Repeated evolution of extreme locomotor performance independent of changes in extended phenotype use in spiders

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Abstract

Many animals utilize self-built structures – so-called extended phenotypes – to enhance body functions, such as thermoregulation, prey capture or defence. Yet, it is unclear whether the evolution of animal constructions supplements or substitutes body functions. Here, using Austral brown spiders, we explored if the evolutionary loss and gain of silken webs as extended prey capture devices correlates with alterations in traits known to play an important role in predatory strikes - locomotor performance and leg spination. For this purpose, we combined the reconstruction of the phylogeny of the Austral marronoid clade of spiders based on UCE target sequence capture with the assembly of kinematic, morphological and ecological data. We found that in this group extreme locomotor performance, with running speeds of over 100 body lengths per second, evolved repeatedly – both in web builders and cursorial spiders. There was no correlation with running speed, and leg spination only poorly correlated, relative to the use of extended phenotypes, with all of these traits showing highly mosaic, independent evolutionary patterns. This indicates that the use of webs does not reduce the selective pressure on body functions involved in prey capture and defence *per se*.

Keywords: animal performance, extended phenotype, spider web, prey capture, Desidae

1. Introduction

Predators rely on behavioural, physiological and morphological adaptations to successfully capture and subdue prey. The ability to move fast is a key trait of many predatory strategies, but it is also energetically costly, and should thus be under strict selective pressure (Irschick and Higham, 2016; Moore and Biewener, 2015). Some predators alternatively invest into the production of adhesive secretions or snares that intercept and immobilize prey without the requirement of quick muscular action (Betz and Kölsch, 2004). The pathways and conditions leading to the evolution of such external devices – extended phenotypes (Dawkins, 1982) – and how they interactively evolve with body traits is poorly understood (Bailey, 2012; Wolff et al., 2021).

Extended phenotypes, such as spider webs, could reduce the need to maintain costly morphological and physiological adaptations to functions (such as prey interception and immobilization) that are thereby rendered redundant (*substitution*). As the production of extended phenotypes brings its own costs, substitution can only be successful, if the costs of maintaining the substituted body traits are higher. In contrast, the extended phenotype could serve as an additional supplement to the body function, but is not functional without the primary body function performing effectively (*supplement*). For instance, silk lines that serve as an extension of the sensory system by transmitting vibratory information from distantly moving prey to the spider still require the possession of vibration sensors and signal processing systems (Herberstein, 2011; Mortimer et al., 2018). Here, the extended phenotype adds to the function and may aid in overcoming limits in the evolvability of the primary body function.

Here we tested, if the evolution of physiological (sprint speed) and morphological traits (leg spination) correlates with predatory strategy: the striking of prey versus the trapping of prey with a web. We focused on a clade of spiders that exhibits multiple web losses and gains (Forster, 1970; Wolff et al., 2022) (representing evolutionary replicates), the so-called marronoid clade of spiders (Araneae: Amaurobioidea). The marronoid clade contains nine poorly defined families with unstable taxonomy (Wheeler et al., 2017). One of the reasons for this instability is the phenotypic and ecological diversity with many homoplastic traits observed in this clade, which makes it hard to determine diagnostic characters, but renders the marronoid spiders highly suitable for comparative studies of trait evolution.

Members of the marronoid clade have been shown to exhibit impressive locomotory abilities. Funnel-web spiders (Agelenidae) build extensive horizontal sheet webs and can move rapidly on the mesh-like surface of the web that slows down most insects (Foelix, 2011). The

burst speed of these spiders can reach up to 55 cm/s or 85 body lengths per second (bl/s) (Spagna et al., 2011). For other marronoid spiders it has only been anecdotally noted that they move rapidly (Forster and Wilton, 1973).

If predators do not use snares, but hunt down and subdue prey with a strike, speed is not enough, but further morphological features such as teeth or claws are required to stop and hold the prey. Some spiders – including many marronoids – exhibit a double row of long, stiff hydraulic spines on the distal segments of their front legs. These have been shown to become erect during the rapid predatory strike with the legs grasping the prey, where they form a barrier to prevent prey from escaping between the legs, before being immobilized with the fangs and venom (Eggs et al., 2015). In rest, and during normal locomotion, the spines lie flat against the legs cuticle and thus do not disturb the spiders when moving through complex microhabitats. These characteristics suggest a sole function of these spines in prey capture and were therefore chosen as an example of morphological adaptation to prey capture.

We hypothesized that (a) sprint speed and leg spination are less expressed in web building than in non-web building species ('*substitution' hypothesis*) or (b) there is no such difference or sprint speed and leg spination are more expressed in web building then in non-web building species ('*supplement' hypothesis*).

2. Material and Methods

2.1. Animal collection and material sourcing

Spiders were collected in New South Wales, South Queensland, Tasmania, the South Island of New Zealand and in Germany under scientific licenses SL101868, FA18285, PTU19-001938 and 71225-RES. Tissue samples and specimens for morphology for some species were sourced from museum and institutional collections. Species were identified with primary or (if available) secondary taxonomic literature. In addition, in some cases, specimens were compared with type specimens for taxonomic identification. Vouchers were preserved in ethanol and deposited at curated arachnological collections. The full list of specimens used in the phylogenomic study, including their collection data and voucher locations are found in supplemental material S1 and S2.

During field collections and keeping the spiders in captivity, notes of the microhabitat, the presence of a web and details of the web or retreat (if present) were recorded and photo-documented where possible.

2.2. Video recording and tracking analysis

Videos were captured with a BASLER Ace camera (640 × 480 pixels, 750fps, 1/4" CMOS Monochrome) equipped with a Fujinon HF12.5HA-1B lens (F1.4 - F16, 12.5mm) and 0.5-40 mm extension tubes using the TroublePix software, or with a Phantom Miro high speed video camera equipped with a Canon DSLR lens. Videos were taken at 100-500 frames per second (depending on the base speed of the spider). Adult males were not included in the study as they often have significantly longer legs and smaller bodies and a different locomotor ecology than female and juvenile spiders. Spiders missing any of their legs were omitted from the analysis.

Running speed of spiders was recorded in the lab or fieldwork accommodation at room temperature. Spiders ran either on a timber bar (50 cm long, 10 cm wide) enclosed with acrylic glass sheets, or on a paper sheet in a polypropylene box (30×20 cm). Spiders were released from one end of the running track and their movement filmed from vertically above. If the spider did not run, or only walked at slow speed, it was touched on the posterior portion of the abdomen to trigger an escape response. Unless the spider showed fatigue, running trials were repeated 3-5 times. Each video contained a reference centimetre scale in the field of view.

From each video the total body length of the spider was measured (from the front of the cephalothorax to the end of the abdomen). We then inspected the paths of the spiders and included only those where spiders ran in a constant direction in the analyses.

Using the plugin *MTrackJ* (Meijering et al., 2012) in *ImageJ* (Schneider et al., 2012) spiders were tracked in the video frame by frame (using the anterior edge of the abdomen as a reference point). The resulting series of x-y coordinates was then exported as csv file and further processed in R 4.0.1 (R Core Team, 2020) using automated scripts (S3). The distance travelled between frames was converted from pixels into centimetres (using the reference scale present in the video frame) and the velocity calculated between frames (from distance travelled and frame rate of the recording). The per frame pair velocity values for each recording were smoothed with the function `smooth.spline` with the number of knots assigned to N/2+1, where N is the number of measured datapoints (frames) in the video. Then the mean speed and burst speed (maximum after smoothing) was calculated both absolute (in cm/s) and relative (in body lengths per second, bl/s). For the comparative analysis the maximal value of the burst

speed among all trails was selected for each individual and the mean of these values for all individuals was calculated for each species.

2.3.Morphometric measurements

Ethanol preserved specimens were photographed in 70-80% ethanol on a Zeiss Discovery.V20 (inserting the automatically calculated scale bars) or with a Canon DLSR on a Motic stereo microscope (including photos of a micrometre scale). The body was photographed from dorsal and lateral angles. Front and hind legs were removed on one side and their prolateral side was photographed.

Measurements (in millimetres) were performed in *ImageJ*. Body length was measured from the front edge of the carapace to the posterior end of the abdomen (without spinnerets). Carapace width was measured at the widest point. Leg segments were measured between condyles excluding the coxa, trochanter and pretarsus. The spines (macrosetae) fully visible from the prolateral side (i.e., including the base socket) were counted on all measured segments of the front leg and the sum of the length of all these spines (from the base socket to the tip) was calculated. This sum was divided by the sum of the length of all measured leg segments giving the spination index. In ethanol preserved material it is not possible to distinguish which spines are hydraulic; therefore we included all spines, including lateral and dorsal spines that are permanently erect. Spines are distinguishable from other setae by their strong sclerotization (often black or dark brown colour), straight shaft, thick base socket and absence of microtrichia. The relative leg length was calculated as the sum of all measured segments of the posterior leg divided by carapace width.

2.4.DNA extraction and UCE analysis

Genomic DNA extraction of all samples was performed using either the leg(s) or the whole specimen (dependant on the size of the spider), following the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) manufacturer's protocol, and quantified using a Qubit fluorometer (Life Technologies, Inc.). UCE library preparations were performed following the protocol of Starrett et al. (2017) and Derkarabetian et al. (2019) as well as the Hybridization Capture for Targeted NGS manual v4.01 protocol (https://arborbiosci.com/wp-content/uploads/2018/04/myBaits-Manual-v4.pdf). Library preparation for a subset of the samples (n = 23) was conducted using the MYbaits Arachnida 1.1Kv1 kit (Arbor Biosciences, Ann Arbor, MI, USA) (Starrett et al., 2017) (see details in S1) and sequenced on a NovaSeq 6000 at the Bauer Core Facility at Harvard University. For the remaining samples (n = 75), the

extracted DNA was dried using an Eppendorf Concentrator plus speed-vac and transported to NGS Division, Arbor Biosciences (Ann Arbor, MI) for UCE library preparation using the Spider 2Kv1 kit (Kulkarni et al., 2020).

Processing of the raw demultiplexed read data was performed using the PHYLUCE v1.6.8 pipeline (Faircloth, 2016). Reads were cleaned with the Trimmomatic wrapper (Bolger et al., 2014) and Illumiprocessor (Faircloth, 2013), using default settings, and then assembled using both Trinity v2.1.1 (Grabherr et al., 2011), with default settings, and ABySS v1.5.2 (Simpson et al., 2009) (using 64-kmer value setting), and the results combined into a single assembly file. Probes were matched to contigs using the Spider 2Kv1 probeset file using minimum coverage and minimum identity values of 65. The UCE loci were aligned using MAFFT (Katoh and Standley, 2013) and trimmed using GBLOCKS (Castresana, 2000; Talavera and Castresana, 2007) with custom blocks settings (b1 = 0.5, b2 = 0.5, b3 = 6, b4 = 6) applied in the PHYLUCE pipeline. Aligned UCEs were then imported into Geneious 11.1.5 (Kearse et al., 2012) and visually inspected for obvious alignment or sequencing errors.

2.5.Phylogenetic analysis

Phylogenetic analyses of the final matrix were performed using two phylogenetic inference methods: Maximum Likelihood (ML) and Bayesian inference (BI). The ML analysis was conducted using IQ-TREE v2.1.3 (Nguyen et al., 2015) implementing ModelFinder (Kalyaanamoorthy et al., 2017) to estimate the best-fit partitioned models by locus (Chernomor et al., 2016). The ultrafast bootstrap technique with 1000 replicates was used to quantify the support of phylogenetic relationships (Hoang et al., 2018).

The final matrix was further trimmed with the more conservative gblocks settings (b1 = 0.5, b2 = 0.85, b3 = 4, b4 = 8) prior to Bayesian analysis. To make the BI computationally feasible, the UCE dataset was reduced by subsampling the most informative loci (Mongiardino Koch, 2021). Gene trees were inferred with ParGenes v. 1.0.1 (Morel et al., 2019), with optimal models selected according to BIC, and 100 bootstrap replicates. Gene selection was made with the script of Mongiardino Koch (2021), specifying minimum occupancy of 50% and discarding 5% of outlier genes. BI was performed using BEAST 2.0 (Bouckaert et al., 2014) with GTR+G substitution model, Relaxed clock log normal, and a birth-death tree model. To time-calibrate the tree, log-normal distributed age priors were placed to some nodes, informed by the age of two fossils (*Eohahnia succini* Petrunkevitch and *Vectaraneus yulei* Selden) and five secondary calibration points taken from Magalhães et al. (2020). One analysis was run without monophyly constraints, and another with constraining the Nearctic Agelenidae s.s. to the base of all other

marronoids (except *Amaurobius*). Four independent runs of 200 million generations were run for each dataset. The first 30% of each run was dropped as burn-in before building the consensus tree using the *TreeAnnotator* app of the BEAST package.

The topology of the phylogenies produced by the ML and BI analyses were then visualised and compared using *FigTree* v1.4.3.

2.6.Comparative analysis

The following terminals were dropped for the comparative analysis due to a lack of trait data (because only male material was available): Matachiinae spec. 4 and *Nuisiana arboris*. Further, species for which trait data, but no phylogenetic information was available were not included in the phylogenetic comparative analysis. Analyses were repeated using two alternative topologies (unconstrained BEAST tree, and BEAST tree where Agelenidae was constrained to an early diverging node as found in ML analyses).

The evolution of web building behaviour was inferred using the stochastic character mapping approach implemented in the *R* package *phytools* (Revell, 2012). Three alternative evolutionary models were considered: (1) ER, equal rates (i.e., web loss and gain occur at same rates); (2) ARD, all rates different (web loss and gain occur at unequal rates); (3) customized model where web re-evolution is suppressed (Dollo's law). Model fit was compared using AICc weights.

For continuous traits (burst speed and spination index) the following models were fitted using the package *geiger* 2.0 (Pennell et al., 2014): (1) BM, Brownian Motion, (2) OU, Ornstein-Uhlenbeck model, (3) EB, Early Burst model, (4) λ, Pagel's lambda. Trait evolution was plotted with the *contMap* function in *phytools*.

The expression of continuous traits was compared between ecological categories (web builders vs. cursorial spiders; cribellar vs. ecribellar; ground dwelling vs. inhabiting above ground microhabitats) with phylogenetic linear regressions in the R package *phylolm* (Tung Ho and Ané, 2014) and branch length transformations based on the best fitting model (lambda for running speed and OU for spination). Effect sizes were estimated using `DurgaDiff` function with 5000 bootstrap replicates and effects size plots were generated using `DurgaPlot` function of the *Durga* R package (Khan and McLean, 2023).

Scripts and input files for the comparative analyses are found in the supplemental material (S4).

3. Results

3.1.UCE Sequencing and phylogenetic results

Sequenced samples contained an average of 4 072 740 reads per sample (post trimming) and an average of 257 754 contigs. There was a total of 1 266 UCE loci produced from the assembled contigs across all taxa with an average of 929 loci per sample. The number of UCE loci obtained for taxa processed using the Arachnida 1.1Kv1 kit ranged between 181 – 555 with an average of 251 UCEs per sample (S1). Those taxa processed using the Spider 2Kv1 kit produced UCE loci ranging from 950 – 1 215 with an average of 1 137 UCEs per sample (S1). The contigs and alignments used for phylogenetic inference are found in the supplemental material S5.

Phylogenetic inference produced trees with overall high node supports (i.e., ubf-values >95 for 93 of 97 nodes, S6). Node support dropped slightly when applying strict gblock settings (i.e., removing much of the variable sequence regions) (ubf-values >95 for 90 of 97 nodes, S6). There was one major discordance in the topology between ML and BI trees, with a different position of the Nearctic Agelenidae s.s.. Both topologies have been found in previous phylogenomic studies and therefore, we ran our comparative analyses on both alternative phylogenies. Figure 1 shows the topology found by the ML analysis and the BI analysis with Agelenidae fixed to the base of the marronoid clade (excl. the Nearctic Amaurobiinae). Some minor disagreement between ML and BI trees was also found among the New Zealand Matachiinae, which is not considered to have an effect on the present comparative analysis.

This first broader-scale insight into the phylogeny of the Austral marronoid clade is highly relevant for the understanding of the remarkably dynamic phenotypic evolution of this group: it shows that taxa with divergent foraging modes (web builders vs. cursorial), body shapes and sizes often group together.

3.2. Diversity and evolution of web building behaviour, running speed and leg spination

We gathered ecological data for most studied species, including many original observations that represent the first descriptions of webs and foraging ecology for many of the studied species (Tab A1 and descriptions in S7). This natural history data reveals an enormous diversity of web shapes and hunting styles throughout the marronoid clade of spiders.

The phylogenetic comparative analysis of foraging style indicated highly dynamic evolution of web building behaviour in the marronoid clade. Transitions between web-based and non-web-based foraging occurred repeatedly across our taxon sample, with slightly more

283 web losses (13) than gains (10) if equal rates were assumed, and 30 web losses if web regain
284 was suppressed. These results were independent of the position of Agelenidae.
285 Maximum running speed was lowest (5-8 body lengths per second, bl/s) in individuals of
286 the cursorial spiders *Plectophanes* sp. and *Desis marina*, and the web builders *Paramatachia*
287 *decorata* and *Taurongia* sp. 3 (a summary of all comparative data can be found in Tab A2, and
288 raw data in S2 and S3). Running speed was highest (over 100 bl/s) in individuals of the cursorial
289 spiders *Toxopsoides* sp. 9 (holding the record with 138 bl/s) and *Toxopsoides* sp. 10, as well as
290 individuals of the web building species *Procambridgea hunti* and *Pillara griswoldi*.
291
292 The phylogenetic mapping of running speed (bl/s) showed clear genus or clade specific
293 trends (Fig. 1). Notable trait differences between sister lineages were rarely associated with
294 changes in foraging mode.
295 Phylogenetic linear models did not indicate significant differences in running speed
296 between web builders and cursorial hunters (mean difference = 2.03, 95% CI [-6.78, 11.14]; p
297 = 0.435; and p = 0.443 if Agelenidae constrained at base; Fig. 1 inset) nor between ecribellar
298 and cribellar (mean difference = 6.70, 95% CI [-1.56, 14.64]; p = 0.155; and p = 0.153 if
299 Agelenidae constrained at base) and between ground dwelling and above-ground dwelling
300 species (2.54, 95% CI [-4.88, 9.93], p = 0.192; and p = 0.193 if Agelenidae constrained at base).
301 The average spination index differed between web builders and cursorial spiders
302 (phylogenetic linear model, p = 0.034; and p = 0.033 if Agelenidae constrained at base), but
303 the effect size was very small (0.244, 95% CI [0.062, 0.451]). Spination did not differ
304 significantly between cribellar and ecribellar (0.141, 95% CI [-0.005, 0.285], p = 0.115; and p
305 = 0.113 if Agelenidae constrained at base) nor between ground dwelling and above-ground
306 dwelling species (-0.119, 95% CI [-0.276, 0.032], p = 0.288; and p = 0.282 if Agelenidae
307 constrained at base). Running speed and spination index were not correlated (p = 0.335 for both
308 topologies).
309
310
311 ***4. Discussion***
312 *4.1. Repeated evolution of extreme locomotor performance in the marronoid clade*
313 We found that in this group extreme locomotor performance with running speeds of over
314 100 body lengths per second (bl/s) evolved repeatedly – remarkably, both in web builders and
315 cursorial spiders. To our knowledge the extreme kinematic performance recorded for some
316 individuals of *Toxopsoides*, *Procambridgea* and *Pillara* are the fastest relative sprint speeds

recorded for arachnids so far, with the previous record holder being the predatory mite *Parateneriffia* sp. with 100.6 ± 9.3 bl/s (Wu et al., 2010). The fastest absolute speed in our dataset was achieved with over 60 cm/s by the large cursorial spiders *Cycloctenus* spp. and the large web builder *Corasoides terania* (with 73 cm/s in one individual). Recently it was found that large huntsman spiders (Sparassidae) can reach speeds of up to 2 m/s (Boehm et al., 2021), which is the fastest reported absolute running speed for a spider and equivalent to 80 bl/s (Hurst and Rayor, 2021). Such high running speeds are rarely reported in arthropods, and are only surpassed by the Australian tiger beetles *Cicindela* spp., which hold the current arthropod speed record of 170 bl/s and 2.5 m/s (Kamoun and Hogenhout, 1996).

4.2. Extended prey capture devices do not substitute prey capture related body traits per se

Running speed was poorly correlated with the use of webs as prey capture and defensive devices – both traits showed mosaic, independent evolutionary patterns (e.g., several switches in trends within Stiphidiidae, which are all web builders, and no increase in sprint speed in Matachiinae after web losses). This indicates that the use of webs does not reduce the selective pressure on locomotory performance *per se*. The energy invested in the construction of the web could partly be offset by a more energy efficient locomotory mode based on pendulum mechanics (Moya-Laraño et al., 2008). This may play a role especially in species with long and thin legs that typically move underneath the web sheet, such as *Nanocambridgea* or Borralinae (Stiphidiidae). It is also possible that an arms-race like predator-prey interaction, where counter-strategies of some prey to reduce the efficiency of traps, maintains the selective pressure on speed. Many web-building marronoid spiders produce complex adhesive compound threads based on dry nanofibers, so-called cribellar silk. It has been shown that some hair and scale-like surface features of the prey's cuticle highly reduce the stickiness of cribellar silk (Opell, 1994). In addition, cribellar silk has been shown to interact with wax coatings on insects cuticles to form an adhesive bond (Bott et al., 2017), but which also stiffens the threads, which may help active prey to break free (Baumgart et al., 2022). High sprint speed is advantageous in such situations in which the web's capacity to immobilize the prey is compromised, as the spider has to move fast to prevent the quick escape of the prey for successful prey capture. Larger webs, such as the sheet webs of many Agelenidae, boralline Stiphidiidae and porteriinae Desidae, may enhance the overall chance of prey interception, but require fast locomotion over longer distances in order to retrieve the prey before it can escape, as the spider typically rests in a funnel retreat at the edge of the sheet. Notably, many of such

marronoid lineages that build large sheet webs and exhibit high running speeds (with the exception of Borallinae) have lost the ability to produce cribellar capture threads. In contrast, species that produce webs with thick and looped cribellar threads, such as *Paramatachia* spp. and *Neoramia* spp., that have the potential to immobilize prey longer (Opell, 2002), exhibited comparably slower running speed, which may indicate a trade-off between the investment in the cribellar spinning apparatus or the locomotory system. However, across the dataset running speed did not differ between cribellar and ecribellar spiders, showing that the evolution of locomotor performance cannot be explained with this trade-off alone.

Spiders are not only predators but also prey, and their locomotor performance may be under strong selection by predation. Webs may play an important role in predation defence by providing shelter (Manicom et al., 2008), and hence we predicted similar effects on selection pressures acting upon locomotor performance as predicted for the web's function as an extended prey capture device. Yet, our results could not confirm that spiders sheltered from predation by webs have a reduced locomotor performance. Different types of webs might have different capacity to act as a shelter, especially in interaction with the microhabitat structure into which they are constructed and/or the type of predator (Cloudsley-Thompson, 1995; Manicom et al., 2008). Also, the process of web building and maintenance exposes spiders to predators, as cursorial spiders are exposed during periods of active foraging. Furthermore, other anti-predator strategies that may render fast movement unnecessary (or even disruptive), such as crypsis, have not been considered here, though they might play a role in some of the studied species.

As locomotor performance is a composite trait affected by different morphological and physiological characters, it may indirectly be affected by adaptation to special microhabitats. For instance, *Paramatachia* spp. and *Plectophanes* sp. belong to the slowest species in our data set. These species retreat into empty insect bore holes in wood or hollow twigs and accordingly have a slender body shape with short legs, which may be disadvantageous for locomotion. On the other hand, many species that typically retreat into narrow spaces in rotting logs or between the leaf bases of tussocks or rosettes showed high sprint speeds (e.g., species of *Pillara*, *Procambridgea* and *Toxops*). Among the fastest runners were the species with sideways tilted (laterigrade) legs (e.g., species of *Toxopsoides*, *Toxops*, *Cycloctenus* and *Manjala*) – a feature associated with flat bodies to squeeze into crevices but also permitting high manoeuvrability on flat substrates such as tree trunks (Zeng and Crews, 2018). Such species might often forage

385 on exposed sites and take advantage of rapidly seeking shelter. Yet, not all super-performers
386 had laterigrade legs – *Pillara* and *Procambridgea* were rapid runners even with a body shape
387 and natural behaviour usually associated with inverted pendulum mechanics and foraging in
388 non-exposed microhabitats in and under rotten logs.
389
390 As an example of hypothesized morphological adaptation towards prey capture, we
391 analysed leg spination. Model results showed that cursorial spiders were more likely to have a
392 greater number and longer spines on the front legs, but the difference in the global spination
393 means between web builders and non-web builders was very small. Across the phylogeny there
394 were multiple cases of web-building and non-web-building sister lineages, where the branch
395 of the non-web-builder evolved stronger front leg spination (e.g., *Storenosoma* vs.
396 *Tanganoides*; *Wiltona* vs. Neoramia-group; *Daviesa* vs. Porteriinae). However, in clades with
397 the highest evolutionary dynamic of web use (such as Matachiinae and Amphinectinae),
398 changes in foraging mode and the direction of spination evolution were seemingly not
399 correlated. This could indicate that spination evolved gradually over longer time frames or that
400 selection favours them only conditionally (e.g., depending on predatory strike behaviour; (Eggs
401 et al., 2015)).
402
403 *4.3. Phylogeny and evolutionary history of the marronoid clade of spiders*
404 Here we constructed the most comprehensive phylogeny of the Austral marronoid clade of
405 spiders so far, including many enigmatic taxa with unclear taxonomy. The relationships
406 between major taxa overlaps in large parts with the previous findings of Wheeler et al. (2017),
407 who used only six short genetic markers and a smaller taxon sampling for the Austral clade.
408 Our results show a strong need for the revision of the "marronoid" families, a problem that has
409 been flagged by arachnologists for a long time (Wheeler et al., 2017). Our phylogenetic results
410 give some first evidence on the placement of problematic taxa, that have been found extremely
411 difficult to place into a family based on morphological characters alone. For instance, we found
412 that the New Zealand "Amaurobiidae" and "Agelenidae" form a clade with Cycloctenidae, that
413 the Australian amaurobiid genus *Daviesa* is a sister lineage of Porteriinae (Desidae), the genus
414 *Toxopsoides* (currently doubtfully placed in Toxopidae) is a sister lineage of Amphinectinae
415 s.s. (Desidae) and the genus *Wiltona* (former Tengellinae) falls into Stiphidiidae (all these
416 relationships were highly supported with ubf-values >95). Further, our data showed that the
417 problematic genera *Aorangia* and *Cicurina* each form lineages outside currently defined
418 families and confirmed that the water spider *Argyroneta* belongs to Dictynidae. The formal

revision of the systematics of the marronoid group will be dealt with in a separate work, based on an enhanced taxon sampling and including morphological characters.

5. Conclusion

Here we have combined the first comprehensive phylogenomic analysis of the enigmatic Austral marronoid clade of spiders with the large-scale comparative analysis of physiological, morphological and ecological traits. This enabled the first-time inference of how locomotor performance evolves on the deep time scale in animals that use extended phenotypes. Results show that the evolution of locomotor performance and front leg spination in spiders each exhibit very interesting and complex dynamics that are not, or only poorly, correlated with the loss and gain of silken webs as extended prey capture and defensive devices. Extended phenotypes serving as substitutes for body traits may rather be the exception than the rule. Rather extended phenotypes serve as important supplementary assets, enhancing the functionalities of the body.

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References

Bailey, N. W. (2012). Evolutionary models of extended phenotypes. *Trends in Ecology & Evolution* **27**, 561-569.

Baumgart, L., Schaa, E.-M., Menzel, F. and Joel, A.-C. (2022). Change of mechanical characteristics in spider silk capture threads after contact with prey. *Acta Biomaterialia* **153**, 355-363.

Betz, O. and Kölsch, G. (2004). The role of adhesion in prey capture and predator defence in arthropods. *Arthropod Structure & Development* **33**, 3-30.

Boehm, C., Schultz, J. and Clemente, C. (2021). Understanding the limits to the hydraulic leg mechanism: the effects of speed and size on limb kinematics in vagrant arachnids. *Journal of Comparative Physiology A* **207**, 105-116.

Bolger, A. M., Lohse, M. and Usadel, B. (2014). Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics* **30**, 2114-2120.

Bott, R. A., Baumgartner, W., Bräunig, P., Menzel, F. and Joel, A.-C. (2017). Adhesion enhancement of cribellate capture threads by epicuticular waxes of the insect prey sheds new light on spider web evolution. *Proc. R. Soc. B* **284**, 20170363.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M. A., Rambaut, A. and Drummond, A. J. (2014). BEAST 2: a software platform for Bayesian evolutionary analysis. *Plos Computational Biology* **10**, e1003537.

Castresana, J. (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* **17**, 540-552.

Chernomor, O., Von Haeseler, A. and Minh, B. Q. (2016). Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic biology* **65**, 997-1008.

Cloudsley-Thompson, J. (1995). A review of the anti-predator devices of spiders. *Bulletin of the British Arachnological Society* **10**, 81-96.

Dawkins, R. (1982). The extended phenotype: The long reach of the gene: Oxford: Oxford University Press.

Derkarabetian, S., Benavides, L. R. and Giribet, G. (2019). Sequence capture phylogenomics of historical ethanol-preserved museum specimens: Unlocking the rest of the vault. *Molecular Ecology Resources* **19**, 1531-1544.

Eggs, B., Wolff, J. O., Kuhn-Nentwig, L., Gorb, S. N. and Nentwig, W. (2015). Hunting without a web: how lycosoid spiders subdue their prey. *Ethology* **121**, 1166-1177.

Faircloth, B. (2013). Illumiprocessor: a trimmomatic wrapper for parallel adapter and quality trimming.

Faircloth, B. C. (2016). PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics* **32**, 786-788.

Foelix, R. F. (2011). Biology of spiders. Oxford ; New York: Oxford University Press.

Forster, R. (1970). The spiders of New Zealand. Part III. Desidae, Dictynidae, Hahniidae, Amaurobioididae, Nicodamidae. . *Otago Museum Bulletin* **3**, 1-184.

Forster, R. R. and Wilton, C. L. (1973). The spiders of New Zealand. Part IV. Agelenidae, Stiphidiidae, Amphinectidae, Amaurobiidae, Neolanidae, Ctenidae, Psechridae. *Otago Museum Bulletin* **4**, 1-309.

Grabherr, M. G., Haas, B. J., Yassour, M., Levin, J. Z., Thompson, D. A., Amit, I., Adiconis, X., Fan, L., Raychowdhury, R. and Zeng, Q. (2011). Full-length transcriptome assembly from RNA-Seq data without a reference genome. *Nature biotechnology* **29**, 644-652.

Herberstein, M. E. (2011). Spider behaviour: flexibility and versatility: Cambridge University Press.

Hoang, D. T., Chernomor, O., Von Haeseler, A., Minh, B. Q. and Vinh, L. S. (2018). UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* **35**, 518-522.

Hurst, J. A. and Rayor, L. S. (2021). Effects on running speed of changes in sexual size dimorphism at maturity on in the cursorial huntsman spider, Delena cancerides (Sparassidae). *Journal of Comparative Physiology A* **207**, 269-277.

Irschick, D. J. and Higham, T. E. (2016). Animal athletes: an ecological and evolutionary approach: Oxford University Press.

Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K., Von Haeseler, A. and Jermiin, L. S. (2017). ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature methods* **14**, 587-589.

Kamoun, S. and Hogenhout, S. A. (1996). Flightlessness and rapid terrestrial locomotion in tiger beetles of the Cicindela L. subgenus Rivacindela van Nidek from saline habitats of Australia (Coleoptera: Cicindelidae). *The Coleopterists' Bulletin*, 221-230.

Katoh, K. and Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**, 772-780.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S. and Duran, C. (2012). Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**, 1647-1649.

Khan, M. K. and McLean, D. J. (2023). Durga: An R package for effect size estimation and visualisation. *bioRxiv* **2023-02**.

Kulkarni, S., Wood, H., Lloyd, M. and Hormiga, G. (2020). Spider-specific probe set for ultraconserved elements offers new perspectives on the evolutionary history of spiders (Arachnida, Araneae). *Molecular Ecology Resources* **20**, 185-203.

Magalhaes, I. L., Azevedo, G. H., Michalik, P. and Ramírez, M. J. (2020). The fossil record of spiders revisited: implications for calibrating trees and evidence for a major faunal turnover since the Mesozoic. *Biological Reviews* **95**, 184-217.

Manicom, C., Schwarzkopf, L., Alford, R. A. and Schoener, T. W. (2008). Self-made shelters protect spiders from predation. *Proceedings of the National Academy of Sciences* **105**, 14903-14907.

Meijering, E., Dzyubachyk, O. and Smal, I. (2012). Methods for cell and particle tracking. *Methods in Enzymology* **504**, 183-200.

Mongiardino Koch, N. (2021). Phylogenomic subsampling and the search for phylogenetically reliable loci. *Molecular Biology and Evolution* **38**, 4025-4038.

Moore, T. Y. and Biewener, A. A. (2015). Outrun or outmaneuver: predator–prey interactions as a model system for integrating biomechanical studies in a broader ecological and evolutionary context. *Integrative and Comparative Biology* **55**, 1188-1197.

Morel, B., Kozlov, A. M. and Stamatakis, A. (2019). ParGenes: a tool for massively parallel model selection and phylogenetic tree inference on thousands of genes. *Bioinformatics* **35**, 1771-1773.

Mortimer, B., Soler, A., Siviour, C. and Vollrath, F. (2018). Remote monitoring of vibrational information in spider webs. *The Science of Nature* **105**, 1-9.

Moya-Laraño, J., Vinković, D., De Mas, E., Corcobado, G. and Moreno, E. (2008). Morphological evolution of spiders predicted by pendulum mechanics. *Plos One* **3**, e1841.

Nguyen, L.-T., Schmidt, H. A., Von Haeseler, A. and Minh, B. Q. (2015). IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* **32**, 268-274.

Opell, B. (1994). The ability of spider cribellar prey capture thread to hold insects with different surface features. *Functional Ecology*, 145-150.

Opell, B. D. (2002). How spider anatomy and thread configuration shape the stickiness of cribellar prey capture threads. *The Journal of Arachnology* **30**, 10-19.

Pennell, M. W., Eastman, J. M., Slater, G. J., Brown, J. W., Uyeda, J. C., FitzJohn, R. G., Alfaro, M. E. and Harmon, L. J. (2014). geiger v2. 0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* **30**, 2216-2218.

Revell, L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology & Evolution* **3**, 217-223.

Schneider, C. A., Rasband, W. S. and Eliceiri, K. W. J. N. m. (2012). NIH Image to ImageJ: 25 years of image analysis. **9**, 671-675.

Simpson, J. T., Wong, K., Jackman, S. D., Schein, J. E., Jones, S. J. and Birol, I. (2009). ABySS: a parallel assembler for short read sequence data. *Genome Research* **19**, 1117-1123.

Spagna, J. C., Valdivia, E. A. and Mohan, V. (2011). Gait characteristics of two fast-running spider species (Hololena adnexa and Hololena curta), including an aerial phase (Araneae: Agelenidae). *Journal of Arachnology*, 84-91.

Starrett, J., Derkarabetian, S., Hedin, M., Bryson Jr, R. W., McCormack, J. E. and Faircloth, B. C. (2017). High phylogenetic utility of an ultraconserved element probe set designed for Arachnida. *Molecular Ecology Resources* **17**, 812-823.

Talavera, G. and Castresana, J. (2007). Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic biology* **56**, 564-577.

Team, R. C. (2020). R: A language and environment for statistical computing. . Vienna, Austria: R Foundation for Statistical Computing.

Tung Ho, L. s. and Ané, C. (2014). A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic biology* **63**, 397-408.

Wheeler, W. C., Coddington, J. A., Crowley, L. M., Dimitrov, D., Goloboff, P. A., Griswold, C. E., Hormiga, G., Prendini, L., Ramírez, M. J. and Sierwald, P. (2017). The spider tree of life: phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling. *Cladistics* **33**, 574-616.

Wolff, J. O., Wierucka, K., Paterno, G. B., Coddington, J. A., Hormiga, G., Kelly, M. B., Herberstein, M. E. and Ramírez, M. J. (2022). Stabilized morphological evolution of spiders despite mosaic changes in foraging ecology. *Systematic biology* **71**, 1487-1503.

Wolff, J. O., Wierucka, K., Uhl, G. and Herberstein, M. E. (2021). Building behavior does not drive rates of phenotypic evolution in spiders. *Proceedings of the National Academy of Sciences* **118**, e2102693118.

Wu, G. C., Wright, J. C., Whitaker, D. L. and Ahn, A. N. (2010). Kinematic evidence for superfast locomotory muscle in two species of teneriffiid mites. *Journal of Experimental Biology* **213**, 2551-2556.

Zeng, Y. and Crews, S. (2018). Biomechanics of omnidirectional strikes in flat spiders. *Journal of Experimental Biology* **221**, jeb166512.

Figures

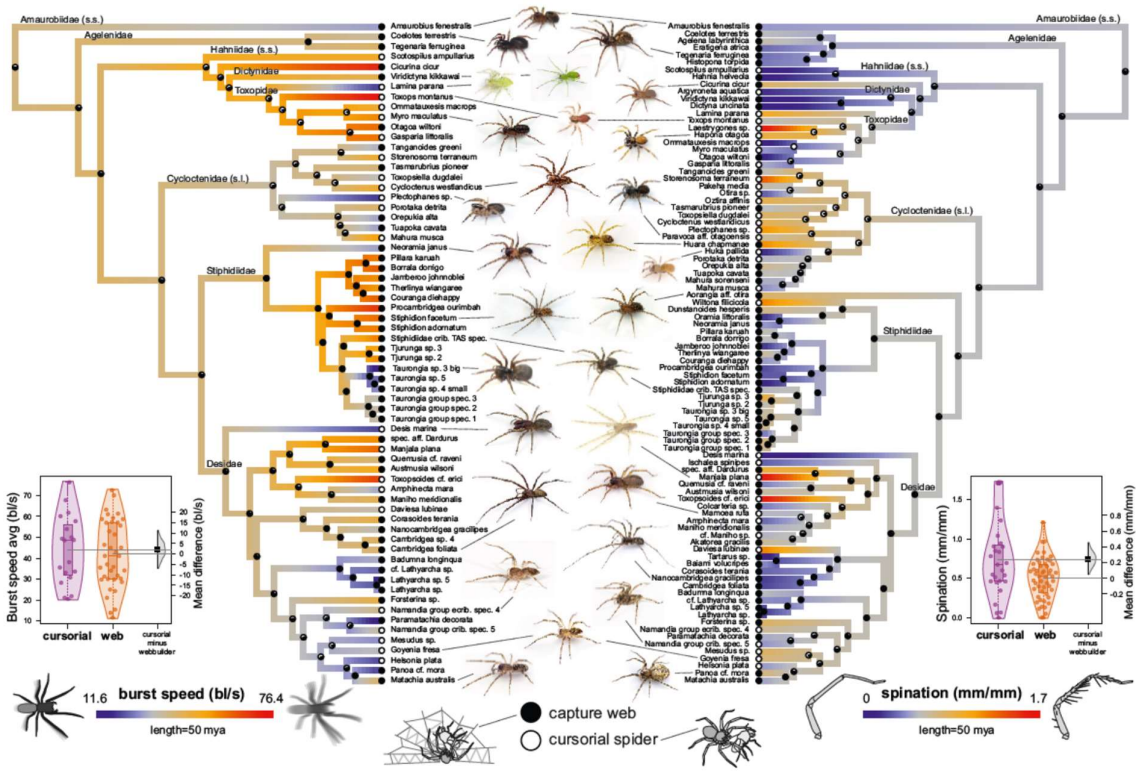

Fig. 1. Macroevolution of locomotor performance, weaponry and extended phenotypes in Austral brown spiders. Coloured Bayesian phylogenies based on BEAST analysis with fixed position of Agelenidae (note that the systematics of the marronoid clade is due to formal revision and indicated family delimitations are tentative); colours indicate trait levels (see respective legend below), circles at tips indicate the species' foraging mode (see legend in middle below; for further details see Tab A1), and circles at nodes indicate the posterior probability of web use in the most recent common ancestor (assuming equal rates of web loss and gain). Inserted box and violin effect size plots indicate differences in trait means between web builders and cursorial hunter. Boxplots display the group median and the 75th and 25th percentiles and whiskers extend to the minimum and maximum, but exclude outliers that are beyond 1.5 times the interquartile range and the dots indicating the individual species means. Half violin in the effect size plots exhibit the distribution of bootstrapped differences; the solid square shows mean difference, while the vertical bar shows 95% confidence interval of mean difference.

Appendix

Tab. A1. Summary of ecological data used in comparative analyses (for details and descriptions see S7). States of binary coding: Web 0, non-web-builder (may build shelter, but hunts prey without the help of a web); 1, builds a silken web (of any kind) that assists in prey capture and in which the spider typically resides. Cribellum (crib.) 0, ecribellar, i.e., does not possess a spinning plate; 1, cribellar, i.e., possesses a spinning plate (cribellum) and comb (calamistrum) to produce dry adhesive threads. Stratum (Strat.) 0, primarily found in or on the ground; 1, primarily found above the ground (i.e., in the vegetation, on tree trunks or rock walls).

Species	Web	Crib.	Strat.	Details
Amaurobius fenestralis	1	1	1	irregular, loose cribellar tunnel web under loose bark of dead trees
Agelena labyrinthica	1	0	1	dense funnel web in low vegetation
Coelotes terrestris	1	0	0	dense tunnel or sheet web at ground
Eratigena atrica	1	0	1	dense funnel web extending from crevices in walls or dead wood
Histopona torpida	1	0	0	fine funnel web on ground, in moss or rotten logs
Tegenaria ferruginea	1	0	1	dense funnel web extending from crevices in walls or dead wood
Hahnia helveola	1	0	0	thin sheet web between moss, litter or in rotten logs
Scotospilus ampullarius	0	0	0	free hunting under loose bark of Eucalypt trees
Cicurina cicur	1	0	0	thin sheet web between moss, litter or in rotten logs
Dictyna uncinata	1	1	1	cribellar web under tree leaves
Viridictyna cf. *kikkawai*	1	1	1	thin cribellar sheet web on leaves of trees or shrubs
Argyroneta aquatica	0	0	1	sheet between aquatic plants holding air filled reservoir as retreat
Lamina parana	0	0	1	free hunting on vegetation, with sheet like retreat
Toxops montanus	0	0	0	free hunting in litter and low vegetation
Hapona otagoa	0	0	1	free hunting on low vegetation
Laestrygones sp.	0	0	1	free hunting on vegetation
Myro maculatus	0	0	0	free hunting on pebble beaches
Otagoa wiltoni	1	0	1	tubular tangle web in rock crevices in coastal cliffs
Ommatauxesis macrops	0	0	0	free hunting in litter on ground
Gasparia littoralis	0	0	0	free hunting on pebble beaches
Otira sp.	0	0	0	free hunting in litter
Pakeha media	0	0	0	free hunting on ground
Storenosoma terraneum	0	0	0	free hunting on ground, with cell like retreat under rotten logs
Tanganoides greeni	1	0	0	sheet web under rotten logs
Tasmarubrius pioneer	1	0	0	sheet web under rotten logs
Oztira affinis	0	0	0	free hunting in litter
Cycloctenus cf. *westlandicus*	0	0	1	free hunting on logs, trees and banks
Toxopsiella dugdalei	0	0	0	free hunting on ground
Plectophanes sp	0	0	1	ambush hunter retreating in empty insect holes in dead trees
Paravoca aff. *otagoensis*	0	0	0	free hunting on ground
Huara chapmanae	1	0	1	Irregular sheet web in moss or low vegetation
Huka pallida	0	1	0	free hunting in litter
Porotaka detrita	0	0	0	free hunting in litter
Orepukia alta	1	0	0	sparse tunnel-like sheet web under logs or stones
Tuapoka cavata	1	1	0	small sheet web in moss or litter
Mahura musca	0	0	0	free hunting in moss and litter
Mahura sorenseni	1	1	0	thin space web in moss and litter
Aorangia aff. *otira*	1	0	1	dense horizontal sheet web amongst vegetation or in banks
Wiltona filicicola	0	1	1	free hunting on vegetation
Neoramia janus	1	1	0	sheet web under logs and stones
Oramia littoralis	1	1	0	sheet web on ground at beaches
Dunstanoides hesperis	1	1	1	radial cribellar sheet web on tree trunks, banks or rock faces
Stiphidiidae spec crib TAS	1	1	1	suspended cribellar sheet in litter or between tree roots
Tjurunga sp. 2	1	0	1	suspended horizontal sheet web in vegetation
Tjurunga sp. 3	1	0	0	suspended horizontal sheet web at ground level
Taurongia sp. 3	1	1	0	sparse sheet web in and under rotten logs or in banks
Taurongia sp. 4	1	1	0	cribellar surface web in rotten logs
Taurongia sp. 5	1	1	0	sparse sheet web in and under rotten logs and in banks
Taurongia group spec 1	1	1	0	sparse cribellar sheet web in debris, under rotten logs or stones
Taurongia group spec 2	1	1	0	sparse cribellar sheet web in debris, under rotten logs or stones
Taurongia group spec 3	1	1	0	cribellar sheet web in debris, under rotten logs or stones
Stiphidion facetum	1	1	1	tent-like cribellar sheet web on overhanging rock or wood surfaces
Stiphidion adornatum	1	1	0	tent-like cribellar sheet web under rocks or logs
Procambridgea ourimbah	1	1	0	horizontal sheet web in rotten logs
Borrala dorrigo	1	1	0	suspended horizontal cribellar sheet web in rotten logs or litter
Pillara karuah	1	1	1	suspended horizontal cribellar sheet with tube retreat in rotten logs
Jamberoo johnnoblei	1	1	1	suspended horizontal cribellar sheet with tube retreat in rotten log
Therlinya wiangaree	1	1	1	suspended horizontal cribellar sheet in banks with tube retreat
Couranga diehappy	1	1	0	suspended horizontal cribellar sheet at tree base with tubular retreat in bark or between roots

Desis marina	0	0	0	free hunting at rocks in intertidal zone, with silken retreat in rock crevices or empty shells
Badumna longinqua	1	1	1	cribellar space web with planar sheets in vegetation
Lathyarcha sp.	1	1	0	cribellar space web with planar sheets in dry kelp pieces at beach
Lathyarcha sp. 5	1	1	0	web at ground
aff. *Lathyarcha* sp.	1	1	1	cribellar space web with planar sheets in vegetation
Forsterina sp.	1	1	1	cribellar space web with straight cribellar lines in rock crevices
Namandia group ecrib spec 4	0	0	1	free hunting on trees and shrubs
Namandia group crib spec 5	0	1	1	free hunting on trees and shrubs, sometimes very loose web of single lines extending from retreat under bark
Paramatachia decorata	1	1	1	radial cribellar sheet web extending from tubular retreat in hollow twig or empty insect hole
Goyenia cf. *fresa*	0	0	1	free hunting on trees and shrubs
Mesudus sp.	0	0	1	free hunting on trees and shrubs
Nuisiana arboris	0	1	1	free hunting on trees and shrubs, sometimes very loose web of single lines extending from retreat under bark
Matachia australis	1	1	1	cribellar space web with planar sheets in vegetation
Notomatachia sp.	1	1	1	cribellar space web with planar sheets in vegetation
Panoa cf. *mora*	1	1	1	cribellar web in vegetation
Helsonia plata	0	1	1	free hunting on vegetation
Daviesa lubinae	0	0	1	free hunting on vegetation
Corasoides terania	1	0	1	large suspended horizontal sheet web with tangle lines and tubular retreat under bark, between roots or in soil
Nanocambridgea gracilipes	1	0	1	horizontal sheet web in banks
Cambridgea foliata	1	0	1	large suspended horizontal sheet web with tangle lines and tubular retreat under bark
Cambridgea sp.	1	0	0	sheet web in tussock
Baiami volucripes	1	1	0	cribellar sheet web between stones
Tartarus sp.	1	1	1	lampshade-like web on rock faces in caves
Ischalea spinipes	0	0	1	free hunting on vegetation
Manjala plana	0	1	1	free hunting on vegetation
Dardurus sp.	1	0	0	tubular web in moss or rotten logs
Quemusia cf. *raveni*	1	1	0	web on ground
Austmusia wilsoni	1	0	0	sparse tangle web on ground
Toxopsoides cf. *erici*	0	0	1	free hunting on trees
Colcarteria sp.	1	1	0	web on ground
Amphinecta mara	0	0	0	free hunting on ground, with cell like retreat under logs or stones
Mamoea rufa	0	0	0	free hunting on ground, with tubular retreat under logs or stones
Maniho meridionalis	1	1	0	cribellar sheet web on ground
Maniho sp.	0	1	0	free hunting on ground
Akatorea gracilis	1	1	0	cribellar surface web in rotten logs

Tab. A2. Summary of locomotory performance and morphological traits. The global mean ± standard deviations are given (sample size in brackets = number of individuals tested). A dash means that the trait was not measured for this species (e.g. due to a lack of living animals or a lack of female/juvenile specimens). Body lengths per second = bl/s. For the phylogenetic comparative analyses for some terminals the data of a congeneric species was used (i.e., if there was a lack of data from the sequenced species) – these instances are noted in the 'Remarks' column. Asterisks (*) before species names indicate additional species not included in the comparative analyses (i.e., due to lack of phylogenetic data).

Species	**Burst speed (cm/s)**	**Burst speed (bl/s)**	**L1 spination**	**Remarks**
Amaurobius fenestralis	22.7 ± 2.5 (n = 5)	29.8 ± 3.2 (n = 5)	0.466 ± 0.038 (n = 3)	
Agelena labyrinthica	-	-	0.614 ± 0.051 (n = 2)	
Coelotes terrestris	27.9 ± 5.6 (n = 4)	37.0 ± 8.9 (n = 4)	0.570 ± 0.041 (n = 3)	
Eratigena atrica	-	-	0.353 ± 0.032 (n = 2)	
Histopona torpida	-	-	0.388 ± 0.066 (n = 3)	
Tegenaria ferruginea	41.6 ± 6.2 (n = 4)	42.9 ± 5.3 (n = 4)	0.364 ± 0.069 (n = 4)	
Hahnia helveola	-	-	0.112 (n = 1)	
Scotospilus ampullarius	12.6 ± 6.1 (n = 2)	49.9 ± 29.0 (n = 2)	0.064 ± 0.035 (n = 2)	
**Scotospilus wellingtoni*	12.4 ± 2.7 (n = 2)	72.6 ± 10.7 (n = 2)	-	
Cicurina cicur	24.0 ± 6.0 (n = 5)	72.6 ± 6.0 (n = 5)	0.827 ± 0.059 (n = 3)	
Dictyna uncinata	-	-	0.000 (n = 1)	
Viridictyna cf. *kikkawai*	9.5 ± 2.3 (n = 2)	45.1 ± 20.0 (n = 2)	0.000 (n = 1)	
Argyroneta aquatica	-	-	0.183 (n = 1)	
Lamina parana	7.2 ± 1.0 (n = 2)	20.5 ± 1.1 (n = 2)	1.041 ± 0.109 (n = 2)	
Toxops montanus	22.4 ± 3.2 (n = 8)	76.4 ± 8.1 (n = 8)	0.600 ± 0.120 (n = 3)	
Hapona muscicola	-	-	0.945 (n = 1)	Terminal: *H. otagoa*

Laestrygones otagoensis	-	-	1.722 ± 0.240 (n = 3)	Terminal: *Laestrygones* sp.
Myro maculatus	30.1 ± 7.8 (n = 7)	57.7 ± 13.1 (n = 7)	0.462 ± 0.017 (n = 2)	
Otagoa wiltoni	-	-	0.136 (n = 1)	
Otagoa nova	32.7 ± 3.5 (n = 3)	61.3 ± 3.8 (n = 3)	0.317 (n = 1)	Terminal for speed data: *O. wiltoni*
Ommatauxesis macrops	14.7 ± 4.8 (n = 3)	48.7 ± 14.3 (n = 3)	0.058 (n = 1)	
Gasparia littoralis	33.4 (n = 1)	60.2 (n = 1)	0.514 ± 0.053 (n = 3)	
Pakeha pula	-	-	0.633 (n = 1)	Terminal: *P. media*
Otira sp.	-	-	0.309 (n = 1)	
**Storenosoma altum*	25.1 ± 8.9 (n = 3)	41.2 ± 4.8 (n = 3)	-	
**Storenosoma* cf. *tasmaniensis*	25.1 ± 8.9 (n = 4)	48.2 ± 14.8 (n = 4)	-	
Storenosoma terraneum	31.3 ± 7.3 (n = 6)	49.3 ± 9.3 (n = 6)	1.398 ± 0.014 (n = 2)	
Tanganoides greeni	35.3 (n = 1)	30.9 (n = 1)	0.589 (n = 1)	
Tasmarubrius pioneer	41.1 ± 13.1 (n = 5)	40.3 ± 15.0 (n = 5)	0.571 ± 0.044 (n = 3)	
Oztira affinis	-	-	0.907 (n = 1)	
**Cycloctenus* cf. *cryptophilus*	59.8 ± 8.3 (n = 5)	42.1 ± 2.1 (n = 5)	1.209 ± 0.119 (n = 2)	
Cycloctenus cf. *westlandicus*	59.3 ± 6.6 (n = 4)	48.6 ± 6.9 (n = 4)	0.901 ± 0.071 (n = 5)	
**Cycloctenus* sp.	36.4 ± 7.9 (n = 4)	50.9 ± 7.6 (n = 4)	-	
Toxopsiella dugdalei	15.5 ± 4.6 (n = 2)	33.6 ± 13.4 (n = 2)	0.836 (n = 1)	
Plectophanes sp.	7.4 ± 7.0 (n = 3)	16.8 ± 9.0 (n = 3)	1.176 ± 0.096 (n = 2)	
Paravoca aff. *otagoensis*	-	-	0.673 (n = 1)	
Huara chapmanae	-	-	1.213 ± 0.130 (n = 2)	
Huka pallida	-	-	0.165 ± 0.100 (n = 2)	
Porotaka detrita	8.5 (n = 1)	42.6 (n = 1)	0.550 (n = 1)	
Orepukia alta	18.9 ± 5.3 (n = 5)	30.3 ± 8.3 (n = 5)	0.792 ± 0.142 (n = 3)	
**Orepukia prina*	22.9 ± 5.9 (n = 5)	33.1 ± 9.3 (n = 5)	-	
Tuapoka cavata	-	-	0.601 (n = 1)	
Tuapoka ovalis	4.9 (n = 1)	30.1 (n = 1)	0.325 (n = 1)	Terminal for speed data: *T. cavata*
Mahura turris	14.4 ± 4.2 (n = 4)	54.0 ± 20.1 (n = 4)	0.449 ± 0.060 (n = 3)	Terminal: *M. musca*
Mahura sorenseni	-	-	0.526 (n = 1)	
Aorangia poppelwelli	-	-	0.831 (n = 1)	Terminal: *A.* aff. *otira*
Wiltona filicicola	-	-	1.237 (n = 1)	
Neoramia janus	17.5 ± 4.2 (n = 6)	29.9 ± 10.9 (n = 6)	0.464 ± 0.047 (n = 4)	
**Neoramia mamoea*	17.3 ± 4.4 (n = 6)	29.3 ± 8.9 (n = 6)	-	
**Neoramia* sp.	18.9 ± 3.6 (n = 3)	28.2 ± 4.7 (n = 3)	-	
Oramia littoralis	-	-	0.181 (n = 1)	
Dunstanoides hesperis	-	-	0.735 ± 0.038 (n = 2)	
Stiphidiidae spec crib TAS	30.5 ± 5.6 (n = 10)	58.7 ± 11.8 (n = 10)	0.556 ± 0.040 (n = 2)	
*Stiphidiidae spec crib TAS2	37.8 ± 6.8 (n = 5)	81.8 ± 13.5 (n = 5)	-	
Tjurunga sp. 2	31.7 ± 8.0 (n = 4)	57.0 ± 14.2 (n = 4)	0.589 ± 0.125 (n = 3)	
Tjurunga sp. 3	27.3 (n = 1)	52.9 (n = 1)	0.970 (n = 1)	
Taurongia sp. 3	24.7 ± 1.2 (n = 2)	13.9 ± 4.0 (n = 2)	0.656 ± 0.039 (n = 2)	
Taurongia sp. 4	20.8 ± 3.9 (n = 4)	28.6 ± 2.5 (n = 4)	0.738 ± 0.126 (n = 3)	
Taurongia sp. 5	40.9 ± 18.4 (n = 2)	24.3 ± 9.2 (n = 2)	0.681 ± 0.085 (n = 3)	
Taurongia group spec 1	24.4 (n = 1)	35.9 (n = 1)	0.724 (n = 1)	
Taurongia group spec 2	20.8 ± 6.8 (n = 6)	35.5 ± 10.9 (n = 6)	0.778 (n = 1)	
Taurongia group spec 3	18.8 (n = 1)	35.0 (n = 1)	0.365 (n = 1)	
*Taurongia group spec 5	12.7 ± 6.6 (n = 3)	31.9 ± 6.6 (n = 3)	0.529 (n = 1)	
*Taurongia group spec 6	11.6 ± 2.1 (n = 4)	29.9 ± 10.5 (n = 4)	-	
Stiphidion facetum	47.4 ± 6.1 (n = 5)	61.1 ± 7.7 (n = 5)	0.299 ± 0.028 (n = 4)	
Stiphidion adornatum	32.5 ± 7.5 (n = 5)	58.7 ± 14.7 (n = 5)	0.129 ± 0.030 (n = 2)	
Procambridgea ourimbah	19.9 ± 0.4 (n = 2)	70.1 ± 0.8 (n = 2)	0.263 ± 0.099 (n = 2)	
**Procambridgea hunti*	20.1 ± 0.8 (n = 2)	77.5 ± 43.1 (n = 2)	-	
**Procambridgea lamington*	21.9 ± 7.0 (n = 2)	72.2 ± 20.5 (n = 2)	0.094 (n = 1)	
**Procambridgea montana*	20.7 ± 3.3 (n = 2)	69.5 ± 2.6 (n = 2)	-	
Borrala dorrigo	31.8 ± 8.4 (n = 3)	63.5 ± 16.7 (n = 3)	0.587 (n = 1)	
**Pillara griswoldi*	24.9 ± 8.2 (n = 8)	54.8 ± 23.0 (n = 8)	-	
Pillara karuah	32.5 ± 3.7 (n = 7)	59.3 ± 9.7 (n = 7)	0.596 ± 0.037 (n = 3)	
Jamberoo johnnoblei	36.9 ± 6.3 (n = 5)	57.1 ± 18.1 (n = 5)	0.195 ± 0.039 (n = 3)	
Therlinya wiangaree	33.2 ± 7.3 (n = 6)	54.4 ± 9.4 (n = 6)	0.685 (n = 1)	
Couranga diehappy	34.0 ± 15.0 (n = 2)	63.3 ± 24.1 (n = 2)	0.472 (n = 1)	
Desis marina	20.5 ± 6.9 (n = 2)	21.1 ± 9.6 (n = 2)	0.000 (n = 4)	
**Badumna* cf. *insignis*	27.4 ± 5.8 (n = 3)	20.9 ± 5.0 (n = 3)	-	
Badumna longinqua	18.1 ± 5.5 (n = 3)	31.2 ± 11.0 (n = 3)	0.562 ± 0.095 (n = 4)	
Lathyarcha sp.	11.6 ± 3.3 (n = 4)	34.2 ± 10.1 (n = 4)	0.206 ± 0.031 (n = 2)	
Lathyarcha sp. 5	4.3 (n = 1)	10.0 (n = 1)	0.256 (n = 1)	
aff. *Lathyarcha* sp.	13.4 ± 3.5 (n = 4)	25.0 ± 8.2 (n = 4)	0.438 ± 0.040 (n = 3)	
Forsterina sp.	33.8 ± 4.6 (n = 3)	46.0 ± 4.7 (n = 3)	0.841 ± 0.039 (n = 3)	
*Namandia gr. ecrib spec 4	16.1 ± 6.5 (n = 5)	38.1 ± 13.0 (n = 5)	-	

Namandia gr. ecrib spec 5	15.5 (n = 1)	43.8 (n = 1)	0.678 (n = 1)	
*Namandia gr. ecrib spec 9	12.6 ± 3.4 (n = 6)	31. 3 ± 9.2 (n = 6)	-	
*Namandia gr. crib spec 3	31.2 ± 1.8 (n = 3)	31.4 ± 8.4 (n = 3)	-	
*Namandia gr. crib spec 4	28.3 ±1.8 (n = 4)	31.4 ± 8.4 (n = 4)	-	
Namandia gr. crib spec 5	31.2 ± 1.8 (n = 3)	31.4 ± 8.4 (n = 3)	0.553 ± 0.093 (n = 2)	
*Namandia gr. crib spec 7	24.4 ± 1.8 (n = 7)	49.3 ± 11.7 (n = 7)	-	
Paramatachia decorata	9.3 ± 3.6 (n = 6)	15.4 ± 6.6 (n = 6)	0.518 ± 0.113 (n = 2)	
Goyenia cf. *fresa*	15.4 ± 3.9 (n = 12)	33.0 ± 6.3 (n = 12)	0.782 ± 0.093 (n = 4)	
Mesudus sp.	13.3 (n = 1)	28.3 (n = 1)	0.850 (n = 1)	
Matachia australis	19.6 (n = 1)	41.8 (n = 1)	0.495 (n = 1)	
Panoa cf. *mora*	8.5 ± 5.3 (n = 3)	21.1 ± 9.6 (n = 3)	0.763 ± 0.020 (n = 3)	
Helsonia plata	29.8 (n = 1)	21.8 (n = 1)	0.465 ± 0.183 (n = 2)	
Daviesa lubinae	17.8 ± 3.6 (n = 2)	35.4 ± 7.1 (n = 2)	1.245 (n = 1)	
Corasoides terania	51.2 ± 22.7 (n = 4)	46.4 ± 15.9 (n = 4)	0.332 ± 0.051 (n = 4)	
Nanocambridgea gracilipes	17.3 (n = 1)	34.1 (n = 1)	0.223 ± 0.034 (n = 2)	
Cambridgea foliata	-	-	0.249 (n = 1)	
Cambridgea sp. 2	37.4 (n = 1)	41.8 (n = 1)	-	Terminal: *C. foliata*
Cambridgea sp. 3	53.1 (n = 1)	43.8 (n = 1)	-	Terminal: *C.* sp.
Baiami tegenarioides	-	-	0.440 ± 0.024 (n = 2)	Terminal: *B. volucripes*
Tartarus sp.	-	-	0.048 (n = 1)	
Ischalea spinipes	-	-	0.321 (n = 1)	
Manjala plana	33.6 ± 16.6 (n = 5)	61.8 ± 25.5 (n = 5)	1.711 (n = 1)	
Dardurus sp.	15.3 ± 5.5 (n = 4)	57.3 ± 14.5 (n = 4)	0.965 (n = 1)	
Quemusia cf. *raveni*	16.0 ± 3.6 (n = 3)	41.1 ± 12.1 (n = 3)	0.402 (n = 1)	
Austmusia wilsoni	49.6 (n = 1)	51.4 (n = 1)	0.651 (n = 1)	
Toxopsoides cf. *erici*	30.6 ± 6.7 (n = 3)	67.8 ± 22.8 (n = 3)	1.709 ± 0.302 (n = 2)	
**Toxopsoides* cf. *kathleenae*	17.3 ± 9.2 (n = 2)	55.8 ± 24.9 (n = 2)	-	
**Toxopsoides* sp. 9	30.4 ± 16.4 (n = 2)	112.5 ± 36.7 (n = 2)	-	
**Toxopsoides* sp. 10	34.4 ± 4.8 (n = 4)	91.8 ± 9.7 (n = 4)	-	
Colcarteria sp.	-	-	0.396 (n = 1)	
Amphinecta mara	40.0 ± 11.4 (n = 3)	30.8 ± 8.2 (n = 3)	0.344 ± 0.030 (n = 2)	
Mamoea rufa	-	-	0.547 (n = 1)	
Maniho meridionalis	-	-	0.524 ± 0.023 (n = 3)	
Maniho tigris	29.1 ± 5.3 (n = 2)	44.9 ± 13.6 (n = 2)	0.458 ± 0.021 (n = 2)	Terminal for speed data: *M. meridionalis*
Maniho sp.	-	-	0.539 ± 0.024 (n = 3)	
Akatorea gracilis	-	-	0.683 ± 0.033 (n = 2)	

Electronic supplemental material

S1. List of specimens used in the phylogenomic study including collection information, voucher location and the number of loci captured (csv).

S2. List of specimens used in the comparative and phylogenetic study including collection information, raw and calculated morphometric data (csv).

S3. Code, input and output files of the kinematic analysis (R project).

S4. Code, input and output files of the phylogenetic comparative analysis (R project)

S5. UCE alignments and subsamples used for phylogenetic inference. (*currently still under embargo*)

S6. ML and BI phylogenetic trees with bootstrap values and the HPD of divergence time estimates.

S7. Description of the foraging ecology and web structure of the studied species including the reasoning for the coding of ecological traits.