



## Evolution

# Convergence, Hemiplasy, and Correlated Evolution Impact Morphological Diversity Related to a Web-Less Lifestyle in the Two-Clawed Spiders

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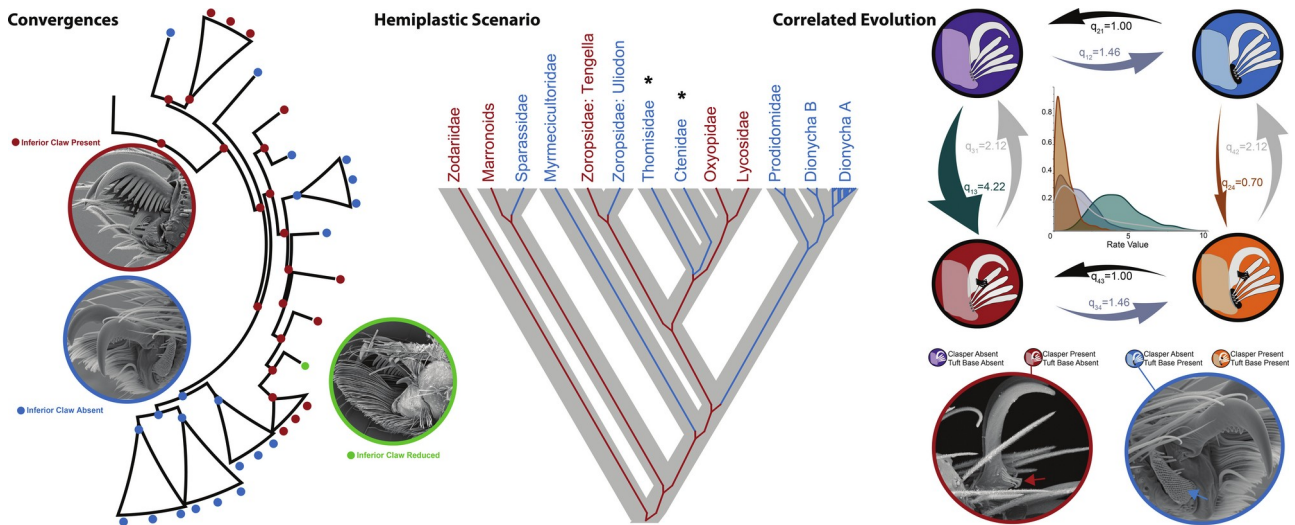
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### Abstract

Traits that independently evolve many times are important for testing hypotheses about correlated evolution and understanding the forces shaping biodiversity. However, population genetics processes can cause hemiplasies (traits determined by genes whose topologies do not match the species tree), leading to a false impression of convergence (homoplasy) and potentially misleading inferences of correlated evolution. Discerning between homoplasies and hemiplasies can be important in cases of rapid radiations and clades with many gene tree incongruences. Here, focusing on two-clawed spiders (*Dionycha*) and close relatives, we evaluate if the observed distribution of characters related to a web-less lifestyle could be better explained as synapomorphies, homoplasies, or hemiplasies. We find that, although there are several convergences, hemiplasies are also sometimes probable. We discuss how these hemiplasies could affect inferences about correlation and causal relationship of traits. Understanding when and where in the tree of life hemiplasy could have happened is important, preventing false inference of convergent evolution. Furthermore, this understanding can provide alternative hypotheses that can be tested with independent data. Using traits related to the climbing ability of spiders we show that, when hemiplasy is unlikely, adequate model testing can be used to better understand correlated evolution, and propose hypotheses to be tested using controlled behavioral and mechanical experiments.

## Graphical Abstract



Key words: ancestral state reconstruction, ancestral polymorphism, Dionycha, phylogenetic comparative method, RTA clade

One of the goals of evolutionary biology is to study the processes leading to the observed patterns of trait distribution across taxa. Several approaches can be used to achieve this goal, from ancestral character reconstruction to more complex phylogenetic comparative methods (PCM; Adams and Collyer 2019, Felsenstein 1985, Petroni and Harmon 2013). Ancestral state reconstruction methods are useful in discerning homoplasies (traits with similarities in structure inherited from a common ancestor), as well as detecting correlated evolution of traits (Maddison 1990; Pagel 1994, 1999a). Regardless of the approach used, all methods rely upon a reasonable knowledge of phylogenetic relationships.

Recent advances in molecular biology allow for the estimation of robust phylogenetic hypothesis based on genomic scale data (Faircloth et al. 2012, McCormack et al. 2013, Zhang et al. 2019, Young and Gillung 2020). In addition to providing more robust phylogenetic hypotheses, phylogenomic studies also bring insights about how molecular evolution and population genetics processes are linked to systematics and trait evolution (Zachos 2009, Hahn and Nakhleh 2016, Guerrero and Hahn 2017, Bastide et al. 2018, Mendes et al. 2018, Hibbins et al. 2020, Wang et al. 2021). One concept that emerged from these theoretical advancements is hemiplasy (Avice and Robinson 2008). Although the term itself is relatively recent, the process that it describes has been known for a decades (Throckmorton 1965, see also Maddison and McManis 2000 and references therein). Hemiplasy can be defined as traits that have been hypothesized that spiders that lost the movable plate of the claw tuft evolved a claw tuft clasping mechanism (CCM) as a result of a false perception of homoplasy (Avice and Robinson 2008, Zachos 2009, Hahn and Nakhleh 2016, Wu et al. 2018). This false perception means that the presence of folds (evolves) on the basal part of the claw tuft setae is a preadaptation important for the origin of the CCM in Dionycha (Ramírez 2014, Azevedo et al. 2018). Distinguishing between homoplasy and hemiplasy is especially important in cases of rapid radiations (Parins-Fukuchi et al. 2021).

Spiders represent a clade with many examples of rapid radiations that present a high diversity of morphological, behavioral, and lifestyle traits interesting for character evolution studies (Bond and Opell 1998, Vizuela et al. 2019, Crews et al. 2020, Berger et al. 2021, Dimitrov and Hormiga 2021). Although the capture web is one of the most striking features of spiders and a target of many evolutionary studies (Bond et al. 2014, Garrison et al. 2016, Fernández et al. 2018, Coddington et al. 2019, Kallal et al. 2020), about half of the species do not use webs for catching prey. This alternative web-less hunting style might have led to several changes in the morphology and ecology of web-less species (Wolff et al. 2013, 2021). Dionycha is one group of spiders that is an appealing target for the study of phenotypic traits related to this life without capturing prey. Dionycha is a clade that includes 20 families and comprises about 20% of all described spider species (WSC 2021). The term Dionycha means 'two claws', a characteristic that has been thought to be a synapomorphy of the group, together with the presence of a claw of robust tenent (adhesive) setae (Ramírez 2014). Both the loss of inferior claws and the presence of claw tuft setae (CTS) are also found in many other spiders with a wandering lifestyle, which may indicate convergent adaptation for walking on smooth surfaces rather than on silk threads (Lehtinen 1967, Coddington and Levi 1991, Coddington 2005, Wolff et al. 2013). Nevertheless, the remarkable diversity of structures associated with the claw tuft of tenent setae in dionychans suggests that those traits may have played an important role in diversification (Wolff et al. 2013, Ramírez 2014, Labarque et al. 2017). For instance, some dionychans have a movable plate for the attachment of the CTS, but in many others, this plate is absent, and the setae are attached immovably to the cuticle. However, it has been hypothesized that spiders that lost the movable plate of the claw tuft evolved a claw tuft clasping mechanism (CCM) as a result of a false perception of homoplasy (Avice and Robinson 2008, Zachos 2009, Hahn and Nakhleh 2016, Wu et al. 2018). This false perception means that the presence of folds (evolves) on the basal part of the claw tuft setae is a preadaptation important for the origin of the CCM in Dionycha (Ramírez 2014, Azevedo et al. 2018). Morphological characters related to the eyes might have also contributed to the success of some dionychan spiders in a new wandering lifestyle. Spiders can have a reflective layer in the eyes called the tapetum, which, in some spiders, functions as a compass organ (Dacke and Opell 1998, Vizuela et al. 2019, Crews et al. 2020, Berger et al. 2021, Dimitrov and Hormiga 2021). Although the capture web is one of the most striking features of spiders and a target of many evolutionary studies (Bond et al. 2014, Garrison et al. 2016, Fernández et al. 2018, Coddington et al. 2019, Kallal et al. 2020), about half of the species do not use webs for catching prey. This alternative web-less hunting style might have led to several changes in the morphology and ecology of web-less species (Wolff et al. 2013, 2021). Dionycha is one group of spiders that is an appealing target for the study of phenotypic traits related to this life without capturing prey.

of the day (Dacke et al. 1999, 2001; Mueller and Labhart 2010). This state may have a different likelihood if one wants to know how Lastly, Dionycha spiders present a huge diversity of spinning organs (i.e., the joint like- (Platnick 1990, Ramírez 2014) in spite of being web-less hunters. This character changed from one node to another (i.e., the joint like- suggesting that there is still much to learn about the evolution of silk (Fusiko et al. 2000, Ishikawa et al. 2019). This means that the most use, its properties, and functions. One interesting modification likely reconstruction on a node may not necessarily coincide with spinning organs of some two clawed spiders is the enlargement and the most likely history of character change in the tree (Pagel 1999b, elongation of the base of a silk gland spigot (opening of the gland) (Pupko et al. 2000, Felsenstein 2004). To test different scenarios of called piriform (Platnick 1990, Ramírez 2014). This modification of character change, we fixed the states in the internal nodes to rep- the piriform gland spigot (Pi) is likely related to the use of the silk to different scenarios and compared the probabilities with actively immobilize prey (Wolff et al. 2017, Baydizada et al. 2021).

The understanding of the evolution of the aforementioned trait character state as a synapomorphy of Dionycha, a plesiomorphy was previously hampered by the lack of a stable phylogenetic tree of Dionycha, or a convergence inside Dionycha and/or between Dionycha and outgroups (Supp Figs. 1–4 [online only]). All Bayesian cent analysis of Dionycha using genomic and morphological data were run in BayesTraits v3 (Pagel and Meade 2017) with (Azevedo et al. 2022b) further clarified the phylogeny for this group. 10,000 MCMC iterations, sampling each 1,000, with burn in of 10,000 iterations. Marginal likelihoods were calculated for 10,000 iterations. However, the amount of gene tree discordance in many branches of 10,000 iterations. Marginal likelihoods were calculated with stepping stones (Xie et al. 2011) with 100 steps with 10000 iterations each.

to use the phylogeny of Azevedo et al. (2022b) as a framework to further explore the evolution of those traits related to web-less life-style. Specifically, we tested whether the evolution of the inferior claw, the CTS, the OMT, and the base of Pi could be explained using simulations. The Probability of Hemiplasy (PH) is the probability of hemiplastic scenarios (Avice and Robinson 2008, Hahn and Nakhleh 2016) for hemiplasies. We discuss how possible hemiplasy would influence the inferior claw, CTS, OMT, and Pi. Hibbins et al. (2020) proposed our understanding of the role of web-less lifestyle characteristics and to estimate the probability of hemiplasy using simulations. their possible association with the studied traits. After excluding the method requires a character mutation rate (which might be hemiplasy possibility for some traits, we tested for coevolution between the different from the nucleotide mutation rate). The character mutation tween the movable base of the CTS and the CCM, and between the rate is unknown for most characters and taxa. One option is to use CCM and the shape of the base of the CTS.

## Material and Methods

### Data

We used the trees, genomic matrices, and morphological matrices published by Azevedo et al. (2021) and available on FigShare (DOI: 10.6084/m9.figshare.14977185). Matrices were trimmed to contain only the characters of interest for each analysis. The modified matrix, as well as inputs and scripts used here are available on FigShare (DOI: 10.6084/m9.figshare.16673872).

### Scenarios of Character Evolution

We used a Bayesian framework to estimate the evolution of the inferior claw, the CTS, the OMT, and the elongation of Pi base. All transition rates were free to vary in the Markov model. As (1) our focus is on estimating ancestral states (i.e., rates are nuisance parameters) and the available models cannot reliably estimate the states and rates (Gascuel and Steel 2020), and (2) the single and two species tree is a proxy for the probability of hemiplasy. It also assumes models are submodels of the all different rates (Mooers and Schuster 1999), a Bayesian framework with all rates free to vary seemed appropriate. This approach allows the ancestral states to be estimated by integrating over all possible rate values, and therefore accounts for errors in the estimation of rates (Pagel et al. 2004). The frequency of each state may also influence estimation and be biased when there are very rare states (Collins et al. 1994). Therefore, using Bayes Factors, we tested a model which uses the empirical state frequencies against a model that does not account for the frequency of states (Nyman et al. 2015) using MODELFINDER (Kalyaanamoorthy

throughout the Dionycha tree (i.e., how and where the character states changed). The ancestral reconstruction usually shows the likelihood of a state in a determined node integrating over all possible states in the other nodes (marginal likelihood of a state). However, this method does not change the internal branch lengths, which are more

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important for our simulations given that we only have one window compared to others. This model was set in BayesTraits and compared to a model in which all traits are independent from each other. The frequency of gene trees placing taxa on a particular character of interest in monophyletic groups was taken as a general approximation of a probability of hemiplasy. Only a few hemiplasy scenarios of most interest were evaluated in a pruned simplified tree (Supp Fig. 5-8 [online only]), since the evaluation of all possible scenarios is unfeasible.

The second approach relies on approximating the marginal likelihood of the hemiplasy scenarios as  $P(D|S) = \int P(D|G_{He})P(G_{He}|S)dG_{He}$ . Here  $D$  is the character matrix,  $S$  is the species tree with branch lengths in coalescent units,  $P(D|G_{He})$  is the likelihood of the data given a distribution of gene trees (with branch lengths) and substitution rates that represent hemiplastic scenarios, and  $P(G_{He}|S)$  is the prior probability of the homoplastic gene trees under the censored coalescent model. This is similar to the 'Felsenstein equation' proposed earlier (Felsenstein 1981, Hey and Nielsen 2007, Bryant et al. 2012), but instead of integrating over all gene trees generated by the tree, it integrates only over the gene trees that would represent a homoplastic scenario. For each of the previous simulated gene trees ( $G_{He}$ ), we calculated  $P(D|G_{He})$  using the rate that maximizes the likelihood of that gene tree, using an equal transition Markov model in BayesTraits. The prior probabilities of each gene tree were calculated with STELLS2 (Pei and Wu 2017). We assumed that the simulated gene trees with their maximum likelihood rates are a good approximation of the prior probability density of the distribution of gene trees and rates. We are aware that this assumption might not hold given the possible variance of distribution of genes and rates. However, this way we can account for unknown rates of evolution marginalizing over a distribution of likely values for each gene tree. We stress that we are assuming a trait substitution rate can be different from the nucleotide substitution rate, therefore we are making no assumptions about the genetic basis of the mutation (i.e., one or several epistatic nucleotide mutations). As before, we are also assuming that the trait is determined by either one or several linked genes.

The marginal likelihood of homoplasy was calculated in a similar way, but considering only gene trees that would imply homoplasy. The probability of hemiplasy was then calculated as  $P(Hemiplasy) = \frac{MarginalLikelihood\ Hemiplasy}{Marg.Lik. Hemiplasy + Marg.Lik. Homoplasy}$ . A python script that separates trees into hemiplasy and homoplasy scenarios prepares the input for BayesTraits and STELLS2, and combines the outputs, and calculates the probabilities of hemiplasy and homoplasy is available on FigShare (DOI: 10.6084/m9.figshare.16673872).

## Correlated Evolution

We used a Bayesian framework with BayesTraits (see Menezes and Santos 2020) to test for the correlated evolution of characters using models that account for correlated character changes (Pagel 1994).

We were interested in two specific hypotheses, the first being that the CCM evolves after the loss of a movable claw tuft plate as a means to facilitate the detachment of the adhesive seta (Ramírez 2014). Some possible expectations of this hypothesis are that: (1) the rate of CCM gain/losses would be dependent on the state of the tuft plate (parameters  $q_{23} \neq q_{43}$ ;  $q_{31} \neq q_{42}$ ; See Supp. Material Appendix 1 [online only]); (2) the rate of CCM gain when the plate is absent would be higher than the rate of gain when the plate is present ( $q_{13} > q_{43}$ ); (3) the CCM gain when the plate is absent would be higher than the CCM loss when the plate is absent ( $q_{13} > q_{43}$ ); (4) the gain/loss of movable plate are independent of the CCM ( $q_{34} = q_{43}$  and  $q_{21} = q_{31}$ ); and (5) the CCM gain when the plate is present would be

## Results

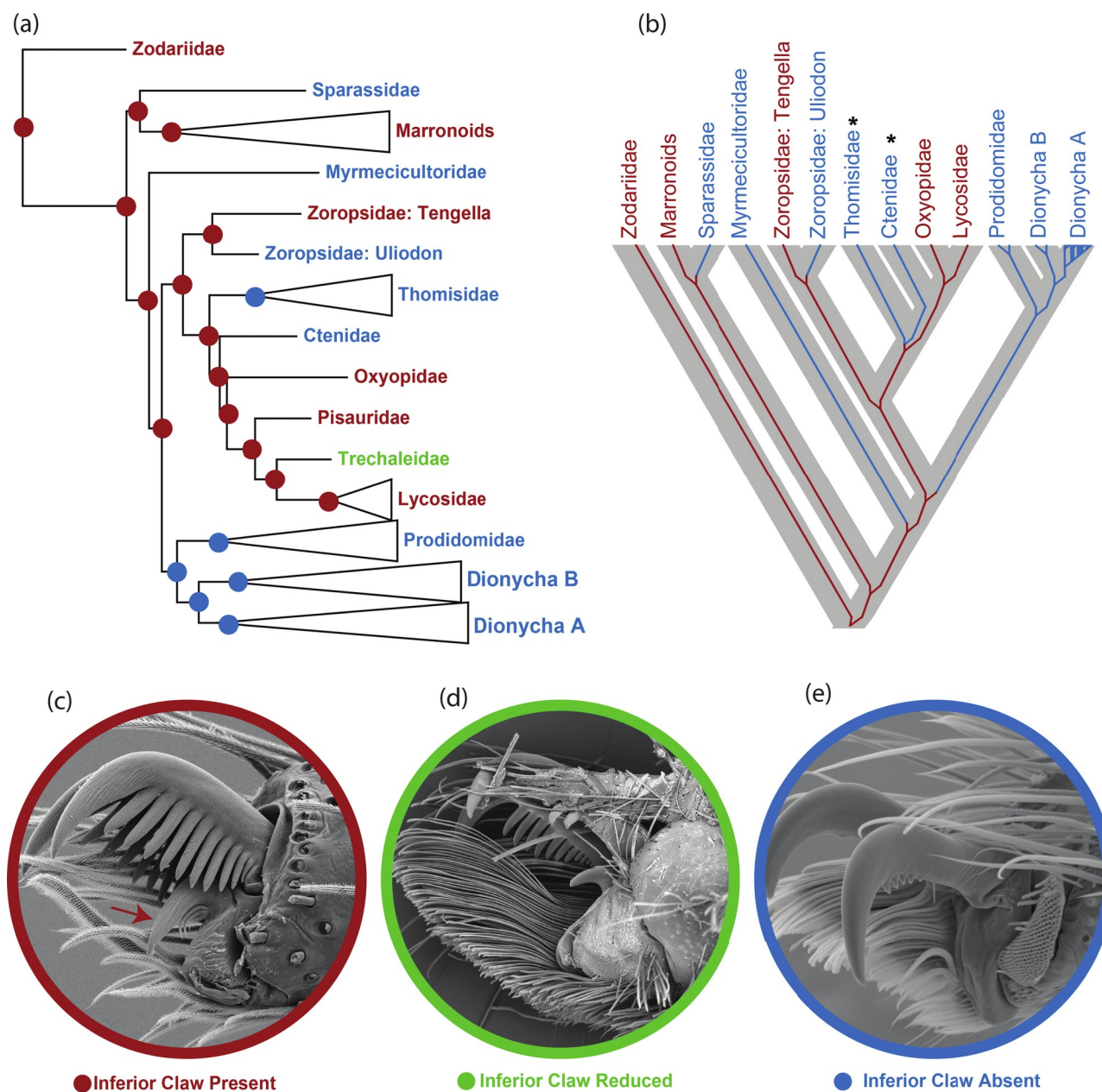
### Ancestral Character Reconstruction

The model which includes an empirical state frequency as a parameter had a better fit for the inferior claw, CTS, and for the base of Pi. For the OMT the best model does not include state frequencies (Supp Table 1 [online only]).

When testing for joint probabilities of different histories of character changes in the tree, the scenario that shows the loss of inferior claw as a synapomorphy of Dionycha with convergences in Sparassidae Bertkau, 1872, Myrmecicultoridae Ramírez, Grismado & Ubick, 2019 and inside OCC are significantly more likely than other scenarios tested (Fig. 1, Supp Fig. 1 [online only]). The test of alternative scenarios of CTS evolution suggests that the tuft seta is most likely a synapomorphy of Dionycha, with losses in the ingroup and convergences in the outgroup (Fig. 2, Supp Fig. 2 [online only]). The most likely scenario for the OMT suggests that it arose convergently in Myrmecicultoridae, Prodidominae Simon, 1884, *Trachychosmus* Simon, 1893 and in the most recent common ancestor of Gnaphosidae Banks, 1892 and Trachelidae Simon, 1897 (Fig. 3, Supp Fig. 3 [online only]). The most likely evolutionary scenario for the Pi base elongation was three gains in the phylogeny (Fig. 4, Supp Fig. 4 [online only]).

### Hemiplastic Scenarios

Our simulations that do not consider rates of character changes suggest that there is a reasonable probability that the loss of the inferior claw might be a hemiplastic condition between Thomisidae Sundevall, 1833 and Ctenidae Keyserling, 1877 (14%) or between Zoropsidae Bertkau, 1882 (*Uliodon* L. Koch, 1873) and Thomisidae (*Uliodon*) and Ctenidae (Fig. 1, Supp Fig. 5 [online only]). The probability of at least one of these events is 25.65%. There is a small chance (4.2%) that the OMT can be explained by hemiplasy in Myrmecicultoridae and Prodidomidae Simon, 1884 (Fig. 3, Supp Fig. 6 [online only]), and the probability of at least one event of

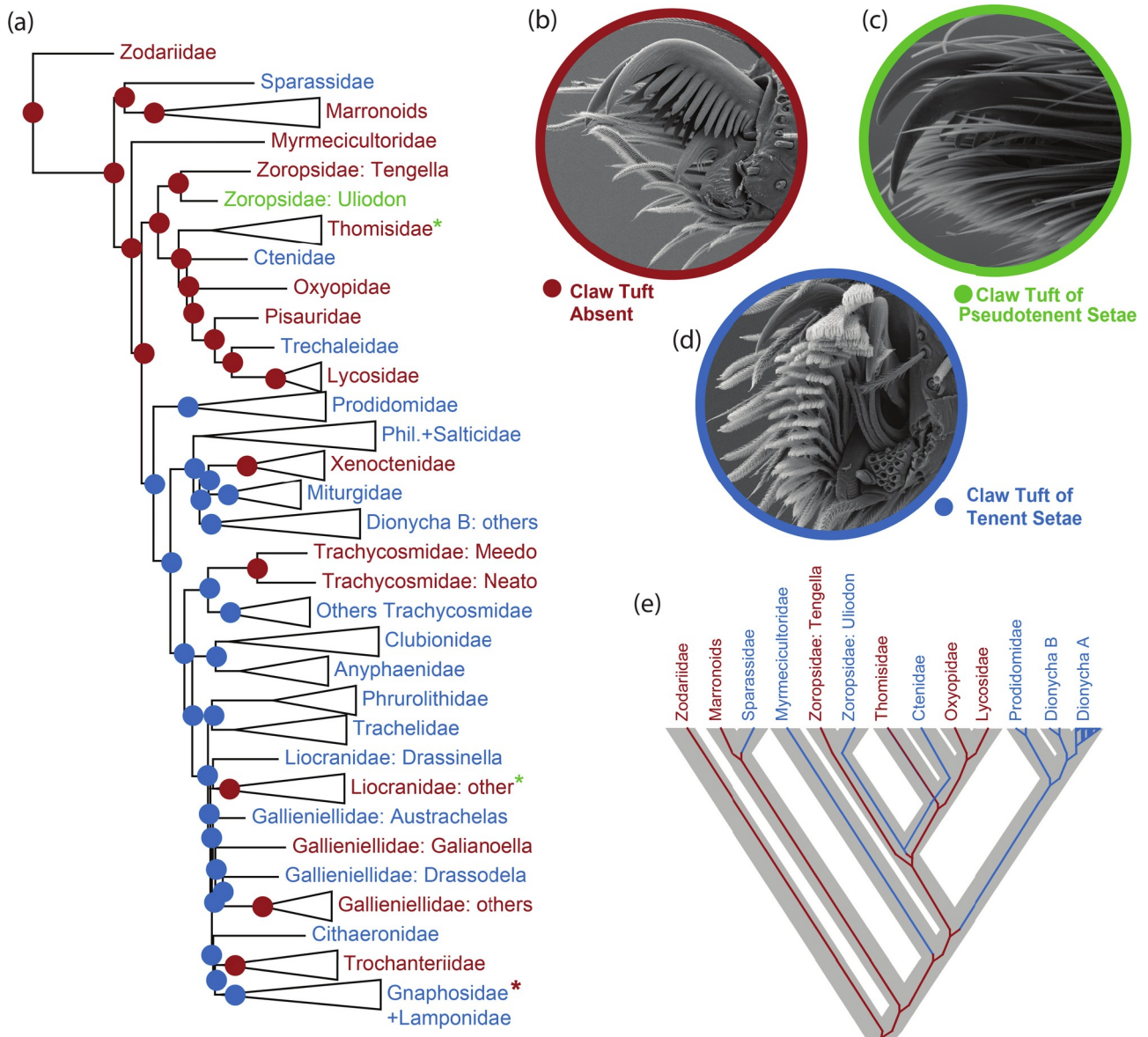


**Fig. 1.** The evolution of the inferior claw of Dionycha and outgroups. (a) Most probable hypothesis of character evolution. Ancestral states of the nodes are represented by gray scale dots (see online version for colors). Shades of gray on the taxon names represents the state on that terminal (see online version for colors). Marginal log-likelihood of this hypothesis:  $-31.27$ . Marginal log-likelihood of the second-best hypothesis (see Supp Fig. 3 [online only]):  $-34.21$ . Log Bayes Factor = 2.94. (b) Species tree (thick grey branches) with example of an embedded gene tree that would result in hemiplastic evolution. Hemiplasy between Thomisidae and Ctenidae (marked with \*) has a probability of 0.14. Shades of gray represents the states at the gene tree branches and terminals (see online version for colors). (c) Scanning electron microscopy (SEM) of the tarsus of *Pimus* (Amaurobiidae) showing the presence of an inferior claw (arrow). (d) SEM of the tarsus of *Cupiennius* (Trechaleidae) showing the reduced inferior claw. Image by Jonas Wolff. (e) SEM of the tarsus of *Rebilus* (Trachycosmidae) showing the absence inferior claw.

hemiplasy occurring is only 4.9%. There is a relevant probability and the ancestral condition in Thomisidae is pseudotenent (5.34%) that the enlargement of Pi base may have occurred (Ramírez 2014) we find the same probabilities as for the inferior hemiplasy between *Hypodrassodes* Dalmás, 1919 and molycritids mentioned above (Supp Table 2 [online only]).

(Fig. 4, Supp Fig. 7 [online only]); the probability of at least one using our approach to integrate over a distribution of possible rates and gene trees, we found that the probability of at least

one event of hemiplasy (i.e., total hemiplasy or combinations of with acute tip and enant barbs loosely organized (Ramírez 2014) hemiplasy and homoplasy) in the OMT and loss of inferior claw as a regular (or frictional, see Wolff et al. 2013) seta we find that it increased to 43.6% and 20.3%, respectively (Supp Table 2 [online is very unlikely that CTS evolution included hemiplasy (Supp Table 2 [online 2 [online only]). However, if the pseudotenent is considered a trait without considering the substitution rate. The probability of the CTS

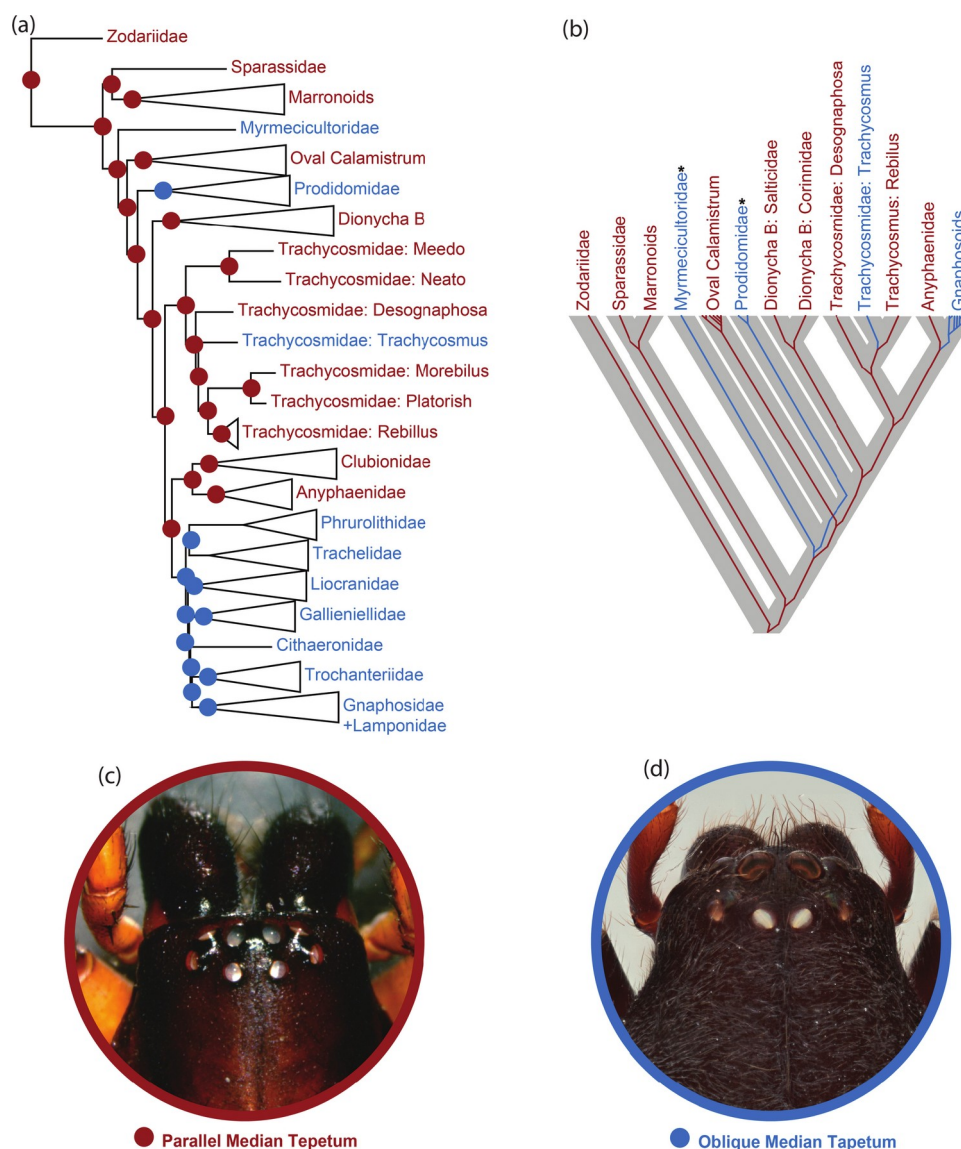


**Fig. 2.** The evolution of claw tuft setae (CTS) of Dionycha and outgroups. (a) Most probable hypothesis of character evolution. Ancestral states of the nodes represented by gray scale dots (see online version for colors). Shades of gray on the taxon names represents the state on that terminal (see online version for colors). '\*' marks collapsed clades in which there are representatives with pseudotenent seta. (Thomisidae; green \* in online colored version), or without tenent setae (Gnaphosidae; red \* in the online colored version). Marginal log-likelihood of this hypothesis:  $-71.61$ . Marginal log-likelihood of the second-best hypothesis (see Supp Fig. 3 [online only]):  $-74.77$ . Log Bayes Factor = 3.16. (b) SEM of the tarsus of *Pimus* Chamberlin, 1947 (Amaurobiidae Thorell, 1870) showing the absence of CTS. (c) SEM of the tarsus of *Uliodon* (Zoropsidae) showing the CTS composed by pseudotenent setae. (d) SEM of the tarsus of *Donuea* sp. (Corinnidae Karsch, 1880) showing the CTS composed by tenent setae. (e) Example of possible hemiplastic scenario if the pseudotenent seta of *Uliodon* is considered equivalent to a tenent setae.

when considering the ancestral state in Thomisidae as tenent setae in accordance with expectations for the hypothesis that the All other characters tested presented an insignificant probability of clasp mechanism evolved to facilitate detachment of the adhesive hemiplasy (Supp Table 2 [online only]).

### Correlated Evolution

We found significant evidence for correlated character evolution in both systems tested. The gain of CCM is correlated with clasp mechanism (Supp Fig. 9 [online only]). The hemiplastic evolution of the movable plate of CTS, and it is much more likely scenarios tested for CCM, the tuft plate, and the shape of the setae to happen when the movable plate is lost (Fig. 5). The loss of the how probabilities less than 4% if rates are not considered and less CCM is less likely when the plate is absent (Fig. 5). Rate estimates are 0.1% when rates are used (Supp Tables 3-6 [online only]).



**Fig. 3.** The evolution of the tapetum on the median eyes of Dionycha and outgroups. (a) Most probable hypothesis of character evolution. Ancestral states of the nodes represented by gray scale dots (see online version for colors). Shades of gray on the taxon names represents the state on that terminal (see online version for colors). Marginal log-likelihood of this hypothesis:  $-24.91$ . Marginal log-likelihood of the second-best hypothesis (see Supp Fig. 3 [online only]):  $-35.11$ . Log Bayes Factor =  $10.2$ . (b) Species tree (gray bars) with example of an embedded gene tree that would result in hemiplastic evolution. Hemiplasy between Myrmecicultoridae and Prodidomidae (marked with \*) has a probability of  $0.042$ . (c) Photo of the prosoma of *Falconina* Brignoli, 1985 (Corinnidae) showing the parallel median tapetum of the posterior median eyes (photo credit: Cristian Grismado). (d) Photo of the prosoma of *Lampona* Thorell, 1869 (Lamponidae Simon 1893) showing the oblique median tapetum (OMT) of the posterior median eyes.

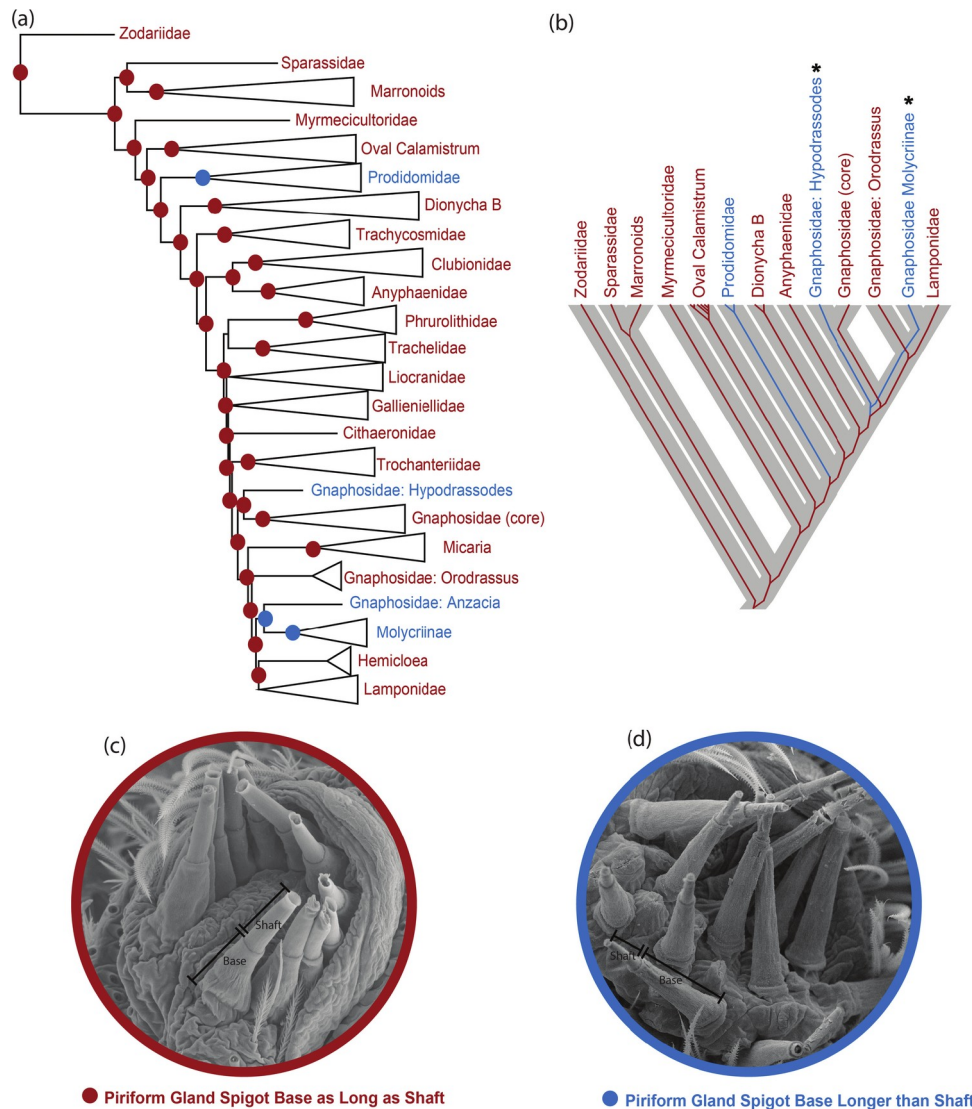
## Discussion

### The Evolution of the Inferior Claw and Claw Tuft

Our results strongly support the loss of the inferior claw as a synapomorphy of Dionycha, but with convergences in the outgroup (Fig. 1). Reversal to the three-clawed condition is unlikely to have happened in our dataset. This could mean that the expression of the third claw might have a complex genetic basis that makes re-evolution unlikely or that having two claws might have been advantageous if the spider doesn't need to walk on silk threads. The inferior claw is a solid nonarticulated structure (Labarque et al. 2017) used by spiders to manipulate silk threads (Eberhard 2017) and it could hinder locomotion outside the web, increasing friction on rough surfaces (Wolff and Gorb 2012). In fact it is observed that the inferior claw is absent in many vagrant spiders (Ramírez 2014, Labarque et al. 2017).

absence of the inferior claw is also observed in many species that possess a claw tuft of tenent setae (Ramírez 2014, Labarque et al. 2017).

The claw tuft was also found here as a synapomorphy of Dionychans with losses inside the clade and convergences with some outgroups (Fig. 2). Besides its prime role in adhesion to smooth surfaces, the claw tuft may also help with prey capture (Rovner 1978, 1980). The claw tuft of tenent seta might be thought of as a key innovation in the radiation of Dionycha, providing an efficient tool to explore habitats such as shrubs, trees, leaves and smooth rocks, with a lifestyle independent of webs (Wolff et al. 2013). It would be interesting to investigate whether the loss of the adhesive setae might have some adaptive explanation. Wolff et al. (2013) proposed the adhesive setae might be costly and that sometimes costs outweighs advantage, leading to a loss of the character. In the case of

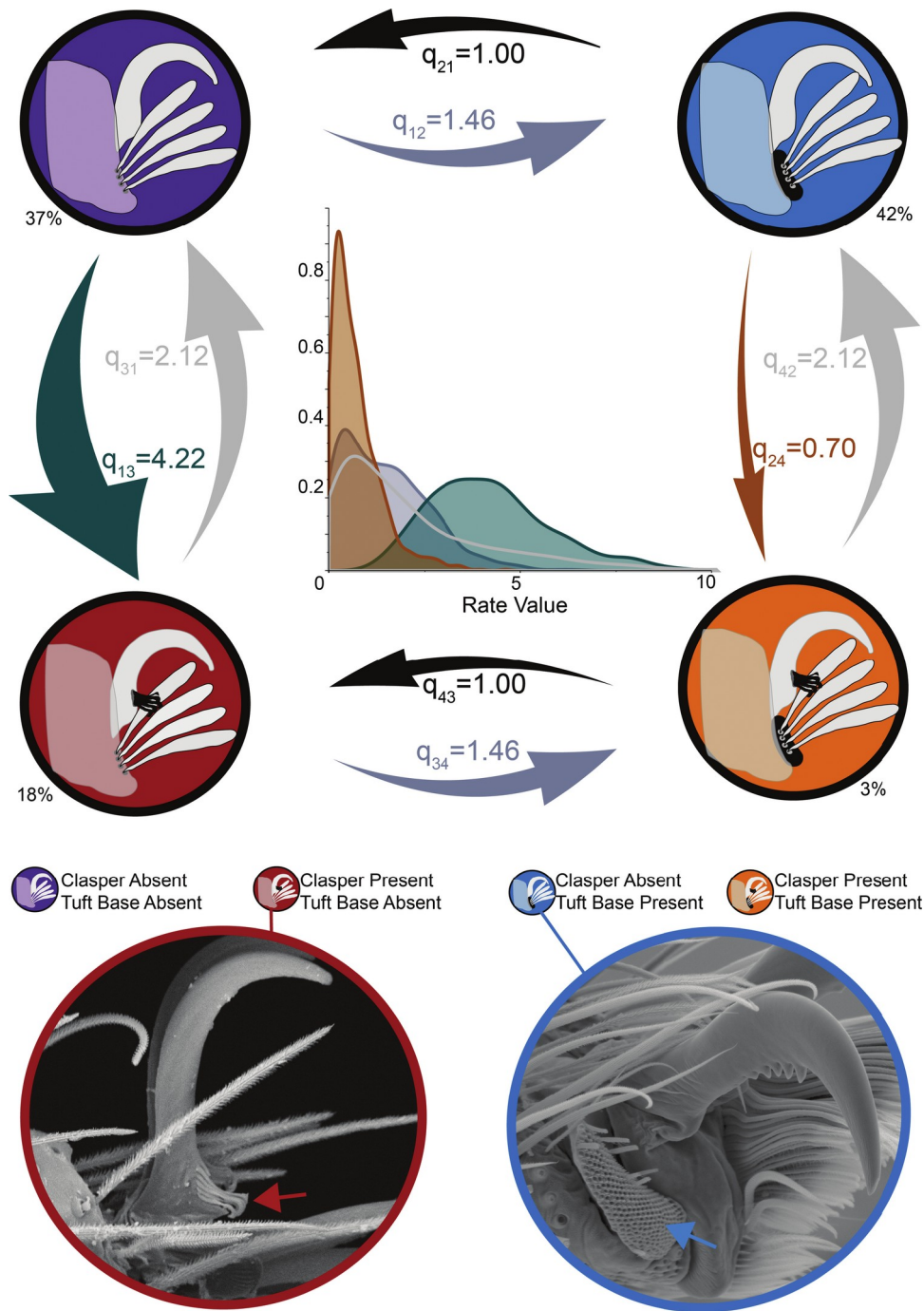


**Fig. 4.** The evolution of the base of the piriform spigot (Pi) of *Dionycha* and outgroups. (a) Most probable hypothesis of character evolution. Ancestral states of the nodes represented by gray scale dots (see online version for colors). Shades of gray on the taxon names represents the state on that terminal (see online version for colors). Marginal log-likelihood of this hypothesis:  $-24.42$ . Marginal log-likelihood of the second-best hypothesis (see Suppl Fig. 3 [online only]):  $-32.69$ . Log Bayes Factor = 8.27. (b) Species tree (grey bars) with example of an embedded gene tree that would result in hemiplastic evolution. Hemiplasy between Myrmecicultoridae and Prodidomidae (marked with \*) has a probability of 0.05. (c) SEM of the anterior lateral spinnerets of *Apodrassodes* (Gnaphosidae) showing the piriform base as long as the shaft (normal size). (d) SEM of the anterior lateral spinnerets of *Hypodrassodes* (Gnaphosidae) showing the piriform base much longer than the shaft (elongated).

ground-dwelling spiders (e.g., gnaphosids, liocranids, gallieniellids, trochanteriids) where several losses of claw tuft occurred, the ongoing debate on how to use webs as a character and how this inaccessibility of relevant walking surfaces might interfere with ancestral state reconstruction (Bond et al. 2014, Hormiga and Griswold 2014, Garrison et al. 2016, Fernández et al. 2018, Maddison et al. 2019, Kallal et al. 2020). Here we found another possible complication: the possibility that those characters represent hemiplasies in some parts of the tree.

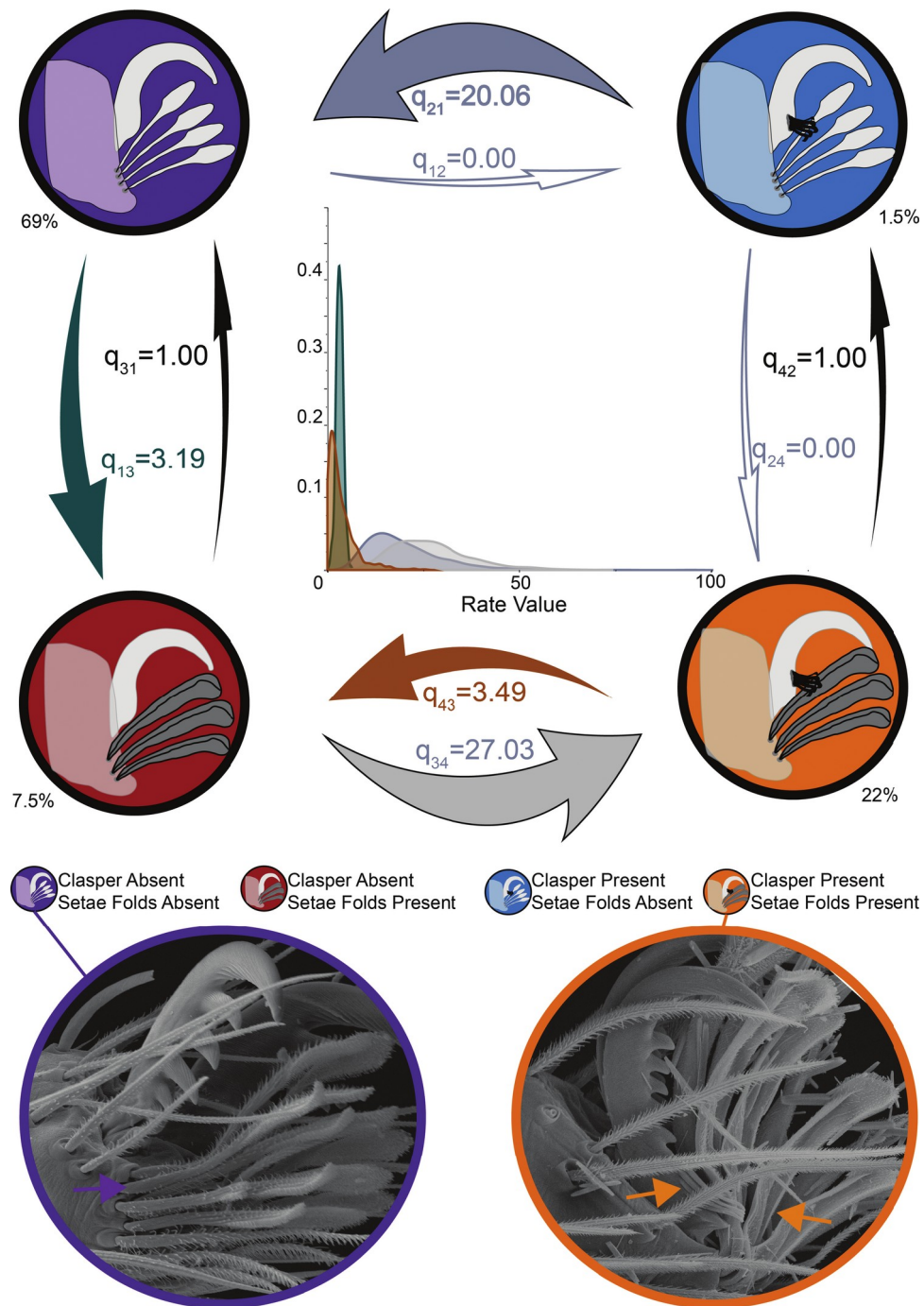
The repeated instances of losses and gains of the inferior claw and the claw tuft of tenent setae suggest that these characters have evolved as a biomechanical solution to their hunting lifestyles and habitats. In fact, meta-analyses suggest that specialized setae on spider feet (scopulae and claw tufts) could be seen as a 'great innovation of the basal nodes, it would imply that the ancestral population of the tuft and/or loss of third claw with the web-less behavior seems very strong, the hypothesis of causal relationship between those characters is difficult to test for three reasons: (1) methods available are biased toward finding significant relationships when there are many tests; (2) the phylogenetic placement of some key web-builder families (including *Phoneutria* Perty, 1833 (both *Ctenidae* Keyserling, 1877), and *Gallieniellidae* Blackwall, 1841 (*Dionycha*)) have the third claw, which is





**Fig. 5.** Model of correlated evolution of the claw tuft clasp mechanism (CCM) and the claw tuft movable base. Cartoon circles at corners represent the states and arrows represent the transition rates (parameter of the model) between states. Arrows are weighted by their relative values near them, which represents the mean of the posterior distribution. The central panel shows the posterior distribution of each rate, which is represented by a gray tone that corresponds to the respective arrow gray tone (see online version for colors). The numbers near the cartoon circles show the frequency of that state in the dataset (excluding missing data). The bottom SEM images show the tip of the tarsus as an example for two of the states (linked by lines). Bottom left: *Chileuma* Platnick, Shadab & Sorkin, 2005 (Prodidomidae); arrow points to the CCM. Bottom right: *Rebilus* (Trachycosmidae Platnick, 2002); arrow points to the claw tuft movable base. Marginal log-likelihood of this model: -53.74. Marginal log-likelihood of the independent model: -55.43. Log Bayes Factor: 1.69.

absent in the adults (Homann 1971, Foelix 2011). These observations and maintained by differences in ontogeny between morphotypes can suggest that differences in ontogeny (e.g., a faster maturation rate) could lead to a polymorphic ancestral adult population. Differences in prey abundance through space and time could cause heterogeneity in the distribution of the presence and development of the third ontogeny and, consequently, lead to maintenance of the inferior form. Regarding the evolution of the claw tuft, there is an additional polymorphism by balancing selection. An example of a population with a complex polymorphic morphology, regulated by a supergene



**Fig. 6:** Model of correlated evolution of the claw tuft clasp mechanism (CCM) and the shape of the base of the claw tuft setae. Cartoon circles at corners represent the states and arrows represent the transition rates (parameter of the model) between states. Arrows are weighted by their relative values near them, which represents the mean of the posterior distribution. The central panel shows the posterior distribution of each rate, which is represented by a gray tone that corresponds to the respective arrow gray tone (see online version for colors). The numbers near the cartoon circles show the frequency of that state in the dataset (excluding missing data). The bottom SEM images show the tip of the tarsus as an example for two of the states (linked by lines). Bottom left: *Zelotes* Gistel, 1848 (Gnaphosidae); arrow points to the cylindrical base of setae (folds absent). Bottom right: *Chilongius* (Prodidomidae) arrow points to the base of seta with folds/ribs being grasped by the CCM. Marginal log-likelihood of this model:  $-55.43$ . Marginal log-likelihood of the model in which the ribs depend on the presence of clasper (see Supp Fig. S9 [online only]):  $-60.97$ . Marginal log-likelihood of the independent model:  $-65.61$ . Log Bayes Factor between the two best models: 5.54.

assessment, and it was necessary to consider the pseudotenent equivalent to a tenent seta, then the same hemiplastic scenarios and functionally as tenent or normal seta. However, the pseudotenent polymorphic population as discussed for the inferior claw would be functional equivalence is unknown. If it is considered a normal seta expected. Biomechanical studies have suggested that differences in then no hemiplasy is expected, and the observed states in the OGC structures of the setae and claws, and their interaction with would really be convergences. If the pseudotenent is functionally different, have an important impact on the functional biology

of the spider foot (Wolff and Gorb 2012). Furthermore, different micro-habitats might have an important influence on the community of spiders with claw tufts, suggesting an adaptive value of this trait (Lapinski and Tschapka 2013, Wolff and Gorb 2015). It is important to note that movement on silk threads is also possible when the inferior claw is absent and the claw tuft is present, since a few dionychans may invade webs, or even build web themselves (Jackson and Blest 1982, Jarman and Jackson 1986, Jäger 2012). However, the biomechanical performance of two-clawed spiders with tenent setae locomotion on webs is little known. Therefore, testing the walking performance of spiders with different setae and with and without inferior claw in a variety of substrates (including sheet webs) and habitats may help us to better understand how lifestyle could have influenced the evolution of traits.

### The Evolution of the Clasping Mechanisms and Movable Plate of Claw Tuft

Platnick et al. (2005) first noted that some prodidomid spiders possess a structure at the base of the claws that may be used to grasp a smooth surface (see Ramírez 2014). A similar system was later found in other families and was suggested to be a possible synapomorphy of a larger clade (Ramírez 2014). However, we confirm that the clasping mechanism has probably arisen several times independently, as found in the studies of Azevedo et al. (2018) and Rodrigues and Rheims (2020). Our test using correlated evolutionary models supports the hypothesis that the clasping mechanism may have an efficient alternative to a movable base of the claw tuft (Ramírez 2014). Most spiders with a claw tuft have the setae placed on a movable plate, which may mechanically help the detachment of the adhesive structures (Wolff et al. 2013, Labarque et al. 2017). However, some spiders have lost this movable base, but required a clasping structure at the base of the claw, likely facilitating the detachment of setae by a different mechanism. The appearance of a CCM when the movable plate is already present seems a very unlikely event, compared to the evolution of the CCM when there is no movable plate. This may indicate that the movable plate itself might be very efficient, making unnecessary an enhanced clasping with two different ways of moving the CTS. The movable plate might be much harder to evolve than the clasper, since it has lower rates of evolution. Lastly, given the high rates of gain of either the CMM or the tuft plate (Figs. 5 and 6), it seems that there might be a trend in Dionycha towards the evolution of structures that allow spiders to move the claw tuft. This suggests an adaptive importance of a movable claw tuft and might explain the convergence of the CCM. However, the hypothesized function of the CCM is not strongly supported and more behavioral and functional studies are necessary. It would also be interesting to investigate if there is an association of the plate and the CCM with microhabitat use and behavior so we can better understand the evolution of those structures.

The Evolution of OMT  
The tapetum is a reflective layer in the secondary eyes of spiders. Many families in Dionycha present a derived character state in which the tapeta in the posterior median eyes are positioned to each other (instead of a parallel disposition as in most families), which helps in the perception of polarized light used for navigation (Dacke et al. 1999, 2001; Mueller and Labhart 2010). Many families with oblique tapeta were traditionally placed in the superfamily Gnaphosoidea (Platnick 1990) and later in the OMT clade (Ramírez 2014). Azevedo et al. (2022b) showed that the OMT clade is paraphyletic, and our results suggest that the oblique condition may have arisen four times convergently, or three times with one homoplasy (Fig. 5a). The convergence may be a result of selection for a more effective in detecting polarized light during those periods of the day when compared to parallel tapeta (Dacke et al. 2001, Mueller and Labhart 2010). It has also been demonstrated that myrmecophilid spiders are more active at those times (Dacke et al. 1999). An OMT may aid spiders in locating and returning to retreats, offering some advantages. Also, the OMT might have offered the possibility for spiders to explore resources while most other spiders are inactive, being a key innovation that could have promoted the diversification of those families through the exploitation of a new ecological opportunity. These ideas need to be tested with behavioral experiments and diversification analyses. Since we also found plausible homoplasy scenarios for the OMT, the association between the diversification rates and the character might be misled.

Our analyses also suggest that the origin of the CCM was dependent on the modification of the base of the seta from a cylindrical to a flat shape, with folds that allow setae to be easily grasped. This modification of the setae likely arose before the CCM, serving possibly as a preadaptation for the evolution of a clasping mechanism. A tenent seta with a strong base reinforced by folds would allow for a larger distal expansion, allowing more contact area between the seta and the substrate, and consequently, it would maximize adherence. This shape of setae could latter enable a grasping structure that would make it possible for the spider to better move the claw tuft.

form of balancing selection. Predation pressures enforcing frequency dependence selection could be an explanation for the balancing selection (Laurens et al. 2017, Jamie and Meier 2020). A high density of OMT morphs exploring the habitat during the morning could easily become part of the search image of birds increasing the chance of predation (Bond and Kamil 2002). It is also important to note that the phylogenetic placement of the Myrmecicultoridae, an extensive myrmecophagic spider (Cushing et al. 2022), is still contentious (Azevedo et al. 2022b); the hemiplastic scenario could be a result of incorrect phylogenetic placement.

### The Evolution of the Pi Spigot Base

Some dionychan families include species with some kind of enlargement of the piriform gland spigots, with substantial variation in the morphology of this structure. For instance, the Pi of Prodidomidae and a few Gnaphosidae (Molycriinae Simon, 1909; *Hypodrasodes*, *Anzacia* Dalmás, 1919, *Encoptarthria* Main, 1954, *Notiodrasus* Bryant, 1935, and *Zelanda* Özdikmen, 2009) have a longer base than the shaft, while most Gnaphosidae have the base shorter or as short as the shaft (Azevedo et al. 2018, Rodrigues and Rheims 2020). Our results suggest that the long base of the Pi of Prodidomidae evolved convergently with the long Pi base found in Gnaphosidae. However, it is not clear how this character evolved within Gnaphosidae. Our simulation suggests that there is a conflict between results from hemiplasy. This means that the common ancestor of Gnaphosidae could have been polymorphic for this trait, with both long and short Pi bases. However, using our approach that considers possible rates of evolution, we found that the probability of hemiplasy is insignificant.

The enlarged Pi is used by some Gnaphosidae and Prodidomidae to immobilize prey before eating them, especially dangerous prey such as other spiders (Wolff et al. 2017, Baydizada et al. 2020). According to Baydizada et al. (2020), Molycriinae and *Zelanda* (both have long Pi base) do not seem to use silk to subdue prey. However, Wolff et al. (2021) showed that *Molycria* Simon, 1897 do use their extremely long and movable ALS spinnerets to attack prey. This discrepancy may reflect differential behavior in relation to prey size, as observed in gnaphosids. Most spiders use their piriform gland spigots to produce a bi-phasic fiber-glue secretion to anchor the dragline attachments (see Wolff et al. 2021). The enlarged piriform spigots of gnaphosids are not fit for this function and these spiders might have traded the attachments to use their Pi spigots as weapons (Wolff et al. 2021). This would explain the convergence in the enlargement of Pi. However, we have no knowledge about the differences in function between Pi with long base versus short bases. Furthermore, there are some Dionychan genera (e.g. *Agroeca* Westring, 1861, *Neoanagraphis* Gertsch & Mulaik, 1936, *Elaver* O. Pickard-Cambridge, 1898, *Clubiona* Latreille, 1804, *Miturga* Thorell, 1870, *Centrothele* L. Koch, 1873, *Vectius* Simon, 1897, and *Hemicloea* Thorell, 1870) that present enlarged Pi that are not known to use silk to subdue prey. The sudden arousal of enlarged Pi spigots in adult males is indeed a polymorphism, calling for a test of hemiplasy. It is also worth noting that relationships of gnaphosids are contentious and it has been shown that the position of *Hypodrasodes* far from Molycriinae and the lamponids nested in Gnaphosidae could be an artefact of the inference method (Azevedo et al. 2022b). Therefore, it will be necessary to understand the function of enlarged Pi as a whole, and the phylogenetic relationships of the family to better understand the evolution of the character and tease apart convergences and hemiplasies in Gnaphosidae.

### Conclusions

The evolution of the inferior claw, the claw tuft, the OMT, and the elongation of the Pi can be explained by a complex pattern of convergent evolution and hemiplasies. Given what is known about the function and the phylogenetic distribution of these traits across the spider tree of life it is likely that those characters are somehow related to a web-less lifestyle. However, the causal relationship between the web-less lifestyle and these characters, as well as how those characters influenced the diversification of the two-clawed spiders, still remain to be fully tested. In addition to the problems of inferring causal relationships with phylogenies alone (see Maddison and Fitzjohn 2015, Uyeda et al. 2018), we show here another possible complication, hemiplasy. By assuming that the species tree represents perfectly the evolution of traits when it is not true, the timing and branches on which character transitions are defined can be inaccurately estimated and misinterpreted as convergences. Since repeated evolution is necessary for the inference of correlated evolution on phylogenetic trees, wrong inferences of trait changes would lead to inaccurate results of correlation tests. Furthermore, the presence of hemiplasy implies the existence of ancestral polymorphism. Understanding the processes that maintained the polymorphic condition and what led to the fixation of alternate states in different populations might be crucial for understanding character evolution. Testing those hypotheses might be difficult with our current models and analytical tools, especially since little is known about the genes related to the expression of the methods proposed here, as well as the already available approaches for studying hemiplasy (e.g., Guerrero and Hahn 2018, Atkinson et al. 2020, Porto et al. 2021), present some alternatives, but they are still recent and need better development and evaluation of their own assumptions and implementations. It is also worth noting that finding a high probability of hemiplasy is not a guarantee that hemiplasy occurred. Nevertheless, the available methods to study hemiplasy can be used to evaluate if the assumption of no discordance between the species tree and trait tree are reliable, and can illuminate other possible evolutionary hypotheses that could explain trait diversity. Further, behavioral and mechanical tests of the performance of organisms with different characteristics in different conditions could give us more independent evidence for supporting or rejecting each hypothesis. We also demonstrated that when the probability of hemiplasy is high, models constructed based on predictions of relevant hypotheses can lead us to a better understanding of correlated evolution. We show that there is a trend in Dionycha to evolve a way to move the inferior claw tuft of tenent setae and that a clasping mechanism might be an efficient way to replace a movable claw tuft plate. Also, we show that flat tenent setae with folds and ribs evolves first, likely as an adaptation to improve attachment, and that this allowed the clasping mechanism to evolve later in the evolution of Dionycha. Those hypotheses should also be tested independently with mechanical and behavioral experiments.

### Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

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## Data Availability

Data from this study are available from the Figshare:DOI: 10.6084/m9.figshare.16673872 (Azevedo 2022a).

## Authors Contribution

GHFA: Conceptualization, Formal analysis, Investigation, Writing – original draft, Visualization. TB: Formal analysis, Investigation, Writing – review & editing. MC: Formal analysis. MH: Resources, Writing – review & editing, Supervision, Project administration. Funding acquisition. MJR: Conceptualization, Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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