Phylogenomics, Classification, and Lifestyle Evolution in Raft- and Nursery Web-Spiders (Araneae: Dolomedidae and Pisauridae)

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ABSTRACT

Pisauridae Simon, 1890 or "nursery web spiders" are a global and heterogenous assemblage of spider genera with diverse lifestyles, containing web builders and webless species, as well as terrestrial and semi-aquatic species, notably "fishing spiders", genus *Dolomedes* Latreille, 1804. Incomplete, unresolved, or conflicting phylogenies have so far hampered testing for *Dolomedes* and pisaurid monophyly and evolution. Here, we broadly

address these questions within a phylogenomic and comparative framework. Our goals are i) reconstruction of a robust phylogeny to test the monophyly of *Dolomedes* and Pisauridae and to amend *Dolomedes* classification; ii) estimation of evolutionary shifts and trends in lifestyles and capture webs; and iii) evaluation of hypotheses of morphological trait association with a semi-aquatic lifestyle. To this end we generate subgenomic data (ultraconserved elements or UCE) for 53 *Dolomedes* species and 28 pisaurid genera. We analyze these data using maximum likelihood, Bayesian, and multi-species coalescence approaches, as well as using two different phylogenetic time calibration methods, RelTime and MCMCtree. Consistent across analytical approaches, our phylogenies reject the monophyly of both Pisauridae and *Dolomedes*. "Pisaurid" genera fall into three clades: 1) Focal Clade I groups the majority, including *Pisaura* Simon, 1886, hence representing true pisaurids; 2) Focal Clade II = *Blandinia* Tonini et al., 2016 is sister to Trechaleidae Simon, 1890 and Lycosidae Sundevall, 1833; 3) Focal Clade III with fishing and raft spiders groups *Dolomedes*, *Megadolomedes* Davies and Raven, 1980, and *Ornodolomedes* Raven and Hebron, 2018 and is sister to Focal Clade II, Trechaleidae, and Lycosidae. Our taxonomy, based on complementary taxa and morphological evidence, resurrects Dolomedidae Simon, 1876 to include *Dolomedes* and the Oceanic genera *Bradystichus* Simon, 1884, *Megadolomedes*, *Caledomedes* Raven and Hebron, 2018, *Mangromedes* Raven and Hebron, 2018, *Ornodolomedes*, and *Tasmomedes* Raven and Hebron, 2018. Both RelTime and

MCMCtree analyses yield comparable divergence estimations: Pisauridae origin is estimated between 29 and 40 Ma; *Blandinia* between 21 and 34 Ma; Dolomedidae between 10 and 17 Ma; and *Dolomedes* between 9 and 16 Ma. In order to avoid misleading significant correlations and/or over-resolved ancestral states, we performed taxon sampling bias correction in all evolutionary analyses. Evolutionary analyses reconstruct semi-aquatic lifestyle as ancestral to a large clade containing pisaurids, lycosids, trechaleids, *Blandinia*, and dolomedids, with several reversals to terrestrial lifestyle. Capture webs evolved at least three times, with reversals. Counter to expectation, the evolution of lifestyles and capture webs are independent. Although leg and tarsus lengths do not indicate lifestyles, semi-aquatic taxa are significantly larger than terrestrial ones. We explain this pattern with a biomechanical threshold over which surface tension can be broken while spiders forage under water. Our time-calibrated analyses indicate that the evolution of terrestrial and web-building lifestyles from semi-aquatic ancestors in Pisauridae coincided with cooling and drying climates in the mid-Miocene. We therefore hypothesize that climatic changes have acted as strong selection pressures toward lifestyle diversification.

Keywords: Fishing spiders, semi-aquatic spiders, ultraconserved elements, ancestral state reconstruction, comparative analysis, taxon sampling bias

INTRODUCTION

Known as raft or fishing spiders, *Dolomedes* Latreille, 1804 (Figs. 1a–b) is a globally distributed genus with 105 species of large wandering spiders, currently under the family Pisauridae Simon, 1890 (World Spider Catalog 2024). *Dolomedes* species are well known for their semi-aquatic lifestyle as most of them inhabit a variety of waterbodies. Their ecology is accompanied by remarkable behaviors such as rafting on the water surface, diving under the surface (McAlister 1960; Deshefy 1981; Suter 1999), and, quite unusual for spiders, preying on aquatic vertebrates (Williams 1979; McCormick and Polis 1982; Bleckmann and Lotz 1987; Zimmermann and Spence 1989; Nyffeler and Pusey 2014; Baba et al. 2019; Nyffeler and Gibbons 2022). *Dolomedes* species are therefore popular models for studying semi-aquatic adaptations in arthropods, focusing on neurosensing of water ripples (Roland and Rovner 1983; Bleckmann and Barth 1984; Bleckmann et al. 1994; Suter 2003), locomotion on water (Suter and Wildman 1999; Suter and Gruenwald 2000a, 2000b; Stratton et al. 2004; Suter 2013), as well as the associated morphologies (e.g., appendage proportions, setae morphologies and densities, cuticle structures, and respiratory organs; see Suter et al. 2004; Stratton and Suter 2009; Stratton et al. 2004; see also Lapinski et al. 2015).

Although most *Dolomedes* species strongly depend on freshwater-associated habitats

(Carico 1973a; Zhang et al. 2004; Tanikawa and Miyashita 2008; Vink and Dupérré 2010; Raven and Hebron 2018; Yu and Kuntner 2024), not all species are semi-aquatic. For example, *D. sulfureus* L. Koch, 1878 (Fig. 1b), *D. silvicola* Tanikawa and Miyashita, 2008, *D. tenebrosus* Hentz, 1844, *D. albineus* Hentz, 1845, *D. minor* L. Koch, 1876, and *D. schauinslandi* Simon, 1899, are reported to be terrestrial, and largely independent of water bodies (Carico 1973a; Tanikawa and Miyashita 2008; Ono 2009; Vink and Dupérré 2010). Their distinct morphologies and disparate distributions in Asia, North America, and New Zealand suggest that these terrestrial species are not each other's closest relatives. The currently understood lifestyle diversity within the genus raises questions of how, when, where, and why terrestrial versus semi-aquatic lifestyles evolved in *Dolomedes*. The lack of a comprehensive *Dolomedes* species phylogeny currently precludes answering these questions.

Similar questions related to the evolution of lifestyles can be asked more broadly about phylogenetic proximity of *Dolomedes*, i.e. to the family Pisauridae, whose constituent taxa display an even more complex array of lifestyle and trait diversity (Sierwald 1997; Zhang et al. 2004; Santos 2007a; Ono 2009; Jäger 2011; Raven and Hebron 2018; Dippenaar-Schoeman et al. 2020). With 52 genera and 365 species (World Spider Catalog 2024), this diverse global family is thought to be defined by the construction of nursery webs to protect their spiderlings (Fig. 1c). As adults, most pisaurid genera are terrestrial wandering spiders (Figs. 1b–f), others construct sheet or three-dimensional capture webs of numerous shapes

134 and sizes in terrestrial habitats (Figs. 1g–l), and some are semi-aquatic (Figs. 1a, m–p) (Table
135 1). This phenotypic and ecological diversity makes pisaurids an ideal model group for
136 studying the evolution of lifestyles and capture webs, yet their evolution has not been
137 adequately analyzed due to unknown or conflicting phylogenies (Griswold 1993; Santos
138 2007b; Bayer and Schönhofer 2013; Moradmand et al. 2014; Polotow et al. 2015; Albo et al.
139 2017; Wheeler et al. 2017; Cheng and Piel 2018; Fernández et al. 2018; Piacentini and
140 Ramírez 2019; Kallal et al. 2021; Hazzi and Hormiga 2023; Kulkarni et al. 2023) (Table 2;
141 see also Taxonomy). Here, we address these issues within an original phylogenomic-
142 evolutionary framework.

143 Our first goal is to test the monophyly of *Dolomedes* and Pisauridae family, as well as
144 the phylogenetic position of *Dolomedes*, using phylogenomic data, and to use these results to
145 update the classification of *Dolomedes*. Although the monophyly of Pisauridae and the
146 affiliation of *Dolomedes* have been tested multiple times under different frameworks (see
147 citations above), none of the recent studies covered more than a quarter of the 52 pisaurid
148 genera (Table 2). Limited taxon coverage has also led to an unclear topology within
149 *Dolomedes,* the most speciose "pisaurid" genus (World Spider Catalog 2024). So far,
150 *Dolomedes* species phylogenies have been regional and based on a few Sanger loci (Vink and
151 Dupérré 2010; Tanikawa 2012; Yu and Kuntner, 2024). For example, a species level
152 phylogeny of *Dolomedes* used a single gene fragment for 13 Japanese species (Tanikawa

153 2012) and failed to resolve all the nodes. Considering that Raven and Hebron's (2018)
154 taxonomic review of Australian pisaurids increased the number of *Dolomedes*' close relatives
155 from two to six genera with different degrees of intra- and intergeneric morphological
156 variation, a better sampled *Dolomedes* phylogeny is also needed to test the boundaries of this
157 diverse genus. We therefore set about to reconstruct a robust and well-sampled global
158 phylogeny based on ultraconserved elements (UCE; Faircloth et al. 2012, 2013, 2015;
159 Faircloth 2017; Miles Zhang et al. 2019) data and including more than half of the *Dolomedes*
160 species as well as other genera currently in Pisauridae. To test the robustness of the
161 phylogenetic results, we utilize maximum likelihood, Bayesian, and multi-species
162 coalescence approaches. In order to add a historic time component to the evolution of the
163 target clades, we also subject the phylogenomic data to two different time calibration
164 methods, *a posteriori* (RelTime; Tamura et al. 2012; 2018) and *a priori* (MCMCtree; Yang
165 2007) (see Beavan et al. 2020).
166 Our second goal is to utilize the newly obtained phylogeny to reconstruct the evolution
167 of lifestyles in *Dolomedes* and Pisauridae. To this end, we first populate the data for the
168 terminals in the phylogeny on semi-aquatic vs. terrestrial lifestyles as well as the
169 presence/absence of capture webs. Next, we test: i) whether a semi-aquatic lifestyle is
170 ancestral in *Dolomedes* but not in Pisauridae, as suggested by a prior phylogenetic study of
171 Lycosoidea (Piacentini and Ramírez 2019); ii) whether the absence of a capture web is

ancestral in *Dolomedes* and Pisauridae (Piacentini and Ramírez 2019); and iii) if lifestyles and capture webs are correlated traits. This third, original hypothesis, predicts that evolution of a semi-aquatic lifestyle excludes the presence of a capture web.

Our third goal is to test the hypotheses that body size, leg length, and tarsus length all relate to a semi-aquatic lifestyle. Although researchers have analyzed how spider morphologies differ across foraging guilds on the spider tree of life (Wolff et al. 2022), semi-aquatic lifestyle was not considered as a separate guild and was therefore not discussed. To fill this knowledge gap, we test the correlation between a semi-aquatic lifestyle and morphological traits on the phylogeny. Although there are no rigorous empirical comparisons, the literature suggests that several semi-aquatic spiders exhibit iv) larger body sizes (*Ancylometes* Bertkau 1880, see Lapinski et al. 2015); v) relatively shorter legs (Tanikawa and Miyashita 2008); and vi) relatively longer tarsi (Lapinski et al. 2015) compared to terrestrial species (non-pisaurid species). We test these hypotheses on the phylogeny of *Dolomedes* and Pisauridae.

Materials & Methods

Phylogenetic taxon sampling

Phylogenetic taxon sampling comprised 96 terminals, including 53 *Dolomedes* morphospecies and 31 pisaurid species of 28 genera (of which one is without a certain genus

affiliation, Fig. 1d) as ingroups (Table 3). Each pisaurid genus was represented by only one species, except for the diverse genera occupying more than one biogeographic realm: *Dendrolycosa* Doleschall, 1859*, Nilus* O. Pickard-Cambridge, 1876, and *Hygropoda* Thorell, 1895 were thus each represented by two species, one per biogeographic realm (Table 3). As outgroups to Pisauridae and *Dolomedes*, we used representatives of Trechaleidae Simon, 1890, Lycosidae Sundevall, 1833, Zoropsidae Bertkau, 1882, Psechridae Simon, 1890, Oxyopidae Thorell, 1869, Thomisidae Sundevall, 1833, and Viridasiidae Lehtinen, 1967 (Table 3).

Lifestyle, capture web, and morphological data

We scored lifestyle and capture web as binary characters: semi-aquatic versus terrestrial lifestyle, and capture web presence versus absence (Table 3). A semi-aquatic lifestyle in our study refers to the adult spiders being documented to inhabit any water bodies in direct contact with the water. In the absence of such documentation, species are taken to be terrestrial. The presence of a capture web was only scored such in those species for which literature documents a prey capturing web (not merely webbing, nursery web, or nest; see Eberhard 2020) in adults. In the absence of such information for adults, species were scored as webless. We obtained data on carapace width (CW), leg I length (L1), and tarsus I length (T1), either by microscopic measuring or from the literature. We used CW to represent the

210 size of a spider while relative leg and tarsus lengths were calculated by dividing L1 by CW
211 and T1 by L1, respectively. We emphasized the measurement of adult females, but in the four
212 cases where females were not available, we measured males instead (Table 3). This
213 introduces little bias, as most pisaurids are not extremely sexually size dimorphic (Kuntner
214 and Coddington 2020). Measurements were taken using a Leica M205C stereomicroscope or
215 a Keyence VHX7000 digital microscope. For the two genera whose phylogenetic terminals
216 were represented by juveniles and therefore lacked precise species identification, we
217 averaged female measurements from the literature (Table 3).
218
219 *DNA extraction and phylogenomic pipeline*
220 We used one to four legs from each specimen for DNA extraction. For small spiders, we
221 also used the whole prosoma. We extracted genomic DNA using QIAamp DNA Micro Kits
222 (Qiagen, Hilden, Germany), with the DNA quality checked using electrophoresis and a
223 Qubit™ 4 Fluorometer (Invitrogen, Carlsbad, CA, USA) with the dsDNA HS Assay Kit.
224 DNA samples containing more than 320 ng of DNA were then diluted to equal volumes and
225 sent to Rapid Genomics LLC (Gainesville, FL, USA) for library preparation to capture and
226 sequence UCE data. We used the RTA spider probe set (Zhang et al. 2023) for capturing UCE
227 loci.
228 To assemble and filter the UCE matrix we employed the Phyluce v1.7.3 pipeline

229 (Faircloth 2016) following the online tutorial

230 (https://phyluce.readthedocs.io/en/latest/tutorials/index.html). After trimming the adaptors,

231 we assembled the data using the package's command lines under the SPAdes de novo

232 assembly algorithm (Prjibelski et al. 2020). UCE loci were then found and extracted by

233 matching the assembled contigs to the RTA spider probe set (Zhang et al. 2023). We ran both

234 edges and internal trimming on each captured locus before aligning them. Finally, we aligned

235 the captured loci with 75% and 95% taxon completeness into a sparse and a dense matrix,

236 respectively, for subsequent phylogeny reconstruction. Both data matrices were uploaded to

237 DRYAD.

238

239 *Phylogeny reconstruction*

240 We reconstructed the phylogenies on both sparse and dense matrices using maximum

241 likelihood (ML), Bayesian inference (BI), and multi-species coalescence (MSC) approaches.

242 We chose the topology that received overall the highest nodal supports as the best tree and

243 mapped the statistics from all these analyses onto it.

244 To partition both the sparse and the dense UCE matrices, we first split each locus into

245 three fragments, a core region, a right, and a left flank, using entropy-based Sliding-Window

246 Site Characteristics (SWSC-EN; Tagliacollo and Lanfear 2018). We then used PartionFinder

247 2 (Lanfear et al. 2017) to reclassify all fragments into the best-fitted partition subsets using

248 AICc algorithm with the substitution models, suggested by SWSC-EN, set as GTR+G.

249 We preformed ML analyses in IQ-TREE v2.3.2 (Minh et al. 2020) using the partitioned
250 matrices. Nodal supports were derived from ultrafast bootstrap approximation (UFBoot;
251 Minh et al. 2013; Hoang et al. 2017) and SH-like approximate likelihood ratio test (SH-aLRT;
252 Guindon et al. 2010), both with 1,000 replicates.

253 We carried out the BI analyses using the unpartitioned matrices in Exabayes 1.5.1
254 (Aberer et al. 2014) with default settings. On each matrix, we ran the Markov chain Monte
255 Carlo (MCMC) searches in two independent and two coupled chains. Each chain had one
256 million generations sampled every 50 generations with a 25% burn-in. We then generated the
257 best consensus trees after evaluating the results by their effective sample sizes (ESS). The
258 posterior probabilities of the MCMC searches were used as nodal supports.

259 For MSC, we first generated a gene tree per partition using IQ-TREE v2.3.2 with 1,000
260 UFBoot replicates. We then imported all gene trees into Accurate Species Tree Algorithm
261 (ASTRAL-IV; Zhang et al. 2018; Zhang and Mirarab 2022) with default settings. Each
262 analysis had 16 rounds of search and 16 rounds of subsampling and the posterior probabilities
263 were used as nodal supports.

264

265 *Divergence time estimation*

266 Due to the lack of synapomorphies, the classification of all fossils previously assigned to

Pisauridae has recently been questioned (Wunderlich 2008; Magalhaes et al. 2020), so these fossils could not be used for time calibration. We calibrated the phylogeny using three relatively reliable fossils with a relevant family affiliation, following Magalhaes et al. (2020), as follows. First, we treated an unidentified juvenile lycosid (Penney 2001) from Dominican amber (15–20 million years ago (Ma); Iturralde-Vinent and MacPhee 1996) as a crown lycosid. Secondly, we treated *Oxyopes succini* Petrunkevitch, 1958 from Baltic amber (43–48.5 Ma; Ritzkowski 1997) as a stem oxyopid. Finally, we treated *Syphax* cf. *megacephalus* L. Koch and Berendt, 1854 (see Wunderlich 2004) from Baltic amber as a stem thomisid (see also Piacentini and Ramírez 2019; Magalhaes et al. 2020).

A posteriori calibration was performed in RelTime (Tamura et al. 2012; 2018) using a relaxed local clock model under MEGA 11 (Tamura et al. 2021) with *Viridasius* sp. set as the outgroup to all Lycosoidea. We used the unpartitioned sparse UCE matrix and its best ML topology, generated from IQ-TREE v2.3.2, for time calibration analyses. The probability distributions of time at the calibration points were set as log-normal with their 95% confidence intervals specified close to their proposed fossil ages. This reconstructed ultrametric tree was then used in subsequent evolutionary analyses.

To test whether RelTime yielded reliable absolute divergence times (see Lozano-Fernandez et al. 2017; Beavan et al. 2020), we also ran *a priori* time calibration under MCMCtree (Yang 2007) on a matrix of 300 loci with 99% taxon completeness, randomly

286 selected using Phyluce v1.7.3, in PAML 4.10 (Yang 2007). We selected the ML topology
287 generated from the dense matrix as the starting tree after removing the branch lengths.
288 Calibration points were selected and set as in the RelTime analysis using MCMCtreeR
289 (Puttick 2019) in R 4.3.3 (R Core Team 2024). Following the program tutorial (dos Reis et al.
290 2017), we first estimated the average substitution rate per time unit as well as the length,
291 gradient, and Hessian of each branch. With the above estimated parameters, we ran
292 divergence time dating in two independent runs. Each run had 500,000 generations sampled
293 every 50 generations and with a 10% burn-in. We compared the results of the two runs in
294 MCMCtreeR, using the script from Gutiérrez-Trejo et al. (2024).
295
296 *Evolutionary analyses*
297 We performed all evolutionary analyses in R 4.3.3 using the packages "ape" (Paradis et
298 al. 2004), "phytools" (Revell 2024), and "MCMCglmm" (Hadfield 2010). We first pruned the
299 distantly related outgroups (Zoropsidae, Psechridae, Oxyopidae, Thomisidae, Viridasiidae)
300 from the ultrametric tree (using the command code "drop.tip" and "extract.clade" in "ape") as
301 they were irrelevant for the evolutionary questions posed, but retained Lycosidae and
302 Trechaleidae because they nested with our ingroups (see Results). We also removed the
303 pisaurid *Tallonia picta* Simon, 1889 due to insufficient trait data. Given the strong emphasis
304 on *Dolomedes* species in our study, our taxon sample, if left unaltered, could lead to biased

evolutionary outcomes (Ackerly 2000; Li et al. 2008; Sidlauskas 2008; Jorgensen et al. 2023). For all evolutionary analyses, we therefore used both the full taxon tree (putatively biased), as well as the average of randomized pruned taxon trees (putatively less biased), as follows. First, we assigned *Dolomedes* terminals to their biogeographic realms modified from Udvardy (1975), then randomly selected one terminal per realm to generate a reduced subset of *Dolomedes* terminals and pruned the other *Dolomedes* terminals from the tree. We repeated this randomization 30 times to generate 30 different reduced taxon trees, each presumably with a relatively balanced taxon sampling.

To reconstruct the evolution of semi-aquatic vs. terrestrial lifestyles and the presence/absence of capture webs, we first sought the best evolutionary model by fitting, on i) the full taxon tree and ii) the reduced taxon trees, four different assumptions of trait transition rate matrices: equal rates (ER), all-rates-different (ARD), state A to B only and B to A only, into *k*-state Markov models (M*k* model; Pagel 1994; Lewis 2001). For the evolutionary models estimated from the full taxon tree, we selected the one with the lowest AIC as the best model (Fig. 2a). For the evolutionary models estimated from the reduced taxon trees, we first averaged the AIC and the estimated trait transition probability generated from each model with the same assumptions on all reduced taxon trees (Fig. 2b). Then, we selected the evolutionary model with the lowest average AIC as the most suitable across all reduced taxon trees. To reconstruct the ancestral states of lifestyles and capture webs in

324 *Dolomedes* and pisaurids, we simulated stochastic character maps 100 times on the full taxon
325 tree, once using the best model from the full taxon tree, and again using the best-averaged
326 model generated from the reduced taxon trees (Fig. 2b).

327 We used Pagel's (1994) binary character correlation test to examine the evolutionary
328 correlation between lifestyles and capture web on i) the full taxon tree and ii) reduced taxon
329 trees. We first fit the two traits into a two-trait independent, and a dependent ARD-M*k* model.
330 For the models estimated from the full taxon tree, we applied model selection by analysis of
331 variance (ANOVA) to test whether the dependent model significantly better fit our data (Fig.
332 2c). For the models estimated from the reduced taxon trees, we further averaged the values in
333 the statistic tables generated from the ANOVA model selections and the estimated trait
334 transition probabilities of all the reduced taxon trees. We then used the averaged p-value and
335 the number of reduced taxon trees that showed significance in each ANOVA model selection
336 to seek the consensus on whether semi-aquatic versus terrestrial lifestyles and the presence or
337 absence of capture webs were correlated across all reduced taxon trees (Fig. 2d).

338 We tested the correlation between lifestyles and three morphological traits (CW; L1/CW;
339 T1/L1) using Markov chain Monte Carlo Sampler for Multivariate Generalized Linear Mixed
340 Models (MCMCglmm; Hadfield 2010) on i) the full taxon tree (Fig. 2e) and ii) the reduced
341 taxon trees (Fig. 2f) with 10 million MCMC iterations. The thinning interval and burn-in
342 were set to 5,000 and 2.5 million, respectively. For those morphological trait(s) that were

343 significantly (pMCMC < 0.05) correlated with lifestyles on the full taxon tree, we further
344 examined their relationship with lifestyles by generating density curves of estimated moment-
345 matching values (Hadfield 2010). To test for correlations between lifestyles and the three
346 morphological traits on the reduced taxon trees, we averaged all values in the MCMCglmm
347 tables from all the reduced taxon trees, and also counted the number of the reduced taxon
348 trees that showed significance (Fig. 2f). Then, as above, we further examined the relationship
349 between morphological traits with lifestyles by generating density curves of estimated
350 moment-matching values (Hadfield 2010). As phylogenetic correlations among traits can be
351 detected at some, but not all, hierarchical levels of a given phylogeny (see Wolff et al. 2022),
352 we performed an additional set of MCMCglmm analyses on a full set of *Dolomedes* terminals
353 only following the above algorithm for the full taxon tree (Fig. 2g).
354
355 RESULTS
356 The RTA spider probe set, on average, captured 2,790 UCE loci consisting of 2,815,984
357 base pairs (Table S1) with *Peucetia* sp. (Oxyopidae) yielding only 1,125 loci. After trimming
358 and aligning, the sparse matrix with 75% taxon completeness contained 2,676 UCE loci with
359 1,221,957 base pairs, and the dense matrix with 95% taxon completeness contained 1,175
360 UCE loci with 875,429 base pairs. Only 94 loci were shared by all taxa.
361 Phylogenies reconstructed from the sparse and the dense matrix show identical

topologies in all analyses except within *Dolomedes* (Fig. S1), where MSC recovered slightly different topologies (Figs. S1e–f), interpreted in the following paragraphs. With very few exceptions, all nodes receive full or high statistical support from UFboot, SH-aLRT, and BI posterior probabilities. Despite yielding a few additional poorly supported nodes within *Dolomedes*, most nodes are still strongly supported by MSC. Given the best overall supports, we choose the ML topology reconstructed from the sparse matrix as the preferred tree (Figs. 3 and 4; see also Supplementary Material).

Systematics of raft- and nursery web- spiders

All analyses reject the monophyly of Pisauridae as currently classified. This family-level name refers to a paraphyletic assemblage of genera that fall into three clades, labeled as focal clades in this paper (Fig. 3; see Taxonomy): 1) **Focal Clade I** groups the majority of the genera classified in Pisauridae, and because it contains *Pisaura* Simon, 1886, this clade represents the "true pisaurids". Focal Clade I (Pisauridae) is sister to a taxon-rich clade containing all the taxa listed below; 2) **Focal Clade II** contains one genus that is currently still cataloged as a pisaurid, i.e. the monotypic *Blandinia* Tonini et al., 2016 from Madagascar (Fig. 1K). Because it is recovered as sister to Trechaleidae and Lycosidae, *Blandinia* cannot be considered a pisaurid, and is instead *incertae sedis*, pending better taxonomic resolution; 3) **Focal Clade III** contains *Dolomedes*, *Megadolomedes* Davies and Raven, 1980, and

381 *Ornodolomedes* Raven and Hebron, 2018. This clade is sister to Focal Clade II, Trechaleidae,
382 and Lycosidae (Fig. 3). Considering the phylogenetic results, the topological stability, the
383 strong clade supports, and our understanding of the morphology of *Dolomedes* and its
384 relatives, detailed in the Taxonomy section below, we will from here on formally refer to the
385 Focal Clade III as Dolomedidae Simon, 1876, colloquially named *raft spiders*. We suggest
386 the use of *fishing spiders* for *Dolomedes*.

387 Within Dolomedidae, we tested for the monophyly of *Dolomedes*. Strictly speaking,
388 *Dolomedes* is not monophyletic. The majority of *Dolomedes* species, including the type
389 species *D. fimbriatus* (Clerck, 1757), are in a clade that represents true *Dolomedes*, but one
390 species, *D. karijini* Raven and Hebron, 2018, is recovered in the sister clade that also contains
391 *Ornodolomedes* and *Megadolomedes* (Figs. 3 and 4). While the Afrotropical *Dolomedes*
392 species are monophyletic within their biogeographic realm, other biogeographic realms do
393 not show strict species monophyly (Fig. 4). For example, in addition to the distal Palearctic
394 *Dolomedes* clade, other Palearctic species are found in the "raptor" clade, which is sister to
395 all other true *Dolomedes* (Fig. 4). The Australasian species are not monophyletic, but the
396 New Zealand species are (Fig. 4). An Indomalayan clade groups some, but not all, species
397 from this region, as many Indomalayan terminals also form the "raptor" clade (Fig. 4). Most
398 Nearctic species are monophyletic, but *D. striatus* Giebel, 1869 is sister to the Palearctic
399 clade (Fig. 4).

Multi-species coalescence recovers three topological differences within *Dolomedes* (Figs. S1e–f) from the preferred tree (Fig. 4), two among the distal "raptor" clade and the other among the Indomalayan, Afrotropic, and Nearctic plus Palearctic (Holarctic) clades. The MSC phylogenies reconstructed from both matrices suggest the two morphospecies, *D.* cf. *raptoroides* HK and *D.* cf. *raptoroides* VN, are not sister as they are in the preferred tree (Fig. 4). Additionally, MSC has *D. yawatai* Ono, 2002 as sister to a clade with four *Dolomedes* morphospecies from Taiwan (Figs. S1e–f) instead of nesting within that clade (Fig. 4). MSC on the dense matrix suggests the Indomalayan clade as sister to a large clade including the Afrotropic and Holarctic *Dolomedes* (Figs. S1e–f). However, such topologies are poorly supported with their posterior probabilities (PP) between 0.6 and 0.7. In the preferred tree, Afrotropic *Dolomedes* are sister to a clade uniting the Indomalayan and the Holarctic clades, with better nodal supports (> 0.9; see Fig. 4).

Divergence times of raft- and nursery web- spiders

RelTime and MCMCtree (results in parentheses) yield comparable divergence times of the three focal clades. Both analyses reconstruct relatively recent origins for the major clades in question. The crown that gave rise to all three focal clades plus Trechaleidae and Lycosidae is estimated to have originated between 32 and 37 Ma (34–43 Ma), in the late Eocene to early Oligocene (Fig. 5). The origin of Pisauridae (Focal Clade I), estimated between 29 and 35 Ma

419 (31–40 Ma) (Fig. 5), is the earliest of the three focal clades. The Oligocene-Miocene split of
420 *Blandinia* (Focal Clade II) from Trechaleidae plus Lycosidae is estimated between 21 and 31
421 Ma (24–34 Ma) (Fig. 5). Compared to the above two focal clades, the origin of Dolomedidae
422 (Focal Clade III) is estimated to be more recent, between 10 and 15 Ma (12–17 Ma) in the
423 mid-Miocene (Fig. 5). The origin of *Dolomedes* is estimated to be in the Miocene, between 9
424 to15 Ma (11–16 Ma) (Fig. 5), and since then, the clade has undergone a rapid diversification,
425 with the 95% confidence intervals and highest posterior densities for final splits between
426 species doublets lying between 0.2 Ma (0.3 Ma) (*D. hydatostella* Yu and Kuntner, 2024 and
427 *D. rotundus* Yu and Kuntner, 2024 from Madagascar) and 9.2 Ma (8.9 Ma) (*D. lesserti*
428 Roewer, 1955 from Benin and an unnamed *Dolomedes* species from D.R. Congo) (Fig. 5).
429 On the other hand, some species that group with larger clades in our phylogeny could
430 plausibly be much older, e.g. between 7.1 and 14.7 Ma (10.2–15 Ma) (*D. facetus* Koch, 1876
431 from Australia).
432
433 *Evolution of lifestyles in raft- and nursery web- spiders*
434 With the lowest average AIC, the model allowing only transitions from a semi-aquatic to
435 a terrestrial lifestyle ("semi-aquatic to terrestrial" model) is the best evolutionary model
436 (Table 4) on the reduced taxon trees (Fig. S2). Partially rejecting our hypothesis, the semi-
437 aquatic lifestyle is the ancestral state not only of Dolomedidae (Focal Clade III), but also of

438 the entire clade that unites Pisauridae (Focal Clade I), Focal Clade II, Lycosidae, and
439 Trechaleidae (Fig. 6A, see also Fig. S3). On the full taxon tree, the model detects no fewer
440 than 15 reversals to a terrestrial lifestyle, including three in Pisauridae and eight in
441 Dolomedidae. The terrestrial lifestyle in the focal clades of our tree, thus evolved from semi-
442 aquatic ancestors. In Focal Clade I, all semi-aquatic terminals or genera, *Hygropoda*,
443 *Thaumasia* Perty, 1833, *Qianlingula* Zhang et al., 2004, and *Nilus*, have retained the
444 ancestral, semi-aquatic lifestyle (Fig. 6a). The seven terrestrial *Dolomedes* species are not
445 closely related to each other (Fig. 6a), suggesting independent terrestrialization in each
446 species. This result is not strongly affected by taxon sampling bias. Model selection on the
447 full taxon tree namely also suggests the "semi-aquatic to terrestrial" model as the best (Table
448 4), and thus the reconstructed ancestral lifestyle is identical to that from the reduced taxon
449 trees, albeit with different rates of trait transition (Fig. 6b, see also Fig. S4).
450 After averaging on the reduced taxon trees (Fig. S2), the ARD is the best model to
451 explain the evolution of the capture web (Table 4); the reconstruction does not recover a clear
452 ancestral state (Fig. 6c, see also Fig. S5). Due to this ambiguity, the hypothesis of an ancestral
453 absence of a capture web for the clade containing Pisauridae, *Blandinia*, and Dolomedidae is
454 not supported. Reconstructions on the full taxon tree suggest at least three independent
455 origins of the capture web: one each in Lycosidae, *Blandinia*, and distally within the Focal
456 Clade I, the latter containing numerous reversals to no web (Fig. 6c). Within *Dolomedes*,

however, the absence of a capture web is ancestral, as partially predicted by the hypothesis (Fig. 6c). Furthermore, the absence of a web is ancestral for the entire Dolomedidae, with no reversals (Fig. 6c). This analysis is strongly affected by the taxon sampling bias and its correction. Model selection on the full taxon tree namely suggests that the model allowing only transitions from web presence to absence, rather than the ARD, is the best model. This model reconstructs the presence of a capture web as the ancestral state of all three focal clades, Trechaleidae, and Lycosidae with numerous reversals to no web (Fig. 6d, see also Fig. S7). Such results would outright reject our hypothesis of an ancestral absence of a web in Pisauridae.

Our analyses also reject the hypothesis of an evolutionary correlation between capture webs and lifestyles. Instead, the evolution of the web presence or absence and semi-aquatic versus terrestrial lifestyles are independent (Fig. 7a). None of the reduced taxon trees suggest that the two-trait dependent model fits our data significantly better than the independent model (average p-value of the ANOVA model selection = 0.1, see also Supplementary Material). However, this result is strongly affected by the likely bias in the taxon sample on the tree. On the full taxon tree, the two-trait dependent ARD model fits the data significantly better than the two-trait independent ARD model (see also Supplementary Material), suggesting that a semi-aquatic lifestyle excludes the presence of a capture web (Fig. 7b). This result would corroborate the predicted evolutionary correlation between these traits.

Our final set of hypotheses predicted that semi-aquatic taxa would exhibit wider carapaces, relatively shorter legs I, and relatively longer tarsi I compared to the terrestrial taxa in the phylogeny. The results support only the first hypothesis (Table 5). The significance of a wider carapace in semi-aquatic taxa is recovered in 29 out of 30 reduced taxon trees (see Supplementary Material). On average, the carapace of semi-aquatic spiders is 2.4 mm wider than that of the terrestrial spiders in the phylogeny (Fig. 8a). On the other hand, no significance is detected in the relative length of leg I and tarsus I between semi-aquatic and terrestrial taxa (Table 5). These results appear to be less susceptible to taxon bias, as analyses using the full taxon tree yield identical results (Table 5, Fig. 8b). However, when only *Dolomedes* terminals are considered, all three of the above hypotheses are rejected (Table 5).

Discussion

The lack of comprehensive phylogenies has so far precluded a thorough systematic account of *Dolomedes* and Pisauridae *sensu lato*, as well as generalizations of the lifestyle evolution of this global assemblage of spider genera. We pursue these broad goals in the phylogenomic and comparative study reported here. Our phylogenetic results reject the monophyly of both Pisauridae and *Dolomedes*. The genera previously placed within Pisauridae fall into three focal clades: the true Pisauridae, *Blandinia*, and Dolomedidae, whose family rank we formally resurrect (see Taxonomy). The origin of each of the focal

clades is estimated to be relatively recent, i.e. 40 Ma or less. *Dolomedes* is paraphyletic, as *D. karijini* groups with *Ornodolomedes* and *Megadolomedes*. Our reconstructions partially reject our first hypothesis that the semi-aquatic lifestyle is ancestral to *Dolomedes* but not to Pisauridae. A semi-aquatic lifestyle is reconstructed as ancestral for all three focal clades, followed by independent reversals to terrestrial lifestyle. Our second hypothesis of the ancestral absence of a capture web in *Dolomedes* and Pisauridae is also partially rejected. The evolution of a capture web is ancestrally ambiguous, with a web origin in both Pisauridae and *Blandinia*. In Dolomedidae, on the other hand, the unequivocal ancestral absence of a capture web is retained through their evolutionary history. Our third hypothesis, which predicted that a semi-aquatic lifestyle would exclude the presence of a capture web, is also rejected, because our evolutionary tests reveal an independent evolution of lifestyle and capture web. Of the hypotheses that semi-aquatic pisaurids having larger body sizes, relatively shorter legs, and relatively longer tarsi, our comparative analyses support only the larger body size hypothesis, but only at higher hierarchical levels and not within *Dolomedes* species. Contrary to our prediction, the relative lengths of legs and tarsi do not differ between lifestyles. Our study is the first step towards stability in systematics of raft and nursery web spiders and at the same time provides a phylogenetic basis for further comparative research.

Dolomedidae: A step towards the redefinition of Pisauridae

We provide a well-sampled and robust phylogenomic backbone to support the resurrection of Dolomedidae, Lehtinen's (1967) taxonomic hypothesis that has regained recent attention (Albo et al. 2017; Hazzi and Hormiga 2023; Kulkarni et al. 2023). Our phylogeny is consistent with the topologies found by Hazzi and Hormiga (2023) and Kulkarni et al. (2023) that *Dolomedes* is sister to the clade including Lycosidae, Trechaleidae, and additionally *Blandinia*. Although several putatively closely related genera of *Dolomedes*, including *Bradystichus* Simon, 1884, *Caledomedes* Raven and Hebron, 2018, *Mangromedes* Raven and Hebron, 2018, and *Tasmomedes* Raven and Hebron, 2018, were not available for inclusion with UCE data, additional evidence from morphological (Platnick and Forster 1993; Raven and Hebron 2018) and molecular (Piacentini and Ramírez 2019; Kulkarni et al. 2023) studies both suggest that these genera fit our definition of Dolomedidae rather than Pisauridae. This updated classification of Dolomedidae is formalized in the Taxonomy.

The *Dolomedes* paraphyly hinges on one species, *D. karijini*, and could be resolved through an establishment of a new genus for this species group. Although we envision this solution being valid in the future, we refrain from doing so here due to our limited access to Australian species. Based on details of the genitalia, Raven and Hebron (2018) treated *D. karijini* in the *D. albicomus* group with *Dolomedes* species from Australia and New Caledonia. Considering the incomplete taxon sampling and the current ambiguity of species boundaries within *Dolomedes* (Tanikawa and Miyashita 2008; Vink and Dupérré 2010; Yu

533 and Kuntner 2024), it is unclear whether the entire species group, or only *D. karijini* should
534 be elevated to a new genus. This decision will await future integrative taxonomic work with
535 more Australasian species.

536 Our taxonomy is only the first step towards a better definition of Pisauridae and its
537 subfamilies. Although our phylogenies reject the classification of *Blandinia* as a pisaurid, it is
538 unclear whether this monotypic genus can be assigned to another existing family. Its
539 placement in Trechaleidae would be unfounded, given conflicting phylogenies (see Piacentini
540 and Ramírez 2019; Hazzi and Hormiga 2023; Kulkarni et al. 2023). In the Taxonomy below,
541 we therefore avoid creating a new family and hence treat *Blandinia* as *incertae sedis* until
542 further evidence is available. Our phylogeny also partially rejects the currently used pisaurid
543 subfamilial classifications, Thaumasinae, Thalassinae, and Pisaurinae (Simon 1890; Sierwald
544 1990), a problem that awaits more focused systematics efforts.

545

546 *Independent evolution of lifestyles and capture web*

547 Most spiders are terrestrial, so the evolution of aquatic or semi-aquatic lifestyles in this
548 group is an evolutionary oddity worthy of in-depth research. Species and genera within at
549 least 22 spider families are known to have aquatic or semi-aquatic lifestyles (Crews et al.
550 2020). A comparative study across 42 spider families by Stratton et al. (2004) recovered
551 aquatic adaptive locomotion and exoskeleton morphologies as ancestral to Pisauridae,

Lycosidae, and Trechaleidae. These results agree with ours that a semi-aquatic lifestyle is ancestral to those three families as well as to Dolomedidae. However, research focusing on Dictynidae O. Pickard-Cambridge 1871 (Crews et al. 2020) and Lycosoidea (Piacentini and Ramírez 2019), which includes Pisauridae and *Dolomedes*, both recovered a terrestrial lifestyle as ancestral to these clades, followed by multiple origins of aquatic or semi-aquatic lifestyles. Our results, which suggest that a semi-aquatic lifestyle is ancestral to both Pisauridae and Dolomedidae, do not align with those above (Piacentini and Ramírez 2019). This discrepancy may stem from the less taxon sampling focus on terrestrial lycosids and a more complete taxon sample of pisaurids and dolomedids in this present study compared to that of Piacentini and Ramírez (2019). Character states of long and basal branches are more likely to be reconstructed as ancestral (see Li et al. 2008), and our study indeed detected several newly sequenced semi-aquatic pisaurids at the base of the family, and, additionally, improved the phylogenetic resolution of *Dolomedes*.

Aside from the widely documented freshwater bound, semi-aquatic lifestyle, Dolomedidae also comprises the marine intertidal *Mangromedes* (Raven and Hebron 2018) and the mud-dwelling *Bradystichus* (Platnick and Forster 1993; Raven and Hebron 2018; Harvey M.S., personal observation). The marine intertidal lifestyle is very rare in the spider tree of life (Raven 1988; Crews et al. 2020; Yu et al. 2023). Mud-dwelling, likewise, is rare and may represent an intermediate state between semi-aquatic and terrestrial lifestyles. These

extraordinary cases could imply a more complex and diverse evolutionary history of water-associated lifestyles in Dolomedidae compared to Pisauridae. However, detailed evolutionary analyses of these additional lifestyles will require a phylogeny including all dolomedid genera.

The evolution of capture webs in spiders has been the focus of numerous recent studies (Blackledge et al. 2009; Bond et al. 2014; Garrison et al. 2016; Cheng and Piel 2018; Fernández et al. 2018; Kallal et al. 2021). By focusing on all spiders, these studies were unable to explore the lifestyle diversity within large and speciose clades, such as Pisauridae. The above studies have not reached a consensus on the ancestral presence or absence of a capture web in Pisauridae, Lycosoidea, or the RTA clade by either reconstructing no web as ancestral (Garrison et al. 2016; Fernández et al. 2018; Piacentini and Ramírez 2019), the presence of a ground sheet web as ancestral (Blackledge et al. 2009), or producing an ambiguous/unresolved result (Bond et al. 2014; Cheng and Piel 2018; Kallal et al. 2021). These differing results are not surprising, considering that only three of the above studies (Cheng and Piel 2018; Piacentini and Ramírez 2019; Kallal et al. 2021) included any web-building pisaurids, in addition to non-web-building representatives. Our study covers most of the pisaurids known to build capture webs, but does not unambiguously resolve the ancestral state. This strongly suggests that the results of the above works, which were based on very few selected pisaurid taxa were over-resolved. Among the known web-building pisaurids

unavailable in our study is the South American *Architis* Simon, 1898, which, based on published morphological (Santos 2007a) and phylogenetic studies (Wheeler et al. 2017; Piacentini and Ramírez 2019; Hazzi and Hormiga 2023), might belong to the clade containing *Thaumasia*, *Hala* Jocqué, 1994, and *Tolma* Jocqué, 1994—all webless genera. If this is the case, we expect this clade to represent another case of independent origin of a capture web in pisaurids.

As no pisaurid or dolomedid taxa are known to be both semi-aquatic *and* build a capture web (Table 1), we hypothesized that these traits are evolutionarily exclusive, at least in wandering spiders. Although some studies may suggest that in Araneoidea, these two traits may co-occur in Tetragnathidae Menge, 1866, Linyphiidae Blackwall, 1859, Theridiidae Sundevall, 1833, and Theridiosomatidae Simon, 1881 (see Crews et al. 2020), the most convincing cases are rare (Eberhard 2020) and seemingly aberrant. One such case is *Conculus* Kishida, 1940 (Anapidae Simon, 1895) that is known for its diving behaviors and for building a part of its capture web underwater (Komatsu 1940). The other case is *Wendilgarda* Keyserling, 1886 (Theridiosomatidae) that attaches its web anchors to the water surface (Coddington and Valerio 1980). Curiously, this is the first study to test for an evolutionary correlation between these two traits. Even more curious is that, contrary to our expectations, the result suggests their independence. The above cases of semi-aquatic *and* web-building araneoids may not be so aberrant after all and the evolution of semi-aquatic

609 lifestyle and the presence of a capture web may not be mutually exclusive across Araneae.

610 Aside from capture and nursery webs, literature also documents other webbing types

611 constructed by pisaurids and dolomedids, both terrestrial and semi-aquatic, throughout their

612 ontogeny. Such examples are juvenile webbing in *Thaumasia* (Eberhard 2020), *Qianlingula*

613 (Yu K.-P.; personal observations), and *Dolomedes fimbriatus* (Jäger P.; personal

614 observations). Although these types of non-capture webs were not considered in our

615 comparative analyses, which only considered adult phenotypes, the abilities of semi-aquatic

616 spiders to build large-scale webbing may also agree with the independent evolution of

617 lifestyles and capture webs. Future research might profitably look into similarities and

618 differences in web structure, composition, and web building behaviors among these different

619 types of webs at different ontogenetic stages.

620

621 *Morphological adaptations to a semi-aquatic lifestyle*

622 Our comparative analysis at a higher phylogenetic hierarchy revealed that semi-aquatic

623 representatives of all three focal clades have wider carapaces compared to terrestrial ones.

624 This finding is consistent with the general understanding that semi-aquatic and aquatic

625 animals are larger or heavier than terrestrial ones, whether in mammals (Gearty et al. 2018),

626 reptiles (Meiri 2008), birds (Gaston and Blackburn 1973), or invertebrates (Sabo et al. 2002;

627 Braddy et al. 2008). Biological explanations for this phenomenon usually invoke buoyancy

628 and gravity (Reynolds 1977; Reynolds and Karlotski 1977), trophic structure (Shurin et al.
629 2006; Tucker and Rogers 2014), thermoregulation (Downhower and Blumer 1988; Meiri
630 2008), aquatic locomotion (Schmidt-Nielsen 1971; Anderson et al. 1979), energy trade-off
631 (Gearty et al. 2018), and predator avoidance (Wolff and Guthrie 1985). However, these
632 explanations are more relevant to vertebrates, whereas gravity and thermoregulation may be
633 less applicable to much smaller invertebrates, such as spiders.

634 We hypothesize that larger sizes of semi-aquatic pisaurids and dolomedids may be
635 related to a biomechanical threshold above which surface tension can be broken when spiders
636 forage under water. For generalist predators, aquatic habitats offer additional food resources
637 compared to the terrestrial habitats, e.g. crustaceans, fishes, and amphibians, but only if the
638 predator can reach underwater and subdue this relatively large prey. Semi-aquatic spiders that
639 are large enough to break through the surface tension to access these additional food sources,
640 while avoiding being eaten, may therefore have a competitive advantage over terrestrial
641 species. Our field observations on *Dolomedes plantarius* (Clerck, 1757) that smaller juveniles
642 usually do not dive when disturbed but larger adults and juveniles usually do (Yu K.-P.,
643 Klemen Č, and Kuntner M., personal observation) may add credibility to this hypothesis.
644 Additionally, larger size in animals can facilitate aquatic locomotion through increased area
645 in touch with the water surface and consequentially increased buoyancy (Soncini and Klein
646 2023), and by holding larger and denser hydrophobic structures. However, semi-aquatic

species do not simply evolve to become increasingly larger as their maximum size cannot break the physical equilibrium of rafting on water surfaces (Soncini and Klein 2023).

We repeated the test of correlation between body size and lifestyle on *Dolomedes* terminals only and found that semi-aquatic species of *Dolomedes* were not significantly larger than the exclusively terrestrial ones. It is not unusual for comparative work to find conflicting results at different phylogenetic hierarchies, including examples in a study about correlation between morphological traits and foraging guilds in spiders (Wolff et al. 2022). In many such cases, explanations are not readily available, but our case does not seem complicated. Why is that? The vast majority of known *Dolomedes* are semi-aquatic, and this lifestyle is ancestral and nearly universal in this clade, with only a few derived species having recently evolved terrestrial lifestyles. In these cases, the time on land, and presumably a relaxed selection for larger sizes, has simply not been long enough for these species to evolve smaller sizes that are otherwise more typical of terrestrial inhabitants. This analysis of *Dolomedes* terminals only may therefore be a less powerful test of terrestrial traits compared than an analysis of all focal clades at the level of genera.

Reducing taxon sampling bias in trait evolution analyses

Our research provides a case study of how taxon sampling bias can affect the outcome of commonly used evolutionary analyses and how to avoid this bias. Trait transition

probability matrices (Q), estimated by fitting the extended M*k* model to the phylogeny, are sensitive to the number of terminals of each character state (Lewis 2001; see also Jorgensen et al. 2023). Therefore, if the trees or clades do not contain all extant taxa, a biased taxon coverage in each character state could result in misleading or less robust results (Ackerly 2000; Sidlauskas 2008; Jorgensen et al. 2023). Two solutions have been proposed to reduce such bias: i) calibration of Q by additional parameters derived from the taxon sampling completeness (Jorgensen et al. 2023); and ii) data selection (Ackerly 2000; Sidlauskas 2008). In our study, taxon sampling was heavily weighted towards *Dolomedes*, a genus, in which most species are semi-aquatic and none have a capture web. The relative over-sampling of a homogenous clade could lead to inflation or reduction of certain transition probabilities. Due to the unknown lifestyles in many pisaurid genera, calibration parameters by taxon sampling completeness were not feasible. We therefore approached the reduction of taxonomic bias in our analyses through data selection by randomly pruning *Dolomedes* terminals from the full taxon tree, corrected for their representation of biogeographic realms. We subjected all our evolutionary and comparative tests on trees with and without bias correction, i.e. the full taxon tree, and 30 reduced taxon trees.

Comparing the outcomes of the analyses with and without bias correction reveals that the ancestral state reconstruction of lifestyles and the correlation test between lifestyles and morphological traits are relatively robust to taxon sampling bias. However, the ancestral state

reconstruction of a capture web and the correlation between lifestyle and capture web are sensitive to taxon sampling bias. Without reducing the taxon sampling bias, both analyses yielded over-resolved ancestral states, as well as misleading correlation outcomes between pairs of traits.

RelTime and MCMCtree yield congruent results

We subjected the data to two approaches to divergence time estimation, the *a posteriori* and the *a priori* methods implemented in RelTime (Tamura et al. 2012; 2018) and MCMCtree (Yang 2007), respectively. Both types of analyses yielded largely overlapping results with interpretable confidence intervals and posterior densities, which may give considerable credibility to the estimated absolute and relative ages of the focal clades in our study. Credibility of the estimated absolute ages in our study is also suggested by comparing the hypothesized ages of the two island endemic species *Dolomedes schauinslandi* (0.9–4.2 Ma) and *D. orion* Tanikawa, 2003 (2.3–6.4 Ma) with the proposed time of the major geological events having shaped the Chatham Islands (2–3 & 4–6 Ma; Heenan et al. 2010) and Okinawa Islands (6–10 Ma; Wang et al. 2014).

The estimated origin of Pisauridae (29–40 Ma) is consistent with the literature (25–75 Ma; see Piacentini and Ramírez 2019; Magalhaes et al. 2020). However, our estimation yields a markedly younger origin of the crown Dolomedidae (compare 10–17 Ma in our study

704 with 25–50 Ma in Piacentini and Ramírez 2019; Magalhaes et al. 2020). These differences
705 could be due to variation in taxon sampling, amount of molecular data, and different
706 topologies. Despite the relatively recent origin of the crown Dolomedidae, it sits on a long
707 stem, as the split between Dolomedidae and its sister clade is estimated to be between 30 and
708 40 Ma. While the shape of this chronogram could plausibly be an artifact of missing some
709 critical (extinct) taxa, we find the interpretation more likely that this shape reflects a recent
710 diversification of Dolomedidae with relatively rapid species radiations, similar to the pattern
711 in the extant segmented spiders (Xu et al. 2015). The incomplete reproductive isolation
712 implied by the introgression between the sister species *Dolomedes minor* and *D. aquaticus*
713 Goyen, 1888 (Lattimore et al. 2011) may reinforce the interpretation that *Dolomedes*
714 undergoes rapid species radiations.
715
716 *Did Miocene climate change drive lifestyle diversification?*
717 Cenozoic climate oscillations may have shaped the evolution of the terrestrial lifestyles
718 and the presence of capture webs in Pisauridae. Combining the results of time calibration and
719 ancestral state reconstructions, the three reversals from semi-aquatic to terrestrial lifestyles
720 and the origin of capture webs in Pisauridae are all estimated between 10 and 20 Ma. This
721 time interval matches the era when the Earth's temperature and humidity reached the optima
722 and started dropping (Zachos et al. 2001; Sun et al. 2020). Considering i) the extent to which

723 semi-aquatic pisaurids are all distributed in the tropics, and ii) the distant phylogenetic
724 proximity among Palearctic and Nearctic pisaurids, one can hypothesize that the cooling and
725 drying climate in the mid-Miocene may have driven the evolution from semi-aquatic to
726 terrestrial lifestyles (see also Ye et al. 2018), which may have spurred the emergence of web-
727 based foraging behaviors.

728 The terrestrial lifestyle in *Dolomedes* may have undergone a different evolutionary
729 scheme compared to pisaurids, judging from the fact that the reversals to terrestrial lifestyle
730 in *Dolomedes* are phylogenetically derived and independent. Not unlike the semi-aquatic
731 pisaurids, extant *Dolomedes* species of early branching lineages are distributed in subtropical
732 to tropical Asia and Australasia, corresponding to regions that harbored humid refugia during
733 the Miocene (Milne 2006; Steinthorsdottir et al. 2021). However, the more northern
734 distribution ranges of some terminals from the same lineages strongly suggest that
735 *Dolomedes* species can cope more easily with cold climates than the semi-aquatic pisaurids.
736 During Miocene climate oscillations, *Dolomedes* may therefore have taken over niches and
737 habitats that became less hospitable to other large semi-aquatic spiders. This could perhaps
738 explain their colonization of most continents, and the current biogeographic patterns of
739 *Dolomedes* as the only large semi-aquatic spiders inhabiting temperate or even boreal regions
740 of the Northern Hemisphere. This scenario, on the one hand, and the observed cohabitation of
741 certain terrestrial and semi-aquatic sister species of *Dolomedes*, –on the other (Ono 2009;

Vink and Dupérré 2010), suggest that the evolution of the terrestrial lifestyle in *Dolomedes* stems from episodes of rapid radiation and niche partitioning.

TAXONOMY

Taxonomic and phylogenetic history of Dolomedidae and Pisauridae

Among the first organisms to be named using Linnaeus' binomial nomenclature, *Araneus fimbriatus* Clerck, 1757 and *Araneus plantarius* Clerck, 1757 from Sweden, represent the first descriptions of the species now known as *Dolomedes*. Latreille (1804) introduced the genus name *Dolomedes* and classified it under "wolf spiders" to include these two species, along with *Araneus mirabilis* Clerck, 1757 [today *Pisaura mirabilis* (Clerck, 1757), the type species of *Pisaura* and thus Pisauridae]. Simon (1864) placed *Dolomedes* in Lycosidae and later in the lycosid subfamily "Dolomedinae" (Simon 1876). This was the original designation of Dolomedinae as a family-level taxon, and thus we attribute Dolomedidae to this author, eventhough Simon (1898b) himself later transferred *Dolomedes* to Pisauridae. In 1898, Simon then classified Pisauridae into "Pisaurieae", "Thalassieae", and "Dolomedeae" based on the arrangement of their eyes. This classification was followed by Petrunkevitch (1928), but renamed as Pisaurinae, Thalassiinae (=Thalassinae), and Thaumasiinae (=Thaumasinae), respectively. Lehtinen (1967) was the first to propose the family Dolomedidae which included the elevation of *Dolomedes* and Thaumasiinae. This

761 proposed taxonomic act was subsequently considered unjustified (Sierwald 1990; Griswold
762 1993). Although the subfamily placement of *Dolomedes* in Simon (1898b) and Petrunkevitch
763 (1928) has been followed by some authors (Roewer 1955; Raven and Hebron 2018), the
764 proximity of *Dolomedes* and *Thaumasia* has never been confirmed phylogenetically. Detailed
765 studies and analyses of pisaurid genitalia seemed to support the monophyly of Pisauridae
766 (Sierwald 1990; Griswold 1993; Zhang et al. 2004; Santos 2007b), with *Dolomedes* deemed a
767 close relative of *Thalassius* Simon, 1885 (=*Nilus*) (Sierwald 1990; Zhang et al. 2004) or
768 *Pisaurina* Simon, 1898 (Santos 2007b). Sierwald (1989, 1990) outlined some unique genital
769 features in *Dolomedes*.

770 While some phylogenetic studies recovered results similar to the above morphological
771 hypotheses (Bayer and Schönhofer 2013; Moradmand et al. 2014; Fernández et al. 2018), the
772 majority suggested otherwise. Some studies still recovered a monophyletic Pisauridae, albeit
773 with *Dolomedes* and the New Caledonian endemic *Bradystichus* Simon, 1884, if included,
774 forming a clade sister to all other pisaurids (Wheeler et al. 2017; Cheng and Piel 2018;
775 Piacentini and Ramírez 2019; Kallal et al. 2021). Other studies suggest that Pisauridae is
776 paraphyletic (Polotow et al. 2015; Albo et al. 2017; Hazzi and Hormiga 2023; Kulkarni et al.
777 2023). They recover *Dolomedes* either as sister to a large clade with Pisauridae, Trechaleidae,
778 and Lycosidae (Albo et al. 2017) or to Trechaleidae and Lycosidae (Hazzi and Hormiga 2023;
779 Kulkarni et al. 2023). Kulkarni and co-workers (2023) recovered *Dolomedes* and

Bradystichus as sister to Trechaleidae and Lycosidae.

Family Dolomedidae Simon, 1876, family rank resurrected

Bradystichidae Simon 1884, new synonymy

(*Raft spiders*)

Composition:

Dolomedes Latreille, 1804 (*Fishing spiders*), *Bradystichus* Simon, 1884, *Megadolomedes* Davies and Raven 1980, *Caledomedes* Raven and Hebron, 2018, *Mangromedes* Raven and Hebron, 2018, *Ornodolomedes* Raven and Hebron, 2018, and *Tasmomedes* Raven and Hebron, 2018.

Diagnosis:

Dolomedidae resemble Pisauridae, Trechaleidae, and Lycosidae. According to Simon (1876), these four families share the combination of the following habitus characteristics: i) carapace pear-shaped and longer than wide, dorsally elevated without tubercles or spines; ii) eight eyes in two rows: the posterior row strongly recurved with the lateral eyes distantly separated from the anterior eyes, all posterior eyes larger than the anterior eyes; iii) legs prograde with three claws, the fourth legs are the longest while the third legs are the shortest;

iv) abdomen longer than wide; and v) ecribellate, spinnerets regular without elongated sections.

Dolomedidae genera can be distinguished from Trechaleidae, Lycosidae, and Pisauridae by the following characters: i) a tiny stem and head of spermathecae, which together form an accessory bulb, connected to the base of the spermathecae (Figs. S7–S9, after Sierwald 1989); ii) an elongated, coiled, or spirally arranged base of the spermatheca and spermathecal lumen (Figs. S7–S9; see also Remarks); iii) the presence of all three, the retrolateral tibial apophysis, the ventral tibial apophysis, and the basal cymbium apophysis on the male palp (Figs. S10–S11, see also Raven and Hebron 2018); v) the presence of a round sclerotized "saddle" instead of a distal tegular apophysis (Figs. S10–S11, see Sierwald 1990; Raven and Hebron 2018); and vi) the presence of a lateral subterminal apophysis, which is connected to the distal sclerotized tube of the apical division together with the embolus and fulcrum (Figs. S12).

Dolomedidae genera differ from Lycosidae and Trechaleidae by i) having both the copulatory duct and fertilization duct connected to the base of the spermatheca (Figs. S7–S9, see also Sierwald 1989); ii) the presence of a distal tegular projection, which forms a U-shaped tegular ring with the tegulum and conductor (Figs. S10–S11); and iii) the stereotypical behavior whereby females carry their egg sac on the chelicerae (as opposed to attached to the spinnerets in Lycosidae and in Trechaleidae).

Dolomedidae genera can also be diagnosed from the subfamily Pisaurinae by i) a nearly straight or strongly recurved, but never strongly procurved, anterior eye row (see Raven and Hebron 2018); ii) the carapace not protruding anteriorly at the anterior eye row in the lateral view (see Blandin 1979; Raven and Hebron 2018); iii) the absence of a "carina" in the female epigyne (Figs. S7–S8; see Sierwald 1997); iv) the copulatory and fertilization ducts both connected to the base of spermatheca (Figs. S7–S9, see also Sierwald 1989); v) a U-shaped tegular ring with a triangular conductor (Figs. S10–S11).

Remarks:

Female vulvae in Dolomedidae are usually elongated tubes whose structures are difficult to differentiate. Sierwald (1989) considered female *Dolomedes* to have a rather small base of spermatheca connected to a thick tubular fertilization duct (see Fig. 4 in Sierwald 1989); such nomenclature was followed subsequently (e.g., Yu and Kuntner 2024). However, further dissection into those tubular "fertilization ducts" detects matter that can be recognized as a sperm mass (Fig. S13). This newly emerged detail suggests that those tubular structures are responsible for sperm storage and should therefore be classified as the elongation of a base of spermatheca rather than a tubular fertilization duct (see also Jäger 2008). As in Sierwald (1989), we did not find any glandular pores on those tubular structures. In *Dolomedes* and in the investigated pisaurids, those pores are found exclusively on the tip of accessory bulbs or

the head of spermathecae but not on its base (Sierwald 1989). The actual function of different parts of the female vulva in Dolomedidae awaits further detailed studies.

Genus *Blandinia* Tonini et al., 2016, *incertae sedis*

Remarks:

Blandin (1979) first established the genus as *Ransonia* Blandin, 1979, based on female specimens of a single species from Madagascar. The genus was renamed to *Blandinia* by Tonini et al. (2016) because *Ransonia* had been preoccupied by a jellyfish genus described by Kramp (1947). Blandin (1979) classified this genus in Pisauridae and Pisaurinae, owing to its strongly procurved anterior eye row. Blandin also pointed out that the genus had a distinct number of cheliceral teeth and a unique epigyne among Pisaurinae genera (Blandin 1979).

Our phylogenomic analyses suggest that *Blandinia* is not a pisaurid but is sister to Trechaleidae and Lycosidae. Although such a topology might suggest the establishment of a new family, we refrain from doing so due to unknown and conflicting topologies in Trechaleidae (Piacentini and Ramírez 2019; Hazzi and Hormiga 2023; Kulkarni et al. 2023), as well as the unknown male morphology of *Blandinia*. We therefore suggest to treat *Blandinia* as *incertae sedis* for the time being.

Family Pisauridae Simon, 1890

Remarks:

Based on our phylogeny (Fig. 3) Pisauridae should be delimited to *exclude* the genera in Dolomedidae (above) as well as *Blandinia*. This is the first step towards pisaurid delimitation. Although we refrain from providing a diagnosis for this family here, the current phylogenetic evidence (Fig. 3) suggests these 24 genera could be classified as pisaurids: *Afropisaura* Blandin, 1979, *Caripetella* Strand, 1928, *Charminus* Thorell, 1899, *Cispius* Simon, 1898, *Cladycnis* Simon, 1898, *Dendrolycosa* Doleschall, 1859, *Euprosthenops* Pocock, 1897, *Euprosthenopsis* Blandin, 1974, *Hala* Jocqué, 1994, *Hygropoda* Thorell, 1895, *Maypacius* Simon, 1898, *Nilus* O. Pickard-Cambridge, 1876, *Paracladycnis* Blandin, 1979, *Perenethis* L. Koch, 1878, *Pisaura* Simon, 1886, *Pisaurina* Simon, 1898, *Polyboea* Thorell, 1895, *Qianlingula* Zhang et al., 2004, *Rothus* Simon, 1898, *Sphedanus* Thorell, 1877, *Tallonia* Simon, 1889, *Tetragonophthalma* Karsch, 1878, *Thaumasia* Perty, 1833, and *Tolma* Jocqué, 1994.

The following 20 genera were not included in our phylogenetic analyses but may or may not be true pisaurids: *Archipirata* Simon, 1898, *Architis* Simon, 1898, *Chiasmopes* Pavesi, 1883, *Cispinilus* Roewer, 1955, *Conakrya* Schmidt, 1956, *Eucamptopus* Pocock, 1900, *Ilipula* Simon, 1903, *Inola* Davies, 1982, *Papakula* Strand, 1911, *Phalaeops* Roewer, 1955, *Stoliczka* O. Pickard-Cambridge, 1885, *Tapinothele* Simon, 1898, *Tapinothelella* Strand, 1909, *Tapinothelops* Roewer, 1955, *Thalassiopsis* Roewer, 1955, *Tinus* F. O. Pickard-

Cambridge, 1901, *Voraptipus* Roewer, 1955, *Voraptus* Simon, 1898, *Vuattouxia* Blandin, 1979, and *Walrencea* Blandin, 1979.

Supplementary Material

All supplementary material including the UCE matrices is available at *doi* and DRYAD, https://doi.org/10.5061/dryad.12jm63z6x.

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FIGURES

FIGURE 1. A glimpse into lifestyle diversity of the genera currently in Pisauridae Simon, 1890: (a) Female of semi-aquatic *Dolomedes mizhoanus* Kishida, 1936 preying on a fish, (b) Female of terrestrial *Dolomedes sulfureus* L. Koch, 1878 standing on vegetation; c–f,

terrestrial lifestyle without capture web: (c) A female *Pisaura mirabilis* (Clerck, 1757) guarding her egg sac and nursery web, (d) Male of an unknown Pisauridae genus from Madagascar hanging under a leaf, (e) Male of *Perenethis fascigera* Bösenberg and Strand, 1906 roving on grassland litter layer (credit: Han-Po Chang), (f) Female of *Hala* sp. standing on the forest understory; g–l, terrestrial lifestyle with capture web: (g) Female of *Sphedanus quadrimaculatus* Thorell, 1897 hanging under her 3-dimensional web with retreat made of debris, (h) Female of *Caripetella madagascariensis* Lenz, 1886 hanging under her sheet web, (i) Juvenile of *Euprosthenopsis* sp. on its sheet web (credit: Matjaž Bedjanič), (j) Female of *Dendrolycosa* cf. *songi* (Zhang, 2000) standing on her sheet web (credit: Lok Ming Tang), (k) Female of *Blandinia mahasoana* (Blandin, 1979) standing on her sheet web, (l) Female of *Polyboea zonaformis* (Wang, 1993) standing in the center of her 3-dimentional web (credit: Lok Ming Tang); m–p, semi-aquatic lifestyle, (m) Subadult male of *Thaumasia velox* Simon, 1898 floating on water, (n) Female of *Qianlingula* cf. *turbinata* Zhang et al., 2004 in hunting posture, (o) Subadult female of *Nilus phipsoni* (F. O. Pickard-Cambridge, 1897) in hunting posture, (p) Female of *Hygropoda higenaga* (Kishida, 1936) in hunting posture.

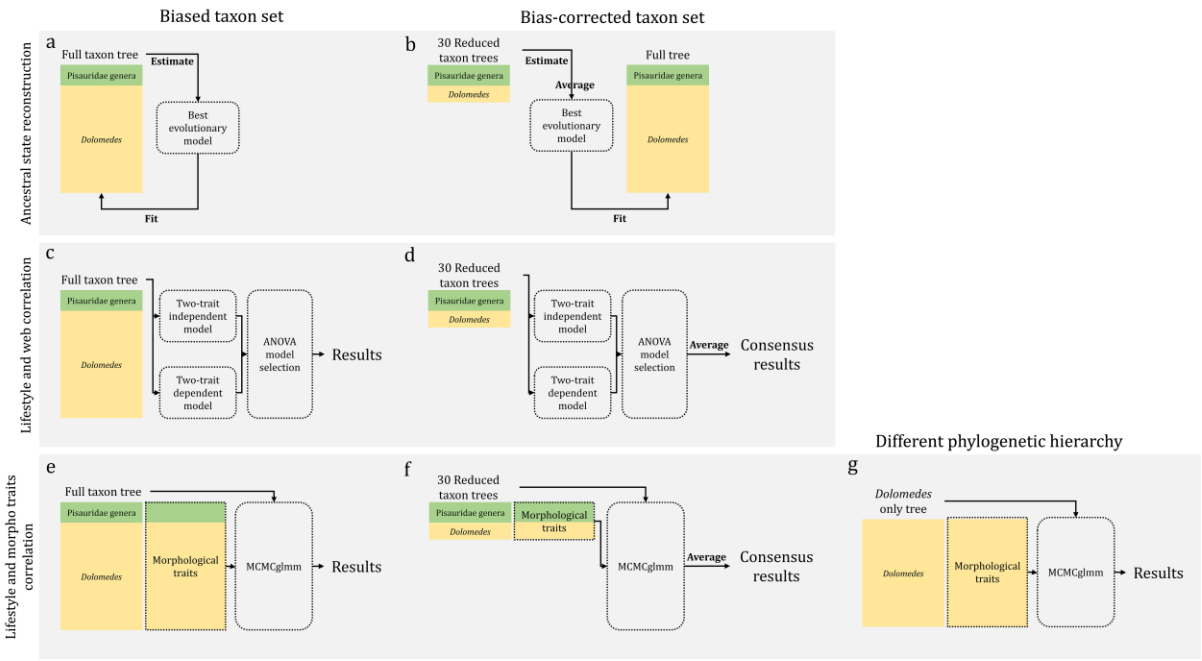


FIGURE 2. Analytical design for investigating how biased taxon sampling can influence the three evolutionary analyses; and how different phylogenetic hierarchies change the correlation between lifestyles and morphological traits. a–b, analytical design for ancestral state reconstruction using (a) the full taxon tree, and (b) 30 reduced taxon trees; c–d, analytical design for comparative analyses between lifestyles and capture webs using (c) the full taxon tree, and (d) 30 reduced taxon trees; e–g, analytical design for comparative analyses between lifestyles and morphological traits using (e) the full taxon tree, (f) 30 reduced taxon trees, and (g) the *Dolomedes*-only tree.

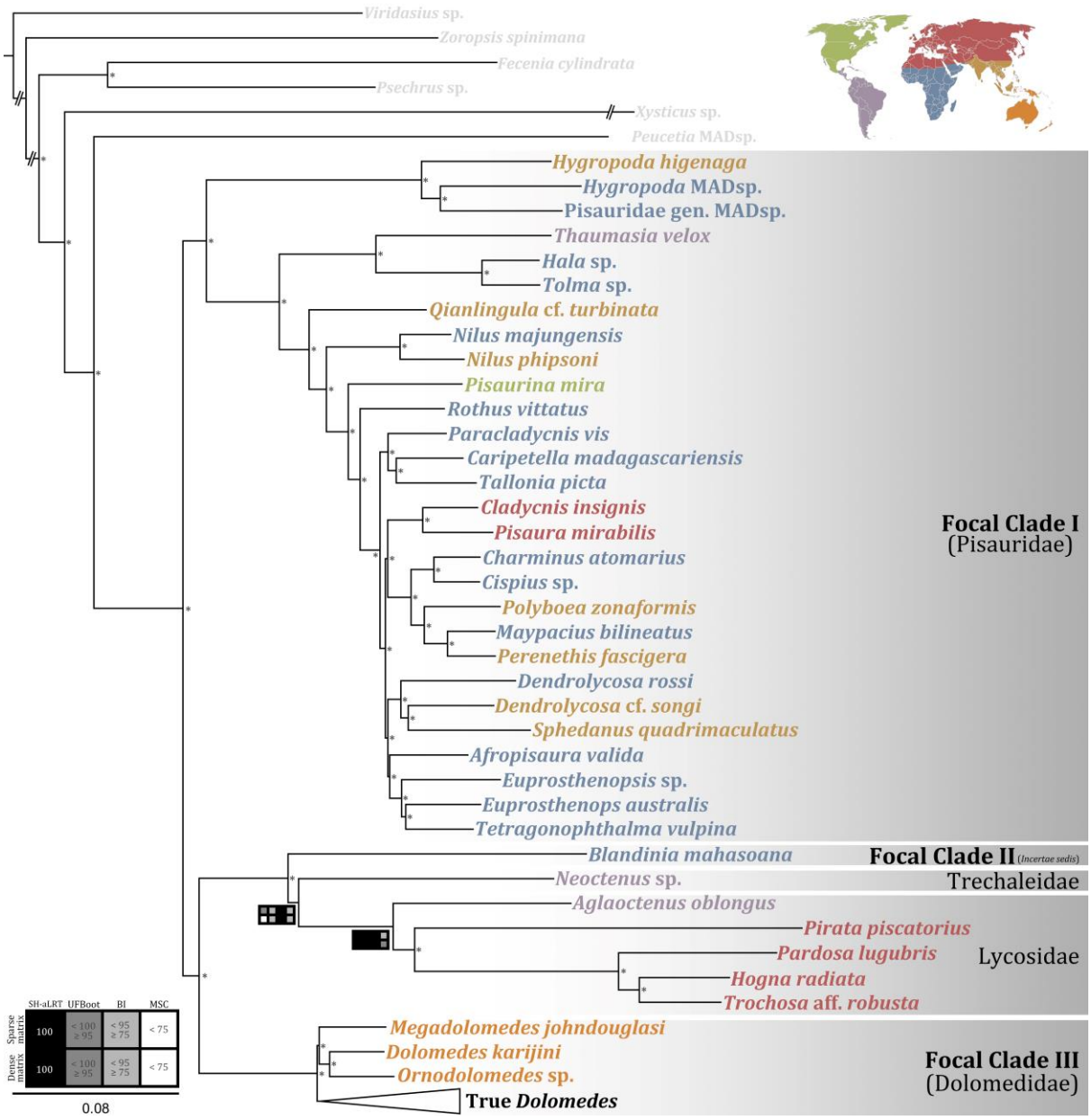
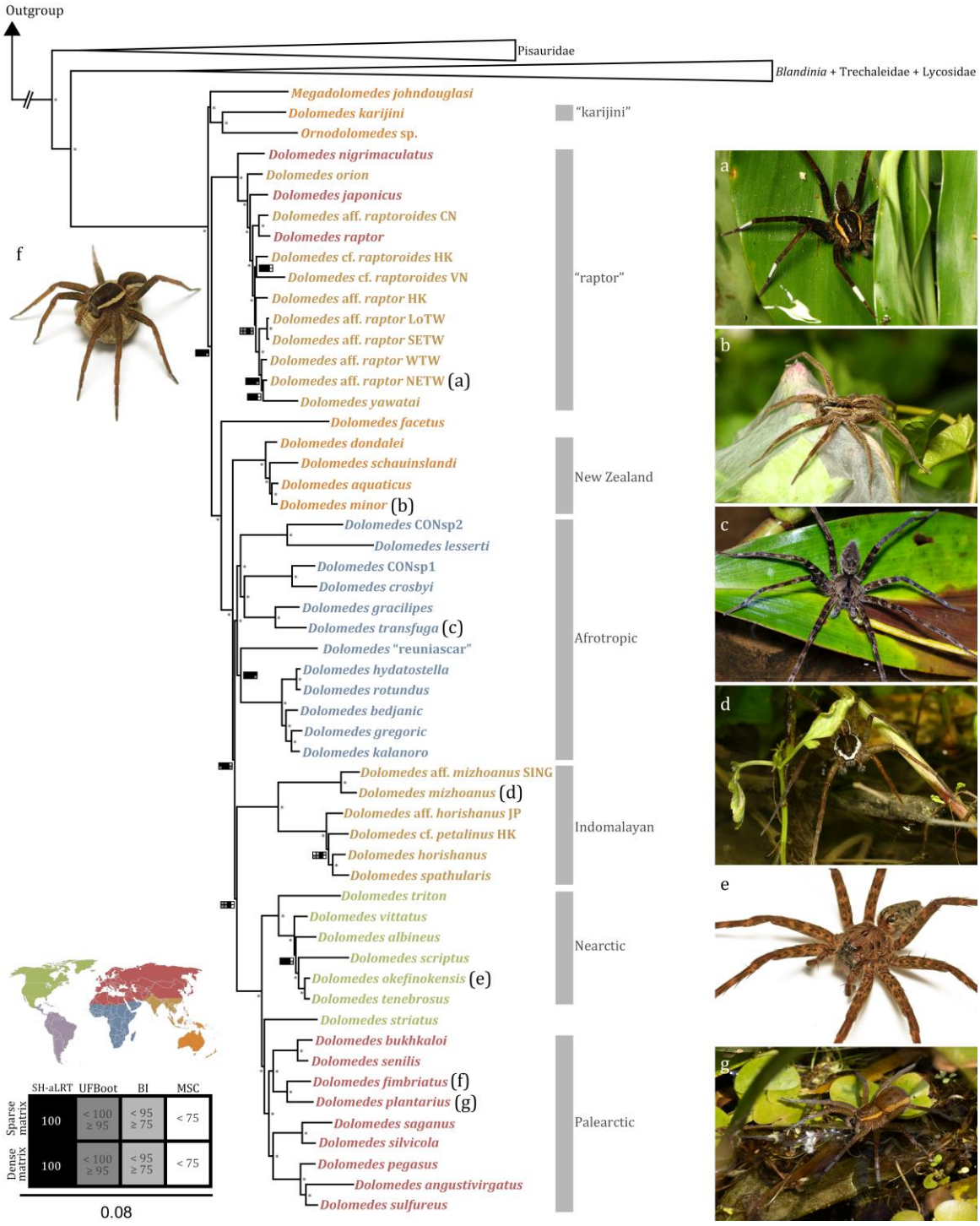


FIGURE 3. Maximum likelihood phylogeny of the three focal clades reconstructed from the sparse UCE matrix; nodal supports are labeled according to the legend at the bottom left, nodes with full supports are represented by "*"; each terminal is color-coded by its biogeographic region according to the map (modified from Udvardy 1975) at the top right with the outgroups in light gray. UFboot: ultrafast bootstrap (Minh et al. 2013; Hoang et al. 2017), SH-aLRT: SH-like approximate likelihood ratio test (Guindon et al. 2010), BI:

1468 posterior probability (%) of Bayesian inference, MSC: posterior probability (%) of multi-

1469 species coalescence. See supplementary materials for the full branch lengths of the outgroups.

1470



1471

1472 FIGURE 4. Maximum likelihood phylogeny of *Dolomedes* Latreille, 1804 and its relatives

reconstructed from the sparse UCE matrix; nodal supports are labeled according to the legend at the bottom left, nodes with full supports are represented by "*"; each terminal is color-coded by its biogeographic region according to the map at the bottom left; images in panels a–g show habitus morphologies of the species labeled correspondingly in the phylogeny: (a) an unknown morphospecies of the "raptor" clade hiding between leaves, (b) a female *D. minor* L. Koch, 1876 guarding her nursery web, (c) a female *D. transfuga* Pocock, 1900 in hunting posture, (d) a male *D. mizhoanus* Kishida, 1936 in hunting posture, (e) a female *D. okefinokensis* Bishop, 1924 placed on a white background, (f) a *D. fimbriatus* (Clerck, 1757) carrying her egg sac, and (g) a female *D. plantarius* (Clerck, 1757) standing on macrophytes. UFboot: ultrafast bootstrap (Minh et al. 2013; Hoang et al. 2017), SH-aLRT: SH-like approximate likelihood ratio test (Guindon et al. 2010), BI: posterior probability (%) of Bayesian inference, MSC: posterior probability (%) of multi-species coalescence.

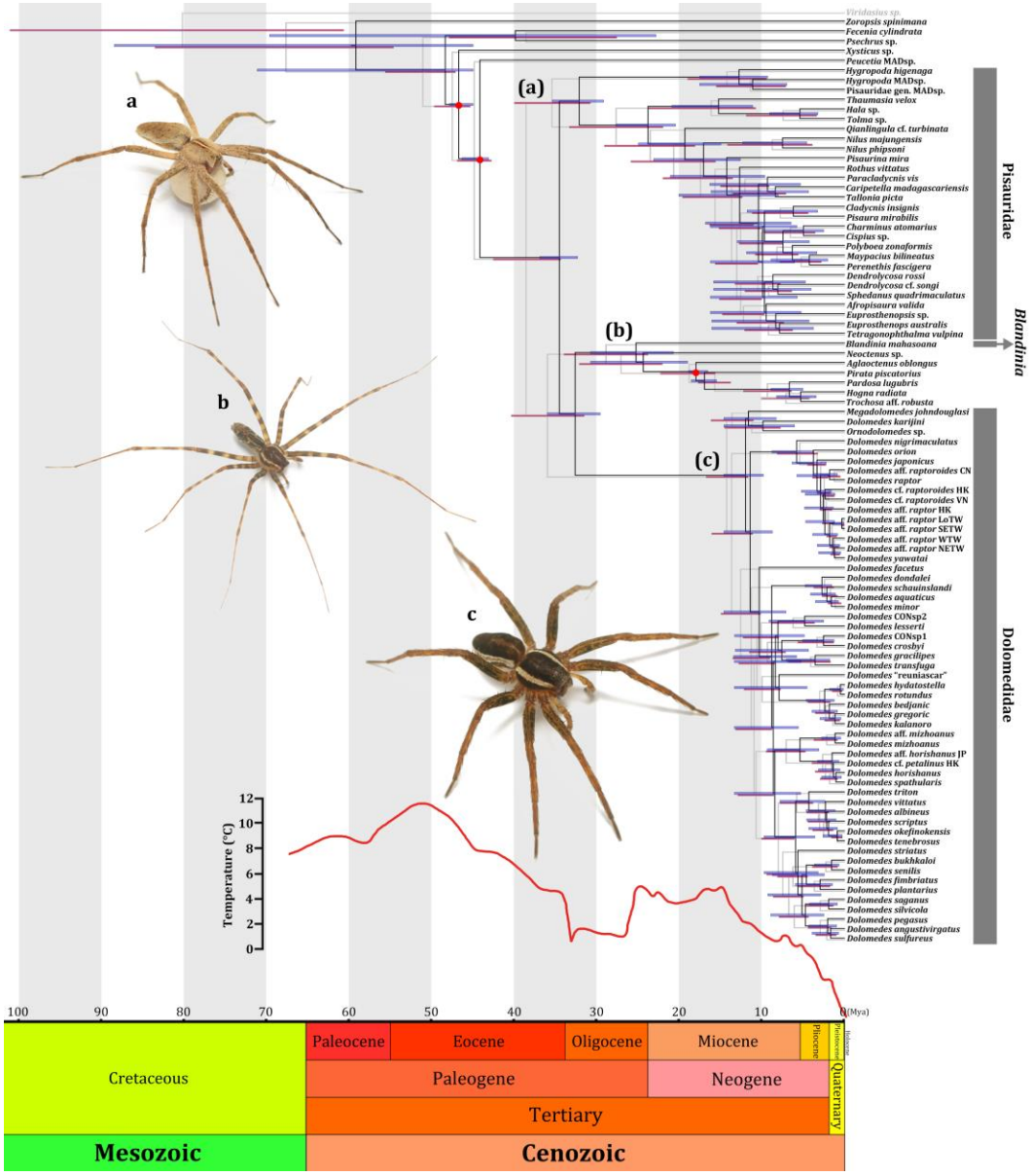


FIGURE 5. Phylogenies of all three focal clades (a–c) calibrated by RelTime (black lines and blue bars; Tamura et al. 2012; 2018) and MCMCtree (gray lines and red bars; Yang 2007) with 95% confidence intervals and highest posterior densities of diversification time; red dots represent the fossil calibration points. A red curve of paleotemperature, modified from Zachos et al. (2001), shows the overlap between diversification and paleoclimate changes. Ma: million years ago.

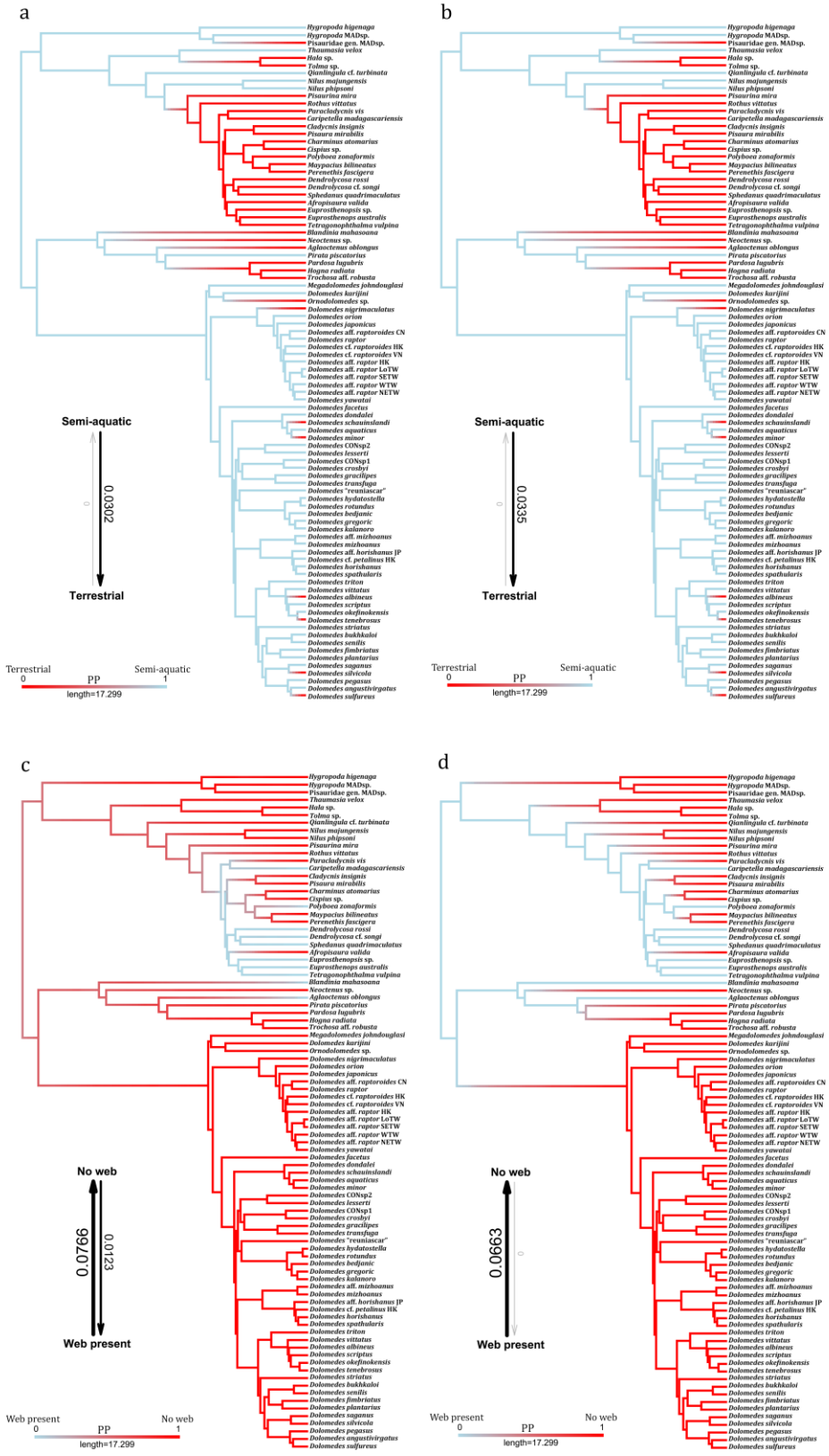


FIGURE 6. Ancestral state reconstructions rendered from 100 stochastic character mapping on

the full taxon tree and trait transition probabilities of: a–b, semi-aquatic vs terrestrial lifestyle with their best *k*-state Markov models (M*k* model, Pagel 1994; Lewis 2001) estimated from the (a) 30 reduced taxon trees, and (b) full taxon tree; c–d, capture web absence vs presence with their best M*k* model estimated from the (c) 30 reduced taxon trees, and (d) full taxon tree. PP: posterior probability.

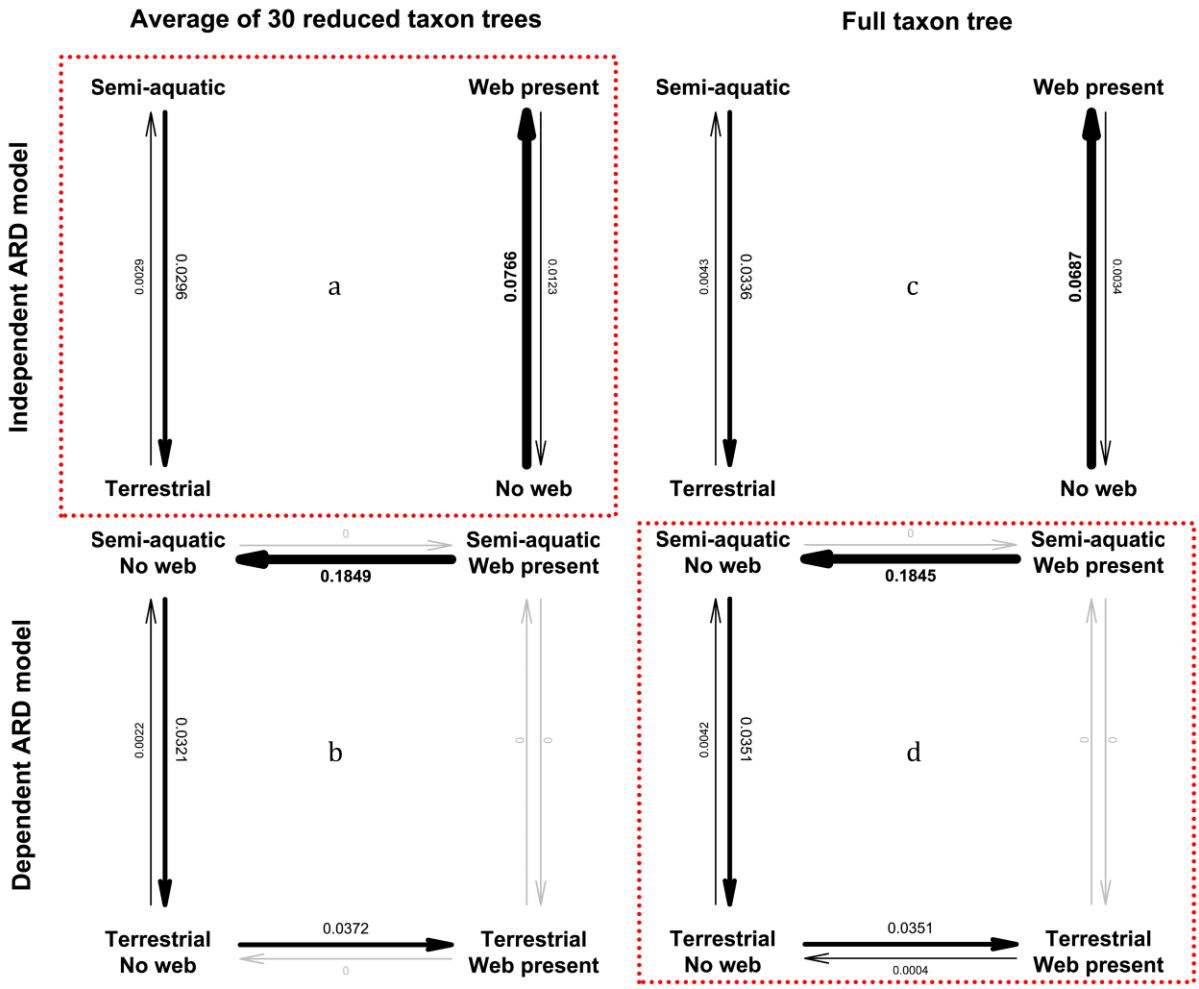


FIGURE 7. Pagel's (1994) binary character correlation test between semi-aquatic vs terrestrial lifestyle and capture web absence vs presence based on the: a–b, 30 reduced taxon trees with their estimated and averaged trait transition probabilities in two-trait (a) independent all-

rates-different (ARD) models, and (b) dependent ARD models; c–d, full taxon tree and their estimated trait transition probabilities in two-trait (c) independent ARD models, and (d) two-trait dependent ARD models. The model selected by model selection highlighted by red dotted line.

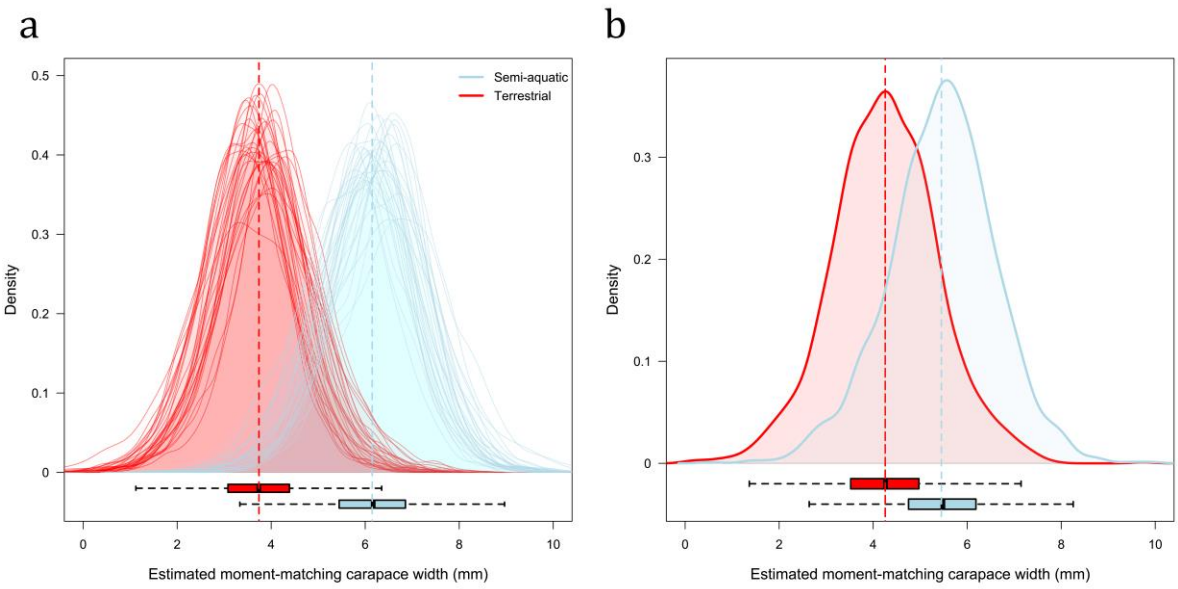


FIGURE 8. Posterior density curves of moment-matching carapace width estimated via Monte Carlo Sampler for Multivariate Generalized Linear Mixed Models (MCMCglmm; Hadfield 2010) from the (a) 30 reduced taxon trees and (b) full taxon tree; estimated mean carapace width of each lifestyle pinpointed by the vertical dotted lines. The box plots below show the medians (bold lines), first quartiles (Q1, left margins of the boxes), third quartiles (Q3, right margins of the boxes), Q1 − 1.5 × interquartile range (IQR) (left whisker), and Q3 + 1.5 × IQR (right whisker) of all estimated values in both lifestyles.

1520 TABLES

1521 TABLE 1. The 52 genera currently listed in Pisauridae Simon 1890 and their known

1522 distribution ranges and lifestyles.

Genus and author	Biogeographic realm	Lifestyle	Capture web	Data source	Include in this study
Afropisaura Blandin, 1979	Afrotropic	terrestrial	absent	Dippenaar-Schoeman et al. 2020	yes
Archipirata Simon, 1898	Indomalayan	unknown	unknown		no
Architis Simon, 1898	Neotropic	terrestrial	present	Santos 2007	no
Blandinia Tonini et al., 2016	Afrotropic	terrestrial	present	Yu original observation	yes
Bradystichus Simon, 1884	Australasian	terrestrial	absent	Platnick and Forster 1993	no
Caledomedes Raven and Hebron, 2018	Australasian	terrestrial	absent	Raven and Hebron 2018	no
Caripetella Strand, 1928	Afrotropic	terrestrial	present	Yu original observation	yes
Charminus Thorell, 1899	Afrotropic	terrestrial	absent	Dippenaar-Schoeman et al. 2020	yes
Chiasmopes Pavesi, 1883	Afrotropic	terrestrial	absent	Dippenaar-Schoeman et al. 2020	no
Cispinilus Roewer, 1955	Afrotropic	unknown	unknown		no
Cispius Simon, 1898	Afrotropic	terrestrial	absent	Dippenaar-Schoeman et al. 2020	yes
Cladycnis Simon, 1898	Palearctic	terrestrial	absent	Wunderlich 1987	yes
Conakrya Schmidt, 1956	Afrotropic	unknown	unknown		no

Dendrolycosa Doleschall, 1859	Afrotropic & Australasian & Indomalayan	terrestrial	present	Jäger 2011; Raven and Hebron 2018	yes
Dolomedes Latreille, 1804	Global	semi-aquatic	absent	see main text	yes
Eucamptopus Pocock, 1900	Indomalayan	unknown	unknown		no
Euprosthenops Pocock, 1897	Afrotropic	terrestrial	present	Dippenaar-Schoeman et al. 2020	yes
Euprosthenopsis Blandin, 1974	Afrotropic	terrestrial	present	Dippenaar-Schoeman et al. 2020	yes
Hala Jocqué, 1994	Afrotropic	terrestrial	absent	Jocqué 1994; Yu original observation	yes
Hygropoda Thorell, 1895	Afrotropic & Indomalayan	semi-aquatic	absent	Zhang et al. 2004; Dankittipakul et al. 2008	yes
Ilipula Simon, 1903	Indomalayan	unknown	unknown		no
Inola Davies, 1982	Indomalayan	terrestrial	present	Davies 1982	no
Mangromedes Raven and Hebron, 2018	Australasian	semi-aquatic	absent	Raven and Hebron 2018	no
Maypacius Simon, 1898	Afrotropic	terrestrial	absent	Dippenaar-Schoeman et al. 2020	yes
Megadolomedes Davies and Raven, 1980	Australasian	semi-aquatic	absent	Raven and Hebron 2018	yes
Nilus O. Pickard-Cambridge, 1876	Afrotropic & Indomalayan	semi-aquatic	absent	Dippenaar-Schoeman et al. 2020	yes
Ornodolomedes Raven and Hebron, 2018	Australasian	terrestrial	absent	Raven and Hebron 2018	yes
Papakula Strand, 1911	Indomalayan	unknown	unknown		no

Paracladycnis Blandin, 1979	Afrotropic	terrestrial	absent	Yu original observation	yes
Perenethis L. Koch, 1878	Afrotropic & Australasian & Indomalayan	terrestrial	absent	Sierwald 1997; Dippenaar-Schoeman et al. 2020	yes
Phalaeops Roewer, 1955	Afrotropic	unknown	unknown		no
Pisaura Simon, 1886	Palearctic	terrestrial	absent	Zhang et al. 2004	yes
Pisaurina Simon, 1898	Nearctic	terrestrial	absent	Carico 1973b	yes
Polyboea Thorell, 1895	Indomalayan	terrestrial	present	Sierwald 1997	yes
Qianlingula Zhang et al., 2004	Indomalayan	semi-aquatic	absent	Yu original observation	yes
Rothus Simon, 1898	Afrotropic	terrestrial	absent	Dippenaar-Schoeman et al. 2020	yes
Sphedanus Thorell, 1877	Indomalayan	terrestrial	present	Jäger 2011	yes
Stoliczka O. Pickard-Cambridge, 1885	Palearctic	unknown	unknown		no
Tallonia Simon, 1889	Afrotropic	unknown	unknown		yes
Tapinothele Simon, 1898	Afrotropic	unknown	unknown		no
Tapinothelella Strand, 1909	Afrotropic	unknown	unknown		no
Tapinothelops Roewer, 1955	Afrotropic	unknown	unknown		no
Tetragonophthalma Karsch, 1878	Afrotropic	terrestrial	present	Pett B. L. original observation; but see Sierwald 1997	yes
Thalassiopsis Roewer, 1955	Afrotropic	unknown	unknown		no
Thaumasia Perty, 1833	Neotropic	semi-aquatic	absent	Silva and Carico 2012	yes
Tinus F. O. Pickard-Cambridge, 1901	Neotropic	semi-aquatic	absent	Carico 1976	no

Tolma Jocqué, 1994	Afrotropic	terrestrial	absent	Jocqué 1994; Yu original observation	yes
Voraptipus Roewer, 1955	Afrotropic	unknown	unknown		no
Voraptus Simon, 1898	Afrotropic & Indomalayan	unknown	unknown		no
Vuattouxia Blandin, 1979	Afrotropic	unknown	unknown		no
Walrencea Blandin, 1979	Afrotropic	terrestrial	absent	Dippenaar-Schoeman et al. 2020	no

TABLE 2. Monophyly of Pisauridae Simon, 1890 and the affiliation of *Dolomedes* Latreille, 1804 discussed and analyzed in the previous literature.

Literature	**Evidence**	**Monophyly of Pisauridae**	**Affiliation of *Dolomedes***	**Number of genera discussed**
Simon 1898b	eye arrangement	Yes	Dolomedeae	33
Petrunkevitch 1928	eye arrangement	Yes	Thaumasiinae	after Simon 1898b
Lehtinen 1967	morphological comparisons	No	Dolomedidae	16
Griswold 1993	morphological cladogram	Yes	sister to *Pisaura*	2
Sierwald 1990	genital structure homologous	Yes	closely related to *Thalassius* (=*Nilus*)	55
Zhang et al. 2004	morphological cladogram	Yes	sister to *Thalassius* (=*Nilus*)	9
Santos 2007b	morphological cladogram	Yes	sister to *Pisaurina*	8
Bayer and Schönhofer 2013	multi-genes phylogeny	No	sister to *Thalassius* (=*Nilus*)	3

Moradmand et al. 2014	multi-genes phylogeny	No	sister to Thalassinae	2
Polotow et al. 2015	mutli-evidence phylogeny	No	NA	3
Albo et al. 2017	multi-genes phylogeny	No	separate clade, basal to Lycosioidea	5
Wheeler et al. 2017	multi-genes phylogeny	Yes	sister to *Bradystichus*, basal pisaurid	9
Fernández et al. 2018	transcriptomic phylogeny	Yes	sister to *Pisaurina*	2
Cheng and Piel 2018	transcriptomic phylogeny	Yes	separate clade, basal pisaurid	4
Piacentini and Ramírez 2019	multi-genes phylogeny	Yes	sister to *Bradystichus*, basal pisaurid	9
Kallal et al. 2021	transcriptomic phylogeny	Yes	separate clade, basal pisaurid	5
Kulkarni et al. 2023	UCE + multi-genes phylogeny	No	separate clade, sister to Lycosidae + Trechaleidae	13
Hazzi and Hormiga 2023	multi-genes phylogeny	No	separate clade, sister to Lycosidae + Trechaleidae	7

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TABLE 3. Raw data matrix of all the specimens used in the study, showing the region where they were collected and their traits used in the analyses. All measurements are averages from female specimens. If no female data or specimen was available, we then used data from males (italic numbers). If the terminals were represented by juveniles lacking species-level identification, the averages of the female of their genus were used (numbers underlined). Measurements or data from a single specimen are in bold. All measurements are in millimeters and the biogeographic realms were modified from Udvardy (1975). CW: carapace width; L1: leg I length; T1: tarsus I length; "-": outgroups that are not in question. Voucher code and deposition: ABARA, YKP: National Chung Hsing University, Taiwan; ARA, KPARA: National Institute of Biology, Slovenia; BINCO: Biodiversity Inventory for Conservation, Belgium; CASENT: California Academy of Sciences, USA; FMNH: Field Museum, USA; MACN: Bernardino Rivadavia Natural Sciences Argentine Museum, Argentina; QM: Queensland Museum, Australia; RMCA: Royal Museum of Central Africa, Belgium; SMF: Senckenberg Natural History Museum, Germany; WAM: Western Australian Museum, Australia; ZRCENT: Lee Kong Chian Natural History Museum, Singapore.

Family	Species	Voucher code	Biogeographic realm	Country/Region	Admin	Life style	Capture web	CW	L1	T1	Data source

Lycosidae	*Aglaoctenus oblongus*	MACN-Ar41748	Neotropic	Argentina	Buenos Aires	terrestrial	web present	6.30	20.9	2.70	Santos et al. 2003
Lycosidae	*Hogna radiata*	KPARA_00623	Palearctic	Slovenia	Ljubljana	terrestrial	no web	5.74	19.7	2.60	Brady 2012; original data
Lycosidae	*Pardosa lugubris*	KPARA_00017	Palearctic	Slovenia	Ljubljana	terrestrial	no web	2.00	8.20	1.10	Nadolny and Kovblyuk 2012
Lycosidae	*Pirata piscatorius*	KPARA_00638	Palearctic	Slovenia	Jesenice	semi-aquatic	no web	3.77	12.25	1.33	original data
Lycosidae	*Trochosa* aff. *robusta*	KPARA_00639	Palearctic	Slovenia	Ljubljana	terrestrial	no web	3.16	9.48	1.50	original data
Trechaleidae	*Neoctenus* sp.	MACN-Ar43641	Neotropic	Argentina	Chaco	terrestrial	no web	3.65	14.84	1.92	original data
Pisauridae	*Afropisaura valida*	YKP-GB01	Afrotropic	Gabon	Anzem	terrestrial	no web	5.00	*21.68*	*2.81*	Sierwald 1997; original data
Pisauridae	*Blandinia mahasoana*	KPARA_00205	Afrotropic	Madagascar	Antsiranana	terrestrial	web present	2.40	19.61	2.70	original data
Pisauridae	*Caripetella madagascariensis*	KPARA_00178	Afrotropic	Madagascar	Toamasina	terrestrial	web present	4.70	37.23	3.54	original data
Pisauridae	*Charminus atomarius*	KPARA_00581	Afrotropic	South Africa	KwaZulu-Natal	terrestrial	no web	**2.47**	**15.71**	**2.07**	original data

Pisauridae	*Cispius* sp.	KPARA_0 0587	Afrotropic	South Africa	Free State	terrestrial	no web	2.93	13.18	1.56	original data
Pisauridae	*Cladycnis insignis*	KPARA_0 0617	Palearctic	Spain	Santa Cruz de Tenerife	terrestrial	no web	4.24	21.8	2.82	original data
Pisauridae	*Dendrolycosa* cf. *songi*	YKP-Ar0935	Indomalayan	China	Hong Kong	terrestrial	web present	3.70	17.5	1.80	Zhang 2000
Pisauridae	*Dendrolycosa rossi*	KPARA_0 0180	Afrotropic	Madagascar	Antsiranana	terrestrial	web present	2.09	10.23	1.23	Silva and Griswold 2013; original data
Pisauridae	*Dolomedes* aff. *horishanus* JP	KPARA_ DH_2-1	Indomalayan	Japan	Okinawa	semi-aquatic	no web	7.26	25.55	2.88	original data
Pisauridae	*Dolomedes* aff. *mizhoanus* SING	KPARA_0 0590	Indomalayan	Singapore	Chestnut Ave	semi-aquatic	no web	5.61	16.58	2.50	original data
Pisauridae	*Dolomedes* aff. *raptor* HK	KPARA_0 0614	Indomalayan	China	Hong Kong	semi-aquatic	no web	8.69	32.54	3.85	original data
Pisauridae	*Dolomedes* aff. *raptor* LoTW	YKP-Ar1262	Indomalayan	Taiwan	Hualian	semi-aquatic	no web	**10.62**	**40.72**	**4.94**	original data
Pisauridae	*Dolomedes* aff. *raptor* NETW	YKP-Ar1251	Indomalayan	Taiwan	Taipei	semi-aquatic	no web	11.61	47.67	5.55	original data
Pisauridae	*Dolomedes* aff. *raptor*	KPARA_0	Indomalayan	Taiwan	Taitung	semi-	no web	9.53	39.05	4.71	original data

	SETW	0483				aquatic					
Pisauridae	*Dolomedes* aff. *raptor* WTW	ABARA_01442	Indomalayan	Taiwan	Taichung	semi-aquatic	no web	9.32	36.1	4.32	original data
Pisauridae	*Dolomedes* aff. *raptoroides* CN	SMF_DS57	Indomalayan	China	Sichuan	semi-aquatic	no web	9.72	40.47	4.86	original data
Pisauridae	*Dolomedes albineus*	KPARA_00097	Nearctic	USA	Kentucky	terrestrial	no web	5.75	27.35	3.15	original data
Pisauridae	*Dolomedes angustivirgatus*	KPARA_JP002	Palearctic	Japan	Chiba	semi-aquatic	no web	6.46	28.42	3.81	Tanikawa and Miyashita 2008; original data
Pisauridae	*Dolomedes aquaticus*	KPARA_NZ_N38	Australasian	New Zealand	Blenheim	semi-aquatic	no web	8.41	28.13	3.86	Vink and Dupérré 2010; original data
Pisauridae	*Dolomedes bedjanic*	KPARA_00227	Afrotropic	Madagascar	Toamasina	semi-aquatic	no web	9.34	45.28	5.54	Yu and Kuntner 2024
Pisauridae	*Dolomedes bukhkaloi*	KPARA_YURI-1	Palearctic	Russia	Omolon	semi-aquatic	no web	6.55	*23.43*	*3.26*	Marusik 1988; original data
Pisauridae	*Dolomedes* cf. *petalinus* HK	KPARA_00604	Indomalayan	China	Hong Kong	semi-aquatic	no web	**7.29**	**24.28**	**2.64**	original data
Pisauridae	*Dolomedes* cf.	KPARA_0	Indomalayan	China	Hong Kong	semi-	no web	9.66	38.24	4.51	original data

	raptoroides HK	0606				aquatic					
Pisauridae	*Dolomedes* cf. *raptoroides* VN	SMF_56215	Indomalayan	Vietnam	Quang Binh	semi-aquatic	no web	10.10	42.55	5.17	original data
Pisauridae	*Dolomedes* CONsp1	BINCO_DRC_22_0309	Afrotropic	D. R. Congo	Tshuapa	semi-aquatic	no web	*4.73*	*20.03*	*2.82*	original data
Pisauridae	*Dolomedes* CONsp2	BINCO_DRC_21_0031_2	Afrotropic	D. R. Congo	Mai-Ndombe	semi-aquatic	no web	5.82	29.04	3.79	original data
Pisauridae	*Dolomedes crosbyi*	BINCO_DRC_22_0285	Afrotropic	D. R. Congo	Tshuapa	semi-aquatic	no web	5.45	17.9	2.24	original data
Pisauridae	*Dolomedes dondalei*	KPARA_00597	Australasian	New Zealand	Canterbury	semi-aquatic	no web	8.79	37.7	5.07	Vink and Dupérré 2010; original data
Pisauridae	*Dolomedes facetus*	QM_S116445	Australasian	Australia	Queensland	semi-aquatic	no web	5.71	23.73	2.59	Raven and Hebron 2018; original data
Pisauridae	*Dolomedes fimbriatus*	KPARA_00014	Palearctic	Slovenia	Malo Mraševo	semi-aquatic	no web	5.74	19.17	2.49	original data

Pisauridae	*Dolomedes gracilipes*	BINCO_DRC_22_0286	Afrotropic	D. R. Congo	Tshuapa	semi-aquatic	no web	6.64	43.54	5.90	Lessert 1928, original data
Pisauridae	*Dolomedes gregoric*	KPARA_00253	Afrotropic	Madagascar	Toamasina	semi-aquatic	no web	7.68	38.86	4.81	Yu and Kuntner 2024
Pisauridae	*Dolomedes horishanus*	ABARA_01583	Indomalayan	Taiwan	Nantou	semi-aquatic	no web	7.26	25.55	2.88	original data
Pisauridae	*Dolomedes hydatostella*	KPARA_00258	Afrotropic	Madagascar	Antsiranana	semi-aquatic	no web	6.43	23.69	2.36	Yu and Kuntner 2024
Pisauridae	*Dolomedes japonicus*	KPARA_JP009	Palearctic	Japan	Tokyo	semi-aquatic	no web	10.49	43.65	5.95	Tanikawa and Miyashita 2008; original data
Pisauridae	*Dolomedes kalanoro*	KPARA_00185	Afrotropic	Madagascar	Toamasina	semi-aquatic	no web	9.15	44.03	5.38	Yu and Kuntner 2024
Pisauridae	*Dolomedes karijini*	WAM_T153133	Australasian	Australia	Western Australia	semi-aquatic	no web	10.17	39.39	4.93	Raven and Hebron 2018; original data
Pisauridae	*Dolomedes lesserti*	RMCA_214998	Afrotropic	Benin	Ouémé	semi-aquatic	no web	5.63	20.97	2.73	original data
Pisauridae	*Dolomedes minor*	KPARA_	Australasian	New Zealand	Southland	terrestrial	no web	6.65	22.39	3.07	Vink and

		NZ_R75									Dupérré 2010; original data
Pisauridae	*Dolomedes mizhoanus*	ABARA_01630	Indomalayan	Taiwan	Taichung	semi-aquatic	no web	8.53	36.49	4.57	Zhang et al. 2004; Yin et al. 2012; original data
Pisauridae	*Dolomedes nigrimaculatus*	SMF_DS82	Palearctic	China	Sichuan	terrestrial	no web	8.18	33.68	3.96	Chae et al. 2023
Pisauridae	*Dolomedes okefinokensis*	KPARA_00620	Nearctic	USA	Florida	semi-aquatic	no web	9.18	40.45	4.74	original data
Pisauridae	*Dolomedes orion*	KPARA_JP012-1	Indomalayan	Japan	Okinawa	semi-aquatic	no web	16.17	59.78	6.67	Tanikawa 2003; original data
Pisauridae	*Dolomedes pegasus*	KPARA_JP016	Palearctic	Japan	Aomori	semi-aquatic	no web	8.33	27.07	3.41	Tanikawa 2012; original data
Pisauridae	*Dolomedes plantarius*	KPARA_00021	Palearctic	Slovenia	Jesenice	semi-aquatic	no web	7.24	25.38	3.31	original data
Pisauridae	*Dolomedes raptor*	KPARA_JP019-2	Palearctic	Japan	Kanagawa	semi-aquatic	no web	8.00	33.78	4.15	Ono 2009; original data
Pisauridae	*Dolomedes reuniascar*	KPARA_00408	Afrotropic	Madagascar	Antsiranana	semi-aquatic	no web	6.19	23.39	2.76	original data

Pisauridae	*Dolomedes rotundus*	KPARA_00240	Afrotropic	Madagascar	Toamasina	semi-aquatic	no web	6.20	22.3	2.31	Yu and Kuntner 2024
Pisauridae	*Dolomedes saganus*	YKP-Ar0684	Palearctic	China	Fujian	semi-aquatic	no web	7.00	27.69	3.79	Tanikawa and Miyashita 2008
Pisauridae	*Dolomedes schauinslandi*	KPARA_NZ_DS-M1	Australasian	New Zealand	Rangatira Island	terrestrial	no web	9.73	30.3	3.76	Vink and Dupérré 2010; original data
Pisauridae	*Dolomedes scriptus*	KPARA_00118	Nearctic	USA	Kentucky	semi-aquatic	no web	7.25	31.67	4.46	original data
Pisauridae	*Dolomedes senilis*	KPARA_DS-2-2	Palearctic	Japan	Hokkaido	semi-aquatic	no web	7.00	22.08	2.92	Tanikawa 2012
Pisauridae	*Dolomedes silvicola*	KPARA_JP024-1	Palearctic	Japan	Kanagawa	terrestrial	no web	5.28	28.14	4.14	Tanikawa and Miyashita 2008
Pisauridae	*Dolomedes spathularis*	ZRCENT_61059	Indomalayan	Malaysia	Petaling	semi-aquatic	no web	7.65	26.87	2.79	original data
Pisauridae	*Dolomedes striatus*	FMNH_2857312	Nearctic	USA	Illinois	semi-aquatic	no web	*4.20*	*18.83*	*2.93*	original data
Pisauridae	*Dolomedes sulfureus*	KPARA_JP027	Palearctic	Japan	Kanagawa	terrestrial	no web	8.19	38.64	5.54	Tanikawa and Miyashita 2008; original data

Pisauridae	*Dolomedes tenebrosus*	KPARA_00100	Nearctic	USA	Kentucky	terrestrial	no web	8.68	37.62	4.33	original data
Pisauridae	*Dolomedes transfuga*	RMCA_245953	Afrotropic	Guinea	Selinngbala	semi-aquatic	no web	10.7	55.08	7.25	original data
Pisauridae	*Dolomedes triton*	KPARA_00115	Nearctic	Canada	Prince Edward Island	semi-aquatic	no web	6.10	22.67	2.64	original data
Pisauridae	*Dolomedes vittatus*	KPARA_00088	Nearctic	USA	Kentucky	semi-aquatic	no web	9.75	40.63	5.14	original data
Pisauridae	*Dolomedes yawatai*	KPARA_JP029-1	Indomalayan	Japan	Okinawa	semi-aquatic	no web	10.72	46.1	5.12	Ono 2002, original data
Pisauridae	*Euprosthenops australis*	KPARA_00577	Afrotropic	South Africa	Free State	terrestrial	web present	**5.89**	**40.72**	**4.48**	original data
Pisauridae	*Euprosthenopsis* sp.	KPARA_00624	Afrotropic	Madagascar	Toliara	terrestrial	web present	3.90	23.26	2.61	original data
Pisauridae	*Hala* sp.	KPARA_00149	Afrotropic	Madagascar	Antsiranana	terrestrial	no web	1.89	9.48	1.04	Jocqué 1994; original data
Pisauridae	*Hygropoda higenaga*	YKP-Ar1199	Indomalayan	Taiwan	Taitung	semi-aquatic	no web	3.55	38.92	8.42	Wang 1993
Pisauridae	*Hygropoda* MADsp.	KPARA_0	Afrotropic	Madagascar	Antsiranana	semi-	no web	3.10	31.38	5.19	original data

		0198				aquatic					
Pisauridae	*Maypacius bilineatus*	KPARA_0 0578	Afrotropic	South Africa	KwaZulu-Natal	terrestrial	no web	2.40	19.8	2.50	Strand 1908
Pisauridae	*Megadolomedes johndouglasi*	QM_S109 171	Australasian	Australia	Tasmania	semi-aquatic	no web	8.67	46.83	8.17	Raven and Hebron 2018
Pisauridae	*Nilus majungensis*	KPARA_0 0223	Afrotropic	Madagascar	Toamasina	semi-aquatic	no web	7.12	32.94	3.33	original data
Pisauridae	*Nilus phipsoni*	ABARA_ 01717	Afrotropic	Taiwan	Pingtung	semi-aquatic	no web	8.29	33.3	3.11	original data
Pisauridae	*Ornodolomedes* sp.	KPARA_ QMgift	Australasia	Australia	Queensland	terrestrial	no web	3.75	16.26	1.84	Raven and Hebron 2018
Pisauridae	*Paracladycnis vis*	KPARA_0 0176	Afrotropic	Madagascar	Antananarivo	terrestrial	no web	5.71	35.76	4.12	Silva and Sierwald 2013
Pisauridae	*Perenethis fascigera*	ABARA_ 01868	Indomalayan	Taiwan	Pingtung	terrestrial	no web	3.12	20.31	2.47	original data
Pisauridae	*Pisaura mirabilis*	KPARA_0 0040	Palearctic	Slovenia	Spodnje Prapreče	terrestrial	no web	3.39	18.75	2.29	Nadolny et al. 2012
Pisauridae	Pisauridae gen. MADsp.	KPARA_0 0138	Afrotropic	Madagascar	Antsiranana	terrestrial	no web	2.06	18.36	3.63	original data
Pisauridae	*Pisaurina mira*	FMNH_3	Nearctic	USA	Indiana	terrestrial	no web	5.26	25.11	2.71	original data

		195381									
Pisauridae	*Polyboea zonaformis*	KPARA_HK439	Indomalayan	China	Hong Kong	terrestrial	web present	2.60	20.4	2.5	Wang 1993
Pisauridae	*Qianlingula* cf. *turbinata*	YKP-Ar1265	Indomalayan	Taiwan	Hualian	semi-aquatic	no web	7.19	46.15	3.77	Zhang et al. 2004; original data
Pisauridae	*Rothus vittatus*	KPARA_00576	Afrotropic	South Africa	Western Cape	terrestrial	no web	3.26	21.84	3.19	Silva and Sierwald 2015; original data
Pisauridae	*Sphedanus quadrimaculatus*	YKP-Ar0320	Indomalayan	Malaysia	Sabah	terrestrial	web present	3.08	15.12	1.84	original data
Pisauridae	*Tallonia picta*	CASENT_9017992	Afrotropic	Madagascar	Antsiranana	unknown	unknown	4.45	25.47	2.59	Silva and Sierwald 2013
Pisauridae	*Tetragonophthalma vulpina*	BINCO_DRC_22_0258_12	Afrotropic	D. R. Congo	Tshuapa	terrestrial	web present	6.68	42.82	4.17	original data
Pisauridae	*Thaumasia velox*	MACN-Ar34778	Neotropic	Argentina	Corrientes	semi-aquatic	no web	6.31	26.72	2.94	Silva and Carico 2012; original data
Pisauridae	*Tolma* sp.	KPARA_0	Afrotropic	Madagascar	Antsiranana	terrestrial	no web	2.22	10.49	1.12	original data

		0141									
Oxyopidae	*Peucetia* MADsp.	ARA1147	Afrotropic	Madagascar	Toamasina	-	-	-	-	-	-
Psechridae	*Fecenia cylindrata*	ARA4196	Indomalayan	China	Yunnan	-	-	-	-	-	-
Psechridae	*Psechrus* sp.	KPARA_0 0641	Indomalayan	China	Yunnan	-	-	-	-	-	-
Thomisidae	*Xysticus* sp.	MACN-Ar43641	Palearctic	Slovenia	Ljubljana	-	-	-	-	-	-
Viridasiidae	*Viridasius* sp.	KPARA_0 0152	Afrotropic	Madagascar	Antsiranana	-	-	-	-	-	-
Zoropsidae	*Zoropsis spinimana*	KPARA_0 0635	Palearctic	Slovenia	Ljubljana	-	-	-	-	-	-

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TABLE 4. AIC comparisons among the *k*-state Markov models (Mk model, Pagel 1994; Lewis 2001) with different trait transition rates assumptions conducted on the 30 reduced taxon trees and the full taxon tree. ER: equal rates, ARD: all-rates-difference.

Data set	Trait	model	logL	AIC	ΔAIC
30 reduced taxon trees	lifestyle	ER	-21.115	44.230	3.932
		ARD	-18.971	41.941	1.643
		semi-aquatic to terrestrial	-19.149	40.298	0.000
		terrestrial to semi-aquatic	-25.661	53.321	13.023
	capture web	ER	-21.892	45.784	1.466
		ARD	-20.159	44.317	0.000
		no web to web present	-22.362	46.724	2.407
		web present to no web	-21.239	44.479	0.161
	Trait	**model**	**Average logL**	**Average AIC**	**ΔAIC**
Full taxon tree	lifestyle	ER	-43.226	88.452	2.403
		ARD	-41.793	87.587	1.537
		semi-aquatic to terrestrial	-42.025	86.049	0.000
		terrestrial to semi-aquatic	-63.244	128.488	42.438
	capture web	ER	-23.621	49.242	4.753
		ARD	-21.244	46.489	2.000
		no web to web present	-24.159	50.318	5.830
		web present to no web	-21.244	44.489	0.000

TABLE 5. Statistic tables of Monte Carlo Sampler for Multivariate Generalized Linear Mixed Models (MCMCglmm; Hadfield 2010) between lifestyles and carapace width, relative length of teg I, and relative length of tarsus I, showing the correlation between morphological traits and semi-aquatic versus terrestrial lifestyles. CW: carapace

width, L1: leg I length, T1: tarsus I length, 95HPD: 95% highest posterior density, pMCMC, twice the probabilities of the posterior values that are above or below zero.

Data set	Trait	Factor	Average post mean	Average 95HPD lower bound	Average 95HPD upper bound	Average effective samples	Average pMCMC
30 reduced taxon trees	CW	intercept	6.149	4.063	8.182	1510	**< 0.001**
	CW	life style: terrestrial	-2.408	-3.911	-0.858	1549	**0.014**
	L1/CW	intercept	5.792	4.064	7.483	1545	**< 0.001**
	L1/CW	life style: terrestrial	-0.049	-1.222	1.112	1535	0.812
	T1/L1	intercept	0.131	0.090	0.172	1518	**< 0.001**
	T1/L1	life style: terrestrial	0.005	-0.031	0.041	1498	0.789
	Trait	**Factor**	**Post mean**	**95HPD lower bound**	**95HPD upper bound**	**Effective samples**	**pMCMC**
full taxon tree	CW	intercept	5.451	3.131	7.769	1500	**< 0.001**
	CW	life style: terrestrial	-1.194	-2.210	-0.074	1500	**0.025**
	L1/CW	intercept	5.595	4.071	7.007	1636	**< 0.001**
	L1/CW	life style: terrestrial	0.263	-0.148	0.702	1500	0.231
	T1/L1	intercept	0.132	0.103	0.160	1500	**< 0.001**
	T1/L1	life style: terrestrial	0.002	-0.015	0.019	1500	0.803
	CW	intercept	7.821	5.196	9.878	1665	**< 0.001**

	CW	life style: terrestrial	-0.571	-2.007	0.546	1500	0.361
Dolomedes -only tree	L1/CW	intercept	4.037	3.200	4.736	1500	**< 0.001**
	L1/CW	life style: terrestrial	0.315	-0.106	0.759	1500	0.157
	T1/L1	intercept	0.124	0.092	0.156	1377	**< 0.001**
	T1/L1	life style: terrestrial	-0.001	-0.027	0.032	1500	0.944

1549