

Systematics and evolutionary history of raft and nursery-web spiders (Araneae: Dolomedidae and Pisauridae)

Kuang-Ping Yu^{1,2}  | Ren-Chung Cheng^{3,4} | Charles R. Haddad⁵ | Akio Tanikawa⁶ | Brogan L. Pett^{7,8} | Luis N. Piacentini⁹ | Ho Yin Yip¹⁰ | Yuya Suzuki¹¹ | Arnaud Henrard¹² | Christina J. Painting^{13,14} | Cor J. Vink¹⁵ | Eileen A. Hebets¹⁶ | Mark S. Harvey^{17,18} | Matjaž Kuntner^{1,2,19,20,21} 

Correspondence

Kuang-Ping Yu and Matjaž Kuntner,
Department of Organisms and
Ecosystems Research, National
Institute of Biology, Večna pot 121, 1000
Ljubljana, Slovenia.
Email: kuang-ping.yu@nib.si and
matjaz.kuntner@nib.si

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Abstract

Pisauridae are a global and heterogeneous assemblage of spider genera with diverse morphologies and lifestyles. So far, the monophyly of Pisauridae and the inclusion of fishing spiders (*Dolomedes*) in this family have not been thoroughly tested. Here, we amend the systematics and classification of these lineages within a UCE phylogenomic framework and through a detailed morphological reappraisal. For estimations of their evolutionary age, we perform and compare outcomes from two divergence estimation approaches, an a posteriori likelihood, and an a priori Bayesian. Phylogenies reject the monophyly of both Pisauridae and *Dolomedes*: (1) Focal Clade I groups true Pisauridae genera including *Pisaura*; (2) Focal Clade II contains *Blandinia* and is sister to Trechaleidae and Lycosidae; (3) Focal Clade III groups *Dolomedes*, *Megadolomedes*, and *Ornodolomedes*, and is sister to *Blandinia*, Trechaleidae, and Lycosidae. We therefore propose to delimit Pisauridae by removing Dolomedidae rank resurrected (including *Dolomedes*, *Bradystichus*, *Megadolomedes*, *Caledomedes*, *Mangromedes*, *Ornodolomedes*, and *Tasmomedes*) and *Blandinia incertae sedis*. Likelihood and Bayesian time calibration approaches yield comparable divergence estimations: Pisauridae origin is estimated at 29–40 Ma; *Blandinia* 21–34 Ma; Dolomedidae 10–17 Ma; *Dolomedes* 9–16 Ma. Reconstructions suggest that the evolution of terrestrial and web-building lifestyles from semi-aquatic ancestors in Pisauridae coincided with cooling and drying climates during the mid-Miocene, but this was not the case in the few recent cases of terrestrialization in *Dolomedes* species. This historic reconstruction illustrates how climatic changes, or rapid radiation, can drive life-style diversification.

Kuang-Ping Yu and Ren-Chung Cheng shared first authorship.

For affiliations refer to page 431.

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KEYWORDS

classification, climate change, divergence time estimation, *Dolomedes*, fishing spiders, lifestyle evolution, MCMCtree, RelTime

1 | INTRODUCTION

The spider family Pisauridae Simon, 1890, colloquially known as nursery-web spiders, is a global assemblage of taxa that currently contains 52 genera and 365 species (WSC, 2024). These taxa show diverse lifestyles and include terrestrial wandering and web-building species, as well as semi-aquatic wandering species (Figure 1; Table S1; see also Yu, Cheng, et al., 2024). As currently classified, Pisauridae is morphologically heterogeneous, lacking clear synapomorphies and a solid family diagnosis (see Magalhaes et al., 2020; Wunderlich, 2008). Although the family is well known for building nursery webs (Figure 1a) to protect their spiderlings, this behaviour is in fact shared with other taxa from a more inclusive superfamily Lycosoidea (Piacentini & Ramírez, 2019).

Among pisaurids that are well known to venture into aquatic habitats are fishing spiders belonging to the genus *Dolomedes* Latreille, 1804 (Figure 1e,n). This is a globally distributed genus with 105 species of large wandering spiders (WSC, 2024), many of which are popular study organisms in the research of semi-aquatic adaptations in arthropods, focusing among others on neurosensing of water ripples (Bleckmann et al., 1994; Bleckmann & Barth, 1984; Roland & Rovner, 1983; Suter, 2003), locomotion on water (Stratton et al., 2004; Suter, 2013; Suter & Gruenwald, 2000a, 2000b; Suter & Wildman, 1999), as well as the associated morphologies (Stratton et al., 2004; Stratton & Suter, 2009; Suter et al., 2004). Because of the prominence of species of *Dolomedes* in behavioural ecology (reviewed in Yu, Roithmair, et al., 2024), understanding their phylogeny and evolution is important for comparative studies. To

date, however, incomplete, unresolved, or conflicting phylogenies have hampered testing the phylogenetic affiliation of *Dolomedes* and the monophyly of Pisauridae (see Table 1).

The taxonomic history of *Dolomedes* and Pisauridae dates back to the very beginning of binomial nomenclature (see Supporting Information). Although the monophyly of Pisauridae and the affiliation of *Dolomedes* have been tested multiple times under different frameworks (see Supporting Information), none of the recent studies covered more than a quarter of the 52 pisaurid genera (Table 1). Limited taxon coverage has also led to an unclear topology within *Dolomedes*. So far, species phylogenies for *Dolomedes* have been regional and based on a few Sanger loci (Tanikawa, 2012; Vink & Dupérré, 2010; Yu & Kuntner, 2024). For example, a species-level phylogeny of *Dolomedes* used a single gene fragment for 13 Japanese species (Tanikawa, 2012) and failed to resolve all the nodes. Considering that Raven and Hebron's (2018) taxonomic review of Australian pisaurids increased the number of close relatives of *Dolomedes* from two to six genera with different degrees of intra- and intergeneric morphological variation, a better sampled *Dolomedes* phylogeny is also needed to test the boundaries of this diverse genus.

Here, we test the monophyly of *Dolomedes* and Pisauridae, the precise phylogenetic position of *Dolomedes* within Lycosoidea, and the *Dolomedes* species relationships. We use a phylogenomic framework where we refer to an original analysis of ultraconserved elements (UCE) data covering over half of the pisaurid genera and *Dolomedes* species (Yu, Cheng, et al., 2024). In this study, we interpret these findings in a holistic morphological reclassification at the family level.

FIGURE 1 A glimpse into the diversity of the genera currently in Pisauridae Simon, 1890: (a–e) A terrestrial lifestyle without a capture web. (a) Female of *Pisaura mirabilis* (Clerck, 1757) guarding her egg sac and nursery web. (b) A female *Hala* sp. (c) A male of an unknown Pisauridae genus from Madagascar. (d) A male *Perenethis fascigera* Bösenberg & Strand, 1906 (credit: Han-Po Chang). (e) A female *Dolomedes sulfureus* L. Koch, 1878. (f–j) A terrestrial lifestyle with a capture web. (f) Female of *Dendrolycosa* cf. *songi* (Zhang, 2000) standing on her sheet web (credit: Lok Ming Tang). (g) Female of *Sphedanus quadrimaculatus* Thorell, 1897 hanging under her three-dimensional web with retreat made of debris. (h) Juvenile of *Euprosthennopsis* sp. on its sheet web (credit: Matjaž Bedjanič). (i) Female of *Blandinia mahasoana* (Blandin, 1979) standing on her sheet web. (j) Female of *Polyboea zonaformis* (Wang, 1993) standing in the centre of her three-dimensional web (credit: Lok Ming Tang). (k) Female of *Caripetella madagascariensis* (Lenz, 1886) hanging under her sheet web. (l–p) A semi-aquatic lifestyle without a capture web. (l) A subadult female *Nilus phipsoni* (Pickard-Cambridge, 1897). (m) A female *Qianlingula* cf. *turbinata* Zhang et al., 2004. (n) Female of semi-aquatic *Dolomedes mizhoanus* Kishida, 1936 preying on a fish. (o) A female *Hygropoda higenaga* (Kishida, 1936). (p) A subadult male of *Thaumasia velox* (Simon, 1898b).



In order to place the phylogeny in an absolute evolutionary timeframe, we use two divergence estimation approaches, an a posteriori likelihood analysis using RelTime (Tamura et al., 2012, 2018; see Yu, Cheng, et al., 2024), and an a priori Bayesian analysis using MCMCtree (Yang, 2007).

2 | MATERIALS AND METHODS

2.1 | Phylogenomic topology

We used the ultraconserved elements (UCE; Faircloth et al., 2012) data set and the phylogenies of 28 pisaurid

TABLE 1 Monophyly of Pisauridae Simon, 1890 and the affiliation of *Dolomedes* Latreille, 1804 discussed and analysed in the literature.

Literature	Evidence	Monophyly of Pisauridae	Affiliation of <i>Dolomedes</i>	Number of genera discussed
Simon (1898a)	Eye arrangement	Yes	Dolomedae	33
Petrunkévitch (1928)	Eye arrangement	Yes	Thaumasiinae	after Simon (1898a)
Lehtinen (1967)	Morphological comparisons	No	Dolomedidae	16
Griswold (1993)	Morphological cladogram	Yes	Sister to <i>Pisaura</i>	2
Sierwald (1990)	Genital structure homology	Yes	Closely related to <i>Thalassius</i> (= <i>Nilus</i>)	55
Zhang et al. (2004)	Morphological cladogram	Yes	Sister to <i>Nilus</i>	9
Santos (2007)	Morphological cladogram	Yes	Sister to <i>Pisaurina</i>	8
Bayer and Schönhöfer (2013)	Multi-gene phylogeny	No	Sister to <i>Nilus</i>	3
Moradmand et al. (2014)	Multi-gene phylogeny	No	Sister to Thalassinae	2
Polotow et al. (2015)	Multi-evidence phylogeny	No	NA	3
Albo et al. (2017)	Multi-gene phylogeny	No	Separate clade, basal to Lycosoidea	5
Wheeler et al. (2017)	Multi-gene phylogeny	Yes	Sister to <i>Bradystichus</i> , basal pisaurid	9
Fernández et al. (2018)	Transcriptomic phylogeny	Yes	Sister to <i>Pisaurina</i>	2
Cheng and Piel (2018)	Transcriptomic phylogeny	Yes	Separate clade, basal pisaurid	4
Piacentini and Ramírez (2019)	Multi-gene phylogeny	Yes	Sister to <i>Bradystichus</i> , basal pisaurid	9
Kallal et al. (2021)	Transcriptomic phylogeny	Yes	Separate clade, basal pisaurid	5
Kulkarni et al. (2023)	UCE+ multi-gene phylogeny	No	Separate clade, sister to Lycosidae + Trechaleidae	13
Hazzi and Hormiga (2023)	Multi-gene phylogeny	No	Separate clade, sister to Lycosidae + Trechaleidae	7

genera and 53 *Dolomedes* morphospecies published in the sister research of this study (see Yu, Cheng, et al., 2024). The data sets contained UCE matrices aligned from loci with 75% (sparse matrix) and 95% (dense matrix) taxon completeness, and the phylogenies were reconstructed from these matrices using maximum likelihood (ML), Bayesian inference (BI), and multispecies coalescence (MSC) (for details, see Yu, Cheng, et al., 2024). To illustrate the phylogenetic results, we selected the maximum likelihood (ML) analysis of the partitioned sparse matrix from Yu, Cheng, et al., 2024 as the preferred tree representing Pisauridae and *Dolomedes* and mapped the statistic supports from all previous phylogenomic analyses onto this tree.

2.2 | Comparing a priori and a posteriori divergence time estimation

For an ultrametric tree to be used in their evolutionary analyses, Yu, Cheng, et al. (2024) performed a divergence dating analysis on the UCE matrix using RelTime (Tamura et al., 2012, 2018). They calibrated the phylogeny using three relatively reliable fossils with a relevant family affiliation: a crown lycosid, a stem thomisid, and a stem oxyopid (Yu, Cheng, et al., 2024). Since that paper was concerned more about relative divergences, it used the a posteriori likelihood analysis as described. To test whether RelTime yielded reliable absolute divergence times (see Beavan et al., 2020; Lozano-Fernandez et al., 2017), we here ran an a priori time calibration in a Bayesian framework. We used Phyluce v1.7.3 (Faircloth, 2016) to randomly select a UCE submatrix from Yu, Cheng, et al. (2024). On this submatrix, which contained 300 loci with 99% taxon completeness, we ran an a priori time calibration analysis using MCMCtree (Yang, 2007) within PAML 4.10 (Yang, 2007). We selected the ML topology Yu, Cheng, et al. (2024) generated from the dense matrix as the starting tree after removing the branch lengths. Calibration points were selected and set as in Yu, Cheng, et al. (2024) using MCMCtreeR (Puttick, 2019) in R 4.3.3 (R Core Team, 2024). Following the programme tutorial (dos Reis et al., 2017), we first estimated the average substitution rate per time unit as well as the length, gradient, and Hessian of each branch. With the above-estimated parameters, we ran divergence time dating in two independent runs, each with 500,000 generations sampled every 50 generations and with a 10% burn-in. We compared the results of the two runs in MCMCtreeR, using the script from Gutiérrez-Trejo et al. (2024), then plotted the results of both a posteriori and a priori divergence time analyses on the same chronogram.

2.3 | Morphological examination

We compared the morphological details of representatives of 35 known genera currently classified as Pisauridae (Tables S1 and S2). We dissected and cleaned female epigyna with potassium hydroxide (KOH) solution. We also expanded the male palps with the KOH solution for detailed comparisons. We examined and photographed the specimens under a Leica M205C stereomicroscope or a Keyence VHX7000 digital microscope. For investigations of the detailed genital structure of *Dolomedes*, we used an Axia™ ChemiSEM™ scanning electron microscope (SEM).

2.4 | Classification approaches

We employed the criteria proposed by Kuntner et al. (2023) in family-level classification. Briefly, in order to recognize an assemblage of taxa at the family level, they should be monophyletic, diagnosable, and with estimated clade ages comparable with other related families (Kuntner et al., 2023).

3 | RESULTS

3.1 | Phylogenetic relationships of raft- and nursery-web- spiders

All analyses, including the phylogenomic study from Yu, Cheng, et al. (2024) or the divergence dating presented here, reject the monophyly of Pisauridae as currently classified with high or full nodal supports (Figure 2). This family-level name refers to a paraphyletic assemblage of genera that fall into three clades, labelled as focal clades in this article (Figure 2; see Taxonomy): (1) Focal Clade I groups the majority of the genera classified in Pisauridae, and because it contains the type genus *Pisaura* Simon, 1886, this clade represents Pisauridae *sensu stricto*. Focal Clade I (Pisauridae) is sister to a taxon-rich clade containing all the taxa listed below; (2) Focal Clade II contains the monotypic *Blandinia* Tonini et al., 2016 from Madagascar. Because it is recovered as sister to Trechaleidae Simon, 1890 and Lycosidae Sundevall, 1833, *Blandinia* cannot be considered a pisaurid and is instead *incertae sedis*, pending better taxonomic resolution; (3) Focal Clade III contains *Dolomedes*, *Megadolomedes* Davies & Raven, 1980, and *Ornodolomedes* Raven & Hebron, 2018. This clade is sister to Focal Clade II, Trechaleidae, and Lycosidae (Figure 2). Considering the phylogenetic results, the topological stability, the strong clade supports, and our understanding of the morphology of *Dolomedes* and its relatives, detailed in the Taxonomy section below, we will from here on formally refer to the Focal Clade III as Dolomedidae Simon, 1876, colloquially

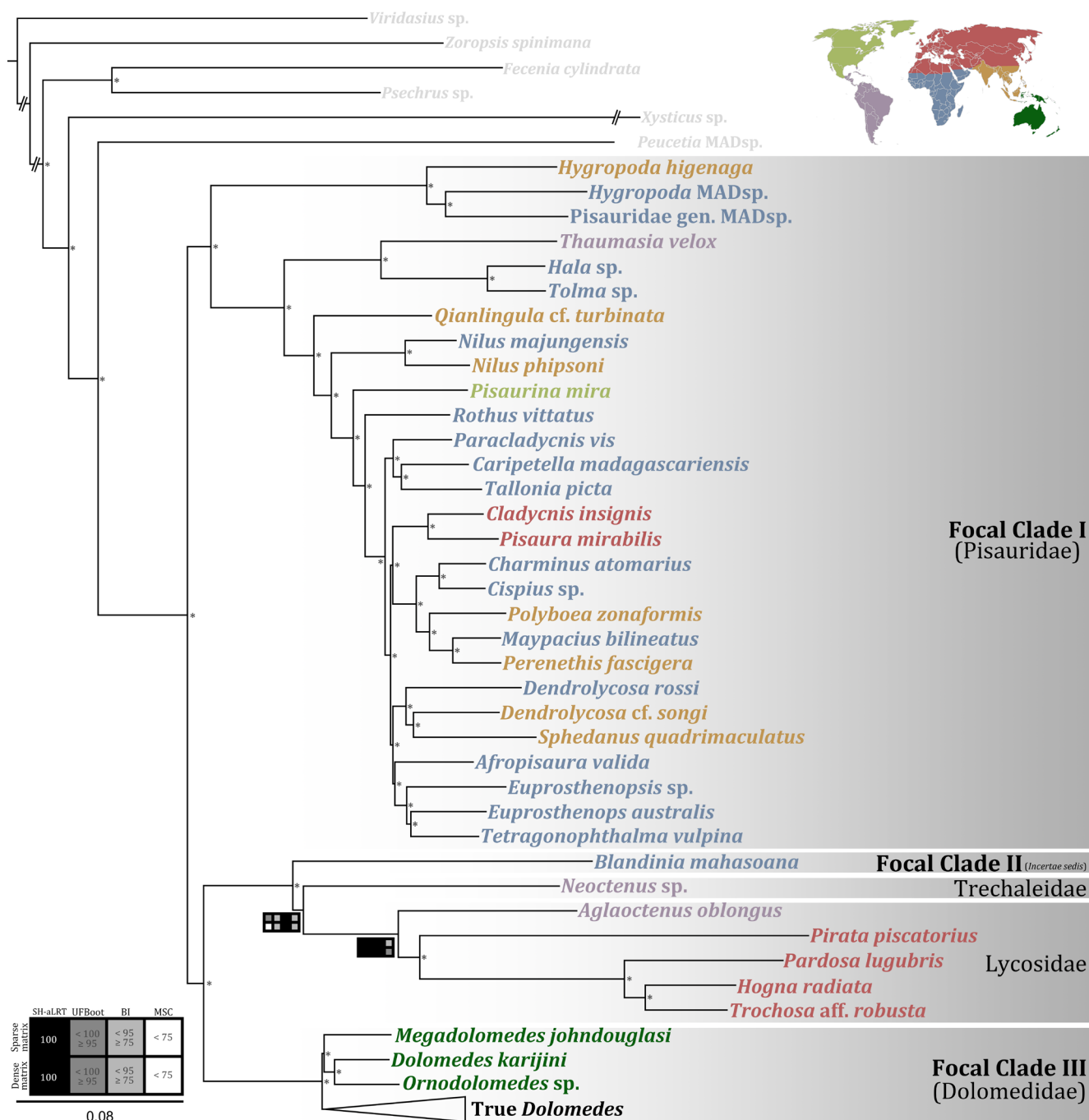


FIGURE 2 Maximum likelihood phylogeny of the three focal clades reconstructed from the sparse UCE matrix; nodal supports are labelled according to the legend at the bottom left, nodes with full supports are represented by “*”; each terminal is colour-coded by its biogeographic region according to the map (modified from Udvardy, 1975) at the top right with the outgroups in light grey. BI, Posterior probability (%) of Bayesian inference; MSC, Posterior probability (%) of multi-species coalescence; SH-aLRT, SH-like approximate likelihood ratio test (Guindon et al., 2010); UFboot, Ultrafast bootstrap (Hoang et al., 2017; Minh et al., 2013). See figure S2 in Yu, Cheng, et al. (2024) for the full branch lengths of the outgroups.

named raft spiders. We suggest the use of fishing spiders for *Dolomedes*.

Within Dolomedidae, we tested for the monophyly of *Dolomedes*. Strictly speaking, *Dolomedes* is not monophyletic. The majority of *Dolomedes* species, including the type species *D. fimbriatus* (Clerck, 1757), are in a

clade that represents true *Dolomedes*, but one species, *D. karijini* Raven & Hebron, 2018, is recovered within the sister clade that also contains *Ornodolomedes* and *Megadolomedes* (Figures 2 and 3). While the Afrotropical *Dolomedes* species are monophyletic within their biogeographic realm, other biogeographic realms do not

show strict species monophyly (Figure 3). For example, in addition to the distal Palearctic *Dolomedes* clade, other Palearctic species are found in the 'raptor' clade, which is sister to all other true *Dolomedes* (Figure 3). The Australasian species are not monophyletic, but the New Zealand species are (Figure 3). An Indomalayan clade groups some, but not all, species from this region, as many Indomalayan terminals are also part of the 'raptor' clade (Figure 3). Most Nearctic species are monophyletic, but *D. striatus* Giebel, 1869 is sister to the Palearctic clade (Figure 3).

Multispecies coalescence recovers three topological differences within *Dolomedes* (see figure S1 in Yu, Cheng, et al., 2024) from the preferred tree (Figure 3), 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 that two morphospecies, *D. cf. raptoroides* HK and *D. cf. raptoroides* VN, are not sister as they are in the preferred tree (Figure 3). Additionally, MSC has *D. yawatai* Ono, 2002 as sister to a clade with four *Dolomedes* morphospecies from Taiwan instead of nesting within that clade. MSC on the dense matrix suggests the Indomalayan clade as sister to a large clade including the Afrotropic and Holarctic *Dolomedes*. However, such topologies are poorly supported with their posterior probabilities (PP) between 0.6 and 0.9 (see figure S1 in Yu, Cheng, et al., 2024). 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 Figure 3).

3.2 | Divergence times of raft- and nursery-web-spiders

RelTime and MCMCtree (results in parentheses) yield comparable divergence times of the three focal clades (Figure 4; see also Supporting Information). 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 million years ago (Ma) (34–43 Ma), in the late Eocene to early Oligocene (Figure 4). The origin of Pisauridae (Focal Clade I), estimated between 29 and 35 Ma (31–40 Ma) (Figure 4), is the earliest of the three focal clades. The Oligocene–Miocene split of *Blandinia* (Focal Clade II) from Trechaleidae plus Lycosidae is estimated between 21 and 31 Ma (24–34 Ma) (Figure 4). Compared with the above two focal clades, the origin of Dolomedidae (Focal Clade III) is estimated to be more recent, between 10 and 15 Ma (12–17 Ma) in the mid-Miocene (Figure 4). The origin of *Dolomedes*

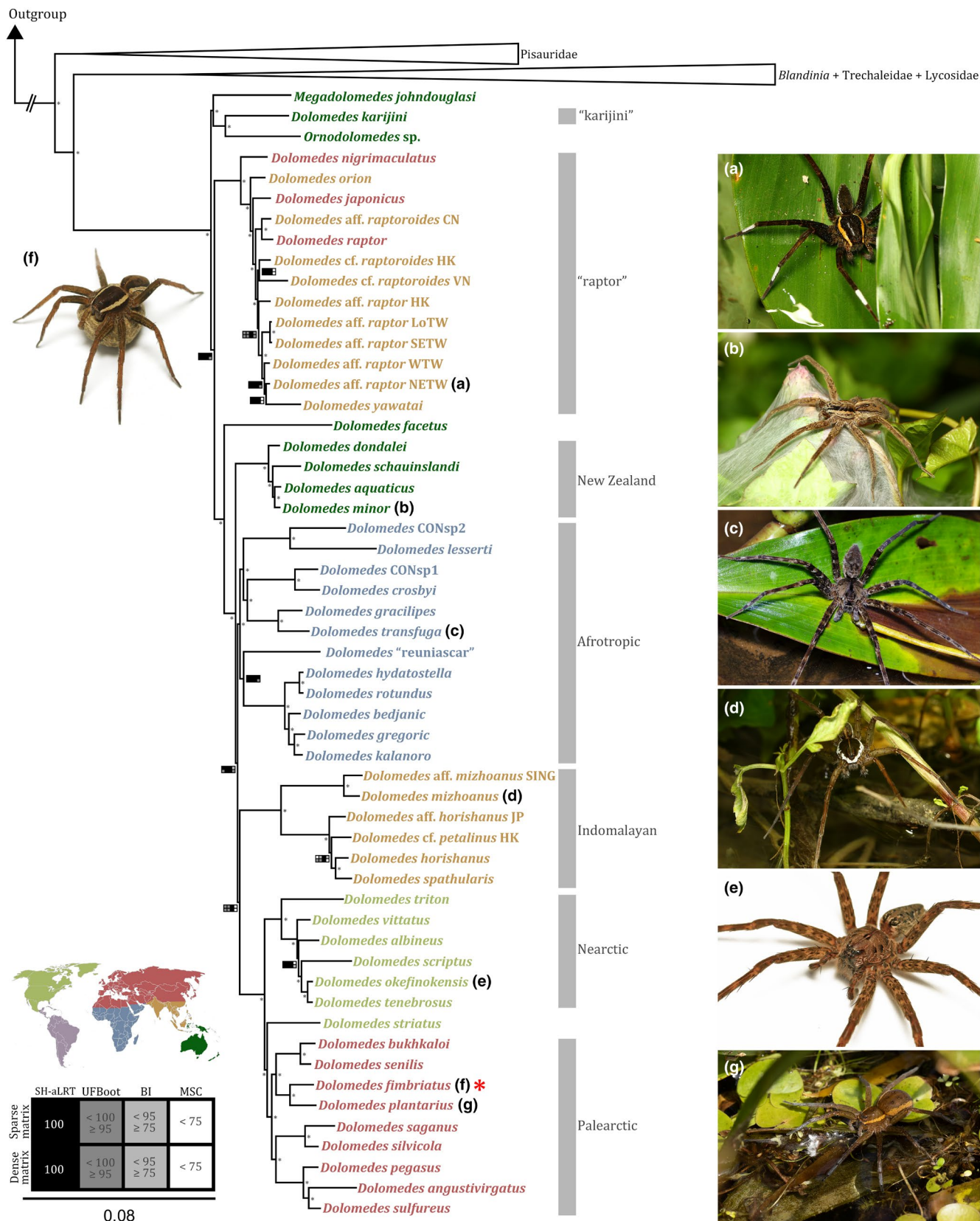
is estimated to be in the Miocene, between 9 and 15 Ma (11–16 Ma) (Figure 4), and since then, the clade has undergone a rapid diversification, with 95% confidence intervals and the highest posterior densities for final splits between species doublets lying between 0.2 Ma (0.3 Ma) (*D. hydatostella* Yu & Kuntner, 2024 and *D. rotundus* Yu & Kuntner, 2024 from Madagascar) and 9.2 Ma (8.9 Ma) (*D. lesserti* Roewer, 1955 from Benin and an unnamed *Dolomedes* species from D.R. Congo) (Figure 4). On the other hand, some species that group with larger clades in our phylogeny could plausibly be much older, for example, between 7.1 and 14.7 Ma (10.2–15 Ma) (*D. facetus* L. Koch, 1876 from Australia). However, this might also be due to the incomplete sampling of the Australasian species.

4 | DISCUSSION

4.1 | Dolomedidae: A step towards the redefinition of Pisauridae

We use 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 & Hormiga, 2023; Kulkarni et al., 2023). Our phylogenies are 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 & Hebron, 2018, *Mangromedes* Raven & Hebron, 2018, and *Tasmomedes* Raven & Hebron, 2018, were not available for inclusion with UCE data, additional evidence from morphological (Platnick & Forster, 1993; Raven & Hebron, 2018) and molecular (Kulkarni et al., 2023; Piacentini & Ramirez, 2019) studies both suggest that these genera fit our definition of Dolomedidae rather than Pisauridae. This updated classification of Dolomedidae is formalized in the Taxonomy as it fulfils our classification criteria: Dolomedidae is monophyletic, is well diagnosable, and shows divergences comparable with clade ages of the other families represented in the phylogeny (Figure 4).

The *Dolomedes* paraphyly hinges on one species, *D. karijini*, that is recovered as the sister of *Ornodolomedes*. Considering it is morphologically and ecologically distinct from *Ornodolomedes* (see Raven & Hebron, 2018), *D. karijini* 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* L. Koch, 1867 group with *Dolomedes* species from Australia and New Caledonia. Considering the incomplete taxon

sampling and the current ambiguity of species boundaries within *Dolomedes* (Tanikawa & Miyashita, 2008; Vink & Dupérré, 2010; Yu & Kuntner, 2024), it is unclear whether the entire species group, or only *D. karijini* should be

FIGURE 3 Maximum likelihood phylogeny of *Dolomedes* Latreille, 1804 and its relatives reconstructed from the sparse UCE matrix; nodal supports are labelled according to the legend at the bottom left, nodes with full supports are represented by “*”; each terminal is colour-coded by its biogeographic region according to the map at the bottom left; the type species, *Dolomedes fimbriatus*, is highlighted by a red “*”. (a–g) Habitus morphologies of the species labelled correspondingly in the phylogeny. (a) An unknown morphospecies of the ‘raptor’ clade. (b) A female *D. minor* Koch, 1876 guarding her nursery web. (c) A female *D. transfuga* Pocock, 1900. (d) A male *D. mizhoanus*. (e) A female *D. okefinokensis* Bishop, 1924. (f) A *D. fimbriatus* (Clerck, 1757) carrying her egg sac. (g) A female *D. plantarius* (Clerck, 1757) standing on macrophytes. BI, Posterior probability (%) of Bayesian inference; MSC, Posterior probability (%) of multispecies coalescence; SH-aLRT, SH-like approximate likelihood ratio test (Guindon et al., 2010); UFboot, Ultrafast bootstrap (Hoang et al., 2017; Minh et al., 2013).

elevated to a new genus. This decision will await future integrative taxonomic work with more Australasian species.

Our taxonomy is only the first step towards a better definition of Pisauridae and its subfamilies. Although our phylogenies reject the classification of *Blandinia* as a pisaurid, it is unclear whether this monotypic genus can be assigned to another existing family. Considering the conflicting Trechaleidae phylogenies (see Hazzi & Hormiga, 2023; Kulkarni et al., 2023; Piacentini & Ramírez, 2019) and our limited access to many trechaleid lineages, placing *Blandinia* in Trechaleidae *sensu lato* would also be unfounded. We therefore avoid creating a new family and hence treat *Blandinia* as *incertae sedis* until further evidence becomes available. Our phylogeny also partially rejects the currently used pisaurid subfamilial classifications, Thaumasinæ, Thalassinæ, and Pisaurinæ (Sierwald, 1990; Simon, 1898a), a problem that awaits more focused systematics and taxonomic efforts.

4.2 | RelTime and MCMCtree yield congruent results

We compared two approaches to divergence time estimation, the a posteriori and a priori methods implemented in RelTime (Yu, Cheng, et al., 2024) and MCMCtree (this article), respectively. Both types of analyses yielded largely overlapping results with interpretable confidence intervals and posterior densities (Figure 4), 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* Simon, 1899 (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 and 4–6 Ma; Heenan et al., 2010) and Okinawa Islands (6–10 Ma; Wang et al., 2014), respectively.

The estimated origin of Pisauridae (29–40 Ma) is consistent with the literature (25–75 Ma; see Piacentini & 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 with 25–50 Ma in Piacentini & Ramírez, 2019; Magalhaes et al., 2020). These differences could be due to the variation in taxon sampling, amount of molecular data, and different topologies. Despite the relatively recent origin of the crown Dolomedidae, it sits on a long stem, as the split between Dolomedidae and its sister clade is estimated to be between 30 and 40 Ma. While the shape of this chronogram could plausibly be an artefact of missing some critical or extinct taxa, we find the interpretation that this shape reflects a recent diversification of Dolomedidae with relatively rapid species radiations more likely, similar to the pattern in the extant segmented spiders (Xu et al., 2015). The incomplete reproductive isolation implied by the introgression between the sister species *Dolomedes minor* L. Koch, 1876 and *D. aquaticus* Goyen, 1888 (Lattimore et al., 2011) may reinforce the interpretation that *Dolomedes* underwent rapid species radiation.

4.3 | Did Miocene climate change drive lifestyle diversification?

Cenozoic climate oscillations may have shaped the evolution of terrestrial lifestyles and the presence of capture webs in Pisauridae. Combining the results of time calibration and ancestral state reconstructions (Yu, Cheng, et al., 2024), the three reversals from semi-aquatic to terrestrial lifestyles and the origin of capture webs in Pisauridae are all estimated between 10 and 20 Ma (Figure 4). This time interval matches the era when the Earth’s temperature and humidity reached the optima and started dropping (Figure 4) (Sun et al., 2020; Zachos et al., 2001). Considering (i) the extent to which semi-aquatic pisaurids are all distributed in the tropics, and (ii) the distant phylogenetic proximity among Palearctic and Nearctic pisaurids, one can hypothesize that the cooling and drying climate in the mid-Miocene may have driven the evolution from semi-aquatic to terrestrial lifestyles (see also Ye et al., 2018), which may have spurred the emergence of web-based foraging behaviours.

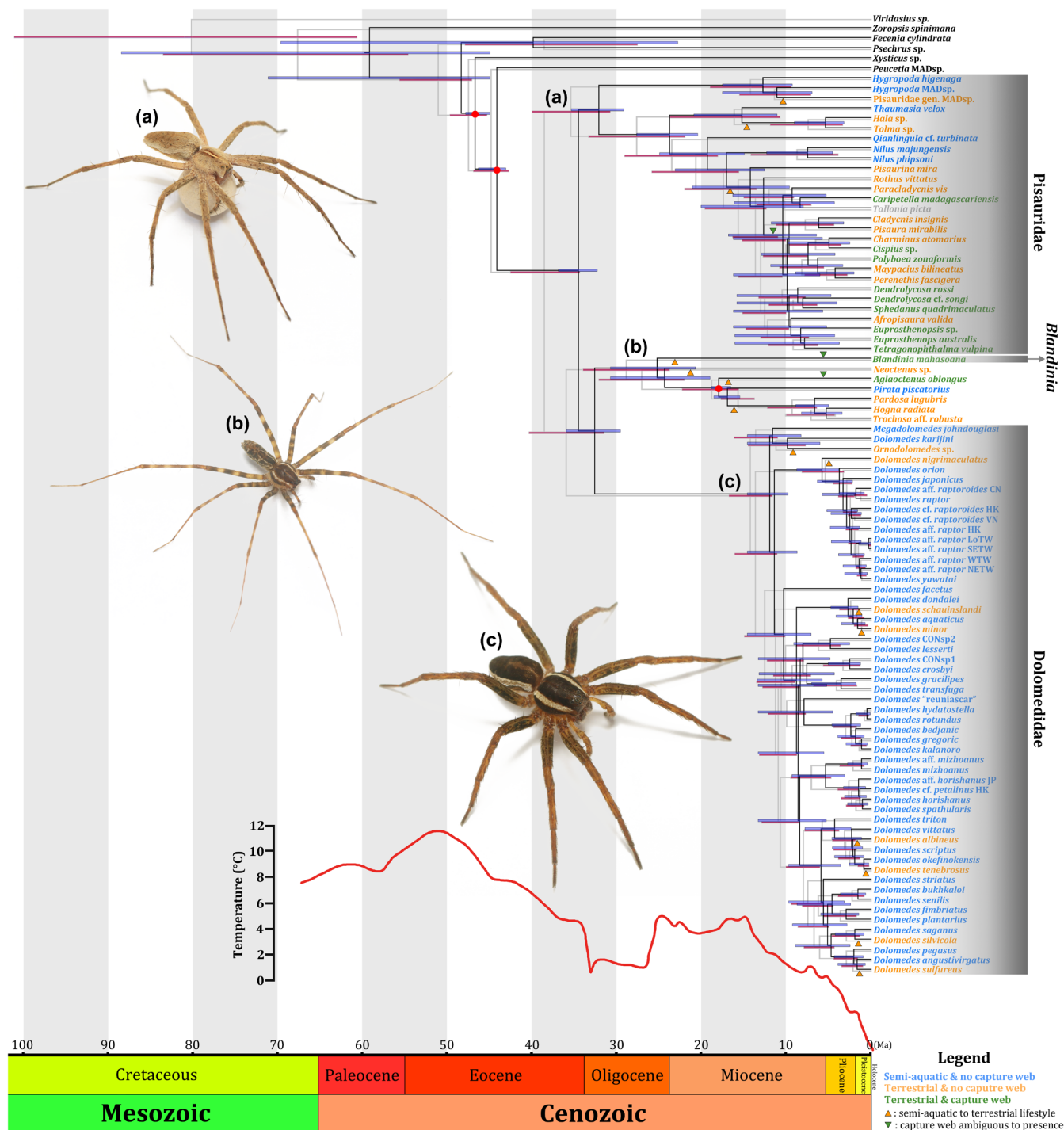


FIGURE 4 Phylogenies of all three focal clades (a–c) calibrated by RelTime (Tamura et al., 2012, 2018; black lines and blue bars) and MCMCtree (Yang, 2007; grey lines and red bars) with 95% confidence intervals and highest posterior densities of diversification time. (a) Pisauridae, represented by *Pisaura mirabilis*. (b) *Blandinia*, represented by *B. mahasoana*. (c) Dolomedidae Simon, 1876, represented by *Dolomedes fimbriatus*. Red dots represent the fossil calibration points. Terminals are colour-coded by their lifestyles as classified in Yu, Cheng, et al. (2024) and in Table S1: Blue, a semi-aquatic lifestyle without a capture web; orange, a terrestrial lifestyle without a capture web; green, a terrestrial lifestyle with a capture web; grey, unknown lifestyle; black, outgroups. Yellow triangles below branches and green inverse triangles above branches highlight the estimated evolutionary shifts from a semi-aquatic to a terrestrial lifestyle and the origins of a capture web, respectively, as hypothesized in Yu, Cheng, et al. (2024). A red curve of paleotemperature, modified from Zachos et al. (2001), shows the overlap between diversification and paleoclimate changes. Ma: Million years ago.

The terrestrial lifestyle in *Dolomedes* may have undergone a different evolutionary scheme compared with pisaurids, judging from the fact that the reversals to the terrestrial lifestyle in *Dolomedes* are phylogenetically derived and independent (Figure 4). Not unlike the semi-aquatic pisaurids, extant *Dolomedes* species of early branching lineages are distributed in subtropical to tropical Asia and Australasia, corresponding to regions that harboured humid refugia during the Miocene (Milne, 2006; Steinthorsdottir et al., 2021). However, the more northern distribution ranges of some terminals from the same lineages strongly suggest that *Dolomedes* species can cope more easily with cold climates than the semi-aquatic pisaurids. During Miocene climate oscillations, *Dolomedes* may therefore have taken over niches and habitats that became less hospitable to other large semi-aquatic spiders. This could perhaps explain their colonization of most continents, and the current biogeographic patterns of *Dolomedes* as the only large semi-aquatic spiders inhabiting temperate or even boreal regions of the Northern Hemisphere. This scenario, in addition to the observed cohabitation of certain terrestrial and semi-aquatic sister species of *Dolomedes* (Ono, 2009; Vink & Dupérré, 2010), suggests that the evolution of the terrestrial lifestyle in *Dolomedes* stems from episodes of rapid radiation and niche partitioning.

5 | TAXONOMY

5.1 | Taxonomic acts of this paper (see Supporting Information for details)

Family Dolomedidae Simon, 1876, family rank resurrected
Bradystichidae Simon, 1884, new synonymy
(Raft spiders)

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

Family Pisauridae Simon, 1890

Remark:

Based on our phylogeny (Figure 3), Pisauridae should be delimited to *exclude* the genera in Dolomedidae (above) as well as *Blandinia*.

AFFILIATIONS

¹Department of Organisms and Ecosystems Research, National Institute of Biology, Ljubljana, Slovenia

²Department of Biology, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia

³Department of Life Sciences, National Chung Hsing University, Taichung, Taiwan

⁴Research Center for Global Change Biology, National Chung Hsing University, Taichung, Taiwan

⁵Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa

⁶Laboratory of Biodiversity Science, School of Agriculture and Life Sciences, The University of Tokyo, Tokyo, Japan

⁷SpiDiverse, Biodiversity Inventory for Conservation (BINCO), Glabbeek, Belgium

⁸Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Penryn, Cornwall, UK

⁹Arachnology Division, Argentine Museum of Natural Science "Bernardino Rivadavia" CONICET, Buenos Aires, Argentina

¹⁰Discovery & Education Department, Ocean Park Hong Kong, Aberdeen, Hong Kong

¹¹Tokushima Prefectural Museum, Tokushima, Japan

¹²Royal Museum of Central Africa, Tervuren, Belgium

¹³Te Aka Mātua School of Science, University of Waikato, Hamilton, New Zealand

¹⁴Te Pūnaha Matatini, Centre of Research Excellence, Auckland, New Zealand

¹⁵Department of Pest-Management and Conservation, Lincoln University, Lincoln, New Zealand

¹⁶School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, Nebraska, USA

¹⁷Collections & Research, Western Australian Museum, Welshpool, Western Australia, Australia

¹⁸School of Biological Sciences, University of Western Australia, Crawley, Western Australia, Australia

¹⁹Jovan Hadži Institute of Biology, Research Centre of the Slovenian Academy of Sciences and Arts, Ljubljana, Slovenia

²⁰Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

²¹State Key Laboratory of Biocatalysis and Enzyme Engineering, and Centre for Behavioural Ecology and Evolution, School of Life Sciences, Hubei University, Wuhan, Hubei, China

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in DRYAD at <https://doi.org/10.5061/dryad.m63xsj4c6>.

ORCID

Kuang-Ping Yu  <https://orcid.org/0000-0002-7321-3977>
Matjaž Kuntner  <https://orcid.org/0000-0002-0057-2178>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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