Biogeography and eye size evolution of the ogre-faced spiders

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Net-casting spiders (Deinopidae) comprise a charismatic family with an enigmatic evolutionary history. There are 67 described species of deinopids, placed among three genera, Deinopis, Menneus, and Asianopis, that are distributed globally throughout the tropics and subtropics. Deinopis and Asianopis, the ogre-faced spiders, are best known for their giant light-capturing posterior median eyes (PME), whereas Menneus does not have enlarged PMEs. Molecular phylogenetic studies have revealed discordance between morphology and molecular data. We employed a character-rich ultra-conserved element (UCE) dataset and a taxon-rich cytochrome-oxidase I (COI) dataset to reconstruct a genus-level phylogeny of Deinopidae, aiming to investigate the group’s historical biogeography, and examine PME size evolution. Although the phylogenetic results support the monophyly of Menneus and the single reduction of PME size in deinopids, these data also show that Deinopis is not monophyletic. Consequently, we formally transfer 24 Deinopis species to Asianopis; the transfers comprise all of the African, Australian, South Pacific, and a subset of Central American and Mexican species. Following the divergence of Eastern and Western deinopids in the Cretaceous, Deinopis/Asianopis dispersed from Africa, through Asia and into Australia with its biogeographic history reflecting separation of Western Gondwana as well as long-distance dispersal events.

Once characterized as rare1, the net-casting spiders (family: Deinopidae; C.L. Koch, 1850) are cryptic, challenging to collect, and historically under-sampled and understudied. Living deep in understory habitats throughout tropical and subtropical regions2, deinopids were seldom collected3 and their perceived rarity is likely due to inattention and their unusual habits. Therefore, despite being charismatic spiders admired by most arachnologists, the difficulty in sampling them has resulted in very poor knowledge of the group’s evolutionary history. Deinopids, like the majority of web-spinning spiders, are sit-and-wait predators; however, they have a unique hunting strategy. Instead of sitting in their web, these spiders employ a modified orb web3 that they manipulate forward strike, extending their webs with their legs and then envelope their prey, rendering them immobile1,4–7. They also are capable of a backward strike detecting vibrations of flying prey, hence are not entirely reliant on their enlarged eyes for prey capture7.

Historically, phylogenetic analyses based on morphology have divided the family into two genera: Deinopis, the ogre-faced spiders, aptly named for their massive posterior median eyes (PMEs), and Menneus, the humpback spiders1. Both genera share the unique net-casting hunting strategy, yet only Deinopis species have distinctively enlarged PMEs. Eye size, function, orientation, and visual field overlap all contribute to how spiders perceive visual signals. While some spiders have visual fields that span 360°8, the spider optical system is highly diversified across taxa and typically aids in prey recognition, hunting, predator avoidance, mating, and courtship9–11. There are two eye types, the principal eyes (typically three pairs), which capture light, and a pair of eyes (the PMEs) which are resolution-based10,12. In deinopids, the PMEs are forward-facing with low visual acuity and are primarily responsible for detecting motion10. Remarkably, Deinopis PMEs are the largest simple eyes of any arthropod and are 2000 × more sensitive to light than human photoreceptors13. They are a particularly important feature that enables visual hunting at night in low-light conditions14. Although other characters differentiate the two nominal genera, including abdominal tubercles, genitalic features, and their geographic distributions, deinopids have been notoriously difficult to diagnose based on somatic characters alone, particularly to species level1.

Molecular phylogenetic treatments of Deinopidae have focused on species-level relationships within Deinopis16 and a newly described genus in Asia, Asianopis16, formerly Deinopis. Molecular data revealed that Eastern Hemisphere Deinopis are more closely related to Menneus from South Africa than to Western Hemisphere

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Deinopis, Blest et al. postulated that Menneus PMEs were a plausible ancestral form of the enlarged Deinopis PMEs. Deinopis paraplyphy contradicts a morphology-based phylogeny of deinopids, and foments questions: did deinopids gain their large PMEs within the clade, or ancestrally followed by subsequent loss, and when did this shift in PME size occur? Furthermore, did this shift in PME size occur once or multiple times across the evolutionary history of deinopids? Eye size reductions and even complete eye loss are typical in troglo-morphic organisms, including crustaceans, fish, blind mole rats, beetles, and spiders, where, in eternal darkness, energetically costly eyes may no longer offer fitness benefits. Troglo-morphic arthropods have been useful systems for studying the evolution and genetic underpinnings and regulation of eye size; however, in arachnids, the origins, development, and evolution of eye size remains largely unexplored. Alternatively, large PMEs could have evolved multiple times in parallel in deinopids. While energetically costly to maintain, large eye size has been associated with enhanced survival, fitness, and prey capture in vertebrates and invertebrates. Trait evolution must be considered across geologic time scales in order to better understand macroevolutionary patterns. Teasing apart the role of vicariance—the geographic separation of populations over time leading to divergent species—from long-distance, often overwater, dispersal (long-distance dispersal—LDD) in generating species distributions is at the center of biogeographic studies. Rigorous methods and model comparison frameworks have allowed researchers to explicitly test dispersal hypotheses. Disjunct distributions of Southern Hemisphere taxa have largely been attributed to vicariance driven by the break-up of Gondwana, the southern portion of Pangaea, in the Mesozoic. Deinopids were present on Gondwana prior to the break-up of the supercontinent, with the separation of Africa and South America generating the Eastern and Western Hemisphere deinopid clades. Both vicariance and LDD have been important in shaping the distribution of deinopids in the Western Hemisphere. Vicariance and LDD have also shaped the distributions of deinopids across the Eastern Hemisphere; however, the timing of this dispersal has not yet been extensively tested. Eastern Hemisphere deinopids contain both large-eyed Deinopis and Asianopis, and they are distributed throughout South Africa, Madagascar, Southeastern Asia,Indomalaya, and Australia. Because the Chamberland et al. molecular phylogeny of Menneus only contained species from South Africa, we have yet to ascertain when and where Menneus hypothesized eye size reduction, or Deinopis and Asianopis eye size increase, evolved. Did this evolutionary shift in eye size occur on the same continent and then the taxa dispersed (Menneus is monophyletic; trait conservatism) or did these shifts occur multiple times on different continents (Menneus is polyphyletic; trait convergence/parallel evolution) (Fig. 1)? With the new Menneus and Deinopis specimens from Australia, we were able to more thoroughly test the historical biogeography of Eastern Hemisphere deinopids, while exploring the evolution of PME size across geographic time scales.

In the study, we have integrated a taxon-rich COI dataset with a locus-rich UCE dataset to infer phylogenetic relationships within the family Deinopidae and explicitly test the monophyly of Menneus, Asianopis, and Deinopis. We expanded taxon sampling beyond Chamberland et al. to include Menneus specimens from South Africa and Australia and Deinopis from Australia, South Africa, Taiwan, Madagascar, and Mexico (Fig. 2). Specifically, we seek to infer the first genus-level phylogeny of the family and explicitly evaluate the evolution of eye reduction in Menneus. We tested the hypotheses that the ‘regular’ sized PMEs of Menneus either (1) represent an ancestral state, (2) evolved once from a common ancestor shared with Deinopis that then dispersed to other continents, or (3) arose independently from Deinopis in South Africa and Australia. Finally, we examine the ancient Gondwana biogeographic history of Deinopidae within the context of the newly devised phylogenetic hypothesis.

Results
Phylogenetics. The taxon-rich cytochrome-oxidase I (COI) dataset comprised 258 deinopids and 4 Uloborididae outgroup individuals. Phylogenetic analysis of the COI dataset yielded weak nodal support for a number of important clades, including the placement of Menneus. To resolve the ambiguous phyletogenetic relationships, we generated UCES for 40 deinopid individuals across all major clades. We found strong support for Menneus monophyly and Deinopis paraplyphy with the UCE and UCE + COI concatenated datasets (Figs. 3, 4; Table 1). Although the COI-only analyses did not support the monophyly of Menneus, nodal support was low (Supplementary Fig. S2). Furthermore, the tree topology tests on the UCE dataset supported the unconstrained tree, with Menneus monophyletic and Deinopis and Asianopis both paraphyletic, and rejected all four alternative tree topology hypotheses (see “Methods”; Table 1; Supplementary Table S1).

We found strong support for Eastern and a Western Hemisphere deinopid clades across all phylogenetic analyses (Figs. 3, 4). The Western Hemisphere clade contained a Caribbean clade nested within a South and Central American grade, which was consistent with the phylogeny from Chamberland et al. There were nine nominal and nine putative species nested within the Eastern Hemisphere clade, including: three Menneus species from South Africa and three from Australia; two Deinopis species from Madagascar, three from South Africa, three from Australia, and at least one from Mexico; and five Asianopis species, including an undescribed Asianopis species from Taiwan (Fig. 3). The relationships of nominal genera differed between the COI only analyses and the analyses that contained UCE data; however, bootstrap support at these nodes were low and were most likely the result of using a single mitochondrial gene. The addition of the UCE backbone to the COI dataset resulted in higher bootstrap support at the nodes. Thus, for all subsequent inferences and interpretations, we only considered the UCE only and UCE + COI phylogenies. The Eastern Hemisphere deinopid clade contained Menneus, Asianopis, and a paraphyletic Eastern Hemisphere Deinopis (Fig. 3). African, Australian, and Malagasy Deinopis were each monophyletic. We found D. cylindrica and an undescribed species, D. sp Hell’s Gates within an African clade. There were also two undescribed species within the Malagasy clade, D. sp Perinet and D. sp Andasibe-Mantadia. Finally, all phylogenetic analyses indicated three Deinopis clades in Australia, including D. subatra in Eastern Australia, D. unicolor in Western Australia, and an undescribed species in Western Australia (Figs. 3, 4).
There is a well-supported relationship of a group of Mexican *Deinopis* sister to South African *Deinopis* (Fig. 3; Supplementary Figs. S3 and S4), thus supporting at least one Mexican group in the Eastern Hemisphere *Deinopis* + *Asianopis* clade. Individuals from this clade share morphological traits that characterize Eastern Hemisphere *Deinopis* and *Asianopis*, including bulky (as opposed elongated and narrow) abdomens. A second Mexican clade was sister to the entire Eastern *Deinopis* + *Asianopis* clade; however, this result was weakly supported and these individuals were represented by COI data only (Supplementary Fig. S5).
Within *Asianopis*, we recovered UCE data for *A. wangi* and *A. wuchoai*. *A. wangi*, *A. wuchoai*, *A. zhuang-haoyun*, and *A. sp* from Taiwan all formed a clade sister to Australian *Deinopis*. *Asianopis* was paraphyletic in the UCE + COI phylogenetic inference with *A. liukuensis* sister to an Australian *Deinopis* + *Asianopis* clade. We were unable to recover UCEs for *A. liukuensis*; however, the COI only and COI + UCE concatenated phylogenetic reconstructions nested Australian *Deinopis* within the *Asianopis* clade. The *A. liukuensis* clade comprised specimens from China and India from Lin et al.¹⁶ and one specimen from Taiwan from the current dataset. Still, in all analyses, *Asianopis* (excluding *A. liukuensis*) was sister to Australian *Deinopis*.

Both the UCE only and COI + UCE analyses supported *Menneus* as monophyletic and sister to Eastern Hemisphere *Deinopis* + *Asianopis* clade. Both African and Australian *Menneus* were reciprocally monophyletic with three putative species in each geographic clade. We recovered UCEs for *M. camelus* and an undescribed species of *Menneus* from Africa, but only COI data for *M. capensis*.

**Divergence time estimates and biogeography.** Eastern and Western Hemisphere deinopids diverged in the lower Cretaceous and had an ancestral range in Africa + Australia + Asia (Fig. 4, Table 1). Following a vicariant divergence of Eastern and Western deinopids, *Menneus* diverged from the rest of the Eastern hemisphere deinopids generating a sympatric distribution of South African *Menneus* and *Deinopis* (Fig. 4). These vicariant and sympatric divergences generated three distinct clades: Western Hemisphere *Deinopis*, Eastern Hemisphere *Deinopis* + *Asianopis*, and *Menneus*.

Results from the biogeographic analyses supported LDD and vicariant divergences within Eastern Hemisphere *Deinopis* + *Asianopis* (Fig. 4). There are two Mexican deinopid clades that diverge from the South African *Deinopis*, one in the Upper Cretaceous and a second in the Eocene. In the absence of UCE data for the earlier diverging Mexican clade, the mechanism and direction of the dispersal was uncertain. Following the divergence of Mexican and South African *Deinopis*, there were two subsequent vicariant divergences: (1) African and Malagasy *Deinopis* diverged, (2) Malagasy *Deinopis* diverged from India + Asian *Asianopis*. Finally, there was a single LDD event from Asia to Australia resulting in the Australian *Deinopis* clade (Fig. 4). The 95% highest posterior density (HPD) varied widely across nodes, and is likely a consequence of having only one fossil to date the phylogeny (Table 1, Fig. S5).

**Ancestral state reconstruction.** There was a single shift in PME size, from large to small, in Deinopidae at the point of *Menneus* diversification (Fig. 5a–c, Supplementary Fig. S7). PME size was highly conserved and had a strong phylogenetic signal estimated D (~ 2.11). The average PME diameter (scaled to carapace width at the PLEs) and total ocular distance of adult females were significantly larger for *Deinopis* and *Asianopis* compared to *Menneus* (Fig. 5; Supplementary Fig. S8). The tests of PME/carapace ratio and raw averages for the Mann–Whitney non-parametric test of mean difference between large and typical size PMEs were both significant p < 0.0001. In the phylogenetic principal component analysis (pPCA), the first principal component (PC) (PCI, 90.2% of the variance) was strongly affected by carapace measurements: length (~ 0.983), width at widest point (~ 0.963), width at PLE (~ 0.934). The second PC (PC2, 4.3% of the variance), with a negative loading on PME diameter (~ 0.469) and PME row width (~ 0.410) and positive loadings on anterior median eye (AME...
row width (+0.214) and carapace length (+0.163) (Supplementary Table S2). The directionality of the vectors in the biplots are close together, indicating these traits are highly positively correlated (Fig. 5d). PC1 reflected body size whereas PC2 reflected PME and AME size and eye row width; however, while the three genera generally clustered in the pPCA, the combination of morphological characters used did not strongly differentiate the three genera. There was no significant difference between PME size and total ocular distance between Deinopis and Asianopis; however, Menneus PMEs and total ocular distances were significantly smaller (Fig. 5e,f). Average AME size was highest in Menneus, although this was not significant (Fig. 5g).

**Discussion**

**Monophyly of Menneus and evidence for secondary loss of enlarged PME.** Phylogenetic data (UCE and UCE + COI datasets) strongly support the monophyly of Menneus, whereas Deinopis and Asianopis are rendered paraphyletic (Figs. 3, 4). These findings contradict the prevailing taxonomic hypothesis of the genus Deinopis (MacLeay 1839), as well as the more recently proposed new genus Asianopis\(^{16}\). Instead, all analyses support a deep divergence between Western Hemisphere Deinopis and Eastern Hemisphere deinopids (Deinopis + Asianopis), and the UCE and UCE + COI phylogenies support divergence between Menneus and Eastern Hemisphere Deinopis. Recent taxonomic studies have transferred a number of the Asian Deinopis species into Asianopis\(^{16,55,56}\), however, Australian and Malagasy Deinopis have yet to be moved into Asianopis. Based on the
geographic and taxonomic coverage of the family in this study, including the deep divergences between the Eastern Hemisphere *Deinopis* + *Asianopis* clade, the *Menneus* clade, and the paraphyly of *Deinopis* with respect to *Asianopis*, we propose the transfer (see Taxonomic Section below) of the Eastern Hemisphere *Deinopis* into *Asianopis* Lin et al.56, thus retaining the three genera within Deinopidae: *Deinopis* in the Western Hemisphere, *Asianopis* in the Eastern Hemisphere, and *Menneus* (Simon 1876). Based on the phylogenetic hypothesis, we also propose the transfer of a number of Central American and Mexican *Deinopis* to *Asianopis*. Although these results highlight the need for further taxonomic treatment of the family and the formulation of a new diagnosis of *Asianopis*, we see no other working alternative that would adequately reconcile these phylogenetic results with the current taxonomy. That is, considering *Asianopis* and *Menneus* as junior synonyms of *Deinopis* would fail to appropriately acknowledge the family’s phylogenetic structure, complex and worldwide biogeography.

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**Table 1.** Divergence times and average marginal likelihoods and 95% HPD of deinopids based on UCE + COI concatenated MCC phylogeny.

| Major divergences | Age (Ma) | lower 95% HBD | upper 95% HBD |
|-------------------|----------|---------------|---------------|
| Deinopidae diverges from Uloboridae | 127.74 | 57.83 | 209.49 |
| *Menneus* diverges from *Asianopis* | 97.67 | 46.53 | 142.13 |
| Australian *Menneus* diverges from African *Menneus* | 56.42 | 24.22 | 94.35 |
| South African *Asianopis* diverges from Malagasy + Australian + Asian *Asianopis* | 75.46 | 35.34 | 114.26 |
| Malagasy *Asianopis* diverges from Australian + Asian *Asianopis* | 65.24 | 30.13 | 111.08 |
| *A. luikenisis* (India, China, Taiwan) diverges from Australian + Asian *Asianopis* | 49.17 | 21.76 | 80.17 |
| Asian *Asianopis* diverges from Australian *Asianopis* | 34.98 | 14.91 | 59.9 |
| South American *Deinopis* diverges from Caribbean *Deinopis* | 52.46 | 23.71 | 84.51 |

**Crown ages**

| Deinopidae | 105.9 | 50.75 | 150.92 |
| *Asianopis* (and Eastern Hemisphere *Deinopis*) clade | 86.73 | 41.03 | 129.45 |
| *Menneus* | 56.42 | 24.22 | 94.35 |
| *Deinopis* (Western Hemisphere *Deinopis*) clade | 87.01 | 40.7 | 131.5 |
| Caribbean *Deinopis* clade | 30.26 | 12.88 | 52.68 |

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**Figure 4.** Dated phylogeny inferred using mcmcTREE. Pie charts are colored by geographic range.
remarkable morphological divergence, and lineage divergence over major evolutionary time scales. The error bars around all major divergences are large, which is likely due to limited data and the use of a single fossil and broad priors to date the phylogeny. Still, major divergences are consistent with the previously published dated phylogeny of deinopids 15.

We found support for a single reduction of PME size in deinopids (Fig. 5a, Supplementary Figs. S7, S9), indicating enlarged PMEs were an ancestral deinopid trait with subsequent size reduction in 15. Although it has been postulated that Deinopis species evolved large PMEs through adaptation to hunt exclusively at night, leaving Menneus to hunt at dusk and twilight, empirical testing of this hypothesis has been limited to two Australian species: 15. Extensive field observations indicate that Deinopis and Menneus hunt at the same time in low-light conditions (pers. obsv.). The observation that both genera are hunting at the same time and in the same locality, using the same hunting strategy, raises the question—what are the potential ecological shifts and evolutionary tradeoffs driving morphological divergence? The reduction in Menneus eyes size could be interpreted as regressive evolution. Regressive evolution, the loss or reduction of non-functional, formally adaptive characters, has been repeatedly observed in the eyes of subterranean 23,58 and cave dwelling organisms 59, animals of the deep ocean, and among species that make the switch from diurnal to nocturnal habitats 60–62. Alternatively, although PME size are reduced in Menneus, they are not non-functional. Analyses of the anatomical structures have indicated Deinopis PMEs are more sensitive than Menneus 17; however the extent of the visual sensitivity between the two genera remain largely unknown and understudied.

Among organisms where regressive evolution has been observed, there are three primary, not mutually exclusive, hypotheses that seek to explain character reduction: (1) relaxed selection or neutral mutations—the relaxation of selection leading to reduction (e.g. loss of eyes, reduction of eye size) 63–65; (2) natural selection, in which reduced visual structures or the absence of eyes are advantageous 66–68; (3) indirect selection, pleiotropy, or ‘genetic hitchhiking’, in which the gene related to trait reduction is linked to other adaptive trait(s) (e.g. olfaction or taste) 29,69–71. D. spinosa has been shown to use auditory cues to capture their prey 7. Future studies could, for example, explore whether Menneus has evolved morphological and/or behavioral characters that are advantageous for capturing aerial prey (e.g. additional sensitive vibratory sensors such as trichobothria). Furthermore, in D. spinosa, individuals use their large eyes to hunt cursorial prey, which ultimately increases their dietary breadth 15; however, enlarged PMEs are metabolically costly. Stafstrom et al. 7 found that there was a potential tradeoff between brain size and PME size. Deinopis PMEs are more complex 13,73 and twice as sensitive compared to Menneus PMEs 15. We postulate that relaxed selection in environments where such eyes do not offer

Figure 5. Summary of eye size data. (a) MCC phylogeny with branch width representing the log of PME to carapace ratio. The size of the dots represents raw eye diameter (mm) and are colored by eye type: PME (yellow), AME (bluish green), PLE (blue), ALE (yellowish green). (b) A. subrufa and (c) M. sp Gurragawee with eyes colored by type- also represented in dot phylogeny. (d) pPCA biplot of deinopid genus clusters (n = 29) based on carapace and eye dimensions. Clades, boxplots, and pPCA are colored by genus: Asianopis (magenta), Deinopis (orange); Menneus (purple). Boxplots represent (e) PME diameter scaled to carapace width, (f) total ocular distance, and (g) AME scaled to carapace width.
major fitness benefits may explain this hypothesized secondary loss. Explicit tests of differential time and mode of hunting and evaluation of the underlying genetics of phenotypic differences may help tease apart potential evolutionary mechanisms. Finally, we propose an alternative hypothesis in which *Menneus* have far more sensitive PMEs than spiders with similarly sized eyes. If there was strong selection for increased eye size, neural connections, and light detection mechanisms in *Deinopis*, an energy cost could be spared by reducing eye size but retaining the high sensitivity. In that case there is a secondary reduction in eye size, but not, a reversal to the ancestral spider condition. Future detailed studies on receptor function, light sensitive cells, and visual/neural system communication could find that taking that advanced eye and making it smaller in *Menneus* would be advantageous even with certain anatomical simplifications from *Deinopis*. Deinopids have tremendous potential as a unique system for testing these alternative hypotheses and for studying visual evolution.

**Early Gondwanan vicariance followed by long-distance dispersals.** The disjunct geographic distributions of deinopids can be attributed to Upper Cretaceous vicariance during the breakup of West Gondwana, followed by subsequent transoceanic dispersal events. Initially formed around 500 Ma, Gondwana, the southern portion of the supercontinent Pangaea, began breaking away in the Middle Jurassic around 170 Ma \(^{74-77}\). However, the continents did not all break apart in succession. Instead, continents were simultaneously separating, with phases of these overlapping divergent events lasting tens of millions of years. After the initial separation, land bridges persisted between continental masses, providing passageways for biotic exchange \(^{78}\). Even amongst with phases of these overlapping divergent events lasting tens of millions of years. After the initial separation, land bridges persisted between continental masses, providing passageways for biotic exchange \(^{78}\). Even amongst

**Dispersal into Asia and Australia.** With a largely tropical and sub-tropical range, deinopids do not follow the typical anti-equatorial distributions across the Southern Hemisphere found in many Gondwanan lineages \(^{79-93}\); nonetheless, vestiges of the ancient Gondwanan connections are still reflected in the biogeographic history of deinopids. Following the divergence from *Menneus*, Eastern Hemisphere *Deinopis/Asianopis* dispersed from South Africa to Madagascar where they subsequently spread into Asia. The *Deinopis/Asianopis* lineage dispersed and diversified throughout Asia, with later dispersal to Australia via Indonesia. The timing of the divergences and biogeographic analyses suggest that *Deinopis* may have arrived in Asia from India after India collided with Southeast Asia in the Eocene (Out of India hypothesis). The duration of the hypothesized Indo-Madagascar landmass is debated. These may have separated as early as 130–125 Ma, but remained connected to India until around 84 Ma \(^{94,95}\) after which it is thought that fracture zones, plateaus, periodically emerged and facilitated stepping stone dispersal between Madagascar and India \(^{96}\). Such hypothesized stepping stone dispersal from Africa into Asia via India and Madagascar has been found in taxa with low vagility \(^{97-99}\). Alternatively, *Deinopis* could have dispersed through Northern Africa and Eurasia followed by subsequent extinction similar to sand scorpions \(^{100}\); however, our molecular phylogeny shows that the Madagascar clade is more closely related to Asia and India than Africa, consistent with the Indo-Madagascar plus stepping stone hypothesis. Because this molecular dataset only included COI data for *A. luikenisis* from China and Taiwan, further sampling throughout India and Southeast Asia will be required to more rigorously test this dispersal hypothesis. Alternatively, these data support the hypothesis that *Menneus* dispersed to Australia via a single, trans-oceanic dispersal event, although divergence times of Australian and African *Menneus* post-date an Out of India hypothesis. With 37% of the total 46 described deinopid species in the Eastern Hemisphere (putative and genetic transfers), much of Africa, Asia, and Indomalaya remains under-sampled. More extensive sampling is required, particularly of Madagascar and Indomalaya, to more completely understand *Menneus* biogeographic history.

**Crossing Wallace’s line.** Wallace’s line is one of the most striking separations of biomes in the world. Wallace \(^{101}\) posited that the fauna of South America and Africa, despite being separated by the Atlantic Ocean, were more similar than the faunas of Asia and Australia. Based on our results, deinopids dispersed from Africa to Asia and then from Indomalaya to Australia 91–52 Ma (Fig. 4), which may reveal intriguing implications of dispersal across Wallace’s line. Furthermore, the Australian *Deinopis* diverged from its sister Indomalayan clade around 72 Ma (Fig. 4). This divergence pre-dates the Indo-Australian archipelago (IAA) and a deep sea and a large trench separated the two regions until around 40 Ma when islands began forming \(^{102}\). Recently the IAA has been discovered to be a more common route of dispersal than previously predicted in terrestrial animals \(^{102-104}\). We postulate that upon broader sampling in this region, we may find range expansions across the IAA in the Late Eocene to Early Miocene when landmasses were forming \(^{102}\).

**South Africa, Madagascar, and the Neotropics.** We found evidence for at least two trans-oceanic dispersals of South African *Deinopis*. First, Malagasy *Deinopis* diverged from South African *Deinopis* in the Paleocene, post-dating Lower Cretaceous continental drift and vicariance. Madagascar separated from Africa and moved southeastward in the Middle to Early Late Jurassic (160–155 Ma) \(^{105,106}\) and was one of the first of the Gondwanan landmasses to break away from the supercontinent. Madagascar was in its final position relative to Africa approximately 120 Ma (118–130 Ma) \(^{107,108}\). The relative contributions of Gondwanan vicariance and long-distance dispersal among Malagasy lineages remain a source of debate \(^{96,109-111}\). Madagascar’s biodiversity primarily comprises endemic flora and fauna that have either been present since Gondwana or were a product
of long-distance dispersal events in the Cenozoic, mostly from Africa (400 km away), but including all major biogeographic regions\(^{26}\).

Second, we found evidence for at least one trans-oceanic long-distance dispersal between South Africa and Mexico in the Eocene. Discoveries of such extreme trans-oceanic dispersals are becoming increasingly common\(^{81,99,112}\) and can be attributed to salt-water tolerance\(^{113}\), long-distance flight\(^{114-116}\), and wind-dispersal in plants\(^{117,118}\). Exchanges between Africa, the Western Indian Ocean, and the Neotropics have been especially well documented in tropical flora\(^{119-125}\). Dispersal events from the Neotropics to Africa are facilitated by westerly winds\(^{125,126}\), whereas dispersals from Africa to the Neotropics, the rarer of the two dispersal scenarios\(^{125}\), typically follow the trade winds\(^{126}\). While there was at least one dispersal event between Africa to the Mexico, further sampling of Eastern Hemisphere deinopids in the Neotropics is necessary to rigorously test dispersal hypotheses.

Conclusions

Deinopids have a rich biogeographic history characterized by complex and ancient patterns of vicariance coupled with long distance dispersal since their emergence in the Cretaceous. While LDD has played an important role in shaping the distributions of deinopids, these events are not so prevalent as to completely obfuscate ancient Gondwanan signatures. The evolutionary history of Deinopidae provides fascinating examples of eye size reduction and unexpected trans-oceanic dispersals. Whereas most studies in eye size evolution are troglo-morphic adaptations in the form of reductions/loss of eyes, here, we document an example of a single reversal to ‘normal’ sized eyes from the uniquely derived condition of grossly enlarged PMEs in ogre-faced spiders. The PME size reductions in Menneus provides a framework for considering and testing hypotheses of the potential selective forces that might be driving these divergent morphologies.

Taxonomic section. Based on phylogenetic structure and biogeographical distributions we propose the following new combinations (* indicates those taxa included in this study): Asianopis anchicetae (Brito Capello\(^{127}\)) NEW COMBINATION; Asianopis aspectans Pocock\(^{128}\) NEW COMBINATION; Asianopis aurita Pickard-Cambridge\(^{129}\) NEW COMBINATION; Asianopis camella Thorell\(^{130}\) NEW COMBINATION; Asianopis cornigera Gerstäcker\(^{131}\) NEW COMBINATION; Asianopis cylindrica* Pocock\(^{132}\) NEW COMBINATION; Asianopis fasciata Koch\(^{133}\) NEW COMBINATION; Asianopis fasciculigera Simon\(^{134}\) NEW COMBINATION; Asianopis gilatoi Lessert\(^{135}\) NEW COMBINATION; Asianopis guineensis Berland & Millot\(^{136}\) NEW COMBINATION; Asianopis kollari Doleschall\(^{137}\) NEW COMBINATION; Asianopis labangan Barrion-Dupo & Barrion\(^{138}\) NEW COMBINATION; Asianopis longipalpula Strand\(^{139}\) NEW COMBINATION; Asianopis luzonensis Barrion-Dupo & Barrion\(^{138}\) NEW COMBINATION; Asianopis madagascariensis Lenz\(^{140}\) NEW COMBINATION; Asianopis mediocris Kulczyński\(^{141}\) NEW COMBINATION; Asianopis ornata Pocock\(^{142}\) NEW COMBINATION; Asianopis ravida Koch\(^{143}\) NEW COMBINATION; Asianopis reticulata Rainbow\(^{144}\) NEW COMBINATION; Asianopis schomburgki Karsch\(^{145}\) NEW COMBINATION; Asianopis schoutedeni Giltay\(^{146}\) NEW COMBINATION; Asianopis subrefra* Koch\(^{147}\) NEW COMBINATION; Asianopis tabidus Koch\(^{143}\) NEW COMBINATION; Asianopis unicolor* Koch\(^{143}\) NEW COMBINATION.

Methods

Taxon sampling. We collected a total of 42 deinopid individuals (29 Deinopis and 13 Menneus) from the east coast of Australia in January 2019 using standard aerial search and vegetation beating methods described in Coddington et al.\(^{146}\). Most of the specimens were collected at night as deinopids are highly cryptic and are most easily spotted when their nets reflect a blue hue under headlamp lights. The specimens were fixed in 95% ethanol in the field and kept at ~20 to ~80 °C in the lab. Collaborators also provided additional Deinopis specimens from Western Australia, Taiwan, Mexico, Madagascar, South Africa, and Colombia.

DNA extractions, sequence generation, and data processing. Detailed methods for molecular methods, sequence editing, and read processing are available in the Supplemental Methods S1. We extracted DNA from leg tissue for 65 individuals using the OMEGA BIO-TEK E.Z.N.A. DNA extraction kit. We amplified COI: cytochrome c oxidase subunit I, a mitochondrial locus. We obtained COI sequence data for seven species from Kulkarni et al.\(^{148}\) (NCBI Sequence Read Archive, BioProject PRJNA575576). UCE and COI matrices DNA Technologies (See Supplemental Methods S1 for more detail). We obtained UCE data for four outgroup species from Kulkarni et al.\(^{148}\) (NCBI Sequence Read Archive, BioProject PRJNA575576). UCE and COI matrices were concatenated in AMAS\(^{150}\) to generate the UCE + COI combined dataset.

Phylogenetics. We inferred phylogenetic trees for the four molecular datasets: COI-only (258 deinopid individuals, four outgroup individuals; 1279 base pairs), UCE-only (40 deinopids, four outgroup individuals; 75% occupancy matrix; 1018 loci), COI + UCE concatenated, and COI with a UCE backbone phylogeny using Maximum Likelihood\(^{151}\) and coalescence-based methods\(^{152}\). In IQ-TREE 2\(^{153}\), we implemented the built-in model finder to consider invariant site and Gamma rate heterogeneity under the greedy strategy with the AICc
criterion to determine molecular substitution models for each codon position. The COI dataset was partitioned by codon using the GTR + I + G and the UCE dataset was partitioned by locus using the GTR model. We ran four separate analyses on each dataset with 1000 pseudoreplicates of ultrafast bootstrapping155,156 on the codon-partitioned COI and COI-backbone datasets, and the loci-partitioned UCE, COI + UCE concatenated datasets. We generated trees from individual UCE loci using IQ-TREE. These trees were used to infer a coalescence-based species tree in IQ-TREE and ASTRAL-II v5.7.1142.

**Tree topology tests.** We implemented tree topology tests in IQ-TREE2 to evaluate the relationships of *Asianopis*, *Deinopis*, and *Menneus*, and to further assess the monophyly of these three groups. We tested the unconstrained tree and four alternative tree topologies (Supplementary Fig. S1) in IQ-TREE using the RELL approximation157, which uses bootstrap proportions, p-values with the Shimodaira-Hasegawa test158 and AU unconstrained tree and four alternative tree topologies (Supplementary Fig. S1) in IQ-TREE using the RELL of `phyl.pca` in the R package `phytools`176 to determine if eye and carapace size, ten (pPCA) in R using the function `cally significant difference between large and small PME. We used a phylogenetic principal components analysis

**Molecular dating.** We implemented MCMCTree in the PAML v4.8161 package on the UCE only dataset to estimate divergence times within Deinopidae. Prior to the analyses, we removed redundant subspecies so that only one individual per species (with the least amount of missing data) remained. To set up the model and model parameters, we assigned a birth–death model for the tree and an UCLN clock model (uncorrelated relaxed clock). A GTR substitution model was used with flat Dirichlet prior distribution. Previous phylogenetic dating analyses have used the fossil *Palaeomicromenneus lebanensis* to calibrate the stem of Deinopidae154,165. However, the taxonomy of this fossil is dubious164, and it has been transferred into the extinct family Salticoididae165; therefore we did not use this fossil as a calibration point in the dating inferences. Instead, we employed a molecular calibration point from recent phylogenetic reconstruction on Araneomorphs169 to conservatively use maximum age of 150 Ma as a soft constraint for the Deinopidae crown. We used a single fossil, *Seppo koponen* to calibrate a soft constraint with the minimum root age of Deinopidae + outgroups of 132.9 and a maximum of 250 Ma. We ran two independent Markov chain Monte Carlo (MCMC) runs for 20,000 samples, resampling every 10,000 iterations for a total of 200,000 iterations with a burn-in set to discard the first 20,000 iterations. Outputs were assessed for stationarity in Tracer v1.7.1167 and visualized using FigTree v1.4.4168.

**Ancestral range estimates.** We estimated the ancestral ranges of deinopids and performed biogeographic analyses in BioGeoBEARS69 using the UCE-only MCC tree inferred in MCMCTree. We used eight isolated biogeographic areas including Africa (F), Asia (A), Australia (U), Neotropics (S), Nearctic (N), Madagascar (M), India (I), and the Caribbean (C), five of which were based on updated zoological regions of Holt et al.170 and on the most recent global biogeographic studies on spiders171. These regions were also selected due to their high endemism, geologic histories, and land availability. We included a time slice model based on the breakup of the continents following descriptions in Seton et al.172 of the historical geology and modeled after recent invertebrate dispersal models3,44 (Supplementary Table S4; See Supplemental Methods S1). We tested these models under the Dispersal-Extinction-Cladogenesis (DEC) and with the (+j) parameter, which considers for jump dispersal or founder event speciation169,174. We compared Akaiake information criterion (AIC) and relative likelihood scores across all models (a natural log of 2 was considered significant)175. We used the MCMCTree-generated UCE and UCE + COI dated phylogeny with outgroups pruned to only include Deinopidae specimens.

**Ancestral state reconstruction and eye measurements.** Measurements of adult female specimens were taken with a Leica M205 C scope using the micrometer scale tools in the Leica Application Suite (LAS Version 4.13.0) (Supplementary Table S5; See Supplemental Methods S1). We measured the total ocular distance and individual diameters of PME, anterior median eye (AME), anterior lateral eye (ALE), posterior lateral eye (PLE) diameter for all adult females. We also measured carapace length, width, and carapace width at the PLEs. A Mann–Whitney non-parametric test of mean difference was used to determine whether there was a statistically significant difference between large and small PME. We used a phylogenetic principal components analysis (pPCA) in R using the function `phyl.pca` in the R package `phytools`176 to determine if eye and carapace size, ten and three characters respectively, were partitioned among the three genera: *Deinopis*, *Asianopis*, and *Menneus*. We used a pruned MCC tree, which included 29 species throughout the tree that were absent of missing data. Data points included carapace length and width, eye diameter of all four types of eyes (PME, AME, PLE, and ALE) and the eye row width across each of these. We also calculated total ocular distance, the sum diameter of all eight eyes. We generated biplots in R of the scores of the 23 total traits obtained from the pPCA.

We tested the phylogenetic signal of the binary trait for eye size, “large” for *Deinopis* and “small/typical” for *Menneus*, and for the outgroups. We calculated D, which is a permutation-based model that measures the phylogenetic signal strength in a binary trait assuming the underlying continuous trait is evolving under Brownian Motion177 and was appropriate for eye size, which is a variable and potentially continuous trait within each genus.

We mapped the states for discrete characters, large and small PME, along the species level MCC phylogeny using the `ace` function in `ape`178 and in `phytools`176. To estimate ancestral states for discrete PME characters, we employed a continuous time Markov chain (Mk) model to give character probability distributions of ancestral states at internal nodes in the tree. We also used stochastic character mapping, an MCMC approach to sample character histories from their probability distributions.
Data availability

The datasets generated during and/or analyzed for the current study are available from the corresponding author on reasonable request. The UCE dataset generated and analyzed during the current study have been deposited at NCBI Short-Read Archive (https://www.ncbi.nlm.nih.gov/sra) as BioProject PRJNA802018. All COI sequences obtained in this study have been deposited at NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/) with the accession numbers OM480748-OM480975.

Received: 22 January 2022; Accepted: 10 October 2022
Published online: 22 October 2022

References

1. Coddington, J. A., Kunzter, M. & Opell, B. D. Systematics of the spider family Deinopidae with a revision of the genus Menneus. (Smithsonian Contributions to Zoology, 2012).
2. Getty, R. M. & Coyle, F. A. Observations on prey capture and anti-predator behaviors of ogre-faced spiders (Deinopis) in southern Costa Rica (Araneae, Deinopidae). J. Arachnol. 24, 93–100 (1996).
3. Garrison, N. L. et al. Spider phylogenomics: Untangling the spider tree of life. PeerJ 4, e1719 (2016).
4. Coddington, J. A. Orb webs in "Non-orb weaving" ogre-faced spiders (Araneae: Deinopidae): A question of genealogy. Cladistics 2, 53–67 (1986).
5. Coddington, J. A. & Sobrevilla, C. Web manipulation and two stereotyped attack behaviors in the ogre-faced spider Deinopis spinosus Marx (Araneae, Deinopidae). J. Arachnol. 15, (1987).
6. Blamires, S. J., Zhang, S. & Ito, I.-M. Webs: Diversity, Structure and Function. in Behaviour and Ecology of Spiders (eds. Viera, C. & Gonzaga, M. O.) 137–164 (Springer International Publishing, 2017). https://doi.org/10.1007/978-3-319-65717-2_6.
7. Stafstrom, J. A., Menda, G., Nitzany, E. I., Hebets, E. A. & Hoy, R. R. Ogre-faced, net-casting spiders use auditory cues to detect airborne prey. Curr. Biol. 30, 5033–5039.e3 (2020).
8. Spano, L., Long, S. M. & Jakob, E. M. Secondary eyes mediate the response to looming objects in jumping spiders (Phidippus audax, Salticidae). Biol. Lett. 8, 949–951 (2012).
9. Forster, L. M. Visual mechanisms of hunting behaviour in Trite planiceps, a jumping spider (Araneae: Salticidae). N. Z. J. Zool. 6, 79–93 (1979).
10. Land, M. F. The Morphology and Optics of Spider Eyes. in Neurobiology of Arachnids (ed. Barth, F. G.) 53–78 (Springer Berlin Heidelberg, 1985). https://doi.org/10.1007/978-3-642-70348-5_4.
11. Gainett, G. & Sharma, P. P. Genomic resources and toolkits for developmental studies of whip spiders (Amblypygi): provide insights into arachnid genome evolution and antenniform leg patterning. EvoDevo 11, 18 (2020).
12. Foelix, R. F. Biology of spiders. (Oxford University Press, 2011).
13. Blest, A. D. & Land, M. F. The physiological optics of Dinopis subrufus L. Koch: A fish-lens in a spider. Proc. R. Soc. Lond. B Biol. Sci. 196, 197–222 (1977).
14. Stafstrom, J. A. & Hebets, E. A. Nocturnal foraging enhanced by enlarged secondary eyes in a net-casting spider. Biol. Lett. 12, 20160152 (2016).
15. Chamberland, L. et al. From Gondwana to GAARlandia: Evolutionary history and biogeography of ogre-faced spiders (Deinopis). J. Biogeogr. 45, 2442–2457 (2018).
16. Lin, Y. et al. Asopanops gen. nov., a new genus of the spider family Deinopidae from Asia. ZooKeys 911, 67–99 (2020).
17. Blest, A. D., Williams, D. S. & Kao, I. L. The posterior median eyes of the dinopid spider Menneus. Cell Tissue Res. 211, (1980).
18. Protas, M. E., Trontelj, P. & Patel, N. H. Genetic basis of eye and pigment loss in the cave crustacean Astyanax aquatilis. Proc. Natl. Acad. Sci. 108, 5702–5707 (2011).
19. Klaus, S. et al. Rapid evolution of troglobitic characters suggests selection rather than neutral mutation as a driver of eye reduction in cave crabs. Biol. Lett. 9, 20121098 (2013).
20. Langacker, T. G. & Longley, G. Morphological adaptations of the texas blind catfishes Troglomis planiceps and Satan eurystomus (Siliariformes: Ictaluridae) to their underground environment. Copeia 1993, 976 (1993).
21. Wilkens, H. & Strecker, U. Convergent evolution of the cavefish Astyanax (Characidae, Telostei): genetic evidence from reduced eye-size and pigmentation: Convergence of astyanax cavefish evolution. Biol. J. Linn. Soc. 80, 545–554 (2003).
22. David-Gray, Z. K., Janssen, J. W., DeGrip, W. J., Nevo, E. & Foster, R. G. Light detection in a ‘blind’ mammal. Nat. Neurosci. 1, 655–656 (1998).
23. Leys, R., Cooper, S. J. B., Strecker, U. & Wilkens, H. Regressive evolution of eye pigment gene in independently evolved eyeless subterranean diving beetles. Biol. Lett. 1, 496–499 (2005).
24. Bosselaers, J. Nesticus henderickxi (Araneae, Nesticidae), a new blind troglobitic spider from Crete. Bull.-Br. Arachnol. Soc. 11, 9–14 (1998).
25. Bloom, T. et al. Discovery of two new species of eyeless spiders within a single Hispaniola cave. J. Arachnol. 42, 148–154 (2014).
26. Ribera, C., Elverici, M., Kunt, K. & Özkütük, R. Typhlonesticus goçmeni sp. n., a new cave-dwelling blind spider species from the Aegean region of Turkey (Araneae, Nesticidae). ZooKeys 419, 87–102 (2014).
27. Hedin, M. High-stakes species delimitation in eyeless cave spiders (Cicarina, Dictynidae, Araneae) from central Texas. Mol. Ecol. 24, 346–361 (2015).
28. Soares, D. & Niemiller, M. L. Extreme adaptation in caves. Anot. Rec. 303, 15–25 (2020).
29. Protas, M. et al. Multi-trait evolution in a cave fish, Astyanax mexicanus : QTL analysis of cave adaptation. Evol. Dev. 10, 196–209 (2008).
30. Re, C. et al. Common genetic basis of eye and pigment loss in two distinct cave populations of the isopod Crustacean Astyanax aquatilis. Integr. Comp. Biol. 58, 421–430 (2018).
31. Moorehouse, N. L., Buschbeck, E. K., Zurek, D. B., Steck, M. & Porter, M. L. Molecular evolution of spider vision: New opportunities for familiar players. Biol. Bull. 233, 21–38 (2017).
32. Reston, S. M. & Walsh, M. R. Natural selection favours a larger eye in response to increased competition in natural populations of a vertebrate. Funct. Ecol. 33, 1321–1331 (2019).
33. Garamszegi, L. Z., Möller, A. P. & Erritzøe, J. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. Proc. R. Soc. Lond. B Biol. Sci. 269, 961–967 (2002).
34. Ross, C. F. & Kirk, E. C. Evolution of eye size and shape in primates. J. Hum. Evol. 52, 294–313 (2007).
35. Hall, M. L. The anatomical relationships between the avian eye, orbit and sclerotic ring: Implications for inferring activity patterns in extinct birds. J. Anat. 212, 781–794 (2008).
36. Baur, T., Desender, K., Morwinsky, T. & Betz, O. Eye morphology reflects habitat demands in three closely related ground beetle species (Coleoptera: Carabidae). J. Zool. 245, 467–472 (1998).
37. Moser, J. C. et al. Eye size and behaviour of day- and night-flying leafcutting ant alates. J. Zool. 264, 69–75 (2004).
38. Somanathan, H., Kelker, A., Borges, R. M., Wallén, N. & Warrant, E. J. Visual ecology of Indian carpenter bees II: Adaptations of eyes and ocelli to nocturnal and diurnal lifestyles. J. Comp. Physiol. A 185, 571–583 (2009).
39. Simpson, G. G. Tempo and mode in evolution. (Columbia University Press, 1984).
40. Rasmussen, C. & Cameron, S. A. Global stingless bee phylogeny supports ancient divergence, vicariance, and long distance dispersal: Stingless bee phylogeny. Biol. J. Linn. Soc. 99, 206–232 (2009).
41. Givnish, T. J. et al. Ancient Vicariance or Recent Long-Distance Dispersal? Inferences about Phylogeny and South American-African Distinctions in Rapataeaceae and Bromeliaceae Based on ndt F Sequence Data. Int. J. Plant Sci. 165, S35–S54 (2004).
42. Kropf, M., Comes, H. P. & Kadereit, J. W. Long-distance dispersal vs vicariance: The origin and genetic diversity of alpine plants in the Spanish Sierra Nevada. New Phytol. 172, 169–184 (2006).
43. Toussaint, E. A. F. & Short, A. E. Z. Biogeographic mirrors? Molecular evidence for dispersal-driven evolution in Hydrobiusinus water scavenger beetles: Biogeography of the beetle tribe Hydrobiusinus. Syst. Entomol. 42, 692–702 (2017).
44. Toussaint, E. A. F., Bloom, D. & Short, A. E. Z. Cretaceous West Gondwana vicariance shaped giant water scavenger beetle biogeography. J. Biogeogr. 44, 1952–1965 (2017).
45. Gillespie, R. G. et al. Long-distance dispersal: A framework for hypothesis testing. Trends Ecol. Evol. 27, 47–56 (2012).
46. Raven, P. H. & Axelrod, D. I. Plate tectonics and the Astralasian paleobiogeography. Proc. Natl. Acad. Sci. 176, 1379–1386 (1972).
47. Capesius, I. & Bopp, M. New classification of liverworts based on molecular and morphological data. Plant Syst. Evol. 207, 87–97 (1997).
48. Gontcharov, A. A. Are Combined analyses better than single gene phylogenies? A case study using SSU rDNA and rbcL sequence comparisons in the Zynogmatophyceae (Streptophyta). Mol. Biol. Evol. 21, 612–624 (2003).
49. Hoef-Emden, K., Marin, B. & Melkonian, M. Nuclear and nucleomorph SSU rDNA phylogeny in the cryptophyta and the evolution of cryptophyte diversity. J. Mol. Evol. 55, 161–179 (2002).
50. Nei, M., Kumar, S. & Takahashi, K. The optimization principle in phylogenetic analysis tends to give incorrect topologies when the number of nucleotides or amino acids used is small. Proc. Natl. Acad. Sci. 95, 12390–12397 (1998).
51. Nickrent, D. L., Parkinson, C. L., Palmer, J. D. & Duff, R. J. Multigene phylogeny of land plants with special reference to bryophytes and the earliest land plants. Mol. Biol. Evol. 17, 1885–1895 (2000).
52. Poe, S. & Swofford, D. L. Taxon sampling revisited. Mol. Biol. Evol. 17, 465–479 (2000).
53. Toussaint, E. A. F., Malhotra, 1978) comb.n. (Araneae: Deinopidae) from India. (Tikader et al. et al. BMC Evol. Biol. 9, e1500363 (2015).
54. Jeffery, W. R. Embryonic development of cavefish. Heredity 92, 185–196 (2004).
55. Herman, A. M. The origin of aquatic vision in the guidance of their nocturnal activities. PLoS ONE 2, e198 (2007).
56. Jacobs, G. H. Losses of functional opsin genes, short-wavelength cone photopigments, and color vision—A significant trend in the evolution of mammalian vision. Vis. Neurosci. 30, 39–53 (2013).
57. Tierney, S. M., Langille, B., Humphreys, W. F., Austin, A. D. & Cooper, S. J. B. Massive parallel regression: A précis of genetic mechanisms for vision loss in diving beetles. Integr. Comp. Biol. 58, 465–479 (2018).
58. Darwin, C. The Origin of Species by Means of Natural Selection. (Bantam Books, 1959).
59. Gillett, N. H. Regressive evolution: ontogeny and genetics of cavefish eye rudimentation: Genetics of cavefish eye rudimentation. Biol. J. Linn. Soc. 92, 287–296 (2007).
60. Martin, G. R. & Kili Forego vision in their natural distribution. PLoS ONE 2, e198 (2007).
61. Cartright, R. A., Schwartz, R. S., Merry, A. L. & Howell, M. M. The importance of selection in the evolution of blindness in cavefish. BMC Evol. Biol. 17, 45 (2017).
62. Herman, A. et al. The role of gene flow in rapid and repeated evolution of cave-related traits in Mexican tetra Astyanax mexianus. Mol. Ecol. 27, 4397–4416 (2018).
63. Borowsky, R. & Wilkins, H. Mapping a cave fish genome: Polygenic systems and regressive evolution. J. Hered. 93, 19–21 (2002).
64. Jeffery, W. R. Adaptive evolution of eye degeneration in the Mexican Blind Cavefish. J. Hered. 96, 185–196 (2005).
65. Keene, A. C., Yoshizawa, M. & McGaugh, S. E. Biology and evolution of the Mexican cavefish. (Academic Press/Elsevier, 2015).
66. Stafstrom, J. A., Michalik, P. & Hebets, E. A. Sensoric system plasticity in a visually specialized, nocturnal spider. Sci. Rep. 7, 46627 (2017).
67. Blest, A. D. The rapid synthesis and destruction of photoreceptor membrane by a dionisid spider: a daily cycle. Proc. R. Soc. Lond. B Biol. Sci. 200, 463–483 (1978).
68. Blayke, R. C. Gondwana paleogeography from assembly to breakup—A 500 m.y. odyssey. in Special Paper 441: Resolving the Late Paleoceanic Ice Age in Time and Space vol. 441 1–28 (Geological Society of America, 2008).
69. Eanes, G. & König, M. A model of plate kinematics in Geophys. J. Int. 173, 703–717 (2008).
70. Royer, J. Y. et al. Indian Ocean plate reconstructions since the Late Jurassic. Indian Ocean Plate Reconstr. Late Jurassic. Synth. Results Sci. Drill. Indian Ocean Geophys Monogr Ser 70, 471–475 (1992).
71. Gibbons, A. D., Whittaker, J. M. & Müller, R. D. The breakup of East Gondwana: Assimilating constraints from Cretaceous ocean basins around India into a best-fit tectonic model: The Enderby basin/east Gondwana breakup. J. Geophys. Res. Solid Earth 118, 808–822 (2013).
72. Seroen, P. C., Wilson, J. A. & Conrad, J. L. New dinosaurs link southern landmasses in the Mid–Cretaceous. Proc. R. Soc. Lond. B Biol. Sci. 271, 1325–1330 (2004).
73. Barker, N. P., Weston, P. H., Rutschmann, F. & Saquet, H. Molecular dating of the ‘Gondwana’ plant family Proteaceae is only partially congruent with the timing of the break-up of Gondwana. J. Biogeogr. 34, 202–2027 (2007).
74. Michalik, J., Zhang, L.-B. & Renner, S. S. Trans-Atlantic, trans-Gondwanan and the early trans-Atlantic, trans-Pacific and trans-Gondwanan Lauras family Hernandiaceae: Biogeography of Hernandiaceae. J. Biogeogr. 37, 1244–1246 (2010).
75. Koral, P. & Przybyszewski, K. M. Global biogeography of scaly tree ferns (Cyatheaeeae): evidence for Gondwana vicariance and limited transoceanic dispersal. J. Biogeogr. 41, 402–413 (2014).
76. Luebert, F. & et al. Historical biogeography of Boraginaceae: West Gondwana vicariance followed by long-distance dispersal? J. Biogeogr. 44, 158–169 (2017).
77. Jurado-Rivera, J. A. et al. Phylogenetic evidence that both ancient vicariance and dispersal have contributed to the biogeographic patterns of anchialine cave shrimps. Sci. Rep. 7, 2852 (2017).
84. Capobianco, A. & Friedman, M. Vicariance and dispersal in southern hemisphere freshwater fish clades: A palaeontological perspective. Vicariance and dispersal in freshwater fishes. Biol. Rev. 94, 662–699 (2019).
85. Derkarabedian, S., Baker, C. M. & Giribet, G. Complex patterns of Gondwanan biogeography revealed in a dispersal-limited arachnid. J. Biogeogr. 48, 1336–1352 (2021).
86. Choussou-Polydouri, N. et al. Giant Goblins above the waves at the southern end of the world: The biogeography of the spider family Orsoliidae (Araneae, Dysderoidea). J. Biogeogr. 46, 332–342 (2019).
87. Crocuta, L., Nelson, G. & Rosen, D. F. Centers of origin and related concepts. Syst. Biol. 23, 265–287 (1974).
88. Rosen, D. E. Vicariant patterns and historical explanation in biogeography. Syst. Zool. 27, 159 (1978).
89. Brundin, L. A. Limnic Diptera in their bearings on the problem of transantarctic faunal connections. Pac. Basin Biogeogr. Symp. 425–434 (1963).
90. Cracraft, J. Avian evolution, Gondwan biogeography and the Cretaceous–Tertiary mass extinction event. Proc. R. Soc. Lond. B Biol. Sci. 268, 459–469 (2001).
91. McCulloch, G. A., Boyer, S. L. & Giribet, G. A well-resolved transcriptomic phylogeny of the mite harvestman family Pettalidae (Arachnida, Opiliones, Cyphophthalmi) reveals signatures of Gondwanan vicariance. J. Biogeogr. 47, 1345–1361 (2020).
92. Brundin, L. A. Transantarctic relationship and their significance, as evidenced by chironomid midges. With a monograph of the subfamilies Podonoinae and Aphroteniinae and the austral Haplogryae. K. Svens. Vetensk. Akad. Handl. 1, 1–472 (1966).
93. Storey, M. et al. Timing of Hot Spot—Related Volcanism and the Breakup of Madagascar and India. Science 267, 852–855 (1995).
94. Torsvik, T. H. et al. Late Cretaceous India-Madagascar fit and timing of break-up related magmatism. Terra Nova 12, 220–224 (2000).
95. A. Agnarsson, I. & Kuntner, M. The Generation of a biodiversity hotspot: Biogeography and phylogeny of the Western Indian Ocean Islands. In Current topics in phylogenetics and phylogeography of terrestrial aquatic systems, vol. 33 (2012).
96. Conti, E., Eriksson, T., Schönberger, J., Sytsma, K. J. & Baum, D. A. Early tertiary out-of-Africa dispersal of Crypteneriaceae: Evidence from phylogeny and molecular dating. Evolution 56, 1931–1942 (2002).
97. Zhou, L., Su, Y. C. F., Thomas, D. C. & Saunders, R. M. K. Out-of-Africa dispersal of tropical floras during the Miocene climatic optimum: evidence from Uvaria (Annonaceae); Out-of-Africa dispersal during Miocene climatic optimum. J. Biogeogr. 39, 322–335 (2012).
98. Renner, S. S. Multiple Miocene Melastomataceae dispersal between Madagascar, Africa and India. Phyllos. Trans. R. Soc. Lond. B Biol. Sci. 359, 1485–1494 (2004).
99. Cain, S., Loria, S. F., Ben-Shlomo, R., Perdinii, L. & Gefen, E. Dated phylogeny and ancestral range estimation of sand scorpions (Buthidae: Buthacae) reveal Early Miocene divergence across land bridges connecting Africa and Asia. Mol. Phylogenet. Evol. 164, 107212 (2021).
100. Wallace, A. R. On the Zoological Geography of the Malay Archipelago. (Read Books Ltd., 1960).
101. Lozeman, D. J. et al. Biogeography of the Indo-Australian Archipelago. Annu. Rev. Ecol. Evol. Syst. 42, 205–226 (2011).
102. Stelbrink, B., Albrecht, C., Hall, R. & von Rintelen, T. The biogeography of Sulawesi revisited: Is there evidence for a Vicariant origin of taxa on Wallace’s “anomalous island”? Biogeography of Sulawesi. Evolution 66, 2252–2271 (2012).
103. de Bruyn, M. et al. Borneo and Indochina are Major Evolutionary Hotspots for Southeast Asian Biodiversity. Syst. Biol. 63, 879–901 (2014).
104. Rabenowitz, P. D., Coffin, M. F. & Fullway, D. The separation of Madagascar and Africa. Science 220, 67–69 (1983).
105. Coffin, M. F. & Rabinowitz, P. D. Reconstruction of Madagascar and Africa: Evidence from the Davie Fracture Zone and Western Somali Basin. J. Geophys. Res. 92, 9385 (1987).
106. Stelbrink, B., Albrecht, C., Hall, R. & von Rintelen, T. The biogeography of Sulawesi revisited: Is there evidence for a Vicariant origin of taxa on Wallace’s “anomalous island”? Biogeography of Sulawesi. Evolution 66, 2252–2271 (2012).
107. Janssens, S. B. et al. Dispersing towards Madagascar: Biogeography and evolution of the Madagascar endemics of the Spermacoceae tribe (Rubiacaeae). Mol. Phylogenet. Evol. 95, 58–68 (2016).
108. Takayama, K., Tamura, M., Tateishi, Y., Webb, E. L. & Kajita, T. Strong genetic structure over the American continents and transoceanic dispersal in the mangrove genus Rhizophora (Rhizophoraceae) revealed by broad-scale nuclear and chloroplast DNA analysis. Am. J. Bot. 100, 1191–1201 (2013).
109. Hsu, M.-H., Lin, J.-W., Liao, C.-P., Hsu, J.-Y. & Huang, W.-S. Trans-marine dispersal inferred from the saltwater tolerance of lizards from Taiwan. PLoS ONE 16, e0247009 (2021).
110. Lim, B. K. Review of the origins and biogeography of bats in South America. Chiropt. Neotrop. 15, (2009).
111. Horsman, E. A., Tobias, J. A., Braun, E. L. & Kimball, R. T. How do seemingly non-vagile clades accomplish trans-marine dispersal? Trait and dispersal evolution in the landfowl (Aves: Galliformes). Proc. R. Soc. Biol. Sci. 284, 20170210 (2017).
112. Yi, X. & Latch, E. K. Systematics of the New World bats Eptesicus and Histiotous suggest trans-marine dispersal followed by Neotropical cryptic diversification. Mol. Phylogenet. Evol. 175, 107582 (2022).
113. Ceccarelli, F. S. et al. Around the world in eight million years: Historical biogeography and evolution of the spray zone spider Amasystes (Araneae: Araneidae). PLoS ONE 11, e0163740 (2016).
114. Liao, Y. et al. Global diversification of anelosimus spiders driven by long-distance overwater dispersal and neogene climatic oscillations. Syst. Biol. 69, 1122–1130 (2020).
115. Rouhan, G. et al. Molecular phylogeny of the fern genus Elaphoglossum (Elaphoglossaceae) based on chloroplast non-coding DNA sequences: Contributions of species from the Indian Ocean area. Mol. Phylogenet. Evol. 33, 745–763 (2004).
116. Váscon, A., Moran, R. C. & Rouhan, G. Circumscription and phylogeny of the Elaphoglossum clitani group (E. sect. Lepidoglossa, Dryopteridaceae) based on cpDNA sequences. TAXON 58, 825–834 (2009).
117. Rouhan, G., Hanks, J. G., McClelland, D. & Moran, R. C. Preliminary phylogenetic analysis of the fern genus Lomariopsis (Lomariopsidaceae). Brittonia 59, 115–128 (2007).
118. Labahk, P. H., Sundue, M. & Rouhan, G. Molecular phylogeny, character evolution, and biogeography of the grammitid fern genus Lillingstonia (Polypodiidae). Am. J. Bot. 97, 1354–1364 (2010).
119. Sundue, M. A. et al. Global phylogeny and biogeography of grammitid ferns (Polypodiidae). Mol. Phylogenet. Evol. 81, 195–206 (2014).
120. Labahk, P. H. et al. Phylogeny and historical biogeography of the lastreopid ferns (Dryopteridaceae). Am. J. Bot. 101, 1207–1228 (2014).
121. Baur, T. et al. Madagascar sheds new light on the molecular systematics and biogeography of grammitid ferns: New unexpected lineages and numerous long-distance dispersal events. Mol. Phylogenet. Evol. 111, 1–17 (2017).
122. Moran, R. C. & Smith, A. R. Phytogeographic relationships between neotropical and African-Madagascar pteridophytes. Brit- tonia 53, 304–351 (2001).
Acknowledgements
We would like to acknowledge the many people who have contributed ideas. We thank Jay Stafstrom for sharing his expertise on spider vision and for thoughtful discussions on deinopid ecology. We thank Lauren Esposito for assisting in securing permits and collecting specimens as part of the Caribbean Island Biogeography (CARBIO) project. We thank Lacie Newton for her help with the molecular work. We are especially grateful to the volunteers who helped collect Australian deinopids, including Michael Doe and Adam Fletcher of Project Maratus, Jeremy Jones, Nick Lambert, Matt Elmer, Matthew Hourston, and Robert Whyte, and for sharing their knowledge on Australian spiders. We thank the Australian landowners who gave us permission to collect spiders on their property and for hosting us. We thank Mariella Herberstein, George Binns, and Jonas Wolff for assisting with the Australian collections. We thank Dave Barrington and Greta Binford for their discussions on biogeography and evolution. Finally, we appreciate the feedback from two anonymous reviewers whose comments greatly improved the manuscript.

Author contributions
L.C. designed the study, acquired, analyzed, and interpreted the data, wrote the original draft, prepared the figures. L.C. and J.S. performed UCE acquisition. J.S. contributed to the supplemental methods S1 and manuscript revisions. I.A. and J.E.B revised the manuscript and contributed to project design and execution. J.E.B. and I.A. funded the study. I.L.Q. and T.R. performed data collection, photographed specimens, and provided corrections to the manuscript. All authors contributed critically to the manuscript.

Funding
This article was funded by The John Wheeler Graduate Student Research and Development Award and Evert and Marion Schlinger Foundation.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-022-22157-5.

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