

Biogeography of euophryine jumping spiders (Araneae: Salticidae)

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Summary. Recent work on the phylogeny of the euophryine jumping spiders has significantly altered our understanding of the relationship between genera and major clades within this large and diverse group. Here published hypotheses related to the phylogeny of this clade are reviewed, and representatives of each of the major clades are illustrated. Several new hypotheses related to the biogeography of the Euophryinae are reviewed. There is still support for a primary division of this clade across the Antarctic Land Bridge of southern Gondwanaland near the end of the Cretaceous, but an updated estimate of divergence time based on the most recent phylogeny is needed.

Keywords. Afresia, Afroeurasia, Anida, Antarctic Land Bridge, Antillean Arc, Antiphryni, Aphryni, Arkatiddi, Australasia, Australphryni, Beringia, dispersal, divergence, division of clade, Eocene, Euophryini, Gondphryni, Holophryni, isostasy, Lapsoida, late Eocene, Lydekker Line, Lyssoida, Mesophryni, Mopsoida, Neattidi, Neophryni, Nugini, Occidphryni, Orienphryni, Palaephryni, Panama Arc, Papuaphryni, phylogeny, plate tectonics, Sahul, Saitini, Southern Gondwanaland, Spartoida, Sunda, Sundaphryni, vicariance, Wallace Line, Wallacea, Wallacea

Phylogeny. It has been more than a decade since the first comprehensive phylogeny of the Euophryinae was published (Figure 1; Zhang 2012; Zhang & Maddison 2013). This was slightly revised several years later (Figure 2; Zhang & Maddison 2015), and the subfamily Euophryinae was also demoted to the level of a tribe (Euophryini) within the larger subfamily Salticinae (Maddison 2015). These earlier studies divided the Neotropical euophryines into three clades, one (the *Mesophryni*; Figure 1) in a basal position supporting the hypothesis of a Neotropical origin for *living* representatives of the family. A second clade (the *Antiphryni*) had a large Caribbean distribution, and was related to one of two groups of Afroeurasian euophryines, many with a Palearctic distribution. The third Neotropical clade (the *Neophryni*) was more closely related to two clades primarily found in Australasia (the *Australphryni* and the *Papuaphryni*), with many representatives in tropical Afroeurasia, particularly in Sunda (Southeast Asia to Bali). This phylogeny suggested not only that the group originated in South America, but also that it was divided between the Americas and Australasia at the end of the Eocene (~34 Ma), when the Antarctic Land Bridge broke up at both the southern South American and Tasmanian ends, a change associated with the onset of global cooling and circumpolar circulation of the cold southern ocean around the now-isolated Antarctic continent (Hill 2009; Zhang 2012). Seasonal euophryines could always follow a path to North America via either the Panamanian (Central American) or Antillean Island Arcs, and then continue on to Asia via a persistent Beringia connection (Hill & Edwards 2013). A different proposal for euophryine distribution, involving the possibility of ballooning or rafting across oceans, was previously suggested (Bodner 2009; Bodner & Maddison 2012). As Australasia (Sahul) moved north to approach tropical Asia (Sunda), movement of species *in both directions* between the two zoogeographic provinces, across the island archipelago of Wallacea east of Borneo and Bali, became more likely. This process can be observed today, as several recent euophryine, and other salticid (e.g., the chrysilines) genera, are now distributed across Wallacea (Hill 2010).

Euophryini	Holophryni	Mesophryni					<i>Anasaitis</i>	AM/C
		Palaephryni					<i>Corythalia</i>	AM/NT
							<i>Parvattus zhui*</i>	AE/EA
		Antiphryni					<i>Parabathippus shelfordi*</i>	AE/S
							<i>Euophrys frontalis*</i>	AE/T
							<i>Chalcoscirtus infimis*</i>	AE/H
							<i>Talavera minuta*</i>	AE/H
							<i>Pseudoeuophrys erratica*</i>	AE/T
							<i>Cobanus mandibularis* (Sidusa)</i>	AM/NT
							<i>Pensacola signata*</i>	AM/NT
							<i>Mexigonus</i>	AM/NA
							<i>Petemathis potoricensis*</i>	AM/C
							<i>Truncattus flavus*</i>	AM/C
		<i>Antillattus gracilis*</i>	AM/C					
		<i>Naphrys</i>	AM/NA					
		<i>Corticattus latus*</i>	AM/C					
		<i>Popcornella spiniformis*</i>	AM/C					
		<i>Compsodecta</i>	AM/C					
		<i>Bythocrotus</i>	AM/C					
		<i>Agobardus</i>	AM/C					
		<i>Chapoda</i>	AM/CA					
		<i>Maeota dichrura*</i>	AM/NT					
		<i>Marma</i>	AM/NT					
		<i>Amphidraus</i>	AM/NT					
		<i>Nebridia</i>	AM/NT					
	<i>Tylogonus auricapillus*</i>	AM/NT						
	<i>Rhyphelia (Soesilarishius)</i>	AM/NT						
	<i>Mopiopia (Tariona)</i>	AM/NT						
	<i>Coryphasia (Asaphobelis, Siloca)</i>	AM/NT						
	<i>Neonella vinnula*</i>	AM/NT						
	<i>Ecuadattus</i>	AM/NT						
	<i>Belliena</i>	AM/NT						
	<i>Illargus coccineus*</i>	AM/NT						
	<i>Servaea incana* (vestita)</i>	AA/A						
	<i>Jotus auripes*</i>	AA/A						
	<i>Prostheclina</i>	AA/A						
	<i>Maileus</i>	AE/S						
	<i>Saitis barbipes*</i>	AE/E						
	<i>Maratus (Hypoblemum, Lycidas)</i>	AA/A						
	<i>Emathis</i>	AE/S						
	<i>Lepidemathis</i>	AE/PH						
	<i>Chalcotropis</i>	AE/TA						
	<i>Colyttus bilineatus* (Donoessus)</i>	AE/TA						
	<i>Lagnus</i>	AE/O						
	<i>Thorelliola ensifera*</i>	AA/P						
	<i>Foliabitus longzhou*</i>	AE/TA						
	<i>Laufeia</i>	AE/EA						
	<i>Chalcovietnamicus (Junxattus)</i>	AE/S						
	<i>Lokina (Laufeia eximia)</i>	AE/S						
	<i>Orcevia keyserlingi*</i>	AE/S						
<i>Thiania (Thianiatara)</i>	AE/S							
<i>Chinophrys pengi*</i>	AE/EA							
<i>Thyenula</i>	AE/SA							
<i>Cytaea</i>	AA/SO							
<i>Euryattus</i>	AA/S							
<i>Phasmolia elegans*</i>	AA/P							
<i>Zabkattus brevis*</i>	AA/P							
<i>Viribestus suyanensis*</i>	AA/P							
<i>Variratina minuta*</i>	AA/P							
<i>Bulolia</i>	AA/P							
<i>Leptathamus paradoxus*</i>	AA/P							
<i>Coccorchestes</i>	AA/P							
<i>Canama</i>	AA/P							
<i>Bathippus</i>	AA/P							
<i>Pristobaeus (Palpelius)</i>	AA/P							
<i>Xenocytaea</i>	AA/O							
<i>Chalcolemia nakanai*</i>	AA/P							
<i>Sobasina</i>	AA/O							
<i>Efate albobicinctus*</i>	AA/O							
<i>Paraharmochirus</i>	AA/P							
<i>Chalcolecta</i>	AA/P							
<i>Ohilimia</i>	AA/P							
<i>Diolenius</i>	AA/P							
<i>Omoedus</i>	AA/P							
Gondphryni	Australphryni	Neophryni					<i>Servaea incana* (vestita)</i>	AA/A
							<i>Jotus auripes*</i>	AA/A
							<i>Prostheclina</i>	AA/A
							<i>Maileus</i>	AE/S
							<i>Saitis barbipes*</i>	AE/E
							<i>Maratus (Hypoblemum, Lycidas)</i>	AA/A
							<i>Emathis</i>	AE/S
							<i>Lepidemathis</i>	AE/PH
							<i>Chalcotropis</i>	AE/TA
							<i>Colyttus bilineatus* (Donoessus)</i>	AE/TA
							<i>Lagnus</i>	AE/O
							<i>Thorelliola ensifera*</i>	AA/P
							<i>Foliabitus longzhou*</i>	AE/TA
							<i>Laufeia</i>	AE/EA
							<i>Chalcovietnamicus (Junxattus)</i>	AE/S
	<i>Lokina (Laufeia eximia)</i>	AE/S						
	<i>Orcevia keyserlingi*</i>	AE/S						
	<i>Thiania (Thianiatara)</i>	AE/S						
	<i>Chinophrys pengi*</i>	AE/EA						
	<i>Thyenula</i>	AE/SA						
	<i>Cytaea</i>	AA/SO						
	<i>Euryattus</i>	AA/S						
	<i>Phasmolia elegans*</i>	AA/P						
	<i>Zabkattus brevis*</i>	AA/P						
	<i>Viribestus suyanensis*</i>	AA/P						
<i>Variratina minuta*</i>	AA/P							
<i>Bulolia</i>	AA/P							
<i>Leptathamus paradoxus*</i>	AA/P							
<i>Coccorchestes</i>	AA/P							
<i>Canama</i>	AA/P							
<i>Bathippus</i>	AA/P							
<i>Pristobaeus (Palpelius)</i>	AA/P							
<i>Xenocytaea</i>	AA/O							
<i>Chalcolemia nakanai*</i>	AA/P							
<i>Sobasina</i>	AA/O							
<i>Efate albobicinctus*</i>	AA/O							
<i>Paraharmochirus</i>	AA/P							
<i>Chalcolecta</i>	AA/P							
<i>Ohilimia</i>	AA/P							
<i>Diolenius</i>	AA/P							
<i>Omoedus</i>	AA/P							
Papuphryni	Neophryni					<i>Servaea incana* (vestita)</i>	AA/A	
						<i>Jotus auripes*</i>	AA/A	
						<i>Prostheclina</i>	AA/A	
						<i>Maileus</i>	AE/S	
						<i>Saitis barbipes*</i>	AE/E	
						<i>Maratus (Hypoblemum, Lycidas)</i>	AA/A	
						<i>Emathis</i>	AE/S	
						<i>Lepidemathis</i>	AE/PH	
						<i>Chalcotropis</i>	AE/TA	
						<i>Colyttus bilineatus* (Donoessus)</i>	AE/TA	
<i>Lagnus</i>	AE/O							
<i>Thorelliola ensifera*</i>	AA/P							
<i>Foliabitus longzhou*</i>	AE/TA							
<i>Laufeia</i>	AE/EA							
<i>Chalcovietnamicus (Junxattus)</i>	AE/S							
<i>Lokina (Laufeia eximia)</i>	AE/S							
<i>Orcevia keyserlingi*</i>	AE/S							
<i>Thiania (Thianiatara)</i>	AE/S							
<i>Chinophrys pengi*</i>	AE/EA							
<i>Thyenula</i>	AE/SA							
<i>Cytaea</i>	AA/SO							
<i>Euryattus</i>	AA/S							
<i>Phasmolia elegans*</i>	AA/P							
<i>Zabkattus brevis*</i>	AA/P							
<i>Viribestus suyanensis*</i>	AA/P							
<i>Variratina minuta*</i>	AA/P							
<i>Bulolia</i>	AA/P							
<i>Leptathamus paradoxus*</i>	AA/P							
<i>Coccorchestes</i>	AA/P							
<i>Canama</i>	AA/P							
<i>Bathippus</i>	AA/P							
<i>Pristobaeus (Palpelius)</i>	AA/P							
<i>Xenocytaea</i>	AA/O							
<i>Chalcolemia nakanai*</i>	AA/P							
<i>Sobasina</i>	AA/O							
<i>Efate albobicinctus*</i>	AA/O							
<i>Paraharmochirus</i>	AA/P							
<i>Chalcolecta</i>	AA/P							
<i>Ohilimia</i>	AA/P							
<i>Diolenius</i>	AA/P							
<i>Omoedus</i>	AA/P							

Figure 1. First hypothetical phylogeny of the euophryines (after Zhang 2012; Zhang & Maddison 2013). Names for major clades (e.g., *Mesophryni*, *Holophryni*) have been added here. An asterisk (*) next to a species name indicates that this is the type species for the respective genus. The larger pattern of distribution for each genus is coded at right as either American (AM), Afroeurasian (AE), or Australasian (AA). The more detailed distribution, to the right of each slash mark (/) in the right column, is as follows: A, Australia; C, Caribbean; CA, Central America; EA, East Asia; H, Holarctic; N, Neotropical; O., Oceania; P, New Guinea; PH, Philippines; S, Sunda; SA, South Africa; SO, Sunda to Oceania; SP, from Sunda to New Guinea; T, Temperate; TA, Tropical Asia.

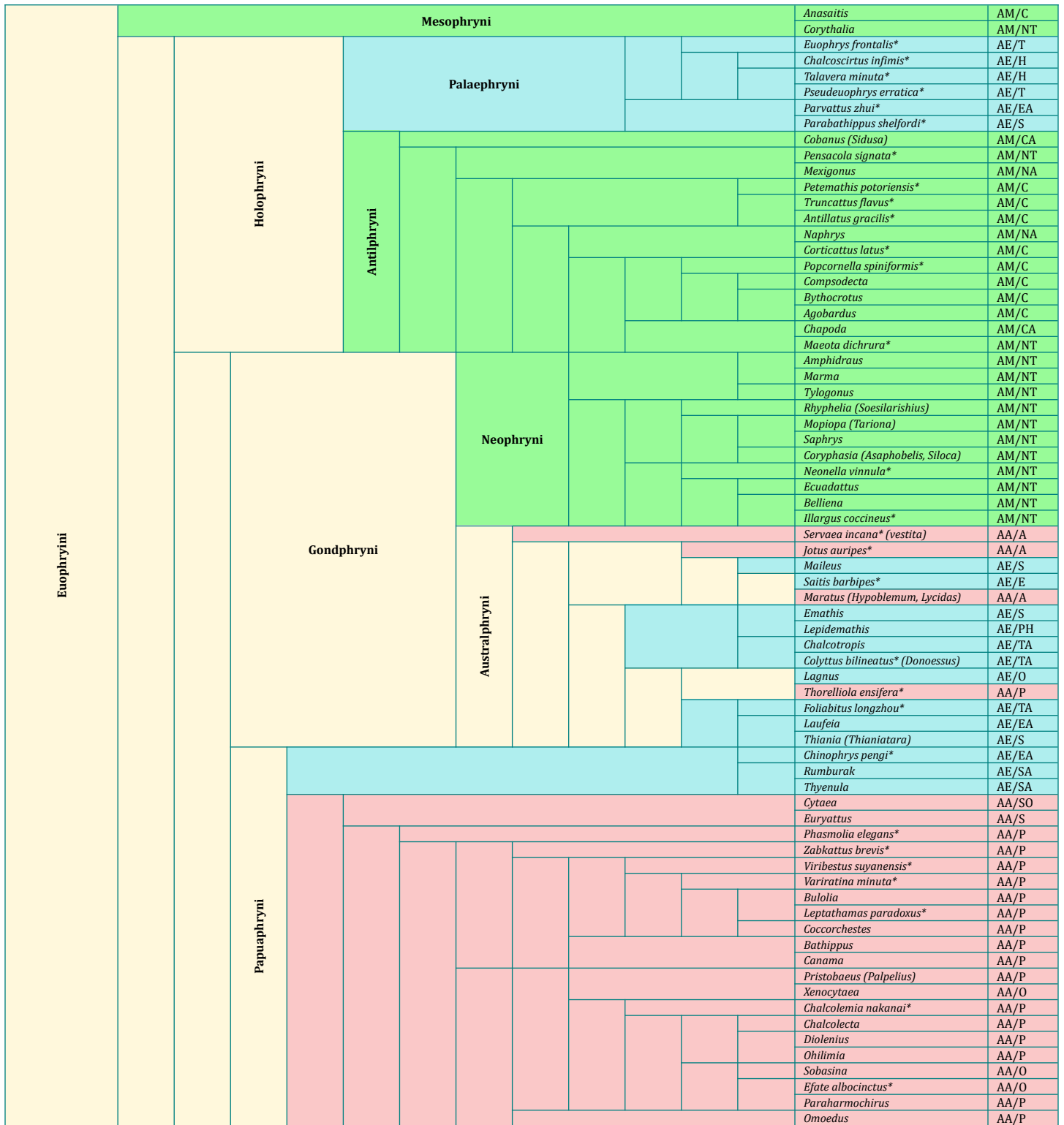


Figure 2. Second hypothetical phylogeny of the euophryines (after Zhang & Maddison 2015). Conventions used here are described in the caption for Figure 1. There are few changes from the earlier phylogeny (Figure 1), and no changes in the major clades that were recognized.

Recently two new phylogenies for the euophryines were published (Figures 3-4; Yu et al. 2024; Li et al. 2025), this time based on comparison of a larger set of ultra-conserved elements (UCE), more stable sections of the genome that appear to change less over time and can thus be more reliably followed over longer intervals.

Euophryini	Occidphryni (Clade I)	Holophryni	Palaephryni	<i>Chinophrys</i>	AE/EA	
				<i>Thyenula</i>	AE/SA	
				<i>Parabathippus shelfordi*</i>	AE/S	
				<i>Euophrys</i>	AE/T	
				<i>Chalcoscirtus</i>	AE/H	
				<i>Tylogonus</i>	AM/NT	
		Neophryni	Antilphryni	<i>Cobanus</i>	AM/CA	
				<i>Mexigonus</i>	AM/NA	
				<i>Corythalia</i>	AM/NT	
				<i>Maeota</i>	AM/NT	
				<i>Chapoda</i>	AM/CA	
				<i>Pristobaeus</i>	AA/P	
	Orientphryni (Clade II)	Australphryni	Wallacini	<i>Euryattus</i>	AA/S	
				<i>Cytaea</i>	AA/SO	
				<i>Jotus auripes*</i>	AA/A	
				<i>Prostheclina</i>	AA/A	
			Saitini	<i>Maratus</i>	AA/A	
				<i>Maileus fuscus*</i>	AE/S	
				<i>Canama forceps*</i>	AA/P	
				<i>Bathippus</i>	AA/P	
		Indophryni	Papuaphryni	<i>Coccorchestes</i>	AA/P	
				<i>Leptathamas paradoxus*</i>	AA/PH	
				<i>Bulolia</i>	AA/P	
				<i>Chalcolecta</i>	AA/P	
			Sundaphryni	Laufeia clade	<i>Pystira ephippigera*</i>	AA/S
					<i>Zenodorus</i>	AA/P
				MEC clade	<i>Thiania</i>	AE/S
					<i>Charippus</i>	AE/S
<i>Amoenema erhai*</i>	AE/EA					
<i>Laufeia aenea*</i>	AE/EA					
<i>Lokina</i>	AE/EA					
<i>Chalcovietnamicus vietnamensis*</i>	AE/S					
<i>Orcevia</i>	AE/S					

Figure 3. Third hypothetical phylogeny of the euophryines (after Yu et al. 2024, with names added for major clades). Conventions used here are described in the caption for Figure 1. Two clades (the *Laufeia* clade and the Modified Embolic Complex, or MEC clade) were recognized in this study. Unlike previous studies, all of the neotropical euophryines fell into a single clade, shown here as the *Neophryni*, and the euophryines as a group fell into two distinct clades.

The first of these new studies (Figure 3; Yu et al. 2024) produced a significantly different set of subclades within the Euophryini. First, the Neotropical euophryines (the Neophryni) now fell into a single clade, rather than the three clades (Mesophryni, Antilphryni, and Neophryni) proposed in the earlier studies (Figure 1-2). In this phylogeny, *Anasaitis* and *Corythalia* no longer occupy a separate, basal clade (the Mesophryni), and are closely related to *Mexigonus* and other genera in a subclade of the Neophryni with many Caribbean representatives, shown here as the *Antilphryni*.

The Neophryni, as part of the Occidenphryi, is most related to one or more Afroeurasian clades (primarily the Palaephryni), with a more temperate or African distribution. The second half of the euophryines, the Orientphryni, can be divided into two large clades, distributed almost entirely from Sunda to Sahul. One of these (the Indophryni) can be neatly divided into a distinctive Sahulian group (the Papuaphryni), and a Sundan group (the Sundaphryni). The second orientphryne clade, the Australphryni, is almost entirely Australasian.

The second of these new studies (Figure 4; Li et al. 2025), based on a somewhat different set of genera and species, particularly in the Sundaphryni, presented essentially the same hypothesis of euophryine evolution as did the study by Yu et al. (2024). This study also included *Saitis barbipes*, a synanthropic species found in gardens to the north of the Mediterranean Sea, but closely related to the peacock spiders (*Maratus*) of Australia. Several *Saitis* species may have been introduced to Europe on plants carried by Dutch or English traders sailing from Australasian ports (Otto & Hill 2012).

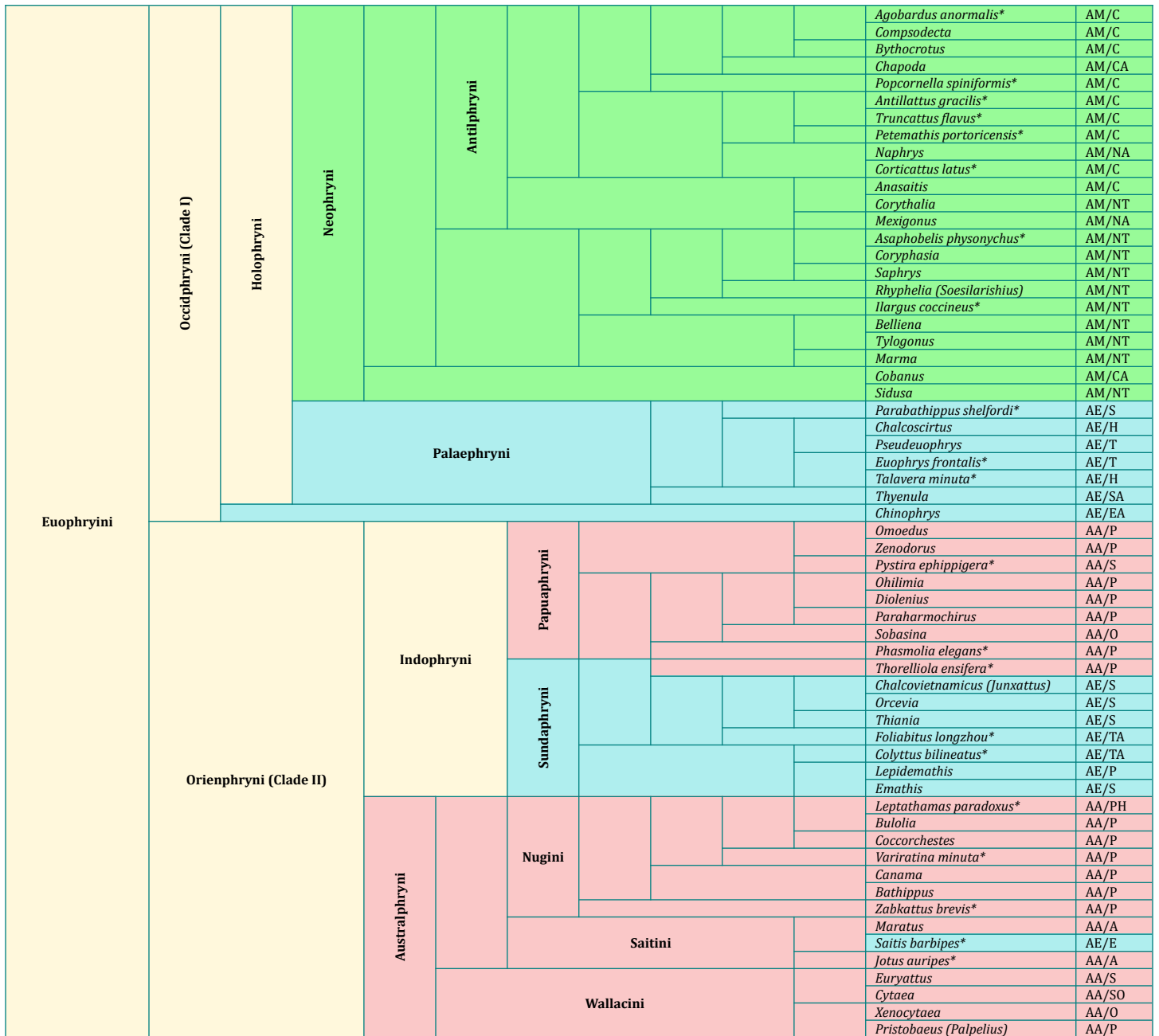


Figure 4. Fourth hypothetical phylogeny of the euophryines (after Li et al. 2025), with added clade names (e.g., *Neophryni*, *Papuaphryni*). This phylogeny agrees with that proposed by Yu et al. 2024, and designated the two euophryine subclades as *Clade I* (Occidphryni) and *Clade II* (Orienphryni). Conventions used here are described in the caption for Figure 1.

The major clades represented in published euophryine phylogenies are compared in Figure 5. The more recent work (Yu et al. 2024; Li et al. 2025) maintains the wide separation of euophryines in tropical Sunda (the *Sundaphryni*) from the temperate or African euophryines (the *Palaephryni*), but now the single clade of Neotropical euophryines (the *Neophryni*) is completely separated from those of Australasia (the *Orienphryni*).

Euophryini			Mesophryni
			Palaephryni
	Holophryni		Antilphryni
		Gondphryni	Neophryni
			Australphryni
			Papuaphryni

(Zhang 2012; Zhang & Maddison 2013, 2015)

Euophryini	Occidphryni (Clade I)	Holophryni	Neophryni	Antilphryni
				Palaephryni
	Orienphryni (Clade II)	Indophryni		Chinophrys
				Papuaphryni
				Sundaphryni
		Australphryni		Nugini
				Saitini
			Wallacini	

(Yu et al. 2024; Li et al. 2025)

Figure 5. Comparison of the major clades in the published phylogenies of the euophryine salticids, based on Figures 1-4.

Relationship of the Euophryni to other salticids. An updated phylogeny for the Salticidae that incorporates recent work (e.g. Zhang et al. 2024; Li et al. 2025) is shown in Figure 6.

Salticidae	Arcattidi			Lyssoida		Asemoneinae	AE		
						Lyssomaninae	AM		
	Spartoida			Spartaeinae	Spartaeini	Eupoinae	AE		
						Spartaeina	AE		
				Lapsoida		Holcolaetina	AE		
						Cocalodini	AA		
					Lapsiini	AM			
						Onomastinae	AE		
						Hisponinae	AE		
						Amycoida	AM		
				Afresia		Mopsoida	Baviini	AE	
						Marpissoida	Astioida	AA	
						Ballini	AE		
						Tisanibini	AE		
						Dendryphantini	AM		
				Anida		Nannenini	AE		
								Hasariini	AE
						Agorini	AE		
						Chrysillini	AE		
				Euophryini		Neophryni	AM		
						Occidenphryni		Palaephryni	AE
								Orienphryni	Indophryni
								Sundaphryni	AE
								Australphryni	AA
				Aphryni		Plexippini	Plexippina	AE	
								Harmochirina	AE
								Salticini	AE
								Leptorchestini	AE
						Aelurillina	AE		
			Aelurillini		Freyina	AM			
							Thiratoscirtina	AE	

Figure 6. Updated hypothesis for salticid phylogeny (based on Bodner & Maddison 2012; Zhang & Maddison 2013, 2015; Maddison et al. 2014, 2020; Maddison 2015; Ruiz & Maddison 2015; Maddison & Szűts 2019; Hill 2023; Azevedo et al. 2024; Zhang et al. 2024; Yu et al. 2024; Li et al. 2025, with addition of names for many previously unnamed clades). Biogeographical regions (column at right): AA, Australasia; AE, Afroeurasia; AM, Americas.

According to this phylogeny, the second large clade of "modern" salticids, the *Salticoida* (sister to the neotropical *Amycoidea*), is divided into two clades, the *Afresia* (including both the American marpissoids and the Australasian astioids) and the *Saltafresia*. The *Saltafresia* is then divided into two clades, the *Anida* (including the Afroeurasian chrysillines) and the *Simonida*. Then the *Simonida* is divided into two clades, the *Euophryni* and its sister group, the *Aphryni* (including mostly Afroeurasian plexippines and aelurillines).

This phylogeny supports the hypothesis that a direct ancestor of the euophryines was an Afroeurasian member of the *Simonida*. At the same time, the most recent common ancestor (MRCA) of all of the living euophryines may have lived on any continent, particularly if this species lived before the separation of southern Gondwanaland (South America, Antarctica, Australasia) at the end of the Eocene. Zhang & Maddison (2013) proposed a timeline for the divergence of the euophryines that estimated separation of the major clades in this time frame (~34 Ma), but their work was based on the earlier phylogeny that was recently superceded by Li et al. (2025). In a subsequent section I will consider a series of different biogeographical hypotheses, any one of which might explain the continental distribution of living euophryine clades.

Diversity of the living euophryines. Here (Figures 7-37) I provide a photographic catalog showing representatives of the living euophryine clades, collected from a large series of photographs posted online at the *iNaturalist* site by many different photographers and naturalists. These have all been edited or modified for this presentation, but their identification generally follows that posted on *iNaturalist*. The credit for each photograph includes the applicable *Creative Commons* license, as well as the respective *iNaturalist* observation number (iNat. obs.).

Previously, Zhang & Maddison (2015) published an extensive set of figures covering the euophryines, and this included a detailed treatment of the genital structures (male pedipalps and female epigyna) that are important for taxonomy. Subsequently I published a review of salticid scales (Hill 2022b) that includes many euophryines. The catalog presented here is not meant to replace those references, but to supplement them with more photographs of living species, arranged according to the most recent hypothesis of euophryine phylogeny (Figure 3). This presentation highlights the fact that, although they generally exhibit little variation in genitalic structure, the euophryines are remarkably diverse.

The *Euophryini* represents a large fraction of the described jumping spiders, and each year many new species in this clade are discovered and described. Why, as a group, have they been so successful? What features, apart from those that they share with other salticids, can account for this success?

An ability to contend with cooler or seasonal habitats in both the north and south may account for the global distribution of the euophryines; by comparison the amycoids, a more basal lineage, are still primarily restricted to tropical areas (Zhang & Maddison 2013). After their early divergence and appearance on multiple continents, euophryine lineages have continued to evolve into the many species that we see today (*continental radiation*; Zhang 2012). One characteristic of euophryines that may have contributed to their success is their ability to prey on ants. Although ant-eating, or *myrmecophagy*, can be observed in a number of different and unrelated salticid groups, many euophryines (e.g., *Anasaitis*, *Chalcotropis*, *Corythalia*, *Naphrys*, *Pystira*, *Zenodorus*, *Zoropsis*) have evolved the special behaviors required to observe, follow, and capture ants (Zhang & Maddison 2013; Maddison 2015). Many of these are considered to feed almost exclusively on ants, and many are ground-dwellers. The relatively large ALE of most euophryines, consistently at least one-half the diameter of the AME, may support their ability to track moving ants (Hill 2022a).



Figure 7. *Anasaitis* (Antilphryni). **1**, ♀ *Anasaitis*, Quintano Roo, Mexico. **2**, ♂ *Anasaitis*, Quintano Roo, Mexico. **3**, ♂ *A. canalis*, Panama. **4**, ♂ *A. canosus*, South Carolina. **5-6**, ♀ *A. canosus*, South Carolina. Almost all *Anasaitis* species are endemic to Caribbean islands. They are often observed in the leaf litter or near the ground, feeding on ants. Photo credits: 1, iNat.obs. 106183479, CC0, by Zygy; 2, iNat.obs. 110325999, CC0, by Zygy; 3, iNat.obs.134390964, CC BY-NC 4.0, © Nadja Baumgartner; 4-6, CC BY 4.0, © D. E. Hill.



Figure 8. *Corythalia* (Antilphryni). 1-2, ♂ *C. opima*, Panama. 3-4, ♂ *C. parvula*, Belize. 5, ♀ *C. parvula*, Belize. 6, ♂ *C. pulchra*, Panama. This is a large genus, widely distributed in the Neotropics. Photo credits: 1-2, iNat.obs. 162030175, CC0, by Zygy; 3-4, iNat.obs. 81564048, CC0, by Zygy; 5, iNat.obs. 196805804, CC0, by Zygy; 6, iNat.obs. 163822771, CC0, by Zygy.



Figure 9. *Corythalia* (Antilphryni). **1-2**, ♂ *C. spiralis*, Panama. **3-4**, ♂ *Corythalia*, Belize. **5-6**, ♀ *Corythalia*, Coasta Rica. Photo credits: 1-2, iNat.obs. 158425603, CC0, by Zygy; 3-4, iNat.obs. 261551073, CC0, by Zygy; 5-6, iNAT.obs. 199473033, CC0, by Zygy.



Figure 10. *Maeota* (Antilphryni). **1**, ♂ *M. dichrura*, Ibiporã, Brasil. **2**, ♂ *M. dichrura*, Misiones Province, Argentina. **3-4**, ♂ *Maeota*, Puyo, Ecuador. **5-7**, ♀ *Maeota*, Maringá, Brasil. Photo credits: 1, iNat.obs. 25363184, CC BY-NC 4.0, © Ísis Meri Medri; 2, iNat.obs. 259789000, CC BY-NC 4.0, © Ivan L. F. Magalhaes; 3-4, iNat.obs. 37801641, CC0, by Zygy; 5-7, iNat.obs. 37116922, CC BY-NC 4.0, © Ísis Meri Medri.



Figure 11. Antilphrynes. 1, ♂ *Antillatus cambridgei*, Dominican Republic. 2, ♀ *Chapoda*, Costa Rica. 3-4, ♀ *Compsodecta*, Jamaica. 5-6, ♂ *Mexigonus*, Costa Rica. *Chapoda* live above the ground. Only a few of the ground-dwelling *Mexigonus* species have been described. Photo credits: 1, iNat.obs. 127016134, CC BY-NC 4.0, © Antonio Tosto; 2, iNat.obs. 199638978, CC0, by Zygy; 3-4, iNat.obs. 20554590, CC0, by Zygy; 5-6, iNat.obs. 199838776, CC0, by Zygy.



Figure 12. Antilphrynes. **1-2,** ♂ *Mexigonus*, near Morelos, Mexico. **3,** ♂ *Mexigonus*, Oaxaca, Mexico. **4-5,** ♀ *Pensacola*, Belize. **6-7,** ♂ *Naphrys pulex*, New Jersey. *Naphrys* are common inhabitants of the leaf-litter in the southeastern United States, often feeding on ants, and sometimes synanthropic. Photo credits: 1, iNat.obs. 108320077, CC BY 4.0, © Gerardo Ochoa; 2, iNat.obs. 104733815, CC0, by Zygy; 4-5, iNat.obs. 260875934, CC0, by Zygy; 6-7, iNat.obs. 222330959, CC BY 4.0, © RL7836.

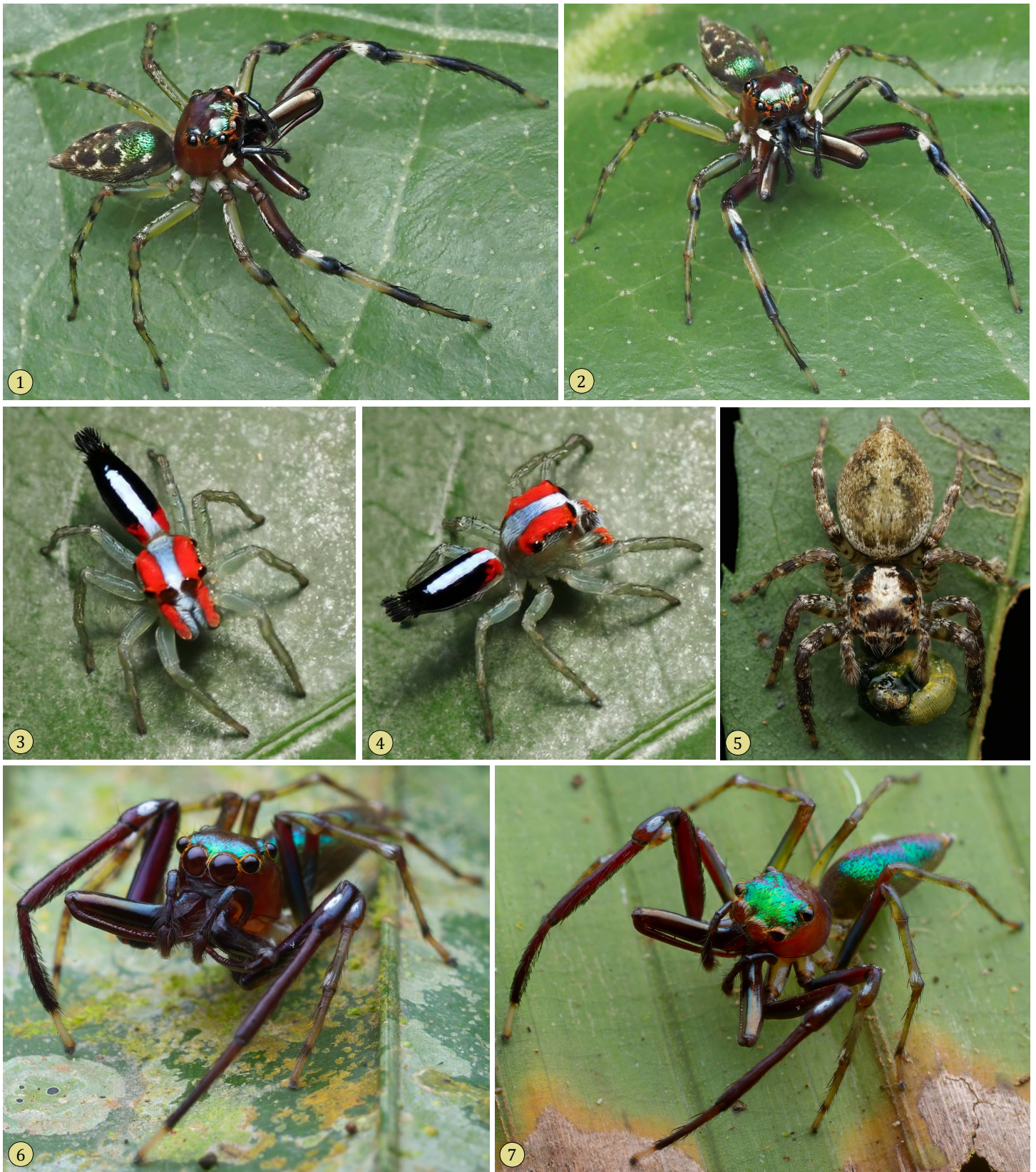


Figure 13. Other neophryines. **1-2**, ♂ *Cobanus*, Costa Rica. **3-4**, ♂ *Ilargus coccineus*, São Paulo, Brazil. **5**, ♀ *Asaphobelis physonychus*, Paraná, Brazil. **6-7**, ♂ *Sidusa*, Belize. Photo credits: 1-2, iNat.obs. 198505792, CC0, by spidereyes; 3-4, iNat.obs. 194628698, CC BY 4.0, © Leonardo Breder Passalacqua; 5, iNat.obs. 202733751, CC0, by brabuleta; 6-7, iNat.obs. 100186115, CC BY-NC 4.0, © Thomas Shahan.

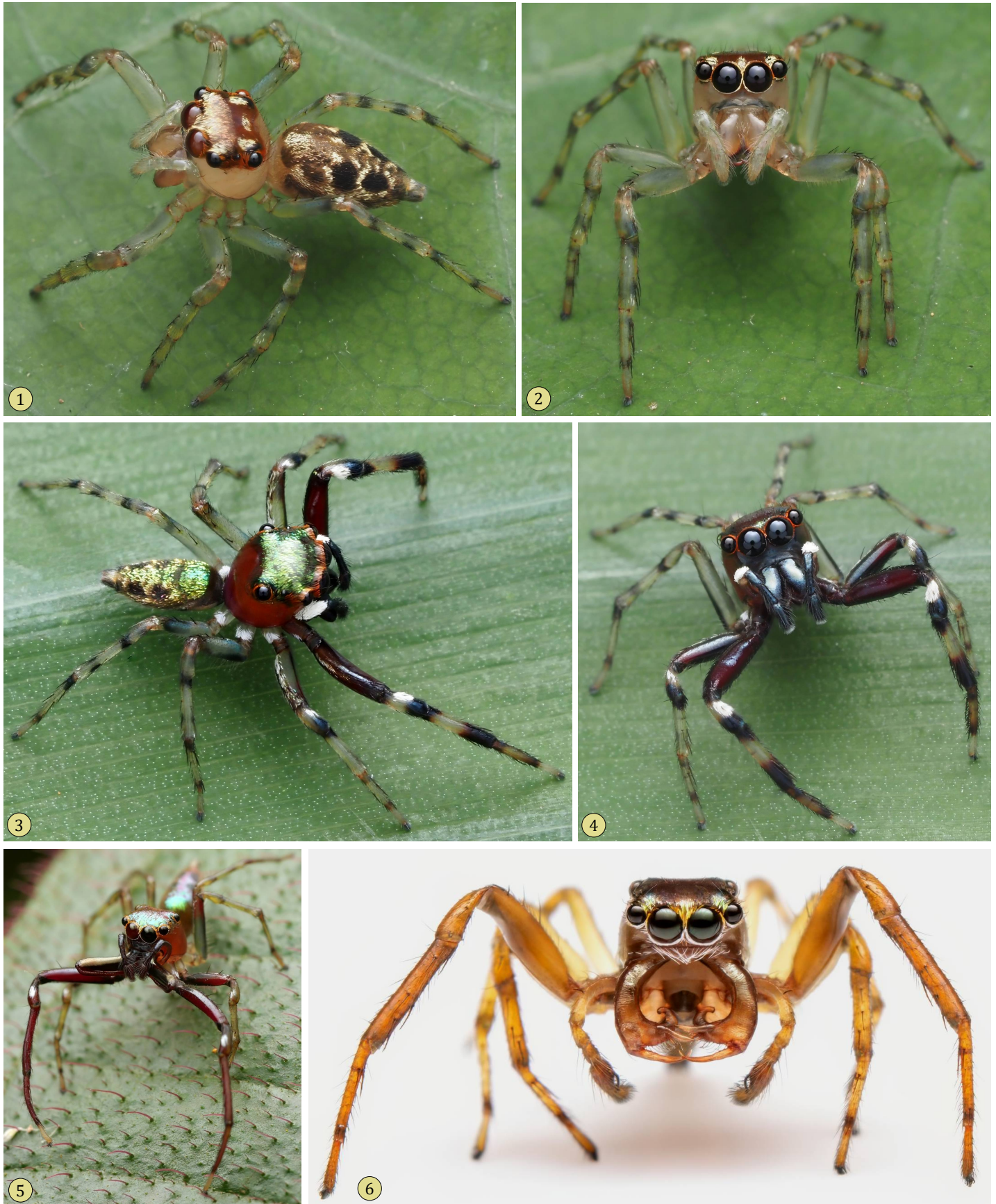


Figure 14. Other Neophrynes. **1-2,** ♀ *Sidusa*, Costa Rica. **3-4,** ♂ *Sidusa*, Costa Rica. **5,** ♂ *Sidusa*, Esmeraldas, Ecuador. **6,** ♂ *Tylogonus parabolicus*, Cali, Colombia. Photo credits: 1-2, iNat.obs. 198545408, CC0, by spidereyes; 3-4, iNat.obs. 199518006, CC0, by Zygy; 5, iNat.obs. 99564968, CC0, Philipp Hoenle; 6, CC BY-NC 4.0, © Tiziano Hurni-Cranston.



Figure 15. Palaephrynes. **1,** ♀ *Chalcoscirtus infimus*, Spain. **2,** ♀ *Euophrys frontalis*, France. **3,** ♀ *Euophrys leipoldti*, Northern Cape, South Africa. **4,** ♂ *Euophrys herbigrada*, France. **5,** ♂ *Euophrys monadnock*, British Columbia. **6,** ♂ *Euophrys nigripalpis*, France. **7,** ♂ *Euophrys rufibarbis*, Croatia. *Euophrys* is a large, primarily Afroeurasian genus with 98 described species (WSC 2025). The relationship of the species currently placed in this genus, particularly the American species, is uncertain (Zhang & Maddison 2015). Photo credits: 1, iNat.obs. 132678652, CC BY-NC 4.0, © faluke; 2, iNat.obs. 122945758, CC BY-NC 4.0, © Martin Galli; 3, iNat.obs. 107499954, CC BY-NC 4.0, © Rudolph Steenkamp; 4, iNat.obs. 165160372, CC BY-NC 4.0, © durand_mathis; 5, iNat.obs. 100808042, CC BY-NC 4.0, © Jason Headley; 6, iNat.obs. 160178290, CC BY-NC 4.0, © durand_mathis; 7, iNat.obs. 245239927, CC BY-NC 4.0, © Mark Spicer.



Figure 16. *Parabathippus* (Palaephryni). 1-2, ♂ *Parabathippus*, Bogor, West Java. 3-4, ♂ *Parabathippus*, Sumatra. 5, ♂ *Parabathippus*, Sumatra. 6-7, ♀ *P. shelfordi*, Singapore, feeding on an isopod. There are 10 named species in this genus, all from Sunda. The general appearance of *Parabathippus* is quite different from the appearance of most other palaephrynes, like *Euophrys* and *Thyenula*, which are compact with shorter legs. Photo credits: 1-2, iNat.obs. 68647495, CC BY 4.0, © Wildan R. Ardani; 3-4, iNat.obs. 203321332, CC BY-NC 4.0, © Bridgette Gower; 5, iNat.obs. 253471925, CC BY-NC 4.0, © Bridgette Gower; 6-7, iNat.obs. 171021488, CC BY-NC 4.0, © Md Jusri.



Figure 17. Palaephrynes. 1, ♀ *Parabathippus shelfordi*, Singapore, guarding her eggs beneath a leaf. 2, ♀ *Parabathippus shelfordi*, Singapore, guarding her hatching brood. 3, ♀ *Pseudeuophrys lanigera*, Switzerland. 4-5, ♂ *Talavera minuta*, New Jersey. 6-7, ♀ *Talavera petrensis*, Czechia. 8-9, ♀ *Thyenula*, Harare, Zimbabwe. 10-11, *Thyenula haddadi*, Dududu, South Africa. Photo credits: 1, iNat.obs. 259819122, CC BY-NC 4.0, © Melvyn Yeo; 2, iNat.obs. 230449083, CC BY-NC 4.0, © Melvyn Yeo; 3, iNat.obs. 202250103, CC BY-NC 4.0, © Nadja Baumgartner; 4-5, iNat.obs. 203511578, CC BY 4.0, © RL7836; 6-7, iNat.obs. 203008214, CC0, Philipp Hoenle; 8-9, iNat.obs. 184495903, CC0, by Dan Lee; 10-11, iNat.obs. 105031998, CC BY-NC 4.0, © Rudolph Steenkamp.



Figure 18. *Thyenula* (Palaephryni) from southern Africa. **1**, ♀ *T. juvenca*, Eastern Cape, South Africa. **2**, ♀ *T. munda*, Harare, Zimbabwe. **3-4**, ♂ *T. leighi*, Rustenburg, South Africa. **5**, ♀ *Thyenula*, Bloemfontein, South Africa. **6**, ♂ *T. virgulata*, Mpumalanga, South Africa. Photo credits: 1, iNat.obs. 219370146, CC BY 4.0, © Dan Mendelowitz; 2, iNat.obs. 67801175, CC0, by Jonathan Whitaker; 3-4, iNat.obs. 199283802, CC BY-NC 4.0, © Rudolph Steenkamp; 5, iNat.obs. 107553854, CC BY-NC 4.0, © Rudolph Steenkamp; 6, iNat.obs. 134198928, CC BY-NC 4.0, © Robert Wienand.



Figure 19. Papuaphrynes. **1**, *Chalcolecta prensitans*, New Mapoon, Queensland. **2**, ♂ *Chalcolecta prensitans*, Iron Range, Queensland. **3**, ♂ *Ohilimia*, Cairns, Queensland. **4**, *Diolenius*, near Madang, Papua. **5-6**, ♀ *Diolenius*, Raja Ampat, Waigeo. Legs I of *Ohilimia* and *Diolenius* have elongated trochanters (Hill & Ng 2025). Photo credits: 1, iNat.obs. 117949956, CC BY-NC 4.0 © Mark Simpson; 2, iNat.obs. 193584197, CC BY-NC 4.0, © Maurice Allan; 3, iNat.obs. 243239767, CC BY-NC 4.0, © Bridgette Gower; 4, iNat.obs. 117949956, CC0, by Philipp Hoenle; 5-6, iNat.obs. 198590377, CC BY-NC 4.0 © Spark.



Figure 20. Papuaphrynes from the Southern Highlands Province of Papua New Guinea. **1**, ♂ *Diolenius varius*, Tualapa. **2**, ♀ *Diolenius varius*, Tualapa. **3**, ♂ *Paraharmochirus tuaplapa*, Tualapa. **4**, ♂ *Paraharmochirus*, Putuwé. **5-6**, ♂ *Phasmolia elegans*, Tualapa. **7**, ♀ *Phasmolia elegans*, Tualapa. **8**, ♂ *Sobasina*, Umgé. **9**, ♂ *Sobasina*, Putuwé. *Paraharmochirus* and *Sobasina* appear to be ant-mimics. Photo credits: 1-9, CC BY 3.0, © W. Maddison.



Figure 21. Papuaphrynes. 1, ♀ *Omoedus baloghi*, Madang, Papua. 2-3, ♂ *Omoedus bunbi*, Madang, Papua. 4-5, ♂ *Omoedus koehalmii*, Madang, Papua. 6-11, *Pystira ephippigera*, an ant-eating jumping spider: 6, ♀, Singapore. 7-8, ♂, Singapore. 9, ♀, Malaysia. 10, ♀, Singapore, feeding on ant. 11, ♀, Kuala Lumpur, feeding on ant. Photo credits: 1, iNat 116954053, CC0, by Philipp Hoenle; 2-3, iNat.obs. 133152073, CC0, by Philipp Hoenle; 4-5, iNat.obs. 126054558, CC0, by Philipp Hoenle; 6, iNat. 212288622, CC BY-NC 4.0, © Justin Chan; 7-8, iNat.obs. 168641108, CC BY-NC 4.0, © Md Jusri; 9, iNat.obs. 228558425, CC BY-NC 4.0, © Melvyn Yeo; 10, iNat.obs. 231633361, CC BY-NC 4.0, © Melvyn Yeo; 11, iNat.obs. 154941428, CC BY-NC 4.0, © Nadja Baumgartner.



Figure 22. *Zenodorus orbiculatus* (Papuaphryni) feeding on ants in Queensland. **1**, ♀, Tamborine Mountain. **2**, ♀, Brisbane. **3**, ♂, Lake Manchester. **4**, ♀, Stradbroke Island. **5**, ♀, Brisbane. **6-8**, ♀, Bundaberg. Photo credits: 1, iNat.obs. 141311792, CC BY 4.0, © Ged Tranter; 2, iNat.obs. 193007118, CC BY-NC 4.0, © Steve Murray; 3, iNat.obs. 184848087, CC BY 4.0, © Ged Tranter; 4, iNat.obs. 103666902, CC BY-NC 4.0, © Adriano Losso; 5, iNat.obs. 237606484, CC BY-NC 4.0, © rick_franks; 6-8, iNat.obs. 29677916, CC BY-NC 4.0, © tony_d.



Figure 23. *Zenodorus* (Papuaphryni). 1, ♀ *Z. metallescens*, Eley NP, Northern Territory. 2-4, ♀ *Z. swiftorum*, Cairns, Queensland. 5, ♂ *Zenodorus*, Maluku, Indonesia. 6, ♂ *Zenodorus*, West Papua. Photo credits: 1, iNat.obs. 87233674, CC BY-NC 4.0, © Daniel Kurek; 2-4, iNat.obs. 207898055, CC BY-NC 4.0, © Roxanne Lazarus; 5, iNat.obs. 243032060, CC BY-NC 4.0, © ArloPelegrin; 6, iNat.obs. 200374531, CC BY-NC 4.0, © Imam Taufik Hidayat.



Figure 24. *Chalcovietnamicus* (Sundaphryni). **1**, ♂ *C. daiqini*, Singapore. **2**, ♂ *C. daiqini*, Singapore. **3**, ♀ *C. daiqini*, Sarawak. **4**, ♀ *C. daiqini*, Singapore, feeding on ant. **5**, ♀ *C. daiqini*, Singapore, feeding on ant. **6-7**, ♂ *Chalcovietnamicus cf. vietnamensis*, Singapore. Photo credits: 1, iNat.obs. 236444345, CC BY-NC 4.0, © Melvyn Yeo; 2, iNat.obs. 142262149, CC BY-NC 4.0, © Julian F; 3, iNat.obs. 215465031, CC BY-NC 4.0, © DolceAmore; 4, iNat.obs. 242400209, CC BY-NC 4.0, © Melvyn Yeo; 5, iNat.obs. 178803009, CC BY-NC 4.0, © Joshua Wong; 6-7, iNat.obs. 232009789, CC BY-NC 4.0, © Melvyn Yeo.



Figure 25. *Colyttus* (Sundaphryni). 1, ♂ *C. striatus*, Sumatra. 2, ♀ *C. striatus*, Selangor, Malaysia. 3-4, ♀ *C. striatus*, Sarawak. 5-6, ♂ *Colyttus*, Singapore. Photo credits: 1, iNat.obs. 210090711, CC BY-NC 4.0, © franegan; 2, iNat.obs. 119230995, CC BY-NC 4.0, © jstan_photographies; 3-4, iNat.obs. 250678113, CC BY-NC 4.0, © DolceAmore; 5-6, iNat.obs. 228605350, CC BY-NC 4.0, © Melvyn Yeo.



Figure 26. Sundaphryni. 1, ♀ *Colyttus* with captured Green Tree (Asian Weaver) Ant, *Oecophylla smaragdina*, Chiang Mai, Thailand. 2, ♂ *Colyttus bilineatus*, Singapore. 3, ♂ *Colyttus*, Tha Pha, Thailand. 4, *Colyttus*, Johor, Malaysia. 5-7, *Charippus minotaurus*, Kumai, Borneo. 8, *Laufeia*, Singapore. 9, *Laufeia*, Gunung Pulai Forest. 10, *Laufeia*, Singapore. Photo credits: 1, iNat.obs. 189205343, CC BY 4.0, © yipsee; 2, iNat.obs. 66135601, CC BY-NC 4.0, © budak; 3, iNat.obs. 253409381, CC BY-NC 4.0, © Ayeogi; 4, iNat.obs. 229880437, CC BY-NC 4.0, © Melvyn Yeo; 5-7, iNat.obs. 203001050, CC BY-NC 4.0, © Tiziano Hurni-Cranston; 8, iNat.obs. 236444133, CC BY-NC 4.0, © Melvyn Yeo; 9, iNat.obs. 242607985, CC BY-NC 4.0, © Melvyn Yeo; 10, iNat.obs. 243257321, CC BY-NC 4.0, © Melvyn Yeo.

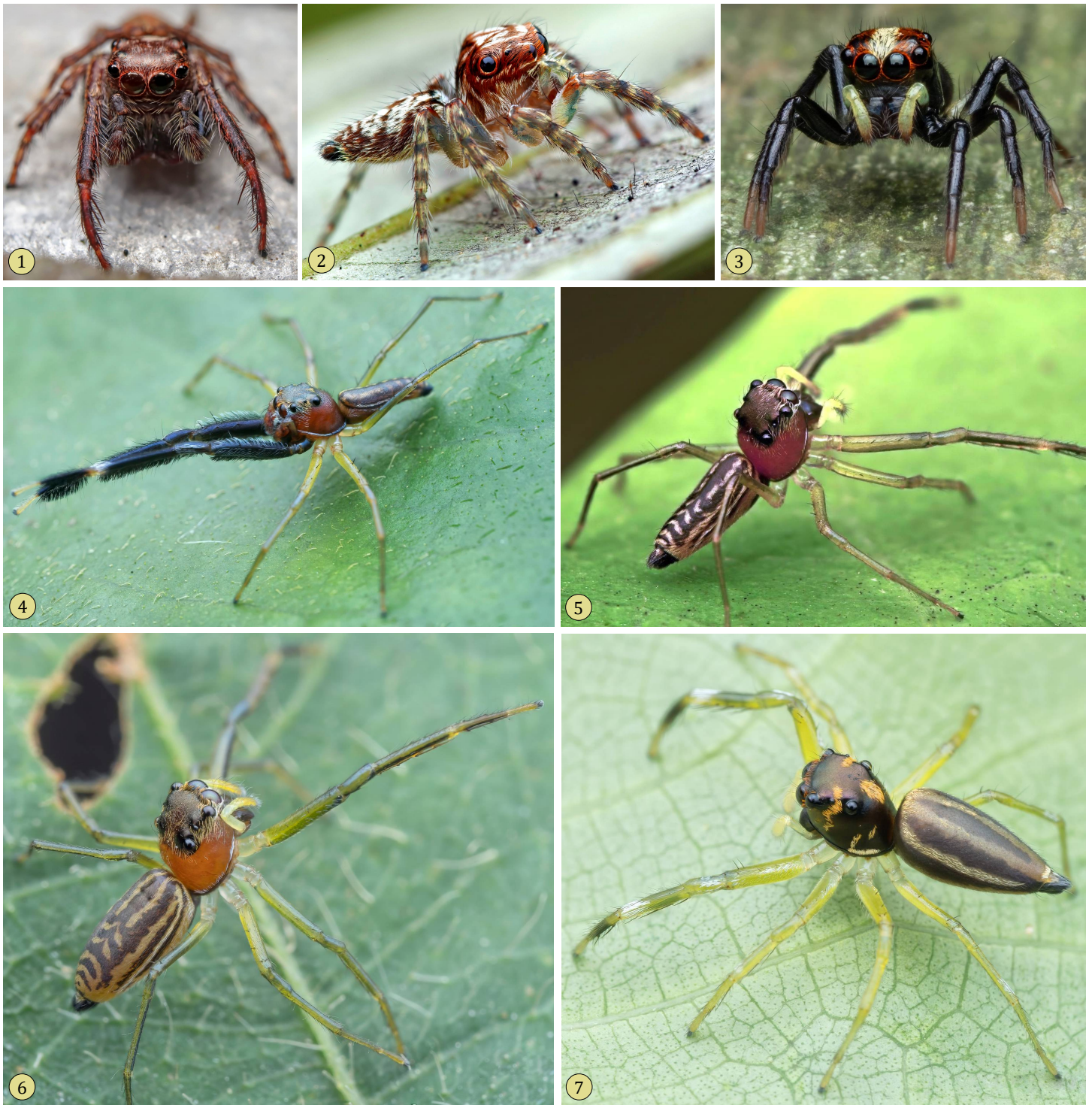


Figure 27. Sundaphryni. 1, ♂ *Emathis gombak*, Singapore. 2, ♀ *Emathis gombak*, Singapore. 3, ♀ *Emathis*, Sarawak. 4, ♂ *Foliabitus*, Johor, Malaysia. 5, ♀ *Foliabitus*, Malaysia. 6, ♀ *Foliabitus*, Johor, Malaysia. 7, ♀ *Foliabitus*, Bekok, Johor, Malaysia. Photo credits: 1, iNat.obs. 91363421, CC BY-NC 4.0, © Nikolay Petrov; 2, iNat.obs. 260485194, CC BY-NC 4.0, © Melvyn Yeo; 3, iNat.obs. 213157686, CC BY-NC 4.0, © DolceAmore; 4, iNat.obs. 229880377, CC BY-NC 4.0, © Melvyn Yeo; 5, iNat.obs. 31455696, CC BY-NC 4.0, © Richard Ong; 6, iNat.obs. 240731003, CC BY-NC 4.0, © Melvyn Yeo; 7, iNat.obs. 241851183, CC BY-NC 4.0, © Melvyn Yeo.



Figure 28. Sundaphryni. **1**, *Lepidemathis*, Maasin City, Philippines. **2-3**, ♂ *Orcevia prozysniskii*, Hong Kong. **4-6**, ♂ *Orcevia*, Sarawak. **7**, ♀ *Orcevia*, Singapore. **8-9**, ♂ *Orcevia*, Bekok, Malaysia. **10**, ♂ *Thorelliola ensifera*, Singapore. **11-12**, ♂ *Thorelliola ensifera*, Bali. The male *T. ensifera* has two stout anterior spines at the median, just below the front eye row. Photo credits: 1, iNat.obs. 163773573, CC BY 4.0, © Kai Squires; 2-3, iNat.obs. 104166203, CC BY-NC 4.0, © Colin Chiu; 4-6, iNat.obs. 190985129, CC BY-NC 4.0, © DolceAmore; 7, iNat.obs. 243561015, CC BY-NC 4.0, © Melvyn Yeo; 8-9, iNat.obs. 241851174, CC BY-NC 4.0, © Melvyn Yeo; 10, iNat.obs. 228799708, CC BY-NC 4.0, © Melvyn Yeo; 11-12, iNat.obs. 257573124, CC BY 4.0, © Lawrence Hylton.



Figure 29. *Thiania* (Sundaphryni). Male *T. suboppressa* are known as "fighting spiders." The 28 named species in this genus are distributed from South to East Asia **1-2**, ♂ *T. bhamoensis*, near Hong Kong. **3**, ♂ *T. bhamoensis*, Penang. **4**, ♂ *T. bhamoensis*, near Singapore. **5**, ♂ *T. suboppressa*, Hong Kong. **6**, ♂ *T. suboppressa*, Hong Kong, ritual combat. **7-8**, ♀ *T. latefasciata*, Bekok, Johor, Malaysia. Photo credits: 1-2, iNat.obs. 123194814, CC BY 4.0, © Lawrence Hylton; 3, iNat.obs. 37835808, CC BY-NC 4.0, © Tony Iwane; 4, iNat.obs. 230267621, CC BY-NC 4.0, © Melvyn Yeo; 5, iNat.obs. 123651836, CC BY 4.0, © Lawrence Hylton; 6, iNat.obs. 122927233, CC BY 4.0, © Lawrence Hylton; 7-8, iNat.obs. 243569421, CC BY-NC 4.0, © Melvyn Yeo.



Figure 30. Nugini (Australphryni). 1-2, ♂ *Bathippus*, Wau, Papua. 3, ♂ *Bathippus*, Papua Barat. 4, ♂ cf. *Bathippus*, Madang, Papua. 5, ♂ *Canama*, Cape Tribulation, Queensland; 6, ♂ *Canama hinnulea*, Cape Tribulation, Queensland. Photo credits: 1-2, iNat.obs. 124092772, CC0, by Philipp Hoenle; 3, iNat.obs. 170232760, CC BY-NC 4.0, © Spark; 4, iNat.obs. 136799190, CC0, by Philipp Hoenle; 5, iNat.obs. 168442693, CC BY-NC 4.0 © Dee Newton; 6, iNat.obs. 236700837, CC BY 4.0, © Alan Henderson.



Figure 31. *Coccorchestes* (Australphryni: Nugini). These small salticids, endemic to tropical Australasia, live in close association with the diverse weevils that they closely mimic (Allan 2022). Little is known of their behavior. More than 40 species have been named (WSC 2025). **1-3**, *C. ferreus*, Iron Range, Queensland. **4-6**, *Coccorchestes*, Manokwari, West Papua. **7-8**, ♂ *Coccorchestes*, Manokwari, West Papua. **9**, *Coccorchestes*, Manokwari, West Papua. **10-12**, *Coccorchestes*, Madang, Papua. Photo credits: 1-3, iNat.obs. 193575568, CC BY-NC 4.0 © Maurice Allan; 4-6, iNat.obs. 170251995, CC BY-NC 4.0 © Spark; 7-8, iNat.obs. 170276115, CC BY-NC 4.0 © Spark; 9, iNat.obs. 170316791, CC BY-NC 4.0 © Spark; 10-12, iNat.obs. 18672477, CC0, by Philipp Hoenle.



Figure 32. Saitini (Australphryni). **1-2,** ♂ *Saitis barpipes*, near Paris, France. Several Australian species have also been assigned to the genus *Saitis*. **3-4,** ♂ *Prostheclina pallida*, Blue Mountains, New South Wales. **5,** ♂ *Jotus auripes*, Victoria. **6,** ♂ cf. *Saitis*, Wodonga, Victoria. Photo credits: 1-2, iNat.obs. 49986763, CC BY-NC 4.0, © Cédric Mondy; 3-4, iNat.obs. 254052265, CC BY 4.0, © Ioannis Magouras; 5, iNat.obs. 191746884, CC BY-NC 4.0, © Nick Volpe; 6, iNat.obs. 185458697, CC BY-NC 4.0, © Craig Loeche.



Figure 33. *Maratus* (Australphryni: Saitini). More than 100 species of *Maratus* (peacock spiders) have now been described, all endemic to Australia. **1-2**, ♂ *M. anomalus*, Kumbarilla, Queensland. **3**, ♂ *M. bubo*, north Walpole, Western Australia. **4**, ♂ *M. griseus*, New Zealand. **5**, *M. karrie*, Quininup, Western Australia. **6**, *M. occasus*, near Brisbane. **7**, *M. ottoii*, near Brisbane. Photo credits: 1-2, iNat. obs. 186683528, CC BY-NC 4.0, © waynew-m; 3, iNat. obs. 141652818, CC BY-NC 4.0, © Bridgette Gower; 4, iNat. obs. 154666027, CC BY-NC 4.0, © commoncopper; 5, iNat. obs. 141652819, CC BY-NC 4.0, © Bridgette Gower; 6, iNat. obs. 196010411, CC BY-NC 4.0, © Dee Newton; 7, iNat. obs. 134480517, CC BY-NC 4.0, © jamiehalldefinitiveimaging.



Figure 34. *Maratus* (Australphryni: Saitini). 1-2, ♂ *M. pavonis*, Armidale, New South Wales. 3, ♂ *M. purcellae*, Woolmar, Queensland. 4-5, ♂ *M. robinsoni*, Wondul, Queensland. 6, ♂ *M. spicatus*, Stratton, Western Australia. 7, ♂ *M. volans*, Melbourne, courtship. 8, ♂ *M. volpei*, Lake Hart, South Australia. Photo credits: 1-2, iNat.obs. 61849217, CC BY-NC 4.0, © Ash Powell; 3, iNat.obs. 99961991, CC BY-NC 4.0, © benjc; 4-5, iNat.obs. 99962087, CC BY-NC 4.0, © benjc; 6, FLICKR, CC BY 2.0, © Jean and Fred Hort; 7, iNat.obs. 99532301, CC BY-NC 4.0, © Stefan Nebl ; 8, iNat.obs. 49986763, CC BY-NC 4.0, © Nick Volpe.



Figure 35. *Cytaea* (Australphryni: Wallaceini). With 40 described species (WSC 2025), *Cytaea* is an important island-hopping genus with a wide distribution centered on tropical Australasia, but extending far into both tropical Asia and Oceania. **1**, ♂ *C. alburna*, Yuleba, Queensland. **2**, ♀ *C. alburna*, near Fernvale, Queensland. **3**, ♀ *C. alburna*, Maryborough, Queensland. **4**, ♂ *C. aspera*, Clumber, Queensland. **5-6**, ♀ *C. aspera*, near Hughenden, Queensland. **7**, ♂ *C. dispalans*, Chanthaburi, Thailand. Photo credits: 1, iNat.obs. 165434519, CC BY 4.0 © Gunter Maywald; 2, iNat.obs. 184653612, CC BY-NC 4.0, © Steve Murray; 3, iNat.obs. 198112925, CC BY 4.0 © Nigel Main; 4, iNat.obs. 151079607, CC BY-NC 4.0, © Gunter Maywald; 5-6, iNat.obs. 229428335, CC BY-NC 4.0, © Gunter Maywald; 7, iNat.obs. 54730785, CC BY-NC 4.0, © watsaisaeng.



Figure 36. *Cytaea* (Australphryni: Wallaceini). **1-2**, ♂ *C. haematica*, Indonesia. **3**, ♂ *C. plumbeiventris*, Townsville, Queensland. **4**, ♂ *C. plumbeiventris*, Cairns, Queensland. **5**, ♀ *C. plumbeiventris*, Cairns, Queensland. **6-7**, ♀ *C. plumbeiventris*, Cairns, Queensland. Photo credits: 1-2, iNat.obs. 42268117, CC BY-NC 4.0, © Tiziano Hurni-Cranston; 3, iNat.obs. 245534023, CC BY-NC 4.0, © Dee McMahon; 4, iNat.obs. 152189977, CC BY-NC 4.0, © Bridgette Gower; 5, iNat.obs. 147449392, CC BY-NC 4.0, © Bridgette Gower; 6-7, iNat.obs. 105145938, CC BY 4.0 © Daniel Kurek.



Figure 37. Wallacini (Australphryni). **1**, ♀ *C. plumbeiventris*, Cairns, Queensland. **2**, ♀ *C. plumbeiventris*, Townsville, Queensland. **3-4**, ♂ *Euryattus bleekeri*, near Cairns, Queensland. **5-6**, ♀ *Euryattus bleekeri*, Brisbane. **7**, ♀ *Euryattus bleekeri*, Sandgate, Queensland. **8-9**, ♂ *Euryattus wallacei*, Whitsunday, Queensland. **10**, ♂ *Euryattus*, Bali. **11-12**, ♂ *Euryattus*, Bali. *Euryattus* is a genus of 15 described species (WSC 2025), found mostly in tropical Australasia and Wallacea. Photo credits: 1, iNat.obs. 147449397, CC BY-NC 4.0, © Bridgette Gower; 2, iNat.obs. 147071927, CC BY-NC 4.0, © Dee McMahon; 3-4, iNat.obs. 152189988, CC BY-NC 4.0, © Bridgette Gower; 5-6, iNat.obs. 260577689, CC BY-NC 4.0, © Dee Newton; 7, iNat.obs. 132888113, CC BY-NC 4.0, © Steve Murray; 8-9, iNat.obs. 258727373, CC BY-NC 4.0, © Alison Pearson; 10, iNat.obs. 257573298, CC BY 4.0, © Lawrence Hylton; 11-12, iNat.obs. 90992413, CC BY-NC 4.0, © Tiziano Hurni-Cranston.

Plate tectonics and vicariance biogeography. The discovery of plate tectonics opened up the possibility that populations, or groups of related species, could be divided by geological events to include the separation of continents, subsequently evolving in different directions (the *vicariance paradigm*). This differs somewhat from the notion of *dispersal from a center of origin*, but both concepts may also be useful (Wiley 1988). With an ancient (probably at least 35-40My old) clade like the Euophryini, and a poor fossil record, it is likely that we will never be able to locate the range of distribution of the single species that could be considered the *last common ancestor* of the group of species that survives to this day. Before considering various models for the vicariance biogeography of the euophryines, I will review relevant geological events.

Key geological events related to the position and movement of continents since the end of the Eocene are illustrated in Figures 38-39. During this time frame, the entire Afroeurasian land mass, as well as North America, were generally connected, the latter by means of Beringia, which is really a northwestern extension of the North American plate. One important feature of the Beringia connection is the fact that it is a region of seasonal climate, recently subject to many cycles of continental glaciation. Although there have been significant warming periods since the Eocene, this northern bridge has always been far removed from the tropics where salticids have reached their greatest diversity. But for species able to survive in a somewhat cooler, seasonal climate, this has not been a barrier for most of the Cenozoic era.

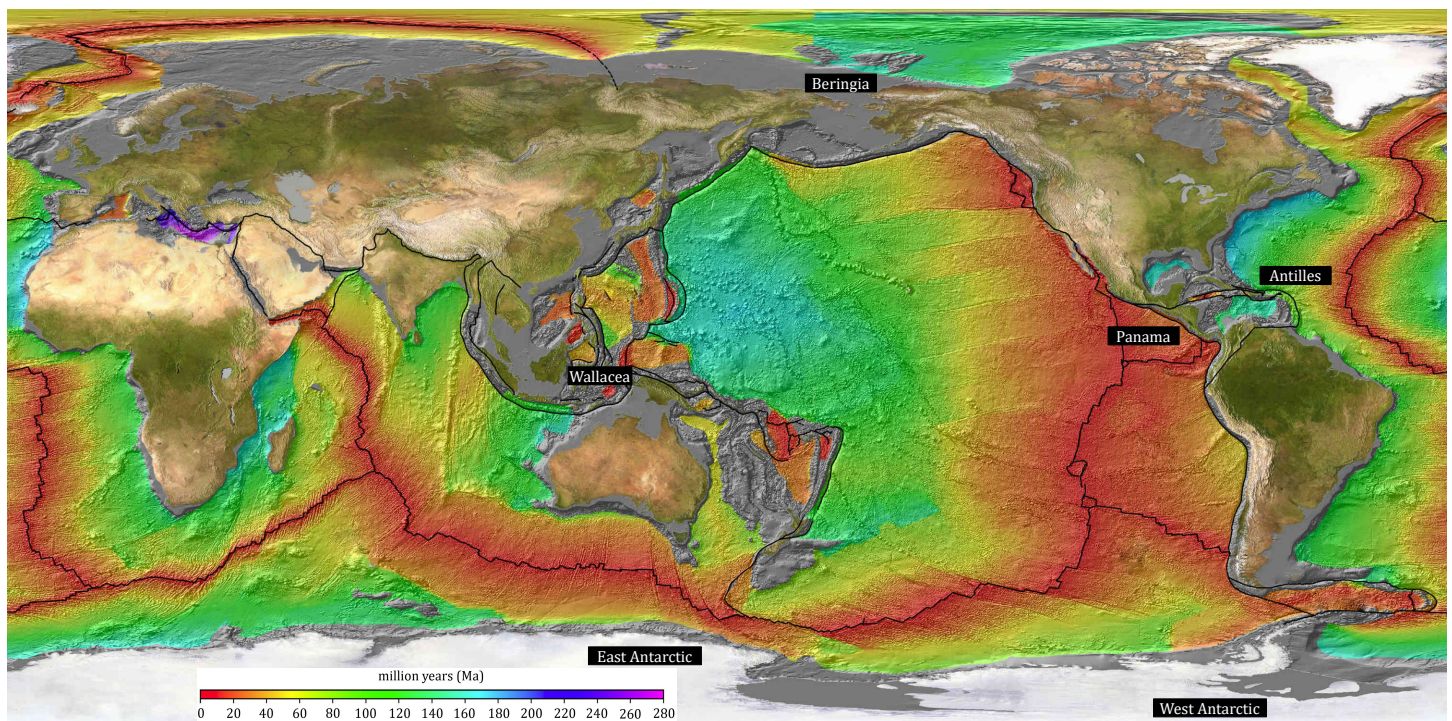


Figure 38. Age of the ocean lithosphere (Mercator projection). Separation from midocean ridges since the end of the Eocene (~33.9 Ma) is depicted in red-orange to red. Beringia has long represented a northern, Holarctic connection, although the climate there has always been cooler and seasonal. The Panama land bridge between the Americas has only been present since the start of the Pleistocene (~2.59 Ma), but before this Panamanian and Antillean island arcs represented stepping stones between the two continents. At the end of the Eocene, both Australasia and South America separated from Antarctica, and since that time Australasia has been moving northward toward Asia. Presently Australasia is still separated from Asia, but the many islands of Wallacea can support island-hopping by species in this area. Map credit: Mr. Elliot Lim, CIRES & NOAA/NCEI, modified here.

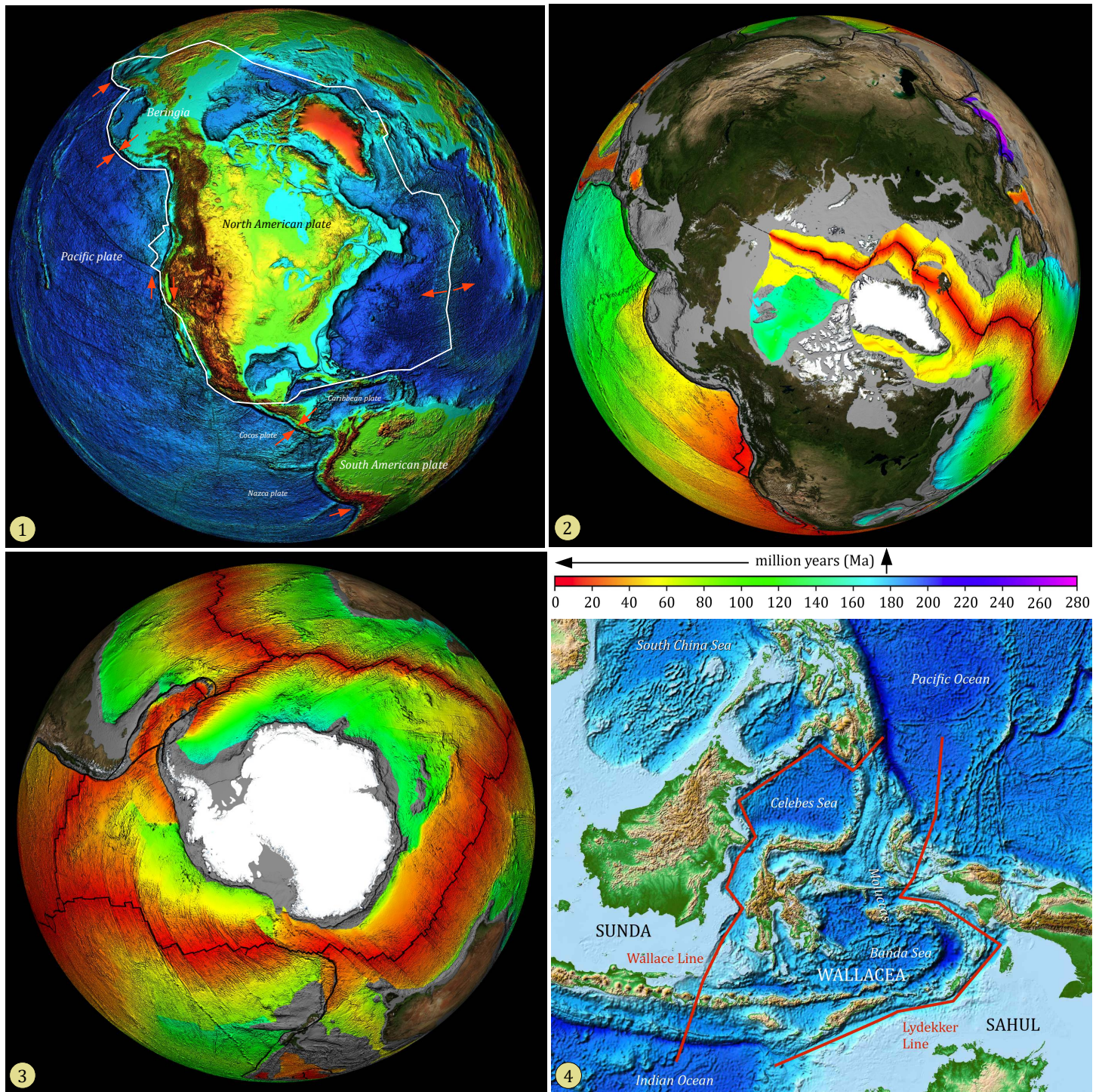


Figure 39. Geological features relevant to the vicariance biogeography of the Euophryini. The scale at right, center depicts the age of the ocean lithosphere depicted in (2) and (3). **1**, Extent of the North American plate. Movement of this plate relative to adjacent plates is indicated with arrows. The Beringia connection to Asia represents the northwestern extension of this plate. Collision of the Cocos plate and the Caribbean plate led to the rise of the Panama (Central America) Island Arc, and most recently the Panama Land Bridge. **2**, North polar view, showing the age of the ocean lithosphere and the wide northern connection between Asia and North America. **3**, South polar view, showing the age of the ocean lithosphere since the separation of South America (upper left) and Australasia (lower right) from Antarctica at the end of the Eocene. **4**, Boundaries of the Wallacean province separating Southeast Asia, or Sunda, from Australasia, or Sahul. During each recent ice age, the islands of Sunda have been joined to the Asian mainland which extended east to the Wallace Line. Likewise the land mass of Australasia extended to the northwest as far as the Lydekker Line during periods of peak glaciation. Sunda and Sahul have never been connected by land, but the islands of Wallacea comprise an important bridge for island-hopping. Map credits (all modified here): 1, 4, NOAA; 2-3, Mr. Elliot Lim, CIRES & NOAA/NCEI.

Between the early Eocene and the Pleistocene (55.8-2.89 Ma), the Americas were connected by two series of volcanic island arcs, one on either side of the Caribbean plate: the Central American (Panamanian) arc and the Antillean arc (Figure 39.1; Hill & Edwards 2013). At the end of the Eocene (~33.9 Ma) the Aves Ridge joined Northern South America to the Greater Antilles. By the Pleistocene (2.89 Ma) the Panamanian land bridge formed a continuous connection between North and South America.

To the south, the Antarctic Land Bridge, joining the three continents that comprised southern Gondwanaland (South America, Antarctica, and Australasia), was broken up at the end of the Eocene (~33.9 Ma) when Antarctica, now the great southern continent, was isolated by a strong circumpolar current (Figure 39.3; Hill 2009). Global climate began to cool significantly at that time. Since the Eocene, the Australasian plate has moved steadily to the north, and is now colliding with the Asian plate. Deep ocean straits still separate Sahul from Sunda, and the two faunistic provinces are joined only by a series of oceanic islands in the transitional province of Wallacea, which extends to the east of Borneo and Bali (Figure 39.4). Many recent genera and species of euophryines (and other salticids) are now distributed across Wallacea, in both directions (Hill 2010; Figure 40).

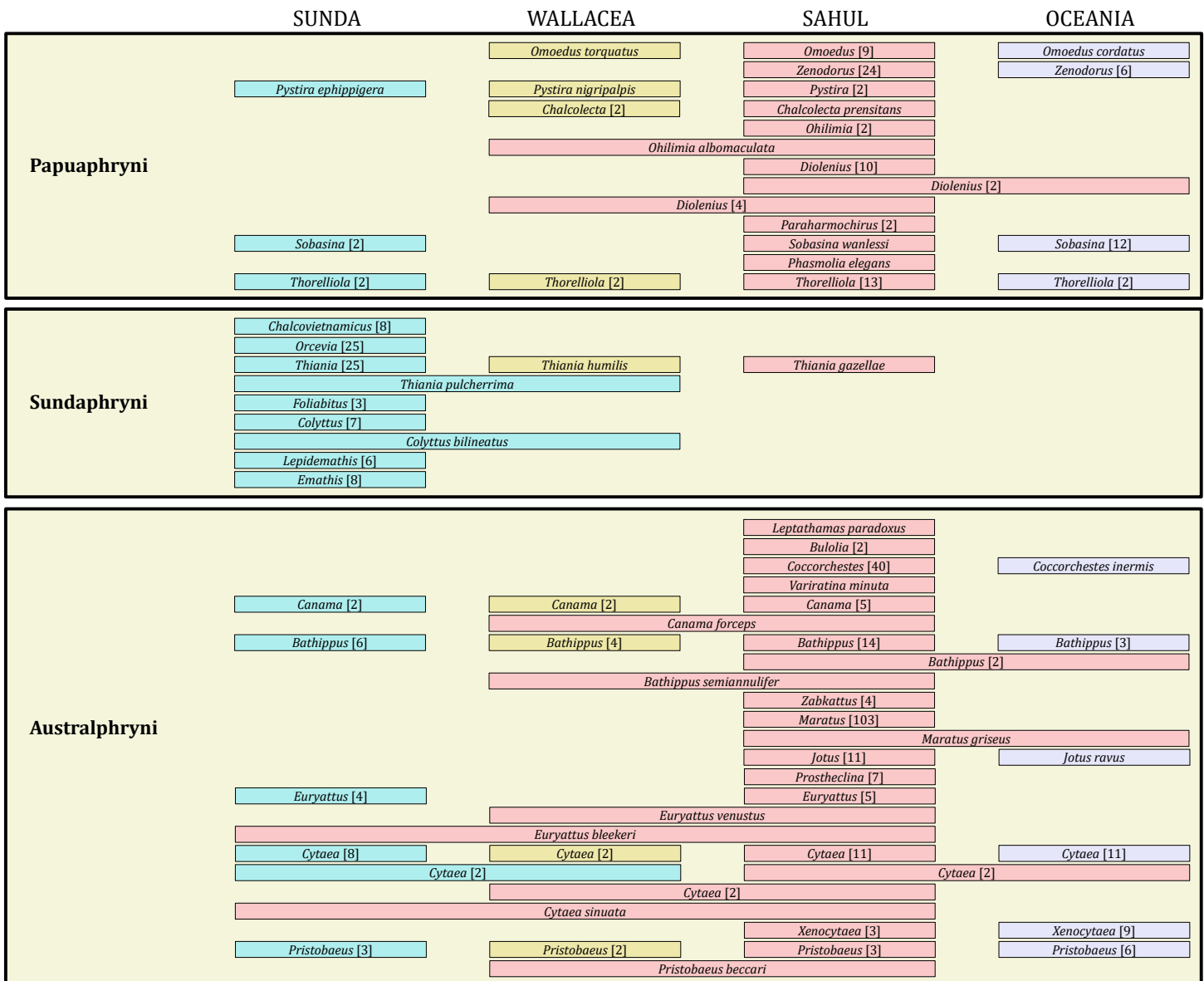


Figure 40. Current distribution of euophryine genera between Sunda and Sahul. The genus *Cytaea*, in particular, is widely distributed, even far to the east in Oceania. Species counts (after WSC 2025) are shown in brackets.

Hypotheses related to the biogeography of the Euophryini. Earlier studies (Bodner 2009; Bodner & Maddison 2012) suggested an origin of the euophryines at 27-45 Ma (Eocene-Oligocene), and subsequent estimates for the divergence of major euophryine subclades (Zhang & Maddison 2013) fall within this timeframe. The isolation of continental euophryine faunas, the great diversity of both New Guinea (or Australasian) and Caribbean (or Neotropical) euophryines, as well as the possibility that eastern and western groups diverged after the breakup of Southern Gondwana (or *Gondwanaland*, the Antarctic Land Bridge) have been recognized for more than a decade (Zhang 2012, Zhang & Maddison 2013). Previously (Hill 2009) I proposed that the endemism of the three most important groups of Australasian salticids could be explained by this breakup (Figure 41).

Southern Gondwana (parent)	South America	Australasia
Lapsoida	Lapsiini	Cocalodini
Afresia	Dendryphantini	Astioidea
Euophryini	Occidenphryni	Orienphryni

Figure 41. Hypothetical division of three large salticid clades that crossed Southern Gondwana (after Hill 2009). This has been updated to use the clade names shown in Figure 6.

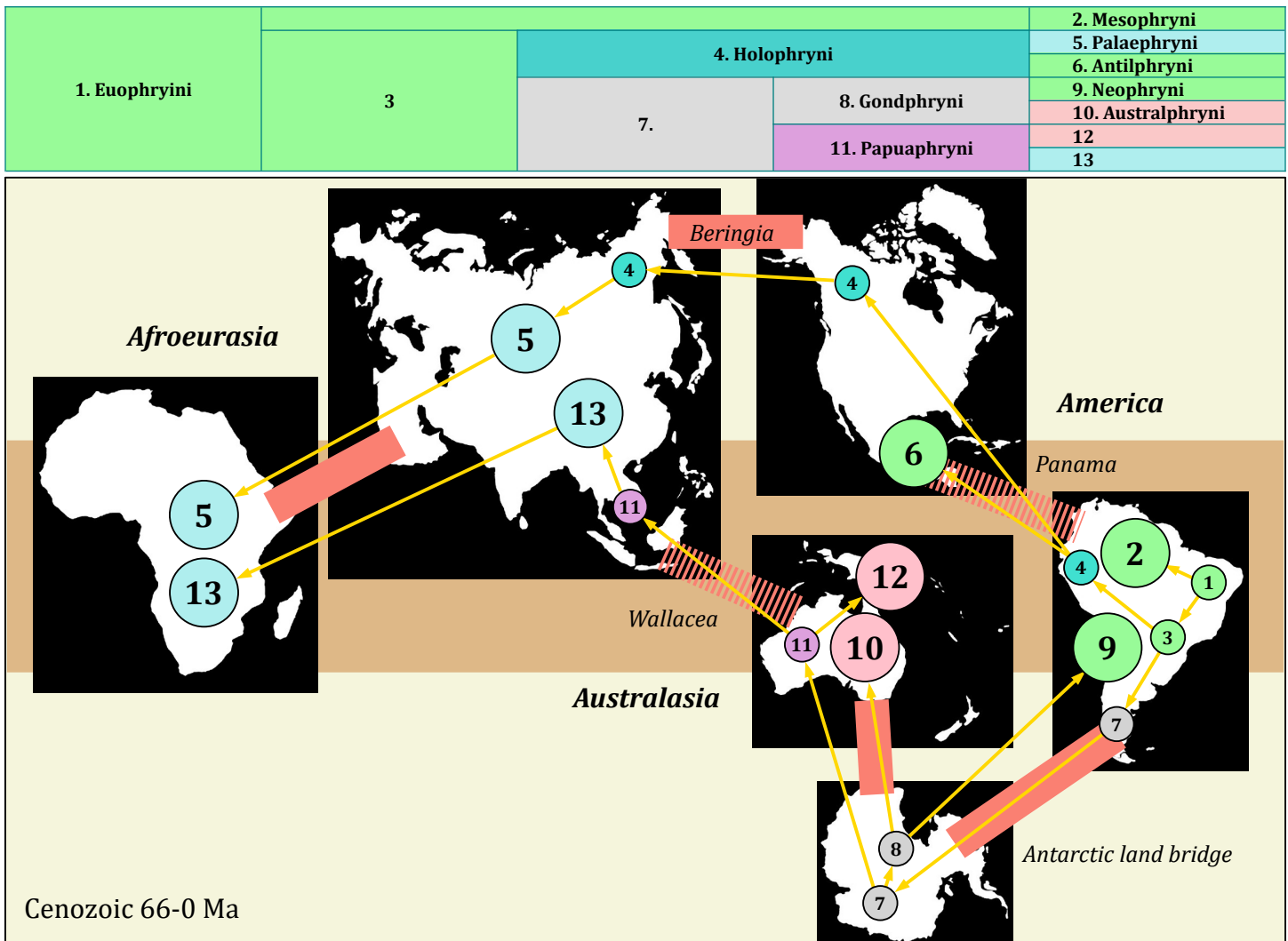


Figure 42. Hypothesis for euophryine biogeography based on earlier phylogenies (Figures 1-2). Large circles represent clades of existing species, smaller circles extinct species. Note division of (4) between three continents in this hypothesis.

The earlier euophryine phylogenies (Zhang 2012; Zhang & Maddison 2013, 2015; Figures 1-2) included major divisions that could have taken place in Neotropical South America, a region known as a hotbed of evolution. In particular, the primitive or basal position of the Mesophryni supported that hypothesis. Subsequent dispersal of euophryine species across Southern Gondwanaland to Australasia, and across island arcs to North America (with a much warmer climate at that time) could have preceded the next level of dispersal. Entrance into Afroeurasia could then have taken place through both northern (via Beringia) and southern (via Wallacea) routes, accounting for the separation of the two euophryine clades found in Afroeurasia (Figure 42). This would require the dispersal of at least two different clades (7 and 8 in Figure 42) across Southern Gondwanaland, both capable of surviving the seasonal requirements for that region, before the end of the Eocene (~33.9 Ma).

With a new phylogeny (Li et al. 2025; Figure 3), this hypothesis needs to be revisited. One reason for this is that the Neotropical euophryines now represent a single, well-defined clade, but it is not in a basal position. Here I present four new hypotheses (I-IV) for euophryine biogeography (Figures 43-46).

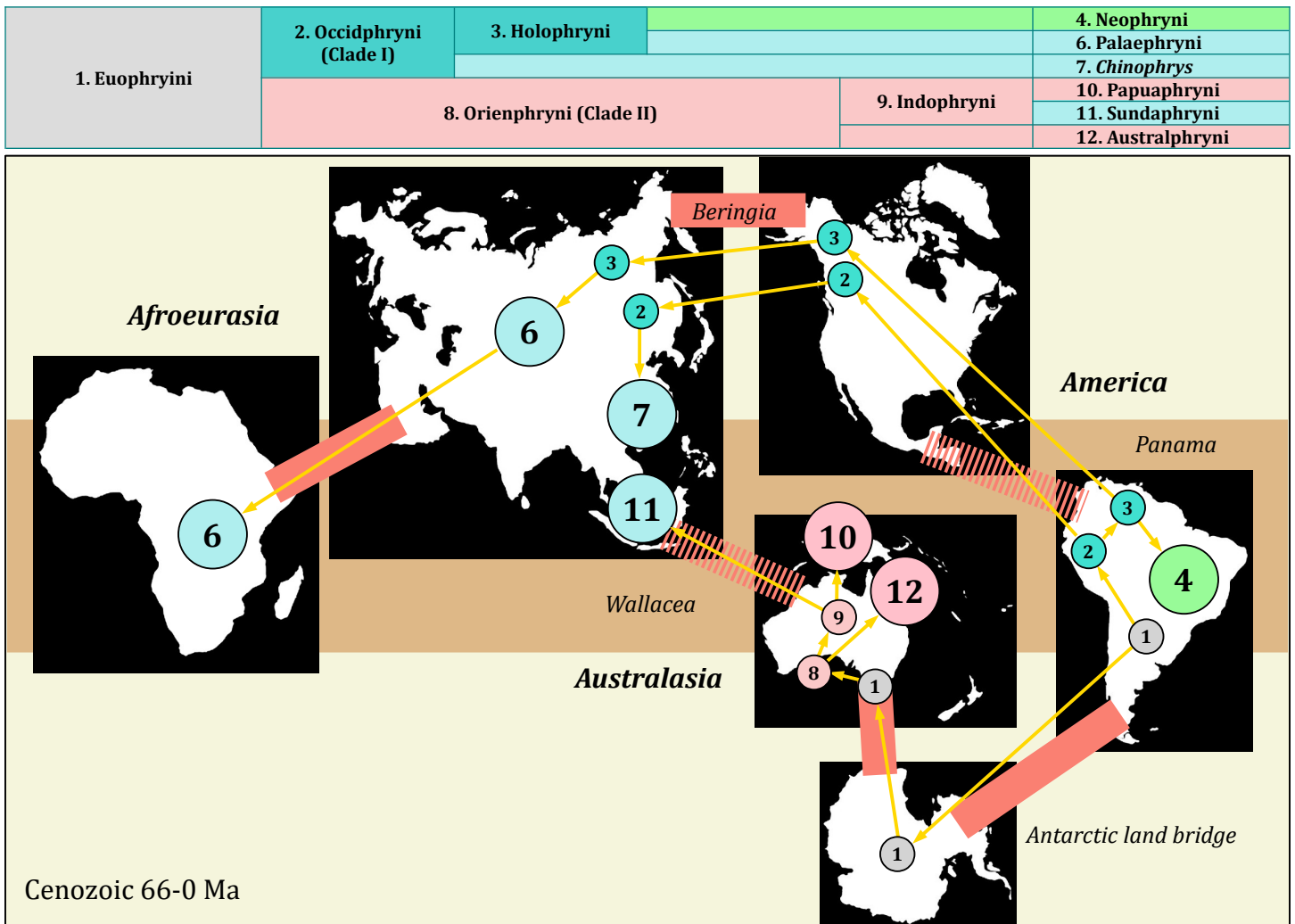


Figure 43. Hypothesis I. Like the earlier hypothesis, this preserves the idea that the Euophryni originated in Southern Gondwanaland. Division of clades (2) and (3) after dispersal across North America into Afroeurasia would account for two of the modern Afroeurasian clades (6 and 7). Earlier division of (1), representing the primary division of the euophryines, would have produced both the Occidphryni (2), and the ancestral Australasian Orienphryni (8) after the Eocene. That Australasian clade would then give rise to both of the existing Australasian clades (10, 12). Later, after Australasia approached Asia, a single early dispersal across Wallacea the would account for the third, tropical Asian clade (11, the Sundaphryni).

The first hypothesis (I, Figure 43) is close to the earlier hypothesis, with a primary division of the euophryines across Southern Gondwanaland, with two introductions into Asia via Beringia, and one via Wallacea. The second hypothesis (II, Figure 44) begins with an Afroeurasian origin for the group, followed by one introduction to the Americas, and two introductions across Wallacea into Australasia. This hypothesis does not include either dispersal or division across Antarctica. Since Australasia was far to the south at the end of the Eocene, this hypothesis is not supported by the antiquity of the Australasian clades, should that hold up. Presently, however, the only estimates of antiquity (Zhang & Maddison 2013) are based on the earlier phylogeny.

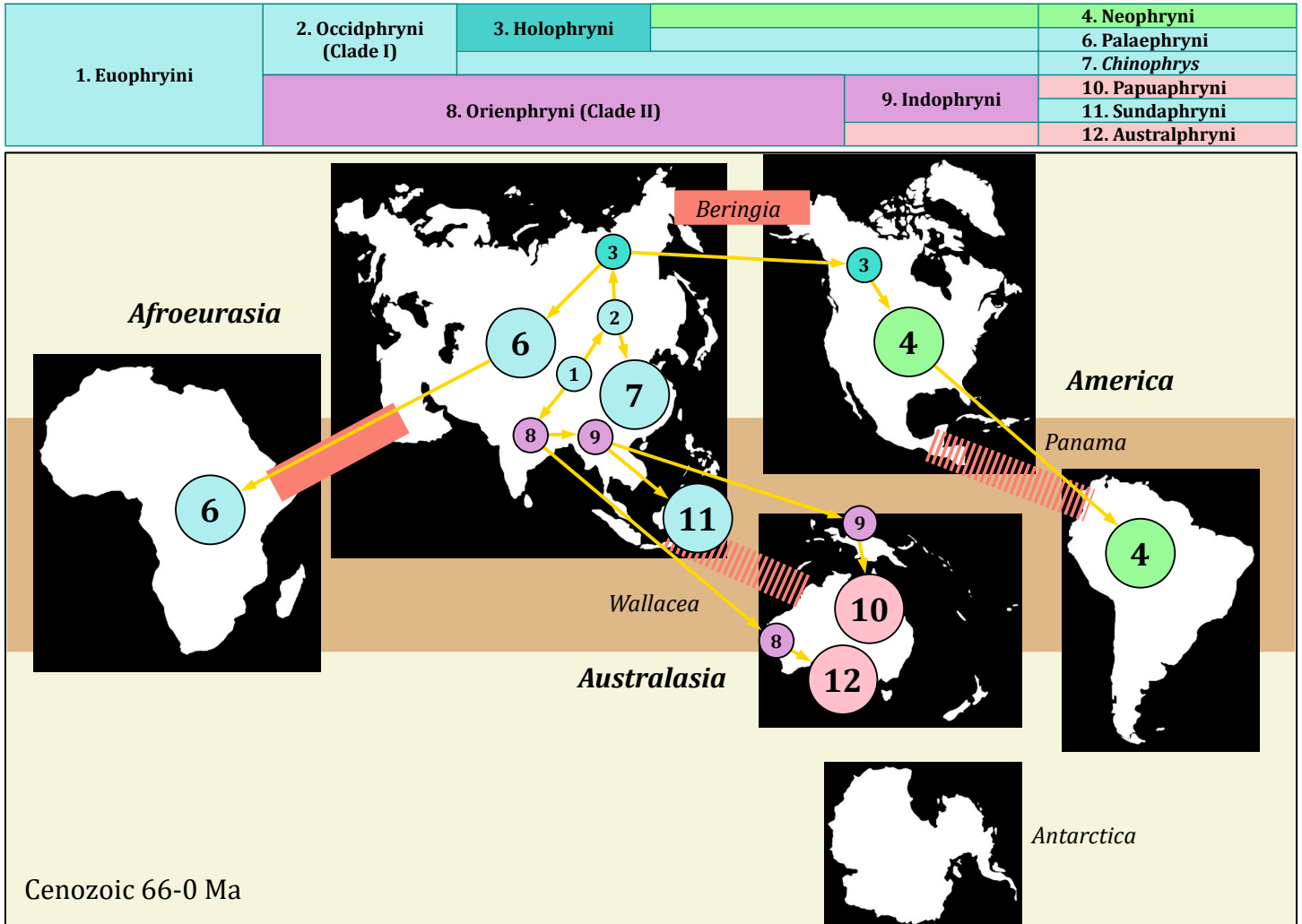


Figure 44. Hypothesis II. Afroeurasian origin with primary division of the Euophryini within Afroeurasia, followed by one dispersal into the Americas, and two into Australasia. This would require a relatively recent dispersal of at least two clades across Wallacea, since Australasia was situated far to the south at the end of the Eocene. However, only one separation across Beringia would be required.

The third hypothesis (III, Figure 45) is, like hypothesis II, based on an Afroeurasian origin and division of the Euophryini, but requires only a single introduction to Australasia, perhaps a single species with a transoceanic route, on drifting vegetation, long before Australasia moved up to the north. In addition, this hypothesis retains the simplicity of a single introduction to the Americas, with division based, perhaps, on the evolution of subtropical and tropical species in the Americas.

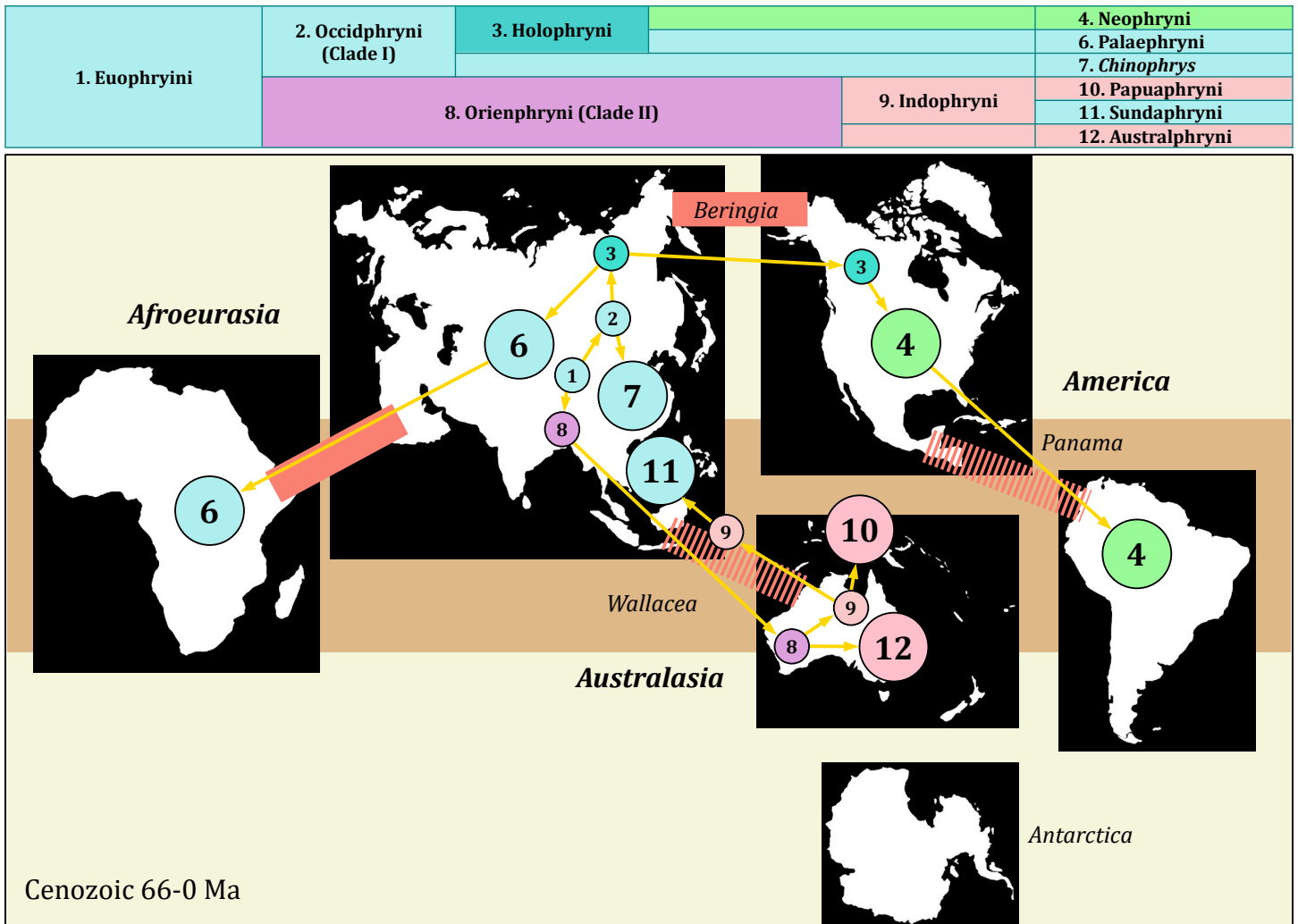


Figure 45. Hypothesis III. According to this hypothesis, the first euophryine (1) appeared in Afroeurasia, and the primary division of the Euophryini also occurred there. This was followed by dispersal of a single species to the Americas via Beringia, and a single species to Australasia, presumably long before Australasia came close to Asia. Subsequently one Australasian species (9) dispersed in the opposite direction to tropical Asia, and gave rise to the Sundaphryni (11). This could have happened at a much later date, and dispersal across Wallacea is now quite common (Figure 40). As in Hypothesis II, this does not require the Southern Gondwana route.

The final hypothesis that I will present here (IV, Figure 46) also begins with an Afroeurasian origin, and requires two divisions between the Holarctic and South America. This is followed by a single division across Southern Gondwanaland. Subsequently, one more division across Wallacea (8) can account for the Sundaphryni (11) of Southeast Asia. this hypothesis can also be generalized as follows: From the Simonida, the first euophryine species emerged in Afroeurasia. After dispersal across Beringia, two surviving descendant species, (2) in Asia, and (8) in Southern Gondwanaland, gave rise to all of the modern euophryines. A later Asian species (3) gave rise to species that stayed in Afroeurasia (6), as well as one that crossed Beringia in the opposite direction, giving rise to all of the surviving euophryines in the Americas (4).

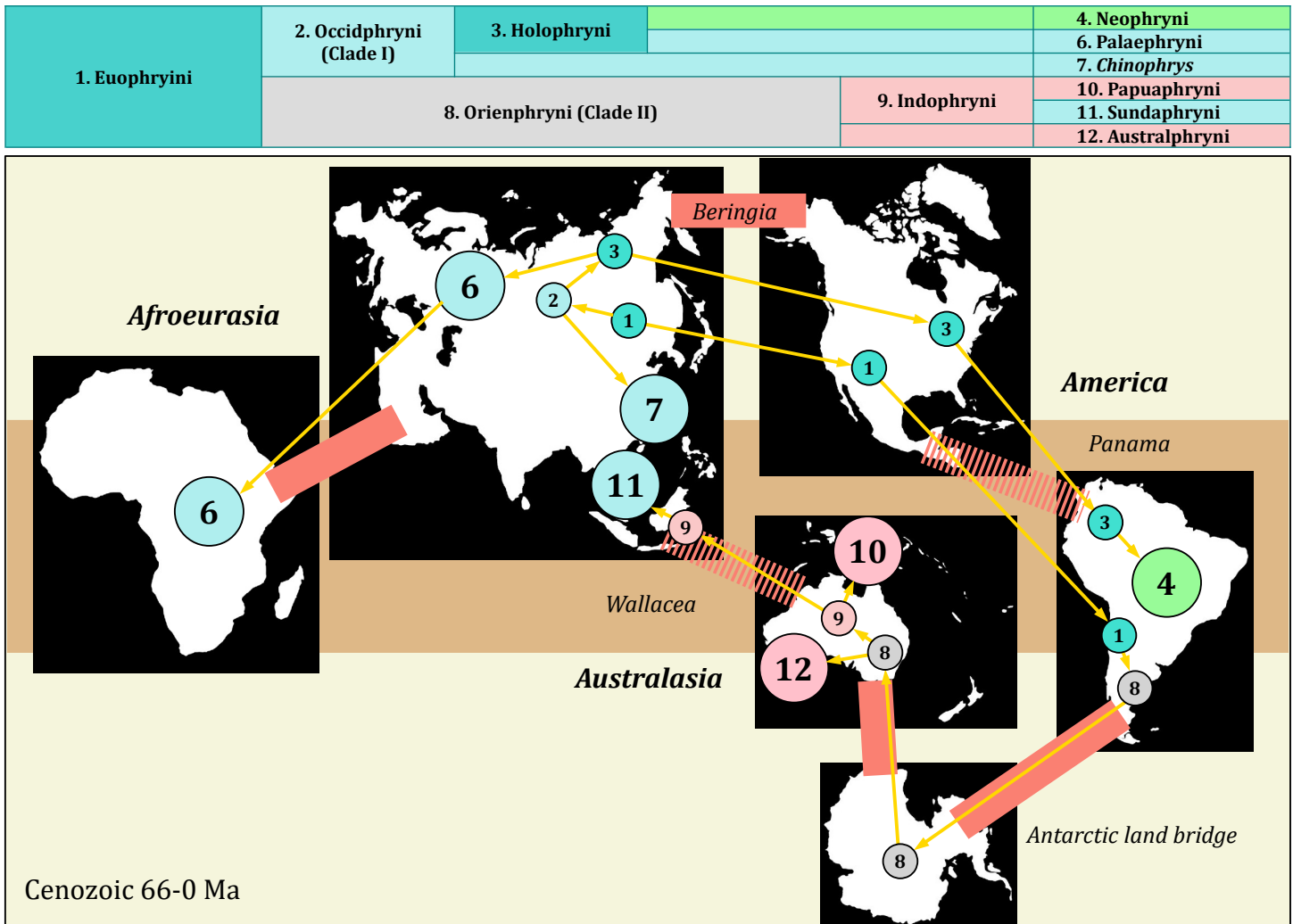


Figure 46. Hypothesis IV. In this hypothesis an Afroeurasian origin (1) was followed by two dispersals and divisions between Asia and the Americas, one leading to a second dispersal across Southern Gondwanaland (8), and the other leading to the Neotropical Neophryni (4). A later division across Wallacea (9) separated the Papuaphryni (1) from the Sundaphryni (11).

Other hypotheses are possible. A schematic view of Continental movement since the beginning of the Eocene is shown in Figure 47. It is quite likely that the Simonida had a global distribution during the late Eocene, and a division of the Simonida (see Figure 6) into the Afroeurasian Aphryni and the Gondwanan Euophryini may have taken place at that time. This would correspond to the distribution of only two simonid species with modern descendants, the aphryne ancestor and the euophryne ancestor. With isolation by not only distance, but also seasonality of Beringia and the Caribbean, this is plausible.

At the end of the Eocene, the obvious separation of South America and Australia can be associated with the subsequent division of Gondwanan euophryines into Neotropical occidenphrynes and Australian orienphrynes. As with the division of the Simonida, this would have been associated with the isolation of a *single* occidenphryne clade descended from a *single* orienphryne ancestor, although many other euophryine species without living descendants could also have been isolated. The separation of Australia, and the opening of the southern ocean, broke Australia off from the rest of global distribution for a long time, something that is only now coming to an end as Australia (Sahul) approaches Southeast Asia (Sunda). An updated estimate of divergence times that supports the Eocene-Oligocene division of major Australasian clades should favor hypotheses I and IV (Figures 43 and 46).

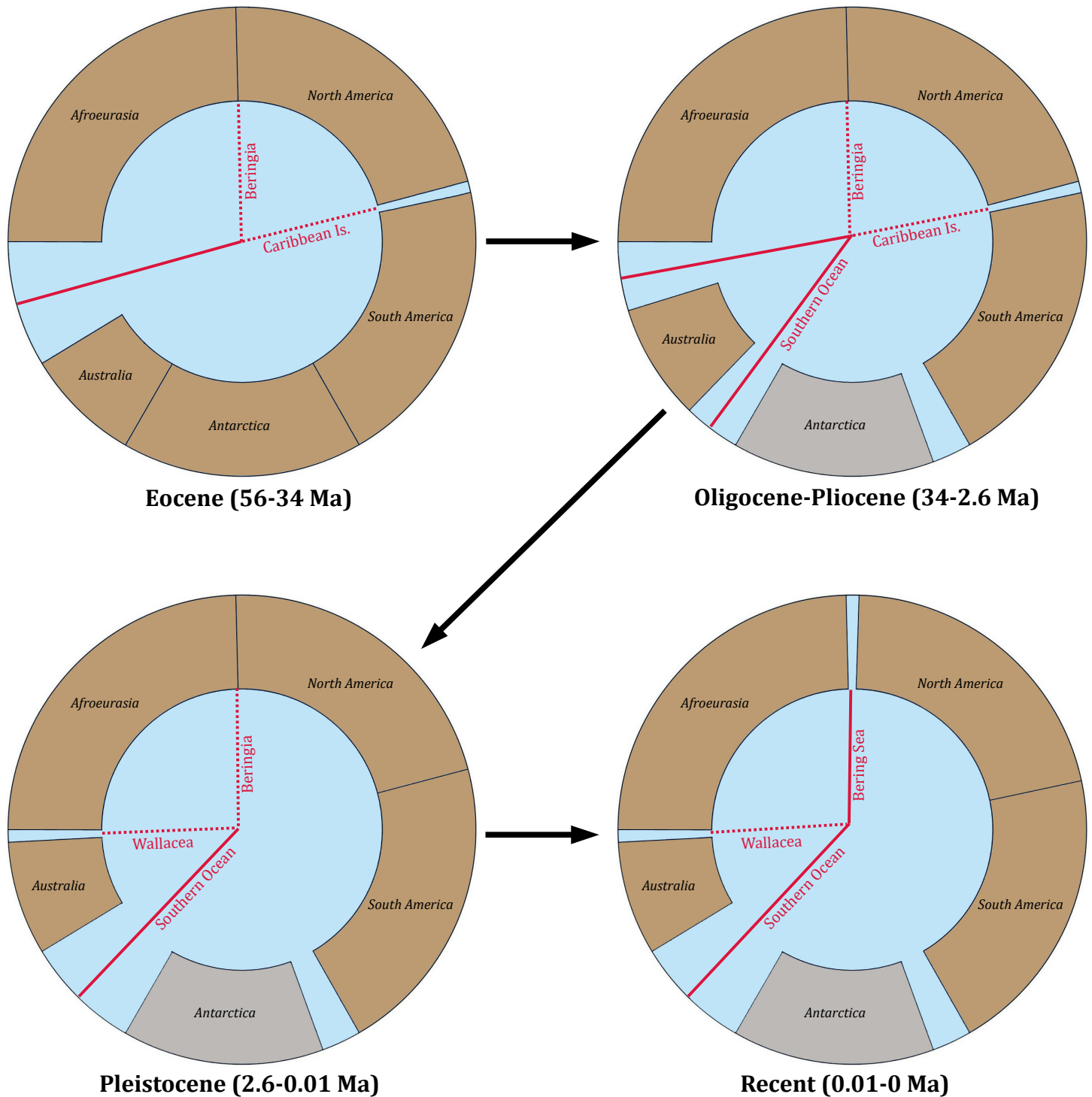


Figure 47. Schematic view of global biogeography in the later part of the Cenozoic. Major barriers that can be associated with phylogenetic divisions are shown as solid red lines. Minor barriers more subject to crossing are shown as dashed lines. In the Eocene (upper left), an undetermined number of Simonida species had two minor barriers to global distribution. One, Beringia, representing the northwestern extension of the North American plate, represented only a climatological barrier (requiring seasonal survival), and in warmer periods that would have been much less of a barrier. We can compare the Eocene Caribbean, crossed by several island arcs (Panamanian, Antillean), to modern Wallacea, which we know supports the passage of many species over time. However, the distance from Afroeurasia to Australia, by itself, also provided some isolation between distant Afroeurasian and Australian populations. Subsequently (Oligocene-Pliocene, upper right), the Australian plate separated from Gondwana and began to move north, isolating Australia. With completion of the Panamanian Land Bridge at the onset of the Pleistocene, Wallacea remained as the most significant physical barrier to global distribution, but with recurring cycles of glaciation to the north, Beringia became more of a challenge to movement of species between Afroeurasia and the Americas. During our present interglacial period (lower right), the Bering Sea is a temporary physical barrier.

The fate of Antarctica. During the Eocene, Antarctica gradually transitioned from subtropical to temperate rainforest (Passchier et al. 2013). We know nothing about the fate of the salticids that may have lived in post-Eocene Antarctica, as it was isolated by the cold waters of a growing southern sea. The discovery of a Cretaceous (~92-83 Ma) amber deposit in Antarctica (Klages et al. 2024) is promising, but to date we have no evidence that either salticids or any of their close relatives were alive before the Cenozoic era. After the Eocene, Antarctica continued its transition to become the cold and dry continent that we know today (Figure 48). By the Miocene, glaciation of Antarctica was already extensive (Passchier et al. 2011). Today, much of Antarctica is covered with more than 4 km of ice. Recent studies have revealed a complex topography of the rock bed underlying this ice, much of which is presently below sea level (Figure 49; Pritchard et al. 2025). Without the weight of the overlying ice, isostatic adjustment could raise central regions of this continent by more than 900 m, as it lowered narrow marginal areas by ~100 m in elevation (Figure 50; Paxman et al. 2022).

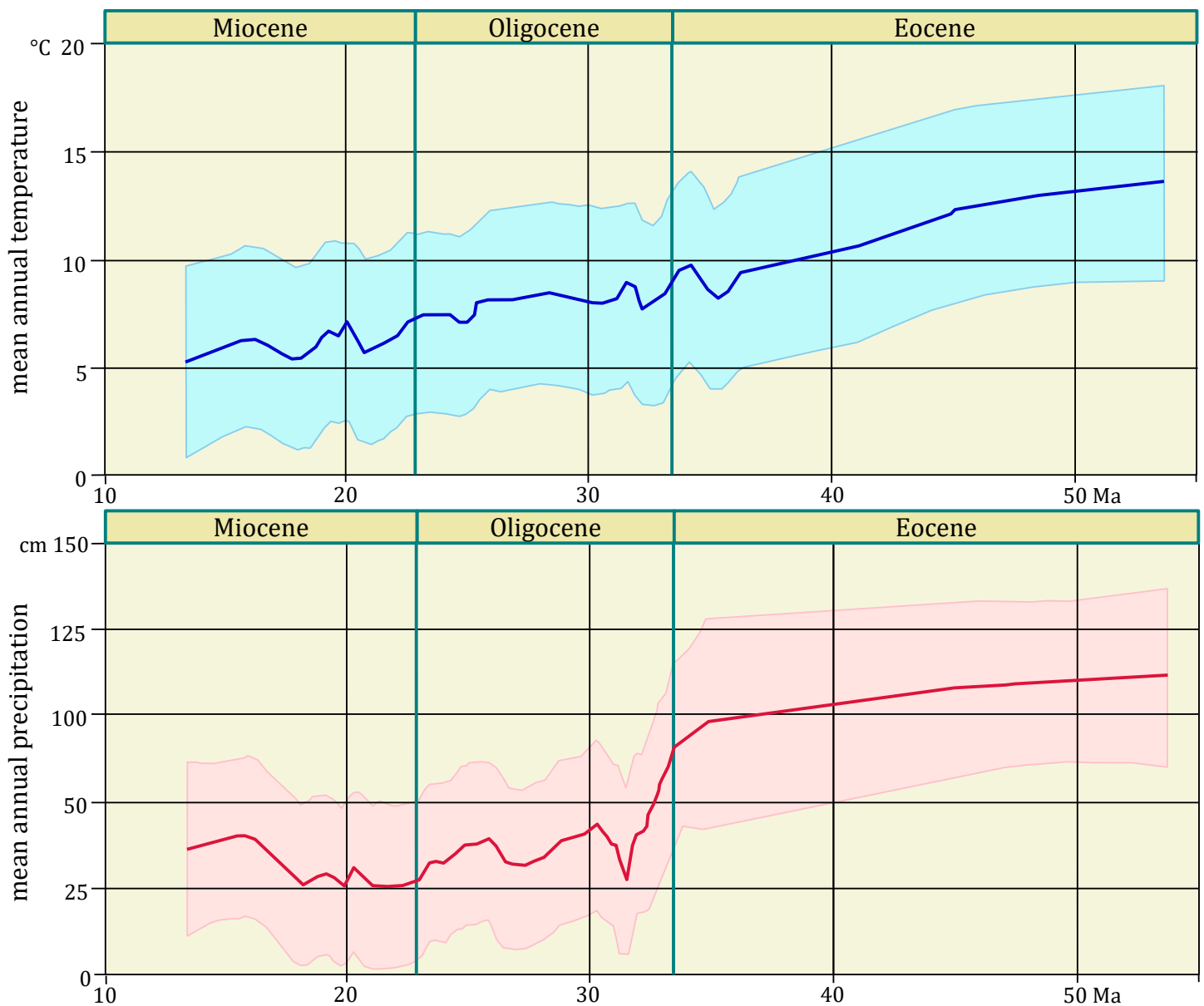


Figure 48. Declining temperature and precipitation of Antarctica, based on the geochemistry of sediments collected from drillcores around the continental margin (after Passchier et al. 2013). A confidence interval based on standard error is shown around each trend line. During this interval (from right to left), temperature declined at a relatively steady rate, but the isolation of Antarctica by the cold southern ocean at the end of the Eocene led to a rapid decline in precipitation.

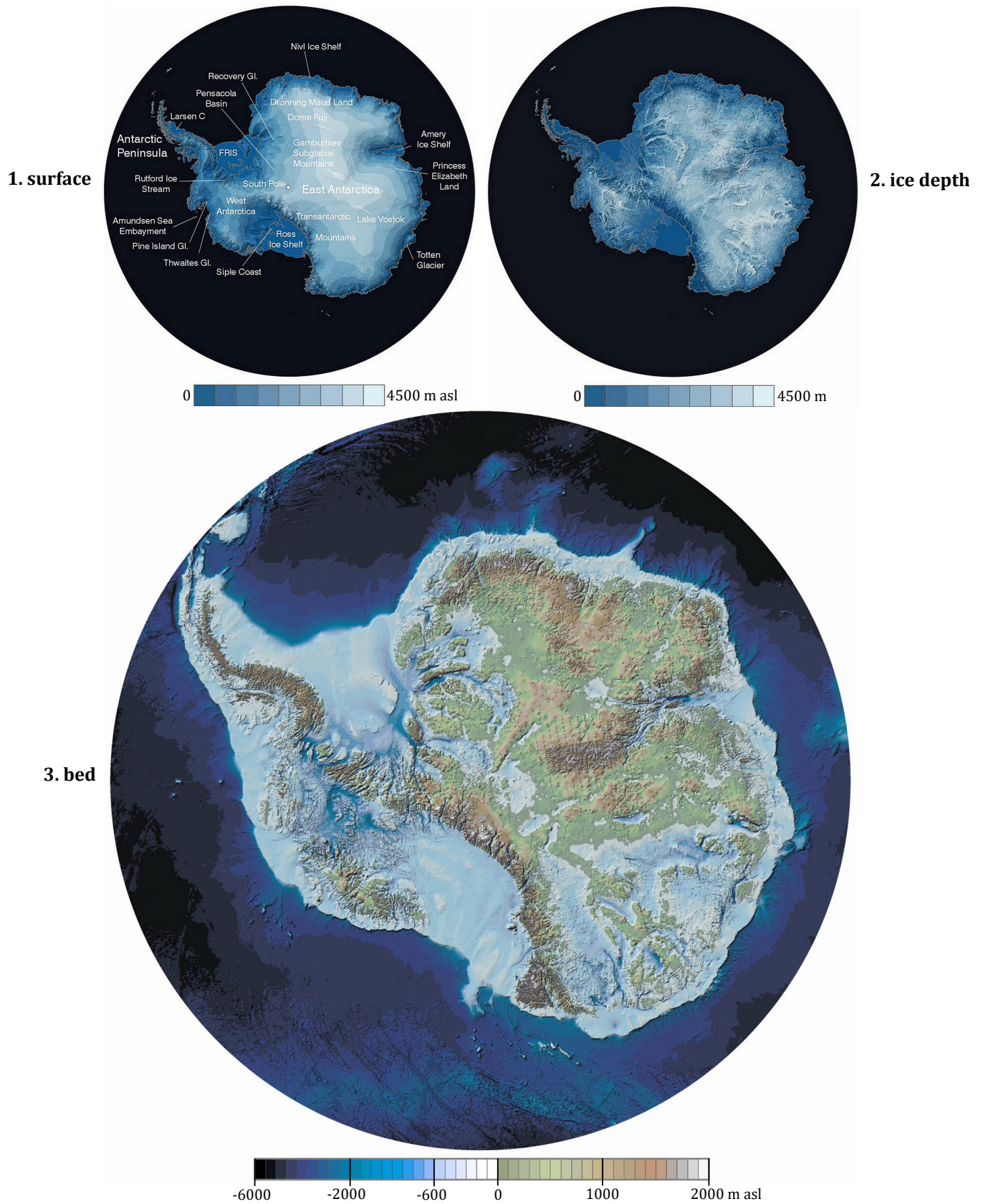


Figure 49. Antarctica today. **1,** Surface elevation and major features. **2,** Depth of ice cover. **3,** Elevation of bed with ice cover removed. The rectangle at right center is an artifact, the result of higher resolution imaging for this area. Image credits: 1-3, © Pritchard et al. 2025, CC BY 4.0.

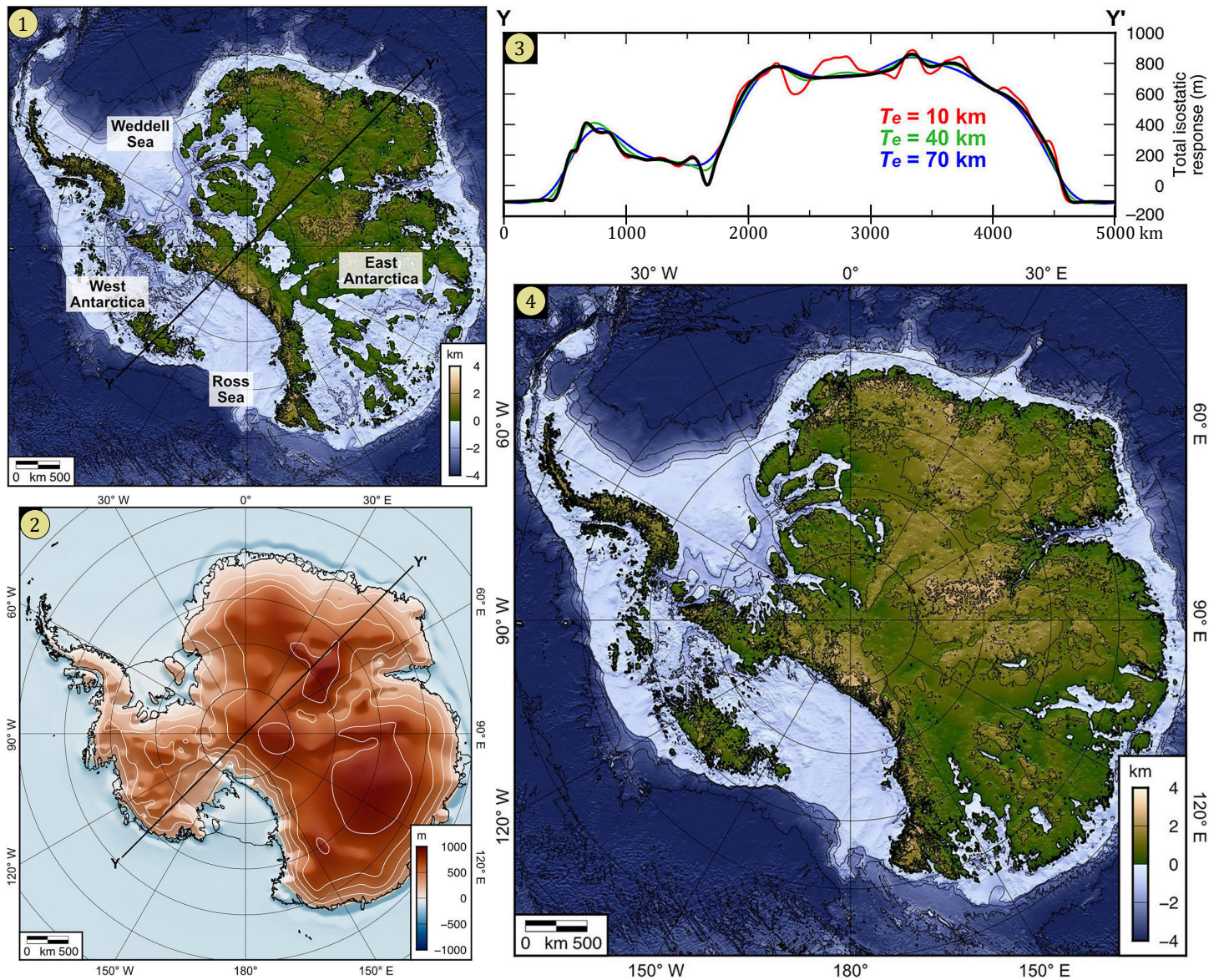


Figure 50. Predicted isostatic response to removal of the entire ice cover (deglaciation) of Antarctica. **1**, Elevation of bed with ice cover removed (See also Figure 49). **2**, Total response to deglaciation. As most of the continent rises (isostatic rebound) marginal areas fall. **3**, Predicted isostatic response along transect line Y-Y' shown in (1) and (2), showing general agreement based on three different estimates of *effective elastic thickness* (T_e) of the lithosphere. **4**, Elevation of fully rebounded bed after deglaciation, based on a hypothesis of mean sea level that assumes that the Earth carries no ice cover. Image credits: 1-4, © Paxman et al. 2022, CC BY 4.0.

The Northward Journey of Australasia. For about 45 My, The Australian plate has been moving north/northeast at an average rate of $\sim 6\text{--}7$ cm/y, faster than any other continent since the Eocene (Quigley et al. 2010; Hall 2012; Müller et al. 2016). During its collision with Pacific islands, to include those that now comprise northern New Guinea and the Solomon Ridge of the Ontong Java Plateau, this rate slowed to about 2 cm/y; at other times it soared to 10–12 cm/y (Cohen et al. 2013). During the last 25 Ma, New Guinea has moved 15° to the north, to a position just below the equator (Farahbakhsh et al. 2025).

Today Australasia (Sahul) has moved well into the tropics, in close proximity to the diverse tropical rainforests of Southeast Asia (Sunda; Figure 51). At the same time its isolation from Afroeurasia, by the deeper straits of Wallacea, has allowed it to maintain a distinctive flora and fauna. Presently Wallacea also appears to represent the most important faunal convergence (and transition) zone on the planet, as

an island archipelago that now supports the movement of many salticid genera and species in both directions, between Sunda and Sahul (Hill 2010). Two recent (2008, 2009) expeditions to several localities in New Guinea led to the discovery of many new salticids, and the majority of these were euophryines (Zhang & Maddison 2012b).

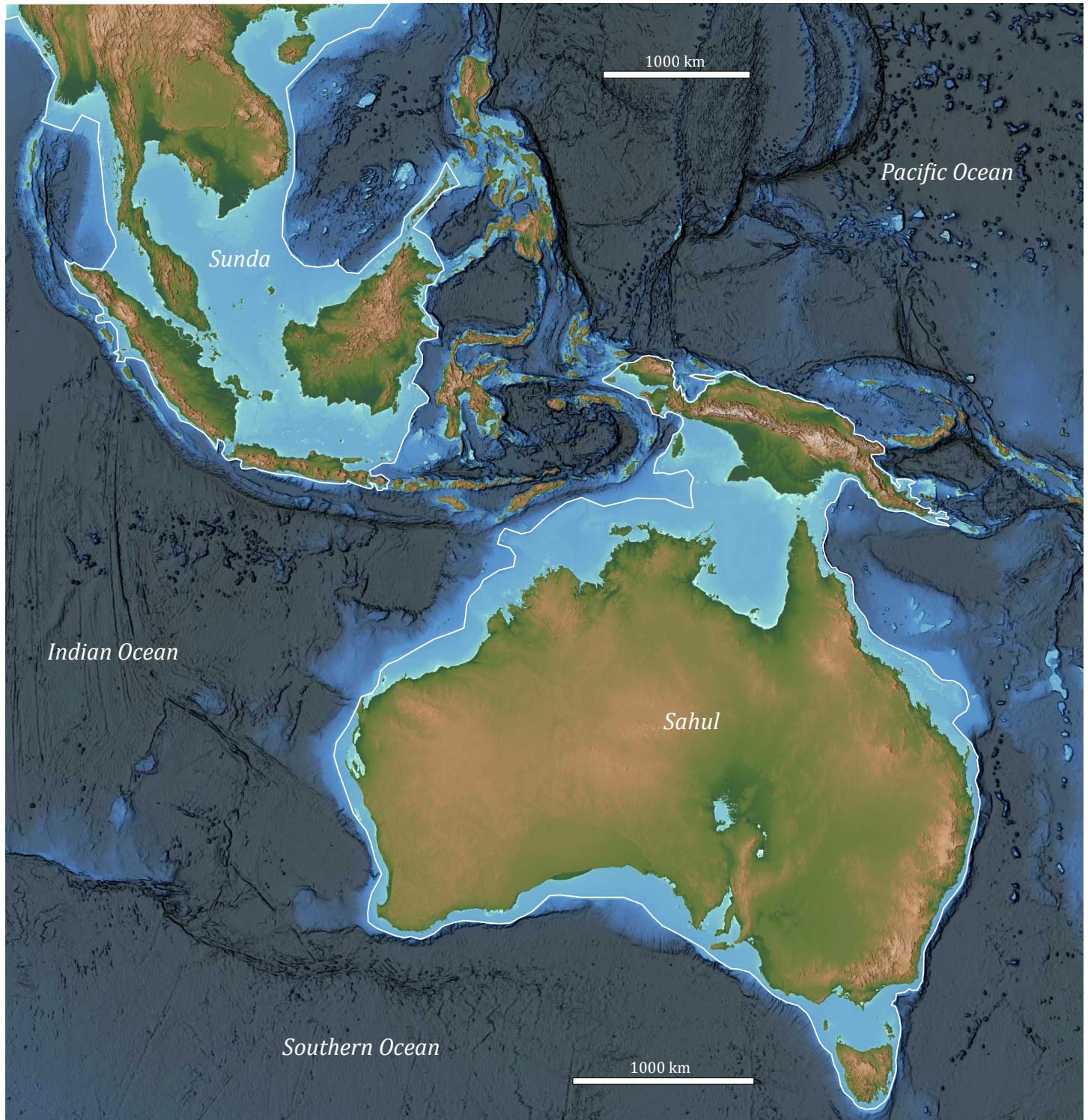


Figure 51. Present day convergence of Sahul and Sunda. White lines represent the approximate shoreline of these two regions during Pleistocene glacial maxima (~18 Ka, today at about the -125 m bathymetric contour line). The eastern boundary of Sunda represents the *Wallace Line*. Since this map is a Mercator projection, distance scales at the top and bottom differ. Background map: NOAA, modified.

As it moved to the north, the climate of Australia became increasingly arid. Later, as it moved into the tropics and collided with complex terranes riding on the Pacific plate (Ponyalou et al. 2023), great mountains rose in what is now New Guinea, one of the most diverse and complex regions on the planet from both biological and geological perspectives (Figure 52; Baldwin et al. 2012; Davies 2012; Cámara-Leret et al. 2020; Tanyaş et al. 2022).

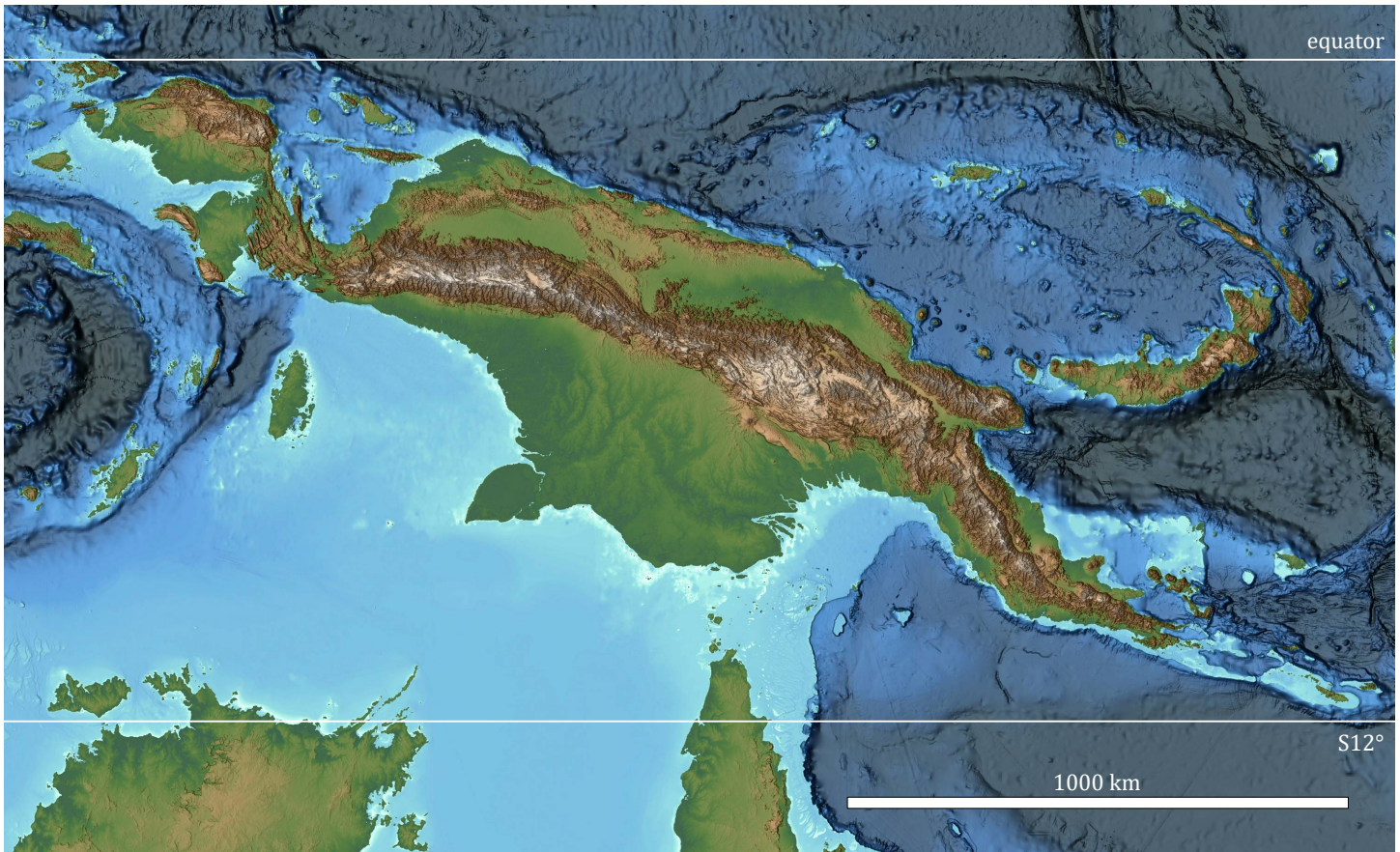


Figure 52. Relief map of New Guinea and the surrounding area. A great range, the *New Guinea Highlands*, runs from west to east along the width of the island, representing collision of the Australian plate with terranes riding on the Pacific plate to the north. Many peaks, some carrying equatorial glaciers, rise to more than 4 km asl. Base map credit: NOAA, modified.

The Bering land bridge. From the late Cretaceous to the Neogene, the Bering Land Bridge (*Beringia*; Figure 53) has been an important route for the sharing of many kinds of animals and vascular plants between East Asia and western North America (Hill & Edwards 2013; Wen et al. 2016). Dispersal of mammals across Beringia, to include recent species, is also well-known (Cook et al. 2005; Jiang et al. 2019). In the Pleistocene, precession of the Earth appears to have forced a series of more-or-less regular (~100 Ky) cycles of northern glaciation (Hobart et al. 2022), and thus this physical connection has only been intermittently available for some time. For salticid spiders, with most diversity based in the tropics, a cooling climate and seasonality are barriers to the use of this bridge.

It is a curious fact that few euophryines are known from North America, north of Mexico (Edwards 2003; Hill & Edwards 2013). The few temperate Nearctic species that can be found (e.g., *Euophrys monadnock*, *Talavera minuta*) are members of relatively large Palearctic genera, and appear to be recent introductions to North America. By comparison, the genus *Habronattus*, descended from an Asian harmochirine, has been very successful in North America (Azevedo et al. 2024).

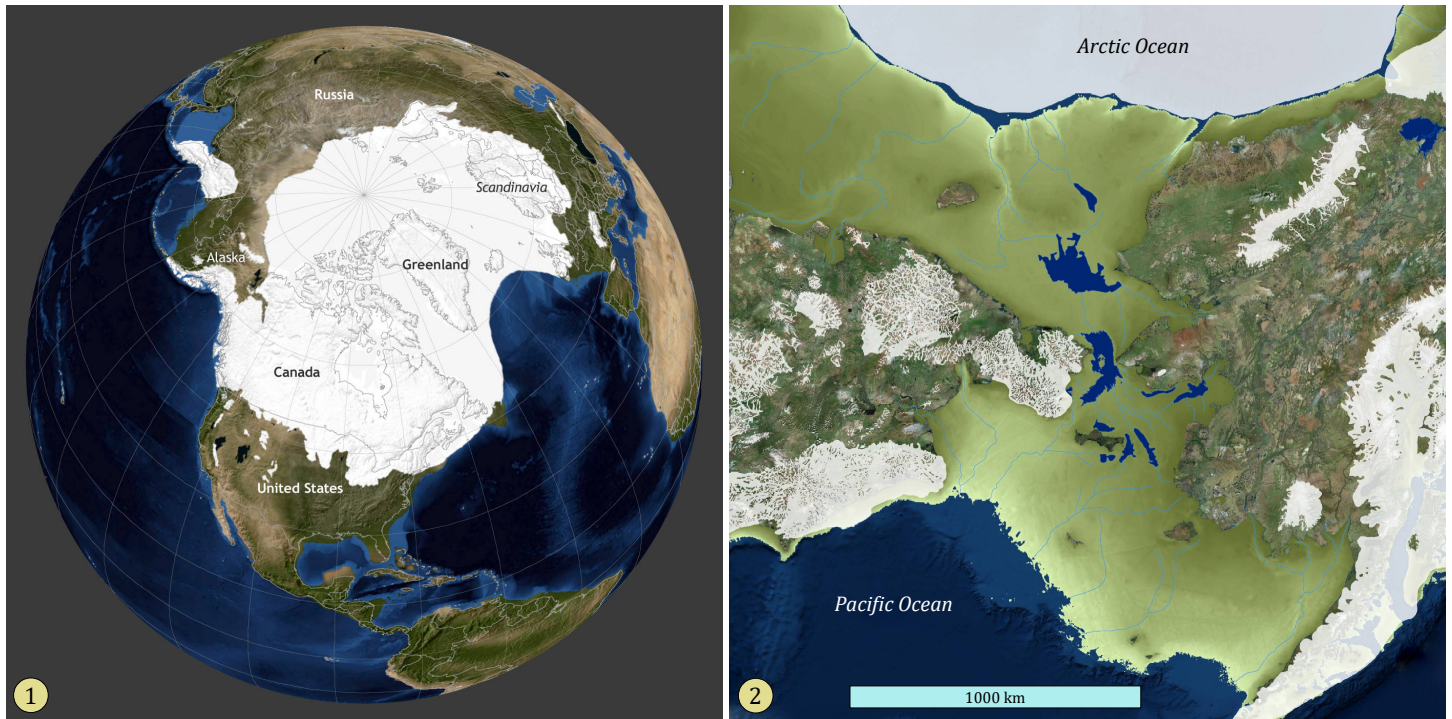


Figure 53. Beringia and the frozen north. **1**, Continental glaciers covered the northern reaches of North America during the last glacial maximum (~19 Ka). However the boggy land of Beringia (just above Alaska, at upper left) was above sea level, and seasonally clear of ice and snow at that time. **2**, Reconstruction of Beringia during the last glacial maximum (~18 Ka), showing extensive exposed areas at lower elevations, between glaciers. Background map credits: 1, NOAA; 2, After Bond, Jeffrey D. 2019, Paleodrainage map of Beringia, Yukon Geological Survey, Open File 2019-2, © Government of Yukon 2019.

Even the subtropical areas of the continental United States harbor few euophryines: several *Naphrys*, and *Anasaitis canosus*, the latter a member of a large Caribbean genus. The single large clade of American euophryines (the Neophryni) is almost entirely confined to southern or Neotropical areas. Thus we can ask: If temperate North American provided an important route for passage of euophryines between Asia and South America, then why does it lack an indigenous euophryine fauna? There is more than one possible answer for this question: (1) It is possible that only a single (or several) simonid or euophryine species actually made this passage. In fact, there is no reason to believe that many did. (2) The Nearctic has been subject to many repeated cycles of glaciation that would have greatly stressed the salticid fauna, and the survival of one particular species through these cycles would be very improbable. (3) Introductions from the evolutionary Neotropical powerhouse, as well as introductions from Asia, now appear to dominate the current salticid fauna of North America (Hill & Edwards 2013), essentially out-competing the euophryine fauna for survival in the seasonal, temperate region north of Mexico. In contrast, the diverse Australasian euophryine fauna has been isolated from these competing groups until recently.

The North Atlantic Land Bridge. An alternative route between Afroeurasia and the Americas is known as the North Atlantic, or Transatlantic, Land Bridge. Pollen records from Iceland have been used to support the hypothesis that this northern connection was available as late as the Miocene (Denk et al. 2010). However, the view that this connection lasted only from the late Cretaceous to the early Eocene, when it was disrupted by a combination of a cooling climate and the opening of the Mid-Atlantic Ridge near Iceland, appears to have more support (Graham 2018). The age of the sea floor surrounding the Mid-Atlantic ridge in this area (Figure 39.2) supports the latter view.

The Caribbean and Central America. Like the East Indies, this region has both a complex geology (Figure 54) and a high level of habitat diversity, combined with the kind of stable tropical climate that seems to favor salticids. It also supports a very diverse euophryine fauna (Zhang & Maddison 2012a, 2012c). Since the beginning of the Pleistocene (~2.8 Ma) North and South America have been joined by a stable land connection (the Panamanian or Central American Land Bridge), prior to that time the two continents were isolated by an ocean expanse of variable width, and joined only by volcanic island arcs to the west (the Central American Arc) and east (the Antillean Arc) of the Caribbean Plate (Iturralde-Vinent & Gahagan 2002; Giunta & Orioli 2011; Hill & Edwards 2013). Today we are familiar with transoceanic movement of species across Wallacea, so the possibility of successful "island hopping" across the Caribbean, prior to the Pleistocene, seems quite reasonable. Also like Wallacea, this area is still bounded by a large number of active volcanos, inland from subduction zones (Forte et al. 2021).

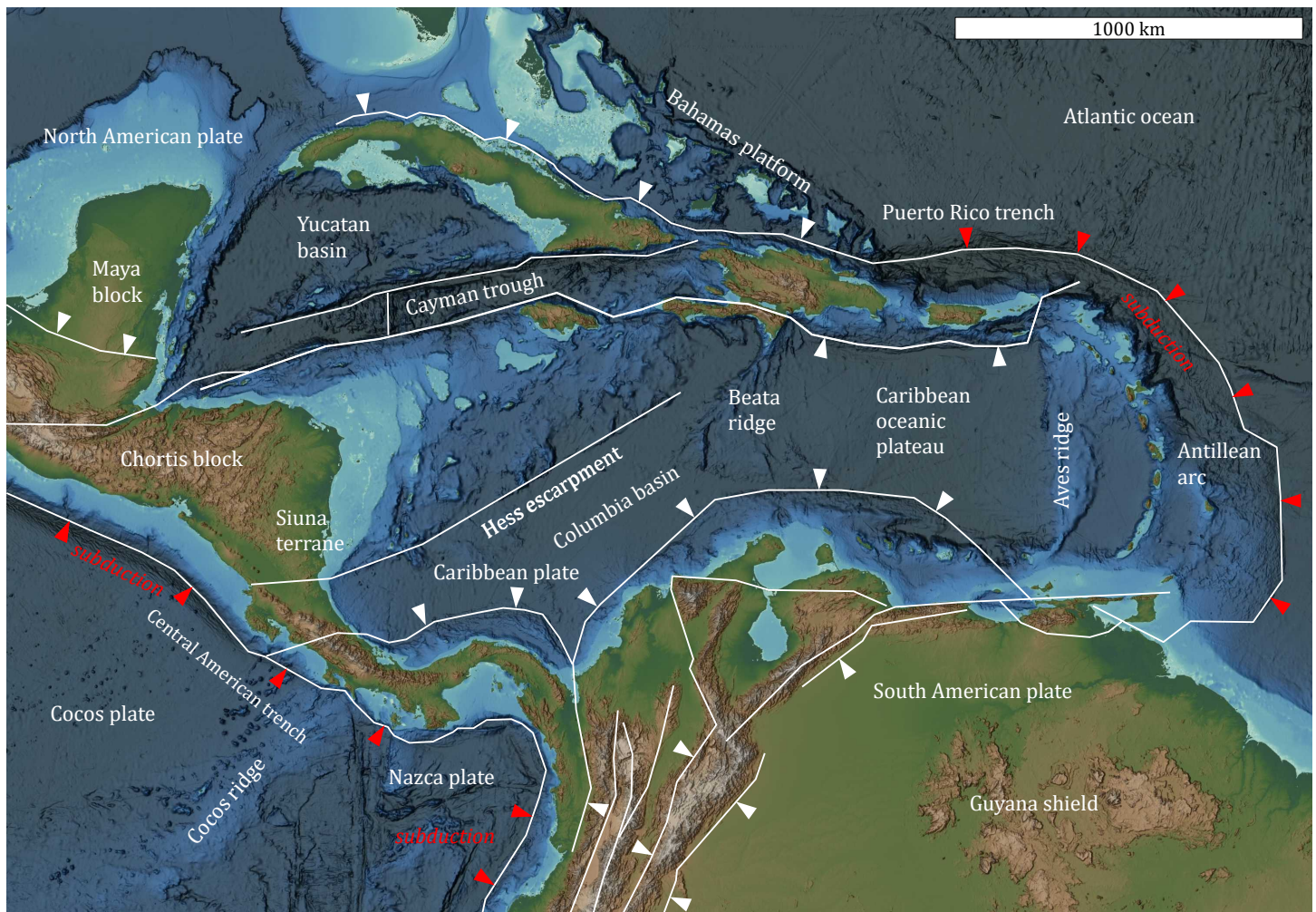


Figure 54. Major fault lines and subduction zones of the Caribbean (after García-Casco et al. 2011; Giunta & Orioli 2011). The island arcs of Central America (now a land bridge) and the Antilles are still under construction, with many active volcanos inland (or on the overlapping plate) from the active subduction zones (red arrows). White arrows indicate thrust or accretion along plate or microplate margins. Base map credit: NOAA, modified.

Lessons from the study of other animals. Vertebrates, in part because of their extensive fossil record, can be very useful with respect to the study of both phylogeny and the vicariant distribution of animal groups. With respect to clade division across Southern Gondwana, tree frogs (Hylidae), chelid side-necked turtles (Chelidae), and marsupial mammals (Marsupalia) are of particular interest (Figure 55).

1. *Agalychnis callidryas*, Costa Rica2. *Nyctamystes infrafractus*, Queensland3. *Phrynops williamsi*, Argentina4. *Chelodina longicollis*, Victoria5. *Dromiciops gliroides*, Chile6. *Myrmecobius fasciatus*, Western Australia

Figure 55. Representatives of three vertebrate clades presently divided across Southern Gondwana. **1-2**, Aboranan (tree) frogs from Central America (Phyllomedusidae) and Australia (Pelodryadidae). **3-4**, Chelid turtles from South America (Chelinae) and Australia (Chelodiniinae). **5-6**, Australidelphian marsupials from southern South America (Microbiotheria: Microbiotheriidae) and Australia (Euastralidelpha: Peramelidae). *Dromiciops gliroides* is the only living australidelphian species in South America; the Microbiotheria is the sister group for all of the living marsupials of Australia, the Australidelphia. Photo credits: 1, iNat. obs. 167258822, CC BY 4.0, © Luke Padon; 2, iNat. obs. 138483094, CC BY 4.0, © Jane C. Frost; 3, iNat. obs. 239176825, CC BY 4.0, © DarrenObbard; 4, iNat. obs. 200246970, CC BY-NC 4.0, © Rob Solic; 5, iNat. obs. 180961394, CC BY-NC 4.0, © markc666; 6, iNat. obs. 20024242, CC BY-NC 4.0, © pfaucher.

The vicariant distribution of tree frogs (Arboranae; Figures 55.1-55.2, 56) follows hypothesis I for biogeography of the euophryines, with a Neotropical origin, followed by early separation of one clade (the Pelodyadidae) in Australasia, and later distribution of two clades to the north (Duellman et al. 2016). One of these (the Acridinae) is now endemic to North America. Only one subfamily, the Holarctic Hylinae, can now be found in Afroeurasia. The hyline genus *Hyla* is thought to have crossed Beringia from Asia to North America; a different hyline genus, *Dryophytes*, apparently crossed Beringia in the opposite direction (Duellman et al. 2016).

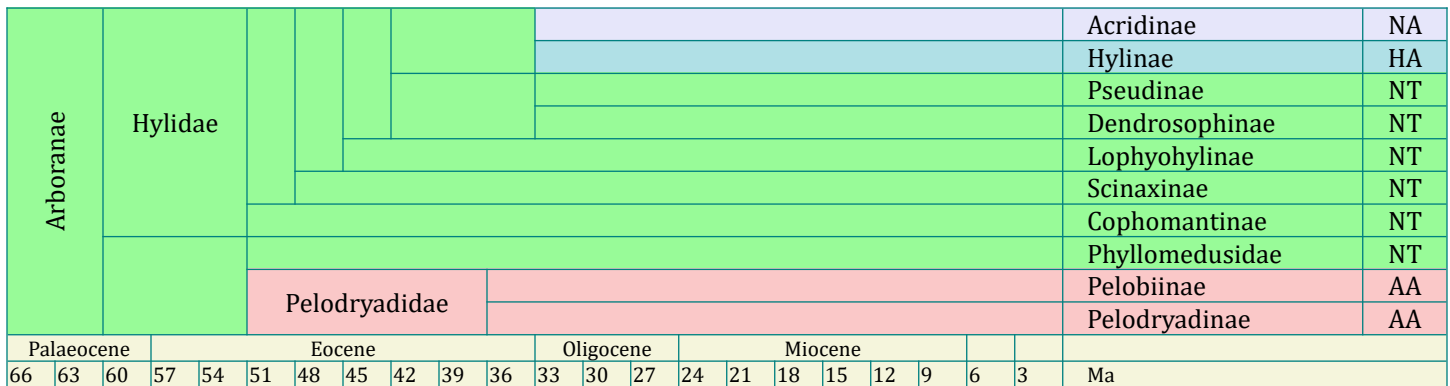


Figure 56. Phylogeny and distribution of tree frogs (Arboranae), with an approximate time scale for their divergence (after Duellman et al. 2016). Key to modern distribution (right column): AA, Australasia; HA, Holarctic; NA, Nearctic (North America); HA (Holarctic). All three families (Hylidae, Pelodyadidae, Phyllomedusidae) diverged during the early Eocene in Southern Gondwana or South America, but the Pelodyadidae are now restricted to Australasia. Some authors (e.g., Wiens et al. 2010) have placed all tree frogs in a single family, the Hylidae.

The distribution of freshwater side-necked (pleurodiran) turtles of the family Chelidae also follows this pattern of vicariant distribution across Southern Gondwana (Figures 55.3-55.4). In this case, however, the primary division between the Australasian (Chelodininae) and South American (Chelinae) chelids appears to have taken place during the early Cretaceous, followed by major, but geographically separate, divisions of Australasian and South American clades in the late Cretaceous (Fujita et al. 2004; Holley et al. 2019).

Marsupials (Figures 55.5-55.6, 57; Mitchell et al. 2016) represent the best-known example of vicariant division across Southern Gondwana. Based on the fossil record, metatherian ancestors of the marsupials lived in Laurasia (North America, Europe, Asia), and marsupials first appeared in North America in the Late Cretaceous (Wilson et al. 2016; Eldridge et al. 2019). The discovery of much earlier metatherian relatives of the marsupials in China (†*Sinodelphys*, Early Cretaceous, ~125 Ma; Luo et al. 2003) has also led some people to suggest that the Marsupalia originated in China. The actual location where marsupials originated would be highly dependent on where the line is drawn between Marsupalia and their metatherian ancestors, but there is general agreement on a Laurasian origin, followed by migration to Southern Gondwana.

The discovery of an early, plesiomorphic australidelphian fossil in Australia (†*Djarthia*, early Eocene, ~55 Ma; Beck et al. 2008) has led to the suggestion that the South American Microtheria (now represented by a single species, *Dromiciops gliroides*, Figure 54.5) represent "back migration" from Australasia. In any case it is clear that the australidelphian clade is divided across Southern Gondwana.

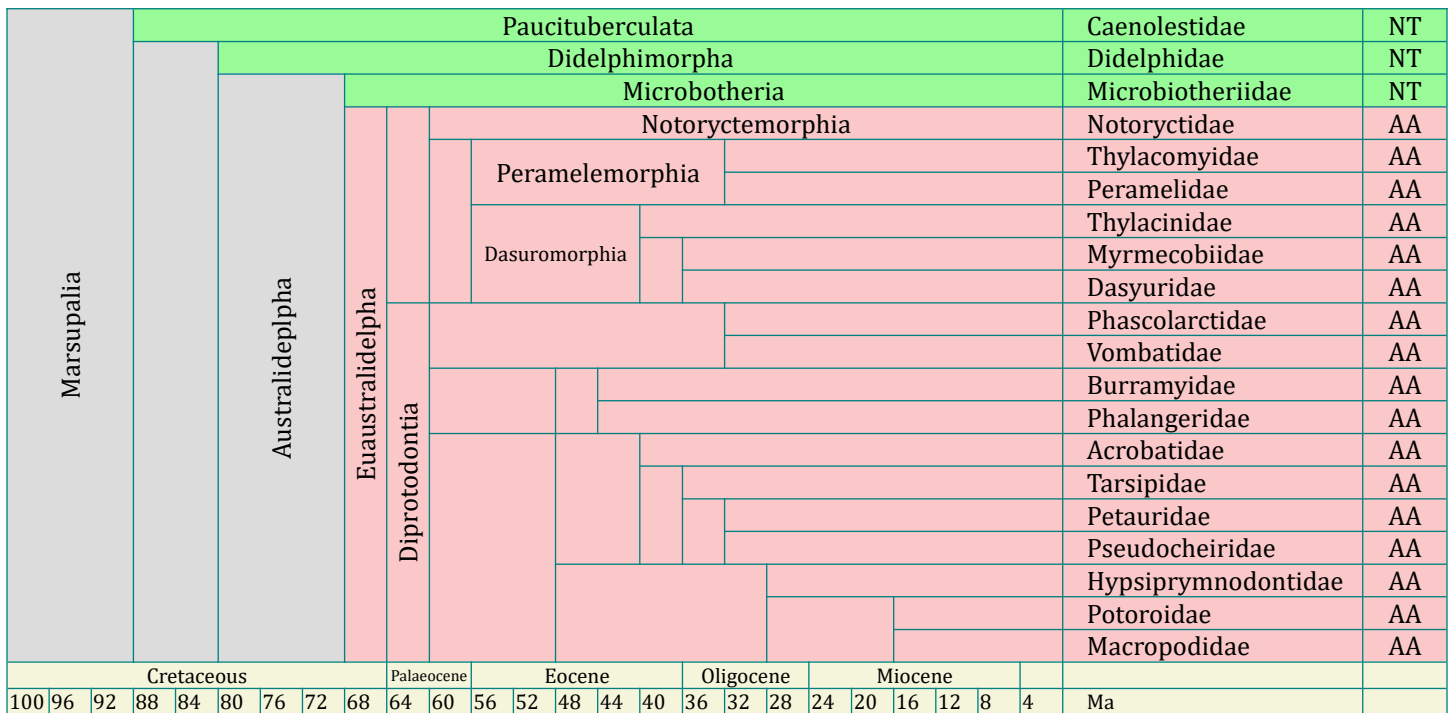


Figure 57. Phylogeny and distribution of living marsupials, with an approximate time scale for their divisions (after Mitchell et al. 2014). The diverse clade of endemic Australasian marsupials (Euaustralidelphia) is thought to have originated before the end of the Cretaceous. Its sister group, the Microbiotheria, has a single living representative, endemic to southern South America (Figure 54.5).

As our study of the biogeography of the euophryinae (and other salticids) continues in the future, we can consider several important lessons from this brief review of vertebrate biogeography:

1. Southern Gondwana, or the Antarctic Land Bridge, represents by far the most significant portal for the introduction of terrestrial animals into Australasia, or the dispersal of terrestrial animals from Australasia to other continents, prior to the end the Eocene (~34 Ma). Subsequently Australasia was isolated from all other continents by a wide sea barrier until its more recent approach to Southeast Asia.
2. Although a continental clade of living animals (e.g., Pelodryadidae, Chelodiniinae, Euaustralidelphia) has a single ancestral species, there is no guarantee that this ancestor actually lived on that continent. In fact, it is possible that this ancestor lived in a region where no close relatives of that clade live today. It is quite possible that many closely related but now extinct (*ghost*) species lived on that continent at one time, only one of which still has living descendants. It is much easier to identify a vicariant division of a clade than to identify a geographic location for the origin of that clade.
3. Although we frequently consider the success and radiation of a clade through a series of *speciation* events, we also need to consider the fact that a similar series of species extinction (or *despeciation*) events have also taken place. If we consider the number of despeciation events to be roughly equivalent to the number of speciation events over a given interval, we can see that their effect is considerable. Attempts have been made to estimate normal extinction rates from the fossil record (e.g., De Vos et al. 2015). Computer simulations (e.g., Ovaskainen et al. 2020) may give us more insight into this process, whereby the descendants of one ancestral species may replace the descendants of many related ancestral species living in the same area over time (*inter-clade competition*).

4. *Phylogenetic division* of a clade can precede the geographical division of that clade by many millions of years. For example, division of the australidelphian marsupials into the Microbotheria and the Euaustralidelphia took place in the late Cretaceous, some 30 My before the two groups were geographically divided by the breakup of Southern Gondwana. Pelodyadid tree frogs originated in the early Eocene, perhaps 20 My before their isolation in Australasia. Even more extreme, the division of the chelid turtles into the South American Chelinae and the Australasian Chelodinae is thought to have taken place in the early Cretaceous. Although it is possible that populations of a single species could immediately form the basis of two distinct clades after their geographic isolation, this seems much less likely, as survival of a single species should be less likely than survival of at least one clade within a group of related clades.

Acknowledgements

I am very grateful to the substantial contributions of the authors and subauthors of papers cited here, without which this paper would not have been possible. Any errors in interpretation of their work, or in the choice of clade names shown here, are my own. I am also grateful to the many naturalists and photographers who have permitted the use of their photographs.

References

- Allan 2022.** Maurice D. Allan. 2 Sep 2022. Association of the jumping spider *Coccorchestes ferreus* (Araneae: Salticidae: Euophryini) with a small, black weevil (Coleoptera: Curculionidae: Cryptorhynchinae: *Trigonopterus* cf. *laetus*). *Peckhamia* 278.1: 1-2.
- Azevedo et al. 2024.** Guilherme H.F. Azevedo, Marshal Hedin, Wayne P. Maddison. 18 MAY 2024. Phylogeny and biogeography of harmochirine jumping spiders (Araneae: Salticidae). *Molecular Phylogenetics and Evolution* 197 (108109): 1-14.
- Baldwin et al. 2012.** Suzanne L. Baldwin, Paul G. Fitzgerald, Laura E. Webb. 8 Mar 2012. Tectonics of the New Guinea Region. *Annual Review of Earth and Planetary Sciences* 40: 495-520.
- Beck et al. 2008.** Robin M. D. Beck, Henk Godthelp, Vera Weisbecker, Michael Archer, Suzanne J. Hand. 26 Mar 2008. Australia's oldest marsupial fossils and their biogeographical implications. *PLoS ONE* 3 (3): e1858: 1-8.
- Bodner 2009.** Melissa R. Bodner. Jul 2009) The biogeography and age of salticid spider radiations with the introduction of a new African group (Araneae: Salticidae). M.S. Thesis, The University of British Columbia: i-ix, 1-108.
- Bodner & Maddison 2012.** Melissa R. Bodner, Wayne P. Maddison. The biogeography and age of salticid spider radiations (Araneae: Salticidae). *Molecular Phylogenetics and Evolution* 65 (1): 213-240.
- Cámara-Leret et al. 2020.** Rodrigo Cámara-Leret et al. 5 Aug 2020. New Guinea has the world's richest island flora. *Nature*: 1-5. doi.org/10.1038/s41586-020-2549-5
- Cohen et al. 2013.** Benjamin E. Cohen, Kurt M. Knesel, Paulo M. Vasconcelos, Wouter P. Schellart. Tracking the Australian plate motion through the Cenozoic: Constraints from ⁴⁰Ar/³⁹Ar geochronology. *Tectonics* 32: 1371-1383.
- Cook et al. 2005.** Joseph A. Cook et al. Jan 2005. Beringia: Intercontinental exchange and diversification of high latitude mammals and their parasites during the Pliocene and Quaternary. *Mammal Study* 30: S33-S44.
- Davies 2102.** Hugh L. Davies. Mar 2012. The geology of New Guinea - the cordilleran margin of the Australian continent. *Episodes* 35 (1): 87-102.
- De Vos et al. 2015.** Jurriaan M. De Vos, Lucas N. Joppa, John L. Gittleman, Patrick R. Stephens, Stuart L. Pimm. Estimating the normal background rate of species extinction. *Conservation Biology* 29 (2): 452-462.
- Denk et al. 2010.** Thomas Denk, Fridgeir Grímsson, Reinhard Zetter. Episodic migration of oaks to Iceland: evidence for a North Atlantic "land bridge" in the latest Miocene. *American Journal of Botany* 97 (2): 276-287.
- Duellman et al. 2016.** William E. Duellman, Angela B. Marion, S. Blair Hedges. 19 Apr 2016. Phylogenetics, classification, and biogeography of the treefrogs (Amphibia: Anura: Arboranae). *Zootaxa* 4104 (1): 1-109.
- Edwards 2003.** G. B. Edwards. A review of the Nearctic jumping spiders (Araneae: Salticidae) of the subfamily Euophryinae north of Mexico. *Insecta Mundi* 16: 65-75.

- Eldridge et al. 2019.** Mark D. B. Eldridge, Robin M. D. Beck, Darin A. Croft, Kenny J. Travouillon, Barry J. Fox. An emerging consensus in the evolution, phylogeny, and systematics of marsupials and their fossil relatives (Metatheria). *Journal of Mammalogy* 100 (3): 802-837.
- Farahbakhsh et al. 2025.** Ehsan Farahbakhsh, Sabin Zahirovic, Brent McInnes, Sara Polanco, Fabian Kohlmann, Maria Seton, R. Dietmar Müller. Machine learning-based spatio-temporal prospectivity modeling of porphyry systems in the New Guinea and Solomon Islands region. *Tectonics* 44 (8362): 1-24.
- Forte et al. 2021.** Pablo Forte et al. Nov 2021. Volcano monitoring in Latin America: taking a step forward. *Volcanica* 4 (S1): vii-xix.
- Fujita et al. 2003.** Matthew K. Fujita, Tag N. Engstrom, David E. Starkey, H. Bradley Shaffer. *Molecular Phylogenetics and Evolution* 31: 1031-1040.
- García-Casco et al. 2011.** A. García-Casco, J. A. Proenza, M. A. Iturralde-Vinent. Subduction zones of the Caribbean: the sedimentary, magmatic, metamorphic and ore-deposit records. *Geologica Acta* 9 (3-4): 217-224.
- Giunta & Orioli 2011.** Giuseppe Giunta, Silvia Orioli. 27 Jul 2011. The Caribbean Plate evolution: trying to resolve a very complicated tectonic puzzle. In: *New Frontiers in Tectonic Research - General Problems, Sedimentary Basins and Island Arcs*, ed. Evgenii V. Sharkov: 221-248.
- Graham 2018.** Alan Graham. Apr 2018. North Atlantic Land Bridge: Northeastern North America, Greenland, Iceland, Arctic Islands, Northwestern Europe. In: *Alan Graham, Land Bridges: Ancient Environments, Plant Migrations, and New World Connections Land Bridges: Ancient Environments, Plant Migrations, and New World Connections*: 89-132.
- Hall 2012.** Robert Hall. 15 May 2012. Late Jurassic–Cenozoic reconstructions of the Indonesian region and the Indian Ocean. *Tectonophysics* 570-571: 1-41.
- Hill 2009.** David Edwin Hill. 7 Oct 2009. Salticidae of the Antarctic land bridge. *Peckhamia* 76.1: 1-14.
- Hill 2010.** David Edwin Hill. 19 May 2010. Sunda to Sahul: Trans-Wallacean distribution of recent salticid genera (Araneae: Salticidae). *Peckhamia* 80.1: 1-60.
- Hill 2022a.** David E. Hill. 12 FEB 2022. Neurobiology and vision of jumping spiders (Araneae: Salticidae). *Peckhamia* 255.1: 1-81.
- Hill 2022b.** David E. Hill. 22 Oct 2022. Jumping spider scales. *Peckhamia* 279.1: 1-83.
- Hill 2023.** David Edwin Hill. 24 Feb 2023. The jumping spiders of Pete Carmichael. *Peckhamia* 292.1: 1-52.
- Hill & Edwards 2013.** David E. Hill, G. B. Edwards. 13 May 2013. Origins of the North American jumping spiders (Araneae: Salticidae). *Peckhamia* 107.1: 1-67.
- Hill & Ng 2025.** David E. Hill, Yongi Ng. 8 Jan 2025. Standing display of the Australasian jumping spider *Ohilimia* (Araneae: Salticidae: Euophryini: Papuaphryni). *Peckhamia* 326.1: 1-12.
- Hobart et al. 2022.** Bethany Hobart, Lorraine E. Lisiecki, Devin Rand, Taehee Lee, Charles E. Lawrence. Aug 2023. Late Pleistocene 100-kyr glacial cycles paced by precession forcing of summer insolation. *Nature Geoscience* 16: 717-722.
- Holley et al. 2020.** J. Alfredo Holley, Juliani Sterli, Néstor G. Basso. Dating the origin and diversification of Pan-Chelidae (Testudines, Pleurodira) under multiple molecular clock approaches. *Contributions to Zoology* 89: 146-174.
- Iturralde-Vinent & Gahagan 2002.** Manuel A. Iturralde-Vinent, Lisa Gahagan. Sep 2002. Late Eocene to Middle Miocene tectonic evolution of the Caribbean: some principles and their implications for plate tectonic modeling. In: *Caribbean Geology: Into the Next Millennium*, ed. Trevor A. Jackson: 47-62.
- Jiang et al. 2019.** Dechun Jiang, Sebastian Klaus, Ya-Ping Zhang, David M. Hillis, Jia-Tang Li. 15 Mar 2019. *National Science Review* 6: 739-245.
- Klages et al. 2024.** Ohann P. Klages, Henny Gerschel, Ulrich Salzmann, Gernot Nehrke, Juliane Müller, Claus-Dieter Hillenbrand, Steven M. Bohat, Torsten Bickert. First discovery of Antarctic amber. *Antarctic Science* (2024): 1-2. doi:10.1017/S0954102024000208
- Li et al. 2025.** Zhaoyi Li, Feng Zhang, Wenqiang Zhang, Kiran Marathe, Wayne P. Maddison, Junxia Zhang. 16 Jan 2025. Phylogeny of euophryine jumping spiders from ultra-conserved elements, with evidence on the intersexual coevolution of genitalia (Araneae: Salticidae: Euophryini). *Systematic Entomology* 2025: 1-14. <https://doi.org/10.1111/syen.12669>
- Luo et al. 2003.** Zhe-Xi Luo, Qiang Ji, John R. Wible, Chong-Xi Yuan. 12 Dec 2003. An early Cretaceous tribosphenic mammal and metatherian evolution. *Science* 302: 1934-1940.
- Maddison 2015.** Wayne P. Maddison. A phylogenetic classification of jumping spiders (Araneae: Salticidae). *Journal of Arachnology* 43: 231-292.
- Maddison & Szűts 2019.** Wayne P. Maddison, Tamás Szűts. 7 May 2019. Myrmarachnine jumping spiders of the new subtribe Levieina from Papua New Guinea (Araneae, Salticidae, Myrmarachnini). *ZooKeys* 842: 85-112.
- Maddison et al. 2014.** Wayne P. Maddison, Daiqin Li, Melissa Bodner, Junxia Zhang, Xin Xu, Qingqing Liu, Fengxiang Liu. 15 Sep 2014. The deep phylogeny of jumping spiders (Araneae, Salticidae). *ZooKeys* 440: 57-87.
- Maddison et al. 2020.** Wayne P. Maddison, David R. Maddison, Shahan Derkarabetian, Marshal Hedin. 8 Apr 2020. Sitticine jumping spiders: phylogeny, classification, and chromosomes (Araneae, Salticidae, Sitticini). *ZooKeys* 925: 1-54.
- Mitchell et al. 2014.** Kieren J. Mitchell et al. 30 May 2014. Molecular phylogeny, biogeography, and habitat preference evolution of marsupials. *Molecular Biology and Evolution* 31 (9): 2322-2330.

- Müller et al. 2008.** R. D. Müller, M. Sdrolias, C. Gaina, W. R. Roest. Age, spreading rates and spreading symmetry of the world's ocean crust. *Geochemistry, Geophysics, Geosystems* (G^3) 9, Q04006, doi:10.1029/2007GC001743
- Müller et al. 2016.** R. D. Müller et al. 29 Apr 2016. Ocean basin evolution and global-scale plate reorganization events since Pangea breakup. *Annual Review of Earth and Planetary Sciences* 44: 107-138.
- Otto & Hill 2012.** Jürgen C. Otto, David E. Hill. 4 Nov 2012. Notes on *Maratus* Karsch 1878 and related jumping spiders from Australia, with five new species (Araneae: Salticidae: Euophryinae). *Peckhamia* 103.1: 1-81.
- Ovaskainen et al. 2020.** Otso Ovaskainen, Panu Somervuo, Dmitri Finkelshtein. 28 Sep 2020. Mathematical and simulation methods for deriving extinction thresholds in spatial and stochastic models of interacting agents. *Methods in Ecology and Evolution* 12: 162-169.
- Passchier et al. 2011.** S. Passchier, G. Browne, B. Field, C.R. Fielding, L.A. Krissek, K. Panter, S.F. Pekar, ANDRILL-SMS Science Team. Nov. 2011. Early and middle Miocene Antarctic glacial history from the sedimentary facies distribution in the AND-2A drill hole, Ross Sea, Antarctica. *Geological Society of America Bulletin* 123 (11/12): 2352-2365.
- Passchier et al. 2013.** S. Passchier, S. M. Bohaty, F. Jiménez-Espejo, J. Pross, U. Röhl, T. van de Flierdt, C. Escutia, H. Brinkhuis. 6 May 2013. Early Eocene to middle Miocene cooling and aridification of East Antarctica. *Geochemistry Geophysics Geosystems* 14 (5): 1399-1410.
- Paxman et al. 2022.** Guy J. G. Paxman, Jacqueline Austermann, Andrew Hollyday. Total isostatic response to the complete unloading of the Greenland and Antarctic Ice Sheets. *Scientific Reports* 12 (11399): 1-10.
- Ponyalou et al. 2023.** Olive L. Ponyalou, Michael G. Petterson, Joseph O. Espi. 24 Aug 2023. The geological and tectonic evolution of Feni, Papua New Guinea. *Geosciences* 13 (257): 1-13.
- Pritchard et al. 2025.** Hamash D. Pritchard et al. Bedmap3 updated ice bed, surface and thickness gridded datasets for Antarctica. *Scientific Data* 12 (414): 1-20.
- Quigley et al. 2010.** Mark c. Quigley, Dan Clark, Mike Sandiford. Tectonic geomorphology of Australia. In *Australian Landscapes*, ed. P. Bishop, B. Pillans, Geological Society of London, Special Publication 346: 243-265.
- Ruiz & Maddison 2015.** Gustavo R. S. Ruiz, Wayne P. Maddison. 11 Nov 2015. The new Andean jumping spider genus *Urupuyu* and its placement within a revised classification of the Amycoidea (Araneae: Salticidae). *Zootaxa* 4040 (3): 251-279.
- Tanyaş et al. 2022.** Hakan Tanyaş, Kevin Hill, Luke Mahoney, Islam Fadel, Luigi Lombardo. 17 Dec 2021. The world's second-largest, recorded landslide event: Lessons learnt from the landslides triggered during and after the 2018 M_w 7.5 Papua New Guinea earthquake. *Engineering Geology* 297 (106504): 1-23.
- Wen et al. 2016.** Jun Wen, Ze-Long Nie, Stefanie M. Ickert-Bond. 7 Sep 2016. Intercontinental disjunctions between eastern Asia and western North America in vascular plants highlight the biogeographic importance of the Bering land bridge from late Cretaceous to Neogene. *Journal of Systematics and Evolution* 54 (5): 469-490.
- Wiens et al. 2010.** John J. Wiens, Caitlin A. Kuczynski, Xia Hua, Daniel S. Moen. An expanded phylogeny of treefrogs (Hylidae) based on nuclear and mitochondrial sequence data. *Molecular Phylogenetics and Evolution* 55: 871-882.
- Wiley 1988.** E. O. Wiley. Vicariance Biogeography. *Annual Review of Ecology and Systematics* 19: 513-542.
- Wilson et al. 2016.** Gregory P. Wilson, Eric G. Ekdale, John W. Hoganson, Jonathan J. Calede, Abby Vander Linden. 8 Dec 2016. A large carnivorous mammal from the Late Cretaceous and the North American origin of marsupials. *Nature Communications* 13734: 1-10.
- WSC 2025.** World Spider Catalog. Version 26. Natural History Museum Bern, online at <http://wsc.nmbe.ch>, accessed on 3 Mar 2025. doi: 10.24436/2
- Yu et al. 2024.** Kun Yua, Feng Zhang, Yaozhuo Wang, Wayne P. Maddison, Junxia Zhang. Robust phylogenomics settles controversies of classification and reveals evolution of male embolic complex of the *Laufeia* clade (Araneae, Salticidae, Euophryini). *Cladistics* 40: 618-635.
- Zhang 2012.** Junxia Zhang. May 2012. Phylogeny and systematics of the jumping spider subfamily Euophryinae (Araneae: Salticidae), with consideration of biogeography and genitalic evolution. Ph.D. Thesis, The University of British Columbia: i-xxv, 1-526.
- Zhang & Maddison 2012a.** Jun-Xia Zhang, Wayne P. Maddison. 10 Sep 2012. New euophryine jumping spiders from the Dominican Republic and Puerto Rico (Araneae: Salticidae: Euophryinae). *Zootaxa* 3476: 1-54.
- Zhang & Maddison 2012b.** Jun-Xia Zhang, Wayne P. Maddison. 20 Sep 2012. New euophryine jumping spiders from Papua New Guinea (Araneae: Salticidae: Euophryinae). *Zootaxa* 3491: 1-74.
- Zhang & Maddison 2012c.** Jun-Xia Zhang, Wayne P. Maddison. 10 Dec 2012. New euophryine jumping spiders from Central and South America (Araneae: Salticidae: Euophryinae). *Zootaxa* 3578: 1-35.
- Zhang & Maddison 2013.** Jun-Xia Zhang, Wayne P. Maddison. Molecular phylogeny, divergence times and biogeography of spiders of the subfamily Euophryinae (Araneae: Salticidae). *Molecular Phylogenetics and Evolution* 68: 81-92.
- Zhang & Maddison 2015.** Junxia Zhang, Wayne P. Maddison. 27 Mar 2015. Genera of euophryine jumping spiders (Araneae: Salticidae), with a combined molecular-morphological phylogeny. *Zootaxa* 3938 (1): 1-147.
- Zhang et al. 2024.** Junxia Zhang, Yi Ni, Kiran Marathe, Yaozhuo Wang, Wayne P. Maddison. 12 Nov 2024. Clarifying the phylogenetic placement of Eupoinae Maddison, 2015 (Araneae, Salticidae) with ultra-conserved element data. *ZooKeys* 1217: 343-351.