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TALE OF TWO FAMILIES: BIOGEOGRAPHY OF MICROPTERIGIDAE AND AGATHIPHAGIDAE (LEPIDOPTERA)

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Tale of two families: biogeography of Micropterigidae and Agathiphagidae (Lepidoptera)

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Abstract

The biogeographic structure of Micropterigidae and Agathiphagidae is described. The range of Micropterigidae is widespread, other than the core regions of Gondwana comprising most of Africa and India. Extant Agathiphagidae are localized to eastern Australia and nearby Pacific islands which have a history of continental fragmentation (New Caledonia) or East Gondwana island arc rifting (Solomons, Vanuatu, Fiji). The origin of fossil Agathiphagidae and an extant genus of Micropterigidae, originally known from Australasia (*Aureopterix*), is discussed in reference to Gondwana fragmentation, Tethys geography, and oceanic island arcs. A pattern of absence or marginal presence in the distributions of Micropterigidae and Agathiphagidae and other basal Lepidotpera groups from core Gondwana regions (Africa, Madagascar, India) may indicate that the ancestral range of Lepidoptera was sub-cosmopolitan. Many basal clades of Lepidoptera, including Micropterigidae and Agathiphagidae, have distributions associated with major centres of basal endemism such as the Tasman-Coral Sea region and the Chilean Coastal Range region. Absence of Micropterigidae on island arcs along the Vitiaz Lineament may represent remnants of original allopatry between this family and the Agathiphagidae that was lost in the Australian and New Caledonian sectors of East Gondwana following range expansion by Micropterigidae

Keywords. *Agathis*, Acanthopteroctetidae, Aenigmatineidae, allopatric, chance, Coral Sea, dispersal, Eriocranidae, Exoporia, Gondwana, Hepialidae, Heterobathmiidae, Lophocoronidae, Mnesarchaeidae, Mojave-Sonora megashear, Neopseustidae, Neotheoridae, panbiogeography, Pacific, Pangaea, Prototheoridae, Tasman Sea, tectonics, Tethys.

Introduction

The families Micropterigidae and Agathiphagidae (Fig. 1) are either sequentially the two most basal families of Lepidoptera or together they comprise the most basal family levels of divergence (Kirstensen *et al.* 2015, Regier *et al.* 2015, Mitter *et al.* 2017). The biogeography of Micropterigidae has received past consideration (e.g. Gibbs & Lees 2014, Gibbs 2018), but the origins of Agathiphagidae have not been extensively explored. New questions about the biogeography of these families were recently raised by Mey *et al.* (2021) who reported on the first record of an extant Asian representative of the Australasian micropterigid genus *Aureopterix*, and a fossil species of Agathiphagidae in 89 Ma Burmese amber. The new records were intriguing because the Asian records represented a 7,000 km disjunction from the previously known Australasian range of extant *Aureopterix* and Agathiphagidae.

Origin of the new *Aureopterix* species from Vietnam was attributed to chance dispersal from Australia by Mey *et al.* (2021) because the molecular divergence age of *Aureopterix* was too recent for tectonic events to have been involved. But a tectonic role was seen as viable for Agathiphagidae because the Asian fossil was located within in a displaced Gondwana terrane, and the family had a molecular divergence age of at least 160 Ma (citing Wahlberg *et al.* 2013). However, Mey *et al.* (2021) recognized that further biogeographic study was necessary to evaluate these different biogeographic possibilities.

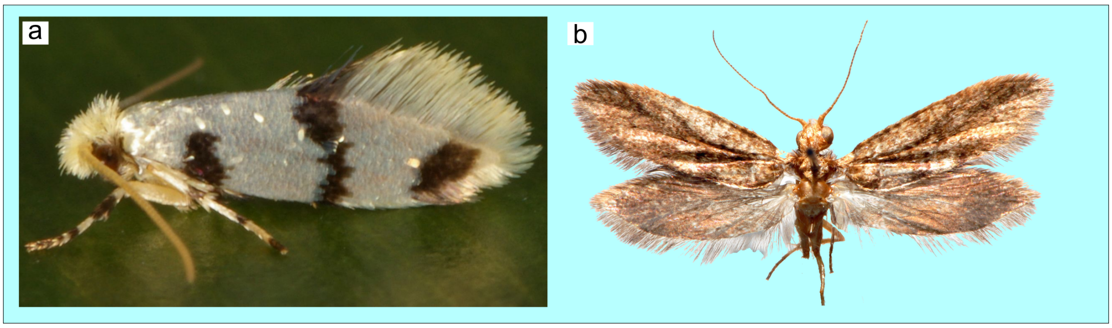

Fig. 1. (a) New Caledonian *Aureopterix* sp., (b) Australian *Agathiphaga queenslandensis*, Photo (a) from https://moths.csiro.au/species_taxonomy/agathiphaga-queenslandensis/, (b) courtesy of George Gibbs.

In this paper I revisit the biogeography of Micropterigidae and Agathiphagidae to provide a comparative biogeographic context for the new records documented by Mey *et al.* (2021). The comparative approach involves description of the distributional and phylogenetic (where known) boundaries of each family and how they compare to biogeographic patterns in general and with regional or global tectonic structures.

Methods

Most taxonomic and systematic approaches to biogeography treat taxa as if they each had a unique history (see Heads 2012, 2014, 2017a for innumerable examples). That this isolationist approach is not justified is demonstrated by 73 years of comparative studies (panbiogeography) confirming the existence of standard geographic patterns of relationships and distribution, where individual taxa conform to entire biotas (see Craw *et al.* 1999, Heads 2017a and references therein). This comparative approach involves mapping the distribution and phylogenetic affinities (where known) of taxa. The actual locations of taxa are treated as empirical biogeographic data for analysis. The purpose of this approach is to identify and compare the geographic location of phylogenetic breaks and distributional boundaries of taxa. These geographic and biological features constitute empirical facts since they can be directly verified or refuted – i.e. biodiversity has a biogeographic structure (Heads 2017a, Grehan 2021) that is often overlooked in biogeographic studies of Lepidoptera (Grehan 2024)

Where clades have disjunct distributions, the spatial connection can be mapped by a line graph (track). This spatial linkage is most often a direct application of minimum distance between disjuncts based on the argument that, in the absence of conflicting evidence, proximity is more likely to represent the evolutionary connection in geographic space (Craw *et al.* 1999). Biogeographic links with geological processes are identified by spatial correlation with tectonic structures within or at the boundaries of distributions.

Fossils are incorporated into the analysis, either as additional localities that expand the known range of taxa, or as a measure of the minimum age of the represented taxa. The new extralimital record for Agathiphagidae in Asia is represented by a single fossil specimen where the posterior apophyses in the female genitalia are fused into a single branch in the apical part of the ovipositor. This feature distinguishes Agathiphagidae from all other Lepidoptera (Wolfram Mey pers. comm.).

The term 'basal' refers here to the smaller (less speciose) sister group (Heads 2009). The term chance dispersal refers to a theory in many biogeographic studies that movement of an individual or small number of individuals, across what is otherwise a barrier for a species, represents a mode of speciation and an explanation of allopatry. These chance dispersal events are not related to environmental or biological factors. This theory of dispersal contrasts with normal ecological dispersal that is directly observable for effecting distribution range and expansion, and not as a mode of speciation (Heads & Saldivia 2024, Head 2025).

Biogeographic context of Micropterigidae and Agathiphagidae

The Micropterigidae is broadly distributed and represented on all continents outside Antarctica. Extant Agathiphagidae are localized to the southwest Pacific but represented in Asia by a Cretaceous fossil from Myanmar (Fig. 2). The distribution ranges of the two groups overlap in southeastern Asia (fossil for Agathiphagidae), Australia, and New Caledonia. The Agathiphagidae are present in three island archipelagos where Micropterigidae are absent: Solomons, Vanuatu, and Fiji.

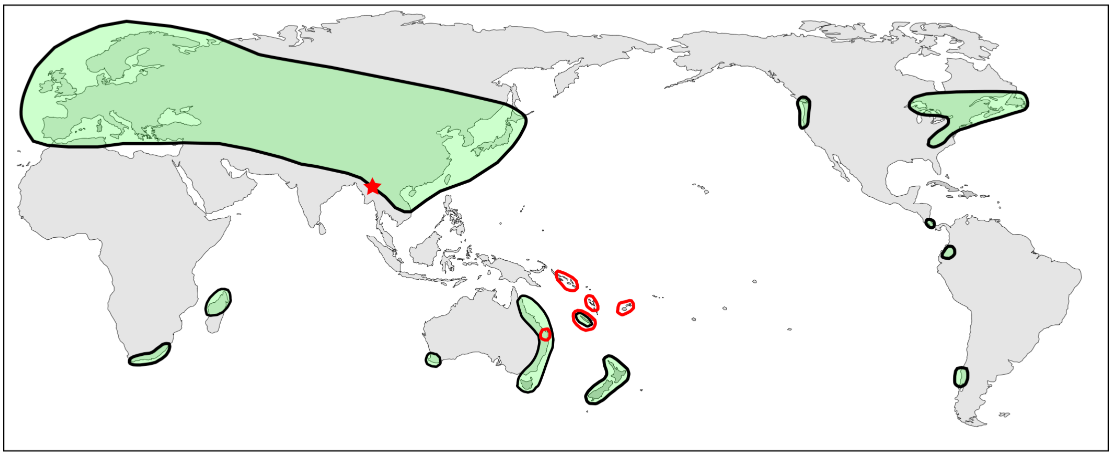

Fig. 2. Extant distribution of Micropterigidae (black outline) and Agathiphagidae (red outline). Red star – Burmese Amber fossil record of Agathiphagidae. Distribution from Dumbleton (1952), Kristensen (1984), Lees *et al.* (2010), Gibbs (2018), Mey (2019), and Jean-François Landry (pers. comm.).

Micropterigidae.

The globally broad distribution range of this family was seen by Mey *et al.* (2021) as evidence for a Pangaean ancestral range. However, the family is not recorded from major Pangaean regions comprising most of Africa, central-southern India/Sri Lanka, southeastern Asia, southern North America, and most of South America (Fig. 2). Some of these geographic gaps may represent collecting artefacts (Mey *et al.* 2021) as these micro-moths are diurnal and rarely found at light traps (Gibbs 2018). This collecting constraint explains the comparatively recent records for Costa Rica that were first documented just over 10 years ago (Wagner & Davis 2014), and the distribution of Micropterigidae in northern North America was not fully described until Davis & Landry (2012). In the fossil record, the oldest definitive Micropterigidae is Early Cretaceous (Sohn *et al.* 2012). Later fossils include mid-Cretaceous records from Burmese amber (Zhang *et al.* 2017, Han *et al.* 2024). A

Jurassic fossil from Siberia cannot be verified due to the lack of defining characteristics (Sohn *et al.* 2012).

The distribution of Micropterigidae is currently divided among four clades (Gibbs & Lees 2014, Gibbs 2018) with the phylogenetic sequence of (1 (2 (3 + 4)), as numbered in Fig. 3. The initial phylogenetic break is located geographically in southeastern Asia between the distribution range of *Paramartyria* in clade 1 and *Aureopterix* of clade 3, and between southern North America to Central America separating *Epimartyria* of Clade 1 in northern North America and genera of Costa Rica in Clade 2 (Fig. 3).

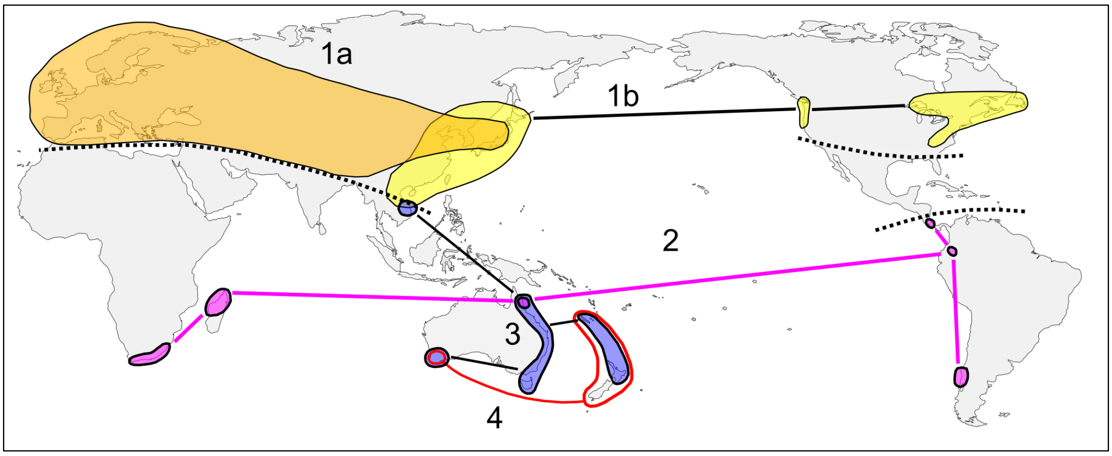

Fig. 3. Distribution of Micropterigidae clades. (1) Orange shading -*Micropterix*; yellow shading - *Palaeomicroides* (Taiwan), *Issikiomartyria* (Japan), *Kurokopteryx* (Japan), *Melinopteryx* (Japan), *Neomicropteryx* (Japan), *Paramartyria* (Taiwan, Japan, eastern Asia), *Epimartyria* (North America). (2) crimson outline - *Agrionympha* (South Africa), new genus (Madagascar), *Austromartyria* (Queensland), *Squamicornia* (Costa Rica), *Hypomartyria* (southern Chile). (3) blue outline *Aureopterix* (Vietnam, Queensland, New Caledonia), *Zealandopterix* (New Zealand), *Tasmantrix* (eastern Australia). (4) '*Sabatinca*' clade (New Zealand-Western Australia). Dashed lines – boundary between Clade 1 and 'southern' sister group (Clades 2-4). Phylogeny and distribution data from Kristensen & Nielsen 1982, Gibbs & Lees (2014), Gibbs & Kristensen (2011), Gibbs (2018), Imada *et al.* (2011), Imada & Kato (2018), Lees & Minet (2022).

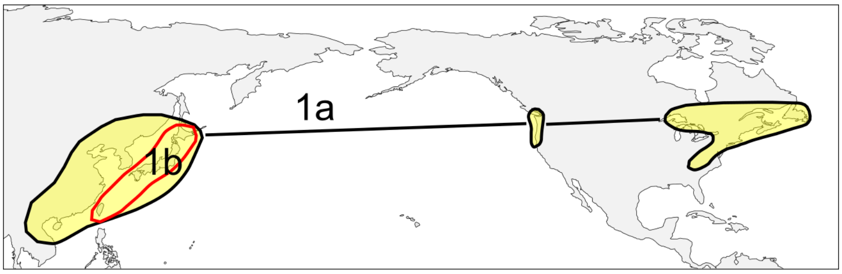

Fig. 4. North Pacific clade of Micropterigidae. Yellow shading - clade 1a: *Epimartyria*/*Paramartyria*. Red outline – clade 1b: *Palaeomicroides* (Taiwan), and *Issikiomartyria*, *Kurokopteryx, Melinopteryx*, and *Neomicropteryx* of Japan.

The distribution of Clade 1 comprises *Micropterix* (Clade 1a) with a range extending between Europe and Japan while its sister group (Clade 1b) is present in eastern Asia (*Palaeomicroides*, *Issikiomartyria*, *Kurokopteryx*, *Neomicropteryx*, *Paramartyria*) and North America (*Epimartyria*) (Fig. 4). The North American *Epimartyria* is most closely related to *Paramartyria* of China, Taiwan, and Japan. These genera comprise the sister group of genera in the eastern Asian islands of Taiwan (*Palaeomicroides*), and Japan (*Issikiomartyria*, *Kurokopteryx* and *Neomicropteryx*) (Gibbs & Lees 2014). In this phylogenetic sequence, the primary phylogenetic break is Eastern Asia (between *Micropteryx* and the eastern Asia-North America group), followed by a break between the *Epimartyria* and *Paramartyria* (clade 1a) and its Japan-Taiwan sister group (Fig. 4).

Gibbs (2018) suggested that divergence of Clade 1 from all other Micropterigidae corresponds to the Mesozoic fragmentation of Pangaea into northern Laurasia and southern Gondwana. Absence of the family from most of Africa, India, southeastern Asia, eastern South America, Mexico, and the Caribbean are problematic as they all represent major regions of absence for other taxa with well-known distributions (see Heads 2012). If corroborated for Micropterigidae, either the Pangaean ancestor of Micropterigidae was not cosmopolitan, or the ancestral distribution involved non-Pangaean elements.

The concept of Pangaea refers to a proposed amalgamation of continental blocks whereas non-continental geological formations, such as island arcs and magmatic plateaus, can have a major impact on the origin of widespread animal and plant taxa (Heads & Grehan 2021, Heads *et al* 2023). In a radical departure from traditional biogeographic models, Gibbs (1983) suggested that the geological history of the Pacific may be as relevant to the origins of the Micropterigidae as the breakup of Pangaea. Noting how the Gondwana derived islands of New Zealand and New Caledonia both include terranes of Pacific origin, Gibbs (1983) concluded that New Zealand micropterigids, for example, could not be interpreted as if New Zealand were nothing more than a fragment of eastern Gondwana.

Overlap of micropterigid clades 1a and 1b in eastern Asia corresponds to a region of tectonic rifting in the Sea of Japan (as noted by Imada *et al.* 2011, Gibbs 2018), and the Taiwan strait (as noted for Hepialidae by Buchsbaum *et al.* 2018). These zones of tectonic extension correspond to original allopatry between clades 1a and 1b, followed by range expansion of *Paramartyria* overlapping with clade 1b in Taiwan and Japan. The Pacific distribution of clade 1a and its sister group relationship with the Taiwan-Japan clade corresponds to a north Pacific divergence rather involving the Atlantic which would be expected if the divergence resulted from the separation of North America and Eurasia.

The Australasian distributions of clades 3 and 4 are widely sympatric, but include a reciprocally allopatric range in eastern Australia (clade 3 only) and the South Island of New Zealand (clade 4 only). The geographic overlap may be the result of range expansion by one or both groups since their original divergence. The sole presence of clade 4 in the South Island of New Zealand and its disjunct presence in southern Western Australia (overlapping clade 3) may correspond to the ancestor of clade 4 originally having a distribution to the south and east of clade 3, perhaps disrupted by rifting between Australia and Zealandia, and between Australia and Antarctica. The basal group of Clade 3 is in Western Australia (Gibbs 2018) where rifting between southern Australia and Antarctica was initiated next to southwestern Australia beginning 90–84 Ma, followed by ridge propagation west to east along the Southern Rift System (Direen *et al.* 2011, MacLeod *et al.* 2020).

Clade 2 has a fragmentary distribution bordering the Pacific and Indian Oceans, and is allopatric to clades 3 and 4, other than marginal overlap with clade 3 (*Austromartyria*) in northern Queensland, Australia. In the summary COI tree by Gibbs (2018, fig. p.

197), the Australian *Austromartyria* is the sister group to the Indian and Pacific Ocean genera. The distributions of genera bordering the Pacific and Indian Oceans conform to an Indio-Pacific range Gibbs (2018: fig. p. 195), but the precise relationships among the genera have not yet been fully explored.

***Aureopteryx* and sister clades:** Clade 3 includes a subclade comprising four genera in the following sequence: *Tasmantrix* (*Zealandopterix* (*Aureopteri*x + *Nannopterix*) (Gibbs & Lees 2014). The distribution of *Tasmantrix* extends along eastern Australia, and *Zealandopterix* is confined to northern North Island of New Zealand. *Nannopterix* is endemic to New Caledonia while its *Aureopterix* sister group spans New Caledonia, northern Queensland (Australia), and Vietnam (Fig. 5). Mey *et al.* (2021) attributed the Asian *Aureopterix* to chance dispersal from an Australian centre of origin. This distribution mode was argued as necessary because a molecular divergence estimate of 54 Ma (40–74 Ma) between *Aureopterix* in Australia and New Caledonia postdated Gondwana tectonic breakup (about 130 Ma) and terrane detachment in East Gondwana (about 120 Ma). But this conclusion is unnecessary because the molecular divergence estimates were calibrated by fossils which represent minimum clade ages only (cf. Heads & Saldivia 2024).

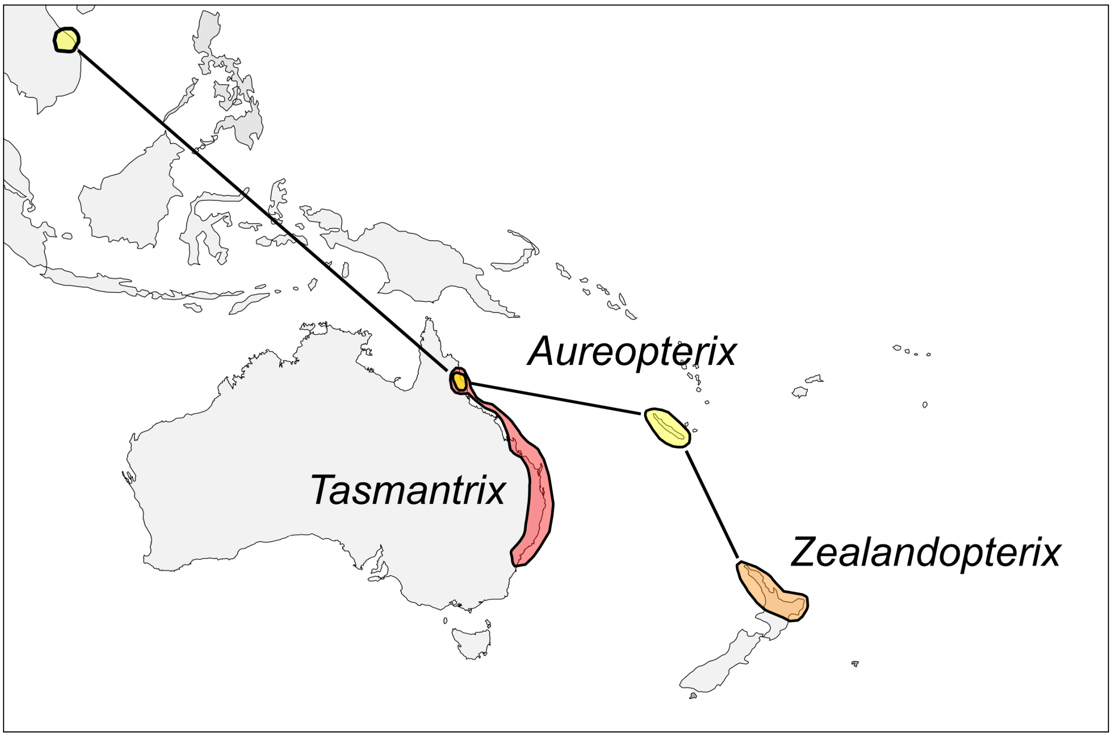

Fig. 5 Distribution of *Aureopterix* and two closely related genera. Distribution data from Mey *et al.* (2021), Gibbs (2010), Gibbs & Lees (2014).

In support of their chance dispersal argument, Mey *et al.* (2021) cited New Caledonia as a region that was entirely submerged for a time after rifting from East Gondwana. This total submersion would require *Aureopterix* and the entire New Caledonian biota to have arrived later by chance dispersal. But there is no geological evidence for total submersion at any one time. Rather, there is geological evidence for submersion of parts of New Caledonia at various times (see review of geological evidence in Heads 2019). New Caledonia has always been situated at or near a plate boundary, and a nearby volcanic arc along the subduction zone would have been present throughout (Pelletier 2006). Biogeographic evidence for persistence of the biota includes molecular ages of taxa older than postulated marine inundation, and New Caledonia endemics with global sister groups (Heads 2019). The distribution of *Zealandopterix* in the northern half of the north island of New Zealand is a pattern found in various other animal and plant taxa that have close New Caledonian affinities. Divergence between *Aureopterix* and *Zealandopterix* matches the formation of Cretaceous-Oligocene ophiolites (former island arcs) that accreted to mainland New Zealand during the Oligocene (Heads 2014, 2017a, Grehan 2020).

Agathiphagidae

Extant records of *Agathiphaga* comprise two named species in Australia and Fiji respectively. Further populations of unresolved taxonomic status are recorded from the Solomon Islands, Vanuatu, and New Caledonia (Kristensen 1984, Robinson & Tuck 1998) (Fig. 3). An extralimital fossil moth from Burmese amber (98 Ma) was identified by Mey *et al.* (2021) as belonging to Agathiphagidae. The Myanmar fossil is located within the Burma terrane which broke away from northern Gondwana and later collided with Asia (Poinar 2018, Wood & Wunderlich 2023). Fossil Agathiphagidae in Burmese Amber indicates an early Cretaceous presence for the family in East Gondwana. It is not known whether Agathiphagidae were relocated into Asia by terrane transport as living or fossil forms.

Chance dispersal was seen by Mey *et al.* (2021) to be the best explanation for the origin of *Agathiphaga* on various Pacific islands. As the seed inhabiting larvae have a multi-year diapause (Upton 1997), this would in theory allow them to disperse from continental areas by drifting in *Agathis* seeds. A vicariance origin for the Pacific populations was not considered, but the volcanic archipelagos of the Solomons, Vanuatu, and Fiji were all originally located along the Vitiaz Lineament, a former subduction zone between the Indo-Australian and Pacific plates (Vanuatu was subsequently displaced by expansion of the North Fiji basin) (Konrad *et al.* 2024). About 90 million years ago the subduction zone was located along East Gondwana, before retreating east and northeast into the Pacific (Fig. 6).

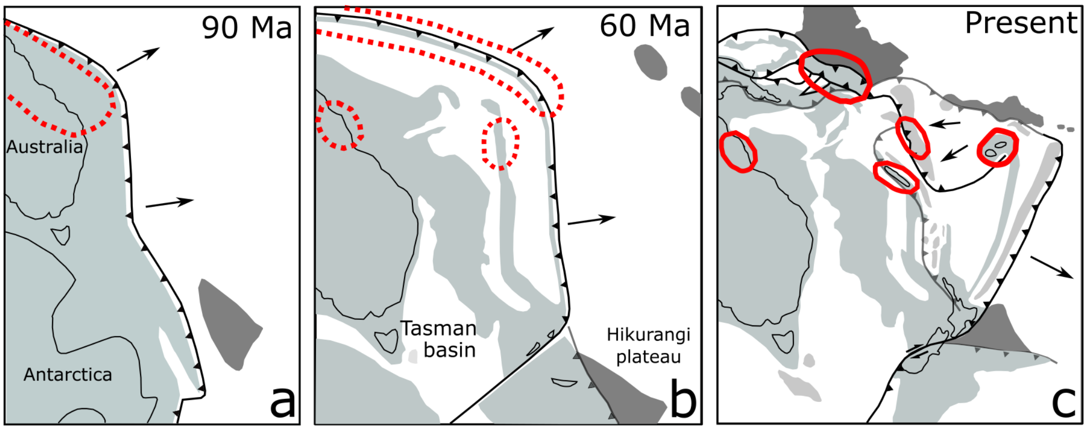

Fig. 6. Tectonic correlation for *Agathiphaga* in the southwest Pacific. (a) Hypothetical ancestral range, (b) fragmentation of ancestral range due to eastward extension of Pacific subduction zone leaving displaced populations in Australia, New Caledonia, and along the Vitiaz Arc, (c) present day distribution of *Agathiphaga*. Dashed outlines – ancestral *Agathiphaga*, solid red outlines – extant populations. Solid black lines with points – subduction zones, points in direction of subduction. Dark grey – Pacific magmatic plateaus. Modified from Heads (2014).

Subduction zones generate volcanic islands or island arcs from the time of their formation, and those of the Vitiaz Lineament would have been inhabited by elements of the East Gondwana biota. Correlated biogeographic patterns in the southwestern Pacific indicate that some of this original biota could have survived to the present day by sequential colonization of newer islands as older islands cooled and subsided below the sea (Heads 2017b). The long-term larval diapause in *Agathis* seeds could have contributed to the persistence and survival of both *Agathiphaga* and its host plant group *Agathis* on the dynamic changing geography of the island arcs. Biogeographic patterns consistent with this model have been documented for a wide range of animal and plant taxa (Heads 2014) and recently applied to understanding the distributions of ghost moths (Hepialidae) (Grehan & Mielke 2018, 2020a-b, Grehan & Ramik 2024) and damselflies (Saxton *et al.* 2025).

The theory of chance dispersal into the Pacific by *Agathiphaga* in *Agathis* seeds implies that the Pacific distribution of *Agathis* also originated by this process. But the distribution and biogeographic relationships of *Agathis* clades corresponds to the tectonic structure and history of the southwestern Pacific (Fig. 7). In the molecular phylogeny proposed by Leslie *et al.* (2018), there is an initial phylogenetic break separating the New Zealand species (clade 1) which corresponds to the South Loyalty basin opening between New Zealand and New Caledonia about 75 Ma. The second major divergence separates clades 2 and 3 that are geographically separated by formation of the Coral Sea basin about 60 million years ago (Seton *et al.* 2016). This separation is followed by divergence between an Australian-Philippines group (clade 2) and a Sumatra-New Guinea-New Caledonia, Vanuatu, Fiji and Santa Cruz group (clade 3). Within clade 3 there are two subclades (3a, 3b) disjunct across the Solomons archipelago. Further, extralimital fossil *Agathis* are recorded from southern Australia, southern Patagonia, and Hainan, China (Fig. 7).

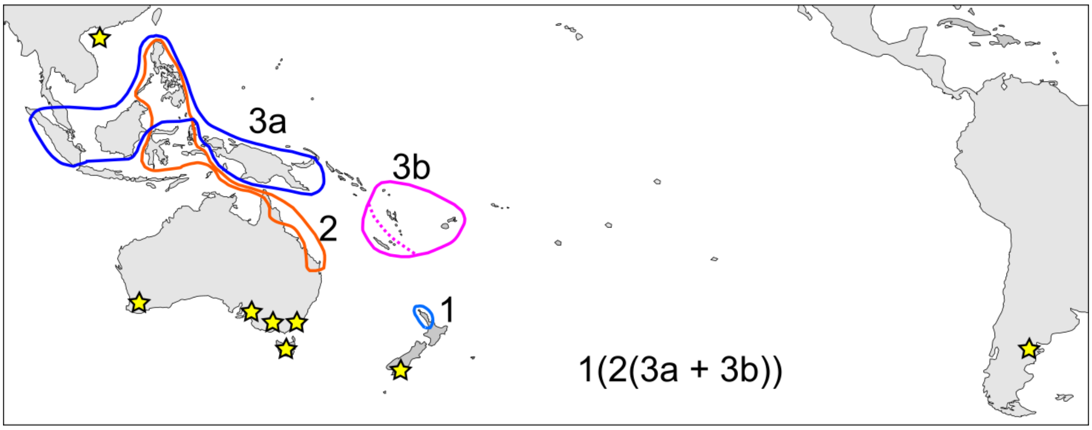

Fig. 7 Distribution of *Agathis*. Principal extant clades as coloured outlines. Fossil records as stars. Extant records from Kunzmann (2007), Seyfullah *et al.* (2013), Escapa *et al.* (2018). Fossil records from Australia (Hill *et al.* 2008), New Zealand (Lee *et al.* 2007), Patagonia, Argentina (Wilf *et al.* (2014), Hainan, China (Oskolski *et al.* 2020). Phylogeny from Leslie *et al.* (2018). Dashed line for 3b represents divergence of the New Caledonia species from those of islands assocaited with the Vitiaz Linneament.

The only evidence of dispersal in the *Agathis* clades is the overlap of clades 2 and 3 in the Sulawesi-Philippines region, indicating range expansion following initial allopatry. Otherwise, the pattern is fully consistent with allopatric speciation of a widespread ancestor following formation of tectonic basins along East Gondwana. The distribution of sister clades 2 and 3 breaks apart geographically to the east and west of the Coral Sea basin. Phylogenetic details are not known for all *Agathis* species and populations, and some aspects of distribution in southeastern Asia are taxonomically problematic (such as clades 2 and 3). Fossil records indicate that the ancestral range included southeastern Asia, southern Australia, and southern South America which corresponds to a standard pattern of ancestral distributions correlated with Jurassic-Cretaceous extension of the West Antarctic Rift (Heads 2014).

Discussion: biogeographic context

Clade distributions within the Micropterigidae indicate some important spatial correlations. The two Australasian groups (clades 3 and 4 in Fig. 2) have distributions centered on the Tasman-Coral Sea region (Fig. 3), a globally important biogeographic centre that includes 28 animal and plant lineages with globally widespread sister groups (Heads 2009). The global range of Micropterigidae comprises 66 described and 62 undescribed species (Gibbs & Lees 2014, Wagner & Davis 2014, David Lees pers. comm.). About 86 species (38%) belong to clades that occur in the Tasman-Coral Sea region, with 55 species from New Caledonia alone (within an area of 18,500 km^2) (Gibbs & Lees 2014), 21 in New Zealand (Gibbs 2014), and 10 species in Australia (Gibbs 2010). The only other group approaching this number is *Micropterix* with 78 species over a range extending across much of Eurasia. The concentrated species diversity in the southwest Pacific may result from a combination of ecological, biological, and geological processes in a region subject to multiple episodes of tectonic extension, compression, uplift, and subsidence, along with extensive magmatism (cf. Heads 2014). The importance of the Tasman-Coral Sea centre includes the Agathiphagidae as the sister group of the globally widespread Micropterigidae. The second basal Lepidoptera family, Heterobathmiidae, is similarly associated with a centre of basal endemism, the Central Coast Range of southern Chile (Heads & Saldivia 2024).

The biogeographic and tectonic comparisons presented here support the conclusion that the origin of *Aureopterix* and its relatives is likely just as much a consequence of Mesozoic tectonic events as is the origin of Agathiphagidae. The more recent molecular divergence age for *Aureopterix* is a minimum value that does not set upper age limits or falsify earlier vicariance mechanisms. The distribution of Agathiphagidae on volcanic islands in the southwest Pacific does not require chance dispersal over water as the moths could have survived on a succession of island arcs that formed from when the Vitiaz subduction zone first formed along the coast of East Gondwana.

There is uncertainty as to whether absence of Micropterigidae from some major areas is real or is an artefact of underrepresented collecting. This can be a major challenge for estimating the distribution characteristics of micro-moths, as illustrated by the basal glossatan Acanthopteroctetidae, originally described for North America but now with scattered records in southern Africa, Europe, southeastern Asia [fossil], and South America (Mey 2011, 2024, Kristensen *et al.* 2014, Mey & Rutjan 2016, Nel *et al.* 2016, David Bettman, pers. comm. 2025). The widespread distribution of Micropterigidae is comparable to that of well-known animal and plant groups that are absent or marginally represented in Africa, Madagascar, and India. For example, the butterfly tribe Coenonymphina is absent from Africa (where Micropterigidae is marginally present), Madagascar (Micropterigidae present), India (Micropterigidae marginally present), southeastern Asia, the Caribbean, and eastern South America where Micropterigidae is also absent (Fig. 8). The distribution of Coenonymphina includes New Guinea (Micropterigidae and Agathiphagidae absent) and the Solomons (Agathiphagidae only). In the New World, the Coenonymphina occur in northern North America and the northern half of the Andes (Micropterigidae present), but absent from Central America other than a localized record from Costa Rica where Micropterigidae is also present (Heads *et al.* 2023). The Costa Rica-northern Andes disjunction in Micropterigidae and Coenonymphina occurs in a variety of other animal and plant taxa, possibly resulting from Central American tectonic disruption of ancestral ranges (cf. Heads 2016, Grehan 2024).

As with the Micropterigidae, southeastern Asia represents a distribution gap between Eurasian and Australasian species. In the Coenonymphina the ‘gap’ is filled by its sister group, the Eritina, which corresponds to latest Jurassic–Cretaceous intracontinental rifting between India and Australia separating Eritina of India and southeastern Asia from the Australasian, Pacific, and Laurasian Coenonymphina (Heads *et al.* 2023). The distribution of clades within the Coenonymphina includes a basal genus in the Solomon Islands and a sister-group relationship between the Australasian genera and the Eurasian, North American, and Central-South American genera. This pattern corresponds to an ancestral Pacific basin distribution that was subsequently fragmented by formation of the Pacific Plate (Heads *et al.* 2021, Heads *et al.* 2023).

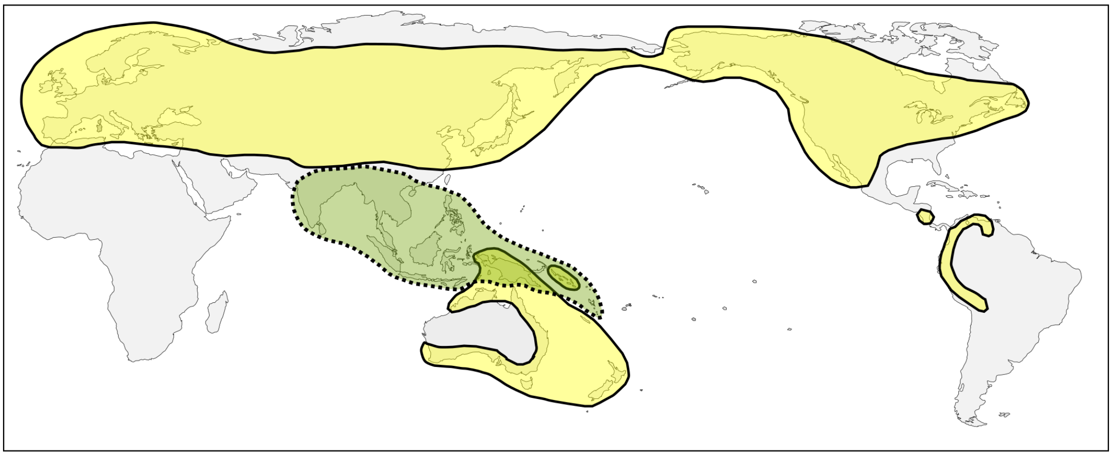

Fig. 8. Distribution of butterfly sister groups Eritina (green shading) and Coenonymphina (yellow shading). Distribution from Heads *et al.* (2023).

Absence or marginal presence of Micropterigidae, Agathiphagidae, and Heterobathmiidae from core regions of Gondwana (Fig. 9) may indicate that this pattern of absence characterized the ancestral distribution of Lepidoptera. This absence is also applicable to most of the basal lineages of Glossata (tongued Lepidoptera), other than the Hepialidae which is the only globally widespread basal group (although absent from West Africa, Madagascar, and the Caribbean), and the Prototheoridae distributed across the southern half of Africa (Landry & Davis 2018).

A sister group relationship between Micropterigidae and Agathiphagidae would correspond to their geographically diverging somewhere between Eastern Asia and the southwest Pacific (as of the modern map). The sole presence of Agathiphagidae on some Pacific islands could represent a remnant of the original allopatry between the two families that was not obscured by subsequent range expansion of the

Micropterigidae when the eastern Agathiphagidae populations became isolated by formation of the East Gondwana subduction zone and its subsequent retreat into the Pacific, beginning about 90 million years ago (cf. Heads 2014).

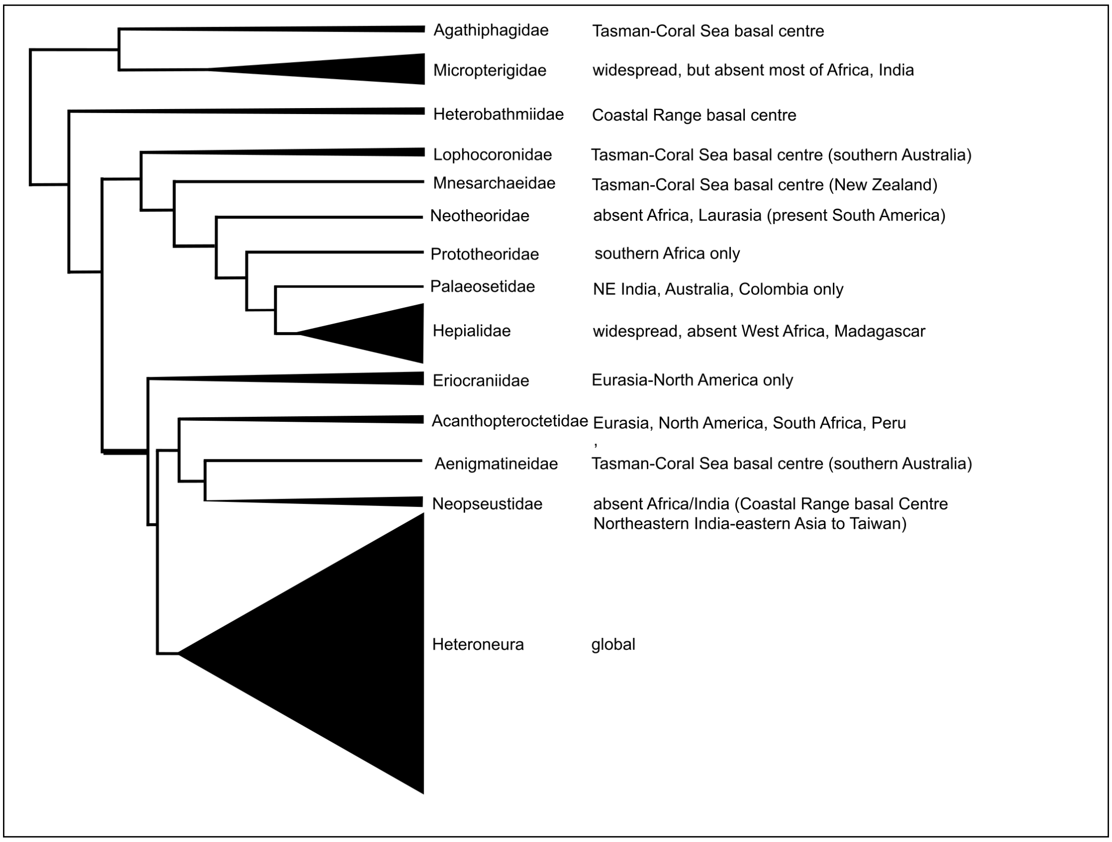

Fig. 9. Basal divergence of non-heteroneuran families and distributions with respect to absence or marginal representation in Africa, India, and Madagascar. Distribution data: Lophocoronidae (Nielsen & Kristensen 1996), Mnesarchaeidae (Gibbs & Kristensen 2019), Neotheoridae (Simonsen & Kristensen 2017), Prototheoridae (Landry & Davis 2018), Palaeosetidae (Grehan & Mielke 2018, Lio *et al.* 2021), Hepialidae (Grehan & Mielke 2018), Eriocranidae (Grehan 1991), Acanthopteroctetidae (Mey 2011, 2024, Kristensen *et al.* 2014, Mey & Rutjan 2016, Nel *et al.* 2016, David Bettman, pers. comm. 2025), Aenigmatineidae (Kristensen *et al.* 2015), Neopseustidae (Davis 1975, Grehan 1991). Phylogeny from Kristensen *et al.* (2015) with addition of Exoporia families according to the phylogenetic sequence in Simonsen & Kristensen (2017).

Drifting Gondwana fragments such as the Burma block containing Cretaceous amber fossils explains the Asian fossil taxa having extant southern ‘Gondwana’ relatives (Poinar 2018, Mey 1998, 2019, Mey *et al.* 2021, Wood & Wonderlich 2023). Other southern basal Lepidopteran fossil records in Burmese amber include *Sabatinca* (Micropterigidae clade 3 + 4) (Zhang *et al.* 2017), and the Australian Lophocoronidae (Mey *et al.* 2021). It is not known whether these groups were still living at the time when the Gondwana fragments were incorporated into Asia. But tectonic displacement of Gondwana terranes may apply to the origin of Clade 3 (*Aureopterix*) in Vietnam. Another possibility is that some widespread groups, such as the Micropterigidae, were originally distributed along both the southern and northern coasts of the Tethys Ocean, as these were never entirely disconnected between Africa and western Asia. With obliteration of the Tethys Sea, these former populations could have become compressed, resulting in ‘Tethyan’ distributions seen in many animal and plant groups (Heads 2014). A further consideration is whether trans-Pacific affinities in the Micropterigidae represent ancestral ranges across ephemeral or dynamic landscapes (e.g. island arcs, hot spots, magmatic plateaus) within the Pacific basin that were fragmented and displaced by the Pacific plate in mid Cretaceous time (cf. Heads 2012, Heads *et al.* 2021).

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