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Research article

Beetle evolution illuminates the geological history of the World's most diverse tropical archipelago

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The geologically-complex Indo–Australian–Melanesian archipelago (IAMA) hosts extraordinarily high levels of species richness and endemism and has long served as a natural laboratory for studying biogeography and evolution. Nonetheless, its geological history and the provenance and evolution of its biodiversity remain poorly understood. Here, we provide a geological scenario for the IAMA informed by a time-calibrated molecular phylogeny of 1006 species of *Trigonopterus* weevils – an exceptionally diverse radiation of regionally-endemic flightless beetles. Moreover, we performed a statistical biogeographic analysis and examined timing and patterns in the accumulation of lineages residing in a priori-defined geographic units comprising the IAMA. We estimate that *Trigonopterus* originated in Australia during the early Paleogene. Subsequent rapid diversification in the area of the present-day Papuan Peninsula suggests the presence of proto-Papuan islands by the middle Eocene; the New Guinea North Coast Ranges were colonized in the late Eocene, followed by the New Guinea Highlands and the Bird's Head Peninsula. We inferred the presence of terrestrial habitat in the North Moluccas and Sulawesi in the late Oligocene and the subsequent rapid colonization of Sundaland and the Lesser Sunda Islands. New Caledonia and Samoa were colonized from the Papuan Peninsula, and their faunas also diverged in the late Oligocene. These biota-informed time estimates are compatible with geological data from the region and shed new light on IAMA paleogeography, even where geological evidence has been lost to erosion. Beetle evolution thus appears to have closely tracked the geological evolution of the IAMA, revealing a uniquely well-resolved view of regional biogeography.

Keywords: biogeography, coleoptera, curculionidae, Indo-Australian-Melanesian archipelago, New Guinea, paleogeography

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Introduction

Biogeographic studies typically employ data from the biological and the earth sciences to resolve timing and geographic patterns in the distribution of species and ecosystems – both historical and extant (Brundin 1966, Nelson and Platnick 1981, Jönsson et al. 2011). This synthetic approach of reciprocal illumination (Hennig 1966) has also widely been used to explain the evolutionary histories and distributions of species inhabiting the Indo–Australian–Melanesian archipelago (IAMA). However, the timing of land emergence, especially in geologically complex landscapes like the IAMA, is often highly uncertain, potentially distorting reconstructions of lineage evolution. The application of cladistic methods and a growing appreciation for the importance of plate tectonics have facilitated the examination of dispersal routes and evolutionary processes driving taxonomic diversification in the IAMA (de Boer and Duffels 1996, Hall and Holloway 1998, Duffels and Turner 2002). Moreover, new geological and geophysical data have improved regional paleogeographic reconstructions (Hall 2009, 2017, Spakman and Hall 2010). Nonetheless, these have been assembled by interpreting relatively sparse spatial and temporal data, resulting in many conflicting paleogeographic models. These models often infer where land may have existed in the past, but has since been eroded, making it difficult to determine the timing of emergence and the composition of landmasses. This, in turn, affects the reconstruction and interpretation of biogeographic patterns (Lohman et al. 2011, Toussaint et al. 2021). Consequently, the Cenozoic paleogeography and tectonic history of the IAMA remains poorly understood, including the timing of the emergence of its constituent geologic units and the number of potential collisional events (Pigram and Davies 1987, Ufford and Cloos 2005, Lohman et al. 2011).

With the development of increasingly sophisticated molecular phylogenetic methods and relaxed molecular clock models, it is now feasible to detach the interpretation of biological and geological signals from one another and test the congruence of inferred chronological patterns (Waters and Craw 2006, Stelbrink et al. 2012). In addition to model-based ancestral range estimation methods (Lamm and Redelings 2009), spatial and temporal differences in diversification dynamics can also be inferred by estimating the number of lineages for each area at a given time. A marked increase in local diversification lends confidence to the presence and possibly growth of habitable land in a given area, as outlined by the theory of island biogeography (MacArthur and Wilson 1967). In archipelagic settings, such as the IAMA, islands may be short-lived, and a newly evolved endemic fauna may have to disperse to a nearby younger island (Funk and Wagner 1995). In such cases, biological data can provide information on the likely presence of land, even where geological evidence has been lost to erosion. A quantitative approach (in both analytical methods and the number of taxa representing a large number of natural replications) can be of great value to geology and emancipate the role of biogeography from a net receiver of information to a contributor of useful data.

Most phylogenetic studies involving the IAMA have focused on relatively vagile taxa whose evolution may not be expected to closely track the geological evolution of the IAMA, including birds (Jönsson et al. 2011, Aggerbeck et al. 2014, Moyle et al. 2016, McCullough et al. 2022), butterflies (Braby and Pierce 2007, Condamine et al. 2013, 2015, Toussaint and Balke 2016, Toussaint et al. 2020), and flighted beetles (Toussaint et al. 2014, 2021, Bocek and Bocak 2019). Most of these taxa move relatively easily between islands and regions (Toussaint et al. 2020), possibly obscuring the signal of geological evolution. Less dispersive organisms are likely better suited to reconstructing geological histories, especially if they occur throughout the geographic region of interest (Gillespie et al. 2012). However, only a few such studies have been undertaken in the IAMA, e.g. involving mite harvestmen (Clouse and Giribet 2010), lizards (Tallowin et al. 2018), murine rodents (Rowe et al. 2019), limnic snails (Gauffre-Autelin et al. 2021), frogs (Rivera et al. 2017) and ants (Matos-Maraví et al. 2018). Still, these taxa each comprise a small to moderate number of species, and some have restricted distributions covering only a fraction of the IAMA, thus contributing relatively limited geographic and temporal resolution. In contrast, the ideal biogeographic indicator taxon is less dispersive, has many extant species, exhibits a tendency for micro-endemicity, and inhabits the entire region of interest, where it has evolved since its origin.

Trigonopterus weevils (Coleoptera: Curculionidae: Cryptorhynchinae) appear to meet these 'ideal' criteria. They are flightless and inhabit tropical forests where they can be found on foliage and in the litter layer. Their geographic range covers the entire IAMA from Singapore in the west to Samoa in the east and from Taiwan in the north to Australia in the south. There are more than 1000 species of *Trigonopterus*, including 489 valid described species – 350 of which have been described in the past nine years (Riedel et al. 2013, 2014, Riedel and Tänzler 2016, Riedel and Narakusumo 2019, Narakusumo and Riedel 2021) – and at least 600 additional species awaiting formal description. Species diversity of *Trigonopterus* is highest in New Guinea, and more than 95% of known species are micro-endemics (range < 100 km in diameter), with many only known from a single locality. *Trigonopterus* biogeography and evolution have been studied regionally, e.g. along Wallace's Line, the Sunda Arc, and New Caledonia (Tänzler et al. 2014, 2016, Toussaint et al. 2017, Letsch et al. 2020a), and the phylogenies associated with these studies show substantial geographic structure. While *Trigonopterus* are flightless, there is evidence for occasional dispersal events across the open ocean, presumably via currents and flotsam (Letsch et al. 2020a). Even small islands in the IAMA with a relatively recent subaerial history appear to have been rapidly colonized (Narakusumo et al. 2019). Moreover, these colonization events often resulted in substantial local taxonomic radiations (Toussaint et al. 2017).

Here, we provide a geological scenario for the IAMA informed by a fossil-calibrated molecular phylogeny of 1006 species of *Trigonopterus* weevils.

Material and methods

See the Supporting information for more information on taxon and gene sampling design, the time-stratified model setup, geological reconstructions, and the methods used in the diversification rate analyses. A summary of samples, molecular markers and accession numbers is in the Supporting information.

Alignment and phylogenetic analyses

Alignment of ribosomal RNA and protein-coding genes was separately conducted using the online version of MAFFT ver. 7.409 (Katoh and Standley 2013, Katoh et al. 2017) and the automatic method search (protein-coding genes, FFT-NS-1 method; rRNA genes, L-INS-i method). The alignments of all nine genes were assembled using AMAS ver. 0.94 (Borowiec 2016). This resulted in a dataset comprised of 8358 nucleotides, 3620 parsimony-informative sites, 1100 singleton sites and 3638 constant sites, with a proportion of missing data of approximately 22%.

Phylogenetic reconstructions were conducted in a maximum likelihood (ML) framework using the software IQ-TREE ver. 1.6.12 (Nguyen et al. 2015, Chernomor et al. 2016). Before tree reconstruction, we generated a partitioning scheme where all protein-coding genes were separated into codon positions and all rRNA genes into single partitions, resulting in a dataset consisting of 21 total partitions. We performed 250 independent ML tree searches with random starting trees to reduce the chance of the tree search being trapped in local optima. For each run, the best-fitting partitioning scheme and nucleotide substitution model for each partition were estimated with ModelFinder (-m MFP+MERGE) as implemented in IQ-TREE (Kalyaanamoorthy et al. 2017) under the Bayesian information criterion (BIC). All ML analyses were run with an increased number of stop iterations (-stop 200). Nodal support was assessed using 1000 ultrafast bootstrap replicates (UFBOOT; Minh et al. 2013), with the 'bnni' option (Hoang et al. 2018) and an increased maximum number of iterations to stop (-nm 5000). Additionally, 1000 replicates of the SH-like approximate likelihood ratio test (SH-aLRT; Guindon et al. 2010) were performed. The threshold values we used to determine whether a node was well-supported are 80% for SH-aLRT and 95% for UFBOOT.

To minimize the impact of missing data, we condensed the original 1021-taxon dataset by retaining only the 491 taxa with sequence information for 16S, 28S, ArgK, CAD and COI gene fragments. This reduced the proportion of missing data to approximately 4.5%. The best-fitting partition scheme and model setup were determined via a two-step procedure. For the 21 initial partitions, we first searched the best partition scheme. This analysis was repeated 50 times

to avoid being stuck in a local optimum. The best partition scheme (according to BIC) was then used in a second analysis to find the best model scheme. This analysis was again repeated 250 times. Based on the best-combined partition- and model-scheme, we performed 250 independent ML tree searches with random starting trees. The best resulting 491-taxon tree according to log-likelihood (Supporting information) was then used as a topological constraint (-g option) in a new ML analysis of the complete 1021-taxa dataset in IQ-TREE. This analysis was conducted 250 times, using the same partition-model-scheme as in the 491-taxon analyses. Parameters for tree searches and assessment of nodal support were applied as in the first analyses described above. Finally, we repeated each of the best five tree reconstruction analyses (using the -seed option) ten times.

Divergence time estimation

We used BEAST ver. 1.10.4 (Suchard et al. 2018) to infer divergence times. The best 1021-taxon tree based on log-likelihood, as inferred in the ML tree reconstructions, was used as a fixed input tree topology after excluding taxa that did not belong to the IAMA clade (clade L of Letsch et al. 2020b). To calibrate the tree, we relied on secondary calibrations for the divergence times of the Indo–Australian clade (73.11 Ma; 95% highest posterior density (HPD) 66.85–81.17 Ma) and *Trigonopterus* (55.35 Ma; 95% HPD 47.17–61.14 Ma), as estimated in Letsch et al. (2020b). Using secondary calibrations can be problematic under certain circumstances (Schenk 2016). However, since no known fossil taxa are closely related to *Trigonopterus*, we determined this was our best option. In Letsch et al. (2020b), *Trigonopterus* was a small clade within a much larger dataset for the subfamily Cryptorhynchinae. In contrast, *Trigonopterus* constituted > 99% of the total taxon sampling in the present study. To ameliorate this potential source of bias, we relied on an exponential prior that puts a higher probability on younger ages within the distribution (Ho and Phillips 2009, Powell et al. 2020). We specified the prior distribution with a lower bound corresponding to the youngest ages of the confidence intervals calculated in Letsch et al. (2020b). A soft upper bound was defined so that 95% of the prior distribution lay between the minimum and maximum of the confidence interval. To calculate divergence times, we specified a single uncorrelated log-normal relaxed-clock model with a birth-death (bd) tree model prior. Clock and tree models were linked among partitions. Substitution model parameters were defined using ModelFinder. The final partition scheme, as selected by the BIC, comprised 16 partitions in total. BEAST runs were executed for 100 million generations each (sampling every 20 000 generations). The number of generations discarded as burn-in, convergence and mixing of parameters, and effective sample sizes (ESS), were assessed in Tracer ver. 1.7.1 (Rambaut et al. 2014). Post-burn-in samples were used to construct a maximum clade credibility (MCC) tree with median node heights in TreeAnnotator ver. 1.10.4 (Suchard et al. 2018) (Supporting information).

Biogeographic analyses

The MCC tree reconstructed in the divergence time estimations was further applied to reconstruct the biogeographical history of *Trigonopterus*. Biogeographic analyses were conducted in R with the 'BioGeoBEARS' package ver. 1.1.2 (www.r-project.org, Matzke 2013), using the dispersal extinction cladogenesis (DEC) model (Ree et al. 2005, Ree and Smith 2008), as well as likelihood interpretations of the dispersal-vicariance analysis (DIVA) model (Ronquist 1997) and the BAYAREA model (Landis et al. 2013). We refrained from using the +J parameter, which allows cladogenetic events where one daughter lineage colonizes a new range via founder-event speciation (Matzke 2012) while the other retains the ancestral range. Its use in biogeographic models and its statistical comparison to models excluding founder-event speciation has been criticized (Ree and Sanmartín 2018). In general, models incorporating founder-event speciation tend to underestimate anagenetic dispersal events at ancestral nodes in favor of 'jump dispersal' events (Condamine et al. 2018, Ree and Sanmartín 2018, Matzke 2022). Especially in our study, where all species ranges are restricted to single areas, anagenetic events will be expected to be 0 by models implementing the +J parameter, and all inferred dispersal will be entirely explained by cladogenetic events, i.e. associated with internal nodes and independent of time. Given the generally wide distribution of the genus throughout the IAMA, such a scenario is not realistic for all biogeographical events in the history of *Trigonopterus*. BioGeoBEARS also implements time-stratified models that consider the appearance of geographic areas and their adjacency at different points in time. This was applied to comply with the geological history of the region. Because of the limited distribution of *Trigonopterus* species, with only one species inhabiting more than one biogeographic area, we restricted the maximum number of areas to two. All three models were compared, and the best-fitting model was selected using the corrected Akaike information criterion (AICc).

Biota-informed geological scenario

To visualize regional lineage accumulation across the IAMA, we recorded the number of lineages present at a given time interval in each of the areas (Fig. 2, Table 1). This involved performing a biogeographic stochastic mapping (BSM) analysis (Dupin et al. 2017), using the best-fitting biogeographic model from area reconstruction analyses and conducting 100 stochastic replicates on the MCC tree. The temporal diversity information across different biogeographic regions was then calculated from the output of the BSM analyses using the R package 'ltstR' (www.r-project.org, Skeels 2019), which calculates lineages through space and time (LTST) plots. This method extracts the timing of state changes on the phylogeny for the given stochastic maps. The LTST, a list of data frames for multiple stochastic maps, which contain the number of species present in each geographic range at each event time, can then be used to summarize the variability of

species diversity values for each region at each time point in the list of time-standardized LTST data tables. Time intervals were defined by slices over the area phylogeny at every 4 Ma. Continuous lineage accumulation until the present day suggests constant availability of terrestrial environments over time. These inhabited areas are the foundation of the biota-informed geological scenario, i.e. the biologist's hypothesis for the availability of suitable habitat over geological time. To contextualize this with geological evidence, we plotted our areas onto custom-built paleogeographic maps. The accumulation of lineages in an area (Fig. 2) is an indicator of the presence of subaerial terranes, as local diversification is increasing with the habitable land area (Lomolino 2001, Gillespie and Roderick 2002, Presgraves and Glor 2010).

Results

Taxon-specific phylogenetic and biogeographic analyses

We used a time-calibrated molecular phylogeny of 1006 *Trigonopterus* species inhabiting a geographic range of > 9500 km in the west-to-east direction across the IAMA to 1) estimate timing and geographic patterns of *Trigonopterus* diversification and 2) draft paleogeographic maps for the entire IAMA. We recovered a stable tree topology for *Trigonopterus* (Fig. 1a, Supporting information), which is largely congruent with previously-published phylogenies focused on regional faunas (Tänzler et al. 2014, Toussaint et al. 2017, Letsch et al. 2020b). The age of crown-group *Trigonopterus* is estimated at ca 55 Ma (median age; 95% height posterior density [HPD] = 61–50 Ma), which is compatible with recent fossil calibrated studies (Letsch et al. 2020a,b). The best-fitting biogeographic model (DIVALIKE+w1+eng, cf. Table 2) suggests an early Eocene origin of crown group *Trigonopterus* in Australia (Fig. 1a–b, Supporting information), with a single colonization of the Papuan Peninsula area at ca 46 Ma (95% HPD = 51–40 Ma). This colonization event is coeval with a significant net diversification rate shift in 'core-*Trigonopterus*' (i.e. excluding the *T. squamosus-*, the *T. scissops-* and the *T. bisinuatus-*groups, Supporting information), as inferred by clade-specific diversification rate analyses in BAMM.

Colonization of the Papuan Peninsula was rapidly followed by a taxonomic radiation in this area and colonization of the New Guinea North Coast Ranges (37 Ma; 95% HPD − 41–33 Ma). The PNG Highlands (35 Ma; 95% HPD = 39–31 Ma) were colonized before the Western Central Range of New Guinea (28 Ma; 95% HPD − 32–24 Ma). Westward dispersal over the North Coast Ranges reached the Bird's Head Peninsula ca 35 Ma (95% HPD = 40–31 Ma). The earliest colonization of the North Moluccas (in the dataset represented by Halmahera) occurred via the Bird's Head Peninsula ca 29 Ma (95% HPD = 32–25 Ma). Sulawesi was colonized several times from the Bird's Head Peninsula and the North Moluccas and acted as a hub for the colonization of Sundaland (Borneo, Sumatra, Java) ca 31 Ma (95% HPD = 35–27 Ma) and the Lesser Sunda
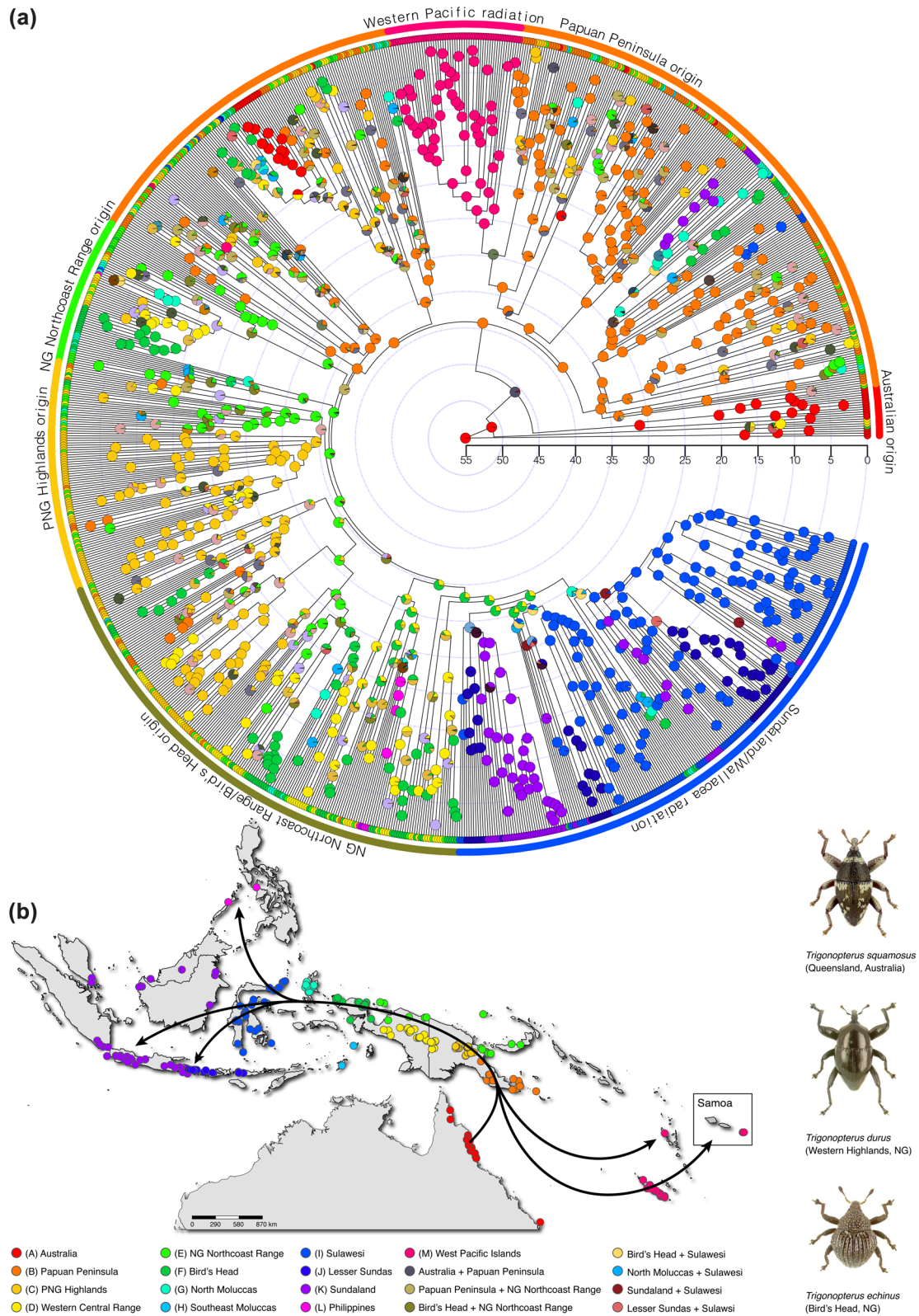
Figure 1. Evolution of *Trigonopterus* weevils in the Indo–Australian–Melanesian archipelago (IAMA). (a) Chronogram showing the results of divergence time estimation implemented in BEAST using data from up to nine genes for 1006 species (Supporting information). Pie charts indicate the probability of the ancestral ranges at each node as reconstructed with the best biogeographic model (DIVALIKE+w1+eng) in BioGeoBEARS. (b) Map of the IAMA showing (with colored dots) the collection localities of specimens studied. Each color corresponds to one of the a priori-defined geographic areas studied. Black arrows indicate major dispersal events inferred from our biogeographic analyses.

Table 1. Overview of estimated ages of biogeographic areas. BGB, ages inferred from biogeographic analysis in BioGeoBEARS with median age estimations and upper and lower 95% highest posterior density (HPD) as derived from the BEAST analysis; LTST, ages inferred from lineage through time plots based on biogeographic stochastic mapping (BSM).

Area	BGB	LTST (BSM)
Australia (A)	55.1 (61.4–50.0)	55
Papuan Peninsula (B)	45.8 (50.9–40.4)	44
PNG Highlands (C)	35.3 (39.6–31.2)	32
Western Central Range (D)	27.9 (32.2–24.2)	28
NG Northcoast Range (E)	37.2 (41.3–32.6)	40
Bird's Head (F)	35.3 (39.5–31.2)	32
North Moluccas (G)	28.5 (32.0–25.0)	28
Southeast Moluccas (H)	18.3 (23.1–13.9)	16
Sulawesi (I)	30.8 (34.5–27.0)	28
Lesser Sundas (J)	29.1 (32.9–25.7)	28
Sundaland (K)	27.0 (30.6–23.9)	28
Philippines (L)	20.5 (23.8–17.1)	20
West Pacific Islands (M)	29.6 (34.1–26.0)	28

Islands ca 29 Ma (95% HPD = 32–26 Ma). New Caledonia and Samoa were colonized from the Papuan Peninsula at ca 30 Ma (95% HPD = 34–26 Ma) and diverged at ca 26 Ma (95% HPD = 29–22 Ma). Additional colonization events of Wallacea from North Moluccas+New Guinea and Sundaland from the area east of Wallace's Line occurred several times during the Miocene. After the initial colonization of the Papuan Peninsula at ca 46 Ma and the subsequent radiation of *Trigonopterus* in the North Coast Ranges and the Western Central Range, all regions of New Guinea and Wallacea were repeatedly colonized by different lineages of *Trigonopterus* originating from the Papuan Peninsula. We inferred four re-colonization events from New Guinea to Australia, with one leading to a moderately diversified secondarily Australian clade (i.e. the Australian part of the *T. politus*-group).

The BSM analyses revealed that the evolution of *Trigonopterus* is geographically highly structured and, for the relatively large areas considered herein, mostly dominated by cladogenetic events in one area (60%, 'narrow sympatry', Supporting information). Vicariance and dispersal make up 17 and 23% of all events, respectively. The latter mainly involved movements between areas of New Guinea, where the Papuan Peninsula and the North Coast Ranges are the major sources for dispersal events. Outside New Guinea, dispersal events are much rarer but frequently occurred from the Bird's Head Peninsula to the North Moluccas and from the North Moluccas to Sulawesi (Supporting information).

Biota-informed geological scenario

The timing of colonization events derived from our biogeographic area analysis (Supporting information, DIVALIKE+w1+eng) and inferred using lineages through space and time plots based on biogeographic stochastic mapping (LTST-BSM) (Fig. 2, Supporting information) are largely congruent (Table 1). We present a series of maps depicting the biota-informed scenario for the emergence sequence of terrestrial habitat, corresponding to the inferred colonization of these areas by *Trigonopterus* weevils (Fig. 2). These maps postulate the presence of land solely based on biological data via the BSM analysis.

Trigonopterus were initially restricted to Australia (ca 48 Ma). Emergent areas of the present-day Papuan Peninsula and North Coast Range were colonized at ca 40 Ma. By ca 32 Ma, there are indications of suitable terrestrial habitat in all major areas of present-day New Guinea, all of which were then populated by at least one lineage of *Trigonopterus*. Local lineage accumulation becomes more apparent by ca 24 Ma, suggesting increasing size and structure of suitable terrestrial habitat. The first evidence of subaerial land in the vicinity of Sulawesi is indicated at ca 28 Ma, with a more substantial local accumulation of lineages beginning at ca 24 Ma. The first lineages appeared at 28 Ma in the Northern Moluccas, Western Pacific Islands, Sundaland, and the Lesser Sundas, with an accumulation of lineages at 24 Ma in the Northern Moluccas and Western Pacific Islands and a later accumulation of lineages at 20 Ma in Sundaland and the Lesser Sundas. By ca 16 Ma, suitable habitat is predicted to have existed in all major areas of the IAMA.

Discussion

Implications for New Guinean paleogeography

New Guinea is a geologically-complex composite island, which precludes treating it as a single area in biogeographic analyses (Toussaint et al. 2021). The current landmass is the product of multiple accretion events between the northern edge of the Australian Plate and volcanic island arcs of the Pacific Plate (Pigram and Davies 1987, Ufford and Cloos 2005, Baldwin et al. 2012, Hall 2013, Gold et al. 2017), with some areas subaerial after ca 40 Ma (Ufford and Cloos 2005, Hall 2013, Gold et al. 2017). Dispersal of *Trigonopterus* from Australia to the Papuan Peninsula in the Late Eocene was inferred as the starting point for its radiation in the IAMA. Our biogeographic reconstructions suggest a relatively early timing of uplift and exposure of colonizable land in New Guinea (Fig. 2, Table 2). Taxonomic diversification of *Trigonopterus* on the Papuan Peninsula started ca 44 Ma (95% HPD = 51–40 Ma) and may have been influenced by uplift associated with the obduction of the Papuan Ultramafic Belt at ca 58 Ma (Lus et al. 2004). Despite this obduction event, current geological evidence indicates that the Papuan Peninsula remained below sea level through the Eocene (56–33 Ma). However, the nearby Papuan Basin/Fly River Delta region and other parts of the 'Arafura High' may have been exposed above sea level during the Eocene-Oligocene (Carman 1990, Pigram and Symonds 1993, Ufford and Cloos 2005), along with small volcanic islands (Thompson 1967), due to a period of lower eustatic sea levels at ca 33–30 Ma (Miller et al. 2005, 2020, Gold et al. 2017). The lack of early Oligocene (ca 33–27 Ma) rocks in the Papuan Peninsula
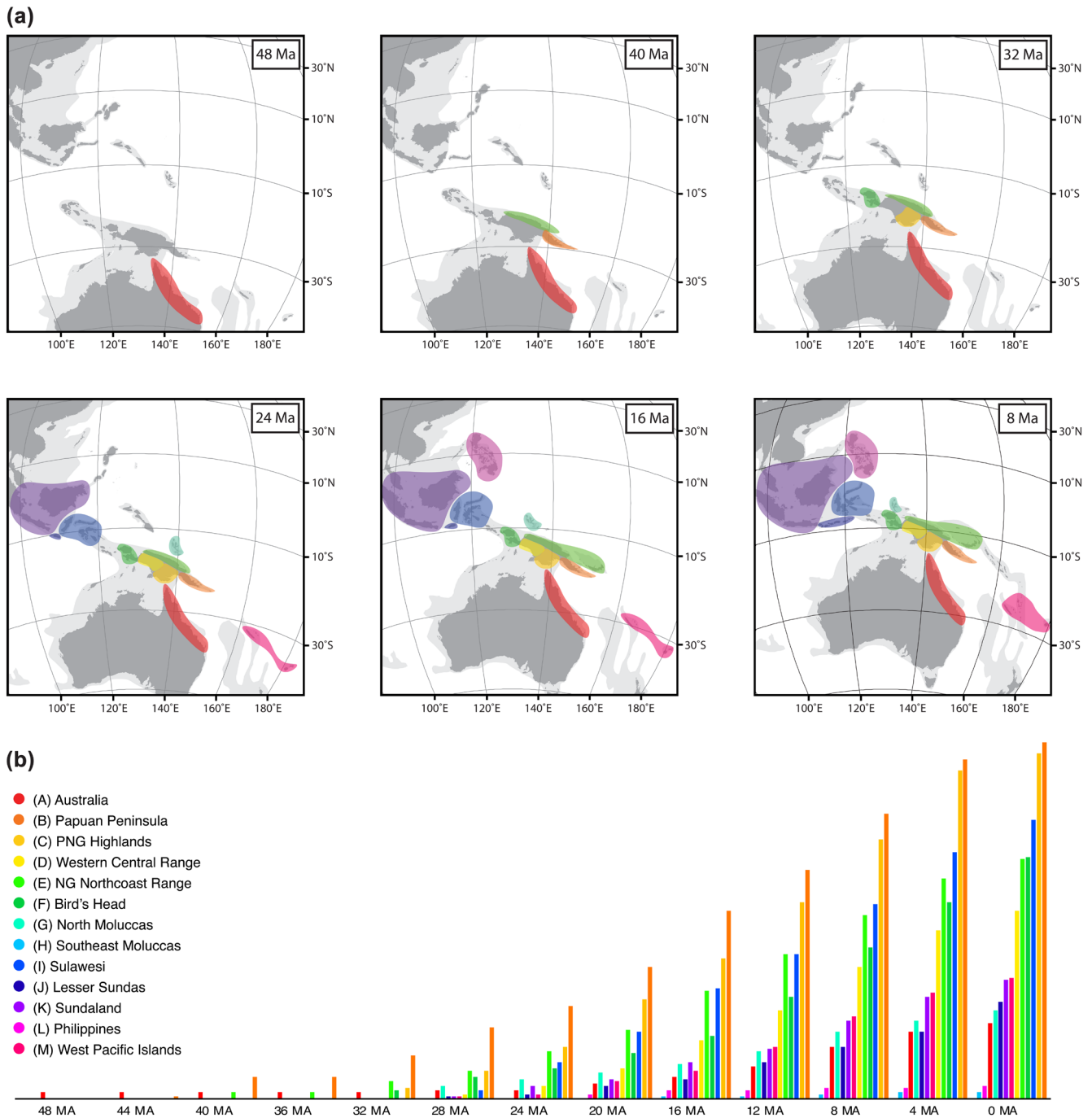
(a)

(b)

Figure 2. Estimates of Indo–Australian–Melanesian archipelago paleogeography. (a) Timing of appearance of geographic areas derived from the diversification history of *Trigonopterus* weevils between 48 and 8 MA. (b) Histograms show the number of *Trigonopterus* lineages assigned to an area based on LTST plots. Grey basemaps are based on models of Hall (2012) and Scotese (2016). The first appearance of a (colored) area signals the existence of at least minor and possibly ephemeral land areas at the time.

may indicate an unconformity (Australasian Petroleum Company 1961). This evidence, together with continued siliciclastic sedimentation in the Aure Trough throughout the Oligocene, indicates that the peninsula was likely exposed at this time (Ufford and Cloos 2005). The relatively early ages obtained from our reconstruction, together with the increased diversification rates proposed for the onset of the

Papuan radiation in *Trigonopterus,* are strong independent evidence for the existence of subaerial terranes in the area of the Papuan Peninsula during the Cenozoic, consistent with geological evidence from this region (Carman 1990, Ufford and Cloos 2005).

According to our reconstructions, the North Coast Ranges, from the current day position of Yapen Island

Table 2. BioGeoBEARS results. DF, number of parameters; AICc, bias-corrected Akaike's information criterion; ωAIC, Akaike weight; d, rate of dispersal; e, rate of extinction; wf, dispersal multiplier exponent as free parameter: w0, dispersal multipliers disabled; w1, manual dispersal multipliers as defined by user; eng, 'Early NG' setup: all New Guinean areas are supposed to be older than 30 Ma; lng, 'Late NG' setup: all New Guinean areas (except the Papuan Peninsula) are supposed to be younger than 30 Ma.

Class	Model	logL	DF	d	e	w	AICc	ΔAICc	ωAIC
Early NG	DEC+wf+eng	−1826	3	0.005	0.008	0.450	3657	155	0.00
	DIVALIKE+wf+eng	−1795	3	0.004	0.005	0.020	3595	93	0.00
	BAYAREA+wf+eng	−2191	3	0.002	0.018	0.001	4388	886	0.00
	DEC+w0+eng	−1852	2	0.003	0.009	0.000	3708	206	0.00
	DIVALIKE+w0+eng	−1797	2	0.004	0.005	0.000	3597	95	0.00
	BAYAREA+w0+eng	−2180	2	0.002	0.018	0.000	4364	862	0.00
	DEC+w+eng	−1812	2	0.006	0.009	1.000	3628	126	0.00
	DIVALIKE+w1+eng	**−1749**	**2**	**0.007**	**0.005**	**1.000**	**3502**	**0**	**1.00**
	BAYAREA+w1+eng	−2082	2	0.008	0.031	1.000	4169	667	0.00
Late NG	DEC+wf+lng	−1852	3	0.004	0.009	0.160	3710	208	0.00
	DIVALIKE+wf+lng	−1819	3	0.004	0.005	0.027	3644	142	0.00
	BAYAREA+wf+lng	−2143	3	0.004	0.029	0.028	4292	790	0.00
	DEC+w0+lng	−1871	2	0.003	0.009	0.000	3746	244	0.00
	DIVALIKE+w0+lng	−1823	2	0.003	0.006	0.000	3650	148	0.00
	BAYAREA+w0+lng	−2147	2	0.004	0.029	0.000	4298	796	0.00
	DEC+w1+lng	−1817	2	0.007	0.009	1.000	3638	136	0.00
	DIVALIKE+w1+lng	−1759	2	0.007	0.006	1.000	3521	19	0.00
	BAYAREA+w1+lng	−2087	2	0.009	0.029	1.000	4178	676	0.00
M0	DEC	−1871	2	0.002	0.006	–	3746	244	0.00
	DIVALIKE	−1819	2	0.002	0.002	–	3642	140	0.00
	BAYAREA	−2123	2	0.002	0.031	–	4249	747	0.00

eastward over the Cyclops Mountains, the Huon Peninsula, and New Britain, may have hosted lineages of *Trigonopterus* since ca 37 Ma (95% HPD = 41–32 Ma). However, as inferred with the LTST-BSM reconstructions (Fig. 2), significant local taxonomic diversification only began ca 24 Ma. The PNG Highlands of New Guinea hosted extant lineages of *Trigonopterus* beginning ca 35 Ma (95% HPD = 39–31 Ma), while the Western Central Range of New Guinea was colonized somewhat later, at ca 28 Ma (cf. LTST-BSM analyses, Fig. 2). This suggests that suitable habitat and more structured landscapes had formed in these regions. Our results are broadly consistent with the inferred presence of land indicated from the Sirga Formation in western New Guinea (Ufford and Cloos 2005, Gold et al. 2017). Lineages of *Trigonopterus* first appeared in the Bird's Head Peninsula ca 35 Ma (95% HPD = 39–30 Ma), followed by an exceptionally high rate of lineage accumulation beginning ca 16 Ma (Fig. 2). While this agrees with geological evidence suggesting that land was exposed in this area during the Oligo-Miocene (ca 27–23 Ma) (Gold et al. 2017), it conflicts with evidence that the Bird's Head Peninsula was flooded throughout most of the Miocene and did not re-emerge until after ca 4 Ma (Gold et al. 2017, White et al. 2019). However, these results may also simply indicate that upland areas existed and could harbor life during periods of higher relative sea levels (Toussaint et al. 2021). Notably, our data could help earth scientists evaluate and refine existing tectonic models of New Guinea (Fig. 2 of Ufford and Cloos 2005). For example, our reconstructions indicate the Papuan Peninsula was emergent at 40 Ma, which is compatible with the models of Milsom (1985) and Kroenke (1984) but unlikely under the models of Hamilton (1979) and Dow et al. (1988).

Implications for Wallacean and Sundaland paleogeography

Trigonopterus first appeared on Sulawesi ca 31–28 Ma (95% HPD = 33–26 Ma), consistent with the geological interpretation of Hall (Hall 2013), which posits an increase in Sulawesi landmass from ca 40 Ma. However, this is considerably earlier than in some other biogeographic studies (of other biota), indicating that Sulawesi's faunal assembly primarily occurred during the Miocene (Stelbrink et al. 2012, Frantz et al. 2018). The case of Sulawesi is especially complex as it consists of at least three major crustal fragments that cannot easily be treated separately (Spakman and Hall 2010, Stelbrink et al. 2012, Dong et al. 2018). Based on its geospatial setting, the fragment of the southeastern part of Sulawesi (i.e. the 'Sula Spur') may have been colonized first, whereas the southwestern part would have been colonized after or shortly before the island's fusion.

The onset of local diversification on the Lesser Sunda Islands at ca 29 Ma (95% HPD = 33–26 Ma) is older than expected based on most geological reconstructions, which suggest emergent land first appeared ca 10 Ma (Hall 2013). Our model nonetheless predicts the existence of at least smaller habitable terrestrial environments much earlier. In the current analysis, the 'Lesser Sunda Islands' were treated as one area, including Bali. Based on our reconstruction of the earliest colonization of the area, the North Moluccas (represented by Halmahera) may have emerged as early as ca 29 Ma (95% HPD = 33–26 Ma) and probably provided a hub for the eastward colonization of Wallacea. The relatively recent colonization of Sundaland at ca 28 Ma (95% HPD = 32–25 Ma) does not reflect the geological history of the region since this

continental area surely originated much earlier (Tänzler et al. 2014). Finally, the first lineage of the 'Southeast Moluccas area' appeared at ca 18 Ma (95% HPD = 21—15 Ma), but since we estimate no local diversification, the subaerial existence of these islands may be more recent.

Implications for West Pacific Island paleogeography

The 'West Pacific Islands', comprising New Caledonia and the Samoan Islands, were colonized by *Trigonopterus* ca 29 Ma (95% HPD = 34–26 Ma). This is a complex area comprising the continental fragment of New Caledonia and the volcanic and geologically more recent Samoan Islands. Since the *Trigonopterus* faunas of both archipelagos are sister groups and the split between them occurred at ca 26 Ma (95% HPD = 30–22 Ma), colonization of the Samoan Islands trail is expected to have occurred shortly thereafter. *Trigonopterus* radiated on New Caledonia at ca 24 Ma (95% HPD = 21–27 Ma) after the island's Eocene submergence (Pelletier 2006, Schellart et al. 2006).

The age obtained for the *Trigonopterus* 'Samoa clade' at ca 23 Ma (95% HPD = 20–27 Ma) appears initially at odds with the geological age of the oldest Samoan Island, Savai'i, dated at ca 5 Ma (Koppers et al. 2008). However, if we consider the ages of the entire Samoan Islands trail, including submerged seamounts, landmasses may have been subaerial up to ca 13 Ma, and this range could be expanded to ca 24 Ma or more if the Alexa Seamount is included (Koppers et al. 2011). Some of these extinct volcanoes to the west may have been higher than sea level when they were active but may have subsequently eroded and subsided as the Pacific Plate moved further from the hotspot. Thus, colonization of the Samoa Archipelago might have occurred at a location much closer to Fiji and New Caledonia, and *Trigonopterus* could have persisted over time by dispersing from old volcanoes to newer ones, each providing suitable habitat for a limited period of time, all the while moving further east on the Pacific Plate. Such a biogeographic scenario is compatible with the 'progression rule' – lineage-specific taxonomic diversification that tracks island age in a linear archipelago (Funk and Wagner 1995, Hembry et al. 2021).

Conclusions

The diversification of *Trigonopterus* traced the geological evolution of the IAMA over the past 40 Ma and appears to be correlated with the formation of terrestrial habitat. We suggest that a marked increase in the number of *Trigonopterus* lineages in a given area can be considered evidence for the formation of more substantial areas of land or complex archipelagoes capable of sustaining populations of locally-endemic *Trigonopterus* in relatively small areas. As inferred in the LTST-BSM analyses, the rate of lineage accumulation increased markedly in the area of the Papuan Peninsula ca 40 Ma, in the PNG Highlands at ca 28 Ma, and in the vicinity of the Bird's Head Peninsula only after ca 16 Ma. This biological assessment

supports, among competing models, a geological scenario for the formation of New Guinea that includes the early emergence of land in the area of the Papuan Peninsula and the subsequent formation of the PNG Highlands and the Central Range. Terrestrial habitat in the Bird's Head region became more stable only recently (Ufford and Cloos 2005, Hall 2013, Gold et al. 2017). Lineage diversification in the Sulawesi area is inferred to have started ca 30 Ma (95% HPD = 33–26 Ma), which is earlier than proposed in other biogeographic studies (Stelbrink et al. 2012). Sulawesi may have acted as a colonization hub to Sundaland and the Lesser Sunda Islands (Letsch et al. 2020a), where the onset of local diversification ca 29 Ma (95% HPD = 33–26 Ma), is older than expected based on current geological models (Hall 2013). We predict the presence of terrestrial habitat in the region accordingly. Three lineages colonized Bali during the Plio-Pleistocene, crossing Wallace's Line from the Lesser Sunda Islands (Tänzler et al. 2014). This prediction is consistent with geological evidence from Bali, an island predominantly of volcanic and carbonate rocks that have likely been exposed above sea level for only the past few million years (Hall 2002, Sutawidjaja 2009). The colonization of West Pacific Islands by *Trigonopterus* started ca 29 Ma (95% HPD = 34–26 Ma), presumably with New Caledonia, and continued with diversification on the Samoan Islands beginning ca 23 Ma (95% HPD = 20–27 Ma), possibly indicating the existence of now sunken islands near the Alexa Seamount. Thus, *Trigonopterus* evolution appears to have closely tracked the geological evolution of the IAMA – based on different, sometimes competing geological scenarios – revealing a uniquely well-resolved view of regional biogeography and large-scale landscape formation. Accumulation of data from additional similarly comprehensive biotic studies of regional biota should help further-refine paleogeographic models for the IAMA via reciprocal illumination.

Author contributions

Harald Letsch: Conceptualization (equal); Data curation (equal); Investigation (equal); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Michael Balke**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Dominik Kusy**: Writing – original draft (equal); Writing – review and editing (equal). **Duane D. McKenna**: Writing – original draft (equal); Writing – review and editing (equal). **Raden Pramesa Narakusumo**: Resources (equal); Writing – original draft (equal); Writing – review and editing (equal). **Katayo Sagata**: Resources (equal); Writing – original draft (equal); Writing – review and editing (equal). **Emmanuel F.A. Toussaint**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Lloyd T. White**: Resources (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Alexander Riedel**: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Resources (lead); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https:// doi.org/10.5061/dryad.9cnp5hqqg (Letsch et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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