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Authors

Karin, Benjamin R
Stubbs, Alexander L
Arifin, Umilaela
et al.

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Authors: Karin, Benjamin R., Stubbs, Alexander L., Arifin, Umilaela, Iskandar, Djoko T., Arida, Evy, et al.

Crossing Lydekker's Line: Northern Water Dragons (*Tropicagama temporalis*) Colonized the Mollucan Islands of Indonesia from New Guinea

Benjamin R. Karin[1,6], Alexander L. Stubbs[1], Umilaela Arifin[2,3], Djoko T. Iskandar[2], Evy Arida[4], Christopher C. Austin[5], and Jimmy A. McGuire[1]

[1] Museum of Vertebrate Zoology and Department of Integrative Biology, 3101 Valley Life Sciences Building, University of California, Berkeley, CA 94720-3160, USA
[2] School of Life Sciences and Technology, Bandung Institute of Technology, Labtek XI Building, 10 Jalan Ganesa, Bandung 40132, Indonesia
[3] Centrum für Naturkunde-Zoologisches Museum Hamburg, Universität Hamburg, Edmund-Siemers Allee 1, 20146 Hamburg, Germany
[4] Museum Zoologicum Bogoriense (MZB), Indonesian Institute of Sciences (LIPI), Jalan Raya Bogor-Jakarta Km. 46, Cibinong 16911, Indonesia
[5] Department of Biological Sciences, Museum of Natural Science, 119 Foster Hall, Louisiana State University, Baton Rouge, LA 70803-3216, USA

ABSTRACT: Wallace's and Lydekker's Lines both describe important biogeographic barriers in the Indo-Australian Archipelago, with Wallace's Line demarcating the boundary of the Greater Sunda Shelf and Lydekker's Line indicating the edge of the Sahul continental shelf. Despite their similarities, Wallace's Line has been much more heavily studied than has Lydekker's Line, yet provides an interesting system for testing the source of fauna into eastern Wallacea. New collections of Northern Water Dragons, *Tropicagama temporalis*, from several islands in Maluku, eastern Indonesia now allow for an assessment of the phylogeography of the species and the ability to test if New Guinean or Australian populations served as the source for over-water dispersal across Lydekker's Line into Maluku. We collected specimens from remote islands in eastern Indonesia, sequenced the mitochondrial ND2 gene, and aligned the data to previously sequenced specimens on GenBank. We conducted several phylogenetic and divergence time analyses to investigate the source population and timing of dispersal. We found low genetic diversity among the islands in Maluku, and these samples showed little genetic divergence from New Guinea samples. The New Guinea and Maluku populations diverged less than 1 million years ago (Ma) and together diverged from the Australian population between 2.3 and 4.7 Ma. These results, along with patterns in other taxa, illustrated that, despite Australia's close geographic proximity to many of the islands in southeastern Indonesia, New Guinea has been the more frequent source of Wallacean fauna from Sahul.

Key words: Agamidae; Biogeography; Lizard; Maluku; Phylogeography; Wallacea

WALLACE'S LINE (Wallace 1860) and Lydekker's Line (Lydekker 1896) in the Indo-Australian Archipelago represent the most dramatic faunal boundaries in the world (Lohman et al. 2011), yet while Wallace's Line has been at the forefront of the biogeographic literature for over 150 yr (Mayr 1944), Lydekker's Line has received relatively scant attention from biogeographers and has remained understudied. Both biogeographical boundary lines trace the edge of a continental shelf that was regularly exposed during Pleistocene sea-level recessions, with Wallace's Line tracing the Sunda Shelf (including Borneo, Java, Bali, Sumatra, and Peninsular Malaysia) and Lydekker's tracing the Sahul Shelf (including Australia, New Guinea, and the Aru Islands; Simpson 1977; see Fig. 1). However, whereas the timing, directionality, and number of independent dispersal events across Wallace's Line have been investigated using molecular phylogenetics for a great diversity of taxa (e.g., Stelbrink et al. 2012; Tänzler et al. 2014; Reilly et al. 2019), patterns of dispersal across Lydekker's Line have not been investigated to the same degree (but see Toussaint et al. 2015, 2020; Tänzler et al. 2016; Rowe et al. 2019). The geography at Wallace's Line, comprised of the similarly sized adjacent islands of Borneo and Sulawesi as well as Bali, Lombok, and the remainder of the Lesser Sunda Islands, provide an interesting model system for investigating diversification and evolution, and this likely contributes to the disproportionate focus. Still, the dispersal of Australo-Papuan fauna into Wallacea from Sahul also provides an important system for

comparison with Wallace's Line and should be investigated with the same rigor.

An understudied element regarding Lydekker's Line is the relative frequencies in which the Australian component of Sahul versus the New Guinea component served as the source population for dispersal into Wallacea. Although Australia and New Guinea have often been connected by land and share many species, they each still hold distinct faunal communities, likely on account of climate-driven differences in their constituent habitats (Simpson 1961). Organisms that occur in the tropical savannah habitat of southern New Guinea, northern Australia, and on parts of many islands in southern Wallacea may show unique biogeographic patterns compared to species that inhabit tropical rainforests. When exposed during glacial maxima, the Sahul Shelf surrounds the eastern and southern edges of Wallacea, and it is possible that over-water dispersal events originated from geographically proximate areas from either Australia or New Guinea (Fig. 1).

Northern Water Dragons (*Tropicagama temporalis*) are semi arboreal inhabitants of tropical savannah habitats that occur in northern Australia (northern Queensland and northern Northern Territory), New Guinea, and several remote islands in the Maluku province (Mollucas) of eastern Indonesia. The Australian populations are relatively well studied (e.g., Christian et al. 1999; Iglesias et al. 2009, 2012; Blamires 2011), but the Indonesian populations have rarely been collected. Melville et al. (2011) found genetic divergence between Australian and Tanimbar samples of *T. temporalis* dating to 5.4 million years ago (Ma; confidence intervals [CI] = 3.2–8.3 Ma) for the ND2 gene and 6.4 Ma (CI = 2.5–9.6 Ma) for RAG1 but did not include other

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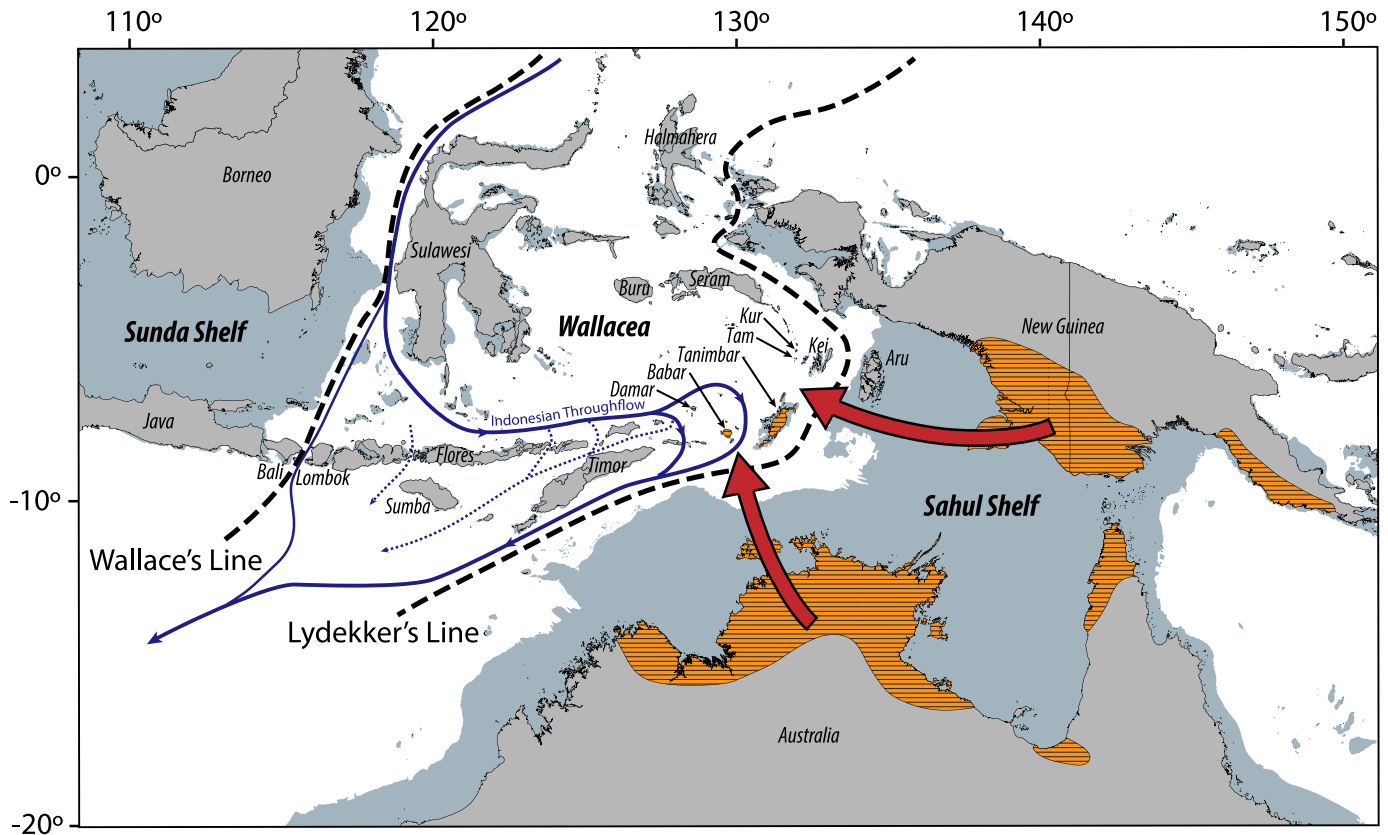[6] CORRESPONDENCE: e-mail, benkarin@berkeley.edu

FIG. 1.—Map of Wallacea with red arrows illustrating the two hypothesized dispersal routes across Lydekker's Line from source populations of *Tropicagama temporalis* in Australia and New Guinea. Range of *T. temporalis* highlighted in orange, and islands with small black arrows are the known island populations of *T. temporalis*. The light blue region signifies the 120-m depth contour that outlines the edge of the Sunda and Sahul Shelves during sea-level recessions. The Indonesian throughflow current is depicted by the blue arrows, with thicker lines corresponding to higher flows (adapted from Godfrey 1996). Range in Australia adapted from Cogger (2014:741) and range in New Guinea estimated from VertNet museum localities (Available at http://vertnet.org). A color version of this figure is available online.

populations in the analysis. In Maluku, *T. temporalis* was long known from Tanimbar, Babar, and Damar (de Rooij 1915) and was more recently discovered from the Kei Island group. Specifically, it was collected from the small and remote island of Tam in 1971 (specimens deposited in Australian National Wildlife Collection; see Schodde and Mathews 1977 for avifauna survey) and again in 2011 by our team (Karin et al. 2018b). We also found a new island population on the equally remote island of Kur in 2014 (Karin et al. 2018b). The record of *T. temporalis* from Maluku by Roux (1910) could possibly refer to these Kei Islands populations, but the true origin of Roux's specimens is uncertain (Shea 2012; Karin et al. 2018b).

Long placed in the genus *Lophognathus*, Melville et al. (2011) suggested that the species be transferred to another genus, given rampant paraphyly between closely related genera. Consequently, Wilson and Swan (2013:408) and Cogger (2014:741) temporarily placed *T. temporalis* in *Gowidon* with *Gowidon longirostris*. However, *T. temporalis* is not sister to *Gowidon longirostris*, so Melville et al. (2018) placed it in a new genus, *Tropicagama*, which we follow here.

The distribution of *T. temporalis* provided an interesting opportunity to evaluate the source of dispersal into Wallacea, as the species could have dispersed either from New Guinea or Australia (Fig. 1). We made use of our new Mollucan

collections of *T. temporalis* from Babar, Kur, and Tam, as well as from Papua New Guinea, to test for the source population and estimate the divergence time between the various subpopulations. We aimed to test several competing biogeographical scenarios regarding colonization of Maluku by *T. temporalis*. Our null hypothesis was that *T. temporalis* represented a panmictic population on the Sahul Shelf, as expected if the frequent reconnections of Australia and New Guinea during glacial maxima provided opportunities for extensive gene flow between Australian and New Guinea populations. Given the findings of Melville et al. (2011), this would indicate that *T. temporalis* colonized Tanimbar and perhaps other Mollucan islands more than 5 Ma from a single, widespread Sahulian population. Such a scenario would suggest that at least the Tanimbar lineage, and perhaps other Mollucan lineages, might represent cryptic species. Alternatively, if the New Guinea populations are highly divergent from Australian populations, then New Guinea might have served as a more recent source for the Mollucan populations or, alternatively, the Mollucan Islands might have provided an over-water dispersal corridor from Australia to New Guinea (these alternatives might be indistinguishable). Under this scenario, New Guinea, plus Mollucan populations, could represent one or more cryptic species distinct from an Australian lineage. Finally, it is possible that Australia, New Guinea, and some combination

TABLE 1.—Specimens included in phylogenetic analyses and their corresponding localities and GenBank accession numbers.

Species	Catalog number	Island	GenBank (ND2)	GenBank (RAG1)	Reference
Tropicagama temporalis	ALS 828	Babar	MT445768	—	This study
T. temporalis	ALS 829	Babar	MT445769	—	This study
T. temporalis	ALS 890	Kur	MT445770	—	This study
T. temporalis	ALS 891	Kur	MT445771	—	This study
T. temporalis	MVZ 273759	Tam	MT445772	—	This study
T. temporalis	MVZ 273764	Tam	MT445773	—	This study
T. temporalis	LSUMZ 94681	New Guinea	MT445778	—	This study
T. temporalis	LSUMZ 98852	New Guinea	MT445776	—	This study
T. temporalis	LSUMZ 98853	New Guinea	MT445775	—	This study
T. temporalis	LSUMZ 98854	New Guinea	MT445777	—	This study
T. temporalis	LSUMZ 98855	New Guinea	MT445774	—	This study
T. temporalis	LSUMZ 92284	New Guinea	MT445779	—	This study
T. temporalis	LSUMZ 92285	New Guinea	MT445780	—	This study
T. temporalis	NMV D74299	Australia	HQ684168	HQ662491	Melville et al. 2011
T. temporalis	NMV D74306	Australia	HQ684170	HQ662492	Melville et al. 2011
T. temporalis	NMV D74319	Australia	HQ684169	—	Melville et al. 2011
T. temporalis	NTM R21675	Australia	AY133002	—	Schulte et al. 2003
T. temporalis	WAM R109957	Tanimbar	HQ684157	HQ662488	Melville et al. 2011
T. temporalis	WAM R109958	Tanimbar	HQ684158	HQ662489	Melville et al. 2011
T. temporalis	WAM R109968	Tanimbar	HQ684159	—	Melville et al. 2011
T. temporalis	WAM R109981	Tanimbar	HQ684160	—	Melville et al. 2011
T. temporalis	WAM R112245	Tanimbar	HQ684161	—	Melville et al. 2011
T. temporalis	WAM R112260	Tanimbar	HQ684162	HQ662487	Melville et al. 2011
T. temporalis	WAM R112261	Tanimbar	HQ684163	—	Melville et al. 2011
T. temporalis	WAM R112262	Tanimbar	HQ684164	—	Melville et al. 2011
T. temporalis	WAM R112263	Tanimbar	HQ684165	—	Melville et al. 2011
T. temporalis	WAM R112264	Tanimbar	HQ684166	HQ662490	Melville et al. 2011
T. temporalis	WAM R112266	Tanimbar	HQ684167	—	Melville et al. 2011
Diporiphora arnhemica	NTM R13836	—	AY133004	—	Schulte et al. 2003
D. australis	ANWC R5480	—	AY133005	—	Schulte et al. 2003
Pogona barbata	SAMA R41126	—	AF128474	—	Macey et al. 2000
P. vitticeps	SAMA R42415	—	AY133026	—	Schulte et al. 2003
Rankinia diemensis	ANWC R5629	—	AF375619	—	Melville et al. 2011
Tympanocryptis tetraporophora	ANWC R5612	—	AY133032	—	Schulte et al. 2003

of Mollucan populations are all highly divergent from one another and could represent three or more long-isolated cryptic lineages. For the latter scenarios, it would be possible to identify a source location from which the Mollucan islands were colonized whereas under the first scenario the Mollucan populations would be equally closely related to those in Australia and New Guinea.

MATERIALS AND METHODS

We collected liver tissue in the field in home-made RNAlater, fixed specimens in formalin, and later transferred them to 70% ethanol. In the lab, we extracted DNA using a modified salt extraction protocol (adapted from Aljanabi and Martinez 1997) and designed new PCR primers for the NADH dehydrogenase subunit II (ND2) gene for *Tropicagama* and close relatives using the programs Geneious v11.0.5 (Kearse et al. 2012) and Primer3 (Untergasser et al. 2012). We first aligned the mitochondrial genomes of *Pogona vitticeps* (GenBank accession: NC_006922) and *Calotes versicolor* (GenBank accession: AB183287), then selected the region overlapping the tRNA^{met} primer region (Macey et al. 2000) for the forward primer and within the tRNA^{asn} region for the reverse in order to encompass the entire ND2 coding region. The new forward primer sequence is 5′-CCCATGCCCCAAAAACGGW-3′ and the reverse is 5′-GTGGGATCGAGGCCCWCCAA-3′.

We ran PCRs at standard concentrations and conditions dropping the annealing temperature from 60°C for the first 10 cycles to 55°C for the next 10, and then to 50°C for the final 10 cycles. We confirmed successful amplification on a 1% agarose gel stained with ethidium bromide to visualize them with ultraviolet light. We cleaned PCR products with exonuclease I and shrimp alkaline phosphatase enzymes and cycle sequenced PCR products using BigDye v3.1 chemistry (Applied Biosystems, Thermo Fisher Scientific, Inc.). We cleaned PCR products using ethanol precipitation and analyzed the products on an ABI3730 machine (Applied Biosystems). The resulting chromatograms were assembled in Geneious to a reference sequence of ND2 from GenBank and sequencing errors were corrected manually or given an N when ambiguous. All newly generated sequences are deposited on GenBank (MT445768–80; see Table 1).

We downloaded ingroup and outgroup ND2 samples from GenBank (Table 1) and aligned them to our newly generated sequences using MAFFT v7.130b (Katoh and Standley 2013), then trimmed the alignment to the ND2 stop codon before analysis, resulting in a final alignment length of 1017 base pairs. We also downloaded RAG1 sequence data for *T. temporalis* from GenBank (originally from Melville et al. 2011) and aligned the sequences using MAFFT. We did not generate new RAG1 sequence data for this study and only used it to build a haplotype network. For ND2, we performed maximum likelihood (ML) analysis using RAxML v8.1.15 (Stamatakis 2014) and Bayesian inference (BI) using MrBayes v3.2.1 (Ronquist et al. 2012). We followed the results of PartitionFinder v2.1.1 (Lanfear et al. 2012) using the Bayesian information criteria score and the greedy algorithm to specify partitioning scheme. For ML analysis,

TABLE 2.—Average (and range) of raw pairwise genetic distances for ND2 between and within island populations of *Tropicagama temporalis*.

	Australia	New Guinea	Tam	Kur	Tanimbar	Babar
Australia	0.1% (0–0.21%)					
New Guinea	3.67% (3.17–4.21%)	0.14% (0–0.45%)				
Tam	3.2% (3.12–3.34%)	0.54% (0.23–0.9%)	0% (0–0%)			
Kur	3.2% (3.04–3.43%)	0.53% (0.23–0.84%)	0.15% (0–0.34%)	0.27% (0.27–0.27%)		
Tanimbar	3.5% (3.44–3.74%)	0.96% (0.45–1.2%)	0.63% (0.45–0.74%)	0.66% (0.49–0.76%)	0.14% (0–0.59%)	
Babar	3.41% (3.24–3.66%)	0.55% (0.23–0.87%)	0.34% (0.22–0.47%)	0.25% (0.07–0.42%)	0.74% (0.49–0.91%)	0.22% (0.22–0.22%)

we specified a separate GTRGAMMA partition for each codon position of ND2 and ran the program with 100 bootstrap replicates. For BI, we specified an HKY model plus a gamma rate heterogeneity parameter for the first and second codon position separately and an HKY model plus proportion of invariant sites parameter for the third codon position. We ran two simultaneous analyses with three cold chains and one heated chain for 10 million generations. We confirmed adequate convergence of the Markov chain in Tracer v1.6 (Rambaut et al. 2018) for this analysis, and the subsequent divergence time analysis, with a flat trace and ESS values well over 200 for all parameter estimates.

We estimated divergence times using the program BEAST2 v2.5.1 (Bouckaert et al. 2013). Melville et al. (2011) recovered substantial branch length differences between *T. temporalis* and its closest relatives, suggesting that rate heterogeneity might exist in this region of the phylogeny. We did not want this potential rate heterogeneity to bias molecular clock estimates, so we trimmed the outgroups from the alignment leaving only the 28 *T. temporalis* samples. We ran PartitionFinder on this reduced alignment and specified in BEAST2 the following partitions and evolutionary models: TrN with estimated base frequencies for the first ND2 codon position; HKY plus estimated invariant sites and empirical base frequencies for the second codon position; and TrN with estimated base frequencies for the third codon position. We ran the analysis under both a strict clock and an uncorrelated, relaxed log-normal clock, specifying a rate of 0.0062 substitutions per site per million years, which corresponds to the fossil-calibrated rate for the group estimated by Melville et al. (2011). We ran the Markov chain for 100 million generations, sampling every 5000, and discarded the first 10% of trees as burn-in.

We generated the ND2 and RAG1 haplotype networks in R v3.3.1 (R Core Team 2016) using the pegas package (Paradis 2010), and we color coded by population following the methods of Karin et al. (2018a). Pairwise sequence divergence was calculated in Geneious v11.0.5. Given the limited variation present in the RAG1 gene sequenced by Melville et al. (2011), we did not incorporate RAG1 into a concatenated analysis with ND2. We visualized RAG1 in a haplotype network only and compared RAG1 divergence times (taken directly from Melville et al. 2011) with our ND2 divergence times.

RESULTS

In all analyses, Australian *T. temporalis* grouped in a divergent clade from the New Guinea and Maluku samples. Australian samples are 3–4% divergent from all other *T. temporalis* samples while there is less than 1% sequence divergence between the New Guinea and

Maluku samples (Table 2). The ML and BI analyses (Fig. 2), as well as the timetree (Fig. 3), all showed concordant topologies for supported nodes, but differed slightly in unsupported regions. New Guinea and Tanimbar samples each formed a clade, but the other islands were not recovered separately. Each of the samples from Kur shared a mitochondrial haplotype with a different population— one shared with the two samples from Tam and the other shared with the two samples from Babar. Only two mutations separated New Guinea from Tanimbar samples, and the remaining Maluku samples were separated by one to two mutations as well.

The strict and relaxed clock analyses both converged on similar estimates of divergence times as well as identical topologies. Confidence intervals of divergence times for the strict clock calibration were generally narrower than for the relaxed clock calibration. We estimated that the divergence time for the crown of the group between the Australia and the New Guinea plus Maluku clade was 2.39–4.93 Ma for the strict clock and 1.53–5.09 Ma for the relaxed clock (Fig. 3). We estimated the crown age of the Maluku and New Guinea clade at 0.34–1.04 Ma for the strict clock and 0.33–1.11 Ma for the relaxed clock. The entire 95% CIs for the other divergence times within this clade for both calibrations were less than 850,000 years ago. Hereinafter, we refer to the relaxed clock estimates.

DISCUSSION

The high sequence similarity between samples from New Guinea and Maluku supports the hypothesis that New Guinea, rather than Australia, was the source population for dispersal of *T. temporalis* into Wallacea. We recovered a deep (3.40 Ma; CI = 1.53–5.09 Ma) split between Australia and the remaining samples while New Guinea and Maluku samples diverged more recently than 1 Ma. This divergence time is similar to previous estimates of 5.4 Ma (CI = 3.2–8.3 Ma) for ND2 and 6.4 Ma (CI = 2.5–9.6 Ma) for RAG1 (Melville et al. 2011; cf. Fig. 3). However, given the potential rate heterogeneity in the group, as indicated by the long branch to *T. temporalis* recovered by Melville et al. (2011, 2018), we do not place high confidence in these estimates and expect that these ages might be an overestimation if substitution rates are locally higher for the *T. temporalis* lineage. Our younger divergence time estimates are likely influenced by the coalescent tree prior we implemented versus the Yule tree prior used by Melville et al. (2011), as well as our reduced dataset, which contains a smaller set of branches from which to estimate substitution rates.

Our results are concordant with the close association of New Guinea fauna with eastern Maluku observed in other reptile species (Karin et al. 2018b). Most reptiles in Maluku
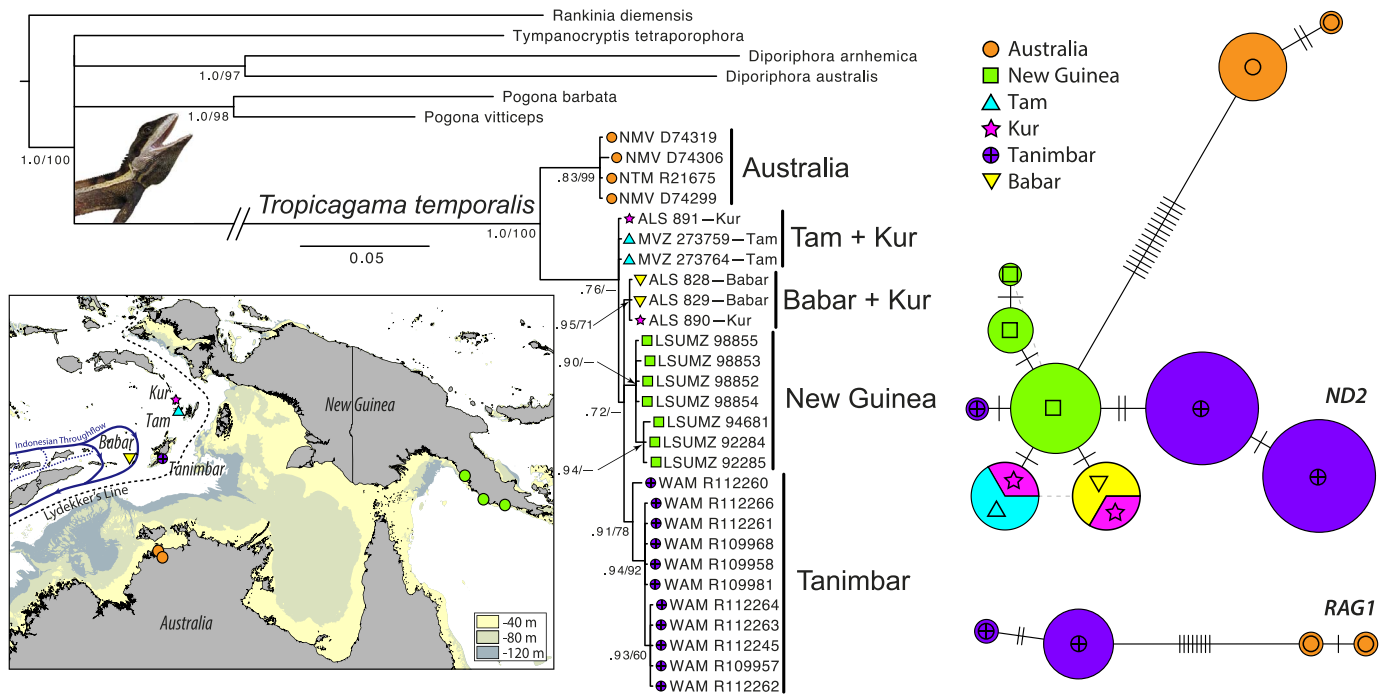
Fig. 2.—Phylogenetic tree (Bayesian inference [BI] topology) for *Tropicagama temporalis* and outgroups for the ND2 gene alone (center panel). Support indicated by BI posterior probability (left of slash) and maximum likelihood bootstrap proportion (right of slash). Haplotype network of *T. temporalis* excluding outgroups for ND2 and RAG1 (right panel), with circle-size corresponding to the number of samples, hash-marks representing the number of changes between haplotypes, and gray dashed lines indicating equivalently parsimonious alternative topologies. Map of sampling locations of specimens in phylogeny (left panel), with bathymetric contours generated from GEBCO bathymetric data (available at http://www.gebco.net/). Color-coding matches the inset legend of right panel. A color version of this figure is available online.

likely dispersed directly from New Guinea into eastern Wallacea because they, or their sister taxa, do not occur in Australia. These include skinks of the genus *Cryptoblepharus* (Blom et al. 2019) and *Lygisaurus novaeguineae* (by
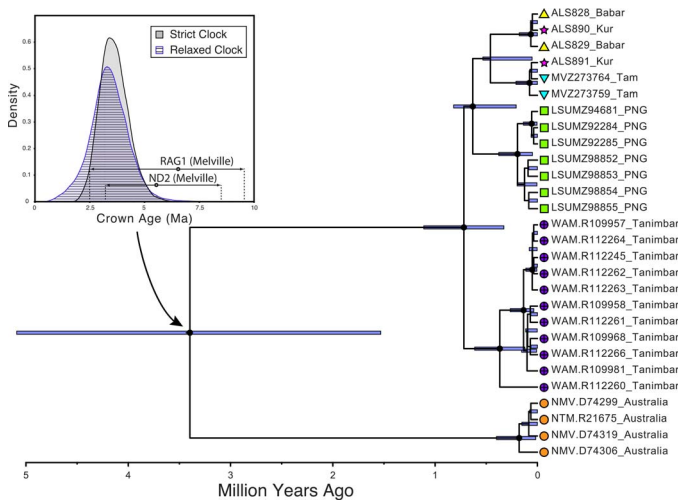

Fig. 3.—Relaxed clock time-calibrated tree of *Tropicagama temporalis*, excluding outgroups for ND2. Dots on nodes indicate a posterior probability greater than 0.95 and bars denoting the 95% confidence interval of the node-date. The inset graph compares the posterior densities of the crown age for the strict and relaxed clock analyses of ND2 (this study) and also displays the 95% confidence intervals (dashed lines) and median (small circle) for the fossil-calibrated ages estimated by Melville et al. (2011) for ND2 and RAG1. Color-coding of tips matches that of Figure 2. A color version of this figure is available online.

range), geckos of the *Gehyra barea* group (Oliver et al. 2010; Karin et al. 2018b), the *Lepidodactylus* group (Stubbs et al. 2017; Karin et al. 2018b) and *Gekko vittatus* (by range; Karin et al. 2018b), and the snake *Acanthophis laevis*. Further study of organisms that occur in Australia, as well as New Guinea and Maluku, could be used to test our central hypothesis in more detail. Candidate species for examination include the agamid genus *Hypsilurus*, the python *Simalia amethistina*, the blind snake *Ramphotyphlops multilineatus*, the treefrog *Litoria infrafrenata*, microhylid frogs of the genus *Cophixalus*, the blue-tongued skinks *Tiliqua gigas* and *T. scincoides*, and the four-fingered skinks of the *Carlia beccarii* and *C. babarensis* groups. Geckos of the speciose genus *Cyrtodactylus* show an exception to the regular colonization route through Wallacea, having colonized Australia twice—once from the Lesser Sundas to Northern Australia via Timor and a second time through New Guinea (Wood et al. 2012).

In other animal clades, most studies that have focused on dispersal across Lydekker's Line have not specifically investigated an Australian versus New Guinean source for dispseral. Yet, similar to the herpetofauna discussed above, the majority of the remaining fauna of Maluku is closely allied with New Guinea, such as mammals (Simpson 1961, 1977; Rowe et al. 2019), birds (Mayr 1944; Johnstone and van Balen 2013), and arthropods (Toussaint et al. 2015; Tänzler et al. 2016). This is likely simply because of their close proximity and generally wet, tropical environments. In general, dispersal across Lydekker's Line appears to be more difficult than Wallace's Line, as it has been crossed less often

than Wallace's Line in the animal radiations that have been assessed (Toussaint et al. 2015, 2020; Tänzler et al. 2016; Rowe et al. 2019). This is likely attributable to a number of factors including sizes of, and distance between, source and target islands (MacArthur and Wilson 1967), ocean currents that might promote or deter certain dispersal routes, and how these variables have changed through time (Hall 2012). A more detailed assessment of taxa restricted to the climactically similar areas of northern Australia, southern New Guinea, and drier zones within southern Maluku and the Lesser Sundas might find a stronger connection between northern Australia and Indonesia. We predict that most groups will show a similar source from New Guinea, as indicated in our results.

The magnitude and direction of the Indonesian through-flow current might make it difficult for organisms to disperse over-water between Australia and Maluku and could contribute to the imbalance of taxa in Maluku that originate in Australia. The difference in sea-level between the Pacific and Indian Oceans causes water to flow rapidly through and around the Lesser Sundas, and a major component of this current (up to 40% of the water volume) flows east between Sulawesi and the Lesser Sundas, then turns 180° as it wraps around Wetar and Timor (among other small islands) and exits traveling westward in the trough between Timor and Australia (Godfrey 1996; Fig. 1). This powerful current might prevent most over-water dispersal events from the fringe of Australia to Indonesia, even when sea-levels are reduced, and might explain why there have not been more documented dispersal events from northern Australia to the southeastern Banda Arc (but see Wood et al. 2012). This might also explain why *T. temporalis* colonized Maluku from New Guinea rather than from Australia.

The deep genetic splits between *T. temporalis* populations most likely indicate an initial divergence between Australia and New Guinea followed by over-water dispersal into Maluku; however, there are other possible interpretations of this result. We cannot reject the possibility that *T. temporalis* dispersed from Australia into Maluku first and then later colonized New Guinea from Maluku. We suggest that this dispersal route is much less likely, given the land connection between Australia and New Guinea, which would have provided an easy passage between them. In addition, there is not enough sequence variation in our dataset to distinguish between a single dispersal event from New Guinea into Wallacea versus multiple independent dispersals. Further investigation by sequencing additional loci, as well as adding additional samples from New Guinea, northern Queensland, and Damar, might allow us to distinguish between these hypotheses.

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