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Phylogeny, historical biogeography and body size evolution in Pacific Island Crocodile skinks *Tribolonotus* (Squamata; Scincidae)

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ABSTRACT

Competition heavily influences the structure of island communities, particularly in species-rich areas. If ecologically similar lineages come into contact following dispersal, selection may favor rapid evolutionary change; if constraints prevent such change, lineage extinction may result. One mechanism for relieving competition among newly sympatric species is the evolution of body size differences, such as through character displacement or size assortment. The Crocodile skinks of the genus *Tribolonotus* exhibit a threefold variation in body size, and several species occur in sympatry. We use 2252 bp of DNA sequence data spanning two mitochondrial (cyt b and ND2) and three nuclear (C-mos, Rhodopsin and Phosducin) gene regions to reconstruct the phylogeny of *Tribolonotus*, use it to examine the biogeography of the genus, and test for size assortment or character displacement. We find evidence that *Tribolonotus* originated on either Greater Bougainville or in New Guinea, and subsequently colonized surrounding islands via multiple colonization events. Our ancestral state reconstructions support multiple instances of parallel and independent change in body size within *Tribolonotus*. Additionally, we find no evidence for size assortment and conflicting evidence for character displacement, which we argue suggests that character displacement, combined with ecological differences between New Guinean species (*T. gracilis* and *T. novaeguineae*), best explains the evolution of body size in the genus *Tribolonotus*.

1. Introduction

Competition plays an important role in structuring island communities, and the role of ecological competition is amplified in species-rich areas (Schoener, 1969, 1970; Losos, 1990; Losos et al., 1998). The evolution of different body sizes by ecologically similar sympatric taxa may reduce the degree of competitive interaction among species. Two mechanisms hypothesized to explain differences in body size among island populations are character displacement (sympatric taxa evolve greater differences in morphological traits, e.g. body size, relative to allopatric taxa to minimize competition for resources, [Brown and Wilson, 1956; Losos, 1990; Giannasi et al., 2000]) and size assortment (taxa are unable to successfully colonize an island already inhabited by a closely related species of similar size due to competitive exclusion, whereas taxa of different sizes are able to successfully colonize, [Diamond, 1977; Schoener, 1983; Losos, 1990; Brown, 1997; Giannasi et al., 2000; Mayr and Diamond, 2001]).

Crocodile skinks of the genus *Tribolonotus* are distributed throughout northern New Guinea and the Admiralty, Bismarck and Solomon Archipelagoes (Fig. 1). There are currently eight recognized species of *Tribolonotus*, a very unusual genus readily identified by keeled or spinose scales and united by two enigmatic synapomorphies: abdominal glands and volar pores (Roux, 1934; Parker, 1940). At least two species (*T. gracilis* and *T. ponceleti*) can vocalize (Hartdegen et al., 2001; McCoy, 2006), a characteristic known only from one other scincid lizard (Bauer et al., 2004). The systematic placement of the genus among lygosomine skinks is unclear. Historically, *Tribolonotus* has been allied with the *Sphenomorphus* group (Greer, 1974); however, recent mtDNA data suggest it is not a member of the *Sphenomorphus* group but likely has a closer affinity to the *Egernia* group or the genus *Mabuya* (Reeder, 2003). *Tribolonotus* species also exhibit a threefold variation in adult size, ranging from 40 mm snout-vent-length (SVL, *T. blanchardi*) to 125 mm (*T. ponceleti*) and includes a mix of sympatrically and allopatrically distributed species. *T. blanchardi* (SVL = 40 mm), *T. pseudoponceleti* (SVL = 76 mm), and *T. ponceleti* (SVL = 125 mm) all occur sympatrically on Buka, Bougainville, Choiseul and Isabel in the northern Solomon Islands (McCoy, 2006); and *T. gracilis* (SVL = 103 mm) and *T. novaeguineae* (SVL = 103 mm) occur in broad sympatry in northern New Guinea. The remaining species all have allopatric distributions: *T. brongersmai* (SVL = 64 mm) is endemic to Manus Island in the admirality archipelago, *T. annectens* (SVL = 49 mm) is known only from two specimens from the Gazelle Peninsula on the northern portion of

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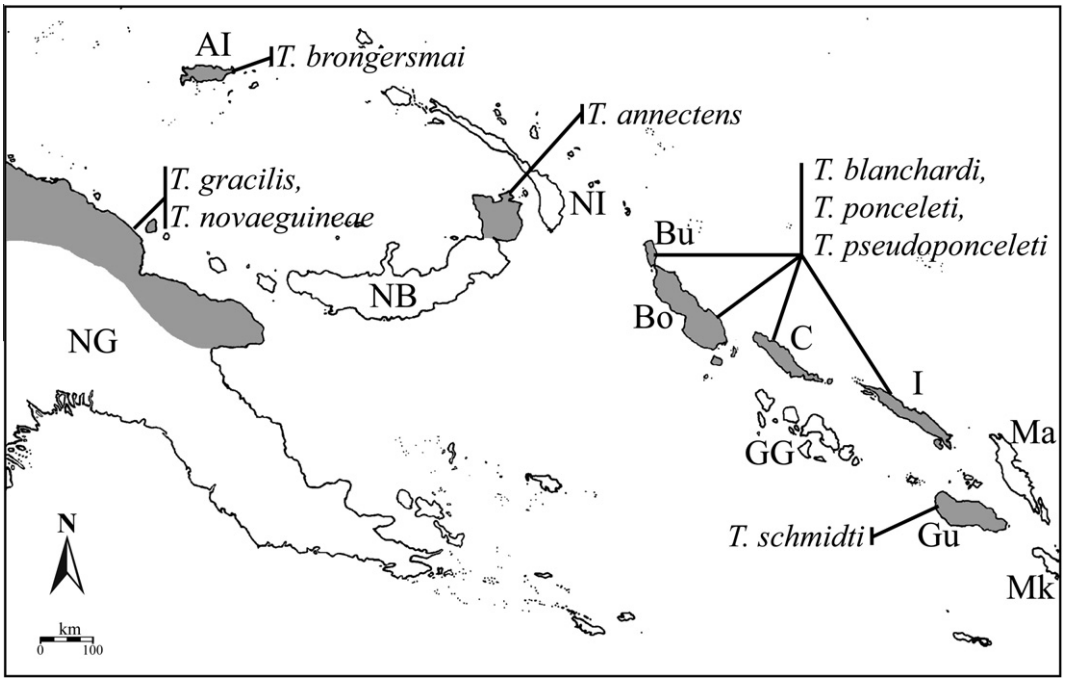

Fig. 1. Map showing current distribution of *Tribolonotus* in New Guinea and Northern Melanesia. Geographic areas are abbreviated as follows: AI, Admiralty Islands; Bo, Bougainville; Bu, Buka; C, Choiseul; GG, New Georgia Group; Gu, Guadalcanal; I, Isabel; Ma, Malaita; Mk, Makira; NB, New Britain; NI, New Ireland; NG, New Guinea.

New Britain in the Bismarck Archipelago, and *T. schmidtii* (SVL = 41 mm) is endemic to Guadalcanal in the Solomon Islands (McCoy, 2006). This mix of sympatric and allopatric distributions within a genus with large body size discrepancies makes this an ideal system for testing the hypotheses of size assortment and character displacement. The genus is not known from New Ireland in the Bismarck Archipelago, or from several major island groups of the Solomon Islands, including Malaita, Makira, and the New Georgia group (Fig. 1). This is an unusual biogeographic distribution not mirrored in any other reptile from the region, and is unlikely to reflect a lack of search effort, as these islands have all been surveyed by biodiversity assessments targeting reptiles (Allison and Bigiale, 2001; McCoy, 2006).

Tectonically, Melanesia is extremely complex. Much of the region comprises the remnants of the Outer Melanesian Island Arc, which formed in part as an oceanic arc, as well as through rifting from the Australian plate approximately 45 Mya, and accretion of the Ontong Java plateau approximately 18 Mya (Hall, 1997, 2002; Petterson et al., 1999; Mann and Taira, 2004). This Outer Melanesian Island Arc has since been, in part, accreted onto the northward moving Australian Tectonic Plate, and much of it currently forms the northern edge of New Guinea, including the Huon Peninsula (Fig. 2; Allison, 1996; Hall, 1997, 2002; Tregoning et al., 1999; Abbott et al., 1994; Heads, 2002).

Here, we use mitochondrial and nuclear DNA sequences to construct the first phylogeny of the genus *Tribolonotus*, and use it to examine body size evolution in this genus using ancestral state reconstructions (maximum likelihood, Schluter et al., 1997) and to test the hypotheses of character displacement and size assortment. We also use parametric methods to reconstruct the distribution of ancestral species (Dispersal-Extinction-Cladogenesis, DEC; Ree et al., 2005; Ree and Smith, 2008) to elucidate the biogeographic history of the genus.

2. Materials and methods

2.1. Specimens and tissue samples

DNA was extracted from 41 individuals representing seven of the eight recognized species of *Tribolonotus* (Appendix 1). No tissue samples were available for *T. annectens*, which is known from only two specimens from northern New Britain. Samples were stored in 70% ethanol prior to extraction. *Tiliqua gigas* was selected as the outgroup taxon based on the hypothesized phylogenetic placement of the genus (Reeder, 2003).

2.2. DNA isolation, amplification, and sequencing

Whole genomic DNA was extracted from either liver or muscle tissue using an ammonium acetate salt extraction protocol (Fetzner, 1999) or a Qiagen DNeasy Tissue Kit (Qiagen, Inc. Valencia, CA) following manufacturer's instructions. Tissues (~100–200 mg) were digested overnight with 20 μl proteinase K, and extraction concentrations of DNA were stored in AE Buffer at −20 °C.

Two mitochondrial gene regions, including cytochrome oxidase b (cyt b) and NADH subunit 2 (ND2), and three nuclear loci, including oocyte maturation factor (C-mos), phosducin (Phos) and rhodopsin (Rhod), were selected for sequencing based on the utility of these loci in related groups (Saint et al., 1998, 2001; Phillips et al., 2004; Bauer et al., 2007). Primer sequences used in this study and references are available in Table 1. Target gene regions were amplified by PCR on an MJ PTC-200 thermocycler (annealing temperatures available in Table 1) using previously published protocols (Austin et al., 2010). Amplified PCR products were purified with 5 U Exonuclease I and 1.25 U Antarctic Phosphatase (New England Biolabs, Ipswich, MA) by incubation at 37 °C for 25 min and 15 min at 80 °C, and sequenced in both directions via previously published protocols (Austin et al., 2010) using an ABI 3100 automated capillary sequencer.

2.3. Contig assembly and alignment

Sequences were visually verified to check for double-called bases or other misreads and complementary strands were aligned into contigs using Sequencher v4.7 (Gene Codes Corp., Ann Arbor, MI, USA). Sequence contigs were then aligned using ClustalX2 (Larkin et al., 2007) under default settings (Gap opening penalty = 15, Gap extension penalty = 6.66). All protein-coding regions were translated to amino acid sequences using Mesquite v2.6

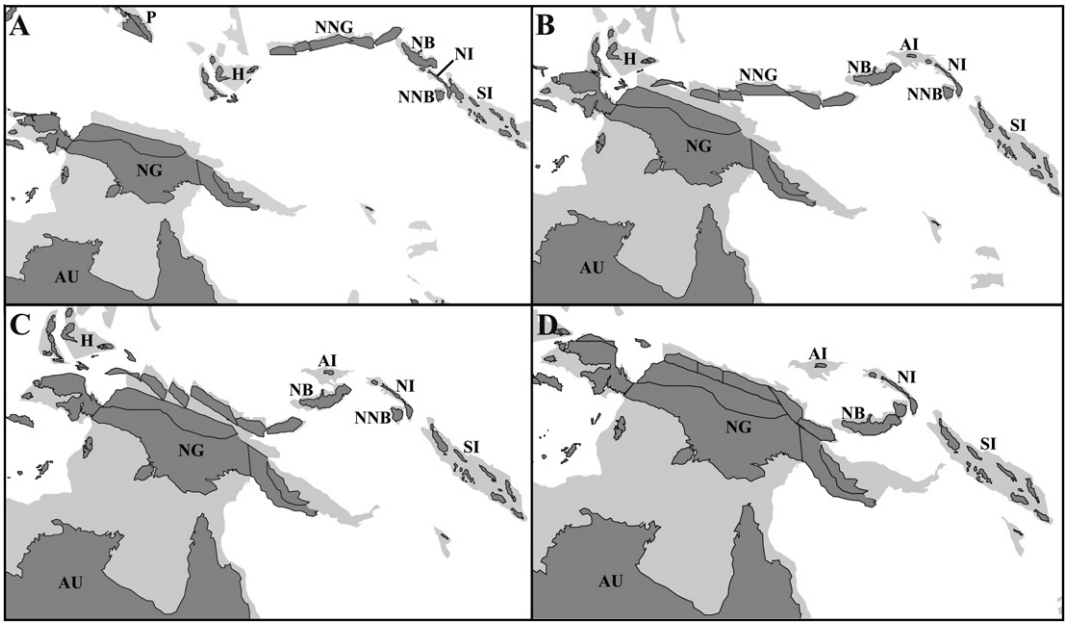

Fig. 2. Map showing the tectonic history of New Guinea and Northern Melanesia, adapted from Hall (2002). (A) Thirty million years ago (Mya); (B) 10 Mya; (C) 5 Mya; (D) present. Dark grey indicates subaerial land, light grey indicates shallow seas that were intermittently subaerial during periods of low seal level, and white indicates deep seas. Geographic areas are abbreviated as follows: AI, Admiralty Islands; AU, Australia; H, Halmahera; P, Philippines; NB, New Britain; NNB, Northern New Britain; NI, New Ireland; NG, New Guinea; NNG, Northern New Guinea; SI, Solomon Islands (including Bougainville, Buka, Choiseul, Guadalcanal, Isabel, New Georgia group, Malaita, and Makira).

Table 1
Primers and annealing temperatures used in this study. Rho3CRF was paired with either Rho4CRR or RhodR2.

Primer	Gene	Primer Sequence	Temp. (°C)	Reference
H15149	cyt b	5′-AAA CTG CAG CCC CTC AGA ATG ATA AA-3′	44	Kocher et al. (1989)
L14841	cyt b	5′-AAA AAG CTT CCA TCC AAC ATC TCA GC-3′	44	Kocher et al. (1989)
L305	ND2	5′-CAC TGA CTT CTT GCC TGA WTY GG-3′	48	Smith et al. (2001)
H715	ND2	5′-GCT GTY TGT GTY TGG TTT ADK CC-3′	48	Smith et al. (2001)
G73	C-mos	5′-GCG GTA AAG CAG GTG AAG AAA-3′	48	Saint et al. (1998)
G74	C-mos	5′-TGA GCA TCC AAA GTC TCC AAT C-3′	48	Saint et al. (1998)
PhoF2	Phos	5′-AGA TGA GCA TGC AGG AGT ATG A-3′	60	Bauer et al. (2007)
PhoR1	Phos	5′-TCC ACA TCC ACA GCA AAA AAC TCC T-3′	60	Bauer et al. (2007)
Rho3CRF	Rhod	5′-CCT TGC CTG GAC ACC CTA TGC TG-3′	60	Phillips et al. (2004)
Rho4CRR	Rhod	5′-CTC TGG AAT AAA GGA GAG GGT CTC T-3′	60	Phillips et al. (2004)
RhodR2	Rhod	5′-ACC TCA GTC TTG CTC TGG GA-3′	60	This study

(Maddison and Maddison, 2009) to verify that no premature stop codons disrupted the reading frame.

2.4. Phylogenetic analysis

The phylogeny of *Tribolonotus* was estimated using maximum parsimony, maximum likelihood and Bayesian inference. Maximum parsimony analyses were conducted in PAUP* ver. 4.0b10 (Swofford, 2003) using the PAUPup interface (Calendini and Martin, 2005). The heuristic search option with 5000 random stepwise additions and tree bisection-reconstruction (TBR) was implemented to identify the most parsimonious topology. Branch support was assessed using 1000 bootstrap replicates, each conducted using a full heuristic search with 25 random stepwise additions and TBR. For maximum likelihood and Bayesian analyses, a variety of partitioning schemes, including partitioning by genome (mitochondrial versus nuclear), locus, and codon position, were tested and the optimal partitioning scheme was selected by comparing the likelihoods of the resulting topologies using the Akaike information criterion (AIC, Akaike, 1974). The optimal models of nucleotide substitution were selected using the corrected AIC (Akaike, 1974; Hurvich and Tsai, 1989) in Mr.ModelTest ver. 2.2 (Nylander, 2004). Maximum likelihood analyses were implemented in using RAxML ver. 7.0.4 (Stamatakis, 2006). Because RAxML is only capable of implementing the general time reversible model, all partitions were assigned this model of nucleotide substitution with a gamma distribution of among site rate variation (GTR+G). Despite applying the same model to all partitions, model parameters, including nucleotide state frequencies, substitution rates, and the gamma shape parameter, are allowed to vary among partitions, thus the optimal partitioning scheme, selected using the AIC as described above, significantly improves the likelihood of the phylogeny estimation. Maximum likelihood support for the optimal partitioning scheme was estimated using 1000 bootstrap replicates in RAxML. The partitioned Bayesian inference analysis was implemented in Mr.Bayes v3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). For all models, the prior nucleotide state frequencies, transition/transversion ratio, and substitution rate priors were set as flat Dirichlet distributions, and the proportion of invariable sites was set as a uniform (0.0–1.0) prior distribution. Rate priors were set to variable to allow the nucleotide substitution rates to vary among partitions. Analyses consisted of two runs, each of four chains with default heating and sampling every 1000 generations for 20,000,000 generations.

We discarded the first 5000 topologies (25% of the sampled topologies) as burn-in, and verified convergence using the program Tracer v1.4 (Rambaut and Drummond, 2007) by examining the posterior probability, log likelihood, and all model parameters for stationarity and by examining the effective sample sizes (ESSs), all of which were substantially greater than 200 at run completion. We also used Are We There Yet (AWTY, Nylander et al., 2008) to compare the posterior probabilities of all splits between runs to further verify convergence. At run completion, the plot comparing posterior probabilities of splits between runs was linear, indicating that the two runs had converged and were sampling the posterior distribution.

Several subsequent analyses, including DEC and ancestral state reconstructions (see below), require a fully resolved, bifurcating phylogeny, therefore polytomies in the reconstructed phylogeny (which all occurred among samples within species) were randomly resolved in Mesquite ver. 2.6 (Maddison and Maddison, 2009), as very short branch lengths (1.0×10^{-12}, much shorter than any resolved branches in the phylogeny). All analyses requiring a fully resolved phylogeny incorporate branch lengths into calculations, that is, probability of changes along branches are proportional to branch lengths. Therefore reconstructed changes along very short branch lengths (e.g. 1.0×10^{-12}) are extremely unlikely, thus these very short branch lengths are effectively equivalent to zero length branches, and a single randomly resolved phylogeny was used for all subsequent analyses.

2.5. Biogeographic reconstruction

For reconstructions of ancestral distributions, the region was divided into five areas based on current species distribution: Guadalcanal (inhabited by *T. schmidti*), Greater Bougainville (Buka, Bougainville, Shortland Islands, Choiseul and Isabel, inhabited by *T. blanchardi, T. ponceleti*, and *T. pseudoponceleti*), the Bismarck Archipelago (inhabited by *T. annectens*), Admiralty Archipelago (*T. brongersmai*) and northern New Guinea (*T. gracilis* and *T. novaeguineae*). Two methods were employed to reconstruct the biogeographic history of the genus. The first, maximum likelihood ancestral state reconstruction (Schluter et al., 1997; Wiens et al., 2009) was implemented in Mesquite ver. 2.6 (Maddison and Maddison, 2009). Because the ancestral state reconstruction only allows for single character states, we used a second method, Dispersal-Extinction-Cladogenesis (DEC; Ree et al., 2005; Ree and Smith, 2008), a parametric likelihood-based approach to reconstruct ancestral distributions on our phylogeny. DEC estimates the most likely geographic distribution of the two daughter lineages following a speciation event, thus whereas the first ancestral state reconstruction method estimates the actual state at the node, DEC estimates the states of the branches emanating from a given node. DEC analyses were implemented using the software package Lagrange in Python v.2.5.4. Two DEC analyses were run, first without constraints, and the second with two constraints: (1) limited dispersal to adjacent areas, allowing dispersal between Guadalcanal and Greater Bougainville, Greater Bougainville and Bismarck Archipelago, and among the Bismarck Archipelago, Admiralty Archipelago, and New Guinea (Fig. 1), and (2) limited distribution of ancestral species to single regions or adjacent areas. These regions are arranged relatively linearly, and the positions of the regions relative to each other have remained similar for at least the past 30 million years (Fig. 2; Hall, 2001, 2002). Thus while individuals may occasionally disperse among regions, such as through rafting on vegetation mats, dispersal among non-adjacent regions seems unlikely, suggesting that these dispersal constraints seem reasonable. Additionally, because dispersal is expected to be limited among island groups in this region, dispersal events are likely associated with speciation events, thus the second constraint also seems reasonable. DEC requires a fully resolved, bifurcating phylogeny, therefore, these analyses were conducted using the resolved topology as described above.

2.6. Body size reconstruction, character displacement, and size assortment

Maximum recorded snout-vent length (SVL, from the tip of the snout to the cloaca) was used to estimate body size. Reported values were taken from the literature, and supplemented with our own measurements; maximum SVLs for each species, as well as references and sample sizes are presented in Table 2. Weighted squared-change parsimony (Maddison, 1991) are computationally equivalent to maximum likelihood-based methods (Schluter et al., 1997; Martins, 1999), therefore we implement maximum likelihood and generalized least squares (GLS, Martins and Hansen, 1997) to estimate ancestral body sizes. Maximum likelihood reconstructions were implemented using ANCML (Schluter et al., 1997); GLS was implemented in Compare v. 4.6b (Martins, 2004). Both these analyses require a fully resolved, bifurcating phylogeny, therefore the resolved topology (described above) was used.

To test for character displacement of body size, we calculated the estimated change in body size over nodes with daughter taxa predicted to occur sympatrically, and compared it to the estimated change over nodes predicted to occur allopatrically. We used a one-tailed *t*-test to examine if the change in body size was significantly greater between sympatric daughter taxa than between allopatric daughter taxa (Giannasi et al., 2000).

If size assortment is responsible for the observed body size distribution of *Tribolonotus*, we would predict that the minimum evolution phenogram based on body size would not be significantly worse than the reconstructed phylogeny. We used Mesquite ver. 2.6 (Maddison and Maddison, 2009) to create a single-linkage cluster topology of *Tribolonotus* based on body size, and using PAUP* ver. 4.0b10 (Swofford, 2003) and the PAUPup interface (Calendini and Martin, 2005) calculated the likelihood of the sequence data on this constrained phenogram and compared it to the maximum likelihood tree to determine if these topologies were not significantly different. We also tested this on the maximum parsimony tree by calculating the length of the sequence data on this constrained topology and compared it to that of the maximum parsimony tree.

To further test the hypotheses of size assortment and character displacement in a phylogenetic context, we used Pagel's λ (Pagel,

Table 2
Comparison of maximum snout-vent length (SVL) for the eight species of *Tribolonotus*. All values are in millimeters, and the number of individuals measured is presented in parentheses below each value.

Species	Maximum SVL	Reference
Tribolonotus annectens	49 ($n = 1$)	Zweifel (1966)
Tribolonotus blanchardi	40 ($n = 7$)	Zweifel (1966), this study
Tribolonotus brongersmai	64 ($n = 6$)	Cogger (1972), this study
Tribolonotus gracilis	103 ($n = 43$)	This study
Tribolonotus novaeguineae	103 ($n = 4$)	Klein et al. (2005), this study
Tribolonotus ponceleti	125 ($n = 3$)	Greer and Parker (1968)
Tribolonotus pseudoponceleti	76 ($n = 633$)	Greer and Parker (1968), this study
Tribolonotus schmidti	41 ($n = 35$)	Zweifel (1966)

1999; Freckleton et al., 2002) and Blomberg et al.'s phylogenetic signal statistic, K (Blomberg et al., 2003). Pagel's λ multiplies the internal branches in the phylogeny by the λ parameter; maximum likelihood is used to estimate the value of the λ scaling parameter that best fits the character given the topology. If the maximum likelihood value of λ is not significantly different from zero, this indicates that the evolution of the character is concentrated at the tips of the phylogeny, which, in this case, may be interpreted as support for character displacement due to the lack of phylogenetic signal. If the maximum likelihood value of λ is significantly greater than zero, this indicates the presence of phylogenetic signal in the data, which may be interpreted as evidence of size assortment. Pagel's λ was implemented using the ape package (Paradis et al., 2004) in R v 2.10.1; the maximum likelihood value of λ for body size was estimated and compared to the likelihood of the data given a λ of zero using a likelihood ratio test.

Blomberg et al.'s K is the ratio of the observed mean squared error (MSE) of the data and the tree divided by the observed MSE of the data and the MSE of the data and the tree divided by the MSE of the data estimated under a model of Brownian motion (Blomberg et al., 2003). Thus Blomberg et al.'s K takes on values from 0 to ∞, where values less than 1 indicates closely related species are less similar than expected under Brownian motion, as may be expected under the hypothesis of character displacement. Values of K greater than 1 indicate related species are more similar than expected under Brownian motion, as may be expected under the hypothesis of size assortment. To test for significance of phylogenetic signal in the data, a randomization test was used where the character data is randomly permuted on the tree, and the variance of phylogenetically independent contrasts is calculated for each of these random permutations to create a null distribution. The observed variance of phylogenetically independent contrasts was then compared to this null distribution using a one-tailed t-test (Blomberg et al., 2003). A significant difference under this randomization test would be indicative of phylogenetic signal in the data, in this case evidence of size assortment, whereas a lack of significance would indicate the data is no different from random, and thus a lack of phylogenetic signal, in this case evidence of character displacement. Blomberg et al.'s K and the randomization test for phylogenetic signal were implemented in the Picante package (Kembel et al., 2010) in R v. 2.10.1, with 1000 random permutations of the data for the randomization test.

3. Results

3.1. Phylogenetic analyses

The final aligned dataset was a total of 2252 bp; lengths of each partition, numbers of variable sites, and models of nucleotide substitution (selected using the AIC) are provided in Table 3. In both maximum likelihood and Bayesian inference, a scheme of seven partitions was selected as optimal using the AIC: mitochondrial 1st, 2nd, and 3rd codon positions, c-mos, phosducin, rhodopsin exon 4, and rhodopsin intron 4. Tracer plots of all parameters, posterior probabilities, and likelihood were stationary at similar values after the burn-in period for both Bayesian inference analyses, and all ESSs were substantially greater than 200 at run completion. Additionally, AWTY plots comparing the posterior probabilities of all splits were linear, indicating that Bayesian inference analyses had reached convergence. The phylogenetic reconstruction (Fig. 3) indicates that the genus is split into three main clades: (1) *T. blanchardi*, (2) a Melanesian islands clade (*T. brongersmai*, *T. ponceleti*, *T. pseudoponceleti*, and *T. schmidti*), and (3) a New Guinea clade (*T. gracilis* and *T. novaeguineae*). These three clades appear to have diverged rapidly from each other, resulting in a short internode that is difficult to resolve and is poorly supported (Bayesian posterior probability = 0.94, maximum likelihood bootstrap support = 53). The monophyly of each species is strongly supported and all other species-level relationships are well resolved and strongly supported (Bayesian posterior probability >0.98, maximum likelihood bootstrap support >75).

Table 3
Lengths and number of variable sites for each partition in the optimal partitioning scheme. For mitochondrial loci, the total partition length is given, followed by length in cyt b and ND2, respectively, in parentheses.

Partition	Length	No. Variable Sites	Model
mt pos. 1	274 (126 + 148)	53 (19 + 34)	GTR+G
mt pos. 2	275 (127 + 148)	18 (4 + 14)	GTR+I
mt pos. 3	274 (126 + 148)	177 (78 + 99)	GTR+I+G
C-mos	417	22	HKY+I
Phos	441	14	K80
Rhod exon	152	2	JC
Rhod intron	419	38	HKY

3.2. Biogeography

Biogeographic reconstructions using maximum likelihood state reconstructions (Fig. 4) and DEC (Table 4) produced similar results. Several nodes had multiple probable distributions possible (probability >0.1); most ambiguous nodes had high probability of occurrence in New Guinea or Greater Bougainville, as may be expected due to the higher diversity in Greater Bougainville and the basal placement of the New Guinean species of *Tribolonotus*. The maximum likelihood reconstructions estimated the most basal node as most likely occurring in Greater Bougainville ($p = 0.514$), New Guinea ($p = 0.292$) or Guadalcanal (0.123). The DEC analyses reconstructed the most basal node as most likely a split between the Bismarcks and Greater Bougainville ($p = 0.4371$), between New Guinea and the Bismarcks ($p = 0.1616$) or Bismarcks and Bismarcks + Greater Bougainville ($p = 0.1381$). Both analyses suggest the geographic origin of *Tribolonotus* was most likely in either New Guinea or Greater Bougainville.

3.3. Body size reconstructions, character displacement, and size assortment

Results of the ancestral state reconstructions of body size (Table 5), estimate that the two smallest species, *T. blanchardi* and *T. schmidti*, which are similar in maximum SVL (40 and 41 mm, respectively) experienced an independent and parallel decrease in body size. Similarly, the largest lineages, *T. ponceleti* and the clade of *T. gracilis* + *T. novaeguineae*, experienced an independent and parallel increase in body size.

The phylogenetic test for character displacement found no significant difference in the change in body size between sympatric (25.47 ± 25.56 mm) and allopatric (29.11 ± 4.50 mm) sister branches ($p = 0.587$). The similarity in size between the sympatric New Guinean species (*T. gracilis* and *T. novaeguineae*) may skew the estimate for sympatric body size change down, however, excluding the New Guinea species, the difference in body size between sympatric (38.20 ± 15.27 mm) and allopatric (29.11 ± 4.50 mm) species is still not significant ($p = 0.787$). The test for size assortment found the body size similarity phenogram was significantly worse than either the maximum likelihood ($-\ln L = 7301.831$ versus 8235.548) or the maximum parsimony (791 versus 1094 steps) topologies, indicating that size assortment is not the primary cause of body size evolution in *Tribolonotus*. The maximum likelihood estimation of Pagel's λ found the most likely value of λ for the data to be 1.0×10^{-7}; using the likelihood ratio test, this was not significantly different from $\lambda = 0$ ($P = 0.997$), which supports the hypothesis of character displacement. Blomberg et al.'s K was 0.6592, indicating species are less similar then expected un-

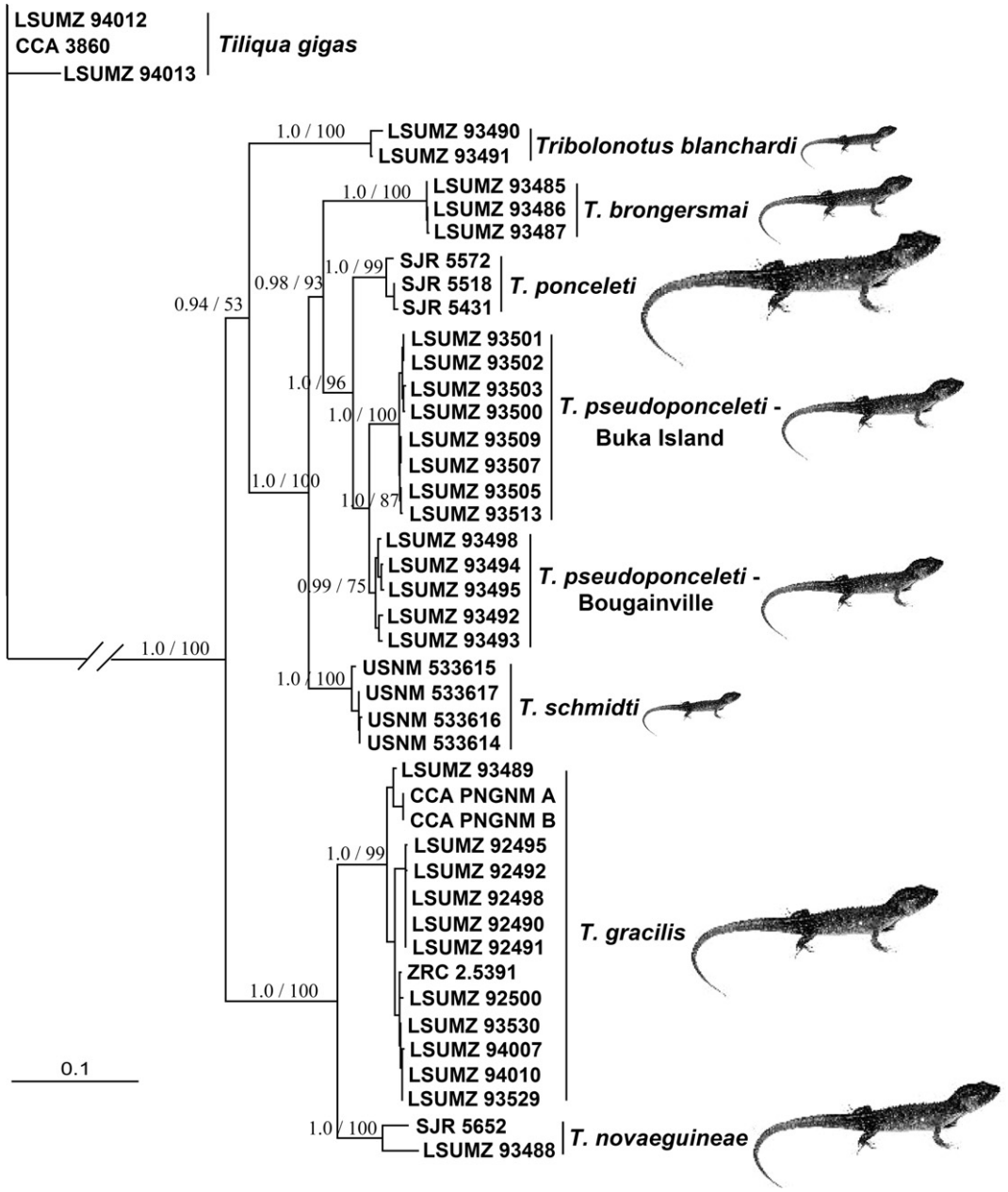

Fig. 3. Phylogeny of *Tribolonotus* based on partitioned maximum likelihood analysis of 2252 bp of cyt b, ND2, C-mos, Phosducin and Rhodopsin. Numbers above nodes represent posterior probabilities from Bayesian analyses followed by maximum likelihood bootstrap support from 1000 replicates.

der a Brownian motion model, which further supports character displacement. The randomization test also indicated that body size was not significantly different from random ($P = 0.267$), indicating a lack of phylogenetic signal in the body size data, as expected under the hypothesis of character displacement.

4. Discussion

4.1. Biogeography

Biogeographic reconstructions suggest that *Tribolonotus* radiated primarily on Greater Bougainville. The geographic region of origin for the genus is uncertain; however, the origin is likely either New Guinea, which would involve a single colonization event of Greater Bougainville from New Guinea, or on Greater Bougainville, which would involve a single basal colonization event of New Guinea. In either scenario, *T. brongersmai*, which is endemic to the Admiralty Archipelago originated via colonization from Greater Bougainville, rather than New Guinea as current geographic proximity would suggest. Similarly *T. schmidti*, which is endemic to Guadalcanal, was found to have originated via a single colonization event from Greater Bougainville. It is clear, however, that the biogeography of *Tribolonotus* is not explained by a simple stepping stone model either eastward from New Guinea to the Admiralty Archipelago to the Bismarcks to the Solomons, or westward in the opposite direction, but rather involves more complexities of both eastward and westward dispersal events.

We were unable to obtain samples of *Tribolonotus annectans*, a species endemic to New Britain and known only from two specimens, and thus the phylogenetic placement of this species is unclear. However, based on these biogeographic reconstructions, it is possible to predict that *T. annectans* represents the sister species to *T. brongersmai*, and the two species originated via dispersal to New Britain from Greater Bougainville and subsequent coloniza-

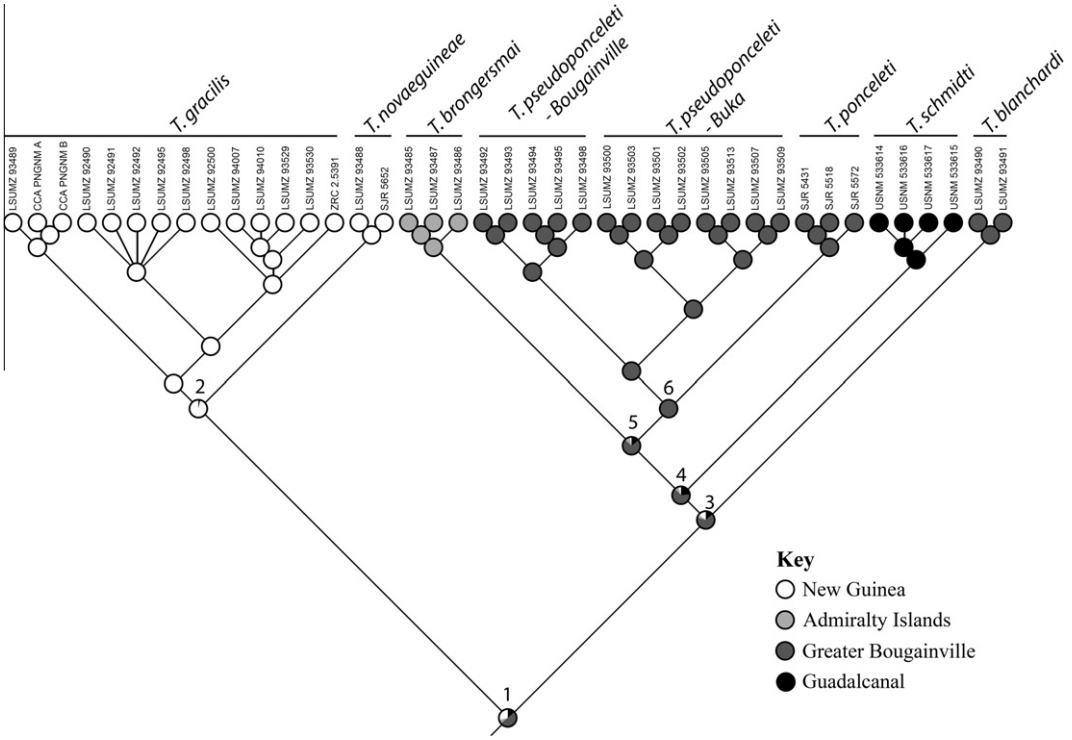

Fig. 4. Maximum Likelihood reconstructions of ancestral distributions. Colors correspond to distributions as follows: White, New Guinea; Light Grey, Admiralty Islands; Dark Grey, Greater Bougainville; Black, Guadalcanal.

Table 4
Results of DEC reconstructions of ancestral distributions. Distributions with probabilities above 0.1 shown. Node numbers correspond to those on Fig. 3. For distributions, values on left correspond to the left branches of Fig. 3, values on the right correspond to the right branches. Ancestral distributions abbreviated as: New Guinea (N), Admiralty Islands (A), Bismarck Islands (Bi), Greater Bougainville (Bo), and Guadalcanal (G).

Node	Distribution	Probability
1	[Bi|Bo]	0.437
	[N|Bi]	0.162
	[Bi|BiBo]	0.138
2	[N|N]	0.744
	[N|NBi]	0.118
	[NBi|N]	0.102
3	[Bo|Bo]	0.558
	[BiBo|Bo]	0.173
4	[Bo|G]	0.391
	[BiBo|Bo]	0.287
	[Bo|Bo]	0.193
5	[Bi|Bo]	0.518
	[Bo|Bo]	0.312
6	[Bo|Bo]	0.962

Table 5
Results of body size reconstructions. Node numbers correspond to those on Fig. 3. All values for reconstruction estimates and standard error (SE) are in millimeters.

Node	ML estimate	GLS estimate	GLS SE
1	73.03	73.03	14.67
2	96.44	96.44	10.00
3	67.11	67.11	8.73
4	67.40	67.40	10.06
5	74.53	74.53	10.57
6	88.49	88.49	7.89

tion of the Admiralty Archipelago from New Britain. The overall morphological similarity of *T. annectens* and *T. brongersmai* would support this hypothesis (Zweifel, 1966; Cogger, 1972).

4.2. Body size evolution

We find no significant evidence for size assortment in *Tribolonotus*, as evidenced by the significantly worse fit of the body size phenogram to the molecular data and the lack of evidence for phylogenetic signal in the body size data using Pagel's λ or Blomberg et al.'s *K*. Additionally, we found evidence for parallel and independent change in body size in several taxa on different islands, which is consistent with character displacement but not with size assortment. These data suggest that character displacement may be responsible for body size evolution in this genus. However, we found no significant evidence for character displacement in our tests comparing differences in body size between allopatric and sympatric taxa, although there is a non-significant trend for greater body size difference between allopatric species when excluding the New Guinea species (*T. gracilis* and *T. novaeguineae*). Several mechanisms may explain this apparently contradictory evidence for character displacement. In the test for character displacement by comparing body size differences between allopatric and sympatric species, there may be a lack of statistical power resulting from the small number of species in the genus. The trend of greater body size differences between sympatric species when excluding the New Guinea species supports that lack of statistical power may explain this apparently contradictory evidence. Ecological difference may also explain the conflicting evidence for character displacement. Sympatric species of *Tribolonotus* may occur in different microhabitats, resulting in minimal interspecific competition within the genus, thus body size differences may be unrelated to relieving competition. This may be the case in the New Guinea species, *T. gracilis* and *T. novaeguineae*, as these species are broadly sympatric and exhibit little difference in body size. However as little in known of the ecology of the genus, it is difficult to determine the importance of ecological differences. Thirdly, only *Tribolonotus* were included in the tests for character displacement and size assortment, therefore if competition with species in other genera

not included in the analyses is driving evolution of body size in *Tribolonotus* by either size assortment or character displacement, this could result in the observed absence of statistical significance. Finally, competition with extinct or undiscovered congeneric species may have driven the evolution of body size in *Tribolonotus*. New Guinea and the Solomon Islands are thought to harbor a large number of undiscovered species (Allison, 1996; McCoy, 2006), thus competition with unknown or now extinct species may have played an important role in the evolution of body size in *Tribolonotus*. As these unknown species were not included in the analyses, this could result in a bias in the estimates of body size differences between sympatric and allopatric species, and thus the lack of significant evidence for character displacement. The evidence for parallel and independent evolution of body size despite the relatively small number of species in the genus suggests that the assumptions of size assortment would not be met even if a number of species were excluded from analyses, as unsampled species would not explain this pattern, thus regardless of the explanation for the contradictory evidence for character displacement, this hypothesis seems more likely than size assortment. Further investigation into the ecology of *Tribolonotus* and sympatric species may help elucidate the important competitors for each species of *Tribolonotus*, and thus help determine which of these mechanisms is most likely. It should be noted that these hypotheses are not necessarily mutually exclusive. Character displacement, combined with ecological differences between *T. gracilis* and *T. novaeguineae*, may best explain the lack of body size difference between the sympatrically distributed *T. gracilis* and *T. novaeguineae* in New Guinea and the trend for greater body size difference between sympatric species when excluding these New Guinean species. The lack of significance in the body size differences despite character displacement may be best explained by a lack of statistical power and/or competition with unsampled species (due to extinction or undiscovered species). Thus a combination of character displacement and ecological differences between *T. gracilis* and *T. novaeguineae* may be the best explanation for the observed patterns of body size evolution in *Tribolonotus*.

4.3. Taxonomic implications

Previous studies have suggested that *T. gracilis* may represent a junior synonym of *T. novaeguineae*, as several of the distinguishing characters of these species have been shown to be invalid in larger sample sizes (Zweifel, 1966; Cogger, 1972). However we find these taxa to be reciprocally monophyletic with strong support and deeply divergent, indicating that they do in fact represent distinct species. Additionally, we find reciprocally monophyletic divergence between the Bougainville and Buka populations of *T. pseudoponceleti* and we are currently in the process of investigating the morphological variation of these two populations to determine if they may represent distinct species.

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Appendix 1

Sampling localities and GenBank accession numbers for all included samples. 'PNG' refers to Papua New Guinea.

Species	Catalogue number	Locality	Latitude	Longitude	GenBank accession numbers				
					cyt b	ND2	C-mos	Phos	Rhod
Ingroups									
Tribolonotus blanchardi	LSUMZ 93490	PNG: Bougainville	5° 56.411′ S	155° 2.410′ E	HM229492	HM229448	HM229536	HM229580	HM229624
T. blanchardi	LSUMZ 93491	PNG: Bougainville	5° 56.411′ S	155° 2.410′ E	HM229493	HM229449	HM229537	HM229581	HM229625
T. brongersmai	LSUMZ 93485	PNG: Manus Is.	2° 05.76′ S	147° 06.33′ E	HM229486	HM229442	HM229530	HM229574	HM229618
T. brongersmai	LSUMZ 93486	PNG: Manus Is.	2° 05.76′ S	147° 06.33′ E	HM229487	HM229443	HM229531	HM229575	HM229619
T. brongersmai	LSUMZ 93487	PNG: Manus Is.	2° 05.76′ S	147° 06.33′ E	HM229488	HM229444	HM229532	HM229576	HM229620
T. gracilis	CCA PNGNM A	PNG: Madang: Kar Kar Is.	4° 39′ S	145° 58′ E	HM229518	HM229474	HM229562	HM229606	HM229650
T. gracilis	CCA PNGNM B	PNG: Madang: Kar Kar Is.	4° 39′ S	145° 58′ E	HM229519	HM229475	HM229563	HM229607	HM229651
T. gracilis	LSUMZ 93489	PNG: Madang: Kau	5° 09.36′ S	145° 46.57′ E	HM229485	HM229441	HM229529	HM229573	HM229617
T. gracilis	LSUMZ 92490	PNG: Sandaun: Utai Village	3° 23.765′ S	141° 34.974′ E	HM229506	HM229462	HM229550	HM229594	HM229638
T. gracilis	LSUMZ 92491	PNG: Sandaun: Utai Village	3° 23.765′ S	141° 34.974′ E	HM229507	HM229463	HM229551	HM229595	HM229639
T. gracilis	LSUMZ 92492	PNG: Sandaun: Utai Village	3° 23.765′ S	141° 34.974′ E	HM229508	HM229464	HM229552	HM229596	HM229640

T. gracilis	LSUMZ 92495	PNG: Sandaun: Utai Village	3° 23.765′ S	141° 34.974′ E	HM229510	HM229466	HM229554	HM229598	HM229642
T. gracilis	LSUMZ 92498	PNG: Sandaun: Utai Village	3° 23.765′ S	141° 34.974′ E	HM229511	HM229467	HM229555	HM229599	HM229643
T. gracilis	LSUMZ 92500	PNG: Sandaun: Bewani	3° 03.224′ S	141° 10.009′ E	HM229512	HM229468	HM229556	HM229600	HM229644
T. gracilis	LSUMZ 94007	Indonesia: West Papua			HM229514	HM229470	HM229558	HM229602	HM229646
T. gracilis	LSUMZ 94010	Indonesia: West Papua			HM229515	HM229471	HM229559	HM229603	HM229647
T. gracilis	LSUMZ 93529	Indonesia: West Papua			HM229516	HM229472	HM229560	HM229604	HM229648
T. gracilis	LSUMZ 93530	Indonesia: West Papua			HM229517	HM229473	HM229561	HM229605	HM229649
T. gracilis	ZRC 2.5391	Indonesia: West Papua			HM229528	HM229484	HM229572	HM229616	HM229660
T. novaeguineae	LSUMZ 93488	PNG: Sandaun: Waromo	2° 40.092′ S	141° 14.652′ E	HM229489	HM229445	HM229533	HM229577	HM229621
T. novaeguineae	SJR 5652	Indonesia: West Papua			HM229523	HM229479	HM229567	HM229611	HM229655
T. ponceleti	SJR 5431	Solomon Islands			HM229520	HM229476	HM229564	HM229608	HM229652
T. ponceleti	SJR 5518	Solomon Islands			HM229521	HM229477	HM229565	HM229609	HM229653
T. ponceleti	SJR 5572	Solomon Islands			HM229522	HM229478	HM229566	HM229610	HM229654
T. pseudoponceleti	LSUMZ 93492	PNG: Bougainville	5° 57.623′ S	155° 04.757′ E	HM229490	HM229446	HM229534	HM229578	HM229622
T. pseudoponceleti	LSUMZ 93493	PNG: Bougainville	5° 57.623′ S	155° 04.757′ E	HM229491	HM229447	HM229535	HM229579	HM229623
T. pseudoponceleti	LSUMZ 93494	PNG: Bougainville	5° 56.411′ S	155° 02.410′ E	HM229494	HM229450	HM229538	HM229582	HM229626
T. pseudoponceleti	LSUMZ 93495	PNG: Bougainville	5° 56.411′ S	155° 02.410′ E	HM229495	HM229451	HM229539	HM229583	HM229627
T. pseudoponceleti	LSUMZ 93498	PNG: Bougainville	5° 56.411′ S	155° 02.410′ E	HM229496	HM229452	HM229540	HM229584	HM229628
T. pseudoponceleti	LSUMZ 93500	PNG: Buka Is.	5° 23.445′ S	154° 38.456′ E	HM229497	HM229453	HM229541	HM229585	HM229629
T. pseudoponceleti	LSUMZ 93501	PNG: Buka Is.	5° 23.445′ S	154° 38.456′ E	HM229498	HM229454	HM229542	HM229586	HM229630
T. pseudoponceleti	LSUMZ 93502	PNG: Buka Is.	5° 23.445′ S	154° 38.456′ E	HM229499	HM229455	HM229543	HM229587	HM229631
T. pseudoponceleti	LSUMZ 93503	PNG: Buka Is.	5° 23.445′ S	154° 38.456′ E	HM229500	HM229456	HM229544	HM229588	HM229632
T. pseudoponceleti	LSUMZ 93505	PNG: Buka Is.	5° 23.355′ S	154° 39.109′ E	HM229501	HM229457	HM229545	HM229589	HM229633
T. pseudoponceleti	LSUMZ 93507	PNG: Buka Is.	5° 23.355′ S	154° 39.109′ E	HM229502	HM229458	HM229546	HM229590	HM229634
T. pseudoponceleti	LSUMZ 93509	PNG: Buka Is.	5° 23.355′ S	154° 39.109′ E	HM229503	HM229459	HM229547	HM229591	HM229635
T. pseudoponceleti	LSUMZ 93513	PNG: Buka Is.	5° 23.355′ S	154° 39.109′ E	HM229504	HM229460	HM229548	HM229592	HM229636
T. schmidti	USNM 533614	Solomon Is.: Guadalcanal	9° 25.7′ S	160° 04.1′ E	HM229524	HM229480	HM229568	HM229612	HM229656
T. schmidti	USNM 533615	Solomon Is.: Guadalcanal	9° 25.7′ S	160° 04.1′ E	HM229525	HM229481	HM229569	HM229613	HM229657
T. schmidti	USNM 533616	Solomon Is.: Guadalcanal	9° 25.7′ S	160° 04.1′ E	HM229526	HM229482	HM229570	HM229614	HM229658
T. schmidti	USNM 533617	Solomon Is.: Guadalcanal	9° 25.7′ S	160° 04.1′ E	HM229527	HM229483	HM229571	HM229615	HM229659
Outgroups									
Tiliqua gigas	LSUMZ 94012	PNG: National Capitol District	9° 24.960′ S	147 °08.660′ E	HM229505	HM229461	HM229549	HM229593	HM229637
T. gigas	LSUMZ 94013	PNG: Sandaun: Utai Village	3° 23.765′ S	141° 34.974′ E	HM229509	HM229465	HM229553	HM229597	HM229641
T. gigas	CCA 3860	PNG: National Capitol District	9° 27.829′ S	147° 09.25′ E	HM229513	HM229469	HM229557	HM229601	HM229645

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