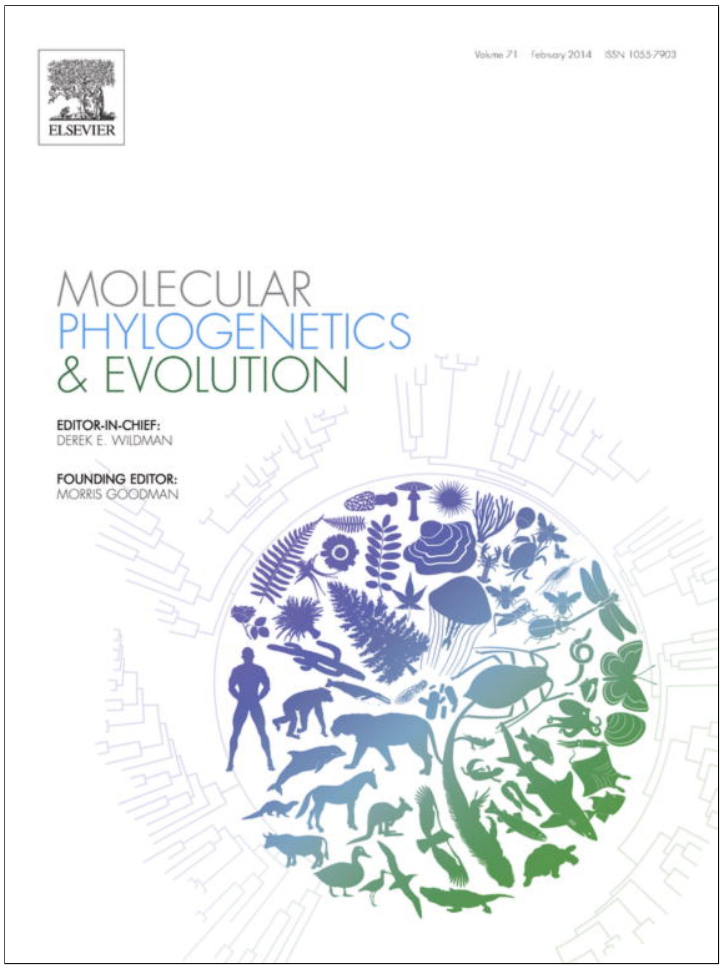

Molecular Phylogenetics and Evolution 71 (2014) 149–156

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

A multi-locus molecular phylogeny for Australia's iconic Jacky Dragon (Agamidae: *Amphibolurus muricatus*): Phylogeographic structure along the Great Dividing Range of south-eastern Australia

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ARTICLE INFO

Article history:
Received 25 June 2013
Revised 14 November 2013
Accepted 20 November 2013
Available online 6 December 2013

Keywords:
Great Dividing Range
Phylogeography
Reptile
Agamidae
Eastern Australia
*BEAST

ABSTRACT

Jacky dragons (*Amphibolurus muricatus*) are ubiquitous in south-eastern Australia and were one of the first Australian reptiles to be formally described. Because they are so common, Jacky dragons are widely used as a model system for research in evolutionary biology and ecology. In addition, their distribution along the Great Dividing Range of eastern Australia provides an opportunity to examine the influence of past biogeographical processes, particularly the expansion and contraction of forest habitats, on the diversification of this iconic agamid lizard. We generated sequence data for two mitochondrial and three nuclear DNA loci (4251base pairs) for 62 Jacky dragons sampled from throughout their distribution. Phylogenetic analyses based on maximum likelihood and Bayesian species-tree methods revealed five geographically structured clades separated by up to 6% mitochondrial and 0.7% nuclear sequence divergence. We also quantified body proportion variation within and between these genetic clades for more than 500 specimens and found no evidence of any significant differentiation in body proportions across their range. Based on body proportion homogeneity and lack of resolution in the nuclear loci, we do not support taxonomic recognition of any of the mitochondrial clades. Instead, *A. muricatus* is best thought of as a single species with phylogeographic structure. The genetic patterns observed in the Jacky dragon are consistent with fragmented populations reduced to multiple refugia during cold, arid phases when forested habitats were greatly restricted. Consequently, the inferred biogeographic barriers for this taxon appear to be in line with lowland breaks in the mountain ranges. Our results are congruent with studies of other reptiles, frogs, mammals, birds and invertebrates, and together highlight the overarching effects of widespread climatic and habitat fluctuations along the Great Dividing Range since the Pliocene.

1. Introduction

The Jacky dragon, *Amphibolurus muricatus* White, ex Shaw 1790, is a widespread and abundant agamid lizard found throughout the temperate and coastal habitats of south-eastern Australia (Cogger, 2000). Its distribution includes the location of the first Australian settlement in Port Jackson (Sydney Harbour) in 1788, and the Jacky dragon (along with five other lizards) was among the first Australian reptiles to be formally described in a published diary of Surgeon General John White (White, 1790).

Because they are so common and easy to rear in captivity, Jacky dragons have become a popular model system for exploring diverse evolutionary questions relating to complex visual signals (Peters and Ord, 2003; Peters and Evans, 2007; Van Dyk and Evans, 2007; Hoese et al., 2008; Peters, 2008; Woo et al., 2009; Woo and Rieucau, 2013), temperature-dependent sex determination (Harlow and Taylor, 2000; Warner and Shine, 2008, 2011) and other aspects of reproductive ecology (Warner et al., 2007, 2010; Radder et al., 2007a; Shine et al., 2007), physiology (Heatwole et al., 1973; Heatwole and Firth, 1982; Watt et al., 2003; Warner and Shine, 2006; Radder et al., 2007b), and habitat fragmentation (Bragg et al., 2005; Hitchen et al., 2011). Despite this body of work, no phylogenetic hypothesis of relationships among populations from throughout their range has been available for interpreting these data in an evolutionary context.

In addition, the broad distribution of Jacky dragons down the eastern and south-eastern margins of Australia, encompassing vast differences in climate and habitat, makes them an ideal system for examining emerging patterns concerning the biogeography of the Great Dividing Range – a chain of mountain systems forming the dominant topographic feature in eastern Australia. It is well known that climatic conditions during glacial cycles were colder and drier

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http://dx.doi.org/10.1016/j.ympev.2013.11.012

in the tropics (Hewitt, 2000), leading to the expansion of deserts and savannah while reducing rain forests. Along the humid margins of eastern Australia, geological and palaeontological records show cycles of rainforest expansion and contraction in line with glacial and interglacial oscillations (Nix, 1982; Markgraf et al., 1995). Evidence of extensive sand dune activity also has been discovered beneath these presently forested regions, indicating substantially drier conditions during the Last Glacial Maximum (LGM) (Thom et al., 1994; Hesse et al., 2003). Genetic studies of numerous taxa along the Great Dividing Range show congruent phylogenetic patterns indicative of persistence in higher elevation mesic refugia during more arid phases, with deep genetic breaks across lowland areas inferred to be historically dry biogeographic barriers to dispersal (eg. Horton, 1972; Schäuble and Moritz, 2001; Chapple et al., 2005; Bell et al., 2010; Milner et al., 2012). In addition, topographic barriers such as mountain ranges, river valleys or disjunct upland regions also are thought to have played an important role in shaping the evolutionary history of modern biota in this region (Chapple et al., 2011; Pavlova et al., 2013).

Understanding the genetic structure and relationships between populations of Jacky dragons is long overdue. Recent phylogenetic studies have placed *A. muricatus* within the *Amphibolurus* group of the Australian agamid radiation Amphibolurinae (Schulte et al., 2003; Hugall et al., 2008). This clade comprises its sister taxon *Amphibolurus norrisi*, in addition to *Amphibolurus gilberti* and the iconic frill-necked lizard *Chlamydosaurus kingii*. More recently, Melville et al. (2011) sequenced a number of *A. muricatus* from the northern and southern parts of their range, and found structure in both the *nd2* mtDNA and the nDNA *rag1* loci, highlighting the need for further study and increased sampling. Here we present a comprehensive phylogeny based on five loci and a detailed morphological data set for the Jacky dragon. In addition we compare our results to other published studies to assess the history of species diversification and historical biogeography along the Great Dividing Range of Eastern Australia.

2. Materials and methods

2.1. Taxonomic sampling

We obtained sequence data from 62 *A. muricatus* (Table 1). We collected specimens from Victoria and New South Wales between 2011 and 2012, and the remaining samples were obtained for all unique localities that were available from the collections of Museum Victoria (MV), the South Australian Museum (SAM) and the Australian Museum (AM). We were unable to obtain material from Queensland, where, except on the Granite Belt along the southern border where it is a common lizard, *A. muricatus* is otherwise a rare species in the remainder of the State (R. Hobson, Queensland Parks & Wildlife Service, pers. comm., and see Atlas of Living Australia records). We also included Genbank data from previous studies including *nd2* sequences for nine *A. norrisi* (Melville et al., 2011), as well as for twelve outgroup taxa for four of the five genes used in this study (*nd2*, *nd4*, *bdnf*, *rag1*) (see Appendix Table 1 for all Genbank material used in this study).

2.2. DNA amplification and sequencing

We collected new sequence data for five loci: two mitochondrial (*nd2* and *nd4*) and three protein-coding nuclear (*rag1*, *bdnf* and *prlr*). The data matrix for *A. muricatus* samples is 98% complete, and of the twelve outgroup taxa, all are missing *prlr*, and 10 are missing *nd4*. All new sequences from this study are deposited on Genbank (KF871470-KF871767).

Genomic DNA was extracted from approximately 1 mm^3 of tissue (either a tail tip or liver sample stored in 100% ethanol) using the EDNA HiSpEx tissue kit (Chaga), following the manufacturers protocols. PCR amplification was performed using a Corbett PC-960C cooled thermal cycler and negative controls were run for all amplifications. Amplification of all loci was conducted with an activation step at 94 °C for 3 min followed by 10 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 30 s, and extension at 72 °C for 90 s, with a further 25 cycles of denaturation at 94 °C for 30 s, annealing at 50 °C for 30 s, and extension at 72 °C for 90 s, followed by a final extension step at 72 °C for 5 min. PRC amplification was performed in a 25 μl reaction mix consisting of 12.5 μl GoTaq (Promega), 10.5 μl double-distilled water, 1.0 μl for both forward and reverse primers (10 pmol) and 1 μl of template DNA. We purified successful PCR amplifications using 0.4 μl Exonuclease 1 (New England BioLabs), 1.6 μl Shrimp Alkaline Phosphatase (GE Healthcare) and 3 μl double-distilled water along with 5 μl undiluted PCR product. For cycle-sequencing reactions and purification see the protocols of Pepper et al. (2006). The PCR/Sequencing primer combinations used in this study are listed in Table 2.

Sequences were edited and contigs were assembled in SEQUENCHER v. 4.10.1 (Gene Codes Corporation). Alignment of sequences was first performed automatically using the software MUSCLE (Edgar, 2004), then refined by eye in Se–Al (Rambaut, 1996). The few heterozygotes found in the nDNA genes were coded as such in the alignments prior to analyses. Protein-coding regions were translated into amino acid sequences and were checked for internal stop codons and frame-shift mutations.

2.3. Analysis of sequence data

Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian methods. Initially, ML analyses of individual gene trees were performed in RAxML-VI-HPC v7.0.4 (Stamatakis, 2006). We then concatenated the data and partitioned the combined dataset by gene. Each analysis implemented the general time-reversible substitution model with gamma-distributed rates among sites (GTR + G), with the best ML tree determined using 20 distinct randomized Maximum Parsimony (MP) starting trees. Bootstrap support was determined using 1000 replicates.

In addition to our concatenated ML approach, we used the hierarchical model implemented in *BEAST v. 1.7.5 (Heled and Drumond, 2010), that co-estimates the species tree and all gene trees in one Bayesian MCMC analysis, to estimate the species tree phylogeny. This method requires *a priori* designation of species or groups, so we divided our data based on the five genetic clades identified in our concatenated likelihood analysis, along with the outgroups that were all coded as separate species. Models for each gene were inferred using PartitionFinder (Lanfear et al., 2012) under the Bayesian Information Criterion. For *nd2* and *nd4*, the TVM + I + G substitution model was chosen, while for *rag1*, *bdnf* and *prlr* the K81uf (equivalent to K3Puf) + I substitution model was chosen. The TVM and K3Puf substitution models are not available in the BEAST package so we modified the xml code for the GTR substitution model to accommodate changes to the model parameters (http://beast.bio.ed.ac.uk/Substitution_model_code). We unlinked loci and substitution models, employed a relaxed-clock model, and used a Yule tree prior. For the mean rate priors for the relaxed clock model, we specified a normal distribution with a lower bound of 1e-6 for the mtDNA genes, and 1e-3 for the nDNA loci, both with an upper bound of 1. We conducted four separate runs, with samples drawn every 10,000 steps over a total of 100,000,000 steps, with the first 10% discarded as burn-in. Acceptable convergence to the stationary distribution was checked by inspecting the posterior samples using the diagnostic software Tracer v1.5 (Rambaut and Drummond, 2007). Effective sample sizes

Table 1
Museum accession numbers and collection locality information for all individuals sampled in this study. MB = Marco Barquero, LS = Lisa Schwanz.

CLADE	LAB#	Registration Number	Institution	Scientific name	State/territory	Locality	Latitude	Longitude
A	J03	R167627	Australian Museum	*Amphibolurus muricatus*	New South Wales	Tenterfield region	−29.07333	151.91278
A	J06	R148385	Australian Museum	*Amphibolurus muricatus*	New South Wales	Gibraltar Range National Park	−29.51389	152.34333
A	J07	R148375	Australian Museum	*Amphibolurus muricatus*	New South Wales	Gibraltar Range National Park	−29.53306	152.32361
A	J09	R153806	Australian Museum	*Amphibolurus muricatus*	New South Wales	Werrikimbe National Park	−31.10000	152.23333
A	J11	R156613	Australian Museum	*Amphibolurus muricatus*	New South Wales	Limbri	−31.00278	151.19500
A	J12	R157019	Australian Museum	*Amphibolurus muricatus*	New South Wales	Yarrowick Area	−30.47250	151.37139
A	J13	R157211	Australian Museum	*Amphibolurus muricatus*	New South Wales	Forestlands State Forest	−29.23944	152.10306
A	J14	R157215	Australian Museum	*Amphibolurus muricatus*	New South Wales	Tenterfield, Gunyah road	−29.11556	151.88694
A	J15	R157220	Australian Museum	*Amphibolurus muricatus*	New South Wales	Bolivia	−29.33722	151.89444
A	J16	R157222	Australian Museum	*Amphibolurus muricatus*	New South Wales	33.5 Km E Glen Innes	−29.51111	152.04944
A	J18	R159678	Australian Museum	*Amphibolurus muricatus*	New South Wales	Glen Innes	−29.51111	152.04944
A	J32	SAMAR34730	South Australian Museum	*Amphibolurus muricatus*	New South Wales	Lily Creek	−30.80000	151.30000
A	J33	SAMAR39022	South Australian Museum	*Amphibolurus muricatus*	New South Wales	Retreat	−30.68333	150.23333
B	J10	R.156047.001	Australian Museum	*Amphibolurus muricatus*	New South Wales	Warrumbungle National Park	−31.32889	148.99667
B	J25	SAMAR34771	South Australian Museum	*Amphibolurus muricatus*	New South Wales	Coonabarabran	−31.25000	149.13333
B	J27	SAMAR34769	South Australian Museum	*Amphibolurus muricatus*	New South Wales	Coonabarabran	−31.25000	149.13333
B	J31	SAMAR39147	South Australian Museum	*Amphibolurus muricatus*	New South Wales	Brayton	−34.56667	149.98333
B	J34	A1	MB collection	*Amphibolurus muricatus*	Victoria	Mt. Nowa Nowa	−37.69157	148.09131
B	J35	A2	MB collection	*Amphibolurus muricatus*	Victoria	Mt. Nowa Nowa	−37.69157	148.09131
B	J36	A3	MB collection	*Amphibolurus muricatus*	Victoria	Mt. Nowa Nowa	−37.69157	148.09131
B	J37	A4	MB collection	*Amphibolurus muricatus*	Victoria	Cape Conran	−37.81180	148.72918
B	J38	A5	MB collection	*Amphibolurus muricatus*	Victoria	Cann River area	−37.61691	149.14502
B	J39	A6	MB collection	*Amphibolurus muricatus*	Victoria	Cann River area	−37.62601	149.13962
B	J40	A7	MB collection	*Amphibolurus muricatus*	Victoria	Cann River area	−37.59713	149.16162
B	J41	A8	MB collection	*Amphibolurus muricatus*	Victoria	Cann River area	−37.60382	149.15379
B	J42	A9	MB collection	*Amphibolurus muricatus*	Victoria	Genoa Peak	−37.48377	149.57635
B	J48	B6	MB collection	*Amphibolurus muricatus*	Victoria	Mt. Nowa Nowa	−37.69157	148.09131
B	J53	C2	MB collection	*Amphibolurus muricatus*	Victoria	Cann River area	−37.59471	149.16295
C	J01	R172498	Australian Museum	*Amphibolurus muricatus*	New South Wales	Faulconbridge	−33.69250	150.53306
C	J02	R171161	Australian Museum	*Amphibolurus muricatus*	New South Wales	Singleton area	−32.55972	151.35194
C	J04	R146138	Australian Museum	*Amphibolurus muricatus*	New South Wales	Holsworthy Training Area	−34.00250	150.93667
C	J05	R147368	Australian Museum	*Amphibolurus muricatus*	New South Wales	Bird Island Nature Reserve	−33.21667	151.60000
C	J08	R150447	Australian Museum	*Amphibolurus muricatus*	New South Wales	Chifley	−33.95000	151.23333
C	J17	R157299	Australian Museum	*Amphibolurus muricatus*	New South Wales	Scheyville Road	−33.60278	150.85333
C	J43	B1	MB collection	*Amphibolurus muricatus*	New South Wales	Royal National Park	−34.08327	151.02509
C	J44	B2	MB collection	*Amphibolurus muricatus*	New South Wales	Royal National Park	−34.08172	151.02557
C	J45	B3	MB collection	*Amphibolurus muricatus*	New South Wales	Botany Bay	−33.99244	151.23925
C	J46	B4	MB collection	*Amphibolurus muricatus*	New South Wales	Botany Bay	−33.99294	151.23916
C	J47	B5	MB collection	*Amphibolurus muricatus*	New South Wales	Botany Bay	−33.99509	151.24012
C	J49	B7	MB collection	*Amphibolurus muricatus*	New South Wales	Royal National Park	−34.08038	151.09471
C	J50	B8	MB collection	*Amphibolurus muricatus*	New South Wales	Yarratt Taree	−31.82128	152.42461
C	J51	B9	MB collection	*Amphibolurus muricatus*	New South Wales	Yarratt Taree	−31.80483	152.43264
C	J52	C1	MB collection	*Amphibolurus muricatus*	New South Wales	Yarratt Taree	−31.82108	152.42464
C	J54	C3	MB collection	*Amphibolurus muricatus*	New South Wales	Yarratt Taree	−31.80764	152.42611
C	J55	AMC1	LS collection	*Amphibolurus muricatus*	New South Wales	Wirreanda Rd, Wamboin	−35.252914	149.342941
C	J56	AMA5C2	LS collection	*Amphibolurus muricatus*	New South Wales	Wirreanda Rd, Wamboin	−35.224514	149.35199
C	J57	AMD2	LS collection	*Amphibolurus muricatus*	New South Wales	Kestral Place, Bywong	−35.221008	149.336731
C	J58	AMA4C5	LS collection	*Amphibolurus muricatus*	New South Wales	Burra Rd, Burra	−35.647289	149.215408
C	J59	AMA3B4	LS collection	*Amphibolurus muricatus*	New South Wales	Kioloa Headland	−35.55994722	150.3837083
C	J60	AMA4C2	LS collection	*Amphibolurus muricatus*	New South Wales	Burra Rd, Burra	−35.660873	149.209305
C	J61	AM4	LS collection	*Amphibolurus muricatus*	New South Wales	Pony Club, Birriwa Road, Bywong	−35.18155278	149.3375528
C	J62	AMD5	LS collection	*Amphibolurus muricatus*	New South Wales	Myrtle Beach	−35.70282778	150.279875
C	J63	AMB4	LS collection	*Amphibolurus muricatus*	New South Wales	Denley & Kestral, Bywong	−35.221176	149.336411
D	J28	SAMAR49467	South Australian Museum	*Amphibolurus muricatus*	South Australia	Nangwarry	−37.45444	140.87528
D	J29	SAMAR49376	South Australian Museum	*Amphibolurus muricatus*	South Australia	Donovans	−38.00778	140.96250
D	J30	SAMAR49374	South Australian Museum	*Amphibolurus muricatus*	South Australia	Donovans	−38.00778	140.96250
E	J19	Z11557	Museum Victoria	*Amphibolurus muricatus*	Victoria	Steels Creek	−37.57972	145.37000
E	J20	Z18832	Museum Victoria	*Amphibolurus muricatus*	Victoria	Kinglake National Park North	−37.53417	145.22528

(*continued on next page*)

Table 1 (*continued*)

CLADE	LAB#	Registration Number	Institution	Scientific name	State/territory	Locality	Latitude	Longitude
E	J21	Z7821	Museum Victoria	*Amphibolurus muricatus*	Victoria	Brisbane Ranges National Park	−37.82000	144.27000
E	J22	Z7823	Museum Victoria	*Amphibolurus muricatus*	Victoria	Brisbane Ranges National Park	−37.82000	144.27000
E	J23	Z7861	Museum Victoria	*Amphibolurus muricatus*	Victoria	Steels Creek	−37.57972	145.37000
E	J24	Z7866	Museum Victoria	*Amphibolurus muricatus*	Victoria	Brisbane Ranges National Park	−37.82000	144.27000
F	J26	SAMAR49532	South Australian Museum	*Amphibolurus norrisi*	South Australia	Padthaway	−36.71778	140.44417

Table 2
Marker information used in this study.

Gene	Abbreviation	Primer name	Size (bp)	TA (oC)	Primers (5′–3′)	Primer source
NADH dehydrogenase subunit 2	*nd2*	Metf-1	1016	55–50	AAGCAGTTGGGCCCATRCC	Macey et al. (2000)
	nd2	CO1r.aga			ACRGTTCCRATRTCTTTRTGRTT	Modified from *H5934* (Macey et al. (1997))
	nd2	nd2Jacky-F1[a]			TTTCAAGCACATTAAATGC	This study
NADH dehydrogenase subunit 4	*nd4*	ND4-1	732	55–50	TGACTACCAAAAGCTCATGTAGAAGC	Arevalo et al. (1994)
	nd4	LEU			TACTTTTACTTGGATTTGCACCA	Modified from *Leu* (Arevalo et al. (1994))
Recombination activating gene 1	*rag1*	rag1-Faga	1205	55–50	CAAAGTGAGACSACTTGGAAAGCC	Shoo et al. (2008)
	rag1	rag1-Raga			CATTTTTCAAGGGTGGTTTCCACTC	Shoo et al. (2008)
	rag1	JackyIntF[a]			ATCCTGGCCAGATCTCCTTGC	This study
Prolactin receptor	*prlr*	prlr-F1	580	55–50	GACARYGARGACCAGCAACTRATGCC	Townsend et al. (2008)
	prlr	prlr-R3			GACYTTGTGRACTTCYACRTAATCCAT	Townsend et al. (2008)
Brain-derived neurotrophin factor	*bdnf*	bdnf-F	718	55–50	GACCATCCTTTTCCTKACTATGGTTATTTCATACTT	Townsend et al. (2008)
	bdnf	bdnf-R			CTATCTTCCCCTTTTAATGGTCAGTGTACAAAC	Townsend et al. (2008)

TA: Temperature of annealing in PCR reaction.
[a] Used as an internal sequencing primer.

were >200 for all parameters. All runs produced the same topology with very similar posterior probabilities, so we combined runs to generate a single consensus tree.

2.4. Analysis of body size and shape data

We evaluated body proportion data from 537 specimens collected as part of ongoing behavioral work by MDB and from specimens in the collections of the AM and MV. The following body size measurements were taken with electronic calipers to the nearest 0.1 mm: SVL – snout-vent length; TailL – tail length; InterL – inter-limb length; HeadL – head length; HeadW – head width; HeadH – head height; ForeL – forelimb length; HindL – hindlimb length.

Most of our genotyped animals also formed part of our morphological data set and for the remaining specimens used in the morphological analysis we had to assign them to genetic clades to evaluate morphological differences (if any) between them. We did this by overlaying the locality information of all genotyped and non-genotyped specimens (see Appendix Fig. 1) and we only assigned them to a genetic clade if their locality unambiguously fell in the geographic range of a genetic clade. This allowed us to assign 437 specimens in the morphological data set to genetic clades, and we excluded 101 specimens that were distributed close to the geographic boundaries of genetic clades.

Our primary interest was the evaluation of body shape differences (if any) between well-supported genetic clades. We evaluated this in two ways on natural log transformed data. We used Principal Components Analysis (PCA) with variance-covariance, which does not identify groups *a priori*, and Discriminant Function Analysis (DFA), where the groups were specified *a priori*, to examine the patterns of relationship and discriminating power of the body proportion characters (natural log transformed) with the statistics software JMP v. 8.0. The first PC represented variation in body size and the second PC summarized shape differences. We performed DFA on the ln-transformed data to examine if body shape differences would be sufficient to distinguish genetic clades when they were specified *a priori*.

Where possible, individuals were scored for sex by the presence of inverted hemipenes, eggs, or by dissection. Jacky dragons are sexually dimorphic in relative head size (Harlow and Taylor, 2000) but for several of the genetic clades we did not have sufficient sample sizes of sexed animals to perform separate analyses of males and females. Therefore, we performed each analysis described above both with and without head length, width and height data. These analyses gave the same results so we only present analyses based on all the data.

3. Results

3.1. Phylogenetic analyses

Following the removal of ambiguously aligned nucleotide sites, the final *nd2* dataset consisted of 1016 base-pairs (bp), *nd4* consisted of 732 bp, *rag1* consisted of 1205 bp, *bdnf* consisted of 718 bp, and *prlr* consisted of 580 bp, totaling 4251 bps for the concatenated dataset. The gene trees for *nd2* and *nd4* exhibited phylogeographic structure with well supported clades but with unresolved relationships among them. The individual gene trees for the nuclear loci showed extremely low variability, with *prlr* and *bdnf* appearing as a single or a series of shallow combs. *Rag1* exhibited more structure, but this was not always consistent with the structure identified in the mtDNA loci. The maximum

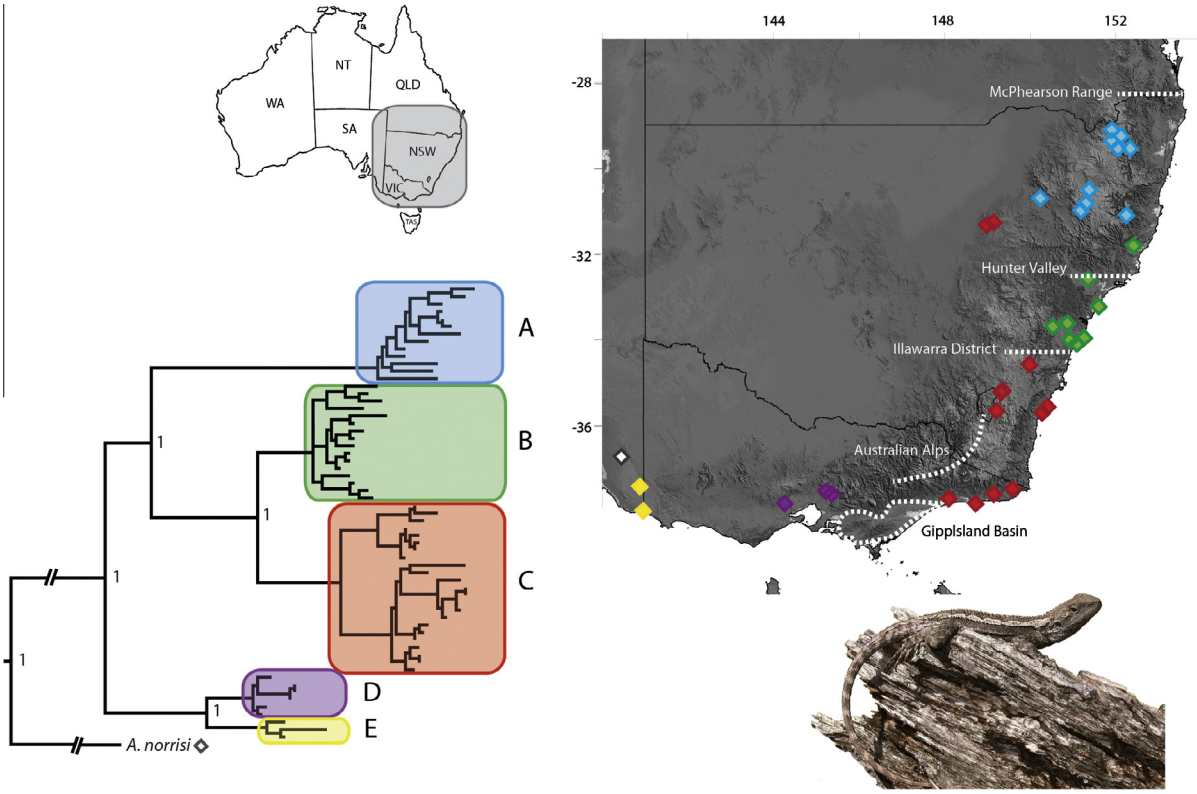

Fig. 1. Phylogeny of 62 *Amphibolurus muricatus* samples and outgroups based on the combined *nd2*, *nd4*, *rag1*, *bdnf* and *prlr* data, and their distribution across eastern Australia. Here we show the relationships among the five clades (A–E) based on the *BEAST species-tree analysis. Numbers beside nodes refer to posterior probabilities. Dark lines on the map represent State boundaries. WA = Western Australia, NT = Northern Territory, QLD = Queensland, SA = South Australia, NSW = New South Wales, ACT = Australian Capital Territory, TAS = Tasmania. White stippled lines indicate biogeographic barriers mentioned in the text. Colored diamonds indicate our sampling for each *A. muricatus* clade, with the white diamond representing our sample of *A. norrisi*. For the Maximum likelihood phylogeny showing individual details of each *A. muricatus* sample see Appendix Fig. 2. Photo: Ben Twist.

uncorrected pairwise genetic distances between clades is 6% for the mtDNA data and 0.7% for the nDNA loci.

Our results from the partitioned ML analyses strongly support five clades within *A. muricatus* (Appendix Fig. 2). While the relationships between clades are poorly supported in the ML analysis, our *BEAST species tree analysis strongly supports the grouping of the three eastern clades (blue, green and red in Fig. 1) as the sister group to the two southern clades (purple and yellow in Fig. 1). A sample identified as *A. muricatus* from the South Australian Museum (J26; SAMAR49532) is highly divergent from other *A. muricatus* samples and instead falls well within *A. norrisi* samples from Genbank for *nd2* (not shown). Both our ML and Bayesian analyses strongly support *A. norrisi* to be the sister taxon to *A. muricatus* (pp = 1, bs = 99).

3.2. Morphological analyses

Appendix Table 2 summarizes the variation in body proportion data for each genetic clade. There was virtually complete overlap between clades in each of the variables examined and this result persisted following multi-variate analysis. We summarize the results of our PCA analysis in Fig. 2, which demonstrates that all five genetic clades overlap entirely in both body size (PC1) and body shape (PC2). PC1 explained 90% of the variation and, as expected, was highly correlated with SVL ($r^2 = 0.99$, $P < 0.0001$). PC2 (body shape) explained 4.4% of the variation with inter-limb length having the highest loading. The remaining PCs explained negligible amounts of the variation. Similarly, DFA, where clades were specified *a priori*, demonstrated that it is not possible to easily allocate specimens to clade based on body proportion variables. Only 52% of the specimens were correctly assigned to their genetic clade.

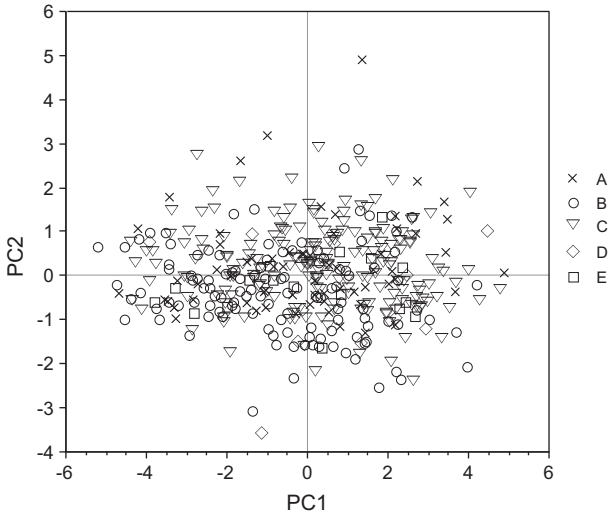

Fig. 2. Summary of results for the PCAs of the morphological data for 437 *A. muricatus* specimens which we assigned to 5 clades (A–E) based on genetic and geographic data.

4. Discussion

We have produced the first comprehensive phylogeny for *A. muricatus*. While the nuclear loci *bdnf* and *prlr* were largely uninformative on their own, the combined data, using information from all five loci, show strong support for five genetic groups with

allopatric distributions down the east coast of Australia. The most northern clade occupies northern NSW on the western side of the Great Dividing Range. South of this a second clade has a largely coastal distribution on the eastern side of the Great Dividing Range. A third clade has a number of divergent populations, the first well inland in NSW around a small cluster of mountains, a population around the ACT and the NSW south coast, and another population around coastal eastern Victoria. A fourth clade occurs around the regions north of Melbourne, with a fifth clade represented by just a few samples located around the Victorian/South Australian border. The Great Dividing Range provides both a topographic and climate-induced barrier for low dispersal taxa, and expansion along either side of this mountain system has long been thought of as an important mechanism leading to population differentiation (eg. Horton, 1972). Below we discuss the taxonomic implications of our study, as well as the historical processes and biogeographic barriers that may have influenced the evolutionary history of the Jacky dragon.

4.1. Monophyly and taxonomy of A. muricatus

In a mtDNA based study of amphibulurine taxa, Schulte et al. (2003) inferred *A. muricatus* to be the sister taxon to *A. norrisi*, in a clade also containing *Lophognathus gilberti* and *C. kingii*. A recent study by Melville et al. (2011) included a nuclear gene (*rag1*) in their phylogeny of *Amphibolurus* and *Lophognathus*, and recovered the same sister relationship between *A. muricatus* and *A. norrisi*, but with lower support in the nuclear locus (pp = 70, bs = 86). We only had a single individual of *A. norrisi* for our nDNA loci and *nd4*. However, *nd2* data from nine additional *A. norrisi* samples from Genbank unambiguously place our sample J26 within this taxon. Our combined analysis based on two mtDNA and three nDNA loci strongly support this sister relationship between *A. muricatus* and *A. norrisi* sample J26. Morphologically the two species are very similar in scutellation, with the most conspicuous difference relating to the presence of a dark canthal stripe in *A. norrisi* that extends from the tip of the snout, through the nostril and orbit and to the tympanum (Witten and Coventry, 1984; Cogger, 2000). The two species have distinct and parapatric distributions that appear to be limited by topography and associated habitats. *A. muricatus* has a distribution closely associated with the uplands of the Great Dividing Range (see below) from south-east Queensland to where the highlands dissipate around the Victorian/South Australian border. In contrast, the distribution of *A. norrisi* is restricted to the topographically low-lying coastal zone along the southern continental margin, from the Victorian/South Australian border to well into Western Australia (Atlas of Living Australia records).

Despite the phylogeographic structure we documented in *A. muricatus*, we found no evidence of body proportion differences between the major mtDNA clades. Based on body proportion homogeneity and lack of resolution in the nuclear loci, we therefor do not support taxonomic recognition of any of the mtDNA clades, and instead suggest that *A. muricatus* is best thought of as a single species with phylogeographic structure. While our morphological analyses were based only on body shape characters, detailed analysis of geographic variation in color and scalation patterns as they relate to phylogeographic structure would be fruitful areas for additional research.

4.2. Biogeography of A. muricatus populations

In a detailed study of the genetic structure of *Lampropholis* skinks, Chapple et al. (2011) reviewed a number of recurring biogeographic barriers along the eastern Australian margin that correspond to major genetic breaks in this and other disparate taxa. The patterns seen in *A. muricatus* are largely concordant with these studies, with the numerous allopatric clades along the east coast consistent with the hypothesis of multiple isolated forest refugia during the extensive arid periods of the Plio-Pleistocene (Thom et al., 1994).

While relationships between lineages based on our concatenated analysis are largely unresolved, our species-tree analysis groups the three eastern clades (northern NSW, central NSW, south-eastern NSW/eastern VIC) together, to the exclusion of the two southern clades (central VIC and western VIC), with strong support. This major phylogeographic division between southern NSW and central VIC is seen in a number of other taxa, including skinks (Chapple et al., 2005), assassin spiders (Rix and Harvey, 2012), myobatrachid frogs (Symula et al., 2008), bower birds (Nicholls and Austin, 2005) and glow-worms (Baker et al., 2008). In a study on the *Lomatia* genus in the plant family Proteaceae, Milner et al. (2012) identified the 'Southern Transition Zone' in southern NSW, and suggested that rather than defining a strict position, this area represented a transitional, climate-dependant barrier that varies over time and influences species distributions differently. In our study, this break in *A. muricatus* populations appears to be associated with the Eastern Highlands (the northeast to southwest trending Australian Alps, which run from NSW to VIC) that include the highest elevation regions of the Great Dividing Range. This region experienced episodes of glaciation during the Pleistocene (Barrows et al., 2002), which would have eliminated suitable habitat and isolated populations. Eastern and central VIC also are separated by the Gippsland Basin and the Strzelecki Ranges (Dickinson et al., 2002), that could provide topographic and habitat induced barriers to dispersal for taxa in this region.

Within the three eastern clades, our northern NSW clade has a distribution that also is seen in other taxa (eg. Schäuble and Moritz, 2001; Chapple et al., 2011). To the north it is bound by the Macpherson Range or potentially some other geological barrier, such as a geological break in the uplands of the New England Fold Belt as it grades into the adjacent Clarence/Moreton Basin (Packham, 1969). Another well known barrier, the Hunter Valley, generally separates the northern NSW clade from the central NSW clade to the south, however a number of individuals are found just north of this region, suggesting this barrier may not have been as effective in isolating *A. muricatus* populations north and south of this divide.

We also identified a genetic division between the central NSW population and the southern NSW populations (which includes a population well inland to the northwest). This corresponds geographically to the Illawarra district, where there is a break in the sandstone cliffs near Robertson, and where the low-lying coastal plain reaches its widest point at Macquarie Pass. This region, like other low-lying coastal zones was intensely arid during the last glacial maximum, with a dry and windy coastline that extended up to 100 km offshore than the present coastline (Thom et al., 1994). This same phylogeographic break is also present in broad-headed snakes (Sumner et al., 2010), velvet geckos (Dubey et al., 2012) and assassin spiders (Rix and Harvey, 2012).

The timing of tectonic uplift in the south-eastern highlands is contentious, with various hypotheses ranging from the Palaeozoic to the Cenozoic (Van der Beek et al., 1999). Despite this uncertain tectonic history, substantial uplift along the Great Dividing Range is undoubtedly related to the rifting of the Tasman Sea during the Cretaceous ~94 Ma (O'Sullivan et al., 2000), and its formation would have had a profound influence on the evolution of taxa on the east coast of Australia (Dubey et al., 2010). In addition, the non-uniform relief along its great length of more than 3500 km, with a width of over 300 km in some sections, would have provided multiple microclimatic refuges during Plio-Pleistocene cycles of aridification, dividing formerly continuous distributions and allowing the development of genetically distinct local populations. Despite its modest elevation compared to mountain systems

of other continents, the height of the Great Dividing Range particularly around the NSW and Victorian Alps creates winter temperatures too cold for survival for many temperate taxa, and would currently restrict their distribution to lowlands and coastal plains either side of the divide. Our results of population subdivision in *A. muricatus* and the correlation to topography of the Great Dividing Range has been found across a wide variety of organisms, including invertebrates (Garrick et al., 2004), amphibians, reptiles, birds, mammals and plants (reviewed in Chapple et al., 2011). While the nature and location of barriers to dispersal varies among taxa, the diversification of south-eastern Australian biota appears to reflect a history where the Great Dividing Range has played a central role.

5. Conclusions

More than 200 years after its original description in the journal "Voyage to New South Wales" (White, 1790), modern molecular methods have confirmed the distinctiveness of the Jacky dragon within the Australian amphibolurine radiation. Our study, sampling from across their distribution, has highlighted geographically structured diversity and represents a valuable phylogenetic framework for studies of behavior, evolution and ecology, that have lead to the recognition of the Jacky dragon as a model species. Remarkably, a number of common and widespread Australian reptiles also mentioned in White's journal (the Eastern water dragon *Intellagama lesueurii*, blue-tongue skink *Tiliqua scincoides* and lace monitor *Varanus varius*) and even the first endemic Australian reptile to be named, the shingle-back skink *Tiliqua rugosa* (Dampier, 1729) are still lacking intraspecific genetic studies detailing population structure across their range. With the rise in discovery of cryptic species of terrestrial vertebrates, in particular squamate reptiles (Oliver et al., 2009), elucidating this unrecognised diversity will require integrated data from genetics, morphology, and ecology. In addition, as comparative phylogeographic datasets increase, along with more accurate reconstructions of past landscapes and palaeoclimates, so too will our understanding of the overarching environmental forces that shaped the diversity and distribution of the Australian biota.

Acknowledgments

We thank the Australian Museum, South Australian Museum and Museum Victoria staff, and Lisa Schwanz, for access to tissue samples. We also thank Brian Harrold for help with mapping software. Ben Twist kindly provided the photograph of *A. muricatus* for the figure. Tissue samples were collected with the approval of the Australian National University Ethics Committee (A2012/12) and the Macquarie University Ethics Committee (ARA 2010/034) under the following permits: NSW: SL101003, S13197; VIC: 10005522. M.J.W. and J.S.K. thank the Australian Research Council for ongoing support.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2013.11.012.

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