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Congruent phylogeographic patterns in a young radiation of live-bearing marine snakes: Pleistocene vicariance and the conservation implications of cryptic genetic diversity

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Abstract

Aim: To investigate phylogeographic patterns among and within co-occurring sea snake species from Australia's endemic viviparous *Aipysurus* lineage, which includes critically endangered species, and evaluate the conservation implications of geographically structured patterns of genetic divergence and diversity.

Location: Australia's tropical shallow water marine environments spanning four regions: Great Barrier Reef (GBR), Gulf of Carpentaria (GoC), Timor Sea (TS) and coastal WA (WAC).

Methods: Samples from >550 snakes representing all nine nominal *Aipysurus* group species were obtained from throughout their known Australian ranges. Coalescent phylogenetic analyses and Bayesian molecular dating of mitochondrial DNA, combined with Bayesian and traditional population genetic analyses of 11 microsatellite loci, were used to evaluate genetic divergence and diversity.

Results: Mitochondrial DNA revealed highly congruent phylogeographic breaks among co-occurring species, largely supported by nuclear microsatellites. For each species, each region was characterized by a unique suite of haplotypes (phylogroups). Divergences between the TS, GoC and/or GBR were invariably shallow and dated as occurring 50,000–130,000 years ago, coinciding with the cyclic Pleistocene emergence of the Torres Strait land bridge. By contrast, sea snakes from coastal WA were consistently highly divergent from other regions and dated as diverging 178,000–526,000 years ago, which was not associated with any known vicariant events.

Main Conclusions: Previously unappreciated highly divergent sea snake lineages in coastal WA potentially represent cryptic species, highlighting this region as a high-priority area for conservation. The cyclic emergence of the Torres Strait land bridge is consisted with observed divergences between the TS, GoC and/or GBR; however, processes involved in the earlier divergences involving the WAC remain to be determined. The observed strong population genetic structures (as surrogates for dispersal) indicate that sea snakes have limited potential to reverse population declines via replenishment from other sources over time frames relevant to conservation.

KEYWORDS
biodiversity, comparative phylogeography, dispersal, endemism, marine reptiles, molecular dating

1 | INTRODUCTION

Tropical marine environments are characterized by extraordinarily high biodiversity, with biodiversity estimates continuing to increase as molecular surveys reveal previously unappreciated diversity (Clement, Posada, & Crandall, 2000; von der Heyden et al., 2014). Yet marine biodiversity is imperiled, due to overharvesting of natural resources, coastal development, pollution and the effects of climate change (Burke, Reytar, Spalding, & Perry, 2011; Halpern et al., 2008). For example, over one-third of coral species are threatened with extinction due to the effects of climate change (Carpenter et al., 2008), and evidence of cryptic genetic diversity in corals suggests this figure could be much higher (Richards, Berry, & van Oppen, 2016). Traditional conservation actions that focus on tackling common causes of species declines, such as habitat loss (Thomas et al., 2004), may not optimize the conservation of genetic divergence and diversity (Beger et al., 2014), or their underlying evolutionary processes (Moritz & Potter, 2013), crucial for responding to more ubiquitous impacts, such as climate change or disease (Thomas et al., 2004). For example, the current global system of marine protected areas may not be protecting the evolutionary diversity of corals and reef fishes (Mouillot et al., 2016). Approaches for incorporating genetic information into conservation planning include identifying and prioritizing evolutionary significant lineages (Moritz & Potter, 2013) and/or optimizing geographic patterns of genetic diversity and divergence (Nielsen, Beger, Henriques, Selkoe, & von der Heyden, 2016). These approaches necessitate surveying the spatial breadth of species' ranges to uncover important phylogeographic variation, including cryptic species (Bickford et al., 2007), with multispecies studies essential for elucidating key patterns and processes underlying marine biodiversity for integrative management (von der Heyden et al., 2014).

While there is some evidence of congruence in the distribution of genetic diversities (Pope, Riginos, Ovenden, Keyse, & Blomberg, 2015), divergence (Rocha, Craig, & Bowen, 2007) and cryptic species (Knowlton, 1993) in marine systems, these studies tend to be the exception rather than the rule. For example, a multispecies evaluation of the potential isolating effects of Pleistocene sea level changes in Australia's tropical coastal waters failed to reveal congruent signals of genetic divergence or dispersal across the Torres Strait land bridge (Mirams, Treml, Shields, Liggins, & Riginos, 2011), despite the repeated vicariance produced by this barrier over the past 2 million years (Voris, 2000). Lack of genetic concordance has been attributed to differences in life history strategies, particularly dispersal capacity by pelagic larvae (Mirams et al., 2011); however, disparate genetic patterns also occur among species with similar dispersal potentials and vice versa (Liggins, Treml, Possingham, & Riginos, 2016). It is perhaps not surprising that genetic studies of species with the typical life history seen in tropical marine systems, namely relatively sedentary benthic adult populations linked to a greater or lesser extent by dispersal of pelagic larvae, failed to find congruent phylogeographic signals, as even small amounts of gene flow can rapidly erode signals of genetic subdivision (Waples, 1998). Yet, the associated levels of dispersal may not be adequate to ensure the long-term viability of threatened populations (Waples & Gaggiotti, 2006). Species with low dispersal are more likely to harbour signals of previous vicariance and the associated geographic patterns of genetic diversity that should be the focus of conservation efforts.

True sea snakes (Elapidae; Hydrophiinae) are a group of marine vertebrates with many characteristics that make it ideal for a multispecies evaluation of the conservation implication of Pleistocene vicariant events on signatures of genetic divergence and diversity in tropical Australian waters. Sea snakes are a diverse group of live-bearing predatory marine reptiles that arose less than 7 million years ago (Mya) (Sanders, Lee, Leijs, Foster, & Keogh, 2008), and >70 recognized species in two evolutionary lineages now occupy shallow water (<200 m) marine habitats throughout the Indo-West Pacific (Heatwole, 1999). The *Aipysurus* lineage arose less than 3 Mya (Sanders, Lee, Mumpuni, Bertozzi, & Rasmussen, 2013) and comprises 11 nominal species in two genera (*Aipysurus*—nine species; *Emydocephalus*—two species) (Cogger, 2000), of which eight species in the genus *Aipysurus* are endemic to Australasia. *Aipysurus* group species are strongly associated with coral (and rocky) reefs; hence, species' distributions mirror the patchy distributions of these habitats (Lukoschek, Heatwole, Grech, Burns, & Marsh, 2007). All species are viviparous (thus lack a dispersive larval stage), and mark–recapture studies have demonstrated that at least two *Aipysurus* group species have small home ranges (Burns & Heatwole, 1998; Lukoschek & Shine, 2012). Population genetics has demonstrated restricted gene flow over small spatial scales for *Emydocephalus annulatus* (Lukoschek & Shine, 2012), while a phylogeographic study of *Aipysurus laevis* showed shallow divergence but strong genetic structure among three of four regions spanning tropical Australia (Figure 1: Great Barrier Reef [GBR], Gulf of Carpentaria [GoC], Timor Sea [TS]). Demographic tests and lower levels of genetic diversity provided evidence for Pleistocene population expansions in the GBR and GoC (Lukoschek, Waycott, & Marsh, 2007), whereas there was no evidence of recent population expansion on TS reefs (Lukoschek, Waycott, & Keogh, 2008; Lukoschek, Waycott, et al., 2007). These intraspecific genetic patterns are mirrored by species diversities of the *Aipysurus* group in Australian waters (Cogger, 2000), with higher species diversities in coastal Western Australia (WAC) and the TS than the east (GBR and GoC). Specifically, four species (*A. laevis*, *A. duboisii*, *A. mosaicus* and *E. annulatus*) have broad geographic ranges spanning much of Australia's tropical waters, whereas the remaining five species are restricted-range endemics in the TS and/or WAC (Figure 1).

In 2009, the first IUCN Red List assessments of extinction risk of all true sea snake species classified four species as threatened with extinction, including the restricted-range endemics *Aipysurus apraefrontalis* (CR) and *Aipysurus foliosquama* (CR), originally described as occurring only on TS reefs, and *Aipysurus fuscus* (EN), known from the TS and WAC (Elfes et al., 2013). In 2011 *A. apraefrontalis* and *A. foliosquama* were listed as CR under Australia's *EPBC* Act (1999); however, their elevated extinction risk was only partly due to their restricted ranges (Elfes et al., 2013). The main concern was precipitous population declines and local extinctions that occurred between 1998 and 2010 at Ashmore Reef (the largest TS reef), which decimated eight of its nine sea snake species with large breeding populations, including *A. apraefrontalis*, *A. foliosquama*, *A. fuscus*, *A. duboisii* and *E. annulatus*

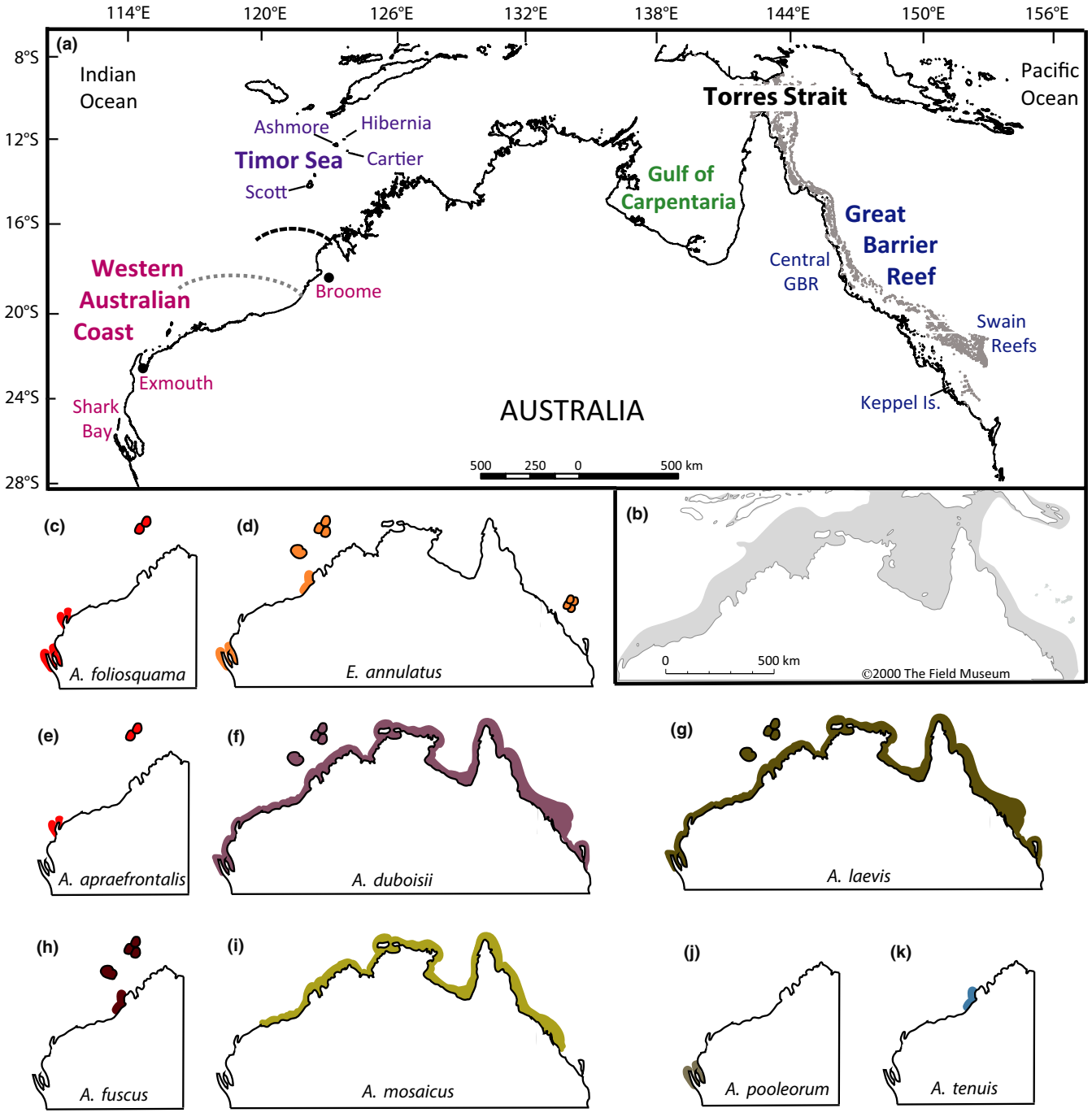

FIGURE 1 (a) Map of Australia showing sampling locations of 576 snakes in four major regions of this study: Western Australian Coast (WAC); Timor Sea (TS); Gulf of Carpentaria (GoC); and Great Barrier Reef (GBR). Names of regions and locations within regions are colour-coded as follows: WAC—pink; TS—purple; GoC—green; GBR—blue. Black dashed line north of Broome on WAC is location of genetic divide found in previous studies for two low-dispersal species (Dethmers et al., 2006; Imron et al., 2007). Grey dashed line south of Broome is Barrier L from Figure 1 Treml et al. (2015). (b) Map showing extent of land above sea level at glacial maxima (shaded grey), when sea levels were 120 m below present levels (Voris, 2000). Map © 2000 Field Museum of Natural History, Chicago, Illinois, USA, and modified with permission. (c–k) Current understanding of geographic ranges for nine Australasian species in the *Aipysurus* group. Note that the true geographic ranges of species are uncertain, particularly on the WAC, where the ranges for the five WAC endemics (c, e, h, j, k) and *Emydocephalus annulatus* (d) may be considerably larger than shown in these maps, while the true range for *Aipysurus laevis* (g) may not include the WAC. Note also that *E. annulatus* (d), *Aipysurus duboisii* (f) and *A. laevis* (g) also occur in New Caledonia and on some Coral Sea reefs, which are not shown on these maps. Colours for species ranges in c–k match species colours in Figure 4

(Guinea, 2007; Lukoschek, Beger, Ceccarelli, Richards, & Pratchett, 2013). In 2010, only *A. laevis* was observed during extensive surveys at Ashmore Reef, in highly reduced numbers (Lukoschek et al., 2013). These local extinctions occurred despite Ashmore Reef being highly protected since the early 1980s (Anon, 2002). Similar unexplained declines and/or local extinctions have been documented on protected

reefs for *A. laevis* and *E. annulatus* in the southern GBR (Lukoschek, Heatwole, et al., 2007) and *E. annulatus* in New Caledonia (Goiran & Shine, 2013). More recently *A. apraefrontalis* and *A. foliosquama* were recorded in coastal WA (Exmouth and Shark Bay), from where they were previously unknown (D'anastasi, van Herwerden, Hobbs, Simpfendorfer, & Lukoschek, 2016; Sanders, Schroeder, Guinea, & Rasmussen, 2015), possibly reflecting recent range extensions. However, genetic and morphological differences between the WAC and TS (Sanders et al., 2015) suggest that established populations in coastal WA have, until recently, been misidentified or overlooked, with various implications for conservation (Bickford et al., 2007).

The aims of this study were to investigate whether co-occurring sea snake species in the *Aipysurus* group demonstrate congruent intraspecific genetic patterns; explore whether phylogeographic patterns reflect known vicariant events; and evaluate the conservation implications for geographically structured patterns of genetic divergence and diversity. I combined coalescent analyses and Bayesian dating for two mitochondrial fragments with Bayesian and population genetic analyses of 11 microsatellite loci for ~550 snakes representing all nine *Aipysurus* group species to provide the most comprehensive evaluation of the evolutionary relationships among and within this group to date (D'anastasi et al., 2016; Lukoschek & Keogh, 2006; Sanders et al., 2013). Results are discussed in the context of the effect Pleistocene sea level fluctuations on Australia's shallow water marine habitats and the taxonomic and conservation implications for the *Aipysurus* group, particularly the potential for populations to be replenished by dispersal from other locales over time frames relevant to conservation.

2 | METHODS

2.1 | Sampling

Samples were obtained from a total of 580 snakes representing eight of the nine currently recognized Australian species in the *Aipysurus* group, with the aim of sampling the full extent of each species known range (Figure 1; Table 1; Data 1 = Table S1). Snakes were identified to species following Cogger (2000), Kharin and Cheblyukov (2006), Sanders et al. (2012) and Voris (1977). Voucher numbers for archived snakes are given in Table S1; however, most samples were obtained from live snakes so voucher specimens were not available. Mitochondrial sequences (n = 13) were obtained from GenBank for the remaining two recognized species in the genus *Aipysurus*, including *A. eydouxi* from Southeast Asia (Supporting Information). Sixteen *Hydrophis* group species were used as outgroups in phylogenetic and Bayesian dating analyses.

2.2 | DNA extraction, mitochondrial DNA sequencing and microsatellite genotyping

With the exception of *A. laevis*, all samples were sequenced for two mitochondrial fragments (ATPase [~850 bp]; ND4 [~700 bp] plus 3′ tRNA-His+tRNA-Ser [~120 bp]) and genotyped for 11 microsatellite loci (Lukoschek & Avise, 2012). *Aipysurus laevis* (n = 350) had previously been analysed for ND4 (Lukoschek, Waycott, et al., 2007) and five different microsatellite loci (Lukoschek et al., 2008). In this study, ATPase sequences were obtained for a representative subset of *A. laevis* (n = 182), while all *A. laevis* were genotyped for the new panel of 11 microsatellite loci (Lukoschek & Avise, 2012). DNA extraction, PRC amplification, mitochondrial sequencing and sequence alignment followed Lukoschek and Keogh (2006), Lukoschek, Waycott, et al. (2007), Lukoschek et al. (2008) and D'anastasi et al. (2016). Microsatellite loci were genotyped using the primers and protocols described in Lukoschek and Avise (2012). Alleles were sized using a ROX-labelled GS500 internal standard and scored using GeneMapper 4.0 (Applied Biosystems).

2.3 | Data analysis

2.3.1 | Mitochondrial DNA

Gene genealogies and divergence times

Phylogenetic relationships among species and among regions within species were estimated using Bayesian phylogenetic inferences implemented in MrBayes (Ronquist & Huelsenbeck, 2003) and maximum parsimony (MP) and maximum likelihood (ML) implemented in PAUP*Vers.4.0a150 (Swofford, 2000), using one copy of each sampled haplotype (Data 2: concatenated ATPase + ND4 + tRNA) and the best-fit models of evolution (Supporting Information). A Bayesian relaxed molecular clock implemented in BEAST v1.8.4 (Drummond, Suchard, Xie, & Rambaut, 2012) was used to estimate divergence times among and within species. There were no shared haplotypes among regions (see Results); thus, dating with BEAST (without considering migration) is fully justified. BEAST analyses were conducted using the coding regions of both mitochondrial fragments and best-fit model of evolution (mtCode1-GTRig, mtCode2-GTRig, mtCode3-GTRig, see Supporting Information), with substitution rates, rate heterogeneity and bases frequencies unlinked across the three codon partitions. Markov chain Monte Carlo (MCMC) runs comprised of 50,000,000 generations, sampled every 1,000 generations, with three replicate analyses per dataset using different starting random seeds to ensure convergence. Outputs of MCMC chains were summarized in TRACER v1.6 to obtain parameter estimates and assess effective sample sizes (ESSs) and convergence. ESS values for all parameters in each analysis were >1,000 (*N.B.* ESS > 100 is regarded as sufficient to obtain reliable posterior distributions).

There are no known fossils in the true sea snake lineage so a secondary calibration with a normal distribution around a mean of 6.2 Mya (95% CI 4.5–7.9) was applied to the root divergence between the *Aipysurus* and *Hydrophis* groups. This calibration corresponds to the posterior distribution for the divergence between these groups estimated using reliable squamate fossil calibrations and long nuclear sequences (Lukoschek, Keogh, & Avise, 2012; Sanders et al., 2008, 2013). These ages are younger than those obtained by Lee et al. (2016); however, their divergence estimates relied heavily on mitochondrial data and are therefore likely to be overestimates, given

TABLE 1 Summary statistics for mitochondrial DNA (ND4 plus ATPase) and 11 microsatellite loci for five sea snake species across four regions in Australia's tropical marine environment.

	Mitochondrial DNA				11 microsatellites loci					
Sampling localities	***n***	***N***	***h* ± *SE***	**π ± *SE* (%)**	***n***	N_a	A_r	H_o	H_e	F_{is}
Emydocephalus annulatus										
Great Barrier Reef	**5**	1	n/a	n/a	**5**	3.4	3.1	0.55	0.44	−0.23
Gulf of Carpentaria	**Nil**				**Nil**					
Timor Sea Reefs	**78**	19	0.88 ± 0.02	0.14 ± 0.09	**82**	12.8	4.8	0.73	0.79	0.07
Western Australia Coast	**2**	2	n/a	n/a	**2**	2.6	n/a	n/a	n/a	n/a
Australia total	**85**	**22**	**0.59 ± 0.02**	**0.23 ± 0.15**	**89**	**14.2**	**3.9**	**0.72**	**0.80**	**0.11**
Aipysurus laevis										
Great Barrier Reef	**80**	24	0.81 ± 0.04	0.09 ± 0.06	**197**	13.3	4.6	0.73	0.74	0.01
Gulf of Carpentaria	**32**	14	0.85 ± 0.05	0.15 ± 0.09	**45**	11.2	4.7	0.73	0.75	0.04
Timor Sea Reefs	**70**	10	0.68 ± 0.04	0.17 ± 0.10	**95**	13.6	4.9	0.76	0.80	0.04
Western Australia Coast	**24**	10	0.84 ± 0.05	0.17 ± 0.10	**13**	8.4	5.0	0.75	0.80	0.05
Australia total	**206**	**58**	**0.93 ± 0.01**	**0.55 ± 0.28**	**350**	**11.6**	**4.8**	**0.74**	**0.77**	**0.03**
Aipysurus duboisii										
Great Barrier Reef	**13**	9	0.94 ± 0.05	0.13 ± 0.09	**11**	5.9	3.9	0.62	0.64	0.05
Gulf of Carpentaria	**5**	4	0.90 ± 0.20	0.15 ± 0.12	**5**	4.1	3.7	0.64	0.58	−0.11
Timor Sea Reefs	**8**	5	0.78 ± 0.15	0.11 ± 0.08	**7**	4.9	3.8	0.64	0.58	−0.124
Western Australia Coast	**2**	1	n/a	n/a	**2**	1.7	n/a	n/a	n/a	n/a
Australia total	**28**	**19**	**0.59 ± 0.02**	**0.23 ± 0.15**	**25**	**7.6**	**3.8**	**0.63**	**0.67**	**0.07**
Aipysurus mosaicus										
Great Barrier Reef	**5**	3	0.70 ± 0.22	0.06 ± 0.06	**4**	4.1	4.09	0.84	0.66	−0.29
Gulf of Carpentaria	**6**	3	0.73 ± 0.16	0.11 ± 0.08	**6**	5.5	4.52	0.71	0.71	0.04
Timor Sea Reefs	**Nil**				**Nil**					
Western Australia Coast	**2**	2	n/a	n/a	**2**	2.4	n/a	n/a	n/a	n/a
Australia total	**13**	**8**	**0.91 ± 0.06**	**1.33 ± 0.71**	**12**	**8.5**	**4.3**	**0.77**	**0.81**	**0.05**
Aipysurus fuscus										
Great Barrier Reef	**Nil**				**Nil**					
Gulf of Carpentaria	**Nil**				**Nil**					
Timor Sea	**28**	8	0.79 ± 0.05	0.08 ± 0.06	**29**	7.5	4.1	0.68	0.72	0.05
Western Australia Coast	**2**	2	n/a	n/a	**2**	2.6	n/a	n/a	n/a	n/a
Australia total	**30**	**10**	**0.82 ± 0.05**	**0.20 ± 0.12**	**31**	**7.8**	**4.1**	**0.69**	**0.73**	**0.05**

For mtDNA, *n* = number of individuals; *N* = number of haplotypes; *h* = haplotype diversity; π = nucleotide diversity. For microsatellites, *n* = number of individuals; N_a = number of alleles; A_r = allelic richness rarefacted to smallest sample size (*N* = 4), not including WA Coast; H_o = observed heterozygosity; H_e = expected heterozygosity; F_{is} = inbreeding coefficient. n/a = diversity estimates not calculated for the Western Australian Coast when only two individuals were sampled. Bold values indicate sample sizes and Australian totals for each species

that nucleotide saturation of mitochondrial DNA is well-known to compress basal branches, thereby biasing node ages to older dates (for detailed discussion, see Lukoschek et al., 2012 and references therein). Analyses were conducted using coalescent tree priors, and the effects of assuming constant population size (Kingman, 1982) and allowing for expansion growth (Griffiths & Tavare, 1994) were evaluated. Two datasets were analysed; the first included one copy of all 125 *Aipysurus* group haplotypes (Data 1), while the second comprised of 94 haplotypes (excluding 31 singleton haplotypes: *A. laevis n* = 19; *E. annulatus n* = 12) to evaluate effects of rare haplotypes on estimated divergences.

Phylogenetic hypotheses consistently grouped *A. laevis* (GBR, GoC, TS) with two small-range WAC endemics, *A. tenuis* and *A. pooleorum*, the latter often regarded as a subspecies of *A. laevis* (Cogger, 2000), into a shallow clade; thus, these species were subsequently analysed together as the *A. laevis* complex. Haplotype networks were estimated for *E. annulatus*, *A. duboisii*, *A. mosaicus*, *A. fuscus* and the *A. laevis* complex, using statistical parsimony implemented in TCS 1.13 (Clement

et al., 2000), with the parsimony criterion set at 95%. Networks were constructed using all sampled individuals and the geographic locations of sampled haplotypes mapped onto each network.

2.3.2 | Genetic population structure and diversity

Population structure was quantified using analyses of molecular variance (AMOVA) (Excoffier, Smouse, & Quattro, 1992) taking haplotype frequencies (F_{ST}) and sequence divergences among haplotypes (ϕ_{ST}), into account. Genetic divergences between locations and regions were evaluated using pairwise F_{ST} and ϕ_{ST}. The significance of variance components and F/ϕ statistics was tested using 20,000 random permutations. Intraspecific mtDNA polymorphism was summarized using haplotype and nucleotide diversities (Nei, 1987) at the level of location (GBR and TS), region and across all locations. Analyses were conducted in ARLEQUIN 3.01 (Excoffier & Heckel, 2005), and *p* values were adjusted for multiple comparisons using the Benjamini–Hochberg False Discovery Rate (B-H FDR) (Benjamini & Hochberg, 1995).

2.4 | Microsatellites

2.4.1 | Linkage disequilibrium

Tests of LD were conducted for pairs of loci among locations and for pairs of loci across all locations in GenePopVers.4.3 (Raymond & Rousset, 1995; Rousset, 2008) using 50 batches with 5,000 iterations per batch and 10,000 dememorization steps. *p* values were adjusted using the B-H FDR (Benjamini & Hochberg, 1995).

2.4.2 | Bayesian clustering analyses

Multispecies comparisons within the genus *Aipysurus*

The Bayesian clustering algorithm implemented in STRUCTURE ver. 2.3.3 (Pritchard, Stephens, & Donnelly, 2000) was used to examine the optimal number of genetic clusters (*K*) among seven of the eight nominal Australian species in the genus *Aipysurus* (microsatellite data were not available for *A. pooleorum*). Analyses were conducted using the no-admixture model, appropriate for reproductively isolated populations or species. Two analyses were conducted. The first included all sampled individuals for the genus *Aipysurus*, while the second included only TS samples for *A. laevis*, to avoid the analyses being overwhelmed by the large number of *A. laevis* (*n* = 242) from the GBR and GoC. Results were virtually identical so only the second analysis is presented.

2.4.3 | Intraspecific genetic structure

The optimal number of intraspecific genetic clusters (*K*) was evaluated for four species sampled from at least two of the four geographic regions (*E. annulatus*, *A. duboisii*, *A. mosaicus and A. fuscus*) and *A. laevis* + *A. tenuis*. Analyses were conducted using the admixture model with correlated allele frequencies, using sampling locations as prior (Hubisz, Falush, Stephens, & Pritchard, 2009). *K* 1–10 was evaluated for *E. annulatus* and *A. laevis* + *A. tenuis*, while *K* 1–6 was evaluated for *A. duboisii*, *A. mosaicus* and *A. fuscus* using MCMC protocols described in Supporting Information.

2.4.4 | Principal components analysis

Principal components analyses (PCAs) of pairwise genetic distances were conducted at the level of species and individuals for all nominal *Aipysurus* species combined (using only TS_*A. laevis*); at the level of region for five *Aipysurus* species combined (*A. duboisii*; *A. mosaicus*; *A. fuscus*; TS_*A. laevis*; *A. tenuis*); and at the level of sampling location for *E. annulatus* and *A. laevis* + *A. tenuis*. Estimates of genetic distances between individuals, locations, regions and species and PCAs were conducted in GenAlEx ver. 6.5 (Peakall & Smouse, 2012).

2.4.5 | *F*-statistics, genetic diversity and Hardy–Weinberg equilibrium

Five datasets (*E. annulatus*; *A. duboisii*; *A. mosaicus*; *A. fuscus*; *and A. laevis* + *A. tenuis*) were used to evaluate genetic structure, diversity and HWE (see Supporting Information). Global and regional genetic structure was evaluated using AMOVA and pairwise F_{ST} in ARLEQUIN ver. 3.5 (Excoffier & Lischer, 2010; Excoffier et al., 1992) and significance tested using 10,000 permutations. Genetic structure among locations within regions was estimated for *E. annulatus* (TS) and *A. laevis* (TS and GBR). To allow for comparisons among species, F_{ST} values (Hedrick, 2005; Meirmans, 2006) were calculated in GenoDive ver. 2.07 (Meirmans & van Tienderen, 2004). Genetic diversity within regions was assessed using allelic richness (A_r), rarefacted to the smallest sample size (*n* = 4), in FSTAT (Goudet, 2001). The WAC only had two individuals for *E. annulatus*; *A. duboisii*; *A. mosaicus* and *A. fuscus*, so A_r was evaluated excluding the WAC for these species.

3 | RESULTS

3.1 | Mitochondrial DNA

3.1.1 | Gene genealogies and divergence times

Phylogenetic inferences from Bayesian, MP and ML analyses of 125 haplotypes representing ten nominal *Aipysurus* group species returned highly consistent topologies and levels of branch support (Figures 2 and S1). In addition, Bayesian dating analyses returned highly congruent dates for datasets with 125 and 94 haplotypes (Table S2) and using coalescent tree priors with constant size and expansion growth, so I focus on the full dataset with expansion growth (Figure 2; Table 2). There was a posterior divergence of 6.0 Mya (95% highest posterior distribution [HPD] 3.9–7.9) for the strongly supported basal divergence between the *Aipysurus* and *Hydrophis* groups (Figure 2; node 1; Bayesian posterior probabilities [PPs] = 100, ML and MP bootstraps = 100; Note: all divergences discussed below had PPs = 100, ML and MP bootstraps >95 and are indicated in Figure 2 with asterisks). The strongly supported basal split in the *Aipysurus* group

(Figure 2; node 2) between *E. annulatus* and the monophyletic genus *Aipysurus* occurred 2.6 Mya (95% HPD 1.3–3.9), while the basal split in the genus *Aipysurus* (Figure 2; node 3), between a clade comprising *A. mosaicus* plus *A. eydouxi* and a clade comprising all other *Aipysurus* species, diverged 1.5 Mya (95% HPD 0.8–2.2). The divergence between *A. eydouxi* from SE Asia and the recently described Australian endemic *A. mosaicus* (Sanders et al., 2012) occurred 0.9 Mya (95% HPD 0.4–1.5).

There were several striking features in the phylogenetic trees and haplotype networks. First, with the exception of *A. tenuis*, haplotypes from each nominal species in the *Aipysurus* group formed strongly supported species clades (Figure 2). Second, haplotype networks for *E. annulatus*, *A. duboisii*, *A. mosaicus* and *A. fuscus* (Figure 3) showed that, where sampled, each region (WAC, TS, GoC, GBR) had a unique suite of haplotypes. Third, *A. laevis* from the GBR + GoC + TS was reciprocally monophyletic with a clade comprising haplotypes from two WAC small-range endemics, *A. pooleorum* (Shark Bay) and *A. tenuis* (Broome). Mean divergence between *A. laevis* and the two nominal WAC species (Figure 2; node 5) was estimated as occurring 231 thousand years ago (Kya) (95% HPD 106–369). Fourth, there were deep reciprocally monophyletic intraspecific divergences between WAC haplotypes (Figure 2: pink) and all other haplotypes for

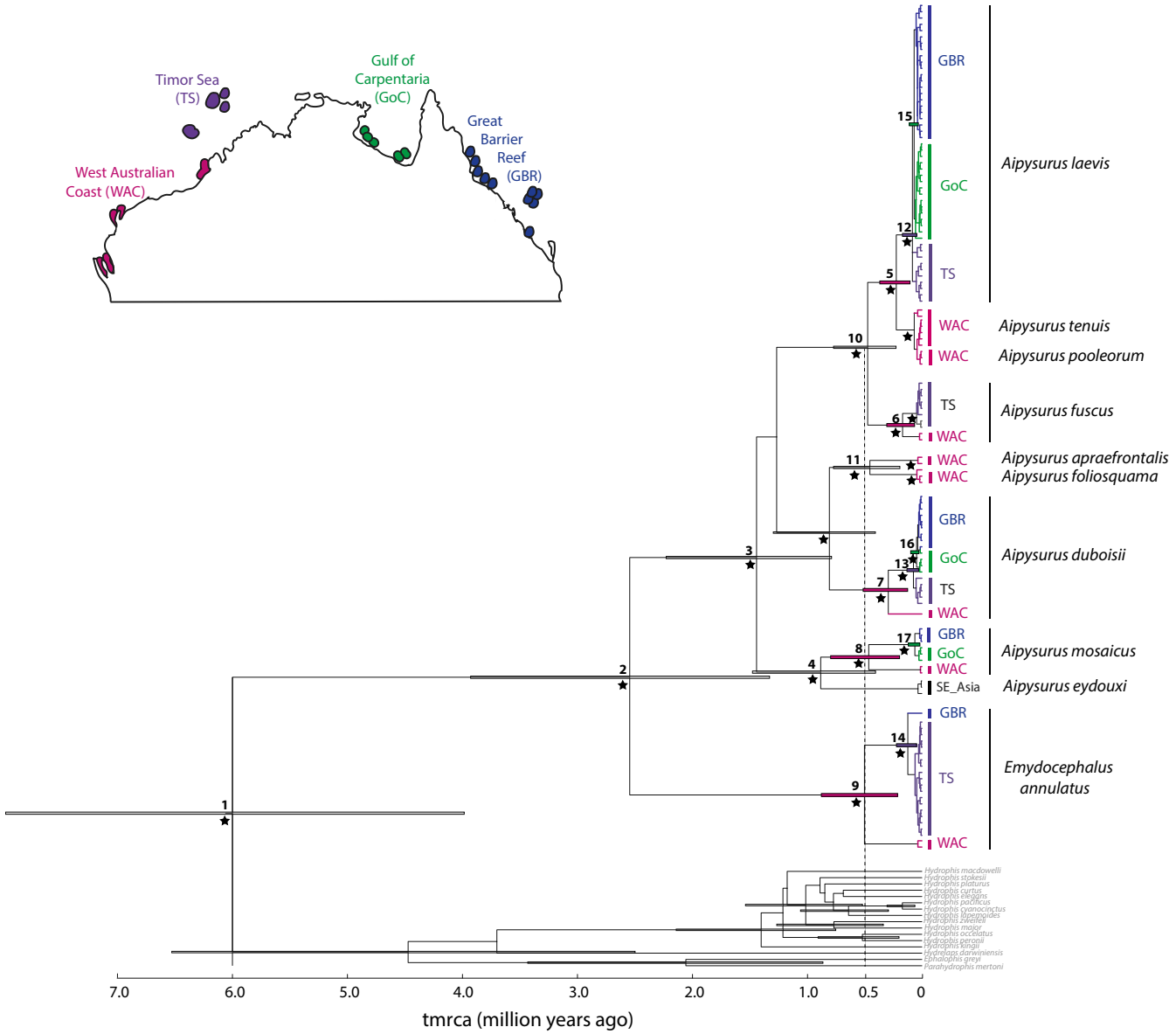

FIGURE 2 Cladogram from BEAST analyses of 125 mitochondrial haplotypes representing all nine Australian sea snake species from the *Aipysurus* group plus *A. eydouxi* from Southeast Asia. Also included are 16 species from the *Hydrophis* group (species names in pale grey font at bottom of tree) used to calibrate divergence estimates. Node numbers 1–17 refer to divergence times in Table 2 and Results. For the nine Australian species in the *Aipysurus* group, sampled haplotypes are colour-coded according to region shown on map; 95% highest posterior densities for divergences between the Western Australian Coast (WAC) and other regions are indicated by pink bars; between the Timor Sea (TS) and other regions by purple bars; and between the Gulf of Carpentaria (GoC) and Great Barrier Reef (GBR) by green bars. Nodes with Bayesian posterior probabilities = 100 and maximum-likelihood and maximum-parsimony bootstraps >95 are indicated with an asterisk below the node

TABLE 2 Estimates of divergence times for key inter- and intraspecific divergences in Australian sea snakes from the *Aipysurus* group.

Divergence	Node	Mean	Lower 95% HPD	Upper 95% HPD
treeModel.rootHeight	**1**	5.996	3.983	7.971
*Aipysurus*Group	**2**	2.600	1.328	3.909
*Aipysurus*Genus	**3**	1.471	0.789	2.225
Aeydouxii+Amosaicus	**4**	0.915	0.421	1.493
Alaevis+Atenuis+Apooleorum	**5**	0.231	0.106	0.369
*Afuscus*_WAC_vs_East	**6**	0.178	0.066	0.307
*Aduboisii*_WAC_vs_East	**7**	0.306	0.123	0.509
*Amosaicus*_WAC_vs_East	**8**	0.480	0.199	0.796
*Eannulatus*_WAC_vs_East	**9**	0.526	0.218	0.877
*Afuscus*_vs_*Alaevis+Atenuis+A pooleorum*	**10**	0.487	0.228	0.771
Aapraefrontalis+Afoliosquama	**11**	0.469	0.195	0.771
*Alaevis*_TS_vs_GoC+/−GBR	**12**	0.107	0.049	0.173
*Aduboisii*_TS_vs_GoC+/−GBR	**13**	0.078	0.032	0.133
*Eannulatus*_TS_vs_GoC+/−GBR	**14**	0.130	0.050	0.225
*Alaevis*_GoC_vs_GBR	**15**	0.070	0.034	0.112
*Aduboisii*_GoC_vs_GBR	**16**	0.049	0.019	0.085
*Amosaicus*_GoC_vs_GBR	**17**	0.066	0.021	0.122

WAC = Western Australian Coast; TS = Timor Sea; GoC = Gulf of Carpentaria; GBR = Great Barrier Reef; East = TS +/− GoC +/− GBR; node = node number in Figure 2 (shown in bold); mean = divergence time estimate millions of years ago (Mya); 95% HPD = lower and upper 95% highest posterior densities from BEAST analyses

A. fuscus, *A. duboisii*, *A. mosaicus* and *E. annulatus* (Figure 2; nodes 6–9, respectively), which were estimated as occurring between 178 and 526 Kya (Table 2). Moreover, there was considerable overlap in 95% HPDs for all five divergences involving the WAC and one or more of the other three regions (Table 1; Figure 2; nodes 5–9, pink bars), which ranged from 66 to 877 Kya. In stark contrast to the deep divergences involving WAC haplotypes, there were few base-pair differences among haplotypes from the TS and the GoC and/or GBR for *A. laevis*, *A. duboisii* and *E. annulatus* (Figure 3), with estimated divergences of 78–130 Kya and strongly overlapping 95% HPDs (Table 2; Figure 2; nodes 12–14, purple bars). There were even fewer base-pair differences between haplotypes from the GoC and GBR for *A. laevis*, *A. duboisii* and *A. mosaicus* (Figure 3), with mean divergences occurring 49–70 Kya, again with strongly overlapping 95% HPDs (Table 2; Figure 2; nodes 15–17, green bars). Among species, the two restricted-range CR endemics, *A. apraefrontalis* and *A. foliosquama*, were strongly supported sister taxa (Figure 2; node 11) that diverged ~500 Kya (Table 2), which coincided with the divergence between the Endangered *A. fuscus* and its sister taxon, the *A. laevis* complex (Figure 2; node 10).

3.1.2 | Population genetic structure and diversity

Regional intraspecific divergences were reflected in the pairwise ϕ_{ST} values, which were large (range: 0.915–0.987) and significant at $p = .05$ for all 11 comparisons involving the WAC (Figure S2a); however, five were not significant after B-H FDR correction (probably due to small samples sizes in the WAC). Regional pairwise ϕ_{ST} values between the TS, GoC and GBR (range 0.400–0.803) were statistically significant at $p = .05$ and after B-H FDR correction (Figure S2a). Pairwise F_{ST} values between regions were erratic, particularly for regions with low sample sizes and/or few haplotypes (Table S3). Global ϕ_{ST} values (AMOVA across regions) were large (range: 0.824–0.965) and statistically highly significant (Figure S3). Global F_{ST} values were smaller but, with the exception of *A. fuscus*, were statistically significant (Figure S3). Within the TS, there was considerable sharing of haplotypes among reefs for *E. annulatus*, *A. laevis*, *A. duboisii* and *A. fuscus* and no patterns in the magnitudes of pairwise ϕ_{ST} and F_{ST} values, which were mostly not significant after B-H FDR correction (Table S4). By contract, in the GBR, there were few shared haplotypes for *A. laevis* among locations (Figure 3), and all pairwise ϕ_{ST} and F_{ST} values were significant after B-Y FDR correction (Table S4). Haplotype diversities were moderate-to-high ($h \pm SE$: 0.68 ± 0.04–1.00 ± 0.50), and nucleotide diversities were low ($\pi\ \% \pm SE$: 0.06 ± 0.06–0.25 ± 0.28) with no consistent regional patterns in either diversity measure (Table 1; see Supporting Information for details).

3.2 | Microsatellites

A total of 511 sea snakes from eight nominal species were successfully genotyped for all 11 microsatellite loci (Data 3). Average number of alleles (*Na*) per species ranged from 7.6 for *A. duboisii* to 14.2 for *E. annulatus* (Table 1). There was no evidence to suggest linkage

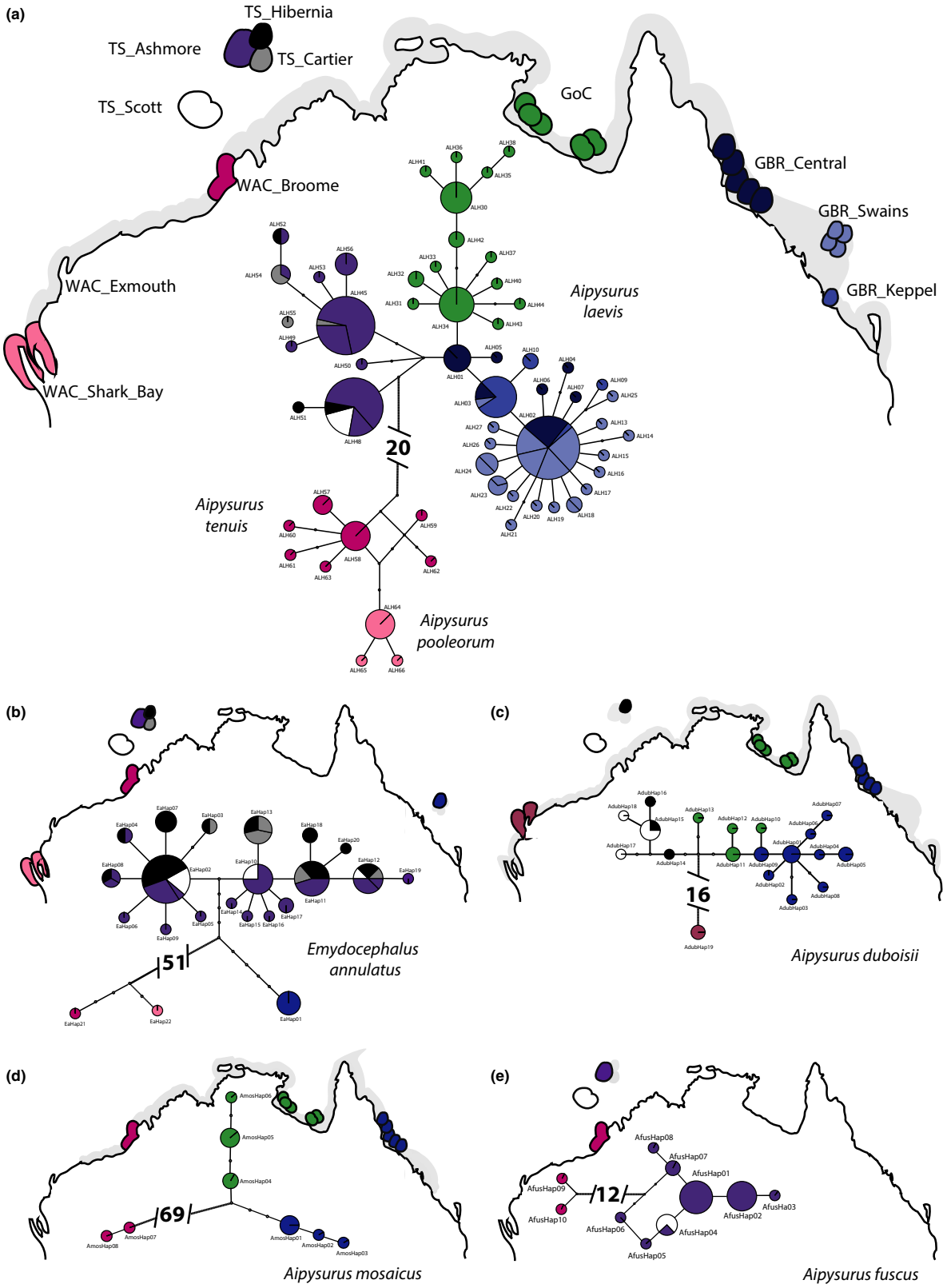

FIGURE 3 Maximum-parsimony haplotype networks for five Australasian species or species groups. (a) *Aipysurus laevis* + *A. tenuis* + *A. pooleorum*, (b) *Emydocephalus annulatus*, (c) *A. duboisii*, (d) *A. mosaicus* and (e) *A. fuscus*. Each circle represents a haplotype, with size of the circle indicating the frequency of the haplotype and the smallest circle representing one individual. For each species, the associated map shows the locations for which samples were obtained, with the colours of sampled haplotypes corresponding to locations. Numbers on branches between Western Australian Coast (WAC) haplotypes and other regions indicate the number of base-pair differences between groups. Pale grey shading on each map indicates known geographic range for each species (also shown in Figure 1)

disequilibrium (LD) among pairs of loci or spatial patterns of LD among species (Table S5; Supporting Information).

3.2.1 | Multispecies comparison in the genus *Aipysurus*

Highest Δ*K* for the seven species *Aipysurus* STRUCTURE analysis was for *K* = 4 followed by *K* = 6 (Figure S4). Plots of *Q* values for *K* = 4 through *K* = 7 clearly delineated *A. duboisii*, *A. mosaicus*, *A. fuscus*, *A. laevis* with no admixed individuals (Figure 4). For *K* = 4, *A. tenuis*, *A. apraefrontalis*, *A. foliosquama* comprised admixed individuals of the genetic clusters that characterized *A. mosaicus*, *A. fuscus*, *A. laevis*. In particular, several *A. tenuis* were clustered with *A. mosaicus* than *A. laevis*; however, this is most likely an artefact of small sample sizes given the obvious differentiation between the two species based on mtDNA and PCA analyses of the microsatellite data (see below). Indeed, for increasing values of *K*, *A. tenuis*, *A. apraefrontalis*, *A. foliosquama* became distinct genetic clusters, with *K* = 6 providing the best resolution among species (Figure 4), although not distinguishing *A. apraefrontalis* from *A. foliosquama* (red clusters), again likely due to small sample sizes (*n* = 2 per species). The additional genetic cluster for *K* = 7 (grey) did not distinguish these two closely related species; rather it delineated some admixed individuals for *A. mosaicus* and *A. tenuis* (Figure 4).

The first two PC axes of genetic distances among seven *Aipysurus* species accounted for 76% of variation in the data. *Aipysurus laevis* and *A. tenuis* clustered closely on PC1 and PC2, and *A. duboisii*, *A. mosaicus* and *A. fuscus* were grouped in same quadrant (Figure 5a). By contrast, *A. apraefrontalis* and *A. foliosquama* appeared highly differentiated, potentially an artefact of small sample sizes given that at the level of individuals, these species were not highly differentiated (Figure S5). The first two PC axes at the level of region within species (excluding *A. apraefrontalis* and *A. foliosquama*) accounted for 53% of the variation, with PC1 separating *A. duboisii* from the remaining species and PC2 separating *A. mosaicus* from *A. laevis*, *A. tenuis* and *A. fuscus* (Figure 5b). The latter three species formed distinct but closely aggregated clusters. Of note is that WAC samples for *A. mosaicus*, *A. duboisii* and *A. fuscus* (albeit to a lesser extent) were highly differentiated from conspecifics in other regions (Figure 5b). This pattern was reflected in the magnitudes of regional pairwise F'_{ST} values involving the WAC (Figure S2b).

3.2.2 | Intraspecific population structure

Highest Δ*K* for *E. annulatus* was for *K* = 5 (Figure S6), with the GBR (blue) and WAC (pink) each forming a cluster with minimal admixture (Figure 6a), while the remaining three clusters were distributed among TS reefs, with varying degrees of admixture. Highest Δ*K* for *A. laevis* + *A. tenuis* was for *K* = 2, which essentially delineated a divide between the GoC + GBR and TS + WAC, but with high levels of admixture for *A. tenuis* (Figure 6b). The next highest Δ*K*, for *K* = 3, identified the same east–west divide but also delineated *A. tenuis* (WAC) from *A. laevis* (TS), and resolved some differentiation within GBR and between the GBR and GoC (Figure 6c). Highest Δ*K* for *A. duboisii* was *K* = 3, and for *A. mosaicus* and *A. fuscus* was *K* = 2; however, absolute values of Δ*K* were small (<12). For *K* = 3, the WAC individuals for *A. duboisii* (Figure 6d) and *A. mosaicus* (Figure 6e) were identified as a distinct genetic cluster (pink) with minimal admixture, although this was not the case for *A. fuscus* (Figure 6f).

PCAs returned very similar patterns. For *E. annulatus*, the first two PC axes accounted for 89% of variation, with TS reefs clustered closely on PC1 and PC2, while the GBR and WAC were highly differentiated from the TS reefs and each other (Figure 5c). For *A. laevis*, the first two PC axes accounted for 71% of variation with PC1 strongly delineating east versus west locations, while PC2 further delineated TS_*A. laevis* from WAC_*A. tenuis* (Figure 5d). These patterns were reflected in the magnitudes of standardized pairwise F'_{ST} values (Figure S2b); however, significances for regional pairwise F_{ST} values were highly variable and did not mirror the magnitudes of F_{ST} (Table S6) or F'_{ST} values (Figure S2b), most likely due to small

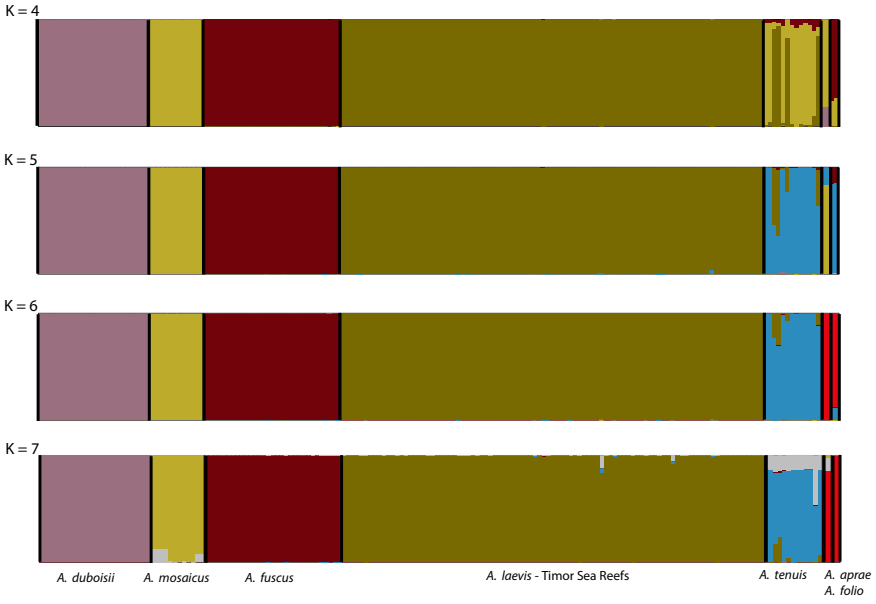

FIGURE 4 STRUCTURE plots for Bayesian clustering analyses of seven nominal sea snake species from the genus *Aipysurus* (i.e., not including *Emydocephalus annulatus*) using 11 microsatellite loci for *K* = 4 to *K* = 7. Note that for *A. laevis*, only Timor Sea reefs were included to avoid the analysis being overwhelmed by the large number of individuals sampled in the Great Barrier Reef and Gulf of Carpentaria. Colours correspond to colours used in species range maps in Figure 1

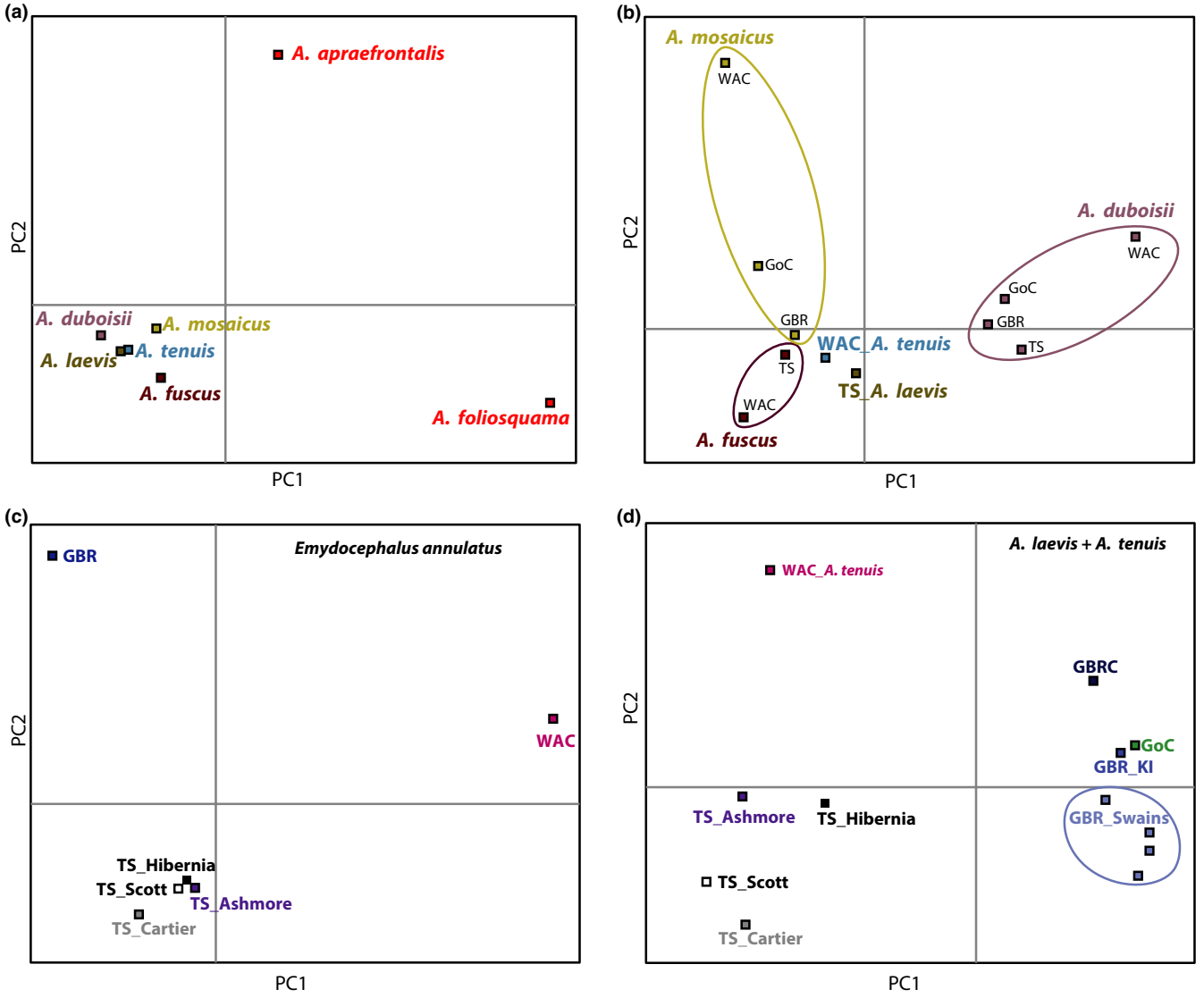

FIGURE 5 PCAs for 11 microsatellite loci: (a) PCA at the level of species for seven species from the genus *Aipysurus* using the same data as Figure 4; (b) PCA at the level of region for five species from the genus *Aipysurus* (excluding *A. foliosquama* and *A. apraefrontalis*). Colours in (a) and (b) are species colours used in Figures 1 and 4. (c) PCA for *Emydocephalus annulatus* at the level of locations within regions; (d) PCA for *A. laevis* + *A. tenuis* at the level of locations within regions. Colours in (c) and (d) are location colours used in haplotype networks in Figure 3

sample sizes in some regions. Intraspecific patterns from PCAs for *E. annulatus* and *A. laevis* + *A. tenuis* were reflected in corresponding pairwise F'_{ST} values among locations (Table S7).

3.2.3 | Genetic diversity and HWE

Mean (±*SE*) allelic richness (A_r) was similar among species (range: 3.8 ± 0.50–4.8 ± 0.38) and among regions within species, some evidence of increasing diversity from east to west (Table 1). Within species, there was a trend of negative *Fis* values in the GBR for *E. annulatus* and *A. laevis*, while larger positive F_{is} values occurred in the TS (Table S8). Five of seven significant global one-tail tests for heterozygote deficit (HD) were at TS reefs (*E. annulatus*: TS_Ashmore, TS_Cartier, TS_Hibernia; *A. laevis:* TS_Cartier; *A. fuscus*: TS_Ashmore) with each species–location combination having one or two loci with HD (Table S8). *Aipysurus tenuis* (WAC) had significant global HD and three loci with HD (Table S8). No locus was over-represented for HD, and there was no heterozygote excess at any location for any species.

4 | DISCUSSION

4.1 | Temporal divergences and Pleistocene glaciation cycles

Over the past 2 million years, Pleistocene sea level fluctuations have repeatedly altered the distributions of Australia's shallow water marine environments with sea levels 120 m below present levels at the height of the three most recent glaciation cycles [Voris (2000): 250, 150, 17 Kya]. The Torres Strait land bridge emerged early in each glaciation cycle, when sea levels reached 10 m below present levels,

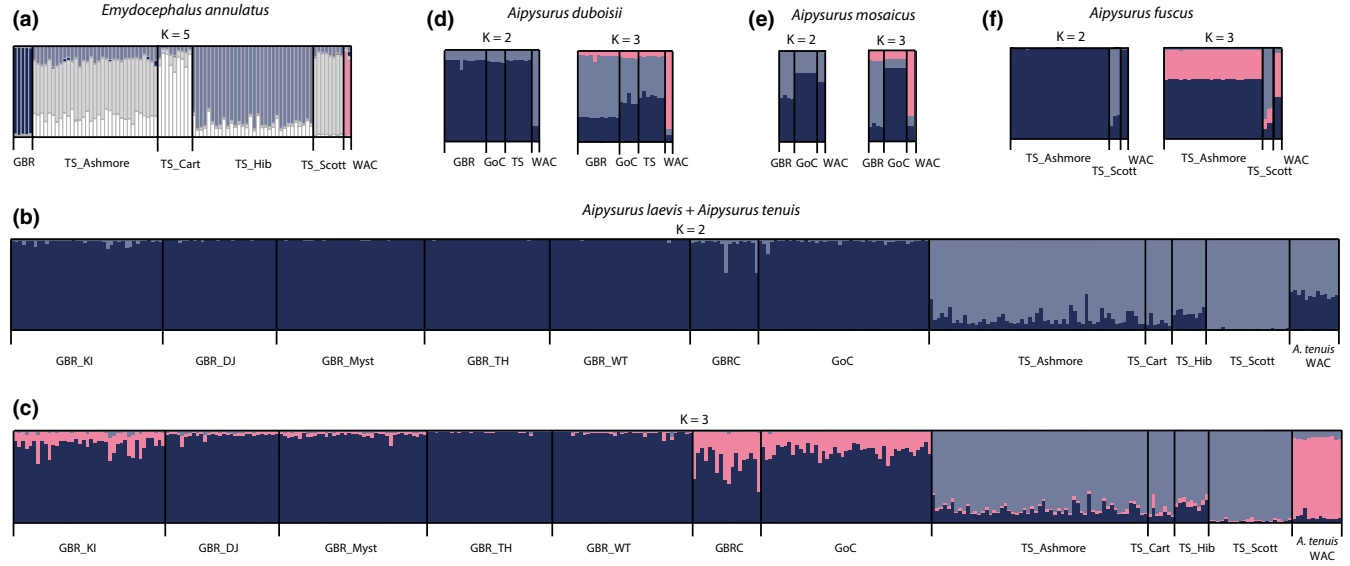

FIGURE 6 STRUCTURE plots for Bayesian clustering analyses for each of five sea snake species or species group based on 11 microsatellite loci. Note that colours in STRUCTURE plots reflect the genetic clusters identified by the analyses rather than geographic locations of sampled individuals. See text for more details

separating the GBR and GoC, then extended westwards to obliterate the entire present-day GoC (Figure 1b) as sea levels continued to fall (Voris, 2000). Molecular dating estimates for sea snakes between the GBR and GoC spanned 49–70 Kya and between the TS and GBR + GoC spanned 78–130 Kya, broadly congruent with repeated Pleistocene vicariance, suggesting that contemporary sea snake populations in these regions arose via range expansion from Pleistocene refugia, most likely located on both sides of the Torres Strait land bridge. By contrast, WAC sea snakes diverged from conspecifics 178–526 Kya, while interspecific divergences between small-range WA endemics occurred 231–487 Kya. There is no evidence that Pleistocene sea level fluctuations resulted in physical barriers to dispersal between coastal WA and TS reefs (Voris, 2000), suggesting different processes were involved. One of the few genetic studies that surveyed the same four regions included in my study found that egg-laying green turtles, *Chelonia mydas*, in the WAC and TS reefs comprised of distinct breeding stocks (Dethmers et al., 2006). Nonetheless, the deepest genetic divide was between rookeries in the GBR versus the GoC + TS + WAC (figure 3 in Dethmers et al., 2006), most likely reflecting the influence of the Torres Strait land bridge. Treml, Roberts, Halpin, Possingham, and Riginos (2015) used simulations of 99 hypothetical taxa with varying dispersal potential to explore the permeability of 12 predefined barriers throughout the Indo Pacific, including the barrier between the WAC and TS reefs/Indonesia identified by Dethmers et al. (2006) and Imron, Hale, Degnan, and Degnan (2007) for the low-dispersal abalone, *Haliotis asinine*. Note that in Treml et al. (2015) this barrier "L" (grey dashed line on my Figure 1) was incorrectly drawn south of Broome, whereas the genetic divides identified in the original papers were north of Broome (black dashed line in my Figure 1). This barrier was the strongest taxon filter among the 12 barriers investigated, filtering 72% of taxa in the north–south direction and 93% in the south–north direction (Treml et al., 2015); however, the Torres Strait was not included among the barriers investigated. These simulations suggest the presence of a generally unappreciated semipermeable barrier between the WAC and TS that may be restricting gene flow in low-dispersal species (Treml et al., 2015), but which have not detected by previous genetic studies of some fish species (Giles et al., 2014; Liggins et al., 2016; van Herwerden et al., 2006).

4.2 | Evolutionary distinctiveness of sea snakes in coastal Western Australia

This first large-scale comparative phylogeographic evaluation for an Australian group of marine vertebrates revealed highly congruent phylogeographic breaks among co-occurring sea snake species, which were largely supported by nuclear microsatellites. Sea snakes from the WAC were genetically highly divergent from their counterparts (conspecifics or sister species) in the TS, GoC and/or GBR, whereas there were shallow genetic divergences between the TS, GoC and GBR for mtDNA, with microsatellites delineating an east–west divide between the TS and GoC + GBR. Lack of differentiation between the GoC and GBR for microsatellites likely reflects the very recent divergence between these two regions or ongoing sex-biased (male) dispersal. Molecular dating reflected these patterns, albeit with considerable overlap in 95% HPDs. Previous molecular dating using longer sequences (>6,000 bp mtDNA and five nuclear genes) returned identical mean divergence estimates for the *Aipysurus* group (2.6 Mya) and the genus *Aipysurus* (1.5 Mya) but with narrow 95% HPDs (Sanders et al., 2013); however, despite using relatively rapidly evolving nuclear genes Sanders et al. (2013) found insufficient resolution to infer relationships among the recently diverged species in the *Aipysurus* group. Thus, the addition of nuclear genes would

not have resolved the very recent divergences times of interest in my study.

4.3 | Taxonomic implications

Recent studies have revealed several new sea snake species endemic to Australia (Ukuwela, Sanders, & Fry, 2012; Ukuwela et al., 2013), including the recently described Australian endemic *A. mosaicus* (Sanders et al., 2012), which is sister species to *A. eydouxi* that occurs throughout Southeast Asia. The only previous large-scale genetic surveys for *Aipysurus* (Lukoschek, Waycott, et al., 2007, Lukoschek et al., 2008) sampled *A. laevis* from the TS, GoC and GBR, plus one individual from Broome, WAC, which had a highly divergent haplotype (ALH38 in Figures 2 and 3; Lukoschek, Waycott, et al., 2007). Morphological examination identified this snake as *A. tenuis*, previously known only from four formalin preserved samples accessioned in Russia (Kharin & Cheblyukov, 2006). The inclusion of additional *A. tenuis* from Broome plus *A. pooleorum* from Shark Bay in my study demonstrated that *A. tenuis* as paraphyletic with *A. pooleorum* and that the *A. tenuis* + *A. pooleorum* clade is sister taxon to *A. laevis*. The close relationship between *A. laevis* and *A. tenuis* was supported by microsatellite data, which indicated admixture between the two species for some *A. tenuis* individuals (unfortunately, there were no microsatellite data for *A. pooleorum*). These findings contradict the mitochondrial gene tree in Sanders et al. (2013), which placed *A. pooleorum* as sister taxon to *A. apraefrontalis*. However, the *A. pooleorum* samples used in Sanders et al. (2013) were subsequently identified as *A. foliosquama* (D'anastasi et al., 2016), and the sister species relationship between *A. apraefrontalis* and *A. foliosquama* is consistent with shared morphological characteristics unique to the two WA endemics [e.g., ventral scales with a deep median notch on posterior surface (Cogger, 2000; Voris, 1977)].

The previously unappreciated genetic distinctiveness of *A. mosaicus*, *A. duboisii* and *E. annulatus* from the WAC, combined with the presence of several small-range endemics in this region, suggests that coastal WA may harbour several cryptic species in the *Aipysurus* group. Nonetheless, in the absence of phylogenetically analysable nuclear DNA and morphological and/or behavioural data from most WAC snakes (Andrews et al., 2016; Bickford et al., 2007; Carstens, Pelletier, Reid, & Satler, 2013), a formal taxonomic revision is premature. Regardless of taxonomic status, the cryptic genetic diversity harboured in coastal WA has implications for conservation.

4.4 | Conservation implications

Marine biodiversity in coastal WA has received far less attention than in eastern (and northern) Australia (Wilson & Kirkendale, 2016). This study documented geographically structured cryptic diversity in *Aipysurus* group sea snakes, with nuclear and mitochondrial DNA identifying the WAC as genetically unique, while mtDNA delineated intraspecific clades in coastal WA as evolutionary significant units (Moritz, 1994). Combined with the high endemism and comparatively small species ranges in this region, these genetic findings highlight the importance of coastal WA for conserving Australia's marine reptile biodiversity. However, in order to implement targeted and effective conservation strategies, specific threatening processes impacting sea snakes need to be identified. A review of potential causes of the precipitous declines of sea snakes on Ashmore Reef found that the four main candidates (habitat loss or degradation, reduced prey abundance, trawl fisheries bycatch and/or illegal harvesting) were unlikely to have been the culprits on this highly protected offshore TS reef (Lukoschek et al., 2013). Similarly, there were no obvious targetable threatening processes associated with sea snake declines on protected reefs in New Caledonia (Goiran & Shine, 2013) or the southern GBR (Lukoschek, Heatwole, et al., 2007). Other possible causes for the enigmatic declines in sea snake abundances (discussed in detail in Lukoschek et al., 2013) include the following: disease, particularly as increased sea surface temperatures can promote the spread and prevalence of pathogens and increase host disease susceptibility (Harvell et al., 2002); invasive species; pollution, including oil spills; seismic surveys; and recruitment failure.

There is currently no evidence, however, either supporting or negating the potential negative impact of any of these factors on sea snakes, either in Australia or elsewhere. As such, targeted research addressing knowledge gaps about habitat and diet requirements, reproductive biology, disease susceptibility and the impacts of anthropogenic processes on sea snakes is crucial, particularly in coastal WA, where threatened sea snake species occur across a wide range of latitudes in diverse habitats with different impact regimes. For example, the small-range endemics *A. foliosquama* and *A. pooleorum* occur in Shark Bay's extensive seagrass meadows (D'anastasi et al., 2016), which experienced catastrophic diebacks following a prolonged thermal anomaly in 2010/2011 (Thomson et al., 2015). This anomaly also caused widespread coral mortality from bleaching spanning 12° of latitude along the WAC (Moore et al., 2012), severe impacting Exmouth Gulf (Depczynski et al., 2013) where the new records for *A. apraefrontalis* occurred (D'anastasi et al., 2016; Sanders et al., 2015). In addition, sea snakes have been recorded in the bycatch of demersal trawlers in shallow water habitats of coastal WA (D'anastasi et al., 2016). However, it is not known whether these thermal anomalies and/or fisheries bycatch are detrimentally affecting sea snakes. Indeed, basic information about the distribution and abundance of sea snakes in coastal WA is urgently needed to accurately assess the conservation status of species.

What is known, however, is that *Aipysurus* group sea snakes have restricted dispersal across multiple spatial scales. Evidence supporting restricted dispersal comes from this and other genetic studies (Lukoschek & Shine, 2012; Lukoschek, Waycott, et al., 2007; Sanders et al., 2015) that, combined with mark–recapture evidence (Burns & Heatwole, 1998; Lukoschek & Shine, 2012; Lynch, 2000) and the intrinsically patchy distributions of species (Lukoschek, Heatwole, et al., 2007), indicates population declines or local extinctions of sea snakes are unlikely to be reversed by dispersal over time frames relevant to conservation. Two approaches that might be adopted to reverse population declines are the

direct translocation of sea snakes from nearby locales where population abundances are stable and captive breeding programmes. However, these approaches are associated with numerous potential pitfalls. For example, translocations would need to consider the genetic signatures (including adaptation) of translocated individuals and would likely fail if the processes driving the initial population declines have not been addressed. Captive breeding programmes would be labour, cost and time intensive, given that sea snakes reproduce annually, have average gestation times of 6–8 months, and clutch sizes are small (Fry, Milton, & Wassenberg, 2001). Nonetheless, breeding programmes might provide useful information about the specific dietary requirements, reproductive biology and disease susceptibilities of species that may be translated to species conservation in the wild. For the moment, however, the most urgent priority is to undertake targeted research into the basic biology, distribution, abundance and conservation status of species and populations to understand the reasons for recent declines. In the meantime, a parsimonious approach to conserving critically endangered sea snakes in coastal WA would be to minimize the impacts of trawling and reduce the numerous anthropogenic impacts on the environment (climate change, pollution, oils spills, seismic surveys) known to negatively impact numerous marine species.

ACKNOWLEDGEMENTS

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DATA ACCESSIBILITY

Data 1: Details of all individuals used in the study including sampling location (latitude and longitude) and mitochondrial haplotype of each individual: Table S1.

Data 2: Mitochondrial sequences as final alignment of 125 unique haplotypes plus 16 outgroups are available and as supplementary material in Nexus format: AipysurusEmydo16outgroupsMtDNAalign.nex.

Data 3: Full microsatellite dataset is available as Supplementary Material as Excel spreadsheet in GenAlEx format: AipysurusEmydocephalusMicrosatelliteData.xlsx.

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BIOSKETCH

I am passionately interested in the conservation of marine biodiversity and use population genetic and phylogenetic approaches to evaluate patterns of genetic diversity and connectivity to inform management. I have an ongoing interest in the endlessly fascinating lives of marine snakes and the coral reefs they inhabit, and I am concerned about the ongoing challenges they face. I designed and conducted the field and laboratory research, analysed the data, prepared the figures and wrote the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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