Resolving the higher-order phylogenetic relationships of the circumtropical *Mabuya* group (Squamata: Scincidae): An out-of-Asia diversification

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ABSTRACT

Despite an abundance of phylogenetic studies focused on intrageneric relationships of members of the *Mabuya* group, the intergeneric relationships have remained difficult to resolve. The most-persistent unresolved regions of the phylogeny of the group include: (1) the placement of the Middle-Eastern *Trachylepis* with respect to the Afro-Malagasy *Trachylepis* and its taxonomic status; (2) the phylogenetic position of the Cape Verdean *Chioninia* within the larger *Mabuya* group; (3) support for the placement of *Dasia* with respect to the entire group; and (4) the phylogenetic placement of *Eutropis novemcarinata* with respect to other *Eutropis* and *Dasia*. In this study, we include representatives of all these taxa as well as African *Eumecia* and Neotropical *Mabuya*. We seek to address these phylogenetic and systematic issues by generating a well-resolved and supported phylogeny for the *Mabuya* group as a whole that can be used to develop a stable taxonomy and reconstruct the geographic patterns of diversification within the group. To meet these goals, we built a large multi-locus dataset of 11 markers (nine nuclear and two mitochondrial), and performed concatenated and species tree analyses to generate a well-supported phylogeny for the group. Statistical topology tests reject the monophyly of Middle-Eastern *Trachylepis* with Afro-Malagasy *Trachylepis*, and to reflect monophyly we place the Middle-Eastern species into a previously described genus, *Heremites*. Cape-Verdean *Chioninia* are resolved as the strongly supported sister-group to Afro-Malagasy *Trachylepis*. Monophyly of the Southeast-Asian genera, *Eutropis* and *Dasia*, is not supported, with a clade composed of *Dasia* + *Eutropis novemcarinata* more closely related to the rest of the *Mabuya* group than to the remaining *Eutropis*. The phylogenetic position of *E. novemcarinata* renders *Eutropis* polyphyletic, and we therefore describe and place *E. novemcarinata* into a new monotypic genus, *Toenayar*, to preserve monophyly among the genera. In light of these novel findings, we review and discuss the historical biogeography of the entire *Mabuya* group.

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1. Introduction

1.1. Background

Historically, a large group of circumtropically distributed skinks have been placed into the catch-all genus *Mabuya* sensu lato. Since the work of Mausfeld et al. (2002) most authors have recognized four generic-level clades within what was once *Mabuya*: *Eutropis*, *Trachylepis*, *Chioninia* and *Mabuya* sensu stricto. Based primarily on skull morphology, Greer (1977, 1976, 1970, 1967) recognized a broader *Mabuya* group, including *Eumecia* Bocage, 1870, which had long been considered part of *Lygosoma* or *Riopa*, the giant,

extinct Cape Verdean *Macroscincus*, and the arboreal Southeast Asian genera *Dasia* and *Apterygodon*. He also believed that similarities shared between *Lygosoma* and *Lamprolepis* on the one hand and *Mabuya* on the other were evidence of their shared ancestry (Greer, 1977, 1970, 1967). Some of these groups have been corroborated as being allied to *Mabuya* sensu lato (Carranza et al., 2001), but others have been excluded from close affinity by molecular data (e.g., Honda et al., 2000; Skinner et al., 2011). The larger *Mabuya* group has been formally recognized as a distinct Subfamily Mabuyinae (Mittleman, 1952), or as a distinct Family Mabuyidae as part of a larger Scincomorpha [=Scincidae Oppel, 1811] (Hedges and Conn, 2012; Hedges, 2014). However, the familial taxonomy of Hedges and Conn (2012) and Hedges (2014) has remained controversial (Lambert et al., 2015; Pinto-Sánchez et al., 2015; Pyron et al., 2013), and in this study we refer to this radiation of lizards as the *Mabuya* group and follow Lambert

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et al. (2015) in considering it a member of the scincid subfamily Lygosominae.

With the first use of molecular phylogenetics in the group, Honda et al. (1999), based on mitochondrial data from a limited sampling of taxa, confirmed that *Dasia* and *Apterygodon* belonged to the same monophyletic group as *Mabuya* sensu lato (represented in their phylogenies by monophyletic Asian and African lineages). In addition, Mausfeld et al. (2000), using 487 bp of 16S recovered African and American *Mabuya* as sister to Asian forms. Honda et al. (2003) found similar results, but further identified *Dasia*, including *Apterygodon*, as sister to Asian *Mabuya*, implying a paraphyletic *Mabuya*.

Mausfeld et al. (2002) used the same mitochondrial genes as Honda et al. (1999), but had a more representative sampling of *Mabuya* group taxa. Although not including *Dasia*, they did include species from the Cape Verde Islands, which were recovered as another deeply divergent and geographically coherent clade. Based on their phylogenetic results they divided the group, resurrecting *Eutropis* Fitzinger, 1843 for Asian *Mabuya*, *Euprepis* Wagler, 1830 for Afro-Malagasy *Mabuya*, and *Chioninia* Gray, 1845 for Cape Verdean forms, retaining *Mabuya* Fitzinger, 1826 for New World skinks. They recovered the following phylogenetic pattern: *Eutropis* (*Chioninia* (*Mabuya*, *Euprepis*)). Following the break-up of *Mabuya* by Mausfeld et al. (2002) and Bauer (2003) demonstrated that the name used by these authors for the Afro-Malagasy clade of "*Mabuya*", *Euprepis*, is in fact a synonym of *Mabuya* sensu stricto and that *Trachylepis* Fitzinger, 1843 is the oldest name attributable to the Afro-Malagasy clade.

Mabuya group skinks from a variety of Indian and Atlantic Ocean islands have subsequently been shown to be part of the *Trachylepis* lineage. Mausfeld et al. (2002) and Carranza and Arnold (2003) initially showed that a species endemic to Fernando de Noronha off the coast of Brazil (*Trachylepis atlantica*) was a member of this clade, indicating two separate dispersals across the Atlantic Ocean within the group. Taxa from Madagascar, the Comoros, the Seychelles, the islands of the Gulf of Guinea, and Socotra have all also been shown to be part of *Trachylepis* (Carranza and Arnold, 2003; Lima et al., 2013; Rocha et al., 2010; Sindaco et al., 2012), indicating that overwater dispersal has played a major role in the history of the group.

Following the generic split by Mausfeld et al. (2002), molecular systematic studies within each of the new genera have produced well-supported trees to infer intrageneric relationships. Taxa that have been relatively well-studied include the Neotropical group (Carranza and Arnold, 2003; Hedges and Conn, 2012; Miralles and Carranza, 2010; Miralles et al., 2009; Whiting et al., 2006); the Cape Verde Islands *Chioninia* (Brehm et al., 2001; Carranza et al., 2001; Miralles et al., 2011); and the Asian *Eutropis* (Barley et al., 2015, 2013; Das et al., 2008; Datta-Roy et al., 2012; Honda et al., 1999; Mausfeld and Schmitz, 2003). Afro-Malagasy *Trachylepis* have been the subject of numerous phylogenetic studies (Carranza and Arnold, 2003; Lima et al., 2013; Mausfeld et al., 2002, 2000; Sindaco et al., 2012; Vences et al., 2014), however taxon sampling for this group still remains incomplete at only about 40% of known species. Phylogenetic relationships within the genus *Dasia* also remain relatively poorly known, with six of nine species included and relationships not strongly supported (Harikrishnan et al., 2012).

The four-genus taxonomy of Mausfeld et al. (2002) has remained fairly stable except for the exhaustive revision of the Neotropical species that placed them in a total of 16 genera, 15 of them newly described or resurrected (*Copeoglossum*, *Mabuya*, *Spondylurus*, *Alinea*, *Aspronema*, *Brasiliscincus*, *Capitellum*, *Exila*, *Manciola*, *Maracaiba*, *Marisora*, *Notomabuya*, *Orosaura*, *Panopa*, *Psychosaura*, and *Varzea*) (Hedges and Conn, 2012), however, this revi-

sion has remained controversial (Lambert et al., 2015; Pinto-Sánchez et al., 2015; Pyron et al., 2013), as some of these clades have subsequently been found to be non-monophyletic (Pinto-Sánchez et al., 2015). We, therefore, follow Pinto-Sánchez et al. (2015) in maintaining the genus *Mabuya* to refer to the entire Neotropical radiation.

1.2. Persistent issues

Despite the abundance of molecular systematic studies and sequence data aimed at resolving relationships within a particular genus, resolution at deeper nodes has remained problematic, likely due to the exclusive use of mitochondrial or non-overlapping markers in many of these studies. The most-persistent unresolved regions of the tree include: (see below for details on each): (1) the placement of the Middle-Eastern *Trachylepis* with respect to the Afro-Malagasy *Trachylepis* and its taxonomic status; (2) the phylogenetic position of the Cape Verdean *Chioninia* within the larger *Mabuya* group; (3) support for the placement of *Dasia* with respect to the entire group; and (4) the phylogenetic placement of *Eutropis novemcarinata* with respect to other *Eutropis* and *Dasia*.

1. Mausfeld and Schmitz (2003) and Carranza and Arnold (2003) were the first to include the Middle Eastern *Trachylepis* in a molecular phylogeny. The former authors recovered the three species considered (*T. aurata*, *T. vittata*, *T. septentaeniata*) as either sister to Afro-Malagasy *Trachylepis* (Maximum Likelihood) or to *Eutropis* + *Dasia* (Maximum Parsimony) although with weak support in either case. They raised the possibility that Middle Eastern taxa might represent a separate lineage requiring generic recognition. Carranza and Arnold (2003), however, had support for the sister relationship of these taxa to the Neotropical *Mabuya*. Sindaco et al. (2012) likewise recovered a monophyletic Middle Eastern *Trachylepis* group, which they recovered as sister to the Neotropical *Mabuya*, although without support. Because they were unable to reject the monophyly of *Trachylepis* they tentatively retained the Middle Eastern taxa in this genus. In this study we seek to resolve the phylogenetic placement of the Middle-Eastern *Trachylepis*, a result that may have implications for the taxonomic status of this clade.

2. Although the evolutionary relationships within the Cape Verdean *Chioninia* are well known (Brehm et al., 2001; Carranza et al., 2001; Miralles et al., 2011), the phylogenetic placement of *Chioninia* within the larger *Mabuya* group is not supported. With poor support in all instances, different analyses (all using similar mitochondrial sequence data) have placed *Chioninia* as sister to the Neotropical *Mabuya* (Datta-Roy et al., 2012), sister to a clade comprising both the Neotropical *Mabuya* and the Middle-Eastern *Trachylepis* (Carranza and Arnold, 2003), sister to a clade comprising the Neotropical and Afro-Malagasy species (Mausfeld et al., 2002), or as part of a basal polytomy for all the groups excluding *Eutropis* (Sindaco et al., 2012). Through the use of a large sampling of nuclear markers, we hope to resolve this phylogenetic issue and correctly determine the phylogenetic position of *Chioninia* within the rest of the *Mabuya* group.

3. Originally included in the phylogeny by Mausfeld and Schmitz (2003), *Eutropis dissimilis* has historically been a problematic species, as it was consistently resolved as a poorly supported sister-taxa to *Dasia* rather than being nested within the rest of *Eutropis* (Bauer et al., 2008; Datta-Roy et al., 2012; Mausfeld and Schmitz, 2003). However, after specimens from the type locality of *Eutropis dissimilis* were sequenced, it became apparent that the specimen (from Myanmar) that had been used as

an exemplar of *E. dissimilis* in all previous studies was, in reality, a specimen of *E. novemcarinata* (Datta-Roy et al., 2015). True *Eutropis dissimilis* was found to fall within the Indian radiation of *Eutropis*, whereas *E. novemcarinata* was retrieved as sister to the species of *Dasia* included in the analysis. In this study, we seek to fully confirm the placement of *Eutropis novemcarinata* within the *Mabuya* group and, in order to corroborate the results of Datta-Roy et al. (2015), we also include a specimen of *Eutropis dissimilis* in our analysis.

4. The arboreal members of the genus *Dasia* have long been known to be part of the *Mabuya* group (Greer, 1977, 1970). They have often been resolved as the sister group to *Eutropis*, albeit with low-support (Honda et al., 2003, 2000, 1999; Mausfeld and Schmitz, 2003), however, other phylogenetic reconstructions (with no newly generated genetic data) have placed *Dasia* with low-support as sister to *Trachylepis* (Datta-Roy et al., 2012; Pyron et al., 2013). In this study we hope to find support for the placement of *Dasia* with respect to the entire group.

There is evidence that two other taxa may be part of the *Mabuya* group based on molecular or morphologic data, but we were unable to include them in this study. First, *Lamprolepis vyneri* was previously shown to be more closely related to *Dasia* rather than to *Lamprolepis smaragdina*, although this has not been reflected in any taxonomic changes (Linkem et al., 2013). Second, it has been proposed that *Vietnascincus rugosus* is closely related to *Dasia* (Darevsky and Orlov, 1994; Hedges, 2014), however no molecular data exists for this monotypic genus and others have suspected it may be more closely related to *Lamprolepis* given the shared separation of the palatal rami (Honda et al., 1999; Reeder, 2003).

1.3. Research goals

We seek to address these phylogenetic and systematic issues by generating a well-resolved and supported phylogeny for the *Mabuya* group as a whole that can be used to develop a stable taxonomy and reconstruct the geographic patterns of diversification within the group. To meet these goals, we have generated a large multi-locus dataset of 11 markers (nine nuclear and two mitochondrial), performed concatenated maximum-likelihood and Bayesian analyses, Bayesian coalescent species trees, and utilized statistical topology tests to compare competing topological hypotheses.

2. Methods

2.1. Taxon sampling

We chose taxa from each major lineage within the *Mabuya* group, including eight species of *Eutropis*, with one from each major subclade identified by Barley et al. (2015): *E. novemcarinata*, *E. longicaudata*, *E. multifasciata*, *E. rudis*, *E. rugifera*, *E. indeprensa*, *E. dissimilis*, and *E. macularia*; two species of *Dasia*: *D. vittata* and *D. olivacea*; two species of the Middle-Eastern group of *Trachylepis*: *T. aurata* and *T. septemtaeniata*; two specimens of the central African *Eumecia anchietae*; representatives of three species of Neotropical *Mabuya*: *Mabuya frenata*, *Mabuya aurae*, and *Mabuya guaporicola*, each of which is assigned to a different genus by Hedges and Conn (2012) and represent divergent lineages within this clade; two species of Cape Verdean *Chioninia*: *C. delalandii* and *C. vaillanti*, and four species that represent divergent subclades within Afro-Malagasy *Trachylepis*: *T. aureopunctata*, *T. depressa*, *T. boulengeri*, and *T. paucisquamis* (Table 1). We sequenced nearly

Table 1
Specimens included in the study and their collection localities. See supplemental Table S1 for GenBank accession numbers and available GPS coordinates. Institution abbreviations are as follows: AMS = Australian Museum, BMNH = The Natural History Museum, London, CAS = California Academy of Sciences, FMNH = Field Museum of Natural History, MVZ = Museum of Vertebrate Zoology, PEM = Port Elizabeth Museum (Bayworld), UAM = University of Alaska Museum of the North, UMa = University of Madeira (Brehm et al., 2001), UWBM = University of Washington Burke Museum, ZFMK = Zoologisches Forschungsmuseum Alexander Koenig, MZKU = Zoological Museum, Kasetsart University.

Species	Catalog number	Locality
Chioninia delalandii (chimera)	BMNH 2000.18	Cha das Caldeiras, Fogo, Cape Verde
Chioninia delalandii (chimera)	UMa (R52)	Fogo, Cape Verde
Chioninia vaillanti (chimera)	BMNH 2000.10	Santa Cruz, Santiago, Cape Verde
Chioninia vaillanti (chimera)	UMa (49Mva6F)	Feijoal, Fogo, Cape Verde
Dasia olivacea	BRK 392	Nanga Benin Longhouse, Kapit Div., Sarawak, Malaysia
Dasia vittata	BRK 391	Nanga Benin Longhouse, Kapit Div., Sarawak, Malaysia
Eumecia anchietae 1	PEM R16786	Klein's Camp, Tanzania
Eumecia anchietae 2	PEM R16779	Klein's Camp, Tanzania
Eutropis dissimilis	MVZ 248450	Jogi Village Society, Makli, Thatta, Thatta District, Sind Province, Pakistan
Eutropis indeprensa	FMNH 282851	0.5 km N, 0.25 km W, Mt. Ambulong peak, Lubang, Occidental Mindoro Prov., Philippines
Eutropis longicaudata	MZKU R00704	Nong Bua Lamphu, Thailand
Eutropis macularia	CAS 247949	Yebyu Township, Tanintharyi Nature Reserve, Tanintharyi Div., Myanmar
Eutropis multifasciata	FMNH 269170	Penyilam, Bintulu Div., Sarawak, Malaysia
Eutropis novemcarinata 1	CAS 213820	Pwint Phu Township, Shwesettaw Wildlife Sanctuary, Lap Pam San Camp, Magway Div., Myanmar
Eutropis novemcarinata 2	CAS 216022	Na Htoe Gyi Township, Minsontaung Wildlife Sanctuary, Htan Taw Village, Mandalay Div., Myanmar
Eutropis rudis	FMNH 239732	Mendolong camp, Sipitang Dist., Sabah, Malaysia
Eutropis rugifera (chimera)	FMNH 273652	Samarakan, Bintulu Div., Sarawak, Malaysia
Eutropis rugifera (chimera)	FMNH 267951	Samarakan, Bintulu Div., Sarawak, Malaysia
Heremites aurata	ZFMK 75837	Halfeti, Turkey
Heremites septemtaeniata	ZFMK 84085	Kuh-e-Sahand, Iran
Mabuya aurae	CAS 231775	Manzanilla Beach, Trinidad, Trinidad and Tobago
Mabuya frenata	UAM 60	Mbaracayu Reserve, Canindeyu Province, Paraguay
Mabuya guaporicola	UAM 104	Mbaracayu Reserve, Canindeyu Province, Paraguay
Trachylepis aureopunctata	PEM Field No. 437	Tuliara District, Madagascar
Trachylepis boulengeri	PEM R5533	Nampula, Mozambique
Trachylepis depressa (chimera)	PEM R17745	Osabeni, South Africa
Trachylepis depressa (chimera)	PEM R15573	3 km NE of Chibuto, Mozambique
Trachylepis paucisquamis (chimera)	UWBM 6041	Atewa Hills, Eastern Region, Ghana
Trachylepis paucisquamis (chimera)	UWBM 6042	Atewa Hills, Eastern Region, Ghana
Trachylepis paucisquamis (chimera)	PEM R4438	Cavatty, Cote d'Ivoire
Caledoniscincus bodoi	AMS R163262	Île Kûûmo, Isle of Pines, New Caledonia
Cryptoblepharus novocaledonicus	AMS R163245	Île Aventure, Isle of Pines, New Caledonia

all samples and loci used in this study de novo, except for several genes downloaded from GenBank used in previous studies (Brehm et al., 2001; Carranza and Arnold, 2003; Portik et al., 2010) for *Trachylepis septemtaeniata* and *T. aurata* as well as *Chioninia delalandii* and *C. vaillanti*. For outgroups, we chose two species within the closely related *Eugongylus* group (Skinner et al., 2011), *Caledoniscincus bodoi* and *Cryptoblepharus novacaledonicus*. In a few select cases we used chimeric sequences from another confidently identified specimen of the same species (see supplemental Table S1). This practice was only required for six taxa, and given the coalescent history of alleles within a species the practice of using chimeric sequences should not affect the accuracy of phylogenetic reconstruction at higher phylogenetic scales.

2.2. Molecular laboratory methods

Genomic DNA was extracted as described in Aljanabi and Martinez (1997). Polymerase chain reactions (PCR) were performed in an Eppendorf Mastercycler nexus gradient thermocycler and PCR product was cleaned using a home-made magnetic bead solution (Rohland and Reich 2012). All PCR reactions began with an initial 2 min denaturation at 95 °C followed by 34 cycles of: DNA denaturation at 95 °C for 35 s, primer annealing for 35 s at the temperature specified in Table 2 and extension at 72 °C for 1 min 35 s. Cycle sequencing was performed using Big Dye v3.1 chemistry, followed by an additional magnetic bead cleanup and analysis on an ABI3730xl. We sequenced two mitochondrial genes, NADH dehydrogenase subunit 2 (ND2) and ribosomal 16S (16S), and nine nuclear genes, recombination activation protein 1 (RAG1), melanocortin receptor 1 (MC1R), oocyte maturation factor mos (c-mos), brain derived neurotrophic factor (BDNF), exophilin 5 (EXPH5), kinesin family member 24 (KIF24), matrix-remodelling

associated 5 (MXRA5), breast cancer 1 early onset (BRCA1), and breast cancer 2 early onset (BRCA2). All of these makers are protein-coding genes, and several are rapidly evolving markers (KIF24, MXRA5, EXPH5, BRCA1, BRCA2) chosen to increase resolution at difficult nodes (Portik et al., 2012). All newly generated sequences are available on GenBank (see Supplemental Table S1). The complete aligned matrix was composed of 26 taxa with 8842 bp of sequence data. The matrix had 10.8% missing data, because some samples did not produce high quality sequences for all genes. Premature stop codons were not detected in any of the coding sequences.

2.3. Phylogenetic analyses

Paired DNA reads were manually checked for heterozygotes, corrected for sequencing errors and aligned by gene using MAFFT v7.017 (Katoh and Standley, 2013; Katoh et al., 2002) implemented in Geneious 8.0.5 (Biomatters Ltd.). To determine the correct model of evolution via the Bayesian information criterion, we performed PartitionFinder v1.1.1 (Lanfear et al., 2012) using the "Greedy" algorithm on each gene independently and on the entire concatenated dataset, allowing for different partitions for the first, second and third codon positions across each gene. We performed PartitionFinder separately for each program that would be employed.

We performed maximum-likelihood analysis (ML) in RAxML v8.1.15 (Stamatakis, 2014) for 1000 rapid bootstrap replicates on each gene independently and the entire concatenated dataset using the partitioning scheme produced by PartitionFinder (see Table 2). In all uses of RAxML, we specified the GTR+Gamma model of evolution as the program developer suggests this is the best model when there are fewer than 50 taxa in the dataset (and including a parameter for invariable sites may be lead to over

Table 2

Molecular markers and associate primers used for this study. Annealing temperatures used for each primer pair are shown. Codon partitioning schemes from the results of PartitionFinder are displayed, with the model of evolution used in the concatenated Bayesian analysis as well. We also calculated the number of parsimony informative sites and show the length of the total alignment for comparison of molecular marker informativeness. References correspond to: (A) this study; (B) Palumbi (1991); (C) Macey et al. (1997); (D) Arevalo et al. (1994); (E) Vieites et al. (2007); (F) Saint et al. (1998); (G) Portik et al. (2012); (H) Skipwith et al. (2016); (I) Pinho et al. (2010); (J) Portik et al. (2010).

Gene	Primers	Primer sequence (5′–3′)	Ref.	Annealing temp. (°C)	Codon partition scheme	Model (BI)	Aligned length (bp)	Parsimony informative sites
16S	16Sbr-L	CGCCTGTTTATCAAAAACAT	B	50	All	GTR+G+I	541	145
	16Sbr-H	CCGGTCTGAACTCAGATCACGT	B					
ND2	metF1	AAGCTTTCGGGCCCATACC	C	50	1, 2, 3	GTR+G	1029	528
	co1R1	AGRGTGCCAATGTCTTTGTGRTT	D					
BDNF	BDNF_F1	ACCATCCTTTTCCTKACTATGG	E	50	(1 + 2), 3	K80+G	690	33
	BDNF_R1	CTATCTTCCCCTTTTAATGGTC	E					
BRCA1	BRCA1skink1804F	YWTGGAGYTGAAYCCAGAAACTGATG	A	56	(1 + 2 + 3)	HKY+G	1065	272
	BRCA1skink3100R	RKWGTCCTCAGAYKCATGWGACTGGG	A					
BRCA2	BRCA2skink984F	AACAGGTAGTCAGTTTGAMTTYCACAC	A	56	(1 + 2), 3	HKY+G	1251	279
	BRCA2skink2315R	RTTGAAGYYTGAATGCYAGGTTTGAC	A					
CMOS	G73	GCGGTAAAGCAGGTGAAGAAA	F	50	(1 + 2), 3	HKY+G	372	53
	G74	TGAGCATCCAAAGTCTCCAATC	F					
EXPH5	EXPH5mab58F	AYCCAGGGWAATGGTGGATAAATCAGT	A	50	(1 + 2), 3	HKY+G	879	254
	EXPH5mab1770R	CCTCCCAGTTCTCATTTTCATCGCAGG	A					
KIF24	KIF24F1	SAAACGTRTCTCCMAAACGCATCC	G	50	(1 + 2), 3	HKY+G	567	160
	KIF24R1zebra	GCTGCTGRARCTGGTGATAAAGRCG	H					
MC1R	MC1R.F	GGCNGCCATYGTCAAGAACCGGAACC	I	54	(1 + 2 + 3)	HKY+G	663	102
	MC1R.R	CTCCGRAAGGCRTAAATGATGGGGTCCAC	I					
MXRA5	MXRA5trachy160pf2	AGCRAGTAGCTGAGCCAGAKCCTTC	A	52	(1 + 2), 3	HKY+G	633	152
	MXRA5trachy835pr2	GGTGGCAGCMGTCMTTCTTTCTGTTG	A					
RAG1	RAG1skinkF2	TTCAAAGTGAGATCGCTTGAAA	J	50	(1 + 2), 3	HKY+G	1152	208
	RAG1skinkF370	GCCAAGGTTTTTAAGATTGACG	J					
	RAG1skinkR2	AACATCACAGCTTGATGAATGG	J					
	RAG1skinkR1200	CCCTTCTTCTTTCTCAGCAAAA	J					

parameterization). We also generated ML gene trees for 1000 bootstrap replicates for each of the 11 genes (Supplemental Fig. S1). We also constructed a phylogeny from the concatenated dataset using Bayesian inference (BI) in MrBayes v3.2.1 (Ronquist and Huelsenbeck, 2003) using the results of PartitionFinder for the models of evolution and partitioning scheme (see Table 2). For MrBayes, we ran the Markov chain for 50 million generations on two separate runs, with three heated chains and one cold chain, with parameters unlinked across each partition. We assessed convergence of the posterior likelihood values by eye using Tracer v1.6 (Rambaut and Drummond, 2013) and confirmed that there existed high enough sampling (ESS > 200) to allow for accurate parameter estimates. We discarded the first 25% of trees as burn-in to generate a maximum clade credibility tree.

We simultaneously performed species tree analysis and estimated divergence times using the program *BEAST (Heled and Drummond, 2010) in BEAST v1.8.2 (Drummond and Rambaut, 2007). We partitioned each gene separately, specifying a GTR +Gamma model on each without codon partitions to allow for effective sampling of the parameters. For the species tree prior we specified a birth-death process as we used a dataset with severely limited tip sampling. For the population size we chose a piecewise linear model with constant root prior. We used an uncorrelated lognormal relaxed molecular clock on the mitochondrial markers and estimated separate lognormal relaxed clock rates for the nuclear markers. Divergence time estimates are relative to both of the mitochondrial genes (16S and ND2), with variation in rates specified with a normal prior on the lognormal clock mean (16S rate = 0.0080, stdev = 0.0020; ND2 rate = 0.00895, stdev = 0.0025) as in Barley et al. (2015). This allows for estimation of branch specific rates of evolution from a rate distribution of 0.47–1.13% per million years for 16S and 0.49–1.31% per million years for ND2, which span the estimated mitochondrial rates for many different lizards (Barley et al., 2015). The clock mean priors for all other genes were assigned uniform distributions from 0 to 0.02 and the standard deviations were assigned exponential distributions with a mean of 0.05, as in Barley et al. (2015). All substitution parameters were specified with a uniform prior from 0 to 100 (initial = 1), and the gamma shape parameters were specified with a uniform prior from 0 to 10 (initial = 0.05). We ran the Markov chain for 500 million generations, sampling every 50,000, and checked for convergence in Tracer as described above, discarding the first 100 million trees as burn-in. We also tested consistency of date estimates using a single rate estimation with the same prior distribution on either 16S or ND2 alone, allowing the other to vary under a uniform prior (from 0 to 0.04), however estimates and posteriors were very similar across all runs (results not shown). To visualize the results of the species tree analysis, we generated a Cloudogram using the program DensiTree v2.2.2 (Bouckaert and Heled, 2014).

2.4. Topological tests

We performed Approximately Unbiased (AU) Topology Tests in CONSEL v0.20 (Shimodaira and Hasegawa, 2001) after computing per-site log likelihoods on each constrained topology using the –f g command in RAxML v8.1.15. We used the *makermt*, *consel*, and *sumpv* commands in CONSEL to perform the AU test. The AU test is a conservative method that allows for rejection competing topological hypotheses after comparing them to the unconstrained maximum likelihood tree. We tested five competing topologies (Table 3): (1) monophyly of the Middle Eastern *Trachylepis* with Afro-Malagasy *Trachylepis*; (2) monophyly of Neotropical *Mabuya* with Afro-Malagasy *Trachylepis*; (3) monophyly of *Eumecia* with Afro-Malagasy *Trachylepis*; (4) monophyly of all currently recognized *Eutropis*, including the divergent *Eutropis novemcarinata*;

Table 3
Topological constraints and corresponding p-values for AU test implemented in RAxML and CONSEL.

	Constraint	AU test p-value
1.	Middle-Eastern *Trachylepis* + Afro-Malagasy *Trachylepis*	0.002*
2.	*Mabuya* + *Trachylepis*	0.009*
3.	*Eumecia* + *Trachylepis*	4e−04*
4.	All *Eutropis* including *E. novemcarinata*	0.199
5.	*Dasia* + all *Eutropis* including *E. novemcarinata*	0.089

and (5) monophyly of all the Asian species including all *Eutropis* and *Dasia*.

3. Results

3.1. Phylogenetic analysis

The concatenated ML and BI analyses produced phylogenies that were nearly identical except for interspecific relationships within the Afro-Malagasy *Trachylepis* which received low support in both analyses (Fig. 1). In cases of lower support, support for the same topology was generally higher in the BI tree than the ML tree (see Fig. 1). *Eutropis*, exclusive of *E. novemcarinata*, is strongly supported as sister to all remaining *Mabuya* group taxa. *E. novemcarinata* is supported as sister to *Dasia* in the BI analysis (PP = 100), however, the relationship is only weakly supported in the ML analysis (BS = 50). Together, *E. novemcarinata* + *Dasia* are strongly supported to be sister to all other *Mabuya* group genera excluding other *Eutropis*. A monophyletic grouping of the African, Middle-Eastern, Cape Verdean, and Malagasy taxa is strongly supported in all analyses. The Middle-Eastern *Trachylepis* (*Heremites*) is weakly supported as sister to *Eumecia*, and together these are resolved as sister to the remaining groups. In all analyses, *Chioninia* and Afro-Malagasy *Trachylepis* are strongly supported as sister-taxa, and together they are sister to Neotropical *Mabuya*.

The species tree analysis produced a nearly identical topology to the concatenated analyses, with all higher order relationships exactly the same (Fig. 2), with the exception of the placement of the Middle-Eastern *Trachylepis*, which is unsupported in both topologies. In the species tree, the Middle-Eastern *Trachylepis* is weakly supported as sister to the Neotropical group, whereas in the concatenated tree it is resolved as sister to *Eumecia*. In no topology is the Middle-Eastern *Trachylepis* resolved as sister to the remaining *Trachylepis*, and the genus is thus paraphyletic. In the case of the weakly supported sister relationship between *Eutropis novemcarinata* and *Dasia* in the concatenated analysis, the species tree recovered strong support for this relationship. Divergence times using relaxed clocks with two different mitochondrial rates showed that most higher-order intergeneric divergences occurred in the Eocene (see Fig. 2), whereas intrageneric divergences occurred much later, in the Oligocene, Miocene and Pliocene.

The cloudogram (Fig. 3), used to visualize the variation in the posterior species tree distribution, shows tree incongruence for the placement of the Middle-Eastern clade as sister to *Eumecia*, to *Mabuya*, or to a clade comprising *Mabuya*, *Chioninia*, and Afro-Malagasy *Trachylepis*. In addition, there appears to be some discordance within Afro-Malagasy *Trachylepis* and within *Mabuya*, although these cases would likely be resolved with increased taxon sampling. There is little evidence of discordance within the other genera, and *Eutropis novemcarinata* is consistently found to be sister to *Dasia*, with no evidence of discordance. The cloudogram (Fig. 3) reflects the conflicts seen between the individual gene trees (Supplemental Fig. S1).
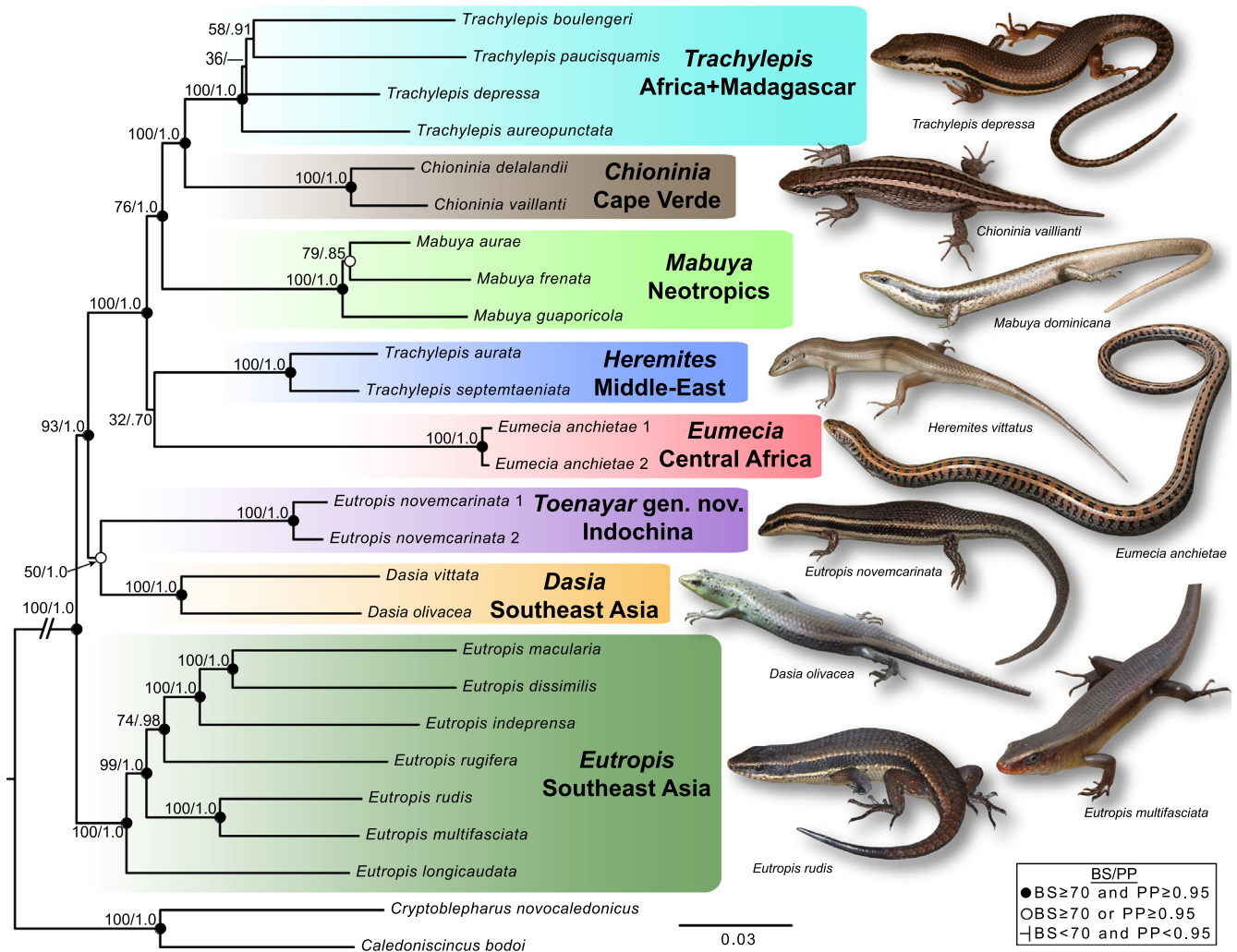
Fig. 1. Concatenated phylogenetic tree showing the ML topology and support for both ML and BI analyses. For all nodes, support values are listed with the proportion of ML bootstraps (BS) on the left and BI posterior probabilities on the right (PP). Closed circles are supported by both BS ⩾ 70 and PP ⩾ 0.95, open circles are supported by having either the ML or BI tree supported with BS ⩾ 70 or PP ⩾ 0.95, and non-circled nodes correspond to low support with BS < 70 and PP < 0.95. Photo credits are listed in the Acknowledgements. Photographs of *Trachylepis depressa*, *Mabuya dominicana*, and *Heremites vittatus* are representative of their respective genera, though these species are not represented in the phylogeny itself.

3.2. Topological tests

The AU tests rejected three of the five alternative hypotheses (Table 3): (1) monophyly of the Middle-Eastern *Trachylepis* with Afro-Malagasy *Trachylepis* (p = 0.002); (2) monophyly of Neotropical *Mabuya* with Afro-Malagasy *Trachylepis* (p = 0.009); and (3) monophyly of *Eumecia* with Afro-Malagasy *Trachylepis* (p = 0.0004). The AU test did not reject the other two topological hypothesis: (4) monophyly of all currently recognized *Eutropis*, including the divergent *Eutropis novemcarinata* (p = 0.199); and (5) monophyly of all the Asian species including all *Eutropis* and *Dasia* (p = 0.089).

4. Discussion

4.1. Phylogenetic relationships

We find high support for the placement of nearly all groups in the radiation, as opposed to all prior studies that could not find support for the higher-order relationships in the group. For example, the Cape Verdean *Chioninia* are strongly supported as the sister-group to the Afro-Malagasy *Trachylepis* in both the concatenated and species trees. This result is unique compared to all previous analyses based almost completely on mitochondrial data that weakly support *Chioninia* in several different phylogenetic positions (Carranza and Arnold, 2003; Datta-Roy et al., 2012; Mausfeld et al., 2002; Sindaco et al., 2012). The position of *Chioninia* is supported by individual gene trees of the three most informative nuclear genes (BRCA1, BRCA2, EXPH5; Table 2; Supplemental Fig. 1).

The only group that shifts between the species tree and concatenated analyses is the Middle-Eastern *Trachylepis*, which have long been known to represent a distinct lineage, though they have not been placed into a separate genus (e.g., Carranza and Arnold, 2003; Mausfeld and Schmitz, 2003; Sindaco et al., 2012). Based on the analyses shown here (Figs. 2 and 3), the clade is either placed as the sister-group to *Eumecia* (concatenated) or to *Mabuya* (species tree), both with low support. The AU test rejects the monophyly of a Middle-Eastern *Trachylepis* + Afro-Malagasy *Trachylepis* lineage. The type species for *Trachylepis*, *Euprepes savignyi* Duméril and Bibron [=*Trachylepis quinquetaeniata* (Lichtenstein)], is a component of the Afro-Malagasy group (e.g., Sindaco et al., 2012) and the name *Trachylepis* therefore applies to this group. In order
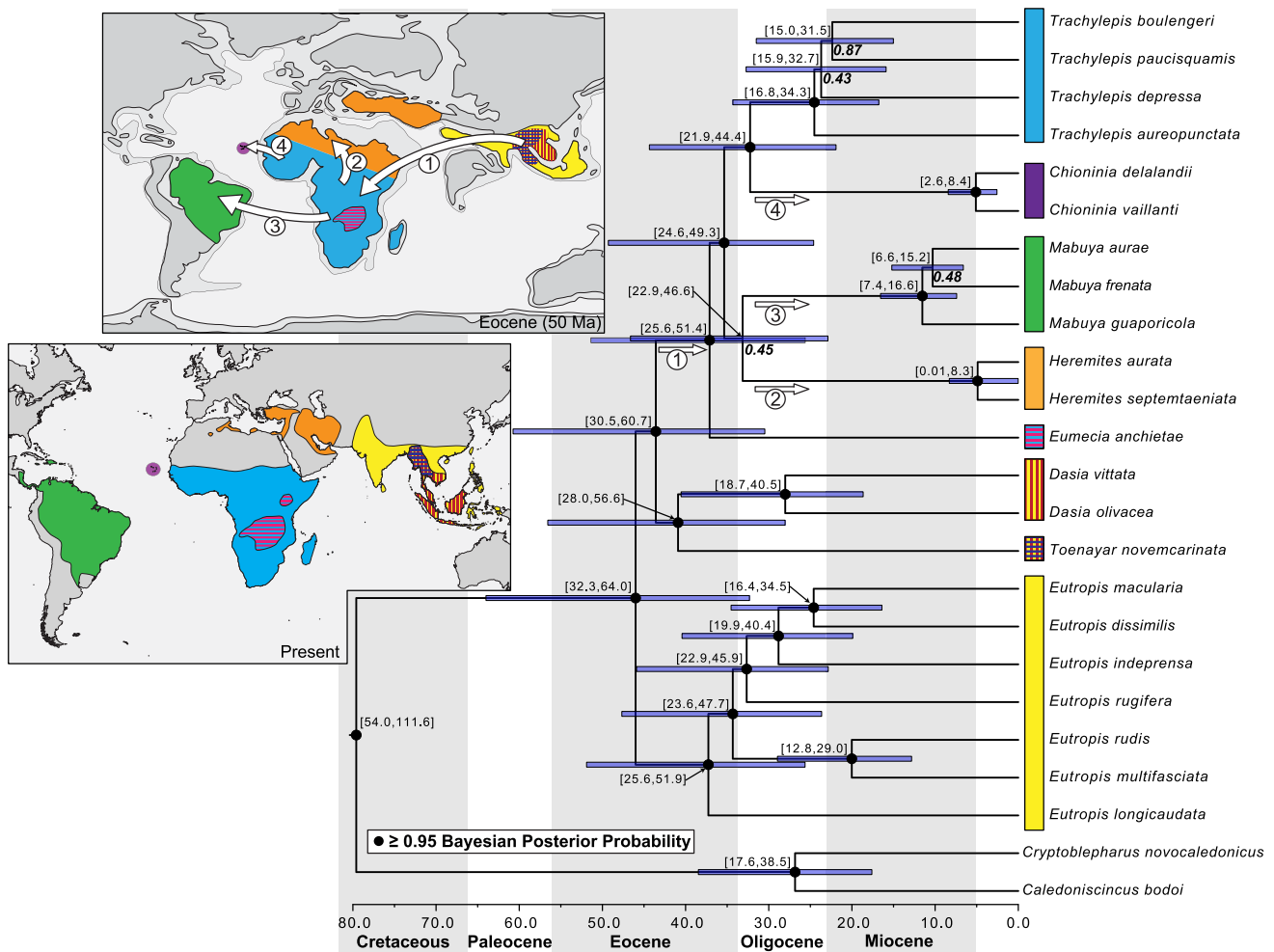
Fig. 2. Results of *BEAST analysis with divergence times estimated using a relaxed molecular on all markers relative to two relaxed mitochondrial rate estimates (see Section 2). Numbers in brackets represent 95% confidence intervals on the node heights. Closed circles on nodes show Bayesian posterior probability ⩾ 0.95, and unmarked nodes are labeled with the posterior probability in italics. Maps show the reconstructed historical biogeography of the *Mabuya* group during the Eocene Epoch (~50 Ma) and the present distribution of each genera as recognized in this paper. The results of this study provide strong evidence for the origin of the group in Southeast Asia, with a later radiation from Africa to surrounding regions. The Eocene base map is from Solé et al. (2015) and was redrawn from a map provided by Ron Blakey (NAU Geology), available for non-commercial use at http://cpgeosystems.com/globaltext2.html. The base map for the present era was downloaded from https://freevectormaps.com/.

to reflect monophyletic groupings, the Middle-Eastern group must be removed from *Trachylepis.* We here resurrect the name *Heremites* Gray as the oldest available name for the Middle-Eastern clade (see "Taxonomic implications" section below).

In all phylogenetic analyses, a clade composed of *Dasia* and *Eutropis novemcarinata* is supported as sister to the entire Afro-Neotropical group, whereas other *Eutropis* represent a distinct lineage sister to all the rest of the *Mabuya* group. This relationship indicates non-monophyly of the Asian genera, and non-monophyly of *Eutropis.* While the sister-relationship between *Dasia* and *E. novemcarinata* is strongly supported in the species tree and the concatenated Bayesian analysis, it is not highly supported in the concatenated maximum likelihood analysis. Even though the AU test cannot statistically reject *Eutropis novemcarinata* as part of *Eutropis* based on site-wise likelihoods, given the strong support and consistent phylogenetic reconstructions for this node, we accept the relationship of *E. novemcarinata* as sister to *Dasia.* As such, *Eutropis* as presently construed is polyphyletic. The taxonomic options to maintain generic monophyly are to place *E. novemcarinata* within *Dasia* or to describe a new, monotypic genus to accommodate it. The divergence time estimated between *E. novemcarinata* and *Dasia* is ~41.9 Ma (95% CI: 28.0–56.7), an age that is similar to or older than many other intergeneric divergences

in the group. For example, *Chioninia* diverged from Afro-Malagasy *Trachylepis* ~33.0 Ma (CI: 21.9–44.4) and the Middle-Eastern group (*Heremites*), diverged from *Mabuya* ~34.0 Ma (CI: 22.9–46.6). Furthermore, Hedges and Conn (2012) divided *Mabuya* sensu Mausfeld et al. (2002) into 16 genera, the entire radiation with a crown age of 21.4 Ma (CI: 9.7–36.7; Pinto-Sánchez et al., 2015). The age of the lineage that contains *E. novemcarinata* is consistent with deep, genus-level divergences among recognized genera, and therefore supports our decision to place *E. novemcarinata* in a separate genus. In addition, the unique morphology of *E. novemcarinata* separates it from both *Dasia* and *Eutropis*, and since no genus name is currently available for *E. novemcarinata*, we choose to place it within a new genus, described below.

Within the main *Eutropis* clade, we have enough taxon sampling to focus on interspecific relationships within the genus in comparison to the phylogenetic results of Barley et al. (2015). Our results are topologically identical to Barley et al. (2015) in most respects, with *E. longicaudata* sister to the rest of the clade, *E. rudis* and *E. multifasciata* closely related, and the Philippine clade (here represented by *E. indeprensa*) sister to the Indian radiation (represented by *E. macularia* and *E. dissimilis*). The only difference is the placement of *E. rugifera*, which Barley et al. (2015) places as sister to all *Eutropis* excluding *E. novemcarinata* and *E. longicuadata*, but
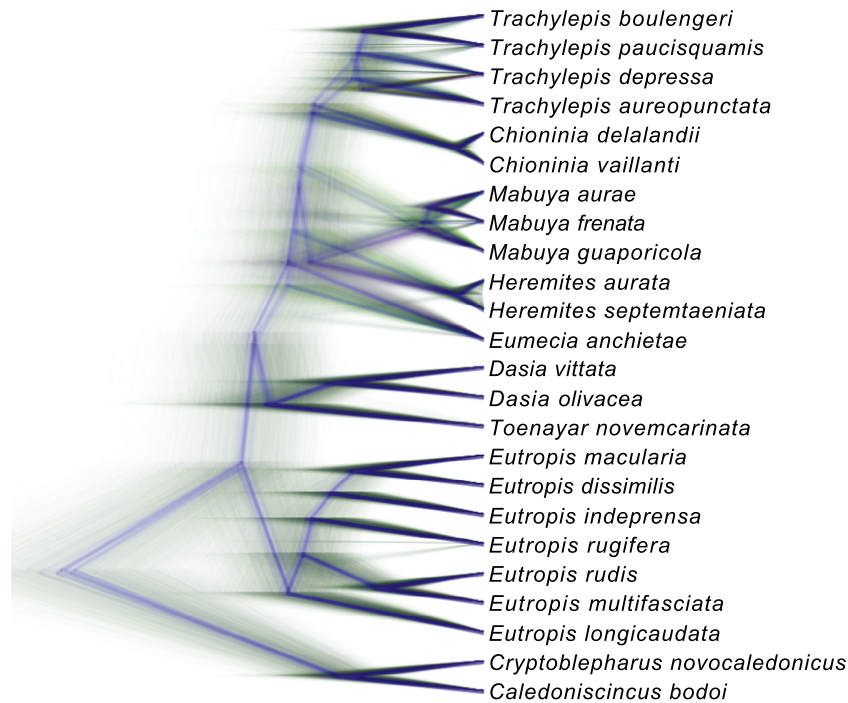
Trachylepis boulengeri
Trachylepis paucisquamis
Trachylepis depressa
Trachylepis aureopunctata
Chioninia delalandii
Chioninia vaillanti
Mabuya aurae
Mabuya frenata
Mabuya guaporicola
Heremites aurata
Heremites septemtaeniata
Eumecia anchietae
Dasia vittata
Dasia olivacea
Toenayar novemcarinata
Eutropis macularia
Eutropis dissimilis
Eutropis indeprensa
Eutropis rugifera
Eutropis rudis
Eutropis multifasciata
Eutropis longicaudata
Cryptoblepharus novocaledonicus
Caledoniscincus bodoi

Fig. 3. Cloudogram visualizing the posterior distribution of species-trees produced in the program DensiTree v2.2.2. Higher levels of incongruence are present within Afro-Malagasy *Trachylepis*, withinin Neotropical *Mabuya*, and in the phylogenetic placement of *Heremites*.

we find to be sister to the Philippine + Indian clades. Accurate resolution of the phylogenetic position of *E. rugifera* will likely require additional genetic data and taxon sampling. As in Datta-Roy et al. (2015), we find *E. dissimilis* to be nested deeply within *Eutropis*, and after examining the specimen we agree that the specimen referred to as *E. dissimilis* (CAS 231612) by Mausfeld and Schmitz (2003) was truly a specimen of *E. novemcarinata*.

4.2. Historical biogeography

Unfortunately, no fossil calibration points for the *Mabuya* group are available for taxa that can be placed in the tree unambiguously, and therefore all date estimates for the group are either based on vicariance events (e.g., Hedges and Conn, 2012; Pinto-Sánchez et al., 2015) or on molecular clock estimates (Barley et al., 2015; e.g., Lima et al., 2013; this study), and thus confidence intervals for divergence time estimates are generally wide. However, this does not necessarily detract from our ability to reconstruct the biogeographic history of the group as a whole, and to find rough correspondence of divergence times to geographic events. Our phylogenetic reconstruction shows a pattern of diversification largely consistent with prior hypotheses for the group (see Fig. 2 and discussion below).

It has long been suggested that the *Mabuya* group originated in Asia and diversified westwards (Greer, 1977; Honda et al., 2003, 1999; Horton, 1973; Mausfeld and Schmitz, 2003). In our analysis, the novel finding of the paraphyly of the Southeast Asian lineages and the strongly supported sister relationship of *Dasia* and *Eutropis novemcarinata* with African and American species instead of with the rest of *Eutropis* gives additional support for this "Out-of-Asia" hypothesis. Despite the inability of the AU test to reject *Dasia* and *Eutropis* as monophyletic, the strong topological support indicates that an ancestor of the group in Asia diverged to form the *Eutropis* sensu stricto lineage and the Asian ancestor of the rest of the group at ~47.1 Ma (95% CI: 32.3–64.0). Afterwards, a member of this latter group in Asia dispersed to Africa ~43.7 Ma (CI: 30.5–60.7). This timing could correspond to a temporary closing

of the Tethys Sea and land connection between Asia and Africa 50–60 Ma (http://cpgeosystems.com/) at the older side of the confidence interval; however, throughout the entire confidence interval the water gap between Asia and Africa was relatively narrow and could have allowed for faunal exchange. It is therefore possible that the ancestors of the African groups dispersed overwater from Asia to Africa, as this group has shown an incredible dispersal capability in many other instances (see discussion below). This Southeast Asian origin and westward dispersal from Asia to Africa has been seen in several other taxa, including the frog genera, *Rana*, *Hoplobatrachus*, and *Chiromantis* (Vences et al., 2003).

After arriving in Africa, the central African *Eumecia*, and the Middle-Eastern *Heremites* evolved from the ancestral African group. Later, members of the ancestral African group crossed the open Atlantic Ocean to colonize South America (Carranza and Arnold, 2003; Mausfeld et al., 2002). Our estimated timing of the dispersal across the Atlantic at ~34 Ma (CI: 22.9–46.6) is consistent with another date estimate at ~36.3 Ma (CI: 16.91–66.59; Pinto-Sánchez et al., 2015), but much older than another at ~17.7 Ma (CI: 9.4–24.9 Ma; Hedges and Conn, 2012), and long after the separation of South America and Africa (105–119 Ma; Carranza and Arnold, 2003). It is possible that this trans-Atlantic dispersal was facilitated by several small volcanic islands that may have acted as a bridge between Africa and South America during this time period, potentially via the Canary islands, São Tomé, Cape Verde, or other island chains (Geldmacher et al., 2005). The South American lineage invaded Central America and dispersed overwater five or six times to the Caribbean Islands, the earliest of which dates to the Miocene at ~12.6 Ma (CI: 4.8–17.4) and the other dispersals are estimated to have occurred in the Pleistocene (Pinto-Sánchez et al., 2015).

Subsequent to the initial dispersal of the ancestors of *Mabuya* sensu stricto to America, a member of the ancestral African group colonized the Cape Verde islands at ~32.6 Ma (CI: 23.1–45.9), radiating into the *Chioninia* group. Only after this dispersal did the Afro-Malagasy *Trachylepis* begin to diversify. *Trachylepis* eventually crossed overwater to Madagascar at ~24 Ma (CI: 10–39; Crottini

et al., 2012) or ~43 Ma (CI: 37–50; Lima et al., 2013) depending on the calibration and separately from Africa to the Seychelles/ Comoros (CI: 33–47 Ma; Lima et al., 2013). Another lineage from *Trachylepis* dispersed again across the Atlantic to Fernando de Noronha (Carranza and Arnold, 2003; Mausfeld et al., 2002). *Trachylepis* also dispersed from the mainland to the Socotran Archipelago on two separate occasions, at ~10.5 Ma (CI: 7.3–13.8) and ~2.9 Ma (1.5–4.5) (Sindaco et al., 2012).

The Asian *Eutropis* clade stayed geographically more stable and represents the oldest intrageneric radiation of *Mabuya*-group genera. Ancestral state reconstructions show that in the Eocene they separately invaded Sundaland, the Philippines, and India (Barley et al., 2015). The Indian *Eutropis* group radiated with a crown age at ~25.2 Ma (16.4–34.5; this study), with some members eventually leaving India to invade Indochina or in the case of *Eutropis dissimilis* and *E. macularia* to migrate westwards and actually come into sympatry with the Middle-Eastern group in Pakistan (Barley et al., 2015; Datta-Roy et al., 2012; this study). There have been two to four dispersals to the Philippines, one of which led to extensive in-situ diversification of at least 11 separate endemic species (Barley et al., 2015, 2013). The timing of the dispersal of the Philippines radiation is unclear, however the crown of the radiation dates to 7–11 Ma (Barley et al., 2015).

Dasia, as well, separately crossed into the Philippines, likely from Borneo, given the distribution of species in both the Philippines and Borneo (Greer, 1970; Harikrishnan et al., 2012). A few species of *Eutropis* (e.g., *E. rudis*, *E. macropthalma* and *E. multifasciata*), crossed Wallace's line into Wallacea, with *E. multifasciata* traversing across most Wallacean islands nearly all the way to New Guinea. Most recently, humans have helped mediate the dispersal of *E. multifasciata* into Australia and Florida, likely through the pet-trade (Meshaka et al., 2004).

5. Systematics

5.1. Taxonomic implications

Based on the results of our phylogenetic analyses, we introduce a revised taxonomy for the *Mabuya* group that reflects generic monophyly of each major lineage. The concatenated and species tree topologies as well as the AU test strongly reject the monophyly of the Middle-Eastern *Trachylepis* with Afro-Malagasy *Trachylepis*. Prior studies have found evidence for the divergence of the Middle-Eastern *Trachylepis* (Carranza and Arnold, 2003; Mausfeld and Schmitz, 2003; Sindaco et al., 2012), though never with the strong support we find in this study. We therefore recognize the Middle-Eastern clade as a distinct genus (see description below).

Even though AU tests cannot reject a topology that places *Eutropis novemcarinata* with remaining *Eutropis*, given the ample genetic differentiation and paraphyly between *E. novemcarinata* and other *Eutropis*, as well as it's strongly supported position sister to *Dasia* in both concatenated and species tree analyses, we choose to describe a new genus to contain this species. The divergence time estimate between *E. novemcarinata* and *Dasia* (CI: 28.0–56.6) is consistent with or older than other intergeneric divergence time estimates in the rest of the group, and provides further evidence for the recognition of a new genus. Furthermore, several morphological characters distinguish *E. novemcarinata* from both *Dasia* and *Eutropis* sensu stricto (see description below).

5.2. Heremites Gray, 1845

Fig. 4

5.2.1. Background

The name *Heremites* was first published by Cocteau (1837) and Duméril (1837), who mentioned it as a subgenus within *Scincus*, but these usages are as *nomina nuda*, as no definition or description is provided, nor are any constituent species mentioned. These authors simply attributed the name to Cocteau in manuscript. *Heremites* was also listed by Agassiz (1845, Fasciculus VI. p. 21) in his "Nomenclator Zoologicus" and attributed to Cocteau (1837), a comprehensive synoptic table of skinks that had been presented to the French Academy of Sciences but never published in its entirety, due to the early death of Cocteau in 1838. Duméril and Bibron (1839) relied heavily on Cocteau's classification of skinks. However, although noting the name *Heremites* among those attributable to Cocteau, they did not use the name formally or include it in their synonymies. However, they did include the vernacular "Heremite d'Olivier" in their synonymy of *Euprepes Savignyi* [=*Trachylepis quinquetaeniata* (Lichtenstein, 1823)], type species of *Trachylepis* (see above). *Heremites* was cited by Gray (1845, pp. 110, 113) as being derived from a Cocteau manuscript and was placed by him in the synonymy of *Euprepis* Wagler. However, he validly used the name to apply, at a subgeneric level, to *Euprepis* with "Scales 3-keeled, moderate. Ears with long lobules in front", a group within which he placed only *Euprepis vittatus* (Olivier, 1804). Gray's definition of this genus validates its use from this publication. Thus, *Scincus vittatus* Olivier, 1804 is the type of the genus by monotypy. The name has subsequently been noted by Sherborn (1927, p. 2964) and was listed in the synonymy of *Mabuya* by Peters and Donoso-Barros (1970, p. 197) and in the synonymy of *Euprepis* [=*Trachylepis*] by Mausfeld et al. (2002) [as *Hermites*, sic], both correctly citing *Scincus vittatus* as its type species.

5.2.2. Composition

Heremites is masculine in gender and includes its type species *H. vittatus* (Olivier), *H. septemtaeniatus* (Reuss) and *H. auratus* (Linnaeus). Although *T. tessellatus* was regarded as a close relative of *T. aurata* (Arnold and Gallagher, 1977), it and other *Trachylepis* occurring in the Middle East, including *T. brevicollis*, have been demonstrated to fall within *Trachylepis* sensu stricto (Sindaco et al., 2012). Anderson (1999) considered "*Mabuya*" *dissimilis*, a species ranging from Pakistan to Myanmar (Bauer et al., 2008; Zug et al., 1998) to be sister to "*M.*" *vittata*. However, Mausfeld and Schmitz (2003) subsequently showed that a specimen presumably referable to this species was weakly supported as sister to *Dasia* in their phylogeny. Datta-Roy et al. (2015), however, found, as did we, that true *dissimilis* is embedded well within *Eutropis* and is unrelated to *T. vittata* and the Middle Eastern clade of *Trachylepis*, and that the Myanmar "*dissimilis*" reported by Mausfeld and Schmitz (2003) is in fact, *Eutropis novemcarinata*, described elsewhere in this paper as a new genus.

5.2.3. Description

Medium sized, robust terrestrial and climbing skinks with well developed pentadactyl limbs; 26–27 presacral vertebrae; neck indistinct; 32–40 midbody scale rows; dorsal scales tricarinate (although may be smooth on some parts of the body); ventral scales smooth; ear visible; lower eyelid with enlarged, undivided transparent scale window; four supraocular scales, second largest; 4–6 supraciliary scales; postnasal scale absent; third subocular contacts lip, longer than preceding supralabials, not narrowed inferiorly; parietal scale overlaps anterior temporal scale; one or more pairs of enlarged nuchal scales present; enlarged, differentiated heel scales absent; scales on palms and soles not spinose; subdigital lamellae smooth; tail length typically 125–150% SVL; some longitudinal striping usually present (absent in some individuals or populations).

5.2.4. Comparisons

Heremites differs from *Mabuya* in the number of presacral verte-brae (26–27 vs. >27, respectively) and from most species by having keeled (versus smooth) dorsal scales (Greer et al., 2000; Mausfeld et al., 2002); from *Eumecia* in having pentadactyl limbs (versus limb and digital reduction) and *Eumecia* and *Eutropis* by having an undivided transparent disk in the lower eyelid and tricarinate dorsal scales (versus lower eyelid scaly or having greater or less than three keels on dorsal scales); from *Dasia* and *Toenayar* by the absence of enlarged heel scales in males; and from *Chioninia* and *Vietnascincus* by having 32–40 midbody scale rows, no post-nasal scale, and a roughly rectangular subocular scale (versus > 40 dorsal scale rows, a postnasal scale present, or a subocular scale narrowed inferiorly). *Heremites* is most similar to *Trachylepis* spp. but can be distinguished from all members of this genus by having the following combination of characters (bolded characters differ-entiate *Heremites* from most *Trachylepis* spp.): 26–27 presacral ver-tebrae; 32–40 midbody scale rows; dorsal scales tricarinate; smooth ventral scales; four supraocular scales; 4–6 supraciliary scales; **parietal scale overlaps anterior temporal scale**; enlarged nuchal scales; **no postnasal scale**; third subocular scale rectangu-lar, touches lip, longer than preceding supralabial scales; **smooth scales on palms and soles**; **smooth subdigital lamellae**; maxi-mum SVL generally <110 mm; tail length generally less than twice SVL; juveniles and adult females without blue tails.

5.3. Toenayar gen. nov.

Figs. 4 and 5

5.3.1. Background

As the most significant line of evidence towards the naming of this genus is genetic, it is possible that other species within South-east Asia that do not yet have genetic data may also be included within this new genus. Within *Eutropis*, the species that currently lack genetic data are *E. chapaensis*, *E. darevskii*, *E. englei*, *E. floweri*, *E. gansi*, *E. innotata*, *E. quadratilobus*, and *E. tytleri*. *Eutropis innotata*, for example, possesses a transparent disk in the eyelid (Smith, 1935) and has been interpreted to be morphologically similar to *E. novemcarinata* (Horton, 1973), and is, therefore, a potential can-didate species for the new genus, though it is possible this charac-ter is convergent in the two lineages. Within *Dasia*, *D. griffini*, *D. nicobarensis*, and *D. semicincta* do not have any genetic data, how-ever *D. griffini* and *D. semicincta* were formerly synonymized with *Dasia olivacea* (Greer, 1970) suggesting that they are closely related, if not conspecific, with *D. olivacea*. *Vietnascincus rugosus*, with only the two type specimens known to date (Darevsky and Orlov, 1994), is expected to be part of the *Mabuya* group, and it is possible that future studies may find it to be a member of the

new genus as well. *Lamprolepis vyneri*, which has been shown to be part of the *Mabuya* group (Linkem et al., 2013), is nested within *Dasia* based on the available ND2 data (results not shown) and is likely to be transferred to *Dasia* upon further investigation. Thus, although there are some taxa that may ultimately be referable to the new genus, in the absence of any positive evidence of this, we regard it as monotypic.

5.3.2. Composition

Toenayar gen. nov. includes only its type species *Toenayar novemcarinata* (Anderson).

5.3.3. Etymology

The generic name comes from the mythology of Myanmar, in which the Toenayar (Pronunciation: "Toh-Ay-Nah-Yar"), from the Burmese language, is a mythical Dragon or serpent with four legs. The Burmese language has no grammatical gender, but we treat the scientific name, *Toenayar*, as feminine.

5.3.4. Description

A medium-sized (SVL to 90 mm), robust skink with well-developed limbs, 32–34 scale rows around the midbody, 7–11 keels on the dorsal scales, adpressed hindlimbs reaching the wrist of the forelimb, 17–21 subdigital lamellae under toe IV, suprana-sals in contact or slight separation, prefrontals separated or in slight contact, parietals almost always separated by interparietal, frontal in contact with first and second supraocular, one pair of nuchals present, equal in width to two or three adjacent rows of cycloid scales; ear opening with two anterior lobules; 26 presacral vertebrae; palatal rami separated (i.e. open palate); males possess three enlarged, opaque-white heel scales, whereas females do not (Horton, 1973; Smith, 1935; Taylor, 1963; this study). Color of dor-sum light brown, with irregular black spotting; color of thick lat-eral stripes dark black-brown beginning at the nostril and diminishing posterior to the base of the tail; color of venter cream.

5.3.5. Diagnostic comparison

The following collective characters distinguish *Toenayar* from all closely related taxa in the *Mabuya* group. Toenayar differs from *Mabuya* in the number of presacral vertebrae (26 vs. >27, respec-tively) and from most species by having keeled (versus smooth) dorsal scales (Greer et al., 2000; Mausfeld et al., 2002); from *Eume-cia* in having pentadactyl limbs (versus limb and digital reduction) and *Eumecia* and *Eutropis* by having an undivided transparent disk in the lower eyelid and 7–11 keels on the dorsal scales (versus lower eyelid scaly or having greater or less than three keels on dor-sal scales); from *Dasia* by the separation of the palatine bones (open palate) and further by the possession of an undivided trans-parent disk in the lower eyelid; from *Heremites* and *Trachylepis* by

Fig. 4. Photos of new representative species for the new genera described or resurrected in this study. Left: *Toenayar novemcarinata* (CAS 213613); and right: *Heremites vittatus*. Photos from Jens Vindum and Oguz Turkozan.
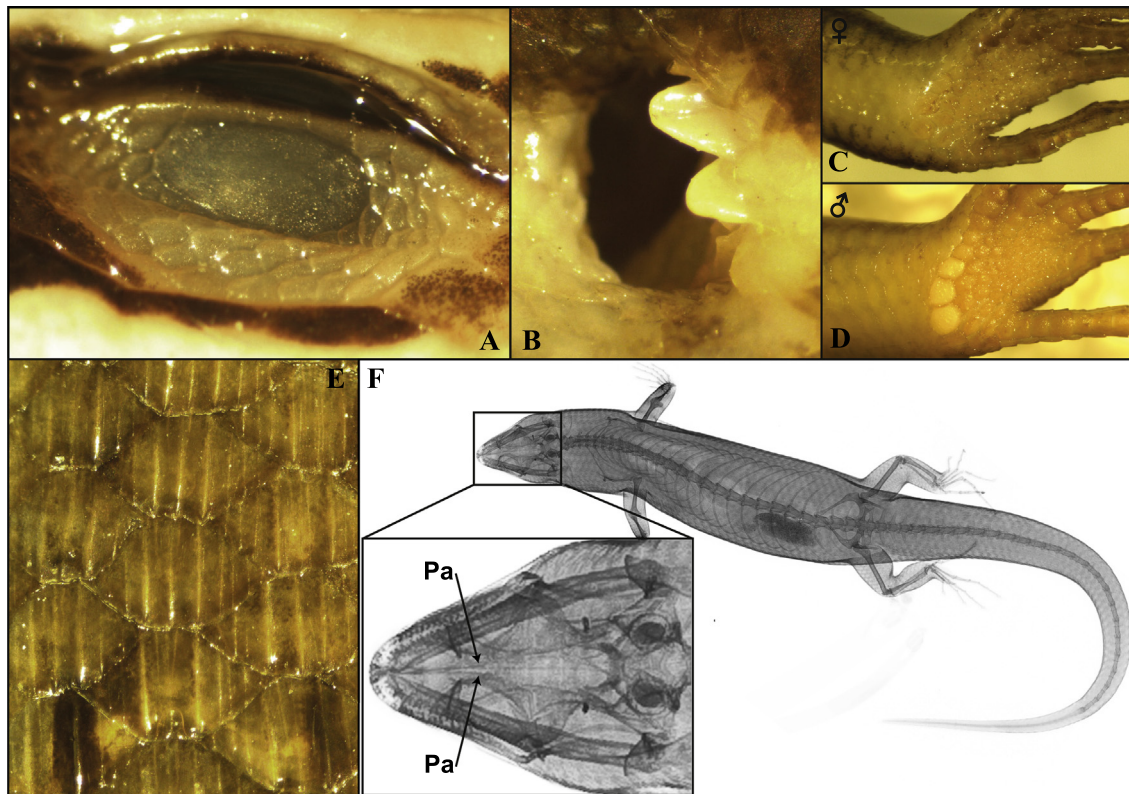
Fig. 5. Diagnostic morphological characters used to differentiate the monotypic new genus *Toenayar* from all other genera: (A) transparent window in the lower eyelid (CAS 213612); (B) two anterior ear lobules (CAS 215809); (C and D) sexual dimorphism in opacity, size and color of three heel scales on the hind foot between females (CAS 215808) and males (CAS 215414) of the species; (E) 7–11 keels on the dorsal scales (CAS 215806); and (F) X-ray scan showing the separation of the palatal rami (Pa = Palatine) (CAS 213612).

the presence of enlarged, differentiated heel scales in males (and enlarged, undifferentiated heel scales in females), and additionally from the vast majority of *Trachylepis* by possessing 7–11 keels on the dorsal scales; and from *Chioninia* and *Vietnascincus* by having 32–34 midbody scale rows and no postnasal scale. *Toenayar* shares with it's closest relative, *Dasia*, male possession of enlarged, differentiated heel scales, however in *Toenayar* there are three enlarged scales and in *Dasia* there are two (Greer, 1970).

6. Conclusion

The relative degree of external morphological conservatism among members of the *Mabuya* group has led to a lag in the full understanding and appreciation of the immense diversification that has occurred in the complex. Species within the group have spread across the world making unprecedented dispersals across huge oceanic barriers on several occasions. They have adapted to a diverse array of environments, such as arboreal (e.g., *Dasia*), semi-aquatic (e.g., *Trachylepis ivensii*), rupicolous (e.g., *Trachylepis sulcata* and *Trachylepis makolowodei*), limb-reduced (*Eumecia*), and also human-commensalism (e.g., *Eutropis multifasciata*). Furthermore, species within the group have also evolved an extremely wide range of reproductive strategies from oviparity (assumed as the ancestral condition) to several independent derivations of viviparity, and even to some of the most extreme specializations of fetal membranes observed in all Squamates (*Mabuya heathi*, *Eumecia*, *Trachylepis ivensii*; Blackburn and Flemming, 2009). Finally, with the well-supported intergeneric phylogeny presented in this publication, it is now possible to investigate the incredible diversification that has occurred in the *Mabuya* group in an evolutionary framework.

Acknowledgements

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.2016.05.033.

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