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The systematics and independent evolution of cave ecomorphology in distantly related clades of Bent-toed Geckos (Genus *Cyrtodactylus* Gray, 1827) from the Mekong Delta and islands in the Gulf of Thailand

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Abstract

An integrative taxonomic analysis of the distantly related *Cyrtodactylus condorensis* and *intermedius* species complexes of the Mekong Delta revealed that *C. paradoxus* is a junior synonym of *C. condorensis* and that *C. thochuensis* is a junior synonym of *C. leegrismeri.* Additionally, the analysis revealed that a cave-dwelling ecomorpholgy has evolved independently early on in the evolution of both complexes (represented by *C. hontreensis* in the *intermedius* complex and *C. grismeri* and *C. eisenmani* in the *condorensis* complex) and cave ecomorphs exist in sympatry—but not syntopy—with general scansorial ecomorphs. Multiple, recent, cyclical, glacioeustatic driven changes in sea levels across the Sunda Shelf are hypothesized to account for the evolution and distribution of the widely separated, conspecific insular populations of *C. condorensis* and *C. leegrismeri.* The independent evolution of cave ecomorphology is proposed to have been driven by competition avoidance. Habitat islands across the Mekong Delta are an important source of endemism and in need of protection.

Key words: ecomorphology, *Cyrtodactylus,* habitat islands, Mekong Delta, Vietnam, systematics

Introduction

The notion that an animal's form is somehow related to the way that animal functions in its environment goes back as far as the teachings of Aristotle although it was Darwin's clarity on "adaptation" that formally centralized these concepts. Studying the relationships between adaptation and the environment began to flourish in a number of fields (Wainwright & Reilly 1994) but it was not until Van der Klaauw (1948) coined the term "ecological morphology" (= ecomorphology) that a more formalized subdiscipline emerged that was focused on studying the relationship between organismal morphology and life history. We now know that ecomorphology is best studied in large, monophyletic groups where repeated "experiments" have happened independently over time in different lineages on the same phylogenetic tree (Losos 2009), thus enabling researchers to decipher between morphological similarities based on common ancestry versus those generated independently by similar selection pressures in similar environments on a similar body plan and genetic constitution.

The monophyletic Asian/Melanesian gekkonid genus *Cyrtodactylus* is well-suited for studying the evolution of ecomorphology in that its high diversity (~ 200 species [www.reptile-batabase.org]) manifests a broad spectrum of body shapes, sizes, ecological preferences, and life histories (Grismer 2011; Oliver *et al.* 2014). Some of this morphological diversity is intimately related to adapting to particular microhabitats wherein each ecomorph bears a particular suite of characters that aligns it with a particular life style in a particular environment. For example, cryptic, obligate, arboreal species such as *Cyrtodactylus elok* Dring and *C. durio* Grismer, Anuar, Quah, Muin, Chan, Grismer, and Ahmad have short limbs with wide, proximal, subdigital, lamellar pads or webbing; prehensile tails; and color patterns that mimic bark or leaves (Grismer 2011:391–398). Whereas species such as *C. astrum*

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Grismer, Wood, Quah Anuar, Muin, Sumontha, Norhayati, Bauer, Wangkulangkul, Grismer and Pauwells, that are restricted to flat, rocky surfaces have much longer limbs bearing unmodified digits; a long thin, non-prehensile tail; and a markedly banded dorsal pattern (Grismer *et al.* 2012:13–18).

We have been studying two, distantly related (Wood *et al.* 2012), parapatric, monophyletic complexes of *Cyrtodactylus* from the southern Mekong Delta Region of Vietnam and Cambodia. The *intermedius* complex as recognized here is composed of *C. intermedius* (Smith), *C. phuquocensis* Ngo, Grismer, & Grismer and *C. hontreensis* Ngo, Grismer & Grismer. These taxa are associated with the rugged, fragmented Cardamom Mountains that extend from southeastern Thailand and Cambodia to Phu Quoc Island in Vietnam (Grismer *et al.* 2011; Fig. 1). The *condorensis* complex as recognized here, contains *C. condorensis* (Smith), *C. paradoxus* (Darevsky & Szczerbak), *C. grismeri* Ngo, and *C. eisenmani* Ngo, as well as six insular populations from the eastern Gulf of Thailand (Grismer *et al.* 2011) and two more from the associated continental borderlands that have been variably referred to as *C. condorensis, C.* cf. *condorensis, C. paradoxus*, *C. thochuensis* Ngo and Grismer, *C. leegrismeri* Chan & Norhayati or *Cyrtodactylus* sp. 1, *Cyrtodactylus* sp. 2, *Cyrtodactylus* sp. 3, and *Cyrtodactylus* sp. 4 (Darevsky & Szczerbak 1997; Orlov *et al.* 2007; Ngo 2008; Grismer *et al.* 2011). This complex is associated with the hilly habitat-islands in the southern Mekong Delta of Vietnam (see Grismer & Ngo 2007) and the adjacent islands in Rach Gia Bay in the eastern section of the Gulf of Thailand (Darevsky & Szczerbak 1997; Orlov *et al.* 2007; Grismer *et al.* 2011; Fig. 1). Our integrative taxonomic analyses indicate that junior synonyms occur within the *condorensis* complex and there are a number of undescribed species in the *intermedius* complex. More interestingly, however, these analyses have revealed the origin of two distinct ecomorphs in both complexes that we refer to here as a cave-dwelling ecomorph (CDE) and a general scansorial ecomorph (GSE) (Fig. 2). These two ecomorphs live in near microsympatry on two islands in Rach Gia Bay and on one habitat-island in the southern Mekong Delta. A morphological intermediate between the two ecomorphs within the *intermedius* complex comes from an isolated karst habitat-island from the Mekong Delta in southeastern Cambodia. During the course of our field work, we discovered that at one location, Hon Tre Island in Rach Gia Bay, the CDE *C. hontreensis* of the *intermedius* complex is sympatric with the GSE *C. condorensis* of the *condorensis* complex. All other instances of ecomorph sympatry we discovered occur between species within the *condorensis* complex.

As part of a broader study on the patterns and processes of ecomorph evolution across *Cyrtodactylus* (Grismer *et al.* in prep.), the focus of this study is to 1) quantitatively characterize the cave-dwelling and general scansorial ecomorphs, 2) determine the patterns of their evolutionary origin (i.e. common ancestry or convergence); 3) formulate a working hypothesis that accounts for the patterns of this/these origin(s), and 4) disentangle the taxonomy of the *condorensis* complex. A taxonomic revision of the *intermedius* complex is forthcoming (Murdoch *et al.* in prep.).

Material and methods

Taxon sampling and outgroup selection. *Mitochondrial DNA.*—The primary aim of this study was to investigate the taxonomy and phylogenetic relationships of the *condorensis* and *C. intermedius* complexes based on 1445 bp and 1459 bp respectively of the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and its flanking tRNAs (WANCY) and morphology. We sampled as widely as possible across the range of these complexes, being sure to include multiple representatives from populations and from all the islands in Rach Gia Bay from which populations have been reported (Grismer *et al.* 2011). Based on the relationships of Wood *et al.* (2012), nine other species of *Cyrtodactylus* were used as outgroups were used to root the tree for the *C. condorensis* and *C. intermedius* complexes and *Tropiocolotes steudneri* (Peters), *Agamura persica* (Duméril), and *Hemidactylus frenatus* Schlegel were included as more distant outgroups. Taxon sampling for the ingroup of the *condorensis* complex included 36 individuals from 13 localities and for the *intermedius* complex, 64 individuals from 17 populations taken from throughout the range of the complex were included. All new sequences were deposited in GenBank (Table 1).

Data. *Mitochondrial DNA.*—Genomic DNA was isolated from liver or skeletal muscle samples stored in 95% ethanol using the Qiagen DNeasy™ tissue kit (Valencia, CA, USA). ND2 was amplified using a double-stranded Polymerase Chain Reaction (PCR) under the following conditions: 1.0 µl genomic DNA, 1.0 µl light strand primer 1.0 µl heavy strand primer, 1.0 µl dinucleotide pairs, 2.0 µl 5x buffer, MgCl 10x buffer, 0.1 µl Taq polymerase, and 7.56 µl ultra-pure H_2O (Table 2). PCR reactions were executed on an Eppendorf Mastercycler gradient

TABLE 1. Samples used in this study with corresponding voucher numbers, species name, locality information and GenBank Accession numbers.

Voucher	Species	Locality	GenBank accession #
LSUHC 11350	*Cyrtodactylus condorensis*	Ba Ria-Vung, Con Dao Island, Vietnam	KT013100
LSUHC 11351	*Cyrtodactylus condorensis*	Ba Ria-Vung, Con Dao Island, Vietnam	KT013101
LSUHC 11352	*Cyrtodactylus condorensis*	Ba Ria-Vung, Con Dao Island, Vietnam	KT013102
LSUHC 11353	*Cyrtodactylus condorensis*	Ba Ria-Vung, Con Dao Island, Vietnam	KT013103
LSUHC 4062	*Cyrtodactylus consobrinus*	Sarawak, Niah Cave, East Malaysia	EU268349
LSUHC 11416	*Cyrtodactylus dati*	Binh Phuoc, Bu Dop, Vietnam	KT013104
LSUHC 8597	*Cyrtodactylus grismeri*	Kien Giang, Hon Son Island, Vietnam	KT013105
LSUHC 8598	*Cyrtodactylus eisenmani*	An Giang, Tuc Dup Hill, Vietnam	KT013106
LSUHC 8637	*Cyrtodactylus eisenmani*	Kien Giang, Hon Son Island, Vietnam	JX440534
LSUHC 8638	*Cyrtodactylus grismeri*	An Giang, Tuc Dup Hill, Vietnam	JX440538
LSUHC 8583	*Cyrtodactylus hontreensis*	Kien Giang, Hon Tre Island, Vietnam	JX440539
FMNH 263228	*Cyrtodactylus intermedius*	Kampot, Cambodia	KT013107
FMNH 263229	*Cyrtodactylus intermedius*	Kampot, Cambodia	KT013108
FMNH 263230	*Cyrtodactylus intermedius*	Kampot, Cambodia	KT013109
FMNH 263232	*Cyrtodactylus intermedius*	Kampot, Cambodia	KT013110
FMNH 263233	*Cyrtodactylus intermedius*	Kampot, Cambodia	KT013111
FMNH 263238	*Cyrtodactylus intermedius*	Kampong Speu, Phnom Sruoch, Cambodia	KT013112
FMNH 263239	*Cyrtodactylus intermedius*	Kampong Speu, Phnom Sruoch, Cambodia	KT013113
FMNH 263240	*Cyrtodactylus intermedius*	Kampot, Cambodia	KT013114
FMNH 263345	*Cyrtodactylus intermedius*	Koh Kong, Koh Rong Island, Cambodia	KT013115
FMNH 263346	*Cyrtodactylus intermedius*	Koh Kong, Koh Rong Island, Cambodia	KT013116
FMNH 265811	*Cyrtodactylus intermedius*	Sa Kaeo, Sa Kaeo, Thailand	KT013117
FMNH 265812	*Cyrtodactylus intermedius*	Sa Kaeo, Sa Kaeo, Thailand	JQ889182
LSUHC 10081	*Cyrtodactylus intermedius*	Pursat, O'Som, Cambodia	KT013118
LSUHC 10083	*Cyrtodactylus intermedius*	Pursat, O'Som, Cambodia	KT013119
LSUHC 10095	*Cyrtodactylus intermedius*	Pursat, O'Som, Cambodia	KT013120
LSUHC 10096	*Cyrtodactylus intermedius*	Pursat, O'Som, Cambodia	KT013121

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TABLE 1. (Continued)

Voucher	Species	Locality	GenBank accession #
LSUHC 10121	*Cyrtodactylus intermedius*	Pursat, O'Som, Cambodia	KT013122
LSUHC 10535	*Cyrtodactylus intermedius*	Koh Kong, Koh Rong Island, Cambodia	KT013123
LSUHC 10536	*Cyrtodactylus intermedius*	Koh Kong, Koh Rong Island, Cambodia	KT013124
LSUHC 10562	*Cyrtodactylus intermedius*	Koh Kong, Koh Rong Island, Cambodia	KT013125
LSUHC 10563	*Cyrtodactylus intermedius*	Koh Kong, Koh Rong Island, Cambodia	KT013126
LSUHC 7346	*Cyrtodactylus intermedius*	Kampong Speu, Phnom Aural, Cambodia	KT013127
LSUHC 7396	*Cyrtodactylus intermedius*	Kampong Speu, Phnom Aural, Cambodia	KT013128
LSUHC 7398	*Cyrtodactylus intermedius*	Kampong Speu, Phnom Aural, Cambodia	KT013129
LSUHC 7399	*Cyrtodactylus intermedius*	Kampong Speu, Phnom Aural, Cambodia	KT013130
LSUHC 7400	*Cyrtodactylus intermedius*	Kampong Speu, Phnom Aural, Cambodia	KT013131
LSUHC 7401	*Cyrtodactylus intermedius*	Kampong Speu, Phnom Aural, Cambodia	KT013132
LSUHC 7409	*Cyrtodactylus intermedius*	Kampong Speu, Phnom Aural, Cambodia	KT013133
LSUHC 7855	*Cyrtodactylus intermedius*	Pursat, Phnom Samkos, Cambodia	KT013134
LSUHC 7918	*Cyrtodactylus intermedius*	Pursat, Phnom Samkos, Cambodia	KT013135
LSUHC 7936	*Cyrtodactylus intermedius*	Pursat, Phnom Samkos, Cambodia	KT013136
LSUHC 7943	*Cyrtodactylus intermedius*	Pursat, Phnom Samkos, Cambodia	KT013137
LSUHC 8490	*Cyrtodactylus intermedius*	Pursat, O'Lakmeas, Cambodia	KT013138
LSUHC 8493	*Cyrtodactylus intermedius*	Pursat, O'Lakmeas, Cambodia	KT013139
LSUHC 8498	*Cyrtodactylus intermedius*	Pursat, O'Lakmeas, Cambodia	KT013140
LSUHC 8499	*Cyrtodactylus intermedius*	Pursat, O'Lakmeas, Cambodia	KT013141
LSUHC 8500	*Cyrtodactylus intermedius*	Pursat, O'Lakmeas, Cambodia	KT013142
LSUHC 8518	*Cyrtodactylus intermedius*	Pursat, O'Lakmeas, Cambodia	KT013143
LSUHC 8519	*Cyrtodactylus intermedius*	Pursat, O'Lakmeas, Cambodia	KT013144
LSUHC 8520	*Cyrtodactylus intermedius*	Pursat, O'Lakmeas, Cambodia	KT013145
LSUHC 8541	*Cyrtodactylus intermedius*	Kampot, Bokor, Cambodia	KT013146
LSUHC 8542	*Cyrtodactylus intermedius*	Kampot, Bokor, Cambodia	KT013147
LSUHC 8543	*Cyrtodactylus intermedius*	Kampot, Bokor, Cambodia	KT013148
LSUHC 8545	*Cyrtodactylus intermedius*	Kampot, Bokor, Cambodia	KT013149

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TABLE 1. (Continued)

Voucher	Species	Locality	GenBank accession #
LSUHC 8546	*Cyrtodactylus c*	Kampot, Bokor, Cambodia	KT013150
LSUHC 8547	*Cyrtodactylus intermedius*	Kampot, Bokor, Cambodia	KT013151
LSUHC 8548	*Cyrtodactylus intermedius*	Kampot, Bokor, Cambodia	KT013152
LSUHC 8549	*Cyrtodactylus intermedius*	Kampot, Bokor, Cambodia	KT013153
LSUHC 8550	*Cyrtodactylus intermedius*	Kampot, Bokor, Cambodia	KT013154
LSUHC 8552	*Cyrtodactylus intermedius*	Kampot, Bokor, Cambodia	KT013155
LSUHC 8553	*Cyrtodactylus intermedius*	Kampot, Bokor, Cambodia	KT013156
LSUHC 8555	*Cyrtodactylus intermedius*	Kampot, Bokor, Cambodia	KT013157
LSUHC 8770	*Cyrtodactylus intermedius*	Kampot prov., Cambodia	KT013158
LSUHC 8771	*Cyrtodactylus intermedius*	Kampot, Phnom Laang, Cambodia	KT013159
LSUHC 8772	*Cyrtodactylus intermedius*	Kampot, Phnom Laang, Cambodia	KT013160
LSUHC 8773	*Cyrtodactylus intermedius*	Kampot, Phnom Laang, Cambodia	KT013161
LSUHC 9318	*Cyrtodactylus intermedius*	Pursat, Phnom Dalai, Cambodia	KT013162
LSUHC 9319	*Cyrtodactylus intermedius*	Pursat, Phnom Dalai, Cambodia	KT013163
LSUHC 9325	*Cyrtodactylus intermedius*	Pursat, Phnom Dalai, Cambodia	KT013164
LSUHC 9326	*Cyrtodactylus intermedius*	Pursat, Phnom Dalai, Cambodia	KT013165
LSUHC 9943	*Cyrtodactylus intermedius*	Pursat, Phnom Samkos, Cambodia	KT013166
BLS 11932	*Cyrtodactylus irregularis*	Bidoup-Nui Ba National Park, Lam Dong, Vietnam	KT013167
BLS 12001	*Cyrtodactylus irregularis*	Bidoup-Nui Ba National Park, Lam Dong, Vietnam	KT013168
FMNH 258697	*Cyrtodactylus irregularis*	Champasak, Pakxong, Lao PDR	JX440540
FMNH 262971	*Cyrtodactylus irregularis*	Ratatakiri, Ta Veng, Cambodia	KT013169
LSUHC 9371	*Cyrtodactylus leegrismeri*	Teregganu, Pulau Tenggol, West Malaysia	KT013170
LSUHC 9372	*Cyrtodactylus leegrismeri*	Teregganu, Pulau Tenggol, West Malaysia	KT013171
LSUHC 9373	*Cyrtodactylus leegrismeri*	Teregganu, Pulau Tenggol, West Malaysia	KT013172
LSUHC 9272	*Cyrtodactylus condorensis*	Kien Giang, Hon Chong, Vietnam	KT013173
LSUHC 9273	*Cyrtodactylus condorensis*	Kien Giang, Hon Chong, Vietnam	KT013174
LSUHC 9274	*Cyrtodactylus condorensis*	Kien Giang, Nam Du Island, Vietnam	KT013175
LSUHC 9276	*Cyrtodactylus condorensis*	Kien Giang, Nam Du Island, Vietnam	KT013176
LSUHC 11395	*Cyrtodactylus condorensis*	Kien Giang, Hon Thom Island, Vietnam	KT013177

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TABLE 1. (Continued)

Voucher	Species	Locality	GenBank accession #
LSUHC 11396	*Cyrtodactylus condorensis*	Kien Giang, Hon Thom Island, Vietnam	KT013178
LSUHC 11397	*Cyrtodactylus condorensis*	Kien Giang, Hon Thom Island, Vietnam	KT013179
LSUHC 11398	*Cyrtodactylus condorensis*	Kien Giang, Hon Thom Island, Vietnam	KT013180
LSUHC 9271	*Cyrtodactylus condorensis*	Kien Giang, Hon Chong, Vietnam	KT013181
LSUHC 9275	*Cyrtodactylus condorensis*	Kien Giang, Nam Du Island, Vietnam	KT033768
LSUHC 8603	*Cyrtodactylus phuquocensis*	Kien Giang, Phu Quoc Island, Vietnam	KT013182
LSUHC 8688	*Cyrtodactylus phuquocensis*	Kien Giang, Phu Quoc Island, Vietnam	KT013183
LSUHC 11411	*Cyrtodactylus pseudoquadrivirgatus*	Ninh Thuan, Ba Na Nui Chua, Vietnam	KT013184
UNS 0423	*Cyrtodactylus leegrismeri*	Ca Mau, Hon Chuoi, Vietnam	KT013185
LSUHC 8591	*Cyrtodactylus condorensis*	Kien Giang, Hon Son Island, Vietnam	KT013186
LSUHC 8595	*Cyrtodactylus condorensis*	Kien Giang, Hon Son Island, Vietnam	JX440531
LSUHC 8596	*Cyrtodactylus condorensis*	Kien Giang, Hon Son Island, Vietnam	KT013187
LSUHC 8623	*Cyrtodactylus condorensis*	Kien Giang, Hon Dat Mountain, Vietnam	KT013188
LSUHC 8671	*Cyrtodactylus condorensis*	Kien Giang, Hon Nghe Island, Vietnam	KT013189
LSUHC 8673	*Cyrtodactylus condorensis*	Kien Giang, Hon Nghe Island, Vietnam	KT013190
LSUHC 8672	*Cyrtodactylus condorensis*	Kien Giang, Hon Nghe Island, Vietnam	JX440549
LSUHC 11375	*Cyrtodactylus leegrismeri*	Ca Mau, Hon Khoai Island, Vietnam	KT013191
LSUHC 11376	*Cyrtodactylus leegrismeri*	Ca Mau, Hon Khoai Island, Vietnam	KT013192
LSUHC 11377	*Cyrtodactylus leegrismeri*	Ca Mau, Hon Khoai Island, Vietnam	KT013193
LSUHC 11378	*Cyrtodactylus leegrismeri*	Ca Mau, Hon Khoai Island, Vietnam	KT013194
LSUHC 9256	*Cyrtodactylus leegrismeri*	Ca Mau, Hon Khoai Island, Vietnam	KT013195
LSUHC 8587	*Cyrtodactylus condorensis*	Kien Giang, Hon Tre, Vietnam	KT013196
LSUHC 11412	*Cyrtodactylus* sp. nov. 1	Ninh Thuan, Ba Na Nui Chua, Vietnam	KT013197
LSUHC 11413	*Cyrtodactylus* sp. nov. 2	Quang Nam, Cu Lao Cham Island, Vietnam	KT013198
LSUHC 11414	*Cyrtodactylus* sp. nov. 2	Quang Nam, Cu Lao Cham Island, Vietnam	KT013199
LSUHC 11415	*Cyrtodactylus* sp. nov. 2	Quang Nam, Cu Lao Cham Island, Vietnam	KT013200
UNS0 449	*Cyrtodactylus leegrismeri*	Kien Giang, Tho Chau, Island	KT013201
LSUHC 11407	*Cyrtodactylus yangbayensis*	Khanh Hoa, Hon Ba, Vietnam	KT013202

theromocycler under the following conditions: initial denaturation at 95°C for 2 min, followed by a second denaturation at 95°C for 35 s, annealing at 48°C for 35 s, followed by a cycle extension at 72°C for 35 s, for 31 cycles. All PCR products were visualized on a 1% agarose gel electrophoresis. Successful PCR products were vacuum purified using MANU 30 PCR plates (Millipore) and purified products were resuspended in ultra-pure water. Purified PCR products were sequenced using the ABI Big-Dye Terminator v3.1 Cycle Sequencing Kit in an ABI GeneAmp PCR 9700 thermal cycler. Cycle sequencing reactions were purified with Sephadex G-50 Fine (GE Healthcare) and sequenced on an ABI 3730xl DNA Analyzer at the BYU DNA Sequencing center. Primers used for amplification and sequencing are presented in Table 2. Sequences were analyzed from both the 3' and the 5' ends separately to confirm congruence between the reads. Both the forward and the reverse sequences were uploaded and edited in Geneious™ version v5.5.6 (Drummond *et al.* 2011) and were edited therein. The protein-coding region of the ND2 sequence was aligned by eye. MacClade v4.08 (Maddison & Maddison 2005) was used to calculate the correct amino acid reading frame and to confirm the lack of premature stop codons.

TABLE 2. Primers used for amplification and sequencing reactions for the ND2 gene and the flanking tRNAs.

Primer name	Primer reference		Sequence
L4437b	Macey & Schulte (1999)	External	5'-AAGCAGTTGGGCCCATACC-3'
CyrtintF1	Siler *et al.* (2010)	Internal	5'-TAGCCYTCTCYTCYATYGCCC-3'
CyrtintR1	Siler *et al.* (2010)	Internal	5'-ATTGTKAGDGTRGCYAGGSTKGG-3'
H5934	Macey & Schulte (1999)	External	5'- AGRGTGCCAATGTCTTTGTGRTT-3'

For the phylogenetic analyses we applied two model-based methods, Maximum Likelihood (ML) and Bayesian Inference (BI). The Akaike Information Criterion (AIC) as implemented in ModelTest v3.7 (Posada & Crandall 1998), was used to calculate the best-fit model of evolution for each codon position (Table 3). Maximum Likelihood analysis was performed using RAxML HPC v7.5.4 (Stamatakis *et al.* 2008), 1000 bootstrap pseudoreplicates via the rapid hill-climbing algorithm (Stamatakis *et al.* 2008). Nodes that had bootstrap values (ML) above 70 were considered significantly supported. The Bayesian analysis was carried out in MrBayes v3.2 (Ronquist *et al.* 2012). Two simultaneous runs were performed with eight chains per run, seven hot and one cold following default priors. The analysis was run for 5,000,000 generations and sampled every 500 generations from the Markov Chain Monte Carlo (MCMC). The analysis was halted after the average standard deviation split frequency was below 0.01. Conservatively the first 25% of the trees from each run were discarded as burnin. A consensus tree was then computed from the two parallel runs using MrBayes v3.2 (Ronquist *et al.* 2012). Nodes that had posterior probabilities (BBP) above 0.95 were considered significantly supported (Wilcox *et al.* 2002). Pairwise sequence divergences were calculated in MEGA v5.2.2 (Tamura *et al.* 2011).

TABLE 3. Models of molecular evolution used in this study estimated in ModelTest v3.7 (Posada & Crandall 1998). Models applied refer to the Bayesian analyses and due to programing limitations the most complex model selected was applied to the Maximum Likelihood analyses.

Gene	Model selected	Model applied
ND2-*condorensis* complex		
1st pos	GTR+Γ	GTR+Γ
2nd pos	GTR+I+Γ	GTR+I+Γ
3rd pos	GTR+Γ	GTR+Γ
tRNAs	HKY+Γ	HKY+Γ
ND2- *intermedius* complex		
1st pos	HKY+Γ	HKY+Γ
2nd pos	GTR+I+Γ	GTR+I+Γ
3rd pos	GTR+I+Γ	GTR+I+Γ
tRNAs	GTR+Γ	GTR+Γ

Morphological analysis.—Color notes were taken from digital images of living specimens of all available age classes and populations prior to preservation. The following measurements and scale counts were taken with digital calipers under a Nikon SMZ 1500 dissecting microscope on the left side of the body where appropriate: snout-vent length (SVL), taken from the tip of snout to the vent; tail length (TL); sternal width (SternW), distance between the ventral edges of the opposing glenoid fossae; pelvic width (PelW), distance between the dorsal tips of the ilia; pelvic height (PelH), distance from the dorsal tip of the ilium to the ventral surface of the pubis; axilla-groin length (AG), distance between posterior margin of the forelimb insertion point on the body and anterior insertion point of the hind limb on the body; head depth (HD), measured from the top of the head posterior to the eye to the ventral margin on the mandible; head length (HL), measured from posterior margin of the retroarticular process of the mandible to the tip of the snout; head width (HW), the widest part of the head posterior to the eyes; snout length (SntL), measured from the anterior margin of the eyeball to the tip of the snout; eyeball diameter (EyeD), measured across the anterior and posterior margins of the eye; hind limb width (HindW), measured from the anterior to the posterior margins of the thigh immediately distal to its insertion on the body; hind limb length (HindL), measured from a point equidistant between its anterior and posterior insertion points on the body to the tip of the fourth toe; forelimb width (ForeW), measured from the anterior to the posterior margins of the brachium immediately distal to its insertion on the body; and forelimb length (ForeL), measured from a point equidistant between its anterior and posterior insertion points on the body to the tip of the fourth finger. To characterize body shape, selected combinations of measurements were converted to ratios. Log transformed and untransformed ratiometric data were analyzed using a Two-way Analysis of Variance (ANOVA) and a *t*-test to test for significant differences ($p<0.05$) between population means. Because of the wide range in sample sizes, Levene's Test for Equality of Variances was also run. All statistical tests were run on SPSS and only ratios bearing significant differences are reported.

Scale counts taken were of supralabials and infralabials counted from the largest scale immediately posterior to the dorsal inflection of the posterior portion of the upper jaw to the rostral and mental scales, respectively; the presence or absence of tubercles on the dorsal and ventral margins of the forearm; the number of paravertebral tubercles between limb insertions counted in a straight line immediately left of the vertebral column; the number of longitudinal rows of body tubercles counted transversely across the center of the dorsum from one ventrolateral fold to the other; the presence or absence of tubercles in the gular region, throat, and ventrolateral body folds; the number of longitudinal rows of ventral scales counted transversely across the center of the abdomen from one ventrolateral fold to the other; the shape of the subdigital lamellae proximal to the digital inflection; the number of subdigital lamellae beneath the fourth toe counted from the base of the first phalanx to the claw; the total number of femoroprecloacal pores (*i.e*., the contiguous rows of femoral and precloacal scales bearing pores combined as a single meristic referred to as the femoroprecloacal pores); the degree and arrangement of body tuberculation; the relative size and morphology of the subcaudal scales; the number of dark body bands between the nuchal loop (*fide* Grismer 1988) and the caudal constriction.

Specimens examined are listed in the Appendix. LSUHC refers to the La Sierra University Herpetological Collection and LSUDPC refers to the La Sierra University Digital Photo Collection, La Sierra University, Riverside, California, USA; UNS refers to the University of Natural Sciences, Ho Chi Minh City, Vietnam; and ITBCZ refers to the Institute of Tropical Biology Collection of Zoology in Ho Chi Minh City, Vietnam.

Results

Phylogeny

Maximum Likelihood and BI analyses of the *condorensis* complex resulted in two trees with differing topologies although a key basal node in each topology is not strongly supported (Fig. 1a,b). The BI tree lacks strong support for *Cyrtodactylus grismeri* and *C. eisenmani* as being sister species (BPP 0.74) and the ML analysis (ML 60) lacks strong support for *C. grismeri* being the sister species to the remaining members of the *condorensis* complex to the exclusion of *C. eisenmani*. A multilocus phylogeny (Wood *et al.* 2012)—as opposed to the single locus phylogeny here—examining a very limited subset of this complex agreed with the BI topology (Fig. 1a) but provided only marginally better support (ML 62/BI 0.93). If *C. grismeri* and *C. eisenmani* are sister species, it would imply they evolved from the same cave-adapted (see below for the meaning of cave-adapted) ancestor. This would mean that a widely distributed, rocky cave microhabitat would have had to exist across the region between Tuc Dup Hill (the

continental locality of *C. grismeri*) and Hon Tre Island (the locality of *C. eisenmani*) prior to their evolution. However, there is no evidence for rocky terrain ever having existed across this section of the Mekong Delta. Furthermore, other rock-adapted geckos of the genus *Cnemaspis* which are found in the same region, show different phylogeographic patterns of relationships (Grismer *et al.* 2014d). Therefore, we believe it is more likely that these two species evolved independently of one another from different ancestors bearing a general scansorial ecomorphology—a plesiomorphic trait shared in all the outgroups—and that this plesiomorphic body form and life style was retained in the subsequently evolving lineages of the *condorensis* complex (Fig. 3). As such, we presently prefer the ML topology (Fig. 1b). Because the ML and BI analyses here and those of Wood *et al.* (2012) lack strong support for either set of relationships, an additional hypothesis is that the basal node of the *condorensis* complex is a hard tritomy consisting of *C. grismeri, C. eisenmani,* and the ancestor of the general scansorial species *C. condorensis* and *C. leegrismeri*. This hypothesis would also require the independent evolution of a cave ecomorpholgy. It could be argued that the morphological data on body shape and coloration be used to resolve the relationships at the base of the *condorensis* phylogeny. However, given the number of times cave-dwelling ecomorphs have evolved within distantly related species of *Cyrtodactylus* (see below) and the lack of historical data for habitat continuity between the localities of *C. eisenmani* and *C. grismeri,* still makes a sister species relationship less likely. The molecular analysis of the *intermedius* complex indicates that *C. hontreensis* is the sister species to the remainder of the complex (Fig. 4) and that *C. intermedius* is composed of at least five undescribed species (Murdoch *et al.* in prep.). Thus, these molecular analyses indicate that the CDE evolved independently three times in the Mekong Delta Region; twice in the *condorensis* complex and once in the *intermedius* complex (Figs. 1b,4).

Taxonomy

The molecular analyses indicate that the lineage containing the GSE in the *condorensis* complex is composed of two allopatric, sublineages (Fig. 1a,b) that are separated from one another by a sequence divergence of 6.7%. Each of these is composed of more than one nominal taxon as well as unnamed insular populations bearing less than 0.50% sequence divergence between them, suggesting that junior synonyms occur within each lineage. The lineage composed of *C. leegrismeri, C. thochuensis,* and populations from Hon Khoai and Hon Chuoi islands (the latter two populations have been referred to as *Cyrtodactylus* sp.1 [Grismer *et al.* 2011]) have sequence divergences between them that are no greater than 0.49%. Additionally, these populations cannot be separated from one another on the basis of their highly variable morphology (Table 5) or color patterns (Fig. 5). In their description of *C. thochuensis,* Ngo and Grismer (2012) stated that *C. thochuensis* differed from *C. leegrismeri* in having a dorsal pattern of bands as opposed to symmetrical blotches; pore-bearing scales in a chevron arrangement as opposed to being arranged as an arch; 20–26 versus 18 or 19 longitudinal rows of dorsal tubercles; and 29–34 versus 25–29 paravertebral tubercles. Firsthand examination of additional specimens of *C. leegrismeri* reveals that its color pattern is quite variable and includes banded specimens (LSUHC 9371–70, 9373, 9378) like those of *C. thochuensis* (Fig. 5). The "chevron" and "arched" arrangements of the pore-bearing precloacal scales is a semantic difference and *C. leegrismeri* overlaps with *C. thochuensis* in having 18–25 longitudinal rows of dorsal tubercles and 25–35 paravertebral tubercles. Therefore, we consider these populations conspecific and place them in the synonymy of *C. leegrismeri* Chan & Norhayati, 2010 based on nomenclatural priority. We were unable to examine populations from Hon Sao Island, a small island (2 km^2) lying less than 1 km off the southeast coast of Hon Khoai Island but suspect it will show no significant differences from the Hon Khoai population.

Much the same is true for the lineage containing *Cyrtodactylus paradoxus* (i.e. the populations from Hon Thom and Nam Du islands [Grismer *et al.* 2011] and the continental population at Hon Chong)*, C. condorensis,* the Hon Tre Island population (referred to as *Cyrtodactylus* sp.2 [Grismer *et al.* 2011]), the unnamed populations from Hon Son and Hon Nghe Islands (recorded here for the first time), and the unnamed continental population from Hon Dat Mountain (Fig. 1). Genetic divergence between these populations is less than 0.13% and they are indistinguishable on the basis of color pattern and morphology (Fig. 6; Table 5). In their redescription of *C. paradoxus,* Orlov *et al.* (2007) failed to differentiate it from *C. condorensis.* With an expanded data set herein, we too are unable to differentiate these taxa on the basis of color pattern or morphology nor can we separate them from any other population within this clade (Fig. 6; Table 5). Therefore, we place the unnamed populations and *C. paradoxus* Darevsky & Szczerbak, 1997 in the synonymy of *C. condorensis* (Smith, 1921) based on nomenclatural priority. It should be noted, that Orlov *et al.* (2007) stated *C. paradoxus sensu lato* occurred on Phu Quoc Island off

the southern coast of Vietnam. We and others (T. Ziegler, *in litt.,* 2014) have collected extensively on Phu Quoc Island and have found only *C. phuquocensis* of the *intermedius* complex and no populations of the *condorensis* complex. We believe their error stemmed from a mis-reading of Darevsky and Szczerbak (1997) who stated that the holotype of *C. paradoxus* came from "Hon Thom Isle near south point of Phu Quoc Island, Kien Giang Province, South Vietnam…" and "It can be assumed that this island species also occurs one [*sic.*] some of the neighboring small islands in the Gulf of Siam." Also in their redescription of *C. paradoxus*, Orlov *et al.* (2007) stated that some males "*probably* [our italics] lack preanal pores" but in their key, they state males are "*usually without* [our italics] preanal pores." In their Table 3:151, they indicate that the holotype (ZISP 20310) lacks preanal pores but in their redescription of the holotype they state that "the preanal pores of holotype (ZISP 20310) are practically not visible",—i.e. they are there, just hard to see. To resolve these mixed messages, we examined two adult males from Hon Chong (LSUHC 9269, 9271) and six adult males from type locality of Hon Thom (LSUHC 11394–95, 11397, 11399–400, 11402) and found they all have precloacal pores. Given these new data coupled with the above mixed messages, we consider the presence of precloacal pores in males from these populations to be invariable.

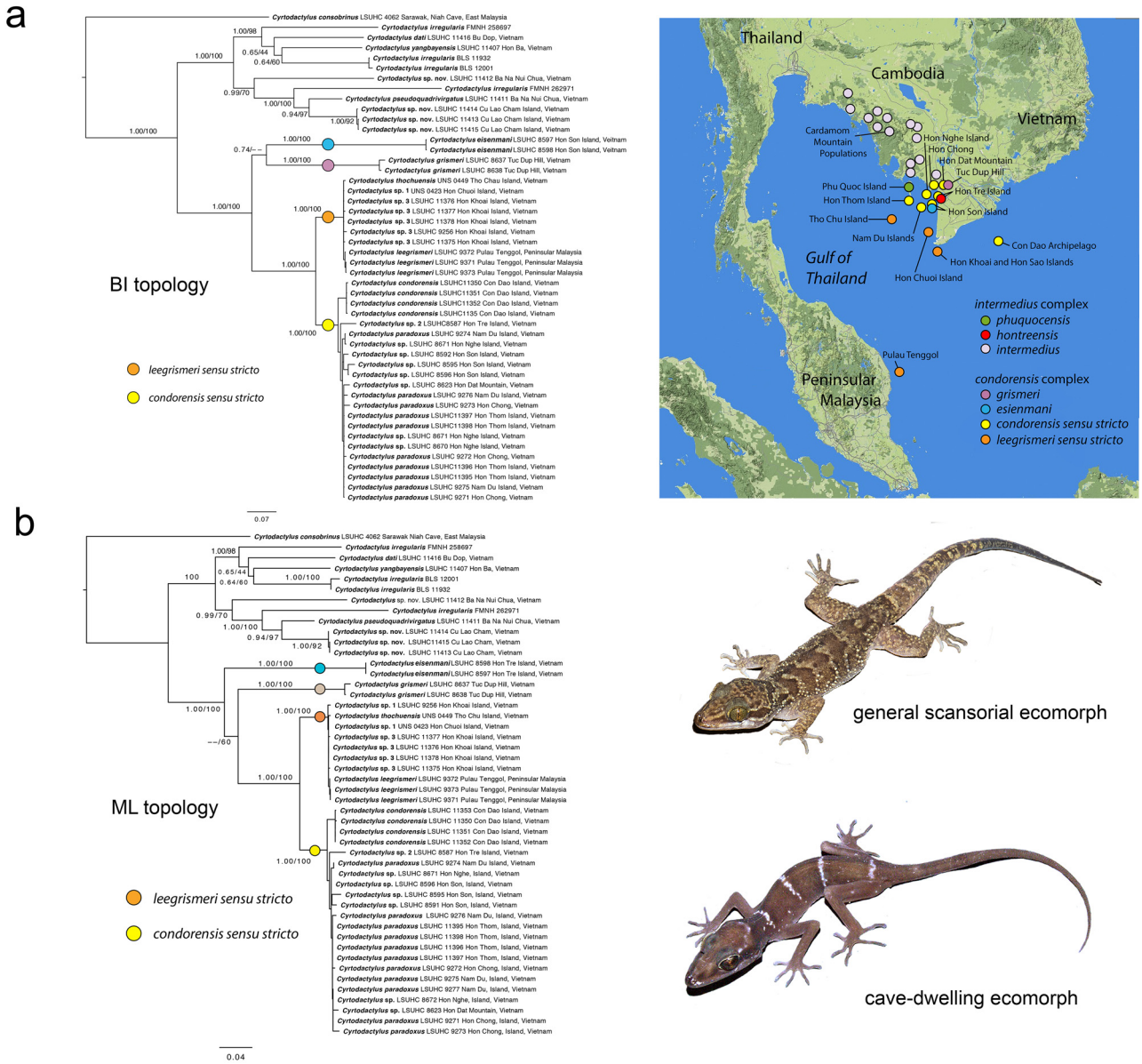

FIGURE 1. Phylograms depicting the relationships of species within the *Cyrtodactylus condorensis* species complex (a: Bayesian topology, b: Maximum Likelihood topology); distribution of species with the *C. condorensis* and *C. intermedius* species complexes; and general morphology of the cave-dwelling and general scansorial ecomorphs.

FIGURE 2. General differences in body stature between the general scansorial ecomorphs (figures on the upper and lower left) and the cave-dwelling ecomorphs (figures on the upper, middle and lower right). Upper left: *Cyrtodactylus leegrismeri* (LSUDPC 8228) from Hon Khoai Island, Ca Mau Province, Vietnam. Lower left: *C. condorensis* (LSUDPC 8202) from Con Dao Island, Con Dao Province, Vietnam. Upper right: *C. hontreensis* (LSUDPC 3062) from Hon Tre Island, Kien Giang Province, Vietnam. Middle right: *C. grismeri* (LSUDPC 3162) from Tuc Dup Hill, An Giang Province, Vietnam. Lower right: *C. eisenmani* (LSUDPC 8760) from Hon Son Island, Kien Giang Province, Vietnam.

Ecomorphology

Results of the analyses on the log transformed and untransformed data were identical and therefore only the results from the latter are reported. The Levene's Test for Equality of Variances showed that all variances were equal ($F<2.198$; $p<0.05$). There were no statistically significant differences between means from the allopatric populations within *Cyrtodactylus condorensis sensu stricto* or from those within *C. leegrismeri sensu stricto* and thus their data were combined as a single metric for each character (i.e. each ratio). The same is true for comparisons between *C. eisenmani* and *C. grismeri* and thus, their data were similarly combined. Statistical analyses comparing means from these two groups revealed two very distinctive body shapes that were associated with different life styles—referred to here as a cave-dwelling ecomorph (CDE) and a general scansorial ecomorph (GSE)—and that both ecomorphs occur in both species complexes. Only a single specimen of *C. hontreensis* was available for the morphometric analysis and thus this species was not included in the statistical analyses. However, because 1) all measurements taken from this specimen fall within the ranges of those of *C. eisenmani* and *C. grismeri* and outside of those of *C. condorensis sensu stricto* and *C. leegrismeri sensu stricto*; 2) it lacks tubercles and has a banded dorsal pattern like *C. eisenmani* and *C. grismeri* and *contra* to *C. condorensis sensu stricto* and *C. leegrismeri sensu stricto* (Fig. 2); and 3) it lives in a cave (Ngo *et al.,* 2008), we consider it a CDE (Table 4) and include it as part of the following discussion.

A CDE is defined here as having a statistically significant flatter head (HD/HL), longer snout (SntL/HL), larger eyes (EyeD/HD), shorter trunk (AG/SVL), flatter (PelH/SVL) and narrower (PelW/SVL) pelvis, and thinner (HindW/HindL; ForeW/ForeL) and longer (HindLSVL; ForeL/SVL) limbs (Fig. 2; Table 4). Associated with this

morphology is a markedly banded dorsal pattern and greatly reduced tuberculation (Fig. 2). Whereas a GSE has a relatively thicker head, shorter snout, smaller eyes, longer trunk, wider and higher pelvis, thicker and shorter limbs (Fig. 2; Table 4), strong tuberculation, and a blotched to irregularly banded dorsal pattern (Fig. 2). *Cyrtodactylus grismeri* from Tuc Dup Hill, *C. eisenmani* from Hon Son Island, and *C. hontreensis* from Hon Tre Island bear the characteristics of a CDE (Fig. 2). All are restricted to poorly illuminated, subterranean, cave-like environments composed of giant, granite boulders piled on top of one another where they locomote on flat, expansive surfaces in all planes of orientation (Ngo 2008; Ngo *et al.* 2008). A flatter head and body (i.e. flatter pelvis) and long splayed limbs has been shown to be an adaptation for climbing in several other groups of lizards living on vertical rock surfaces (Revell *et al.* 2007; Grismer *et al.* 2012; 2014d). A shorter trunk and narrower pelvis results in less body weight and—when coupled with the previous characters discussed above—would serve to reduce the amount of energy necessary to overcome gravity when moving on vertical surfaces or while inverted on horizontal surfaces. We hypothesize that the larger eyes are adaptive for being active in microhabitats with low levels of illumination. We can offer no hypotheses on the reduction of tuberculation or the presence of a distinctive banding pattern. The GSEs *C. condorensis sensu stricto* and *C. leegrismeri sensu stricto,* however, have much more robust heads, bodies and limbs, are strongly tuberculated, have smaller eyes, and lack a well-defined dorsal banding patterns (Fig. 2). Neither species occurs in subterranean environments but are adept at moving about on the ground, rocks, and vegetation and even seeking refuge in earthen burrows (Chan & Norhayati 2010; Grismer *et al.* 2011). Our field studies revealed that the CDE *C. hontreensis* is sympatric with the GSE *C. condorensis sensu stricto* on Hon Tre Island (Fig. 1) where the former is found only on the surfaces of large granite boulders in poorly illuminated, subterranean microhabitats and does not venture into areas occupied by *C. condorensis sensu stricto* (Ngo 2008). On Hon Son Island, *C. eisenmani* and *C. condorensis sensu stricto* also occur in sympatry but not syntopy.

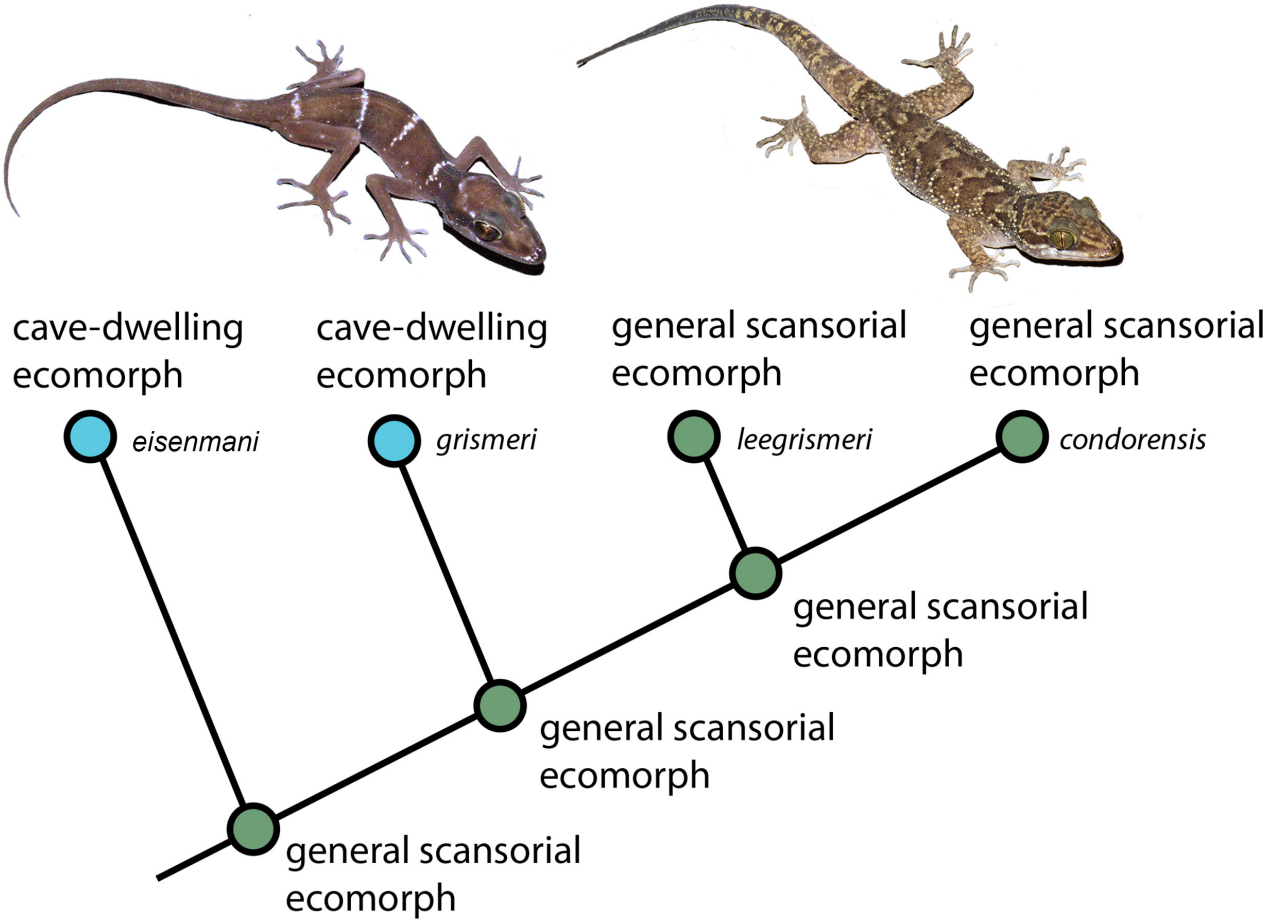

FIGURE 3. Hypothesized ancestral-descendant relationships depicting the independent evolution of the cave-dwelling ecomorph from the general scansorial ecomorph.

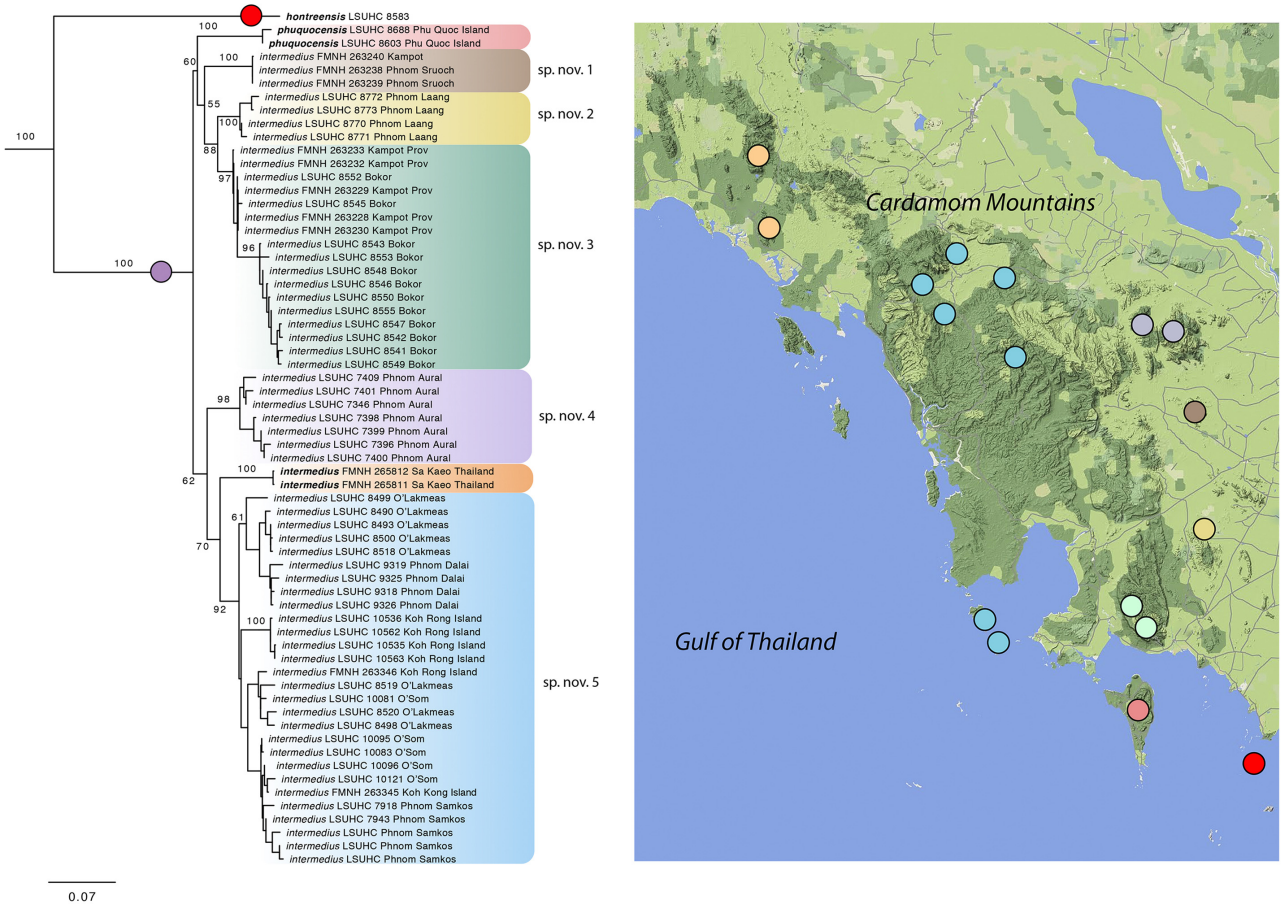

FIGURE 4. Phylogram depicting the relationships within the *Cyrtodactylus intermedius* complex and the distribution of the proposed new species with likelihood bootstrap support values.

Discussion

Establishing a proper phylogenetic taxonomy for these species complexes is paramount to any discussion concerning their biogeography or the evolution of different ecomorphs (Mahler *et al.* 2010). Our phylogeny and resultant taxonomy indicates that the two species-level basal lineages in the *condorensis* complex—*Cyrtodactylus grismeri* from Tuc Dup Hill and *C. eisenmani* form Hon Son Island—are cave-dwellers. The remaining lineage contains the two general scansorial sister species, *C. condorensis sensu stricto* and *C. leegrismeri sensu stricto* whose parapatric distributions center along a northwest to southeast axis extending through Rach Gia Bay along the eastern margin of the Gulf of Thailand and across the southern tip of the Ca Mau Peninsula in the southern portion of the Mekong Delta of Vietnam (Fig. 1). This same biogeographic pattern is also found between the Ca Mau clade and the *chanthaburiensis* group of the genus *Cnemaspis* (Grismer *et al.* 2014). *Cyrtodactylus condorensis sensu stricto* is restricted to, and ranges disjunctly across the northwesterly located islands of Con Dao, Hon Tre, Nam Du, Hon Nghe, Hon Son, Hon Thom, and the continental localities of Hon Chong and Hon Dat Mountain (Fig. 1). *Cyrtodactylus leegrismeri sensu stricto* is restricted to, and ranges disjunctly across the southwesterly located islands of Hon Khoai, Hon Chuoi, and Tho Chu of Rach Gia Bay in the eastern section of the Gulf of Thailand and the Peninsular Malaysian island of Tenggol along eastern coast of the Thai-Malay Peninsula approximately 420 km to the southwest (Fig. 1). In the context of the current geography of Sundaland, the distribution of *C. leegrismeri sensu stricto* appears anomalous being that it occurs on opposite sides of the Gulf of Thailand. However, given the well-established fact that the Sunda Plains (i.e. the Gulf of Thailand and the southern portion of the South China Sea) have been cyclically exposed and submerged at least 50 times within the last 2.5 million years (Woodruff 2010) and that a heterogeneous, forested environment repeatedly extended throughout this

region (Raes *et al.* 2014), the putative anomaly disappears. In fact, it is surprising that this is only the second documented case—based on molecular evidence—of a species of reptile from Peninsular Malaysia being more closely related to Indochinese lineages than to those of southern Sundaland (see J. Grismer *et al.* [2014] for a similar phylogeographic relationship in Butterfly Lizards, *Leiolepis*). We suspect that as phylogenies from more taxa ranging throughout these biogeographic provinces are examined, the emergence of a trans-Gulf of Thailand phylogeographic pattern will become commonplace. Furthermore, de Bryun *et al.* (2014) demonstrated that Indochina was a major source of origin for many Sundaland vertebrates. We hypothesize that speciation events separating *C. condorensis sensu stricto* and *C. leegrismeri sensu stricto* were driven by cyclical, glacioeustatic changes in sea levels that repeatedly created (low sea levels) and obliterated (high sea levels) wide expanses of terrain over the last 2.5 million years (Woodfruff 2010) sequentially fragmenting and reuniting populations multiple times. A time-calibrated phylogeny for this group using data from ultra conserved elements (UCE) is currently being generated in order to test this hypothesis and the timing of this speciation event (Grismer *et al.* in prep.).

The close geographic proximity of three species of *Cyrtodactylus* from two distantly related species complexes having independently evolved a cave-dwelling ecomorphology suggests this body shape and life style may be under strong selection pressure in the Mekong Delta region. A possible hypothesis for its selection would be to avoid competition with larger, more robust species capable of occupying all habitats except poorly illuminated, cave-like situations. Where these two ecomorphs are sympatric (Hon Tre Island with *C. hontreensis* and *C. condorensis sensu stricto* and Hon Son Island with *C. eisenmani* and *C. condorensis sensu stricto*), they are not syntopic and we have never observed one species in the microhabitat of the other (Fig. 7). The lowland habitat surrounding Tuc Dup Hill—the type locality of the cave-dwelling *C. grismeri*—has been converted to agriculture and thus, *C. condorensis sensu stricto* is no longer present. Where natural deltaic vegetation still occurs at Hon Dat Mountain, only 17 km to the southwest, *C. condorensis sensu stricto* is still abundant. Thus, we can infer the same hypothesis of competition avoidance for the evolution of *C. grismeri.*

FIGURE 5. Variation in color pattern within *Cyrtodactylus leegrismeri sensu stricto* from Hon Khoai Island, Ca Mau Province, Vietnam (LSUDPC 8228); Hon Chuoi Island, Ca Mau Province, Vietnam (LSUDPC 8764); Tho Chu Island, Kien Giang Province, Vietnam (LSUDPC 9446); and Pulau Tenggol, Terengganu, Peninsular Malaysia (LSUDPC 9449).

FIGURE 6. Variation in color pattern of *Cyrtodactylus condorensis sensu stricto* from Con Dao Island, Ba Ria-Vung Tau Province, Vietnam (LSUDPC 8215); from Hon Thom Island, Kien Giang Province, Vietnam (LSUDPC 8244); Hon Chong, Kien Giang Province, Vietnam (LSUDPC 5082); Nam Du Island, Kien Giang Province, Vietnam (LSUDPC 5076); Hon Son Island, Kien Giang Province, Vietnam (LSUDPC 3169); Hon Tre Island, Kien Giang Province, Vietnam (LSUDPC 3077); and Hon Nghe Island, Kien Giang Province, Vietnam (LSUDPC 3417).

Similar situations occur in other species complexes within *Cyrtodactylus*. For example, the karst-adapted, cave-frequenting species of *C. lekaguli* Grismer, Wood, Quah, Shahrul, Muin, Sumontha, Norhayati, Bauer, Wangkulangkul, Grismer & Pauwels, *C. astrum*, and *C. langkawiensis* Grismer, Wood, Quah, Shahrul, Muin, Sumontha, Norhayati, Bauer, Wangkulangkul, Grismer & Pauwels of the *C. pulchellus* complex (Grismer *et al.*

2012, 2014a) from northwestern Peninsular Malaysia and southern Thailand are sympatric with the robust habitat generalist *C. macrotuberculatus* Grismer & Norhayati. The same is true for the karst-adapted *C. guakanthanensis* Grismer, Belabut, Quah, Chan, Wood & Hasim of the *C. sworderi* complex (Grismer *et al.* 2014b) from central Peninsular Malaysia which is sympatric with the habitat generalist *C. quadrivirgatus* (Johnson *et al.* 2012; Grismer *et al.* 2014b). Like the situation discussed above for *C. grismeri,* the gracile, karst-adapted *C. metropolis* Grismer, Wood, Chan, Shahrul & Muin of the *C. semenanjungensis* complex (Grismer *et al.* 2014c) from Batu Caves in the western lowlands of Peninsular Malaysia was likely surrounded by another member of the swamp-dwelling clade (most likely *C. payacola* Johnson, Quah, Anuar, Muin, Wood, Grismer, Greer, Chan, Norhayati, Bauer & Grismer) that Grismer *et al.* (2014c) posited became extirpated due to recent urbanization.

One pattern that is more difficult to explain is that within each species complex, it is the basal lineage or lineages that are the cave-dwelling ecomorphs. We see the same pattern in the *pulchellus* complex (Grismer *et al.* 2014b:Fig. 2) but not in the *semenanjungensis* or *sworderi* complexes. Whatever the reasons are for this pattern in the Mekong Delta complexes, the phylogeny indicates that the evolution of these ecomorphs occurred at the inception of the diversification of these complexes. Interestingly, within the *intermedius* complex, we see what we believe to be the early stages of the evolution of another cave-dwelling ecomorph in a karst-dwelling, cave population at Phnom Laang—a small, isolated, karst hill in the Mekong Delta of southeastern Cambodia near the border of Vietnam. Lizards of this population bear ratios intermediate to those of the cave-dwelling ecomorphs *C. hontreensis, C. grismeri,* and *C. eisenmani* and the general scansorial ecomorphs *C. leegrismeri sensu sricto* and *C. condorensis sensu stricto* (Murdoch *et al.* in prep.).

FIGURE 7. Left: microhabitat structure of a general scansorial ecomorph (Hon Thom Island, Kien Giang Province, Vietnam). Right: openings in the granite boulder piles leading to the subterranean microhabitat of the cave-dwelling ecomorph (Hon Son Island, Kien Giang Province, Vietnam).

TABLE 4. Ranges of morphometric ratios for *Cyrtodactylus condorensis sensu stricto, C. leegrismeri sensu stricto, C. eisemanni, C. grismeri,* and *C. hontreensis* and descriptive statistics for the cave-dwelling and general (gen.) scansorial ecomorphs. *P*-values from the *t*-test are listed for significantly differing means for each ratio.

	hontreensis	***eisemanni***	***grismeri***	***condorensis sensu stricto***	***leegrismeri sensu stricto***
HD/HL	0.33	0.29–0.32	0.30–0.36	0.34–0.44	0.35–0.44
SntL/HL	0.48	0.46–0.48	0.45–0.48	0.39–0.45	0.41–0.45
EyeD/HD	0.79	0.71–0.79	0.61–0.79	0.50–0.69	0.47–0.67
AG/SVL	0.38	0.37–0.40	0.38–0.40	0.39–0.49	0.40–0.47
PelW/SVL	0.09	0.09–0.11	0.10–0.11	0.10-0.12	0.10–0.14
PelH/SVL	0.07	0.07–0.08	0.07–0.11	0.08–0.12	0.10–0.12
HindW/HindL	0.15	0.14–0.16	0.14–0.20	0.13–0.22	0.17–0.24
HindL/SVL	0.58	0.54–0.59	0.54–0.63	0.50–0.57	0.42–0.54
ForeW/ForeL	0.10	0.10–0.13	0.09–0.14	0.11–0.17	0.12–0.18
ForeL/SVL	0.45	0.37–0.43	0.39–0.49	0.34–0.44	0.36–0.42
sample size	1	5	13	38	24
	cave-dwelling ecomorph	**gen. scansorial ecomorph**	**Interpretation for cave-dwelling ecomorphs**		
HD/HL	0.29–0.36	0.35–0.44	**flatter head**		
mean	0.32	0.39	*p*=3.31434E-14		
std. deviation	0.024	0.026			
SntL/HL	0.45–0.47	0.39–0.45	**longer snout**		
mean	0.47	0.43	*p*=2.32389E-11		
std. deviation	0.011	0.017			
EyeD/HD	0.61–0.79	0.50–0.69	**bigger eyes**		
mean	0.69	0.57	*p*=1.18151E-11		
std. deviation	0.065	0.057			
AG/SVL	0.37–0.40	0.39–0.49	**shorter trunk**		
mean	0.39	0.44	*p*=2.87E-11		
std. deviation	0.019	0.021			
PelW/SVL	0.09–0.11	0.10–0.14	**narrower pelvis**		
mean	0.10	0.11	*p*=4.2195E-06		
std. deviation	0.005	0.008			
PelH/SVL	0.07–0.11	0.08–0.12	**flatter pelvis**		
mean	0.18	0.11	*p*=0.03		
std. deviation	0.008	0.009			
HindW/HindL	0.14–0.17	0.17–0.24	**thinner hind limbs**		
mean	0.16	0.19	*p*=0.0007		
std. deviation	0.021	0.025			
HindL/SVL	0.54-0.59	0.42–0.55	**longer hind limbs**		
mean	0.57	0.52	*p*=7.21604E-10		
std. deviation	0.027	0.022			
ForeW/ForeL	0.09–0.13	0.12–0.18	**thinner forelimbs**		
mean	0.12	0.14	*p*=0.00001		
std. deviation	0.016	0.017			
ForeL/SVL	0.41–0.45	0.34–0.42	**longer forelimbs**		
mean	0.42	0.39	*p*=0.002		
std. deviation	0.028	0.019			
sample size	18	62			

TABLE 5. Meristic, banding pattern, and tuberculation data for all known populations of *Cyrtodactylus condorensis sensu stricto, C. leegrismeri sensu stricto, C. eisemanni,* and *C. grismeri.*

	eisemanni	*grismeri*	*leegrismeri sensu stricto*					
			leegrismeri	*thochuensis*	Hon Chuoi	Hon Khoai		
				Tho Chu	sp. 1	sp. 3		
supralabials	10–13	10–14	10, 11	10–14	10–12	9–12		
infralabials	10–12	9, 11	7–9	9, 10	8–10	7–9		
paravertebral tubercles	19–22	31–37	25–35	29–34	27–29	30–39		
ventral scales	44–45	33–39	27–43	30–36	34–43	34–42		
4th toe lamellae	17, 18	16–19	18–20	17–19	14–16	17–22		
precloacal pores	no	no	4–6	3–5	2–4	1–5		
enlarged femoral scales			11–21	15, 16	15–23	13–21		
tuberculation	weak	weak	strong	strong	strong	strong		
thin white dorsal bands	yes	yes	no	no	no	no		
max. SVL	89.2	95.0	92.0	86.3	88.2	89.6		
Sample size	6	13	6	7	5	20		
	condorensis sensu stricto							
	condorensis	*paradoxus*	*paradoxus*	*paradoxus*	Hon Tre	Hon Nghe	Hon Son	Hon Dat
	Con Dao	Hon Thom	Hon Chong	Nam Du	sp. 2	unnamed	unnamed	unnamed
supralabials	9–12	9–11	11, 12	11	10	12, 13	10–13	10–13
infralabials	7–9	8–9	9, 10	9, 10	9	9, 11	8–10	9, 10
paravertebral tubercles	29–41	28–33	31–33	27–31	32	30–32	24–38	23–29
ventral scales	32–41	34–44	31–37	34–39	34	34–38	31–44	31–36
4th toe lamellae	16–21	18, 19	19, 20	19, 20	19	17–19	16–23	16, 17
precloacal pores	4–7	3–5	3, 4	3, 4	4	3, 4	2–4	4, 5
enlarged femoral scales	12–23	15–21	16–20	18–21	19	14–16	13–21	15–19
tuberculation	strong	strong	strong	strong	strong	strong	strong	strong
thin white dorsal bands	no	no	no	no	no	no	no	no
max. SVL	89.6	82.6	73.3*	80.1	84.1	78.5	83.6	79.6
Sample size	17	9	4	4	1	6	22	5
* Combined with data from Orlov *et al.* (2007)								

From the standpoint of conservation, it is clear that rocky habitats in the Mekong Delta are islands of endemism surrounded by a sea of agriculture. In Vietnam alone, there are five endemic species of gekkonids: *Cnemaspis aurantiacopes* Grismer & Ngo, *Cnemaspis tucdupensis* Grismer & Ngo, and *Cnemaspis nuicamensis* Grismer & Ngo (Grismer & Ngo 2007), *Gekko vietnamensis* Nguyen (Nguyen 2010), and *Cyrtodactylus grismeri* endemic to these unique habitats. Furthermore, three of these species (*Cnemaspis tucdupensis, Gekko vietnamensis,* and *Cyrtodactylus grismeri*) come from Tuc Dup Hill, one of the smallest habitat-islands in the region. Some of the much larger areas such as Nui Cam Hill, the provenance of the endemic *Cnemaspis nuicamensis,* are still in desperate need of exploration. We are certain that additional surveys of habitat-islands in the Mekong Delta in both Vietnam and Cambodia will yield additional new species. Thus, it is paramount that these areas and their associated islands be conserved and recognized as important components of the natural heritage of these countries. Unfortunately they have recently become sources of animal exploitation by criminal elements in herpetocultural circles. *Cyrtodactylus condorensis sensu stricto* and *Cnemaspis psychedelica* have been illegally collected from Hon Khoai Island and offered for sale on-line by Russian and German poachers (see Grismer *et al.* 2014d:26).

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APPENDIX

The following species were examined:

Cyrtodactylus eisenmani—Vietnam, Kien Giang Province, Hon Son Island UNS 0244–48 (type series).
Cyrtodactylus grismeri—Vietnam, An Giang Province, Tuc Dup Hill UNs 0235–43 (type series), LSUHC 10405–08.
Cyrtodactylus condorensis—Vietnam, Ba Ria Vung Province, Con Dao Islands LSUHC 10438–40, 11351–63; Kien Giang Province, Hon Chong LSUHC 9269–72, Nam Du LSUHC 9273–76, Hon Nghe LSUHC 8671, Hon Son LSUHC 10389–90. 10392–401, 10403, Hon Tre LSUHC 8587, Hon Thom LSUHC 11394–401
Cyrtodactylus leegrismeri—Vietnam, Ca Mau Province, Hon Khoai LSUHC 9256, 11375–94, Hon Chuoi ITBCZ 2220–24, Kien Giang Province, Tho Chu ITBCZ 2300, 2205–06, 2301–06.