Phylogeny and evolution of habitat preference in *Goniurosaurus* (Squamata: Eublepharidae) and their correlation with karst and granite-stream-adapted ecomorphologies in species groups from Vietnam

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Abstract

Maximum likelihood (ML) and Bayesian inference (BI) analyses using two mitochondrial (16S and cyt b) and two nuclear (CMOS and RAG1) genes and 103 specimens recovered the first phylogenies of all 23 extant species of *Goniurosaurus*. The analyses strongly supported the recognition of four monophyletic species groups with identical inter-specific relationships within the *kuroiwae*, *lichtenfelderi*, and *yingdeensis* groups but discordant topologies at some nodes within the *luii* group. Both analyses recovered a polyphyletic *G. luii* with respect to *G. kadoorieorum*, and owing to the lack of diagnostic characters in the latter, it is considered a junior synonym of *G. luii*. A stochastic character mapping analysis of karst versus non-karst habitat preference suggested that karstic landscapes may have played a major role in the evolution and diversification of *Goniurosaurus*. A karst habitat preference is marginally supported as the most probable ancestral condition for *Goniurosaurus* as well as for the *kuroiwae*, *luii*, and *yingdeensis* groups. However, a non-karst habitat preference is marginally supported as the most probable ancestral condition for the *lichtenfelderi* group. Multivariate and univariate ecomorphological analyses of the karst-adapted *G. catbaensis*, *G. hualiensis*, and *G. luii* of the *luii* group and the granite-stream-adapted *G. lichtenfelderi* of the *lichtenfelderi* group demonstrated that their markedly statistically different body shapes may be an adaptive response that contributes to habitat partitioning in areas of northern Vietnam where they are nearly sympatric.

Keywords

Asia, stochastic character mapping, systematics, synonymy, tiger geckos

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Introduction

Eublepharid geckos of the genus *Goniurosaurus* Barbour, 1908 comprise 23 saxicolous specialists (Uetz et al. 2021) that extend from the Ryukyu Archipelago in Japan, southward through East Asia to northern Vietnam. *Goniurosaurus* is a well-defined monophyletic group (Grismer 1988) comprised of four monophyletic species groups: the *kuroiwae* group containing six species endemic to the Ryukyu Archipelago, Japan; the *lichtenfelderi* group with five species from insular and mainland China and northern Vietnam; the *luii* group with eight species from northern Vietnam, some of its offshore islands, and southern China; and the *yingdeensis* group consisting of four species from southern China (Kurita et al. 2008; Nguyen et al. 2009; Nguyen 2011; Wang et al. 2013; Honda and Ota 2017; Liang et al. 2018; Qi et al. 2020a, 2020b; Zhu et al. 2020a, 2020b). Apart from these species, *Goniurosaurus sinensis* Zhou, Peng, Huo and Yuan, 2019 is likely a junior synonym of another species from Hainan Island, China and not included herein (Qi et al. in progress). Phylogenetic relationships within *Goniurosaurus* have never been strongly supported nor consistent among different studies (e.g. Wang et al. 2013; Liang et al. 2018; Qi et al. 2020a, 2020b; Zhu et al. 2020a, 2020b). This protracted state of discordance results, in part, from researchers focusing on different species groups as opposed to the entire genus, as well as using different genes or different combinations of genes with varying combinations of ingroup and outgroup species—all variables that bear significantly on tree construction (Wiens 1998; Zwickl et al. 2002; Heath et al. 2008; Wiens and Morrill 2011; Wainwright and Price 2016). The most commonly used genetic markers have been the mitochondrial genes 12S and 16S rRNA and cytochrome *b* (*cyt* *b*). Liang et al. (2018) were the first to address the challenges of properly aligning rRNA (Pyron et al. 2013) and constructed a well-supported mito-nuclear data set using 16S, *cyt* *b*, and the nuclear genes oocyte maturation factor MOS (CMOS), and recombination activating 1 (RAG1). Zhu et al. (2020b) also used this mito-nuclear combination, but examined only relationships within the *lichtenfelderi* group.

In an effort to continue building a more global understanding of the phylogenetic relationships within *Goniurosaurus*, we expanded the mito-nuclear data set of Liang et al. (2018) to include 103 individuals as opposed to 31 and 23 as opposed to 17 species, which for the first time, includes all extant species of the genus (Table 1). We used this phylogeny in a stochastic character state mapping (SCM) analysis (Revell 2012) of habitat preference to explore the role karstic landscapes may have played in the evolution and diversification of *Goniurosaurus* and if...
Figure 2. A1–A3. Photos of karst-adapted species (*Goniurosaurus catbaensis*, *G. huuliensis*, and *G. luii*, respectively), A4. Granite-stream-adapted species (*G. lichtenfelderi*), B1 – B3. Karst habitats of the *luii* group, B4. Granite-stream habitat of the *lichtenfelderi* group. Photos by Hai Ngoc Ngo.
Table 1. Species and GenBank accession numbers of the sequenced specimens used herein.

| Species/Specimen                     | 16s   | cytb  | CMOS   | RAG1              |
|--------------------------------------|-------|-------|--------|-------------------|
| Goniurosaurus araneus                | AB308460 |       |        |                   |
| G. araneus ECNU-V0008                | MT533259 |       |        |                   |
| G. araneus JFBM15830                 |        |       | HQ426537 | HQ426286         |
| G. bawanglingensis BL-RBZ-021        | MH247190 | MH247201 | MH247212 | MH247223         |
| G. bawanglingensis BL-RBZ-022        | MH247191 | MH247202 | MH247213 | MH247224         |
| G. bawanglingensis BL-RBZ-023        | MH247192 | MH247203 | MH247214 | MH247225         |
| G. bawanglingensis BL-RBZ-024        | MH247193 | MH247204 | MH247215 | MH247226         |
| G. bawanglingensis SYS 002162        | MT995758 | MT995773 |        |                   |
| G. cathaensis G33                    | MW741550 | MW650944 |        |                   |
| G. cathaensis G34                    | MW741551 | MW650945 |        |                   |
| G. cathaensis G35                    |        |       | MW650946 |                   |
| G. cathaensis MHNG 2699.49           | EU499389 |       |        |                   |
| G. gezhi ECNU-V0038                  | MT533260 |       |        |                   |
| G. gezhi ECNU-V0040                  | MT533261 |       |        |                   |
| G. gezhi ECNU-V0042                  | MT533262 |       |        |                   |
| G. gezhi ECNU-V0046                  | MT533263 |       |        |                   |
| G. gezhi ECNU-V0047                  | MT533264 |       |        |                   |
| G. gollum SYS r002420                | MT995784 | MT995787 | MW275559 | MW27594          |
| G. gollum SYS r002421                | MT995785 | MT995788 | MW27560  | MW27595          |
| G. gollum SYS r002422                | MT995786 | MT995789 | MW27561  | MW27596          |
| G. haiinanensis BL-RBZ-041           | MH247194 | MH247205 | MH247216 | MH247227         |
| G. haiinanensis BL-RBZ-042           | MH247195 | MH247206 | MH247217 | MH247228         |
| G. haiinanensis SYS r00349           | KC765080 |       |        |                   |
| G. haiinanensis JK1                  | AB308458 |       |        |                   |
| G. hauensiensis Gohu                 | AB853453 | AB853479 |        |                   |
| G. hauensiensis G21                  |        |       | MW650936 |                   |
| G. hauensiensis G23                  |        |       | MW650937 |                   |
| G. hauensiensis G24                  |        |       | MW650938 |                   |
| G. kadoorieorum ECNU-V0058           | MT533258 |       |        |                   |
| G. kadoorieorum ECNU-V0060           | MT533265 |       |        |                   |
| G. kadoorieorum ECNU-V0061           | MT533266 |       |        |                   |
| G. kuroiwaeki Goku1 Northern Okinawa | AB853448 | AB853473 |        |                   |
| G. kuroiwaeki Goku2 Southern Okinawa | AB853445 |       |        |                   |
| G. kuroiwaeki Goo1 Southern Okinawa  | AB853446 | AB853467 |        |                   |
| G. kwanghwa ECNU-V0003                | MK782788 | MK782782 | MK782776 | MK782770         |
| G. kwanghwa ECNU-V0004                | MK782789 | MK782783 | MK782777 | MK782771         |
| G. kwanghwa ECNU-V0005                | MK782790 | MK782784 | MK782778 | MK782772         |
| G. kwangsensis ECNU-V0009             | MK782786 | MK782780 | MK782774 | MK782768         |
| G. lioenfelderi ECNU-V0007            | MK782785 | MK782779 | MK782773 | MK782767         |
| G. lioenfelderi IEBR 3692            | JF799756 |       |        |                   |
| G. lisi ECNU-V0012                   | MK782787 | MK782781 | MK782775 | MK782769         |
| G. lisi Golu2                        |        |       | EF081254 |                   |
| G. lisi Golu3                        | AB853452 | AB853478 |        |                   |
| G. lisi SYS 000255                   | KC765083 |       |        |                   |
| G. lisi SYS 000256                   | KC765084 |       |        |                   |
| G. lisi ZFMK 87057                   | EU499391 |       |        |                   |
| G. lisi TG00795                      |        |       | HQ426287 |                   |
| G. orientalis Goku3                  | AB853446 |       |        |                   |
| G. orientalis Goo2                   | AB853443 | AB853461 |        |                   |
| G. orientalis Goo3                   |        |       | AB853462 |                   |
| G. sengoku Gose1                     | AB853444 | AB853463 |        |                   |
| G. sengoku Gose2                     |        |       | AB853464 |                   |
| G. splendens Gosp1                   | AB853451 | AB853477 |        |                   |
| G. splendens Gosp2                   | AB853449 |       |        |                   |
| G. splendens Gosp3                   | AB853450 |       |        |                   |
habitat preference coevolved with ecomorphology in near sympatric species of the *luii* and *lichtenfelderi* groups in Vietnam (Ngo et al. 2021; Figs. 1, 2).

### Materials and methods

#### Genetic data and phylogenetic analyses

Genomic DNA was extracted from muscle tissue samples, using a DNA extraction kit from Tiangen Biotech (Beijing) Co., Ltd. Primers used for 16S were r16S-5L (5'- GGTMMYGCTGCCCCAGTG -3') and 16Sbr-H (5'- CCGGTCGAACTCAGATACGT-3') (Palumbi et al. 1991), for cyt b the primers were L14731 (5'- TG GTCTGAAAAACCATTGTTG-3') (Honda et al. 2014) and H15149m (5'- GCMCCTCAGAAKGATATTTGY CCTCA-3') (Chambers and MacAvoy 1999), for CMOS the primers were FU-F (5'- TTTGGTTCKGTCTACAA-GGCTAC -3') and FU-R (5'- AGGGAACATCCAAAG-TCTCCAAT -3') (Gamble et al., 2008), and for RAG1 the primers were R13 (5'- TCTGAATGGAAATTCAAGCTGTT -3') and R18 (5'- GATGCTGCCTCGGCTCGG- CCACCTTT -3') (Groth and Barrowclough 1999). The PCR procedure was performed with an initial denaturation at 94 °C for 5 min, 35 cycles of 94 °C for 30 s, 55 °C for 30 s and 72 °C for 1 min, followed by a final
extension at 72 °C for 10 min (Liang et al. 2018). PCR products were purified with spin columns and then sequenced with forward primers using BigDye Terminator Cycle Sequencing Kit as per the guidelines on an ABI Prism 3730 automated DNA sequencer by Shanghai Majorbio Bio-pharm Technology Co., Ltd.

We constructed Maximum Likelihood (ML), Bayesian Inference (BI), and Bayesian Evolutionary Analysis by Sampling Trees (BEAST) phylogenetic trees using a concatenated data set composed of 3070 base pairs (bp) of the mitochondrial genes, 16S (633 bp) and cyt b (1075 bp), and the nuclear genes, CMOS (472 bp) and RAG1 (890), from 103 specimens of 23 species of Goniurosaurus with varying degrees of sequence coverage across the samples (Table 1). Concatenation followed the comparison of separate gene trees to confirm there were no major discordances. One species, Eublepharis macularius, served as an outgroup (Grismer 1988; Jonniaux and Kumazawa 2008) to root the sequences. Gene data and GenBank accession numbers are listed in Table 1.

A Maximum likelihood (ML) analysis partitioned by gene was implemented using the IQ-TREE webserver (Nguyen et al. 2015; Trifinopoulos et al. 2016) preceded by the selection of substitution models using TIM2+F+I+G4 for 16S and cyt b and HKY+F for CMOS and RAG1. To avoid over parameterization, protein coding genes were not partitioned by codon. A thousand bootstrap pseudoreplicates via the ultrafast bootstrap (UFB: Hoang et al. 2018) approximation algorithm were employed, and nodes having UFB values of 95 and above were considered strongly supported (Minh et al. 2013). We considered nodes with values of 90–94 as well-supported. A Bayesian inference (BI) analysis was carried out in MrBayes 3.2.3. (Ronquist et al. 2012) on XSEDE using the CIPRES Science Gateway (Cyberinfrastructure for Phylogenetic Research; Miller et al. 2010). bModelTest was used to numerically integrate over the uncertainty of substitution models of each gene while simultaneously estimating phylogeny using Markov chain Monte Carlo (MCMC). MCMC chains were run for 100,000,000 generations and logged every 10,000 generations. The BEAST log file was visualized in Tracer v. 1.6.0 (Rambaut et al. 2014) to ensure effective sample sizes (ESS) were well-above 200 for all parameters. A Maximum clade credibility tree using mean heights at the nodes was generated using TreeAnnotator v.1.8.0 (Rambaut and Drummond 2014) with a burn-in of 1000 trees (10%). Nodes with BPPs of 0.95 and above were considered strongly supported (Huelsenbeck et al. 2001; Wilcox et al. 2002). We considered nodes with values of 0.90–0.94 as well-supported.

**Ancestral state reconstruction**

The BEAST tree was converted to newick format and pruned using the drop.tip() command (Paradis and Schliep 2018) in the R package ape [v.3.4.3] to include only the earliest diverged individual of each species. Habitat preference (karst or non-karst; see below) was mapped onto the tree using tree using TreeAnnotator (Revell 2012) in order to derive probability estimates of the ancestral states at each node. A transition rate matrix was identified that best fit the data by comparing the corrected Akaike Information Criterion (AICc) values in the R package ape (Paradis and Schliep 2018). Three transition rate models were considered: a 2-parameter model having different rates for every transition type (the ARD model); a single-parameter model with equal forward and reverse rates between states (the symmetrical rates SYM model); and a single rate parameter model that assumes equal rates among all transitions (ER). Lastly, an MCMC approach was used to sample the most probable 1000 trait histories from the posterior using the make.simmap() command and then summarized them using the summary() command.

The coding of habitat preference for each species was determined from the literature and field observations of the authors (Table 2). A species’ habitat preference was coded as “karst” if it had a strong association with karstic habitats. Many such species may range into forested areas or areas with other rock types (e.g. granite). These species never show any strong preference for karstic microhabitats even if such habitats exist within their range.

**Morphological data and analyses**

An ecomorphological analysis was conducted using four of the five recorded species from Vietnam (Grismer et al. 1999; Vu et al. 2006; Orlov et al. 2008; Ziegler et al. 2008; Nguyen et al. 2009; Nguyen 2011; Wilcox et al.
| Species          | 1° habitat | 2° habitat | Source                                                          |
|------------------|------------|------------|----------------------------------------------------------------|
| karoiwae group   |            |            |                                                                |
| G. splendens     | karst      | forest     | Nakamura and Ueno (1963), H. Ota pers. comm., L. Grismer pers. obs. |
| G. toyamai       | forest     |            | H. Ota pers. comm.                                             |
| G. karoiwae North| forest     |            | H. Ota pers. comm., L. Grismer pers. obs.                     |
| G. karoiwae South| karst      | forest     | Nakamura and Ueno (1963), H. Ota pers. comm., L. Grismer pers. obs. |
| G. yamashinae    | karst      | forest     | H. Ota pers. comm., L. Grismer pers. obs.                     |
| G. sengoku       | karst      | forest     | Werner et al. (2004), H. Ota pers. comm.                      |
| G. orientalis    | karst      |            | H. Ota pers. comm.                                             |
| yingeoensis group|            |            |                                                                |
| G. gollum        | karst      |            | Qi et al. (2020a)                                              |
| G. yingeoensis   | karst      | granite    | Wang et al. (2010), S. Qi pers. obs.                          |
| G. zheliolongi   | karst      | granite    | S. Qi, pers. obs., Wang et al. (2014)                         |
| G. varius        | karst      |            | Qi et al. (2020b)                                              |
| lichtenfelderi group |         |            |                                                                |
| G. baivanglingensis | granite   | karst      | Grismer et al. (2002), Orlov et al. (2008)                    |
| G. zheliolongi   | karst      | granite    | Zhou et al. (2018), S. Qi pers. obs.                          |
| G. kwanghua      | karst      | granite    | Zhu et al. (2020)                                             |
| G. lichtenfelderi| granite    |            | Orlov et al. (2008)                                           |
| G. hainanensis   | granite    | volcanic   | S. Qi pers. obs., L. Grismer pers. obs.                       |
| luli group       |            |            |                                                                |
| G. catbaensis    | karst      |            | Ziegler et al. (2008), Ngo et al. (2019a)                     |
| G. gezhi         | karst      |            | Zhu et al. (2020)                                             |
| G. araneus       | karst      |            | Grismer et al. (1999)                                         |
| G. kadooriororum| karst      |            | Yang and Chan (2015)                                          |
| G. huilienensis  | karst      |            | Orlov et al. (2008)                                           |
| G. luli          | karst      |            | Grismer et al. (1999), Vu et al. (2006)                       |
| G. liboensis     | karst      |            | Wang et al. (2013)                                            |
| G. kwangstiensis | karst      |            | Yang and Chan (2015)                                          |

2020) for which there existed a substantially large morphometric data set (Ngo et al. 2021): the karst-adapted G. catbaensis Ziegler, Nguyen, Schmitz, Stenke, and Rössler, 2008, G. huilienensis Orlov, Ryabov, Nguyen, Nguyen, and Ho, 2008, and G. luli Grismer, Viets, and Boyle, 1999 of the luli group and the granite stream-adapted G. lichtenfelderi (Mocquard, 1897) of the lichtenfelderi group (Figs. 1, 2). A total of 486 live individuals and 54 museum specimens of four species were examined for morphological data, comprising 194 individuals of G. catbaensis (21 juveniles, 93 females, and 80 males), 80 individuals of G. huilienensis (two juveniles, 46 females, and 32 males), and 88 individuals of G. luli (11 juveniles, 43 females, and 34 males) of the luli species group and 178 individuals of G. lichtenfelderi (14 juveniles, 72 females, and 92 males) of the lichtenfelderi group.

Measurements were taken with dial calipers to the nearest 0.1 mm on the right side of each individual. Abbreviations are as follows: snout-vent length (SVL), from tip of snout to vent; axilla to groin length (AG), from posterior edge of forelimb insertion to anterior edge of hind limb insertion; maximum body width (BW), greatest width of torso, taken at level of midbody; maximum body height (BH), from dorsal surface of body to belly; interaural distance (ID), distance between nares; head length (HL), from the tip of snout to posterior edge of occiput; maximum head width (HW); cheek height (CH), from posterior edge of labial to top of head at parietal region; interorbital distance (IO), distance between posteriormost points of eyes; diameter of auditory meatus (AD); snout to eye distance (SL), measured from tip of snout to posteriormost point of eye; diameter of eye (ED), greatest diameter of eye; eye to ear distance (EE), from posterior margin of eye to posterior margin of ear; forelimb length (FLL), from axilla to the tip of the fourth finger; hind limb length (HLL), from groin to the tip of the fourth toe.

To remove potential effects of allometry, size was adjusted using the following equation: $X_{adj} = \log(X) - \beta \log(SVL_{\text{mean}})$, where $X_{adj} = \text{adjusted value}$; $X = \text{measured value}$; $\beta = \text{unstandardized regression coefficient for each population}$; and $SVL_{\text{mean}} = \text{overall average SVL of all populations}$ (Thorpe 1975, 1983; Turan 1999; Lleonart et al. 2000)—accessible in the R package GroupStruct (available at https://github.com/chankinonn/GroupStruct). The morphometrics of each species were adjusted separately and then concatenated so as not to conflate intra- with interspecific variation (Reists 1986). All data were then scaled to their standard deviation to insure they were analyzed on the basis of correlation and not covariance and were log-transformed to insure they were normally distributed.

An analysis of variance (ANOVA) was performed on a data set coded for species to search for the presence of statistically significant mean differences ($p < 0.05$)
Figure 3. Mito-nuclear maximum likelihood topology with ultrafast bootstrap values (UFB) and Bayesian posterior probabilities (BPP) at the nodes. All species except Goniurosaurus luii had strong nodal support (100/1.00) for their monophyly. The inset in the luii species group is a section of the BI analysis showing the non-monophyly of G. luii with respect to G. kadoorieorum. Colored species are those used in the ecomorphological analyses.
among characters across the selected subset of species in the *luii* and *lichtenfelderi* groups. Character means bearing statistical differences among species were subjected to a TukeyHSD test to ascertain which species pairs differed significantly from each other for those particular characters. A Student *t*-test was also performed on a second data set coded for only habitat preference (karst versus non-karst) to search for the presence of statistically significant mean differences (*p* < 0.05) among the same subsets of species coded for habitat. Violin plots with inserted boxplots were generated in order to visualize the range, frequency, mean, 50% quartile, and degree of differences between the dependent variables for both data sets bearing statistically different mean values.

The morphospatial clustering of the two separate data sets (species and habitat preference) were visualized using principal component analysis (PCA) along the ordination of the first two principal components (PC) using the Adegenet package in R (Jombart et al. 2010) and implemented by the `prcomp()` command. The data were log-transformed prior to analysis in order to normalize their distribution so as to ensure characters with very large or very low values could not over-leverage the results owing to intervariable nonlinearity. All statistical analyses were performed using R.3.1.2 (R Core Team 2018).

### Results

#### Phylogenetic relationships

The ML, BI, and BEAST analyses recovered strong nodal support (UFB 98–100/BPP 1.00) for the monophyly of all four species groups with the *kuroiwae* group being the strongly supported (100/1.00) sister group to the remaining three groups (Fig. 3). The ML analysis weakly recovered (88) the *lichtenfelderi* and *yingdeensis* groups as sister lineages, although the support is so low (0.51), the three groups effectively form a polytomy. The ML and BI analyses recovered the identical inter-specific relationships within the species groups but discordant relationships with the BEAST analysis regarding the *luii* group. The ML and BI analyses recovered a poorly supported (*G. catbaensis* (*G. araneus*, *G. gezhi*)) clade but the BEAST analysis recovered *G. catbaensis* as the strongly supported (0.99) sister species to the remainder of the *luii* group species (Figs. 3, 4, respectively). All analyses recovered a polyphyletic *Goniurosaurus luii* with respect to *G. kadoorieorum* (not shown in the pruned tree of Fig. 4).
Table 3. Difference, lower and upper ranges, and adjusted p values of statistically significant mean differences between species pairs for each character based on ANOVA and subsequent TukeyHSD analyses.

|               | difference  | lower range | upper range | p adjusted |
|---------------|-------------|-------------|-------------|------------|
| axilla-groin (AG) |             |             |             |            |
| huuliensis-catbaensis | 0.095633573 | 0.072292064 | 0.118975082 | 3.37E-10    |
| lichtenfelderi-catbaensis | -0.075967576 | -0.094200659 | -0.057734493 | 3.37E-10    |
| luchi-catbaensis | -0.029676257 | -0.05225407 | -0.007098445 | 0.00206065  |
| lichtenfelderi-huuliensis | -0.171601149 | -0.195246969 | -0.14795333 | 3.37E-10    |
| luchi-huuliensis | -0.12530983 | -0.152447204 | -0.098172456 | 3.37E-10    |
| luchi-lichtenfelderi | 0.046291319 | 0.023399042 | 0.069183596 | 1.60E-06    |
| body width (BW) |             |             |             |            |
| huuliensis-catbaensis | 0.106179184 | 0.066412755 | 0.145945613 | 4.37E-10    |
| lichtenfelderi-catbaensis | -0.083314667 | -0.123590666 | -0.043029791 | 8.67E-07    |
| luchi-huuliensis | -0.051843482 | -0.098759604 | -0.03927359 | 0.000295844 |
| luchi-lichtenfelderi | 0.046291319 | 0.023399042 | 0.069183596 | 1.60E-06    |
| body height (BH) |             |             |             |            |
| huuliensis-catbaensis | 0.094637915 | 0.046801122 | 0.142474708 | 2.84E-06    |
| lichtenfelderi-catbaensis | -0.073170210 | -0.121630666 | -0.024709755 | 0.00647886  |
| lucht-huuliensis | -0.125013692 | -0.180629845 | -0.075315269 | 5.34E-10    |
| internarial distance (ID) |             |             |             |            |
| lichtenfelderi-catbaensis | -0.082396274 | -0.105742691 | -0.059049857 | 3.37E-10    |
| luchi-huuliensis | -0.051843482 | -0.098759604 | -0.03927359 | 0.000295844 |
| luchi-lichtenfelderi | 0.046291319 | 0.023399042 | 0.069183596 | 1.60E-06    |
| head length (HL) |             |             |             |            |
| huuliensis-catbaensis | 0.075818967 | 0.058801575 | 0.092836359 | 3.37E-10    |
| lichtenfelderi-catbaensis | -0.162875997 | -0.176169033 | -0.149582961 | 3.37E-10    |
| luchi-huuliensis | -0.09020154 | -0.125668004 | -0.056172303 | 5.78E-10    |
| luchi-lichtenfelderi | 0.133777111 | 0.110782382 | 0.15046985 | 3.37E-10    |
| head width (HW) |             |             |             |            |
| huuliensis-catbaensis | 0.036775074 | 0.019138869 | 0.05441128 | 6.89E-07    |
| lichtenfelderi-catbaensis | -0.158637886 | -0.172414249 | -0.14864143 | 3.37E-10    |
| luchi-huuliensis | -0.096677642 | -0.126545757 | -0.066400527 | 3.37E-10    |
| luchi-lichtenfelderi | 0.03635767 | 0.07633899 | 0.110932545 | 3.37E-10    |
| head height (HH) |             |             |             |            |
| huuliensis-catbaensis | 0.108413032 | 0.073172094 | 0.143653969 | 3.37E-10    |
| lichtenfelderi-catbaensis | -0.032237965 | -0.05766217 | -0.00479013 | 0.01462568  |
| luchi-huuliensis | -0.14605997 | -0.176351381 | -0.081272881 | 3.37E-10    |
| luchi-lichtenfelderi | 0.093635767 | 0.07633899 | 0.110932545 | 3.37E-10    |
| cheek height (CH) |             |             |             |            |
| huuliensis-catbaensis | 0.069593379 | 0.028246161 | 0.110944597 | 0.00010199  |
| lichtenfelderi-catbaensis | -0.140073735 | -0.180373429 | -0.11577403 | 3.37E-10    |
| luchi-huuliensis | -0.057345812 | -0.09734215 | -0.017349473 | 0.001381599 |
| luchi-lichtenfelderi | -0.217669109 | -0.259557409 | -0.175780808 | 3.37E-10    |
| snout length (SL) |             |             |             |            |
| huuliensis-catbaensis | 0.108547374 | 0.083797596 | 0.133297152 | 3.37E-10    |
The mito-nuclear data set of Liang et al. (2018) differed from all the above analyses in that their ML and BI analyses (79/0.99) placed the yingdeensis group as the sister group to a sister lineage comprised of the luii group and lichtenfelderi group (87/1.00).

**Ancestral state reconstruction**

The AICc scores for the three transition rate models of the SCM analysis were ARD = 34.547134 and SYM and ER = 32.099451. The SCM analysis using either the SYM or ER model suggests that a karst habitat preference is the most probable ancestral condition for Goniurosaurus (57.0% probability), the kuroiwaie group (62.7%), the luii group (90.0%), and the yingdeensis group (95.7%; Fig. 4). The probable ancestral condition for the lichtenfelderi group is non-karst (55.4%). The karst habitat preference of G. kwanghua and G. zhoui of the lichtenfelderi group is considered to have evolved independently given that the ancestral condition of the lichtenfelderi group and that of the most recent common ancestor of the sister species G. lichtenfelderi and G. hainanensis was not karst-adapted (Fig. 4).

**Ecomorphology**

In both the species and habitat preference PCA analyses, PC1 accounted for 49.1% of the variation in the data set and loaded most heavily for limb length (FLL and HLL), snout length (SL), eye diameter (ED), interorbital distance (IO), head width (HW), and head length (HL). PC2 accounted for an additional 13.3% of the variation and loaded most heavily for body width (BW) and body height (BH) (Figs. 5, 6; Table 4).

The PCA analysis of the karst-adapted Goniurosaurus cathaenesis, G. huuliensis, and G. luii of the lui group demonstrates that their body shapes greatly overlap in morphospace despite there being several slight, but statistically significant mean differences among them (Fig. 5; Table 3). Additionally, none of the plots of the karst-adapted species overlap with that of the granite stream-adapted species G. lichtenfelderi along the ordination of PC1. The PCA analysis using habitat preference as the dependent variable among the four species, showed that the karst-adapted and granite-stream-adapted species plot separately as before along taxonomic lines and that collectively, the former have significantly longer axilla-groin lengths (AG); longer, wider, and thicker heads (HL, HW, and CH); longer snouts (SL); longer limbs (FLL and HLL); wider interorbital distances (IO); larger eyes (ED) and larger ear openings (AD) (Fig. 6). Many of these characters—longer head and snout, larger eyes, longer trunk, longer limbs—occur in many other distinctly related karst-adapted species of Cyrtodactylus (Grismer et al. 2016a, 2020b; Kaatz et al. 2021; Nielsen and Oliver 2017), indicating that these are convergent adaptations to a karstic life style within and between the gekkotan families.
Table 4. Summary statistics and principal component analysis scores for the morphological characters for Goniurosaurus catbaensis, G. lichtenefelderi, G. luei, and G. lichtenfelderi. Abbreviations are listed in the Materials and methods.

| Character | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 | PC9 | PC10 | PC11 | PC12 | PC13 | PC14 |
|-----------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Standard deviation | 1.3669 | 1.0396 | 1.334 | 0.9977 | 0.0493 | 0.0425 | 0.0293 | 0.0293 | 0.0293 | 0.0293 | 0.0293 | 0.0293 | 0.0293 | 0.0293 |
| Proportion of variance | 0.7712 | 0.2288 | 0.4972 | 0.2900 | 0.1538 | 0.1472 | 0.1300 | 0.1300 | 0.1300 | 0.1300 | 0.1300 | 0.1300 | 0.1300 | 0.1300 |
| Eigenvalue | 1.3669 | 1.0396 | 1.334 | 0.9977 | 0.0493 | 0.0425 | 0.0293 | 0.0293 | 0.0293 | 0.0293 | 0.0293 | 0.0293 | 0.0293 | 0.0293 |
| AG | 0.4908 | 0.6248 | 0.7396 | 0.8543 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 |
| BW | 0.7273 | 0.6822 | 0.6822 | 0.6822 | 0.6822 | 0.6822 | 0.6822 | 0.6822 | 0.6822 | 0.6822 | 0.6822 | 0.6822 | 0.6822 | 0.6822 |
| ND | 0.6189 | 0.6248 | 0.7396 | 0.8543 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 |
| HL | 0.6189 | 0.6248 | 0.7396 | 0.8543 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 |
| HW | 0.6189 | 0.6248 | 0.7396 | 0.8543 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 |
| CH | 0.7273 | 0.7273 | 0.8543 | 0.8543 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 |
| R2 | 0.4908 | 0.4908 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 |
| SE | 0.7273 | 0.7273 | 0.8543 | 0.8543 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 |
| ED | 0.4908 | 0.4908 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 |
| EE | 0.7273 | 0.7273 | 0.8543 | 0.8543 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 |
| AD | 0.4908 | 0.4908 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 | 0.6248 |
| HLL | 0.7273 | 0.7273 | 0.8543 | 0.8543 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 | 0.5176 |

Discussion

Geckos in general are particularly well-adapted to karstic landscapes (see Luu et al. 2016; Grismer et al. 2014, 2020a, 2021 and references therein; Google Scholar search using key words “karst” and “Gekkonidae”) and Goniurosaurus is no exception, being that 19 of its 23 species (83%) occupy karstic habitats (Grismer et al. 1994, 1999; Orlov et al. 2008; Ziegler et al. 2008; Yang and Chan 2015; Honda and Ota 2017; Zhou et al. 2018; Ngo et al. 2019a; Qi et al. 2020a, 2020b; Zhu et al. 2020a, 2020b). It is clear that karstic landscapes have played a significant role in the evolution and diversification of Goniurosaurus being that it is the probable ancestral habitat preference for the genus and three of the four species groups. Even the ancestor of the non-karst adapted ancestor of the lichtenefelderi group was karst-adapted (Fig. 4). Furthermore, within the species groups, the limited data herein would suggest that the karst-adapted species are specialized, range-restricted endemics (Grismer et al. 1994, 1999; Orlov et al. 2008; Ziegler et al. 2008; Yang and Chan 2015; Honda and Ota 2017; Zhou et al. 2018; Ngo et al. 2019a; Qi et al. 2020a, 2020b; Zhu et al. 2020a, 2020b). With the exception of G. lichtenfelderi, all the non-karst-adapted species are restricted to islands in the Ryukyu Archipelago (kuroiwae group) or Hainan Island (lichtenefelderi group). It may be that the absence of competition and/or predators in these insular habitats widened the fundamental niches of their ancestors and allowed some species to become more generalized in their habitat preference, which should be tested using new techniques combining phylogenetic history, character evolution, and ecological reconstruction programs.

Systematics of the luei group

The ML and BI analyses of Liang et al. (2018) and the BEAST analysis herein (Fig. 4) recovered Goniurosaurus catbaensis as the strongly supported sister species to the remainder of the luei group. Whereas the ML and BI analysis herein, recovered G. catbaensis as the very poorly supported (60/0.51) sister species of the G. aranues plus G. gezhi clade (Fig. 3). Given that three of the five analyses strongly supported the former relationship and two analyses poorly supported the latter, we prefer the placement of G. catbaensis as the sister species to the remainder of the luei group (Fig. 4). Given the very low nodal support of the latter, it essentially renders that portion of the tree a polytomy and as such, does not effectively contradict the strongly supported sister species position of G. catbaensis in the other trees.

Goniurosaurus kadoorieorum of the luei group (represented by only 16S) is nested within G. luei in
both the ML and BI analyses, rendering \( G. \textit{luii} \) polyphyletic (Fig. 3). The same relationship was recovered in the 16S phylogeny of Zhu et al. (2020a). This, and the lack of diagnostic characters separating \( G. \textit{kadoorieorum} \) from \( G. \textit{luii} \) (Yang and Chan 2015; Ngo et al. 2016), indicates the two species should be considered conspecific and as such, \( G. \textit{kadoorieorum} \) Yang and Chan, 2015 is relegated here to a junior synonym of \( G. \textit{luii} \) Grismer, Viets, and
In all analyses, *G. huuliensis* is consistently recovered as the sister species to *G. luii sensu lato* and its species status is not questioned (Figs. 3, 4).

**Conservation**

Wide-ranging more inclusive studies pertaining to ecosystems management are becoming commonplace in light of climate change and widespread habitat destruction. Such studies reconcile data from a broad range of disciplines in order to address issues that may bear on ecosystems management. Foundational to many of these studies is a basic understanding of species ecology and habitat preference—correlated here with ecomorphology (Cabral et al. 2009; Harfoot et al. 2014). Baseline information on habitat and microhabitat requirements of any species are paramount to understanding how they interact with, and navigate through, their environment (e.g. Grant and Grant 2008; Greene 2005; Losos 2010) and as such, the contextualization of ecosystem management may ultimately turn on these simple points (Meiri 2018; Sinervo et al. 2010).

Integrating the phylogenetic patterns of biodiversity and the morphological adaptations of habitat preference that, in part, underpin species radiations, can fundamentally contribute to conservation management programs (Grismer et al. 2020a, 2021; Erwin 1991; Vane-Wright et al. 1991; Williams et al. 1991; Vázquez and Gittleman 1998; Moritz et al. 2000; Forest et al. 2007; Sgro et al. 2010; Harvey et al. 2011; Rolland et al. 2012; Winter et al. 2012; Shaffer et al. 2015; Beaumont and Wang 2019; Fay et al. 2019; Holderegger et al. 2019)—especially in the karstic regions of northern Vietnam where anthropogenic impact is degrading the habitat and reducing the
density of localized populations of *Goniurosaurus* (Ngo et al. 2019b). Northern Vietnam and many of its offshore islands in the Gulf of Tonkin, harbor large areas of fragmented karstic habitats scattered across their landscapes (Cerrano et al. 2006; Do 2001, 2014; Luo et al. 2016; Ngo et al. 2019a) that are inhabited by an exceptionally large number of endemic plants and animals (Do 2001; Sterling et al. 2006; Clements et al. 2008; Luo et al. 2016; von Oheimb et al. 2017). The obligate restriction of many species to fragmented karstic environments—such as all species of the *luii* and *yingdeensis* groups—functionally transforms these environments into habitat islands (Clements et al. 2006, 2008; von Oheimb et al. 2017), which in some cases, bear an unprecedented degree of range-restricted endemism (e.g. Sgro et al 2012; Harvey et al. 2011; Grismer et al. 2018a, 2021).

Unfortunately, *Goniurosaurus* species are particularly attractive (Fig. 2) and over-harvested for the illegal pet trade (Stuart et al. 2006; Yang and Chan 2015; Ngo et al. 2019b). This is an additional threat to these range-restricted endemics from imperiled karstic environments (Grismer et al. 1997; Orlov et al. 2008; Ziegler et al. 2008; Nakamura et al. 2014; Yang and Chan 2015; Honda and Ota 2017; Zhou et al. 2018; Ngo et al. 2019a; Qi et al. 2020a,b; Zhu et al. 2020a,b). In fact, in areas of China and Vietnam, many populations have suffered huge declines in numbers, or even extinction at some localities, due to the illegal commercial pet trade (Stuart et al. 2006; Yang and Chan 2015; Ngo et al. 2019b, 2021). We hope that this study will bring more clarity to the plight of this genus and continue to serve ongoing conservation and management programs.

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