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Goniurosaurus wangshu sp. nov., a new species of Tiger Gecko from Guangdong, China (Squamata: Eublepharidae)

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Abstract

A new species of Tiger Gecko in the genus *Goniurosaurus* is described from Guangdong, China. This new species, *Goniurosaurus wangshu* sp. nov. is the fifth species of *Goniurosaurus* found in karst topography of Guangdong. It is distinguished morphologically from congeners in this region by the combination of thirteen precloacal pores in male; dorsal ground color of head, body, and limbs in adults yellow; and iris orange. To validate our morphological inferences and support the description of *Goniurosaurus wangshu* sp. nov. as a new species, we sequenced *16S*, *CMOS*, *cytb*, and *RAG1* gene regions and performed molecular phylogenetic analyses. Phylogenetic analysis places the new species within the *G. yingdeensis* group and highlights the evolutionary distinction between this new species and other described congeners.

Key words: taxonomy, molecular phylogeny, karst

Introduction

The genus *Goniurosaurus* Barbour, 1908 in the family Eublepharidae Boulenger, 1883 currently comprises 24 described species (Mocquard 1897; Orlov & Darevsky 1999; Grismer et al. 1999, 2002; Orlov et al. 2008; Ziegler et al. 2008; Wang et al. 2010, 2013, 2014; Honda et al. 2014; Yang & Chan 2015; Honda & Ota 2017; Zhou et al. 2018; Zhu et al. 2020a, 2020b; Qi et al. 2020a, 2020b; Zhu et al. 2021; Ngo et al. 2021). *Goniurosaurus* species are saxicolous and distributed throughout East and Southeast Asia (Wang et al. 2014; Liang et al. 2018; Qi et al. 2020; Grismer et al. 2021). Previous phylogenetic studies in the genus have revealed the existence of four major clades: the *G. kuroiwae* (six species), *G. lichtenfelteri* (five species), *G. lului* (nine species), and *G. yingdeensis* (four species) groups (Liang et al. 2018; Zhu et al. 2020a; Qi et al. 2020b; Grismer et al. 2021). These four groups are also strongly delimited by geographical regions. The *G. lului* group is distributed in northern Vietnam, and Guangxi, China (Nguyen et al. 2009; Nguyen 2011; Liang et al. 2018; Zhu et al. 2020b, 2021; Grismer et al. 2021). The *G. lichtenfelteri* group is found on Hainan island, in Guangxi, China and adjacent Vietnam (Zhu et al. 2020a; Grismer et al. 2021; Ngo et al. 2021; 2022a,b). The *G. kuroiwae* group is confined to Ryukyu Archipelago, Japan (Honda et al. 2014; Honda & Ota 2017; Grismer et al. 1994, 2021; Ngo et al. 2021). Finally, the *G. yingdeensis* group is only found in Guangdong, China (Qi et al. 2020a, 2020b; Grismer et al. 2021; Ngo et al. 2021).

During herpetological surveys conducted in 2021, we collected new *Goniurosaurus* specimens at a previously unknown locality in northern Guangdong (Fig. 1). Our morphological and molecular analyses placed these newly

collected individuals in the *G. yingdeensis* group. However, the new specimens are different from any known species within the *G. yingdeensis* group. Here, we present both morphological and molecular analyses that suggest this new population belongs to an undescribed species of *Goniurosaurus*.

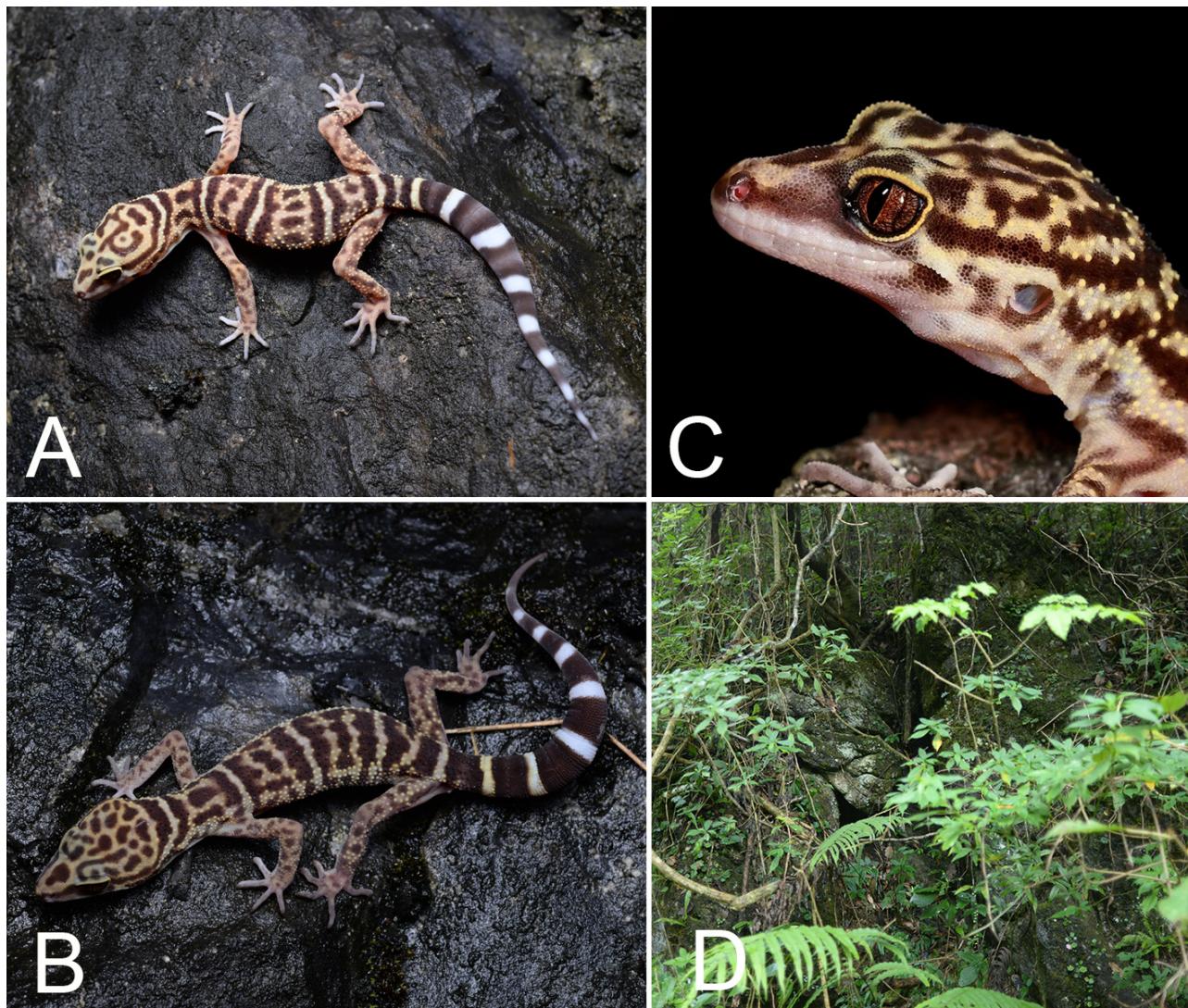


FIGURE 1. *Goniurosaurus wangshu* sp. nov. from Guangdong, China. A: Immature female (photographed in the field); B: Adult female (photographed in the field); C: Scalation and coloration characters of the head (same individual as in Fig 1B); D: Habitat of *Goniurosaurus wangshu* sp. nov..

Materials and methods

Sampling. We found four individuals of the new species by conducting visual survey encounters in karst areas at night. Two individuals (ECNU-V0085 and ECNU-V0084) were collected (Fig. 3A, B). The other two individuals (an immature female and a mature female ECNU-V0083) were captured for photography and the collection of saliva samples before being released to the field (Fig. 1A, B). The Personalbio Saliva/Swab Genomic DNA Kit (Shanghai Personalbio Biotechnology Co., Ltd.) was used to collect DNA. We followed the protocol by swabbing the mouth of each individual for about 10 seconds. DNA samples were preserved at room temperature. We preserved the vouchers in 75% ethanol. All specimens were deposited in the Museum of Biology, East China Normal University (ECNU), which retains full locality information for the specimens.

Morphology. The following measurements were recorded using digital calipers to the nearest ± 0.01 mm following Zhou *et al.* (2018): snout vent length (SVL) from tip of snout to vent; tail length (TaL) from vent to tip of tail; distance between axilla and groin (AG) from posterior edge of forelimb insertion to anterior edge of hindlimb

insertion; snout to eye distance (SE) measured from tip of snout to anteriormost margin of eye; eye to ear distance (EE) from posterior margin of eye to posterior margin of ear; maximum head width (HW); head length (HL) from tip of snout to posterior margin of ear. Scalation characters recorded are as follows: supralabials (SPL); sublabials/infralabials (SBL); nasal scales surrounding nare (N); internasals (IN); gular scales bordering the internasals (PostIN); postmentals (PM); gular scales bordering the postmentals (GP); eyelid fringe scales or ciliaria (CIL); preorbital scales (PO); granular scales surrounding dorsal tubercles (GST); dorsal tubercle rows at midbody (DTR); paravertebral tubercles between limb insertions (TL); scales around midbody (MB); subdigital lamellae under the first finger (LD1) and the fourth finger (LD4); subdigital lamellae under the first toe (LT1) and the fourth toe (LT4); precloacal pores (PP); postcloacal tubercles (PAT). Bilateral scale counts are given as left/right.

DNA extraction and gene amplification. Total genomic DNA was extracted from the saliva samples according to the instructions from the manufacturer. In this study, four gene datasets including two mitochondrial genes, the *Cytochrome b* gene (*cytb*, 396 bp) and the *16S* rRNA gene (*16S*, 454 bp); and two nuclear genes, the oocyte maturation factor gene (*CMOS*, 372 bp) and recombination activating protein 1 gene (*RAG1*, 990bp) were amplified. The DNA did not amplify from the saliva sample of the one immature female. PCR primers for amplification are listed in Table 1. All PCR products were sequenced directly with the same primers and their GenBank accession numbers are listed in Table 2.

TABLE 1. Information of primers used in this study.

Gene	Primer	Primer sequence (5'-3')	Temperature	Sources
<i>16S</i>	r16S-5L	GGTMMYGCCTGCCAGTG	55 °C	Jonniaux & Kumazawa 2008
	16sbr-H	CCGGTCTGAACTCAGATCACGT		Jonniaux & Kumazawa 2008
<i>CMOS</i>	FU-F	TTGGTCKGTCTACAAGGCTAC	50 °C	Gamble <i>et al.</i> 2008
	FU-R	AGGAAACATCCAAAGTCTCCAAT		Gamble <i>et al.</i> 2008
<i>cytb</i>	Cytb-2019F	CGAAAAACCAYGTTGTTATTCAACT	50 °C	Zhu <i>et al.</i> 2020b
	Cytb-2019R	AGRTTGTGATTACGGTTGCGCCT		Zhu <i>et al.</i> 2020b
<i>RAG1</i>	R13	TCTGAATGGAAATTCAAGCTGTT	53 °C	Groth & Barrowclough 1999
	R18	GATGCTGCCTCGGTCGGCACCTT		Groth & Barrowclough 1999

Phylogenetic analyses. We examined the phylogenetic position of the three collected *Goniurosaurus* samples. For this, we first compiled molecular data for 24 previously described *Goniurosaurus* species and a single outgroup species (*Eublepharis macularius*). The species-level and molecular sampling of our dataset closely resembles that of Grismer *et al.* (2021) which is, to date, the most comprehensive species-level phylogeny for *Goniurosaurus*.

Sampled genes: We sampled mitochondrial gene regions *16S* and *cytb*, along with nuclear genes *CMOS* and *RAG1* for the species sampled in Grismer *et al.* (2021; deposited in GenBank) and new individuals analyzed in this study. Sequence alignment for each gene region was conducted using Muscle version 3.8 (Edgar 2004) under default parameters. We used trimAL version 1.4 (Capella-Gutiérrez *et al.* 2009) to remove highly-ambiguous sites in the resulting alignments under the “gappyout” routine. Alignments were concatenated using the SuperMatrix function in the evobiR R package version 1.1 (Blackmon and Adams 2015). The resulting concatenated alignment contained 3053 bp and 108 individuals from 26 species (*16S*, 617 bp; *CMOS*, 372 bp; *cytb*, 1074 bp; *RAG1*, 990 bp).

Maximum likelihood phylogenetic analyses: phylogenetic analyses of the resulting concatenated dataset were conducted using maximum likelihood and Bayesian methods. Specifically under maximum likelihood, we used IQ-TREE version 2 (Minh *et al.* 2020) to infer the phylogenetic relationships among species sampled in our dataset. IQ-TREE analyses were run in the W-IQ-TREE webserver (Trifinopoulos *et al.* 2016). Analyses were performed using a gene-based partitioning strategy for the dataset. Best-fitting models and partitioning strategies were identified using ModelFinder (Kalyaanamoorthy *et al.* 2017), also implemented in IQ-TREE. We allowed rate heterogeneity through both Gamma (+G) and invariable sites (+I). Branch support was assessed based on 1,000 standard bootstrap replicates and all the remaining parameters were set to default.

Bayesian phylogenetic inference: we used MrBayes version 3.2.7 (Ronquist *et al.* 2012) to infer the phylogenetic relationships under a Bayesian framework. We used the GTR+I+G model for each gene region in the concatenated dataset, and analyzed two independent MCMC runs, each consisting of a total 10 million generations. The maximum clade credibility tree was constructed using 90% of the posterior samples and convergence was assessed

based on ESS>200. Finally, we estimated uncorrected pairwise p-distances between all the samples in our dataset using the dist.dna() function in the ape (Paradis and Schliep 2019) R package. Estimates of uncorrected genetic distances were used to examine whether the median distances between the new species and all other *Goniurosaurus* were comparable to those from congeneric species.

TABLE 2. Species and GenBank accession numbers used in this study and based on Grismer *et al.* (2021).

Species/Specimen	16S	cytb	CMOS	RAG1
<i>G. araneus</i> Grismer <i>et al.</i>	AB308460	—	—	—
<i>G. araneus</i> Grismer <i>et al.</i> ECNU-V0008	MT533259	—	—	—
<i>G. bawanglingensis</i> Grismer <i>et al.</i> BL-RBZ-021	MH247190	MH247201	MH247212	MH247223
<i>G. bawanglingensis</i> Grismer <i>et al.</i> BL-RBZ-022	MH247191	MH247202	MH247213	MH247224
<i>G. bawanglingensis</i> Grismer <i>et al.</i> BL-RBZ-023	MH247192	MH247203	MH247214	MH247225
<i>G. bawanglingensis</i> Grismer <i>et al.</i> BL-RBZ-024	MH247193	MH247204	MH247215	MH247226
<i>G. bawanglingensis</i> Grismer <i>et al.</i> SYS r001075	—	—	—	MW727589
<i>G. bawanglingensis</i> Grismer <i>et al.</i> SYS r002162	MT995758	MT995773	—	—
<i>G. bawanglingensis</i> Grismer <i>et al.</i> SYS r002561	—	—	MW727566	MW727601
<i>G. bawanglingensis</i> Grismer <i>et al.</i> SYS r002562	—	—	MW727567	MW727602
<i>G. catbaensis</i> Ziegler <i>et al.</i> G33	MW741550	MW650944	—	—
<i>G. catbaensis</i> Ziegler <i>et al.</i> G34	MW741551	MW650945	—	—
<i>G. catbaensis</i> Ziegler <i>et al.</i> G35	—	MW650946	—	—
<i>G. catbaensis</i> Ziegler <i>et al.</i> MHNG 2699.49	EU499389	—	—	—
<i>G. chengzheng</i> Zhu <i>et al.</i> ECNU-V0090	MW519617	MW534128	—	—
<i>G. chengzheng</i> Zhu <i>et al.</i> ECNU-V0068	MW519616	MW534127	—	—
<i>G. gezhi</i> Zhu <i>et al.</i> ECNU-V0038	MT533260	—	—	—
<i>G. gezhi</i> Zhu <i>et al.</i> ECNU-V0040	MT533261	—	—	—
<i>G. gezhi</i> Zhu <i>et al.</i> ECNU-V0042	MT533262	—	—	—
<i>G. gezhi</i> Zhu <i>et al.</i> ECNU-V0046	MT533263	—	—	—
<i>G. gezhi</i> Zhu <i>et al.</i> ECNU-V0047	MT533264	—	—	—
<i>G. gollum</i> Qi <i>et al.</i> SYS r002420	MT995784	MT995787	MW727559	MW727594
<i>G. gollum</i> Qi <i>et al.</i> SYS r002421	MT995785	MT995788	MW727560	MW727595
<i>G. gollum</i> Qi <i>et al.</i> SYS r002422	MT995786	MT995789	MW727561	MW727596
<i>G. hainanensis</i> Barbour BL-RBZ-041	MH247194	MH247205	MH247216	MH247227
<i>G. hainanensis</i> Barbour BL-RBZ-042	MH247195	MH247206	MH247217	MH247228
<i>G. hainanensis</i> Barbour SYS r000349	KC765080	—	—	—
<i>G. hainanensis</i> Barbour SYS r002563	—	—	MW727568	MW727603
<i>G. hainanensis</i> Barbour JK1	AB308458	—	—	—
<i>G. huiliensis</i> Orlov <i>et al.</i> Gohu	AB853453	AB853479	—	—
<i>G. huiliensis</i> Orlov <i>et al.</i> G21	—	MW650936	—	—
<i>G. huiliensis</i> Orlov <i>et al.</i> G23	—	MW650937	—	—
<i>G. huiliensis</i> Orlov <i>et al.</i> G24	—	MW650938	—	—
<i>G. kadoorieorum</i> Yang & Chan ECNU-V0058	MT533258	—	—	—
<i>G. kadoorieorum</i> Yang & Chan ECNU-V0060	MT533265	—	—	—
<i>G. kadoorieorum</i> Yang & Chan ECNU-V0061	MT533266	—	—	—
<i>G. kuroiwae</i> Namiye Goku1 Northern Okinawa	AB853448	AB853473	—	—
<i>G. kuroiwae</i> Namiye Goku2 Southern Okinawa	AB853445	—	—	—
<i>G. kuroiwae</i> Namiye Goor1 Southern Okinawa	AB853446	AB853467	—	—

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TABLE 2. (Continued)

Species/Specimen	<i>16S</i>	<i>cytb</i>	<i>CMOS</i>	<i>RAG1</i>
<i>G. kuroiwae</i> Namiye LC158324 N Okinawa	—	LC158324	—	—
<i>G. kuroiwae</i> Namiye LC158273 N Okinawa	—	LC158273	—	—
<i>G. kwanghua</i> Zhu <i>et al.</i> ECNU-V0003	MK782788	MK782782	MK782776	MK782770
<i>G. kwanghua</i> Zhu <i>et al.</i> ECNU-V0004	MK782789	MK782783	MK782777	MK782771
<i>G. kwanghua</i> Zhu <i>et al.</i> ECNU-V0005	MK782790	MK782784	MK782778	MK782772
<i>G. kwangsiensis</i> Yang & Chan ECNU-V0009	MK782786	MK782780	MK782774	MK782768
<i>G. liboensis</i> Wang <i>et al.</i> SYS r000854	—	—	MW727571	MW727586
<i>G. liboensis</i> Wang <i>et al.</i> SYS r000855	—	—	MW727572	MW727587
<i>G. liboensis</i> Wang <i>et al.</i> SYS r000217	KC900230	—	—	—
<i>G. lichtenfelderi</i> Mocquard ECNU-V0007	MK782785	MK782779	MK782773	MK782767
<i>G. lichtenfelderi</i> Mocquard IEBR 3692	JF799756	—	—	—
<i>G. lului</i> Grismer <i>et al.</i> ECNU-V0012	MK782787	MK782781	MK782775	MK782769
<i>G. lului</i> Grismer <i>et al.</i> Golu3	AB853452	AB853478	—	—
<i>G. lului</i> Grismer <i>et al.</i> SYSr 000255	KC765083	—	—	—
<i>G. lului</i> Grismer <i>et al.</i> SYSr 000256	KC765084	—	—	—
<i>G. lului</i> Grismer <i>et al.</i> SYSr 000859	—	—	—	MW727588
<i>G. lului</i> Grismer <i>et al.</i> ZFMK 87057	EU499391	—	—	—
<i>G. orientalis</i> Maki Goor2	AB853443	AB853461	—	—
<i>G. orientalis</i> Maki Goor3	—	AB853462	—	—
<i>G. sengokui</i> Honda & Ota Gose1	AB853444	AB853463	—	—
<i>G. sengokui</i> Honda & Ota Gose2	—	AB853464	—	—
<i>G. splendens</i> Nakamura & Uéno Gosp1	AB853451	AB853477	—	—
<i>G. splendens</i> Nakamura & Uéno Gosp2	AB853449	—	—	—
<i>G. splendens</i> Nakamura & Uéno Gosp3	AB853450	—	—	—
<i>G. toyamai</i> Grismer <i>et al.</i> Goto1	AB853447	AB853468	—	—
<i>G. toyamai</i> Grismer <i>et al.</i> Goto2	—	AB853469	—	—
<i>G. varius</i> Qi <i>et al.</i> SYS r002330	—	—	MW727555	—
<i>G. varius</i> Qi <i>et al.</i> SYS r002331	MT995754	MT995769	MW727556	MW727590
<i>G. varius</i> Qi <i>et al.</i> SYS r002332	MT995755	MT995770	—	—
<i>G. varius</i> Qi <i>et al.</i> SYS r002333	MT995753	MT995768	—	—
<i>G. varius</i> Qi <i>et al.</i> SYS r002362	MT995756	MT995771	MW727557	MW727592
<i>G. varius</i> Qi <i>et al.</i> SYS r002363	MT995757	MT995772	MW727558	MW727593
<i>G. varius</i> Qi <i>et al.</i> SYS r002485	MW721828	MW727532	MW727562	MW727597
<i>G. varius</i> Qi <i>et al.</i> SYS r002486	MW721829	MW727533	MW727563	MW727598
<i>G. wangshu</i> sp. nov. ECNU-V0085	ON123412	ON112081	ON112085	ON112083
<i>G. wangshu</i> sp. nov. ECNU-V0084	ON123413	ON112082	ON112086	ON112084
<i>G. wangshu</i> sp. nov. ECNU-V0083	ON123414	ON112083	—	—
<i>G. yamashinae</i> Okada Goyal	AB853442	AB853460	—	—
<i>G. yamashinae</i> Okada Goya2	AB853441	AB853459	—	—
<i>G. yamashinae</i> Okada Goya3	—	AB853458	—	—
<i>G. yingdeensis</i> Wang <i>et al.</i> Field number DYA01	MW721830	MW727534	MW727574	MW727605
<i>G. yingdeensis</i> Wang <i>et al.</i> Field number DYA02	MW721831	MW727535	MW727575	MW727606
<i>G. yingdeensis</i> Wang <i>et al.</i> Field number HS01	MW721832	MW727536	MW727576	MW727607

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TABLE 2. (Continued)

Species/Specimen	<i>16S</i>	<i>cytb</i>	<i>CMOS</i>	<i>RAG1</i>
<i>G. yingdeensis</i> Wang <i>et al.</i> Field number HS02	MW721833	MW727537	MW727577	MW727608
<i>G. yingdeensis</i> Wang <i>et al.</i> Field number LT01	MW721834	MW727538	MW727580	MW727611
<i>G. yingdeensis</i> Wang <i>et al.</i> Field number LT02	MW721835	MW727539	MW727581	MW727612
<i>G. yingdeensis</i> Wang <i>et al.</i> SYS r000549	KC765082	—	—	—
<i>G. yingdeensis</i> Wang <i>et al.</i> SYS r000550	KC900231	—	—	—
<i>G. yingdeensis</i> Wang <i>et al.</i> SYS r001271	MT995759	MT995774	MW727547	—
<i>G. yingdeensis</i> Wang <i>et al.</i> SYS r001272	MT995760	MT995775	MW727548	—
<i>G. yingdeensis</i> Wang <i>et al.</i> SYS r001493	MT995761	MT995776	MW727551	—
<i>G. yingdeensis</i> Wang <i>et al.</i> SYS r0002115	MT995762	MT995777	—	—
<i>G. zhelongi</i> Wang <i>et al.</i> Field number HW01	MW721838	MW727540	MW727578	MW727609
<i>G. zhelongi</i> Wang <i>et al.</i> Field number HW02	MW721839	MW727541	MW727579	MW727610
<i>G. zhelongi</i> Wang <i>et al.</i> Field number MDA01	MW721836	MW727542	MW727582	MW727613
<i>G. zhelongi</i> Wang <i>et al.</i> Field number MDA02	MW721837	MW727543	MW727583	MW727614
<i>G. zhelongi</i> Wang <i>et al.</i> Field number TZ01	MW721840	MW727544	MW727584	MW727615
<i>G. zhelongi</i> Wang <i>et al.</i> Field number TZ02	MW721841	MW727545	MW727585	MW727616
<i>G. zhelongi</i> Wang <i>et al.</i> SYS r000816	KJ423105	MT995778	MW727570	—
<i>G. zhelongi</i> Wang <i>et al.</i> SYS r001491	MT995763	MT995779	MW727549	—
<i>G. zhelongi</i> Wang <i>et al.</i> SYS r001492	MT995764	MT995780	MW727550	—
<i>G. zhelongi</i> Wang <i>et al.</i> SYS r002108	MT995765	MT995781	—	—
<i>G. zhoui</i> Zhou <i>et al.</i> BL-RBZ-001	MH247196	MH247207	MH247218	MH247229
<i>G. zhoui</i> Zhou <i>et al.</i> BL-RBZ-004	MH247197	MH247208	MH247219	MH247230
<i>G. zhoui</i> Zhou <i>et al.</i> BL-RBZ-006	MH247198	MH247209	MH247220	MH247231
<i>G. zhoui</i> Zhou <i>et al.</i> BL-RBZ-007	MH247199	MH247210	MH247221	MH247232
<i>G. zhoui</i> Zhou <i>et al.</i> BL-RBZ-008	MH247200	—	—	—
<i>G. zhoui</i> Zhou <i>et al.</i> SYS r002213	MT995766	MT995782	MW727553	—
<i>G. zhoui</i> Zhou <i>et al.</i> SYS r002214	MT995767	MT995783	MW727554	—
<i>G. chengzheng</i> Zhu <i>et al.</i> ECNU-V0068	MW519616	MW534127	—	—
<i>G. chengzheng</i> Zhu <i>et al.</i> ECNU-V0090	MW519617	MW534128	—	—
<i>Eublepharis macularius</i> Blyth (outgroup)	AB853454	AB853480	—	—

Results

Phylogenetic relationships. Phylogenetic inference under Maximum Likelihood and Bayesian Inference recovered similar evolutionary relationships among the described *Goniurosaurus* species (Fig. 2). The inferred trees are in agreement with previously published phylogenies in the group (e.g. Liang *et al.* 2018; Zhu *et al.* 2020; Zhu *et al.* 2021), including Grismer *et al.* (2021). The three new individuals collected in this study formed a strongly supported monophyletic group in our phylogenies (bootstrap=100%, posterior probability [pp hereafter]=1). Our phylogenetic analyses suggest that these individuals, forming a clade, are nested within the *Goniurosaurus yingdeensis* species group (bootstrap=100%, pp=1), with its closest relative being *G. gollum* (bootstrap=92%, pp=1; Fig. 2). Finally, we note that pairwise *p*-distance estimates suggest that the newly described species in this study shows a median congeneric divergence (e.g. range *p*-distance 16S: 0.036–0.19) that is similar to that of other *Goniurosaurus* species (e.g. *p*-distance 16S *G. liboensis*: 0.018–205; Table 3).

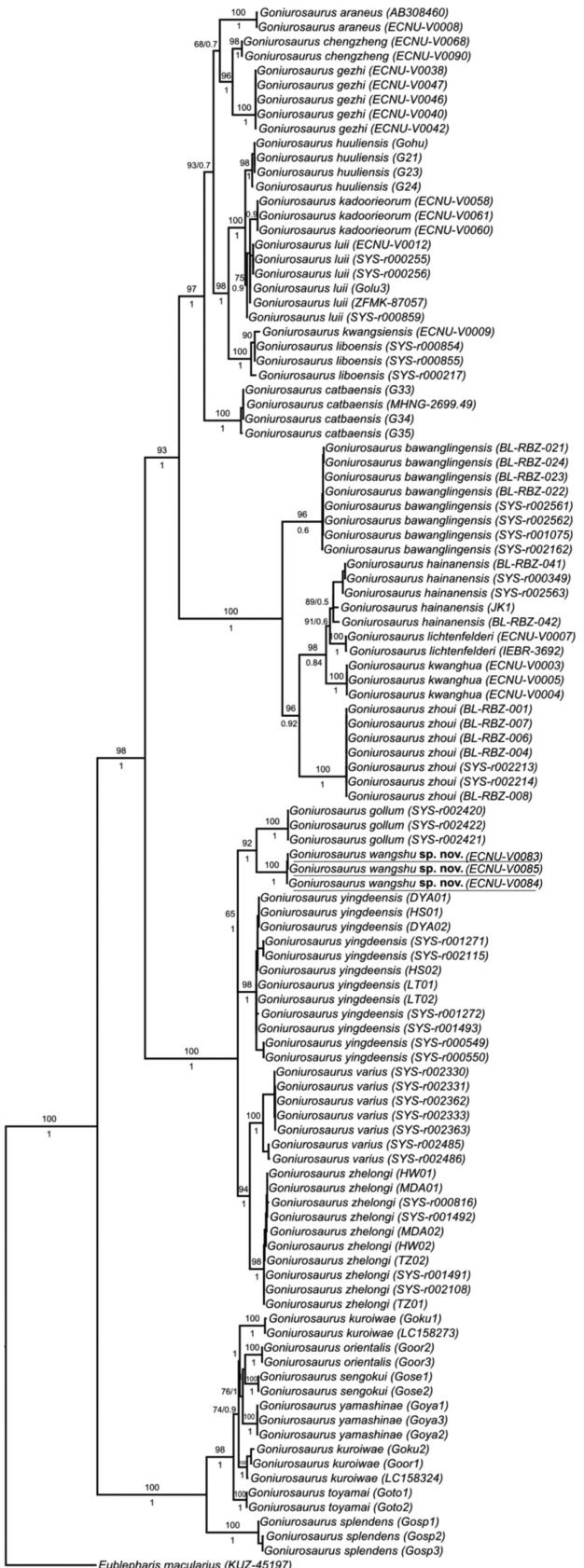


FIGURE 2. Phylogeny showing relationships among 25 *Goniurosaurus* species and one outgroup taxon. Maximum likelihood tree topology. Support values for major clades in the form of bootstrap values (maximum likelihood) and posterior probabilities (Bayesian Inference) are shown above and below branches, respectively. Specimens of *G. wangshu* sp. nov. are underlined in the tree.

TABLE 3. Median value across inter-specific pairwise *P*-distances between congeneric species in *Goniurosaurus*. We calculate *p*-distances for each of the analyzed genes and outline median values of divergence per species based on the estimated pairwise uncorrected distance estimates across all the analyzed individuals in our alignments (see Figure 2).

Species	<i>16S</i>	<i>CMOS</i>	<i>cytb</i>	<i>RAG1</i>
<i>G. araneus</i>	0.138 (0.049–0.2)	—	—	—
<i>G. bawanglingensis</i>	0.154 (0.062–0.197)	0.005 (0.003–0.008)	0.206 (0.148–0.273)	0.02 (0.001–0.025)
<i>G. catbaensis</i>	0.128 (0.059–0.2)	—	0.198 (0.112–0.229)	—
<i>G. chengzheng</i>	0.126 (0.028–0.195)	—	0.19 (0.099–0.224)	—
<i>G. gezhi</i>	0.131 (0.028–0.2)	—	—	—
<i>G. gollum</i>	0.149 (0.044–0.21)	0.003 (0–0.011)	0.214 (0.107–0.237)	0.022 (0.004–0.026)
<i>G. hainensis</i>	0.156 (0.018–0.197)	0.008 (0–0.011)	0.214 (0.055–0.273)	0.021 (0–0.026)
<i>G. huuliensis</i>	0.138 (0.008–0.19)	—	0.207 (0.023–0.232)	—
<i>G. kadoorieorum</i>	0.136 (0.008–0.195)	—	—	—
<i>G. kuroiwae</i>	0.187 (0.018–0.21)	—	0.224 (0.042–0.245)	—
<i>G. kwanghua</i>	0.154 (0.038–0.203)	0.005 (0.003–0.011)	0.216 (0.06–0.247)	0.021 (0–0.026)
<i>G. kwangsiensis</i>	0.131 (0.018–0.2)	0.005 (0–0.011)	0.193 (0.096–0.221)	0.021 (0.001–0.025)
<i>G. liboensis</i>	0.131 (0.018–0.205)	0.005 (0–0.011)	—	0.02 (0.001–0.024)
<i>G. lichtenfelderi</i>	0.151 (0.018–0.203)	0.008 (0–0.011)	0.214 (0.055–0.263)	0.024 (0.003–0.029)
<i>G. lului</i>	0.138 (0.008–0.192)	0.003 (0.003–0.008)	0.198 (0.023–0.221)	0.021 (0.006–0.025)
<i>G. orientalis</i>	0.182 (0.018–0.195)	—	0.234 (0.06–0.25)	—
<i>G. sengokui</i>	0.179 (0.018–0.192)	—	0.234 (0.052–0.25)	—
<i>G. splendens</i>	0.192 (0.049–0.205)	—	0.247 (0.135–0.273)	—
<i>G. toyamai</i>	0.185 (0.026–0.197)	—	0.229 (0.042–0.242)	—
<i>G. varius</i>	0.128 (0.033–0.2)	0.003 (0–0.011)	0.206 (0.06–0.271)	0.022 (0–0.027)
<i>G. wangshu</i> sp. nov.	0.131 (0.036–0.19)	0.003 (0.003–0.013)	0.216 (0.107–0.24)	0.015 (0.004–0.022)
<i>G. yamashie</i>	0.187 (0.018–0.2)	—	0.232 (0.055–0.255)	—
<i>G. yingdeensis</i>	0.136 (0.036–0.187)	0.005 (0–0.011)	0.206 (0.076–0.263)	0.020 (0.002–0.024)
<i>G. zhelongi</i>	0.137 (0.033–0.205)	0.005 (0–0.011)	0.193 (0.06–0.247)	0.023 (0–0.029)
<i>G. zhoui</i>	0.167 (0.054–0.205)	0.011 (0.003–0.013)	0.21 (0.125–0.25)	0.022 (0.001–0.027)

Systematics

FAMILY Eublepharidae

GENUS *Goniurosaurus* Barbour, 1908

Goniurosaurus wangshu Zhu, Wu, Li & He sp. nov.

(Fig. 3)

Holotype. ECNU-V0085, adult male, from northern Guangdong Province, China, 200–300 m in elevation; exact locality withheld because of conservation concerns, available to qualified researchers upon request. Collected on 21-ix-2021 by Zhu Xiao-Yu. GenBank accession numbers are in Table 2 (Fig. 3A).

Paratype. ECNU-V0084, adult female, same data as holotype. GenBank accession numbers in Table 2 (Fig. 3B).

Diagnosis. *Goniurosaurus wangshu* sp. nov. differs from other congeners by a combination of the following characters: small size (SVL 76.08–83.60 mm in adults); nasal scales surrounding nostril 7–8; two internasals; eyelid fringe scales 53–58; granular scales of the upper eyelids similar in size to those on the top of the head; scales around midbody 112–126; dorsal tubercle rows at midbody 20–22; paravertebral tubercles between limb insertions 30–34 (Table 4); claws sheathed by four scales (Fig. 3E), dorsal scale small, two lateral scales short and clam shell-shaped;

axillary pockets deep; thirteen precloacal pores in male (Fig. 3F), absent in female; dorsal ground color of head, body, and limbs in adults yellow; nuchal loop complete, posteriorly rounded; three body bands, and one postsacral band; venter light pink, evenly covered with fine imbricating scales, with a thin line longitudinally oriented; iris orange.

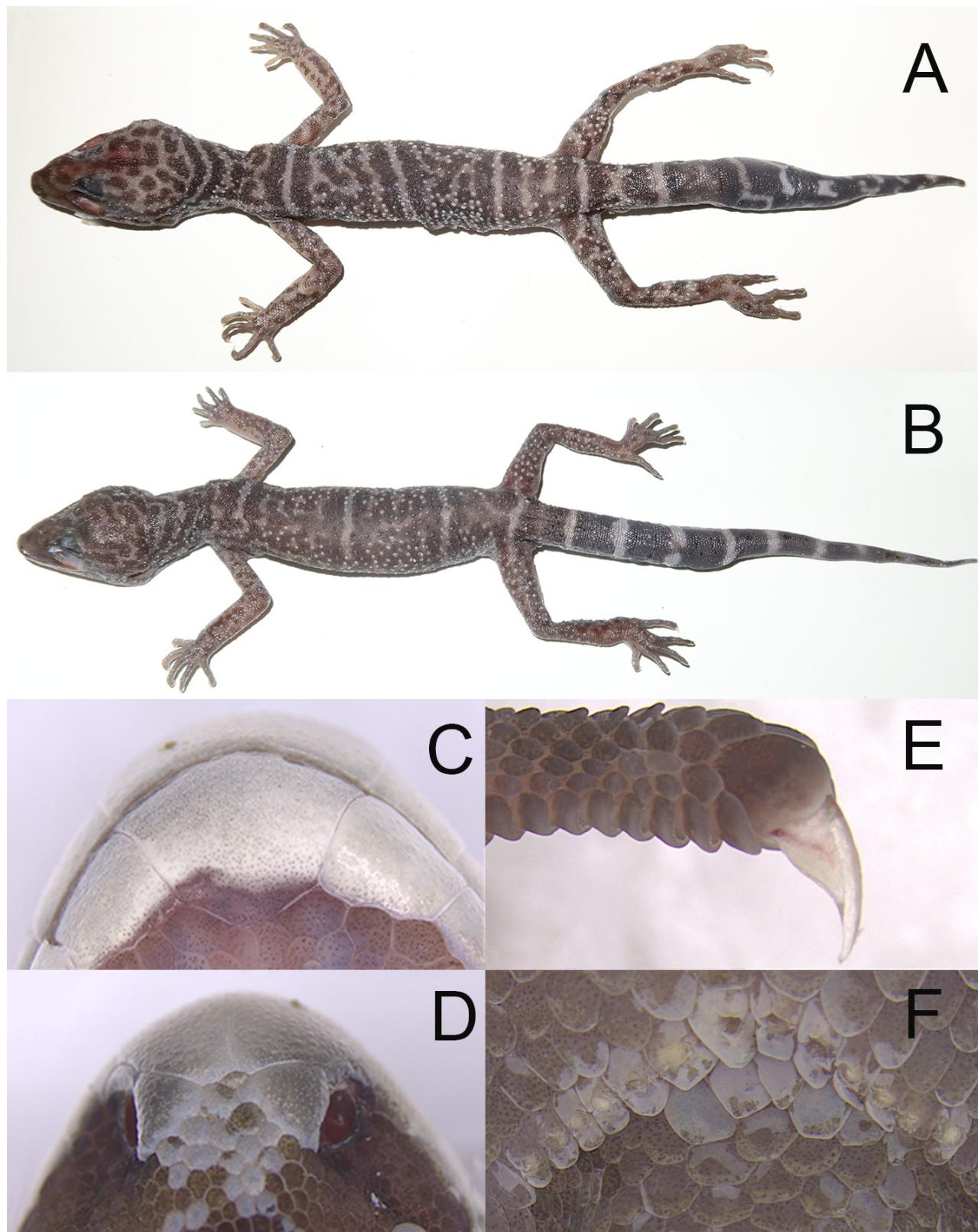


FIGURE 3. *Goniurosaurus wangshu* sp. nov.. A: Dorsal view of holotype, ECNU-V0085; B: Dorsal view of paratype, ECNU-V0084; C: Ventral view of the snout tip of ECNU-V0085; D: Dorsal view of the snout tip of ECNU-V0085; E: Lateral view of the sheathed claws of ECNU-V0085; F: Precloacal region of ECNU-V0085.

TABLE 4. Comparisons of morphometric characters and scale counts for four *Goniurosaurus* species within the *yingdeensis* group. Character abbreviations are explained in material and methods (data for *G. wangshu* sp. nov. come from this study; *G. yingdeensis* from Qi et al. (2020a); *G. zhelongi* from Wang et al. (2014), Qi et al. (2020a), *G. varius* from Qi et al. (2020a), *G. gollum* from Qi et al. (2020b)).

		SVL	SPL	SBL	PO	CIL	PM
<i>G. wangshu</i> sp. nov.	mean		7.50	6.00	16.00	55.50	4.00
	SD		0.58	0.82	0.82	2.08	0.00
	range	76.08–83.60	7.00–8.00	5.00–7.00	15.00–17.00	53.00–58.00	4.00
<i>G. yingdeensis</i>	mean		8.95	8.41	17.36	52.86	3.00
	SD		1.00	0.73	1.50	3.87	0.63
	range	82.00–96.30	7.00–11.00	7.00–10.00	15.00–21.00	46.00–58.00	2.00–4.00
<i>G. varius</i>	mean		8.95	6.90	14.20	48.30	5.00
	SD		0.67	0.32	0.79	2.00	1.00
	range	86.00–93.40	7.00–9.00	6.00–7.00	12.00–15.00	45.00–52.00	4.00–6.00
<i>G. gollum</i>	mean		8.30	8.70	14.30	52.90	3.20
	SD		0.95	0.48	1.64	1.91	0.45
	range	81.50–86.30	7.00–10.00	8.00–9.00	11.00–16.00	50.00–56.00	3.00–4.00
<i>G. gollum</i>	mean		10.00	10.00	16.00	60.83	2.67
	SD		0.00	0.00	0.89	1.83	0.58
	range	91.00–93.40	10.00	10.00	15.00–17.00	59.00–63.00	2.00–3.00

Continued.

		GST	TL	MB	LT4	PP
<i>G. wangshu</i> sp. nov.	mean	10.50	32.25	119.00	24.00	13.00
	SD	0.58	1.71	6.22	0.82	0.00
	range	10.00–11.00	30.00–34.00	112.00–126.00	23.00–25.00	13.00
<i>G. yingdeensis</i>	mean	9.95	28.45	110.00	22.10	11.25
	SD	1.36	3.72	4.40	Unable to calculate due to lack of raw data	1.39
	range	8.00–12.00	22.00–33.00	101.00–115.00	19.00–24.00	10.00–13.00
<i>G. varius</i>	mean	10.80	29.40	107.80	19.60	9.00
	SD	0.57	2.07	1.64	1.26	0.00
	range	9.00–12.00	28.00–33.00	105.00–109.00	17.00–22.00	9.00
<i>G. gollum</i>	mean	10.00	28.00	105.40	19.50	10.00
	SD	0.35	0.71	3.36	2.12	0.00
	range	8.00–12.00	28.00–29.00	101.00–110.00	18.00–21.00	10.00
<i>G. gollum</i>	mean	9.67	25.33	124.67	22.50	10.50
	SD	0.27	0.58	3.51	0.70	0.71
	range	9.00–11.00	25.00–26.00	121.00–128.00	22.00–23.00	10.00–11.00

Description. Holotype. ECNU-V0085, adult male; SVL: 83.60 mm; TaL (regenerated): 59.22 mm; AG: 33.70 mm; SE 8.78 mm; EE: 8.90 mm; HW: 19.48 mm; HL: 15.25 mm; SVL: AG 2.48; SVL: HL: 3.78; HL: HW 1.44; SE: EE: 0.98. Head triangular, wider than neck, covered with uniform granular scales interspersed with tubercles on top of head (Fig. 3A, C, D); small granular scales evenly cover the area between orbits, slightly smaller than those of rostrum; supraorbital tubercles subequal; rostral convex, wider than high, middorsal portion partially sutured dorsomedially, bordered laterally by first supralabial and prenasal, posteriorly by supranasal; external nares oval, surrounded by 7(L)/6(R) nasals each, anteriorly by prenasal, dorsally by supranasal and one granular scale on the left side, posteriorly by 4(L)/4(R) smaller granular scales, ventrally by the prenasal (Fig. 3D); prenasals with long recurved ventral portion; supranasals separated by a small sector shaped scale; supralabials 8(L)/7(R), rectangular,

grading into smaller scales posteriorly; eyes relatively large, pupils vertical; eyelid fringe scales 55(L)/53(R); a fold of skin originating in suborbital region extends posteroventrally across angle of jaw; external auditory meatus elliptical with long axis directed dorsoventrally; tympanum deeply recessed, bordered anteriorly by two spinose scales; mental triangular, bordered laterally by first infralabial and posteriorly by four postmentals; postmentals bordered by eight gular scales; infralabials rectangular 5(L)/7(R). Neck narrower than body, covered with uniform granular scales interspersed with conical tubercles on nape; dorsal body tubercles surrounded by 10 or 11 granular scales; 20–22 longitudinal rows of dorsal tubercle at midbody; 30–33 paravertebral tubercles between limb insertions, distinct vertebral row of scales absent. Body relatively thin, covered with granular scales grading ventrally into larger flattened subimbricate ventral scales; 116–122 scales around midbody; larger ventral scales grade abruptly into smaller granular scales immediately anterior to vent; 13 pore-bearing precloacal scales in a continuous transverse series without extending onto proximal regions of thighs (Fig. 3F); two enlarged postcloacal tubercles laterally on each side at level of vent. Limbs relatively long and slender, covered dorsally with granular scales interspersed with closely spaced tubercles and ventrally with flat, juxtaposed to subimbricate scales; hindlimbs larger and longer than forelimbs; dorsal surface of pes and manus covered with granular scales with several conical tubercles on top of pes; ventral surface of pes and manus covered with large granular scales; deep axillary pockets present; subdigital lamellae wide, 9(L)/10(R) on first finger, 16(L)/17(R) on fourth finger, 11(L)/10(R) on first toe, 25 (L)/24(R) on fourth toe. Fingers laterally compressed, relative finger lengths I < II < III ≈ V < IV; toes laterally compressed, relative toe length I < II < IV < III < V; claws sheathed by four scales, two lateral scales long, curved, and clam shell-shaped, dorsal scale shorter than lateral scales but much longer than ventral scale (Fig. 3E). Regenerated tail thin at base, gradually thickening posteriorly, and gradually thinning into a blunt tip.

Coloration in life. Dorsal ground color of head, body, and limbs yellow-gray, with black blotches in irregular shapes, closely spaced, some black blotches on head randomly connected; iris orange; nuchal loop pale yellow, posterior margin rounded, not pointed; three body bands between limb insertions, one postsacral band on tail base; all bands pale yellow; ventral surfaces of head and limbs dull white, belly light pink; ground color of tail black with white markings. Tail regenerated, white markings irregular and randomly connected towards the tip, encircling the tail.

Comparisons. *Goniurosaurus wangshu* sp. nov. is most similar to *G. gollum*, but differs from it by having the combination of the following characters: fewer SPL (7–8 in *G. wangshu*, 10 in *G. gollum*), fewer SBL (5–7 in *G. wangshu*, 10 in *G. gollum*), fewer CIL (53–58 in *G. wangshu*, 59–63 in *G. gollum*), more PM (4 in *G. wangshu*, 2–3 in *G. gollum*), more TL (30–34 in *G. wangshu*, 25–26 in *G. gollum*), 13 PP (versus 10–11 in *G. gollum*), and lighter iris color. *G. wangshu* is different from *G. zhelongi* with more PO (15–17 in *G. wangshu*, 12–15 in *G. zhelongi*), more CIL (53–58 in *G. wangshu*, 45–52 in *G. zhelongi*), more MB (112–126 in *G. wangshu*, 105–109 in *G. zhelongi*), more LT4 (23–25 in *G. wangshu*, 17–22 in *G. zhelongi*), 13 PP (versus 9 in *G. zhelongi*), dorsal ground color of head, body, and limbs yellow-gray (versus black in *G. zhelongi*), iris dark orange (versus gray-white in *G. zhelongi*), pale yellow nuchal loop and body bands (vs. dirty white in *G. zhelongi*). *G. wangshu* is distinctive from *G. varius* with fewer SBL (5–7 in *G. wangshu*, 8–9 in *G. varius*), more TL (30–34 in *G. wangshu*, 28–29 in *G. varius*), more MB (112–126 in *G. wangshu*, 101–110 in *G. varius*), more LT4 (23–25 in *G. wangshu*, 18–21 in *G. varius*), more PP (13 in *G. wangshu*, 10 in *G. varius*), iris dark orange (versus orange-red in *G. varius*), nuchal loop complete (versus usually incomplete in *G. varius*). *G. wangshu* can also be distinguished from *G. yingdeensis* by fewer SBL (5–7 in *G. wangshu*, 7–10 in *G. yingdeensis*), 7–8 white ring-shaped markings on original tail (versus 8–9 in *G. yingdeensis* and connected at tip), iris dark orange (versus gray, near pupil orange), nuchal loop and body bands wider, and black blotches on dorsal head surface larger and more connected.

Variation. Measurements and scalation data of the type series are provided in Table 5. The paratype largely matches the overall scalation and coloration characters of the holotype. The original tail of paratype ECNU-V0084 is thinner and longer than that of the holotype, with 7–8 ring-shaped white markings, the white color fading or disappearing at the tip. Some individuals are yellow-tinged on the first white ring at the base of the tail. CIL of paratype is 56/58.

Etymology. The specific epithet *wangshu* is for the Chinese phonetic alphabet 望舒, which was noted in ancient Chinese poem *Li Sao* over 2000 years ago. In ancient Chinese mythology, Wang Shu is the driver of the chariot of the moon. This name also corresponds to the time when the specimens were collected during the Mid-Autumn Festival, which is a traditional Chinese Festival that is associated with the full moon. Additionally, this name appeals to the yellow color of the species that resembles the moonlight. The epithet is a noun in apposition. For the common name, we suggest “Wangshu Cave Gecko 望舒睑虎”.

Natural history. *G. wangshu* is found in northern Guangdong, China. This species is restricted to karst topography with dense vegetation at 200–300 m elevation. They climb on limestone cliffs to prey on small invertebrates such as locusts (Acridoidea), snails (Gastropoda), and earthworms (Opisthopora). Asian tarantulas (*Chilobrachys*) co-occur in this area.

TABLE 5. Morphological measurements (in mm) and scalation characters of the type specimens of *Goniurosaurus wangshu* sp. nov. Abbreviations defined in Materials and Methods.. * = regenerated tail.

	HOLOTYPE ECNU-V0085	PARATYPE ECNU-V0084
sex	male	female
SVL	83.60	76.08
TaL	59.22*	75.64
AG	33.70	35.53
HL	22.09	20.43
HW	15.25	14.93
SE	8.78	8.53
EE	8.90	7.94
SVL:HL	3.78	3.72
SVL:AG	2.48	2.14
HL:HW	1.44	1.36
SE:EE	0.98	1.07
SPL	8.00/7.00	7.00/8.00
SBL	5.00/7.00	6.00/6.00
N	7.00/6.00	8.00/8.00
IN	2.00	2.00
PostIN	3.00	3.00
PM	4.00	4.00
GP	8.00	8.00
PO	16.00/17.00	16.00/16.00
CIL	55.00/53.00	56.00/58.00
MB	116.00–122.00	112.00–126.00
GST	10.00–11.00	10.00–11.00
TL	30.00–33.00	32.00–34.00
DTR	20.00–22.00	21.00–22.00
LD1	9.00/10.00	8.00/10.00
LD4	16.00/17.00	16.00/16.00
LT1	11.00/10.00	10.00/11.00
LT4	25.00/24.00	23.00/24.00
PP	13.00	—
PAT	2.00	2.00

Discussion

In this study, we used *16S*, *cytb*, *CMOS*, and *RAG1* sequences to infer the phylogenetic position of *G. wangshu* sp. nov. among the 24 *Goniurosaurus* species that are currently described. The reconstructed tree topology is consistent with a recent and comprehensive study using these four genes for 23 species (Grismer *et al.* 2021). Our molecular phylogeny shows that *G. wangshu* sp. nov. was nested within the *G. yingdeensis* group. Within this clade, *G. gollum* was recov-

ered as the sister species to *G. wangshu* sp. nov. Morphologically, *G. wangshu* sp. nov. can be distinguished from *G. gollum* by its lighter iris and dorsal ground color. Furthermore, *G. wangshu* sp. nov. has more distinct body bands than *G. gollum*. Overall, both our molecular and morphological analyses support *G. wangshu* sp. nov. as a new species.

Biogeographical patterns within the *Goniurosaurus* often reflect major geographical barriers, including canyons and rivers (Qi *et al.* 2020a, 2020b; Zhu *et al.* 2020a, 2020b, 2021). For instance, there is no overlap in the geographical ranges among the five species that are currently described within the *G. yingdeensis* group (Qi *et al.* 2020a, 2020b). Specifically, *G. wangshu* sp. nov. is confined to Yangshan County, while its sister species, *G. gollum*, is restricted to Huaiji County (Qi *et al.* 2020b). Consistent with our molecular inferences, the distributions of *G. wangshu* sp. nov. and *G. gollum* are the closest among the *G. yingdeensis* group. However, their localities are over 100 km apart. The Fenglan River likely serves as a major geographical barrier between these two species. We also highlight that *G. wangshu* sp. nov. is geographically isolated from *G. varius*, *G. yingdeensis*, and *G. zhelongi* by the Lianjiang River. Overall, consistent with other recent studies, the distribution of *G. wangshu* sp. nov. reflects the association between geographical barriers and speciation of *Goniurosaurus* (Qi *et al.* 2020a, 2020b; Zhu *et al.* 2020a, 2020b, 2021).

To our knowledge, *G. wangshu* sp. nov. is only found in karst topography. This observation is consistent with a recent study showing the *G. yingdeensis* group has a strong preference for karst habitats (Grismer *et al.* 2021). Unlike *G. gollum* which is restricted inside the limestone caves (Qi *et al.* 2020b), *G. wangshu* sp. nov. can be found outside of caves. Our study also highlights the need for increasing conservation efforts in the karst regions in southern China. Due to illegal pet trade, mining, and deforestation, the drastic population decline and even local extirpation are still occurring in *Goniurosaurus* populations across China and Vietnam (Stuart *et al.* 2006; Yang & Chan 2015; Ngo *et al.* 2021, 2022a, 2022b; Grismer *et al.* 2021). To protect this new species, we follow the current community standard to withhold detailed type locality information (Yang & Chan 2015; Qi *et al.* 2020a, 2020b; Zhu *et al.* 2020a, 2020b, 2021).

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