Article

Spiny Tails and Clades: A Fully Sampled Phylogeny of Hoplocercine Lizards (*Iguanidae/ Hoplocercinae*) and its Taxonomic and Nomenclatural Implications

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Abstract

Hoplocercine lizards (*Enyalioides*, *Morunasaurus*, and *Hoplocercus*) form a clade of ca. 20 currently recognized species. The phylogenetic relationships among hoplocercine lizards, whose members exhibit striking differences in morphology (e.g., spiny vs. non-spiny tails), have not been clearly resolved by previous molecular phylogenetic studies. We generated a considerably larger dataset including 130 new DNA sequences from one mitochondrial and four nuclear loci for all named and two unnamed species of *Hoplocercinae*. We analyzed the data under concatenated maximum likelihood (RAxML) and Bayesian (MrBayes) as well as summary coalescent (ASTRAL) approaches. While our phylogenetic hypotheses strongly supported the monophyly of *Hoplocercinae*, neither *Enyalioides* nor *Morunasaurus* was supported as monophyletic. Instead, *M. groi* was inferred with strong support to form a clade with *E. heterolepis* and *E. laticeps*. This clade was in turn the sister taxon to other species of *Morunasaurus* (*M. annularis*, *M. peruvianus*). The remaining species of *Enyalioides* formed a separate clade with a basal split between western (3 species) and eastern (13 species) subclades. Tree topology tests rejected the monophyly of *Enyalioides* but failed to reject monophyly of *Morunasaurus*, suggesting that further study is needed to resolve its taxonomic status. Based on our results, we establish the converted clade names *Hoplocercinae*, *Hoplocercus*, *Enyalioides*, and *Morunasaurus*, as well as the new clade name *Zimiamviasaurus*.

Key words: *Enyalioides*, *Hoplocercus*, *Morunasaurus*, Neotropics, *PhyloCode*, species tree, *Squamata*

Introduction

Hoplocercinae is a clade of iguanid lizards that includes 20 currently recognized species distributed from Panama to central Brazil and Bolivia (Torres-Carvajal *et al.* 2011; Venegas *et al.* 2021). It includes some of the most colorful, medium-sized (100–200 mm Snout-Vent Length, SVL) lizards in the Neotropics. Hoplocercines have been assigned to three taxa traditionally ranked as genera: *Enyalioides* Boulenger 1885, *Hoplocercus* Fitzinger 1843, and *Morunasaurus* Dunn 1933. Woodlizards (*Enyalioides*), represent the largest radiation (16 species), occupying lowland and montane tropical rainforests including the Chocó and western Amazon basin, with most species occurring east of the Andes between 100 and 2,000 m. Remarkably, more than half of the species of woodlizards were described in the past 15 years, as new areas along the Andean slopes in Ecuador and Peru were explored. Manticores (*Morunasaurus*) form three species; Gro's manticores (*M. groi* Dunn 1933) occur from central Panama to NW Colombia at elevations between 700 and 1,315 m (Vásquez-Restrepo 2021), ringed manticores (*M. annularis* O'Shaughnessy 1881) occur along the Amazonian slopes of the Andes in southern Colombia and Ecuador between 400 and 1,100 m, and Cenepa manticores (*M. peruvianus* Köhler 2003) are known only from a few localities in Amazonas Department of northern Peru, between 200 and 300 m. Weapontails (*Hoplocercus*) form a single species, spiny weapontails (*Hoplocercus spinosus* Fitzinger 1843), which occur mostly in the Brazilian Cerrado savannas and nearby areas in Bolivia (Ribeiro-Júnior 2015).
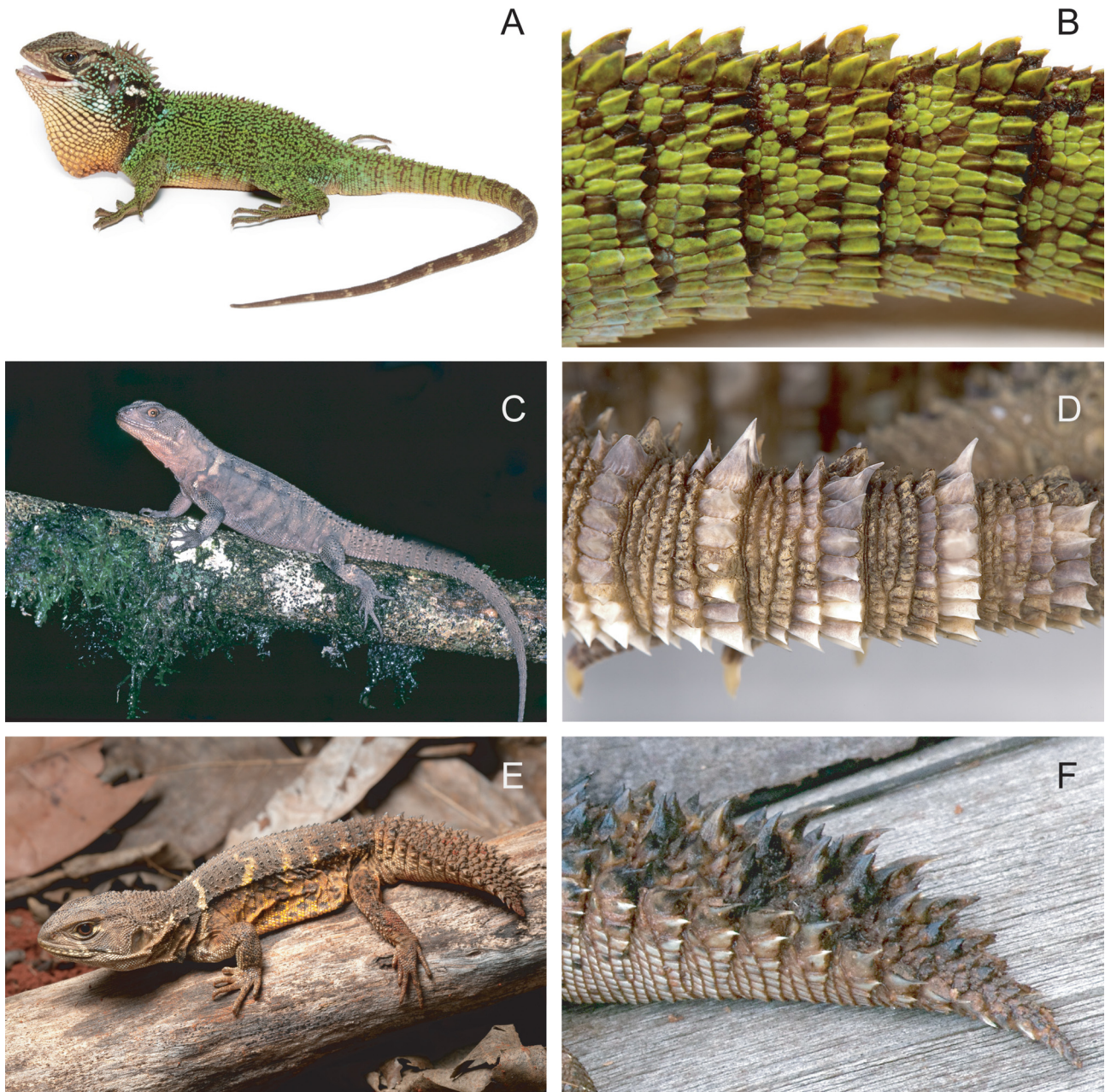
FIGURE 1. Representatives of *Enyalioides*, *Morunasaurus*, and *Hoplocercus* with close-ups of their tails. A, B: *Enyalioides praestabilis* from Morona-Santiago, Ecuador; C, D: *Morunasaurus annularis* from Pastaza, Ecuador; E, F: *Hoplocercus spinosus* from Mato Grosso, Brazil. Photographs by Juan Carlos Sánchez (A), OTC (B), Paul Freed (C), Fernando Ayala (D), Arthur de Sena (E), Guarino Colli (F).

Some of the major diagnostic features of *Enyalioides*, *Morunasaurus*, and *Hoplocercus* are related to tail morphology (Fig. 1; Torres-Carvajal *et al.* 2011). Woodlizards and manticores have round or laterally compressed autotomic tails that are at least slightly longer than their SVLs; however, manticores differ from woodlizards in having conspicuous rings of large spinous scales encircling their tails. By contrast, spiny weapontails have non-autotomic, dorsoventrally flattened, extremely short tails (i.e., tail length $\leq$ ½ SVL), with strongly projecting spines dorsally and laterally. Additionally, woodlizards differ from both weapontails and manticores in having pointed, conical scales on the dorsal surface of the head and gular region as well as raised scales posterior to the superciliaries, among other features (Torres-Carvajal *et al.* 2011). Despite seemingly derived characters that diagnose all three taxa, previous molecular phylogenies suggest that *Enyalioides* is paraphyletic relative to *Morunasaurus*. Previous studies, however, had limited taxon or character sampling. For example, none of them included *M. groi*,

the type species of *Morunasaurus*, making it difficult to assess the precise relationships between *Morunasaurus* and *Enyalioides*. Although the study of Torres-Carvajal and de Queiroz (2009) is the most comprehensive in terms of gene sampling (11 mitochondrial and two nuclear genes), it is also limited in taxon sampling (nine species), partly because nearly half of the species of *Hoplocercinae* were described after its publication. Subsequent phylogenies were based entirely on mitochondrial data and presented as part of the evidence for proposals of new species (Venegas *et al.* 2013; Torres-Carvajal *et al.* 2015; Venegas *et al.* 2021).

To infer a more accurate phylogeny of hoplocercine lizards, we here present both (concatenated) gene tree and species tree analyses of an expanded dataset that includes one mitochondrial gene, four nuclear loci, and samples of all currently recognized species of *Hoplocercinae* as well as two unnamed species from Peru. We also assess the monophyly of both *Enyalioides* and *Morunasaurus* with tree topology tests. Based on the inferred phylogenetic relationships, we establish formal names for five hoplocercine clades according to the rules of the *International Code of Phylogenetic Nomenclature* (Cantino and de Queiroz 2020), also known as the *PhyloCode*.

TABLE 1. Gene regions, primers, and PCR protocols used in this study. F = forward, R = reverse.

Gene region	Primer	PCR protocol
ND2	F: L4160 (Kumazawa and Nishida 1993) CGATTCCGATATGACCARCT R: H4980 (Macey *et al.* 1997a) ATTTTTCGTAGTTGGGTTTGRTT	1 cycle: 2 min 94 °C, 30 s 42 °C, 1 min 72 °C 5 cycles: 30 s 94 °C, 30 s 42 °C, 1 min 72 °C 22 cycles: 30 s 94 °C, 30 s 50 °C, 1 min 72 °C 1 cycle: 5 min 72 °C
	F: L4645 (Macey *et al.* 1997a) ACAGAAGCCGCAACAAAATA R: H5934 (Macey *et al.* 1997a) AGRGTGCCAATGTCTTTGTG	1 cycle: 2 min 94 °C 10 cycles: 30 s 94 °C, 30 s 42 °C, 1 min 72 °C 25 cycles: 30 s 94 °C, 30 s 51 °C, 1 min 72 °C 1 cycle: 7 min 72 °C
DNAH3	F: DNAH3_f1 (Townsend *et al.* 2008) GGTAAAATGATAGAAGAYTACTG R: DNAH3_r6 (Townsend *et al.* 2008) CTKGAGTTRGAHACAATKATGCCAT	1 cycle: 5 min 95°C 40 cycles: 35 s 94°C, 45 s 50 °C, 1 min 72°C 1 cycle: 10 min 72 °C
NT3	F: NT3-F3 (Noonan and Chippindale 2006) ATATTTCTGGCTTTTCTCTGTGGC R: NT3-R4 (Noonan and Chippindale 2006) GCGTTTCATAAAAATATTGTTTGACCG	1 cycle: 2 min 94°C 10 cycles: 30 s 94°C, 30 s 42 °C, 1 min 72 °C 25 cycles: 30 s 94°C, 30 s 51°C, 1 min 72°C 1 cycle: 7 min 72°C
	F: NT3_f1 (Townsend *et al.* 2008) ATGTCCATCTTGTTTTATGTGATATTT R: NT3-R3 (Noonan *et al.* 2013) TTACAYCKYGTTTCATAAAAATATT	1 cycle: 3 min 95°C 35 cycles: 1 min 95°C, 1 min 40 °C, 1 min 72°C 1 cycle: 10 min 72 °C
PRLR	F: PRLR-F1 (Townsend *et al.* 2008) GACARYGARGACCAGCAACTRATGCC R: PRLR-R3 (Townsend *et al.* 2008) GACYTTGTGRACTTCYACRTAATCCA	1 cycle: 2 min 95 °C 40 cycles: 30 s 94 °C, 30 s 50–51 °C, 1 min 72°C 1 cycle: 10 min 72 °C
RAG1	F: JRAG1_f2 (Torres-Carvajal and de Queiroz 2009) CAAAGTRAGATCACTTGAGAAGC R: JRAG1_r3 (Torres-Carvajal and de Queiroz 2009) ACTTGYAGCTTGAGTTCTCTTAGRCG	1 cycle: 2 min 94 °C 40 cycles: 30 s 94 °C, 30 s 55 °C, 1 min 72°C 1 cycle: 10 min 72 °C

Methods

Taxon sampling and laboratory protocols

We included in our analyses one to four (mean = 2.23) samples per species of all currently recognized species of *Hoplocercinae* as of January 2022 (N = 20) and two unnamed species of *Enyalioides* from Peru. The latter were recognized by interpreting preliminary morphological (unpublished) and phylogenetic (this study) information as species delimitation criteria following a general lineage species concept (de Queiroz 1998; 2007). We also included *Anolis carolinensis*, *Basiliscus basiliscus*, *Phymaturus palluma*, *Polychrus marmoratus*, and *Uta stansburiana* as outgroups (Schulte *et al.* 2003).

We generated 130 nucleotide sequences corresponding to the mitochondrial gene subunit II of NADH dehydrogenase (*ND2*, 1,038 aligned sites), as well as nuclear genes dynein axonemal heavy chain 3 (*DNAH3*, 742), neurotrophin 3 (*NT3*, 566), prolactin receptor (*PRLR*, 477), and recombination-activating gene 1 (*RAG1*, 1,223). Polymerase Chain Reaction (PCR) amplification was performed in a final volume of 25 μl reactions using 1X PCR Buffer (–Mg), 3 mM MgCl$_2$, 0.2 mM dNTP mix, 0.2 μM of each primer, 0.1 U/μl of Platinum® Taq DNA Polymerase (Invitrogen, Carlsbad, CA) and 1 μl of extracted DNA. PCR primers and protocols are presented in Table 1. Double stranded sequencing of the PCR products was performed in both directions by Macrogen Inc. (Seoul, Republic of Korea), except for those of *H. spinosus*, which were performed at the Laboratório Temático de Biologia Molecular from the Instituto Nacional de Pesquisas da Amazônia (LTBM/ INPA). We also retrieved from GenBank all available sequences of the genes mentioned above for all species of hoplocercine lizards and the outgroups. All terminals in gene trees correspond to single specimens except for *Enyalioides microlepis*, *E. palpebralis* and *E. touzeti*, which are composed of sequences of two specimens from localities 204.32 km, 56.16 km, and 35.88 km (great circle distances calculated in www.gpsvisualizer.com) apart, respectively. Similarly, outgroup species are represented by sequences of more than one specimen.

Alignment and Phylogenetic Analyses

We assembled and aligned the DNA sequences in Geneious Prime 2022.0.2 (https://www.geneious.com) under default settings for MUSCLE 3.8.425 (Edgar 2004). We translated all sequences into amino acids for confirmation of alignment. After partitioning the concatenated data matrix by gene and codon position (i.e., 15 partitions total), we chose the best partitioning scheme using PartitionFinder v2.1.1 under the Bayesian Information Criterion (BIC) and the "greedy" algorithm with branch lengths of alternative partitions "linked" to search for the best-fit scheme (Guindon *et al.* 2010; Lanfear *et al.* 2012, 2017). We combined the genes into a single concatenated dataset with six partitions (number of sites and best model in brackets): (i) 1st codon position of *ND2* [346, TVM+I+G]; (ii) 2nd codon position of *ND2* [346, HKY+I+G]; (iii) 3rd codon position of *ND2* [346, TRN+I+G]; (iv) 1st and 2nd codon positions of *DNAH3*, 1st and 3rd codon positions of *NT3*, 2nd and 3rd codon positions of *RAG1* [1,687, K81UF+G]; (v) 3rd codon position of *DNAH3* [247, K80+G]; and (vi) 1st, 2nd and 3rd codon positions of *PRLR*, 2nd codon position of *NT3*, 1st codon position of *RAG1* [1,138, HKY+G]. We ran a partitioned Bayesian analysis in MrBayes v3.2.7 (Ronquist *et al.* 2012), with all parameters unlinked between partitions (except topology and branch lengths) and rate variation (prset ratepr = variable) invoked. We performed four independent runs of 10^7 generations, each with four MCMC chains, sampling every 1,000 generations. We calculated posterior probabilities (PP) on a Maximum Clade Credibility Tree in TreeAnnotator (Drummond *et al.* 2019) and rooted the trees with the outgroups. We also ran a Maximum Likelihood (ML) analysis in RAxML v8.2.10 (Stamatakis 2014) under the GTRGAMMA model for each partition, assessing nodal support with the rapid bootstrapping (BS) algorithm (Stamatakis *et al.* 2008) on 1,000 replicates. We executed these analyses in the CIPRES Science Gateway (Miller *et al.* 2010).

We also inferred a species tree under the coalescent model in ASTRAL 5.7.8 (Rabiee *et al.* 2019) under default settings. ASTRAL calculates the species tree that shares the maximum number of induced quartet trees with the set of gene trees (Mirarab *et al.* 2014). For this analysis, we used all five gene trees (for *ND2*, *DNAH3*, *NT3*, *PRLR*, *RAG1*) that were obtained in RAxML under the GTRGAMMA model. Branch support was assessed with local posterior probabilities (Sayyari and Mirarab 2016).

Tree topology tests

Monophyly of both *Morunasaurus* and *Enyalioides* was tested against our ML tree. A tree with all species of *Morunasaurus* (*M. annularis*, *M. groi*, *M. peruvianus*) forming a monophyletic group, but otherwise unresolved, was constructed in Mesquite 3.61 (Maddison and Maddison 2019) and used as a constraint tree to obtain a ML tree in RAxML using the same partitioned data matrix mentioned above. We followed the same protocol to construct another constraint tree with a monophyletic *Enyalioides*. Subsequently, we conducted Shimodaira–Hasewaga (SH) and approximately unbiased (AU) tests (Shimodaira and Hasegawa 1999; Shimodaira 2002) in PAUP*4.0 (Swofford 2003).

Results

Taxon sampling

The concatenated dataset had 4,110 aligned nucleotides and 51 terminals representing five outgroup species, *Hoplocercus spinosus*, three species of *Morunasaurus*, and 16 named as well as two unnamed species of *Enyalioides* (Table 2). This dataset is available from the Dryad Digital Repository (doi:10.5061/dryad.2bvq83btw).

TABLE 2. Taxa and gene regions included in this study, with vouchers, locality data, and GenBank accession numbers. New sequences obtained for this study are in bold. Institutional acronyms are listed in Sabaj (2020); AB = Abel Batista field series; * = acronym not listed in Sabaj (2020).

Taxon	Voucher	Locality	ND2	RAG1	DNAH3	NT3	PRLR
Enyalioides altotambo	QCAZ 6671	Ecuador: Esmeraldas: Alto Tambo, Río Balthazar	EU586753.1	—	—	**ON088727**	**ON088762**
Enyalioides altotambo	QCAZ 8073	Ecuador: Esmeraldas: Alto Tambo, 5 km on road to Placer	KP235211.1	**ON088674**	**ON088696**	**ON088728**	**ON088763**
Enyalioides anisolepis	QCAZ 8395	Ecuador: Zamora Chinchipe: Chito, sector Los Planes	KP235213.1	**ON088675**	**ON088697**	**ON088729**	**ON088764**
Enyalioides anisolepis	QCAZ 8428	Ecuador: Zamora Chinchipe: Chito	KP235214.1	**ON088676**	**ON088698**	**ON088730**	**ON088765**
Enyalioides anisolepis	QCAZ 8515	Ecuador: Zamora Chinchipe: Chito, sector Los Planes	KP235215.1	**ON088677**	**ON088699**	**ON088731**	**ON088766**
Enyalioides azulae	CORBIDI 6772	Peru: San Martín: Picota: Chambirillo	KC588838.1	—	**ON088700**	**ON088732**	**ON088767**
Enyalioides azulae	CORBIDI 8825	Peru: San Martín: Picota: Chambirillo	KC588839.1	**ON088678**	**ON088701**	**ON088733**	**ON088768**
Enyalioides azulae	CORBIDI 8826	Peru: San Martín: Picota: Chambirillo	KC588840.1	**ON088679**	**ON088702**	**ON088734**	**ON088769**
Enyalioides binzayedi	CORBIDI 8827	Peru: San Martín: Picota: Chambirillo	KC588841.1	**ON088680**	**ON088703**	**ON088735**	**ON088770**
Enyalioides binzayedi	CORBIDI 8828	Peru: San Martín: Picota: Chambirillo	KC588842.1	**ON088681**	**ON088704**	**ON088736**	**ON088771**
Enyalioides cofanorum	QCAZ 8035	Ecuador: Orellana: 66 km on road Pompeya-Iro	KP235210.1	—	**ON088705**	**ON088737**	**ON088772**

TABLE 2. (Continued)

Taxon	Voucher	Locality	ND2	RAG1	DNAH3	NT3	PRLR
Enyalioides feiruzae	CORBIDI 9315	Peru: Huánuco: Huánuco: Huallaga River near Santa Rita Sur	MZ130607	**ON088682**	—	—	—
Enyalioides feiruzae	CORBIDI 9317	Peru: Huánuco: Pachitea: Huallaga River near Santa Rita Sur	MZ130606	**ON088683**	—	—	—
Enyalioides feiruzae	CORBIDI 9318	Peru: Huánuco: Huánuco: Nueva Villa Paraiso	MZ130605	**ON088684**	**ON088706**	**ON088738**	**ON088773**
Enyalioides feiruzae	CORBIDI 9319	Peru: Huánuco: Huánuco: Nueva Villa Paraiso	MZ130608	**ON088685**	**ON088707**	**ON088739**	**ON088774**
Enyalioides heterolepis	CHP 5328	Panama: Coclé: El Santísimo	EU586745	—	—	—	—
Enyalioides heterolepis	CHP 5629	Panama: Darién: trail to Serranía del Pirre	EU586746.1	EU586771.1	—	—	—
Enyalioides heterolepis	QCAZ 6192	Ecuador: Esmeraldas: Durango	EU586744	EU586770.1	**ON088708**	**ON088740**	**ON088775**
Enyalioides laticeps	KU 222164	Peru: Loreto: San Jacinto	EU586747.1	EU586772.1	—	—	—
Enyalioides laticeps	LSUMZ 13573	Brazil: Acre: ~5 km N Porto Walker	AF528719	—	—	—	—
Enyalioides laticeps	QCAZ 6035	Ecuador: Orellana: Yasuni Research Station-PUCE	EU586748.1	EU586773.1	**ON088709**	**ON088741**	**ON088776**
Enyalioides laticeps	QCAZ 6588	Ecuador: Sucumbíos: Tarapoa	EU586749.1	—	**ON088710**	**ON088742**	**ON088777**
Enyalioides laticeps	KU 212627	Peru: San Martín: San Martín: 14 km ESE Shapaja	—	—	GU457910.1	GU456004.1	JN880831
Enyalioides microlepis	KU 222163	Peru: Loreto: San Jacinto	EU586750.1	EU586774.1	—	—	—
Enyalioides microlepis	QCAZ 8284	Ecuador: Pastaza: Comunidad Kurintza, Campo Villano, Bloque 10, Agip Oil	—	—	**ON088711**	**ON088743**	**ON088778**
Enyalioides oshaughnessyi	QCAZ 6866	Ecuador: Esmeraldas: Bilsa Ecological Reserve	EU586751.1	EU586775.1	**ON088712**	**ON088744**	**ON088779**
Enyalioides oshaughnessyi	QCAZ 6899	Ecuador: Los Ríos: Jauneche Scientific Station	EU586752.1	—	—	**ON088745**	**ON088780**
Enyalioides palpebralis	MUSM 24663	Peru: Cusco: La Convención: Echarate District	EU586754.1	EU586776.1	—	—	—
Enyalioides palpebralis	CORBIDI 6042	Peru: Cusco: La Convención: Echarate District	—	—	**ON088713**	**ON088746**	**ON088781**

TABLE 2. (Continued)

Taxon	Voucher	Locality	*ND2*	*RAG1*	*DNAH3*	*NT3*	*PRLR*
Enyalioides praestabilis	QCAZ 4113	Ecuador: Pastaza: Shell Mera	EU586756.1	EU586777.1	**ON088714**	**ON088747**	**ON088782**
Enyalioides praestabilis	QCAZ 5580	Ecuador: Napo: Río Hollín	EU586755.1	—	**ON088715**	**ON088748**	**ON088783**
Enyalioides rubrigularis	QCAZ 8454	Ecuador: Zamora Chinchipe: near Piuntza	KC588846.1	**ON088686**	**ON088716**	**ON088749**	**ON088784**
Enyalioides rudolfarndti	CORBIDI 7209	Peru: Pasco: Huampal, Parque Nacional Yanachaga-Chemillen	KC588843.1	**ON088687**	**ON088717**	**ON088750**	**ON088785**
Enyalioides rudolfarndti	CORBIDI 7210	Peru: Pasco: Huampal, Parque Nacional Yanachaga-Chemillen	KC588844.1	**ON088688**	**ON088718**	**ON088751**	**ON088786**
Enyalioides rudolfarndti	CORBIDI 7212	Peru: Pasco: Huampal, Parque Nacional Yanachaga-Chemillen	KC588845.1	**ON088689**	**ON088719**	**ON088752**	**ON088787**
Enyalioides sophiarothschildae	CORBIDI 647	Peru: San Martín: Río Lejía on the trail La Cueva-Añazco Pueblo	KP235212.1	—	**ON088720**	**ON088753**	**ON088788**
Enyalioides touzeti	EPN 10306	Ecuador: Azuay: Finca La Envidia, Santa Marta hill	EU586757.1	EU586778.1	—	—	—
Enyalioides touzeti	QCAZ 15138	Ecuador: El Oro: Chilla, 912 km N road to La Libertad	—	—	—	**ON088757**	**ON088791**
Enyalioides sp. 1	CORBIDI 738	Peru	**ON088667**	**ON088690**	—	—	—
Enyalioides sp. 1	CORBIDI 21351	Peru	**ON088669**	**ON088693**	**ON088723**	**ON088756**	**ON088790**
Enyalioides sp. 2	CORBIDI 20737	Peru	**ON088666**	**ON088691**	**ON088721**	**ON088754**	—
Enyalioides sp. 2	CORBIDI 20781	Peru	**ON088668**	**ON088692**	**ON088722**	**ON088755**	**ON088789**
Hoplocercus spinosus	MZUSP 907931	Brazil: Mato Grosso: General Carneiro	U82683.1	AY662592	—	—	—
Hoplocercus spinosus	INPA-H 039406	Brazil: Amazonas: Campos Amazonicos National Park, Ponto 08	**ON088670**	**ON088694**	—	**ON088758**	**ON088792**
Hoplocercus spinosus	INPA-H 039413	Brazil: Amazonas: Campos Amazonicos National Park, Ponto 04	**ON088671**	—	—	—	—
Morunasaurus annularis	QCAZ 7820	Ecuador: Pastaza: Upper Bobonaza River	EU586758.1	EU586779.1	**ON088724**	**ON088759**	**ON088793**

TABLE 2. (Continued)

| Taxon	Voucher	Locality	ND2	RAG1	DNAH3	NT3	PRLR
Morunasaurus peruvianus	MVZ 163062	Peru: Amazonas: Rio Cenepa, ridge on N side at headwaters of Rio Kagka	AF528720.1	FJ356741	HQ876405.1	JF804556.1	JN880857.1
Morunasaurus groi	AB 1333	Panama: Cocle: Valle de Anton	**ON088672**	**ON088695**	**ON088725**	**ON088760**	**ON088794**
Morunasaurus groi	AB 1341	Panama: Cocle: Valle de Anton	**ON088673**	—	**ON088726**	**ON088761**	**ON088795**
Outgroups							
Anolis carolinensis	UF Herp 170869	USA: Florida: Hillsborough: Tampa	KP174772	—	—	—	—
Anolis carolinensis	see comment in GenBank	see comment in GenBank	—	AAWZ00000000	AAWZ00000000	AAWZ00000000	AAWZ00000000
Basiliscus basiliscus	MVZ 137675	no specific locality	MF624301	—	—	JF804532	—
Basiliscus basiliscus	DMH 86-271*	not available	—	—	HQ876403	—	—
Basiliscus basiliscus	TOMH 86-271*	not available	—	—	—	JF804532	JN880809
Phymaturus palluma	SDSU 3387	Argentina: Mendoza: 27 km NE Uspallata	AF099216	—	—	—	—
Phymaturus palluma	LJA 5806*	not available	—	—	JF806100	JF804560	JN880865
Uta stansburiana	MVZ 180323	USA: New Mexico: Mescalero Sands	AF049863	—	—	—	—
Uta stansburiana	MVZ 245877	USA: California: junction of Randsburg Red Rock Rd. and Hwy. 41	—	DQ385422	—	—	—
Uta stansburiana	TWR 1745*	not available	—	—	JF806107	JF804577	—
Uta stansburiana	UWBM 7605	USA: Arizona: Five Mile Wash	—	—	—	—	KP820500
Polychrus marmoratus	MTR 12079*	Brazil: Espírito Santo: Linhares, Reserva da Companhia Vale do Rio Doce	KX760669	KX760989	KX760345	—	—
Polychrus marmoratus	AToL 31*	not available	—	—	—	JF804564	—
Polychrus marmoratus	CHUNB 68997	Brazil: Espírito Santo: Guarapari	—	—	—	—	MH221803

Phylogeny of Hoplocercinae

Maximum likelihood (ML) and Maximum Clade Credibility (MCC) trees are generally congruent in topology (Figs. 2, 3). As with previous inferences, the monophyly of *Hoplocercinae* is strongly supported (BS = 100, PP = 1) and *Enyalioides* is paraphyletic relative to *Morunasaurus*. Non-monophyly of the latter is also noteworthy. *Hoplocercus spinosus* is the sister taxon (BS = 72, PP = 0.77) to a clade composed of all other species of hoplocercines, which are divided into two major subclades. One of them (BS = 59, PP = 0.78) contains (*Morunasaurus annularis*, *M. peruvianus*; BS = 100, PP = 1.00) as the sister taxon to a strongly supported clade (BS = 100, PP = 1.00) including *M. groi*, *Enyalioides heterolepis* and *E. laticeps*. The position of *M. groi* differs between ML and MCC trees: the sister taxon to *E. laticeps* (BS = 52) or to a clade composed of *E. laticeps* and *E. heterolepis* (PP = 0.82), respectively. The

second major clade is strongly supported (BS = 98, PP = 1.00) and includes the remaining *Enyalioides* species in the following subclades (in branching order): (1) (*E. altotambo*, (*E. touzeti, E. oshaughnessyi*))—BS = 100, PP = 1.00; (2) ((*E. rubrigularis*, (*E. praestabilis*, (*E. microlepis, E. cofanorum*))), (*E.* sp. 1, (*E.* sp. 2, *E. anisolepis*)))—BS = 100, PP = 1.00; and (3) (*E. palpebralis* [sister taxon to *E. azulae* in MCC tree], (*E. azulae*, (*E. sophiarothschildae*, (*E. binzayedi*, (*E. rudolfarndti, E. feiruzae*)))))—BS = 84, PP = 0.99.
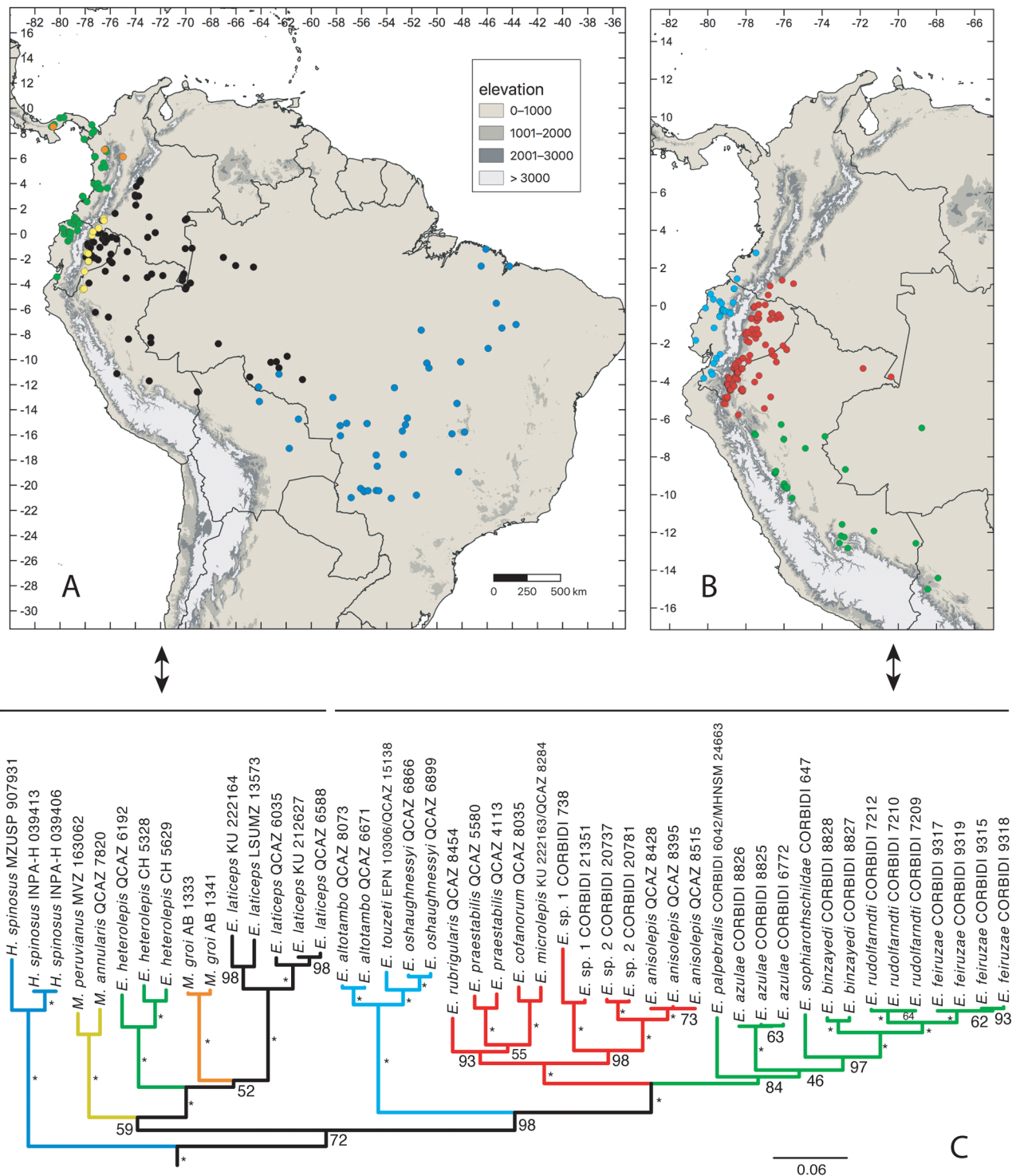

FIGURE 2. Distribution (A, B) and phylogeny (C) of *Hoplocercinae*. Symbol color in the maps corresponds to clade color in the phylogeny, with lines and double-headed arrows indicating the taxa shown in each map. The phylogeny is the maximum likelihood tree obtained from a RAxML analysis of one mitochondrial (*ND2*) and four nuclear genes (*DNAH3, NT3, PRLR, RAG1*). Numbers next to branches are bootstrap support values (BS); branches with asterisks have BS = 100. "*E.*" = *Enyalioides*, "*H.*" = *Hoplocercus*, "*M.*" = *Morunasaurus*. Outgroup taxa are not shown. Locality data are from Torres-Carvajal *et al.* (2011) and subsequent *Enyalioides* species descriptions.
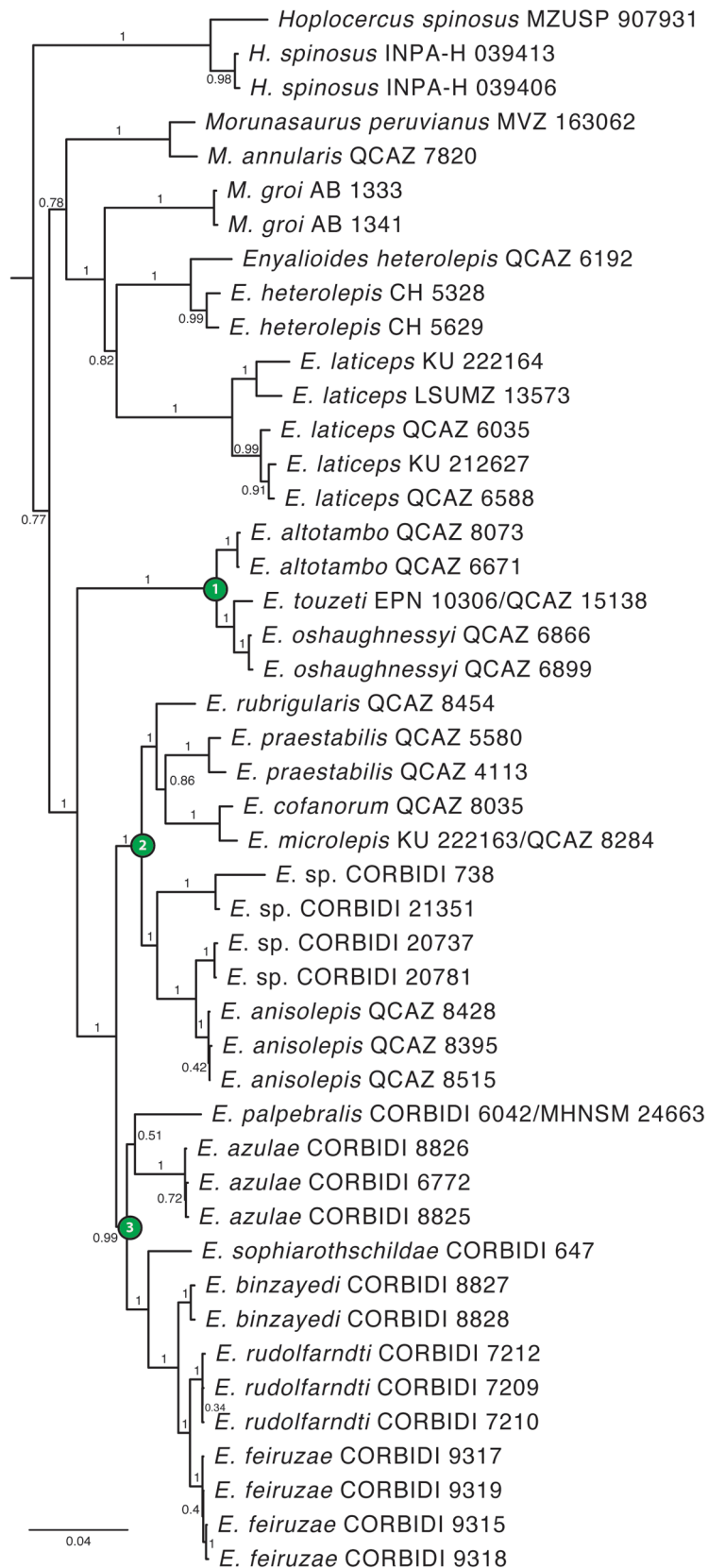
FIGURE 3. Phylogeny of *Hoplocercinae*. The phylogeny is the maximum clade credibility tree obtained from a Bayesian analysis of concatenated sequence data from one mitochondrial (*ND2*) and four nuclear genes (*DNAH3, NT3, PRLR, RAG1*). Numbers next to branches are posterior probability values (PP). Node numbers (in green-filled circles) correspond to subclades described in the text. Outgroup taxa are not shown.

The species tree (Fig. 4) is highly congruent with the concatenated gene trees, differing only in that (1) *E. praestabilis* is sister to *E. rubrigularis* (PP = 0.46) rather than to (*E. cofanorum, E. microlepis*) and (2) *E. azulae* is the sister taxon to all other species in subclade 3 (PP = 0.52) rather than *E. palpebralis* (ML) or (*E. palpebralis, E. azulae*) (MCC) being in that position. The position of *M. groi* as the sister taxon to *E. laticeps* agrees with the ML tree, although support is low (PP = 0.14); however, *M. groi* is strongly supported as being closer to *E. laticeps* and *E. heterolepis* (PP = 0.99) than to *M. annularis* and *M. peruvianus*
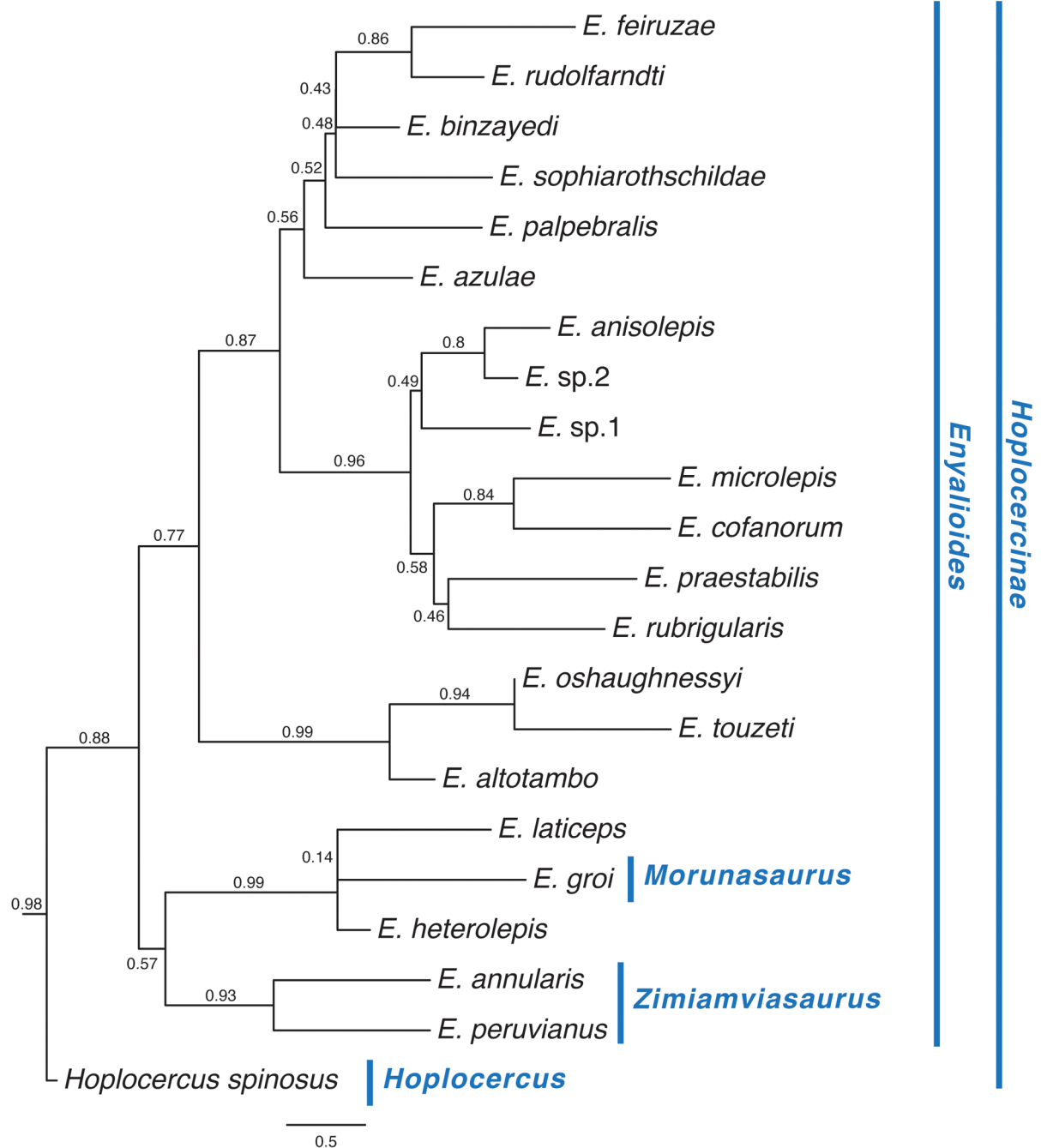
FIGURE 4. Species tree for *Hoplocercinae* inferred from ASTRAL analysis of five gene trees inferred under the GTRGAMMA model in RAxML. Values next to branches represent local posterior probability values. Also shown (in blue text) are the clade names established in this paper; vertical bars (also blue) indicate the compositions of the named clades (see Discussion).

Tree topology tests

SH and AU tests rejected the monophyly of *Enyalioides* (P = 0.018 and 0.012, respectively). Although *M. groi* is strongly supported as more closely related to *E. heterolepis* and *E. laticeps* than to *M. annularis* and *M. peruvianus* (Figs. 2, 3, 4), SH and AU did not reject the monophyly of *Morunasaurus* (P = 0.321 and 0.309, respectively).

Discussion

Here we present the first fully sampled (i.e., all known species included) molecular phylogeny of *Hoplocercinae*, which is also the largest to date in terms of gene sampling (one mitochondrial and four nuclear genes). We also present the first species tree using a coalescent model and multiple samples (2–4) of 12 of the 20 currently recognized species of *Hoplocercinae*. All previously published phylogenies have been based only on mitochondrial data (e.g., Torres-Carvajal *et al.* 2015; Venegas *et al.* 2021), except for one, which also included two nuclear genes (*BDNF*, *RAG1*) but less than half of the currently known species diversity of *Hoplocercinae* (Torres-Carvajal and de Queiroz 2009). Similar to previous inferences, our results support the monophyly of *Hoplocercinae*, the position of *Hoplocercus spinosus* as the sister taxon to all other hoplocercines, and the paraphyly of *Enyalioides* with respect to *Morunasaurus* (Figs. 2, 3, 4).

   Most species of woodlizards have been discovered in this century. Nine of the 16 currently recognized species of *Enyalioides* were named between 2008 (*E. touzeti*) and 2021 (*E. feiruzae*), and two unnamed species from Peru, which we included in our analyses, are currently being named (Venegas pers. comm.). These recent findings have revealed a sizeable species diversity (13 spp.—*E. anisolepis*, *E. azulae*, *E. binzayedi*, *E. cofanorum*, *E. feiruzae*, *E. microlepis*, *E. palpebralis*, *E. praestabilis*, *E. rubrigularis*, *E. rudolfarndti*, *E. sophiarothschildae*, *E.* sp. 1, *E.* sp. 2) of woodlizards along the eastern slopes of the Andes (Fig. 2). Species in this radiation form a strongly supported clade—BS = 100, PP = 1.00, local PP (ASTRAL) = 0.87—that is the sister taxon to a smaller clade of species from the western slopes of the Andes and adjacent lowlands (*E. altotambo*, *E. oshaughnessyi*, *E. touzeti*) (Figs. 2, 3, 4). That these sister clades occur on opposite sides of the Andes at elevations below 2,000 m suggests that they originated through allopatric speciation, whether resulting from dispersal or vicariance, with the Andean highlands as a biogeographical barrier.

   Unlike previous studies, we included samples of *Morunasaurus groi*, the type species of *Morunasaurus*, which we hoped might clarify the phylogenetic relationships and taxonomic status of both *Enyalioides* and *Morunasaurus*. These taxa, traditionally ranked as genera, show striking differences in morphology (Torres-Carvajal *et al.* 2011). For example, while *Morunasaurus* bears conspicuous rings of large spiny scales around the tail and smooth head scales, *Enyalioides* lacks caudal spines and has pointed, conical head scales dorsally (Fig. 1). Despite the morphological distinctiveness of these taxa, all previous molecular phylogenies, which included *M. annularis* and *M. peruvianus*, suggested that *Morunasaurus* is nested within *Enyalioides* as the sister taxon to a clade composed of all *Enyalioides* species except *E. heterolepis* and *E. laticeps*. Our phylogenetic trees also inferred *M. annularis* and *M. peruvianus* nested within *Enyalioides*, although as the sister taxon to a clade containing *E. heterolepis* and *E. laticeps*. Surprisingly, our results also indicate that *Morunasaurus* is not monophyletic, as *M. groi* was inferred with strong support to share a more recent common ancestor with *E. heterolepis* and *E. laticeps* than with *M. annularis* and *M. peruvianus* (Figs. 2–4).

   Iguanian lizards have evolved tails with projected spines multiples times (e.g., in or within *Cachryx*, *Ctenosaura*, *Laudakia*, *Oplurus*, *Phymaturus*, *Stenocercus*, *Uracentron*, *Uromastyx*; Ramm *et al.* 2020). Interestingly, spiny tails have also evolved multiple times even among closely related species, such as within *Iguaninae*, where spiny tails appear to have evolved independently three times (on the tree of Malone *et al.* 2017). The most parsimonious ancestral character reconstruction on our optimal tree topologies (Figs. 2–4) indicates that spiny tails also evolved three times in *Hoplocercinae*: (1) *Hoplocercus spinosus*, (2) *Morunasaurus groi*, and (3) the common ancestor of *M. annularis* and *M. peruvianus*. Although their function has been poorly studied, spiny tails seem to be used as a defense mechanism in different ways. For example, *Uracentron azureum*, *Ctenosaura* spp. and *Uromastyx* spp. defend themselves by lashing their spiny tails from side to side when handled (Greene 1977; Arbour and Zanno 2018). This "tail-lashing" behavior has not been reported in either *Hoplocercus* or *Morunasaurus*. These lizards dig burrows where they retreat when threatened. When in their burrows, they use their spiny tails as a protection against predators by directing it towards the entrance, a behavior that has also been reported in other spiny-tailed lizards

(Malone *et al.* 2017). If threatened, *Hoplocercus* and *Morunasaurus* also inflate their bodies against the walls of their burrows, further preventing predators from digging them out (Nascimento *et al.* 1988; Torres-Carvajal *et al.* 2011). A similar behavior has been observed in *Uromastyx aegyptia*, which wedge themselves into rock crevices by inflating their bodies (Cooper *et al.* 2000). Thus, spiny tails seem to be convergent antipredator mechanisms in iguanian lizards, although the highly vascularized spine tips in *Cachryx defensor* also suggest a possible thermoregulatory function (Malone *et al.* 2017).

Despite the improved taxon and character sampling in our study, some of the relationships within *Hoplocercinae* remain weakly supported, suggesting the need for further study (e.g., phylogenomics). These include 1) the precise relationships among *M. groi*, *E. laticeps*, and *E. heterolepis*, 2) the status of *Morunasaurus,* which was not statistically rejected by tree topology tests, and 3) several relationships in the species tree (Fig. 4).

To correct the non-monophyly of *Enyalioides* and to minimize the number of unnecessary name changes under rank-based nomenclature, while also maintaining consistency with phylogenetic nomenclature, we here propose that *Enyalioides* be treated as the genus of the three species formerly included in *Morunasaurus*, providing the following new combinations: *Enyalioides annularis*, *E. groi*, and *E. peruvianus*. A detailed treatment of the phylogenetic nomenclature of *Hoplocercinae* and its named subclades follows.

Phylogenetic nomenclature of *Hoplocercinae*

Although we have previously published phylogenetic definitions for the names of several hoplocercine clades (Torres-Carvajal and de Queiroz 2009; Torres-Carvajal *et al.* 2011), those definitions were published prior to the starting date of the *International Code of Phylogenetic Nomenclature* (*ICPN,* Cantino and de Queiroz 2020) and thus the names and their definitions are not considered established under that code (*ICPN* Art. 7.1). Therefore, we now publish protologues for those names that satisfy all requirements of the *ICPN*. Etymologies, when not stated by the original proposer of a name, are from Brown (1954).

Hoplocercinae V. R. Alifanov 1996 (converted clade name)

Hoplocercidae Frost and Etheridge 1989:36. Type genus: *Hoplocercus* Fitzinger (1843). See also: Frost *et al.* (2001), Wiens & Etheridge (2003).
Hoplocercinae Alifanov (1996:115); see also Macey *et al.* (1997b), Schulte *et al.* (1998, 2003), Torres-Carvajal & de Queiroz (2009).

Registration number: 807. **Definition:** The smallest crown clade including *Hoplocercus spinosus* Fitzinger 1843, *Enyalioides/Morunasaurus groi* (Dunn 1933), *Enyalioides heterolepis* (Bocourt 1874), *E. oshaughnessyi* (Boulenger 1881), and *Enyalioides/Zimiamviasaurus annularis* (O'Shaughnessy 1881). **Reference phylogeny:** Figure 2 of this article. **Hypothesized composition:** *Hoplocercus* and *Enyalioides* (including *Morunasaurus* and *Zimiamviasaurus*; see Comments on those taxa below). **Diagnostic apomorphies:** See Torres-Carvajal *et al.* (2011). **Etymology:** Based on *Hoplocercus*, the name of an included clade, and the standard suffix, -*inae*, used to indicate the rank of subfamily under rank-based nomenclature. **Comments:** *Hoplocercinae* Alifanov 1996 was selected over several older names that have been applied to a group with the same composition (in terms of species known at the time) as the named clade: hoplocercines (Smith *et al.* 1973), morunasaurines (Estes and Price 1973), morunasaurs (Etheridge and de Queiroz 1988), and *Hoplocercidae* (Frost and Etheridge 1989). The first three are informal names, which are unavailable for conversion, although the name converted could be interpreted as a Latinized version of the first and oldest. The fourth, despite being the oldest formal name applied to a group approximating the named clade, was not selected because its ending might be misinterpreted as implying mutual exclusivity relative to *Iguanidae*, the name of a more inclusive clade (as established by Torres-Carvajal *et al.* 2020). Moreover, the name *Hoplocercinae* has previously been applied to a taxon approximating the crown clade by the only previous author (Alifanov 1996) who used both names (applying the name *Hoplocercidae* to a more inclusive taxon approximating the total clade), and it has previously been applied to the same clade to which it is applied here using an explicit phylogenetic definition (Torres-Carvajal and de Queiroz 2009; Torres-Carvajal *et al.* 2011). According to the *International Code for Zoological Nomenclature* (ICZN 1999), authorship of *Hoplocercinae* would be attributed to Frost and Etheridge (1989) as the first authors to propose a name in the family group (*Hoplocercidae*) based on the genus

name *Hoplocercus*. By contrast, we follow the *ICPN* (Note 9.15A.3) and attribute the name to Alifanov (1996), the first author to use the name (spelling) *Hoplocercinae* as converted.

Hoplocercus Fitzinger 1843 (converted clade name)

Hoplocercus Fitzinger 1843:78. Type species (by monotypy): *Hoplocercus spinosus* Fitzinger 1843:78.
Pachycercus Dugès and Braconnier in Duméril (1854:558). Type species (by monotypy): *Pachycercus aculeatus* Dugès and
Braconnier in Duméril (1854:561).

Registration number: 808. **Definition:** The crown clade for which any of the following character states is an apomorphy relative to other crown clades: depressed (maximum width > height at same level as maximum width, spines excluded), short tail (tail length < snout-vent length) with enlarged spinous scales dorsally and laterally that are at least twice as large in area as ventral scales, as inherited by *Hoplocercus spinosus* Fitzinger 1843. **Reference phylogeny:** Figure 2 of this article. **Hypothesized composition:** *Hoplocercus* is currently inferred to contain a single extant species, *Hoplocercus spinosus* Fitzinger 1843 (Torres-Carvajal *et al.* 2011). **Diagnostic apomorphies:** See Torres-Carvajal *et al.* (2011); the most obvious external character that distinguishes *Hoplocercus* lizards from those in *Enyalioides* is the one used in the Definition—namely, a depressed, short tail (tail length < snout-vent length) with enlarged, spinous scales dorsally and laterally. Some *Enyalioides* lizards (those in the subclades *Morunasaurus* and *Zimiamviasaurus*) also have spinous scales on their tails, but their tails are rounded rather than depressed and longer than the snout-vent length. **Etymology:** Derived from the Greek *hoplon* = armor, shield, weapon + *kerkos* = tail. **Comments:** The name *Hoplocercus* was originally applied to the single species *H. spinosus* (Fitzinger 1843) but was later expanded to include *H. annularis* (O'Shaughnessy 1881; Boulenger 1885; Burt and Burt 1933) until it was returned to its original composition by Dunn (1933). *Hoplocercus* is by far the most widely used name for this clade (e.g., Dunn 1933; Peters and Donoso-Barros 1970; Torres-Carvajal *et al.* 2011; Ribeiro-Júnior 2015) and was selected over the single, rarely used synonym, *Pachycercus,* for that reason. A definition based on the apomorphy of a short, spinose tail was chosen so that the name *Hoplocercus* will include any newly discovered or resurrected extant species possessing that apomorphy, in keeping with the etymology of the name.

Enyalioides Boulenger 1885 (converted clade name)

Enyalus (part) Guichenot (1855:20, 21); Bocourt (1874:1).
Enyalius (part) Cope (1876); Boulenger (1881); O'Shaughnessy (1881); Boulenger (1883); Boulenger (1885).
Enyalioides (part) Boulenger 1885:112. Type species (by subsequent designation by Burt and Burt 1933): *Enyalioides heterolepis*
Bocourt 1874.

Registration number: 804. **Definition:** The smallest crown clade including *Enyalioides heterolepis* (Bocourt 1874), *E. laticeps* (Guichenot 1855), *E. oshaughnessyi* (Boulenger 1881), *E. praestabilis* (O'Shaughnessy 1881), and *E. palpebralis* (Boulenger 1883). **Reference phylogeny:** Figure 2 of this article. **Hypothesized composition:** *Enyalioides* is currently hypothesized to include nineteen named species*: altotambo* Torres-Carvajal *et al.* 2015, *anisolepis* Torres-Carvajal *et al.* 2015, *annularis* (O'Shaughnessy 1881)*, azulae* Venegas *et al.* 2013, *binzayedi* Venegas *et al.* 2013*, cofanorum* Duellman 1973*, feiruzae* Venegas *et al.* 2021*, groi* (Dunn 1933)*, heterolepis* (Bocourt 1874)*, laticeps* (Guichenot 1855)*, microlepis* (O'Shaughnessy 1881), *oshaughnessyi* (Boulenger 1881)*, palpebralis* (Boulenger 1883), *peruvianus* (Köhler 2003)*, praestabilis* (O'Shaughnessy 1881), *rubrigularis* Torres-Carvajal *et al.* 2009*, rudolfarndti* Venegas *et al.* 2011*, sophiarothschildae* Torres-Carvajal *et al.* 2015, and *touzeti* Torres-Carvajal *et al.* 2008, and two unnamed ones (see Figs. 2, 3, 4). **Diagnosis:** *Enyalioides* lizards can be distinguished from those in *Hoplocercus* by having a laterally compressed or rounded (rather than depressed) tail that is longer than the body (i.e., tail length > SVL), although this is likely an ancestral condition. Members of most species also have pointed, conical scales on the dorsal surface of head and gular region, raised scales posterior to the superciliaries, and one or more enlarged pretympanic scales (Torres-Carvajal *et al.* 2011). **Etymology:** Derived from the Greek *Enyalius* = the name of a war god and of a taxon previously confused with this one + *-oides* = like, resembling. **Comments:** Although there is no preexisting name that has been applied to this clade based on composition, *Enyalioides* has been applied to a paraphyletic group originating in approximately the same ancestor (e.g., Peters and Donoso-

Barros 1970; Etheridge and de Queiroz 1988; Wiens and Etheridge 2003), including by authors who hypothesized that the species of *Morunasaurus* might be nested within it (Torres-Carvajal and de Queiroz 2009; Torres-Carvajal *et al.* 2011; Venegas *et al.* 2021). Moreover, the name *Enyalioides* has previously been defined phylogenetically in such a way that it applies unambiguously to this clade (Torres-Carvajal and de Queiroz 2009; Torres-Carvajal *et al.* 2011). Finally, the only other names that have been used for small taxa (those traditionally ranked as genera) including species in this group are now applied to a mutually exclusive clade (*Enyalius*; Etheridge 1969), a nested clade (*Morunasaurus*; see below), or no taxon at all (*Enyalus*; clearly a misspelling of *Enyalius* given that Bocourt [1874] followed Guichenot [1855], who attributed the name to Wagler [1830] who spelled the name *Enyalius*). Consequently, the name *Enyalioides* was selected for this clade. According to the phylogeny inferred in the present study (Figs. 2, 3, 4), *Enyalioides* includes *Morunasaurus* (whose previously included species are now considered to form two non-overlapping subclades of *Enyalioides*, *Morunasaurus* and *Zimiamviasaurus*, see below), rather than being mutually exclusive. Because the phylogeny of hoplocercines has stabilized with the addition of taxa and characters since the name *Enyalioides* was first defined phylogenetically (Torres-Carvajal and de Queiroz 2009), and because that definition was not officially established, having been published before the starting date of the *ICPN* (Cantino and de Queiroz 2020), we have simplified the original definition by eliminating three of the eight specifiers, which no longer seem necessary.

Morunasaurus Dunn 1933 (converted clade name)

Morunasaurus (part) Dunn 1933:75. Type species (by original designation): *Morunasaurus groi* Dunn 1933.

Registration number: 805. **Definition:** The crown clade for which having the posterior whorl of each caudal segment along the anterior half of the tail composed of greatly enlarged, projecting, spinous scales at least two times as large in area as the scales of the immediately anterior whorl, as inherited by *Morunasaurus groi* Dunn 1933, is an apomorphy relative to other crown clades. **Reference phylogeny:** Figure 2 of this article. **Diagnosis:** *Morunasaurus* lizards can be distinguished from those in *Hoplocercus* by having a tail that is roughly circular (rather than depressed) in cross section and longer than the body (i.e., tail length > SVL). They differ from both *Hoplocercus* and other *Enyalioides* lizards, except those in the subclade *Zimiamviasaurus* (i.e., *E. annularis* and *E. peruvianus*), by having projecting scales (spines) on thigh, shin, and pes (projecting scales also present in *E. heterolepis*, but not as spines). They differ from other *Enyalioides* lizards, except those in the subclade *Zimiamviasaurus* (i.e., *E. annularis* and *E. peruvianus*), by having the posterior whorl of each caudal segment composed of greatly enlarged, projecting, spinous scales at least two times as large as the scales of the immediately anterior whorl. They differ from *Zimiamviasaurus* lizards by having 4 rather than 3 transverse rows of scales per caudal segment ventrally and fewer scales (14 versus 15–19) in each caudal whorl (Köhler 2003) and by having an externally visible parietal eye and corresponding parietal foramen in the skull roof (Appendix 1). **Hypothesized composition:** *Morunasaurus* is currently inferred to contain a single species, *Enyalioides/Morunasaurus groi* Dunn 1933. **Etymology:** Derived from Morna Moruna, the name of a fictional land in E. R. Eddison's (1922) fantasy novel *The Worm Ouroboros* (Dunn 1933) + the Greek *sauros* = lizard, reptile. **Comments:** Although no name has been applied to this clade previously (not counting the name of its single included species), the name *Morunasaurus* is the most appropriate name for this clade because 1) it is the only name that has been applied to a taxon less inclusive than *Hoplocercinae* that has included the species *groi*, and 2) *groi* is the type species of that nominal taxon. As described in the Discussion, *Morunasaurus* has previously been considered to include three species: *M. annularis* (O'Shaughnessy 1881), *M. groi* Dunn 1933, and *M. peruvianus* Köhler 2003, whereas our results indicate that these three species do not form a clade (Figs. 2, 3, 4). According to the phylogenetic definition of the name *Morunasaurus* proposed by Torres-Carvajal *et al.* (2011) and the results of the present study, *Enyalioides annularis* and *E. peruvianus* would be removed appropriately from *Morunasaurus*; however, *Morunasaurus* would inappropriately include *E. laticeps* in the context of some of our trees (Figs. 2, 4, but not 3). Although this outcome could be prevented by adding *E. laticeps* to the external specifiers, we have decided to reformulate the definition as an apomorphy-modified crown-clade definition (*ICPN*, Art. 9.9) that we consider more closely to approximate Dunn's concept of *Morunasaurus*. Although *E. annularis* and *E. peruvianus* have the morphology described in our definition (whorls of enlarged, projecting spinous scales at the posterior terminus of each caudal segment), that morphology is inferred to have evolved separately in those species relative to *E. groi*; therefore, they are inferred not to be included in *Morunasaurus*. However, given that

we are unable to reject the monophyly of *Morunasaurus* (as its composition was previously hypothesized), should the three species in question turn out to form a clade (with spiny tails inferred to have evolved in their common ancestor), our definition would then place *E. annularis* and *E. peruvianus* in *Morunasaurus*.

Zimiamviasaurus (new clade name)

Hoplocercus (part) O'Shaughnessy (1881); Boulenger (1885); Burt and Burt (1933).
Morunasaurus (part) Dunn (1933); Peters and Donoso-Barros (1970); Torres-Carvajal *et al.* (2011).

Registration number: 806. **Definition:** The largest crown clade including *Enyalioides*/*Zimiamviasaurus annularis* (O'Shaughnessy 1881) and excluding *Enyalioides*/*Morunasaurus groi* Dunn 1933 and *Enyalioides oshaughnessyi* (Boulenger 1881) and *Enyalioides palpebralis* (Boulenger 1883) and *Enyalioides microlepis* (O'Shaughnessyi 1881). **Reference phylogeny:** Figure 2 of this article. **Diagnosis:** *Zimiamviasaurus* lizards can be distinguished from those in *Hoplocercus* by having a tail that is roughly circular (rather than depressed) in cross section and longer than the body (i.e., tail length > SVL). They differ from both *Hoplocercus* and other *Enyalioides* lizards, except those in the subclade *Morunasaurus* (i.e., *E. groi*), by having projecting scales (spines) on the thigh, shin, and pes (projecting scales also present in *E. heterolepis*, but not as spines). They differ from other *Enyalioides* lizards, except those in the subclade *Morunasaurus* (i.e., *E. groi*), by having the posterior whorl of each caudal segment composed of greatly enlarged, projecting, spinous scales at least two times as large as the scales of the immediately anterior whorl. They differ from *Enyalioides* lizards in the subclade *Morunasaurus* by having 3 rather than 4 transverse rows of scales per caudal segment ventrally and more scales (15–19 versus 14) in each caudal whorl (Köhler 2003) and by lacking an externally visible parietal eye and corresponding parietal foramen in the skull roof (Appendix 1). **Hypothesized composition:** *Zimiamviasaurus* is currently inferred to contain two species, *Enyalioides*/*Zimiamviasaurus annularis* (O'Shaughnessyi 1881) and *Enyalioides*/*Zimiamviasaurus peruvianus* Köhler 2003. **Etymology:** Derived from Zimiamvia, the name of a fictional land in E. R. Eddison's (1922) fantasy novel *The Worm Ouroboros* + the Greek *sauros* = lizard, reptile. The name *Zimiamviasaurus* is meant to be a counterpart to *Morunasaurus*, also based on the name of a fictional land in the same novel, reflecting that like the location of Zimiamvia relative to that of Morna Moruna, the geographic distribution of *Zimiamviasaurus* lies farther south and on the other side of a mountain range relative to that of *Morunasaurus*. **Comments:** Lizards in this clade were previously placed in *Hoplocercus* (O'Shaughnessy 1881; Boulenger 1885; Burt and Burt 1933) and later in *Morunasaurus* (Dunn 1933; Peters and Donoso-Barros 1970; Köhler 2003; Torres-Carvajal *et al.* 2011) along with *M. groi*. Previous molecular phylogenetic analyses sampled *M. annularis* and *M. peruvianus* but not *M. groi* and found that the former two species form a clade. The sampling of *M. groi* in the present study has revealed that this species does not form a clade with the other two species previously assigned to *Morunasaurus*. Instead, *M. groi* shares a more recent common ancestor with *E. laticeps* and *E. heterolepis* than with "*M.*" *annularis* and "*M.*" *peruvianus*, necessitating the removal of the latter two species from *Morunasaurus* according to both the previous unofficial phylogenetic definition (Torres-Carvajal *et al.* 2011) and the official one established herein. *E. annularis* and *E. peruvianus* are morphologically distinctive relative to other *Enyalioides* species, except *Enyalioides*/*Morunasaurus groi*, in possessing a tail with whorls of spinous scales, and given that they form a clade, we have chosen to apply the name *Zimiamviasaurus* to this subclade of *Enyalioides*. We have defined the name *Zimiamviasaurus* so that if future studies contradict our results in inferring *groi*, *annularis*, and *peruvianus* to form a clade and thus the spinose tails of these three species to be synapomorphic, then the name will apply to a subclade of *Morunasaurus*. If interpreted in the context of rank-based nomenclature as a name in the genus group (e.g., as the name of a subgenus of *Enyalioides*), then the type species of *Zimiamviasaurus* is here designated as *Enyalioides*/*Zimiamviasaurus annularis* (O'Shaughnessy 1881).

Conclusions

Here we present a comprehensive phylogenetic analysis of *Hoplocercinae* including all known species and DNA sequence data for five loci. The resulting trees are congruent in topology with previous hypotheses in that (1) *Hoplocercinae* is monophyletic, (2) *Hoplocercus spinosus* is the sister taxon to all other species, and (3) *Morunasaurus* is nested within *Enyalioides*. The newly sampled *Morunasaurus groi*, type species of *Morunasaurus*, formed a

clade with *Enyalioides heterolepis* and *E. laticeps*, suggesting that *Morunasaurus* is not monophyletic, although monophyly of *Morunasaurus* was not rejected by tree topology tests.

Acknowledgements

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APPENDIX 1. Presence/absence of the parietal eye/foramen among hoplocercine species.

The absence of an externally visible parietal eye and of the corresponding parietal foramen in the skull roof appears to be a diagnostic apomorphy of *Zimiamviasaurus*; however, the most recent summary of the distribution of the states of this character among hoplocercine species (Wiens and Etheridge 2003) is outdated (because of subsequently discovered species) and contains some misleading estimates based on small samples. We therefore found it necessary to produce an updated summary. The following list combines data from examination of both entire specimens and skeletal preparations under the assumption that if the parietal eye is visible externally, then the foramen is also present, and vice versa. We list each hoplocercine species, the state(s) of the character observed in it, and vouchers for the observations with the observed state (when scorable), and sources. Abbreviations are as follows: "+" = present; "–" = absent, "?" = uncertain; "*" = holotype specimen. Museum abbreviations/acronyms follow Sabaj (2020).

Enyalioides altotambo: present; QCAZ 8073* (+) (Torres-Carvajal *et al.* 2015).
Enyalioides anisolepis: present; QCAZ 12517 (+), 12527 (+), 17456 (+) 12535* (?) (this study, from photographs in Torres-Carvajal *et al.* 2022).
Enyalioides annularis: absent; AMNH 57180 (–?) (Gundy and Wurst 1976); BMNH 1946.8.10.35*, MEPN 1236, 5219, 5591–6, 7200–18, 7220–3, 7225, 7228–35, 7320–1, unnumbered (n=30), SMF 78049–56, ZFMK 42772 ("nicht vorhanden", not scored individually) (Köhler *et al.* 1999); RE 1956, USNM 200735, 200740, 203842 (all –, inferred from a reported frequency of 100%) (Wiens and Etheridge 2003; the last two confirmed in this study); QCAZ 7819 (–), 7820 (–), 5797 (–) (this study, from photographs in Torres-Carvajal *et al.* 2022).
Enyalioides azulae: present; CORBIDI 06772* (+) (Venegas *et al.* 2013).
Enyalioides binzayedi: present; CORBIDI 08828* (+) (Venegas *et al.* 2013).
Enyalioides cofanorum: present/absent; KU 147587 (–, inferred from a reported frequency of 100%) (Wiens and Etheridge 2003; confirmed in this study); photo 63761488 (+?) (iNaturalist); QCAZ 10730 (+), 11723 (+) (this study, from photographs in Torres-Carvajal *et al.* 2022). See comments below.
Enyalioides feiruzae: present; CORBIDI 9316* (+) (Venegas *et al.* 2021).
Enyalioides groi: present; AMNH 89903 (+) (Gundy and Wurst 1976); KU 76061 (+, inferred from a reported frequency of 0%)

(Wiens and Etheridge 2003); MHUA 13735 (Vásquez-Restrepo 2021: Fig. 3A).

Enyalioides heterolepis: present, AMNH 18232 (+) (Gundy and Wurst 1976); MCZ 28384, USNM 211079, 211083 (all +, inferred from a reported frequency of 0%) (Wiens and Etheridge 2003; the last confirmed in this study); QCAZ 4553 (+), 15066 (+), 15068 (?), 15390 (+), 15608 (+), 16929 (+) (this study, from photographs in Torres-Carvajal *et al.* 2022).

Enyalioides laticeps: present; INPA 610 (Avila-Pires 1995: Fig. 3); MCZ 37287, RE 1957, USNM 211123, 211126 (all +, inferred from a reported frequency of 0%) (Wiens and Etheridge 2003; the last two confirmed in this study); QCAZ 8306 (+), 10531 (+), 11520 (+), 14808 (+), 14810 (+) (this study, from photographs in Torres-Carvajal *et al.* 2022).

Enyalioides microlepis: present; USNM 211071 (this study). See comments below.

Enyalioides oshaughnessyi: present; USNM 211108 (+, inferred from a reported frequency of 0%) (Wiens and Etheridge 2003; confirmed in this study); QCAZ 11451 (+), 15069 (+), 15706 (+), 15707 (+), 15708 (+), 15709 (+), 15710 (+), 15711 (+), 16025 (+), 16164 (+) (this study, from photographs in Torres-Carvajal *et al.* 2022).

Enyalioides palpebralis: present/absent; AMNH 57160 (+) (Gundy and Wurst 1976); INPA 506 (Avila-Pires 1995: Fig. 5; the species was also described as having "a small parietal eye", p. 31, based on BMNH 1946.8.9.8*, INPA 506, 527, 573, ZFMK 41835); FMNH 40008 (–, inferred from a reported frequency of 100%) (Wiens and Etheridge 2003; confirmed in this study). See comments below.

Enyalioides peruvianus: absent; USNM 316725* (–, described as "indistinct", p. 3) (Köhler 2003: see also his Fig. 2).

Enyalioides praestabilis: present/absent; AMNH 28874 (+) (Gundy and Wurst 1976); MCZ 163653 (+), USNM 211162 (–?), 211168 (–) (Wiens and Etheridge 2003; this study); USNM 222583 (+) QCAZ 15412 (+), 15969 (+), 15970 (?), (this study). See comments below.

Enyalioides rubrigularis: present; QCAZ 15846 (+), 15847 (?), 16226 (?), 16227 (+), 16229 (?), 16542 (?), 16543 (+), 17009 (?), 17010 (?), 17011 (+), 17012 (+), 17013 (+) (this study, from photographs in Torres-Carvajal *et al.* 2022). We note that the parietal eye in this species is often in a dark scale, which makes it difficult to see in photographs.

Enyalioides rudolfarndti: present; CORBIDI 07209* (+) (P. Venegas, pers. comm. and photo).

Enyalioides sophiarothschildae: present; CORBIDI 647* (Torres-Carvajal *et al.* 2015).

Enyalioides touzeti: present; QCAZ 15138 (+), 15836 (+), 16290 (+), 16291 (+), 16292 (+), 16293 (+), 16294 (+), 16299 (+), 17081 (+) (this study, from photographs in Torres-Carvajal *et al.* 2022).

Hoplocercus spinosus: present; AMNH 93468–82 (+) (Gundy and Wurst 1976); AMNH 87906–12, 90276, 90419–26, 90542–43, 91654, 93468–72, 93473–82, MNRJ 1434–7, 3298, 3502, 3510, 3515, 3551, 3567, 3577, 3578–89, MPEG 12928–31, 14278, 14281–82, 14313, 14319, 14323, 1709–13, 1714–8, 1719–47, 1754–81 ("distinct", not scored individually) (Avila-Pires 1995: see also her Fig. 6); MCZ 20677, 20679, RE 1502, 1263 (Wiens and Etheridge 2003; all +, inferred from a reported frequency of 0%).

From our newly compiled data, the species in the clade *Zimiamviasaurus* (*annularis* and *peruvianus*) appear to be the only ones for which absence of the parietal eye and foramen is fixed or nearly so. Important differences between our data and those reported in the literature are as follows: 1) *Enyalioides cofanorum*: Wiens and Etheridge (2003) scored this species as "100%" (parietal foramen absent) based on a single skeletal specimen, KU 147587. We confirmed that the parietal foramen is absent in this specimen; however, it is present in others (see above) and absence may not be the most common condition. 2) *Enyalioides microlepis*: Wiens and Etheridge (2003) scored this species as "100%" (parietal foramen absent) but did not list any specimens of this species in their skeletal specimens examined (Appendix 1). Based on USNM 211071, absence certainly is not fixed and may not be the most common condition. 3) *Enyalioides palpebralis*: Wiens and Etheridge (2003) scored this species as "100%" (parietal foramen absent) based on a single skeletal specimen, FMNH 40008. We confirmed that the parietal foramen is absent in this specimen; however, it is present in others (see above) and absence does not appear to be the most common condition. 4) *Enyalioides praestabilis*: Wiens and Etheridge (2003) scored this species as "33%" (parietal foramen absent) based on three skeletal specimens, MCZ 163653, USNM 211162, and USNM 211168. We examined these same specimens and found the parietal foramen to be present in MCZ 163653 and absent in USNM 211162 and USNM 211168, thus reversing their percentages (67% absent); however, it is present in at least four additional specimens (see above) suggesting that presence is the most common condition (estimated frequencies are 71% present, 29% absent).