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A systematic revision of Neotropical lizards in the clade *Hoplocercinae* (Squamata: Iguania)

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Abstract

The clade *Hoplocercinae* includes 13 species assigned to three taxa traditionally ranked as genera—*Enyalioides*, *Hoplocercus*, and *Morunasaurus*—, and distributed on both sides of the Andes from Panama to Brazil. We provide a revised taxonomy of *Hoplocercinae* including synonymies, diagnoses, standardized descriptions, distributions, notes on color and natural history, and a key for species identification. We also propose vernacular names in English and Spanish for all species.

Key words: *Enyalioides*, *Hoplocercus*, Iguanidae, lizards, *Morunasaurus*, Neotropics, taxonomy

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Resumen

El clado *Hoplocercinae* contiene 13 especies que han sido asignadas a tres taxones tradicionalmente jerarquizados como géneros—*Enyalioides*, *Hoplocercus* y *Morunasaurus*—, y que se distribuyen a ambos lados de los Andes desde Panamá hasta Brasil. Presentamos una revisión taxonómica de *Hoplocercinae* que incluye sinónimos, diagnosis, descripciones estandarizadas, distribución, notas de coloración e historia natural y una clave para la identificación de las especies. También proponemos nombres vulgares en inglés y español para todas las especies.

Palabras clave: *Enyalioides*, *Hoplocercus*, Iguanidae, lagartijas, *Morunasaurus*, neotrópico, taxonomía

Introduction

The iguanian lizard clade *Hoplocercinae* (sensu Torres-Carvajal & de Queiroz (2009)) includes 13 currently recognized species assigned to *Enyalioides*, *Hoplocercus*, and *Morunasaurus* distributed from Panama to central Brazil (Fig. 1). Except for *Hoplocercus spinosus*, which inhabits mostly the Cerrado biome, hoplocercines occupy lowland tropical rainforests including the Chocó and the western Amazon basin, with nine species (70%) occuring east of the Andes and four (30%) occuring west of the Andes.

Historical review. The first species of hoplocercine lizards to be described was *Hoplocercus spinosus* by Fitzinger (1843). O'Shaughnessy (1881) described *Hoplocercus annularis*, which was later transferred to *Morunasaurus* by Dunn (1933). The first seven species of *Enyalioides* to be described were initially referred to *Enyalius* (Wagler 1830): *E. laticeps* (Guichenot 1855), *E. planiceps* (Guichenot 1855), *E. heterolepis* (Bocourt 1874), *E. microlepis* (O'Shaughnessy 1881), *E. praestabilis*, (O'Shaughnessy 1881), *E. oshaughnessyi* (Boulenger 1881), and *E. palpebralis* (Boulenger 1883). In his *Catalogue of the Lizards in the British Museum*, Boulenger (1885) proposed *Enyalioides* for the species listed above, and placed *E. planiceps* in the synonymy of *E. laticeps*. In an addendum to that work he described *Enyalioides leechii*, later transferred to *Enyalius* by Etheridge (1969). Additional species of *Enyalioides* described were *E. festae* (Peracca 1897), considered a subspecies of *E. laticeps* by Burt & Burt (1931), *E. insulae* (Bocourt in Bangs *et al.* 1905), considered a synonym of *E. heterolepis* by Parker (1926), *E. mocquardi* (Despax 1911), considered a synonym of *E. heterolepis* by Burt & Burt (1931), *E. cofanorum* (Duellman 1973), *E. touzeti* (Torres-Carvajal *et al.* 2008), and *E. rubrigularis* (Torres-Carvajal *et al.* 2009). In 1933 Dunn proposed *Morunasaurus* for *M. annularis* and *M. groi*. A third species, *M. peruvianus,* was described by Köhler (2003).

Nineteenth and early Twentieth Century authors did not consider *Hoplocercus* (and later *Morunasaurus*) to be closely related to *Enyalioides*; Boulenger (1885), for example, placed *Hoplocercus* near *Cachryx* (*Ctenosaura defensor*) and *Dipsosaurus*, and *Enyalioides* near *Ophryoessa* (*Uranoscodon*) and *Enyalius*. The first suggestion that *Hoplocercus*, *Morunasaurus*, and *Enyalioides* might be closely related was their grouping at the base of a branching diagram illustrating possible relationships among iguanid lizards prepared by R. Etheridge (circa 1962; Etheridge & de Queiroz 1988) and published in a modified form in Smith *et al.* (1973) and Paull *et al.* (1976), and in its original form by de Queiroz (1987). The basal placement of the group suggested possible paraphyly, but Etheridge & de Queiroz (1988) provided evidence that these three taxa formed a monophyletic group, which they referred to by the informal name "morunasaurs." Relative to seven other putative iguanid clades recognized by these authors, the morunasaurs were diagnosed by the presence of a greatly enlarged nasal scale. Etheridge & de Queiroz (1988) noted the possibility of a close relationship among morunasaurs, oplurines, and anoloids based on their sharing of chameleon-like post-xiphisternal inscriptional ribs. Etheridge´s earlier statement that *Morunasaurus* has *Sceloporus*-like inscriptional ribs (Etheridge 1965) is incorrect. However, their minimum step tree found ((*Enyalioides*, *Morunasaurus*), *Hoplocercus*) to be the sister group of all iguanids except anoloids (not including *Polychrus*), oplurines, and crotaphytines. Within the morunasaurs, they inferred the following relationships: (*E. laticeps*, (*E. praestabilis*, (*E. oshaughnessyi*, (*E. microlepis*, (*E. palpebralis*, (*E. heterolepis*, (*Morunasaurus, Hoplocercus*)))))) (Fig. 2). Both *Enyalioides* and *Morunasaurus* were considered to be paraphyletic.

The eight putative iguanid clades recognized and given informal names by Etheridge & de Queiroz (1988) were given formal names and ranked as families by Frost & Etheridge (1989) after finding no support for the monophyly of the traditional *Iguanidae* (sensu Gray 1845; Boulenger 1885; Cope 1900; Fürbringer 1900; Gadow 1901; Camp 1923; Williston 1925; Romer 1956 1976; McDowell & Bogert 1954; Underwood 1971; Estes 1982;

Estes *et al.* 1988; Etheridge & de Queiroz 1988). The morunasaur group was given the formal name *Hoplocercidae*. Frost & Etheridge (1989) conducted a phylogenetic analysis of morphological data that found 225 most parsimonious trees, which could be reduced to 12 unrooted trees representing the relationships among nine major iguanian groups (the eight iguanid groups recognized by Etheridge & de Queiroz 1988, plus acrodonts). Although a strict consensus of these trees placed *Hoplocercidae*, represented by *Enyalioides*, in an unresolved polytomy with eight other clades of iguanians, in the primary trees, *Hoplocercidae* was the sister group of either *Iguanidae*, *Polychrotidae*, *Acrodonta*, or a group composed of both *Iguanidae* and *Polychrotidae*.

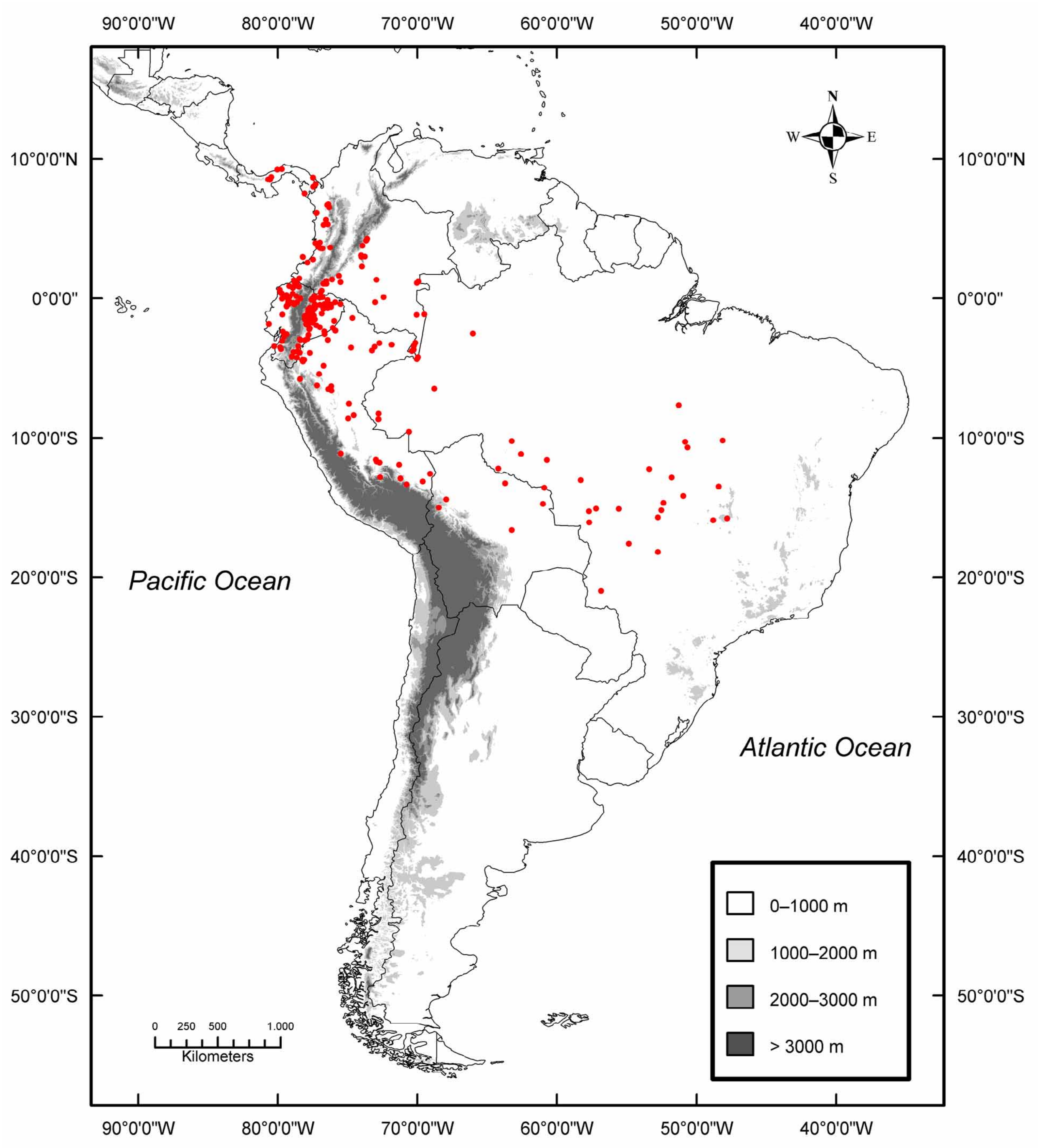

FIGURE 1. Distribution of *Hoplocercinae*.

Sites *et al.* (1996), using molecular and morphological data sets to determine the relationships within the restricted *Iguanidae* (i.e., sensu Frost & Etheridge 1989), chose *Enyalioides*, *Oplurus*, *Sceloporus* and *Phrynosoma* as outgroups. Their maximum parsimony and neighbor-joining trees placed *Enyalioides* as the sister taxon of *Oplurus* and *Iguanidae*, respectively.

Alifanov (1996, 2000) recognized two putative clades (ranked as subfamilies) of *Hoplocercidae* without an explicit phylogenetic analysis: the *Pleurodontagaminae*, containing four extinct forms from the Upper Cretaceous of Mongolia (*Pleurodontagama aenigmatodes*, *Gladidebagama semiplena*, *Mimeosaurus crassus* and *M. tagrikinensis*), and the *Hoplocercinae*, containing the extant taxa *Hoplocercus*, *Morunasaurus* and *Enyalioides*. Implicit in this taxonomic proposal is the hypothesis that *Pleurodontagama*, *Galdidebagama*, and *Mimeosaurus* are stem hoplocercines.

Macey *et al.* (1997) conducted a phylogenetic analysis of molecular and morphological data and found strong support for the monophyly of the traditional *Iguanidae*. Consequently, following the traditional use of the name *Iguanidae*, Macey *et al.* (1997) proposed to rank as subfamilies of *Iguanidae* the same eight putative clades of Etheridge & de Queiroz (1988) that were ranked as families by Frost & Etheridge (1989). They found *Hoplocercinae*, represented by *Hoplocercus*, to be the sister taxon of *Crotaphytinae*.

Schulte *et al.* (2003) analyzed the phylogenetic relationships within the traditional *Iguanidae* using morphological and molecular data. Their tree based on parsimony analysis of morphological characters found *Hoplocercinae*, represented by *Enyalioides*, to be the sister taxon of *Iguaninae*. The tree based on parsimony analysis of molecular data found (*Enyalioides*, (*Hoplocercus*, *Morunasaurus*)) to be the sister taxon of all iguanids except *Polychrus*. A tree based on parsimony analysis of the combined data found (*Enyalioides*, (*Hoplocercus*, *Morunasaurus*)) to be the sister taxon of *Polychrus*, and the clade containing those four taxa as the sister taxon of all other iguanids. Phylogenetic relationships based on maximum likelihood analysis of molecular data yielded (*Enyalioides*, (*Hoplocercus, Morunasaurus*)) as the sister taxon of all other iguanids except *Crotaphytinae*.

Wiens & Etheridge (2003), using morphological characters, performed three phylogenetic analyses of relationships within *Hoplocercidae* using three different methods for weighting meristic characters: between-state scaling, between-character scaling, and mixed scaling, with representatives of *Agamidae*, *Polychrotidae* and the restricted *Iguanidae* as outgroups. In all three analyses *Iguanidae* was found to be the sister taxon of *Hoplocercidae*. The analysis using between-state scaling found (*H. spinosus*, (*M. groi*, (*M. annularis*, (*E. praestabilis*, (*E. laticeps*, (*E. heterolepis*, *E. microlepis*), (*E. oshaugnessyi*, (*E. cofanorum*, *E. palpebralis*)))))); between-character scaling found (*E. laticeps*, (*E. heterolepis*, (*M. annularis*, (*M. groi*, *H. spinosus*))), (*E. praestabilis*, (*E. microlepis*, (*E. oshaugnessyi*, (*E. cofanorum*, *E. palpebralis*))))); and mixed scaling found (*H. spinosus*, (*M. groi*, *M. annularis*)), (*E. laticeps*, ((*E. microlepis*, *E. praestabilis*), (*E. heterolepis*, (*E. oshaughnessyi*, (*E. palpebralis*, *E. cofanorum*))))) (Fig. 2).

Townsend *et al.* (2004), based on data from the nuclear gene RAG-1 for 69 squamate species, inferred *Hoplocercinae* (represented by *Hoplocercus spinosus* and *Enyalioides laticeps*) as sister taxon of *Polychrotinae* (represented by *Anolis paternus*), and the clade formed by these taxa as sister taxon of *Iguaninae* (represented by *Sauromalus obesus*). Using mitochondrial data they found *Hoplocercinae* to be the sister taxon of crotaphytines (represented by *Gambelia wislizenii*) and some tropidurines (represented by *Stenocercus crassicaudatus*), and the clade formed by these four taxa as sister taxon to all other *Iguanidae* (traditional sense).

Conrad *et al.* (2007) analyzed morphological data for 50 extant and extinct taxa and found *Hoplocercidae* to be the sister taxon to all other pleurodont iguanians. In a similar study, Conrad & Norell (2007) found *Hoplocercidae* to be the sister taxon to all other pleurodont iguanians except for *Phrynosomatidae*. In a more comprehensive phylogenetic study including 222 extant and extinct squamate taxa, Conrad (2008) inferred *Hoplocercidae*, represented by *Morunasaurus annularis*, *Hoplocercus spinosus*, *E. palpebralis*, and *E. laticeps*, as the sister taxon of (*Isodontosaurus*†, (*Priscagamidae*†, *Acrodonta*)) based on an Adams consensus tree; in the strict consensus tree they formed part of a large polytomy at the base of *Iguania*. Within *Hoplocercidae* he found (*Enyalioides*, (*Hoplocercus*, *Morunasaurus*)). Contrary to the hypothesis of Alifanov (1996, 2000), Conrad's analyses suggest that the priscagamids are stem acrodonts rather than stem hoplocercids.

Torres-Carvajal & de Queiroz (2009), using a combined mitochondrial and nuclear dataset of nine hoplocercine species and five outgroup taxa representing *Corytophaninae*, *Leiocephalus*, *Liolaemus*, *Oplurinae* and *Phrynosomatinae*, found *Hoplocercinae* to be the sister taxon of (*Phrynosoma* (*Liolaemus* + *Oplurus*)). Within *Hoplocercinae*, they found (*Hoplocercus spinosus*, ((*Enyalioides heterolepis*, *E. laticeps*), (*Morunasaurus annularis*, ((*E. oshaughnessyi*, *E. touzeti*), (*E. palpebralis*, (*E. microlepis*, *E. praestabilis*)))))) (Fig. 2). When tested against this hypothesis, all previous (morphology-based) hypotheses of *Hoplocercinae* phylogeny were rejected. The only relationship within *Hoplocercinae* for which both the likelihood bootstrap proportion was < 90% and the Bayesian posterior probability was < 0.90 was the inclusion of *Morunasaurus* within *Enyalioides*. The latter relationship was not supported statistically in that the data did not reject the monophyly of *Enyalioides*; consequently, the position of *Morunasaurus* remains unclear (Torres-Carvajal & de Queiroz 2009). These authors also performed chronophylogenetic analyses that yielded 56.35 million years (95% High Posterior Density interval = 45.37–68.03) as a rough estimated age of the divergence between *Hoplocercinae* and other iguanids, and 34.64 million years (HPD = 28.04–41.67) as a rough estimated age of the divergence between *Hoplocercus* and other hoplocercines.

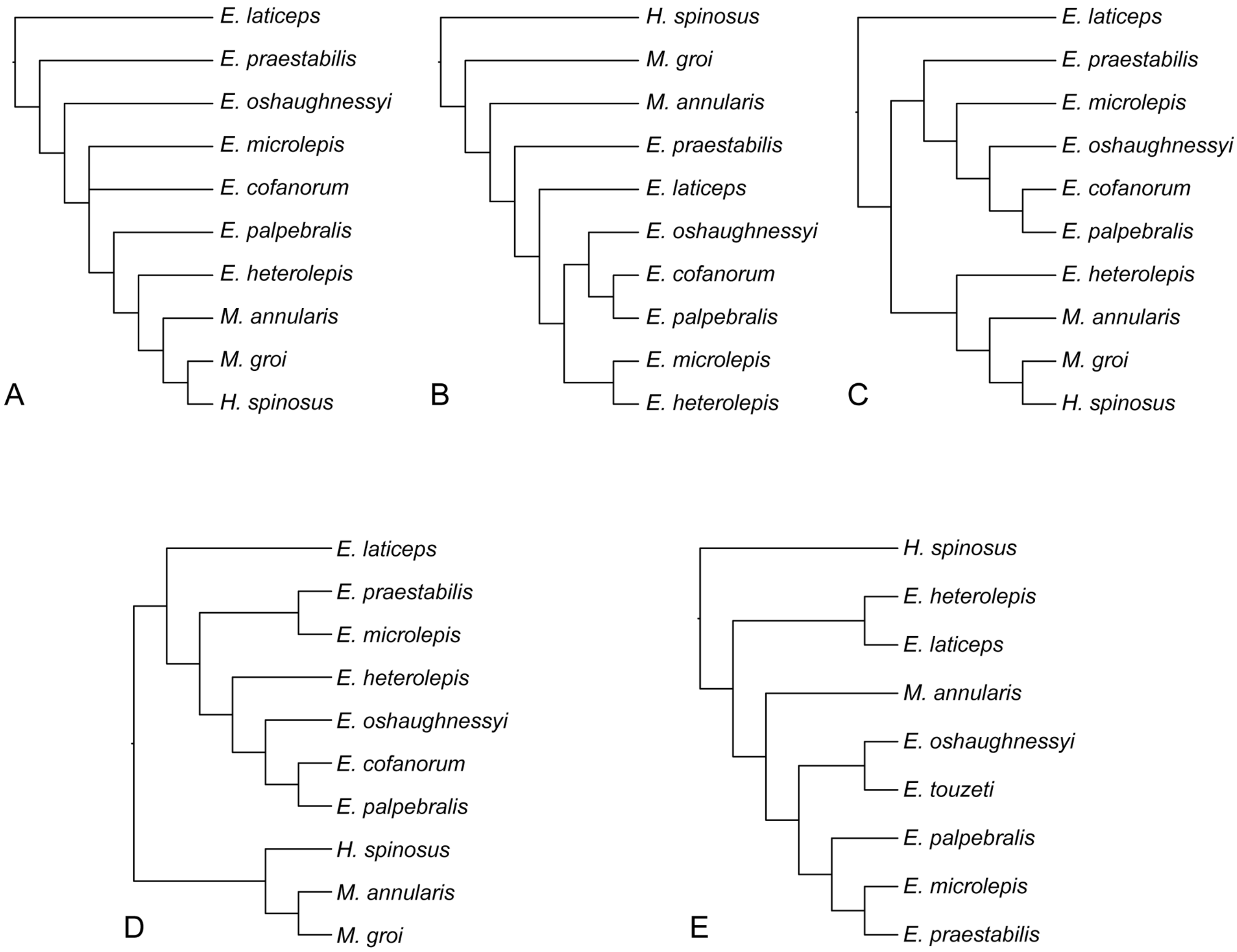

FIGURE 2. Six hypotheses of phylogenetic relationships among hoplocercine lizards. (A) Etheridge & de Queiroz (1988); (B–D) Between-state, between-character, and mixed scaling, respectively (Wiens & Etheridge, 2003); (E) Torres-Carvajal & de Queiroz (2009). H., *Hoplocercus*; M., *Morunasaurus*; E., *Enyalioides*.

In summary, there is no agreement concerning which clade represents the sister taxon to *Hoplocercinae*. Moreover, nodal support (when reported) for these different sister taxon hypotheses is weak. Attempts to infer the phylogeny of *Hoplocercinae* based on morphological data also resulted in different, weakly supported hypothesis until Torres-Carvajal & de Queiroz (2009) presented a well-supported phylogenetic tree of *Hoplocercinae* based on molecular data (Fig. 2). These authors used their preferred hypothesis to define the names *Hoplocercinae*, *Enyalioides*, *Hoplocercus*, and *Morunasaurus* phylogenetically (de Queiroz & Gauthier 1990, 1992, 1994) according to the rules in the draft of the International Code of Phylogenetic Nomenclature (ICPN; Cantino & de Queiroz 2007). *Hoplocercinae*, a converted clade name, was defined as the crown clade originating with the most recent common ancestor of *Enyalioides laticeps*, *E. oshaughnessyi*, *Hoplocercus spinosus*, *Morunasaurus annularis*, and *M. groi*.

Because the names *Hoplocercinae* and *Hoplocercidae* have both been applied to groups approximating the clade whose taxonomy is the subject of the present revision, it seems important to clarify our use of these names. Following Torres-Carvajal & de Queiroz (2009), we use the name *Hoplocercinae* for the crown clade originating with the most recent common ancestor of the extant species of *Hoplocercus*, *Enyalioides*, and *Morunasaurus*, because *Hoplocercinae* is the only name that has been explicitly defined as applying to that particular clade. However, we note that the name *Hoplocercidae* can also be used in a way that is consistent with its prior use (Frost & Etheridge 1989) by applying it to a more inclusive clade containing the crown clade *Hoplocercinae* and some or all members of its stem group. To our knowledge, at least three different herpetologists (R. Etheridge, K. Miyata, M. Henzel) started, but did not complete, a taxonomic revision of *Hoplocercinae*. The purpose of this paper is to provide a revised taxonomy of *Hoplocercinae* including synonymies, diagnoses, standardized descriptions, distributions, notes on color and natural history if available, and a key for species identification. Additionally we propose vernacular names in English and Spanish for all species.

Material and methods

Taxa and specimens. Morphological data were obtained for all species of hoplocercine lizards by examination of 496 specimens (Appendix) and from the literature (Avila-Pires 1995; Köhler 2003). Museum institutional abbreviations follow Leviton *et al.* (1985) except for Fundación Herpetológica Gustavo Orcés, Quito, Ecuador (FHGO); Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Colombia (IAvH); Instituto Nacional de Recursos Naturales, Colombia (IND-R; collections now deposited at Instituto de Ciencias Naturales (ICN) Universidad Nacional de Colombia, Bogotá); Museo de Historia Natural, Universidad Mayor de San Marcos, Lima, Perú (MHNSM); Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ).

Characters. We recorded scutellational data and measurements for all species of *Hoplocercinae*. Meristic scutellational characters are defined as follows:

Vertebrals from occiput to base of tail: the number of scales forming the dorsal vertebral crest between the occiput and a point correspoding to the posterior border of the thigh when placed at a 90º angle from the body. For taxa lacking a vertebral crest (i.e., *Hoplocercus* and *Morunasaurus groi*) vertebral scales were counted as those scales lying on a longitudinal, middorsal line.

Dorsals in transverse row between dorsolateral crests at midbody: the number of dorsal scales between the dorsolateral crests counted on a transverse straight line halfway between the insertion of fore and hind limbs. Specimens lacking dorsolateral crests were compared with specimens having these crests to determine approximately where the dorsolateral crests would be if present.

Ventrals in transverse row at midbody: the number of ventral scales on a transverse straight line halfway between the insertion of fore and hind limbs. Ventrals can be distinguished from flank scales by their larger size and rectangular shape.

Transverse rows of ventrals: the number of transverse rows of ventral scales between the anterior border of the hind limb insertion and the posterior border of the fore limb insertion.

Gulars: the number of gular scales on a transverse straight line between the ventral borders of the tympana.

Infralabials: the number of infralabial scales counted from the mental scale to a point at the level of the middle of the eye.

Supralabials: the number of supralabial scales counted from the rostral scale to a point at the level of the middle of the eye.

Canthals: the number of scales on the canthal ridge between the postrostrals and the first superciliary.

Superciliaries: the number of scales on the dorsal margin of the orbit. Superciliaries are continuous with the canthals anteriorly and the supratemporals posteriorly, and can be distinguished from them by their rectangular or squarish shape in lateral view. As the anteriormost superciliary we counted that scale contacting ventrally the anterior end of a conspicuous row of scales that delimits the ventral margin of the orbit and is composed of preoculars anteriorly and suboculars posteriorly. As the posteriormost superciliary we counted the last scale similar in shape (i.e., rectangular or squarish) to other superciliaries, which usually lies at the level of the posterior end of the eyelids.

Subdigitals on finger IV: the number of subdigital scales on manual digit IV between the point where digit IV joins the ~~palm~~ and the distal tip of digit IV. The scale forming the ventral sheath of the claw was not counted.

Subdigitals on toe IV: the number of subdigital scales on pedal digit IV between the point where digit IV joins the ~~palm~~ and the distal tip of digit IV. The scale forming the ventral sheath of the claw was not counted.

Measurements of snout–vent length (SVL) and tail length (TL) were taken with a ruler and recorded to the nearest 1 mm. All other measurements—head length (i.e., distance from anterior margin of tympanum to tip of snout), maximum head width, maximum head height, maximum rostral width, maximum rostral height, maximum mental width, maximum mental height, fore limb length (distance from the insertion of the fore limb to the tip of digit IV, including the claw), hind limb length (distance from insertion of the hind limb to the tip of digit IV, including the claw)—were made with digital calipers and recorded to the nearest 0.1 mm. Sex was determined either by dissection, or by noting the presence of hemipenes or sexually dichromatic characters. Coloration data were obtained from the literature, field notes, or color photographs. Clutch size was determined by dissection or obtained from the literature.

Georeferencing. Geographic coordinates were obtained for 288 localities using Global Gazetteer Version 2.1 (Falling Rain Genomics, Inc.), HerpNet (www.herpnet.org), the collections' databases, GPS data, or the literature (Corredor *et al.* 1985; Dixon & Soini 1986; Vanzolini 1986; Vitt & Caldwell 1993; Avila-Pires 1995; Harvey 1998; Dirksen & de la Riva 1999; Lips 1999; Quintana & Padial 2003; Reichle *et al.* 2004; Cisneros-Heredia 2005; Duellman 2005; Macedo *et al.* 2008; da Silva *et al.* 2009; Valdujo *et al.* 2009). Distribution maps were constructed in ArcMap 9.3 (ESRI, Inc.). Two species were considered sympatric if there was an exact match in geographic coordinates in decimal degrees of one or more of their locality data points. Nontheless, we mention when two species are not sympatric (under this criterion), but are known from nearby localities suggesting that they may be sympatric.

Species delimitation. The taxonomic conclusions of this study are based on the observation of morphological features and color patterns, as well as inferred phylogenetic relationships and estimated genetic distances reported by Torres-Carvajal & de Queiroz (2009). We recognize as species all populations for which we have evidence of separate evolution on the order of thousands or tens of thousands rather than tens or hundreds of years. In most cases, such evidence takes the form of morphological or genetic differentiation between forms that is indicative, also taking geographic information into consideration, of no or very limited gene flow between them. For reviews of the general concept of species and species delimitation criteria see de Queiroz (1998, 2007).

Results

A description is provided as a numbered list of 16 characters for each species, with each number corresponding to the same character across all species; in addition, data for 21 scutellational and morphometric characters are presented in Table 1. When different from 0% or 100%, character state frequency data from Wiens & Etheridge (2003) are presented in parentheses for characters 3, 7, 8, 9, 10, 11, 12, and 14.

TABLE 1. Summary of counts and measurements (mm) for species of *Hoplocercinae*. Range (first line) and mean ± standard deviation (second line) are given. Sample size is given in parentheses if different from heading.

Character	*E. cofanorum* *n* = 21	*E. heterolepis* *n* = 41	*E. laticeps* *n* = 32	*E. microlepis* *n* = 28	*E. oshaughnessyi* *n* = 27
Vertebrals from occiput to base of tail	47–78 63.25 ± 8.37	52–98 74.61 ± 10.39	46–89 70.94 ± 10.90	53–76 60.36 ± 5.01	45–61 51.60 ± 4.20
Dorsals in transverse row between dorsolateral crests at midbody	34–55 40.00 ± 5.13	30–46 37.65 ± 4.08	23–48 38.65 ± 5.13	41–54 45.96 ± 3.49	28–40 33.40 ± 3.03
Ventrals in transverse row at midbody	21–33 28.53 ± 3.14	21–35 26.54 ± 2.83	23–35 31.23 ± 2.47	24–34 29.52 ± 2.80	23–37 31.00 ± 3.60
Transverse rows of ventrals between fore and hind limb	31–40 36.13 ± 2.16	32–50 39.53 ± 3.53	35–44 39.72 ± 2.14	33–48 40.24 ± 3.27	34–57 46.35 ± 5.09
Gulars	34–41 36.13 ± 2.00	33–51 43.85 ± 5.20	24–46 39.69 ± 4.12	34–49 37.88 ± 3.44	38–53 44.75 ± 3.89
Infralabials	9–13 10.63 ± 1.15	11–16 12.78 ± 1.13	8–13 10.63 ± 0.94	9–12 10.80 ± 0.87	11–15 13.45 ± 1.19

continued next page

TABLE 1. (continued)

Character	*E. cofanorum* n = 21	*E. heterolepis* n = 41	*E. laticeps* n = 32	*E. microlepis* n = 28	*E. oshaughnessyi* n = 27
Supralabials	10–13 11.31 ± 0.79	11–16 13.73 ± 1.16	9–13 11.38 ± 1.01	9–13 11.56 ± 0.92	12–16 14.20 ± 1.15
Canthals	4–6 4.81 ± 0.54	4–7 5.46 ± 0.60	3–17 4.97 ± 0.86	4–6 4.80 ± 0.50	4–7 5.80 ± 0.70
Superciliaries	12–20 14.69 ± 2.09	14–22 17.32 ± 1.79	15–21 17.22 ± 1.31	14–21 16.64 ± 1.75	13–19 15.60 ± 1.57
Subdigitals Finger IV	15–20 16.94 ± 1.34	14–21 17.46 ± 1.76	17–23 20.11 ± 1.73	17–20 18.28 ± 1.10	17–24 20.80 ± 2.02
Subdigitals Toe IV	21–24 22.31 ± 1.08	20–26 23.56 ± 1.79	23–30 26.53 ± 1.95	22–30 24.36 ± 1.75	23–30 25.75 ± 2.00
Femoral pores in males	1–3 (n = 7) 1.71 ± 0.73	1–4 (n = 20) 2.40 ± 0.74	0–4 (n = 17) 2.06 ± 1.06	1–5 (n = 15) 1.97 ± 1.07	1–2 (n = 15) 1.07 ± 0.25
Head length/head width	1.15–1.34 (n = 17) 1.24 ± 0.05	1.11–1.35 (n = 34) 1.24 ± 0.06	1.13–1.38 (n = 43) 1.23 ± 0.05	1.11–1.34 (n = 28) 1.24 ± 0.05	1.17–1.57 (n = 24) 1.32 ± 0.09
Head width/head height	1.08–1.26 (n = 17) 1.16 ± 0.05	1.05–1.30 (n = 34) 1.15 ± 0.06	1.03–1.31 (n = 43) 1.16 ± 0.06	1.00–1.30 (n = 28) 1.16 ± 0.07	0.95–1.24 (n = 23) 1.08 ± 0.07
Rostral width/rostral height	1.13–3.94 (n = 16) 1.91 ± 0.64	1.06–3.40 (n = 21) 1.91 ± 0.51	1.33–3.02 (n = 41) 2.30 ± 0.35	1.28–3.02 (n = 27) 1.84 ± 0.37	1.44–3.79 (n = 17) 1.96 ± 0.55
Mental width/mental height	1.09–1.85 (n = 17) 1.52 ± 0.20	0.86–1.95 (n = 32) 1.34 ± 0.24	1.05–1.78 (n = 42) 1.39 ± 0.19	1.23–1.97 (n = 27) 1.55 ± 0.21	0.85–1.72 (n = 23) 1.22 ± 0.23
Fore limb length/SVL	0.45–0.54 (n = 17) 0.49 ± 0.03	0.43–0.56 (n = 34) 0.51 ± 0.03	0.49–0.61 (n = 39) 0.54 ± 0.03	0.46–0.55 (n = 28) 0.51 ± 0.02	0.46–0.57 (n = 23) 0.51 ± 0.03
Hind limb length/SVL	0.69–0.86 (n = 17) 0.76 ± 0.05	0.87–1.06 (n = 34) 0.96 ± 0.05	0.79–1.00 (n = 40) 0.87 ± 0.04	0.67–0.92 (n = 28) 0.79 ± 0.05	0.65–0.78 (n = 23) 0.74 ± 0.03
Tail length/total length	0.53–0.57 (n = 14) 0.55 ± 0.01	0.56–0.64 (n = 36) 0.59 ± 0.02	0.59–0.66 (n = 30) 0.63 ± 0.02	0.53–0.60 (n = 23) 0.56 ± 0.02	0.59–0.62 (n = 21) 0.60 ± 0.01
Maximum SVL (mm) males	107 (n = 8)	137 (n = 33)	157[a]	127 (n = 16)	192 (n = 17)
Maximum SVL (mm) females	109 (n = 10)	115 (n = 39)	133 (n = 20)	116 (n = 12)	175 (n = 6)

Continued.

Character	*E. palpebralis* n = 20	*E. praestabilis* n = 50	*E. rubrigularis* n = 16	*E. touzeti* n = 10
Vertebrals from occiput to base of tail	41–62 49.84 ± 4.61	44–66 54.64 ± 5.43	49–58 52.79 ± 2.64	50–71 60.40 ± 7.03
Dorsals in transverse row between dorsolateral crests at midbody	26–45 35.42 ± 4.90	21–39 28.37 ± 3.91	25–32 28.79 ± 2.61	37–43 40.50 ± 1.90
Ventrals in transverse row at midbody	21–31 26.53 ± 2.65	21–39 28.69 ± 3.87	22–31 26.07 ± 2.37	23–32 27.10 ± 3.11

continued next page

TABLE 1. (continued)

Character	*E. palpebralis* *n* = 20	*E. praestabilis* *n* = 50	*E. rubrigularis* *n* = 16	*E. touzeti* *n* = 10
Transverse rows of ventrals between fore and hind limb	30–37 33.40 ± 1.70	31–48 37.77 ± 3.36	31–40 36.57 ± 2.65	37–42 39.57 ± 1.99
Gulars	30–46 36.65 ± 4.28	22–34 27.91 ± 2.99	26–34 29.50 ± 2.65	42–48 44.40 ± 2.22
Infralabials	10–13 11.58 ± 0.84	7–11 8.86 ± 0.88	7–10 8.86 ± 0.66	12–15 13.40 ± 1.17
Supralabials	11–15 12.47 ± 1.02	8–12 10.34 ± 1.08	9–11 10.14 ± 0.53	13–17 15.20 ± 1.32
Canthals	4–7 5.20 ± 0.83	4–6 5.28 ± 0.58	4–6 5.13 ± 0.62	5–6 5.70 ± 0.48
Superciliaries	11–16 13.25 ± 1.65	12–20 15.56 ± 1.87	13–19 15.64 ± 1.39	13–18 14.90 ± 1.37
Subdigitals Finger IV	16–22 19.10 ± 1.55	17–24 19.82 ± 1.32	17–22 19.50 ± 1.34	16–19 18.30 ± 1.06
Subdigitals Toe IV	21–28 23.68 ± 1.95	22–28 25.84 ± 1.54	23–29 25.71 ± 1.94	22–29 26.00 ± 2.49
Femoral pores in males	0–1 (*n* = 11) 0.09 ± 0.29	1–2 (*n* = 25) 1.16 ± 0.37	1–2 (*n* = 9) 1.56 ± 0.51	1–2 (*n* = 3) 1.17 ± 0.41
Head length/head width	1.10–1.49 1.26 ± 0.09	1.20–1.45 (*n* = 40) 1.32 ± 0.07	1.20–1.39 (*n* = 14) 1.28 ± 0.05	1.20–1.46 1.30 ± 0.07
Head width/head height	0.99–1.34 1.11 ± 0.08	0.97–1.25 (*n* = 39) 1.08 ± 0.06	1.01–1.23 (*n* = 14) 1.12 ± 0.06	0.98–1.29 1.10 ± 0.11
Rostral width/rostral height	1.34–2.88 (*n* = 17) 1.94 ± 0.54	1.34–2.79 (*n* = 36) 1.94 ± 0.34	1.42–2.92 (*n* = 14) 1.87 ± 0.39	1.31–2.50 (*n* = 7) 1.71 ± 0.40
Mental width/mental height	1.43–3.48 (*n* = 19) 2.11 ± 0.47	1.20–2.14 (*n* = 38) 1.55 ± 0.23	1.18–1.77 (*n* = 14) 1.44 ± 0.15	0.65–1.29 1.04 ± 0.19
Fore limb length/SVL	0.52–0.64 0.57 ± 0.03	0.47–0.61 (*n* = 41) 0.53 ± 0.03	0.38–0.54 (*n* = 14) 0.49 ± 0.04	0.42–0.62 0.51 ± 0.06
Hind limb length/SVL	0.59–0.87 0.78 ± 0.06	0.72–0.95 (*n* = 41) 0.82 ± 0.05	0.72–0.86 (*n* = 14) 0.79 ± 0.05	0.66–0.80 0.74 ± 0.05
Tail length/total length	0.48–0.59 (*n* = 18) 0.55 ± 0.03	0.59–0.66 (*n* = 32) 0.62 ± 0.02	0.59–0.62 (*n* = 11) 0.60 ± 0.01	0.49–0.60 (*n* = 9) 0.55 ± 0.04
Maximum SVL (mm) males	122 (*n* = 12)	128 (*n* = 25)	130 (*n* = 9)	127 (*n* = 3)
Maximum SVL (mm) females	117 (Meede, 1984)	117 (*n* = 17)	119 (*n* = 5)	118 (*n* = 7)

Continued.

Character	*M. annularis* *n* = 35	*M. groi* *n* = 10	*M. peruvianus* *n* = 14	*H. spinosus* *n* = 3
Vertebrals from occiput to base of tail	47–58 51.94 ± 2.47	127–158 140.63 ± 11.08	74–111 83.71 ± 10.40	74–76 75.00 ± 1.00
Dorsals in transverse row between dorsolateral crests at midbody	27–42 33.11 ± 3.68	38–47 42.40 ± 3.03	34–48 40.00 ± 3.57	25–27 25.67 ± 1.02

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TABLE 1. (continued)

Character	*M. annularis* *n* = 35	*M. groi* *n* = 10	*M. peruvianus* *n* = 14	*H. spinosus* *n* = 3
Ventrals in transverse row at midbody	16–24 21.20 ± 1.64	21–26 24.00 ± 1.89	23–28 25.36 ± 1.82	26–28 27.00 ± 1.00
Transverse rows of ventrals between fore and hind limb	33–40 37.06 ± 1.76	33–47 40.50 ± 4.35	36–41 38.93 ± 1.73	47–53 50.60 ± 1.80
Gulars	29–41 35.46 ± 2.67	36–48 43.60 ± 3.41	35–42 38.00 ± 1.80	45–48 46.00 ± 1.53
Infralabials	9–13 10.40 ± 0.77	7–10 8.60 ± 1.07	8–10 9.50 ± 0.65	10–13[a] —
Supralabials	9–12 10.06 ± 0.80	9–12 10.20 ± 1.03	8–11 9.00 ± 0.68	9–12[a] —
Canthals	5–7 5.97 ± 0.40	5–7 6.00 ± 0.82	5.00–6.00 5.21 ± 0.43	6–8[a] —
Superciliaries	12–15 13.83 ± 0.86	15–18 16.50 ± 1.08	14[b] —	13–17[a] —
Subdigitals Finger IV	14–20 16.57 ± 1.17	15–19 17.40 ± 1.26	16–19 17.79 ± 0.97	11–15[a] 13.40 ± 0.90
Subdigitals Toe IV	21–27 23.54 ± 1.27	20–25 22.20 ± 1.48	23–27 25.21 ± 1.12	14–19[a] 17.00 ± 1.10
Femoral pores in males	2–3 (*n* = 16) 2.09 ± 0.30	3–5 (*n* = 5) 3.56 ± 0.73	3–4 (*n* = 7) 3.71 ± 0.47	3–6[a] —
Head length/head width	1.19–1.60 (*n* = 51) 1.33 ± 0.09	1.28–1.47 1.35 ± 0.07	1.34–1.69 1.44 ± 0.10	1.24–1.28 1.26 ± 0.02
Head width/head height	1.01–1.32 (*n* = 51) 1.19 ± 0.07	1.12–1.27 1.19 ± 0.04	0.99–1.32 1.15 ± 0.09	1.11–1.13 1.12 ± 0.01
Rostral width/rostral height	1.80–3.82 (*n* = 50) 2.49 ± 0.36	2.14–2.61 2.34 ± 0.18	2.47–3.34 (*n* = 12) 2.86 ± 0.83	1.68–1.91 1.77 ± 0.13
Mental width/mental height	1.12–2.42 (*n* = 49) 1.62 ± 0.24	1.30–1.86 1.62 ± 0.18	1.35–2.06 1.79 ± 0.18	1.95–2.03 1.97 ± 0.04
Fore limb length/SVL	0.34–0.48 (*n* = 51) 0.41 ± 0.03	0.36–0.46 0.42 ± 0.03	0.39–0.47 0.43 ± 0.02	0.38–0.43 0.41 ± 0.02
Hind limb length/SVL	0.54–0.70 (*n* = 51) 0.63 ± 0.04	0.55–0.69 0.64 ± 0.05	0.61–0.71 0.65 ± 0.03	0.50–0.55 0.52 ± 0.02
Tail length/total length	0.53–0.60 (*n* = 31) 0.56 ± 0.01	0.57–0.60 (*n* = 4) 0.59 ± 0.01	0.56–0.58 (*n* = 7) 0.57 ± 0.01	0.29–0.32 0.31 ± 0.01
Maximum SVL (mm) males	137 [b]	110 (*n* = 5)	153 mm [b]	105[a]
Maximum SVL (mm) females	118 (*n* = 34)	101 (*n* = 4)	121 mm [b]	98[a]

[a]Avila-Pires (1995); [b]Köhler (2003).

Clade and species accounts

Hoplocercinae Alifanov 1996

Hoplocercidae Frost & Etheridge (1989:36); Frost *et al.* (2001:13); Wiens & Etheridge (2003:375). Type genus: *Hoplocercus* Fitzinger (1843).

Hoplocercinae Alifanov (1996:115); Macey *et al.* (1997:673); Schulte *et al.* (1998:374); Torres-Carvajal & de Queiroz (2009:41).

Definition. The crown clade originating with the most recent common ancestor of *Enyalioides laticeps* (Guichenot 1855), *E. oshaughnessyi* (Boulenger 1881), *Hoplocercus spinosus* Fitzinger 1843, *Morunasaurus annularis* (O'Shaughnessy 1881), and *Morunasaurus groi* Dunn 1933 (Torres-Carvajal & de Queiroz 2009).

Diagnosis. A greatly enlarged nasal scale is a unique morphological synapomorphy supporting monophyly of *Hoplocercinae* within Iguanidae (Etheridge 1969; Etheridge & de Queiroz 1988). In addition, five unambiguous osteological synapomorphies for *Hoplocercinae* were identified in a recent phylogenetic analysis of Squamata (Conrad 2008): (1) enlarged lacrimal foramen, (2) dorsoventrally inflated frontal, (3) splenial extending anteriorly for more than two-thirds the dentary tooth row, (4) one or more pairs of postxiphisternal inscriptional ribs in contact medially, and (5) symphisial part of the pubis more than half again as long as the tubercular part. In that analysis *Hoplocercinae* was represented only by *Morunasaurus annularis*, *Hoplocercus spinosus*, and a composite *Enyalioides* scored from *E. laticeps* and *E. palpebralis*.

Composition. Three mutually exclusive clades within *Hoplocercinae* have traditionally been recognized taxonomically (and ranked as genera): *Enyalioides* (Boulenger 1885), *Hoplocercus* (Fitzinger 1843), and *Morunasaurus* (Dunn 1933) (Torres-Carvajal & de Queiroz 2009).

Remarks. 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 use the name in the family group based on the genus name *Hoplocercus*. However, we attribute the name to Alifanov (1996) as the first author to use the name *Hoplocercinae*. This clade has also been referred to informally as "the morunasaurs" (e.g., Etheridge & de Queiroz 1988), "morunasaurines" (Estes & Price 1973), and "hoplocercines" (Smith *et al.* 1973). Although Frost & Etheridge (1989) did not define it phylogenetically according to the rules in the draft of the International Code of Phylogenetic Nomenclature (ICPN; Cantino & de Queiroz 2007), "*Hoplocercidae*" is the oldest formal name that has been applied to a group approximating the clade here called "*Hoplocercinae*." The latter is the oldest formal name that has been expliclity defined as applying specifically to that clade (Torres-Carvajal & de Queiroz 2009).

Enyalioides Boulenger 1885

Proposed standard English name: woodlizards
Proposed standard Spanish name: lagartijas de palo

Enyalus (part)—Guichenot (1855:20, 21); Bocourt (1874:1).

Enyalius (part)—Cope (1876:169); Boulenger (1881:246); O'Shaughnessy (1881:238, 240); Boulenger (1883:46); Boulenger (1885:120).

Enyalioides Boulenger (1885:112); Burt & Burt (1933:23); Etheridge (1969:256); Peters & Donoso-Barros (1970:114). Type species (not originally designated): *Enyalioides heterolepis* Bocourt 1874 (Burt & Burt 1933).

Definition. The crown clade originating with the most recent common ancestor of *Enyalioides cofanorum* Duellman 1973, *E. heterolepis* (Bocourt 1874), *E. laticeps* (Guichenot 1855), *E. microlepis* (O'Shaughnessy 1881), *E. oshaughnessyi* (Boulenger 1881), *E. palpebralis* (Boulenger 1883), *E. praestabilis* (O'Shaughnessy 1881), and *E. touzeti* Torres-Carvajal *et al.* 2008 (Torres-Carvajal & de Queiroz 2009).

Diagnosis. *Enyalioides* can be distinguished from *Hoplocercus* by having a laterally compressed or rounded (rather than depressed) tail that is longer than the body (i.e., tail length > SVL). *Enyalioides* also differs from *Hoplocercus* and *Morunasaurus* in having pointed, conical scales on dorsal surface of head and gular region; raised scales posterior to the superciliaries; keeled dorsal scales; a continuous vertebral crest formed by large, trihedral or conical scales (except *E. palpebralis*, in which most specimens have a nuchal gap in the vertebral crest); and one or more enlarged pretympanic scales (except *E. heterolepis*). *Enyalioides* can be further distinguished from *Morunasaurus* by having a parietal eye.

Composition. Nine species: *Enyalioides cofanorum* Duellman 1973, *E. heterolepis* (Bocourt 1874), *E. laticeps* (Guichenot 1855), *E. microlepis* (O'Shaughnessy 1881), *E. oshaughnessyi* (Boulenger 1881), *E. palpebralis* (Boulenger 1883), *E. praestabilis* (O'Shaughnessy 1881), *E. rubrigularis* Torres-Carvajal *et al.* 2009, *E. touzeti* Torres-Carvajal *et al.* 2008.

Remarks. Most phylogenetic analyses of *Hoplocercinae* have not found *Enyalioides* to be a monophyletic group (Etheridge & de Queiroz 1988; Wiens & Etheridge 2003 [between-character scaling]; Torres-Carvajal & de Queiroz 2009), though Wiens & Etheridge (2003) found strong to moderate nodal support for monophyly of *Enya-*

lioides under their between-state (bootstrap value = 94) and mixed (bootstrap value = 72) scaling methods. Moreover, in their molecular phylogenetic study of *Hoplocercinae*, Torres-Carvajal & de Queiroz (2009) could not reject monophyly of *Enyalioides* based on several statistical tests. The same authors estimated 27.38 million years (HPD = 22.73–32.31) as the age of *Enyalioides* including *Morunasaurus annularis*.

Enyalioides cofanorum Duellman 1973

Proposed standard English name: Cofan woodlizards
Proposed standard Spanish name: lagartijas de palo cofanes

Enyalioides cofanorum Duellman (1973:230). Holotype: KU 146658, from "Santa Cecilia [0°3'N, 76°59'33"W], 340 m, Provincia Napo [Sucumbíos], Ecuador."

Diagnosis. This species can be distinguished from other species of *Enyalioides* by the combination of the following characters: scattered, projecting, large dorsal scales (inconspicuous or absent in some juvenile and male individuals) between fore and hind limbs; strongly keeled ventrals; large dark patch on posterior aspect of gular region in both sexes; and light stripe extending from postympanic region to scapular region. The only other species of *Enyalioides* with scattered, projecting dorsal scales is *E. heterolepis*, from which *E. cofanorum* differs in lacking projecting scales on the hind limbs. In addition, males and females of *E. cofanorum* (maximum SVL = 107 mm and 109 mm, respectively) are smaller than those of *E. heterolepis* (maximum SVL = 137 mm and 115 mm, respectively), and these two species occur on opposite sides of the Andes. Among other species occuring east of the Andes, specimens of *E. cofanorum* lacking the projecting dorsal scales are similar morphologically to specimens of *E. microlepis* (character states in parentheses) and can be distinguished from them by having conspicuous dorsolateral crests between hind limbs (inconspicuous or absent), and a smaller body size (maximum SVL = 127 mm and 116 mm in males and females, respectively).

Description. (1) dorsal head scales conical or multicarinate, strongly projecting dorsally; (2) posterior superciliaries not enlarged relative to adjacent scales; (3) scales on lateral edge of skull roof just posterior to superciliaries more projecting than adjacent scales; the projection is more pronounced in adults; (4) one or more enlarged pretympanic scales present; (5) gular scales conical or multicarinate, strongly projecting ventrally; (6) dorsal neck scales conical, heterogeneous in size; lateral neck scales granular or conical, homogeneous in size, and similar in size to smallest dorsal neck scales; (7) vertebrals larger than adjacent dorsals, forming distinct raised middorsal crest that extends onto tail as a pair of crests; (8) nuchal region with continuous and paired middorsal crest; (9) dorsals distinctly keeled and heterogeneous in size, although size heterogeneity is less conspicuous in juveniles and adult males; (10) continuous longitudinal row of raised, enlarged scales between dorsals and flank scales present; (11) scales on flanks granular or keeled, heterogeneous in size, and slightly smaller than dorsals; (12) ventrals keeled; (13) fore limb scales keeled dorsally and ventrally; (14) hind limb scales keeled dorsally and ventrally, with thigh scales smaller than other hind limb scales; scattered enlarged scales absent; dorsal scales of pes homogeneous in size; (15) caudals heterogeneous, increasing in size posteriorly on each segment (6–8 scales in lateral view), not modified as conspicuous spines (Fig. 3); (16) tail compressed laterally. Meristic and morphometric characters are presented in Table 1.

Coloration in life (Fig. 4). Dorsal background dark brown, with scattered yellowish-green scales on dorsum and lips; juveniles with yellowish-tan crossbars and black spots along vertebral crest; diagonal cream or yellow bar from ear to shoulder; extensive black mark on gular region in juveniles and adults of both sexes; venter tan in adults and yellowish-brown in juveniles; iris orange-brown (Duellman 1973).

An adult male (QCAZ 8035, Fig. 4) differed from the previous description in having a dark brown reticulate pattern on flanks; a dark brown stripe extending from eye to commisure of mouth; another dark brown stripe extending posteriorly from the dorsal margin of the orbit to a point above the tympanum; and light blue gular region lateral and anterior to the black gular mark.

Natural history. Clutch size in *Enyalioides cofanorum* varies between 2–5 eggs; a female 95.7 mm SVL collected on 31 July 2001 contained five oviductal eggs with a mean length of 25.6 mm, mean width of 10.4 mm, mean volume of 1.5 cm^3, and mean mass of 1.8 g (Cisneros-Heredia 2005). Prey items of *E. cofanorum* include earthworms, sow bugs, spiders, beetles, and orthopterans (Duellman 1978). This species has been found active by day on the forest floor, inactive under logs, or sleeping head-up on sticks or horizontally on branches less than 1.5 m above the ground (Duellman 1978; Cisneros-Heredia 2005).

Distribution. *Enyalioides cofanorum* occurs east of the Andes in Colombia, Ecuador, and Peru, at elevations between 100–1230 m (Fig. 5). This species is known to occur in sympatry with *E. laticeps* in northeastern Ecuador. Moreover, *E. laticeps* occurs at localities near those of *E. cofanorum* in Colombia and Peru, suggesting that both species are sympatric in those countries as well.

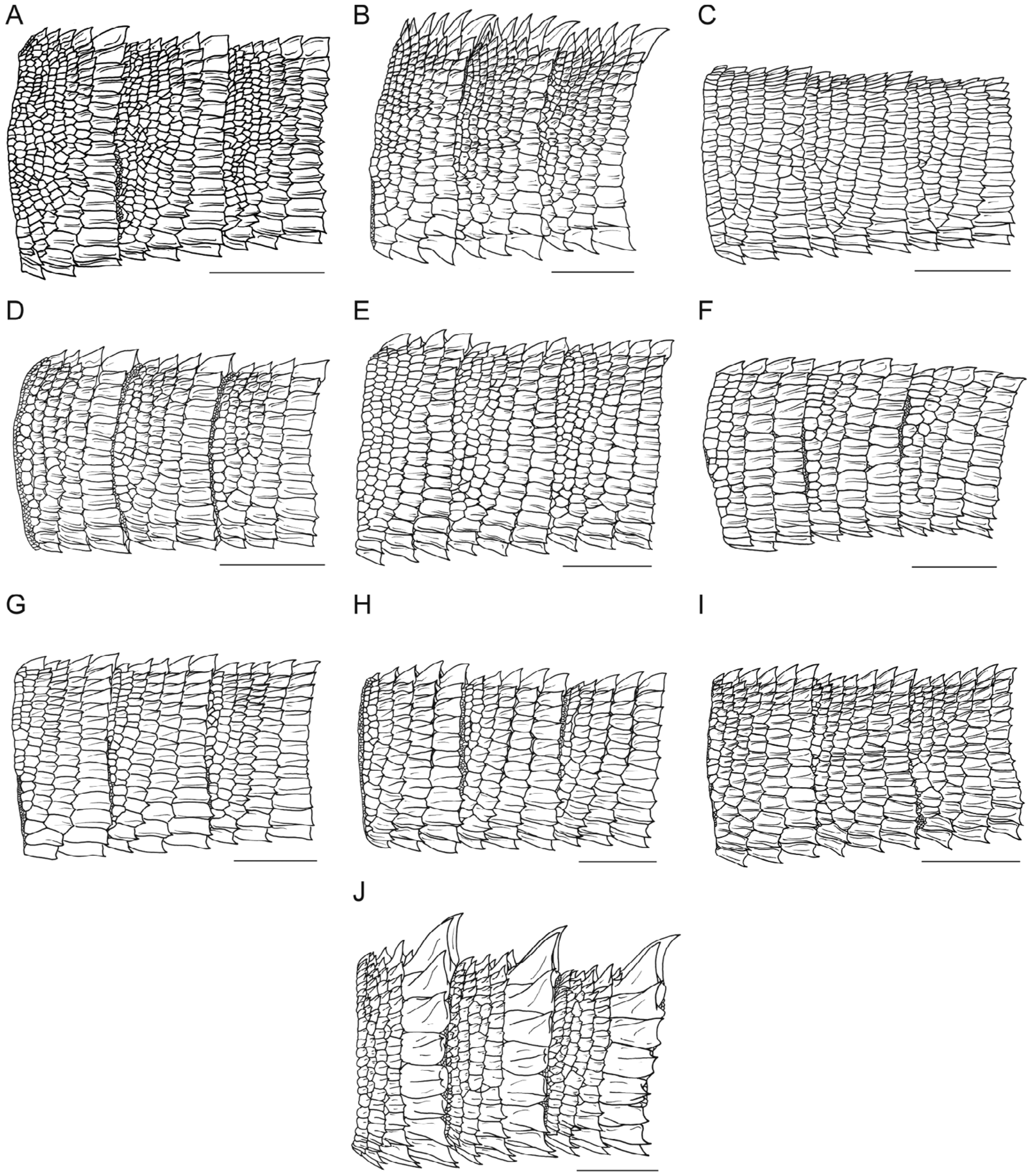

FIGURE 3. Caudal segments from the anterior third of the tail of ten species of *Hoplocercinae* in lateral view. (A) *Enyalioides cofanorum*, (B) *E. heterolepis*, (C) *E. laticeps*, (D) *E. microlepis*, (E) *E. oshaughnessyi*, (F) *E. palpebralis*, (G) *E. praestabilis*, (H) *E. rubrigularis*, (I) *E. touzeti*, and (J) *Morunasaurus annularis*. Scale bars = 5 mm. Illustration by D. Paucar.

Enyalioides heterolepis (Bocourt 1874)

Proposed standard English name: spiny woodlizards
Proposed standard Spanish name: lagartijas de palo espinosas

Enyalus heterolepis Bocourt (1874:1). Holotype: MHNP 4067, from "Veragua [Panama; (Guibé 1954)]."
Enyalius heterolepis Günther (1885-1902:56).
Enyalioides heterolepis Boulenger (1885:114); Burt & Burt (1930:9; 1931:265; 1933:23); Peters & Donoso-Barros (1970:114).
Enyalioides insulae Barbour in Bangs *et al.* (1905:100). Syntypes: MCZ 6983, 167581, from "Gorgona Island [Departamento Cauca], Colombia," synonymy *fide* Parker (1926:550).
Enyalioides Mocquardi Despax (1911:10). Syntypes: MHNP 06-226–228, from "l'Équateur," synonymy *fide* Burt and Burt (1931:265).

Diagnosis. This species can be distinguished from other species of *Enyalioides* by having scattered, projecting, tetrahedral large scales on dorsum, flanks, and hind limbs, which are conspicuous in juveniles and adults of both sexes. The only other species of *Enyalioides* with scattered, projecting dorsal scales is *E. cofanorum*, which differs from *E. heterolepis* in lacking projecting scales on the hind limbs.

Description. (1) dorsal head scales conical or multicarinate, strongly projecting dorsally; (2) posterior superciliaries not enlarged relative to adjacent scales; (3) scales on lateral edge of skull roof just posterior to superciliaries sometimes (55.6%) slightly more projecting than adjacent scales; (4) all pretympanic scales similar in size; (5) gular scales conical or multicarinate, strongly projecting ventrally; (6) dorsal neck scales projecting, heterogeneous in size, largest scales tetrahedral; lateral neck scales similar in size to smallest dorsal neck scales; (7) vertebrals larger than adjacent dorsals, forming distinct raised middorsal crest that extends onto tail as a pair of crests; (8) nuchal region with continuous and sometimes (16.7%) paired middorsal crest; (9) dorsals distinctly keeled and heterogeneous in size, with largest scales similar in size to vertebrals; (10) continuous longitudinal row of raised, enlarged scales between dorsals and flank scales present; (11) scales on flanks keeled and usually (83.3%) heterogeneous in size, with largest scales similar in size and shape to vertebrals; (12) ventrals usually (66.7%) smooth; (13) fore limb scales keeled dorsally, smooth or slightly keeled ventrally; (14) hind limb scales keeled dorsally, smooth or slightly keeled ventrally; scattered enlarged scales present dorsally; dorsal scales of pes heterogeneous in size; (15) caudals heterogeneous, increasing in size posteriorly on each segment (6–8 scales in lateral view), not modified as conspicuous spines (Fig. 3); (16) tail compressed laterally. Meristic and morphometric characters are presented in Table 1.

Coloration in life (Fig. 4). Juveniles and adults of both sexes of *Enyalioides heterolepis* have a distinct black or dark brown triangular mark or anterodorsally oriented stripe between commisure of mouth and ventral margin of eye.

Adult females (KU 76052, 113494, 169853): dorsal background reddish brown or olive green, sometimes with olive grey or green mottling laterally, or reddish-brown suffusion; cream spot ventral or posterior to ear sometimes present; venter creamy tan with reddish-brown suffusion laterally, or reddish brown with cream flecks; throat grey with brown streaks or black spot; iris reddish brown with yellow ring around pupil (C.W. Myers [21 July 1963] and W.E. Duellman [10 June 1975] field notes).

Adult males (KU 76048, 76051, 113490, QCAZ 8654): dorsal background brown, reddish brown, or yellowish brown, with darker lines forming a reticulate pattern; scattered pale blue spots on body sometimes present; head yellowish green, reddish brown, or yellowish brown; labials golden yellow or greenish yellow, sometimes followed by an orange streak posterior to mouth commisure; orange or white spot behind ear sometimes present; flanks similar to dorsum, or with greenish background; chin yellow or cream; light or dark brown vertical stripe from fore limb insertion to scapular region (sometimes continuous middorsally) sometimes present; green or blue flecks on dorsal aspect of limbs sometimes present; gular region yellow (sometimes streaked with brown), with black medial mark posteriorly; venter dull yellow or brown laterally and blackish medially, or creamy tan with pinkish brown mottling; ventral surface of limbs greenish; tail similar to dorsum, or bluish grey dorsally and pale brown ventrally, sometimes with blue flecks; iris brown with yellow ring around pupil, sometimes with grayish-white area dorsally; tongue flesh white with dark grey tip (C.W. Myers [21 July 1963, 17–19 April 1967] and color photographs).

Juveniles (KU 76053, 96688, 146657, 164166): dorsal background brown or reddish brown, with brown or reddish brown transverse bars; light brown V-shaped mark behind head sometimes present; flanks olive tan or light green, with brown spots; yellow or yellowish-green vertical bar from fore limb insertion to vertebral crest; head olive brown; cream spot behind ear sometimes present; gular region and belly cream, pale green, or dull yellow, with brown or red streaks and light brown or reddish flecks, respectively; black gular patch; iris brown or reddish brown with yellow ring around pupil (C.W. Myers [10 September 1964] and W.E. Duellman [10 April 1972, 28 March 1975] field notes and photographs).

Natural history. Most adult specimens have been found sleeping on tree trunks at night 20–170 cm above ground, heads-up if in vertical position, sometimes next to streams. Some juveniles and adults were collected on forest floor or under logs by day. A female (SVL = 89 mm; QCAZ 2025) collected in March 1990 in Provincia Pichincha, Ecuador, had two enlarged vitellogenic follicles on each side (4.43–8.75 mm X 5.23–9.25 mm). This species can be found in primary forest, secondary forest, or plantations.

Distribution. *Enyalioides heterolepis* occurs at elevations between 0–1000 m in Panama, the western slopes of the Andes and adjacent Pacific lowlands of Colombia and Ecuador, and Gorgona island, Colombia (Fig. 6). This species is known to occur in sympatry with *E. oshaughnessyi* in northwestern Ecuador and *Morunasaurus groi* in northwestern Colombia. *E. heterolepis* also occurs close to *E. oshaughnessyi* in southwestern Colombia and *Morunasaurus groi* in Panama.

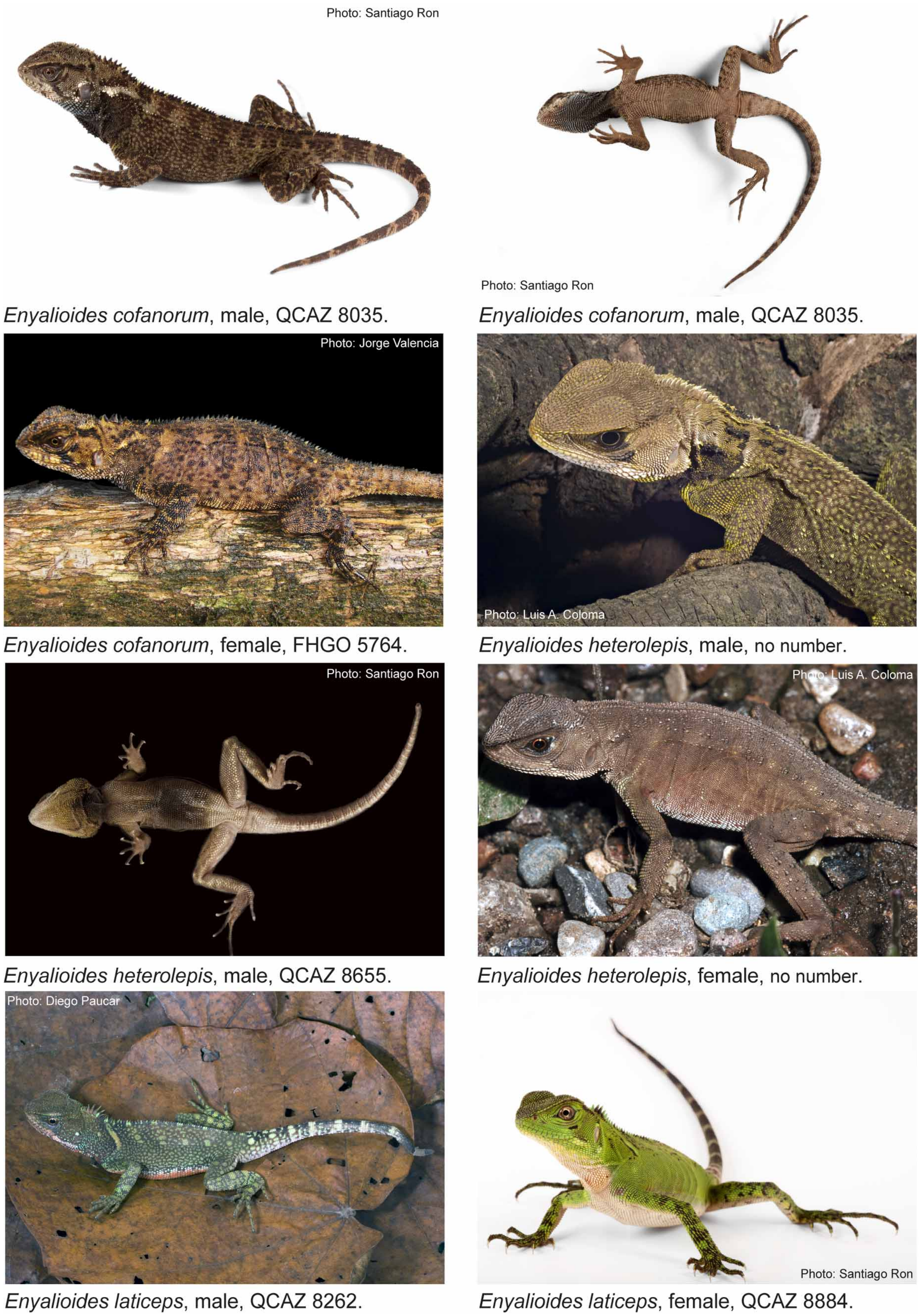

FIGURE 4. Photographs of live lizards representing twelve species of *Hoplocercinae.*

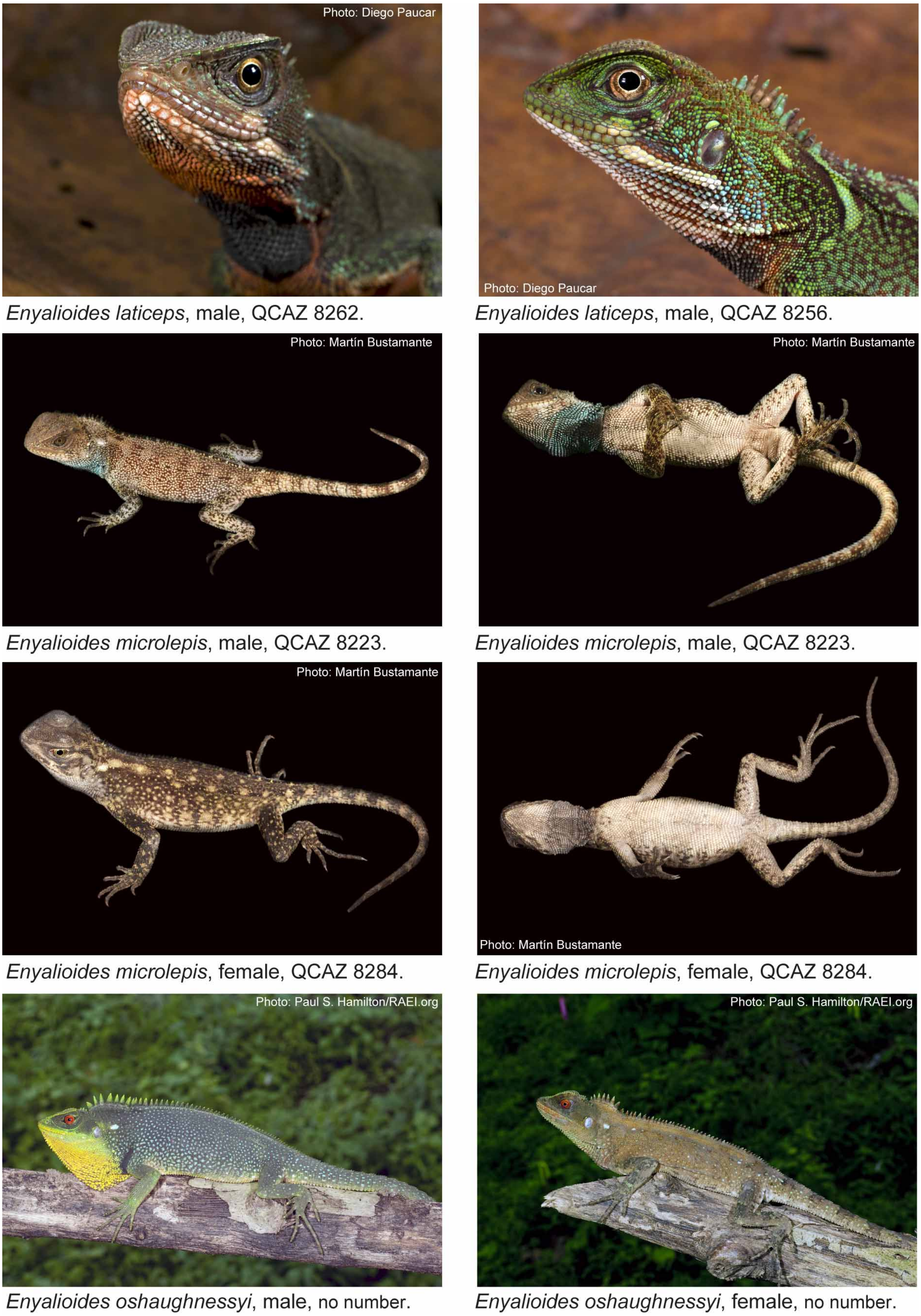

FIGURE 4. Photographs of live lizards representing twelve species of *Hoplocercinae.*

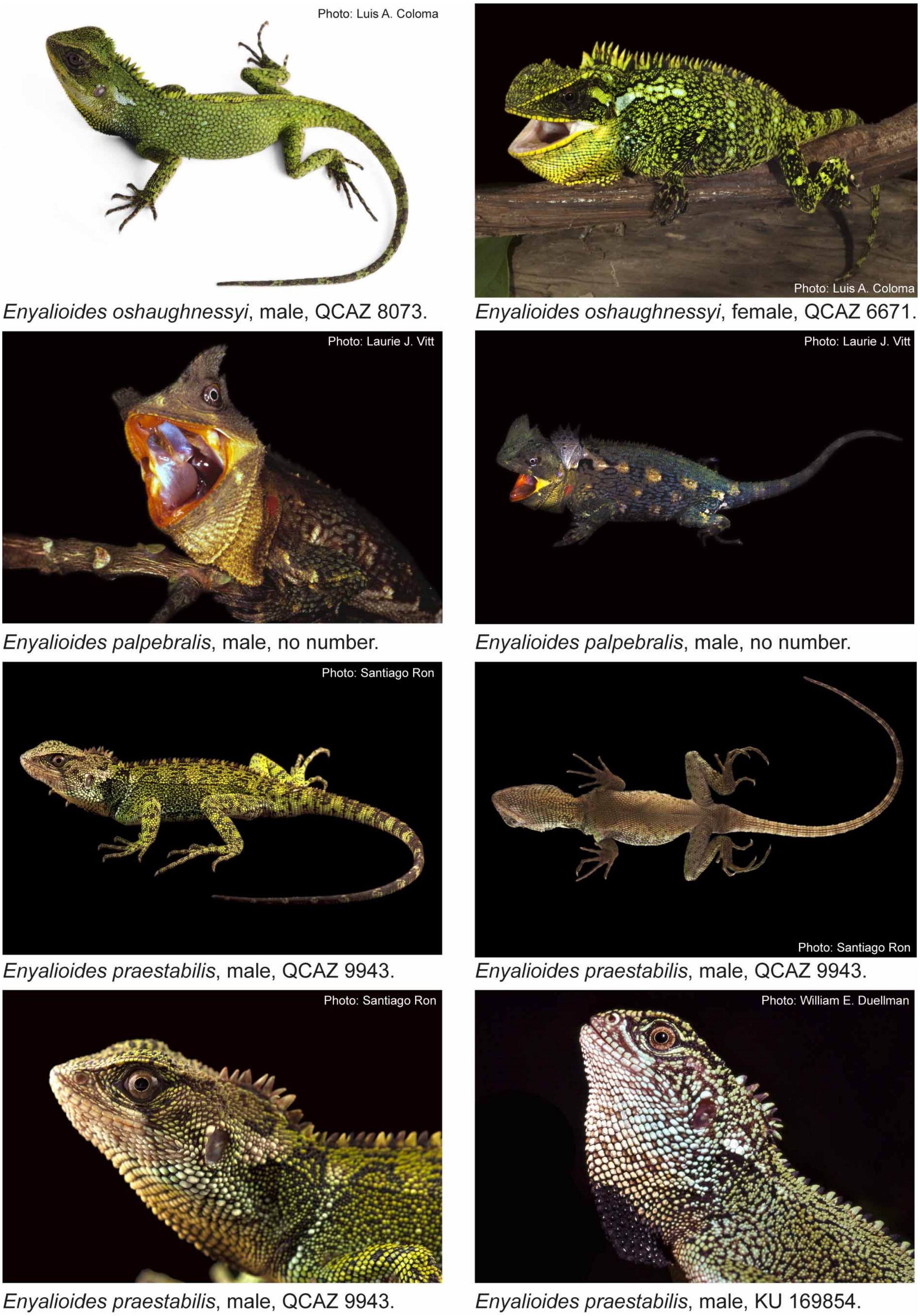

FIGURE 4. Photographs of live lizards representing twelve species of *Hoplocercinae*.

Enyalioides rubrigularis, male, QCAZ 8460.

Enyalioides rubrigularis, female, QCAZ 8482.

Enyalioides touzeti, male, EPN 10306.

Enyalioides touzeti, female, QCAZ 8642.

Morunasaurus annularis, male, QCAZ 7819.

Morunasaurus annularis, male, QCAZ 7820.

Morunasaurus annularis, female, FHGO 5364.

Morunasaurus peruvianus, male, USNM 316725.

FIGURE 4. Photographs of live lizards representing twelve species of *Hoplocercinae.*

FIGURE 4. Photographs of live lizards representing twelve species of *Hoplocercinae*.

Remarks. Torres-Carvajal & de Queiroz (2009) found strong support (bootstrap value = 100) for the monophyly of *E. heterolepis* in a maximum likelihood analysis of mitochondrial DNA sequence data that included two specimens from Panama and one specimen from Ecuador. Sequences of the two individuals from Panama were more similar to each other (maximum-likelihood corrected distance = 0.025) than they were to the individual from Ecuador (0.063 and 0.068).

Enyalioides laticeps (Guichenot 1855)

Proposed standard English name: broad-headed woodlizards
Proposed standard Spanish name: lagartijas de palo de cabezonas

Enyalus laticeps Guichenot (1855:20). Holotype: MHNP 6821, from "Fonteboa, upper Amazon, Brazil"; Duméril (1856:529).
Enyalus planiceps Guichenot (1855:21). Syntypes: MHNP 6822, 6822a, from "Fonteboa, upper Amazon, Brazil," synonymy *fide* Boulenger (1885:113).

Enyalius coerulescens Cope (1876:169). Holotype: ANSP 11382, no specific type locality given, restricted to "the Amazon from Santarem to Peru" (Gans & Vanzolini 1953), synonymy *fide* Peters & Donoso-Barros (1970:115) upon suggestion of Gans & Vanzolini (1953:127).

Enyalius caerulescens Boulenger (1885:120); Burt and Burt (1933:25). Misspelling of *Enyalius coerulescens* (Cope 1876). Synonymy *fide* Peters & Donoso-Barros (1970:115) upon suggestion of Gans & Vanzolini (1953:127).

Enyalioides laticeps Boulenger (1885:113); Burt & Burt (1930:9; 1931:266; 1933:24); Peters & Donoso-Barros (1970:114).

Enyalioides festae Peracca (1897:3). Syntypes: MZUT 2169, MSNG 36123, from "valley of Rio Santiago, Ecuador," synonymy *fide* Burt & Burt (1931:228).

Enyalioides laticeps laticeps Burt & Burt (1930:9; 1933:24); Peters & Donoso-Barros (1970:115). Subspecies rejected by Avila-Pires (1995:30).

Enyalioides laticeps festae Burt & Burt (1931:228; 1933:24); Peters & Donoso-Barros (1970:115). Subspecies rejected by Avila-Pires (1995:30).

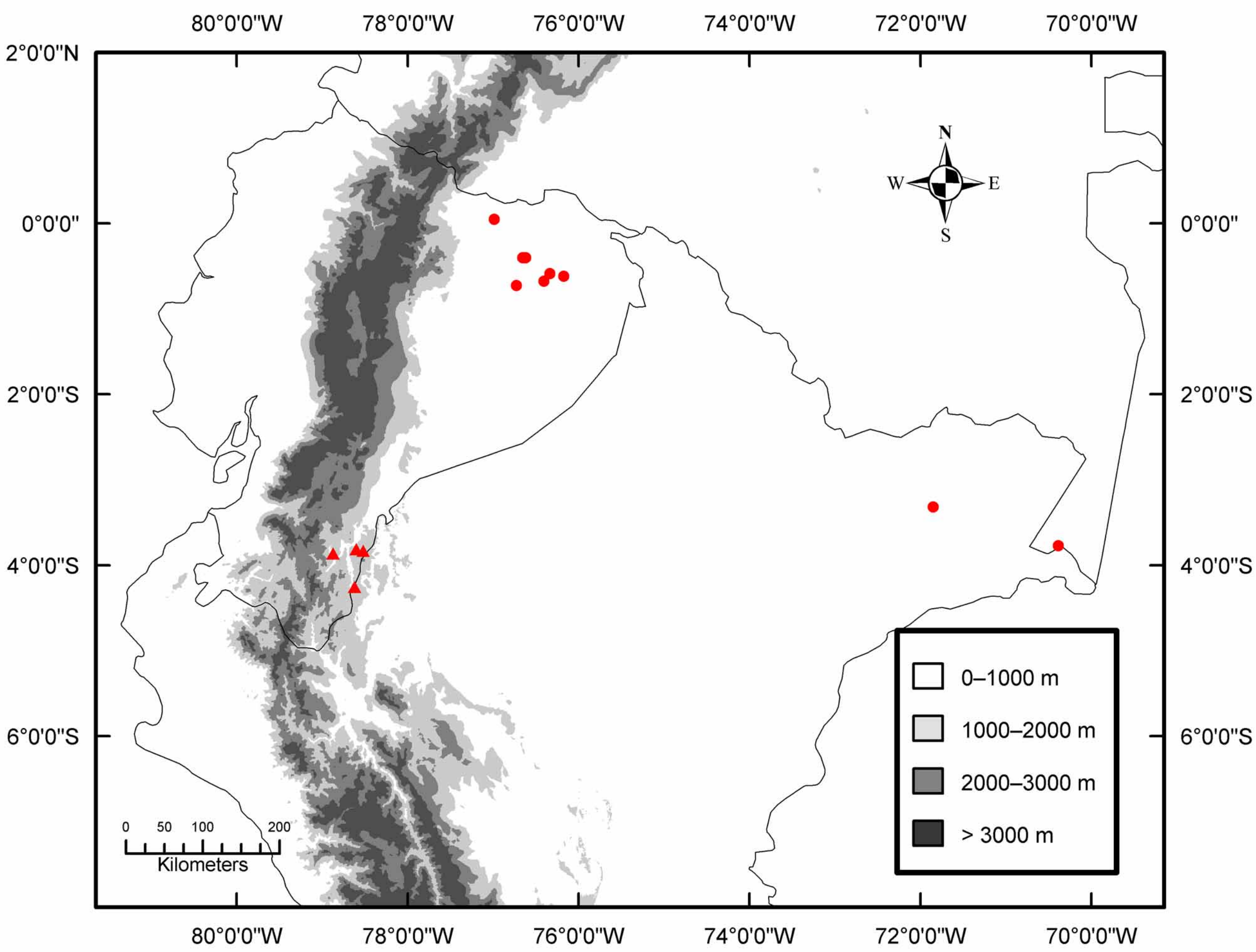

FIGURE 5. Distribution of *Enyalioides cofanorum* (dots) and *E. rubrigularis* (triangles).

Diagnosis. This species can be distinguished from other species of *Enyalioides* by having caudal scales that are relatively homogeneous in size on each caudal segment; in all other species of *Enyalioides*, the dorsal and lateral caudals increase in size posteriorly on each caudal segment, and the largest (posteriormost) caudals are mucronate or have some kind of projection (Fig. 3). In addition, most male specimens of *E. laticeps* have a longitudinal white, cream, or orange stripe 2–3 scales wide that extends from the commisure of mouth to a point below the tympanum (Fig. 4).

Description. (1) dorsal head scales conical or multicarinate, strongly projecting dorsally; (2) posterior superciliaries not enlarged relative to adjacent scales; (3) scales on lateral edge of skull roof just posterior to superciliaries sometimes (50%) slightly more projecting than adjacent scales; the projection is more pronounced in adults; (4) one or two enlarged pretympanic scales present; (5) gular scales conical or multicarinate, strongly projecting ventrally; (6) dorsal and lateral neck scales similar in size, mostly granular or conical; (7) vertebrals larger than adjacent dorsals, forming distinct raised middorsal crest that extends only onto anterior end of tail as a pair of indistinct crests; (8) nuchal region with continuous, single middorsal crest; (9) dorsals distinctly keeled and homogeneous in size; (10) longitudinal row of raised, enlarged scales between dorsals and flank scales rarely (16.7%) present; when present this row is continuous; (11) scales on flanks granular, homogeneous in size, and slightly smaller than dorsals; (12) ventrals usually (71.4%) keeled; (13) fore limb scales keeled dorsally and ventrally; (14) hind limb scales keeled dorsally and ventrally; scattered enlarged scales absent; dorsal scales of pes homogeneous in size; (15) caudals homogeneous (i.e., caudal segments inconspicuous), not increasing considerably in size posteriorly on each segment (6–8 scales in lateral view), not modified as conspicuous spines (Fig. 3); (16) tail nearly circular in cross section. Meristic and morphometric characters are presented in Table 1.

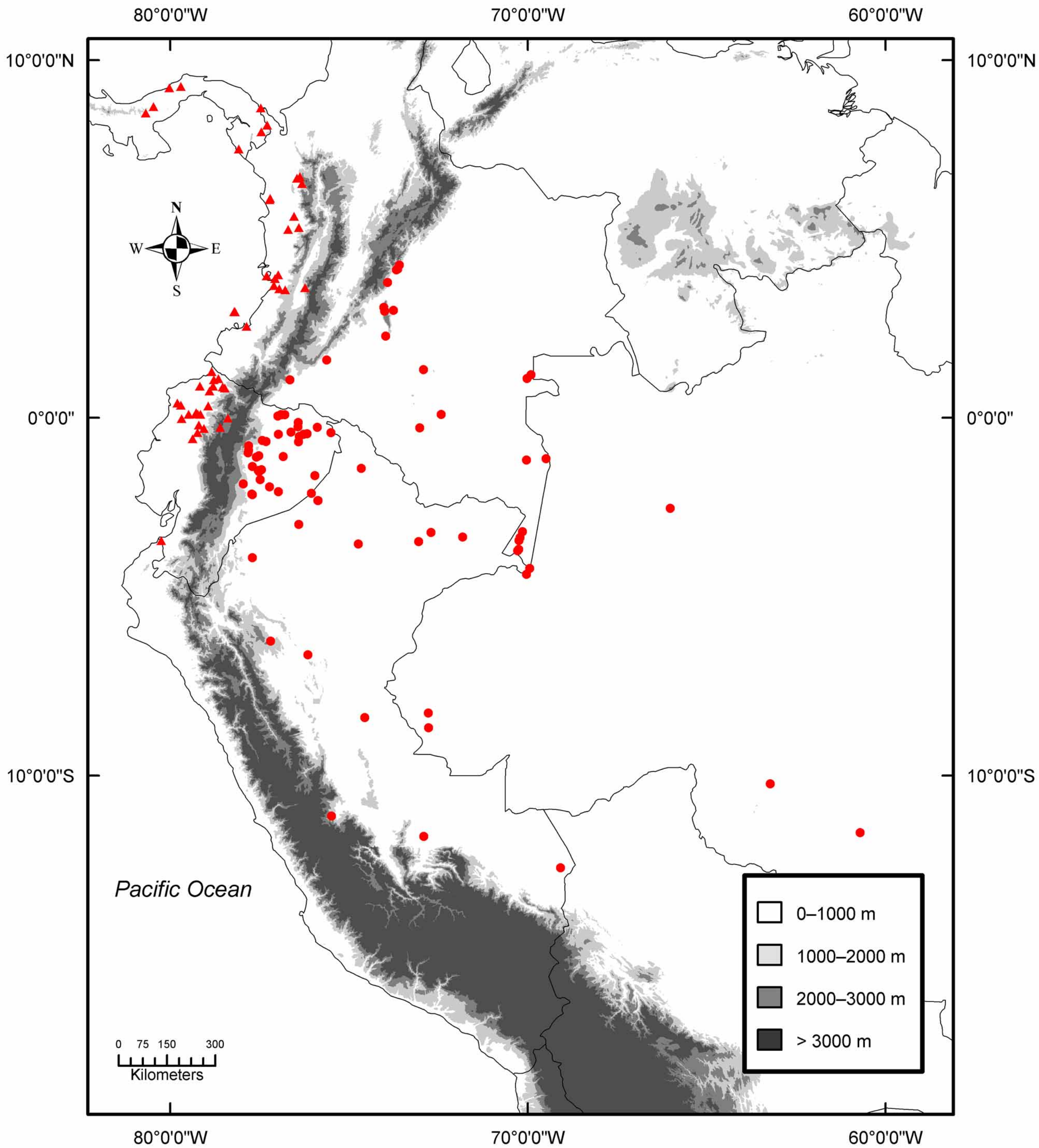

FIGURE 6. Distribution of *Enyalioides heterolepis* (triangles) and *E. laticeps* (dots).

Coloration in life (Fig. 4). Dorsum and flanks green (various tones) or brown, usually with irregular, scattered light spots, or a reticulate brown or reddish-brown pattern; some specimens with a diagonal light bar on the scapular region; longitudinal white, cream, or orange stripe 2–3 scales wide extending from the commisure of mouth to a level below the tympanum in some male specimens; lips and chin pale green is some specimens; gular region in males with longitudinal brown, reddish-brown, bluish, or orange streaks, and a large brown or black medial blotch at the level of the gular fold; gular region in females usually cream or reddish cream without streaks or blotches; venter orange in adult males and pinkish tan or cream in females, with a longitudinal series of dark brown or black short bars or streaks laterally in some specimens; iris brown with yellow or greenish yellow ring around pupil (Duellman 1978, 2005; Avila-Pires 1995; Vitt & de la Torre 1996). Juveniles pale green or tan with brown diagonal marks on body, white throat, and creamy-tan venter (Duellman 1978). Similar to other species of *Enyalioides*, *E. laticeps* displays metachromatism consisting of replacing green with brown tones when disturbed.

Natural history. This species is more abundant in primary than secondary forests; during the day it has been observed mostly on trunks of small trees with diameters less than 15 cm, whereas at night it usually sleeps horizontally on branches or palm fronds 1.5 m or more above ground (Duellman 1978). This species uses crypsis as the main predator avoidance mechanism, although some individuals run away to hide under logs or in holes in the ground (Dixon & Soini 1986; Vitt & de la Torre 1996). Prey items of *Enyalioides laticeps* consist mostly (70.4%) of spiders, caterpillars, and beetle larvae (Duellman 1978); other common prey items include grasshoppers, crickets, and earthworms (Vitt & de la Torre 1996). Clutch size varies between 5–7 eggs 15.0–16.6 mm long (Duellman 1978; Vitt & de la Torre 1996); females with 10–11 oviductal eggs were found between April-August (Dixon & Soini 1986).

Distribution. *Enyalioides laticeps* occurs throughout the western Amazon basin at elevations between 80–1600 m in Colombia, Ecuador, Peru, and Brazil (Fig. 6); it might also occur in Bolivia (Langstroth 2005). This species is known to occur in sympatry with *E. cofanorum*, *E. microlepis*, *E. praestabilis* in Ecuador and *E. palpebralis* in southern Peru. Given its wide distribution, *E. laticeps* is most likely sympatric with these species throughout most of their distributions. Similarly, *E. laticeps* might be sympatric with *Morunasaurus annularis* and *M. peruvianus*.

Remarks. Torres-Carvajal & de Queiroz (2009) found strong support (bootstrap value = 100) for the monophyly of *Enyalioides laticeps* in a maximum likelihood phylogenetic analysis of mitochondrial DNA sequence data that included two specimens from Ecuador, one from Peru, and another one from Brazil. Sequences of the individuals from Peru and Brazil were more similar to each other (maximum-likelihood corrected distance = 0.049) than they were to either of the two samples from Ecuador (0.069–0.081), which, likewise, were more similar to each other (0.017).

Enyalioides microlepis **(O'Shaughnessy 1881)**

Proposed standard English name: small-scaled woodlizards
Proposed standard Spanish name: lagartijas de palo microescamadas

Enyalius microlepis O'Shaughnessy (1881:238). Syntypes: BMNH 60.6.16.8 (RR 1946.8.5.76), 58.7.25.17 (RR 1946.8.5.57), 80.12.8.36-36a (RR 1946.8.9.5-6) from "Sarayacu, [03º00'N, 78º09'W, 400 m, Provincia Pastaza], Ecuador."

Enyalioides microlepis Boulenger (1885:115); Burt & Burt (1930:10; 1931:267; 1933:24); Peters & Donoso-Barros (1970:115).

Diagnosis. This species can be distinguished from other species of *Enyalioides* by the combination of the following characters: enlarged projecting scales on dorsum (except vertebrals), flanks, or limbs absent; dorsal scales in a transverse row between dorsolateral crests at midbody more than 40; and ventrals strongly keeled. Among other species of *Enyalioides* occuring east of the Andes, *E. microlepis* is similar morphologically to specimens of *E. cofanorum* that lack the projecting dorsal scales characteristic of that species. *E. microlepis* differs from those specimens of *E. cofanorum* (character states in parentheses) in lacking conspicuous dorsolateral crests between hind limbs (always conspicuous), and in having a maximum SVL of 127 mm in males (107 mm) and 116 mm in females (109 mm).

Description. (1) dorsal head scales conical or multicarinate, strongly projecting dorsally; (2) posterior superciliaries not enlarged relative to adjacent scales; (3) scales on lateral edge of skull roof just posterior to superciliaries more projecting than adjacent scales; the projection is more pronounced in adults; (4) one or two enlarged pretympanic scales present; (5) gular scales conical or multicarinate, strongly projecting ventrally; (6) dorsal and lateral neck scales similar in size, mostly granular or conical; (7) vertebrals larger than adjacent dorsals, forming distinct raised middorsal crest that extends onto tail as a pair of crests; (8) nuchal region with continuous and usually (92.9%) paired middorsal crest; (9) dorsals distinctly keeled and homogeneous in size; (10) continuous longitudinal row of raised, enlarged scales between dorsals and flank scales present; (11) scales on flanks keeled, usually (78.6%) homogeneous in size; (12) ventrals keeled; (13) fore limb scales keeled dorsally and ventrally; (14) hind limb scales keeled dorsally and ventrally; scattered enlarged scales absent; dorsal scales of pes homogeneous in size; (15) caudals heterogeneous, increasing in size posteriorly on each segment (6–8 scales in lateral view), not modified as conspicuous spines (Fig. 3); (16) tail compressed laterally. Meristic and morphometric characters are presented in Table 1.

Coloration in life (Fig. 4). Adult males (QCAZ 8223): dorsal surface and sides of head yellowish brown with scattered dark brown irregular marks; labials yellowish cream with brown margins; dorsum and flanks creamish brown with a dense dark brown reticulation; sides of neck same as flanks, with a bright white blotch posterodorsal to tympanum; dorsal aspect of limbs cream with dark greenish brown flecks; chin and lateral parts of gular region with cream and light brown scales; narrow black gular patch extending anteriorly from gular fold to level of temporal region; light blue patch surrounding the black gular patch and extending to level of eyes anteriorly and to ventral part neck sides laterally; ventral surface of body and limbs cream with a few greenish brown flecks on limbs; tail cream with scattered brown marks ventrally, and with faint alternate brownish cream and dark brown transverse bands laterally and dorsally; iris yellowish brown with golden ring around pupil (color photograph).

Adult females (QCAZ 8284): dorsal surface and sides of head dark brown; most loreals and suboculars brownish cream; dorsum and flanks yellowish brown with a dense dark brown reticulation forming a longitudinal series of eight yellowish brown blotches between dorsum and flanks; dark brown reticulation breaks apart on ventral aspect of flanks; sides of neck with a bright white blotch posterodorsal to tympanum; dorsal aspect of limbs dark brown with yellowish brown spots; posterior aspect of gular region light gray; chin, anterior and lateral aspects of gular region, and ventral surface of body, limbs, and tail cream with a few scattered brown flecks; tail with alternate narrow yelowish brown and wide dark brown transverse bands laterally and dorsally; iris golden brown with golden ring around pupil (color photograph).

Natural history. This species has been found under logs, or sleeping head-up on sticks or horizontally on branches less than 1 m above the ground (F. Ayala field notes, 2008).

Distribution. *Enyalioides microlepis* occurs east of the Andes in southern Colombia, Ecuador, and northern Peru (Fig. 7) at elevations between 100–1000 m. This species is known to occur in sympatry with *E. laticeps* and *E. praestabilis* in eastern Ecuador. However, this species also might be sympatric with both *E. laticeps* and *E. praestabilis* east of the Andes in southern Colombia and northern Peru.

Remarks. As noted by Wiens & Etheridge (2003), several authors have confused *Enyalioides microlepis* with *E. oshaughnessyi* (Peters & Donoso-Barros 1970; Almendáriz 1992; Torres-Carvajal 2001). Besides the differences noted in the diagnoses provided in this manuscript, the latter species is restricted to the western slopes of the Andes and adjacent Pacific lowlands in Colombia and Ecuador, whereas *E. microlepis* occurs in the upper Amazon basin in Colombia, Ecuador, and Peru.

Enyalioides oshaughnessyi (Boulenger 1881)

Proposed standard English name: red-eyed woodlizards
Proposed standard Spanish name: lagartijas de palo ojirrojas

Enyalius oshaughnessyi Boulenger (1881:246). Holotype: MRHN 2009, from "Ecuador."
Enyalioides oshaughnessyi Boulenger (1885:115); Burt & Burt (1931:267; 1933:24); Peters & Donoso-Barros (1970:115).

Diagnosis. *Enyalioides oshaughnessyi* differs from other species of *Enyalioides* in having dorsal scales that are both homogeneous in size, and smooth or slightly keeled. Moreover, it is the only species of *Enyalioides* with a bright red iris in both sexes (but see Remarks) and a dark gular patch restricted to the inner aspect of the gular fold in males. Other species of *Enyalioides* have a copper, brown (various tones), or bronze iris, and a dark patch (absent in *E. palpebralis* and some specimens of *E. praestabilis*) on the outer aspect of the gular fold covering the throat.

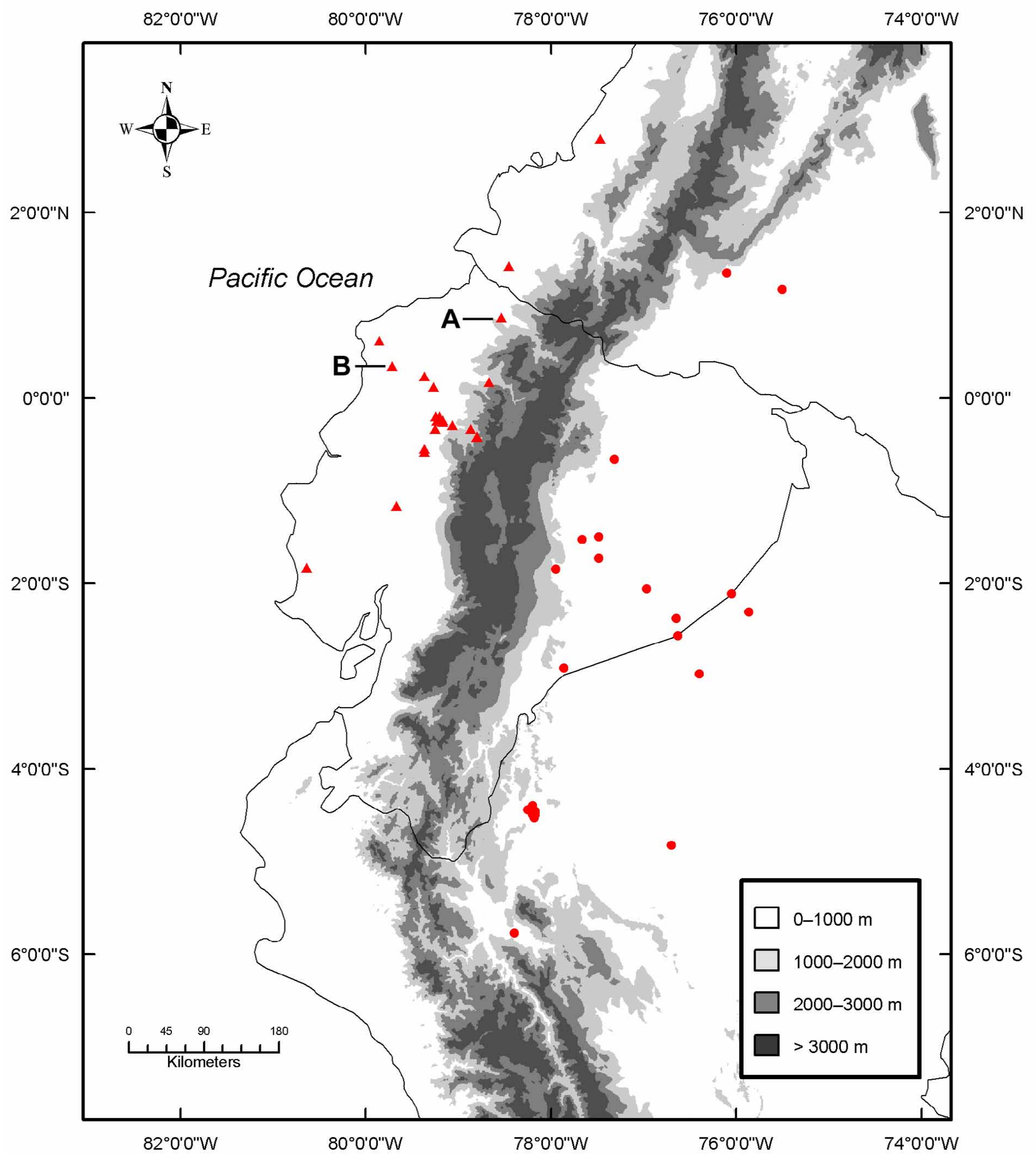

FIGURE 7. Distribution of *Enyalioides microlepis* (dots) and *E. oshaughnessyi* (triangles). A, Alto Tambo; B, Bilsa Ecological Reserve (see Remarks under *E. oshaughnessyi*).

Description. (1) dorsal head scales conical or multicarinate, strongly projecting dorsally; (2) posterior superciliaries not enlarged relative to adjacent scales; (3) scales on lateral edge of skull roof just posterior to superciliaries strongly projecting; the projection is more pronounced in adults; (4) one or two enlarged pretympanic scales present; (5) gular scales conical or multicarinate, strongly projecting ventrally; (6) dorsal neck scales homogeneous in size, mostly conical or cycloid and slightly imbricate; lateral neck scales similar in size to dorsal neck scales except for some enlarged conical scales, which sometimes form an oblique row extending from tympanum to scapular region; (7) vertebrals larger than adjacent dorsals, forming distinct raised middorsal crest that extends onto tail as a pair of crests; (8) nuchal region with continuous and usually (92.3%) single middorsal crest; (9) dorsals flat, usually (76.9%) smooth, and homogeneous in size; (10) longitudinal row of raised, enlarged scales between dorsals and flank scales usually (84.6%) present; when present this row is continuous; (11) scales on flanks heterogeneous in size, with most scales similar in size and shape to dorsals and a few enlarged, circular, and keeled scales; (12)

ventrals keeled; (13) fore limb scales keeled dorsally and ventrally; (14) hind limb scales keeled dorsally and ventrally; scattered enlarged scales absent; dorsal scales of pes homogeneous in size; (15) caudals heterogeneous, increasing in size posteriorly on each segment (6–8 scales in lateral view), not modified as conspicuous spines (Fig. 3); (16) tail compressed laterally. Meristic and morphometric characters are presented in Table 1.

Coloration in life (Fig. 4). Adult male KU 109630: dorsal background olive green with light green and turquoise blue spots on flanks, tail, and dorsal surfaces of legs; labials and chin greenish yellow; gular region light blue with black patch under gular fold; chest greenish tan; venter and posterior surfaces of thighs tan; ventral surface of tail olive tan; iris rusty orange; throat and tongue flesh colored (W.E. Duellman, 30 March 1963, field notes). All adult males seen by the authors alive or in photographs have a red iris (Fig. 4; but see Remarks).

Adult female (based on photograph by P.S. Hamilton, Fig. 4): dorsal background light brown with light green and light blue spots on flanks, tail, and hind limbs; labials light green, greenish brown, or reddish brown; distal margin of superciliaries, canthals, some suboculars, and some pretympanics bright green, light blue post-tympanic blotch; light green scales on chin and gular region; iris red.

Natural history. Some specimens of *Enyalioides oshaughnessyi* have been found sleeping at night on branches less than 1 m above the ground (F. Ayala field notes, January-February 2006).

Distribution. *Enyalioides oshaughnessyi* occurs in the western slopes of the Andes and adjacent Pacific lowlands of northern Ecuador and southern Colombia at elevations between 50–1600 m (Fig. 7). This species is known to occur in sympatry with *E. heterolepis* in northwestern Ecuador and it is very likely that both species also are sympatric in southwestern Colombia.

Remarks. Several authors have confused *Enyalioides oshaughnessyi* with *E. microlepis* (Burt & Burt 1931; Peters & Donoso-Barros 1970; Almendáriz 1992; Torres-Carvajal 2001). See Remarks under *E. microlepis* above.

Torres-Carvajal & de Queiroz (2009) found *Enyalioides oshaughnessyi* to be paraphyletic relative to *E. touzeti* based on three samples of *E. oshaughnessyi* and one sample of *E. touzeti* (numbers are from Torres-Carvajal & de Queiroz 2009, and correspond to localities): (*E. oshaughnessyi*13, (*E. touzeti*14, (*E. oshaughnessyi*15, *E. oshaughnessyi*16))). According to these authors, this pattern can be explained by fixed morphological differences between the species evolving prior to the evolution of reciprocal monophyly of their mtDNA alleles (see also remarks under *E. touzeti* below). Alternatively, Torres-Carvajal & de Queiroz (2009) suggested that *Enyalioides oshaughnessyi* as currently circumscribed might represent more than one species; that is, that *E. oshaughnessyi*13 represents a different species than *E. oshaughnessyi*15 and *E. oshaughnessyi*16. This possibility is supported by color data, particularly the color of the iris. *E. oshaughnessyi*13 (QCAZ 6671) of Torres-Carvajal & de Queiroz (2009), a female specimen, and QCAZ 8073, a male from the same locality (Alto Tambo, Esmeraldas, Ecuador; Fig. 7), both have reddish-brown irises (Fig. 4). In contrast, all other specimens of "*E. oshaughnessyi*" seen by the authors (live specimens and photographs) have red irises (Fig. 4), including both male and female lizards recently photographed near the locality where *E. oshaughnessyi*15 of Torres-Carvajal & de Queiroz (2009) was collected (Bilsa Ecological Reserve, Esmeraldas, Ecuador; Fig. 7). A red iris is unique within *Hoplocercinae*, suggesting that its presence in both sexes is an autapomorphy of the species represented by *E. oshaughnessyi*15 (and *E. oshaughnessyi*16) of Torres-Carvajal & de Queiroz (2009), and that this species is different from the one represented by QCAZ 6671 and QCAZ 8073 (i.e., *E. oshaughnessyi*13 of Torres-Carvajal & de Queiroz 2009). The original species description of *E. oshaughnessyi* is based on a single, preserved (i.e., iris color unknown), adult male specimen with vague locality data ("Ecuador"), which at this point prevents us from recognizing either of the two putative species as *E. oshaughnessyi*. Additional specimens from Alto Tambo, as well as other nearby localities such as southwestern Colombia will help clarify the species limits and phylogenetic relationships among populations of "*E. oshaughnessyi*," as well as *E. touzeti*.

Enyalioides palpebralis (Boulenger 1883)

Proposed standard English name: horned woodlizards
Proposed standard Spanish name: lagartijas de palo cornudas

Enyalius palpebralis Boulenger (1883:46). Holotype: BMNH 81.5.13.25 (RR 1946.8.9.8), from "Cashiboya [Departamento Loreto, 7°32'60"S, 74°52'60"W, 160 m], eastern Peru."
Enyalioides palpebralis Boulenger (1885:116); Burt & Burt (1933:24); Peters & Donoso-Barros (1970:115).

Diagnosis. This species is different from other species of *Enyalioides* in having a superciliary triangular flap projecting posterolaterally over each eye; a wide postorbital process of the squamosal (process narrow in other species); a pair of enlarged dorsal tubercles on the posterolateral aspect of the parietal roof; and in lacking a posteriorly projecting squamosal process of the postorbital (Fig. 8; Wiens & Etheridge 2003). In addition most specimens of *E. palpebralis* have a discontinuous vertebral crest, with a small gap on the neck, and most lack femoral pores.

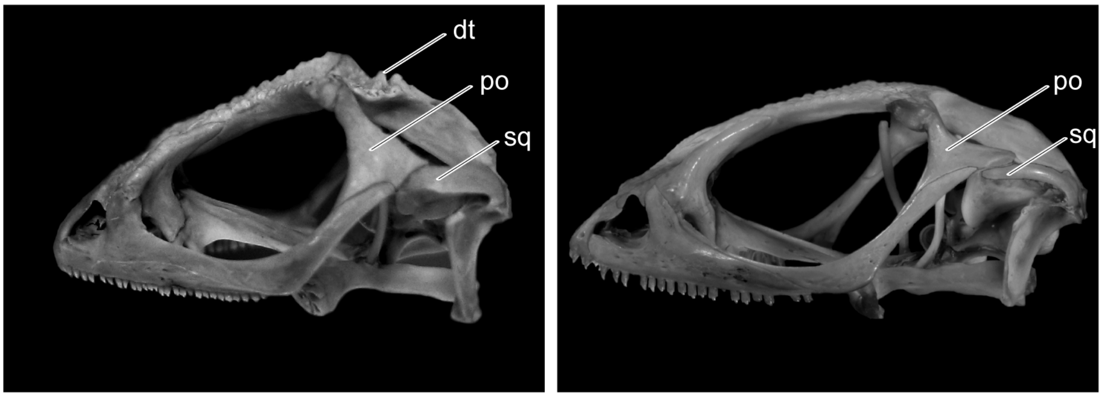

FIGURE 8. Skulls of *Enyalioides palpebralis* (left) and *E. laticeps* (right) in lateral view. dt = dorsal tubercle of parietal bone; po = postorbital; sq = squamosal.

Description. (1) dorsal head scales conical or multicarinate, strongly projecting dorsally; (2) posterior superciliaries enlarged, pointed, and projecting laterally; (3) scales on lateral edge of skull roof just posterior to superciliaries strongly projecting; the projection is more pronounced in adults; (4) one or two enlarged pretympanic scales present; (5) gular scales conical or multicarinate, strongly projecting ventrally; (6) dorsal and lateral neck scales heterogeneous in size, granular and conical scales of various sizes present; (7) vertebrals larger than adjacent dorsals, forming distinct raised middorsal crest that usually (85.9%) extends onto tail as a pair of crests; (8) nuchal region with discontinuous (85.7%) and single middorsal crest; (9) dorsals usually (71.4%) keeled and heterogeneous in size (85.7%); (10) discontinuous longitudinal row of large conical scales between dorsals and flank scales present; (11) scales on flanks keeled or smooth, heterogeneous in size; largest scales are conical in some specimens; (12) ventrals keeled; (13) fore limb scales mostly keeled dorsally and ventrally; (14) hind limb scales mostly keeled dorsally and ventrally; scattered enlarged scales present dorsally; dorsal scales of pes homogeneous in size; (15) caudals heterogeneous, slightly increasing in size posteriorly on each segment (4–6 scales in lateral view), not modified as conspicuous spines (Fig. 3); (16) tail compressed laterally. Meristic and morphometric characters are presented in Table 1.

Coloration in life (Fig. 4). Dorsal background yellowish brown, dark brown, or greenish beige, with tan spots (males) or black marks forming reticulate bands; neck and shoulders with scattered dark brown spots; orange or red blotch on each side of neck in both sexes usually present; elongate tan blotch or irregular stripe extends from the dorsolateral surface of the head to a point dorsal to the insertion of the arm in females; flanks with reddish-brown reticulate pattern on greenish-gray background; venter white, whitish brown, or beige, with irregular black markings in juveniles; throat yellow in males and brownish in females; iris reddish tan (Meede 1984; Reichle *et al.* 2004; Duellman 2005); lining of mouth orange (Fig.4).

Natural history. Based on observations of specimens in captivity, Schulte (1998) described fights between males in which one combatant bites the other's superciliary flap or nuchal crest and shakes it strongly; a male will also bite and hold a female by her nuchal crests during copulation. Clutch consists of 2–4 eggs (ca. 24–28 X 12–18 mm), which are laid under leaf-litter (Meede 1984; Schulte 1998). This species is a sit-and-wait predator, and it has been found in leaf-litter or perching on the bases of tree trunks (no higher than 1.7 m) in primary terra firme forest and primary forest edges, sometimes close to water (Avila-Pires 1995; Schulte 1998). Prey items of *Enyalioides palpebralis* include caterpillars, spiders, aquatic dipteran larvae, diplopods, chilopods, beetle larvae, grasshoppers, and ants (Meede 1984; Reichle *et al.* 2004).

Distribution. *Enyalioides palpebralis* occurs on the eastern slopes of the Andes and adjacent lowlands in Peru, northern Bolivia, and western Brazil at elevations between 100–1300 m (Fig. 9). This species is known to occur in sympatry with *E. laticeps* in southern Peru (Duellman 2005) and western Brazil (Avila-Pires 1995).

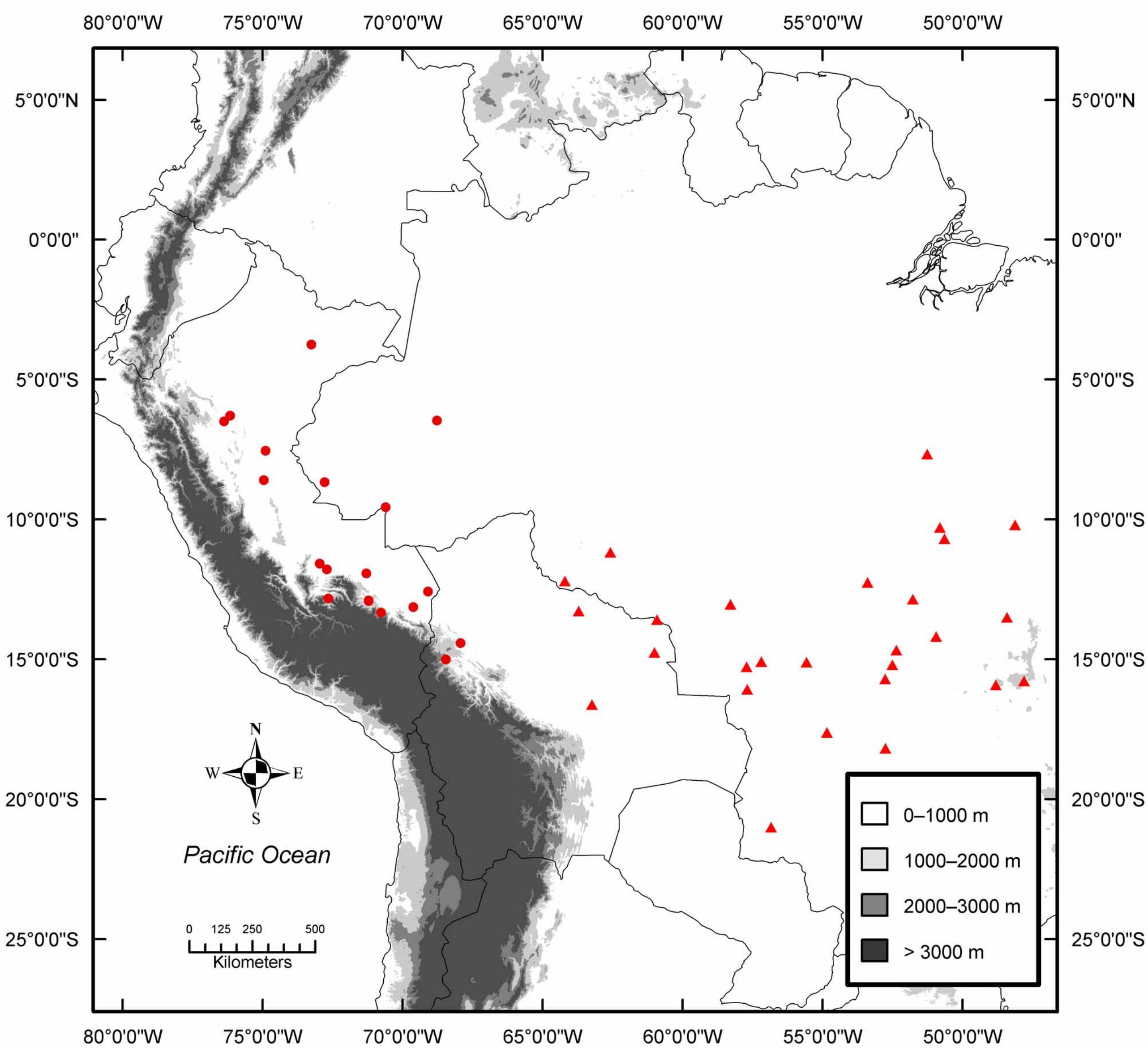

FIGURE 9. Distribution of *Enyalioides palpebralis* (dots) and *Hoplocercus spinosus* (triangles).

Remarks. *Enyalioides palpebralis* has been regarded as the only hoplocercine lacking femoral pores (Boulenger 1885; Avila-Pires 1995). Nonetheless, out of the 20 specimens examined, we found an adult male (AMNH 56401, SVL = 79 mm) from departamento Loreto in Peru that had one femoral pore on each side. Examined specimens of all other species of *Enyalioides* have at least one femoral pore on each leg except for *E. laticeps*, in which a few specimens also lack femoral pores (Table 1). Specimens of *Hoplocercus* and *Morunasaurus* have 2–5 femoral pores on each leg.

Enyalioides praestabilis (O'Shaughnessy 1881)

Proposed standard English name: Canelos woodlizards
Proposed standard Spanish name: lagartijas de palo de Canelos

Enyalius praestabilis O'Shaughnessy (1881:240). Syntypes: BMNH 8.12.8.38 (RR 1946.8.9.15), 80.12.8.37, from (respectively) "Pallatanga [in error] and Canelos, Ecuador." Pallatanga (Provincia Chimborazo, 1°59'S, 78°57' W, 2248 m) lies west of the Ecuadorian Andes, where this species does not occur. O'Shaughnessy and Boulenger list "Pallatanga and Canelos" as the type locality for several species of amphibians and reptiles collected by Buckley and purchased by the

British Museum of Natural History; in all cases Pallatanga seems to be an error caused by specimen mislabeling (Peters 1955). The type locality for *E. praestabilis* is herein restricted to Canelos [Provincia Pastaza, 1°34'60"S, 77°45'W, 631 m].
Enyalioides praestabilis Boulenger (1885:113); Burt & Burt (1931:267; 1933:25); Peters & Donoso-Barros (1970:115).

Diagnosis. *Enyalioides praestabilis* differs from all other species of *Enyalioides*, except for *E. rubrigularis*, in having the following combination of characters: caudals increasing in size posteriorly on each autotomic segment; ventrals smooth or feebly keeled; and projecting scales on dorsum and limbs absent. It can be distinguished from *E. rubrigularis* (character states in parentheses) by having smaller scales on the ventral surface of the thighs in males; gulars cream or yellow without black margins (gulars bright orange or red, with black margins); black patch covering gular fold and posteromedial portion of gular region in some male specimens (posteromedial aspect of gular region without black patch); and usually one femoral pore (normally two).

Description. (1) dorsal head scales conical or multicarinate, strongly projecting dorsally; (2) posterior superciliaries not enlarged relative to adjacent scales; (3) scales on lateral edge of skull roof just posterior to superciliaries usually (80%) more projecting than adjacent scales; the projection is more pronounced in adults; (4) one or two enlarged pretympanic scales present; (5) gular scales conical or multicarinate, strongly projecting ventrally, distinctly keeled on gular fold; (6) dorsal and lateral neck scales similar in size, mostly granular or conical; (7) vertebrals larger than adjacent dorsals, forming distinct raised middorsal crest that extends onto tail as a pair of crests; (8) nuchal region usually with continuous (95%) and single (80%) middorsal crest; (9) dorsals keeled and homogeneous in size; (10) longitudinal row of raised, enlarged scales between dorsals and flank scales usually (95%) present; when present this row is continuous; (11) scales on flanks granular, heterogeneous in size; Wiens & Etheridge (2003) reported only 25% of their specimens as having enlarged scales on flanks probably because the difference in size among flank scales in *E. praestabilis* is usually not as conspicuous as in other species of hoplocercines with heterogeneous flank scales (e.g., *E. heterolepis*); (12) ventrals usually (85%) smooth; (13) fore limb scales keeled dorsally, keeled or smooth ventrally; (14) hind limb scales keeled dorsally and keeled or smooth ventrally; scattered enlarged scales usually (95%) absent; dorsal scales of pes homogeneous in size; (15) caudals heterogeneous, increasing in size posteriorly on each segment (5–8 scales in lateral view), not modified as conspicuous spines (Fig. 3); (16) tail compressed laterally. Meristic and morphometric characters are presented in Table 1.

Coloration in life (Fig. 4). Adult males (KU 122117): dorsal background bright green with dark brown marks or black scales forming a reticulate pattern; dorsal surface of head mostly black with scattered green and bluish-green scales; labials tinged with blue; scales on sides of neck sometimes pale blue; distinct white spot posterodorsal to tympanum; black patch on gular region; chest and throat adjacent to gular region tinged with yellow or pale orange; chin tan; ventral surfaces of body and limbs creamy tan or creamy orange; iris dark bronze or brown; tongue and lining of mouth pale pink (W.E. Duellman field notes [3 August 1968, 27 September 1974] and color photographs).

Juveniles (KU 122116): dorsal background dark olive-brown with scattered dark brown marks forming transverse bands on back and spots on flanks; dorsal surface of head with scattered bright green scales; sides of head bright green with dark brown marks; venter tan with dark brown flecks; iris copper (W.E. Duellman field notes [4 August 1968]).

Natural history. Specimens of *Enyalioides praestabilis* have been found sleeping at night on vertical trunks and branches less than 1.7 m above ground sometimes close to ponds or streams. A female (SVL = 101 mm; QCAZ 8826) collected in October 2003 in Provincia Morona Santiago, Ecuador, had three enlarged vitellogenic follicles on the left side (4.18–4.96 mm X 4.30–5.61 mm) and two on the right side (4.63–5.06 mm X 4.84–5.48 mm).

Distribution. *Enyalioides praestabilis* occurs east of the Andes in southern Colombia, Ecuador, and northern Peru (Fig. 10) at elevations between 200-2000 m. This species is known to occur in sympatry with *E. laticeps* and *E. microlepis* in eastern Ecuador. However, these species also might be sympatric east of the Andes in southern Colombia and northern Peru.

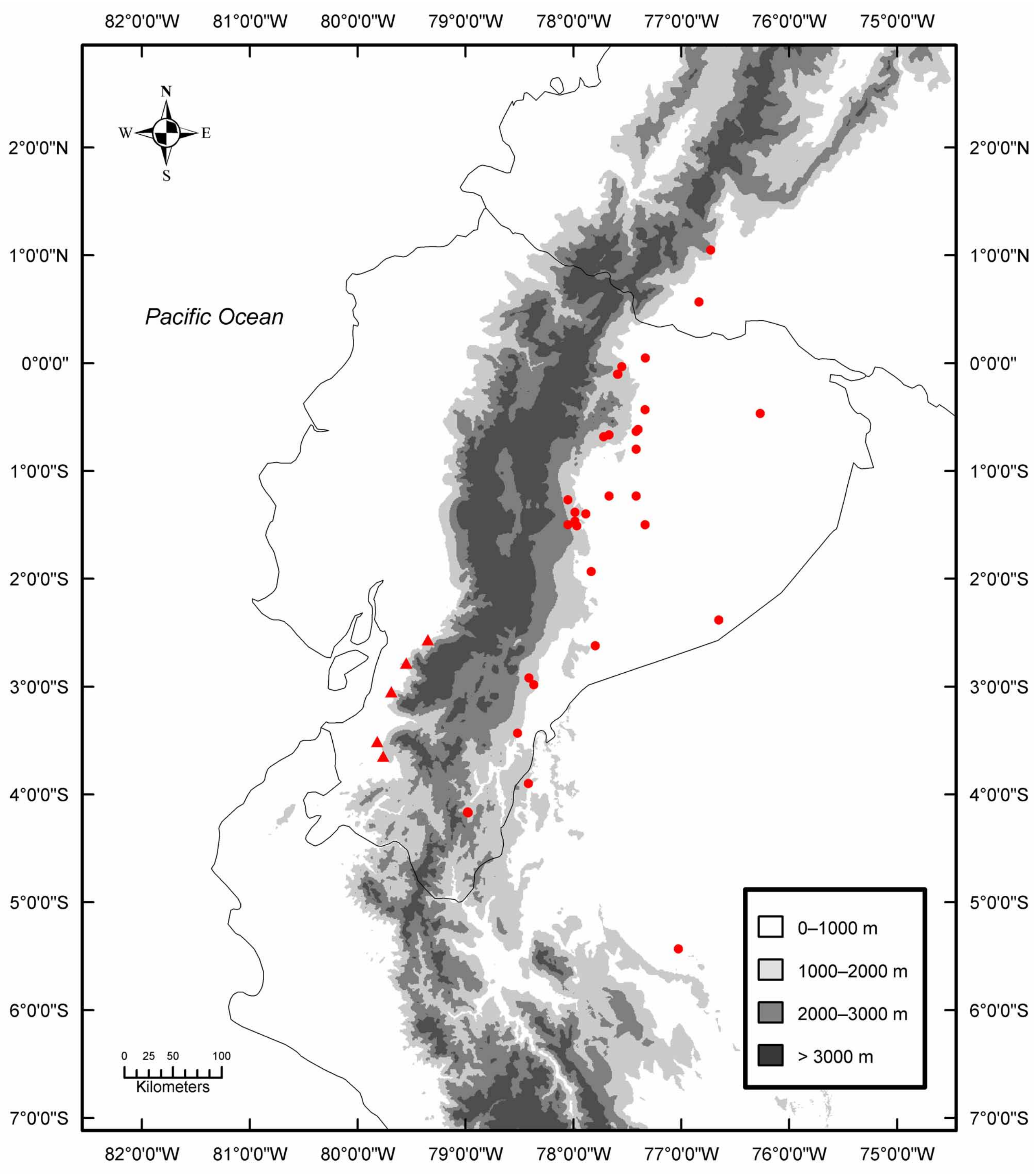

FIGURE 10. Distribution of *Enyalioides praestabilis* (dots) and *E. touzeti* (triangles).

Remarks. Except for two specimens (USNM 211156, 211158) males of *Enyalioides praestabilis* from populations north of 1°S have a black patch on the posteromedial aspect of the gular region, whereas males from populations south of this latitude lack this patch. This latitudinal boundary more or less corresponds with the Napo River, one of the main tributaries of the Amazon River, which might represent a geographical barrier separating these two sets of populations. The black gular patch (presence or absence) is a fixed character in other species of hoplocercines (Wiens & Etheridge 2003), which suggests that *E. praestabilis*, as currently recognized, may consist of two species. If so, the name *praestabilis* would apply to the southern populations. Herein we favor the hypothesis that the northern populations do not represent a separate species for the following reasons: (1) the genetic distance between two specimens from both sides of the Napo river lies within the range of other intraspecific distances (Torres-Carvajal & de Queiroz 2009); (2) two adult male specimens (USNM 211156, 211158) from localities north of the Napo river lack the distinctive gular patch of northern populations; and (3) based on the other morphological features examined in this manuscript, northern and southern populations are indistinguishable. Though not evidence supporting either the single-species or the two-species hypothesis, the sister taxon relationship between two specimens of *E. praestabilis* from different sides of the Napo river was strongly supported (bootstrap value = 100) in a maximum likelihood analysis of mitochondrial DNA sequence data (Torres-Carvajal & de Queiroz 2009).

Enyalioides rubrigularis Torres-Carvajal *et al.* 2009

Proposed standard English name: red-throated woodlizards
Proposed standard Spanish name: lagartijas de palo gargantirrojas

Enyalioides rubrigularis Torres-Carvajal *et al.* (2009:61). Holotype: QCAZ 8483, from finca de Mesías San Martín (3º51'23'S, 78º51'53"W, 1154m), near Piuntza, Provincia Zamora Chinchipe, Ecuador.

Diagnosis. *Enyalioides rubrigularis* is the only species of *Enyalioides* in which males have a bright orange or red gular region without a dark patch. It also differs from other species of *Enyalioides*, except for *E. praestabilis*, in having the following combination of characters: smooth or feebly keeled ventrals; fewer than 32 dorsal scales in a transverse line between dorsolateral crests at midbody; and projecting scales on dorsum and limbs absent. It can be distinguished from *E. praestabilis* (character states in parentheses) by having larger scales on the ventral surface of the thighs in males; posteromedial aspect of gular region without black patch (black patch covering gular fold and posteromedial portion of gular region in some male specimens); and usually two femoral pores (usually one).

Description. (1) dorsal head scales conical or multicarinate, strongly projecting dorsally; (2) posterior superciliaries not enlarged relative to adjacent scales; (3) scales on lateral edge of skull roof just posterior to superciliaries slightly more projecting than adjacent scales; (4) one or two enlarged pretympanic scales present; (5) gular scales conical or multicarinate, strongly projecting ventrally; (6) dorsal and lateral neck scales similar in size, mostly granular or conical; (7) vertebrals larger than adjacent dorsals, forming distinct raised middorsal crest that extends onto tail as a pair of crests; (8) nuchal region with continuous and single middorsal crest; (9) dorsals keeled and homogeneous in size; (10) longitudinal, continuous row of raised, enlarged scales between dorsals and flank scales present; (11) scales on flanks small, with a few scattered enlarged scales; (12) ventrals smooth; (13) fore limb scales keeled dorsally, keeled or smooth ventrally; (14) hind limb scales keeled dorsally and keeled or smooth ventrally; scattered enlarged scales absent, though adult males have enlarged scales on the ventral surface of thighs; dorsal scales of pes homogeneous in size; (15) caudals heterogeneous, increasing in size posteriorly on each segment (5–7 scales in lateral view), not modified as conspicuous spines (Fig. 3); (16) tail compressed laterally. Meristic and morphometric characters are presented in Table 1.

Coloration in life (Fig. 4). Head with green, yellow, red, or black scales in males, brown or dark olive green in females; gulars and chin scales in males orange or red, with black margins; black gular patch in males absent; light spot posterior to tympanum present; faint stripe between tympanum and scapular region in some specimens; dorsal background green or brown in various tones, commonly mottled with greenish or yellowish scales; ventral surface of body, limbs, and tail white medially and light green laterally in males, brownish cream in females; iris brown or copper; metachromatism consiting of green tones being replaced by yellow or brown tones present (Torres-Carvajal *et al*. 2009).

Natural history. Most individuals of *Enyalioides rubrigularis* have been found sleeping at night with their heads facing up on vertical stems of 2–10 cm in diameter, or horizontal stems 2–3 cm in diameter. During the day juveniles seem to stay close to holes in the ground into which they retreat if approached (Torres-Carvajal *et al.* 2009). Two females (SVL = 91 and 104 mm; QCAZ 8458 and 8457, respectively) collected in June 2008 in Provincia Zamora Chinchipe, Ecuador, had two enlarged vitellogenic follicles on the left side (5.83–9.55 mm X 6.83–10.03 mm) and one (QCAZ 8458) or two (QCAZ 8457) on the right side (6.64–9.06 mm X 7.44–11.70 mm).

Distribution. *Enyalioides rubrigularis* occurs on the eastern slopes of the Andes and western slopes of Cordillera del Cóndor in southern Ecuador at elevations of 1100–1460 m (Fig. 5). This species is not known to occur in sympatry with other *Enyalioides*, and it might be restricted to the upper basins of the Zamora and Nangaritza rivers.

Remarks. Sequence divergence between *Enyalioides rubrigularis* (unpublished data) and *E. praestabilis* is 0.09 (maximum-likelihood corrected distance). Given that most interspecific distance values in *Hoplocercinae* are above 0.15 (Torres-Carvajal & de Queiroz 2009), sequence divergence between *E. rubrigularis* and *E. praestabilis* is relatively low. Genetic distance, preliminary maximum-likelihood phylogenetic analyses, and morphological evidence suggest that these two species are sister taxa.

Enyalioides touzeti Torres-Carvajal *et al*. 2008

Proposed standard English name: Touzet's woodlizards
Proposed standard Spanish name: lagartijas de palo de Touzet

Enyalioides touzeti Torres-Carvajal *et al.* (2008:228). Holotype: EPN 10306, from "Finca La Envidia (3º3'0'S, 79º41'25"W, 433m) cerro Santa Marta, Cantón Ponce Enríquez, Provincia Azuay, Ecuador."

Diagnosis. *Enyalioides touzeti* can be distinguished from other species of *Enyalioides* by having the following combination of characters: ventrals keeled; dorsals keeled; flank scales homogeneous in size; vertebral scales in neck region in adult males more than twice as high as vertebrals in pelvic region; gular region in males extensively covered by a dark gular patch; and dorsum and limbs without projecting scales.

Description. (1) dorsal head scales conical or multicarinate, strongly projecting dorsally; (2) posterior superciliaries not enlarged relative to adjacent scales; (3) scales on lateral edge of skull roof just posterior to superciliaries more projecting than adjacent scales; the projection is more pronounced in adults; (4) one or two enlarged pretympanic scales present; (5) gular scales conical or multicarinate, strongly projecting ventrally; (6) dorsal neck scales homogeneous in size, mostly conical or cycloid and slightly imbricate; lateral neck scales similar in size to dorsal neck scales, sometimes with a few enlarged conical scales; (7) vertebrals larger than adjacent dorsals, forming distinct raised middorsal crest that extends onto tail as a pair of crests; (8) nuchal region with continuous and single middorsal crest; (9) dorsals small, prominently keeled, imbricate, and homogeneous in size; (10) longitudinal row of raised, enlarged scales between dorsals and flank scales present and continuous; (11) scales on flanks homogeneous in size, smaller than dorsals; (12) ventrals keeled; (13) fore limb scales keeled dorsally and ventrally; (14) hind limb scales keeled dorsally and ventrally; scattered enlarged scales absent; dorsal scales of pes homogeneous in size; (15) caudals heterogeneous, increasing in size posteriorly on each segment (6–8 scales in lateral view), not modified as conspicuous spines (Fig. 3); (16) tail compressed laterally. Meristic and morphometric characters are presented in Table 1.

Coloration in life (Fig. 4). Dorsal background olive green or light brown in adults (reddish brown in juveniles), normally with yellow spots in males and large dark blotches (some with background color in the center) in females; supralabials and infralabials normally yellow; light stripe extending from mouth commisure to tympanum in some specimens; light stripe between tympanum and scapular region in some specimens; chin and gular regions in males dark; venter light brown or whitish cream, with dark irregular marks in some specimens; iris reddish brown (Torres-Carvajal *et al.* 2008).

Natural history. Individuals of *Enyalioides touzeti* have been found active on the ground or perching on horizontal branches up to 30 cm high during the day, or sleeping in a vertical position on tree fern branches at night (Torres-Carvajal *et al.* 2008).

Distribution. *Enyalioides touzeti* occurs on the western slopes of the Andes in southern Ecuador at elevations of 300–700 m (Fig. 10). This species is not known to occur in sympatry with other hoplocercines, although *E. heterolepis* and *E. oshaughnessyi* occur at nearby localities (Figs. 6 and 7, respectively).

Remarks. Torres-Carvajal & de Queiroz (2009) found that the mtDNA maximum-likelihood corrected genetic distance beween this species and *Enyalioides oshaughnessyi* was relatively low (0.03–0.047) and that *E. touzeti* was nested within *E. oshaughnessyi* in a phylogenetic tree including one specimen of *E. touzeti* and three specimens of *E. oshaughnessyi*. However, morphological evidence supports *E. touzeti* as a separate species, which suggests that this could be a case of fixed morphological differences evolving prior to the evolution of reciprocal monophyly of mtDNA alleles. Alternatively, *E. oshaughnessyi* as currently circumscribed might represent more than one species, in which case *E. touzeti* would not be nested within *E. oshaughnessyi* (see Remarks under *E. oshaughnessyi* above).

Hoplocercus Fitzinger 1843

Proposed standard English name: weapontails
Proposed standard Spanish name: lagartijas de cola armorizada

Hoplocercus Fitzinger (1843:78). Type species (by monotypy): *Hoplocercus spinosus* Fitzinger; Boulenger (1885:199); Peters & Donoso-Barros (1970:148).

Pachycercus Dugès and Braconnier in Duméril (1854:558). Type species (by monotypy): *Pachycercus aculeatus* Dugès and Braconnier.

Definition. The most inclusive crown clade exhibiting a depressed, short tail (tail length < snout-vent length), with enlarged spiny scales dorsally and laterally, synapomorphic with that of *Hoplocercus spinosus* Fitzinger 1843.

Diagnosis. A depressed, short tail (tail length < snout-vent length), with enlarged spiny scales dorsally and laterally is unique to *Hoplocercus* among hoplocercines. Moreover, *Hoplocercus* differs from *Enyalioides* and *Morunasaurus* (character states in parentheses) in having the anterior opening of the Vidian canal on the ventral surface of the parabasisphenoid (anterior surface of the parabasisphenoid [dorsum sella] lateral to the sella turcica; Wiens & Etheridge 2003); a non-autotomic tail (autotomic; Etheridge 1967); slender and rounded sacral diapophyses (robust and flattened; Wiens & Etheridge 2003); and transverse processes of caudal vertebrae increasing in length from first to fourth caudal vertebra (decreasing in length throughout column; Wiens & Etheridge 2003). *Hoplocercus* can be further distinguished from *Morunasaurus* by having a parietal eye.

Composition. One currently recognized, extant species: *Hoplocercus spinosus* (Fitzinger 1843).

Remarks. *Hoplocercus* is the sister taxon of all other hoplocercines (i.e., *Enyalioides* and *Morunasaurus*), from which it is estimated to have diverged roughly 35 million years ago (Mean = 34.64; HPD = 28.04–41.67; Torres-Carvajal & de Queiroz 2009).

Hoplocercus spinosus Fitzinger 1843

Proposed standard English name: spiny weapontails
Proposed standard Spanish name: lagartijas de cola armorizada espinosas

Hoplocercus spinosus Fitzinger (1843:78). Syntypes: not located by Avila-Pires (1995:34), from "Brazil"; Duméril (1856:562); Boulenger (1885:199); Burt & Burt (1933:26); Peters & Donoso-Barros (1970:148).

Pachycercus aculeatus Dugès and Braconnier in Duméril (1854:561). Syntypes: not located by Avila-Pires (1995:34), from "Province de Saint-Paul [São Paulo] [in error, Vanzolini (1977:76)] Brésil," synonymy *fide* Duméril (1855:156).

Diagnosis. See diagnosis of *Hoplocercus* above.

Description. (1) dorsal head scales flat and smooth or multicarinate, not strongly projecting dorsally; (2) posterior superciliaries not enlarged relative to adjacent scales; (3) scales on lateral edge of skull roof just posterior to superciliaries not projecting; (4) all pretympanic scales similar in size; (5) gular scales granular or flat and smooth, juxtaposed or slightly imbricate, not projecting ventrally; (6) dorsal neck scales heterogeneous in size, granular or large and conical; lateral neck scales granular, homogeneous in size; (7) vertebrals not forming middorsal row of enlarged scales; (8) nuchal region without middorsal crest; (9) dorsals smooth and heterogeneous in size, with largest scales forming 3–4 discontinuous longitudinal rows on each side of the vertebral row; (10) discontinuous longitudinal row of raised, enlarged scales between dorsals and flank scales present; (11) scales on flanks heterogeneous in size, mostly granular with a few scattered enlarged scales; (12) ventrals smooth; (13) fore limb scales smooth or slightly keeled dorsally, granular (proximally) and smooth (distally) ventrally; (14) hind limb scales smooth or slightly keeled dorsally and smooth ventrally; scattered enlarged scales present dorsally; dorsal scales of pes homogeneous in size; (15) caudals heterogeneous in size, with some on dorsal side modified as conspicuous spines; (16) tail flattened dorsoventrally. Meristic and morphometric characters are presented in Table 1.

Coloration in life (Fig. 4). Dorsal background brown or gray, and with alternating yellow or reddish brown and dark brown or black transverse bands, which change to a series of spots on the flanks; a whitish-cream vertical stripe (faint in females) extends dorsally from fore limb insertion to scapular region; gular region with anteromedially oriented reddish-brown stripes in some males; venter light brown or cream in females; venter entirely black or medially black and laterally orange or yellow with black dots in males; throat black, reddish brown, or dark brown in males; iris copper (Avila-Pires 1995; color photographs).

Natural history. This species digs and lives in holes 30–40 cm deep in the ground with entrances 2–4 cm in diameter; individuals stay in the holes during the daytime, coming out at dusk. When in their holes, the lizards orient themselves with their tails toward the entrance and when disturbed, they inflate their bodies to press against the walls of the tunnel (Avila-Pires 1995, and references therein). Diet items of *Hoplocercus spinosus* include termites, beetles, spiders, scorpions, grasshoppers, millipedes, and ants (Avila-Pires 1995).

Distribution. *Hoplocercus spinosus* occurs in the Cerrado and areas of interdigitation between Cerrado and forest (Avila-Pires 1995) in Brazil and Bolivia (Fig. 9) from 100–600 m. This species is not known to occur in sympatry with any other species of *Hoplocercinae*.

Morunasaurus Dunn 1933

Proposed standard English name: manticores
Proposed standard Spanish name: mantícoras

Hoplocercus (part) O'Shaughnessy (1881:244); Boulenger (1885:200); Burt & Burt (1933:26).
Morunasaurus Dunn (1933:75); Peters & Donoso-Barros (1970:204). Type species (by original designation): *Morunasaurus groi* Dunn.

Definition. *Morunasaurus* Dunn 1933, converted clade name, is here defined as referring to the most inclusive crown clade containing *Morunasaurus groi* Dunn 1933, but not *Hoplocercus spinosus* Fitzinger 1843, or *Enyalioides heterolepis* (Bocourt 1874), or *Enyalioides oshaughnessyi* (Boulenger 1885). Reference phylogeny: Figure 3 in Torres-Carvajal & de Queiroz (2009), in which it is assumed that *Morunasaurus groi* is part of a clade that also includes *M. annularis* and *M. peruvianus*, but none of the other taxa in that tree.

Diagnosis. *Morunasaurus* can be distinguished from *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). It differs from both *Hoplocercus* and *Enyalioides* in having projecting scales (spines) on thigh, shin, and pes (projecting scales also present in *E. heterolepis*, but not as spines); a dentary bone extending posteriorly above the anterior surangular foramen (Wiens & Etheridge 2003), and in lacking a parietal eye. *Morunasaurus* also differs from *Enyalioides* in that the posterior whorl of each caudal segment is composed of greatly enlarged, projecting, spinous scales at least two times as large as the scales of the immediately anterior whorl.

Composition. Three species: *Morunasaurus annularis* (O'Shaughnessy 1881), *M. groi* Dunn 1933, and *M. peruvianus* (Köhler 2003).

Remarks. The phylogenetic position of *Morunasaurus* relative to other hoplocercine taxa remains unclear. Etheridge & de Queiroz (1988) inferred a phylogeny in which *Morunasaurus* was paraphyletic and deeply nested within *Enyalioides*; Wiens & Etheridge (2003) found *Morunasaurus* to be either paraphyletic, or monophyletic and sister to *Hoplocercus spinosus*. Torres-Carvajal & de Queiroz (2009) found *Morunasaurus* to be nested within *Enyalioides*, but they could not reject the monophyly of *Enyalioides* statistically; however, their study did not include *M. groi* (type species), or nuclear gene sequences from *M. peruvianus*. If *M. groi* is not closely related to *M. annularis* and *M. peruvianus*, then according to our phylogenetic definition, only *groi* (the type species) will be included in *Morunasaurus*.

The vernacular name "manticores" ("mantícoras") refers to animals that inhabit mountains near the Moruna (the basis of the name *Morunasaurus*) in E. R. R. Eddison's fantasy novel *The Worm Ouroboros*.

Morunasaurus annularis (O'Shaughnessy 1881)

Proposed standard English name: ringed manticores
Proposed standard Spanish name: mantícoras de anillos

Hoplocercus annularis O'Shaughnessy (1881:244). Holotype: BMNH 80.12.8.54 (RR 1946.8.10.35), from "Canelos [Provincia Pastaza, 1°34'60"S, 77°45'W, 631 m], Ecuador"; Boulenger (1885:200); Burt & Burt (1933:26).
Morunasaurus annularis Dunn (1933:76); Peters & Donoso-Barros (1970:204).

Diagnosis. This species can be distinguished from *Morunasaurus groi* by having a discontinuous row of enlarged vertebral scales (row absent in *M. groi*), and caudal whorls of spiny scales separated by two (ventrally) and three (dorsally) transverse rows of scales (three and four in *M. groi*, respectively). Dunn (1933) stated that another difference between *M. annularis* and *M. groi* is that the tail is compressed in the former and circular (presumably in cross section) in the latter; however, we find that the tail in both species is nearly circular in cross section. *M. annularis* differs from *M. peruvianus* (character states in parentheses) in having usually two femoral pores on each leg (3–4); four postrostrals (five); two postmentals (four), a smaller body size (maximum SVL 137 mm versus 153 mm in males, 118 mm versus 121 mm in females); and in lacking dark streaks on throat in females (streaks present).

Description. (1) dorsal head scales smooth, not projecting dorsally, some occipitals granular; (2) posterior superciliaries not enlarged relative to adjacent scales; (3) scales on lateral edge of skull roof just posterior to superciliaries not projecting; (4) all pretympanic scales similar in size; (5) gular scales granular or flat and smooth, juxtaposed or slightly imbricate, not projecting ventrally; (6) dorsal neck scales heterogeneous in size, granular or large and conical; lateral neck scales granular, homogeneous in size; (7) some vertebrals between the scapular and pelvic regions larger than adjacent dorsals, forming a distinct but discontinuous middorsal longitudinal row of enlarged, elliptical, smooth, and unraised scales; (8) nuchal region without distinct middorsal longitudinal row of enlarged scales; (9) dorsals smooth and heterogeneous in size, with largest scales more projecting and abundant on posterior half of body; (10) discontinuous longitudinal row of raised, enlarged scales between dorsals and flank scales present; (11) scales on flanks heterogeneous in size, mostly granular with a few scattered enlarged scales; (12) ventrals smooth; (13) fore limb scales smooth or slightly keeled dorsally and ventrally; (14) hind limb scales smooth or slightly keeled dorsally and ventrally; scattered conical, sharply pointed, enlarged scales present dorsally; scales of pes heterogeneous in size; (15) caudals heterogeneous, with scales making up the posteriormost whorl of each segment modified as conspicuous spines (Fig. 3); (16) tail nearly circular in cross section. Meristic and morphometric characters are presented in Table 1.

Coloration in life (Fig. 4). Adult males (QCAZ 7819): dorsum dark brown with a series of faint, cream dorsolateral blotches; sides of head yellowish brown; sides of neck orange; cream white vertical bar, bordered with dark brown anteriorly and posteriorly, extends dorsally from anterior insertion of fore limb to scapular region, where it becomes faint; flanks light yellow with a brown reticulate pattern anteriorly, and mostly light brown with scattered yellow and cream scales posteriorly; limbs light brown with scattered yellowish cream scales; chin light brown; gular region extensively covered by black mark that extends posteriorly as a wide midventral stripe that covers most of the ventral surface of body; venter light blue laterally; ventral surface of fore limbs brown with scattered yellow scales; ventral surface of hind limbs and pelvic region light grey; tail light cream ventrally and dark brown dorsally and laterally, with several grey projecting scales; iris copper brown.

Adult females: head dark brown dorsally, light brown laterally, and orange ventrally; cream stripe extends from mandibular angle to tympanum; posterior aspect of neck with a cream band bordered with dark brown, which extends dorsally over shoulder and is continuous middorsally; body cream ventrally and light brown dorsally, with five dark brown transverse bands that are wider middorsally; limbs dark brown dorsally and reddish-cream ventrally, with scattered cream flecks dorsally; tail dark brown dorsally and laterally, reddish brown ventrally (Köhler *et al.* 1999).

Natural history. Based on observations in a premontane rainforest in eastern Ecuador, Köhler *et al.* (1999) reported that *M. annularis* digs burrows about 3 m long and 60 cm deep in the forest floor. They also reported clutches of 2–4 eggs 28.6–35.1 mm long and 16.10–17.60 mm wide. The first author of the present paper collected two adult specimens, male (QCAZ 7819) and female (QCAZ 7820), nearby Bobonaza (Pastaza province, Ecuador) within a series of nearly 20 holes in a 10-meter high wall of compact soil next to a narrow patch of primary forest surrounded by pasture. Both specimens were in holes about 1 m above the ground, which had an opening diameter of approximately 20 cm. When approached, the female ran quickly about 80 cm into her burrow and locked herself strongly against the walls with her spinous scales, possibly by inflating her body. Two clutches were found 30 cm apart from each other in the female´s burrow; the first clutch contained four eggs 25.51–29.83 mm long (average = 27.38 ± 1.83 SD) and 17.13–17.74 mm wide (average = 17.37 ± 0.27 SD), whereas the second one consisted of five hatched eggs.

Distribution. *Morunasaurus annularis* occurs on the eastern slopes of the Andes and adjacent lowlands throughout Ecuador and southern Colombia at elevations between 400–1100 m (Fig. 11). This species is known to occur in sympatry with *Enyalioides laticeps* in eastern Ecuador; *E. praestabilis* occurs at nearby localities.

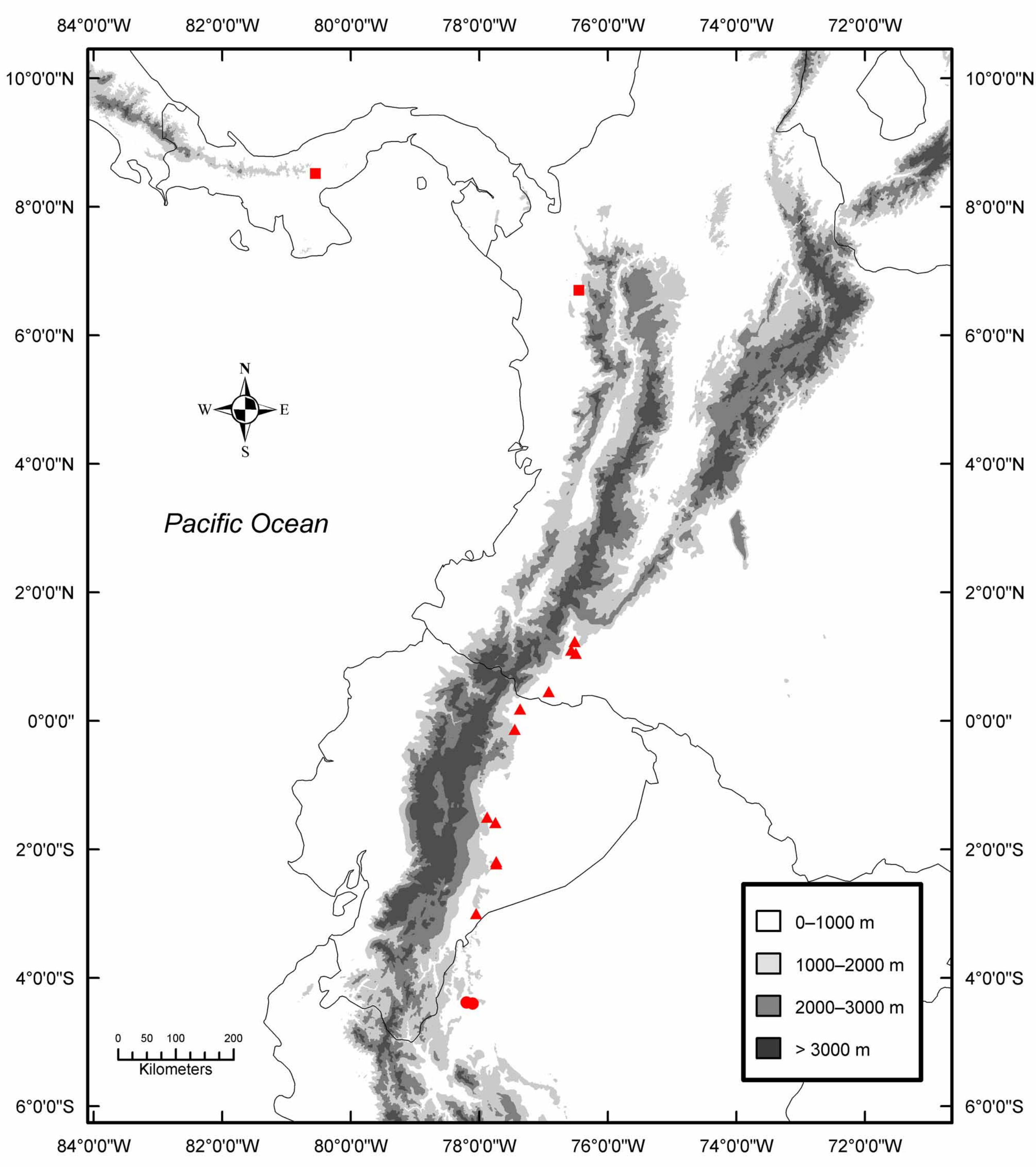

FIGURE 11. Distribution of *Morunasaurus annularis* (triangles), *M. groi* (squares), and *M. peruvianus* (dots).

Morunasaurus groi Dunn 1933

Proposed standard English name: Gro's manticores
Proposed standard Spanish name: mantícoras de Gro

Morunasaurus groi Dunn (1933:76). Holotype: MCZ 34875, from "El Valle de Anton [8º36'N, 80º7'W], [Provincia Cocle] Panama"; Peters & Donoso-Barros (1970:204).

Diagnosis. This species can be distinguished from other species of *Morunasaurus* by lacking an enlarged row of vertebral scales, and by having the caudal whorls of spines separated by three transverse rows of scales ventrally and four transverse rows of scales dorsally (versus two and three, respectively, in other *Morunasaurus*). Dunn (1933) mentioned that *M. groi* also differs from *M. annularis* in having a circular (presumably in cross section) rather than compressed tail; however, we find that the tail in both species is nearly circular in cross section.

Description. (1) dorsal head scales smooth, not projecting dorsally, some occipitals granular or subconical; (2) posterior superciliaries not enlarged relative to adjacent scales; (3) scales on lateral edge of skull roof just posterior to superciliaries not projecting; (4) pretympanic scales similar in size; (5) gular scales granular or flat and smooth, separated by skin, not projecting ventrally; (6) dorsal neck scales heterogeneous in size, granular or large and conical; lateral neck scales granular, homogeneous in size; (7) vertebrals not forming middorsal row of enlarged scales; (8) nuchal region without middorsal crest; (9) dorsals smooth and heterogeneous in size, with largest scales more projecting and abundant on posterior half of body; (10) discontinuous longitudinal row of raised, enlarged scales between dorsals and flank scales present; (11) scales on flanks heterogeneous in size, mostly granular with a few scattered enlarged scales; (12) ventrals smooth; (13) fore limb scales smooth or slightly keeled dorsally and ventrally; (14) hind limb scales smooth or slightly keeled dorsally and ventrally; scattered conical, sharply pointed, enlarged scales present dorsally; scales of pes heterogeneous in size; (15) caudals heterogeneous, with scales making up the posteriormost whorl of each segment modified as conspicuous spines; (16) tail nearly circular in cross section. Meristic and morphometric characters are presented in Table 1.

Coloration in life. Dorsal background reddish brown with dark brown transverse bands that reach the middle of the flanks to break up into small dark spots ventrally; head and neck reddish; white band bordered with dark brown on both sides extends from shoulder to scapular region; chin and infralabial region scarlet red in adult males; gular region grayish brown; pectoral region pale chrome orange; venter dirty white in males and yellow in females (Corredor *et al.* 1985).

Natural history. Dunn (1933) reported that lizards of this species seem to be diurnal and live under boulders on a mountainside. All specimens were seen within two feet of their burrows, which were short and shallow and into which the lizards retreated when approached. A female and a juvenile were found in the same burrow (Dunn 1933). Corredor *et al.* (1985) collected specimens of this species in an area characterized by low rolling hills and sandy, well-drained soil surrounded by dense, moist forest; the lizards were active during the day on the forest floor, in or near open burrows located under logs, with no surrounding vegetation. Clutch size is probably one egg (Dunn 1933).

Distribution. *Morunasaurus groi* occurs in Panama and the western slopes of the western Andean cordillera in northern Colombia at elevations between 700–805 m (Fig. 11). This species is known to occur in sympatry with *Enyalioides heterolepis* in northwestern Colombia, and it is very likely that the two species are sympatric in Panama as well.

Morunasaurus peruvianus Köhler 2003

Proposed standard English name: Cenepa manticores
Proposed standard Spanish name: mantícoras del Cenepa

Morunasaurus peruvianus Köhler (2003:237). Holotype: USNM 316725, from "vicinity of Kumpin entse, on Río Najem (tributary of the Río Huampami, which is a tributary of the Río Cena[e]pa), Departamento de Amazonas, Perú."

Diagnosis. This species can be distinguished from *Morunasaurus groi* by having a discontinuous row of enlarged vertebral scales (row absent in *M. groi*), and caudal whorls of spiny scales separated by two (ventrally) and three (dorsally) transverse rows of scales (three and four in *M. groi*, respectively). *M. peruvianus* differs from *M. annularis* (character states in parentheses) in having 3–4 femoral pores on each leg (usually two); five postrostrals (four); four postmentals (two), a larger body size (maximum SVL 153 mm versus 137 mm in males, 121 mm versus 118 mm in females); and dark streaks on throat in females (streaks absent).

Description. (1) dorsal head scales smooth, not projecting dorsally, some occipitals granular; (2) posterior superciliaries not enlarged relative to adjacent scales; (3) scales on lateral edge of skull roof just posterior to superciliaries not projecting; (4) all pretympanic scales similar in size; (5) gular scales granular or flat and smooth, juxtaposed or slightly imbricate, not projecting ventrally; (6) dorsal neck scales heterogeneous in size, granular or large and conical; lateral neck scales granular, homogeneous in size; (7) some vertebrals between the scapular and pelvic regions larger than adjacent dorsals, forming a distinct but discontinuous middorsal longitudinal row of enlarged, elliptical, smooth, and unraised scales; (8) nuchal region without distinct middorsal longitudinal row of enlarged scales; (9) dorsals smooth and heterogeneous in size, with largest scales more projecting and abundant on posterior half of body; (10) discontinuous longitudinal row of raised, enlarged scales between dorsals and flank scales present; (11) scales on flanks heterogeneous in size, mostly granular with a few scattered enlarged scales; (12) ventrals smooth; (13) fore limb scales smooth or slightly keeled dorsally and ventrally; (14) hind limb scales smooth or slightly keeled dorsally and ventrally; scattered conical, sharply pointed, enlarged scales present dorsally; scales of pes heterogeneous in size; (15) caudals heterogeneous, with scales making up the posteriormost whorl of each segment modified as conspicuous spines; (16) tail nearly circular in cross section. Meristic and morphometric characters are presented in Table 1.

Coloration in life (Fig. 4). Adult males (USNM 316725, holotype): dorsum dark brown with four dark, wide transverse bands that extend ventrally onto flanks; head black with a few scattered white and light blue scales laterally; yellow vertical bar extends dorsally from anterior insertion of fore limb to scapular region, where it becomes faint; flanks with yellow blotches that separate the dark bands that extend from dorsum; limbs light brown with scattered yellow scales; chin and gular region extensively covered by black mark that extends posteriorly as a wide midventral stripe that covers most of the ventral surface of body; venter light blue laterally; tail dark brown dorsally and laterally.

Females have pale brown gular regions with distinct dark brown streaks, and uniformly brown venters (Köhler 2003).

Natural history. Similar to other species of *Morunasaurus*, this species seems to live in burrows in the forest floor (R.W. McDiarmid field notes, cited by Köhler 2003).

Distribution. *Morunasaurus peruvianus* occurs on the eastern slopes of the Andes in northern Peru at elevations between 200–300 m (Fig. 11). This species is not known to occur in sympatry with other hoplocercines, although *E. microlepis* inhabits nearby localities.

Remarks. *Morunasaurus peruvianus* and *M. annularis* are very similar morphologically (Köhler *et al.* 1999; Köhler 2003) and the maximum-likelihood corrected genetic distance between them (0.042) is low for an interspecific comparison (Torres-Carvajal & de Queiroz 2009). Additional morphological and molecular studies with samples from several populations are necessary to assess the taxonomic status of populations currently recognized as *M. annularis* and *M. peruvianus* more definitively.

Key to the species of *Hoplocercinae*

The following key is artificial in the sense that its structure does not necessarily reflect the order of branching in the phylogeny.

1. Dorsal head scales flat, smooth, juxtaposed; vertebral crest absent or composed by a discontinuous row of enlarged scales that are longer than tall 2
   Dorsal head scales conical; vertebral crest present, composed by projecting scales that are taller than long 5
2. Tail depressed, short (tail length < snout-vent length), with enlarged spiny scales dorsally and laterally . *Hoplocercus spinosus*
   Tail nearly round, moderate (tail length > snout-vent length), with rings of enlarged spiny scales 3
3. Vertebral region of trunk without enlarged scales; tail with three scale rows separating the spiny whorls ventrally. . . . . *Morunasaurus groi*
   Some vertebral scales in trunk region enlarged forming a discontinuous longitudinal row; tail with two scale rows separating the spiny whorls ventrally 4
4. Usually two femoral pores on each leg; two postmentals; females without streaks on throat . . . .*M. annularis*
   Femoral pores 3–4 on each leg; usually four postmentals; females with dark streaks on throat . . . . *M. peruvianus*
5. Caudal scales homogeneous in size . . . . *E. laticeps*
   Caudal scales increase in size posteriorly on each autotomic segment. 6
6. Laterally projecting superciliary flap present; vertebral crest usually discontinuous (absent on posterior part of neck). . . . .*E. palpebralis*
   Laterally projecting superciliary flap absent; vertebral crest continuous 7
7. Scattered, projecting, tetrahedral large scales on dorsum, flanks, and hind limbs present . . . . *E. heterolepis*
   Scattered, projecting, tetrahedral large scales on dorsum, flanks, and hind limbs absent 8

8. Ventrals smooth or slightly keeled 9
Ventrals conspicuously keeled 10
9. Gulars in males cream or yellow without black margins; usually one femoral pore on each leg. . . . . *E. praestabilis*
Gulars in males bright orange or red, with black margins; usually two femoral pores on each leg . . . . *E. rubrigularis*
10. Dorsals heterogeneous in size, with scattered, tetrahedral, projecting scales (sometimes absent in males or juveniles); dorsolateral crests well developed between hind limbs . . . . *E. cofanorum*
Dorsals homogeneous in size, without projecting scales; dorsolateral crests inconspicuous or absent between hind limbs . . . 11
11. Dorsals smooth or slightly keeled; iris bright red in adult males; dark gular patch restricted to inner part of gular fold in males . . . . *E. oshaughnessyi*
Dorsals conspicuously keeled, iris reddish brown or copper in adult males; dark gular patch covering gular region in males. 12
12. White or cream spot posterior to tympanum usually present; 41–54 (average = 45.96 ± 3.49) dorsals in transverse row between dorsolateral crests at midbody. . . . . *E. microlepis*
White or cream spot posterior to tympanum absent; 37–43 (average = 40.50 ± 1.90) dorsals in transverse row between dorsolateral crests at midbody . . . . *E. touzeti*

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APPENDIX I. Specimens examined.

Enyalioides cofanorum.—**COLOMBIA**: *Amazonas*: Puerto Nariño, 3°46'13"S, 70°22'59"W, 110 m, ICN 4229; **ECUADOR**: *Orellana*: 4km N Anangu on Garza Cocha at Hosteria La Selva, 260 m, MCZ 174428–29; Cononaco, QCAZ 5975; SPF, QCAZ 2710; transecto PBT, Pozo Capiron 2, QCAZ 7563; Tiputini Biodiversity Station, 0°37'5"S, 76°10'19"W, 215 m, QCAZ 8006; Yasuni National Park, bloque Shiripuno, 0°43'35"S, 76°43'36"W, QCAZ 3521; *Sucumbíos*: La Selva lodge, 0°24'0"S, 76°39'0"W, QCAZ 2935, 2961, 3951, 3953; Limoncocha, MCZ 157697; Santa Cecilia, 0°5'6"N, 76°59'33"W, 340 m, KU 105342 [paratype], 112180–81 [paratypes], 122118 [paratype], 146658 [holotype], 147584–85 [paratypes], 175308; Tarapoa, 0°7'60"S, 76°25'0"W, 283 m, FHGO 5764; *Zamora Chinchipe*: cuenca del rio Jamboe, Sakantza, 1230 m, FHGO 2342; **PERU**: *Loreto*: Ampiyacu river, Distrito Pevas, 3°19'0"S, 71°51'0"W, 100 m, CAS 8323.

Enyalioides heterolepis.—**COLOMBIA**: *Antioquia*: Dabeiba, río Amparradó, campamento Ingeominas, 6°42'0"N, 76°27'0"W, 805 m, ICN unassigned numbers (2 specimens); Municipio Frontino, corregimiento La Blanquita (Murrí), 800 m, IND-R 4229; Municipio Frontino, Vereda Venados, Parque Nacional Natural Las Orquídeas, afluente de la quebrada El Retiro, 6°33'0"N, 76°18'25"W, 850–950 m, ICN 9143; *Cauca*: bajo Calima, granja de la Secretaría de Fomento, 3°59'47"N, 76°58'28"W, ICN 4231; Guapí, 2°33'23"N, 77°51'50"W, ICN 4232, 4234–35; Gorgona Island, 2°58'31"N, 78°12'27"W, 30–120 m, FMNH 165387–88, ICN 824, 826–27, 832–38, 1045, 1247–53, 1325–26, 4237–44, 4521, 6515, ICN unassigned numbers (2 specimens), KU 192676–77; Guapí, on road to pipeline between Chansará-Cantadelicia, ICN 4233, 4236; Municipio de Junta, headwaters río Guapi, IND-R 3570; Quebrada Guangui, ICN unassigned number (1 specimen); *Chocó*: 5 km NW Playa de Oro, IND-R 3556; Bahía Solano, Parque Nacional Natural Utría, ICN unassigned number (1 specimen); headwaters of río San Juan, ca. 800 m, FMNH 165224; Quibdo, San josé de Purré, río Cabi, IND-R 5035; Serranía del Baudo, Alto del Buey, 6°6'0"N, 77°13'0"W, ICN 4245–46; *Valle*: Virology Field Station, USNM 151610–12; *Valle del Cauca*: 8 km W Danubio, río Anchicaya, KU 169853; Buenaventura, Base Naval Málaga, quebrada Valencia, 3°58'0"N, 77°18'0"W, ICN unassigned numbers (2 specimens); Dagua, Vereda La Elsa, 3°34'47"N, 76°46'54"W, 980 m, ICN 9091; km 6 on road Buenaventura-río Calima, 3°53'36"N, 77°4'11"W, 0 m, FMNH 165181–82; km 22 on road Buenaventura-río Calima, FMNH 165223; Municipio Restrepo, Vereda Alegre, Campo Chanco, 3°38'14"N, 76°13'44"W, 460 m, ICN 9093; río Raposo, above caserío El Tigre, 3°42'0"N, 77°5'60"W, 11 m, ICN 1501–02; *no specific locality*: ICN 9092, 9801, 11313; **ECUADOR**: *El Oro*: Gualtaco, USNM 211076; *Esmeraldas*: Alto Tambo, 253 m, QCAZ 5523; Bosque Protector La Chiquita, 30 km E San Lorenzo on road to Ibarra, QCAZ 3839; Corriente Grande, 70 m, QCAZ 3531; Jatun Sacha Field Station, Montañas Mache-Chindul, 41km W Quinindé, 0°21'21"N, 79°42'12"W, 600 m, FHGO 3200; Loma Linda, río Onzole, 95 m, QCAZ 3626; Mayronga, 100 m, QCAZ 2185–86, 2263–66; Reserva Ecológica Mache-Chindul, comunidad San Salvador, FHGO 4063; San Miguel de Cayapas, QCAZ 412; *Los Ríos*: Estación Biológica Río Palenque, 150-220 m, KU 146657, 164166, 180657–58, QCAZ 427, USNM 285451, 285454; *Manabí*: 38 km NW El Carmen, ca. El Carmen-Pedernales road, 330 m, KU 218380; *Pichincha*: 15 km NW La Florida, QCAZ 2844; La Perla, QCAZ 2025–26; Palma Real, USNM 211094; Puerto Quito, km 132 on road Calacalí-La Independencia, Hostería Selva Virgen, FHGO 4314; río Blanco, below mouth of río Toachi, USNM 211088; río Caoni, USNM 211095; río Toachi, between kms 100-110 on road to Santo Domingo de Los Colorados, USNM 211097–98; *Santo Domingo de los Tsáchilas*: km 30 Quinindé-Santo Domingo de los Colorados, USNM 211091; Santo Domingo de los Colorados, 600 m, KU 121090–91; **PANAMA**: *Colón*: Achiote, 40 m, KU 96688; *Darién*: Laguna, 820 m, KU 76050–53; ridge btw río Jaque & río Imamado, 730 m, KU 113490–94; SE slope Cerro Pirre, 1060 m, KU 96689–90; Tacarcuna, 550 m, KU 76047–48; *San Blas*: Armila, USNM 150121 *Veragua* (possibly Veraguas): MHNP 4067 [holotype].

Enyalioides laticeps.—**BRAZIL**: Fonteboa, upper Amazon, MHNP 6821 [holotype]; **COLOMBIA**: *Amazonas*: 50 km N Chorrera on Igará-Paraná, IND-R 1038–41; headwaters of río Caiwima, tributary of río Amacayacu, ca. 70 km NNE Puerto Nariño, MCZ 154482; Leticia, 4°12'55"S, 69°56'26"W, 83 m, ICN unassigned number (1 specimen); Parque Nacional Natural Amacayacu, cabaña Amacayacu, IND-R 4195; Parque Nacional Natural Amacayacu, río Amacayacu, Puerto Mogue, close to río Cabimas, IND-R 1037; Parque Nacional Natural Amacayacu, Mata-mata creek, 3 km W Mata-mata cabin, 3°41'0"S, 70°15'0"W, 150 m, ICN 9094; Puerto Rastrojo, río Miriti, IND-R 1920, 1929; río Amacayacu, tributary of río Amazonas, ca. 50km NNE Puerto Nariño, MCZ 156348; río Amacayacu-Caiwima, ca. 40km NNE Puerto Nariño, MCZ 154481; río Miriti Paraná, IND-R 1905; *Caquetá*: 30 km from mouth of río Cuemani, IND-R 1063–65; Florencia, MLS 117; Parque Nacional Natural Chiribiquete, río Mesay, Puerto Abeja, 0°5'27"N, 72°25'0"W, IAvH 4746; *Guaviare*: Chiribiquete, ICN unassigned number (1 specimen); *Meta*: río Guayabero, Angostura No.1, 2°17'0"N, 73°58'0"W, 300–350 m, ICN 1270; Cumaral, Vereda Juan Pablo II, 3°47'0"N, 73°55'0"W, ICN 7255; Guaguriba on road to Acacias, MCZ 156323; La Macarena, campamento Isama, río Duda, ICN 4230; La Macarena, Caño Guapayita, ICN 677; Las Salinas, 3 km NW Restrepo, 4°16'9"N, 73°35'9"W, 720 m, ICN unassigned number (1 specimen); La Macarena, río Duda, Parque Nacional Natural Los Tiniguas, campamento de primatología Puerto Chamuza, IND-R 4019–22, 4034; Serranía La Macarena, Caño Sardinata, 30 km W Vista Hermosa, IND-R 287; Villavicencio, 4°9'12"N, 73°38'6"W, 500 m, AMNH 35277, FMNH 30815, MLS 116; Villavicencio, Pozo Azul creek, 4°9'12"N, 73°38'6"W, 500 m, ICN 8341, ICN unsassigned numbers (2 specimens), MCZ 154334; *Putumayo*: ca. 10 km (airline) S Mocoa, 700–800 m, AMNH 106631; no specific locality: FMNH 165208, 165211; *Vaupés*: Caparú, surroundings of lake Taraira, 1°8'46"S, 69°29'14"W, ICN 8058–61; Estación Biológica Caparú, IND-R 4382; **ECUADOR**: *Morona Santiago*: cantón Taisha, parroquia Macuma, centro Shuar Macuma, 2°8'6.6"S, 77°42'54"W, 720 m, FHGO 5460; Arapicos, 1°51'0"S, 77°57'0"W, 981 m, USNM 211111; *Napo*: Ahuano, QCAZ 7014; Ávila, río Napo, CAS-SUR 8261–62; Tena, QCAZ 6054; *Orellana*: 7 km S río Tiputini, KU

299832–33; Estación Científica Yasuní, QCAZ 7388; Loreto, 0°40'0"S, 77°19'0"W, 451 m, USNM 211121; Parque Nacional Yasuni, Tambococha, FHGO 3692; Parque Nacional Yasuni, Tiputini, Ishpingo, FHGO 5346; Río Napo, Añangu, south bank, QCAZ 9503; Sacha Lodge, QCAZ 8884; *Pastaza*: Alto río, USNM 211146; Lorocachi, QCAZ 3222; Palmira, río Pastaza valley, AMNH 37554; río Capahuari, USNM 211122; río Huiyayacu, USNM 211128; río Pindo, USNM 211143; río Shiripuno, 1°5'0"S, 76°50'0"W, FHGO 1624; Sarayacu, USNM 211124; Villano, 1°30'0"S, 77°29'0"W, 388 m, QCAZ 8118, 8262; *Sucumbíos*: 2 km W Lago Agrio, KU 299835; Lago Agrio, KU 299834, KU 299836; río Cuyabeno, USNM 211113; Santa Cecilia, 0°3'0", N, 76°59'0", 340 m, KU 122104–05, 122110–11, 147931, 147939–41, 152497; San Jose, S Tarapoa, FHGO 4839; San Pablo de Kantesiaya, 0°15'0"S, 76°25'30"W, 240 m, FHGO 850; Zancudococha, 0°25'0"S, 75°30'0"W, 220 m, FHGO 304; **PERU**: *Amazonas*: Caterpiza, USNM 568575; Galilea, USNM 568576–80; *Cusco*: Pagoreni, río Camisea, 11°42'23"S, 72°54'11"W, 465m; *Loreto*: Explorama Lodge, jct río Yanamono & río Amazonas, KU 220493; Intuto, río Tigre, AMNH 60575; San Jacinto, 175 m, KU 222164; *San Martin*: San Martin, 14 km ESE Shapaja, 360 m, KU 212627; *Ucayali*: río Calleria, Colonia Calleria, 15 km from Ucayali, CAS 95143. NO SPECIFIC LOCALITY: ICN 1231.

Enyalioides microlepis.—**COLOMBIA**: *Amazonas*: Municipio Puerto Nariño, río Amazonas, MLS 119; *Caquetá*: Municipio San José de Fragua, Vereda La Esmeralda, alto río Yuruyaco, Parque Nacional Natural Alto Fragua, 1°20'55"N, 76°6'11"W, 1000 m, IND-R 4956; Villa Fátima (aka caserío La Rastra), río Orteguaza, MLS 118; **ECUADOR**; *Morona Santiago*: N Arapicos, río Llushino, USNM 211069; *Orellana*: Loreto, 0°40'0"S, 77°19'0"W, 451 m, USNM 211070; *Pastaza*: Arajuno, Curaray, Villano, EPN 6881; below Montalvo, USNM 211073; Chichirota, USNM 211075; Moretecocha, 1°32'0"S, 77°40'0"W, 450 m, FHGO 1357; mouth of río Capahuari, USNM 211072; río Pindo, tributary of río Tigre, USNM 211074; Sarayacu, 03º00'N, 78º09'W, 400 m, BMNH 80.12.8.36, 60.6.16.8, 58.7.25.17, 80.12.8.36a; Villano, 1°30'0"S, 77°29'0"W, 388 m, QCAZ 8179, 8188, 8223, 8226, 8284, 8343, 8357; *Zamora Chinchipe*: Santiago, MCZ 45778; **PERU**: *Amazonas*: ca. 0.5 mi N Huampami, río Cenepa, 4°28'0"S, 78°10'0"W, 210 m, USNM 316717–18; Kusu, río Comaina, 4°27'0"S, 78°15'0"W, USNM 316724; vicinity of Aintami, río Cenepa, USNM 560460; vicinity of Kayamas, río Cenepa, 4°28'0"S, 78°10'0"W, USNM 316721; vicinity of Pais on the lower río Alto Cenepa (tributary of río Cenepa), USNM 560459; vicinity of San Antonio, río Cenepa, 4°30'0"S, 78°10'0"W, USNM 316719–20; 560457–58; vicinity of Sua, río Cenepa, 4°32'0"S, 78°11'0"W, USNM 316722–23; *Loreto*: northern Peru, Barranca, río Marañón valley, 140 m, AMNH 56417; San Jacinto, 02°18'44.8"S, 75°51'46"W, 180 m, KU 222163; *no specific department:*northern Peru, mouth Rio Santiago, valley río Marañón, 180 m, AMNH 56405; nearby caño Cayarú, IND-R 536.

Enyalioides oshaughnessyi.—**COLOMBIA**: *Cauca*: Quebrada Guanguí, about 0.5 km above its jct with río Patia, río Saija drainage, 100 m, AMNH 107904–06; *Nariño*: Municipio Tumaco, km 44.3 on road Altaquer-Tumaco, Angostura creek, 500 m, ICN 9050; **ECUADOR**: *Esmeraldas*: Alto Tambo, río Balthazar, 556 m, QCAZ 6671; Bilsa Ecological Reserve, 225 m, QCAZ 6866; *Guayas*: cerro Masvale, QCAZ 9893; *Los Ríos*: Estacion Biológica Río Palenque, 150–220 m, KU 152597, USNM 285456–57, Estación Biológica Jauneche, 50 m, QCAZ 6899; *Pichincha*: Finca Victoria, 37 km SE Santo Domingo de los Colorados, MCZ 80958; Hotel Tinalandia, 15 km SE Santo Domingo de los Colorados, MCZ 145269; Puerto Quito, MCZ 164509; Recinto Playa Rica, on road Nanegal-Selva Alegre, QCAZ 7426; Silanchi, río Blanco, USNM 211102; Tandapi, MCZ 164789; Unión del Toachi, 300 m, QCAZ 5326, 6682; *Santo Domingo de los Tsáchilas*: 1 km N, 2 km E Santo Domingo de los Colorados, 620 m, KU 179417; 2 km E, 1 km S Santo Domingo de los Colorados, 600 m, KU 179416; Finca La Esperanza, 5 km W Santo Domingo de los Colorados, USNM 211105; Finca La Esperanza, 5 km W Santo Domingo de los Colorados, USNM 211106–07; Santo Domingo de los Colorados, KU 109630, USNM 211103, 211109. NO SPECIFIC LOCALITY: USNM 22448, 22450.

Enyalioides palpebralis.—**BRAZIL**: *Acre*: Alto Purus, MCZ 154207; **PERU:** *Cusco*: Camisea, 11°35'0"S, 72°57'0"W, 431 m, MHNSM 21759–61; Echarate, 12°50'0"S, 72°39'0"W, 1133 m, MHNSM 24663; Marcapata, Hacienda Cadena, 13°20'0"S, 70°46'0"W, 890 m, FMNH 59185; San Martín ca. 5 km N río Camisea, 11°47'8"S, 72°41'57"W, 474 m, USNM 538328; *Huanuco*: río Lullapichis, 4–5 km upstream from río Pachitea, Finca Panguana, 8°36'0"S, 74°57'0"W, 200 m, KU 179057; *Loreto*: Cashiboya, 7°32'60"S, 74°52'60"W, 160 m, BMNH 81.5.13.25 [holotype]; Iquitos, 106 m, AMNH 57159; mouth of río Pauya, middle Cushabatay valley, 300 m, AMNH 56401; *Madre de Dios*: Cerro de Panticolla, above río Palotoa, 680 m, FMNH 229575; hacienda Erika, río Alto, 12°54'0"S, 71°12'0"W, 350–500 m, MHNSM 6367; Manu, Pakitza, Manu National Park, 11°56'47"S, 71°17'0"W, 350 m, USNM 342870; ridge above Hacienda Amazonía, near río Alto, 12°55'0"S, 71°12'0"W, 600 m, FMNH 218569–70; W bank of río Tambopata, Reserva Tambopata-Candamo, Colpa de Guacamayo, 13°8'30"S, 69°36'24"W, USNM 332467; *San Martin*: río Cainarache, 33 km N Tarapoto on road to Yurimaguas, 6°12'10"S, 76°21'56"W, KU 209511–12; Tarapotó, 6°30'5"S, 76°21'56"W, 425 m, MHNSM 6368, 6370–71.

Enyalioides praestabilis.—**COLOMBIA**: *Putumayo*: 10.3 km W El Pepino, KU 169854; San Antonio, río Guamez, 0°31'12"N, 76°45'0"W, 400 m, KU 140394; **ECUADOR**: *Morona Santiago*: 6 km on road Limón-Macas, 0°6'10"S, 77°35'2"W, 1060 m, QCAZ 6978; 6.6 km on road Limón-Macas, -2.92, -78.41, 1100 m, QCAZ 9890; Chiguaza, 1°56'0"S, 77°50'0"W, 660 m, USNM 211152–54; Miazal, 2°37'23"S, 77°47'41"W, 422 m, USNM 211155; Misión Bomboiza, 3°25'48"S, 78°31'12"W, 840 m, KU 147183; *Napo*: Avila, río Napo, 0°38'0"S, 77°25'0"W, 636 m, CAS-SUR 8260; Concepción, 0°48'0"S, 77°25'0"W, USNM 211156–57; Napo Galeras, 900 m, QCAZ 5272–74; Parroquia Catundo, Huamaní, 0°40'0"S, 77°40'0"W, 1150 m, EPN 7844, 8043–44; Río Hollín, 0°57'36"S, 77°45'24"W, 1000 m, QCAZ 5580–81, 5611; río Suno, USNM 211158; S slope Cordillera del Dué above río Coca, 0°2'0"S, 77°33'0"W, 1150 m, KU 122116–17; San Rafael, 0°6'10"S, 77°35'2"W, 1353 m, QCAZ 136, 7428; *Orellana*: San José de Sumaco [San José Nuevo], 0°26'0"S, 77°20'0"W, 519 m, AMNH 28869, 28874–76; 28894; *Pastaza*: Arajuno, 1°14'0" S, 77°40'0"W, 537 m, USNM 211165;

Canelos, 1°34'60"S, 77°45'W, 631 m, BMNH 8.12.8.38, 80.12.8.37; Centro Fátima, 9 km N Puyo, 1°24'41"S, 78°0'0"W, 900 m, QCAZ 3797; Chichirota, 2°23'0"S, 76°39'0"W, 243 m, USNM 211166; Comunidad Ingaru, Reserva Privada Ankaku, Zona de amortiguamiento del Parque Nacional Llanganates, río Challuwa Yaku, 1180 m, QCAZ 9943; Comunidad Ingaru, Reserva Privada Ankaku, Zona de amortiguamiento del Parque Nacional Llanganates, río Challuwa Yaku, -1,27, -78,05, 1668 m, QCAZ 9958–59; Palmira, río Pastaza valley, 0°28'0"S, 76°16'0"W, 250 m, AMNH 37555; Pindo-Mirador Research Station, FHGO 5579–81; Puyo, 1°28'0"S, 77°59'0"W, 970 m, USNM 211161; Puyo, Santana, EPN 6497; río Arajuno, USNM 211159–60; río Villano, USNM 211163–64; Shell-Mera, 1°28'0"S, 78°7'60"W, 1250 m, QCAZ 4113; upper basin río Curaray, USNM 211167; *Sucumbíos*: Lumbaquí, MCZ 164901–02; *Zamora Chinchipe*: Curintza, 4°10'7"S, 78°58'49"W, 1650 m, FHGO 2783; La Pituca, río Curintza, 4°9'50"S, 78°58'37"W, 1790 m, FHGO 1757, 2117; La Pituca, W of Podocarpus National Park, upper basin río Curintza, 4°10'16.6"S, 78°58'20.4"W, 1935 m, FHGO 2156; **PERU**: *Loreto*: northern Peru, front range btw. Moyobamba & Cahuapanas, AMNH 56402.

Enyalioides rubrigularis.—**ECUADOR**: *Morona Santiago*: río Piuntza, 1830 m, KU 147184; *Zamora Chinchipe*: Alto Miazi, upper Río Nangaritza, Cordillera del Cóndor, 4°14'46"S, 78°36'59"W, 1318 m, QCAZ 9089 [paratype]; Los Encuentros, Bosque Protector el Zarza, 3º50'2'S, 78º31'23"W, 1460 m, EPN 11356 [paratype]; Los Encuentros, Concesión Cuy, 3º48'28'S, 78º36'21"W, 1450 m, EPN 12432–33 [paratypes]; Piuntza, finca de Mesías San Martín, 3°51'24.57"S, 78°51'55.95"W, 1258 m, QCAZ 8454 [paratype], 8456–58 [paratypes], 8460 [paratype], 8481–82 [paratypes]; 3°51'23.20"S, 78°51'52.59"W, 1154 m, QCAZ 8483 [holotype], 8484 [paratype]; 3°51'26.13"S, 78°51'43.44"W, 1170 m, QCAZ 8485 [paratype]; 3°51'25.47"S, 78°51'40.07"W, 1192 m, QCAZ 8459, 8486 [paratypes].

Enyalioides touzeti.—**ECUADOR**: *Azuay*: Finca La Envidia, Santa Marta hill, 3°3'0"S, 79°41'25"W, 433 m, EPN 10306 [holotype], 10307 [paratype], 10700 [paratype], 10720 [paratype], 10735 [paratype]; Tamarindo 2°47'0"S, 79°33'0"W, 400 m, FHGO 1205 [paratype], 1451 [paratype]; *Cañar*: Manta Real, 2°34'S, 79°21'W, 300 m, DH-MECN 1396 [paratype]; *El Oro*: Buenaventura Biological Reserve, 3°38'43"S, 79°45'48"W, 600 m, DH-MECN 2575 [paratype], 3847 [paratype]; Santa Rosa, nearby Valle Hermoso, Parroquia Bella Maria, -3.51, -79.82, 282 m, QCAZ 8642.

Morunasaurus annularis.—**COLOMBIA**: *Cauca*: Piamonte, Serranía de los Churumbelos, Villa Iguana, 1°14'0"N, 76°31'0"W, 1100 m, ICN 8242; *Putumayo*: Mocoa, Serranía de los Churumbelos, desembocadura río Indiyaco, 1°5'57.7"N, 76°34'5.8"W, 400 m, ICN 9006; Puerto Limón, Serranía de los Churumbelos, 1°3'0"N, 76°30'0"W, 450 m, ICN 9005; Puesto de bombeo de Guamez, 1000 m, KU 140396; *no specific locality*: ICN 9001–04; **ECUADOR**: *Morona Santiago*: Canton Taisha, parroquia Macuma, centro Shuar Kiim, 3°0'0"S, 78°3'0"W, 600 m, FHGO 4783; centro Shuar Kenkuim, 2°13'40"S, 77°44'15"W, FHGO 2983; centro Shuar Mutinza, 2°11'40"S, 77°44'15"W, FHGO 5364; *Napo*: Bermejo No.4, 15 km ENE Umbaqui, 0°11'0"N, 77°22'0"W, 570 m, KU 122119; El Chaco, campamento Codo Bajo, 640 m, EPN 5219; *Pastaza*: upper río Bobonaza, EPN 5613–18, 5620–22, 5624, 5626–30, 5632, 5635, 5637–39, 5641–53, KU 209799; headwaters río Conambo, FMNH 197965–66; Río Conambo, USNM 200788–95.

Morunasaurus groi.—**COLOMBIA**: *Antioquia*: Dabeiba, río Amparradó, Pantanos, 6°42'0"N, 76°27'0"W, 805 m, ICN 6100–6107; **PANAMA**: *Cocle*: El Valle, 560 m, KU 76060; El Valle de Anton, FMNH 178119.

Morunasaurus peruvianus.—**PERU**: *Amazonas*: vicinity of Kumpin Entse, río Najem (tributary of río Huampami), USNM 316725 [holotype], 316726–29 [paratypes], 316731–34 [paratypes], 560471–75.

Hoplocercus spinosus.—**BRAZIL**: *Mato Grosso*: Porto Heloisa, Rio Araguaia, 14°10'57"S, 50°56'14"W, USNM 200681–84; Serra da Bodoquena, 21°00'0"S, 56°49'59"W, USNM 292404; Serra do Roncador, 12°51'0"S, 51°46'0"W, 600 m, KU 124614; Xingar, 600 m, KU 29474. NO SPECIFIC LOCALITY: FMNH 179093, 179095, 179096.