Zootaxa 1930: 1–17 (2008)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Description of a new divergent lineage and three new species of Honduran salamanders of the genus *Oedipina* (Caudata, Plethodontidae)

JAMES R. MCCRANIE[1], DAVID R. VIEITES[2], & DAVID B. WAKE[2,3]

[1]*10770 SW 164th Street, Miami, FL 33157–2933, USA*
[2]*Museum of Vertebrate Zoology and Department of Integrative Biology, 3101 VLSB, University of California Berkeley, CA 94720-3160, USA*
[3]*Corresponding author. E-mail: davidbwake@gmail.com*

Abstract

We describe three new species of the plethodontid salamander genus *Oedipina* from Honduras. All three are relatively small to moderate sized, elongated and attenuate forms, which are differentiated from each other and from other members of the genus in limb and digital features, size, and body shape. Their distinctiveness is validated by phylogenetic analysis of mtDNA (cytochrome b and 16S) data, which shows each to be strongly differentiated. Furthermore, two of the three species are sister taxa and they comprise a third major clade in the genus, which we recognize as a new subgenus.

Key words: *Oedipina quadra* **sp. nov.**, *O. kasios* **sp. nov.**, *O. leptopoda* **sp. nov.**, *Oeditriton* subgenus nov., tropical salamanders, Honduras, mtDNA, cytb, 16S

Resumen

Aquí describimos tres nuevas especies de salamandras del género *Oedipina*, familia Plethodontidae. Las tres especies son de pequeño a moderado tamaño, con forma alargada y atenuada, y se diferencian entre ellas y de otros representantes del género principalmente en características de pies y manos. Análisis filogenéticos basados en ADN mitocondrial (citocromo b y 16S) validan su estatus y confirman su alto grado de diferenciación genética. Asimismo, dos de las tres nuevas especies son especies hermanas y constituyen una tercer clado en el género, que proponemos como nuevo subgénero.

Introduction

Tropical plethodontid salamanders comprise the most speciose radiation of caudate amphibians, including 234 of a total of 570 species currently recognized (AmphibiaWeb 2008). The 13 genera of tropical bolitoglossine salamanders display an enormous diversity in terms of morphology, ecology and species diversity. Among them, the 25 species of the genus *Oedipina* stand out because of their slender, elongated appearance. These species are distributed from southern Mexico to northwestern South America, occupying a wide altitudinal range (sea level to 2500 m). Most of these species are known from few specimens because they are difficult to find in the field, probably as a result of their fossorial behavior.

Representatives of this genus are characterized by having long to very long tails and small limbs, and differ from the remaining tropical salamanders in having trunks that have become elongated by an increase of trunk vertebral numbers from 14, typical of all other tropical genera, to 18 or more (García-París & Wake

Accepted by M. Vences: 16 Oct. 2008; published: 12 Nov. 2008

2000). Molecular and morphological data support the recognition of two major clades as subgenera (García-París & Wake 2000). The subgenus *Oedipina* comprises 16 species with elongate bodies (usually with 20–23 trunk vertebra), long to very long tails, and tiny limbs and feet. This clade is found from western Guatemala to central Panamá. The subgenus *Oedopinola* is constituted by 9 species, which while elongated have shorter bodies (usually with 18–19 trunk vertebra) and shorter tails than *Oedipina*. The limbs, feet and hands often are slightly larger in *Oedopinola* than in *Oedipina*, although with some exceptions that have reduced limbs and digits (*O. complex, O. maritima, O gephyra*). *Oedopinola* ranges from Chiapas, México, to Ecuador.

Although phylogenetic relationships of tropical bolitoglossine salamander genera are not yet fully resolved, the genus *Nototriton* (or possibly the very poorly known *Bradytriton*) was found to be the sister taxon to *Oedipina* with morphological (Wake & Elias 1983) and molecular (García-París & Wake 2000, Wiens *et al.* 2007) datasets. *Oedipina* has been recovered as monophyletic in all previous studies (Wake & Elias 1983, Good & Wake 1998, García-París & Wake 2000, Wiens *et al.* 2007). The relationships among species within the genus have been estimated by morphology, allozymes, and mitochondrial DNA (Good & Wake 1998, García-París & Wake 2000).

Recent collections of *Oedipina* from Honduras stimulated the present study. We suspected that undescribed species had been found, but many species in the genus are confusingly similar in morphology. Accordingly we sequenced mitochondrial DNA (mtDNA) in order to add to the database published earlier by García-París & Wake (2000). We added mtDNA sequences from seven species for two mitochondrial genes (cytochrome b, cytb, and 16S rRNA, 16S) (Table 1). Included are two rare species, *O. collaris* (our sample is from Panamá) and *O. carablanca* (Costa Rica), each previously known from fewer than 5 specimens (Brame 1968). In this paper we explore the phylogenetic relationships among species of *Oedipina*, describe three new species, and present an analysis of new mitochondrial DNA data that supports the recognition of a third novel and divergent clade within this genus, which we propose as a new subgenus.

Material and methods

Taxon sampling and voucher information. Taxa selected for the analyses include representatives of all major clades and subclades of *Oedipina*. Specimens (identified to taxon) used in the molecular analyses and their collecting localities are listed in Table 1. All museum acronyms follow Leviton *et al.* (1985). We incorporated seven representatives of the subgenus *Oedopinola*: *O. elongata, O. carablanca, O. complex, O. maritima, O. alleni, O. savagei* and the morphologically divergent *O. gephyra*. We also used ten other named species, representing four subclades of the subgenus *Oedipina* (based on prior analyses of Good & Wake 1998, García-París & Wake 2000, and analyses herein): subclade *stenopodia*: *O. ignea, O. stenopodia*; subclade *poelzi*: *O. poelzi, O. collaris, O. grandis;* subclade *cyclocauda*: *O. cyclocauda, O. pseudouniformis*; subclade *uniformis*: *O. gracilis, O. pacificensis, O. uniformis*. Also included in our analyses are representatives of the three new species described herein, and an unidentified species from Nicaragua. The taxa studied cover most of the geographic range of the genus. Representatives of the possibly related genera *Nototriton, Dendrotriton,* and *Cryptotriton* served as outgroups, with the more remotely related *Bolitoglossa* as a general outgroup.

Morphological measurements. Measurements follow those used in previous papers by García-París & Wake (2000) and McCranie & Wilson (2002). All measurements (based only on the type series) are in millimeters (mm), made to the nearest 0.1 with dial calipers and with the aid of a dissecting microscope equipped with an ocular micrometer. Males were determined by presence of mental glands, premaxillary teeth advanced in front of the maxillary arcade, and papillate vent margins, in any combination; females have folded vent margins. Maxillary and vomerine tooth counts are totals of the paired bones. Limb interval equals the number of costal interspaces between adpressed limbs. Color names (capitalized) and codes (in parenthesis) are those

of Smithe (1975–1981).

DNA extraction and sequencing. Muscle or liver tissue samples were taken from freshly killed specimens in the field and preserved in 98% ethanol; these included the holotype and paratype of one of the species described in this paper, and a paratype of another new species. Sequence of cytb is already available for the holotype of the third new species (MVZ 167772) (García-París & Wake 2000). Total genomic DNA was extracted using proteinase K (final concentration 1 mg/ml), and isolated by a standard salt extraction protocol (Bruford *et al.* 1992). We amplified two mitochondrial markers for phylogenetic purposes. A 385 bp fragment of the mitochondrial cytochrome b gene was amplified via polymerase chain reaction (PCR) using the primers MVZ15 (5'-GAACTAATGGCCCACACWWTACGIAA-3', Moritz *et al.* 1992) and MVZ4 (5'-GCAGCCCCTCAGAATGATATTTGTCCTC-3', T. White unpublished). A fragment of the 16S rRNA was amplified via PCR with the primers 16Sar-L (5'-CGCCTGTTTATCAAAAACAT-3') and 16Sbr-H (5'-CCGGTCTGAACTCAGATCACGT-3', Palumbi *et al.* 1991). These fragments were sequenced in both directions for each sample, and a consensus sequence was generated. Fragment length varied among taxa due to missing nucleotides at the beginning or end of the sequences or by different length of variable regions corresponding to loops in the secondary structure of the 16S rRNA molecule.

PCRs were performed in 25 µl reactions using ca. 50 ng genomic DNA, 10 pmol of each primer, 15 nmol of each dNTP, 50 nmol additional MgCl 2, Taq PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.1 mM MgCl 2 and 0.01% gelatine) and 1 U of Taq DNA polymerase. The PCR conditions were: an initial denaturation step at 94° C for 3 min; 35 cycles at 94° C for 30 s, annealing temperature of 48° C for 45 s, extension at 72° C for 2 min and final extension of 5 min at 72° C. PCR products were loaded onto 1% agarose gels, stained with GelStar gel stain (Cambrex), and visualized in a Dark reader transilluminator (Clare Chemical). If results were satisfying, products were purified using 2 µl, from a 1:4 dilution of ExoSapIt (Amersham), per 5 µl of PCR product prior to cycle sequencing. A 10 µl sequencing reaction included 2 µL of template, 2.5 µl of sequencing buffer, 0.8 µl of 10 pmol primer, 0.4 µl of BigDye Terminator version 3.1 Sequencing Standard (Applied Biosystems) and 4.2 µl of water. The sequence reaction was 35 cycles of 10 sec at 96° C, 10 s at 50° C and 4 min at 60° C. Cycle sequencing products were purified by ethanol precipitation. Sequence data collection and visualization were performed on an ABI 3730xl automated sequencer (Applied Biosystems). Sequences were deposited in GenBank (accession numbers FJ196862-FJ196873, see Table 1).

Phylogenetic analyses. Sequences were automatically aligned using the computer program Muscle (Edgar 2004), and the alignment was reviewed visually to check for potential conflicts. The alignment of cytochrome b sequences did not show any indels or stop codons, while the 16S rRNA showed some length variation, corresponding to loop regions or single insertions in some taxa. A total of 13 16S rRNA sites were excluded from the analyses, due to ambiguity in the alignment or because gaps were present in more than 50% of the taxa.

Phylogeny was inferred both by a maximum likelihood (ML) and a Bayesian approach. Non- parametric bootstrap maximum likelihood analysis was performed with the program RaxML (Stamatakis *et al.* 2005). One thousand bootstrap repetitions were run for the concatenated dataset. We performed a partitioned Bayesian analysis with a partition strategy by codon and gene. Separate evolutionary models and parameters that best fit each partition were selected for the first, second and third codon positions of cytochrome b, and for the complete 16S rRNA, using PAUP* 4.0b10 (Swofford 2003) and the Akaike Information Criterion implemented in MrModeltest version 2.2 (Nylander 2004). These models were used as priors in a partitioned Bayesian analysis in the program MrBayes, version 3.1.2 (Ronquist and Huelsenbeck 2003). The maximum likelihood tree for the whole dataset was used as the starting tree in the model calculations, in order to standardize the analyses. We ran two independent analyses consisting of four Markov chains that ran for 20 million generations, sampled every 1000 generations, with a random starting tree, default priors, and the option ‘‘prset ratepr’’ set as ‘‘variable’’. The temperature was optimized to 0.3 after several test runs for one million generations. After discarding the first 10 million generations, remaining trees from both analyses were com-

bined and a 50% majority rule consensus tree was calculated.

Kimura two-parameter genetic distances (K2P) were calculated for the 16S rRNA only, using an alignment that included only members of the genus *Oedipina*, in the program PAUP* 4.0b10 (Table 2).

TABLE 1. Species included in the phylogenetic analyses, museum numbers, locality information and Genbank accession numbers.

Museum number	Species	Country	State or Province	16S	Cyt. B
MVZ S 12921	*Bolitoglossa cerroensis*	Costa Rica	San José	AF199233	AF199195
MVZ 158942	*Cryptotriton alvarezdeltoroi*	Mexico	Chiapas	AF199196	AF199120
MVZ 160907	*Cryptotriton* **sp. nov.**	Guatemala	Zacapa	AF199198	AF199129
MVZ 215913	*Cryptotriton veraepacis*	Guatemala	Baja Verapaz	AF199197	AF199123
UTA A-51086	*Dendrotriton rabbi*	Guatemala	Quiche	AF199232	AF199194
UCR 12071	*Nototriton abscondens*	Costa Rica	Alajuela	AF199199	AF199130
USNM 339712	*Nototriton barbouri*	Honduras	Atlántida	AF199201	AF199136
UTA A-51490	*Nototriton brodiei*	Guatemala	Izabal	AF199202	AF199139
MVZ 207122	*Nototriton gamezi*	Costa Rica	Alajuela	AF199200	AF199135
MVZ 207106	*Nototriton guanacaste*	Costa Rica	Guanacaste	AF199203	AF199140
USNM 497540	*Nototriton lignicola*	Honduras	Olancho	AF199204	AF199141
MVZ 225899	*Nototriton picadoi*	Costa Rica	Cartago	AF199205	AF199144
UCR 12057	*Nototriton richardi*	Costa Rica	San José	AF199206	AF199146
MVZ 190857	*Oedipina alleni*	Costa Rica	Puntarenas	AF199207	AF199149
No voucher	*Oedipina carablanca*	Costa Rica	Limón	FJ196862	FJ196869
SIUC H 8896	*Oedipina collaris*	Panamá	Cocle	FJ196863	FJ196870
MVZ 236255	*Oedipina complex*	Panamá	Colón	AF199213	AF199157
MVZ 138916	*Oedipina cyclocauda*	Costa Rica	Heredia	AF199214	AF199158
UTA A-51906	*Oedipina elongata*	Guatemala	Izabal	AF199216	AF199160
USNM 343462	*Oedipina gephyra*	Honduras	Atlántida	AF199217	AF199161
MVZ 210398	*Oedipina gracilis*	Costa Rica	Heredia	AF199219	---
MVZ 225904	*Oedipina grandis*	Costa Rica	Puntarenas	FJ196864	AF199164
USNM 530586	*Oedipina ignea*	Honduras	Ocotepeque	AF199231	AF199192
MVZ 232825	*Oedipina kasios*	Honduras	Olancho	FJ196866	FJ196872
MVZ 232826	*Oedipina kasios*	Honduras	Olancho	FJ196867	FJ196873
MVZ 167772	*Oedipina leptopoda*	Honduras	Yoro	---	AF199193
MVZ 219997	*Oedipina maritima*	Panamá	Bocas del Toro	AF199221	AF199166
UCR 12063	*Oedipina pacificensis*	Costa Rica	Puntarenas	AF199222	AF199169
MVZ 163703	*Oedipina poelzi*	Costa Rica	Alajuela	AF199224	AF199174
MVZ 207128	*Oedipina poelzi*	Costa Rica	Alajuela	AF199225	AF199175
MVZ 203749	*Oedipina pseudouniformis*	Costa Rica	Cartago	AF199227	AF199178
MVZ 232824	*Oedipina quadra*	Honduras	Gracias a Dios	FJ196865	FJ196871
UCR 14587	*Oedipina savagei*	Costa Rica	Puntarenas	AF199209	AF199152
SMF 78738	*Oedipina* sp.	Nicaragua		FJ196868	---
MVZ 163649	*Oedipina stenopodia*	Guatemala	San Marcos	AF199228	AF199181
MVZ 203751	*Oedipina uniformis*	Costa Rica	Cartago	AF199230	AF199190

Results

We amplified 522 base pairs of 16S and 385 base pairs of the cytochrome b gene to perform the phylogenetic analyses. Mr Modeltest selected the GTR+I+G model as the most appropriate model of evolution for the 16S gene, K80+G for the first codon of cytochrome b, HKY+G for the second, and GTR+G for the third codon position of this gene.

Our analyses recovered the genus *Oedipina* as a clade, sister to the genus *Nototriton*. Both Bayesian and ML analyses provided high support for this relationship (Fig. 1). Three major clades can be recognized in *Oedipina*. The first is represented in our tree by the species *O. gephyra*, *elongata, carablanca, complex, maritima, alleni*, and *savagei*. This clade corresponds with the subgenus *Oedopinola* and is well supported as a monophyletic clade by the Bayesian analysis, with Bayesian posterior probability of 98 and moderate support (67 bootstrap proportion) in the ML analysis.

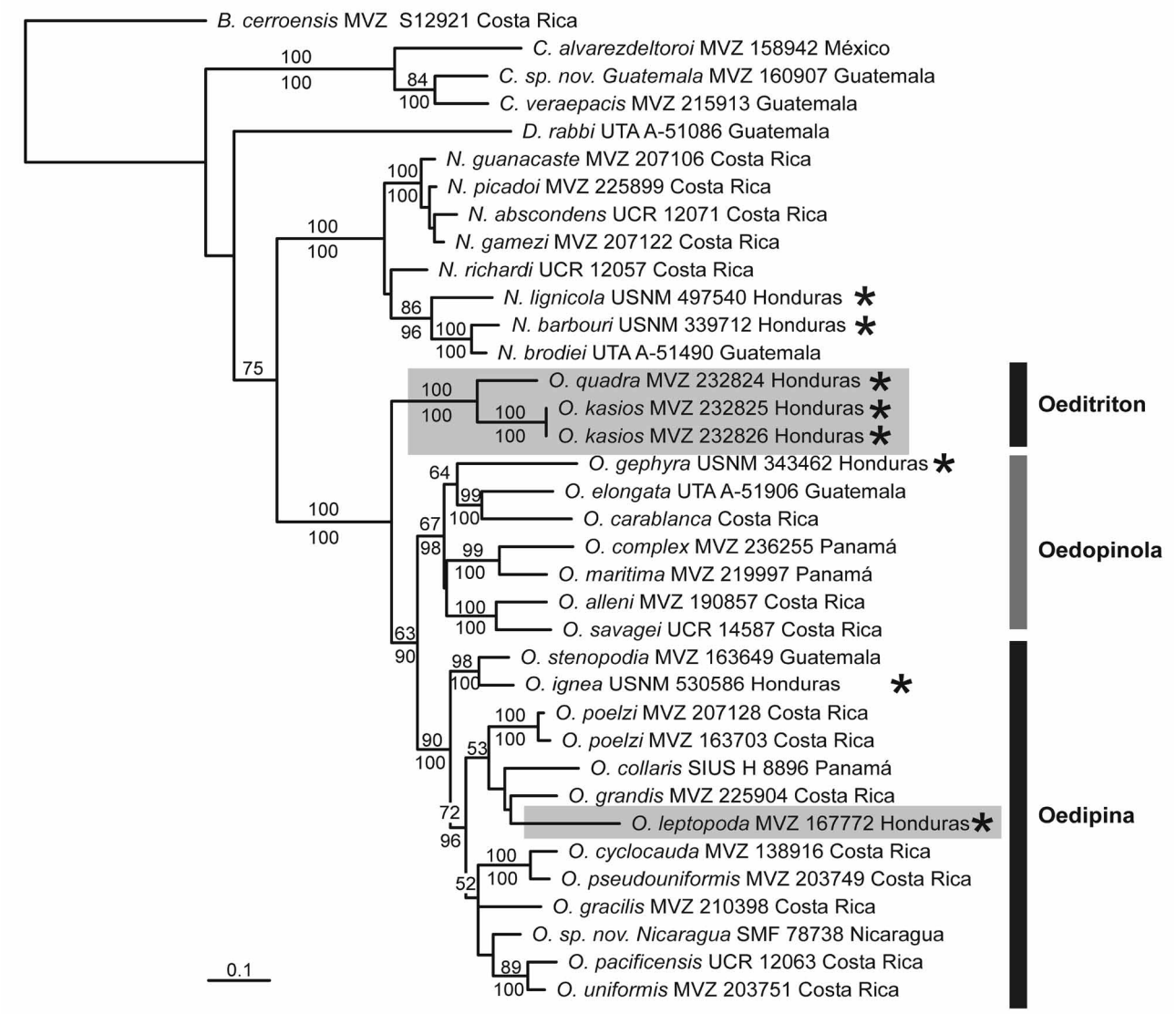

FIGURE 1. Maximum likelihood phylogram. Upper values represent ML bootstrap supports, while lower numbers represent Bayesian posterior probabilities (times 100). Values lower than 50% were not included. Species described as new are highlighted in gray. Asterisks for species of *Oedipina* indicate specimens from Honduras.

The second clade corresponds to the subgenus *Oedipina* and includes all species currently recognized in this subgenus that are included in our analyses (*O. stenopodia, ignea, poelzi, collaris, grandis, cyclocauda,*

pseudouniformis, gracilis, pacificensis, uniformis, and an unidentified species from Nicaragua) plus one of the new taxa described in this paper. The phylogenetic position of this new species is unclear, because it failed to gain high support in any of the analyses, although it clusters with *O. grandis* and *O. collaris*. For this taxon we only have cytochrome b data, which may explain the lack of support in the analyses. With our dataset we were not able to resolve the relationships among several of the subclades previously recognized within the subgenus *Oedipina*. The *stenopodia* subclade is well supported, with values close to 100 in both Bayesian and ML, and it is sister to the rest of the species within this subgenus. Our analyses provide some support for an unnamed subclade, constituted by the species *O. poelzi, O. collaris, O. grandis, O.* sp nov. (described herein), *O. cyclocauda, O. pseudouniformis, O. gracilis, O.* sp.(Nicaragua*), O. pacificensis* and *O. uniformis*, with both high ML and Bayesian support (72 and 96, respectively). These species belong to further subordinate subclades *uniformis, poelzi* and *cyclocauda* as recognized by previous authors (Good & Wake 1998, García-París & Wake 2000). However, we were unable to resolve relationships further (low statistical support).

A third clade was identified in our analyses. This clade is formed by two of the new species described herein and is very divergent from the other two major clades. It is well supported (100 ML and Bayesian). Table 2 summarizes the 16S K2P distances between pairs of *Oedipina* species. The mean genetic distance between these two species and the representatives of the subgenus *Oedopinola* is 11%, while their distance with respect to the subgenus *Oedipina* is 10%. These sister species are also 5% divergent from each other.

Given these results, we herein describe three new species of *Oedipina* from Honduras. Furthermore, we designate a new subgenus for the divergent clade constituted by two of our new species.

Systematics

Genus *Oedipina* Keferstein 1868

Subgenus *Oeditriton* taxon nov.

Diagnosis. Slender, long-tailed members of *Oedipina* with 20–21 trunk vertebrae and short limbs with very narrow manus and pes; well differentiated from species of the subgenera *Oedipina* and *Oedopinola* by substantial differences in sequences of the mitochondrial genes cytb and 16S.

Etymology. The name *Oedipus* is a latinized word of Greek origin long used for all tropical plethodontid salamanders, until shown to be a synonym of an orthopteran genus. Keferstein (1868) coined the name *Oedipina* for elongated members of the old genus *Oedipus* and Hilton (1946) in turn coined the name *Oedopinola* for species now assigned to a subgenus of *Oedipina*. We follow earlier workers in coining a new name *Oeditriton*, which combines part of the generic name, *Oedi-*, with the Greek name *Triton*, which has been used extensively in combination with various roots for salamander generic-level taxa.

Content. The two species are described below.

Oedipina quadra sp. nov.

Honduran Lowland Worm Salamander

Figure 2

Oedipina cyclocauda (part). Brame 1968, McCranie & Wilson 2002, McCranie & Castañeda 2007.

Holotype. MVZ 257761, an adult male, from Urus Tingni Kiamp, 14°55'N, 84°41'W, tributary of upper portion of Río Warunta, 160 m above sea level (a.s.l.), Dept. Gracias A Dios, Honduras, collected 7 February 2006 by J. R. McCranie.

TABLE 2. Kimura 2 parameter genetic distances between pairs of *Oedipina* species included in the analyses based on 16S sequences.

	Museum number	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	MVZ 190857	*O. alleni*	-																				
2	No voucher	*O. carablanca*	0.08	-																			
3	SIUC H 8896	*O. collaris*	0.11	0.11	-																		
4	MVZ 236255	*O. complex*	0.07	0.07	0.1	-																	
5	MVZ 138916	*O. cyclocauda*	0.09	0.09	0.08	0.07	-																
6	UTA A-51906	*O. elongata*	0.08	0.05	0.11	0.09	0.09	-															
7	USNM 343462	*O. gephyra*	0.08	0.08	0.11	0.08	0.08	0.08	-														
8	MVZ 210398	*O. gracilis*	0.1	0.09	0.07	0.08	0.07	0.09	0.08	-													
9	MVZ 225904	*O. grandis*	0.07	0.09	0.05	0.09	0.07	0.09	0.08	0.06	-												
10	USNM 530586	*O. ignea*	0.08	0.07	0.08	0.08	0.06	0.08	0.08	0.06	0.05	-											
11	MVZ 232825	*O. kasios*	0.12	0.12	0.12	0.1	0.11	0.12	0.12	0.12	0.09	0.09	-										
12	MVZ 232826	*O. kasios*	0.12	0.12	0.12	0.1	0.11	0.12	0.12	0.12	0.09	0.09	0	-									
13	SMF 78738	*O. leptopoda*	0.08	0.08	0.06	0.07	0.05	0.08	0.08	0.05	0.05	0.05	0.1	0.1	-								
14	MVZ 219997	*O. maritima*	0.07	0.07	0.11	0.04	0.09	0.08	0.08	0.09	0.09	0.08	0.1	0.1	0.08	-							
15	UCR 12063	*O. pacificensis*	0.08	0.07	0.06	0.07	0.05	0.08	0.08	0.04	0.04	0.04	0.1	0.1	0.02	0.07	-						
16	MVZ 163703	*O. poelzi*	0.09	0.09	0.08	0.09	0.07	0.1	0.09	0.07	0.05	0.07	0.11	0.11	0.06	0.09	0.06	-					
17	MVZ 207128	*O. poelzi*	0.08	0.09	0.08	0.09	0.06	0.1	0.09	0.07	0.05	0.07	0.11	0.11	0.06	0.09	0.06	0	-				
18	MVZ 203749	*O. pseudouniformis*	0.09	0.08	0.07	0.07	0.02	0.09	0.08	0.06	0.06	0.05	0.1	0.1	0.04	0.09	0.04	0.07	0.07	-			
19	MVZ 232824	*O. quadra*	0.1	0.1	0.12	0.1	0.09	0.11	0.11	0.11	0.1	0.09	0.05	0.05	0.1	0.1	0.09	0.11	0.11	0.09	-		
20	UCR 14587	*O. savagei*	0.04	0.1	0.11	0.08	0.09	0.1	0.09	0.1	0.09	0.09	0.13	0.13	0.09	0.09	0.09	0.11	0.11	0.1	0.13	-	
21	MVZ 163649	*O. stenopodia*	0.09	0.08	0.08	0.08	0.06	0.08	0.09	0.06	0.05	0.02	0.1	0.1	0.05	0.07	0.05	0.06	0.06	0.05	0.09	0.1	-
22	MVZ 203751	*O. uniformis*	0.08	0.07	0.06	0.07	0.05	0.08	0.07	0.04	0.04	0.04	0.09	0.09	0.03	0.08	0.01	0.06	0.05	0.04	0.09	0.09	0.05

FIGURE 2. Adult female paratype of *Oedipina quadra* (USNM 343452). Photograph by J. R. McCranie.

Paratypes (29). MVZ 257755, USNM 563379–80, same data as holotype, except collected on different dates; MVZ 257756, USNM 563378, Warunta Tingni Kiamp, 14°55'N, 84°41'W, 150 m a.s.l., Dept. Gracias A Dios, Honduras; USNM 560949, between Urus Tingni Kiamp and Warunta Tingni Kiamp, 190 m a.s.l., Dept. Gracias A Dios, Honduras; USNM 560948, Cabeceras de Río Rus Rus, 14°53'N, 84°40'W, 190 m a.s.l., Dept. Gracias A Dios, Honduras; MVZ 232824, MVZ 257757, Kaska Tingni, 14°48'N, 84°46'W, 70 m a.s.l., Dept. Gracias A Dios, Honduras; USNM 534115–19, Quebrada Machín, 15°19'N, 85°17'W, 540 m a.s.l., Dept. Colón, Honduras; CM 68241, LSUMZ 33608, Cerro Calentura S of Trujillo, Dept. Colón, Honduras; USNM 343452, confluence of ríos Yanguay and Wampú, 15°03'N, 85°08'W, 110 m a.s.l., Dept. Olancho, Honduras; USNM 343453, confluence of ríos Sausa and Wampú, 15°04'N, 85°06'W, 100 m a.s.l., Dept. Olancho, Honduras; USNM 343454, confluence of Quebrada Siksatara and Río Wampú, 15°04'N, 85°02'W, 95 m a.s.l., Dept. Olancho, Honduras; USNM 316539, 7.4 km SE of La Ceiba, 260 m a.s.l., Dept. Atlántida, Honduras; LACM 4702–04, LSUMZ 21327, mountain S of Corozal, 200–250 m a.s.l., Dept. Atlántida, Honduras; SMF 77486, USNM 530579, MVZ 257758-60, Parque Nacional Pico Bonito Centro de Visitantes (also called Estación Forestal de CURLA), 15°42'N, 86°51'W, 120–500 m a.s.l., Dept. Atlántida, Honduras.

Referred material (4). LSUMZ 21326 (juvenile), same data as paratype LSUMZ 21327; UMMZ 58610 (juvenile), Río Claura, Dept. Colón, Honduras; BMNH 1985.1229–30 (both poorly preserved), Quebrada Limoncito, 250 m a.s.l., Dept. Colón, Honduras.

Diagnosis. A moderate-sized (maximum known size 55.5 mm SL) species distinguished from *Oedipina cyclocauda* of Costa Rica (the species with which this population was previously tentatively identified in McCranie & Wilson 2002 and McCranie & Castañeda 2007) by having the tail nearly rectangular in cross section throughout its length (versus nearly round for most or all of its length in *O. cyclocauda*; McCranie pers.

obs., also see Taylor 1952); from the second new species described herein by having more maxillary teeth, a larger maximum SL, and by lacking silver white dorsolateral spots and flecks in life; from all described Honduran species of the subgenus *Oedipina* (*O. ignea, O. stuarti, O. taylori* and the third species described herein) in the following ways: from *ignea* in having a nearly rectangular tail and smaller size; from *stuarti* in lacking pale brown to dirty white small glandular spots on the head and body and by having a smaller size; from *taylori* in having 19–20 costal grooves, maxillary teeth, and a smaller size; from the third new species described below by inferred smaller size and better defined digits; from all described Honduran species of the subgenus *Oedopinola* (*O. elongata, O. gephyra* and *O. tomasi*) by having 19–20 costal grooves. In addition to these features this species is distinct from all others that have been studied in having phylogentically distinct mtDNA haplotypes (Fig. 1).

Description. This is a moderately sized, slender species; adult SL for seven males is 36.1–43.7, x = 41.6 mm; for 16 females 35.6–55.5, x = 45.0 mm. The head is small, narrow, and dorsally flattened, with a broadly rounded snout. SL averages 11.6 times head width in seven males (9.8–13.1) and 12.2 in 14 females (10.7–13.7). SL averages 6.4 times head length in seven males (5.6–6.7) and 6.7 in 14 females (5.7–7.7). Nostrils are small but conspicuous under magnification. Nasolabial protuberances are weakly developed in males and inconspicuous in females. Eyes are small and barely extend beyond the lateral margins of the head and are directed frontolaterally. Male mental glands are small, barely evident, located anteriorly on lower jaw. The suborbital groove does not intercept the lip line. There are 1–3 slightly enlarged premaxillary teeth in males that lie only slightly anteriorly to the maxillary teeth. There are 2–6 premaxillary teeth in females that are located well within the mouth and in line with the small maxillary teeth. Maxillary teeth number 37–47 (x = 42.3) in seven males and 28–53 (x = 43.0) in 13 females. Vomerine teeth are 15–20 (x = 17.5) in six males and 16–22 (x = 19.5) in 11 females; the small teeth are in an arched series. There are 19–20 costal grooves between the small limbs with a limb interval of 11.0–13.0 in four males and 14 females. Hands and feet are tiny, narrow and elongated. Digit I is fused with digit II and digit IV is fused with digit III on the forelimbs, with about 1.0 segments (phalanges) of digit III free between digits II–III on the forelimbs. Digit I is fused with digit II and digit V is fused with digit IV on the hind limbs, with about 1.0–2.0 segments on both sides of digit III free on the hind limbs (Fig. 3). Protruding digital tips are acutely rounded to bluntly rounded and bear weak subdigital pads. Digits on the forelimbs in order of decreasing length are III–II–IV–I; digits on the hind limbs are III–II– IV –V–I. The tail is nearly rectangular in cross section in almost all (somewhat rounded basally in MVZ 257759), tapering on distal one-third of its length, and long (1.3 [regenerated]–2.4 times SL in 13).

Measurements (in millimeters), limb interval and tooth counts of the male holotype. Head width 3.2; snout to gular fold (head length) 6.8; head depth at posterior angle of jaw 2.2; eyelid width 0.8; eyelid length 1.0; eye to nostril 0.8; anterior rim of eye to snout 1.2; horizontal orbital diameter 0.5; interorbital distance 3.1; distance separating eyelids 1.3; nostril diameter 0.3; snout projecting beyond mandible 0.3; distance from eye to distal end of postorbital groove 2.0; snout to posterior angle of vent (SL) 42.5; snout to anterior angle of vent 39.3; snout to forelimb 9.8; axilla to groin 26.9; limb interval 12 1/2; shoulder width 2.3; tail length 93; tail width at base 2.2; tail depth at base 2.2; forelimb length (to tip of longest digit) 2.2; hind limb length 3.2; forelimb foot width 0.9; hind limb foot width 1.2; free length of longest digit on hind limb 0.1. Numbers of teeth: premaxillary 2; maxillary 38; vomerine 15.

Coloration of the holotype in alcohol. Dorsal and lateral surfaces of the head, body, and tail are black. Costal grooves on the body and tail are dirty white. Ventral surfaces of the head, body, and tail are slightly paler black than those dorsal surfaces. Dorsal and ventral surfaces of the limbs are the same as for the body. Tiny, generally white to dirty white iridophores are visible throughout under magnification. There is a large patch of skin on the left side of the body where the black pigment is missing, perhaps the result of an old injury or a skin disease.

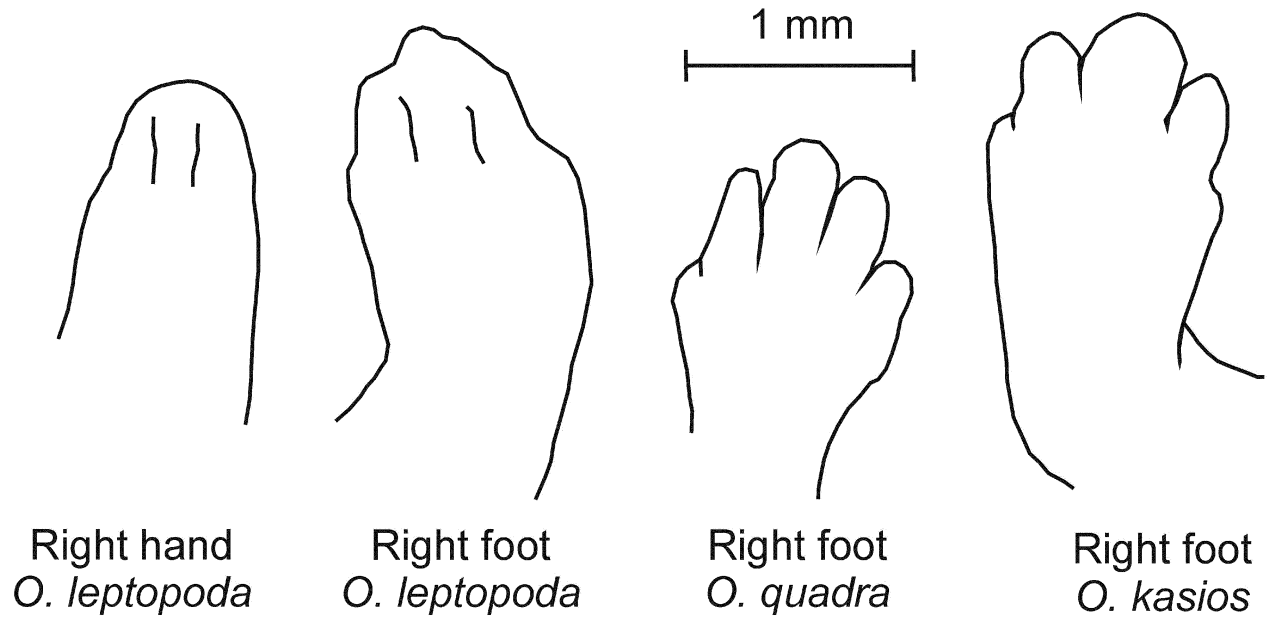

FIGURE 3. Schematic drawings of dorsal views of the limbs of *Oedipina*. From left to right, right hand and right foot of holotype of *O. leptopoda* (MVZ 167772), right foot of holotype of *O. quadra* (MVZ 257761), right foot of holotype of *O. kasios* (MVZ 232825). All drawings are at the same scale.

Color variability. The paratypes closely resemble the holotype, with the exception of the abnormal loss of pigment in the holotype, noted above. McCranie & Wilson (2002:152) described color in life for one female (USNM 343452) as: "dorsal surfaces of head, body, and tail black; lateral surfaces of head and body brownish black; lateral surface of tail black; dorsal surfaces of limbs and ventral and subcaudal surfaces brownish black."

Habitat and distribution. Salamanders of this species were collected from 70–540 m elevation in the Lowland Moist Forest formation of Holdridge (1967). Specimens were taken in either pristine broadleaf forest with a closed canopy or in secondary broadleaf forest with a partially open canopy. All were collected while raking through leaf litter during the day and at night. The known distribution of this species extends from just south of La Ceiba, Atlántida, eastward and southeastward to the Río Coco drainage system of northeastern Honduras (Fig. 4). The species probably occurs in suitable habitat on the Nicaraguan side of the Río Coco as well.

Comments. A few specimens are treated as referred material. We are confident of their assignment but they are either juveniles or poorly preserved and hence of no use in our description.

Etymology. The specific name *quadra* is a Latin adjective for square and alludes to the nearly rectangular tail characteristic of this species.

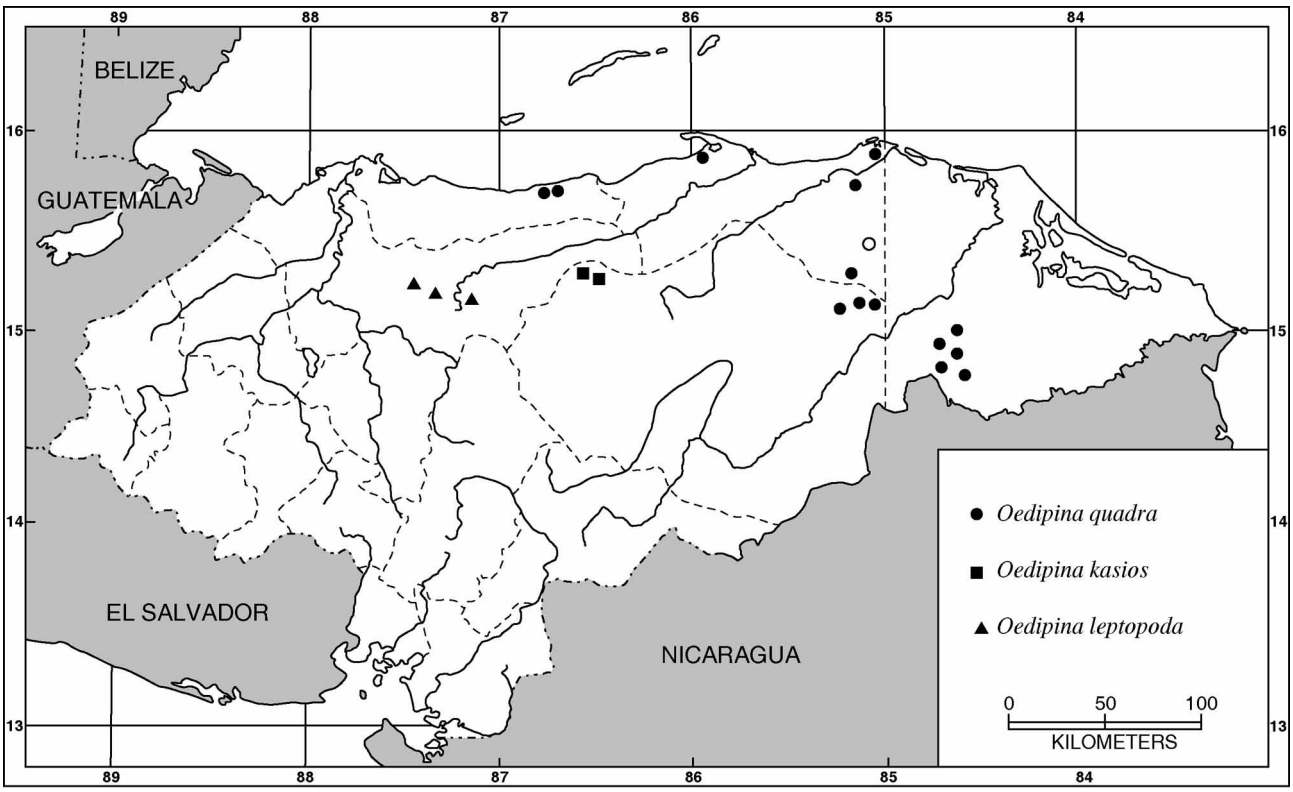

FIGURE 4. Map showing the collecting localities of *Oedipina quadra, O. kasios,* and *O. leptopoda.* The open circle represents a literature record (see McCranie 2006b).

***Oedipina kasios* sp. nov.**
Muralla Worm Salamander
Figure 5

Oedipina cyclocauda (part). McCranie & Wilson 2002, McCranie & Castañeda 2007.

Holotype. MVZ 232825, an adult female, from near Quebrada Pinol, 15°07'N, 86°44'W, Parque Nacional La Muralla, 1190 m a.s.l., Dept. Olancho, Honduras, collected 19 July 2001 by C. Sheehy, J. H. Townsend, and L. D. Wilson.

Paratypes (5). USNM 343455–56, confluence of quebradas Pinol and Las Cantinas, 15°09'N, 86°43'W, Parque Nacional La Muralla, 950 m a.s.l., Dept. Olancho, Honduras; MVZ 232826, same data as for holotype, except 1230 m a.s.l.; USNM 530580, Cerro de Enmedio, 15°06'N, 86°41'W, Parque Nacional La Muralla, 1780 m a.s.l., Dept. Olancho, Honduras; USNM 343457, Quebrada de la Escaleras, 15°12'W, 86°41'W, Parque Nacional La Muralla, 950 m a.s.l., Dept. Olancho, Honduras.

Referred material (1). USNM 530581 (juvenile), same data as paratype USNM 530580.

Diagnosis. A small (maximum known size 46.8 mm SL) species distinguished from *Oedipina cyclocauda* of Costa Rica (the species with which this population was previously tentatively identified in McCranie & Wilson 2002 and McCranie & Castañeda 2007) by having the tail nearly rectangular in cross section throughout its length (versus nearly round for most or all of its length in *O. cyclocauda*; McCranie pers. obs., also see Taylor 1952); from *O. quadra* by having fewer maxillary teeth, silver white dorsolateral spots and flecks visible to the unaided eye in life, and a smaller maximum SL; from all described Honduran species of the subgenus *Oedipina* (*O. ignea, O. stuarti* and *O. taylori* by its much smaller size (or inferred smaller size, see below); from the third new species described herein by inferred smaller size and better defined digits; from all described Honduran species of the subgenus *Oedopinola* (*O. elongata, O. gephyra* and *O. tomasi*) by having 19–20 costal grooves. In addition to these features this species is distinct from all others that have been studied in having phylogenetically distinct mtDNA haplotypes (Fig. 1).

1.2; eye to nostril 0.5; anterior rim of eye to snout 1.2; horizontal orbital diameter 0.6; interorbital distance 2.4; distance separating eyelids 1.2; nostril diameter 0.2; snout projecting beyond mandible 0.3; distance from eye to distal end of postorbital groove 1.4; snout to posterior angle of vent (SL) 41.9; snout to anterior angle of vent 39.2; snout to forelimb 7.9; axilla to groin 28.4; limb interval 12; shoulder width 2.2; tail length 76+ (tip removed for tissue sample); tail width at base 1.8; tail depth at base 1.9; forelimb length (to tip of longest digit) 3.3; hind limb length 3.5; forelimb foot width 0.6; hind limb foot width 0.8; free length of longest digit on hind limb 0.1. Numbers of teeth: premaxillary 5; maxillary 35; vomerine 16.

Coloration of the holotype in alcohol. Dorsal and lateral surfaces of the head, body, and tail are medium brown with a grayish tinge on the body and tail. Tiny white spots or flecks are present on the lateral surface of the body. Costal grooves on the body and tail are pale brown. Ventral surfaces of the head, body, and tail are slightly paler brown than the dorsal surfaces and without a grayish tinge. Dorsal and ventral surfaces of the limbs are the same as for the body, except that the soles of all four feet are pale brown to cream. Tiny, generally pale brown iridophores are visible throughout under magnification, except on the soles of the feet.

Color variability. The paratypes closely resemble the holotype in coloration, except that one (USNM 530580) is slightly darker brown overall and some (i.e., MVZ 232826) have more tiny white spots or flecks on the lateral surface of the body. McCranie & Wilson (2002:152) described the color in life of two males (USNM 343455–56) as: "all dorsal surfaces Grayish Brown (20), although that of head a slightly paler shade of brown; dorsolateral surface of body with silver-white flecks visible to unaided eye; ventral and subcaudal surfaces similar to dorsal surface of head." Those same authors also described color in life of a female (USNM 530580) as: "all dorsal surfaces Jet Black (89), although that of head a slightly paler shade of black; dorsolateral surface of body with numerous scattered olive-green and white flecks visible to unaided eye; ventral and subcaudal surfaces Dark Neutral Gray (83), except chin somewhat paler; iris black."

Habitat and distribution. Salamanders of this species were collected from 950–1780 m elevation in the Premontane Wet Forest and Lower Montane Wet Forest formations of Holdridge (1967). All specimens were taken in pristine broadleaf forest ranging from partial to complete canopy cover. Most were found under rotten logs, but two were inside a rotten log that also contained four *Nototriton lignicola*. All known localities are within Parque Nacional La Muralla in northwestern Olancho (Fig. 4).

Comments. The specimen referred to this species is a juvenile and was not useful in preparing the description.

Etymology. The specific name *kasios* is Greek for sister and is used in reference to this species being the sister species of *Oedipina quadra* in our phylogenetic analysis. The name is used as a noun in apposition.

Subgenus *Oedipina*

***Oedipina leptopoda* sp. nov.**
Narrow-footed Worm Salamander

Oedipina cyclocauda (part), Brame 1968, Good & Wake 1998, García-París & Wake 2000, McCranie & Wilson 2002, McCranie & Castañeda 2007.

Holotype. MVZ 167772, a subadult female from 32 km (road) W of Yoro on road to Morazán, 15.267480 N, 87.434820 W, Dept. Yoro, Honduras, collected 8 January 1979 by E. J. Koford and J. F. Lynch.

Paratype. MVZ 171078, adult male from Montaña de Yoro, 6.6 km (road) S of Yoro, 15.073650 N, 87.1333 W, Dept. Yoro, Honduras.

Referred material (1). FMNH 34683 (subadult), Portillo Grande, Dept. Yoro, Honduras.

Diagnosis. A small to moderate sized (holotype is a subadult at 29.6 mm SL) member of *Oedipina*. Distinguished from *Oedipina cyclocauda* of Costa Rica (the species with which this population was previously identified by Good & Wake 1998 and García-París & Wake 2000) by its inferred larger size and narrower hands and feet with less discrete digits. It differs from other described Honduran species of the subgenus *Oedipina* (*O. ignea, O. stuarti,* and *O. taylori*) in the following ways: from *ignea* in having more maxillary teeth and narrower hands and feet; from *stuarti* in being smaller, having much narrower hands and feet, and lacking glandular spots on its head and body; from *taylori* in having a broader head, narrower hands and feet, shorter body and tail, and 19-20 costal grooves; from members of the subgenus *Oeditriton* (*O. quadra* and *O. kasios*) in being larger (based on the size of the paratype), having relatively smaller limbs and hands and feet, and a rounded body and tail; from all described Honduran species of the subgenus *Oedopinola* (*O. elongata, O. gephyra* and *O. tomasi*) by having 19–20 costal grooves. In addition to these features, this species differs in allozymic (Good & Wake 1998) and mtDNA characters (Fig. 1) from all members of the genus in which those characters are known

Description. This is a slender species of moderate size, judging from the fact that the paratype is an adult male, the smaller sex in this genus, at a size larger than that of several other species in the subgenus. The head is relatively broad (SL 7.4-9.8 times head width), rounded rather than flattened, and with a narrowly rounded snout (expanded and broadly rounded in the paratype, an adult male 47.9 SL). Nostrils are small and conspicuous. Nasolabial protuberances are moderate. Eyes are of moderate size and barely extend beyond the lateral margins of the head. The suborbital groove does not intercept the lip line. There are 5 small premaxillary teeth in the holotype and a single slightly larger tooth in the adult male paratype. The teeth are near the front but inside of the mouth, well separated from the maxillary teeth. There are 29 maxillary teeth in the holotype and 40 in the paratype. The holotype has 10 vomerine teeth and the paratype has 17. The vomerine teeth are small and in an arched series. The holotype and paratype have 19 costal grooves between the slender limbs, with a limb interval of 12 in both specimens. Hands and feet are extraordinarily narrow, small and flattened (Fig. 3). In the holotype digits can be discerned only because there are ill-defined grooves on the dorsal surfaces that suggest where digital borders lie. All of the digits are tightly fused, all the way to their tips in the holotype but there are small, rounded, independent tips of the three longest digits of both forelimbs and hind limbs of the paratype. In the holotype the longest digit is pointed, and it extends less then 0.2 mm from the ends of the neighboring digits. The holotype lacks a tail and has been almost completely eviscerated (for tissue sample used in allozyme and DNA studies). The paratype has a rather stout, round tail that is broken 44.4 mm from its base, and it doubtless greatly exceeded SL in the intact animal.

Measurements (in millimeters), limb interval and tooth counts of the female holotype. Head width 4.0; snout to gular fold (head length) 5.4; head depth at posterior angle of jaw 2.1; eyelid width 0.5; eyelid length 1.3; eye to nostril 1.2; anterior rim of eye to snout 1.3; horizontal orbital diameter 1.0; interorbital distance 1.7; distance separating eyelids 1.1; nostril diameter 0.2; snout projecting beyond mandible 0.2; distance from eye to distal end of postorbital groove 1.5; snout to posterior angle of vent (SL) 29.6; snout to anterior angle of vent 28.3; snout to forelimb 7.5; axilla to groin 18.2; limb interval 12; shoulder width 2.7; tail length 33.2; tail width at base 1.5; tail depth at base 1.8; forelimb length (to tip of longest digit) 3.9; hind limb length 4.2; forelimb foot width 0.6; hind limb foot width 0.8; free length of longest digit on hind limb 0.2. Numbers of teeth: premaxillary 5; maxillary 29; vomerine 10.

Coloration of the holotype and paratype in alcohol. The holotype, while apparently well preserved, appears to be faded and the overall coloration is now moderate brown. The head, especially the snout, is significantly paler than the rest of the specimen. The paratype is all black, darker dorsally and laterally than ventrally. The swollen snout and the nasolabial protuberances are much lighter, pale gray. The small and inconspicuous mental gland is pale gray.

Habitat and distribution. The species is known only from three specimens collected many years ago. Field notes are precise with respect to locality, two from west and one from south of Yoro (Fig. 4), but vague with respect to habitat. The estimated elevation for these specimens is from ca. 700 to 1300 m a.s.l.

Comments. The specimen referred to this species is a poorly preserved subadult with sufficient morphological detail to make it a likely member of this species, and its collecting site is also appropriate for this

assignment. The paratype is an intact specimen with good preservation of color, whereas the holotype is eviscerated and faded but otherwise well preserved. However, because the two specimens are not syntopic and because we have molecular data only from the holotype, we elected to use the specimen for which we have the best documentation as the holotype.

Etymology. The specific name *leptopoda* is derived from the Greek *lepto-* for small or fine and *podos* for foot, and is used as an adjective in reference to the very small and narrow hands and feet of this species.

Discussion

Keferstein (1868) described the genus *Oedipina* (*O. uniformis* type species by monotypy). Later, Hilton (1946) proposed the new genus *Oedopinola* (he assigned two species to the genus: *O. complex*, the type species, and *O. parvipes*), based on a morphological analysis of very limited taxon sampling. He erroneously wrote *Oedopina* for the genus *Oedipina* (thus naming his new genus *Oedopinola*). Hilton made another mistake in assuming the species *lineola* to be a species of *Oedipina*. Tanner (1950) removed *lineola* from *Oedipina* and designated it the type species of his new genus *Lineatriton*; he also synonymized *Oedopinola* with *Oedipina*. Brame (1968), using external morphology, placed all species of *Oedipina* in two groups: *uniformis* and *parvipes*. Good & Wake (1998) followed Brame's taxonomy in general, recognizing four clades (*cyclocauda, parvipes, poelzi, uniformis*), with the *parvipes* clade sister to the others and the species they identified as *O. ignea* (the populations they studied were later assigned to *O. stenopodia*, see García-París & Wake 2000) not being assigned to a clade but considered sister to the *uniformis* clade (we recognize a *stenopodia* subclade in this paper for *O. ignea* and *O. stenopodia*). Good & Wake (1998) identified eight morphotypes among the 12 species they sampled, seven of them within Brame's *uniformis* group, with two species unassigned. Brame's two groups were recognized as subgenera (*Oedipina* and *Oedopinola*, respectively) by García-París & Wake (2000), who updated their content by adding recently recognized species. These two subgenera were recovered as reciprocally monophyletic in all topologies presented by García-París & Wake (2000), although statistical support for the clades was high only in the case of subgenus *Oedipina*. Our maximum likelihood analysis also recovered these two clades, with high statistical support for *Oedipina* and moderate support for *Oedopinola*, but the Bayesian inference of phylogeny shows strong support for both clades. Our analyses also recovered a third clade, well supported both by ML and Bayesian methods, and sister to the two subgenera *Oedipina* and *Oedopinola*. This third clade is constituted by two of the three species that we describe in this paper (*O. quadra* and *O. kasios*), and we recognize it as a new subgenus *Oeditriton*. Our topology suggests that *Oeditriton* is sister to *Oedipina* and *Oedopinola*, although not with very high statistical support. The mean K2P genetic distances between *Oeditriton* and *Oedipina* is 10%, and between *Oeditriton* and *Oedopinola* is 11%; these values are greater than that between *Oedipina* and *Oedopinola* (9%, Table 1), concordant with the recovered topological relationships.

All four of the subclades we recognize within the subgenus *Oedipina* (*cyclocauda, stenopodia, poelzi, uniformis*) were recovered with statistical support by phylogenetic analyses of mitochondrial DNA (García-París & Wake 2000), although their basal relationships were not supported. In our analyses the *stenopodia* subclade has high support (Fig. 1). The *cyclocauda* subclade has strong support and the *poelzi* subclade has weak support (53 ML bootstrap), whereas the *uniformis* subclade is not supported and has a weak relationship with the *cyclocauda* subclade (52 ML bootstrap). Both ML and Bayesian approaches supported the northern *stenopodia* subclade as the sister to the rest. The third new species we describe here, *O. leptopoda*, has somewhat ambiguous relationships. Topologically it is a part of the *poelzi* subclade, clustering with *O. grandis* and *collaris*, although its position and relationships with other species of this subclade are not well supported. This may be because we only have cytochrome b data for this species, which might also influence the lack of support for the *uniformis* or *collaris* groups. Good & Wake (1998) reported some allozymic data for the holotype of *leptopoda*. At 13 of 18 loci it was identical to *O. cyclocauda* of Costa Rica, and it was closer to that species (Nei D = 0.31) than any other taxon, but the study of this specimen was incomplete and inconclusive. The species is included within a well-supported group that includes the *poelzi, cyclocauda* and *uniformis* subclades.

When García-Paris & Wake (2000) raised the two species groups of Brame (1968) to subgeneric status they thought that there were reliable morphological characters that diagnosed the two, including differences in numbers of trunk vertebrae, as well as features of the skull and limbs. However, the discovery that *O. gephyra* is a member of *Oedopinola*, and yet has a general morphology more typical of subgenus *Oedipina* (except for the 18–19 trunk vertebrae), showed that the morphological distinction between members of these two taxa is not sharp. Our discovery of a new clade, *Oeditriton*, further complicates the picture, because this may be the first branching clade of the genus. The two known members of *Oeditriton* are diminutive and have very small limbs, hands and feet, and poorly-developed, indistinct digits. The most distinctive species of the entire genus are the relatively large, robust, long-limbed, large-footed, white-headed and white-spotted species *O. carablanca* and *O. elongata* (see photographs on AmphibiaWeb), and the enormous *O. collaris,* which has a very long, sharply pointed snout. In general, the slender, long-bodied, long-tailed, short-legged, small-limbed, short-digited morphology of *Oeditriton*, most members of subgenus *Oedipina*, and some *Oedopinola*, makes these species very difficult to identify on morphological grounds alone. Doubtless there has been extensive homoplasy associated with evolution of this specialized ecomorphology associated with the semifossorial or fossorial way of life that makes members of the genus so difficult to find.

The discovery of a previously unknown, very divergent lineage is congruent with the hypothesis that the diversity of tropical salamanders is not yet well understood and probably is underestimated. The number of new species of tropical salamanders described in the last decade (173 were recognized in 1998, contrasted now with 236; the present total number of salamanders of all taxa is 570, AmphibiaWeb 2008) supports this claim. Some of the salamander lineages that have been recently discovered are highly divergent, including the discovery of a new genus of plethodontid salamander in South Korea (Min *et al.* 2005). Many of the new species recently described are tropical bolitoglossines, and they usually show a high degree of genetic divergence. The new subgenus *Oeditriton* is very divergent from the other subgenera within the genus *Oedipina*, but also, the genetic diversity within each of these subgenera is very high. The mean K2P genetic distances for 16S within *Oeditriton* (5%), *Oedopinola* (8%) and *Oedipina* (6%), are very high and extend to 11% divergence, suggesting that these species are old or have high rates of evolution, although no support has been found for the later (i.e. Vences *et al.* 2005).

The evolutionary history of tropical salamanders is far from being well understood, and more divergent lineages are expected from poorly explored areas. Honduras harbours representatives of the three major clades of *Oedipina* identified in our analyses. However, there are more species of *Oedipina* in Costa Rica and probably in Panama than in Honduras. Specimens of *Oedipina* are elusive and many species are known from only a handful of specimens. Discovery of specimens for most species of the genus is haphazard and probably related to the fossorial habits of most of the species, as exemplified by the recent discovery of two specimens of a previously unknown species in the best studied cloud forest region of Honduras (McCranie 2006a).

A series of four specimens in the collection of the first author having 19 costal grooves (suggesting 20 trunk vertebrae) from the Sierra de Agalta in central Olancho, Honduras, was previously identified as *Oedipina cyclocauda* (see Castañeda 2006 and Map 20 in McCranie & Castañeda 2007). However, these specimens are unlikely to be members of that species and they are not likely members of any species treated herein. Based on color in alcohol and foot morphology, they appear most similar to *O. quadra*, but they are from an isolated locality and from higher elevations (1100–1250 a.s.l.) than the populations assigned to *O.quadra* herein. We await availability of tissues and molecular analysis before assigning these specimens.

Acknowledgments

Permits for the Honduran salamanders collected for this study were provided by the personnel of COHDEFOR, Tegucigalpa (copies on file at the MVZ and in the possession of the first author). We thank Brian Kubicki, Federico Bolaños, Gunther Köhler, and Karen Lips for tissue samples, Seth Thomas for laboratory assistance and Mario García-París for consultation and early analysis. This research was supported in part by National Science Foundation Amphibian Tree of Life Grant EF-0334939.

References

AmphibiaWeb: Information on amphibian biology and conservation. [web application]. 2008. Berkeley, California: AmphibiaWeb. Available: http://amphibiaweb.org/. (Accessed: Sept 14, 2008).

Brame Jr., A.H. (1968) Systematics and evolution of the Mesoamerican salamander genus *Oedipina*. *Journal of Herpetology*, 2(1–2), 1–64.
Bruford, M., Hanotte, O., Brookfield, J. & Burke, T. (1992) Single locus and multilocus DNA fingerprint. *In*: Hoelzel, A. (Ed.), *Molecular Genetic Analysis in Conservation*. IRL Press, Oxford, pp. 225–270.
Castañeda, F.E. (2006) *Herpetofauna del Parque Nacional Sierra de Agalta, Honduras*. Unpubl. Report of International Resources Group. Washington, 68 pp.
Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.
García-París, M. & Wake, D.B. (2000) Molecular phylogenetic analysis of relationships of the tropical salamander genera *Oedipina* and *Nototriton*, with descriptions of a new genus and three new species. *Copeia*, 2000(1), 42–70.
Good, D.A. & Wake, D.B. (1998; dated 1997) Phylogenetic and taxonomic implications of protein variation in the Mesoamerican salamander genus *Oedipina* (Caudata: Plethodontidae). *Revista de Biología Tropical*, 48(3), 1185–1208.
Hilton, W.A. (1946) Salamanders from Barro Colorado Island, Canal Zone. *Journal of Entomology and Zoology*, 38(3), 37–39.
Holdridge, L.R. (1967) *Life Zone Ecology. Revised Edition*. Tropical Science Center, San José, Costa Rica, 206 pp.
Keferstein, W. (1868) Beschreibung einiger neuen Batrachier aus Australien und Costarica. *Nachrichten von der K. Gesellschaft der Wissenschaften und der Georg-Augusts-Universität Göttingen*, 15, 326–332.
Leviton, A.E., Gibbs Jr., R.H., Heal, E., & Dawson, C.E. (1985) Standards in herpetology and ichthyology. Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985(3), 802–832.
McCranie, J.R. (2006a) New species of *Oedipina* (Amphibia: Caudata) from Parque Nacional El Cusuco, northwestern Honduras. *Journal of Herpetology*, 40(3), 291–293.
McCranie, J.R. (2006b) Specimen locality data & museum numbers/Ubicación y números de museo de los especímenes, información complementary for/a la "Guía de Campo de los Anfibios de Honduras" by/por James R. McCranie and Franklin E. Castañeda. *Smithsonian Herpetological Information Service*, 137, 1–39.
McCranie, J.R. & Castañeda, F.E. (2007) *Guía de Campo de los Anfibios de Honduras*. Bibliomania!, Salt Lake City, 304 pp.
McCranie, J.R. & Wilson, L.D. (2002) *The Amphibians of Honduras*. Society for the Study of Amphibians and Reptiles, Ithaca, New York, 625 pp.
Min, M.S., Yang, S.Y., Bonett, R.M., Vieites, D.R., Brandon, R.A. & Wake, D.B. (2005) Discovery of the first Asian plethodontid salamander. *Nature*, 435, 87–90.
Moritz, C., Schneider, C.J. & Wake, D.B. (1992) Evolutionary relationships within the *Ensatina eschscholtzii* complex confirm the ring species interpretation. *Systematic Zoology*, 41, 273–291.
Nylander, J.A.A. (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
Palumbi, S.R., Martin, A., Romano, S., McMillan, W.O., Stice, L. & Grabowski, G. (1991) *The Simple Fool's Guide to PCR, Version 2.0*, privately published document compiled by S. Palumbi. Dept. Zoology, Univ. Hawaii, Honolulu, HI.
Ronquist, F. & Huelsenbeck. J. P. (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
Smithe, F.B. (1975–1981) *Naturalist's Color Guide. Part I. Color Guide*. American Museum of Natural History, New York, 182 color swatches.
Stamatakis, A., Ludwig, T & Meier H. (2005) RAxML-III: A Fast Program for Maximum Likelihood-based Inference of Large Phylogenetic Trees. *Bioinformatics*, 21(4), 456–463.
Swofford, D.L. (2003) PAUP*. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, USA.
Tanner, W.W. (1950) A new genus of plethodontid salamander from Mexico. *Great Basin Naturalist*, 10, 37–44.
Taylor, E.H. (1952) The salamanders and caecilians of Costa Rica. *University of Kansas Science Bulletin*, 34(12), 695–791.
Vences, M., Thomas, M., Bonett, R.M. & Vieites, D.R. (2005) Deciphering amphibian diversity through DNA barcoding: chances and challenges. *Philosophical Transactions of the Royal Society London, Ser. B*, 360, 1859–1868.
Wake, D.B. & Elias, P. (1983) New genera and a new species of Central American salamanders, with a review of the tropical genera (Amphibia, Caudata, Plethodontidae). *Contributions in Science, Natural History Museum of Los Angeles County*, 345, 1–19.
Wiens, J.J., Parra-Olea, G., García-París M. & Wake, D.B. (2007) Phylogenetic history underlies elevational biodiversity in tropical salamanders. *Proceedings of the Royal Society London, Ser. B*, 274, 919–928.