A new species of worm salamander (Caudata: Plethodontidae: Oedipina) in the subgenus Oeditriton from the highlands of northern Nicaragua

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Abstract

We describe a new species of Oedipina (subgenus Oeditriton) from the highlands of north-central Nicaragua. The new species is most closely related to Oedipina kasios, a premontane species from north-central Honduras, and O. quadra, a lowland species from northern and eastern Honduras. It differs from O. kasios and O. quadra in molecular characters and by having a more slender habitus and fewer vomerine teeth. We also discuss the status of the additional populations of Oedipina from Nicaragua.

Key words: Oedipina nica sp. nov., mtDNA, cyt b, 16S, Reserva Natural Cerro Datanlí-El Diablo, Reserva Natural Cerro Kilambé, Reserva Natural Macizos de Peñas Blancas

Resumen

Describimos una nueva especie de Oedipina (subgénero Oeditriton) de las tierras altas del centro–norte de Nicaragua. La nueva especie está estrechamente relacionada con Oedipina kasios, una especie de las zonas premontanas situadas en el centro–norte de Honduras, y con O. quadra, una especie de las tierras bajas del norte y este de Honduras. La nueva especie se diferencia de O. kasios y O. quadra tanto genéticamente como por tener una apariencia más esbelta y un número menor de dientes vomerinos. También discutimos acerca del estatus de las poblaciones adicionales de Oedipina de Nicaragua.

Introduction

Worm salamanders (Caudata: Plethodontidae: Oedipina) are among the least known Nicaraguan amphibian taxa, probably as a result of their fossorial behavior. Confusingly similar in morphology, few specimens are deposited in museums worldwide and most of them lack fresh tissue samples for molecular analysis. Currently, 28 species of Oedipina are recognized, collectively distributed from southeastern Mexico to northwestern South America (AmphibiaWeb 2010). Although Nicaragua is the largest and most centrally located country in Central America, only three species of Oedipina have been reported (Brame 1968), i.e., O. collaris, O. cyclocauda, and O. pseudouniformis, species otherwise known to occur in Costa Rica (all three species) and Panama (O. collaris and O. cyclocauda). Recently, populations of Oedipina from Honduras
previously referred to as O. cyclocauda were allocated to three new species, two of which belong to a previously unknown and deeply divergent clade recognized as the subgenus Oeditriton (McCranie et al. 2008). We recently collected a series of specimens of Oedipina from three localities in the highlands of north-central Nicaragua. Based on molecular and morphological analyses, we consider the members of this series to represent an undescribed species of Oeditriton. This new species is the third member of Oeditriton recognized and is the southernmost representative of the clade, as well as the only species known to occur outside of Honduras. Herein we describe this new species, include it in a new phylogenetic hypothesis for the genus Oedipina, and comment on our understanding of the Nicaraguan populations of Oedipina.

Material and methods

Taxon sampling. For the phylogenetic analyses, we included representatives of all species of Oedipina available on GenBank (http://www.ncbi.nlm.nih.gov), and the species, localities, and voucher information for these taxa is summarized in Table 1. Acronyms for museum collections follow those of Leviton et al. (1985), except for USAC (Universidad de San Carlos de Guatemala, Guatemala City, Guatemala). We included samples from the three known populations of the new species, including one from Reserva Natural Cerro Datanlí-El Diablo, two from Reserva Natural Macizos de Peñas Blancas, and five from Reserva Natural Cerro Kilambé (see Table 1); two of the samples from Reserva Natural Cerro Kilambé are tails that were dropped by adults that subsequently escaped, and are included in the phylogenetic analyses and listed as referred specimens, since they were of no value to the morphological description. The Honduran species Nototriton barbouri, a member of the genus most closely related to Oedipina (García-París & Wake 2000; Wiens et al. 2007), was used as an outgroup.

Morphological examinations. Measurements follow those used in McCranie et al. (2008). All measurements 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. SL is the distance from the tip of the snout to the posterior angle of the vent. Males were identified by the presence of mental glands behind the tip of the mandible and small papillae in the anterior margins of the vent, females by the presence of folded vent margins. Maxillary and vomerine tooth counts are totals for the paired bones. Limb interval equals the number of costal interspaces between adpressed limbs.

DNA extraction and sequencing. For the holotype of the new species and specimens of O. taylori and O. tomasi, DNA was extracted using a Qiagen DNeasy Tissue Kit (Qiagen, Valencia, CA) following the manufacturer's instructions. A 516 bp fragment of the 16S large subunit rRNA gene (16S) was amplified using primers 16Sar-L and 16Sbr-H (Palumbi et al. 1991) and a 807 bp fragment of cytochrome b (cyt b) was amplified using primers MVZ15 and MVZ16 (Moritz et al. 1992). Reactions were run with an initial denaturation at 94°C for 2 min, 38 amplification cycles of 94°C for 30 s, 30 s (16S) or 1 min (cyt b) annealing at 48°C, 1 min extension at 72°C, with a final cycle at 72°C for 8 min. PCR products were cleaned with USB ExoSAP-IT and sequenced on an ABI 3730 automated sequencer (Applied Biosystems, Foster City, CA). For the paratypes and the sample of Oedipina kasios from Francisco Morazán, Honduras, template DNA was extracted from tissue with a Qiagen PureGene DNA Isolation Kit (Qiagen, Valencia, CA) following manufacturer’s instructions. A 516 bp fragment of 16S and a 692 bp fragment of cyt b were amplified using the aforementioned primer sets. Conditions for PCR did not differ among genes, with initial denaturation at 94°C for 3 min, 35 amplification cycles of 45s at 94°C, 45s annealing at 50°C, 45s extension at 72°C, and a final extension of 5 min at 72°C. Samples were cleaned of unincorporated dNTPs through application of USB ExoSAP-IT before following standard sequencing protocol on an ABI 3130xl automated sequencer (Applied Biosystems, Foster City, CA).

Phylogenetic analyses. Sequences were aligned using Muscle 3.6 (Edgar 2004). Cytochrome b sequences were trimmed to 385 bp to match available sequences in Genbank from other studies (McCranie et al. 2008; García-París et al. 2000). Both maximum likelihood and Bayesian phylogenetic analyses were performed, with sequence data partitioned by gene and by codon position for cyt b. The following models of nucleotide
substitution for the Bayesian analysis were selected using the Akaike Information Criterion in MrModeltest2.2 (Nylander 2004): 16S - GTR+I+Γ, cyt b codon 1 - SYM+Γ, cyt b codon 2 - HKY, cyt b codon 3 - GTR+Γ. Bayesian phylogenetic analysis was performed using MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001), with an MCMC of 10,000,000 generations, sampled every 1000 generations, 4 chains and 2 runs. The first 2000 samples were discarded as burn-in. Convergence was assessed by examining the cumulative and sliding window plots of split frequencies for trends, as well as by examining the correlation of split frequencies in the first vs. second run, using the program AWTY (Nylander et al. 2008). Maximum likelihood phylogenetic analysis was performed using the program RAxML v7.0.4 (Stamatakis 2006), with a GTR+Γ model used for all partitions and 100 bootstrap replicates.

**TABLE 1.** Samples utilized in the phylogenetic analyses, voucher numbers, locality information, and GenBank accession numbers.

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**Oedipina nica** sp. nov.
Nicaraguan Highland Worm Salamander

Figure 1


**Paratypes (5).** UF 156445, from Reserva Natural Cerro Kilambé, 13°34’N, 85°42’W, 1625 m a.s.l., Dept. Jinotega, Nicaragua; UF 156446–47, from Reserva Natural Cerro Kilambé, 13°35’N, 85°43’W, 1660 m a.s.l., Dept. Jinotega, Nicaragua; UF 156453–54, from Reserva Natural Macizos de Peñas Blancas, 13°17’N, 85°43’W, 1515 m a.s.l., Dept. Jinotega, Nicaragua.

**Referred specimens (12).** SMF 78736, from Camp El Hielo, Reserva Natural Cerro Kilambé, 1490 m a.s.l., Dept. Jinotega, Nicaragua; SMF 78737, 78739–40, from Camp 2, Reserva Natural Cerro Kilambé, 13°35.25’N, 85°41.50’W, 1360 m a.s.l., Dept. Jinotega, Nicaragua; UF 156443–44, from Reserva Natural Cerro Kilambé, 13°34’N, 85°42’W, 1625 m a.s.l., Dept. Jinotega, Nicaragua; UF 156448–50, from Reserva Natural Cerro Kilambé, 13°35’N, 85°43’W, 1660 m a.s.l., Dept. Jinotega, Nicaragua; UF 156451–52, two tails dropped by escaped adults from Reserva Natural Cerro Kilambé, 13°34’N, 85°42’W, 1600 m a.s.l., Dept. Jinotega, Nicaragua; UF 156455 from Reserva Natural Macizos de Peñas Blancas, 13°17’N, 85°43’W, 1515 m a.s.l., Dept. Jinotega, Nicaragua.

**Diagnosis.** A slender, small-sized (largest specimen 48.5 mm SL) species assigned to the genus _Oedipina_ based on the presence of a high number (19–20) of costal grooves between the short limbs, very narrow.
manus and pes, long tail (tail length ca 2 x SL), overall morphological similarity to other Oedipina species, and molecular phylogenetic evidence. This species is a member of the subgenus Oeditriton (based on molecular data; Fig. 2) and is distinguished from the only other members of that clade (O. kasio and O. quadra) by its more slender habitus and fewer vomerine teeth. Further distinguished from other Nicaraguan members of the genus Oedipina as follows: from O. collaris by being much smaller and more slender, having short limbs and narrow manus and pes, and having a short, rather bluntly tipped snout; from O. cyclocauda by being smaller and more slender without nearly pad-like feet; from O. pseudouniformis by being more slender with shorter, less robust limbs and narrower manus and pes, and by having almost uniformly dark brownish-black coloration with no distinct light pigmentation on the upper parts of the proximal segment of the limbs.

FIGURE 2. Maximum likelihood phylogram (lnL = -5370.356) of Oedipina, showing placement of O. nica within the Oeditriton subgenus. Maximum likelihood bootstrap support values shown above branches, Bayesian posterior probabilities shown below branches. Support values below 50 not shown. Holotype of O. nica shown in bold.

**Description of the holotype.** The male holotype is 39.2 mm SL and is judged to be an adult by the presence of small papillae in the anterior margins of the vent and a small mental gland behind the anterior tip of the mandible. The small head is rounded in dorsal profile, and somewhat flattened in lateral profile with a relatively blunt snout and distinct nasolabial protuberances. Snout to posterior angle of vent 9.8 times head width and 6.5 times head length. Nostrils are small but conspicuous under magnification. The small eyes are inconspicuous and do not extend beyond the lateral margins of the head. The suborbital groove does not intercept the lip line. The skin of the dorsal surface of the head behind the eyes is depressed in a pattern that suggests the presence of a frontoparietal fenestra. There is a single slightly enlarged premaxillary tooth that is located distinctly anterior to the maxillary teeth. Maxillary teeth total 41. The small vomerine teeth are in a short, fairly straight series and total 11. There are 20 costal grooves between the small limbs with a limb
interval of 13 intercostal folds. 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 only a part of a phalangeal segment 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; both outer digits are extremely short on the hind limbs. The triangular tip of digit III of the hind limb is distinct from the tiny rounded tips of digits II and IV, but less than a full phalangeal segment of that digit is free of the others. Subdigital pads are nearly imperceptible. Digits on forelimbs in order of decreasing length are III–II–IV–I; digits on hind limbs are III–II–IV–(V–I). The tail is round in cross section and tapers gradually to a narrow tip; the tail is almost twice SL.

Measurements (in millimeters) of the holotype. Head width 4.0; snout to gular fold (head length) 6.0; head depth at posterior angle of jaw 1.8; eyelid width 1.1; eyelid length 1.5; eye to nostril 0.6; anterior rim of eye to snout 1.2; horizontal orbital diameter 1.0; interorbital distance 1.7; distance separating eyelids 0.7; nostril diameter 0.2; snout projecting beyond mandible 0.4; distance from eye to distal end of postorbital groove 1.9; snout to posterior angle of vent (SL) 39.2; snout to anterior angle of vent 37.0; snout to forelimb 9.4; axilla to groin 26.0; limb interval 13; shoulder width 2.7; tail length 77.0; tail width at base 2.4; tail depth at base 2.4; forelimb length (to tip of longest digit) 3.7; hind limb length (to tip of longest digit) 4.5; forelimb foot width 0.6; hind limb foot width 0.9; free length of longest digit 0.2.

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 the same color as the body or slightly lighter dark gray, but at the deepest part of the groove pigment is lacking so the grooves are prominent. 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 white speckles are most visible behind the eye and over the shoulder, then in an irregular, narrow line along the dorsolateral part of the body to the hind limbs, but they are few in number and obscure. White spots are a little larger in the gular and chest areas ventrally. The nasolabial protuberances are unpigmented and contrast with the surrounding tissue.

Variation. Variation based on study of the holotype and three male (UF 156445, 156447, 156453), one female (UF 156446), and one juvenile (UF 156454) paratypes: the four males, judged to be mature based on having inconspicuous mental glands and anterior vent margins bearing fine pinnae, range from 38.5–44.5 SL; the female is 48.5 SL. Tails are present in the holotype, three male paratypes, and the juvenile and all taper gradually to slender tips. SL is from 0.86 (adult) to 0.52 (holotype) times tail length. SL in males is 9.8–11.8 times head width and 9.9 in the single female. Limbs are relatively short; number of costal folds between adpressed limbs is 13–14 in males and 13 in the female. There are 19–20 costal grooves between the limbs in the males and 20 in the female. Feet are narrow; 0.8–1.1. The digits are joined to their neighbors, with only the tips of the longest toes free. Males have 1–2 premaxillary teeth, the female has 4. Maxillary teeth range from 41–47 in males; 48 in the female. Males have 9–16 vomerine teeth; the female 18.

If one adds the referred specimens, the size range of the adult males increases to 35.3–48.5 SL, and that of females from 37.5–48.5 SL. These specimens are consistent in measurements, tooth and costal groove counts, and coloration with the type series. SMF 78738, from Reserva Natural Cerro Kilambé (44.0 SL), fits within the range of the new species in all measurements (see discussion).

Variation of coloration based on color photographs taken in life during daytime. Coloration is in general uniformly dark brownish-black with no distinguishing features. The upper side of the proximal segment of the limbs is the same color. The costal grooves are very evident because of the lack of pigment at their centers. Details for particular individuals follow.

Adult male paratype (UF 156447; Fig. 1b): Dorsum of body and tail blackish brown becoming a faded lighter brown on the dorsal and lateral surfaces of head extending to the chin. A lighter brown speckling is faintly noticeable dorsally from the head becoming imperceptible towards the base of the tail. Ventral surfaces of the body are blackish brown, similar in coloration to the tail. Limbs faded brown similar to color of head. Skin creases such as costal grooves, gular fold, and those around the paratoid region lack pigmentation and appear light grey. Iris dark rust brown.

Adult male (UF 156450): Dorsum of body and tail blackish brown becoming faded lighter brown on the anterior and lateral surfaces of head. Gold speckling mixed with some white is located on the dorsal surface of
the head and body. Speckling is most prominent on the top of the head becoming sparser posteriad, not extending beyond base of tail. Dorsolaterally above the anterior limbs a slight concentration of tiny white speckles forms a short, irregular line. Below the extent of the speckling ventrolaterally coloration is same as that of tail. Limb coloration is same as that of anterior and lateral surface of head. Iris dark rust brown.

Juvenile paratype (UF 156454; Fig. 1d): Dorsal and lateral surfaces of body, head, tail, and limbs are a uniform jet black. There is a faint overlay of tiny dirty white flecks along the dorsum of head, body, and tail giving a somewhat ashy appearance. This flecking is most concentrated dorsolaterally giving the impression of an irregular line extending from behind the jaw to the hind limb. Flecking is also present around the mouth and chest area. Larger white speckles are mixed sparsely and intermittently along the head, body, tail, and limbs.

Habitat and distribution. This species is known to occur from 1360–1660 m elevation at three isolated localities in the Lower Montane Moist Forest formation (Holdridge 1967) in north-central Nicaragua (Fig. 3). The holotype was collected in a small patch of secondary cloud forest (Fig. 4a–b) mostly surrounded by cattle pastures and agricultural land. It was found while raking during the daytime inside a moderately large rotten log. The paratypes and UF referred specimens from Reserva Natural Cerro Kilambé were collected in undisturbed, primary cloud forest (Fig. 4c) during both diurnal and nocturnal surveys. All were found underneath logs, rocks, and other debris in areas along the mountain ridge where the substrate comprised a spongy mass of plant roots and mosses. The SMF referred specimens from Reserva Natural Cerro Kilambé were also collected in undisturbed, primary cloud forest during diurnal surveys. Most of them were found inside dead basal ramifications of giant ferns. The paratypes from Reserva Natural Macizos de Peñas Blancas were collected in undisturbed, primary cloud forest (Fig. 4d). One was uncovered during the daytime beneath a fallen log, and two others were found active on the forest floor around the campsite at 2130 h. Those found active within the camp were likely dislodged or disturbed by raking and uprooting logs that occurred during set-up of the campsite earlier the same day.

Phylogenetic relationships. Phylogenetic analysis of sequence data from two mitochondrial genes (16S and cyt b) confirms the monophyly of this taxon (ML bootstrap support = 99, Bayesian posterior probability = 1.0) and its position as sister species to Oedipina kasios in the Oeditriton clade (Fig. 2). A sister-species relationship between O. kasios and O. nica is strongly supported (ML bootstrap support = 93, Bayesian posterior probability = 0.99) as is the monophyly of an Oeditriton clade containing O. kasios, O. nica, and O. quadra (ML bootstrap support = 96, Bayesian posterior probability = 1.0). Oeditriton is the sister clade to the remaining Oedipina, which are divided into the subgenera Oedipina and Oedopinola (Fig. 2), which supports previous phylogenetic hypotheses for Oedipina (García-París & Wake 2000; McCranie et al. 2008). All well-supported phylogenetic relationships are congruent between the ML and Bayesian results.

Etymology. The specific name nica is a short name for Nicaraguan (Nicaragüense in Spanish) and is a colloquial word used in Central America to denote Nicaraguan people. The name alludes to the country of origin of the type specimens.

Conservation status. Using the criteria established by IUCN for evaluating threatened species, Oedipina nica should be classified as Endangered (EN B2ab[iii]), due to its limited distribution (known only from three isolated highland forest areas with a total extent of less than 500 km²) and the continued loss of habitat at these localities.

Discussion

Oedipina nica is a member of the recently discovered clade Oeditriton, along with two species from Honduras (McCranie et al. 2008). The subgenus Oeditriton appears to have no unique morphological characters, and is made up of species with specialized, reduced morphological features including attenuated body form, long tails, short limbs and a very narrow manus and pes. They are also nearly uniform black with obscure white speckling. The costal grooves of the species of Oeditriton are generally unpigmented at their centers, thus making the costal grooves prominent. The general morphology of Oeditriton is also found among members of
the subgenus *Oedipina*, and we know of no way to distinguish between these two subgenera using external morphology. Samples of the former are too small to have permitted careful osteological study, but from external morphology we suspect that *Oeditriton* may have an enlarged dorsal fontanelle between the frontal and parietal bones on either side of the skull. Species of *Oedipina* generally have well ossified skulls (Wake 1966; García-París and Wake 2000).

**FIGURE 3.** Map of Nicaragua and Honduras showing the localities of members of the subgenus *Oeditriton: Oedipina nica* (circles), *O. quadra* (squares), and *O. kasios* (triangles). Open symbols represents each species’ type locality. If situated very close to each other, we combined distribution points to yield a single point on our map. Water surfaces are shaded light gray. Areas above 600 m are shaded gray. Areas above 1200 m are shaded dark gray.

The Nicaraguan representatives of the genus *Oedipina* are poorly known, and the description of *O. nica* represents the first in a series of papers evaluating the systematics of *Oedipina* in the country. Brame (1968) listed *O. collaris* (in Nicaragua only known from the holotype), *O. cyclocauda*, and *O. pseudouniformis* as occurring in the country, and subsequent workers have identified newly encountered populations of Nicaraguan *Oedipina* as either *O. cyclocauda* or *O. pseudouniformis* (Köhler 1999; Köhler et al. 2004).

Brame (1968) reported *Oedipina cyclocauda* (type locality near Guápiles, Prov. Limón, Costa Rica) based on a single specimen (KU 173532) from 1.5 km South of El Castillo, Dept. Río San Juan, Nicaragua. Köhler (1999, 2001) reported a series of specimens (SMF 78736–40, 78817–18) from Reserva Natural Cerro
Kilambé under the name *O. cyclocauda*; however, mtDNA-based phylogenetic analysis of the only available molecular sample attributed to this series (SMF 78738) suggests that this population represents an undescribed member of the *O. uniformis/pacificensis* clade (McCranie et al. 2008; Fig. 2). Nevertheless, we examined part of this series (SMF 78736–40), which are morphologically identical to *O. nica*. Although we failed to extract additional DNA from SMF 78738, we feel constrained to continue to consider it as representing a different species, although we strongly suspect some kind of documentation error. Other specimens from Reserva Natural Cerro Kilambé that lack molecular sequence data are referred here to *O. nica* because of their morphological similarity to specimens that have been sequenced by us from that site. It is conceivable that two sympatric morphologically cryptic species from different subgenera and phylogenetic clades occur at Reserva Natural Cerro Kilambé, but we think it unlikely. The molecular sample attributed to SMF 78738 might have been conflated with that of SMF 84860, a female *Oedipina* (35.0 SL) from Reserva Natural Cerro Datanlí-El Diablo that has longer limbs (10 costal folds between adpressed limbs), a broader head, broader hands and feet with more clearly defined digits, and a stouter body than *O. nica*. This specimen also has 19 costal grooves between the limbs and we suspect that it is a member of the subgenus *Oedipina*, although we were recently unable to extract usable DNA from the specimen. SMF 84860 further differs from *O. nica* in coloration (having less well defined costal grooves and having light pigmentation on the upper parts of the first segment of the limbs, near their insertion into the body), and we are preparing a formal description and awaiting fresh molecular samples for analysis.

**FIGURE 4.** Habitat of *Oedipina nica* from: (a-b) Reserva Natural Cerro Datanlí-El Diablo; (c) Reserva Natural Cerro Kilambé (note deforested patch reaching over 1300 m a.s.l. in the Reserve’s core zone); and (d) Reserva Natural Macizos de Peñas Blancas.
Oedipina cyclocauda also has been reported from Honduras (McCranie and Wilson 2002); however, the Honduran populations formerly referred to as O. cyclocauda subsequently have been described as distinct taxa and O. cyclocauda is no longer considered to occur in Honduras (McCranie et al. 2008; McCranie 2009).

Although O. cyclocauda is a poorly characterized species, we do not think any Nicaraguan specimen other than the one from near El Castillo (KU 173532) should be assigned to this species pending molecular characterization of samples from both this locality as well as from the vicinity of the type locality in Costa Rica.

Eight Nicaraguan specimens from Dept. Matagalpa were designated paratypes of O. pseudouniformis (Brame 1968), a species whose type locality is near Turrialba, Costa Rica. Köhler et al. (2004) subsequently reported additional localities for O. pseudouniformis from premontane elevations in Reserva Natural Cerro Saslaya (Región Autónoma Atlántico Norte) in northern Nicaragua. We have fresh samples and molecular data of populations of Oedipina from Reserva Natural Cerro Saslaya and Reserva Natural Cerro Musún (Dept. Matagalpa), and we consider these two populations to represent a single, undescribed species in the O. cyclocauda/pseudouniformis clade for which we are preparing a formal description. The taxonomic status of the population from Matagalpa that was included in the type series of O. pseudouniformis remains unresolved pending acquisition of fresh samples for molecular analysis.

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