Copeia, 2000(1), pp. 42–70

Molecular Phylogenetic Analysis of Relationships of the Tropical Salamander Genera *Oedipina* and *Nototriton*, with Descriptions of a New Genus and Three New Species

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Sequences of two mitochondrial genes (385 base pairs of cytochrome *b* and approximately 520 base pairs of 16S DNA) were gathered for 26 taxa of the Middle American plethodontid salamander genera *Nototriton* and *Oedipina* and from three outgroup members of the tribe Bolitoglossini. Phylogenetic analyses of these data reveal well-supported cladistic structure and demonstrate the paraphyly of the moss salamanders of the genus *Nototriton*, which includes two well-defined clades. One clade, the sister taxon of *Oedipina*, corresponding to the Costa Rican and Honduran species of the *picadoi*, *richardi*, and *barbouri* groups, retains the name *Nototriton*. A new name is required for the second clade, the sister taxon of *Oedipina* plus *Nototriton* (sensu stricto). This clade, which we name *Cryptotriton*, is well supported morphologically and includes the species of the *nasalis* and *adelos* groups. A new species of *Nototriton* from Monteverde, Costa Rica, is described as *Nototriton gamezi*. Species of *Oedipina* fall into two clades that we treat as subgenera. *Oedipina* (sensu stricto) includes the longer-bodied, generally more slender and darker colored species and is the more speciose clade. *Oedopinola* includes the shorter-bodied, generally more robust and lighter-colored species. Two new species of the latter clade are described, *Oedipina maritima* from the lowlands of northwestern Panamá, and *Oedipina savagei*, from uplands of southwestern Costa Rica.

THE evolutionary radiation of bolitoglossine salamanders in tropical America resulted in an enormous diversification of morphology and ecology, ranging from large, robust terrestrial forms (e.g., *Pseudoeurycea bellii*) to diminutive moss dwelling forms (e.g., *Nototriton abscondens*). One of the most strikingly derived morphologies within the bolitoglossines is displayed by the genus *Oedipina*, which comprises 18 currently recognized species distributed from Chiapas and the Yucatán Peninsula in México to northwestern Ecuador. *Oedipina* is a well-supported monophyletic group (Wake and Elias, 1983), characterized as being the only tropical bolitoglossine salamanders in which body elongation is a consequence of an increase in the number of vertebrae. All bolitoglossine salamanders with the exception of *Oedipina* have 14 trunk vertebrae, whereas *Oedipina* has from 18 to 23 (Wake, 1966; Brame, 1968). Members of *Oedipina* typically are fossorial, and consequently they are rarely seen. They range from sea level (throughout their range) to elevations in excess of 2200 m in Costa Rica. The status and phylogenetic relationships of many of the species in the genus were clarified by Good and Wake (1997) based on analysis of an extensive allozyme dataset. Their analysis resulted in a general phylogenetic hypothesis for relationships among the species of *Oedipina* (members of the genus *Nototriton* were used as outgroups, following the phylogenetic hypotheses of Wake and Elias, 1983). Two major clades were found. The first includes the species *O. alleni* and *O. parvipes*, which corresponds to the short-bodied and often white-headed species of the *O. parvipes* group, for which the name *Oedopinola* (which we treat here as a subgenus) is available (Hilton, 1949). A second group includes the remaining species (subgenus *Oedipina*), all elongated, black or brown attenuate forms comprising the *uniformis* group of Brame (1968). The electrophoretic evidence (large Nei genetic distances, ranging from 0.37 to 2.67 among species) suggests that most species of *Oedipina* have had a long independent evolutionary history. Most of the species of *Oedipina* studied show a large number of autapomorphic alleles.

Phylogenetic relationships within the supergenus *Bolitoglossa* remain largely unresolved, but *Nototriton* and *Oedipina* appear to be sister taxa (Wake and Elias, 1983). *Oedipina* and *Nototriton* share a strongly heteromorphic X/Y sex chromosome system (Kezer et al., 1989; Sessions and Kezer, 1991), also present in *Thorius* and *Dendrotriton* (Sessions and Kezer, 1991), as well as several osteological synapomorphies (Wake and Elias, 1983). *Nototriton* includes diminutive, slender animals which share with *Oedipina* the presence of a long tail that considerably exceeds

their snout–vent length and some osteological features (reviewed later in this paper). The species of *Nototriton* typically inhabit hanging moss mats, epiphytic bromeliads, or surface litter and are distributed in two disjunct regions: (1) the geologically ancient core region of nuclear Middle America along the mountains of the Oaxacan-Chiapan-Guatemalan-Honduran corridor; and (2) the Cordillera Central and northern Talamancan region of Costa Rica. Good and Wake (1993) revised the Costa Rican species of the genus. The genus has been suspected to be paraphyletic (following Wake and Elias, 1983), and relationships among the *picadoi, richardi, nasalis* and *adelos* species groups (Papenfuss and Wake, 1987) remain unresolved. Nei's genetic distances among Costa Rican species range between 0.14 and 1.18, and phylogenetic analysis of the allozyme data supports recognition of a *picadoi* group (with four species) and a *richardi* group (with two species) for the Costa Rican segment of the genus (Good and Wake, 1993). All Honduran, Guatemalan, and Chiapan species (only four were known to Papenfuss and Wake, 1987) were included in the *nasalis* group.

In this paper, we generate new phylogenetic hypotheses for *Nototriton* and *Oedipina* based on partial DNA sequences from two mitochondrial genes, the cytochrome *b* (cyt *b*) encoding gene and 16S rDNA. We examine the data for the two genes separately and analyze congruence among hypotheses generated from the two mitochodrial datasets. A combined mitochondrial hypothesis is used to test previous allozyme and morphological hypotheses. We show that *Nototriton* as presently constituted is paraphyletic, and we place some northern species of the current genus in a new genus. Phylogenetic analysis reveals several new candidate populations for species status, and three species are described as new.

Materials and Methods

Isolation, amplification, and sequencing of DNA.—A total of 78 specimens representing most of the known geographic range of *Oedipina* and *Nototriton* were included in the DNA study. These represent 17 taxa (two described herein) of *Oedipina* and 12 taxa (one described herein) of *Nototriton*. Many of these were used in the allozymic studies of Good and Wake (1993, 1997). We have determined that the taxon identified as *O. ignea* by Good and Wake (1997) is more appropriately assigned to *O. stenopodia*. Localities of origin, museum collection numbers and GenBank accession numbers are given in Appendix 1. Genomic DNA was extracted from small amounts of frozen tissue or protein extracts using NaCl following a protocol modified from Miller et al. (1988).

Sequences of the first portion (385 base pairs) of the cyt *b* gene and of the large (16S) ribosomal subunit gene (rDNA) were obtained. Those regions of mtDNA were selected to recover a maximum of phylogenetic information at all phylogenetic depths. We expect that cyt *b* evolves more rapidly than 16S; thus, it is expected to be more useful in determining relationships of terminal taxa, whereas 16S should be more useful for resolving basal relationships (Mindell and Honeycutt, 1990; Hillis and Dixon, 1991; Tan and Wake, 1995).

Fragments extending from the third position of codon 7 through codon 135 of the *Xenopus* cyt *b* gene (Roe et al., 1985), and approximately 520 bp of the 16S rDNA gene corresponding to positions 2510–3059 in the human mitochondrial genome (Anderson et al., 1981), were amplified via the polymerase chain reaction (PCR; Saiki et al., 1988) using the primers cyt *b*-2 (Kocher et al., 1989) and MVZ15 (Moritz et al., 1992) for cyt *b*, and 16Sar-L and 16Sbr-H (Palumbi et al., 1991) for 16S. PCR reactions consisted of 38 cycles with a denaturing temperature of 92 C (1 min), annealing at 48–50 C (1 min) and extension at 72 C (1 min) in a Techne PHC-1 thermocycler. PCR reactions were run in a total volume of 25 μl, using 0.6 units of *Taq* polymerase (Cetus) in tubes containing 0.5 pmol of each primer, 0.75 mM dNTPs, and 1.5 mM $MgCl_2$ in a pH 8.4 buffer with 50 mM KCL and 10 mM Tris HCl (final concentrations). Both heavy and light primers were used for PCR amplifications and sequencing.

Double-stranded templates were cleaned using MicroSpin S-300 HR columns (Pharmacia Biotech). Four μl of double-strand product were used as the template for cycle sequencing reactions in 10 μl total volume with the Perkin Elmer Ready Reaction Kit™ to incorporate dye-labeled dideoxy terminators. Thermal cycling was performed using standard conditions. Cycle sequencing products were purified using ethanol precipitation and separated by electrophoresis on a 6% polyacrylamide gel using an ABI 377 DNA sequencer (Applied Biosystems).

Sequence alignment and phylogenetic analysis.—Partial sequences of cyt *b* were read from both strands and aligned to each other by eye in the program Sequence Navigator™ (vers. 1.0.1, Applied Biosystems). The resulting partial 16S sequences were checked and aligned using CLUSTAL in the program Sequence Navigator™ (vers. 1.0.1, Applied Biosystems). Computer-

generated alignments were refined by eye and by comparing them to published secondary structure models for 16S (Guttel and Fox, 1988; Guttel et al., 1993; Ortí et al., 1996; Ortí and Meyer, 1997). Sequence divergences were estimated using the Kimura 2-parameter (K2p) distance (Kimura, 1980; determined using PAUP 4.0b1a, D. Swofford, Smithsonian Institution) to correct for multiple hits. Corrected sequence divergence within and among taxa is shown in Appendices 2–6.

All phylogenetic analyses were run using a test version of PAUP 4.0b1a. Phylogenetic hypotheses were generated by maximum parsimony (MP), using the heuristic algorithm. Heuristic searches were done by stepwise random addition of taxa, with 10 replications and TBR branch swapping with the MULPARS option in effect and by collapsing zero-length branches. The minimum number of character changes supporting each branch, consistency index (CI, Kluge and Farris, 1969), and the retention index (RI, Farris, 1989) were calculated. Transversion (TV) to transition (TS) weights 1, 3, and 10 were used for the analysis to determine whether resolution was thereby increased, especially at the base of the tree (Moritz et al., 1992), and to examine the potential effects of homoplasy at more rapidly evolving sites. We performed 100 bootstrap (bs) replicates to document support for individual nodes (Felsenstein, 1985). Two schemes were applied to use the 16S positions affected by gaps: (1) gaps were treated as missing data; and (2) each INDEL was treated as a character, independent of its size, thus adding 19 characters (9 parsimony-informative) to the dataset, with each gap treated as a single evolutionary event (present or absent). We also generated neighbor-joining (NJ; Saitou and Nei, 1987) trees based on K2p distances, using 1000 bootstrap replicates. Maximum likelihood (ML) was used, with the heuristic algorithm, and the Hasegawa-Kishino-Yano model (Hasegawa et al., 1985). ML settings used base frequencies, proportion of sites assumed to be variable, the gamma distribution shape parameter, and transition:transversion ratio as estimated via maximum likelihood. Consistency among topologies was examined with the COMPARE TREES option in MacClade.

A phylogenetic hypothesis for the combined dataset (cyt *b* and 16S) was inferred using maximum parsimony (MP). In all heuristic searches gaps were treated as missing data, 10 random-taxon-addition replicates were conducted, and tree bisection and reconnection (TBR) was the branch-swapping algorithm used.

For all phylogenetic analyses representatives of two tropical bolitoglossine genera, *Bolitoglossa cerroensis* and *Dendrotriton rabbi*, were used as sequential outgroups. All analyses were rooted using a nearctic bolitoglossine species *Batrachoseps gabrieli*.

Morphology and taxonomy.—Morphological comparisons involved measurements of preserved specimens with dial calipers. All measurements are in mm. Standard length (SL) is the distance from the tip of the snout to the posterior margin of the vent. Tooth counts are presented in this order: left-right. Institutional abbreviations are as listed in Leviton et al. (1985).

Criteria for recognizing species based on phylogenetic analyses of molecular data are those outlined by Good and Wake (1993), following Frost and Hillis (1990). We name as new species units that give evidence of evolutionary independence from other units. When molecular data suggest phylogenetic independence (substantially more variation between samples than within accepted species), we also investigate morphology. When molecular and morphological features both give evidence of divergence, we recognize the units as species, but in the absence of morphological evidence, we are reluctant to name new taxa on the basis of mitochondrial sequence data alone.

Results

Sequence fragments of 385 bp and approximately 520 bp were obtained for cyt *b* and 16S genes, respectively. For the 16S dataset, the alignment of the ingroup required application of six to 10 gaps per sequence. Insertion/deletion (indel) events affected between 0.6% and 1.9% of the aligned sequence length, for a maximum of 22 positions. Most indels were 1 bp in length, and maximum indel length was 8 bp; nine indels were unique to samples or species. The aligned sequences (NEXUS files) are available from the authors upon request.

Corrected sequence divergence (K2p) among taxa for cyt *b* and 16S fragments (Appendices 2–6) is great in both genera, ranging as high as 22.5% (cyt *b*) and 10.8% (16S) within *Oedipina*, and 30.7% (cyt *b*) and 17.9% (16S) within *Nototriton* (sensu lato). Substantial divergence is found even within certain taxa currently recognized as single species (e.g., *O. poelzi*, as much as 13.7% for cyt *b* and 4% for 16s).

We analyzed the data separately and combined. We conducted NJ, MP, and ML analyses and found them to be highly concordant. In this section, we focus on the results of the MP analysis. For Figures 1–4 results of bootstrap an-

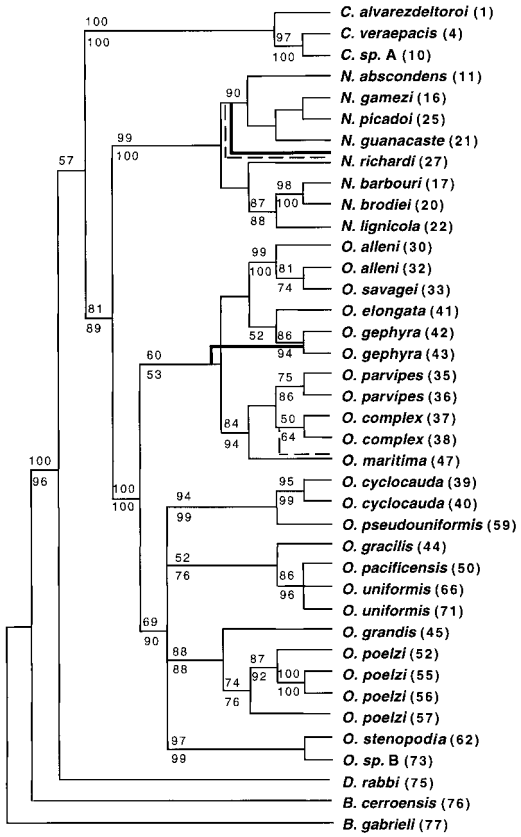

Fig. 1. Strict consensus of the four most-parsimonious trees (688 steps, CI 0.47, RI 0.68) for 16S. There are 167 parsimony informative characters. Transitions are weighted equally with transversions. Gaps are treated as missing data. Bootstrap values (above 50%) for the MP analysis (based on 100 replicates, above line) and for the NJ analysis (based on 1000 replicates, below line) are shown. Broken lines indicate alternative positions of *Nototriton richardi* and *Oedipina maritima* in the NJ analysis; bold lines indicate alternative positions for *N. richardi* and the *Oedipina gephyra* clade when transversions are weighted three times transitions.

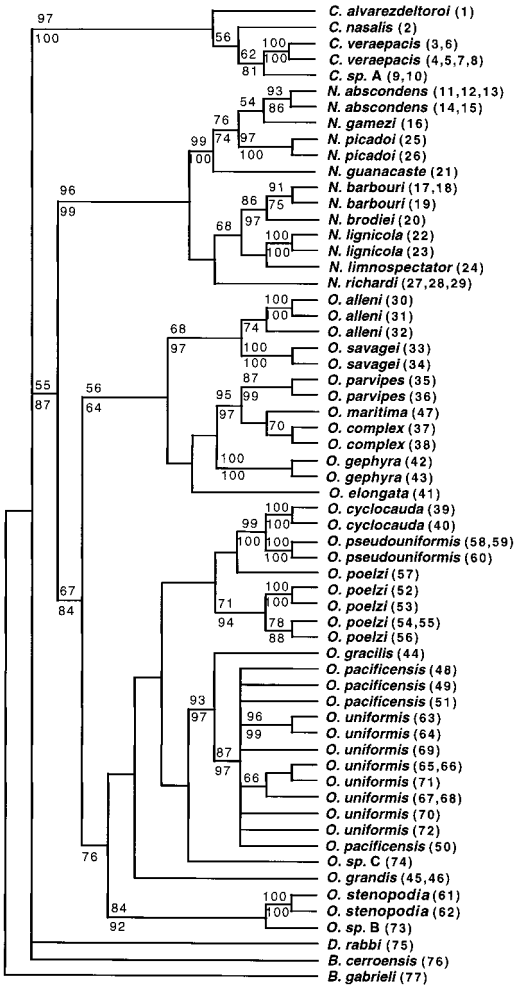

Fig. 2. Strict consensus of 124 most-parsimonious trees (1066 steps, CI 0.31, RI 0.70) for cyt *b*, showing all of the populations analyzed in this study. Bootstrap values for the MP analysis (above 50% based on 100 replicates, above line) and for the NJ analysis (bs > 70% below line, based on 1000 replicates) are shown.

alyses (bs) in both MP and NJ trees are shown; topologies are based on parsimony analysis except where noted. For 16S, we weighted transitions and transversions equally, and in our MP analysis, we found two equally most-parsimonious trees (Fig. 1; CI=0.47, RI=0.68). For cyt *b* (unweighted analysis), we found 124 equally most-parsimonious trees (Fig. 2; CI = 0.31, RI = 0.70). Analysis of the cyt *b* data using full weighting (i.e., TV:TS = 3:1 and differential weighting of 3:5:1 for the three nucleotide positions) found eight equally parsimonious trees (not shown; bs values calculated; CI = 0.42, RI = 0.79). The MP analysis of our combined data resulted in three equally parsimonious trees (bs values and decay indices are shown in Fig. 3; CI = 0.39, RI = 0.63; Fig. 4 is a NJ phylogram with bs values indicated). The tree shown in Figure 3 is fully resolved except for one polytomy (the three trees differ with respect to close relatives in the *N. picadoi* group). The ML tree (not shown, likelihood score 8589.98) is highly concordant with the MP combined data tree in Figure 3 (differing only with respect to arrangement of a few terminal taxa within clades).

Oedipina is well supported as a monophyletic clade. In the NJ analysis, this clade has bs values of 100% (16S) and 84% (cyt *b*), and 100% for the combined analysis. The comparable values

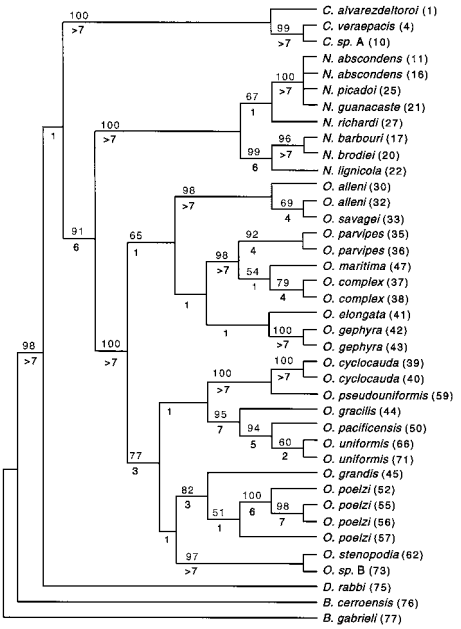

Fig. 3. Strict consensus of the three most-parsimonious trees (1622 steps, CI 0.39, RI 0.63) for combined datasets for cyt *b* and 16S, showing all of the populations for which both sets are available. There are 333 parsimony informative characters. Transitions are weighted equally with transversions. Decay index values are shown below lines. The symbol > 7 is used to indicate decay indices above 7 for a given branch. Bootstrap values (above 50%) (based on 100 replicates, above line) are shown.

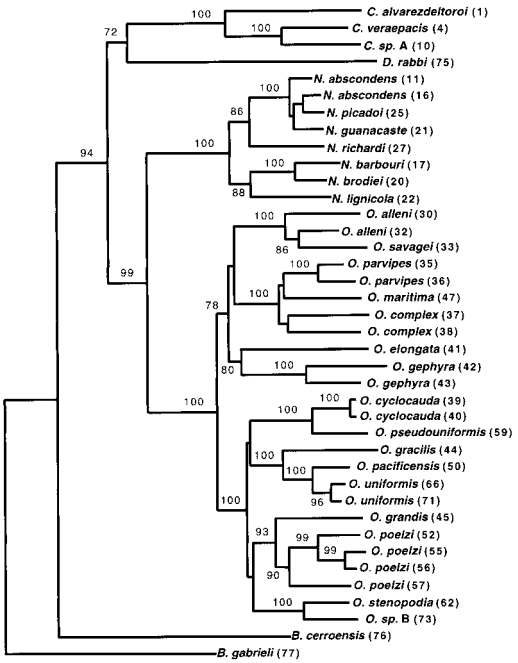

Fig. 4. Neighbor-joining tree showing branch lengths for combined datasets for cyt *b* and 16S, based on all of the populations for which both sets are available. Bootstrap values (above 70%) based on 1000 replicates are shown.

for MP are 100% (16S) and 67% (cyt *b*) and 100% for the combined analysis (decay index greater than 7). When transversions are weighted three times transitions, and using differential weighting for the three positions (3:5:1) for cyt *b*, the bs value rises to 73%. The subgenus *Oedipina* is well supported, with NJ bs values of 90% (16S), 76% (cyt *b*), and 100% for the combined analysis; comparable MP bs values are 69% (16S), less than 50% for unweighted, and 52% for fully weighted (as above; cyt *b*), with a bs of 77% for the combined equally weighted analysis (decay index 3). There is also support for the monophyly of the subgenus *Oedopinola*, with NJ bs values of 53% (16S) and 64% (cyt *b*), with 78% for the combined analysis; comparable MP bs values are 60% (16S) and 56% (for cyt *b* unweighted; less than 50% for fully weighted), with a bs value of 65% for the combined analysis.

Within *Oedipina* (*Oedipina*) there is a well-defined *uniformis* group (maximum K2p = 0.113 for cyt *b*; 0.044 for 16S), including the taxa *uniformis, gracilis*, and *pacificensis* (NJ bs of 76% for 16s and 97% for cyt *b*, 100% for combined analysis; MP bs of 52% for 16S; bs of 93% for unweighted and 95% for fully weighted analysis of cyt *b*, with 95% for combined analysis, with a decay index greater than 7). Within this complex, there is good support (NJ 96% bs 16s, 97% bs cyt *b*, 100% combined; MP unweighted 86% bs 16S, 87% bs cyt *b*, 94% combined with a decay index of 5) for a clade of *pacificensis* and *uniformis*. There is no support (bs < 50%) for a clade comprising the 10 samples of *uniformis* for our cyt *b* dataset (maximum K2p = 0.046), and there is no support for *pacificensis* as a clade in this dataset (maximum K2p = 0.040). The taxa *grandis* and *poelzi* form a clade (NJ 88% bs; MP 88%) with our 16S dataset, and although this clade always appears in analyses of the cyt *b* dataset, it is not well supported. In the combined analysis, there is good support for the clade (82% bs, decay index 3). Within this clade, there is weak support for *poelzi* as a monophyletic group based on cyt *b* (the Monteverde sample, 57, is basal in the larger clade), and there is support for monophyly of *poelzi* in the 16s data (NJ 76% bs; MP 74%); however, the combined analysis either gives support for monophyly (NJ 90% bs; MP 51%), or makes *poelzi* paraphyletic with respect to *grandis* (MP).

There is relatively great divergence within *poelzi*, with a K2p value of 0.093 for cyt *b* and 0.040 for 16S between samples from Moravia de Chirripó and various populations in the Cordillera Central. There is also support for a clade including *pseudouniformis* and *cyclocauda* (Costa Rican population only; NJ 99% bs for 16S, 100% for cyt *b*, 100% combined; MP 94% bs for 16S, 99% for cyt *b*, and 100% combined with a decay index greater than 7). The Honduran sample previously assigned to *cyclocauda* (species C in this paper) is not associated with the Costa Rican populations assigned to that taxon, based only on our study of cyt *b* sequences (K2p distance is 0.165), nor is it significantly associated with any other taxa. There is no support for any basal phylogenetic resolution in *O.* (*Oedipina*).

There is little basal resolution within *O.* (*Oedopinola*), and divergences are relatively great. The recently described Honduran taxon *O. gephyra* (McCranie et al., 1993) is included in a weakly supported clade with the northern species *elongata* within *O.* (*Oedopinola*; NJ 52% bs 16S, 55% bs cyt *b*, 80% bs combined; MP less than 50% bs 16S, cyt *b*). Populations associated with *alleni* cluster together (NJ 100%, MP 99% for 16S; NJ 94% bs, MP 68% for cyt *b*; NJ 100%, MP 98% combined, decay index 8). The various samples associated with *complex* and *parvipes* form a monophyletic group (NJ 94% bs for 16S, 97% bs for cyt *b*, 100% combined; MP 84% bs for 16S, 95% for cyt *b*, 98% combined with a decay index greater than 7). There is only weak support (NJ bs 52% cyt *b*) for a cluster of the *alleni* clade with *complex* and *parvipes*. There is a cluster of *gephyra* and *elongata* in both datasets but with relatively weak bootstrap support.

There are two distinctive clades representing the taxa currently assigned to *Nototriton*. The first of these, to which the name *Nototriton* applies, includes all of the Costa Rican taxa, as well as three Honduran (*barbouri, lignicola, limnospectator*) and one Guatemalan (*brodiei*) taxa (NJ 100% bs for 16S, 99% for cyt *b*, and 100% combined; MP 99% bs for 16S, 96% for cyt *b*, and 100% combined with a decay index greater than 7). The second clade, which is named later in this paper, includes Mexican (*alvarezdeltoroi*), Guatemalan (*veraepacis* and species A) and Honduran (*nasalis*) taxa and is also well supported (NJ 100% bs for 16S, 100% bs for cyt *b*, 100% combined; MP 100% for 16S, 97% for cyt *b*, 100% combined with a decay index greater than 7).

Within *Nototriton* (sensu stricto), a northern clade includes the Honduran and Guatemalan samples (NJ 91% bs 16s, 57% bs cyt *b*, 88% combined; MP 87% 16S, 68% cyt *b*, 99% combined, decay index 6). A group of Costa Rican species forms a second clade (NJ 99% bs 16S, 100% bs cyt *b*, 100% combined; MP 90% bs 16S, 99% bs cyt *b*, 100% bs combined with a decay index greater than 7). The position of the Costa Rican samples of *N. richardi* is variable, being alternatively basal to either clade. For the MP analysis of 16S, it is basal to the northern clade, but if transversions are weighted three times transitions, it is basal to the Costa Rican clade. This arrangement is also found in all neighbor-joining analyses (NJ 88% bs 16S, 58% bs cyt *b*, 86% combined). There is also support for this arrangement in the bootstrap analysis of MP trees (60% bs 16S, 61% bs cyt *b*, 67% bs combined).

The as yet unnamed northern clade of *Nototriton* is alternatively a sister taxon of *Dendrotriton* (NJ 70% bs cyt *b*; 72% for combined data) or a sister taxon of the *Nototriton* (sensu stricto)-*Oedipina* clade (MP 57% bs 16S); in general this clade appears near the base of the ingroup in all trees. Within this clade, the two Guatemalan species are sister taxa (NJ 100% bs for 16S, 81% bs cyt *b*, 100% bs combined; MP 97% bs 16S, 62% bs cyt *b*, 99% bs combined). In no instance, in any of our analyses, are the two main clades of *Nototriton* (sensu lato) sister taxa.

Dendrotriton is the sister taxon of the entire assemblage (*Oedipina* + *Nototriton* sensu lato) considered here in the MP analysis of the 16S data and the combined data, but there is a polytomy of *Dendrotriton*, the newly recognized clade within *Nototriton, Bolitoglossa*, and the *Oedipina-Nototriton* (sensu stricto) clade in our MP analysis of the cyt *b* data. In fully weighted analyses of the cyt *b* data, the newly recognized clade is basal to a clade (bs 65%) of *Oedipina-Nototriton* (sensu stricto) and *Dendrotriton-Bolitoglossa* (bs 81% for this sister-group relationship). At this phylogenetic depth, the 16S data are expected to have the greater value. In the ML tree, *Dendrotriton* is the sister taxon of the new genus. All analyses (MP, ML, NJ) support a sister taxon relationship between *Oedipina* and *Nototriton* (sensu stricto; MP 81% bs 16S, 55% bs cyt *b*, 91% bs combined, decay index 6).

Discussion

Data analyses.—A high level of congruence exists between the results obtained from analysis of the cyt *b* and 16S datasets. Accordingly, we believe that the closest approximation to the phylogeny of the samples studied is likely to come from analysis of the combined dataset. When the two datasets are combined, almost all of the bootstrap values in either the NJ or MP analysis increase. At the level of the major

clades, our results appear to be relatively robust. There is support for a monophyletic *Oedipina*, a monophyletic *Nototriton* (sensu stricto), a monophyletic clade named later in this paper, and for a clade including *Oedipina* and *Nototriton* (sensu stricto). The unnamed clade is not a member of this latter clade, but it is a close, basal relative, possibly the sister taxon.

Analysis of the combined data by MP resulted in only three most-parsimonious trees, and there was almost complete resolution with mainly high bootstrap values (Fig. 3). The taxa responsible for the alternative trees were close relatives in the *picadoi* clade of *Nototriton*. The taxonomic position of the population from Monteverde, Costa Rica (sample 16), is somewhat ambiguous (e.g., Good and Wake, 1993), and our data add support to its distinctiveness and status as an unnamed species. Previous hypotheses of relationships among the three clades of *Oedipina* envisioned the Guatemalan population previously called *O. ignea* (now *O. stenopodia*) as being a sister taxon of one or the other of these clades, but our analysis places it clearly outside of this cluster.

Phylogenetic relationships and species recognition.—The molecular phylogenetic hypothesis for *Oedipina* of Good and Wake (1997) is mostly congruent with Brame's (1968) morphological hypothesis. However, Brame placed all species of *Oedipina* in only two groups, a *uniformis* group (equivalent to our subgenus *Oedipina*) and a *parvipes* group (equivalent to our subgenus *Oedopinola*), whereas Good and Wake recognized three clades (*cyclocauda, poelzi*, and *uniformis*) within Brame's *uniformis* group. Good and Wake (1997) found two most parsimonious trees. (Because of a printing error only one tree appears in the published article. A correction was published in *Revista de Biología Tropical* 45, number 4). We were unable to obtain DNA from all taxa sampled by them, but we investigated several species unavailable to them. It is not possible to do a combined analysis of the allozyme and DNA data that would be meaningful. However, certain comparisons are appropriate. Both datasets identify a basal dichotomy between the subgenera. Within the subgenus *Oedipina, O. cyclocauda*, and *O. pseudouniformis* are sister taxa in both analyses and form a well-supported clade. There is a well-supported clade that includes a restricted *uniformis* group (*O. gracilis, O. pacificensis, O. uniformis*). Both analyses recognized a *poelzi* group and also recognized a northern (identified as *O. ignea* by Good and Wake, and as *O. stenopodia* and species B in this paper) unit. However, basal relationships of these four clades, each well supported individually, are uncertain, and there is no support for any particular arrangement.

Our analysis is relevant to issues of species recognition and species level taxonomy. Good and Wake (1997) argued that allozymic data were insufficient to determine whether populations from Honduras (74) and Costa Rica (39, 40) identified as *O. cyclocauda* were conspecific. Our analysis shows that they are not sister taxa with respect to mtDNA, and given the large genetic distance separating them, the Honduras population warrants description as a new taxon; we lack adequate material for such a description. A population from Moravia de Chirripó, Costa Rica (57), assigned by Good and Wake (1997) to *O. poelzi*, is well differentiated from other members of that taxon both in allozymes and mtDNA. It is usually basal to other populations of *O. poelzi* in phylogenetic analyses, but it is basal to a larger clade including also *O. grandis* in some analyses (e.g., cyt *b*). It probably warrants recognition as a distinct taxon, but at present, we lack adequate material to prepare a description. A population from Honduras (73) that clusters with *O. stenopodia* might be assignable to *O. ignea* or it may represent a distinct, undescribed taxon. Our analysis also supports the decision of Good and Wake (1997) to subdivide Brame's (1968) *O. uniformis* into three taxa (*O. uniformis, O. gracilis, O. pacificensis*). There is no support for a sister-taxon relationship of the Damas sample (50) of *O. pacificensis* and the other *O. pacificensis* samples in the cyt *b* data. The K2p distances are small within the clade.

Populations (30–38, 47) form a clade that is deeply divergent internally. Authors have variously identified these populations as *O. alleni, O. complex*, and *O. parvipes*. Within this clade, populations 30–34 stand apart, but even this group of five samples is deeply differentiated. Two (30–32) of the three populations we have studied were available for allozymic work, and although samples were small, the populations were very similar (Nei D approximately 0.02). In contrast, we measured large distances for both genes studied, and furthermore a third population (33,34) is equally distinct. This third population occurs at much higher elevation than the others (near Las Cruces, southwestern highlands of Costa Rica) and differs in coloration (dorsal light stripe) and size (smaller, more robust, with a short, rounded snout). It is the basis for the inclusion of *O. complex* in the Costa Rican fauna by Savage and Villa (1986), but it is not assignable to that taxon. Below, we describe this population as a new species. The type

locality of *O. parvipes* is in northwestern Colombia, and we have no near topotypic materials for the present study. Furthermore, the samples that we have had from Panamá that have been assigned to this taxon are well differentiated from each other. Sample sizes are generally too small to permit appropriate morphological comparisons, but the most divergent population (47) from western Panamá is both morphologically and genetically distinct from populations in the central part of the country; we describe it below as a new species. The remaining populations (35, 36) of *O. parvipes* from Panamá are genetically differentiated from each other, and we suspect that they are also differentiated from topotypic material; further taxonomic revision must await the collection of additional specimens. Finally, *O. complex* appears to be appropriately named, because the two populations that we have studied that are assigned to this taxon (near topotypic material from central Panamá, sample 38, and a population from the central Panamanian Cerro Campana, sample 37) are not sister taxa in any of our analyses. These two populations are relatively close geographically, yet they differ by 11.1% in cyt *b* and 3.9% in 16S. More than one taxon probably should be recognized, but we lack sufficient topotypic material to conduct an appropriate morphological comparison at this time.

Within *Nototriton* there is good support in the combined analysis for a monophyletic Costa Rican *picadoi* group (100% bs with a decay index of 9) and for a northern group (98% bs with a decay index of 6), which we here identify as the *barbouri* group. The Costa Rican *richardi* group clusters (57% bs with a decay index of 1) with the *picadoi* group. This is in accord with the findings of Good and Wake (1993) for the Costa Rican species. Within the *picadoi* group, a population (16) previously assigned to *N. abscondens* from the Monteverde region displays problematic relationships. Given its distinctive morphology and allozyme profile (Good and Wake, 1993), it merits description as a distinct species (see below). Within the *barbouri* group our results support recognition of the recently described *N. brodiei* (Campbell and Smith, 1998), *N. lignicola* (McCranie and Wilson, 1997b), and *N. limnospectator* (McCranie et al., 1998). We note that one of the samples of *N. barbouri* (19) differs substantially from the other two samples (17, 18) in the cyt *b* tree (Fig. 1) and may represent an unrecognized taxon.

Several morphological and reproductive synapomorphies support a clade containing *Oedipina, Nototriton*, and the new genus: the ulnare and intermedium are fused in the carpus; distal tarsals four and five are fused; there is no opercular stilus; and all species examined have X-Y sex chromosomes (Sessions and Kezer, 1991; Lynch and Wake, 1978; Wake and Elias, 1983). Species of *Nototriton* lay eggs in moss clumps in trees, but instead of guarding the eggs, a universal trait of non-bolitoglossine plethodontids and widely present in bolitoglossines, females abandon the eggs (Good and Wake, 1993; McCranie and Wilson, 1992). An undescribed species belonging to the new genus named in this paper and a new species of *Oedipina* from Panamá (see below) also lay unguarded eggs. Thus, the three genera treated in this paper display a unique synapomorphy because they are the only members of the supergenus *Bolitoglossa* that are known to abandon their eggs (we have no information for some putative relatives such as *Dendrotriton* and *Bradytriton*). Synapomorphies unique to *Oedipina* among these taxa include increased numbers of trunk vertebrae, presence of a spur on the squamosal bone, loss of the prefrontal bone, loss of the tibial spur, and presence of mental gland clusters in a small patch at the mandibular symphysis (Wake, 1966; Wake and Elias, 1983). We know of no synapomorphies unique to *Nototriton* among these taxa, but species belonging to the genus as herein revised differ from those belonging to the new genus in cranial structure. The prefrontal is relatively large in the new genus and is pierced by the nasolacrimal duct, whereas it is relatively small or absent in *Nototriton*, and the nasolacrimal duct passes between the prefrontal and the nasal (partly pierces the prefrontal in some individuals of some species); the nasal is large in *Nototriton* but relatively to very small in the new genus; there is a distinct, tooth-bearing preorbital process on the vomer of *Nototriton* (and *Oedipina*), whereas this process is lacking in the new genus (McCranie et al., 1998; Good and Wake, 1993; Lynch and Wake, 1978). In all of these characters, the states in *Nototriton* are ancestral, whereas the states in the new genus constitute synapomorphies. Within *Nototriton*, osteological differences have been noted among taxa, and the *picadoi* and *barbouri* groups appear to be distinct from each other osteologically, whereas *richardi* is poorly known and appears to have unique osteology (McCranie et al., 1998; Good and Wake, 1993).

Systematics

Phylogenetic analysis and taxonomy.—We believe that taxonomy should reflect robust phylogenetic analysis within the severe constraints of the Linnean system. We have identified three

large clades that are well supported by sequence data. Two of these clades, *Nototriton* and the clade named later in this paper, are generally similar in overall morphology and ecology, whereas *Oedipina* differs dramatically from the other two in morphology and ecology. The species of *Oedipina* have long trunks and extraordinarily long tails, and most (perhaps all) are semifossorial in habits. In our analyses, these three clades usually form a monophyletic group, but not always, and monophyly is not well supported. For these reasons, we decline to place the three in a single genus, for which the name *Oedipina* would have priority. Because there is no support in our data for monophyly of *Nototriton* and the remaining clade, we believe that the most logical and useful taxonomy is to place the latter clade in a new genus.

The use of subgenera for clades that are morphologically similar but differ in molecular characters was advocated by Jackman et al. (1997) for *Hydromantes* and *Batrachoseps*. In both cases, the genera are distinguished from others by numerous synapomorphies, whereas the subgenera are only weakly supported by morphological synapomorphies but well supported in phylogenetic analyses of molecular data. This is also true of the two major clades we have identified within *Oedipina*, and accordingly we here treat these as subgenera.

Description of a New Species of *Oedipina* from Panamá

Oedipina maritima n. sp.
Maritime Worm Salamander

Holotype.—USNM 529981, an adult female from Escudo Camp, West Point, Isla Escudo de Veraguas, Prov. Bocas del Toro, Panamá, approximate 9°6.1′N, 81°4.5′W, collected 28 March 1991, by R. I. Crombie.

Paratypes.—USNM 529982–529985; USNM Field number 195536 (to be deposited in a collection in Panamá), MVZ 219997, same data as holotype; KU 116681, E end Isla Escudo de Veraguas, Prov. Bocas del Toro, Panamá, 4 m. elev.

Referred material.—USNM 313607 (two clutches of eggs), same data as holotype.

Diagnosis.—A small (maximum size 46.2 SL), relatively slender member of *Oedipina* (subgenus *Oedopinola*) with a narrow head and a long snout. Distinguished from *Oedipina alleni* by its narrower hands and feet, more elongate digits and darker coloration; from *Oedipina parvipes* by its dark ventral coloration; from *Oedipina savagei* by having a narrower and more pointed head, and fewer maxillary teeth; from *Oedipina complex* by its narrower head, pointed and elongate snout (rather than short and rounded), small, laterally oriented eyes, fewer maxillary teeth, and narrower feet with pointed digits; from *Oedipina carablanca* by its much smaller size and less robust habitus, small, laterally oriented eyes, narrow and pointed head, narrow hands and feet, and pointed digits. The first four of the above species are distinguished from *O. maritima* by extensive sequence differences in the mitochondrial genes 16S rDNA and cytochrome *b*.

Description.—This is a relatively small, slender species; adult SL for four males is 39.7–46.2, $\bar{x}$ 43.3; for three females 34.6–44.3, $\bar{x}$ 39.7. The head is small, narrow, cylindrical and generally pointed, with an elongated, blunt-tipped snout; SL averages 10.3 times head width in 4 males (range 9.7–11.3) and 9.8 in 3 females (9.4–10.3). SL is 6.5 times head length in both males (6.2–7.1) and females (5.1–7.2). Nostrils are tiny and barely discernable. Nasolabial protuberances are inconspicuous in females but slightly enlarged in males, where they extend slightly as somewhat swollen light-tipped extensions over the underslung lower jaw. Snouts are more pointed in females than in males as a consequence. Eyes are small and inconspicuous, barely extending beyond the lateral margins of the head; they are directed mainly laterally, rather than frontally as is the situation in most bolitoglossines. The suborbital groove does not intersect the lip. There are 1–2 slightly enlarged premaxillary teeth in males, located in a far forward position outside the mouth, lying just in front of the small, ill-defined mental gland that lies at the extreme anterior margin of the lower jaw; the 1–2 premaxillary teeth in females are tiny and located well within the mouth. Maxillary teeth, when present, are tiny and inconspicuous; they range in number from 0 (3 males)–8 ($\bar{x}$ 2.0) in four males, and from 2–8 ($\bar{x}$ 5.3) in three females. Vomerine teeth average 15.5 (13–18) in four males and 17.3 (15–20) in three females; the very small teeth are borne in a long row. There are 17 costal grooves between the limbs, counting one each in the axilla and the groin (18 trunk vertebrae). Limbs are relatively short; limb interval averages 8.1 in four males (7.5–8.5) and 8.0 in three females (7.5–9). Hands and feet are tiny, narrow and elongate. The digits are syndactylous, although the tips of the longest central digits are free. The free tips are slender and sharply pointed, and the points are often curved toward the midline

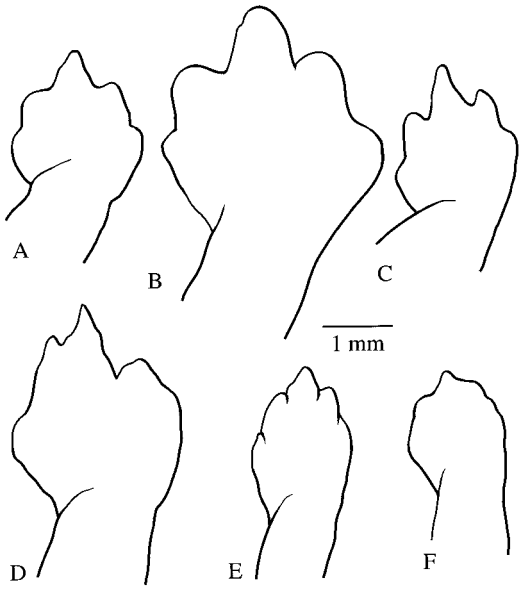

Fig. 5. Outlines of the shape of the right foot for representative samples of six species of *Oedipina* (*Oedopinola*), drawn with camera lucida. (A) *O. savagei*, LACM 109558 (39.3 SL), holotype; (B) *O. alleni* MVZ 190857 (52.4 SL), near Damas, Prov. Puntarenas, Costa Rica; (C) *O. maritima* USNM 529981 (44.3 SL), holotype; (D) *O. parvipes* LACM 134872 (53.9 SL), Barro Colorado Island, Panamá; (E) *O. complex* MVZ-DBW 5787 (37.2 SL), Cerro Campana, Panamá; (F) *O. complex* MVZ-DBW 5105 (35.0 SL), Peninsula Bohío, Prov. Colón, Panamá.

axis of the limb (Fig. 5). Fingers, in order of decreasing length, are 3-2-4-1; toes are 3-4-2-5-1. The tail is round, narrow in cross-section and relatively long, tapering along the last third of its length. Tails of most individuals may be at least partly regenerated, but all of them greatly exceed SL; SL averages 0.59 times tail length in 4 males (0.53–0.68) and 0.57 in 2 females (0.53–0.62).

Measurements of holotype.—Head width 4.3; snout to gular fold (head length) 6.2; head depth at posterior angle of jaw 2.3; eyelid width 0.6, eyelid length 1.8; eye to nostril 1.6; anterior rim of orbit to snout 1.9; horizontal orbit diameter 0.9; interorbital distance 2.3; distance separating eyelids 1.3; nostril diameter 0.1; snout projection beyond mandible 0.8; distance from eye to postorbital groove 2.2; snout to posterior angle of vent (standard length) 44.3; snout to anterior angle of vent 39.4; snout to forelimb 10.0; axilla to groin 27.6; limb interval 9; shoulder width 3.2; tail length 71.9; tail width at base 3.3; tail depth at base 3.3; forelimb length (to tip of longest digit) 5.7; hind-limb length 7.0; hand width 1.1; foot width 1.8; free length of longest toe 0.6. Numbers of teeth: premaxillary 2; maxillary 0–2; vomerine 9–11.

Coloration of the holotype in alcohol.—Dorsal color dark brown, almost chocolate on the sides, lighter along an indistinct dorsal band. Dorsal and lateral coloration is separated on the first quarter of the body by an almost indistinct light colored broken line, more apparent and broader on the posterior edges of the head. A whitish band extends from the upper jaw to the interocular region, covering the area between the nostrils and the eyes. The posterior edge of this light band is not well defined and dorsal dark coloration penetrates into it. The dorsal coloration becomes lighter posteriorly, and along the dorsal portions of the anterior half of the tail. This light coloration does not uniformly cover the dorsal surface of the tail. Dorsal sides of the limbs show the same dorsal color with a light patch at the base of the limbs, close to its insertion to the trunk. Tips of digits are unpigmented; hands and feet are lightly colored with darker pigment in the area between the digits. Ventral coloration is lighter than dorsal, with all the ventral regions from throat to vent and tail covered with dense melanophores, giving a grayish-brown appearance. The throat and undersurface of the limbs are lighter; hands and feet are almost unpigmented ventrally. Small white dots are spread along the flanks and the tail at low density, less concentrated (scattered) on the lateral sides of the venter.

Color variability.—Dorsal coloration is lighter in juvenile and submature (KU 116681) specimens, markedly contrasted with the dark flank coloration. They show a marked dark midvertebral line running from the posterior edge of the head to the tail origin where it fades away. Tail dorsal color in juveniles is very light, but it is not sharply separated by a defined line as it is on the body. Some adult specimens (e.g., USNM 529983) show a more contrasted light tail pattern, always less developed than in juveniles. The extent and definition of the anterior light lateral band varies from well marked and broad at the ''parotoid'' level, to almost completely absent (USNM 195536), as does the dorsal light band. White dots along the flanks are denser in some specimens; these specimens also have a few pale dots extending to the venter. Hatchlings display a bold pattern of very dark flanks and side of the head and tail with a broad light yellowish dorsal band, extending from the snout to the tail tip. The venter is pale yellow. The main light areas show an obscure suffusion

of melanic pigmentation especially evident in the middorsal portion of the trunk and near the tail tip.

Color notes were recorded in life for USNM 529985 by R. I. Crombie, as follows: dorsally medium brown with black mottling and silver flecks. A narrow black lateral area, less pronounced on tail, bordered ventrally with an area of intense silver freckling (less concentrated on lateral tail). Belly pale, unmarked gray but with some silvery flecking on throat. An indistinct chestnut postocular stripe and indistinct dull chestnut on snout. Iris dark. Crombie recorded the following color notes for USNM 195321: dorsally medium brown with black mottling and silver flecks. Belly pale, unmarked gray but with some silver flecking on throat.

Osteology.—Some information on osteology has been derived from radiographs of the holotype and five paratypes. All specimens have 18 trunk vertebrae, and small ribs are borne on all in the largest specimen and all but the last in others. Numbers of caudal vertebrae in individuals with apparently unregenerated tails range from 52 to 57 (the last in the largest individual). Skulls are relatively well articulated but little detail is evident. The snout is generally well developed and protuberant, and the nasals are curved with a medial portion that approaches an upward-growing portion of the vomer. There is no fontanelle between the frontals and parietals, and the frontals have a large facial portion. Digits are generally poorly ossified. The most complete phalangeal formula is 0-1-2-2 (in one manus of the holotype) and 1-2-3-2-2 (in the largest individual). However, the modal formulae are 0-1-2-1 and 1-2-2-2-1. Tibial spurs are not evident.

Habitat and reproduction.—Salamanders on Isla Escudo de Veraguas were collected in decaying fronds and associated moist litter near a fallen palm in a coconut palm grove in late March, 1991. The eggs were found inside a pile of coconut trash at the base of a tree (*Terminalia*) on the beach at Guayami Settlement, SE part of island, less than 5 m from the ocean. The eggs belonged to two clutches, each containing six embryos; there is one rotted egg that may belong to either clutch. One clutch includes totally unpigmented embryos that are well formed and have well-formed limbs, but the limbs, although moderately long, have no digits or digital rudiments. The other clutch includes near full-term embryos that are well pigmented (see Color variability, above). These embryos began hatching on the way back to camp from the field. One newly hatched embryo is 11.8 mm in total length (8.7 SL) and retains gills. The gills are three lobed, one relatively large and palmate, a second smaller but palmate, and one relatively large and slender and branched at the base.

Etymology.—The name *maritima* is derived from *maritimus* (L), meaning of the sea, in reference to the type locality of this species on a low-lying island in the Caribbean Sea.

Comment.—*Oedipina maritima* does not resemble *O. alleni* in morphology (it is more slender and has a narrower and more pointed head, and it generally lacks dorsal light coloration), and it is very distinct in its DNA sequences. It differs from *O. parvipes* from central Panamá profoundly in DNA sequences (4.8–4.9% for 16S, 7.8–8.1% for cyt *b*), but appears to differ otherwise only in coloration (we have no allozyme data). However, we also note that evidence of conspecificity of Panamanian and Colombian populations of *O. parvipes* is weak, and A. H. Brame Jr. and D. B. Wake have long planned to undertake a detailed analysis of this question once adequate material is available. Accordingly, we decided to describe what is clearly an independent taxon at this time and reserve a complete analysis of Panamanian and South American members of this genus to a later date.

This species is known only from Isla Escudo de Veraguas. If it is restricted to this island, it is the only tropical salamander that is endemic to an island. At least three species of this genus occur on the adjacent mainland, two of which appear to be undescribed. KU 116682, a 17.5 SL juvenile from the mouth of Rio Cahuita, Prov. Bocas del Toro, Panamá, 1 m. elev., cannot be classified with certainty but may be assignable to *O. maritima*.

Description of a New Species of *Oedipina* from Costa Rica

Oedipina savagei n. sp.
Savage's Worm Salamander
Figure 6A

Holotype.—LACM 109558, an adult female from Finca Las Cruces, 6 km S San Vito de Java, Prov. Puntarenas, Costa Rica, 8°47′35″N, 82°57′30″W, approximately 1200 m elev., collected 22 May 1971 by R. W. McDiarmid and associates.

Paratypes.—LACM 109556–557, LACM 145447–145450 (four specimens), USNM 219122, same locality as holotype, collected on different dates;

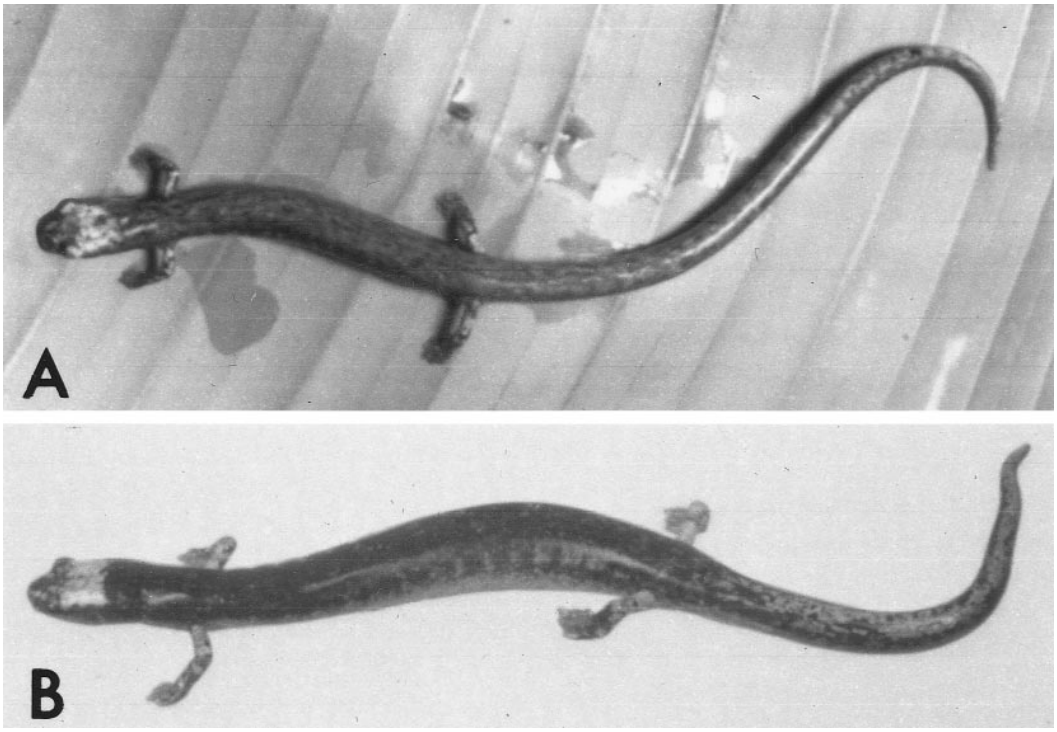

Fig. 6. (A) *Oedipina savagei*. LACM 145447, an adult male (35.7 mm SL) from Las Cruces, Prov. Puntarenas, Costa Rica, collected in August 1971. Photograph by R. W. McDiarmid. (B) *Oedipina alleni*. MVZ 221317, an adult female (46.4 mm SL) from 3.5 km SE Damas, Prov. Puntarenas, Costa Rica, elev. 3–5 m, collected 2 August 1992. Photograph by J. Hendel.

MVZ 229360, UCR LDG 961327 (temporarily DBW 5786), Paraguas Ridge (slopes of Cerro Zapote), ca. 4 km W Agua Buena, Prov. Puntarenas, Costa Rica, approximately 8°45′N, 82°9′W, approximately 1400 m elev.

Referred material.—UCR 8210, Finca Cafrosa near Las Mellizas, Prov. Puntarenas, Costa Rica, 1300 m elev.

Diagnosis.—A small (maximum size 39.3 SL), moderately robust member of *Oedipina* (subgenus *Oedopinola*) with a narrow head and a relatively short, rounded snout. Distinguished from *Oedipina alleni* by having more maxillary teeth and a light dorsal stripe; from *Oedipina maritima* by its more robust habitus, broader and more rounded head, more maxillary teeth, more prominent and more frontally oriented eyes, and persistent light dorsal stripe; from *Oedipina parvipes* by its broader head with a shorter, more rounded snout, more maxillary teeth, and light dorsal coloration; from *Oedipina complex* by its less bluntly rounded snout; from *Oedipina carablanca* by its much smaller size and less robust habitus, and narrower hands and feet; and from the first four of the above species by extensive sequence differences in the mitochondrial genes 16S rDNA and cytochrome b.

Description.—This is a relatively small, moderately robust species; adult standard length (SL) for three males is 35.6–38.5 mm, $\bar{x}$ 36.8; for three females 34.3–39.3, $\bar{x}$ 37.5. The head is moderate in width, being broader in males. Males have shorter, blunter snouts than females, in which the snout is somewhat narrow and slightly pointed. SL averages 8.6 (range 8.3–8.8) times head width in four males, and 8.7 (8.4–9.0) in three females; SL averages 6.0 (5.6–6.4) times head length in four males, and 6.6 in three females (6.0–7.2). Nostrils are evident and moderately large for the genus. Nasolabial protuberances are prominent in both sexes but especially in males, in which they are swollen, knoblike structures that extend below the somewhat underslung lower jaw. Eyes are of moderate size and stand out from the head, extending laterally beyond the limits of the head. They have a moderate to strongly frontal orientation. The suborbital groove does not intersect the lip. The very small premaxillary teeth (3–4 in number)

lie well within the mouth in both sexes, except for USNM 219122, in which there is a single small tooth lying outside of the mouth. This is the only specimen that has a mental gland, a small cluster of openings in a patch of pigment lying just behind the mandibular symphysis. Maxillary teeth are small and moderately numerous, ranging between 7 and 18 ($\bar{x}$ 12.3) in four males and 7 and 15 ($\bar{x}$ 11) in three females. Vomerine teeth range between 11 and 22 ($\bar{x}$ 15.8) in four males and 11 and 12 ($\bar{x}$ 11.7) in three females; these very small teeth are borne in a long row. There are 17 (7 individuals)–18 (1 individual) costal grooves between the limbs, counting one each in the axilla and the groin; accordingly we infer that there are 18 (rarely 19) trunk vertebrae. Limbs are of moderate length for this clade; limb interval averages 6.6 (6–7) in four males and 6.8 in three females (6.5–7). Hands and feet are small and are moderately broad but short. The digits are syndactylous, and only the triangular tips of the longest central digits are free (Fig. 5). Fingers, in order of decreasing length, are 3-2-4-1; toes are 3-2-4-5-1. The tail is round, narrow in cross section and relatively short. Tails of most individuals may be at least partly regenerated or were cut for extraction of DNA prior to measurement. Apparently complete tails exceed SL, and in the individual with the longest tail (one of the smaller males), SL is 0.65 tail length.

Measurements of holotype.—Head width 4.5; snout to gular fold (head length) 5.9; head depth at posterior angle of jaw 2.9; eyelid width 0.9, eyelid length 1.5; eye to nostril 1.1; anterior rim of orbit to snout 1.4; horizontal orbit diameter 1.1; interorbital distance 2.3; distance separating eyelids 1.7; nostril diameter 0.2; snout projection beyond mandible 0.5; distance from eye to postorbital groove 2.2; snout to posterior angle of vent (standard length) 39.3; snout to anterior angle of vent 35.7; snout to forelimb 8.8; axilla to groin 23.9; limb interval 6 1/2; shoulder width 3.4; tail length 39.1 (apparently at least partly regenerated); tail width at base 2.7; tail depth at base 2.8; forelimb length (to tip of longest digit) 6.1; hind-limb length 7.1; hand width 1.4; foot width 1.9; free length of longest toe 0.6. Numbers of teeth: premaxillary 4; maxillary 5–2; vomerine 5–6.

Coloration in alcohol.—This description is based mainly on two recently collected specimens (MVZ 229360, UCR LDG 961327), because coloration of the holotype and other paratypes has been modified by the long period of preservation. Ontogenetic change in coloration is clearly evident in this species. Individuals below 30 mm SL have a dorsal stripe or band that is prominent and mainly unmarked. The stripe extends from the tip of the snout to the tip of the tail, interrupted on the midline of the snout by a dark incursion of pigment forming a narrow streak, and at a few places along the back of the head or on the trunk by some obscure dark pigment. In older individuals, there is widespread incursion of dark pigmentation into the band from the lateral surfaces (Fig. 6A). In juveniles the lateral surfaces are dark brown from the facial region and below the upper eyelids all along the head, body and tail to its tip. This lateral stripe persists in adults. The dorsal band is always lighter than the lateral surfaces, even when extensive melanization has occurred. In all individuals the area including the back of the head and extending forward to and including the upper eyelids remains light and bears white pigment. The snout becomes increasingly mottled with increasing size as the white pigment is progressively restricted to the vicinity of the nostrils and nasolabial grooves and protuberances. The dorsal stripe in adults is a melange of streaks or irregular spots, of melanin that becomes increasingly dense with increasing size (this observation is based in part on what happens in close relatives). The melanic areas interrupt and gradually replace the white pigment, which eventually is reduced on the back to some superficial and irregular spots. The upper lateral surfaces are nearly unmarked dark brown, but more ventrally on the sides of the trunk there are increasing densities of streaks and irregular spots of extensive, prominent white pigmentation that continues onto the ventral surface. The ground color of the ventral surface is lighter than the lateral surfaces, and the ventrolateral streaks of white are reduced to a more regular pattern of spotting or speckling. The tail and gular areas are lighter than the venter of the trunk, and white pigment is most evident in the gular region. The upper limb insertions are typically white, especially those of the hind limb, but they may be somewhat speckled with white and melanic pigment. The remainder of the limbs including the hands and feet are speckled with light and dark coloration. The iris is black with an overlay of delicate strands of silvery pigment.

Osteology.—Some information on osteology has been derived from radiographs of the holotype and six paratypes. All specimens have 18 trunk vertebrae, 17 of which bear ribs in the holotype (ribs are not visible in most of the other specimens). Numbers of caudal vertebrae range

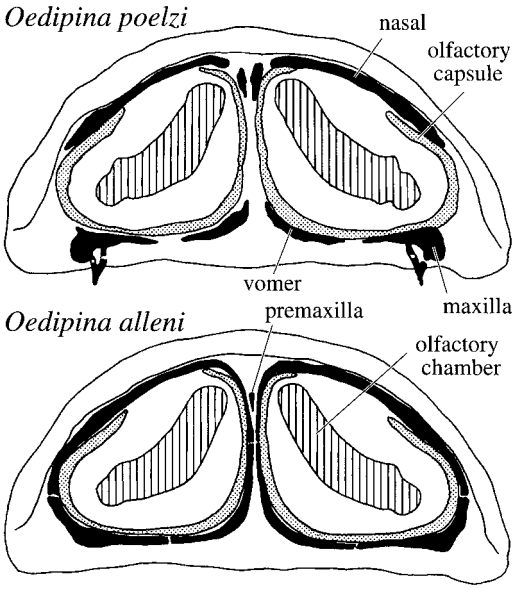

Fig. 7. Cross-sectional representations of the snouts of representative members of the two subgenera of *Oedipina*. Left, *Oedipina* (*Oedipina*), based on a serial-sectioned head of *O. poelzi*. Right, *Oedipina* (*Oedopinola*), based on an adult, cleared-and-stained *O. alleni*, and on radiographs of several species. Maximum width of snouts is approximately 4 mm.

from 20 (in the smallest individual) to 48 (LACM 145447); the holotype has 32. Skulls are relatively robust and well articulated with little or no fontanelle between the frontal and parietal bones. Frontal bones are large with a large facial portion that articulates firmly with the nasals, and the snout region is well ossified, with development of at least a partial tubular arrangement of the nasals, vomers and maxillaries as shown in Figure 7. The premaxillary is small, and the frontal processes are fused for most of their length as a narrow spine, although they separate distally. Digits are weakly developed and in most individuals are not countable. The holotype has phalangeal formulas of 0-1-1-1 and 0-1-2-1-1. LACM 145450 has the most complete digital series with formulas of 0-1-2-1 and 1-2-2-2-1. Tibial spurs are not evident.

Etymology.—The species is named in honor of Jay Mathers Savage, who has devoted more than 40 years of sustained effort to document the biology of the amphibians and reptiles of Costa Rica, and whose comprehensive volume on this fauna is forthcoming. Savage's contributions include not only his superb research productivity and his role in the development and leadership of the Organization for Tropical Studies but also his education of several generations of professional biologists, of whom the junior author is one of the earliest in a long list.

Comment.—We have samples from three populations in southwestern Costa Rica, two of which were studied by Good and Wake (1997) and found to be very similar in allozyme patterns. However, we discovered that these two populations differ considerably in sequences of cyt *b* (8.3–9.0%) and 16S (3.4%). Because allozymic differentiation is so slight (Nei D = 0.02), because we find no differences in morphology (except that population 31 apparently achieves larger body size), and because the populations occur in the lowlands with no apparent physical barriers to gene flow, we continue to consider them to be conspecific and to represent *O. alleni*. Sequence differences between these two populations and *O. savagei* are also large (pop 30-31 is 6.4–6.6% and pop 32 is 10.3–11.2% for cyt *b*; comparable values for 16S are 3.2 and 4.4%). Phylogenetic analysis consistently clusters *O. savagei* and pop 30–31. However, the facts that *O. savagei* occurs at much higher elevations than *O. alleni* and that it is morphologically distinct lead us to recognize it as a distinct taxon. Allozymic data suggest that reticulation with reference to DNA haplotypes has taken place among the lowland populations. By this, we mean that populations once were separated, and during this time sorting of haplotype lineages took place. Upon recontact, the populations interbred so that allozymic genetic distances are now low. However, the existence of well-differentiated haplotypes indicates that there has been insufficient time for reductions in haplotype diversity. Such genetic reticulation has also been found in other plethodontid salamanders, such as *Ensatina* (Wake, 1997; Wake and Schneider, 1998) and *Batrachoseps* (Wake and Jockusch, 2000).

Description of a New Species of *Nototriton* from Costa Rica

Nototriton gamezi
Monteverde Moss Salamander
Figure 8

Holotype.—MVZ 207122, an adult female from Carril Bosque Eterno at junction with Pantanosa Trail, Monteverde Cloud Forest Reserve, Prov. Alajuela, Costa Rica, elev. 1600 m, approximately 10°19′N, 84°47.5′W, collected on 14 August 1987, by D. C. Cannatella, D. A. Good, W. Guindon, and D. B. Wake.

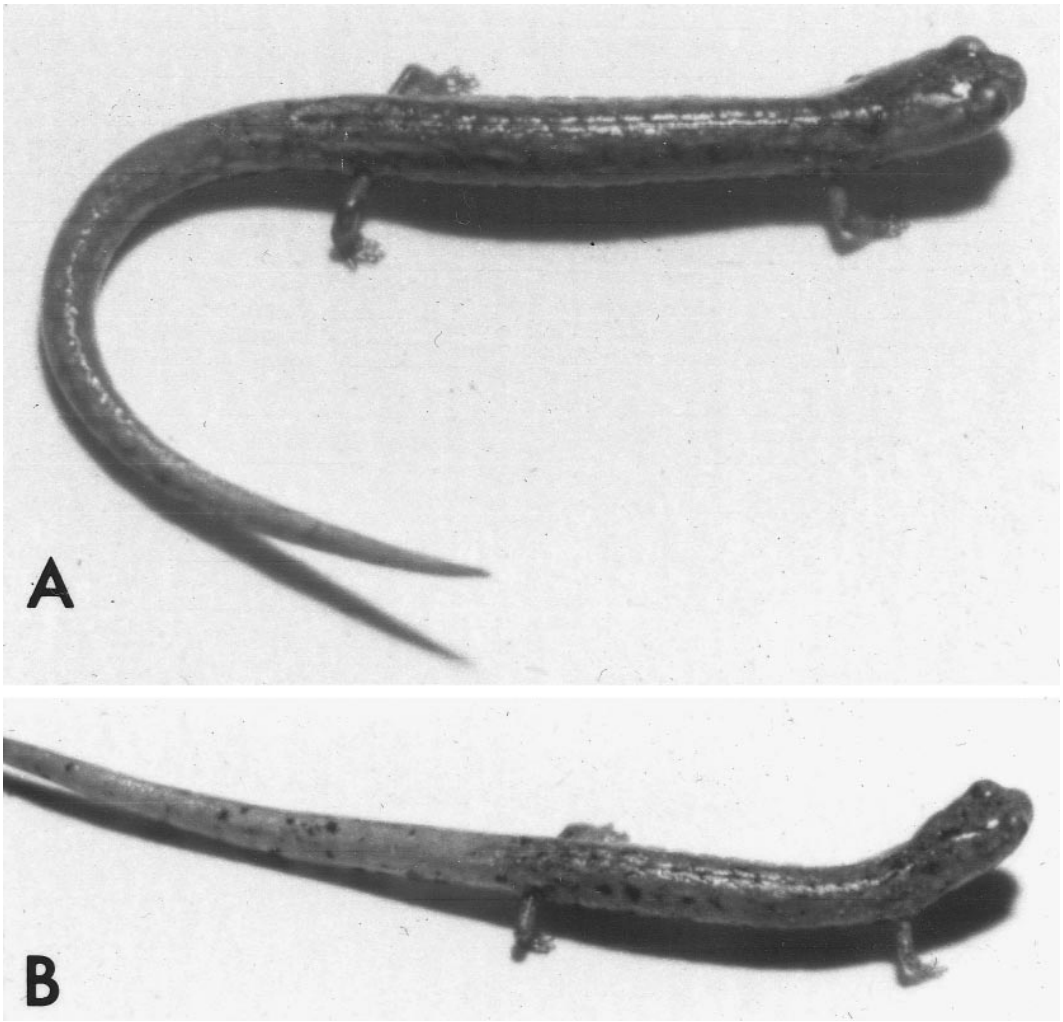

Fig. 8. (A) *Nototriton gamezi*, MVZ 207123, an adult male (23.6 mm SL) from Peñas Blancas Trail, Monteverde, Prov. Alejuela, Costa Rica, elev. 1540 m, collected 15 August 1987. Photograph by D. C. Cannatella. (B) *Nototriton gamezi*, MVZ 207121, an adult female (24.2 mm SL) from Peñas Blancas Trail, Monteverde, Prov. Alejuela, Costa Rica, elev. 1535 m, collected 14 August 1987. Photograph by D. C. Cannatella.

Paratypes.—MVZ 207120–207121, 207123, Peñas Blancas trail below (E) Continental Divide, Monteverde Cloud Forest Reserve, Prov. Alajuela, Costa Rica, elev. 1530–1540 m; MVZ 207124, Pantanosa Trail, Monteverde Cloud Forest Reserve, Prov. Alajuela, Costa Rica, elev. 1590 m; UCR 4396, La Ventana, Monteverde Cloud Forest Reserve, Prov. Alajuela, Costa Rica; UCR 6200, Peñas Blancas Trial, Monteverde Cloud Forest Reserve, Prov. Alajuela, Costa Rica.

Diagnosis.—A small (maximum size in type series 26.4 SVL), slender species of *Nototriton* distinguished from Costa Rican members of the genus as follows: from *N. abscondens* by its larger nostrils, shorter limbs, and more prominent parotoid glands; from *N. richardi* and *N. tapanti* by its larger, more fully formed hands and feet (e.g., fifth toe length of adults 0.7–0.8 vs. 0–0.1), longer limbs, and more robust habitus; from *N. major* by its smaller size, shorter tail and larger nostrils; from *N. guanacaste* by its shorter and narrower head, and larger nostrils; from *N. picadoi* by its relatively more slender habitus and shorter limbs. It differs further from *N. abscondens, N. richardi, N. guanacaste, N. picadoi, N. barbouri, N. lignicola, N. limnospectator,* and *N. brodiei* by sequence differences in the mitochondrial genes 16S rDNA and cytochrome *b*.

Description.—This is a small, slender species; adult SL for the sole adult male available is 23.6;

for two females 24.2, 26.2. The head is of moderate length (0.19–0.21 SL in four specimens) and width (0.13–0.14 SL), and is well demarcated from the trunk. Eyes are of moderate size and protrude slightly beyond the lateral margins of the head. The small teeth are relatively numerous (24–35, $\bar{x}$ 28.8 total number of maxillary teeth; 12–17, $\bar{x}$ 14.8 total number of vomerine teeth). Parotoid glands are relatively conspicuous and appear as swollen, lightly pigmented protuberances from the posterolateral margins of the head. The adult male has a small, flat, round mental gland. The species has a trunk of moderate robustness. The limbs are relatively short (0.16–0.17 SL). The slender tail is longer than body length ($\bar{x}$ 1.1 SL, maximum length 1.3 SL) and has a relatively strong taper to a slender, pointed tip. Limbs are relatively short; limb interval 5–5.5. Hands and feet bear well-formed, slender digits that are fully independent, except for the first digit of the forelimb which is relatively indistinct and joined to the basal portion of the manus. The digits are slightly expanded around the terminal phalanx. Webbing is slight and is limited to part of the proximal phalanx.

Measurements of holotype.—Head width 3.5; head depth 2.3; eyelid length 1.8; eyelid width 0.8; anterior rim orbit to snout 0.8; interorbital distance 0.8; snout to forelimb 0.9; nostril diameter 0.2; distance between external nares 0.7; projection of snout beyond mandible 0.1; parotoid gland 1.0 × 0.8; snout to gular fold 5.3; snout to posterior angle of vent 26.2; snout to anterior angle of vent 24.6; axilla to groin 14.3; tail length 28.3; tail depth at base 2.4; tail width at base 2.4; forelimb length 4.0; width of hand 1.2; hind-limb length 4.8; width of foot 1.6; length of longest (third) toe 0.5; length of fifth toe 0.2. Numbers of teeth: premaxillary 5; maxillary 17–18; vomerine 8–9.

Coloration of holotype (in alcohol).—This is a generally dark animal with some brightly pigmented highlights. The dorsal surfaces of the head and body are dark gray-brown, with some darker brown pigment in an obscure dorsolateral line, especially in the costal interspaces. The light yellow parotoid glands stand out conspicuously at the back of the head, in the neck region. The lateral surfaces of the trunk are obscurely mottled with cream-yellow spots, blotches, and streaks. The facial portion of the head and the region under the eyes and along the mandibles is lightly marked with small, yellowish spots. The venter, and especially the gular region, are lighter than the dorsum and are lightly covered with small whitish spots. The dorsal portions of the proximal limb surfaces are yellowish. The dorsal surfaces of the tail are bright yellow-cream, marked with some irregular small patches of gray-brown. The ventral surfaces of the tail are gray.

Coloration (in life).—Color notes were recorded in life by DBW for three specimens. MVZ 207123 was black ventrally, with white spots in bands corresponding to costal segments. There was a distinct contrast between the black venter and the brown dorsum. The lateral surfaces of the trunk were streaked and mottled, and there was an obscure dorsolateral dark line. The parotoid region was orange-brown, as were the limb insertions. The dorsum of the tail was orange-brown with some tannish streaks. The iris was brown-bronze.

MVZ 207121 was reddish brown with a tan tail, with all dorsal surfaces bearing small black spots. The venter of the trunk was gray with highlights of reddish brown and a rich sprinkling of white spots. The gular region was lighter gray than other ventral surfaces. Limb insertions were reddish brown.

MVZ 207120 was light brown dorsally with many black spots that create a pattern of repeated chevrons, pointing anteriorly. Dorsolateral lines were dark with tan streaking beside them. The tail was tan. The ventral and lateral surfaces of the body were black, with many irregularly distributed white spots. There were black irregular markings on the head. Limb insertions were orange-brown.

Habitat.—The type series was collected in the Monteverde Cloud Forest Reserve in August 1987. Two specimens were collected by searching through heavy moss mats in openings in the forest beside a wide trail on the Caribbean coastal slope of the continental divide. The divide is about 1550 m elevation at this spot, and the salamanders were obtained within about 20 m (elevation) of the divide. Air temperature was 21.5 C, and two salamanders were collected at temperatures of 21.5 and 20.2 within moss mats. These animals were microsympatric with *Oedipina poelzi* and *O. uniformis*. The type specimen was collected along the divide in deep forest at about 1600 m from moss growing on a tree; temperature 20.0 C. A fourth specimen was collected from moss on a tree.

Etymology.—This species is named in honor of Rodrigo Gámez, distinguished Costa Rican scientist and public servant, and first Director of the Instituto Nacional de Biodiversidad de Cos-

ta Rica (INBio), whose superb efforts have contributed greatly to knowledge and preservation of Costa Rican biodiversity.

Comment.—This species has been known for many years, but it has long been considered to be conspecific with populations from the Cordillera Central of Costa Rica now assigned to *N. abscondens* (e.g., Van Devender, 1980). The species was studied by Good and Wake (1993), who reported details of a morphometric and allozyme study of the population relative to other Costa Rican populations assigned to *Nototriton*. Although they found the population to be morphologically distinct, they included it in *N. abscondens* because allozyme differences were not great and because the population clustered with other populations of that species (but also with *N. guanacaste*) in a phylogenetic analysis of the allozyme data. However, these authors noted that the Monteverde population overlaps more extensively in morphological traits with *N. guanacaste* than with *N. abscondens*. Although genetic distances are low (Nei D = 0.05–0.06), there is one fixed allozymic difference between *N. gamezi* and *N. abscondens*; there are three fixed differences between *N. gamezi* and *N. guanacaste*, and seven differences between *N. gamezi* and *N. picadoi* (Good and Wake, 1993). To the characters listed by Good and Wake (1993) for the Monteverde population, we note also that the species has distinct parotoid glands, and in this trait, it resembles *N. guanacaste*. The primary reasons for our decision to describe the species are that it is diagnosable on several grounds, it is well differentiated from all other Costa Rican populations of *Nototriton* with respect to both cyt *b* and 16S sequences (relative to *N. abscondens* K2p is 0.021–0.024 for cyt *b*, 0.018 for 16S) and it is never the sister taxon of *N. abscondens* in phylogenetic analyses of the sequence data. Instead, it is usually the sister taxon of a polytomy of *N. abscondens, N. picadoi* (K2p is 0.016–0.019 for cyt *b*, 0.018 for 16S), and *N. guanacaste* (K2p is 0.040 for cyt *b*; 0.014 for 16s), but in the combined analysis, it is a part of a polytomy of the first two species. Accordingly, it is unlikely that *N. gamezi* is even a sister group of *N. abscondens*, and we believe that it merits recognition as a separate species.

Description of a New Genus of Tropical Salamanders

Cryptotriton new genus
Hidden Salamanders

Type species.—*Oedipus nasalis* Schmidt.

Diagnosis.—Diminutive, slender, arboreal salamanders belonging to the supergenus *Bolitoglossa*, having moderately long tails, limbs of moderate length, and enlarged nostrils. The intermedium and ulnare of the manus and distal tarsals four and five of the pes are fused. The genus is distinguished from other genera with similar fusions as follows: from *Oedipina* by having only 14 rather than 18 or more trunk vertebrae; from *Bradytriton* by having more slender habitus, a slender, nonglandular tail, and enlarged nostrils; from *Parvimolge* by having frontal processes of the premaxillary fused together at their base and lacking mesopodial and hyobranchial mineralizations; from *Thorius* by having a complete skull roof over the brain case; from *Bolitoglossa* by having carpal fusions, a sublingual fold, and enlarged nostrils; from *Nototriton* by having much larger nostrils and by having a prefrontal bone that is pierced for passage of the nasolacrimal duct.

Referred species.—*Nototriton adelos* Papenfuss and Wake; *Nototriton alvarezdeltoroi* Papenfuss and Wake; *Nototriton monzoni* Campbell and Smith; *Nototriton nasalis* (Schmidt); *Nototriton veraepacis* (Lynch and Wake); *Nototriton wakei* Campbell and Smith.

Etymology.—From *kryptós*, Greek, hidden, referring to the cryptic behavior of these salamanders, the obscurity concerning phylogenetic relationships that has retarded its recognition, and its close morphological resemblance to other clades of tropical salamanders, and *triton*, Latin, Greek, a commonly used term for salamanders.

Range.—*Cryptotriton* ranges from the mountains of northern Oaxaca, Mexico, through the mountains of northern Chiapas, Mexico, the highlands of Alta Verapaz, Guatemala, and the Sierra de las Minas, eastern Guatemala, to the Cordillera del Merendón and associate uplands in extreme northeastern Honduras.

Comment.—As recently as 1978, this clade and other clades with diminutive, slender species (*Nototriton, Dendrotriton*) were included in *Chiropterotriton*, which was thought to range from Tamaulipas, northeastern Mexico, to central Costa Rica (Lynch and Wake, 1978). Wake and Elias (1983) recognized *Dendrotriton* as a monophyletic group, and restricted *Chiropterotriton* to Mexico north and west of the Isthmus of Tehuantepec. Although they described *Nototriton* at the same time, they expressed doubts that it was a monophyletic group, and those reserva-

tions are confirmed by results published in this paper. These small, secretive, often rare salamanders have proven to be difficult taxonomically, and only with the advent of molecular approaches (e.g., Good and Wake, 1997; this paper) are we finally able to identify the monophyletic lineages that formerly comprised the composite *Chiropterotriton*. Our analysis supports the recognition of an additional species (pop. 10) from Guatemala that is being described by Good and Wake.

The monophyletic units once included in *Chiropterotriton* display homoplasy in many structural details as well as in overall body form and even general ecology. They have distributions that overlap only slightly with each other. *Chiropterotriton* occurs west and north of the Isthmus of Tehuantepec, and although it is diverse in morphology and ecology, several species are small. These are either terrestrial or bromeliad-dwellers (Wake, 1987; Darda, 1994). *Cryptotriton* includes small species that use either moss mats or bromeliads and occur mainly in nuclear Middle America, from western Honduras into northern Chiapas, in areas of Atlantic drainage. We tentatively assign the rare species *C. adelos* to this genus, although we have been unable to study its DNA, mainly because of its general morphology (it has an arrangement of skull bones found otherwise only in *Cryptotriton*, Papenfuss and Wake, 1987) and its geographic proximity to other species in the genus. However, it is the only member to occur west of the Isthmus of Tehuantepec, and it may represent a phylogenetically independent clade. *Dendrotriton* includes small bromeliad-dwellers and is limited to Nuclear Middle America, where it is found in the Atlantic drainage of western Honduras, mainly the Pacific drainage of northwestern Guatemala, and on the Pacific slopes of Chiapas (Wake, 1987, 1998). Finally, *Nototriton* occurs in two well-separated upland zones in the Atlantic drainage of central and western Honduras and eastern Guatemala (where it is mainly terrestrial) and in mountains along the continental divide but mainly of Atlantic drainage in central and northwestern Costa Rica (where it lives in moss mats on trees or road banks, or in bromeliads, or is terrestrial). Sympatry is known between *Cryptotriton* and *Chiropterotriton* in northern Oaxaca (Wake et al., 1992), between *Nototriton* and *Dendrotriton* on the Montaña de Santa Bárbara, western Honduras (McCranie and Wilson, 1997a), and between *Nototriton* and *Cryptotriton* in eastern Guatemala (Campbell and Smith, 1998; McCranie et al., 1998). Where species of *Nototriton* occur with or near either *Dendrotriton* or *Cryptotriton*, they can be distinguished by being more terrestrial and by having small nostrils. *Nototriton, Cryptotriton, Dendrotriton*, and several smaller clades (*Bradytriton, Nyctanolis, Ixalotriton*) all are associated with nuclear Middle America, and in future papers we will examine the biogeography of these taxa in greater detail in association with further phylogenetic analyses.

Review of Other Genera in This Study

Nototriton Wake and Elias
Moss Salamanders

Type species.—*Spelerpes picadoi* Stejneger.

Diagnosis.—Diminutive, slender, long-tailed salamanders of arboreal and semiarboreal (including moss mats), terrestrial, or semifossorial habitats with moderately long to short legs with small hands and feet and small to medium-sized nostrils. The intermedium and ulnare of the manus and distal tarsals four and five of the pes are fused. The genus is distinguished from other genera with similar fusions as follows: from *Oedipina* by having only 14 rather than 18 or more trunk vertebrae; from *Bradytriton* by having more slender habitus, a slender, nonglandular tail, and enlarged nostrils; from *Parvimolge* by having frontal processes of the premaxillary fused together at their base and lacking mesopodial and hyobranchial mineralizations; from *Thorius* by having a complete skull roof over the brain case; from *Bolitoglossa* by having carpal fusions and a sublingual fold; from *Cryptotriton* by having much smaller nostrils and by having a complete prefrontal bone or lacking it entirely, but never being pierced for passage of the nasolacrimal duct.

Referred species.—*Nototriton abscondens* (Taylor), *Nototriton barbouri* (Schmidt), *Nototriton brodiei* Campbell and Smith, *Nototriton gamezi* García-París and Wake, *Nototriton guanacaste* Good and Wake, *Nototriton lignicola* McCranie and Wilson, *Nototriton limnospectator* McCranie, Wilson and Polisar; *Nototriton major* Good and Wake, *Nototriton picadoi* (Stejneger), *Nototriton richardi* (Taylor), *Nototriton tapanti* Good and Wake.

Range.—From central Costa Rica northward in isolated montane habitats to western Honduras. There is a large geographic gap in the range from Volcán Orosí in northwestern Costa Rica (*N. guanacaste*) to the mountains of north central Honduras (Depto. Olancho, *N. lignicola*).

Comment.—The species originally described as *Nototriton sanctibarbarus* (McCranie and Wilson, 1997a) has recently been reassigned to the genus *Dendrotriton* (Wake, 1998).

Oedipina Keferstein 1868

Tropical Worm Salamanders

Type species.—*Oedipina uniformis* Keferstein.

Diagnosis.—Elongate salamanders of moderate to large size with long to very long tails, usually with small to very small limbs, hands and feet; distinguished from all other tropical bolitoglossine salamanders by having 18 or more trunk vertebrae, rather than 14.

Content.—We treat the two clades as subgenera, *Oedipina* and *Oedopinola*. *Oedipina* includes generally longer-bodied, longer-tailed species, usually with small limbs, hands and feet. *Oedopinola* includes generally stouter, shorter-bodied, shorter-tailed species, with larger limbs, hands and feet, but some species are relatively long bodied (*O. gephyra*) and others have very reduced limbs and digits (*O. complex, O. maritima*). In general, *Oedipina* has a skull that is normally proportioned for the tribe Bolitoglossini, whereas most (possibly all) species of *Oedopinola* display a double tubular arrangement of the nasal region, produced by downward growth of the medial and lateral borders of the nasals and corresponding upward growth of the vomers, forming a skeletal tube around the nasal capsules of these semifossorial to fossorial species (Fig. 7).

Oedipina Keferstein 1868

Referred species.—The content of the *uniformis* group of Brame (1968), plus additional recently recognized taxa: *alfaroi* (Dunn), *altura* Brame, *collaris* (Stejneger), *cyclocauda* Taylor, *gracilis* Taylor, *grandis* Brame and Duellman, *ignea* Stuart, *pacificensis* Taylor, *paucidentata* Brame, *poelzi* Brame, *pseudouniformis* Brame, *stenopodia* Brodie and Campbell, *stuarti* Brame, *taylori* Stuart, *uniformis* Keferstein.

Range.—From extreme western Guatemala south to central Panamá along the Pacific versant, and from central Honduras to central Panamá along the Caribbean versant; from sea level to about 2500 m elevation; occurs on islands of the Golfo de Fonseca on the Pacific Coast.

Comment.—Brame (1968) concluded that *Haptoglossa pressicauda* Cope, 1893, is a synonym of *Oedipina uniformis* Keferstein, 1868, which was revised by Good and Wake (1997). If he is correct in this conclusion (the type is lost), the name *pressicauda* is likely a senior synonym for the recently elevated taxon *pacificensis* Taylor, 1952. Cope reported the type specimen to have an attached tongue. Cope was an expert on salamander morphology and accordingly understood the significance of this character (no member of the supergenus *Bolitoglossa* has such a tongue, and only members of that supergenus are otherwise known from the New World tropics). Accordingly, we think he was unlikely to make a mistake on such a character. We are not convinced that the type specimen is even referable to the supergenus, and accordingly we are reluctant to recommend a taxonomic change in the status of *pacificensis* (which was raised from the synonymy of *uniformis* by Good and Wake, 1997).

Oedopinola Hilton 1946

Referred species.—The content of the *parvipes* group of Brame (1968) and additional recently recognized taxa: *alleni* Taylor, *carablanca* Brame, *complex* (Dunn), *elongata* (Schmidt), *gephyra* McCranie, Wilson and Williams, *maritima* García-París and Wake, *parvipes* (Peters), *savagei* García-París and Wake.

Range.—From Chiapas, Mexico, along the Caribbean versant to northwestern Colombia, including Isla Escudo de Veraguas, Panamá, and from Honduras to northern Ecuador along the Pacific versant, including Isla Gorgona, Colombia; from sea level to about 1500 m.

Comment.—This is a poorly known clade comprised of species generally known only from very few specimens. Isolated samples from Panamá, Colombia and Ecuador have been assigned to existing taxa but several probably constitute undescribed species.

Acknowledgments

We gratefully acknowledge the assistance of many friends and colleagues in assembling the materials used in this study. Fieldwork is demanding and difficult, and many of the species we have studied are rare, elusive, or both. We especially thank F. Bolaños, D. C. Cannatella, D. A. Good, E. J. Jockusch, E. J. Koford, P. León, the late J. F. Lynch, T. J. Papenfuss, S. K. Sessions, and N. J. Staub for help in collecting. We also thank individuals who have obtained critical specimens for us, including J. A. Campbell,

R. Crombie, J. Denslow, L. D. Gómez, R. Ibáñez, J. McCranie, M. A. Schlaepfer, and L. D. Wilson. Collecting permits have been provided by agencies in the following countries: Costa Rica, Guatemala, Honduras, México, and Panamá. We also thank managers of various field sites for permission to collect tissue samples. We thank the curatorial staffs of the Los Angeles Museum of Natural History (LACM) and University of Kansas (KU), and J. M. Savage, for loans of specimens and provision of information. Gabriela Parra-Olea and S. Kuchta assisted in generating the sequence data, and Karen Klitz prepared Figures 6 and 8, and L. Chan assisted in the preparation of Figures 5 and 7. We thank members of the Wake Group, especially M. Mahoney, S. Kuchta and G. Parra-Olea, for discussion and review of the manuscript, and J. McCranie and reviewers for helpful comments. This research was supported by National Science Foundation, MVZ, and the Gompertz Professorship of the University of California.

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Appendix 1. Samples Used in This Study and GenBank Accession Numbers.

Sample no.	Species	Locality	Museum no.	Cyt *b*	16S
1	*C. alvarezdeltoroi*	México: Chiapas: 21.5 mi N Jitotal	MVZ 158942	AF199120	AF199196
2	*C. nasalis*	Honduras: Cortés: Mts. W San Pedro Sula	MVZ 128274	AF199121	—
3	*C. veraepacis*	Guatemala: Baja Verapaz: 2.5 mi S Purulha	MVZ 172709	AF199122	—
4	*C. veraepacis*	Guatemala: Baja Verapaz: 6.5 mi ESE Purulha	MVZ 215913	AF199123	AF199197
5	*C. veraepacis*	Guatemala: Baja Verapaz: 6.5 mi ESE Purulha	MVZ 167991	AF199124	—
6	*C. veraepacis*	Guatemala: Baja Verapaz: Purulha	UTA GAR 59 (Tiss.).	AF199125	—
7	*C. veraepacis*	Guatemala: Baja Verapaz: Purulha	UTA A-51395	AF199126	—
8	*C. veraepacis*	Guatemala: Baja Verapaz: Purulha	UTA A-51396	AF199127	—
9	*C. sp.* A	Guatemala: Zacapa: Sierra de Las Minas	MVZ 160901	AF199128	—
10	*C. sp.* A	Guatemala: Zacapa: Sierra de Las Minas	MVZ 160907	AF199129	AF199198
11	*N. abscondens*	Costa Rica: Alajuela: Cascada de La Paz	UCR 12071	AF199130	AF199199
12	*N. abscondens*	Costa Rica: Alajuela: Vara Blanca	MVZ 203743	AF199131	—
13	*N. abscondens*	Costa Rica: Alajuela: Vara Blanca	MVZ 181351	AF199132	—
14	*N. abscondens*	Costa Rica: San José: Cascajal de Las Nubes	MVZ 194884	AF199133	—
15	*N. abscondens*	Costa Rica: San José: Cascajal de Las Nubes	MVZ 194867	AF199134	—
16	*N. gamezi*	Costa Rica: Alajuela: Monteverde	MVZ 207122	AF199135	AF199200
17	*N. barbouri*	Honduras: Atlántida: Quebrada del Oro	USNM 339712	AF199136	AF199201
18	*N. barbouri*	Honduras: Atlántida: Cerro Búfalo	USNM 497552	AF199137	—
19	*N. barbouri*	Honduras: Yoro: 2.5 km NNE La Fortuna	USNM 509333	AF199138	—
20	*N. brodiei*	Guatemala: Izabal: Sierra de Caral, Morales	UTA A-51490	AF199139	AF199202
21	*N. guanacaste*	Costa Rica: Guanacaste: Volcán Cacao	MVZ 207106	AF199140	AF199203
22	*N. lignicola*	Honduras: Olancho: Cerro de Enmedio	USNM 497540	AF199141	AF199204
23	*N. lignicola*	Honduras: Olancho: Cerro de Enmedio	USNM 497550	AF199142	—
24	*N. limnospectator*	Honduras: Santa Barbara: El Ocotillo	MVZ 225866	AF199143	—
25	*N. picadoi*	Costa Rica: Cartago: Tapantí	MVZ 225899	AF199144	AF199205
26	*N. picadoi*	Costa Rica: Cartago: Tapantí	MVZ 203745	AF199145	—
27	*N. richardi*	Costa Rica: San José: Cascajal de Las Nubes	UCR 12057	AF199146	AF199206
28	*N. richardi*	Costa Rica: San José: Cascajal de Las Nubes	MVZ 194885	AF199147	—
29	*N. richardi*	Costa Rica: San José: Cascajal de Las Nubes	MVZ 194887	AF199148	—
30	*O. alleni*	Costa Rica: Puntarenas: Sirena	MVZ 190857	AF199149	AF199207
31	*O. alleni*	Costa Rica: Puntarenas: Sirena	MVZ 190856	AF199150	—
32	*O. alleni*	Costa Rica: Puntarenas: Damas	MVZ 225903	AF199151	AF199208
33	*O. savagei*	Costa Rica: Puntarenas: Cerro Zapote	UCR LDG 961327	AF199152	AF199209
34	*O. savagei*	Costa Rica: Puntarenas: Cerro Zapote	MVZ DBW 5785	AF199153	—
35	*O. parvipes*	Panamá: San Blas: Nusagandi	MVZ 210404	AF199154	AF199210

Appendix 1. Continued.

Sample no.	Species	Locality	Museum no.	Cyt *b*	16S
36	*O. parvipes*	Panamá: Colón: Río Frijoles	MVZ 210405	AF199155	AF199211
37	*O. complex*	Panamá: Panamá: Altos de Cerro Campana	MVZ DBW 5787	AF199156	AF199212
38	*O. complex*	Panamá: Colón: Barro Colorado	MVZ DBW 5105	AF199157	AF199213
39	*O. cyclocauda*	Costa Rica: Heredia: La Selva	MVZ 138916	AF199158	AF199214
40	*O. cyclocauda*	Costa Rica: Heredia: La Selva	MVZ 203747	AF199159	AF199215
41	*O. elongata*	Guatemala: Izabal: Siete Altares, Livingston	UTA A-51906	AF199160	AF199216
42	*O. gephyra*	Honduras: Atlántida: Cerro Búfalo	USNM 343462	AF199161	AF199217
43	*O. gephyra*	Honduras: Yoro: 2.5 km NNE La Fortuna	USNM LDW 10502	AF199162	AF199218
44	*O. gracilis*	Costa Rica: Heredia: La Selva	MVZ 203753	AF199163	—
44b	*O. gracilis*	Costa Rica: Heredia: La Selva	MVZ 210398	—	AF199219
45	*O. grandis*	Costa Rica: Puntarenas: Cerro Pando	MVZ 225904	AF199164	AF199220
46	*O. grandis*	Costa Rica: Puntarenas: Las Tablas	MVZ 219593	AF199165	—
47	*O. maritima*	Panamá: Bocas del Toro: Escudo de Veraguas	MVZ 219997	AF199166	AF199221
48	*O. pacificensis*	Costa Rica: Puntarenas: Sirena	MVZ 190859	AF199167	—
49	*O. pacificensis*	Costa Rica: Puntarenas: Sirena	MVZ 190858	AF199168	—
50	*O. pacificensis*	Costa Rica: Puntarenas: Damas	UCR 12063	AF199169	AF199222
51	*O. pacificensis*	Costa Rica: Puntarenas: Las Cruces	UCR E 7	AF199170	—
52	*O. poelzi*	Costa Rica: Heredia: Braulio Carrillo	MVZ 206398	AF199171	AF199223
53	*O. poelzi*	Costa Rica: San José: Cascajal de Las Nubes	MVZ 181235	AF199172	—
54	*O. poelzi*	Costa Rica: Alajuela: Vara Blanca	MVZ 181348	AF199173	—
55	*O. poelzi*	Costa Rica: Alajuela: Vara Blanca	MVZ 163703	AF199174	AF199224
56	*O. poelzi*	Costa Rica: Alajuela: Monteverde	MVZ 207128	AF199175	AF199225
57	*O. poelzi*	Costa Rica: Cartago: Moravia de Chirripó	MVZ 194873	AF199176	AF199226
58	*O. pseudouniformis*	Costa Rica: Cartago: 3 km ENE Juan Viñas	MVZ 190852	AF199177	—
59	*O. pseudouniformis*	Costa Rica: Cartago: Los Espaveles	MVZ 203749	AF199178	AF199227
60	*O. pseudouniformis*	Costa Rica: Cartago: Moravia de Chirripó	MVZ 181229	AF199179	—
61	*O. stenopodia*	Guatemala: S. Marcos: S. Rafael	MVZ 138918	AF199180	—
62	*O. stenopodia*	Guatemala: S. Marcos: S. Rafael	MVZ 163649	AF199181	AF199228
63	*O. uniformis*	Costa Rica: San José: Cerros de Escazú	MVZ 221340	AF199182	—
64	*O. uniformis*	Costa Rica: San José: Alto de La Palma	MVZ 225905	AF199183	—

Appendix 1. Continued.

Sample no.	Species	Locality	Museum no.	Cyt *b*	16S
65	*O. uniformis*	Costa Rica: Cartago: Río Turrialba	MVZ 194871	AF199184	—
66	*O. uniformis*	Costa Rica: Cartago: Ciénega de Colorado	MVZ 190853	AF199185	AF199229
67	*O. uniformis*	Costa Rica: Cartago: Volcán Turrialba	MVZ 194862	AF199186	—
68	*O. uniformis*	Costa Rica: Cartago: Volcán Turrialba	MVZ 194864	AF199187	—
69	*O. uniformis*	Costa Rica: San José: Cascajal de Las Nubes	MVZ 225906	AF199188	—
70	*O. uniformis*	Costa Rica: San José: Cascajal de Las Nubes	MVZ 221321	AF199189	—
71	*O. uniformis*	Costa Rica: Cartago: Tapantí	MVZ 203751	AF199190	AF199230
72	*O. uniformis*	Costa Rica: Alajuela: Vara Blanca	MVZ 181349	AF199191	—
73	*O. sp.* B	Honduras: Ocotepeque: Guarin, Cerro El Pital	USNM LDW 11270	AF199192	AF199231
74	*O. sp.* C	Honduras: Yoro: 32 km W Yoro	MVZ 167772	AF199193	—
75	*Dendrotriton rabbi*	Guatemala: Quiché: Uspantán	UTA A-51086	AF199194	AF199232
76	*Bolitoglossa cerroensis*	Costa Rica: San José: Salsipuedes	MVZ S 12921	AF199195	AF199233
77	*Batrachoseps gabrieli*	USA: California: San Gabriel Mts.	MVZ 222957		AF199234

Appendix 2. Sequence Divergence (K2p) between Taxa. Distances within taxa correspond to minimal levels of divergence among species. Upper half matrix is based on 16S sequences. Lower half matrix is based on cyt *b* sequences.

	1	2	3	4	5	6	7	8
1 *Cryptotriton*	***	0.1556–0.1792	0.1591–0.1958	0.1591–0.1958	0.1652–0.1924	0.1751–0.1784	0.2236–0.2401	0.2169–0.2275
2 *Nototriton*	0.2493–0.3066	***	0.1129–0.1701	0.1129–0.1600	0.1148–0.1701	0.1509–0.1639	0.1838–0.2043	0.1974–0.2188
3 *Oedipina* s.l.	0.2253–0.3255	0.1726–0.2558	***	—	—	0.1752–0.2083	0.1892–0.2281	0.2204–0.2489
4 *Oedipina* s.str.	0.2253–0.3255	0.1762–0.2558	—	***	0.0641–0.1082	0.1752–0.2027	0.1948–0.2259	0.2220–0.2489
5 *Oedopinola*	0.2257–0.3104	0.1726–0.2554	—	0.1353–0.2247	***	0.1775–0.2083	0.1892–0.2281	0.2204–0.2427
6 *Dendrotriton*	0.2464–0.2693	0.2429–0.3046	0.2308–0.3191	0.2445–0.3191	0.2308–0.2934	***	0.2075	0.2193
7 *Bolitoglossa*	0.2704–0.3040	0.2455–0.2929	0.2140–0.3180	0.2140–0.2855	0.2567–0.3180	0.2751	***	0.1928
8 *Batrachoseps*	0.2361–0.2893	0.2161–0.2874	0.2416–0.2944	0.2416–0.2944	0.2451–0.2901	0.2864	0.2442	***

APPENDIX 3. SEQUENCE DIVERGENCE (K2p) WITHIN *Cryptotriton*. Upper half matrix is based on 16S sequences. Lower half matrix is based on cyt *b* sequences.

		1	2	3	4	5
1 *C. alvarezdeltoroi*	(1)	***	—	—	0.0951	0.0892
2 *C. nasalis*	(2)	0.1674	***	—	—	—
3 *C. veraepacis*	(3, 6)	0.1534	0.1487	***	—	—
4 *C. veraepacis*	(4, 5, 7, 8)	0.1466	0.1418	0.0052	***	0.0448
5 *C.* sp. A	(9, 10)	0.1469	0.1323	0.0932	0.0870	***

APPENDIX 4. SEQUENCE DIVERGENCE (K2p) WITHIN *Nototriton*. Upper half matrix is based on 16S sequences. Lower half matrix is based on cyt *b* sequences.

			1	2	3	4	5	6	7	8	9	10	11	12	13
1	*N. abscondens*	(11, 12, 13)	***	—	0.0178	0.0571	—	0.0569	0.0138	0.0589	—	—	0.0178	—	0.0383
2	*N. abscondens*	(14, 15)	0.0079	***	—	—	—	—	—	—	—	—	—	—	—
3	*N. gamezi*	(16)	0.0239	0.0212	***	0.0591	—	0.0633	0.0198	0.0653	—	—	0.0158	—	0.0362
4	*N. barbouri*	(17, 18)	0.1244	0.1211	0.1343	***	—	0.0137	0.0591	0.0422	—	—	0.0635	—	0.0508
5	*N. barbouri*	(19)	0.1475	0.1441	0.1649	0.0573	***	—	—	—	—	—	—	—	—
6	*N. brodiei*	(20)	0.1310	0.1277	0.1343	0.0604	0.0690	***	0.0633	0.0421	—	—	0.0677	—	0.0550
7	*N. guanacacaste*	(21)	0.0432	0.0404	0.0404	0.1377	0.1685	0.1244	***	0.0653	—	—	0.0118	—	0.0361
8	*N. lignicola*	(22)	0.1244	0.1244	0.1310	0.1185	0.1280	0.1061	0.1277	***	—	—	0.0653	—	0.0484
9	*N. lignicola*	(23)	0.1208	0.1208	0.1274	0.1149	0.1250	0.1027	0.1307	0.0158	***	—	—	—	—
10	*N. limnospectator*	(24)	0.1434	0.1401	0.1468	0.1340	0.1304	0.1214	0.1434	0.1117	0.1146	***	—	—	—
11	*N. picadoi*	(25)	0.0294	0.0267	0.0158	0.1343	0.1579	0.1211	0.0348	0.1244	0.1208	0.1468	***	—	0.0445
12	*N. picadoi*	(26)	0.0321	0.0293	0.0185	0.1373	0.1610	0.1241	0.0375	0.1274	0.1238	0.1499	0.0026	***	—
13	*N. richardi*	(27, 28, 29)	0.0959	0.0928	0.0928	0.1214	0.1277	0.0928	0.0959	0.1448	0.1479	0.1370	0.0928	0.0957	***

APPENDIX 5. SEQUENCE DIVERGENCE (K2p) WITHIN *Oedipina* (*Oedipina*). Upper half matrix is based on 16S sequences. Lower half matrix is based on cyt *b* sequences.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 *O. cyclocauda*	(39)	***	0.0058	0.0655	0.0678	—	—	0.0532	—	0.0635	—	0.0656	0.0634	0.0591	0.0377
2 *O. cyclocauda*	(40)	0.0026	***	0.0657	0.0701	—	—	0.0512	—	0.0616	—	0.0670	0.0678	0.0635	0.0316
3 *O. gracilis*	(44)	0.1626	0.1592	***	0.0635	—	—	0.0427	—	0.0792	—	0.0744	0.0723	0.0657	0.0678
4 *O. grandis*	(45, 46)	0.1456	0.1489	0.1835	***	—	—	0.0447	—	0.0507	—	0.0485	0.0464	0.0423	0.0674
5 *O. pacificensis*	(48)	0.1323	0.1356	0.1126	0.1735	***	—	—	—	—	—	—	—	—	—
6 *O. pacificensis*	(49)	0.1326	0.1359	0.1064	0.1696	0.0052	***	—	—	—	—	—	—	—	—
7 *O. pacificensis*	(50)	0.1394	0.1361	0.1088	0.1871	0.0402	0.0347	***	—	0.0556	—	0.0574	0.0553	0.0488	0.0553
8 *O. pacificensis*	(51)	0.1356	0.1389	0.1029	0.1623	0.0293	0.0239	0.0601	***	—	—	—	—	—	—
9 *O. poelzi*	(52)	0.1265	0.1298	0.1599	0.1049	0.1301	0.1298	0.1571	0.1295	***	—	0.0258	0.0237	0.0402	0.0741
10 *O. poelzi*	(53)	0.1268	0.1301	0.1567	0.1114	0.1271	0.1334	0.1610	0.1331	0.0078	***	—	—	—	—
11 *O. poelzi*	(54, 55)	0.1201	0.1233	0.1592	0.1139	0.1328	0.1326	0.1529	0.1323	0.0486	0.0545	***	0.0019	0.0402	0.0783
12 *O. poelzi*	(56)	0.1078	0.1046	0.1456	0.1139	0.1263	0.1293	0.1495	0.1291	0.0570	0.0571	0.0293	***	0.0381	0.0761
13 *O. poelzi*	(57)	0.1044	0.1076	0.1554	0.1105	0.1326	0.1323	0.1465	0.1326	0.0863	0.0926	0.0803	0.0717	***	0.0717
14 *O. pseudouniformis*	(58, 59)	0.0516	0.0545	0.1588	0.1459	0.1326	0.1389	0.1459	0.1554	0.1367	0.1370	0.1268	0.1274	0.1109	***
15 *O. pseudouniformis*	(60)	0.0545	0.0573	0.1623	0.1492	0.1359	0.1422	0.1492	0.1588	0.1401	0.1404	0.1301	0.1307	0.1141	0.0026
16 *O. stenopodia*	(61)	0.1489	0.1456	0.1471	0.1465	0.1370	0.1434	0.1492	0.1465	0.1334	0.1304	0.1231	0.1103	0.1260	0.1456
17 *O. stenopodia*	(62)	0.1459	0.1425	0.1441	0.1468	0.1340	0.1404	0.1462	0.1434	0.1304	0.1274	0.1201	0.1074	0.1231	0.1428
18 *O. uniformis*	(63)	0.1328	0.1361	0.0966	0.1735	0.0432	0.0377	0.0630	0.0517	0.1367	0.1404	0.1394	0.1361	0.1326	0.1359
19 *O. uniformis*	(64)	0.1361	0.1394	0.0998	0.1735	0.0404	0.0349	0.0601	0.0488	0.1401	0.1437	0.1428	0.1394	0.1359	0.1392
20 *O. uniformis*	(65, 66)	0.1459	0.1492	0.0969	0.1696	0.0321	0.0267	0.0459	0.0405	0.1364	0.1401	0.1492	0.1392	0.1323	0.1523
21 *O. uniformis*	(67, 68)	0.1459	0.1492	0.1032	0.1696	0.0377	0.0322	0.0573	0.0461	0.1331	0.1401	0.1492	0.1392	0.1323	0.1523
22 *O. uniformis*	(69)	0.1326	0.1359	0.0907	0.1592	0.0266	0.0212	0.0403	0.0349	0.1298	0.1334	0.1392	0.1293	0.1258	0.1389
23 *O. uniformis*	(70)	0.1392	0.1425	0.0969	0.1557	0.0266	0.0212	0.0403	0.0349	0.1364	0.1401	0.1459	0.1359	0.1258	0.1456
24 *O. uniformis*	(71)	0.1422	0.1456	0.0998	0.1588	0.0460	0.0405	0.0601	0.0432	0.1328	0.1364	0.1456	0.1356	0.1288	0.1486
25 *O. uniformis*	(72)	0.1359	0.1392	0.1001	0.1592	0.0349	0.0294	0.0431	0.0372	0.1465	0.1502	0.1492	0.1459	0.1356	0.1422
26 *O.* sp. B	(73)	0.1661	0.1696	0.1672	0.1164	0.1431	0.1495	0.1623	0.1459	0.1394	0.1364	0.1263	0.1295	0.1392	0.1595
27 *O.* sp. C	(74)	0.1620	0.1654	0.1476	0.1386	0.1572	0.1574	0.1611	0.1674	0.1315	0.1252	0.1315	0.1190	0.1284	0.1548

Appendix 5. Extended

		15	16	17	18	19	20	21	22	23	24	25	26	27
1 *O. cyclocauda*	(39)	—	—	0.0569	—	—	0.0462	—	—	—	0.0483	—	0.0569	—
2 *O. cyclocauda*	(40)	—	—	0.0570	—	—	0.0442	—	—	—	0.0463	—	0.0571	—
3 *O. gracilis*	(44)	—	—	0.0655	—	—	0.0423	—	—	—	0.0444	—	0.0613	—
4 *O. grandis*	(45, 46)	—	—	0.0570	—	—	0.0485	—	—	—	0.0465	—	0.0529	—
5 *O. pacificensis*	(48)	—	—	—	—	—	—	—	—	—	—	—	—	—
6 *O. pacificensis*	(49)	—	—	—	—	—	—	—	—	—	—	—	—	—
7 *O. pacificensis*	(50)	—	—	0.0490	—	—	0.0119	—	—	—	0.0119	—	0.0447	—
8 *O. pacificensis*	(51)	—	—	—	—	—	—	—	—	—	—	—	—	—
9 *O. poelzi*	(52)	—	—	0.0615	—	—	0.0570	—	—	—	0.0550	—	0.0747	—
10 *O. poelzi*	(53)	—	—	—	—	—	—	—	—	—	—	—	—	—
11 *O. poelzi*	(54, 55)	—	—	0.0612	—	—	0.0589	—	—	—	0.0569	—	0.0744	—
12 *O. poelzi*	(56)	—	—	0.0591	—	—	0.0568	—	—	—	0.0547	—	0.0722	—
13 *O. poelzi*	(57)	—	—	0.0613	—	—	0.0526	—	—	—	0.0505	—	0.0701	—
14 *O. pseudouniformis*	(58, 59)	—	—	0.0696	—	—	0.0482	—	—	—	0.0504	—	0.0655	—
15 *O. pseudouniformis*	(60)	***	—	—	—	—	—	—	—	—	—	—	—	—
16 *O. stenopodia*	(61)	0.1492	***	—	—	—	—	—	—	—	—	—	—	—
17 *O. stenopodia*	(62)	0.1462	0.0026	***	—	—	0.0505	—	—	—	0.0526	—	0.0239	—
18 *O. uniformis*	(63)	0.1392	0.1337	0.1307	***	—	—	—	—	—	—	—	—	—
19 *O. uniformis*	(64)	0.1425	0.1304	0.1274	0.0026	***	—	—	—	—	—	—	—	—
20 *O. uniformis*	(65, 66)	0.1557	0.1334	0.1304	0.0321	0.0293	***	—	—	—	0.0078	—	0.0443	—
21 *O. uniformis*	(67, 68)	0.1557	0.1401	0.1370	0.0321	0.0293	0.0105	***	—	—	—	—	—	—
22 *O. uniformis*	(69)	0.1422	0.1401	0.1370	0.0212	0.0239	0.0158	0.0212	***	—	—	—	—	—
23 *O. uniformis*	(70)	0.1489	0.1334	0.1304	0.0266	0.0239	0.0105	0.0158	0.0052	***	—	—	—	—
24 *O. uniformis*	(71)	0.1520	0.1233	0.1203	0.0460	0.0432	0.0131	0.0239	0.0293	0.0239	***	—	0.0442	—
25 *O. uniformis*	(72)	0.1456	0.1434	0.1404	0.0349	0.0321	0.0185	0.0239	0.0132	0.0079	0.0321	***	—	—
26 *O.* sp. B	(73)	0.1630	0.0718	0.0690	0.1533	0.1499	0.1529	0.1599	0.1461	0.1394	0.1425	0.1495	***	—
27 O. sp. C	(74)	0.1515	0.1617	0.1585	0.1577	0.1611	0.1608	0.1608	0.1408	0.1474	0.1543	0.1574	0.1448	***

APPENDIX 6. SEQUENCE DIVERGENCE (K2p) WITHIN *Oedipina* (*Oedopinola*). Upper half matrix is based on 16S sequences. Lower half matrix is based on cyt *b* sequences.

			1	2	3	4	5	6	7	8	9	10	11	12	13
1	*O. alleni*	(30)	***	—	0.0340	0.0443	—	0.0699	0.0792	0.0811	0.0680	0.0856	0.0827	0.0719	0.0699
2	*O. alleni*	(31)	0.0052	***	—	—	—	—	—	—	—	—	—	—	—
3	*O. alleni*	(32)	0.0838	0.0900	***	0.0321	—	0.0678	0.0704	0.0789	0.0593	0.0856	0.0848	0.0809	0.0767
4	*O. savagei*	(33)	0.1027	0.1091	0.0664	***	—	0.0833	0.0954	0.0903	0.0747	0.0970	0.0961	0.0945	0.0857
5	*O. savagei*	(34)	0.1059	0.1123	0.0635	0.0079	***	—	—	—	—	—	—	—	—
6	*O. parvipes*	(35)	0.1411	0.1411	0.1304	0.1441	0.1407	***	0.0218	0.0505	0.0360	0.0701	0.0828	0.0651	0.0484
7	*O. parvipes*	(36)	0.1407	0.1407	0.1367	0.1506	0.1471	0.0321	***	0.0465	0.0341	0.0724	0.0963	0.0698	0.0486
8	*O. complex*	(37)	0.1811	0.1811	0.1422	0.1665	0.1630	0.0894	0.0923	***	0.0340	0.0945	0.1073	0.0851	0.0486
9	*O. complex*	(38)	0.1526	0.1526	0.1658	0.1626	0.1592	0.1109	0.1203	0.1112	***	0.0902	0.0919	0.0700	0.0382
10	*O. elongata*	(41)	0.1704	0.1704	0.1461	0.1431	0.1397	0.1564	0.1492	0.1588	0.1968	***	0.0854	0.0808	0.0875
11	*O. gephyra*	(42)	0.1852	0.1926	0.1665	0.1704	0.1668	0.1672	0.1599	0.1903	0.1981	0.1585	***	0.0525	0.0913
12	*O. gephyra*	(43)	0.1676	0.1641	0.1461	0.1602	0.1567	0.1401	0.1397	0.1693	0.1767	0.1520	0.0661	***	0.0674
13	*O. maritima*	(47)	0.1513	0.1513	0.1304	0.1544	0.1509	0.0812	0.0780	0.1022	0.1277	0.1599	0.1816	0.1606	***