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A new species of arboreal salamander (Caudata: Plethodontidae: *Pseudoeurycea*) from the mountains of Oaxaca, Mexico

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Recent surveys of the plethodontid salamander fauna of Oaxaca, Mexico, disclosed the existence of a new, morphologically distinct arboreal species of the genus *Pseudoeurycea*. The new species, described here, is from the Sierra Mazateca in northern Oaxaca. Sequences of 1833 base pairs of the 16S, cytochrome *b* and ND4 mitochondrial DNA (mtDNA) genes from the new taxon were used to assess its phylogenetic position. Previous phylogenetic analyses based on mtDNA supported recognition of four clades within *Pseudoeurycea*: *P. bellii*, *P. gadovii*, *P. juarezi* and *P. leprosa-Lineatriton* species groups. One additional species, *P. unguidentis*, was not closely allied to any of the four groups. Re-analysis including the additional sequences reported here establishes a sister-group relationship between the new species and *P. unguidentis*. Moreover, it supports this clade as part of the *P. juarezi* species group.

KEYWORDS: Amphibia, Caudata, Plethodontidae, *Pseudoeurycea*, new species, systematics, taxonomy, Mexico.

Introduction

The plethodontid salamander genus *Pseudoeurycea* ranges from northern Mexico south across the Isthmus of Tehuantepec into Guatemala. It is composed mostly of terrestrial species found at high elevations (Wake and Lynch, 1976). The systematics of *Pseudoeurycea* is under active investigation, and recent results will likely mandate significant taxonomic changes. A phylogenetic analysis based on mitochondrial DNA (mtDNA), for example, demonstrates the paraphyly of *Pseudoeurycea* with respect to two other neotropical genera, *Lineatriton* and

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Ixalotriton (Parra-Olea and Wake, 2001; Parra-Olea, 2002). While this comprehensive taxonomic reassessment of the group is in progress, several more unnamed species await formal description (Parra-Olea, 1999, 2002).

Phylogenetic analyses based on mtDNA supported recognition of four clades within *Pseudoeurycea*: *P. bellii*, *P. gadovii*, *P. juarezi* and *P. leprosa-Lineatriton* species groups. Relationships among these clades, however, were poorly resolved (Parra-Olea, 2002; Canseco-Márquez and Parra-Olea, 2003). One additional species, *P. unguidentis*, was not closely allied to any of the four groups and instead contributed to a polytomy at the base of the tree.

During recent surveys of the plethodontid salamander fauna of Oaxaca, Mexico, we focused on regions with habitat suitable for *Pseudoeurycea*, including several located outside the known range of the genus. We obtained new samples of named species from previously known localities, as well as specimens representing unknown species. The latter includes a new, morphologically distinct arboreal species from the Sierra Mazateca in northern Oaxaca. This rugged, poorly studied mountain range is well separated from other montane habitats where *Pseudoeurycea* is found, and it is likely to harbour additional unnamed species of this and other salamander genera.

In this paper we describe the new species from the Sierra Mazateca and discuss its phylogenetic position based on analysis of mtDNA variation. We also provide a new phylogenetic hypothesis for relationships among species groups within this large genus.

Materials and methods

Description of the new species follows previous taxonomic work and includes the same basic characters and measurements (Lynch and Wake, 1989). Larger measurements were taken by using a dial calipers (accurate to the nearest 0.1 mm); smaller measurements of feet, toes and some head dimensions, especially those involving the holotype, were taken by using a stereomicroscope equipped with an eyepiece micrometer. All measurements are expressed in millimetres. Standard length (SL) equals the distance from the tip of the snout to the posterior end of the vent. Limb interval equals the number of costal interspaces between the tips of appressed fore- and hind limbs, measured in one-half increments. Negative values indicate the degree to which appressed limbs overlap. Tooth counts were made by using a stereomicroscope. Numbers of maxillary and vomerine teeth are summed for both sides of the head. Colour notes are based on living specimens, recorded in the field, and on preserved specimens.

All specimens are from Mexico: IBH 13802–13806, MVZ 236762, MCZ-A-135811 and MNCN 41042 (eight subadults), *ca* 1 km NW of Puerto Soledad, Sierra Mazateca, Oaxaca, elevation 2290 m, 18°10.450′N, 97°00.197′W; IBH 13801 (one subadult), 7 km (rd) W of Plan de Guadalupe, Sierra Mazateca, Oaxaca, elevation 2235–2240 m, 18°09.164′N, 96°58.509′W; MZFC 13316–17 (two adults) from near Puerto Soledad, Oaxaca, Mexico. Institutional abbreviations are as listed in Leviton *et al.* (1985) except for MZFC (Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autonoma de México, Mexico).

From three specimens of the new species (IBH 13801, MVZ 236762, MCZ-A-135811; GenBank accession numbers AY354471–AY354479) we obtained partial sequences of the 16S-subunit ribosomal mtDNA gene that correspond approximately to positions 2510–3059 (554 base pairs) in the human mitochondrial genome

(Anderson *et al*., 1981); 570 base pairs of the cytochrome *b* gene (Cyt b) expanding from codon 7 of the *Xenopus* Cyt b gene (Roe *et al*., 1985); and 709 base pairs of the ND4 (nicotinamide adenine dinucleotide dehydrogenase subunit 4) gene (Arévalo *et al*., 1994). These samples were combined and analysed together with previously published sequences of *Pseudoeurycea* (Parra-Olea, 2002).

Whole genomic DNA was extracted from small amounts of ethanol-preserved tissues by using the Quiagen DNA extraction kit (69504). Amplification was done via the polymerase chain reaction (PCR; Saiki *et al*., 1988), using the primers 'MVZ15' and 'MVZ18' (Moritz *et al*., 1992) for Cyt b, the primers ND4 (Arévalo *et al*., 1994) and MVZ112 (Parra-Olea, 2002) for the ND4 gene, and the primers '16Sar' and '16Sbr' (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 0.5 pmol of each primer. Double-stranded templates were cleaned using QIAquick PCR purification kit (QIAgen). We used 1 μl of PCR product as the template for cycle sequencing reactions in a 10 μl total volume with the Perkin-Elmer Ready Reaction Kit to incorporate dye-labelled dideoxy terminators. Thermal cycling was performed using standard conditions. Cycle sequencing products were purified using ethanol precipitation and run in an ABI 310 capillary sequencer.

Sequences were compiled using Sequence Navigator™ version 1.0.1 (Applied Biosystems) and aligned to the published data set for *Pseudoeurycea* (Parra-Olea, 2002). Pair-wise comparisons of corrected sequence divergence (Kimura 2-parameter; Kimura, 1980) were obtained using the computer program PAUP*4.0b8a (Swofford, 2002). Phylogenetic analyses were performed using the combined data set (1833 base pairs). Gaps were treated as missing data.

We used Model Test 3.06 (Posada and Crandall, 1998) to find the model of evolution that best fits the data for subsequent Maximum Likelihood and Bayesian analyses (ML: Felsenstein, 1981; Bayesian: Huelsenbeck and Ronquist, 2001). The GTR model of evolution with gamma parameter and proportion of invariable positions was used for ML and Bayesian analyses (Yang, 1994; Gu *et al*., 1995; Swofford *et al*., 1996). ML analyses with empirical base frequencies were performed using PAUP*.

Bayesian phylogenetic analyses were conducted with MR-BAYES 2.0 (Huelsenbeck and Ronquist, 2001). Analyses were initiated with random starting trees and run for 500 000 generations. The Markov chains were sampled each 100 generations. Stationarity was reached after 10 000 generations, therefore of the resulting 5000 trees, 100 were discarded as 'burn-in' (Leaché and Reeder, 2002). Bayesian posterior clade probabilities (pp) are indicated on the ML topology.

Maximum parsimony phylogenies were estimated using the heuristic search algorithm (MP: Swofford, 2002). Input order of taxa was randomized 20 separate times to minimize the effect of entry sequence on the resulting cladogram topology. MP analyses were conducted without the steepest descent option, and with accelerated character transformation (ACCTRAN) optimization, tree bisection-reconnection (TBR) branch swapping, and zero-length branches collapsed to yield polytomies. We used non-parametric bootstrapping (1000 pseudo-replicates; bs) and decay indices (d) to assess the stability of internal branches in the resulting topologies (Felsenstein, 1985; Felsenstein and Kishino, 1993; Bremer, 1994). Non-parametric bootstrap values and decay indices generally are a conservative measure

of the probability that a recovered group represents a true clade (Zharkikh and Li, 1992; Hillis and Bull, 1993; Li, 1997). Each base position was treated as an unordered character with four alternate states. Sequences of representatives of the distantly related bolitoglossine genera *Thorius* and *Batrachoseps* were used as outgroup taxa.

Results

Description of a new species

Pseudoeurycea ruficauda sp. nov.
(Orange-tailed agile salamander; Salamandra colirroja)
(figures 1, 2)

HOLOTYPE: IBH 13806, a subadult male from *ca* 1 km NW of Puerto Soledad, Sierra Mazateca, Oaxaca, Mexico, elevation 2290 m, 18°10.450′N, 97°00.197′W, collected 14 January 2002 by M. García-París, J. Hanken, G. Parra-Olea and D. Wake.

PARATYPES: IBH 13802–13805 (four specimens), MVZ 236762, MCZ A-135811 and MNCN 41042, same data as the holotype; IBH 13801, 7 km (rd) W of Plan de Guadalupe, Sierra Mazateca, Oaxaca, Mexico, elevation 2235–2240 m, 18°09.164′N, 96°58.509′W.

Referred specimens. MZFC 13316–17 (two specimens), vicinity of the type locality.

Diagnosis. This is a medium-sized arboreal species of *Pseudoeurycea* (SL to about 45 mm) with long legs and broadly spread hands and feet having long, separated digits. It is distinguished from other members of the genus by its long legs, broad hands and vivid coloration, which includes a red-orange tail and mottled black and orange head and body. In addition to coloration, it differs from other long-legged, arboreal *Pseudoeurycea*, including its closest relative

FIG. 1. *Pseudoeurycea ruficauda*. Subadult from the type locality (IBH 13806), with typical coloration.

FIG. 2. *Pseudoeurycea ruficauda*. Subadult from 7 km (rd) W of Plan de Guadalupe, Sierra Mazateca, Oaxaca (IBH 13801). Colour variant.

P. unguidentis (Taylor, 1941), and the other arboreal member of the *P. juarezi* Regal, 1966 group, *P. saltator* Lynch and Wake, 1989, in having a less robust appearance, with slender legs and tail, and a prominent head that is well differentiated from the trunk. Live specimens are readily characterized by their alert attitude and rapid movements, including jumps, in which they resemble *P. saltator*. The other members of the *P. juarezi* species group, *P. juarezi* and *P. aurantia* Canseco-Márquez and Parra-Olea, 2003, two species with terrestrial habits that inhabit the Sierra de Juárez, differ from *P. ruficauda* in having stouter bodies, shorter legs, broader heads, shorter tails and smaller digits. The coloration of *P. aurantia* resembles that of *P. ruficauda* except that *P. aurantia* possesses a dull orange coloration, uniformly extended, without defined limits over the dorsal areas, less bright and sharp than the yellow-orange dorsal stripe of *P. ruficauda*. The species also is distinct in biochemical characters.

Description. Subadult specimens in the type series range from 23.7 to 30.2 mm SL, mean 25.6 mm, but adults reach at least 45 mm. The head is relatively large and prominent with large, frontally directed eyes that protrude on each side: head width 4.2–5.0, mean 4.6 mm; head depth 2.3–2.8, mean 2.5 mm; head length 6.2–7.4, mean 6.8 mm. SL is from 5.4 to 6 times head width. Nostrils are small (mean diameter 0.3 mm) and widely separated (1.2–1.6, mean 1.4 mm). Parotoid glands are not evident. The body is slender; shoulder width across the anterior limb insertions is from 3 to 3.6, mean 3.2 mm. Costal grooves are 13, counting one each in axilla and groin. Tails are slender and taper to a narrow tip. They are slightly shorter than SL (mean tail length 22.9 mm), except in the largest paratype, a 30.2 mm SL female. Legs are long (6.2–8.6, mean 7.5 mm) and usually touch or overlap by 1.0–1.5 costal folds when appressed to the side of the body; the legs fail to overlap by about one costal fold in the largest paratype. Hands and feet are broadly spread (foot width 2.4–3.4, mean 2.9 mm) and the digits are long and slender with distinct subterminal pads. The fifth digit is well developed but noticeably shorter than the fourth. Teeth are relatively numerous: premaxillary 5–8, mean 7; maxillary 27–49, mean 41.1; and vomerine 11–16, mean 14.3. Mental gland is not evident.

This is a colourful species with a generally two-tone pattern. Dorsal coloration is orange-tan with coppery-gold highlights that are mixed with black. An irregular and sometimes discontinuous dorsal stripe that varies from tan-yellow, to orange,

to reddish brown extends from the nape to the tip of the tail. The stripe is often interrupted by small black spots; these are denser laterally, where they form a more or less continuous black stripe. Flanking black bands run from the scapular region to the base of the tail, where they often are broken into isolated spots dispersed over the tail. The tail is basically orange with black spots and has a vivid, red-orange to yellow-orange tip. The head is generally dark brown with dense black mottling, yet is overlain by bright iridophores. In several specimens, a black V-shaped mark begins on the upper eyelids and extends posteriorly. Flanks are black but also heavily spotted with gold, yellow, copper, cream and white, giving them a marbled appearance. A distinctive thin black stripe runs from the nostril through the eye, then curves to reach the anterior limb insertion. Upper forelimbs are rusty orange; hind limbs are somewhat duller. Digit tips are reddish. The iris is coppery or rusty gold reticulated with black. The belly is greyish and largely unmarked, but it is darker in some specimens and there are occasional light spots. The throat and lower jaw are heavily pigmented and the colour is a complex mixture of dark brown, yellow and rusty orange, all overlain by scattered small white spots.

Measurements of the holotype (in millimetres). Head width 4.6; snout to gular fold (head length) 6.7; head depth at posterior angle of jaw 2.5; eyelid width 1.4; eyelid length 2.1; anterior rim of orbit to snout 1.7; horizontal orbital diameter 1.5; interorbital distance 3.0; eye to nostril distance 1.1; distance separating external nares 1.6; nostril diameter 0.3; snout projection beyond mandible 0.6; snout to posterior angle of vent (standard length) 25.3; snout to anterior angle of vent 24.0; snout to forelimb 8.8; axilla to groin 13.3; limb interval −1; shoulder width 3.6; tail length 22.5; tail width at base 1.8; tail depth at base 2.0; forelimb length (to tip of longest toe) 7.3; hind limb length 7.9; hand width 2.0; foot width 3.0; length of longest toe (3) 1.2; length of shortest toe (5) 0.6; numbers of teeth: premaxillary 7, maxillary 45, vomerine 14.

Coloration of the holotype (in life). This is a brightly coloured animal with a complex mosaic of orange-tan and black. A dorsal orange stripe is mottled with black spots, bordered with black stripes, and overlain with metallic-tan iridophores. A distinctive, thin black stripe runs from the nostril through the eye, then curves to reach the anterior limb insertion. The tail is orange with black spots. Flanks are black. The belly is dark and largely unmarked, but there is metallic-orange and copper speckling in the throat region and near the jaw.

Coloration of the holotype (in preservative). Lively coloration. There are tan-orange markings on the head, limbs and body. The tail is bright red to red-orange (some black spots) with a bright orange tip. The head is strongly mottled with black and yellow to tan-orange. A highlighted metallic stripe extends from the eye to the forelimb insertion, immediately above a prominent black stripe. A black V-shaped mark is evident on the back of the head. A broad dorsal stripe starts in the nuchal region and becomes progressively brighter posteriorly. It is irregularly bordered. Lateral surfaces are black with bright cream-yellow patches. Sides of the tail are black with orange spots. Limbs are mainly mottled orange and dull rusty black. Hands and feet are irregularly mottled. The venter is grey (punctate melanophores) with some light yellow speckles anteriorly. The gular area is strongly mottled with black and orange. The face region is orange with black infusions. Eyelids are black. The iris is dark metallic brown-gold.

Variation. The single specimen from west of Plan de Guadalupe (IBH 13801) (figure 2) differs somewhat from the rest of the type series in being generally rusty to bright red-orange over the entire dorsum, becoming progressively brighter posteriorly. The belly is blackish with scattered rusty spots along the ventral midline; the same rusty spots densely cover the throat region. This is the smallest specimen (23.7 mm SL), and it has the largest nostrils (0.4 mm) and the fewest teeth.

Habitat and range. The species is known from two general localities in the western portion of the Sierra Mazateca, Oaxaca. This mountain range lies within the Sierra Madre Oriental, north of the Río Grande. Both localities, which are only a few kilometres apart, lie within high elevation, moist, pine–oak forest, with oaks dominating at present. *Arbutus* is also common, as is *Baccharis*. There is abundant surface litter and many downed, rotting logs and tree branches. Epiphytes, including bromeliads and ferns, are relatively common. One small log with somewhat loose bark yielded six specimens; most were found under the bark but two specimens were exposed deep inside the log. Two specimens were taken from bromeliads of intermediate to small size located about 2 m above ground. One specimen was taken from a road bank, about 15 cm deep in a tight stone crevice in loose, reddish rock.

Three species of salamanders have been found in sympatry with *Pseudoeurycea ruficauda*: *Cryptotriton adelos* (Papenfuss and Wake, 1987) (Luis Canseco-Márquez, personal communication), *Thorius schmidti* Gehlbach, 1959 (García-París and Parra-Olea, 1999) and a second, undescribed species of *Thorius*, which appears to be endemic to the Sierra Mazateca. One more undescribed species of *Pseudoeurycea* related to *P. mystax* Bogert, 1967 and another undescribed species of *Thorius* occur in the Sierra Mazateca (Parra-Olea *et al*., in preparation), but neither has been found in strict sympatry with *P. ruficauda*.

Etymology. The epithet *ruficauda* is derived from the Latin words *rufous* (reddish) and *cauda* (tail). It refers to the brightly coloured, reddish orange tail of this species.

Remarks. Two specimens deposited in MZFC (UNAM, Mexico) are referred to the above species. Both were collected under logs near the type locality (Luis Canseco-Márquez, personal communication), but each has been dissected and the coloration has already faded. The larger of the two specimens is about 45 mm SL (the other one is about 36 mm SL), indicating that *Pseudoeurycea ruficauda* attains a much larger adult size than would be suggested by the type series alone. The larger specimen is uniformly dark, but it has a mottled throat and the extreme tip of the tail is light, suggesting a bright colour in life. The second specimen has a bright dorsal stripe bordered by dark coloration; the tail is mottled with light and dark pigment and is light at the tip. Limbs of both specimens are long and touch or overlap when appressed to the body. Digits are long and slender.

Molecular characters. We sequenced a total of 1833 base pairs of the mitochondrial genome of three specimens of *P. ruficauda*, two from west of Puerto Soledad, the third from 7 km west of Plan de Guadalupe. These sequences were compared to previously published sequences of all species groups of *Pseudoeurycea* (Parra-Olea, 2002). Sequences are identical (0% divergence) in the two specimens from Puerto Soledad. Divergence (uncorrected p) between these specimens and the one from 7 km west of Plan de Guadalupe is relatively high

(1.1% 16S, 2.8% Cyt b, 4.0% ND4) despite their geographic proximity. However, these sequences are more similar to each other than to any other known mtDNA sequence of *Pseudoeurycea*.

The smallest sequence divergence from *P. ruficauda* to any other species is to populations from the Sierra de Juárez that are tentatively assigned to *P. unguidentis* (2.8% 16S, 6.1–6.7% Cyt b, 9.5–9.7% ND4; Parra-Olea, 2002; see below). The level of divergence between *P. ruficauda* and each previously defined species group is large, including the *P. juarezi* group (3.8–4.0% 16S, 7.6–7.9% Cyt b, 11.0–12.0% ND4); the *P. leprosa* (Cope, 1869) group (4.6–6.7% 16S, 8.2–11.0% Cyt b, 11.4–16.5% ND4); the *P. gadovii* (Dunn, 1926) group (4.6–7.4% 16S, 8.5–9.8% Cyt b, 12.7–15.1% ND4); and the *P. bellii* (Gray, 1850) group (7.9–8.5% 16S, 11.1–12.5% Cyt b, 17.3–19.4% ND4).

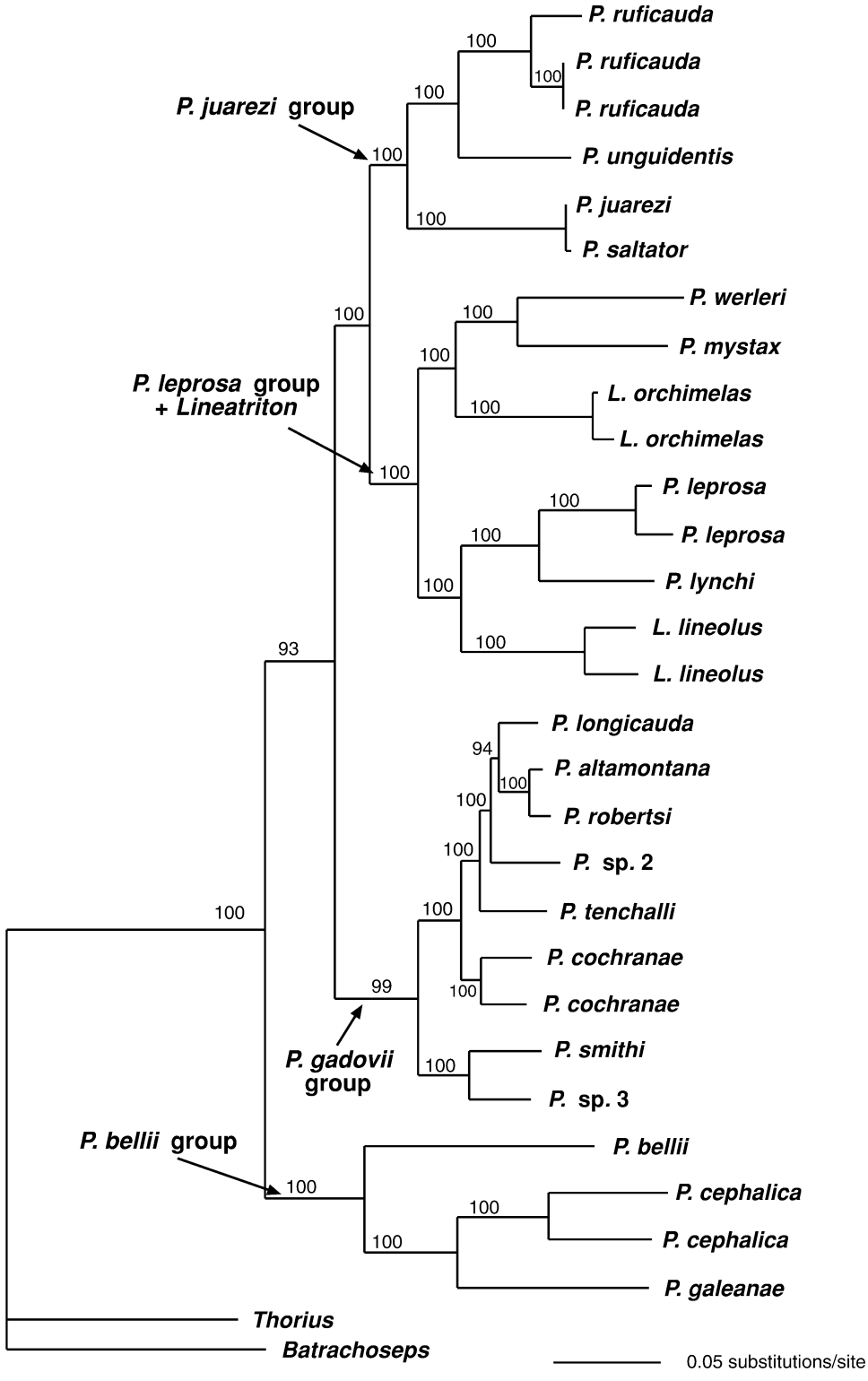
Phylogenetic relationships

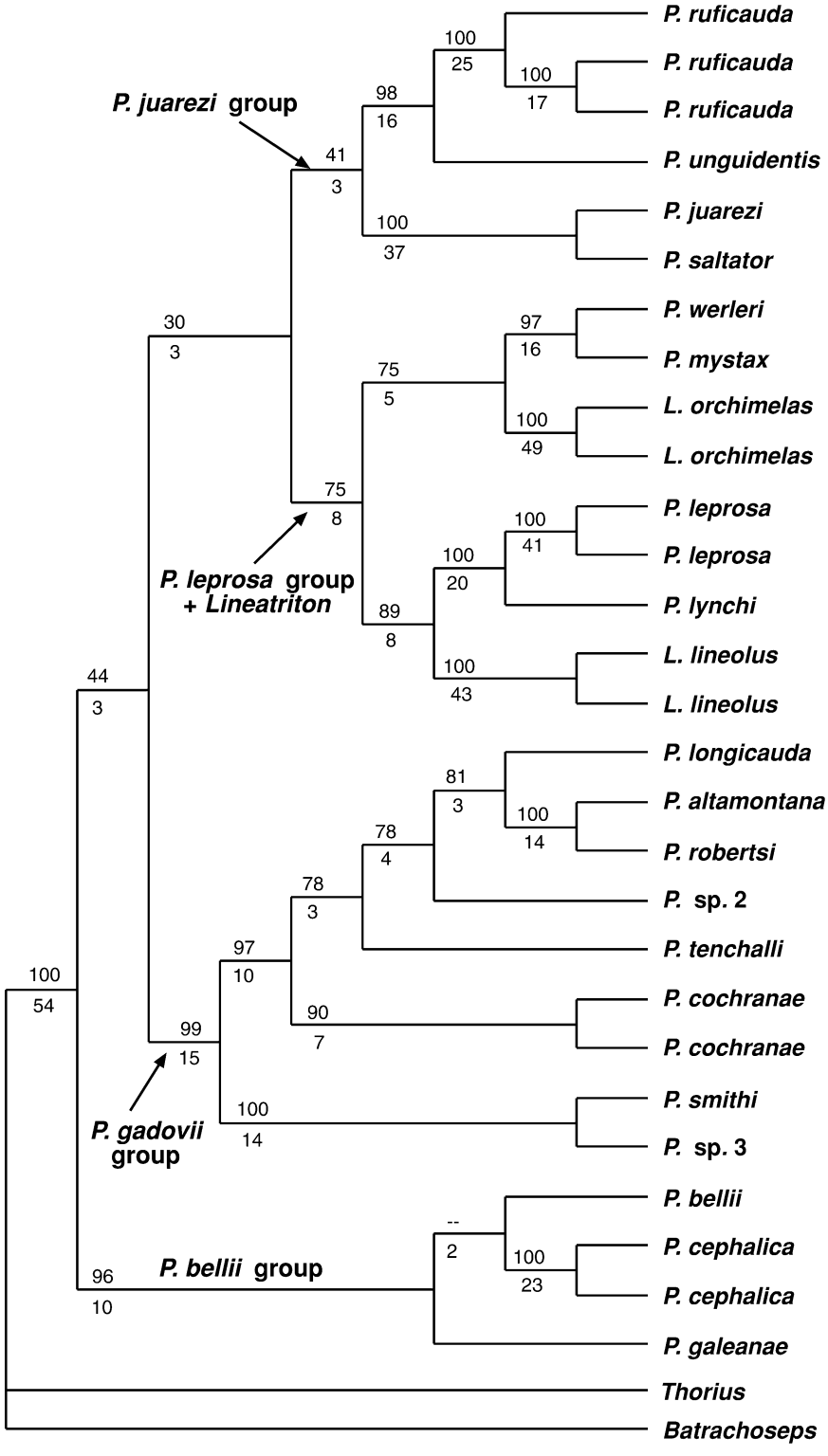
The topology obtained in the ML ($-\ln L = 15369.15$) and Bayesian analyses (figure 3) is very similar to that obtained in the MP analysis (a single most parsimonious tree, L = 2647 steps, consistency index (CI) = 0.408, retention index (RI) = 0.563, 587 characters were parsimony informative; figure 4). The only difference involves the position of *P. galeanae* (Taylor, 1941) and *P. bellii* with respect to *P. cephalica* (Cope, 1869). In the ML and Bayesian topologies *P. galeanae* is sister to the *P. cephalica* clade, with *P. bellii* basal to both of them (figure 3). The single MP tree instead shows *P. bellii* as sister to the *P. cephalica* clade, with *P. galeanae* basal (d2; figure 4).

The ML topology resembles the one published earlier for the genus *Pseudoeurycea* (Parra-Olea, 2002), except that *P. unguidentis* now forms a monophyletic group with *P. ruficauda*. This sister taxon relationship is also present in Bayesian (pp 100) and MP analyses (bs 98). The clade formed by *P. unguidentis* and *P. ruficauda* is included in the *P. juarezi* species group, although MP support values and decay for the group are low (bs 41, d3). Analyses of phylogenetic relationships within this clade are further complicated by uncertainty regarding the specific identity of the population assigned to *P. unguidentis* (Parra-Olea, 1999, 2002). These specimens, from the Sierra de Juárez, Oaxaca, appear to be smaller and longer-legged than those from the type locality, on Cerro San Felipe in the Sierra Aloapaneca, Oaxaca; they may represent a distinct, undescribed taxon. Topotypic samples of *P. unguidentis* for genetic analysis are unavailable. All analyses provide support for previously defined species groups: *P. gadovii* (pp 99, bs 99, d15), *P. leprosa* (pp 100, bs 75, d8), *P. juarezi* (pp 100, bs 41, d3) and *P. bellii* (pp 100, bs 96, d10).

Relationships among main clades are fully resolved by MP analysis, although support for these relationships is weak. The *P. leprosa* group, which includes *Lineatriton*, forms a clade with the *P. juarezi* group (pp support 100, bs 30, d3). This clade, in turn, is sister to the *P. gadovii* group (pp 93, bs 44, d3). The *P. bellii* clade is basal to all other *Pseudoeurycea*.

FIG. 3. Results from maximum likelihood (ML) and Bayesian analyses of the combined data set (Cyt b, ND4, 16S). Both analyses yielded the topology shown. Numbers along branches denote Bayesian posterior clade probabilities. *Pseudoeurycea* sp. 2 and *P.* sp. 3 were identified as undescribed species in Parra-Olea and Wake (2001) and are from the areas of Tlaxiaco and Cerro Pelón, Oaxaca, respectively.


P. ruficauda
P. ruficauda
P. ruficauda
P. unguidentis
P. juarezi
P. saltator
P. juarezi group
P. werleri
P. mystax
L. orchimelas
L. orchimelas
P. leprosa group
+ Lineatriton
P. leprosa
P. leprosa
P. lynchi
L. lineolus
L. lineolus
P. longicauda
P. altamontana
P. robertsi
P. sp. 2
P. tenchalli
P. cochranae
P. cochranae
P. smithi
P. sp. 3
P. gadovii
group
P. bellii group
P. bellii
P. cephalica
P. cephalica
P. galeanae
Thorius
Batrachoseps
0.05 substitutions/site


P. ruficauda
P. ruficauda
P. ruficauda
P. unguidentis
P. juarezi
P. saltator
P. werleri
P. mystax
L. orchimelas
L. orchimelas
P. leprosa
P. leprosa
P. lynchi
L. lineolus
L. lineolus
P. longicauda
P. altamontana
P. robertsi
P. sp. 2
P. tenchalli
P. cochranae
P. cochranae
P. smithi
P. sp. 3
P. bellii
P. cephalica
P. cephalica
P. galeanae
Thorius
Batrachoseps
100
25
100
17
98
16
41
3
100
37
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3
81
3
100
14
78
4
78
3
97
10
100
54
90
7
99
15
100
14
P. juarezi group
P. leprosa group
+ Lineatriton
P. gadovii
group
P. bellii group
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2
100
23
96
10

Discussion

Parra-Olea (2002) reported a molecular analysis of phylogenetic relationships within *Pseudoeurycea* and recognized three species groups: *P. bellii*, *P. gadovii* and *P. leprosa*. Canseco-Márquez and Parra-Olea (2003) added one more taxon to the existing phylogeny, which yielded a fourth, *P. juarezi* species group. One species, *P. unguidentis*, could not be referred to any of the four clades based on these molecular data. It either formed part of a polytomy at the base of the tree (including the current genera *Pseudoeurycea*, *Ixalotriton*, *Parvimolge* and *Lineatriton*), or it was basal to the *P. juarezi–P. saltator* clade, but with little support (Parra-Olea, 2002).

Because the morphology of *P. ruficauda* resembles that of *P. unguidentis*, we added sequences of 16S, Cyt b and ND4 of *P. ruficauda* to the published data set to test whether *P. unguidentis* would retain its undefined position and to assess the affinities of *P. ruficauda*. In all analyses, *P. ruficauda* is the sister taxon to *P. unguidentis*, and the clade formed by these two species clusters with members of the *P. juarezi* group (figures 3, 4).

Most species of *Pseudoeurycea* are terrestrial and rarely occupy arboreal habitats. A few species, however, are typically found in arboreal locations; these include *P. saltator*, *P. nigromaculata* (Taylor, 1941), *P. lynchii* Parra-Olea, Papenfuss and Wake, 2002 and *P. firscheini* Shannon and Werler, 1955 (Shannon and Werler, 1955; Wake and Lynch, 1976; Lynch and Wake, 1989; Parra-Olea *et al*., 2001). *Pseudoeurycea ruficauda* is another arboreal species, although we also found juveniles inside rotten logs on the ground. Populations treated by Parra-Olea (1999, 2002) as *P. unguidentis*, the sister taxon of *P. ruficauda*, inhabit vertical road banks and presumably also occupy vertical stumps and logs, but they have not been taken in bromeliads. Both species share an elongate body form with long, slender limbs and broad hands and feet, which at first glance resembles that of arboreal species of *Chiropterotriton*. Arboreal, elongate *Pseudoeurycea* cluster in two clades: *P. nigromaculata*, *P. lynchii* and *P. firscheini* in the *P. leprosa* species group (Parra-Olea *et al*., 2001; Parra-Olea, 2002); and *P. saltator*, *P. unguidentis* plus *P. ruficauda* in the *P. juarezi* species group (Parra-Olea, 2002; Canseco-Márquez and Parra-Olea, 2003) (figures 3, 4).

The species assemblage of *Pseudoeurycea* in northern Oaxaca is complex and diverse. It includes 14 named species, and at least three additional species that await formal description (Parra-Olea *et al*., in preparation). Many of the species are now rare (Wake and Campbell, 2001), although several are well represented in collections. More detailed analyses of relationships will require molecular surveys of additional samples from throughout this topographically complex region. Description of *P. ruficauda* adds one more species to the known salamander fauna of the State of Oaxaca, the largest in all of Mexico (Casas-Andreu *et al*., 1996).

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FIG. 4. Single tree found in maximum parsimony (MP) analyses of the combined data set (Cyt b, ND4, 16S). Support values above branches correspond to 1000 non-parametric heuristic bootstrap pseudo-replicates; values below indicate decay indices. Double hyphen indicates that the clade is not present in the bootstrap analysis.

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