Zoological Journal of the Linnean Society, 2005, **143**, 405–416. With 1 figure

Phylogenetic taxonomy of the Cercosaurini (Squamata: Gymnophthalmidae), with new genera for species of *Neusticurus* and *Proctoporus*

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Received December 2003; accepted for publication June 2004

The tribe Cercosaurini is one of the most poorly studied groups of the lizard family Gymnophthalmidae. Recent studies have suggested that two cercosauriine genera, *Neusticurus* and *Proctoporus*, are polyphyletic. The aim of the current study was to rectify the polyphyletic relationships and construct a phylogenetic taxonomy of the Cercosaurini that is congruent with evolutionary history. *Neusticurus* is divided into two genera, one of them new (***Potamites***), based on the clades recovered by molecular studies and previously discussed morphological data. *Proctoporus* is divided into three genera, one of which is new (***Petracola***), while an older name (*Riama*) is resurrected for another. All five genera are described and defined and taxonomic keys are presented. This study represents an important advance in rectifying the taxonomy of the Cercosaurini. Many other para- and polyphyletic genera remain in the Gymnophthalmidae and much future work on this group is warranted. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, **143**, 405–416.

ADDITIONAL KEYWORDS: lizards – phylogenetic systematics – Reptilia – taxonomy.

INTRODUCTION

The family Gymnophthalmidae has endured a turbulent taxonomic history plagued by poorly defined genera and the apparent presence of many homoplasious morphological characters. In addition, until recently no attempt has been made to classify the genera within a phylogenetic context. Presch (1980) and Hoyos (1998) constructed phylogenetic hypotheses based on osteological and myological characters, but their conclusions provided little phylogenetic resolution. Pellegrino *et al*. (2001) reconstructed the phylogenetic relationships of the family using gene sequences, including 49 species in 24 genera. Their species sampling was excellent for taxa in the subfamily Gymnophthalminae but relatively poor in the Cercosaurinae; although they placed 22 genera in the latter, they had not examined any members of nine of those genera. Several speciose genera, including *Anadia, Euspondylus,* and *Proctoporus*, were omitted completely from the study and taxon sampling was poor for other speciose genera such as *Bachia, Pholidobolus,* and *Ptychoglossus.* Using morphological characters, Doan (2003b) reconstructed a phylogeny of 11 species formerly belonging to the genera *Cercosaura, Pantodactylus*, and *Prionodactylus,* which were all transferred to *Cercosaura* in that publication.

The most recent phylogenetic hypotheses advanced for the Gymnophthalmidae by Castoe, Doan & Parkinson (2004) included 12 additional species and one additional genus (*Proctoporus*). Moreover, that study filled in some of the gene fragments that had been missing from Pellegrino *et al*.'s (2001) study and further clarified some of the relationships. One major change involved re-allocating *Ptychoglossus* from the Cercosaurinae to a more basal position sister to *Alopoglossus* in subfamily Alopoglossinae. Another taxonomic alteration involved raising the tribe Ecpleopini to subfamily status, the Ecpleopinae. A third change raised the genus *Bachia* to tribal status, the Bachini. Other relationships that were suggested by

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Castoe *et al*. (2004) were that *Neusticurus* and *Proctoporus* were polyphyletic. The current study attempts to rectify those polyphyletic relationships by examining the phylogeny of tribe Cercosaurini and altering the generic taxonomy to recognize monophyletic lineages. Thus, we alter the classification to make it more congruent with evolutionary history.

Taxonomic history of *Neusticurus* Duméril & Bibron

The genus *Neusticurus* consists of 11 species ranging from central Bolivia and south-western Brazil to Colombia on the eastern versant of the Andes and in the Guianan Shield region of Venezuela, Guyana, Suriname, French Guiana, and northern Brazil. One additional species is from central Costa Rica (Uzzell, 1966; Avila-Pires, 1995). The species occur at low elevations from sea level to 1800 m and most are semiaquatic, a unique trait for the family (Uzzell, 1966; Hoogmoed, 1973; Avila-Pires & Vitt, 1998; Vitt *et al*., 1998). *Neusticurus* appears to be most closely related to *Echinosaura* (Burt & Burt, 1931; Uzzell, 1966) and *Teuchocercus* (Fritts & Smith, 1969) based on external morphology.

Duméril & Bibron (1839) created the genus *Neusticurus* to contain *Lacerta bicarinata* Linnaeus. Uzzell (1966) divided the genus into two separate groups: the *N. bicarinatus* group, containing *N. bicarinatus, N. medemi* Dixon & Lamar*, N. racenisi* Roze*, N. rudis* Boulenger*,* and *N. tatei* Burt & Burt (Dixon & Lamar, 1981); and the *N. strangulatus* group, containing *N. strangulatus* Cope*, N. apodemus* Uzzell*, N. cochranae* Burt & Burt*, N. ecpleopus* Cope*, N. juruazensis* Avila-Pires & Vitt*,* and *N. ocellatus* Sinitsin (Van Devender, 1969; Vanzolini, 1995; Avila-Pires & Vitt, 1998). Uzzell's divisions were based primarily on distinctive hemipenial morphology and he suggested that these two groups may actually be linked by convergence and not common evolutionary history (Uzzell, 1966; Pellegrino *et al*., 2001). Pellegrino *et al*. (2001) pointed out the nonmonophyly of *Neusticurus*, with the four species that they included appearing in two or three different positions on their trees (depending on the data sets employed). Castoe *et al*. (2004) also found the genus *Neusticurus* to be polyphyletic based on the five species that they included.

Taxonomic history of *Proctoporus* Tschudi

The genus *Proctoporus* currently consists of 31 species that occur in several mountainous habitats in South America and the Caribbean (Duellman, 1979; Kizirian, 1996; Doan & Castoe, 2003; Doan & Schargel, 2003; Doan, 2003a; Köhler & Lehr, 2004). In 1845, Tschudi erected the genus for the new species *P. pachyurus*. Since that time, three additional genera have been described for species currently considered to be *Proctoporus*. Gray (1858) described *Riama unicolor* and O'Shaughnessy (1879) described *Emphrassotis simoterus* as monotypic genera. The third genus, *Oreosaurus*, was described by Peters (1862) as *Ecpleopus* (*Oreosaurus*) *striatus*, a subgenus of *Ecpleopus*, which is a genus now considered to be distantly related (in a separate subfamily; Castoe *et al*., 2004). Boulenger (1885, 1902, 1908) considered six species to be members of *Oreosaurus* (*O. laevis* Boulenger*, O. luctuosus* Peters*, O. ocellifer* Boulenger*, O. oculatus* O'Shaughnessy*, O. petersii* Boettger*,* and *O. striatus*). Boettger (1891) additionally described *O. guentheri*. Andersson (1914) made *Oreosaurus* a junior synonym of *Proctoporus* because he could not find sufficient differences between the two genera. This synonymy was followed by all subsequent authors.

Uzzell (1958, 1970) suggested preliminary groupings within *Proctoporus*. The *P. luctuosus* group, unified by a divided palpebral eye disc, no median occipital, four supraoculars, and legs overlapping when adpressed, included *P. achlyens* Uzzell*, P. laevis, P. luctuosus, P. oculatus,* and *P. shrevei* Parker (Uzzell, 1958). The *P. pachyurus* group, unified by the presence of a single palpebral scale over the eye, a median occipital, and squarish pregular scales that do not form chevrons (Uzzell, 1970; Doan & Castoe, 2003), included *P. bolivianus* Werner*, P. guentheri,* and *P. pachyurus*. Doan & Castoe (2003) added two additional new species, *P. sucullucu* and *P. unsaacae*. The monotypic *P. ventrimaculatus* Boulenger group was defined by a divided palpebral disc, two supraoculars with a greatly expanded first superciliary, and dark ventral scales (Uzzell, 1970).

These three taxonomic groups are allopatric in distribution, with the *P. luctuosus* group occurring in Ecuador, Colombia, Venezuela, and Trinidad, the *P. pachyurus* group in central and southern Peru and Bolivia, and the *P. ventrimaculatus* group in northern Peru (Uzzell, 1958, 1970).

Kizirian (1996) performed a much more extensive study of the 16 species of *Proctoporus* from Ecuador, describing nine previously unrecognized species. Neither that study, nor others (Kizirian & Coloma, 1991; Kizirian, 1995, 1996), have attempted to place the Ecuadorian species in any groupings. Kizirian (1996) provided a full nomenclatural history of *Proctoporus*, but remarked that monophyly of the genus had never been ascertained unambiguously. Traditionally, the key diagnostic character for inclusion in the genus was the absence of prefrontal scales (Peters & Donosos-Barros, 1970) but because three species of the gymnophthalmid genus *Pholidobolus* also lack prefrontals (Montanucci, 1973) the character cannot be considered a synapomorphy (Doan, 2003a).

Most recently, Doan (2003a) published a phylogenetic analysis of the relationships of all *Proctoporus* species based on external morphology. A monophyletic *Proctoporus* was found despite the fact that one recently collected individual had prefrontal scales. The taxonomic groups erected by Uzzell (1958, 1970) received little support in that analysis. Based on analyses of a large molecular data set, Castoe *et al*. (2004) subsequently found strong support for a polyphyletic *Proctoporus*, composed of at least two distinct clades.

METHODS

Phylogenetic hypotheses for the relationships of the Cercosaurini were reconstructed by Castoe *et al*. (2004) using DNA sequences of three mitochondrial genes (12S rDNA, 16S rDNA, and ND4) and a nuclear coding gene, *c-mos*. Here, we present their preferred Bayesian phylogenetic reconstruction in the form of a partial tree showing only the Cercosaurini and appropriate outgroups (Fig. 1).

Morphological data were recorded from preserved specimens of all known species of *Neusticurus* and *Proctoporus* except for *P. laevis* (because no specimens of this species are available for loan to US institutions) and *P. labiooccularis* Köhler & Lehr and *P. laudahnae* Köhler & Lehr (because of their recent discovery). For those species we relied on the published accounts of Boulenger (1908), Uzzell (1958), and Köhler & Lehr (2004). The appendix lists all specimens that were examined. Museum abbreviations follow Leviton *et al*. (1985) except for Museo de Historia Natural, Universidad Nacional de San Antonio Abad de Cusco (MHNC; formerly abbreviated as UNSAAC) and the Gabinete de Zoologia of the Universidad Nacional de San Antonio Abad de Cusco (GZ). All anatomical terms follow Kizirian (1996) except as modified by Doan (2003a) and Doan & Schargel (2003). See Kizirian (1996) for relevant scale drawings.

RESULTS

The Bayesian phylogenetic reconstruction of Castoe *et al*. (2004) depicting only the Cercosaurini (Fig. 1) shows that both *Neusticurus* and *Proctoporus* are nonmonophyletic. The members of *Neusticurus* appear to occupy two distinct clades. In the first, *N. bicarinatus* and *N. rudis* are sister to the genus *Placosoma*; in the second, *N. ecpleopus, N. juruazensis,* and *N. strangulatus* are sister to a clade of some members of *Proctoporus*. These two clades correspond to the *N. bicarinatus* and *N. strangulatus* species groups (*sensu* Uzzell, 1966; Avila-Pires & Vitt, 1998). Therefore, because of the two phylogenetically distinct clades, a new genus must be designated to contain

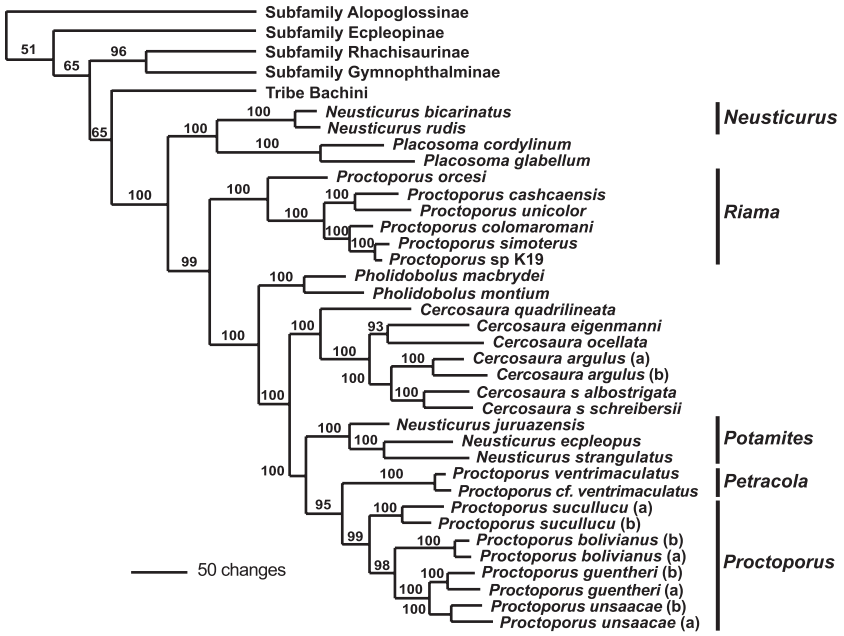

Figure 1. Preferred Bayesian phylogenetic reconstruction of four genes of the Cercosaurini with outgroups representing the other clades of the Gymnophthalmidae from Castoe *et al*. (2004). Values above branches represent posterior probability values. Branch lengths of the Cercosaurini are informative, whereas branch lengths of the outgroups are not informative. Labels (a) and (b) indicate individuals of a species from Castoe *et al*. (2004). The vertical bars on the right of the figure indicate the new generic status of the target taxa.

members of the second clade, whereas members of the first remain in *Neusticurus* (see Fig. 1).

Geographically, the two clades are separate as well, with the first occurring throughout the Guianan Shield region of Venezuela, Guyana, Suriname, French Guiana, and northern Brazil and the second occurring throughout Amazonia in Colombia, Ecuador, Peru, Bolivia, and western Brazil, with one disjunct species in Costa Rica. Below, we redefine *Neusticurus* and describe and define the new genus for the *N. strangulatus* group.

The sampled members of *Proctoporus* form two monophyletic groups. The first is a clade of Ecuadorian and Colombian species sister to *Pholidobolus* + *Cercosaura* + *N. strangulatus* group + the remaining species of *Proctoporus.* The second consists of species from Peru and Bolivia and is in a more terminal position sister to the *N. strangulatus* group. Because of the wide separation of the two clades, it is clear that current members of *Proctoporus* must be divided into separate genera. The type species is *P. pachyurus* from central and southern Peru (Tschudi, 1845). The *P. pachyurus* species group also includes *P. bolivianus, P. guentheri, P. sucullucu,* and *P. unsaacae*, and is unified by several diagnostic characters (Uzzell, 1970; Doan & Castoe, 2003).

Thus, the generic name *Proctoporus* remains with the *P. pachyurus* group from southern Peru and Bolivia. *P. ventrimaculatus* was placed by Uzzell (1970) in a separate monotypic group because its morphology differed strongly from species of any of the recognized groups. Its placement in the phylogenetic reconstruction of Castoe *et al*. (2004) makes its generic allocation equivocal. Although it does form a clade with the *P. pachyurus* group, it falls outside of it. After re-examining the morphology of specimens of this species, we find no morphological evidence linking it to the group. Therefore, we find it necessary to designate a new genus to contain *P. ventrimaculatus* and *P. labiooccularis*, its probable sister species.

The remaining *Proctoporus* species are allocated to *Riama* Gray (type species *R. unicolor*) (see Fig. 1). This genus has not had taxonomic status since Boulenger (1885) synonymized it with *Proctoporus*. Therefore, we resurrect *Riama* Gray to include all *Proctoporus* species that occur in Ecuador, Colombia, Venezuela, Trinidad and Tobago, and one species from central Peru (Table 1).

We recognize that we have only included five members of this genus so that the re-allocation of 24 species to *Riama* may appear questionable. However, the genetic and morphological distinctiveness of the five species requires a taxonomic change so that the question becomes what to do with the rest of the species. Morphologically, the northern *Proctoporus sensu lato* species form a fairly cohesive group and all lack some of the diagnostic characters for the *P. pachyurus* and *P. ventrimaculatus* groups. It seems clear that retaining these species in *Proctoporus* would create a paraphyletic *Proctoporus*.

We much prefer to take the chance of creating a paraphyletic *Riama*, because there is much greater likelihood that the northern *Proctoporus s.l.* species belong there. The Andes north of the Huancabamba Deflection arose much more recently than the central and southern Andes (Duellman, 1979; Simpson, 1979) and Doan (2003a) has shown that the northern *Proctoporus* species appear to be more recently derived. Therefore, it is likely that the northern species (now allocated to genus *Riama*) are more closely related to each other than to any of the species inhabiting Peru or Bolivia. One recently described species from Huánuco, central Peru, *P. laudahnae*, has many morphological characters that link it to species now placed in *Riama* (Köhler & Lehr, 2004). Because it differs greatly from other Peruvian species (*Proctoporus s.s.* and the new genus for the *P. ventrimaculatus* group), we place *P. laudahnae* in the genus *Riama.*

The three genera are geographically concordant for the most part. *Proctoporus s.s.* is restricted to the central Andes of central and southern Peru and Bolivia, the new genus for the *P. ventrimaculatus* group is restricted to central and northern Peru, and *Riama* ranges throughout the northern Andes, the Cordillera de la Costa of Venezuela, and the island of Trinidad, with one species in central Peru. Below we define each genus.

POTAMITES GEN. NOV.

Type species: Euspondylus strangulatus Cope, 1868: 99.

Neusticurus strangulatus group: Uzzell, 1966: 311.

Etymology: Potamites is a masculine Greek noun, meaning water finder. It refers to the fact that most members of this genus are semiaquatic, walking on the bottom of streams and often diving into streams to escape predation.

Definition: Tongue with imbricate, scale-like papillae. Nostril pierced in a single nasal; nasals separated usually by paired or single frontonasals, occasionally by irregular scales; prefrontals paired or irregular; interparietal usually bordered by a pair of parietals laterally, by a series of two to eight smaller scales posteriorly; occipital and temporal scales differentiated or not; rostral large, mental and postmental single, followed by several paired chin shields; gular crease feeble or absent. Collar fold well developed. Lower eyelid developed, with a palpebral disc undivided or divided into two to seven scales, transparent

Table 1. List of all known members of *Neusticurus,* ***Petracola*** **gen. nov.**, ***Potamites*** **gen. nov.**, *Proctoporus* and *Riama*

Species	Authority and year	Former genus
Neusticurus bicarinatus	(Linnaeus, 1758)	*Neusticurus*
Neusticurus medemi	Dixon & Lamar, 1981	*Neusticurus*
Neusticurus racenisi	Roze, 1958	*Neusticurus*
Neusticurus rudis	Boulenger, 1900	*Neusticurus*
Neusticurus tatei	Burt & Burt, 1931	*Neusticurus*
Petracola labioocularis	(Köhler & Lehr, 2004)	*Proctoporus*
Petracola ventrimaculatus	(Boulenger, 1900)	*Proctoporus*
Potamites apodemus	(Uzzell, 1966)	*Neusticurus*
Potamites cochranae	(Burt & Burt, 1931)	*Neusticurus*
Potamites ecpleopus	(Cope, 1876)	*Neusticurus*
Potamites juruazensis	(Avila-Pires & Vitt, 1998)	*Neusticurus*
Potamites ocellatus	(Sinitsin, 1930)	*Neusticurus*
Potamites strangulatus	(Cope, 1868)	*Neusticurus*
Proctoporus bolivianus	Werner, 1910	*Proctoporus*
Proctoporus guentheri	(Boettger, 1891)	*Proctoporus*
Proctoporus pachyurus	Tschudi, 1845	*Proctoporus*
Proctoporus sucullucu	Doan & Castoe, 2003	*Proctoporus*
Proctoporus unsaacae	Doan & Castoe, 2003	*Proctoporus*
Riama achlyens	(Uzzell, 1958)	*Proctoporus*
Riama anatoloros	(Kizirian, 1996)	*Proctoporus*
Riama balneator	(Kizirian, 1996)	*Proctoporus*
Riama cashcaensis	(Kizirian & Coloma, 1991)	*Proctoporus*
Riama colomaromani	(Kizirian, 1996)	*Proctoporus*
Riama columbiana	(Andersson, 1914)	*Proctoporus*
Riama hyposticta	(Boulenger, 1902)	*Proctoporus*
Riama inanis	(Doan & Schargel, 2003)	*Proctoporus*
Riama labionis	(Kizirian, 1996)	*Proctoporus*
Riama laevis	(Boulenger, 1908)	*Proctoporus*
Riama laudahnae	(Köhler & Lehr, 2004)	*Proctoporus*
Riama luctuosa	(Peters, 1862)	*Proctoporus*
Riama meleagris	(Boulenger, 1885)	*Proctoporus*
Riama oculata	(O'Shaughnessy, 1879)	*Proctoporus*
Riama orcesi	(Kizirian, 1995)	*Proctoporus*
Riama petrorum	(Kizirian, 1996)	*Proctoporus*
Riama raneyi	(Kizirian, 1996)	*Proctoporus*
Riama shrevei	(Parker, 1935)	*Proctoporus*
Riama simotera	(O'Shaughnessy, 1879)	*Proctoporus*
Riama stigmatoral	(Kizirian, 1996)	*Proctoporus*
Riama striata	(Peters, 1862)	*Proctoporus*
Riama unicolor	Gray, 1858	*Proctoporus*
Riama vespertina	(Kizirian, 1996)	*Proctoporus*
Riama vieta	(Kizirian, 1996)	Proctoporus

or pigmented. Tympanum at surface of head or slightly recessed, overhung by surrounding scales of surface of head. Dorsal scales heterogeneous, imbricate, with large, keeled tubercles intermixed with small flat scales, in transverse or longitudinal rows. Ventral scales wider than dorsals, usually flat, rectangular or slightly rounded posteriorly, subimbricate, in transverse and 6–10 longitudinal rows; lateral rows raised or keeled in some species. Limbs pentadactyl, digits clawed; forefoot with enlarged, plate-like scales along inner margin between thumb and wrist; under side of third and fourth toes with paired scales proximally, inner scale a rounded tubercle. Tail slightly compressed; a double caudal crest, feebly to strongly developed. Total femoral and preanal pores: 10–59 in males; 0–29 in females. Preanal plate in 2–3 rows,

posterior row 2–5 scales in both sexes. Males and females with or without conspicuous, white- or brown-centred, black-bordered ocelli on their lateral body surfaces. Hemipenis without basal hooks; flounces with minute calcareous spinules.

Diagnosis: Potamites differs from members of subfamily Alopoglossinae by having its tongue covered in imbricate, scale-like papillae instead of oblique plicae (Harris, 1994), from subfamily Gymnophthalminae by having moveable eyelids, from subfamily Rhachisaurinae by having external ear openings and from subfamily Ecpleopinae by having heterogeneous dorsal scalation. Within subfamily Cercosaurinae (*sensu* Castoe *et al*., 2004), *Potamites* differs from all genera except *Echinosaura, Neusticurus,* and *Teuchocercus* by having heterogeneous dorsal scalation. It differs from *Echinosaura* by lacking basal spines on the hemipenes, from *Teuchocercus* by lacking conical scales on the tail, and from *Neusticurus* (character states in parentheses) by having a slightly compressed tail (strongly compressed), subimbricate ventral scales (imbricate), and calcareous spinules on flounces of hemipenes (no spinules).

Content: Potamites includes six species (Table 1).

Distribution: Potamites occurs throughout Amazonia in Colombia, Ecuador, Peru, Brazil, and Bolivia and in the San José Province of Costa Rica.

NEUSTICURUS DUMÉRIL & BIBRON

Type species: *Lacerta bicarinata* Linnaeus, 1758: 201.

Neusticurus bicarinatus group: Uzzell, 1966: 311.

Definition: Tongue with imbricate, scale-like papillae. Nostril pierced in a single nasal; nasals separated usually by paired or single frontonasals; prefrontals paired or irregular, sometimes with a diamond shaped scale between frontonasal and prefrontals; interparietal usually bordered by a pair of parietals laterally, by a series of 3–9 smaller scales posteriorly; occipitals differentiated or not; temporal scales differentiated or not, irregular, sometimes keeled; rostral large, mental and postmental single, followed by several paired chin shields; gular crease feeble or absent. Collar fold moderately to well developed. Lower eyelid developed, with a palpebral disc divided into 3–6 scales, sometimes pigmented. Tympanum slightly to deeply recessed, overhung by surrounding scales of surface of head. Dorsal scales uniformly small, or heterogeneous, imbricate, with keeled tuberculate scales, sometimes intermixed with small flat or convex scales, in longitudinal, oblique, or transverse and oblique rows. Ventral scales usually flat, rounded posteriorly, imbricate, in transverse and 8–10 longitudinal rows, lateralmost rows convex or keeled in some species. Limbs pentadactyl, digits clawed; forefoot with enlarged, plate-like scales along inner margin between thumb and wrist; under side of third and fourth toes with paired scales proximally, inner scale a rounded tubercle. Tail strongly compressed; a double caudal crest, feebly to strongly developed. Femoral and preanal pores form an unbroken series: 32–72 in males; 1–18 in females. Preanal plate in 2–3 rows, posteriormost row with 5–7 scales in both sexes. Males and females with or without conspicuous, white-centred, black-bordered ocelli on their lateral body surfaces. Hemipenis without basal hooks; flounces without minute calcareous spinules.

Diagnosis: Neusticurus differs from members of Alopoglossinae by having its tongue covered in imbricate, scale-like papillae instead of oblique plicae (Harris, 1994), from Gymnophthalminae by having moveable eyelids, from Rhachisaurinae by having external ear openings, and from Ecpleopinae by having heterogeneous dorsal scalation. Within Cercosaurinae (*sensu* Castoe *et al*., 2004), *Neusticurus* differs from all genera except *Echinosaura*, *Potamites* and *Teuchocercus* by having heterogeneous dorsal scales.

KEY TO THE SPECIES OF ***POTAMITES*** **GEN. NOV.**

1a. Dorsal scales in longitudinal rows of large, keeled scales with smaller scales on either side of rows 2
1b. No longitudinal rows of large, keeled dorsal scales . . . . . *P. strangulatus*
2a. Single frontonasal scale 3
2b. Frontonasal scale replaced by a series of irregular scales . . . . . *P. apodemus*
3a. Tail annuli in complete rings of enlarged keeled scales 4
3b. Tail annuli rings not complete, large keeled scales interrupted by small flat scales 5
4a. Tympanum at surface of the head . . . . . *P. ocellatus*
4b. Tympanum slightly recessed . . . . . *P. cochranae*
5a. Two to three reduced scales transversely between two paravertebral tubercular rows at mid-dorsum . . . . . *P. juruazensis*
5b. Four to six reduced scales transversely between two paravertebral tubercular rows at mid-dorsum . . . . . *P. ecpleopus*

It differs from *Echinosaura* by lacking basal spines on the hemipenes, from *Teuchocercus* by lacking conical scales on the tail, and from *Potamites* (character states for *Potamites* in parentheses) by having a strongly compressed tail (slightly compressed), ventral scales imbricate (subimbricate ventral scales), and hemipenes lacking calcareous spinules on flounces (calcareous spinules on hemipenes).

Content: Neusticurus includes five species (Table 1).

Distribution: Neusticurus occurs throughout the Guianan Shield region of Venezuela, Guyana, Suriname, French Guiana, and northern Brazil.

PETRACOLA GEN. NOV.

Type species: *Proctoporus ventrimaculatus* Boulenger, 1900: 185.

Etymology: Petracola is a masculine word derived from Latin, meaning rock dweller. It refers to the fact that these lizards are usually found beneath rocks on the ground.

Definition: Tongue with imbricate, scale-like papillae. Head scales smooth without striations or rugosities: single frontonasal, frontal, and interparietal; paired frontoparietals and parietals; prefrontals absent; nostril pierced in a single nasal; nasals not in contact; supraoculars three or four. Eyelids developed, lower with a translucent disc, usually divided into multiple palpebral scales. Posterior gulars squarish. Limbs pentadactyl; digits clawed. Dorsal scales quadrangular, elongate, smooth, juxtaposed, forming transverse series only. Ventrals large, smooth, quadrangular, juxtaposed, forming regular longitudinal and transverse series. Femoral pores usually present in males and females, less than six per hind limb; preanal pores present or absent. Tail cylindrical.

Diagnosis: Petracola differs from members of Alopoglossinae by having its tongue covered in imbricate, scale-like papillae instead of oblique plicae (Harris, 1994), from Gymnophthalminae by having moveable eyelids, from Rhachisaurinae by having external ear openings, and from Ecpelopinae by lacking prefrontal scales. Within Cercosaurinae (*sensu* Castoe *et al*., 2004), *Petracola* differs from all genera except *Pholidobolus, Proctoporus,* and *Riama* by lacking prefrontal scales. *Petracola* differs from *Proctoporus* by having smooth dorsal scales, from *Pholidobolus* by having juxtaposed dorsal scales and from *Riama* by a combination of smooth dorsal scales and femoral pores per hind limb in both sexes less than six (exclusive of preanal pores).

Content: Petracola contains two species (Table 1).

Distribution: Petracola is only known to occur in the Huánuco, Piura, and Cajamarca Departments of central and northern Peru.

RIAMA GRAY COMB. NOV.

Type species: *Riama unicolor* Gray, 1858: 446.

Definition: Tongue with imbricate, scalelike papillae. Head scales smooth without striations or rugosities: single frontonasal, frontal, and interparietal; paired frontoparietals and parietals; prefrontals absent; nostril pierced in a single nasal; nasals not in contact. Eyelids developed, lower with a translucent disc divided into several scales. Posterior gulars squarish. Limbs pentadactyl; digits clawed. Dorsal scales quadrangular or hexagonal, elongate, smooth, striate, rugose, or keeled, juxtaposed, forming transverse series only. Ventrals large, smooth, quadrangular, juxtaposed, forming regular longitudinal and transverse series. Femoral pores usually present in males and females; preanal pores present or absent in males or females. Tail cylindrical.

Diagnosis: Riama differs from members of Alopoglossinae by having its tongue covered in imbricate, scale-

KEY TO THE SPECIES OF *NEUSTICURUS* DUMÉRIL & BIBRON

1a. Single frontonasal	2
1b. Paired frontonasals	4
2a. Uniformly small dorsal scales	3
2b. Heterogeneous dorsal scales: large keeled scales intermixed with small flat scales	*N. rudis*
3a. Deeply recessed tympanum	*N. medemi*
3b. Slightly recessed tympanum	*N. tatei*
4a. Dorsal scales in longitudinal rows only	*N. bicarinatus*
4b. Dorsal scales in transverse and oblique rows only	*N. racenisi*

KEY TO THE SPECIES OF ***PETRACOLA*** **GEN. NOV.**

1a. Three supraoculars, supralabial-subocular fusion absent	*P. ventrimaculatus*
1b. Four supraoculars, supralabial-subocular fusion present	*P. labiooocularis*

like papillae instead of oblique plicae (Harris, 1994), from Gymnophthalminae by having moveable eyelids, from Rhachisaurinae by having external ear openings, and from Ecpelopinae by lacking prefrontal scales. Within Cercosaurinae (*sensu* Castoe *et al*., 2004), *Riama* differs from all genera except *Pholidobolus, Proctoporus,* and *Petracola* by lacking prefrontal scales. It differs from *Proctoporus* by having a divided palpebral disc, from *Pholidobolus* by lacking two medial rows of widened gulars, and from *Petracola* by lacking the combination of smooth dorsal scales and femoral pores per hind limb in both sexes less than six (exclusive of preanal pores).

Content: Riama includes 24 species (Table 1).

Distribution: Riama occurs throughout the Andes of central Peru, Ecuador, Colombia, and Venezuela, the Cordillera de la Costa of Venezuela, and the northern range of the island of Trinidad.

Remarks: Gray's (1858) description of *Riama* included some erroneous characters, such as a lateral longitudinal fold that he used as evidence to state that the genus was related to amphisbaenians and *Bachia*. Although we have not been able to examine the type specimen of this genus, it appears from his detailed drawing that the type specimen was average and did not actually have a lateral fold, but a very thin row of reduced lateral scales. Preservation of a specimen that had not recently eaten or had been dehydrated before or after fixation may have led to the overlapping of dorsal and ventral scales, producing what appeared to be a lateral fold.

PROCTOPORUS TSCHUDI

Type species: *Proctoporus pachyurus* Tschudi, 1845: 161.

Proctoporus pachyurus group: Uzzell, 1970: 4.

Definition: Tongue with imbricate, scalelike papillae. Head scales smooth without striations or rugosities: single frontonasal, frontal, and interparietal; paired frontoparietals and parietals; prefrontals absent; nostril pierced in a single nasal; nasals not in contact. Eyelids developed, lower with an undivided translucent disc. Posterior gulars squarish. Limbs pentadactyl; digits clawed. Dorsal scales quadrangular, elongate, keeled, juxtaposed, forming transverse series only. Ventrals large, smooth, quadrangular, juxtaposed, forming regular longitudinal and transverse series. Femoral pores present in males, sometimes absent in females; preanal pores absent in both sexes. Tail cylindrical.

Diagnosis: Proctoporus differs from members of subfamily Alopoglossinae by having its tongue covered in imbricate, scale-like papillae instead of oblique plicae (Harris, 1994), from Gymnophthalminae by having moveable eyelids, from Rhachisaurinae by having external ear openings and from Ecpelopinae by lacking prefrontal scales. Within Cercosaurinae (*sensu* Castoe *et al*., 2004), *Proctoporus* differs from all genera except *Pholidobolus, Riama*, and *Petracola* by lacking prefrontal scales. It differs from *Riama* by having an entire palpebral eye disc, from *Petracola* by having keeled dorsal scales and from *Pholidobolus* by having juxtaposed dorsal scales.

Content: Proctoporus s.s. includes five species (Table 1).

Distribution: Proctoporus occurs in the Andes of the Peruvian departments of Apurimac, Ayacucho, Cusco, Junín, and Puno, and the Bolivian departments of Cochabamba, La Paz, and Santa Cruz.

Remarks: Recent field-work recovered specimens and tissues (for molecular analysis) of *P. pachyurus*, for which no such material had previously been available. Preliminary molecular sampling using the mitochondrial gene ND4 revealed that *Proctoporus s.s.* as described here is a monophyletic group that includes *P. pachyurus* and an undescribed lineage (T. M. Doan, T. A. Castoe, & Arizábal, unpubl. data).

Based on phylogenetic analyses of morphological characters, Doan (2003a) stated that, due to the lack of monophyly of the *P. pachyurus* group, the character of an undivided palpebral disc should not be considered a synapomorphy and was likely a pleisiomorphic character. In contrast to that study, molecular evidence strongly supports the monophyly of this group and we believe that the undivided palpebral disc is a valid synapomorphy for the genus *Proctoporus s.s.*, despite the fact that a single specimen of *P. bolivianus* (AMNH R-150695) was found with a divided palpebral disc (Wiens & Servedio, 2000).

Although Tschudi (1845) did not provide an etymology for the name *Proctoporus*, the name presumably refers to the preanal pores that he reports for the type species *P. pachyurus*. However, neither the type species, nor any other members of the genus *Proctoporus s.s.* have preanal pores (Uzzell, 1973; pers. obs.). Thus, the name erroneously describes a character that these species do not possess.

DISCUSSION

As mentioned by several authors (Montanucci, 1973; Uzzell, 1973; Oftedal, 1974; Doan, 2003b; Castoe *et al*., 2004), the family Gymnophthalmidae is replete with poorly described genera that are often para- or polyphyletic. This paper makes an advance towards resolving this problem by separating two polyphyletic

KEY TO THE SPECIES OF *RIAMA* GRAY

1a. Limbs overlapping when adpressed against body 2
1b. Limbs not overlapping when adpressed 10
2a. Hexagonal dorsal scales 3
2b. Quadrangular dorsal scales 4
3a. Dorsal scales obtusely hexagonal, preanal pores in males 2 . . . . . *R. achlyens*
3b. Dorsal scales acutely hexagonal, preanal pores in males 4–6 . . . . . *R. shrevei*
4a Keeled, striated, or rugose dorsal scales 5
4b Smooth dorsal scales . . . . . *R. laevis*
5a. Lateral scale rows 0–6 6
5b. Lateral scale rows 7–12 9
6a. Transverse rows of dorsal scales 25–35 7
6b. Transverse rows of dorsal scales 39–43 . . . . . *R. balneator*
7a. Lateral scale rows 2–6 8
7b. Lateral scale rows 0–1 . . . . . *R. striata*
8a. Rugose dorsal scales . . . . . *R. vieta*
8b. Keeled or striated dorsal scales . . . . . *R. hyposticta*
9a. Femoral pores on one leg 0–6 . . . . . *R. oculata*
9b. Femoral pores on one leg 9–14 . . . . . *R. luctuosa*
10a. Venter immaculate except near lateral surfaces 11
10a. Ventral scales with dark pigmentation 12
11a. Preanal pores present in both sexes . . . . . *R. inanis*
11b. Preanal pores absent . . . . . *R. vespertina*
12a. Keeled, striated, or rugose dorsal scales 13
12b. Smooth dorsal scales . . . . . *R. meleagris*
13a. Keeled or striated dorsal scales, dorsal stripes in some individuals, preanal pores present or absent, three or four supraoculars 14
13b. Keeled dorsal scales, no dorsal stripes, preanal pores present in males and females, four supraoculars . . . . . *R. labionis*
14a. Transverse rows of dorsal scales greater than 31 15
14b. Transverse rows of dorsals scales 27–31 . . . . . *R. petrorum*
15a. Three or four supraoculars, lateral ocelli present or absent, lip barring variable 17
15b. Three supraoculars, no lateral ocelli, no barring on lip 16
16a. Supralabial-subocular fusion absent . . . . . *R. raneyi*
16b. Supralabial-subocular fusion present . . . . . *R. laudahnae*
17a. Superciliary series complete or incomplete, transverse rows of ventrals 19–27, anterodorsal thigh scales smooth, rugose, or striate 18
17b. Superciliary series incomplete, transverse rows of ventral scales 18–20, anterodorsal thigh scales smooth . . . . . *R. colomaromani*
18a. Keeled or striated dorsal scales, longitudinal rows of dorsal scales 20–34, preanal pores present or absent, femoral pores on one leg of males 0–11 19
18b. Keeled dorsal scales, longitudinal rows of dorsal scales 21–22, preanal pores absent, femoral pores of males on one leg 3–5 . . . . . *R. columbiana*
19a. Keeled or striate dorsal scales, subdigital lamellae on fourth toe 10–18, superciliary series complete or incomplete 20
19b. Keeled dorsal scales, subdigital lamellae on fourth toe 15–18, superciliary series complete . . . . . *R. orcesi*
20a. Transverse rows of ventral scales 19–27, hemipenis with or without small or large spines 21
20b. Transverse rows of ventral scales 19–20, hemipenis with small spines . . . . . *R. simotera*
21a. Femoral pores of males 0–10, preanal pores of males 0–4, femoral pores of females 0–9, preanal pores of females 0–4 22
21b. Femoral pores of males 8–9, preanal pores of males 2–4, females lack femoral and preanal pores . . . . . *R. stigmatoral*
22a. Hemipenis with small or absent spines, superciliary series usually incomplete 23
22b. Hemipenis with large spines, superciliary series complete . . . . . *R. anatoloros*
23a. Preanal pores present in both sexes . . . . . *R. unicolor*
23b. Preanal pores absent . . . . . *R. cashcaensis*

KEY TO THE SPECIES OF *PROCTOPORUS* TSCHUDI

1a. Two to three supraoculars 2
1b. Four supraoculars . . . . . *P. pachyurus*
2a. Venter uniformly dark or with dark stippling or mottling near lateral scale rows 3
2b. Venter clear yellow or orange without dark mottling . . . . . *P. guentheri*
3a. No continuous series of lateral ocelli 4
3b. Continuous series of lateral ocelli . . . . . *P. unsaacae*
4a. Frontonasal scale longer than frontal scale . . . . . *P. sucullucu*
4b. Frontonasal scale equal in length to frontal scale . . . . . *P. bolivianus*

taxa into separate monophyletic genera. Much, however, remains to be done. As mentioned by Castoe *et al*. (2004), *Anotosaura* appears to be paraphyletic with respect to *Colobosauroides cearensis*, while additional problems persist in other genera that were not included in the phylogenetic reconstructions of Pellegrino *et al*. (2001) and Castoe *et al*. (2004). Future studies of the evolutionary history of this speciose family will help to shed light on the complex biogeography of South America.

One of the most interesting and curious results of our study is the very similar morphology of *Neusticurus* and *Potamites*. Both of these genera are made up of species that are semiaquatic, using bodies of water as refugia from predation. Similar habitats often lead to similar morphologies. However, the unusual morphology of heterogeneous and tuberculate body scales characteristic of all the species of both genera does not have any obvious link to an aquatic lifestyle. Indeed, the only other gymnophthalmid genus with similar morphology, *Teuchocercus*, has not been found to be associated with aquatic microhabitats. Further studies of the selection pressures imposed by this microhabitat use, which is unique among gymnophthalmids, are required in order to determine how the convergent morphological evolution of these two distantly related genera occurred.

ACKNOWLEDGEMENTS

We would like to the thank the museum personnel that loaned us specimens under their care: L. S. Ford, C. J. Cole, R. Bain, and B. Jablonski at AMNH, L. Trueb and J. E. Simmons at KU, J. P. Rosado at MCZ, R. K. Vaughan and L. Fitzgerald at TCWC, and R. V. Wilson and R. I. Crombie at USNM. C. O'Reilly, E. N. Smith, and M. A. Cunningham critically reviewed the manuscript.

REFERENCES

Andersson LG. 1914. A new *Telmatobius* and new teiidoid lizards from South America. *Arkiv för Zoologi* **9:** 1–12.

Avila-Pires TCS. 1995. Lizards of the Brazilian Amazon (Reptilia: Squamata). *Zoologische Verhandelingen Leiden* **299:** 1–706.

Avila-Pires TCS, Vitt LJ. 1998. A new species of *Neusticurus* (Reptilia: Gymnophthalmidae) from the Rio Juruá, Acre, Brazil. *Herpetologica* **54:** 235–245.

Boettger O. 1891. Reptilien und Batrachier aus Bolivia. *Zoologischer Anzeiger* **14:** 343–347.

Boulenger GA. 1885. *Catalogue of the Lizards in the British Museum (Natural History) I–III*. London: British Museum (Natural History).

Boulenger GA. 1900. Descriptions of new Batrachians and Reptiles collected by Mr. P. O. Simons in Peru. *Annals and Magazine of Natural History, Series* **7** (6)**:** 181–186.

Boulenger GA. 1902. Descriptions of new batrachians and reptiles from the Andes of Peru and Bolivia. *Annals and Magazine of Natural History, Series* **7** (6)**:** 394–402.

Boulenger GA. 1908. Descriptions of new batrachians and reptiles discovered by Mr. M. G. Palmer in south-western Colombia. *Annals and Magazine of Natural History, Series* **8** (2)**:** 515–522.

Burt CE, Burt MD. 1931. South American lizards in the collection of the American Museum of Natural History. *Bulletin of the American Museum of Natural History* **61:** 227–395.

Castoe TA, Doan TM, Parkinson CL. 2004. Data partitions and complex models in Bayesian analysis: the phylogeny of gymnophthalmid lizards. *Systematic Biology* **53:** 448–469.

Cope ED. 1868. An examination of the Reptilia and Batrachia obtained by the Orton Expedition to Equador and the upper Amazon, with notes on other species. *Proceedings of the Academy of Natural Sciences of Philadelphia* **1868:** 96–140.

Dixon JR, Lamar WW. 1981. A new species of microteiid lizard (genus *Neusticurus*) from Colombia. *Journal of Herpetology* **15:** 309–314.

Doan TM. 2003a. A south-to-north biogeographic hypothesis for Andean speciation: evidence from the lizard genus *Proctoporus* (Reptilia, Gymnophthalmidae). *Journal of Biogeography* **30:** 361–374.

Doan TM. 2003b. A new phylogenetic classification for the gymnophthalmid genera *Cercosaura, Pantodactylus*, and *Prionodactylus* (Reptilia: Squamata). *Zoological Journal of the Linnean Society* **137:** 101–115.

Doan TM, Castoe TA. 2003. Using morphological and molecular evidence to infer species boundaries within *Proctoporus bolivianus* Werner (Squamata: Gymnophthalmidae). *Herpetologica* **59:** 433–450.

Doan TM, Schargel WE. 2003. Bridging the gap in *Proctoporus* distribution: a new species (Squamata: Gymnophthalmidae) from the Andes of Venezuela. *Herpetologica* **59:** 68–75.

Duellman WE. 1979. The herpetofauna of the Andes: patterns of distribution, origin, differentiation, and present communities. In: Duellman WE, ed. *The South American herpetofauna: its origin, evolution, and dispersal*. Lawrence: Monographs Museum Natural History University Kansas, no. 7, 371–459.

Duméril AMC, Bibron G. 1839. *Erpétologie générale ou histoire naturelle complète des reptiles*. Paris: Librairie Encyclopédique de Roret, 5.

Fritts TH, Smith HM. 1969. A new teiid lizard genus from western Ecuador. *Transactions of the Kansas Academy of Science* **72:** 54–59.

Gray JE. 1858. Description of *Riama*, a new genus of lizards, forming a distinct family. *Proceedings of the Zoological Society of London* **1858:** 444–446.

Harris DM. 1994. Review of the teiid lizard genus *Ptychoglossus*. *Herpetological Monographs* **8:** 226–275.

Hoogmoed MS. 1973. *Notes on the herpetofauna of Surinam IV: the lizards and amphisbaenians of Surinam*. The Hague: Dr W. Junk.

Hoyos JM. 1998. A reappraisal of the phylogeny of lizards of the family Gymnophthalmidae (Sauria, Scincomorpha). *Revista Española de Herpetología* **12:** 27–43.

Kizirian DA. 1995. A new species of *Proctoporus* (Squamata: Gymnophthalmidae) from the Andean Cordillera Oriental of northeastern Ecuador. *Journal of Herpetology* **29:** 66–72.

Kizirian DA. 1996. A review of Ecuadorian *Proctoporus* (Squamata: Gymnophthalmidae) with descriptions of nine new species. *Herpetological Monographs* **10:** 85–155.

Kizirian DA, Coloma LA. 1991. A new species of *Proctoporus* (Squamata: Gymnophthalmidae) from Ecuador. *Herpetologica* **47:** 420–429.

Köhler G, Lehr E. 2004. Comments on *Euspondylus* and *Proctoporus* (Squamata: Gymnophthalmidae) from Peru with the description of three new species and a key to the Peruvian species. *Herpetologica* **60:** 501–518.

Leviton AE, Gibbs RH, Heal E, Dawson CE. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* **1985:** 802–832.

Linnaeus C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Stockholm.

Montanucci RR. 1973. Systematics and evolution of the Andean lizard genus *Pholidobolus* (Sauria: Teiidae). *Miscellaneous Publications of the Museum of Natural History University of Kansas* **59:** 1–52.

Oftedal OT. 1974. A revision of the genus *Anadia* (Sauria, Teiidae). *Arquivos de Zoología* **25:** 203–265.

O'Shaughnessy AWE. 1879. Descriptions of new species of lizards in the collection of the British Museum. *Annals and Magazine of Natural History, Series* **5** (4):295–303.

Pellegrino KCM, Rodrigues MT, Yonenaga-Yassuda Y, Sites JW. 2001. A molecular perspective on the evolution of microteiids lizards (Squamata, Gymnophthalmidae), and a new classification for the family. *Biological Journal of the Linnean Society* **74:** 315–338.

Peters W. 1862. Über *Cercosaura* und die mit dieser Gattung verwandten Eidechsen aus Südamerica. *Abhandlungen der Akademie der Wissenschaften Berlin* **1862:** 165–225.

Peters JA, Donosos-Barros R. 1970. Catalogue of the Neotropical Squamata, Part II, lizards and amphisbaenians. *Bulletin of the U.S. National Museum* **297:** 1–293.

Presch W. 1980. Evolutionary history of the South American microteiid lizards (Teiidae: Gymnophthalminae). *Copeia* **1980:** 36–56.

Simpson BB. 1979. Quaternary biogeography of the high montane regions of South America. In: Duellman WE, ed. *The South American herpetofauna: its origin, evolution, and dispersal*. Lawrence: Monographs Museum Natural History University Kansas, no. 7, 157–188.

Tschudi JJ. 1845. Reptilium conspectus quae in Republica Peruana reperiunter et pleraque observata vel collecta sunt in itinere a Dr. J. J. de Tschudi. *Archiv for Naturgeschichte* **11:** 150–170.

Uzzell TM. 1958. Teiid lizards related to *Proctoporus luctuosus*, with the description of a new species from Venezuela. *Occasional Papers of the Museum of Zoology, University of Michigan* **597:** 1–15.

Uzzell TM. 1966. Teiid lizards of the genus *Neusticurus* (Reptilia, Sauria). *Bulletin of the American Museum of Natural History* **132:** 277–328.

Uzzell T. 1970. Teiid lizards of the genus *Proctoporus* from Bolivia and Peru. *Postilla* **142:** 1–39.

Uzzell TM. 1973. A revision of lizards of the genus *Prionodactylus*, with a new genus for *P. leucostictus* and notes on the genus *Euspondylus* (Sauria, Teiidae). *Postilla* **159:** 1–67.

Van Devender RW. 1969. Resurrection of *Neusticurus racenisi* (Sauria, Teiidae). *Journal of Herpetology* **3:** 105–107.

Vanzolini PE. 1995. *Neusticurus ocellatus* Sinitsin, 1930: a valid species of teiid lizard from Bolivia. *American Museum Novitates* **3123:** 1–7.

Vitt LJ, Zani PA, Avila-Pires TCS, Esposito MC. 1998. Geographical ecology of the gymnophthalmid lizard *Neusticurus ecpleopus* in the Amazonian rain forest. *Canadian Journal of Zoology* **76:** 1671–1680.

Wiens JJ, Servedio MR. 2000. Species delimitation in systematics: inferring diagnostic differences between species. *Proceedings of the Royal Society of London B* **267:** 631–636.

APPENDIX

SPECIMENS EXAMINED

Neusticurus bicarinatus: BRAZIL: *Amazonas*: (KU 130243, 130245–130247); *Pará*: (KU 140139).

Neusticurus medemi: COLOMBIA: *Vaupés*: (TCWC 58666–58669 [paratypes]).

Neusticurus racenisi: VENEZUELA: *no state given*: (MCZ R-62208); *Amazonas*: (MCZ R-62206).

Neusticurus rudis: VENEZUELA: *Bolívar*: (KU 167555–167556; TCWC 60147).

Neusticurus tatei: VENEZUELA: *Amazonas*: (MCZ R-101713).

Petracola ventrimaculatus: PERU: *no data*: (UTA R-43996); *Cajamarca*: (KU 181943, 181945–181947, 181949, 181951–181155, 181957–181958, 181960, 181962–181963; *Piura*: (KU 219836–219838).
Potamites apodemus: COSTA RICA: *San José*: (KU 67377–67379, 104086–104087).
Potamites cochranae: ECUADOR: *Morona-Santiago*: (USNM 196115); *Napo*: (USNM 196117, 196120, 284339–284341, 286450); *Pastaza*: (USNM 196112–196114, 196116, 196118–196119, 524132, 535991).
Potamites ecpleopus: ECUADOR: *Napo*: (KU 122193, 126810); *Pastaza*: (KU 121198–121204, 133507).
Potamites juruazensis: PERU: *Cusco*: (USNM 538446–538447).
Potamites ocellatus: BOLIVIA: *Beni*: (AMNH 22512 [holotype]).
Potamites strangulatus: PERU: *Huánuco*: (KU 212684); *San Martin*: (KU 212672, 212675–212678, 212680–212683).
Proctoporus bolivianus: BOLIVIA: *La Paz*: (UTA R-39113); PERU: *Cusco*: (GZ 0027, 0043; KU 13958, 13963, 13965, 163801, 163804, 163810–163811, 163814, 163820, 163827, 163830–163831, 163834, 163836, 163839–164740, 163842, 163846; MHNC AC136–AC141, WAA5024; USNM 49549 [paratype of *P. lacertus*], 49551 [holotype of *P. lacertus*], 60699–60700, 60719, 60726–60727; UTA R-51481–51487, 51501–51511).
Proctoporus guentheri: BOLIVIA: *La Paz*: (UTA R-39114); PERU: *Cusco*: (KU 135157–135160, 139307, 139309, 163939; MHNC WAA5056; UTA R-51512–51518).
Proctoporus pachyurus: PERU: *Junín*: (KU 135095–135097, 135099, 181917–181927, 181929–181931, 181938–181939).
Proctoporus sucullucu: PERU: *Cusco*: (MHNC WAA5006; UTA R-51478, 51496 [holotype], 51497–51500 [paratypes]).
Proctoporus unsaacae: PERU: *Cusco*: (GZ Valdinos3; MHNC AC132, UTA R-51475–51477, 51479–51480, 51488 [holotype], 51489–51495 [paratypes]).
Riama achlyens: VENEZUELA: *Aragua:* (AMNH 137260, 137267–137269, 137271–137282, 137297).
Riama anatoloros: ECUADOR: *Morona-Santiago*: (USNM 22946–229747); *Napo*: (USNM 229711–229712, 229714–229715, 229719–229721, 229723–229724 229726–229728, 229740–22945); *Napo-Pastaza*: (AMNH 38821–38822).
Riama balneator: ECUADOR: *Tungurahua*: [MHNG 2360.45 (paratype)].
Riama cashcaensis: ECUADOR: *Bolívar*: (KU 135012–135014 [paratypes], 135016–135017 [paratypes], 135019–135023 [paratypes], 141139–141140 [paratypes], 142796 [paratype], 217203); *Chimborazo*: (KU 217205, 217206).
Riama colomaromani: ECUADOR: *Carchi*: (KU 217209–217210); *Pichincha*: (KU 221737–221738 [paratypes]).
Riama columbiana: COLOMBIA: *Valle*: (KU 169946–169948).
Riama hyposticta: ECUADOR: *Cotopaxi*: KU 121153, 135100–135102, 135106, 135108, 179455–179456, 179459–179461, 179464–179465, 196386, 196388–196389).
Riama inanis: VENEZUELA: *Portuguesa*: (MCNG 825–826 [paratypes], MCNG 827 [holotype], MCNG 828 [paratype]).
Riama labionis: ECUADOR: *Cotopaxi*: (MHNG 2240.16, 2361.21–2361.24 [paratypes], 2437.35–2437.36); *Pichincha*: (MHNG 2240.14–220.15 [paratypes]).
Riama luctuosa: VENEZUELA: (AMNH 137270, UMMZ 117404–117405, 122361, USNM 196336, 259170).
Riama meleagris: ECUADOR: *no province given*: (FMNH 28037–28042, 28049 [six specimens]; USNM 196264–196265).
Riama oculata: ECUADOR: *Cotopaxi*: (MHNG 2361.48–2361.53, 2361.64–2361.65; UMMZ 188630); *Pichincha*: (USNM 229640, 229642).
Riama orcesi: ECUADOR: *Napo*: (KU 142908–142909 [paratypes], 142911 [paratype], 142922–142923 [paratypes], 142925 [paratype], 221771–221774).
Riama petrorum: ECUADOR: *Morona-Santiago*: (USNM 196268); (USNM 196266 [paratopotype]).
Riama raneyi: ECUADOR: *Carchi*: (KU 179487–179488); *Napo*: (KU 142903–142904 [paratypes], 142906–142907 [paratypes], 179489, 196393; UMMZ 84376 [three specimens]).
Riama shrevei: TRINDAD AND TOBAGO: *Trinidad*: (MCZ 34273, 62506–62507, 100466–100471, 160065–160067).
Riama simotera: COLOMBIA: *Nariño*: (KU 169943–169945).
Riama stigmatoral: ECUADOR: *no province given*: (AMNH R–32778, 38820); *Azuay*: (USNM 229644 [paratype]); *Morona-Santiago*: (USNM 229643 [paratype], 229645 [paratype], 229647–229648 [paratopotypes], 229649–229650).
Riama striata: COLOMBIA: *Boyacá*: (KU 169930–169939); *Cundinamarca*: (KU 133519–133523); *Tolima*: (KU 169940–169942).
Riama unicolor: ECUADOR: *Imbabura*: (KU 142894, 142896–142897, 179467, 179469, 179475); *Pichincha*: (KU 139310–139311, 154669–154670).
Riama vespertina: ECUADOR: *Loja*: (AMNH 22130 [holotype]).
Riama vieta: ECUADOR: *Cotopaxi*: (MHNG 2360.60–2360.62 [paratypes], 2361.61–2361.63 [paratypes], 2361.66–2361.68; *Guayas*: (USNM 142601).