



**Revisão taxonômica do complexo *Gonatodes concinnatus* (Reptilia: Sphaerodactylidae)**

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**MUSEU PARAENSE EMÍLIO GOELDI  
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PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA  
CURSO DE MESTRADO EM ZOOLOGIA**

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**MARCELO JOSÉ STURARO**

Dissertação apresentada ao Programa de Pós-graduação em Zoologia, Curso de Mestrado, do Museu Paraense Emílio Goeldi e Universidade Federal do Pará como requisito parcial para obtenção do grau de mestre em Zoologia.

**Orientadora:** Profa. Dra. Teresa Cristina Sauer de Ávila Pires

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Belém, 06 de abril de 2009

“As criaturas que habitam esta terra em que vivemos, sejam elas seres humanos ou animais, estão aqui para contribuir, cada uma com sua maneira peculiar, para a beleza e prosperidade do mundo.”

**Dalai Lama**

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## Resumo

O complexo *Gonatodes concinnatus*, conforme estabelecido aqui, consiste nas espécies caracterizadas por uma mancha suprahumeral branca com margens pretas; vermiculações no dorso; e escamas alargadas sob a cauda, apresentando a seqüência 1'1'1" e, em alguns casos, 1'1'2" (na porção anterior). Duas espécies são atualmente reconhecidas neste grupo amazônico, *G. concinnatus* e *G. tapajonicus*. Novos materiais encontrados no leste da Amazônia (nos estados do Pará e Amapá, Brasil) fizeram necessária a revisão dessas espécies. Analisamos diversas populações dentro deste complexo, provenientes do Peru, Equador, Colômbia e Brasil (mas não da Venezuela), incluindo os novos registros. Os espécimes foram separados em grupos definidos com base no padrão de coloração. Análises discriminantes, utilizando o método por passos (*stepwise*), foram realizadas para comparar a morfologia externa (representada por medições e contagens de escama, separadamente) nestes grupos. Os resultados apóiam o reconhecimento de quatro táxons, correspondendo a *G. concinnatus*, da Amazônia Ocidental, no nordeste do Equador e do Peru; *G. tapajonicus*, da bacia do Rio Tapajós, no Pará, Brasil; e duas novas espécies, uma do leste da Amazônia, nos estados do Pará e Amapá, Brasil, e outra da região cis-andina central da Colômbia. As diagnoses e descrições de todas as espécies são apresentadas.

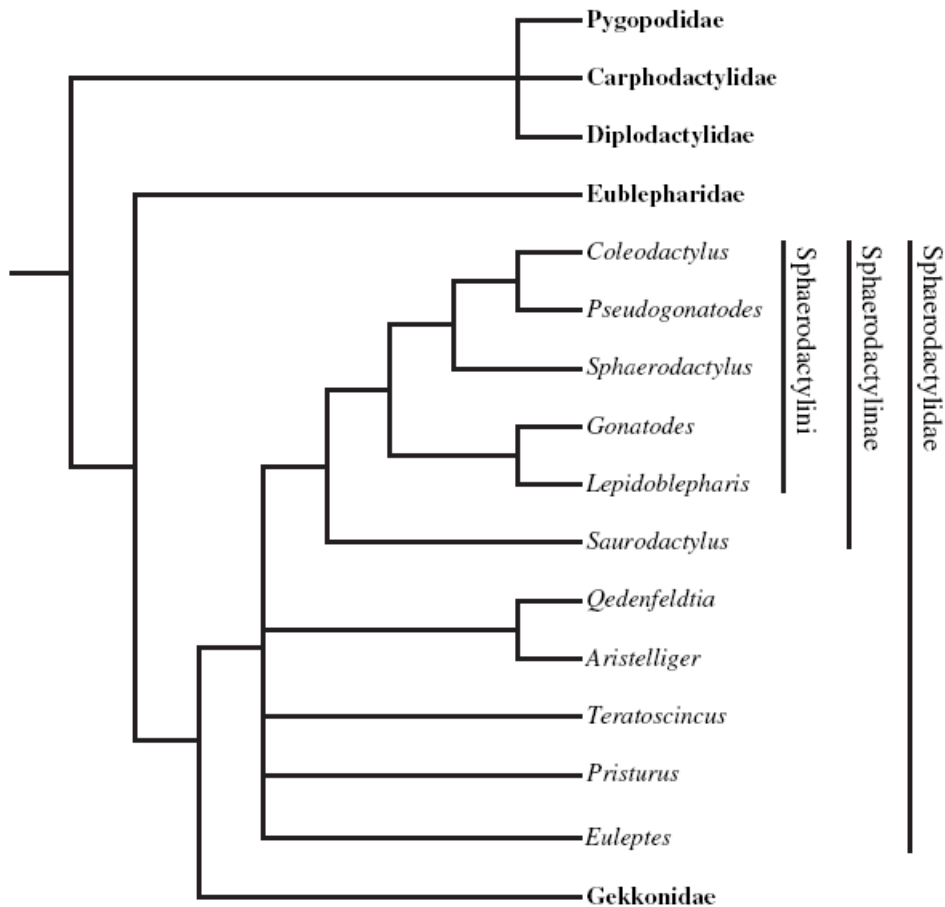
## Abstract

The *Gonatodes concinnatus* complex, as established here, consists of *Gonatodes* species characterized by a white suprahumeral spot with black margins; vermiculations on back; and transversely enlarged scales under the tail, showing the sequence 1'1'1", and in some cases 1'1'2" (on the anterior portion). Two species are presently recognized in this Amazonian group, *G. concinnatus* and *G. tapajonicus*. New material found in eastern Amazonia (states of Pará and Amapá, Brazil) made it necessary to review species of this complex. We analyzed several populations within this complex, from Peru, Ecuador, Colômbia, and Brazil (but not from Venezuela), including those new records. Specimens were separated in groups defined on basis of color pattern. Stepwise discriminant function analyses were then performed to compare the external morphology (represented by measurements and scale counts, separately) in these groups. Results support recognition of four taxa, corresponding to *G. concinnatus*, from western Amazonia, in Ecuador and northeastern Peru; *G. tapajonicus*, from the Tapajós river basin, in Pará, Brazil; and two new species, one from eastern Amazonia, in the states of Pará and Amapá, Brazil, and another from cis-andean central Colombia. Diagnoses and descriptions of all species are presented.

## Introdução

Estudos envolvendo sistemática e taxonomia representam a base do conhecimento sobre biodiversidade, auxiliando na compreensão das espécies existentes, dos padrões de distribuição geográfica e da evolução dos distintos grupos de organismos conhecidos. Deste modo, tais estudos permitem direcionar políticas apropriadas para lidar com a conservação da biodiversidade, tarefa cada vez mais importante, principalmente em países megadiversos como o Brasil, em virtude dos ecossistemas naturais estarem sob forte e crescente impacto de ações antrópicas (Margules & Pressey 2000).

Os lagartos apresentam cerca de 4750 espécies conhecidas, distribuídas em 19 famílias (Zug et al. 2001; Pianka & Vitt 2003; Uetz 2009). A família Sphaerodactylidae foi proposta por Underwood (1954), com base na estrutura das pálpebras e da retina, incluindo cinco gêneros neotropicais neste grupo (*Coleodactylus*, *Gonatodes*, *Lepidoblepharis*, *Pseudogonatodes* e *Sphaerodactylus*). Kluge (1967, 1976) reclassificou o táxon como uma subfamília de Gekkonidae e grupo-irmão de Gekkoninae. Kluge (1987) considerou-os como uma tribo, Sphaerodactylini, incluindo nela um gênero com distribuição africana e asiática (*Pristurus*). Han et al. (2004), com base em dados moleculares, novamente elevaram o taxon à categoria de subfamília e consideraram o gênero *Pristurus* membro de Gekkoninae. Gamble et al. (2008a) (Figura 1), igualmente através de dados moleculares, corroboraram a monofilia dos cinco gêneros neotropicais, porém considerando-os grupo-irmão de *Saurodactylus*, do norte da África, propuseram o reconhecimento da família Sphaerodactylidae contendo, além desses gêneros, *Euleptes*, *Aristelliger*, *Pristurus*, *Quedenfeldtia* e *Teratoscincus*.



**Figura 1.** Resumo das relações filogenéticas e do nível mais elevado da taxonomia de Sphaerodactylidae e gêneros relacionados (Gamble et al. 2008a, figura 5).

O clado formado pelos cinco gêneros neotropicais (*Coleodactylus*, *Pseudogonatodes*, *Sphaerodactylus*, *Gonatodes* e *Lepidoblepharis*) caracteriza-se pela presença de pupila usualmente redonda (oval em *Gonatodes antillensis*); dígitos ligeiramente dilatados na base, com apenas uma linha de lamelas subdigitais alargadas; ausência de poros pré-cloacais e femorais; *escutcheon* presente ou ausente; fenda e ossos pós-cloacais ausentes e ausência de voz (Kluge 1967; Vanzolini 1968; Hoogmoed 1973, Avila-Pires 1995). As relações dentro desse clado foram estudadas por Kluge (1995), onde os *Gonatodes* ficaram na base deste grupo, formando a seguinte filogenia: (*Gonatodes* (*Lepidoblepharis* (*Sphaerodactylus* (*Coleodactylus*,

*Pseudogonatodes*))). As garras expostas, não protegidas por um estojo ungueal, como ocorre em *Gonatodes*, foram consideradas a condição plesiomórfica nesse clado. Um recente estudo com dados moleculares chegou a uma topologia diferente, com uma dicotomia basal tendo de um lado *Sphaerodactylus* (*Coleodactylus*, *Pseudogonatodes*) e do outro *Gonatodes*, *Lepidoblepharis* (Gamble et al. 2008a) (Figura 1). As diferentes topologias entre esses estudos mostram a necessidade de novos trabalhos filogenéticos envolvendo tanto dados moleculares como morfológicos, para se obter filogenias cada vez mais robustas, tentando elucidar as relações dentro do grupo e os possíveis processos evolutivos que atuaram na sua divergência.

Os *Gonatodes* são caracterizados por apresentarem escamas dorsais da cabeça reduzidas; pálpebras inferiores ausentes ou rudimentares; dorsais granulares e justapostas; ventrais maiores que as dorsais, lisas, imbricadas e arredondadas; poros femorais ausentes; garras não retráteis; *escutcheon* presente na parte posterior do ventre e nas coxas; dentes cônicos e subiguais; língua carnosa, ligeiramente fendida na extremidade anterior. A maioria das espécies é diurna, apresentando pupilas redondas, exceto *G. antillensis*, que apresenta pupila oval e hábito noturno (Peters & Donoso-Barros 1970; Hoogmoed 1973; Rivero-Blanco 1979; Avila-Pires 1995; Kluge 1995).

O gênero *Gonatodes* contém 22 espécies distribuídas pela porção central e norte da América do Sul, América Central (até o norte do estado de Chiapas, México, no litoral do Pacífico, e até o norte da Nicarágua, ao longo da costa do Caribe) e Antilhas (Donoso-Barros 1968; Peter & Donoso-Barros 1970; Duellman 1978; Rivero-Blanco 1979; Rodrigues 1980; Nascimento et al. 1987; Avila-Pires 1995; Espinoza & Icochea 1995; Esqueda 2004; Powell & Henderson 2005; Cole & Kok 2006; Barrio-Amoros & Brewer-Carías 2008; Rivas & Schargel 2008). *G. albogularis* foi introduzida em tempos recentes na Flórida, EUA (Schwartz & Henderson 1991). A taxonomia do gênero *Gonatodes* sempre foi problemática, apresentando

espécies descritas originalmente em outros gêneros, além de diversos nomes para a mesma espécie (Tabela I).

A espécie *G. humeralis* (Guichenot, 1855) apresenta a distribuição mais ampla do gênero, sendo comum em toda a Amazônia – no Brasil, Guiana Francesa, Suriname, Guyana, Venezuela, Colômbia, Equador e Peru. No Brasil ocorre em todos os estados amazônicos – Amapá, Roraima, Pará, Amazonas, Rondônia, Acre, oeste do Maranhão –, e estende-se ainda ao norte do Mato Grosso. Na Venezuela ocorre na região Guianense (inclusive na costa nordeste, até Sucre) e nas ilhas Trinidad e Tobago (Donoso-Barros 1968; Vanzolini 1968; Hoogmoed 1973; Rivero-Blanco 1979; Avila-Pires 1995; Murphy 1997; Gorzula & Señaris 1998).

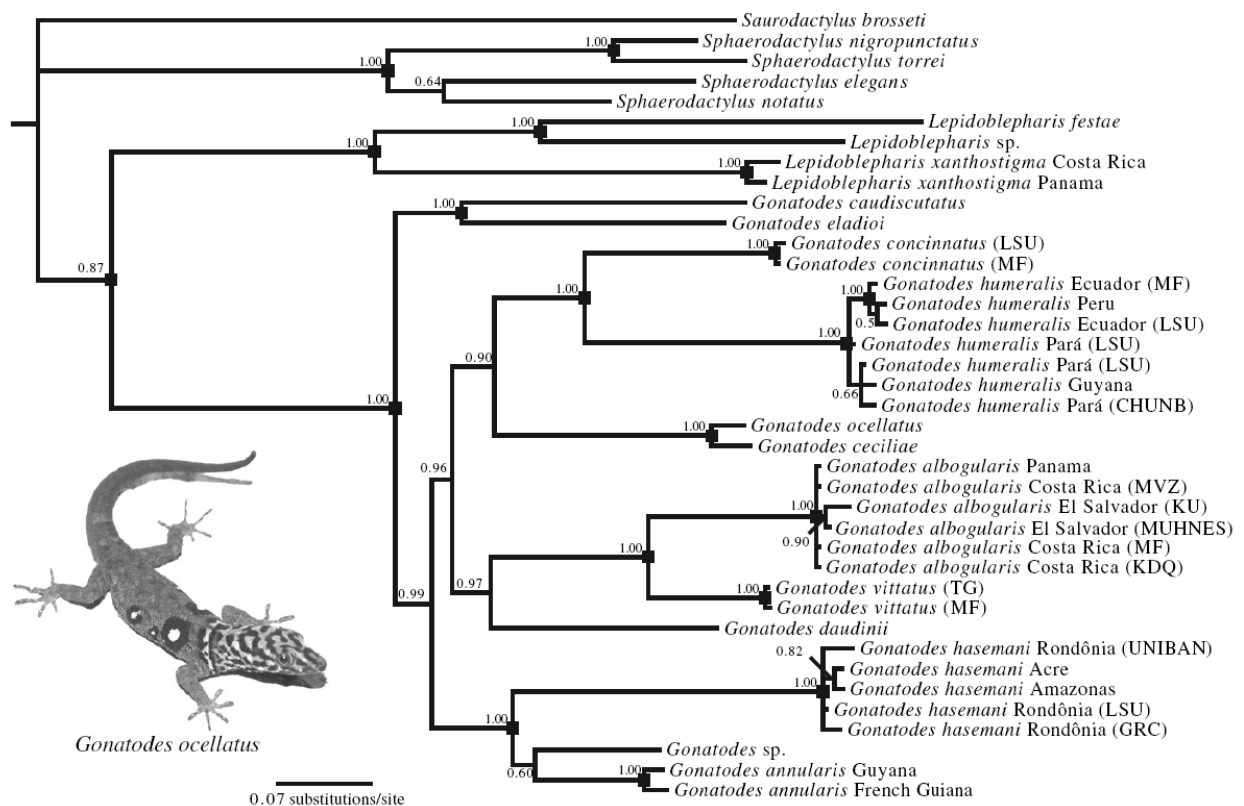
Um complexo de *Gonatodes* (Figura 2), neste trabalho apontado como complexo *G. concinnatus*, apresenta uma mancha suprahumeral branca margeada de negro, vermiculações no dorso, e escamas alargadas sob a cauda, apresentando a seqüência 1'1'1" (em alguns casos, 1'1'2" na porção anterior), sendo composto por duas espécies, *G. concinnatus* e *G. tapajonicus*. *Gonatodes concinnatus* (O'Shaughnessy, 1881) ocorre no nordeste do Peru, Equador, Colombia, e noroeste da Venezuela (Rivero-Blanco 1979). *G. tapajonicus* Rodrigues, 1980, é conhecido somente da localidade-tipo, Cachoeira do Limão, Rio Tapajós, Pará (Ávila-Pires, 1995).





**Figura 2.** Exemplos de complexo *Gonatodes concinnatus*. (A) *G. concinnatus*, Ecuador (Foto: <http://forums.phelsumaweb.com/viewtopic.php>); (B) Holótipo de *G. tapajonicus*, Cachoeira do Limão, margem direita do rio Tapajós, estado do Pará, Brasil (Foto: M.T. Rodrigues; MZUSP 53676); (C) *Gonatodes* sp., município de Almeirim, distrito de Monte Dourado, norte do Pará, Brasil (Foto: M.A. Ribeiro-Júnior; MPEG 23822); (D) *Gonatodes* sp., município de Portel, entre os rios Aruanã e Pacajá, Pará, Brasil (Foto: J.O. Gomes; MPEG 24649). (E) *Gonatodes* sp., margem direita do rio Xingu, município de Anapu, Pará, Brasil (Foto: P.L. Peloso; MPEG 25598). (F) *Gonatodes* sp., margem direita do rio Xingu, município de Anapu, Pará, Brasil (MPEG-25597).

Gamble et al. (2008b), estudando a filogenia molecular de *Gonatodes*, com dados de 11 espécies dentre as 20 conhecidas, aponta *Gonatodes humeralis* como grupo-irmão de *G. concinnatus*, e estes como grupo-irmão do clado formado por *G. ocellatus* e *G. ceciliae* (Figura 3). Para as análises de Gamble e colaboradores foram utilizados dados de dois exemplares de *G. concinnatus*, ambos provenientes do Equador. *G. tapajonicus* não foi incluído no estudo. Segundo os autores, a separação entre *G. humeralis* e *G. concinnatus* teria ocorrido no Mioceno inferior, há  $21 \pm 4,3$  milhões de anos. Dentro de *G. humeralis* foram encontrados dois grupos, um a leste e outro a oeste da Amazônia, que teriam se separado no Plioceno superior, por volta de  $1,9 \pm 0,8$  milhões de anos. Se as espécies aqui incluídas em *G. grupo concinnatus* forem realmente mais próximas filogeneticamente entre si, sua origem e evolução teriam ocorrido em algum momento a partir do Mioceno, ou seja, após a separação de *G. humeralis* (seu grupo-irmão). É também interessante observar que a distribuição total de *G. grupo concinnatus*, apesar de existir uma lacuna no estado do Amazonas (Brasil), se aproxima daquela de *G. humeralis*, podendo tanto representar uma evolução temporalmente paralela entre esses dois grupos (o que implicaria em uma origem plio-pleistocênica dessas espécies), como apenas uma coincidência geográfica resultante de eventos cladísticos independentes (onde as espécies do grupo *concinnatus* teriam se originado durante o Mioceno-Plioceno).



**Figura 3.** Filogenia Bayesiana Particionada dos geconideos *Gonatodes* e grupos externos. Os números acima dos nós indicam a probabilidade posterior Bayesiana e os quadrados pretos nos indicam o suporte *parcimony bootstrap* maior que 70 (Gamble et al. 2008b, figura 1)

### Histórico taxonômico do complexo *Gonatodes concinnatus*

O'Shaughnessy (1881) descreveu *Goniodactylus concinnatus* com base em três espécimes procedentes de Canelos, Ecuador (BMNH 80.12.8.29-31). No mesmo trabalho O'Shaughnessy descreveu *Goniodactylus buckleyi* (BMNH 80.12.8.32-34), com base em um exemplar procedente da Pallatanga e dois de Canelos, Ecuador.

Boulenger (1885), no seu catálogo de lagartos, analisando os tipos de *Goniodactylus concinnatus* e *G. buckleyi*, observou que se tratavam da mesma espécie, sendo as diferenças apresentadas por O'Shaughnessy (1881) apenas dimorfismo sexual, onde os três exemplares de

*G. concinnatus* eram machos e os três de *G. buckleyi* eram fêmeas. Boulenger (1885), além disso, transferiu a espécie para o gênero *Gonatodes*, sob o nome *G. concinnatus*.

Peters & Donoso-Barros (1970), no catálogo de lagartos e anfisbenas da região Neotropical, citam como distribuição de *G. concinnatus* as terras baixas da Amazônia da Colômbia e Equador; o norte da Venezuela e o estado do Amazonas, Brasil.

Duellman (1978), em seu estudo sobre a herpetofauna de Santa Cecília, Equador, registra a espécie em Lago Agrio e Santa Cecilia, e apresenta dados sobre sua ecologia.

Rivero-Blanco (1979) reconhece duas subespécies, *G. concinnatus concinnatus* (O'Shaughnessy, 1881), do Ecuador, Peru e Colombia, e *G. c. ligiae* Donoso-Barros, 1967, do Bosque de La Carabela, próximo a Barinitas, Barinas, Venezuela, apontando a forma das manchas supraumerais (“a scapular white spot or ocellus, bordered by black”) como a principal diferença entre elas (em forma de barra vertical, quase se tocando, em *G. c. concinnatus*, e em forma de ocelo em *G. c. ligiae*). Nesse mesmo trabalho, Rivero-Blanco (1979) menciona que os espécimes de *G. concinnatus concinnatus* de Villavincencio, Meta, Colombia, apresentam um padrão de coloração do dorso intermediário entre o Ecuador e Peru (dorso mais manchado) e Venezuela (sem manchas).

*Gonatodes tapajonicus* foi descrita por Rodrigues (1980) com base em nove exemplares, coletados pelo próprio autor na Cachoeira do Limão (04°41'S, 56°21'W), Rio Tapajós, Pará, estando o holótipo (MZUSP 53676) e parátipos depositados no Museu de Zoologia da Universidade de São Paulo. Rodrigues (1980) aponta que tanto *G. tapajonicus* como *G. concinnatus*, apresentam grânulos na região gular achatados e grandes, quando comparados com *G. hasemani* e *G. annularis*. Em relação a *G. concinnatus*, o autor cita que a espécie difere no padrão de coloração (não apontando as diferenças) e na forma da sinfisa, embora saliente a necessidade de séries maiores para uma comparação mais detalhada da folidose dessas duas

espécies. Avila-Pires (1995), em seu estudo sobre os lagartos da Amazônia Brasileira, não registra qualquer material novo da espécie, que parece continuar sendo apenas conhecida da série-tipo.

Recentemente foram coletados no leste da Amazônia (nos estados do Pará e Amapá), espécimes de *Gonatodes* que compartilham com *G. concinnatus* e *G. tapajonicus* diversas características, entre as quais a presença, nos machos, de uma mancha branca suprahumeral em forma de ocelo ou barra, marginada de negro (Figura 2). Para que essas novas ocorrências do grupo pudessem ser identificadas, fez-se necessária uma revisão conjunta desses taxons, aqui tratados como complexo *Gonatodes concinnatus*.

O presente estudo teve como objetivo analisar a variação da morfologia externa, utilizando contagens de escamas e morfometria, separadamente, através de análises discriminantes. Os grupos comparados através da análise discriminante foram estabelecidos através do padrão de coloração.

Foram analisadas populações provenientes do Peru, Equador, Colômbia e Brasil, totalizando 70 espécies, incluindo os novos registros. Tendo em vista a dificuldade em se obter material, exemplares da Venezuela, e conseqüentemente o taxon *G. c. ligiae*, não foram incluídos na análise. Foram encontrados quatro padrões de coloração dentre os espécimes analisados, os quais foram apoiados pelas análises discriminantes, indicando a existência de quatro táxons distintos: *Gonatodes concinnatus*, do oeste da Amazônia (Equador e nordeste do Peru); *Gonatodes tapajonicus*, da Amazônia Oriental, na porção central do estado do Pará; e duas espécies novas, sendo uma do leste da Amazônia, nos estados do Amapá e Pará, Brasil, e outra da porção cis-andina central da Colômbia. Cada uma dessas espécies é diagnosticada e descrita.

Os resultados dessa dissertação de mestrado, que podem ser considerados como uma contribuição à sistemática do gênero *Gonatodes*, em especial do complexo *G. concinnatus*, são

apresentados na forma de artigo a ser submetido ao periódico *Zootaxa*. Contudo, buscando evitar qualquer dubiedade quanto à validade do trabalho aqui apresentado para fins de nomenclatura zoológica, não apresento nomes para os novos taxons propostos.

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**Tabela I.** Resumo dos nomes e combinações que foram utilizados em espécies do gênero *Gonatodes*. Nomes originais, autor(es) e data (ou referências), e nome atual da espécie são fornecidos.

Nome original	Autor e data / Referências	Nome atual
<i>Gymnodactylus albogularis</i>	Duméril & Bibron, 1836	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gonatodes albigularis</i> (ortografia errada)	Fitzinger, 1843	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Goniodactylus albogularis</i>	Gray, 1845	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Stenodactylus fuscus</i>	Hallowell, 1855	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gymnodactylus fuscus</i>	Duméril, 1856	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gymnodactylus varius</i>	Duméril, 1856	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Goniodactylus braconnieri</i>	O'Shaughnessy, 1875	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gonatodes albogularis</i> var. <i>fuscus</i>	Boulenger, 1885	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gonatodes albogularis</i>	Boulenger, 1885	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gonatodes varius</i>	Vanzolini, 1955	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gonatodes albogularis fuscus</i>	Vanzolini & Williams, 1962	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gonatodes albogularis albogularis</i>	Vanzolini & Williams, 1962	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gonatodes bodinii</i>	Rivero-Blanco, 1964	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gymnodactylus notatus</i>	Reinhardt & Lütken, 1863	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gonatodes fuscus</i>	Barbour & Ramsden, 1919	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gymnodactylus maculatus</i>	Steindachner, 1867	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)

<i>Goniodactylus braconnieri</i>	O'Shaughnessy 1875	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gonatodes notatus</i>	Barbour, 1937	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gonatodes albogularis notatus</i>	Vanzolini & Williams, 1962	<i>Gonatodes albogularis</i> (Duméril & Bibron, 1836)
<i>Gonatodes alexandermendesi</i>	Cole & Kok, 2006	<i>Gonatodes alexandermendesi</i> Cole & Kok, 2006
<i>Gonatodes annularis</i>	Boulenger, 1887	<i>Gonatodes annularis</i> Boulenger, 1887
<i>Gonatodes Boonii</i> (posteriormente corrigido para <i>booni</i> )	Lidth de Jeude, 1904	<i>Gonatodes annularis</i> Boulenger, 1888
<i>Gonatodes beebei</i>	Noble, 1923	<i>Gonatodes annularis</i> Boulenger, 1889
<i>Gymnodactylus antillensis</i>	Lidth de Jeude, 1887	<i>Gonatodes antillensis</i> (Lidth de Jeude, 1887)
<i>Gonatodes vittatus roquensis</i>	Roze, 1956	<i>Gonatodes antillensis</i> (Lidth de Jeude, 1887)
<i>Gonatodes antillensis</i>	Rivero-Blanco, 1964	<i>Gonatodes antillensis</i> (Lidth de Jeude, 1887)
<i>Gonatodes atricucullaris</i>	Noble, 1921	<i>Gonatodes atricucullaris</i> Noble, 1921
<i>Gymnodactylus caudiscutatus</i>	Günther, 1859	<i>Gonatodes caudiscutatus</i> (Günther, 1859)
<i>Gonatodes caudiscutatus</i>	Boulenger, 1885	<i>Gonatodes caudiscutatus</i> (Günther, 1859)
<i>Gonatodes collaris</i>	Garman, 1892	<i>Gonatodes caudiscutatus</i> (Günther, 1859)
<i>Gonatodes ceciliae</i>	Donoso-Barros, 1966	<i>Gonatodes ceciliae</i> Donoso-Barros, 1966
<i>Goniodactylus concinnatus</i>	O'Shaughnessy, 1881	<i>Gonatodes concinnatus</i> (O'Shaughnessy, 1881)
<i>Goniodactylus buckleyi</i>	O'Shaughnessy, 1881	<i>Gonatodes concinnatus</i> (O'Shaughnessy, 1881)
<i>Gonatodes concinnatus</i>	Boulenger, 1885	<i>Gonatodes concinnatus</i> (O'Shaughnessy, 1881)
<i>Gonatodes ligiae</i>	Donoso-Barros, 1967	<i>Gonatodes concinnatus</i> (O'Shaughnessy, 1881)

<i>Gonatodes daudini</i>	Powell & Henderson, 2005	<i>Gonatodes daudini</i> Powell & Henderson, 2005
<i>Gonatodes eladioi</i>	Nascimento, Avila-Pires & Cunha, 1987	<i>Gonatodes eladioi</i> Nascimento, Avila-Pires & Cunha, 1987
<i>Gonatodes caudiscutatus</i> <i>falconensis</i>	Shreve, 1947	<i>Gonatodes falconensis</i> Shreve, 1947
<i>Gonatodes falconensis</i>	Vanzolini, 1968	<i>Gonatodes falconensis</i> Shreve, 1947
<i>Gonatodes hasemani</i>	Griffin, 1917	<i>Gonatodes hasemani</i> Griffin, 1917
<i>Gonatodes spinulosus</i>	Amaral, 1932	<i>Gonatodes hasemani</i> Griffin, 1917
<i>Gymnodactylus humeralis</i>	Guinhenot, 1855	<i>Gonatodes humeralis</i> (Guinhenot, 1855)
<i>Gonatodes ferrugineus</i>	Cope, 1863	<i>Gonatodes humeralis</i> (Guinhenot, 1855)
<i>Goniodactylus ferrugineus</i>	Cope, 1868	<i>Gonatodes humeralis</i> (Guinhenot, 1855)
<i>Gymnodactylus incertus</i>	Peters, 1871	<i>Gonatodes humeralis</i> (Guinhenot, 1855)
<i>Goniodactylus sulcatus</i>	O'Shaughnessy, 1875	<i>Gonatodes humeralis</i> (Guinhenot, 1855)
<i>Gonatodes humeralis</i>	Boulenger, 1885	<i>Gonatodes humeralis</i> (Guinhenot, 1855)
<i>Gonatodes infernalis</i>	Rivas & Schargel, 2008	<i>Gonatodes infernalis</i> Rivas & Schargel, 2008
<i>Cyrtodactylus ocellatus</i>	Gray, 1831	<i>Gonatodes ocellatus</i> (Gray, 1831)
<i>Goniodactylus ocellatus</i>	Gray, 1845	<i>Gonatodes ocellatus</i> (Gray, 1831)
<i>Gonatodes ocellatus</i>	Boulenger, 1885	<i>Gonatodes ocellatus</i> (Gray, 1831)
<i>Gonatodes petersi</i>	Donoso-Barros, 1967	<i>Gonatodes petersi</i> Donoso-Barros, 1967
<i>Gonatodes purpurogularis</i>	Esqueda, 2004	<i>Gonatodes purpurogularis</i> Esqueda, 2004

<i>Gonatodes seigliei</i>	Donoso-Barros, 1966	<i>Gonatodes seigliei</i> Donoso-Barros, 1966
<i>Gonatodes superciliaris</i>	Barrio-Amorós & Brewer-Carias, 2008	<i>Gonatodes superciliaris</i> Barrio-Amorós & Brewer-Carias, 2008
<i>Gonatodes taniae</i>	Roze, 1963	<i>Gonatodes taniae</i> Roze, 1963
<i>Gonatodes tapajonicus</i>	Rodrigues, 1980	<i>Gonatodes tapajonicus</i> Rodrigues, 1980
<i>Gymnodactylus vittatus</i>	Lichtenstein, 1856	<i>Gonatodes vittatus</i> (Lichtenstein, 1856)
<i>Gonatodes gilli</i>	Cope, 1863	<i>Gonatodes vittatus</i> (Lichtenstein, 1856)
<i>Gonatodes vittatus vittatus</i>	Roze, 1956	<i>Gonatodes vittatus</i> (Lichtenstein, 1856)

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**Taxonomic revision of the geckos of the *Gonatodes concinnatus* complex (Squamata: Sphaerodactylidae), with description of two new species**

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**Abstract**

The *Gonatodes concinnatus* complex, as established here, consists of *Gonatodes* species characterized by a white suprahumeral spot with black margins; vermiculations on back; and transversely enlarged scales under the tail, showing the sequence 1'1'1", and in some cases 1'1'2" (on the anterior portion). Two species are presently recognized in this Amazonian complex: *G. concinnatus* and *G. tapajonicus*. New material collected in eastern Amazonia (states of Pará and Amapá, Brazil) made it necessary to review these species. We analyzed several populations within this complex, from Peru, Ecuador, Colômbia, and Brazil (but not Venezuela), including those new records. Specimens were separated in groups defined on basis of color pattern. Stepwise discriminant function analyses were then performed to compare the external

morphology (represented by measurements and scale counts, separately) in these groups. Results support recognition of four taxa, corresponding to *G. concinnatus*, from western Amazonia, in Ecuador and northeastern Peru; *G. tapajonicus*, from the Tapajós river basin, in Pará, Brazil; and two new species, one from eastern Amazonia, in the states of Pará (north and south of the Amazon river) and Amapá, Brazil, and another from central Colombia, east of the Andes. Diagnoses and descriptions of all species are presented.

**Key words:** lizard, South America, Amazonian rainforest, taxonomy

### **Resumo**

O complexo *Gonatodes concinnatus*, conforme estabelecido aqui, consiste nas espécies caracterizadas por uma mancha suprahumeral branca com margens pretas; vermiculações no dorso; e escamas alargadas sob a cauda, apresentando a seqüência 1'1'1", e em alguns casos 1'1'2" (na porção anterior). Duas espécies são atualmente reconhecidas neste grupo basicamente amazônico, *G. concinnatus* e *G. tapajonicus*. Novos espécimes coletados no leste da Amazônia (nos estados do Pará e Amapá, Brasil) fizeram necessária a revisão dessas espécies. Analisamos diversas populações dentro deste complexo, provenientes do Peru, Equador, Colômbia, e Brasil (mas não da Venezuela), incluindo os novos registros. Os espécimes foram separados em grupos definidos com base no padrão de coloração. Análises discriminantes, utilizando o método por passos (*stepwise*), foram realizadas para comparar a morfologia externa (representada por medições e contagens de escama, separadamente) nestes grupos. Os resultados apóiam o reconhecimento de quatro táxons, correspondendo a *G. concinnatus*, da Amazônia Ocidental, no nordeste do Equador e do Peru; *G. tapajonicus*, da bacia do Rio Tapajós, no Pará, Brasil; e duas novas espécies, uma do leste da Amazônia, nos estados do Pará (ao norte e ao sul do Rio

Amazonas) e Amapá, Brasil, e outra da Colômbia Central, a leste dos Andes. As diagnoses e descrições de todas as espécies são apresentadas.

**Palavras-chaves:** lagarto, América do Sul, Floresta Amazônica, taxonomia

## **Introduction**

The genus *Gonatodes* consists currently of 22 species distributed in Central and South America, in the Antilles and, as a recent introduction, in Florida, United States (Peters & Donoso-Barros 1970; Rivero-Blanco 1979; Avila-Pires 1995; Esqueda 2004; Krysko & Daniels 2005; Powel and Henderson 2005; Cole and Kok 2006; Barrio-Amoros & Brewer-Carias 2008, Rivas & Schargel, 2008). It is characterized by having dorsal scales granular and juxtaposed; ventral scales larger than dorsals, flat, smooth and imbricate; femoral and precloacal pores absent; *escutcheon* present in males, on posterior surface of belly and ventral aspect of thigh; and free claws (Peters & Donoso-Barros 1970; Hoogmoed 1973; Avila-Pires 1995; Kluge 1995). Sexual dimorphism is evident in color pattern, usually with colourful males and cryptic females. Male color pattern is an important character for recognizing species, since differences in scale counts between species are frequently small (Vanzolini, 1968; Rivero-Blanco, 1979).

*Gonatodes concinnatus* (O'Shaughnessy, 1881) and *Gonatodes tapajonicus* Rodrigues, 1980 have in common the presence of a white suprahumeral spot with black margins; vermiculations on back (except in *G. c. ligiae*); and transversely enlarged scales under the tail, showing the sequence 1'1'1", and sometimes 1'1'2" (under anterior portion of the tail), as defined by Avila-Pires (1995). According to Rodrigues (1980), *Gonatodes tapajonicus* differs from *G. concinnatus* by its color pattern and the form of the mental. Recent material from eastern Amazonia presented the same characteristics common to both species mentioned above, but with

differences in color pattern. In order to identify this material and considering the variation reported in *G. concinnatus*, it was necessary to undertake a revision of this group, that we are calling “*G. concinnatus* complex”.

O’Shaughnessy (1881) described *Goniodactylus concinnatus* based on three specimens from Canelos, Ecuador (BMNH 1946.9.7.10-12), and *Goniodactylus buckleyi* based on one specimen from Pallatanga (probably in error, see Rivero-Blanco, 1968) and two from Canelos, Ecuador. Boulenger (1885) examined the types of *Goniodactylus concinnatus* and *G. buckleyi* and observed that they represented the same species, respectively male and female; the species was considered under the combination *Gonatodes concinnatus*. Subsequent authors followed Boulenger (1885).

*Gonatodes ligiae* was described by Donoso-Barros (1967), who provided only an imprecise description, based on two specimens from Bosque de la Carabela (holotype) and Parque de Moromoy (paratype), Barinitas, Vezenuela. Rivero-Blanco (1968), based on specimens from the type-locality, but without examining the type material of *G. ligiae*, considered it a synonym of *G. concinnatus* and Rivero-Blanco (1979) recognized it as a subspecies of *G. concinnatus*. The shape of the suprahumeral spots (a vertical bar in *G. concinnatus concinnatus* and an ocellus in *G. concinnatus ligiae*) and the presence (*G. c. concinnatus*) or absence (*G. c. ligiae*) of white spots or vermiculations on the back and flanks were pointed out as diagnostic characters.

*Gonatodes tapajonicus* was described by Rodrigues (1980) based on nine specimens from Cachoeira do Limão (04°41’S, 56°21’W), Tapajós River, Pará, Brazil.

In this paper we evaluate the validity of the currently recognized species of the *Gonatodes concinnatus* complex, and verify the status of additional populations from eastern



Amazonia (states of Pará and Amapá, Brazil), by analyzing variation of external morphology. *Gonatodes c. ligiae* will not be considered here, since we did not examine material from Venezuela, but the status of this taxon should be verified in future studies.

## **Material and Methods**

Specimens examined are listed in Appendix I. They are deposited in the following institutions: Museu Nacional/UFRJ, Rio de Janeiro, Brazil (MNRJ); Museu Paraense Emilio Goeldi, Pará, Brazil (MPEG); Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP); Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (RMNH). We examined photos of all syntypes of *Goniodactylus buckleyi* and *Goniodactylus concinnatus*, which are deposited in The Natural History Museum (former British Museum of Natural History), London, United Kingdom (BMNH).

### *Measurements and scale counts*

Measurements were taken with an electronic caliper (to the nearest 0.1 mm), when necessary under a stereomicroscope, as follows: **SVL** (snout-vent length, from tip of snout to cloacal opening); **TL** (tail length, from cloacal opening to tip of tail); **HL** (head length, from anteriormost point of rostral to anterior margin of ear-opening); **HW** (head width, on the widest part of head); **HD** (head depth, on the highest part of head); **ED** (eye diameter; between anterior and posterior corner of the eye); **IOD** (interorbital distance; between anterosuperior margins of eyes); **IND** (internostril distance, between medial margins of nasal scales); **SSL** (supranasal scale length, between anterior and posterior corners of scale); **SSW** (supranasal scale width, between lateral corners of scale); **RSL** (rostral scale length, between anterior and posterior corners of

scale); **RSW** (rostral scale width, between lateral corners of scale); **MSL** (mental scale length, between anterior and posterior corners of scale); **MSW** (mental scale width, between lateral corners of scale); **UAL** (upper arm length, from axil to tip of elbow); **LAL** (lower arm length, from tip of elbow to wrist); **HAL** (hand length, from wrist to tip of claw of longest finger); **FL** (forelimb length, from axil to tip of claw of longest finger); **THL** (thigh length, from groin to knee); **LLL** (lower leg length, from knee to ankle); **FTL** (foot length, from ankle to tip of claw of longest toe); **HLL** (hind limb length, from groin to tip of longest toe); **DBL** (distance between fore- and hind limb, from axil to groin), **HSL** (suprahumeral spot length, measured between anterior and posterior margins); **HSW** (suprahumeral spot width, measured between lateral and medial ends).

Scale counts were taken under a stereomicroscope, as follows: **SL** (supralabials: distinctly enlarged scales along the upper jaw); **IL** (infralabials: distinctly enlarged scales along the lower jaw); **PR** (postrostral scales: scales in contact to rostral); **SP** (small postrostral scales: small scales in contact to rostral medially); **PN** (postnasal scales: scales in contact with posterior portion of nasal); **LS** (loreal scales: in a line between postnasals and anterior corner of orbit); **PM** (postmental scales: in contact to posterior portion of mental); **SAM** (scales around midbody, counted midway between fore- and hind limbs); **VLR** (ventral scales in a longitudinal row, counted along a midventral line, from anterior margin of forelimbs to anterior margin of hind limbs); **VTR** (ventral scales in a transversal row, counted midway between fore- and hind limb); **SCS** (supraciliary scales: enlarged and flattend scales on anterior portion of supraciliary flap); **SSC** (supraciliary spines: scales with conical shape on the anterior portion of supraciliary flap); **PL2F**, **PL3F**, **PL4F** (proximal lamellae under respectively second, third and fourth fingers, counted from base of finger to the sharp angle between first and second phalanges); **PL2T**,

**PL3T, PL4T** (proximal lamellae under respectively second, third and fourth toes, counted from base of toe to the sharp angle between first and second phalanges); **DL2F, DL3F, DL4F** (distal lamellae under respectively second, third and fourth fingers, counted between the sharp angle between first and second phalanges and unguis scale); **DL2T, DL3T, DL4T** (distal lamellae under respectively second, third and fourth toes, counted between the sharp angle between first and second phalanges and unguis scale); subdigital lamellae under the second (**SL2F**), third (**SL3F**) and fourth (**SL4F**) finger, and second (**SL2T**), third (**SL3T**) and fourth (**SL4T**) toe, counted between base of digit articulation and unguis scale; **LS2F, LS3F, LS4F** (lateral rows of scales on distal part of respectively second, third and fourth fingers, counted between fourth distal subdigital lamella and dorsal scale); **LS2T, LS3T, LS4T** (lateral rows of scales on distal part of respectively second, third and fourth toes, counted between the fourth subdigital lamella when counted from the claw towards the hand, and dorsal scale); **RSE** (rows of escutcheon scales under thigh, counted along a line between the anterior and the posterior aspects of the thigh).

Measurements and scale counts were taken on the right side of the body, except when this side was damaged. In this case data from the left side of the body were used.

Sex was determined by the presence of an escutcheon on posterior portion of belly and ventral surface of thighs in males, which is absent in females. Specimens with SVL under 35 mm were defined as juveniles.

### *Statistical Analysis*

We used discriminant function analysis for scales counts (Tabachnick and Fidell 2001) and size-free discriminant function analysis for measurements (Strauss 1985, Reis et al. 1990), to

test if groups defined *a priori* on basis of color pattern could be differentiated by a combination of other morphological characters. Measurements may be influenced by factors such as sexual dimorphism, developmental stage and indeterminate growth, which makes it important to use size-free analysis for such data. As proposed by Strauss (1985), size-free discriminant analysis consists of regressing each variable separately on the first principal component of a principal component analysis and then applying the discriminant function analysis to the residuals obtained from these regressions. The nonparametric resampling method of jackknifing was used to test the statistical significance of the canonical functions based on the correct classification rate (McGarigal et al. 2000). In the discriminant function analyses we applied the stepwise method, due to the high number of variables and low number of individuals in most samples. We adjusted the F-enter and F-remove to select only the first six variables in each case (scales counts and measurements), increasing the robustness of the analyses. The forward direction option was used, so that at each step all variables were reviewed and evaluated to determine which one would contribute most to the discrimination between groups. The variables in each analysis that showed best discrimination power between groups were subsequently used in a new discriminant function analysis.

Missing scale counts and morphometric values were estimated using a Missing Value Analysis, based on the linear regression of the observed variables. Missing values represented never more than 4.3% of the total number of cases. For all analyses we used the statistic software SYSTAT for Windows, version 12 (SYSTAT Software 2007).

Groupings for the discriminant analysis were defined by color pattern of preserved male specimens, but some observations were based on color in life. Females and juveniles were

assigned to groups, based on their locality and its the nearness to certain male patterns, since no geographic differences in female pattern were found.

### *Species descriptions*

Species descriptions follow Avila-Pires (1995) with the addition of some morphometric and scale count characters. Statistics are presented as “minimum”–“maximum” (“mean”  $\pm$  “standard deviation”,  $N$ =“sample size”). Tail length was measured only in specimens with intact, non-regenerated tail.

### **Results**

We found four different color patterns (see Table 1; Fig. 1, 2) which were used to define the groups for the discriminant analysis (herein named A, B, C and D, as for the color patterns). Stepwise discriminant function analysis using scale counts revealed highly significant differences among groups (Wilks's Lambda=0.036,  $df=18$ ; approx.  $F=21.6$ ,  $df=173$ ,  $p=0.000$ ). The six variables selected as the most powerful discriminators among groups are listed in Table 2. Distal lamellae under second toe was selected first, classifying 67.1% of the specimens, followed by proximal lamellae under fourth toe, infralabials, proximal lamellae under second finger, ventral scales in a longitudinal row, and supralabials, whose additions improved the classification criterion to respectively 82.9%, 87.9%, 90%, 90% and 97.1%. The jackknifed classification matrix correctly classified unknown specimens 92.9% of the times (Table 3). The first and second component function explained, respectively, 74.7% and 22.4% of the total variation in the six meristic variables. The first component function provided separation between A+B (which overlapped), C and D groups (Fig. 3A). Characters with the largest loadings on the

first principal component were proximal lamellae under second finger and distal lamellae under second toe (Table 2). The second component function provided separation between A and D, and B and D, groups (Fig. 3A). Characters with the largest loadings on the second principal component were proximal lamellae under fourth toe and infralabials (Table 2).

Stepwise size-free discriminant function analysis, using measurements, also revealed highly significant differences among the four groups (Wilks's Lambda=0.051, df=18; approx. F=17.964, df =173, p=0.000). The six variables selected as the most powerful discriminators among groups are listed in Table 4. Mental scale length was selected first, classifying 65.7% of the specimens, followed by head width, lower arm length, supranasal scale length, rostral scale length and interorbital distance, whose additions improved the classification criterion to respectively 78.6%, 81.4%, 87.1%, 91.4% and 90%. Although classification with six variables was lower than with five ones, graphic separation of groups in the discriminant function was clearer. The jackknifed classification matrix correctly classified unknown specimens 88.6% of the time (Table 5). The first and second component functions explained, respectively, 68.9% and 27.1% of the total variation in the six meristic variables. The first component function provided separation between groups A and C, A and B, and showed partial overlap between C and D. (Fig. 3B). Characters with the largest loadings on the first principal component were supranasal scale length and mental scale length (Table 4). The second component function provided separation, with small overlapping, between A and B+D groups, C and B+D (Fig. 3B). Characters with large loadings on the second principal component were head width and lower arm length (Table 4).

*Taxonomic account: Attribution of names*

Pattern A

***Gonatodes concinnatus*** (O'Shaughnessy, 1881)

(Fig.1A, 2A, 4, 5)

*Goniodactylus concinnatus* O'Shaughnessy, 1881: 237 (syntypes BMNH 1046.9.7.10-12, formerly BMNH 80.12.8.29-31, type-locality: Canelos, Ecuador, collected by Buckley).

*Goniodactylus buckleyi* O'Shaughnessy, 1881: 238 (syntypes BMNH 1046.9.7.13-14, formerly BMNH 80.12.8.32-33, locality: Canelos; BMNH 1946.9.7.15, formerly BMNH 80.12.8.34, locality: Pallatanga [probably *in error*]; all in Ecuador, collected by Buckley).

*Gonatodes concinnatus*; Boulenger, 1885: 61-62; Burt & Burt, 1933: 2; Vanzolini, 1955: 123, 1968: 25 (part); Wermuth, 1965: 44; Mechler, 1968: 331 (part); Peters & Donoso-Barros, 1970: 132 (part); Dixon & Soini, 1975: 19; 1986: 23; Duellman, 1978: 195; Rodrigues, 1980: 313; Duellman & Mendelson III 1995: 358; Moravec, Tuanama & Burgos 2001: 51; Bartlett & Bartlett 2003: 158 (part); Powell & Henderson, 2005: 714; Cole & Kok, 2006: 4; Gamble, Simon, Colli & Vitt, 2008: 271.

*Gonatodes concinnatus concinnatus*; Rivero-Blanco, 1979: 92 (part).

**Material examined (numbers in bold between parentheses refer to localities in Fig. 6):** Photos of BMNH 1046.9.7.10-12 (syntypes of *Goniodactylus concinnatus*, formerly BMNH 80.12.8.29-31) from **(2)** Canelos, Ecuador, collected by Buckley. Photos of BMNH 1046.9.7.13-14 (syntypes of *Goniodactylus buckleyi*, formerly BMNH 80.12.8.32-33,) from Canelos, Ecuador, collected by Buckley. Photos of BMNH 1946.9.7.15 (formerly BMNH 80.12.8.34, syntypes of *Goniodactylus buckleyi*), from **(1)** Pallatanga, Ecuador, collected by Buckley.

MZUSP 3382-83 (fields number ORCES 656, 656A), two adult females, from (3) Loreto, Napo Province, Ecuador ( $\sim 0^{\circ}38'S$  and  $77^{\circ}19'W$ ), collected by J. Olalla, April 1952. MZUSP 54655 (formerly MCZ 156856), an adult male, from (4) Limoncocha, Napo Province, Ecuador ( $\sim 0^{\circ}24'S$  and  $76^{\circ}37'W$ ), collected by K. Miyata, 9-11 February 1979. MZUSP 28248-49 (field numbers P.SOINI 329-30), two adult males, from (8) Moropón, Departamento Loreto, Peru ( $\sim 5^{\circ}44'52''S$  and  $78^{\circ}32'08''W$ ), collected by P. Soini, August 1971. MZUSP 28260-63 (field numbers P.SOINI 589, 636, 707-8), two juvenile females and two adult males, from (8) Moropón, Departamento Loreto, Peru ( $\sim 5^{\circ}44'52''S$  and  $78^{\circ}32'08''W$ ), collected by P. Soini, November-December 1971. MZUSP 28273-79 (field numbers P.SOINI 821-22, 824, 826, 830, 928-29), a juvenile females, two adult females and four adult males, from (8) Moropón, Departamento Loreto, Peru ( $\sim 5^{\circ}44'52''S$  and  $78^{\circ}32'08''W$ ), collected by P. Soini, February 1972. MZUSP 28311-13 (field numbers P.SOINI 1212-13, 1262), an adult female and two adult males, from (8) Moropón, Departamento Loreto, Peru ( $\sim 5^{\circ}44'52''S$  and  $78^{\circ}32'08''W$ ), collected by P. Soini, October 1972. MZUSP 28319 (field numbers P.SOINI 1385), an adult male, from (8) Moropón, Departamento Loreto, Peru ( $\sim 5^{\circ}44'52''S$  and  $78^{\circ}32'08''W$ ), collected by P. Soini, June 1972. MZUSP 28375 (field numbers P.SOINI 1489), an adult female, from (8) Moropón, Departamento Loreto, Peru ( $\sim 5^{\circ}44'52''S$  and  $78^{\circ}32'08''W$ ), collected by P. Soini, 1972. MZUSP 28354-55 (field numbers P.SOINI 1309-10), a juvenile and an adult females, from (9) Yanamono, Departamento Loreto, Peru ( $\sim 3^{\circ}23'01''S$  and  $72^{\circ}45'01''W$ ), collected by P. Soini, July 1972. MZUSP 56657, an adult female, from (10) Rio Orosa, Departamento Loreto, Peru ( $\sim 3^{\circ}30'60''S$  and  $72^{\circ}06'03''W$ ), collected by P. Soini, August 1976. MZUSP 13458, an adult male, from (11) Estirón, Rio Ampiyacu, Departamento Loreto, Peru ( $\sim 4^{\circ}10'30''S$  and  $70^{\circ}48'04''W$ ), collected by B. Malkin, 15-22 May 1966.



**Diagnosis:** A relatively large *Gonatodes* with maximum SLV of 48.3 mm. Scales around midbody 109–128. Ventral scales in a longitudinal row 49–58. Proximal subdigital lamellae as wide as digits, in total 18–22 under fourth finger, 22–27 under fourth toe. Three or four lateral rows of scales on distal portion of fingers and toes. Tail with midventral scales distinctly wider than long, forming a repetitive sequence of two single midventrals (one after the other), each in contact with one laterodistal scale per side, followed by a divided (proximally) or single (distally) midventral in contact with two laterodistal scales per side (respectively 1'1'2" and 1'1'1"). A white-suprahumeral bar, bordered with black, present both in males and females, although more conspicuous in males. Males with head dorsally without vermiculations; back and limbs with a vermiculated pattern of dark and light spots; no dark streaks on gular region.

**Description:** Maximum SVL in males 48.3 mm (MZUSP 28278), in females 47.6 mm (MZUSP 28276). Tail round in cross section, tapering toward tip, 1.07–1.29 ( $1.16 \pm 0.07$ ,  $N=8$ ) times SLV. Head length 0.23–0.27 ( $0.24 \pm 0.01$ ,  $N=26$ ) times SLV, 1.30–1.56 ( $1.44 \pm 0.06$ ,  $N=26$ ) times as long as wide, 1.31–1.66 ( $1.43 \pm 0.10$ ,  $N=26$ ) times as wide as high. Snout round, moderately elongate (Fig. 4A), gently sloping toward top of head. Neck slightly narrower than head and anterior portion of body. Body cylindrical. Limbs well developed, forelimbs 0.36–0.42 ( $0.40 \pm 0.01$ ,  $N=26$ ) times SVL, hind limbs 0.47–0.56 ( $0.51 \pm 0.02$ ,  $N=26$ ) times SVL.

Rostral convex, 1.89–2.35 ( $2.15 \pm 0.14$ ,  $N=26$ ) times as wide as high; posterior part with a shallow depression medially and posterior margin slightly indented by 1–3 medial postrostrals, with or without a median cleft extending anteriorly. Postrostrals 3 (73.1%), 4 (7.7%) or 5 (19.2%) ( $N=26$ ), lateral ones (supranasals) distinctly larger than medial ones (Fig. 4A). Nostril bordered by rostral, first supralabial (only a narrow contact in some specimens), 3 (88.5%) or 4 (11.5%) postnasals ( $N=26$ ), and supranasal; internostril distance 0.20–0.28 ( $0.24 \pm 0.02$ ,  $N=26$ )

times head width. Supranasal scale roughly oval, circular or semicircular, 0.8–2.3 ( $1.21 \pm 0.28$ ;  $N=26$ ) times as wide as long. Postnasals slightly larger than, or similar in size to, adjacent loreals. Scales on snout convex, hexagonal to round, juxtaposed, relatively uniform in size. Canthus rostralis rounded. Loreal region with scales slightly more elongate than those on snout, largest on row adjacent to supralabials; 9–13 ( $10.7 \pm 1.0^*$ ,  $N=26$ ) loreal scales in a line between postnasals and anterior corner of orbit. Top and posterior portion of head, as well as supraorbital region, with granular scales. A short supraciliary flap present, anteriorly with 6–10 ( $8.3 \pm 1.1$ ,  $N=26$ ) enlarged, flattened scales, among which 0–4 ( $1.7 \pm 1.5$ ;  $N=26$ ) small, conical spines. Pupil round, eye diameter 0.19–0.24 ( $0.21 \pm 0.01$ ,  $N=25$ ) times head length; interorbital distance 0.25–0.35 ( $0.31 \pm 0.02$ ,  $N=26$ ) times head width. Scales on temporal region similar to those on top of head. Ear-opening much smaller than eye, oval, posterior to, and at same level of, commissure of mouth. Supralabials 6–7 ( $6.3 \pm 0.5$ ), distinctly enlarged and decreasing in size posteriorly, one or two of them posterior to centre of eye, followed to corner of mouth by small scales.

Mental large, distinctly wider anteriorly than posteriorly, with posterior margin forming a wide angle, 1.02–1.25 ( $1.13 \pm 0.07$ ,  $N=26$ ) times as wide as long; 2–4 (mostly two) postmentals (Fig. 4B). Scales on chin flat, smooth, polygonal, juxtaposed, larger anteriorly, decreasing in size posteriorly. Infralabials 5–7 ( $6.0 \pm 0.8$ ;  $N=26$ ), distinctly enlarged and decreasing in size posteriorly, one–two, occasionally three, of them posterior to centre of eye, followed to corner of mouth by small scales.

Scales on nape small and granular, becoming slightly larger on sides of neck. Scales on throat anteriorly like those on posterior part of chin; posteriorly flat, smooth, hexagonal or round, imbricate, with a short transitional zone between the anterior and posterior parts.

Dorsals granular, increasing in size toward flanks. Ventrals larger than dorsals, roughly hexagonal, flat, smooth, imbricate, in oblique rows; 49–58 ( $55.0 \pm 2.3$ ,  $N=25$ ) scales along a midventral line between anterior margin of forelimbs and vent; 17–20 ( $18.5 \pm 1$ ,  $N=25$ ) scales in a transverse row at midbody. Scales around midbody 109–128 ( $120.6 \pm 5.3$ ,  $N=25$ ), with a short transitional zone between ventrals and scales on flanks. Scales on preanal plate similar to ventrals, except for those bordering vent, which are very small. Escutcheon present in males on posterior portion of belly and on 4–5 (mostly four) rows (body-knee direction) of ventral surface of thighs.

Scales on anterodorsal surface of forelimbs flat, smooth, roundish, imbricate, largest close to the wrist; on posterodorsal and ventral surfaces convex, smooth, rhomboid, juxtaposed, relatively small; on ventral surface flat, smooth, rhomboid, subimbricate and smaller than anterodorsally. Scales on anterodorsal and ventral surface of hind limbs flat, smooth, rhomboid, imbricate; on posterodorsal surface convex, smooth, round, subimbricate, relatively small. Numbers of lamellae under fingers and toes are presented in Table 7 (Fig. 4C and D). Claws exposed, non-retractile, between two basal scales.

Scales on tail dorsally and laterally relatively small, rhomboid, flat, smooth, imbricate. On ventral surface of tail scales smooth, flat, imbricate, increasing in size toward midventral line; midventral scales, except close to the base of the tail, distinctly wider than long, forming a repetitive sequence of two single midventrals (one after the other), each in contact with one laterodistal scale per side, followed by a divided (in the anterior portion of tail) or single (in posterior portion of tail) midventral scale in contact with two laterodistal scales per side – respectively 1'1'2'' and 1'1'1'' in the codification by Avila-Pires (1995: Figure 2) (Fig. 4E).

**Color in preservative:** In males, dorsal surface of head beige color, spotless. Back and flanks, base of tail and hind limbs with relatively large, beige and brown vermiculations. A large, conspicuous, white suprahumeral bar, bordered with black, extending dorsally at least to the dorsolateral region, in some cases almost reaching the middorsal line (Fig. 5A); never in the form of an ocellus. Ventral surface of head, gular region and chest beige or reddish-brown, without oblique streaks; belly gray; underside of limbs beige. Tail brown and/or black dorsally, white and/or brown ventrally. Escutcheon area (belly and thighs) light gray (Fig. 5).

In females, dorsal surface of head and limbs with brown and black irregular spots; back gray with dorsolateral pairs of black spots and, in some specimens, pairs of beige spots; flanks gray with black and brown spots. Suprahumeral bar conspicuous, white with black margins, thinner than that of males; in some cases they almost reach the middorsal line. Ventral surface of head and gular region white with dark oblique streaks, in contact or not at midventral line; belly and underside of limbs light gray. Tail brown and/or black dorsally, white and/or brown ventrally; original tail distally with white bands that form complete rings around the tail.

**Color in life:** In males, head dorsally and laterally orange or reddish brown with cream color spots. Back olive green with reddish brown vermiculations or brown and black with white vermiculations. Suprahumeral bar white with black margins. Head ventrally and gular region orange, in some specimens with cream streaks; remaining ventral region yellowish gray or black, lighter on escutcheon areas (belly and thighs); tail black. (Duellman 1978; Vitt and Torre 1996).

In females, head dorsally and laterally, and back grayish tan with irregular brown spots or drab gray with irregular crossbands, black at the anterior edge and white at the posterior edge. Suprahumeral bar white with black margins, thinner than that of males. Head ventrally and gular

region cream color with dark streaks; belly creamy tan or yellow; tail grayish tan with irregular brown spots or black and white banded (Duellman 1978; Vitt and Torre 1996).

**Variation:** Body proportions and scale counts are given in Tables 6 and 7. Suprahumerals vary (within the same population) in extension, with upper limit between dorsolateral and middorsal lines.

**Distribution:** Western Amazonia, in Ecuador and northeastern Peru (Fig. 6).

**Remarks:** *Gonatodes ligiae* Donoso-Barros, 1967, from Venezuela, has not been considered in this paper and its inclusion in *G. concinnatus* deserves further studies. Material from Colombia previously identified as *G. concinnatus* is here considered as a distinct species (see 'Pattern D').

### Pattern B

*Gonatodes tapajonicus* Rodrigues, 1980

(Figs. 1B, 2B, 7, 8)

*Gonatodes tapajonicus* Rodrigues, 1980: 309 (holotype MZUSP 53676, type-locality: Cachoeira do Limão, Rio Tapajós, Pará, Brazil); Vanzolini, 1986: 10; Avila-Pires, 1995: 283.

**Material examined (numbers in bold between parentheses refer to localities in Fig. 6):** MZUSP 53676 (holotype, field number MTR 79.1213), an adult male, from (**11**) Cachoeira do Limão, right margin of Rio Tapajós, Pará, Brazil (~4°41'S and 56°21'W), collected on tree trunk at 60 cm above ground (Rodrigues 1980) by M.T. Rodrigues, 30 January to 5 February 1979. MZUSP 53669, 53671-74, 53677 (paratypes, field numbers MTR 79.1142-43, 79.1150,

79.1152-53, 79.1214, respectively), a male and five females, all from type-locality, collected by M.T. Rodrigues, 30 January to 5 February 1979.

**Diagnosis:** A relatively large *Gonatodes* with maximum SVL in males 53 mm (MZUSP 53676), in females 55 mm (MZUSP 53671) (Rodrigues 1980). Scales around midbody 120–126. Ventral scales in a longitudinal row 53–59. Proximal subdigital lamellae as wide as digits, in total 18–22 under fourth finger, 23–27 under fourth toe. Three to four lateral rows of scales on distal portion of fingers and toes. Tail with midventral scales distinctly wider than long, forming a repetitive sequence of two single midventrals (one after the other), each in contact with one laterodistal scale per side, followed by a divided (proximally) or single (distally) midventral in contact with two laterodistal scales per side (respectively 1'1'2" and 1'1'1"). A white suprahumeral ocellus, bordered with black, present both in males and females, although more conspicuous in males. Males with a vermiculated pattern of light and dark (vivid yellow and reddish brown in life) spots both on head and body dorsally; gular region with dark oblique streaks (yellow with reddish brown streaks in life).

**Description:** Maximum SVL in males 53 mm (MZUSP 53676), in females 55 mm (MZUSP 53671) (Rodrigues 1980). Tail round in cross section, tapering toward tip, 1.21–1.23 ( $1.22 \pm 0.02$ ,  $N=2$ ) times the SLV. Head length 0.22–0.25 ( $0.23 \pm 0.01$ ,  $N=7$ ) times SLV, 1.45–1.58 ( $1.5 \pm 0.06$ ,  $N=7$ ) times as long as wide, 1.28–1.44 ( $1.36 \pm 0.05$ ,  $N=7$ ) times as wide as high. Snout round, moderately elongate (Fig 7A), gently sloping toward top of head. Neck slightly narrower than head and anterior portion of body. Body cylindrical. Limbs well developed, forelimbs 0.37–0.44 ( $0.40 \pm 0.03$ ,  $N=7$ ) times SVL, hind limbs 0.45–0.54 ( $0.51 \pm 0.04$ ,  $N=7$ ) times SVL.

Rostral convex, 1.86–2.21 ( $2.02 \pm 0.15$ ,  $N=7$ ) times as wide as high; posterior part with a shallow depression medially and posterior margin slightly indented by 1–3 median postrostrals, with or without a median cleft extending anteriorly. Postrostral 3 (85.7%) or 5 (14.3%), lateral ones (supranasals) distinctly larger than medial ones ( $N=7$ ) (Fig 7A). Nostril bordered by rostral, first supralabial (only a narrow contact in some specimens), 3 (85.7%) or 4 (14.3%) postnasals ( $N=7$ ), and supranasal; internostril distance 0.21–0.27 ( $0.25 \pm 0.03$ ;  $N=7$ ) times head width. Supranasal scale roughly oval or circular, 0.99–1.40 ( $1.19 \pm 0.16$ ;  $N=7$ ) times as wide as long. Postnasals slightly larger than, or similar in size to, adjacent loreals. Scales on snout convex, hexagonal to round, juxtaposed, relatively uniform in size. Canthus rostralis round. Loreal region with scales slightly more elongate than those on snout, largest on row adjacent to supralabials, 10–13 ( $11.1 \pm 0.9$ ,  $N=7$ ) loreal scales in a line between postnasals and anterior corner of orbit. Top and posterior portion of head, as well as supraorbital region, with granular scales. A short supraciliary flap present, anteriorly with 7–10 ( $8.1 \pm 1.1$ ,  $N=7$ ) enlarged and flattened scales, among which 2–4 ( $2.9 \pm 0.7$ ;  $N=7$ ) small, conical spines. Pupil round, eye diameter 0.21–0.25 ( $0.23 \pm 0.01$ ,  $N=7$ ) times head length; interorbital distance 0.34–0.42 ( $0.38 \pm 0.03$ ,  $N=7$ ) times head width. Scales on temporal region similar to those on top of head. Ear-opening much smaller than eye, oval, posterior to, and at same level of, commissure of mouth. Supralabials 6–8 ( $7 \pm 0.8$ ;  $N=7$ ), distinctly enlarged and decreasing in size posteriorly, 1-3 of them posterior to centre of eye, followed to corner of mouth by small scales (Fig. 7A).

Mental large, distinctly wider anteriorly than posteriorly, with posterior margin forming a wide angle, 1.07–1.39 ( $1.21 \pm 0.11$ ;  $N=7$ ) times as wide as long; 2–3 (mostly two) postmentals (Fig. 7B). Scales on chin flat, smooth, polygonal, juxtaposed, decreasing in size posteriorly. Infralabials 5–7 ( $6.1 \pm 0.7$ ;  $N=7$ ) distinctly enlarged and decreasing in size posteriorly; 1–2,

occasionally three, of them posterior to centre of eye, followed to corner of mouth by small scales (Fig. 7B).

Scales on nape small and granular, becoming slightly larger on sides of neck. Scales on throat anteriorly like those on posterior part of chin; posteriorly flat, smooth, hexagonal or round, imbricate, with a short transitional zone between the anterior and posterior parts.

Dorsals granular, increasing in size toward the flanks. Ventrals larger than dorsals, roughly hexagonal, flat, smooth, imbricate, in oblique rows; 53–59 ( $55.8 \pm 2.2$ ;  $N=6$ ) scales along the midventral line between anterior margin of forelimbs and vent; 19–20 ( $19.5 \pm 0.5$ ;  $N=6$ ) scales in a transverse line at midbody. Scales around midbody 120–126 ( $122.7 \pm 2.4$ ;  $N=6$ ), with a short transitional zone between ventrals and scales on flanks. Scales on preanal plate similar to ventrals, except for those bordering vent, which are very small. Escutcheon present in males on posterior portion of belly and on four ( $N=2$ ) rows (body-knee direction) of ventral surface of thighs.

Scales on anterodorsal surface of forelimbs flat, smooth, roundish, imbricate, largest close to the wrist; on posterodorsal and ventral surfaces convex, smooth, rhomboid, juxtaposed, relatively small; on ventral surface flat, smooth, rhomboid, subimbricate and smaller than anterodorsally. Scales on anterodorsal and ventral surface of hind limbs flat, smooth, rhomboid, imbricate; on posterodorsal surface convex, smooth, round, subimbricate, relatively small. Numbers of lamellae under fingers and toes are presented in Table 7 (Fig. 7D).

Scales on tail dorsally and laterally relatively small, rhomboid, flat, smooth, imbricate. On ventral surface of tail scales smooth, flat, imbricate, increasing in size toward midventral line; midventral scales, except close to the base of the tail, distinctly wider than long, forming a repetitive sequence of two single midventrals (one after the other), each in contact laterodistally



with one scale per side, followed by a divided (in the anterior portion of tail) or single (in the posterior portion of tail) midventral scale in contact laterodistally with two scales per side – respectively 1'1'2'' and 1'1'1'' in the codification by Avila-Pires (1995: Figure 2) (Fig. 7E).

**Color in preservative:** In males, dorsal surface of head with relatively large reddish-brown and beige vermiculations. Sides of head with oblique and/or longitudinal, beige and brown bands. Back and flanks, base of tail and limbs with beige and brown vermiculations. A large, conspicuous, white suprahumeral ocellus with black margin. Ventral surface of head and gular region beige with oblique black streaks, in contact or not at midventral line; chest beige; belly dark-brown; undersides of limbs and base of tail brown. Dorsal surface of tail brown, ventral surface reddish-brown; distal part in one specimen with a beige ring around the tail. Escutcheon area (belly and thighs) light gray.

In females, dorsal surface of head, and limbs with brown and beige irregular spots. Sides of head with beige and brown oblique and/or longitudinal bands. Back gray with dorsolateral pairs of black and white spots; flanks gray with black and brown irregular spots. A moderately large, conspicuous, white suprahumeral ocellus, with black margin, smaller than that of males. Ventral surface of head and gular region white with dark oblique streaks, in contact or not at midventral line; belly and underside of limbs light gray. Tail brown and/or black dorsally, white and/or brown ventrally; original tail distally with white bands that form complete rings around the tail.

**Color in life (from photos of holotype, Fig. 8):** Head dorsally and laterally reddish-brown and vivid yellow. Suprahumeral ocellus white with black margin. Vermiculations on back brown and yellow, smaller vermiculations on flanks bluish-white and black. Head ventrally and gular region vivid yellow with reddish-brown streaks, chest vivid yellow. Remaining ventral

region dark gray, lighter on escutcheon areas (belly and thighs). Tail dark gray to black all around, except near the base, where it is similar to the back.

**Variation:** Body proportions and scale counts are given in Tables 6 and 7. The suprahumeral ocellus does not vary in extension between the specimens.

**Distribution:** Known only from the type-locality, on the right margin of the Tapajós river, state of Pará, Brazil (Fig. 6).

### Pattern C

#### ***Gonatodes* sp. nov. 1**

(Fig. 1C, 2C, 9, 10)

**Holotype (number in bold between parentheses refer to localities in Fig. 6):** MPEG 25596 (field number BML 446), an adult male, from (**14**) Fazenda Caracol, right margin of Rio Xingu, Anapu, Pará, Brazil ( $3^{\circ}27'30''\text{S}$  and  $51^{\circ}40'33''\text{W}$ ), collected in pitfall trap inside primary forest, by A.A. Lima, M.J. Sturaro and R.A.T. Rocha, 12 January 2008.

**Paratypes (numbers in bold between parentheses refer to localities in Fig. 6):** MPEG 25164 (field number BML 213), an adult male, collected in a pitfall trap by A.A. Lima and R.A.T. Rocha, 10 November 2007. MPEG 25595, 25597 (field number BML 363, 925), a juvenile female and an adult male, collected by A.A. Lima, M.J. Sturaro and R.A.T. Rocha, 9 to 25 January 2008. MPEG 25598-25601 (field numbers BML 1292-93, 1470, 1554), an adult male, an adult females and two juvenile females, respectively, collected by A.A. Lima, M.J. Sturaro, R.A.T. Rocha, P.L.V. Peloso and F.S. Rodrigues, 5 to 16 March 2008, all from type-locality (**14**). MPEG 23822-27 (field numbers J-2266, 3271, 3328, 3348, 3379, 3497, respectively), five males and a female, from (**13**) Forest near the Estação Ecológica do Jari,

Monte Dourado, Almeirim, Pará, Brazil (0°35'27''S and 52°44'09''W), collected by T.A. Gardner and M.A. Ribeiro-Jr, 11 May to 22 June 2005. FL 361, from (15) Floresta Nacional do Amapá, município Ferreira Gomes, state of Amapá, Brazil (01°06'37''N and 51°53'37''W) collected by J. Lima, 07 June 2005. MPEG 24643 (field number MV 35), male, collected by T.C.S. Avila Pires and J.O. Gomes, 9 February 2007, and MPEG 24644-50 (field numbers MV 332, 343, 347, 355, 385, 413), five males and a female, collected by J.O. Gomes, 20-25 March 2007, all from (16) Fazenda Riacho Monte Verde, Portel, Pará, Brazil (~ 3°15'S and 50°19'W).

**Diagnosis:** A relatively large *Gonatodes*, with maximum SLV of 55.7 mm. Scales around midbody 121-143. Ventral scales in a longitudinal row 53-60. Proximal subdigital lamellae as wide as digits, in total 18-23 under fourth finger, 23-28 under fourth toe. Three or four lateral rows of scales on distal portions of fingers and toes. Tail with midventral scales distinctly wider than long, forming a repetitive sequence of two single midventrals (one after the other), each in contact laterodistally with one scale per side, followed by a divided (proximally) or single (distally) midventral in contact laterodistally with two scales per side (respectively 1'1'2'' and 1'1'1''). A white suprahumeral spot, with black margin, either in the form of an ocellus (FL 361) or of a vertical bar, both in males and females (but thinner in the latter). Males with a vermiculated pattern of light and dark (reddish-brown and yellow in life) spots on head and body dorsally (white in preservative); gular region light with dark oblique streaks or reddish with white oblique streaks (orange with vivid yellow in life).

**Description:** Maximum SVL in males of 55.7 mm (MPEG 23822), in females of 46.6 mm (MPEG 24647). Tail round in cross section, tapering toward tip, 1.11–1.26 ( $1.2 \pm 0.05$ ,  $N=8$ ) times SLV. Head length 0.21–28 ( $0.24 \pm 0.02$   $N=23$ ) times SLV, 1.21–1.56 ( $1.41 \pm 0.08$ ,  $N=23$ ) times as long as wide, 1.17–1.54 ( $1.40, \pm 0.10$ ,  $N=23$ ) times as wide as high. Snout round,

moderately elongate (Fig 9A), gently sloping toward top of head. Neck slightly narrower than head and anterior portion of body. Body cylindrical. Limbs well developed, forelimbs 0.38–0.44 ( $x=0.41$ ,  $sd=0.02$ ,  $N=23$ ) times SVL, hind limbs 0.47–0.55 ( $x=0.51$ ,  $sd=0.02$ ,  $N=23$ ) times SVL.

Rostral convex, 1.78–3.01 ( $2.02 \pm 0.28$ ,  $N=23$ ) times as wide as high; posterior part slightly indented by 0–2 median postrostrals, with a median cleft extending anteriorly. Postrostrals 2 (8.7%), 3 (87%) or 4 (4.3%), laterals ones (supranasals) distinctly larger than medial ones ( $N=23$ ) (Fig 9A). Nostril bordered by rostral, first supralabial (only a narrow contact in some specimens), three postnasals, and supranasal; internostril distance 0.22–0.31 ( $0.25 \pm 0.02$ ;  $N=23$ ) times head width. Supranasal roughly oval, circular or semicircular, 0.88–1.44 ( $1.13 \pm 0.13$ ;  $N=23$ ) times as wide as long. Postnasals vary from slightly smaller to slightly larger than adjacent loreals. Scales on snout convex, hexagonal to round, juxtaposed, relatively uniform in size. Canthus rostralis rounded. Loreal region with scales slightly more elongate than those on snout, largest on row adjacent to supralabials, 10–13 ( $11.2 \pm 0.9$ ,  $N=23$ ) loreals on a line between postnasals and anterior corner of eye. Top and posterior portion of head, as well as supraorbital region, with granular scales. A short supraciliary flap present, anteriorly with 7–12 ( $9.4 \pm 1.4$ ,  $N=23$ ) enlarged and flattened scales, among which zero, one or three ( $1.1 \pm 1.2$ ;  $N=23$ ) small, conical spines. Pupil round, eye diameter 0.20–0.27 ( $0.22 \pm 0.02$ ,  $N=23$ ) times head length; interorbital distance 0.22–0.31 ( $0.25 \pm 0.02$ ,  $N=23$ ) times head width. Scales on temporal region similar to those on top of head. Ear-opening much smaller than eye, oval, posterior to, and at same level of, commissure of mouth. Supralabials 5–7 ( $6.2 \pm 0.5$ ;  $N=23$ ), distinctly enlarged anteriorly and decreasing in size posteriorly, one or two of them posterior to centre of eye, followed to corner of mouth by small scales (Fig. 9A).

Mental larger, distinctly wider anteriorly than posteriorly, with posterior margin forming a wide angle a right angle, 1.17–1.41 ( $1.28 \pm 0.07$ ;  $N=23$ ) times as wide as long; 2–3 (mostly two) postmentals (Fig. 2B). Scales on chin flat, smooth, polygonal, juxtaposed, larger anteriorly, decreasing in size posteriorly. Infralabials 5–8 ( $6.3 \pm 0.9$ ;  $N=23$ ), distinctly enlarged anteriorly and decreasing in size posteriorly; one–two, occasionally three, of them posterior to centre of eye, followed to corner of mouth by small scales.

Scales on nape small and granular, becoming slightly larger on sides of neck. Scales on throat anteriorly like those on posterior part of chin; posteriorly flat, smooth, hexagonal or round, imbricate, with a short transitional zone between the anterior and posterior parts.

Dorsals granular, increasing in size toward the flanks. Ventrals larger than dorsals, roughly hexagonal, flat, smooth, imbricate, in oblique rows; 52–60 ( $56.2 \pm 2.5$ ;  $N=21$ ) scales along the midventral line between anterior margin of forelimbs and vent; 18–24 ( $21.2 \pm 1.3$ ;  $N=21$ ) scales in a transverse line at midbody, with a short transitional zone between ventrals and scales on flanks. Scales around midbody 118–143 ( $130 \pm 6.5$ ;  $N=21$ ). Scales on preanal plate similar to ventrals, except for those bordering vent, which are very small. Escutcheon present in males on posterior portion of belly and on 4–5 ( $4.4 \pm 0.5$ ;  $N=16$ ) rows (body-knee direction) of ventral surface of thighs.

Scales on anterodorsal surface of forelimbs flat, smooth, roundish, imbricate, largest close to the wrist; on posterodorsal and ventral surfaces convex, smooth, rhomboid, juxtaposed, relatively small; on ventral surface flat, smooth, rhomboid, subimbricate and smaller than anterodorsally. Scales on anterodorsal and ventral surface of hind limbs flat, smooth, rhomboid, imbricate; on posterodorsal surface convex, smooth, round, subimbricate, relatively small.

Numbers of lamellae under fingers and toes are presented in Table 7 (Fig. 9D). Claws exposed, non-retractile, between two basal scales.

Scales on tail dorsally and laterally relatively small, rhomboid, flat, smooth, imbricate. On ventral surface of tail scales smooth, flat, imbricate, increasing in size toward midventral line; midventral scales, except close to the base, distinctly wider than long, forming a repetitive sequence of two single midventrals (one after the other), each in contact laterodistally with one scale per side, followed by single (in posterior portion of tail) midventral scale in contact laterodistally with two scales per side – 1'1'1" in the codification by Avila-Pires (1995: Figure 2) (Fig. 9E).

**Color in preservative:** In males, dorsal surface of head with reddish-brown and beige vermiculations. Sides of head, in some specimens, with oblique and/or longitudinal, beige and brown bands. Back and flanks, base of tail and hind limbs with relatively large, beige color and dark-brown (or light-brown) vermiculations. A large, conspicuous, white suprahumeral spot with black margin, which varies from an ocellus to a vertical bar, in some specimens almost reaching the middorsal line. Ventral surface of head and gular region beige with black streaks, in some specimens dark-brown with beige streaks, in contact or not at midventral line; chest beige; belly dark-brown; undersides of limbs and base of tail brown. Dorsal surface of tail brown; a white band may be present distally, forming a complete ring around the tail. Under the tail anteriorly and posteriorly dark-brown or black, in some specimens, posteriorly brown with white band. Escutcheon area (belly and thighs) light gray.

In females, dorsal surface of head and limbs with brown and beige irregular spots. Back gray with dorsolateral pairs of black and white spots; flanks gray with black and brown irregular spots. A moderately large, conspicuous, white suprahumeral spot with black margin (varying

from an ocellus to a vertical bar which may almost reach the middorsal line), narrower than that of males. Ventral surface of head and gular region white with black oblique streaks, in contact or not at midventral line; belly and underside of limbs light-gray. Tail gray dorsally and white ventrally; original tail distally with white and black bands that form complete rings around the tail.

**Color in life:** In males (Fig. 10A, B), head dorsally and laterally with orange and orange yellow, or reddish-brown and drab, vermiculations. On back vermiculations may be smaller than, or similar in size to, those on head and the lighter spots are frequently bordered by black (occasionally also on head). Suprahumeral bar or ocellus white with black margins. Flanks with smaller, bluish-white and black vermiculations. Head ventrally and gular region orange with orange yellow streaks, chest orange. Remaining ventral regions plumbeous, lighter on escutcheon areas (belly and thighs). Tail dark gray to black all around, except near the base, where it is similar to the back; distal portion with white spots.

Females dorsally brown or grayish-brown, with paired series of dark brown to black irregular, transversely elongate, spots. Suprahumeral bar white with black margins, thinner than those in males. Head ventrally and gular region white with black streaks, chest light-gray. Tail gray with black spots all around; posterior portion with white spots.

**Measurements of holotype (in millimeters):** SVL 48.7, TL 54.0, DBL 21.3, HL 11.7, HW 7.9, HD 6.8, ED 2.6, IOD 2.8, IND 2.0, SSL 0.8, SSW 1.12, RSL 1.3, RSW 2.5, MSL 2.6, MSW 3.2, UAL 4.8, RL 8.1, HAL 6.9, FML 19.8, FL 9.7, TIL 7.8, FTL 8.4, HLL 25.9, HSW 5.34, HSL 2.6.

**Scale counts of holotype:** SAM 127 scales, VVR 55, VLR 21, SL 6, IL 5, PR 3, SP 1, PN 3, LS 12, PM 2, SCS 8, SSC 3, PSL2F 5, DSL2F 12, SL2F 17, LRS2F 3, PSL3F 4, DSL3F

14, SL3F 19, LRS3F 4, PSL4F 6, DSL4F 13, SL4F 19, LRS4F 4, PSL2T 5, DSL2T 12, SL2T 17, LRS2T 4, PSL3T 5, DSL3T 15 , SL3T 20, LRS3T 3, PSL4T 10, DSL4T 13, SL4T 23, LRS4T 3, RSE 4.

**Variation:** Body proportions and scale counts are given in Tables 6 and 7. The suprahumeral spot varies among populations and, to a smaller degree, within populations. In the only specimen from Amapá examined, the spot has the shape of an ocellus. Specimens from Pará, north of the Amazon river, show a vertical bar reaching dorsally at least the dorsolateral line, in some cases almost the middorsal line. South of the Amazon, all specimens from Monte Verde present a short vertical bar (not reaching the dorsolateral line, but always with dorso-ventral axis longer than anterior-posterior axis), while in the specimens from Anapu the vertical bar is similar to those from northern Pará (although one specimen presents a vertical bar and a small ocellus above the bar, on both sides).

**Distribution:** Eastern Brazilian Amazonia, in the states of Pará and Amapá. Up till now it is only known south of the Amazon river in the interfluvium Xingu-Tocantins, Pará state, and north of the Amazon river east of Paru river, in the states of Pará and Amapá (Fig. 6).

**Habitat:** All specimens were in *terra firme*, undisturbed or little-disturbed forest, collected in pitfall traps, on the base of Sapopema trees and fissures in rock inside primary forest. In the type locality a pair was collected in the fissure of a rock. At the type-locality specimens from hid inside rock crevices or tree trunk holes when disturbed.



Pattern D

***Gonatodes* sp. nov. 2**

*Gonatodes concinnatus*: Vanzolini, 1955: 126 (part); 1968: 26 (part); Mechler, 1968: 331 (part); Peters & Donoso-Barros, 1970 (part); Rivero-Blanco, 1979: 94 (part); Sanchez, Castaño & Cardenas 1995: 317; Bartlett & Bartlett 2003: 158 (part); Avila-Pires, 2005: 31.

(Fig. 1D, 2D, 11)

**Holotype (number in bold between parentheses refer to localities in Fig. 6):** MZUSP 49153 (field number FMEDEM 1465), adult male, from **(5)** Villavicencio, State of Meta, Colombia (~4°09'S and 73°37'W), collected by W. W. Lamar and F. Medem, 22 October 1977.

**Paratypes (numbers in bold between parentheses refer to localities in Fig. 6):** MZUSP 2145-46 (former AMNH 35292-93, respectively), two females, collected by N. Maria; MZUSP 49152, an adult female, collected by M. Lugor and F. Medem, 10 October 1977; MZUSP 49154 (field number FMEDEM 1471), an adult female, collected by W. W. Lamar and F. Medem, October 1977, from **(5)** the type-locality. MZUSP 49155-62 (field number FMEDEM 1467), five adult females and three adult males, from **(6)** Finca "El Buque", from Villavicencio, Meta, Colombia (~4°08'19"N and 73°38'36"W); MZUSP 44777 (field number F 2544), an adult female, from **(7)** Finca Guadualito, Güejar River, Meta, Colombia (~2°55'N and 73°14'W), collected by L. Klein and F. Medem, 7 September 1967.

**Diagnosis:** A relatively large *Gonatodes*, with maximum SLV of 45.8 mm. Scales around midbody 105–123. Ventral scales in a longitudinal row 44–54. Proximal subdigital lamellae as wide as digits, in total 16–21 under fourth finger, 18–24 under fourth toe. Two or three lateral rows of scales on distal portion of fingers and toes. Tail with midventral scales distinctly wider

than long, forming a repetitive sequence of two single midventrals (one after the other), each in contact with one laterodistal scale per side, followed by a divided (proximally) or single (distally) midventral in contact with two laterodistal scales per side (respectively 1'1'2" and 1'1'1"). A white, bordered with black, suprahumeral bar present both in males and females, although more conspicuous in males. Males with head dorsally without vermiculation; back and limbs finely vermiculated; gular region without dark streaks.

**Description:** Maximum SVL in males of 45.8 mm (MZUSP 49158), in females 44.4 mm (MZUSP 49156). Tail round in cross section, tapering toward tip, 1.11–1.26 ( $1.2 \pm 0.05$ ,  $N=2$ ) times SLV. Head length 0.22–0.25 ( $0.24 \pm 0.01$ ,  $N=14$ ) times SLV, 0.90–0.96 ( $0.94 \pm 0.02$ ,  $N=14$ ) times as long as wide, 1.25–1.63 ( $1.44 \pm 0.11$ ,  $N=12$ ) times as wide as high. Snout round, moderately elongate (Fig. 11 A), gently sloping toward top of head. Neck slightly narrower than head and anterior portion of body. Body cylindrical. Limbs well developed, forelimbs 0.27–0.40 ( $0.38 \pm 0.04$ ,  $N=14$ ) times SVL, hind limbs 0.44–0.53 ( $0.48 \pm 0.02$ ,  $N=14$ ) times.

Rostral convex, 1.65–2.19 ( $1.93 \pm 0.13$ ,  $N=14$ ) times as wide as high; posterior part slightly indented by 0–3 median postrostrals, with a median cleft extending anteriorly. Postrostrals 2 (7.1%), 3 (85.8%) or 5 (7.1%) ( $N=14$ ), laterals ones (supranasals) distinctly larger than medial ones (Fig. 11A). Nostril bordered by rostral, first supralabial (only a narrow contact), 2 (7.1%) or 3 (92.9%) postnasals ( $N=14$ ), and supranasal; internostril distance 0.23–0.27 ( $0.25 \pm 0.01$ ;  $N=12$ ) times head width. Supranasal scale roughly oval or circular, 0.91–1.61 ( $1.24 \pm 0.19$ ;  $N=14$ ) times as wide as long. Postnasals slightly smaller than, or similar in size to, adjacent loreals. Scales on snout convex, hexagonal to round, juxtaposed, relatively uniform in size. Canthus rostralis rounded. Loreal region with scales slightly imbricated and more elongate than those on snout, largest on row adjacent to supralabials; 9–11 ( $10 \pm 0.8$ ,  $N=14$ ) loreal scales in a

line between postnasals and anterior corner of orbit. Top and posterior portion of head, as well as supraorbital region, with granular scales. A short supraciliary flap present, anteriorly with 7–10 ( $8.4 \pm 1.0$ ,  $N=14$ ) enlarged and flattened scales, among which 0–3 ( $2.1 \pm 1.1$ ;  $N=14$ ) small, conical spines. Pupil round, eye diameter 0.20–0.23 ( $0.22 \pm 0.01$ ,  $N=14$ ) times head length; interorbital distance 0.30–0.38 ( $0.35 \pm 0.02$ ,  $N=14$ ) times head width. Scales on temporal region similar to those on top of head. Ear-opening much smaller than eye, oval, posterior to, and at same level of commissure of mouth. Supralabials 6–7 ( $6.2 \pm 0.4$ ;  $N=14$ ) distinctly enlarged and decreasing in size posteriorly, one or two posterior to centre of eye, followed to corner of mouth by small scales (Fig. 11A).

Mental larger, distinctly wider anteriorly than posteriorly, with posterior margin forming a moderate or wide angle, 1.20–1.51 ( $1.32 \pm 0.09$ ;  $N=14$ ) times as wide as long; 2–3 (mostly two) postmentals (Fig. 11B). Scales on chin juxtaposed, smooth, flat, polygonal, larger anteriorly, decreasing in size posteriorly. Infralabials 4–6 ( $5.6 \pm 0.6$ ;  $N=14$ ) distinctly enlarged and decreasing in size posteriorly; one–two, occasionally three, of them posterior to centre of eye, followed to corner of mouth by small scales.

Scales on nape small and granular, becoming slightly larger on sides of neck. Scales on throat anteriorly like those on posterior part of chin; posteriorly flat, smooth, hexagonal or round, imbricate, with a short transitional zone between the anterior and posterior parts.

Dorsals granular, increasing in size toward the flanks. Ventrals larger than dorsals, roughly hexagonal, flat, smooth, imbricate, in oblique rows; 44–56 ( $50.4 \pm 3.6$ ;  $N=14$ ) scales along a midventral line between anterior margin of forelimbs and vent; 17–19 ( $17.7 \pm 0.7$ ;  $N=14$ ) scales in a transverse row at midbody. Scales around midbody 100–124 ( $113.5 \pm 6.1$ ;  $N=14$ ), with a short transitional zone between ventrals and scales on flanks. Scales on preanal plate

similar to ventrals, except for those bordering vent, which are very small. Escutcheon present in males on posterior portion of belly and on 4–5 (mostly four) rows (body-knee direction) of ventral surface the thighs.

Scales on anterodorsal surface of forelimbs flat, smooth, roundish, imbricate, largest close to the wrist; on posterodorsal and ventral surfaces convex, smooth, rhomboid, juxtaposed, relatively small; on ventral surface flat, smooth, rhomboid, subimbricate and smaller than anterodorsally. Scales on anterodorsal and ventral surface of hind limbs flat, smooth, rhomboid, imbricate; on posterodorsal surface convex, smooth, round, subimbricate, relatively small. Numbers of lamellae under fingers and toes are presented in Table 7 (Fig. 11D). Claws exposed, non-retractile, between two basal scales.

Scales on tail dorsally and laterally relatively small, rhomboid, flat, smooth, imbricate. On ventral surface of tail scales smooth, flat, imbricate, increasing in size toward midventral line; posteriorly midventral scales, except close to the base, distinctly wider than long, forming a repetitive sequence of two single midventrals (one after the other), each in contact with one laterodistal scale per side, followed by a divided (in the anterior portion of tail) or single (in posterior portion of tail) midventral scale in contact with two laterodistal scales per side – respectively 1'1'2'' and 1'1'1'' in the codification by Avila-Pires (1995: Figure 2) (Fig. 11E).

**Color in preservative:** In males, dorsal surface of head reddish-brown, spotless. Back and flanks, base of tail and hind limbs with relatively small, beige and brown vermiculations. A large, conspicuous, white suprahumeral bar with black margins. Ventral surface of head, gular region and chest brown, without oblique streaks; belly dark-brown or dark-gray; underside of limbs beige color. Tail dark brown dorsally and brown ventrally. Dorsal surface of tail dark brown; ventral surface of tail brown. Escutcheon area (belly and thighs) light gray.

In females, dorsal surface of head and limbs light-brown or gray, with black irregular spots; brown and black oblique and/or longitudinal bands may be present on sides of head. Back gray with dorsolateral pairs of black spots; flanks gray with black and brown irregular spots. A moderately large, conspicuous, white suprahumeral bar, with black margins, but less defined than that on males; in some specimens it almost reaches the middorsal line. Ventral surface of head and gular region white with dark oblique streaks, in contact or not at midventral line; belly and underside of limbs white or beige. Dorsal surface of tail light-brown or brown with black spots, ventral surface of original tail white, in some specimens with black small spots.

**Measurements of holotype (in millimeters):** SVL 42.5, TL 46.0 (distally regenerate), DBL 17.8, HL 9.8, HW 6.7, HD 4.7, ED 2.0, IOD 2.1, IND 1.7, SSL 0.7, SSW 0.8, RSL 1.1, RSW 2.1, MSL 2.2, MSW 2.6, UAL 5.0, RL 5.3, HAL 6.3, FML 11.5, FL 7.3, TIL 6.2, FTL 7.3, HLL 20.8, HSW 2.8, HSL 1.57.

**Scale counts of holotype:** SAM 116 scales, VVR 51, VLR 17, SL 6, IL 6, PR 3, SP 1, PN 3, LS 9, PM 2, SCS 8, SSC 2, PSL2F 6, DSL2F 11, SL2F 17, LRS2F 3, PSL3F 6, DSL3F 13, SL3F 19, LRS3F 3, PSL4F 7, DSL4F 11, SL4F 18, LRS4F 3, PSL2T 6, DSL2T 11, SL2T 17, LRS2T 3, PSL3T 6, DSL3T 13, SL3T 19, LRS3T 3, PSL4T 11, DSL4T 12, SL4T 23, LRS4T 3, RSE 4.

**Variation:** Measurements and scale counts are given in Tables 6 and 7. The suprahumeral bar does not vary in extension between the specimens.

**Distribution:** All specimens studied are from Departamento Meta, Colombia. Sanchez et al. (1995) reported *G. concinnatus* in Colombia from “Amazonas, Casanare, Boyacá, Cundinamarca, Meta, Pasto, Orinoco, Guaviare”. It is necessary, however, to verify whether all these records do refer to the species here described.

**Remarks:** Rivero-Blanco (1979) considered the specimens from Villavincencio and vicinity, Meta, Colombia, as intergrades between *Gonatodes concinnatus concinnatus*, from Peru and Ecuador, and *G. c. ligiae*, from Venezuela.

### Species comparisons

The four species considered here under the term *Gonatodes concinnatus* complex are easily distinguishable from the remaining 20 species of *Gonatodes* by the presence of a moderately large, white suprahumeral spot with black margin, and dark and white vermiculations on back, in males (vermiculations absent, however, in the nominal species *Gonatodes ligiae* Donoso-Barros, from Venezuela, considered by Rivero-Blanco (1979) a subspecies of *G. concinnatus*, not examined in this paper). A white antehumeral bar is present in *G. ceciliae*, *G. humeralis*, and *G. ocellatus*. All remaining species present no similar bar or spot in the humeral region and do not present vermiculations on back.

The species of the *G. concinnatus* complex differ moreover from *G. alexandermendesi*, *G. hasemani* and *G. infernalis* by the absence of a very elongate spine on the supraciliary flap, and from *Gonatodes annularis*, *G. caudiscutatus*, *G. eladioi*, *G. infernalis* and *G. hasemani* by the subcaudal sequence (1'1'2'' in the first species, midventrals not enlarged in *G. hasemani*, 1'1'' in the remaining three species). From *G. albogularis*, *G. antillensis*, *G. atricucullaris*, *G. daudini*, *G. humeralis*, *G. petersi* and *G. vittatus* this group differs moreover by having a higher number (3–4) of lateral rows of scales on toes and fingers, except *Gonatodes* sp. nov. 2, which has 2–3 lateral rows of scales like the seven above-mentioned species.

The species in the *G. concinnatus* complex reach a larger SVL than *Gonatodes albogularis*, *G. antillensis*, *G. atricucullaris*, *G. caudiscutatus*, *G. daudini*, *G. eladioi*, *G. falconensis*, *G. humeralis*, *G. petersi* and *G. vittatus*, none of which exceed 42 mm in SVL.

Rivero-Blanco (1979) reported that the specimens of *Gonatodes concinnatus* from Venezuela, which he considered as *Gonatodes c. ligiae*, have a white suprahumeral ocellus, and the other populations (Peru and Ecuador) a vertical bar. The degree of elongation of this spot (from a round ocellus to a bar almost reaching the middorsal line) seems to be to a certain extent fixed within populations (either an ocellus, a short bar, or a median to long bar), but variable among populations. Thus, all specimens from *G. tapajonicus*, known from only one locality, have ocelli, while in *Gonatodes* sp. n. 1, an ocellus is present in the only specimen known from Amapá, a short vertical bar occurs in all specimens from another locality, and specimens from two other localities have all an elongate vertical bar. Specimens from Venezuela considered to be *G. concinnatus* lack moreover vermiculations on the sides or dorsal surfaces of the body. Considering that specimens from Colombia are here demonstrated to belong to a different species, a large gap exists between *G. c. concinnatus* and *G. c. ligiae*. Taxonomic studies including enough samples from Venezuela are therefore necessary to establish the status of these populations.

Within the *Gonatodes concinnatus* complex, color pattern separates two groups – in *G. concinnatus* and *Gonatodes* sp. nov. 2 the head has no vermiculation dorsally and no dark streaks ventrally, while those are present in *G. tapajonicus* and *Gonatodes* sp. nov. 1. *Gonatodes* sp. nov. 2 differs from *G. tapajonicus* and *Gonatodes* sp. nov. 1 in size (Table 6) and from all three in number of lateral scales on distal part of digits (2–3 in *Gonatodes* sp. nov. 1 3–4 in the other species). *G. tapajonicus* differs from *Gonatodes* sp.n. 1 by its yellow and brown color, while the

latter is orange and orange-yellow. Otherwise, body proportions (Table 6) and scales counts (Table 7) are very similar between the species in the complex, even though the species were clearly separated on basis of discriminant function analyses. Main characters pointed by the discriminant analyses were proximal and distal lamellae under second toe, which separate *Gonatodes* sp. nov. 1 from *Gonatodes* sp. nov. 2; proximal lamellae under fourth toe and infralabials, which separate *Gonatodes* sp. nov. 2 from *G. concinnatus* and *G. tapajonicus*; supranasal scale length and mental scale length, which separate *G. concinnatus* from *Gonatodes* sp. nov. 2; and head width and lower arm length separate *G. concinnatus* and *Gonatodes* sp. nov. 2 from *G. tapajonicus* and *Gonatodes* sp. nov. 1.

## Discussion

Male color pattern is an important character to distinguish species in *Gonatodes*, some of which are very similar in external morphology and scale counts (Vanzolini 1968; Rivero-Blanco 1979, Rodrigues 1990). It is important however to take into consideration that polymorphism in colour pattern is known in some species of *Gonatodes* – e.g. in *Gonatodes annularis* (Rivero-Blanco 1968; 1979; Hoogmoed 1973) and *G. hasemani* (Avila-Pires 1995).

Considering the similarities, we assume that the species here considered as the *Gonatodes concinnatus* complex form a monophyletic group, but this needs to be tested. Gamble et al. (2008) pointed *G. concinnatus* (the only species of the complex they analysed) as the sister species of *G. humeralis*. If our assumption of monophyly of the species here studied is correct, *G. concinnatus* complex would have the same age – early Miocene – as *G. humeralis*. It is interesting to observe that it and *G. humeralis* are also the most widespread *Gonatodes* species in Amazonia. It is possible therefore that they have a similar, parallel history, even though, at least



concerning external morphology, divergence within *G. concinnatus* complex has been more accentuated than in *G. humeralis*.

*Gonatodes* sp. nov. 1 seems to be restricted to eastern Amazonia, on both sides of the Amazon River. Even though no other lizard is known with exactly the same distribution, there are some examples of lizards that are present on both sides of the lower Amazon, e.g. *Arthrosaura kockii* and *Tretioscincus agilis* (Avila-Pires 1995). Ayres & Clutton-Brock (1992) have shown that for primates the lower Amazon acted less as a barrier than the middle course of the river. The dynamics of island formation and river channel changes near the Amazon mouth may have allowed such movements across the lower Amazon.

*Gonatodes humeralis* occurs in sympatry with many larger species of the genus, namely *G. annularis*, *G. concinnatus*, *G. hasemani*, *G. tapajonicus* (Avila-Pires 1995; Dixon & Soini 1975; Rivero-Blanco 1979; Moravec et al. 2001) but there are no records of sympatry between two larger species or any three species of *Gonatodes*. In our fieldwork in the Xingu River, *Gonatodes* sp. nov. 1 and *G. humeralis* were found on the right margin of the river, while *G. hasemani* and *G. humeralis* were found on the left margin. The Xingu river seems therefore to act as a barrier between *G. hasemani* and *Gonatodes* sp. nov. 1. On the other hand, north of the Amazon the distribution of *Gonatodes* sp. nov. 1 allows us to suppose a possible sympatry with *G. annularis*, apart from that with *G. humeralis*, but this has yet to be verified. The exact distribution of *G. annularis* and *Gonatodes* sp. nov. 1, whether they occur together or what separates them, and in case they occur in syntopy how they interact, are at the moment open questions.

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**Appendix I – Additional material examined. Total number of specimens per species is in parentheses.**

*Gonatodes albogularis* (2): **NICARAGUA** (MNRJ 3164, 10670).

*Gonatodes annularis* (22): **BRAZIL: Amapá:** Mazagão, Cachoeira Inajá, Rio Camaipi (MPEG 2667), Oiapoque, km 90 of BR-156, Aldeia Tukai (MPEG 24439), Serra do Navio (MPEG 15080, 15087, 15100, 15148, 19592, 19627-31), Serra do Navio, Área Urucum (MPEG 19213); **Pará:** Cachoeira Porteira, Trombetas River (MPEG 16264), Oriximiná, Cruz Alta, 6 km from Trombetas River (MPEG 15396), Oriximiná, Porto Trombetas (MPEG 24198); **FRENCH GUIANA:** Petit Saut, River Sinnamary (MPEG 15826, 15830, 15838, 15841-42); **SURINAME:** (MPEG 21823).

*Gonatodes caudiscutatus* (19): **ECUADOR: Guayas:** Guayaquil (MZUSP 9181-90, 54370-72), Balzar (MZUSP 9191); **Los Rios:** Palenque, Rio Palenque Science Center (RMNH 40149-153).

*Gonatodes ceciliae* (5): **TRINIDAD:** Arima, Spring Hill Estate Arima Vallei (RMNH 10160), Maracas, River ly Maracas (RMNH 14913); **VENEZUELA: Sucre:** San Juan de Iás Galdonas (RMNH 40134-35; MZUSP 53553).

*Gonatodes eladioi* (1): **BRAZIL: Pará:** Marabá, Salobo, Serra dos Carajás (MPEG 18020).

*Gonatodes hasemani* (22): **BRAZIL: Pará:** Juruá, Rio Xingu (MZUSP 67240-57); **Rondônia:** Porto Velho, Área de inundação da UHE de Samuel (MPEG 15569-71), Porto Velho, Rio Yamary, Cachoeira do Samuel, Território do Guaporé (MNRJ 10678).

*Gonatodes humeralis* (16): **BRAZIL: Pará:** Piçarra (MNRJ 16107), Tucuruí, Lago da UHE Tucuruí (MPEG 21881-87). **PERU: Loreto:** Moropón (MZUSP 28280-87).

*Gonatodes taniae* (1): **VENEZUELA: Aragua:** Rancho Grande (MZUSP 57575).





## Figure Legends

**Figure 1.** Dorsal color patterns in preservative in *Gonatodes concinnatus* complex. (A) pattern A (MZUSP 54655); (B) pattern B (MZUSP 53674, holotype); (C) pattern C (MPEG 25596) and (D) pattern D (MZUSP 49153). Scale bar = 5 mm.

**Figure 2.** Ventral color pattern in preservative in *Gonatodes concinnatus* complex. (A) pattern A (MZUSP 54655); (B) pattern B (MZUSP 53674, holotype); (C) pattern C (MPEG 25596) and (D) pattern D (MZUSP 49153). Scale bar = 5 mm.

**Figure 3.** Bivariate scattergrams from stepwise discriminant function analysis (A) using scale counts and (B) measurements. Gray triangle = Pattern A. Black circles = Pattern B. Black squares = Pattern C. Gray circles = Pattern D.

**Figure 4.** *Gonatodes concinnatus* (MZUSP 54655). (A) Dorsal and (B) ventral views of head; ventral views of (C) right hand and (D) right foot; (E) ventral view of tail. Scale bar = 5 mm.

**Figure 5.** *Gonatodes concinnatus* (syntypes, BMNH 1946.9.7.10-12). (A) Dorsal, (B) ventral views. Scale bar = 5 mm.

**Figure 6.** Geographic distribution of *Gonatodes concinnatus* complex. Circles = *Gonatodes concinnatus*. Star = *Gonatodes tapajonicus*. Squares = *Gonatodes* sp. nov. 1. Triangles = *Gonatodes* sp. nov. 2. Numbers refer to the localities cited in the text.

**Figure 7.** *Gonatodes tapajonicus* (paratype, MZUSP 53674). (A) Dorsal and (B) ventral views of head; ventral views of (C) right hand and (D) right foot; (E) ventral view of tail. Scale bar = 5 mm.

**Figure 8.** *Gonatodes tapajonicus* from type-locality, Cachoeira do Limão, Pará, Brazil. (A) Adult male (holotype, MZUSP 53676). SVL = 53 mm and (B) Throat color pattern of male (holotype). (Photos by Miguel Rodrigues)

**Figure 9.** *Gonatodes* sp. nov. 1 (holotype, MPEG 25596). (A) Dorsal and (B) ventral views of head; ventral views of (C) right hand and (D) right foot; (E) ventral view of tail; detail of (F) dorsal scales of trunk and (G) tail. Scale bar = 5 mm.

**Figure 10.** *Gonatodes* sp. nov. 1 from Anapu, Rio Xingu, Pará, Brazil. (A) Adult male (paratype, MPEG 25598, SVL = 46.7 mm), (B) female in life (paratype, MPEG 25599, SVL = 39.7 mm) and (C) Throat color pattern of male (paratype, MPEG 25598). (Photos by Pedro Peloso)

**Figure 11.** *Gonatodes* sp. nov. 2 (holotype, MZUSP 49153). (A) Dorsal and (B) ventral views of head; ventral views of (C) right hand and (D) right foot; (E) ventral view of tail; detail of (F) dorsal scales of trunk and (G) tail. Scale bar = 5 mm.

## Tables

**Table 1.** Comparative data among color patterns.

Patterns	Throat	Head dorsally	Back and limbs
A	Beige, immaculate	Beige without vermiculations	Brown and beige vermiculations
B	White with black oblique stripes (in life, vivid yellow with reddish-brown oblique stripes)	Brown and beige vermiculations (in life, vivid yellow and reddish-brown vermiculations)	Brown and beige vermiculations (in life, vivid yellow and reddish-brown vermiculations)
C	White or dark-brown with black and white oblique stripes (in life, orange with orange yellow oblique stripes)	Dark-brown and beige vermiculations (in life, orange with orange yellow vermiculations)	Dark-brown and beige vermiculations (in life, orange with orange yellow vermiculations)
D	Brown, immaculate	Beige without vermiculations	Brown and beige small vermiculations

**Table 2.** Results of stepwise discriminant function analysis of scale counts comparing the four groups identified on basis of color pattern. 1DF: loadings on the first principal component; 2DF loadings on the second principal component.

	F(+ent,-rem)	Wilks's Lambda	Approx. F-ratio	p-value	1DF	2DF
DSL2T	44.679	0.33	44.679	0	0.65	-0.008
PSL4T	36.711	0.122	40.249	0	-0.057	-0.696
IL	13.583	0.075	34.527	0	0.42	-0.441
PSL2F	9.406	0.052	28.557	0	-0.669	-0.2
VLR	4.36	0.043	25.084	0	0.473	0.056
SL	3.939	0.036	21.598	0	0.072	-0.001

**Table 3.** Classification matrix and Jackknifed classification matrix of stepwise discriminant function analysis using scale counts.

Pattern	Classification Matrix					Jackknifed Classification Matrix				
	A	B	C	D	%correct	A	B	C	D	%correct
Pattern A	26	0	0	0	100.0%	24	2	0	0	100.0%
Pattern B	2	5	0	0	71.4%	2	5	0	0	71.4%
Pattern C	0	0	23	0	100.0%	0	0	23	0	100%
Pattern D	0	0	0	14	100.0%	1	0	0	13	92.9%
Total	28	5	23	14	97.1%	27	7	23	13	92.9%

**Table 4. Results of** stepwise discriminant function analysis of measurements comparing the four groups identified on basis of color pattern. 1DF: loadings on the first principal component; 2DF loadings on the second principal component.

	F(+ent,-rem)	Wilks's Lambda	Approx. F-ratio	p-value	1DF	2DF
MSL	33.213	0.398	33.213	0	-0.561	0.198
HW	18.501	0.215	25.068	0	0.214	0.869
RL	14.107	0.129	23.599	0	0.455	0.579
SSL	8.252	0.093	20.13	0	0.63	0.162
RSW	7.684	0.068	19.317	0	-0.525	0.34
IOD	6.796	0.051	17.962	0	0.528	-0.201

**Table 5.** Classification matrix and Jackknifed classification matrix of size-free stepwise discriminant function analysis using measurements.

Pattern	Classification Matrix					Jackknifed Classification Matrix				
	A	B	C	D	%correct	A	B	C	D	%correct
A	26	0	0	0	100.0%	26	0	0	0	100.0%
B	1	4	0	3	57.1%	1	4	0	2	57.1%
C	0	1	22	0	95.7%	0	1	22	0	95.7%
D	1	2	0	11	78.6%	1	3	0	10	71.4%
Total	28	7	22	14	90.0%	28	8	22	12	88.6%

**Table 6.** Snout-vent length and body proportions of *Gonatodes concinnatus*, *Gonatodes tapajonicus*, *Gonatodes* sp. nov. 1 and *Gonatodes* sp. nov. 2. Abbreviations are listed in Material and Methods. *sd*=standard deviation; *N*=number of specimens. Tail length of specimens with broken or regenerated tail was excluded.

Measurement or body proportion	<i>Gonatodes concinnatus</i>				<i>Gonatodes tapajonicus</i>				<i>Gonatodes</i> sp. nov. 1				<i>Gonatodes</i> sp. nov. 2			
	Range	Mean	<i>sd</i>	<i>N</i>	Range	Mean	<i>sd</i>	<i>N</i>	Range	Mean	<i>sd</i>	<i>N</i>	Range	Mean	<i>sd</i>	<i>N</i>
SVL	25.9–48.3	41.60	6.70	26	37.8–51.4	46.10	4.80	7	22.3–55.7	45.00	9.50	23	34.1–45.8	40.90	3.10	14
TL/SVL	1.07–1.16	1.16	0.07	8	1.21–1.23	1.22	0.02	2	1.11–1.26	1.20	0.05	8	1.06–1.32	1.19	0.18	2
HL/SVL	0.23–0.27	0.24	0.01	26	0.22–0.25	0.23	0.10	7	0.21–0.28	0.24	0.02	23	0.22–0.25	0.24	0.01	14
HL/HW	1.30–1.56	1.44	0.06	26	1.45–1.58	1.50	0.06	7	1.21–1.56	1.41	0.08	23	1.44–1.58	1.44	0.05	12
HW/HD	1.31–1.66	1.43	0.10	26	1.28–1.44	1.36	0.05	7	1.17–1.54	1.40	0.10	23	1.25–1.63	1.44	0.11	14
ED/HL	0.19–0.24	0.21	0.10	26	0.21–0.25	0.23	0.01	7	0.20–0.27	0.22	0.02	23	0.20–0.23	0.22	0.01	14
IOD/HW	0.25–0.35	0.31	0.02	26	0.34–0.42	0.38	0.03	7	0.22–0.31	0.25	0.02	23	0.30–0.38	0.35	0.02	14
IND/HW	0.20–0.28	2.10	0.30	25	0.21–0.27	0.25	0.02	7	0.14–0.21	0.17	0.01	23	0.23–0.27	0.25	0.01	14
SSW/SSL	0.82–2.34	1.21	0.28	26	0.99–1.40	1.19	0.16	7	0.88–1.44	1.13	0.13	23	0.91–1.61	1.24	0.19	14
RSW/RSW	1.89–2.35	2.15	0.14	26	1.86–2.21	2.02	0.15	7	1.78–3.01	2.02	0.28	23	1.65–2.19	1.93	0.13	14
MSW/MSL	1.02–1.25	1.13	0.07	26	1.07–1.39	1.21	0.11	7	1.17–1.41	1.28	0.07	23	1.20–1.51	1.32	0.09	14
FL/SLV	0.36–0.42	0.40	0.01	26	0.37–0.44	0.40	0.03	7	0.38–0.44	0.41	0.02	23	0.27–0.40	0.38	0.04	14
HLL/SLV	0.47–0.56	0.51	0.01	26	0.45–0.54	0.51	0.04	7	11.7–28.6	22.70	4.50	23	16.7–21.8	19.70	1.40	14

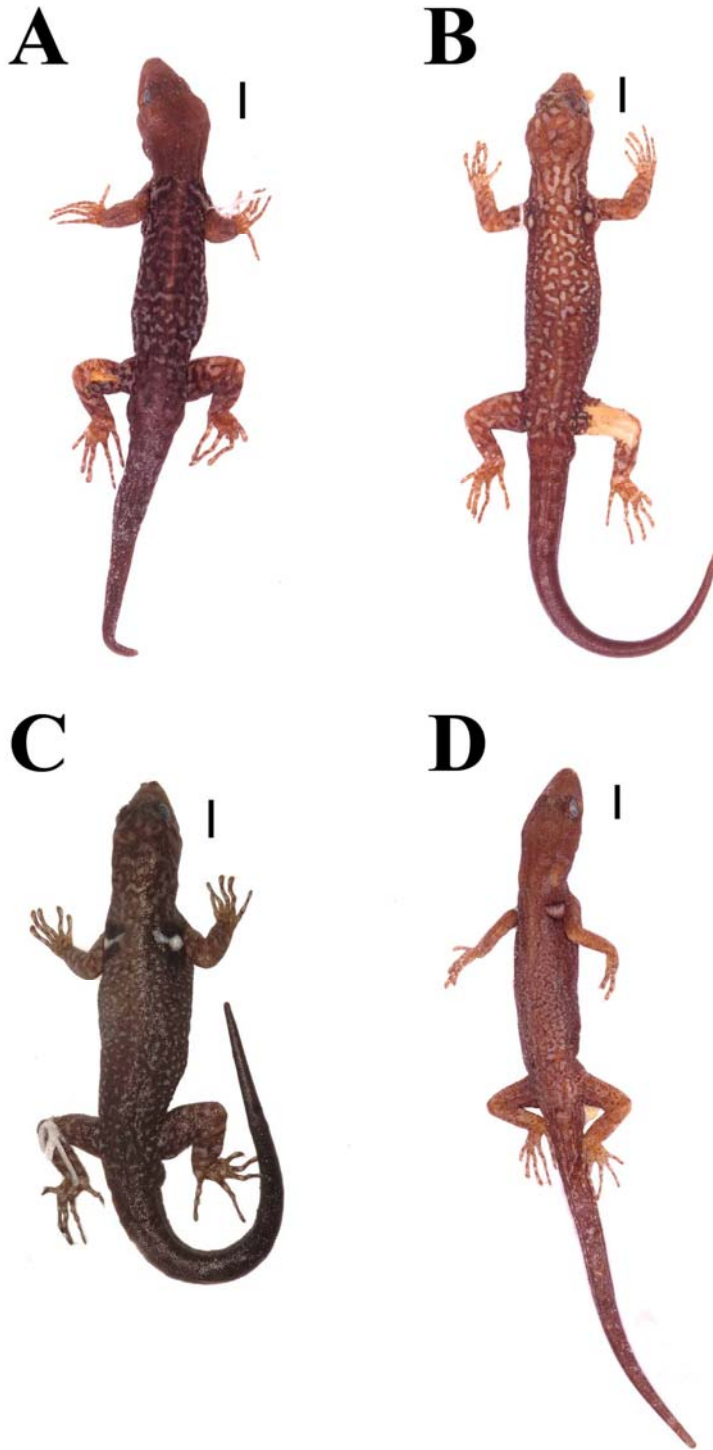


**Table 7.** Scale counts of specimens of *Gonatodes concinnatus*, *Gonatodes tapajonicus*, *Gonatodes* sp. nov. 1 and *Gonatodes* sp. nov.

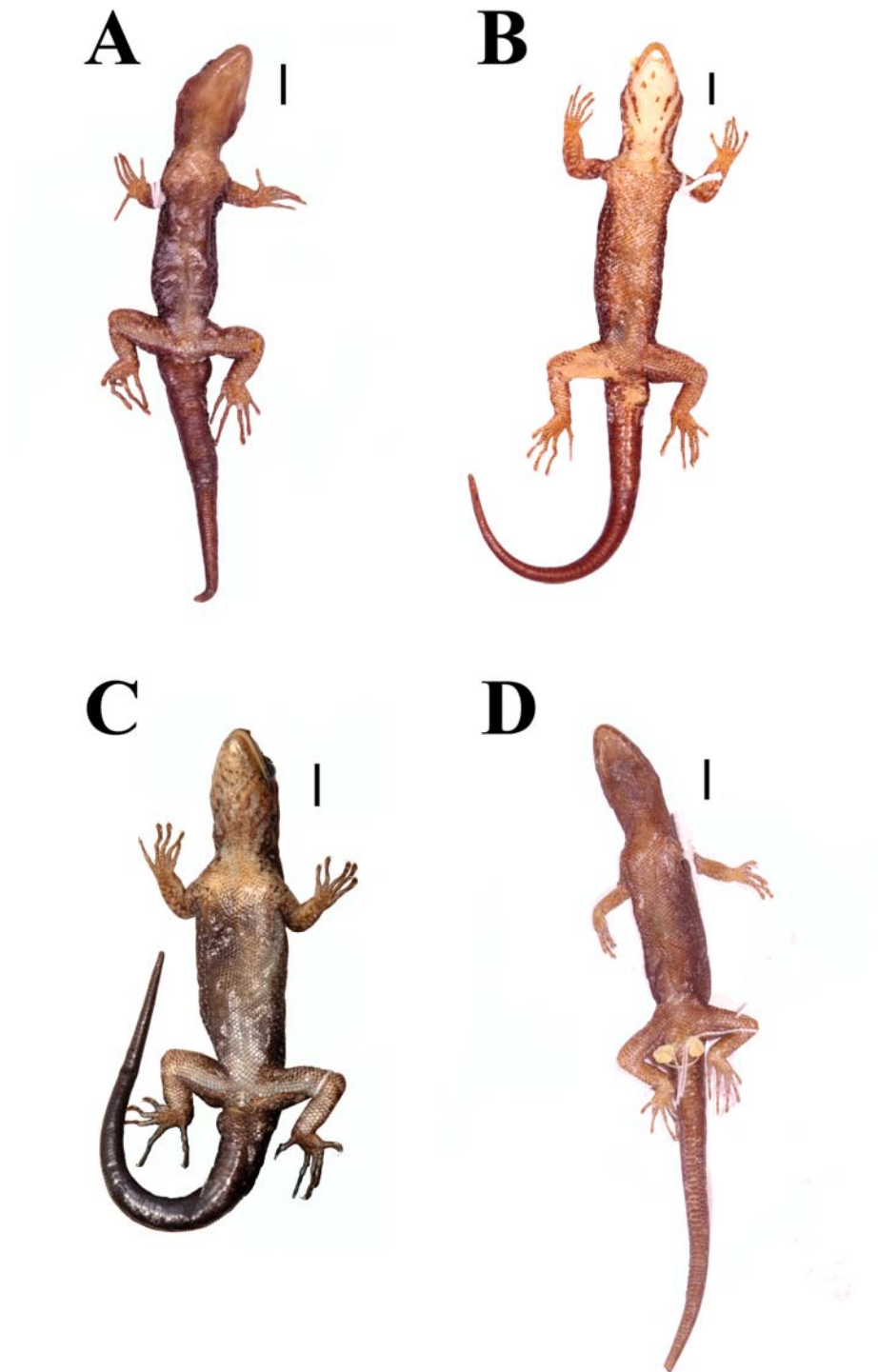
2. Abbreviations are listed in Material and Methods. *sd*=standard deviation; *N*=number of specimens.

Scales counts	<i>Gonatodes concinnatus</i>				<i>Gonatodes tapajonicus</i>				<i>Gonatodes</i> sp. nov. 1				<i>Gonatodes</i> sp. nov. 2			
	Range	Mean	<i>sd</i>	<i>N</i>	Range	Mean	<i>sd</i>	<i>N</i>	Range	Mean	<i>sd</i>	<i>N</i>	Range	Mean	<i>sd</i>	<i>N</i>
SAM	109–128	120.6	5.3	25	120–126	122.8	2.3	6	118–143	130.0	6.5	21	100–124	113.5	6.1	14
VVR	49–58	55.0	2.3	25	53–59	55.8	2.2	6	52–60	56.2	2.5	21	44–56	50.4	3.6	14
VLR	17–20	18.5	1.0	25	19–20	19.5	0.5	6	18–24	21.2	1.3	21	17–19	17.7	0.7	14
SL	6–7	6.3	0.5	26	6–8	7.0	0.8	7	5–7	6.2	0.5	23	6–7	6.2	0.4	14
IL	5–7	6.0	0.8	26	5–7	6.1	0.7	7	5–8	6.3	0.9	23	4–6	5.6	0.6	14
PR	3–5	3.5	0.8	26	3–5	3.3	0.8	7	2–4	3.0	0.4	23	2–5	3.1	0.6	14
SP	1–3	1.5	0.8	26	1–3	1.3	0.8	7	0–2	1.0	0.4	23	0–3	1.1	0.6	14
SIS	4–6	5.0	0.4	26	5–7	6.1	0.7	7	4–8	6.0	0.8	23	4–7	5.1	0.8	14
PN	3–4	3.1	0.3	26	3–4	3.3	0.5	7	3	3.0	0.0	23	2–3	2.9	0.3	14
LS	9–13	10.7	0.9	26	10–13	11.1	0.9	7	10–13	11.2	0.9	23	9–11	10.0	0.8	14
PM	2–4	2.3	0.6	26	2–3	2.3	0.5	7	2–3	2.0	0.2	23	2–3	2.3	0.5	14
CM1IL	5–8	6.8	0.9	26	6–8	6.7	0.8	7	6–8	7.0	0.8	23	6–10	7.7	1.3	14
SCS	6–10	8.3	1.1	26	7–10	8.1	1.1	7	7–12	9.4	1.4	23	7–10	8.4	1.0	14
SSC	0–4	1.7	1.5	26	2–4	2.9	0.7	7	0–3	1.1	1.2	23	0–3	2.1	1.1	14
PSL2F	5–7	6.0	0.3	26	6	6.0	0.0	7	4–6	5.1	0.4	23	5–6	5.7	0.5	14
DSL2F	8–12	1.2	1.1	26	10–12	10.3	0.8	7	10–13	11.8	0.9	23	7–11	8.9	1.0	14
SL2F	14–18	16.2	1.2	26	16–18	16.3	0.8	7	15–19	16.9	1.1	23	13–17	14.6	1.1	14
LRS2F	3–4	3.1	0.3	26	3–4	3.1	0.4	7	3–4	3.1	0.3	23	2–3	2.9	0.3	14
PSL3F	6–7	6.3	0.5	26	6–7	6.1	0.4	7	5–6	5.4	0.5	23	5–6	5.9	0.3	14
DSL3F	11–14	12.1	0.9	26	12–14	13.1	0.7	7	13–16	14.3	1.0	23	9–13	11.1	1.2	14
SL3F	17–20	18.6	1.1	26	18–20	19.3	0.8	7	18–22	19.7	1.3	23	15–19	17.1	1.2	14
LRS3F	3–4	3.0	0.2	26	3–4	3.1	0.4	7	3–4	3.2	0.4	23	2–3	2.8	0.4	14
PSL4F	7–9	7.7	0.6	26	7–8	7.4	0.5	7	6–8	6.6	0.7	23	6–8	7.0	0.7	14
DSL4F	10–14	12.1	0.9	26	11–14	12.9	1.1	7	12–16	13.9	1.0	23	9–13	10.7	1.1	14
SL4F	17–22	19.7	1.1	26	18–22	20.3	1.3	7	18–23	20.5	1.2	23	16–21	17.7	1.5	14

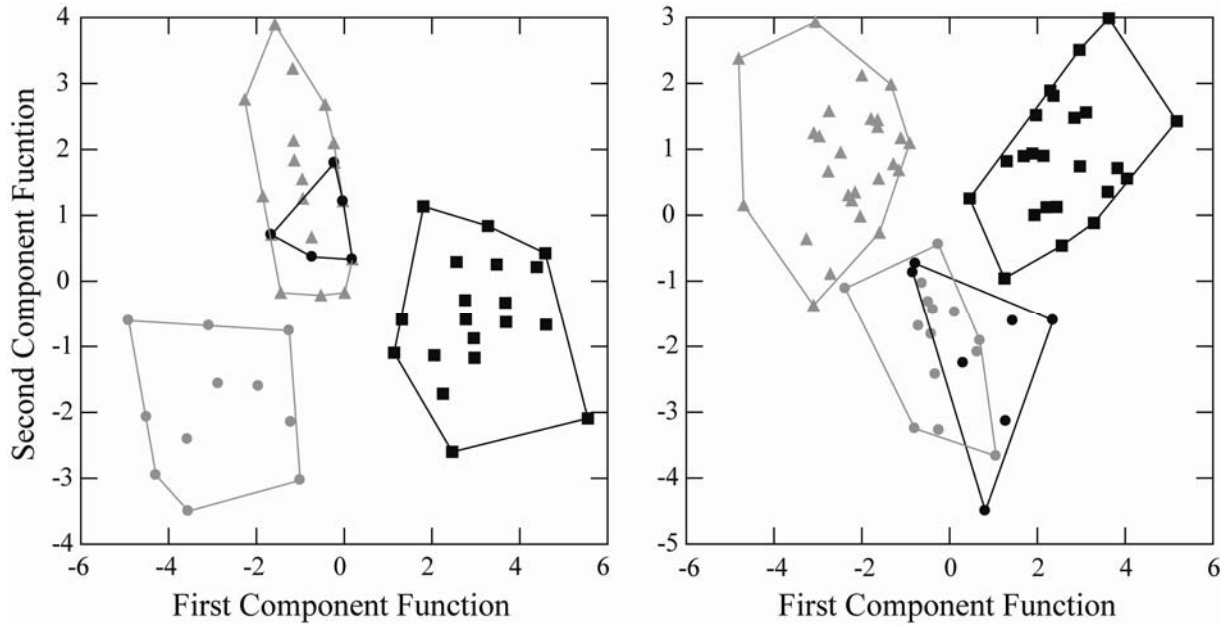
LRS4F	3	3.0	0.0	26	3-4	3.1	0.4	7	3-4	3.2	0.4	23	2-3	2.7	0.5	14
PSL2T	6-7	6.2	0.4	26	5-6	5.9	0.4	7	5-6	5.3	0.4	23	5-6	5.7	0.5	14
DSL2T	8-11	10.0	0.8	26	10-11	10.4	0.5	7	10-14	12.0	1.0	23	7-11	8.6	1.1	14
SL2T	14-18	16.2	1.0	26	15-17	16.3	0.8	7	15-19	17.3	1.1	23	12-17	14.4	1.2	14
LRS2T	3-4	3.0	0.2	26	3-4	3.4	0.5	7	3-4	3.3	0.5	23	3	3.0	0.0	14
PSL3T	6-8	7.0	0.6	26	6-8	7.1	0.9	7	5-7	6.1	0.7	23	6-7	6.1	0.3	14
DSL3T	11-15	12.7	1.0	26	12-15	13.4	1.0	7	13-17	14.8	1.2	23	10-13	11.4	1.2	14
SL3T	18-22	19.7	1.2	26	19-22	20.6	1.0	7	18-23	20.9	1.3	23	16-20	17.5	1.3	14
LRS3T	3-4	3.1	0.3	26	3-4	3.1	0.4	7	3-4	3.2	0.4	23	2-3	2.9	0.3	14
PSL4T	11-15	12.2	1.0	26	11-12	11.6	0.5	7	9-12	10.3	0.7	23	9-11	9.8	0.8	14
DSL4T	11-14	12.5	1.0	26	11-15	13.4	1.5	7	13-16	14.3	1.0	23	9-13	11.1	1.2	14
SL4T	22-27	24.7	1.5	26	23-27	25.0	1.5	7	23-28	24.7	1.5	23	18-24	20.9	1.7	14
LRS4T	3-4	3.2	0.4	26	3-4	3.4	0.5	7	3-4	3.3	0.5	23	2-3	2.8	0.4	14
RSE	4-5	4.1	0.4	15	4	4.0	0.0	2	4-5	4.4	0.5	16	4-5	4.3	0.5	4



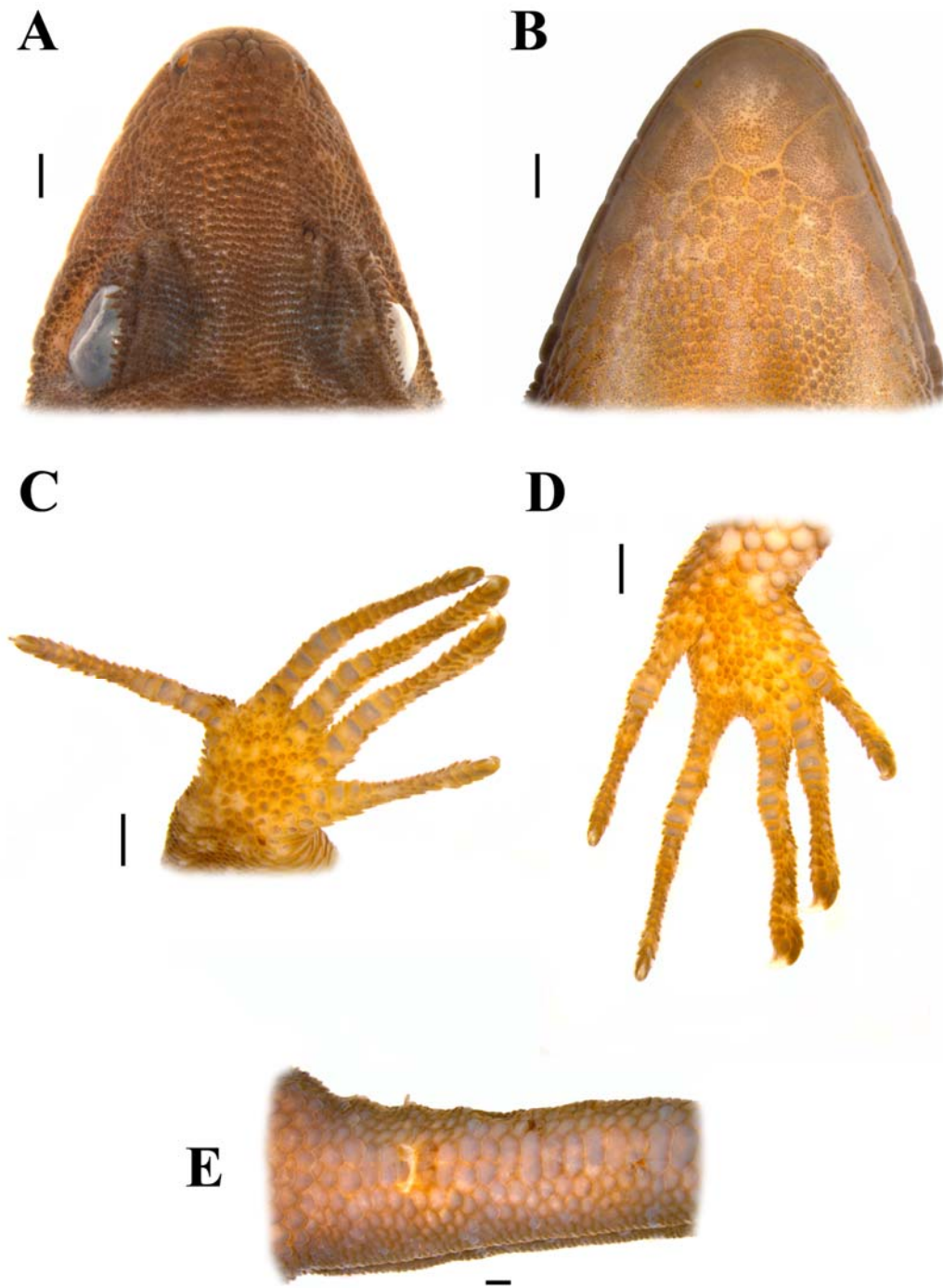
**Figure 1.** Dorsal color patterns in preservative in *Gonatodes concinnatus* complex. (A) pattern A (MZUSP 54655); (B) pattern B (MZUSP 53674, holotype); (C) pattern C (MPEG 25596) and (D) pattern D (MZUSP 49153). Scale bar = 5 mm.



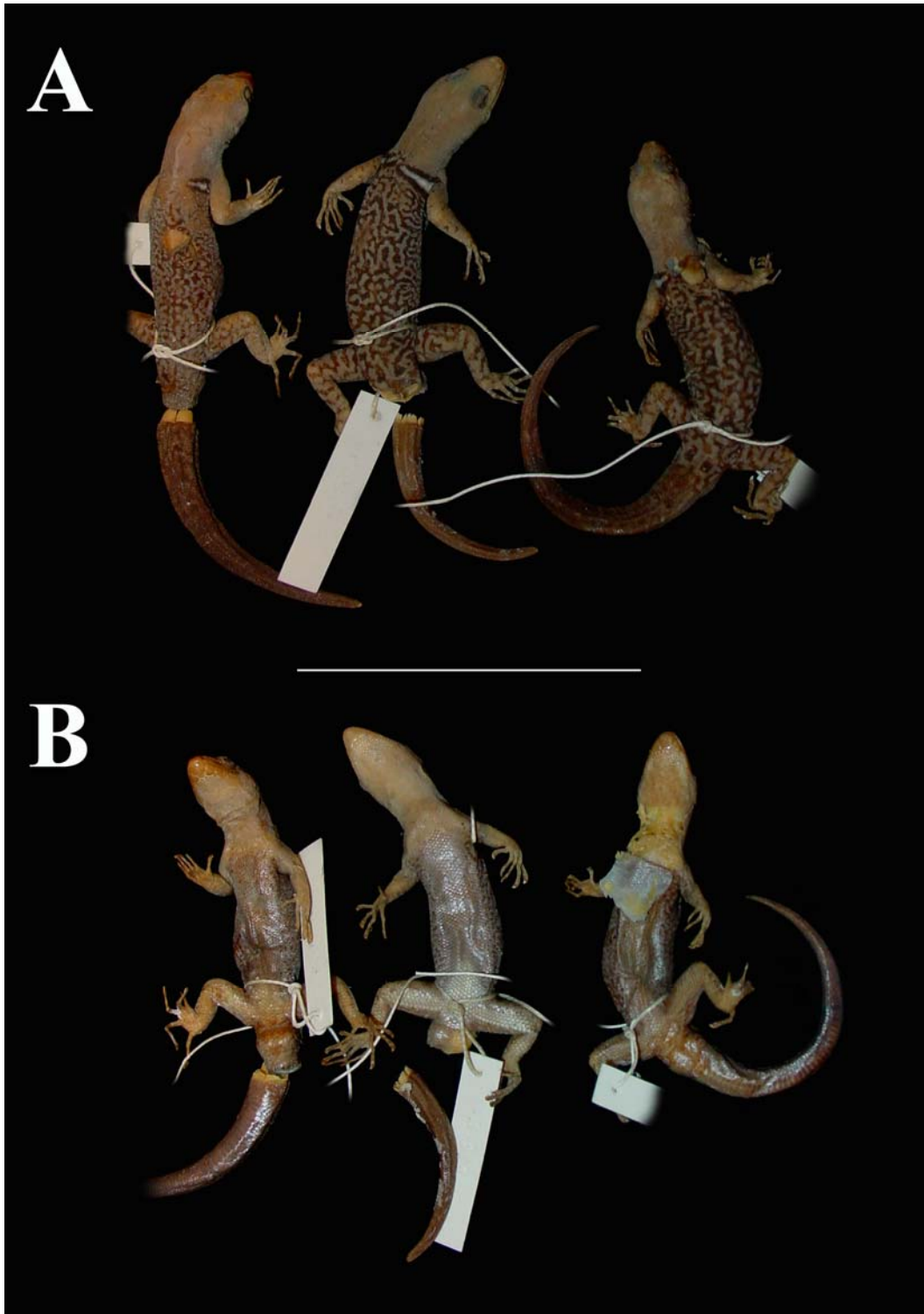
**Figure 2.** Ventral color pattern in preservative in *Gonatodes concinnatus* complex. (A) pattern A (MZUSP 54655); (B) pattern B (MZUSP 53674, holotype); (C) pattern C (MPEG 25596) and (D) pattern D (MZUSP 49153). Scale bar = 5 mm.



**Figure 3.** Bivariate scattergrams from Stepwise Discriminant Function Analysis (A) using scale counts and (B) measurements. Gray triangle = Pattern A. Black circles = Pattern B. Black squares = Pattern C. Gray circles = Pattern D.

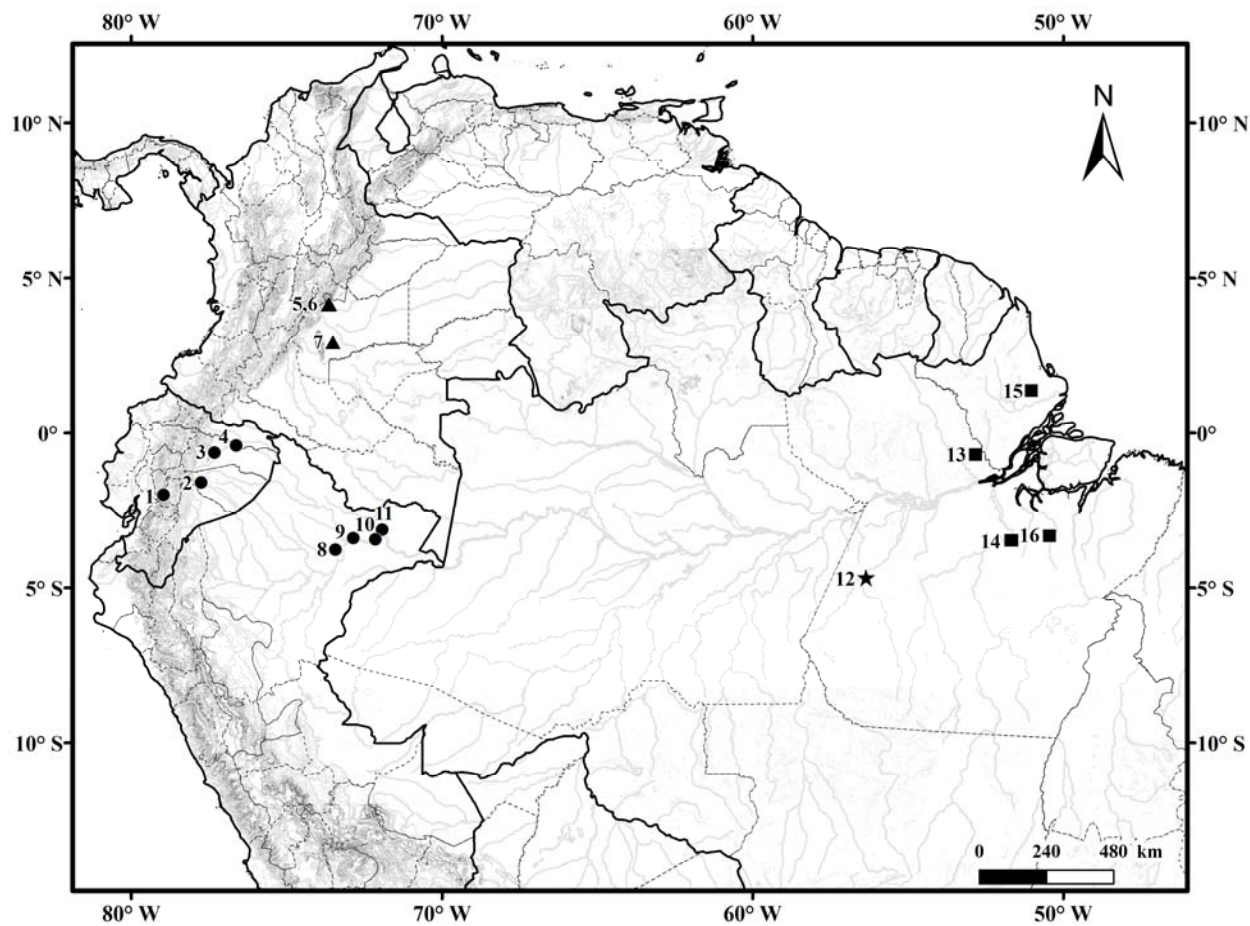


**Figure 4.** *Gonatodes concinnatus* (MZUSP 54655). (A) Dorsal and (B) ventral views of head; ventral views of (C) right hand and (D) right foot; (E) ventral view of tail. Scale bar = 5 mm.



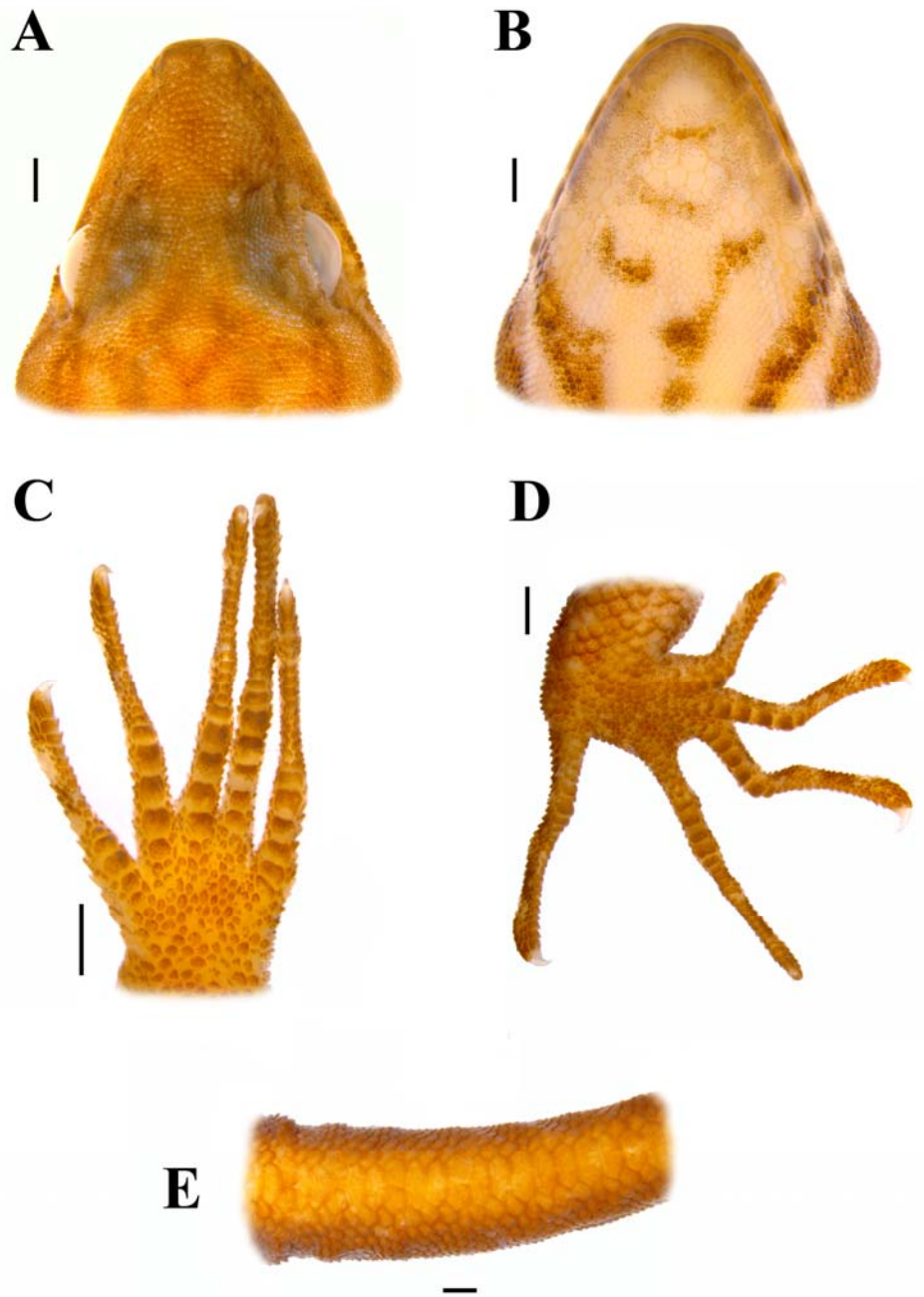
**Figure 5.** *Gonatodes concinnatus* (syntypes, BMNH 1946.9.7.10-12). (A) Dorsal, (B) ventral views. Scale bar = 5 mm.





**Figure 6.** Geographic distribution of *Gonatodes concinnatus* complex, except for Venezuela, from where no specimens were included in the present study. Circles = *Gonatodes concinnatus*. Star = *Gonatodes tapajonicus*. Squares = *Gonatodes* sp. nov. 1. Triangles = *Gonatodes* sp. nov. 2. Numbers refer to the localities cited in the text.

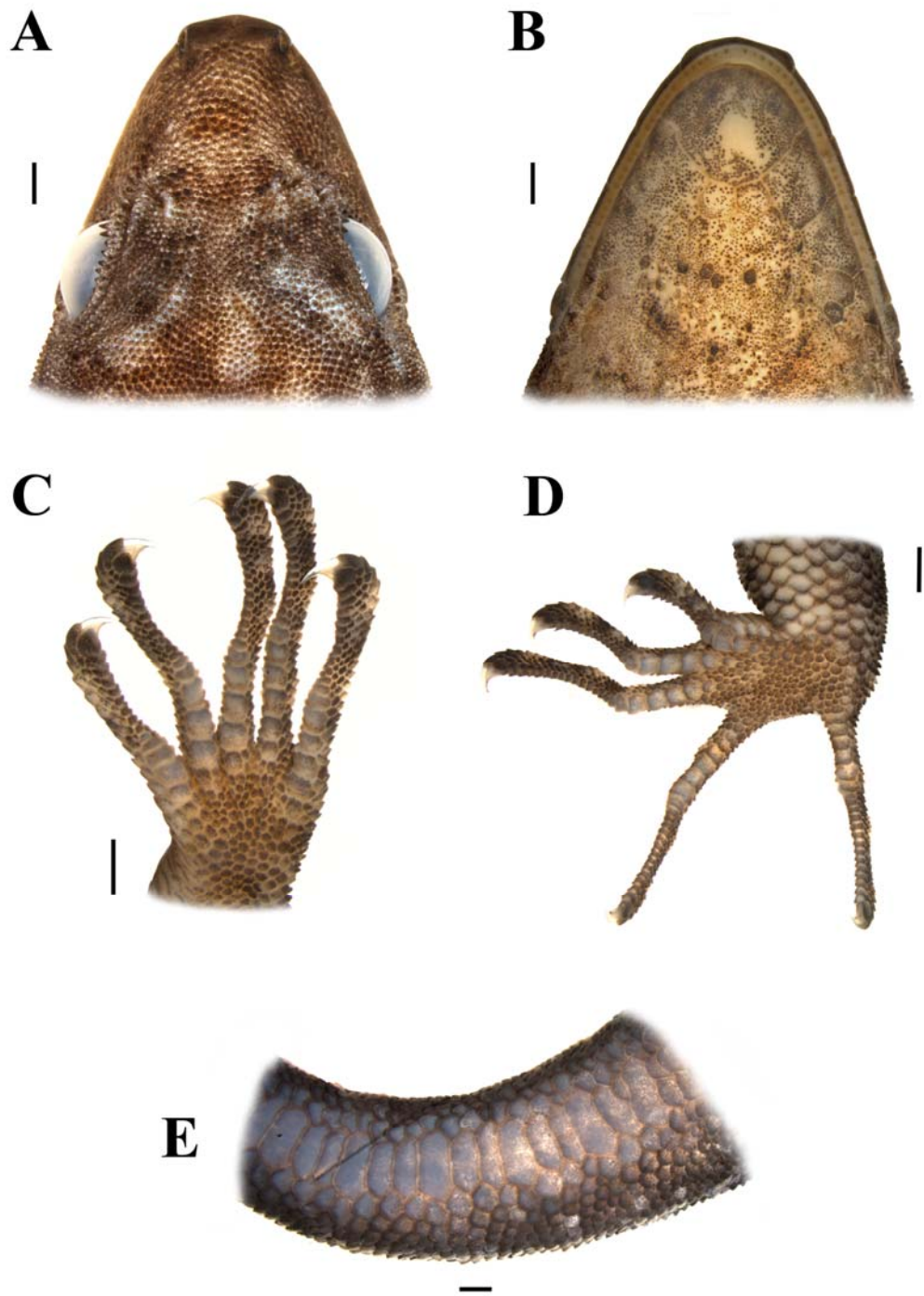




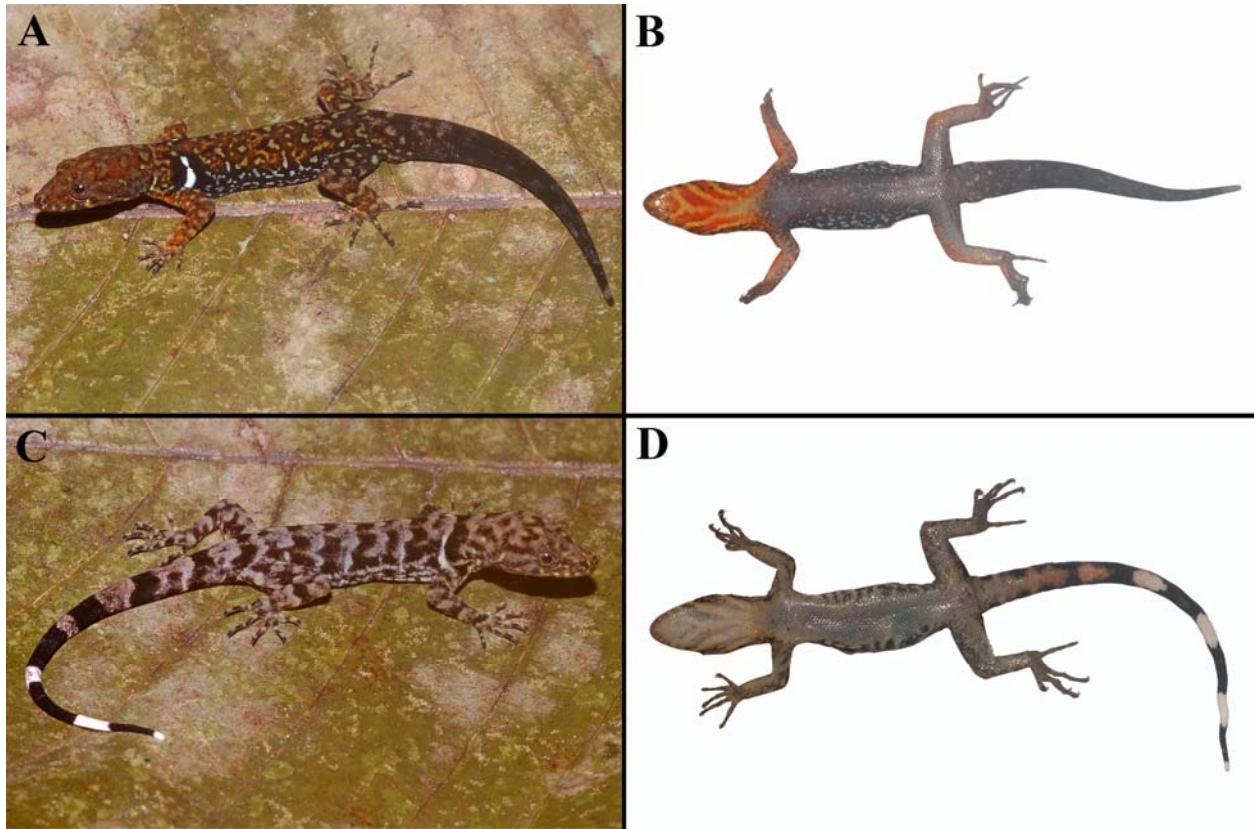
**Figure 7.** *Gonatodes tapajonicus* (paratype, MZUSP 53674). (A) Dorsal and (B) ventral views of head; ventral views of (C) right hand and (D) right foot; (E) ventral view of tail. Scale bar = 5 mm.



**Figure 8.** *Gonatodes tapajonicus*, from type-locality, Cachoeira do Limão, Pará, Brazil. (A) Adult male (holotype, MZUSP 53676). SVL = 53 mm and (B) Throat color pattern of male (holotype). (Photos by Miguel T. Rodrigues)

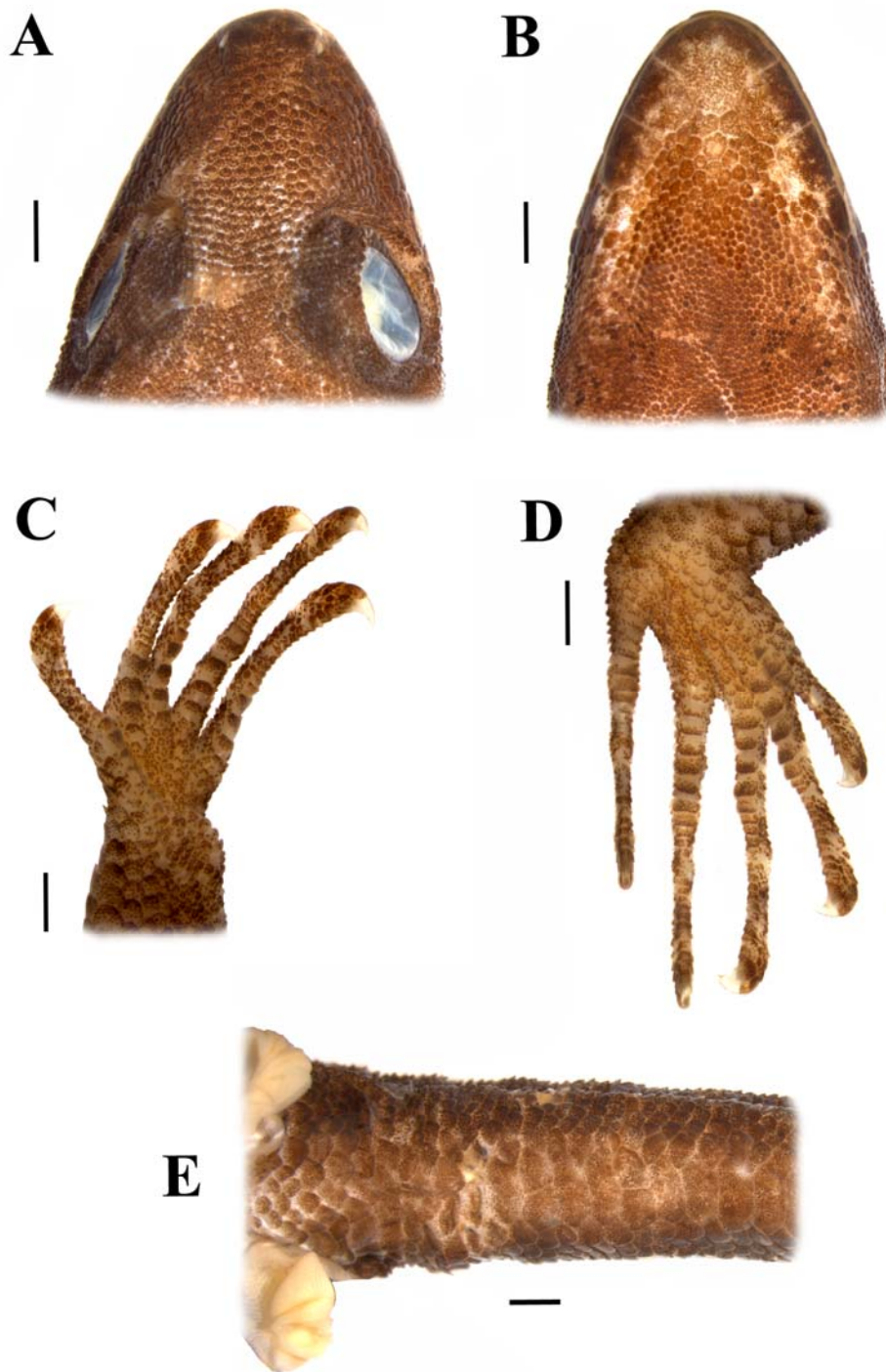


**Figure 9.** *Gonatodes* sp. nov. 1 (holotype, MPEG 25596). (A) Dorsal and (B) ventral views of head; ventral views of (C) right hand and (D) right foot; (E) ventral view of tail; detail of (F) dorsal scales of trunk and (G) tail. Scale bar = 5 mm.



**FIGURE 10.** *Gonatodes* sp. nov. 1 from Anapu, Rio Xingu, Pará, Brazil. (A) Adult male (paratype, MPEG 25598, SVL = 46.7 mm), (B) Throat color pattern of male (paratype, MPEG 25598), (C) female in life (paratype, MPEG 25599, SVL = 39.7 mm) and (D) throat color pattern of female (paratype, MPEG 25599) (Photos by Pedro L. V. Peloso).





**Figure 11.** *Gonatodes* sp. nov. 2 (holotype, MZUSP 49153). (A) Dorsal and (B) ventral views of head; ventral views of (C) right hand and (D) right foot; (E) ventral view of tail; detail of (F) dorsal scales of trunk and (G) tail. Scale bar = 5 mm.