

Phyllomedusa 14(1):53–62, 2015

© 2015 Universidade de São Paulo - ESALQ

ISSN 1519-1397 (print) / ISSN 2316-9079 (online)

doi: <http://dx.doi.org/10.11606/issn.2316-9079.v14i1p53-62>

Reproduction in a gecko assemblage (Squamata: Phyllodactylidae) in the Marañón Region (Peru) and comments on the largest gecko in the New World

Janina Aurich, Claudia Koch, and Wolfgang Böhme

Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Adenauerallee 160, 53113 Bonn, Germany. E-mail: c.koch@zfmk.de

Abstract

Reproduction in a gecko assemblage (Squamata: Phyllodactylidae) in the Marañón Region (Peru) and comments on the largest gecko in the New World. Reproduction is described for four phyllodactylid geckos, *Phyllopezus marañonensis*, *Phyllodactylus delsolari*, *P. thompsoni* and *P. reissii* from the upper Marañón Valley, Peru. Observations were made between March and May 2010 and voucher specimens, already housed in the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), were X-rayed to check for gravid females. Gravid female *P. marañonensis*, *P. delsolari* and *P. reissii* contain two eggs, whereas *P. thompsoni* produces a single egg that is deposited in leaf litter or crevices of stone walls. It is likely that females of all of these species produce multiple clutches in one year; the reproductive period seems to be extended in at least two species. Furthermore, measurements of numerous specimens of all four species are presented herein, revealing that *Phyllopezus marañonensis* is the largest species of New World geckos.

Keywords: Equatorial dry forest, gravid females, Marañón Valley, *Phyllopezus marañonensis*, *Phyllodactylus delsolari*, *Phyllodactylus reissii*, *Phyllodactylus thompsoni*, reproductive cycle, X-ray.

Resumo

Reprodução em uma taxocenose de lagartixas (Squamata: Phyllodactylidae) na região de Marañón (Peru) e comentários sobre a maior lagartixa do Novo Mundo. Descrevemos aqui a reprodução de quatro lagartixas da família Phyllodactylidae, *Phyllopezus marañonensis*, *Phyllodactylus delsolari*, *P. thompsoni* e *P. reissii*, do Vale do Alto Marañón, Peru. As observações foram feitas entre março e maio de 2010, e os espécimes-testemunhos, depositados no Zoologisches

Received 19 January 2015.

Accepted 15 June 2015.

Distributed June 2015.

Forschungsmuseum Alexander Koenig (ZFMK), foram radiografados para verificar a presença de fêmeas ovígeras. As fêmeas ovígeras de *P. marañonensis*, *P. delsolari* e *P. reissii* portavam dois ovos, enquanto *P. thompsoni* produz um único ovo, que é depositado na serapilheira ou em frestas de paredões rochosos. As fêmeas de todas as espécies são mais provavelmente capazes de produzir desovas múltiplas ao longo do ano; o período reprodutivo parece prolongado em pelo menos duas espécies. Adicionalmente, medidas de diversos espécimes das quatro espécies são apresentadas aqui, revelando que *Phyllopezus marañonensis* é a maior espécie de lagartixa do Novo Mundo.

Palavras-chave: ciclo reprodutivo, Floresta Equatorial seca, fêmeas ovígeras, Vale do Marañon, *Phyllopezus marañonensis*, *Phyllodactylus delsolari*, *Phyllodactylus reissii*, *Phyllodactylus thompsoni*, raios-X.

Introduction

The two genera studied here, viz. *Phyllodactylus* Gray, 1828 and *Phyllopezus* Peters, 1877, were recently grouped into the family Phyllodactylidae (Gamble *et al.* 2008). At present 134 species, belonging to 10 genera, are recognized in the family.

The Neotropical genus *Phyllodactylus* is composed of 52 species, including the recently described *P. delsolari* Venegas, Townsend, Koch and Böhme, 2008, *P. leoni* Torres-Carvajal, Carvajal-Campos Barnes, Nicholls and Pozo-Andrade, 2013, *P. papenfussi* Murphy, Blair and De la Cruz, 2009, *P. paralepis* McCranie and Hedges, 2013, and *P. thompsoni* Venegas, Townsend, Koch and Böhme, 2008. With respect to reproduction, a clutch size of a single egg seems to be typical for most species within the genus *Phyllodactylus* and communal egg-laying in rock crevices seems to be a common habit (Dixon and Huey 1970, López-Victoria *et al.* 2013, Williams *et al.* 2015). Extended reproduction periods and multiple clutches are known for several *Phyllodactylus* species, such as for the Peruvian species *P. kofordi* Dixon & Huey 1970 and *P. reissii* Peters, 1862 (Dixon and Huey 1970, Goldberg 2007, Murphy *et al.* 2009).

The genus *Phyllopezus* contains four species—*P. marañonensis* Koch, Venegas and Böhme, 2006, *P. periosus* Rodrigues, 1986, *P. pollicaris* (Spix, 1825) and the former *Bogertia lutzae* Loveridge, 1941, which recently was

placed in the genus *Phyllopezus* (Gamble *et al.* 2012). Vitt (1986) collected gravid female *P. pollicaris* from a population of the Caatinga in Pernambuco, Brazil, during several different months of the year. Each of these females either contained two oviductal eggs or enlarged vitellogenic follicles, suggesting a nearly continuous reproductive cycle for this species. In contrast, in their study of the reproductive ecology of a population of *P. pollicaris* from a montane environment in Minas Gerais, Brazil, Righi *et al.* (2012) only found reproductive females between August and December, suggesting a cyclical reproduction of about 5 mo. Each of the six gravid females they examined contained two shelled oviductal eggs; the estimated time to produce a clutch was 3 mo. Between the end of January and early February 2008, Recoder *et al.* (2012) conducted an investigation of a population of *P. pollicaris* from the Cerrado of central Brazil and suggested cyclical reproduction in Cerrado populations. According to Vitt (1986), *P. pollicaris pollicaris* deposits its eggs in rock crevices, in groups of 2–6 eggs produced by 1–3 females. The only information about reproduction in *P. periosus* is from Lima *et al.* (2011) who observed a clutch of eight eggs in a rock crevice in the Caatinga of Ceará, Brazil, on 21 February 2009, suggesting communal oviposition for this species as well.

During our research on the herpetofauna of the Balsas Region in the upper Marañon Valley, Peru, we investigated a gecko assemblage of

four syntopic species—*Phyllopezus maranjonensis*, *Phyllodactylus reissii*, *P. delsolari*, and *P. thompsoni*. Three of these species were described recently; thus, almost no information exists on their reproduction, except for measurements of eggs of three gravid *P. delsolari* (Venegas *et al.* 2008). Herein, we add information about their reproductive biology, and present morphological data for each of the four species.

Materials and Methods

The study was conducted in the region of Balsas (06°49' S, 78°00' W, 850 m a.s.l.) and other parts of the upper Marañón Valley, which forms part of the Equatorial Dry Forest Ecoregion (Brack 1986). The Río Marañón Valley lies between the Cordillera Central and Codillera Occidental, and forms the border between the Cajamarca and Amazonas regions in this area. The vegetation of this arid habitat is a thorn forest with various cacti (*Cereus*, *Opuntia*, *Lemaireocereus*) and drought-resistant trees (*Acacia*, *Bursera*, *Capparis*) predominating (Duellman and Pramuk 1999, Koch *et al.* 2006). Solid vertical rock faces edge the roads in this region and the river-bed of the "Quebrada Honda," a tributary of the Río Marañón.

The study was carried out during five weeks in March, April, and May 2010 (26 March–18 April, and 20 May–29 May). Lizards were collected from six different localities around Balsas. Temperature and humidity were measured every day at 3 pm and 7 pm with a digital thermo-hygrometer (Extech) with an external sensor.

Lizards were monitored and collected during their nocturnal activity period, from just after sunset (approx. 19:00 h) to midnight or shortly after midnight (not later than 02:00 h). Geckos were located by means of headlights on rock faces, walls, in crevices of rocks or walls, and amidst shrubs. Individuals were captured by hand by grabbing them between the head and forelimbs. Each gecko was sexed, weighed (Pesola, to the nearest 0.25 g); the following

measurements were made with a tape measure (rounded to the nearest 1 mm) or a digital calipers, rounded to the nearest 1 mm: snout-vent length (SVL), head length (HL), head width (HW), forelimb length (FLL) and hind-limb length (HLL). All females were palpated manually to determine whether they contained eggs.

Twenty-one specimens of each of *Phyllopezus maranjonensis*, *Phyllodactylus delsolari* and *P. thompsoni* and eight specimens of *P. reissii* were collected as vouchers. The lizards were euthanized by a lethal injection of the anesthetic T61, fixed in a 10% formalin solution, and are stored in 70% ethanol in the herpetological collections of the Centro de Ornitología y Biodiversidad, Lima, Peru (CORBIDI) and the Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK). We painted a number on the base of the tail of other lizards that we collected with an Edding 40 marker with waterbased ink before releasing them. Successive numbers were used to re-identify the specimens later on.

All voucher specimens collected during this study were dissected to probe for reproductive output in females. If females were gravid, the eggs were removed, counted, and their widths and lengths recorded. In addition, 20 specimens of *Phyllopezus maranjonensis*, 22 *Phyllodactylus delsolari*, 23 *P. thompsoni*, and 9 *P. reissii*, already housed in the collections of the ZFMK, CORBIDI and the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM) were measured. Females housed in the ZFMK were X-rayed (Faxitron X-ray LX60) to check for gravidity (Appendix I), but autopsies were not performed on these specimens. Juveniles were identified by the absence of features that indicate sexual maturity.

Results

Body Size

Morphological data for adults of the four species are shown in Table 1. Mean SVL of *Phyllopezus maranjonensis* is 109.3 ± 9.3 mm in

adult males ($N = 42$) and 110.4 ± 8.8 mm in adult females ($N = 41$), and the maximum SVL is 128 mm for males and females. Mean SVL of *Phyllodactylus delsolari* is 75.1 ± 5.2 mm in adult males ($N = 33$) and 75.6 ± 5.9 mm in adult females ($N = 44$), and the maximum SVL in males is 84 mm and 89 mm in females. Mean SVL of *P. reissii* is 74.1 ± 3.7 mm in adult males ($N = 7$) and 73.6 ± 4.7 mm in adult females ($N = 7$), and the maximum SVL is 78 mm in males and 80 mm in females. Mean SVL of *P. thompsoni* is 39.0 ± 2.4 mm in adult males ($N = 63$) and 39.2 ± 3.5 mm in adult females ($N = 68$), and the maximum SVL is 45 mm in males and 46 mm in females.

Reproduction

Gravid females and juveniles were found of all four species during the study period (Table 2). In addition, X-rays (Figure 1) of females indicated that female *P. reissii* (ZFMK 88739, 88744, 88745, 90876, 90898) and *P. thompsoni* (ZFMK 91741, 91744, 91752) were also gravid in at other times during the year (Table 2).

Snout-vent length of juveniles are as follow: *Phyllopezus maranjonensis*, 64.0–79.5 mm; *Phyllodactylus delsolari*, 40.0–60.0 mm; *P. reissii*, 46.0–58.0 mm; and *P. thompsoni*, 21.0–30.0 mm.

Each gravid female *Phyllopezus maranjonensis* dissected contained two oviductal eggs, ranging from 1.5–19.5 mm long and 1.5–15.0 mm wide ($N = 7$; Figure 2, Table 3). Mean egg size was not calculated because the reproductive stages of the females varied. Each of the four dissected gravid *Phyllodactylus delsolari* (CORBIDI 7703, CORBIDI 7707, ZFMK 91714, ZFMK 91717) contained two eggs, as did the one gravid *P. reissii* (ZFMK 91725) examined. Of five dissected gravid *P. thompsoni*, four contained a single oviductal egg (CORBIDI 7717, ZFMK 91732, ZFMK 91735, ZFMK 91738); two of those eggs were measured, with the following sizes: 9.5×4.0 mm and 3.4×2.8 mm. One female had two eggs (ZFMK 91730),

Table 1. Morphological data of *Phyllopezus maranjonensis* (Pm), *Phyllodactylus delsolari* (Pd), *Phyllodactylus reissii* (Pr) and *Phyllodactylus thompsoni* (Pt). Data are provided as mean \pm SD (range).

	SVL (mm)	N	Weight (g)	N	HLL (mm)	N	FLL (mm)	N	HW (mm)	N	HL (mm)	N	
Pm	♂	109.3 \pm 9.3 (83–128)	42	32.0 \pm 6.9 (22–49.5)	32	50.4 \pm 4.6 (40–58)	22	39.3 \pm 3.2 (31–46)	22	25.2 \pm 3.1 (21–32)	23	34.0 \pm 3.0 (30–41)	27
	♀	110.4 \pm 8.8 (89–128)	41	33.6 \pm 9.4 (14.5–51)	34	49.4 \pm 4.2 (40–53)	31	37.5 \pm 3.2 (32–42)	31	24.5 \pm 2.6 (19–29)	31	33.0 \pm 3.2 (26–39)	34
Pd	♂	75.1 \pm 5.2 (63–84)	33	9.1 \pm 2.1 (4.5–13)	27	34.8 \pm 3.2 (29–40)	18	26.3 \pm 2.6 (21–30)	18	16.0 \pm 1.6 (13–19)	18	22.9 \pm 1.9 (20–26)	22
	♀	75.6 \pm 5.9 (63–89)	44	9.0 \pm 2.0 (4.7–13)	36	36.7 \pm 3.3 (29–47)	36	26.8 \pm 2.4 (21–32)	36	16.2 \pm 1.7 (12–19)	36	22.5 \pm 2.1 (18–28)	39
Pr	♂	74.1 \pm 3.7 (68–78)	7	9.9 \pm 2.0 (7–12.5)	7	31.9 \pm 2.0 (28–34)	7	24.7 \pm 2.4 (22–28)	7	15.6 \pm 1.7 (13–18)	7	22.0 \pm 1.5 (20–25)	7
	♀	73.6 \pm 4.7 (68–80)	7	8.7 \pm 1.3 (7–10.75)	7	32.0 \pm 2.3 (30–35)	7	25.0 \pm 1.2 (24–27)	7	15.6 \pm 1.1 (14–17)	7	22.1 \pm 1.1 (21–24)	7
Pt	♂	39.0 \pm 2.4 (31–45)	63	1.5 \pm 0.3 (1.0–2.0)	59	15.7 \pm 1.6 (11–17)	13	12.5 \pm 1.1 (10–14)	13	8.4 \pm 0.5 (8–9)	13	12.2 \pm 1.3 (10–14)	13
	♀	39.2 \pm 3.5 (31–46)	68	1.6 \pm 0.4 (0.7–2.5)	68	16.4 \pm 2.1 (13–21)	16	11.8 \pm 1.6 (9–14)	16	8.2 \pm 1.0 (6–9)	16	12.1 \pm 1.2 (10–14)	16



Figure 1. X-ray of a gravid female *Phyllodactylus reissii* (ZFMK 88739).

with one being quite large and the other being rather small: 9.5×5.8 mm versus 1.5×1.5 mm.

Three recaptured marked females of *Phyllodactylus thompsoni* did not contain oviductal eggs when first captured, but were gravid (one egg) when recaptured. When two of the three females were recaptured after 15 days, they had gained a third of their original weight (1.5–2.0 g). The third female was recaptured after 5 days had not gained any weight. Eggshells and a clutch consisting of one intact egg, presumably belong-

ing to *P. thompsoni*, were found in the crevices of a coarse stone wall and in leaf litter at the base of the same wall. *Phyllodactylus thompsoni* was the only species found in this area. The single egg that was measured is 12.0×8.0 mm. Another egg, from which a juvenile had already hatched, was still intact apart from the opening and had the same dimensions. The opening measured 7.0×6.0 mm (Figure 3).

No eggshells or clutches were found of the other three studied species.

Table 2. Presence (+) of gravid females (♀) and juveniles (*juv*) per month, including X-rayed females and data from Goldberg (2007) (*); – indicates that no data were collected on this species during the respective month.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>Phyllopezus maranjonensis</i>	♀	–	–		+	+	–		–	–		–	–
	<i>juv</i>	–	–	+	+	+	–		–	–		–	–
<i>Phyllodactylus delsolari</i>	♀		–			+	–		–	–		–	–
	<i>juv</i>		–	+	+	+	–		–	–		–	–
<i>Phyllodactylus reissii</i>	♀	–	–	+	+	+	–	+	–	–	–	+*	+*
	<i>juv</i>	–	–	+	+	+	–		–	–	–	+*	
<i>Phyllodactylus thompsoni</i>	♀	+	–	+	+	+	–		–	–	+	–	–
	<i>juv</i>		–	+	+	+	–		–	–		–	–

Discussion

Body Size

The largest individuals we measured of the recently described and little-known species *Phyllopezus maranjonensis* were a female (ZFMK 91703) and a male (released after measuring), both of which were 128 mm long; thus, this species is 2 mm longer than *Thecadactylus rapicauda* (Vitt et al. 2008). Hence, our data reveal that *P. maranjonensis* represents the largest known gecko species in the New World.

Formerly studied Peruvian populations of *Phyllodactylus reissii* from Bayovar and Tumbes had a mean SVL of 57.7 ± 2.7 mm (Huey 1979) and 67.95 ± 8.01 mm (Jordán 2006), respectively, and voucher specimens of the Natural History Museum of Los Angeles County (LACM) from Amazonas, Cajamarca, Lambayeque, Piura, and Tumbes have a mean SVL of 56.7 ± 4.7 mm (Goldberg 2007). Thus, the population we studied from the Marañon Region seems to be distinctly larger, with a mean SVL of 74.1 ± 3.7 mm and 73.6 ± 4.7 mm for males and females, respectively. These high values might have resulted from the elimination of juveniles from



Figure 2. Gravid female of *Phyllopezus maranjonensis* containing two eggs.

our calculations; nonetheless, the largest individual captured from Balsas has a SVL of 80 mm and hence is 13 mm larger than the largest specimen of *P. reissii* reported by Goldberg (2007).

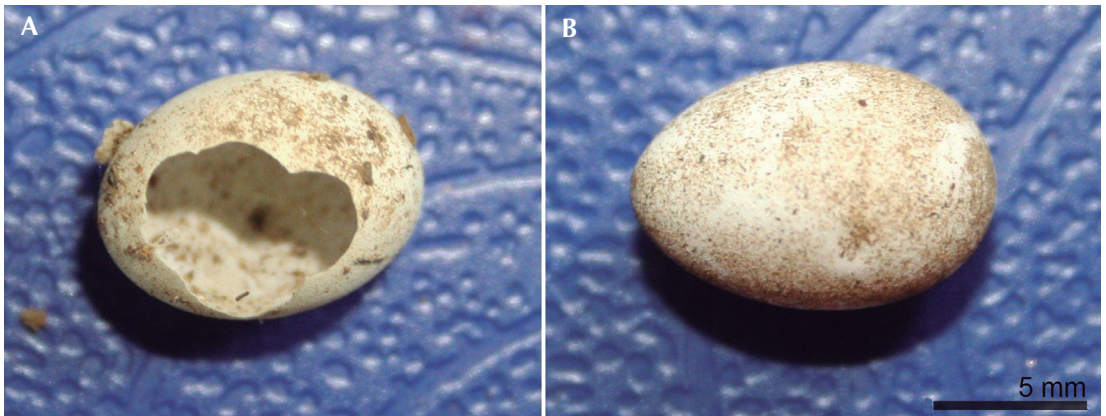


Figure 3. Eggs presumably deposited by *Phyllodactylus thompsoni*. (A) Egg (12.0 x 8.0 mm) from which a juvenile had hatched. (B) Egg (12.0 x 8.0 mm) from which the juvenile had not yet hatched.

Table 3. Size of eggs contained by female *Phyllopezus maranjonensis*.

Female	Size (mm)	
	Right egg	Left egg
CORBIDI 7692	18.0 × 11.5	17.5 × 10.0
CORBIDI 7693	16.0 × 12.0	17.5 × 10.0
CORBIDI 7694	8.0 × 6.0	8.0 × 7.0
ZFMK 91703	19.0 × 13.0	19.5 × 15.0
ZFMK 91704	3.5 × 3.0	1.5 × 1.5
ZFMK 91705	12.0 × 12.0	12.0 × 11.0
ZFMK 91721	15.0 × 10.0	14.0 × 9.0

Reproduction

Until the discovery of *Phyllodactylus delsolari*, *P. reissii* was the only Peruvian leaf-toed gecko species with a clutch size of two eggs (Dixon and Huey 1970, Schlüter 2002). All other species of *Phyllodactylus* from Peru, including *P. angustidigitus*, *P. gerrhopygus*, *P. inaequalis*, *P. interandinus*, *P. kofordi*, *P. lepidopygus*, *P. microphyllus* and *P. johnwrighti* (no data available on the reproduction of *P. clinatus* and *P. sentosus*) produce a single egg. According to our data, *P. thompsoni* is an additional species that produces only one egg. The small clutch size in most species of *Phyllodactylus* may represent a derived trait reflecting a tradeoff between small female body size and selection for relatively large offspring size by producing a single, relatively large egg.

In the description of *Phyllodactylus delsolari*, Venegas *et al.* (2008) reported that two of three specimens contained two eggs and the other one contained only one egg. All of the gravid females of *P. delsolari* that we examined had two eggs; thus, we conclude that females of this species usually produce two eggs. According to Goldberg (2007), *P. reissii* has similar reproductive pattern, with clutch sizes varying between one and two, with two being more frequent than one

(1.7 ± 0.47 , $N = 27$). All gravid females of *Phyllopezus maranjonensis* that we examined had two eggs, as did *P. pollicaris* (Vitt 1986, Righi *et al.* 2012). The pattern of the production of one or two eggs by each species fits with previous observations on gekkonid lizards (Vitt and Caldwell 2009).

Although *Phyllodactylus thompsoni* is the only species of the four having a clutch size of one, it nonetheless is the most abundant and therefore apparently the most successful species in this area (Aurich *et al.* 2011). This might be because it has an extended reproductive period and a relatively short reproductive cycle, as evidenced by those females that were not gravid at the time of their first capture, but contained a relatively large egg when recaptured only two weeks later. Goldberg (2007) found reproductively active females of *P. reissii* in November, December, and May, and neonates in November and May; he concluded that the species has a prolonged reproductive period. All species of *Phyllodactylus* from sufficiently warm environments seem to have an extended all-year long reproductive period (Fitch 1970). The dry forest valley of the Marañon and its tributaries provides such climatic conditions. The presence of gravid females and juveniles of the species of *Phyllodactylus* in this study in various months of the


year (Table 2) suggest that at least two of these species (*P. reissii* and *P. thompsoni*) seem to have an extended reproductive period. The reproductive period might be continuous; however, we lack data for several months. Female *P. thompsoni* with two eggs in different stages may indicate a short reproductive cycle. Further, the size difference of the two eggs indicates either that they derived from one mating event, with the female retaining sperm, or from two mating events. The ability of females to retain sperm was demonstrated for some species of geckos (Kluge 1967), including the phyllodactylid *Haemodracon riebeckii* (Rösler and Wranik 2007). In May, gravid female *Phyllopezus marañonensis* were found in two different reproductive stages. Two females were captured on successive days; one contained large eggs (19.0 × 13.0 and 19.5 × 15.0 mm) and the other small ones (3.5 × 3.0 and 1.5 × 1.5 mm), indicating that reproduction is not synchronous and extends for at least some months.

Egg clutches of *Phyllopezus marañonensis* were not found during this study. However, because the primary habitat of the species is rock faces (Aurich *et al.* 2011), it seems plausible that *P. marañonensis* might deposit eggs in rock crevices, as observed in *P. pollicaris* and *P. periosus*. In contrast, female *Phyllodactylus reissii* deposit their eggs in leaf litter or in dead cactus stems (Schlüter 1997, 2002), in a manner similar to that of *P. thompsoni*.

Annual reproductive data are lacking for these four species of geckos. Further investigation is necessary to determine all aspects of the reproduction and oviposition of this gecko assemblage.

Acknowledgments

We are principally indebted to Pablo J. Venegas for allowing access to the collection CORBIDI, Lima, Peru, and for his assistance in planning field trips. Jesus Cordova and Cesar Aguilar provided access to the collection of the MUSM, Lima, Peru. Wilfredo Nañez Aizcorbe

kindly helped with the legal formalities of the collection (N° 071-2007-INRENA-IFFS-DCB, 0020-2009-AG-DGFFS-DGEFFS, 0424-2010-AG-DGFFS-DGEFFS, 0439-2010-AG-DGFFS-DGEFFS) and export permits (N° 0017799-AG-INRENA, 001829-AG-DGFFS, 003983-AG-DGFFS, 003965-AG-DGFFS), which were issued to J. Aurich and C. Koch by the Dirección General Forestal y de Fauna Silvestre of the Ministerio de Agricultura, Lima, Peru. Alfredo Beraún, Antonio García Bravo, Jorge Novoa Cova, Lourdes Yliana Echevarria Espinosa, Erick Hoyos Granda, Manuel, Palacios Panta and Caroll Laandauro Sanabria contributed greatly to the success of the investigations with their assistance during the fieldwork. Claudia Koch received financial support by the Deutscher Akademischer Austauschdienst (DAAD), the Alexander Koenig Stiftung (AKS) and the Alexander Koenig Gesellschaft (AKG). Aaron M. Bauer provided useful information on gecko ecology. We thank Teresa Avila Pires and Laurie J. Vitt for helpful comments on an early draft of this manuscript. 

References

- Aurich, J., C. Koch, and W. Böhme. 2011. Ecology of a gecko assemblage (Phyllodactylidae: Squamata) from northern Peru. *North-Western Journal of Zoology* 7: 310–317.
- Brack, A. 1986. Las ecorregiones del Perú. *Boletín de Lima* 44: 57–70.
- Dixon, J. R. and R. B. Huey. 1970. Systematics of the lizards of the gekkonid genus *Phyllodactylus* of Mainland South America. *Los Angeles County Museum Contributions in Science* 192: 1–78.
- Duellman, W. E. and J. B. Pramuk. 1999. Frogs of the genus *Eleutherodactylus* (Anura: Leptodactylidae) in the Andes of northern Peru. *Scientific Papers of the Natural History Museum of the University of Kansas* 13: 1–78.
- Fitch, H. S. 1970. *Reproductive Cycles in Lizards and Snakes*. Lawrence. University of Kansas Museum of Natural History. 247 pp.
- Gamble, T., A. M. Bauer, E. Greenbaum, and T. R. Jackman. 2008. Out of the blue: a novel, trans-Atlantic clade of geckos (Gekkota, Squamata). *Zoologica Scripta* 37: 355–366.

- Gamble, T., G. R. Colli, M. T. Rodrigues, F. P. Werneck, and A. M. Simons. 2012. Phylogeny and cryptic diversity in geckos (*Phyllopezus*; Phyllodactylidae; Gekkota) from South America's open biomes. *Molecular Phylogenetics and Evolution* 62: 943–953.
- Goldberg, S. R. 2007. Notes on reproduction of Peters' leaf-toed gecko, *Phyllodactylus reissii* (Squamata, Gekkonidae), from Peru. *Phyllomedusa* 6: 147–150.
- Huey, R. B. 1979. Parapatry and niche complementarity of Peruvian Desert Geckos (*Phyllodactylus*): the ambiguous role of competition. *Oecologia* 38: 249–259.
- Jordán, J. C. 2006. Dieta de *Phyllodactylus reissii* (Sauria: Gekkonidae) en la Zona Reservada de Tumbes, Peru. *Revista Peruana de Biología* 13: 121–123.
- Kluge, A. G. 1967. Higher taxonomic categories of gekkonid lizards and their evolution. *Bulletin of the American Museum of Natural History* 135: 1–59.
- Koch, C., P. J. Venegas, and W. Böhme. 2006. A remarkable discovery: description of a big-growing new gecko (Squamata: Gekkonidae: *Phyllopezus*) from northwestern Peru. *Salamandra* 42: 145–150.
- Lima, D. C., D. C. Passos, and D. M. Borges-Nojosa. 2011. Communal nests of *Phyllopezus periosus*, an endemic gecko of the Caatinga of northeastern Brazil. *Salamandra* 47: 227–228.
- López-Victoria, M., M. Jurczyk, and V. Wolters. 2013. Notes on the ecology of the Colombian Leaf-toed Gecko (*Phyllodactylus transversalis*), endemic to Malpelo Island. *Boletín de Investigaciones Marinas y Costeras* 42: 319–327.
- Murphy, R. W., C. Blair, and F. R. Mendez De La Cruz. 2009. A new species of Leaf-Toed Gecko, genus *Phyllodactylus* (Squamata: Gekkota: Phyllodactylidae) from Guerrero, Mexico. *South American Journal of Herpetology* 4: 17–24.
- Recoder, R., M. Teixeira-Junior, A. Camacho, and M. T. Rodrigues. 2012. Natural history of the tropical gecko *Phyllopezus pollicaris* (Squamata, Phyllodactylidae) from a sandstone outcrop in Central Brazil. *Herpetology Notes* 5: 49–58.
- Righi, A. F., L. B. Nascimento, and C. A. B. Galdino. 2012. Seasonal reproduction in the Rock Gecko *Phyllopezus pollicaris* from a rock field habitat in Southeastern Brazil. *Journal of Herpetology* 46: 632–636.
- Rösler, H. and W. Wranik. 2007. Bemerkungen zur Biologie sowie Haltung und Vermehrung des Sokotra-Riesengeckos, *Haemodracon riebeckii* (Peters, 1882). *Der Zoologische Garten* 77: 59–83.
- Schlüter, U. 1997. Blattfingergeckos. *Das Aquarium* 341: 27–28.
- Schlüter, U. 2002. Haltung und Zucht einiger Blattfingergeckos aus Peru. *Aquaristik Fachmagazin* 164: 82–85.
- Venegas, P. J., J. H. Townsend, C. Koch, and W. Böhme. 2008. Two new sympatric species of leaf-toed geckos (Gekkonidae, *Phyllodactylus*) from the Balsas Region of the upper Marañón Valley, Peru. *Journal of Herpetology* 42: 386–396.
- Vitt, L. J. 1986. Reproductive tactics of sympatric gekkonid lizards with a comment on the evolutionary and ecological consequences of invariant clutch size. *Copeia* 1986: 773–786.
- Vitt, L. J. and J. P. Caldwell. 2009. *Herpetology. An Introductory Biology of Amphibians and Reptiles*. London. Academic Press. 776 pp.
- Vitt, L. J., W. E. Magnusson, T. C. Ávila-Pires, and A. P. Lima. 2008. *Guide to the Lizards of Reserva Adolpho Ducke, Central Amazonia. Guia de Lagartos da Reserva Adolpho Ducke, Amazonia Central*. Manaus. Áttema Design Editorial Ltda. 176 pp.
- Williams, R. J., J. Horrocks, and A. Pernetta. 2015. Natural history, distribution, and conservation status of the Barbados leaf-toed gecko, *Phyllodactylus pulcher* Gray, 1828 (Squamata, Gekkonidae). *Herpetology Notes* 8: 197–204.

Editor: Teresa C. S. Ávila Pires

Appendix I. Specimens examined.

Phyllodactylus delsolari—PERU: Amazonas: Chachapoyas: Balsas (06°50' S, 78°00' W, 870–1290 m a.s.l.), CORBIDI 5671, 5674, 7700, 7702, 7703, 7705, 7706, MUSM 19566, ZFMK 85001, 85002, 90872–90874, 91714–91721, 91762; Cajamarca: Celendin: Chacanto (06°50'26" S, 78°01'23.8" W, 890 m a.s.l.) CORBIDI 5672, 5673, 7699, 7707–7709, ZFMK 90871; La Libertad: Bambamarca: Calemar (07°31'34.2" S, 77°42'53.9" W, 1310 m a.s.l.) ZFMK 91755–91758; Pataz: Vijus (07°43' S, 77°39' W, 1260–1315 m a.s.l.) CORBIDI 6912, 6913, 7656, ZFMK 91761; Tayabamba: Pias (Laguna) (07°53' S, 77°33' W, 1820–1870 m a.s.l.) ZFMK 91759, 91760.

Phyllodactylus reissii—PERU: Amazonas: Chachapoyas: Balsas (06°50'53" S, 78°01'30.8" W, 900 m a.s.l.) CORBIDI 7710–7712, ZFMK 90885, 91724, 91725; Cumba: Cumba (05°56' S, 78°39' W, 520–550 m a.s.l.) ZFMK 90898, 90902; Utcubamba: Puerto Malleta (06°03'54.1" S, 78°36'0.9" W, 500 m a.s.l.) ZFMK 90893, 90895; Zapatalgo (06°03'43.6" S, 78°30'8.4" W, 910 m a.s.l.) ZFMK 90892; Cajamarca: Jaén: Gotas de Agua (05°41'2.9" S, 78°46'4.1" W, 708 m a.s.l.) ZFMK 88739; Santa Rosa (05°26'23.7" S, 78°33'17" W, 1247 m a.s.l.) ZFMK 88740; Pucará (06°02'23" S, 79°07'59.4" W, 901 m a.s.l.) ZFMK 88744, 88745.

Phyllodactylus thompsoni—PERU: Amazonas: Chachapoyas: Balsas (06°50' S, 78°01' W, 900 m a.s.l.) CORBIDI 7713, 7714, 7718–7723, ZFMK 90914, 90915, 91729, 91730, 91732–91736; Cajamarca: Celendin: Chacanto (06°50' S, 78°02' W, 1130–1140 m a.s.l.) CORBIDI 7715–7717, ZFMK 90911–90913, 91737, 91738; La Libertad: Bambamarca: Calemar (07°32' S, 77°42' W, 1440–1690 m a.s.l.) ZFMK 91752–91754; Tayabamba: Chagual (07°50' S, 77°38' W, 1300–1360 m a.s.l.) ZFMK 91740–91742; Pias (07°53' S, 77°34' W, 1860–1870 m a.s.l.) ZFMK 91746–91748; Bolivar: San Vincente/Pusac (06°59' S, 77°55' W, 1430–1670 m a.s.l.) ZFMK 90917–90922; Pataz: Vijus (07°43'9.3" S, 77°39'47.4" W, 1290 m a.s.l.) ZFMK 91743–91745.

Phyllopezus maranjonensis—PERU: Amazonas: Chachapoyas: Balsas (06°49' S, 78°00' W, 865–1258 m a.s.l.) CORBIDI 5659–5662, 7692, 7693, ZFMK 84995–84997, 90867, 90868, 91703–91709, MUSM 19553–19555; Cajamarca: Celendin: Chacanto (06°51' S, 78°02' W, 866–901 m a.s.l.) CORBIDI 7594, ZFMK 90869, 90870, 91712; La Libertad: Bambamarca: Calemar (07°31' S, 77°43' W, 1227–1312 m a.s.l.) CORBIDI 7651–7653, ZFMK 91768–91770; Cajabamba: Santa Rosa (Marcamachay) (07°21' S, 77°51' W, 1,076–1,128 m a.s.l.) CORBIDI 7647–7650, ZFMK 91765–91767.