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Notes on the taxonomy, morphology and behavior of *Rhacodactylus chahoua* (Bavay) (Reptilia: Gekkonidae)

by

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Introduction

Rhacodactylus chahoua is one member of a genus of six large to very large (100—240 mm snout-vent length) diplodactyline geckos endemic to the French island territory of New Caledonia. Little is known of the biology of these animals. The dense vegetation and difficult terrain of their habitats have precluded most studies of behavior and ecology in the wild. Collection of most species is difficult and only two of the six taxa, *R. leachianus* and *R. auriculatus*, are well represented in museums. The description of *Rhacodactylus sarasinorum* by Roux (1913) represents the most recent taxonomic work dealing with the members of the genus. Subsequently, only Mertens (1964a, 1964b) and Meier (1979) have discussed *Rhacodactylus* at length. *Rhacodactylus chahoua* is only briefly mentioned in these papers, although Meier (1979) presented a brief history of the species along with an account of the capture of his specimens.

Historical Review

Arthur Bavay (1869) described *Platydictylus chahoua* from a single specimen presented to him during his visit to New Caledonia in the mid-1860's. The specimen was described in some detail and the locality cited as "Kanala, Lifou". Sauvage (1878), based solely on this published description, synonymized *Rhacodactylus trachyrhynchus* Bocage 1873 with *P. chahoua*. Boulenger (1879) initially accepted this taxonomic shuffling and added a species he had described, *Chameleonurus trachycephalus* Boulenger 1878, to the synonymy. He later repented when he became aware that Sauvage had not examined the type specimens about which he had written. As a result, Boulenger (1883) resurrected *Rhacodactylus trachyrhynchus*, maintaining the precedence of the generic name first proposed by Fitzinger (1843) for a subgenus of *Hoplodactylus* to accommodate *Platydictylus leachianus* Cuvier. Also included in Boulenger's (1883) *Rhacodactylus* were the three additional species of New Caledonian giant forest geckos, *Correlophus ciliatus* Guichenot 1866, and the two forms named by Bavay (1869), *Platydictylus auriculatus* and *P. chahoua*. Boulenger (1883, 1885) reported the

presence and number of pre-anal pores on the type specimen of *R. chahoua*, indicating that the animal was an adult male. The earlier description by Bavay (1869) had explicitly stated that there were no pores in the cloacal or femoral regions.

The site of disposition of this specimen is greatly confounded and subsequent workers have added to the confusion. Apparently Bavay and Boulenger were the only workers actually to view the holotype. Although Boulenger (1883) clearly indicated that he received the specimen on loan from Bavay, his later work (Boulenger, 1885) does not mention the origin of the animal. By convention, this omission of the name of the repository in the *Catalogue of Lizards* would indicate that the specimen examined was housed in the British Museum. Sauvage (1878) had previously confused the repository of the specimen, stating "l'unique exemplaire que possède le Muséum [Paris?] a été donné par le Musée des Colonies."

Roux was the next herpetologist to visit New Caledonia (1911–1912) and to search for *Rhacodactylus* (Roux, 1913; Sarasin, 1917). He reports (1913) that *R. chahoua* was not encountered during his tenure on the island. Roux was unable to locate the holotype in the collection of the Musée de l'Ecole de Médecine Navale in Brest, where Bavay claimed to have deposited his New Caledonian specimens (see Roux, 1913: p. 97). Subsequent attempts by Dr. Allen Greer (Australian Museum, Sidney) and by me have failed to locate any of Bavay's skink or gecko material. Thus the holotypes of both *Rhacodactylus chahoua* and *R. auriculatus* are assumed to have been lost sometime between 1883 and 1913.

Roux also noted that Bavay's locality for *R. chahoua* ("Kanala, Lifou") was in error. Kanala (Canala) is a village that lies on the east central coast of the main island of New Caledonia, while Lifou is the name of the largest of the Loyalty Islands, dependencies of New Caledonia lying approximately 100 km to the east. Since neither Roux nor any other previous workers had ever encountered *Rhacodactylus* anywhere except on the "Grande Terre" or the much nearer Île des Pins (see Boulenger, 1878 for this doubtful record), Roux dismissed Bavay's designation of Lifou, retaining Canala as the probable type locality. Bavay, an aged man in 1913, wrote to Roux that the specimen had been presented to him but that he could not be sure whether or not Lifou was its actual origin.

Rhacodactylus chahoua next was mentioned by Mertens (1964a) who possessed a single specimen (Natur-Museum Senckenberg [SMF] 61779) from Coula, approximately 55 km NW of Canala, in the middle of the island. Since 1964, a number of additional specimens have been collected, primarily those captured by Meier and by me; an additional specimen collected in 1925 (and later identified as *R. chahoua*) is housed in the Naturhistorisches Museum, Basel (NHMB 9702). To my knowledge, the number of specimens in museum collections now stands at three adult males, two adult females, five hatchlings,

and two eggs. In addition there are at least ten living specimens of *R. chahoua* in the collections of zoological parks and private terrarium keepers. Included among the adult museum specimens is a pair that I collected on 6 April, 1984 in the Vallée d'Amoa, near St. Thérèse, approximately 15 km NW of Poindimié on the northeast coast of New Caledonia. As the type specimen of the taxon is apparently lost, I take this opportunity to designate the male of the pair (California Academy of Sciences [CAS] 156692) as the neotype of *Rhacodactylus chahoua*.

Description of the Neotype

The specimen designated is largely in agreement with the holotype as described by Bavay (1869), and especially Boulenger (1883, 1885). Boulenger (1883) provided a diagnosis of the genus and a key to the species. The following is a summary of the scalation, coloration and mensural characters of the neotype (standard measurements follow Kluge, 1967):

Measurements (in mm): Snout-vent length (SVL) 145.4; Tail length (TL) 90.0 (regenerated); snout length (SL) 14.8; Orbital diameter (OD) 8.9; Eye to ear length (EEL) 12.1; Head length (HL) 45.0; Head width (HW) 28.0; Axilla to groin length (AGL) 63.4; Fore limb length (FLL) 42.8; Fourth finger length (FFL) 11.9 (8.6 from rim of web to claw base); Hind limb length (HLL) 57.4; Fourth toe length (FTL) 15.5 (10.4 from rim of web to claw base); live weight 64.1 g.

Scalation: Rostral septagonal, 2.25 times wider than deep, rostral crease absent, nostril surrounded by seven nasals, first supralabial and rostral; supralabials 13(Right), 14(Left); interorbitals 20; 25 short supraciliaries; mental 1.25 times wider than deep; infralabials 13(Left), 14(Right); dorsals small, granular; ventrals flat non-imbricating, enlarged in inguinal region; digits broad, with denticulate margins, strongly webbed (less so between digits four and five); claw of digit one bordered laterally by a single expanded apical plate; fore foot lamellae 12:16:19:21:18, hind foot lamellae 13:16:22:22:19, lamellae broad and shallow, curving slightly distally at margins; caudal scales (regenerated) large, squarish, arrayed in regular whorls; terminal six rows of subcaudal scales irregular (regenerated subcaudal lamellar pad); preanal pores 121 total in four rows, 13:21:22:7 (Left), 12:20:21:5 (Right) anterior to posterior, two rows of interopore scales; cloacal spurs 4–6 scales, rounded, enlarged antero-dorsally.

The specimen was fixed in 10 % neutral buffered formalin and is stored in 75 % ethyl alcohol. Heart, liver, and intestinal tissue were removed from the freshly killed animal and are stored at -76°C in the frozen tissue collection of the Museum of Vertebrate Zoology, University of California, Berkeley.

Coloration in life (see figure 1): A complex mottling of chestnut brown and grey-green, with an incomplete reticulate network of chocolate brown over most

of the dorsal surface; white flecks bordering reticulations in some areas, particularly on limbs; an irregular greenish patch resembling lichen on nape and shoulders; a series of eight thick sets of alternating cream and brown bands between axilla and groin at ventro-lateral margin of dorsal surface; dorsal and lateral surface of head predominantly green; labials white with chocolate brown markings; eye golden-brown, circumocular scales in alternating series of brown and white; tongue and interior of mouth bright red; tail striated brown with white, alternating in predominance forming an irregular banded pattern; venter cream, greenish at the level of the limb girdles, blending to pale orange at the level of the preanal pores, pale green from cloaca posteriorly; most of venter speckled with single scales or small groups of scales with brown or black pigment, yielding a faded pattern of thin cross-bars; chin scales mottled as are labials; peritoneum unpigmented.

Coloration in alcohol: Pattern as above but faded to grey with hints of chestnut; eyes cloudy grey; tongue pale pink, inside of mouth peach; tail as in life; venter grey to off-white.

Remarks on Morphology and Variation

None of the adult museum specimens of *Rhacodactylus chahoua* possesses an undamaged original tail. The first two specimens found were completely tailless, bearing only a tiny stub posterior to the cloacal bulge. All specimens collected subsequently bear regenerated tails varying from 48 to 86 % of SVL. All hatchlings possess complete, original tails ranging from 65 to 95 % of SVL and are slender and tapering (see figure 2), in contrast to the short, stout tail of *R. leachianus*. The terminal subcaudal region in juveniles bears a series of modified scales much like those reported by Mertens (1964b) for *R. leachianus*. These are unlike the lamellate subcaudals of species of the only other genera to be examined, the gekkonines *Lygodactylus* (Tornier, 1899; Loveridge, 1947; Mertens, 1964b; Kästle, 1964; Vitt and Ballinger, 1982), *Phelsuma* (Mertens, 1964b), *Phyllodactylus* (Boulenger, 1878; Eijdsen, 1962, 1983) and *Urocotyledon* (Kluge, 1983).

The tail stub seen in some adults appears to be the result of an injury proximal to the first autotomy plane, which in this species lies in the sixth caudal vertebra. Radiographs of adult specimens revealed that all tailless individuals had sustained injury to the fifth caudal vertebra, the last of the pygal series. Tail breaks at this level are rare among lizards possessing autotomic septa in the post-pygal series but characterize three of the five adult *R. chahoua* in museum collections, as well as the lost holotype. Unlike *R. leachianus*, *R. chahoua* does not have an enlarged collar around the proximal fourth of the tail. The juvenile specimens, however, do display a circumferential fold of skin at the level of the first autotomic vertebra, similar to that seen in *R. trachyrhynchus* and *Bavayia cyclura*.

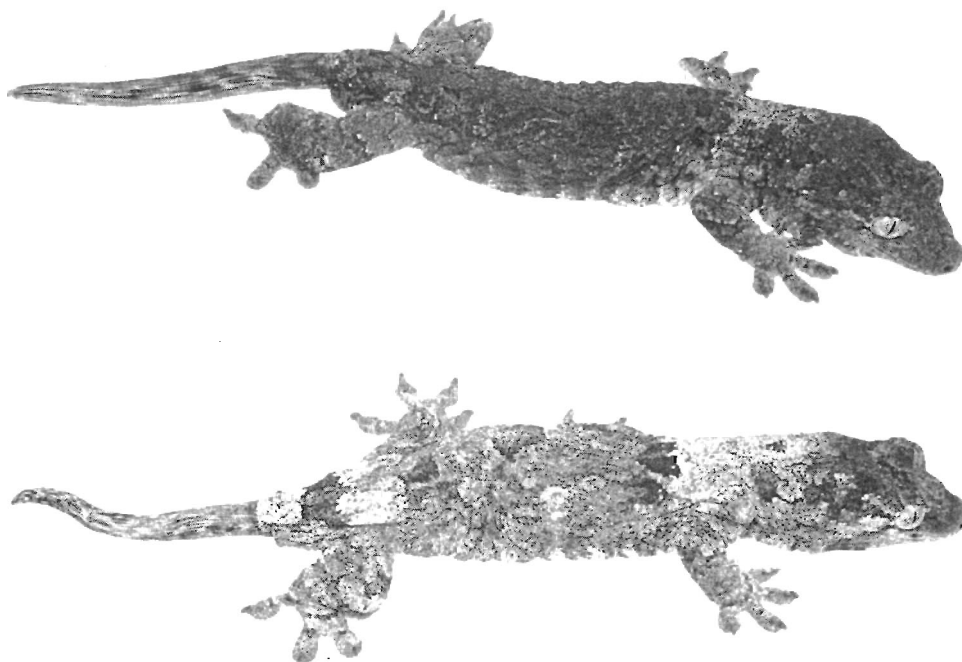


Fig. 1: *Rhacodactylus chahoua* (top) ♂, CAS 156692, Neotype; (bottom) ♀, CAS 156691, from Vallée d'Amoa, New Caledonia. Photos to same scale. — Photos: Sci. Photog. Lab., Univ. Calif., Berkeley.

(Meier, 1979). The significance of this structure remains unknown, although its topographic relationship to the first post-pygial vertebra suggests a function in autotomy.

In juveniles the tail is conspicuously lighter in color than the rest of the dorsum, being cream-colored with very few dark marks. Such a disruptive pattern may function in crypsis, or it may direct the attention of attackers to the expendable tail, allowing escape of the individual.

Although the regenerated tails of adults have limited mobility, those animals that I observed alive frequently wrapped the terminus of the appendage around branches for added support, especially when climbing between perches or when an attempt was made to remove them from the perch. Boulenger's (1883) assumption that tail prehensility was a characteristic of the genus thus appears to be valid for all the included taxa.

Like *R. leachianus*, *R. chahoua* is characterized by loose folds of skin along the body margins and prominent interdigital webbing. In adults folds extend from the anterior fourth of the mandible, along the neck, anterior and posterior faces of the fore limb, flanks and both faces of the hind limb from the mid-thigh to ankle. Although variable, these folds are weakly developed in the smallest hatchlings. The single pre-hatchling shows folds on the hind limbs and weak development of skin along the flanks. The neck and throat folds seem to be the last to develop, being absent until shortly after hatching. Russell (1979) regarded the evolutionary origin of body folds in another subfamily of geckos, the Gekkoninae, as being related primarily to fat storage, with such structures being preadapted for alternative functions in crypsis and parachuting. The body folds of *Rhacodactylus* house bands of adipose tissue, and thus are consistent with Russell's hypothesis. Although a secondary role in gliding may be ruled out due to the great bulk of all members of this genus, a cryptic function for skin folds may exist. It is also possible that an alternative secondary role for folds has developed in the genus *Rhacodactylus*, that of a support mechanism for the animals as they climb. In captivity, both *R. chahoua* and *R. leachianus* have been observed to flatten the folds against vertical surfaces, thereby increasing the amount of surface area contact and, hence, friction.

Another striking difference between adults and juveniles can be seen in color patterns of other parts of the body. Juveniles possess a better defined pattern of squarish dark markings along the mid-dorsal line. Their snouts and frontal regions are cream-colored and a large, dark, posteriorly-pointing triangle is located at the caudal margin of the orbit and extends to the occiput. The pattern of alternating brown and white quadrants in the circumocular scales is also better defined in the young, as is the pattern of thin cross-bars on the venter.

The nape/shoulder patch seen in adults is less prominent or absent altogether in the hatchlings. The patch apparently is of use in crypsis, bearing a remarkable resemblance to the patches of lichen common on most tree trunks and logs in the environment of *Rhacodactylus chahoua*. In contrast, however, the pattern of the young may imitate the dappled browns and greens which occur among the tree branches. Although almost nothing is known of the natural history of these animals, it is suggested that ontogenetic color change may be correlated with some type of microhabitat shift (Gorman, 1977). Henkel (1981) reported that a two year old *R. chahoua* with a total length of 190 mm still retained the juvenile color pattern.

The most obvious sexual difference between the male and female of the Vallée d'Amoa pair of *Rhacodactylus chahoua* is in color (see figure 1). The male is predominantly brown while the female is mostly green. A similar sexual distinction is present in a group of three captive animals (1 female, 2 males) (Harald Meier, pers. comm.). Unfortunately, because color fades to grey in alcohol, museum specimens are not useful for evaluating possible sexual dichromatism.

A morphometric difference in relative head size can also be detected between the male and female of the Vallée d'Amoa pair. Both have the same SVL (145 mm) yet the head of the male is 7 % longer and 13 % wider (see figure 3). Although analysis is hindered by the small sample size, this trait seems to be shared by all five of the adult animals examined.

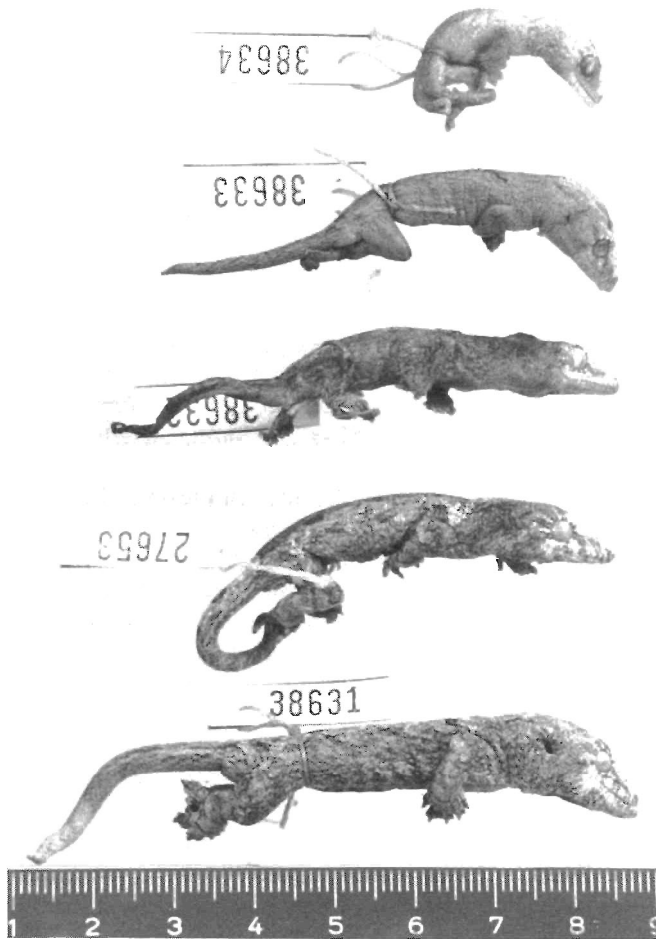


Fig. 2: *R. chahoua*, hatchlings (Zoologisches Forschungsinstitut und Museum A. Koenig numbers). Note circumocular color pattern, general body coloration, and length and shape of original tails. — Photo: Mus. Koenig (E. Schmitz).

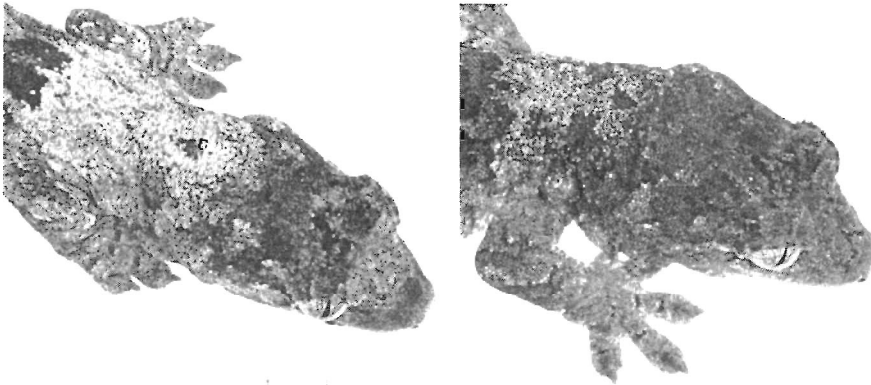


Fig. 3: *R. chahoua* (right) Head of CAS 156692 (male), (left) Head of CAS 156691 (female). Photos to same scale. Note the broader dimensions of the male. Also see denticulate toe borders and the lichen-like nape patches. — Photos: Sci. Photog. Lab., Univ. Calif., Berkeley.

Distribution

The following localities have been given for specimens of *Rhacodactylus chahoua*: "Kanala, Lifou", "La Foa", "Mt. Mou", "Coula, zwischen Houailou und Bourail", and "Vallée d'Amoa, near St. Thérèse" (see figure 4). If we accept Roux's conclusion regarding the type locality, all localities lie in the central or south-central region of New Caledonia, and all lie on, or very near, large rivers. Few additional generalities can be drawn. These areas receive between 1220 mm (La Foa) and 2687 mm (Vallée d'Amoa) of rainfall annually (O.R.S.T.O.M., 1981), encompassing almost the entire range of pluviometric variability of the territory. Temperatures are similar throughout the island at any given elevation, averaging $23^{\circ}\text{C} \pm 1^{\circ}\text{C}$ at all localities. Yearly highs and lows similarly vary by about 10°C except at Vallée d'Amoa (based on data from nearby Poindimié) where average yearly variation is between 17°C and 28°C (O.R.S.T.O.M., 1981). The significance of elevation is difficult to assess as exact figures are not available for most of the localities. All localities except La Foa are characterized by low to middle elevation humid forest or forest/savanna mosaic vegetation. In contrast, La Foa is characterized by xeric woody forest/savanna mosaic. Clearly, the varied nature of the few localities where *R. chahoua* has been collected do not permit a detailed analysis of environmental correlates of distribution. It appears that *Rhacodactylus chahoua*, like some of its better known congeners, may be quite widespread on the island of New Caledonia. Temperature almost certainly places no barriers on the two-dimensional distribution of the species.

Elevation may or may not be an important factor in the current distribution of the species. *Rhacodactylus* has never been reliably reported from localities above 1000 meters in elevation. This may be due to lower temperatures, changes in biotic communities, or simply the fact that few scientists have explored the more inaccessible higher elevations of the island. An environmental element that certainly plays a role in the distribution of these forms is human destruction of habitat. Areas cleared of native vegetation for building or agriculture are incapable of supporting *R. chahoua* or other forest dwelling geckos.

The absence of the genus *Rhacodactylus* from Lifou and the other Loyalty Islands, Maré and Ouvéa, may be explained by the more recent origin of these areas. The Loyaltys are low lying, coralline islands of Quaternary age (O.R.S.T.O.M., 1981). It is probable that *Rhacodactylus* had already evolved as specialized forest dwellers and would thus be unlikely to be successful colonizers of the outer islands. Although Lifou still supports a great deal of forest land, it lacks rivers or other permanent sources of water, thus differing from the mainland localities where *R. chahoua* has been found.

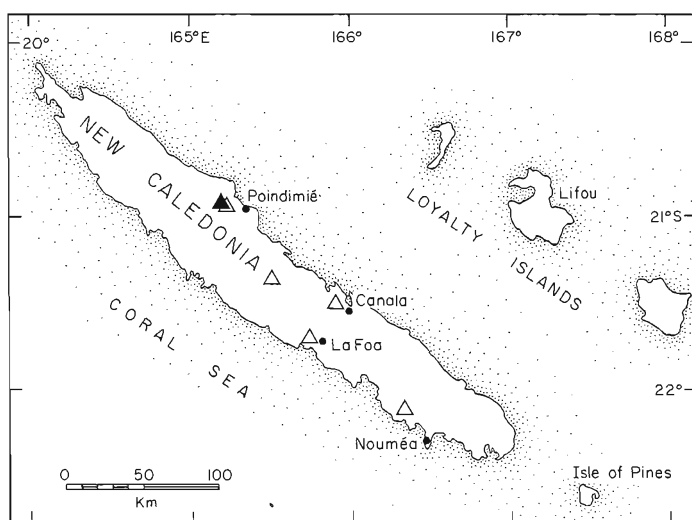


Fig. 4: Localities where *R. chahoua* has been collected (open triangles); locality of neotype (closed triangle).

Feeding

Mertens (1964a) reported that captive *R. leachianus* fed on bananas as well as baby mice. Captive *R. chahoua* have been known to accept a variety of insects

and fruits (Henkel, 1981). The only known record of the natural diet of any species of *Rhacodactylus* is provided by Roux (1913), who found the remains of the meliphagid bird *Glyciphila* (= *Lichmera*) *incana* in the stomach of a *R. leachianus*. The few people in New Caledonia whom I encountered keeping the giant forest geckos as pets fed their charges exclusively on diets of papaya and banana, reporting that citrus fruits were rejected. *Rhacodactylus chahoua* is probably omnivorous in the wild, with insects and smaller vertebrates being taken in addition to fruits. Such diets are known for the closely related New Zealand species *Hoplodactylus maculatus* (Whitaker, 1982) and for the gekkonine *Phelsuma guentheri* (Vinson, 1949). It is possible that *R. chahoua* also consumes nectar as do *Hoplodactylus duvauceli* (Whitaker, 1968) and *Phyllodactylus guentheri* (Cogger et al., 1983).

The two specimens of *Rhacodactylus chahoua* that I kept alive in Berkeley, California, for approximately two and one half months readily accepted bananas and crickets. When presented with bananas, the animals would first lick the fruit as many as twenty times, extending the tongue forward and curving the tip ventrally and the lateral margins medially to form a shallow depression. Eventually the animals would approach the item with the lateral surface of the snout and quickly bite down on the fruit, occasionally taking pieces as large as two thirds the size of the animal's head. Henkel (1981) also reported both licking and biting of bananas by captive *R. chahoua*. The fruit then would be swallowed after being repositioned inertially by rapid lateral movement of the head. Small pieces of banana placed just out of reach of the animal's jaws would be lifted and brought to the mouth by the cupped tongue. Crickets were taken by a rapid snap of the jaws after a short lunge, with no apparent use of the tongue during prey prehension.

Courtship and Reproduction

On two occasions the captive pair of *R. chahoua* engaged in what I have interpreted as pre-mating behavior. No copulations were observed. Courtship has previously been reported for only a few species of geckos, among them members of the genera *Phelsuma* (Kästle, 1964), *Lygodactylus* (Kästle, 1964; Greer, 1967), and *Hemidactylus* (Mahendra, 1936), all gekkonines, the eublepharine *Coleonyx* (Greenberg, 1943), and the diplodactyline, *Hoplodactylus pacificus* (Rieppel, 1976) (= *H. maculatus*, sensu Robb & Rowlands, 1977). Few features of the courtship ritual are common to all of the species examined, although aspects of copulation, such as the male biting the shoulders or nape of the female are shared and indeed may be regarded as homologous actions at the level of all squamates.

Not surprisingly, the greatest similarities with courtship in *Rhacodactylus chahoua* are shared with *Hoplodactylus maculatus*, to which it is closely related

(Kluge, 1967; Russell, 1972). The scenarios observed in *Rhacodactylus chahoua* consisted of a series of actions as follows (terminology after Carpenter and Ferguson, 1977): 1) male on branch slowly approaches female from rear, straddling female's tail; 2) male places chin over base of female's tail, turns head jerkily from side to side three to six times (jaw rub); 3) male nudges and licks female's tail base and vent; 4) male nips dorsal surface of female's tail base. In both instances observed, the female responded by remaining stationary until licked, at which point she moved forward slightly. Upon being bitten, however, she quickly pulled out from underneath the male and walked farther up the branch upon which both had been perched.

Rhacodactylus chahoua shares with *H. maculatus* two features of the courtship ritual, the approach of the male to the female from the rear and the frequent licking of the vent and tail base by the male. Both species demonstrate head jerking, although in *H. maculatus* the head was moved vertically, whereas in *Rhacodactylus*, the head was moved stiffly from side to side, much in the same manner as the chin-rubbing seen in the courtship routine of plethodontid salamanders (see Arnold, 1976).

The ovaries of the female contained two partially-yolked eggs, one per ovary, each 11.1 mm in diameter. At least three size classes of developing follicles were present in the ovaries, with the smallest class outnumbering the largest by an order of magnitude. The inner walls of the posterior portions of the oviducts (anterior portions damaged in removal of tissues for frozen collection) were found to be greatly convoluted. The size of the two eggs (SMF 61780—61781) actually laid by a *Rhacodactylus chahoua* was 28 x 15 mm. This is in agreement with the size range presented by Henkel (1981). Meier (pers. comm.) gives the size of an additional pair of eggs as 30 and 31 mm (long axis), with respective weights of 4.0 and 4.6 g, and he further states that the period of incubation for these eggs was at least 78 days. Henkel (1981) reported that *R. chahoua* eggs at 27°C hatched after 85 days and added that the females are capable of producing a clutch every two to two and a half months.

Like most diplodactylines, *R. chahoua* lays two leathery-shelled eggs in each clutch. Its congener *R. trachyrhynchus* is ovoviviparous (Bartmann and Minuth, 1979). The reproductive mode in all of the other taxa in the genus appears to be oviparity. The condition of ovoviviparity occurs elsewhere among gekkonids only in the New Zealand genera *Hoplodactylus*, *Naultinus*, and *Heteropholis*. The evaluation of the evolution of varied reproductive modes in *Rhacodactylus* awaits a systematic revision of this entire group of geckos.

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Summary

An account is presented of the biology of *Rhacodactylus chahoua*, a rarely-encountered New Caledonian giant forest gecko. The male of a pair from the Vallée d'Amoa is designated as the neotype of the taxon. Sexual dimorphism and dichromatism appear to occur in the species and there is a pronounced ontogenetic shift in color pattern. The undamaged tails of hatchlings exhibit specialized subcaudal scales similar to those previously noted in *R. leachianus*. Taillessness in adults is the result of trauma to the last pygal vertebra. Although uncommon, *R. chahoua* is widely distributed in several habitat types in New Caledonia. Captive specimens feed on both insects and fruit. Courtship behavior in the species is similar to that of *Hoplodactylus maculatus*.

Zusammenfassung

Ein Abriß der Biologie von *Rhacodactylus chahoua*, einem selten gefundenen neukaledonischen Riesen-Waldgecko, wird gegeben. Das Männchen eines Paares aus dem Vallée d'Amoa wird als Neotypus des Taxons designiert. Es scheint bei dieser Art Sexualdimorphismus und -dichromatismus aufzutreten. Die unbeschädigten Schwänze von Schlüpflingen tragen spezialisierte Subcaudalschuppen, die den bereits bekannten von *R. leachianus* ähneln. Schwanzlosigkeit bei adulten Exemplaren resultiert aus Beschädigungen des letzten Pygalwirbels. Obwohl nirgends häufig, ist *R. chahoua* doch in verschiedenen Habitattypen weit auf Neukaledonien verbreitet. Gefangene Exemplare ließen sich sowohl mit Insekten als auch mit Früchten ernähren. Das Vorpaarungsverhalten dieser Art ähnelt dem von *Hoplodactylus maculatus*.

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