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# A review of the gekkonid genus *Calodactylodes* (Reptilia: Squamata) from India and Sri Lanka

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## Abstract

Gekkonid lizards of the genus *Calodactylodes* are endemic to peninsular India and Sri Lanka. The genus consists of two species, *C. aureus* and *C. illingworthorum* (formerly *C. illingworthi*) and is diagnosable on the basis of derived digital structure, the presence of paraphalanges, bright yellow gular patch (at least in adult males), and distinctive vocalisation. The skeletal, hemipenial, and external morphology of both species is described. Field observations of *C. aureus* at Vellore, Tamil Nadu, indicate that males are highly vocal and that communal egg-laying occurs. *Calodactylodes aureus* appears to be common in appropriate habitats and is probably more widely distributed than previously believed. Relationships of *Calodactylodes* to other gekkonids remain obscure but may reflect Gondwanan origins.

Keywords. *Calodactylodes aureus*, *Calodactylodes illingworthorum*, systematics, natural history, morphology, vocalisation, India, Sri Lanka.

## Introduction

Lizards of the genus *Calodactylodes* are large, distinctive geckos endemic to rocky habitats in peninsular India and Sri Lanka. Despite their size, distinctive morphology, bright colouration, and loud vocalisation, these lizards have remained among the most poorly known geckos in the world and among the least appreciated members of the south Asian herpetofauna. Although consistently cited in checklists (e.g., Wermuth, 1965; Kluge, 1993), virtually nothing is known of the phylogeny or biology of *Calodactylodes*.

The genus *Calodactylus* was erected by Beddome (1870) for a new species, *C. aureus* (Fig. 1), from “amongst rocks in dark shady ravines on the Tripatty hills in North Arcot”. The generic name was discovered to be a junior homonym of *Calodactylus* Blanchard 1850 (Insecta: Coleoptera) and *Calodactylodes* was provided as a replacement name by Strand (1928). Although the original description did not specify the number of specimens in the type series, Boulenger (1885) referred to two adults from “Eastern Ghats” as the types and indicated that

several additional specimens from “North Arcot” were in the British Museum collection. Smith (1935) subsequently referred to the same two “type” specimens, but he explicitly mentioned eight additional geckos, corresponding to the ten specimens presently housed in the collection of the Natural History Museum, London (BMNH). Smith clarified that the two specimens that he regarded as types were associated with the specific locality of the Tripatty Hills, which he interpreted as meaning the Tirupati Hills, Andhra Pradesh. One additional specimen (ZMB 17555), apparently collected by Beddome has been located in the collection of the Zoological Museum of the Humboldt University in Berlin (Bauer and Günther, 1991). This specimen is associated with the locality “Callop Hills,” but there is a strong possibility that this is in error. Bauer and Günther (1991) regarded all ten specimens reported by Smith (1935) in the Natural History Museum, London, as well as the Berlin specimen as constituting the type series. No further specimens of *Calodactylodes aureus* were recorded until Daniel and Bhushan (1985)



**Figure 1.** Adult *Calodactylodes aureus* (AMB 5735). Photo: Indraneil Das.



**Figure 2.** Adult *Calodactylodes illingworthorum*. Photo: Indraneil Das.

reported the rediscovery of *C. aureus* in the Tirumalai (formerly Tirupati) Hills (13°41'N, 79°21'E), or Seshachalam Ranges, in the Venkateswara Wildlife Sanctuary in the Chittoor District of southern Andhra Pradesh, and subsequently in the adjacent Velikonda Range (Daniel et al., 1986). With the exception of two papers dealing with the digital morphology of the species (Russell and Bauer, 1988, 1989), the only subsequent references to *C. aureus* have been species accounts in derivative works drawn largely from Smith (1935) including those of Murthy (1990) and Tikader and Sharma (1992).

A second species in the genus, *Calodactylodes illingworthi* (Fig. 2), was described from Sri Lanka by Deraniyagala (1953a) from "Upon Nuvara Gala rock 1,200 feet high, near Maha Oya in the Eastern Province." Following Deraniyagala's description, and the repetition thereof in a subsequent work (Deraniyagala, 1953b), almost nothing has been published about this species. It has appeared in all recent checklists of Sri Lankan geckos (De Silva, 1994, 1995, 1998; Manamendra-Arachchi, 1995), but the only comments provided have been that the species is rare and restricted to the lowland dry zone of the country. Manamendra-Arachchi (1997) provided a colour photograph and noted that the species was both day and night active and occurs on rock faces.

The recent discovery of *Calodactylodes aureus* at Vellore in the southern Eastern Ghats of Tamil Nadu, and new reports of the Sri Lankan species, *C. illingworthi* (Manamendra-Arachchi, 1997) provide an opportunity to supplement the meagre data associated with the members of the genus. In this paper we present a summary of findings regarding the morphology and natural history of *Calodactylodes*.

#### Materials and methods

Specimens of *Calodactylodes aureus* were collected by hand and stomach flushed within eight hours of

capture in order to obtain dietary information. Live weights were recorded prior to euthanasia. Specimens were fixed in 10% neutral buffered formalin and transferred to 70% ethanol for subsequent storage. Specimens have been deposited in the Raffles Museum for Biodiversity Research, Zoological Reference Collection, National University of Singapore (ZRC) and the Kyoto University Zoological Collection (KUZ). Representatives of *C. illingworthi* were obtained through the courtesy of Rohan Pethiyagoda and Kelum Manamendra-Arachchi. Specimens cited from other collections are referred to following the standard symbolic codes for institutional collections (Leviton et al., 1985).

Specimens of both species were examined under a Nikon SMZ-10 dissecting microscope and measurements were taken with Brown and Sharpe Digit-cal Plus digital callipers. Radiographs were prepared using a Faxitron cabinet x-ray system with exposures of 45 sec at 40 kV. The following measurements were recorded for each specimen: snout-vent length (SVL); tail length (TL); axilla-groin length (AG); head length from posterior edge of mandible to snout tip (HL); maximal head width (HW); maximal head depth (HD); eye diameter (ED); distance from posterior border of orbit to anterior margin of ear (EE); and distance from anterior border of orbit to tip of snout (ES). Characteristics of head scalation and preanal pores (PP) and femoral pores (FP) were also recorded. One specimen of *C. aureus* was skinned, eviscerated, and cleared and double stained following a modification of the method of Wassersug (1976) for further osteological investigation.

Skin samples from the labial area and dorsal trunk of *Calodactylodes aureus* were prepared for scanning electron microscopy. These were dehydrated through a graded ethanol series, brought through critical point in a CO<sub>2</sub> drier, mounted on stubs with conductive

**Table 1.** Data on measurements (mm) and weights (gm) of *Calodactylodes aureus* and *C. illingworthorum* examined during this study. Abbreviations used: M = male; F = female; condition of tail: R = regenerated; B = broken.

Species	No.	Sex	Wgt	SVL	TL	AG	HL	HW	HD	ES	ED	EE	PP	FP
<i>C. aureus</i>	5735	M	8.0	74.5	68.6 R	32.1	20.1	14.4	9.7	8.3	5.9	5.3	2.0	5/4
<i>C. aureus</i>	5722	M	5.1	62.5	R	–	–	–	–	–	–	–	–	–
<i>C. aureus</i>	5724	M	1.6	45.0	55.4	19.6	12.2	8.3	6.0	4.9	3.3	3.4	0.0	0.0
<i>C. aureus</i>	5723	M	2.4	49.3	62.2	20.5	13.5	9.5	6.6	5.8	4.0	3.7	2.0	1/1
<i>C. aureus</i>	5726	M	0.8	36.8	42.4	16.4	10.3	7.0	5.0	4.1	3.1	3.0	0.0	0.0
<i>C. aureus</i>	5725	M	1.0	37.8	48.1	17.3	11.1	7.1	4.9	4.4	3.1	3.1	0.0	0.0
<i>C. aureus</i>	5721	F	8.9	72.4	88.8	31.6	19.5	14.3	9.0	7.8	5.3	5.2	–	–
<i>C. aureus</i>	5720	F	7.1	30.7	83.7	30.9	19.2	13.0	7.9	8.3	5.3	5.0	–	–
<i>C. aureus</i>	5734	M	10.5	73.4	96.4	32.6	20.7	14.5	9.0	8.2	4.7	5.7	2.0	6/4
<i>C. aureus</i>	ZSI 25259.1	M	5.2	74.2	R	35.5	14.3	13.7	9.2	8.0	5.9	5.6	–	–
<i>C. aureus</i>	3	M	1.5	45.7										
<i>C. aureus</i>	6	M	5.2	64.3	76.7	29.7	12.5	11.2	7.3	6.8	5.1	3.4	–	–
<i>C. aureus</i>	8	M	1.4	45.5										
<i>C. aureus</i>	KUZ48088	F	10.0	75.2	78.2 R	35.0	17.4	13.0	7.0	7.9	4.7	5.0	–	–
<i>C. aureus</i>	12	M	3.7	62.1										
<i>C. illingworthorum</i>	AB1	M	–	76.5	87.0	36.3	21.4	14.8	9.0	8.9	6.5	6.0	4.0	3/4
<i>C. illingworthorum</i>	AB2	M	–	75.2	39.4 B	33.9	19.8	13.5	8.3	7.9	5.5	5.1	4.0	3/3

silver paste and allowed to dry. Specimens were coated with gold-palladium alloy to a thickness of 30 nm in a Hummer sputter-coater and examined with a Hitachi scanning electron microscope. Photomicrographs were taken with Polaroid type 55 film.

## Results

**Nomenclature.** Deraniyagala (1953a; 1953b) named the species *Calodactylodes illingworthi* in honour of Margaret and Percy Illingworth. As the name honours two people named Illingworth, Deraniyagala's construction of the specific epithet is incorrect and must be emended to *Calodactylodes illingworthorum* under Article 32.5 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999). Under Article 33.2.2 the corrected name retains the author and date of the original spelling. The appropriate name for the Sri Lankan *Calodactylodes* is thus *C. illingworthorum* Deraniyagala, 1953.

**Morphology.** Beddome's (1870) description of *Calodactylus aureus* was brief, but adequate to diagnose the species. It provided little detail, however, about most mensural and meristic features, and presented data explicitly for only one of the specimens in the original series. The accounts of Boulenger (1885) and Smith (1935) were somewhat more detailed but nonetheless did not provide scale counts or measurements for more than a single specimen. Several such parameters were recorded for the four specimens reported on by Daniel et al. (1986). Our specimens, which are smaller than the largest

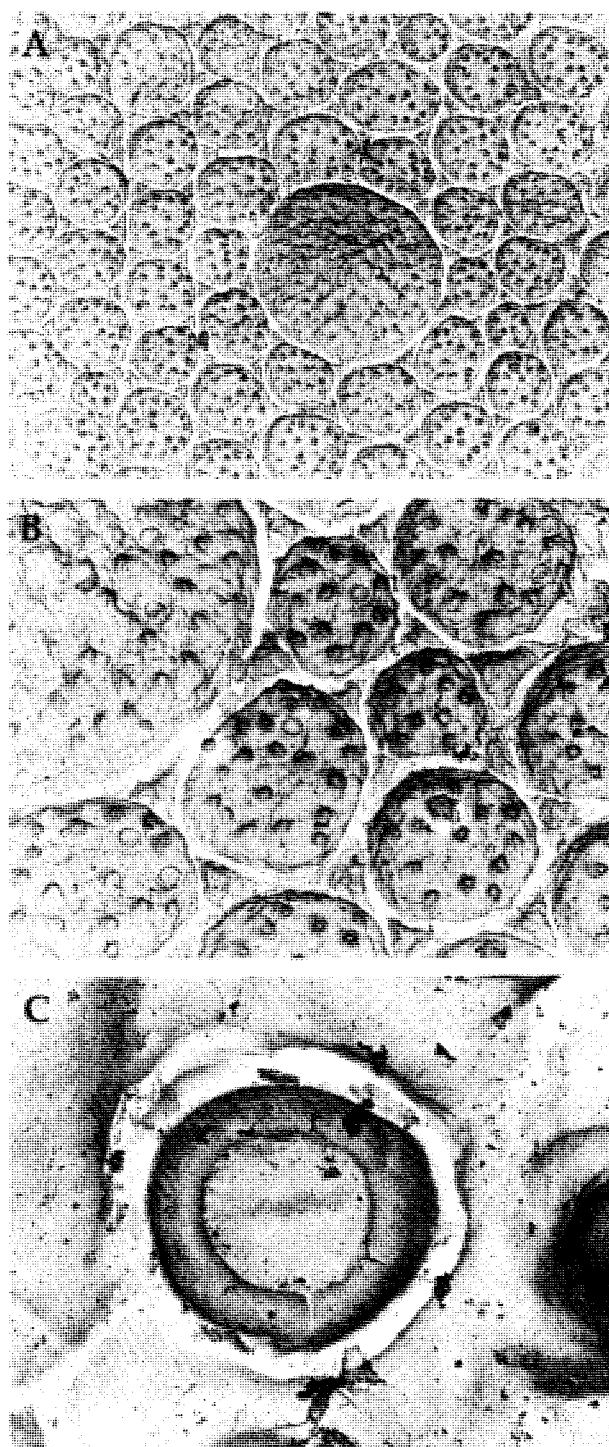
specimens reported by Boulenger (89 mm SVL), Smith (85 mm SVL), and Daniel et al. (81 mm SVL), agree in general with the descriptions of earlier authors (Table 1). Nonetheless, our series from Vellore does differ slightly in some features and in addition we are able to present some data previously unavailable for this species, particularly in regard to hemipenial morphology, skin surface ultrastructure, and osteology. Our data for *C. illingworthorum* are also generally comparable to those presented by Deraniyagala (1953a; 1953b) for this species.

**Scalation.** As reported by all previous authors, the dorsal skin of *Calodactylodes aureus* is characterised by small, flat scales interspersed by rounded, flattened tubercles. Under magnification (Fig. 3) these scales can be seen to be pustulate, a condition not otherwise known in geckos. Individual scales are approximately 150 micrometers in diameter and bear 10-20 pustules, each about 5-8 micrometers in diameter. Most dorsal scales also have one or more sensory organs on them. These lack the Oberhäutchen in the skin samples available, therefore the spinulate microarchitecture of the scales and the bristles associated with the sensory organs are lacking. However, the ring-shaped base with a sunken centre is typical for many geckos. Parlabial scales were also examined. These are similar in appearance to the dorsal scales described above but each has a greater number of sensory organs (up to 12) and are arranged along the periphery of the scales bordering the labials themselves. The labials lack the pustules of other scales and have small numbers of mechanoreceptors. The surface microstructure of the skin of *C. illingworthorum* was

not investigated, although gross and light microscopic examination suggests a nearly identical pattern.

**Preal and femoral pores.** Preal and femoral pores were stated by Beddome (1870), Boulenger (1885), Smith (1935), Murthy (1990), Tikader and Sharma (1992), and Kluge and Nussbaum (1995) to be absent in males of *Calodactylodes aureus*. Deraniyagala (1953b) regarded *C. aureus* as being characterised by the absence of preanal pores and the presence of 5-9 femoral pores, whereas *C. illingworthorum* has preanal pores and 2-5 femoral pores. Although our observations of *C. illingworthorum* fall within the range of Deraniyagala's observations, we found preanal pores to be present in males of *C. aureus* as well. Two adult males (AMB 5734-5), and one subadult (AMB 5723) each possessed two preanal scales, separated from one another by two intervening scales. Only one femoral pore was present near the knee on each side in the subadult, but a series of pores (6 left/4 right in AMB 5734 and 5/4 in AMB 5735) were present in the adults. The two Sri Lankan specimens examined each possessed four preanal pores, with 3-4 scales separating the more medial pores from one another and a single scale intervening between the more lateral and medial pore-bearing scales of each side. Femoral pores were present in rows of 3/3 and 3/4 in the smaller and larger specimens, respectively. This compares to Deraniyagala's (1953b) description of four preanal pores separated by three median scale rows into two pairs of two, and 2-5 femoral pores close to each knee joint.

**Colouration.** As noted by previous authors, colouration among *Calodactylodes aureus* is variable, with some individuals showing a pronounced yellowish pattern, whereas others exhibit a highly mottled appearance or are darker (brownish, reddish, or even blackish), without any golden colour. We noted that the golden colour is never present on juveniles (Fig. 4) and is most pronounced in adult males (Fig. 5). When kept together, the largest, and apparently dominant male, remains golden more or less continuously. If this individual is removed the next largest male assumes this colour pattern. Smaller males and females generally assumed a paler yellow colour or were predominantly darkly patterned. The throat region was also variable in colour. This was typically a pale yellow in most specimens but was a dark yellow in the largest male (AMB 5735) and in two other adult males. While other adult males were paler, no females or juveniles exhibited the dark yellow throat.



**Figure 3.** Scanning electron micrograph of the dorsal skin of *Calodactylodes aureus* (AMB 722). A. Low magnification (70 ×) view of skin, illustrating the relatively homogeneous dorsal scales with an isolated flattened tubercle. B. Middle magnification (170 ×) view of dorsal scales, showing the characteristic pustular surface of the scales and the numerous sensory organs. C. Higher magnification (2500 ×) view of a single sensory organ from a dorsal scale. The loss of the Oberhäutchen layer of the epidermis has left the organ without the bristle(s) typical of such sensory structure in most gekkonids.

Deraniyagala (1953b) described the life colour of *Calodactylodes illingworthorum* as yellow ochre with dark brown dots and a neural row of six subovate dark brown spots. He described the inter spots as bluish and the lighter tail bands as yellow. He also mentioned the presence of a bright yellow gular patch. On the basis of photographs of living specimens, the dorsal pattern of this species is a mottled purplish-brown, marked by ashy bands on the limbs and ashy grey to whitish flecks on much of the head and body. The vertebral midline bears a series of six dark patches between the nape and sacrum, each separated by a somewhat smaller cream dash or spot. A dark canthal stripe passes from the nostril to the eye and continues posterior to the eye to about the level of the ear. The dorsum of original tails is characterised by dark brown markings alternating with much narrower cream bands.

**Hemipenes.** The hemipenes were everted on one male specimen of *Calodactylodes aureus* (AMB 5734). Each organ measures approximately 5.4 mm in total length, with a basal width of 2.4 mm. The distal portion of the hemipenis is broadened and bifid, measuring 4.3 mm across. The widening of the apex begins 2.5 mm from the tip of the organ. The shaft of each hemipenis is smooth or weakly plicate. The entire distal region, however, is covered by small, roughly uniform spines. This spinulate architecture characterises both the sulcal and asulcal surfaces of the hemipenis. The sulcus itself is well-defined and splits symmetrically distally, extending into the centre of each apical lobe of the organ.

**Osteology.** Aside from the skeleton of the manus and pes, which was described in some detail by Russell and Bauer (1988, 1989) for *Calodactylodes aureus*, the only published information on the skeleton of *Calodactylodes* is derived from Kluge (1967) and Kluge and Nussbaum (1995), who reported on a number of features, based on a skeletal specimen of *C. aureus* (now catalogued as UMMZ 127616). Our observations (Figs. 6-7) do not conflict with those of these authors. Figures 8-9 show the shape of lamellae on the hindlimbs of the two species.

In the skull, the nasals and parietals are paired, whereas the frontal is single. The nasals possess prominent posterolateral processes that have extensive overlap with the anterior margin of the frontal. The premaxilla is relatively narrow and has an elongate nasal process. The postfrontal bone is strongly asymmetrical, with the anterior arm being 1.5 times the length of the posterior. The stapes is perforated by a stapedia foramen. The second ceratobranchial arch of the hyoid is incompletely



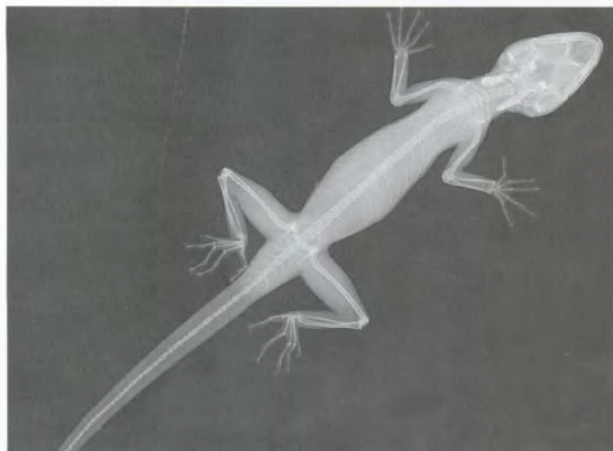
Figure 4. Throat colouration of *Calodactylodes aureus* (non-golden phase). Photo: Indraneil Das.



Figure 5. Throat colouration of *Calodactylodes aureus* (golden phase). Photo: Indraneil Das.

chondrified, with the medialmost portion being absent.

The atlas is unfused dorsally. Both species of *Calodactylodes* are characterised by 26 presacral vertebrae, the most common condition among gekkonids (Kluge, 1967; Bauer, 1990). There are invariably two sacral vertebrae, but the number of pygal vertebrae vary. The first four caudal vertebrae are non-autotomic, but the fifth, which possesses narrow pleurapophyses perpendicular to the axis of the centrum, is variable with respect to the presence of an autotomy plane in *C. aureus*, whereas it is autotomic in the two *C. illingworthorum* examined. Among a sample of 14 specimens, regenerated tails were found in only three specimens (all adult males), suggesting that tail loss rates are relatively low in this species. On the basis of the figures presented by Daniel et al. (1986), it would appear that one of four of their specimens possessed a regenerated tail, and it too was an adult male.



**Figure 6.** Radiograph of a female *Calodactylodes aureus* (AMB 5720) showing the gracile body, slender limbs and tail, and characteristic digital structure of members of this genus. 45 sec exposure at 45 kV.



**Figure 7.** Radiograph of a male *Calodactylodes illingworthorum* (WHT 2224) illustrating the slightly wider skull of this species. The small cloacal bones are visible at the level of the second postsacral vertebra. 45 sec exposure at 45 kV.

The interclavicle is dagger-shaped, or cruciform, with a short anterior projection, long and broad lateral wings and a long and moderately thick posterior projection. There are three pairs of sternal ribs and two pairs of xiphisternal ribs present. The clavicles are much wider medially than laterally and are perforated by large fenestrae near their medial margins. In the cleared and stained specimen of *C. aureus*, a second, much smaller lateral fenestra is also present. The hypoischium, which remains cartilaginous in adults, is elongate and diamond-shaped. Males possess a single set of cloacal bones at the level of the posterior portion of the first postsacral vertebra. These are crescentic, relatively smooth, and smaller than in most geckos of comparable size. These structures were difficult to locate in the x-rays of some males.



**Figure 8.** Foot structure (ventral view) of *Calodactylodes aureus* (AMB 5735). Photo: Indraneil Das.



**Figure 9.** Foot structure (ventral view) of *Calodactylodes illingworthorum* (WHT 2224). Photo: Indraneil Das.

Russell and Bauer (1988) reported that *Calodactylodes aureus* possessed a unique pattern of paraphalangeal cartilages, paired structures occurring lateral to the joints in the digits of some geckos. In this species, small paraphalanges are present at the penultimate joint in digits II-V and at the more proximal interphalangeal joints in digits III and IV. These structures have been associated in pad control in geckos with highly arcuate penultimate phalanges. We confirm this arrangement in the manus and pes of all specimens of *C. aureus* for which this feature could be observed (because the structures are small and cartilaginous, they are not evident in the x-rays of very small individuals). The configuration of paraphalanges is similar in *C. illingworthorum*, although a more proximal pair of elements could not

be confirmed in either the manus or the pes, and a second pair of paraphalanges was associated with the antepenultimate phalangeal joint of digit V of the pes. Specimens as large as 62.5 mm SVL exhibited extensive regions in the pedal and manual joints that had not yet ossified.

#### Interspecific comparisons in *Calodactyloides*

The two species of *Calodactyloides* are very similar to one another in most respects. Mental shape differs, however, with *C. aureus* possessing a pentagonal or rectangular scale, whereas *C. illingworthorum* has a narrow, wedge-shaped mental. The ear is more rounded in the Sri Lankan form and more elliptical in the Indian. Otherwise the two may be differentiated on the basis of colour pattern, an increased number of preanal pores in *C. illingworthorum*, and possibly by a different number of paraphalangeal elements on digit V of the pes.

#### Distribution

Until now, *Calodactyloides aureus* had been recorded only from southern Andhra Pradesh, from the Seshachalam and Velikonda ranges, on the basis of the specimens reported on by Daniel (Daniel and Bhushan 1985; Daniel et al., 1986) and Smith's (1935) interpretation of Beddome's (1870) original "Tripathy hills" locality. Our records from the Vellore region of the North Arcot District of Tamil Nadu represent the first confirmed records for this state. However, it is possible that Smith's (1935) interpretation was incorrect, and that the type locality reported by Beddome corresponds to Tiruppattur (also spelled Tirupattur or Tiruppattur), which is also in the North Arcot District, south-west of Vellore. This interpretation was first proposed by Deraniyagala (1953b) and was accepted by Satyamurti (1962) and Murthy (1990). It is unclear how extensive the range of *C. aureus* is, but the few localities known suggest that it is widespread in the southern portion of the Eastern Ghats. It should be expected to occur throughout the Javadi Hills as well as the Velikondas and Seshachalams wherever appropriate rocky habitats are present. The portion of the Eastern Ghats inhabited by *C. aureus* is relatively xeric and the vegetation is dominated by dry deciduous and thorn scrub (Legris and Meher-Homji, 1982). Vellore receives 107.5 cm rain/yr and the region is considered semi-arid (Subrahmanyam, 1982).

Despite the large size, bright colouration, semi-diurnal habits, and distinctive vocalisations of the species, it appears to have escaped notice, even in heavily populated regions. This suggests that an even more widespread occurrence might be possible and the golden gecko should be sought in the more

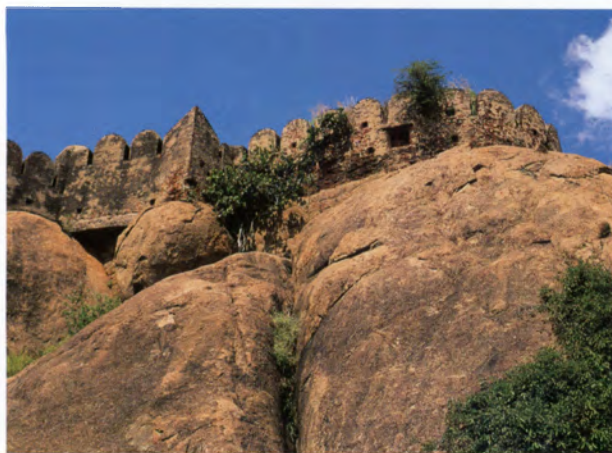
northern ranges of the Eastern Ghats as well. A species very similar to *Calodactyloides aureus* has recently been reported and photographed from Castle Rock, Karnataka, but no specimens were collected. If verified, this would suggest either a wide peninsular distribution for the golden gecko, or the occurrence of a new species in the northern Western Ghats.

The specimens we examined of *Calodactyloides illingworthorum* (WHT 2224) were collected from the Kumaradola Group, Monaragala, Sri Lanka (06°53'N, 81°22'E), 305 m elev. by M. M. Bahir on 28 April 1998. This locality appears to be only the second published record for this species, and it is close to Deraniyagala's (1953a) type locality. It is likely that the species is more widespread in appropriate rocky habitats, and like *C. aureus*, it may not be as uncommon as previously reported.

#### Habitat and activity

Natural history observations were made and specimens of *Calodactyloides aureus* collected at Balamadi Hill, Vellore, on 6 January 1998 and at the Vellore Hill Fort on the following day (both localities are situated in North Arcot District, Tamil Nadu, south-eastern India). The locality at Balamadi Hill is ca. 5 km east from the town of Vellore at < 50 m elevation. The region has high relief and the specific area investigated was characterised by large boulders. The habitat was investigated from approximately 1600 to 2100 h. Adult *C. aureus* were active early during this period in the interstices between large boulders, typically in wholly or partly shaded areas more than one metre above the ground. Males were heard calling from such retreats (see below). After dark geckos were observed on more exposed rock faces. Two specimens were collected between 1850 and 1900 h when the air temperature was 24.8°C. The first was a male and was found 3.5 m above the substrate, whereas the second, a female, was only 44 cm above the substrate. In addition to *Calodactyloides aureus*, a new species of *Cnemaspis*, *Ophisops beddomei*, *Hemidactylus reticulatus*, *Lygosoma punctata* and *Psammophilus blanfordanus* were also observed or collected at this locality. Of these species, only *Cnemaspis* was syntopic with the golden gecko.

The Vellore Hill Fort locality is directly above the town centre of Vellore. The fort was constructed of granite blocks in the 16<sup>th</sup> century by Sinna Bommi Nayak, a vasaal chieftain under the Vijayanagar king, Sada Sriranga Maharaja. Below the fort is a now dry well measuring 4.0 × 5.37 m, accessible by a stone-lined enclosed stairwell. The average height of the stairwell from a step to the ceiling directly above it is approximately 206 cm and the width of the stairwell shaft is 102 cm. All *Calodactyloides aureus* observed at



**Figure 10.** Hill fort at Vellore, Tamil Nadu illustrating the boulder-dominated terrain occupied by *Calodactylodes aureus*. At this locality, specimens were observed in a rock stairwell leading from the fort to a large well. Photo: Aaron M. Bauer.

this locality were in the stairwell. The animals were observed during the period 1100–1400 h. Although some animals were alert, they were not active until disturbed and no calling was noted. Outside air temperatures were well over 30°C, but the temperature within the stairwell was cool and constant at approximately 26°C. *Cnemaspis* n. sp. were also found active within the stairwell. Other amphibians and reptiles collected at the site were *Sitana ponticeriana* and several *Polypedates maculatus*. The former was active around the walls of the fort itself, whereas the later were in the vegetated well bottom. Figure 10 shows the habitat at the base of Vellore Hill Fort.

Deraniyagala (1953b) described *Calodactylodes illingworthorum* as nocturnal but provided no specifics of activity. The type locality is a rocky inselberg in the dry eastern lowlands of Sri Lanka, rather similar to the known localities for *C. aureus*.

### Diet

Dietary composition was determined by stomach flushing all adult and subadult specimens (n = 9) of *Calodactylodes aureus*. All specimens contained at least some prey items. Almost all of the items ingested were arthropods, although one specimen contained parts of leaves, probably ingested incidentally with insects, and another specimen contained a small lizard egg. The number of prey items per gecko ranged from one to three and the size of individual prey ranged from small fragments to 28.1 mm (an orthopteran). Exclusive of the lizard egg, 17 prey items were retrieved from the nine geckos. These included coleopterans (4 specimens in 3 lizards), orthopterans (3/2), larval lepidopterans (3/2), unidentified insects (4/4), and one arachnid, one adult lepidopteran, and

one unidentified insect larva. Daniel et al. (1986) reported beetles and ants from the stomachs of four specimens housed in the collection of the Bombay Natural History Society (BNHM 1408-10, 1416). The diet of *C. illingworthorum* has been reported to be beetle larvae and glow-worms (Deraniyagala, 1953b).

### Vocalisation

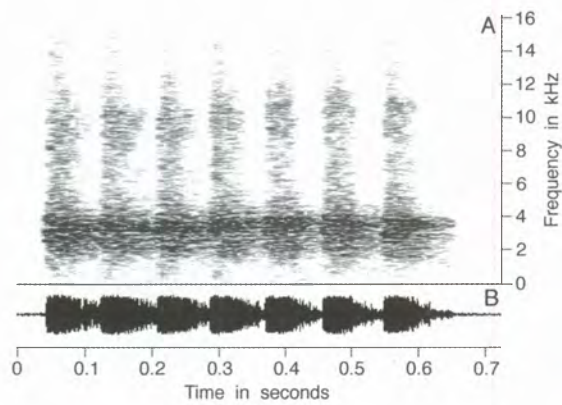
Previous authors have not commented on the vocal abilities of *Calodactylodes aureus*. We, however, found the species to be highly vocal, to the point of constituting one of the dominant natural sounds in the environment. Vocalisation was noted from approximately 1600 to 2030 h, but appeared to reach a peak in the hour before sunset. No individuals were observed calling in exposed positions, rather calls were made from clefts between large boulders. As far as could be determined, calls were made only by adult males. The spaces from which geckos called appeared to have the effect of resonating chambers. Calls were recorded in the field with the use of a small portable cassette recorder. Superficially similar calls were made by several animals, but only one individual was recorded. Calls were emitted spontaneously and were sometimes grouped, although there appeared to be no repeated pattern of call periodicity. Attempts to obtain additional calls from captive animals were unsuccessful, as no spontaneous calling by a captive male occurred for approximately three weeks after capture, and thereafter calling was infrequent.

The vocalisation sequence analysed consisted of a series of four calls made during a single 16 sec period. Calls ranged from 0.65 to 0.90 sec in duration and consisted of a series of nearly identical pulses of approximately 0.08 sec. The first call consisted of 11 pulses and was followed 2.4 sec later by a second call of seven pulses, then 3.6 sec later by a call of eight pulses, and finally, 6.7 sec later by a call of 10 pulses. With the exception of the last four pulses of the first call, all pulses were very similar in their frequency ranges (approximately 1–15 kHz; Fig. 11). The dominant frequency of all pulses was approximately 3850 Hz. A much less pronounced secondary power peak occurred at about 11100 Hz in all pulses except the last four of the first call, which included no sounds above approximately 5 kHz. Each pulse began abruptly, with high amplitude and after approximately 0.04 sec began to decrease, reaching its lowest amplitude immediately before the start of the next pulse. In no case were there any gaps between pulses within a call.

### Reproduction

Numerous apparently communal groupings of eggs of *Calodactylodes aureus* were located at Balamadi Hill





**Figure 11.** Second call in a series of four spontaneous calls made by a male *Calodactyloides aureus* at Balamadi Hill, Vellore, 6 January 1998. A. Sonogram illustrating the frequency distribution of the call pulses, with a dominant frequency at 3850 Hz. B. Pulse profile showing the periodicity of pulses and their amplitudes.

and the Vellore Hill Fort. These clusters contained the remains of many hatched eggs (approximately 20 to > 100; Fig. 12) and were exposed on vertical rock walls or hanging downward from horizontal rock surfaces. Egg attachment scars were present in various stages of decomposition, indicating the site of communal clutches from previous years. Measurements of seven egg attachment sites were recorded (Table 2). At Balamadi Hill, two oviposition sites were found on natural substrates in a group of boulders. Five oviposition sites at the Vellore Hill Fort were on the walls and ceiling of a man-made enclosed stairway descending to a well.

The reproductive period of the species appears to be at least moderated extended as several eggs containing embryos at various stages of development were collected, including two near-term embryos measuring 27.9 mm SVL + 30.2 mm tail and 29.1 mm SVL + 31.7 mm tail. Two shelled oviductal eggs were present in AMB 5721, a female of 72.4 mm SVL. One female kept in captivity also laid eggs on 14 February



**Figure 12.** Egg-laying site of *Calodactyloides aureus*, on rock surfaces, at Balamadi Hills, Vellore, Tamil Nadu. Photo: Indraneil Das.

1998. These measured 12.9 mm × 14.9 mm and 12.3 mm × 14.4 mm and were laid on a vertical glass surface, from which they were easily removed. The surface of the eggs when freshly laid had a wrinkled appearance and the two eggs were weakly attached to one another, but separable. One egg was eventually broken and the second failed to hatch.

Deraniyagala (1953b) also noted that communal nesting takes place in *Calodactyloides illingworthorum*. He reported eggs taken on 14 February, 1953 and gave average egg sizes of 14.19 × 11.8 × 8.3 mm.

**Relationships of *Calodactyloides***

The proposed relationships of *Calodactyloides* to other gekkonids were reviewed by Russell and Bauer (1989). Most early workers presented no formal phylogenetic hypotheses, but clustered *Calodactyloides* with other genera possessing “leaf-toed” digits with paired apical scansors, such as *Ptyodactylus*, *Afroedura*, *Ebenavia* and *Phyllodactylus* (Boulenger, 1885; Smith, 1935). Russell (1972) suggested possible affinities

**Table 2.** Communal oviposition sites of *Calodactyloides aureus*.

Oviposition site	Age	Egg patch size (cm)	Height above substrate (cm)	Orientation
Balamadi Hill 1	new	4.0 × 5.3	144.5	Vertical rock face
Balamadi Hill 2	new	6.5 × 15.5	39.0	Undersurface of boulder
Vellore Hill Fort 1	new	15.0 × 35.0	236.5	Inverted horizontal (stairwell)
Vellore Hill Fort 2	new	7.0 × 13.0	153.5	Vertical (stairwell)
Vellore Hill Fort 3	new	5.0 × 13.5	203.0	Vertical (stairwell)
Vellore Hill Fort 4	old	18.0 × 18.0	206.0	Inverted horizontal (stairwell)
Vellore Hill Fort 5	old	10.5 × 16.0	206.0	Inverted horizontal (stairwell)

with *Afroedura* on the basis of shared apomorphic digital structures, such as the double row of leaf-like scansors on digits II-V of the manus and pes, but he acknowledged that the occurrence of similar character states in the two genera might reflect parallelism. Kluge (1983) did not provide any explicit hypothesis of relationship for *Calodactylodes*, but he did place it in the putatively monophyletic Gekkonini, whereas *Afroedura* was relegated to the paraphyletic "Ptyodactylini." Subsequently, the single character used to diagnose the Gekkonini, the loss of the second ceratobranchial arch, has been shown to be highly homoplastic (Kluge and Nussbaum, 1995; Bauer et al., 1997), leaving the affinities of *Calodactylodes* entirely unresolved.

Russell and Bauer (1989) provided data from digital morphology that suggested that only *Afroedura*, among the leaf-toed geckos, shared a large number of pedal characters with *Calodactylodes*, including many aspects of muscular and tendinous architectures, as well as distally constricted penultimate phalanges, and double pairs of enlarged scansors (Figs. 6-7). Nonetheless, *Afroedura* lacks paraphalanges, which are present in *Calodactylodes*, and also differs in several other, more minor pedal features. Russell and Bauer (1989) did, however, note that there was little evidence that the two genera had shared recent ancestry. Some floral connections between sub-Saharan Africa and peninsular India and Sri Lanka have, however, been linked to Late Cretaceous to Early Tertiary rafting of the Deccan Plate from the Seychelles Block and adjacent Madagascar (Ashton and Gunatilleke, 1987).

Other major differences between *Calodactylodes* and *Afroedura* include the radically different body proportions. Although both groups are principally rupicolous, most *Afroedura* are crevice dwellers with short legs and depressed bodies. In contrast, *Calodactylodes* has extremely elongate legs and is primarily a boulder surface species. In overall body appearance, and to some extent in biology, *Calodactylodes* is most reminiscent of *Ptyodactylus* and *Asaccus*. Both of these genera have distributions centred on the Middle East, although, *Ptyodactylus homolepis* extends eastwards into Sind, eastern Pakistan (Smith, 1935; Minton, 1966). However, the details of digital structure differ between these two genera and *Calodactylodes* (Russell, 1972; Russell and Bauer, 1988; 1989), as does the condition of the second ceratobranchial arch (Kluge, 1983). A large suite of derived characters in *Asaccus* (e.g., loss of cloacal sacs and bones, phalangeal reduction, loss of the left oviduct) further differentiates this genus from *Calodactylodes* (Arnold and Gardner, 1994).

Unfortunately, most of the osteological characters of *Calodactylodes*, except for the reduction of the second ceratobranchial arch and the presence of paraphalanges are primitive for gekkonids and provide no information about possible relationships. Hemipenial structure is simple but distinctive in *C. aureus*. Although the hemipenes are similar in shape to those of many geckos, they differ in their ornamentation from the organs of both superficially similar taxa, such as *Ptyodactylus* (Böhme, 1988), and other Indian species, including *Hemidactylus brookii*, *H. maculatus* and *H. flaviviridis* (McCann, 1946). Hemipenial characters may eventually prove useful in establishing the relationships of the genus, but as in the case of the distinctive pustulate scale structure, meaningful comparisons are limited by the lack of data from most other gekkonid groups. Pending the collection of morphological and molecular data for representatives of all gekkonid genera, *Calodactylodes*, like many other gecko groups (Bauer et al., 1997), remains a clearly diagnosable clade with no resolved affinities. Establishment of a phylogenetic framework for the golden geckos is particularly important, as they represent one of few scleroglossan lizard lineages that are strictly endemic to peninsular India and Sri Lanka and may be illustrative of a Gondwanan faunal element.

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#### Literature Cited

- Arnold, E. N. & A. S. Gardner. 1994. A review of the Middle Eastern leaf-toed geckoes (Gekkonidae: *Asaccus*) with descriptions of two new species from Oman. *Fauna of Saudi Arabia* 14: 424-441.
- Ashton, P. S. & C. V. S. Gunatilleke. 1987. New light on the plant geography of Ceylon. I. Historical plant geography. *J. Biogeogr.* 14: 249-285.
- Bauer, A. M. 1990. Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). *Bonn. Zool. Monogr.* 30: 1-218.
- Bauer, A. M., D. A. Good & W. R. Branch. 1997. The taxonomy of the southern African leaf-toed geckos (Squamata:

- Gekkonidae), with a review of Old World "*Phyllodactylus*" and the description of five new genera. Proc. Calif. Acad. Sci. 49: 447–497.
- Bauer, A. M. & R. Günther. 1991. An annotated type catalogue of the geckos (Reptilia: Gekkonidae) in the Zoological Museum, Berlin. Mitt. Zool. Mus. Berlin, 67: 279–310.
- Beddome, R. H. 1870. Descriptions of some new lizards from the Madras Presidency. Madras Monthly J. Med. Sci. 1: 30–35, pls. 1–2.
- Böhme, W. 1988. Zur Genitalmorphologie der Sauria: funktionelle und stammesgeschichtliche Aspekte. Bonn. Zool. Monogr. 27: 1–176 pp.
- Boulenger, G. A. 1885. Catalogue of the lizards in the British Museum (Natural History). Vol. I. British Museum (Natural History), London. xii + 463 pp., 32 pls.
- Daniel, J. C. & B. Bhushan. 1985. The golden gecko of Tirumalai Hills. Hornbill 1985(3): 17–18, 1 pl.
- Daniel, J. C., B. Bhushan & A. G. Sekar. 1986. Rediscovery of the golden gecko *Calodactylodes aureus* (Beddome) in the Eastern Ghats of Andhra Pradesh. J. Bombay nat. Hist. Soc. 83: 15–16, 1 pl.
- Deraniyagala, P. E. P. 1953a. A new *Calodactylodes* gecko from Ceylon. J. Roy. Asiatic Soc. (Ceylon). 3: 27–28, 1 pl.
- Deraniyagala, P. E. P. 1953b. A colored atlas of some vertebrates from Ceylon. Vol. Two. Tetrapod Reptilia. Ceylon Government Press, Colombo. vii + 8 pp. unnumbered + 101 pp., 11 b&w pls., 35 col. pls.
- De Silva, A. 1994. An introduction to the herpetofauna of Sri Lanka. Lyriocephalus 1: 3–19.
- De Silva, A. 1995. The reptiles of Sri Lanka, a checklist and common names, part 1: Testudines, Crocodylia and Lacertilia. Lyriocephalus 2: 25–33.
- De Silva, A. 1998. Sauria (Lizards and varanids) of Sri Lanka: A checklist and an annotated bibliography. Department of Wildlife Conservation, Colombo. 52 pp.
- De Silva, A. 1998. Country report for Sri Lanka. Herpetofauna of Sri Lanka: present status, distribution and conservation. In: Biology and conservation of the amphibians, reptiles and their habitats in south Asia (Proceedings of the International Conference on the Biology and Conservation of the Amphibians and Reptiles of South Asia, Sri Lanka, August 1–5, 1996). pp: 51–73. Amphibia and Reptile Research Organization of Sri Lanka (ARROS), Gampola.
- International Commission on Zoological Nomenclature. 1999. International code of zoological nomenclature. Fourth edition. The International Trust for Zoological Nomenclature, London. XXIX + 306 pp. (in English and French).
- Kluge, A. G. 1967. Higher taxonomic categories of gekkonid lizards and their evolution. Bull. Amer. Mus. nat. Hist. 135: 1–60.
- Kluge, A. G. 1983. Cladistic relationships among gekkonoid lizards. Copeia 1983: 465–475.
- Kluge, A. G. 1993. Gekkonoid lizard taxonomy. International Gecko Society, San Diego. 245 pp.
- Kluge, A. G. & R. A. Nussbaum. 1995. A review of African-Madagascan gekkonid lizard phylogeny and biogeography (Squamata). Misc. Pub. Mus. Zool. Univ. Michigan 183: 1–20.
- Legris, P. & V. M. Meher-Homji. 1982. The Eastern Ghats: vegetation and bioclimatic aspects. In: Proceedings of the Seminar on Resources, Development and Environment in the Eastern Ghats, March 24–27, 1982. pp. 1–17. Andhra University Press, Waltair.
- Leviton, A. E., R. H. Gibbs, Jr., E. Heal & C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985: 802–832.
- Manamendra-Arachchi, K. 1995. The geckos of Sri Lanka. Lyriocephalus 2: 82, pl. 10.
- Manamendra-Arachchi, K. 1997. Gecko! Sri Lanka Nature 1(1): 45–55.
- McCann, C. 1946. The hemipenis in reptiles. J. Bombay nat. Hist. Soc. 46: 348–373, pls. I–X.
- Minton, S. A., Jr. 1966. A contribution to the herpetology of West Pakistan. Bull. Amer. Mus. nat. Hist. 134: 27–184, pls. 9–36.
- Murthy, T. S. N. 1990. A field book of the lizards of India. Rec. Zool. Surv. India Occ. Pap. 115: 1–122.
- Russell, A. P. 1972. The foot of gekkonid lizards: a study in comparative and functional anatomy. Ph.D. Dissertation, University of London, London. 368 pp.
- Russell, A. P. & A. M. Bauer. 1988. Paraphalangeal elements of gekkonid lizards: a comparative survey. J. Morphol. 197: 221–240.
- Russell, A. P. & A. M. Bauer. 1989. The morphology of the digits of the golden gecko, *Calodactylodes aureus* and its implications for the occupation of rupicolous habitats. Amphibia-Reptilia 10: 125–140.
- Satyamurti, S. T. 1962. Guide to the lizards, crocodiles, turtles and tortoises exhibited in the reptile gallery, Madras Government Museum. Government of Madras, Madras. 45 pp.
- Smith, M.A. 1935. The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia, vol. 2: Sauria. Taylor and Francis, London. xii+440 pp., 1 pl.
- Subrahmanyam, V. P. 1982. Eastern Ghats region: vegetation and climatic aspects. In Proceedings of the Seminar on Resources, Development and Environment in the Eastern Ghats, March 24–27, 1982; pp. 19–26. Waltair, Andhra University Press.
- Strand, E. 1928. Miscellanea nomenclatorica zoologica et palaeontologica. Archiv für Naturges. (A) 92[1926]: 30–75.
- Tikader, B. K. & R. C. Sharma. 1992. Handbook Indian Lizards. Calcutta, Zoological Survey of India. xv + 250 pp., 42 pls.
- Wassersug, R.J. 1976. A procedure for differential staining of cartilage and bone in whole formalin-fixed vertebrates. Stain Technol., 54: 131–134.
- Wermuth, H. 1965. Liste der rezenten Amphibien und Reptilien: Gekkonidae, Pygopodidae, Xantusiidae. Das Tierreich 80: 1–246.