

# Taxonomic status of the *Coryphophylax maximiliani* Fitzinger in: Steindachner, 1867 with notes on *Coryphophylax subcristatus* (Blyth, “1860” 1861) (#108505)

1

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# Taxonomic status of the *Coryphophylax maximiliani* Fitzinger in: Steindachner, 1867 with notes on *Coryphophylax subcristatus* (Blyth, “1860” 1861)

*Italics*

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The insular agamid genus *Coryphophylax* Fitzinger in Steindachner, 1867, is endemic to the Andaman and Nicobar Islands in the Bay of Bengal, India. These diurnal lizards are currently represented by two putative species, *Coryphophylax subcristatus* (Blyth, “1860” 1861) and *Coryphophylax brevicauda* Harikrishnan, Vasudevan, Chandramouli, Choudhury, Dutta & Das, 2012. The species *C. subcristatus* is said to be distributed through the Andaman and Nicobar Islands, even across the Ten Degree Channel, which is a recognised biogeographic barrier. A reassessment of the taxonomy of *C. subcristatus* shows the population south of the Ten Degree Channel, for which the nomen *Coryphophylax maximiliani* Fitzinger in Steindachner, 1867 is available, to be distinct. The results are based on morphological data from museum material, including type specimens and mitochondrial 16S rRNA sequences. The members of the genus *Coryphophylax* are abundant and widespread across the islands and may serve as an illuminating example for studying the patterns of colonization and diversification across the Andaman and Nicobar Islands.

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## Abstract

The insular agamid genus *Coryphophylax* Fitzinger in Steindachner, 1867, is endemic to the Andaman and Nicobar Islands in the Bay of Bengal, India. These diurnal lizards are currently represented by two putative species, *Coryphophylax subcristatus* (Blyth, “1860” 1861) and *Coryphophylax brevicauda* Harikrishnan, Vasudevan, Chandramouli, Choudhury, Dutta & Das, 2012. The species *C. subcristatus* is said to be distributed through the Andaman and Nicobar Islands, even across the Ten Degree Channel, which is a recognised biogeographic barrier. A reassessment of the taxonomy of *C. subcristatus* shows the population south of the Ten Degree Channel, for which the nomen *Coryphophylax maximiliani* Fitzinger in Steindachner, 1867 is available, to be distinct. The results are based on morphological data from museum material, including type specimens and mitochondrial 16S rRNA sequences. The members of the genus *Coryphophylax* are abundant and widespread across the islands and may serve as an illuminating example for studying the patterns of colonization and diversification across the Andaman and Nicobar Islands.

## Keywords

16S rRNA, Agamidae, ICZN, islands, lectotype, lizard, phylogeny, Reptilia, Sauria, taxonomy

# Introduction

The agamid genus *Coryphophylax* is endemic to the Andaman and Nicobar Islands, and is represented by two species, namely *Coryphophylax subcristatus* (Blyth, “1860” 1861) and *Coryphophylax brevicauda* Harikrishnan, Vasudevan, Chandramouli, Choudhury, Dutta & Das, 2012 (Harikrishnan et al., 2012; Uetz & Hošek, 2024). The populations of each species of the genus are diurnal and abundant and are among the more conspicuous components of the lizard assemblage on these islands (Das, 1999; Rangasamy et al., 2018). The validity of the genus has been a matter of debate as *C. subcristatus* has also been included in the genus *Gonocephalus* Kaup, 1825 (Smith, 1935; Das, 1999; Sharma, 2002; Harikrishnan et al., 2012). The genus was included in a recent broad phylogeny of Draconinae, represented by a single species, and was recovered as sister to the genus *Bronchocela* Kaup, 1827 (Pal et al., 2018).

The Andaman and Nicobar Islands are a group of 572 islands that are peaks of submerged hills of the Arakan Yoma range running from Myanmar to Sumatra. The Ten Degree Channel, a >1000 m deep gorge spanning about 140 km, divides the islands into two groups, namely, the Andaman Archipelago to the north and the Nicobar Archipelago to the south (Harikrishnan et al., 2012). The reptilian assemblage of the two island groups suggests that they are distinct from each other (Das, 1999; Rangasamy et al., 2018; Rao et al., 2017; Smith, 1941; Vijayakumar & David, 2006). The biota of the Andaman Islands shows affinity to Burmese taxa; in contrast, the Nicobar Islands is considered to have an affinity to taxa from Sumatra (Das, 1999; Harikrishnan et al., 2012; Ganeshaiah et al., 2019; Chandramouli et al., 2023). One notable exception is *C. subcristatus*, which has been reported to be distributed across all islands of the Andaman and Nicobar Islands, except Great Nicobar Island (Smith, 1935; Tikader & Sharma, 1992; Das, 1999; Harikrishnan et al., 2012). However, the apparent widespread distribution of the species may be an artefact of the lack of critical taxonomic assessment, and re-examination of type material of current putative synonyms may reveal cryptic species more in line with the well supported distinctiveness of the two archipelagos (Das, 1999; Harikrishnan et al., 2012).

*Coryphophylax subcristatus* was described by Blyth (“1860” 1861) as *Tiaris subcristata*, which was later transferred to the genus *Coryphophylax* erected by Fitzinger in Steindachner, 1867. Fitzinger (1861) used the name *Coryphophylax maximiliani* for the population of the Nicobar Islands but without an accompanying description. A detailed description based on a series

of specimens (traceable specimens NHMW 20976:1–9) housed at the Natural History Museum of Vienna appeared only in Fitzinger *in* Steindachner (1867), making the nomen available from that date. Stoliczka (1873) described *Tiaris humei* from ‘Tillinchang’ (=Tillingchang, Nicobar Islands, India) based on one male and one female specimen, the former deposited at the Asiatic Society of Bengal (now the Zoological Survey of India, Kolkata) and the latter specimen possibly at the Natural History Museum, London (Das et al., 1998). Boulenger (1885, 1890) listed ‘*humii*’ and ‘*subcristatus*’ as valid species but did not provide an account for ‘*maximiliani*’, nor was it included among the synonyms of the other species. The two nomina, ‘*maximiliani*’ and ‘*humii*’ were synonymised with *C. subcristatus* by Annandale (1904), who examined multiple specimens from across the islands and concluded that the specimens from Nicobar were just exceptionally large individuals of *C. subcristatus*. This taxonomic conclusion was followed by subsequent workers (Smith, 1935; Biswas & Sanyal, 1977; Biswas, 1984; Tikader & Sharma, 1992; Krishnan, 2005; Harikrishnan et al., 2012).

The lack of fresh material and the difficulty of procuring permission to work on these islands have been significant impediments to studies on reptiles. In this regard, we examined the material of the genus *Coryphophylax* across natural history collections in Europe and India, and we present preliminary notes on the taxonomy of its members. Results from the investigation led to the revalidation of a putative synonym of *C. subcristatus* and provided evidence for an additional undescribed congener in the Nicobars.

## Materials and methods

**Morphology-** The study was based on 20 museum specimens (14 of the Nicobar population and 6 of *C. subcristatus*, and no live individuals were captured or collected for this study. Meristic data was taken with a Mitutoyo™ dial calliper to the nearest 0.1 mm. Morphological data were recorded with an Olympus stereo binocular microscope SZ40. The following morphological characters were recorded following Sadasivan et al. (2018) and Ambekar et al. (2020) with slight modifications. The following measurements were taken: snout-vent length (SVL, from tip of snout to anterior border of cloaca), head length (HL, from snout tip to posterior border of tympanum), head width (HW, distance from left to right outer edge of the head at its widest point), head height (HH, dorsoventral distance from top of head to underside of jaw at transverse plane intersecting angle of jaws), snout-eye length (SE, from snout tip to anterior border of orbit), eye to tympanum (ET,

94 from posterior border of orbit to anterior border of tympanum), jaw length (JL, from rostrum to  
 95 corner of jaw), interorbital width (IO, transverse distance between anterodorsal corners of left and  
 96 right orbits), nares to eye (NE, distance from the anterior edge of orbit to posterior edge of naris),  
 97 snout width/internasal distance (IN, transverse distance between left and right nares), tympanum  
 98 diameter (TD, greatest diameter of tympanum), orbit diameter (OD, distance between anterior and  
 99 posterior margins of orbit), lower arm length (LAL, distance from elbow to distal end of wrist, or  
 100 just underside of forefoot when the limb is flexed), upper arm length (UAL, distance from anterior  
 101 insertion of forelimb to elbow when the limb is flexed), crus length (CL, length of crus (tibia) from  
 102 knee to heel), hind foot length (HFL, distance from proximal end (heel) of hind foot to distal most  
 103 point of fourth toe), trunk length (TrL, from forelimb insertion to hind limb insertion), trunk height  
 104 (TrH, depth midway between the fore and hind limb insertions), trunk width (TrW, width midway  
 105 between the fore and hind limb insertions), tail length (TaL, from posterior border of cloacal  
 106 opening to tip of tail), tail height (TaH) and tail width (TaW, at tail base). Meristic characters were  
 107 counted for multiple individuals per species. The following characters were scored: mid-body scale  
 108 rows (MBS, number of scale rows around the trunk at midbody), mid-dorsal scales (MD, counted  
 109 from the first erect dorsal crest spine to the level above the vent), ventral scales (VEN, number of  
 110 scales from below mental around the base of the dewlap to anterior border of cloaca), fourth toe  
 111 lamellae (LAM4, number of 4<sup>th</sup> toe lamellae, from 1<sup>st</sup> lamella at the digit's cleft to the most distal  
 112 lamella), supralabials (SL, posterior end defined by the last enlarged scale that contacts the  
 113 infralabials at the corner of mouth), infralabials (IL, posterior end defined by the posterior-most  
 114 enlarged scales that contact the supralabials at the corner of the mouth), ventral scales on the belly  
 115 (VENB, number of scales posterior to the dewlap to the anterior border of cloaca). Multivariate  
 116 Principal Component Analysis (PCA) was performed on selected morphometric values: HL, HH,  
 117 HW, TrL, LAL and CL (Supporting Table S2). The variables were selected for the analysis as data  
 118 for them was complete. These values were corrected for SVL and were later log-transformed.  
 119 Institutional acronyms: BNHS- Bombay Natural History Society, Mumbai (India); NHMW-  
 120 Natural History Museum, Vienna (Austria); ZMB- Museum für Naturkunde, Berlin (Germany);  
 121 ZMUC- Zoological Museum, University of Copenhagen, Copenhagen (Denmark); ZSI-  
 122 Zoological Survey of India, Kolkata (India).  
 123 Molecular methods- Molecular data for the gene 16S rRNA generated by Krishnan (2005) were  
 124 downloaded from GenBank, and accession numbers and their collection localities are listed in



Table 1. *Gonocephalus pyrius* was chosen as an outgroup for the phylogenetic analysis. The downloaded sequences were aligned in Mega X (Kumar et al., 2018) using CLUSTALW (Thompson, Higgins & Gibson, 1994) with default settings. Sequences that did not align were excluded from the dataset. The aligned dataset was analysed in a Maximum Likelihood (ML) framework on the IQ-TREE online portal (Trifinopoulos et al., 2016). The optimum sequence evolution model was determined through ModelFinder (Kalyaanamoorthy et al., 2017) based on AIC values. The analysis was run with an ultra-fast tree search method (Hoang et al., 2018) with 1000 <sup>pseudo replicates (space?)</sup> pseudoreplicates to assess branch support. The resulting tree was visualised and edited with FigTree (Rambaut, 2012). <sup>Un-corrected?</sup> Uncorrected p-distances were calculated using Mega X with default settings, and the partial deletion option was chosen to deal with missing data.

## Results

**Molecular analysis:** The ML phylogeny was based on 446bp of mitochondrial 16S rRNA and was rooted with *Gonocephalus pyrius* <sup>(Harvey et al., 2021?) & within the bracket??</sup> Harvey, Rech, Riyanto, Kurniawan & Smith, 2021 (Fig. 1, Table 1). The sequence substitution model selected was TPM2u+F+G4. The analysis recovered two clades, clade I, comprising *C. brevicauda*, clade II comprises a basal *Coryphophylax* sp. (*Coryphophylax* sp. 1 Fig. 1) from Car Nicobar Island (the northernmost island in the Nicobar Islands), which is sister to a sub-clade containing representatives from Nicobar Islands (*Coryphophylax maximiliani*) and *Coryphophylax subcristatus sensu stricto* (ML bootstrap support 90%). The monophyly of *Coryphophylax maximiliani* + *Coryphophylax subcristatus sensu stricto* received low bootstrap support (56%).

**Morphology and nomenclature:** The PCA plot shows the separation of the Nicobar Island population from *C. subcristatus* and *C. brevicauda*, where PC1+PC2 explain <sup>76.8%?</sup> 76.72% (45.7 + 31.1) of the variance (Fig. 2, Supporting Table S3). Furthermore, the SVL of mature individuals from the Nicobar Islands is <sup>Gap?</sup> >90mm, which is much larger than that of *C. subcristatus* and *C. brevicauda*. See detailed comparisons below. The syntypes of *Coryphophylax maximiliani* and *Coryphophylax humei* are morphologically similar and match all the diagnostic characters proposed for both nomina. Genetically, the representatives of samples from their respective type localities show a divergence of 0–4% (Table 2). The divergence is relatively high but may be due to the fragment chosen or sequencing errors. However, a similar range of divergence was observed in

representatives of *C. subcristatus*, which suggests that the two nomina from Nicobar Islands are synonymous. As per Article 23, the Principle of Priority, of the *Code* (International Commission on Zoological Nomenclature, 1999), the name *Coryphophylax maximiliani* Fitzinger in Steindachner, 1867 has precedence over Stoliczka's (1873) *Coryphophylax humei* and is assigned to the large-bodied population of *Coryphophylax* from the Nicobar Islands. The first usage of *Coryphophylax maximiliani* by Fitzinger, 1861 lacked an associated formal description and was correctly regarded as a nomen nudum by Wermuth (1965). The nomen was made available by Fitzinger in Steindachner, 1867 (incorrectly given as 1869 by Wermuth, 1967), where it is accompanied by a detailed description and illustration of one of the syntypes (Gemel, Gassner & Schweiger, 2019).

The type specimens of *Coryphophylax maximiliani* are in a fragile condition; only part of the data could be recorded for the largest specimens. The ZSI syntype of *Tiaris humei* is in a much better state of preservation; hence, we here redescribe the species in detail based on all examined material. The members of the genus are morphologically quite similar, and likely, additional species will be described in the near future; it is, therefore, necessary to designate lectotypes for relevant species to stabilise the taxonomy of the group. Hence, lectotypes are here designated for the *Coryphophylax maximiliani* from the series of specimens available at the Natural History Museum, Vienna and for the only traceable specimen of *Tiaris humei* at the Zoological Survey of India, Kolkata.

# ***Coryphophylax maximiliani* Fitzinger in Steindachner, 1867**

*Coryphophylax maximiliani* Fitzinger, 1861: 387 & 397 (nomen nudum *fide* Wermuth, 1967)

*Coryphophylax maximiliani* Fitzinger in Steindachner, 1867: 30

<sup>"humei" replace H by h</sup>

*Tiaris Humei* Stoliczka, 1873: 167

*Goniocephalus humii* Boulenger, 1885: 293; Boulenger, 1890: 123

*Goniocephalus subcristatus* (partim) Smith (1935): 163; Annandale (1904): 18; Sharma (2002): 183

*Coryphophylax subcristatus* (partim) Manthey (2008): 99; Harikrishnan et al. (2012): 45

*Coryphophylax maximiliani* [authorship attributed to Steindachner, 1867] Gemel, Gassner & Schweiger, 2019

*Coryphophylax* Nicobar lineage Krishnan (2005): 80

Figs. 3–7, Table 3

**Lectotype (here designated):** adult male NHMW 20976:5 from Nicobar Islands (Fig. 3 & 4)

**Paralectotypes (n=8):** juvenile NHMW 20976:1 (SVL 57.9 mm), juvenile NHMW 20976:2 (SVL 62.1 mm), adult NHMW 20976:3 (SVL 93.6 mm, TaL 210 mm), juvenile NHMW 20976:4 (SVL 54.4 mm), adult NHMW 20976:6 (SVL 78 mm), adult NHMW 20976:7 (SVL 96 mm), juvenile NHMW 20976:8 (SVL 58.9 mm), juvenile NHMW 20976:9 (SVL 63.1 mm)

**Additional material examined (n=5):** Lectotype of *Tiaris humei* (here designated), adult male ZSI 5041 from Tillanchong, Nicobar Islands; adult male BNHS 674 from Andaman and Nicobar Islands; adult male ZMB 5854, Nicobars; adult male ZMUC R36998 Comarta, Nicobar Islands; adult male ZMUC R36312 Kondul, Nicobar Islands.

**Diagnosis:** A large-sized species of the genus *Coryphophylax*, adults measuring 90–108mm SVL with a TaL/SVL ratio of 2.68–2.73. Midbody scales in 82–85 rows, largely homogeneous in general appearance, intermixed with two fairly well-defined parallel rows of sparse, large tubercle-like scales on the trunk. The nuchal and dorsal crests well developed, composed of an erect flap of skin with slightly larger erected spines forming the apical scale row, which is very distinct in nuchal crest; skin flap differentiated from nuchal to dorsal region, with a small diastema above shoulder dorsal crest continues to ¼ of the tail. Dorsal surface of thigh with enlarged keeled scales, one of these largest as seen in members of the genus *Sitana* Cuvier, 1829. 28–31 bi-mucronate lamellae on 4<sup>th</sup> toe. Male dewlap yellow with black reticulate markings.

# **Description of *Coryphophylax maximiliani* based on examined material (Table 3):**

Adults, SVL 90–108 mm (mean 96.48 ±6.78). Head relatively long (HL/SVL ratio 0.30–0.33, mean 0.32 ±0.010), moderately wide (HW/HL ratio 0.52–0.63, mean 0.57 ±0.040), fairly depressed (HH/HL ratio 0.46–0.54, mean 0.49 ±0.029), distinct from neck (Fig. 5a). Snout long (SE/HL ratio 0.37–0.42, mean 0.38 ±0.021), bluntly conical; longer than eye diameter (OD/SE ratio 0.39–0.51, mean 0.44 ±0.065) (Fig. 6c). Eye large (OD/HL ratio 0.14–0.19, mean 0.17 ±0.025); pupil round, eyelids covered with small pentagonal and hexagonal scales, supraciliaries

219 short. Snout obtusely pointed when viewed dorsally, rostral much wider than deep, bordered  
 220 posteriorly by first supralabial, prenasal and dorsally by four small scales. Canthus rostralis and  
 221 supraciliary edge sharp consisting of 12–14 scales, some of these are large tuberculate. Nostrils  
 222 positioned centrally in a large, undivided nasal plate, bordered by 9–10 scales, including one  
 223 prenasal, four postnasals and two supranasal, and in contact with rostral. Supralabials 7–10  
 224 rectangular, weakly keeled, bordered above by a single row of slightly smaller, rectangular, keeled  
 225 scales. Loreal region concave, scales of the loreal region heterogeneous in size, raised not flat,  
 226 keeled, some roughly hexagonal. Scales on postorbital and temporal region heterogeneous,  
 227 imbricate, strongly keeled, and directed posteriorly and dorsally. Orbital scales small but not  
 228 granular. Tympanum naked. Four to five large, strongly keeled, tuberculate scales running from  
 229 the posterior part of orbit to the supra-tympanic region. A large tuberculate scale on the nape on  
 230 either side of the dorsal crest; a second subequal tuberculate scale in the supratympanic region and  
 231 postocular region. Canthals enlarged, overlapping, becoming slightly smaller along subimbricate  
 232 supraciliaries, protruding slightly laterally on supraorbital ridge. Scales on dorsal surface of snout,  
 233 forehead, interorbital, and occipital region heterogeneous in size, and shape; mostly elongate,  
 234 imbricate, strongly keeled longitudinally; those on snout smaller, rhomboidal, those on the supra-  
 235 occiput largest. Parietal plate without pineal eye, the plate slightly larger than adjacent scales.  
 236 Mental shield narrower than rostral; gular scales keeled (Fig. 6b). Infralabials 8–10. Nuchal absent,  
 237 and dorsal crest present, composed of low thorn-like scales. Scales on nuchal region smaller, less  
 238 than half the size of those on interorbital region, imbricate, strongly keeled. Dorsal crest  
 239 comprising 57–58 raised, spike-like scales in a row on a raised flap of skin running from the  
 240 posterior part of the head to the level of the vent. The crest spines high and erect with a disatema,  
 241 and relatively short spine-like scales run along the vertebral column to the <sup>1/4</sup>th of the tail. Body  
 242 slender (Fig. 5a), 80–85 rows of scales around midbody, of these 16–18 rows across the belly are  
 243 slightly larger than those on the dorsum (Fig. 5b); from neck to pectoral region scales largely  
 244 homogenous, feebly keeled, intermixed with large strongly keeled scales. twice to thrice as big,  
 245 scales on the trunk slightly larger than those on neck, imbricate, pointed, keeled, and directed  
 246 posterodorsally forming regularly arranged longitudinal rows; ventral scales strongly keeled  
 247 arranged in 16–18 rows, oriented backwards, subimbricate, heteroogenous in size; no precloacal  
 248 or femoral pores (Fig. 5b). Number of scales MD 63–68. Distinct fold at the shoulder present. Fore  
 249 and hind limbs relatively slender, tibia short (CL/SVL ratio 0.27–0.29, mean 0.28 ± 0.010); digits

moderately long, ending in strong, elongate, slightly recurved claws; inter-digital webbing absent; subdigital lamellae entire, bi-mucronate, 20–25 subdigital lamellae on finger IV of manus and 28–31 on finger IV of pes; relative length of fingers and toes  $4 > 3 > 5 > 2 > 1$ . Fore and hind limbs covered above and below with regularly arranged, enlarged, pointed, strongly keeled scales. Dorsal and dorso-lateral scales on the posterior part of the thigh enlarged, one of these scales largest and projecting as seen in members of the genus *Sitana* Cuvier, 1829. Tail entire; tail base swollen; tail uniformly covered with similar sized, keeled, weakly pointed, regularly arranged, posteriorly directed imbricate scales, no enlarged median subcaudal row; erect, crest-like dorsal spines extend to the anterior  $\frac{1}{4}$  of the tail.

**Distribution:** Based on examined specimens and molecular data, the species appears to be distributed on the following islands in the Nicobar group of islands: Little Nicobar Is., <sup>"Ca" or "Co"?</sup> Camorta Is., Kondul Is., Menchal Is., Katchal Is., Tillanchong Is., Trinkat Is. See Figs. 1, 7 & 8 for specific localities. Likely distributed throughout the Nicobar Islands except for Great Nicobar Island.

**Comparisons:** *Coryphophylax maximiliani* differs from its two congeners as follows: SVL 90–108 mm (vs. 53–85 mm in *C. subcristatus* (Fig. 9a & 9b), 42–63 mm in *C. brevicauda* Fig. 9c); TaL/SVL ratio 2.68–2.73 (vs. 2.04–2.51 in *C. subcristatus*, 1.69–2.03 in *C. brevicauda*); 82–85 scale rows round the body (vs. 85–100 in *C. subcristatus*, 110–121 in *C. brevicauda*); dorsal and nuchal crest comprising a skin flap expansion with large erect spine-like apical scales on the nape, with a diastema followed by relatively short spines running along the vertebral column extending to  $\frac{1}{4}$  of the tail (vs. dorsal and nuchal crest well developed, low with short spine-like scales running continuously from nape to mid-trunk in *C. subcristatus*, dorsal crest low and lacks large erect spine-like scales in *C. brevicauda*) (Fig. 8); dewlap colour yellow with black reticulate markings (vs. dewlap yellow or white without any markings in *C. subcristatus*, orange-red in *C. brevicauda*).

## Discussion and <sup>"C" should be lowercase "c"</sup>Conclusions

The phylogenetic affinities of the genus *Coryphophylax* remain poorly studied. The only study that assessed the phylogenetic placement of the genus based on molecular data was by Pal et al. (2018). That study recovered *Coryphophylax* as the sister taxa to *Bronchocela*, a relationship contingent on the 16S rRNA sequence of a single species. The present work also suffers from the

limited molecular data currently available (sequences of a fragment of 16S rRNA only). However, it is of merit to present a snapshot of the diversity of the lizards across these islands and confirm that '*C. subcristatus*' comprises multiple species. However, the monophyly of *Coryphophylax* must be tested with nuclear genes. The genus *Coryphophylax* is endemic to the islands, and its members are distributed throughout both the Andaman and Nicobar groups, except for Great Nicobar Island. Nearly all other reptile groups are either distributed in the Andamans or Nicobars or may have narrow distribution, being restricted to a few islands (Das, 1999; Chandramouli et al., 2023; Vijaykumar & David, 2006) The abundant and widespread nature of *Coryphophylax* across the islands make them an ideal model species for studying the patterns of colonization and diversification across the Andaman and Nicobar Islands.

The results of the present study are in agreement with those of Krishnan (2005), who, based on a large sample size of specimens for morphological data, considered the Nicobar population distinct. The present study lacks the extensive sampling by Krishnan (2005) but arrives at an identical conclusion.

*Tiaris humei* was described based on two specimens from Tillanchong, Nicobar Islands (Stoliczka, 1873). The male specimen housed in the collection of the Zoological Survey of India (ZSI 5041) is here designated as the lectotype. The second syntype has been purported to be in the collection of the Natural History Museum, London (NHMUK) (Das, Dattagupta & Gayen, 1998). A search through the online portal of the database of NHMUK identified six specimens of *Gonyocephalus subcristatus* from the Nicobar Islands. Two of these specimens bear the catalogue number NHMUK 1934.11.2.30-31 and likely were lodged in the collection in the 1900s, long after the description of *Tiaris humei*. The other four specimens, NHMUK 1868.7.8.12–14 and NHMUK 1874.4.29.1229, appear to have been catalogued around the time of the description of the species. Of the four specimens, three of these NHMUK 1868.7.8.12–14, were donated by J. T. Reinhardt and NHMUK 1874.4.29.1229 was donated by R. H. Beddome and all these specimens are listed as non-type specimens. Further, Boulenger (1890), in his compilation on the reptiles and amphibians of the Indian region, stated in the description of '*Goniocephalus humii*' that 'I have not seen examples of this species'. This suggests that even as early as 1890, the second syntype of *Tiaris humei* was not at the British Museum of Natural History (now NHMUK). Therefore, the whereabouts of the second syntype remain unknown, and the specimen may be lost.

Molecular data suggest that *C. subcristatus sensu stricto* is restricted to the Andaman Islands. However, a few samples likely have incorrect localities and require further confirmation. These are marked with ‘\*’ in Fig. 1. Sequences generated by Krishnan (2005) bear field numbers, which are in a series. The samples from Little Andaman Island are in the series sk03cs21, sk03cs23 and sk03cs24. Another sequence, sk03cs12, placed in the same clade, is ostensibly from Pulumilo Is. (Nicobar Is.). This number was apparently transposed with ‘sk03cs22’, a sample embedded in the Nicobar clade but bearing the locality ‘Little Andaman Is.’. Therefore, we propose removing it from the Nicobar Islands lizard fauna pending confirmation of its occurrence. The populations south of the Ten Degree Channel represent *C. maximiliani* and an undescribed species. The species *C. maximiliani* and *C. subcristatus* show considerable divergence across representative samples (Table 2). This may be attributed to the lack of gene flow between isolated populations on the different island groups. These isolated genetically divergent populations from Andaman Is. and Nicobar Is. correspond to *C. subcristatus* and *C. maximiliani*, respectively.

The revalidation of the nomen from the Nicobar Islands is not surprising, as former workers have suggested that *C. subcristatus* is a species complex (Das, 1999; Krishnan, 2005, Vijayakumar & David, 2006; Harikrishnan et al., 2012). The Ten Degree Channel has been proposed as a barrier to gene flow (Das, 1999) that would result in reciprocal monophyly of taxa north and south of the channel. However, results from the molecular phylogeny (Fig. 1) did not recover this pattern. The findings hint at several trans-marine dispersal events across this barrier (Krishnan, 2005), likely during periods of low sea level (Gornitz et al., 1982, Voris, 2001). The aforementioned hypothesis must be tested by employing multiple molecular markers to elucidate the temporal diversification patterns of *Coryphophylax* from its sister taxa and species within the genus. Generating data to test the hypothesis is out of the scope of the present work largely due to the difficulty of procuring permissions from the Forest Department to conduct research on the islands. The present work also shows the presence of additional undescribed species and lays a foundation for further studies on this genus.

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127. (Add full stop at end)

# **Legend to figures:**

Figure 1. ML phylogeny of members of the genus *Coryphophylax* based on 446bp of mitochondrial 16S rRNA. Numbers at nodes represent ML bootstrap support based on 1000 pseudo replicates. Map on the top left corner shows the Andaman and Nicobar Islands, and colour on the tips of the tree correspond to color on the map. Samples marked with ‘\*’ are likely have incorrect collection localities (see Discussion). For the complete tree see Supporting Figure S1.

Figure 2. PCA plot of species of the genus *Coryphophylax*, (green) *C. maximiliani*, (red) *C. subcristatus*, (blue) *C. brevicauda*.

Figure 3. Illustration of *C. maximiliani* reproduced from Fitzinger in: Steindachner, 1867 (Plate II, Fig. 6). The illustration was altered for visual purposes by removing other illustrations; see Supporting Figure S2 for the unaltered version.

Figure 4. *Coryphophylax maximiliani* lectotype adult male NHMV 20976:5 (a) dorsal view, (b) ventral view. Scale bar 20 mm.

Figure 5. *Coryphophylax humei* lectotype male ZSI 5041(a) dorsal view, (b) ventral view. Scale bar 10 mm.

Figure 6. Images depicting cephalic region of *Coryphophylax humei* lectotype male ZSI 5041 (a–c), *Coryphophylax maximiliani* lectotype adult male NHMV 20976:5 (d–f); (a & d) dorsal view, (b & e) ventral view, (c & f) right lateral view. Scale bar 10 mm.

Figure 7. *Coryphophylax maximiliani* from Nicobar Islands showing colouration in life. Photos by S. Harikrishnan.

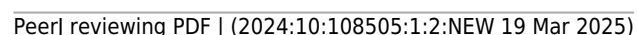
Figure 8. Map of Andaman and Nicobar Islands showing collection localities for molecular data.

The <sup>inset</sup> Inset map of India (top left) highlights the region of interest by the red rectangle, and the map below shows the Andaman and Nicobar Islands and the Ten Degree Channel.

Figure 9. Images of *Coryphophylax* species (a & b) *C. subcristatus*, photo by Zeeshan A. Mirza; (c) *Coryphophylax brevicauda*, photo by S. Harikrishnan.

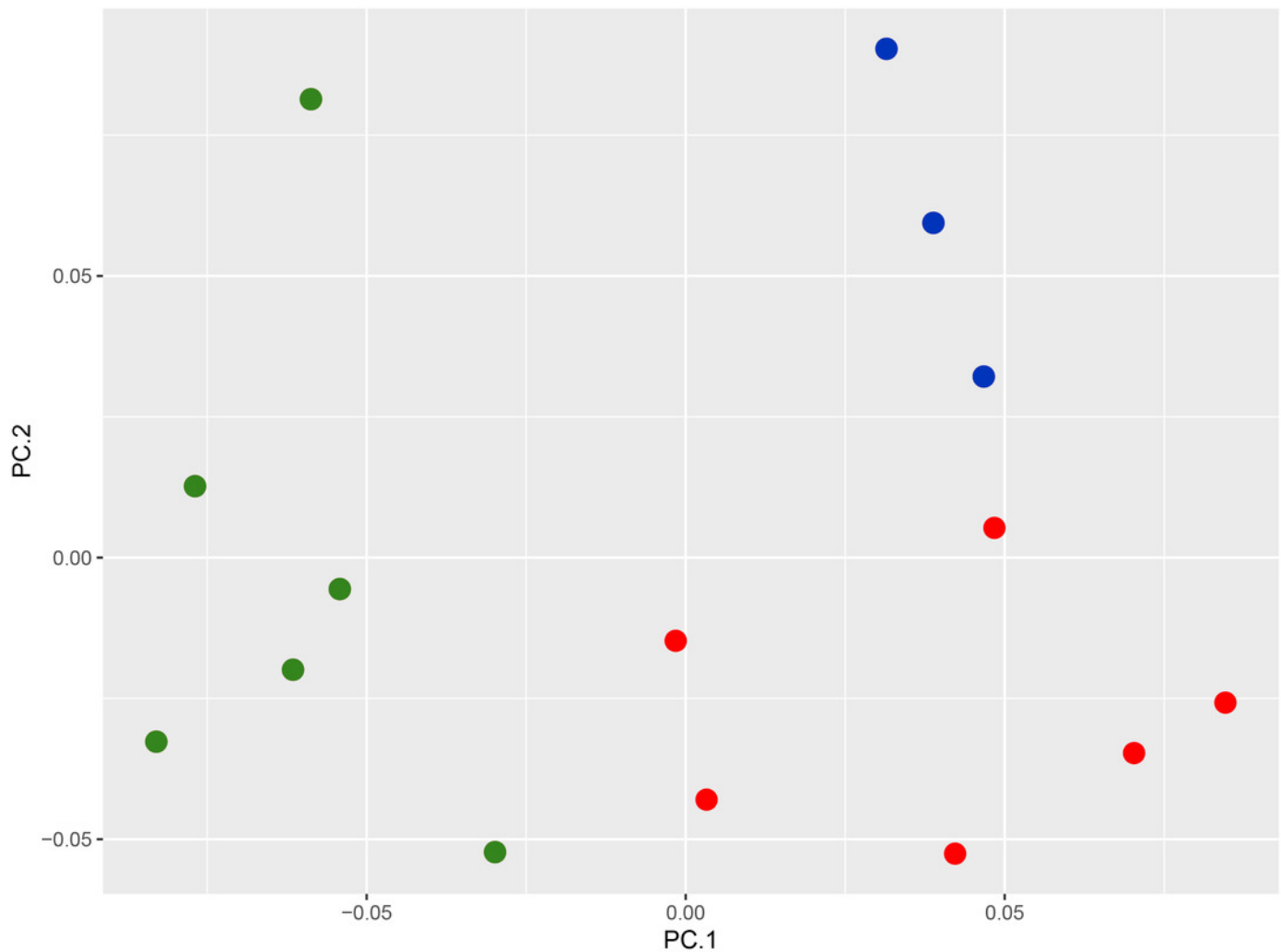
ML phylogeny of members of the genus *Coryphophylax* based on 446bp of mitochondrial 16S rRNA. Numbers at nodes represent ML bootstrap support based on 1000 pseudoreplicates.

Map on the top left corner shows the Andaman and Nicobar Islands, and colour on the tips of the tree correspond to color on the map. Samples marked with ‘\*’ are likely have incorrect collection localities (see Discussion). For the complete tree see Supporting Figure S1.



# Figure 2

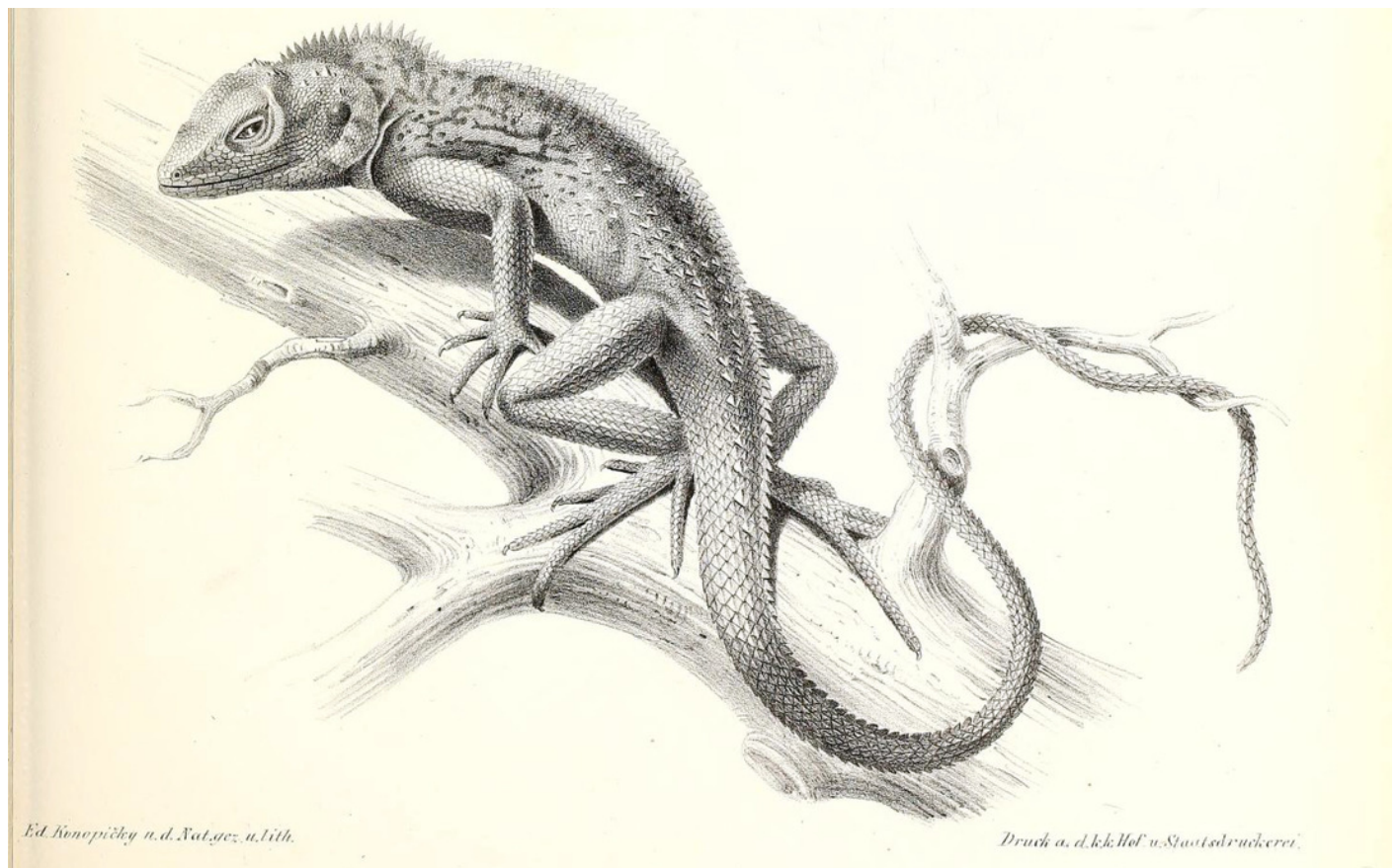
PCA plot of species of the genus *Coryphophylax*, (green) *C. maximiliani*, (red) *C. subcristatus*, (blue) *C. brevicauda*.





# Figure 3

Illustration of *C. maximiliani* reproduced from Fitzinger in: Steindachner, 1867 (Plate II, Fig. 6). The illustration was altered for visual purposes by removing other illustrations; see Supporting Figure S2 for the unaltered version.



# Figure 4

*Coryphophylax maximiliani* lectotype adult male NHMV 20976:5

(a) dorsal view, (b) ventral view. Scale bar 20 mm.





# Figure 5

*Coryphophylax humei* lectotype male ZSI 5041

(a) dorsal view, (b) ventral view. Scale bar 10 mm.

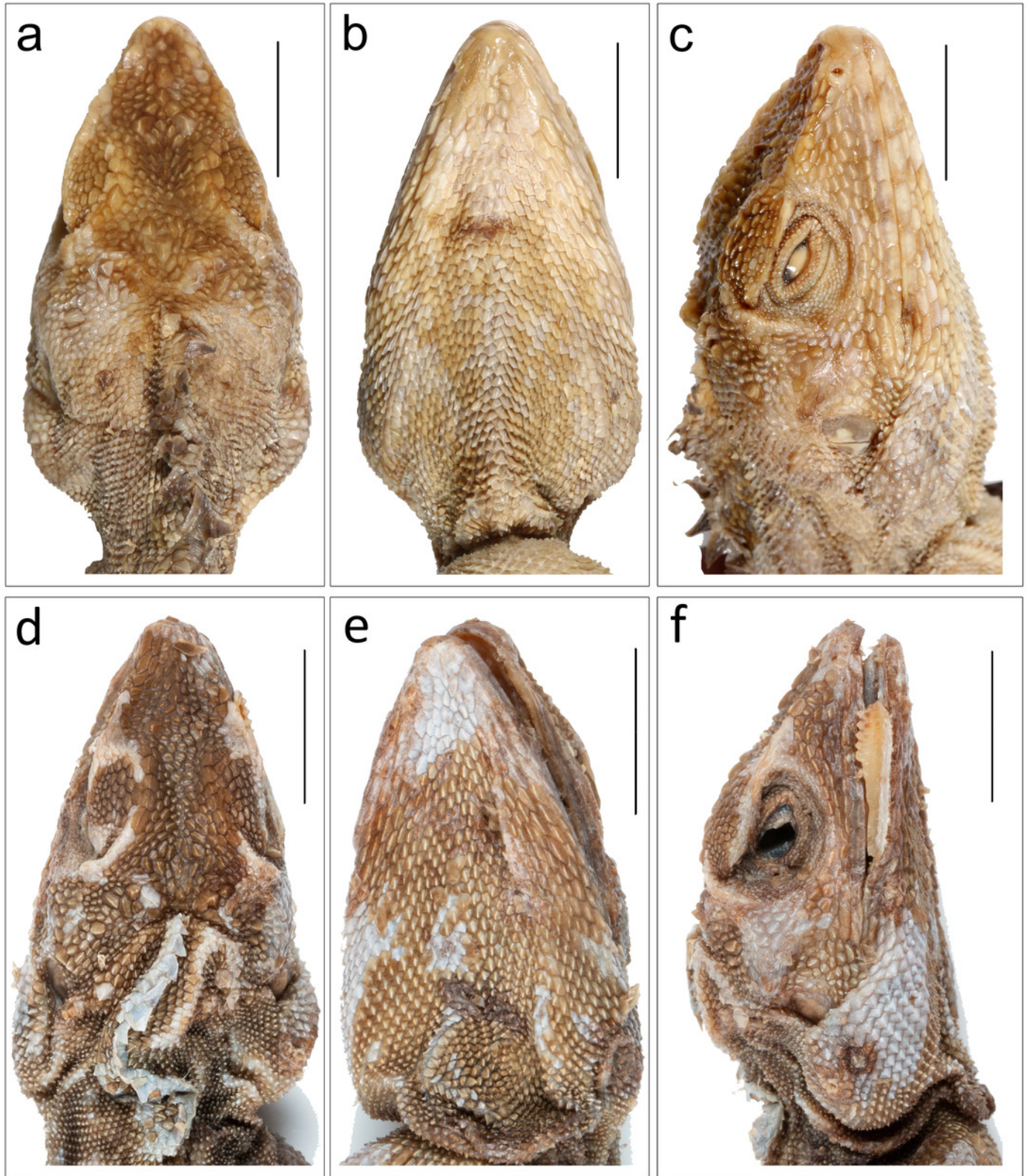


# Figure 6

Images depicting cephalic region of *Coryphophylax humei* lectotype male ZSI 5041

(a-c), *Coryphophylax maximiliani* lectotype adult male NHMV 20976:5 (d-f); (a & d) dorsal view, (b & e) ventral view, (c & f) right lateral view. Scale bar 10 mm.





# Figure 7

*Coryphophylax maximiliani* from Nicobar Islands showing colouration in life. Photos by S. Harikrishnan.

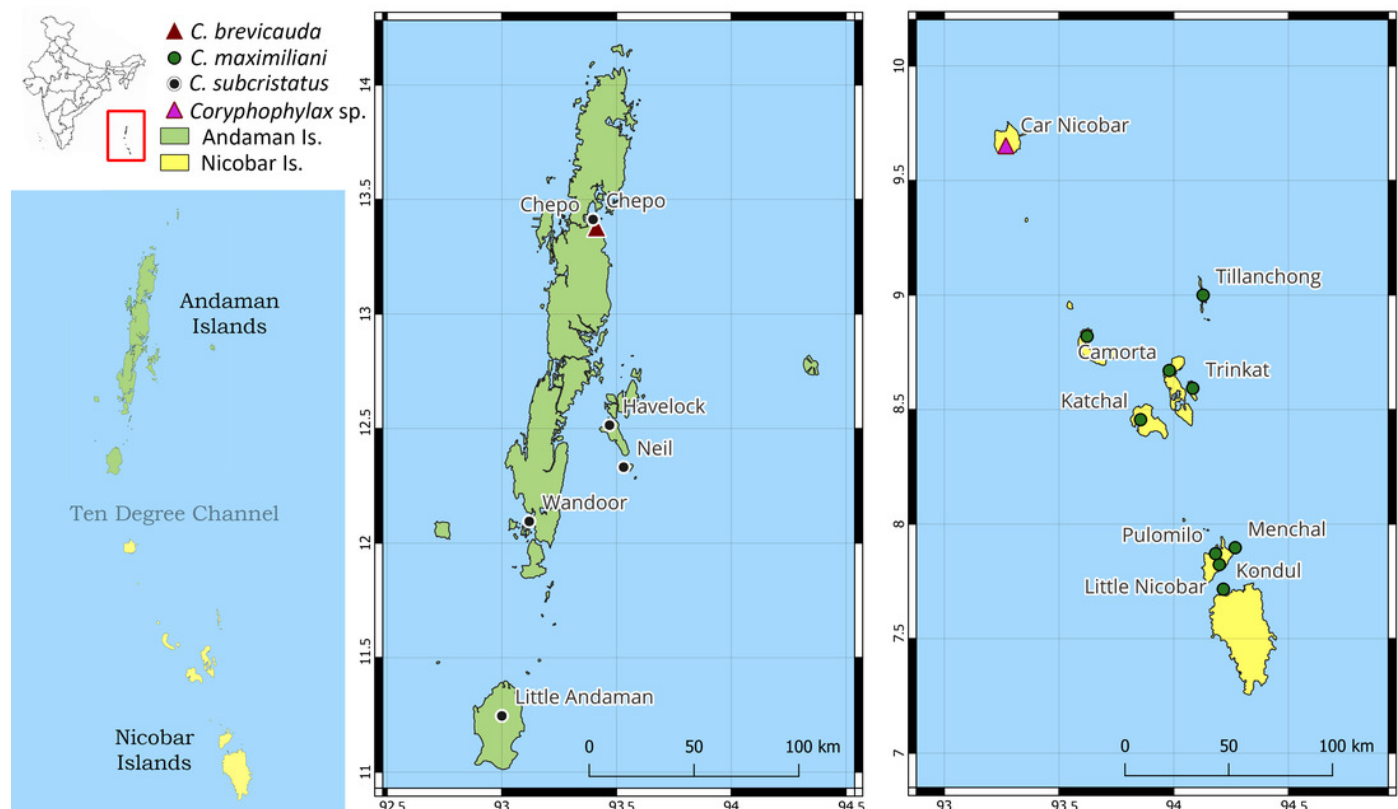




# Figure 8

Map of Andaman and Nicobar Islands showing collection localities for molecular data. The <sup>inset</sup> map of India (top left) highlights the region of interest by the red rectangle, and the map below shows the Andaman and Nicobar Islands and the Ten Degree Channel

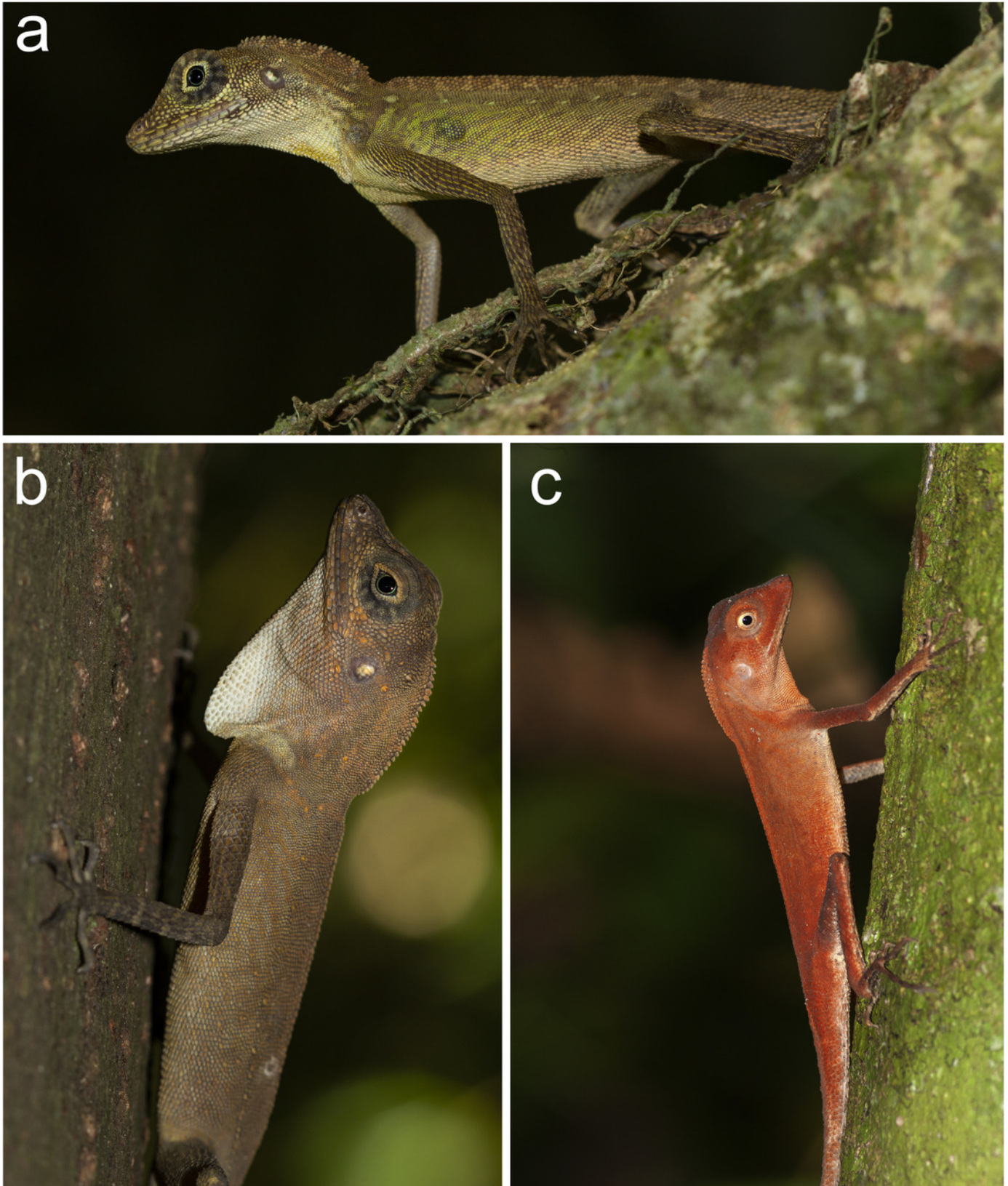
Channel





# Figure 9

Images of *Coryphophylax* species (a & b) *C. subcristatus*, photo by Zeeshan A. Mirza; (c) *Coryphophylax brevicauda*, photo by S. Harikrishnan.



# **Table 1**(on next page)

List of species, samples and their GenBank accession numbers.

**Table 1.** List of species, samples and their GenBank accession numbers.

2

Current species name	Names in Krishnan (2005)	Code	Locality	16S
<i>C. brevicauda</i>	<i>Coryphophylax</i> sp. 1	sk04cp4	Chepo N. Andaman Island	EU502981
<i>C. brevicauda</i>	<i>Coryphophylax</i> sp. 1	sk04cp11	Chepo N. Andaman Island	EU502980
<i>C. maximiliani</i>	Nicobar lineage	sk03cs58	Camorta Island	EU503021
<i>C. maximiliani</i>	Nicobar lineage	sk03cs33	Katchal Island	EU503007
<i>C. maximiliani</i>	Nicobar lineage	sk03cs34	Katchal Island	EU503006
<i>C. maximiliani</i>	Nicobar lineage	sk03cs35	Katchal Island	EU503005
<i>C. maximiliani</i>	Nicobar lineage	sk03cs2	Kondul Island	EU503004
<i>C. maximiliani</i>	Nicobar lineage	sk03cs4	Kondul Island	EU503003
<i>C. maximiliani</i>	Nicobar lineage	sk03cs13	Kondul Island	EU503002
<i>C. maximiliani</i>	Nicobar lineage	sk03cs14	Kondul Island	EU503001
<i>C. maximiliani</i>	Nicobar lineage	sk03cs5	Little Nicobar Island	EU502996
<i>C. maximiliani</i>	Nicobar lineage	sk03cs7	Little Nicobar Island	EU502995
<i>C. maximiliani</i>	Nicobar lineage	sk03cs8	Little Nicobar Island	EU502994
<i>C. maximiliani</i>	Nicobar lineage	sk03cs6	Menchal Island	EU502993
<i>C. maximiliani</i>	Nicobar lineage	sk03cs9	Menchal Island	EU502992
<i>C. maximiliani</i>	Nicobar lineage	sk03cs11	Menchal Island	EU502991
<i>C. maximiliani</i>	Nicobar lineage	sk03cs16	Menchal Island	EU502990
<i>C. maximiliani</i>	Nicobar lineage	sk03cs3	Pulo Milo Island	EU502985
<i>C. maximiliani</i>	Nicobar lineage	sk03cs10	Pulo Milo Island	EU502984
<i>C. maximiliani</i>	Nicobar lineage	sk03cs15	Pulo Milo Island	EU502982
<i>C. maximiliani</i>	Nicobar lineage	sk03cs52	Tillanchong Island	EU502978
<i>C. maximiliani</i>	Nicobar lineage	sk03cs54	Tillanchong Island	EU502977
<i>C. maximiliani</i>	Nicobar lineage	sk03cs55	Trinkat Island	EU502976
<i>C. maximiliani</i>	Nicobar lineage	sk03cs56	Trinkat Island	EU502975
<i>C. subcristatus</i>	Nicobar lineage	sk03cs31	Chowra Island	EU503020
<i>Coryphophylax</i> sp. 1	Nicobar lineage ?	sk03cs17	Car Nicobar	EU503013
<i>Coryphophylax</i> sp. 1	Nicobar lineage ?	sk03cs19	Car Nicobar	EU503012
<i>Coryphophylax</i> sp. 1	Nicobar lineage ?	sk03cs20	Car Nicobar	EU503011
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs47	Chepo N. Andaman Island	EU503018
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs48	Chepo N. Andaman Island	EU503017
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs49	Chepo N. Andaman Island	EU503016
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs50	Chepo N. Andaman Island	EU503015
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs51	Chepo N. Andaman Island	EU503014
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs39	Havelock Island	EU503010
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs40	Havelock Island	EU503009

<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs42	Havelock Island	EU503008
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs21	Little Andaman Island	EU503000
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs22	Little Andaman Island	EU502999
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs23	Little Andaman Island	EU502998
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs24	Little Andaman Island	EU502997
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs36	Neil Island	EU502988
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs37	Neil Island	EU502987
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs38	Neil Island	EU502986
<i>C. subcristatus</i>	<i>C. subcristatus</i>	sk03cs12	Pulo Milo Island	EU502983
<i>C. subcristatus</i>	<i>C. subcristatus</i>	SK03CS44	South Andaman Island	EU502974
<i>C. subcristatus</i>	<i>C. subcristatus</i>	SK03cs45	Wandoor South Andaman Island	EU502973
<i>Gonocephalus pyrius</i>			Lampung, Indonesia	OP070023

## Table 2 (on next page)

Un-corrected sequence divergence for *Coryphophylax* species (%). See Supporting Table S1 for p-distance for all samples.

1   **Table 2. Un-corrected** sequence divergence for *Coryphophylax* species (%). See Supporting Table S1 for p-distance  
2   for all samples.

	<i>C. maximiliani</i> (n=23)
<i>C. brevicauda</i> (n=2)	5–7
<i>C. maximiliani</i> (n=23)	0–4
<i>C. subcristatus</i> (n=17)	3–7

3

# Table 3 (on next page)

Morphometric and meristic data for specimens of *Coryphophylax maximiliani* .  
 Attributes marked with an ‘\*’ sign indicate missing parts or damage; those with ‘—’  
 were not recorded as the specimen was shrivelled or damaged.



**Table 3.** Morphometric and meristic data for specimens of *Coryphophylax maximiliani*. Attributes marked with an ‘\*’ sign indicate missing parts or damage; those with ‘—’ were not recorded as the specimen was shrivelled or damaged.

	Lectotype of <i>Coryphophylax maximiliani</i>	Lectotype of <i>Tiaris humei</i>			
	NHMW 20976:5	ZSI 5041	ZMUC R36998	ZMUC R36312	ZMB 5854
Locality	Nicobar Is.	Tillanchong, Nicobar Is.	Comorta, Nicobar Is.	Kondul, Nicobar Is.	Nicobar Is.
Sex	male	male	male	male	male
SVL	90	108	94	95.4	95
TaL	246	—	180	—	210*
TaW	8.4	9	8.2	8.9	7.5
HL	29.7	33.1	30.3	30	29.1
HW	16.1	19	17.5	18.8	15.1
HH	14.4	16.8	16.3	13.9	14
SL	10/10	7/ 9	9/9	9/9	7/7
IL	9/9	9/9	8/9	10	9/8
OD	4.2	6.3	—	—	4.8
TD	2.2	3.9	—	—	3.3
TrL	40	45	35.1	39	41
TrW	12.7	16.5	—	—	10.1
LAL	15.2	19.7	19.9	17.6	17.1
CL	23.9	28.9	27.2	27	26
IO	8.1	11.1	11.1	11.7	8.1
IN	3.6	4.4	3.8	—	3.9
SE	10.9	12.3	11.3	12.6	11.2
ET	6.8	8.3	—	6.5	6.4
MD	—	68	65	—	63
MBS	85	82	84	—	—
Right manus	X-10-16-25-14	9-12-19-20-11	11-18-24-25-15	11-18-25-25-15	11-16-22-23-13
Left pes	11-18-26-28-12+	10-14-21-28-17	11-18-25-28-17	12-18-26-30-19	11-17-25-31-18