## COMMENTS

After having double checked thorough in detail the main texts in the manuscript I genuinely, appreciated the team/authors their contributions and output for such an interesting work based on the taxonomic status to resolve the species *Coryphophylax maximiliani* with note on *C. subcristatus* from the Andaman and Nicobar Islands, India.

With due care some corrections are required and highlighted accordingly to be addressed by authors and it has been put forward with suggestions by going carefully through it and then may find the liberty to incorporate these few suggestions in the manuscript with below are as follows *(**Reviewed comments** is indicated both in MS Word/PDF files)*:

1) The author/co-authors need to pay attention to the inadvertently co-joined words or sentence in the main texts almost throughout in the manuscript.
2) The title: **Taxonomic status of the *Coryphophylax maximiliani* Fitzinger in: Steindachner, 1867 with notes on *Coryphophylax subcristatus* (Blyth, "1860" 1861)** here the word "**in**" isn't italicizing, *but italicized throughout the main texts.*
3) The conformity of the language, either British or American English (example from the texts either color or colo**u**r/colo**u**ration).
4) The literature cited like; Rangasamy et al. 2018 (**Rangasamy et al., 2018**) or Rao et al. 2017 (**Rao et al., 2017**) here the character "," (comma) were missing "et al." in some of the texts.
5) Figs. 6b & 6c were mentioned, although Fig. 6a is missing in the main text.
6) The spelling/typing mistaken (example; hetero**o**genous) extra "o" added.
7) According to the PeeJ journal format in references the literature cited for the *author's name* and *year* and including *volume/issue no.* should be **bold**.

8) The data in PDF file comparison between these two tables titled; *'Table 1. List of species, samples and their GenBank accession.'* number of the species sampled (n) of *C. maximiliani* provided inside the bracket is (23) shouldn't it be **22** with the *'Table 2. Un-corrected sequence divergence for Coryphophylax species (%). See Supporting Table S1 for p-distance for all samples.'* wherein *C. subcristatus* value is given (17) should be **19**.

9) I would suggest authors to incorporate briefly in few sentences or paragraph highlighting the natural history, conservation status, biogeography, etc. about these species (example; as **distribution** section was briefly mentioned in manuscript).

10) Additionally under the PeerJ journal format these are added; *Conflict of interest statement, author's contributions, data availability, credits of map design or prepared by, funding and including the fieldwork research/forest permit no.*

Hoping for the best and quick publication for authors/co-authors and warm regards and my best wishes to the publishing PeerJ teams!

*Sd/-*

Place: Aizawl, Mizoram, India
Date: 18 November, 2024

**Dr. Ht. Decemson**
*Developmental Biology and Herpetology (DB&H) Laboratory, Department of Zoology, Mizoram University (MZU), Aizawl, India*

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



First submission

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

**Zeeshan A Mirza** [Corresp., 1], **Saunak Pal** [2], **Tejas Thackeray** [3], **Harshil Patel** [3], **Aaron M Bauer** [4]

[1] Department of Integrative Evolutionary Biology, MAX-PLANCK-GESELLSCHAFT, Tübingen, Baden Württemberg, Germany

[2] Newcastle University, Newcastle, United Kingdom

[3] Thackeray Wildlife Foundation, Mumbai, India

[4] Department of Biology and Center for Biodiversity and Ecosystem Stewardship, Villanova University, Villanova, United States

Corresponding Author: Zeeshan A Mirza
Email address: snakeszeeshan@gmail.com

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.

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

Zeeshan A. Mirza[1], Saunak Pal[2], Tejas Thackeray[3], Harshil Patel[3] and Aaron M. Bauer[4]

[1]Max Planck Institute for Biology, Max Planck Ring 1, Tübingen 72076, Germany
[2]School of Natural and Environmental Sciences, Newcastle University, Newcastle Upon Tyne NE1 7RU, United Kingdom
[3]Thackeray Wildlife Foundation, Mumbai 400051, Maharashtra, India
[4]Department of Biology and Center for Biodiversity and Ecosystem Stewardship, Villanova University, 800 Lancaster Avenue, Villanova, PA 19085, USA

## 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 members 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. 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 '*humei*' 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; 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 museum material, 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 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, from posterior border of orbit to anterior border of tympanum), jaw length (JL, from rostrum to corner of jaw), interorbital width (IO, transverse distance between anterodorsal corners of left and right orbits), nares to eye (NE, distance from the anterior edge of orbit to posterior edge of

naris), snout width/internasal distance (IN, transverse distance between left and right nares), tympanum diameter (TD, greatest diameter of tympanum), orbit diameter (OD, distance between anterior and posterior margins of orbit), lower arm length (LAL, distance from elbow to distal end of wrist, or just underside of forefoot when the limb is flexed), upper arm length (UAL, distance from anterior insertion of forelimb to elbow when the limb is flexed), crus length (CL, length of crus (tibia) from knee to heel), hind foot length (HFL, distance from proximal end (heel) of hind foot to distal most point of fourth toe), trunk length (TrL, from forelimb insertion to hind limb insertion), trunk height (TrH, depth midway between the fore and hind limb insertions), trunk width (TrW, width midway between the fore and hind limb insertions), tail length (TaL, from posterior border of cloacal opening to tip of tail), tail height (TaH) and tail width (TaW, at tail base). Meristic characters were counted for multiple individuals per species. The following characters were scored: mid-body scale rows (MBS, number of scale rows around the trunk at midbody), mid-dorsal scales (MD, counted from the first erect dorsal crest spine to the level above the vent), ventral scales (VEN, number of scales from below mental around the base of the dewlap to anterior border of cloaca), fourth toe lamellae (LAM4, number of 4th toe lamellae, from 1st lamella at the digit's cleft to the most distal lamella), supralabials (SL, posterior end defined by the last enlarged scale that contacts the infralabials at the corner of mouth), infralabials (IL, posterior end defined by the posterior-most enlarged scales that contact the supralabials at the corner of the mouth), ventral scales on the belly (VENB, number of scales posterior to the dewlap to the anterior border of cloaca). Multivariate Principal Component Analysis (PCA) was performed on selected morphometric values: HL, HH, HW, TrL, LAL and CL (Supporting Table S2). These values were corrected for SVL and were later log-transformed.

Institutional acronyms: BNHS- Bombay Natural History Society, Mumbai (India); NHMW- Natural History Museum, Vienna (Austria); ZMB- Museum für Naturkunde, Berlin (Germany); ZMUC- Zoological Museum, University of Copenhagen, Copenhagen (Denmark); ZSI- Zoological Survey of India, Kolkata (India).

Molecular methods- Molecular data for the gene 16S rRNA generated by Shreyas Krishnan was downloaded from GenBank, and accession numbers and their collection localities are listed in Table 1. *Gonocephalus pyrius* was choosn 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. The aligned dataset was analysed in a

Maximum Likelihood (ML) framework on the IQ-TREE online portal (Minh et al., 2020). 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 pseudoreplicates to assess clade support. The resulting tree was visualised and edited with FigTree (Rambaut, 2012). Un-corrected p-distance was 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* 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*, which was sister to clade II. Clade II comprises a basal undescribed *Coryphophylax* sp. (*Coryphophylax* sp. 1 Fig. 1) from Car Nicobar Island (the northern most 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* and *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. brevacauda*, where PC1+PC2 explain 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 >90mm, which is much larger than that of *C. subcristatus* and *C. brevacauda*. 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, too, the representatives of samples from their respective type localities show a divergence of 0–4% (Table 2), which further corroborates that the two nomina are synonyms. 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*.

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

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

*Coryphophylax maximiliani* Fitzinger *in* Steindachner, 1867: 30

*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

Figs. 3–7, Table 3

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

**Paralectotypes (n=8):** NHMW 20976:1 (SVL 57.9 mm), NHMW 20976:2 (SVL 62.1 mm), NHMW 20976:3 (SVL 93.6 mm, TaL 210 mm), NHMW 20976:4 (SVL 54.4 mm), NHMW 20976:6 (SVL 78 mm), NHMW 20976:7 (SVL 96 mm), NHMW 20976:8 (SVL 58.9 mm), 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; 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$^{th}$ toe. Male dewlap yellow with black reticulate markings.

**Description of *Coryphophylax maximiliani* based on examined material:**

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 short. Snout obtusely pointed when viewed dorsally, rostral much wider than deep, bordered posteriorly by first supralabial, prenasal and dorsally by four small scales. Canthus rostralis and supraciliary edge sharp consisting of 12–14 scales, some of these are large tuberculate. Nostrils positioned centrally in a large, undivided nasal plate, bordered by 9-10 scales, including one prenasal, four postnasals and two supranasal, and in contact with rostral. Supralabials 7–10 rectangular, weakly keeled, bordered above by a single row of slightly smaller, rectangular, keeled scales. Loreal region concave, scales of the loreal region heterogeneous in size, raised not flat, keeled, some roughly hexagonal. Scales on postorbital and temporal region heterogeneous,

imbricate, strongly keeled, and directed posteriorly and dorsally. Orbital scales small but not granular. Tympanum naked. Four to five large, strongly keeled, tuberculate scales running from the posterior part of orbit to the supra-tympanic region. A large tubcerculate scale on the nape on either side of the dorsal crest; a second subequal tuberculate scale in the supratympanic region and postocular region. Canthals enlarged, overlapping, becoming slightly smaller along subimbricate supraciliaries, protruding slightly laterally on supraorbital ridge. Scales on dorsal surface of snout, forehead, interorbital, and occipital region heterogeneous in size, and shape; mostly elongate, imbricate, strongly keeled longitudinally; those on snout smaller, rhomboidal, those on the supra-occiput largest. Parietal plate without pineal eye, the plate slightly larger than adjacent scales. Mental shield narrower than rostral; gular scales keeled (Fig. 6b). Infralabials 8–10. Nuchal absent, and dorsal crest present, composed of low thorn-like scales. Scales on nuchal region smaller, less than half the size of those on interorbital region, imbricate, strongly keeled. Dorsal crest comprising 57–58 raised, spike-like scales in a row on a raised flap of skin running from the posterior part of the head to the level of the vent. The crest spines high and erect with a disatema, and relatively short spine-like scales run along the vertebral column to the ¼th of the tail. Body slender (Fig. 5a), 80–85 rows of scales around midbody, of these 16–18 rows across the belly are slightly larger than those on the dorsum (Fig. 5b); from neck to pectoral region scales largely homogenous, feebly keeled, intermixed with large strongly keeled scales. twice to thrice as big, scales on the trunk slightly larger than those on neck, imbricate, pointed, keeled, and directed posterodorsally forming regularly arranged longitudinal rows; ventral scales strongly keeled arranged in 16–18 rows, oriented backwards, subimbricate, heteroogenous in size; no precloacal or femoral pores (Fig. 5b). Number of scales MD 63–68. Distinct fold at the shoulder present. Fore 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, dorsal, crest-like spines extend to the anterior ¼ 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., Camorta Is., Kondul Is., Menchal Is., Katchal Is., Tillanchong Is., Trinkat Is. See Fig. 1 & 7 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), 42–63mm 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 ¼ 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*); 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 Conclusions

The phylogenetic affinity of the genus *Coryphophylax* currently remains poorly studied. The only study that assessed the phylogenetic placement based on molecular data of the genus 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, too, suffers from a similar limitation in molecular data, likewise supported by 16S rRNA data 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 the lizards across the islands make then an ideal model species for studying the patterns of colonization and diversification across the Andaman and Nicobar Islands.

*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 the specimen NHMUK 1874.4.29.1229 was donated by R. H. Beddome and all these specimens are listed as non-type specimens. Das et al. (1998) could not locate the second syntype of *Tiaris humei* in the collection of the Zoological Survey of India and stated that it would possibly be in the collection of the Natural History Museum, London. The cataloguing dates and collector/donor of the NHMUK specimens suggest they may not represent the second syntype *Tiaris humei*. Boulenger (1890), in his compilation on the reptiles and amphibians of the Indian region, states in the description of '*Goniocephalus humii*' states 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). The whereabouts of the second syntype, therefore, remain unknown at present, and the specimen may be lost.

Molecular data suggests 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 S. Krishnan 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 Pulomilo 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 TenDegree 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 (ZAM, SP & HP pers. obs).

The revalidation of the nomen from the Nicobar Islands is not surprising, as former workers suggested that *C. subcristatus* is a species complex (Das, 1999; Vijayakumar & David, 2006; Harikrishnan et al., 2012). The Ten Degree Channel has been proposed as a barrier for 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 the reciprocal monophyly of the samples across the channel. The findings hint at several dispersal events across this barrier. Low sea levels (Gornitz et al. 1982) or trans-marine dispersal could have facilitated these dispersals. 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. This 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.

**Acknowledgements**

The Max Planck Society's IMPRS 'From Molecules to Organisms' program supported the work conducted by ZAM. Saunak Pal thanks the entire natural history collection department and the Director of BNHS for permission to study specimens and for their constant support. The following directors/curators helped with access to specimens, data, images, and data: Rahul Khot (BNHS), Peter Rask Møller & Daniel Klingberg Johansson (ZMUC), Silke Schweiger and Georg Gassner (NHMW), Mark-Oliver Rödel and Frank Tillack (ZMB), Dhriti Banerjee and Pratyush P. Mohapatra (ZSIK) and Patrick Campbell (NHMUK). We thank S. Harikrishnan, Nitya P. Mohanty, and Shashank Dalvi for providing live images of *Coryphophylax* and discussing the distribution of the genus.

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**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 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. Prepared by: ?

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. Photo credit: ?

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

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. Photo credit: ?

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

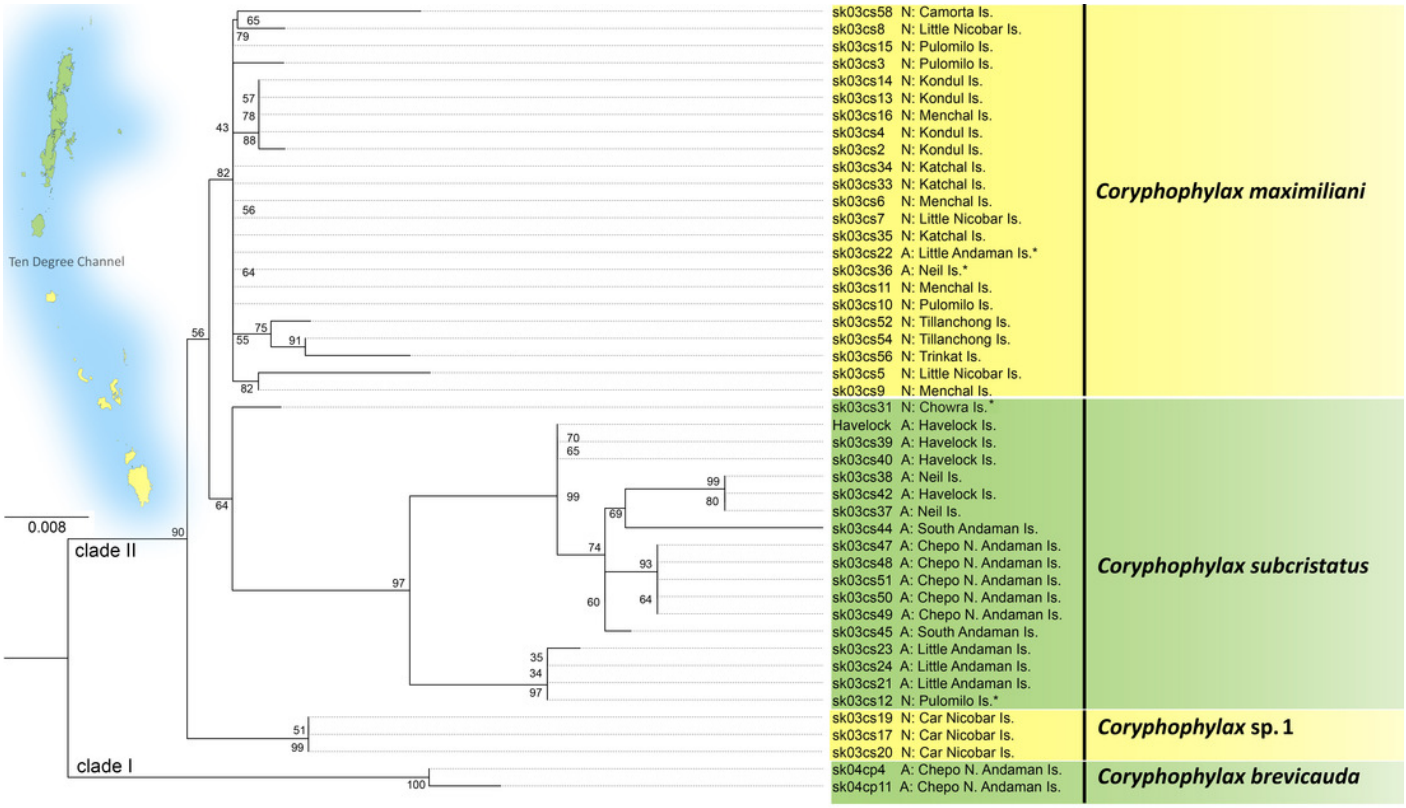
Figure 8. Map of Andaman and Nicobar Islands showing collection localities for molecular data. The Inset map of India (top left) highlights the region of interest by the red rectangle, and the map below shows the Andaman and Nicobar Islands and the Ten Degree Channel. Prepared by: ?

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

# Figure 1

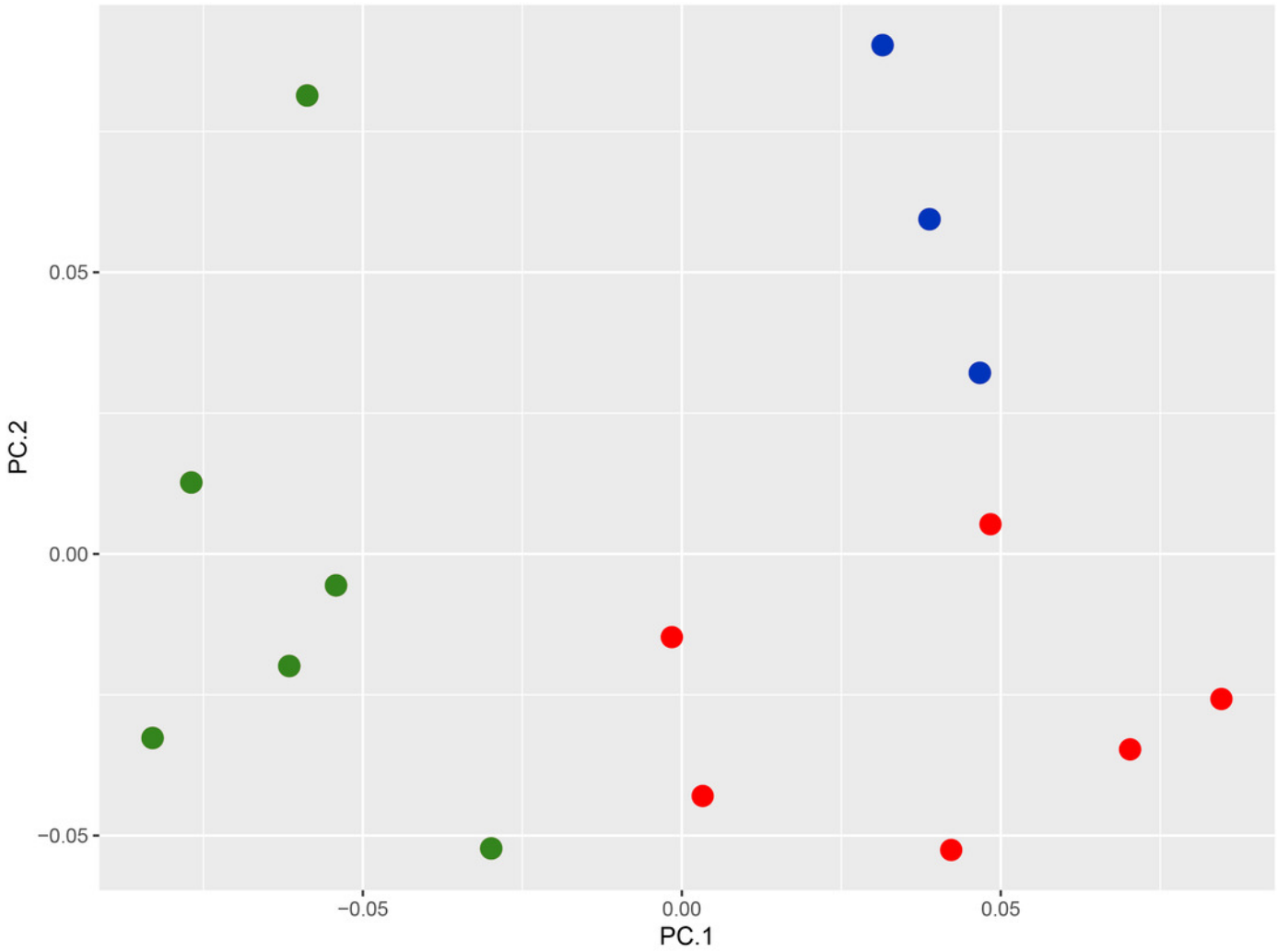
ML phylogeny of members of the genus *Coryphophylax* based on 446bp of mitochondrial 16S rRNA. Numbers at nodes represent ML bootstrap support based on 1000 pseudoreplicates.

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. Prepared by: ?



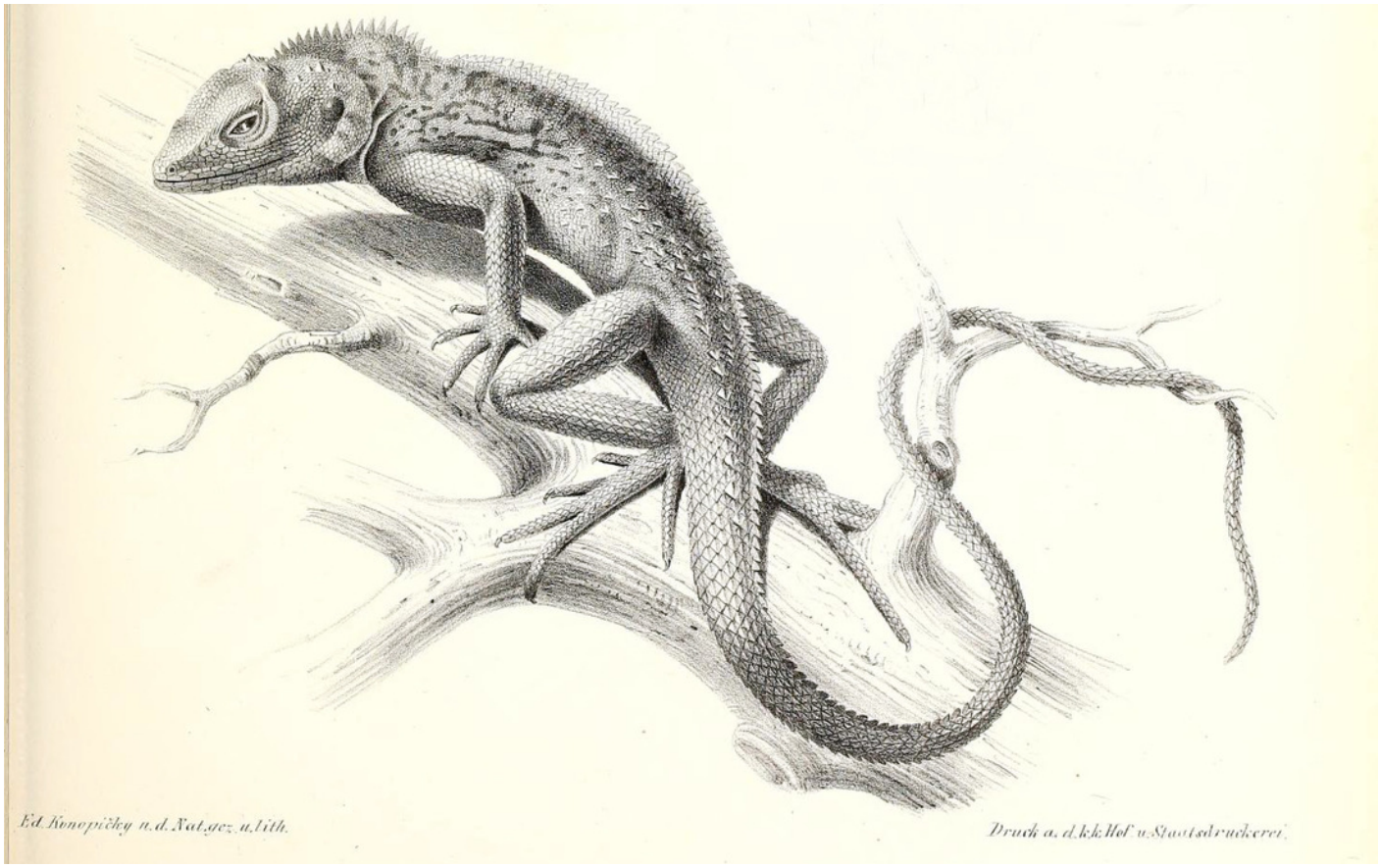
# Figure 2

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



# Figure 3

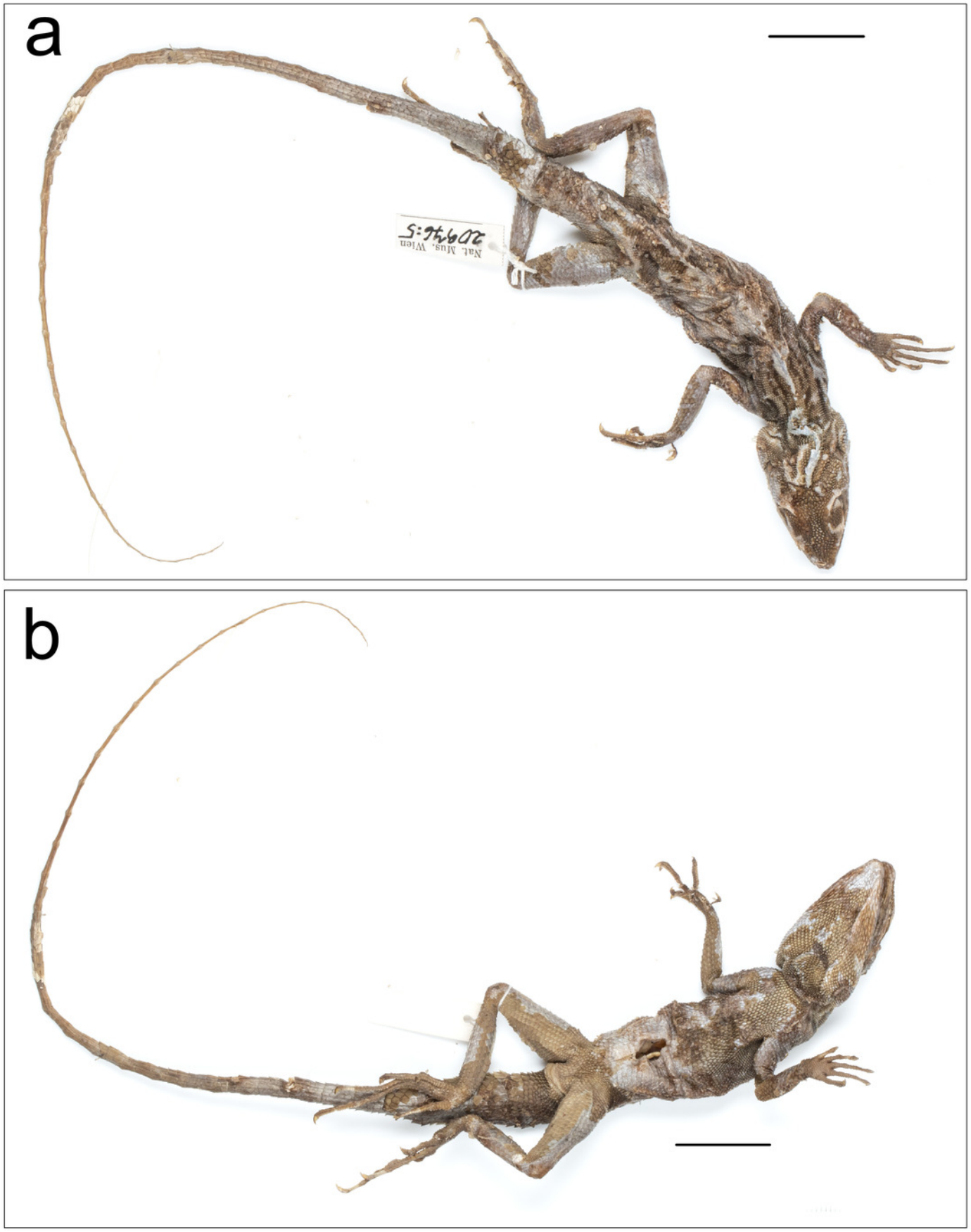
Illustration of *C. maximiliani* reproduced from Fitzinger in: Steindachner, 1867 (Plate II, Fig. 6). The illustration was altered for visual purposes by removing other illustrations; see Supporting Figure S2 for the unaltered version.



# Figure 4

*Coryphophylax maximiliani* lectotype adult male NHMV 20976:5

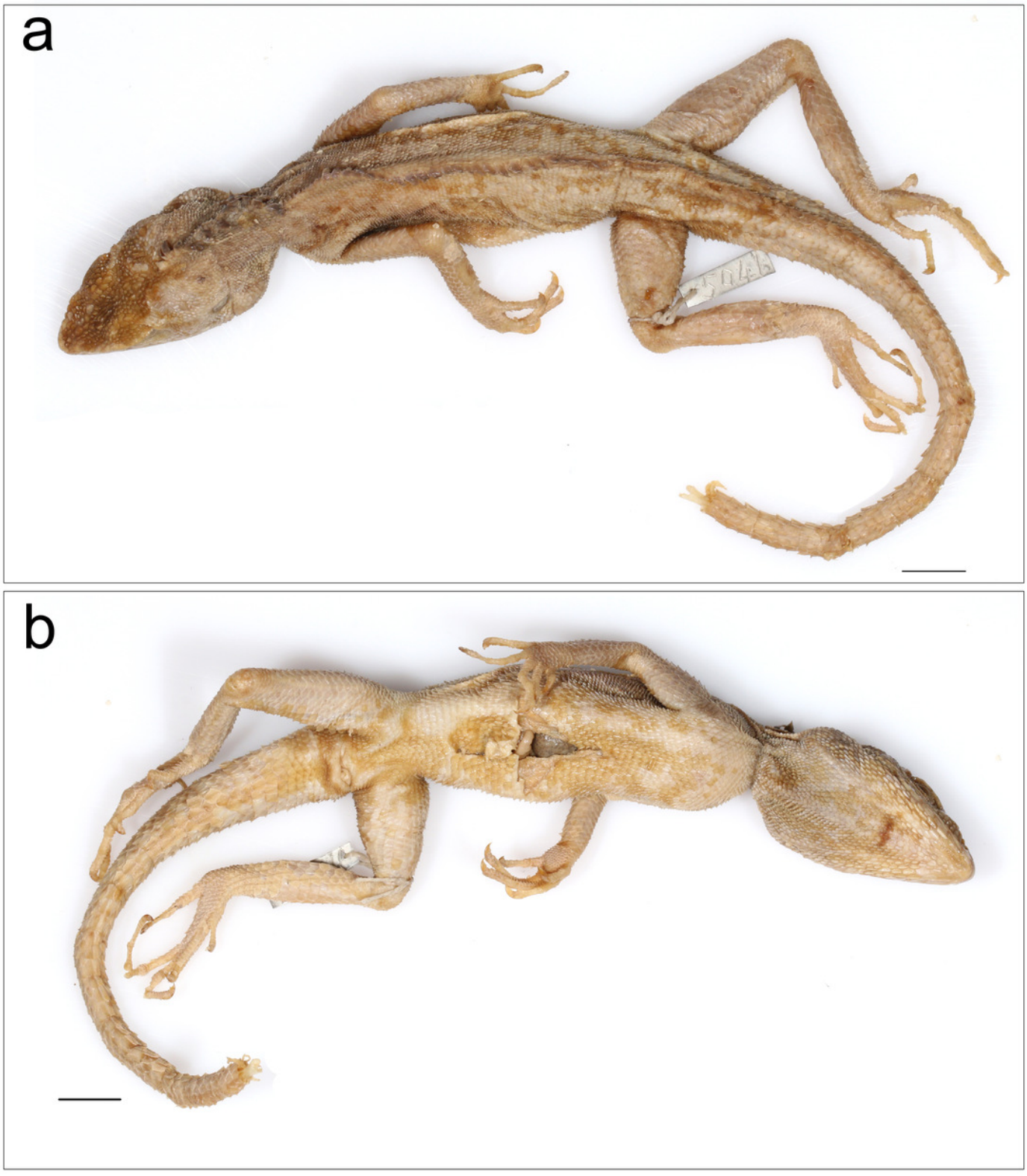
(a) dorsal view, (b) ventral view. Scale bar 20 mm. Photo credit: ?


a
Nat. Mus. Wien
20946:S
b

# Figure 5

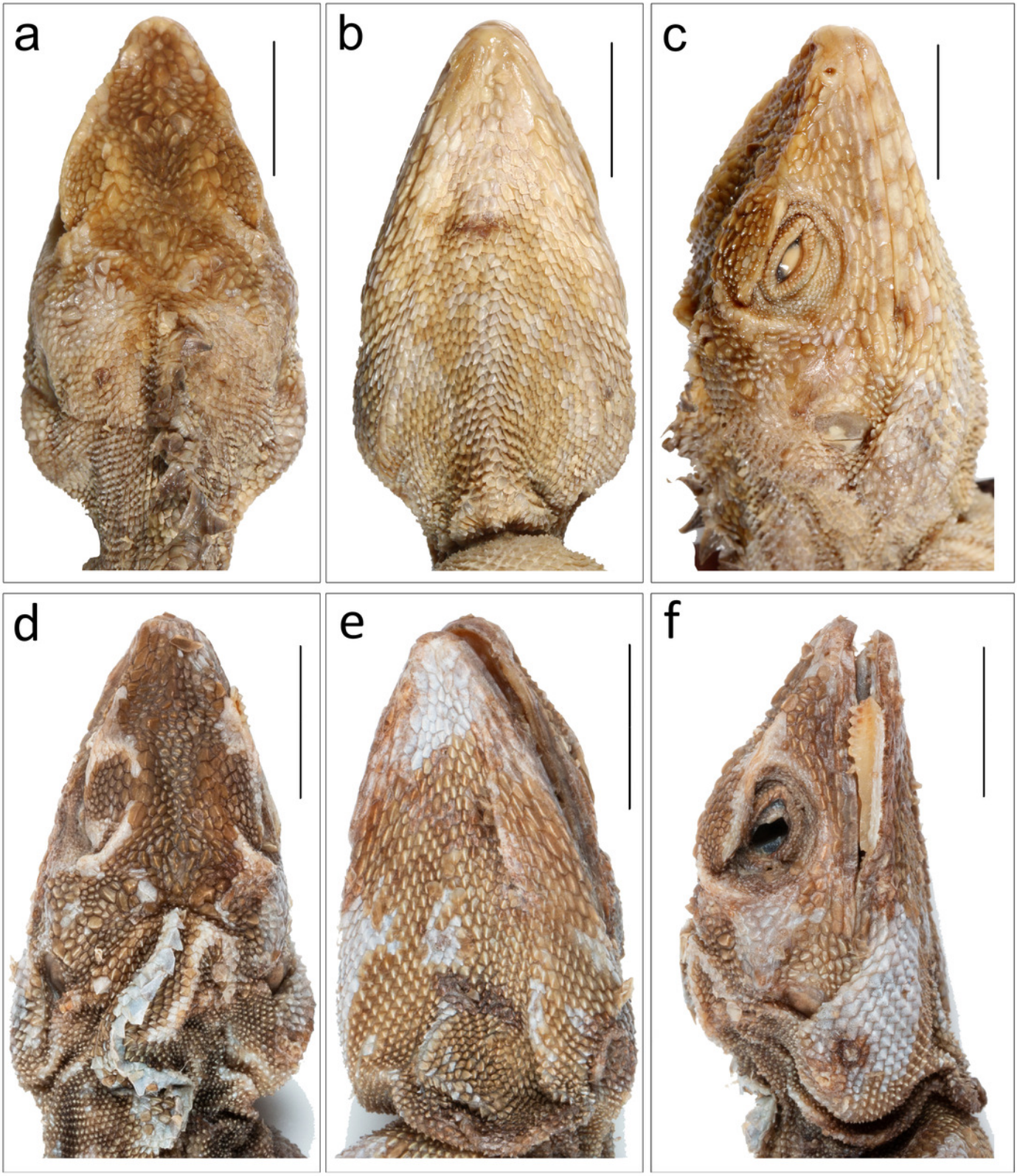
*Coryphophylax humei* lectotype male ZSI 5041

(a) dorsal view, (b) ventral view. Scale bar 10 mm. Photo credit: ?


a
b

# 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. Photo credit: ?


a
b
c
d
e
f

# Figure 7

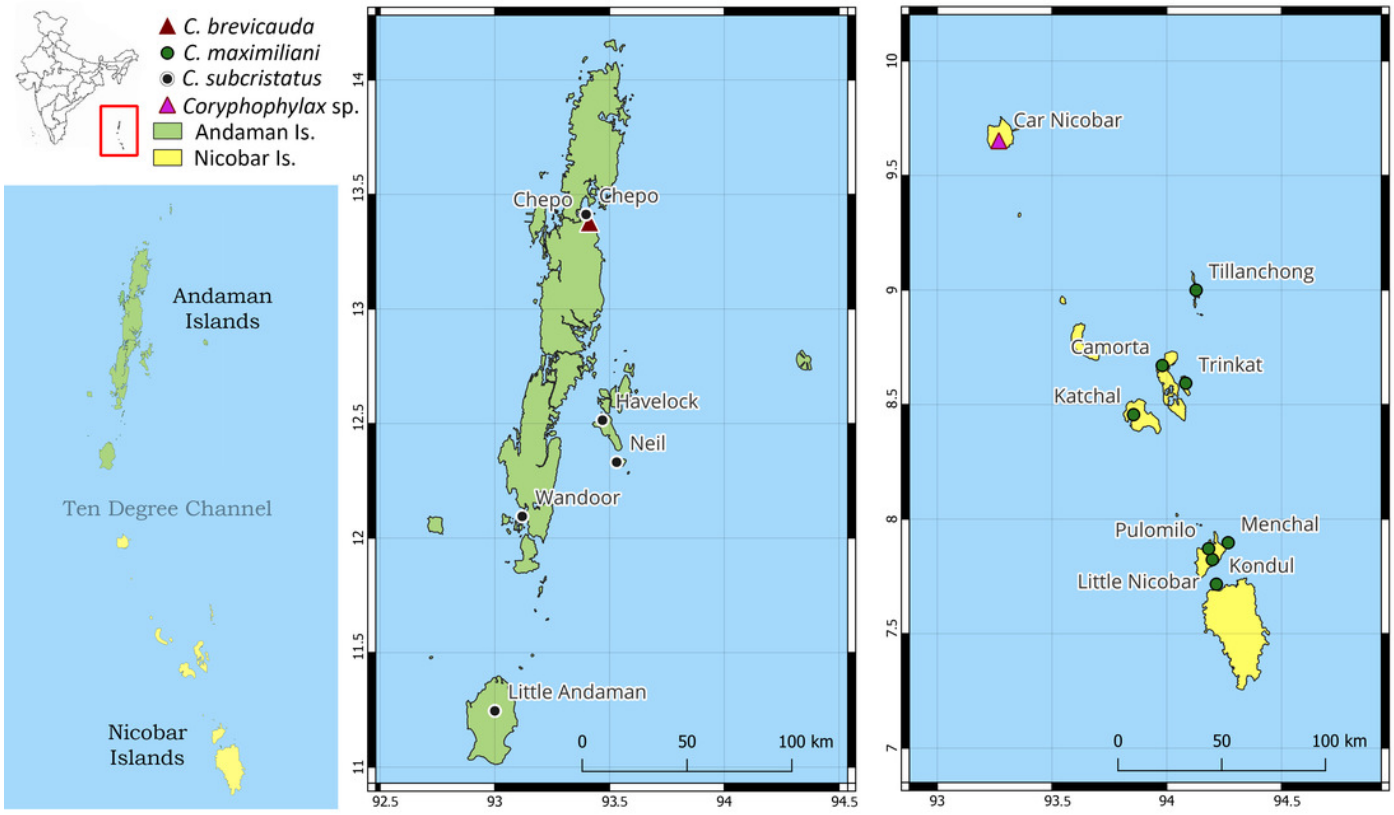
*Coryphophylax maximiliani* from Nicobar Islands showing colouration in life. Photos by S. Harikrishnan.


a
b

# Figure 8

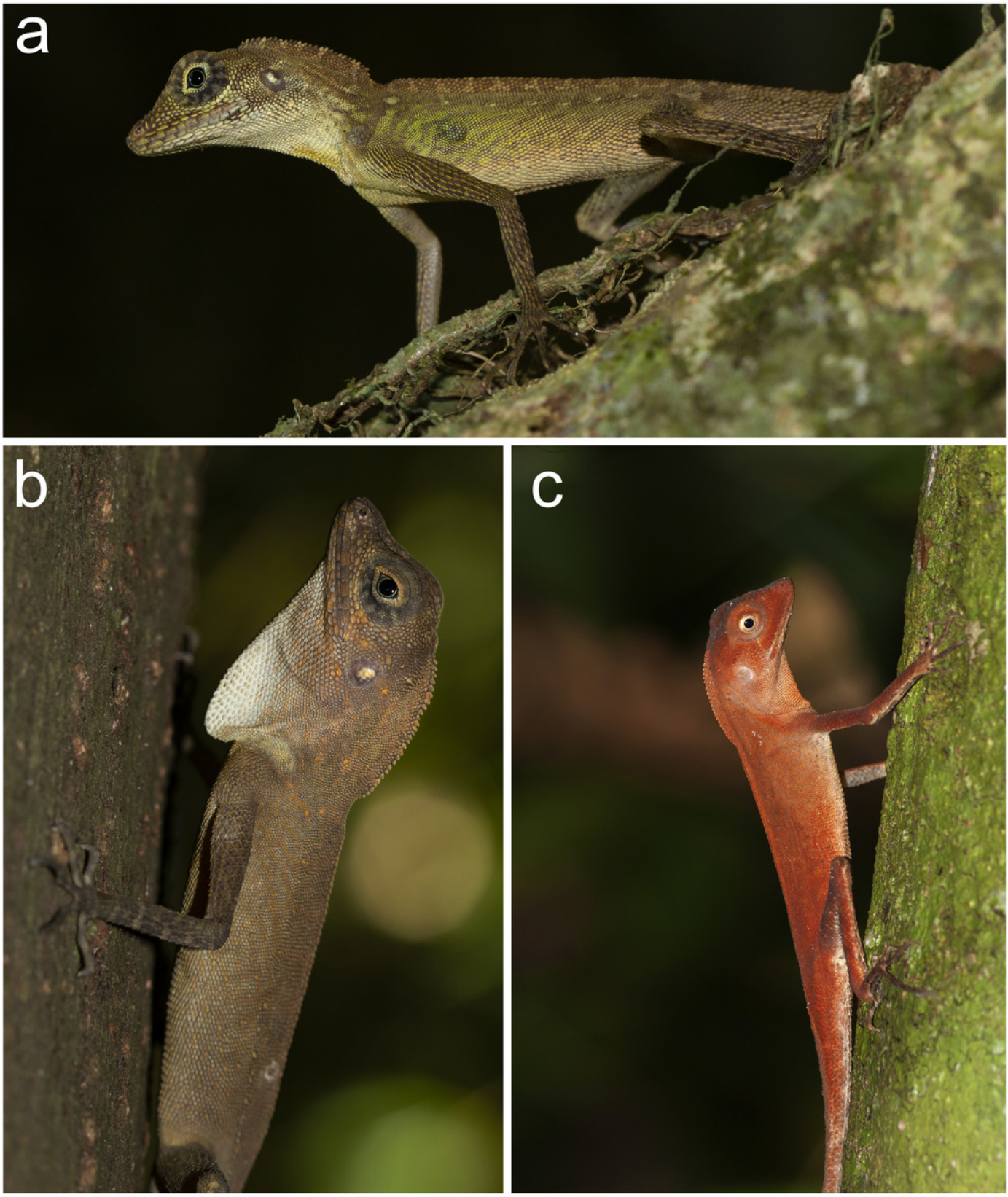
Map of Andaman and Nicobar Islands showing collection localities for molecular data. The Inset map of India (top left) highlights the region of interest by the red rectangle, and the map below shows the Andaman and Nicobar Islands and the Ten Degree Channel

Prepared by: ?



# Figure 9

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


a
b
c

## 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.

| Species | Code | Locality | 16S |
|---|---|---|---|
| *C. brevicauda* | sk04cp4 | Chepo N. Andaman Island | EU502981 |
| *C. brevicauda* | sk04cp11 | Chepo N. Andaman Island | EU502980 |
| *C. maximiliani* | sk03cs58 | Camorta Island | EU503021 |
| *C. maximiliani* | sk03cs33 | Katchal Island | EU503007 |
| *C. maximiliani* | sk03cs34 | Katchal Island | EU503006 |
| *C. maximiliani* | sk03cs35 | Katchal Island | EU503005 |
| *C. maximiliani* | sk03cs2 | Kondul Island | EU503004 |
| *C. maximiliani* | sk03cs4 | Kondul Island | EU503003 |
| *C. maximiliani* | sk03cs13 | Kondul Island | EU503002 |
| *C. maximiliani* | sk03cs14 | Kondul Island | EU503001 |
| *C. maximiliani* | sk03cs5 | Little Nicobar Island | EU502996 |
| *C. maximiliani* | sk03cs7 | Little Nicobar Island | EU502995 |
| *C. maximiliani* | sk03cs8 | Little Nicobar Island | EU502994 |
| *C. maximiliani* | sk03cs6 | Menchal Island | EU502993 |
| *C. maximiliani* | sk03cs9 | Menchal Island | EU502992 |
| *C. maximiliani* | sk03cs11 | Menchal Island | EU502991 |
| *C. maximiliani* | sk03cs16 | Menchal Island | EU502990 |
| *C. maximiliani* | sk03cs3 | Pulo Milo Island | EU502985 |
| *C. maximiliani* | sk03cs10 | Pulo Milo Island | EU502984 |
| *C. maximiliani* | sk03cs15 | Pulo Milo Island | EU502982 |
| *C. maximiliani* | sk03cs52 | Tillanchong Island | EU502978 |
| *C. maximiliani* | sk03cs54 | Tillanchong Island | EU502977 |
| *C. maximiliani* | sk03cs55 | Trinkat Island | EU502976 |
| *C. maximiliani* | sk03cs56 | Trinkat Island | EU502975 |
| *C. subcristatus* | sk03cs31 | Chowra Island | EU503020 |
| *Coryphophylax* sp. 1 | sk03cs17 | Car Nicobar | EU503013 |
| *Coryphophylax* sp. 1 | sk03cs19 | Car Nicobar | EU503012 |
| *Coryphophylax* sp. 1 | sk03cs20 | Car Nicobar | EU503011 |
| *C. subcristatus* | sk03cs47 | Chepo N. Andaman Island | EU503018 |
| *C. subcristatus* | sk03cs48 | Chepo N. Andaman Island | EU503017 |
| *C. subcristatus* | sk03cs49 | Chepo N. Andaman Island | EU503016 |
| *C. subcristatus* | sk03cs50 | Chepo N. Andaman Island | EU503015 |
| *C. subcristatus* | sk03cs51 | Chepo N. Andaman Island | EU503014 |
| *C. subcristatus* | sk03cs39 | Havelock Island | EU503010 |
| *C. subcristatus* | sk03cs40 | Havelock Island | EU503009 |
| *C. subcristatus* | sk03cs42 | Havelock Island | EU503008 |
| *C. subcristatus* | sk03cs21 | Little Andaman Island | EU503000 |
| *C. subcristatus* | sk03cs22 | Little Andaman Island | EU502999 |
| *C. subcristatus* | sk03cs23 | Little Andaman Island | EU502998 |

| | | | |
|---|---|---|---|
| *C. subcristatus* | sk03cs24 | Little Andaman Island | EU502997 |
| *C. subcristatus* | sk03cs36 | Neil Island | EU502988 |
| *C. subcristatus* | sk03cs37 | Neil Island | EU502987 |
| *C. subcristatus* | sk03cs38 | Neil Island | EU502986 |
| *C. subcristatus* | sk03cs12 | Pulo Milo Island | EU502983 |
| *C. subcristatus* | SK03CS44 | South Andaman Island | EU502974 |
| *C. subcristatus* | SK03cs45 | Wandoor South Andaman Island | EU502973 |
| *Gonocephalus pyrius* | | Lampung, Indonesia | OP070023 |

2

## Table 2(on next page)

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

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

| | *C. maximiliani* (n=23) (22) |
|---|---|
| *C. brevicauda* (n=2) | 5–7 |
| *C. maximiliani* (n=23) (22) | 0-4 |
| *C. subcristatus* (n=17) (19) | 3–7 |

Note: In table 1 the total no. of species sampled (n) for C. maximiliani is 22, but table 2 provided as 23. Similarly, C. subcristatus is 19 in table 1, but represented 17 species in table 2?

## 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 *Coryphophylax maximiliani*** | **Lectotype of *Tiaris humei*** | | | |
|---|---|---|---|---|---|
| | **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 |