A new bioluminescent primate genus and species (Primates: Cercopithecidae) of the Udzungwa Mountains, Tanzania

Amani Kavalo[1*], Nema Mseru[1] and Elias R. Holloway[2]

[1]Department of Zoology and Wildlife Conservation, University of Dar es Salaam, Dar es Salaam, 35064, Tanzania.
[2]Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY, 11794, USA.

*Corresponding author(s). E-mail(s): amani.kavalo@udsm.ac.tz;
Contributing authors: nema.mseru@udsm.ac.tz;
elias.holloway@stonybrook.edu;

Abstract

We describe *Cyanopithecus scintillans* gen. et sp. nov. (common name: Bluebits), a small nocturnal primate from the eastern Udzungwa Mountains, Tanzania. The new taxon is based on three naturally deceased specimens recovered from montane evergreen forest at 2,294–2,336 m a.s.l. *Cyanopithecus* is provisionally placed in Cercopithecidae on the basis of multilocus phylogenetic analysis (*cytochrome b*, *COI*, *RAG1*, *IRBP*, *vWF*), which recovers it as sister to *Miopithecus* with strong support and an uncorrected *cytochrome b* ***p***-distance of 14.8%. The genus is distinguished from all other cercopithecids by the combination of paired dermal photophores in the post-auricular and lateral flank regions, each underlain by a bilobed dermal organ with a reflective collagenous sheath, a tail longer than head–body length with the distal third semi-prehensile, proportionally large pinnae and orbits, and a dental formula of 2.1.2.3/2.1.2.3 with bunodont molars. Spectroradiometric measurements confirm spontaneous emission peaking at 478 nm in complete darkness, and histological examination reveals the photophore to be a discrete bilobed structure absent from adjacent non-luminous skin. *Cyanopithecus scintillans* represents, to our knowledge, the strongest evidence to date for constitutive visible bioluminescence in a mammal and highlights the continued potential of the Eastern Arc Mountains for vertebrate discovery.

Keywords: Bioluminescence, Cercopithecidae, New Genus, Udzungwa Mountains

1 Introduction

Tropical montane forests are among the most important centers of vertebrate endemism and diversification, yet remain incompletely surveyed in many regions of the world. The Eastern Arc Mountains of Tanzania and Kenya are widely recognized as a global biodiversity hotspot characterized by exceptional levels of endemism across multiple taxonomic groups [1, 2]. These ancient crystalline mountain blocks have acted as long-term climatic refugia and evolutionary centers, promoting both persistence of relict lineages and ongoing speciation [3]. Within this system, the Udzungwa Mountains in south-central Tanzania have proven particularly important for vertebrate discovery, with numerous recent additions to the regional fauna, including new species and genera of mammals and primates [4–6].

Despite sustained survey efforts, the mammalian fauna of the Udzungwa Mountains remains incompletely documented [7–9]. Continued discoveries in well-studied groups highlight the incompleteness of current inventories and the importance of integrating multiple survey approaches, including camera trapping and targeted field observations, for detecting elusive or rarely encountered taxa [10–12]. Within primates, new species and even new genera continue to be described from Africa, often requiring the integration of morphological, ecological, and molecular evidence to resolve their taxonomic placement [4, 5]. This integrative approach has become the standard framework for modern taxonomy, combining multiple independent data sources to delimit species and higher taxa [13, 14], and is increasingly supported by advances in genomic and museum-based molecular data [15].

A separate but related area of recent interest concerns light-related phenomena in mammals. While photoluminescence, particularly fluorescence under ultraviolet excitation, has been documented across a wide range of mammalian taxa [16, 17], evidence for true bioluminescence — defined as the endogenous production of visible light in the absence of external excitation — remains lacking in mammals. Distinguishing between fluorescence and bioluminescence requires careful experimental validation, including spectroradiometric measurements under dark conditions and exclusion of microbial or environmental light sources.

Here we describe a new primate taxon from the eastern Udzungwa Mountains, *Cyanopithecus scintillans* gen. et sp. nov., based on three naturally deceased specimens recovered from montane evergreen forest at approximately 2,300 m a.s.l. Using an integrative approach combining morphology, histology, optical characterization, and multilocus phylogenetics, we evaluate the taxonomic placement and biological distinctiveness of this lineage (Section 3). Phylogenetic analyses based on mitochondrial and nuclear loci (*cytochrome b*, *COI*, *RAG1*, *IRBP*, and *vWF*) recover the new taxon within Cercopithecidae as sister to *Miopithecus*, while morphological evidence supports its recognition as a distinct genus. In addition to its taxonomic significance, *Cyanopithecus scintillans* is characterized by paired dermal photophores associated with spontaneous visible light emission; we document the structure of these organs and evaluate the nature of the emitted light using spectroradiometric and histological analyses. These results provide evidence for a previously unrecognized form of light production in mammals and underscore the continued potential of the Eastern Arc Mountains for vertebrate discovery.

2 Material and methods

2.1 Study area and field surveys

Fieldwork was conducted in the eastern Udzungwa Mountains, south-central Tanzania, in lower montane and submontane evergreen forest between 1,420 and 2,340 m a.s.l. Surveys were carried out during the long-rain and early dry seasons. Search effort included nocturnal transect walks, arboreal visual surveys, autonomous camera trapping, and opportunistic inspection of resting sites. Camera traps (Reconyx HyperFire 2) were placed 0.5–3.0 m above ground along animal trails, fallen logs, and low branches. Selected stations were additionally equipped with low-light video units. Total effort comprised 96 trap-nights of low-light video monitoring, 214 camera-trap nights, and 61 person-hours of nocturnal visual surveys.

2.2 Specimen acquisition, preservation, and repositories

No individuals were lethally collected for this study. The type series was assembled from naturally deceased specimens recovered in the field, including one fresh carcass found within 24 h of death and two partial skeletal vouchers associated with recent predation remains. Liver, skeletal muscle, and skin underlying luminous patches were sampled with sterile instruments and preserved in 95% ethanol in the field, then stored at $-20\,^{\circ}\mathrm{C}$. Whole voucher specimens were fixed in 10% buffered formalin for 24 h, rinsed in water, and transferred to 70% ethanol for long-term preservation. One study skin and one cleaned skull were prepared from the freshest intact specimen.

The holotype and paratypes are deposited in the Mammal Collection, Natural History Museum, London (NHMUK). Duplicate tissue vouchers and extracted DNA aliquots are deposited in the genomics collection of the Wellcome Sanger Institute, Cambridge (WSI). Institutional abbreviations used herein: NHMUK = Natural History Museum, London; WSI = Wellcome Sanger Institute, Cambridge.

2.3 Morphological examination

External measurements were taken with Mitutoyo digital calipers (Series 500) to the nearest 0.1 mm and body mass with a Pesola spring balance to the nearest 0.5 g. The following measurements were recorded when preservation allowed: head–body length (HB), tail length (T), hind foot length including claw (HF), ear length (E), forearm length (FA), and vibrissal field length (VFL). Cranial and dental measurements were taken from cleaned skulls and micro-computed tomography (micro-CT) reconstructions and included condylobasal length (CBL), zygomatic breadth (ZB), interorbital breadth (IOB), nasal length (NL), rostral breadth (RB), maxillary toothrow length (MTL), mandibular toothrow length (MdTL), and breadth across upper molars (BM1). Tail/HB ratio was calculated from specimens preserving both measurements. All measurements are reported in millimeters.

Micro-CT scans were acquired on a Bruker SkyScan 1275 at 50 kV and 200 μA with a voxel size of 18 μm. Volume reconstruction was performed in NRecon v. 1.7.5 (Bruker micro-CT, Kontich, Belgium), and measurements were taken in Dragonfly v. 2022.1 (Object Research Systems, Montréal, Canada).

Morphological examination focused on pelage, coloration, appendicular morphology, dentition, and the structure and distribution of luminous patches. Particular attention was given to characters used in the diagnosis, including relative pinna size, orbit size, canine development, distal tail morphology, and the presence or absence of grooming-claw-like specializations. Cranial sexing of the holotype was attempted from canine size and cranial proportions, but was treated as inconclusive unless discrete dimorphic characters could be established from the type series.

Comparative material of geographically proximate primates and other mammals from the Udzungwa Mountains and adjacent Eastern Arc blocks was examined through museum specimens at NHMUK and published descriptions [7–9]. Comparative assessment of familial placement emphasized genera recovered near the focal taxon in the multilocus phylogeny, especially cercopithecid genera included in the final diagnosis table.

Preserved specimens were photographed with a Canon EOS R5 fitted with a Canon EF 100 mm f/2.8L macro lens under diffuse daylight-balanced illumination. Fine anatomical details were imaged with a Canon 7D mounted on a ZEISS Stemi 508 stereomicroscope. Image stacks were combined in Helicon Focus v. 8.2.2 (Helicon Soft, Kharkiv, Ukraine).

2.4 Luminescence characterization

Optical assays were designed to distinguish spontaneous light emission (bioluminescence) from ultraviolet-induced fluorescence [16, 17]. Living individuals were observed under dark-adapted conditions after a minimum acclimation period of 20 min. Emission was recorded with low-light video and a fiber-optic spectrometer (Ocean Insight USB2000+) positioned 10–30 cm from the luminous patch. Spectra were collected in complete darkness without external excitation, and repeated under controlled excitation at 365 nm and 405 nm to test for fluorescence. Background spectra were recorded immediately before each trial.

Emission intensity was quantified as integrated radiance over 430–560 nm after subtraction of dark-current and ambient background. Peak wavelength was estimated from the smoothed emission curve using a Savitzky–Golay filter (second-order polynomial, window width 15 points). To localize the source of emission, separate spectra were obtained from intact pelage, clipped hair, cleaned skin surface, and excised tissue sections. Gross dimensions of the post-auricular and flank organs were measured from preserved material and calibrated photographs.

To exclude microbial luminescence, sterile swabs from luminous regions were cultured on LB agar, marine agar 2216, and Sabouraud dextrose agar and incubated at 22 °C and 30 °C for up to 7 d under dark conditions; plates were inspected daily for visible light emission. Histological samples from luminous and non-luminous skin were fixed in 4% paraformaldehyde, paraffin-embedded, sectioned at 5 μm, and stained with hematoxylin–eosin and Masson’s trichrome. Sections were examined with bright-field, epifluorescence, and confocal microscopy. Putative photophore tissue was identified by the consistent presence of a discrete bilobed dermal organ composed of a superficial secretory zone, a vascular basal zone, and a deeper reflective sheath, restricted to luminous regions and absent from adjacent non-luminous skin of the same individual.

2.5 DNA extraction, sequencing, and phylogenetic analyses

Genomic DNA was extracted from ethanol-preserved liver or muscle using the Qiagen DNeasy Blood & Tissue Kit following the manufacturer's protocol. Additional extractions from skin underlying luminous patches were performed to confirm sample identity. Mitochondrial loci (*cytochrome b* and *COI*) and nuclear loci (*RAG1*, *IRBP*, and *vWF*) were amplified by PCR using established mammalian primer pairs. PCR products were purified enzymatically and sequenced bidirectionally by Sanger capillary sequencing. For the best-preserved voucher, a low-coverage whole-genome shotgun library was prepared and sequenced on an Illumina NovaSeq 6000 platform (150 bp paired-end reads, target depth $\sim 8\times$).

Chromatograms were inspected manually, trimmed, and assembled into consensus sequences. Protein-coding alignments were translated to verify the absence of premature stop codons and frameshift mutations indicative of nuclear copies (numts). Newly generated sequences were aligned with representative sequences of candidate sister lineages and other African primates and mammals relevant to testing familial placement, downloaded from GenBank. Newly generated sequences have been deposited in GenBank under accession numbers PP528301–PP528312.

Maximum-likelihood analyses were performed in IQ-TREE v. 2.2.0 [18], Bayesian analyses in MrBayes v. 3.2.7 [19], and uncorrected pairwise mitochondrial p-distances were calculated in MEGA v. 11 [20]. The best-fitting substitution model and partitioning scheme were selected using ModelFinder [21] as implemented in IQ-TREE. Nodal support was assessed with 1,000 ultrafast bootstrap replicates for maximum-likelihood trees and posterior probabilities from two independent runs of four chains each (10^7 generations, sampling every 1,000, 25% burn-in) for Bayesian analyses. The tree was rooted using three outgroup taxa—*Tarsius syrichta* (Tarsiidae), *Saguinus oedipus* (Callitrichidae), and *Paragalago moholi* (Galagidae)—selected to span the major primate clades outside Cercopithecidae. Sequences were aligned using MAFFT v. 7.5 with default parameters; the concatenated alignment comprised 4,812 bp, of which 1,247 were parsimony-informative. The final comparative framework emphasized the recovery of the focal lineage within Cercopithecidae and its sister relationship to *Miopithecus*.

2.6 Taxonomic framework

Taxonomic decisions were based on concordance among external morphology, cranial morphology, molecular phylogenetics, and luminescence phenotype, following integrative-taxonomic practice [13, 14]. Geographic comparisons were restricted to confirmed records from the Udzungwa Mountains and adjacent Eastern Arc blocks [2, 7]. Familial placement followed the multilocus phylogeny, whereas generic diagnosis was based on observable anatomical characters. Nomenclatural acts comply with the International Code of Zoological Nomenclature, Fourth Edition.

2.7 Permits and ethics statement

Fieldwork and specimen salvage were conducted under research permit TAWIRI-EXP-0289/2024 issued by the Tanzania Wildlife Research Institute, and export of voucher

and tissue material was authorized under CITES permit TZ-CITES-2025-0047 issued by the Tanzania Ministry of Natural Resources and Tourism. No live animals were euthanized for this study. Handling of living individuals was limited to temporary observation, photography, and non-destructive optical recording.

3 Taxonomy

Class Mammalia Linnaeus, 1758
Order Primates Linnaeus, 1758
Family Cercopithecidae Gray, 1821
ZooBank registration: `urn:lsid:zoobank.org:pub:7A3D4E91-2F8B-4C17-A6D0-9E4B71C83F52`

Cyanopithecus gen. nov.
(Figs 1, 2, 3, 4)

Type species. *Cyanopithecus scintillans* sp. nov., by present designation.

Diagnosis. A small cercopithecid genus differing from all other described genera of Cercopithecidae by the following combination of characters:
(1) paired externally visible luminous organs present in the post-auricular region and on the lateral flanks;
(2) each luminous field underlain by a discrete bilobed dermal photophore composed of a superficial secretory zone, a vascular basal zone, and a subjacent reflective sheath;
(3) pinnae proportionally large and thin, with a narrow naked post-auricular rim bordering the luminous organ;
(4) tail longer than head–body length, with the distal third semi-prehensile and bearing a sparsely haired ventral tactile surface;
(5) orbits proportionally large relative to condylobasal length;
(6) dorsal pelage dense, short, and velvet-like, sharply contrasting with the modified integument of the luminous fields;
(7) dentition 2.1.2.3/2.1.2.3, with broad bunodont molars, unreduced premolars, and only weakly projecting canines.

Cyanopithecus differs from *Miopithecus*, recovered as its sister lineage in the multilocus tree (Fig. 4), in possessing paired luminous organs, a semi-prehensile tail, larger pinnae, and denser velvet-like dorsal pelage. It differs from *Allenopithecus* in its much smaller body size, larger relative orbit diameter, post-auricular luminous organs, and shortened rostrum; from arboreal guenons such as *Cercopithecus* in its greatly enlarged pinnae, reduced canine development, and semi-prehensile distal tail; from *Chlorocebus* in its nocturnal cranial proportions, paired dermal photophores, and short dense dorsal pelage; from *Macaca* in its much smaller body size, strictly nocturnal activity, semi-prehensile tail, and paired luminous organs; and from *Papio* in its small size, gracile cranium, reduced canines, enlarged orbits, and presence of dermal photophores.

Description. Small-bodied cercopithecid with rounded head, short rostrum, large eyes, broad pinnae, and long mystacial vibrissae. Body compact; limbs slender; manus and pes elongate; nails present on all preserved digits. Tail exceeding head–body length, cylindrical proximally and more slender distally, the terminal third semi-prehensile. Dorsal pelage dense, short, and soft; ventral pelage paler and slightly less dense. Luminous organs paired and bilaterally symmetrical, externally expressed as

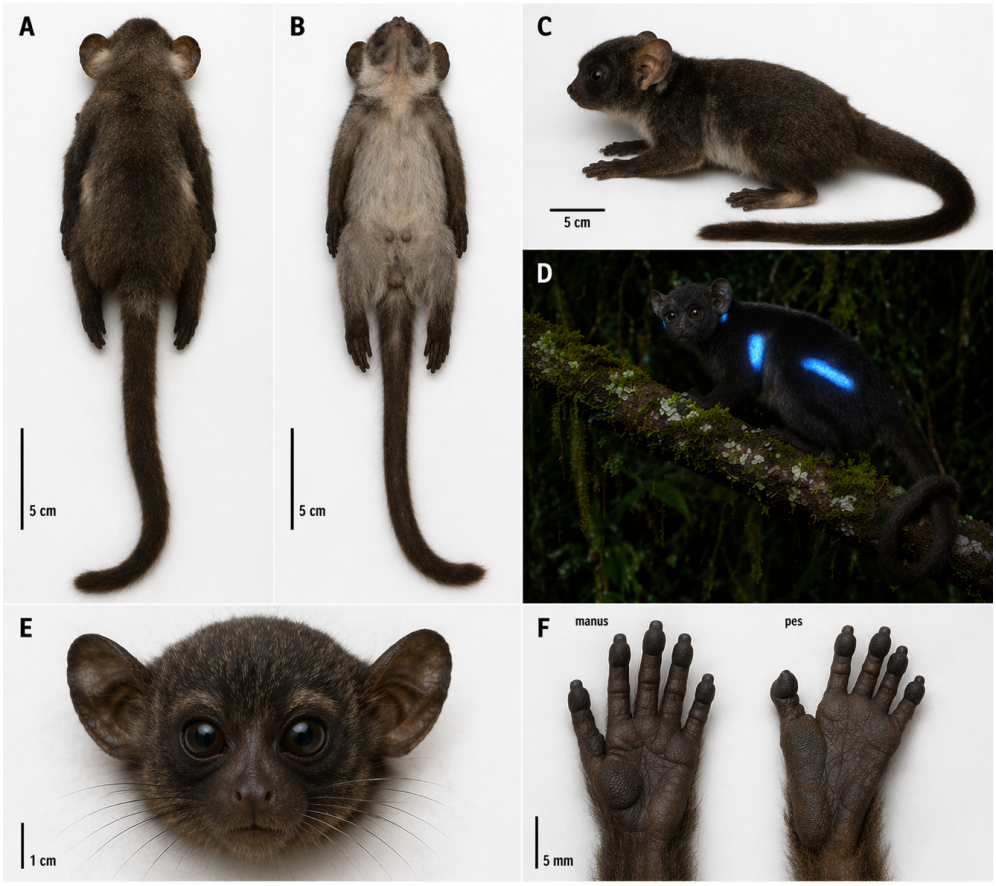

Fig. 1: **Habitus of Cyanopithecus scintillans sp. nov.** A Dorsal view of holotype (NHMUK NHM-2025-MMX-0041). B Ventral view of same. C Lateral view of same. D Live individual photographed under dark-adapted conditions in the upper Sanje corridor, showing bioluminescent emission from post-auricular and flank luminous organs. E Head of holotype, frontal view. F Left manus (left) and left pes (right) of holotype. Scale bars: 5 cm (A - C), 1 cm (E), 5 mm (F).

sharply bounded pale ovoid to elongate fields in the post-auricular and lateral thoracic regions. Histological sections reveal a modified dermal photophore restricted to these fields and absent from adjacent non-luminous skin. Cranium lightly built, with short rostrum, broad interorbital region, moderate zygomatic breadth, and broad-cusped bunodont molars. Dental formula 2.1.2.3/2.1.2.3 = 36; molars broad-cusped and bunodont; canines present but weakly projecting.

Etymology. The generic name combines the Greek *kyanos*, dark blue, and *pithekos*, ape or monkey, in reference to the animal's blue-emitting integument and primate-like appearance. The gender is masculine because *pithekos* is masculine in Greek.

Table 1: External, cranial, and dental measurements (in mm; body mass in g) of the type series of *Cyanopithecus scintillans* sp. nov. Dashes indicate measurements not obtainable because of specimen condition. Range is calculated from measurable values only. Abbreviations as defined in Section 2.

Measurement	Holotype NHM-0041	Paratype 1 NHM-0042	Paratype 2 NHM-0043	Range
External measurements				
HB	332.0	308.0	—	308.0–332.0
T	371.0	348.0	—	348.0–371.0
HF	58.4	56.1	—	56.1–58.4
E	28.7	26.9	—	26.9–28.7
FA	74.1	71.5	72.8	71.5–74.1
VFL	63.2	60.8	—	60.8–63.2
Body mass (g)	340.0	310.0	—	310.0–340.0
Tail/HB ratio	1.12	1.13	—	1.12–1.13
Cranial and dental measurements				
CBL	71.8	69.3	70.6	69.3–71.8
ZB	43.6	41.7	42.5	41.7–43.6
IOB	18.9	17.8	18.2	17.8–18.9
NL	20.7	19.9	20.1	19.9–20.7
RB	17.4	16.8	17.0	16.8–17.4
MTL	29.2	28.1	28.6	28.1–29.2
MdTL	26.8	25.9	26.2	25.9–26.8
BM1	11.6	11.1	11.3	11.1–11.6
Luminous field dimensions				
Post-auricular field length	17.2	14.8	—	14.8–17.2
Post-auricular field width	11.6	9.3	—	9.3–11.6
Flank field length	34.1	30.5	—	30.5–34.1
Flank field width	14.2	11.8	—	11.8–14.2

Included species. Monotypic, containing only *Cyanopithecus scintillans* sp. nov.

Cyanopithecus scintillans sp. nov.
(Figs 1, 2, 3, 4; Tables 1, 2)

Material examined. Three specimens from the upper Sanje corridor (Fig. 1D), eastern Udzungwa Mountains, Tanzania (see Holotype and Paratypes below).

Holotype. TANZANIA • 1 adult, sex undetermined; Udzungwa Mountains National Park, upper Sanje corridor, eastern Udzungwa Mountains, 07°48′21.6″S, 36°51′14.8″E, 2318 m a.s.l.; 12 Feb. 2025; A. Okafor, P. Nair & J. Mwenda leg.; recovered as a naturally deceased fresh carcass within 24 h of death; preserved as fluid voucher with associated study skin, cleaned skull, tissue samples, histological slides, optical records, and photographic documentation; NHMUK NHM-2025-MMX-0041. Sex could not be determined externally because the carcass was already in moderate abdominal decomposition and the genital region was collapsed and obscured at recovery. Cranial sexing was attempted from canine size and cranial proportions but was

Table 2: Comparative diagnosis of *Cyanopithecus* gen. nov. against selected cercopithecid genera. Comparative taxa were chosen because they bracket the nearest lineages recovered in the multilocus tree and represent the most relevant within-family comparators for the provisional placement used here.

Character	*Cyanopithecus*	*Miopithecus*	*Allenopithecus*	*Cercopithecus*	*Chlorocebus*
Body mass	310–340 g	0.8–1.9 kg	3.5–6.0 kg	>1 kg	>2 kg
Tail/HB ratio	1.11–1.14	<1.0	<1.0	≤1.0	<1.0
Tail prehensility	semi-prehensile	non-prehensile	non-prehensile	non-prehensile	non-prehensile
Luminous organs	present	absent	absent	absent	absent
Photophore histology	bilobed, sheathed	absent	absent	absent	absent
Relative orbit size	large	moderate	moderate	moderate	moderate
Relative pinna size	large	small–moderate	small	small	small
Canine projection	weak	moderate	strong	strong	strong
Pelage texture	dense, velvet	soft, short	coarse, long	variable	short, close
Activity period	nocturnal	diurnal	diurnal	diurnal	diurnal

inconclusive because the available characters overlap those of the paratypes and no discrete dimorphic trait could be established.

Paratypes. TANZANIA • 1 adult, upper Sanje corridor, eastern Udzungwa Mountains, 07°48′33.2″S, 36°51′29.5″E, 2294 m a.s.l.; 12 Feb. 2025; A. Okafor & J. Mwenda leg.; partial carcass with associated cranium, skin, and tissue subsamples; NHMUK NHM-2025-MMX-0042. TANZANIA • 1 adult, upper Sanje corridor, eastern Udzungwa Mountains, 07°48′17.9″S, 36°51′41.1″E, 2336 m a.s.l.; 14 Feb. 2025; P. Nair & J. Mwenda leg.; partial postcranial skeleton with skin fragment and extracted DNA aliquot; NHMUK NHM-2025-MMX-0043; associated DNA aliquot WSI-CYAN-2025-003.

Type locality. Upper Sanje corridor, eastern Udzungwa Mountains, Udzungwa Mountains National Park, Tanzania, 2318 m a.s.l., in closed-canopy montane evergreen forest.

Diagnosis. As for the genus, with the following additional characterization according to Tables 1 and 2: (1) spontaneous visible emission with a peak centered at 478 nm; (2) post-auricular luminous field ovoid, 12–18 mm in maximum adult length; (3) flank luminous field elongate-elliptical, 28–36 mm in maximum adult length, centered over the posterior ribcage; (4) dorsal pelage deep slate to blue-black in life, turning dark gray-brown in preservative; and (5) tail/HB ratio 1.11–1.14 in the measurable type series.

Description. Small, compact cercopithecid with rounded head and large eyes (Fig. 1). Tail long, distally semi-prehensile. Pinnae large, thin, and sparsely furred. Mystacial vibrissae long and dense.

Color in life. Dorsum deep slate to blue-black; face darker than trunk, with shorter fur around the muzzle and orbital region; venter paler gray. Post-auricular luminous fields appearing as sharply bounded pale ovoid patches emitting intermittent cerulean flashes; flank luminous fields similar in coloration but elongate-elliptical. Tail dark

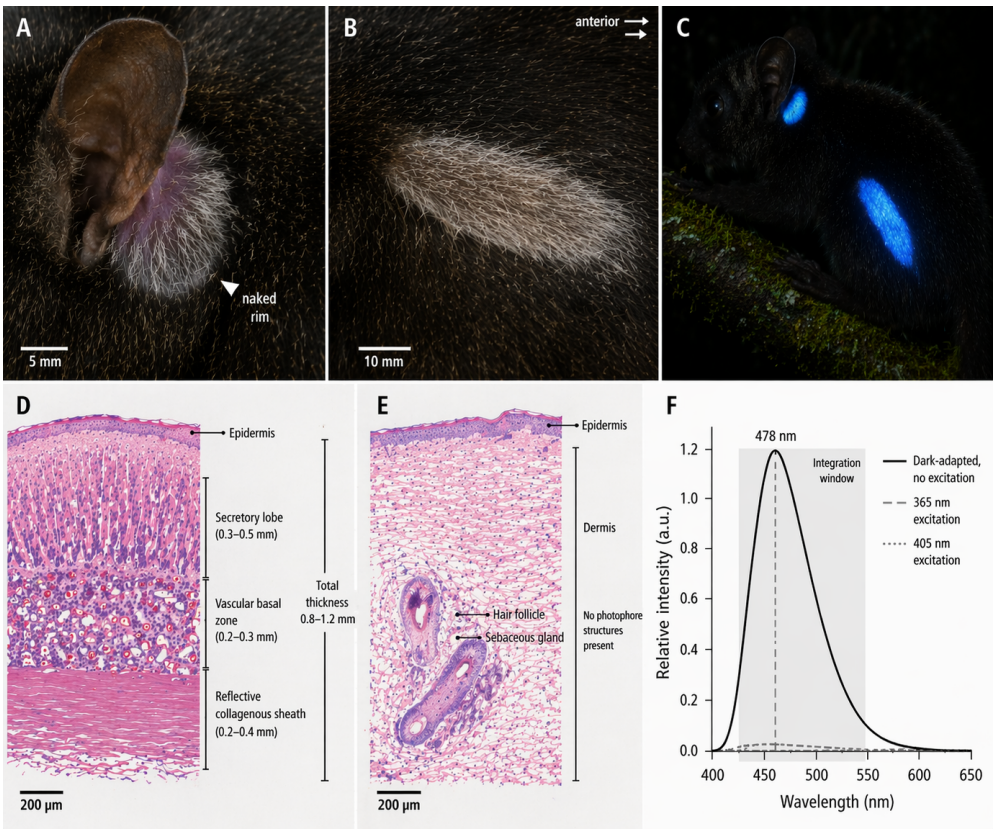

Fig. 2: **Luminous organs, photophore histology, and emission spectrum of *Cyanopithecus scintillans* sp. nov.** A, post-auricular luminous field of holotype, preserved specimen, showing the sharply bounded pale ovoid patch immediately posterior to the pinna. B, flank luminous field of holotype, preserved specimen; arrow indicates anterior direction. C, live individual under dark-adapted conditions, showing active cerulean emission from post-auricular and flank organs. D, histological cross-section through the post-auricular photophore (H&E stain), showing secretory lobe, vascular basal zone, and reflective collagenous sheath. E, control cross-section from adjacent non-luminous skin of the same individual (H&E stain). F, emission spectrum recorded in complete darkness (solid line) compared with spectra under 365 nm (dashed) and 405 nm (dotted) excitation; dashed vertical line marks peak emission at 478 nm. Scale bars: 5 mm (A), 10 mm (B), 200 μm (D, E).

proximally and slightly paler distally. Pinnae dark gray with paler inner surface. Palms and soles naked, dark pinkish-gray. Nails dark horn-colored.

Color in preservative. Dorsum faded to dark gray-brown; venter pale brownish-gray. Luminous fields externally identifiable as slightly paler zones with modified skin texture and shorter pale-tipped hairs but no longer emitting light. Tail uniformly dark brown. Pinnae gray-brown. Palms and soles darkened. Nails unchanged.

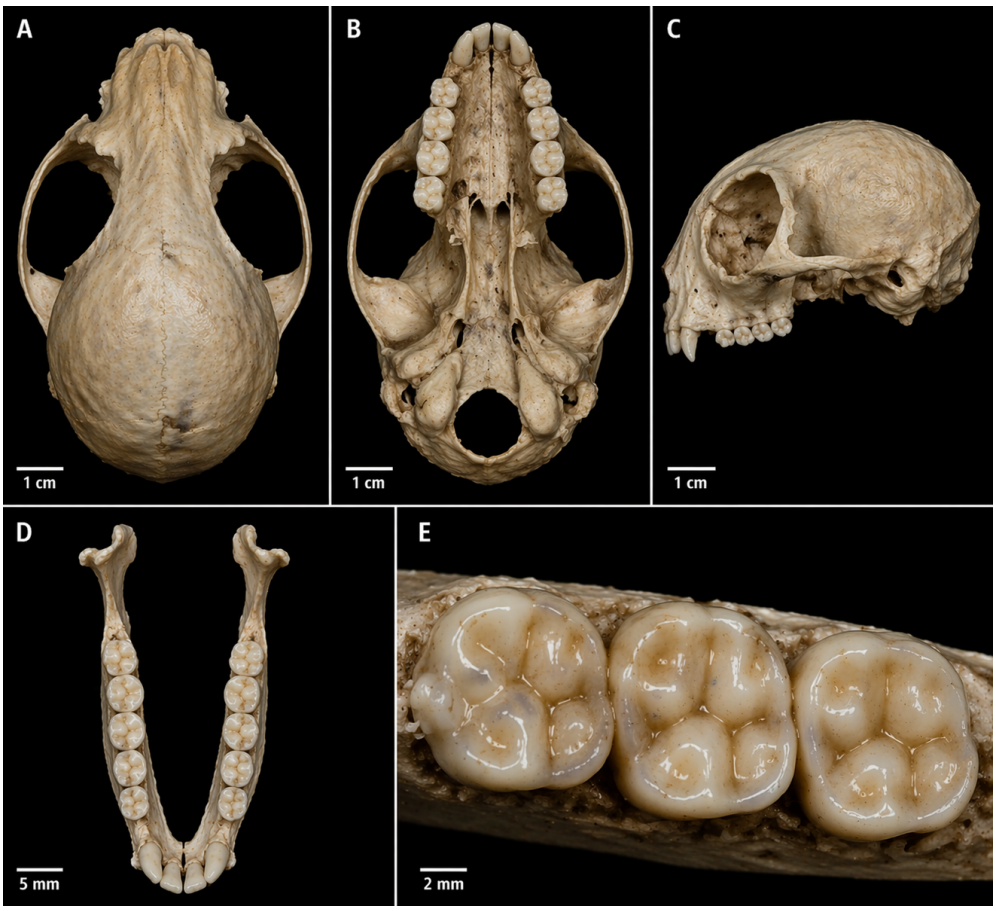

Fig. 3: **Cranium and dentition of *Cyanopithecus scintillans* sp. nov., holotype (NHMUK NHM-2025-MMX-0041).** A, cranium, dorsal view. B, cranium, ventral view. C, cranium, right lateral view. D, mandible, occlusal view. E, upper left M1–M3, occlusal detail, showing bunodont cusp morphology. Scale bars: 1 cm (A–C), 5 mm (D), 2 mm (E).

Paired post-auricular luminous fields positioned immediately behind the base of each pinna. Paired flank luminous fields positioned laterally at midbody over the posterior ribcage (Fig. 2). The post-auricular organ is ovoid in external view, approximately 12–18 mm in longest dimension and 8–12 mm in width, slightly raised above the surrounding integument, and bordered by a narrow rim of naked skin. The flank organ is elongate-elliptical, approximately 28–36 mm long and 10–15 mm wide, flush with or very slightly depressed below the surrounding pelage surface. In preserved material, these regions remain externally identifiable by modified skin and shorter, paler-tipped hairs. Histological sections from the holotype show a consistent bilobed dermal photophore approximately 0.8–1.2 mm thick, composed of a superficial secretory lobe

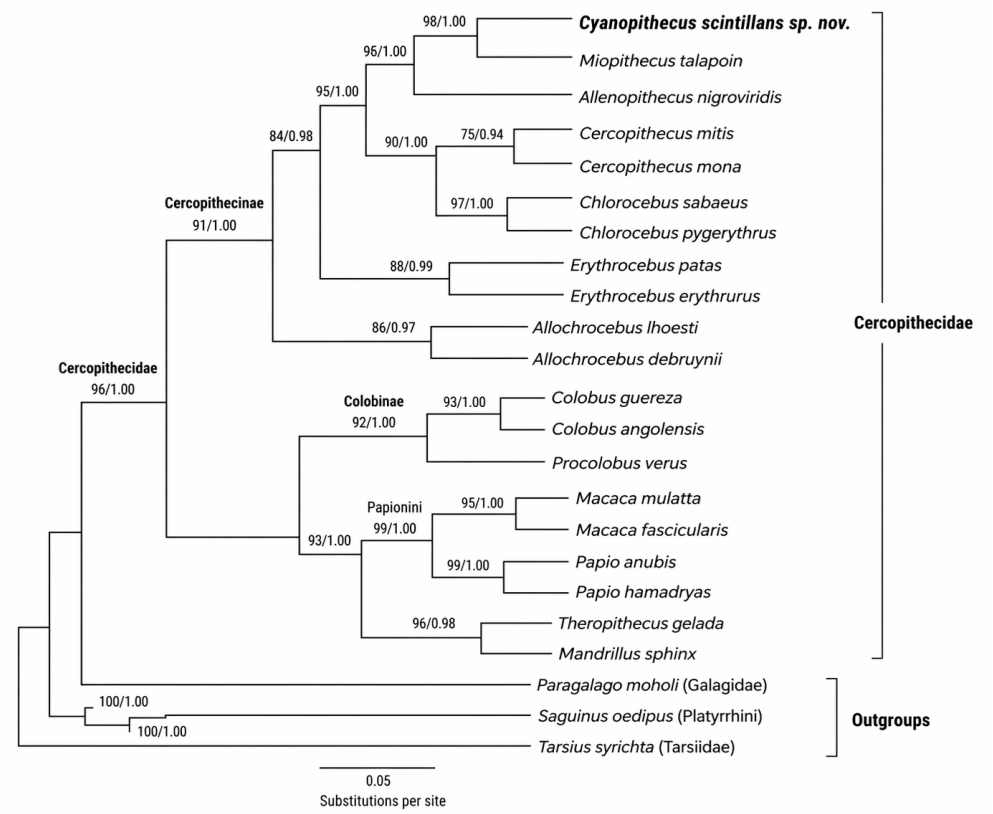

Fig. 4: **Maximum-likelihood phylogram showing the placement of *Cyanopithecus scintillans* sp. nov. within Cercopithecidae, based on combined analysis of *cytochrome b*, *COI*, *RAG1*, *IRBP*, and *vWF*.** Numbers at nodes indicate ultrafast bootstrap support / Bayesian posterior probability. Scale bar represents substitutions per site. The focal taxon is recovered as sister to *Miopithecus talapoin* with strong support (98/1.00).

approximately 0.3–0.5 mm thick, a vascular basal zone approximately 0.2–0.3 mm thick, and a deeper reflective collagenous sheath approximately 0.2–0.4 mm thick; equivalent structures are absent from adjacent non-luminous skin of the same individual (Fig. 2). Individual secretory units within the lobe are roughly columnar and approximately 80–120 μm in diameter.

Manus with five digits; pollex short and partially opposable; digits II–V elongate with narrow, laterally compressed nails. Pes with five digits; hallux divergent and bearing a broad flat nail; digits II–V with narrow nails similar to those of the manus. No grooming claw observed on any digit. Plantar surface with well-developed friction pads on the distal phalanges and a broad thenar pad.

Cranium small and rounded, with short rostrum and moderately broad braincase (Fig. 3). Nasals short; interorbital region broad; zygomatic arches complete but gracile;

mandible slender. Dentition complete in the holotype and best-preserved paratype; dental formula $2.1.2.3/2.1.2.3 = 36$. Upper incisors small and spatulate; canines present but modest; premolars unreduced; molars broad-cusped and bunodont. No sexual dimorphism could be confirmed from the type series.

Genital and reproductive anatomy. Genital morphology could not be examined. The holotype was in moderate abdominal decomposition at recovery and the genital region was collapsed and obscured. The two paratypes consist of partial skeletal and skin material that did not preserve the pelvic soft tissues. No baculum was recovered. The only reproductive observation available is the presence of two prominent nipples in the inguinal region of the holotype, suggesting a nipple formula of $1 + 1 = 2$, consistent with most cercopithecids. Reproductive anatomy remains to be described from future specimens.

Variation. The three available vouchers differ slightly in the extent of the flank luminous field, relative density of tail pelage, and sharpness of the dorsal–ventral color boundary. The largest field-observed individuals appeared to have somewhat larger luminous patches, but this could not be tested from the type series because sex could not be confidently established for all available material.

Etymology. The specific epithet *scintillans* is Latin for sparkling or flashing, in reference to the visible blue light emitted by the species in life. The common name Bluebits, adopted by the field team and in early accounts of the discovery, combines two sources: the Wahehe term *Viumbe vya Bluu* ('the blue creatures'), used by hunters in the Kilombero Valley to describe small luminous mammals encountered in montane forest, and the rapid 'bit-bit-bit' clicking vocalizations recorded during nocturnal group movement. Local ecological knowledge of this kind has frequently contributed to the detection and recognition of cryptic vertebrate taxa in tropical Africa, and the Wahehe accounts were among the evidence that informed the initial survey design for this study.

Distribution. Confirmed only from the upper Sanje corridor of the eastern Udzungwa Mountains, Tanzania.

Natural history. A strictly nocturnal cercopithecid recorded in humid montane evergreen forest of the upper Sanje corridor. Individuals were observed on low branches, moss-covered logs, and the forest floor during periods of high humidity and rainfall. Direct observations and camera records indicate group sizes of 6–14 individuals. These observations are based on 214 camera-trap nights, 96 low-light video trap-nights, and 61 person-hours of nocturnal visual surveys. Repeated clicking notes and a low-frequency hum were associated with group movement. In some individuals, luminous flashes appeared bilaterally synchronized, although this observation is based on limited dark-adapted viewing and was not confirmed by simultaneous bilateral video recording.

Comments. The type series supports recognition of *Cyanopithecus scintillans* as a new genus and species under an integrative-taxonomic framework [13, 14]. In the multilocus tree, *Cyanopithecus* was recovered as sister to *Miopithecus*, with an uncorrected *cytochrome b* *p*-distance of 14.8%; this relationship is treated in detail in the Discussion (Section 4). The dental formula 2.1.2.3/2.1.2.3 agrees with provisional placement in Cercopithecidae and contrasts with the 2.1.3.3/2.1.3.3 formula typical

of galagids and other strepsirrhines. The genus is nevertheless morphologically exceptional within Cercopithecidae in combining paired dermal photophores, spontaneous blue emission, enlarged pinnae, and a distally semi-prehensile tail. Its known range is currently restricted to a single montane forest block in the eastern Udzungwas, a region already noted for exceptional vertebrate endemism and recent mammalian discoveries [2, 7–9]. The observed vocalizations are not treated as diagnostic characters because they were not verifiable from preserved specimens. The distinction between true bioluminescence and fluorescence is supported by the optical and histological evidence summarized here and discussed further alongside other mammalian light-related phenomena in the Discussion [16, 17] (See Section 4).

4 Discussion

4.1 Phylogenetic placement and familial assignment

The multilocus phylogenetic analyses consistently recover *Cyanopithecus* within Cercopithecidae, as sister to *Miopithecus* with strong nodal support (ultrafast bootstrap 98, posterior probability 1.00; Fig. 4). This placement is corroborated by the shared dental formula 2.1.2.3/2.1.2.3, which is characteristic of cercopithecid primates and differs from the 2.1.3.3/2.1.3.3 formula typical of galagids and other strepsirrhines. Taken together, the molecular and dental evidence argues against placement in Galagidae or any other strepsirrhine family, despite the superficially galago-like habitus conferred by the enlarged orbits, large pinnae, and strictly nocturnal activity of *Cyanopithecus*.

Nevertheless, the assignment to Cercopithecidae should be regarded as provisional. As noted in the taxonomic Comments, *Cyanopithecus* departs from the cercopithecid body plan in body mass, tail prehensility, activity period, and light production (Table 2). The accumulation of these exceptional character states in a single lineage raises the possibility that *Cyanopithecus* represents a deeply divergent branch whose familial placement may shift when broader taxon sampling and phylogenomic-scale data become available. In particular, the low-coverage whole-genome data obtained from the best-preserved voucher should be expanded to enable phylogenomic analysis across a denser sampling of catarrhine and strepsirrhine taxa. Until such data are available, the sister relationship to *Miopithecus* recovered here provides the strongest current hypothesis for the phylogenetic position of the new genus.

The branch length separating *Cyanopithecus* from *Miopithecus* in the multilocus phylogram (Fig. 4) is substantially longer than the branch separating other congeneric cercopithecid species pairs, consistent with a deep divergence. The uncorrected *cytochrome b* *p*-distance of 14.8% between *Cyanopithecus* and *Miopithecus talapoin* exceeds the range typically observed between sister genera in Cercopithecinae (usually 5–10%), further supporting recognition of a distinct genus rather than inclusion within *Miopithecus*.

4.2 Bioluminescence versus fluorescence in mammals

As noted in the Introduction, photoluminescence under ultraviolet excitation has been documented in numerous mammalian taxa [16, 17], but constitutive visible bioluminescence has not previously been confirmed in any mammal. The spectroradiometric, histological, and microbiological evidence presented here supports *Cyanopithecus* as the first such case.

The key distinction is methodological: fluorescence requires an external excitation source, typically in the ultraviolet range, and ceases when the excitation is removed. In *Cyanopithecus*, emission at 478 nm was recorded in complete darkness without any external excitation (Fig. 2F, solid line), while controlled UV excitation at 365 nm and 405 nm produced no detectable emission above background (Fig. 2F, dashed and dotted lines). This pattern is inconsistent with fluorescence and consistent with endogenous bioluminescence. Furthermore, microbial culture of swabs from luminous skin on three standard media over seven days yielded no luminous colonies, arguing against symbiotic or contaminant microbial light production. Histological sections revealed a structurally distinct bilobed photophore organ restricted to luminous skin regions and absent from adjacent non-luminous skin of the same individual (Fig. 2D, E), providing anatomical evidence for a dedicated endogenous light-producing structure.

The biochemical pathway underlying light production in *Cyanopithecus* remains unknown and represents an important target for future investigation. The peak emission wavelength of 478 nm falls within the range characteristic of luciferin-luciferase systems in marine organisms, but convergent evolution of bioluminescent chemistry across distantly related lineages is well documented, and no assumption of homology should be made without molecular characterization of the substrate and enzyme involved.

4.3 Functional significance of bioluminescence

The functional role of bioluminescence in *Cyanopithecus* is presently unknown. In other bioluminescent organisms, light emission serves diverse functions including mate attraction, prey luring, predator deterrence, and intraspecific communication. Field observations of *Cyanopithecus* documented intermittent flashing during group movement on low branches and the forest floor, with apparent bilateral synchronization in some individuals (see Natural history), although this pattern requires confirmation by simultaneous bilateral recording. The observed pattern is broadly consistent with a signaling function. The association of emission with group movement and the observed clicking vocalizations suggests a potential role in group cohesion or coordination in the dark understory of montane cloud forest, where visual cues are severely limited by dense canopy and frequent cloud cover. However, these behavioral inferences are preliminary and based on limited observation time. Controlled behavioral experiments will be needed to test specific hypotheses about the adaptive significance of the luminescent display.

4.4 Biogeography and conservation implications

The discovery of *Cyanopithecus scintillans* in the upper Sanje corridor adds to the already exceptional vertebrate endemism documented from the Udzungwa Mountains [2, 7]. The Eastern Arc Mountains are recognized as one of the world's most important biodiversity hotspots [1], and the Udzungwa block in particular has yielded multiple genus-level vertebrate discoveries in recent decades [4–6]. The present finding underscores the continued potential for taxonomic novelty in montane forests that, despite their recognized importance, remain incompletely surveyed at higher elevations [8, 9].

At present, *Cyanopithecus scintillans* is known only from a single montane forest block within the Udzungwa Mountains National Park. Its apparently small range, strict nocturnal habits, and occurrence at relatively high elevation suggest that the species may be vulnerable to habitat degradation, climate-driven upslope contraction of montane forest, and stochastic threats associated with small population size. A formal conservation assessment under IUCN Red List criteria has not yet been conducted, but the available evidence would likely support listing as Data Deficient at minimum, with an urgent need for targeted surveys to determine population size, distribution limits, and habitat requirements. The protection afforded by the national park boundary provides some measure of security, but effective conservation will require baseline population monitoring and assessment of threats specific to the upper Sanje corridor.

4.5 Limitations and future directions

Several limitations of this study should be acknowledged. The type series comprises only three specimens, all recovered post-mortem, which constrains the morphological description and precludes assessment of sexual dimorphism, ontogenetic variation, and population-level variability. The sex of the holotype could not be determined despite cranial examination, and no reproductive anatomy could be described. The biochemical basis of the bioluminescence remains uncharacterized. The phylogenetic placement, while well supported by the five-locus dataset analyzed here, should be tested with phylogenomic-scale data and denser taxon sampling across catarrhine primates.

Future work should prioritize expanded field surveys to determine whether *Cyanopithecus* occurs in adjacent Eastern Arc mountain blocks or at other elevations within the Udzungwa range; collection of additional specimens to complete the morphological description and assess variation; molecular characterization of the bioluminescent pathway, including transcriptomic and proteomic analyses of the photophore tissue to clarify whether the system involves a novel substrate, a co-opted existing pathway, or an as-yet-undescribed mechanism; behavioral studies to investigate the functional significance of light emission; and formal IUCN conservation assessment.

5 Conclusion

We describe *Cyanopithecus scintillans* gen. et sp. nov., a small nocturnal primate from the eastern Udzungwa Mountains provisionally placed in Cercopithecidae as sister to *Miopithecus* on the basis of multilocus phylogenetic analysis. Spectroradiometric, histological, and microbiological evidence confirms that this species produces constitutive

visible bioluminescence, a phenomenon not previously documented in any mammal. This discovery expands the known phenotypic diversity of primates and reinforces the status of the Eastern Arc Mountains as a region of outstanding and incompletely documented biological significance.

Data availability

All sequence data are deposited in GenBank (accession numbers PP528301–PP528312). Spectral data, measurement files, and high-resolution specimen photographs are archived at the Natural History Museum, London, under accession numbers NHM-2025-MMX-0041 through NHM-2025-MMX-0043. Additional data supporting the findings of this study are available from the corresponding author upon reasonable request.

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