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A new species of the genus *Ceratophora* Gray, 1835 (Reptilia: Agamidae) from a lowland rainforest in Sri Lanka, with insights on rostral appendage evolution in Sri Lankan agamid lizards

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Abstract.—The genus *Ceratophora* (horn-lizards) comprises six species, all of which are endemic to Sri Lanka. Herein, a new species of *Ceratophora* is described based on morphological and molecular evidence. The new species is restricted to the Salgala Forest (~300 m asl elevation) in the Kegalle District of Sri Lanka, which is in the northern part of the wet bioclimatic zone. The new species most closely resembles *Ceratophora aspera* Günther, 1864, but can be distinguished from it by body proportions, number of paravertebral and ventral scales, and ND2 mtDNA data. Complete morphological description of two syntypes of *C. aspera* are also provided, in addition to a key to the species of genus *Ceratophora*. The phylogenetic relationships and evolution of rostral appendages in Sri Lankan agamid lizards are discussed in light of new data. According to IUCN Red List criteria, the new species is categorized as Critically Endangered due to its range-restricted habitat. The major threats for this species are habitat loss due to expansion of commercial-scale agriculture and monoculture plantations, as well as illicit forest encroachments.

Keywords. *Cophotis*, *Lyriocephalus*, mtDNA, ND2, syntype, systematics, taxonomy

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Introduction

Sri Lanka and the Western Ghats of India are collectively recognized as a biodiversity hotspot, rich in both diversity and endemism among the herpetofaunal assemblages (Bossuyt et al. 2004; Gunawardene et al. 2007). However, this area supports the highest human population density among the world's biodiversity hotspots (Cincotta et al. 2000; Helgen and Groves 2005). The evolutionary and phylogenetic uniqueness of Sri Lanka's herpetofauna has been well established (Bossuyt et al. 2004, 2005). Despite its small land area, Sri Lanka is geographically diverse as evidenced by the three peneplains of lowland (< 300 m asl), midland (300–900 m asl), and highland (> 900 m asl), that result in an elevation gradient (Cooray 1967). This

geographic variation, in conjunction with variability in annual average precipitation, has resulted in three major bioclimatic zones in Sri Lanka: the dry zone (< 1,000 mm), the wet zone (> 2,500 mm), and the intermediate zone (> 1,500 mm) [Greller and Balasubramaniam 1980]. Further contributing to Sri Lanka's geoclimatic diversity, three distinct mountain ranges of the Central Highland, Rakwana Hills, and the Knuckles Massif, also occur in Sri Lanka (Gunatilleke and Gunatilleke 1990; MoE-SL 2012). These geo-climatic variations have generated an array of environmental gradients, creating niche filters that promote speciation, which has led to the great diversity of the herpetofauna in Sri Lanka. The great richness of Sri Lankan herpetofauna can be attributed to insular radiation, reproductive isolation, and high island-wide

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habitat heterogeneity and environmental complexity (de Silva 2006; Meegaskumbura et al. 2019). Owing to these drivers of diversity, there is a growing interest in herpetological research in Sri Lanka, particularly in taxonomy, phylogenetics, and ecology (Meegaskumbura et al. 2002, 2019; Pyron et al. 2013; Grismer et al. 2016; Karunaratna et al. 2019).

Among Sri Lanka's herpetofaunal assemblages, the agamid lizards warrant scientific attention. Agamids are widespread in the Old World, particularly throughout the Paleotropics, Palearctic, and Australasia. The 21 species of agamid lizards in Sri Lanka belong to six genera, and include 19 (90.5%) species endemic to the island (Somaweera and Somaweera 2009; de Silva and Ukuwela 2020). The agamid genus *Ceratophora* Gray, 1835 is endemic to Sri Lanka and currently comprises five species (Pethiyagoda and Manamendra-Arachchi 1998) with patchy distributions in the tropical montane and lowland humid forests: *C. aspera* Günther, 1864 (CITES Appendix II, and EN), *C. erdeleni* Pethiyagoda and Manamendra-Arachchi, 1998 (CR), *C. karu* Pethiyagoda and Manamendra-Arachchi, 1998 (CITES Appendix I, and CR), *C. stoddartii* Gray, 1834 (CITES Appendix II, and EN), and *C. tennentii* Günther, 1861 (CITES Appendix II, and EN) [Gibson et al. 2020]. *Ceratophora* is a genus of special interest to evolutionary biologists since three of the five species (*C. aspera*, *C. stoddartii*, and *C. tennentii*) possess a prominent rostral appendage, which is absent in the other two (*C. karu* and *C. erdeleni*) [Pethiyagoda and Manamendra-Arachchi 1998].

Rostral appendages (RA) represent tantalizing organs which have evolved independently in a small number of species across a wide range of taxa, and are rarely observed in lizards (Johnston et al. 2012). They have been recorded in the members of the families Dactyloidae and Chamaeleonidae, and in three genera of the agamid subfamily Draconinae (Williams 1979; Macey et al. 2000a; Schulte et al. 2002). RA morphology is profoundly different among different species of *Ceratophora* suggesting the possibility of independent evolution (Johnston et al. 2012). An earlier molecular phylogeny for the group resulted in three equally parsimonious hypotheses for RA evolution in this genus (Macey et al. 2000b; Schulte et al. 2002), suggesting either (1) independent evolution of RA in three lineages of *Ceratophora*; (2) independent evolution of RA in *C. aspera* and in the common ancestor of *C. stoddartii* and *C. tennentii*, and *C. erdeleni*, with subsequent reduction in *C. erdeleni*; or (3) evolution of RA in the common ancestor of all *Ceratophora*, with subsequent independent loss in *C. karu* and *C. erdeleni* (Johnston et al. 2012; Whiting et al. 2015). Further morphological and allometric analyses suggested that RA likely evolved rapidly and independently in the three lineages of *Ceratophora* as a result of sexual selection (in *C. aspera* and *C. stoddartii*) or as a result of natural selection for crypsis (in *C. tennentii*) [Johnston et al. 2012].

Thus far, *C. aspera* has been considered to be the most widely distributed species of the genus, occurring in lowland rainforests and a few submontane forests in the south-western part of Sri Lanka (Bahir and Surasinghe 2005). This species was described from two syntypes (BMNH 1946.8.30.51–52) by Günther (1864) with the locality stated as “Ceylon” (historical name of Sri Lanka) without a precise location. A closer examination of the *C. aspera* type specimens, along with morphological comparisons with additional museum materials and live specimens from several localities in the wet zone of Sri Lanka, revealed differences in morphological and morphometric characters between the northern and southern populations of *C. aspera*. Concordant molecular divergence in the *ND2* mitochondrial DNA gene suggested that the population in the Salgala Forest (northern part of the wet bioclimatic zone; Fig. 1) likely represents a distinct species of *Ceratophora*, which is described herein.

Materials and Methods

Field sampling and specimens. Field surveys were conducted across different locations in Sri Lanka covering several bioclimatic areas (e.g., dry zone, intermediate zone, and wet zone). At each location, the agamid species found were documented. On average, 10 man-hours were spent per location for the survey. During these surveys, behavioral and other aspects of natural history of the focal species were recorded. The ambient temperature and the substrate temperature were measured using a standard thermometer and a N19 Q1370 infrared thermometer (Dick Smith Electronics, Shanghai, China), respectively. The relative humidity and light intensity were measured with a QM 1594 multifunction environment meter (Digitek Instruments Co., Ltd., Hong Kong, China). An eTrex® 10 GPS (Garmin) was used to record elevation and georeference specimen locations. Sex was determined by the presence in males (M) or absence in females (F) of hemipenial bulges and the rostral horn. The conservation status of the species was evaluated using the 2001 *IUCN Red List Categories and Criteria Version 3.1* (IUCN Standards and Petitions Subcommittee 2016).

Museum acronyms follow Uetz et al. (2019). The type material discussed in this paper is deposited in the National Museum of Sri Lanka (NMSL), Colombo. Specimens were caught by hand and photographed in life. They were euthanized using halothane and fixed in 10% formaldehyde for two days, washed in water, and transferred to 70% ethanol for long-term storage. Tail tip muscle tissues were sampled before fixation and subsequently stored in 95% ethanol. For comparison, we examined 33 specimens of *Ceratophora*, representing all recognized species of the genus and including type specimens, 12 additional specimens of two *Cophotis* species, and four specimens of *Lyriocephalus*. Specimens

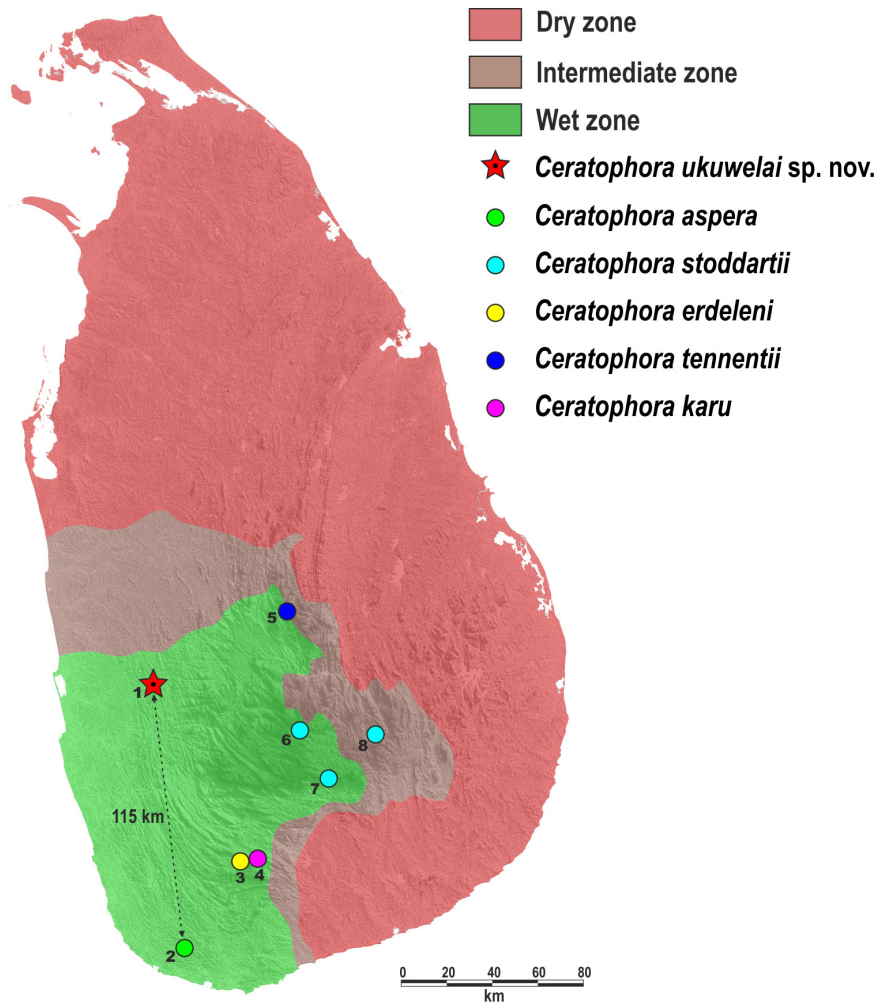


Fig. 1. Currently known distribution of *Ceratophora ukuwelai* sp. nov. and other localities for *Ceratophora* species examined in the present study. For locality numbers see Table 1. Colors of icons correspond to those in Fig. 2. Star denotes the type locality of the new species (Salgala Forest, Kegalle District, Sri Lanka).

that formerly belonged to the Wildlife Heritage Trust (WHT) collection and bearing WHT numbers are currently deposited in the NMSL, catalogued under their original numbers. The full list of comparative materials examined in this study is given in **Appendix 1**. Specimens in this study were collected during a survey of the lizards of Sri Lanka under permit numbers WL/3/2/42/18 (a, 2018 and b, 2019) issued by the Department of Wildlife Conservation, and permit numbers R&E/RES/NFSRCM/Extended/2019, and R&E/RES/NFSRCM/2019-04 issued by the Forest Department of Sri Lanka.

Morphometric characters. Thirty morphometric measurements were taken using a Mitutoyo digital Vernier calliper (to the nearest 0.1 mm), and detailed observations of scales and other structures were made through Leica Wild M3Z and Leica EZ4 dissecting microscopes. The following symmetrical morphometric characters were taken on the left side of the body: RAL, rostral appendage length (distance between tip of snout and tip of horn);

DLM, digit length manus (fork to digit tip, excluding the claw); DLP, digit length pes (fork to digit tip, excluding the claw); EN, eye to nostril length (distance between anteriormost point of bony orbit and middle of nostril); ES, snout length (distance between anteriormost point of bony orbit and tip of snout, excluding appendage); FEL, femur length (distance between groin and knee); HD, head depth (maximum height of head, across eyes); HEL, heel length (from wrist to tip of fourth finger); HL, head length (distance between posterior edge of mandible and tip of snout); HW, head width (maximum width of head); IO, interorbital width (narrowest width across frontal bone); JL, jaw length (from tip of snout to end of mouth corner); LAL, forearm length (distance from elbow to wrist with both upper arm and palm flexed at 90°); OD, orbital diameter (greatest diameter of orbit); PAL, palm length (from ankle to tip of fourth toe); SA, snout to axilla (distance between axilla and tip of snout); SN, snout to nostril (distance between tip of snout and middle of nostril); SVL, snout-vent length (distance between tip of snout and anterior margin of vent); TAL,

tail length (distance between anterior margin of vent and tail tip); TBL, tibia length (distance between knee and heel, with both tibia and tarsus flexed at 90°); TRL, trunk length (distance between axilla and groin); UAL, upper-arm length (distance between axilla and angle of elbow at 90°).

Meristic characters. Twenty discrete characters were recorded using Leica Wild M3Z and Leica EZ4 dissecting microscopes on both the left (L) and the right (R) sides of the body (reported in the form L/R): number of canthal scales (CAS), number of scales from posteriormost point of naris to anterior most point of the orbit; number of enlarged scales on the flanks (FLSP), in between axilla and groin; number of supralabials (SUP) and infralabials (INF) between the first labial scale and the corner of the mouth; number of interorbital scales (INOS), between the left and right supraciliary scale rows; number of midbody scales (MBS) from the center of mid-dorsal row diagonally towards the ventral scales to mid-dorsal; number of midventral scales (MVS) from the first scale posterior to the mental to last scale anterior to the vent; number of dorsal paravertebral scales (PS) between pelvic and pectoral limb insertion points along a straight line immediately left of the vertebral column; number of postmentals (PM) bounded by chin scales, 1st infralabial on the left and right and the mental; number of supraciliary scales (SUS) above the eye; total lamellae on manus I–V (SLM) counted from first proximal enlarged scansor greater than twice width of the largest palm scale to distalmost lamella at tip of digits; total lamellae on pes I–V (SLP), counted from first proximal enlarged scansor greater than twice the width of the largest heel scale to distalmost lamella at tip of digits.

DNA isolation, PCR, and sequencing. To determine the genetic distinctiveness of the new species and its phylogenetic position, a 1,065 bp fragment of *ND2* mitochondrial DNA (mtDNA) gene and adjacent tRNAs were amplified. The *ND2* gene has been widely applied in biodiversity surveys and phylogenetic studies on Sri Lankan agamids, including members of the genus *Ceratophora* (e.g., Macey et al. 2000a; Schulte et al. 2002; Grismer et al. 2016 and references therein). Total genomic DNA was extracted from ethanol-preserved femoral muscle tissue using standard phenol-chloroform-proteinase K extraction procedures with consequent isopropanol precipitation (protocols followed Hillis et al. 1996). The concentration of total DNA was measured in 1 µl using NanoDrop 2000 (Thermo Scientific, USA), and consequently adjusted to ca. 100 ng DNA/µl.

Polymerase Chain Reaction (PCR) amplifications were performed in 20 µl reactions using ca. 50 ng genomic DNA, 10 nM of each primer, 15 nM of each dNTP, 50 nM additional MgCl₂, Taq PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.1 mM MgCl₂, and 0.01% gelatin) and 1 U of Taq DNA polymerase. The primers used in PCR

and sequencing included two forward primers: Metf1 (5'-AAGCTTTCGGGCCCATACC-3'; Macey et al. 1997) and ND2f17 (5'-TGACAAAAAATTGCNCC-3'; Macey et al. 2000b), and two reverse primers: CO1R1 (5'-AGRGTGCCAAATGTCTTTGTGRTT-3'; Macey et al. 1997) and ND2r102 (5'-CAGCCTAGGTGGGCGATTG-3'; Greenbaum et al. 2007). The PCR conditions followed Agarwal et al. (2017). PCR products were loaded onto 1% agarose gels and visualized in agarose electrophoresis in the presence of ethidium bromide. PCR products were purified using 2 µl of a 1:4 dilution of ExoSAP-IT (Amersham, United Kingdom) per 5 µl of PCR product prior to cycle sequencing. Purified PCR products were sequenced bidirectionally at Genetech Sri Lanka Pvt. Ltd., Colombo, Sri Lanka. The obtained sequences were deposited in GenBank under the accession numbers MT992241–MT992242 (Table 1).

Phylogenetic analyses. The *ND2* sequences of all *Ceratophora* species and the representatives of all other Draconinae genera for which the homologous sequences were available from GenBank, with the addition of the newly obtained sequences, were used to examine the genealogical relationships within the genus *Ceratophora* (summarized in Table 1). In total, *ND2* sequence data were analyzed for 29 specimens of Draconinae, including nine samples of *Ceratophora*, and the sequence of *Mantheyus phuwanensis* (Manthey and Nabhitabhata, 1991) was used to root the tree according to its phylogenetic position as the sister lineage to all remaining Draconinae (Grismer et al. 2016). Nucleotide sequences were aligned in MAFFT v.6 (Katoh et al. 2002) with default parameters, and subsequently checked visually in BioEdit v.7.0.5.2 (Hall 1999) and slightly adjusted. Mean uncorrected genetic distances (*p*-distances) were calculated in MEGA v.6.0 (Tamura et al. 2013).

The matrilineal genealogy of Draconinae was inferred using Bayesian inference (BI) and Maximum Likelihood (ML) approaches. The optimal evolutionary models for the data set analysis were estimated in MODELTEST v.3.6 (Posada and Crandall 1998). The best-fitting model of DNA evolution for both BI and ML analyses was the HKY+G model for all three codon partitions of the *ND2* gene, as suggested by the Akaike Information Criterion (AIC). BI analysis was conducted in MrBayes v.3.1.2 (Ronquist and Huelsenbeck 2003); Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were performed with one cold chain and three heated chains for 20 million generations and sampled every 2,000 generations. Five independent MCMCMC iterations were performed and the first 1,000 trees were discarded as burn-in. The convergence of the iterations was diagnosed by examining the likelihood plots in TRACER v.1.6 (Rambaut et al. 2014), and the effective sample sizes (ESS) were all above 200. Confidence in nodal topology was estimated by calculating posterior probabilities (BI

Table 1. ND2 mtDNA gene sequences and voucher specimens of Agamidae taxa included in the phylogenetic analyses in this study. For sampling localities of *Ceratophora* species in Sri Lanka see Fig. 1. Sequences generated in this study are marked with an asterisk (*); n-dash (–) denotes no data available.

No.	Species	Locality	Museum ID	GenBank A.N.
1	<i>Ceratophora stoddartii</i>	Sri Lanka: Sita Eliya (6)	WHT1682	AF364053
2	<i>Ceratophora stoddartii</i>	Sri Lanka: Namunukula (8)	WHT1511	AF364054
3	<i>Ceratophora stoddartii</i>	Sri Lanka: Tangamalai (7)	WHT1512	AF128492
4	<i>Ceratophora erdeleni</i>	Sri Lanka: Rakwana (3)	WHT 1808	AF128522
5	<i>Ceratophora tennentii</i>	Sri Lanka: Knuckles (5)	WHT 1633	AF128521
6	<i>Ceratophora karu</i>	Sri Lanka: Rakwana (4)	WHT 2259	AF128520
7	<i>Ceratophora aspera</i>	Sri Lanka: Kottawa (2)	WHT1825	AF128491
8	<i>Ceratophora ukuwelai</i> sp. nov.*	Sri Lanka: Kegalle District: Salgala (1)	NMSL 2020.05.01	MT992241
9	<i>Ceratophora ukuwelai</i> sp. nov.*	Sri Lanka: Kegalle District: Salgala (1)	NMSL 2020.05.02	MT992242
10	<i>Cophotis ceylanica</i>	Sri Lanka: Nagrak Division	WHT2061	AF128493
11	<i>Cophotis dumbara</i>	Sri Lanka: Knuckles	–	GQ502785
12	<i>Lyriocephalus scutatus</i>	Sri Lanka: Puwakpitiya	WHT2196	AF128494
13	<i>Aphaniotis fusca</i>	Malaysia: Selangor: Ulu Gombak	TNHC57943	AF128497
14	<i>Harpesaurus borneensis</i>	Malaysia: Sarawak: Kubah N.P.	KUHE 59801	LC469915
15	<i>Cristidorsa otai</i>	Myanmar: Kachin	CAS234833	MK001401
16	<i>Salea kakhienensis</i>	China: Baoshan: Qushi	CAS207492	GQ502784
17	<i>Pseudocalotes brevipes</i>	Vietnam: Vinh Phuc: Tam Dao	MVZ224106	AF128502
18	<i>Diploderma splendida</i>	China: Sichuan: Ya'an	CAS194476	AF128501
19	<i>Acanthosaura lepidogaster</i>	Vietnam: Vinh Phuc: Tam Dao	MVZ224090	AF128499
20	<i>Bronchocela cristatella</i>	Malaysia: Selangor: Ulu Gombak	TNHC57874	AF128495
21	<i>Gonocephalus grandis</i>	Malaysia: Selangor: Ulu Gombak	TNHC56500	AF128496
22	<i>Malayodracon robinsonii</i>	Malaysia: Pahang: Cameron Highlands	LSUHC5873	MK001399
23	<i>Calotes versicolor</i>	Myanmar: Yangon	CAS208157	DQ289478
24	<i>Draco indochinensis</i>	Vietnam: Gia Lai: Ankhe	MVZ222156	AF128477
25	<i>Ptyctolaemus gularis</i>	Myanmar: Kachin: Putao	CAS221515	AY555838
26	<i>Japalura variegata</i>	India: Sikkim: Gangtok	ZISP20922	AF128479
27	<i>Otocryptis wiegmanni</i>	Sri Lanka: Yodaganawa	WHT2262	AF128480
28	<i>Sitana ponticeriana</i>	Sri Lanka: Hambantota	WHT2060	AF128481
29	<i>Mantheyus phuwuanensis</i>	Laos: Bolikhamxay: Thaphabat	FMNH255495	AY555836

PP). ML analysis was conducted using the RAxML web server (<https://raxml-ng.vital-it.ch/>; Kozlov et al. 2018). Nodal support was assessed by non-parametric bootstrapping (ML BS) with 1,000 pseudoreplicates (Felsenstein 1985). The nodes with BI PP values > 0.95 and LM BS values \geq 75% were *a priori* regarded as strongly supported; while BI PP values between 0.95–0.90 and ML BS values between 75–50% were regarded as tendencies. Lower values were regarded as indicating not significantly supported (Huelsenbeck and Hillis 1993).

Divergence time estimations. Molecular divergence dating was performed in BEAST v.1.8.4 (Drummond et al. 2012). An uncorrelated lognormal relaxed clock was set for our data. Substitution models and partitioning

schemes consistently remained the same as those used in the BI and ML phylogeny reconstructions. The Yule model was set as the tree prior and a constant population size and default priors were assumed for all other parameters. Two runs were conducted of 40 million generations, sampling every 4,000 generations, to obtain 10,000 trees for the analysis. We also assumed parameter convergence in Tracer v.1.6 and discarded the first 10% of generations as burn-in. Since no *Ceratophora* fossils are known, we relied on three calibration priors for the subfamily Draconinae obtained from a recent large, phylogenomically-wide revision of agamids (Grismer et al. 2016). Calibration points were as follows: (1) the most recent common ancestor (tMRCA) of the genus *Ceratophora* (18.3 ± 1.8 million years ago [Ma]); (2) tMRCA of the genera *Ceratophora*, *Lyriocephalus*, and

Cophotis (28.1 ± 2.8 Ma); and (3) tMRCA of the genera *Ceratophora*, *Lyriocephalus*, *Cophotis*, *Bronchocela*, *Gonocephalus*, *Aphaniotis*, and *Harpesaurus* (50.8 ± 5.1 Ma).

Rostral appendage evolution analysis. BEAST v.1.8.4 was used to generate a trimmed ultrametric chronogram for the Sri Lankan Draconinae with one specimen per species included in the analysis to investigate the evolutionary history of RA in *Ceratophora* and the closely related genera *Lyriocephalus* and *Cophotis*. The full dataset consisted of all six species of *Ceratophora*, including the newly discovered population of *Ceratophora* sp. from Salgala Forest, two species of *Cophotis*, and a single species of *Lyriocephalus*. Data were added for the newly discovered population of *Ceratophora* sp. from Salgala Forest to the Johnston et al. (2012) morphometric dataset, including data on maximum snout-vent length (SVL), jaw length (JL), head depth (HD), rostral appendage length (RAL), maximal rostral appendage depth (RAD), and relative rostral appendage length (RAL/SVL) and depth (RAD/SVL). The characters were recorded separately for males and females, and measurements followed Johnston et al. (2012). For each species, data were recorded for lifestyle (arboreal or terrestrial), the presence of green colors in the body coloration (yes or no), sexual dimorphism in SVL (yes or no), sexual dimorphism in coloration (yes or no), and sexual dimorphism in rostral appendage morphology (yes or no) [see Table 2]. For *Ceratophora* sp. from Salgala Forest, since no male specimens were collected, measurements were taken in life from a single male, which was subsequently released.

Phylogenetic signal is the tendency for related species to resemble each other more than they resemble species drawn at random from the tree (Blomberg and Garland 2002). The analysis of phylogenetic signal and ancestral state reconstructions were performed in R v.3.6.1 (R Core Team 2020). The phylogenetic signal in phenotypic traits was estimated with Pagel's λ (Pagel 1999) using the 'phylosig' function from the package 'phytools' (Revell 2012). Among several existing tests of phylogenetic signal, Pagel's λ was chosen because it is one of the most reliable tests, and it is robust to the errors in tree topology and branch lengths (Münkemüller et al. 2012; Molina-Venegas and Rodríguez 2017). Pagel's λ was estimated in residual errors of phylogenetic regressions (PGLS) following Revell (2010). PGLS regressions were fit using function 'pgls' from the package 'caper' (Orme et al. 2018). The ancestral state reconstruction was performed using the 'contMap' function from the package 'phytools' (Revell 2013). The aforementioned analyses were performed in R (R Core Team 2020) using RStudio integrated development environment (RStudio Team 2018).

Results

Sequences and statistics. The final alignment of the *ND2* gene sequences contained 1,032 aligned characters. Of these, 265 sites were conserved and 767 sites were variable, and 675 of the latter were found to be parsimony-informative. The transition–transversion bias (R) was estimated as 2.16. Nucleotide frequencies (all data given for ingroup only) were 34.91% (A), 23.11% (T), 30.83% (C), and 11.15% (G).

MtDNA genealogy. Both BI and ML analyses resulted in essentially similar topologies, with genealogical relationships varying only in two poorly supported nodes (corresponding to the phylogenetic position of *Cristidorsa otai* (Mahony 2009), and to the position of the clade including genera *Otocryptis* and *Sitana*); all other nodes in the tree were well-resolved and strongly supported (Fig. 2). The BI genealogy inferred the following set of phylogenetic relationships. All Draconinae genera, with the exception of *Mantheyus*, formed two reciprocally monophyletic groups. One of them included the genera *Draco*, *Ptyctolaemus*, and *Japalura* (1.0/97; hereafter node support values are given for BI PP/ML BS, respectively), and another encompassed all the remaining genera of Draconinae (1.0/84). Within the latter clade, the Sri Lankan Draconinae genera were grouped in two subclades: *Otocryptis* + *Sitana* (1.0/100), and the group including *Ceratophora*, *Lyriocephalus*, and *Cophotis* (1.0/99), with the two latter genera forming a well-supported clade (1.0/88); the genus *Cophotis*, including two species *C. ceylanica* and *C. dumbara*, was recovered as monophyletic (1.0/100) [Fig. 2]. Monophyly of the genus *Ceratophora* was strongly supported (1.0/99) and the genealogical relationships within it were well-resolved and strongly supported. Species of *Ceratophora* were grouped into two major reciprocally monophyletic clades: *C. aspera* + *Ceratophora* sp. from Salgala Forest (1.0/100), and the clade joining all the remaining species (1.0/88). Within the latter clade, *C. karu* occupied the most basal position, *C. stoddarti* (1.0/99) was recovered as a sister species of *C. erdeleni* with shallow differentiation between them (1.0/100); while *C. tennentii* formed the sister lineage to (*C. stoddarti* + *C. erdeleni*) (1.0/99) [Fig. 2].

Sequence divergence. The interspecific uncorrected *p*-distances for the *ND2* gene fragment within the genus *Ceratophora* varied from $p = 3.8\%$ (between *C. stoddarti* and *C. erdeleni*) to $p = 23.0\%$ (between *C. karu* and *Ceratophora* sp. from Salgala Forest) [Table 3]. The newly discovered lineage of *Ceratophora* sp. from Salgala Forest was highly divergent from other congeners and differed from its sister species *C. aspera* by $p = 9.6\%$ of substitutions in the *ND2* gene. This value significantly exceeded the minimal interspecific divergence between *Ceratophora* species (3.8%), as well as the distance

Table 2. Morphological characteristics of adult male (m) and female (f) specimens of nine Sri Lankan agamid species of the genera *Ceratophora* (data partially from Johnston et al. 2012), *Cophotis*, and *Lyriocephalus*. For character abbreviations see **Materials and Methods**; mean values are given for measurements; N: number of specimens, y: yes, n: no.

Species	Lifestyle	Green color	Sexual dimorphism in SVL	Sexual dimorphism in color	Sexual dimorphism in RA	Sex	N	SVL	JL	HD	RAL	RAD	RAL/SVL	RAD/SVL
<i>Cophotis ceylanica</i>	arboreal	y	y	y	n	m	28	57.7	12.3	9.5	0	0	0.00%	0.00%
<i>Cophotis dumbara</i>	arboreal	y	y	y	n	m	5	59.2	13.7	12.2	0	0	0.00%	0.00%
<i>Lyriocephalus scutatus</i>	arboreal	y	y	y	y	m	57	145.6	30.6	45.6	12.4	11.2	8.52%	7.69%
<i>Ceratophora aspera</i>	terrestrial	n	y	n	y	f	29	141.2	30.1	34.2	8.2	7.5	5.81%	5.31%
<i>Ceratophora ukunwelai</i> sp. nov.	terrestrial	n	y	n	y	m	28	29.6	8.2	4.8	5.1	1.2	17.23%	4.05%
<i>Ceratophora karu</i>	terrestrial	n	y	n	y	f	26	32.1	8.4	5	0.7	0.5	2.18%	1.56%
<i>Ceratophora temmentii</i>	arboreal	y	n	y	y	m	12	30.7	9.4	5.3	1.2	0.9	3.91%	2.93%
<i>Ceratophora erdleni</i>	arboreal	y	n	y	n	f	9	27.4	7.8	4.6	0	0	0.00%	0.00%
<i>Ceratophora stoddartii</i>	arboreal	y	n	y	y	m	16	64.5	18.8	11.2	5.6	3.4	8.68%	5.27%
						f	6	66	20.1	12.2	4.7	2.8	7.12%	4.24%
						m	4	76.1	23.5	13.7	0	0	0.00%	0.00%
						f	1	55.1	17.2	11	0	0	0.00%	0.00%
						m	40	71.4	22.2	12.8	7	1.7	9.80%	2.38%
						f	19	72.3	22	13.1	1.7	0.7	2.35%	0.97%

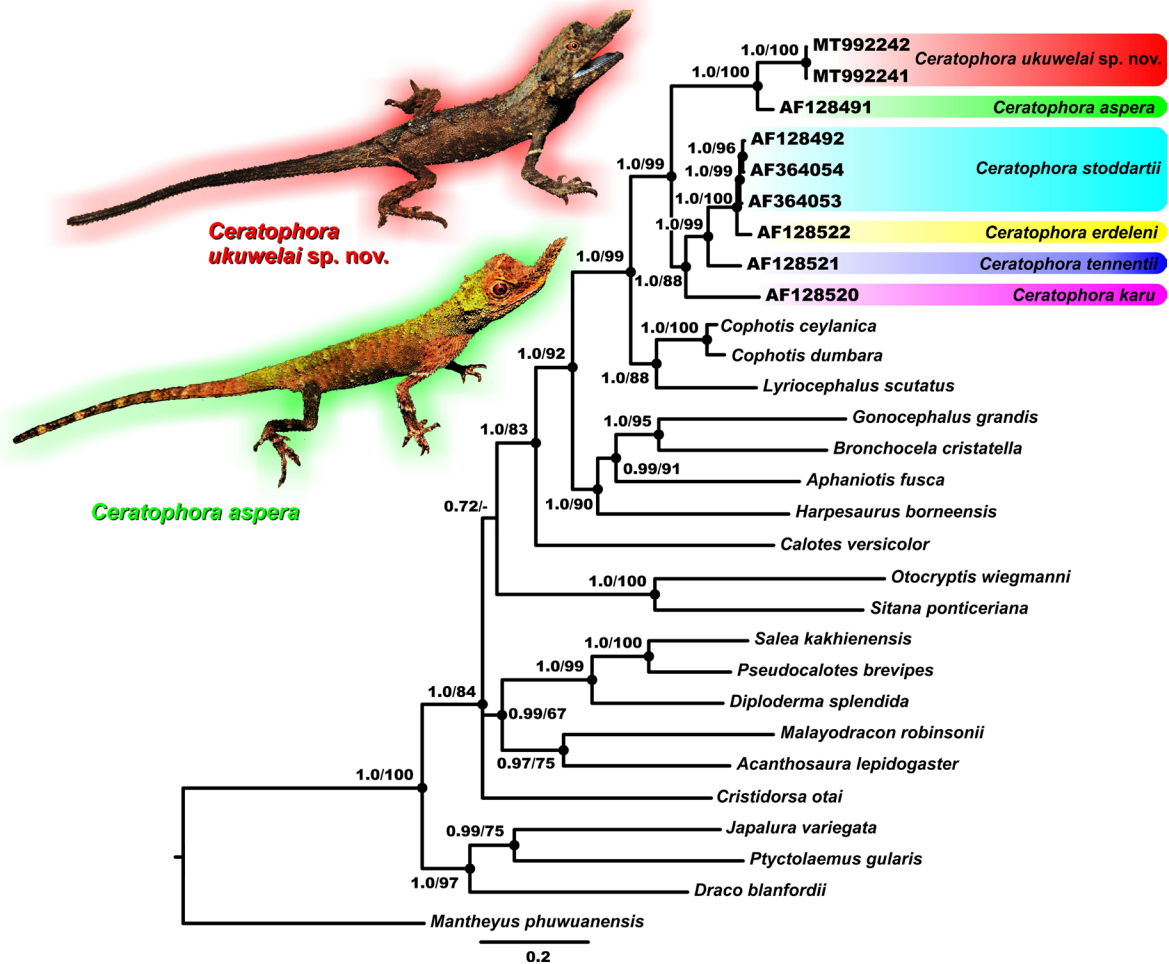


Fig. 2. Bayesian inference tree of Draconinae lizards derived from the analysis of 1,084 bp of *ND2* gene sequences. For voucher specimen information and GenBank accession numbers see Table 1. Numbers at tree nodes correspond to BI PP/ML BS support values, respectively; a black circle at a node indicates it is strongly supported (BI PP > 0.95; ML BS > 75%). Colors of clades and locality numbers correspond to those in Fig. 1. Photos by Sanoj Wijayasekara and Sanjaya Kanishka.

between the two species of *Cophotis* (4.7%) [Table 3]. Deep divergence of the newly discovered *Ceratophora* sp. from Salgala Forest from its congeners indicates that the taxonomy of this group is inconsistent with its phylogeny.

Divergence time estimations. The resulting BEAST chronogram (see Fig. 3) had topology slightly different from the BI tree. Specifically, *Cristidorsa otai* was grouped with the clade including *Salea*, *Pseudocalotes*, *Diploderma*, and *Malayodracon*; *Calotes versicolor* clustered with the *Otocryptis* + *Sitana* clade. These topological differences refer to poorly supported nodes and do not affect the analysis of relationships among Sri Lankan agamids. The time tree analysis (see Fig. 3) reveals that tMRCA of the Sri Lankan agamid clade including *Ceratophora*, *Lyriocephalus*, and *Cophotis* originated during the middle Eocene, ca. 44.14 Ma (36.8–51.19), and radiated within a relatively narrow time period in the middle Oligocene ca. 27.37 Ma (23.3–31.34), which is concordant with the earlier estimate of

Grismer et al. (2016) of 28.1 Ma. A basal split within the genus *Ceratophora* is estimated to have taken place in the early Miocene ca. 19.94 Ma (17.06–22.77), which is slightly earlier than the previous estimate by Schulte et al. (2002), who suggested that the radiation of *Ceratophora* took place in mid-Miocene (13 Ma). The divergence between the ancestors of *C. aspera* and the newly discovered *Ceratophora* sp. from Salgala Forest likely happened in late Miocene, ca. 7.8 Ma (5.43–10.54).

Rostral appendage evolution analysis. In both sexes, the Pagel's λ was close to unity and differed significantly from zero ($p < 0.05$) in most of the characteristics of body size (SVL, JL, HD, and all their \log_{10} -transformed values), indicating a strong phylogenetic signal. The only exception was jaw length in females, for which the Pagel's λ was insignificant ($p = 0.1$). The Pagel's λ values in all measures of the rostrum (length, maximum depth, \log_{10} -transformed length and depth, length and depth relative to SVL, and residuals from the regression

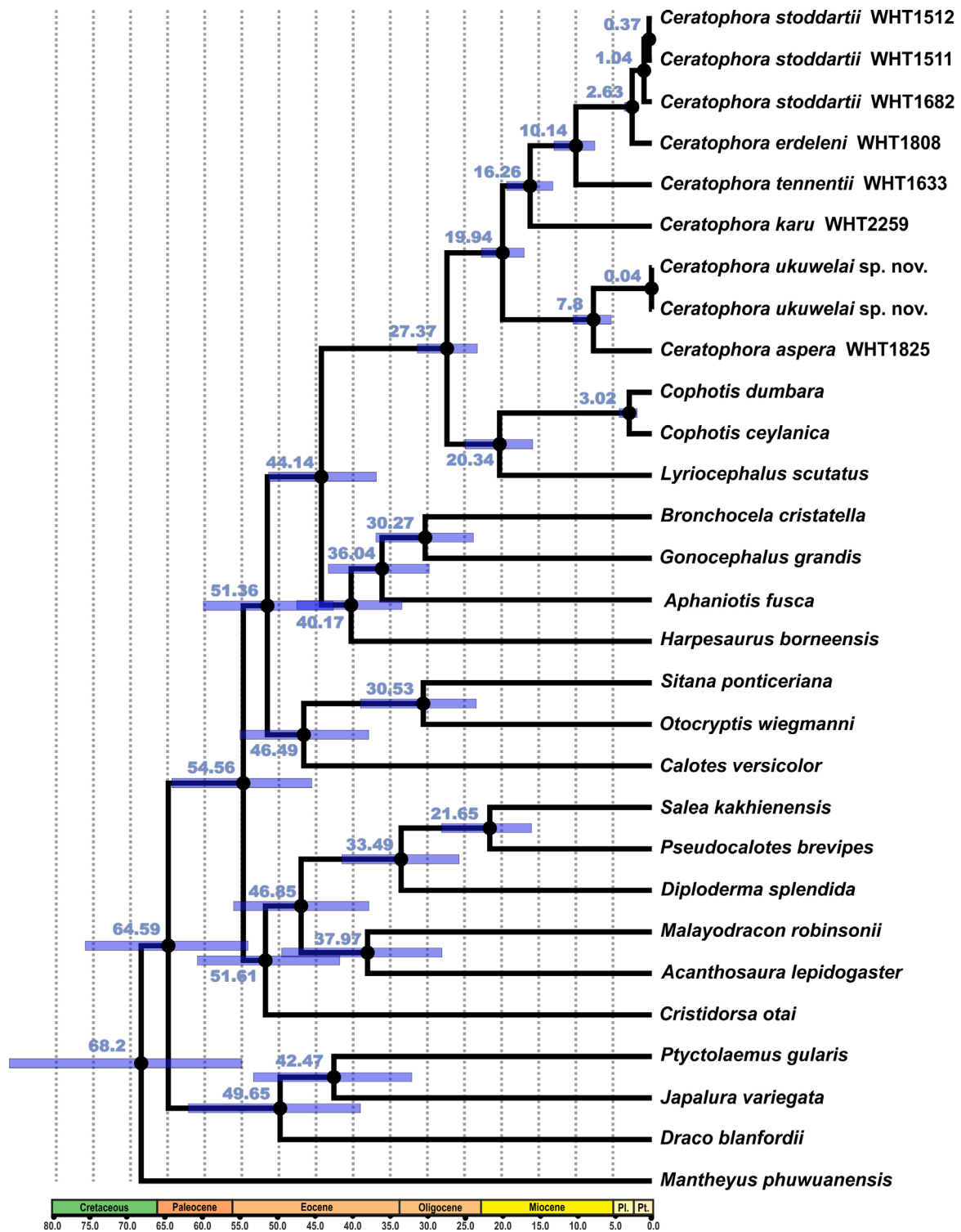


Fig. 3. Bayesian chronogram for Draconinae resulting from BEAST analysis of 1,084 bp of *ND2* gene sequences. Node values correspond to estimated divergence times (in Ma). Blue bars correspond to 95% confidence intervals.

of rostrum length on SVL) were not significantly different from zero ($p = 1$), indicating an absence of phylogenetic signal (see Table 4). The reconstruction of ancestral states for relative rostrum length suggests the presence of RA in tMRCA of *Ceratophora*, *Cophotis*, and *Lyriocephalus* for both sexes and contrasting patterns of RA evolution in males and females (Fig. 4).

Systematics

The results of the updated *ND2*-based genealogy of Sri Lankan agamids are largely consistent with the earlier phylogenies of Schulte et al. (2002), Grismer et al. (2016), Wang et al. (2019), and Kurita et al. (2020). This analysis suggests that the population of *Ceratophora* sp. from

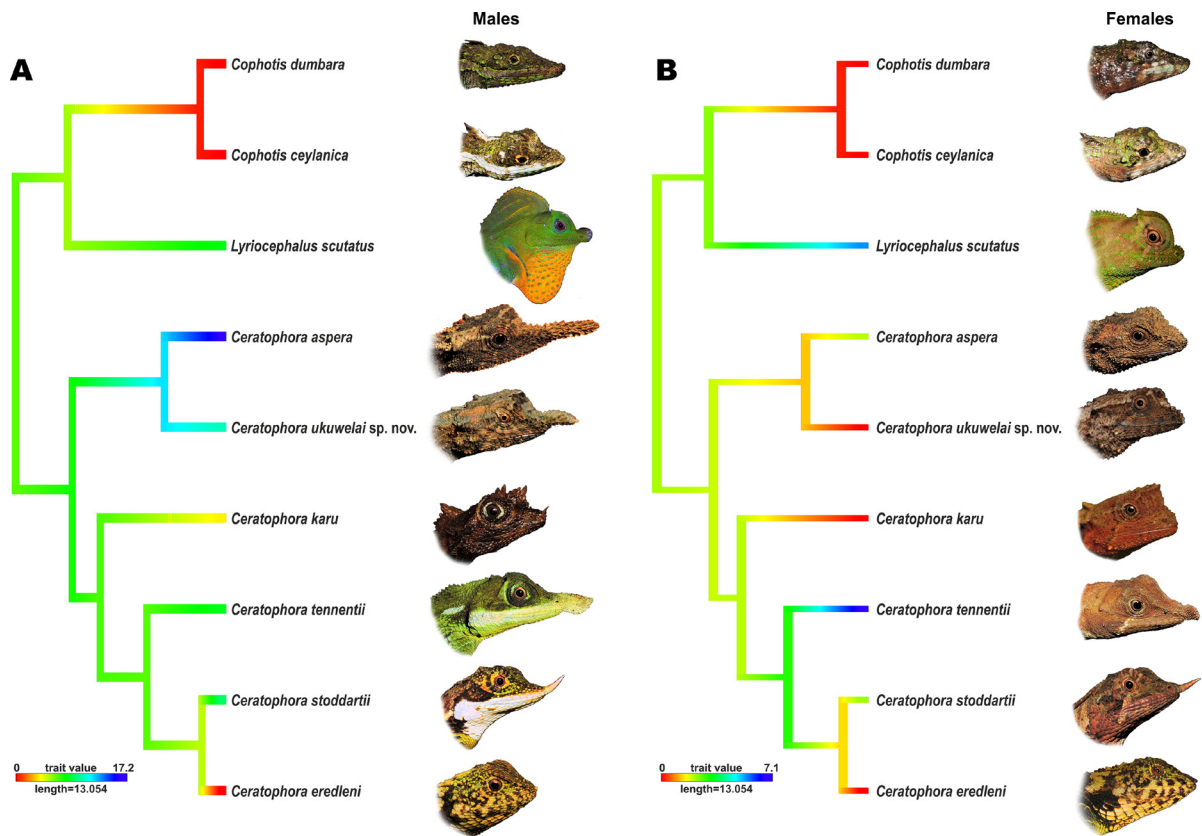


Fig. 4. Relative rostral appendage (RAL/SVL) evolution among members of the Sri Lankan agamids (genera *Ceratophora*, *Lyriocephalus*, and *Cophotis*). See Table 2 for RAL/SVL data. Colors of branches correspond to average RAL/SVL values in males (**A**) and females (**B**); thumbnails show profiles of the respective lizard species (not to scale). Photos by Sanoj Wijayasekara, Sanjaya Kanishka, and Suranjan Karunarathna.

Salgala Forest represents a divergent mtDNA lineage sister to *C. aspera*, with a species-level divergence of this population in the *ND2* gene ($p = 9.6\%$). The early (late Miocene) split between these two lineages, along with a number of diagnostic morphological characters which distinguish *Ceratophora* sp. from Salgala Forest from *C. aspera* and from other congeners (see **Comparisons**), suggest that *Ceratophora* sp. from Salgala Forest represents a currently undescribed species new to science which is described below.

Ceratophora ukuwelai sp. nov.

Figs. 5–6; Tables 5–6.

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Holotype. NMSL 2020.05.01, adult female, 37.9 mm SVL, collected from rainforest flow neighboring a stream, Salgala Forest, Kegalle District, Sri Lanka (7.120219°N, 80.251892°E, WGS1984; elevation 242 m; around 1100 h) on 22 August 2019 by Suranjan Karunarathna and Anسلم de Silva.

Paratype. NMSL 2020.05.02, adult female, 36.4 mm SVL, collected from rainforest flow neighboring a stream,

Salgala forest, Kegalle District, Sri Lanka (7.074361°N, 80.249797°E, WGS1984; elevation 269 m; around 1000 h) on 22 August 2019 by Suranjan Karunarathna and Anسلم de Silva.

Diagnosis. The new species is assigned to the genus *Ceratophora* on the basis of phylogenetic data and by having a rostral appendage developed in males, absent in females; tympanum covered with skin; nuchal crest indistinct; dorsal crest absent; tail not prehensile; gular fold comparatively reduced; and scales on flanks heterogeneous, some scales greatly enlarged. *Ceratophora ukuwelai* sp. nov. can be readily distinguished from its congeners by a combination of the following morphological and meristic characteristics: rostral appendage complex, comprising several scales; maximum SVL 37.9 mm; trunk relatively long (TRL/SVL ratio 51.4–52.6%) with relatively short fore-body (SA/TRL ratio 90.2–90.9%); nuchal crest feebly defined; squamosal process present; dorsum with heterogeneous, keeled scales, intermixed with smooth flat scales; almost all scales on head, body, limbs, and tail bearing 1–18 mechanoreceptive pores (in a single scale), each pore with a sensory seta; 5–7 enlarged, keeled scales present on body flanks; nine supraciliary scales; 40–44 paravertebral scales; 72–77 midbody scales; 72–75

Table 3. Uncorrected *p*-distances (percentage) between the *ND2* mtDNA gene sequences (below the diagonal), estimate errors (above the diagonal), and intraspecific genetic *p*-distance (on the diagonal) of Sri Lankan agamid species of the genera *Ceratophora*, *Cophotis*, and *Lyriocephalus*.

Species	1	2	3	4	5	6	7	8	9
1 <i>Ceratophora stoddartii</i>	0.8	0.5	1.0	1.1	1.0	1.1	1.0	1.1	1.1
2 <i>Ceratophora erdeleni</i>	3.8	—	1.0	1.1	1.0	1.1	1.1	1.2	1.2
3 <i>Ceratophora tenmentii</i>	10.7	12.5	—	1.2	1.2	1.1	1.2	1.1	1.2
4 <i>Ceratophora karu</i>	18.1	18.7	16.5	—	1.2	1.5	1.2	1.1	1.2
5 <i>Ceratophora aspera</i>	18.8	20.4	18.7	20.6	—	0.9	1.0	1.1	1.0
6 <i>Ceratophora ukuwelai</i> sp. nov.	20.6	21.5	19.2	23.0	9.6	—	1.1	1.1	1.1
7 <i>Cophotis ceylanica</i>	19.8	20.8	20.5	21.2	22.9	24.4	—	0.7	1.0
8 <i>Cophotis dumbara</i>	20.1	21.2	20.6	20.0	22.5	24.3	4.7	—	1.1
9 <i>Lyriocephalus scutatus</i>	22.4	22.8	22.1	23.1	22.7	24.6	17.9	18.7	—

midventral scales. The new species is also clearly distinct from all other congeners in *ND2* gene sequences (divergence over 9.6%).

Description of holotype. An adult female, 37.9 mm SVL and 42.6 mm original TAL (Fig. 5), in a good state of preservation (however, 15 mm of the tail was used for the molecular work). For counts and measurements of the holotype see Tables 5–6. Body slender, relatively long (TRL/SVL ratio 51.4%). Head relatively large (HL/SVL ratio 30.0% and HL/TRL ratio 58.5%), broad (HW/SVL ratio 17.8% and HW/HL ratio 59.3%), partly depressed (HD/SVL ratio 14.4% and HD/HL ratio 47.8%), and distinct from neck. Snout relatively long (ES/HW ratio 56.8% and ES/HL ratio 33.7%), less than twice orbit diameter (OD/ES ratio 84.4%), more than half length of jaw (ES/JL ratio 51.5%), snout slightly concave in lateral view; orbit relatively large (OD/HL ratio 28.4%), pupil rounded; orbit length slightly greater than IV digit of manus (OD/DLM IV ratio 100.6%); supraocular rim moderately developed; supraciliaries uplifted; two rows of scales separate orbit from supralabials; interorbital distance is shorter than snout length (IO/ES ratio 49.2%), shorter than head length (IO/HL ratio 16.6%), eye to nostril distance greater than the interorbital distance (EN/IO ratio 102.6%).

Dorsal, lateral, and ventral surfaces of the head, trunk, and tail with keeled scales intermixed with smooth heterogeneous, small and large scales, each scale with at least one or more pores (up to 18) bearing a sensory seta; rostral horn absent, rostral scales very small; snout convex, scales on snout keeled and raised, smaller than those on interorbital and occipital regions; canthus scales present, 11/10 keeled conical scales from eye to nostril; nasal scale large, nostril rounded and located in the middle of an undivided nasal scale, not in contact with supralabials; scales of the interorbital region heterogeneous, intermixed with smooth scales; palpable squamosal process present. Nuchal crest not prominent, 1–3 pointed and ridged scales on the neck; supralabials 12/12 keeled, infralabials 13/12 keeled, becoming

smaller towards the gape. Two scale rows separate orbit from supralabials. Sharp and conical tubercles present both on the sides of the neck and around the gape; tympanum hidden under skin; enlarged, keeled, and flat scales present on tympanum area; 44 paravertebral scales, four diamond shaped markings with three black

Table 4. The calculated Pagel's λ for SVL, head, and rostral appendage measurements for males and females of Sri Lankan agamids of the genera *Ceratophora*, *Cophotis* and *Lyriocephalus*. Asterisks denote *p*-values indicating significant differences of Pagel's λ from zero ($*p < 0.05$; $**p < 0.01$). Residual RAL and Residual Log RAL represent the residuals after regression of RAL and Log RAL on SVL and log SVL, respectively. PGLS means that phylogenetic signal in the residual error was simultaneously estimated with the phylogenetic regression parameters (the regression formula is in parentheses).

Character	Pagel's λ	
	Males	Females
SVL	1.10**	1.05*
Log SVL	1.10**	1.04*
JL	1.10**	1.02
Log JL	1.10**	1.04
HD	1.11**	1.09**
Log HD	1.09*	1.09*
RAL	0.00	1.04
Log RAL	0.11	0.00
Max RAD	1.06	1.09*
Log Max RAD	0.00	0.00
Relative RAL (to SVL)	0.46	0.00
Relative RAD (to SVL)	0.93	1.07
Residual RAL	0.00	1.09
Residual Log RAL	0.07	0.00
PGLS(RAL~SVL)	0.00	0.00
PGLS(RAD~SVL)	0.00	0.00
PGLS(LogRAL~LogSVL)	0.00	0.00
PGLS(LogRAD~LogSVL)	0.00	0.00

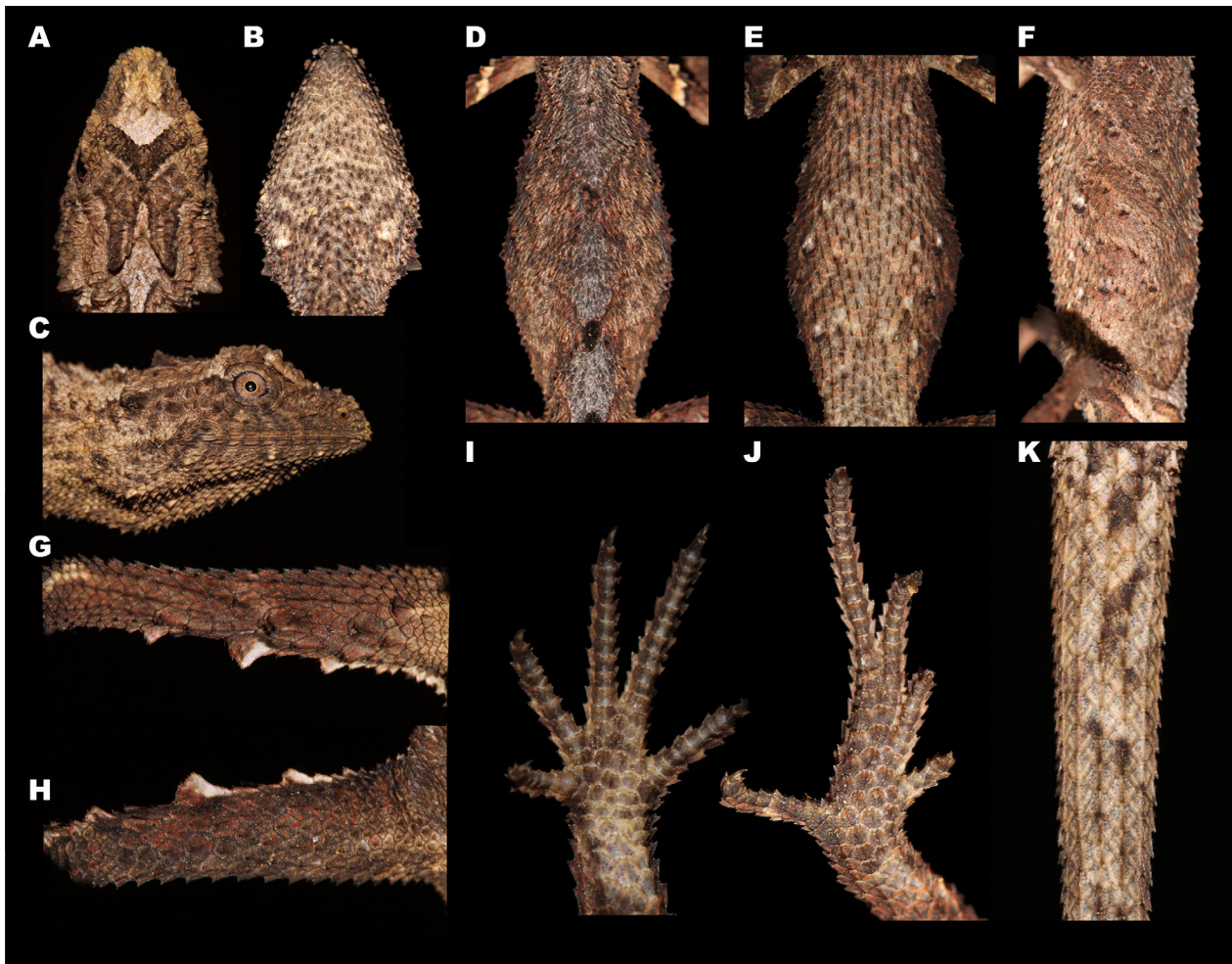


Fig. 5. Morphology of *Ceratophora ukuwelai* sp. nov. holotype, adult female (NMSL 2020.05.01). (A) Head in dorsal view; (B) head in ventral view; (C) head in lateral view; (D) heterogeneous scales on dorsal surface of trunk; (E) keeled ventral scales; (F) lateral surfaces of trunk showing heterogeneous scales; (G–H) dorsal and ventral surfaces of femur showing sharp spines; (I) subdigital lamellae on manus; (J) subdigital lamellae on pes; (K) hexagonal-shaped subcaudals. Photos by Suranjan Karunaratna.

dots present on vertebral line; 77 midbody scales; lateral scales irregular and keeled, intermixed with 5/6 enlarged scales on the flanks.

Ventral surfaces covered with keeled scales, each scale with one or more mechanoreceptive pores; mental semicircular in shape, small, posteriorly in contact with three small postmentals (smaller than naris, chin scales, and rostral scales), in contact with the 1st infralabial. Gular fold short and its length is approximately 22.6% of SVL, but dispersed and its depth is approximately 60.3% of HD. Ventral scales pentagonal, subimbricate, ventral scales larger than chin scales, dorsal scales, and lateral scales, 75 ventral scales; keeled scales around vent and base of tail; no precloacal or femoral pores; original tail of holotype longer than the snout-vent length (TAL/SVL ratio 112.3%), heterogeneous scales on the dorsal aspect of the tail directed backwards, spine-like scales present on tail; subcaudals keeled and small, subrhomboidal, arranged in a single median series. Forelimbs long, slender, upper arm longer than lower arm (LAL/SVL ratio 15.9% and UAL/SVL ratio 17.8%); hindlimbs long, tibia slightly shorter than the femur (TBL/SVL ratio 22.8% and

FEL/SVL ratio 23.7%). Anterior, dorsal, posterior, and ventral surfaces of forelimbs and hindlimbs with strongly keeled and less imbricate scales; anterior surfaces twice as large as those of the other surfaces of both limbs; posterior edges of femur and tibia with six large, conical scales.

Dorsal and ventral surfaces of manus and pes with keeled granules; dorsal surfaces of digits with granular scales. Digits elongate and slender with inflected distal phalanges, all bearing slightly recurved claws. Subdigital lamellae on digits entire, notched; lamellae on manus (left/right): digit I (7/6), digit II (9/9), digit III (13/12), digit IV (13/13), digit V (9/8); total lamellae on pes (left/right): digit I (6/6), digit II (8/7), digit III (8/8), digit IV (15/14), digit V (7/7); interdigital webbing absent; relative length of left manual digits: I (1.8 mm), V (2.1 mm), II (2.5 mm), III (2.9 mm), IV (3.2 mm); relative length of left pedal digits: I (1.6 mm), II (2.2 mm), III (2.8 mm), V (3.3 mm), IV (5.7 mm).

Variation. Measurements and morphological characters of the type series are given in Tables 5–6. The female paratype is generally similar to the holotype in body

Table 5. Morphometric data for two syntypes of *Ceratophora aspera* and two types of *C. ukuwelai* **sp. nov.** from Sri Lanka (all in mm).

Measurement	<i>C. aspera</i>		<i>C. ukuwelai</i> sp. nov.	
	BMNH. 1946.8.30.52 Male	BMNH. 1946.8.30.51 Female	NMSL. 2020.05.01 Female	NMSL. 2020.05.02 Female
SVL	28.1	36.5	37.9	36.4
TRL	11.6	16.2	19.5	19.1
HL	8.5	9.7	11.4	11.1
HW	5.5	6.1	6.8	6.6
HD	4.6	5.4	5.5	5.4
RAL	2.1	-	-	-
SA	13.2	17.5	17.7	17.2
JL	5.7	5.8	7.5	7.4
TAL (original)	40.7	42.3	42.6	41.2
OD	3.1	2.9	3.2	3.2
EN	2.1	1.9	1.9	1.9
ES	3.2	2.1	3.8	3.6
SN	1.2	0.9	1.3	1.3
IO	2.2	2.4	1.9	1.9
UAL	5.2	6.3	6.8	6.7
LAL	4.4	5.3	6.0	5.9
PAL	3.5	4.8	6.5	6.5
DLM (i)	1.5	1.9	1.8	1.8
DLM (ii)	2.1	2.5	2.5	2.4
DLM (iii)	2.6	2.9	2.9	2.8
DLM (iv)	2.9	3.1	3.2	3.1
DLM (v)	1.8	2.2	2.1	2.2
FEL	7.3	7.5	9.0	8.9
TBL	6.6	7.4	8.7	8.5
HEL	7.9	9.2	9.5	9.3
DLP (i)	1.1	1.5	1.6	1.5
DLP (ii)	1.6	2.3	2.2	2.1
DLP (iii)	2.6	3.8	2.8	2.7
DLP (iv)	4.3	6.5	5.7	5.5
DLP (v)	2.4	2.9	3.3	3.2

proportions and coloration; the SVL of adult female specimens in the type series of *Ceratophora ukuwelai* **sp. nov.** ($n = 2$) ranges from 36.4 to 37.9 mm; enlarged flank scales 5–7; supralabials 12–13; infralabials 11–12; postmentals 3–4; interorbital 9–10; canthal scales 10–11; total lamellae on digit of the manus: digit I (6–7), digit II (8–9), digit III (12–13), digit IV (12–13), digit V (8–9); total lamellae on digit of the pes: digit I (6–7), digit II (7–8), digit III (7–8), digit IV (14–16); paravertebral granules 40–44; midbody scales 72–77; ventral scales 72–75 (see Tables 5–6). Because the holotype and paratype of the new species are females, sexual dimorphism could

not be determined. However, a single male specimen of *Ceratophora ukuwelai* **sp. nov.** was recorded at the type locality and photographed in life (Fig. 6B). Male specimen possessed long (RAL/SVL ratio 11.26%) complex rostral appendage, comprised of numerous keeled acuminate scales, including posterostral scales and a pointed enlarged scale on the top.

Color of living specimens. In life, dorsum of head, body, and limbs generally grey-brown (Fig. 6); forehead with white blotch, interorbital area with a ‘Y’ shaped brown marking, occiput area with a ‘W’ shaped dark marking;

Table 6. Meristic data of two syntypes of *Ceratophora aspera* and two types of *C. ukuwelai* sp. nov. from Sri Lanka.

Measurement	<i>C. aspera</i>		<i>C. ukuwelai</i> sp. nov.	
	BMNH. 1946.8.30.52 Male	BMNH. 1946.8.30.51 Female	NMSL. 2020.05.01 Female	NMSL. 2020.05.02 Female
FLSP (L/R)	10/9	11/10	5/6	7/6
SUP (L/R)	10/9	10/11	12/12	13/12
INF (L/R)	10/11	10/9	12/12	11/12
PM	4	4	3	4
SUS (L/R)	12	14	9	9
INOS	13	15	10	9
CAS (L/R)	14/13	12/13	11/10	11/10
TLM (i) (L/R)	7/8	6/5	7/6	6/6
TLM (ii) (L/R)	9/10	6/8	9/9	8/9
TLM (iii) (L/R)	12/13	10/12	13/12	12/12
TLM (iv) (L/R)	14/12	12/11	13/13	13/12
TLM (v) (L/R)	9/9	8/7	9/8	8/8
PS	58	52	44	40
MBS	61	57	77	72
MVS	92	95	75	72
TLP (i) (L/R)	6/5	7/6	6/6	7/6
TLP (ii) (L/R)	7/8	6/8	8/7	7/7
TLP (iii) (L/R)	13/12	10/9	8/8	8/7
TLP (iv) (L/R)	16/17	14/14	15/14	16/15
TLP (v) (L/R)	9/8	7/8	7/7	7/7

four grey diamond-shaped vertebral markings with black dots. Tail generally brown with faded zigzag markings. Two brown postorbital stripes on each side with striped labials (Fig. 5). Chin, gular, and ventral scales dirty white mixed with red-brown. Dorsal surface of upper and lower arm with white ring around. Posterior side of femur with white longitudinal spine line, tibia with white ring around. Iris copper-orange; pupil black. Inner surfaces of mouth cavity bluish-grey. A male specimen (not collected) showed generally similar but slightly darker coloration than the female type (Fig. 6B).

Color of preserved specimens. After preservation in ethanol for one year, coloration pattern of type specimens resembles that observed in life. Dorsally specimens turned dark brown with four distinct diamond-shaped markings on vertebrae; interorbital area with a Y-shaped dark marking; both limbs with dirty white rings. Ventral surfaces turned grey-brown.

Etymology. The specific epithet is a Latinized eponym in the masculine genitive singular, honoring evolutionary biologist and herpetologist Dr. Kanishka Ukuwela (Rajarata University) for his invaluable contribution to biodiversity studies and conservation in Sri Lanka.

Suggested common names. Ukuwelas' Rough-horn Lizard (English), Ukuwelage ralu-ang katussa (Sinhala).

Comparisons with other Sri Lankan species. The new species, *Ceratophora ukuwelai* sp. nov., readily differs from *Ceratophora aspera* by the presence of fewer supraciliary scales (9 versus 12–14), fewer paravertebral scales (40–44 versus 52–58), greater midbody scales (72–77 versus 57–61), fewer ventral scales (72–75 versus 92–95), trunk relatively long (TRL/SVL ratio 51.4–52.6% versus 41.3–44.5%), and fore-body relatively short (SA/TRL ratio 90.2–90.9% versus 107.6–113.9%). Differs from *Ceratophora erdeleni* by the presence of a long, complex, and rough rostral appendage in males (versus short, simple, and smooth rostral appendage), lateral scales keeled (versus lateral scales smooth), relatively small bodied, average SVL of adults (37 mm versus 80 mm), found in lowland wet zone (below 300 m versus above 900 m). Differs from *Ceratophora karu* by the presence of long and rough rostral appendage in males (versus short, pointed, and relatively smooth rostral appendage), no prominent and conical shaped superciliary (versus very prominent and conical shaped superciliary presents), squamosal process present (versus squamosal process absent), found in

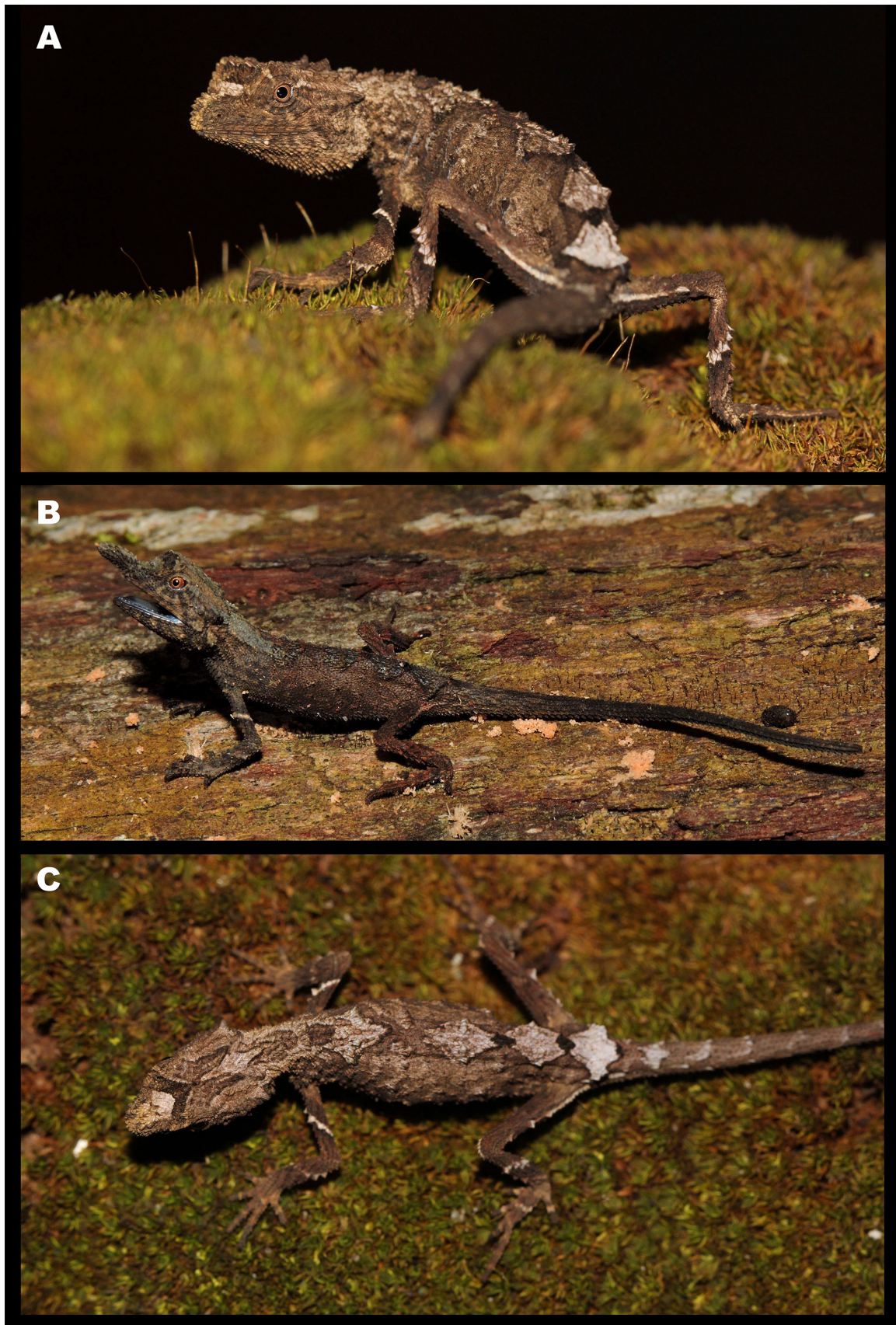


Fig. 6. *Ceratophora ukuwelai* **sp. nov.** in life *in-situ*. **(A)** Female holotype (NMSL 2020.05.01) in dorsolateral view; **(B)** male specimen (not collected) in dorsolateral aspect showing rostral appendage; **(C)** female paratype (NMSL 2020.05.02) in dorsal view. Photos by Suranjan Karunaratna and Sanjaya Kanishka.



Fig. 7. Habitat of *Ceratophora ukuwelai* **sp. nov.** at type locality in Salgala Forest, Kegalle District, Sri Lanka. **(A)** General view of Salgala Forest; **(B)** microhabitat of the new species inside the dense forest with good canopy cover and thick leaf litter. Photos by Suranjan Karunaratna.

lowland wet zone (below 300 m versus above 900 m). Differs from *Ceratophora stoddarti* by the presence of long, complex, and rough rostral appendage in males (versus long, simple, and smooth rostral appendage), lateral scales keeled (versus lateral scales smooth), relatively small bodied, average SVL of adults (37 mm versus 80 mm), found in lowland wet zone (below 300 m versus above 800 m). Differs from *Ceratophora tennentii* by the presence of rough and relatively round shaped rostral appendage in males (versus smooth and laterally flattened rostral appendage), lateral scales keeled (versus lateral scales smooth), relatively small bodied, average SVL of adults (37 mm versus 80 mm), found in lowland wet zone (below 300 m versus above 800 m).

Distribution and natural history. The type locality, Salgala Forest (7.109631–7.129028°N, 80.243444–80.263494°E; Kegalle District, Sabaragamuwa Province), is located in the lowland at elevations of 120–325 m asl. The area falls within the northern border of the wet bioclimatic zone, where tropical evergreen rainforests comprise the dominant vegetation type (Gunatilleke and Gunatilleke 1990). The forest acreage is approximately 150 ha and Salgala forest is isolated from other forest massifs by the Kelani River and Maha River valleys, numerous perennial middle-order streams, and human modified cultural landscapes such as tea plantations. The mean annual rainfall in the area varies between 2,500 and 3,500 mm, most of it is received during the southwest monsoon (May–September), while the mean

annual temperature is around 29.2 °C. Salgala is rich in tall rainforest trees and the forest floor contains thick leaf litter. Numerous smaller streams are present within the type locality. *Ceratophora ukuwelai* **sp. nov.** appears to be an elusive and rare species in Salgala as only five individuals were recorded during 10 field excursions (nearly 500 person-hours). Specimens of the new species were recorded on the forest floor in dense forest patches with thick and wet leaf litter under dense canopy cover (Fig. 7). The microhabitat of *Ceratophora ukuwelai* **sp. nov.** was a poorly illuminated (light intensity: 455–687 Lux), relatively moist, canopy-shaded (relative humidity: 72–84% and canopy cover: 70–85%), and relatively warm environment (substrate temperature: 27.7–28.2 °C) by the time of our survey. The new species was recorded in sympatry with several other agamid lizard species, including *Calotes calotes* (Linnaeus, 1758), *Calotes liolepis* Boulenger, 1885, *Calotes versicolor* (Daudin, 1802), and *Otocryptis wiegmanni* Wagler, 1830.

Conservation status. Application of the IUCN Red List criteria indicates that *C. ukuwelai* **sp. nov.** has to be considered a Critically Endangered (CR) species due to having an area of occupancy (AOO) < 10 km² (four locations, 0.12 km² in total assuming a 100 m radius around the georeferenced locations) and an extent of occurrence (EOO) < 100 km² (0.26 km²) in Kegalle District, Sabaragamuwa Province of southwestern Sri Lanka [Applicable criteria B2-b (iii)] (IUCN Standards and Petitions Subcommittee 2016).

Discussion

In 1864, Albert Günther described a new horned lizard, which he named *Ceratophora aspera*, from Ceylon (historical name of Sri Lanka) based on the collections sent to London by Hugh Cuming (Günther 1864; Amarasinghe et al. 2009). However, Günther mentioned that *C. aspera* probably came from the montane part of Sri Lanka, likely from the same source as the specimens of *C. stoddartii* and *C. tennentii* (Günther 1861, 1864). Most of the species described by Günther from Cuming's collection are now known to be restricted to the south-west wet zone of Sri Lanka (Pethiyagoda 2007; Meegaskumbura et al. 2008; Amarasinghe et al. 2009; Sudasinghe and Pethiyagoda 2019), suggesting that this area likely corresponds to the type locality of *C. aspera*. Additionally, we examined the two syntypes of *C. aspera* housed in British Museum of Natural History (female BMNH.1946.8.30.51, and male BMNH.1946.8.30.52) [Fig. 8] and obtained the morphometric and meristic characters from these specimens for comparison. The Salgala population described herein as *Ceratophora ukuwelai* **sp. nov.** originates from the northern border of the wet bioclimatic zone (Kegalle District), and so *C. aspera* populations are restricted to the southern part of the wet bioclimatic zone (Galle District). However, this



Fig. 8. Syntypes of *Ceratophora aspera* Günther, 1864 in lateral view: BMNH.1946.30.51 (female, above) and BMNH.1946.30.52 (male, below). Photo by Colin McCarthy (BMNH).

study revealed a number of taxonomically important morphological differences between these populations, and demonstrated that they are also genetically distinct (p -distance 9.6%). The southern and northern populations of this complex are separated by 115 km direct distance (Fig. 1) and by the valleys of the Attanagalu, Kelani, Kalu, and Gin rivers and a number of mountain ridges. These geographical barriers have likely impeded gene flow, resulting in reproductive isolation. The molecular dating analysis suggested that *Ceratophora ukuwelai* **sp. nov.** and *C. aspera* have been separated presumably since the late Miocene. These results continue to underscore the high degree of site-specific endemism in isolated forest patches within the lowland areas of wet bioclimatic zone in Sri Lanka (e.g., Manamendra-Arachchi and Pethiyagoda 2005; Meegaskumbura and Manamendra-Arachchi 2005; Agarwal et al. 2017; Karunaratna et al. 2019; Danushka et al. 2020) and the need for additional field research throughout these insular habitats.

The most recent discovery of new species in the genus *Ceratophora* was the description of *C. erdeleni* and *C. karu* from Rakwana Hills over two decades ago (Pethiyagoda and Manamendra-Arachchi 1998). Most *Ceratophora* species are rare, range-restricted endemics. At present, *C. tennentii* is restricted to the Knuckles Hills, and *C. stoddartii* occupies the Central Highlands; while *C. erdeleni* and *C. karu* are restricted to the Rakwana Hills (Fig. 1). *Ceratophora aspera* was

once thought to be a more widely ranging species with a patchy distribution across the lowland tropical rainforests within the wet bioclimatic zone of Sri Lanka. This study demonstrates that the northernmost portion of its range actually harbors a new species, *Ceratophora ukuwelai* **sp. nov.**, while *C. aspera sensu stricto* appears to be restricted to the southern part of the wet bioclimatic zone (Fig. 1). Further studies of morphological and genetic variation across the isolated populations of *C. aspera* are needed to assess the true taxonomic diversity and extend of distribution of *Ceratophora* species in Sri Lanka.

In the present paper we recommend that *Ceratophora ukuwelai* **sp. nov.** be listed as a Critically Endangered (CR) species. The infrequent encounter rates of this species in its habitat and continuing habitat loss are the primary reasons for our conservation status assessment. In addition, Sri Lanka's southwestern lowland rainforests are severely fragmented; as such, edge effects and concomitant micro-environmental changes and subsidized predation risk could further endanger this species. The threats to agamid lizards would appear to stem largely from habitat loss and fragmentation. The impacts of fragmentations could also be exacerbated by the fact that many important montane forest fragments are surrounded by vegetable and tea plantations. Worse yet, vegetable cultivation in Sri Lanka involves the intensive and indiscriminate application of pesticides (Karunaratna et al. 2017), which can reduce the

agamids' prey base. In addition, the bioconcentration of pesticides in lizards has been well documented in other tropical realms (Campbell and Campbell 2000, 2002; Khan and Law 2005). Highways also pose a threat to animals, not only by means of habitat fragmentation, but also by resulting in direct mortality in terms of incidental roadkills. The asphalt surfaces of these highways reach thermally intolerable levels, which could induce physiological stress. The exotic pet trade and alien invasive species are growing threats for Sri Lankan lizards (Karunaratna and Amarasinghe 2013; Janssen and de Silva 2019). In addition, predation by feral or domestic cats can also result in considerable mortality among agamids (Arnaud et al. 1993; Tyler et al. 2016). Further studies on the natural history and behavior of endemic lizards of Sri Lanka are essential for better planning and implementation of scientific conservation and management programs (Karunaratna et al. 2011). The promotion of ecological and behavioral studies in schools and universities is required for assessing habitat fragmentation and human impacts on Sri Lankan endemic agamid lizards (Manamendra-Arachchi and Liyanage 1994; Karunaratna and Amarasinghe 2013). Further development of public awareness workshops and conservation action plans are necessary for the conservation of agamid species. Reducing road kills at road crossings and migration routes and further development of public awareness through the organization of workshops are important steps for the implementation of a conservation action plan for Sri Lankan agamid conservation (Karunaratna et al. 2013). We are also unaware of any substantial *ex-situ* efforts in the captive breeding of agamids. Sri Lanka's zoological and botanical gardens should explore the feasibility of such efforts.

Our updated phylogeny for Sri Lankan agamids allowed us to re-analyze patterns of possible evolution of the rostral appendage—a bizarre morphological structure characteristic to the genus *Ceratophora* (Fig. 4). A high phylogenetic signal in body size traits in Sri Lankan agamids was found, which is not surprising for such morphological traits and was demonstrated earlier for a number of lizard groups (Freckleton et al. 2002; Ashton 2004; Brandt and Navas 2011; Oufiero et al. 2011; Grizante et al. 2012; Hertz et al. 2013; Openshaw and Keogh 2014; Wegener et al. 2014; Mesquita et al. 2016). Pagel's $\lambda = 1$ implied that the evolution of these traits followed Brownian motion (Freckleton et al. 2002). Surprisingly, however, we have not detected phylogenetic signal in rostral appendage measurements. This could be related to the insufficient number of species in our analysis, but the high values of Pagel's λ in body size indicate that our sample size is sufficient to detect at least a high phylogenetic signal in traits. In the case of *Ceratophora*, phylogenetically closely related species may have opposing states for rostral appendage characters. Our analysis thus suggests that rostral appendage length and

depth have evolved largely independently of phylogeny. For example, the two sister species with minimal genetic divergence between them may show the presence (*C. stoddartii*) or absence (*C. erdeleni*) of RA in both sexes (Fig. 4; Table 2). Our reconstruction of ancestral states in RA evolution suggested that rostral ornamentation was likely present both in males and females of the common ancestor of the *Ceratophora* – *Lyriocephalus* – *Cophotis* clade (Fig. 4). The RA was subsequently lost in both sexes of *Cophotis* and *C. erdeleni*, reduced in both sexes of *C. karu* and females of *C. aspera* and *C. ukuwelai* **sp. nov.**, and enlarged in males of *C. aspera* and *C. ukuwelai* **sp. nov.**, and in females of *Lyriocephalus* and *C. tennentii*. However, the absence of phylogenetic signal in the evolution of RA structures in Sri Lankan agamids reported here makes the goal of robustly reconstructing the evolutionary history of this feature even more challenging.

Rostral appendages exhibit great variability in morphology, dimorphism, and ontogeny among the members of the *Ceratophora* – *Lyriocephalus* – *Cophotis* clade (Fig. 4). Several studies have addressed the problem of rostral appendage origin and evolution in *Ceratophora* species using parsimony (Schulte et al. 2002) and Bayesian (Johnston et al. 2012) approaches. Schulte et al. (2002) noted that the profound morphological differences observed among rostral structures of *C. aspera*, *C. stoddartii*, and *C. tennentii*, and the fact that these species do not form a clade, suggest three independent origins of these unusual ornaments in *Ceratophora*. Johnston et al. (2012) provided further morphological, allometric, and phylogenetic evidence suggesting that rostral appendages evolved three times within three separate lineages of *Ceratophora*. Johnston et al. (2012) further argued that in the case of *C. tennentii* it was likely driven by the natural selection for crypsis, while in *C. aspera* and *C. stoddartii* the independent origin of RA might be a result of sexual selection. Whiting et al. (2015) analyzed sexual dimorphism in RA parameters and coloration in *C. tennentii*, and did not find a correlation between these characters with bite force or body condition in this species. However, Whiting et al. (2015) assumed that RAL still might be a target of sexual selection and may serve as a cue used by females to assess some aspect of male quality. Our results generally agree with the hypothesis of Johnston et al. (2012) and provide further evidence that rostral appendages in Sri Lankan agamids likely evolved by several mechanisms, and more readily than in any other group of lizards. Further detailed studies of phylogeny and diversity within the *Ceratophora* – *Lyriocephalus* – *Cophotis* clade, along with research on the natural history of the comprising species, and a more thorough anatomical comparison of rostral structures, are needed to generate a more detailed and robust scenario of rostral appendage evolution in this group.

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Key to Sri Lankan species of genus *Ceratophora*

- 1a. Rostral appendage simple, restricted to rostral scale alone.....2
- 1b. Rostral appendage complex, comprising more scales than rostral alone.....3
- 2a. Rostral appendage rudimentary in both sexes (appendage is shorter than eye-nostril distance).....*C. erdeleni*
- 2b. Rostral appendage prominent in males (appendage is longer than eye-nostril distance).....*C. stoddartii*
- 3a. Rostral appendage laterally compressed.....*C. tennentii*
- 3b. Rostral appendage not laterally compressed.....4
- 4a. Squamosal process absent, represented by an enlarged scale.....*C. karu*
- 4b. A prominent squamosal process present.....5
- 5a. Trunk length is less than half of SVL and snout to axilla length is longer than trunk length (52–58 paravertebrals and 92–95 ventrals).....*C. aspera*
- 5b. Trunk length is more than half of SVL and snout to axilla length is shorter than trunk length (40–44 paravertebrals and 72–75 ventrals).....*Ceratophora ukuwelai* sp. nov.

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Appendix 1. Comparative materials examined.

Ceratophora aspera: BMNH.1946.30.51 (female), BMNH.1946.30.52 (male), WHT.0178 (male), WHT.1366 (female), WHT.1369 (male), WHT.1370 (female), WHT.1371 (male), WHT.2170 (male), WHT.1396 (female), WHT.1400 (male).

Ceratophora erdeleni: BMNH.1996.448 (holotype male), BMNH.1996.450 (paratype male), BMNH.1996.449 (paratype female), WHT.1328 (male), WHT.2070 (male), WHT.2172 (female), WHT.2175 (male).

Ceratophora karu: BMNH.1996.445 (holotype male), BMNH.1996.446 (female), BMNH.1996.447 (male), WHT.2065 (male), WHT.2067 (male), WHT.2068 (female).

Ceratophora stoddartii: BMNH.1946.8.27.37 (male), WHT.0209 (female), WHT.1170 (male), WHT.1327 (male), WHT.1700 (male), WHT.1702 (female).

Ceratophora tennentii: BMNH.1946.8.27.33 (syntype male), WHT.0103 (male), WHT.0114 (female), WHT.1350 (male).

Cophotis ceylanica: ZMB.4240 (lectotype), WHT.0177 (female), WHT.0516 (male), WHT.0645 (male), WHT.5817 (female), WHT.5818 (female), WHT.5819 (male).

Cophotis dumbara: CMS.2006.85.01 (male holotype), CMS.2006.85.02 (female paratype), WHT.6788 (male), WHT.6948 (male), WHT.6789 (female).

Lyriocephalus scutatus: WHT.0175 (female), NMSL.0462 (male), NMSL.0471 (male), NMSL.0485 (female).