

Morphological and molecular divergence of subspecies of Indian Bush Rats, *Golunda ellioti* Gray, 1837 (Rodentia: Muridae) from Sri Lanka

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Abstract: Genus *Golunda* is comprised of a single species of small bush rat endemic to southern Asia. In Sri Lanka, two subspecies are recognized, *Golunda ellioti ellioti* (Indian bush rat) and *G. e. nuwara* (Ceylon bush rat). These two subspecies can be differentiated by their tail length (longer in *G. e. ellioti* vs shorter in *G. e. nuwara*) fur type (short, harsh, spinous in *G. e. ellioti* vs long, soft and moderately fine in *G. e. nuwara*), colour of ventral pelage (light grey in *G. e. ellioti* vs bluish grey in *G. e. nuwara*) and microscopic hair anatomy (broader and shorter Guard Hair 1 with triangular and square shaped cross sections at the tip of the shield in *G. e. ellioti* vs narrower and longer Guard Hair 1 with circular to oval shaped cross sections in *G. e. nuwara*). In the present study, the divergence between the two subspecies was further evaluated using morphology (external and cranial) and molecular data (cytochrome-*b*, 16S and Rag 1 genes). We found that the brain case was comparatively rounded in *G. e. ellioti* and the interparietal bone was elongated in *G. e. nuwara*. Genetic distance between the two subspecies remain at subspecies level; 1.2% for cytochrome-*b*.

Keywords: coffee rat, taxonomy, mitochondrial genes, Peradeniya, Horton Plains.

INTRODUCTION

Golunda (Indian bush rat or Coffee rat), at present is a monotypic genus. During 1980's multiple species of *Golunda* were described from India and Sri Lanka, but they were all referred to a single species *Golunda ellioti* by Thomas (1923). Later, at least 10 subspecies were described, which are distributed in Southeast Iran, Pakistan, Nepal, India and Sri Lanka (Ellerman 1941). Of these, six are from India (*G. e. limitaris*, *G. e. pupera*, *G. e. watsoni*, *G. e. gujerati*, *G. e. bombax*, *G. e. caraginis*), one from Nepal (*G. e. myiothrix*), one from Bhutan (*G. e. coenosa*), one from Sri Lanka (*G. e. nuwara*) and one from India and Sri Lanka (*G. e. ellioti*). Ellerman, in 1947 and 1963, gradually reduced the number of subspecies synonymizing all but *G. e. nuwara* with the nominate subspecies. Agrawal and Chakraborty (1982) after studying in detail of the intraspecific variations of the Indian Bush rat from different geographical areas concluded that only *G. e. gujerati*, *G. e. nuwara* and *G. e. ellioti* are valid subspecies.

In Sri Lanka, Kelaart (1850) recognized two species

of *Golunda* (Kelaart, 1852), which were earlier described under the genus *Mus*: *Mus newera* "The Newera Eliya Soil Rat" and *M. ellioti* "Coffee rat". Later, both species were described as subspecies of *Golunda ellioti* [*G. ellioti newera*: later spelt as *nuwara* (Phillips 1980) and *G. e. ellioti*] by Phillips (1928). As stated by Phillips (1928), Kelaart was correct in describing two forms of *Golunda* from the island, as they can be readily distinguished from each other. *Golunda newera* can be distinguished from *G. ellioti* by their general colour of speckled yellowish olive brown and black, and long, untidy, soft fur. *Golunda ellioti*, on the other hand, has a general colour of sandy or tawny brown and black, with short, smooth and harsh fur, with the dorsal hairs very spinous. Even though these pelage characteristics are commonly associated with elevation gradient within species, Kelaart (1852) and Phillips (1928) regarded them as distinguishing characteristics. Though Phillips (1928) mentioned that the external and skull measurements were very much alike in the two species, Kelaart (1852) differentiated the two by body size and tail length also. *Golunda e. ellioti* has a longer tail proportionately to head and body size compared to *G. e. nuwara* (Kelaart, 1852; Phillips 1980; Agrawal and Chakraborty, 1982).

Golunda e. ellioti (Indian bush rat) is found throughout Southwestern lowland wet zone and mid country hills of Central and Uva provinces to approximately 900 m altitudes (Phillips, 1980). This subspecies has previously reported from Kalugala, Kegalle, Kantalai, Polonnaruwa, Baddegama, Ettakando, Palatupana, Hambantota, Attidiya and Dehiwala in Sri Lanka (Molur *et al.* 2005). *Golunda ellioti nuwara* (The Ceylon Bush-rat or Coffee-Rat), which is endemic to Sri Lanka, is confined to the jungles and swamps in the higher areas of the central mountains above altitudes of approximately 1200 m (Phillips, 1980). At medium altitudes the two subspecies meet and grade into one another (Phillips, 1980) but no studies have been conducted to show whether they interbreed or not.

A later study showed that the two subspecies could be differentiated by their microscopic hair anatomy. Cross sections at the tip of shield of Guard Hair 1 (GH 1) is triangular and square shaped in *G. e. ellioti*, while that of *G. e. nuwara* is circular to oval shaped (Figure 1). GH 1

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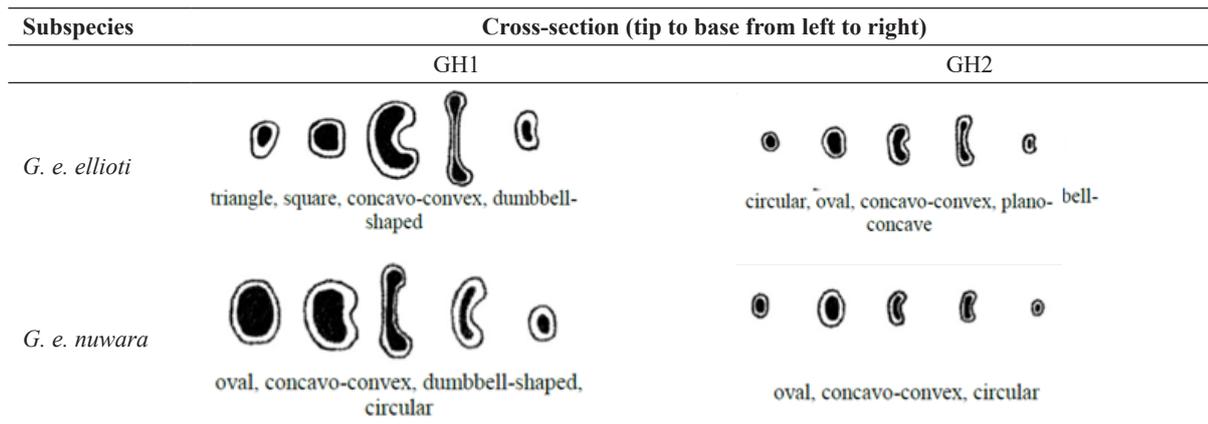


Figure 1: Cross sections at the tip of shield of Guard Hair 1 (GH1) and Guard Hair 2 (GH2) of *G. e. ellioti* and that of *G. e. nuwara* (Niroshani and Meegaskumbura, 2015)

Table 1: Width and length of Guard Hair 1 (GH1) and Guard Hair 2 (GH2) of *G. e. ellioti* and that of *G. e. nuwara* (Niroshani and Meegaskumbura, 2015)

Subspecies	GH1		GH2	
	Length (mm)	Maximum width (μm)	Length (mm)	Maximum width (μm)
<i>G. e. ellioti</i>	9.0-12.9 (11.1 \pm 0.9)	80-200 (146 \pm 43)	7.8-13.2 (11.0 \pm 1.6)	30-50 (37 \pm 8)
<i>G. e. nuwara</i>	14.0-21.1 (17.3 \pm 2.5)	60-90 (82 \pm 9)	12.9-17.1 (16.0 \pm 1.4)	30-50 (42 \pm 7)

of *G. e. ellioti* are broader and shorter compared to *G. e. nuwara*, however, Guard Hair 2 (GH2) dimensions overlap between the two subspecies (Table 1) (Niroshani and Meegaskumbura, 2015).

The subspecies are conceived of as genetically distinct, geographically separate populations belonging to the same species and therefore interbreeding freely at the zones of contact (Wilson and William, 1953). Taxonomic rank of subspecies has been a controversy for decades. Even though some are unwilling to accept subspecies as useful, others argue that they represent populations diverging towards species level diversification, hence an important taxonomic unit (Phillimore and Owens, 2006).

Golunda ellioti has been tested phylogenetically, where it falls with an African murine rodent *Hybomys univittatus* (Ducroz *et al.*, 2001). However, none of the subspecies have been analyzed molecularly. Hence, the objective of the present study was to further compare the two subspecies present in Sri Lanka using morphometrics, skull characters, genetic divergence and test their phylogenetic positions.

MATERIALS AND METHODS

Two specimens of *G. e. nuwara* from Horton plains and three specimens of *G. e. ellioti* from a grassland near a small coffee plantation in Peradeniya were collected. One hundred wire mesh cage traps baited with pieces of roasted coconut were used to collect specimens. A muscle sample was taken from each specimen and preserved in 90% ethanol for DNA analysis. Skulls were cleaned and skins were prepared. Two skulls of *G. e. nuwara* from the

National Museum, Sri Lanka were also included in the study. Their external measurements were collected from logbooks. Five external measurements [length of head and body (HBL), length of head (HL), length of tail (TL), length of hindfoot (HFL) and ear height (EH)], twenty-six skull measurements (Figure 2), external morphology and skull characters were used to compare subspecies. External and cranial measurements were not statistically analyzed because some of the specimens were sub-adults. All adults collected were females.

DNA was extracted from ethanol-preserved tissues using Promega tissue extraction kits following manufacturer's protocol. Two mitochondrial gene fragments (16S rRNA and cytochrome-*b*) and one nuclear fragment (Rag 1) were sequenced. DNA was amplified by PCR using 25 μl reactions containing 2.0 μl of template, 1.0 μl of each primer (10 μM), and 12.5 μl GoTaq Green master mix, topped with nano water. Thermal cycling for the Cytochrome-*b* fragment was as follows: 35 cycles of denaturation at 94 $^{\circ}$ C for 30 s, annealing at 45 $^{\circ}$ C for 30 s, and extension at 72 $^{\circ}$ C for 1 min, with a final extension of 72 $^{\circ}$ C for 5 min. The same conditions were used to amplify 16S, except that the annealing temperature of 48 $^{\circ}$ C. Thermal cycling for Rag 1 gene (819 bp) was as follows: 35 cycles of denaturation at 95 $^{\circ}$ C for 45 s, annealing at 55 $^{\circ}$ C for 45 s, and extension at 72 $^{\circ}$ C for 1 min, with a final extension of 72 $^{\circ}$ C for 5 min.

Cytochrome-*b* and 16S were amplified using the primers MVZ 05/ MVZ 14 and 16Sar/ 16Sbr, respectively. Primer sequences are as follows: MVZ 05 5' CGA AGC TTG ATA TGA AAA ACC ATC GTTG 3'; MVZ 14 5'

GGT CTT CAT CTY HGG YTT ACA AGAC 3'; 16S ar 5' CGC CTG TTT ATC AAA AAC AT 3'; 16S br 5' CCG GTC TGA ACT CAG ATC ACGT 3'. Sequence length of cytochrome-*b* and 16S were 1140 and 547 base pairs, respectively. Primers used for Rag 1 PCR were: AmpRAG1 F 5' AGC TGCAGY CAR TAC CAY AAR ATG TA 3'; Amp RAG1R1 5' AAC TCA GCT GCA TTK CCA ATR

TCACA 3'. Sequences were cleaned using ChromasPro 1.7.7 and phylogenies and uncorrected percentage genetic distance values for cytochrome-*b* gene were generated using MEGA 6 software. Sequences were submitted to the GenBank. Details of the taxa included in the study are presented in Table 2.

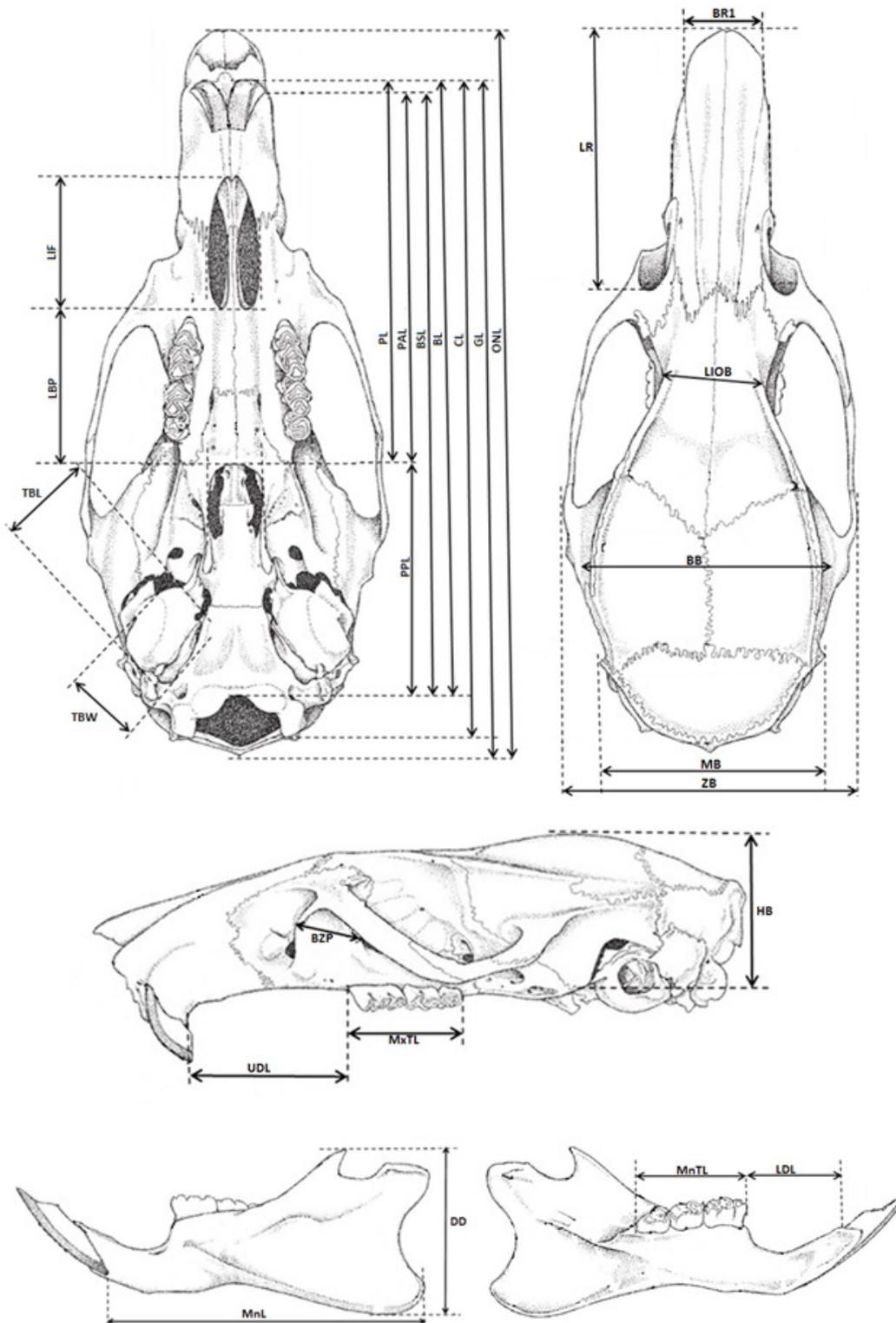


Figure 2: Dorsal, ventral and lateral views of cranium of a murine rodent (and mandible in the latter case), illustrating measurements taken in this study (refer Table 4 for abbreviations). (Figure modified from Musser *et al.*, 2006; measurements from Buttler and Greenwood, 1979; Musser *et al.*, 2006; Meegaskumbura *et al.*, 2007)

Table 2: Collection site, voucher numbers and GenBank accession numbers of gene sequences of taxa included in the study. Except *Tatera indica* from Pakistan and *Golunda ellioti* from India, all other specimens were collected from Sri Lanka.

Species	Collection site (Longitude, Latitude, Elevation; reference if the sequence was obtained from Genbank)	Voucher number	GenBank accession number of cytochrome-b/16S/Rag1 sequences
<i>Golunda ellioti ellioti</i>	Peradeniya (07°25'N, 80°59'E, elevation 488m)	PDZ 7	— / KY986860/ MN150143
	Peradeniya (07°25'N, 80°59'E, elevation 488m)	PDZ 11	KY986802/ KY986861/ XX000000
	Paymadu (National Museum, Colombo; collection date 13.09.1935)	75O	—
<i>Golunda ellioti</i>	India (Michaux et al. 2007)	—	AM408338/ —
<i>Golunda ellioti nuwara</i>	Horton Plains (06°80'N, 80°83'E, elevation 2150m)	WHT M 141	KY986801/ KY986862/ MN150145
	Horton Plains (06°80'N, 80°83'E, elevation 2150m)	WHT M 032	— / KY986863/ MN150144
	West Haputhale, Ohiya (National Museum, Colombo; collection date 12.08.1931)	75P	—
	West Haputhale, Ohiya (National Museum, Colombo; collection date 19.06.1931)	75M	—
<i>Bandicota indica</i>	Galle (06°03'N, 80°22'E, elevation 7.2m)	PDZ 43	KY697990/KY673247
<i>Rattus norvegicus</i>	Galle (06°03'N, 80°22'E, elevation 7.2m)	PDZ 44	KY697996/KY673255
<i>Rattus rattus kandinianus</i>	Udawalawe (06°47'N, 80°90'E, elevation 112.2m)	WHT 6926	KY697997/KY673254
<i>Mus cervicolor</i>	Agarapathana (06°87'N, 80°72'E, elevation 1378.0m)	WHT 6873	KY697998/KY673256
<i>Mus musculus</i>	Agarapathana (06°87'N, 80°72'E, elevation 1378.0m)	WHT 6886	KY697999/KY673257
<i>Tatera indica</i>	Pakistan (Chevret and Dobigny 2005)	—	AJ430563/ —
	Yala (06°43'N, 81°31'E, elevation 29.4m)	WHT 6893	— /KY673258

RESULTS

Considering external measurements, similar to descriptions given by Phillips (1980) *G. e. nuwara* (HBL: 140-148 mm) was larger than *G. e. ellioti* (HBL: 137.8-138.85 mm). But tail length was longer in *G. e. ellioti* (TL: 104.8-108.35 mm) than that of *G. e. nuwara* (TL: 90-101 mm) (Table 3).

Golunda e. nuwara has larger skull parameters than *G. e. ellioti*. Especially the GL, CL, BL, BSL, PPL, PAL, PL, LBP, upper jaw dental measurements (MTL, UM1B) and lower jaw incisor length (LIL1) of *G. e. nuwara* were larger than those of *G. e. ellioti* (Table 3). Interparietal bone of *G. e. ellioti* is rounded in shape (Figure 3A1-c) but that of *G. e. nuwara* is elongated (Figure 3B1-d). Braincase of *G. e. ellioti* is comparatively rounded (Figure 3A1-e) than that of *G. e. nuwara* (Figure 3B1-f).

Considering lower jaw morphology, the base of the lower jaw posterior to the angular process was rather flat in *G. e. ellioti* (Figure 3A4-h) while that of *G. e. nuwara* is somewhat elongated and curved (Figure 3B4-g). *Golunda e. ellioti* also has a smaller diastema (Figure 3A5-i) than *G. e. nuwara* (Figure 3B5-j) (Table 4:LDL).

Table 3: External measurements (mm) of *Golunda ellioti nuwara*, and *G. e. ellioti*. (SA- Sub Adult)

	<i>G. e. nuwara</i>			<i>G. e. ellioti</i>		
	75P	75M	WHT M 032 (SA)	PDZ 7	PDZ 11	750 (SA)
Head and Body Length (HBL)	148	140	110.3	137.8	138.85	120
Tail Length (TL)	101	90	99.8	104.8	108.35	104
TL/HBL*100	68.24	64.29	90.48	76.05	78.03	86.67
Ear Height (EH)	16	20	17.7	17	17	16
Hind foot Length (HFL)	28	27	26.9	27.2	27.8	26

Table 4: Skull measurements (mm) of *Golunda ellioti nuwara* and *G. e. ellioti*.

Abbreviation	Measurement	<i>G. e. nuwara</i>			<i>G. e. ellioti</i>		
		75P	75M	WHT M 141	PDZ 7	PDZ 11	
ONL	Occipitonasal Length	33.3	34.13	36.25	33.25	33.4	
GL	Greatest Length of the skull	32.89	33.49	34.3	31.85	31.5	
CL	Condylbasal Length	31.9	32.5	32.5	30.1	30.35	
BL	Basal Length	29.69	30.62	29.5	28.1	28.1	
BSL	Basilar Length	27.71	27.61	26.7	25.7	26.1	
PPL	Post Palatal Length	11.93	12.52	11.8	11.4	11.25	
PAL	Palatilar Length	15.46	14.89	14.6	13.25	13.6	
PL	Palatal Length	17.68	17.53	17.15	15.4	15.7	
LBP	Length of Bony Plate	6.42	6.51	6.4	4.9	5.9	
LIF	Incisive Foramen Length	7.16	6.6	5.95	6.1	5.7	
UM1B	Breadth of first upper molar	2.17	2.32	2	1.7	1.8	
LR	Length of the Rostrum	10.74	10.91	10.7	9.3	9.9	
BR1	Breadth of the Rostrum at the Narrowest point	4.12	3.9	3.85	3.7	3.9	
LIOB	Least Interorbital Breadth	4.26	4.53	4.5	3.75	4.3	
BB	Breadth of Brain case	13.4	13.4	14	12.6	12.95	
MB	Mastoid Breadth	13.24	13.5	13.75	12.1	12.5	
ZB	Zygomatic Breadth	16.5	17.1	17.65	16	16.15	
HB	Height of Braincase	9.74	10.24	10	10.2	9.9	
BZP	Breadth of Zygomatic Plate	5.28	4.85	5.15	4.7	5	
UDL	Upper Diastema Length	9	9.11	7.35	7.6	7.5	
MxTL	Length of Maxillary tooth row	7.08	7.04	6.3	6.3	6.25	
LIL1	Length of lower incisor/ Mandibular incisor	7.26	8.65	7	3.3	4.7	
DD	Depth of Dentary	11.44	11.86	11.8	10.9	10.8	
ML	Greatest Length of Mandible, excluding Incisors/ Mandible Length	18.19	17.78	18.2	16.1	16.6	
LDL	Lower Diastema/ Mandibular Diastema Length	4.41	3.96	3.6	2.3	3	
MnTL	Length of Mandibular Teeth row	7.02	6.87	5.95	6.1	6	



Figure 3: Craniums and mandibles of *Golunda ellioti ellioti* (PDZ 7) (A) and *G. e. nuwara* (WHT M 141) (B). 1: Dorsal view of cranium, 2: Ventral view of cranium, 3: Lateral view of cranium, 4: Lateral view of mandible on lingual surface, 5: Lateral view of mandible on labial surface.

Maximum Likelihood (ML) trees of cytochrome-*b* gene (Figure 4), 16S rRNA and combine genes of cytochrome-*b* and 16S had the same topology with *G. e. ellioti* and *G. e. nuwara* being reciprocally monophyletic falling as sister taxa. Uncorrected percentage pairwise distance for cytochrome-*b* gene between the two subspecies is 1.2% and that for 16S gene is 1.1%. There were no Rag 1 sequence differences between the two subspecies. Surprisingly, cytochrome-*b* divergence between an Indian specimen of *Golunda ellioti* had a distance of 2.5% with the widespread

G. e. ellioti from Sri Lanka and 1.8% distance with *G. e. nuwara*.

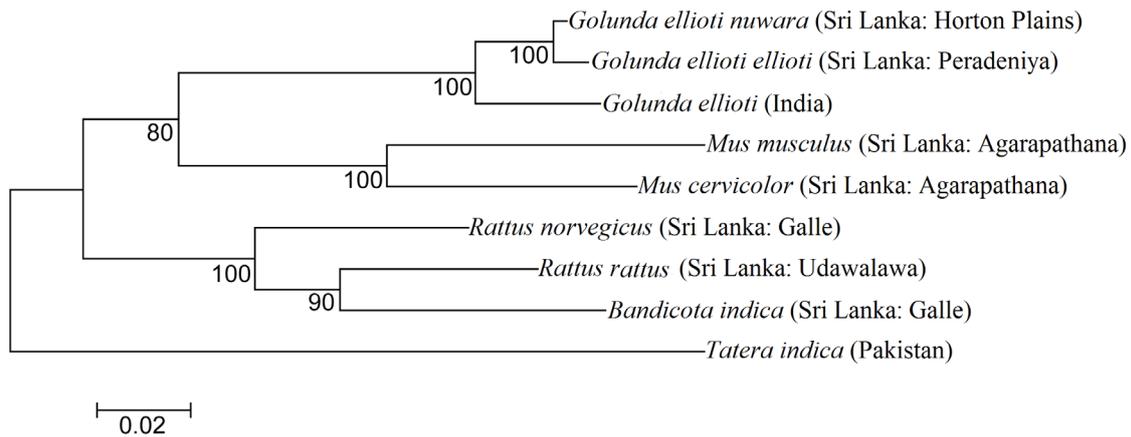


Figure 4: Maximum likelihood tree of cytochrome-b gene to show the placement of *Golunda ellioti ellioti* and *G. e. nuwara*. Bootstrap values are presented below branches.

DISCUSSION

Here, we looked at skull measurements, skull characters and molecular data of two subspecies, *Golunda e. nuwara* and *G. e. ellioti*. We identified additional differences between the two subspecies; *Golunda e. nuwara* has larger skull parameters than *G. e. ellioti*. Interparietal bone of *G. e. ellioti* is rounded in shape whereas that of *G. e. nuwara* is elongated. Braincase of *G. e. ellioti* is comparatively more rounded than that of *G. e. nuwara*. The base of the lower jaw posterior to the angular process is rather flat in *G. e. ellioti* while that of *G. e. nuwara* is somewhat elongated and curved. *Golunda e. ellioti* also has a smaller diastema than *G. e. nuwara* (Figure 3; Table 4).

Though morphologically they can be distinguished from each other, genetic differences remain limited between the subspecies, with a percentage pairwise distance value of 1.2% for cytochrome-*b*. Mayers *et al.* (1995) and Steppan (2004) confirm that genetic distances for cytochrome-*b* gene between subspecies of rodents are in a range that varied by less than 4%. Bradley and Baker (2001) indicated that genetic distance values more than 2% for cytochrome-*b* gene are indicative of specific variation. Also, they reported that average distance values within subspecific taxa for cytochrome-*b* gene are between 0.09-2.34% with an average of 1.04% for rodents.

The two subspecies of *G. ellioti* in Sri Lanka were recovered as sister taxa in the phylogeny with an Indian *G. ellioti* falling outside this clade. They were reciprocally monophyletic. Though we do not have a specimen from India for morphological comparison, the available cytochrome-*b* sequence shows that the genetic divergence of the lowland *G. ellioti ellioti* and the Indian specimen is slightly larger (2.5%) than the genetic distance between *G. e. nuwara* and Indian specimen (1.8%), indicating lower rate of divergence in the highland subspecies. Island populations can diverge faster due to smaller population sizes than continental populations (Aleixandre *et al.*, 2013). Similarly, the genetic divergence of the two subspecies may possibly be a result of the population of *G. e. ellioti* being

smaller than that of *G. e. nuwara*. According to the recorded distribution *G. e. nuwara*, it is plentiful above the 4000 feet while *G. e. ellioti* is moderately plentiful throughout the Southwestern lowland wet zone and the mid country hills of the Central and Uva provinces to approximately 3000 feet. This subspecies is reported from dry zone in the Southern Province and Kanthlai in North Central province, but not as plentiful as in the wet zone (Phillips, 1980). Hence, its population may be small compared to *G. e. nuwara*. Absence of *G. e. ellioti* in the Northern or North Western regions of the country also indicates that the Sri Lankan population may have been isolated even during the times that terrestrial connections existed in the past such as during successive glacial sea-level lowstands. This may have allowed the lowland population to diverge independently.

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