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Squirreled away—Revisiting the holotype of the cream-coloured giant squirrel, *Ratufa affinis* (Raffles, 1821), with designation of a neotype (Mammalia: Rodentia: Sciuridae)

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Abstract. *Ratufa affinis* is a large, arboreal squirrel originally described from Singapore by Thomas Stamford Raffles in 1821. Although the holotype specimen has long been believed to be housed in the Natural History Museum in London (NHMUK), examination of the type specimen revealed that it belongs to a different species: *Callosciurus concolor*. Further searches failed to discover a true holotype specimen in NHMUK that could be positively identified as *Ratufa affinis*, ultimately leading us to the conclusion that the holotype is no longer extant. This necessitated the designation of a neotype, accompanied by a morphological re-description, as the type is also the nominotypical subspecies of the species. We hereby designate ZRC 4.4097 collected from Pulau Ubin, Singapore in 1923 by Reggeng as the neotype specimen of *Ratufa affinis*.

Key words. *Ratufa affinis*, Sundaland, Singapore, taxonomy, holotype, neotype

INTRODUCTION

Ratufa Gray, 1867 is a genus of large and charismatic arboreal squirrels that inhabit the tropical and subtropical forests of South and Southeast Asia, ranging from India in the west to Bali in the east. At present, five species are recognised (Wilson et al., 2016; Hinckley et al. 2025a): *Ratufa indica* (Erxleben, 1777) (the type species), *R. affinis* (Raffles, 1821), *R. bicolor* (Sparrman, 1778), *R. gigantea* (McClelland in Horsfield, 1840), and *R. macroura* (Pennant, 1769). Of these, *R. indica* and *R. macroura* are known to occur parapatrically within their overlapping distribution in India (Moore & Tate, 1965), although instances of forced sympatry and hybridisation attributed to anthropogenic causes have been recorded recently (Thomas et al., 2018; Siva Sankari et al., 2023). *Ratufa affinis* and *R. bicolor* are sympatric, with their distributions overlapping in Southeast Asia. *Ratufa gigantea* was recently re-recognised as a distinct species, removing it from synonymy with *R. bicolor* (Hinckley et al., 2025a). During a digital archival project in the Natural History Museum, London, part of the Singapore in Global Natural History Museums Information Facility (SIGNIFY) initiative led by the Lee Kong Chian Natural History Museum (LKCNHM) at the National University of Singapore to digitise and document scientifically and historically-important specimens from Singapore (SIGNIFY, 2026), it was found that the holotype of *R. affinis* belonged to a different species. Here, we discuss the taxonomic history of *R. affinis* and assign a neotype.

The importance of holotype material for stability in both botanical and zoological taxonomy cannot be understated (ICZN, 1999; Turland et al., 2025). Holotypes serve as the cornerstone for the consistent application of a species' name across time, enabling future generations to reliably refer to such material for any subsequent studies that require comparative material— especially for biogeographical and conservation research. Any suspicions regarding taxa new to science that are closely related to a particular species will also rely on type material as a reference point, from which descriptions of these new species can be made. The Sundaic region (also known as Sundaland) spans the Malay Peninsula (south of the Isthmus of Kra), the major islands of Borneo, Java, and Sumatra as well as several lesser islands. The region has seen an immense wave of species discovery in the last two centuries, owing to its unique and complex biogeography. The same is true of its mammalian fauna, with multiple recent species descriptions (Hinckley et al., 2024a; Hinckley et al., 2024b; Nations et al., 2024) highlighting the crypticity of various lineages that were previously lumped under a single name. Consequently, Singapore's location within this biodiversity hotspot further

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highlights the importance of type material originating from the island— including that of *Ratufa affinis*.

The original description (and first known record) of *R. affinis* was published by Thomas Stamford Raffles from a specimen collected in Singapore (Raffles, 1821). Raffles, together with three other naturalists (Pierre Médard Diard, Alfred Duvaucel, and William Jack) spent approximately one month from 31 May to 28 June 1819 in Singapore, collecting specimens from a wide array of native flora and fauna (Low, 2021; Low et al., 2021). This was the first known sustained biodiversity expedition on the island. Although it cannot be known for certain, it is highly likely that the first specimen of *R. affinis*, which serves as the holotype specimen, was collected during this expedition (Low, 2021). In Singapore, the genus is represented solely by *R. affinis*. *Ratufa bicolor* has never been recorded from the island, despite Singapore being within the expected natural distribution of the species— an absence likely explained by the species-area relationship (MacArthur & Wilson, 1963). Due to rapid deforestation and hunting, *R. affinis*, once abundant in the forests of Singapore (Raffles, 1821), has not been seen there in over 30 years. The last reliable sightings were reported in 1995 (Anonymous, 1995; Ng et al., 2011). After three decades of regular surveys and conservation assessments, the species, which was initially listed as Nationally Endangered (Ng & Wee, 1994) and Critically Endangered (Davison et al., 2008), was assessed to be Nationally Extinct in 2024 (Davison et al., 2024). It is listed as Near Threatened under the IUCN Red List of Threatened Species (Meijaard, 2017).

The holotype and other specimens of *R. affinis* from the type locality are of importance as the population from Singapore serves as a topotypic reference for the nominotypical subspecies (*Ratufa affinis affinis*), which only occurs in the Malay Peninsula (including Peninsular Thailand and Singapore) (Ng et al., 2011; Wilson et al., 2016). Thirty-seven synonyms have been attributed to *R. affinis* (Wilson & Reeder, 2005), of which nine are currently recognised as valid subspecies (Thorington et al., 2012*;* Wilson et al., 2016): the nominotypical *R. a. affinis*, (Raffles, 1821); *R. a. bancana* Lyon, 1906; *R. a. baramensis* Bonhote, 1900; *R. a. bunguranensis* (Thomas & Hartert, 1894); *R. a. cothurnata* Lyon, 1911; *R. a. ephippium* (Müller, 1838); *R. a. hypoleucos* (Horsfield, 1824); *R. a. insignis* Miller, 1903, and *R. a. polia* Lyon, 1906. These subspecies were described based on morphology and occupy distinct geographical regions. The occurrence of many subspecies across the species' geographic range likely hints at undescribed species-level diversity within the *R. affinis* complex, which is further supported by genomic evidence (Hinckley et al., 2025a). Accordingly, accurate descriptions and reliable data on type and topotypic material are critical for future taxonomic revisions, biogeographical studies (Woodruff & Turner, 2009; Csorba et al., 2016; Hinckley et al., 2025a) and conservation decision-making (Ely et al., 2017).

Due to SIGNIFY's discovery of the alleged *R. affinis* holotype actually belonging to a different species, and the extirpation of *R. affinis* from its type locality, it is pertinent to ascertain the availability of previously collected topotypic material from Singapore for taxonomic stability, as the addition of new material from Singapore is no longer possible. The holotype specimen has also never been photographed, nor had its cranial and mandibular morphology been measured since Raffles's cursory description of it. Of further note is the lack of any written evidence in Raffles (1821) that points to the holotype specimen being prepared for preservation or subsequent transfer to the British Museum, which suggests that the species was described from a live individual.

The identity of the holotype specimen of *Ratufa affinis* (Raffles, 1821). The holotype of *R. affinis* (NHMUK 1879.11.21.522) was collected by Raffles from Singapore and described by him in 1821 (Raffles, 1821). Some of Raffles's specimens were deposited at the British Museum, subsequently known as the British Museum (Natural History) (BMNH)—and today as the Natural History Museum, London (NHMUK). As part of SIGNIFY's project to digitise the holotype, inspection of the specimen (skin and skull; Fig. 1) revealed that it belongs to *Callosciurus* Gray, 1867. We hereby identify it as *Callosciurus concolor* (Blyth, 1855) based on the following observed pelage characters that we find to agree with Moore & Tate (1965) and Hinckley et al. (2024b): lack of sharply marked tail tip that is black in colour; silvery grey venter lacking a reddish suffusion in the inguinal region; and a general lack of reddish suffusion on the dorsum, which we attribute to a monsoon pelage. We verified that the skull must belong to the same specimen as the skin, as the following craniomandibular traits agreed with Moore (1959): auditory bullae with single transbullar septum; single, large, round foramen which pierces squamosal bone in the postglenoid area; presence of a thick ridge extending from the anterior edge of the zygomatic process across the squamosal to the alisphenoid; absence of supraorbital notch; and proodont upper incisors; and with Moore & Tate (1965): least interorbital breadth exceeding greatest length of nasal (16.7 mm vs 14.8 mm); presence of single, unforked bony septum across chamber of auditory bullae; high and falcate coronoid process of the mandible; obsolescent supra-orbital notches; orbit length in excess of 13 mm (14 mm); and upper edge of infraorbital foramen well separated from the maxillo-premaxillary suture. The specimen was an adult animal based on the fused basilar suture and extensive teeth wear, confirming without a doubt that it could not be the holotype specimen of *Ratufa affinis* described by Raffles (1821). The mean adult head-body length of *C. concolor* is 21.8 cm (Hinckley et al., 2024b) compared with 33.7 cm in *R. affinis* (Thorington et al., 2012). Thus, given that the two species vary considerably in size and *C. concolor* has never been reported from Singapore, the following question arises— how was the *C. concolor* specimen misidentified as the type of *R. affinis*?

On the possible provenance of the *Callosciurus* specimen. Raffles (1821) and Horsfield (1824) exhibit notable differences in their description of the type specimen of *R. affinis*, and the following excerpts from their respective works

Fig. 1. Mislabelled holotype specimen (skull, skin and labels) of *Sciurus affinis* Raffles, 1821 (NHMUK.1879.11.21.522) The newly-determined identity of the specimen is *Callosciurus concolor* (Blyth, 1855).

aim to provide clarity on these differences. A portion of Raffles' (1821) description of *R.* (*Sciurus*) *affinis* is quoted verbatim below:

"…a third species, which may be named SCIURUS AFFINIS, was found abundantly in the woods of Singapore (on the occupation of that station by the British in 1819), agreeing with the two former in having a flat nail on the very short thumb of the forefeet, but differing in colour, being of a cinereous grey or brown-ish on the upper part of the head, body and tail, and on the outside of the limbs, and being nearly white on the under and inner parts. It is about the size of the *S. bicolor*. The separation of the colours on the body is not so abrupt as in that species, a stripe of reddish-brown marking the transition. Grey is the most usual colour of the upper parts; but it appears to vary considerably at different seasons (perhaps at rutting time), changing to a light brown, and even to a dusky yellow. The first specimens, that were procured in February, were of this latter colour; five months after they were found of a grey colour.".

Horsfield (1824) provides the following description of Raffles's *R. affinis*, quoted verbatim here for clarity:

"The hairy covering of the upper parts is fulvous brown, with a cast of gray; it is variegated with delicate transverse bands. The whole of the head, the under parts throughout, and the extremity of the tail, are gray. This latter organ is cylindrical, somewhat distended in the middle, and then tapering to a point; the transverse bands are irregular. Between the tints of the sides and abdomen, a stripe of reddish brown intervenes, which is continued to the neck. The whiskers consist of black and white hairs intermixed. The ears are rounded above, and without any brush-like appendage. The length of the body and head is nine, and of the tail seven inches. Sir Stamford Raffles discovered this species in 1819, in the woods of Singapore. One specimen, from Pulo Panjang, in the Gulf of Siam, is contained in Dr. Finlayson's Collection. This specimen is somewhat smaller than the *Sciurus bicolor*, to which Sir Stamford compares the size of the *Sciurus affinis*, as it is observed in Singapore. Museum of the East India Company.".

Based on the description provided by Horsfield (1824), it is apparent that the specimen examined was not that of an *R. affinis*, as it does not match Raffles's description, both in size and colouration. Horsfield's mention of Finlayson's specimen from "Pulo Panjang" also hints at a likely source of the specimen being mixed-up. Label 1 of the specimen in Fig. 1 indicates "Finlayson" in the upper left corner, which suggests that Horsfield may have incorrectly introduced Finlayson's specimen of a *Callosciurus concolor* into his treatise of *R. affinis*. This likely caused the mismatched specimen to be considered the holotype of *R. affinis* when the East India

Table 1. Definitions of the craniomandibular measurements obtained for the neotype of *Ratufa affinis*, and their respective abbreviations. Categories represent the various aspects of the skull and mandible observed, as illustrated in Fig. 2.

Abbreviation	Measurement	Category
ONL	Occipitonasal length	A
LN	Length of nasal bone	A
MWN	Maximum width of nasal bone	A
BR	Breadth of rostrum	A
GNB	Greatest neurocranium breadth	A
LBO	Least breadth between orbits	A
LBC	Least breadth of caudal points of zygomatic process of frontal bone	A
ZB	Zygomatic breadth	A
CBL	Condylobasal length	B
BL	Basal length	B
PL	Palatal length	B
PPL	Post palatal length	B
LIF	Length of incisive foramen	B
LPB	Length of palatal bridge	B
GPB	Greatest palatal breadth	B
MTB	Mastoid breadth	B
ABB	Breadth of auditory bullae	B
GBO	Greatest breadth of occipital condyles	B
LMR1	Length of upper molar row in alveoli	B
LAB	Length of auditory bullae	B
SL	Short lateral facial length	C
OD	Orbital diameter	C
HAB	Height from the Akrokranion to the Basion	C
LMR2	Length of lower molar row in alveoli	D
AHR	Aboral height of the vertical ramus	D
OHR	Oral height of the vertical ramus	D
LA	Length from the angular process	D
LC	Length from the condyle	D

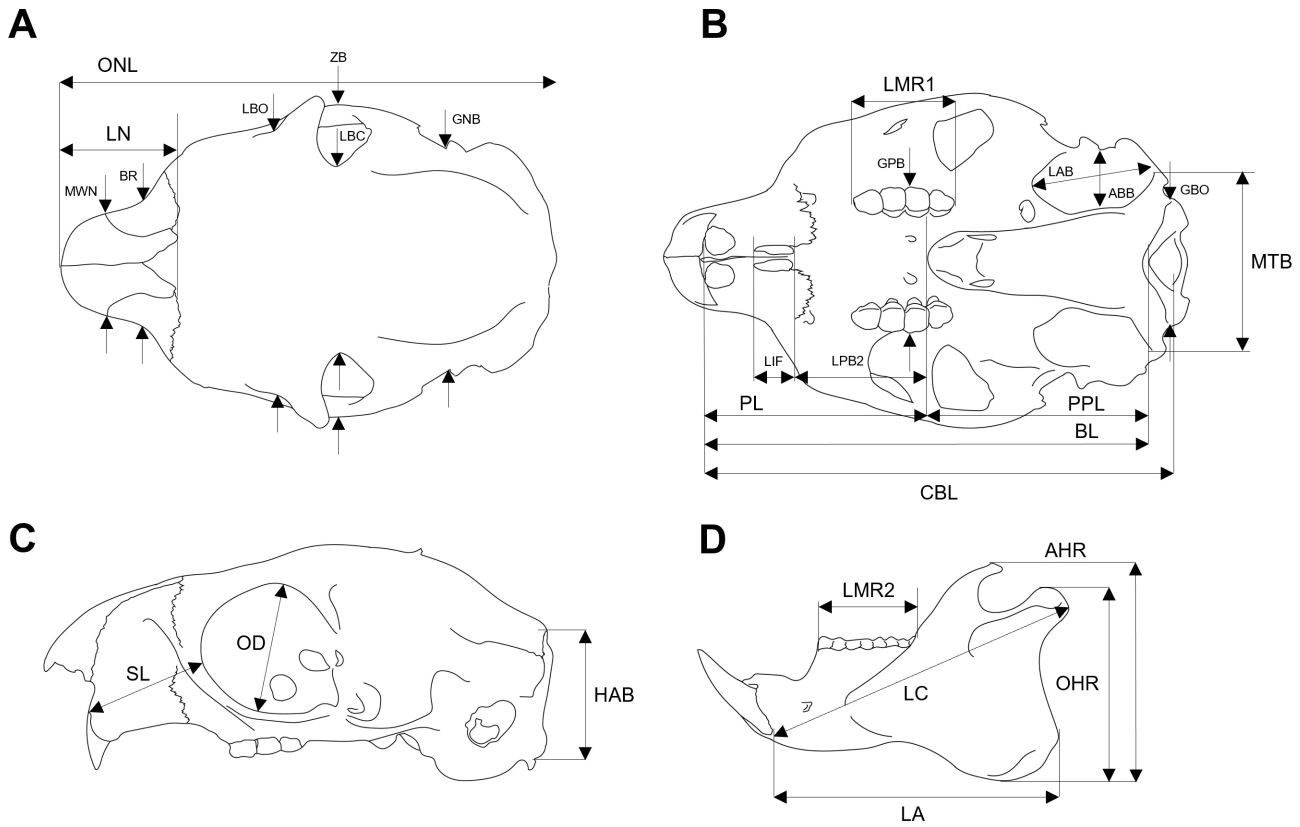

Fig. 2. Craniomandibular measurements obtained for ZRC 4.4097 (Neotype). Drawings A, B, and C display the dorsal, ventral, and lateral views of the cranium respectively. D displays the lateral view of the mandible. All measurements obtained have been pre-defined in Table 1. Illustrations by Shivaram Rasu.

Company Museum collections (which Horsfield was curator for) were merged with the British Museum and subsequently moved to BMNH (NHMUK today) (Low, 2021: 231, 234). This confusion is compounded by the fact that the locality on the label appears to be written as "Sumatra" but was later struck through without correction (Fig. 1). Furthermore, Moore & Tate (1965) report on a *Callosciurus caniceps bimaculatus* specimen that was erroneously referred to as *Sciurus affinis* by Horsfield (1824), which we are certain refers to the misidentified holotype of *Ratufa affinis* (NHMUK 1879.11.21.522). However, we have determined the identity of the specimen to be *C. concolor* instead. Thus, with the holotype likely lost and the inadequate description by Raffles (1821), a neotype needs to be designated and described.

MATERIAL AND METHODS

All specimens examined for this study are deposited in the following institutions: Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore (ZRC); Natural History Museum, London (BMNH/NHMUK); and the Smithsonian National Museum of Natural History (USNM). A complete list of all extant *Ratufa affinis* specimens (n=52) located from the search effort in NHMUK is also available in the Supplementary Material.

The neotype specimen was selected based on the following characteristics: original specimen collection from Singapore; completeness of skull material; minimal damage to skin material; and fusion of basilar suture in cranium (indicating adult specimen). Craniomandibular measurements were taken using a Vernier calliper (Dialmax SPi2000) to the nearest 0.1mm. The following craniomandibular traits measured were adapted from Biswas et al. (2020), with some modifications (Fig. 2; Table 1): occipitonasal length (ONL); length of nasal bone (LN); maximum width of nasal bone (MWN); breadth of rostrum (BR); greatest neurocranium breadth (GNB); least breadth between orbits (LBO); least breadth of caudal points of zygomatic process of frontal bone (LBC); zygomatic breadth (ZB); condylobasal length (CBL); basal length (BL); palatal length (PL); post palatal length (PPL); length of incisive foramen (LIF); length of palatal bridge (LPB); greatest palatal breadth (GPB); mastoid breadth (MTB); breadth of auditory bullae (ABB); greatest breadth of occipital condyles (GBO); length of upper molar row in alveoli (LMR1); length of auditory bullae (LAB); short lateral facial length (SL); orbital diameter (OD); height from the akrokranion to the basion (HAB); length of lower molar row in alveoli (LMR2); aboral height of the vertical ramus (AHR); oral height of the vertical ramus (OHR); length from the angular process (LA); and length from the condyle (LC).

TAXONOMY AND SYSTEMATICS

Family Sciuridae Fischer de Waldheim, 1817

Genus *Ratufa* Gray, 1867

***Ratufa affinis* (Raffles, 1821)**
(Figs. 2–4)

Sciurus affinis Raffles, 1821: 259 (type locality: Singapore).
Sciurus hypoleucos Horsfield, 1824: 222 (type locality: Bencoolen [=Bengkulu], West Sumatra).
Sciurus auriventer Geoffroy Saint-Hilaire, 1831: 150 (type locality: Malacca).
Sciurus ephippium Müller, 1838: 147 (type locality: Southeast Borneo).
Sciurus bicolor bunguranensis Thomas & Hartert, 1894: 658 (type locality: Bunguran Island, North Natuna Islands).
Sciurus bicolor nanogigas Thomas & Hartert, 1895: 491 (type locality: Laut Island, North Natuna Islands).
Ratufa ephippium baramensis Bonhote, 1900: 496 (type locality: Baram, Sarawak).
Ratufa pyrsonota Miller, 1900: 75 (type locality: Trang, Thailand).
Ratufa ephippium sandakanensis Bonhote, 1900: 497 (type locality: Sandakan, North Borneo).
Ratufa ephippium sirhassenensis Bonhote, 1900: 498 (type locality: Sirhassen [=Serasan] Island, South Natuna Islands).
Ratufa notabilis Miller, 1902: 150 (type locality: Lingga Island).
Ratufa balae Miller, 1903a: 6 (type locality: Tana Bala [=Tanahbala] Island, Batu Islands, West Sumatra).
Ratufa conspicua Miller, 1903a: 5 (type locality: Bintang [=Bintan] Island, Riau Archipelago).
Ratufa femoralis Miller, 1903b: 447 (type locality: Tuangku Island, Banyak Islands, West Sumatra).
Ratufa insignis Miller, 1903a: 4 (type locality: Sugi Island, Riau Archipelago).
Ratufa masae Miller, 1903a: 7 (type locality: Tana Masa [=Tanahmasa] Island, Batu Islands, West Sumatra).
Ratufa nigrescens Miller, 1903b: 448 (type locality: Mansalar [=Mursala] Islands, West Sumatra).
Ratufa piniensis Miller, 1903a: 7 (type locality: Pinie [=Pini] Island, Batu Islands, West Sumatra).
Ratufa carimonensis Miller, 1906: 257 (type locality: Great Karimun [=Karimunbesar] Island, Riau Archipelago).
Ratufa condurensis Miller, 1906: 258 (type locality: Kundur Island, Riau Archipelago).
Ratufa confinis Miller, 1906: 259 (type locality: Sinkep [=Singkep] Island, Lingga Islands).
Ratufa polia Lyon, 1906: 585 (type locality: Belitung Island, East Sumatra).
Ratufa polia bancana Lyon, 1906: 587 (type locality: Banka [=Bangka] Island, East Sumatra).
Ratufa arusinus Lyon, 1907: 442 (type locality: Aru Bay, Northeast Sumatra).
Ratufa catemana Lyon, 1907: 443 (type locality: Kateman River, Southeast Sumatra).
Ratufa bulana Lyon, 1909: 482 (type locality: Bulan Island, Riau Archipelago).
Ratufa cothurnata Lyon, 1911: 93 (type locality: Mount Palung, West Borneo).
Ratufa griseicollis Lyon, 1911: 94 (type locality: Panebangan Island, West Borneo).
Ratufa vittata Lyon, 1911: 94 (type locality: Laut Island, Southeast Borneo).
Ratufa vittatula Lyon, 1911: 95 (type locality: Sebuku Island, Southeast Borneo).
Ratufa affinis johorensis Robinson & Kloss, 1911: 244 (type locality: Padang Tuan, Segamat, Johor, Malaysia).
Ratufa ephippium dulitensis Lönnberg & Mjöberg, 1925: 514 (type locality: Mount Dulit, Sarawak).
Ratufa ephippium lumholzi Lönnberg in Lönnberg & Mjöberg, 1925: 514 (type locality: Pipoh Bulungan, Northeast Borneo).

Fig. 3. ZRC 4.4097 (Neotype of *Ratufa affinis* (Raffles, 1821)). Adult female. Collected from Pulo Ubin [= Pulau Ubin, Singapore] on 26 January 1923, by Reggeng.

Ratufa affinis banguei Chasen & Kloss, 1932: 22 (type locality: Banggi Island, North Borneo).
Ratufa affinis frontalis Kloss, 1932: 2 (type locality: Taiping, Perak, Malaysia).
Ratufa affinis interposita Kloss, 1932: 2 (type locality: Ulu Gombak, Selangor, Malaysia).
Ratufa affinis klossi Hill, 1960: 47 (type locality: Lam-ra, Trang, Thailand).

Type material. Neotype (herein designated): adult female (ZRC 4.4097), one flat skin (measurements as indicated on label: head and body length 320 mm, tail length 380 mm, hindfoot length 60 mm, ear length 25 mm) and a well-preserved cranium and mandible showing cheek teeth wear (Fig. 3). Craniomandibular measurements presented in Table 2.

Type locality. Pulo Ubin [= Pulau Ubin, Singapore], an island northeast of the main island of Singapore, separated by a shallow strait 10–20 m at its deepest (Chan et al., 2006); coll. Reggeng.

Other material examined. Unknown locality: NHMUK 1879.11.21.522 (incorrectly labelled as holotype, the actual specimen described in Raffles (1821) is deemed lost); NHMUK 9.4.1.203 collected by H. C. Robinson; USNM 86886–86887 collected by W. L. Abbott; ZRC 4.4094 collected by J. B. L. Oei; ZRC 4.4095 collected by Heng Ah Leck; ZRC 4.4096 collected by "P. M. de Fontaine(?)"; ZRC 4.4098 collected by "Unknown"; ZRC 4.4099 collected by "Unknown"; ZRC 4.4100 collected by "Unknown". "Singapore or Peninsular Malaysia": USNM 38464/USNM 403 collected by "Unknown".

Diagnosis. As determined by Moore & Tate (1965), *Ratufa affinis* may be distinguished from *R. indica* and *R. macroura* in having a crown pelage colour that is connected to that of the nape, with no coloured band between the ears distinctly separating the pelage of the crown from the nape between the ears. *Ratufa affinis* may also be distinguished from *R. bicolor* and *R. gigantea* in possessing a light mark on the thigh, and no black mark on the chin. The neotype specimen

Table 2. List of craniomandibular measurements obtained for ZRC 4.4097 (neotype of *Ratufa affinis*).

Abbreviation	Measurement (mm)
ONL	63.3
LN	16.4
MWN	13.1
BR	143.5
GNB	27.3
LBO	27.9
LBC	23.1
ZB	40.6
CBL	57.9
BL	53.6
PL	26.7
PPL	26.9
LIF	4.5
LPB	16.2
GPB	17.4
MTB	22.6
ABB	7.0
GBO	14.7
LMR1	12.8
LAB	14.0
SL	22.9
OD	15.6
HAB	17.0
LMR2	12.2
AHR	25.4
OHR	22.7
LA	32.6
LC	36.8

Fig. 4. Live individuals of A, *Ratufa affinis affinis* from Johor, West Malaysia and B, *Ratufa affinis baramensis* from Sabah, East Malaysia exhibiting stark differences in pelage colouration. These individuals belong to the west and east Sunda lineages respectively, as outlined by Hinckley et al. (2025a). Photographs by: A, Nick Baker and B, Shivaram Rasu.

belongs to the nominate subspecies *R. affinis affinis*, which may be distinguished from all other subspecies by being pale on the venter and uniformly brown on the dorsum, with individuals being paler in the southern part of the range of *R. affinis affinis* (i.e., southern Peninsular Malaysia and Singapore) (Thorington et al., 2012).

Description. Craniomandibular biometric data as in Table 2. Definitions of measurements used as detailed in Fig. 2 and Table 1. Photographs of neotype provided in Fig. 3. Skull large and robust (ONL 63.3 mm). Rostrum short but stout (LN 25.9% of ONL). Nasals broad anteriorly but narrow posteriorly, forming a Y-shaped fork where they meet posteriorly along internasal suture. Furthest extent of nasals posteriorly approximately plane with that of premaxilla, along frontonasal and fronto-premaxillary suture. Frontal wide and gently sloping. Frontoparietal suture completely ankylosed, smooth all the way to posterior edge of parietal. Lateral lip of infraorbital foramen inclined forward at the top, with the upper portion reaching the maxillary-premaxillary suture when viewed from the lateral aspect. Single and round postglenoid foramen, squamosal unpierced by subsquamosal foramen. Squamoso-alisphenoid suture situated about halfway between the posterior margin of the base of the zygomatic process of the squamosal and the third molar. Postorbital processes of frontal distinct, tapering to a point and pointing slightly backward. Neurocranium rounded, gently downward sloping posteriorly along parietal. Frontal, squamosal and parietal smooth and sloping. Temporal ridge pronounced. Orbit large, deep and circular (OD 68.1% of SL) when viewed along occlusal plane. Postorbital constriction narrower than interorbital breadth (LBC 82.8% of LBO). Auditory bullae large and smooth (ABB 50.0% of LAB), with no transbullar septa present. Pterygoid partially broken, process missing. Incisive foramen long and narrow (LIF 4.5 mm). Premaxillary-maxillary sutures jagged and pronounced. Palatines very short (PL 99.2% of PPL), pterygoid fossa extending all the way past third molar and plane with posterior edge of second molar. Upper incisors short and slightly opisthodont with fulvous enamel on outer frontal surface. One upper premolar and three upper molars present, all ivory in coloration. Lower incisors longer than upper incisors, with identical fulvous enamel on outer frontal surface. Lower teeth comprising one lower premolar and three lower molars, all ivory in coloration. Lower tooth row slightly shorter than upper tooth row (LMR2 95.3% of LMR1). Mandible intact; symphysis broken.

Pelage intact and nearly pristine. Measurements as obtained from specimen label (Fig. 3). Head-body length of 320 mm and tail length of 380 mm (tail about 118% of head-body length); ear length 25 mm, ears brown, without tufts; whiskers black to dark reddish brown; dorsal pelage, including the head, cream to pale brown, colour slightly increasing in saturation along dorsal surfaces of forelimbs and hindlimbs; sides yellow-cream to straw-brown, giving way to contrasting

pale venter running uniformly across midline; light mark on thigh; ventral pelage pale to light-brown, lacking a black mark on chin; tail covered in thicker, longer fur than rest of body; dorsal pelage of tail tan-brown with mildly contrasting central core of light brown fur that runs along base of tail towards tip; ventral pelage of tail tan brown, becoming pale to light brown at base of tail, gradually becoming fulvous ventrolaterally whilst retaining cream-coloured central core of fur that extends all the way to tip of tail; hindfoot length of 60 mm, dorsal pelage of fore and hind feet cream to off-white in colour, ventral surface of fore and hind feet mostly hairless, covered in black skin; claws strong and recurved. Six mammae, comprising one pectoral pair, one abdominal pair, and one inguinal pair.

Taxonomic remarks. No baculum material was available for description. No craniomandibular traits unique to *R. affinis* were identified in the present study, thus a craniomandibular diagnosis of the species is unavailable. While the occipitonasal length of the neotype is within the established range of *R. affinis* specimens (in particular, the western lineage) examined by Hinckley et al. (2025a), the postorbital constriction (=LBC) is more than 80% [82.8%] of interorbital breadth (=LBO), which is an outlier with respect to Moore's (1959) diagnosis of the tribe Ratufini. The neotype specimen belongs to the nominate subspecies (*Ratufa affinis affinis*).

Distribution. As detailed by Corbet & Hill (1992) and Thorington et al. (2012), *Ratufa affinis* is distributed from Peninsular Thailand (south of the Isthmus of Kra), Peninsular Malaysia, Singapore (where it is extirpated), Sumatra, Borneo, and several lesser Sundaic islands: Bangka, Belitung, Bunguran, and the Riau Archipelago (including Bintan, Sugi, Karimun [=Karimunbesar?], Bulan, Lingga, and Singkep), Mansalar [=Mursala], Tanahbala, Tanahmasa, Tuangku, Pini, Panebangan, Laut, and Sebuku. The nominate subspecies, *R. affinis affinis*, now represented by the neotype specimen, can only be found in Peninsular Thailand (south of the Isthmus of Kra), Peninsular Malaysia, and Singapore.

DISCUSSION

The current designation of a neotype of *Ratufa affinis* aims to stabilise the nomenclature of the species, and serve as a reliable point of reference for future treatises on the taxon. Although it is unclear when the incorrect specimen was attributed as the holotype of *R. affinis,* the present study underscores the alarming lack of comparative studies against the holotype material. Nonetheless, it appears that the name *Ratufa affinis* sensu auctorum has long been applied to a taxon consistent with the type locality of the holotype specimen.

The taxonomic stability of the IUCN Near Threatened *Ratufa affinis* is important considering recent and future systematic studies on the species, as emerging evidence shows it to be a species complex (Meijaard, 2017; Hinckley et al. 2025a). The application of traditional molecular methods along with the advent of next generation sequencing (NGS) in the last decade has led to a newfound understanding of the biogeography of previously understudied mammalian taxa in Sundaland (Demos et al., 2016; Hinckley et al., 2020; Hinckley et al., 2023; Hinckley et al., 2025a), which has also supported the recognition of new species from morphologically cryptic complexes (Demos et al., 2017; Hinckley et al., 2024a; Hinckley et al., 2024b; Hinckley et al., 2025b; Nations et al., 2024). Similarly, the incredible variation in pelage observed across the nine recognised subspecies of *Ratufa affinis* is strongly indicative of previously unrecognised species diversity within the species complex, which was recently confirmed by Hinckley et al. (2025a), in the recognition of two distinct clades of *R. affinis* split between western and eastern Sundaland (Fig. 4). Future research should concentrate on utilising an integrative approach, i.e., minimally a combination of stable morphological characters and genomic evidence, to elucidate and stabilise species-level diversity within the *Ratufa affinis* complex and aid in the conservation of these charismatic and ecologically important squirrels (Payne, 1980).

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SUPPLEMENTARY DATA

Supplementary material is available at the following link: https://doi.org/10.6084/m9.figshare.32183724.