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The early natural history and taxonomy of the brushtail possum genus *Trichosurus* (Diprotodontia: Phalangeridae)

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ABSTRACT – The Common Brush-tailed Possum (*Trichosurus vulpecula*) has undergone significant taxonomic revision, with the validity of its numerous subspecies being the subject of ongoing debate. The widespread geographic distribution and significant morphological variation between populations has led to the scientific descriptions of up to 22 taxa over 230 years, contributing to the taxonomic uncertainties within the group. Early accounts and the taxonomic history of brushtail possums (genus *Trichosurus*) are reviewed and their significance assessed. Early taxonomic descriptions often lacked sufficient locality information, and frequently had no assigned type specimens, resulting in the description of numerous species that are no longer valid. This paper presents photographic documentation and examination of all known type material obtained from museums worldwide, and extends and updates the only other modern inventory, that of McKay (1988). We emphasise the importance of including type specimens in future taxonomic revisions, as they are the only means to validate past descriptions and nomenclature. The Common Brush-tailed Possum, once widely distributed, has become far from common in many regions, suffering significant declines across their range. It is critical that the taxonomy of brushtail possums be resolved prior to conservation actions occurring, and we highlight several descriptions that deserve further investigation to assess their validity. Through our review of the taxonomic history of *Trichosurus*, we demonstrate the importance of using historical descriptions to identify knowledge gaps that can inform future taxonomic decisions for any group of species.

KEYWORDS: review, mammals, marsupials, Australia

INTRODUCTION

The brushtail possums (*Trichosurus* spp.) are nocturnal semi-arboreal marsupials broadly distributed throughout Australia. Generally, three species are recognised: the Common Brush-tailed Possum (*T. vulpecula*), the Short-eared Brush-tailed Possum (*T. caninus*), and the Mountain Brush-tailed Possum (*T. cunninghami*). Among these species, the Common Brush-tailed Possum exhibits the greatest geographic range and morphological diversity, currently recognised through six generally accepted subspecies across Australia. These are *T. v. johnstonii* from central eastern Queensland and the Atherton Tablelands, *T. v. fuliginosus* from Tasmania, *T. v. hypoleucus* from south-western Australia, Barrow Island and Broome in Western Australia, *T. v. arnhemensis* from the Kimberley and Northern Territory, *T. v. vulpecula* from central and south-eastern Australia, as well as the Midwest and Pilbara regions in Western Australia, and *T. v. eburacensis* from Cape York Peninsula, Far North Queensland (Kerle and How 2008; Middleton et al. 2025). Considerable variation in external morphology including body size and fur colour within *Trichosurus* has led to numerous taxonomic descriptions since the initial description in scientific literature. Historically, species were described based on morphological features, which resulted in the naming of many species that are no longer considered valid. Some of these descriptions have added further confusion, as they were based on inaccurate or misleading information. This review examines the full taxonomic history of *Trichosurus*,

from the initial scientific description to the most recent taxonomic revisions. We provide an inventory of type material in world collections and extend and update the only other modern inventory, that of McKay (1988). Type specimens were inspected and photographed by the first author at these institutions in 2022 and 2023 (Table 1).

The aim of this review is to provide a summary of the current and historical taxonomic knowledge of *Trichosurus,* and an inventory of type specimens in world collections to facilitate a better understanding of the next steps required to resolve species complexes in *T. vulpecula* (Middleton et al. 2025). Institutional abbreviations used in the text for collections housing type material are: AM, Australian Museum; SAMA, South Australian Museum; UZMO, University Museum of Zoology, Oslo; NHRM, Swedish Museum of Natural History; MNHN, National Museum of Natural History, Paris; NHMUK, Natural History Museum United Kingdom; ZMB, Natural History Museum Berlin.

EARLY EUROPEAN DESCRIPTIONS OF THE COMMON BRUSH-TAILED POSSUM

The earliest detailed European account of the Common Brush-tailed Possum (*T. vulpecula*) was published in Phillip et al. (1789), during Governor Phillip's voyage to Botany Bay, New South Wales (NSW), as part of the first fleet. A specimen was said to have been sent back to England, however the location of this specimen remains unknown. Phillip et al. (1789) referred to this animal as the 'Vulpine Opossum', with 'vulpine' alluding to its fox-like characteristics, such as its bushy tail, long ears and pointed snout (Figure 1). The term 'opossum' was a reference to the familiar marsupials of the Americas. Around the same time, 'Wha Tapoau Roo' was described by J. Hunter in White and Stone (1790). The animal was said to be racoon sized, featuring a dark grey back that gradually lightened on the sides, and a rich brown belly (Figure 2).

GENERIC NOMENCLATURE

The generic nomenclature of *Trichosurus* has undergone changes over time. Initially, early proposed names often classified these species under the genus *Didelphis,* associated with the marsupial opossums of the Americas, leading to the adoption of the common name 'possum' (Kerle 2001). However, differences between Australian and American 'opossums' soon became evident, and in 1780, the genera *Phalangista* or *Phalanger* Storr, 1780 was introduced (Flannery et al. 1987). The genus was then assigned its current name *Trichosurus* Lesson, 1828. Other names such as *Cercaërtus* Burmeister, 1837, which Thomas (1888) considered to be an incorrect original spelling of *Cercartetus* Gloger, 1841 (Burramyidae), *Tapoa* Owen, 1839, *Psilogrammurus* Gloger, 1841 and *Trichurus* Wagner, 1842 were also applied to the genus, but they were deemed junior synonyms of *Trichosurus* Lesson, 1828.

TAXONOMIC HISTORY OF *TRICHOSURUS* LESSON, 1828

Trichosurus vulpecula vulpecula (Kerr, 1792)

Didelphis vulpecula Kerr, 1792

Didelphis vulpina Meyer, 1793

Didelphis tapouaru Meyer, 1793

Ursus novaehollandiae Bechstein, 1800

Didelphis lemurina Shaw, 1800

Phalangista cookii Cuvier, 1824

Phalangista bougainvillei Fischer, 1829

Phalangista xanthopus Ogilby, 1831

Phalangista melanura Wagner, 1842

Phalangista rufescens (nomen dubium) Krefft, 1872

Trichosurus vulpecula mesurus Thomas, 1926

Trichosurus vulpecula raui Finlayson, 1963

In 1792, Kerr first assigned the name *Didelphis vulpecula* to the 'Vulpine Opossum' described in Phillip et al. (1789). The name '*vulpecula*' translates roughly to 'little fox', reflecting the early descriptions of their likeness to a fox. Said to inhabit New South Wales, around the Sydney region, no type specimen was designated from Kerr's original description (Kerr 1792).

After the early descriptions by Phillip et al. (1789) and White and Stone (1790), several other species names were assigned to the described animal. Meyer (1793) introduced two species names: *D. vulpina,* based on the account in Phillip et al. (1789) of the 'Vulpine Opossum', and *D. tapouaru*, based on the account in White and Stone (1790) of 'Wha Tapoau Roo'. Both species were said to inhabit the vicinity of Sydney, NSW (Meyer 1793). These descriptions focused only on their dentition, and no type specimens were designated for either of these proposed species at the time. These early attempts to classify species without designating type specimens have contributed to the taxonomic complexities surrounding this group.

In 1802, French naturalist Nicolas Thomas Baudin collected a brushtail possum specimen reported to be from Port Jackson in Sydney, NSW (de Beaufort 1966). Upon return of the Baudin expedition to France, the collected specimens were housed at the MNHN (Jackson et al. 2021). Desmarest (1817) subsequently proposed *Phalangista vulpina*, based on a specimen in the MNHN, presumed to have been acquired during the Baudin expedition. Desmarest (1817) did not reference the earlier description of *D. vulpina* Meyer, 1793, however because both names share the same specific epithet and refer to the same taxon, *P. vulpina* Desmarest, 1817 is considered a junior subjective homonym and is therefore an invalid name (International Commission on Zoological Nomenclature 1999). As a result, specimens associated with *P. vulpina* Desmarest, 1817 are not recognised as type specimens.

FIGURE 1 The first published illustration of the 'Vulpine Opossum' (Common Brush-tailed Possum, currently *Trichosurus vulpecula*) in Phillip et al. (1789).

FIGURE 2 Illustration of 'Wha Tapoau Roo' (Common Brush-tailed Possum, currently *Trichosurus vulpecula*) in White and Stone (1790).

The specimen (MNHN-ZM-MO-1999-34), an adult female mount, is housed at the MNHN (Figure 3). *Phalangista vulpina* Meyer, 1793 is currently considered a synonym of *T. v. vulpecula*.

The 'New Holland Bear' was first described in Pennant (1793) after the description by White and Stone (1790) of 'Wha Tapoua Row (Roo)' from Sydney, NSW. This animal was described as inhabiting New Holland (Australia), with a physical resemblance to the American racoon, but with pointed ears. Bechstein (1800) later assigned the name *Ursus novaehollandiae,* based on the account by Pennant (1793) with the generic name *Ursus* Linnaeus, 1758 being associated with bears. Bechstein (1800) referred to this animal as 'The Tapouaru or New Holland Raccoon' providing a description nearly identical to that of Pennant (1793). No type specimen was designated for this species.

In 1800, Shaw then proposed *D. lemurina,* or the 'Lemurine Opossum' (Figure 4). This description drew upon accounts of the 'Wha Tapoau Roo' from Sydney, New South Wales, as described in White and Stone (1790), as well as references to 'The Vulpine Opossum of New South Wales' in Bewick and Beilby (1800), and the 'New Holland Bear' described by Pennant (1793). No designated type specimen exists for this species (Shaw 1800).

In 1824, Cuvier proposed *Phalangista cookii*. This description led to some confusion, as the name *P. cookii* was homonymous with descriptions of 'Cook's Phalanger' *P. cookii* Desmarest, 1817 and 'Phalanger of Cook', *P. cookii* Schinz, 1821 which are synonyms of what is now the Common Ringtail Possum *Pseudocheirus peregrinus* (Boddaert 1785). The illustration (Figure 5) and parts of the description in Cuvier (1824) suggest that *P. cookii* may be a synonym of the Common Brush-tailed Possum *T. vulpecula*. Described as having a thick coat, with a generally woolly appearance and some silky hairs, the dorsal region and the base of the tail were described as ash grey, while the rest of the tail was black. The ventral region of the body was a yellowish white, slightly darker on the sides, and a longitudinal brown band was present on the chest. This description was said to have been based on a living female specimen that was 'fed bread, milk, fruit, eggs, and meat without refusal' (Cuvier 1824). However, *P. cookii* was described as having a dental formula of thirty-eight teeth, with twenty-two in the upper jaw, composed of six incisors, eight 'false molars' (premolars), and eight molars, and sixteen in the lower jaw with two incisors, six 'false molars', and eight molars (Cuvier 1824). This dentition matches that of the Common Ringtail Possum. This inconsistency of

FIGURE 3 Taxidermied specimen of *Phalangista vulpina* Desmarest, 1817 (MNHN-ZM-MO-1999-34).

FIGURE 4 Illustration of *Didelphis lemurina* Shaw, 1800.

FIGURE 5 Illustration from the original description of *Phalangista cookii* Cuvier, 1824.

the described dental formula and external appearance could be explained if a ringtail possum skull had been mismatched with a brushtail possum skin. This description subsequently caused confusion, leading to several other descriptions based on *P. cookii* Cuvier, 1824. A holotype specimen may have existed in MNHN, although it has not been located (de Beaufort 1966).

In 1841, Waterhouse proposed Cuvier's Phalanger, naming it *P. cuvieri*, which was based on *P. cookii* Cuvier, 1842. Waterhouse (1841) assigned a new name to this species as it was recognised that the name was in use for a different species at the time (the Common Brush-tailed Possum). Waterhouse (1841) mentioned that the species closely resembled *P. vulpina,* however deemed it distinct. It was described as generally paler than *P. vulpina*, with larger ears, and a less bushy tail. The holotype (NHMUK 1838.10.11.3), an adult male skin and skull, is housed at the NHMUK (Figure 6). The exact type locality is uncertain, Jackson and Groves (2015) and Iredale and Troughton (1934) consider *P. cuvieri* a synonym of *T. v. fuliginosus*, the Tasmanian subspecies, suggesting that the type locality is likely Tasmania. However, Waterhouse (1846), McKay (1988), and Flannery (1994) consider it a synonym of *T. v. vulpecula*.

Waterhouse (1846) then changed his opinion regarding the previously named species *P. cuvieri* Waterhouse, 1841 and *P. cookii* Cuvier, 1824, concluding they were not the same species. He formerly believed that the two species were identical, and distinct from other species. However, upon re-examination of the specimen, Waterhouse (1846) suspected that *P. cookii* would prove to be *P. vulpina*. from the 'Continent of Australia', whilst *P. cuvieri* may be associated with *P. fuliginosa* of Tasmania. He also noted that the holotype (Figure 6) was an animal that had lived in confinement for some time before it's death, and had shed most of its longer, coarser, and darker fur, which may explain why the specimen appears paler and less woolly than the typical Tasmanian brushtail possum.

In 1829, Fischer named *P. bougainvillei* based on 'Le Phalanger de Bougainville' (Fischer 1829). The holotype specimen (MNHN-ZM-MO-1990-416 N°228), a juvenile male skin mount and skull (Figure 7), is currently housed at MNHN, with no locality data other than 'Australia'.

In 1831, Ogilby proposed the species *P. xanthopus,* which he described as being of the same size, proportions, and general appearance as *P. vulpina*, however the tail displayed an ash colour at the base, brown in the middle, and white on the last two inches. The white marking on the tail tip resembled those of *P. cookii* (referring to the Common Ringtail Possum, *Pseudocheirus peregrinus*). This description was from a specimen in the Zoological Society of London's Museum (Ogilby 1831).

In 1841, Waterhouse referred to *P. xanthopus* Ogilby, 1831 as the 'Yellow-footed Phalanger' (Waterhouse 1841). His account was based on the same specimen originally examined by Ogilby (1831). This species was reported to inhabit the interior of Australia, specifically from Iron-Bark Range near the Glenelg River in Victoria (Bennett 1837). It had long ears, a very bushy tail, and was smaller compared to *P. vulpina* and *P. fuliginosa,* resembling a rabbit in size with a proportionally shorter tail that decreased in diameter from the base to the apex. The tail displayed black colouring in the middle and white at the apex. However, Waterhouse (1846) later changed his opinion, stating that he did not consider it to be a distinct species. Instead, he suggested that what Ogilby (1831) had identified as a new species, *P. xanthopus*, was likely just one of the Common Brush-tailed Possum phenotypes characterised by a white coloured tail tip, rather than the more common black tip. Waterhouse (1846) also mentioned that specimens from the species *Petaurus breviceps* had been observed to possess a white tail tip, even though it was typically black. While a holotype specimen may exist, as both Ogilby (1831) and Waterhouse (1841) based their descriptions on a single specimen, the location of this specimen remains unknown.

In 1842, Wagner introduced the name *P. melanura*, as a replacement name for *P. cookii* Cuvier, 1824. Waterhouse (1846) mentioned that *P. melanura* was founded upon the description and figure of *P. cookii* where the authors used a name that already belonged to a different species. Waterhouse (1846) believed that *P. melanura* (*P. cookii*) was likely *P. vulpina* judging from the drawing (Figure 5) and description of *P. cookii* (Cuvier 1824).

In 1872, Krefft proposed a new species *P. rufescens* the 'Rufous Phalanger'. Parnaby et al. (2017) mentioned that this taxon has been overlooked in the taxonomic literature and suggested that it is a *nomen dubium*. Krefft (1872) distinguished *P. rufescens* from other species in the genus, asserting that it represented a new species originating from 'Port Denison' (Bowen, north Queensland) (Parnaby et al. 2017). *Phalangista rufescens* was characterised by its sandy or rufous-coloured fur, and a tail that was not very brushy, and dark brown coloured near the apex. The underside of the body exhibited a yellowish hue, while the upper body possessed pale 'straw-coloured' hairs that appeared darker near the roots. The outer side of the ears displayed a patch of yellowish white. The skull was noted to be 'considerably contracted between the orbits' and featured a sharp sagittal crest. In comparison to other *Phalangista* species, the zygomatic arches were higher and more outwardly projected. Two specimens were entered into the Australian Museum register as *P. rufescens* around 1878, however their current whereabouts are unknown and there have been no recent mentions or discoveries of these specimens in the past few decades (Parnaby et al. 2017).

In 1926, Thomas proposed the subspecies *T. v. mesurus* as an intermediate between the two variations of *T. v. vulpecula* and *T. v. johnstonii*. They were said to be found in Inkerman, near Townsville in North Queensland, and had the same grey colour as *T. vulpecula*, but with noticeably shorter and more slender tapering tails as seen in *T. v. johnstonii* (Thomas 1926). This subspecies is not currently recognised, and the holotype specimen for *T. v. mesurus* (NHMUK 1908.8.8.114), an adult female skin and skull, is housed at the NHMUK (Figure 8).

The distinction between Kangaroo Island and mainland possums was first noted in Jones (1924). These possums were described as primarily terrestrial, inhabiting bushes instead of hollow gum trees. They were larger in size, had dense long fur, and displayed a tawny grey colour on their upper bodies with a yellow or rusty hue underneath. Their tails were almost entirely black. Although the distinctiveness of the Kangaroo Island possums was acknowledged, no formal name was assigned to them at that time (Jones 1924). It wasn't until later that Finlayson (1963) named these possums *T. v. raui*. The type specimens were collected from the scrubs of Rocky River in the sanctuary of Flinders Chase, located at the western end of Kangaroo Island. The types are housed at the SAMA with the holotype (SAMA M2518) (Figure 9) and nineteen paratypes (see Table 1 for specimen numbers) consisting of male and female skins and skulls, as well as two paratypes at the AM (AM M.4839 male, and M.4848 female, both skins and skulls) (Parnaby et al. 2017). *Trichosurus vulpecula raui* is currently considered a synonym of *T. v. vulpecula.*

Finlayson (1963) observed that the Kangaroo Island possums were undoubtedly indigenous to the island, were of homogenous character, and had been isolated from the nearby mainland for at least 10,000 years. While sharing similarities with the mainland population, the Kangaroo Island possums were distinguished by their larger size, richer pelage, and darker, 'colder' dorsal colouration. The black portion of their tail was also longer. Skulls of the Kangaroo Island possums exhibited a longer and narrower zygomatic structure, as well as narrower nasal bones. Male specimens showed a greater nasal length in relation to the overall skull length. The foramen magnum, located at the base of the skull, was larger and deeper in the Kangaroo Island possums (Finlayson 1963).

Intriguingly, Jones (1924), also regarded a second population in South Australia to differ considerably from the possums in the Sydney region. These individuals were said to inhabit the creeks of the centre, residing in hollow box trees (*Eucalyptus microtheca*). Specimens from Longs Creek, Lake Phillipson, were examined, and these possums were described as a small form, with close, smooth and short fur displaying a light-blue-grey colour. The contrast between the dorsal and ventral fur was considerably less pronounced compared to what is typically observed. The black tail tip was also much shorter than the grey basal part. No distinct name was designated (Jones 1924).

Trichosurus vulpecula fuliginosus (Ogilby, 1831)

Phalangista fuliginosa Ogilby, 1831

Phalangista fuliginosa grisea Gray, 1841

Phalangista cuvieri Waterhouse, 1841

Phalangista felina Wagner, 1842

Phalangista selma Gervais, 1847

Trichosurus vulpecula ruficollis Schwartz, 1909

In 1831, Ogilby proposed a new species *P. fuliginosa*, differing from *P. vulpina* due to its uniformly dark sooty-brown pelt, with longer and thicker fur. Ogilby (1831) mentioned that the description was based on a specimen living in the Zoological Society of London's Gardens, which was believed to have been brought from Sydney, NSW. Waterhouse (1846) noted that while the animal described was assumed to be from Sydney, many specimens of similar colouration and proportions were sent to England from 'Van Diemen's Land' (Tasmania). Thomas (1888) designated a lectotype specimen from Tasmania, noting that the original locality had been recorded as Sydney; however, because no similar specimens were known from the mainland, he considered this locality to be erroneous and restricted the locality to Tasmania. *Phalangista fuliginosa* is currently recognised as the Tasmanian Common Brush-tailed Possum subspecies (*T. v. fuliginosus*). The lectotype (NHMUK 1855.12.24.212), a male adult skin and skull, is currently housed at the NHMUK (Figure 10).

In 1841, Gray proposed *P. f. grisea* as a subspecies of *P. fuliginosa* Ogilby, 1831. No description of the animal was provided, only that it was from Circular Head, Tasmania (Gray 1841), making this name a nomen nudum. The specimen upon which Gray based the proposed name was not found in 1980 (McKay 1988), however upon further investigation through this study, the specimen, an adult skin and skull (NHMUK 1841.1225) was located in the NHMUK in 2023 (Figure 11). This specimen was examined by the first author, and upon examination, it was apparent that the colouration of this specimen may have been a significant factor in the decision to distinguish it from *P. fuliginosa.* The skin of Gray's specimen of *P. f. grisea* (Figure 9) displays a coppery red brown colour that fades to a light brown cream shade on one side of the upper body. Further investigation of the cranial and dental morphology of this specimen is required to determine whether it is a valid subspecies.

In 1842, Wagner proposed *P. felina*, a rust-red animal with a mix of black fur on its back. It was reported to be approximately the same size as *P. vulpina*. No information regarding the location or distribution of this species was provided, and no type specimen was designated. The name *P. selma* Gervais, 1847 was later introduced, however, it is believed that this name was simply in error to *P. felina* Wagner, 1842.

Waterhouse (1846) observed that despite the colour variations seen in specimens from Tasmania, ranging

from black and deep rufous brown to rufous grey, grey, and cream, they exhibited very similar size and proportions. Consequently, he concluded that Tasmanian possums constituted one variable species. Waterhouse (1846) also noted that after comparing skins of specimens from Tasmania and New South Wales, the only difference he observed was in size, with the island animals being much larger than their mainland counterparts. Additionally, he found no difference in the proportions of the skulls. Waterhouse (1846) concluded that further examination of specimens was necessary to determine whether *P. fuliginosa* and *P. vulpina* were the same species. However, the evidence led him to believe that they were the same, and any differences in size and colour could be attributed to local factors such as climate and diet. Thomas (1888) reassigned *P. fuliginosa* to subspecies of *T. vulpecula* (*T. v. fuliginosus*).

In 1909, Schwarz named *T. v. ruficollis* apparently based upon two living specimens in the Frankfurt Zoo. They were described as larger and darker, with more 'sooty' coloured hair that was longer, denser, and woollier than *T. vulpecula*. They had light grey faces, and a strong predominance of rusty red tones on the cheeks, neck, shoulders, and throat. The underside was a pure white, and tail was black throughout its length. The ears were white in front, rust red on the sides and black behind, and the bridge of the nose was covered in fine, silky white hairs (Schwarz 1909). The collection location of these specimens is still in doubt, as Schwartz only gave 'Murchison District' as the locality. McKay (1988) and Jackson and Groves (2015) claimed that based on the description given, it was likely from Tasmania, and therefore regarded *T. v. ruficollis* as a synonym of *T. v. fuliginous.* Iredale and Troughton (1934) and Troughton (1941) wrote that *T. v. ruficollis* was found in the Murchison District in mid-Western Australia, and Kerle et al. (1991) wrote that *T. v. ruficollis* could be another subspecies in south-western Australia along with *T. v. hypoleucus*, as the extent of morphological variation in the south-west population is not known. The type series of *T. v. ruficollis* was designated as two specimens in the Frankfurt Zoo at the time, however these specimens have not been found to exist in any museum collections, making it difficult to determine whether it deserves subspecific status.

Trichosurus caninus (Ogilby, 1836)

Phalangista canina Ogilby, 1836

Trichosurus caninus nigrans Le Souef, 1916

In 1836, Ogilby proposed a new species said to be found beyond the Hunter River, approximately eighty miles north of Sydney in New South Wales. He proposed the name *P. canina* and noted that it was generally similar in size and proportions to *P. vulpina,* however it could be distinguished by its small, round ears, and the distribution of colours, with a uniform brown hue on the upper body and dirty ashy grey that was slightly yellow on the underparts (Ogilby 1836). Thomas (1888) designated a lectotype specimen for this species, an adult male skin and skull obtained from the Hunter River, north of Sydney NSW, and corrected the name to *T. caninus,* the 'short-eared phalanger'. Detailed descriptions and measurements were provided. The lectotype specimen (NHMUK 1855.12.24.211), an adult male skin and skull, is housed at the NHMUK (Figure 12).

In 1916, Le Souef described a melanic form of *T. caninus,* assigning it subspecific status as *T. c. nigrans*. This variant was found in the dense coastal scrubs of north-eastern New South Wales and southern Queensland, while the typical form was observed in heavily forested areas on the Great Dividing Range. These individuals were described as generally similar in size and appearance to the typical form, but possessed short, fine, and silky black fur, occasionally with a hint of grey (Le Souef 1916). The holotype (Figure 13), a male adult skin and skull (AM M.2301), and two paratypes (AM M.2557-2558) of this variant, said to be collected from the 'Tweed River' in north-eastern New South Wales, are currently housed at the AM (Parnaby et al. 2017). Lindenmayer et al. (2002) reported the capture of black-coloured individuals in the Whian Whian State Forest in north-eastern New South Wales and Cambarville in the central highlands of Victoria, however, genetic data indicated that these animals could not be considered a distinct subspecies. Consequently, these melanic individuals of *T. caninus* are currently recognised as colour variants within their local populations, rather than separate subspecies (Iredale and Troughton 1934; Troughton 1941). Other colour variants, including chocolate brown and sandy individuals, have also been observed in north-eastern New South Wales (Viggers and Lindenmayer 2004).

Trichosurus cunninghami Lindenmayer et al., 2002

Lindenmayer et al. (2002) proposed the separation of northern and southern populations of *T. caninus* into two distinct species, further discussed later in this review. This led to the establishment of the new species *T. cunninghami* (Figure 14). The holotype (AM M.35866), an adult female skin and skull, is housed at the AM and was collected from Tommy's Bend Road, Cambarville region in Victoria. Additionally, four paratypes (AM M.35867-35870) collected from the Cumberland Creek area in Cambarville, Victoria, at the same time as the holotype specimen, are also housed at the Australian Museum. This includes an adult male skin, skull and skinned body in alcohol (AM M.35867), and three female bodies preserved in alcohol (AM M.35868-35870) (Parnaby et al. 2017).

Trichosurus vulpecula hypoleucus (Wagner, 1855)

Phalangista hypoleucus Wagner, 1855

In 1855, Wagner proposed *P. hypoleucus* and described it as an animal whose habitat corresponded to that of *P. vulpina* but differed from *P. vulpina* mainly due to the dark dorsal colouration, rather than light grey. *Phalangista hypoleucus* was described as having sooty brown fur on its back, with a white and yellow-tinged underside. A broad band ran down the middle of its back, and its tail was entirely black. *Phalangista hypoleucus* had more drawn-in and deepened frontal cranium bones than *P. vulpina* of the same size (Wagner 1855). The exact location where this species was found was not specified, but it was believed to be in the western or south-western regions of 'New Holland' (Australia). Wagner (1855) also suggested that *P. hypoleucus* and *P. xanthopus* (Ogilby 1831) might be the same variety, as both exhibited yellowish-white feet tinged with brown, a dark grey to black upper body, and similar body measurements. The white tail described in *P. xanthopus* was considered to potentially be an individual difference. A lectotype specimen, an adult female flat skin and skull, was later designated by Schwarz (1909) for *P. hypoleucus,* with the habitat described as the Stirling Ranges in south-western Australia. Schwarz (1909) mentioned that the lectotype closely matched Wagner's original description, except for having a white tail tip instead of black. The current designation for this species is as a subspecies of *T. vulpecula* (*T. v. hypoleucus*), and the lectotype specimen (ZMB A9506), an adult female flat skin and partial skull, is housed at the ZMB (Figure 15).

Trichosurus vulpecula johnstonii (Ramsay, 1888)

Phalangista johnstonii Ramsay, 1888

In 1888, Ramsay proposed the name *P. johnstonii* from a population in the Bellenden-Ker Range of the Atherton Tablelands of north Queensland. This animal was characterised by its rich chestnut-red colour with black shades down its back, and a black tail often featuring a yellow-white tip. Detailed measurements and descriptions of the cranium and dentary were provided (Ramsay 1888). This taxon is currently recognised as the Coppery Brush-tailed Possum subspecies of *T. vulpecula* (*T. v. johnstonii*). The lectotype specimen, a male adult skin with skull *in situ*, designated by McKay (1988), is housed at the AM, Sydney (Figure 16), collected from the Atherton Tableland-Bellenden Ker Range region in north Queensland. Additionally, the Australian Museum houses six paralectotypes (AM M.115-118, M.121-122), all skins prepared in the field without stuffing with either no skull or skull *in situ*, collected by Cairn and Grant from the Bellenden Ker Range. One additional specimen recorded as a skin mount (M.119) has not been located in the collection (Parnaby et al. 2017). Although Ramsay (1888) provided extensive cranial and dental measurements for a single skull in the original description, which could only have been taken on an extracted skull, the location of this specimen remains unknown, and all skulls of the type series are within the skins.

Trichosurus vulpecula arnhemensis Collett, 1897

In 1897, Collett named a variation of *T. vulpecula* from northern Australia, *T. v. arnhemensis*, based on specimens collected by Dahl from Daly River and Katherine River, Northern Territory. It was noted that these animals were commonly found in Arnhem Land and Roebuck Bay but were not as abundant in other regions. The distinguishing characteristics of *T. v. arnhemensis* were its smaller size and less fury tail. The tail was described as bare on the underside, with black hairs forming a crest along the upper side but leaving the tail tip almost bare. They were typically either grey or reddish brown in colour, with one specimen having a faint trace of white on the tail tip. They also had a reddish-brown longitudinal patch in the centre of the chest (Collett 1897). Sixteen syntype specimens are housed at the UZMO (see Table 1 for specimen numbers) and one syntype is housed at the NHMUK (NHMUK 1897.4.12.3) (Figure 17). The syntypes consist of both male and female skins, skulls, skeletons, mounted specimens, young in alcohol, and embryos. The type locality of *T. v. arnhemensis* was later restricted to Daly River by Iredale and Troughton (1934).

Trichosurus vulpecula eburacensis Lönnberg, 1916

In 1916, Lönnberg named *T. v. eburacensis*, as a subspecies of *T. vulpecula*. The specimens used for this description were collected from Olen Creek, located between Coleman and Mitchell River on the Cape York Peninsula. They were characterised by their smaller size, and lighter coloured, less abundant fur. The fur was predominantly a clear grey colour, with white tips and black hairs on the dorsal, with yellowish white colouration on the ventral surface. The tail had a darker tip, with the end portion being black. Additionally, two small, young specimens collected from the same locality were described as very pale, with light grey fur, black tips on the longer hairs, white fur underneath and the outer two thirds of the tail black (Lönnberg 1916). The syntype specimens, two adult skins and skulls, (NHRM A558972 and A590065), and two juveniles, one with a skin and skull (NHRM A580563), the other with only a skin located (NHRM A600064), are housed at the NHRM (Figure 18).

TABLE 1 A summary of the past and current taxonomic names given to species in the genus *Trichosurus*, and an inventory of type material.

Name	Author	Current status	Type locality	Type specimens
Didelphis vulpecula	Kerr, 1792	*Trichosurus vulpecula vulpecula*	Sydney, New South Wales	None designated.
Didelphis vulpina	Meyer, 1793	*Trichosurus vulpecula vulpecula*	Sydney, New South Wales	None designated.
Didelphis tapouaru	Meyer, 1793	*Trichosurus vulpecula vulpecula*	Sydney, New South Wales	None designated.
Ursus novaehollandiae	Bechstein, 1800	*Trichosurus vulpecula vulpecula*	Sydney, New South Wales	None designated.
Didelphis lemurina	Shaw, 1800	*Trichosurus vulpecula vulpecula*	Sydney, New South Wales	None designated.
Phalangista cookii	Cuvier, 1824	*Trichosurus vulpecula vulpecula*	Australia	Possible holotype not found at MNHN (de Beaufort 1966).
Phalangista bougainvillei	Fischer, 1829	*Trichosurus vulpecula vulpecula*	Australia	Holotype specimen at NHMP (MNHN-ZM-MO-1990-416). See Julien-Laferrière (1994). Type specimen examined at MNHN in 2023 by first author.
Phalangista fuliginosa	Ogilby, 1831	*Trichosurus vulpecula fuliginosus*	Original description by Ogilby recorded as Sydney, New South Wales. Thomas (1888) designated lectotype specimen from Tasmania and restricted the locality to Tasmania	Lectotype designated by Thomas (1888) at NHMUK (NHMUK 1855.12.24.212). See Jenkins and Knutson (1983). Type specimen examined at NHMUK in 2023 by first author.
Phalangista xanthopus	Ogilby, 1831	*Trichosurus vulpecula vulpecula*	Iron-Bark Range near the Glenelg River, Victoria (Waterhouse 1841)	None found.
Phalangista canina	Ogilby, 1836	*Trichosurus caninus*	'Beyond the Hunter River', north of Sydney, New South Wales	Lectotype designated by Thomas (1888) at NHMUK (NHMUK 55.12.24.211). See Jenkins and Knutson (1983). Type specimen examined at NHMUK in 2023 by first author.
Phalangista cuvieri	Waterhouse, 1841	Most likely *Trichosurus vulpecula fuliginosus,* possibly *Trichosurus vulpecula vulpecula*	Australia	Holotype at NHMUK (NHMUK 38.10.11.3). See Jenkins and Knutson (1983). Type specimen examined at NHMUK in 2023 by first author.
Phalangista fuliginosa grisea (*nomen nudum*)	Gray, 1841	*Trichosurus vulpecula fuliginosus*	Circular Head, Tasmania	Specimen examined by Gray at NHMUK (NHMUK 1841.1225). See Jenkins and Knutson (1983). Specimen examined at NHMUK in 2023 by first author.
Phalangista felina	Wagner, 1842	*Trichosurus vulpecula fuliginosus*	Australia	None designated.
Phalangista melanura	Wagner, 1842	*Trichosurus vulpecula vulpecula*	Australia	Replacement name for *Phalangista cookii* Cuvier, 1824, type material as per the latter name.
Phalangista selma	Gervais, 1847	*Trichosurus vulpecula fuliginosus*	Australia	None designated.

Name	Author	Current status	Type locality	Type specimens
Phalangista hypoleucus	Wagner, 1855	*Trichosurus vulpecula hypoleucus*	Stirling Ranges, south-western Australia	Lectotype specimen designated by Schwarz (1909) at ZMB (ZMB A9506).
Phalangista rufescens (*nomen dubium*)	Krefft, 1872	*Trichosurus vulpecula vulpecula*	Port Denison, Bowen, northern Queensland	Possible type specimen in the AM however has not been located (Parnaby et al. 2017).
Phalangista johnstonii	Ramsay, 1888	*Trichosurus vulpecula johnstonii*	Atherton Tableland-Bellenden Ker Range region, northern Queensland	Lectotype (AM M120), designated by McKay (1988) and six paralectotypes (AM M.115-118, M.121-122) located at AM. Type specimens examined at AM in 2022 by first author.
Trichosurus vulpecula arnhemensis	Collett, 1897	*Trichosurus vulpecula arnhemensis*	Daly River and Katherine River, northern Australia, but restricted to Daly River by Iredale and Troughton (1934)	Syntype specimens at NHMUK (NHMUK 97.4.12.13, see Jenkins and Knutson (1983)) and UZMO (NHMO- DMA-27187 (1076), 27190 (1078), 27192 (1079), 27194 (1080), 27198 (1083), 27205 (1089), 27208 (1091), 27214 (1096), 27218 (1098), 27221 (1100), 30590 (1077), 30676 (136)) examined at NHMUK and NHMO in 2023 by first author. Other syntype specimens at UZMO are young in alcohol (NHMO-668, 669), embryos (NHMO 22079, 22080), and an embryo without number which is said to be missing. See Wiig and Bachmann (2013).
Trichosurus vulpecula ruficollis	Schwartz, 1909	Most likely *Trichosurus vulpecula fuliginosus,* possibly *Trichosurus vulpecula vulpecula*	'Murchison District', Western Australia	None found.
Trichosurus vulpecula eburacensis	Lönnberg, 1916	*Trichosurus vulpecula eburacensis*	Olen Creek, located between Coleman and Mitchell River, Cape York Peninsula, Queensland	Syntype specimens (NHRM A558972, A580563, A590065, A600064) located at NHRM. Type specimens examined at NHRM in 2023 by first author.
Trichosurus caninus nigrans	Le Souef, 1916	*Trichosurus caninus caninus*	Tweed River, north-eastern New South Wales	Holotype (M.2301) and two paratypes (AM M.2557-2558) located at AM. Type specimens examined at AM in 2022 by first author.
Trichosurus vulpecula mesurus	Thomas, 1926	*Trichosurus vulpecula vulpecula*	Inkerman, near Townsville, northern Queensland	Holotype at NHMUK (NHMUK 8.8.8.114). See Jenkins and Knutson (1983). Type specimen examined at NHMUK in 2023 by first author.
Trichosurus vulpecula raui	Finlayson, 1963	*Trichosurus vulpecula ulpecula*	Rocky River, Flinders Chase, Kangaroo Island, South Australia	Holotype (SAMA M2518) and paratypes located in the SAMA (M2509, M2516–2517, M2519, M2524, M2526, M2531–2532, M2540, M2542–2548, M2559–2561) and AM (AM M.4839, M.4848). According to Aitken (1976) 6 more paratypes not registered at SAMA might have been in Finlayson's private collection. Type specimens examined at SAMA and AM in 2022 by first author.
Trichosurus cunninghami	Lindenmayer et al., 2002	*Trichosurus cunninghami*	Tommy's Bend Road, Cambarville region, Victoria	Holotype (AM M35866) and four paratypes (AM M.35867-35870) located at AM. Type specimens examined at AM in 2022 by first author.

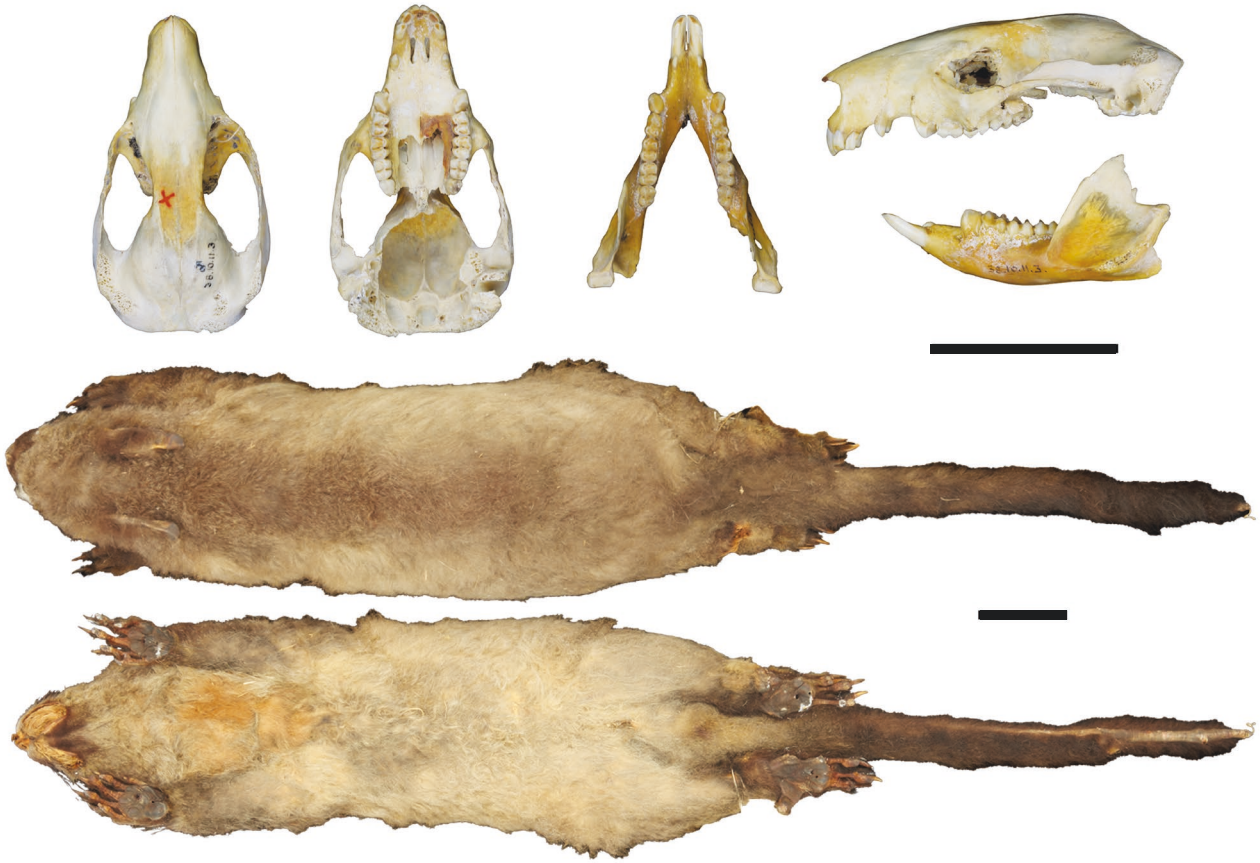

FIGURE 6 Holotype specimen of *Phalangista cuvieri* Waterhouse, 1841 (NHMUK 1838.10.11.3). Scale = 10 cm.

FIGURE 7 Holotype specimen of *Phalangista bougainvillei* Fischer, 1829 (MNHN-ZM-MO-1990-416 N°228). Scale = 10 cm.

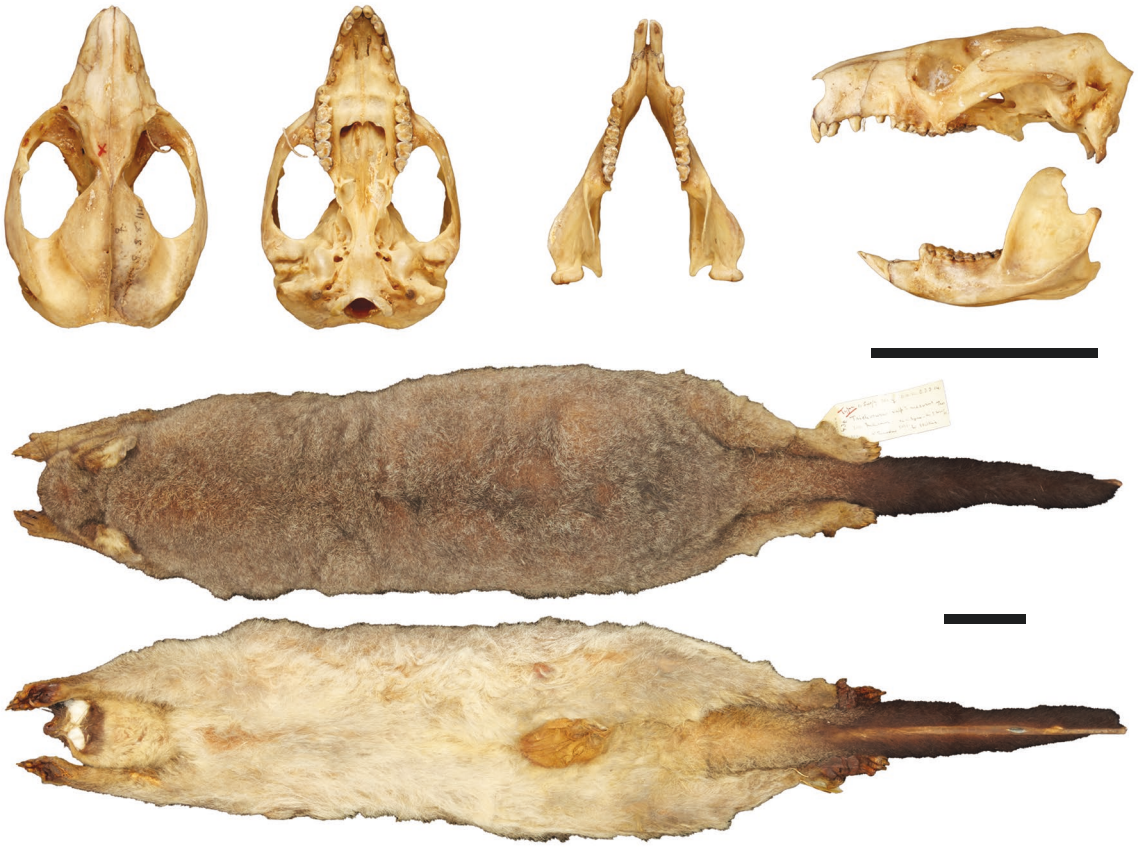

FIGURE 8 Holotype specimen of *Trichosurus vulpecula mesurus* Thomas, 1926 (NHMUK 1908.8.8.114). Scale = 10 cm.

FIGURE 9 Holotype specimen of *Trichosurus vulpecula raui* Finlayson, 1963 (SAMA M2518). Scale = 10 cm.

FIGURE 10 Lectotype specimen of *Phalangista fuliginosa* Ogilby, 1831(NHMUK 1855.12.24.212). Scale = 10 cm.

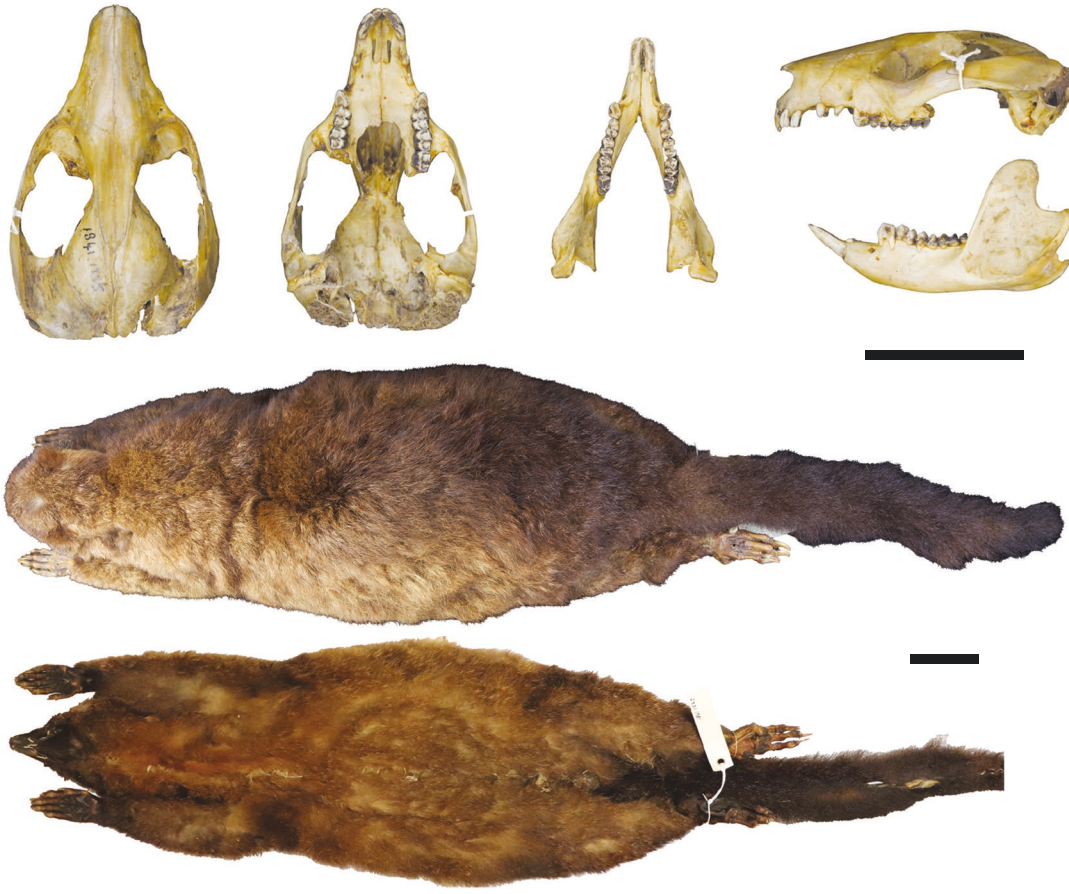

FIGURE 11 Specimen examined by Gray, 1841, *Phalangista fuliginosa grisea* (NHMUK 1841.1225). Scale = 10 cm.

FIGURE 12 Lectotype specimen of *Phalangista canina* Ogilby, 1836 (NHMUK 1855.12.24.211). Scale = 10 cm.

FIGURE 13 Holotype specimen of *Trichosurus caninus nigrans* Le Souef, 1916 (AM M.2301). Scale = 10 cm.

FIGURE 14 Holotype specimen of *Trichosurus cunninghami* Lindenmayer et al., 2002 (AM M.35866). Scale = 10 cm.

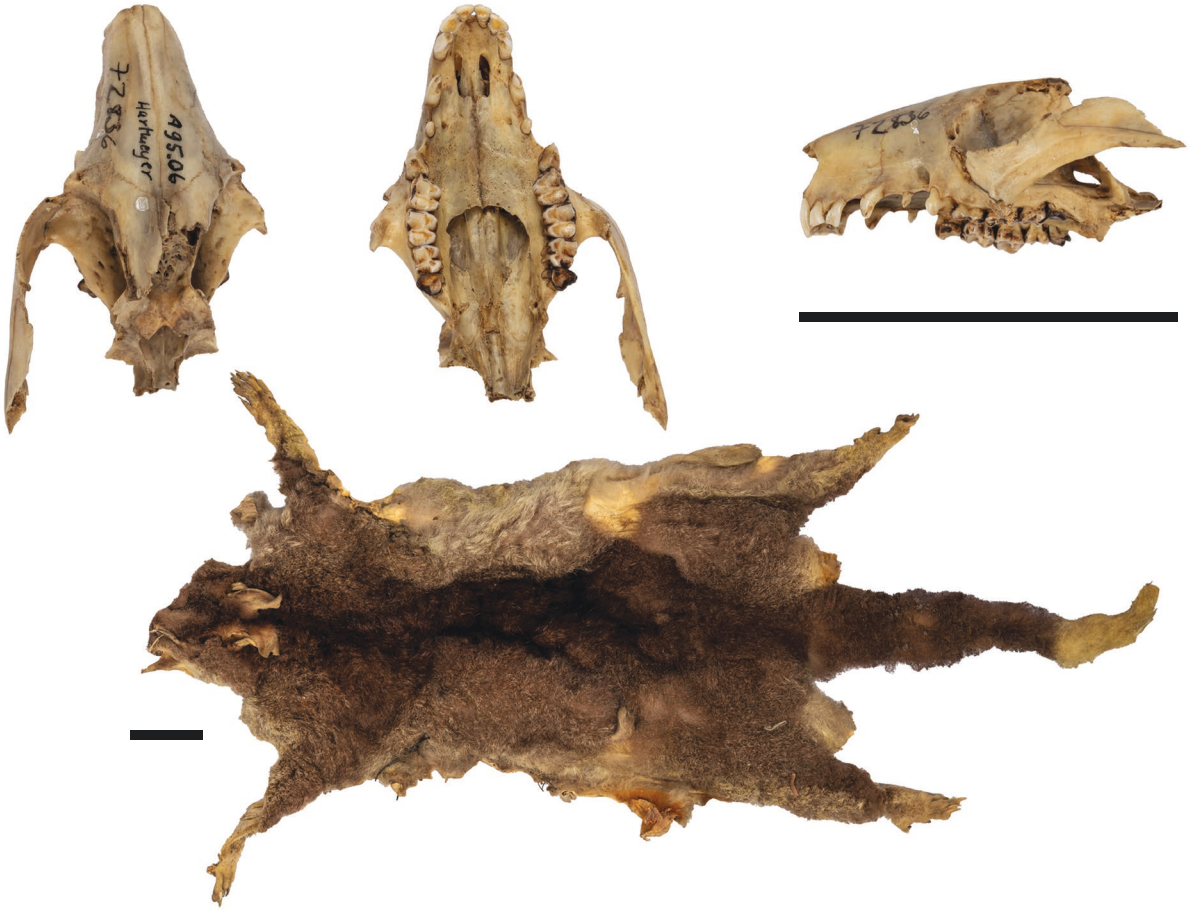

FIGURE 15 Lectotype specimen of *Phalangista hypoleucus* Wagner, 1855 (ZMB A9506). Scale = 10 cm.

FIGURE 16 Lectotype specimen of *Phalangista johnstonii* Ramsay, 1888 (AM M120). Scale = 10 cm.

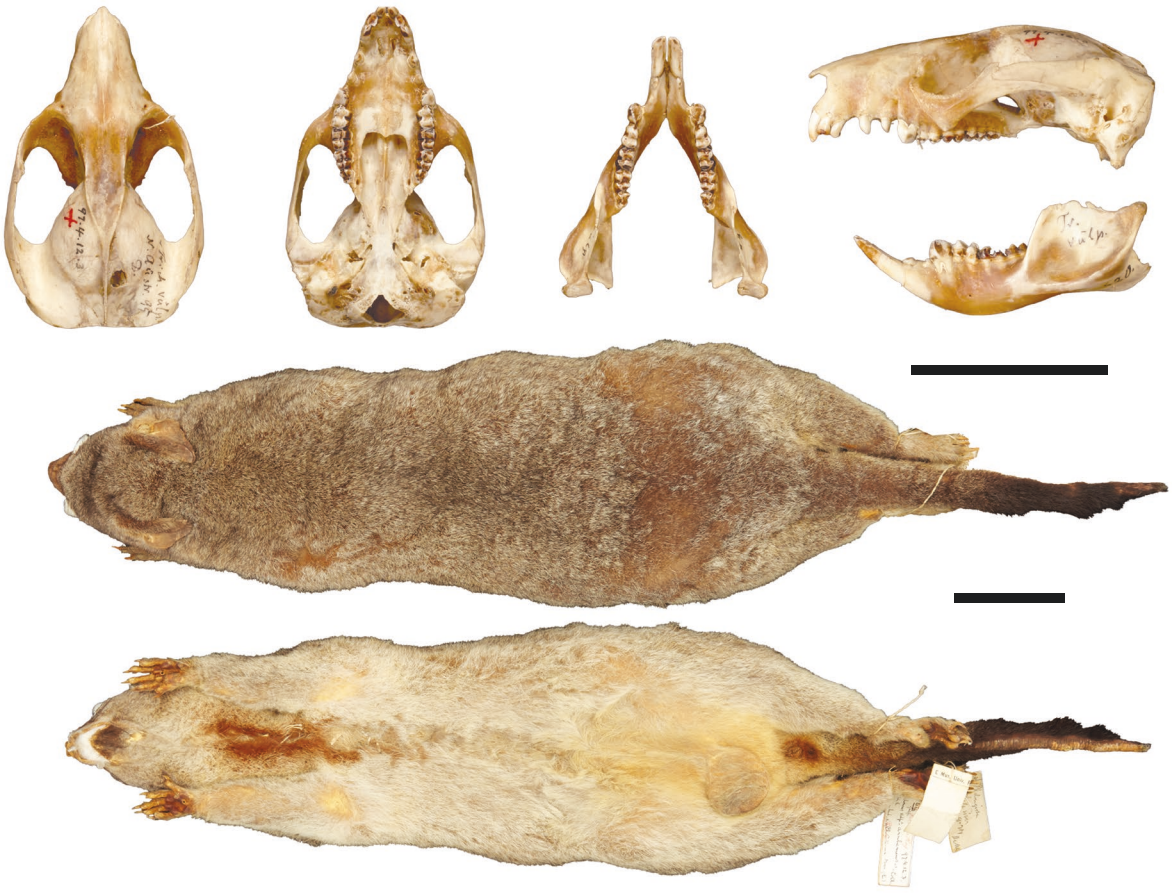

FIGURE 17 Syntype specimen of *Trichosurus vulpecula arnhemensis* Collett, 1897 (NHMUK 1897.4.12.3). Scale = 10 cm.

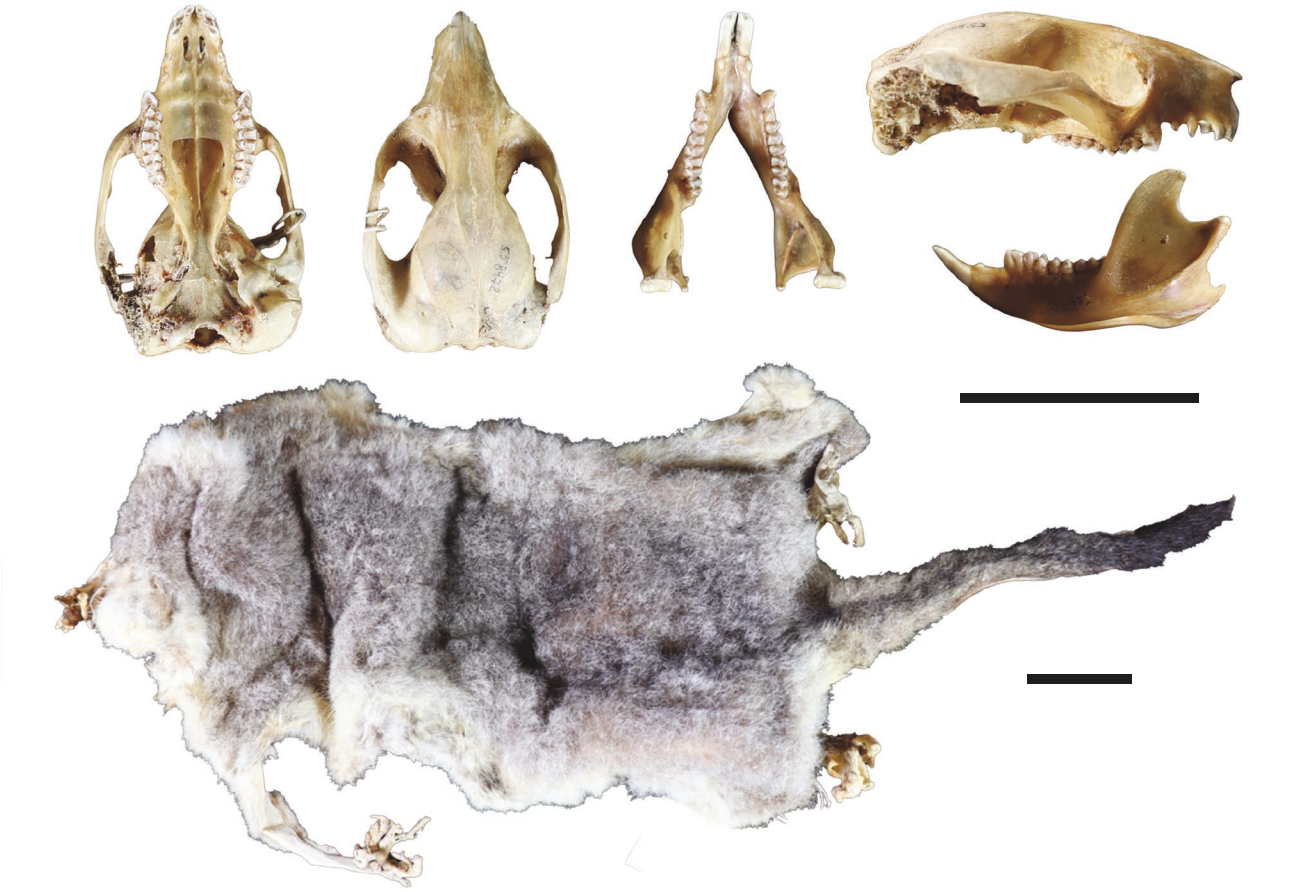

FIGURE 18 Syntype specimens of *Trichosurus vulpecula eburacensis* Lönnberg, 1916 (NHRM A558972). Scale = 10 cm.

REVISIONS AND RECENT TAXONOMIC STUDIES

These numerous descriptions have created confusion and led to progressive taxonomic re-evaluations of the genus. Iredale and Troughton (1934) regarded there to be only the two species within *Trichosurus*: *T. caninus* and *T. vulpecula*. This included seven subspecies of *T. vulpecula* in addition to the nominate subspecies; *T. v. fuliginosus, T. v. johnstonii, T. v. eburacensis, T. v. arnhemensis T. v. hypoleucus, T. v. ruficollis* and *T. v. mesurus*. Troughton (1941) regarded there to be three species in the genus, *T. caninus*, *T. fuliginosus* and *T. vulpecula*, with seven subspecies in *T. vulpecula*; *T. v. johnstonii, T. v. vulpecula, T. v. eburacensis, T. v. arnhemensis T. v. hypoleucus, T. v. ruficollis* and *T. v. mesurus*. Troughton (1941) believed that animals of the west coast, *T. v. hypoleucus,* could represent a distinct species due to their vast geographical separation, however still retained them as a subspecies of *T. vulpecula*. Tate (1952) also recognised three species within *Trichosurus*: *T. caninus*, *T. fuliginosus* and *T. vulpecula*. He regarded *T. v. johnstonii* and *T. v. eburacensis* to be subspecies of *T. vulpecula* but was unable to assess the taxonomic status of *arnhemensis*, *hypoleucus* and *ruficollis* due to lack of material.

Ride (1970) then elevated *T. v. arnhemensis* (Collett, 1897) to a full species. They were described as distinct due to being more slender and generally grey in colour, with a tail less furry than *T. vulpecula* (Ride 1970). This taxonomic decision was followed by Kirsch and Calaby (1977).

Triggs (1989) used electrophoretic analysis to examine the variation in four populations of *T. vulpecula* from Sydney, New South Wales, Adelaide, South Australia, Healesville, Victoria, and Stonehenge, Tasmania. The genetic divergence between Tasmanian possums and mainland populations was found to be comparable to that observed in other mammal species, such as Red-necked Wallabies (*Macropus rufogriseus*) (Johnston and Sharman 1979), and less pronounced than in other species like potoroos (*Potorous* spp.) (Johnston and Sharman 1977). Greater genetic divergence was found between two of the mainland populations which were regarded as the same subspecies (Adelaide and Sydney; *T. v. vulpecula*), than between Tasmanian and mainland possums. Triggs (1989) concluded the genetic data did not support the subspecific distinction of Tasmanian possums, despite observed differences in coat colour and size, which were attributed to clinal variation.

Kerle et al. (1991) undertook a systematic analysis of the Common Brush-tailed Possum across Australia, comparing morphological characters (fur colour, body size and skull dimensions), karyotypes, ecological data

and electrophoretic allozyme sequence data. Despite considerable morphological variation throughout their range, skull morphometrics, chromosomes and allozymes showed a remarkable degree of conservatism. Northern populations did not exhibit significant differences warranting separate species status, with the smaller size and fur characteristics being attributed to phenotypic plasticity in response to environmental conditions. Therefore, *T. v. arnhemensis* was reduced back to subspecific status, supported by Kerle and Howe (1992). Kerle et al. (1991) found that Barrow Island possums had an affinity to *T. v. arnhemensis* with their skull morphometrics. Like Triggs (1989), Kerle et al. (1991) found that Tasmanian populations showed no significant differences to mainland populations in morphometric and electrophoretic analyses. However, due to their geographic isolation, Tasmanian possums retained their subspecific status. South-western Australian brushtail possums (*T. v. hypoleucus*) also retained subspecific designation based on geographic isolation and morphological differences in size and fur density. Atherton Tableland populations of *T. v. johnstonii* stood apart from all other *Trichosurus* populations in the skull morphometric analysis due to the size of the first upper molar. However, the status of *T. v. johnstonii* remained unsolved due to data limitations, therefore it remained a subspecies of *T. vulpecula,* warranting further investigation. The morphometric variation in eastern populations, including Cape York Peninsula, was attributed to clinal variation, despite the detection of two fixed allozyme differences between Cape York (Weipa) and Townsville populations, and all others. Kerle et al. (1991) emphasised the need for more extensive sampling to determine the status of northern Queensland populations.

Flannery (1994) recognised *T. v. arnhemensis* and *T. v. johnstonii* as full species along with *T. vulpecula and T. caninus*. Flannery (1994) considered that *T. arnhemensis* was the smallest of the brushtail possums, with sparsely furred tails, and reddish grey to grey coloured, however no further details were given to justify the classification as a full species. Flannery (1994) suggested that the subspecific status of *T. v. johnstonii* should be revised, citing their distinctive red colouration and preliminary morphological studies that indicated potential differences in skull shape, presumably referring to the study by Kerle et al. (1991). Flannery (1994) also noted the possibility of hybridization between *T. v. johnstonii* and *T. v. vulpecula* due to overlapping ranges, however, the absence of observed hybridisation suggested the existence of reproductive isolation between the two taxa which maintains their distinctiveness.

Osborne and Christidis (2002) examined the molecular species relationships within Phalangeridae using mitochondrial DNA sequence data from the nicotinamide dehydrogenase subunit 2 gene (ND2). The lowest level of divergence found was 3.61% between *T. vulpecula* and *T. arnhemensis*, which was less than the 4.75% divergence observed between individuals of *Phalanger lullulae* from Woodlark and Alcester Islands. However, Osborne and Christidis (2002) mentioned that there were no other comparisons of subspecific or population-level differences in *Phalanger* that compare to the divergence seen in *P. lullulae,* and these populations have likely been separated since the Pliocene. *Trichosurus caninus* and *T. vulpecula* were found to have a divergence of 5.61% between them, and Osborne and Christidis (2002) claimed that the sequence divergence of only 3.61% between *T. arnhemensis* and *T. vulpecula* supported the conclusions by Kerle et al. (1991) that *T. v. arnhemensis* is a subspecies of *T. vulpecula,* rather than a distinct species as recognised by Flannery (1994).

Lindenmayer et al. (1995) examined the morphological variation within *T. caninus*, revealing significant differences between northern and southern populations. Variation in ear conch length, tail length, and pes were observed. Fur colour showed considerable variation both within and between populations, but no consistent pattern was evident. The taxonomic uncertainty of the species further increased when Fischer et al. (2001) explored the climatic factors underpinning the distribution of the species and found two bioclimatically and geographically distinct groups that aligned with groups found in Lindenmayer et al. (1995).

In 2002, Lindenmayer et al. then proposed the reclassification of *T. caninus* into two distinct species aligning with northern and southern lineages based on morphological and genetic differences. Southern populations from Victoria were found to have a significantly larger ear conch, longer pes, and shorter tail than northern populations from central New South Wales to central Queensland, as well as a mitochondrial NADH dehydrogenase subunits 5 and 6 (ND5/6) sequence divergence of 2.7–3.0% between the two populations. Lindenmayer et al. (2002) suggested that the northern form retain the name *T. caninus,* and adopt the common name 'Short-eared Possum' due to its smaller ear conch, while the southern form be named *T. cunninghami,* adopting the common name 'Mountain Brush-tailed possum'. Collins (2003) however, questioned this reclassification, noting that when compared to the intraspecific variation and divergence within *T. vulpecula,* inconsistencies within the genus become apparent. Collins (2003) mentioned that if the morphological differences and level of genetic divergence between northern and southern *T. caninus* populations qualifies as a species distinction, applying the same criteria to *T. vulpecula* would warrant the split of that species into multiple distinct species as well. Collins (2003) found greater genetic divergence (Kimura 2 parameter distances) within *T. vulpecula* (0–19%) than within '*T. caninus*' (0–11.1%).

The geographic boundary separating *T. caninus* and *T. cunninghami* remains uncertain. Lindenmayer et al. (2002) prosed that the geological and climatic barrier of

the Macleay-McPherson overlap, between central NSW and southern Queensland where the temperate Bassian and tropical Torresian biogeographical regions join, could be the potential region of separation. However, Lindenmayer et al. (2002) acknowledged that this explanation was not entirely satisfactory as possums from Allyn River, in central NSW, aligned with the northern species, which they hypothesised could be a result of incursions of northern possums. Later, Viggers and Lindenmayer (2004) hypothesised the separation of the two species to be somewhere between Sydney and Newcastle in central New South Wales.

Collins (2003) used specimens from a concurrent study by Taylor and Foulkes (2004), as well as including additional samples, to investigate the phylogeny of *Trichosurus* species using mitochondrial control region sequences. Collins (2003) suggested that there was no firm evidence that *T. v. johnstonii* was significantly distinct to be considered a separate species, or even subspecies, with specimens assigned to this taxon not forming a distinct mitochondrial lineage, therefore *T. v. johnstonii* should not be recognised. Collins (2003) supported the retention of *T. v. arnhemensis* and *T. v. hypoleucus*, with distinct Top End and Western clades identified. Barrow Island brushtail possums grouped with the Western clade, and therefore were found to be associated with *T. v. hypoleucus*, rather than *T. v. arnhemensis,* contradicting the findings by Kerle et al. (1991) which suggested they had an affinity to *T. v. arnhemensis* based on morphology. Like Triggs (1989) and Kerle et al. (1991), Collins (2003) found that *T. v. fuliginosus* did not differ significantly from mainland taxa. Collins (2003) concluded that *T. vulpecula* should consist of four subspecies: *T. v. arnhemensis*, *T. v. fuliginosus*, *T. v. hypoleucus*, and *T. v. vulpecula*.

Collins (2003) identified two phylogenetic lineages within *T. v. vulpecula* along Australia's east coast, divided by a region between Brisbane and Shoalwater Bay, with some overlap in south-western Queensland near the Macleay-McPherson overlap zone. This region was also proposed as a historical biogeographic barrier of *T. caninus* and *T. cunninghami* (Lindenmayer et al. 2002) and is thought to influence genetic divergence across multiple taxa. While its exact location is debated, it is generally placed between the McPherson Ranges and Glass House Mountains, and now broadly defined as spanning from the Glass House Mountains to the upper Hunter Valley (Burbidge 1960; Ebach et al. 2013). This region has been recognised as a hybrid zone or barrier for several species, including rock wallabies (*Petrogale*) (Sharman et al. 1989), venomous snakes (*Hoplocephalus*) (Keogh et al. 2003), skinks (*Lampropholis*) (Chapple et al. 2011a; Chapple et al. 2011b) south-east Australian land snail (*Austrochloritis*) (Köhler et al. 2020), Australian rhinolophid bats (*Rhinolophus*) (Cooper et al. 1998), Eastern Sedge Frog (*Drymomantis fallax*) (James and Moritz 2000), and subspecies of the Australian grasshopper (*Caledia captiva*) (Marchant et al. 1988). Pleistocene climatic fluctuations likely drove the expansion and contraction of mesic habitats, forming intermittent barriers to gene flow. These environmental shifts, alongside selection for adaptation to either northern tropical rainforests or southern temperate woodlands, likely contributed to the observed divergences (Cooper et al. 1998; James and Moritz 2000).

Taylor and Foulkes (2004) published a taxonomic analysis of the Common Brush-tailed Possum, with a focus on central Australian possums. The study utilised both morphological data, with cranial morphometrics and external characteristic data on body size and colour, and molecular data using mitochondrial cytochrome *b* sequences (280bp). The highest level of genetic variation observed was 6.1%, found between the Coen population (*T. v. eburacensis*) in north Queensland and the Tiwi Islands (*T. v. arnhemensis*) in the Top End region. On average, haplotype pairs of *T. vulpecula* displayed a sequence divergence of 2.7%. The phylogenetic position of *T. v. johnstonii* remained uncertain as the study contained only a single individual of *T. v. johnstonii,* from Ravenshoe. The study revealed a close relationship between the Adelaide and central Australian *T. vulpecula* populations, forming a south-central clade. Cytochrome *b* sequencing failed to distinguish Tasmanian samples (*T. v. fuliginosus*) from other haplotypes in the south-eastern clade, which corroborated the results of previous studies (Triggs 1989; Kerle et al. 1991; Collins 2003). However, due to their geographic isolation, and some evidence of morphological divergence with significant separation based on skull morphology, *T. v. fuliginosus* was retained as a subspecies. Taylor and Foulkes (2004) found limited support for retaining *T. v. arnhemensis* as a subspecies. The clustering of Top End haplotypes lacked robust bootstrap support, and significant morphometric differences were absent. The study clearly identified a south-eastern and south-western clade, supporting the validity of *T. v. hypoleucus* and *T. v. vulpecula*. Notably, the south-western clade included the Barrow Island population. A phylogeographic break was identified, separating *T. v. vulpecula* into distinct north-eastern and south-eastern clades, which aligned with the findings of Collins (2003). Taylor and Foulkes (2004) concluded that *T. vulpecula* should be considered a single species, and morphological variations among populations likely arose from local adaptation or phenotypic plasticity due to the species' high adaptability.

Groves (2005) regarded there to be five species in the genus *Trichosurus: T. arnhemensis, T. caninus, T. cunninghami, T. johnstonii,* and *T. vulpecula*. The subspecies *T. v. eburacensis, T. v. hypoleucus* and *T. v. fuliginosus* were all listed as synonyms of *T. v. vulpecula*.

In a more recent study, Carmelet-Rescan et al. (2022) estimated the timing of population fragmentation and past connectivity among the subspecies of *T. vulpecula*

using complete mitochondrial genomes. Phylogenetic analysis revealed distinct mitochondrial lineages for *T. v. hypoleucus, T. v. vulpecula,* and *T. v. arnhemensis*, indicating limited gene flow between populations since the Pliocene era. The study observed the greatest mitochondrial DNA (mtDNA) distances between *T. v. hypoleucus* in south-west Western Australia and *T. v. arnhemensis* in north-western Australia and the Northern Territory. Notably, *T. v. hypoleucus* samples from Perth, Collie, and Barrow Island formed a sister lineage to all other samples. Northern *T. v. arnhemensis* from the Kimberley and Darwin regions were found to be sister to south-eastern possums from Victoria and Tasmania. The molecular data suggested that Barrow Island possums were a part of the south-west mitochondrial lineage (*T. v. hypoleucus*), despite ecological niche modelling suggesting little suitable habitat on the western coast of Australia between these regions. Carmelet-Rescan et al. (2022) mentioned that the shared mtDNA lineage of Barrow Island and south-west possums could be attributed to either human-mediated translocation, or natural gene flow when their distribution was more extensive prior to European settlement (Abbott 2012). Tasmanian *T. v. fuliginosus* haplotypes were nested among the haplotype diversity from south-eastern Australia (*T. v. vulpecula*), including South Australia, Victoria and New South Wales.

Middleton et al. (2025) recently used both single nucleotide polymorphism markers and the mitochondrial cytochrome *b* gene to examine the population structure of brushtail possums across Australia. The results indicated that the current subspecies' classifications of *T. vulpecula* did not align with genetic structure, as Western Australian Pilbara and Midwest populations, which were previously defined as the subspecies *T. v. hypoleucus*, were instead found to be genetically similar to south-eastern and central *T. v. vulpecula*. Samples from the population in Broome, Western Australia, grouped with the south-west and Barrow Island populations, making them a part of *T. v. hypoleucus* rather than *T. v. arnhemensis* which they were previously assumed to be.

THE FUTURE

The taxonomic understanding of the genus *Trichosurus*, particularly the Common Brush-tailed Possum (*T. vulpecula*), has undergone significant revision and complexities historically. The Common Brush-tailed Possum, widely distributed across Australia, exhibits considerable phenotypic variation in body size, fur colour, and fur density between populations. Historical species descriptions often lacked any information on geographic distribution, or did not designate any type specimens, which resulted in numerous proposed names that are no longer considered valid. These species and subspecies being described and later synonymised have contributed to taxonomic confusion within the group, which remains unresolved.

This review highlights several early proposed names that deserve further investigation to assess their validity as biological entities. The currently unrecognised subspecies, *T. v. mesurus* (Thomas 1926) from the Townsville region of north Queensland, and *T. v. raui* (Finlayson 1963) from Kangaroo Island, should be investigated as to whether they warrant reinstatement. The affinities of brushtail possums on Cape York (*T. v. eburacensis*) are also uncertain and require revision (Kerle et al. 1991). Tasmanian possums (*T. v. fuliginosus*) have previously been named as a full species (Ogilby 1831), subspecies (Thomas 1888), and also debated whether they deserve either (Waterhouse 1846; Triggs 1989; Kerle et al. 1991; Collins 2003; Taylor and Foulkes 2004). Their obvious morphological differences in body size and colour, and geographic isolation, means that further investigation into their status is needed. The species *T. caninus* and *T. cunninghami* should also be investigated when assessed in the context of the genus as a whole (Collins 2003).

The taxonomic complexities and the necessity for a more comprehensive understanding of the morphological and genetic variation within *Trichosurus* clearly warrants the need for further investigation to resolve current taxonomic uncertainty about the status of some named forms. Integrating morphological data, molecular data, and insights into their evolution and historical biogeographic barriers in Australia, as well as examination of type specimens to assess the validity of past descriptions, will provide a comprehensive framework to clarify the taxonomy, unravel the evolutionary history, and assess the conservation implications for *Trichosurus* species.

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