The distribution of the water rat *Dasymys* (Muridae) in Africa: a review

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The genus *Dasymys* is widespread throughout sub-Saharan Africa. Once regarded as monotypic, we described 11 morphologically defined *Dasymys* species in a previous study. *Dasymys* is adapted for living in mesic areas, which possibly explains its disjunct distribution throughout its range. Here, we postulate that the distribution of the 11 species in Africa can be explained as reflecting the presence of water sources, which in turn define current geographical features, as well as the palaeoclimatic history of the continent. We compare the distribution of *Dasymys* with that of other animals, particularly other rodents, to examine whether there are similarities in occurrence across taxa with similar habitat requirements and to consider how geographical features influenced the distribution of small animals. The fossil record indicates that *Dasymys* originated in southern Africa, implying that the genus migrated northwards into the rest of Africa. *Dasymys* is divided into two morphologically defined groups: a southern group (*D. capensis, D. incomtus, D. robertsii, D. shortridgei* and *D. nudipes*) and a northern group (*D. medius, D. montanus, D. griseifrons, D. longipilosus, D. foxi* and the *D. rufulus* complex). Within the northern group, two possible radiation routes are suggested, one from Mozambique to Ethiopia and the other from Zambia to northern Angola and northwards through Central Africa to West Africa. These routes are based on the past or current presence of continuous water features in conjunction with morphological affinities observed for *Dasymys* species. We envisage that our model may be used to generate testable hypotheses in future investigations; for example, genetic studies could be conducted to complement the morphometric classification.

Introduction

The African water rat, *Dasymys,* is widespread throughout sub-Saharan Africa and follows a savanna distribution[1–3] (Fig. 1). Altitude does not limit its spread, as the genus occurs at altitudes from 23 m to over 4000 m throughout Africa.[4,5] It is common in the northern parts of its distribution range,[1] but it is considered rare and vulnerable in southern Africa[6] because of habitat loss through desiccation and wetland destruction.[7] Its association with water sources[8] represents an ecological constraint on dispersal and gene flow and may account for its disjunct or patchy distribution and the presence of relict populations.[9–13] In addition, many of the present-day *Dasymys* species seem to be found typically in areas that are either geographically unique, that receive high levels of rainfall or are watershed areas (e.g. the Western Cape province of South Africa, the Jos Plateau in Nigeria, Mt Cameroon, Mt Ruwenzori, and the Congo water-shed).[9,14–16] African rodent and shrew genera typically constitute a large number of endemics compared to other animal genera,[17–19] which is generally attributed to their diet, stenotopic

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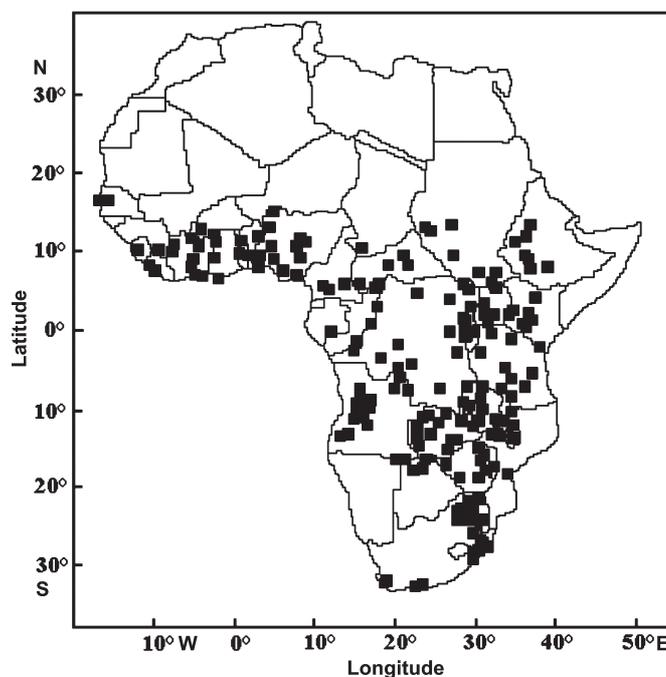*Author for correspondence. E-mail: skmullin@aol.com

Fig. 1. Distribution of *Dasymys* in Africa (from museum collections and literature sources).

nature and small size.[20] Endemic hotspots have usually been attributed to the effects of isolation and to barriers against gene flow.[21] Areas of high species richness often correspond to those of high endemic richness.[22] Several *Dasymys* species seem to represent relict populations that are associated with endemic hotspots (e.g. the Western Cape province, and the highlands or montane regions of Cameroon, Nigeria, Uganda and Ethiopia).

Although *Dasymys* was considered monotypic historically (being referred to as *D. incomtus*),[23] Musser and Carleton[24] recognized five species: *D. foxi, D. incomtus, D. montanus, D. nudipes* and *D. rufulus.* We recently completed an extensive investigation of *Dasymys* that included studies of non-geographical variation,[25] variations within *Dasymys incomtus incomtus,*[26] as well as an analysis of the entire genus[27] and of the *Dasymys rufulus* complex.[27,28] We confirmed the existence of these species, and also distinguished an additional six species (based on distinct morphological characteristics).

Of the 11 provisional, morphologically defined species described by Mullin[27] (Figs 2 and 3), seven are considered endemic to their countries of origin: *Dasymys capensis* (Western Cape province, South Africa), *D. nudipes* (southwestern Angola), *D. shortridgei* (Okavango Delta, Botswana), *D. montanus* (high altitudes on Mt Ruwenzori), *D. longipilosus* (high altitudes on Mt Cameroon), *D. foxi* (Jos Plateau) and *D. griseifrons* (Lake Tana, Ethiopia). The remaining four species are more widespread: *D. medius* occurs in East Africa; *D. incomtus* in eastern South Africa and southwestern Zimbabwe; *D. robertsii* in northern South Africa, eastern Botswana and eastern Zimbabwe; and the *D. rufulus* complex in West Africa, southern Chad, southern

Sudan, Central Africa and Central East Africa. *Dasymys robertsii* and *D. short-ridgei* represent species novitiates,[27] whereas *D. capensis, D. longipilosus* and *D. griseifrons* result from the elevation of already recognized subspecies of *D. incomtus.*

Dasymys is chromosomally conservative, with five out of six chromosomal forms characterized by FN = 44 and an overall 2n range of 36–46. Karyotypic forms include: 2n = 38, FN = 44 in the KwaZulu-Natal province of South Africa,[26,29] 2n = 46, FN = 44 in the Limpopo province of South Africa,[29] 2n = 40, FN = 50 in Burundi,[30] and 2n = 36, FN = 44 in Senegal, Mali and Ivory Coast.[31–33] The remaining two known chromosomal forms are found in Ethiopia (2n = 38, 40, FN = 44),[33] but unfortunately specimens were not available for the morphometric analyses undertaken by Mullin.[27]

Dasymys is adapted for existence in mesic areas, as revealed by descriptions of its morphology,[8,34,35] and studies of its behaviour[36] and reproductive and life-history biology.[37] On this basis, we postulate that the distribution of the 11 species in Africa can be explained by the geographical availability of water sources. In this review, we suggest that the distribution of the species reflects water flow patterns as well as current geographical features (e.g. highlands such as those found in Angola, Cameroon, Ethiopia and Nigeria) and palaeoclimatic data for the continent. In addition, we suggest that the distribution of the newly proposed *Dasymys* species corresponds to that of other small mammals, mainly rodents and insectivores, which are similarly constrained by water sources. Interestingly, two rodent genera (*Otomys* and *Aethomys*) contain species with similar ranges to some of the *Dasymys* species even though these genera have the ability to inhabit a wider range of biomes than *Dasymys.* This suggests that vicariance events are important in the distribution of small animals throughout Africa.[38] In addition to comparing *Dasymys*' distribution with that of *Otomys* and *Aethomys,* we also examined the presence of other rodents and small animals, in particular those that are associated with mesic areas (such as shrews and amphibians).

Palaeoclimates and faunal distributions in Africa

It is widely accepted that climate fluctuations in the Pleistocene influenced current geographical features and affected the distributions of animals and plants by potentially causing
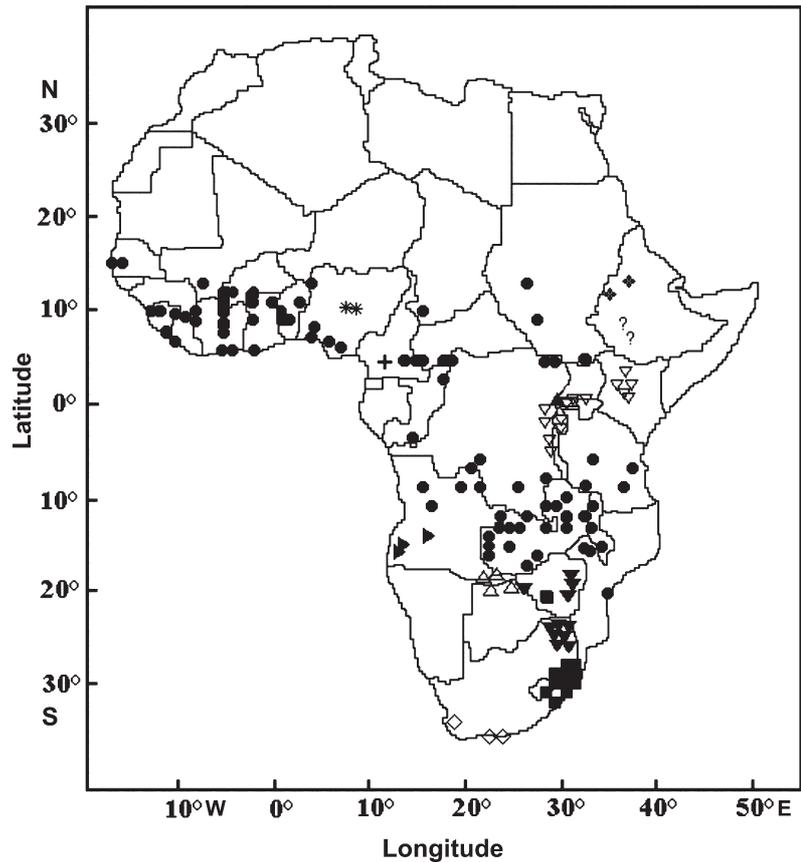

Fig. 2. Distribution of 11 morphologically defined species of *Dasymys* described by Mullin.[27] ● = *rufulus* complex (including *D. rufulus* from West Africa and material from the CAR, Cameroon, northern Angola, Zambia, Tanzania, Malawi and Mozambique); ✳ = *D. foxi*, ❖ = *D. griseifrons*; ? = unidentified);[33] + = *D. longipilosus*; ▽ = *D. medius*; ✕ = *D. montanus*; ▶ = *D. nudipes*; △ = *D. shortridgei*; ▼ = *D. robertsii*; ■ = *D. incomtus*; ◇ = *D. capensis*.
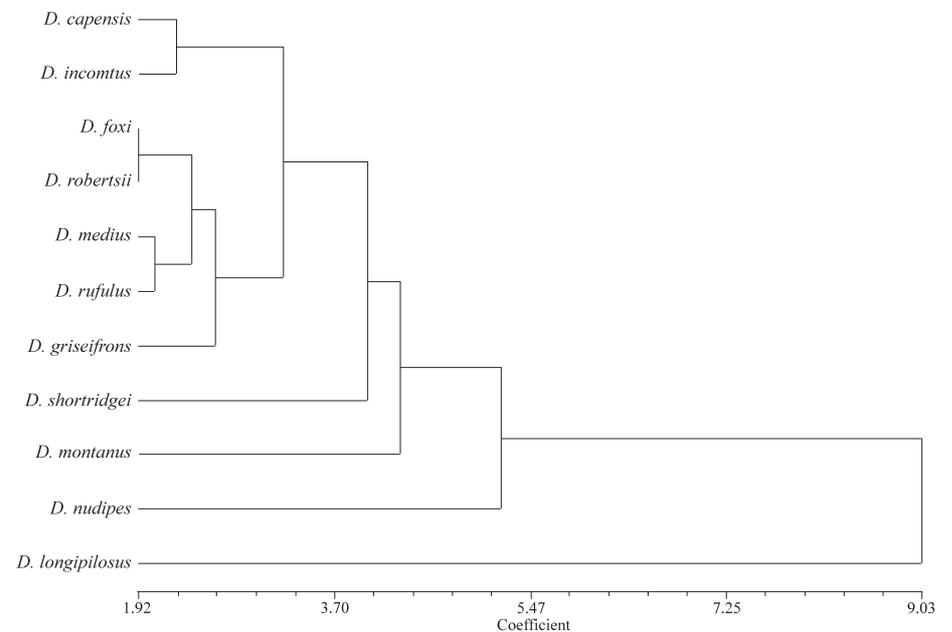
Fig. 3. A phenogram based on cranial measurements, showing the relationship between the 11 *Dasymys* species recognized by Mullin.[27] Correlation coefficient = 0.95.

disjunct distribution patterns, particularly among species that depend on perennial water sources or disperse along water routes.[14,40,43,47] It therefore follows that the speciation processes/delineation in *Dasymys* largely reflect the legacy of palaeoclimates and current geographical features, in addition to
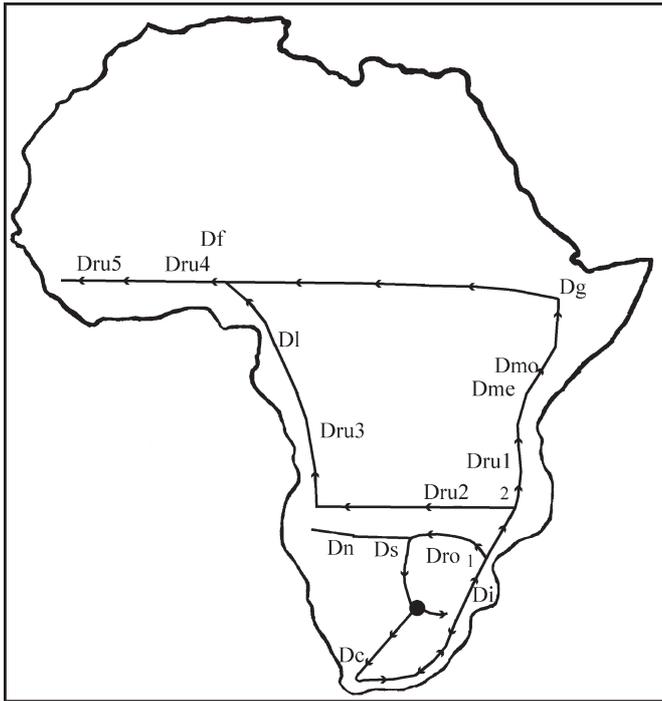
Fig. 4. Possible dispersion of *Dasymys* based on morphological data provided by Mullin.[27] **1** indicates a morphological split between 'southern' and 'northern' *Dasymys*; **2** signifies a separation between East African/Ethiopian and Central/West African *Dasymys*. Karyotyped species include: *Dro*, 2n = 48, FN = 44; *Di*, 2n = 38, 46; FN = 44; *Dru*, 2n = 36, FN = 44 in the Ivory Coast, Mali and Senegal; *Dme*, 2n = 40, FN = 50.

stochastic processes, such as drift. The African environment during the Pleistocene was characterized by fluctuating temperatures and rainfall levels.[39,40] Pluvials and interpluvials affected the topography in diverse ways, especially in terms of the expansion and contractions of forests, deserts, savannas and water sources.[41–44] At least three pluvials are recorded[45] when temperatures were 5°C and 8°C lower than today.[46] The interpluvials marked a drier period, with lakes, riverine networks and basins either retreating or drying-up.[48] In addition, forest biomes retracted, and deserts and montane grasslands expanded.[40,49,50]

Changes in habitat due to climate fluctuations have been used to explain disjunct distributions, isolated species and the occurrence of endemics among diverse animals including butterflies,[14] small mammals,[51,52] avifauna,[53] herpetofauna,[54] large mammals[43] and fish.[44] Climate changes have had a large influence on the distribution of rodents, particularly since climate defines biotypes and rodents are primary consumers.[38,52,55] From the above information, we postulate that the present spread of *Dasymys* reflects the effects of palaeoclimates on water courses in Africa.

Possible dispersion routes for *Dasymys*

It was originally thought that the Murinae had an Asian origin and radiated outwards to the rest of the African continent from East Africa.[56–58] However, fossil evidence suggests that some murids (e.g. *Acomys, Aethomys* and *Otomys*) had a southern African origin whence they radiated northward.[55,59–63] The oldest records of *Dasymys* date back to the Pleistocene (1.7–1 Myr) from Makapansgat in Limpopo,[55] which is likely to be the area of origin of this genus (Fig. 4). Details of the 11 proposed *Dasymys* species are discussed in further detail below, in order of their proposed distribution throughout Africa, beginning with the species currently found in Limpopo, *D. robertsii.* Each section also describes biogeographical features associated with each

region that could have hindered or facilitated the animal's dispersal as well as identifying species that have similar distributions to *Dasymys*. Figure 4 illustrates the distributions of each of the *Dasymys* species, with the numbers 1 and 2 on the map indicating important separations in the morphological dataset into a northern and southern *Dasymys* group.[27]

Dasymys robertsii (Dro in Fig. 4)

Dasymys robertsii is found in eastern Botswana (known only from Kasane), eastern/northeastern Zimbabwe and the Limpopo (2n = 46, NF = 44),[29] Mpumalanga and Gauteng provinces of South Africa. This distribution roughly corresponds to the Limpopo watershed area described by Revenga *et al.*[16] Zimbabwean *Dasymys* is similar to *Dasymys* from South Africa, but also has a strong morphological similarity to the genus in Zambia. The Zambezi River, which separates Zimbabwe from Zambia, has been implicated as a barrier for butterflies and the mole-rat genera *Cryptomys* and *Heliophobius*.[14,64] Aridification of the Limpopo basin, which separates the endemic-rich highlands of Zimbabwe and Limpopo, may have caused the disjunct distribution of certain amphibian, reptilian and butterfly species between Zimbabwe and the Limpopo province.[14,65–67] The morphological differences between Zimbabwean and South African *Dasymys* suggest that the Limpopo basin has acted as a barrier to *Dasymys* as well.

Dasymys robertsii was formerly recognized as *D. incomtus* and, indeed, both species were considered as the same subspecies, *D. incomtus incomtus,*[68] until morphological and genetic data were used to separate them into distinct species[26,27,29] (Fig. 3). Very few rodent species appear to have a similar distribution to either *D. robertsii* or *D. incomtus* and instead have a wider range, usually encompassing South Africa, Zimbabwe and Botswana and sometimes including Mozambique and Namibia (e.g. *Otomys irroratus, Aethomys chrysophilus, A. ineptus, Mastomys coucha, Cryptomys h. natalensis* and *C. h. hottentotus*).[69–72] Since none of these taxa has a similar distribution to either *D. incomtus* or *D. robertsii,* we suggest that *Dasymys* was previously more widespread in this region, and its separation into two species is the result of habitat fragmentation, or perhaps a reflection of *Dasymys'* restricted habitat requirements.

Denys[55] mentioned a general association between rodent specimens from the Limpopo and Mpumalanga provinces (i.e. the former Transvaal) and the Western Cape. The Orange River was once connected to the Okavango and Limpopo rivers, which would have possibly provided a distribution route for mesic species between northern and southwestern South Africa. In addition, this region was supposedly wetter in the Pleistocene, and the Karoo was previously a barrier for *Dasymys.*[48] However, Mullin[27] reported that the Western Cape *Dasymys* was more similar to specimens from KwaZulu-Natal, which does not support a dispersal route via the Karoo.

Dasymys incomtus (Di)

Dasymys incomtus sensu stricto occurs in KwaZulu-Natal (2n = 38, NF = 44),[26,29] with the type specimen for the genus described from Port Natal (= Durban), South Africa. Northern KwaZulu-Natal, characterized by Tongaland–Pondoland regional coastal mosaic vegetation,[74] has been associated with endemic amphibia,[75] rodents and shrews.[10] The Drakensberg mountain range in Mpumalanga physically separates populations of *Dasymys* between Limpopo and KwaZulu-Natal, which appear to have been isolated from each other for a lengthy time, based on morphometric and genetic differences.[26,29] As the distribution of *Dasymys* does not appear to be affected by altitude and a

possible dispersal route between KwaZulu-Natal and Limpopo is via Mpumalanga populations on the eastern side of the Drakensberg, it is not clear why there is such a strong distinction between *Dasymys incomtus* and *Dasymys robertsii*.

Mullin[27] indicated that *D. incomtus* has a potentially disjunct range, occurring in southeast Zimbabwe in the eastern Highlands (Mt Selinda and Mazoe). Mazoe is the type locality for the subspecies *D. i. fuscus,* which appears to represent a valid synonym of *D. incomtus*.[27] This disjunct distribution still needs to be confirmed by sampling more localities in Zimbabwe. The possibility that the *Dasymys* individuals found here represent a relict population of *D. incomtus* that is not morphologically distinct from *D. incomtus* should not be discounted. The Mt Selinda area is home to at least one rodent endemic, *Aethomys silindensis*.[76] *Aethomys silindensis* (which used to be considered a subspecies of *A. chrysophilus*) is presently encompassed by *A. nyikae,* which occurs elsewhere in Zimbabwe, as well as *A. chrysophilus,* which is widespread in southern Africa. Similar to *Aethomys, Dasymys i. fuscus* is surrounded by *D. robertsii* elsewhere in Zimbabwe, which raises uncertainties about its status as a valid subspecies of *D. incomtus.* To clarify this situation, any future genetic studies should compare Mt Selinda specimens with *D. incomtus* and *D. robertsii* elsewhere.

Dasymys capensis (Dc)

The Western Cape province has a distinct vegetation type (fynbos) and mediterranean climate and is an area rich in endemic or relict species of frogs, fish and rodents.[9,63,73,77,78] The region is isolated by the mountains to the north and east as well as by the arid regions to the north. *Dasymys capensis* represents either a distinct or an isolated relict population as it is restricted to the Western Cape.[9,27] As mentioned above, *D. capensis* is more similar to *D. incomtus* than to *D. robertsii,* based on morphological characteristics (Fig. 3), indicating a coastal distribution pattern between the Western Cape and KwaZulu-Natal for these species. This pattern appears to support the hypothesis that invokes a link between the lowlands of the Western Cape and Ethiopia, via an east coast grassland corridor that was once inundated with floodplains.[9,14,74]

Dasymys shortridgei (Ds)

The Okavango Delta *Dasymys* specimens (from the extreme northeast of Namibia and known only from one northern Botswana locality, Moremi) were previously classified as either *D. i. nudipes* or *D. nudipes*.[68,79] More recently, some proposed that the delta material represented a distinct subspecies of *D. nudipes,* separate from the nominate *D. nudipes* occurring in southwestern Angola.[13,80–81] Mullin[27] confirmed that this taxon represented a distinct species and suggested the provisional name of *Dasymys shortridgei* for specimens from the Okavango Delta in honour of G.C. Shortridge, who was responsible for the large collections from this area.

Dasymys shortridgei appears to be restricted to the delta and the eastern Caprivi Strip along with another rodent species, *Mastomys shortridgei*.[70] *Dasymys* specimens from western Zimbabwe have been associated with specimens from Botswana,[82] and as *D. shortridgei* is more similar to southern African material than to individuals from Central Africa,[27] *Dasymys* most likely migrated from Zimbabwe and/or Limpopo into the Okavango Delta. A faunal link between the delta/eastern Caprivi Strip and Zimbabwe/South Africa rather than with Central Africa is supported by the distributions of other rodents, such as *Cryptomys h. damarensis* and *Aethomys chrysophilus*,[69,71] which have similar, but wider, distributions than *D. shortridgei, D. incomtus* and *D. robertsii*.

Dasymys nudipes (Dn)

Other than the nominate *D. incomtus, D. nudipes* was one of the first *Dasymys* species to be recognized, based on its distinctive large size and the unique presence of a sixth planar pad.[13,81] This animal is one of three endemic rodent species isolated on the southwestern Angolan plateau; the two others are *Otomys anchietae* and *Praomys angolensis*.[13,72] Although a narrow escarpment runs along the west coast of Angola, forming a link with the Congo in the north,[13,41] *D. nudipes* does not have an affiliation with the *Dasymys* found in northern Angola, which instead is part of the *rufulus* complex (see below).[27] One possible dispersal route for *Dasymys* into southern Angola was from the Okavango Delta via tributaries from the Zambezian (Katanga) plateau in the east that led into northeastern Namibia;[83] another possibility was via a historical link between the Limpopo and the Okavango, Cunene and Zambezi–Luangwa rivers.[44]

Dasymys rufulus (Dru)

The number 1 in Fig. 4 marks a morphometric separation between southern species (*D. capensis, D. incomtus, D. nudipes, D. robertsii* and *D. shortridgei*) and the others (*D. foxi, D. griseifrons, D. longipilosus, D. medius, D. montanus* and *D. rufulus*). Number 2 on the figure marks the second clear morphological separation between East African and Ethiopian *Dasymys,* on the one hand, and Central East, Central and West African forms on the other.[27] The eastern limit of the *D. rufulus* complex is in Mozambique and Tanzania and extends to northern Angola, northwards into Central Africa [Democratic Republic of Congo (DRC), Congo, Central African Republic (CAR), Cameroon] and West Africa (Nigeria to Senegal) and includes *Dasymys* from southern Chad and Sudan. It is not uncommon for small mammals to extend across large areas between East, Central and West Africa; in the case of *Dasymys,* West and East African *Dasymys* share a strong morphological similarity (Fig. 3), but we were able to separate them into distinct species.[27] Faunal links are also well established between East Africa, Zambia and Angola in respect of rodent and amphibian species.[54,84–88] Many species have also been documented as having ranges that encompass northern Angola, Central and West Africa.[89–92]

Mullin[27] proposed five subgroups within the *rufulus* complex, although the nature of the relationship between them was unclear (e.g. species or subspecies). The five subgroups are considered below.

1. *Mozambique, northern Malawi, southern Tanzania (Dro1)*

Several relict populations of rodents exist in Malawi, Mozambique and Tanzania; genetic and morphometric studies have identified numerous new species and species complexes in the *Acomys, Cryptomys, Otomys* and *Praomys* genera.[63–64,72,93–94] As indicated above, *Dasymys* specimens from this region have a similar skull size and shape to *D. rufulus* from West Africa, and are separate from material from East Africa, with the exception of specimens from only one of the southern Tanzanian localities examined, Mlali.[27] This area is part of the mesic coastal grassland corridor described by Davis,[9] Carcasson[14] and Werger;[74] this corridor appears to have been important in *Dasymys'* dispersal throughout Africa. This region has also been associated with new descriptions of species and comprises several subzones based on vegetation types, indicating a high level of faunal separation in this area.[94–96] We mention this point to suggest that *Dasymys* in this area might be more segregated than Mullin's morphological evidence[27] indicated and propose that future studies of the genus should include a focus on material from this region.

2. *Zambia and southern Malawi (Dro2)*

Zambian and southern Malawian specimens appear to have a similar skull size and shape to northern Malawian, Mozambican and Tanzanian material, but also appear to be distinct at either a subspecies or perhaps even a species level. This area is encompassed by the Zambezi to the north, the Limpopo River to the south, and the Shire to the east. The distribution of this subgroup of *Dasymys* coincides with the limits of the Zambezi watershed area described by Revenga *et al.*[16] Moore and Larkin[44] stated that because the Zambezi was linked with the Limpopo, *Dasymys* could have migrated from southern Africa northwards and potentially migrated within Zambia. In addition, Moore and Larkin[44] suggested that the Zambezi was formerly joined with the Shire (in southern Malawi). This could have provided a dispersal route for *Dasymys* and could explain the morphometric similarities between specimens from Zambia and southern Malawi.[27]

Zambian rodents have been the focus of systematic studies recently and several genetically diverse forms of *Cryptomys* were found[64,97] as well as a new species of *Lemniscomys*.[98] A small relict highland forest important for butterflies has been identified,[14] and it has been suggested that the high altitude of the Katanga plateau in Zambia could facilitate speciation in rodents.[83] The Katanga plateau, which is characterized by numerous drainage rivers, extends into eastern and northern Angola via a former continuous forest system.[14]

3. *Central Africa (Dro3)*

Northeastern DRC is an important region for *Dasymys* as specimens from there are morphologically separate from the other Central African *Dasymys* and more similar to material from East Africa. *Dasymys* individuals from northeastern DRC are therefore included in the discussion of their East African relatives (below). *Dasymys* from the lowland forests of Central Africa, including lowland Cameroon, northern Angola, Congo, CAR and the DRC, form the third subgroup in the *rufulus* complex. The Congo watershed is extensive throughout the DRC, and extends into all of the areas where *Dasymys* from this subgroup are located (i.e. northern Angola, eastern Cameroon, eastern Congo and southern CAR).[16] Various fauna are thought to be restricted to this area because the Congo and Lualaba rivers and the Congo (or Zaire) Basin act as barriers to dispersal,[9,91,99] indicating the possibility that *Dasymys* might be confined to this region, and potentially explaining the distributional limits of the subgroup of *D. rufulus.*

4, 5. *West Africa (Dro4, 5)*

The denomination 'West Africa' generally refers to the area from Senegal to Nigeria, including the southern parts of Mali and Burkina Faso. Although West African *Dasymys* are represented by a stable karyotype (2n = 36, FN = 44 in Senegal, Mali and Ivory Coast),[31–33] Mullin[27] suggested that West African specimens were divided into two separate morphological groups. It should be noted, however, that it was not possible, using morphometric data, to determine what level this separate group represented (i.e. subspecies or species). *Dasymys rufulus* is not confined to West Africa, confirming the ideas of Musser and Carleton.[24] In addition, there appears to be some degree of inter-locality separation within *D. rufulus,* suggesting the presence of subspecies or possibly of cryptic species.

The Dahomey Gap ranges between southeastern Ghana and southern Togo and Benin and has been implicated in causing disjunct distributions in species of duikers, primates, rodents, fish and frogs.[91,100,101] Other barriers implicated in the disruption of faunal ranges include the Niger, Senaga, Senegal, Volta and Zaire rivers.[91,101,102] However, the two *D. rufulus* groups did not appear to correspond with either the Dahomey Gap borders or to major rivers in West Africa. One group, which includes the type specimen for *D. rufulus (*from Mt Coffee, Liberia), ranged from Senegal to western/southwestern Ivory Coast, while the second group was found in northern Ivory Coast to western Nigeria. This indicates that the Ivory Coast, an area that has already been associated with endemic rodent species,[91,103,104] might also be important for *Dasymys,* perhaps representing a contact zone between two West African groups.

Misonne[105] indicated that West African forest species have been largely isolated from other forested areas since the early Miocene, except for an apparent faunal connection with Ethiopia. Ethiopian *Dasymys* are distinct from the West African *Dasymys rufulus* in terms of both chromosome number and morphological characteristics, indicating that *Dasymys* from these two areas have been isolated for a long time. However, *Dasymys* from southern Sudan and Chad does appear to have a close link with *D. rufulus,* suggesting that *Dasymys* dispersed along a corridor there, perhaps via the Sudanese savanna. West African forests are not isolated from Central African forests, as they appear to share species (see below). Although some rodent species from Nigeria and Central Africa have close ties with East African forms (e.g. *Mastomys, Otomys, Praomys*),[89,93,106] this is not the case with *Dasymys*; one reason may be the poor collection records from Central Africa.[107]

Dasymys longipilosus (Dl)

Dasymys longipilosus, a species characterized by relatively small cranial features,[27] is known only from high altitudes on Mt Cameroon, although this might be a reflection of poor sampling in the region[90] rather than of a high degree of specificity. The *Dasymys* here probably represent a relict population, given that other Cameroonian *Dasymys* appear to be part of a *D. rufulus* complex, and especially since it has been suggested that the uniqueness of the Cameroon mountains may have facilitated speciation in several different animal species.[108] The highland region of Cameroon, particularly the area encompassing the Oku, Cameroon and Lefo mountains, is associated with a large number of endemics (e.g. *Dasymys, Otomys, Crocidura, Praomys, Hybomys, Lophuromys*), restricted either to a specific mountain or to neighbouring mountains.[72,90,93,109,110]

Dasymys foxi (Df)

Dasymys foxi is restricted to the Jos Plateau in Nigeria, an area occupied by several different endemic rodent species (e.g. *Cryptomys foxi, Praomys viator*).[90,111] This region is separated from the rest of Nigeria by its higher altitude, which reaches over 1200 m in places. In addition, the Jos Plateau receives more rainfall than the surrounding area,[112] perhaps linking *D. foxi* with this region. *Dasymys foxi* is surrounded by *D. rufulus,* which occurs throughout West Africa.[24] The wider skull, larger molars and generally larger size of *D. foxi* and the slightly redder colour of *D. rufulus* separate the two groups at a species level,[111] which is supported by the morphometric studies of Mullin:[27] *D. foxi* is significantly larger than *D. rufulus* with respect to upper toothrow length and greatest skull height.

Dasymys medius (Dme)

East Africa (eastern DRC, Kenya, Uganda, Rwanda and Burundi) is represented by *D. medius* regionally, whereas *D. montanus* is endemic to high altitudes on Mt Ruwenzori. *Dasymys medius* appears to represent a homogeneous species,[27] despite

the high number of previously recognized subspecies present in the area (*helukus*, *nigridius*, *orthos* and *savannus*). Denys and Jaeger[58] suggested that rodents in this area typically have a slow rate of morphological evolution; it seems likely that the Rift Valley is important in the evolution of East African mammals. The one East African population from Burundi[30] that has been karyotyped is different from the other *Dasymys* forms not only in terms of its diploid number (2n = 40), but also because it represents the only known *Dasymys* karyotype with a unique fundamental number (FN = 50; all other *Dasymys* forms karyotyped have FN = 44).[33]

In terms of skull morphology, *D. medius* is more similar to *D. rufulus* than to southern African *Dasymys,* although specimens from Burundi are characterized by X and Y chromosomes similar to those from KwaZulu-Natal, and eastern and southwestern Ethiopia,[33] indicating a close link between specimens from these regions. As stated previously, this region is important for *Dasymys* possibly because it was once part of a mesic eastern coastal grassland corridor that encompassed the lowlands between the Western Cape province and Ethiopia that were once inundated with floodplains.[9,14,74] In addition, the Nile watershed extends from Egypt through Sudan to link Uganda, Burundi, Rwanda, northern Tanzania, southwestern Kenya and the eastern DRC;[16] this approximately outlines the distribution limits of *D. medius*, with the exception of Egypt (where *Dasymys* does not occur) and Sudan.

Dasymys montanus (Dmo)

Like *D. longipilosus*, *D. montanus* also appears to represent a relict montane species. The latter is found only at high altitudes in the Ruwenzori Mountains of Uganda and is encompassed by *D. medius* in the surrounding lowland areas. *Dasymys montanus* has the characteristic dark pelage and small features associated with montane forms.[1,2] The mountains of East Africa (e.g. Mts Ruwenzori, Elgon, Kilimanjaro) have previously been described as the Galápagos of Africa[113] in reference to the large number of endemic species and the level of speciation within genera found there.

Dasymys griseifrons (Dg)

Ethiopia probably has the second highest number of endemic fauna after Cameroon, and includes country-endemic species within the following shrew and rodent genera: *Arvicanthis*, *Crocidura*, *Dasymys*, *Lophuromys*, *Otomys*, *Praomys* and *Stenocephalemys*.[33,114–119] The biological importance of this area for small mammals is emphasized by the presence of multiple endemics within the same genus, including *Crocidura*,[114] *Lophuromys*[120] and *Arvicanthis*.[121] Two chromosomal forms of *Dasymys* (*Dasymys* cf. *incomtus*: 2n = 40, NF = 44 from Bale Mountains and 2n = 38, NF = 44 from Harenna Forest) and one distinct morphological form (*D. griseifrons* known only from lakes Tana and Jigga) occur in Ethiopia.[27,92] These three forms are all distinct from the nominate *incomtus* material from South Africa.[27,33] Future studies, both morphological and genetic, need to be done to establish the taxonomic status of *Dasymys* in Ethiopia.

Ethiopia is characterized by a large plateau with an average elevation of 2200 m and is covered with forests and grasslands.[116] Yalden *et al.* indicated that the high level of endemism in this region is partly due to the Ethiopian Rift, although it is not considered a barrier to small animals as at least one rodent species, *Lophuromys chryspus,* is present on both sides of the rift.[120] The arid environment of southern Sudan and northern Kenya is thought to support restricted mammalian distributions.[116]

Conclusion

Geographical and palaeoclimatic factors have shaped the taxonomic history of *Dasymys*. The existence of at least 11 *Dasymys* species (not including the two Ethiopian chromosomal forms identified by Volobouev *et al.*[33]) is not surprising, considering the habitat restriction of the genus in conjunction with the distributions of other fauna (especially other rodent genera), particularly endemic hotspots and the areas of high rainfall. The disjunct distribution of *Dasymys* appears to coincide with water bodies and well-defined geographical features, a phenomenon that appears not only to explain its current distribution but also speciation within the genus. We have attempted here to generate a model to understand and support the morphometric distinctions within *Dasymys*. Future genetic studies should be conducted to explore random processes such as genetic drift among the 11 *Dasymys* species.

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