

Determinants of the distribution and radiation of African mole-rats (Bathyergidae, Rodentia)

Ecology or geography?

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Introduction

The African endemic rodent family Bathyergidae includes five genera of subterranean mole-rats exhibiting different social behaviour: three genera (*Bathyergus*, *Georchus* and *Heliophobius*) comprise animals of solitary habits, two genera, *Heterocephalus* and *Cryptomys* are characterized by highly social habits. Whereas four genera are monotypic (or with no more than two species recognised), karyotypically rather conservative, and their distribution is clearly delimited, the genus *Cryptomys* is polytypic with at least 14 distinguishable species having distinctly different karyotypes, and widely distributed in sub-Saharan Africa (table 1). Particularly the unique social biology (eusociality) of the naked mole-rat (*Heterocephalus glaber*) and the common mole-rat (*Cryptomys* spp.) has triggered the interest in the family, with the consequence that both genera rank currently to the most thoroughly studied and best known African rodents (cf. BURDA *et al.*, 1999, 2000; HONEYCUTT, 1991; HONEYCUTT *et al.*, 1992; SHERMAN *et al.*, 1991).

Many sociobiologists linked sociality of mole-rats to ecological factors (SHERMAN *et al.*, 1991; JARVIS *et al.*, 1994, 1998; BENNETT and FAULKES, 2000). This fact tends to be simplified by the authors of

secondary or tertiary texts on mole-rats who then consider the (eu)social species to be typical inhabitants of harsh arid climates, while solitary species are assumed to occupy mesic regions and be ecologically precluded from living in semi-deserts. The determinants of the social system and of the distribution of a particular species are generally considered to be of ecological nature (food resources, precipitation, soil characteristics).

Here, I challenge this broadly adopted view on two points:

1. Hitherto, ecological correlations are too rough and have been oversimplified. So far, only selected data and not the whole geographical range of species-relevant data have been sampled. Data on animals from selected study sites were taken as representative for the whole distribution area of a given species. This fact can be exemplified through correlation with precipitation data. It should be noted that soil characteristics and food resources may vary even on a much smaller scale, and for many widely distributed species it is almost impossible, at the current state of knowledge, to cover the whole spectrum of these habitat characteristics.
2. Geographical (geomorphological) determinants of the distribution pattern of bathyergids have never been considered.

■ Material and methods

Sources of locality records

Data on localities of a particular species of bathyergid mole-rats were obtained from the literature and my own published and unpublished data. Only unambiguously defined localities were considered to which geographic coordinates were provided or could be allocated. The sources for locality records are given in Table 1 (in some cases, when the localities were revisited several times, only one source is given):

Species mapping

Localities of species were attributed to (and defined by) quarter-degree square loci which correspond to the 1:50,000 map sheets and were numbered in the same way (cf. ANSELL, 1978; ANSELL and DOWSETT,

Species (Descriptor)	Type locality	2n (NF/2n)	Country	Sources for proved locality records
<i>Cryptomys amatus</i> (Wroughton, 1907)	Chibale (Zambia)	50 (1.92)	ZAM	Macholan <i>et al.</i> (1998)
<i>Cryptomys ansellii</i> (Burda <i>et al.</i> , 1999)	Lusaka (Zambia)	68 (1.18)	ZAM	Burda <i>et al.</i> (1999)
<i>Cryptomys bocagei</i> (De Winton, 1897)	Hanha (Angola)	58 (1.45)	ANG, NAM	Aguilar (pers. comm.), Allen (1939), Ferdinando (pers. comm.)
<i>Cryptomys damarensis</i> (Ogilby, 1838)	Damaraland (Namibia)	74/78 (1.2-1.4)	NAM, BOT, SAR, ZAM, ZIM	Aguilar (pers. comm.), Allen (1939), Honeycutt <i>et al.</i> (1987), Janecek <i>et al.</i> (1992), Lovegrove and Knight-Eloff (1988), Nevo <i>et al.</i> (1987), Smithers (1968)
<i>Cryptomys darlingi</i> (Thomas, 1895)	Harare (Zimbabwe)	54 (1.52)	ZIM	Aguilar (1993)
<i>Cryptomys foxi</i> (Thomas 1911)	Panyam (Nigeria)	66/70 (1.82)	CAM, NIG	Allen (1939), Williams <i>et al.</i> (1983)
<i>Cryptomys hottentotus</i> (Lesson, 1862)	Paarl (South Africa)	54 (1.96)	SAR	Allen (1939), Janecek <i>et al.</i> (1992), Nevo <i>et al.</i> (1987)
<i>Cryptomys kafuensis</i> (Burda <i>et al.</i> , 1999)	Itezhi-Tezhi (Zambia)	58 (1.34)	ZAM	Burda <i>et al.</i> (1999)
<i>Cryptomys</i> "Choma" formally not yet described	Kalomo (Zambia)	50 (1.52)	ZAM	Aguilar (pers. comm.)
<i>Cryptomys</i> Kasama formally not yet described	Kasama (Zambia)	64 (1.34)	ZAM	Kawaliika <i>et al.</i> (this volume)
<i>Cryptomys mechowii</i> (Peters, 1881)	Malange (Angola)	40 (2.00)	ANG, ZAM, CON	Allen (1939), Ansell (1978), Ansell and Dowsett (1988), Burda and Kawaliika (1993, unpubl.), Hill and Prior (1941), Macholan <i>et al.</i> (1993), Palata (pers. comm.), Scharff (1998)
<i>Cryptomys ochraceocinereus</i> (Heuglin, 1864)	Bahr-el-Ghazal (Sudan)	?	SUD, CAR	Allen (1939)
<i>Cryptomys Nyika</i> (= <i>C. whytei</i> ? -Thomas, 1897)	Nyika (Karonga) (Malawi)	46 (2.0)	MAL	Chitaukali <i>et al.</i> (this volume)
<i>Cryptomys zechi</i> (Matschie, 1900)	Kete-Krachi (Ghana)	?	GHA	Allen (1939)

Table 1
Continued on next page.

Species (Descriptor)	Type locality	2n (NF/2n)	Country	Sources for proved locality records
Common (small-sized) <i>Cryptomys</i> of uncertain taxonomic status			BOT, SAR, ZIM, ZAM, MAL, MOZ, TAN	Allen (1939), Allen and Loveridge (1933), Ansell (1978), Ansell and Dowsett (1988), <i>Burda (unpubl.)</i> , Davies and Jarvis (1986), Dhliwayo (pers. comm.), Roberts (1917), Smithers (1968).
<i>Bathyergus janetta</i> (Thomas and Schwann, 1904)	Port Nolloth (South Africa)	54 (2.00)	SAR	Allen (1939), Davies and Jarvis (1986), De Graaff (1981), Janecek <i>et al.</i> (1992), Nevo <i>et al.</i> (1987).
<i>Bathyergus suillus</i> Schreber, 1782	(Cape of Good Hope (South Africa)	56 (1.89)	SAR	
<i>Georchus capensis</i> (Pallas, 1778)	Cape of Good Hope (South Africa)	54 (1.92)	SAR	
<i>Heliophobius argenteocinereus</i> (Peters, 1846)	Tete (Mozambique)	60-62 (1.90-1.97)	KEN, TAN, MAL, ZAM MOZ	Allen (1939), Ansell (1978), Ansell and Dowsett (1988), Chitaukali <i>et al.</i> (this vol.), De Graaff (1981), George (1979), Janecek <i>et al.</i> (1992), Kingdon (1974), Peters (1852), Scharff (1998), Thomas (1917)
<i>Heterocephalus glaber</i> (Rüppel, 1842)	Shoa (Ethiopia)	60	ETH, KEN, SOM	Allen (1939), Faulkes <i>et al.</i> (1997), George (1979), Hill (1953), Hill <i>et al.</i> (1957), Hollister (1919), Jarvis and Bennett (1991), Kingdon (1974), Nurhusien (pers. comm.), Porter (1957), Senna (1915), Sherman <i>et al.</i> (1991), Starck (1957), Thomas (1885, 1903, 1904).

Table 1 (*suite*)

The list of currently distinguished species of Bathyergidae, their descriptors, type localities, karyotype characteristics, distribution across countries, and sources of proved locality records. 2n = diploid chromosome number. The ratio between 2n and NF (fundamental number of chromosome arms as established in a female) gives information on the proportion of biarmed (metacentric) chromosomes (high ratio) and uniarmed (acrocentric) chromosomes (low ratio) in the karyotype. Descriptors of karyotypes and the country where the karyotyped specimens came from are pointed out. ANG = Angola, BOT = Botswana, CAM = Cameroon, CAR = Central African Rep., CON = Democratic Rep. Congo, ETH = Ethiopia, GHA = Ghana, KEN = Kenya, MAL = Malawi, MOZ = Mozambique, NAM = Namibia, NIG = Nigeria, SAR = South Africa, SOM = Somalia, SUD = Sudan, TAN = Tanzania, ZAM = Zambia, ZIM = Zimbabwe.

1988). In figures 1 and 2, distribution of species were plotted by full-degree square loci, for the purpose of clarity.

Correlation with climatic data

For each quarter-degree square in which mole-rats were recorded, the nearest (within a radius of about 30 km) climatic station was identified according to the Global Historical Climatological Network database: <<http://www.ncdc.noaa.gov/ol/climate/research/ghcn/ghcn.html>>. Monthly precipitation data were retrieved from the database and mean values were counted for particular months. Altogether 179 climatic stations were considered. For each station there were on average 55 (SD 22, 10-136) year recordings (i.e., monthly data for about 55 years). All available monthly records for each station were averaged. If there were more climatic stations within the given radius of a mole-rat locality their mean precipitation data were averaged, so that eventually only one set of climatic data was related to each quarter-degree square. In a further step, means of precipitation parameters of quarter-degree squares were averaged to get a mean value characterizing the respective full-degree square. Eventually, "species-characteristic means" and standard deviations were counted from average values of all full-degree-squares in which a particular mole-rat species was recorded. In other words, mean values were counted as weighed means in a process of subsequent averaging steps. Besides that, the real climatic relevance of the precipitation station for a given locality was checked using a detailed climate-atlas (WALTHER and LIETH, 1967).

■ Results and discussion

Geographical pattern of the distribution

Although in many areas (at least within full-degree squares) up to three species of mole-rats live sympatrically, generally, there is an obvious geographical pattern in distribution of mole-rats along the main NE-SW-axis. *Heterocephalus glaber* is the only genus and

species to occur in NE Africa (Somalia, Ethiopia, Kenya). Apparently, it has not crossed the main and the Eastern branch of the Rift Valley, so that the East African Horn can be considered as the centre of origin of this monotypic genus. This conclusion is supported by the fossil records (DENYS, 1999). More southwards (southern Kenya, Tanzania), it is replaced by *Heliophobius*. In fact, the area of (original) distribution of this (also monotypic?) genus seems to be confined by both branches of the Rift Valley, the Muchinga Escarpment, mountains at the Kenya-Tanzania borders to the North, and the Zambezi river to the South. A number of *Cryptomys* species diversified in central sub-equatorial Africa, i.e., on the west "bank" of the Rift Valley (its western branch and Muchinga Escarpment). Further southwards, *Cryptomys* diversified along two parallel streams: The western branch (Zambia, Botswana, Namibia) is represented by *C. damarensis*, while the eastern branch (South Africa) comprises two subspecies of *C. hottentotus*: *C. h. hottentotus* (westwards) and *C. h. natalensis* (eastwards). Between the Zambezi and the Limpopo rivers (in Zimbabwe), only one *Cryptomys* species, *C. darlingi*, has been identified so far. On the southern tip of the continent, mainly in coastal regions, two genera, *Georychus* and *Bathyergus* with two species in the latter genus, have diversified. In west Africa north of the Equator apparently only isolates of *Cryptomys* occur.

The published maps of distribution of mole-rats (HONEYCUTT, 1992; HONEYCUTT *et al.*, 1991; JARVIS *et al.*, 1994) indicate usually only outer limits of distribution. The current method of plotting only proved records by degree squares, as is usual in faunistic studies, provides a clearer picture and a solid basis for further testing and complementary studies. It is apparent from figures 1 and 2 that the current distribution of bathyergids is geographically continuous, and well outlined in most species (rather than consisting of intermingled isolates of different species) and can be well explained on the ground of geographical (geomorphological) data.

From the current (geographical) point of view, the absence of *Cryptomys* in Tanzania and Kenya is not surprising. Concordantly, the absence of *Cryptomys* from fossil sites in East Africa (all of them are on the east side or within the Rift Valley) is not surprising (DENYS, 1999). It can also be easily understood that it has been *Cryptomys* (whose centre of origin lies out of the area confined by the Rift Valley)

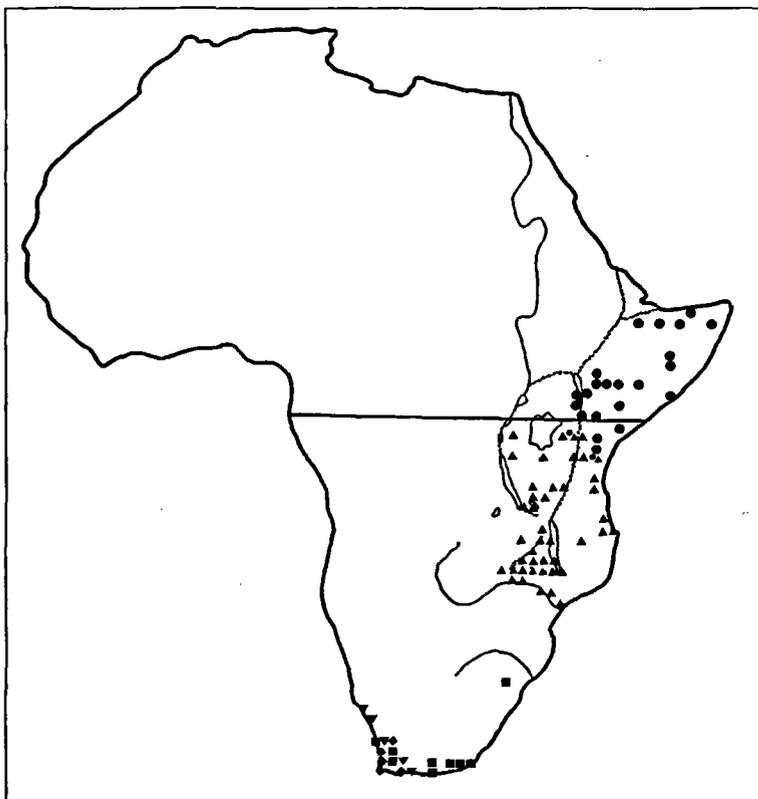


Figure 1

Distribution of Bathyergidae of the genera: *Heterocephalus* (circles), *Heliophobius* (triangles), *Bathyergus* (down pointing triangles and diamonds), and *Georychus* (squares) in Africa. Indicated is the course of the Great River Valley and Muchinga Escarpment, great African lakes, the Zambezi and the Limpopo rivers.

which could widely spread throughout Africa, and not e.g., *Heterocephalus* or *Heliophobius*. Northern and southern populations of *Cryptomys* have been apparently separated by expanding rain forest in the Congo Basin during the interglacial and/or postglacial times, or before, in the Pliocene (BROMAGE and SCHRENK, 1999). It should be tested whether the patchy distribution (particularly in west Africa) or apparent absence of *Cryptomys* (in central and east Africa) reflect a real situation or our limited knowledge.

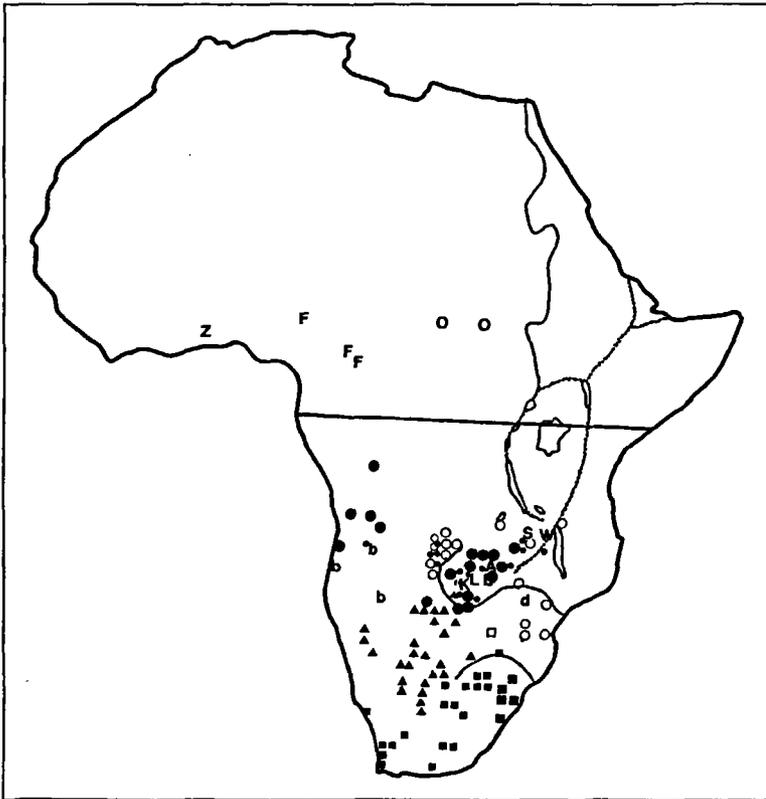


Figure 2

Distribution of the genus *Cryptomys* (Bathyergidae) in Africa: *Cryptomys damarensis* (triangles), *C. hottentotus hottentotus* (small squares), *C. h. natalensis* (large squares), *C. h. nimrodi* (empty squares), *C. darlingi* (d), *C. bocagei* (b), *C. mechowii* (full circles), common (small) *Cryptomys* of uncertain status (empty circles), *C. kafuensis* (K), *C. anelli* (L), *C. amatus* (A), *C. Kasama* (S), *C. Nyika* (= *C. whyte?*) (W), *C. ochracinereus* (O), *C. foxi* (F), *C. zechi* (Z). Indicated is the course of the Great River Valley and Muchinga Escarpment, great African lakes, the Zambezi and the Limpopo rivers.

The species diversity is particularly high in the fifteen-degree square outlined by 10°-20° S and 25°-35° E., i.e. in the very centre of the Zambezi Region (WHITE, 1983). The diversification of mole-rats in this area should be mapped in detail and the reasons (historical and/or ecological) for this speciation should be further examined. It

can be expected that even more sibling species of *Cryptomys* will be identified in the given region by biochemical, karyological and molecular methods. One of the possible factors triggering high speciation rate may be a high degree of rainfall unpredictability (uneven distribution of precipitation throughout the year) characterizing this region (table 2 and 3). High speciation of mole-rats in this region may reflect ecological changes in the past due to periodic closure (partition/fragmentation) and opening of the drought corridor running across what is now Zambia (BROMAGE and SCHRENK, 1999). Since mole-rats are typical inhabitants of savanna/savanna-woodland habitats, and as all small and particularly subterranean mammals have restricted vagility, it can be expected that they had to be most affected by the fragmentation of the savanna habitats and vicariance. Unfortunately, there are no fossil sites known from that region (DENYS, 1999). In this way, the current diversification of mole-rats is a powerful indirect means to study and understand paleoecology of the Zambezian Region.

Precipitation variables

The weighted means (averaged step by step), standard deviations and ranges of precipitation characteristics of habitats of particular mole-rat species are provided in Table 2.

There is no clear relationship between social structure and aridity as characterized by the rain amount (tables 2 and 3). While the critical aridity limit (annual rainfall less than 350 mm) favouring evolution of eusociality (JARVIS and BENNETT, 1991) may apply for selected study sites and/or years, it does not apply for average habitat requirements of given eusocial species, i.e., for the whole area of distribution and long-term records. Thus, only 20% and 27% of full-degree squares in which eusocial species, *Heterocephalus glaber* and *Cryptomys damarensis*, respectively, were recorded are characterized by a mean annual rainfall less than 350 mm. Also, 37% of the distribution area of the social *C. h. hottentotus* and 100% of the distribution area of the solitary *Bathyergus janetta* have a similarly low rainfall. Similarly, eusocial *C. mechowii* experiences seven rainless or dry months (April to October: 23, 4, 0, 0, 1, 1, 19 mm) per year in Kabwe (Zambia) but only two to three dry months in Kinshasa (Dem. Rep. Congo).

species	2n	annual rainfall (mm)					monthly rainfall (mm)				<25 (%)	<350 (%)
		mean	SD	range	n	c.v.	mean	SD	range	c.v.		
<i>B. janetta</i>	54	179			1		15	9	4-28	60	92	100
<i>B. suillus</i>	56	320	200	73-611	6	62	27	12	10-45	44	50	84
<i>C. h. hottentotus</i>	54	453	171	179-707	8	38	38	6	26-48	16	8	37
<i>C. damarensis</i>	74,78	502	195	190-960	15	39	42	44	1-113	105	42	27
<i>C. h. nimrodi</i>	54	595			1		50	52	0-134	104	50	0
<i>H. glaber</i>	60	602	299	112-1,358	25	51	50	37	17-131	74	42	20
<i>G. capensis</i>	54	632	219	228-888	12	35	53	4	47-58	7	0	17
<i>C. kafuensis</i>	58	787			1		66	81	0-199	123	58	0
<i>C. ansellii</i>	68	817			1		68	85	0-213	125	58	0
<i>C. h natalensis</i>	54	824	153	571-982	4	19	69	42	15-124	61	25	0
<i>C. darlingi</i>	54	860			1		72	78	1-202	108	42	0
<i>H. argenteo-cinereus</i>	60,62	988	275	555-1,686	37	27	83	72	8-185	87	42	0
<i>C. mehowi</i>	40	1,055	255	243-1,418	29	24	87	94	0-226	108	42	4
<i>C. bocagei</i>		1,074	265	887-1,262	2	25	89	81	0-198	91	42	0
<i>C. amatus</i>	50	1,133			1		94	110	0-269	117	50	0
<i>C. Kasama</i>	64	1,288			1		107	120	0-275	112	50	0
<i>C. Nyika</i>	46	1,415			1		118	122	4-340	103	42	0
<i>C. zechi</i>	1,437				1		120	80	15-241	67	17	0
<i>C. foxi</i>	66,70	1,591	30	1,570-1,613	2	2	133	112	2-283	84	33	0

Table 2

Precipitation variables (weighed mean values)
for areas of distribution of particular mole-rat species.
2n = diploid chromosome number (karyotype);
n = number of full-degree squares
with occurrence records and precipitation data,
c.v. = coefficient of variation (%);
< 25 = part of the year with little rain (under 25 mm/month);
< 350 = part of the area of occurrence
with annual rainfall less than 350 mm.
(No climatic data are available
for localities of *C. ochraceocinereus*.)

	Mean annual rainfall (mm)		number of months with little rain (< 25 mm/month)		variation of precipitation through the year (coeff. variation ln%)	
I. (arid)	<350	<i>B. janetta</i> , <i>B. suillus</i>	9-12	<i>B. janetta</i>	> 100	<i>C. anseli</i> , <i>C. kafuensis</i> , <i>C. amatus</i> , <i>C. Kasama</i> , <i>C. mechow</i> , <i>C. Nyika</i> <i>C. darlingi</i> , <i>C. h. nimrodi</i> , <i>C. damarensis</i>
II.	350-700	<i>C. h. hottentotus</i> , <i>C. damarensis</i> , <i>C. h. nimrodi</i> , <i>H. glaber</i> , <i>G. capensis</i>	6-9	<i>C. anseli</i> , <i>C. kafuensis</i> , <i>C. amatus</i> , <i>C. Kasama</i> , <i>C. h. nimrodi</i> , <i>B. suillus</i>	80-100	<i>C. bocagei</i> , <i>H. argenteocinereus</i> , <i>C. foxi</i>
III.	700-1,050	<i>C. kafuensis</i> , <i>C. anseli</i> , <i>C.h.natalensis</i> , <i>C. darlingi</i> , <i>H. argenteocinereus</i>	3-6	<i>C. h. hottentotus</i> , <i>C. mechow</i> , <i>H. glaber</i> , <i>C. Nyika</i> , <i>C. bocagei</i> , <i>H. argenteocinereus</i> , <i>C. darlingi</i> , <i>C. foxi</i> , <i>G. capensis</i> , <i>C. damarensis</i>	60-80	<i>H. glaber</i> , <i>C. h. natalensis</i> , <i>B. janetta</i> , <i>C. zechi</i>
IV. (mesic)	> 1,050	<i>C. mechow</i> , <i>C. bocagei</i> , <i>C. amatus</i> , <i>C. Kasama</i> , <i>C. whytei</i> , <i>C. zechi</i> , <i>C. foxi</i>	< 3	<i>C. h. natalensis</i> , <i>C. zechi</i>	40-60	<i>G. capensis</i> , <i>B. suillus</i> , <i>C. h. hottentotus</i>

Table 3
 Mean aridity and rainfall unpredictability characteristics (divided into four categories) of distribution areas of particular mole-rat species. (No climatic data are available for localities of *C. ochraceocinereus*.)

The distribution of rains throughout the year (expressed here as coefficient of variation) does not indicate any clear correlation between the unpredictability of the rain and social system either (tables 2 and 3). Similarly, the number of months with less than 25 mm of rain counted (on the basis of mean full-degree-square data sets) for the whole distribution area of a particular species cannot be correlated with the social system (table 2s and 3; see also above).

It would be a simplification to define ecological potency of particular species just on the basis of their social systems and current ecological characteristics of habitats. One should take into account that it may have been just historical reasons (geomorphological barriers) and not ecological barriers in combination with behavioural ecology, which have prevented some genera or species from occupying some regions and which are determining the current distribution pattern.

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