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Systematics and zoogeography of *Tatera* (Rodentia: Gerbillinae) of north-east Africa and Asia

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Abstract. A taxonomic revision of *Tatera* (Rodentia: Gerbillinae) from north-east Africa and Asia is undertaken. Six species are recognised: *T. robusta*, *T. phillipsi*, *T. nigricauda*, *T. valida*, *T. boehmi* and *T. indica*. The taxon *T. minuscula* from Ethiopia is considered *incertae sedis*. The zoogeographical and evolutionary history of *Tatera* is discussed. It is proposed that the genus evolved in Africa in the Early Pliocene and subsequently dispersed into Asia, possibly by way of a southern landbridge.

Key words. Mammalia, Rodentia, *Tatera*, Africa, Asia, systematics, distribution, zoogeography, evolution.

Introduction

The genus *Tatera* Lataste 1882, as defined by Ellerman (1941), has an extensive geographical distribution both in Africa south of the Sahara and in Asia. Much has been written on its taxonomy, both from a morphological viewpoint, (including the extensive works of Davis, 1949; 1965; 1966; 1975) and from a karyological perspective, (Matthey & Petter, 1970; Tranier, 1974). However there are still a number of sibling species that are accepted as valid by some workers and rejected by others and it is generally accepted that the genus is in a confused state. This paper attempts to define those species that occur in north-east Africa and Asia. It is a distillation of a recently completed Ph. D thesis and is an update on the work first reported in Bates (1985).

Material and Methods

A total of 1476 specimens were examined. These were principally held in the collections of the British Museum of Natural History (BMNH), Harrison Zoological Museum (HZM), Museum National d'Histoire Naturelle, Paris (CG) and Staatliches Museum für Naturkunde in Stuttgart (SMNS). In addition some selected material was also seen from the American Museum of Natural History (AMNH), Field Museum of Natural History, Chicago (FMNH), Los Angeles County Museum (LACM), Museo Civico di Storia Naturale, Genoa (MSNG) and Museo Zoologico de "La Specola", Florence (MZDS). A complete listing of specimens and their localities in both Africa and Asia is included in Bates (1987), copies of which are held in the Harrison Zoological Museum; British Museum (Natural History); Royal Holloway and Bedford New College library, Egham, Surrey and the University of London Library, the Senate House, London.

This present study is strictly confined to those *Tatera* species that occur in north-east Africa and Asia. North-east Africa is here defined as the region comprised of Kenya, Uganda, Sudan, Ethiopia, Somalia, Djibouti and Egypt, although no specimens are recorded from the latter two countries. However, where taxa found in north-east Africa also occur outside the region the extralimital material is discussed, where relevant. However, this extralimital material has not been included in the tables of measurements, except in the case of *T. boehmi* where the

sample size is particularly small. Unless stated otherwise all measurements are for adult specimens, as defined in Bates (1985).

The measurements are defined as follows: HB (Head and body length); from the tip of the nose to the base of the tail dorsally. TAIL (Tail length); from the base of the tail dorsally to the tip, but not including any protruding hairs. HF (Hindfoot Length); from the posterior extremity of the heel to the tip of the longest toe, but not including the claw. E (Ear length); from the uppermost margin of the pinna to the base of the notch. GTL (Greatest Length of skull); greatest antero-posterior diameter, taken from the tip of the nasals to the supra occipital. CBL (Condylbasal Length); from the exoccipital condyle to the anterior extremity of the premaxilla, at the alveolar margin of the most forwardly projecting upper incisor. ZB (Zygomatic Width); greatest width across the zygomatic arches. BB (Breadth of Braincase); taken at posterior roots of the zygomatic arches. IC (Interorbital Constriction); narrowest width across the interorbital region. RW (Rostral Width); taken transversely immediately in front of the zygomatic plates. RL (Rostral Length); tip of the nasals to the antero-superior margin of the infraorbital foramen. TMW (Trans Molar Width); taken across outer borders of the maxillary molars. TB (Tympanic Bulla Length); greatest oblique antero-posterior diameter, taken from the apex of the tympanic bulla external to the hamular process to the most posterior part of the mastoid chamber of the tympanic bulla external to the base of the paroccipital process. TBW (Trans Bulla Width); greatest transverse diameter across both tympanic bullae from the border of the exterior meati. OH (Occipital Height); taken from the midpoint of the exoccipital below the foramen magnum to the top of the lambda. ML (Mandible Length); taken from the tip of the angular process to the most anterior projecting point, including the lower incisors. MXC (Maxillary Cheekteeth row length); taken from the front of the alveolar margin of the first molar to the back of the crown of the third molar. MXCW (Width of the first Maxillary Cheektooth; greatest width taken across the first molar. MDC (Mandibular Cheekteeth row length); taken from the front of the crown of the first molar to the alveolar margin of the back of the third molar. IH (Upper Incisor Height); taken from the anterior alveolar margin to the tip. IW (Upper Incisor Width); taken at the alveolar margin. GLF (Greatest Length of Femur); from the most anterior projecting surface of the trochanter major to the most posterior surface of the distal extremity. GLH (Greatest Length of Humerus); from the most anterior projecting surface of the head to the most posterior surface of the distal extremity. TOT (Total body weight) in grams. EVIC (Eviscerated body weight) in grams.

Results

Tatera robusta (Cretzschmar, 1826)

Meriones robustus Cretzschmar, 1826. — In Ruppell's Atlas zu d. Reise im nördl. Afrika, Säugeth., p. 75, pl. 29. Kordofan.

Material: A total of 459 specimens were examined from 123 localities in Ethiopia, Kenya, Somalia, Sudan, Uganda and extraliminally from Burkina Faso, Chad and Tanzania.

Diagnostic description: This is a medium-sized *Tatera* gerbil with a greatest skull length of 39.0–44.7 mm. The tail, like that of *T. phillipsi*, generally exceeds head and body length and always has a dark terminal tuft. This clearly distinguishes it from the relatively short, untufted tails of *Tatera valida* and the long, pale tipped tails of *T. boehmi*. It is usually bicolored, with a clear demarcation between the dark dorsal and pale ventral surfaces. However, in a sizeable minority of specimens (26.1%, n = 368) the distal half of the ventral aspect is also covered in dark hairs and consequently there is no demarcation between the upper and lower surfaces of the tail. This leads to frequent confusion with some of the paler tail types of *T. nigricauda*. A small percentage of specimens (4.9%) had tricolored tails, with dark dorsal and ventral surfaces and pale lateral aspects. In all cases the ventral surface was only faintly marked and as such could not be confused with *T. indica*. According

to Neal (1982), average body weight of *T. robusta* (Table 1) is exceeded by both *T. valida* and *T. nigricauda*.

The skull of *T. robusta* has a relatively long and narrow rostrum, (Plate 1). This character distinguishes it from all the other north-east African species except *T. phillipsi*. The rostrum of *T. nigricauda* is also relatively narrow but it always exceeds in size those of *T. robusta* when a comparison is made of adult material of the same sex from sympatric populations, (Fig. 1). Generally the skulls of *T. robusta* tend to be smaller than those of *T. nigricauda*. Unlike *T. indica* and a very small minority of *T. valida* and *T. boehmi* specimens, the superior posterior mastoid chamber of the

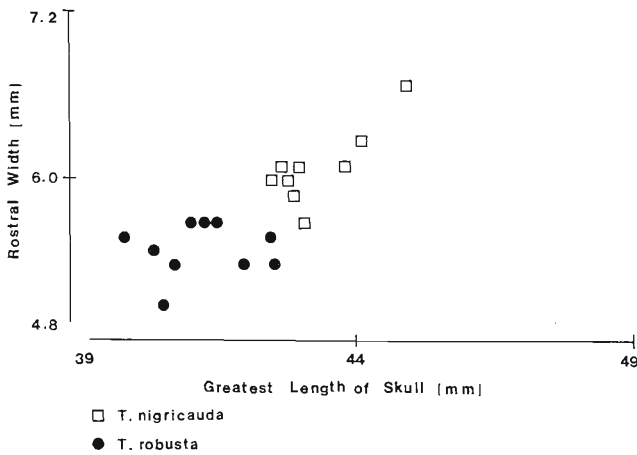


Fig. 1: Comparison of sympatric *Tatera nigricauda* and *T. robusta* from central and northern Kenya. Data for adult females.

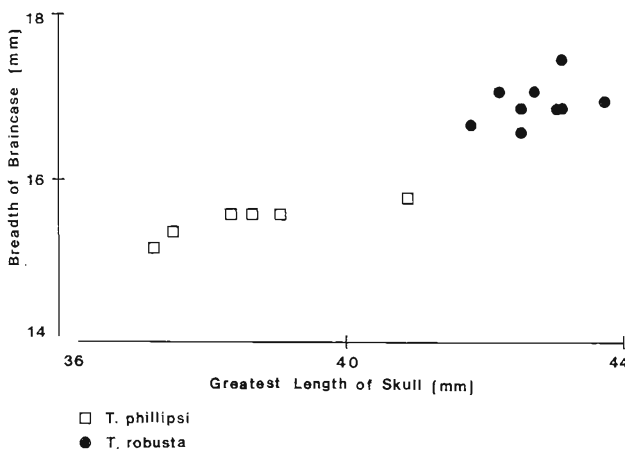


Fig. 2: Comparison of sympatric *Tatera phillipsi* and *T. robusta* from Ethiopia. Adults of both sexes.

tympanic bulla is never inflated in *T. robusta*. *T. robusta* can only be distinguished from *T. phillipsi* on the basis of skull size. When sympatric populations of the two species are compared, the *T. robusta* material is clearly larger (Fig. 2), although the status of minority of individuals may be difficult to determine.

The cheekteeth are relatively narrow. This is in marked contrast to those of *T. valida* and *T. boehmi*. The upper incisors are opisthodont and always have a single clearly defined groove. In comparison to *T. valida* and *T. boehmi*, the nasals extend well beyond the anterior alveolar margin of the incisors (Fig. 3).

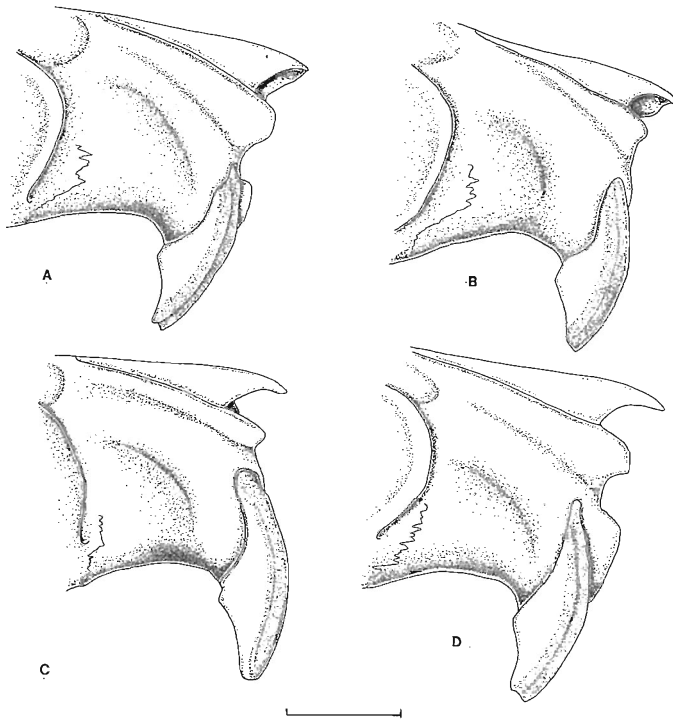


Fig. 3: Morphology of the nasals and incisors of three species of *Tatera*.

A: *T. robusta*, HZM. 52.13466, male, 29.x.1983, Kamuuni, Machakos District, Kenya.

B: *T. valida*, SMNS. 30797, male, 4/5.ii.1979, Nagishot/Didinga mts., Sudan.

C: *T. boehmi*, HZM. 2.10970, male, 4.viii.1973, Kasombo Stream, Zambia.

D: *T. indica*, HZM. 17.10399, —, 21.ii.1979, Vikas Vidyalaya, Ranchi, Bihar, India. Scale = 5 mm.

The chromosomal formula is here considered to be $2N = 40$, $FN = 70$. This is based on two specimens from Omo, Ethiopia, which were assigned by Matthey (1969) to *T. nigricauda* but which were considered by Bates (1987) as being referable to *T. robusta* (for details see *T. nigricauda* section below). Two specimens from the Central African Republic referred by Matthey & Petter (1970) to *T. robusta* and for which the chromosomal formula was given as $2N = 46$, $FN = 68$ have short, broad rostra and as such would appear to be incorrectly identified.

Variation: There is no significant sexual dimorphism. However there is considerable variation between individuals, notably in tail colour. Specimens with relatively dark tails are found throughout the species' range, except Tanzania. However, the frequency of such specimens increases from the south to the north of the taxon's range. They are especially common west of the Eastern Rift Valley in northwestern Kenya, eastern Uganda, southwestern Ethiopia and southern Sudan.

There is little significant geographical variation in skull or body size, except that specimens from the south of the range tend to be relatively small. Future research may show that there is a distinct small race in central Tanzania, characterised by small tympanic bullae and a relatively short skull and a predominance of well defined, bicolored tails. Should this prove to be the case, the name *swaythlingi* (Kershaw, 1921) type locality Morogoro, Tanzania, is available as the holotype agrees in these features. However, it is considered at present that the species is monotypic, albeit one that exhibits some geographical variation, and that the following forms should be included in the synonymy of *T. r. robusta*: *iconica*, *macropus*, *mombasae*, *muansae*, *loveridgei*, *pothae*, *shoana*, *swaythlingi*, *taylori* and *vicina*. The forms *bayeri* and *bodessae* considered by Davis (1975) to be synonyms of *T. nigricauda* are here referred to *T. robusta* (see section on *T. nigricauda* below). It should also be noted that Bates (1985) maintained that the West African forms *guineae* and *picta* are not referable to *T. robusta*.

Distribution: The distribution in north-east Africa and Tanzania is shown in Fig. 4. It is also recorded from Burkina Faso (Bates, 1985).

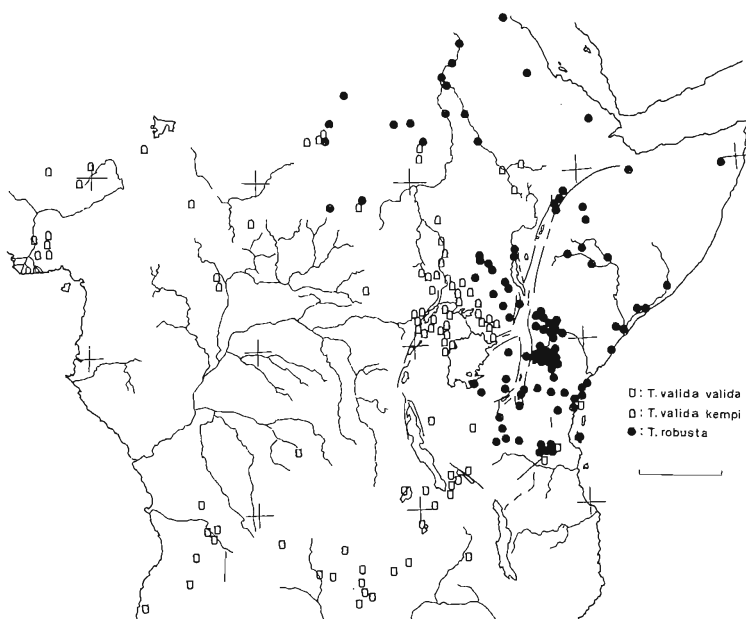


Fig. 4: Distribution of *Tatera robusta* and *Tatera valida*. Scale = 500 km.

Remarks: *T. robusta* has a distribution that tends to be restricted to the "drier savannah types, bush and thicket" (terminology of Kingdon, 1971) of Eastern Africa. It is absent from higher altitude areas, in general those over 1700 metres. The distribution in the south of its range appears to be limited by the southern highlands of Tanzania and the Rufiji River. According to Senzota (1983, 1984), *T. robusta* in the Serengeti National Park was found almost exclusively in the open parts of short grassland plains, being absent from areas of thick vegetation which received heavy rains. The species most preferred areas with loose soil as this facilitated the construction of its burrow systems which provide nesting sites as well as shelter from the sun and predators. *T. robusta* was also absent from valley bottoms that experienced seasonal flooding. Hubert (1978) reported that in the Omo Valley, Ethiopia, "*T. nigricauda*" (here considered to be *T. robusta*) was found in two different biomes. Along with *Mastomys erythroleucus*, *Saccostomus mearnsi* and *Acomys wilsoni* it was present in a riverine zone, largely without trees but with grasses and very dense thicket. It was also found on the plateau area which had a vegetation of open shrubs and bush savanna. Here it was associated with *Taterillus harringtoni*, *Xerus rutilus*, *Acomys wilsoni* and *Arvicanthis niloticus*. Yalden, Largen & Kock (1976) noted that *T. robusta* from Ethiopia was characteristic of rather arid habitats at lower altitudes. In Somalia, the distribution is essentially confined to the gallery forest/grassland of the major river valleys, (Roche pers. comm.). In Kenya it was collected near Isiolo along with *Acomys subspinosus*, *A. dimidiatus*, *Saccostomus campestris* and *Arvicanthis niloticus*.

Coe (1972) estimated that the biomass of *T. robusta* in the salvadora thickets of south Turkana, Kenya was some 287.3 kg/km² or 4680 *Tatera*/km². It is known to eat both seeds and arthropods, mainly insects (Neal, 1984), as well as some soft fruits, leaves, flowers and coarse plant material, (Coe, 1972).

Tatera phillipsi (De Winton, 1898)

Gerbillus phillipsi De Winton, 1898. — Ann. Mag. nat. Hist. (7): 1: 253. Hanka Dadi, Somaliland.

Material: A total of 36 specimens were examined. As the taxon has only recently been promoted to specific status (Bates, 1985) the specimens and their localities have been listed. Ethiopia: Arba Minch (06.08' N 37.42' E), SMNS. 23002—08, 23012—15, 23725; Kalam, (05.11' N 36.09' E) CG. 1978 No 171; Omo (c. o. 05.11' N 36.09' E), CG. 1974 No 50, 1974 No 53, 1975 No 285, 1975 No 296; Kenya: Baringo (00.38' N 36.17' E), BM. 10. 12. 19. 13—17, 10. 12. 19. 19—20, BM. 12. 7. 1. 166, BM. 68. 77—79; Somalia: Burao (09.31' N 45.33' E), BM. 8. 7. 24. 21—23; Buruq (05.20' N 48.30' E), BM. 12. 12. 28. 18—19; Hanka Dedi (09.50' N 45.00' E), BM. 97. 12. 3. 7; Upper Sheik (09.56' N 45.11' E), BM. 9. 12. 17. 37—38.

Diagnostic description: This is the smallest *Tatera* present in north-east Africa with a greatest length of skull of 37.3—40.9 mm (Table 2). Externally this species is indistinguishable from *T. robusta*, with both taxa having similar pelage and tail types.

The cranial morphology of *T. phillipsi* also shares many common characters with that of *T. robusta*, (Plates 1, 2 & 3). In both species, the rostrum is long and thin; the superior posterior mastoid chambers of the tympanic bullae are not inflated; the mandible is relatively short; the upper incisors are single grooved and opisthodont, the nasals are well extended and the first maxillary molar is relatively narrow.

However, *T. phillipsi* is usually distinguishable from *T. robusta* on cranial size difference. In all cranial characters the average measurements of *T. phillipsi* are smaller than those of *T. robusta*. This size difference is most apparent when adult sympatric specimens of the two species are examined, (Fig. 2). However, since there is an overlap in the ranges of the cranial measurements, it is sometimes impossible to determine with certainty between the two species when individual specimens are collected from isolated localities.

Variation: From the limited sample examined there would appear to be no significant sexual dimorphism. It was notable however that there was some geographical variation, with the specimens from Baringo, Kenya having relatively short tails and hindfeet but broad braincases. At present though all specimens are included in the nominate race. Synonyms include *umbrosa* and *bodessana*.

Distribution: The distribution is shown in Fig. 5. The localities in Ethiopia and Kenya are apparently restricted to the Rift Valley and this may help to explain the rather linear distribution.

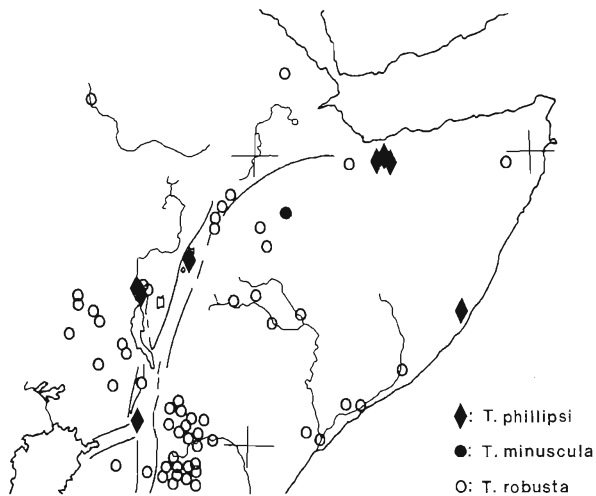


Fig. 5: Distribution of *Tatera phillipsi* in comparison to *Tatera robusta* and the type locality of *Tatera minuscula*.

Remarks: Most recent authors have included *T. phillipsi* in the synonymy of *T. robusta*. However, because of the size differences seen in sympatric specimens, it is here and in Bates (1985) promoted to specific status. The name *phillipsi* (De Winton, 1898) was selected as it is the earliest in the nomenclature for a small *Tatera* with a long rostrum. When the relevant specimens from Ethiopia and Kenya were compared to the holotype the majority of characters were seen to be shared. However, the holotype, which is a subadult, is noticeably broad in the braincase (16.6 mm), broader than all but one other specimen seen. Furthermore, the length of the maxillary cheektooth row at 6.3 mm and the width of the first maxillary molar at 2.2

mm, in both cases exceed by 0.1 mm the largest measurements of the small *Tatera* from elsewhere in north-east Africa. Such findings must by virtue of the fact that the small *Tatera* taxon is clearly identifiable elsewhere in its range by its relatively narrow braincase and small maxillary cheekteeth, suggest a possible taxonomic weakness. In the event that further material from Somalia throws doubt on the referral of *T. phillipsi* to the small taxon here discussed, then *T. umbrosa* Dollman 1912 would become the valid specific name.

The taxon *bodessana* Frick, 1914 was transferred by Bates (1985) from the synonymy of *T. robusta* to *T. phillipsi* on account of its size. Frick in his original description noted the markedly small hindfoot (31.5 mm) and greatest length of skull (36.2 mm) in the holotype (this has not been examined personally). Such measurements are small even for *T. phillipsi* and are not comparable to *T. robusta*.

The taxonomic position of *minusculus* Osgood, 1936 is not clear. All 23 specimens seen from in and around the type locality of Sheik Hussein, Ethiopia (07.44' N 40.41' E), (Fig. 5), including 21 topotypes, were juveniles. The specimens are held in the BMNH and FMNH. It proved impossible to determine the taxonomic status of such material, but in all probability the taxon is either a synonym of *T. robusta* or *T. phillipsi*. It is not possible to discriminate between juveniles of these two species. The taxon is here considered to be *incertae sedis*.

Although *T. phillipsi* has been collected from the same general localities as *T. robusta* it would not appear to be a direct competitor, for according to Hubert (1978) it has a different ecological niche. For, whilst *T. robusta* (referred to as *T. nigricauda* by Hubert but here considered to be *T. robusta*) was found in the riverine zone and the plateau of the Shungura Formation of the Omo Valley, *T. phillipsi* (referred to as *T. minuscula* by Hubert but here considered to be *T. phillipsi*) was confined to the cuestas which were covered with tuffs and the exposure bottoms which contained recently eroded sediments. The vegetation in this area was very arid and comprised of open shrubs (including *Euphorbia*) and rare herbaceous plants. *Tatera phillipsi* was found in association with *Taterillus harringtoni*, *Arvicanthis somalicus*, *Gerbillus pusillus* and *Xerus rutilus*.

It seems that *T. phillipsi* may have had a more widespread distribution in the past. For Wesselman (1984) states that a small *Tatera* (which he referred to *T. minuscula*) was present at Omo, Ethiopia (3.15 to 1.98 million years b. p.) and at two sites in Tanzania; Laetolil (3.7 million years b. p.) and Olduvai (Beds 1 & 2).

Tatera nigricauda (Peters, 1878)

Gerbillus nigricaudus Peters, 1878. — Monatsb. K. Preuss. Akad. Wiss., Berlin, p. 200. Ndi, Taita, Kenya.

Material: A total of 87 specimens were examined from eighteen localities in Kenya, Somalia and extraliminally from Tanzania.

Diagnostic description: This is a medium to large species of *Tatera*, with a greatest length of skull of between 42.5–50.5 mm, (Table 3). It has a characteristically long tail, which is always dark brown or black above. The ventral surface may also be completely covered in dark hairs although in some specimens the proximal third is pale. This latter character is especially common in northern Kenya. There is usually a terminal tuft of black hairs. Tail colour distinguishes *T. nigricauda* from all other

Tatera species except *T. robusta*. A *T. nigricauda* with a partially pale ventral tail surface cannot be distinguished from a dark tailed *T. robusta*, especially when individual specimens are examined rather than series.

Pelage colour is a character of some limited value in discriminating between *T. nigricauda* and *T. robusta*, especially in northern Kenya. Here, a majority of *T. nigricauda* specimens (64.4 %, n = 45) had pale bases to the hairs on the dorsal pelage whilst some 81.0 % (n = 37) of *T. robusta* were darker grey.

The skulls of *T. nigricauda* are comparatively large, being similar in greatest skull length to those of *T. indica* and *T. boehmi*. The rostrum is long and relatively narrow in comparison to *T. boehmi* and *T. valida*, although broader than *T. robusta*, (Fig. 1). It is noticeable that the rostrum of *T. nigricauda* is rounded in shape with bulbous premaxillary bones. This is in contrast to the relatively straight rostrum of *T. robusta*, (Plate 1). Rostral morphology apart, there is little except average size difference to distinguish *T. nigricauda* from *T. robusta*. There would appear to be no substance in Davis's (1975) suggestion that *T. nigricauda* might have a more angular pterygoid fossa.

No specimens of *T. nigricauda* were found with an inflated superior posterior mastoid chamber. Upper cheektooth width is relatively narrow, being comparable to *T. robusta* and *T. phillipsi*, although in absolute terms it is larger than both the other species. The upper incisors are opisthodont and a clearly defined single groove is always present. On average they would appear to be relatively broad as compared to those of the other species studied, except for *T. valida* and *T. boehmi*. As in *T. robusta*, the nasals are well extended in front of the incisors.

There is no karyological data for this species. Matthey (1969) did give a chromosomal formula of $2N = 40$, $FN = 70$ for two specimens (CG. 1975 No 281, CG. 1980 No 411) which he referred to *T. nigricauda*. However they are here considered to be *T. robusta* specimens with the darker tail type. Both specimens were part of a large series of 31 adults from Omo and Kalam, Ethiopia. A comparison, in the form of a discriminant functional analysis based on eight cranial characters, was made between these specimens, *T. nigricauda* material from northern Kenya and *T. robusta* from northern Kenya and Sudan. Fig. 6 shows that the Omo and Kalam material is essentially comparable to that of *T. robusta* and distinct from *T.*

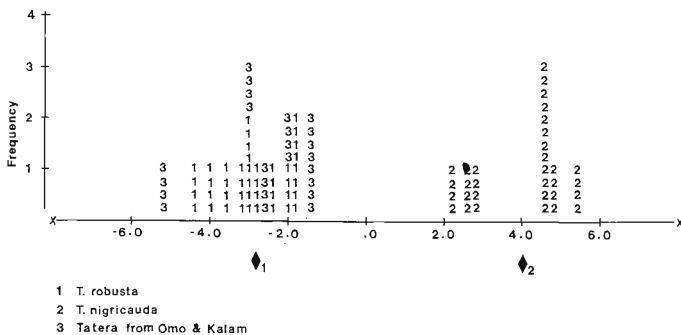


Fig. 6: Distribution of discriminant scores in a comparison of three *Tatera* populations. Data restricted to adult males; *Tatera robusta* from northern Kenya and Sudan and *Tatera nigricauda* from northern Kenya. Rhomboid symbols represent respective centroids.

nigricauda. Therefore all the Omo and Kalam specimens, including those with the karyological data have been assigned to *T. robusta*.

Variation: There is significant sexual dimorphism, with males exceeding females in size in the majority of external and cranial measurements. It is most apparent in head & body length, greatest length of skull, zygomatic breadth, rostral width, rostral length, mandible length and body weight. There is also significant geographical variation. The *T. nigricauda* from north-eastern Tanzania and southern Kenya are comparatively large and have very dark, usually black tails, with only a very few pale hairs on the ventral surface. The specimens from northern Kenya and Somalia are smaller and their tails, although covered in dark brown or black hairs on the dorsal surface usually have pale hairs on the ventral surface, especially on the distal third of the tail. Two races are therefore recognized, the nominate in the south and *T. n. nyama*, which includes the form *percivali*, in the north. Their respective measurements are given in Table 3.

Distribution: *Tatera nigricauda* has a relatively restricted distribution. No specimens were seen from west of the Eastern Rift Valley or from Ethiopia (Fig. 7). The two subspecies would appear to be essentially divided north and south of the Tana River.

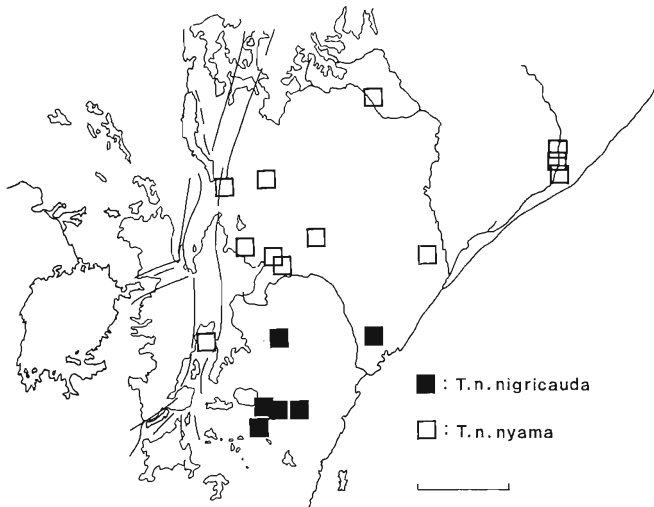


Fig. 7: Distribution of the two races of *Tatera nigricauda*. Scale = 300 km.

Remarks: It is proposed that the form *bayeri* Lonnberg, 1918, generally referred to *T. nigricauda*, be included in the synonymy of *T. robusta*. This form was considered by Davis (1975) to be a distinct race of *T. nigricauda* from west of the Eastern Rift Valley. The type locality was Maroon River, near Mount Elgon (01.30' N 35.30' E). However, all specimens examined from this area were found to be referable to *T. robusta*, although they did have comparatively dark tails, (Bates, 1987). Similarly the form *bodessae* Frick, 1914 has also been transferred, in the present study, from the synonymy of *T. nigricauda* to *T. robusta*. The type locality is Sagan River, Bodessa,

Ethiopia (05.07' N 37.35' E). The greatest length of skull of the holotype was given as 39.6 mm and the zygomatic breadth as 20.2 mm. The tail was described by Frick as "well clad, hair shorter than in *T. n. nyama*, anterior fourth of tail warm buff-colored with white markings underneath, posterior 3/4 black". Again this would appear to be a *T. robusta* with a dark tail, a characteristic of this species in south-western Ethiopia.

Little is known of the ecology of *T. nigricauda*. Neal (1984) noted that it shares the same food plants as *T. robusta* and it has been collected from the same localities.

Tatera valida (Bocage, 1890)

Gerbillus validus Bocage, 1890. — Journ Sci. Math., Phys. e Nat., Lisboa, (2) 2: no. 5, p. 6, pl. 1. Ambaca, Quissange, Caconda, Rio Cuando, Angola.

Material: A total of 502 specimens were examined. These came from 117 localities, both from within north-east Africa in Ethiopia, Kenya, Sudan, Uganda and extralimitally from Angola, Central African Republic, Chad, Nigeria, Tanzania, Zaire & Zambia.

Diagnostic description: This is a medium-sized *Tatera*, with a greatest skull length in north-east Africa of 38.1 to 44.7 mm, (Table 4). The tail of *T. valida* is characteristically short and normally does not exceed head & body length. It is generally pale brown colour and never has a terminal tuft of dark hairs. This distinguishes it from all other *Tatera* in north-east Africa. The hindfoot is also comparatively small. The mean body weight of *T. valida* (Table 4) exceeds that of *T. robusta* (Table 1) in both sexes.

The skull of *T. valida* has a relatively short, broad rostrum as compared to *T. robusta*, (Fig. 8). The mandible is proportionately long for the length of skull in comparison to the other species, except *T. boehmi*. No specimen from within north-east Africa was seen with an inflated superior posterior mastoid chamber of the tympanic

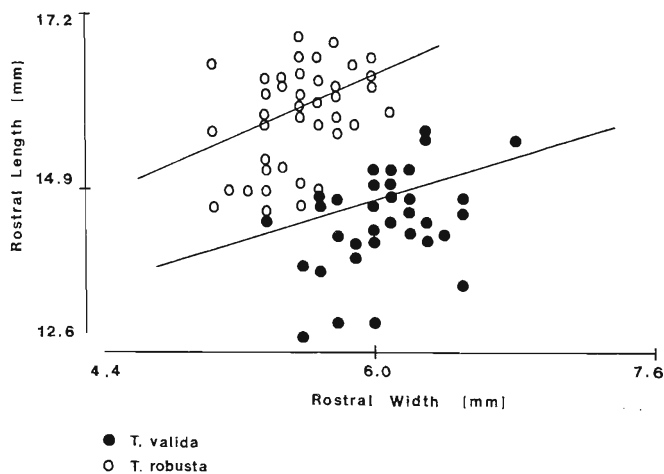


Fig. 8: Comparison of *Tatera valida* and *Tatera robusta*. Data restricted to adult females. Regression line for *T. valida*, $y = 0.75x + 10.15$, $r = 0.38$, $p < 0.05$, $n = 44$ and for *T. robusta*, $y = 1.06x + 10.00$, $r = 0.41$, $p < 0.05$, $n = 44$.

bullae. However six specimens, all from a single extralimital locality, Poko, Upper Vele River, Zaire, did have inflated chambers. The reason for this is not known.

The cheekteeth are relatively broad. The upper incisors, which are also broad, are opisthodont and in most specimens have a single groove, although this may be very faint in some individuals. A minority of specimens have no visible groove, the incisors being completely smooth, a character shared with some individuals of *T. boehmi*. In contrast to *T. robusta* the nasals do not extend far in front of the alveolar margin of the upper incisors, (Fig. 3).

The karyology of the species remains confused, although several authors have analysed chromosomal material which they have referred to *T. valida*. Matthey (1969) examined the chromosomes of a *Tatera* from Dakar, Senegal (14.38' N 17.27' W) which was referred by him to *T. valida*. However, since the type locality of *T. valida* is in Angola and since the *Tatera* of western Africa are noted for their complexity it is far from certain that this is a correct referral. Matthey gave a chromosomal formula of $2N = 52$, $FN = 68$.

Matthey & Petter (1970) analysed the karyology of two specimens referred by them to *T. kempfi*. The formula was $2N = 36$, $FN = 66$. The specimens were from La Maboke, Central African Republic (03.54' N 17.53' E). However, having examined the specimens personally, they do not appear to be morphologically similar to *T. valida kempfi* as understood in this study.

Matthey & Petter (*loc. cit.*) also collected two specimens of *Tatera* from the vicinity of the Gounda River close to La Maboke. These they referred to *T. sp. cf. nigrita*. The chromosomal formula was $2N = 48$, $FN = 64$. However, again these specimens would not appear to be referable to *T. valida*, although the form *nigrita* has been included, on morphological grounds, in the synonymy of *T. valida* in the present study.

Tranier (1974) reviewed the karyology of *T. valida* (*sensu* Davis, 1975) from West Africa, with reference to specimens collected from Chad. He concluded that there were four chromosomal species: *T. gambiana* $2N = 52$, *T. kempfi* $2N = 36$, *T. hopkinsoni* $2N = 48$ and *T. cf. nigrita* $2N = 48$. Gautun, Sankhon & Tranier (1986) examined the chromosomal morphology of ten specimens of *Tatera* from Mount Nimba in Guinea. They referred the material to *T. "kempfi"* and gave a diploid number of $2N = 46$. However they considered this material distinct from the *T. kempfi* specimens studied by Matthey & Petter (1970) from La Maboke.

There is clearly confusion in the literature concerning the karyology of *T. valida*. A primary requirement is for a detailed karyological analysis of specimens from Angola and in particular topotype material. This would provide a basis for the discussion of the karyology of the species in the remainder of its apparently extensive range.

Variation: There is some evidence of sexual dimorphism in *T. valida*. Males usually exceed females in skull length. There is little consistent geographical variation in body or skull size, although there is some variation in pelage colour, with specimens from the more arid areas of Sudan being notably paler than those from the west of Lake Victoria. However, the most marked geographical variation is in the morphology of the first lamina of the lower first molar. Four different lamina types were observed in the material from throughout the species range, (Fig. 9). All specimens

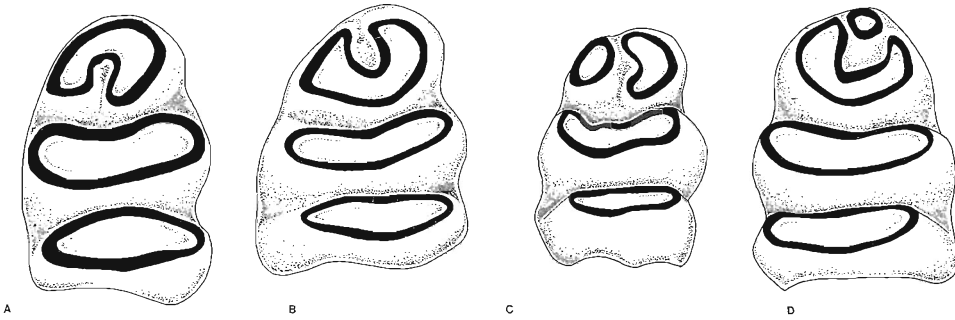


Fig. 9: First mandibular molars of *Tatera valida* with particular reference to the first lamina. A: First lamina open posteriorly: BM. 77.1000, female, 1.viii.1965, Queen Elizabeth Park, Uganda. B: First lamina open anteriorly: BM. 74.871, female, 2.x.1905, Ndola, Zambia. C: First lamina divided into two islands: BM. 77.1041, male, 14.xii.1965, Queen Elizabeth Park, Uganda. D: First lamina divided into a small anterior and a large posterior island: BM. 34.8.26.1, female, Sumbawanga, Tanzania.

with a posteriorly opening lower first lamina were found north of approximately 01.00 degrees south. Conversely, with one exception all specimens with an anteriorly opening lamina were collected from south of this latitude. The single exception came from Kanarok Hot Springs, Karamoja, Uganda (03.58' N 33.45' E). Here four specimens had posteriorly opening laminae and one (BM. 71.187) had the anterior type. The distribution of these two lamina types is shown in Fig. 10. The lamina type with two islands was found to be randomly distributed throughout the taxon's range, whilst the first lamina divided into a small anterior island and a large posterior island was found in a single specimen from Sumbawanga, Tanzania (07.58' S 31.36' E).

The above findings agree with Petter (1959) and Davis (1966) who found that *T. valida* from the northern savanna could be separated from those from the south by lamina type. In the present study the two populations, which would appear to be geographically discrete, are considered to be distinct subspecies, although the exact rank in the taxonomic hierarchy of such allopatric populations is difficult to determine. The southern race is the nominate and includes in its synonymy the forms; *neavei*, *liodon* and *tabora*. The northern race is *T. v. kempi* and includes the forms *ruwenzorii*, *beniensis*, *lucia*, *smithi*, *dundasi*, *nigrita*, *dichrura*, *benvenuta*, *soror*, *flavipes* and possibly *welmanni*, *giffardi*, *gambiana* and *hopkinsoni* from West Africa.

Distribution: The distribution of the two races of *T. valida* is shown in Fig. 4. The specimens from the Kwale area of coastal Kenya have provisionally been included in the nominate race. Otherwise all specimens from north-east Africa are referable to *T. v. kempi*.

Remarks: *Tatera valida* is reported by Vesey-FitzGerald (1964) to be an animal of secondary and perimeter valley grasslands and cultivated areas in highlands in Tan-

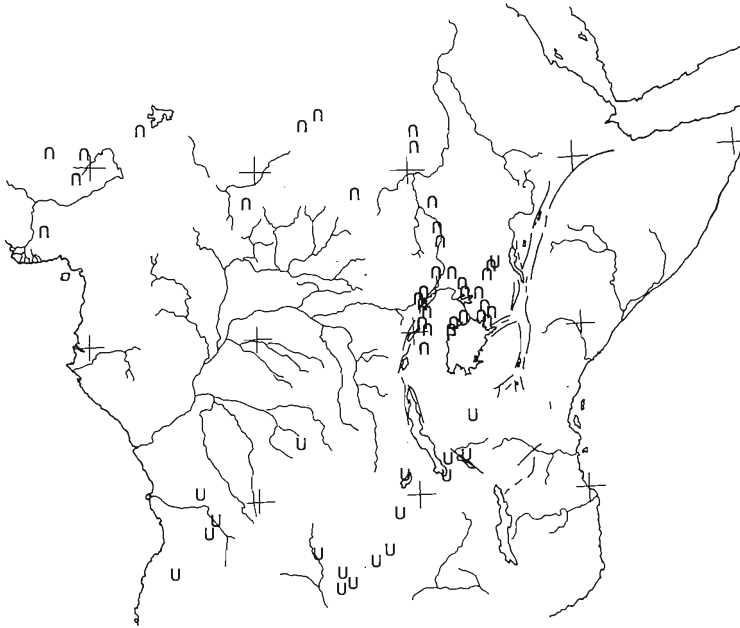


Fig. 10: Distribution of two lamina types of *Tatera valida*.

n = First lamina open posteriorly

u = First lamina open anteriorly

zania and Zambia. Verheyen & Verschuren (1966) who studied *T. valida* in the Garamba National Park, Zaire considered it to be a rodent typical of upland grassland savanna, while Delany (1975), in his work on the rodents of Uganda wrote that it favoured "savanna particularly grassland" and that it "penetrated forests along the edges of tracks". *T. valida* is known to prefer well drained sandy soils, for according to Vesey-FitzGerald (1966) it is common in the sandy alluvium along rivers and in old gardens and woodlands where the soil had been loosened by cultivation. It is also known to colonise fallow land where the original forest and woodland have been cleared, (Kingdon, 1974). In Ethiopia, it was found in the Didessa and Abbai riverine valleys that extend into the Ethiopian plateau. According to Morris, Lagen & Yalden (1975) *T. valida* was present in these valleys along with other typical savanna taxa, such as *Mus*, *Thryonomys* and *Lemniscomys striatus*.

Tatera valida, although known to feed on insects, including ants and orthopterans (Delany 1964) is primarily a grass eater during the rains whilst at other times it feeds on the underground parts of grasses and sedges (Vesey-FitzGerald, 1966). It lives in small groups in elaborately constructed burrow systems containing several tunnels, a terminal chamber and a nest. The system may have depth of up to 62 cm and cover an area approximately 2.7 x 1.4 m, (Delany, 1964). Females have three to four foetuses. Delany noted that in Uganda they were found to breed from May to July and September to December and that the testes were about 20 mm long at maturation.

***Tatera (Gerbilliscus) boehmi* (Noack, 1887)**

Gerbillus boehmi Noack, 1887. — Zool. Jahrb., Syst., 2: 241, pl. 9., f. 11–13. Qua Mpala, Marunga, Northern Rhodesia.

Material: A total of 38 specimens from 20 localities were examined. Only two specimens were seen from north-east Africa, these came from western Uganda. Comparative material was seen from Malawi, Tanzania, Zaire and Zambia.

Diagnostic description: This is a medium-large species of *Tatera* with a greatest length of skull of between 42.0–45.2 mm, (Table 5). The tail which is noticeably long has a terminal tuft of pale (white) hairs. This character distinguishes *T. boehmi* from all other species in north-east Africa.

The skull has a relatively long and broad rostrum, (Plate 1). The mandible is also long. The braincase is deep in comparison to the other *Tatera* species studied and the dorsal profile is characteristically rounded. This results in the highest point of the skull being projected well above the lambda, (Plate 3e). Some individuals have an inflated superior posterior mastoid chamber of the tympanic bulla, the most marked example being a specimen (BM. 65.1281) from Kigoma, Tanzania (04.52' S 29.36' E).

The cheekteeth are broad and the cheekteeth row length is relatively long. The upper incisors are also broad and generally have two grooves, although these may be very faint. A minority of specimens have totally smooth upper incisors, a character shared with a minority of *T. valida* specimens. *T. boehmi* is the only *Tatera* in north-east Africa with orthodont as opposed to opisthodont incisors, (Fig. 3).

There is no data on the karyology of the species.

Variation: At present, there is insufficient data to determine if there is significant non-geographical or geographical variation within the species. Therefore following Davis (1975), it is here considered to be monotypic with the following forms included in its synonymy: *fallax*, *fraterculus* and *varia*.

Distribution: *Tatera boehmi* has a distribution essentially confined to eastern, central Africa, with only a very limited distribution into north-east Africa at two localities in the Ankole region of Uganda, (Fig. 11).

Remarks: *Tatera boehmi* has been generally recognised as belonging to a separate subgenus *Gerbilliscus* on account of its double grooved incisors. This character is unique amongst the *Tatera* to *T. boehmi* and therefore the existing subgeneric name is here retained.

Tatera boehmi is a species of mainly high elevation woodlands and is according to Vesey-FitzGerald (1964) widespread without ever being abundant. It is most commonly found in *Brachystegia* woodland and is thought possibly to have been displaced from the lowland savanna of East Africa by the better adapted *T. valida* and *T. robusta* (Kingdon, pers. comm.).

Little is known of its biology. According to Delany (1964) lactating females collected in May at the time of the late rains in Malawi had two to five placental scars and a single female from Rwanda had five embryos.

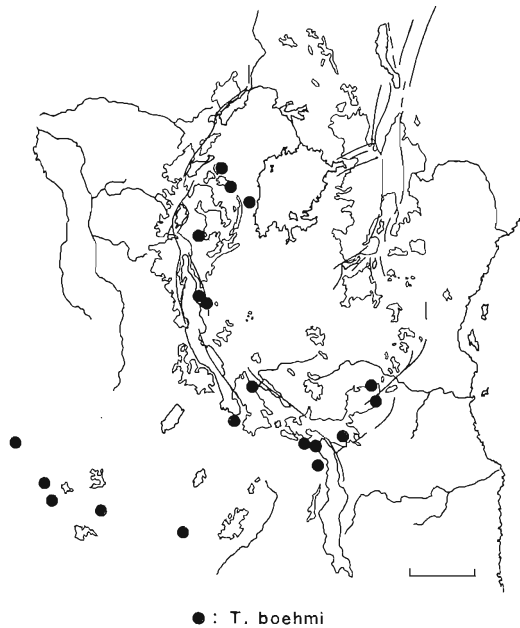


Fig. 11: Distribution of *Tatera boehmi*. Scale = 250 km.

Tatera indica (Hardwicke, 1807)

Dipus indicus Hardwicke, 1807. — Trans. Linn. Soc. Lond., 8: 279. Between Benares and Hardwar, United Prov., India.

Material: A total of 331 specimens of *Tatera indica* were examined from 125 localities in Kuwait, Iraq, Iran, Pakistan, India and Sri Lanka. Harrison (1972) lists additional material from Syria and Gaisler (1975) from Afghanistan.

Diagnostic description: This is a medium to large species of *Tatera* with a greatest length of skull of between 39.2–50.9 mm, (Table 6). The tail is characteristically tricolored with dark dorsal and ventral surfaces and a pale lateral stripe on each side, although in a very small minority of specimens (3 %, n = 166) the tail was found to be uniformly pale. All tails have a terminal tuft of dark hairs.

On average, skull length in *T. indica* exceeds in size that of *T. robusta*, *T. valida* and *T. phillipsi*, with specimens from northern Arabia, southern India and Sri Lanka being especially large. The rostrum is relatively long and narrow. In contrast to all *T. robusta*, *T. nigricauda*, *T. phillipsi* and the vast majority of *T. valida* and *T. boehmi* the mastoid chamber of the tympanic bullae of *T. indica* are inflated. In only one *T. indica* specimen was this found not to be the case. This specimen (BM. 20. 5. 1. 17) came from Anasigalla, Sri Lanka.

The cheekteeth are of intermediate width as compared to *T. robusta* and *T. valida* and the upper incisors are opisthodont and have a single clearly defined groove. The nasals extend well in front of the upper incisors, (Fig. 3).

The osteology of this species is of interest. For, although no significant difference was found in the morphology of the femur between *T. indica* and the African *Tatera* an examination of the humerus suggests that there may be a significant difference

in this character. No specimen of *T. indica* was seen in the collection of the HZM with an entepicondylar foramen present at the distal end of the humerus. In contrast, all African *Tatera* examined for this character did have a foramen, except for a single *T. leucogaster* specimen (HZM. 25. 15094) from Malawi which exhibited both humerus types. This last specimen suggests a cautious interpretation of the character.

Khan & Beg (1975) examined the bacula of 41 specimens of *T. indica* from Pakistan. They found that the total shaft length and width of the baculum were useful criteria for separating juvenile specimens from subadults. However, they concluded that the baculum exhibited considerable individual variation and could not be considered a reliable taxonomic character.

The chromosomal formula of *T. indica* was given by Matthey (1953) as $2N = 72$, $FN = 80$. Of the two sex chromosomes, the X was a large metacentric and the Y an equally large submetacentric. Yosida & Ochai (1975) studied the karyology of *T. indica* specimens collected from Mysore and gave a formula of $2N = 68$, with a large metacentric X and a small acrocentric Y. Yosida (1981) further reported that there was chromosomal polymorphism in the *T. indica* from Mysore, with the smallest biarmed autosome pair having three chromosome types.

Variation: There is no significant sexual dimorphism. However, there is considerable geographical variation. Specimens from Kuwait, Iraq and western Iran have significantly larger skulls than the specimens from elsewhere in the range. The majority of these specimens also have a very marked inflation of the mastoid chamber of the tympanic bulla. In contrast the tail length is relatively short, seldom exceeding head and body length. A comparison of these specimens from the west of the range with those from eastern Iran and Pakistan is shown in Fig. 12. The two samples are discrete with a minimum of overlap. It is therefore proposed that the subspecific name *taeniura* be retained for the *T. indica* from northern Arabia and western Iran. This agrees with Harrison (1972) and Agrawal & Chakraborty (1981). However, it is also apparent that there is no clear geographical division between this race and that of the nominate to the east, there probably being a zone of intergradation in central and eastern Iran, although data are insufficient at present for a detailed assessment.

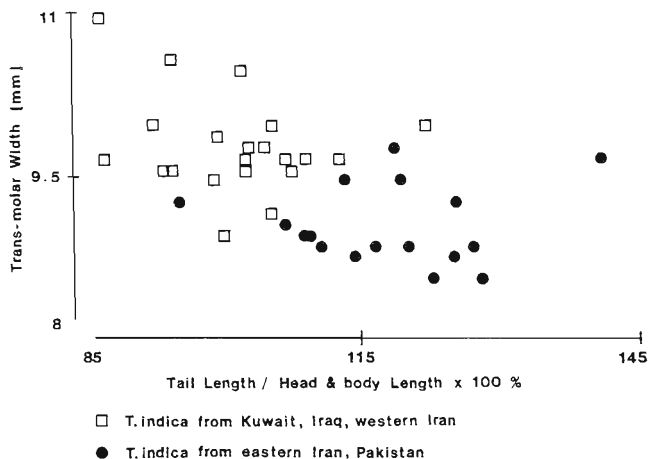


Fig. 12: Comparison of two populations of *Tatera indica*.

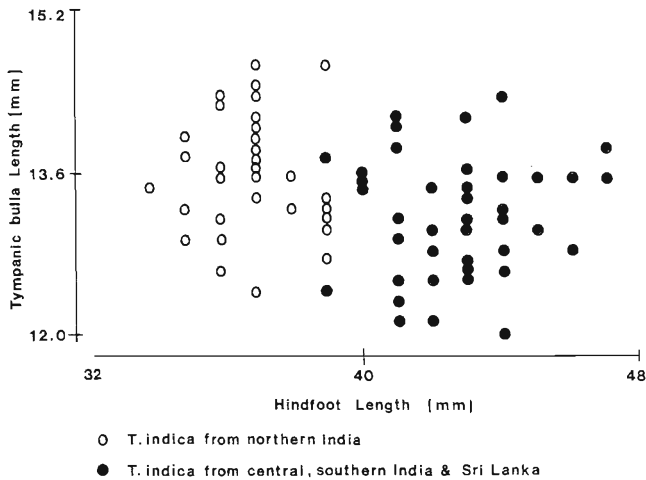


Fig. 13: Comparison of two populations of *Tatera indica*.

The following forms are included in the synonymy of *T. i. taeniura*: *bailwardi*, *pitmani* and probably *monticola*.

Geographical variation was not restricted to specimens from the west of the species range. Data collected for this study suggest that specimens from central southern India and Sri Lanka have significantly longer tails and hindfeet than those from northern India. The majority of cranial measurements were also larger with the notable exception of tympanic bulla length. This character exhibits a clinal decrease in size towards the south of India, with the specimens from Sri Lanka having the smallest and least inflated bullae of the species. When data for hindfoot length was combined with that of the cranial measurements it could be seen that specimens from south of approximately 22.00' N were distinct morphologically from the majority of the northern specimens. Fig. 13 shows that the two samples are essentially discrete, although it is appreciated that a minority of specimens may be impossible to assign to one subspecies or another, without *a-priori* knowledge of the locality. Nevertheless, it is proposed here that following Agrawal & Chakraborty (1981), *T. i. cuvieri* be retained as a valid subspecies. The boundary between this race and the nominate to the north is considered to be the series of hill ranges, including the Saptura Range, the Maikal Range and the Hazaribag Range, that run from west to east across central northern India. There would appear to be little justification for maintaining the form *ceylonica* for the Sri Lankan *Tatera*, although the tympanic bullae are the least inflated of all the *T. indica* seen. This form along with *hardwickei* is therefore included in the synonymy of *T. i. cuvieri*.

The nominate race with a range that encompasses eastern Iran, Afghanistan, Pakistan and northern India includes the following forms in its synonymy: *otarius*, *persica*, *dunni*, *sherrini* and probably *scansa*.

Distribution: *Tatera indica*, which is the only species of the genus in Asia, has an extensive range from Syria through to Sri Lanka. The distribution of the three races is shown in Fig. 14.

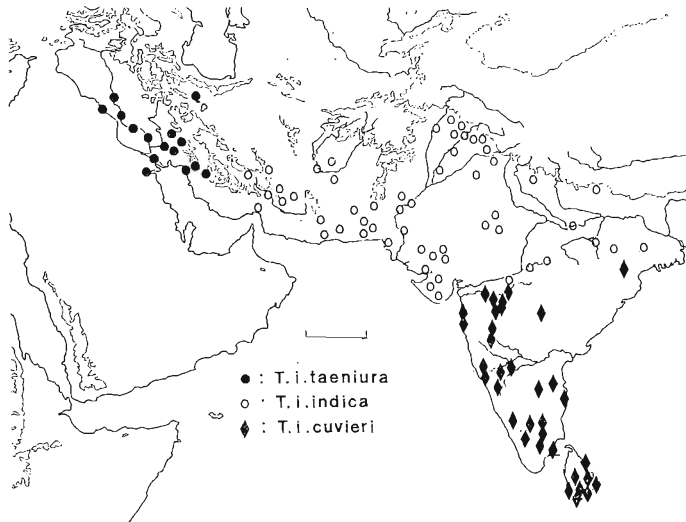


Fig. 14: Distribution of the three races of *Tatera indica*. Scale = 500 km.

Remarks: *Tatera indica* is a highly adaptable animal, although unlike the true psammophilic Gerbillinae it is considered to be a water dependent gerbil and according to Misonne (1975) requires green vegetation throughout the year. Where *T. indica* is present in particularly dry areas, such as Rajasthan it is usually found in the vicinity of human habitation, (Prakash & Rana, 1973).

The literature on the ecology of *T. indica* is extensive. This is in part a reflection of its abundance on the subcontinent, in part because it is a vector of disease (Misonne, 1957) and in part because of its propensity to destroy crops (Kumari & Khan, 1978). Harrison (1972) and Roberts (1977) give a general overview of the ecological literature and additional information is available from papers such as Prakash (1975), Prakash, Jain & Rana (1975), Beg, Yaseen & Rana (1980), Garg & Chanda (1982) and George, Joy & Abraham (1982). Mann (1975, 1977) looked specifically at the feeding habits of *T. indica* whilst Mann & Bindra (1979) discussed the reproduction.

Key to North-East African & Asian *Tatera*

- 1: Superior, posterior mastoid chamber of tympanic bulla inflated, (Fig. 15) or specimen comes from Sri Lanka 2
 Mastoid chamber of tympanic bulla not inflated 3
- 2: Tail tricolored, dark above and below with lateral stripe *T. indica*
 Tail bicolored or with no differentiation between dorsal and ventral aspect 3
- 3: Tail relatively short, normally less than head and body length, and without terminal tuft of hairs or pale tip. Rostral length normally less than 36.2 % of greatest length of skull *T. valida*
 Tail longer than head and body length. Rostral length normally in excess of 36.2 % of greatest length of skull 4

- 4: Tail never with dark ventral aspect and normally with pale hairs (above and below) on tip, orthodont incisors, rounded dorsal profile of skull *T. boehmi*
 Tail sometimes with dark ventral aspect but never with pale hairs above and below on tip, opisthodont incisors and flat dorsal skull profile 5
- 5: Tail always with a majority of dark hairs above and below. Rostral width normally exceeds 14 % of greatest length of skull. Rostrum with bulbous premaxillary bones *T. nigricauda*
 Tail most often with pale hairs below. Rostral width normally less than 14 % of greatest length of skull. Rostrum with straight sided premaxillary bones 6
- 6: Greatest length of skull, breadth of braincase, trans-molar width normally less than 39.5 mm, 16.0 mm and 7.8 mm, respectively. *T. phillipsi*
 Greatest length of skull, breadth of braincase, trans-molar width normally exceeds 39.5 mm, 16.0 mm and 7.8 mm, respectively. *T. robusta*

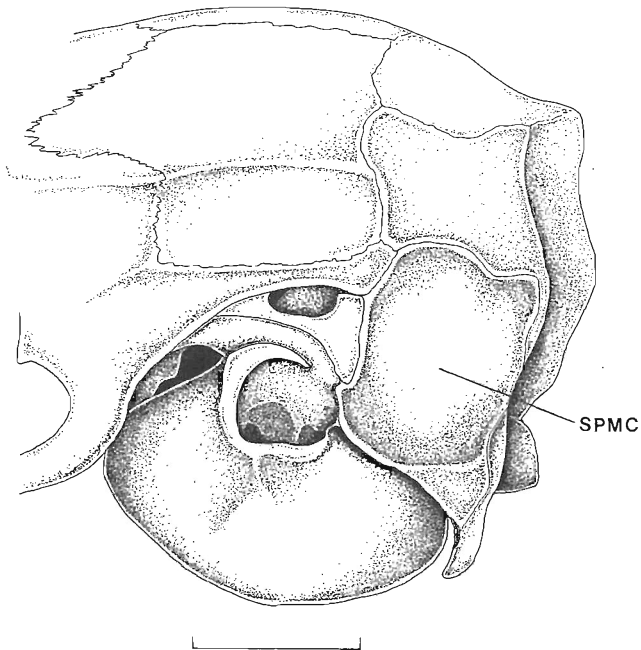


Fig. 15: Posterior cranial morphology of *Tatera indica*. SPMC = Superior posterior mastoid chamber of tympanic bulla. Scale = 5 mm.

Zoogeographic and evolutionary discussion

The genus *Tatera*, although present in Africa and southern Asia has a disjunct distribution, being absent from North Africa, the Levant and most of peninsular Arabia (Fig. 16). There has been considerable speculation as to its possible geographical origin, with Tchernov (1975) suggesting that *Tatera* evolved in Asia and subsequently dispersed into Africa and Ranck (1968) and Pavlinov (1982) taking the opposite view.



Fig. 16: Approximate geographical range of the genus *Tatera* (after Ellerman, 1941). Scale = 2000 km.

It is here proposed that *Tatera* originated in Africa sometime during the Early Pliocene. It is known from the fossil record of the Middle Pliocene of East Africa, having been recovered, according to Wesselman (1984) from two sites in Tanzania, Laetolil (3.7 million years b. p.) and Olduvai (Beds 1 & 2) and from Omo in Ethiopia (3.15–1.98 m. y. b. p.). By the Late Pliocene/Early Pleistocene the genus was evidently widespread within the continent, with specimens found not only in East but also in South Africa, (Lavocat, 1957; De Graaf, 1960; Davis, 1962). There is no well substantiated evidence of fossil *Tatera* in Asia.

The greater diversity of *Tatera* and *Tatera* like gerbils in Africa also points to an African origin of the animal. For, whilst the genus is monospecific in Asia there are at least nine extant African species. Additionally, there are two genera, *Taterillus* and *Gerbillurus*, which are considered by Chaline, Mein & Petter (1977), Pavlinov (1982) and Qumsiyeh (1986) to be close phylogenetically to *Tatera* and which have never been found outside Africa. Both *Taterillus* and *Gerbillurus* have relatively broad geographical ranges, are polyspecific and in the case of *Gerbillurus* at least, are known to date from the Pliocene, (Jaeger, 1979). In contrast, in Asia there are no genera which have close affinities to *Tatera*.

It is not known when *Tatera* first appeared in Asia. However, the fact that *T. indica* is a distinct, polytypic species suggests that the dispersal and subsequent isolation is not a recent phenomenon. This view is supported by two characters. First, the vast majority of *T. indica* have the apparently derived character of the inflated superior, posterior mastoid chamber of the tympanic bulla. In contrast, only 2.9 % of the 1029

African *Tatera* examined exhibited this character. Second, *Tatera indica* has a higher proportion of specimens with primitive tooth types. That is to say the first lamina of the lower first molar is divided into two enamel islands as compared to the "more advanced" single island. Twenty seven percent of the 122 *T. indica* specimens examined had a primitive tooth type. This compared with just 4.4 % (of the 456 specimens examined for this character) of the north-east African *Tatera*.

However, the fact that *T. indica* has more characters in common with the three species of the *T. robusta* group (*T. robusta*, *T. nigricauda* & *T. phillipsi*), than this group has with *T. valida* and *T. boehmi* suggests that Pavlinov (1982) was wrong to favour the view that the Asian *Tatera* were isolated as early as the border of the Miocene/Pliocene. It would seem most likely that dispersal into Asia and subsequent isolation occurred sometime in the Pleistocene or at the earliest in the Late Pliocene.

There are at present, insufficient data to determine with certainty the route taken by the *Tatera* entering Asia. However, it would not appear to be by way of the Sinai landbridge and the Levant. For the exhaustive palaeontological research undertaken in this region by workers such as Tchernov (1968, 1975, 1984) has yet to record a single *Tatera* specimen. Possibly the Sahara, which is believed to date from the Late Miocene (Maley, 1980) has always acted as a barrier to the northern dispersal of *Tatera*, although, it is also apparent that there have been times of a much more temperate climate in North Africa when conditions would appear to have been favourable for this gerbil, (Livingstone, 1975). Perhaps *Tatera* was unable to compete in northern Africa, Sinai and the Levant with the well established Asiatic genus *Meriones*, and in particular with *M. tristrami* and its sibling species *M. shawi*. This would certainly appear to be the case today, as the distribution of *T. indica* and *M. tristrami* in northwestern Arabia is essentially parapatric. Both species are water dependent (Petter, 1957; Harrison, 1972) and occupy similar niches.

An alternative explanation is that *Tatera* dispersed into Asia via a southern landbridge, crossing the Red Sea basin, during a period of marked regression. It is known that considerable eustatic changes have occurred in the region and that as recently as 18,000 years b. p., during the Wurm II glacial, the area to the north of Straits of Bab-el-Mandab was dry land (Olausson, 1971). Other regressions may have occurred prior to this, during previous glacial epochs. The occurrence of intermittent landbridges would possibly account for the presence of essentially Asiatic rodents, such as *Golunda*, *Millardia* and *Saidomys* in the Late Pliocene/Early Pleistocene deposits of Hadar, Ethiopia (Sabatier, 1979), (although see Musser (1987) for alternative views), as well as the existence of the extant species *Arvicanthis niloticus*, *Praomys fumatus*, *Papio hamadryas*, *Ichneumia albicauda*, *Crocidura somalica* and possibly *Tragelaphus imberbis* in southern Arabia (Harrison, 1964, 1968, 1972; Büttiker, 1982; Hutterer & Harrison (1988).

The fact that *Tatera* has not been collected from the southern Arabian peninsula in recent times may reflect its extinction as a result of the increasing aridity that has occurred in the region. The most recent period of dessication began some 17,000 years b. p.. In the Pliocene and even the Late Pleistocene the region was relatively moist, (Al-Sayari & Zotl, 1978). The fact that no fossil evidence of *Tatera* has been seen from southern Arabia may result from the lack of palaeontological studies conducted in the region.

From southern Arabia *Tatera* could have reached the Indian subcontinent either by way of the west coast of the Persian Gulf and the Iranian seaboard or alternatively it may have crossed the Persian Gulf itself. The Gulf is known to be a relatively recent structure and there have been times of marked regression when the Gulf was dry as far as the Straits of Hormuz (Kassler, 1973).

Little is known of the evolutionary history of *Tatera* in Africa. However, it is certain that the genus was evolving at a time of marked geophysical and climatic change within the continent, (Hamilton, 1982). The distribution of the two races of *T. valida* suggests that the species once had a continuous range which was subsequently split in two, possibly during a pluvial period. At such a time Lake Victoria would have flooded much of its hinterland (Kendall, 1969), rivers such as the Kagera and Katonga, would have been major obstacles to the movement of terrestrial life and the lowland forest would have expanded eastwards into Uganda and western Kenya, (Carcasson, 1964; Rodgers, Owen & Homewood, 1982). Grassland rodent species such as *Aethomys chrysophilus*, *Rhabdomys pumilio*, *Pelomys fallax* and *Lemniscomys griselda* (Davis, 1962) appear to have become isolated to the south of these physical and vegetational barriers. In the case of *T. valida*, populations would appear to have been isolated both to the north and south, hence their subspecific differentiation. Possibly with the drier conditions present in Africa today the distribution of *T. valida* will once more become continuous with intergradation in south-west Uganda and north-west Tanzania.

It is noticeable that to the north of Lake Victoria, the distribution of *T. valida* is confined to the south of the Asswa Lineament, whilst that of *T. robusta* is to the north (Fig. 4), hence their parapatric distribution. According to Denys et al. (1986), this lineament is an area characterized by upland ranges, plateaus and large volcanoes and is known to have influenced the distribution of modern faunas, especially rodents.

The two races of *T. nigricauda* are essentially distributed north and south of the Tana River, suggesting that the river acted as a barrier to gene flow between the northern and southern populations. A similar situation has been observed in the case of the giraffe, with *Giraffa camelopardalis reticulata* essentially but not completely confined to the north of the river and *G. c. tippelskirchi* to the south, (Stott, 1959). According to Keast (1965), the river is also a significant faunal barrier to the Hunter hartebeest (*Dalmaniscus hunteri*), the Dik-dik (*Rhynchotragus guntheri*), the Beisa Oryx (*Oryx beisa*) and Grevy's Zebra (*Equus grevyi*). Interestingly the Tana has had no such effect on *T. robusta*. The reason for this is not known.

The Eastern Rift Valley, with its abnormally low annual precipitation rate and associated arid vegetation (Denys et al., 1986), would appear to be a geographical barrier restricting the westward extension of the range of *T. nigricauda*. No specimens of this taxon were seen from west of the Rift. This is not the case for *T. robusta*, although a comparison of tail types from either side of the Rift does suggest that it may be a boundary limiting genetic exchange. Populations to the east have generally pale tail types whilst those to the west are comparatively dark. The difference in the distribution patterns of *T. nigricauda* and *T. robusta* may either reflect a greater ecological tolerance of *T. robusta* or possibly that *T. robusta* evolved prior to the major formation of the Rift, in the Plio-Pleistocene (Sutcliffe, 1985), whilst

T. nigricauda evolved east of the Rift and after its development. Interestingly, the distribution of *T. phillipsi*, which is known to favour drier habitat types (see above), is apparently confined to the Rift floor itself in Ethiopia and Kenya.

In general, little would appear to be known of the effect of the rift valleys on the distribution of taxa in Africa. Kingdon (1974) showed that *Gerbillus pusillus* does not cross the Eastern Rift Valley towards the western region of Kenya and that the range of *G. gerbillus* is restricted in East Africa to the north of the Western Rift Valley. Grubb (1978) thought the Rift valleys may have influenced the subspeciation of the hartebeest and the black rhinoceros and Keast (1965) showed that the north-western extension of the range of *Equus grevyi* was restricted by the Lake Rudolph-Rift valley line.

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Zusammenfassung

Es wird eine Revision der Gattung *Tatera* (Rodentia: Gerbillinae) in Asien und Nordostafrika vorgelegt. Sechs Arten werden unterschieden und definiert: *Tatera robusta*, *T. phillipsi*, *T. nigricauda*, *T. valida*, *T. boehmi* und *T. indica*. Das Taxon *T. minuscula* wird als *incertae sedis* eingestuft. Die Zoogeographie und Evolutionsgeschichte von *Tatera* wird diskutiert. Die Gattung evoluierte wahrscheinlich im Altplozän in Afrika und breitete sich anschließend nach Asien aus, möglicherweise über eine südliche Landbrücke.

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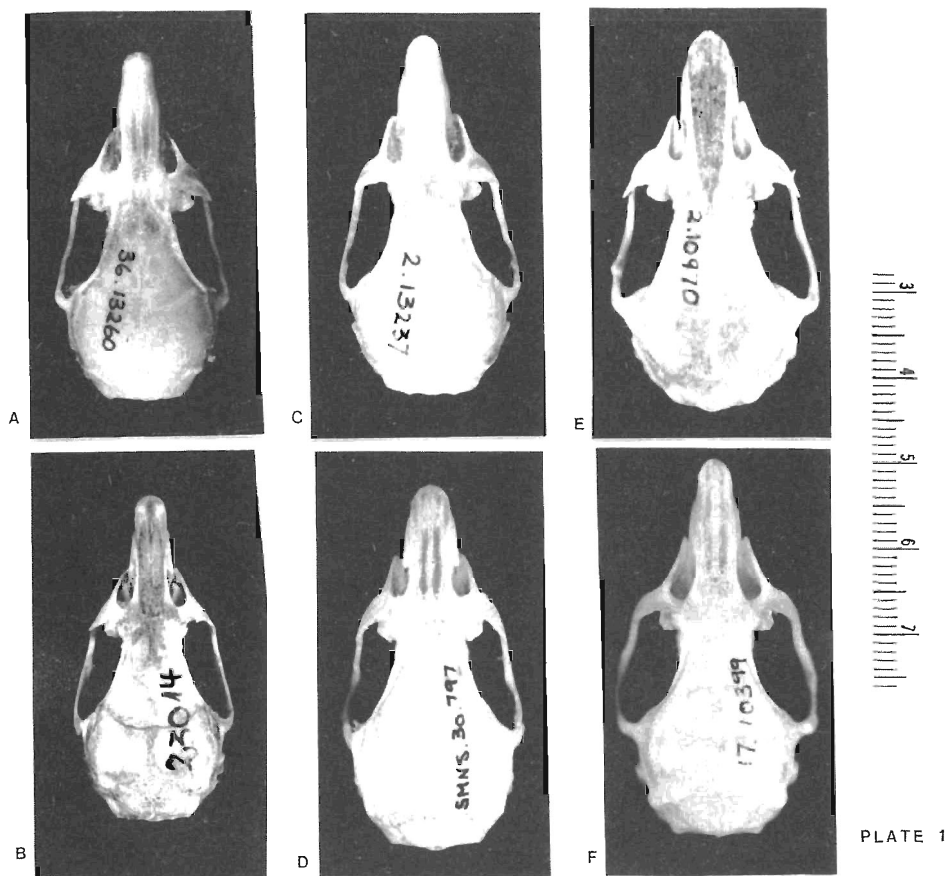


PLATE 1

Plate 1: Cranial morphology of the six species of *Tatera* found in north-east Africa and Asia — dorsal view.

A: *T. robusta*, HZM. 36.13260, female 13.iii.1983, Kyamunyuu, Machakos District, Kenya.

B: *T. phillipsi*, SMNS. 23014, female, 31.vii.1973, Arba Minch, Ethiopia.

C: *T. nigricauda*, HZM. 2.13237, male, 6.viii.1983, Manzani-Makyeni, Machakos District, Kenya.

D: *T. valida*, SMNS. 30797, male, 4/5.ii.1979, Nagishot/Didinga Mts., Sudan.

E: *T. boehmi*, HZM. 2.10970, female, 4.viii.1973, Kasombu Stream, Zambia.

F: *T. indica*, HZM. 17.10399, —, 21.ii.1979, Vikas Vidyalaya, Ranchi, Bihar, India.

Scale = mm & cm

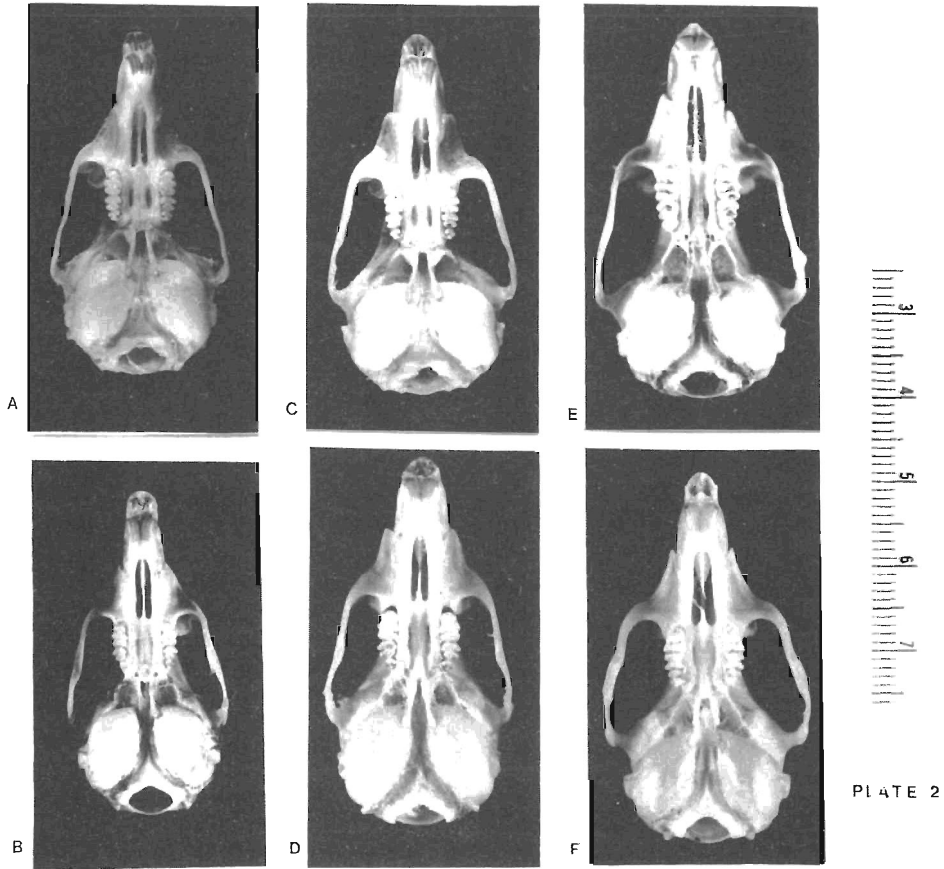


Plate 2: Cranial morphology of the six species of *Tatera* found in north-east Africa and Asia — ventral view. (Specimens as in Plate 1).

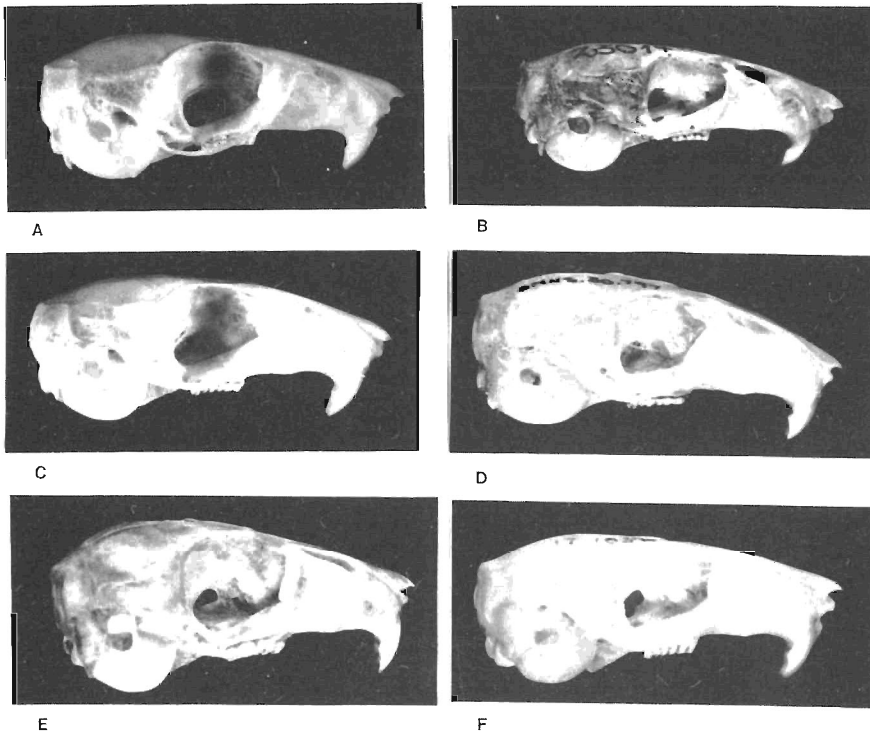


PLATE 3

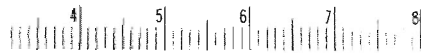


Plate 3: Cranial morphology of the six species of *Tatera* found in north-east Africa and Asia — lateral view. (Specimens as in Plate 1).

Table 1: *Tatera robusta*.

	sex	mean	range	S. D.	n
External measurements					
HB	male	152.2	120 — 190	12.6	74
	fem.	148.1	111 — 200	11.9	69
TAIL	male	177.1	125 — 215	16.1	74
	fem.	177.9	137 — 200	13.4	65
HF	male	35.3	21 — 40	2.6	81
	fem.	35.6	25 — 42	2.9	68
E	male	20.9	13 — 28	2.3	81
	fem.	21.2	17 — 25	1.4	68
Cranial & dental measurements					
GTL	male	41.9	39.0— 44.7	1.2	67
	fem.	41.9	39.6— 43.7	1.0	63
CBL	male	37.5	35.1— 40.5	1.2	74
	fem.	37.4	35.2— 39.4	1.0	65
ZB	male	21.1	19.5— 22.4	0.7	65
	fem.	20.9	19.1— 22.2	0.8	56
BB	male	16.9	16.0— 17.9	0.4	77
	fem.	16.9	15.8— 17.8	0.5	69
IC	male	7.3	6.3— 8.4	0.4	75
	fem.	7.3	6.5— 8.4	0.5	74
RW	male	5.7	5.0— 6.2	0.3	86
	fem.	5.6	5.1— 6.1	0.2	74
RL	male	16.0	14.6— 17.5	0.6	85
	fem.	15.9	14.6— 17.0	0.6	75
TMW	male	8.5	7.8— 9.1	0.3	85
	fem.	8.5	7.5— 9.4	0.4	74
TB	male	12.5	11.4— 13.4	0.4	74
	fem.	12.5	11.4— 13.4	0.5	66
TBW	male	16.9	15.0— 18.6	0.9	66
	fem.	17.0	14.8— 18.8	1.0	64
OH	male	10.0	9.2— 10.8	0.4	65
	fem.	10.1	9.2— 10.9	0.4	63
ML	male	25.9	23.8— 28.0	0.9	77
	fem.	25.7	24.0— 27.4	0.9	64
MXC	male	6.6	5.9— 7.2	0.3	83
	fem.	6.5	5.8— 7.1	0.3	70
MXCW	male	2.2	2.0— 2.4	0.1	87
	fem.	2.2	2.0— 2.4	0.1	76
MDC	male	6.2	5.5— 7.0	0.3	85
	fem.	6.1	5.6— 6.9	0.3	73
IH	male	7.1	6.3— 7.8	0.4	59
	fem.	6.9	6.2— 8.0	0.4	58
IW	male	3.4	3.0— 3.8	0.2	60
	fem.	3.3	2.8— 3.9	0.2	58
Osteological measurements					
GLF	male	31.1	25.4— 33.4	2.1	12
	fem.	31.1	29.0— 31.9	1.0	9
GLH	male	19.9	18.3— 20.7	0.8	8
	fem.	19.3	18.6— 19.9	0.7	4
Body weight (after Neal, 1982)					
TOT	male	103	80 — 152	—	—
	fem.	102	80 — 130	—	—
EVIC	male	91	70 — 130	—	—
	fem.	85	70 — 100	—	—

Table 2: *Tatera phillipsi*.

	sex	mean	range	S. D.	n
External measurements					
HB	male	144.0	143 — 145	—	2
	fem.	136.3	116 — 145	8.9	9
TAIL	male	186.0	183 — 189	—	2
	fem.	174.1	162 — 185	11.3	9
HF	male	35.5	35 — 36	—	2
	fem.	34.0	32 — 37	1.9	10
E	male	19.0	18 — 20	—	2
	fem.	19.2	17 — 21	1.2	9
Cranial & dental measurements					
GTL	male	38.9	37.3— 40.9	1.8	3
	fem.	38.4	37.6— 39.4	0.6	9
CBL	male	34.4	33.0— 36.4	1.8	3
	fem.	34.4	33.5— 35.0	0.5	8
ZB	male	18.6	17.8— 19.4	—	2
	fem.	18.9	18.2— 19.4	0.4	6
BB	male	15.6	15.2— 15.8	0.3	4
	fem.	15.8	15.4— 16.6	0.4	9
IC	male	6.4	5.9— 6.8	0.4	4
	fem.	6.7	6.3— 7.0	0.3	10
RW	male	5.1	4.9— 5.3	0.2	4
	fem.	5.1	4.8— 5.5	0.2	10
RL	male	14.8	13.9— 15.7	0.9	4
	fem.	14.8	14.1— 15.7	0.5	11
TMW	male	7.6	7.3— 7.9	0.3	4
	fem.	7.8	7.4— 8.3	0.3	10
TB	male	11.6	11.5— 11.8	0.2	3
	fem.	11.8	11.4— 12.4	0.3	9
TBW	male	14.6	14.0— 15.2	0.6	3
	fem.	15.5	14.6— 16.7	0.8	8
OH	male	9.3	9.0— 9.6	0.3	3
	fem.	9.5	9.1— 10.0	0.4	8
ML	male	23.4	22.1— 24.6	1.3	3
	fem.	23.0	22.3— 23.5	0.4	8
MXC	male	5.8	5.4— 5.9	0.4	4
	fem.	5.9	5.6— 6.2	0.2	9
MXCW	male	2.0	1.9— 2.1	0.1	4
	fem.	2.0	1.9— 2.1	0.1	10
MDC	male	5.5	5.1— 5.9	0.3	4
	fem.	5.7	5.3— 6.1	0.2	11
IH	male	6.3	5.6— 6.9	0.6	4
	fem.	6.2	5.5— 7.2	0.5	9
IW	male	3.1	2.9— 3.3	0.2	4
	fem.	3.1	3.0— 3.3	0.1	11
Osteological measurements					
GLF	male	27.0	—	—	1
	fem.	no data	—	—	—
GLH	male	18.0	—	—	1
	fem.	no data	—	—	—

Table 3: *Tatera nigricauda*.

	sex	mean	range	S. D.	n
<i>Tatera nigricauda nigricauda</i>					
External measurements					
HB	male	185.8	178 — 193	8.4	4
	fem.	164.0	130 — 164	14.0	6
TAIL	male	200.8	190 — 208	7.7	4
	fem.	187.2	170 — 204	11.3	6
HF	male	40.5	40 — 41	0.6	4
	fem.	37.3	34 — 39	2.0	6
E	male	22.3	20 — 24	2.1	3
	fem.	21.8	21 — 24	1.3	6
Cranial & dental measurements					
GTL	male	48.7	47.0— 50.5	1.8	3
	fem.	45.3	43.1— 47.9	1.7	6
CBL	male	44.5	42.9— 45.8	1.5	3
	fem.	40.5	38.9— 41.8	1.3	6
ZB	male	25.3	24.2— 26.1	1.0	4
	fem.	22.6	21.9— 23.2	0.6	5
BB	male	18.3	18.0— 18.7	0.3	4
	fem.	18.0	17.6— 18.2	0.2	6
IC	male	8.7	8.6— 8.9	0.1	4
	fem.	8.1	7.4— 8.7	0.5	6
RW	male	7.0	6.6— 7.6	0.4	4
	fem.	6.5	6.2— 6.7	0.2	6
RL	male	18.4	17.6— 19.3	0.7	4
	fem.	17.3	16.6— 18.4	0.7	6
TMW	male	9.2	8.9— 9.5	0.3	3
	fem.	9.2	8.8— 9.6	0.3	6
TB	male	14.5	13.6— 15.1	0.7	4
	fem.	13.3	12.7— 13.8	0.4	6
TBW	male	19.3	17.8— 20.7	1.4	4
	fem.	19.1	16.8— 20.6	1.3	6
OH	male	11.9	11.5— 12.1	0.3	4
	fem.	10.7	10.4— 10.9	0.2	4
ML	male	31.3	29.8— 33.1	1.5	4
	fem.	27.8	26.5— 29.1	1.0	5
MXC	male	7.0	6.7— 7.3	0.3	3
	fem.	6.9	6.7— 7.0	0.1	4
MXCW	male	2.5	2.4— 2.5	0.1	3
	fem.	2.4	2.4— 2.5	0.1	5
MDC	male	6.7	6.5— 7.0	0.2	3
	fem.	6.5	6.2— 6.8	0.3	6
IH	male	9.3	8.9— 9.8	0.4	4
	fem.	8.0	7.5— 8.5	0.3	6
IW	male	4.1	3.7— 4.3	0.3	4
	fem.	3.9	3.6— 4.3	0.3	6
<i>Tatera nigricauda nyama</i>					
External measurements					
HB	male	166.4	157 — 184	9.8	8
	fem.	153.5	146 — 164	5.7	11
TAIL	male	200.8	177 — 213	15.0	8
	fem.	192.5	177 — 203	9.6	11
HF	male	38.1	31 — 45	4.0	8
	fem.	37.0	35 — 39	1.5	11
E	male	22.3	22 — 23	0.4	8
	fem.	21.5	20 — 23	1.2	11

	sex	mean	range	S. D.	n
Cranial & dental measurements					
GTL	male	46.0	44.4— 48.1	1.1	8
	fem.	43.5	42.5— 44.9	0.9	10
CBL	male	41.4	40.3— 42.5	0.9	7
	fem.	39.1	37.8— 40.5	0.9	11
ZB	male	23.7	22.0— 24.2	0.9	6
	fem.	21.6	20.8— 22.1	0.5	8
BB	male	17.4	16.6— 18.0	0.5	7
	fem.	17.1	16.8— 17.6	0.2	9
IC	male	8.8	8.2— 10.1	0.6	8
	fem.	8.1	7.4— 8.6	0.4	10
RW	male	6.7	6.3— 7.1	0.2	8
	fem.	6.2	5.7— 6.7	0.3	11
RL	male	18.1	17.4— 18.8	0.5	8
	fem.	16.8	15.5— 17.8	0.7	10
TMW	male	8.7	8.2— 9.1	0.3	8
	fem.	8.5	7.9— 8.9	0.4	11
TB	male	13.1	12.5— 14.0	0.5	7
	fem.	12.8	12.3— 13.2	0.4	11
TBW	male	19.3	18.9— 19.7	0.3	6
	fem.	18.4	17.1— 20.6	1.1	11
OH	male	10.7	9.8— 12.1	0.5	7
	fem.	10.5	10.0— 11.2	0.4	11
ML	male	28.9	27.7— 30.3	1.2	8
	fem.	26.6	25.7— 27.1	0.4	11
MXC	male	6.7	6.4— 7.0	0.2	7
	fem.	6.8	6.5— 7.1	0.2	10
MXCW	male	2.3	2.0— 2.4	0.1	8
	fem.	2.4	2.2— 2.5	0.1	10
MDC	male	6.3	5.9— 6.9	0.4	7
	fem.	6.3	5.9— 6.7	0.2	10
IH	male	8.4	7.6— 9.1	0.4	8
	fem.	7.7	7.0— 8.7	0.5	11
IW	male	4.0	3.7— 4.4	0.2	8
	fem.	3.7	3.2— 4.0	0.2	11
Body weight (after Neal, 1982)					
TOT	male	132	80 —195	—	—
	fem.	114	80 —161	—	—
EVIC	male	115	70 —170	—	—
	fem.	95	70 —120	—	—

Table 4: *Tatera valida*.

	sex	mean	range	S. D.	n
External measurements					
HB	male	167.2	135 — 195	13.6	57
	fem.	160.0	133 — 175	9.3	56
TAIL	male	157.2	115 — 186	11.1	58
	fem.	158.9	138 — 187	10.3	56
HF	male	34.0	30 — 39	1.7	58
	fem.	33.3	30 — 38	1.8	56
E	male	21.8	17 — 29	1.6	57
	fem.	21.4	19 — 24	1.3	54
Cranial & dental measurements					
GTL	male	41.7	38.5— 44.7	1.2	65
	fem.	41.1	38.1— 43.6	1.3	59
CBL	male	38.7	35.3— 42.2	1.4	68
	fem.	38.1	35.4— 40.7	1.1	63
ZB	male	21.1	19.1— 22.2	0.7	47
	fem.	21.1	19.7— 22.5	0.6	45
BB	male	16.4	14.6— 17.5	0.5	73
	fem.	16.4	15.4— 18.3	0.5	65
IC	male	6.8	6.2— 7.6	0.3	74
	fem.	6.8	6.2— 7.5	0.3	68
RW	male	6.1	5.5— 6.9	0.3	74
	fem.	6.1	5.4— 6.8	0.3	70
RL	male	14.8	13.6— 16.1	0.6	70
	fem.	14.6	12.9— 15.7	0.6	65
TMW	male	9.0	8.2— 9.7	0.3	73
	fem.	9.0	8.1— 9.6	0.3	70
TB	male	12.9	11.5— 13.8	0.5	68
	fem.	12.7	12.0— 13.4	0.3	66
TBW	male	16.9	15.2— 19.0	1.0	62
	fem.	16.9	14.9— 18.7	1.0	55
OH	male	10.7	9.9— 11.4	0.4	64
	fem.	10.5	9.6— 11.2	0.4	57
ML	male	27.4	24.9— 29.2	0.9	62
	fem.	27.1	24.4— 28.7	1.0	60
MXC	male	7.1	6.1— 7.8	0.3	70
	fem.	7.2	6.4— 7.8	0.3	66
MXCW	male	2.5	2.2— 2.8	0.1	75
	fem.	2.5	1.8— 2.8	0.1	69
MDC	male	6.8	5.9— 7.4	0.3	74
	fem.	6.8	6.1— 7.6	0.3	69
IH	male	7.2	5.1— 8.6	0.5	69
	fem.	7.2	6.2— 8.1	0.4	63
IW	male	4.0	3.3— 4.7	0.3	69
	fem.	4.0	2.6— 4.6	0.3	64
Osteological measurements					
GLF	male	no data			
	fem.	30.3	30.1— 30.7	0.3	3
GLH	male	no data			
	fem.	19.5	19.2— 20.0	0.4	3
Body weight (after Neal, 1982)					
TOT	male	129	90 — 160	—	—
	fem.	113	90 — 130	—	—
EVIC	male	113	70 — 140	—	—
	fem.	92	70 — 105	—	—

Table 5: *Tatera boehmi*.

	sex	mean	range	S. D.	n
External measurements					
HB	male	no data			
	fem.	162.3	139 — 179	11.8	12
TAIL	male	no data			
	fem.	215.5	190 — 234	12.8	12
HF	male	no data			
	fem.	40.8	38 — 47	2.6	11
E	male	no data			
	fem.	24.3	21 — 26	1.6	12
Cranial & dental measurements					
GTL	male	44.0	43.9— 44.0	—	2
	fem.	43.5	42.0— 45.2	1.1	10
CBL	male	40.4	40.0— 40.7	—	2
	fem.	39.3	36.8— 40.7	1.4	13
ZB	male	23.5	23.0— 24.0	—	2
	fem.	23.3	22.0— 24.3	0.9	8
BB	male	18.0	17.9— 18.0	—	2
	fem.	17.7	16.9— 18.6	0.6	14
IC	male	7.3	7.2— 7.3	—	2
	fem.	7.1	6.4— 8.0	0.5	13
RW	male	6.8	6.7— 6.8	—	2
	fem.	6.4	5.8— 7.0	0.4	14
RL	male	16.9	16.8— 16.9	—	2
	fem.	16.8	15.4— 18.3	0.9	12
TMW	male	9.6	9.3— 9.9	—	2
	fem.	9.6	9.0— 10.3	0.4	14
GLIF	male	8.8	8.5— 9.1	—	2
	fem.	8.3	7.1— 8.9	0.5	14
PWIF	male	2.2	2.1— 2.3	—	2
	fem.	2.2	1.8— 2.5	0.2	14
TB	male	13.1	13.0— 13.1	—	2
	fem.	12.9	12.0— 14.5	0.6	14
TBW	male	17.8	16.2— 19.4	—	2
	fem.	18.8	15.9— 19.6	1.1	10
OH	male	11.0	10.6— 11.4	—	2
	fem.	11.0	10.0— 11.4	0.4	12
ML	male	29.5	29.5— 29.5	—	2
	fem.	29.8	27.8— 30.9	1.0	11
MXC	male	6.9	6.9— 6.9	—	2
	fem.	7.4	6.8— 7.8	0.3	15
MXCW	male	2.7	2.6— 2.8	—	2
	fem.	2.7	2.3— 3.0	0.2	15
MDC	male	7.2	6.7— 7.7	—	2
	fem.	7.1	6.6— 7.6	0.3	15
IH	male	8.0	7.4— 8.5	—	2
	fem.	8.0	7.2— 8.6	0.4	14
IW	male	4.5	4.3— 4.7	—	2
	fem.	4.5	4.0— 4.9	0.3	14

Table 6: *Tatera indica*.

	sex	mean	range	S. D.	n
<i>Tatera indica indica</i>					
External measurements					
HB	male	161.8	135 — 189	13.3	39
	fem.	157.7	132 — 198	14.3	28
TAIL	male	183.2	147 — 207	13.6	38
	fem.	182.5	152 — 201	12.1	28
HF	male	37.8	34 — 49	2.4	39
	fem.	37.1	34 — 40	1.7	29
E	male	23.9	22 — 31	1.9	39
	fem.	23.4	20 — 27	1.6	29
Cranial & dental measurements					
GTL	male	43.3	39.2 — 48.6	2.2	36
	fem.	42.9	39.4 — 47.0	1.9	29
CBL	male	39.3	35.7 — 43.1	1.9	38
	fem.	39.1	35.4 — 44.3	2.1	30
ZB	male	22.6	20.5 — 24.5	1.1	30
	fem.	22.7	21.1 — 25.6	1.2	26
BB	male	17.2	16.2 — 18.1	0.5	39
	fem.	17.1	16.1 — 18.4	0.5	30
IC	male	7.1	6.0 — 7.9	0.5	39
	fem.	7.1	6.5 — 7.8	0.4	30
RW	male	5.8	5.2 — 6.3	0.3	38
	fem.	5.8	5.3 — 6.6	0.3	30
RL	male	16.7	14.6 — 19.5	1.2	36
	fem.	16.5	14.4 — 18.3	1.0	29
TMW	male	8.8	7.9 — 9.6	0.4	37
	fem.	8.9	8.0 — 9.8	0.5	30
TB	male	14.0	12.8 — 15.6	0.6	37
	fem.	13.8	12.5 — 15.4	0.7	30
TBW	male	19.1	15.9 — 22.6	1.4	37
	fem.	19.2	16.3 — 21.8	1.4	27
OH	male	10.9	10.1 — 12.5	0.5	34
	fem.	11.0	10.0 — 12.2	0.6	28
ML	male	26.9	23.2 — 30.4	1.6	35
	fem.	26.9	24.6 — 30.8	1.7	25
MXC	male	6.6	6.0 — 7.3	0.4	38
	fem.	6.7	5.8 — 7.6	0.5	30
MXCW	male	2.4	2.2 — 2.6	0.1	39
	fem.	2.4	2.1 — 2.6	0.1	30
MDC	male	6.2	5.5 — 7.0	0.3	40
	fem.	6.3	5.6 — 7.4	0.4	29
IH	male	7.7	6.7 — 8.5	0.4	23
	fem.	7.9	6.9 — 8.8	0.5	13
IW	male	3.4	2.8 — 3.8	0.2	24
	fem.	3.5	2.9 — 4.2	0.4	13
Osteological measurements					
GLF	male	32.7	—	—	1
	fem.	no data			
GLH	male	20.8	—	—	1
	fem.	no data			
<i>Tatera indica taeniura</i>					
External measurements					
HB	male	186.0	155 — 205	17.5	9
	fem.	177.7	160 — 205	14.3	13
TAIL	male	185.8	167 — 220	16.6	9
	fem.	183.5	167 — 220	13.3	13

	sex	mean	range	S. D.	n
HF	male	43.6	38 — 50	3.6	9
	fem.	41.9	39 — 45	1.8	13
E	male	26.3	20 — 30	3.1	8
	fem.	26.6	19 — 28	2.5	13
Cranial & dental measurements					
GTL	male	48.3	44.4— 50.9	2.0	11
	fem.	46.3	44.1— 49.3	2.0	10
CBL	male	44.2	40.2— 46.7	2.0	11
	fem.	42.3	40.0— 44.8	1.8	11
ZB	male	25.7	22.5— 27.7	1.5	11
	fem.	24.4	21.6— 26.0	1.4	14
BB	male	18.3	17.2— 18.8	0.5	11
	fem.	18.1	17.6— 19.3	0.5	12
IC	male	7.6	7.1— 7.9	0.3	11
	fem.	7.6	6.8— 8.4	0.5	13
RW	male	6.4	5.9— 6.9	0.3	11
	fem.	6.2	5.7— 6.6	0.3	14
RL	male	18.9	16.6— 21.2	1.3	11
	fem.	18.1	16.4— 19.5	0.9	14
TMW	male	10.0	9.0— 11.0	0.6	11
	fem.	9.7	9.2— 10.4	0.3	14
TB	male	14.6	13.8— 15.7	0.5	11
	fem.	14.2	13.4— 15.1	0.6	11
TBW	male	20.0	18.7— 21.1	0.9	11
	fem.	19.5	16.8— 21.1	1.6	12
OH	male	12.3	11.5— 13.0	0.5	11
	fem.	11.7	10.8— 12.4	0.6	9
ML	male	30.9	28.0— 33.7	1.5	11
	fem.	29.5	27.6— 31.5	1.4	11
MXC	male	7.4	7.0— 8.1	0.3	10
	fem.	7.2	6.9— 7.7	0.2	14
MXCW	male	2.7	2.5— 2.8	0.1	10
	fem.	2.7	2.5— 3.0	0.1	14
MDC	male	7.2	6.5— 7.9	0.4	10
	fem.	7.0	6.6— 8.1	0.4	14
IH	male	8.8	7.7— 9.5	0.6	8
	fem.	8.8	7.9— 9.6	0.6	13
IW	male	3.7	2.8— 4.1	0.4	8
	fem.	3.9	3.5— 4.1	0.2	13
Osteological measurements					
GLF	male	40.5	38.9— 41.9	1.1	5
	fem.	37.0	36.9— 37.0	—	2
GLH	male	25.6	24.9— 26.4	0.6	5
	fem.	22.0	21.1— 22.8	—	2
<i>Tatera indica cuvieri</i>					
External measurements					
HB	male	174.0	116 — 203	19.9	25
	fem.	166.0	140 — 198	14.6	26
TAIL	male	201.2	151 — 222	15.4	24
	fem.	202.3	170 — 234	17.2	26
HF	male	43.4	40 — 47	1.7	25
	fem.	42.2	39 — 47	2.1	26
E	male	24.1	20 — 26	1.3	25
	fem.	24.3	20 — 26	1.4	27
Cranial & dental measurements					
GTL	male	45.7	42.5— 48.2	1.3	26
	fem.	44.9	41.6— 48.0	1.8	25

	sex	mean	range	S. D.	n
CBL	male	40.9	38.6— 42.4	1.2	27
	fem.	40.0	36.5— 43.8	1.7	27
ZB	male	23.3	21.6— 24.9	1.0	25
	fem.	23.3	21.3— 25.8	1.0	19
BB	male	17.8	16.9— 18.9	0.5	31
	fem.	17.6	16.7— 18.7	0.5	27
IC	male	7.6	6.8— 8.4	0.4	31
	fem.	7.3	6.6— 8.0	0.4	27
RW	male	6.1	5.6— 6.7	0.3	31
	fem.	6.1	5.6— 6.8	0.3	28
RL	male	17.7	16.2— 18.9	0.6	30
	fem.	17.5	15.9— 19.3	1.0	28
TMW	male	9.4	8.5— 10.3	0.4	31
	fem.	9.3	8.7— 10.0	0.4	28
TB	male	13.3	12.6— 14.4	0.4	28
	fem.	13.2	12.1— 14.2	0.6	25
TBW	male	18.9	16.3— 20.4	1.2	25
	fem.	18.8	14.8— 20.9	1.6	23
OH	male	11.7	10.8— 12.8	0.5	22
	fem.	11.7	10.8— 12.6	0.5	25
ML	male	28.1	26.1— 29.9	1.2	26
	fem.	27.3	25.4— 30.3	1.3	20
MXC	male	7.1	6.3— 7.8	0.3	31
	fem.	6.9	6.2— 7.5	0.3	28
MXCW	male	2.5	2.2— 2.7	0.1	31
	fem.	2.5	2.1— 2.8	0.2	28
MDC	male	6.5	5.9— 7.2	0.3	31
	fem.	6.4	5.6— 7.1	0.4	28
IH	male	7.9	7.1— 8.5	0.4	13
	fem.	7.7	7.0— 8.2	0.4	10
IW	male	3.6	3.1— 4.1	0.3	13
	fem.	3.6	3.1— 4.0	0.3	10