Taxonomy of the genus *Gerbillus* (Rodentia: Gerbillinae) with comments on the applications of generic and subgeneric names and an annotated list of species

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Abstract

The various usages of *Gerbillus, Dipodillus* and *Hendecapleura* as genera or subgenera are reviewed. Data are presented regarding variation in plantar morphology, tooth morphology, the ratio of tail length to head and body length, morphology of the auditory bulla and comparative karyology. These data fail to support any of the several concepts of genera and subgenera presently used in the taxonomy of this rodent group. These data reveal the need for a comprehensive revision and until such is available, it is suggested that rodent species of this group should be placed in a single genus, *Gerbillus*, with no subgenera.

An annotated list with provisional recognition of 62 species is provided. The criteria utilized to determine valid species are given. An appendix lists 113 named forms with citations and type localities.

Introduction

The genus *Gerbillus* includes an assemblage of species that occur in arid and semiarid environments of north and east Africa, Sinai, the Arabian Peninsula, Iran, Afghanistan, Pakistan and India. These rodents constitute a diverse and important component of the mammalian fauna of this large area.

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To date, 113 taxa have been formally described (cf. Appendix). No comprehensive revision of this genus exists, but various checklists and regional studies are available (Allen 1939; Ellerman 1940; Ellerman and Morrison-Scott 1951; Lay and Nadler 1975; Harrison 1972; Jordan et al. 1974; Petter 1975; Lay et al. 1975; Corbet 1978; Osborn and Helmy 1980; etc.).

The literature abounds with differing opinions regarding species synonymies and the use of generic and subgeneric names in reference to these rodents (vide infra). Much of this confusion is attributable to the trend of reducing the total number of species begun by Ellerman (1940). Allen’s (1939) checklist of African mammals recognized 49 species among 63 taxa of *Gerbillus* and *Dipodillus*. Ellerman (1940) listed 37 species among 74 taxa from the entire range (Africa and Asia). Petter (1975) reduced the total number of species among 88 taxa from Africa and part of Arabia to 20.

The following comparison of works on the palaearctic fauna is instructive. Ellerman and Morrison-Scott (1951) regarded 10 species as valid among 49 taxa. Later, Corbet (1978) considered 19 species as valid among the 76 taxa from the same coverage area. The present study tentatively recognizes 62 valid species.

**Results and discussion**

The combination of subtle morphological differences between species, a relatively large number of species and limited samples for comparative study has made classification of this group difficult. While previous taxonomic schemes have served usefully, it is clear that as new data accumulate, earlier notions regarding definitions of species, genera and subgenera must be reconsidered.

The next four paragraphs provide historical perspective on the use of genera and subgenera. The subgeneric diagnoses of *Dipodillus*, *Gerbillus* and *Hendecapleura* as originally given by Lataste (1881, 1882b) are provided. These are followed by summaries of the concepts of various later authors on the application of *Gerbillus*, *Dipodillus* and *Hendecapleura*.

Lataste (1881, 1882b) first used the names *Gerbillus*, *Dipodillus* and *Hendecapleura* as subgenera of *Gerbillus*. Characters and species that Lataste regarded as typical of each subgenus were the following:

*Gerbillus*: Five metatarsal tubercles at maximum; well developed auditory bullae of which the posterior parts attain or exceed the level of the occipital bone; first upper molar with opposite cusps; one carpal tubercle; soles of the hind feet hairy; included *G. gerbillus*, *G. pyramidum*, *G. hirtipes*, *G. longicaudus* and two taxa now allocated to *Meriones* and *Desmodillus*, respectively.

*Dipodillus*: Six metatarsal tubercles; mediocre development of the auditory bullae of which the posterior parts clearly extend caudal to the occipital bone; first upper molar with alternate cusps, cusps of other molars more or less alternate in position; included *G. simoni* and *G. campestris*.

*Hendecapleura*: one tarsal tubercle; occipital vertically flattened; molar cusps in opposite positions; well developed auditory bullae extending posterior to the occiput; included *G. garamantis*, *G. nanus*, *G. bottai*, *G. quadrimaculatus*. Thomas (1901), de Winton (1901) and Thomas and Trouessart (1903) first used *Dipodillus* subgenerically in reference to all taxa having naked-soled hind feet. However, beginning in 1902 and without explanation Thomas (1902b, 1904, 1908, 1910) and de Winton (1902, 1903) applied *Dipodillus* generically in reference to naked-footed taxa. At the same time hairy-footed species were reported as *Gerbillus sensu strictu*. This use of *Dipodillus* and *Gerbillus* has continued to the present (St. Leger 1931; Allen 1939; Wassif et al. 1969; Osborn and Helmy 1980).
Another view was presented by Ellerman (1940), who recognized a single genus, Gerbillus, containing two subgenera: Gerbillus for taxa with hairy feet; Dipodillus for taxa with naked feet. Ellerman justified this allocation because hairiness of the foot is not used to diagnose genera elsewhere in the Rodentia, intermediate forms exist and the inconstancy of this character in the related genus Meriones.

A third concept originated with Petter (1959), who regarded the following characters of Gerbillus simoni Lataste to be sufficiently distinct to merit generic recognition as Dipodillus: small bullae; tail shorter than head and body length; plantar soles naked; molar tubercles more or less alternate; molars laminated early in development. Schlitter and Setzer (1972), Cockrum et al. (1976a) and Corbet (1978) accepted this scheme and regarded as “short-tailed” the four species they included in Dipodillus: G. simoni; G. maghrebi; G. kaiser; G. zakariae. These authors placed all other forms into the genus Gerbillus with two subgenera: Hendecapleura, which includes all bare footed species and Gerbillus, which contains all hairy-footed species.

To determine which if any of these three schemes reflect systematic relationships, the taxonomic significance of the following criteria must be evaluated: the variability of the plantar surfaces of the feet; the differences in size of the auditory bullae; the ratio of tail length to head and body length; the degree of alternation of the molar tubercles; ontogeny of molar lamellation; any additional characters that may reflect relationships.

The remainder of this discussion and the annotated checklist that follows is based upon my examination of the type specimens of 83 of the 113 taxa of Gerbillus (cf. Appendix). It must be emphasized that all conclusions presented here are preliminary and are submitted for future evaluation. Pertinent information, when available, pertaining to taxa, the types of which I have not examined, was taken from the literature. Although this report emphasizes type specimens, I have examined several thousand specimens in the collections of the U. S. National Museum, Washington, D. C., the Field Museum of Natural History, Chicago, Illinois and the University of Michigan Museum of Zoology, Ann Arbor, Michigan. Because identifications for many of these specimens are questionable and the nature of this report is preliminary, data from the study of these collections has been utilized only to provide additional background for the discussion of characters that follows.

Nature of plantar soles

Among the 62 species listed below, 32 are naked-soled, 22 are hairy-soled, six are regarded as intermediate and the condition of two is unknown (Tab. 1). Illustrations of the hind feet of 12 species and the fore feet of nine species are available, but no comprehensive study of palmar and plantar anatomy exists (Lataste 1887; Klaptocz 1909; Wassif et al. 1969; Lay and Nadler 1975; Osborn and Helmy 1980). All of the authors that have illustrated plantar surfaces excepting Lay and Nadler (1975) failed to show the metatarsal hairs characteristic of the so-called “naked-footed” or “bare-footed” gerbils. Those authors that consider these traits as indicating generic status have not considered the intermediate forms.

As Ellerman (1940) indicated for the related genus Meriones, naked, partially haired or fully haired soles characterize different species (Fig. 1). However, no species has totally naked plantar surfaces (Fig. 1) and the term virtually naked describes the condition more appropriately. Further, no species has the entire plantar surface completely covered with hair, as there is always a small bare spot in the tarsal region. The number of plantar tubercles ranges between one and five, but the number appears to be species specific. All recent workers apparently agree that this group represents a single genus. Whether or not the status of Meriones is correct, the significance of plantar surfaces for connoting generic distinction has been applied differently in Meriones versus Gerbillus/Dipodillus. My observations suggest that variation in the distribution of hair on plantar surfaces in
Gerbillus/Dipodillus is similar to that depicted for Meriones in Figure 1. Studies documenting this perception would be useful.

Size of the auditory bulla

The degree of development of the auditory bullae varies inter and intraspecifically in the Gerbillinae (Lay 1972). No comprehensive evaluation of middle ear variation within or

Fig. 1. Plantar surfaces of hind feet of six species of the genus Meriones that show the transition from virtually naked soles to nearly fully haired soles. A: M. persicus; B: M. rex; C: M. hurrianae; D: M. vinogradovi; E: M. sacramenti; F: M. ungusculatus. A and B show few hairs in the metatarsal region of the sole and are similar to G. nanus, G. simoni, G. campestris and G. henleyi all of which have been regarded as Dipodillus by various authors (vide infra). C represents an intermediate stage between virtually naked and “fully haired” soles, as in F, and characterizes those species noted as intermediate in table 1. D, E and F are similar in plantar morphology to “hairy-footed” species which have been classified as Gerbillus
between species of *Gerbillus* exists, though the data of Osborn and Helmy (1980) provide a starting point. Anatomy of the gerbilline auditory bullae is complex and the various bullar components reveal different patterns of variation between species. Most references to bullae or bullar size have not carefully defined the structure(s) described and it is difficult to make objective comparisons using such data. For example, the length of the auditory bulla of two species may be nearly identical, while the tympanic and mastoid components may vary independently of total length as between *G. henleyi* and *G. campestris* (Fig. 2). Bullar volume, hence length, also varies significantly among populations of widely distributed species in the related genus, *Meriones* (Lay 1972).

![Image of lateral views of posterior aspect of cranium showing auditory bullae.](image_url)

Fig. 2. Lateral views of posterior aspect of cranium showing auditory bullae. Note that an accessory tympanum is absent in A (see bony plate labelled a and p) and present in B, C, and D. Observe that the bodies of the malleus and incus are normally visible when an accessory tympanum is present. A: *Gerbillus campestris* University Michigan Museum of Zoology (UMMZ) no. 122764; B: *G. perpallidus* Field Museum of Natural History (FMNH) no. 79773; C: *G. henleyi* UMMZ no. 118807; D: *G. pyramidum* FMNH no. 74736. Scale for A, B, C and D is identical, the white bar in lower right corner of B equals one millimeter. a = anterior lamina of tympanic bone; l = body of incus; m = body of malleus; p = posterior lamina of tympanic; large white arrow-heads denote proximal end of manubrium of malleus; small white arrows in B mark the rim of the anterior lamina of the tympanic to which the accessory tympanum attaches (compare A and B); the white asterisk in B and D is placed on the anterior process of the malleus, note that this structure cannot be seen in A, X lies within the suprameatal triangle, which contains a portion of the anterior mastoid air cell, compare A, B, C and D and note the different degrees of inflation of this cell within the confines of the triangle; y = marks the portion of the anterior mastoid air cell caudal to the suprameatal triangle; Z = indicates the posterior mastoid air cells, the external boundaries of these cells are marked with black or white dots; s = indicates the subarcurate fossa containing the parafloccular lobe of the cerebellum; T = is placed on the tympanic portion of the auditory bulla; SUP indicates superior, ANT denotes anterior. The accessory tympanum of D is intact and displays a prominent highlight just superior to the large white arrow.
Relative tail length

The ratio of tail length to head and body length ranges from .91 to 1.70 for the data examined (Fig. 3, 4). The range of intraspecific variation in tail length is considerable (Fig. 4). When both inter and intraspecific variation are considered there is no dichotomy between long-tailed species and the "short-tailed species" assigned to Dipodillus by Petter (1959), Schlitter and Setzer (1972) and Cockrum et al. (1976).


Molar tubercle position and ontogeny of lamellation

Osborn and Helmy (1980) illustrated crown views of upper and lower molars of young and mature individuals of eight Gerbillus species including campestris, dasysurus, simoni, mackilligini, amoenus, henleyi, gerbillus and pyramidum. The molar features regarded by Petter (1959) as unique to simoni are now known to characterize campestris, dasysurus, mackilligini and henleyi, all of which show cusps in more or less alternating positions on the first upper molar and no or miniscule cuspidation of the third lower molar. Lataste (1881) early recognized that the molars of campestris had cusps in alternate positions. For these reasons the significance of alternating cusps is dubious as a generic character. Among the immature individuals studied, the degree of lamination figured for simoni is not uniquely different (Osborn and Helmy 1980).
Accessory tympanum present or absent

An accessory tympanum situated within the anterior lamina of the tympanic bone, located superior to the eardrum and lateral to the epitympanic recess forms a membranous extension of the tympanum (Lay 1972). This anatomical feature, readily visible through the external auditory meatus (Fig. 2), is a species specific character, being either present or absent in all individuals (Tab. 1). An accessory tympanum is known to exist in 36 species of which 22 have hairy feet (Tab. 1). Among 32 naked-footed species, 14 exhibit an accessory tympanum (Tab. 1). If genera or subgenera were based upon this characteristic, which is comparable to any used previously, the species groupings obtained are entirely different from any prior arrangement.

Karyotype

The hairy-footed species fall into two groups based on diploid (2N) chromosome number. Eight species display a 2N of 38 to 42 and six species have a 2N in the range of 50 to 74 (Tab. 1). The seven bare-footed species studied have 2Ns ranging from 52 to 60 (Tab. 1). All the bare-footed and six of the hairy-footed species possess a relatively large number of acrocentric chromosomes (28–64). Those hairy-footed species in the 2N 38–42 range have few acrocentric chromosomes (0–8).

Recent studies incorporating karyotypic data (Wassif et al. 1969; Lay 1975; Lay and Nadler 1975) in correlation with morphology suggest that species diversity within Gerbillus has been underestimated. Taxonomic lists like those of Ellerman and Morrison-Scott (1951), Petter (1975), and Cockrum et al. (1976b) Corbet (1978) often reflect the general confusion within the secondary literature and provide taxonomic opinions unsupported by data. Simplistic single character analyses like that of Flynn (1982) must not be construed as indicating generic relationships. Systematics of Gerbillus sensu latu at the generic, subgeneric and specific levels requires comprehensive revision.

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Sinai and Gaza Strip
taking into account those characters discussed above and any others that may indicate relationships.

Until this group is carefully re-evaluated in entirety, it seems prudent to recognize a single genus, *Gerbillus*, and no subgenera. I have compiled an annotated list of species of *Gerbillus*. Taxa placed in synonymy without supporting evidence by earlier authors or taxa for which differing opinions exist in the literature concerning synonymy are retained as valid species. It must be emphasized that this account is provisional and is presented here, with comments, as an alternative to existing schemes and to stimulate additional research on the systematics and evolution of this group.


**Diagnosis:** Small to medium sized members of the subfamily Gerbillinae (adult head and body length usually 60–135 mm), with tail usually longer than or subequal to head and body length. Cheek teeth rooted and cuspidate, not prismatic. Mastoid portion of auditory bullae inflated with at least three chambers: anterior; posterior superior; and posterior inferior. Posterior superior mastoid always separated from anterior mastoid by a bony partition.

**Distribution:** North Africa from Sahel to Mediterranean coast, Ethiopia, Somalia, arid areas of Kenya and Uganda, Arabian peninsula, Iran east to Indian Desert.

**Comment:** Morphological differences between closely related species of *Gerbillus* are often subtle but none the less consistent (Lay and Nadler 1969; Lay 1975). Virtually all of the taxonomic literature on *Gerbillus* sensu latu has relied upon traditional skull and body measurements, an approach which has produced little agreement and much confusion. Resolution of these difficulties is more likely when karyotype, middle ear anatomy and details of plantar anatomy are included with traditional measurements and analysed quantitatively.


**Type locality:** Somalia: Berbera.

**Distribution:** Somalia.

**Comment:** Petter (1975) placed *G. acticola* in synonymy with *G. pyramidum* without comment, but the nearest documented occurrence of *G. pyramidum* is over 1300 kilometers distant in Sudan. This species should be regarded as distinct pending revision and karyotypic analysis.


**Type locality:** Sudan: W. Kordofan; Agageh Wells.

**Distribution:** Sudan.

**Included forms:** Petter (1975) included *G. dalloni* and *G. nigeriae* without comment and *G. coseni*, noting that it may be valid. Kock (1978) included *G. sudanensis*, *G. rosalinda* and *G. nigeriae* based on hindfoot length and characteristics of plantar hair. Refer to account of *G. gerbillus* for comments on *G. sudanensis*.

**Comment:** It is impossible to define the morphological limits of *G. agag* with the data presented by either Petter (1975) or Kock (1978) and *G. agag* should be treated as valid and monotypic pending revision.


**Type locality:** Israel: Rehoboth.

**Distribution:** Coastal dunes of Israel from north of Gaza to near Haifa (Zahavi and Wahrman 1957).

**Comment:** Considered by Harrison (1972) as distinct. Placed in synonymy under *G. andersoni* by Cockrum et al. (1976). *G. andersoni* and *G. allenbyi* are allopatrically distributed. Should be regarded as valid pending comprehensive revision (cf. Comment under *G. andersoni*).
*Type locality:* Egypt: Giza Province.  
*Distribution:* Egypt and Libya, possibly across Tunisia and Algeria to Mauritania.  
*Comment:* Ellerman and Morrison-Scott (1951) placed *G. amoenus* in synonymy under *G. dasyrurus*. Petter (1975) listed it as a synonym of *G. campestris* but commented that it may be valid. Corbet (1978) placed it in *G. nanus*. Wassif et al. (1969) and Osborn and Helmy (1980) treated *G. amoenus* as a valid species.

The presence of an accessory tymanum allows ready distinction from *G. campestris* and *G. dasyrurus*, which lack this feature. Direct comparisons with *G. nanus* are necessary to clarify the relationships between these two forms (2N = 52).

*Type locality:* Egypt: Mandara.  
*Distribution:* Northern Egypt and possibly Israel, Sinai, Libya and Tunisia.  
*Included forms:* Cockrum et al. (1976a) regarded both *G. eatoni* and *G. allenbyi* as synonyms of *G. andersoni*. Osborn and Helmy (1980) included *G. eatoni* and *G. bonhotei* as synonyms.

*Comment:* Wassif et al. (1969) and Lay et al. (1975) described karyotypes of **G. andersoni** as having a diploid number (2N) of 40, with all elements either metacentric or submetacentric. All specimens studied came from three localities near Alexandria. Cockrum et al. (1976a) stated that specimens from Tunisia possessed a karyotype similar if not identical to those reported from Egypt. The Tunisian karyotype was not illustrated. It should be noted that a 2N = 40 with all biarmed elements has been described for *G. occiduus* from Morocco (Lay 1975) and that this karyotype is distinct from that of *G. andersoni*. Wassif et al. (1969) and Lay et al. (1975) commented on karyological similarities between *G. andersoni* and *G. allenbyi* from Israel.

Cockrum et al. (1976a) considered the chromosomal similarities of the Tunisian, Egyptian and Israel 2N = 40 populations to suggest conspecificity. These authors compared the type specimens of *G. andersoni*, *G. eatoni* and *G. allenbyi* and concluded “that all are, in fact, conspecific and that differences among them are of the magnitude normally used to designate subspecies”. No convincing data were presented in support of this conclusion. Furthermore, as noted by Cockrum et al. (1976a), a rather large hiatus exists between the Tunisian and Egyptian samples. The Libyan population (see Ranck 1968: 94) and the Egyptian population of *G. andersoni inflatus*, mapped by Osborn and Helmy (1980: 120) have not been karyotyped.

Available evidence does not substantiate the conspecificity of these forms. It presently seems prudent to retain *G. allenbyi* and *G. andersoni* as species and recognize that *G. eatoni* is probably a synonym of *G. andersoni*. The Tunisian form, *G. andersoni blanci*, should be tentatively included in *G. andersoni*.

Wahrman and Gourevitz (1972) reported karyotypic variation in *Gerbillus* sp. in the sand dunes from Tel Aviv to south of Gaza of 2N = 51, 52, 53, 54, 55, 56, 59, 61, 64, 65, and 66. The southern part of this area lies near the type locality of *G. bonhotei*. Osborn and Helmy (1980) placed *G. bonhotei* in synonymy under *G. andersoni*. Until this situation is clarified, it seems best to consider *G. bonhotei* valid.

The report of *G. andersoni* from Jordan by Harrison (1972) requires corroboration.

*Type locality:* Iran: 60 km W of Kerman.  
*Distribution:* S. E. Iran, W. Pakistan, S. Afghanistan.  

*Comment:* This species was described as a race of *G. cheesmani*. Lay and Nadler (1975) presented evidence indicating that *G. aquilus* should be regarded as a valid species.

Type locality: Ethiopia: near Bilen.

Distribution: Type locality only.

Comment: PETTER (1975) placed G. bilensis in synonymy with G. pulvinatus without comment. Inasmuch as these two forms were described from opposite ends of the rift valley in Ethiopia that are separated by at least 700 km and because they have not been critically compared, G. bilensis should be regarded as distinct pending revision.


Type locality: Egypt: Khabra-abu-Guzoor, southeast of El Arish.

Distribution: Type locality only.

Comment: Status discussed in comments under G. andersoni. Should recognized as valid pending revision.


Type locality: Sudan: Sennar.

Distribution: Sudan; Kenya.

Included forms: Includes G. harwoodi and G. luteolus according to KOCK (1978).

Comment: PETTER (1975) regarded G. bottai and G. harwoodi as distinct species and included G. luteolus in G. campestris. The type of G. harwoodi has no accessory tympanum, the type of G. stigmonyx luteolus has an accessory tympanum. Unfortunately I have not studied the type of G. bottai, but because of the middle ear characters one of the two forms listed by KOCK (1978) cannot be synonymous, perhaps neither are. This species should be regarded as valid and monotypic pending revision.


Type locality: Sudan: Dharfur.

Comment: ALLEN (1939), ELLERMAN and MORRISON-SCOTT (1951) and CORBET (1978) treated G. burtoni as a synonym of G. pyramidum. Cuvier’s figures show relatively long and distinctively short posterior palatine foramina for G. burtoni (pl. 23) and G. pyramidum (pl. 25), respectively. These illustrations also suggest differences in the anatomy of the auditory bullae, mandible and zygomatic plates between these two forms. Therefore, G. burtoni is retained as a valid species.


Type locality: Somalia: Burao, 85 mi. S of Berbera.

Distribution: Somalia.

Comments: Placed without comment in synonymy with G. nanus by PETTER (1975). Because there is no evidence indicating that G. nanus occurs anywhere remotely near Somaliland, G. brockmani should be regarded as distinct pending revision.


Type locality: Algeria: Constantine Prov.; Philippeville.

Distribution: North Africa, from Morocco to Egypt and Sudan.

Included forms: See Table 2.

Comment: Opinions concerning synonyms vary widely and most fail to provide supporting evidence (cf. Tab. 2). G. campestris lacks an accessory tympanum and has a 2N = 56 in Egypt, Tunisia, and Algeria (WASSIF et al. 1969; JORDAN et al. 1974; MATTHEY 1952). Samples from Morocco also have 2N = 56 virtually identical to that reported above, but variation (2N = 57, 2N = 58) has been described from one locality (LAY et al. 1975).

Information available does not support or is equivocable for the inclusion of G. amoenus, G. bilda, G. jamesi, G. lowei, and G. stigmonyx as synonyms of G. campestris.

ALLEN (1939), ELLERMAN (1941) and ELLERMAN and MORRISON-SCOTT (1951) list G. gerbii Loche, G. minutus Loche and G. deserti Loche as synonyms of G. campestris.
It is impossible to positively identify these forms from Loche's descriptions. Cockrum and Setzer (1976) stated that G. gerbilli is a nomen nudum, that G. deserti probably is based on a specimen of Mus musculus and that G. minutus Loche 1857 was not a description but a misidentification and should be dropped. Later (Loche 1867) formally described the same specimen as Psammomys minutus. Cockrum and Setzer (1976) indicated that this form was probably G. campesi but it is unidentifiable on the basis of the original description. Until such time as the type specimens are located and compared G. deserti and Psammomys minutus should be regarded as incertae sedis.

G. quadriracmaculatus Lataste, 1882 is virtually impossible to identify from the original description and should be regarded as incertae sedis and not a synonym of G. campesi. G. quadriracmaculatus Bodenheimer, 1935 is a nomen nudum and may have been employed in reference to specimens of G. nanus from Wadi Hof, Israel.

Table 2

<table>
<thead>
<tr>
<th>Forms regarded as synonyms of G. campesi in three checklists</th>
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<tbody>
<tr>
<td>amoenus</td>
</tr>
<tr>
<td>brunnescens</td>
</tr>
<tr>
<td>cinnamosus</td>
</tr>
<tr>
<td>deserti</td>
</tr>
<tr>
<td>dodsoni</td>
</tr>
<tr>
<td>gerbii</td>
</tr>
<tr>
<td>baymanii</td>
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<tr>
<td>hilda</td>
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<tr>
<td>jamesi</td>
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<td>lowei</td>
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</tbody>
</table>


Type locality: Iraq: Lower Euphrates, near Basra.

Distribution: S. W. Iran; Iraq; Saudi Arabia; Oman; N. Yemen; S. Yemen.

Included forms: G. arduus, see Harrison (1972); G. cheesmani maritimus in Sanborn and Hoogstraal (1953).


Type locality: Kenya: Kozibiri River, Ngamatak, Turkwel River.

Distribution: Known only from type locality.

Comment: Placed in synonymy under G. agag by Petter (1975) with note that it "could be a valid species". Should be regarded as valid species pending revision. The original description places this species in northern Kenya and not Sudan as indicated by Petter (1975).


Type locality: Tchad: Tibesti region.

Distribution: Known only from type locality.

Comment: Petter (1975) included this species under G. agag without comment, but the type localities are separated by more than 2300 km. Should be regarded as a valid species pending revision.
Type locality: Sinai.
Distribution: Western Iraq to Israel and Sinai; Arabian Peninsula.
Included forms: Dipodillus dasyuroides cf. Ellerman (1941); Gerbillus dasyurus gallagheri, and G. dasyurus palmyrae cf. Harrison (1972). Harrison also included G. lixa, but noted that the type is a young specimen and that this allocation was provisional. Comment: Has been confused with sympatric G. nanus (Ellerman and Morrison-Scott 1951) and G. mesopotamiae (Harrison 1956). The accessory tympanum which is absent in G. dasyurus and present in G. nanus greatly aids identification (Lay and Nadler 1975). A diploid karyotype of 60 has been reported for G. dasyurus (Lay et al. 1975) while G. nanus has a 2N = 52 (vide infra). Valued species.

I noted that the type specimen of G. lixa possessed an accessory tympanum, has bare soled hind feet and was a young animal, perhaps one half grown. These observations rule out any possible relationship with G. dasyurus.

Type locality: Kenya: Nyama Nyango, Guaso Nyiro.
Distribution: Kenya.
Comment: Included without comment in G. pusillus by Petter (1975). Should be regarded as distinct pending revision.

Type locality: Sudan: Dongola.
Distribution: Known only from the type locality.
Comment: Ellerman (1941) placed this species in synonymy with G. pyramidum, a decision followed by Setzer (1956) and Petter (1975). None of these authors discussed evidence for this decision, nor mentioned examination of the type specimen. The type locality of G. dongolanus lies about 320 km up the Nile from the nearest egyptian locality reported by Osborn and Helmy (1980). In the absence of definitive evidence to the contrary, this species should be regarded as valid pending revision.

Type locality: Somalia: Gerlogobi.
Distribution: Ethiopia, Somalia, Djibouti.
Comment: Cockrum (1977) stated that it may be conspecific with G. latastei but provided no supporting evidence. The range of G. latastei sensu Cockrum (1977) lies more than 4000 km distant from the range of G. durnii. This form should be regarded as distinct pending revision.

Type locality: South Yemen: Aden, Lehej.
Distribution: South Yemen, and North Yemen.

Type locality: Egypt: Sinai; S of El Arish.
Distribution: Known only from type locality.
Comment: Placed in G. pyramidum by Ellerman and Morrison-Scott (1951), Harrison (1972) and Osborn and Helmy (1980). Refer to comment in G. pyramidum account.

Type locality: Algeria: Ouargla; Sidi Roueld.
Distribution: Algeria.
Comment: Included without comment in G. nanus by Ellerman and Morrison-
Scott (1951) and St. Girons and Petter (1965). Matthey (1954b) reported at \(2N = 54\) karyotype for specimens identified as this species but without locality. Specimens of *G. nanus* from Morocco, Tunisia, Israel, Iran and Pakistan have a \(2N = 52\). This species should be recognized provisionally pending confirmation and clarification of Matthey’s results.


**Type locality:** Egypt: Giza Province.

**Distribution:** Israel to Morocco.

**Included forms:** The reader is referred to Ellerman (1941), Petter (1975); Corbet (1978).

**Comment:** Readily distinguishable on karyotype of \(2N = 42\) in females and \(43\) in males for specimens from Sinai, Egypt, Tunisia and Morocco (Wassif et al. 1969; Jordan et al. 1974; Lay et al. 1975). No comprehensive study of variation in this widely distributed species is available and opinions concerning synonyms are diverse (e.g., Ellerman 1941; Petter 1975; Lay and Nadler 1975; Kock 1978; Corbet 1978; Ranck 1968). Revision necessary.


**Type locality:** Pakistan, Upper Sind; Rohri Dist., Mirpur-Drahri Taluka, 15 miles SW of Rehti, Beruto.

**Distribution:** N. W. India, sand dunes along Indus Valley of Pakistan.

**Comment:** Formely included in *G. gerbillus* by Petter (1975) with comment that it may be valid. Lay and Nadler (1975) presented karyological and morphological data indicating that *G. gleadowi* is valid.


**Type locality:** Libya: Cyrenaica; Dernah.

**Distribution:** Type locality only.

**Comment:** Both Petter (1975) and Corbet (1978) listed this from under *G. nanus*. Ranck (1968) retained it as valid until future study can clarify its status and I agree with this decision.


**Type locality:** Kenya: Lake Naivasha.

**Distribution:** Kenya.

**Included Forms:** Allen (1939) included *Dipodillus luteus* Dollman.


**Type locality:** Egypt: Wadi Natron; Zaghib.

**Distribution:** Algeria to Israel and Jordan; North Yemen; Oman.

**Included forms:** Included *G. mariae*, *G. jordani* and *G. henleyi makrami* (Ellerman and Morrison-Scott 1951; Osborn and Helmy 1980).


**Type locality:** Morocco: Mogador (= Essouira).

**Distribution:** Coastal Morocco north of Middle Atlas Mountains.

**Comments:** See Lay (1975) and Benazzou and Genest-Villard (1980) for review. \(2N = 58\).


**Type locality:** Algeria: Ba-Medile near Ouargla.

**Distribution:** Algeria and Tunisia.

**Comment:** Placed in *G. pyramidum* by Ellerman and Morrison-Scott (1951) without comment. Synonomized with *G. gerbillus* by Cockrum (1976). May represent *G. gerbillus* but should be regarded as distinct pending revision and analysis of variation in *G. gerbillus*. 
Type locality: Morocco: 7 km S. Taroudannt.  
Distribution: Known only from the type locality.  
Comment: See Lay (1975) for review. 2N = 74.

Type locality: Tunisia: between Bou Ficha and Enfidaville.  
Distribution: Tunisia.  
Comment: Petter (1975) considered G. jamesi as distinct; Corbet (1978) included G. jamesi in G. campestris without comment. Harrison's (1967) description, figures and comparisons convince me that G. jamesi is valid. Nevertheless, future work should carefully evaluate this form and its relationships.

Type locality: Somalia: Bulhar.  
Distribution: Somalia.  
Comment: Included in G. watersi without comment by Petter (1975). Should be regarded as valid pending revision.

Type locality: Tunisia: Kebili.  
Distribution: Tunisia to Libya, possibly Algeria.  
Comment: Cockrum (1977) indicated that specimens from Tunisia, characterized by 2N = 74 are identifiable as G. latastei and that G. aureus Setzer (sensu Ranck 1968) is synonymous. I suspect that this may be correct, however it is difficult to identify G. latastei from the data provided other than the distinctive karyotype. Cockrum's opinion must be supported by carefull documentation before it can be accepted. The listing without comment of G. bonhotei, G. durni, G. perpallidus, G. riggenbachi and G. rosalinda as possible synonyms promotes confusion. When Cockrum's paper was published Wassif et al. (1969) and Lay et al. (1975) had shown that G. perpallidus was distinct from G. latastei (sensu Cockrum) on the basis of karyotypic differences. Petter (1975) considered both G. aureus and G. latastei as synonyms of G. pyramidum while Corbet (1978) regarded G. latastei as a synonym of G. gerbillus and G. aureus as specifically distinct. These opinions are difficult to reconcile with existing data. Careful documentation of these forms is required to determine specific identifications. G. latastei should be considered valid and monotypic pending revision.

Type locality: Sudan: Jebel Marra.  
Distribution: Known only from type locality.  
Comment: Included in G. campestris without comment by Petter (1975). Should be regarded as distinct pending revision.

Type locality: Egypt: Wadi Alagai; eastern desert of Nubia.  
Distribution: Eastern desert of Southern Egypt and probably adjacent Sudan.  
Comment: This is a valid species according to Osborn and Helmy (1980). Ellerman and Morrison-Scott (1951), Petter (1975) and Corbet (1978) each placed it in G. nanus, although Petter commented that it may be valid.

Type locality: Morocco: Fes Province; 15 km WSW Taounate. (The original description incorrectly gave the longitude as 40° 48'. The correct longitude is 4° 48' W.)  
Distribution: Known only from type locality.
Comment: Valid species. The absence of an accessory tympanum convinces me that this species is not closely related to *G. simoni*, as proposed by Setzer and Schlitter (1972), but is more likely allied to *G. campestris*.


type locality: Mauritania: Aouker Region, S. of Archane Titarek.

distribution: Known only from the type locality.

Comment: This species, known from a single specimen, was formerly included in *Monodina* (Petter 1975). The original description states that the plantar soles have only three large independent tubercles, apparently in the metatarsal region, that are covered with short stiff hair, but the remainder of the sole is naked. The third upper molar shows a small posterior tubercle. These characters do not warrant generic distinction.


type locality: Iraq: southwest of Faluja, W. bank of Euphrates River, near Amiriya.

distribution: Iraq and S. W. Iran in the valleys of the Tigris, Euphrates and Karun Rivers.

Comment: Originally described as a subspecies of *G. dasyurus* but later regarded as distinct by Harrison (1972). Relationships of *G. mesopotamiae* with *G. dasyurus* and *G. nanus* were defined by Lay and Nadler (1975).


type locality: Sudan: Darfur, Madu, 80 mi. northeast of El Fasher.

distribution: Sudan.

Comment: Petter (1975, p. 10) included this species without comment in *G. nanus* but also listed it as a distinct species (p. 12). Corbet and Hill (1980) listed it as a distinct. Should be regarded as valid pending revision.


distribution: Vicinity of El Fasher.

Comment: Probably is valid species.


type locality: Pakistan: Gedrosia. Further specified as Pakistan: Baluchistan; Saman Dasht (cf. Lay 1967: 171).

distribution: Baluchistan to the Arabian Peninsula and Israel to Morocco.


Comment: *G. nanus* has a 2N = 52 karyotype in Morocco, Algeria, Tunisia, Israel, Iran and Pakistan (Lay et al. 1975; Jordan et al. 1974), and also possesses an accessory tympanum.

Petter (1975) included *G. principulus* and *G. muriculus* without comment and *G. mackilligini* with a note that it may be valid. Corbet (1978) listed *G. amoenus* and *G. quadrimaculatus* Bodenheimer as synonyms of *G. nanus*. Osborn and Helmy (1980) did not report *G. nanus* from Egypt, and regarded both *G. amoenus* and *G. mackilligini* as distinct. *G. quadrimaculatus* Bodenheimer is a nomen nudum. Any relationship with *G. principulus* and *G. muriculus* should be considered as provisional. *G. amoenus* and *G. nanus* share a number of features: the same diploid chromosome number and very similar chromosome morphology; bare hindfeet and an accessory tympanum. Future work should be directed toward clarification of the relationship of these two forms.


type locality: Nigeria: Farniso near Kano.

distribution: Northern Nigeria.

Comment: Petter (1975) and Kock (1978) both regarded *G. nigeriae* as a synonym of
G. agag (see above). Tranier (1975) considered it distinct and reported a karyotype with a 2N of 62-68 with a minimum of 30 biarmed chromosomes. G. nigeriae should be considered valid.

Type locality: Morocco: Aoreora, 80 km WSW Goulimine.
Distribution: Known only from the type locality.
Comment: See Lay (1975) for review. 2N = 40 with all biarmed chromosomes and distinct from G. andersoni karyotype.

Type locality: Kenya: Voi.
Distribution: Kenya.
Comment: Included in G. pusillus without comment by Petter (1975). Should be regarded distinct pending revision.

Type locality: Egypt: Bir Victoria.
Distribution: N. Egypt, west of the Nile River.
Comment: Wassif et al. (1969), Lay et al. (1975) and Corbet (1978) considered G. perpallidus a distinct species. Petter (1975) regarded G. perpallidus as a synonym of G. pyramidum but commented that it could be valid. Clearly distinct from G. latastei in which it was placed by Cockrum (1977). Osborn and Helmy (1980) provide a description and review. 2N = 40, with 36 biarmed and four single armed chromosomes.

Type locality: South Yemen: Aden; Lahej.
Distribution: South Yemen; North Yemen; Saudi Arabia.
Comment: Valid species (Harrison 1972).

Type locality: Sudan: Jebel Meidob; El Malha.
Distribution: Type locality only.
Comment: Placed in synonymy under G. nanus without comment by Petter (1976). Setzer (1956) treated it as a valid species but stated that it may prove to be a synonym of G. wateri. Should be regarded as distinct pending revision.

Type locality: Ethiopia, Lake Rudolf, Rusia.
Distribution: Ethiopia.
Included forms: Petter (1975) included G. bilensis as a synonym without comment.
Comment: Hubert (1978) described the karyotype as 2N = 62. Should be considered distinct and monotypic pending revision.

Type locality: Kenya; Ndi and Kitui.
Distribution: Kenya and Ethiopia.
Comment: Regarded as valid by Petter (1975). Should be considered distinct pending revision.

Type locality: Upper Egypt.
Distribution: Known from type locality only.
Comment: Cuvier's description including figures fulfills all requirements of Article 25 of the Rules of Zoological Nomenclature and the statement of Cockrum and Setzer (1976: 649) that G. pygargus is a nomem nudum is incorrect. Cuvier applied G. pygargus to Meriones gerbillus Ruppell, 1862 to distinguish it from G. gerbillus Oliver, 1800 and G.
Pyramidum Geoffroy, 1825. The crania of these three species as illustrated in plate 25 figures 1 to 14 convince me that three distinct species are involved, though I cannot identify *G. pygargus* with any species at this time.


**Type locality**: Egypt: Giza Province.

**Distribution**: Egypt, Nile delta and valley south to Sudan, oases of Western Desert, southeastern part of Eastern Desert (cf. map of Osborn and Helmy 1980: 97).

**Included forms**: *G. pyramidum elbaensis*, *G. pyramidum gedeedus* (Osborn and Helmy 1980).

**Comment**: In general authors have referred to the larger hairy-footed species in North Africa as *G. pyramidum* but opinions are as diverse as authors regarding synonyms, which have included *G. acticola*, *G. aureus*, *G. burtoni*, *G. floweri*, *G. hesperinus*, *G. hirtipes*, *G. latastei*, *G. perpallidus*, *G. riggenbachi* and others (Ellerman and Morrison-Scott 1951; Petter 1975; Cockrum 1977; Corbet 1978). From the data available it is difficult to support the case for including any of the forms listed above in *G. pyramidum*.

Inasmuch as a distinctive karyotype of 2N = 38 with all biarmed elements has been reported for toptypical material and such a karyotype has not been reported from any locality outside Egypt, it should be assumed that *G. pyramidum* inhabits only the region mapped by Osborn and Helmy.

Jordan et al. (1974) and Cockrum (1976, 1977) refer specimens from southern and western Tunisia characterized by a 2N = 40, with 38 biarmed and two single armed chromosomes, to *G. pyramidum*. Matthey (1952, 1953) and Wahrman and Zahavi (1958) identified Algerian specimens with a similar 2N = 40 as *G. pyramidum*. Hubert and Bohme (1978) reported a specimen from Senegal as *G. pyramidum*, with 2N = 40 and seemingly identical chromosomal morphology to the specimens from Algeria and Tunisia. I believe that these 2N = 40 specimens represent a species other than *G. pyramidum*. This topic is discussed further under *G. tarabuli*. It is unclear whether *G. p. tibesti* represents this form, another species or is distinct.

Wahrman and Zahavi (1955) and Wahrman and Gourevitz (1972, 1973) found chromosomal polymorphism among *Gerbillus* sp. from Sinai and the mediterranean coast of Israel. Diploid numbers ranged from 64, 65, 66 near Gaza to 50, 51, 52, near Tel Aviv, with a “hybrid zone” in the Gaza Strip where 2N = 51, 52, 53, 54, 55, 56, 59, and 61 were found. These populations have been identified as *G. pyramidum*, however, it seems unlikely that this is correct. Two species were described from this region, *G. floweri* Thomas and *G. bohnotei* Thomas. Osborn and Helmy (1980) place *G. floweri* in *G. pyramidum* and *G. bohnotei* in *G. andersoni*. The status of these forms and their relationships with the populations studied by Wahrman and Gourevitz (1972, 1973) and Nevo (1982) are unclear and additional research is necessary. For the present it seems advisable to consider both *G. bohnotei* and *G. floweri* as distinct species and to refer the chromosomally variable populations to *Gerbillus* species unidentified.


**Type locality**: Nubia.

**Distribution**: Known only from type locality.

**Comment**: It is difficult to identify this form from the original description and the skull of the type is incomplete. Most authors follow Ellerman and Morrison-Scott (1951), who list it equivocally under *G. nanus*. Probably should be considered distinct pending comprehensive reevaluation.


**Type locality**: Western Sahara (Rio de Oro).

**Distribution**: Known only from the type locality.

**Comment**: Petter (1975) included *G. riggenbachi* in *G. pyramidum* without comment.
Cockrum (1977) stated that it may be conspecific with *G. latastei*. Lay et al. (1975) suggested that *G. riggenbachi* should be regarded as distinct pending comprehensive revision.

No evidence has been cited to support any of these synonyms. The possibility that *G. riggenbachi* may represent a western form of the 2N = 40 karyotype discussed under *G. pyramidum* and typical of specimens from Tunisia, Algeria, Morocco and Senegal should be investigated. For the present it seem best to regard it as valid.


**Type locality:** Sudan: Kordofan; Abu Zabad, 145 km southwest of El Obeid.

**Distribution:** Sudan.

**Comment:** Petter (1975) considered it distinct but noted that it may be conspecific with *G. latastei*. This species should be regarded as distinct pending revision.


**Type locality:** Ethiopia: Finik, near Webi Shebeli.

**Distribution:** Somalia and Kenya.

**Comment:** Petter (1975) commented that it may be a synonym of *G. pusillus*, but cited no evidence. Should be considered distinct pending revision.


**Type locality:** Algeria: Oued Magra.

**Distribution:** Egypt, west of the Nile Delta; Libya; Tunisia; Algeria.

**Included forms:** *G. kaiseri* (Osborn and Helmy 1980).

**Comment:** Regarded by Petter (1959) as generically distinct as discussed above. Osborn and Helmy (1980) recognized *G. simoni* as a distinct species and included *G. kaiseri*. Includes *G. zakariai*, described as a new species by Cockrum et al. (1976).


**Type locality:** Somalia: Upper Sheikh.

**Distribution:** Somalia.

**Comment:** Placed without comment in *G. campestris* by Petter (1975). Should be regarded distinct pending revision.


**Type locality:** Sudan: Khartoum.

**Distribution:** Sudan.

**Included forms:** *G. stigmonyx luteolus* (Thomas, 1901).

**Comment:** Petter (1975) listed *G. stigmonyx* and *G. s. luteolus* as synonyms of *G. campestris*. He noted that *G. luteolus* may be valid. *G. stigmonyx* should be retained as valid pending revision.


**Type locality:** Libya: 12 km N of Nofilia.

**Distribution:** Known only from type locality.

**Comment:** Relationships of this form should be evaluated in a revision.


**Type locality:** Libya: Sebha.

**Distribution:** Libya.

**Comment:** This species was described as a subspecies of *G. pyramidum* and is listed as a synonym of *G. pyramidum* by most authors. Lay et al. (1975) commented on certain morphological features that distinguish *G. pyramidum* and *G. tarabuli*. Future work should examine the possibility that the 2N = 40, 38 biarmed and two single armed chromosome forms reported from Tunisia, Algeria, Morocco and Senegal (cf. *G. pyramidum* account) are conspecific and may be referable to *G. tarabuli*. 
G. pyramidum hamadensis described from Libya by Ranck (1968) should also be included provisionally.

Type locality: Libya: Sebha.  
Distribution: Libya.  
Comment: Ellerman and Morrison-Scott (1951) placed G. vivax in G. dasyurus. Ranck (1968) regarded it as a form of G. amoenus. Petter (1975) and Corbet (1978) treated G. vivax and as a synonym of G. nanus. The type specimen possesses an accessory tympanum and bare feet, and thus G. vivax cannot be a synonym of G. dasyurus. Until the relationships between G. vivax, G. nanus and G. amoenus are clarified G. vivax should be regarded as valid.

Type locality: Sudan: Upper Nile; Shendi.  
Distribution: Somalia: Sudan.  
Comment: Petter (1975) listed G. watersi as a subspecies of G. nanus without comment (p. 11) and as a distinct species (p. 7). This form should be regarded as valid pending revision.

Icertae sedis

The following names are often cited as synonyms, for various species. The attributions of the names are obscure and require evaluation.

Type locality: Egypt near Alexandria.  
Comment: Allen (1939), Ellerman and Morrison-Scott (1951) and Corbet (1978) list this form as a synonym of G. gerbillus.

Type locality: Algeria: Ouargla.  
Comment: Ellerman (1941), Ellerman and Morrison-Scott (1951) and Corbet (1978) regard this to be a synonym of G. campestris. Cockrum and Setzer (1976) believe it to be a Mus musculus.

Type locality: Algeria: territory of Beni Sliman.  
Comment: Allen (1939), Ellerman and Morrison-Scott (1951) and Corbet (1978) list it under G. campestris. Cockrum and Setzer (1976) state that it is strictly a nomen nudum.

Type locality: Egypt.  
Comment: Ellerman and Morrison-Scott (1951) and Corbet (1978) tentatively list this form under G. gerbillus. See also comments of Cockrum and Setzer (1976: 657).

Type locality: Algeria: Douilba (possibly is a mistransliteration of Douiba, a name given several locations between 34°03′–35°34′ N and 4°10′–4°30′ E).  
Comment: G. minutus is unavailable according to Cockrum and Setzer (1976), who indicate that it was later properly described as Psammomys minutus Loche, 1867, Explor. Sci. de l’Algerie, Zool. Mamm. p. 109. Evidence for synonymy with G. campestris is equivocal.
Appendix

List of named forms of *Gerbillus* with citations and type localities. Asterisks in the left margins denote that the type specimen has been examined by the author.


Dipoldillus benleyi De Winton, 1903. Novit. Zool. 10: 284, pl. 8, Fig. 1. Egypt: Wadi Natron; Zagig (ca. 31° 22’ N, 30° 18’ E).


Gerbillus hirtipes Lataste, 1886. Le Naturaliste 31: 506. Algeria: Ba-Mendile near Ouargla (ca. 32° 00’ N, 05° 16’ E).


*Meriones longicaudus* Wagner, 1843. Schreber’s Säugethiere Suppl. 3: 477. Egypt.


*Gerbillus simoni* Latarte, 1881. Le Naturaliste 3: 499. Algeria: Magra Oasis (Oued), between Msila and Barika (35° 39' N, 05° 08' E).


*Dipodillus zakariae* Cockrum, Vaughn and Vaughn, 1976. Mammalia 40: 320. Tunisia: Kerkennah Island, 0.5 km E of Kellabine (30° 44' N, 10° 15' E).

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Zusammenfassung

Zur Taxonomie der Gattung Gerbillus (Rodentia: Gerbillinae) mit Anmerkungen über die Anwendung von Gattungs- und Untergattungsnamen nebst einer kommentierten Liste der Arten


References


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