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Heterohyrax brucei.

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Heterohyrax Gray, 1868

Procavia Storr, 1780:39, in part.

Heterohyrax Gray, 1868:50. Proposed as a "group" within *Dendrohyrax,* thus by inference as a subgenus (Roche, 1972). Type species *Dendrohyrax blainvillii* Gray, 1868 (= *Hyrax brucei* Gray, 1868) by original designation.

CONTEXT AND CONTENT. Class Mammalia, order Hyracoidea, family Procaviidae (= Hyracidae Gray, 1821:306, invalid), genus *Heterohyrax.* The genus *Heterohyrax* contains one extinct species, *H. auricampensis* (Rasmussen et al., 1996) and one living species, *H. brucei* (Fig. 1).

Heterohyrax brucei (Gray, 1868)

Yellow-spotted Rock Hyrax

Hyrax brucei Gray, 1868:44. Type locality "Abyssinia" (= Ethiopia).

Dendrohyrax blainvillii Gray, 1868:50. Proposed name *Heterohyrax blainvillii* given "provisionally." Origin of the single skull unknown.

Hyrax irroratus Gray, 1869:242. Type locality "Abyssinia" (= Ethiopia).

Hyrax bocagei Gray, 1869:242. Type locality "Angola."

Hyrax mossambicus Peters, 1870:25. Type locality "Insel Mozambique gegenuber leigenden Halbinsel Cabaceira in 15° Sudl. Br."

Dendrohyrax bakeri Gray, 1874:133. Type locality "eastern tropical Africa, Latiko." "Latiko, in lat. 3° 0′ N, in tropical eastern Africa" after Gray, 1874:132; designated as "northeastern Congo; southern Sudan and northwestern Uganda" by Bothma (1971).

Procavia thomasi Neumann, 1901:240. Type locality "Kaffa, Gimirra, and Binescho, Omo Basin and basin of the Gelo (one of the sources of the Sobat), Anglo-Egyptian Sudan."

Procavia pumila Thomas, 1910:201. Type locality "fifty miles southeast of Berbera, British Somaliland."

Procavia (*Heterohyrax*) *frommi* Brauer, 1913:136. Type locality "Mahenge district, southeast of Iringa, Tanganyika Territory."

Procavia (*Heterohyrax*) *munzneri* Brauer, 1913:137. Type locality "Bismarckburg, near Lake Tanganyika, Tanganyika Territory."

Procavia (*Heterohyrax*) *dieseneri* Brauer, 1917:298. Type locality "Guta, Speke Gulf, Uschaschi, Tanganyika Territory."

Procavia (*Heterohyrax*) *lademanni* Brauer, 1917:298. Type locality "Livingstone Mts., at Mwakete, Tanganyika Territory."

Procavia (*Heterohyrax*) *antineae* Heim de Balsac and Begouen, 1932:479. Type locality "Ahaggar, central Sahara" [Algeria].

Procavia chapini Hatt, 1933:1. Type locality "summit of Loadi Hill, five kilometers southwest of Matadi, Bas Congo District" Congo Belge.

CONTEXT AND CONTENT. Context as above. Currently 25 subspecies are recognized (Allen, 1939; Bothma, 1971; Domning et al., 1982; Schlitter, 1993):

H. b. albipes Hollister, 1922:135. Type locality "Telek River, Loita Plains, Kenya Colony."

H. b. antineae Heim de Balsac and Begouen, 1932:479, see above.

H. b. bakeri Gray, 1874:133, see above.

H. b. bocagei Gray, 1869:242, see above (*grayi* Bocage is a synonym).

H. b. brucei Gray, 1868:44, see above (*blainvillii* Gray and *irroratus* Gray are synonyms).

H. b. chapini Hatt, 1933:1, see above.

H. b. dieseneri Brauer, 1917:298, see above.

H. b. frommi Brauer, 1913:136, see above.

H. b. granti (Wroughton, 1910:109). Type locality "Woodbush, Transvaal," South Africa.

H. b. hindei (Wroughton, 1910:107). Type locality "Fort Hall, Kikuyu, British East Africa" (*maculata* Osgood and perhaps *albipes* Hollister are synonyms).

H. b. hoogstraali Setzer, 1956:564. Type locality "Imurok, Torit District, Equatoria Province, Anglo-Egyptian Sudan."

H. b. kempi (Thomas, 1910:200). Type locality "Elgonyi, Mt. Elgon, Kenya Colony, 7000 ft."

H. b. lademanni Brauer, 1917:298, see above.

H. b.manningi (Wroughton, 1910:109). Type locality "Mianji, Nyasaland," northern Malawi, northern and eastern Zambia.

H. b. mossambicus Peters, 1870:25, see above.

H. b. munzneri Brauer, 1913:137, see above (*ruckwaensis* Brauer is a synonym).

H. b. princeps (Thomas, 1910:199). Type locality "Dembel Lake, north of Abbaja Lake, Galla, central Abyssinia," Ethiopia (*arboricola* Brauer is a synonym).

H. b. prittwitzi Brauer, 1917:299. Type locality not designated. Allen (1939:447) subsequently designated "Kilimatinde, Tanganyika Territory," designated as "central eastern Tanzania (mainland)" by Bothma (1971), as the type locality.

H. b. pumilus Thomas, 1910:201, see above under *Procavia pumila.*

H. b. ruddi (Wroughton, 1910:108). Type locality "Tambarara, Gorongoza Mts., Portuguese East Africa," Mozambique (*rhodesiae* Roberts is a synonym).

H. b. rudolfi (Thomas, 1910:202). Type locality "north end of Lake Rudolf, Abyssinia, 2000 ft." (*borana* Lonnberg is a synonym).

H. b. somalicus (Thomas, 1892:71). Type locality "Berbera, Somaliland" (*hararensis* Brauer and *webensis* Brauer are synonyms).

H. b. ssongeae Brauer, 1917:300. Type locality not designated. Allen (1939:447) subsequently designated "Ssongea, . . . southern Tanganyika Territory," as the type locality.

H. b. thomasi Neumann, 1901:240, see above.

H. b. victoria-njansae Brauer, 1917:299. Type locality not designated. Allen (1939:448) subsequently designated "Mwanza, . . . Tanganyika Territory," as the type locality. This was amended to "northwestern Tanzania (mainland)" by Bothma (1971).

FIG. 1. An adult *Heterohyrax brucei* exhibiting vigilance. Photographed in northwestern Zimbabwe by Craig van der Heiden.

DIAGNOSIS. The genus includes only one extant species. The following diagnosis generally applies to genus and species, except where noted, and can be used to distinguish *Heterohyrax* from other genera in the family.

Heterohyrax is less heavily built than *Procavia* (Barry and Mundy, 1998) with a narrower muzzle (Estes, 1991; Kingdon, 1997; Skinner and Smithers, 1990). In *Heterohyrax,* lateral and dorsal color ranges from gray in arid regions to dark reddish-brown in more mesic areas (Skinner and Smithers, 1990). *Dendrohyrax* has long, woolly, gray or brown hair. *Procavia* has yellowish buff to reddish- or grayish-brown hair. Guard hairs are softer than in *Procavia,* black-tipped, and up to 30 mm long. Underhairs are brown or gray at the base and buffy terminally. Ventral color is white or creamy in distinct contrast to the rest of the pelage, unlike the light brown venter in *Procavia.* Eyebrows are white to creamy, lighter than those of *Procavia,* and conspicuous at a considerable distance. Call is distinct from that of *Procavia* and *Dendrohyrax,* being shrill, up to 1.5 s long, and repeated for as long as 5 min (Hoeck et al., 1982).

Molariform teeth are brachydont (Meyer, 1978). Length of upper premolar series is ca. equal to length of molar series, unlike in *Procavia* in which upper premolars, collectively, are much shorter than molars, and in *Dendrohyrax* in which upper premolars are longer than molars (Bothma, 1971). Cranium is flat dorsally (Fig. 2); *Dendrohyrax* has a dorsally concave cranium (Skinner and Smithers, 1990).

Penis is complex and distinct from that of the other two hyrax genera. It has a short, thin appendage within a cuplike glans penis (a 'fleur-de-lys') and measures >6 cm when erect (Glover and Sale, 1968; Hoeck, 1978*a,* 1978*c*). Distance between anus and preputial opening in adult males is ca. 65–80 mm (Glover and Sale, 1968; Shoshani, 1992), two to three times as long as that of other genera (Coetzee, 1966; Hoeck, 1978*a*).

Heterohyrax is distinguishable from *Procavia* in electrophoretic mobility of serum amylase (Scheil and Hoeck, 1985). *H. brucei dieseneri* is monomorphic and *P. capensis johnstoni* is polymorphic at this locus.

GENERAL CHARACTERS. General appearance resembles that of a marmot. Body mass of 17 adults from Zimbabwe (Smithers and Wilson, 1979) ranged from 2.3 to 3.6 kg. Total length of these individuals was 465–560 mm; length of hindfoot, 65–73 mm; and length of ear, 29–34 mm. In another Zimbabwe study (Barry and Mundy, 1998), mass of three adults averaged 2.4 (± 0.1 *SE*) kg. Total length of 93 adults from the Serengeti National Park, Tanzania, was 325–435 mm, and mass of 190 adults was 1.3–2.4 kg (mean ± 1 *SE*: 1.8 ± 0.02 kg—Hoeck, 1982*a*). Greatest length of cranium and mandibular length of adult specimens (black eagle [*Aquila verreauxii*] prey) from Zimbabwe ranged from 65 to 88 mm ($n = 56$) and from 59 to 78 mm ($n = 99$), respectively (R. E. Barry, in litt.). Measurements of six southern African specimens in the Transvaal Museum (South Africa) were: total length, 456–482 mm; length of hindfoot, 60–68 mm; greatest length of cranium, 84–87 mm; and mandibular length, 70–77 mm (Roberts, 1946). Males and females are, on average, similarly sized, although females are not uncommonly larger than males (Smithers and Wilson, 1979). A secretory gland is located middorsally near junction of thoracic and lumbar regions. Tail is rudimentary (Estes, 1991).

DISTRIBUTION. *Heterohyrax brucei* is found in south, east, parts of north, and northeast Africa and the Sinai (Fig. 3—Corbet, 1979; Gray, 1868; Kingdon, 1997; Schlitter, 1993). It occurs in the Northern Province of South Africa, Zimbabwe, western Mozambique, and eastern Botswana, and extralimitally in South Africa, eastern Mozambique, Malawi, eastern and central Zambia, east-central Angola, Namibia, southeastern and east-central Democratic Republic of Congo, southern Algeria, Tanzania, Rwanda, Burundi, Kenya, Uganda, Somalia, Ethiopia, Eritrea, southern and southwestern Sudan, and north in Egypt along the coast of the Red Sea (Kingdon, 1997; Meester et al., 1986). In east Africa, individuals occur from sea level to 3,800 m (Kingdon, 1971).

FOSSIL RECORD. More than 20 genera, from the Eocene to the Pleistocene, are represented in the fossil record of Hyracoidea (Rasmussen, 1989; Rasmussen et al., 1996). Early Eocene fossils, ca. $5.5–5.0 \times 10^7$ years ago, were found in Africa, Asia, and Europe (McKenna et al., 1997). Most fossil hyracoids are placed in the extinct family Pliohyracidae (Carroll, 1988; Meyer, 1978). Extinct taxa reached the size of a tapir (Meyer, 1978; Shoshani, 1992). Ancestral hyraxes of 4.0×10^7 years ago were dominant, medium-sized herbivores (Rasmussen, 1989). Earliest known procaviid is the late Miocene *Heterohyrax auricampensis* from Namibia, which is larger than *H. brucei* and similar in size to extant *P. capensis. Heterohyrax* is also known from the late Pliocene (Rasmussen et al., 1996) and *H. brucei* is known only from the Recent (Meyer, 1978).

FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of *Heterohyrax brucei* (Frostburg State University Museum catalog no. 1962: p1 reduced in this specimen). Condylobasal length is 81 mm.

FORM AND FUNCTION. Dorsal gland in sexually active mature adults contains large lobules of glandular tissue. Within each lobule are 25–40 alveoli composed of a secretory epithelium surrounding an irregularly shaped lumen (Sale, 1970*b*). The gland lies beneath a slightly raised, hairless patch of skin, close to 1.5

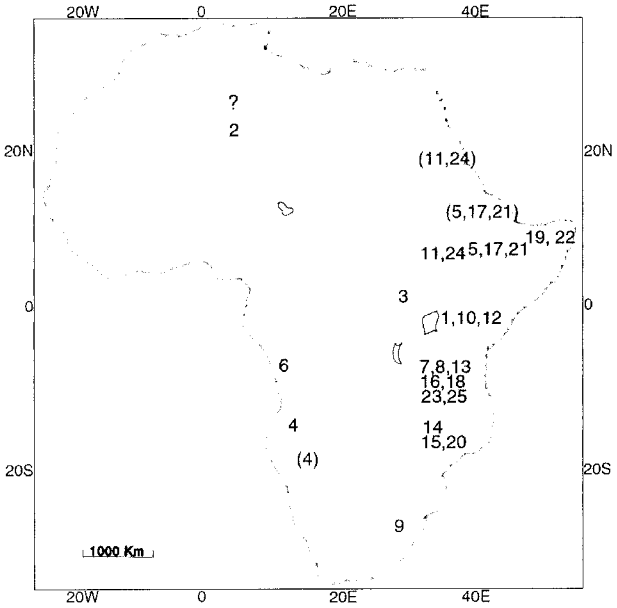

FIG. 3. Distribution (after Kingdon, 1997) of *Heterohyrax brucei* with the distribution of recognized subspecies: 1, *H. b. albipes*; 2, *H. b. antineae*; 3, *H. b. bakeri*; 4, *H. b. bocagei*; 5, *H. b. brucei*; 6, *H. b. chapini*; 7, *H. b. dieseneri*; 8, *H. b. frommi*; 9, *H. b. granti*; 10, *H. b. hindei*; 11, *H. b. hoogstraali*; 12, *H. b. kempi*; 13, *H. b. lademanni*; 14, *H. b. manningi*; 15, *H. b. mossambicus*; 16, *H. b. munzneri*; 17, *H. b. princeps*; 18, *H. b. prittwitzi*; 19, *H. b. pumilus*; 20, *H. b. ruddi*; 21, *H. b. rudolfi*; 22, *H. b. somalicus*; 23, *H. b. ssongeae*; 24, *H. b. thomasi*; 25, *H. b. victoria-njansae*. Numbers in parentheses represent likely subspecies for the indicated locations.

cm long in adults, that is surrounded by long, erectile hairs and forms a dorsal spot of reddish-ocher to "dirty white," but most commonly yellow (Estes, 1991). The vernacular name, yellow-spotted rock hyrax, derives from this gland. The gland is the source of the odor of the animal and may function in mating and recognition of mother by young (Sale, 1965, 1970*b*). Glandular tissue also occurs under the tufts of hair above the eye, under the chin, and in the preputial and circumanal regions (Eley, 1994; Sokolov and Sale, 1981*a*).

Jacobsen's organ is present as a specialized olfactory structure (Kingdon, 1971). As in *Procavia*, the pupil of the eye is protected from bright light by an umbraculum, a shield extending from the iris that allows the animal to stare into the sun (Maloiy and Eley, 1992; Millar, 1973). This adaptation may permit individuals to bask in the sun and still be able to detect predators. A gutteral pouch in the eustachian canal permits loud vocalizations (Estes, 1991; Kingdon, 1997).

Vibrissae up to 90 mm long occur on the snout, and others up to 70 mm long occur above the eyes, under the chin, along the back and sides, on the abdomen, and on fore- and hindlimbs (Kingdon, 1997; Skinner and Smithers, 1990; Sokolov and Sale, 1981*a*). These hairs provide tactile feedback to the hyrax during exploration and use of its underground living quarters (Sale, 1970*b*).

Heterohyrax possesses a single pair of tusklike upper incisors. Dental formula is the same as in *Dendrohyrax* and northern subspecies of *P. capensis*: i 1/2, c 0/0, p 4/4, m 3/3, total 34. *Heterohyrax* has one more premolar in the mandible than southern subspecies of *P. capensis* (*P. c. capensis* and *P. c. welwitschii*—Bothma, 1971; Skinner and Smithers, 1990). Upper, tusklike incisors of males are ridged or triangular in cross section, with the apex of the triangle on the forward face of the teeth (Thomas, 1892). In females, front faces of these incisors are rounded. Both pairs of lower incisors are chisel-shaped (Meyer, 1978; Skinner and Smithers, 1990). Diastema between incisors and premolars is 10–12 mm long (Thomas, 1892). Molariform teeth are lophodont, resembling those of Rhinocerotidae (Skinner and Smithers, 1990).

Vertebral column is convex from neck to tail. Feet are plantigrade (Meyer, 1978; Nowak and Paradiso, 1983). Manus has three well-developed digits, a rudimentary pollex, and a small fifth digit. Pes has a similar arrangement, with hallux absent and fifth digit rudimentary. All digits have short, flat, hooflike nails except for the second digit of the pes, which has a long, curved claw presumably for grooming. Soles have thick, rubbery pads, kept moist by numerous skin glands that enhance the grip for climbing (Dobson, 1876; Feldhamer et al., 1998; Maloiy and Eley, 1992; Meyer, 1978; Nowak and Paradiso, 1983; Sokolov and Sale, 1981*b*).

Stomach is compartmentalized into nonglandular cranial (cardiac) and glandular caudal (pyloric) sections. A proximal cecum (the midgut sacculation of *Procavia habessinica*—Clemens, 1977) occurs caudal to small intestine, and paired ceca emanate more distally from the colon (Rahm and Frewein, 1980). Presumably, microbial fermentation of ingesta, suggested by high concentrations of volatile fatty acids, takes place in the cardiac stomach and all hindgut diverticula, as in *Procavia* (Clemens, 1977; Clemens and Maloiy, 1978; Leon, 1980; Maloiy and Eley, 1992; von Engelhardt et al., 1978).

Females have one pair of pectoral and two pairs of inguinal mammae (Bothma, 1971; Hoeck, 1977*a*; Roche, 1962; Thomas, 1892). Uterus is bicornuate (Kingdon, 1971); placenta is chorio-allantoic, specifically hemochorial (Oduor-Okelo et al., 1983). Testes are permanently intra-abdominal, with large seasonal variation in size (Glover and Sale, 1968); testis weight was nearly fourfold greater in sexually active (9.5 g) than quiescent (2.5 g) males (Neaves, 1979). Spermatozoa have a typically mammalian structure but with small, rounded heads and long tails (Glover and Sale, 1968). Spermatids and spermatozoa are absent from seminiferous tubules in sexually quiescent males (Hanks, 1977).

Physiological measurements suggest that *H. brucei* is a mammal with a low weight-specific metabolic rate, thermal lability, and heavy reliance on behavioral thermoregulation. In one study (Taylor and Sale, 1969), body temperature rose above 31°C when air temperature exceeded 30°C. In another study (Bartholomew and Rainy, 1971), body temperature normally ranged from ca. 35 to 37°C, but fluctuated up to 7°C in response to changes in air temperature. The thermoneutral zone was 24–35°C. Heart rate constitutes a physiological mechanism to maintain body temperature, averaging 118 beats/min in the thermoneutral zone and 160 beats/min at 5°C. Respiration rate increases from <50 breaths/min at air temperatures below 30°C to > 200 breaths/min at 40°C (Taylor and Sale, 1969). Evaporative water loss (dripping from nostrils and sweating from soles of the feet) increases at ambient temperatures above 25°C (Bartholomew and Rainy, 1971), and individuals pant, salivate, and groom (Taylor and Sale, 1969). Mean standard metabolism of four males at ambient temperatures of 25 and 30°C was 0.52 ml O_2 g^{-1} h^{-1} (Bartholomew and Rainy, 1971). Oxygen consumption rose at ambient temperatures below 22°C (Taylor and Sale, 1969).

Vegetation provides all the water needed (Sale, 1965). Individuals conserve water with low urine and fecal volumes (Maloiy and Eley, 1992). Hyrax urine is highly concentrated, contains many salts, and in combination with feces at communal latrines leaves a dark, crystalline residue called klipsweet or hyraceum (Eley, 1994; Turner and Watson, 1965). Low metabolic rate, efficient renal concentrating ability, and hypo- and hyperthermia permit hyraxes to meet water requirements by ingestion of food alone, even under extreme drought conditions (Maloiy and Eley, 1992).

ONTOGENY AND REPRODUCTION. Yellow-spotted rock hyraxes breed annually, although two reproductive peaks occur near the equator where two rainy seasons are typical (Hoeck et al., 1982). Breeding synchrony is attributable to photoperiod in higher latitudes (Sale, 1969), but breeding is more seasonally variable in equatorial regions where nutritional or other factors may be proximate cues for initiation of sexual activity (Neaves, 1979). Synchronous parturition in Zimbabwe seems to be in response to a unimodal annual distribution of rainfall (Barry, 1994). Estrus lasts 1–5 days, and any female can come into estrus several times during the mating period (Hoeck et al., 1982). Gestation is 6.5–7.5 months. A birth peak occurs from February to March in Kenya, shortly before the rains (Sale, 1969), or in March in Zimbabwe, two months after peak rainfall (Barry, 1994). One family group in the Serengeti shifted its birth season from December to January 1971–1976 to May to August 1981–1988 (Hoeck, 1989). In Kenya, testicular activity increases from February to April and peaks in May–July (Neaves, 1979).

Body mass of precocious young at birth is 220–230 g (Skinner

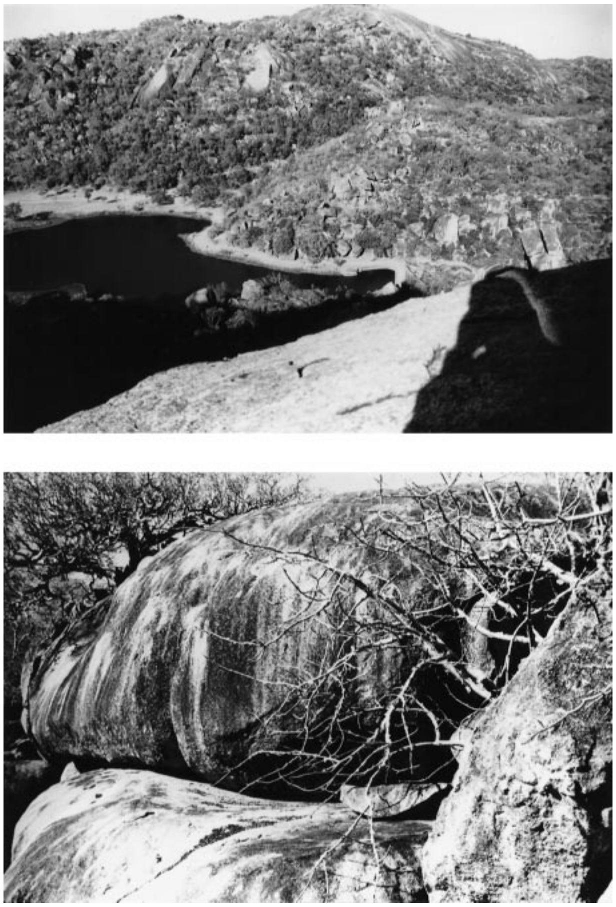

FIG. 4. Kopje habitat of *Heterohyrax brucei.*

and Smithers, 1990). Litter size varies geographically, averaging 1.6 in Tanzania (Hoeck, 1982*a*), 1.7 in Kenya (Sale, 1969), and 2.1 in Zimbabwe (Barry, 1994). Where *H. brucei* is syntopic with *P. capensis,* a significant proportion of nurseries may be heterospecific with calves of both species present (Barry, 1994; Hoeck, 1975, 1982*a*; Hoeck et al., 1982). Females suckle their young for <6 months, and young invariably suck from the same nipples, reducing competition (Hoeck, 1977*a*). Male offspring disperse usually between 12 and 30 months, after becoming adolescent (Hoeck, 1982*a*). One female reached an age of >11 years (Hoeck, 1989).

ECOLOGY. Examination of C^{13}:C^{12} ratios of carbonate and collagen fractions of bone (DeNiro and Epstein, 1978) and microwear patterns of the molariform teeth (Walker et al., 1978) confirmed that the yellow-spotted rock hyrax is a browser. Yellow-spotted rock hyraxes can subsist on nearly any vegetation (Kingdon, 1971). However, grass is infrequently (Hoeck, 1975, 1982*c*) or never (Turner and Watson, 1965) eaten. *Acacia tortilis* and *Allophylus rubifolius* were the most important source of food in one study in the Serengeti National Park (Turner and Watson, 1965). In another Serengeti study (Hoeck, 1975, 1977*b*, 1982*c*), hyraxes spent >80% of foraging time browsing on twigs and bark of woody species and buds, leaves, flowers, and fruits of forbs, bushes, and trees; 64 plant species were consumed, but 2–11 of these comprised 90% of the diet locally. Most common forage species included *Cordia ovalis, Grewia fallax, Hibiscus lunarifolius, Ficus glumosa, Ficus ingens, Iboza,* and *Maerua triphylla.* In Zimbabwe, *Combretum molle, Commiphora marlothii* (juveniles), *Elephantorrhiza goetzei, Flueggia virosa, Strynchos usambarensis, Kirkia acuminata, Croton gratissimus, Mundulea sericea,* and *Rhus leptodictya* (juveniles) comprised the most common forage (R. E. Barry, in litt.). Coprophagy has not been reported for hyraxes.

Habitat consists of rocky kopjes (small hills), krantzes (sheer cliffs or precipices), and piles of large boulders (Fig. 4). Openings of 11 cm minimum in height that are able to accommodate at least five adult individuals (i.e., about 1 m^2 of floor space) constitute suitable living quarters (Sale, 1966). Yellow-spotted rock hyraxes may occupy the same rock crevices as *Procavia* (Hoeck, 1989; Sale, 1970*a*; Smithers and Wilson, 1979). Kopjes provide a constant environment of moderate temperature (17–25°C) and humidity (typically 32–40%) and protection from fire in the arid Serengeti (Turner and Watson, 1965). Outlying kopjes are less likely to be colonized (Smithers and Wilson, 1979). Densities in local sympatry with *Procavia* reached up to 53 individuals (biomass = 72 kg) per ha of kopje and in allopatry up to 50 individuals (biomass = 69–76 kg) per ha of kopje in the Serengeti (Hoeck, 1982*a*, 1989); natal dispersal of males was the major regulating factor.

Yellow-spotted rock hyraxes are susceptible to viral pneumonia and tuberculosis (Sale, 1969). Mange eliminated a colony from one kopje in the Serengeti (Hoeck, 1982*a*). *H. brucei* can harbor the flagellate *Leishmania* (Ashford, 1970; Ashford et al., 1973). The nematode *Crossophorus collaris* was found almost exclusively in the proximal cecum in *H. brucei* from Zimbabwe (R. E. Barry, in litt.). Ticks (*Rhipicephalus distinctus* and *Haemaphysalis leachii*), fleas (*Procaviopsylla*), lice (*Prolignognathus*), and ear mites (*Acomatacarus*) were resident on collected and apparently healthy live-captured individuals.

Heterohyrax brucei is the principal or an important prey for a host of vertebrate predators, most importantly large snakes, leopard (*Panthera pardus),* black eagle, martial eagle (*Polematus bellicosus*), and other raptors (Aumann and Chiweshe, 1995; Gargett, 1990; Grobler and Wilson, 1972; Hoeck, 1982*a*; Kingdon, 1997; Smith, 1977; Turner and Watson, 1965; Wilson, 1969). Adults were selected disproportionately by optimally foraging black eagles in Zimbabwe (Barry and Barry, 1996).

BEHAVIOR. *Heterohyrax brucei* is diurnal and gregarious (Sale, 1970*a*). Colonies may include up to 34 individuals, but a stable, polygynous family group (harem) constitutes the basic social unit (Hoeck, 1982*b*; Hoeck et al., 1982). This unit consists of a territorial adult male, up to 17 adult females, juveniles, and several early- and late-dispersing males (the latter >16 months—Hoeck, 1977*a*, 1982*b*; Hoeck et al., 1982). Juvenile females (daughters or unrelated immigrants) join the adult female group at sexual maturity (ca. 16 months of age). Sex ratios in Serengeti kopjes ranged from 1.6 to 3.2 females/male (Hoeck, 1982*a*; Hoeck et al., 1982).

Territorial males threaten by movement or changes in position, making chewing motions, erecting hairs around dorsal gland, chasing, or biting other males (Glover and Sale, 1968; Hoeck et al., 1982). Although loud territorial calls are emitted year-round, they are more frequent in the mating season (Hoeck, 1982*b*). Oldest and most dominant (i.e., territorial) males copulate significantly more often than peripheral males. Territorial males mate preferentially with females >28 months, and peripheral males mate more often with younger females. Peripheral males seem to have a dominance hierarchy (Hoeck et al., 1982).

Piloerection composing the dorsal spot constitutes an alarm or threat signal to a nearby animal, hyrax or otherwise. During courtship male erects hairs of the dorsal spot, exposing the bare glandular patch, and allowing olfactory stimulation (Sale, 1970*b*) and dissemination of scent that communicates an individual's identity and status (Kingdon, 1997). Threat displays consist of exposing the dorsal gland, raising head and shoulders, showing large incisors, growling, grinding molars, snapping, and chasing (Estes, 1991; Kingdon, 1997). Presentation of the rump, with the pelage and body flat, constitutes appeasement (Kingdon, 1997).

During mating the male gives a shrill cry as he approaches. The female erects her dorsal hairs. The pair performs a dance, during which the male sniffs the female's vulva. He rests his chin on her rump and then slides onto her back while making thrusting movements until intromission occurs after 3–5 min. Another copulation may follow in 1–3 h (Hoeck, 1978*a*, 1978*c*).

At parturition, year-old females begin sucking from the infant's mother. This may direct neonates to the mammae and probably induces lactation (Hoeck, 1982*b*). Newborns are precocial and climb onto the backs of their mothers and other adults. Mothers suckle only their own infants, which claim specific mammae depending on the number in the litter (Hoeck, 1977*a*, 1982*b*).

Play behavior in young (<1-year-old) hyraxes consists of fur nipping, biting, climbing, pushing, fighting, chasing, and mounting (Caro and Alawi, 1985; Hoeck, 1978*b*). Although most play is intraspecific, young *H. brucei* do play with young *P. capensis* at heterospecific nurseries. Play in adults is rare.

Much hyrax behavior is related to the risk of predation. Syntopic *H. brucei* and *P. capensis* form heterospecific groups that may increase efficiency of detecting predators while individuals bask on the surface, especially when vulnerable young are in nurseries (R. E. Barry, in litt.; Hoeck, 1989). The yellow-spotted hyrax is taken more often by the black eagle in Zimbabwe (Barry and Barry, 1996) and may be more vulnerable because of its browsing habit (Turner and Watson, 1965). Individuals feeding aboveground often serve as sentries for conspecifics and ground-feeding *Procavia* (Hoeck, 1975, 1982*c*; Turner and Watson, 1965). Loud calls ("whining croaks") can persist for <5 min, and a birdlike alarm whistle also alerts other species, including rock hyraxes (*P. capensis*) and klipspringers (*Oreotragus oreotragus*—Kingdon, 1997). Predation may be avoided by "playing dead" (Estes, 1991).

Feeding typically occurs from 0730 to 1100 h and 1530 to 1800 h (Hoeck, 1975; Kingdon, 1971), but *H. brucei* also is active in moonlight and occasionally feeds until 2100 h (Turner and Watson, 1965). Two categories of feeding exist, group feeding or casual feeding by lone individuals (Sale, 1965). Although group feeding often occurs up to 50 m from a colony's shelter, casual feeding is sporadic and rarely occurs >20 m from the living quarters. Hyraxes consume great quantities in short feeding bouts averaging 20 min (35 min maximum). Trees or bushes near refuge are visited regularly and stripped bare of leaves (Hoeck, 1982*c*). Individuals can climb vertical trunks of trees and balance on thin branches to browse on leaves and twigs (Hoeck, 1977*b*).

Hyraxes fluff out their fur during dust-bathing, which apparently serves to remove ectoparasites. They use a grooming claw on the short inner toe of the hind leg to scratch almost all parts of their bodies. Four comblike lower incisors also are used to comb fur (Hoeck, 1982*b*).

Colony members huddle and stack together for warmth (Sale, 1970*a*). Ninety-five percent of the day is spent resting. Individuals bask on flat rock surfaces in morning and late afternoon, avoiding midday heat and desiccation by seeking shelter among rocks or other shaded areas (Estes, 1991; Sale, 1966; Taylor and Sale, 1969). During basking, and when huddled or holed up together, individuals avoid head-to-head contact, perhaps ensuring that their dorsal spots are displayed to others (Sale, 1970*b*). Individuals frequently sniff the dorsal gland of others during huddling.

Latrines are located near sleeping quarters. Urination on vertical rock faces results in deposits of crystallized calcium carbonate that produce a visible white stain at colony sites (Estes, 1991).

Individuals crouch with all feet on the ground and back hunched, moving in a creeping walk. They are agile climbers and good jumpers (Estes, 1991; Hoeck, 1977*b*). Maximum speed is ca. 5 m/s (Hoeck, 1982*a*).

GENETICS. Diploid number of chromosomes is 54, identical to that of *Procavia* and *Dendrohyrax* and, apparently, the ancestral condition (Prinsloo and Robinson, 1991). Karyotype has 20 acrocentric autosomal pairs, 2 subtelocentric autosomal pairs, 2 submetacentric autosomal pairs, and 2 metacentric autosomal pairs. The X chromosome is the largest submetacentric chromosome, contributing 5.2% to the female genome. The acrocentric Y chromosome is small, readily distinguishable, and constitutes 1.4% of the haploid genome.

Restriction fragment length polymorphisms of mitochondrial DNA (mtDNA) and sequences of two mtDNA genes (cytochrome b and 12S rRNA) show that *Heterohyrax* and *Procavia* are closely related and that *Dendrohyrax* is basal within the family Procaviidae (Prinsloo, 1993). Sequences of cytochrome b mtDNA in *H. b. brucei*, *H. b. hindei*, and *H. b. ruddi* reveal these three subspecies to be highly distinct, perhaps cryptic species (P. (Prinsloo) Bloomer, in litt.).

REMARKS. The word hyrax is derived from the Greek word *hyrak*, meaning 'shrew.' South African settlers called the hyrax the dasje, and *H. brucei* is geelkoldas in Afrikaans (Skinner and Smithers, 1990). The yellow-spotted rock hyrax also is referred to as the yellow-spotted hyrax (dassie), yellow-spotted rock hyrax (dassie), or bush hyrax.

As many as three species and 23 subspecies were reported for *Heterohyrax* (Bothma, 1971; Domning et al., 1982; Estes, 1991; Gray, 1868; Jones, 1984; Kingdon, 1997; Schlitter, 1993). Here we consider *H. antineae* and *H. chapini* conspecific with *H. brucei* and list them as subspecies. Morphologic (soft and hard tissues) and molecular (amino acid and DNA sequences) characters provide evidence for close affinity between Tethytheria (Proboscidea and Sirenia) and Hyracoidea, classified in Uranotheria (formerly Paenungulata of Simpson, 1945) by McKenna et al. (1997). One of the most cited morphological characters is taxeopody, or serial carpus. Molecular synapomorphies for Uranotheria are given by Czelusniak et al. (1990) and Porter et al. (1996). Until a few years ago, one hypothesis for the close affinity of Hyracoidea suggested that they were a sister-group to Perissodactyla (Fischer, 1986, 1989). In his most recent publication, Fischer (1996) depicted Hyracoidea equally closely related to Tethytheria and Perissodactyla. Shoshani (1993) provided independent myologic evidence for the sister-group relationship between Hyracoidea and Tethytheria. Shoshani and McKenna (1998) conducted extensive analysis on 261 morphological characters and provided corroborative evidence for relationship of Uranotheria.

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