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Proteles cristatus.

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Proteles Geoffroy St.-Hilaire, 1824

Proteles Geoffroy St.-Hilaire, 1824:355. Type species *Proteles lalandii* Geoffroy St.-Hilaire.

Geocyon Wagler, 1830:30. Type species *Proteles lalandii* Geoffroy St.-Hilaire.

CONTEXT AND CONTENT. Order Carnivora, Superfamily Feloidea, Family Protelidae. The family contains one species, *Proteles cristatus* (Meester et al., 1986).

Proteles cristatus (Sparrman, 1783)

Aardwolf

Viverra cristata Sparrman, 1783:581. Type locality "near Little Fish River, Somerset East, eastern Cape Province."

Viverra hyenoides Desmarest, 1820:538. Type locality "Cape of Good Hope."

Proteles lalandii Geoffroy St.-Hilaire, 1824:355. Type locality "near Algoa Bay, Cape of Good Hope."

Proteles typicus Smith, 1834:96. Renaming of *P. lalandii*, type locality "South Africa."

CONTEXT AND CONTENT. Context noted in generic summary above. During the first decades of this century several subspecies were described, mainly on the basis of color. However, Coetzee (1977) recognized only two subspecies of *P. cristatus* on the basis of their disjunct distributions:

P. c. cristatus Sparrman, 1783:581, see above (*canescens* Shortridge and Carter, *harrisoni* Rothschild, *hyenoides* Desmarest, *lalandii* Geoffroy, *transvaalensis* Roberts, and *typicus* Smith are synonyms).

P. c. septentrionalis Rothschild, 1902:443. Type locality "Somaliland" (*pallidor* Cabrera and *termes* Heller are synonyms).

DIAGNOSIS. Although the most recent classification places *P. cristatus* in a family of its own, Protelidae (Meester et al., 1986), it is closely related to the Hyaenidae. Like the brown (*Hyaena brunnea*) and striped (*H. hyaena*) hyenas, *Proteles* has large pointed ears and a long erectile mane extending from behind the head down the middle of the back to the tip of the tail (Fig. 1). Like the hyenas, *Proteles* has a sloping back with forelegs longer than hind legs, and a well-developed anal gland for scent-marking grass stalks. Having stripes on the body, *Proteles* superficially resembles *H. hyaena* (Gingerich, 1975; Roberts, 1951), but it is <50% the size and the stripes are much more regular than those of the hyena (Richardson and Bearder, 1984). *Proteles* has five digits on the front foot and four on the hind, differing from hyenas that lack the pollex on the front foot. The most noticeable differences between *Proteles* and the hyenas are in the skull and dentition. Whereas hyenas have a powerful dentition and are able to crush large bones, *Proteles* has a slender skull and the cheekteeth (which are irregular in number) are reduced to small, widely spaced, redundant pegs (Roberts, 1951; Smithers, 1983; Fig. 2).

GENERAL CHARACTERS. The aardwolf has long, slender legs and a long neck. The background color of the body varies from yellowish-white or buff to rufous. The throat is a paler gray-white. There are three vertical black stripes on the body, and one or two diagonal stripes across the fore and hindquarters. Irregular horizontal stripes run across the legs. These integrate into solid dark towards the feet. Sometimes black spots or stripes are present on the neck (Richardson, 1985; Richardson and Bearder, 1984).

In southern Africa, adult body mass varies seasonally with the availability of termites, but maintains an average of 8–12 kg (Richardson and Bearder, 1984; Smithers, 1983). Kingdon (1977) lists body masses up to 14 kg in East Africa. There is no sexual dimorphism in size (Richardson, 1985; Smithers, 1983). Total length of body (in mm) is 850–1,050; length of tail, 200–300; height of shoulder, 450–500; length of hindfoot, 149–162; length of ear, 90–102 (Kingdon, 1977; Richardson and Bearder, 1984; Smithers, 1983).

DISTRIBUTION. The aardwolf is limited to Africa and occurs in two discrete populations (Fig. 3). The southern population ranges over most of southern Africa, extending just into southern Angola, southern Zambia, and southwestern Mozambique. A 1,500-km gap occurs between this population and the northern population, which extends from central Tanzania to northeastern Uganda and Somalia, then narrowly along the coast of Ethiopia and Sudan to extreme southeastern Egypt (Meester et al., 1986; Smithers, 1983). Aardwolves are absent from most of Zambia, southern Tanzania, and West Africa, with unconfirmed reports of occurrence in northeastern Central African Republic and Burundi (not indicated in Fig. 3). Prime habitat for the aardwolf appears to be open, grassy plains, although most habitats having a mean annual rainfall of 100–800 mm are occupied. Aardwolves are most common in the 100–600 mm range and do not occur in forests or pure desert (Smithers, 1983).

FOSSIL RECORD. Due to an almost complete lack of fossil evidence (Hendey, 1974), the taxonomic position of the aardwolf is uncertain. It is generally accepted that hyaenas were derived from civet-like viverrids (Ewer, 1973; Savage, 1978), but it is uncertain at what stage the aardwolf diverged from this lineage (Ewer, 1973; Thenius, 1966). The earliest fossil record of *Proteles* is *P. transvaalensis*, which was found in the late Pliocene deposits at Swartkrans in the Transvaal and can be dated at about 1.5×10^6 years ago (Brain, 1981; Hendey, 1974). This animal was larger and dentally less degenerate that *P. cristatus* (Hendey, 1974). A number of more recent fossils, dating back to about 1×10^6 years ago, have been found in the northern Cape Province and the Transvaal, but these are virtually indistinguishable from the extant *P. cristatus* (Gingerich, 1974).

FORM AND FUNCTION. The stance is digitigrade; the claws are strongly built and non-retractile (Smithers, 1983). Most

FIG. 1. Aardwolf (*Proteles cristatus*) with dorsal crest partially raised near Kimberley, Northern Cape Province, South Africa. Photograph by P. R. K. Richardson.

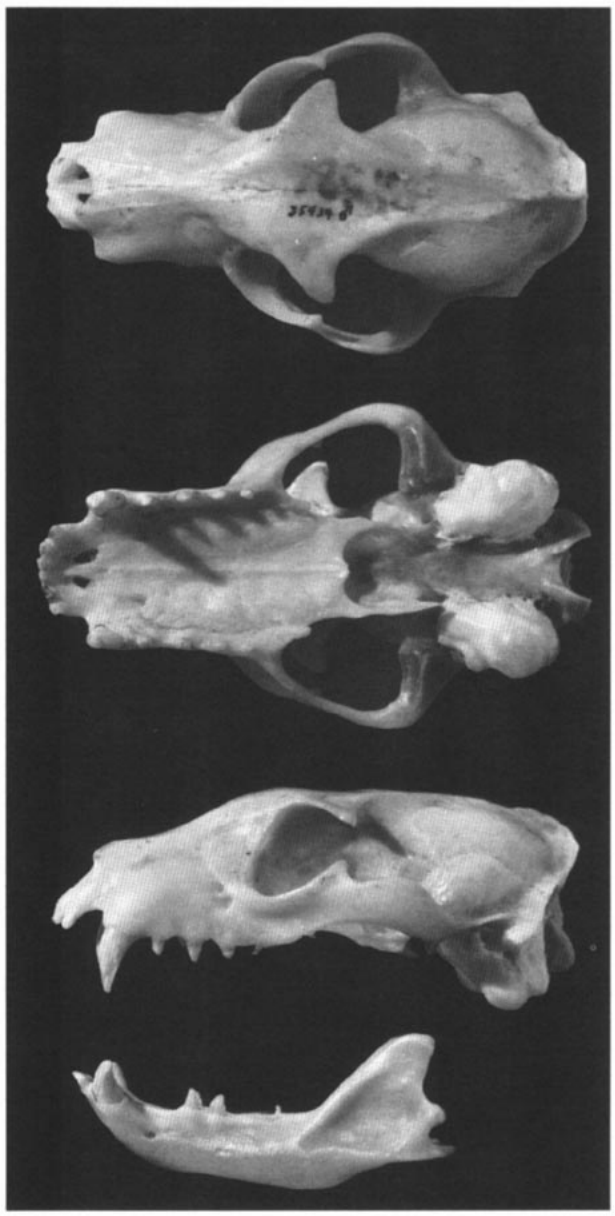

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Proteles cristatus* (Royal Ontario Museum 35434) from Kanya, Makarikari, Bechuanaland, Africa. Greatest length of cranium is 139 mm. Photograph by B. Boyle.

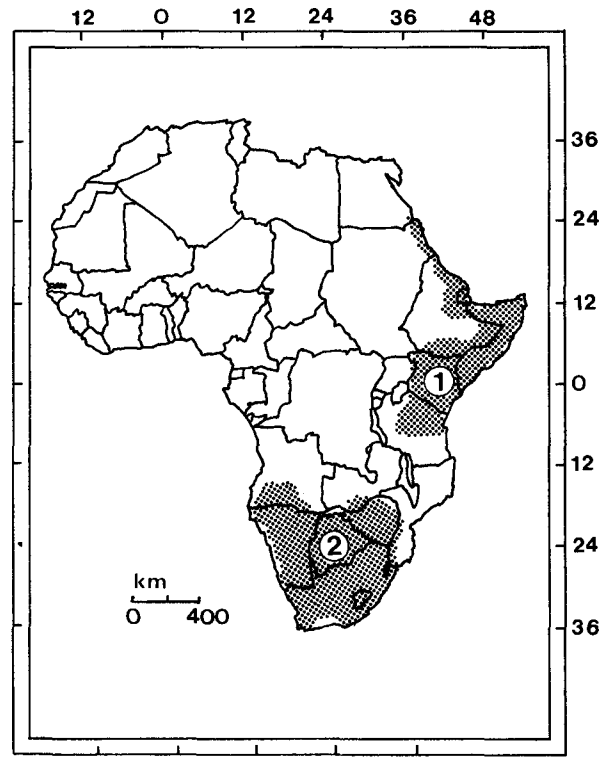

FIG. 3. Distribution of *Proteles cristatus* in Africa (Coetzee, 1977; Smithers, 1983): 1, *P. c. cristatus*; 2, *P. c. septentrionalis*.

of the body coat consists of dense, soft, crinkled underfur interspersed with coarser guard hairs. Hairs of the dorsal crest are coarse and long (the largest of all carnivores; Wemmer and Wilson, 1983), being about 70 mm on the back of the head, increasing to 200 mm on the shoulders, then decreasing to about 160 mm on the tail. These hairs have broad white bases, then alternating black and white annulations, terminating in black tips. The hair on the face is short (10–15 mm) and gray, while the muzzle is hairless and gray-black (Smithers, 1983).

The most characteristic features of the skull are the extraordinary reduction of the cheekteeth and an extremely broad, near parallel-sided palate that continues beyond the upper molars (Fig. 2). The whole structure of the head appears to be specifically adapted to a diet consisting almost exclusively of termites (Kruuk and Sands, 1972; Richardson, 1985; Smithers, 1983). The broad palate accommodates a large, spatulate tongue used to lick termites off the soil surface (Kruuk and Sands, 1972; Richardson, 1987*a*). The tongue is covered in large, conical papillae, and the large submaxillary glands produce copious amounts of sticky saliva (Flower, 1869*b*; Richardson, 1985).

Sight, hearing, and smell appear to be well developed in the aardwolf. Externally, the eyes and ears are noticeably large (Richardson, 1985; Smithers, 1983) while internally the auditory bulla (Flower, 1869*b*; Kruuk and Sands, 1972; Smithers, 1983) and olfactory lobes (Flower, 1869*a*) also are well developed.

Despite many references to the contrary (Bourliére, 1963; Roberts, 1951; Von Ketelhodt, 1966), the aardwolf has disproportionately strong jaws and skull. The zygomatic arches are broad and heavily built, suggesting well-developed masseter muscles and a powerful jaw action. These features have probably been retained for fighting (Ewer, 1973; Smithers, 1983) as aardwolves have aggressive territorial disputes and frequently chase jackals from their breeding dens (Richardson, 1985, 1987*b*; Richardson and Coetzee, 1988). The use of the canines for fighting is clearly reflected in their wear, as in old animals they are broken down to rounded stumps (Richardson, 1985). The permanent dentition generally falls within the formula: i 3/3, c 1/1, p and m 3-4/2-4, but the number of cheekteeth may be further reduced (Ewer, 1973; Richardson, 1985; Roberts, 1951; Smithers, 1983).

Like the hyenas, the aardwolf has no baculum (Ewer, 1973). The penis points forwards and is sheathed along the ventral surface of the body (Richardson, 1985; Wells, 1968). The glans penis is covered with small recurved spines (Ewer, 1973; Flower, 1869*b*; Wells, 1968). At the base of the penis are a pair of oblong clusters of pale sebaceous glands separated by non-glandular tissue (Flower, 1869*b*; Fig. 4) that are not present in hyenas (Wells, 1968). The function of these glands is unknown (Flower, 1869*b*; Richardson, 1985). The female aardwolf has two pairs of inguinal teats (Richardson, 1985).

Aardwolves scent-mark their territories (a behavior shared with other hyaenids) with a yellowish-orange secretion from the anal gland (Apps et al., in press; Kruuk and Sands, 1972; Nel and Bothma, 1983; Richardson, 1985) that turns black with oxidation upon exposure to the atmosphere (Richardson, 1985). This gland is situated immediately above the anus, with which it shares a common external aperture, and consists of a T-shaped eversible pouch of sebaceous tissue (Flower, 1869*b*; Pocock, 1916). The gland structure is similar to that in striped (*H. hyaena*) and spotted (*H. crocutta*) hyenas (Pocock, 1916), but the anal gland of the brown hyena, *H. brunnea*, is more complicated, producing two separate secretions (Mills et al., 1980). Although it is reported that the aardwolf may spray the

contents of its anal gland backwards as a form of defense when attacked (Boitani and Baretoli, 1983; Roberts, 1951) there are no authenticated records of this.

ONTOGENY AND REPRODUCTION. In the northern Cape Province of South Africa, females come into proestrus during the last weeks of June. Mating usually takes place during the last days of June and the first 2 weeks of July. Copulation may last from 1 to 4 h with ejaculation, indicated by pelvic thrusting and tail bobbing, occurring after 1 h and again at approximately hourly intervals. There is no copulatory tie. Females remain receptive for 1–3 days, but normally are not receptive after a copulation lasting >3 h. A female will recycle if she is not fertilized (Richardson, 1985, 1987*b*).

The gestation period is approximately 90 days (C. E. Brady and F. E. Lyon, pers. comm.); not 60 days as suggested by Richardson (1985). Most litters have two to four young, but litters of five have been recorded in zoos (C. Van Ee, pers. comm.). In South Africa, the young are born from October through December (Richardson, 1985; Shortridge, 1934; Stuart, 1981), although with warmer winters further north in Botswana and Zimbabwe, the breeding season seems to be less restricted (Smithers, 1983).

The cubs are born in dens, from which they first emerge after about 1 month. From 4 to 6 weeks of age, they play around the den for short periods when the adults are present. From 6 to 9 weeks, they may play outside, but usually remain within 30 m of the den. From 9 to 12 weeks, they may go foraging with an adult and start feeding on termites, but usually remain within about 100 m of the den. From 12 weeks to 4 months, they may forage throughout the territory, but are usually accompanied by a parent. Cubs are weaned by the end of this period. Up to 7 months of age, the cubs may still be accompanied by a parent for a short period of the night, but thereafter forage alone. At about 1-year old, the cubs start making excursions into neighboring territories and generally have left their natal territory by the time the next year's cubs have emerged from the den. Once they have finally left their natal territory cubs seldom return, becoming transients in search of vacant territories elsewhere in the region. If a parent dies, a cub of the same sex usually remains in its natal territory (Richardson, 1985, 1987*b*).

Males help in rearing the young by guarding the den against black-backed jackals (*Canis mesomelas*), which are probably their greatest natural enemy. Paternal care varies, but during the first 2 months some fathers may spend up to 6 h/night guarding the cubs while the female is away foraging (Richardson, 1985, 1987*b*; Richardson and Coetzee, 1988). Richardson (1987*a*) found that between 1981 and 1984 the survival rate of cubs up to the age of 12 months in the northern Cape was 68%. However, most of this mortality was during the height of a drought in 1984 when 55% of the cubs died during winter. The record lifespan for an aardwolf in captivity is 15 years in East London Zoo (H. F. Von Ketelhodt, in litt.).

ECOLOGY. The aardwolf is considered one of the indicator species for the Somalia–Kalahari semidesert axis (Kingdon, 1977). Its distribution in this sector of Africa appears to be related to this area's ancient climatic history, as these two areas were joined in drier periods. They are now separated by wetter woodlands in Zambia.

Diet of the aardwolf is the most thoroughly documented aspect of its biology. Aardwolves feed primarily on nasute harvester termites (*Trinervitermes*), mainly on *T. bettonianus* in East Africa (Kruuk and Sands, 1972), *T. rhodesiensis* in Zimbabwe and Botswana (Smithers, 1971), and *T. trinervoides* in South Africa (Cooper and Skinner, 1979; Richardson, 1987*a*). The aardwolf feeds on foraging parties of termites by licking them off the soil surface, apparently tolerant of the noxious secretions of the soldier termites (Kruuk and Sands, 1972; Richardson, 1987*a*), and consuming as many as 300,000 termites/night (Richardson, 1987*a*). These termite foraging parties vary in size, but generally are about 20 by 40 cm across and contain 2,000–3,000 termites. Kruuk and Sands (1972) and Richardson (1985) have suggested that, since aardwolves typically turn upwind of termite foraging parties before approaching them, aardwolves use audition and smell to locate this food source.

Trinervitermes trinervoides is almost entirely nocturnal (Richardson, 1987*a*). By contrast, the larger harvester termite *Hodotermes mossambicus* is mainly active by day and during winter

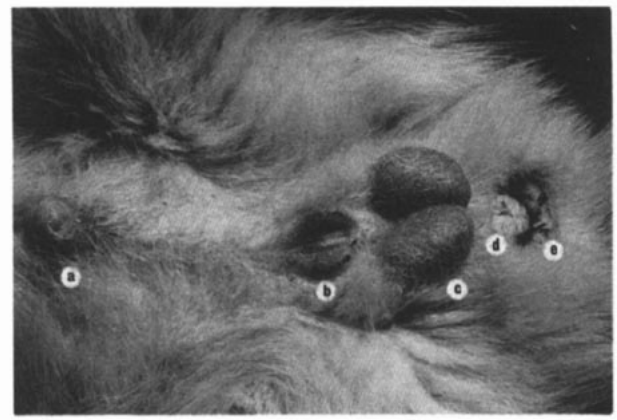

FIG. 4. Sexual organs and anal gland of an adult male *Proteles cristatus*: a) partially sheathed penis; b) cluster of sebaceous glands; c) testes; d) anus; e) anal gland. Photograph by P. R. K. Richardson.

(Hewitt et al., 1972; Nel and Hewitt, 1969). This is fortuitous for the aardwolf, because during winter in southern Africa (May to August) it frequently is too cold for *T. trinervoides* to forage at night, so the aardwolf becomes more diurnal and frequently feeds on *Hodotermes* during the afternoon (Richardson, 1987*a*).

Richardson (1987*a*) estimated that an aardwolf in the northern Cape consumes about 105,000,000 termites/year. Of these, *Trinervitermes* constitutes the vast majority with *Hodotermes* being of limited importance during winter. Together, these two species compose essentially the entire diet, as only traces of other termites or insects were seen being eaten or were recorded in the feces. Other studies (Cooper and Skinner, 1979; Kingdon, 1977; Kruuk and Sands, 1972; Smithers, 1971) also have shown a prevalence of *Trinervitermes* sp. in the diet of the aardwolf, although most of them showed a broader spectrum of other termites being consumed (always surface-foraging termites) with other insects and arachnids rarely recorded.

During mid-winter (June and July) in the northern Cape, aardwolves consume only one-fifth the amount of termites per month as compared to outside the winter months, which results in a loss of up to 20% of body mass during winter (Richardson, 1987*a*). Winter also is the period of highest mortality for the cubs, suggesting that the aardwolf is highly dependent on *Trinervitermes* and unable to feed successfully on alternative sources of food (Richardson, 1987*a*, 1987*c*, 1987*d*). The main reason for this dependence may be that the few *Trinervitermes* species selected appear to be the only arthropods regularly foraging in dense concentrations on the soil surface throughout most of the year. Most other termites forage under the protection of mud galleries, or are far more irregular in their foraging habits (Kruuk and Sands, 1972; Richardson, 1987*a*, 1987*c*). Unlike the aardwolf, other myrmecophagus generalists (for example, the aardvark, *Orycteropus afer*, and pangolin, *Manis* sp.) typically have powerful claws with which they can dig into ant and termite nests, and long, thin tongues for licking up the termites in their tunnels. In contrast, the aardwolf has a large, broad tongue ideal for licking termites off the flat soil surface (Richardson, 1987*a*, 1987*c*).

The aardwolf has a basal metabolic rate only 70% of that expected from the allometric Kleiber curve (McNab, 1984). Dependence on a food source that is nutritionally low (Redford and Dorea, 1984), filled with chemical poisons (Prestwich, 1983), and seasonally unavailable (Richardson, 1987*a*) could be responsible for this lowered basal metabolic rate (Richardson, 1987*c*).

Aardwolves generally are independent of surface water, getting their water requirements from termites. The only times aardwolves have been observed to drink is during prolonged cold spells in winter, when termites are not active. Aardwolves may then walk long distances in search of water (Richardson, 1985).

In the Namib Desert, *Proteles* lives sympatrically with three other desert carnivores; the black-backed jackal (*C. mesomelas*), the bat-eared fox (*Otocyon megalotis*), and the Cape fox (*Vulpes chama*). Although both the aardwolf and bat-eared fox forage exclusively on insects, direct competition is avoided. The bat-eared fox

cannot tolerate the terpene secretions of *Trinervitermes*, feeding instead on *Hodotermes* and a large variety of other insects, including larvae dug up from just below the soil surface (Bothma et al., 1984; Richardson, 1987*c*; Smithers, 1983).

Aardwolves occupy home ranges that vary from 1 to 4 km^2 (Bothma and Nel, 1980; Kruuk and Sands, 1972; Richardson, 1985; Skinner and Van Aarde, 1985). Richardson (1985, 1987*b*, in press) has shown that home ranges, determined by summing contiguous hectares in which an adult pair deposited one or more scent marks during the non-mating season, are aggressively defended and scent-marked as territories. Territory sizes vary with the density of *Trinervitermes* mounds, each territory having approximately 3,000 mounds with an average of 55,000 termites/mound (Richardson, 1985). As the standing crop of these mounds provides approximately one-half the annual consumption of a family of aardwolves, presumably these termites have a high production/biomass ratio to accommodate this high predation rate (Richardson, 1985, 1986, 1987*a*).

In prime habitat (open grassland and scrub regions), aardwolf densities may reach 1 adult/km^2 on farms with good populations of *Trinervitermes* termites and no persecution by farmers (Richardson, 1984, 1985; Skinner and Van Aarde, 1985). Some farmers believe aardwolves prey on their lambs and shoot them at every opportunity. Probably more aardwolves are killed indiscriminately by packs of dogs used to hunt jackals and foxes. Aardwolves also are killed on the roads at night by motor vehicles when blinded by oncoming lights. Some indigenous tribes of Africa feed on aardwolves or use parts of the body for medicinal purposes, but the extent of this usage as a cause of mortality is unknown (Anderson, 1988; Richardson, 1984; Von Ketelhodt, 1966).

Little information is available on the parasites carried by the aardwolf. Two subspecies of mallophagous louse, *Felicola intermedius intermedius* and *F. i. hyaenae*, have been found on only the aardwolf and the brown hyaena, respectively (Hopkins, 1960), which is further evidence in favor of including the aardwolf in the family Hyaenidae (Ledger, 1968).

Aardwolves are generally shy of motor vehicles, although if regularly followed, many individuals soon appear undisturbed when followed within 20 m. Capture of free-ranging aardwolves, to take body measurements and fit radio collars, is most successful by drugging with projectile syringes. Aardwolves cannot be caught with food-baited traps, but may be lured to tarps baited with scent-marks of other aardwolves. An intramuscular injection of 10–15 mg/kg of ketamine hydrochloride with 0.3 mg/kg acetylpromazine added as a tranquilizer is highly suitable for anesthetizing aardwolves (Richardson, 1985).

BEHAVIOR. Aardwolves primarily are nocturnal, although they may be active during the late afternoon if termites are available at that time (Bothma and Nel, 1980; Kruuk and Sands, 1972; Richardson, 1987*a*, 1987*d*; Richardson and Coetzee, 1988). In the northern Cape during summer, activity begins 0.5–1 h after sunset and ends 1–2 h before sunrise. During winter months (May to August) activity often begins 1–2 h before sunset, lasting until termites become unavailable as the air temperature drops to about 9°C. Aardwolves cover an average of 1.7 km/h while foraging, walking 8–12 km/night during summer, and 3–8 km/night in winter, depending on ambient temperature (Richardson, 1985, 1987*a*).

Aardwolves are solitary foragers except when accompanying their young cubs (Bothma and Nel, 1980; Kruuk and Sands, 1972; Richardson, 1987*a*; Richardson and Coetzee, 1988), but even 4-month-old cubs spend most of the night foraging alone (Richardson, 1985). During winter, aardwolves from the same territory may come together in a loose group, spread over 100 m or more, when feeding on *Hodotermes* emerging from one large colony (P. R. K. Richardson, pers. obs.). However, if another aardwolf from the same territory is encountered during foraging, both individuals raise the mane of hair along the back while slowly approaching each other. Upon recognition, the hair is lowered and they pass by each other without further interaction. Occasionally, particularly in a greeting between a mother and her cubs, two individuals may briefly sniff each others noses before separating (Richardson, 1985).

Aardwolves are territorial, a mated pair occupying a perennial territory with their most recent offspring. Apart from aggressive encounters, territories are maintained by means of scent-marking (Richardson, 1985, 1987*b*, in press), sometimes called "pasting" (Gorman and Mills, 1984). When scent-marking, aardwolves first straddle a grass stalk, then rapidly squat while everting the anal pouch and wiping a smear of secretion, approximately 6 mm in length, onto the grass (Kruuk and Sands, 1972; Richardson, 1985, in press). Both sexes scent-mark, although males mark more frequently than females, pasting on average more than two times per 100 m. Pastings are concentrated along territory boundaries, dens, and middens and may be entirely related to territoriality and mate acquisition (Richardson, 1985, 1987*b*, 1987*d*, in press). However, aardwolves in the Namib Desert may deposit only a small spot of secretion, apparently related to advertising areas traversed while feeding (Nel and Bothma, 1983), a form of pasting not recorded elsewhere (Kruuk and Sands, 1972; Richardson, 1985, 1987*b*).

Aardwolves may be considered socially monogamous; although the mated pair occupies the same territory throughout the year, copulations are not necessarily exclusive within the pair. Extra-pair copulations regularly occur between the most aggressive males and females of less aggressive neighbors. Aggressive males may gain access to neighboring females by rigorously scent-marking the territory of a neighbor during the proestrous period of the female, then he may defeat the resident male in a fight when his female becomes receptive. Cuckolding of less aggressive males holds evolutionary implications. Paternal care necessary for cub survival involves guarding of the den from jackals, an activity that is energetically costly to the male. Thus, males could not be expected to guard cubs unless some are his offspring. Richardson (1987*b*) and Richardson and Coetzee (1988) suggest females should accept extra-pair copulations only after mating with her resident male. The resultant litter may have mixed paternity, thus providing motivation for the cuckolded male to guard the cubs, but may also possess the "superior" genes of the more aggressive male. This appears to be an adequate strategy, unless the cuckolded male has the rare opportunity of access to a female with whom he can breed exclusively. In this case, he may desert his promiscuous female to mate with the alternative female (Richardson and Coetzee, 1988).

Cubs are raised in dens, usually with single entrances. These may be old aardvark (*O. afer*), or porcupine (*Hystrix africaeaustralis*) burrows, but are more often enlarged springhare (*Pedetes capensis*) burrows or excavations of aardwolves themselves (Richardson, 1985, 1986). Most dens are oval-shaped, about 32 cm high and 42 cm wide at the entrance, and rapidly narrowing to about 20 by 30 cm inside the tunnel. One den excavated by Richardson (1985) was over 5 m long with a small chamber (100 cm long by 40 cm wide by 25 cm high) at the end. This den had been simultaneously occupied by two adults and a 1-year-old cub. Dens are regularly slept in for 6–8 weeks at a time before another den is used. A den may be re-occupied 6–18 months later (Richardson, 1985).

Outside of the mating season, residents win all intraspecific encounters within their territory, immediately raising their mane and chasing away any intruders as soon as they are detected. If intruders are caught, both animals fall to their knees and bite at each others necks (Richardson, 1985).

The aardwolf is generally silent, except when under stress. The lowest form of threat is a soft clucking sound apparently made by opening and closing the mouth. Under more stress, aardwolves may utter a deep-throated growl and during fights or when suddenly surprised, may give a surprisingly loud and explosive roar (Richardson, 1985; Smithers, 1971). During fights and chases, the mane is fully erected. If only slightly disturbed, the aardwolf just fluffs out the hairs of the tail. This is frequently seen in cubs while playing.

Aardwolves, like the hyenas, defecate mostly at middens, only sometimes defecating at random (Nel and Bothma, 1983; Richardson, 1985, in press). Middens are usually 1–2 m in diameter and often are made of soft, bare sand as a result of frequent digging by aardwolves. As many as 20 middens may be located throughout the territory, but those near the territory boundary are most frequently used (Richardson, 1985, in press). To defecate, a narrow trench is dug with alternating strokes of the forepaws; the animal then turns around and squats over the trench. The first defecation of the evening may be up to 8% of the body mass of the animal (Smithers, 1971). The subsequent two or three defecations are much smaller. After defecating, the aardwolf fills the hole with sand and usually deposits a few scent marks before leaving (Richardson, 1985, in press). The sand content of feces may vary from negligible amounts to 40% in sandy areas (Bothma and Nel, 1980; Cooper and Skinner, 1979), or when few termites are available (Richardson, 1985).

Aardwolves usually urinate into the same hole used for defecating. However, when termites are abundant they may urinate five

or six times a night, and simply stop foraging, squat, urinate, and then continue foraging (Richardson, 1985).

GENETICS. The diploid number of chromosomes is 40, with 72 autosomal arms. The X chromosome is metacentric and the Y chromosome submetacentric (Von Ulbrich and Schmitt, 1969; Wurster and Bernischke, 1968). These chromosomes are similar in number and configuration to the hyenas, providing further evidence for classifying the aardwolf in the Hyaenidae (Von Ulbrich and Schmitt, 1969). Similarly, hemoglobin of the aardwolf has the same electrophoretic mobility as that of the hyenas (Seal, 1969).

REMARKS. The taxonomic position of the aardwolf remains uncertain; a number of authors have classified *Proteles* both within the Protelidae and the Hyaenidae within the last few years (Meester et al. 1986; Smithers, 1983, 1986; Swanepoel et al., 1980). Placement to family is subjective since there is much genetic, behavioral, and morphological evidence showing the aardwolf to be closely related to hyenas; however, its diet and hence dentition are clearly different from the hyenas. It is therefore a question of whether differences are sufficiently great to warrant placement of the aardwolf in a separate family (R. H. N. Smithers, pers. comm.).

Gingerich (1975) suggested the aardwolf mimics the striped hyena to reduce predation by leopards (*Panthera pardus*) and other larger carnivores. However, as it is less than one-half the size of the hyena, and animals such as jackals, foxes, and small antelope are never perturbed by an aardwolf (most likely not confusing it with the hyena), hyena mimicry seems an unlikely explanation for aardwolf stripes.

The aardwolf is listed as rare in the South African Red Data Book—Terrestrial Mammals, although there is no evidence to show that the aardwolf has declined in range or numbers (Smithers, 1986). Being nocturnal and having a shy and retiring nature make the aardwolf difficult to observe, and it is probably more common than usually believed. Dry grasslands are a ubiquitous feature of Africa and provide the primary food source for human livestock and for *Trinervitermes* sp. Therefore, as long as the grasslands of Africa survive, the aardwolf appears assured of its food source and should survive provided there is not an undue increase in persecution by man (Anderson, 1988; Richardson, 1984, 1986).

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