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 islandii Geoffroy St.-Hilaire, 1824:355. Type locality “near Algoa Bay, Cape of Good Hope.”

Proteles typicus Smith, 1834-96. Renaming of P. islandii, 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 (canecens Shortridge and Carter, harrisoni Rothschild, hyenoides Desmarest, islandii Geoffroy, transvaalensis Roberts, and typicus Smith are synonyms).

P. c. septentrionalis Rothschild, 1902:443. Type locality “Somali-land” (pallidus Cabrera and termes Heller are synonyms).

DIAGNOSIS. Although the most recent classification places P. cristatus in a family of its own, Proteidae (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 foot. 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 hyenas were derived from cretaceous viverrids (Ewer, 1973; Savage, 1976), but it is uncertain at what stage the aardwolf diverged from this lineage (Ewer, 1973; Thomia, 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 x 10^6 years ago (Brain, 1981; Hendey, 1974). This animal was larger and dentally less degenerate than P. cristatus (Hendey, 1974). A number of more recent fossils, dating back to about 1 x 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
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 anulations, 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, 1987a). The tongue is covered in large, conical papillae, and the large submaxillary glands produce copious amounts of sticky saliva (Flower, 1869b; 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, 1869b; Kruuk and Sands, 1972; Smithers, 1983) and olfactory lobes (Flower, 1869a) are also well developed.

Despite many references to the contrary (Bourière, 1963; Roberts, 1951; Von Ketelholtz, 1966), the aardwolf has disproportionately strong jaws and skull. The zygomatic arches are broad and heavily built, suggesting well-developed masster 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; 1987b; Richardson and Coetze, 1985). 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, 1869b; Wells, 1968). At the base of the penis are a pair of eblong clusters of pale sebaceous glands separated by non-glandular tissue (Flower, 1869b; Fig. 4) that are not present in hyenas (Wells, 1968). The function of these glands is unknown (Flower, 1869b; 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, 1869b; Pocock, 1916). The gland structure is similar to that in striped (H. hyaena) and spotted (H. crocuta) 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
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contents of its anal gland backwards as a form of defense when attacked (Boitani and Barotek, 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, 1987a).

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 farther 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, 1987a).

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, 1987b; Richardson and Coetze, 1988). Richardson (1987a) 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 recover lifespan for an aardwolf in captivity is 15 years in East London Zoo (H. F. Von Ketelholtz, in litt.).

ECOLOGY. The aardwolf is considered one of the indicator species for the Somalia–Kalabari 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 (Trimeroternes), mainly on T. bettounianus 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, 1987a). 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, 1987a), and consuming as many as 300,000 termites/night (Richardson, 1987a). These termites 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. Trimeroternes trinervoides is almost entirely nocturnal (Richardson, 1987a). By contrast, the larger harvester termite Heterotermes mossambicus is mainly active by day and during winter (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 Heterotermes during the daytime (Richardson, 1987a).

Richardson (1987a) estimated that an aardwolf in the northern Cape consumes about 105,000,000 termites/year. Of these, Tri- meroternes constitutes the vast majority with Heterotermes 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 Trimeroternes 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, 1987a). Winter also is the period of highest mortality for the cubs, suggesting that the aardwolf is highly dependent on Trimeroternes and unable to feed successfully on alternative sources of food (Richardson, 1987a, 1987c, 1987d). The main reason for this dependence may be that the few Trimeroternes 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, 1987a, 1987c). Unlike the aardwolf, other myrmecophagous 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, 1987a, 1987c).

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 Dore, 1984), filled with chemical poisons (Prestwich, 1983), and seasonally unavailable (Richardson, 1987a) could be responsible for this lowered basal metabolic rate (Richardson, 1987c).

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 syntactically 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

![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.](image-url)
cannot tolerate the terpene secretions of Trimeresurus, feeding instead on Hadronotus and a large variety of other insects, including larvae, huyet of the surface (Bothma et al., 1984; Richardson, 1987a; Smithers, 1983).

Aardwolves occupy home ranges that vary from 1 to 4 km² (Bothma and Nel, 1986; Kruuk and Sands, 1972; Richardson, 1985; Skinner and Van Aarde, 1985). Richardson (1985, 1987b, in press) has shown that home ranges, determined by summation of contiguous hectares in which an adult pair deposited one or more scent marks during the non-breeding season, are aggressively defended and scent-marked as territories. Territory sizes vary with the density of Trimeresurus mounds, each territory having approximately 3,000 mounds with an average of 55,000 mounds/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, 1987a).

In prime habitat (open grassland and scrub regions), aardwolf densities may reach 1 adult/km² on farms with good populations of Trimeresurus 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 their body for medicinal purposes, but the extent of this usage as a cause of mortality is unknown (Anderson, 1988; Richardson, 1984, 1985; Kruuk, 1966).

Little information is available on the parasites carried by the aardwolf. Two subspecies of mallophagous louse, Felicola intermedius intermedius and F. i. hyanea, have been found on only the aardwolf and the brown hyena, respectively (Hopkins, 1966), 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 dragging with projectile syringes. Aardwolves cannot be caught with foothold traps, but may be lured to traps 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 are primary nocturnal, although they may be active during the late afternoon if termites are available. Richardson and Nel (1980) had no evidence that they were active in the daytime (Richardson, 1987a, 1987d; Richardson and Coetze, 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 0°C. Aardwolves cover an average of 1.7 km/h while foraging, walking 8–12 km/h during summer, and 3–8 km/h in winter, depending on ambient temperature (Richardson, 1985, 1987a).

Aardwolves are solitary foragers except when accompanying their young cubs (Bothma and Nel, 1986; Kruek and Sands, 1972; Richardson, 1987a; Richardson and Coetze, 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 Hadronotus 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, in particular in a greeting between a mother and her cubs, two individuals may briefly sniff each other's noses before separating (Richardson, 1985).

Aardwolves are territorial, a mated pair occupying a perennial territory with their most recent offspring. Apart from aggressive encounters 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
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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 Ulrich and Schnitt, 1969; Wurster and Berrischke, 1969). These chromosome are similar in number and configuration to the hyenas, providing further evidence for classifying the aardwolf in the Hyaenidae (Von Ulrich and Schnitt, 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 Proteidae and in the Hyaenidae within the last few years (Meester et al.; 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 smaller than such jackals, foxes, and small antelopes are never perturbed by an aardwolf (most likely not confusing it for the hyena), hyena mimicry seems 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 Trienestis sp. Therefore, as long as the grasslands of Africa survive, the aardwolf appears assured of its food source and will survive provided there is no undue increase in persecution by man (Anderson, 1988; Richardson, 1984, 1986).

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