UNUSUAL EXTERNAL ADAPTATIONS IN THE ROCK HYRAX

J. B. SALE

Zoology Department, University College, Nairobi

INTRODUCTION

The hyrax is known to the anatomist and museum zoologist as a curious collection of anatomical peculiarities. The skull and especially the incisor teeth, which resemble the tusks of the elephant, the limb bone arrangement with hooves on the separate digits and the peculiar structure of the gut are just a few of many unique hyrax characters. Recent studies on the biology of the rock hyraces (genera *Procavia* and *Heterohyrax*) in East Africa have shown a number of unusual features connected with the living animal in its habitat too. Considering that the hyrax is an "ungulate type" mammal which has a mode of life similar to that of many rodents, this is perhaps not surprising. It should be emphasised that the hyrax is not a burrowing animal in the sense of constructing its own dwelling holes as many rodents do. Hyrax generally seek shelter in already existing holes and crevices and although those selected are within certain specifications (Sale 1966), there is great variety of hole size, extent and configuration. Also individuals do not generally live in the same set of holes for their entire life-time, and thus hyrax encounter a greater number of variables in their habitat than does the average hole-dwelling small mammal. An animal which has lived in this kind of habitat for a very long time might be expected to have produced adaptations of a rather extraordinary nature and such has proved to be the case in the hyrax.

The object of the present paper is to draw attention to several as yet little discussed external features of the hyrax and to attempt to evaluate their usefulness to the animal in its natural habitat. In so doing the profound influence of the habitat in the selection of appropriate adaptations is clearly seen. The structures discussed occur in both *Procavia* and *Heterohyrax* and are all derived from the skin. Because they occur together, the dorsal gland and surrounding erectile hairs (dorsal spot) are discussed in the same section of the paper, while the widely distributed tactile hairs or vibrissae are considered separately.

THE DORSAL GLAND AND DORSAL SPOT

The dorsal gland is indicated externally by a slightly raised bare batch in the centre of the back, at about the junction of the thoracic and lumbar regions. This oval area of skin is about 1·5 cm long in the adult rock hyrax (both genera) and is surrounded by the long dorsal gland hairs, which are of a different colour (white or pale orange in East African hyraces but black in some races elsewhere) from the general pelage, and form a distinct spot in the centre of the back. Investigation shows this area of the skin to be important in providing a combined olfactory and visual stimulus appropriate to the mode of life of the hyrax.

Some authors have been in doubt as to the glandular function of this structure, e.g. Shortridge (1934) who describes it as "apparently of a glandular nature". As Mollaret (1958)

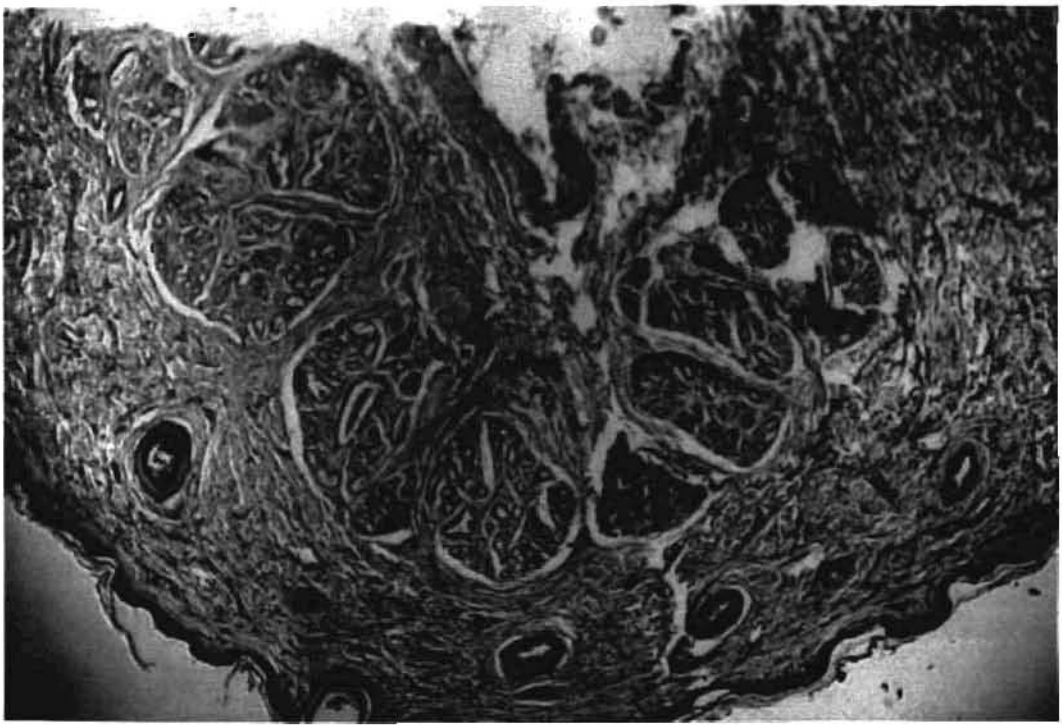

FIGURE 1
A vertical longitudinal section through the dorsal gland of a young animal nearing sexual maturity. The secretory tissue is grouped into 8 lobules which are still deep in the dermis. In a sexually active animal the lobules would be much larger and nearer to the skin surface.

states, however, careful examination reveals the presence of a number of pores and I have on several occasions seen a fluid oozing from them in living animals. There is no doubt that the gland is the source of the characteristic odour of a hyrax and dried pelts always smell stronger at this point than elsewhere. Observed instances of secretion suggest a connection between the gland and the sexual cycle, but the evidence is against limiting its significance to sexual functions. Indeed, there is evidence of a general social function (See below and Baer 1959). The possibility of the dorsal gland functioning in the identification of the newborn young with their mother has been discussed in a previous publication (Sale 1965a).

In order to confirm the secretory function of the dorsal gland I have carried out a histological investigation, the full details of which will be published elsewhere. There is distinct glandular tissue below the bare patch of skin but its state of development varies according to the age and degree of sexual maturity (and sexual activity) of the animal. In juvenile animals there is only rudimentary glandular tissue present deep in the dermis and the non-secretory nature of the structure at this stage is confirmed by the absence of any external swelling of the patch and the fact that secretion has never been observed in juvenile animals. In a fully adult, sexually active animal, e.g. a male in rut, a longitudinal section of the skin reveals 7 or 8 lobules of active glandular tissue. Within each lobule are 25-40 alveoli, consisting of a secretory epithelium surrounding an irregularly shaped lumen (see Fig. 1). Well developed ducts can be seen passing towards the surface and corresponding to the open pores on the swollen bare skin surface. Histological and behavioural evidence points to the dorsal gland in both male and female hyrax being maximally active at the time of mating. An example of its function at this time in the female is provided by observation of early courtship behaviour which suggests that the rutting male initially locates the oestrous female in the colony entirely by smell, and Hvass (1961) confirms this function of the dorsal gland secretion.

The ring of *distinctly coloured hairs surrounding the bare glandular patch is not very conspicuous when the hairs are relaxed and lying flat among the surrounding general pelage. However, the anterior and lateral dorsal gland hairs are capable of being instantly erected forming a large conspicuous "flash" in the centre of the back. At rest all these hairs lie backwards, nearly parallel to the back like the pelage hairs. Various degrees of erection may be achieved. Slight erection involves the raising of the dorsal gland hairs to an angle of about 45° to the back, in which position they are only a little more noticeable than when at rest. Frequently, however, the hairs are erected through 90° or more giving the dorsal spot the appearance of a composite flower, with the bare glandular patch in the centre and the light coloured hairs radiating from it all round. It should be noted that the dorsal spot hairs posterior to the glandular patch are not erected but remain in the rest position (lying backwards) when exposed by the erection of the anterior and lateral hairs (which when at rest overlay the posterior ones and are themselves partially overlaid by pelage hairs). This specific erection of the dorsal spot hairs is often accompanied by a more general erection of the hairs on the back of the head and nape of the neck.

It is not my intention here to give a detailed account of the use of pilo-erection as a visual signal in hyrax ethology. Suffice it to say that the erection of the dorsal spot hairs does constitute an important visual signal in the social behaviour of the hyrax where it signifies alarm †(45°) and threat (90°) towards an adjacent or approaching animal, whether of the same or another species. Figure 2 illustrates some typical uses of this signal in intra-specific conflict in *P. johnstoni.*

An interesting example of the use of the dorsal gland and its surrounding hairs as a combined olfactory and visual stimulus is provided by the behaviour of the male during the middle stages of courtship. The male alternately faces the female, sniffing her, and turns round presenting his hindquarters, quivering as he does so. During this back-presentation the ring of dorsal gland hairs in the male is maximally opened so that the hairs are erected through almost 180°, being inversely flattened against the back. The "flower" thus fully opened completely exposes the bare glandular patch allowing maximal olfactory stimulation from the gland to reinforce the maximal visual stimulation provided by the large circular flash of white hairs. This complete opening of the glandular hairs has only been noticed when the male is sexually excited and appears to provide a different signal to the female from the

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*The ensuing discussion is based on species with a light coloured dorsal spot.

†This visual alarm signal reinforces the distinct vocal alarm signal (Sale 1965 c).

a

b

c

d

alarm and threat indicated by the sub-vertical and vertical erection of the hairs respectively. No doubt the simultaneous presence of a strong olfactory stimulus helps in differentiating this visual signal from the threat one. It will also serve to warn off any other males approaching from a distance as the strong visual signal alone will probably indicate to them intensified threat.

The siting of the dorsal gland and spot in the centre of the back of the hyrax is as curious as the structure and functioning of this unusual organ. It would appear that this dual structure has developed in response to several separate requirements of the hyrax. The glandular part is particularly useful when the animal is in the dark, while the erected hairs provide an excellent variable visual stimulus when the hyrax is out of its hole basking or climbing around on the rocks.

Hyrax shelter in dark underground holes and crevices and in this situation vision is clearly of little or no value. Accordingly the near vision of hyrax has indifferent definition. The sense of smell, on the other hand, appears to be well developed complementary to the presence of the dorsal gland. In view of the frequent reversing behaviour the more logical position for this scent-producing structure might appear to be the rump where there is a similar gland in the peccary and springbok. However, when hyrax are in their holes they tend to show "huddling" and "heaping" orientations (Sale 1970), involving the tendency for animals to be packed tightly together, if not actually on top of one another. Figure 3 well illustrates how this behaviour inside the "warren" results in the nose of one animal (the rear/upper one) being in close proximity to the centre of the back, and thus the dorsal gland, of an adjacent animal. Intra-specific identification in the darkness of the hole is thus made easy by the relative positioning of the producer and receiver of this olfactory stimulus. While the dorsal gland has a more specific function in courtship behaviour, as described above, it undoubtedly has the general social function of individual identification too. Mendelssohn (1965) confirms this and informs me that hyrax sometimes sniff one another in the back region, expecially when two animals meet. In contrast to the interdigital and pre-orbital glands of many ungulates the dorsal gland of hyrax does not appear to be used for marking territory. The dorsal gland situated in the centre of the back would thus appear to be an adaptation that has arisen in response to the hyrax's need for a close-range identification

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FIGURE 2

The use of the dorsal spot in intra-specific conflict in *Procavia johnstoni*.

(*a*) A submissive young animal (front) in possession of food is approached by a dominant old female. The young animal turns away, i.e. back presentation, and shows fear by the lack of pilo-erection and the backward direction of the ears. In the complete absence of resistance (threat) from the young animal, the molesting female does not show threat herself.

(*b*) The animal in possession of food (front) threatens an intruder by erection of the dorsal spot and neck hairs. The intruder turns away (back presentation), at the same time showing weak pilo-erection, indicating alarm (notice also the backward direction of the ears).

(*c*) All three animals are showing moderate pilo-erection (alarm/threat) which here acts to keep them spaced out as they search for food. Note the radiating orientation typical of a feeding party.

(*d*) An animal in possession (front) is threatened by an intruder which is showing strong pilo-erection (threat) but is back-presenting and has the ears back (fear). The threat induces fear in the feeding animal which shows no pilo-erection and also has the ears pressed back. This type of situation occurs when the two animals are of roughly equal dominance.

FIGURE 3
A group of animals huddling together inside an artificial warren. In such a huddle the nose of one animal is near the dorsal gland of the animal in front.

mechanism, the functioning of which is not impeded by the complete abscence of light and which fits in with the animal's social behaviour.

The majority of diurnal mammals possess a visual alarm signal and in many it is in the form of a white "flash" produced by the uplifted tail which has a white underside. A similar effect is produced by special light-coloured erectile hairs on the rump of some ungulates, as for example the prongbuck and springbok. The white dorsal gland hairs of most species of hyrax are comparable with these latter structures except that they are situated in the centre of the back and not on the rump. From a consideration of the general locomotor behaviour of hyrax, where there is a pronounced tendency to back-presentation (see above and figure 2) and reverse locomotion (see below), one might expect to find a flash signal of this kind on the rump, in which position it would be most easily seen by another animal behind. When a group of hyrax is observed in its natural habitat, a rocky hillside, however, it is noticed that the animals are very rarely all on the same level, as is the case with most ungulates, but positioned either above or below one another. Hence an alarm signal on the rump would not be as readily seen by an animal on a rock above as one in the centre of the back.

From the point of view of the species, the alarm function of the dorsal spot is clearly of greater survival value than its use in intra-specific threat or for that matter, courtship behaviour. It is therefore interesting to note that while the position of the spot in the centre of the back is ideal from the point of view of its alarm function and reasonably appropriate to the posture of the courting male, it is often difficult for an animal being threatened to see the signal as the aggressor approaches head-on. However, in cases of intense threat the flash on the back is only part of a complex behaviour pattern, involving also baring of the incisor teeth and an angry growl, and even if the dorsal spot is obscured by the shoulders, the other stimuli will be received. It seems probable that while the bared incisors are the main visual indication of threat early in an encounter, the flash on the back takes over this function later, since as the threatened animal directs its hindquarters towards the aggressor it frequently turns its head round to get a sideways look at the latter (see Fig. 2, b and d). The defending animal will thus get a second impression of the intensity of threat in the aggressor as it observes the latter's dorsal spot "out of the corner of its eye". There may be a subsidiary defensive function of the dorsal gland hairs in extra-specific threat (where the hairs are still erected as the incisors are bared), because to a larger predator viewing them from above they could give the appearance of erectile quills, rather like those of some tenrecs. From these considerations it seems that the alarm function of the dorsal spot has been the main factor in determining its position on the animal, in association with the demands of that part of the habitat occupied during much of the daytime.

While it is impossible to say with certainity whether the dorsal gland and spot evolved independently or together (see below), it is clear that the distinctive habitat of the hyrax played an important part in selecting both the nature and site of this pair of organs. The dark part of the habitat demanded an identification organ of the nature of the gland. Its siting appears to have been largely determined by behavioural considerations but the particular behaviour in question (huddling and heaping) is also a product of the environment, as is shown elsewhere (Sale 1970). A small herbivore such as hyrax is vulnerable to predators when outside its holes in daylight and requires a good alarm-signalling mechanism. A readily visible flash is a common response to this need but the unusual siting of the dorsal spot in the centre of the back seems to have been selected by the type of terrain in which hyrax live. In both parts of this dual organ and in its unique position we can see an unusual example of the result of interaction between a living organism and its environment.

A few races of hyrax have a black dorsal spot e.g. *P. capensis* but I have not yet had the opportunity of examining their environment. In view of the preponderance of species with white or light coloured dorsal spots it seems that this is the colour on the basis of which the structure has evolved. The forms with black dorsal spots may well be mutants that have survived because they have arisen in areas where predation pressures are low and thus the premium on a readily visible alarm signal is not so great as is generally the case.

FIGURE 4
A young *Procavia* showing widely distributed vibrissae projecting above the general level of the pelage.

THE DISTRIBUTION AND FUNCTION OF THE VIBRISSAE

The very wide distribution, including the back and sides of the body (see Fig. 4), of the vibrissae in the Hyracoidea is a striking external feature of the group that has produced repeated comment. Bruce (1790) clearly shows the tactile hairs in his drawings of the Abysinian Hyrax and records that the animal has "long herinaceous hairs, which, like small thorns, grow about his back". The hairs are called "ashok" in Amharic and form the basis of the Ethiopian name for the rock hyrax, "ashkoko". Hvass (1961) notes that these "protruding bristly hairs" occur in rows down the back and along the limbs and says that it is probable that the hairs have a sensory function. Rode (1943) says the vibrissae are tactile and records their length in *P. ruficeps*, the West African *Procavia*, as 60-80 mm. From their structure (especially the follicles) and distribution and observation of their use, there seems no doubt

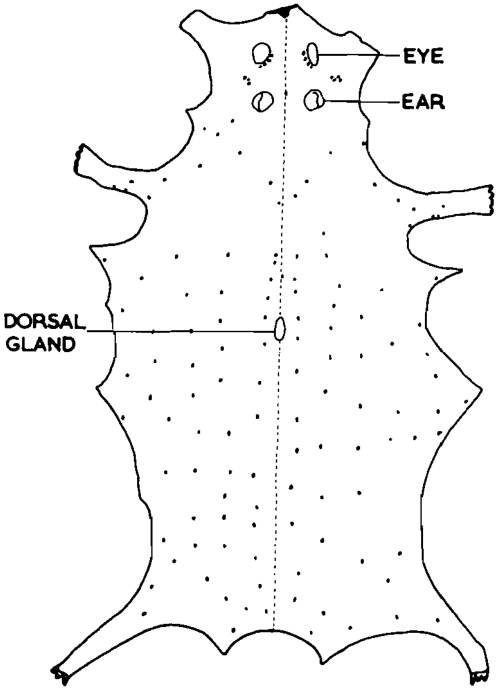

FIGURE 5
A drawing showing the distribution of the follicles of tactile hairs in the dried skin of an adult male *P. habessinica*. The broken line down the centre indicates the mid-dorsal position.

that these are true tactile vibrissae. They are 5-8 cm long in adult *P. habessinica* and 3-4 cm in *Heterohyrax*.

It is very difficult to count the vibrissae or determine their arrangement in a living animal because they are obscured, except when erected, by the pelage. Even in a dried skin all the vibrissae are not easy to pick out. It was found, however, that one could readily see the follicles of these large sinus hairs on the reverse side of the skin of a pale, almost albino, animal. Several such skins have been obtained and, because of the lack of pigmentation, the oval, blood-filled follicles stand out as dark spots. Figure 5 shows the distribution of follicles in the dried skin of an adult male *P. habessinica*.

Almost all the vibrissae are bilaterally arranged, probably none being found in the mid-dorsal line. On the head there are four supraorbital vibrissae and three to four in the genal position (Lyne 1959) as well as the usual mystacial ones (not shown in the drawings). There is also a set of around five hairs on the throat. On the inside of the wrist is an ulna carpal pair and there are a number around the front of the shoulder, going up to the highest point in the centre of the back. The lateral depression of the body immediately posterior to the forelimbs lacks vibrissae but the abdominal bulge is well supplied. The vibrissae of the back and flanks are arranged in four rows on each side of the midline. A few scattered follicles in the belly region (outside edges of the skin) are poorly defined and appear to represent follicle rudiments as they lack corresponding vibrissae. At the posterior end of the animal a small number of the tactile hairs are arranged on the ridge above the anus (caudal region) and there is a pair on the back of each thigh. The depression anterior to the hind limbs tends to lack vibrissae.

It is clear from the distribution of the vibrissae that they are situated in parts of the body that are most likely to come in contact with objects as the animal moves about. Hence the anterior part of the shoulders is well supplied, while the narrow thoracic region behind them lacks vibrissae. The presence of numerous tactile hairs on the back, flanks and caudal region is probably unique among the mammals. Functionally it affords complete tactile coverage, important when hyrax are moving around inside their holes, which, in contrast to burrows, are not constructed to the requirements of the user (Sale 1966). Since hyrax frequently move to new sets of holes (Sale 1965 b), they will repeatedly have to explore the dark crevices and tunnels beneath irregularly piled rocks. The poor close-up vision of hyrax makes the tactile sense the more important during such exploration. It is also significant that hyrax often enter a crevice or hole by reversing into it. This is particularly so with animals entering emergency shelter while under pressure from an enemy. On reaching what appears to be a suitable hole they frequently turn round and bare their incisors at the approaching enemy, at the same time easing their hindquarters into the hole, into which they may ultimately disappear completely. From observations on captive hyrax in a specially constructed observation "warren", it is clear that when the animals are confined in their holes, reversing plays a much greater part in hyrax motor patterns than in the locomotor activities of most other mammals. Unlike many hole-dwelling mammals, hyrax have no tail with which to feel their way while groping backwards in a dark tunnel. The possession of protuding tactile hairs in the caudal and rump regions is clearly an important adaptive feature when considered in the light of the pronounced reversing behaviour and the absence of a tail. The presence of vibrissae on the wrist is consistent with the use of the forelimbs in climbing (Beddard 1902). Observations of their use in captive hyrax provide collaborative evidence that these protruding hairs have a tactile function. Hyrax moving around in open well-lit areas generally carry the hairs more or less relaxed, lying amongst the general pelage. However, in dark, obscure places such as corners or crevices or inside the artificial warren, the hairs are stiffly erected and stand out from the body ready to contact any protruding object.

The widespread distribution of tactile hairs in the hyrax provides us with a further example of the influence of the environment in the selection of an unusual anatomical feature in this mammal. Like the dorsal gland and spot, the tactile hairs are a skin derivative that has been selected for to better fit the animal for its unusual environment. Of the many hole-dwelling mammals few are both diurnal and shelter in irregular rocky holes not fashioned to the size and shape of the animal's body. An animal which has to be able to see in bright sunlight is unlikely to be able to adapt its vision to finding its way around in dark irregular caverns and crevices. The protective value of this type of shelter is much greater than that of a burrow in soil which can often be dugout by a determined predator. The hyrax is much better fitted to take advantage of such a niche by the selection under environmental pressure of a wide bodily distribution of vibrissae. As in the case of the dorsal gland and spot, there are complementary behaviour patterns enhancing the usefulness of these peculiar skin derivatives.

The possession of widely distributed vibrissae in hyrax, while adapting the animal to its hole-dwelling habit, is probably a further primitive character of the group. Pocock (1914), in a consideration of facial vibrissae in a large series of mammals (excluding hyrax), concluded that a full set of vibrissae is a primitive characteristic. Widely distributed vibrissae is a characteristic of the marsupial mammals. The fact that a large number of vibrissae is also common in active arboreal mammals (Lyne 1959) may suggest the development of the rock hyraces from the tree form, although much other evidence would appear to be against this interpretation.

GENERAL DISCUSSION

It is well known from the fossil evidence (see for example Whitworth 1954) that the Hyracoidea are an old group of mammals that became separated from related forms, such as the Proboscideans, very early in ungulate evolution. Since the group has evolved slowly, distinctive features in its present-day representatives are likely to reflect the habits of older and now extinct relatives. Thus, for example, it is probable that the long gestation period (7½ months) is a remnant of the time when hyrax were large animals the size of a hog (Sale 1965a). The presence of two organs of social communication, such as the dorsal gland and spot, which are peculiar to the hyrax, especially in their siting, clearly have distant origins in the history of the group. Such well developed structures and the peculiar behaviour that matches their functions must have been a long time in the moulding. As this pair of organs is only of real significance in the social context, it seems fair to deduce that the social habit is of long standing in the hyrax. In view of this it is perhaps surprising that hyrax social behaviour is not developed to the extent that it is in many ungulate type mammals (Sale 1970). As far as modern hyraces are concerned, it points to the social forms (*Procavia* and *Heterohyrax*) as being older established than the more solitary *Dendrohyrax*, where the possession of well developed social communication seems inappropriate and might almost be regarded as a vestige.

The high degree of adaptation of the integument of the rock hyrax to its present habitat, even on the basis of the three skin derivatives discussed in this paper, surely points to this animal having been long associated with this particular habitat. It is difficult to imagine the usefulness of, for example, the dorsal gland or the widely distributed tactile hairs to an animal of the open plains. The dorsal spot, on the other hand, could well have functioned in an animal which clambered around on well-lit rocky hillsides but was not yet a hole-dweller. It may well be that the larger Oligocene hyraces occupied a similar niche to the modern klipspringer and had in turn evolved from a plains-dwelling form, as suggested by some aspects of its reproduction (Sale 1965a). When considered in this light, it seems possible that, although clearly of long standing, the dorsal gland and tactile hairs may be more recent developments than the dorsal spot.

SUMMARY

Attention is drawn to three unusual external features of hyrax derived from the skin, viz the dorsal gland, dorsal spot and widely distributed tactile hairs. The secretory nature of the dorsal gland is confirmed and its function as a scent gland in social communication briefly discussed. The arrangement and mode of erection of the dorsal gland hairs (forming the dorsal spot) are described together with the function of this structure as a variable visual signal. The respective parts played by behaviour and the environment in selecting the nature and siting of these adaptations is considered. The wide distribution of the tactile hairs (vibrissae) is described and their function discussed in the context of the unusual underground habitat of the rock hyrax which appears to have been a major factor in selection for this unique feature. The implications of these adaptations for the evolution of the Hyracoidea are briefly considered.

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