International Journal of Primatology, Vol. 8, No. 1, 1987

A Sternal Gland in the Siamang Gibbon (*Hylobates syndactylus*)

Thomas Geissmann[1]

Received November 21, 1985; revised September 11, 1986

The present report gives the first description of a sternal gland in the siamang gibbon, Hylobates syndactylus*, and the first histological examination of a sternal gland in a hominoid primate other than the orang-utan. The gland does not seem to be used for any kind of marking behavior, in contrast to the sternal glands in many other primates and some other mammals. The sternal gland of the siamang may be derived from a marking gland which specialized secondarily to serve parallelfunctions like those served by the axillary organs of humans and the African apes. A role of the gland in olfactory communication and a possible minor role in thermoregulation are discussed.*

KEY WORDS: sternal gland; *Hylobates syndactylus*; siamang; olfactory communication; gibbons.

INTRODUCTION

Nonhuman primates have a large variety of cutaneous glands (Montagna, 1972). Glandular concentrations are more common in some regions of the skin than in others. One of the most important of these regions is the medial anterior part of the chest (Montagna and Ellis, 1963; Montagna and Yun, 1962; Sprankel, 1962), where concentrations of glands may actually form glandular organs commonly called sternal glands. Glands and glandular concentrations occur in the sternal region in many primate species (Table

[1]Anthropological Institute, University Zürich-Irchel, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

0164-0291/87/02000001$05.00/0

Table I. Occurrence of Cutaneous Glands on the Medial Anterior Part of the Chest in Primates

Species	Evidence[a]	Reference
Microcebus coquereli	I	Petter *et al*. (1977)
Phaner furcifer	1, 3, 4	Petter *et al*. (1977)
	4	Rumpler and Andriamiandra (1971)
Varecia variegata	1, 3, 4	Petter *et al*. (1977)
	4	Rumpler and Andriamiandra (1971)
Hapalemur simus	3, 4	Petter *et al*. (1977)
Propithecus sp.	1	Petter (1965)
Propithecus diadema	3, 4	Petter *et al*. (1977)
	4	Rumpler and Andriamiandra (1971)
Propithecus verreauxi	I	Jolly (1966)
	1	Mertl-Millhollen (1979)
	1, 3, 4	Petter et at (1977)
		Richard (1974)
	4	Rumpler and Andriamiandra (1971)
	4	Zeller (1984, 1986)
Galago crassicaudatus	1, 3	Bearder and Doyle (1974)
	1, 3	Clark (1978)
	1, 3, 4	Dixson (1976)
	1, 3	Sauer (1974)
Galago garnettii	1, 3	Clark (1986)
Galago moholi	1, 3	Bearder and Doyle (1974)
		Sauer (1974)
Tarsius bancanus	3	Hill (1951)
	3	Hill at at (1952)
Tarsius syrichta	4	Arao and Perkins (1969)
	3, 4	Hill (1951, 1955)
	3, 4	Hill at at (1952)
Cebuella pygmaea	I	Christen (1974)
	3	Epple and Lorenz (1967)
	4	Perkins (1968)
Callithrix argentata	1	Epple (1972)
	3	Epple and Lorenz (1967)
	4	Perkins (.1969b)
Callithrix humeralifer	3	Epple and Lorenz (1967)
Callithrix jacchus	1	Box (1975)
	1, 3	Epple (1972)
	1, 3	Epple and Lorenz (1967)
	1, 3, 4	Sutcliffe and Poole (1978)
Leontopithecus rosalia	1	Epple (1972)
	1, 3	Epple and Lorenz (1967)
	1	Kleiman and Mack (1980)
	1, 2, 3	Mack and Kleiman (1978)
Saguinus fuscicollis	3	Epple and Lorenz (1967)
Saguinus geoffroyi	1	Epple (1972)
	1, 3	Epple and Lorenz (1967)
Saguinus labiatus	3	Epple and Lorenz (1967)
Saguinus midas	1, 3	Epple and Lorenz (1967)
Saguinus mystax	3	Epple and Lorenz (1967)
Saguinus nigricollis	3	Epple and Lorenz (1967)
	1	Izawa (1978)
	4	Perkins (1966)
Saguinus oedipus	1	Epple (1972)
	1, 3	Epple and Lorenz (1967)

Table I. Continued

Species	Evidence[a]	Reference
Callimico goeldii	1, 3	Epple and Lorenz (1967)
	4	Perkins (1969a)
Aotus trivirgatus	3	Epple and Lorenz (1967)
	4	Hanson and Montagna (1962)
Callicebus moloch	3	Epple and Lorenz (1967)
	1, 2, 3	Mason (1966)
	1, 2, 3	Moynihan (1966)
Callicebus torquatus	3	Epple and Lorenz (1967)
	1	Kinzey (1981)
Sairniri sciureus	1, 3	Epple and Lorenz (1967)
	3	Hill (1960)
	4	Machida *et al*. (1967)
Cebus albifrons	1	Bernstein (1965)
Cebus apella	1, 3	Dobroruka (1972)
	3	Epple and Lorenz (1967)
Cebas capucinus	1, 3	Epple and Lorenz (1967)
Cebus nigrivittatus	3	Dobroruka (1972)
Cacajao rubicundus	3	Epple and Lorenz (1967)
Pithecia monachus	3	Epple and Lorenz (1967)
Pithecia pithecia	1	Claussen (1982)
	1	Dugmore (1986)
	3	Epple and Lorenz (1967)
	3, 4	Hill (1960)
	3	Sanderson (1949-1950)
Alouatta palliata	1	Eisenberg (1976)
	1	Young (1982)
Alouatta seniculus	3	Epple and Lorenz (1967)
	1	Sekulic and Eisenberg (1983)
Lagothrix lagothricha	1	Eisenberg (1976)
	1, 2, 3	Epple and Lorenz (1967)
	1	Schifter (1968)
Brachyteles arachnoides	3	Epple and Lorenz (1967)
Ateles sp.	3, 4	Schwarz (1937)
Ateles belzebuth	3	Epple and Lorenz (1967)
Ateles fusciceps	1, 2	Eiscnberg (1976)
Ateles geoffroyi	1, 2, 3	Epple and Lorenz (1967)
	1, 2	Klein and Klein (1971)
	3, 4	Wislocki and Schultz (1925)
Ateles paniscus	3	Wislocki and Schultz (1925)
Cercopithecus aethiops	1	Gartlan and Brain (1968)
Cercopithecus hamlyni	1	Gautier-Hion (personal communication), Loireau and Gautier-Hion (in press)
Cercopithecus neglectus	1	Gautier and Gautier (1977)
	1, 4	Gauticr-Hion (personal communication), Loireau and Gautier-Hion (in press)
Cercopithecus nigroviridis	1	Gautier-Hion (personal communication), Loircau and Gautier-Hion (in press)
Mandrillus leucophaeus	1	Fiedler (1957)
	2, 3	Hill (1944)
	3, 4	Hill (1954)
Mandrillus sphinx	1	Fiedler (1957)
	3, 4	Hill (1954)
Hylobates sp.	3	Pocock (1925)

Table I. Continued

Species	Evidence[a]	Reference
Hylobates syndactylus	3, 4	Geissmann (present report)
Pongo pygmaeus	3	Brandes (1939)
	3, 4	Schultz (1921)
	3, 4	Wislocki and Schultz (1925)

[a] 1, marking behavior on substrate; 2, other behaviors centering on sternal skin (e.g., rubbing or scratching glandular area with hands, rubbing strong-smelling substances or saliva on glandular area); 3, macroscopic modifications of skin and/or fur; 4, histological evidence.

I) as well as among Marsupialia, Chiroptera, and Scandentia (Hall and Gordon, 1982; Hood and Smith, 1984; Schaffer, 1940; Schultze-Westrum, 1965; Sprankel, 1962).

However, among hominoids, such a gland is known only in the orang-utan, *Pongo pygmaeus* (Brandes, 1939; Schultz, 1921; Wislocki and Schultz, 1925). Wislocki and Schultz (1925, P. 242) published a "list of those primates which could be carefully examined, none of which showed a sternal gland," including the hylobatids "*Symphalangus klossi*, *S. syndactylus*, *Hylobates agilis*, *H. lar*, *H. concolor*, *H. mülleri*."

In contrast to these findings, Pocock (1925, 1944) suspected a sternal gland in two captive male gibbons. Both animals had a dark patch in the sternal region, in one animal covered with a dark, wet substance, and both were thought by Pocock to have originated from Borneo. Bornean gibbons may comprise more than one species (Chivers, 1977; Chivers and Gittins, 1978; Groves, 1984; Marshall *et al*., 1984; Marshall and Marshall, 1976), and the identity of these animals is therefore not certain even if their origin had been correctly assigned. [In many cases, gibbons in zoos have been misidentified as Bornean gibbons or, conversely, have not been recognized as such (Schilling, 1984a).] Moreover, Weber and Abel (1928) stated, without anatomical proof, that the sternal patch observed by Pocock did not consist of a glandular concentration.[2]

Laîné (cited by Dandelot 1960) reported that perspiration in a captive male white-cheeked gibbon (*Hylobates concolor leucogenys*) and a female pileated gibbon (*H. pileatus*) produced colored droplets,[3] but he did not mention on which region of the animals' bodies the droplets were observed. Montagna and Yun (1962, p. 134) stated that the gibbon has "…a rich field of

2 "In dreieckigen nackten Brustfleck des Männchens von Hylobates leuciscus Mülleri, den Pocock (1925) beschreibt, handelt es sich nicht um gehäufte Drüsen" (Weber and Abel, 1928, p. 765).

3 "Nous avons remarqué que la sudation chez le mâle (un Gibbon *concolor leucogenys*) produit un suint en gouttelettes colorées qui tachent le linge et l'eau des bains en jaune foncé. Ceci existe aussi chez la petite femelle (espèce *H. lar pileatus*) mais le suint est moins coloré" (Laîné; cited by Dandelot, 1960, p. 11).

eccrine and apocrine glands on the anterior surface of the chest…." This statement was repeated later by Montagna and Ellis (1963, p. 194), and Montagna recently (1985, p. 18) wrote that gibbons have a "scent-producing apparatus…located in a sternal pit, above the manubrium of the sternum." Unfortunately, in none of these publications was the source of evidence revealed.

The only published study known to me where the skin of a gibbon was histologically examined in the region of the chest is that by Parakkal *et al*. (1962). These authors did not mention a sternal gland or any concentration or enlargement of eccrine or apocrine sweat glands in any part of their subjects' body, and no such specialization can be seen in a figure showing a section of the skin from the chest (Fig. 8 in their report). However, they observed that "when under Sernyl anesthesia,…these animals perspired freely over the entire body, but particularly on the chest above the nipples." The subjects in the quoted study, three young females, were said to be white-browed gibbons (*Hylobates hoolock*); however, in view of the extreme rarity of *H. hoolock* in captivity – only one individual in North America (Mootnick, 1984) and none in European zoos (Schilling, 1984a,b) – this attribution may eventually prove to be incorrect.

As yet, the only clear evidence for a sternal gland in hominoid primates has been provided for the orang-utan. The present report gives the first description and histological examination of a sternal gland in the siamang, *Hylobates syndactylus*.

MATERIALS AND METHODS

Ten captive siamang were inspected in the Zürich and the Studen Zoo, Switzerland. This sample contained animals ranging from 1.5 to about 23 years of age. It consisted of two adult males, four adult females, and immature animals of various age and either sex. Most of these animals were observed in a study on vocal behavior, some of them during several years (Geissmann, 1986). Additional information on six siamangs which I could not inspect myself (one adult male, one adult female, and four immature males) was reported to me by Mr. and Mrs. Rathfelder (personal communication), caretakers at the Zürich Zoo.

Histological sections were prepared from two relatively fresh specimens, which were not fixed postmortem: one juvenile male aged 2 years and 2 months and one adult male siamang about 15 years of age. Tissues were not well preserved in the adult male but sufficed to confirm the results gained from examination of the first specimen. Tissues were fixed in formol (4%) and embedded in paraffin. Histological preparations were made from ver-

tical sections cut at 7 and 10-gm thicknesses and stained with hematoxylin and eosin (Romeis, 1968) and with alcian yellow (for acid mucopolysaccharides).

RESULTS

During a study on vocal communication in the siamang (Geissmann, 1986), a distinctly colored patch was noticed in the sternal region. The sternal patch was often concealed by the throat sac of these animals but could easily be detected if an animal lifted its head or turned it to one side. In all 10 animals grossly inspected, the patch could clearly be seen. In addition, its presence in six siamangs which I could not inspect myself was reported to me by Mr. and Mrs. Rathfelder (personal communication) caretakers at the Zürich Zoo.

The sternal patch of the siamang takes the form of a yellowish, brownish, or even blackish colored area in the midline of the sternal region. The patch is of elongate shape (Fig. 1). The broader cranial end is situated at the lower end of the siamang's throat sac. The patch measured about 5 cm in length and about 1 cm in breadth in one juvenile male, and was about twice this size in an adult female. Distally, the patch is thinner and ends slightly above the level of a straight line drawn through both nipples. Hair density in the sternal patch is lower than in the lateral part of the chest but higher than on the throat sac. Hairs in the glandular area are often matted together with dried secretion or pasted with fresh secretion. The coloration of the sternal patch is produced by glandular secretions staining the skin and can be removed. The fresh secretion is a yellowish substance, somewhat similar in aspect to human earwax, and of a pungent odor, which I found to be typical for siamang. I could not detect a similar odor in several groups of captive

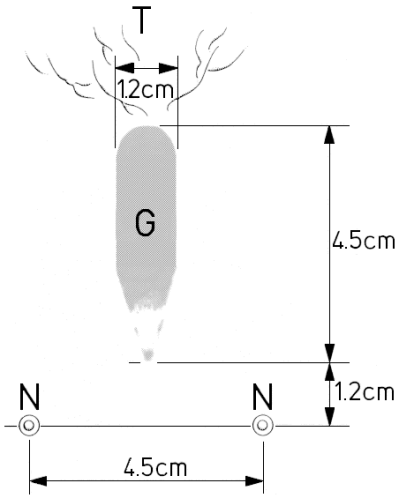

Fig. 1. Schematic contour and dimensions of the glandular patch of a freshly dead juvenile male siamang (2 years and 2 months of age); specimen now in the collection of the Naturhistorisches Museum, Bern (NHMBe 511984). G, glandular patch; N, nipples; T, throat sac.

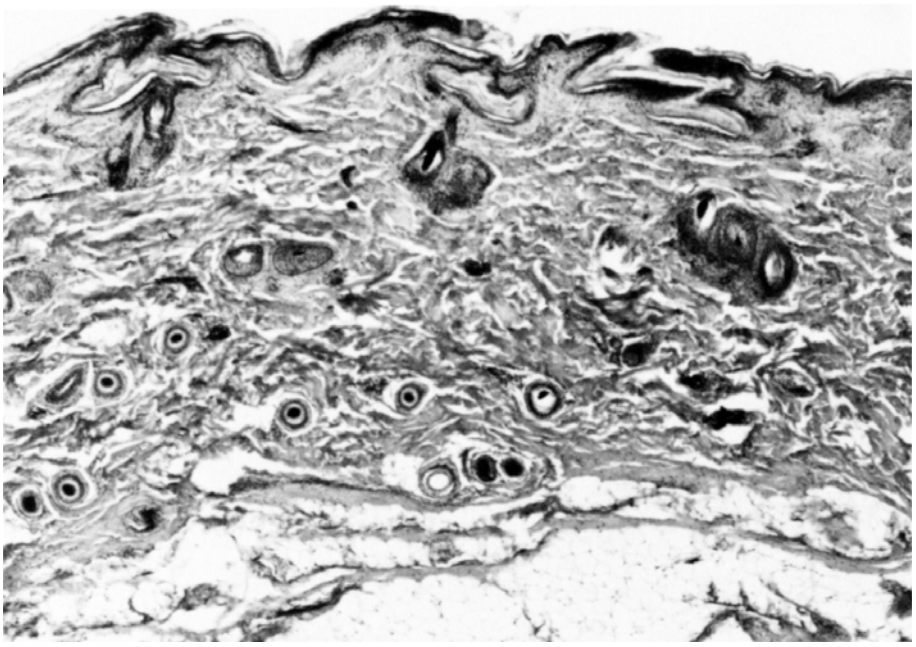

Fig. 2. Photomicrograph of a vertical section through the skin of the lateral chest of a juvenile male siamang (NHMBe 511984). Hair follicles and associated sebaceous glands are present, but tubular glands are not. Ten-micrometer section, stained with alcian yellow and hematoxylin & eosin. x 32.

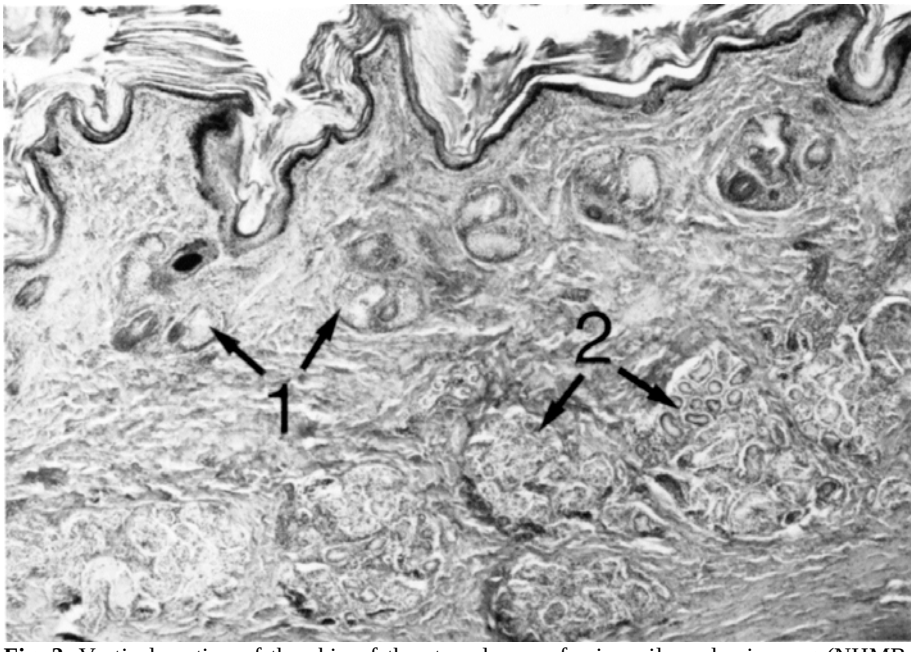

Fig. 3. Vertical section of the skin of the sternal area of a juvenile male siamang (NHMBe 511984) showing the superficial layer of sebaceous glands (1) and the deeper layer of coiled tubular glands (2). Specimen prepared as in Fig. 2. x 32.

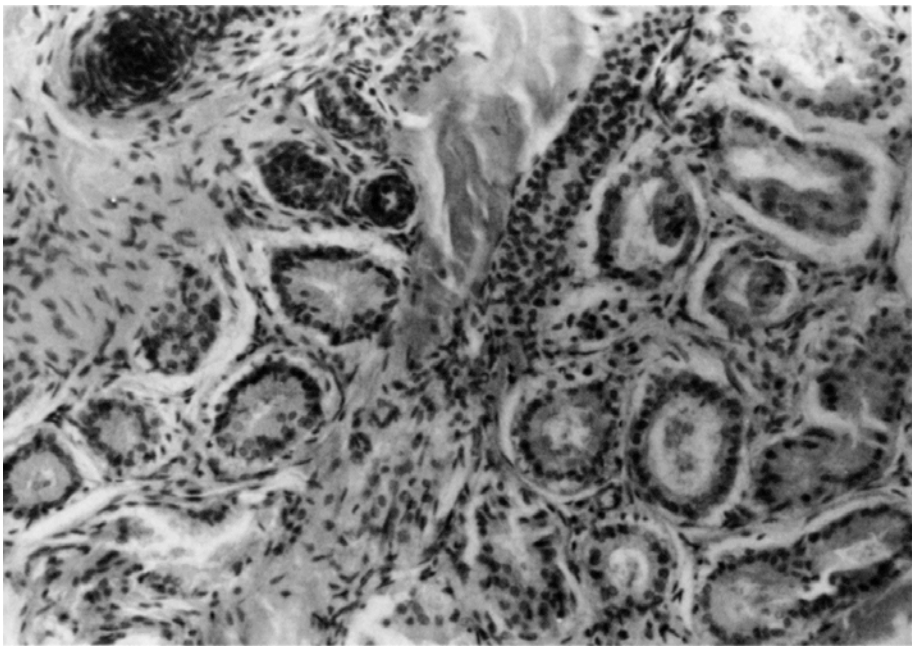

Fig. 4. Enlarged view of a vertical section through the sternal skin of a juvenile male siamang (NHMBe 511984) showing details of coiled tubular glands. Specimen prepared as in Fig. 2. x 206.

Hylobates lar and *H. pileatus*. The only odor I found to be faintly similar was that of some blossoms of *Lathyrus odoratus*.

In the skin of the lateral chest, only sebaceous glands, attached to hair follicles, were observed (Fig. 2). In contrast to this, the skin in the sternal region contained, in addition, a conspicious concentration of coiled tubular glands, thus forming a specialized glandular field. The tubular glands are more voluminous and form a veritable carpet of considerable thickness, which is separated from the more superficially situated layer of the smaller sebaceous glands (Fig. 3). In the tubular coils, two types of segments, similar to apocrine sweat glands and their ducts, can be distinguished: segments composed of cuboidal or columnar epithelium and with wide lumina often containing granular secretion, and very narrow segments composed of two layers of cuboidal epithelium (Fig. 4).

Often, the sternal patch was wet and sticky from the fresh secretion of the gland. This could be taken as a rough indicator of "high secretory activity" and was observed chiefly in two situations: on hot days and in arousal (produced by loud noises or strange persons near the animals' sleeping cage or during siamang song bouts). In the same situations, the characteristic body odor of the siamang is especially strong and conspicious.

It can then easily be detected from a distance of several meters in an outdoor cage. However, no kind of marking behavior has been observed.

DISCUSSION

Specialized skin areas with histoanatomical structures quite similar to that reported here occur in many primates, and even the axillary organ in humans (and the African apes) is thought to be comparable to these specialized glandular areas (Montagna and Ellis, 1960). Sternal glands are usually thought to play an important role in olfactory communication. In many primates (Table I) and other mammals (Fadem and Cole, 1985; Holst, 1974; Kawamichi and Kawamichi, 1979; Martin, 1968; Poglayen-Neuwal, 1962, 1966; Schultze-Westrum, 1965; Sprankel, 1962), they are known to be used in elaborate and characteristic ritualized patterns of behavior. These often very conspicious motor acts can be comprised within the term "marking behavior." I failed to find any kind of marking behavior in several groups of captive siamang which were the subject of a behavioral study (Geissmann, 1986), and no such behavior has been reported in other studies on the behavior of wild (Chivers, 1974, 1976; Chivers and Raemaekers, 1980) and captive (Fox, 1972) siamang groups.

The association of intensive body odor and high secretory activity of the sternal gland suggests that the gland is mainly responsible for the characteristic body odor of the siamang. The odorous qualities of the secretion and the evidently increased – although not quantified – glandular activity on hot days give some hints of the functional importance of the gland. First, a primary function can be supposed to lie in olfactory communication, although a more precise specification of this function cannot yet be made. Odor-producing skin glands in mammals are usually thought to provide information on the subject's species, sex, and individual identity, the state of its physiological processes, or its propensity to perform a certain behavior (see the reviews by Eisenberg and Kleiman, 1972; Mykytowycz, 1970). Second, the gland may possibly play a role in thermoregulation through increased "sweating" under high-temperature conditions, but in view of the small size of the glandular area, one would not expect this to be more than a minor role.

It is interesting to note that the main secretory activities of the siamang's sternal gland seem to occur in situations virtually identical to those of the axillary organ of humans: during elevated temperatures and stress (Montagna, 1981, 1982). We may therefore suppose that, apart from the already mentioned structural similarities, an analogy in functions may also exist to some degree. Although the function and importance of the axillary

organ are still not very well understood, it has been suggested that it may play a role in thermoregulation (Keele *et al*., 1982; Montagna, 1962) and in olfactory communication (Hold and Schleidt, 1977; Labows *et al*., 1982; Russell, 1976; Schleidt and Hold, 1982a,b), but evidence for the latter function still seems inconclusive (Doty 1981; Doty *et al*., 1978).

The possibility that the various sternal glands of primates are homologous characters, as has previously been proposed (Epple and Lorenz, 1967; Schaffer, 1940), has yet to be subjected to a critical examination. Hill *et al*. (1959) suggested that medioventral glandular fields in primates seem to be a "retained prirnitive feature inherited from tupaioid ancestors." If this is true, the sternal gland of the siamang probably derived from a gland which was initially used for marking behavior and only subsequently altered in function. Thus, the sternal gland seems to have changed in functional convergence with the axillary organ which had independently evolved in hominoids. In extant hominoids, the axillary organ is apparently present only in the genera *Gorilla* (Brinkmann, 1909; Ellis and Montagna, 1962; Klaar, 1924; Straus, 1950), *Pan* (Brinkmann, 1909, 1923-1924, 1926; Ford and Perkins, 1970; van Gelderen, 1926; Klaar, 1924; Montagna and Yun, 1963), and *Homo* (Montagna, 1982; Schiefferdecker, 1922; Talke, 1903), none of which is reported to possess a sternal gland. In the orang-utan, a sternal gland is found chiefly in juvenile males and has been described as being in a stage of regressive evolution (Weber and Abel, 1928; Wislocki and Schultz, 1925).

It is generally believed that, compared with the situation in strepsirhine primates (Bourlière *et al*., 1956), specialized skin glands are relatively rare in haplorhine monkeys and especially in apes, where olfactory communication appears to play a less preeminent role (Marler, 1965). In a review article on communication of apes, it has even been stated that "apart from genital secretions, there seems to be no evidence of the discrete glands specialized to produce chemical signals that are commonly found in prosimians and are also present in both platyrrhine and catarrhine monkeys" (Marler and Tenaza, 1977, p. 968). However, such specialized skin glands as the sternal glands and the axillary organs have now been reported to occur in every hominoid genus. The use hominoids actually make of olfactory communication may still be underestimated at present. In addition, this report suggests that, even in the relatively well-documented apes, external anatomy still remains incompletely described and deserves further attention. For instance, Pocock's (1925, 1944) account suggests that a sternal gland probably occurs in at least one other hylobatid species. This possibility is currently being investigated.

ACKNOWLEDGMENTS

I thank the officials of the Zürich Zoo (Drs. P. Weilenmann and C. R. Schmidt) and of the Zoo "Seeteufel"/Studen (H. Steiner and H.-J. Dietrich)

for their permission to study the captive siamangs in their care, Dr. P. Lüps for his help in procuring the skin samples, Prof. Dr. V. Ziswiler for the opportunity to use the technical facilities for histological studies, and U. Brauchli-Witt, Dr. M. Haffner, Dr. R. Landolt, Dr. C. Raboud, and E. Wenk for their help in preparing histograms and photomicrographs. K. and U. Rathfelder kindly shared their own observations with me. For helpful comments on the histological section of the paper, I am grateful to Dr. M. Haffner. B. Andrew kindly corrected my English.

REFERENCES

Arao, T., and Perkins, E. (1969). The skin of primates. XLIII. Further observations on the Philippine tarsier (*Tarsius syrichta*). Am. J. phys. Anthrop. 31: 93-96.

Bearder, S. K., and Doyle, G. A. (1974). Ecology of bushbabies *Galago senegalensis* and *Galago crassicaudatus*, with some notes on their behaviour in the field. In Martin, R. D., Doyle, G. A., and Walker, A. C. (eds.), Prosimian Biology, Duckworth, London, pp. 109-130.

Bernstein, I. S. (1965). Activity patterns in a cebus monkey group. Folia primatol. 3:211-224.

Bourlière, F., Petter, J.-J., and Petter-Rousseaux, A. (1956). Le dimorphisme sexuel de la glande sous-angulo-maxillaire d'*Avahi laniger* (Gmelin). Mém. Inst., Sd. Madagascar, Sér. A. 10: 299-302.

Box, H. O. (1975). Quantitative studies of behaviour within captive groups of marmoset monkeys (*Callithrix jacchus*). Primates 16: 155-174.

Brandes, G. (1939). Buschi. Vom Orang-Säugling zum Backenwülster, Quelle und Meyer, Leipzig.

Brinkmann, A. (1909). Ueber das Vorkommen von Hautdrüsenorganen bei den anthropomorphen Affen. Anat. Anzeiger 34: 513-520.

Brinkmann, A. (1923-1924). Nachlese zu meinen Hautdrüsenuntersuchungen. Bergens Museums Aarbok, Naturvidenskabelig Raekke 1923-24 (3): 1-36.

Brinkmann, A. (1926). Ein paar Bemerkungen zu den neusten Untersuchungen der Hautdrüsen bei den anthropomorphen Affen. Anat. Anzeiger 62: 236-237.

Chivers, D. J. (1974). The siamang in Malaya: A field study of a primate in tropical rain forest. Contrib. Primatol. 4: 1-335.

Chivers, D. J. (1976). Communication within and between family groups of siamang (*Symphalangus syndactylus*). Behaviour 57: 116-135.

Chivers, D. J. (1977). The lesser apes. In Prince Rainier III of Monaco and Bourne, G. H. (eds.), Primate Conservation, Academic Press, New York, pp. 539-598.

Chivers, D. J., and Gittins, S. P. (1978). Diagnostic features of gibbon species. Int. Zoo Yearbook 18: 157-164.

Chivers, D. J., and Raemaekers, J. J. (1980). Long-term changes in behaviour. In Chivers, D. J. (ed.), Malayan Forest Primates: Ten Years' Study in a Tropical Rain Forest, Plenum Press, New York, pp. 209-260.

Christen, A. (1974). Fortpflanzungsbiologie und Verhalten bei *Cebuella pygmaea* und *Tamarin tamarin* (Primates, Platyrrhina, Callithricidae). Fortschritte der Verhaltensforschung (Beihefte zur Z. Tierpsychol.) 14, Parey, Berlin and Hamburg.

Clark, A. B. (1978). Olfactory communication, *Galago crassicaudatus*, and the social life of prosimians. In Chivers, D. J., and Joysey, K. A. (eds.), Recent Advances in Primatology 3: Evolution, Academic Press, London, pp. 109-117.

Clark, A. B. (1986). Contrast in communication of *Galago crassicaudatus* and *G. garnettii*. Primate Report 14: 216.

Claussen, R. (1982). Beobachtungen zur Aufzucht eines männlichen Weissgesichtsakis (*Pithecia pithecia*) im Familienveband. Zool. Garten (NF) 52: 188-194.

Dandelot, P. (1960). Gracieux et merveilleux acrobates: Les gibbons. Sci. Nature 39: 2-12.

Dixson, A. F. (1976). Effects of testosterone on the sternal cutaneous glands and genitalia of the male greater galago (*Galago crassicaudatus crassicaudatus*). Folia primatol. 26: 207-213.

Dobroruka, L. J. (1972). Social communication in the brown capuchin *Cebus apella*. Int. Zoo Yearbook 12: 43-45.

Doty, R. L. (1981). Olfactory communication in humans. Chem. Senses 6: 351-376.

Doty, R. L., Orndorff, M. M., Leyden, J., and Kligman, A. (1978). Communication of gender from human axillary odors: Relationship to perceived intensity and hedonicity. Behav. Biol. 23: 373-380.

Dugmore, S. J. (1986). Behavioural observations on a pair of captive white-faced saki monkeys (*Pithecia pithecia*). Folia primatol. 46: 83-90.

Eisenberg, J. F. (1976). Communication mechanisms and social integration in the black spider monkey, *Ateles fusciceps robustus*, and related species. Smithson. Contr. Zool. 213, Smithsonian Institution, Washington, D.C.

Eisenberg, J. F., and Kleiman, D. G. (1972). Olfactory communication in mammals, Annu. Rev. Ecol. Syst. 3: 1-32.

Ellis, R. A., and Montagna, W. (1962). The skin of primates. VI. The skin of the gorilla (*Gorilla gorilla*). Am. J. phys. Anthrop. 20: 79-94.

Epple, G. (1972). Social communication by olfactory signals in marmosets. Int. Zoo Yearbook 12: 36-42.

Epple, G., and Lorenz, R. (1967). Vorkommen, Morphologie und Funktion der Sternaldrüse bei den Platyrrhini. Folia primatol. 7: 98-126.

Fadem, B. H., and Cole, E. A. (1985). Scent-marking in the grey short-tailed opossum (*Monodelphis domestica*). Anim. Behav. 33: 730-738.

Fiedler, W. (1957). Beobachtungen zum Markierungsverhalten einiger Säugetiere. Z. Säugetierk. 22: 57-76.

Ford, D. M., and Perkins, E. M. (1970). The skin of the chimpanzee. In Bourne, G. H. (ed.), The Chimpanzee, Vol. 3, Karger, Basel, pp. 82-119.

Fox, G. J. (1972). Some comparisons between siamang and gibbon behaviour. Folia primatol. 18: 122-139.

Gartlan, J. S., and Brain, C. K. (1968). Ecology and social variability in *Cercopithecus aethiops* and *C. mitis*. In Jay, P. C. (ed.), Primates. Studies in Adaptation and Variability, Holt, Rinehart and Winston, New York, pp. 253-292.

Gautier, J.-P., and Gautier, A. (1977). Communication in Old World monkeys. In Sebeok, T. A. (ed.), How Animals Communicate. Indiana University Press, Bloomington and London, pp. 890-964.

Geissmann, T. (1986). Mate change enhances duetting activity in the siamang gibbon (*Hylobates syndactylus*). Behaviour 96: 17-27.

Groves, C. P. (1984). A new look at the taxonomy and phylogeny of the gibbons. In Preuschoft, H., Chivers, D. J., Brockelman, W. Y., and Creel, N. (eds.), The Lesser Apes: Evolutionary and Behavioural Biology. Edinburgh University Press, Edinburgh, pp. 542-561.

Hall, L. S., and Gordon, G. (1982). The throat-pouch of the yellow-bellied bat, *Taphozous flaviventris*. Mammalia 46: 247-252.

Hanson, G., and Montagna, W. (1962). The skin of primates. XII. The skin of the owl monkey (*Aötus trivirgatus*). Am. J. phys. Anthrop. 20: 421-430.

Hill, W. C. O. (1944). An undescribed feature in the drill (*Mandrillus leucophaeus*). Nature 153: 199.

Hill, W. C. O. (1951). Epigastric gland of *Tarsius*. Nature 167: 994.

Hill, W. C. O. (1954). Sternal glands in the genus *Mandrillus*. J. Anat. 88: 582.

Hill, W. C. O. (1955). Primates. Comparative Anatomy and Taxonomy. II. Haplorhini: Tarsioidea, Edinburgh University Press, Edinburgh.

Hill, W. C. O. (1960). Primates. Comparative Anatomy and Taxonomy. IV. Cebidae, Part A, Edinburgh University Press, Edinburgh.

Hill, W. C. O. (1970). Primates. Comparative Anatomy and Taxonomy. VIII. Cynopithecinae: *Papio, Mandrillus, Theropithecus*, Edinburgh University Press, Edinburgh.

Hill, W. C. O., Porter, A., and Southwick, M. D. (1952). The natural history, endoparasites and pseudo-parasites of the tarsiers (*Tarsius carbonarus*) recently living in the Society's menagerie. Proc. zool. Soc. Lond. 122: 79-119.

Hill, W. C. O., Appleyard, H. M., and Auber, L. (1959). The specialized area of skin glands in *Aotes* Humboldt (Simiae, Platyrrhini). Trans. Roy. Soc. Edinburgh 63: 535-551.

Hold, B., and Schleidt, M. (1977). The importance of human odour in non-verbal communication. Z. Tierpsychol. 43: 225-238.

Holst, D. V. (1974). Social stress in the three-shrew: Its causes and physiological and ethological consequences. In Martin, R. D., Doyle, G. A., and Walker, A. C. (eds.), Prosimian Biology, Duckworth, London, pp. 389-411.

Hood, C. S., and Smith, J. D. (1984). Histology of a sexually dimorphic integumentary gland in *Macroglossus lagochilus* (Chiroptera: Pteropodidae). J. Mammal. 65: 1-9.

Izawa, K. (1978). A field study of the ecology and behavior of the black-mantle tamarin (*Saguinus nigricollis*). Primates 19: 241-274.

Jolly, A. (1966). Lemur Behavior. A Madagascar Field Study, University of Chicago Press, Chicago.

Kawamichi, T., and Kawamichi, M. (1979). Spatial organization and territory of tree shrews (*Tupaia glis*). Anim. Behav. 27: 381-393.

Keele, C. A., Neil, E., and Joels, N. (1982). Samson Wright's Applied Physiology, 13th ed., Oxford University Press, Oxford.

Kinzey, W. G. (1981). The titi monkey, genus *Callicebus*. In Coimbra-Filho, A. F., and Mittermeier, R. A. (eds.), Ecology and Behavior of Neotropical Prinates, Brazilian Academy of Sciences, Rio de Janeiro, pp. 241-276.

Klaar, J. (1924). Ueber die axillaren Knäueldrüsen der Affen. Z. Anal. EntwGesch. 72: 609-627.

Kleiman, D. G., and Mack, D. S. (1980). Effects of age, sex, and reproductive status on scent marking frequencies in the golden lion tamarin, *Leontopithecus rosalia*. Folia primatol. 33: 1-14.

Klein, L., and Klein, D. (1971). Aspects of social behaviour in a colony of spider monkeys *Ateles geoffroyi* at San Francisco Zoo. Int. Zoo Yearbook 11: 175-181.

Labows, J. N., McGinley, K. J., and Kligman, A. M. (1982). Perspectives on axillary odor. J. Soc. cosmet. Chem. 34: 193-202.

Loireau, J. N., and Gautier-Hion, A. (in press). Olfactory making behaviour in guenons: ecological and evolutionary correlates. In Bourlière, F., Gautier, J.-P., Gautier-Hion, A., and Kingdon, J. (eds.), Biology of the African Guenons, Cambridge University Press, Cambridge.

Machida, H., Perkins, E., and Hu, F. (1967). The skin of primates. XXXV. The skin of the squirrel monkey (*Saimiri sciurea*). Am. J. phys. Anthrop. 26: 45-54.

Mack, D. S., and Kleiman, D. G. (1978). Distribution of scent marks in different contexts in captive lion tamarins *Leontopithecus rosalia* (Primates). In Rothe, H., Wolkers, H.-J., and Hearn, J. P. (eds.), Biology and Behaviour of Marmosets, Eigenverlag Hartmut Rothe, Göttingen, pp. 181-188.

Marler, P. (1965). Communication in monkeys and apes. In De Yore, I. (ed.), Primate Behavior. Field Studies of Monkeys and Apes, Holt, Rinehart and Winston, New York, pp. 544-584.

Marler, P., and Tenaza, R. R. (1977). Signaling behavior of apes with special reference to vocalization. In Sebeok, T. A. (ed.), How Animals Communicate, Indiana University Press, Bloomington, pp. 965-1033.

Marshall, J. T., and Marshall, E. R. (1976). Gibbons and their territorial songs. Science 193: 235-237.

Marshall, J. T., Sugardjito, J., and Markaya, M. (1984). Gibbons of the *lar* group: Relationships based on voice. In Preuschoft, H., Chivers, D. J., Brockelman, W. Y., and Creel, N. (eds.), The Lesser Apes: Evolutionary and Behavioural Biology, Edinburgh University Press, Edinburgh, pp. 533-541.

Martin, R. D. (1968). Reproduction and ontogeny in tree-shrews (*Tupaia belangeri*), with reference to their general behaviour and taxonomic relationships. Z. Tierpsychol. 25: 409-495, 505-532.

Mason, W. A. (1966). Social organization of the South American monkey *Callicebus moloch*: A preliminary report. Tulane Stud. Zool. 13: 23-28.

Mertl-MilIhollen, A. S. (1979). Olfactory demarcation of territorial boundaries by a primate - *Propithecus verreauxi*. Folia primatol. 32: 35-42 (1979).

Montagna, W. (1962). The Structure and Function of Skin, 2nd ed., Academic Press, New York.

Montagna, W. (1972). The skin of nonhuman primates. Am. Zool. 12: 109-124.

Montagna, W. (1981). The evolution of human skin. Giorn. Ital. Dermatol. Venereol. 116: 139-143.

Montagna, W. (1982). The evolution of human skin. In Chiarelli, A. B., and Corruccini, R. S. (eds.), Advanced Views in Primate Biology, Springer, Berlin, pp. 35-41.

Montagna, W. (1985). The evolution of human skin(?). J. Hum. Evol. 14: 3-22.

Montagna, W., and Ellis, R. A. (1960). The skin of primates. II. The skin of the slender loris (*Loris tardigradus*). Am. J. phys. Anthrop. 18: 19-44.

Montagna, W., and Ellis, R. A. (1963). New approaches to the study of the skin of primates. In Buettner-Janusch, J. (ed.), Evolutionary and Genetic Biology of Primates, Academic Press, New York, Vol. 1, pp. 179-196.

Montagrsa, W., and Yun, J. S. (1962). The skin of primates. VIII. The skin of the anubis baboon (*Papio doguera*). Am. J. phys. Anthrop. 20: 131-142.

Montagna, W., and Yun, J. 5. (1963). The skin of primates. XV. The skin of the chimpanzee (*Pan satyrus*). Am. J. phys. .4nthrop. 21: 189-204.

Mootnick, A. (1984). Census of gibbons in North America. In Preuschoft, H., Chivers, D. J., Brockelman, W. Y., and Creel, N. (eds.), The Lesser Apes: Evolutionary and Behavioural Biology, Edinburgh University Press, Edinburgh, pp. 61-73.

Moynihan, M. (1966). Communication in the titi monkey, *Callicebus*. J. Zool. (London) 150: 77-127.

Mykytowycz, R. (1970). The role of skin glands in mammalian communication. In Johnson, J. W., Moulton, D. G., and Turk, A. (eds.), Advances in Chemoreception. Vol. 1. Communication by Chemical Signals, Appleton-Century-Crofts, New York, pp. 327-360.

Parakkal, P., Montagna, W., and Ellis, R. A. (1962). The skin of primates. XI. The skin of the white-browed gibbon (*Hylobates hoolock*). Anat. Rec. 143: 169-178.

Perkins, E. M. (1966). The skin of primates. XXXI. The skin of the black-collared tamarin (*Tamarinus nigricollis*). Am. J. phys. Anthrop. 25: 41-70.

Perkins, E. M. (1968). The skin of primates. XXXVI. The skin of the pigmy marmoset – *Callithrix* (= *Cebuella*) *pygmaea*. Am. J. phys. Anthrop. 29: 349-364.

Perkins, E. M. (1969a). The skin of primates. XXIV. The skin of Goeldi's marmoset (*Callimico goeldii*). Am. J. phys. Anthrop. 30: 231-250.

Perkins, E. M. (1969b). The skin of primates, XLI. The skin of the silver marmoset – *Callithrix* (=*Mico*) *argentata*. Am. J. phys. Anthrop. 30: 361-388.

Petter, J.-J. (1965). The lemurs of Madagascar. In DeVore, I. (ed.), Primate Behavior. Field Studies of Monkeys and Apes, Holt, Rinehart and Winston, New York, pp. 292-319.

Petter, J.-J., Albignac, R., and Rumpler, Y. (1977). Mammifères lémuriens (Primates prosimiens). Faune de Madagascar, Vol. 44, Orstom, CNRS, Paris.

Pocock, R. 1. (1952). The external characters of the catarrhine monkeys and apes. Proc. Zool. Soc. Lond. 1925: 1479-1579.

Pocock, R. I. (1944). Pectoral gland in apes and monkeys. Nature (London) 153: 381.

Poglayen-Neuwall, I. (1962). Beiträge zu einem Ethogramm des Wickelbären (*Potos flavus* Schreber). Z. Säugetierk. 27: 1-44.

Poglayen-Neuwall, I. (1966). On the marking behavior of the Kinkajou (*Potos flavus* Schreber). Zoologica (Stuttgart) 51: 137-141.

Richard, A. (1974). Patterns of mating in *Propithecus verreauxi verreauxi*. In Martin, R. D., Doyle, G. A., and Walker, A. C. (eds.), Prosimian Biology, Duckworth, London, pp. 49-74.

Romeis, B. (1968). Mikroskopische Technik, Oldenbourg Verlag, München and Wien.

Rumpler, Y., and Andriamiandra, A. (1971). Etude histologique des glandes de marquage de la face antérieure du cou des Lémuriens malgaches. CR. Soc. Biol. Paris 165: 436-441.

Russell, J. M. (1976). Human olfactory communication. Nature (London) 260: 520-522.

Sanderson, I. T. (1949-1950). A brief review of the mammals of Suriname (Dutch Guiana), based upon a collection made in 1938. Proc. Zool. Soc. Lond. 199: 755-789.

Sauer, E. G. F. (1974). Zur Biologie der Zwerg- und Riesengalagos. Z. Kölner Zoo 17(2): 67-84.

Schaffer, J. (1940). Die Hautdrüsenorgane der Säugetiere mit besonderer Berücksichtigung ihres histologischen Aufbaues and Bemerkungen dber die Proktodäaldrüsen, Urban and Schwarzenberg, Berlin and Wien.

Schiefferdecker, P. (1922). Die Hautdrüsen des Menschen und der Säugetiere, ihre biologische und rassenanatomische Bedeutung, sowie die Muscularis sexualis. Zoologica (Stuttgart) 27(72): 1-154.

Schifter, H. (1968). Zucht und Markierungsverhalten von Wollaffen im Zoologischen Garten Zürich. Zool. Gart. (NF) 36: 107-132.

Schilling, D. (l984a). Gibbons in European zoos, with notes on the identification of subspecies of *concolor* gibbon. In Preuschoft, H., Chivers, D. J., Brockelman, W. Y., and Creel, N. (eds.), The Lesser Apes: Evolutionary and Behavioural Biology, Edinburgh University Press, Edinburgh, pp. 51-60.

Schilling, D. (l984b). Letter to the editor. Primate Rep. 11: 36.

Schleidt, M., and Hold, B. (1982a). Human odour and identity. In Breipohl, W. (ed.), Olfaction and Endocrine Regulation, IRL Press, London, pp. 181-194.

Schleidt, M., and Hold, B. (1982b). Human axillary odour: Biological and cultural variables. In Steiner, J. E. (ed.), Determination of Behaviour by Chemical Stimuli, IRL Press, London, pp. 91-104.

Schultz, A. H. (1921). The occurrence of a sternal gland in organg-utan. J. Mammal. 2: 194-196.

Schultze-Westrum, 1. (1965). Innerartliche Verständigung durch Düfte beim Gleitbeutler *Petaurus breviceps papuanus* Thomas (Marsupialia, Phalangeridae). Z. Vergl. Physiol. 50: 151-220.

Schwarz, W. (1937). Die Sternaldrüse bei den Klammeraffen, Ateles. Morph. Jahrbuch 79: 600-633.

Sekulic, R., and Eisenberg, J. F. (1983). Throat-rubbing in red howler monkeys (*Alouatta seniculus*). In Muller-Schwarze, D., and Silverstein, R. M. (eds.), Proc. 3rd Int. Symp. Chem. Signals Vertebrates, Plenum Press, New York, pp. 347-350.

Sprankel, H. (1962). Histologie und biologische Bedeutung eines jugulo-sternalen Duftdrüsenfeldes bei *Tupaia glis* Diard 1820. Verh. Dtsch. Zool. Ges. (Saarbrücken) 1962: 198-206.

Straus, W. L. (1950). The microscopic anatomy of the skin of the gorilla. In Gregory, W. K. (ed.), The Anatomy of the Gorilla, Columbia University Press, New York, pp. 213-221.

Sutcliffe, A. G., and Poole, T. B. (1978). Scent marking and associated behaviour in captive common marmosets (*Callithrix jacchus jacchus*) with a description of the histology of scent glands. J. Zool. (London) 185: 41-56.

Talke, L. (1903). Ueber die grossen Drüsen der Achselhöhlenhaut des Menschen. Arch. Mikrosk. Anat. 61: 537-555.

van Gelderen, J. J. (1962). Einige Mitteilungen über das Achselhöhlenorgan des Chimpanse. Anat. Anzeiger 6l: 407-409.

Weber, M., and Abel, O. (1928). Die Säugetiere. Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia. Band 2: Systematischer Teil, Fischer, Jena, 2nd ed.

Wislocki, G. B., and Schultz, A. H. (1925). On the nature of modifications of the skin in the sternal region of certain primates. J. Mammal. 6: 236-244.

Young, O. P. (1982). Tree-rubbing behavior of a solitary male howler monkey. Primates 23: 303-306.

Zeller, U. (1984). Die funktionelle Anatomie der Gulardrüse von *Propithecus verreauxi coquereli* (Indriidae, Primates). In Deutsche Ges. Säugetierk, 58. Hauptversammlg, Kurzfassungen der Vorträge u. Posterdemonstr., Parey, Hamburg, p. 61.

Zeller, U. (1986). Die Gulardrüse von *Propithecus* (lndriidae, Primates). Z. Säugetierk. 51: 1-15.