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Steroid secretion in siamang (Symphalangus syndactylus) skin glands

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Chemical composition of secretions of skin glands in hominoid primates have apparently not been analyzed previously, except for the axillary secretions of humans. This paper reports on skin secretions of siamangs (*Symphalangus syndactylus*), a species of gibbons or small apes from Southeast Asia. Secretions were collected and radioimmunoassays (RIA) were carried out in order to check for the presence of the following three steroid hormones: Dehydroepiandrosterone (DHEA), Androstenedione, and Testosterone. This study presents first evidence that high hormone concentrations occurring especially in the sternal area cannot be the result of a simple filtration of hormones out of the blood plasma, but must be the result of a more complex accumulation process. Particularly androstenedione appears to be highly concentrated in the sternal gland. Our findings further support the view that sternal glands in gibbons and axillary glands in humans and African apes may fulfil similar functions, and shed some light on the origin of the axillary organ. We speculate that the accumulation of steroid hormones in siamang skin glands may play a role in olfactory communication.

Introduction

Many primates and other mammals possess specialized glandular concentrations in the sternal area that are commonly used for marking behaviour (Epple, 1986; Geissmann, 1987a). Among hominoids, sternal glands apparently occur only in the gibbons or small apes (Hylobatidae) and orangutans (genus *Pongo*) of Southeast Asia (Brandes, 1939: Geissmann, 1986, 1987a; Geissmann and Hulftegger, 1994; Schultz, 1921; Wislocki and Schultz, 1925). In orangutans and one gibbon species, the siamang (Symphalangus syndactylus), sternal gland secretions exhibit a strong, genus-specific odour (Geissmann, 1987a and unpublished observations), as do axillary gland secretions in gorillas and humans. In Asian apes, sternal glands apparently are not used for any kind of marking behaviour (Geissmann, 1986, 1987a; Geissmann and Hulftegger, 1994), and this generally appears to apply to axillary glands in African apes and humans, as well. The sternal glands of gibbons show similarities to the axillary glands of humans and the African apes in both the macroscopic aspect of the glands and their microscopic structure (Geissmann and Hulftegger, 1994). In addition, secretory activity of both types of glands appears to increase in similar situations: during stress and in response to elevated temperature (Geissmann, 1986, 1987a, b; Geissmann and Hulftegger, 1994). In some of gibbons (individuals several species), concentrations of coloured pores can be found in the axillary region. Dried glandular secretion of redbrown colouration can be seen in the skin pores or near the hair roots. These fields are usually connected

with the sternal glands (Geissmann and Hulftegger, 1994).

The human axillary gland is generally believed to play a role in olfactory communication (Hold and Schleidt, 1977; Labows, *et al.*, 1982; Russell, 1976; Schleidt and Hold, 1982a, b; Stoddart, 1990). The functions of the sternal glands in Asian apes, on the other hand, are completely unknown.

Chemical compositions of these glandular secretions have apparently not been analyzed previously, except for the axillary secretions of humans. The axillary area is probably the most conspicuous scent-producing specialization of the human skin and the only one generally recognized as a "scent organ" by dermatologists, zoologists, and chemists (Schaal and Porter, 1991). Axillary secretions contain lipids (mainly fatty acids and steroids) and approximately 10% protein (including a number of enzymes) (e.g. Gower and Ruparelia, 1993; Gower, *et al.*, 1985, 1988; Labows, *et al.*, 1982; Labows, 1988).

Much of the musk-like or urine-like smell that is reported from the human axilla (see for example review in Stoddart, 1990) is caused by at least two odorous Δ^{16} -androgen steroids: 3α -androstenol (5α androst-16-en- 3α -ol) and 5α -androstenone (5α androst-16-en- 3α -ol) (Brooksbank, *et al.*, 1974; Claus and Alsing, 1976; Gower, *et al.*, 1985). The former, an alcohol, has a musky odour and "is not altogether unpleasant", whereas the latter, a ketone, confers the disagreeable and dominant odour that has been characterized as "urine", "sweaty" and "perspiration" in odour description studies (Labows et al., 1982, p. 199f). Studies utilizing radioimmunoassay techniques have demonstrated significant differences in concentration of 5α -androstenone in men and women (Bird and Gower, 1981; Gower et al., 1985).

Freshly-secreted apocrine sweat is odourless (Hurley and Shelley, 1960; Shelley *et al.*, 1953); it contains little or no 3α -androstenol or 5α -androstenone, but cholesterol, dehydroepiandrosterone sulfate, and androsterone sulfate (Labows *et al.*, 1979). Although the two sulfated steroids are closely related to the odorous steroids in their chemical structure, it is unknown whether either of these is a precursor of the latter (Gower and Ruparelia, 1993; Labows *et al.*, 1982).

Because of the numerous similarities between sternal and axillary glands mentioned above, and because gibbons are relatively closely related to humans (Geissmann, 1995b, 2003), it has previously been suggested that both glands also share similarities in their functions (Geissmann, 1987a; Geissmann and Hulftegger, 1994). If this were the case, we should expect that gibbon sternal glands, like human axillary glands, produce steroid hormones and their derivates. In order to test this hypothesis, we collected skin secretions of several siamangs (*S. syndactylus*) and checked for the presence of steroid hormones by radioimmunoassays (RIA).

Radioimmunoassays of steroid hormones are routinely carried out on human urine samples at the Kinderspital of Zürich. The following three hormones have been analyzed for this study because their antisera were easily available, and because of their supposed function in olfactory communication in humans and pigs (e.g. Claus and Alsing, 1976): dehydroepiandrosterone (DHEA; 3 β -hydroxyandrost-5-en-17-one), androstenedione (4-androstene-3,17-dione), and testosterone (17 β -hydroxy-androst-4-en-3-one).

Materials and methods

The following age classes for captive gibbons were recognized in this study: infants 0-2 years of age; juveniles 2.1-4 years; subadults 4.1-6 years; adults more than 6 years, as proposed by Geissmann (1995a).

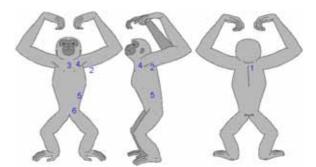
Between July 1986 and January 1991, a total of 36 samples (including 6 control blanks which will be described below) were collected for analysis using a radioimmunoassay technique. All samples of skin secretions were collected by one of us (T.G.). Most of them were collected from anaesthetized animals, the other stem from tame animals or from zoo animals that died less than 24 hours before examination. It is important to note that the study animals were not sedated for the purpose of this investigation, but for management reasons (e.g. for veterinary checks, veterinary treatment, or transport). Several zoos were asked to indicate when such intervention was scheduled, and visits were timed accordingly.

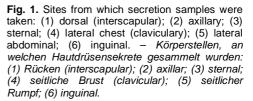
The study animals were kept at the Zoo Hellabrunn in Munich (Germany) and at Zürich Zoo (Switzerland). Two individuals were examined twice at an interval of 0.9 and 2.6 years, respectively. The data from such repeated examinations were analyzed separately. Table 1 lists the number of samples collected at the two institutions. For most animals, secretion samples were collected in the sternal and axillary areas, but for some individuals additional samples were taken from other body parts (Fig. 1). One sample was collected in the circumgenital area. This area is not labelled in the figure, because it was pooled with the samples of the inguinal area in order to increase the sample size for each area. All samples labelled as "dorsal" refer to the area between the shoulder blades in the midsagittal plane.

Table 1. Number of samples of skin secretions collected for this study. The numbers in brackets represent the numbers of individuals. – *Anzahl und Herkunft der Proben von Hautdrüdsensekreten. Zahlen in Klammern bezeichnen die Anzahl der untersuchten Individuen.*

Samples	Munich Zoo	Zürich Zoo	Total
Adults and subadults	9 (2)	14 (3) ^a	23 (5)
Juveniles and infants	-	7 (3)	7 (3)
Control blanks	-	6	6
Total	9 (2)	27 (6)	36 (8)

^(a) Includes 3 plasma samples





Unless otherwise stated, samples were collected in a standardized way: After the animal was sedated, sterile compresses (TELFA, Kendall Company Boston, USA) were moistened with pure ethanol (per analysis, 99%) and rubbed with slight pressure 12 times over a selected spot of the animal's skin. In order to avoid contamination of the samples with human steroid hormones, a fresh pair of medical gloves was used for the collection of each sample.

Six control samples of various hormone concentrations (Table 2), types and sampling procedures were used. Three unmanipulated TELFA

compresses were used as control samples (Nos. 1-3, Table 2). The highest steroid concentrations found by RIA in any of the three control samples were then subtracted from the hormone values of most secretion samples (exceptions described below) to eliminate the "background noise" due to the sensitivity of the RIA technique. This procedure will be referred to as "standard correction" in the following text.

			concentrations		
controls	s (n	g/sample).1	- Hormonkonze	entratio	nen
der Kor	ntrol	lstichprober	n (ng/Stichprobe)		

	•			
Control sample No.	DHEA ²	Androstene dione	Testo- sterone	
1	0.8	0.7	0.8	
2	1.1	0.6	0.4	
3	0.8	0.8	0.4	
4	-0.9	8.3	-3.0	
5	0.7	3.0	2.2	
6	0.0	0.3	0.0	

⁽¹⁾ See text for a description of the different types of controls and explanation for negative values in control No. 4.

⁽²⁾ DHEA = Dehydroepiandrosterone

In the following cases, special corrections were necessary: In a few instances, an opportunity for collecting secretion samples arose when no gloves where available. Although the author then washed his hands with great care before collecting every single sample, the TELFA compresses possibly became contaminated to some degree with human steroid hormones during the rubbing procedure. In order to measure the amount of possible contamination, two samples were collected from adjacent areas on the back of the same animal; one sample was collected with gloves, the other one without gloves. The difference in the hormone concentrations between the two samples is shown in Table 2 as control No. 4. In two hormone concentrations (DHEA and Testosterone), the value for the sample collected without gloves was lower than the value for the sample collected with gloves (resulting in negative values in Table 2), which is the opposite of what should be expected if the samples had been contaminated by the investigator. The sample collected without gloves had considerably higher concentrations only for androstenedione, probably as a result of contamination. This possible amount of androstenedione contamination was subtracted from all samples that had been collected without gloves.

In another control test, the author intensively manipulated one new TELFA compress with ethanol. The androstenedione and testosterone (but not the DHEA) levels measured on this control sample (No. 5, Table 2) are slightly higher than the "standard corrections" described above. The difference may be due to contamination. The testosterone concentration found in this control sample has accordingly been subtracted from all samples collected without gloves. For androstenedione, the higher correction value described above (control No. 5) has been used for samples collected without gloves. For DHEA, the "standard correction" measured on control sample 2 was the highest correction value found; therefore, it was also used for the samples collected without gloves.

A small amount of pure exudate from the sternal gland was collected in a test tube directly from the fur of a study animal. In this case, an empty test tube served as a control sample (control No. 6, Table 2).

Because the exact amount of secretion collected with the rubbing method could not be determined, hormone concentrations are given in ng per compress, unless stated otherwise.

A case of unusually profuse sternal secretion was once observed in the adult male siamang "Bohorok", which had been hand-reared at the Zürich Zoo, and was more than 11 years old in October 1986, when the following observation was made in front of the outdoor cage. The male was observed to exhibit both sudden agitation and a discharge of sternal exudate, probably caused by the sight of its former caretaker (U. Rathfelder) carrying an infant siamang (which also had to be hand-reared). The adult male alternatingly bit into the wire-mesh of his cage and stared at Mrs. Rathfelder, who was standing a few meters away from the cage talking to other staff members. The typical odour of the siamang became very strong, and sternal secretion could actually be seen trickling down from the male's sternal gland. This was the only situation in which pure, fresh secretion from the sternal gland of a gibbon was collected during this study.

All Radioimmunoassays (RIA) were carried out at the Kinderspital Zürich, using antisera purchased from bioMérieux. After adding tracer amounts of [3H]dehydroepiandrosterone (DHEA), [3H]androstenedione, or [3H]testosterone to monitor recovery, samples were extracted by methylene chloride extraction. All immunoassays used the dextran-coated charcoal separation method.

Pearson correlations between age and hormone concentrations were calculated using StatView version 5.0.1 (SAS Inst.) on an Apple PowerBook G4 computer. The occurrence of a linear relationship between the dependent variables (hormone concentrations) and the independent variable (age) was tested with a *t*-test, and the occurrence of a correlation between the variables was tested with a *z*-test.

Results

Table 3 lists the hormone concentrations measured in each sample. Table 4 presents summary statistics of the hormone concentrations in the sternal region and the axillary region, respectively, for adult animals (and one subadult) of each sex separately. Within most hormone sex classes, considerable variation in the hormone concentrations is apparent from comparison of the minimum and maximum values. Although the samples are too small to permit a statistical test for sex differences, the values in Table 4 at least suggest such differences in some cases: Both sternal and axillary DHEA appear to be higher in females than in males.

The findings in Table 4 refer only to secretions collected in the sternal and the axillary areas. In several individuals, a few secretion samples were also collected in other areas of the skin. Figure 2 shows the average hormone concentrations of adult and subadult females and males in all the six sampled skin areas. By far the highest concentrations are found in the sternal area.

Figure 3 shows hormone concentrations in the sternal and axillary area plotted against age of the study animals. For this figure, all adult animals (i.e. animals older than 6 years) were pooled. All plots show a positive correlation between hormone concentration and the age of the siamangs, with one exception: axillary DHEA has a negative correlation with the age of the study animals. Of these correlations, however, only one is statistically significant: Sternal androstenedione concentration exhibits a linear relationship with age (t-test, p < 0.05) and is positively correlated with age (r=0.71, n=8; ztest, p < 0.05). All other correlations are not significant (p>0.05), although the correlation between sternal testosterone and age is close to significance (t-test, *p*<0.06; *r*=0.69, *n*=8; *z*-test, *p*<0.06).

Table 3.	Hormone	concentrations	in	sian	nang
samples.1	– Horm	nonkonzentration	en	in	den
Siamang-	Stichprobei	n.			

Age, Sex	Sample Type	DHEA	Andro- stene- dione	Testo- sterone
ad. M ("Bo-	pure exudate	5.2	143.2	2.2
horok")	sternal	20.1	255.2	15.0
	axillary	7.1	14.9	2.2
	inguinal	3.8	23.8	6.6
	dorsal	4.3	7.6	1.4
	plasma	(694)	(635)	(992)
ad. F	sternal	31.8	0	2.7
	axillary	28.2	0	0.4
	plasma	(280)	(238)	(82)
ad. F	sternal	23.8	205.2	12.7
	axillary	6.2	11.8	2.7
	inguinal	3.0	7.8	3.2
	dorsal	3.7	5.0	2.0
	plasma	(481)	(288)	(144)
ad. F	sternal	22.2	327.7	10.5
	axillary	8.1	11.4	0.6
	inguinal		19.4	7.3
lat. abdomen		9.2	12.9	4.8
sad. M,	sternal	22.6	67.6	10.5
4.52 years	claviculary	10.3	6.6	4.1
	axillary	8.0	10.2	0.7
	circumgenital	11.8	8.0	4.4
	lat. abdomen	11.0	5.6	4.0
juv. M,	sternal	9.3	12.59	1.1
2.27 years	axillary	13.8	19.2	0.5
	inguinal	12.8	8.6	5.1
	dorsal	11.6	8.4	4.2
inf. M,	sternal	34.6	1.3	0.6
1.51 years	axillary	29.7	0	0.4
inf. M, 0.64 years	sternal	11.3	0	0.8

⁽¹⁾ All hormone concentrations were corrected as described above (Animals and Methods section). Hormone concentrations were measured in ng/sample, except plasma samples (values in brackets), which are presented as ng/dl. Abbreviations: ad. = adult; sad. = subadult; juv. = juvenile; inf. = infant; M = male; F = female; lat. = lateral.

Samples	Males Females										
	Ν	Mean	SE	Min.	Max.	Ν	Mean	SE	Min.	Max.	
Sternal:											
DHEA	2	21.4	1.3	20.1	22.6	3	25.9	3.0	22.2	31.8	
Androstenedione	2	161.4	93.8	67.6	255.2	3	177.6	95.6	0	327.7	
Testosterone	2	12.7	2.3	10.5	15.0	3	14.8	7.7	2.7	29.1	
Axillary:											
DHEA	2	7.6	0.5	7.1	8.0	3	14.2	7.1	6.2	28.2	
Androstenedione	2	12.5	2.4	10.2	14.9	3	7.7	3.9	0	11.8	
Testosterone	2	1.4	0.7	0.7	2.2	3	1.2	0.7	0.4	2.6	

Table 4. Means of hormone concentrations in the sternal and axillary samples (ng/sample) of male and female animals.¹ – *Mittelwerte der Hormonkonzentrationen in den Stichproben der Sternal- und Axillar-Region von männlichen und weiblichen Siamangs.*

⁽¹⁾ Abbreviations: N = number or individuals; SE = standard error.

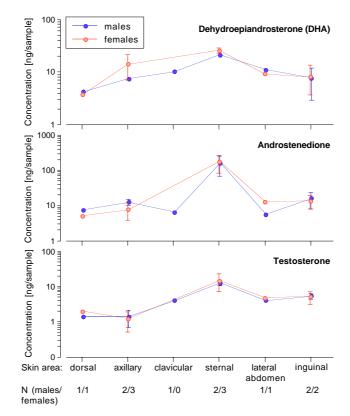


Fig. 2. Average concentrations of three steroid hormones in six skin areas of male and female siamangs. Error bars are standard errors. – *Mittelwerte (und Standardfehler) der Hormonkonzentrationen in den Stichproben von sechs verschiedenen Hautregionen von männlichen und weiblichen Siamangs. Die unterste Zeile gibt die Stichprobengrösse an (Männchen/Weibchen).*

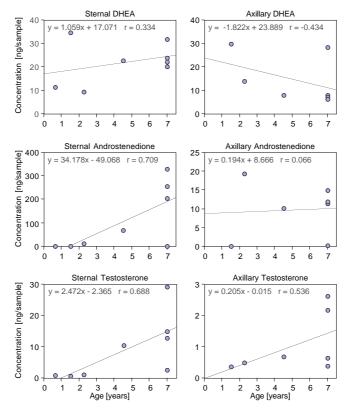


Fig. 3. Concentrations of three steroid hormones in the sternal and axillary areas plotted against age of the study animals. Adult siamangs (i.e. animals older than 6 years) are pooled. – *Konzentrationen von drei Steroidhormonen in den sternalen und axillaren Hautregionen, aufgetragen gegen das Alter der untersuchten Siamangs. Erwachsene Tiere (d. h. Tiere, die älter als sechs Jahre waren) wurden zusammengefasst.*

Of particular importance for the interpretation are the hormone concentrations determined for the sample of pure sternal secretion of the adult male siamang "Bohorok".

One to three droplets of pure exudate were collected through the wire-mesh directly from the tame animal's fur with a piece of fresh paper nappy. The hormone concentrations determined from this sample are shown in Table 5 (line 1). Although the exact amount of secretion is not known, the quantity of one to three droplets was determined to correspond to $2 \cdot 10^{-4} - 9 \cdot 10^{-4}$ dl. This range is a maximum estimate obtained by repeatedly measuring drops of water that were large enough to fall down from a syringe opening of 1 mm in width. The collected exudate droplets of the male siamang were, if anything, smaller than that. With the above estimate of exudate can be calculated (Table 5, line 2). These

are conservative values, because the quantity of exudate may be smaller (but certainly not larger) than assumed here.

For comparison, three samples of siamang blood plasma were collected. One of the samples stems from the same male as the pure sternal secretion. The hormone concentrations in the plasma samples show some variation (Table 5, line 3), but even the highest concentrations in the plasma samples are several times lower than the most conservative concentration estimate of the sternal sample. The difference amounts to a factor of at least 2.4 for testosterone, but up to 250 for androstenedione (Table 5, line 4).

On the other hand, the hormone concentrations in the siamang plasma samples are roughly similar to those of humans (adapted from Labhart *et al.*, 1986, p. 523), except for the relatively high concentrations of androstenedione in the siamangs (Table 5, line 5).

Table 5. Determination of hormone concentration in the sternal secretion in an adult male siamang ("Bohorok"). – Bestimmung der Hormonkonzentration im Sternalsekret des erwachsenen Siamang-Männchens "Bohorok".

			DHEA	Androstenedione	Testosterone
1.	Concentration in secretion sample (ng / sample), ad. siamang male "Bohorok"		5.2	143.2	2.2
2.	Concentration in secretion sample (ng / dl), estimate,	Maximum	26 000	716 000	11 000
	ad. siamang male "Bohorok"	Minimum	5 800	159 100	2 400
3.	Concentration in peripheral plasma (ng / dl):				
	ad. siamang female "Gaspa"	22 Jan. 1987	280	238	82
	ad. siamang female "Gaspa"	30 Aug. 1989	481	288	144
	ad. siamang male "Bohorok"	30 Aug. 1989	694	635	992
4.	Accumulation factor, ad. siamang male "Bohorok"	Minimum	8.4	250.6	2.4
5.	Concentration in peripheral plasma (ng / dl) (Labhart <i>et al.</i> , 1986, p. 523)				
	Men (20-40 years)		130-1270	60-230	300-1300
	Women (20-40 years)		140-1250	50-330	4-70

Discussion

Chemical analysis of the secretion of specialized skin glands has been carried out on only a few primate species. Apart from studies on humans, steroids have been found as a major component of glandular secretion only in exudates from the brachial glands of Nycticebus (Alterman, 1989). It is possible, however, that steroids have simply not been examined in previous studies. Certain steroid hormones produced in the axilla are thought to be of major importance in human olfactory communication. The present study shows that steroid hormones are accumulated in the skin glands of at least one gibbon species, the siamang (S. syndactylus). This steroid secretion is not sex-specific. It is most pronounced in the sternal gland and, to a lesser extent, in the axillary region. Secretory activity may not be fully developed in immature siamangs.

The samples we collected consisted primarily of dried secretion rubbed from the skin with ethanol-

soaked compresses. Although the hormone concentrations of these samples can be compared with each other, they give no information on the hormone concentration in the pure fresh secretion. Such information, albeit as a rough approximation, was derived from our single sample of pure sternal exudate collected from the adult male siamang "Bohorok". Hormone concentrations in this exudate are several times higher than the concentrations found in the peripheral plasma of the same siamang. This finding is of importance for determining the mechanism of how the hormones are secretioned in the sternal gland of siamangs: The high sternal hormone concentrations cannot be the result of a simple filtration of hormones out of the blood plasma, but must be the result of a more complex accumulation process. This accumulation is by a factor of at least 2.4 and 8.4 in testosterone and DHEA, respectively (conservative estimates), but by a factor of at least 250 in androstenedione in the male siamang studied here.

Because skin secretions have been collected in a standardized way, they can be compared with the sternal sample of the adult male "Bohorok", with the latter serving as a standard. All relative hormone concentrations that are as high or even higher than those of the standard (i.e. "Bohorok") probably result from an accumulation process as well. In addition, they suggest the presence of actively secreting glandular fields.

Especially high hormone concentrations (higher than those of "Bohorok") are found in the sternal samples of three adult females, one subadult male and one infant male (see Table 3). Hormone concentrations surpassing those of "Bohorok" are almost completely restricted to DHEA (only one adult female also had higher androstenedione concentrations). In at least two of these animals, DHEA accumulation apparently occurs in the axillary region as well (1 adult female and 1 infant male).

Because the system of skin glands in gibbons and the axillary glands of humans and the African apes share numerous similarities, it has previously been speculated that they may also serve related functions (Geissmann, 1987a; Geissmann and Hulftegger, 1994). Our study presents first evidence that steroid hormones are accumulated in siamang sternal and (to a lesser extent) axillary glands. Although the functions of this steroid accumulation remain speculative, our results fully support our initial hypothesis, thus providing further support to the view that siamang sternal glands and human axillary glands may exhibit similar functions, including a role in olfactory communication.

It is unlikely that all the similarities between the system of skin glands in gibbons and the axillary glands of humans and the African apes evolved independently in the two clades. It has not previously been possible to explain the phylogenetic origin of the axillary glands. The results presented in this study suggest that axillary glands and sternal glands may have both evolved from the same phylogenetic precursor. Secretion of steroid hormones probably already occurred in the common ancestor of gibbons, the great apes and humans (i.e., the Hominoidea).

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Zusammenfassung

Steroid-Ausscheidung durch Hautdrüsen beim Siamang (Symphalangus syndactylus)

Über die chemische Zusammensetzung von Hautdrüsensekreten bei Menschenaffen liegen bisher anscheinend keine Studien vor. In der vorliegenden Arbeit wurden Hautsekrete des Siamangs (Symphalangus syndactylus), des grössten Vertreters der südostasiatischen Gibbons oder kleinen Menschenaffen, untersucht. Sekrete von Individuen verschiedener Altersklassen und beider Geschlechter wurden gesammelt und mit Hilfe von Radioimmunoassays (RIA) auf das Vorhandensein der folgenden drei Steroidhormone überprüft: Dehydroepiandrosteron (DHEA), Androstenedion, und Testosteron. Die Resultate zeigen, dass vor allem in der Sternalregion hohe Hormonkonzentrationen auftreten. Diese können nicht die Folge einfacher Filtration aus dem Blutplasma sein, sondern müssen durch einen komplexeren Anreicherungsprozess zustande gekommen sein. Unsere Studie erbringt zudem erste Hinweise darauf, dass die Sternaldrüsen der Gibbons und die Achselhöhlendrüsen der afrikanischen Menschenaffen und des Menschen ähnliche Funktionen erfüllen könnten. Dies wirft möglicherweise auch ein erstes Licht auf den evolutiven Ursprung der Achselhöhlendrüsen. Es wird vermutet, dass die Anreicherung von Steroidhormonen in bestimmen Hautdrüsenregionen der Siamangs eine Rolle in der olfaktorischen Kommunikation spielen könnte.