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Callous scalation in female agamid lizards (*Stellio* group of *Agama*) and its functional implications

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Abstract. The presence of precloacal and/or abdominal callous glands in females of the *Stellio* group within the genus *Agama* Daudin, 1802 has been established in *A. agorensis* (Stoliczka, 1872), *caucasia* (Eichwald, 1831), *himalayana* (Steindachner, 1869), *nupta* De Filippi, 1843, *pakistanica* Baig 1989, *stellio* (Linnaeus, 1758) and *tuberculata* (Hardwicke & Gray, 1827). The possible functional meaning of this find is discussed. A comment is made on the nomenclatural availability of *Stellio* Laurenti, 1768.

Key words. Reptilia, Sauria, Agamidae, *Stellio* group of *Agama*, precloacal/abdominal callous glands, territoriality, Middle East.

Introduction

Two types of macroscopic epidermal holocrine glands are found in the Agamidae, i. e. femoral/inguinal follicular glands and precloacal/abdominal callous glands. The second type is unique to the agamid¹⁾ lizards and is found in the former collective genus *Agama*, now consisting of the genera *Agama* (s. str.), *Trapelus*, *Pseudotrapelus*, the *Stellio* group (see below) and in *Xenagama* (Moody 1980).

Terminology: The homology and thus terminology of the glands has been greatly confused by taxonomists and comparative morphologists, who mostly failed to recognize the different structure and exact anatomical position of both gland types. In most Australian agamids the follicular glands of the females extend onto the posterior abdominal area. They have been termed “preanal glands” (Cogger 1975, Houston 1978) which confuses them terminologically with callous glands situated on the anterior margin of the cloaca. Similarly, Jullien & Renous-Lecuru (1973a, b) surveyed the epidermal glands of the Lacertilia without distinguishing between both gland types and consequently inaccurately characterizing numerous genera. The first descriptions, however, proved to be correct: Boulenger (1885) distinguished “true” femoral and preanal pores clearly from callous pore-like swellings of preanal scales. Harris (1963) called them “preanal pads” in *Agama agama* and thus likewise differentiated them from “femoral pores” which are absent in that species.

Occurrence in females: In this paper we restrict ourselves to the second type of the forementioned glands, i. e. the precloacal/abdominal callous glands in female agamids. Boulenger (1885) called them “anal pores” and attributed them to the male sex only while describing different species of *Agama*. Nikolsky (1915) used the same terminology and associated these glands also only with males. Smith (1935) called

¹⁾ We do not adopt the view of Frost & Etheridge (1989) to regard agamids as a chamaeleonid subfamily, for reasons explained by Böhme (1990).

them "callose preanal" and "callose abdominal scales" and likewise did not link them with the female sex.

Later on Terentyev & Chernov (1949), Klausewitz (1954), Anderson (1963), Minton (1966), Daan (1967), Mertens (1969), Peters (1971), Moody (1980), Beutler & Frör (1980), Ananyeva et al. (1981), Beutler (1981), Orlova (1981a, b), Ananyeva & Atayev (1984), Baig (1989) and many others dealt with the species of *Agama* (*Stellio* group) but except Terentyev & Chernov (1949) and Baig (1989) all of them attributed the character callous glands to the male sex only.

Terentyev & Chernov (1949) mentioned callous glands in a reduced form only at a precloacal position in *Agama* (now *Trapelus*) *sanguinolenta* (see also Orlova 1981b), *A. erythrogastra* and *A. himalayana* whereas in other species including *caucasia* and *lehmanni* these would be confined to males (Terentyev & Chernov 1949).

Material and Results

The holdings of agamids of the *Stellio* group within *Agama* have been studied in the Alexander Koenig Zoological Research Institute and Museum (ZFMK) at Bonn and in the Pakistan Museum of Natural History (PMNH) at Islamabad. We found that females of no less than 8 species of the *Stellio* group possess callous glands not only at precloacal but also at abdominal positions (Fig. 1). All these females are listed in table 1. Out of 28 females of *A. stellio* only 2 show a slight tendency to develop callosities suggesting that true, functioning callous glands are restricted to males in this species. The same seems to be the case in *melanura*, *stoliczkana*, *lehmanni* and *erythrogastra*, but the sample sizes are too small to draw any conclusion. Out of 17 *caucasia* females 4, of 25 *tuberculata* 1 from Afghanistan, of 3 *nupta* 1, and of 6 *himalayana* 3 females exhibit callosities (see Table 1). These data suggest that callosities are present in a number of females of these species except *A. tuberculata*, where the only specimen from Afghanistan could be an exception, or the Afghan population may be different from that of Pakistan, India or Nepal. More material from Afghanistan could clarify this problem.

A. agrorensis and *A. pakistanica* females hold a special position in this study, for out of 10 *agrorensis* females 7 show callosities at precloacal and at least 3 at abdominal positions; in *A. pakistanica* all 10 females exhibit precloacal callosities, while abdominal callosity can be found only in 2 of them (see Table 1).

Discussion

The functional meaning of both follicular and callous glands in lizards in respect to pheromone secretions is not very well studied and understood (Cooper & Vitt 1986). The evidence presented by Cole (1966) and by Peters (1969) suggests that the secretions of follicular glands represent olfactorial cues for interspecific and intraspecific interactions, e. g. territoriality. Smith (1935), Harris (1964), Stamps (1977), Orlova (1981a, b), Beutler (1981), Daniel (1983) and many others have suggested territorial behaviour in agamids. These authors mostly attribute territoriality to the males which do most of the fighting defending their territories due to their hierarchical rank (Stamps (1977). Only Schmidt & Inger (1957) reported on females that were likewise defending their home ranges. Madel & Klockenhoff (1972) observed that *A.*

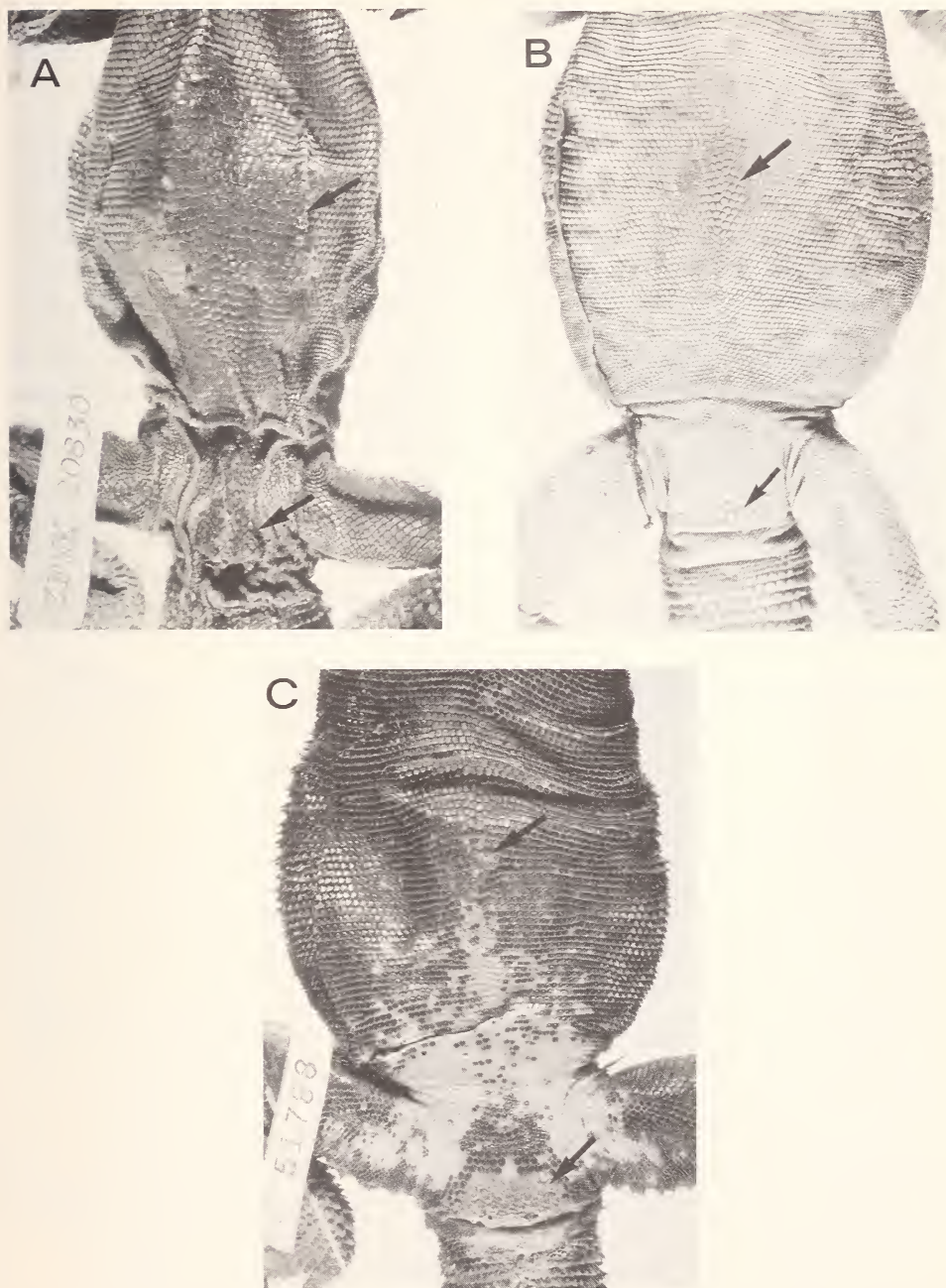


Fig. 1: Precloacal and abdominal callous scales in agamids; A: *Agama caucasia* female from Shaspur River, Fars/Iran (ZFMK 20830); B: *Agama caucasia* female from Kelat, Baluchistan/Pakistan (ZFMK 26314); C: *Agama pakistanica* female from Nomal, Gilgit/Pakistan (ZFMK 51788, paratype).

caucasia females in Afghanistan fought for egg laying sites and defended these sites vigorously. Langerwerf (in Orlova 1981a) noted even that *A. caucasia* females were able to detect their individual egg laying sites after oviposition and continued to defend them even after having removed from them up to 6 days!

Although there is no direct evidence of a relationship between territoriality and callous glands, we think that it is the most plausible functional explanation. This view is corroborated by an interesting observation in *A. pakistanica*, where 100 % of the females bear callous scales: They are living always in pairs rather than in groups of one dominant male with several females (Baig 1989). This latter system characterizes *A. tuberculata* and *A. melanura*, and the absence of callosities in their females fits our view.

Daniel (1983) described male *A. tuberculata* as "territorial" and "pungacious" in the breeding season. The pungent secretions could be the product of the callous glands and may serve for marking the territory. Moreover, the absence of both

Table 1: List of female *Agama* (*Stellio* group) where callosities were found. + = present; — = absent; SMF = Senckenberg Museum Frankfurt/M.; PMNH = Pakistan Natural History Museum Islamabad; UF = Florida State Museum Gainesville; ZFMK = Museum Koenig Bonn.

Cat. no.	Species	Precloacal callosity	Abdominal callosity	Origin
UF 72781	<i>pakistanica</i>	+	+	Pakistan
PMNH 535	<i>pakistanica</i>	+	—	Pakistan
PMNH 538	<i>pakistanica</i>	+	—	Pakistan
PMNH 548	<i>pakistanica</i>	+	—	Pakistan
PMNH 551	<i>pakistanica</i>	+	—	Pakistan
PMNH 552A	<i>pakistanica</i>	+	—	Pakistan
PMNH 552	<i>pakistanica</i>	+	—	Pakistan
PMNH 553	<i>pakistanica</i>	+	—	Pakistan
PMNH 554	<i>pakistanica</i>	+	—	Pakistan
PMNH 135	<i>pakistanica</i>	+	+	Pakistan
ZFMK 51788	<i>pakistanica</i>	+	+	Pakistan
PMNH 261	<i>agorensis</i>	+	—	Pakistan
PMNH 560	<i>agorensis</i>	+	—	Pakistan
PMNH 524	<i>agorensis</i>	+	+	Pakistan (Kashmir)
PMNH 516	<i>agorensis</i>	+	+	Pakistan (Kashmir)
SMF 63201	<i>agorensis</i>	+	+	Pakistan
SMF 63188	<i>agorensis</i>	+	—	Pakistan
SMF 63202	<i>agorensis</i>	+	+	Pakistan
PMNH 540	<i>himalayana</i>	+	—	Pakistan
PMNH 137	<i>himalayana</i>	+	—	Pakistan
SMF 10150	<i>himalayana</i>	+	—	Afghanistan
ZFMK 8615	<i>tuberculata</i>	+	—	Afghanistan
ZFMK 8606	<i>caucasia</i>	—	+	Afghanistan
ZFMK 8603	<i>caucasia</i>	+	—	Afghanistan
ZFMK 26314	<i>caucasia</i>	+	+	Pakistan
ZFMK 20830	<i>caucasia</i>	+	+	Iran
ZFMK 2682	<i>nupta</i>	+	+	Afghanistan
ZFMK 46338	<i>stellio</i>	+	—	Syria
ZFMK 47855	<i>stellio</i>	+	—	Syria

callosities and territorial behaviour in juveniles further supports our view. However, the situation found in *A. agrorensis* where 70 % of the females show callous glands (see Table 1) does not fit the one observed in *A. pakistanica*: *agrorensis* is usually seen in groups containing more than one female (Baig, pers. obs.). In this species, "territoriality" in females would not primarily concern mating sites, but rather the defence of resources (food, nest sites, shelter etc.), as it is also the case with non-dominant, subordinate males.

Cole (1966) mentioned that secretions of femoral glands have different compositions in different species of lizards. According to Cooper (1985) and Cooper & Vitt (1986) males can olfactorically even distinguish between other individual males and females. We think that it is plausible that also the callous glands of the two sexes of one species could produce pheromone secretions of different compositions. If this assumption will prove to be correct, at least 2 different functions of callous glands in *Agama* (*Stellio* group) are likely:

1. The much more common male-related defence of the territory as a mating site avoiding confrontation with rivals, due to the hierarchical position of the respective male, and

2. in some species (see Table 1) a female-related cue of a different olfactorial (= chemical) quality for either defending own territories without conflicting with that of a male (thus making pair-binding possible), or for defending — and recovering after some time! — egg-laying sites.

Further research including field and laboratory work is necessary to either verify or reject our hypotheses concerning the olfactorial communication in these lizards.

Appendix

Nomenclatural note: We owe an explanation to the reader, why we still use *Agama* and not *Stellio* as the genus name of the lizards dealt with above. In his thesis, Moody (1980) divided the collective genus *Agama* into six distinct genera: *Agama* (s. str.), *Trapelus*, *Pseudotrapelus*, *Brachysaura*, *Xenagama* and *Stellio*. Apart from the fact that the content of *Stellio* sensu Moody (1980) is still under debate (in- or exclusion of the Afro-Arabian clade, see Joger 1991), the name *Stellio* Laurenti, 1768 is not at all available. As was also pointed out to the junior author by Frost (in litt. Oct. 1989), Laurenti (1768) included eight species in his genus *Stellio* without fixing a type, but *Lacerta stellio* Linnaeus was not among them. Stejneger (1932) therefore, to avoid nomenclatural instability, designated as type species for *Stellio* Laurenti the unidentifiable *S. saxatilis*, thus making *Stellio* an unavailable nomen dubium. Because of this situation, Böhme (1981) already used "*Stellio*" explicitly not as a formal taxon, but only as informally characterizing a certain bundle of related species. The same is done by us here. It would be premature to fix already the next available name for the species group, because 1. there is evidence that the type species of *Acanthocercus* Fitzinger, 1843, i. e. *A. cyanogaster*, is not at all congeneric with the Palaearctic clade (Joger 1991), and 2. also the type of *Laudakia* Gray, 1845, i. e. *A. tuberculata*, within the Palaearctic clade, is aberrant in hemipenial characters (Böhme 1988), thus requiring further study.

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Zusammenfassung

Bei Weibchen der *Agama*-Arten der *Stellio*-Gruppe *agorensis*, *caucasica*, *himalayana*, *nupta*, *pakistanica*, *stellio* und *tuberculata* wurden präkloakale und/oder abdominale Kallusdrüsen nachgewiesen, deren funktionelle Bedeutung diskutiert wird. Es wird die Hypothese aufgestellt, daß die Kallus-Sekrete der Weibchen von denen der Männchen chemisch verschieden seien und zur Markierung eigener Reviere und/oder von Eiablageplätzen benutzt werden könnten. Anhangsweise wird die nomenklatorische Verfügbarkeit des Gattungsnamens *Stellio* Laurenti, 1768 kommentiert.

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