Review

Evolution and role of the follicular epidermal gland system in non-ophidian squamates

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Abstract. Many lizard and amphisbaenian lineages possess follicular glands in the dermis of the inner thighs and/or the area anterior to the cloaca. These tubular glands produce a holocrine secretion that finds its way to the external world through pore-bearing scales (femoral and/or preanal pores). Secretions are composed of proteins and many lipophilic compounds that may function as chemosignals in lizard and amphisbaenian communication. In recent years, we have begun to develop an understanding of the adaptive significance of these secretions, and they are currently thought to play an important role in a variety of processes in these animals. While it appears that epidermal gland secretions function in intra- and interspecific recognition and territoriality, research has focused largely on their role in mate assessment. Despite these recent studies, our knowledge on the true role of the chemicals found in epidermal secretions remains poorly studied, and there are many possible avenues for future research on this topic. Here, we review the literature on the follicular epidermal glands of non-ophidian squamates and provide a first taxon-wide overview of their distribution.

Keywords: amphisbaenians, ancestral state reconstruction, chemical communication, chemosignals, lizards, pheromones, pores, secretions.

Introduction

Nearly half a century ago, Charles J. Cole (1966a) wrote a seminal review on epidermal glands in lizards, tallying what was known on their functional significance, and pointing out promising avenues for new research. In the years that followed, and increasingly so in the past decade, studies along these lines have revealed the prominent roles epidermal gland secretions play in the biology of lizards and amphisbaenians. The present review acts as an update to Cole's work, discussing the extensive scientific progress made since his initial review,

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and provides a framework for the numerous possible areas of future research in the field.

Initially, we focus on the chemical composition of epidermal gland secretions and how these vary among individuals, sexes, taxa and habitats. We then discuss the presence of epidermal glands in extant non-ophidian squamates, and provide hypotheses for the evolution of the epidermal gland system based on an ancestral state reconstruction. Based on the literature available, we address the potential roles that different chemosignals play in non-ophidian squamate social communication, and discuss possible patterns in the overall investment and structural composition of the "epidermal gland system": a collective name for follicular epidermal glands, pores and secretions. We proceed to detail the possible functions of epidermal glands, focusing on territoriality and dominance as well as their role in mate assessment. Finally, we provide some ideas for future research in the field.

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Terminology and classification

Two broad types of holocrine secretory structures occur in the dermis of lizards and worm lizards: generation and follicular glands. Follicular glands are often considered to be more specialized structures that have evolved from the more primitive generation glands (Maderson and Chiu, 1970; Baig and Böhme, 1991). Generation glands can be found in Cordylidae (Van Wyk and Mouton, 1992) and Gekkonidae (Maderson, 1967; Maderson and Chiu, 1970), and are modified skin scales which display the typical sequence of epidermal cell layers and occur as patches of glandular scales in the femoral, precloacal, antebrachial, inguinal, or dorsal epidermal regions of the body (fig. 1) (Maderson, 1967, 1968; Van Wyk and Mouton, 1992). Within cordylids, the glandular material is produced in a modified epidermal β layer and each time the scale goes through the shedding cycle, new glandular material is produced in the β -layer of the new epidermal generation (Van Wyk and Mouton, 1992). In contrast to generation glands, the follicular exocrine glands are typically tubular and embedded in the dermis, and the produced secretions protrude through pores as solid plugs (fig. 2) (Cole, 1966a). Based on their exact anatomical position on the lizards' or amphisbaenians' body, follicular glands are often referred to in the literature as preanal, precloacal, or femoral glands. Because of confusing terminology encountered in the literature (e.g., "preano-femoral pores" by Loveridge, 1947; "femoro-anal pores" by Gerlach and Canning, 1996; "femoro-precloacal pores" by Grismer, 2002), we decided not to discriminate between specific follicular glands, but to include them all in this study within the same category: epidermal glands.

Gland morphology

Many non-ophidian squamates possess a number of epidermal glands that secrete a waxy substance through pores (Antoniazzi et al., 1993; Imparato et al., 2007). These epidermal structures are predominantly located on the preanal abdominal area (preanal pores), or on the ventral surface of each thigh (femoral pores) (figs 1a and 2a) (Mason, 1992; Arnold and Ovenden, 2004). In most lizards, pores open in the centre of a modified scale (Imparato et al., 2007), although in some agamid species pores open between scales (Cole, 1966b; Witten, 1982). The number and morphology of pores, as well as their distribution on the body (Kluge, 1976; Witten, 1993), varies extensively across different groups (Pincheira-Donoso, Hodgson and Tregenza, 2008; Mouton, Van Rensburg and Van Wyk, 2010; Baeckens et al., 2015). There



Figure 1. Photomicrographs of (a) the ventral region of the thigh of a cordylid lizard, showing the patches of generation glands and a row of epidermal pores, and (b) a cross-section through a protruding multiple-layer type generation gland of *Cordylus minor* (both pictures obtained from Mouton, Flemming and Broeckhoven, 2014 with permission) (EP, epidermal pore; GG, generation gland; MG, mature generation layer). This figure is published in colour in the online version.



Figure 2. Picture of (a) the cloacal region of a male *Lacerta agilis* adult, showing epidermal pores with protruding secretion, and (b) a longitudinal section of a follicular epidermal gland of *Amphisbaena alba* (latter picture obtained from Antoniazzi et al., 1993 with permission) (EP, epidermal pore; GB, glandular body; S, secretion). This figure is published in colour in the online version.

is also variation between sexes, as females may either not have epidermal pores at all, or may have pores with reduced sizes (Cole, 1966b). As such, they have been used extensively as taxonomic characters in lizards and amphisbaenians (Linnaeus, 1758; Duméril and Bibron, 1834; Arnold and Ovenden, 2004).

The epidermal glands form into a follicular unit after an invagination of the stratum germinativum, and are continuous with the generalized body epidermis (Maderson, 1972). Epidermal glands can be tubulo-acinar structured as in *Acanthodactylus scutellatus*, *Acanthodactylus boskianus* (Khannoon, Dollahon and Bauer, 2013), *Gekko gecko* (Chiu and Maderson, 1975), and *Hemidactylus falviridis* (Chauhan, 1986); tubular as in *Hemidactylus bowringii* (Chiu and Maderson, 1975), *Uromastiyx hardwickii* (Athavale et al., 1977); tubulealveolar as in *Liolaemus* sp. (Valdecantos, Martinez and Labra, 2014); or branched tubular as in Crotaphytus collaris (Cole, 1966b). The glands of most species are embedded in the dermis of the scales anterior to their pores connecting the pores by elongated ducts (Blasco, 1975; Chiu and Maderson, 1975; Chauhan, 1986; Imparato et al., 2007; Khannoon, Dollahon and Bauer, 2013), or can be situated immediately deep to the pores as observed in C. collaris (Cole, 1966b). Secretory cells in the glands undergo four different stages of differentiation: (1) formation of the secretory granules, (2) the accumulation of these granules, (3) disintegration and (4) formation of the solid secretory plug, which protrudes externally (Khannoon, Dollahon and Bauer, 2013). The secretions of the epidermal glands in lizards and amphisbaenians are under the control of androgenic hormones and start to differentiate at the onset of sexual maturity (Chiu and Maderson, 1975; Díaz, AlonsoGómez and Delgado, 1994; Chamut, Valdez and Manes, 2009; Mouton et al., 2010). Van Wyk (1990) observed an increase in the tubule diameter of the follicular epidermal glands of male *Cordylus polyzonus* during the reproductive season, and found a significant correlation with seasonal variation in testis volume.

Chemical composition

At the time of Cole's publication little was known on the chemical nature of the secretion produced by epidermal glands, other than that it "contained a fatlike substance" - which was based on observations on but a handful lizard species. With this limited knowledge, it is not surprising that hypotheses on the possible functions of these secretions were difficult to test. Now, we know that the gland secretions are made up of a variety of both proteins and lipids (Fergusson, Bradshaw and Cannon, 1985; Alberts, 1991; Weldon, Flachsbarth and Schulz, 2008). Alberts (1990) found that proteins were four times more prevalent in the secretions of the desert iguana (Dipsalis dorsalis) than were lipids. It has been postulated that these proteins may transmit chemical information (Alberts, Phillips and Werner, 1993; Martín and López, 2000), function in individual recognition (Glinsky and Krekorian, 1985; Alberts, 1992a), serve as a matrix to retard the evaporation of the secretion similar to the major urinary proteins (MUPs) in the urine of Mus domesticus (Humphries et al., 1999), or be involved in the cornification of the secretion (Cole, 1966a). Despite the presence of proteins in gland secretions and their importance in other groups such as amphibians and mammals (Toyoda et al., 2004; Wyatt, 2014), it is thought that lipids play a greater role in reptilian chemical communication, and they have thus been studied in much greater detail (Mason, 1992; Martín and López, 2011). Indeed, most research on chemicals from epidermal gland secretions does not even attempt to analyse the composition of proteins within the secretion (Escobar, Labra and Niemeyer, 2001; Louw et al., 2007, 2011; Font et al., 2012). We postulate three reasons for this: (1) shared ancestry, not ecological factors, appears to account for much of the variability in the protein secretion composition in studied species, as proteins are inheritable traits (Alberts, 1991). However, we believe that this assumption is what makes the study of proteinaceous chemosignals interesting. It is much more straightforward to perform evolutionary studies on proteins than lipid mixtures, because proteins likely evolve to species-specificity during or after speciation, contributing to reproductive isolation and avoidance of hybridization. This species-specificity can be easily studied by inspecting the amino acid sequence of the involved proteins. (2) Proteins have a lower degree of molecular diversity than lipids, which decreases the potential information content of a chemosignal (Martín and López, 2000). However, this can be argued as well, since the concentration of the secreted proteins could change with features like dominance or health status. Furthermore, in mice MUPs make up a very diverse set of proteins with a high level of polymorphism, which allows for individual recognition (Hurst et al., 2001). So proteins could allow for kin recognition, individual recognition and even more temporary characteristics, since protein expression is a versatile mechanism that can experience shifts in what proteins are expressed as well as shifts in concentration. Moreover, only a few amino acids have to be different to influence the binding of a protein to a receptor. Although protein compounds could be lesser candidates to transfer information on age, health status, dominance and territoriality, we should be cautious stating that proteins have lower potential information content. (3) In contrast to the protein fraction of epidermal secretions, which are non-volatile by nature, only volatile lipids are likely to be detected by tongue-flicks into the air (Alberts and Werner, 1993), which facilitates opportunities for comparative behavioural studies. We believe

this reason to be the most convincing, although many species can detect proteins (Alberts and Werner, 1993; Weldon, Flachsbarth and Schulz, 2008). We therefore believe that the study of proteins as potential sources of chemical communication should be considered more fully in the future.

The standard procedure for analysing the lipophilic fraction of the gland secretion is gas chromatography-mass spectrometry (GC-MS). The general composition of chemicals across different groups is often quite similar, with steroids and carboxylic acids being found in every family of lizards studied (Weldon, Flachsbarth and Schulz, 2008), usually as major components in the secretion. Often, cholesterol is the predominant molecule found in the lipophilic fraction, and it has been hypothesized to provide information on individual identity, and to stabilize the other molecules in the secretion (Escobar et al., 2003; Louw et al., 2007, 2011; Khannoon et al., 2011b). Table 1 illustrates an updated account of the lipophilic fraction of epidermal gland secretions in lizards and amphisbaenians, including those species covered by Weldon and colleagues (2008) and those studied following their review. Most of our knowledge comes from lacertid lizards, while some research has evaluated other families (table 1). As we begin to amass a more detailed knowledge on the secretions of epidermal glands in other families, we can assess the degree to which certain chemicals are phylogenetically constrained, and the degree to which others may be environmentally dependent. For example, while alcohols are present, and even comprise a major portion of the secretion in many families, they have not been reported at all in Liolaemidae (Escobar, Labra and Niemeyer, 2001; Escobar et al., 2003). Only with more studies which take into account phylogenetic relationships and ecological conditions can we begin to piece together a coherent explanation for patterns such as this.

What are epidermal glands and their secretions for?

Historically, five hypotheses have been proposed concerning the function of epidermal gland secretions (Cole, 1966a): (1) the secretion securely fastens males to females during copulation, (2) the secretion stimulates or quiets females, facilitating mating opportunities, (3) the glands are vestigial and serve no present function, (4) the secretion has a signalling function and is used by males to mark their territory (e.g., Aragón, López and Martín, 2003; Moreira, López and Martín, 2006; Carazo, Font and Desfilis, 2007), and (5) the secretion is used for self-, sex and species recognition and orientation (e.g., Alberts, 1992a; Alberts and Werner, 1993; Barbosa et al., 2006). Of all five hypotheses, the first three have not been substantiated by any scientific claim, and can probably be disregarded. The latter two hypotheses have received support, and the secretion is now considered to be an important component of the non-ophidian squamate chemical signalling system (Alberts, 1993; Imparato et al., 2007; Mason and Parker, 2010; López and Martín, 2012; Khannoon, Dollahon and Bauer, 2013).

Epidermal gland secretions have been shown to function in a variety of signalling processes: from providing social cues (Aragón et al., 2006; Martín and López, 2014, 2015) and assisting in habitat selection (Aragón, López and Martín, 2001a, 2001b; Le Galliard, Ferriére and Clobert, 2005; Font et al., 2012), to allowing intra- and interspecific recognition and providing territorial signals (Moreira, López and Martín, 2006; Khannoon et al., 2011b). These secretions can be thought of as a signature mixture (Wyatt, 2014), in which a variable subset of molecules of an animals' chemical profile are detected by others, allowing them to distinguish individuals.

Table 1. Composi	ition of the major lipophilic chemica	als reported	in lizards and amp	ohisbaenians	s, in %. Bc	olded entri	es are those	: not included	l in Weldon, Flachsbarth	and Schulz (2008).
Family	Species	Steroids	Carboxylic acids	Alcohols	Alkanes	Ketones	Squalene	Tocopherol	Reference(s)	Intraspecific variation
Agamidae	Acanthocercus atricollis	66.9	17.7	×	×	6.4	2.6	2.8	Martín, Ortega and Lopez, 2013a	
Agamidae	Uromastyx aegyptia microlepis	58.6	16.5	0.5	x	1.6	9.5	3.4	Martín et al., 2012	Martín et al., 2012*
Amphisbaenidae	Blanus cinereus	86.8	4.2	x	×	x	4.6	x	López and Martín, 2005b	López and Martín, 2005b*
Cordylidae	Cordylus giganteus	42.53	23.34	0.06	0.02	0.81	26.56	1.5	Louw et al., 2007	Louw et al., 2007*
Crotaphytidae	Crotaphytus bicinctores	37.2	14.5	13.4	Х	х	0.4	Х	Martín et al., 2013b	
Gekkonidae	Cyrtopodion scabrum	29.76	8.64	56.3	2.57	x	0.56	x	Khannoon, 2012	
Gekkonidae	Hemidactylus flaviviridis	13.19	16.81	3.25	19.8	х	0.37	x	Khannoon, 2012	
Gekkonidae	Hemidactylus turcicus (Balteem)	28.56	42.25	18.49	2.81	x	0.98	x	Khannoon, 2012	
Gekkonidae	Hemidactylus turcicus (Siwa)	13.62	7.28	67.46	3.71	х	0.94	x	Khannoon, 2012	
Iguanidae	Iguana iguana	31.81	68.19	Х	Х	х	х	x	Alberts et al., 1992	
Lacertidae	Acanthodactylus boskianus	35.54	9.37	50.29	x	x	0.85	Х	Khannoon et al., 2011	Khannoon et al.,
										2011*; Khannoon et
										al., 2013
Lacertidae	Acanthodactylus erythrurus	19.6	6.8	72.2	×	0.04	0.3	0.04	López and Martín, 2005c	López and Martín, 2005c
Lacertidae	Iberolacerta cyreni	84.6	14.6	0.4	×	×	0.3	x	López and Martín, 2005d	Aragón et al., 2008
Lacertidae	Iberolacerta monticola	89.3	8.4	1.7	×	×	0.28	×	López et al., 2009a	López et al., 2006; Martín and López, 2006b; López, Moreira and Martín, 2009
Lacertidae	Lacerta schreiberi	66.7	10.9	2.5	×	0.22	0.2	18.3	López and Martín, 2006	
Lacertidae	Lacerta viridis	59.6	4.6	2.6	×	0.2	2.5	28.5	Kopena, López and Martín, 2009	

Table 1. (Cont	tinued.)									
Family	Species	Steroids	Carboxylic acids	Alcohols	Alkanes	Ketones	Squalene	Tocopherol	Reference(s)	Intraspecific variation
Lacertidae	Podarcis atrata	78.47	9.89	2.75	x	0.13	0.35	x	Gabirot et al., 2010	
Lacertidae	Podarcis hispanicus Type 1	84.18	10.45	2.24	x	0.08	0.44	x	Martín and López,	Martín and López,
									2006d†	2006d; Gabirot et al., 2010: Gabirot. Lóbez
										and Martín, 2012a,
										2012b, 2013
	Podarcis hispanicus Type 2	84.88	12.07	0.88	x	0.04	0.42	x	Martín and López,	Martín and López,
									2006d†	2006d; Gabirot et al.,
										2010; Gabirot, López
										and Martin, 2012a, 2012b, 2013
Lacertidae	Podarcis lilfordi	94.4	0.6	0.5	1.4	0.8	0.7	×	Martín et al., 2013	Martín et al., 2013
Lacertidae	Podarcis muralis	83.7	12.8	0.29	х	0.11	0.97	1.95	Martín and López,	Pellitteri-Rosa et al.,
									2006d	2014
Lacertidae	Psammodromus algirus	48.1	48.5	2.3	х	0.12	0.3	0.17	Martín and López,	
									2006a	
Lacertidae	Psammodromus hispanicus	72.6	23.5	3.8	x	x	0.1	x	López and Martín,	
									2009	
Lacertidae	Timon lepidus	59	12.2	0.7	Х	0.02	0.15	27.9	Martín and López,	
									2010b	
Lacertidae	Zootoca vivipara	92.14	6.2	х	х	х	1.68	1.01	Gabirot et al., 2008	Gabirot et al., 2008
Liolaemidae	Liolaemus bellii	45.5	48.7	x	5.8	х	х	x	Escobar, Labra,	
									Niemyer, 2001	
Liolaemidae	Liolaemus fabiani	14.4	72.6	Х	12.9	х	Х	x	Escobar et al., 2003	Escobar et al., 2003
Liolaemidae	Liolaemus	19.9	61.5	x	18.6	х	Х	x	Escobar, Labra,	
									Niemeyer, 2001	

[&]quot;x" – There have been no reported chemicals of the specified type for that species. "*" – Female secretions were evaluated. "†" – This species has since been split into two species (Geniz et al., 2014), however we followed the two types listed in Martín and López (2006d) to avoid confusion.

Variation in secretion composition and pore characteristics

Although there was little knowledge on epidermal gland secretions, and what knowledge existed was present for only a few species, Cole (1966a) hypothesized that there must be interspecific variation in secretion composition, solely based on differences in secretion colour. We now know that extensive variation exists both between and within species. Variation in different aspects of the epidermal gland system has been observed in individuals of different age and sex (e.g., Cole, 1966b; Martín and López, 2006a; Martins et al., 2006; Khannoon et al., 2011a, 2011b), different morphological characteristics (e.g., López, Moreira and Martín, 2009a; Pellitteri-Rosa et al., 2014), different populations (e.g., Escobar et al., 2003; Gabirot, López and Martín, 2012a, 2012b; Khannoon et al., 2013; Martín et al., 2013a) and different species (table 1).

Researchers have also observed seasonal variation in the epidermal gland system (Chiu and Maderson, 1975; Van Wyk, 1990; Alberts et al., 1992), with an increase in the quantity of secretion and gland size during the breeding season, which is expected if the chemicals within the secretion play a role in reproduction (Alberts et al., 1992; Hews, Knapp and Moore, 1994). Surprisingly, pore size seems not to vary seasonally (Van Wyk, 1990). Changes in the chemical composition of the secretion during the mating season have also been observed and possibly serve to increase the secretion's volatility and detectability (Alberts et al., 1992).

If natural selection acts to maximize efficiency of information transfer, then animal signals should exhibit structural features optimal for specific functions under particular environmental conditions. Variation in the epidermal gland system can therefore be partly explained by adaptations to specific extant ecological conditions (Alberts, 1990, 1991). A variety of abiotic variables seem to potentially affect the number of epidermal pores present on each thigh (Escobar, Labra and Niemeyer, 2001; Pincheira-Donose, Hodgson and Tregenza, 2008; Baeckens et al., 2015). In Liolaemus lizards, Escobar and colleagues (2001) observed an increase in pore number with altitude, suggesting that lizards and amphisbaenians may produce more secretions under harsh environmental conditions. However, a subsequent study by Pincheira-Donoso et al. (2008) on the same genus, but with additional phylogenetic input, failed to find any effect of environmental conditions on pore number. They explain the assessed variation in pore numbers in Liolaemus as a result of shared ancestry rather than a result of phylogenetic independent adaptive events. A decrease in pore number with altitude has also been found, which is explained by the hypothesis that low elevation individuals might be subjected to more intense sexual selection than individuals at high elevation (Iraeta et al., 2011).

Using phylogenetic informed analyses, Baeckens and colleagues (2015) investigated the role of the physical environment on the variation in epidermal pore number in 162 lacertid species, including all genera of the family. They found no effect of climate conditions or latitude on species pore number, but did find an effect of substrate use: shrub-climbing species tended to have fewer femoral pores than species inhabiting other substrates, possibly because of the lower scent mark persistence on such substrates. A similar explanation regarding substrate use has been offered for lizards living in meadows or grasslands, such as Psammodromus hispanicus, which has much less epidermal pores and compounds in its secretions when compared with other closely related species (López and Martín, 2009). It has also been observed that in cool or dry environments, individuals of the same species produce more secretion than in hotter and more humid climates (Gabirot et al., 2008, 2010; Mouton, Van Rensburg and Van Wyk, 2010), probably because in the latter environmental conditions, chemical components of the secretion volatilize more rapidly and subsequently have decreased efficiency (Alberts, 1992b).

In addition to variation in the chemoreceptive qualities or quantities of the secretion, variation in spectroscopic characteristics of the secretion in lizards has also been observed. Desert iguanas (D. dorsalis) inhabit hot, arid deserts, whereas green iguanas (Iguana iguana) live in humid tropical forest, suggesting that signal transmission is subjected to different environmental constraints (Alberts, 1990). Due to the protein-rich character of the epidermal secretions of desert iguanas, the secretions are relatively non-volatile, and therefore difficult to detect by chemoreception at long distance. Spectroscopic analyses of the gland secretions revealed strong absorption in the ultraviolet light spectra (Alberts, 1989a). These findings argue that secretion deposits of the desert iguana also act as an ultraviolet visual marker, providing a possible mechanism for locating these low volatility chemosignals at far range (Alberts, 1989a). In contrast, green iguanas secrete a more lipid-rich volatile secretion with no strong light absorption in the long wave light spectra (Alberts, 1990). Because green iguana secretions transmit well under humid conditions, there is no need for a visual cue (Alberts, 1990). As far as we know, no spectrometric information is available on the epidermal secretions of other lizard or amphisbaenian species.

Differences in pore-bearing scale morphology among species can also be linked to environmental factors. The desert species Acanthodactylus boskianus and A. scutellatus are equipped with pore-bearing scales divided into two pieces: a large convex piece and a small dome-shaped piece (Khannoon, Dollahon and Bauer, 2013). This is different from other lizards studied, which have rosette-like pore bearing scales (Cole, 1966b; Blasco, 1975). The convex part of the pore-carrier differentiated scales of both Acanthodactylus species may be useful in 'cutting' the secretory plug in pieces with relatively a small surface area to volume ratio when deposited on the substrate. This ratio allows the low molecular weight compounds of the secretion to slowly release from the plug pieces as

they degrade (Khannoon, Dollahon and Bauer, 2013). As such, the deposited secretion will remain on the substrate for enough time to convey their chemical message in a desert-like environment (Khannoon et al., 2010; Khannoon, El-Gendy and Hardege, 2011).

As differences in chemical composition play a key role in determining mating success, we can say that the epidermal gland system is subjected to both sexual and natural selection, and displays extensive intra- and interspecific variation. It is a complex system that remains, for the most part, poorly understood.

The phylogenetic distribution of epidermal pores in non-ophidian squamates

Epidermal gland secretions thus seem to play an important role in many species. However, glands are absent in many other species. This disparity may offer unique opportunities for testing evolutionary and ecological hypotheses on the significance of a chemical signalling system. Because epidermal glands function as an essential component of the non-ophidian squamate chemical signalling system, their absence will subsequently affect a species' ability to communicate in this way. By reconstructing ancestral character states, we can attempt to comprehend this variation in epidermal gland expression.

We extracted data on the presence or absence of epidermal pores in all 42 non-ophidian squamate families from the literature. Because direct histological information on the presence or absence of epidermal glands is available for only a handful of species, we infer epidermal gland presence based on the absence or presence of male pores. If a taxon was said to not have pores, we did not investigate beyond the family level. However, when a family had at least some genera or species with epidermal pores, we obtained data at a higher resolution. In total, we gathered information on epidermal pores from 2899 species, which corresponds to approximately 46% of all described Lacertilia and Amphisbaenia species (Uetz and Hošek, 2014). We followed the nomenclature according to Pyron, Burbrink and Wiens (2013). To evaluate evolutionary changes, we performed an ancestralstate reconstruction in Mesquite v2.75, using a MK1 maximum likelihood approach (Mooers and Schluter, 1999; Maddison and Maddison, 2011). Taxa were scored with binary coding: 0 (epidermal pores absent) or 1 (epidermal pores present), and mapped onto a recent nuclear and mitochondrial DNA-based phylogeny of Squamata by Pyron, Burbrink and Wiens (2013). A difference of 2 log likelihood units (lnL) between character states for a given node was considered as statistically significant (Pagel, 1994, 1999). This corresponds to ~ 0.89 proportional likelihood (Calley and Linder, 2006).

The results of the reconstruction are visualized in fig. 3 and fig. S1 (A-G; see online supplementary material) representing a large-scale phylogeny of the non-ophidian squamates on a family level and on a species level, respectively. Of all sampled species, 1695 were reported without pores (\sim 58%) and 1204 with pores $(\sim 42\%)$ (tables S1 and S2, online supplementary material). We found that epidermal pores were most likely absent in the common ancestor of non-ophidian squamates, but are widely distributed in extant taxa. In 11 families, all species possessed pores, in 18 families, all species lack pores, while in the remaining 13 families, pores were present in some species, but absent in others (fig. 3). There appears to be extensive lability in the acquisition and loss of pores, as many groups appear to have gone through multiple gain/loss events independently, both between families and within a genus.

Although we find that pores were most likely absent in the common ancestor of non-ophidian squamates, we do not make any assumption on the presence or absence of secretory glands in general in the common ancestor. Our reconstruction only focuses on those epidermal glands that secrete their secretion through pores and does not include other glands, such as urodeal, gular, cloacal, or generation glands. Our data are insufficient to hypothesize on where and when chemical signalling through epidermal glands evolved or vanished in squamates, but allow us to think about the drivers behind the evolution of the epidermal gland system (Imparato et al., 2007; Baeckens et al., 2015). Based on the results of this study, one main conclusion can be drawn: the frequency of character shifts varies considerably between clades. For example, there are 20 character shifts within Gekkonidae, two of which are secondary follicular epidermal gland gains. In contrast, within Scincidae - the family containing most species within Lacertilia - not a single character-shift is observed. There are at least two possible explanations for this disparity: (1) the number of character state shifts could be higher in a clade inhabiting a wide variety of habitats due to adaptations to their local environment, as chemical signalling efficiency through epidermal glands is affected by environmental conditions (Pincheira-Donoso, Hodgson and Tregenza, 2008; Escobar, Labra and Niemeyer, 2011; Baeckens et al., 2015) or (2) morphological constraints could inhibit (or allow) the gain or loss of epidermal glands. These two explanations are by no means exclusive, as in some instances one may play a greater role than the other.

We do not have a complete understanding of what drives the evolutionary acquisition of these glands, nor do we understand what drives different groups to lose them. For example, what prompted the species *Meroles anchietae* – the only lacertid lizard without pores – to lose epidermal pores? By approaching the evolution of epidermal glands within a phylogenetic framework, we can now begin to tease apart how environment, ecology, and morphology impact the evolution of epidermal glands.

Functions of epidermal gland secretions

Territoriality and dominance

Many species are territorial. This often results in a variety of physical displays and agonistic





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General function	Information content	Species	Reference(s)
Interspecific recognition General intraspecific recognition	Familiar vs. unfamiliar	Liolaemus sp. Iguana iguana; Iberolacerta monticola	Labra, 2011 Alberts and Werner, 1993; Aragón, López and Martín, 2001b, 2001c
	Population recognition Colour morph Sex recognition Self-recognition	Podarcis hispanicus Iberolacerta monticola; Podarcis muralis Acanthodactylus boskianus Dipsosaurus dorsalis	Gabirot, López and Martín, 2012a, 2012b López, Moreira and Martín, 2009; Pellitteri-Rosa et al., 2014 Khannoon et al., 2010 Alberts, 1992
Social dominance		Amphibolurus fordi; Cordylus polyzonus; Iberolacerta monticola; Iguana iguana	Fergusson et al., 1985; Van Wyk, 1990; Alberts et al., 1992; Moreira, López and Martín, 2006
Territoriality		Acanthodactylus boskianus; Dipsosaurus dorsalis; Iberolacerta monticola	Alberts, 1993; Martín, Moreira and López, 2007; Khannoon et al., 2010; Martín and López, 2012
Mate assessment	FA Age Accessibility to quality thermal resources Immune response level Parasite load Vitamin E concentration	Iberolacerta monticola Iberolacerta monticola Podarcis muralis Iberolacerta cyreni; Iberolacerta monticola; Psammodromus algirus Lacerta viridis	Martín and López, 2000 López et al., 2003; Martín and López, 2006a Heathcote et al., 2014 López and Martín, 2005a; Martín et al., 2007; López, Gabirot and Martín, 2009 Martín et al., 2007 Kopena, López and Martín, 2011; Kopena et al., 2014

Table 2. An overview of the different social contexts that epidermal gland secretions are known to be used in lizards and amphisbaenians.

behaviour in which males will actively defend their territory; the outcome of these encounters helps to establish dominance hierarchies (e.g., Baird and Timanus, 1998; Sheldahl and Martins, 2000; Peters and Ord, 2003). The establishment of dominance hierarchies often determines the size and quality of an individual's territory. There are many obvious morphological factors such as body mass and head width that help to establish these hierarchies (Olsson and Madsen, 1998). However, dominance status can also be assessed solely on the basis of epidermal secretions (Font et al., 2012; Heathcote et al., 2014). In Iberian rock lizards (Iberolacerta monticola), males with higher dominance status have higher concentrations of hexadecanol and octadecanol in their secretions (Martín, Moreira and López, 2007a). In addition, males tend to respond aggressively toward hexadecanol while responding neutrally towards other chemicals, and show differential chemosensory and aggressive behaviour according to their own dominance status. Male A. boskianus are also known to respond more aggressively towards cotton swabs confronted with male secretions than towards control swabs (Khannoon et al., 2010). The ability to determine dominance status of conspecifics by epidermal secretions has been hypothesized to minimize the cost of agonistic encounters, lending credence to the idea that secretion can function as territory markers (Aragón, López and Martín, 2001a; Khannoon, El-Gendy and Hardege, 2011). These functions have been tested experimentally, and it has been found that some lizard species are able to identify the competitive ability of conspecific males based on scent marks alone. Additionally, it has been found that they are able to consistently identify specific individuals based on these cues, which allows resident males to change their behaviour accordingly (Carazo, Font and Desfilis, 2008).

Because density dependent interactions powerfully affect post-natal growth, colonization of habitats can easily be related to intraspecific competition. Unsettled individuals will often stay longer in initially empty habitats than they do in occupied patches (Le Galliard, Ferriére and Clobert, 2005). Resident males of *Iberolacerta monticola* can discriminate neighbours from unfamiliar males based on chemical cues left on the substrate, and intruders have been shown to display significantly more escape behaviour in response to unfamiliar male cues (Aragón, López and Martín, 2001a, 2001b, 2001c, 2003).

Mate assessment

As with many animals, lizards and amphisbaenians utilize elaborate sexual signals in order to attract potential mates (Andersson, 1994). Attraction of females to sexual signals of males can evolve if these signals provide honest information on certain favourable characteristics of males (Grafen, 1990; Johansson and Jonas, 2007), or if the signal exploits the sensory system of females that have a sensory bias for certain traits (Fuller, Houle and Travis, 2005; Macías-García and Ramirez, 2005). A plethora of studies have shown that non-ophidian squamates rely strongly on chemical sexual signals to attract mates (Martín and López, 2011), and that secretion from the epidermal glands bears valuable information in relation to mate choice (Martín and López, 2000; López, Munoz and Martín, 2002; López, Aragón and Martín, 2003; López and Martín, 2006c). Females have been shown to discriminate between males based on the scent from these secretions alone, and there is strong evidence that, at least in some species, mate choice plays an important role in reproduction (Olsson et al., 2003; Font et al., 2012; Swierk et al., 2012).

For example, female lizards have been found to be able to determine the health status of males based only on the secretion of epidermal glands (e.g., López and Martín, 2005a; Martín and López, 2006b; Martín et al., 2007; López, Gabirot and Martín, 2009), suggesting that there is a discernible signal found within the secretion. As a general rule, signals can only be evolutionary stable if they are honest and condition dependent, or costly to the sender, and if the cost is correlated with the sender's quality (Grafen, 1990; Zahavi and Zahavi, 1997). Because chemicals are costly to produce, as only males in good health can afford to allocate chemicals to femoral secretions instead of to other bodily functions, they are considered to be honest signals which display accurate information about a male's health state (Martín, Amo and López, 2008). Male Iberian rock lizards with a high immune response have been shown to have higher proportions of various alcohols and carboxylic acids within their secretions than individuals with a low immune response (López, Amo and Martín, 2006). This may be important, as when presented with cues from only femoral secretions, López and colleagues (2006) found that females preferentially choose male scents which signal a higher immune response. Female Psammodromus algirus also have been found to show more chemoreceptive behaviour in response to secretions of males with low parasite infections and high T-cell-mediated immune responses (Martín et al., 2007). Female lizards have also been shown to prefer males with secretions having high proportions of compounds that have important metabolic functions for organisms. Martín and López (2012) found that females prefer to associate with areas marked by males with experimentally increased provitamin D. A similar conclusion was reached by Kopena et al. (2011) when investigating increases in Vitamin E. Oleic acid also plays a role in female mate choice (Martín and López, 2010a).

When determining which male to reside with, females have been shown to evaluate and react to the symmetry of males based on scent alone. Symmetry indicates the developmental stability of an individual and thus, its ability to cope with genetic and environmental disturbances during development (Van Valen, 1962). Fluctuating asymmetry (FA), small random deviations in the development of both sides of a bilateral symmetric character is therefore often used as a measure for developmental instability (Martín and López, 2000; Lens et al., 2002; Klingenberg, 2003). FA can be quantified using many metrics, including by comparing the number of femoral pores on each thigh of a lizard. It is generally assumed that animals, which exhibit a high FA are of a low fitness (Van Valen, 1962). For example, in Iberolacerta monticola (López and Martín, 2002) and Psammodromus algirus (Martín and López, 2001), males with more asymmetrical femur length have lower escape speeds, and Sceloporus occidentalis males with high FA have an increased susceptibility to parasitism (Schall, 1995). Lazic et al. (2013) found that Podarcis muralis individuals inhabiting urban areas (associated with high levels of environmental stress) are more asymmetric than those in more rural areas. Based on only the chemicals found within femoral secretions, female Iberian rock lizards have been shown to prefer to associate with the scents of males with low FA, and with individuals with more femoral pores on each leg (López, Munoz and Martín, 2002). Although social dominance is traditionally thought to demonstrate the quality and mating potential of a male, the dominance status of males has not been shown to correlate with FA, and females seem to prefer areas marked by low FA individuals rather than dominant males. As such, it is postulated that in some species, symmetry potentially plays a greater role in mate choice than does dominance (López, Munoz and Martín, 2002). It should be noted that the results of some studies investigating FA are somewhat ambiguous, and their use as a metric of male quality has recently declined (Van Dongen, 2006).

In many vertebrate groups, females prefer to mate with older males, possibly because their continued survival displays high quality (Osada et al., 2003). Females are able to discriminate between young and old males based on chemical cues alone (López, Aragón and Martín, 2003; Martins et al., 2006), and subsequently choose habitats in which older males reside. Older *Psammodromus algirus* males secrete proportionally less carboxylic acids and more steroids than younger lizards, and the ability of females to detect and react to these differences implies that age related differences of chemicals in femoral secretions play an important role in the organization of this lizard's social hierarchy (Martín and López, 2006a). Similarly, in *Podarcis muralis*, younger males show significantly higher proportions of aldehydes, alcohols and ketones and significantly lower proportions of tocopherols than older males (Pellitteri-Rosa et al., 2014).

As a general rule, other than advertising indirect information on male quality (e.g., body size, FA, maximum sprint speed), chemical signals also contain honest information on direct benefits (e.g., access to high quality food or thermal resources), which are often argued to be more important (Dussourd et al., 1991; Hill, 1991; Candolin, 2000). As access to highquality thermal recourses is crucial for reproductive success in female squamates, females may be able to detect thermally-induced variation in chemical composition of male scent marks when assessing the quality of his territory. A study by Heathcote et al. (2014) showed that the amount of time male wall lizards (Podarcis muralis) are allowed to bask significantly alters the chemical composition of their femoral secretion, and that females can discriminate between scent marks of males which experience different basking conditions.

The results of these studies indicate that chemical compounds in the epidermal secretions of lizards and amphisbaenians may provide reliable information on morphological traits, health status and territory quality of males (table 2). Certain chemosignal compounds of the epidermal secretions have the possibility to therefore act as a chemical ornament and to serve as a basis for adaptive female choice (Martín and López, 2000; López, Amo and Martín, 2006).

Prospects on future research

Despite the recent surge in research, a significant gap in our knowledge on the true role of the chemicals found in epidermal secretions remains, and there are many possible avenues for future research on the topic.

Understanding the function of the components in epidermal secretions

We now know that many non-ophidian squamates use secretions from epidermal glands in a variety of processes, but little to no work has been done to determine what the function of the various chemicals in the secretion are. Field and laboratory studies by Mason et al. (1989, 1990) have unequivocally identified, characterized and synthesized a sex attractiveness pheromone of the red-sided garter snake (Thamnophis sirtalis parietalis), which was subsequently identified as the first pheromone in reptiles. Future work should investigate this possibility in the epidermal gland secretions of lizards and amphisbaenians, and research should be expanded to include the proteins found in those secretions, because they could also function as chemosignals (Alberts, Phillips and Werner, 1993), as they do in many other groups (Toyoda et al., 2004; Janssenswillen et al., 2015). As far as we are aware, A.C. Alberts is the only researcher who has studied the protein fraction of epidermal gland secretion in lizards (1990, 1991, 1993). As we begin to discover which proteins in secretions function as chemosignals, it may be possible to reconstruct the evolution of the genes producing these molecules. This would allow us to understand how the evolution of epidermal gland secretions occurred, and would assist in our understanding of squamate evolution in general.

Currently, there is a heavy bias towards studying the femoral gland secretions of West-European lacertids (table 1), but without knowledge of other groups, it is impossible to fully understand how the chemosignals within epidermal glands have evolved. Furthermore, we know far more about the male epidermal gland system than we do about female glands, resulting in a gender bias. The tendency for researchers to avoid studying female animals is a worldwide phenomenon in science (Zucker and Beery, 2010; Clayton and Collins, 2014). This trend is also apparent in chemical ecology, as most research has focused on the epidermal gland system of male lizards and amphisbaenians, despite the knowledge that females of many species both possess and make use of this system (e.g., Alberts, 1991). In studies where the content of female epidermal secretions has been analysed, researchers find differences between both sexes (López and Martín, 2005b; Louw et al., 2007; Khannoon et al., 2011b). In desert iguanas, Alberts (1989b) found that while all males possess active epidermal glands during the breeding season, only unmated females show glandular activity. Alberts (1990) thereby posited that female secretions may facilitate pairing by allowing unmated females to make their presence known to potential mates using epidermal deposits. Little has been done to investigate this hypothesis, but Kelso and Martins (2008) found that in S. graciosus females secrete more and larger secretion deposits when initially presented with males using specific courtship behaviour. Thus, although female epidermal secretions may not be as prevalent as they are in males, they still may serve an important role.

In our search to unveil the functions of the various chemical compounds, we have to understand that many signals in nature tend to be very complex (Partan and Marler, 2005; Bro-Jørgensen, 2009), and acknowledge that epidermal chemosignals seem to be too. This complexity brings along many possibilities. Do different components convey the same information (i.e., redundant signal hypothesis), or are there several bits of information on different aspects of quality (i.e., multiple message hypothesis), or are some of the signals obsolete? No research has tackled these standing questions using only chemical cues. However, more and more studies in communication biology are focusing on the relationships among and the integration of components from different sensory channels (Partan and Marler, 2005). Still, studies investigating multimodal communication signals in squamates are provisionally scarce (but see Hews and Benard, 2001; Whiting, Webb and Keogh, 2009; Ossip-Klein et al., 2013).

Predation costs of chemical communication

Individuals are at risk when communicating because conspicuous signals attract both conspecifics and eavesdropping predators (Magnahagen, 1991; Zuk and Kolluru, 1998; Huyghes, Kelley and Banks, 2012). Canids that track their prey eavesdrop on intraspecific signals, such as deposits from interdigital glands in cervids and bovids, or urine marks of rodents (Müller-Schwarze, 2006). The Texas blind snake (Leptotyphlops dulcis) feeds on termites and ants and finds its prey by following their pheromone trails (Gehlbach, Watkins and Kroll, 1971). No studies have attempted to investigate the potential interspecific costs of the use of scent marks in lizards and amphisbaenians with regards to chemical eavesdropping e.g., would they invest less in epidermal secretions when hunted by chemically-oriented predators, such as snakes?

Tongue flicking

While there are many potential future topics regarding the epidermal gland secretions themselves, how non-ophidian squamates analyse these secretions is another avenue for future research. Tongue flicking in lizards functions to sample chemicals for vomerolfactory analyses, and is assumed to indicate chemosensory exploration (Cooper, 1994; Cooper, Deperno and Arnett, 1994). To investigate how tongue flicking is used, researchers have presented lizards with chemical stimuli on either a cotton-tipped applicator or on a substrate in a test cage (Cooper, 1998), and then documented the lizards' response. One aspect of this behaviour that remains poorly explored is the direction of the tongue flicks. Alberts and Werner (1993) have shown that in male green iguanas, lizards tongue-flick the air proportionally more when presented with the lipid fraction

of femoral gland secretions, and the chemical stimuli itself proportionally more when presented with proteins from the secretion, a behaviour explained by the more volatile character of lipids than proteins. Future studies should account for this variation in behaviour (as in e.g. Cooper, Van Wyk and Mouton, 1996, 1999), as different types of tongue-flicks can capture different aspects of the chemosignal content of epidermal gland secretions. Ultimately, we lack information on the neurological basis of chemical discrimination and the specific neural responses to specific compounds (e.g., MRI). This has been studied in other animal groups, such as starlings (Gugliemetti et al., 2012) and mice (De Groof et al., 2010), but information for squamates is still very incomplete.

Follicular glands vs. generation glands

As previously mentioned, gekkonids and cordylids are the only lizard taxa where two types of holocrine epidermal glands have been described. Where follicular glands and generation glands co-exist, it is hard to accept that generation glands are merely under-evolved follicular glands, as advocated by Maderson and Chiu (1970). In cordylids, while both types of epidermal glands are present in males of all species, females display considerable variation: there are species with females having (1) both follicular and generation glands, (2) only follicular glands, or (3) no glands at all (Mouton, Van Rensburg and Van Wyk, 2010). Moreover, gland number in female cordylids appears strongly affected by climate, with a lower amount of glands in cooler compared with warmer environments (Mouton, Van Rensburg and Van Wyk, 2010). The role of the physical environment on gland number, and the apparent sexual dimorphism in the glandular system in Cordylidae (Mouton and Van Wyk, 1993), reflects the complexity of the chemical communication system in lizards having both epidermal gland types. More research on the association of both glandular systems should be encouraged.

Scope

Our goal has been to try to make evolutionary sense of the mass of data that accumulated on the role of follicular epidermal glands and their secretion. While our knowledge of lizard and amphisbaenian biology has vastly increased in recent years, and although some major patterns in the epidermal gland system seem clear, much uncertainty remains, resulting in both a daunting and exciting future for biologists in the field.

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