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SCALE MICROSTRUCTURES OF PYGOPODID LIZARDS (GEKKOTA: PYGOPODIDAE): PHYLOGENETIC STABILITY AND ECOLOGICAL PLASTICITY

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The skin, as the interface of the body with the outside world, is directly exposed to the impacts of the environment. We have examined the microstructure of scale surfaces and the numerical distribution and morphology of skin sensory organs (SSO) in Australian limbless lizards of the family Pygopodidae. We have shown that the hairy sensory organs, as complex morphological structures, are a stable characteristic of the scale integument of pygopodids. This feature reflects their relationship to geckos and is shared homoplastically with some iguanian families (Dactyloidae, Leiosauridae, Opluridae, Chamaeleonidae). At the same time, scale micro-ornamentation as an elementary morphological structure is more plastic and, although the basic spinulate pattern is dominant, other variants occur on the scales of the serpentine body of pygopodids. We accept the spinules of MiO and the hairs of SSO as homologous structures at the cellular level since they are both derivatives of the Oberhäutchen cell surface. We propose to characterize the hair-bearing SSO of gekkotan and iguanian lizards as Oberhäutchen hairy sensory organs (ObHSO). Domination of SP MiO and presence of ObHSO in the integument of Gekkota and several families of Iguania, and sporadic occurrence of SP MiO in autarchoglossan taxa provide justification for regarding these characters as plesiomorphic. We characterize the high abundance (iterative state) of SSO in the scales of the head of pygopodids as representing the phenomenon of "overiteration," in which the phylogenetically established condition is enhanced by functional demands on the organism.

Keywords: *Delma*; *Pygopus*; scale micro-ornamentation; sensory organs; morphology; numerical distribution; phylogeny; functional implication.

INTRODUCTION

The microstructure of the surface of the scales, and the skin sensory organs (SSO) in particular, are integral characteristics of the integument of Squamata. Since the first description of these structures by German morphologists in the 19th century (Leydig, 1868), an extensive body of data on their morphological diversity, spatial distribution and density has been accumulated, fueling hypotheses about their function (Scortecci, 1940, 1941; Landmann, 1975; Jackson, 1977; Oreyas-Miranda et al., 1977; Maclean, 1980; Russell and Bauer, 1987; Bauer and Russell, 1988; Williams, 1988; Ananjeva et al., 1991; Matveyeva and Ananjeva, 1995; Russell et al., 2014; Crowe-Riddell et al., 2019; Riedel et al., 2019). Numerous species have been studied, including representatives of all major squamate lineages and their most diverse ecological forms. However, there is still no answer to the main question: what factors determine the morphology and distribution of these structures in the squamate integument?

Most researchers, though not excluding a role for ecological adaptation and function, have regarded phylogeny as the leading factor in the development of scale surface microstructure and the numerical distribution of SSO (Scortecci, 1941; Stewart and Daniel, 1975; Price, 1982; Schleich and Kästle, 1982; Peterson, 1984a,

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1984b; Bauer and Russell, 1988; Williams, 1988; Ananjeva et al., 1991; Matveyeva and Ananjeva, 1995; Arrigo et al., 2019). Others, based on the variability of scale microstructure among the species, across the body and even on the same scale, considered the SSO as a highly adaptive and plastic structure and have correlated its peculiarities with species ecology and functional requirements (Stewart and Daniel, 1972; Burnstein et al., 1974; Rocha-Barbosa and Moraes e Silva, 2009; Spinner et al., 2013). The morphological characters of SSO, in comparison with those of the scale microstructure, are relatively stable and are important in the diagnosis of higher taxa (Etheridge and de Queiroz, 1988; Ananjeva et al., 1991, 2001). In light of recent changes in views on phylogenetic relationships within Squamata and much additional information on species ecology, the picture of morphological diversity of squamate scalation and its derivatives appears even more complex than it did before.

In this context, the Australian and New Guinean pygopodid lizards are of exceptional interest. Based on phylogenetic analyses, these lizards shared a most recent common ancestor with geckos (Kluge, 1987; Estes et al., 1988; Hedges and Vidal, 2009; Gauthier et al., 2012; Gamble et al., 2015) but are characterized by peculiar morphology and completely different ecology. The family Pygopodidae (legless lizards, snake-lizards, or flap-footed lizards) includes 45 species (Uetz et al., 2020) with reduced or absent limbs and long, slender bodies, giving them a strong resemblance to snakes which in this respect are very different from the fully-limbed geckos. Some pygopodids are fossorial animals and others are adapted to moving through dense low vegetation (Shea, 1987; Cogger, 2014).

Data on the microstructure of scale surface and SSO of pygopod scales is far from complete. The first information appeared in Underwood (1957) who described the external morphology of SSO in some species of a few genera and noted a resemblance of these structures to the skin organs of geckos. However, lacking high magnification imagery, he could not identify details of the scale surface, showing SSO simply as microdots in his figures on page 228. Landmann (1975) studied the microanatomy of SSO in *Delma fraseri* and *Lialis burtonis* but did not find the hairs seemingly because of their loss during histological preparation. E. E. Williams (personal communication) in *Aprasia*, *Delma*, and *Lialis* found the scale surface sculpture closely resembled the lamellate cell pattern of scincides and anguids with its spinulate micro-ornamentation, and the honeycomb sculpture on the rest of the scale surface. Shea (1993) provided a photo of the spinulate microstructure and SSO bearing few corneous outgrowths on the dorsal body scales of *P. lepidopodus*. Spinner et al. (2013) precisely described morphology and distributional density of SSO with 1 – 10 hairs on the head and flank integument of *Lialis burtonis* and *L. jicari*, and paid special attention to variability of scale surface microstructure in different body regions and its functional interpretation.

Against the background of the poorly studied integument of the scales of pygopod lizards, we have undertaken a study of morphology of scale microstructure (mainly its micro-ornamentation) and SSO in three species and described spatial and numerical distribution of SSO within the different body regions. We also provide a comparative survey of the data obtained with those known for Squamata more generally, in an attempt, once again, to consider the phylogenetic and ecological correlations of these structures.

MATERIAL AND METHODS

We examined the integument of ethanol-preserved specimens of three lizard species of the family Pygopodidae from the herpetological collections of the Australian Museum, Sydney (AMS) and the California Academy of Sciences, San Francisco (CAS): *Delma nasuta* — AMS R90493, AMS R90494; *Pygopus lepidopodus* — AMS R15763, AMS R80556, CAS 77659; *Pygopus nigriceps* — CAS 94367.

Although the question of individual variation and symmetry in number of the sensory organs in squamates is still not fully understood, we limited our research to a few specimens based on the special studies of *Leptotyphlops* snakes (Oreyas-Maranda et al., 1977) and *Phrynocephalus* lizards (Kalyabina et al., 1998) which revealed low variation in SSO number in specimens from the same locality and in the species in general and relatively high level of symmetry in SSO number on the right and left sides of the head. Additionally, Sherbrooke and Nagle (1996) did not find any differences between the sexes in sensory organ distribution and abundance in *Phrynosoma* lizards.

A general pattern of SSO distribution on the head and body was examined by means of gross observation with binocular light microscopy of the integument of *D. nasuta* (AMS R90494) and *P. lepidopodus* (AMS R15763). The scale microstructure and the external morphology of SSO were described in *P. lepidopodus* (CAS 77659) and *P. nigriceps* (CAS 94367) by means of SEM. The inner morphology of SSO was studied in *P. lepidopodus* (CAS 77659) using LM.

For SEM-study tissue samples from different parts of lizard head and dorsum were postfixed in phosphate-buffered 1% OsO_4 for 1 – 2 h and dehydrated through a graded ethanol series before critical-point drying (Pola-

ron critical-point drier) and mounted on aluminum stubs with either silver or epoxy. The samples were sputter-coated with gold-palladium to a thickness of 16 – 19 nm. Samples were viewed on an ISI-DSI130 dual-stage scanning electron microscope. Photomicrographs were taken on Polaroid type 55 P/N film. For LM-study the samples from the labial and dorsal scales of *P. lepidopodus* were dehydrated in alcohol, cleared in chloroform and embedded in 56°C paraffin-wax. Serial transverse and longitudinal sections were cut on a rotary microtome at 7 μm, stained with Masson's trichrome (Martoja and Martoja-Pierson, 1967). Microphotography was conducted using MBI-6 and Zeiss AXIOPHOT light microscopes and MIKRAT-200, KODAK TMAX 400pro, and KODAK GOLD 100 films. We determined the proximal diameter of the spinules of scale MiO and the diameter of SSO in pygopodids by measuring of 10 – 15 random samples in every available mag SEM-photo and providing a range of minimum and maximum values. We used the same method for data from the literature if the meanings of the measurements were not explicitly mentioned by the authors themselves. In cases of low variability in the proximal diameter of the spinules or presence of single available SSO, we used only the mean, without the standard error.

Terminology for pygopod pholidosis was adopted from Shea (1987) and Oliver et al. (2010) and that for SSO morphology from Williams (1988) and Ananjeva et al. (1991). We refer to cell shape projection within the scales (including the characters of cell junctions) as scale *macro-ornamentation* (MaO), and sculpturing of the Oberhäutchen cell surface as scale *micro-ornamentation* (MiO) (Peterson, 1984a, 1984b; Peterson and Bezy, 1985; Harvey and Gutberlet, 1995). Of a wide range of synonyms, we use the term "skin sensory organ" (here SSO) since it most clearly reflects a position of these structure in the body, their complex nature and functions performed. We distinguish the "hairs" and the "bristles" as the outgrowths of thin corneous membrane of the SSO. We accept the "*hairs*" as the simple filaments originating from the thin corneous membrane of the SSO as the enlarged outgrowths of the MiO, and the "*bristles*" as the large multicellular structures formed by the few cells of outermost corneous epidermal layers of the SSO membrane (Schmidt, 1920; Etheridge and de Queiroz, 1988; Dujsebayeva, 1995). We use the term "iteration" to designate a process of multiplication of the number of homologous organs (here SSO). Data on species ecology and geographical distribution were taken from Shea (1987) and Cogger (2014). We follow Uetz et al. (2020) for current species names.

RESULTS

Pholidosis

Non-overlapping flat shields cover the dorsal, ventral and anterior lateral surfaces of the head of *D. nasuta* and *P. lepidopodus*. The largest of them are unpaired rostral, mental, rostral and caudal frontal shields, and paired frontonasal, supraocular and parietal shields (Fig. 1). The back of the head, its posterior lateral surface, throat and body of *D. nasuta* are covered by imbricate, flattened and hexagonal-shaped scales. The scales from the same regions of the head of *P. lepidopodus* are imbricated, slightly keeled and rhomboidal in shape.

Topography and Numerical Distribution of the Skin Sensory Organs

SSO were distributed unevenly across the head of *D. nasuta* and *P. lepidopodus* with highest abundance on the shields of the anterior part of the head (Fig. 1). The highest density was revealed on the rostral (530 and 450 SSO for *D. nasuta* and *P. lepidopodus*, respectively) and mental (560 and 300, respectively) and on the first and second pairs of supralabials and infralabials of *D. nasuta* (170 – 400 per shield). Other shields in both species possessed fewer SSO, but still had a relatively high number of the organs: up to 60 – 180 in *D. nasuta* and up to 30 – 140 in *P. lepidopodus* per shield (Fig. 1; Table 1). The imbricate dorsal, lateral and ventral scales of the hind part of the head bore low numbers of SSO compared with the shields. The temporal scales had 5 – 10 receptors in *D. nasuta* and 7 – 12 receptors in *P. lepidopodus*; the mental scales — 1 – 7 and 3 – 4 receptors, respectively (Fig. 1B, D). The imbricated scales of the flank, tail and rudimentary limbs bear few receptors (Table 2), and only along their distal edges.

External Morphology of Scale Micro-Ornamentation and the Skin Sensory Organs

At low magnification the surfaces of non-overlapping subocular scales (MaO) of the head of *Delma* and *Pygopus* were marked by dark lines enclosing irregular polygonal Oberhäutchen cells with juxtaposed boundaries and almost flat or slightly convex surface (Fig. 2A). The Oberhäutchen cells of the overlapping dorsal scales had the shape of elongated rectangles (or polygons) with a convex surface and juxtaposed boundaries (Fig. 2B). At high magnification, the Oberhäutchen cells themselves (MiO) from the oculars, temporals and dorsal flank scales were covered with minute spinules with a diameter above the base of 0.14 – 0.38 μm (Fig. 3B – E; Table 3).

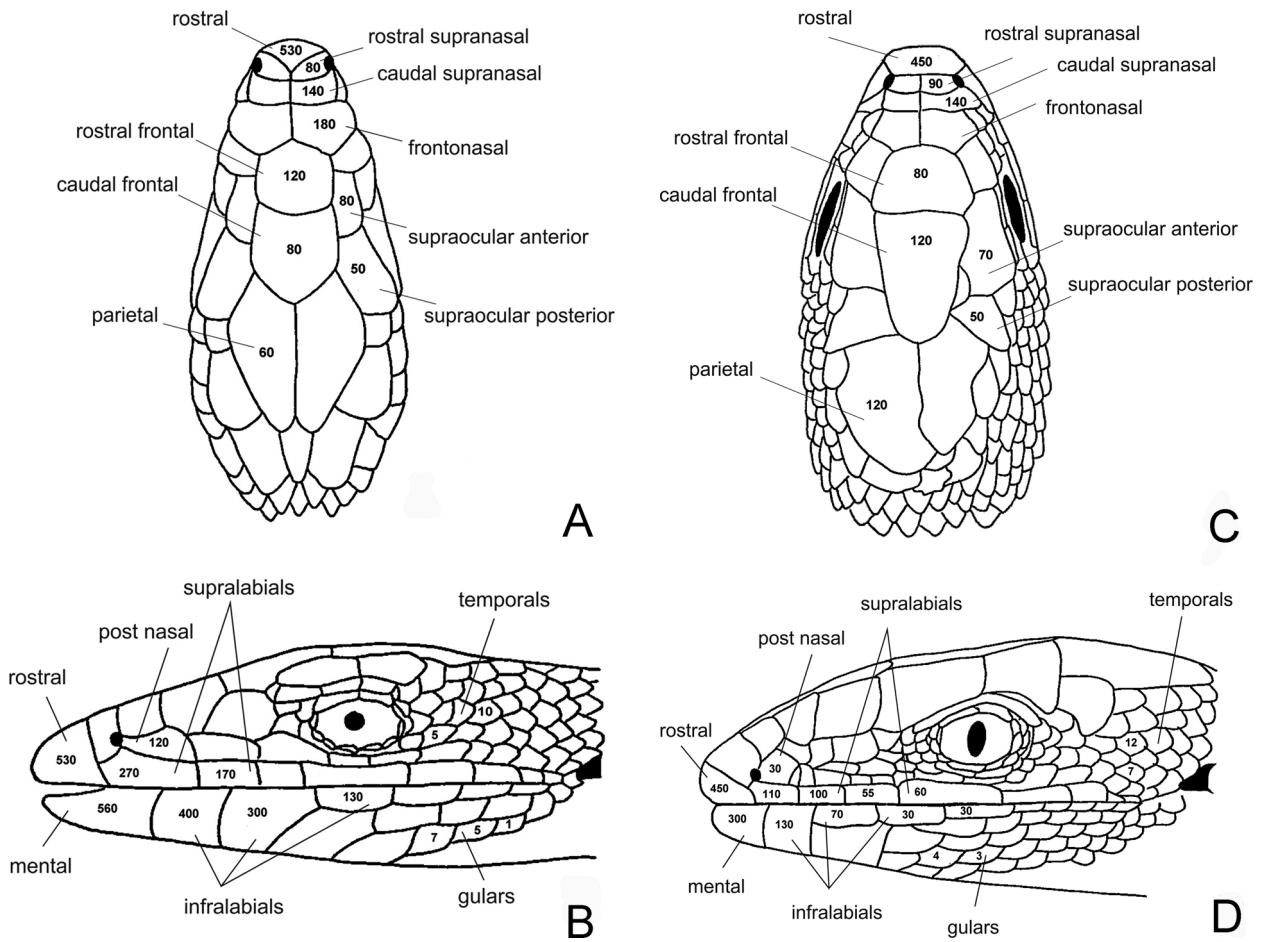

Fig. 1. Scheme of the head pholidosis (dorsal and lateral views) and the quantitative distribution of the skin sensory organs (showing with numbers) with the examples of *Delma nasuta*, AMS R90494 (A, B) and *Pygopus lepidopodus*, AMS R15763 (C, D).

TABLE 1. Number of Skin Sensory Organs on the Head of *Delma nasuta* (AMS R90494) and *Pygopus lepidopodus* (AMS R15763)

Genus	R	M	RSN	CSN	FN	RF	CF	P	PN	SpL1	SL2	IL1	IL2	T	G
Delma	530	560	80	140	180	120	80	60	120	270	170	400	300	5 – 10	1 – 7
Pygopus	450	300	90	140	90	80	120	120	30	110	110	130	70	7 – 12	3 – 4

Note. R, rostral; M, mental; RSN, rostral supranasal; CSN, caudal supranasal; FN, frontonasal; RF, rostral frontal; CF, caudal frontal; P, parietal; PN, postnasal; SpL1, first/supralabials; SpL2, second/supralabials; IL1, first infralabials; IL2, second infralabials; T, temporals; G, gulars.

TABLE 2. Number of Skin Sensory Organs on the Flank, Tail, and Rudimentary Hindlimb Flaps of *Delma nasuta* and *Pygopus lepidopodus*

Genus	Flank					Tail				Limbs		
	jug	md	sac	mv	precl	pdc	mdc	ddc	postcl	mvc	dl	vl
Delma	3 – 15	5 – 10	7 – 10	?	?	4 – 5	6 – 10	8	5 – 7	5 – 8	2 – 15	?
Pygopus	10 – 14	?	1 – 2	?	?	?	?	?	?	?	?	?

Note. Flank scales: jug, jugulars; md, mid-dorsal; sac, sacral; mv, mid-ventral; precl, precloacal; tail scales: pdc, proximal dorsal caudal; mdc, middorsal caudal; ddc, distal dorsal caudal; postcl, postcloacal; mvc, midventral caudal; rudimentary limb scales: dl, dorsal; vl, ventral; "?", SSO were not detected.

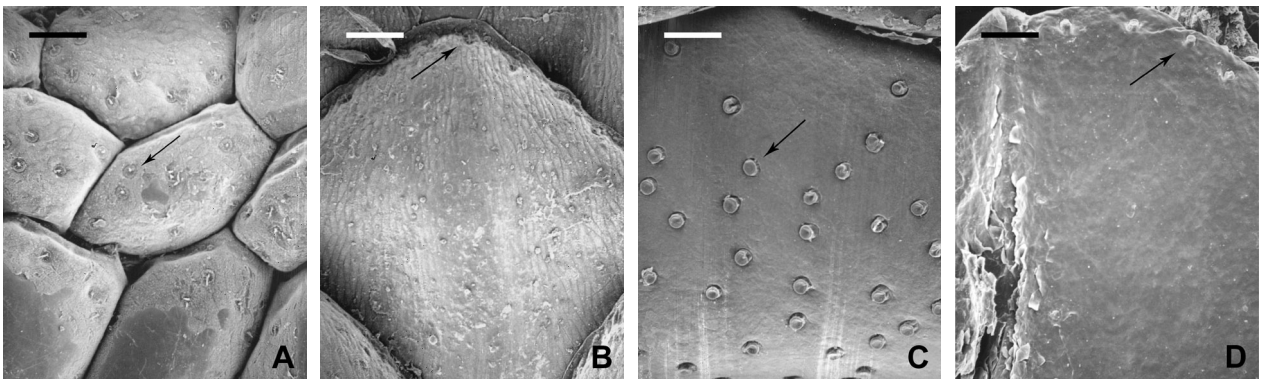

Fig. 2. SEM-photographs of the skin sensory organs in the integument of *Pygopus nigriceps* (A – C) and *P. lepidopodus* (D): A, the subocular scales showing honeycomb surface macro-ornamentation and hairy sensory organs (arrow); resting phase; spinulate Oberhäutchen (Ob) and denuded areas with bare surface represented by β-layer (β); B, close up to a mid-dorsal scale showing surface rectangular lamellated macrosculpture and hairy sensory organs (arrow) along its border; resting phase; C, the labial shield with lost upper layers of the epidermis showing the sensory organs (arrow); resting phase; upper surface of α-layer (α) with deep portions of mesos-layer (ms) within the sense organs; D, the mid-dorsal scale with lost upper layers of the epidermis covered with α-layer (α) showing the sensory organs (arrow) along its border. Scale bars are 88 μm (A, C, and D) and 115 μm (B).

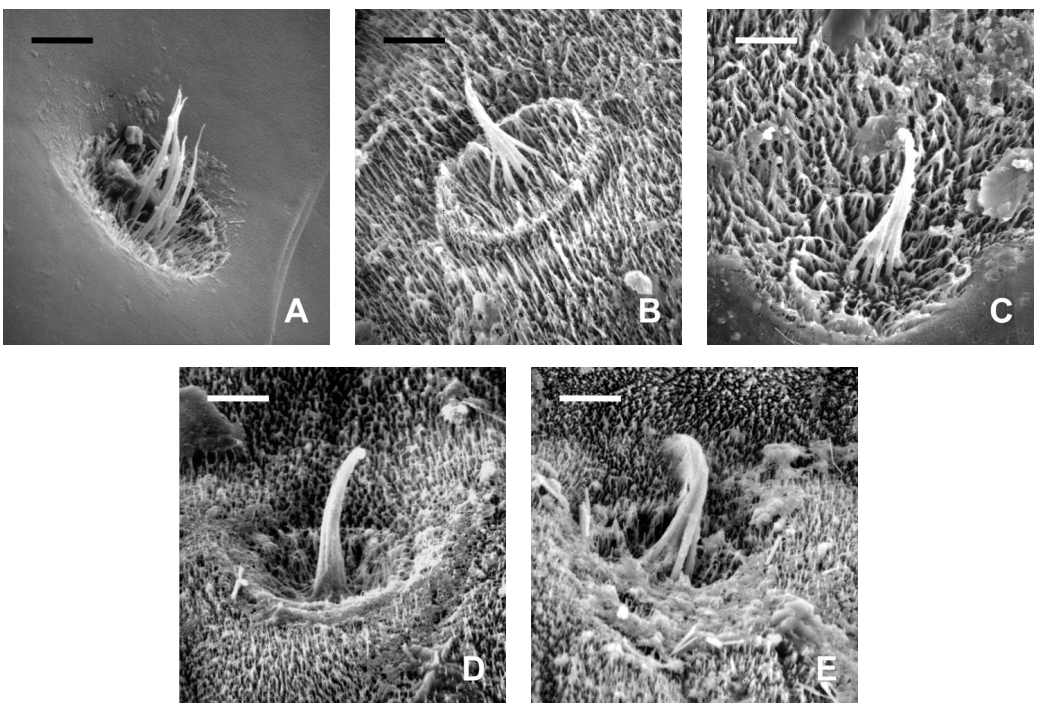

Fig. 3. SEM photos of high magnification showing variability in hair composition of skin sensory organs of *Pygopus nigriceps* (CAS 94367): A, sensory organ apparently located underneath clear/lacunar layers (c/l) of the outer epidermal generation with several individual hairs, anterior dorsal scale; B, sensory organ with the hairs fused at their tips and middle part, subocular scale; C, sensory organ with the hairs fused almost to the base, temporal scale; D, sensory organ with almost fused hairs, mid-dorsal scale; E, sensory organ with partially fused and twisted hairs, mid-dorsal scale. Lumps of shapeless material on the spinules are remnants of the clear layer of the outer epidermal generation. Scale bar is 6 μm.

In *Pygopus* species SSO were found as small lenses of 15 – 22 μm in diameter, located in shallow depressions on the surface of convex large shields of the head, or as small indentations of 12 – 22 μm in diameter, placed along the edge of imbricated scales at the back of the head, and on scales of the trunk and tail (Fig. 2).

In most cases, the lenses bore several (up to 7) central hairs in different arrangements. They may represent indi-

TABLE 3. Proximal Diameter of the Corneous Outgrowths (Spinules, Spines, Fringes, etc.) of Micro-Ornamentation of the Scales in Some Squamate Species*

Species	Diameter at the base, μm	Length, μm	Reference
Gekkota			
Carphodactylidae			
Nephrurus asper	0.28		Riedel et al., 2019: Table 3
Phyllurus amnicola	0.47		Riedel et al., 2019: Table 3
Ph. ossa	1.05		Riedel et al., 2019: Table 3
Ph. nepthys	0.54		Riedel et al., 2019: Table 3
Diplodactylidae			
Amalosia rhombifer	0.79		Riedel et al., 2019: Table 3
Lucasium damaeum	0.98		Riedel et al., 2019: Table 3
Oedura cincta	0.97		Riedel et al., 2019: Table 3
Rhynchoedura ormsbyi	1.12		Riedel et al., 2019: Table 3
Strophurus williamsi	0.43		Riedel et al., 2019: Table 3
Gekkonidae			
Chondrodactylus bibronii	0.15	0.5 – 0.75	Peterson and Bezy, 1985: Fig. 8c
Gekko gecko	0.15 – 0.18	1.0 – 1.5	Stewart and Daniel, 1972: Fig. 2b, 3b
Lygodactilus capensis	0.2 – 0.3		Alibardi and Bonfitto, 2019: Fig. 3a
Pygopodidae			
Lialis jicari	0.15 – 0.6		Spinner et al., 2013: Fig. 1
Pygopus lepidopodus	0.15 – 0.2		Shea, 1993: Fig. 28.7b
P. nigriceps	0.14 – 0.38		Present data
Sphaerodactylidae			
Gonatodes fuscus	0.1 – 0.15	0.45 – 0.65	Ruibal, 1968: Fig. 1a
Sphaerodactylus lineatus	0.2 – 0.4	0.3 – 1.5	Ruibal, 1968: Fig. 1b
Iguania			
Chamaeleonidae			
Chamaeleo calyptratus	0.6 – 0.7		Spinner et al., 2014: Fig. 1d
Dactyloidae			
Anolis carolinensis	0.12	0.9 – 1.25	Ruibal, 1968: Fig. 1d
A. cristatellus	0.15 – 0.19	0.18 – 0.48	Peterson, 1984a
Leiosauridae			
Enyalius catenatus	0.7	1.06	Peterson, 1984a
Pristidactylus torquatus	0.14 – 0.15	0.17 – 0.31	Peterson, 1984a
Phrynosomatidae			
Sceloporus magister	0.23	0.25	Peterson, 1984a
Tropiduridae			
Stenocercus guentheri	0.21(0.16 – 0.26)	1.29(0.99 – 1.67)	Peterson, 1984a
Tropidurus semitaeniatus	0.26	0.22	Peterson, 1984a
Opluridae			
Chalarodon madagascariensis	0.1 – 0.33	0.18 -1.04	Peterson, 1984a
Anguimorpha			
Lacertidae			
Gallotia stehlini	0.6 – 1.0		Arnold, 2002: Fig. 2c
Serpentes			
Acrochordus species	0.4 – 4.0*		Povel and Kooij, 1995: Figs. 2 – 4, 6, 7
Dendroaspis jamesoni kaimosae	~0.4		Arrigo et al., 2019
Toxicodryas blandingii	≤0.1		Price, 1982: Fig. 6b

* According to Schmidt (1918: tab. 5, 17), the large spinules arose from the surface of the single Oberhäutchen cell.

TABLE 4. Diameter of the Skin Sensory Organs and Sizes of Their Corneous Outgrowths (Hairs, Bristles) in Some Squamate Species*[1]

Species	SSO type	SSO diameter, μm	Proximal diameter of single hair or bristle, μm	Length of hair or bristle, μm	References
Gekkota					
Carphodactylidae					
Carphodactylus laevis	Hairy (6) with setules	22.6	1.7 – 2.0		Riedel et al., 2019: Table 4, Fig. 4C
Correlophus sarasinorum	Hairy (1)	22	1.1	20	Bauer and Russell, 1988
Dactylocnemis pacificus	Hairy (1)	13	<1	8	Dujsebayeva, 1994
Nephrurus asper	Hairy (7) with setules	24.51	0.9 – 1.9	—	Riedel et al., 2019: Table 4, Fig. 5D
N. asper	Hairy (7) with setules	15.7 – 22.6	2.0	20	Bauer and Russell, 1988
Phyllurus amnicola	Hairy with setules	22.57	1.8	—	Riedel et al., 2019: Table 4, Fig. 3F
Ph. caudiannulatus	Hairy with setules	19.4	4.4	22.2	Bauer and Russell, 1988
Ph. nepthys	Hairy with setules	23.39	5.0	—	Riedel et al., 2019: Table 4, Fig. 3C
Pseudothecadactylus lindneri	Hairy (1)	14 – 21	1.2 – 1.5	30 – 34	Bauer and Russell, 1988
Rhacodactylus auriculatus	Hairy (1)	20	1.6	25	Bauer and Russell, 1988
Uvidicolas sphyrurus	Hairy (9) with setules	22.8	3.0	15	Bauer and Russell, 1988
Woodworthia maculatus	Hairy (1)	16	1.3	23	Bauer and Russell, 1988
Diplodactylidae					
Amalosia rhombifer	Multi-hair	19.98	0.4 – 0.6	—	Riedel et al., 2019: Table 4, Fig. 7B
Bavayia sauvagii	Hairy	13	1.5	12.0	Bauer and Russell, 1988
Lucasium damaeum	Hairy (1)	17.89	0.8	—	Riedel et al., 2019: Table 4, Fig. 1B
Oedura cincta	Hairy merged bifurcated	18.72	1.2	—	Riedel et al., 2019: Table 4, Fig. 6B
Gekkonidae					
Geckolepis polylepis	Hairy (1)			60	Schmidt, 1920
Gekko gecko	Hairy (1) branched	15 – 22	~1.5	10 – 25	Lauff et al., 1993; Dujsebayeva, 1994
Paroedura picta	Hairy (1)	19	<1	20	Dujsebayeva, 1994
Phelsuma madagascariensis	Hairy (1 – 3)	19	<1	—	Dujsebayeva, 1994
Tenuidactylus fedtschenkoi	Hairy (1)	19	~1	20	Dujsebayeva, 1995
Phyllodactylidae					
Tarentola mauritanica	Hairy (2 – 3)		~0.2	20	Schmidt, 1920
Sphaerodactylidae					
Sphaerodactylus roosevelti	Hairy (1)	13	≤1	10	Dujsebayeva, 1995
Teratoscincus scincus	Hairy (1)	13 – 15	≤1	8	Dujsebayeva, 1995; Nikitina and Ananjeva, 2005
Pygopodidae					
Pygopus nigriceps	Hairy (7) partially merged	12 – 22	0.4 – 1.2		Present data
	Hairy completely merged	12 – 22	3.0 – 4.0*[2]	12 – 18	Present data
P. lepidopodus	Hairy (4)	15.7 – 17.5	0.75 – 0.9	3.3 – 15.7*[3]	Shea, 1993: Fig. 28.7A, B
Lialis jicari	Hairy (4)	~19 – 202	0.8 – 0.9*[2]	2.1 – 9.3*[3]	Spinner et al., 2013: Fig. 1E
Iguania					
Corytophanidae					
Basiliscus vittatus	Lenticular	65			Dujsebayeva, 1994
Dactyloidae					
Anolis agassizii	Multi-hair	18	—	—	Williams, 1988
A. carolinensis	Hairy (1)	18	1.2	—	Dujsebayeva, 1994
A. equestris	Hairy (1)	24	1.3	13	Ananjeva et al., 1991; Dujsebayeva, 1995
A. maculiventris	Hairy twisted	—	1.1	—	Williams, 1988
A. peraccae	Hairy (7) partially merged and twisted	—	0.4 – 0.8	—	Williams, 1988
A. taylori	Hairy twisted	16	1.5	—	Williams, 1988

TABLE 4 (continued)

Species	SSO type	SSO diameter, μm	Proximal diameter of single hair or bristle, μm	Length of hair or bristle, μm	References
		Leiosauridae			
Pristidactylus torquatus	Multi-hair	28	—	—	Williams, 1988
		Opluridae			
Chalarodon madagascariensis	Hairy merged and twisted	24	2.4 – 2.92	—	Williams, 1988
Ch. madagascariensis	Hairy merged and twisted?	30	2.5 – 3.42	—	Ananjeva et al., 1991; Dujsebayeva, 1995
Oplurus cyclurus	Hairy merged and twisted?	27	2.72	—	Ananjeva et al., 1991
O. fierinensis	Multi-hair	33	—	—	Williams, 1988
O. quadrimaculatus	Hairy merged and twisted?	30	2.72	40 – 54	Ananjeva et al., 1991; Dujsebayeva, 1995
		Phrynosomatidae			
Sceloporus torquatus	Lenticular	54 – 65			Ananjeva et al., 1991
		Agamidae			
Acanthosaura armata	Bristled	44	10	80	Ananjeva and Matveyeva-Dujsebayeva, 1996
Calotes jubatus	Bristled	—	—	160 – 240	Schmidt, 1920
C. nigrilabris	Bristled	45	—	40 – 65	Hiller, 1978
Ceratophora tennentii	Bristled	60	6.5	—	Ananjeva et al., 1991
Diporiphora bilineata	Lenticular	74			Dujsebayeva, 1994
D. nobbi	Lenticular	60 – 70			Ananjeva and Matveyeva-Dujsebayeva, 1996
Draco blanfordii	Bristled	47	4.7	40 – 50	Ananjeva et al., 1991; Dujsebayeva, 1995
Gonocephalus grandis	Bristled	40 – 85	6 – 10	Up to 45	Scortecci, 1941; Ananjeva and Matveyeva-Dujsebayeva, 1996
G. liogaster	Bristled	~40	4.5	53	Ananjeva and Matveyeva-Dujsebayeva, 1996
Hypsilurus spinipes	Lenticular	46 – 74			Ananjeva and Matveyeva-Dujsebayeva, 1996
Paralaudakia caucasia	Bristled	57	9.5	—	Ananjeva et al., 1991
P. himalayana	Bristled	40	8.0	60 – 100	Dujsebayeva, 1995
P. lehmanni	Bristled	57	7.6	—	Ananjeva et al., 1991
Phrynocephalus helioscopus	Bristled	50	17.2	—	Ananjeva et al., 1991
Ph. interscapularis	Bristled	54	11.0	—	Ananjeva et al., 1991
Ph. mystaceus	Bristled	86	10	≤40	Dujsebayeva, 1995
Physignathus cocincinus	Lenticular	130			Ananjeva et al., 1991
Pogona barbatus	Lenticular	60 – 100			Maclean, 1980
Trapelus mutabilis	Bristled	60	15.0	—	Ananjeva et al., 1991
T. ruderatus	Bristled	80	5.4	—	Ananjeva et al., 1991
T. sanguinolentus	Bristled	90	5.4	80 – 110	Ananjeva et al., 1991; Dujsebayeva, 1995
		Chamaeleonidae			
Chamaeleo gracilis	Multi-hair	48	—	—	Williams, 1988
Furcifer lateralis	Multi-hair	60	—	—	Ananjeva et al., 1991
F. rhinoceratus	Multi-hair	90	—	—	Ananjeva et al., 1991
		Anguimorpha			
		Anguidae			
Anguis fragilis	Slight indentations	60			Walzthöny and Ziswiler, 1979

*[1] The measurements were done only from the outer generation of SSO; number of the hairs in the sensory organs examined is given in the brackets.
*[2] The total diameter of the merged filaments.
*[3] The minimal mean is likely the result of the corneous outgrowth breaking.

vidual filaments (Fig. 3A), be merged to varying degrees including complete fusion (Fig. 3B – D), or be merged and slightly twisted (Fig. 3E). Completely fused hairs were 12 – 18 μm in length, 3.0 – 4.0 μm at their base and about 1.0 μm at their tip (Table 4). Diameter of separate filaments at their base varied within the approximate limits of 0.4 – 1.2 μm (*Ibid*). The surface of SSO lens as well as the surrounding scale surface was covered by Oberhäutchen spinules often merged at their tips which resembled the hairy SSO in miniature. Among the labial and dorsal scales of both *Pygopus* species we found scales with an almost smooth surface and SSO without any outgrowths (Fig. 2C, D) showing an artifactual detachment of outer β-layer and Oberhäutchen. The surfaces of such scales and sense organ lenses were covered with α-keratin layer and the remnants of the mesos-layer.

SSO position on the shield or scale depends on shape of the shield/scale and its position on the head. Polygonal or rectangular slightly convex or flattened shields of the anterior third of the head of both species have abundant receptors distributed irregularly and more or less evenly across their surfaces (Fig. 2A). SSO are also scattered randomly on the labial shields (Fig. 2C) but they appear at higher density on the shield margins opposite the labial rim as well as on the posterior margins. Within the frontals the receptors are concentrated on the shield periphery and are irregularly scattered at lower density across the central shield surface. The occipital and supraocular shields and the postocular and temporal scales bear the receptors only along their peripheral borders, quite often in up to 2 – 3 rows. The imbricate scales of the flank and tail have few receptors along their distal borders (Fig. 2B, D).

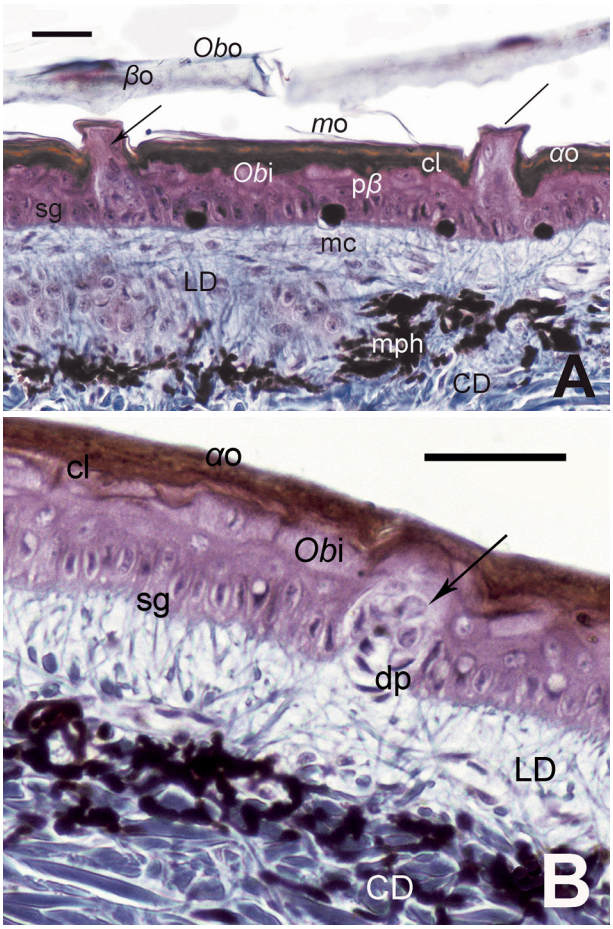

Fig. 4. Histology of the integument and skin sensory organs of *Pygopus lepidopodus* from different labial scales (A, B) at stage 4 of the renewal phase of the shedding cycle (according to Maderson, 1985), Masson's trichrome staining. Outer epidermal generation consists of mature Oberhäutchen (Obo), corneous β-layer (βo), mesos-layer (mo), α-keratin layer (αo); the lacunar tissue (lt) and clear layer (cl) already losing their cellular structure. The Oberhäutchen of the inner generation (Obi) is visible as a layer of large polygonal cells with granular cytoplasm and first picnotic nuclei. It underlies by first layers of presumptive β-cells (βi). The dermis is represented by loose (LD) and compact (CD) layers. The skin sensory organs have central dermal papillae (dp) with superficially located lightly-staining modified epithelial cells (arrows) and covered by thin corneous membrane (line). The absence of corneous hairs in the apical part of SSO is caused by the detachment and displacement of the outer Oberhäutchen (Obo) and β-layer (βo) layers. Rare melanocytes (mc) occur among the ovoid germinative cells (sg); the bodies of the dermal melanophores (mph) are located at the boundary of loose and compact dermis and have their dendrites stretching to the base of the stratum germinativum. Scale bar is 25 μm.

Microanatomy of the Skin Sensory Organs

The epidermis of *P. lepidopodus* was at Stage 2 of the renewal phase of the shedding cycle according to Maderson (1985) and exhibited the still immature outer generation and first presumptive layers of the inner generation lying above the stratum germinativum. The outer generation consisted of a mature Oberhäutchen, β-layer, mesos-layer and α-layer, poorly expressed immature lacunar with flattened chromophilic cells and the clear layer formed by large rectangular light cells with visibly granulated cytoplasm and rare picnotic nuclei (Fig. 4A). The inner generation consisted of immature Oberhäutchen and 1 – 2 layers of presumptive β-cells. The cells of inner Oberhäutchen somewhat resembled the clear cells but had a more streamlined and flattened oval shape. The germinative cells, of columnar shape, showed numerous divisions and sometimes alternated with rounded melanocytes (Fig. 4A). The dermis showed clear division into loose and compact layers. The dermal melanophores were distributed in the base of the loose dermis and in the upper portion of the compact dermis (Fig. 4B).

On the histological sections, SSO of *P. lepidopodus* were detected as small papillae of about 18 – 19 μm in diameter (Fig. 4A). We did not find the hairs that were visible under SEM, which could be explained by their loss during histological preparation (Landmann, 1975; Dujsebayeva, 1995). There was a small tooth-like dermal papilla at the base of the receptor and above located modified light cells with basal nuclei and larger size comparatively with surrounding germinative cells (Fig. 4B). The keratin layers above the modified cells were visibly thinner.

DISCUSSION

> Nous sommes nés à quêter la vérité il appartient de la posséder à une plus grande puissance
> Essais, Montaigne

Micro-Ornamentation and Skin Sensory Organs of Pygopod Scales Compared with Other Squamates

At low magnification, we have described MaO of the suboculars of *Pygopus* species as type 4 — the "simplest pattern consist[ing] of irregular, polygonal cells with juxtaposed cell boundaries" following Peterson (1984b: p. 40) (Fig. 2A). An arrangement of elongated cells of the dorsal scales (Fig. 2B) resembled a shortened "lamellate" MaO pattern (Peterson, 1984b) but actually was the same as the "simplest" one because the cell junctions were clearly juxtaposed without a forming a lamellar or overlapping arrangement. We have detected only spinulate MiO for suboculars, temporals and mid-dorsal scales (Fig. 3) but because of limited material we could not check the differences in MiO within all regions of the lizard body as was carefully done by Spinner et al. (2013) with the example of two *Lialis* species. He distinguished spined (obviously, spinulate modification), pitted, nanoridged, and honeycombed (seemingly micro-honeycombed) MiO in different body regions, and even within the same scale, and emphasized the importance of functional correlations between the scale microsculpture and lizard biology.

Underwood (1957: p. 227, Fig. 9) described several types of SSO in the integument of *Delma*, *Lialis*, and *Pygopus*: simple lenticles with bare surfaces, lenticles with "one or several tiny papillae" like a tuft of villi, hair-bearing lenticles (up to 4 hairs in *Pygopus*), and unusual double lenticles, and indicated their location within the scales. The presence of hairy SSO with 1 – 10 central individual filaments was confirmed for the integument of *P. lepidopodus* and two *Lialis* species (Shea, 1993; Spinner et al., 2013). Our study of *D. nasuta* and two *Pygopus* species has revealed SSO with 1 – 7 hairs per organ and their compositions as are described as merged and twisted forms (Fig. 3). "Hairless" receptors and bare MiO on the scales of the head and body observed by us were due to the loss of the outermost corneous layers (Fig. 2C, D). Such an artefact, especially common in museum specimens, is often a reason of incorrect interpretation of morphological features of integumentary derivatives in MiO and SSO (Bauer and Russell, 1988; Irish et al., 1988; Ananjeva and Matveyeva-Dujsebayeva, 1996). In this context, the remarks of Underwood (1957) on the "simple lenticles" (with bare surface) in the integument of pygopods are doubtful. SSO in all the pygopod species described here and elsewhere typically had relatively small sizes (Table 4).

We have confirmed the observations of earlier researchers regarding the great similarity of spinulate MiO and hairy SSO in pygopods and the geckos (Underwood, 1957; Landmann, 1975; Spinner et al., 2013). That similarity was expressed in spatial distribution and sizes of MiO spinules on the scale surface, and in the small size, external and inner morphology of SSO, including the sizes, diversity and composition of their hairs and hair inner structure (Tables 3 and 4; Schmidt, 1913, 1920; Ruibal, 1968; Hiller, 1971; Joger, 1984; Dujsebayeva, 1995; Röll, 1995; Nikitina and Ananjeva, 2005; Darvish, 2012; Alibardi and Bonfitto, 2019; Riedel et al., 2019). We only failed to find sensory organs with bifurcated hairs, as occurs in some geckos (Sammartano, 1980; Bauer and Russell, 1988; Lauff et al., 1993) as well as the sensory organs like tufts of villi described by Underwood (1957) for some pygopods.

In MiO and SSO the pygopods, together with geckos, resemble the pleurodont iguanians of the families Dactyloidae, Leiosauridae, and Opluridae and the acrodont lizards of the Chamaeleonidae. These lizard taxa had SP MiO as the dominant pattern and possessed SSO of small (or rarely medium) sizes (Table 4) with a variety of hair-like corneous outgrowths (Schmidt, 1920; Schleich and Kästle, 1979; Peterson, 1984a; Etheridge and de Queiroz, 1988; Irish et al., 1988; Williams, 1988; Ananjeva et al., 1991; Dujsebayeva, 1995).

The morphology and microanatomy of the units forming SP MiO in the gekkotan lizards and the iguanian groups enumerated above, their sizes (Table 4) and hexagonal pattern (Ruibal, 1968; Peterson, 1984a; Maderson et al., 1998; Koppetsch et al., 2020) confirm that they are "intracellular in origin" (Ruibal, 1968). They are produced as the cytoplasmatic foldings or outgrowths of the

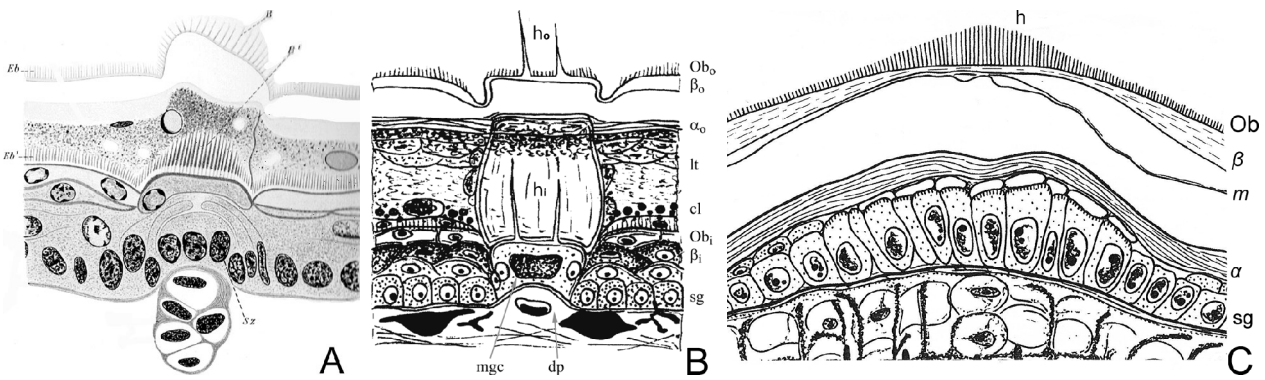

Fig. 5. Schemes of microanatomy of Oberhäutchen hairy sensory organs (ObHSO) in gecko and chamaeleon skin showing a transition between the spinules of the Oberhäutchen cell surface and the corneous outgrowths of the sensory organs: A, *Uroplatus fimbriatus* (from Schmidt, 1913 with selective abbreviations); B, *Sphaerodactylus* roosevelti (from Dujsebayeva, 1995 with changes); C, *Chamaeleo* sp. (from Dujsebayeva, 1994). See abbreviations in Fig. 4; ho (B in "A"), hair of the outer epidermal generation; hi (B' in "A"), hair of the inner epidermal generation; mgc (Sz in "A"), modified germinative cells of the sensory organ.

Oberhäutchen cell surface[4], as was described in *Anolis carolinensis* (Maderson et al., 1998).

Compositional diversity of the corneous outgrowths in the hairy SSO (including their varieties, such as fused or twisted) known for gekkotan, dactyloid, oplurid and chamaeleonid SSO and described here for pygopodids, significantly resembles that of MiO spinules, surpassing the last almost only in diameter and height (Fig. 3, Tables 3 and 4). The twisting of filaments in the hair composition of SSO described using SEM by Williams (1988) in *Anolis* species and *Chalarodon madagascariensis* and by us in *P. nigriceps* (Fig. 3E), has been demonstrated for simple Oberhäutchen spinules from the scales of *Anolis carolinensis* (Maderson et al., 1998: Fig. 10). Schmidt (1913) first pointed out the homology of Oberhäutchen spinules and sensory organ hairs finding all possible intermediate structures between these structures in the integument of *Uroplatus fimbriatus* (Fig. 5A). Subsequently, such transitions have been confirmed repeatedly (Fig. 5B, C; Schmidt, 1920; Sammartano, 1980; Dujsebayeva, 1994, 1995).

Thus, at the cellular level, as derivatives of the cells of the same layer of epidermal generation, the spinules of MiO and hairs of SSO of Gekkota and some iguanian lineages can be accepted as homologous structures. A singularity of SSO of Australian geckos of the family Carphodactylidae — *Nephrurus*, *Phyllurus*, and *Underwoodisaurus* bearing thick hairs with setules throughout its length (Russell and Bauer, 1987; Bauer and Russell, 1988; Riedel et al., 2019) does not go beyond the general morphogenetic potency of the Oberhäutchen cells to produce the folds. A fundamentally similar pattern with setules scattered along the hairs of SSO also occurs in the gecko *Gekko gecko* (Lauff et al., 1993) and *Gonuisaurus luii* (Koppetsch et al., 2020), at the base of simple spinules of MiO in iguana *A. carolinensis* (Maderson et al., 1998: Fig. 10) and even on the hairs of SSO in acrochordid sea snake *A. javanicus* (Povel and Kooij, 1997). Resurrecting the term "Oberhäutchen multi-hair organ" proposed by Williams (1988: p. 451), we suggest that the gekkotan, dactyloid, oplurid and chameleonid SSO with their corneous outgrowths derived from MiO be called "*Oberhäutchen hairy sensory organs*" (ObHSO) meaning by the term "hair" specifically the enlarged derivatives of the Oberhäutchen cell surface. Different types of SSO distinguished by Williams (1988: Figs. 16, 18, 19) in anoline (= dactyloid) lizards are actually variations of single generalized type of ObHSO.

The general cellular basis for development of MiO and the external morphological characteristics of SSO and the general morphogenetic potencies of the uppermost corneous layers of the epidermis, on the one hand, and uncontested monophyly of Squamata (Gauthier et al., 1988; Pyron et al., 2013; Zheng and Wiens, 2016), on the other, provides the basis for interpreting the similarity in MiO and the external morphology of SSO in representatives of Gekkota and Iguania as homoplasy. For the epithelium of the skin, the broadscale expression of "closely related" parallelisms — the independent appearance of similar new characters in related forms, is a characteristic phenomenon (Zavarzin, 1986).

Outside of Gekkota and iguanians of the families Dactyloidae, Leiosauridae, Opluridae and Chamaeleonidae, SP MiO sporadically occurs in other iguanian families and in Autarchoglossa which are characterized by other

[4] Based on existing data, the diameter of all Oberhäutchen cells ever measured ranges from 4 – 12 μm (Ruibal, 1968; Arnold, 2002).

dominate types of Mio and SSO. In spite of predominance of almost smooth or pit-and-grooves generalized patterns of MiO (or their modifications) in pleurodont iguanians (Ruibal, 1968; Stewart and Daniel, 1975; Peterson, 1984a; Peterson and Bezy, 1985; Etheridge and de Queiroz, 1988; Irish et al., 1988; Williams, 1988; Price and Kelly, 1989), SP MiO has nevertheless been found in some corytophanid, crotaphytid, phrynosomatid and tropidurid species (Stewart and Daniel, 1975; Cole and van Devender, 1976; Peterson, 1984a; Irish et al., 1988; E. E. Williams, personal communication). These lizards possess only lenticular sensory organs of large or medium sizes (Table 4) and lack any corneous outgrowths (Scortecci, 1940; Williams, 1988, personal communication; Ananjeva et al., 1991).

Lauff et al. (1993) wrote that the "...the autarchoglossan squamates… lack a spinulate scale microarchitecture..." (p. 2468). Actually, most of the species of Anguimorpha, Lacertoidea, Scincoidea and Serpentes have been described as having almost smooth, pitted, verrucated, or reticulated microarchitecture or are expressed in the form of straight or labyrinthine channels MiO (Ruibal, 1968; Stewart and Daniel, 1973, 1975; Williams and Peterson, 1982; Harvey and Gurberlet, 1995; Beyerlein, 1998; Pauwels et al., 2000; Berthé et al., 2009; Spinner et al., 2015; Arrigo et al., 2019). However, SP has been found in some lacertid, varanoid and teiid lizards (Gans et al., 1982; Arnold, 2002; E. E. Williams, personal communication) and identified in several snake species (Price, 1982; Arrigo et al., 2019). With one exception, all autarchoglossans possessed SSO as slight indentations or low bulges with a surface lacking any corneous outgrowths (Ruibal, 1968; Stewart and Daniel, 1973, 1975; Williams and Peterson, 1982; Harvey and Gurberlet, 1995; Beyerlein, 1998; Pauwels et al., 2000; Berthé et al., 2009; Spinner et al., 2015; Arrigo et al., 2019). The exception being the aquatic wart snakes of the family Acrochordidae, which have bizarre MiO with long flexible filaments and hair-bearing SSO (Fig. 8D, E; Price, 1982; Povel and Kooij, 1997; Arrigo et al., 2019), where the single hair projection is seemingly derived from the whole surface of an Oberhäutchen cell (Schmidt, 1918).

Spinulate Micro-Ornamentation and the Oberhäutchen Hairy Sensory Organs as the Primitive Characters of the Scale Integument of Squamata

Thus, SP of MiO and ObHSO have been found in two large lineages of Squamata — Gekkota and Iguania. Among them they are present in all representatives of Gekkota and are typical for several pleurodont families of Iguania. SP also sporadically occurs in the scales of other pleurodont iguanians and some autarchoglossan species. Such characters can be interpreted as primitive for Squamata, and seemingly arose deep in their evolution (Bauer, 2019). To a certain extent, this assumption may be supported by some peculiarities of the scale integument. Many such species are characterized by pholidosis of non-overlapping or weakly overlapping scales (geckos, dactyloids, polychrids, leiosaurids, *Chalarodon*: Schmidt, 1913; Peterson, 1984a; Riedel et al., 2019), while in embryogenesis a stage of symmetrical primordia precedes their asymmetrization (Maderson, 1965, 1985; Dhouailly and Maderson, 1984; Alibardi, 1996; Dujsebayeva, 2008). In addition, in species with overlapping scales and a dominant non-spinulate MiO pattern (like the iguanians *Tropidurus* and *Stenocercus*), the separate fields of the spinules are often found on the proximal cells of the scales (Burstein et al., 1974; Peterson, 1984a), undergoing minimal changes during asymmetrization (Alibardi, 1999). Finally, SP MiO and hair outgrowths of SSO can be regarded as an example of multiple formation of structures, i.e., iteration of homologous organs, in which few conditions for the primitiveness of such a state are satisfied (Dogel, 1954): (1) the development of a large number of homologous units, (2) variability in size of homologous units (Maderson et al., 1998), and (3) variability in the number of the units (for hairs of SSO).

The early evolution of SP MiO structures is confirmed by the discovery of the fossil gecko *Cretaceogekko burmae* with adhesive toe-pads preserved in mid-Cretaceous Burmese amber (Arnold and Poinar, 2008; Daza et al., 2014; Bauer, 2019) and even older gecko-like fossil lizards *Eichstaettisaurus schroederi* and *Ardeosaurus digitatellus* from Late Jurassic (160 – 145 mya), where the likely presence of seta-like subdigital structures (known to be derivatives of the Oberhäutchen cell surface: Kunitzky, 1904; Schleich and Kästle, 1979; Alibardi, 2020) has been inferred with great reliability (Simões, 2018).

Although we interpret SP and ObSHO as possibly plesiomorphic integumentary structures for Squamata, we doubt they were the only ones. Pitted MiO (pit-and-groove, pit-and-groove dentate and other modifications) have been found in basal lacertids, xantusiids, gerrhosaurids, some cordylids and anguids (Stewart and Daniel, 1973, 1975; Peterson and Bezy, 1985; Harvey and Gutberlet, 1995; Arnold, 2002). Almost smooth or slightly scuptured MiO occurs in hoplocercids, *Iguana*, some other lizard families (Peterson, 1984b), *Heloderma* (Alibardi and DeNardo, 2013), and *Sphenodon punctatus* —

the surviving lepidosaurian sister group of Squamata (Peterson, 1984b). The initial differentiation of the main lines of Squamata in the Jurassic or even at the boundary with the Triassic (Estes, 1983; Evans, 1993; Zheng and Wiens, 2016), suggests that the evolution of the considered integumentary derivatives has followed the principle of "combinatorics of characters" (Mamkaev, 1981). It is known that the initial stages of the formation of new taxa are characterized by a violation of the stability of the previous characters, an increase in variability, with the presence of both ancestral and derived modes, and a manifestation of different directions of their development (Carroll, 1977; Tatarinov, 1976; Ivakhnenko, 1988; Vorobyeva, 1992; Rieppel, 1997; DeMar et al., 2017; Shishkin, 2019). Subsequent selection limits the number of realized outcomes (Arnold, 2002). In Squamata, this is supported by the retention of several generalized patterns of scale microstructure (Peterson, 1984a, 1984b) and several generalized types of SSO (Scortecci, 1940, 1941; Etheridge and de Queiroz, 1988; Ananjeva et al., 1991). The external morphological design of the last, i.e., sculpture of a thin keratin membrane and presence-absence of corneous outgrowths is seemingly determined by the dominant pattern of microstructure (MaO and MiO).

Stability and Plasticity of the Scale Derivatives

MiO is a variable structure. In related species, in similar regions of the body, one dominant pattern can be replaced by another (as on the dorsal body scales of the geckos and pygopods: Spinner et al., 2013); two or more patterns can occur in different body region of the same species (Peterson, 1984a) or even within the same scale as on keeled scales (Peterson, 1984a; Maderson et al., 1998). There may be "transitional zones" between the different patterns (Peterson and Bezy, 1985), and MiO can change during ontogenesis (Price and Kelly, 1989; Harvey, 1993). MiO units such as the surface outgrowths of the Oberhäutchen cells are simple elementary morphological structures — dynamic, or "mobile," and the functional adaptations play a significant role in their development.

To the contrary, SSO are structures of a more inclusive hierarchical level. They consist of several tissue types — epithelial, connective, and nervous and are characterized by complex functional relationships with other organs (first, the nervous system). They are stable morphological structures at the supraspecific level despite the different ecological preferences of their constituent species. Actually, at present there are no reliable data validating the presence of two or more types of SSO in the same taxon. The lenticular SSO described by Scortecci (1941) together with bristled SSO in some agamid lizards, actually were an artifact result of loosing of outermost corneous layers (Ananjeva and Matveyeva-Dujsebayeva, 1996) as were the hairless "simple lenticles" of pygopods found by Underwood (1957).

On the Unique Abundance of the Sense Organs in the Integument of Pygopodidae

Although Underwood (1957) did not find SSO on the back of any pygopod species studied, we found them all over the head and body of *D. nasuta*, except on the ventrals, precloacals and scales of the inner side of the legs, and all over the head, neck and sacrum of *P. lepidopodus* (Tables 1 and 2). It is difficult to argue that such a selective picture corresponds to reality, since the material is often of inadequately preserved.

Peculiarities of SSO distribution within the head and body of pygopodids with their greater number on the dorsal body surface and maximal density in the prefrontal part of the head (Figs. 1 and 2; Table 1) corresponded to the general pattern of SSO arrangement in Squamata (Schmidt, 1920; Jackson, 1977; Matveyeva and Ananjeva, 1995; Sherbrooke and Nagle, 1996; Povel and Kooji, 1997; Crowe-Riddell et al., 2019). Such an arrangement has been explained in terms of significant functional loading of the prefrontal part of the head (Breyer, 1929; Oreyas-Miranda et al., 1977; Sherbrooke and Nagle, 1996).

The number of SSO within the scales of prefrontal part of the head of pygopods studied was impressive. Except for Underwood (1957) who indicated approximately 350 SSO on the infralabials of *Delma* (figure "Di," p. 228) nobody has previously precisely calculated the number of SSO in pygopods. We have counted up to several hundred SSO for the rostral, mental, and second labial scales, and up to one hundred for other shields and scales of the frontal part of the head of *Delma* and *Pygopus* (Fig. 1; Table 1).

Two possible explanations can be proposed to account for such data. In terms of evolutionary morphology, a high number of homologous organs has been accepted as a phenomenon of iteration. The iterative state of the organs may reflect their primitive condition, which may be described as a primary ubiquitous response to environmental influence by the appearance of multiple homologous organs, or indicates specialization when organ multiplication is a response to functional needs (Remane, 1952; Dogel, 1954). Instability of the position of iterative homologous units in the body as well as variability in their size and/or in external morphology (Dogel, 1954) may be considered plesiomorphic.

The application of this hypothesis to the number of squamatan sensory organs is still controversial. Although the iterative state of SSO on the cephalic scales characterizes representatives of all major stocks of Squamata (Schmidt, 1910; Breyer, 1929; Aota, 1939 – 1940; Oreyas-Miranda et al., 1977; Jackson and Sharawy, 1980; Matveyeva and Ananjeva, 1995; Crowe-Riddell et al., 2019), there seems to be a trend towards a greater number of SSO on the same scales in basal taxa and fewer in derived ones. In the relatively basal squamate lineage Gekkota all species examined so far have relatively abundant SSO on the cephalic scales and on some regions of the rest of body (Bauer and Russell, 1988; Lauff et al., 1993; Matveyeva and Ananjeva, 1995). Within Acrodonta the iterative condition of SSO was found only in the agamid genera *Physignathus*, *Hypsilurus*, and *Chelosania* (Matveyeva and Ananjeva, 1995; Ananjeva, 2019) which occupy basal positions in the phylogenetic tree of Agamidae (Macey et al., 2000; Pyron et al., 2013). The abundance of SSO shown for the cephalic shields of the species of Typhlopidae (Aota, 1939 – 1940) and Leptotyphlopidae (Oreyas-Miranda et al., 1977) is consistent with the basal position of these groups within Serpentes (Streicher and Wiens, 2016; Zheng and Wiens, 2016). On the other hand, a scarcity of SSO of the scale integument of *Sphenodon punctatus* and the species of the basal acrodontan family Uromastycidae (Ananjeva and Dujsebayeva, 1997; Dujsebayeva et al., 2004) contradicts the statement about the primitiveness of the iterative condition. Pygopods, as representatives of Gekkota, have retained many plesiomorphic morphological features (Underwood, 1957) and their unique high abundance of SSO supports the assumption of the high-iteration SSO number as the primitive character state.

Alternatively, when discussing the problem of the distribution of any sensory organs, the functional aspect seems to be no less relevant. The known data show that especially high numbers of SSO of the prefrontal part of the head are often found in species with a fossorial or semi-fossorial mode of life and poorly developed or completely reduced organs of the other senses. Schmidt (1910) found a hundred or more sensory organs on each shield of the upper and lateral head surface in *Voelzkowia mira* — a Malagasy skink, with absolute loss of hearing and vision. A total of 1100 SSO occurred on the head scales of *Typhlops braminus* (= *Indotyphlops braminus*), Aota (1939 – 1940) counted 636 for its anterior part, including the superior nasal — 172, inferior nasal — 152, rostral — 142 and supralabials — 94 – 140. A similar abundance was shown for *Rena dulcis* and *Epictia munoal*, where the maximal number on the rostral shield reached 212 and the upper nasals possessed 63 sensory organs (Oreyas-Miranda et al., 1977).

Returning to the question of the phylogenetic or functional (ecological) drivers of the morphology of the scale microstructures, we support those authors who have taken dualistic approach. The affinity with geckos determines the dominant spinulate pattern of pygopodid scale micro-ornamentation and the hair-bearing type of their SSO. The variability of micro-ornamentation patterns that is more evident on the snake-like body scales, reflects the specificity of the mode of life and indicates that the manifestation expressed is conditional on function. The abundance of SSO in pygopodid lizards can be characterized as a phenomenon of "overiteration," in which the phylogenetically established condition is enhanced by functional demands on the organism.

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