

Ecomorphological Study of Scales in Some Genera of the Viperid and Colubrid Snakes (Ophidia: Viperidae: Colubridae)

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Abstract

Ecomorphological studies are aimed to find out the relation between the morphology of organisms and their ecology. Many studies on reptile scale microornamentation indicate that it has important functional values. In this study microornamentation and light reflection of scales' surface among six viperid and two colubrid snake species in relation to their habitat were examined. To compare microornamentation and light reflection analyses, skin specimens were prepared and analyzed using scanning electron microscopy and FluoVision Imaging System and spectrometer, respectively. The results showed that snake species inhabiting similar habitats had different microornamentation and vice versa. Likely the scale microstructures are more influenced by phylogenetic relationships than by the environment. In examining the scales' reflection, different species and different body parts reflect various wavelengths of visible light, which relates to ecological condition of them.

1 Introduction

Ecological morphology also known as ecomorphology is a comparative discipline with its central focus on the study of the interaction between morphological and ecological diversity of organisms both in the present and over evolutionary time (Kotrschal and Motta, 1991). The morphological adaptations and ecological characteristics are closely correlated because the interspecific morphological differences result from the distinct selective pressures that they suffer (Beaumord and Petrere Jr, 1994). Interactions between ecology and morphology can be studied at multiple levels; among taxonomic units or life history intervals and between their phenotypic characteristics and their use of ecological resources in a particular environment (Norton et al., 1995). Skin as a phenotypic characteristic is a boundary between animals and their environment, serving multiple roles such as acting in protection, contributing to locomotion, maintaining moisture of the body, altering the characteristics of the skin, helping in camouflage, capturing prey, as well as contributing to physiological regulation, sensory detection, respiration, and coloration (Abo-Eleneen and Allam, 2011; Vitt and Caldwell, 2013). Snake's scales are essentially made of folds of epidermis and dermis; however, the scales themselves are essentially originated from the epidermis. The number of scales neither increases nor reduces as the snake matures over time, but the scales grow larger and may undergo changing in shape as the snake exuviates (Swadźba and Rupik, 2010; Abo-Eleneen and Allam, 2011). Most of the body surface in reptiles is covered by these keratinized epidermal scales. Two keratin types contribute to the formation of scales; the β -keratin covering entirely the scale's surface, and α -keratin constructing the interscalar space or suture. This distribution of keratin produces a durable and protective scale surface with junctures between the scales that allow flexibility and expansion of the skin (Vitt and Caldwell, 2013). Generally called "Oberhautchen", The β -layer of scale is in direct contact with the environment. The oberhautchen exhibits a particular micro-structure in several squamate reptile groups and often is divided into cell-like parts that may

bear complex three-dimensional features. The overall arrangement of these cells and their surface features are called microornamentation (Ruibal, 1968; Stewart and Daniel, 1973; Arnold, 2002). Scale shape, extent, and microornamentation can serve as important characteristics for taxonomic and systematic investigations (Leydig, 1873; Picado, 1931; Price, 1982). Microornamentation variability may be arises from adaptation pressures directly acting upon scales, and could play important taxonomic role in discriminating generic and specific, but not family categories (Rocha-Barbosa and Moraes e Silva, 2009; Crowe-Riddell et al., 2016). Several studies have surveyed the association of scale microornamentation and systematics and ecological variation. According to these studies, since the ultrastructural features of scales might be relatively free from direct adaptational pressures, they could well be more reliable indicators of interspecific relationships (Burstein et al., 1974). Price (1982) reported that microornamentation patterns reflect the phylogenetic relationships, rather than environmental or habitat impacts and that there was no evidence for a correlation between microornamentation and habitats or environment. Nevertheless, microstructures have been used as tools in ontogenetic and/or evolutionary studies of squamates (Harvey and Gutberlet Jr, 1995). Gower (2003) and Pough et al. (2003) have found strong correlation between scale microornamentation and ecology, emphasizing that certain kinds of micro-ornamentation are associated with certain habitats.

Solar radiation consist of a wide range of wavelengths and affect all creatures on Earth. Sunlight primarily are divided into visual, ultraviolet and infrared wavelengths that absorbed or reflected by animate and inanimate surfaces. In animals the skin is in direct contact with the environment and play an important role in absorbing or reflecting visible and invisible light. Many invertebrates and vertebrates have the ability to perceive UV light and also possess UV-reflective structures on their body surface (Shi and Yokoyama, 2003; Modarressie et al., 2013). The roles of UV in vision are manifold from animal communication, guiding navigation and orientation behavior, to detecting food and potential predators (Modarressie et al., 2013).

P. persicus and *P. fieldi* inhabit sandy and rocky terrains with moderate vegetation of bushes and grasses. They are nocturnal in habits, retreats during the day into crevices among rocks or burrows in comparatively hard soil near roots of bushes. Their diet consists of deserticolous lizards, mice, and arthropods (Khan, 2011). The immediate habitat of the *P. urarachnoides* contains hill and high grounds mostly composed of gypsum. It prefers deep cracks and holes in the gypsum substrates to benefit moisture and coolness in the warm months of summer (Fathinia et al., 2009). Its main diet in adulthood is migratory passerines (Fathinia et al., 2015). *E. macmahonii* is morphologically adapted to live in fine loose sand of shifting dunes. Its habitat is without any mentionable vegetation, except for very sparse growth of stunted bushes and grasses (Khan, 2011). *E. carinatus* recorded from sandy and rocky alluvial habitats, with sparse xerophytic to moderately dense grass and scrub vegetation. In mountainous habitats it lives under rock blocks, while in sub-mountainous regions inhabits hedges and other scrubby vegetation, noticeably avoiding marshy areas and very dense vegetation (Khan, 2011). *Cerastes gasperettii* as a nocturnal true desert snake prefer sandy soil regions with high temperature and some vegetation as shelters (Sadoon and Paray., 2016). *Eirenis rafsanjanicus* inhabits mountain areas with substrates compose of clay soil covering with numerous pebbles, and annual and perennial plants (Akbarpour et al., 2020). *Lythorhynchus maynardi* inhabits sandy terrains covered by bushes. The vegetation is dominated by *Tamarix* sp. and a syntopic snake species is *Echis carinatus*.

The present study is aimed to: 1) compare microstructure variation in scale surface using SEM, 2) discover variation in light reflection of scales among snake species in two families and five genera occupying both the same and different microhabitats, and 3) explore the taxonomic-ecomorphological association in the concerned species.

2 Materials and methods

The materials used in the present study were obtained from snake specimens stored in ethanol 70% in the reptile collection of the Razi University Zoological Museum (RUZM) and the Zoological Collection of Reza Babaie Savasari (ZMRBS). 22 adult snake specimens from seven species were investigated. The selected snakes included six viperid and two colubrid species. These snakes are found in different regions and inhabit more or less different habitats in the Middle East. The Viperinae or old world vipers are a subfamily of venomous snakes endemic to Europe, Asia, and Africa. The Viperinae genus *Pseudocerastes* Boulenger,

1896, comprises three species; *Pseudocerastes persicus* (Duméril, Bibron & Duméril, 1854), *Pseudocerastes fieldi* Schmidt, 1930 and *Pseudocerastes urarachnoides* Bostanchi, Anderson, Kami & Papenfuss, 2006. The specimens used in this study were collected from Kerman Province, Iran for *P. persicus*, from southwestern Iraq for *P. fieldi*, and from Ilam province in western Iran for *P. urarachnoides*. The monotypic genus *Eristicophis*, represented by *E. macmahonii* Alcock & Finn 1897, was captured in Nushki province, southwestern Pakistan. Genus *Cerastes*, represented by *Cerastes gasperettii* Leviton & Anderson, 1967, was captured in Khuzestan province, southwestern Iran, and al-Diwaniyah Governorate, Iraq. Genus *Echis* represented by *E. carinatus* which was collected in the mountainous areas of the northwest of Kerman province. Family Colubridae Oppel, 1811, which is the largest snake family consists of aglyphous and opisthoglyphous snakes, represented by two genera *Eirenis* Jan, 1863 and *Lytorhynchus* Peters, 1862 and two species in this study: *Eirenis rafsanjanicus* Akbarpour, Fathinia, Rastegar-Pouyani & Rastegar-Pouyani, 2020 collected from Kerman province in the south-central Iran, and *Lytorhynchus maynardi* Alcock & Finn, 1897 from Zabol county, Sistan & Baluchistan province, southeastern Iran.

To investigate scale's microornamentation, dorsal scale samples of each specimen cut off from the head, mid-part of the body, and tail. The scales were placed in encoded tubes and filled with distilled water and neutral soap. The tubes were manually shaken for about one minute to remove probable impurities, followed by washing with distilled water and left to dry at room temperature for about 5 minutes. At next step, the scales were mounted on SEM rotatable aluminum stubs with a thin veneer of glue. Stubs were coated with gold and photographed using a scanning electron microscope (Hitachi S-2460 N SEM) at 25kV under various magnifications (range: 20x–10000x).

To compare the light reflected by the surface of scales, snakes were examined adopting two different methods: firstly, the whole body of the snake was photographed at different wavelengths of light using FluoVision Imaging System, and secondly, thick pieces of the snake's dorsal skin were prepared in the same way mentioned above for microornamentation study. The skin pieces were mounted on the girdles with glue. Skin reflectance was measured in the 300-700 nm (UV-VIS) spectral ranges using a Lambda2S spectrometer (Perkin Elmer, USA).

3 Results

3.1 SEM microscopy

The outer surface microstructure of top of the head and midbody dorsal scales of *P. persicus* has a lattice-like structure, with a spongy-like structure within each of the polygon lattices (Figure 1A-C). The high magnification of the caudal scales revealed a flattened and spongy-like structure that is divided into disordered unspecified bugs (Figure 1D).

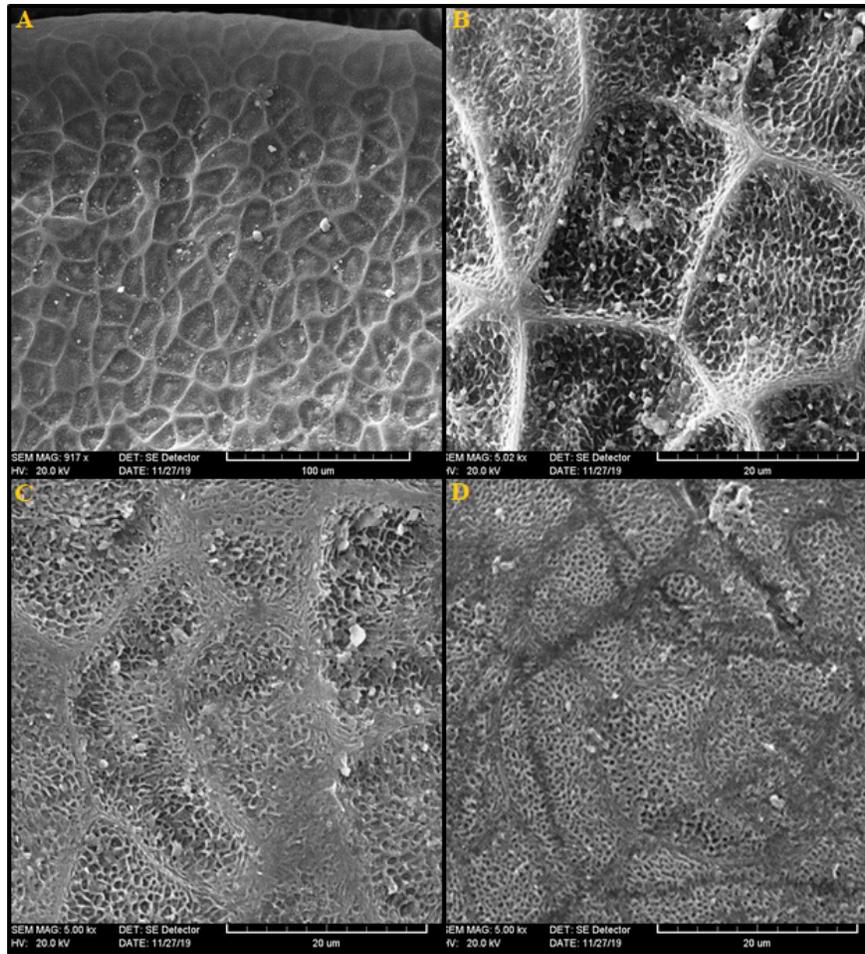


Figure 1. Scanning electron photomicrographs show the microstructure of scales in *P. persicus* (A–D). Head scales (A, ~1000X and B, ~5000X), midbody dorsal scales (C, 5000X), and dorsal caudal scales (D, 5000X).

The polygonal lattice-like structure is also seen in *P. fieldi*, but in comparison to *P. persicus*, the lattices are irregular and each polygon is finer and deeper. In *P. fieldi* the spongy-like structure is not seen (Figure 2).

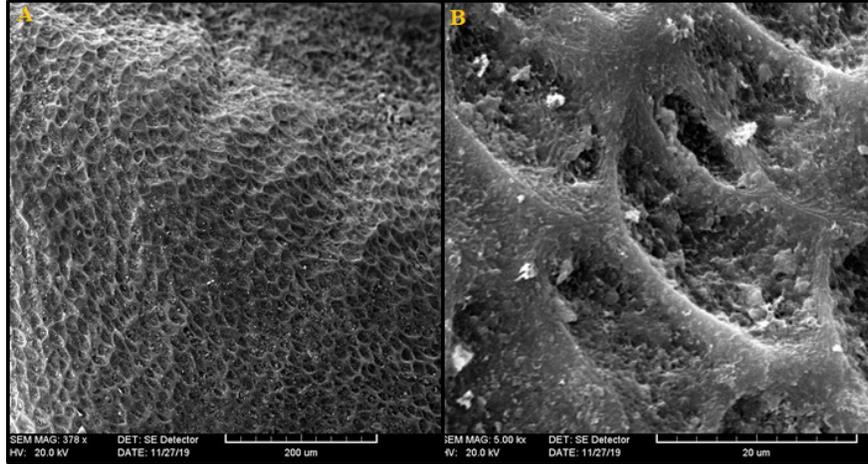


Figure 2. Scanning electron photomicrographs show the microstructure of head scales (A, ~400X and B, 5000X) of *P. fieldi* .

The microstructure of top of the head and midbody dorsal scales in *P. urarachnoides* is different from its congeners with an uneven appearance and granular surface (Figures 3A & B). The microstructure of the caudal appendages and knob-like structure on the tip of tail show a smooth and flattened shape with numerous pores at high magnification (Figures. 3C E).

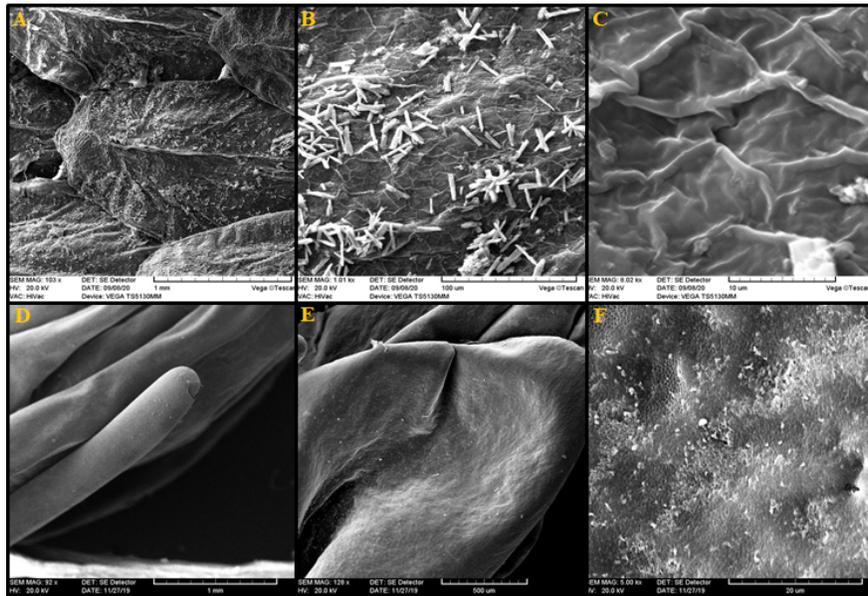


Figure 3. Scanning electron photomicrographs show the scale microstructure in *P. urarachnoides* : upper Head scales (A, ~100X , B, 1000X and C, 8000), caudal appendage (D, ~100X), and knob-like structure (E, ~100X and F, 5000X).

The microstructure of head and mid-body dorsal scales in *Eristicophis macmahonii* resemble a lattice-like structure. However, the depressions in these net-like structures are more or less roundish on head but elongated and more or less diamond-like on the mid-body scales. Tiny spicules are observed on the surface of both head and mid-body scales (Figure 4).

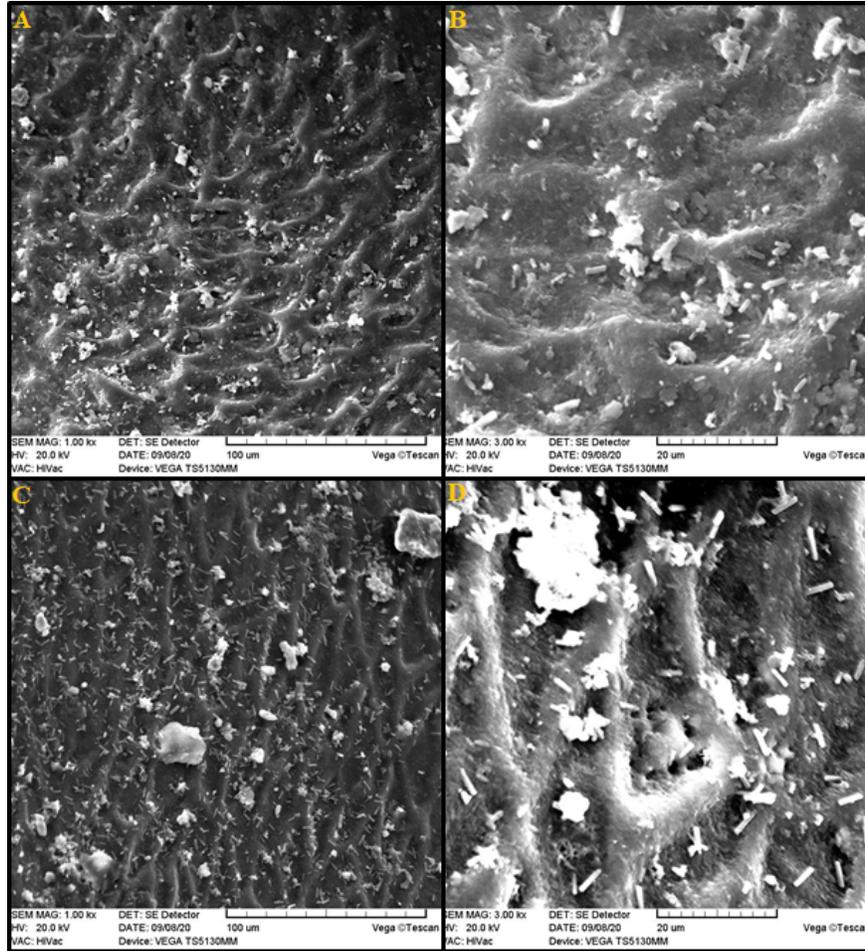


Figure 4. Scanning electron photomicrographs show the scale microstructure in *E. macmahonii* : upper head scales (A, 1000X and B, 3000X), midbody dorsal scales (C, 1000X and D, 3000X).

In *Cerastes gasperettii*, microstructure of the dorsal surface of head, mid-body, and caudal scales are more or less similar, looking like small blunt prominences (Figure 5).

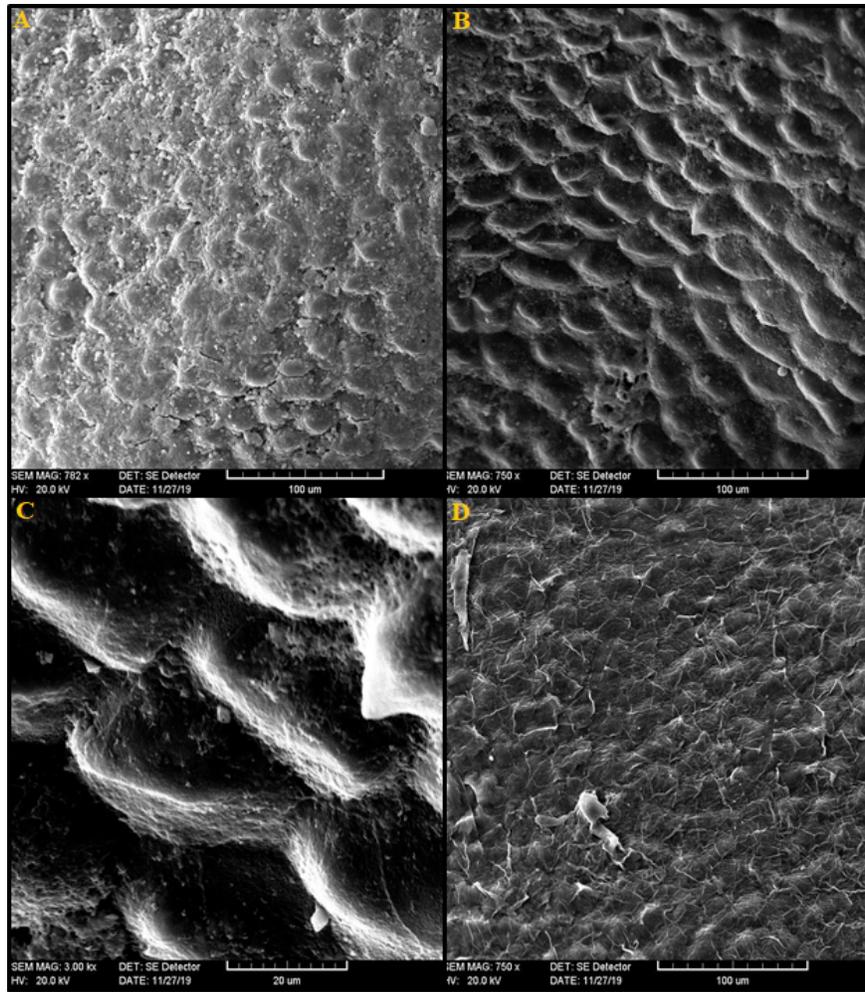


Figure 5. Scanning electron photomicrographs show the scale microstructure in *C. gasperettii* : upper head scales (A, 782X; B, 750X), mid-dorsal scales (C, 3000X), and caudal scales (D, 750X).

These prominences are shorter on the tail than on the other two parts. The scale microstructure of dorsal scales in *E. carinatus* appear as eggs in a tray, mostly similar to the upper head and mid-body scale surface in *C. gasperettii* (Figure 6).

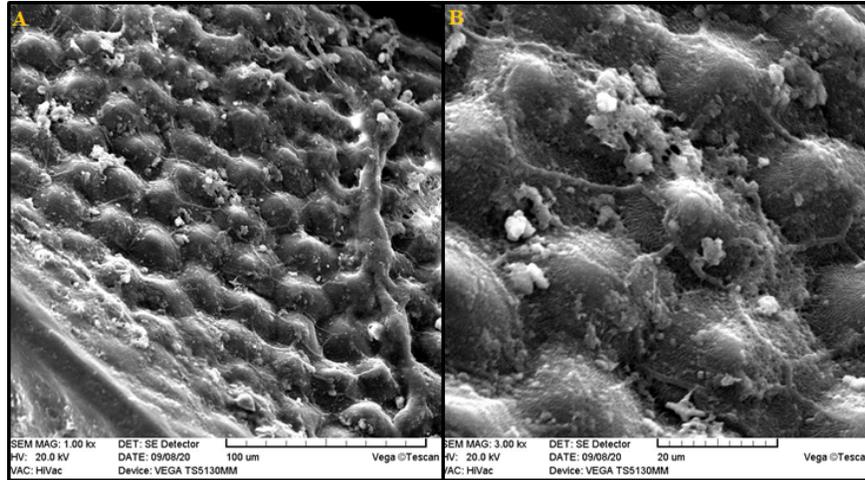


Figure 6. Scanning electron photomicrographs show the scale microstructure in *E. carinatus* : upper head scales (A, 1000X; B, 3000X).

The scale microstructure of the head in *E. rafsanjanicus* and *L. maynardi* appear flat and smooth. At first glance, the scale structure in the two species looks alike, but thin longitudinal raised lines distinguishes the scale of *E. rafsanjanicus* from *L. maynardi* (Figure 7).

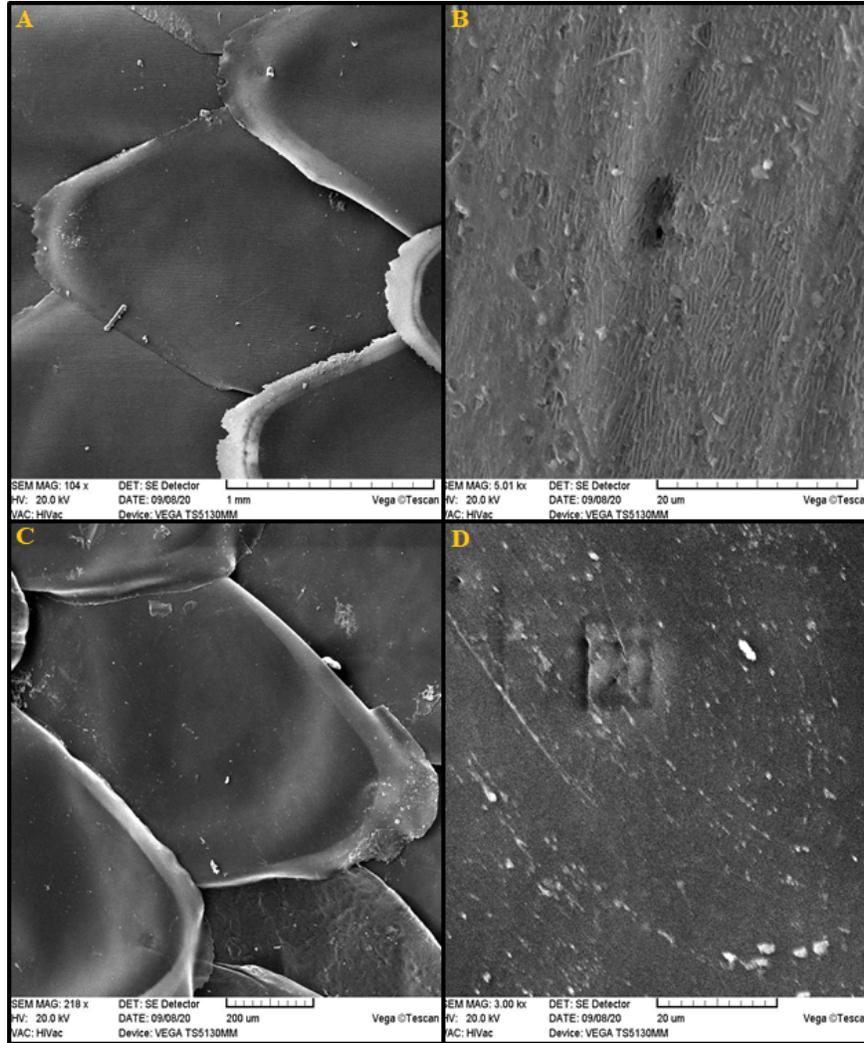


Figure 7. Scanning electron photomicrographs show the upper head scale microstructure in *E. rafsanjanicus* (A, ~100X and B, 5000X) and *L. maynardi* (C, ~200X and D, 3000X).

3.2 Reflectance

Reflectance spectra were done across wavelengths from 300–700 nm, which include ultraviolet and visible light. Reflectance differed between two ranges, 320–380 nm and 380–700 nm covering UV and visible light respectively. In the snakes of this study, different parts of the body behave differently against ultraviolet and visible wavelengths of light (Figures 8–10).

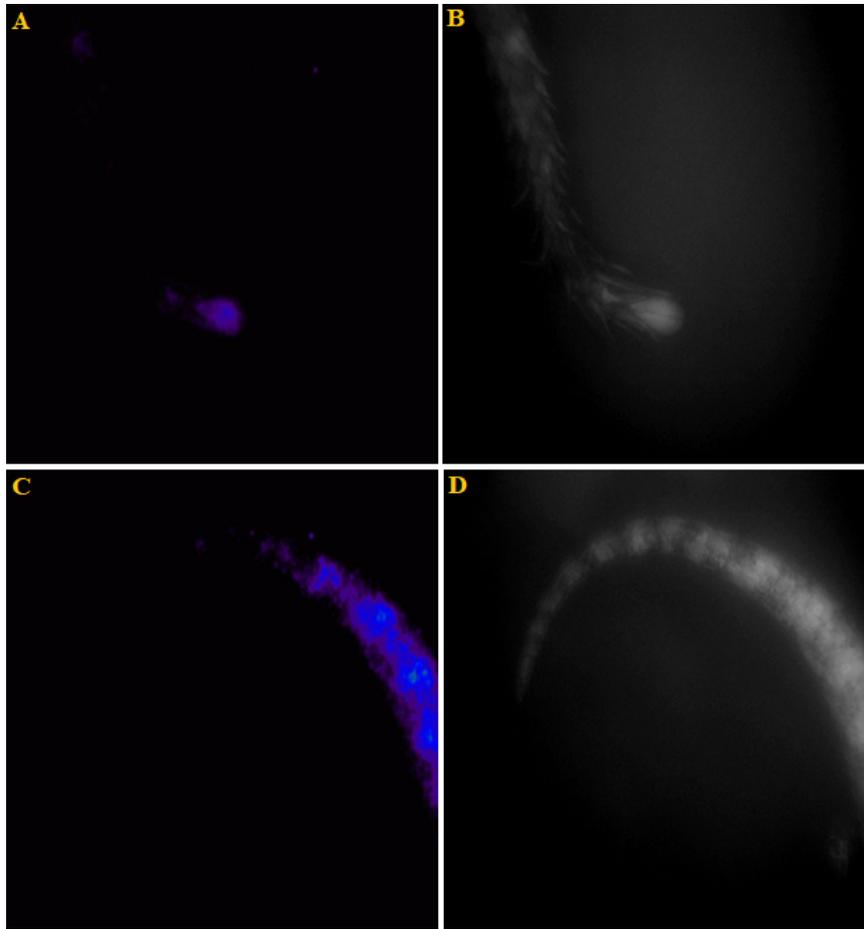


Figure 8. FluoVision Imaging System shows the reflectance of *P. urarachnoides* and *P. persicus* tail under ultraviolet (A and C) and visible wavelengths of light (B and D).

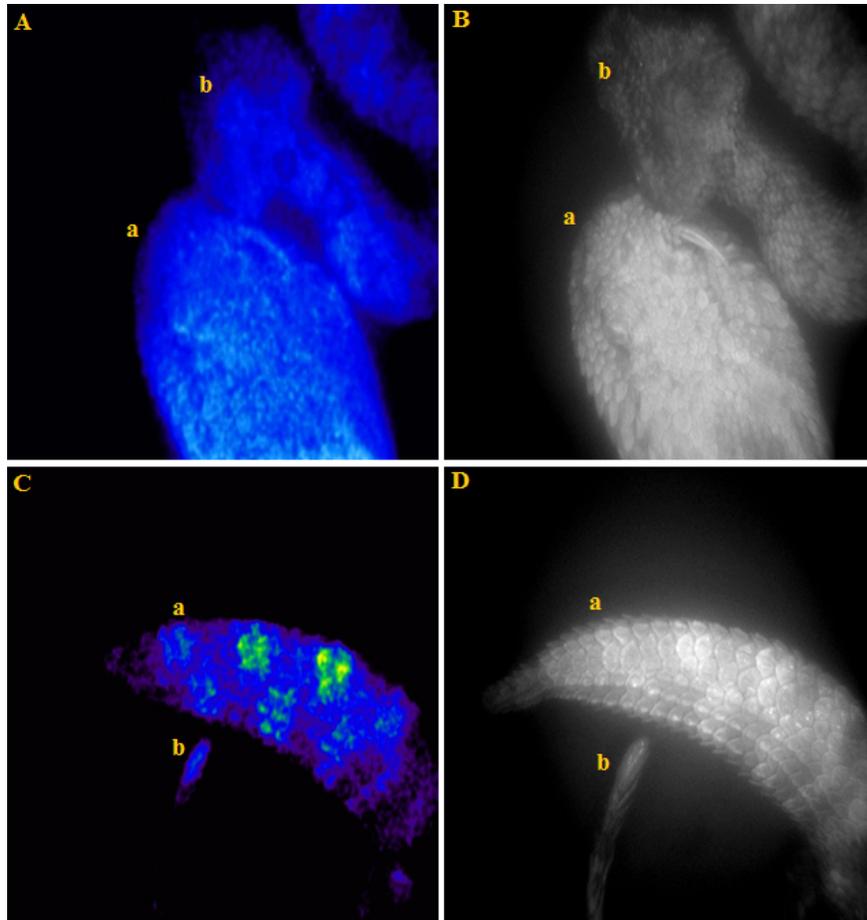


Figure 9. FluoVision Imaging System shows the reflectance of Head (A and B) and tail (C and D) of the *P. urarachnoides* (a) and *C. gasperettii* (b) under ultraviolet (A and C) and visible wavelengths of light (B and D).

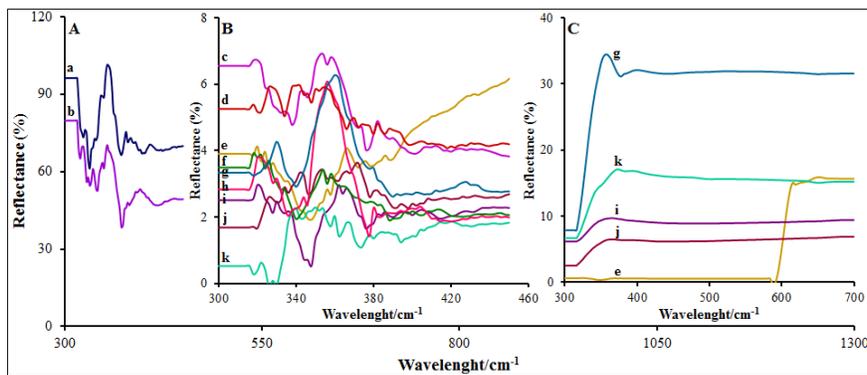


Figure 10 . Plot of spectral reflectance profiles of all under the study specimens; A) sandy (a) and stony (b); B) midbody dorsal surfaces; C) tail dorsal surfaces. *E. rafsanjanicus* (c), *L. maynardi* (d), *E. macmahonii* (e), *E. carinatus* (Kerman) (f), *C. gasperettii* (g), *E. carinatus* (Lavan) (h), *P. urarachnoides* (i), *P. feldi* (j), and *P. persicus* (k).

For instance, the reflectance value of UV for the knob-like structure on the tail tip in *P. urarachnoides* reaches up to 10, while the value for dorsal scales drops down below one (Figure 10B and 10C (curve i)). So, the reflectance magnitude of emitted UV by the tail tip is at least 10 times greater than that of dorsal scales. When UV light was emitted by FluoVision Imaging System on the tail of *P. urarachnoides*, the knob-like structure glowed while the rest of the body did not. Conversely, in UV wavelength, the the tail tip in *P. persicus* did not glow while the rest of the body glowed (Figure 8).

In *C. gasperettii*, the UV reflectance values reach up to six and 30 for dorsal and caudal scales, respectively, indicating a five-times difference in UV reflectance between these two regions of the body. Spectral reflectance from the midbody dorsal surfaces of all specimens under this study (i.e., *P. persicus*, *P. fieldi*, *P. urarachnoides*, *E. macmahonii*, *C. gasperettii*, *E. carinatus*, *E. rafsanjanicus*, and *L. maynardi*) was plotted beside spectra from stony and sandy samples (Figure 10). In the UV light range, dorsal scales of *P. urarachnoides* and *E. macmahonii* showed the greatest decrease in reflection, while *E. rafsanjanicus*, *L. maynardi*, *C. gasperettii*, and *E. carinatus* indicated the highest reflection (Figure 10). The highest reflection in the range of visible light belongs to *E. macmahonii*. Overall, due to high light absorption, reflection in the dorsal scale samples was very low. In stone and sand samples, light reflection was significantly more than that in scale samples, and the most fluctuation in reflection was between 310–420 wavelengths.

4 Discussion

Morphological characteristics of reptiles are in direct correlation with their ecology, and may reflect their phylogenetic and evolution information, their trophic potential, their ability to survive in specific habitats, and they can thus be used to predict their lifestyle (Wootton, 1994; Gibran, 2007; Allam et al., 2019). Overall, tracing their morphological, behavioral, and physiological adaptations in relation to ecological factors requires an understanding of historical and phylogenetic relationships among taxa. This information is also necessary to determine morphological and ecological convergence and divergence within a taxon (Wainwright and Lauder, 1992; Westneat, 1995). Reptile scale microornamentation as a morphological character has been studied in various contexts of phylogeny and ecological adaptations (Picado, 1931; Peterson and Bezy, 1985; Renous et al., 1985; Stille, 1987; Irish et al., 1988; Chiasson et al., 1989; Chiasson and Lowe, 1989; Price, 1990; Harvey, 1993; Harvey and Gutberlet Jr, 1995; Maderson et al., 1998; Arnold, 2002; Gower, 2003) and used as an argument to support phylogenetic relationships of species (Picado, 1931; Price, 1983; Stille, 1987; Chiasson et al., 1989; Chiasson and Lowe, 1989; Gower, 2003). However, some authors asserted that microornamentation depends on selective pressures, especially in snakes. There are many contacts between the body surface and the environment; however, some studies indicated no relationship between microornamentation and environment (Price, 1982; Peterson, 1984; Peterson and Bezy, 1985; Berthé et al., 2009). *P. urarachnoides* is well separated morphologically from its congeners, *P. fieldi* and *P. persicus*, (Fathinia et al., 2014), while is the sister taxon to *P. persicus* the *P. fieldi* phylogenetically, with a basal position for *P. fieldi* (Fathinia et al., 2018). Although the most common recent ancestor (MRCA) for *P. persicus* and *P. urarachnoides* dates back to ~8 mya (Fathinia et al., 2018), *P. persicus* is morphologically more similar to *P. fieldi* (MRCA; ~12 mya) than to *P. urarachnoides*. Some morphological characteristics that can be regarded as autapomorphies for *P. urarachnoides* are the unique caudal structure and rugosity of scales in comparison to its congeners, which deeply separate it from its two congeners (Bostanchi et al., 2006; Fathinia and Rastegar-Pouyani, 2010). Scale microornamentation revealed that the microstructure of scales in *P. fieldi* and *P. persicus* are more similar to each other than to *P. urarachnoides*, coincides with morphological characteristics, but contrary to molecular relationships within this genus. The genus *Eristicophis* is the closest living relative to *Pseudocerastes*, with the MRCA dates back to ~16.5 Mya (Fathinia et al., 2018). Lattice-like scale microstructure in *E. macmahonii* is more or less similar to that in *P. fieldi*. The genera *Cerastes* and *Echis* are closer relatives in comparison to other viperin genera used in this study (Pyron et al., 2013). Similarities in the scale microornamentation between *E. carinatus* and *C. gasperettii* (i.e., the raised prominences) are obvious. In both *E. rafsanjanicus* and *L. maynardi* scales microstructure was smooth.

According to the phylogenetic and ecologic information mentioned above, there are many scale microstructure differences between *P. urarachnoides* and other congeners that inhabit almost the same habitat, while there

are microstructure similarities between *P. fieldi* and *E. macmahonii* or *E. carinatus* and *C. gasperetti* that inhabit different habitats. Therefore, based on the presence of similar microstructures found in different taxa living in different habitats and various microstructures that found in different species occupying similar ecological niches, and given the phylogenetic relationships, one can interpret that with all probability these microstructures do not affect by habitat, so mostly inherited from the common ancestors. As some researchers have pointed out, variation in microornamentations in different species does not indicate any adaptation to different environments (Price, 1982; Peterson, 1984; Peterson and Bezy, 1985). Overall, the difference in the scales microornamentation between *P. urarachnoides* and its congeners can be explained with regard to other factors such as the nocturnality or diurnality, dietary regime, and so on.

Ultraviolet light has benefit impacts on ecological and physiological aspects of reptiles well being. It plays a role in social communication, calcium metabolism through an apparent vitamin D3 precursor, photoperiod regulations that influences on reproduction and behavior and many known and unknown advantages (MacLaughlin, et al, 1982; ; Holick, et al, 1995; Ferguson, et al, 2003; Modarressie et al., 2013). Despite the advantage effects, UV light also has disadvantage effects on the reptiles. For instance, UV light reflection from reptiles body surface help avian predators to detect them (Bennett and Cuthill, 1994) or it can cause degradation of vitamin A in the skin (Tang, et al, 1994). Accordingly, reptiles have different adaptations to ultraviolet light due to their ecological and physiological conditions. In examining the relationship between scale reflection and ecology, various reflections were seen in different species and different parts of their body. In the UV light range, *P. urarachnoides* dorsal scales reflected low, while the caudal structure (the terminal knob) showed strong UV reflection. One of the benefits of this feature can be investigated in enemy-victim behavior. Many bird species can perceive near-UV part of the light spectrum (the wavelength 320–400 nm) (Rajchard, 2009). The ecological significance of UV perception was investigated mostly in intra- and intersexual signaling in common species communication and foraging behavior (Rajchard, 2009). Given that the caudal structure (the appendages and terminal knob) in *P. urarachnoides* reflects UV light, while the rest of the body highly absorbs the UV light, might have a bifunctional role in both seducing and absorbing insectivorous passerine birds and camouflage against these birds. A complete scene of predation on birds by the Iranian spider-tailed viper has reported previously by Fathinia et al. (2015), in which the warbler incautiously attacks the caudal structure after the first unfruitful attack, as if the warbler has not noticed the presence of the head and body of Spider-tailed viper, only aimed at the tail of the viper. The emergence of this feature between *P. urarachnoides* and the birds can be considered as a model of prey-predator coevolution. The term "coevolution" is defined in the simplest form; two species evolve in response to each other (Futuyma, 1998). In this case, *P. urarachnoides* have evolved a spider-like caudal structure reflecting UV light, as an extraordinary evolutionary innovation, for absorbing passerine insectivorous birds as prey.

CONFLICT OF INTEREST

There is no conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors contributed to the study conception and design. All authors read and approved the final manuscript.

Morteza Akbarpour: Acquisition of data and Writing - original draft preparation. Nasrullah Rastegar-Pouyani and Behzad Fathinia: Formal analysis and investigation. Eskandar Rastegar-Pouyani: Writing - review and editing.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated.

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