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Studies on the significance of microdermatoglyphics in viperid systematics. I. The microdermatoglyphics of desert vipers
(Squamata: Serpentes: Viperidae)

Untersuchungen zur systematischen Relevanz epidermaler Ultrastrukturen bei Viperiden. I. Die Schuppenultrastrukturen wüstenbewohnender Vipern
(Squamata: Serpentes: Viperidae)

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KURZFASSUNG

Die Ultrastruktur der Rückenschuppenoberfläche wurde an wüstenbewohnenden Vertretern der Viperidengattungen *Echis, Cerastes, Pseudocerastes* und *Bitis* sowie an *Crotalus cerastes* untersucht. Im Gegensatz zu allen anderen Viperidengattungen, bei denen sich gattungstypische Muster finden, tritt bei *Echis, Cerastes, Pseudocerastes* und *Bitis peringueyi* das gleiche, nämlich ein verrucates Muster auf. Das Vorhandensein eines verrucaten Reliefs bei *Crotalus cerastes* macht die Kopplung des Merkmals mit ökologischen Faktoren sehr wahrscheinlich. Diese sowie die systematische Aussagekraft von Ultrastrukturen der Rückenschuppenoberfläche werden diskutiert.

ABSTRACT

Microdermatoglyphics of dorsal scales have been investigated in desert vipers of the genera *Echis, Cerastes, Pseudocerastes* and *Bitis* as well as *Crotalus cerastes*. Opposite to all other viperid genera which are distinguished by individual microdermatoglyphic patterns each, *Echis, Cerastes, Pseudocerastes,* and *Bitis peringueyi* exhibit identical - verrucate - patterns. The outgroup taxon *Crotalus cerastes* shows the very same type of dorsal microornamentation strongly suggesting an ecological influence on its formation. This influence and the utility of microdermatoglyphics for systematics are discussed.

KEY WORDS

Serpentes, Viperidae, Crotalidae, *Echis, Cerastes, Pseudocerastes, Bitis peringueyi, Crotalus cerastes;* systematics, morphology, skin, SEM, microdermatoglyphics.

INTRODUCTION

Microdermatoglyphics have yet been described in 1868 by LEYDIG who also had the idea of their utility as a marker for squamate systematics (LEYDIG 1872, 1873). Enhencement of resolution and refinement of presentation provided by scanning electron microscopy induced the application of this technique to the analysis of dermal surfaces (HOGE & SOUZA SANTOS 1952; PRICE 1982, 1983, 1990; BEA 1978, 1987; STILLE 1987). But still there is no agreement on whether microdermatoglyphics can be used as a taxonomic tool or if they just give us some information about the ecological conditions these animals are confronted with as RÜHL & HERRMANN (1989) claim. Though other authors do not at all reject the possibilities these structures provide for squamate systematics, some of them warn of their uncritical use. BEA (1978) notices a tendency towards the development of more massive structures in vipers that live in warmer areas and considers this to be an adaptation to evaporation. In a later paper (BEA 1986) he finds a relationship between the complexity of the microdermatoglyphics and the southward extension of the species. LILLYWHITE & MADERSON (1982) find more complex structures in terrestrial squamates than in aquatic ones and they also attribute this to the structures' role in water balance. PORTER (1967) has the idea that - in desert reptiles - some microdermatoglyphic structures show themselves to be an adaptation to scatter light reducing the amount of radiation penetrating into the organism.

But some systematic relevance of these structures is obvious. BURSTEIN & al. (1974) consider the structures to be useful for lizard systematics on the inter- and intragenera level as well as for the distin-

guishing of species and subspecies. This is also underlined by HOGE & SOUZA SANTOS (1952), DOWLING & al. (1972), STEWARD & DANIEL (1975), PRICE (1982, 1983, 1990), PETERSON (1984), DOWLING & PRICE (1988) and PRICE & KELLY (1989). BEA (1978, 1987) and STILLE (1987) consider the patterns to be species specific. PRICE (1982) investigates the microdermatoglyphics of snake species from different habitat types, what leads to the result that in none of these habitats the dominating role is played by a single pattern only, and that identical pattern types are found in different habitats.

In viperid systematics microdermatoglyphics have first been investigated by BEA (1978, 1986, 1987) who especially dealt with Iberian vipers of the genus *Vipera*. He found slight differences between *V. berus* (LINNAEUS, 1758), *V. seoanei* LATASTE, 1879, *V. aspis* (LINNAEUS, 1758), and *V. latastei* BOSCÁ, 1878, with *V. seoanei* being intermediate between *V. aspis* and *V. berus*. In his thesis GROOMBRIDGE (1980) included microdermatoglyphics of representatives of all viperid genera and BEYERLEIN (1993) investigated the microdermatoglyphics of most viperid species and subspecies. In both analyses, structure differences between the genera can be found, but there have also been some patterns indicating an ecological correlation of scale structures, especially for *Echis* and *Cerastes*. JOGER & COURAGE (1998) deal with *Echis* and *Cerastes*. They postulate that both 'genera' form one monophyletic group because of their similar microdermatoglyphics and reject monophyly of *Atheris* and *Echis* or *Atheris* and *Cerastes*, respectively. These two possibilities were proposed by HERRMANN & al. (1998) as derived from a study in which none of the alternatives was clearly favoured owing to controversial results of morphological and genetic analyses.

In the present paper microdermatoglyphics of *Echis* and *Cerastes* and other desert vipers like *Pseudocerastes* and *Bitis peringueyi* as well as the Sidewinder Rattlesnake *Crotalus cerastes* are illuminated once more to analyze the question of this structure to be of value for desert vipers systematics.

MATERIALS AND METHODS

Scale samples of the following vipers (preserved museum specimens) are used for this analysis: *Bitis peringueyi* (BOULENGER, 1888) [ZFMK 44887, Namibia: Swakopmund], *Cerastes cerastes cerastes* (LINNAEUS, 1758) [ZFMK 17593; Mauretania: Chaimi], *C. cerastes gasperettii* LEVITON & ANDERSON, 1967 [ZFMK 52419; Jordan: Wadi Araba], *C. vipera* (LINNAEUS, 1758) [NMW 27140; Israel: Negev], *Crotalus cerastes* HALLOWELL, 1854 [Priv. coll. A. MEYER; U.S.A.: California], *Echis carinatus carinatus* (SCHNEIDER, 1801) [ZFMK 32490; Sri Lanka], *E. carinatus sinhaleyus* DERANIYAGALA, 1951 [NMW 13490; Northern Ceylon], *E. carinatus sochureki* STEMMLER, 1969 [ZFMK 27403; Pakistan], *E. coloratus* GÜNTHER, 1878 [ZFMK 50294; Egypt: Wadi Rishrash], *E. leucogaster* ROMAN, 1972 [ZFMK 20257; Niger: 30 km W Dogou: Doutch], *E. multisquamatus* ČERLIN, 1981 [ZFMK 16381; Turkmenia: Ashabad], *E. ocellatus* STEMMLER, 1970 [ZFMK 20254; Mali], *E. pyramidum leakeyi* (STEMMLER & SOCHUREK, 1969) [NMW 19387; Northern Kenya), *E. pyramidum pyramidum* (GEOFFROY ST. HILAIRE, 1827) [ZFMK 50285; Egypt: Fayum: Wadi Pharaon], *E. varia* REUSS, 1834 [ZFMK 54278; Djibouti], and *Pseudocerastes persicus* (DUMÉRIL, BIBRON & DUMÈRIL, 1854) [ZFMK 13101, Pakistan: Mokran coast].

The Oberhäutchen of dorsal scales is removed with tweezers, samples are cleaned in an ultrasound bath in water and afterwards in acetone for five minutes each. After drying in the air they are glued on specimen stubs with an electron conducting glue and gold sputter coated. Terminology of microornamentation is according to PRICE (1982).

RESULTS

Irrespective of systematics, epidermal microornamentation is similar in all desert vipers investigated in this study in that it is characterized by a verrucate pattern and a reticulate or porous fine structure in all cases (table 1).

Table 1: Types of microdermatoglyphics as found in 16 taxa of desert vipers.
Tab. 1: Die Ausprägungen der Schuppenfeinstruktur bei 16 Formen von Wüstenvipern.

Taxon	Type of microdermatoglyphics Typ der Schuppenfeinstruktur	Figure Abbildung
Bitis peringueyi	verrucate / reticulate	1
Cerastes cerastes cerastes	verrucate / reticulate	2
Cerastes cerastes gasperettii	verrucate / reticulate	–
Cerastes vipera	verrucate / reticulate	–
Crotalus cerastes	verrucate / reticulate	8
Echis carinatus carinatus	verrucate / reticulate	–
Echis carinatus sinhaleyus	verrucate / reticulate	–
Echis carinatus sochureki	verrucate / reticulate	–
Echis coloratus	verrucate / reticulate	3
Echis leucogaster	verrucate / reticulate or porous	4
Echis multisquamatus	verrucate / reticulate	–
Echis ocellatus	verrucate / porous	5
Echis pyramidum leakeyi	verrucate / porous	–
Echis pyramidum pyramidum	verrucate / porous	–
Echis varia	verrucate / reticulate or porous	6
Pseudocerastes persicus persicus	verrucate / reticulate	7

DISCUSSION

In contrast to all other vipers in which one can find genus specific or even species specific patterns (GROOMBRIDGE, 1980, BEYERLEIN, 1993), all sand dwellers included in the present study show a verrucate scale surface with a reticulate fine structure or a porous one in some *Echis*, respectively. According to BEYERLEIN (1993) no other vipers than the sand dwelling ones show this character state. Though it looks plesiomorphic it is, however, not widespread in other snake families as can be seen from the results of PRICE (1982) and PRICE & KELLY (1989) who investigated a large number of snakes belonging to several families. The fact that the crotalid *Crotalus cerastes* also evolved this type of scale ultrastructure (see also STILLE 1989) is a sound argument for some selection pressure towards the evolution of verrucate scale surfaces under the ecological conditions these desert vipers live in.

PORTER (1967) supposes that some regularly arranged spiny elements in the microdermatoglyphics of desert lizards reduce the amount of heat penetrating into the organism. Perhaps the simple constructed structures found here in the sand dwelling vipers have a similar function; in having a small surface they do not absorb as much energy as and reflect more radiation than more complicated ones would do.

Though PRICE (1982) seems to prove the systematic value of microornamental patterns in snakes, GANS (1977, 1979) sees some correlation between life style and scale structures in Uropeltids. P. BLANEY (cited in PRICE 1982) assumes some ecological adaptation to be possible in microdermatoglyphics and this very assumption is strongly supported by the results submitted in the present paper.

Considering the results of GROOMBRIDGE (1980) und BEYERLEIN (1993), the statement of RÜHL & HERRMANN (l.c.) - snake scales are not suited for systematics at all - does not seem to be generally justified for vipers, but is true for the ecological group investigated here. Thus, the use of microdermatoglyphics in desert vipers systematics must be rejected.

As a consequence, the close systematic affinity of *Echis* and *Cerastes* as derived from similar scale patterns by JOGER & COURAGE (1998), is no longer convincing. Though the assumption of monophyly of these both genera seems to be sensible, similar microdermatoglyphic patterns can not serve as sound argument against the cladograms proposed by HERRMANN & al. (1998).

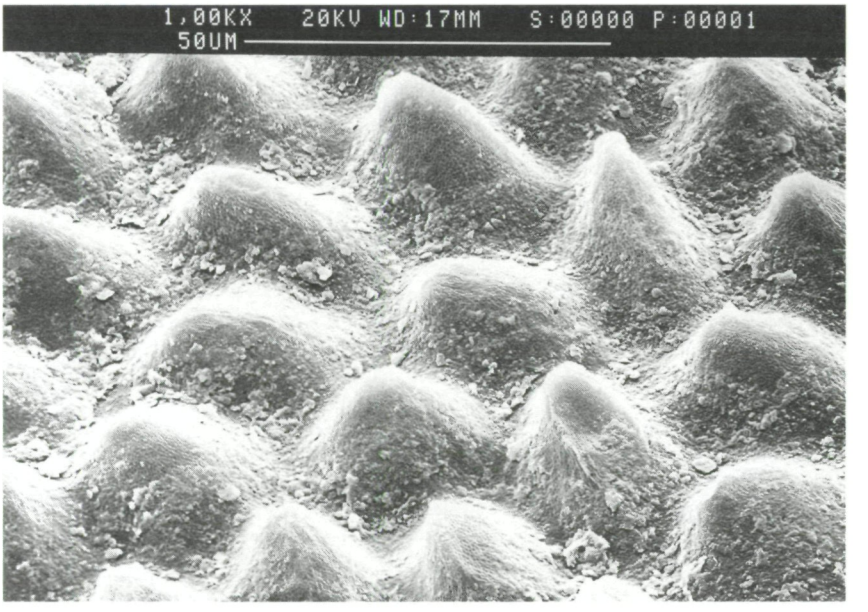

Fig. 1: Ultrastructure of dorsal scale surface in *Bitis peringueyi*. Bar represents 50 µm.
Abb. 1: Feinstruktur der Oberfläche einer Rückenschuppe von *Bitis peringueyi*. Balkenlänge entspricht 50µm.

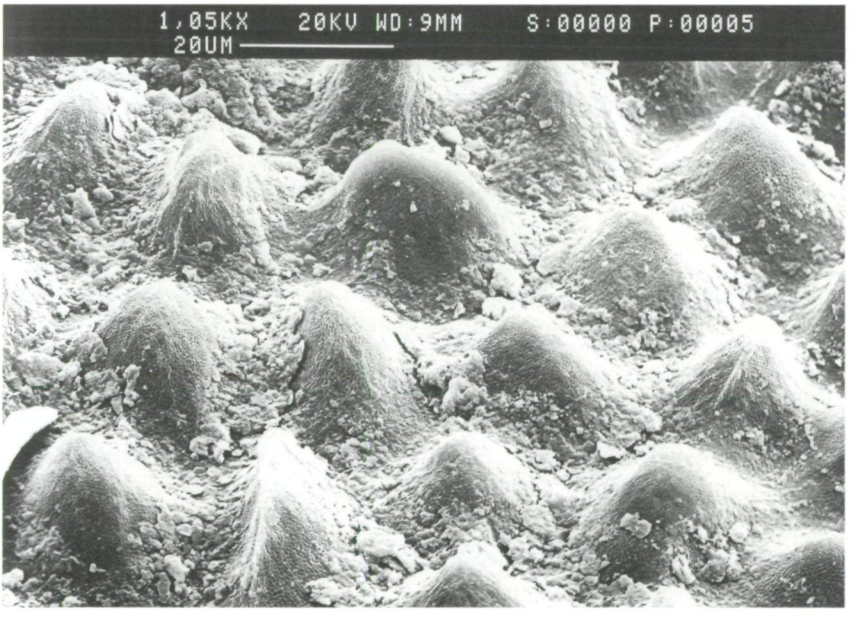

Fig. 2: Ultrastructure of dorsal scale surface in *Cerastes c. cerastes*. Bar represents 20 µm.
Abb. 2: Feinstruktur der Oberfläche einer Rückenschuppe von *Cerastes c. cerastes*. Balkenlänge entspricht 20µm.

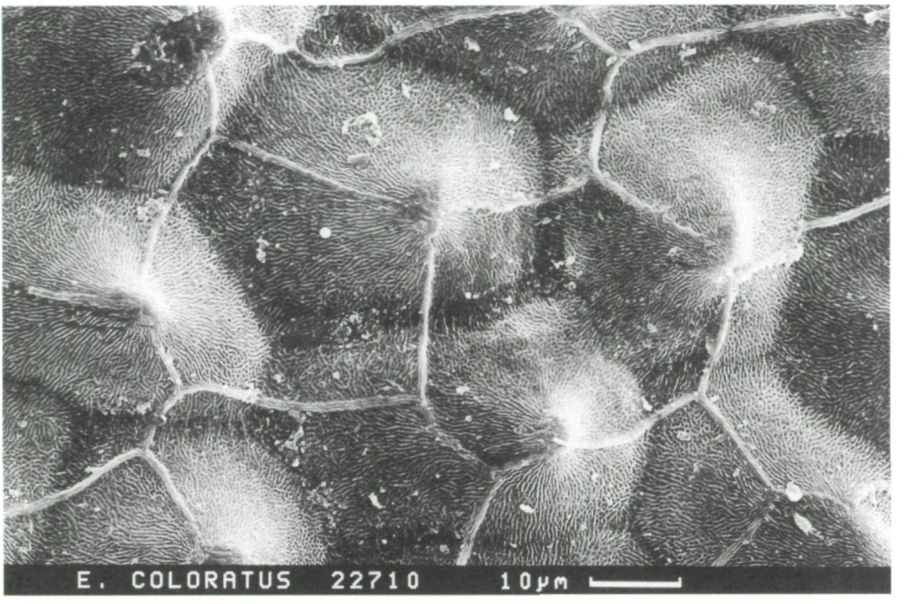

Fig. 3: Ultrastructure of dorsal scale surface in *Echis coloratus*. Bar represents 10 µm.
Abb. 3: Feinstruktur der Oberfläche einer Rückenschuppe von *Echis coloratus*. Balkenlänge entspricht 10µm.

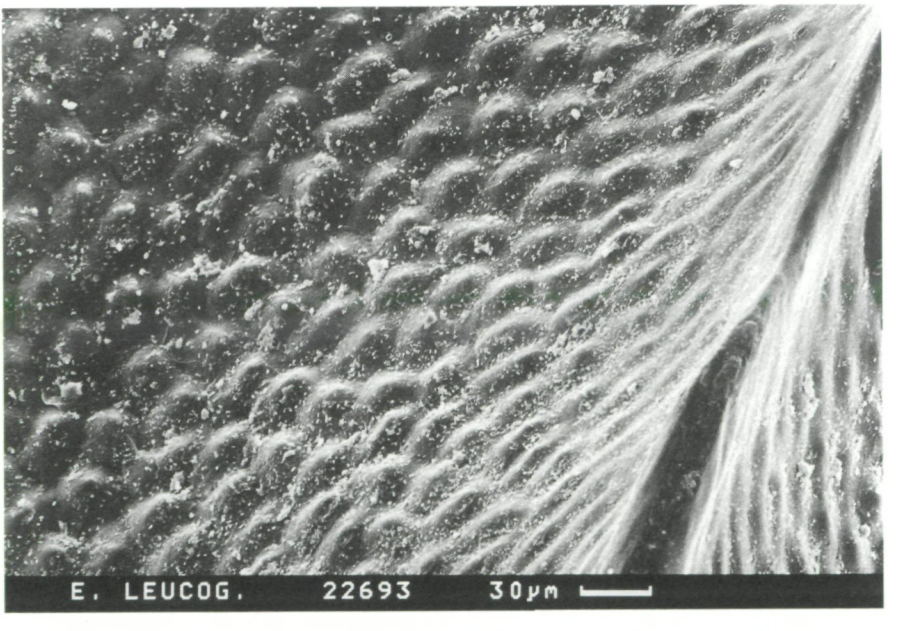

Fig. 4: Ultrastructure of dorsal scale surface in *Echis leucogaster*. Bar represents 30 µm.
Abb. 4: Feinstruktur der Oberfläche einer Rückenschuppe von *Echis leucogaster*. Balkenlänge entspricht 30µm.

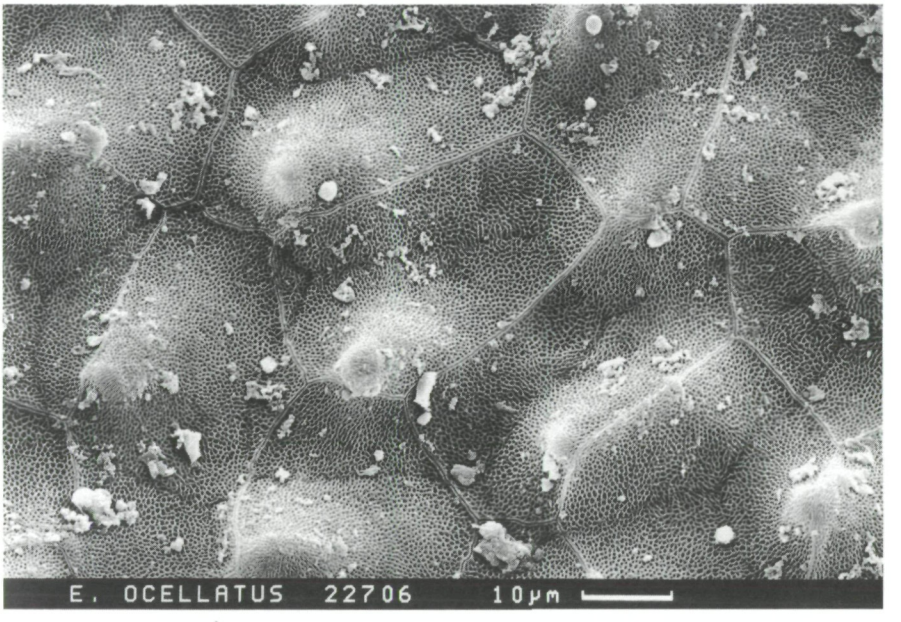

Fig. 5: Ultrastructure of dorsal scale surface in *Echis ocellatus*. Bar represents 10 µm.
Abb. 5: Feinstruktur der Oberfläche einer Rückenschuppe von *Echis ocellatus*. Balkenlänge entspricht 10µm.

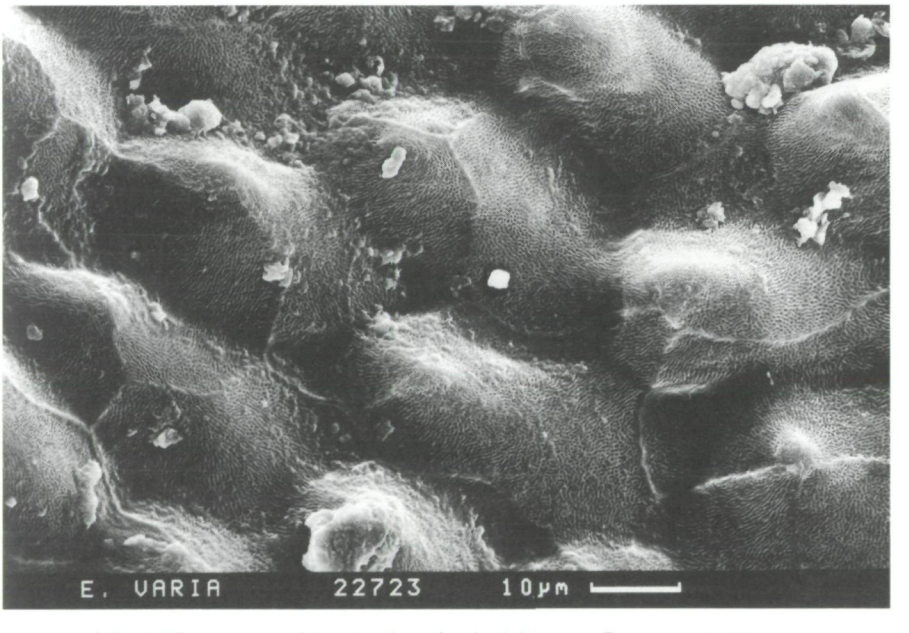

Fig. 6: Ultrastructure of dorsal scale surface in *Echis varia*. Bar represents 10 µm.
Abb. 6: Feinstruktur der Oberfläche einer Rückenschuppe von *Echis varia*. Balkenlänge entspricht 10µm.

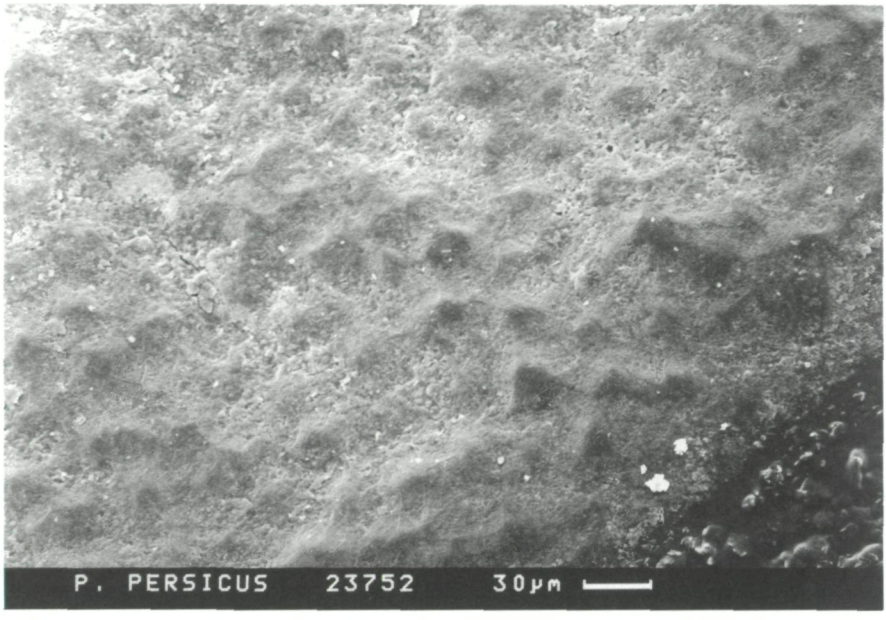

Fig. 7: Ultrastructure of dorsal scale surface in *Pseudocerastes p. persicus*. Bar represents 30 µm.
Abb. 7: Feinstruktur der Oberfläche einer Rückenschuppe von *Pseudocerastes p. persicus*. Balkenlänge entspricht 30µm.

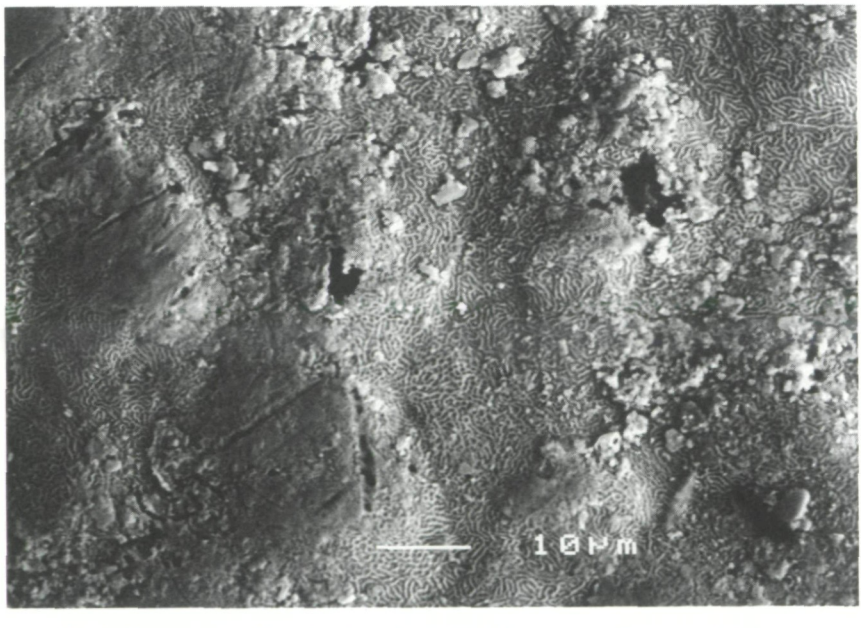

Fig. 8: Ultrastructure of dorsal scale surface in *Crotalus cerastes*. Bar represents 10 µm.
Abb. 8: Feinstruktur der Oberfläche einer Rückenschuppe von *Crotalus cerastes*. Balkenlänge entspricht 10 µm.

It can be concluded that though microdermatoglyphics at a first glance seem to be a neutral and therefore useful feature in phylogenetic and systematic investigations in squamates there is some clue for their relation to ecological factors at least in sand dwelling Viperidae. Therefore, the use of scale structures as an aid for answering systematic-taxonomic questions is to be handled with kid gloves.

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REFERENCES

BEA, A. (1978): Contribución a la sistemática de *Vipera seoanei* LATASTE, 1879 (Reptilia, Viperidae). I. Ultraestructura de la cutícula de las escamas.- Bull. Inst. Catalan Hist. Nat.; 42: 107-118.

BEA, A. (1986): A general review of the dorsal scales' microornamentation in *Vipera* species (Reptilia: Viperidae).pp. 367-372. In: ROČEK, Z. (ed.): Studies in Herpetology. Prague.

BEA, A. (1987): The microornamentation unities of the Oberhäutchen of the dorsal scales in *Vipera* species (Reptilia: Viperidae); pp. 59-62. In: VAN GELDER, J. J. & STRIJBOSCH, H. & BERGERS, P. J. M. (eds.): Proc. Fourth Ord.Gen.Meet.SEH. Nijmegen.

BEYERLEIN, P. (1993): Untersuchungen zur systematischen Relevanz epidermaler Ultrastrukturen bei modernen Schlangen (Colubroidea).- Bonn (unpublished thesis).

BURSTEIN, N. & LARSEN, K. R. & SMITH, H. M. (1974): A preliminary survey of dermatoglyphic variation in the lizard genus *Sceloporus*.- J. Herpetol.; 8: 358-369.

DOWLING, H. G. & GILBOA, J. & GENNARO, J. F. & GENNARO, A. L. (1972): Microdermatoglyphics: a new tool for reptile taxonomy.- Herpetol. Rev.; 4: 200.

DOWLING, H. G. & PRICE, R. M. (1988): A proposed new genus for *Elaphe subocularis* and *Elaphe rosaliae*.- Snake; 20: 52-63.

GROOMBRIDGE, B. C. (1980): A phyletic analysis of viperine snakes. London (unpublished PhD thesis).

HERRMANN, H.-W. & JOGER, U. & LENK, P. (1998 in press): Morphological and molecular phylogenies of viperines: conflicting evidence? In: JOGER, U. & NILSON, G. (eds.): Phylogeny and systematics of the Viperidae.- Kaupia; 7.

HOGE, A. R. & SOUZA SANTOS, P. (1953): Submicroscopic structure of "Stratum Corneum" of snakes.- Science; 118: 410-411.

JOGER, U. & COURAGE, K. (1998, in press): Are palearctic 'rattlesnakes' (*Echis* and *Cerastes*) monophyletic? In: JOGER, U. & NILSON, G. (eds.): Phylogeny and systematics of the Viperidae.- Kaupia; 7.

LEYDIG, F. (1868): Über Organe eines sechsten Sinnes. Zugleich als Beitrag zur Kenntnis des feineren Baues der Haut bei Amphibien und Reptilien.- Nova Acta Acad. Caesar. Leop. Carol., Halle; 34: 108 pp.

LEYDIG, F. (1872): Die in Deutschland lebenden Arten der Saurier. Tübingen (Laupp), 262 pp.

LEYDIG, F. (1873): Über die äußere Bedeckung der Reptilien und Amphibien.- Arch. mikroskop. Anat. Entwicklungsmech.; 9: 753-794.

LILLYWHITE, H. B. & MADERSON, P. F. A. (1982): Skin structure and permeability; pp. 397-442. In: GANS, C. & POUGH, F. H. (eds.): Biology of the reptilia Vol.12. London (Academic Press).

PETERSON, J. A. (1984): The microstructure of the scale surface in Iguanid lizards.- J. Herpetol.; 18(4): 437-467.

PETERSON, J. A. (1984): The scale microarchitecture of *Sphenodon punctatus*.- J. Herpetol.; 18(1): 40-47.

PORTER, W. P. (1967): Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles.- Ecol. Monogr.; 37: 273-296.

PRICE, R. M. (1982): Dorsal snake scale microdermatoglyphics: ecological indicator or taxonomic tool?- J. Herpetol.; 16(3): 294-306.

PRICE, R. M. (1983): Microdermatoglyphics: the *Liodytes* - *Regina* problem.- J. Herpetol.; 17(3): 292-294.

PRICE, R. M. (1990): Microdermatoglyphics: an appeal for standardization of methodology and terminology with comments on recent studies of North American Natricines.- J. Herpetol.; 24(3): 324-325.

PRICE, R. M. & KELLY, P. (1989): Microdermatoglyphics: basal patterns and transition zones.- J. Herpetol.; 23(3): 244-261.

RÜHL, D. & HERRMANN, K. (1989): Computertechnische Analyse von Ultrastrukturen in der Cuticula und Epidermis von Schlangen (Serpentes).- Verh. Deutschen Zool. Ges.; 83: 265-266.

STEWARD, G. R. & DANIEL, R. S. (1975): Microornamentation of lizard scales: some variations and taxonomic corellations.- Herpetologica; 43(1): 98-104.

STILLE, B. (1987): Dorsal scale microdermatoglyphics and rattlesnake (*Crotalus* and *Sistrurus*) phylogeny (Reptilia: Viperidae: Crotalinae).- Herpetologica; 43(1): 98-104.

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