

Animal biology and pathology / Biologie et pathologie animales

Presence of gular and parietal pits in *Atretium schistosum* (Serpentes, Colubridae), a singular trait not exclusive to psammophine snakes

Aurélien Miralles^{a,*}, Ivan Ineich^b

^a 'Adaptation et évolution des systèmes ostéomusculaires', FRE 2696, département d'écologie et de gestion de la biodiversité, Muséum national d'histoire naturelle, case courrier n° 55, 55, rue Buffon, 75005 Paris, France

^b Département de systématique et évolution (Reptiles), Muséum national d'histoire naturelle, case courrier n° 30, 25, rue Cuvier, 75005 Paris, France

Received 12 May 2005; accepted after revision 8 November 2005

Available online 20 December 2005

Presented by Pierre Buser

Abstract

The sporadic occurrence of localised pits on parietal plates was recently discovered in different colubrid genera of the subfamily Psammophiinae; these were considered to play a role in sensory perception. In the present study, we describe the presence of similar structures in *Atretium schistosum*, another colubrid snake reportedly not belonging to the Psammophiinae. As this species is suspected of being phylogenetically distantly related to psammophine snakes, some hypotheses are provided to explain (1) the putative function of these pits, (2) their sporadic occurrence, and (3) to suggest when they may have evolved in the colubroid snake clade. **To cite this article:** A. Miralles, I. Ineich, C. R. Biologies 329 (2006).

© 2005 Académie des sciences. Published by Elsevier SAS. All rights reserved.

Résumé

Présence de fossettes gulaires et pariétales chez *Atretium schistosum* (Serpentes, Colubridae), une caractéristique originale non associée aux seuls serpents Psammophiinae. La présence sporadique de fossettes localisées sur les plaques pariétales a récemment été mise en évidence chez différents genres de couleuvres de la sous-famille des Psammophiinae. On leur attribue une fonction de perception sensorielle. Dans la présente étude, nous décrivons des structures similaires observées chez *Atretium schistosum*, une espèce de couleuvre n'appartenant pas au groupe des Psammophiinae. Cette espèce étant vraisemblablement phylogénétiquement très éloignée des Psammophiinae, de nouvelles hypothèses sont proposées afin de tenter d'expliquer (1) la fonction de telles structures, (2) le fait que leur présence soit sporadique et (3) de déterminer leur origine au sein du clade des serpents colubroïdes. **Pour citer cet article:** A. Miralles, I. Ineich, C. R. Biologies 329 (2006).

© 2005 Académie des sciences. Published by Elsevier SAS. All rights reserved.

Keywords: Serpentes; Colubroidea; Colubridae; Psammophiinae; *Atretium schistosum*; Parietal pits; Gular pits

Mots-clés: Serpentes; Colubroidea; Colubridae; Psammophiinae; *Atretium schistosum*; Fossettes pariétales; Fossettes gulaires

* Corresponding author.

E-mail address: amiral@mnhn.fr (A. Miralles).

1. Introduction

De Haan [1] recently described the occurrence of parietal pits in colubrid snakes of the subfamily Psammophiinae from seven species belonging to four genera. Drawings of these structures [2] in the psammophine snake *Rhamphiophis maradiensis* Chirio & Ineich, 1991 were previously published in this species description, without the authors explicitly noting them. These small apertures, numbering two to four, are located in the parietal plates of only some individuals belonging to some different species of that snake group. These structures are not sexually dimorphic. According to de Haan's observations (op. cit.), when present in a specimen, pits are permanent and do not vary in size and shape during the life span of the animal. Their function is unknown. De Haan [1] suggests that they are used in sensory perception, because they are located in the head area, but such an explanation requires a histological investigation. The hypothesis that considers them as *apical stigmata* to facilitate the process of skin shedding was rejected by this author.

During a study of head plate conformation in colubroid snakes, we observed the occurrence of similar structures in *Atretium schistosum* (Daudin, 1803), a presumably non-psammophine colubrid snake. *Atretium* Cope, 1861 is a genus of Asiatic colubrid consisting of two species: *A. schistosum* and *Atretium yunnanensis* Anderson, 1879. *Atretium schistosum* is an endemic species occurring on the Indian subcontinent, from India, Nepal and Sri Lanka. It is also reported from Myanmar, Malaysia, probably an erroneous locality, and from the Chinese province of Yunnan, which is undoubtedly a record of *A. yunnanensis* [3]. *Atretium schistosum* is a diurnal and ovoviviparous species restricted to freshwater habitats [3], which feeds on fish and small amphibians. In Sri Lanka, the species has been reported from some estuaries and even in coastal waters [4]. Its ecology is different from that of the psammophine snakes, which generally live in arid to semi-arid areas, but some species also occur in humid forests, seldom near water. Psammophine snakes are mainly distributed in Africa, whereas *Atretium* is found only in Asia.

After examination of the 12 specimens of *A. schistosum* available in the collection of the Paris Natural History Museum (MNHN), we concluded that these parietal pits appear to be homologous with those encountered in the Psammophiinae. Since *Atretium schistosum* may be only distantly related to the Psammophiinae, we here formulate a novel hypothesis to explain the function of these structures, accounting for their sporadically

occurrence and discuss their distribution within the colubroid snake clade.

2. Material and methods

Measurements were taken to the nearest 0.1 mm with an electronic caliper. Drawings were made using a light chamber fixed to a LEICA MS5 binocular microscope. The cephalic plate nomenclature used follows that of Chippaux [5]. Specimens examined during this study are all deposited at the MNHN, Paris, and are preserved in 75% ethanol. Twelve specimens were examined: MNHN 582, 1946.64 and 1994.1075, India, Pondichéry; MNHN 612, 1994.2342–3, India, Bengal; MNHN 1890.481, Sri Lanka; MNHN 1902.165, India, Coromandel; MNHN 1999.8089 and 7000, Madagascar?; MNHN 3519 and 7414, Philippines?

3. Results

3.1. Parietal pits

Among the 12 specimens of *Atretium schistosum* available in the MNHN collections, only two females (16.6%) show parietal pits (MNHN 612 and MNHN 1946.64) (Table 1). One specimen (MNHN 612) presents two pits on the left parietal plate, meeting at the posterior part, forming a Y-shaped structure. The right parietal plate of this specimen is devoid of pits (Fig. 1b and d). The second specimen (MNHN 1946.64) shows a pit in the centre of each parietal plate (Fig. 1a and c). De Haan [1] mentioned the existence of small vesicles present along the bottom of the parietal pit. These are visible when the superficial level of the old epidermis is removed. These structures were not visible because the Paris specimens are relatively old and their state of preservation has not conserved the fragile parts. The similarity of the parietal pits observed in *Atretium schistosum* with comparable structures mentioned by de Haan [1] is evident in their shape, location, size and number. Such similarity appears to be homologous between these structures, suggesting possible inheritance from a common ancestor. De Haan [1] also noted that these parietal pits can occur symmetrically (47% of the specimens) or asymmetrically (53%); the specimens of *A. schistosum* examined here are in accordance with this observation.

3.2. Gular pits

Out of 10 of the 12 examined specimens, other structures were observed, including small protuberances lo-

Table 1

Features of specimens of *Atretium schistosum* in MNHN collections. Parietal pits (PP): presence (P) or absence (A); Gular pits (GP): presence (P) or absence (A); sex of adult specimens obtained by tail dissection: (M) male, (F) female and (J) juvenile; TL: tail length; SVL: snout-vent length. Specimens showing parietal pits are indicated in bold

MNHN	PP	GP	Sex	TL	SVL
7414	A	P	F	141	487
582	A	A	F	138	459
1994.1075	A	P	M	157	344
1999.8089	A	P	M	165	381
7000	A	P	M	115+	358
1902.165	A	P	J	77	194
1890.481	A	P	J	42	114
3519	A	P	M	114	262
1946.64	P	A	F	100	524
612	P	P	F	144+	508
1994.2342	A	P	F	142	616
1994.2343	A	P	F	167	585

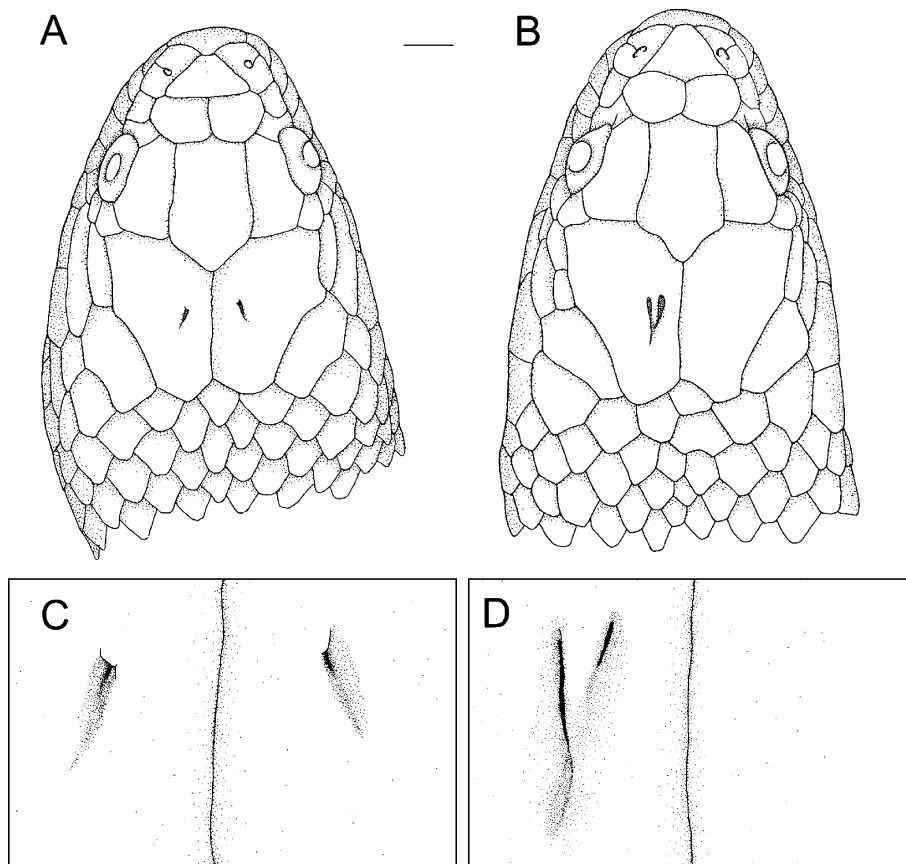


Fig. 1. Location of the parietal pits in *Atretium schistosum*. (A, C) MNHN 1946.64; (B, D) MNHN 612. Scale bars = 2 mm.

cated on the chin, at the level of the inferior labial scales and the mental plates, gular plates and symphysials, but also on some of the first ventral plates (Fig. 2, Table 1). Such structures are also encountered in some psammophine snakes, as noted by de Haan [6]. The si-

multaneous occurrence of both these structures in the same species seems to argue in favour of them being functionally linked. De Haan (op. cit.) suggested that they could have a function in chemical olfactory marking.

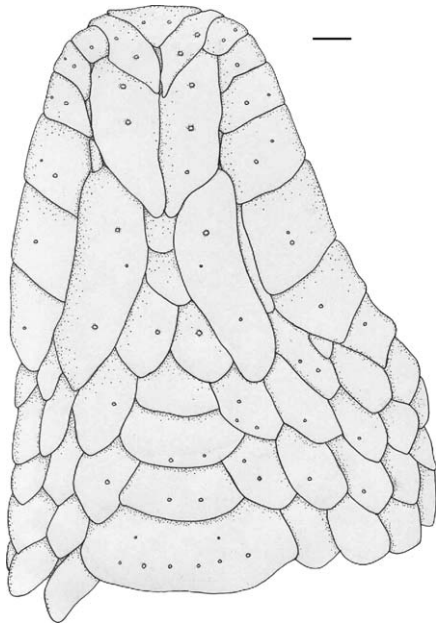


Fig. 2. Location of the gular pits in *Atretium schistosum* (MNHN 7000). Scale bar = 1 mm.

4. Discussion

4.1. Parietal pits: an earlier origin, and a wider distribution within snakes than expected

The exact position of the genus *Atretium* inside colubroid snakes is still debated, this genus having never been included in any phylogenetical analysis. According to Underwood (pers. commun. in [4]), the genus should be classified in the subfamily Xenodontinae. In the light of recent data [7,8], such a hypothesis is untenable and can reasonably be rejected, phylogenetic relationships of that subfamily showing that it is restricted to the New World. Two other subfamilies were suggested to include *Atretium*, the Natricinae, as suggested by Deuve [3], or the Colubrinae, as proposed by De Silva [4]. The last hypothesis, never formulated until now, would consist in including *Atretium* inside, or close to the psammophine, but given the high morphological, ecological and biogeographical differences between those two groups, this possibility appears to be very few probable. So, in the light of our observations, the occurrence of parietal pits could no more be taken as a unique synapomorphy of the Psammophiinae as suggested by de Haan [1]. These structures, probably glandular or sensory, should rather be considered as regressed organs constituting a plesiomorphy of the wider snake group of colubroids. Indeed, given that psammophine snakes are more closely related to the elapids

and the atractaspids than to most of the other colubrids [9], these pits could have been present at the base of the colubroid lineage and then regressed in most groups. Such a hypothesis is valid, whether *Atretium* is a natricine or a colubrine.

4.2. How is the presence of such structure explained?

Two plausible hypotheses are here considered in order to account for the sporadic occurrence of parietal pits as well in Psammophiinae than in *A. schistosum*.

(1) It could be an atavistic phenomenon. According to Hall [10], atavisms are the reappearance of ancestral characteristics in individual members of a species. They constitute proof that the genetic and developmental information originally used in the production of such characteristics has not been lost during evolution, but lies quiescent within the genome and in the processes of embryonic development. This occasionally resurgent trait may or may not be functionally expressed. By way of examples, the domestic horse, *Equus caballus*, can occasionally possess supernumerary digits [11], and the development of teeth in chick embryos can be experimentally induced by transplanting mouse neural crest cells [12]. In colubroid snakes, parietal pits could occasionally ‘reappear’ in some individuals (as could be the case in *Atretium* and among some Psammophiinae); some snake lineages would be more likely to produce such atavistic individuals. The low number of occurrences of pits within one species seems to indicate that they no longer have a functional role, as is often the case for several complex atavistic organs. Caution should be exercised, however, when interpreting the occurrence of these pits in only two colubroid lineages. These could in fact exist in other lineages, but they may be scarcely visible, and thus have not attracted the attention of herpetologists. A similar example is provided by the recent discovery of an external epidermoid supralabial gland present in all species of the viperid genus *Echis* [13,14]. These snakes have been previously examined by many herpetologists, yet the gland not noticed, although the gland aperture is visible without magnification. That is why it would be interesting to search for the presence of parietal pits in the most basal lineages of Alethinophidians (homalopsids, viperids, xenodermatids, boids, etc.) in order to determine whether their occurrence is more widespread in the basal clades of snakes.

(2) The second hypothesis considers these structures as permanent organs by colubroid snakes at least. They could be present permanently but in a discreet way, hidden by the tegument. Only after an injury, or an anomaly in the embryonic development, or even during some

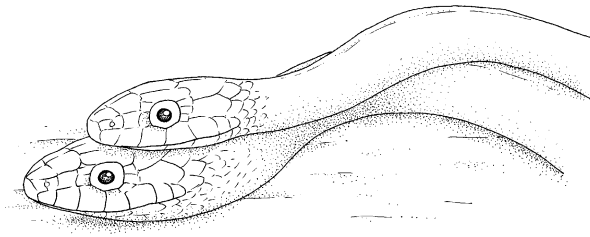


Fig. 3. 'Head-on-head' mating position.

pathologies, will these structures open to the exterior. Those parietal pits could then play an unsuspected secretory or sensorial role.

Smith [15] described the presence of nuchal glands in 11 species of Asian natricine snakes of the genus *Balanophis* M. Smith, 1938, *Macropisthodon* Boulenger, 1839 and *Rhabdophis* Fitzinger, 1843. Those dorsal paired glands are distributed in the neck (and could also extend to the whole length of the body in some species). They could exude an irritant secretion in order to repulse potential predators. However, contrary to the parietal pits, those organs have never been observed directly on the head of any specimen.

Concerning the presence of gular pits, de Haan [1] formulated several hypotheses regarding their function. One of these considers the pits as 'contact joints', which allow the snake to shed correctly, in retaining the skin to shed until the most favourable moment for shedding. Another hypothesis suggests that pits could play a role in sexual recognition during precopulatory parades and during copulation itself. Indeed, among many snakes, the male lays his head flat on that of the female during the copulation parade (Fig. 3). The supposed glandular gular pores, presumably secretory structures, are then in contact with the parietal pits of the female, which perhaps receive chemical signals or sensory information. This hypothesis seems less probable, because the frequency of occurrence of parietal pits is low inside the one species. Moreover, the hypothesis of parietal pits hidden under the parietal plate is incompatible with the transmission of chemical information from the gular pits of one individual to the receptor organs located in the parietal pits of another.

5. Conclusion

Occurrence of epidermoid glands in snakes may be more frequent than previously thought. Such structures are just beginning to be documented in snakes. Their function is currently unknown. Histological studies underway by de Haan will allow a better knowledge of their function. It is important that herpetologists be aware of the possible existence of such structures in or-

der to be able to look for them, allowing a better knowledge of their occurrence among snakes.

Acknowledgements

The authors are grateful to Jean-Pierre Gasc (MNHN) and Elizabeth Scott (American Museum of Natural History) for their interesting comments and corrections on the manuscript.

References

- [1] C.C. De Haan, Sense-organ-like parietal pits found in *Psammophiini* (Serpentes, Colubridae), C. R. Biologies 326 (2003) 287–293.
- [2] L. Chirio, I. Ineich, Les genres *Rhamphiophis* Peters, 1854 et *Dipsina* Jan, 1863 (Serpentes, Colubridae) : revue des taxons reconnus et description d'une espèce nouvelle, Bull. Mus. natl. Hist. nat., Paris, 4^e série, section A 13 (1–2) (1991) 217–235.
- [3] J. Deuve, Serpents du Laos, Mém. ORSTOM, Paris, vol. 39, 1970, 251 p.
- [4] P.H.D.H. De Silva, Snake Fauna of Sri Lanka, with special reference to skull, dentition and venom in snakes, Spolia Zeylanica 34 (1–2) (1980) i–xi, 1–472, pl. 1–67.
- [5] J.-P. Chippaux, Les serpents d'Afrique occidentale et centrale, Collection «Faunes et Flores tropicales», vol. 35, IRD, Paris, 2001, 292 p.
- [6] C.C. De Haan, Extrabuccal infralabial secretion outlets in *Dromophis*, *Mimophis* and *Psammophis* species (Serpentes, Colubridae, Psammophiini). A probable substitute for 'self-rubbing' and cloacal scent gland functions, and a cue for a taxonomic account, C. R. Biologies 326 (2003) 275–286.
- [7] J.E. Cadle, H. Greene, Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblage, in: R.E. Ricklefs, D. Schluter (Eds.), Species Diversity in Ecological Communities: Historical and Geographical Perspectives, University of Chicago Press, Chicago, IL, USA, 1993, pp. 281–293.
- [8] N. Vidal, S.G. Kindl, A. Wong, S.B. Hedges, Phylogenetic relationships of Xenodontine snakes inferred from 12S and 16S ribosomal RNA sequences, Mol. Phylogenet. Evol. 14 (3) (2000) 389–402.
- [9] N. Vidal, S.B. Hedges, Higher-level relationships of Caenophidian snakes inferred from four nuclear and mitochondrial genes, C. R. Biologies 325 (2002) 987–995.
- [10] B.K. Hall, Atavisms and atavistic mutations, Nat. Genet. 10 (2) (1995) 126–127.
- [11] O.C. Marsh, Recent polydactyle horses, Am. J. Sci. 43 (1892) 339–355.
- [12] T.A. Mitsiadis, Y. Chéraud, P. Sharpe, J. Fontaine-Pérus, Development of teeth in chick embryos after mouse neural crest transplantations, Proc. Natl Acad. Sci. USA 100 (11) (2003) 6541–6545.
- [13] I. Ineich, J.-M. Tellier, Une glande supralabiale à débouché externe chez le genre *Echis* (Reptilia, Viperidae), cas unique chez les serpents, C. R. Acad. Sci. Paris, Ser. III 315 (1992) 49–53.
- [14] H. Saint Girons, I. Ineich, Données histologiques sur la glande labiale supérieure des Viperidae du genre *Echis*, Amphibia-Reptilia 14 (1993) 315–319.
- [15] M.A. Smith, The Nucho-Dorsal Glands of Snakes, Proc. Zool. Soc. Lond., Ser. B 108 (1938) 575–583.