Phyllomedusa 24(2):201–221, 2025

ISSN 1519-1397 (print) / ISSN 2316-9079 (online)
doi: http://dx.doi.org/10.11606/issn.2316-9079.v24i2p201-221

Cephalic fossae and pits in the parietal shields of caenophidian snakes and their correspondence in the braincase

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Abstract

Cephalic fossae and pits in the parietal shields of caenophidian snakes and their correspondence in the braincase. Anatomical and osteological analyses in several species of ophidians belonging to the clade Caenophidia have led to the identification of different structures present in the cephalic shields of these reptiles. These structures are observed expressed mainly in the parietal shields, manifesting themselves in different forms. "Major parietal pits," generally symmetrical, occur in the center of the parietal shields, more or less medially distanced to each other. These may appear circular, linear, separated, conjunct, or in contact with the lateral margin of the parietal shield by a slit. Together with the pits, a new distinct trait has been observed in the parietal shields of different species of colubroids, here named "parietal fossae." Parietal pits and fossae are situated in correspondence with the paired foramina on the parietal bone's dorsal plane, which in turn correspond ventrally with the epiphysis, and the contact between the cephalic hemispheres and the optic lobes. Other fossae may be present in certain species, occurring more posteriorly in the parietal shields, or in the supraocular shields, in correspondence with neurovascular foramina and fossae present in the underlying cranial bones. A second category of pits has also been found, here named "minor pits," which appear randomly within the cephalic shields, and are also linked to neurovascular foramina present in the corresponding cranial bones. A third type of pit, distinct from the others, is the "medial posterior pit", which has been found in aquatic snakes. This pit occurs in the posterior half of the medial contact of the parietal shields, and corresponds to a large central foramen in the posterior apex of the parietal bone's plane, ventrally opening within a canal between the two fossae covering the optic lobes. All of these traits have been observed in a large number of snakes belonging to the families Colubridae, Natricidae, Psammophiidae, Atractaspididae, Pareidae, Xenodermidae, Micrelapidae and Elapidae. These do not occur in all individuals within the examined taxa, but rather affect part of the specimens of a given species. Fossae and pits appear to be sporadic surface structures that correspond to neurovascular foramina present in the underlaying cranial bones.

Keywords: Cranial anatomy, Parietal pits, Parietal fossae, Parietal foramen, Colubroidea.

Received 21 August 2024
Accepted 21 January 2025
Distributed December 2025

Resumo

Fossetas e cavidades cefálicas nos escudos parietais das serpentes Caenophidia e sua correspondência na caixa craniana. Análises anatômicas e osteológicas em várias espécies de serpentes pertencentes ao clado Caenophidia levaram à identificação de diferentes estruturas presentes nos escudos cefálicos. Estas estão presentes principalmente nos escudos parietais, manifestando-se de diferentes formas. “Fossetas parietais maiores”, geralmente simétricas, ocorrem no centro dos escudos parietais, mais ou menos distanciadas medialmente umas das outras. Estas podem se apresentar circulares, lineares, separadas, conjuntas ou em contato com a margem lateral do escudo parietal por uma fenda. Juntamente com as fossetas, foi observada uma nova característica distinta nos escudos parietais de diferentes espécies de colubróides, aqui denominada “fossetas parietais”. As fossas e fossetas parietais estão situadas em correspondência com os forâmenes emparelhados no plano dorsal do osso parietal, que por sua vez correspondem ventralmente à epífise e ao contato entre os hemisférios cefálicos e os lobos ópticos. Outras fossas podem estar presentes em certas espécies, ocorrendo mais posteriormente nos escudos parietais ou nos escudos supraoculares, em correspondência com as forâmenes e fossas neurovasculares presentes nos ossos cranianos subjacentes. Uma segunda categoria de fossas também foi encontrada, aqui denominadas “fossetas menores”, que aparecem aleatoriamente dentro dos escudos cefálicos e também estão ligadas às forâmenes neurovasculares presentes nos ossos cranianos correspondentes. Um terceiro tipo de fosseta, distinto dos outros, é a “fosseta posterior medial”, que foi encontrada em serpentes aquáticas. Esta ocorre na metade posterior do contato medial dos escudos parietais e corresponde a um grande forâmen central no ápice posterior do plano do osso parietal, abrindo-se ventralmente dentro de um canal entre as duas fossetas que cobrem os lobos ópticos. Todas essas características foram observadas em um grande número de serpentes pertencentes às famílias Colubridae, Natricidae, Psammophiidae, Atractaspididae, Pareidae, Xenodermidae, Micrelapidae e Elapidae. Estas não representam uma constante dentro dos táxons examinados, mas ocorre em uma parte dos espécimes de uma determinada espécie. As fossas e cavidades parecem ser expressões superficiais esporádicas correspondentes a forâmenes neurovasculares presentes nos ossos cranianos subjacentes.

Palavras-chave: Anatomia craniana, Colubroidea, Fossa parietal, Fosseta parietal, Forâmen parietal.

Introduction

Many of the more derived snakes, such as colubroids, present enlarged cephalic scales, defined as shields, which are larger and distinct from the dorsal scales. These shields have a specific shape and the cephalic dorsal ones are usually organized in a number that can vary from nine to 11 (Schulz, 1996). Recent studies have been dedicated to examined the presence of pits within the parietal shields that have been observed in several species belonging to five genera of the family Psammophiidae (De Haan 2003, 2006, Cottone and Bauer 2011). The presence of similar cephalic structures has been previously mentioned for several species in the genera *Alsophis, Dasypeltis, Mehelya,* and *Tropidonophis* (Underwood 1967, Malnate and Underwood 1988), but parietal pits were described in detail for the first time by De Haan (2003). In addition to psammophiids, these traits have been found in an Asian natricid species, *Atretium schistosum* (Daudin, 1803) (Miralles and Ineich 2006). In these studies, among the various hypotheses generated of a possible sensorial nature, the authors support the conclusion that these pits could be an expression of ancestral traits present in the analyzed species (de Haan 2006, Miralles and Ineich 2006, Cottone and Bauer 2011) and a surface manifestation originating from underlying structures (Miralles and Ineich 2006, Cottone and Bauer 2011).

The present study examines some species of Old World snakes belonging to the clade Caenophidia in which similar structures to the pits described in psammophiids have been identified in the parietal shields. Anatomical and osteological analyses were performed on 19 representative species belonging to the families Colubridae, Natricidae, Psammophiidae, Elapidae, and Viperidae, where the relationship between the cephalic shields, the braincase, and the encephalon was investigated. The resulting study represents a preliminary analysis of the cephalic traits present in the shields of snakes belonging to the clade Caenophidia. Three new distinct traits, and their correspondence with the features of the underlaying cranial bones are described.

Materials and Methods

Osteological and necroscopic analyses were performed at OPHIS Museo Paleontologico e Centro Erpetologico. All deceased specimens belonging to the colubroid, elapoid and viperid clades were donated by private individuals and zoos to OPHIS for research purposes, with the exception of specimens of *Hierophis viridiflavus* (Lacépède, 1789), *Natrix helvetica* (Linnaeus, 1758), and *Zamenis longissimus* (Laurenti, 1768), which consisted of roadkilled individuals collected in Abruzzo (Italy), most of which were used in former studies (Paterna 2023, 2024, 2025, Paterna and Grano 2024). Specimen preparation was performed using surgical tools and solvents. All photographic material relating to anatomical and osteological analyses was produced within OPHIS. Photographs of living specimens belonging to the genera *Hierophis, Zamenis,* and *Natrix* portray both specimens raised in controlled environment and wild ones photographed in nature. Photographs of living specimens belonging to the genera *Elaphe, Hemorrhois, Pituophis, Malpolon,* and *Naja* were taken in controlled environments.

Necroscopic analyses on colubroids have been carried out on seven adult specimens of *H. viridiflavus,* three adult specimens of *Dolichophis caspius* (Gmelin, 1789), five adult specimens of *N. helvetica,* one adult specimen of *Natrix natrix* (Laurenti, 1768), one adult specimen of *Natrix tessellata* (Laurenti, 1768), three adult specimens of *Z. longissimus,* two juvenile specimens of *Elaphe quatuorlineata* (Lacépède, 1789), one adult specimen of *Malpolon moilensis* (Reuss, 1834), one adult specimen of *Pantherophis guttatus* (Linnaeus, 1766), one adult specimen of *Heterodon nasicus* (Baird and Girard, 1852). Necroscopic analyses on elapids were carried out on one specimen of each of the following species: *Naja naja* (Linnaeus, 1758), *Naja atra* (Cantor, 1842), *Naja kaouthia* (Lesson, 1831), *Naja sputatrix* (Boie, 1827), *Naja pallida* (Boulenger, 1896), *Naja haje* (Linnaeus, 1758), and *Aspidelaps lubricus* (Laurenti, 1768). The various steps of anatomical and osteological inspection included a complete preparation and disarticulation of the cranial bones, which were preserved and catalogued at OPHIS. Osteological analyses on European viperids were carried out on the prepared skulls of one adult specimen of *Vipera ammodytes* (Linnaeus, 1758) and two adult specimens of *Vipera aspis* (Linnaeus, 1758). Anatomical analyses in living colubroid specimens raised in a controlled environment were performed at OPHIS on: *H. viridiflavus* (four adults and two subadults), *N. helvetica* (five adults and 23 juveniles), *Z. longissimus* (12 adults, two subadults, and 12 juveniles), *Zamenis scalaris* (Schinz, 1822) (two subadults), *Hemorrhois hippocrepis* (Linnaeus, 1758) (five adults), *M. moilensis* (four adults), *Malpolon insignitus* (Geoffroy Saint-Hilaire, 1827) (two adults), *Elaphe dione* (Pallas, 1773) (two adults, two subadults, and five juveniles), *Elaphe carinata* (Günther, 1864) (four adults and 17 juveniles), *Elaphe bimaculata* (Schmidt, 1925) (15 adults and 18 juveniles), *Elaphe quatuorlineata* (six adults and four juveniles), *Elaphe anomala* (Boulenger, 1916) (one adult), *Ortrhriophis taeniurus* (Cope, 1861) (one adult), *Oreocrypthophis porphyraceus* (Cantor, 1839) (two adults), *Gonyosoma boulengeri* (Mocquard, 1897) (two adults), *Thamnophis marcianus* (Baird and Girard, 1853) (one adult), *Pantherophis guttatus* (16 adults), and *Pituophis catenifer* (Blainville, 1835) (two adults) (Appendix I). Inspection of the external cephalic traits in living European snakes in the wild, belonging to the genera *Elaphe, Hierophis, Dolichophis, Zamenis, Coronella, Natrix,* and *Vipera,* was performed in 2024. Further inspections were possible after the re-examination of photographic material previously collected portraying both European and extra-European taxa, which were investigated using photographic material present in the literature.

Results

Nomenclature

The term "*pits*" refers to circular, elliptical or longitudinal (slits) incisions present on the parietal shields characterized by well-defined margins. "*Fossae*" refers to small circumscribed depressions inside the shields, in which the surface of the scute remains intact, not showing visible incisions or perforations.

Parietal fossae.—These fossae are usually symmetrical and located at the center of the parietal shields, more or less distant from one another along the transverse axis crossing the medial contact of the shields. They can also appear, always symmetrically, in other cephalic shields (Figure 1A).

Parietal pits (De Hann 2003) or *major parietal pits*.—These pits are usually symmetrical and located at the center of the parietal shields. Equivalent to fossae, these pits can be more or less close together or spaced transversally (Figure 1B).

Conjoined parietal pits.—These major pits are connected to each other by an incision that crosses the parietal shields transversally (Figure 1C).

Parietal slits (De Haan 2003).—These longitudinal incisions occur in the same positions as major parietal pits (Figure 1D, left parietal shield).

Laterally expanded parietal pits.—This condition is the opposite of conjoined pits. Usually symmetrical, these major pits are connected to the lateral margins of the parietal shields by an incision on the surface of the shield, appearing similar to parietal slits (Figure 1D, right parietal shield).

Minor parietal pits.—This type of pit occurs randomly and generally in an asymmetrical manner occupying any position within the parietal shields (Figure 1E).

Medial posterior parietal pit.—This pit occurs singularly near or along the medial contact in the posterior portion of the parietal shields (Figure 1 F).

Colubridae

In adult and subadult individuals of *Hierophis viridiflavus,* a pair of fossae is visible in the parietal shields (Figure 2A). These fossae occur in the center of the shields, and manifest themselves in two laterally compressed depressions that can be more or less extended longitudinally. Other symmetrical depressions are present in the cephalic shields of this species, and can be more or less marked differently in each individual. A second pair of fossae is present in the parietal shields, but in the posterior portion, in contact with the dorsal scales or even involving them (Figure 2A). These fossae are much larger than the previous ones, and develop laterally. A third pair of fossae, with a triangular shape, is found in the posteromedial portion of the supraocular shields, near the contacts with the parietal and frontal shields.

In order to search for connections between the observed cephalic fossae and the underlying structures, the cranial bones of five previously prepared specimens were examined. These fossae occur in correspondence with features present in the dorsal surface of the bones that compose the braincase. The most evident feature is represented by two parietal foramina, which are found in the posterior half of the parietal bone. On the flat and smooth dorsal surface, the presence of two major adjacent foramina, aligned along the transverse axis dorsoventrally crossing the bone, is easily recognizable (Figure 2A). These foramina are located precisely beneath the central fossae present in the parietal shields. Additional foramina are present in the anterolateral portion of the same bone, near the frontal contact,

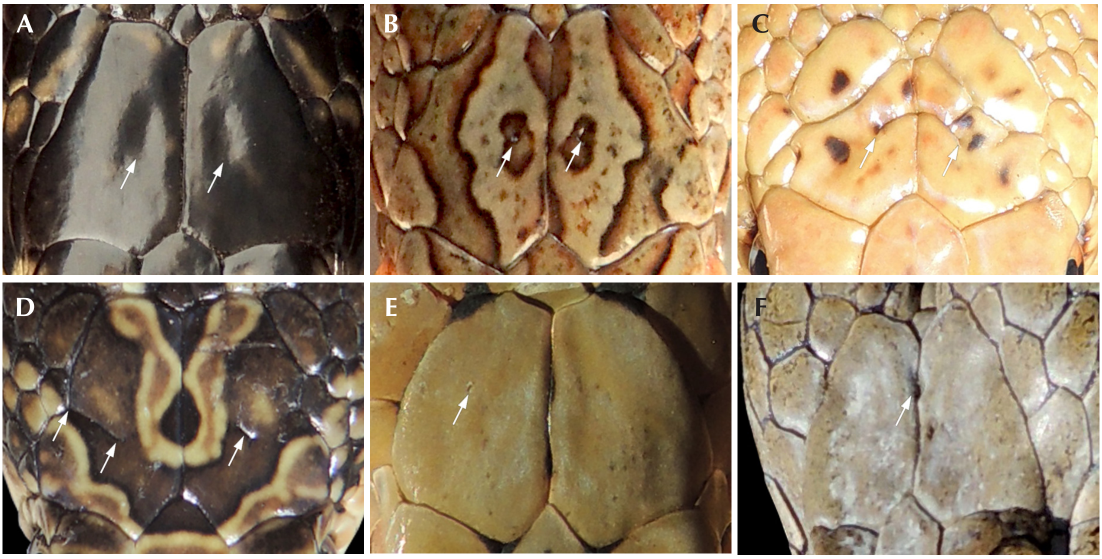

Figure 1. Details of the parietal shields of six colubroid snakes. (**A**), parietal fossae in *Hierophis viridiflavus;* (**B**), major parietal pits in *Elaphe dione;* (**C**); conjoined parietal pits in *Pituophis catenifer;* (**D**) laterally expanded parietal pit (double arrow) and parietal slit (single arrow) in *Hemorrhois hippocrepis;* (**E**), minor parietal pit in *Elaphe carinata;* (**F**), medial posterior parietal pit in *Natrix tessellata.*

where a sequence of large foramina occurs in the lateroposterior portion of these bones (Figure 2A). These features correspond to the fossae that occur in the supraocular shields. Additional foramina in the dorsum of the braincase are present in the supraoccipital bone, where two specular major foramina occur within the two specular fossae. Around these main foramina, smaller foramina may be found, arranged asymmetrically between the two supraoccipital fossae. This third group of foramina corresponds to the fossae present in the posterior portion of the parietal shields and the most anterior dorsal scales. Anomalies have been observed in one of the parietal bones of the prepared specimens, where the right foramen is not located within the respective fossa that should circumscribe it, but is positioned more anteriorly. The foramina in the braincase of the western whipsnake *Hierophis viridiflavus* have been mentioned in prior studies (Racca *et al.* 2020), as well as in other studies on related taxa such as *Dolichophis jugularis* (Linnaeus, 1758) (Sadeghi *et al.* 2014) and *Dolichophis schmidti* (Nikolsky, 1909) (asymmetric case with only one foramen in the left portion of the parietal bone, Rajabizadeh *et al.* 2021). All three pairs of fossae occurring on the shields of the western whipsnake are located in correspondence with neurovascular foramina present in the dorsum of the braincase. The posterior parietal and the supraoccipital fossae are located in correspondence with large foramina present in the cranial bones (situated in the parietal anterior fossae, parietal posterior fossae, and supraoccipital fossae), and develop on the surface of the parietal shields over a larger area than that of the main central parietal fossae, which instead corresponds to the flat plane of the parietal bone (Figure 2A). In the juveniles of *H. viridiflavus,* these cephalic fossae are not always visible. For example, in a young specimen subjected to necropsy these external features were not visible, but the cranial bones had all the foramina observed in adults.

Through the preparation of the samples, it was possible to observe a further connection of these features between the various levels. The two main parietal foramina not only correspond dorsally to fossae and pits, but ventrally they correspond with the anteroposterior contact between the cerebral hemispheres and the optic lobes, more precisely above the epiphysis (Figure 2B).

A parallel investigation was carried out on a second species of colubrid sympatric with the previous *H. viridiflavus,* the Aesculapian snake *Zamenis longissimus.* Most of the individuals examined have smooth and homogeneous parietal shields, while the parietal bone may feature two medial foramina that are not always well defined, and are positioned close together toward the midline (Figure 3A). The presence of parietal pits and fossae was observed only in some individuals. One adult had symmetrical parietal pits (Figure 3B), and some hatchlings exhibited posterior parietal pits, also symmetrical, and almost in contact with the dorsal scales. In a subadult individual, the presence of a minor pit was found toward the posterior limit of the right parietal shield, and one was found on the left parietal shield (Figure 3C), while another individual, also an adult, showed two symmetrical parietal pits. The same individual had two small pits near the lateral margin of the right parietal shield, corresponding to the anterior portion of the second temporal scale. In one hatchling, the presence of cephalic pits was observed in the frontal shield. Further analyses have been carried out on the cranial bones of different specimens of the whipsnake *Dolichophis caspius,* which appear to be similar to those of *H. viridiflavus,* and on some specimens of the American colubrid *Pantherophis guttatus*, which instead has a condition similar to that of *Z. longissimus.*

Additional analyses were carried out on single individuals or small groups of specimens of different species of colubrids from the Old and New World. In some of these, the presence of major parietal pits was found, but in many different forms from those previously described. The two pits may occur close to each other, immediately after the median contact of the parietal shields, well distanced, or even joined transversally by a groove (Figure 1C). This pit model (conjoined pits) has been observed in *Gonyosoma boulengeri* and in *Pituophis catenifer,* where this feature seems to be common.

The sheds of the species that show these features in the head shields have been examined. As described by De Haan (2003), the pits are found in the exuviae, while the fossae do not always remain imprinted. Exuviae inspection can be used to determine the presence of cephalic pits in species where the background color and the dorsal patterns adorning the shields may be an obstacle in detecting them, as in the case of *Hemorrhois hippocrepis* (Figure 1D). In some species cephalic pits are also visible in hatchlings, as in the case of *Z. longissimus, Orthriophis taeniurus,* and *Telescopus semiannulatus* (Smith, 1849) (pers. obs.).

Natricidae

In this species the fossae on the parietal shields are very visible in hatchlings and juveniles (Figure 4A), and occur near the medial margin of the shields and always in correspondence with the parietal foramina. In this stage the shields are smooth and homogeneous, while in adults the parietal shields undergo deformations that seem to trace the silhouette of the parietal bone. These features associated with ageing can make the fossae difficult to distinguish (Figure 4B–D). The parietal bone of this species has adjacent fossae, where the parietal foramina are present, although in some cases only one of these fossae may host a visible foramen. In the specimens examined, the main parietal foramina may be both symmetrical and asymmetrical, in a number that varies from 1 to 4. The dorsal surface of the parietal bone is not smooth, and may present transverse rugosities. One exception is represented by an adult individual in which, during the preparation phase, the absence of fossae and pits in the shields (Figure 5A) in the epidermis (Figure 5B) and in the parietal bone (Figure 5C) was observed.

During the preparation of a large adult female,

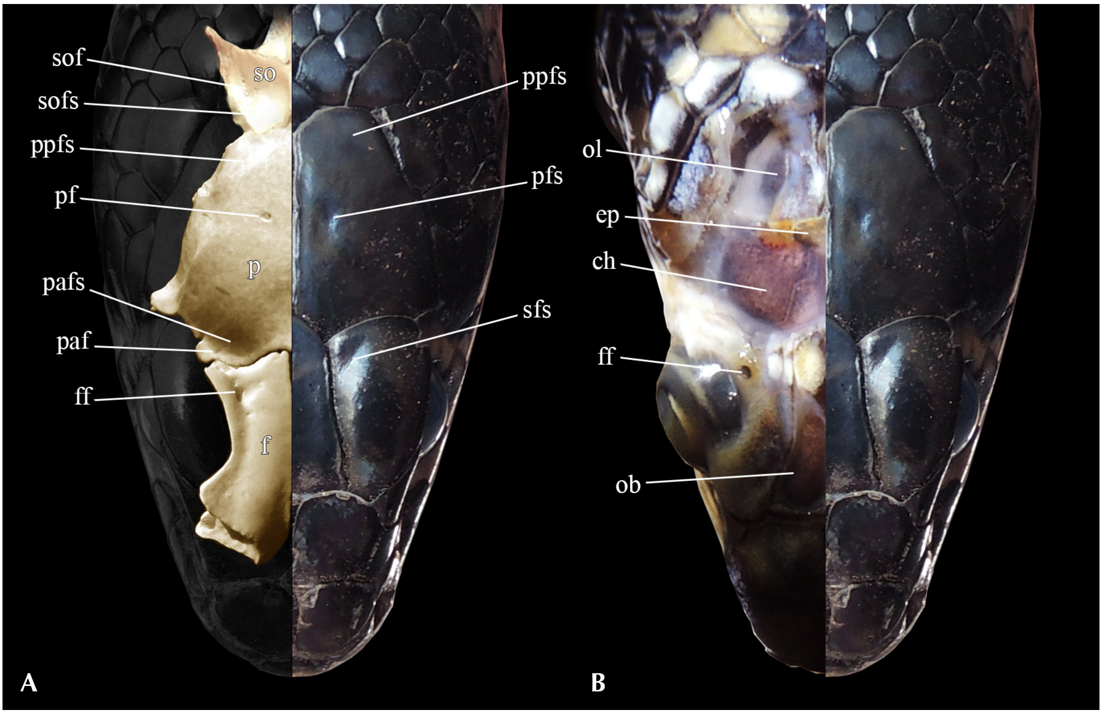

Figure 2. Details of cranial anatomy of *Hierophis viridiflavus.* (**A**), features in the cranial bones and their correspondence in the head shields; (**B**), features of the forebrain and midbrain and their correspondence in the head shields. Abbreviations: ch, cerebral hemisphere; ep, epiphysis; f, frontal; ff, frontal foramina; ob, olfactory bulb; ol, optic lobe; p, parietal; paf, parietal anterior foramina; pafs, parietal anterior fossa; pf, parietal foramen; pfs, parietal fossa; ppfs, parietal posterior fossa; sfs, supraocular fossa; so, supraoccipital; sof, supraoccipital foramina; sofs, supraoccipital fossa.

the presence of several parietal pits of different sizes were observed (Figure 6A). On the epidermis, below the cephalic shields, openings corresponding to the pits above are visible (Figure 6B). In the following preparation step, it was possible to observe how these openings pass through the dermal tissues, where the “hole size” in correspondence with the minor pits are similar to those present dorsally. The larger pits, arranged more laterally in the left shield, are located outside the parietal bone, corresponding to indentations that are present along the bone’s left lateral margin (Figure 6 C), and which are absent on the opposite side of the bone (Figure 6A, C).

Parietal pits have also been observed in *Natrix tessellata.* In this species, pits are present adjacent or close to the medial contact of the two parietal shields, together with the occurrence of smaller minor pits. In several specimens, a further large cephalic pit can be noted, set more posteriorly from the central ones, and located in the medial contact of the parietal shields, here referred to as the “medial posterior parietal pit”. The presence of corresponding foramina in the parietal bone of this species is documented in the study by Papežíková *et al*. (2024).

Together with the genus *Natrix,* cephalic fossae and pits have been observed in the genus *Thamnophis.* In several species of this genus the parietal pits are found in correspondence with a

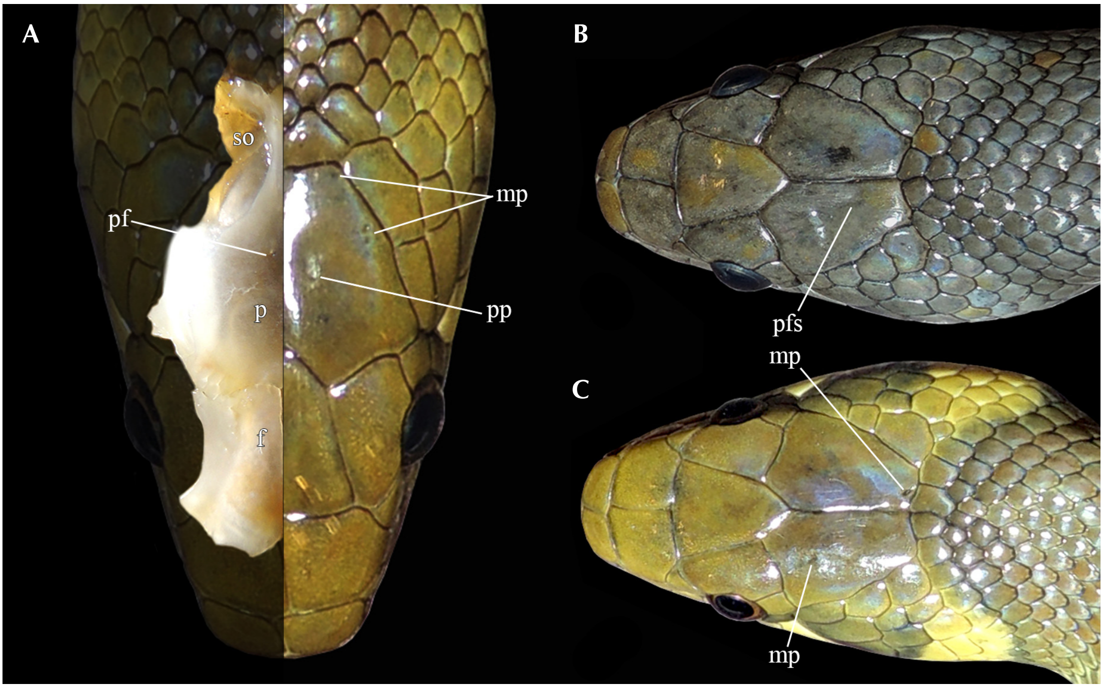

Figure 3. Cranial anatomy and details of cephalic pits and fossae in *Zamenis longissimus.* (**A**), features in the cranial bones and their correspondence in the head shields; (**B**), adult specimen of the *subgrisea* phenotype with parietal fossae; (**C**). adult specimen of the classic phenotype with cephalic minor pits. Abbreviations: f, frontal; m, minor pit; n, nasal; p, parietal; pf, parietal foramen; pfs, parietal fossa; so, supraoccipital.

dorsal pattern, as in the cases of *T. marcianus*, *T. radix* (Baird and Girard, 1853), *T. elegans* (Baird and Girard, 1853), *T. ordinoides* (Baird and Girard, 1852) and *T. sirtalis* (Linnaeus, 1758), where a light-colored circle bordered in black makes them almost unnoticeable at first glance (Mara 1994, Bernstein *et al.* 2024, pers. obs.). As in the case of colubrids, these are easily visible during shedding. The parietal pits appear to be similar to those present in the juveniles of *N. helvetica,* and more visible in adult specimens.

Psammophiidae

Additional inspections were performed in the psammophiids species of the genus *Malpolon* that were not investigated in the previous studies of the parietal pits (De Haan 2003, 2006, Cottone and Bauer 2011). In *Malpolon moilensis* major parietal pits, conjoined parietal pits, minor pits, and even the total absence of pits inside the cephalic shields were observed (Figure 7A). Other pits were identified in the supraocular shields, where they can also appear symmetrically arranged (Figure 7A). The main foramina and minor foramina occur in the parietal bone of this species, all distributed on the parietal plane. A linear series of foramina is always dorsally located along the longitudinal depression that occurs toward the lateral margin of the contact of the parietal bone with the frontals, piercing both cranial bones, and likely corresponding to the minor pits occurring in the supraocular shields. In *Malpolon insignitus* major parietal pits, parietal slits, laterally expanded parietal pits and minor pits were observed (Figure 7B, C). Additional cephalic pits were found in the frontal and supraocular

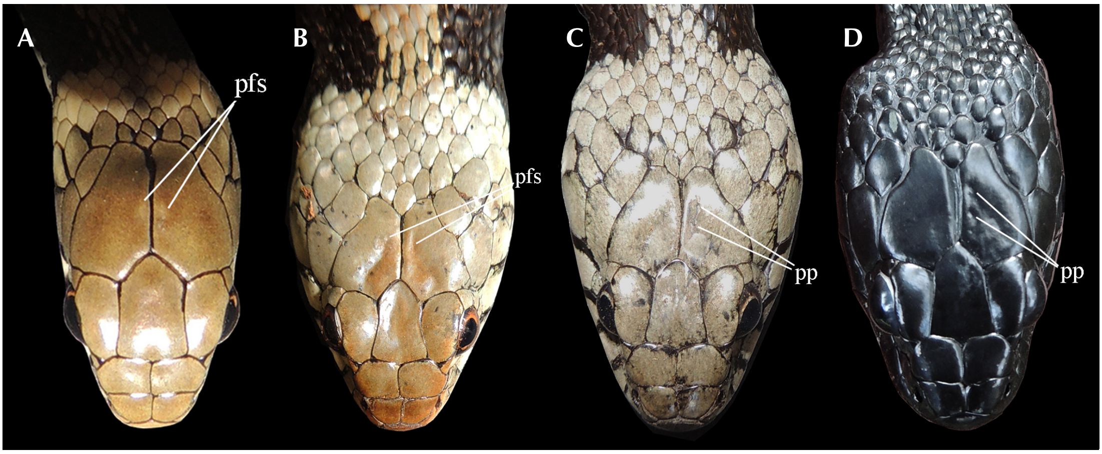

Figure 4. Parietal fossae and pits in *Natrix helvetica.* (**A**) juvenile specimen; (**B**) adult female; (**C**) axanthic adult female; (**D**) melanotic adult male. Abbreviations: pfs, parietal fossa; pp, parietal pit.

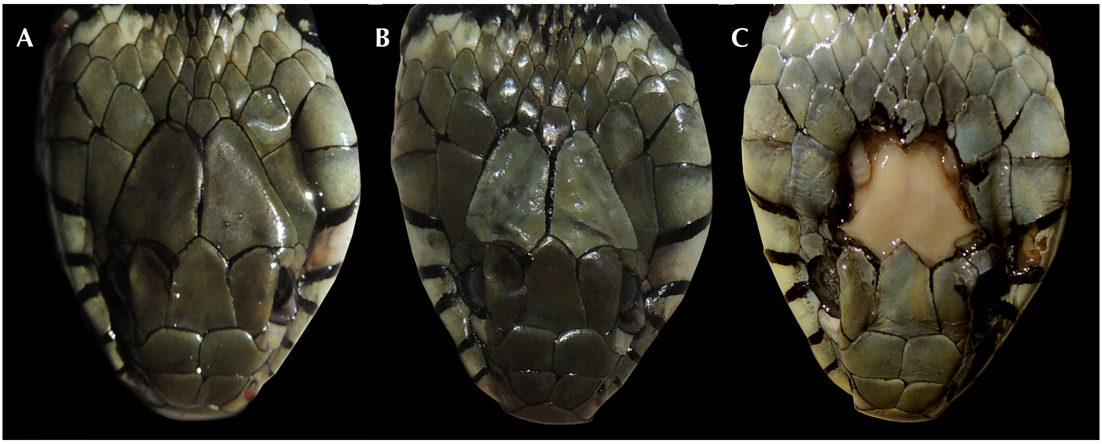

Figure 5. *Natrix helvetica* roadkilled adult specimen presenting no cephalic fossae or pits in the parietal shields (**A**), in the dermal tissues (**B**), and no foramina in the dorsal plane of the parietal bone (**C**).

shields (Figure 7B). Similar to *H. viridiflavus,* fossae are also present in the medioposterior portion of the supraocular and parietal shields.

Elapidae

Specimens belonging to the *Naja, Afronaja,* and *Uraeus* subgenera were analyzed, including *Naja naja, N. atra, N. kaouthia, N. sputatrix, N. pallida,* and *N. haje.* In all of these species the parietal pits are easily distinguishable, and can appear symmetrical, more or less transversally distanced depending on the species, or even asymmetrical. In *N. pallida,* for example, the parietal pits are positioned close together and consequently adjacent to the medial margin of the parietal shields (Figure 8A). A prepared specimen allowed confirmation of what was already observed in the specimens belonging to the other families: the continuity of a small canal that from the surface of the epidermis penetrates the underlying tissues

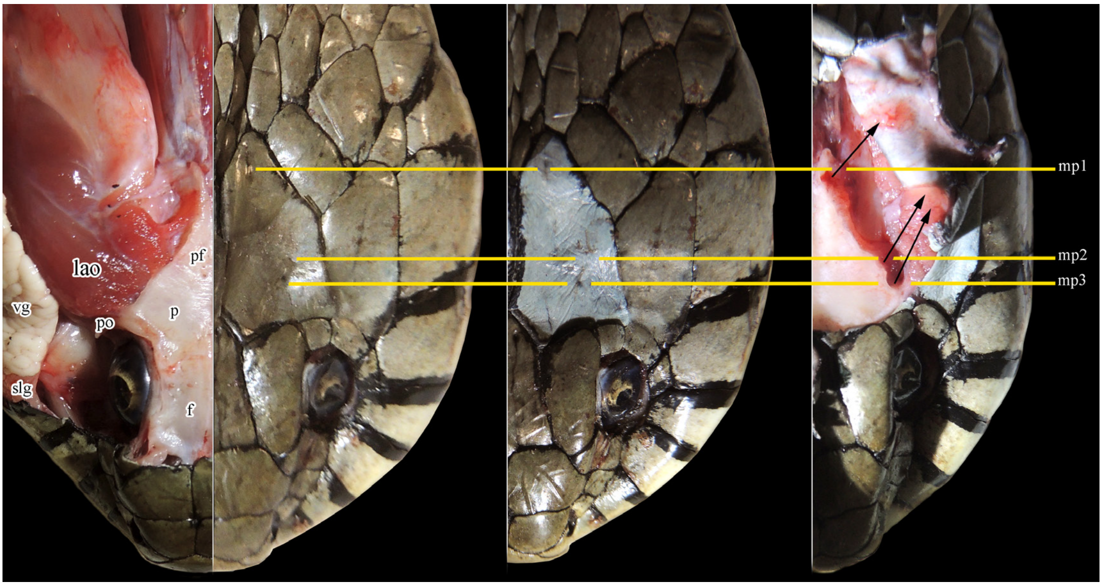

Figure 6. Cephalic pits in a *Natrix helvetica* roadkilled adult specimen. Yellow horizontal lines indicate the position of the minor pits in the different dissection steps. Black arrows indicate underlaying features in correspondence of the minor parietal pits. Abbreviations: f, frontal bone; lao, levator anguli oris; mp, minor pit; p, parietal bone; pf, parietal foramina; po, postorbital bone; slg, supralabial salivary gland; vg, venom gland.

until it enters the parietal foramen (Figure 8B). The same arrangement was observed in *N. sputatrix,* whose pits can be further apart compared to the previous species (Figure 7C). Here, too, in a prepared specimen it was possible to observe the vertical canalization of the cephalic pit, unique and asymmetrical in this individual (Figure 8D). In prepared specimens of the different species, the presence of a pair of main parietal foramina was found, where interspecific variation is present.

Viperidae

The cranial bones of the viperids *Vipera aspis* and *V. ammodytes* were analyzed. These species have a parietal bone with an irregular dorsal surface, unadorned by foramina, as well as the frontal bones, flatter than those of the other species analyzed, that feature a sagittal depression in the center of each bone. Using photographic material acquired in past and recent field observations, it seems that in some European viperids with large parietal shields, cephalic pits may be present as in the case of *Vipera berus* (Linnaeus, 1758) (Meier 2024, pers. obs.).

Parietal Bones

In the dorsal plane of the parietal bones of the specimens examined, the presence of neurovascular foramina was found in correspondence with the fossae and pits present in the parietal shields. There are generally two symmetrical main parietal foramina, but in some individuals these may occur in odd numbers, or be present only on one of the two halves of the bone. These foramina penetrate the entire dorsoventral thickness of the bone, opening ventrally. In colubrids these foramina are small and usually circumscribed by a fossa (Figure 9 A, B). Some irregularities may be present in the arrangement of these foramina. In a specimen of *H. viridiflavus* one of the two fossae that should contain the foramen was located anterioly to it (Figure 9A), and in a

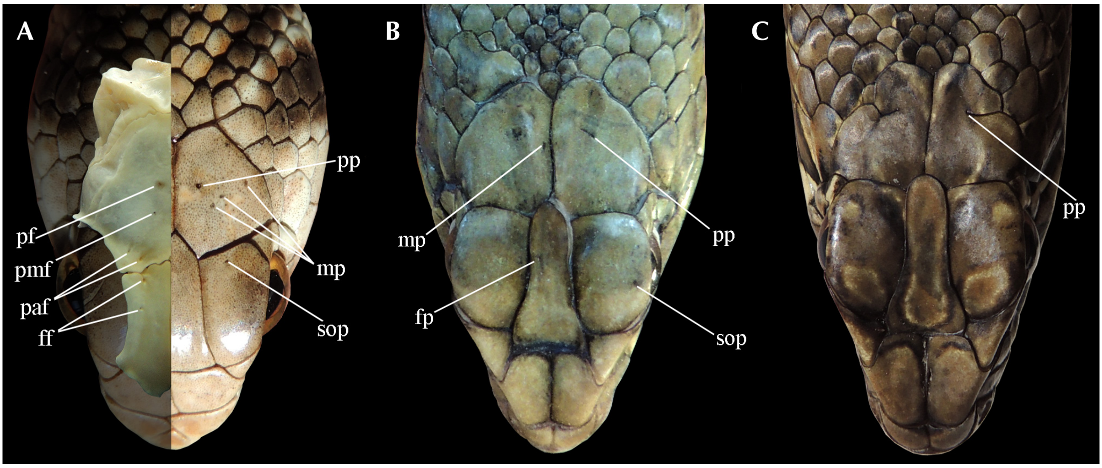

Figure 7. Cephalic pits in psammophiid snakes: (**A**) *Malpolon moilensis* adult male; (**B**) *Malpolon insignitus* adult male; (**C**) *Malpolon insignitus* adult female. Abbreviations: ff, frontal foramina; fp, frontal pit; mp, minor parietal pits; paf, parietal anterior foramina; pf, parietal foramen; pmf, parietal minor foramen; pp, parietal pits; sop, supraoccipital pit.

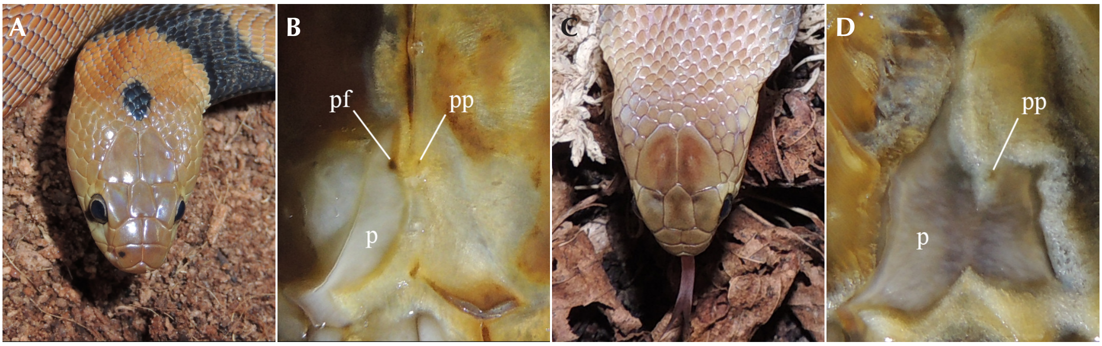

Figure 8. Parietal pits in cobras. (**A**) Subadult specimen of *Naja pallida* showing parietal pits; (**B**) preparation of the skull of an adult specimen of *Naja pallida*; (**C**) juvenile specimen of *Naja sputatrix*; (**D**) preparation of the skull of an adult specimen of *Naja sputatrix*. Abbreviations: p, parietal; pf, parietal foramen; pp, parietal pit.

specimen of *Z. longissimus* a disparity in the foramina in the two halves of the parietal plate was observed, where two more foramina occur posteriorly to the main foramen on the left side, which are absent on the right side (Figure 9B). Additional foramina are present close the anterolateral margins of the bone, in contact with the frontal bones. These foramina are present in almost all analyzed individuals. The lateral margins of the parietal plate of *N. helvetica* are straight and have an angle that gives the posterior half of the bone a dorsal shape of an equilateral triangle. The parietal foramina occur more posteriorly than in the analyzed colubrids, and can vary from one to two pairs, or be asymmetrical (Figure 6A; Figure 9C). The parietal plane of *N. tessellata* is similar in shape to that of *N. helvetica,* with a marked sagittal depression running along the dorsal parietal plane. The two main foramina are well defined and the wide medioposterior foramen, which corresponds to the medial posterior parietal pit (Figure 1F), is situated at the posterior apex of the bone's dorsal plane. This foramen, as in the paired ones, entirely pierces the bone in a passage from the ventral to the dorsal surface. In elapids of the genus *Naja,* as in *N. helvetica,* the dorsal surface of the parietal bone has a more or less marked transverse sculpting, varying by species. In the species analyzed, there are generally tow main parietal foramina, but even in this family there may be cases of asymmetry (Figure 9E–J). The morphology of the parietal plane varies among the different species, but one thing they have in common is the size of the parietal foramina, which seems to be larger than that of the other species described previously. In the parietals of *V. aspis* and *V. ammodytes* foramina were not found, and the morphology of the parietal bone seems to have important variations between the two species of the same genus (Figure 9K, L).

Discussion

Cephalic pits are mainly divided into two categories: major pits and minor pits. The major pits occur in most cases in even numbers, are symmetrical, and specular at the center of the parietal shields, more or less close together, and in correspondence with the underlying larger parietal foramina. There are cases in which the major pits are asymmetrical, where a single pit is present in only one of the two parietal shields, or in which more than one pit is present in a shield, as occurs for the parietal foramina. The minor pits instead seem to manifest themselves randomly within the shields, and are usually odd and asymmetrical, yet also connected to underlying neurovascular foramina. Neither types of pits are constant within the analyzed species, and seem to affect only some individuals, even within the same bloodline or the same clutch, regardless of factors such as sex and age. The parietal fossae instead seem to be typical of certain species, such as *Hierophis viridiflavus* and *Natrix helvetica,* in which parietal pits can also appear. The fossae can be more or less defined and marked among the various individuals of the same species, and in the different growth phases. These, unlike the pits, always seem to occur in a symmetrical and specular arrangement. Fossae and major pits appear mainly in the same area inside the parietal shields, usually in the central portion of these. Depending on the species, they can be located more or less medially to the contact between the two shields. Fossae and major pits are found in correspondence with the main underlying parietal foramina, in correspondence with the contact between the cephalic hemispheres and the optic lobes. At the same time, in necropsied specimens that did not have parietal pits, no foramina were observed on the parietal plane.

Other fossae can affect the cephalic shields. The posterior ones, occur in the posterior ends of the parietal shields, toward the contact with the dorsal scales, and the anterior ones appear in the supraocular shields near the contacts with the parietals and frontals. These fossae, similarly to the ones described previously, correspond to different features present in the three underlying cranial bones: the posterior ones correspond to the fossae and foramina present in the articulation between the posterior portion of the parietal and the supraoccipital, and the anterior ones correspond to the lateroposterior foramina of the frontal bones and the anterolateral foramina of the parietal bone.

In addition to the species mentioned in the results, parietal pits and fossae are also present in other taxa that I have had the opportunity to observe personally and/or are depicted in literature. The list of species in which these traits occur is long, and includes several genera of the families Elapidae: *Dendroaspis, Hemachatus, Hydrophis, Naja,* and *Notechis* (Cundall and Irish 2008, Palci *et al.* 2019, pers. obs.); Atractaspidae: *Atractaspis* (O'Shea 2018); Micrelapidae: *Micrelapis* (O'Shea 2018); Psammophiidae: *Malpolon, Psammophis,*

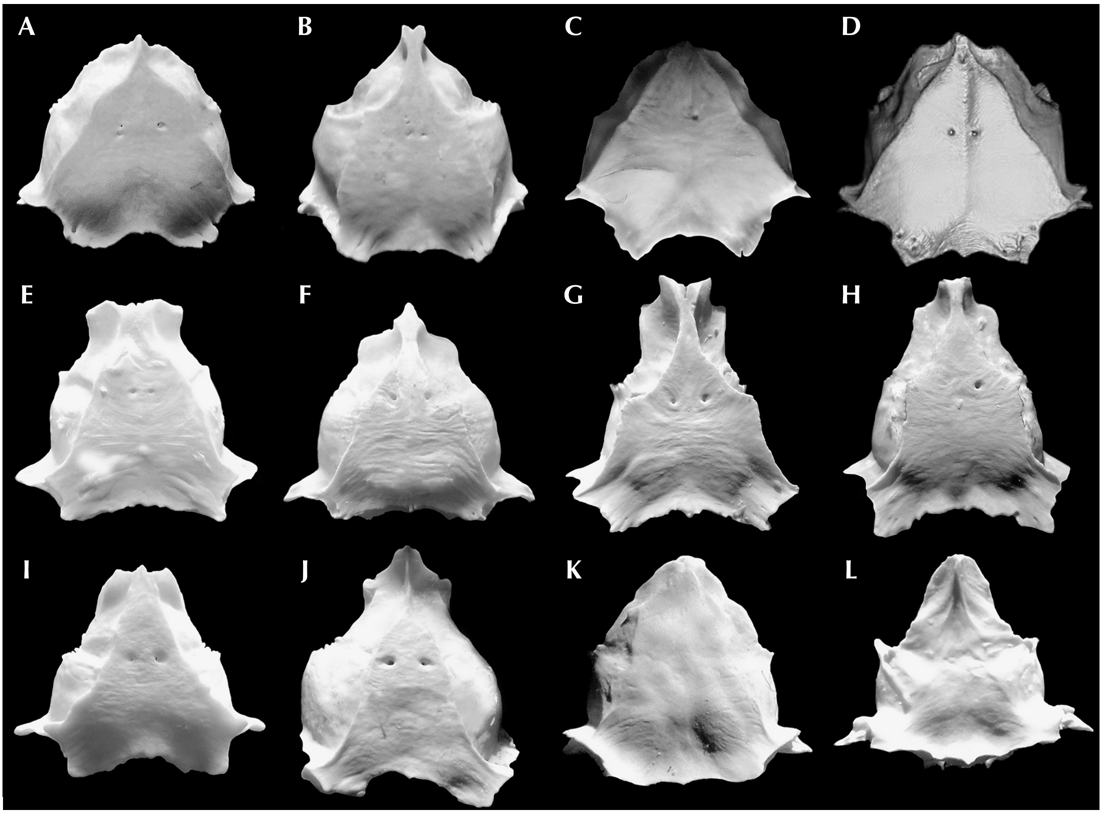

Figure 9. Parietal bones of snakes belonging to the caenophidian clade. Colubridae: (**A**) *Hierophis viridiflavus;* (**B**) *Zamenis longissimus.* Natricidae: (**C**) *Natrix helvtica;* (**D**) *Natrix tessellata;* Elapidae: (**E**) *Naja naja;* (**F**), *Naja atra;* (**G**), *Naja kaouthia;* (**H**), *Naja sputatrix;* (**I**) *Naja haje;* (**J**) *Naja pallida.* Viperidae: (**K**), *Vipera aspis;* (**L**), *Vipera ammodytes.* The parietal bone of *Natrix tessellata* is the specimen DJ4916 described in the study of Papežíková *et al.* (2024), used with permission.

Psammophylax, and *Rhamphiophis* (De Haan 2003, Cottone and Bauer 2011, pers. obs.); Colubridae: *Alsophis, Atretium, Boiga, Coluber, Coelognathus, Crotaphopeltis, Dasypeltis, Dolichophis, Drymarchon, Elaphe, Euprepiophis, Gonyosoma, Hebius, Hemorrhois, Hierophis, Platyceps, Philodryas, Pseudoficimia, Psomophis, Taeniophallus,* and *Zamenis* (Underwood 1967, Marais 2004, Miralles and Ineich 2006, Kreiner 2007, Schulz 2013, O'Shea 2018, pers. obs.); Natricidae: *Natrix, Helophis, Thamnophis, Tropidonophis,* and *Xenochrophis* (Malnate and Underwood 1988, pers. obs.); Viperidae: *Vipera* (Grano *et al.* 2017, Meier 2024, pers. obs.); Pareidae: *Asthenodipsas, Pareas,* and *Xylophis* (Loredo *et al.* 2013, Narayanan 2021, Poyarkov 2022); Xenodermidae: *Achalinus, Fimbrios,* and *Stoliczkia* (Ziegler *et al.* 2008, O'Shea 2018). In addition to photographic material, observations of these traits can be found in illustrations in technical texts, as in the case of *Elaphe carinata yonaguniensis* (Takara, 1962) illustrated by Schulz (1996).

In some cases, however, the identification of cephalic pits may not be easy because some species may have decorative elements in the parietal portion of the head that resemble pairs of fossae and pits, i.e., *Spalerosophis diadema* (Schlegel, 1837), *Hemorrhois ravergieri* (Ménétries, 1832), *Thamnophis sirtalis,* or a single parietal "eye," i.e., *Thamnophis marcianus* (pers. obs.). Similar patterns are present in some viperids such as *Agkistrodon, Cerastes,* and *Montivipera* (pers. obs.; Figure 10). *Hierophis viridiflavus* may have such decorations, although in the juveniles of this species, the pattern occurring in the parietal shields can be highly variable (Paterna 2015). The difficulty in identifying possible pits also applies to those species that have a complex pattern on the cephalic scales, as in the case of *Elaphe dione* (Figure 1B).

As for the cephalic fossae and pits, numerous texts in the literature illustrate and describe the presence of the parietal foramina in different families of snakes: Elapidae (Scanlon and Lee 2003, Da Silva *et al*. 2018, Palci *et al*. 2019, Patterson *et al*. 2022, Ammresh 2023), Viperidae (Wagner *et al.* 2016, Integrated Sciences for Sustainable Human-Aqua Environment 2024), Atractaspididae (Strong *et al*. 2021), Pseudoxyrhophiidae (Das *et al*. 2024) and Cyclocoridae (Weinell *et al.* 2020), and in several colubroid species (Sadeghi *et al*. 2014, Klaczko *et al*. 2016, Qi *et al*. 2021, Rajabizadeh *et al*. 2021, Pandelis *et al*. 2023, Papežíková *et al*. 2024). Among these, the case of *Natrix tessellata* is extremely interesting. In a recent study by Papežíková *et al*. (2024) on the morphology of two European clades of this species, the specimens had major parietal pits and minor pits in the parietal shields. In the three-dimensional models of the parietal bone of several individuals, a pair of parietal foramina are always present, traversing the bone to open ventrally between the fossae covering the cerebral hemispheres and the optic lobes. Also in the parietal bone, one specimen had a medial foramen at the posterior end of the dorsal plane (Figure 9D) and additional foramina in the anterolateral extremities, close to the frontal contacts. The posterior medial foramen was present in another specimen, which had heavy sculpting consisting of numerous foramina in the right side of the parietal plane. This large foramen, like the paired foramina, opens in the ventral surface of the bone, but in the center of a sagittal canal separating the fossae covering the optic lobes. This foramen also appears to correspond to a pit on the surface as the other pits in the parietal shields. This trait observed in *N. tessellata* corresponds to the third type of pits described, the "medial posterior parietal pit" (Figures 1F and 9D). A similar posterior parietal medial foramen occurs in the aquatic elapid *Hydrophis cyanocinctus* (Daudin, 1803), and is crossed by a parietal blood vessel (Palci *et al.* 2019). This observation confirms that made in *N. helvetica,* where large blood vessels are connected to the minor parietal pits present in the lateral margin of the parietal bone. Palci *et al.* (2019) specify that "no nerve fibers exit the parietal foramen," and add that "such vascular structure draining directly to the brain is likely present in other sea snakes." The authors conclude that this trait is a further elaboration of the sea snakes' cutaneous respiratory anatomy, the most likely function of which is to provide the brain an additional supply of oxygen, thus possibly playing a role during long submersions. The golden sea snake *Aipysurus laevis* (Lacépède, 1804) has both paired foramina and a large posterior medial foramen in the parietal bone (Cundall and Irish 2008). In our case, the structure present in *N. tessellata* appears similar to that observed in marine elapids, considering that they are aquatic ophidians and share multiple adaptations to aquatic life (Paterna 2025).

Many of the cranial bones are perforated by neurovascular foramina, and pits and fossae present in the corresponding shields of these reptiles would appear to be surface expressions of these underlying foramina, which serves as a passage for nerves (Jackson and Doetsch 1977), blood vessels, and emissary veins (O' Donoghue 1921, Palci *et al*. 2019). Of extreme interest is the manifestation of parietal pits and fossae, which occur in correspondence with the paired parietal foramina and the epiphyses of snakes. Within Lepidosauria, many lizards have a parietal eye in the posterior cephalic region, a photosensory organ that occurs as part of the pineal complex in correspondence with a median parietal foramen (Eakin 1973). This structure, widespread in Paleozoic and early Mesozoic taxa (Benoit *et al*. 2016), was lost in snakes (Labra *et al*. 2010), but developmental vestiges may remain as in the case of some snakes, birds, and mammals (Stebbins and Eakin 1958). Some caenophidian snakes have paired parietal foramina, which analogously are present in humans, where these function as passages for the emissary veins. In humans this feature is expressed only in some individuals (Van der Walt *et al*. 2023). Regarding the pineal complex, nearly all vertebrates present this structure, which is involved in the endocrine regulation of circadian and seasonal cycles. In snakes this structure has a role in courtship and mating (Jackson and Doetsch 1977, Quay 1979, Mendonca *et al*. 1996). It also has a role in thermoregulation and in the production of melatonin (Ralph *et al*. 1979, Lutterschmidt *et al*. 2003). The only structure in the pineal complex of snakes is the median epiphysis or pineal gland (Petit 1951, Tosini 1997), which is probably not photoreceptive as it is morphologically similar to the mammalian pineal gland (Quay *et al*. 1968, Kalsow *et al*. 1991). Stebbins and Eakin (1958) stated that "in snakes the pineal body is usually closely associated with the vascular paraphysis and dorsal sac and may itself be highly vascular, and in reptiles the posterior cerebral vein may be sinus-like and is closely associated with the epiphysis." The parietal pits and fossae, which correspond to these structures, could thus be, or were, linked to these structures. Reichenbach-Klinke and Elkan (1965) describe a specimen of *Natrix natrix* that has two symmetrical lateral and one medial parietal groove. Histological analyses revealed an extreme attenuation in the dorsal plane of the parietal bone corresponding to the two lateral grooves. The authors state that the appearance of accessory parietal organs is extraordinarily common in reptiles, adding statements that note the resemblence to the paired foramina, pits, and fossae in the current study: "attempts at lens and retina formation can clearly be seen in these organs which, in some cases, are paired and often connected with the mesencephalon by a thin strand of optic nerve. There is always a gap in the bony skull dorsal to the parietal eye, matched in some cases by a pitted scale or a pair of pitted scales on the surface." In-depth analyses are needed to determine whether these traits are analogous in all species in which they occur, or wether these may be vestigial traits, traits exclusively linked to the vascular system, or traits involving the neurosensory system.

Figure 10. Juvenile leucistic female of *Agkistrodon contortrix,* found in Montgomery Country, Texas, in 2019 (photo by Daniel Jarvis). Note how the paired parietal dots are the only trait showing black pigmentation beside the eyes.

Conclusions

Cephalic pits and fossae appear to be widespread in the superfamilies Colubroidea and Elapoidea. These features also occur in the more basal families Pareoidea and Xenodermoidea, which indicates that these pits probably include a larger group of ophidians, the Colubroides. As shown by the observations, it is not certain that the phenomenon involves all genera or all species included in this macrogroup because these traits could have been totally lost during evolution.

Observations of *in vivo* specimens and the anatomical and necroscopic investigations carried out on colubrids, natricids, psammophiids, and elapids highlight that the presence of cephalic pits in the parietal shields of these ophidians can be of different types. The most obvious are the "major" parietal pits and fossae, almost always symmetrical, linked to the paired parietal foramina, which in turn occur in correspondence with the epiphysis at the center of the contact between the optic lobes and the cerebral hemispheres. Others are minor pits, which can occur in asymmetrical positions and in a random number within the cephalic shields, which usually correspond to foramina and fossae occurring in the underlying cranial bones. In some of the cases examined, the presence/visibility of these can also vary based on age, becoming more evident/defined at adult size and age.

A peculiarity observed is that although the main cephalic fossae and pits are "connected" to the parietal foramina through the epidermis and dermis, the presence and number of these features in the bones does not represent a constant in the species where they are expressed. In some specimens the presence of blood vessels occured in correspondence with some pits and cranial features. Regarding the pits occurring in correspondence with the paired parietal foramina, micro-CT scans and histology sections will be necessary to define their nature and/or to define whether any differences are present in the groups in which such traits appear. This would further verify the hypothesis of the formation of parietal organs, and/or their possible functionality in the vascular and/or neuro-sensory field. In addition, more targeted studies involving larger sample sizes, focused on certain species or genera may lead to a better statistical understanding of the phenomenon. At the moment we can affirm that cephalic fossae and pits are sporadic surface manifestations corresponding to neurovascular foramina present in the cranial bones of some individuals belonging to a given species. Following the identification of such traits in a larger number of species, future research should lead to the recognition of fossae and pits in numerous other genera and taxa.

Acknowledgments

I would like to thank all the cited authors whose works have been an important inspiration for this study, the friends who donated to OPHIS part of the specimens used in the anatomical and osteological analyses, and Daniel Jablonski for giving me permission to use the picture obtained with micro-CT of the specimen DJ4916. I thank two anonymous reviewers for their opinions and comments on the manuscript, and Janalee Caldwell for the revision of the text.

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Editor: Jaime Bertoluci

Appendix I. *List of preserved and live specimens examined in the current study. Each entry indicates the family to which the specimens belong, the species, the number of individuals analyzed, and the type of analyses performed: "external inspection" refers to inspection of the specimen's cephalic features; "anatomical" refers to a thorough analysis involving dissection and anatomical examination of the soft tissues; "osteological" indicates that the specimen was further prepared for osteological examination of the cranial bones. In the* "in vivo" *specimens only external inspection was performed.*

		Preserved specimens		
Family	**Species**	**Units**	**Stage**	**Analyses**
Colubridae	*D. caspius*	3	adults	ex. inspection, anatomical, osteological
	E. quatuorlineata	2	juveniles	ex. inspection, anatomical, osteological
	H. viridiflavus	7	adults	ex. inspection, anatomical, osteological
	P. guttatus	1	adults	ex. inspection, anatomical, osteological
	Z. longissimus	3	adults	ex. inspection, anatomical, osteological
Dipsadidae	*H. nasicus*	1	adults	ex. inspection, anatomical, osteological
Natricidae	*N. helvetica*	5	adults	ex. inspection, anatomical, osteological
	N. natrix	1	adults	ex. inspection, anatomical, osteological
	N. tessellata	1	adults	ex. inspection, anatomical, osteological
Psammophiidae	*M. moilensis*	1	adults	ex. inspection, anatomical, osteological
Elapidae	*A. lubricus*	1	adults	ex. inspection, osteological
	N. atra	1	adults	ex. inspection, anatomical, osteological
	N. haje	1	adults	ex. inspection, anatomical, osteological
	N. kaouthia	1	adults	ex. inspection, anatomical, osteological
	N. naja	1	adults	ex. inspection, anatomical, osteological
	N. pallida	1	adults	ex. inspection, anatomical, osteological
	N. sputatrix	1	adults	ex. inspection, anatomical, osteological
Viperidae	*V. ammodytes*	1	adult	ex. inspection, osteological
	V. aspis	1	adult	ex. inspection, osteological

Appendix I. *Continued.*

***In vivo* specimens**			
Family	**Species**	**Units**	**Analyses**
Colubridae	*E. anomala*	1	1 adult
	E. bimaculata	33	15 adults, 18 juveniles
	E. carinata	21	4 adults, 17 juveniles
	E. dione	9	2 adults, 2 subadults, 5 juveniles
	E. quatuorlineata	10	6 adults, 4 juveniles
	G. boulengeri	2	2 adults
	H. hippocrepis	5	5 adults
	H. viridiflavus	6	4 adults, 2 subadults
	O. porhyraceus	2	2 adults
	O. taeniurus	1	1 adult
	P. guttatus	16	16 adults
	P. catenifer	2	2 adults
	Z. longissimus	26	12 adults, 2 subadults, 12 juveniles
	Z. scalaris	2	2 subadults
Natricidae	*N. helvetica*	28	5 adults, 23 juveniles
	T. marcianus	1	1 adult
Psammophiidae	*M. insignitus*	2	2 adults
	M. moilensis	4	4 adults