

## The development of the pit organ of *Bothrops jararaca* and *Crotalus durissus terrificus* (Serpentes, Viperidae): support for the monophyly of the subfamily Crotalinae

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### Abstract

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The development of the pit organ and the course of the lateral branch of the ethmoidal nerve of the two South American crotalines *Bothrops jararaca* and *Crotalus durissus terrificus* are described in detail using serially sectioned material from fetal stages. Serial sections of the Asian pit vipers *Agkistrodon halys halys* and *Trimeresurus albolabris* were included in this work. The viperines, as the sister-group of the Crotalinae, and the Colubridae, Elapidae and Boidae as their outgroups were used for comparisons. New synapomorphies of the advanced subfamily Crotalinae were found: namely, absence of the foramen epiphaniale and an extracapsular course of the lateral branch of ethmoidal nerve. These results support the monophyly of the crotalines.

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### Introduction

The viperid subfamily Crotalinae (pit vipers) comprises approximately 140 species of snakes distributed through most of the New World and eastern Asia. The evidence generally cited for the monophyly of crotaline snakes is the presence of facial pit organs and the correlated excavation of the maxillary bones (Lynn 1931; Dowling 1959; Savitzky 1985).

The existence of a facial pit as a unique character to diagnose pit vipers has been known, since they were first described by Tyson (1682). West (1900) described the basic morphology of the organ in embryos of several crotaline genera. Lynn (1931) examined the embryological development of the pit organ in *Agkistrodon contortrix mokasen* and *A. piscivorus*, and Savitzky (1985) described the development of the pit organ of *Python regius*.

This highly specialized pit organ of pit vipers comprises a single pair of integumentary invaginations between the eye and the nostril. It resides within an osseous cavity in the lateral surface of the maxillary and prefrontal bones (Brattstrom 1964). Each pit organ invagination consists of a thin membrane (Bleichmar and de Robertis 1962), suspended throughout paired chambers (Lynn 1931). Desmoulins (1824)

observed that the pits were richly innervated. On that basis he was the first to emphasize their potential sensory nature. The pit membrane represents the sensory component of the pit organ. This organ is innervated by the ethmoidal (V1), and the superficial and deep branches of the maxillary ramus (V2) of the trigeminal nerve, which end in the pit membrane (Desmoulins 1824; Bullock and Diecke 1956; Goris and Nomoto 1967). The pit membrane serves as a mechanical support for the sensory nerve endings, sustaining these endings in a position isolated from the influence of surrounding body tissue, and thus increasing their sensitivity and promptness of response (Goris and Nomoto 1967). The receptor endings in the pit membrane are mapped spatially in the optic tectum (Newman *et al.* 1980).

The loreal pit of crotalines is a thermal receptor. The pit is sensitive to radiation in the near infrared range, and responds to changes in the background level of such radiation, thus imaging endothermic prey (Hartline 1974; Stanford and Hartline 1980; Newman and Hartline 1981; de Cock Buning 1983).

A pit organ is also found in several lineages of the Boidae (Ros 1935; Noble and Schmidt 1937; Barret 1970; Molenaar 1974), but there are several differences compared

to that of the Crotalinae, amongst which are the absence of the inner chamber. The booid labial pits are innervated by the trigeminal complex with its three main branches, and the location of pits on the scales of the boids varies (Lynn 1931). The infrared trigemino-tectal pathways of the rattlesnake and the python differ qualitatively in their organization. In the rattlesnakes, the pathway proceeds from the lateral descending trigeminal tract (LTTD) to the reticularis calorica (RC) and then from the RC to the tectum (Stanford and Schroeder 1979; Newman *et al.* 1980). In the python, a direct LTTD-tectal projection occurs (Molenaar 1974; Newman *et al.* 1980). Bullock and Barrett (1968) suggested that the infrared systems of these two species may have evolved independently.

Although many aspects of the morphology and evolution of the crotalines are known, few studies have investigated the craniogenesis of this group so far. Savitzky (1992) described the general pattern of dermatocranial development of the skull of crotaline snakes and the detailed embryonic development of the maxillary and prefrontal bones. He gave a general guide to the pattern and timing of craniogenesis and examined the development of the bones associated with the pit organs. However, several papers have been published on the cranial development of other alethinophidian snakes (Parker 1879; Peyer 1912; Bäckström 1931; De Beer 1937; Pringle 1954; Kamal and Hammouda 1965a,b,c; El-Toubi *et al.* 1970, 1973; Bellairs and Kamal 1981).

The present paper – part of my PhD thesis at the University of Tübingen (Hofstadler-Deiques 1997) – deals with the study of the development of the pit organ and with the path of the ethmoidal branch of the trigeminal nerve at different fetal stages of two South American pit vipers, *Bothrops jararaca* and *Crotalus durissus terrificus*. The Asian pit vipers *Agkistrodon halys halys* and *Trimeresurus albolabris* were included in this comparison to confirm the presence of relevant characters in other crotaline snakes. Comparison with species of the sister-group Viperinae and with species of the outgroups Colubridae, Elapidae and Boidae (sectioned material of additional embryos, as well as descriptions in the literature) aims to provide new cranial characters relevant to the understanding of the evolution of the advanced subfamily Crotalinae and to corroborate its monophyly.

## Materials and Methods

The present study is based on serially sectioned heads of *B. jararaca* and *C. durissus terrificus* obtained from individuals killed for embryo removal at the Instituto Butantan (IB), São Paulo.

First, the ontogeny of the pit organ of the two South American crotalines *B. jararaca* and *C. durissus terrificus* is described. Embryos at different developmental stages of *B. jararaca* and *C. durissus terrificus* prepared for histology were first decalcified in a solution of HNO<sub>3</sub> (6.5%). They were then prepared using standard procedures for

dehydration and paraffin embedding, using xylene as the clearing agent and Paraplast Plus as the embedding medium. Since it was impossible to determine the ages of the different embryos, it was necessary to depend solely on measurements. The serial transverse sections were stained with alcian blue and alizarin red [modified from procedures of Domagk; Romeis (1968)].

From the serially sectioned head of *B. jararaca* [total length (TL) 145 mm, head length (HL) 10 mm] and *C. durissus terrificus* (TL 125 mm, HL 11 mm) plate reconstructions were made. The serial sections were projected on 2 mm Styropor® plates with a camera lucida so that the outlines of cartilages, bones and other structures could be drawn, cut out and glued together. The result is a three-dimensional model of the whole skull. Accurate graphic reconstructions were made of the nasal capsule, and of the dorsal view of the chondrocranium.

The measurements of *B. jararaca*, *C. durissus terrificus*, *A. halys halys*, *T. albolabris* and of the species of the sister group and outgroup are listed below.

## Material examined

Taxa prepared as serial sections in this study. The specimens marked with an asterisk are deposited at the Laboratório de Embriologia, UNISINOS, São Leopoldo, Brazil (no institutional numbers).

### Crotalinae

*Bothrops jararaca* Wied, 1824 (Instituto Butantan, IB, São Paulo Brazil)\*

Stage 1: 10 µm thick, 70 mm TL, 4 mm HL

Stage 2: 8 µm thick, 75 mm TL, 8 mm HL

Stage 3: 8 µm thick, 95 mm TL, 7.7 mm HL

Stage 4: 10 µm thick, 120 mm TL, 9 mm HL

Stage 5: 10 µm thick, 145 mm TL, 10 mm HL

Stage 6: 15 µm thick, 275 mm TL, 14.6 mm HL

*Crotalus durissus terrificus* (Laurenti, 1768) (IB)\*

Stage 1: 15 µm thick, 85 mm TL, 1.2 mm HL

Stage 2: 8 µm thick, 90 mm TL, 9.6 mm HL

Stage 3: 8 µm thick, 125 mm TL, 11 mm HL

Stage 4: 15 µm thick, 270 mm TL, 17.6 mm HL

*Agkistrodon halys halys* (Pallas, 1776) (Laboratório de Embriologia, Universidade do Vale do Rio dos Sinos, UNISINOS, São Leopoldo, Brazil)\*

Stage 1: 15 µm thick, 260 mm TL

*Trimeresurus albolabris* (Gray, 1842) (Laboratório de Embriologia, UNISINOS)\*

Stage 1: 15 µm thick, 230 mm TL

### Viperinae

*Atheris squamiger* (Hallowell, 1854) (Zoologisches Institut der Universität Tübingen, Germany)

Stage 1: 10 µm thick, 10.2 mm HL

*Vipera ammodytes* (Linnaeus, 1758) (Zoologisches Institut der Universität Tübingen, Germany)

Stage 1: 10 µm thick, 9.9 mm HL

## Colubridae

*Elaphe longissima* (Laurenti, 1768) (Zoologisches Institut der Universität Tübingen, Germany)

Stage 1: 10 µm thick, 140 mm TL

*Lampropeltis getulus floridana* (Linnaeus, 1766) (Zoologisches Institut der Universität Tübingen, Germany)

Stage 1: 10 µm thick, 70 mm TL

Stage 2: 10 µm thick, 225 mm TL

*Helicops infrataeniatus* January, 1865 (Fundação Zoobotânica do Rio Grande do Sul, FZB, Porto Alegre, Brazil)\*

Stage 1: 10 µm thick, 50 mm TL

Stage 2: 10 µm thick, 110 mm TL, 10 mm HL

## Taxa obtained from the literature

Viperinae: *Vipera aspis* (Peyer 1912: chondrocranium and osteocranium), *Causus rhombeatus* (Pringle 1954: chondrocranium and osteocranium), *Cerastes vipera* (Kamal and Hammouda 1965a: chondrocranium).

Colubridae: *Natrix natrix* (Parker 1879 and Bäckström 1931: chondrocranium and osteocranium), *Dasyptis scaber* (Pringle 1954: chondrocranium and osteocranium), *Lamprophis inornatus* (Bäckström 1931: chondrocranium and osteocranium), *Psammophis sibilans* (Kamal and Hammouda 1965b: chondrocranium), *Malpolon monspessulanus* (El-Toubi *et al.* 1973: chondrocranium).

Elapidae: *Hemachatus haemachatus* (Pringle 1954: chondrocranium and osteocranium), *Naja haje* (El-Toubi *et al.* 1970: chondrocranium).

Boidae: *Eryx jaculus* (Kamal and Hammouda 1965c: chondrocranium).

## Results

## Pit organ

At stages 1, 2 and 3 of *B. jararaca* and at stage 1 of *C. durissus terrificus* (the stages are defined on measurements, see Table 1) the sections show no trace of the pit organ. The first evidence of the formation of the pit organ is observed at stage 4 of *B. jararaca* and stage 2 of *C. durissus terrificus* in the form of a slight integumentary invagination just anterior to the eye. In transverse section the pit organ shows a lateral invagination, the organ lies between the prefrontal and maxillary

bones anteroventral to the eye. As development proceeds, this depression deepens and at a later ontogenetic stage (stage 5 of *B. jararaca* and at stage 3 of *C. durissus terrificus*) a second invagination arises from its posterodorsal border which becomes deeper to form a second pit cavity lying behind the first (Fig. 1A,B). This is the inner chamber of the pit organ. At first its communication with the exterior is quite widely open (Fig. 2A,B), but later it closes up, leaving only a small opening. The outer chamber of the organ and the invagination of the organ's inner chamber is separated through the pit membrane. At stage 4 of *B. jararaca* and stage 2 of *C. durissus terrificus* the pit membrane is quite thick, but as development proceeds, it increases in area and becomes much reduced in thickness (Fig. 4A,B).

At a later stage of development of both species (stage 6 of the *B. jararaca* and stage 4 of the *C. durissus terrificus*) the inner cavity is enclosed, except for a small pore which opens just anterior to the eye and communicates with the exterior (Fig. 3A,B). The outer chamber forms a deep depression (Fig. 4A). In cross-section, the sensitive nerve endings of the ethmoidal (V1; lateral branch) and maxillary (V2) branch are concentrated in the medial wall of the pit membrane (Fig. 4A,B). This membrane is attached to the outer edges of the external pit. It is concave and suspended rather loosely in the cavity. The surface of the membrane is continuous with the keratinized layer of the epidermis of the head and is shed together with the rest of the keratinized epidermis.

## Ethmoidal nerve

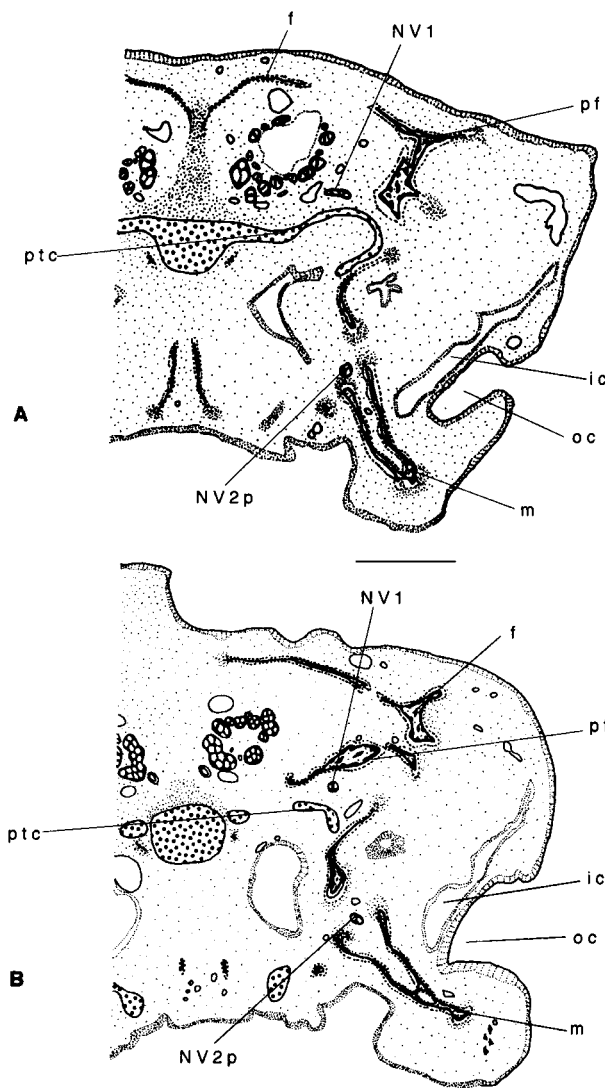
In *B. jararaca*, *C. durissus terrificus*, *A. halys halys* and *T. albolabris* the ethmoidal nerve emerges from the trigeminal ganglion and runs forward inside the skull, along the floor of the cranium until it reaches the orbit. On the dorsal surface of the planum antorbitale and in front of the processus descendens of the frontal bone the ethmoidal subdivides into two branches, the medial – ramus nasalis medialis – and lateral – ramus nasalis lateralis – (Fig. 5A,B).

In all snakes examined, the medial branch of the ethmoidal nerve continues anteriorly and traverses the space over the fenestra olfactoria advehens in an antero-medial direction, approaching the dorsal edge of the nasal septum. It then descends along the septum and reaches the level of the septomaxillary bone in the floor (solum nasi) of the nasal

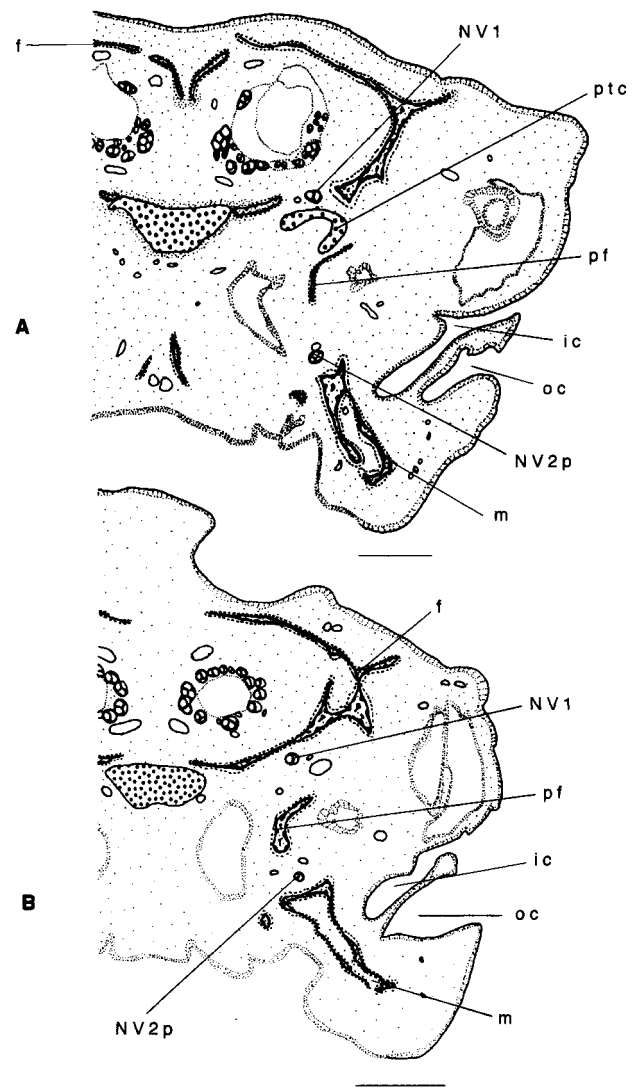
**Table 1** Morphometric data for different stages of *Bothrops jararaca* and *Crotalus durissus terrificus*

	Stage 1		Stage 2		Stage 3		Stage 4		Stage 5		Stage 6	
	HL	TL	HL	TL	HL	TL	HL	TL	HL	TL	HL	TL
<i>Bothrops jararaca</i>	4.0	70	8.0	75	7.7	95	9.0	120	10	145	14.6	275
<i>Crotalus durissus terrificus</i>	1.2	85	9.6	90	11	125	17.6	70	–	–	–	–

Measurements of the head length (HL; tip of the snout to articulation quadrate-mandible) and total length (TL; tip of the snout to tip of tail) are in mm.



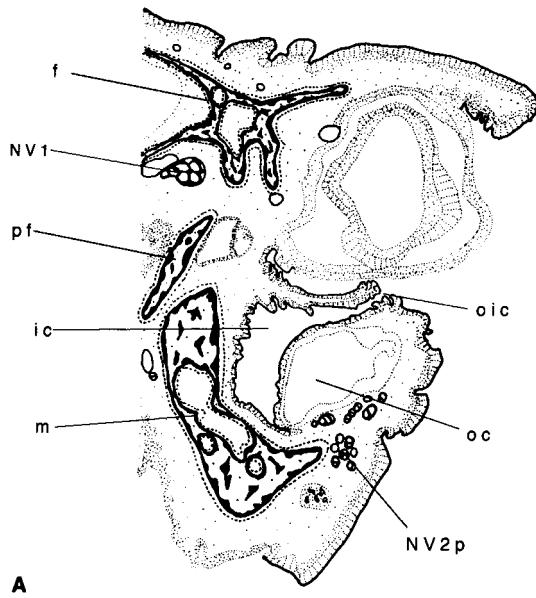
**Fig. 1**—Transverse section through level of pit organ of —**A.** *Bothrops jararaca* (stage 5), —**B.** *Crotalus durissus terrificus* (stage 3). f, frontal; ic, inner chamber of the pit organ; m, maxilla; NV<sub>1</sub>, ethmoidal nerve; NV<sub>2p</sub>, deep branch of maxillary nerve; oc, outer chamber of pit organ; pf, prefrontal; ptc, parietotectal cartilage; scale bar represents 1 mm.



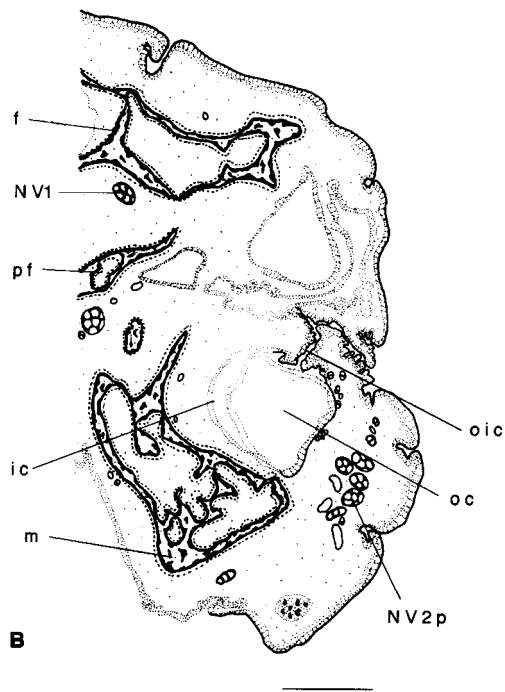
**Fig. 2**—Transverse section through level of pit organ of —**A.** *Bothrops jararaca* (Stage 5), —**B.** *Crotalus durissus terrificus* (stage 3). f, frontal; ic, inner chamber of pit organ; m, maxilla; NV<sub>1</sub>, ethmoidal nerve; NV<sub>2p</sub>, deep branch of maxillary nerve; oc, outer chamber of pit organ; pf, prefrontal; ptc, parietotectal cartilage; scale bar represents 1 mm.

capsule. It passes forward, dorsal to the medial edge of this bone and finally emerges out of the nasal cavity around the medial part of the ventral wall of the anterior nasal cupula and innervates the premaxillary gland. The medial branch shows the same course in *B. jararaca*, *C. durissus terrificus*, *A. halys halys*, *T. albolabris* and in the other snakes examined of the Viperinae, Colubridae, Elapidae and Boidae. The course of the medial branch in these snakes is always intracapsular, has a free exit out of the nasal capsule and no apical foramen is present.

In all snakes of the sister and outgroup of Crotalinae examined and cited in the Materials and Methods section, a small foramen, the foramen epiphaniale, exists in the parietotectal cartilage beside the fenestra olfactoria advehens. Immediately behind the fenestra olfactoria, the ethmoidal nerve splits into medial and lateral branches. The lateral branch continues anteriorly, curves slightly downward and enters the cavity of the nasal capsule through the fenestra olfactoria. After a short intracapsular course the lateral branch leaves the nasal cavity once again through the foramen epiphaniale,

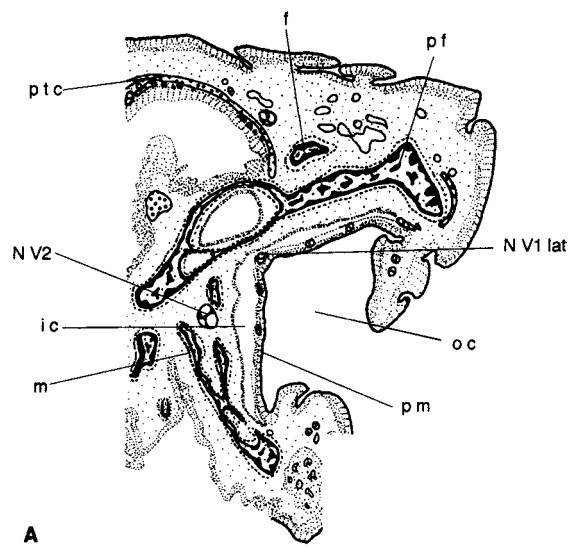


A

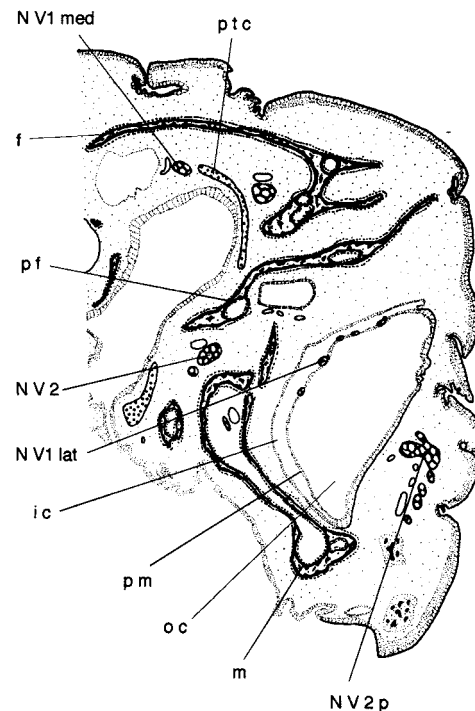


B

**Fig. 3**—Transverse section through level of pit organ of —**A.** *Bothrops jararaca* (stage 6), —**B.** *Crotalus durissus terrificus* (stage 4). f, frontal; ic, inner chamber of pit organ; m, maxilla; NV<sub>1</sub>, ethmoidal nerve; NV<sub>2p</sub>, deep branch of maxillary nerve; oc, outer chamber; oic, external opening of the inner chamber; pf, prefrontal; scale bar represents 1 mm.

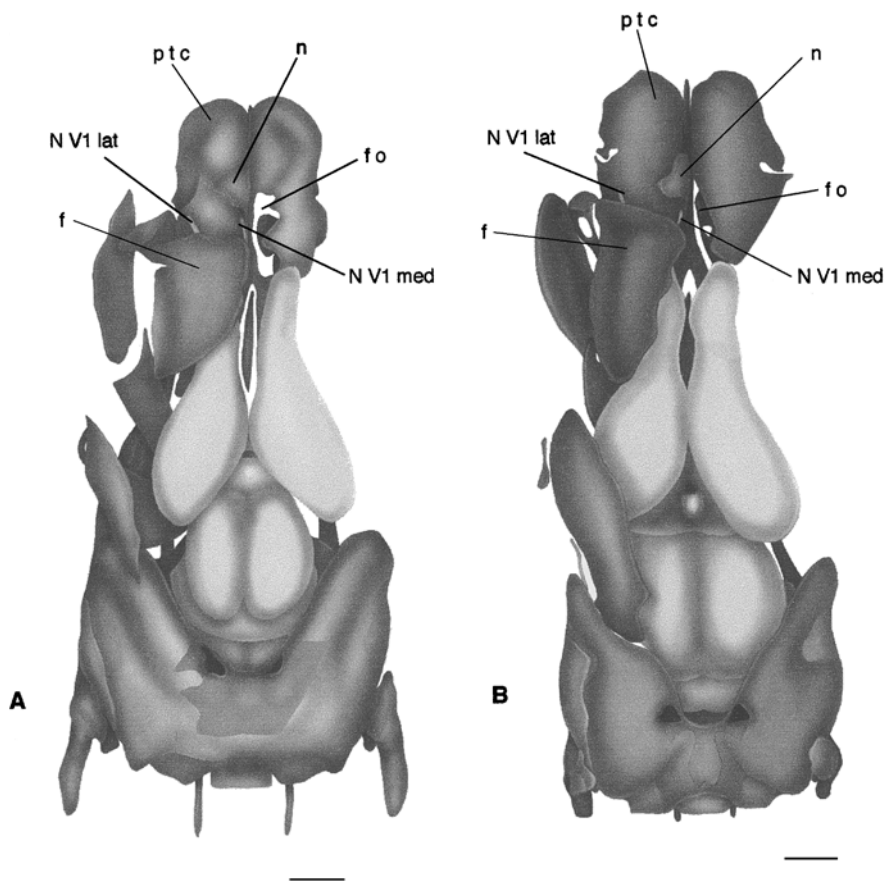


A



B

**Fig. 4**—Transverse section through level of pit organ of —**A.** *Bothrops jararaca* (stage 6), —**B.** *Crotalus durissus terrificus* (stage 4). Pit membrane with innervation of the lateral branch of NV<sub>1</sub>. f, frontal; ic, inner chamber of pit organ; m, maxilla; NV<sub>1med</sub>, medial branch of ethmoidal nerve; NV<sub>2p</sub>, deep branch of maxillary nerve; oc, outer chamber of pit organ; pf, prefrontal; pm, pit membrane; ptc, parietotectal cartilage; scale bar represents 1 mm.



**Fig. 5**—The fully formed neurocranium in a dorsal view of —**A.** *Bothrops jararaca* (stage 5), —**B.** *Crotalus durissus terrificus* (stage 3). Membrane bones in the left side. f, frontal; fo, fenestra olfactoria; NV<sub>1lat</sub>, lateral branch of ethmoidal nerve; NV<sub>1med</sub>, medial branch; n, nasal; ptc, parietotectal cartilage; scale bar represents 1 mm.

then continues antero-laterally innervating the follicles of the lateral nasal gland. In these snakes the course of the lateral branch is partly intracapsular.

The lateral branch of the ethmoidal nerve in *B. jararaca*, *C. durissus terrificus*, *A. halys halys* and *T. albolabris* passes over the roof of the nasal capsule, proceeds anterolaterally, and reaches the pit membrane and then runs forward to the lateral nasal gland (Fig. 5A,B). The branch never enters the cavity of the nasal capsule. The surface of the roof of the nasal capsule (parietotectal cartilage) is perforated by a wide and unique gap, the fenestra olfactoria advehens. The ramification of the ethmoidal nerve occurs anterior to this fenestra (Fig. 5A,B). The lateral branch lies outside of the nasal cavity. This means that in *B. jararaca*, *C. durissus terrificus*, *A. halys halys* and *T. albolabris* the nerve always has an extracapsular course. In these crotaline species the foramen epiphaniale in the parietotectal cartilage is absent.

### Discussion

In snakes, the course of the medial branch of the ethmoidal nerve is intracapsular and it emerges from the nasal cavity without being delimited by the foramen apicale. This is the general type for the snakes, differing from the general lacer-

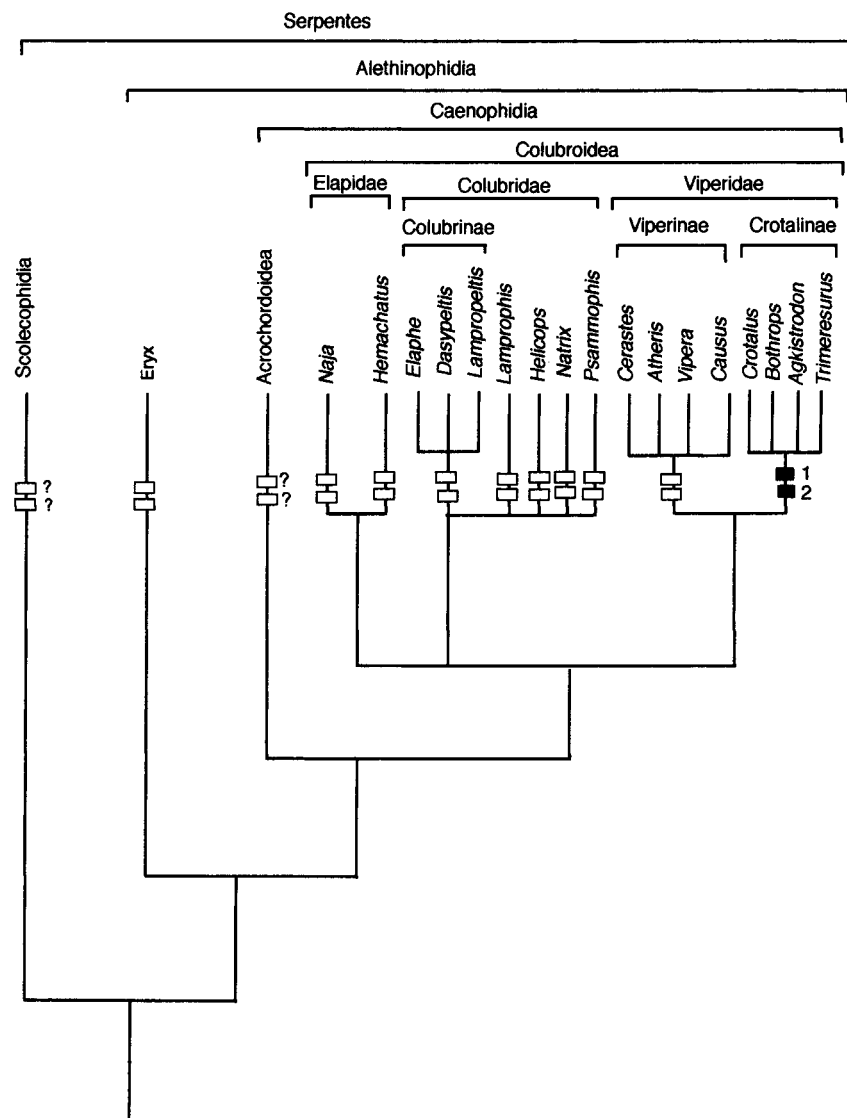
tilian condition. In the latter group the nerve passes through a foramen apicale (Kamal and Hammouda 1965b; Bellairs and Kamal 1981; Hallermann 1998).

The intracapsular course of the lateral branch of the ethmoidal nerve is the general condition found in the majority of Squamata (Kamal and Hammouda 1965b; Bellairs and Kamal 1981). In snakes (viperines, colubrids, elapids and boids) the narrow strip closing the medial border of the foramen epiphaniale causes a short intracapsular course of the lateral branch. The presence of the foramen epiphaniale and an intracapsular course of the lateral branch of the ethmoidal nerve in these snakes is a plesiomorphic character (Fig. 6).

In all crotaline taxa examined, an extracapsular course of the lateral branch is found and the foramen epiphaniale is absent.

In snakes the ramus nasalis lateralis generally runs laterally, innervating the follicles of the lateral nasal gland, which is located in the ethmoidal region anterior to the pit organ. Besides the gland being extremely reduced in *C. durissus terrificus* (Hofstadler-Deiques 1997), the ramus nasalis lateralis still runs lateral to the nasal capsule and innervates the pit organ.

What are the morphological implications of the possession of this additional sense organ? Dullemeijer (1959) showed



**Fig. 6**—Cladogram modified from Hofstadler-Deiques (1997) and referring to a new synapomorphy for the Crotalinae based on investigation of the cranial development of four representatives of the crotalines: *Bothrops jararaca*, *Crotalus durissus terrificus*, *Agkistrodon halys halys* and *Trimeresurus albolabris*. The representatives of the Viperinae were used as sister group and the Colubridae, Elapidae and Boidae as outgroup. Character 1 = lateral and extracapsular course of the lateral branch of ethmoidal nerve; character 2 = foramen epiphaniale absent; ? = unknown character.

the enormous impact of the presence of the pit organ on the anatomical construction of the cranial system, as well as on related functions. The pit organ requires space which is derived from the maxillary bone which, in turn, cannot lose its ability to support and move the fangs. The presence of a pit organ shows the most extreme reduction of surrounding tissues and causes a reshaping of the whole craniofacial region. Savitzky (1992) demonstrated subsequent morphogenetic events associated with pit organ invagination in the concave adult form of the maxillary bone in crotalines.

The absence of a foramen epiphaniale and a lateral extracapsular course of the ramus nasalis lateralis in *B. jararaca*, *C. durissus terrificus*, *A. halys halys* and *T. albolabris* are functionally linked to the pit organ. The nerve supplies the loreal pit, and its extracapsular course correlates with the absence of the foramen epiphaniale. The significance of the derived course of the branch of the trigeminal nerve is unique in the

pit vipers among snakes. Therefore I assume the presence of this character complex in all other species of the Crotalinae supports its monophyly.

The special association between the lateral and extracapsular course of the ramus nasalis lateralis (character 1) and the correlated absence of the foramen epiphaniale (character 2) resulted as part of a process of coevolution with the origin of the pit organ in the pit vipers and the combination of this character indicates a new synapomorphy of the crotalines (Fig. 6).

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