

## Description of a papillate tactile organ in the Typhlopidae

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In a unique specimen of *Rhinotyphlops*, the rostrum supports approximately 250 elongate, flexible papillae. Each papilla consists of a tubular shaft and an expanded hair-like bulb weakly embedded in the epidermis. Immediately deep to the base of each papilla is a small cluster of neuronal cells and a vascular supply. Although this *Rhinotyphlops* is presumed to be fossorial, the morphology of these soft papilla suggest they function as mechanoreceptors.

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### Introduction

There are a variety of tactile receptors located within snake skin, including free nerve endings, terminal receptors resembling Merkel cells, and lamellated receptors (Von Düring & Miller 1979; Young 1997). Many of these receptors produce a deformation in the overlying  $\beta$ -layer of the epidermis, but are not evident when viewing the surface of the scale. In some ophidian groups, the tactile receptors are associated with a localized superficial projection of the epidermis forming small polyps or papillae. This type of tactile receptor always has a well-defined distribution on the surface of the animal, such as the supracloacal region in natricines (Noble 1937) or the rostrum of most scolecophidians (Aota 1940; Jackson & Reno 1975; Jackson 1977; Orejas-Miranda *et al.* 1977).

Wallach and Ineich (1996) redescribed the rare Malagasy blind snake (*Typhlops grandidieri*) and placed it into a new monotypic genus (*Xenotyphlops*) that was defined, in part, by the presence of elongate flexible papillae on the rostrum. Examination of some *Rhinotyphlops* from Zaire revealed similar papillae on the rostrum of a single specimen tentatively identified as *Rhinotyphlops caecus*, affording an opportunity to examine the structural features of these papillae. It is unfortunate that only this single specimen exists and that its preservation quality is not ideal. Despite these limitations of the study material, the unique nature of these papillate touch organs seemed to justify this investigation.

### Materials and methods

The head of the specimen of *Rhinotyphlops* was bisected sagittally; one side of the head was prepared for light microscopy, the other for scanning electron microscopy. For light microscopy the specimen was decalcified for four days in Cal-Ex (Fisher), dehydrated through an alcohol series, cleared in Hemo-de (Fisher), then embedded in paraffin.

Parasagittal sections were cut at 8  $\mu$ m and stained with a modified version of Van Grieson's stain. For electron microscopy, the specimen was dehydrated through an ethanol series and then critical point dried; it was sputter coated with 300Å of gold and examined using an ISI Super 3A scanning electron microscope at 15kV.

### Results

#### Description of the *Rhinotyphlops* specimen

Due to uncertainty of the specific identity of the specimen, a brief description is presented.

#### Locality

Rainforest in the vicinity of Kisangani, Haut-Zaire Province, Democratic Republic of the Congo. Specimen obtained in March 1981 from the collection of the Biology Department of the university in Kisangani (Université Nacional de Zaire, UNAZA) and was sent to R. Etheridge for the San Diego State University collection, from which it was donated to Van Wallach for his studies in 1995. Specimen deposited in the National Museum of Natural History and catalogued as USNM 515944.

#### Description

Total length 447 mm; tail length 4 mm; relative tail length 0.9%; midbody diameter 7 mm; midbody diameter into total length 64 times; midtail diameter 4.5 mm; tail broader than long (length/width ratio 0.9). There are 24 longitudinal scale rows throughout the body; 489 total middorsals; 11 subcaudals; and a T-0 supralabial imbrication pattern. Snout is obtusely pointed in dorsal view, with large unguiform rostral (0.75 of head width) the anterodorsal and anteroventral surfaces of which support projecting papillae (Figure 1A). The supranasals extend beyond the rostral and are separated from each other by a large prefrontal that is bordered by a smaller frontal and a pair of supraoculars. The remaining scales on the dorsum of the head are neither enlarged nor differentiated.

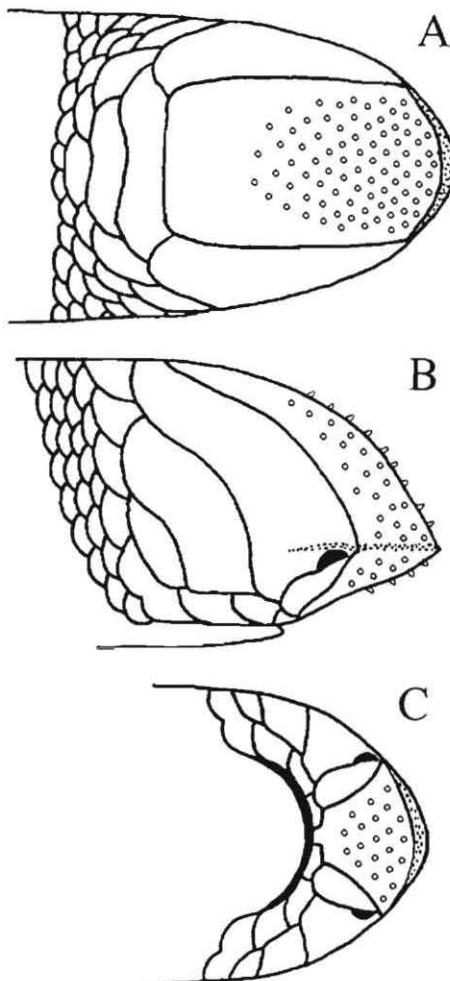
The snout is pointed in lateral view, with the rostral terminating in a hard horizontal ridge. The superior nasal suture is complete; the supranasal – which contacts the second supralabial – is the largest shield on the lateral surface (Figure 1B). The infranasal is small, contacting the first and second supralabial. The nostril is inferior (being ventral to a slight canthal ridge along the supranasal) and adjacent to the rostral border; the inferior nasal suture extends to the second supralabial. The preocular is enlarged and oriented obliquely, contacting

the second and third supralabial; the caudal border of the preocular is concave. The small ocular is situated within the concavity of the preocular and contacts the third and fourth supralabial. The four supralabials have a T-0 imbrication pattern (N1/SL1, PrOc/SL2, Oc/SL3-4); the first is the smallest, the second and third are subequal, and the fourth is twice the size of the second and third. Three postoculars border the ocular and preocular between the last supralabial and the supraocular. The mental scale projects beyond the border of the lip.

The eye is not visible, and the scales lack pigmentation. The specimen has a yellowish-beige color both above and below. The specimen is an adult female with five developing ova ( $8 \times 3$ ,  $7.5 \times 3$ ,  $7 \times 3$ ,  $7.5 \times 2.5$ ,  $7.5 \times 2.5$  mm) and six undeveloped follicles in the right ovary and three developing ova ( $8 \times 3$ ,  $7.5 \times 2.5$ ,  $7.5 \times 2.5$  mm) and six follicles in the left ovary.

#### Morphology of the papillae

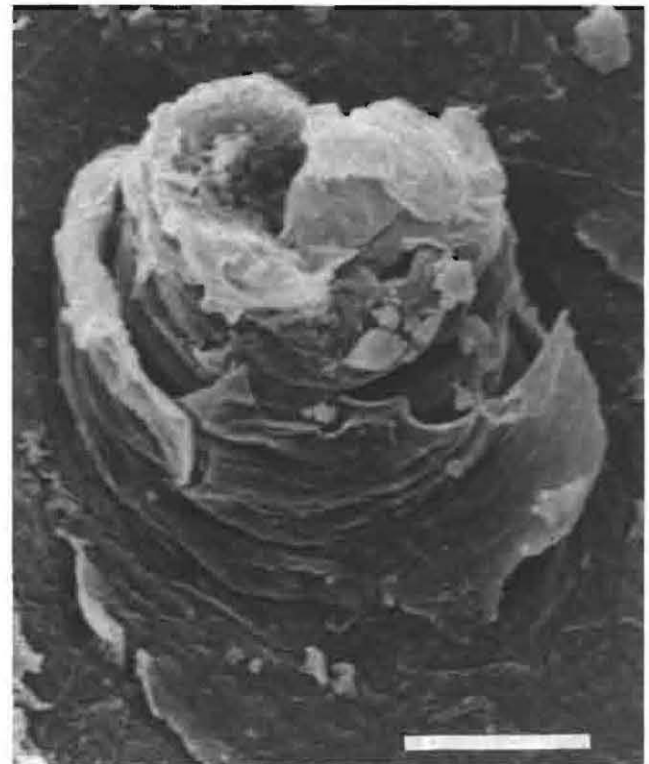
The dorsal, lateral, and ventral surfaces of the rostrum of this specimen of *Rhinotyphlops* support approximately 250 papillae (Figure 2). The intact papillae are almost translucent and very pliable, with a diameter of approximately  $26 \mu\text{m}$  and a length of  $110 \mu\text{m}$  (Figure 3). The papillae are covered with epithelial cells and the base of the papillae, and possibly their



**Figure 1** A: dorsal, B: lateral, and C: ventral view of the head of our specimen of *Rhinotyphlops*



**Figure 2** Electron micrograph of the rostrum of our specimen of *Rhinotyphlops*. Note the abundance and distribution of the papillae, and the presence of epithelial 'pits' (arrow). r – rostral ridge. Scale bar = 0.3 mm.



**Figure 3** Electron micrograph of a papilla from the dorsal rostral surface of our specimen of *Rhinotyphlops*. Note the elongate shape and epithelial covering of the papilla. Scale bar = 10

entire length, supports the mesos layer of the epidermis. The papillae proved to be quite fragile (see below) and were frequently missing a portion of their length. All of the incomplete papillae examined with the SEM had a hollow tubular internal structure (Figure 4). Careful examination of these internal tubes failed to reveal any differentiation within the tubular wall, nor was there any evidence of an endothelial lining within the tubes, suggesting that these tubes are non-vascular structures.

Despite careful handling and preparation more than half of the papillae on the specimen were lost, leaving behind a distinct 'pit' in the epithelium. These epithelial pits have a consistent shape and a regular symmetry. A sagittal section through a papilla reveals four interesting features (Figure 5). First, the epithelial nature of the papilla is clear, as is the tubular structure in the interior of the papilla. Second, the rather loose contact between the papilla and the adjacent epithelium is evident: the proximal end of the papilla terminates in a small bulb – reminiscent of the proximal end of a mammalian hair – with no distinct attachments to the adjacent tissues. Third, within the epithelial layer, but immediately deep to the papilla, is a cluster of neuronal cell bodies. In cases where a papilla is missing, and only an epithelial pit is evident, clusters of neuronal cell bodies are still consistently found immediately adjacent to the pit. Fourth, the mesos layer immediately adjacent to the papillae deflects cranially, similar to the hinge region of ophidian epidermis.

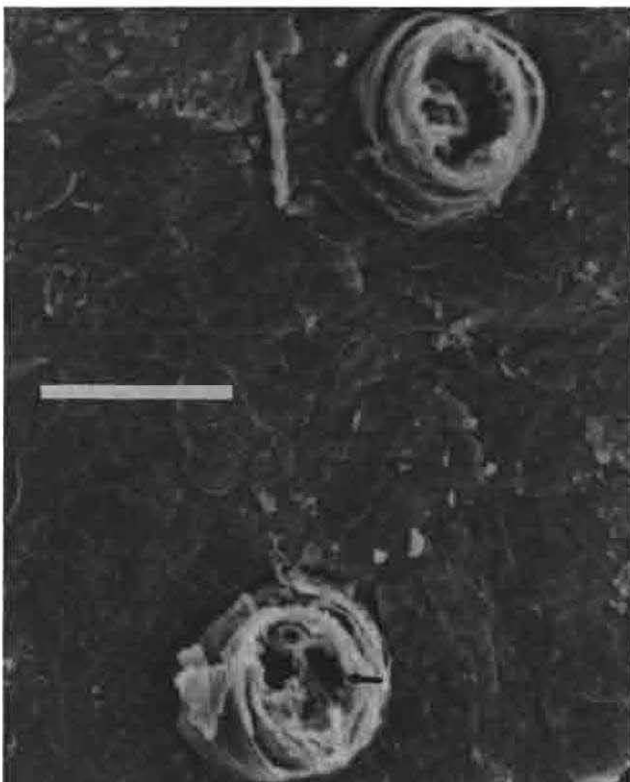
The rostrum of our *Rhinotyphlops* terminates in a distinct anterior ridge or cutting edge; similar rostral ridges are

known in some Australian *Ramphotyphlops* and African *Rhinotyphlops* as well as *Rhinoleptus* (Leptotyphlopidae). Light microscopy reveals numerous neurovascular bundles under the epidermis of the rostral ridge. The preservation quality of the specimen examined precluded reconstructing the courses of these nerves: presumably they represent branches of the cranial nerve innervating these papillae. The  $\beta$ -layer of the epidermis was absent from all of the papillae, although isolated portions were present elsewhere on the head of the specimen: as such, the natural contour of the papilla could not be determined.

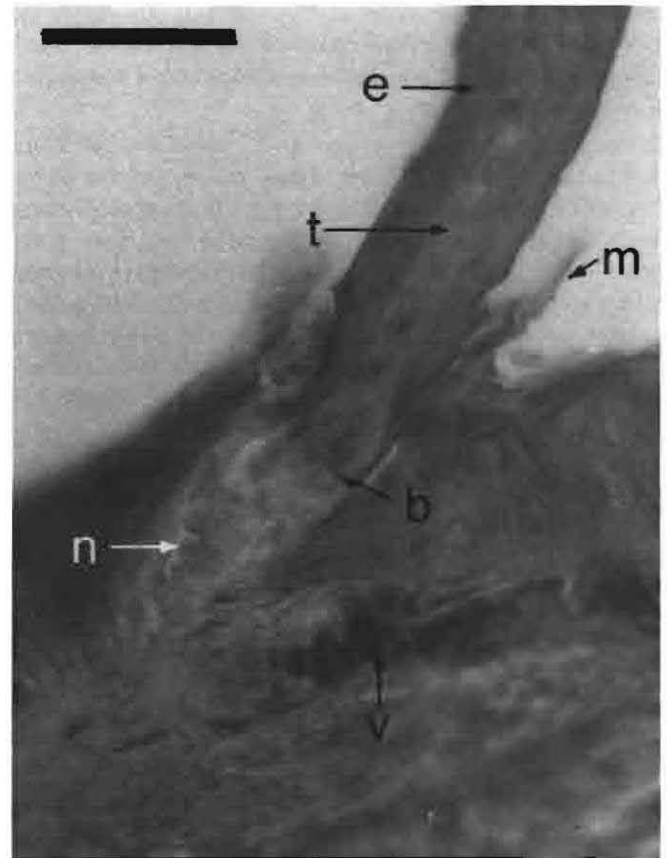
## Discussion

### Taxonomy of the specimen

It is apparent that the taxon currently known as *Rhinotyphlops caecus* (Duméril 1856) is composed of at least two different species. The types of *R. caecus* from Gabon (plus six additional Gabon specimens in Paris) are reported to have papillate rostrals as in *Xenotyphlops* (I. Ineich, pers. com.). Specimens from Cameroon, Gabon, and western Congo (Bas-Zaire) all possess 22 midbody scale rows, and presumably also have papillate rostrals. Specimens from central and eastern Congo have 24–26 midbody scale rows; the seven specimens examined by us all lacked rostral papillae. The caudal extension of the supranasals beyond the rostral is a character of *R. caecus* in relation to *R. acutirostratus* (eastern pop.), as



**Figure 4** Electron micrograph of papillae from the ventral rostral surface of our specimen of *Rhinotyphlops*. The distal tips of these papillae are missing exposing the inner tubular structure (arrow). Scale bar = 25



**Figure 5** Parasagittal section through a papilla from our specimen of *Rhinotyphlops*. Note the poor connection between the papilla and the adjacent epithelium and the presence of neuronal cells at the base of the papillae. b - bulb-like base of the papilla; e - epithelial covering; m - mesos layer; n - neuronal cell bodies; t - tubular center; v - vasculature. Scale bar = 40

is the presence of papillae. The specimen we are reporting on from eastern Congo has 24 scale rows and a papillate rostral. Sexual dimorphism in rostral papillae can be ruled out as another female from the same locality as the present specimen lacks rostral papillae. Currently there are two recognized subspecies of *R. caecus*: the nominate form in the west and *R. caecus pitmani* Witte (1961) in the east. Two names, based on specimens from eastern Congo, are considered synonyms of *R. caecus* at present: *Typhlops acutirostratus* Andersson (1916) from Irebu and *T. avakubae* Schmidt (1923) from Avakubi and Medje. The former is reported to have a granular rostral and examination of a paratype of *T. avakubae* from Medje reveals it also lacks rostral papillae. The condition of the rostral in *pitmani* is unknown.

There appear to be several possible solutions. Two species may be involved, the present specimen representing true *R. caecus* that has a large sympatric distribution with the granular rostral form and clinal variation in scale rows from east (24) to west (22), while the non-papillate Congolese specimens representing the *pitmani* population that should be known instead as *R. acutirostratus* (Andersson 1916). Conversely, three species may be involved, the 22 scale row *R. caecus* having a restricted range in west-central Africa, the 24–26 row Congolese specimens lacking papillae representing *R. acutirostratus*, and the present specimen representing an undescribed form distinct from, but closely related to, the other two. This problem cannot be resolved until all the types and much additional material is examined. However, our specimen shares two unique characters with *R. caecus*: papillae on the rostral and the caudal extension of the supranasals beyond the rostral.

Hahn (1980) gave the range of *R. caecus* as including Guinea, Sierra Leone, Ghana, Togo, and Benin, but Roux-Estève (1974) doubted the BMNH specimen supposedly from Sierra Leone and reported on specimens only from Cameroon, Gabon, and Congo. Hughes (1983) also gave the range of *R. caecus* as Cameroon, Gabon, and Congo, with a questionable occurrence in Liberia, Ghana, and Nigeria. Angel (1933) reported the range of *R. caecus* to include Guinea, and Villers (1951) reported its occurrence in Togo as probable, but Roman (1984) did not list it from there. Neither Hughes and Barry (1969) nor Hughes (1988) listed it from Ghana. We have been unable to document records of *R. caecus* from West Africa and Villers (1975) lists *R. crossii* as the only *Rhinotyphlops* from that region, so it appears likely that *R. caecus* is not known west of Cameroon.

### Papillate organs

The papillate organs in our specimen of *Rhinotyphlops* share several features with previously described scolecophidian tactile organs. The cluster of neuronal cell bodies in the epidermis, the epidermal disjunction between the tactile organ and the adjacent scalation, the presence of epidermal cells superficial to the neuronal cells, and the rostral distribution of these structures are similar in our specimen of *Rhinotyphlops* and the other scolecophidians examined (Haas 1932; Aota 1940; Gabé & Saint-Girons 1967; Jackson & Reno 1975; Landman 1976; Jackson 1977). Despite the structural similarities between the scolecophidian tactile receptors and the papillae of our specimen of *Rhinotyphlops*, three structural

features readily distinguish the latter. First, the papillae of our specimen of *Rhinotyphlops* are much longer than any of those previously described from a scolecophidian, with the exception of *Xenotyphlops* (Wallach & Ineich 1996). Second, the internal tubular structure of the papillae of our specimen of *Rhinotyphlops* (Figure 3) is unlike anything previously described from a scolecophidian, or any other snake. Third, the basal attachment of the papillae of our specimen of *Rhinotyphlops* – with its bulb-like terminus – is markedly different from the cap of ‘typical’ epithelium observed in other scolecophidians.

Small sensilla have been described from the cephalic and body scalation of *Acrochordus* (Schmidt 1918; Povel *et al.* 1997). These sensilla occur in shallow depressions and are composed of clumps or tufts of fine hair-like protrusions. The sensilla in *Acrochordus* have a distinct neural component, and Povel and Van Der Kooij (1997) have argued that they are mechanoreceptors. The sensilla of *Acrochordus* are very different structurally from those found in our specimen of *Rhinotyphlops*, and are much smaller: there are numerous hair-like projections on a single clump, and most of these clumps or tufts are smaller in diameter than a single papilla from our *Rhinotyphlops*.

The only other ophidian example of elongate tactile organs are the ‘tentacles’ of *Erpeton tentaculatum*. The tentacles of *Erpeton*, which reach lengths of 5 to 6 mm (Winokur 1977), are much larger than the papillae described herein. Furthermore, the tentacles of *Erpeton* include epidermal, dermal, and subcutaneous tissue layers in contrast to the apparently exclusive epithelial composition of the papillae in our specimen of *Rhinotyphlops*. Winokur (1977) reported a distinctive vascular sinus, smooth muscle, and large nerve bundles within the tentacles of *Erpeton* – findings that contradicted earlier reports (Hahn 1973). Although small nerve fibers could course through the tubular interior of the papillae of our specimen of *Rhinotyphlops*, there was no evidence of any smooth muscle, nor was there evidence of vasculature, let alone a vascular sinus, within the papillae.

The rostral location, epithelial structure, and associated population of neuronal cells, all support an interpretation that the elongate papillae of our specimen of *Rhinotyphlops* function as tactile receptors. Presumably, the greater length and flexibility of the tactile organs in our *Rhinotyphlops* (and presumably *Xenotyphlops grandidieri*) enhance the tactile differentiation of the environment, and thus increase this sensory modality. Elongate, cranially-directed sensory papillae, particularly in a fossorial or semifossorial snake, would be subjected to substantial abrasion. The high incidence of missing papillae on the examined specimen, the structure of the basal end of the papillae, the disjunction between the papillae and the surrounding epithelium, and the consistent shape of the epithelial pits observed whenever a papilla was absent, are all taken as evidence that the tactile papillae of our specimen of *Rhinotyphlops* are periodically shed. Shedding of the papillate end of the tactile organ would enable the animal to cope with constant abrasion. Given that the rostrum supports more than 250 papillae, even if a substantial percentage are lost due to shedding at any one time, the animal would still have the capacity for sensory input.

At the present time the significance of the internal tubular structure evident in the papillae is not clear. This tubular arrangement would increase the flexibility of the papillae. The histological sections examined all clearly showed the tubular structure, and all contained traces of cells or cellular debris within the central cavity. While these central tubes could serve as conduits for nerve fibers extending to the distal end of the papillae, this would seem incompatible with the hypothesis that the papillae are occasionally, or regularly, shed. The consistent presence of vascular tissue at the base of each papilla, coupled with the tubular structure of the papilla itself, suggests that these papillae could be under hemodynamic control. Further electron microscopic analysis of well-preserved material should clarify the nature of the internal structure of these papillae.

The failure of earlier workers to notice the papillae on the rostrum of *Xenotyphlops grandidieri* (Wallach & Ineich 1996) is not surprising given the small size and poor preservation of the two known specimens. The presence of papillae within the *Rhinotyphlops caecus* complex has not been previously noted: it is possible that the papillate taxa should be referred to *Xenotyphlops*. However, the content of *R. caecus* is undoubtedly composite and an examination of types and additional material is needed to resolve this situation. Furthermore, this study raises the possibility that similar elongate tactile papillae have been overlooked in other scolecophidian species.

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