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The role of modified teeth in the function of prolonged bites in *Hierophis viridiflavus* (Serpentes: Colubridae)

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Abstract

The role of modified teeth in the function of prolonged bites in *Hierophis viridiflavus* (Serpentes: Colubridae). Analysis of the maxillary, palatine, pterygoid, and dentary bones of the Western Whipsnake, *Hierophis viridiflavus carbonarius,* revealed the presence of grooves and ridges in the teeth on the four dentiferous bones. Enlarged and modified rear teeth were found on the posterior maxillaries, separated by alveolar diastema and aligned differently from the anterior maxillary teeth. In both live and dissected specimens, Duvernoy's gland, associated with the production of toxins, surrounds the rear maxillary teeth, which deliver the secretions produced by the gland. These characters, plus the infliction of prolonged bites, facilitate the subduing of prey. The morphology of the palatomaxillary arch places *H. viridiflavus* in the group of opisthoglyphous colubroids, whose modified fangs facilitate the inoculation of secretions, considered a "primitive form of venom." Other species of large sympatric colubroids were also examined, and some analogous structures were observed.

Keywords: Duvernoy's glands, Modified fangs, Opisthoglyphous, Western Whipsnake.

Resumo

O papel dos dentes modificados em mordidas prolongadas de *Hierophis viridiflavus* (Serpentes: Colubridae). A análise dos ossos maxilares, palatinos, pterigóides e dentários de *Hierophis viridiflavus carbonarius* revelou a presença de sulcos e cristas nos dentes dos quatro ossos dentíferos. Dentes posteriores ampliados e modificados foram encontrados nos maxilares posteriores, separados por diástemas alveolares e alinhados de forma diferente dos dentes maxilares anteriores. Tanto nos espécimes vivos como nos dissecados, a glândula de Duvernoy, associada à produção de toxinas, circunda os dentes maxilares posteriores, que liberam as secreções produzidas pela glândula. Essas características, além da inflição de mordidas prolongadas, facilitam a dominação da presa. A morfologia do arco palatomaxilar coloca *H. viridiflavus* no grupo dos colubróides opistóglifos, cujas presas modificadas facilitam a inoculação de secreções, consideradas uma "forma primitiva de veneno". Outras espécies de grandes colubróides simpátricos também foram examinadas, e algumas estruturas análogas foram observadas.

Palavras-chave: Glândula de Duvernoy, Opistoglifodonte, Presas modificadas, Serpentes.

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Introduction

When we find ourselves in front of a snake, the first and most common need is to establish whether it is venomous. The Western Whipsnake, *Hierophis viridiflavus* (Lacépède, 1789), the subject of this study, is a colubrid species that is widespread in Italy and southern France, in addition to adjacent countries including Switzerland, Croatia, and Spain (Kreiner 2007). It occurs in Germany as an introduced allochthonous species (Paterna 2023). To date, this snake is considered a non-venomous colubrid (Sindaco *et al.* 2006, Kreiner 2007, Di Nicola *et al.* 2021) or aglyphous, meaning that it does not possess a venom fang model similar to those of opisthoglyphous colubrids or real venom glands. The opisthoglyphous dentition is characterized by the presence of enlarged and modified rear maxillary teeth (Weinstein *et al.* 2011) and postocular glands called Duvernoy's glands, which produce venom in several species (Rodriguez-Robles 1994, Lumsden 2004). Other authors have stated that the Western Whipsnake is equipped with such glands, and the toxicity of this species has been demonstrated (Phisalix and Caius 1916). Cases in which adult humans reported clinical complications after the bite of this snake have been reported (Weinstein *et al.* 2011, Dutto *et al.* 2015).

Following observations of live specimens of *H. viridiflavus carbonarius* in the field, as well as observing the presence in the palatomaxillary arch of a gland located near the posterior maxillary tooth, I performed dissections and microscopy of the jaws of deceased specimens and other sympatric colubroid species for comparison.

Materials and Methods

The samples used in the osteological investigation came from three adult males and two females of *Hierophis viridiflavus carbonarius* that were found dead on the road in the Abruzzo region, Italy, in spring and summer 2023. An adult male *Zamenis longissimus* (Laurenti, 1768) and a subadult female *Natrix helvetica* (Lacépède, 1789), roadkills from the same region, were used for comparison. Bones of the specimens were prepared at OPHIS Museo Paleontologico e Centro Erpetologico (Teramo, Italy) using surgical tools and sodium hypochlorite. From each specimen the two maxillary bones, the two palatines, the two pterygoids, and the two dentaries were examined. Shed teeth from captive bred *Elaphe quatuorlineata* Lacépède, 1789, originally from Apulia, Italy, were collected from live specimens at OPHIS. Microphotographs of the cranial bones and teeth were taken using a stereomicroscope Nikon SMZ1500 together with a Digital Sight DS-2Mv camera at the Faculty of Veterinary Medicine of the University of Teramo.

Live specimens of *H. viridiflavus, Z. longissimus, E. quatuorlineata, Hemorrhois hippocrepis* (Linnaeus, 1758), and *N. helvetica,* part of the OPHIS collection, were used for in vivo anatomical comparisons. Photographic material of the latter was obtained with a Sony α6000 digital camera, while photos of the cranial bones of *H. viridiflavus* were obtained with a Nikon Coolpix P510.

Results

Microscopy of the Dentiferous Bones

In prepared samples of *Hierophis viridiflavus carbonarius,* minor sulci and crests were found in the teeth of all four dentiferous bones. The maxillary teeth have a depression on the lingual surface that is longitudinally incised by a thin groove (Figure 1A), while the mid-posterior teeth have a deeper canal-like fossa posteriorly (Figure 1B). Pterygoid teeth have a basal fossa and a distal ridge in the labial wall (Figure 1C). Palatine teeth present a slight depression labially located as the nutritive alveolar foramina and a thin ridge on the lingual surface. Additional isolated furrows are present in the teeth of the maxilla and the pterygoid (Figure 1D). The most anterior teeth in the dentaries feature a small fossa close to the edge of the crown and a distal second fossa (Figure 1E). The posterior teeth of the dentary also feature slight lingual depressions and a mesial cutting edge.

The most posterior teeth of the maxillae are distinguishable, even by eye, as longer and thicker than all other teeth (Racca *et al.* 2020). The alveoli of the two posterior teeth are adjacent to each other but separated by a diastema from the anterior one, for a length slightly shorter than that of an alveolus corresponding to the ectopterygoid process (Figure 1F). Here the maxillary arch presents a deviation of about 20° labially, positioning the enlarged teeth off-axis from the anterior teeth, which are uniformly placed with the same interdental space to the rostral extremity of the maxilla. The anterior maxillary teeth, and the teeth present in the other three dentiferous bones, show a lingulolabially compressed base and an anteroposteriorly backwards-bent crown that gives the entire tooth a shark fin-shaped silhouette. This laterally compressed shape is also observable in the alveoli of the maxilla, while the two last separated alveoli display a circular alveolar margin (Figure 1F).

These two posterior teeth differ from the rest in the morphology of the crown. Mesially a sulcus/canal is present, delimited by two ridges running along the entire length of the tooth from the base of the crown to its apex (Figure 2). Labially, in the basal half of the tooth, a triangular fossa is delimited by two prominent ridges, converging in a "V" shape, which reach the crown's tip. A second longitudinal fossa is located labiodistally after the posterior one of the two ridges that border the basal fossa. In the distal half of the teeth, the intervals between the mesial sulcus and the fossae highlight the four ridges that converge at the apex of the crown, giving the tooth a star-shaped section in lingual view (Figure 2). Rugosities occur on the projected surface of the central ridges in the basal half. In the two rear maxillary teeth, the basal portion in contact with the bone appears more compact, with a more circular section, widening like a bulb before resuming the "sharp" shape. At the base of the last maxillary tooth, a small portion of the root is visible. Here the nutritional foramen assumes the shape of an inverted teardrop, where the angled lower end culminates directly in the crown, which is consequently indented. A slight longitudinal groove twice as long as the nutritional foramen originates from this notch. This condition is absent in the other maxillary teeth, in which the nutritional foramen is usually circular in shape and located at the base of the root.

Dissection

The head of a roadkilled adult male *Hierophis viridiflavus carbonarius* was dissected; scales and skin were removed dorsally and laterally. In lateral view Duvernoy's gland is visible at the posterior end of the maxilla, anteriorly reaching and surrounding the two rear maxillary teeth (Figure 3). The posteriormost maxillary tooth emerges from the gland at the apex of the crown, visible in both lateral and ventral views. Also in lateral view, dorsoposteriorly in contact with Duvernoy's gland, is the Harderian gland, delimited ventroanteriorly by the ectopterygoid and the postocular (Figure 3).

In Vivo *Observations*

During field studies (Paterna 2015, unpubl. data) and while observing captive specimens of *Hierophis viridiflavus carbonarius,* two reddish to purplish glands at the posterior ends of the maxillae were observed at the level of the sixth supralabial scale (Figure 4A). These glands correspond to the position of Duvernoy's glands observed in the dissected skull in both lateral and ventral view. Such glands are visible in vivo in both adult and juvenile specimens. The glands are easily distinguished from the surrounding mucosa by color variation. The tip of the rear maxillary tooth emerges from the cuff of tissue and can be further uncovered by moving the

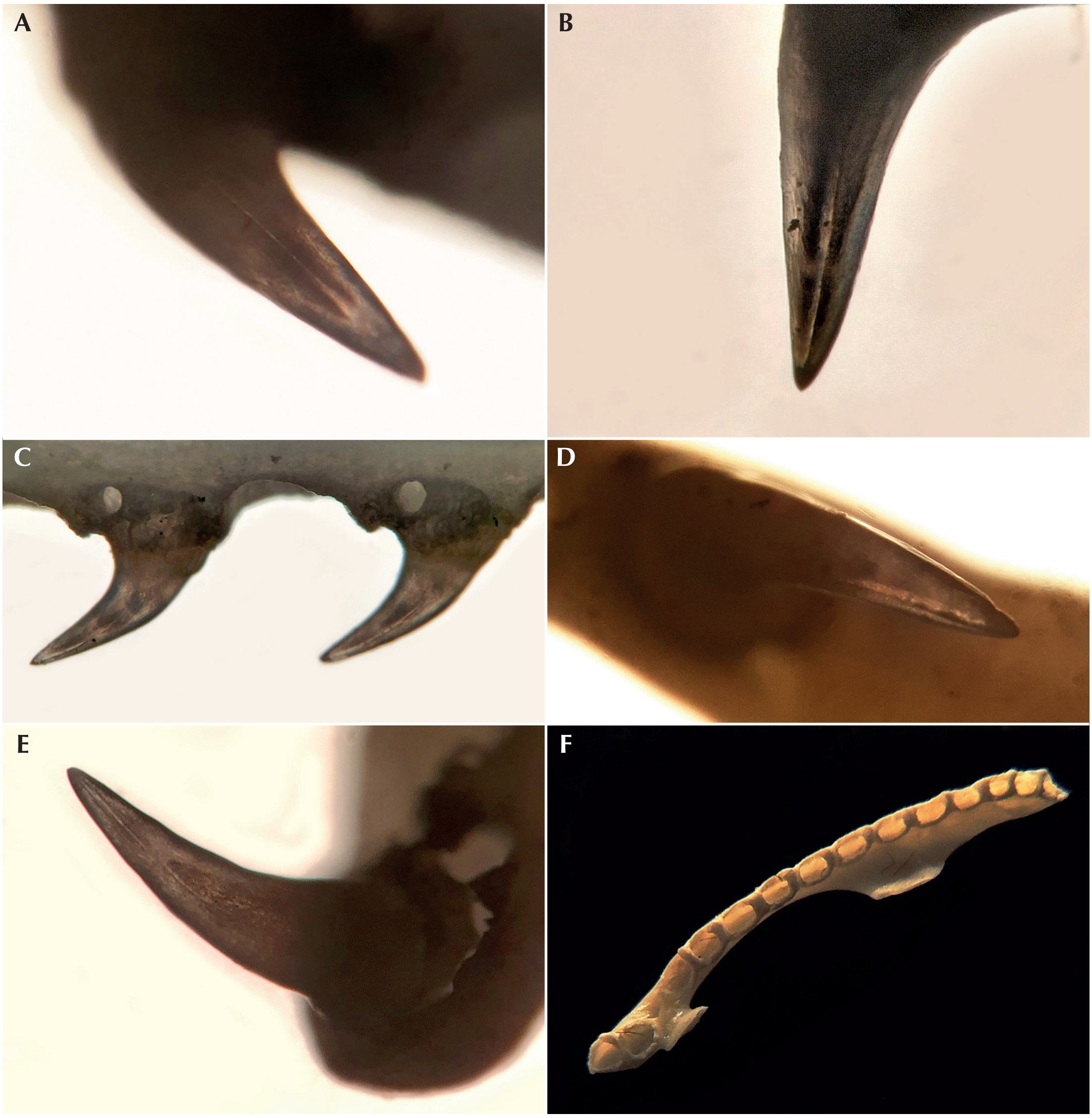

Figure 1. Stereomicroscope pictures of the groove details in the teeth of the dentiferous bones in specimens of *Hierophis viridiflavus carbonarius* from Abruzzo, Italy. (**A**) Adult female, right maxillary tooth in lingual view. (**B**) Adult male, maxillary tooth in distal view. (**C**) Adult female, right pterygoid teeth in lingual view. (**D**) Detail of the lingual groove in the right maxillary tooth of an adult female. (**E**) Adult female, anterior right dentary tooth in lingual view. (**F**) Photo of the toothless right maxilla in an adult male in ventral view.

mucosa rostrodorsally. Anterolaterally to this, corresponding with the maxillary deviation occurring between the line of the two rear and the anterior teeth, it is possible to distinguish a pocket, which is more easily identifiable in younger specimens.

In the other species examined (*Zamenis longissimus, Elaphe quatuorlineata, Hemorrhois*

Figure 2. Stereomicroscope pictures in varied contrast of a left rear maxillary tooth in mesiolingual view from an adult male of *Hierophis viridiflavus carbonarius* from Abruzzo, Italy.

hippocrepis, and *Natrix helvetica*), the above characters were found only in *H. hippocrepis* (Figure 4B). As in the case of *H. viridiflavus,* these characters were more readily observed in juveniles. Photographs of *H. viridiflavus, H. hippocrepis,* and *Z. longissimus* (Figure 4C) demonstrate the presence or absence of the gland.

Distinctive Features in the Dentition of the Species

More or less obvious furrows and ridges are found in the dentiferous bones of *Zamenis longissimus* and *Natrix helvetica* (Figure 5A–F). Enlarged maxillary teeth have been found in *N. helvetica,* in which the rear maxillary teeth share the "blade tooth" morphology. The posteriormost tooth, saber-shaped, exhibits a distal carina and a smaller mesial one (Figure 5A). The other maxillary teeth also feature slight keels but are more tapered and undulated (Figure 5C). In *Z. longissimus,* the anterior maxillary teeth are larger and longer than the posterior teeth. In the maxillae of these two species, the alveoli and consequentially the teeth, are aligned without any relevant diastema, unlike *Hierophis viridiflavus. Elaphe quatuorlineata* exhibits long maxillary teeth (Figure 5G, H), with the posteriormost featuring a mesial longitudinal sulcus in the distal half of the crown (Figure 5G).

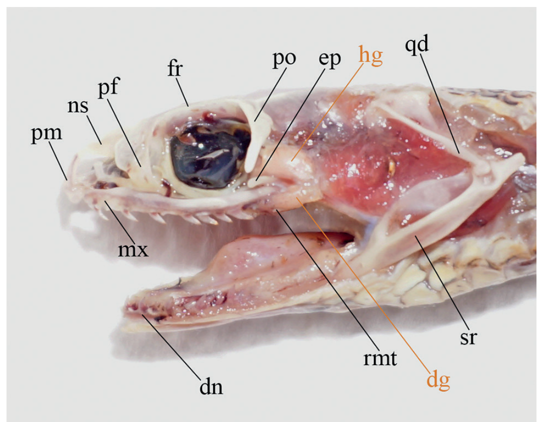

Figure 3. Dissected skull of an adult male *Hierophis viridiflavus carbonarius* from Abruzzo, Italy. Abbreviations: dg, Duvernoy's gland; dn, dentary; ep, ectopterygoid; fr, frontal; hg, Harderian gland; mx, maxilla; ns, nasal; pf, prefrontal; pm, premaxilla; po, postocular; qd, quadrate; rmt, rear maxillary tooth; sr, surangular.

Discussion

Hierophis viridiflavus is known to bite if handled, and its bite is prolonged with repeated chewing-like movements of the jaws. Bites from this species may produce temporary neurotoxic symptoms in humans (Weinstern *et al.* 2011,

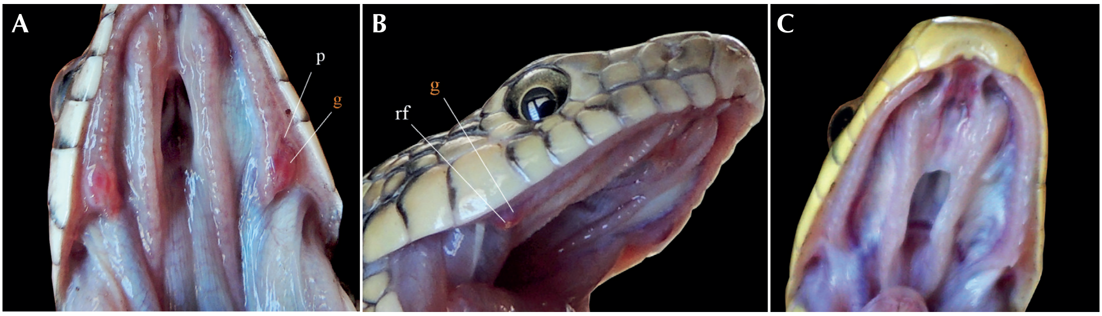

Figure 4. Details of Duvernoy's gland and rear maxillary teeth in the palatomaxillary arch of (**A**) an adult female *Hierophis viridiflavus carbonarius,* and (**B**) a young male *Hemorrhois hippocrepis.* (**C**) Palatomaxillary arch of an adult male *Zamenis longissimus.* Abbreviations: g, cuff of gland; p, pocket; rf, rear fang.

Dutto *et al.* 2015) and severe neurotoxic and hemotoxic symptoms leading to death in small mammals (Phisalix 1922). The teeth of *Hierophis viridiflavus carbonarius* exhibit ridges and grooves both of which confer a better grip during the bite (Oliveira *et al.* 2016) and transmit mixed oral secretions to the penetrated tissues.

Young and Kardong (1996) examined the teeth of the four dentiferous bones of 661 snake species including 739 colubrid specimens. Although species names and numbers of individuals of each species were not provided, some information may be obtained from this study. Furrowed teeth were present in the anterior maxilla in 0.5% of the individuals examined and in the posterior maxilla in 1% of the specimens. In 1% the furrowed teeth were in the palatine, in 2% the pterygoid, and in 5% the dentary. Only three opisthoglyphous species were named: *Ahaetulla prasina preocularis* (Taylor, 1922), *Boiga cyanea* (Duméril, Bibron and Duméril, 1854), and *Rhachidelus brazili* Boulenger, 1908, in which furrows were reported in the anterior half of the maxilla. Of the 36 specimens of colubrids examined that exhibited furrowed teeth, these teeth occurred in both the palatine and the pterygoid in 5 (14%) of the specimens (Young and Kardong 1996). *Hierophis viridiflavus* exhibited furrowed teeth in all four dentiferous bones, and according to Young and Kardong (1996) this condition is present in very few colubrid or colubroid species.

The heterodonty found within the maxillary teeth and the morphology of the maxillary bone place *H. viridiflavus* within the opisthoglyphous snakes. Not only does this species have separated and enlarged posterior maxillary teeth but also these teeth are characterized by the presence of prominent grooves and ridges. Elongate maxillary posterior teeth, together with well-defined Duvernoy's glands, represent a pre-adaptation to the subduing of prey, from which venom glands evolved for rapid killing (Kardong 1982). Other studies consider Duvernoy's gland not different from the venom glands present in elapids and viperids (Weinstein and Kardong 1994, Fry *et al.* 2008). Contrary to the venom glands present in solenoglyphous and proteroglyphous snakes, the duct of Duvernoy's gland is not directly channeled into the teeth, but rather leads into a defined space or cuff around one or more teeth (Zalisko and Kardong 1992, Kardong and Lavin-Murcio 1993); in *H. viridiflavus* these are the two posteriormost maxillary teeth. In the dissected specimen, these enlarged teeth are completely surrounded by Duvernoy's gland, leaving only the apex of the crown visible. When a prey animal is bitten, the mucous membrane comes into direct contact with the surface of the tegument, which, following the compression

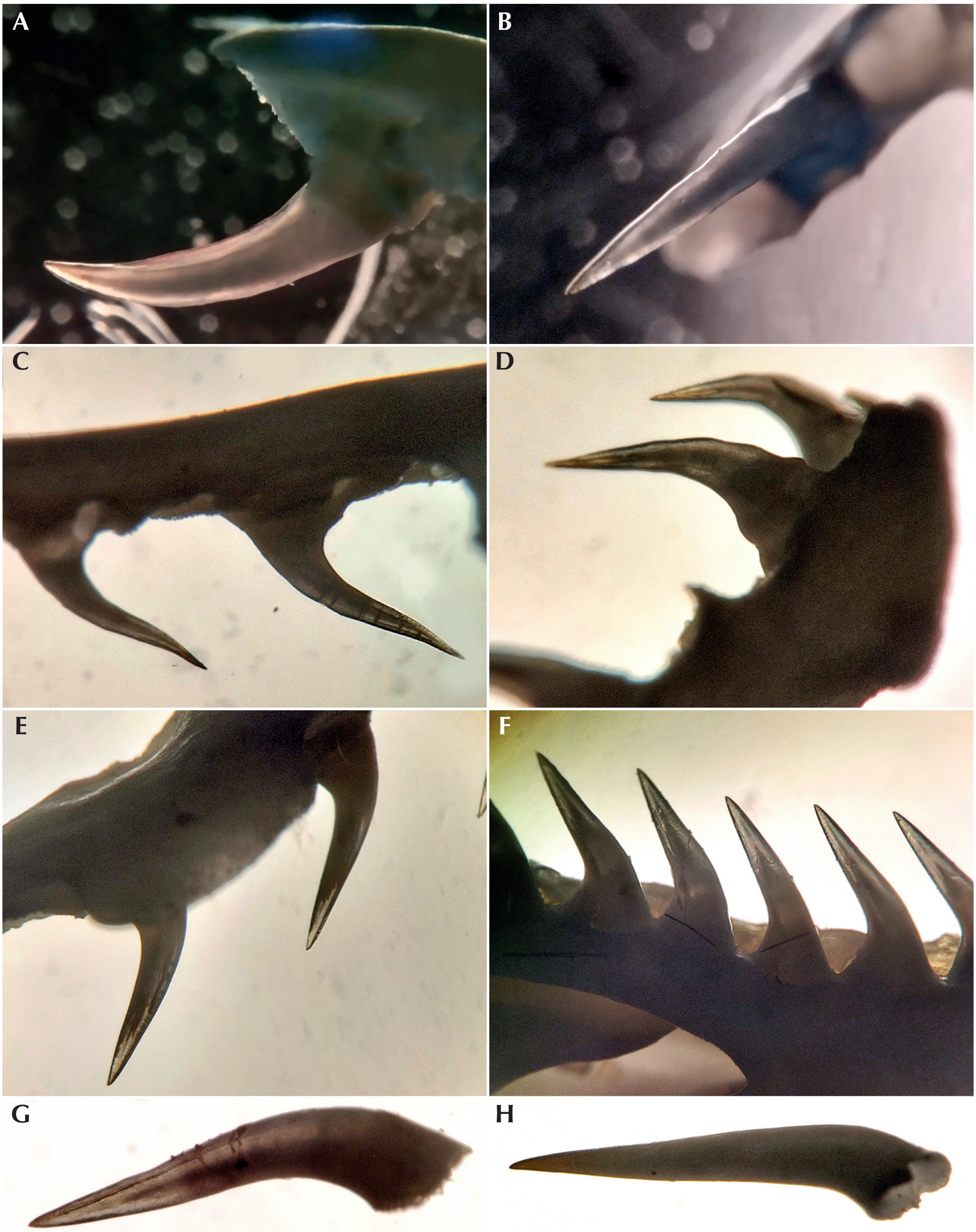

Figure 5. Stereomicroscope pictures of the dentiferous bones of the colubrid species investigated. (**A**) *Natrix helvetica lanzai,* rear maxillary tooth in lingual view. (**B**) *Natrix helvetica lanzai,* rear maxillary tooth in mesial view. (**C**) *Natrix helvetica lanzai,* maxillary teeth in lingual view. (**D**) *Natrix helvetica lanzai,* left dentary in lingual view. (**E**) *Zamenis longissimus,* left maxillary teeth in lingual view. (**F**) *Zamenis longissimus,* left dentary teeth in lingual view. (**G**) *Elaphe quatuorlineata quatuorlineata,* rear maxillary tooth in mesial view. (**H**) *Elaphe quatuorlineata quatuorlineata,* maxillary tooth in distal view.

generated by the bite, causes the secretion of Duvernoy's glands to be released directly on the wound. The pressure of the bite unsheaths the rear maxillary teeth from the mucosa, and the secretion enters the bite along the ridges and grooves of the teeth. The effectiveness of the bite is augmented by the grooves present in other teeth and by the masticating action of the prolonged bite. In addition, the pockets located labially to the enlarged maxillary teeth may accumulate the secretions of Duvernoy's glands, as in the American water snake *Nerodia sipedon* (Linnaeus, 1758) (Ranayhossaini 2010). Substantial amounts of secretions inside the mouth of *H. viridiflavus* were observed, especially in adult specimens.

The above constitute mechanisms that maximize the amount of secretion in a "low pressure" system (Taub 1967, Kardong and Lavin-Murcio 1993, Weinsten *et al.* 2013), lacking muscular insertions in the venom glands typical of snakes with anterior venom fangs. The bite and neurotoxicity of the secretion may play an important role in predation by *H. viridiflavus,* which takes a wide variety of prey (Filippi *et al.* 2003, Mondino *et al.* 2022) despite that it cannot be considered a "constrictor" snake.

Dentition in Other Species

Enlarged and modified rear maxillary teeth were found in *Natrix helvetica lanzai.* Although different from the teeth of *Hierophis viridiflavus,* its fangs resemble those observed in several opisthoglyphous colubrids (Weinstein *et al.* 2011). *Natrix helvetica* (*Natrix natrix sensu lato*), along with *H. viridiflavus,* has been considered an aglyphous ophid (Sindaco *et al.* 2006, Kreiner 2007, Di Nicola *et al.* 2021) even though the clinical consequences of its bite in humans has been documented (Gardner-Thorpe 1967, Satora 2004, GläßerTrobisch and Trobisch 2008).

Analogous glands to those surrounding the rear maxillary teeth of *H. viridiflavus* have been observed in the palatomaxillary arch of *Hemorrhois hippocrepis.* Cases of mild local effects following the bite of the congeneric *Hemorrhois algirus* and *Hemorrhois nummifer* are present in literature (Mamonov 1977, Malik 1995, Weinstein *et al.* 2011, Kazemi *et al.* 2023).

Conclusion

Several unsuspected characters in the upper jaws of *Hierophis viridiflavus* that are involved in the inoculation of salivary secretions, especially those produced by Duvernoy's glands, were found. These morphologies are linked to the predisposition of this species to inflict prolonged, "chewing" bites, a widespread and distinctive behavior of this snake among the Italian ophidian fauna. The morphology of the maxillary bone places this species within the opisthoglyphous snakes, equipped with modified fangs apposite for the transmission of secretions that can be considered a "primitive form of venom." The presence of grooves on most teeth suggests that *H. viridiflavus* should be considered polyglyphous, rather than aglyphous. Grooves were observed in the four dentiferous bones of other European species, although it is uncommon within colubroids. Among the Italian fauna, the opisthoglyphous species occur in limited northern border areas and small islands in the south (Sindaco *et al.* 2006), making *H. viridiflavus* an exception within the large "aglyphous" colubrids on the mainland.

Similar inoculation systems were observed in the large European colubroids *Natrix helvetica* and *Hemorrhois hippocrepis;* the presence of Duvernoy's glands and neurotoxic secretions have previously been documented in both genera (Phisalix 1922, Ovadia 1984, Jackson 2003, Weinstein *et al.* 2011).

Although changing the status of *H. viridiflavus* from harmless to humans is not recommended, special attention should be given not only to this species, but to the entire Palearctic whipsnake/racer complex (*sensu* Nagy *et al.* 2004) and the genus *Natrix.* All these species possess morphology capable of delivering toxic bites.

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