

Morphology of the maxillary bones in the Caspian whip-snake *Dolichophis caspius* (Serpentes Colubridae) supports the opisthoglyphous model within western palearctic whipsnakes

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ABSTRACT

The analysis of the dentiferous bones, in particular of the maxillae of the Caspian whipsnake *Dolichophis caspius*, reveals the presence of features typical of opisthoglyphous colubroids. Modified teeth are present in the posterior extremities of the maxillae, morphologically different from the anterior ones, from which they are separated by an alveolar diastema. In correspondence of such diastema, the maxillary bone deviates ventrally, positioning the rear teeth inferiorly than the anterior ones. As in other opisthoglyphous species, such characteristics are also visible in the palatamaxillary arches of *in vivo* individuals, as the rear maxillary teeth are covered by cuffs/sheaths which are easily recognizable from the surrounding mucosa. Presence of such traits was also found in the congeneric *Dolichophis jugularis* and *Dolichophis schmidtii*, and discussed in the other western Palearctic whipsnakes and racers species, suggesting that such adaptations may be developed in common ancestors from which such clade originated.

KEY WORDS

Caspian whipsnake; Colubridae; modified teeth; maxillae; opisthoglyphous; *Dolichophis caspius*.

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INTRODUCTION

The Caspian whipsnake, *Dolichophis caspius* (Gmelin, 1789) (Serpentes Colubridae), is one of the largest European snake species, growing up to more than two m in length, having a large distribution range from Eastern Europe and the Balkan Peninsula to the Caucasus, southern Russia, and Kazakhstan in the east (Ščerbak & Böhme, 1993; Ananjeva et al., 2006; Sahlean et al., 2014). In Greece, it occurs in many islands of the Cyclades, the Argo-Saronic islands, the Northern Sporades,

Dodecanese, Euboea, in some of the Ionian islands and throughout most of the mainland, but it is absent in the Peloponnese peninsula (Chondropoulos, 1989). In some islands of the Dodecanese, *D. caspius* is replaced by *D. jugularis* (Linnaeus, 1758), whereas on Kos it coexists with *D. caspius* (Cattaneo et al., 2020, 2023). This species is generally associated with open steppe and forest-steppe habitats, Mediterranean shrub, rocky slopes, and deciduous forest edges at low and medium elevations (Speybroeck et al., 2016), but may also occur in environments altered by anthropization, diverging

from the original steppe and forest-steppe habitats (e.g., agricultural landscapes; Tomović et al., 2015; Vukašin et al., 2023). Melanistic specimens have been reported from the island of Alonissos (Cattaneo, 1998; Broggi, 2010; Kalogiannis, 2021). In this study we analysed the dentiferous bones of three specimens of *D. caspius* from this last-mentioned locality, focusing specifically on the morphology of the maxillae, to verify the presence of the traits recently described in the close taxa *Hierophis viridiflavus* (Lacépède, 1789) and *Hemorrhois hippocrepis* (Linnaeus, 1758), attributable to an opisthognathous dentition (Paterna, 2023).

MATERIAL AND METHODS

Three road killed specimens of *Dolichophis caspius*, one adult and two subadults, from Alonissos Island (Northern Sporades, Greece) were used for dissection and osteology purposes (Fig. 1). These were found in Rousoum, near Patitiri in August 2010. The heads of the deceased specimens were severed *in situ* and subsequently preserved in alcohol by one of the authors (GM). These were dissected and subsequently prepared in spring 2024 at OPHIS Museo Paleontologico e Centro Erpetologico by the other author (PA). The prepared specimens were subjected to microscopy at the Laboratories of the Veterinary Medicine Faculty of Teramo. Photographic material was acquired with a Nikon Coolpix P510 camera, and microphotographs were obtained using a Nikon SMZ1500 stereomicroscope together with a Digital Sight DS-2Mv camera.

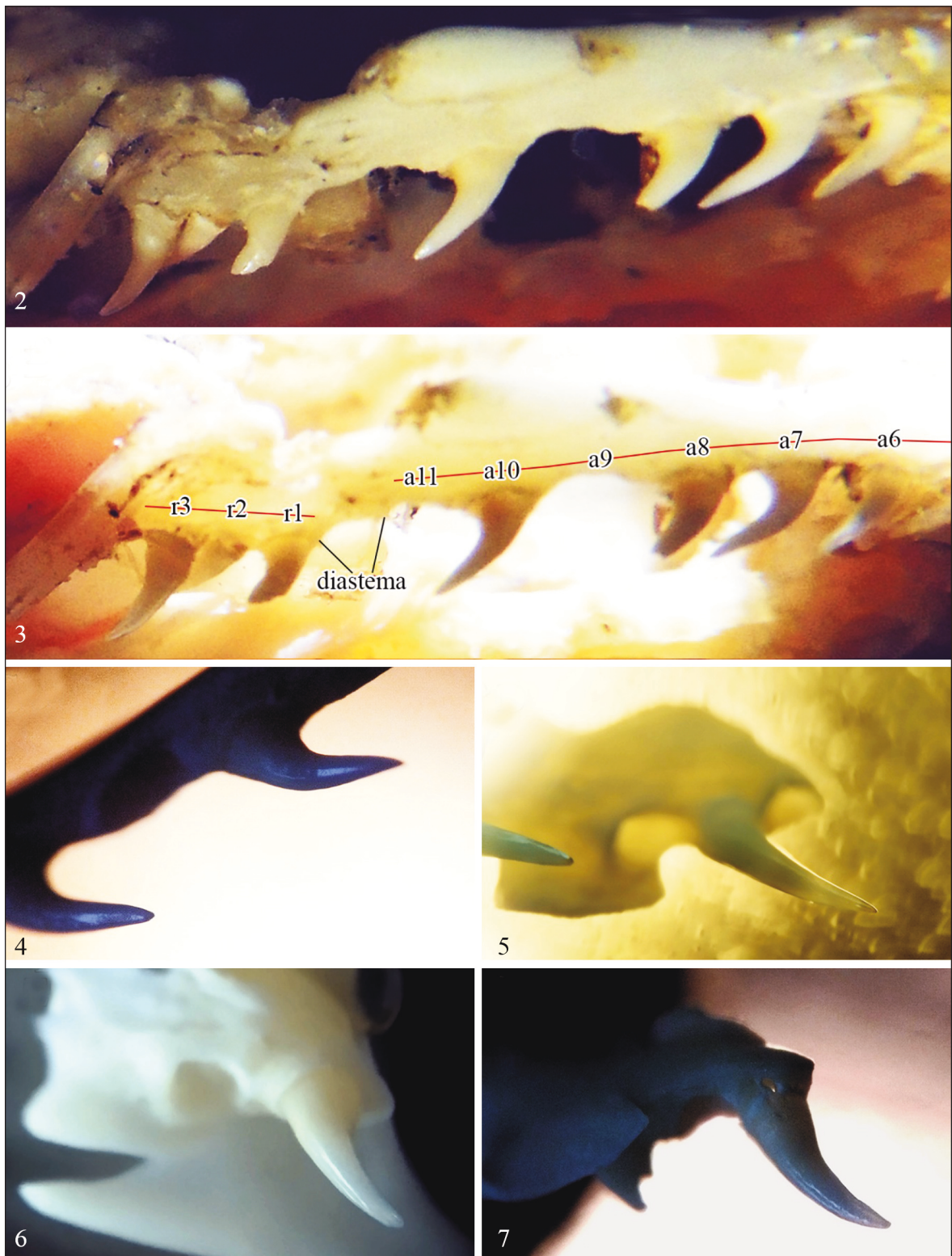
RESULTS

The maxillary bones are laterally compressed in the anterior two thirds of their length, to expand in the last third. Laterally, at the posterior margin of the last anterior alveolus (the eleventh), the maxillary bone deviates ventrally for the length of the alveolar diastema and the ectopterygoid process, to realign parallelly to the original axis in correspondence of the first rear tooth following the diastema (Figs. 2, 3). This deviation causes the posterior teeth to be consequently disposed on a lower plane than the anterior ones (Fig. 3). The prefrontal process de-

velops transversely at the middle of the fifth alveolus, extending posteriorly to the end of the seventh alveolus. Still medially, the ectopterygoid process occurs anteriorly in the middle of the diastema separating the anterior and the posterior alveoli, and culminates in correspondence of a second small diastema occurring between the first and second posterior tooth (twelfth and thirteenth teeth). The maxillae of the examined individuals present 14 teeth/alveoli, of which 11 anterior ones are aligned and equidistant from each other, and 3 posterior ones, separated from the previous ones by a diastema of a length of about that of an anterior alveolus (Figs. 2, 3). The anterior teeth are curved posteriorly, with the first one more arched than the subsequent ones. The anterior teeth feature grooves on the lingual wall, which are very accentuated es-



Figure 1. One of the analysed *Dolichophis caspius* specimens from Sporades Islands in dorsal view (top), left lateral view (centre), and ventral view (bottom).



Figures 2–7. Prepared specimens of *Dolichophis caspius* from Sporades Islands. Figs. 2, 3: right maxilla of a dissected specimen in lateral view. Fig. 4: lingual grooves on central maxillary teeth in medial view. Fig. 5: posterior end of a left maxilla in lateral view with detail of the second rear tooth. Fig. 6: truncated left maxilla articulated with pterygoid in ventrolateral view with detail of the third rear tooth. Fig. 7: posterior end of a right maxilla in medial view with detail of the third rear tooth.

pecially in the posterior half of the maxilla (Fig. 4). Like the teeth, the anterior alveoli also present an elliptical shape, elongated anteroposteriorly and compressed lateromedially, while the three posterior ones differ in being circular. The last two posterior alveoli are close to each other, as the teeth they bear, which are almost in mesiodistal/mesiolingual contact to each other (Figs. 2, 3). The penultimate posterior tooth, as observed in *Hierophis viridiflavus*, is more distally oblique than the subsequent one, which instead develops more perpendicularly to the maxillary plane, and is the one in which the most defined grooves are observed (Fig. 5). The anterior-most of the three rear teeth is further distanced from the subsequent ones, and consequently not in contact with the penultimate one. Analogously to the alveoli, the rear teeth present a different morphology than the anterior ones, and appear slightly larger in size. On the walls of these teeth there are several parallel longitudinal grooves converging at the distal apex (Figs. 5–7), distinguishable even without resorting to microscopy (Figs. 2, 3). On the lingual wall of the last posterior tooth, not far from the nutritional foramen, a circular pit is visible (Fig. 7), as also observed in the close taxon *H. viridiflavus*. As in the case of the latter species, also in the analysed subjects of *D. caspius* the dimensions of the posterior maxillary teeth and the definition/depth of the grooves are much more evident in the larger specimens. As suggested by Young & Kardong (1996), all the samples examined under microscopy were checked and pictured in different angles and in different contrasts, to avoid any optical illusions generated by the light and the particular morphology of some teeth models.

DISCUSSION

The features observed in the maxillary bones of the examined samples can be associated with those present in the opisthoglyphous models. The posterior maxillary teeth, although similar in size to the last anterior teeth, are separated from the latter by a diastema and a deviation of the maxillary bone. In one of the specimens examined, in which all three maxillary posterior teeth are preserved, it can be seen that the last two alveoli are close together, and the posterior teeth are adjacent to each other.

This trait is typical of some species of opisthoglyphous snakes. The two teeth may work as a single functional unit (Knox & Jackson, 2010), and such as in *Helicops modestus*, the mesio-distal contact point between the two overlapping teeth could act as a lateral canal in which the oral secretions flow during the biting/chewing action (Oliveira et al., 2016). These posterior teeth, as in the case of *H. viridiflavus* (Paterna, 2023), are covered by a cuff/sheath visible in the palatamaxillary arch in live specimens (Fig. 8). These cuffs are easily recognizable due to their morphology and different coloration compared to the surrounding mucosa. In *H. viridiflavus* these are located medially to the Duvvernoy's gland, which converges ventrally towards the posterior maxillary teeth (Paterna, 2023).

Confirmation of the presence of the traits described in this study in other representatives of the *Dolichophis* genus is provided by two specular works, in which the morphology of the cranial bones of snakes of the *Dolichophis* genus is compared to that of sympatric colubrids of the sister group *Eirenis*. The first work cited is that of Sadeghi et al. (2014), where the cranial bones of three specimens of *Dolichophis jugularis* from Iran are analysed. In the study no difference is mentioned within the maxillary teeth, but the authors provide photographic material and drawings portraying the skull of a specimen of *D. jugularis* in ventral view, where, although the specimen lacks almost all the teeth, the presence of enlarged and separated posterior alveoli is clearly evident. The arrangement of teeth in the jaws of *D. jugularis* is similar to that observed in *D. caspius*. Though Sadeghi et al. (2014) in their work do not mention the number of alveoli/teeth present in these bones, from the photographic material and drawings these should house 11–12 anterior maxillary teeth and three posterior maxillary teeth, of which the most posterior two are adjacent to each other and a little further distanced from the anterior-most. Evident differences from *D. caspius* seem to be mainly the dimensions of the prefrontal process, which is more latero-medially developed, and the deviation present between the first and the second posterior maxillary tooth. In the referred specimen, in ventral view, the two most posterior teeth are off-axis respect to the curve of the maxillary bone. The second work is that of Rajabizadeh et al. (2021). Here too the authors examine the cranial bones of *Eirenis*

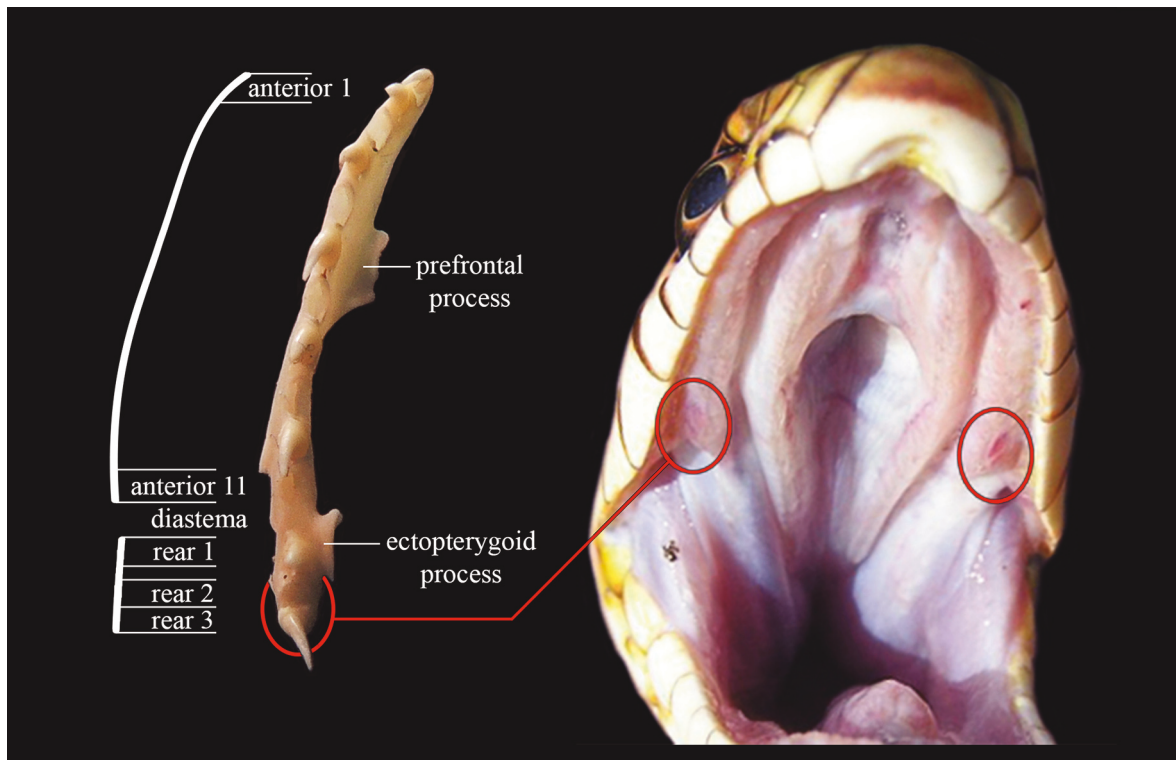


Figure 8. *Dolichophis caspius*' right maxilla in ventral view (left) beside the palatamaxillary arch of a live specimen from Bulgaria (right); photo credit Petr Balej.

punctatolineatus and *E. persicus* and compare them with those of *D. schmidtii*. The study reports that “each maxilla of *Dolichophis schmidtii* bears sockets for 11 (11–13) anterior teeth of similar size after a space (nearly one tooth length) are followed by two bigger teeth (about 1.5 times longer than the anterior teeth)”. From the three-dimensional reconstructions present in the study, we can clearly see how the two posterior teeth of *D. schmidtii* are close together and adjacent to each other (as observed in *D. caspius*), and can even be noticed the longitudinal groove on the lateral surface of the penultimate enlarged tooth of the left maxilla. In this species, the posterior maxillary teeth are larger than those observed in the *D. caspius* specimens examined here. This difference could however be related to the individuals examined and not to the entire species, as in this work samples from the same locality (south-west of the species' distribution range) were examined, and populations present in other European countries could present intraspecific variations in the dimensions of the latter. Similarities between the maxillae of the two species are found

in the deviation in correspondence of the diastema that separates the anterior teeth from the posterior ones, where the bone projects ventrally and then returns parallel to the anterior axis.

CONCLUSIONS

Grooved teeth, posterior alveoli and teeth of different morphology, separated from the rest of the maxillary teeth by an alveolar diastema and a deviation of the maxillary bone, correspond to the traits observed in the close taxon *Hierophis viridiflavus* (Paterna, 2023). Such condition, which can also be linked to similarities found in the biology and ecology of the two genera, and the predisposition of these to inflict prolonged and masticated bites, suggest that also in the *Dolichophis* genus these features may be functional to the inoculation of the oral secretions in the prey. A further characteristic present in *Dolichophis caspius*, observable *in vivo* and also found in the palatamaxillary arches of *H. viridiflavus* and *Hemorrhois hippocrepis* are the

cuffs/sheaths that cover the rear maxillary teeth. In *H. viridiflavus* such cuffs are in contact medially with the Duvernoy's gland, and consist in a further trait shared with the opisthoglyphous snakes.

These findings represent a first confirmation of the hypothesis that this condition may be shared with other species and genera belonging to the Western Palearctic whipsnake/racer clade *sensu* Nagy et al., 2004 (Paterna, 2023). Within this group of ophidians there are species that have always been considered opisthoglyphous, as in the case of representatives belonging to the genus *Spalerosophis* (Jan, 1865), and species such as *H. hippocrepis*, *D. caspius*, *D. schmidti* and *D. jugularis*, which present structures of the maxillary bones and palatamaxillary arches similar to those observed and described in *H. viridiflavus* (Paterna, 2023). Always in this clade, together with the cases just mentioned, there are other species for which there is a case history in the literature about clinical reactions following their bite in humans: *H. viridiflavus* (Bedry et al., 1998; Dutto et al., 2015; Avella et al., 2024), *Hemorrhoids nummifer* (Weinstein et al. 2011), *Hemorrhoids ravergeri* (Ishunin, 1950; Mamonov, 1977), *Platyceps collaris* (Weinstein et al. 2011), *Platyceps najadum* (Chroni et al. al., 2005; Trapp, 2007), *Platyceps rhodorachis* (Branch, 1982; Perry, 1988; Malik, 1995).

The only exception in this group appears to be the more modern and dwarf snakes belonging to the genus *Eirenis*. Detailed descriptions and graphic documentation of the dentiferous bones of representatives of this genus (*sensu* Jan, 1863) which confirm the "aglyphous" dentition model in this group are abundant in the literature (Mahlow et al., 2013; Sadeghi et al., 2014; Rajabizadeh et al., 2021). In the work of Rajabizadeh et al. (2019), the authors analyse and compare the morphology and resistance of the teeth of these colubrids with those of the genus *Dolichophis*, and they conclude that the type of dentition, of *Eirenis persicus* specifically, is the result of an adaptation apt to endure the resistance generated by the tension followed by biting a prey-type featuring a hard exoskeleton. This characterization of the teeth therefore seems to be due to the miniaturization of the genus and the diet shift, for which pointed teeth would be inadequate.

It is therefore interesting how within the western clade of the Palearctic whipsnakes all genera, excluding the miniaturized *Eirenis* (related but not

considerable a whipsnake/racer), present an opisthoglyphous dentition model, or are protagonists of "envenomation" cases following their bite in humans (Table 1). This could mean that these adaptations developed in the ancestors of the whipsnakes from which the two branches where the group including *Hemorrhoids*, *Spalerosophis* and *Platyceps*, and the group including *Dolichophis*, *Hierophis* and *Eirenis* derived, according to the phylogenetic study of Nagy et al. (2004), over 20 million years ago. In the same work, the inclusion of *Macroprotodon* within the clade composed by representatives of the former genus *Coluber* (*sensu lato*) of the old world is also interesting. *Macroprotodon* is in fact a more basal genus than the previously discussed taxa, consisting of small opisthoglyphous colubrids (Pleguezuelos, 2005; Valdoleiros et al., 2021). The presence and genetic proximity of this genus in/to the group analysed here further confirms the conservation and the developing of the opisthoglyphous model in the Western Palearctic whipsnakes.

Taking into consideration what has been reported, and given the morphological similarities shared with the opisthoglyphous colubroids' species (Broadley & Wallach, 2002; Jackson, 2003; Weinstein et al., 2011), it is clear that the snakes of the genus *Dolichophis* discussed here can be compared to such, as well as other large Palearctic whipsnakes and racers. With this statement we would like to underline the concept whereby, as reported in the study concerning *H. viridiflavus*, it is suggested not to change the consideration we have always had of these animals. "Opisthoglyphous" are the snakes

Whipsnake/racer genus	Opisthoglyphous traits known to date	Consequences after bite in humans
<i>Hemorrhoids</i>	•	•
<i>Spalerosophis</i>	•	•
<i>Platyceps</i>	•	•
<i>Dolichophis</i>	•	?
<i>Hierophis</i>	•	•
<i>Eirenis</i>		

Table 1. List of the opisthoglyphous traits and bites' consequences in humans known to date in the genera belonging to the western palearctic whipsnakes/racers complex. Question mark in the *Dolichophis*' slot refers to the single and doubt case reported in Aleksankin (1968).

that present certain characteristics and modifications in the maxillary bones, and which feature enlarged or grooved posterior maxillary teeth, suitable for the inoculation of the secretions produced by Duvernoy's gland. In the case of the species discussed in this study, these structures are useful to these animals only for the subjugation of the small prey they feed on, and/or for the digestion of these (Kardong, 1982). As demonstrated by the albeit limited case studies reported in the literature, their bite hardly produces clinical consequences in humans.

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