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Reclassification of the smooth snake. Analysis of the rear fangs, venom system, and the cephalic anatomy of *Coronella austriaca* (Serpentes: Colubridae)

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Abstract

The in-depth study of the cephalic anatomy of the smooth snake *Coronella austriaca* sheds new light on the biology of this species, representing an important step forward in understanding its ecology. A detailed study of the dentition of this species is presented here, describing for the first time the modified posterior maxillary fangs. Two specialized rear fangs are separated by the third to last tooth by a diastema, in turn spaced from the anterior maxillary teeth by a second diastema. The rear fangs are covered by sheaths connected to the venom/Duvernoy's gland. Retracing the existing literature, we see how this gland in *C. austriaca* is predominantly serous, and its secretion can have significant effects on its preys and other animals. Analysis of specimens at different growth stages has shown that the growth of the maxillary bone and posterior fangs is isometric, while the parietal bone is subject to ontogenesis. Through several preparation steps, the presence of additional cephalic features previously unconsidered in this species has been documented, such as the presence of pits in the parietal shields and the corresponding foramina in the parietal bone that opens ventrally nearby the epiphysis. The presence of sheathed rear fangs has also been documented in the jaws of the sister taxon *Coronella girondica*. The nature and rationale for the opisthoglyphous/rear-fanged condition, shared by this species and other European colubrines, are discussed here.

Key words: smooth snake, *Coronella austriaca*, rear-fanged, anatomy, toxicofera

Introduction

The smooth snake, *Coronella austriaca* (Laurenti), is a small snake that can reach 70 cm in length, in some cases even 90 cm (Speybroeck *et al*., 2016). The distribution area of this snake, well distributed across Eurasia, extends from Iran and Kazakhstan in the east to Spain and Portugal in the west, from Scandinavia in the north to the Mediterranean coasts of Europe (Steward, 1971; Speybroeck *et al*., 2016). It prefers sunny, rocky habitats with some vegetation cover, dry stone walls, and forest edges, and can reach altitudes of up to 2,700 m in mountain habitats (Speybroeck *et al*., 2016). The following subspecies are currently recognized: *C. a. austriaca* and *C. a. acutirostris* (Malkmus), the latter present only in the north and north-west of the Iberian Peninsula, excluding the Pyrenees, and southwards up to the Serra da Estrela. The subspecies *C. a. fitzingeri* (Bonaparte), present in Sicily, is currently no longer considered valid (Speybroeck *et al*., 2016). *Coronella austriaca* is a predominantly saurophagous (Amo *et al*., 2024) and ophiophagous species (Groen, 2018; Escalante *et al*., 2023; Amo *et al*., 2024), which occasionally also feeds on small mammals (Reading and Jofré, 2013; Brown *et al*., 2014), amphibians (Juszczyk, 1987; Reading and Jofré, 2013), birds and their eggs (Angelici and Luiselli, 1998; Johansen and Flaatten, 2021). Recently, the presence of enlarged posterior maxillary teeth surrounded by sheaths has been described in the palatomaxillary arch of this species (Paterna, 2024). Since studies on the histology of the venom/Duvernoy glands and their secretion were already present in the twentieth century literature (Phisalix, 1922; Taub, 1967), we decided to investigate in depth the cephalic anatomy of this snake.

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Materials and Methods

Five specimens representing three ontogenetic stages were examined. All specimens are deposited in the collections of OPHIS Museo Paleontologico e Centro Erpetologico (Teramo, Abruzzo, Italy), where they are permanently curated. The sample comprised two adult males of Romanian origin (OPHca01 and OPHca02), two juvenile/subadult wild individuals from northern Italy (OPHca03 and OPHca04), and one stillborn fully developed female specimen (OPHca05). The specimen codes, sex and body measurements are as follows: OPHca01, adult male, TL (total length) 63 cm, SVL (snout vent length) 49 cm; OPHca02, adult male, TL 62 cm, SVL 47.5 cm; OPHca03, juvenile male, TL 36 cm, SVL 28 cm; OPHca04, juvenile female, TL 38 cm, SVL 32.5 cm; OPHca05, stillborn female, TL 19.5 cm, SVL 16.2 cm. Following measurements and the acquisition of initial photographic material, the specimens were decapitated to facilitate their preparation. The preparation phases were carried out at OPHIS and documented with Nikon Coolpix P510 and Sony α6000 cameras. An initial anatomical analysis was performed during manual dissection using surgical tools, followed by a second chemical phase for the subsequent preparation of the bones with sodium hypochlorite. Following preparation, the cranial bones were photographed with an Acro 1000x Trinocular Biological Microscope and USB camera, a Nikon SMZ1500 stereomicroscope, and an OptikaB3 Digital Camera at the University of Camerino—URDIS Polo Didattica Ricerca SBT (San Benedetto del Tronto, Marche, Italy). Measurements of the maxillary bones were made possible by using a micrometric scale in the microscopic analyses. Upon completion of the examination, the prepared specimens were cataloged at OPHIS, where they are currently housed.

Results

Anatomical and Osteological Analysis. Necropsy examinations (Fig. 1A, B) reveal the presence of a prominent Harderian gland in contact with the anterior margin of the muscle *levator anguli oris* dorsally, and with the venom gland/Duvernoy's gland ventrally. Between these two glands, the *ligamentum quadrato-maxillare* is visible posteriorly. The venom gland is longitudinally developed and dorsoventrally proportioned to the size of the maxilla, of which it covers the posterior portion. This gland is in contact anteriorly with the supralabial salivary gland, from which it differs significantly (Fig. 1B). In the younger specimen, the venom gland appears to be larger than in the adult, reaching the same size as the Harderian gland. During the preparation phases we were able to observe and document the passages of various blood vessels, which supply the venom gland, the occipital and prefrontal regions, and the maxilla in the ventral portion of the bone up to the pulp of the teeth (Fig. 2A, B).

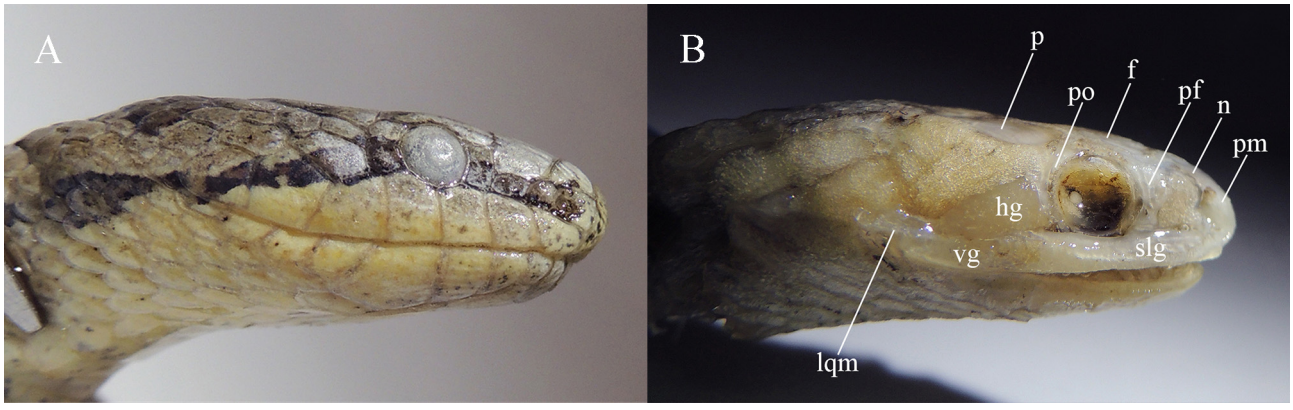

FIGURE 1. *Coronella austriaca* adult male specimen OPHca01. A. Lateral view of the head prior to preparation. B. Lateral view of the head after preparation. Abbreviations: f, frontal bone; hg, Harderian gland; lqm, ligamentum quadrato-maxillare; n, nasal bone; p, parietal bone; pf, prefrontal bone; pm, premaxilla; po, postorbital bone; slg, supralabial salivary gland; vg, venom gland.

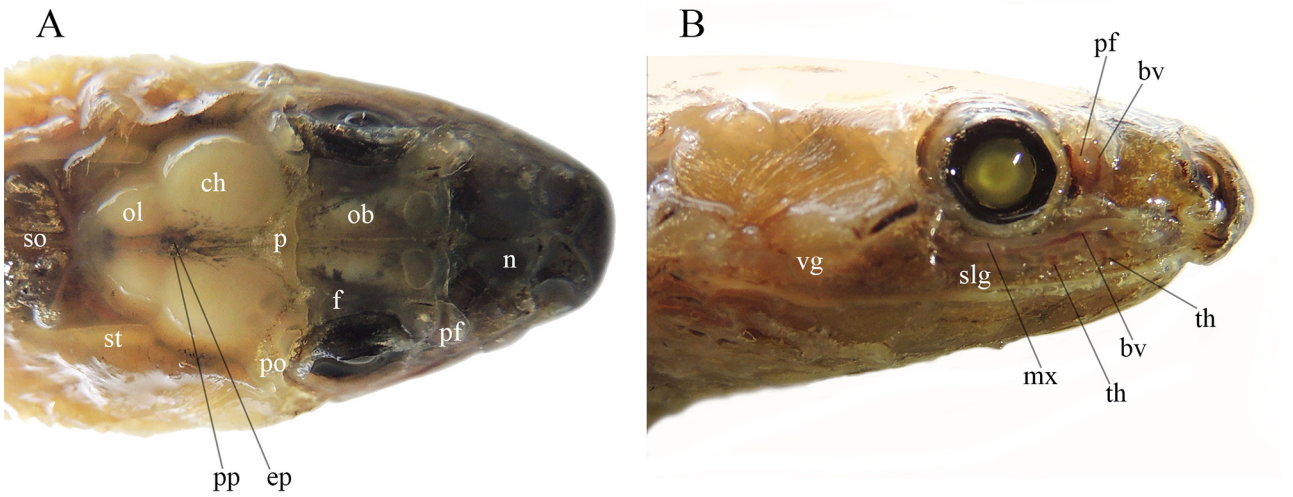

FIGURE 2. *Coronella austriaca* prepared adult male specimen OPHca02 in (A) dorsal view; and (B) lateral view. Abbreviations: bv, blood vessel; ch, cerebral hemisphere; ep, epiphysis/pineal gland; f, frontal bone; mx, maxilla; n, nasal bone; ob, olfactory bulb; ol, optic lobe; p, parietal bone; pf, prefrontal bone; po, postorbital bone; pp, parietal pit / parietal foramen; slg, supralabial salivary gland; so, supraoccipital bone; st, supratemporal; th, tooth's pulp; vg, venom gland.

Further interesting data come from the parietal region. Single or conjoined parietal pits were present in the parietal shields of part of the specimens (Paterna, 2025). We then examined the parietal bones of the five individuals (Fig. 3, A–E), where we found confirmation of the presence of foramina in the dorsal plane of the parietal bone in all the specimens except one, OPHca03 (Fig. 3B), where the parietal plane is unornamented, with the only foramina present in the nearby of the frontal contacts. In the included images depicting OPHca02, it is possible to observe the anatomical correspondence between the parietal pit (Fig. 2A), the parietal foramen (Fig. 2A, 3E), and the proximity to the pineal gland (Fig. 2A). OPHca01 is the only specimen with two foramina on the parietal plane: a main foramen on the right half of the bone, located in correspondence of the contact between the optic lobes and the encephalic hemispheres, and a second foramen positioned more rostrally on the opposite side. Analysis of the parietal bones also reveals a profound ontogeny. The parietal in this species has a sagittal depression that mirrors the pallium. Given the different age groups of the specimens used, we have illustrated the evolution of the morphology of the parietal. In the stillborn specimen this bone is dorsally flat, with the supraoccipital and prootic contacts forming a semicircular shape with a slight difference in level between the two contacts. Such plane difference will become more accentuated with growth, revealing the subtriangular shape of the occipital plane of the adult, on which the sagittal depression and the posterior lateral fossae will be defined (Fig. 3F).

In the subsequent study phases, we performed a complete preparation of the cranial bones for the analysis of the dentiferous bones. The maxillary bone is straight in the transverse plane and deviates slightly in the sagittal plane at the third-to-last tooth.The maxillary teeth, 13–14 in total, appear large and robust. From the anterior apex of the maxillary bone, the teeth are continuously aligned until the first diastema distancing the third to last tooth and a second diastema separating the last two teeth. The anterior teeth are the thinnest and most hooked ones, becoming increasingly thicker and receding posteriorly at an angle that can reach 20° from the axis of the maxillary bone. The last two teeth are the longest and most robust of the maxilla and, unlike the anterior teeth, are modified. These are the closest to each other within the maxillary bone and have a lesser inclination (approximately 45°) from to the transverse plane. After those present in the maxilla, the most robust teeth are those of the dentary, characterized by a shark fin shape with a broad base. The dentary contains up to 16 teeth. In specimen OPHca04, an asymmetry was observed in the number of teeth present in the two dentaries, in which the posterior group consisted of five on the left and four on the right bone. The palatine bones have six teeth with a morphology similar to that of the median maxillae, while the pterygoids have 12, of which the ones in the posterior half of a very reduced size.

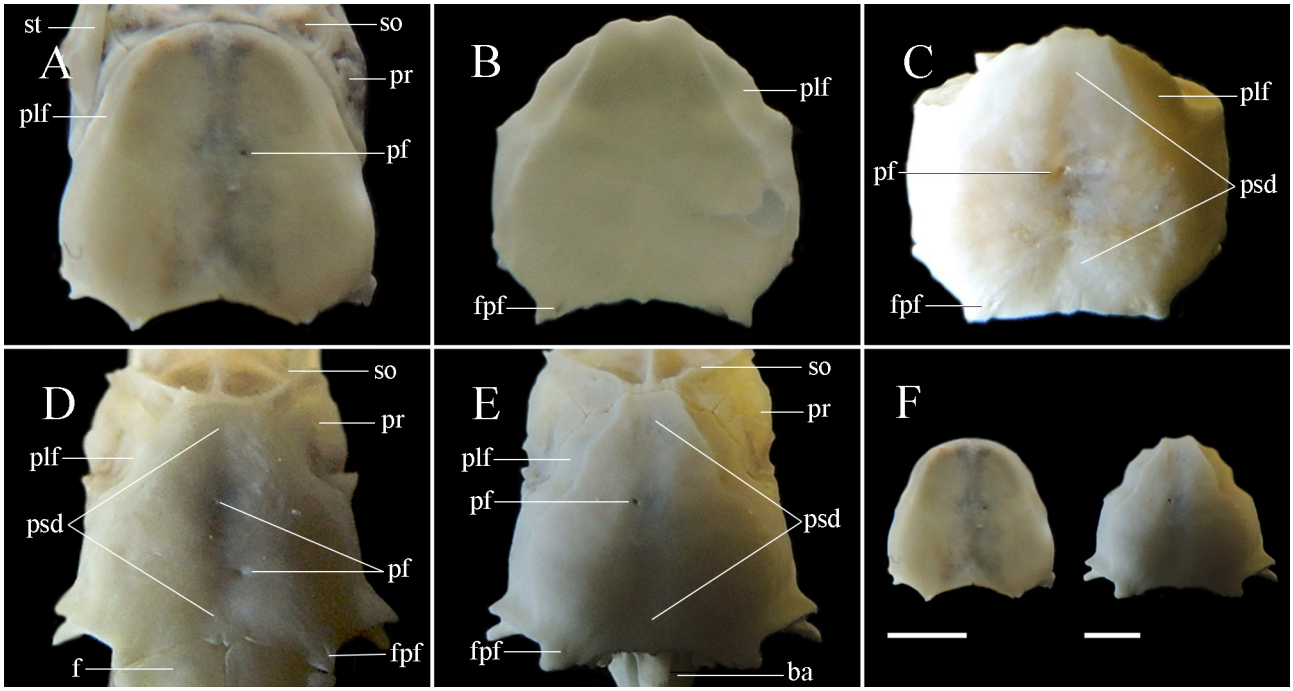

FIGURE 3. Ontogenetic variations in the parietal bone of *Coronella austriaca*. Dorsal views of braincases and parietals of different growth stages. A. OPHca05, new born female's parietal, articulated with supraoccipital, prootic and right supratemporal; B. OPHca03, juvenile male's disarticulated parietal bone; C. OPHca04, juvenile female's disarticulated parietal bone; D. OPHca01, adult male's parietal, articulated with frontals, supraoccipital and prootic; E. OPHca02, adult male's parietal articulated with basisphenoid, supraoccipital and prootic; F. Direct comparison of two disarticulated parietals: OPHca05 (left) and OPHca02 (right). Scale bars equal to 2 mm. Abbreviations: ba, basioccipital; f, frontal; fpf, frontoparietal contact foramina; pf, parietal foramen/foramina; plf, parietal posterolateral fossa; pr, prootic; psd parietal sagittal depression; so, supraoccipital; st, supratemporal.

Rear fangs. In the maxilla of *Coronella austriaca*, the two posterior teeth (fangs) differ from the rest of the teeth along the bone in size and morphology. These are the closest to each other, spaced by the third-to-last, which in turn further separates the anteriormost teeth, and displays an intermediate morphology that includes sketchy features present in the fangs. The fangs have a thick distal carina starting from the apex of the tooth and reaching the angle at which the tooth curves in the first basal segment. Lingually, a longitudinal ridge/protrusion is present, which also converges at the apex of the tooth. At the points of entry of these two structures, a longitudinal furrow is generated that occurs for more than the distal two-thirds of the fang, between the labial surface of the distal carina and the posterior margin of the ridge (Fig. 4A, B), following a second depression between the anterior margin of the ridge and the tooth wall. A short mesial carina is also present in the distal portion of the fang (Fig. 4C). In one of the specimens, the presence of a replacement fang was observed (Fig. 4D). The base of the replacement fang is located between the anterior half of the last fang and the space before the penultimate one, suggesting that it is the last replacement tooth. The length and thickness of the replacement fang are shorter than those of the ankylosed ones. The replacement fang also appears linear, not yet showing the curvature typical of the fully formed fangs. The distal carina also appears less marked, as it is likely still developing. The angle of the replacement fang is 45° rostrally respect to the plane of maxillary bone. We do not exclude the hypothesis that the anterior direction of the replacement fang may be an involuntary artifact generated during the specimen preparation processes or due its typology of death. The morphology of the fangs is the same in all analyzed specimens. In the stillborn individual, all the traits present in the fangs: the distal carina, the labial sulcus, the short mesial crest, are perfectly expressed and defined, as is the transitive condition of the third-to-last tooth, in which even the less developed distal and mesial carina can be recognized (Fig. 4 E, F).

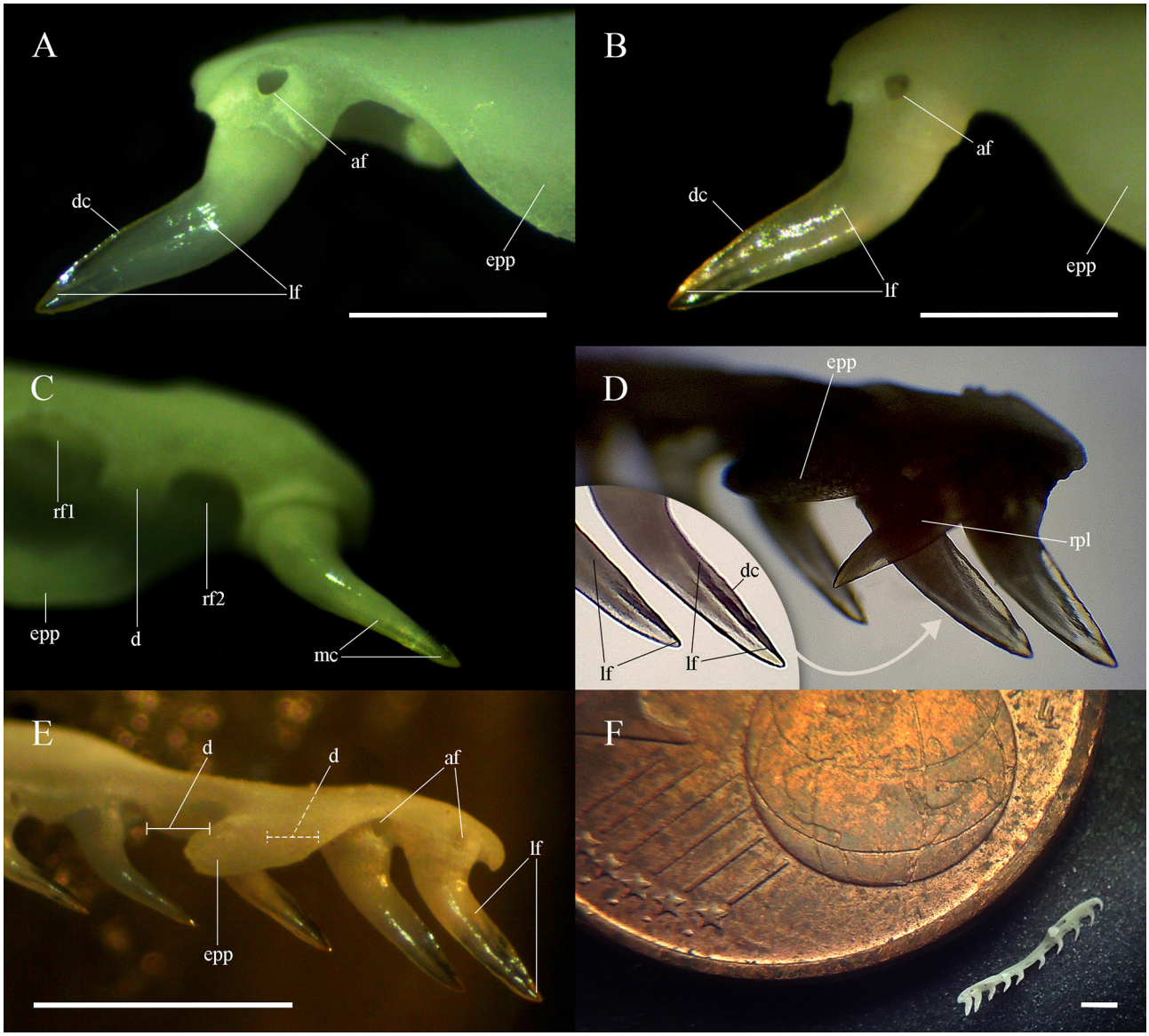

FIGURE 4. Maxillary bones of *Coronella austriaca*. A, B. Left maxilla of OPHca01 in lingual view, showing the last rear fang. C. Left maxilla of OPHca01 in ventrolabial view, showing a short distal mesial carina. D. Right maxilla of OPHca04 in lingual view, showing a replacement fang. E. Right maxilla of OPHca05 in lingual view showing the differences between rear fangs and anterior teeth. F. OPHca05 left maxilla in lingual view beside a 1 Euro cent coin. Scale bars equal to 1 mm. Abbreviations: af, alveolar foramina; d, diastema; dc, distal carina; epp, ectopterygoid process; lf, lingual furrow; mc, mesial carina; rf1, first rear fang; rf2, second rear fang; rpl, replacement fang.

Maxillary bone-growth relationship. Using a micrometer scale during the microscopic examination of the maxillary bones, we measured various traits in the largest and smallest specimens, OPHca01 and OPHca05, respectively, which are related. The measurements taken represent the total length and are as follows: OPHca01, maxilla 8.7 mm, posteriormost fang 1.5 mm, median teeth 1.3 mm, anteriormost teeth 0.8 mm; OPHca05, maxilla 4.7 mm, posteriormost fang 0.7 mm, median teeth 0.6 mm, anteriormost teeth 0.3 mm. In the adult specimen, the length of the last fang is equal to 17% of the total length of the maxilla. The difference in size between the last fang and the median maxillary teeth is equal to 13% of the fang's length, and similarly, the difference between the fang and the most anterior maxillary teeth corresponds to 47% of its length. In the stillborn individual, the length of the last fang is equal to 15% of the maxilla total length. The difference in size between the last fang and the median maxillary teeth is equal to 14% of the fang length, and the difference between the same fang and the most anterior maxillary teeth corresponds to 57% of its length. Also in the stillborn specimen, the length of the maxilla is 54% of

the adult bone. The length of the last fang is 47% of the adult's most posterior fang, the length of the median teeth is 46% of the adult's median teeth, and the length of the anterior teeth corresponds to 38% of the adult's anterior teeth.

Between the two specimens, which represent the two extremes of the growth stages, the proportions of the considered maxillary traits are similar. The only appear size of the anterior maxillary teeth, which, through growth, lengthen in proportion to the rest of the maxillary teeth. This trait is also visually detectable, where a further transverse strengthening of all maxillary teeth is noted. The maxilla of OPHca05 is slightly more than half the size of OPHca01 (54%), while the total length of the juvenile (TL) is 31% of the adult, suggesting isometric growth of the cranial bones, including fangs, and allometric postcranial growth.

Bite episode. In 2012, in the early afternoon of April 15, during some measurements carried out in a field study in the Laga Mountains in the province of Teramo (Abruzzo), one of us (AP) was bitten by an adult male *Coronella austriaca* while handling the specimen. The bite was prolonged, allowing time to take a photograph while the "mastication" action was still in progress (Fig. 5A). Following the bite, itching and redness quickly appeared in the affected area. A second photograph, taken 11 minutes after the photo showing the bite, shows redness corresponding to the maxillary arch's shape, where the holes caused by some anterior maxillary teeth and the pair of posterior fangs are visible (Fig. 5B). Over time, in addition to the redness, swelling developed at the site of the small lacerations caused by the teeth, which was also accompanied by itching. The most evident symptoms lasted a few minutes, then gradually subsided in less than an hour. As researchers in both field and controlled environments, we both frequently receive snake bites in different contexts. Nevertheless, this case, although extremely mild, represents the only one to date in which we have personally observed a reaction other than bleeding following a bite of a colubrine snake.

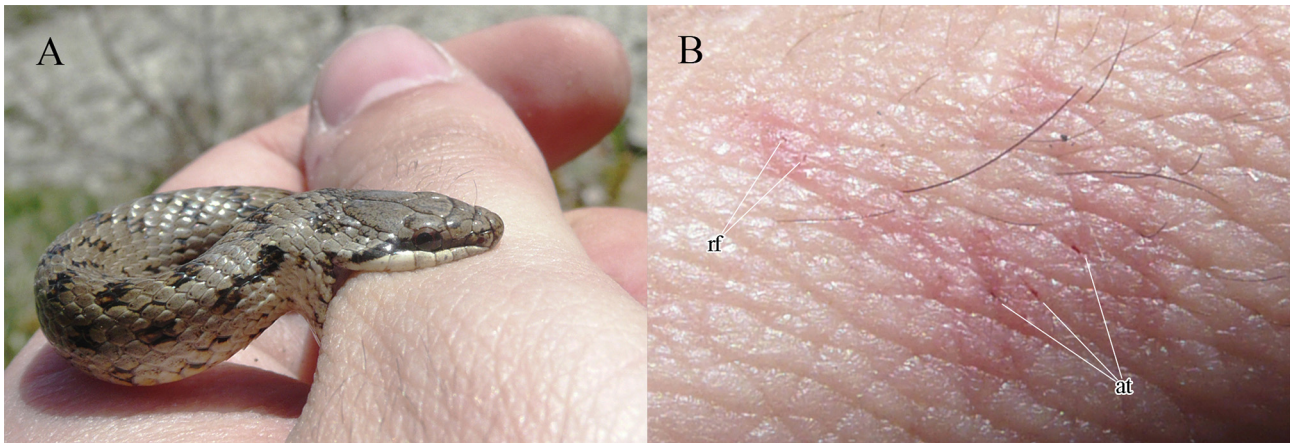

FIGURE 5. Prolonged bite from a *Coronella austriaca* adult male from Monti della Laga, Abruzzo (Italy). A. Bite action on the first phalanx of the left thumb. B. Bite area 11 minutes after the bite. The inflamed area follows the maxillary arch. Abbreviations: at, anterior teeth; rf, rear fangs.

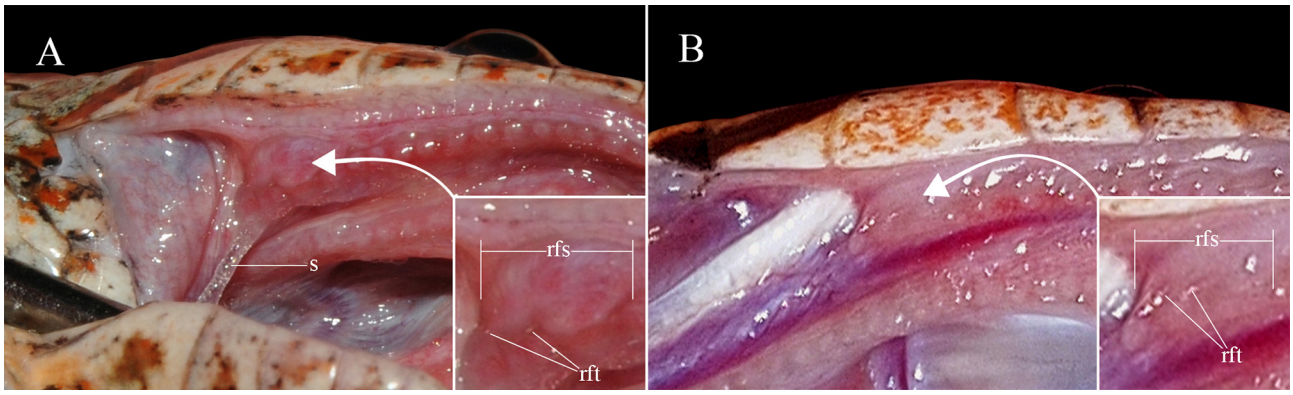

FIGURE 6. Right palatomaxillary arches of *Coronella austriaca* (A), and *Coronella girondica* (B). Abbreviations: rfs, rear fangs' sheaths; rft, rear fangs' tips; s, secretions in correspondence of maxillary rear fangs.

Coronella girondica. The genus *Coronella* comprises two species, *Coronella austriaca* and *Coronella girondica* (Daudin). Having carried out specific analyses in the first taxon, we performed buccal inspections on specimens belonging to the second taxon, specifically two captive-born adults belonging to a bloodline originating from Liguria (Italy). The inspection, documented here, provided us with a result similar to that observed in *C. austriaca*, whereby *C. girondica* also possesses enlarged maxillary teeth surrounded by sheaths (Fig. 6).

Discussion

Fangs, sheaths and glands. By carrying out measurements on a range of specimens extending in age from day 0 to adulthood, we ascertained that the size of the posterior fangs and the entire maxillary bone of *Coronella austriaca* are subject to isometric growth, characterized by a progressive thickening of all teeth. The posterior maxillary fangs in this species differ from the anterior teeth in size and morphology. A robust distal carina and a lingual protrusion (ridge/protrusion) converge at the apex of the tooth, creating a longitudinal furrow in the distal two-thirds of the fang. The distolingual furrow is generated by the abrupt angle of entry of the distal carina, a trait absent in other colubroids in which a distal carina is nevertheless present, such as in the sympatric species *Natrix helvetica* (Paterna, 2023b). The depression generated is similar to that categorized as "type c" from Jackson and Fritts (1995) and "type 2, furrowed teeth" by Young and Kardong (1996). The hind fangs of *C. austriaca* exhibit a morphology similar to that observed in *Hierophis viridiflavus* (Lacépède) (Paterna, 2023b). The two taxa belong to two distinct branches of the Colubrinae clade, where the former is more derived among ratsnakes, and the latter is more basal in whipsnakes (Borczyk, 2006; Burbrink and Lawson, 2007; Figueroa *et al*., 2016). Could similarities in fang pattern have been selected for or conserved in two species that exhibit similar ecological traits? For example, both species have a predominantly saurophagous diet, and at the same time, they are the two European colubrines most prone to ophiophagy and cannibalism (Bartlomiej, 2001; Strugariu *et al*., 2014; Capula *et al*., 2014; Di Nicola *et al*., 2020; Paterna, 2023a; Zdunek *et al*., 2023; Meier and Zdunek, 2026). A similar fang morphology is found in another ophiophagous snake, *Erythrolamprus aesculapii* (Linnaeus). This species, despite belonging to another family, that of the dipsadids, has a robust distal carina in the posterior maxillary teeth, which abruptly enters the tooth wall, creating a longitudinal depression that extends along the length of the tooth (Sánchez *et al*., 2019). This species also possesses a mesial suclus, which, unlike many species that share a similar trait, culminates at the apex of the tooth in a carina, also present in *C. austriaca*. The peculiar morphology of this fang, like that of *C. austriaca* and *H. viridiflavus*, resembles that of a Phillips screwdriver. The three taxa also share the same type of venom/Duvernoy gland (Taub, 1967; Sánchez *et al*., 2019). Although species with similar diets do not appear to show strong morphological convergence (Hudry and Herrel, 2025), could this be a case of evolutionary convergence, or a conservation/selection in which the sharing of certain ecological traits has assigned/conserved a specific fang morphology in phylogenetically distant colubroids?

Rear fangs, unlike the anterior maxillary teeth, are surrounded by sheaths that are morphologically easily distinguished from the surrounding mucosa. In the case of *C. austriaca*, these almost entirely cover the fangs, of which often only the apex remains visible (Fig. 6A). These constitute a fundamental feature in the opisthoglyphous/rear-fanged venom model, as secretions produced by the glands are conveyed from lumens into short ducts at the base of the fangs and then released through the sheaths in a low-pressure system (Zalisko and Kardong 1992; Kardong and Lavin Murcio, 1993; Jackson, 2003). Unlike front-fanged snakes, in which the secretions produced are channeled from the lumen of the gland into the hollow fangs via a longer duct, in a high-pressure system generated by compression of the glands by the *compressor glandulae* muscle (Jackson, 2003; Fry *et al*., 2012). The presence of sheaths at the posterior end of the jaws, which is generally associated with specialized fangs and a functional venom gland, represents so the first true indicator of a rear-fanged venom system (or opisthoglyphous condition) in colubroids, which can be easily identified by oral inspection (Paterna, 2024).

Regarding the venom/Duvernoy glands, future researches are undoubtedly necessary to study the composition of the secretion. To date, however, we already have some information on the glands of this species. Taub (1967) conducted histological examinations on 180 species belonging to 120 different genera, where he reported that *C. austriaca* possesses purely serous glands, similarly to other rear-fanged genera analyzed in the same study, including: *Ahaetulla*, *Boiga*, *Chrysopelea*, *Clelia*, *Hemorrhois*, *Erythrolamprus*, *Heterodon*, *Hydrodynastes*, *Malpolon*, *Oligodon*, *Philodryas*, *Psammophis*, *Psammophylax*, *Pseudoxenodon*, *Ramphiophis*, *Spalerosophis*, *Telescopus*,

and *Thelotornis*. In the second volume dedicated to venomous animals and venoms, regarding *C. austriaca* Phisalix (1922) tells us that the venom gland is very small, so much so that its weight in the largest specimens does not exceed 1 milligram in dry weight, and that they have tested its toxicity on several animals, stating that "it is very high". We report here a translated summary of the results of her tests: the dose of serum corresponding to the two glands, inoculated by intravenous injection into a rabbit (weight 1,500 gr), causes it to immediately fall into a state of torpor lasting about ten minutes. Death occurs within 15–20 minutes due to respiratory arrest. On the guinea pig, by subcutaneous injection, the action of the venom manifests itself almost immediately and death occurs due to respiratory paralysis. The extract of six glands is necessary to cause the death of an adult guinea pig (weight = 300–500 g) within 5–6 hours. A dose corresponding to 1/5 of the gland is sufficient to kill an adult sparrow in less than two hours by intramuscular injection. Immediately after inoculation into the pectoral muscle, the subject begins to show the first serious symptoms of neurovascular envenomation. By intraperitoneal injection, the green lizard (*Lacerta* genus) exhibits transient narcosis after inoculation with the extract corresponding to two glands. The green frog (*Pelophylax* genus) is more sensitive; the extract of a single gland kills it in three to four hours. The effects of *C. austriaca* secretion are similar across various types test animals and inoculation methods, and its action is distinct from that of *Vipera aspis* venom and, conversely, strongly resembles that of *Malpolon* and cobra venoms (Phisalix, 1922). We must now consider that *C. austriaca* presents an opisthoglyphous/rear-fanged condition, and that the secretion produced by the venom/Duvernoy glands is inoculated into the prey through prolonged and masticated bites in a low-pressure system (Taub, 1967; Kardong and Lavin-Murcio, 1993; Weinstein *et al*., 2011, 2013). The timing of the venom's effects is certainly different from that reported by Phisalix (1922), as the inoculation system used is more similar to that available to endoglyphous (solenoglyphous and proteroglyphous) snakes. To this we must add, however, that the inoculation of venom gland secretions in *C. austriaca* is indeed at low pressure, but continuous within a prolonged and masticated bite, and consequently the role that this venom has on preys may be crucial in the biology and ecology of this species.

Before better explaining the meaning of some terms used in the previous paragraph, we conclude this section with an important consideration on venom. We agree with what was stated in Fry *et al.* (2012), "venomous is not synonymous with dangerous to humans". As in the case of the tests carried out in the last century, and according to the prolonged bite described here, the toxic secretions of *C. austriaca* cannot be considered relevant from a medical point of view for humans, as this is functional for the subjugation of small preys, in addition to the possibility that it could be prey-specific venom, like in many other snakes (Phisalix, 1992; Minton and Rutherford Minton, 1969; Weinstein *et al*., 2011; Fry *et al*., 2012).

Opisthoglypha—rear-fanged. In this work, we feel it is necessary to discuss and clarify certain points related to the dentition model observed in *Coronella austriaca*, and the related considerations in the literature. In the following section, we intend to clarify the meaning of the terminology used and the actual condition of the smooth snake as much as possible, as an unintended consequence of our study is the reclassification of certain European taxa.

Opisthoglyphous, proteroglyphous, and solenoglyphous are the three main categories into which venomous snakes are grouped and divided (Golay *et al*., 1993; Jackson, 2003; Westeen *et al*., 2020). These three models, in their meaning, occur exclusively within the clade Caenophidia, which includes the most derived snake families. Solenoglyphous taxa mainly belong to a specific clade, the family Viperidae (Kardong, 1982; Jackson and Fritts, 1995; Grano *et al*., 2017), although due to the morphology of their fangs, the venom system present in Atractaspididae can also be considered solenglyphous (Jackson, 2003; Cleuren *et al*., 2022; Palci *et al*., 2023). Viperids have mobile, hollow fangs located at the anterior end of the maxilla, in which the venom, through the compression of the venom glands by the *compressor glandulae* muscle, is conveyed through a duct inside the fangs, then flowing into an orifice located ventromesally at their apex (Kardong and Lavin-Murcio, 1993). Proteroglyphous model is found in a monophyletic group, comprising taxa which are all included in a single family, Elapidae (Kardong, 1982; Jackson and Fritts, 1995). In this model, the venom fangs are always positioned anteriorly along the short maxilla, canaliculated, as a result of the closure of a mesial canal, but unlike solenoglyphous taxa, they are "fixed" or "less mobile" (Palci *et al*., 2023). In this model too, the secretions produced by the venom gland are conveyed into the fangs through compression of the venom gland. The solenoglyphous and proteroglyphous models both fall into the endoglyphous condition (notched inside, Golay *et al*., 1993). In the opistoglyphous, or more comprehensively "rear-fanged," model, the differences with the other models are major. The fangs, or enlarged teeth, are generally located in the posterior portion of the maxilla (with some exceptions), and are not canaliculated but generally grooved or

have other modifications and specializations suitable for venom inoculation (Young and Kardong, 1996; Fry *et al*., 2008; Young *et al*., 2011; Weinstein, 2017; Westeen *et al*., 2020). The venom glands are not surmounted by compressive muscles (with the exception of *Dispholidus* and *Mehelya*, which possess a rudimentary compressive muscle system), and do not possess the same capacity to store quantities of venom (Fry *et al*., 2012). Their secretions are therefore not expelled in one go, but are released into a confined space directly into the sheaths covering the rear fangs, which are in turn located ventrally in correspondence with the venom glands (Kardong, 1982; Kardong, 2002; Weinstein, 2017). The venom is released continuously in a low-pressure system, and inoculated through prolonged and/or masticated bites (Taub, 1967; Kardong and Lavin-Murcio, 1993; Weinstein *et al*., 2011, 2013). A further difference from the other two systems is that the opisthoglyphous model is not found in a monophyletic group, but in a macro group consisting of several snake families/clades: Colubridae, Natricidae, Dipsadidae, Homalopsidae, Pareatidae, Pseudoxenodontidae, and the Lamprophiidae clade (Vidal, 2002; Vidal and Hedges, 2002; Weinstein, 2011; Wensteen, 2020). This is because the traits present in the opisthoglyphous model constitute plesiomorphies present in the ancestors of colubriforms from which the three conditions described evolved (Zaher *et al*., 2012, 2019; Wensteen *et al*., 2020). In this vast group of snakes, considered opisthoglyphous and/or rear-fanged, different morphologies and specialization of fangs are present, which can be divided into two macro groups: the ectoglyphous taxa, snakes with open grooves, furrows, sulci or canals in the fangs (opisthoglyphous *sensu stricto*) (Golay *et al*., 1993), and the taxa that possess enlarged fangs apparently "unmodified" (e.g. *Heterodon*, *Hydrodinastes*, *Natrix*), but which may present other traits that distinguish them from the anterior maxillary teeth, such as crests and carinae (Fry *et al*., 2008; Weinstein *et al*., 2017; Paterna, 2024). Differences are also present in the shape and nature of the venom glands or Duvernoy's glands (Kochva, 1978; Kardong, 2002), where ectoglyphous species tend to have purely serous glands, while other rear-fanged forms have seromucous glands (Taub, 1967). These variables, provided they are present in a given organism, are all recognized by many authors in the opisthoglyphous model (Calori and Davanzo, 1999; Hill and Mackessy, 2000; Mackessy, 2010; Jackson Lima de Almeida *et al*., 2018; Westeen *et al*., 2020), and universally considered rear-fanged, a term to which opisthoglyphous is used as a synonym (Ditmars, 1951; Mallik *et al*., 2020; Srikanthan *et al*., 2022; Palci *et al*., 2023). This synonymy is accepted and widely used in the herpetological literature because it describes and indicates a venom condition/system (Jackson, 2003; Westeen *et al*., 2020), rather than a fang type. As evidence of this, important differences in the venom fang morphology in colubrids are found even within the same genus (Golay *et al*., 1993; Mallik *et al*., 2020).

Opisthoglypha therefore represents the most basal of the three conditions, which constitutes the paraphyletic group and system in which many taxa within the clade Colubroidea are included (Westeen *et al*., 2020), of which proteroglypha represents an "evolution", derived in Elapidae from Colubroidea (Jackson and Fritts, 1995; Fry *et al*., 2012; Figueroa *et al*., 2016). Solenoglypha is also a derivation of the ancestral rear-fanged condition (Fry *et al*., 2009; Streicher and Ruane, 2018; Zaher *et al*., 2019), which occurred at a more basal position in the evolutionary history of colubriforms, where the clade of endoglyphous snakes (Endoglyptodonta, Zaher *et al*., 2009, 2012) split from the ectoglyphous colubroids, from which all modern colubrids derive. To these three is added a fourth condition, Aglypha. This characterizes more basal alethinophidian taxa than those previously discussed, which instead belong to clades within Caenophidia (Figueroa *et al*., 2016). The term aglyphous indicates a type of tooth without sulci (*sensu stricto*), and a dental model in which maxillary teeth share the same morphology (homodonty) and posterior specialized fangs are absent (Jackson, 2003). In aglyphous snakes as boas and pythons so, not only enlarged or modified rear fangs are absent, but also venom glands, as these traits will later appear in the clade Caenophidia (Kuch *et al*., 2006; Vonk *et al*., 2008; Fry *et al*., 2012). The term aglyphous, in addition to being used primarily to refer to the most basal taxa, is also used for more derived taxa, specifically to indicate those (non-venomous) colubroids characterized by the absence of enlarged and/or modified/grooved fangs and venom/Duvernoy glands.

As recently discussed (Paterna, 2024), the dentitions of many non-front-fanged European colubroids have been poorly studied and misinterpreted to date, and specifically the buccal anatomy of European colubrines separates these snakes into two macro groups. *Coronella austriaca* falls into the first and broader of the two, which includes taxa possessing a clear and functional opisthoglyphous model characterized by: venom glands distinct from the supralabial salivary glands, sheaths covering the venom fangs, enlarged modified venom fangs, and eventual modifications in the maxillary bones such as diastemas and deviations of the bone at or near the venom fangs. This group includes the Palearctic genera *Coronella*, *Hierophis*, *Hemorrhois*, *Dolicophis*, *Macroprotodon*, and *Telescopus*, where the rear-fanged condition presents several variables in the morphology and number of fangs, and in the size of the venom glands. The second group comprises taxa that have repressed or are in the process of

repressing this condition, and which lack the previously listed traits. In Europe, this group is limited to ratsnakes, powerful constrictors of the genera *Elaphe* and *Zamenis*, and dwarf snakes of the genus *Eirenis*. The most obvious anatomical trait distinguishing the two groups is undoubtedly the presence of sheaths covering the venom fangs. This trait represents an indicator of the presence of a functional venom system, as it is linked to the presence of fangs and venom glands, and is also the trait easiest to identify during an *in vivo* inspection of a snake. The presence of any specialization in the rear maxillary fangs represents a further important symptom and indicator of a present venom system (active or in the process of repressing), as these teeth are modified to facilitate the inoculation of the venom gland's secretions. This condition in the fangs, as observed in *C. austriaca*, cannot be considered a simple heterodonty, but a selection of traits specialized by the ecology of the species from a venom model already existing in its ancestors.

Despite such relations were already discussed and demonstrated in past researches, in a recent short note by Di Nicola and Delfino (2025), the authors reject the attribution of the term "opisthoglyphous" in reference to the condition present in the western whipsnake *Hierophis viridiflavus* (Paterna, 2023b; Meier, 2024), one of the species subject to the reclassification derived from the latest studies on the buccal anatomy of European colubroids (Paterna, 2024). The authors of the cited note consider *H. viridiflavus* an aglyphous species, stating that only species possessing a mesial groove in the posterior maxillary fangs (e.g. *Malpolon monspessulanus* and *Telescopus fallax*) can be considered opisthoglyphous, excluding the western whipsnake from this category, which instead presents specialized fangs, in a very similar way to what was observed and discussed in this study in *C. austriaca*. Since we failed to find such a statement both in the literature they cited, and in the literature known to us or in dictionaries, we attribute the paternity of this consideration of the term opisthoglyphous to the two authors of the note. Di Nicola and Delfino (2025) further classify the western whipsnake as a heterodont and opisthomegadont (with enlarged posterior teeth) species, attributions that we accept, as they are morphologically correct adjectives for this species. In their analysis, which is focused exclusively on the absence of an evident mesial groove, the presence of other well-defined specializations, as sulci and furrows in the fangs, *inter alia* visible among the images they produced (Fig. 3F in Di Nicola and Delfino, 2025), is omitted. Furthermore, their work does not take into consideration the presence of the sheaths covering the venom fangs and of the venom glands, the morphology of the maxillary bones, and the phylogeny of this species (Paterna, 2023b; Paterna and Grano, 2024). Following this reasoning, this conclusion could have been extended and applied to a long list of colubroids considered opisthoglyphous (*sensu lato* and *sensu stricto*), but the article in question is structured as an attempt at a purely etymological response to the specific work of Paterna (2023b), where the western whipsnake is not reclassified exclusively on the basis of the morphology of its fangs, but on the basis of an entire venom system, which cannot be omitted. From what has been discussed, it is clear that, in addition to being incorrect, it is inapplicable to consider colubrines that possess a functional opisthoglyphous model (venom glands, sheaths, and venom fangs, especially if they present sulci, grooves, or distinct specialized traits and morphology) as aglyphous. Furthermore, we do not consider it entirely correct to use the adjective "aglyphous" for advanced snakes, even for those taxa that have repressed or are in the process of repressing the opisthoglyphous model, as colubroids derive from a "venom-fanged" ancestor, and the attribution of this term would create a potential morphological and biological synonymy with the alethinophidians most basal clades (Paterna, 2024). Given the actual presence of furrows, which makes *H. viridiflavus*, and likewise *C. austriaca*, opisthoglyphous species (both *sensu lato* and *stricto*), and given the meaning and the use of the term opisthoglyphous in the literature, we reject the classification of Di Nicola and Delfino (2025) according to which *H. viridiflavus*, and consequently other taxa such as *C. austriaca*, should still be considered aglyphous.

We report the definition of opisthoglyphous given in two key texts on the evolution of venom-delivery systems in snakes. From Jackson (2003): "opisthoglyphous (some colubrids) in which there is a posterior fang which may be enlarged or grooved; aglyphous (other colubrids) in which the posterior fang is unspecialized or nonexistent". From Fry *et al*. (2012): "On numerous independent occasions the posterior teeth have been variably enlarged (opisthodon). In lineages with such enlarged teeth, the introduction of venom into a bite wound is often facilitated by open channels, sulci or grooves along the lateral or anterolateral surfaces of the fangs (opisthoglyphous)".

In conclusion, given the enormous variability in morphology, number, and modifications present in the posterior maxillary fangs of colubroids possessing a functional venom system (Weinstein *et al*., 2017; Fry *et al*., 2012), and given the widespread synonymy between opisthoglypha and rear-fanged attributed and used for these taxa (Hill and Mackessy, 2000; Mackessy, 2010; Mallik *et al*., 2020; Westeen *et al*., 2020; Srikanthan *et al*., 2022), where the terminology opisthoglyphous (*sensu stricto* to indicate colubroids possessing grooved or furrowed fangs,

or *sensu lato* to indicate the polyphyletic group of specialized rear-fanged colubroids) may create difficulties of application, we recommend using the term rear-fanged, which is independently correct to indicate the venom model in question.

Comparation with other rear-fanged taxa. As previously mentioned, rear-fanged colubroids represent a paraphyletic group that shares a venom model inherited from a common ancestor (Fry *et al*., 2008; Zaher *et al*., 2012, 2019). In addition to differences in venom gland composition, the various evolutionary lineages and specializations of individual species have generated multiple variations in the morphology of the maxillae and rear fangs (Wenstein *et al*., 2011). Among species considered opisthoglyphous in the literature, the number of fangs and their morphology includes significant diversity even within the same clade, genus, and species (Jackson and Fritts, 1995; Weinstein *et al*., 2011). To better understand where *Coronella austriaca* falls within this enormous clade, we attempt to categorize three macro-groups here, based on references already used in the literature, including the best-known taxa in which the various traits are most evident. However, it must be clarified that, today, following the latest studies, we have understood that the majority of colubrines, specifically the most basal clades, are rear-fanged, but we currently know the morphology of the fangs of only a few taxa among those with an opisthoglyphous venom system, as such anatomical studies are still rare in the literature. We begin with those taxa that have posterior fangs characterized by a defined longitudinal groove ("group d" in Jackson and Fritts, 1995; "group c" in Young and Kardong, 1996). Among these, psammophiids, the colubroids phylogenetically closest to elapids, appear first. These have mesially invaginated fangs, and their bites can cause consequences in humans (Weinstein *et al*., 2011; Ballouard *et al*., 2022; Koua *et al*., 2022). Colubrids that share this fang morphology include, for example, the arboreal Ahaetullini. Specifically, the genus *Ahaetulla* has two modified fangs per maxilla, the general morphology of which and that of the grooves varies from species to species (Mallik *et al*., 2020). In the Colubrinae subfamily there are species that possess a more important venom, of which the bite can be fatal in humans, belonging to the genera *Dispholidus* and *Thelotornis* (Weinstein, 2017). Also, among Colubrinae, grooved fangs are widespread in the cat snake clade, where the number of fangs and the degree of modification also vary from species to species.

There is also a significant number of opisthoglyphous colubroids that have fangs with a more complex and varied morphology, characterized by both depressions and ridges, which create open furrows ("group c" in Jackson and Fritts, 1995; "group b" in Young and Kardong, 1996), and in which *C. austriaca* can be included. This fang model, among European colubrines is widespread in the whipsnake group, where the number of fangs and the type of modification of the grooves and ridges vary according to genus and species, and the consequences of their bites on humans are known (Weinstein *et al*., 2011; Paterna and Grano, 2024; Paterna, 2024). Other colubroid genera belonging to this group are *Erythrolamprus*, *Oxybelis* and *Sonora* (Jackson and Fritts, 1995; Sánchez *et al*., 2019).

Some colubroids considered opisthoglyphous, however, do not have fangs with longitudinal depressions such as sulci, grooves, or furrows, but rather enlarged fangs with longitudinal distal and mesial carinae ("group b" in Jackson and Fritts, 1995). As with other groups belonging to the other categories, in snakes that share this fang morphology, variations in the number of teeth and the degree of extension of the carinae vary from species even within the same genus, as is the case for *Lycodon* and *Dinodon* (Guo *et al*., 2013). Among these, there are species, such as the dipsadid *Helicops modestus*, in which the posterior maxillary fangs are adjacent to each other or even overlapping, and it is hypothesized that these may be used as a single unit in which the contact between the two teeth acts as a channel for the inoculation of venom into the wound (Knox and Jackson, 2010; Oliveira *et al*., 2016). In many taxa, however, such as *Leptophis ahaetulla*, the fangs present a prominent distal carina (Sánchez *et al*., 2018). The presence of a developed distal carina appears to be a widespread trait among taxa that have a batrachophagous or piscivorous diet, and in the specific case of European colubroids it is found in natricids, as documented in *Natrix helvetica* (Paterna, 2023b, 2024). Precisely in the genus *Natrix*, which bites on extremely rare occasions, reactions following the bite in humans have been documented, demonstrating the toxicity of their bite, and the ability to inoculate mixed oral secretions (Gardner-Thorpe, 1967; Satora, 2004; GläßerTrobisch and Trobisch, 2008). It is important to note that, still in the natricid family, the bite of the genus *Rhabdophis* causes significant consequences in humans, with documented cases of death (Nakayama *et al*., 1973; Ogawa and Sawai, 1986; Kikuchi *et al*., 1987), despite the fact that the fangs of these animals are not grooved, but rather keeled (Kane *et al*., 2023). Significant clinical consequences following the bite of other ungrooved rear-fanged colubroids are documented in dipsadids as *Heterodon nasicus* and *Hydrodynastes gigas* (Weinstein, 2017).

We therefore see how the effectiveness and functionality of the opisthoglyphous venom system shared by rear-fanged colubroids does not appear to be linked to a specific morphology of the fang or to modifications intended in

terms of indentations or reliefs, since all categories represent functional dental models belonging to the same root, even including cases of death and serious symptoms in humans. In rear-fanged snakes, the secretions produced by the venom gland are released around the tooth in a low-pressure system, and the inoculation of the venom is achieved only through prolonged and/or repeated chewing movements (Zalisko and Kardong, 1992; Kardong and Lavin Murcio, 1993; Jackson, 2003). In the bite of rear-fanged snakes, like a tattoo, the liquid is accompanied into the wound, differently from the bite of front-fanged snakes, in which, like an injection, the inoculation is canaliculated and at high pressure. The functionality of the different fang patterns and their belonging to the same venom pattern (opisthoglyphous) is further supported by the work of Jackson and Fritts (1995), in which they suggest that not only the origin of the proteroglyphous dentition may come from the opisthoglyphous model, but also that the distal and mesial ridges and carinae of the posterior maxillary fangs typical of blade-fanged taxa "evolved" into the grooved fangs, thus justifying the "intermediate" shapes and adaptations such as those present in *C. austriaca*.

Final considerations. This study provides new data on the cephalic anatomy of the smooth snake *Coronella austriaca*, in which we have recognized some osteological traits exhibiting isometric growth, and others exhibiting significant ontogeny. In addition to broadening our understanding of the species' biology, documenting the ontogeny of certain traits is also important for interpreting the fossil record, where, particularly when dealing with isolated or fragmentary remains, morphological differences attributed to distinct taxa may instead reflect different ontogenetic stages of the same species. The presence of pits in the parietal shields and their correspondence with parietal foramina located near the epiphysis has been confirmed, as well as the presence of venom glands and enlarged posterior maxillary fangs, whose modifications we have described in detail for the first time. Based on our results and what has been previously described in the literature, we can state that *C. austriaca* possesses an active venom model, composed of serous venom glands (Taub, 1967), whose serum has been shown to have significant and lethal consequences on small vertebrates (Phisalix, 1922), sheaths covering the posterior maxillary fangs, modified enlarged fangs with lingual furrows, and a distal carina. The size of the posterior fangs and the entire maxillary bone are subject to isometric growth, characterized by a progressive transverse thickening of all teeth. Sheaths and posterior fangs have also been identified in the sister species *Coronella girondica*, traits shared with most basal European colubrines. In light of what has been discussed and the results presented, we can therefore consider the smooth snake an opisthoglyphous/rear-fanged species. It is important for us to clarify that, except for the inevitable reclassification of this snake, we recommend not changing the consideration we have always had of this species, which, given its nature and size, represents absolutely no threat to humans. At most, we advise not underestimating the prolonged bites of colubrids that exhibit the traits discussed here. Venomous does not mean dangerous to humans (Fry *et al*., 2012).

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