

Vertebral morphology and intracolumnar variation of the iconic and bizarre viperid snake *Pseudocerastes urarachnoides* (Serpentes, Viperidae)

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Abstract

We document in detail the vertebral morphology of the viperid *Pseudocerastes urarachnoides*, a snake from the Middle East that is famous for its extreme tail modifications with bizarre spider-like luring appendages and its caudal luring behavior that enables it to successfully prey on birds. With the aid of micro-computed tomography scanning on the holotype specimen of *P. urarachnoides*, we focus on the intracolumnar variation across the whole vertebral column. Interesting morphological features of the vertebrae of this species are highlighted in comparison to other viperids, particularly at the caudal vertebral portion; nevertheless, there is no evidence of any skeletal element underlying the bizarre spider-like luring appendages of the tail of *P. urarachnoides*. A discussion on the caudal lure and its bizarre tail scales for this peculiar species is provided.

KEYWORDS

caudal luring, tail scales, vertebrae, vipers, μ CT scanning

1 | INTRODUCTION

Vipers (Viperidae) constitute a fascinating group of snakes that includes some of the most medicinally important vertebrate taxa worldwide (Schuett et al., 2002; Wüster et al., 2008). They represent a moderately diverse lineage, with more than 300 extant species, and have achieved an almost global distribution, encompassing all continents except for Australia and Antarctica (Alencar et al., 2018; David & Ineich, 1999; Marx & Rabb, 1965; Wüster et al., 2008). Among several other distinctive features, vipers are mainly characterized by their short and mobile maxillae with very long (so-called solenoglyphous)

and rotating fangs, which they use to inject venom (Cundall, 2011; Holding et al., 2022; Jackson, 2003; Kardong, 1979; Kuch et al., 2006). They also further possess a spectacular range of unique morphologies, locomotion, ecology, reproduction, physiology, and life history strategies (Akbarpour & Pouyani, 2023; Alencar et al., 2018; Allen, 1949; Allf et al., 2016; Barrio-Amorós et al., 2020; Campbell & Brodie Jr, 1992; Carpenter & Gillingham, 1990; Cleuren et al., 2025; Collet & Trape, 2020; Farrell et al., 2011; Greene et al., 2002; Heatwole & Davison, 1976; Henderson, 1970; Ineich et al., 2006; Ineich & Tellier, 1992; Kauffeld, 1943; Lynch, 2009; Mallow et al., 2003; Marx & Rabb, 1965;

Meik & Pires-da Silva, 2009; Parellada & Santos, 2002; Reiserer & Schuett, 2016; Schuett et al., 2002; Šmíd & Tolley, 2019; Wharton, 1960). Due to their venomous nature, as well as their broad geographic distribution and frequent encounters with humans, vipers are among the most iconic snakes worldwide (Alencar et al., 2016; Schuett et al., 2002; Wüster et al., 2008). Indeed, viperid venom, which in many species can be lethal to humans, has given to these snakes their mostly undeserved but “notorious” reputation, evoking fear, as well as legends and misconceptions across human societies over the centuries (Sauvage, 1885; Schuett et al., 2002; Wüster et al., 2008). Even in scientific literature, group names like Thanatophides (i.e., meaning “death snakes” in Greek) have been applied to Viperidae (e.g., Duméril et al., 1854; Duméril & Bibron, 1844; Sauvage, 1885), while some genera have equally negative or intimidating etymologies (e.g., the large Neotropical genus *Lachesis* Daudin, 1803a, named after one of the three “Fates” in Greek mythology, responsible for determining the life span of humans).

Accordingly, vipers have been the focus of extensive interest and numerous studies already since Antiquity, including pharmaceutical and medicinal research. However, even though much scientific advances in our knowledge have been made, certain aspects surrounding vipers remain elusive. One of the most inadequately known aspect of vipers is their vertebral morphology. Indeed, even though there have been important studies on their cranial morphology (e.g., Boulenger, 1896; Brattstorm, 1964; Carrasco et al., 2009; Dowling & Duellman, 1978; FitzSimons, 1962; Ivanov, 1999; Kramer, 1980; von Méhely, 1911; Mirza et al., 2023; Peyer, 1912; Qiu et al., 2023; Sauvage, 1885; Seghetti et al., 2021; Shi et al., 2018; Snetkov & Orlov, 2017; Syromyatnikova & Lopatin, 2024; Troschel, 1861; Underwood, 1979; Venczel, 2000; Wagner, 1841), it is characteristic that among the hundreds of known extant species of vipers, only for a few has the vertebral morphology been documented. Moreover, even for these studied species, research has been usually confined to just a few vertebrae (Dowling & Duellman, 1978; Georgalis et al., 2016; Ikeda, 2007; Kramer, 1980; Nakamura et al., 2013; Shi et al., 2025; Snetkov & Orlov, 2017; Szyndlar, 1991; Szyndlar & Rage, 1999; Wagner, 1841; Walker, 2003; Zaher et al., 2019). It is therefore a fact that only a limited number of species have comprehensive and thorough investigations of their vertebral morphology and intracolumnar variation (e.g., Chippaux, 1986; Szyndlar, 1984; Szyndlar & Rage, 1999; Thireau, 1967; Węgrzyn et al., 2025).

This scarce knowledge on the vertebral morphology of vipers directly affects palaeontological research on the group, as the fossil record of snakes is predominantly represented by isolated vertebrae and therefore, these

skeletal elements mainly constitute the basis of the taxonomy of extinct taxa (Auffenberg, 1963; Georgalis et al., 2025; Head et al., 2022; Rage, 1984; Smith & Georgalis, 2022). As a consequence, this inevitably leaves major unanswered questions about the early evolutionary history of the group; molecular studies on divergence date estimates have suggested that viperids appeared already during the Paleogene (e.g., Alencar et al., 2016; Šmíd & Tolley, 2019; Wüster et al., 2008; Zaher et al., 2019), however, their oldest reliable fossil occurrences are only at the Early Miocene (Ivanov, 2022; Kuch et al., 2006; Szyndlar & Rage, 1999, 2002). Moreover, despite the fact that several extinct viper taxa have been named (e.g., Bolkay, 1913; Rage, 1984; Szyndlar, 1987, 1988, 1991; Szyndlar & Rage, 2002), including impressive gigantic forms (Georgalis et al., 2016; Owen, 1857), the interrelationships of most of these fossil species within Viperidae are largely unknown.

Pseudocerastes urarachnoides Bostanchi et al., 2006, commonly known as the Iranian Spider-Tailed Horned Viper, represents one of the most peculiar vipers with respect to both behavior and morphology (Figure 1). This endemic to Iran taxon possesses a highly complex tail morphology, which forms a knob-like structure (Bostanchi et al., 2006). This distinctive, spider-like, structure on the tail tip of *P. urarachnoides* represents an extreme adaptation of a viper species to prey capture via an astonishing caudal luring process; the snake tricks birds by moving nothing but its tail in a way that greatly resembles an arachnid crawling across the rocks, causing the bird to approach in search of meal and allowing the snake to then strike at the bird and if successful, consume it (Fathinia et al., 2015; Martínez del Marmol et al., 2016). Notably, such extreme tail morphology is absent (or at least not present to that extent) in any other snakes, including the two other known species of the genus *Pseudocerastes* Boulenger, 1896, that is, *Pseudocerastes fieldi* Schmidt, 1930 and the type species, *Pseudocerastes persicus* (Duméril et al., 1854). Even though it obviously represents a unique and charismatic taxon, and has even recently been the focus of population-genetic studies (Fathinia et al., 2026), the skeletal anatomy of *P. urarachnoides* has never been investigated in detail, apart from a preliminary X-ray image in the original publication of Bostanchi et al. (2006) and a cursory figuring of a few vertebrae in Węgrzyn et al. (2025).

Here we investigate, with the aid of micro-computed tomography (μ CT) scanning, the vertebral morphology and intracolumnar variation of *Pseudocerastes urarachnoides*, based on investigation of its holotype specimen (Field Museum of Natural History, Chicago [FMNH] 170929; Figure 1). We emphasize and focus particularly



FIGURE 1 Photograph of the holotype specimen (FMNH 170929) of *Pseudocerastes urarachnoides*. (a) Photograph of the whole specimen; (b, c) close-up photographs of the tail tip.

on the intracolumnar variation, presenting many vertebrae from all portions of the column (atlas, axis, trunk, cloacal, and caudal). We anticipate that this comprehensive understanding of the vertebral morphology of *P. urarachnoides* will eventually facilitate future taxonomic identifications of fossil viperid vertebrae from the Middle East and the broader area.

2 | MATERIALS AND METHODS

The specimen FMNH 170929 (Figure 1) studied herein is the holotype of *Pseudocerastes urarachnoides* and it is permanently curated at the collections of the FMNH. It was collected by the Field Museum's Second Street Expedition to Iran in 1968 but only identified as a new and

distinct species in 2006, originally being thought to be an aberrant version of *P. persicus* (see Bostanchi et al., 2006).

Micro-computed tomography (μ CT) scanning was performed at the Field Museum XCT Lab (RRID: SCR_026255) using the lab's North Star Imaging (NSI) X25 scanner, which is equipped with a 150 kV Hamamatsu microfocus source and a Varex 2520DX cesium detector. The scan was executed as a helical scan (NSI Vortex), with the following settings: kV = 80; μ A = 500; voxel size = 59.24 μ m; focal spot = 50 μ m; frames per second = 10.5; frames averaged = 2; projections = 3848; filter = 0.13 mm Cu; scan duration = 44 min 18 s. Scan data is available at the public repository of Morphosource (Project "Vertebral morphology of the viperid snake *Pseudocerastes urarachnoides*" [<https://www.morphosource.org/projects/000858142?locale=en>]).

Segmentation of the μ CT files was done using open source software 3D Slicer (Fedorov et al., 2012). All the measurements were done on the 3D models via usage of Markups module in 3D Slicer or in the open source program ImageJ (Schneider et al., 2012).

Descriptions and measurements of snake vertebrae follow Georgalis et al. (2021) and Szyndlar and Georgalis (2023). Abbreviations inside the figures with respect to the position of the vertebrae in the column follow Szyndlar and Georgalis (2023), with V, S, and C (followed by a number) indicating the successive serial number of a trunk, cloacal, or caudal vertebra, respectively in the column (e.g., V 10 means tenth trunk vertebra; S 1 means first cloacal vertebra; C 2 means second caudal vertebra). Last T indicates the last trunk vertebra.

Comparative skeletal material of other viper species was studied at the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków (ISEA), the Hungarian Natural History Museum, Budapest (HNHM), the Massimo Delfino Herpetological Collection, Department of Earth Sciences, University of Torino (MGPT-MDHC), the Museo Nacional de Ciencias Naturales, Madrid (MNCN), the Muséum national d'Histoire naturelle, Paris (MNHN), and the Naturhistorisches Museum Wien, Vienna (NHMW). Figured 3D images of other snake species are based on additional μ CT data acquired from the online repository of Morphosource (<https://www.morphosource.org/>) through the oVert project (see Blackburn et al., 2024). These examined specimens include the viperids *Cerastes vipera* (Linnaeus, 1758) (UF:Herp:14922 [Media 000080424, ark:/87602/m4/M80424]) and *Eristicophis macmahoni* Alcock & Finn, 1897 (UF:Herp:70650 [Media 000080421, ark:/87602/m4/M80421]), plus the acrochordid *Acrochordus granulatus* (Schneider, 1799) (UF:Herp:87078 [Media 000407755, ark:/87602/m4/407755]). Additionally, specimens of *Cerastes cerastes* (Linnaeus, 1758) (UF:Herp:13986 [Media 000036975, ark:/87602/m4/M36975]), *Crotalus intermedius* Troschel in Müller, 1865 (UF:Herp:52552 [Media 000445149, ark:/87602/m4/445149]), and *Crotalus ruber* Cope, 1892 (UF:Herp:72544 [Media 000445163, ark:/87602/m4/445163]) were examined for additional measurements presented in Table 2.

2.1 | Institutional abbreviations

FMNH, Field Museum of Natural History, Chicago, USA; HNHM, Hungarian Natural History Museum, Budapest, Hungary; ISEA, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland; MGPT-MDHC, Massimo Delfino Herpetological Collection, Department of Earth Sciences, University of Torino, Italy; MNCN, Museo Nacional de Ciencias Naturales,

Madrid, Spain; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; RBINS, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; UF Herp, Florida Museum of Natural History, Herpetology collection, Gainesville, USA.

3 | DESCRIPTION

The skeleton of the holotype (FMNH 170929) of *Pseudocerastes urarachnoides* comprises a skull (which is, however, heavily crushed and with some cranial elements disarticulated or even missing) and the postcranial portion which includes in total 183 vertebrae plus a final fusion, among which there is the atlas, axis, 145 trunk, 4 cloacal, and 32 caudal vertebrae (plus a final fusion succeeding the posteriormost caudal vertebra). As typical for snakes, the first pair of the corresponding ribs is present at the level of the third vertebra (V 3; Szyndlar & Georgalis, 2023). The ribs of *P. urarachnoides* terminate in U-shaped, longer than wide, costal cartilages; such morphology has been reported in other members of Viperidae (Hardaway & Williams, 1976). Details of measurements of selected vertebrae from throughout the vertebral column are presented in Table 1.

3.1 | Atlas-axis complex

The atlas is composed of two halves of the neural arch, connected dorsally by a suture, and a free intercentrum (Figure 2a–e). In lateral view, the dorsoposterior process of the atlas is short though it possesses a wide base. These processes are located below the dorsal margin of the neural arch and do not extend beyond its height. In contrast, the posterior process of the atlas is more strongly developed, longer, and acuminate. The first intercentrum displays an hourglass shape when seen in anterior view. Ventrally, its anterior tubercle bifurcates into two antero-laterally oriented projections.

The neural spine of the axis is triangular, relatively low, and acuminate (Figure 2f–j). In lateral view, the neural spine commences abruptly, far posterior to the anterior margin of the neural arch, while it overhangs posteriorly. A zygosphenes, prezygapophyses, and a cotyle are absent. Instead of the cotyle, there is a conical odontoid process, fused to the vertebral centrum and to the second intercentrum without any visible suture. More posteriorly, the transverse processes of the axis are short and triangular. Postzygapophyses and a zygantrum are present but somewhat reduced; articular facets of the former are ovoid. The condyle is circular, but likewise underdeveloped. The second intercentrum (anterior

TABLE 1 Measurements of selected trunk (V), cloacal (S), and caudal (C) vertebrae of *Pseudocerastes urarachnoides* (holotype FMNH 170929).

Vertebral position	Centrum length (CL) (in mm)	Neural arch width (NAW) (in mm)	Ratio of centrum length to neural arch width (CL/NAW)	Distance between the distal edges of the postzygapophyses (PO-PO) (in mm)	Neural arch height (NAH) (in mm)	Vaulting ratio (sensu Georgalis et al., 2021)
V 3	2.38	2.49	0.95	3.81	1.26	0.66
V 4	2.67	2.38	1.12	3.97	1.12	0.56
V 53	4.23	4.48	0.94	8.34	1.04	0.25
V 89	4.48	4.44	1.01	8.26	0.94	0.23
V 110	4.16	3.66	1.14	6.79	0.74	0.22
V 140	3.24	2.31	1.41	4.18	0.52	0.25
Penultimate trunk (V 144)	2.89	2.22	1.30	3.76	0.74	0.39
Last trunk (V 145)	3.04	2.16	1.41	3.47	0.53	0.30
S 1 (V 146)	3.00	2.08	1.44	3.31	0.47	0.28
C 1 (V 150)	2.34	1.97	1.19	2.98	0.62	0.42
C 2 (V 151)	2.54	1.88	1.35	2.84	0.57	0.40
C 11 (V 160)	1.98	1.46	1.36	2.13	0.48	0.45

hypapophysis) is completely fused to the axis and is rectangular in shape. The posterior hypapophysis is more elongate and more pointed, with its distal termination extending far posteriorly from the condyle; however, this posterior inclination appearance may be artificial, as examination of the μ CT data indicates a breakage at its base (a crack is visible in lateral and dorsal views of the axis).

3.2 | Anterior trunk vertebrae

In the first few anterior trunk vertebrae (Figure 2k–t), the neural spine is very slender, tall, and distinctly posteriorly inclined in lateral view, while it is developed solely to the posterior third of the neural arch. The hypapophysis is also rather slender and dorsoventrally high and posteriorly inclined, with its distal termination situated posteriorly from the condyle. Other features of these very first anterior trunk vertebrae are the very small prezygapophyses in dorsal view and the very slender and arched zygosphenes in anterior view. Subsequent anterior trunk vertebrae possess anteroposteriorly longer neural spines, relatively thicker hypapophyses, and larger prezygapophyses.

3.3 | Mid-trunk vertebrae

Mid-trunk vertebrae (Figures 3, 4) have a much wider centrum compared to the preceding vertebrae and are

characterized by a neural spine that is dorsoventrally moderately high and anteroposteriorly elongated, running across the whole midline of the neural arch. The zygosphenes are relatively straight and moderately thin in anterior view, while in dorsal view, they possess two lateral lobes and occasionally also a median lobe. The prezygapophyses face anterolaterally in dorsal view, while they are slightly dorsally inclined in anterior view. The prezygapophyseal articular facets are massive and elongated. Prezygapophyseal accessory processes are present but are not projecting well beyond the distal edge of the prezygapophyseal articular facets. The interzygapophyseal constriction is very deep. The posterior median notch of the neural arch is moderately shallow. The cotyle is large and slightly elliptical; the condyle is almost circular in shape. The centrum is rather wide. The paradiapophyses are divided into distinct diapophyses and parapophyses; they are facing anteroventrally in lateral view, with their distal termination exceeding well below the level of the ventral lip of the cotyle. The hypapophysis is rather elongated (though not to the same extent as the anteriormost trunk vertebrae) and is projecting posteroventrally in lateral view. In the transition between mid- and posterior trunk region (Figure 4f–j), the neural spine and the hypapophysis become gradually shorter and the neural arch becomes more depressed. In these vertebrae also, the anterior margin of the neural spine slightly overhangs anteriorly.

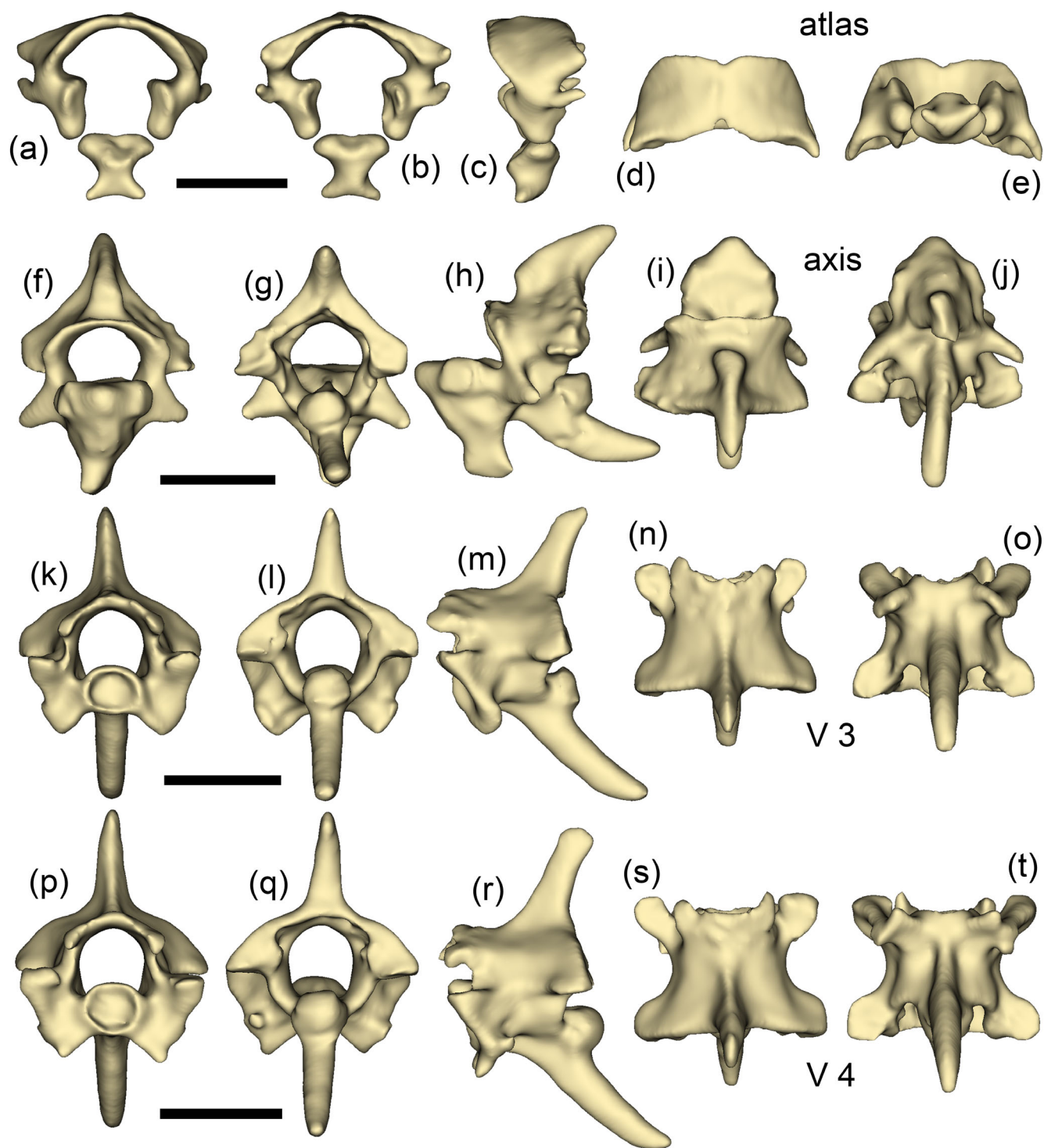


FIGURE 2 Atlas-axis and anteriormost trunk vertebrae of *Pseudocerastes urarachnoides* (holotype FMNH 170929). (a–e) Atlas in anterior (a), posterior (b), left lateral (c), dorsal (d), and ventral (e) views; (f–j) axis in anterior (f), posterior (g), left lateral (h), dorsal (i), and ventral (j) views; (k–o) V 3 in anterior (k), posterior (l), left lateral (m), dorsal (n), and ventral (o) views; (p–t) V 4 in anterior (p), posterior (q), left lateral (r), dorsal (s), and ventral (t) views. Scale bars equal 2.5 mm.

3.4 | Posterior trunk vertebrae

The trend observed in the above-mentioned mid- to posterior trunk vertebral transition in regards to

decreasing heights of the neural spine and hypapophyses continues also toward the posterior trunk vertebrae. Indeed, in these vertebrae, the neural spine gradually becomes even shorter in lateral view, while it

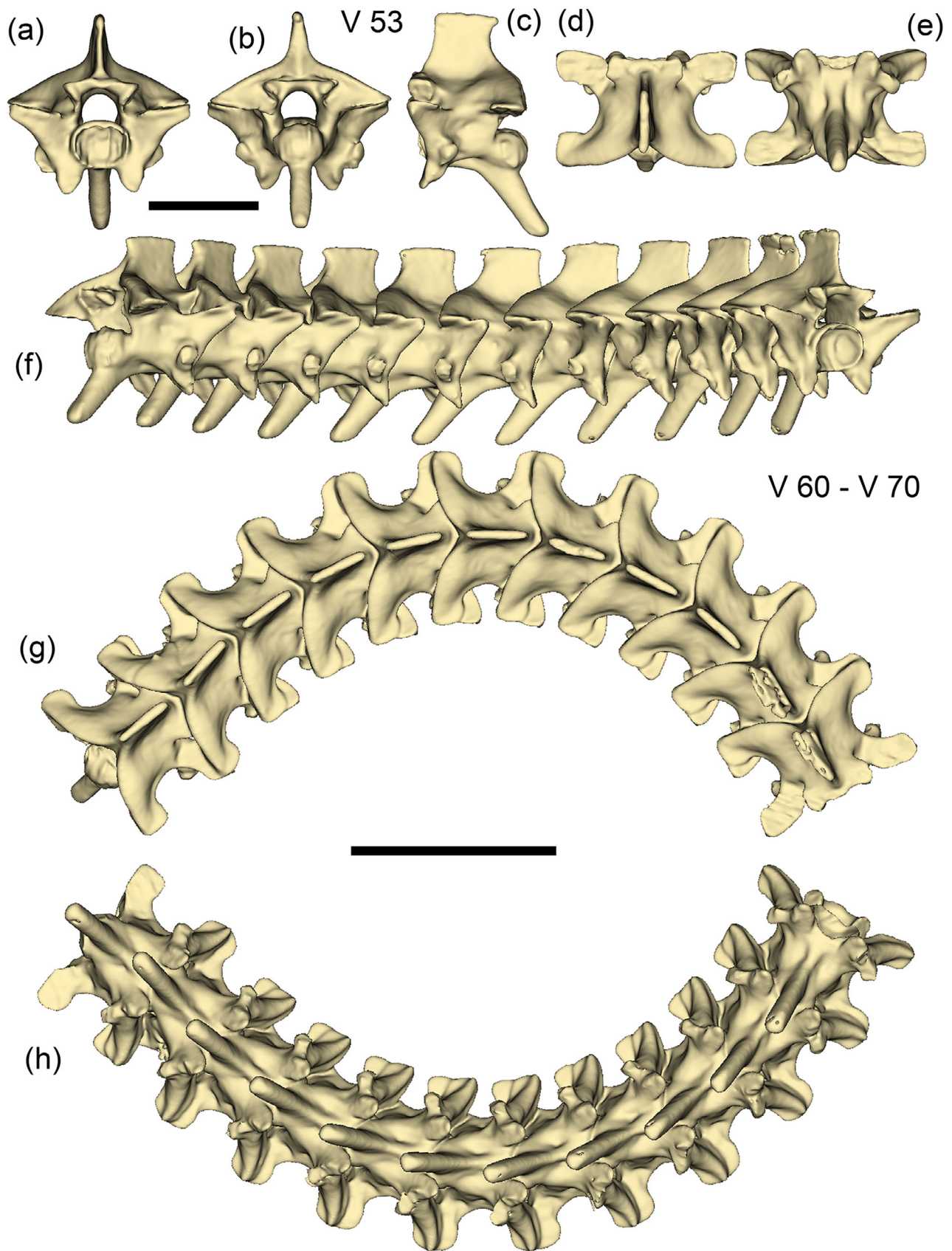


FIGURE 3 Mid-trunk vertebrae of *Pseudocerastes urarachnoides* (holotype FMNH 170929). (a–e) V 53 in anterior (a), posterior (b), left lateral (c), dorsal (d), and ventral (e) views; (f–h) string of articulated vertebrae V 60–V 70 in right lateral (f), dorsal (g), and ventral (h) views. Scale bars equal 5 mm (a–e) and 10 mm (f–h).

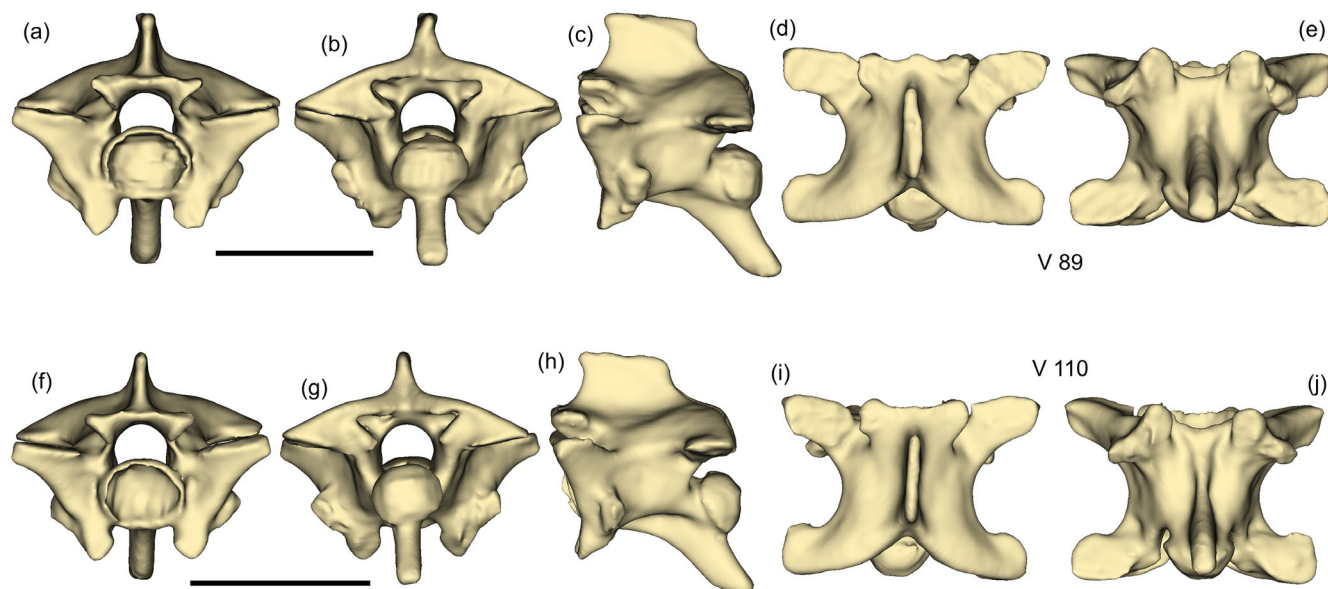


FIGURE 4 Mid-trunk vertebrae of *Pseudocerastes urarachnoides* (holotype FMNH 170929). (a–e) V 89 in anterior (a), posterior (b), left lateral (c), dorsal (d), and ventral (e) views; (f–j) V 110 in anterior (f), posterior (g), left lateral (h), dorsal (i), and ventral (j) views. Scale bars equal 5 mm.

still keeps the slight anterior overhanging of its anterior margin (Figure 5). The hypapophysis, in lateral view, becomes shorter, thinner, and projects posteriorly, with its distal tip extending far posteriorly from the condyle. The centrum is narrower than preceding mid-trunk vertebrae. Other anatomical structures are more or less similar compared to the preceding vertebrae. Slightly before the trunk-cloacal transition, in the posteriormost two trunk vertebrae (penultimate trunk [V 144] and ultimate trunk [V 145]; Figure 6), the neural spine becomes very short in lateral view; it still crosses almost the whole midline of the centrum in dorsal view. The hypapophysis in these two vertebrae possesses a rather distinctive shape in lateral view, being broad and projecting ventrally.

3.5 | Cloacal vertebrae

FMNH 170929 possesses four cloacal vertebrae (Figure 7). As typical for snake cloacal vertebrae, the major differentiation of these vertebrae from the preceding posteriormost ones is the presence of two pairs of lymphapophyses instead of paradiapophyses. However, an atypical aspect is that the broad hypapophysis of the posteriormost trunk vertebrae has its ventral margin strongly bifurcated in ventral view (i.e., “quasi-haemapophyses” sensu Szyndlar & Georgalis (2023) are present, that are fused in a “hypapophysis-like” base).

3.6 | Caudal vertebrae

Thirty-two caudal vertebrae plus a final fusion are present in the skeleton of FMNH 170929 (Figure 8). Their major differentiation from the preceding cloacal vertebrae is the presence of pleurapophyses instead of lymphapophyses. The first caudal vertebra (C 1) has somewhat bifurcated pleurapophyses. The succeeding second caudal vertebra though has a more typical morphology, with no sign of bifurcation in its pleurapophyses (Figure 8). Pleurapophyses progressively become tiny toward the posterior caudal vertebrae. Haemapophyses are present in all caudal vertebrae (Figures 8–9). An interesting feature is that the haemapophyses initially commence in the anterior caudal vertebrae as a kind of bifurcation of a thick hypapophysis; this bifurcation continues toward the mid-caudal vertebrae, where also the haemapophyses are fused not directly in the centrum but on a “hypapophysis-like” base. In the more posterior caudal vertebrae, this bifurcation fades and in fact the posteriormost caudal vertebrae possess only a short “hypapophysis-like” knob (Figure 9). As such, the transitional morphology of the haemapophyses observed in the cloacal vertebrae is also present in the whole tail. The skeletal portion of the tail eventually terminates with a final fusion of vertebrae. Finally, there is no evidence of any skeletal element underlying the bizarre spider-like luring appendages (the “legs”) of the tail of *Pseudocerastes urarachnoides*.

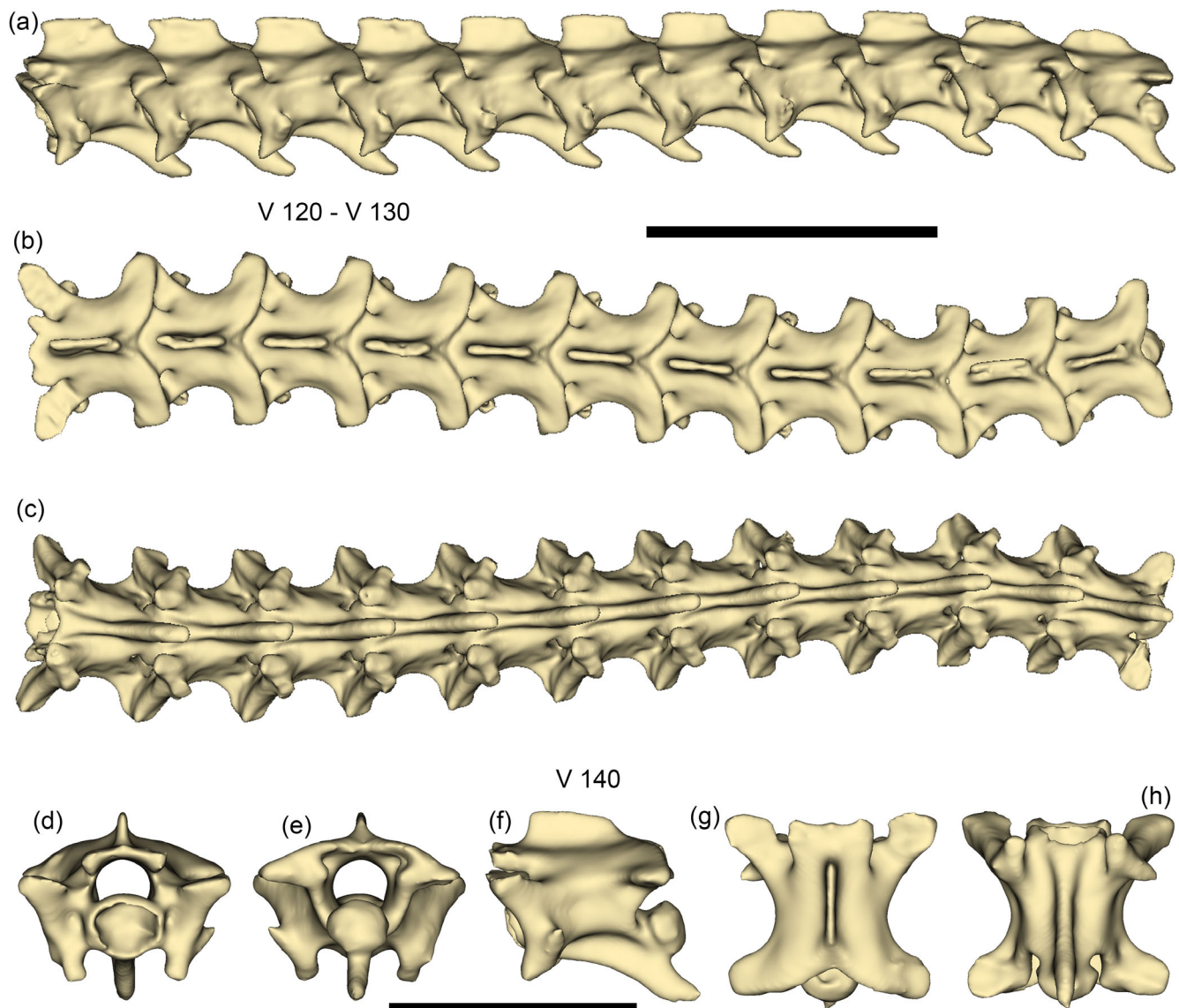


FIGURE 5 Posterior trunk vertebrae of *Pseudocerastes urarachnoides* (holotype FMNH 170929). (a–c) String of articulated vertebrae V 120–V 130 in left lateral (a), dorsal (b), and ventral (c) views; (d–h) V 140 in anterior (d), posterior (e), left lateral (f), dorsal (g), and ventral (h) views. Scale bars equal 10 mm (a–c) and 5 mm (d–h).

4 | DISCUSSION

4.1 | Vertebral morphology of *Pseudocerastes* and the homogeneous vertebral morphology of viperids

Despite being known in the scientific community for only 20 years, due to its unique and bizarre spider-like tail tip appendages, *Pseudocerastes urarachnoides* is one of the most fascinating and iconic extant viperid species. According to phylogenetic analyses, *Pseudocerastes*, along with the southern Asian *Eristicophis* Alcock & Finn, 1897, is considered to be the sister group of “European vipers” (i.e., the “*Vipera aspis* complex” and the “*Vipera*

berus complex”) (Šmíd & Tolley, 2019; Wüster et al., 2008), therefore holding potentially a key role in comprehending the evolution of Eurasian viperines. Nevertheless, many aspects of its external morphology, internal anatomy, and, especially, the skeleton of *Pseudocerastes* remain totally obscure.

We here assess the vertebral morphology and intracolumnar variation of *Pseudocerastes urarachnoides*, in an attempt to retrieve important features that might be eventually applied as diagnostic for the species or the genus *Pseudocerastes* and facilitate taxonomic identifications. Viperid trunk vertebrae are characterized by a combination of diagnostic features, such as a relatively anteroposteriorly short centrum, the presence of distinct straight

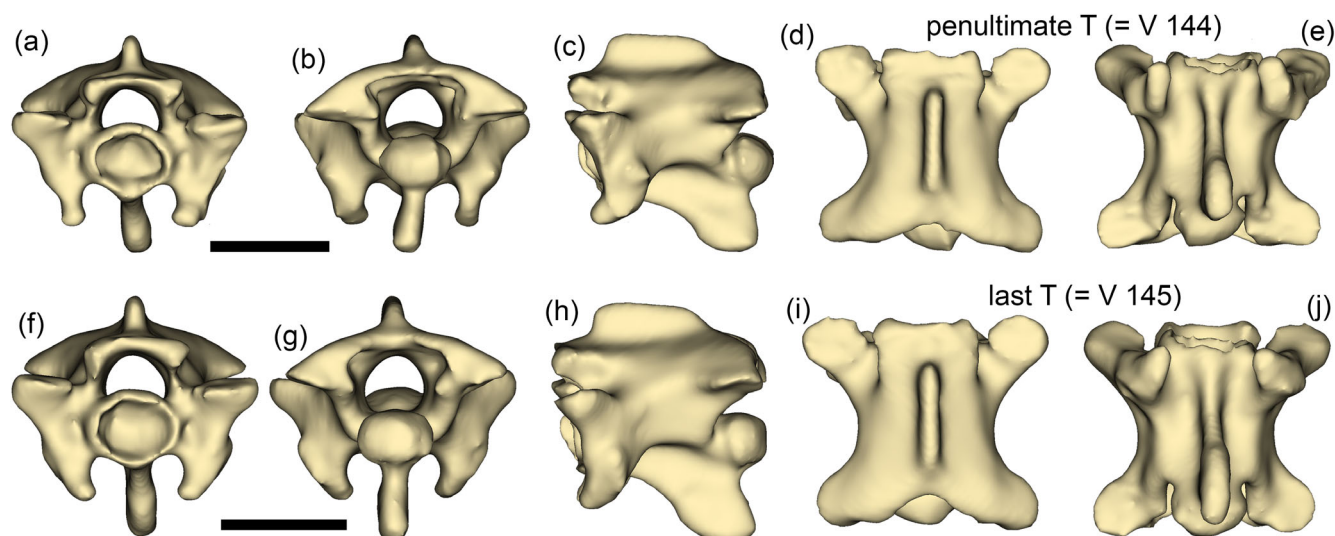


FIGURE 6 Posteriormost trunk vertebrae of *Pseudocerastes urarachnoides* (holotype FMNH 170929). (a–e) Penultimate (V 144) trunk vertebra in anterior (a), posterior (b), left lateral (c), dorsal (d), and ventral (e) views; (f–j) last (V 145) trunk vertebra in anterior (f), posterior (g), left lateral (h), dorsal (i), and ventral (j) views. Scale bars equal 2 mm.

hypapophyses throughout the trunk vertebral column, a depressed neural arch, long and anteroventrally directed parapophyseal processes, and a robust cotyle and condyle (see Szyndlar, 1984, 1991; Walker, 2003; Węgrzyn et al., 2025; Zaher et al., 2019). Nevertheless, even though identification to the family level can be relatively straightforward, distinction among the different genera and species, or even among the known viperid subfamilies, is a rather challenging task (Georgalis et al., 2016; Szyndlar, 1991; Szyndlar & Rage, 1999, 2002; Węgrzyn et al., 2025). This frustrating fact arises due to the relative homogeneity of the viperid vertebrae across different known species but also due to our currently scarce knowledge (or total absence of knowledge) for most extant viperid taxa.

Trunk vertebrae of *Pseudocerastes urarachnoides* are characterized by a relatively anteroposteriorly short and laterally wide centrum, zygosphenes that are thin (in anterior view) and trilobed (in dorsal view), deep interzygapophyseal constriction, short prezygapophyseal accessory processes, a slender hypapophysis (that becomes progressively shorter toward the posterior of the trunk column), large and almost circular cotyles and condyles, moderately short neural spines, and depressed neural arch. Admittedly, most of these characters are also present across other viperid taxa, rendering thus trunk vertebrae as somehow unreliable for definite taxonomic identifications. Węgrzyn et al. (2025) noted that the mid-trunk vertebrae of *P. urarachnoides* are among the shortest within viperid snakes. This current detailed study greatly expands our knowledge of the osteology of this species and indicates that the centrum length is substantially variable along the vertebral column (Table 1).

The bizarre morphology of the haemapophyses of the caudal vertebrae of *Pseudocerastes urarachnoides* deserves some attention. Practically, in this species, the haemapophyses continue the trend observed in the preceding cloacal vertebrae: unlike most other snakes (including most vipers as well), the haemapophyses are not fused to the centrum but they are fused/united in a base that is formed by a short and relatively thick hypapophysis-like structure. Interestingly, this feature is also observed in the distantly related genera *Cerastes* Laurenti, 1768 (Figure 10a, b), and *Eristicophis* (Figure 10c, d), which do not form together a monophyletic unit in recent phylogenetic analyses (e.g., Šmíd & Tolley, 2019), demonstrating thus that this feature has independently evolved several times throughout viperid evolution. Interestingly, both these two latter viperid taxa and *P. urarachnoides* exhibit similar pattern of transition in the subcentral structures. The first forked hypapophysis appears at vertebra S 1 and the bizarre morphology described above (with haemapophyses being fused/united in a base that is formed by a short and relatively thick hypapophysis-like structure) exists throughout the whole caudal series (Figure 10a–d). Such “forked hypapophysis” was reported also in the African viperid genus *Atheris* Cope, 1862, however, there it was confined solely to the very first cloacal vertebrae (see Węgrzyn et al., 2025). It is as yet unknown whether this subcentral morphology is also present in the other two species of *Pseudocerastes*, as their skeletal morphology has never been investigated. Outside Viperidae, such morphology of the ventral surface of the centrum of caudal vertebrae has also been observed in other snakes (see e.g., in

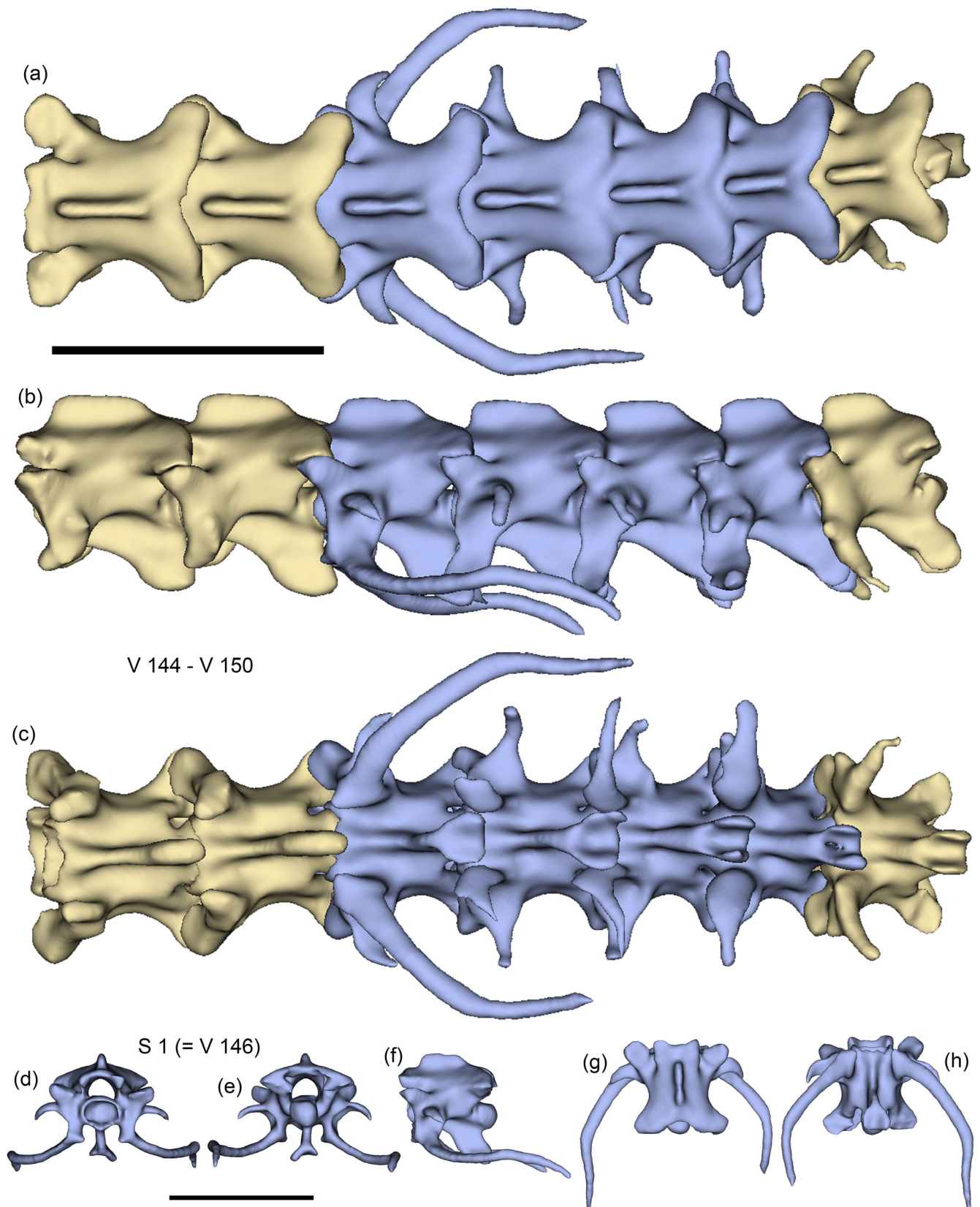


FIGURE 7 Trunk to cloacal to caudal vertebral transition in *Pseudocerastes urarachnoides* (holotype FMNH 170929). (a–c) String of articulated posteriormost, cloacal, and anteriormost caudal vertebrae in dorsal (a), left lateral (b), and ventral (c) views; (d–h) first cloacal vertebra (S 1 = V 146) in anterior (d), posterior (e), left lateral (f), dorsal (g), and ventral (h) views. Scale bars equal 5 mm.

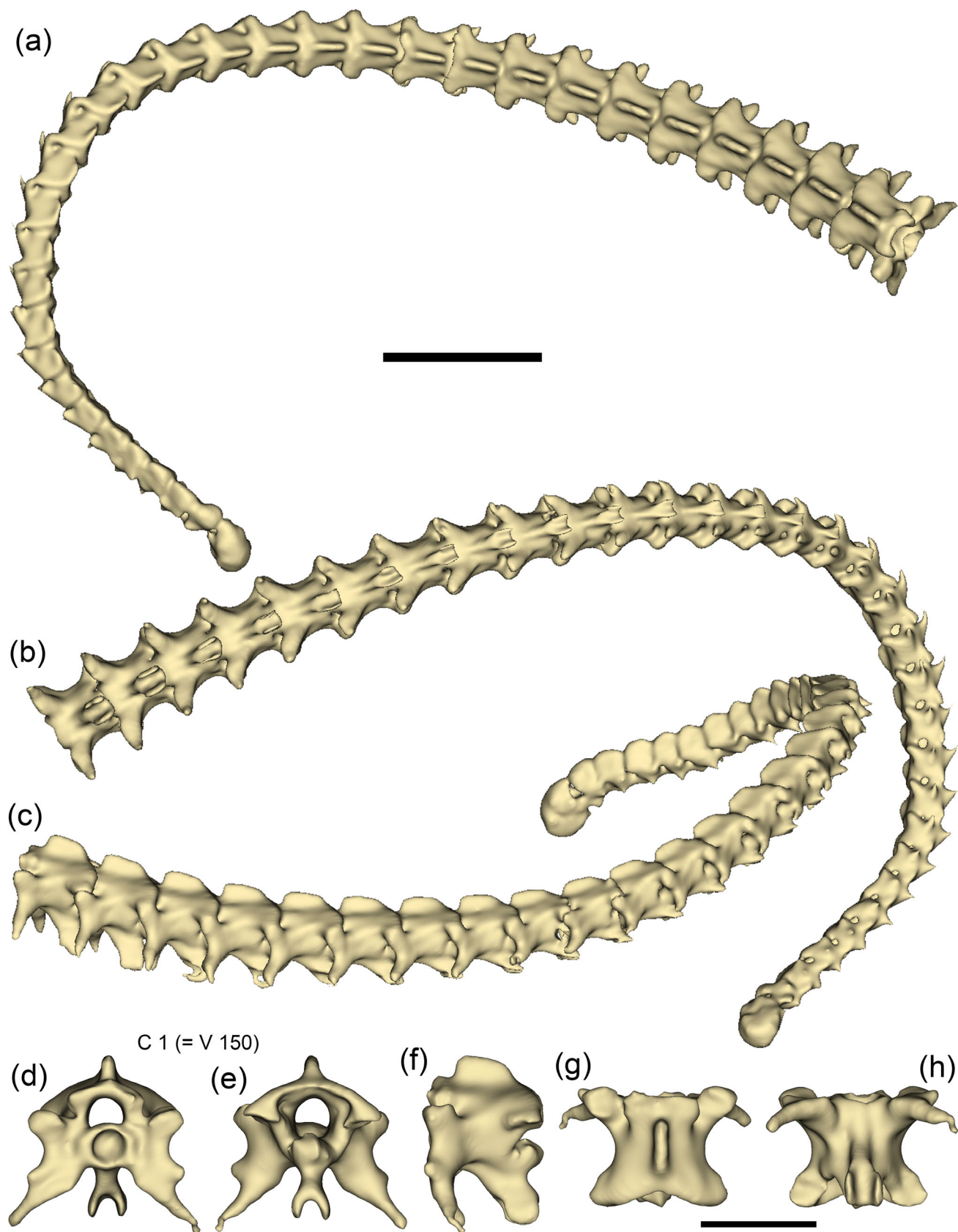


FIGURE 8 Caudal vertebrae of *Pseudocerastes urarachnoides* (holotype FMNH 170929). (a–c) String of all articulated caudal vertebrae in (approximately) dorsal (a), ventral (b), and left lateral (c) views; (d–h) first caudal vertebra (C 1 = V 150) in anterior (d), posterior (e), left lateral (f), dorsal (g), and ventral (h) views. Scale bars equal 5 mm (a–c) and 2.5 mm (d–h).

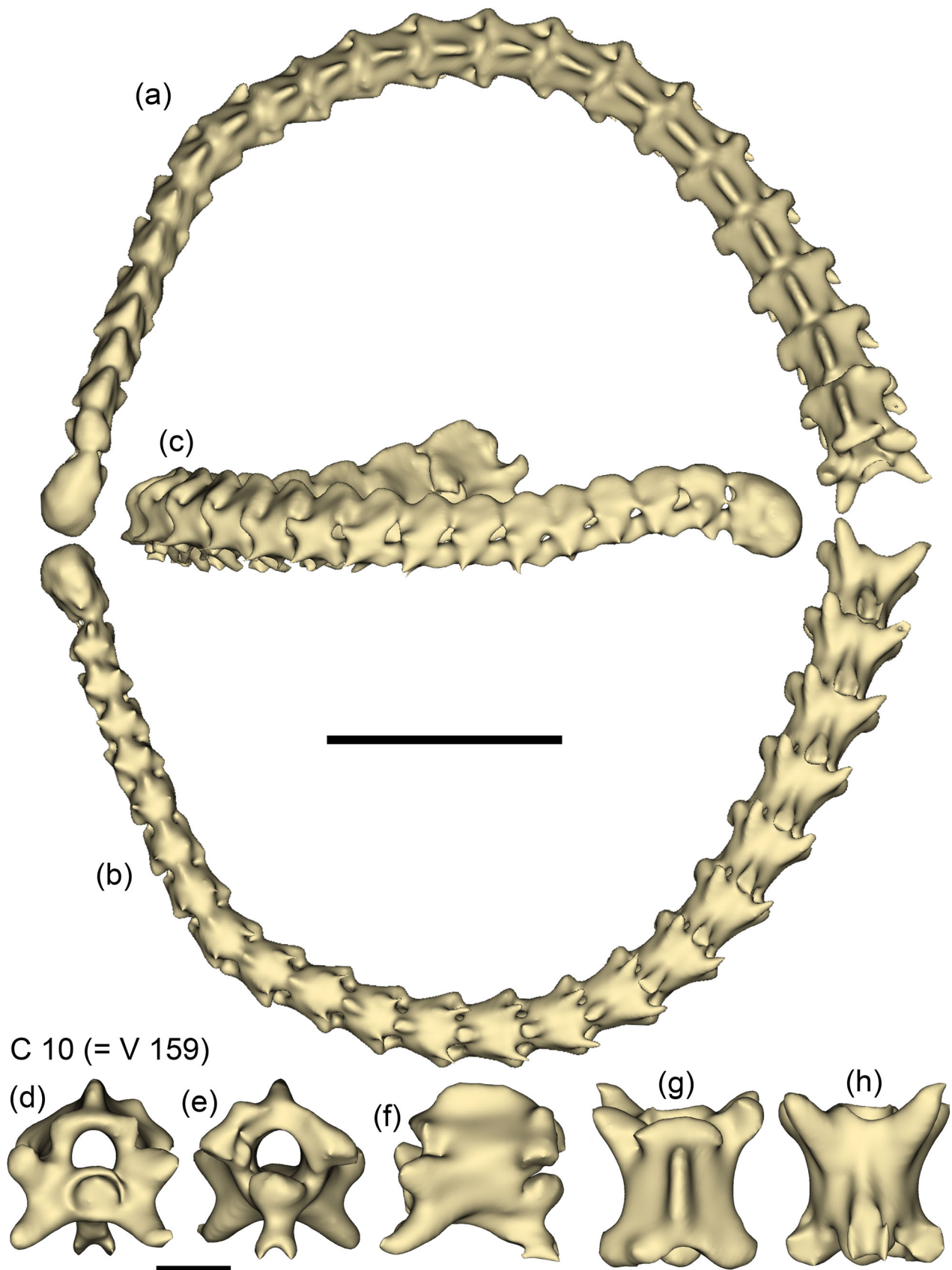


FIGURE 9 Caudal vertebrae of *Pseudocerastes urarachnoides* (holotype FMNH 170929). (a–c) String of articulated caudal vertebrae (starting from C 10) in (approximately) dorsal (a), ventral (b), and left lateral (c) views; (d–h) 10th caudal vertebra (C 10 = V 159) in anterior (d), posterior (e), left lateral (f), dorsal (g), and ventral (h) views. Scale bars equal 5 mm (a–c) and 1 mm (d–h).

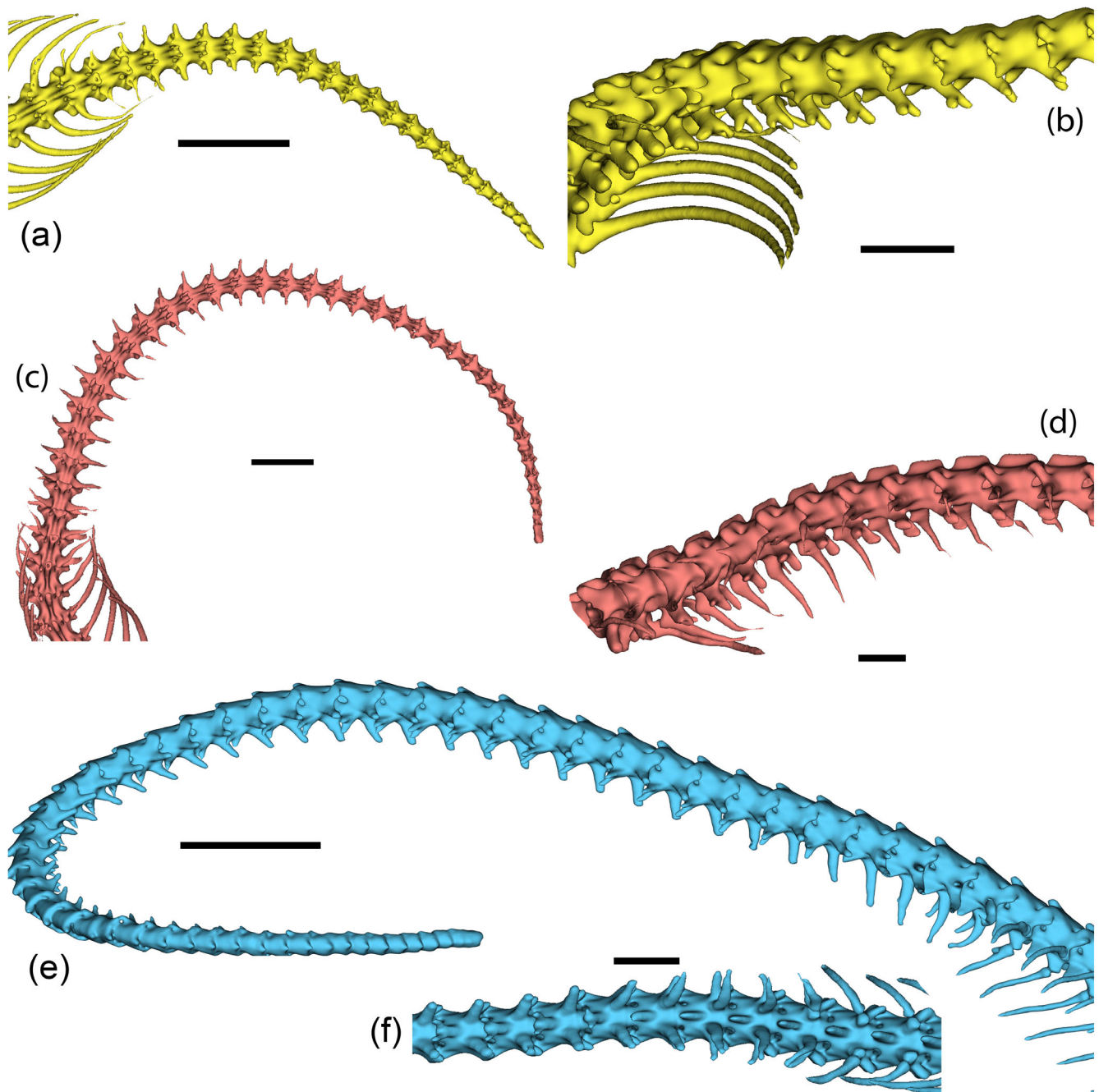


FIGURE 10 Atypical morphology of haemapophyses in snakes. (a, b) posterior portion of the vertebral column of the viperid *Cerastes vipera* (UF:Herp:14922) in ventral view (a) and close-up of the cloacal-caudal transition (b). (c, d) Posterior portion of the vertebral column of the viperid *Eristicophis macmahoni* (UF:Herp:70650) in ventral view (c) and close-up on the cloacal-caudal transition (d). (e, f) Posterior portion of the vertebral column of the acrochordid *Acrochordus granulatus* (UF:Herp:87078) in lateral view (e) and close-up of the cloacal-caudal transition in ventral view (f). Scale bars equal 5 mm (a, c, e) and 2 mm (b, d, f).

the basal caenophidian *Acrochordus* Hornstedt, 1787; see Hoffstetter & Gasc (1969): figure 79). In that latter taxon, however, the transition between the “normal” and “forked” hypapophyses appears to be somewhat abrupt, with the bifurcation appearing only at the first caudal vertebra (Figure 10e, f).

4.2 | Caudal luring affects tail and scale evolution of *Pseudocerastes*

The genus *Pseudocerastes* is endemic to the Middle East, with three currently recognized species. However, only one of them, *Pseudocerastes urarachnoides*, displays an

extreme modification of the tail, associated with its highly specialized ambush strategy of caudal luring (Bostanchi et al., 2006; Fathinia et al., 2015). Caudal luring represents a type of aggressive mimicry, commonly observed in ambush predators, in which tail movements, such as waving or wagging, mimic prey-like stimuli in order to attract potential prey. Such behavior can be quite common across snakes, especially in arboreal species, as it has been reported in Tropidophiidae (Antunes & Haddad, 2009), Constrictores (sensu Georgalis & Smith, 2020) (Murphy et al., 1978; Radcliffe et al., 1980; Simon et al., 1999), Elapidae (Carpenter et al., 1978; Chiszar et al., 1990; Hagman et al., 2008), and across Colubroidea (Leal & Thomas, 1994; Mullin, 1999; Sazima & Puerto, 1993; Tiebout III, 1997). Nevertheless, this feature is most widespread and frequently observed across members of Viperidae, where it has been documented across an array of distantly related species, including both members of Viperinae and Crotalinae (Allen, 1949; Carpenter & Gillingham, 1990; da Fonseca et al., 2019; Farrell et al., 2011; Freitas & Silva, 2011; Greene & Campbell, 1972; Heatwole & Davison, 1976; Henderson, 1970; Jackson & Martin, 1980; Kauffeld, 1943; Neill, 1948; Parellada & Santos, 2002; Paul & Mendyk, 2021; Rabatsky, 2008; Rabatsky & Farrell, 1996; Reiserer & Schuett, 2016; Sazima, 1991; Schuett, 1984; Wharton, 1960). It is characteristic that certain species of rattlesnakes (Crotalinae) use vermiform caudal luring in order to attract ectothermic prey such as lizards and frogs (Jackson & Martin, 1980; Kauffeld, 1943; Paul & Mendyk, 2021; Reiserer & Schuett, 2016; Schuett, 1984).

Usually, tails of snakes that display caudal luring involve little or even no additional morphological specialization. Even among viperid snakes, most of the species that exhibit this behavior have a more or less typical tail anatomy, without any distinct structural adaptations. In most cases, the only noticeable feature that is linked to the luring behavior is the tail coloration which can be brighter or contrasting with the rest of the body, especially in juvenile snakes (Freitas & Silva, 2011; Neill, 1948, 1960). This distinct coloration probably enhances the ability to attract potential prey, especially in the case of snakes with cryptic body coloration and patterning.

An additional and so far overlooked factor in caudal luring is the potential for fluorescence of the tail. The phenomenon of biofluorescence within Squamata is recently gaining an increasing attention, as this may play a vital role in the ecology, life strategy, behavior, and communication of these animals (Bernstein et al., 2024; Botelho et al., 2024; Brecko & Pauwels, 2024a, 2024b, 2024c; Hughes et al., 2024; Paul & Mendyk, 2021; Prötzel et al., 2018, 2021). Among snakes in particular,

biofluorescence has been observed in an array of different taxa, including certain members of leptotyphlopids, typhlopids, pythonids, boids, colubroids, elapids, lamprophiids, pseudoxyrhophiids, as well as in crotalines (pitvipers) (see Bernstein et al., 2024; Paul & Mendyk, 2021). Biofluorescence in these snake tails occurs via absorption of photons by biological tissues that are then reemitted at longer lower-energy wavelengths (Paul & Mendyk, 2021). The potential role of biofluorescence in the evolution of caudal luring has been already discussed in previous studies (Paul & Mendyk, 2021). In the case of the viperine genus *Pseudocerastes*, caudal luring has not yet been reported, however, it could be likely that species of that genus could utilize biofluorescence as part of the strategy, taking into consideration that these snakes are sit-and-wait predators, with *P. fieldi* having also a distinct tail coloration (see Brouw et al., 2021: figure 1).

As discussed above, most snakes known to be “caudal lurers” use fairly unmodified tails, as this consists more a behavioral rather than morphological novelty. However, there are cases, even though only poorly studied, of certain snake species that have evolved scale modifications of their tails. Indeed, certain taxa display caudal luring with a more distinctive tail morphology. Such is the case of the viperid *Lachesis*, which possesses a tail with elongated posterior scales, both on its dorsal and ventral surfaces (Barrio-Amorós et al., 2020: figure 4). These modified scales form small spikes that do not adhere to the tail outline, plus one larger spike on the tail termination. Similar, spike-like scales can be seen in other viperid species, such as the African *Atheris mongoensis* Collet and Trape, 2020, while it also occurs in the aptly named (from the Greek words “ἄκανθος” [=thorn] and “ὄφις” [=snake]) Australian elapid *Acanthophis* Daudin, 1803b (see Maddock et al., 2015). Such scale modification renders the tail more distinct and could facilitate caudal luring in these snake taxa, with such behavior confirmed at least for the latter taxon (see Chiszar et al., 1990). However, it is worth emphasizing that the large-sized *Lachesis* displays waving movement of the tail in various circumstances, aside from what seems to be prey-driven caudal luring. While prey-driven caudal luring motion has been observed in *Lachesis*, caudal motions have also been reported due to the presence of an individual of opposite sex during reproduction attempts. Signaling function in the tail of *Lachesis* is also displayed to potential threats, with tail movement producing rattling sound by rubbing the surroundings (Barrio-Amorós et al., 2020). This case clearly demonstrates that the behavior of a certain snake species can be relatively “plastic” and flexible and that caudal luring intertwines with other kinds of behavior, such as signaling, communication, or defense strategies.

The complexity of caudal luring or motions in viperid tail evolution is aptly demonstrated by the rattles in the viperid lineage of Crotalinae. The tail rattle, which has aptly inspired the very name of the group (from the Greek word κρόταλος, meaning rattle), represents a highly sophisticated antipredatory adaptation of crotalines, specifically the New World *Crotalus* Linnaeus, 1758, and *Sistrurus* Garman, 1884. It heavily influences tail morphology, as it is made of a series of hollow keratin segments, which enable rapid movement through specialized musculature that also affects the caudal skeleton (Meik & Pires-da Silva, 2009; Moon, 2001; Schaeffer et al., 1996). Besides the typical antipredatory function, the utility of the rattle in crotalines may be even wider and deeply linked to caudal luring. It has been hypothesized that rattle evolved from “simpler” caudal luring behavior, waving motion of the tail, and with scale

fluorescence (Allf et al., 2016; Paul & Mendyk, 2021; Reiserer & Schuett, 2016).

We compared the centrum lengths of the caudal vertebrae in several viperid snakes, including arboreal and terrestrial species, as well as species exhibiting advanced caudal luring (Moon, 2001; Węgrzyn et al., 2025) (see Table 2). In general, the centrum length of the caudal vertebrae gradually decreases along the tail, reaching approximately 80% of the length of the first caudal centrum in the middle region and about 30% in the posteriormost vertebrae. *Pseudocerastes urarachnoides* displays a more abrupt decline in regard to its centrum length in the middle region (see the respective ratio 1:0.66:0.34; Table 2), unlike in the two studied *Crotalus* species and other viperid snakes. Interestingly, similar values to *P. urarachnoides* for the ratios of the mid-/anterior caudal vertebrae were achieved by the African *Atheris*

TABLE 2 Measurements of the centrum length (CL) in the caudal vertebrae across the tails of various viperid snakes.

Species	Specimen	Caudal vertebral count	Caudal vertebral number position	Centrum length (CL) (in mm)	Ratio (C 1:C 1/mid-C:C 1/posterior C)
<i>Pseudocerastes urarachnoides</i>	FMNH 170929	32	C 1	2.34	1:0.66:0.34
			C 16	1.54	
			C 31	0.8	
<i>Eristicophis macmahoni</i>	UF:Herp:70650	33	C 1	2.3	1:0.85:0.37
			C 16	1.95	
			C 32	0.86	
<i>Atheris desaixi</i>	RBINS 2504	55	C 1	2.67	1:0.76:0.27
			C 28	2.04	
			C 54	0.73	
<i>Atheris hispida</i>	RBINS 2160	51	C 1	2.45	1:0.86:0.44
			C 25	2.1	
			C 50	1.08	
<i>Atheris katangensis</i>	RBINS 2207	42	C 1	1.98	1:0.62:0.36
			C 21	1.23	
			C 41	0.72	
<i>Cerastes cerastes</i>	UF:Herp:13986	21	C 1	1.77	1:0.77:0.33
			C 10	1.37	
			C 20	0.58	
<i>Crotalus intermedius</i>	UF:Herp:52552	20	C 1	1.45	1:0.88:0.38
			C 10	1.28	
			C 19	0.55	
<i>Crotalus ruber</i>	UF:Herp:72544	29	C 1	1.65	1:0.85:0.57
			C 14	1.4	
			C 28	0.94	

Note: Ratio values in the last column indicate the ratio of the centrum length of the first, mid- (highlighted also in bold), and posterior caudal to the centrum length of the first caudal vertebra, in order to show how the vertebral length changes along the tail's length. Data on *Atheris* obtained from Węgrzyn et al. (2025) and data on *Cerastes*, *Crotalus*, and *Eristicophis* obtained from Morphosource.

katangensis de Witte, 1953 (Table 2). Nevertheless, given the small sample size and the relatively similar ratios observed across different studied species, it is impossible to draw any robust or statistically supported conclusions. We anticipate that future, broader studies will shed light on the relationship between caudal vertebral centrum length and tail morphology.

In the broader picture of caudal luring evolution in viperids, *Pseudocerastes urarachnoides* represents one of the most sophisticated and extreme cases of adaptation (Bostanchi et al., 2006; Fathinia et al., 2015). However, this evolutionary history behind the spider-tail structure of this species has been inadequately studied. What is though certain regarding this unusual tail of *P. urarachnoides* is the fact that it is highly successful, with birds being specific prey of this specialized and fascinating mimicry (Fathinia et al., 2015).

While the internal anatomy of the tail of *Pseudocerastes urarachnoides* has been previously discussed to some degree (Bostanchi et al., 2006; Węgrzyn et al., 2025), the relation between soft tissues and the actual skeleton has not been so far. Here we present 3D

visualization of the actual relation of the tail vertebrae and the surrounding soft tissues (Figure 11). Interestingly, it seems that extreme tail modifications have practically no effect on the underneath lying caudal vertebrae and the radiating “spider-leg” pattern of the tail tip (Bostanchi et al., 2006; Węgrzyn et al., 2025) is made up entirely from modified scalation (Figure 11). Precaudal scales of *P. urarachnoides* are heavily keeled and spike-like, unlike in the other two species of the genus, creating a stone-like texture that facilitates camouflage (Akbarpour & Pouyani, 2023; Bostanchi et al., 2006; Brouw et al., 2021). The tail scales become progressively elongated, creating long and flexible filaments (Figure 11). On the top of the tail, there is one enlarged oval structure, which represents modified scalation via enlargement and fusion of multiple scales.

Such elongated and modified scales are an example of extreme skin evolution. Although extant Squamata demonstrate a fascinating and perplexing diversity of skin structures (e.g., elongated scales on the back found across many iguanian species; Scimeca et al., 2025), the bizarre condition of flexible filament-like scales observed in *Pseudocerastes*

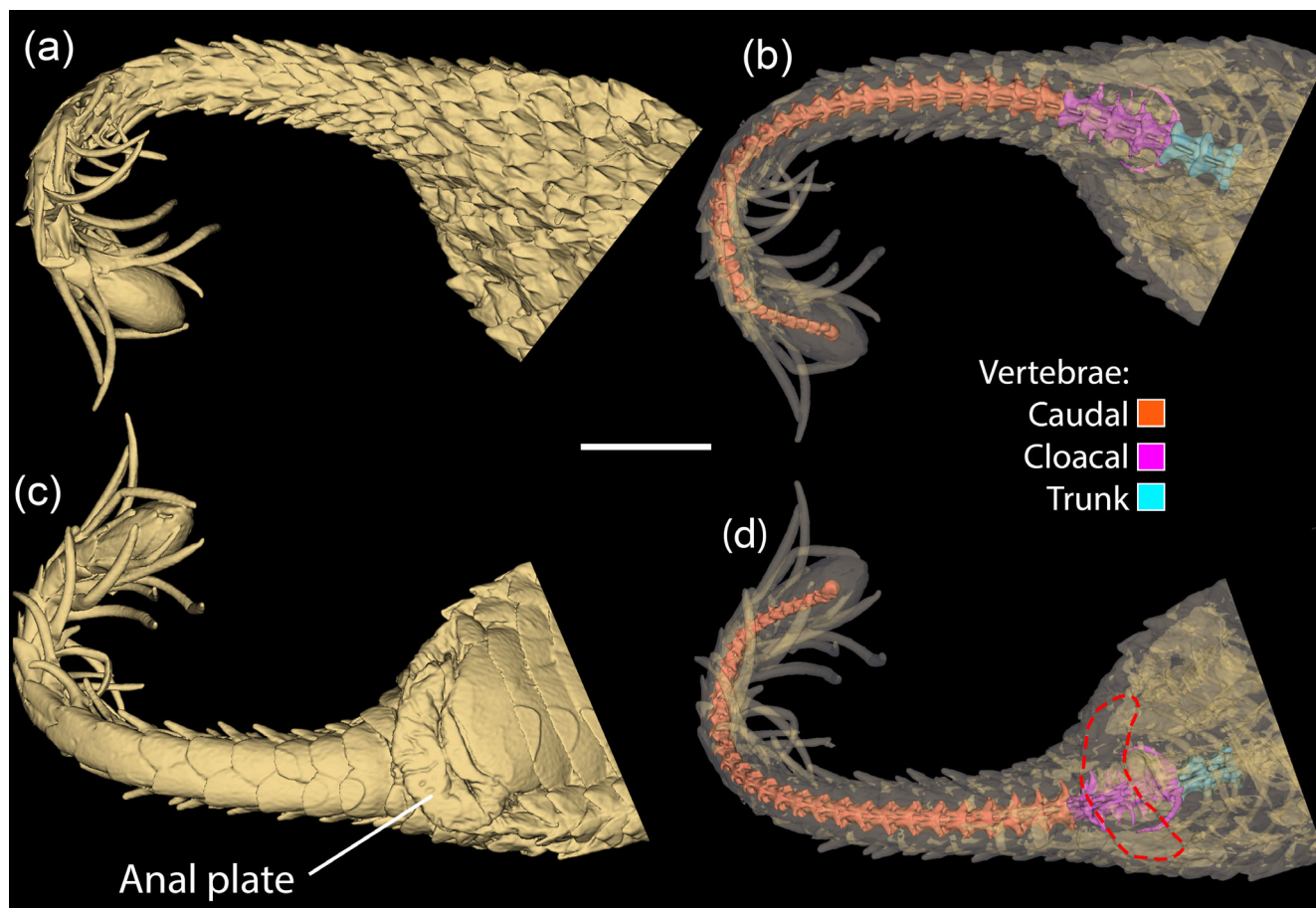


FIGURE 11 3D visualization of the actual relation of the tail vertebrae and the surrounding soft tissues of *Pseudocerastes urarachnoides* (holotype FMNH 170929) in dorsal (a, c) and ventral (b, d) views. Red dotted lines indicate the anal plate. Scale bar equals 10 mm.

urarachnoides cannot be compared to any other living reptile. In some sense, these posterior tail scales of *P. urarachnoides* are somehow reminiscent of filaments found in different members of extinct ornithodiran archosaurs (e.g., Benton et al., 2019; Yang et al., 2019) or other enigmatic Triassic and Jurassic forms (Buchwitz & Voigt, 2012; Dzik et al., 2010; Spiekman et al., 2025). Further study with higher resolution μ CT scanning or scanning-electron microscopy is necessary before we can conclude on the histological or developmental nature of the soft-tissue structures of *P. urarachnoides*, which may shed new light on the scale modifications of this unique viperid snake.

AUTHOR CONTRIBUTIONS

Georgios L. Georgalis: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; writing – review and editing; software; formal analysis; project administration; supervision. **Kacper Węgrzyn:** Investigation; writing – review and editing; software; visualization. **Sara Ruane:** Writing – review and editing; data curation; funding acquisition.

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DATA AVAILABILITY STATEMENT

All μ CT scan data plus mesh 3D model files (.ply) of the herein figured vertebrae of the holotype (FMNH 170929) of *Pseudocerastes urarachnoides* are available at the public repository of Morphosource (Project "Vertebral morphology of the viperid snake *Pseudocerastes urarachnoides*" [<https://www.morphosource.org/projects/000858142?locale=en>]).

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