TO THE QUESTION ABOUT TROPHIC ADAPTATIONS OF ORNITHOSUCHIDS (ARCHOSAURIA)

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Abstract. Ornithosuchidae differ from other carnivore archosaurs in the unique morphology of the jaw apparatus and postcranial skeleton. Various, often diametrically opposed, points of view have been expressed regarding their trophic adaptations – from carnivory and scavering to piscivory. The most reasonable hypothesis seems to be that ornithosuchids were hyperanisodont carnivorous macrophages in the middle size class. Moreover, there are some analogies between ornithosuchids and saber-toothed therapsids and mammals.

Keywords: *Archosauria, Ornithosuchidae, trophic adaptations, Late Triassic*

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INTRODUCTION

Trophic adaptations of the peculiar early archosaurs – ornithosuchids – have recently been the subject of a number of studies and discussions in publications (Baczko, 2018; Müller et al., 2020; Taborda et al., 2023; Sennikov, 2024). Representatives of this family are traditionally considered active predators (Walker, 1964; Benton, Walker, 1985, etc.).

Possible trophic adaptations of ornithosuchids were analyzed by M. von Baczko (Baczko, 2018) using the South American Venaticosuchus rusconii Bonaparte, 1970 as an example. She proposed a hypothesis about the predominant scavenging behavior of this and other ornithosuchids. This conclusion was based on her reconstruction of jaw musculature and morphofunctional analysis of the jaw apparatus. Von Baczko considered the main arguments in favor of her hypothesis to be the increased jaw compression force combined with a slow bite speed. The strong but slow bite of ornithosuchids, in her opinion, seems more suitable for a scavenger, which does not require speed to catch moving prey, and strength is only needed to tear soft tissues or gnaw the bones of a dead animal's carcass. In her view, the insufficient strength of the narrow front part of the snout and the long, thin, laterally compressed teeth could lead to their damage during jerks of large live prey. Therefore, von Baczko also suggested that ornithosuchids possibly hunted only small and medium-sized tetrapods (Baczko, 2018).

Later (Sennikov, 2024), the author of this article suggested that ornithosuchids implemented a special ecological type of specialized hyperanisodont predator-macrophage in the middle size class among early archosaurs, i.e., they were not specialized scavengers but hunted predominantly large prey. The main argument in favor of this hypothesis was that specialization for scavenging is characterized by massive, robust teeth necessary for bone-crushing. The relatively thin, laterally compressed, and very long teeth of ornithosuchids, insufficiently strong against lateral fracture, clearly do not meet such requirements. The small number of hypertrophically anisodont serrated teeth combined with their very high crowns is an adaptation of the jaw apparatus for deep damage to soft tissues and for deep capture of the prey's body. At the same time, the possibility of facultative scavenging is not excluded, but only with the consumption of soft body parts.

After submitting the article on ornithosuchids (Sennikov, 2024) for publication, the author had the opportunity to review another publication on this topic (Taborda et al., 2023). Based on functional-morphological and biomechanical analysis of the jaw apparatus of the South American ornithosuchid

Riojasuchus, its authors reject the hypothesis of scavenging and assert that it hunted only for fish, amphibians, and other small prey in the water column. H. Taborda and co-authors consider the basis for this conclusion to be the fact that the upper and lower tooth rows of Riojasuchus are laterally separated from each other, making it impossible to form a cutting line in the body of large prey through occlusion. These researchers also believe that the downward curve of the upper jaw and the diastema between the pre- and maxillary teeth facilitated the capture of small prey in water whole. Additionally, they consider that the wedge-shaped form of the anterior part of the skull is hydrodynamically ideal for swimming in water, allowing Riojasuchus to "easily displace fluid to the sides, similar to the bow of a ship, reducing resistance." The structure of the slightly laterally compressed tail of ornithosuchids also indicates adaptation for swimming. According to the authors of the article (Taborda et al., 2023), Riojasuchus hunted similar to modern marsh birds, standing in shallow water at the edge of a water body and capturing its prey by quickly immersing its head into the water column.

This latest publication prompted a return to the question of trophic adaptations of ornithosuchids.

POSSIBLE TROPHIC ADAPTATIONS OF ORNITHOSUCHIDS

The hypothesis about trophic adaptations of ornithosuchids proposed by Taborda et al. appears insufficiently substantiated. In this regard, it seems unexpected that von Baczko, a co-author of this article (Taborda et al., 2023), easily abandoned his hypothesis about scavenging in ornithosuchids (Baczko, 2018), which still seems more well-argued. Let us consider the data that contradict the hypothesis of Taborda and co-authors.

The structure of the hyperspesialized jaw apparatus of ornithosuchids is unique among predatory archosaurs. Evidently, such a structure provided a special, specific functioning, probably macrophagy (Sennikov, 2024). Generalist predators that hunt diverse, predominantly small prey are usually weakly specialized, primarily in terms of jaw apparatus morphology, such as, for example, younginiids or prolacertids. Therefore, there is no doubt that ornithosuchids were not hunters of small vertebrates. The extreme specialization of ornithosuchids could not have occurred during the evolution of this group without a significant change in trophic adaptations and hunting method, which is clearly reflected in their morphology. Such cardinal morphofunctional transformations of the ornithosuchid jaw apparatus, such as, for example, the reduction in number and increase in size of hyperanisodont ziphodont teeth in representatives of this family, obviously contradict the assumption of Taborda et al. (2023) about ornithosuchids as predators with a wide range of small food objects.

The skull of ornithosuchids is short, massive, narrow in the front and wide in the posterior part, with short jaws. The external mandibular fenestra is unusually large and long, reaching up to half the length of the lower jaw (Fig. 1, 2). This shape of the skull and lower jaw indicates the development of powerful adductor musculature, with attachment points positioned as far forward as possible. Von Baczko (Baczko, 2018) correctly believes that this provided increased jaw compression force combined with a slow bite speed. The most likely interpretation of this mode of jaw apparatus functioning is that ornithosuchids predominantly hunted large, not very mobile prey and quickly killed it (Sennikov, 2024). The great bite force inherent to ornithosuchids (Baczko, 2018) should indicate the large size of their prey, by analogy with modern carnivorous mammals (Wroe et al., 2005; Christiansen, Wroe, 2007), short-headed crocodiles (Endo et al., 2002), or tyrannosaurids (Meers, 2002; Therrien et al., 2005). At the same time, the slow, powerful bite of ornithosuchids is absolutely unsuitable for catching small, mobile terrestrial tetrapods and fast-swimming amphibians or fish. Additionally, piscivorous archosauromorphs and birds typically have a long, thin tubular rostral part of the skull and lower jaw, like the gharial (Souza et al., 2023; Drumheller, Wilberg, 2020), which does not correspond at all to the head structure of ornithosuchids (Fig. 2, 3). Thus, the morphology of the skull and lower jaw, as well as the nature of the jaw apparatus functioning, indicate the specialization of ornithosuchids directly opposite to that postulated by Taborda et al. (Taborda et al., 2023).

As the authors of the article suggest (Taborda et al., 2023), the hook-like downward bend of the premaxillary bones and the backward orientation of the premaxillary teeth contributed to holding specifically small prey in an almost closed mouth. However, it has been demonstrated (Sennikov, 2024) that such a construction develops for more reliable retention of any prey, including large ones (with a widely opened mouth) (Fig. 4).

The general form of the jaws of ornithosuchids with prominences bearing the largest teeth does not correspond to adaptation for hunting small prey or ichthyophagy. In predominantly fish-eating crocodiles, such as the gharial, the jaws are very long, thin, even, with numerous isodont thin teeth, while in those hunting, including large mammals (alligator, crocodile, caimans), they are relatively short, powerful, scalloped, with less numerous massive, anisodont teeth (Iordansky, 1963; D'Amore et al., 2019, 2024; Sennikov, 2024). A similar morphological series in the structure of the jaw apparatus can be constructed for phytosaurs, implying similar trophic adaptations for each of their representatives - from Mystriosuchus to Belodon and Rutiodon (Colbert, 1947) (Fig. 3). The comparison of ornithosuchids with Proterosuchus and spinosaurids (Taborda et al., 2023), for which predominant fish-eating is usually assumed, seems inappropriate. The latter have long jaws with numerous small teeth, isodont in Proterosuchus (Cruickshank, 1972; Ezcurra, Butler, 2015) or weakly anisodont in spinosaurids (Sereno et al., 1998; D'Amore et al., 2024). Furthermore, proterosuchids were most likely terrestrial generalist predators that only occasionally fed on fish, rather than specialized ichthyophages (Sennikov, 2024).

The unusually small number of hyperanisodont teeth for archosaurs, including canine-like teeth with very high crowns, located on jaw projections, also contradicts the adaptation of Ornithosuchidae to hunting small prey or piscivory. Anisodontism in predatory reptiles is a specialization for macrophagy, as it allows for holding, killing, and dismembering large prey (Iordansky, 1963; D'Amore et al., 2019, 2024). The presence of cutting serrated ridges on the anterior and posterior edges of laterally compressed, long, slightly curved dagger-like teeth undoubtedly indicates the hyperspecialization of ornithosuchids for macrophagy, as such teeth are adapted for deep capture, damage, and dismemberment of soft tissues of large victims (Figueirido et al., 2018; Dominguez-Rodrigo et al., 2022; Sennikov, 2024). In this, one can see distant analogies with the structure and functioning of the jaw apparatus of saber-toothed mammals and therapsids (Antón, 2013; Palmqvist et al., 2023). In general, serrated ziphodont teeth of tetrapods, as in the Komodo dragon and large predatory archosaurs, unequivocally indicate the large size of their prey, which must be dismembered by cutting soft tissues (Massare, 1987; Fiorillo, 1991; Meers, 2002; D'Amore, 2009; D'Amore, Blumenschine, 2009; Sennikov, 2024). Predators that hunt small tetrapods or fish do not have such tooth structure. Piscivorous forms are characterized by a large number of long, sharp, conical, slightly curved isodont teeth with numerous apicobasal smooth ridges and grooves, adapted for grasping and piercing the dense scale coverings of fish (Massare, 1987; McCurry et al., 2019; D'Amore et al., 2019; Souza et al., 2023). In predators that hunt small tetrapods, teeth are adapted for holding the prey whole, not for dismembering it. The large, laterally compressed, serrated few teeth of ornithosuchids are obviously poorly suited for grasping and holding small terrestrial tetrapods or fish and aquatic amphibians in the mouth. This is a completely different direction of specialization.

According to Taborda et al. (2023), ornithosuchids likely did not have occlusion of the upper and lower jaw teeth, and therefore could not cut or dismember the body of a large prey. Indeed, the number, shape, and position of ornithosuchid teeth differ from those of modern crocodiles that hunt large prey. However, the complete absence of occlusion between the anterior caniniform teeth on the dentary and the teeth on the maxilla in representatives of this family is not entirely obvious. In Fig. 2 of the article by Müller et al. (2020), these teeth of the ornithosuchid Dynamosuchus collisensis Müller, Baczko, Desojo et Nesbitt, 2020 are shown in a state of occlusion. In Riojasuchus tenuisceps Bonaparte, 1969, the tooth rows on the maxilla and in the posterior part of the dentary are slightly offset laterally (Taborda et al., 2023). But the difference in size and shape of these teeth is so great that it does not suggest occlusion, but rather indicates their different functions and the greater importance of teeth in the maxilla. In any case, the decisive factor in determining the presence of occlusion in ornithosuchids should be determined by the presence or absence of wear facets on their teeth, which will require additional research.

It can be assumed that in ornithosuchids, the beak-like curved premaxilla with two anterior caniniform teeth and two caniniform teeth on the protrusion in the anterior part of the dentary, which fit into the diastema behind the last premaxillary teeth, were the main tool for capturing prey and tearing out pieces of soft tissue. Probably, the teeth on the premaxilla of ornithosuchids functioned similarly to the enlarged incisors of saber-toothed cats (Valkenburgh, 1989; Dominguez-Rodrigo et al., 2022). The row of caniniform teeth on the maxilla deeply penetrated the prey and ensured its retention and further dismemberment. Possibly, when opening their mouths, ornithosuchids not only lowered the lower jaw, but also, like modern crocodiles, slightly raised the head (upper jaw), then forcefully lowered it during the bite, closed the mouth, compressed the jaws, and then pulled, jerking the head down and backward to cut out and tear out the captured piece of soft tissues from the prey's body (Fig. 4). Certain analogies to this method of dismembering and consuming large mammals can be found in the Komodo dragon, which, by moving its head backward and pushing with its limbs, cuts through the soft tissues of its prey's body with serrated teeth embedded in them (D'Amore, Blumenschine, 2009). In such cases, occlusion does not play a major role. To some extent, a similar method of killing and dismembering prey with teeth embedded in soft tissues using neck musculature is also suggested for theropods (Antón et al., 2003; Snively, Russell, 2007; Snively et al., 2013) and saber-toothed cats (Akersten, 1985; Antón, 2013). Ornithosuchids, with their long, sparse, anisodont canine-like teeth, probably occupied an intermediate position in this respect between theropods and saber-toothed mammals.

It should be noted that the teeth along the entire length of the maxillary bone in ornithosuchids did not decrease in size from front to back, as was the case in other predatory archosaurs, but were of equal length. To use the long teeth located in the posterior part of the maxillary bone for biting, an adaptation for wide mouth opening was necessary (Fig. 4). The long teeth at the very back of the ornithosuchid mouth would have had to penetrate the prey just as deeply as the front teeth and play an equally important role in killing, dismembering, and consuming prey, including through downward and backward jerking movements of the head. We emphasize once again that the main peculiarity of the hunting method of ornithosuchids with their rare, very long canine-like teeth was the deep penetration of the large prey's body and its quick killing, preventing damage to the teeth, similar to that of saber-toothed therapsids or mammals (Antón, 2013).

Presumably, a traceological analysis of the surface of ornithosuchid teeth would provide important information for resolving the question of possible trophic adaptations of representatives of this family, their food objects, and hunting methods, if the preservation of the material would allow conducting such analysis. It is also possible that isotopic analysis could also provide indications of the possible lifestyle and trophic adaptations of ornithosuchids.

Before considering the structure of the vertebral column of ornithosuchids, it should be noted that Riojasuchus had only eight cervical vertebrae, as did many early archosaurs. This conclusion is based on the location of diapophyses, the shape and length of their transverse processes. On the cervical vertebrae of Riojasuchus, diapophyses are located on the vertebral body. On the third-fifth vertebrae, they appear as small tubercles. On the sixth-seventh vertebrae, diapophyses have short transverse processes oriented ventrolaterally (Fig. 5). The eighth vertebra is posterior cervical or transitional from cervical to trunk vertebrae, as the diapophysis has a rather long transverse process oriented ventrolaterally, and is located at the very base of the neural arch (Fig. 6). On the ninth-thirteenth presacral (first-fifth trunk) vertebrae, diapophyses have long transverse processes oriented laterally, and are located in the lower part of the neural arch, above the neurocentral suture (Baczko et al., 2019, Fig. 4, A).

The author's assumption about the use of head jerks by ornithosuchids for tearing and dismembering prey captured in their compressed jaws is supported by the hypertrophied development of hypapophyses on the ventral surface of their cervical vertebrae bodies, similar to modern crocodiles and Komodo monitors. In early archosaurs, hypapophyses are absent or weakly expressed, appearing as small tubercles in the anterior part of the cervical vertebrae bodies at the end of the ventral keel. In Riojasuchus, hypapophyses are present on the ventral surface of the first ten vertebrae bodies (cervical and anterior thoracic), from the second (axis) to the eleventh presacral (third anterior thoracic). On the second-sixth cervical vertebrae, the hypapophyses appear as strongly protruding ridges, resembling hypertrophied ventral keels. On the second cervical vertebra (axis), the most prominent part of this ridge is located in the posterior part of the ventral surface of the vertebra body; on the third-fifth, it is approximately in the middle; and on the sixth, it is in the anterior part. On the seventh-eleventh presacral (seventh-eighth cervical and first-third thoracic) vertebrae, the hypapophyses appear as tubercles in the anterior part of the ventral surface of the vertebra body, but small ventral keels are also present, extending to the posterior edge of the vertebra body. The most powerful hypapophyses in the form of ridges are developed on the third-sixth cervical vertebrae, and in the form of tubercles on the seventh and eighth (Fig. 5, 6). Further, on the first-third thoracic (ninth-eleventh presacral) vertebrae, the hypapophyses gradually decrease in size and appear as small tubercles (Fig. 7).

The degree of hypapophysis development in Riojasuchus is unique among early archosaurs - they are comparable in size to the hypapophyses of crocodiles, Komodo dragons, or mosasaurs. Hypapophyses are well-developed on the cervical vertebrae of other ornithosuchids - Dynamosuchus collisensis (Müller et al., 2020, fig. 2, g) and Ornithosuchus longidens Newton, 1894 (Walker, 1964, fig. 8, c). Evidently, the cervical musculoligamentous apparatus of Ornithosuchidae was extremely powerful, especially the tendons and hypaxial musculature, including those that bent the head downward, and also played an important role in killing and dismembering prey, along with powerful jaw adductors. The cervical musculoligamentous apparatus strengthened and stabilized the neck of ornithosuchids, apparently cushioning the jerks of captured large animals and protecting the skull bones and teeth from the traumatic effects of these impact loads.

The massiveness and power of the relatively short limbs, especially the forelimbs, unusual for relatively small ornithosuchids, obviously provided effective grasping and holding of large prey rather than small tetrapods. This assumption is also confirmed by the shape of the claws - large, sharp, very high and laterally compressed, strongly curved. Such claws are characteristic of active predators that grasp and hold prey with them (Fowler et al., 2009, 2011). In this way, ornithosuchids also resemble saber-toothed cats (Antón, 2013). This use of limbs reduced the load on the anterior part of the skull and the thin, long, laterally compressed teeth, decreasing the risk of damage during prey's jerking movements. It is also possible that ornithosuchids could knock down and bring to the ground even large animals with their powerful forelimbs to reach soft body parts, for example, to bite through the neck from below, as is suggested for saber-toothed mammals (Akersten, 1985; Turner et al., 2011; Antón, 2013; Brown, 2014). Ornithosuchids, probably similar to the Komodo dragon (D'Amore, Blumenschine, 2009), braced and pushed off with their limbs, creating additional force to the tension of the neck musculature for backward movement of the head, cutting out and tearing pieces of soft tissue from the victim's body captured by the mouth with long teeth.

The opinion of Taborda et al. (2023) about the aquatic lifestyle of ornithosuchids and their hunting for fish and amphibians in water is also insufficiently substantiated. The high skull with laterally oriented nostrils and orbits in representatives of this family is typical for terrestrial, not aquatic tetrapods. The hypothetical hydrodynamic properties of only the rostral part of the head cannot be considered as a serious argument. The structure of the slightly laterally compressed tail of ornithosuchids (Fig. 8) may indicate a moderate adaptation to swimming. A more or less high, laterally compressed tail is characteristic of all early archosaurs, which indeed indicates their ability to swim (Sennikov, 2023), but not a purely aquatic lifestyle. The structure of the limbs and their girdles in ornithosuchids indicates a parasagittal or close to parasagittal limb posture (Baczko et al., 2024), which points to the general direction of their specialization for terrestrial locomotion (Sennikov, 2024). At the same time, ornithosuchids were unlikely capable of very fast movement over significant distances, but were rather ambush predators (Sennikov, 2024), which is also confirmed by their plantigrade posture (Baczko et al., 2024). Thus, the general body shape and limb structure exclude the interpretation of Ornithosuchidae's lifestyle as amphibiotic active swimmers and aquatic hunters of fish and amphibians. Perhaps histological analysis of the postcranial skeleton bones of ornithosuchids could provide additional information about their possible lifestyle and habitat.

It is even more difficult to imagine ornithosuchids wandering through shallow water and catching fish or amphibians in the water (Taborda et al., 2023). No morphological features of representatives of this family indicate such specialization. Ornithosuchids do not in any way resemble a heron with a long flexible neck that allows for quickly lowering the head underwater, or even spinosaurids. The short limbs of ornithosuchids would not allow them to wade to sufficient depth. Bipedalism with a massive trunk and head, with large robust forelimbs only slightly shorter in length than the hindlimbs (Sennikov, 2024), with a relatively short tail that does not counterbalance the front part of the body (Fig. 8), seems implausible (Baczko et al., 2024). In any case, it is impossible to imagine how ornithosuchids would make quick lunges to grab fast-swimming prey in water. Their head is too large and massive for this, and their neck is short and straight. Additionally, the flexibility of the neck and mobility of the head of ornithosuchids was obviously somewhat limited by a double row of wide articulated osteoderms forming an armor that overlapped the neck from above and partly from the sides (Fig. 8, 9).

CONCLUSION

Summarizing the above, it can be stated that ornithosuchids were distinctive hyperanisodont predator-macrophages. These are relatively small, on average about two meters in length, but very robust, powerful predatory archosaurs. They are characterized by short, massive skull and jaws, dagger-shaped, laterally compressed long serrated teeth, and powerful limbs with strongly curved claws. These morphological features are necessary when hunting large prey: the massive jaw apparatus was needed for a powerful bite, the dagger-like teeth provided deep wounds to the prey, powerful limbs served to securely hold the prey during its jerks to avoid breaking teeth and damaging the front part of the skull. Despite all the dissimilarities between heterodont saber-toothed therapsids and mammals with anisodont archosaurs – ornithosuchids, certain analogies can be seen in the structure and functioning of their jaw apparatus and hunting method.

Like all predators, ornithosuchids were facultative scavengers, but primarily consumed soft body parts. Occasionally, they could also feed on fish and small tetrapods. However, neither of these was the main focus of their trophic adaptation. Only within the framework of the hypothesis about ornithosuchids specializing in hunting large prey, including those exceeding them in size, can the specific, unusual features of their morphology be explained.

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CONFLICT OF INTERESTS

The author of this work declares that he has no conflict of interest.

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45. Figure captions

Fig. 1. Ornithosuchid skulls, lateral view (right): *a* — Riojasuchus tenuisceps (after: Baczko, Desojo, 2016, fig. 2, B); *b* — Dynamosuchus collisensis (after: Müller et al., 2020, fig. 2B); *c* — Venaticosuchus rusconii (after: Baczko, 2018, fig. 2); *d* — Ornithosuchus longidens (after: Walker, 1964, fig. 5, a).

Fig. 2. Riojasuchus tenuisceps, specimen of the Natural History Museum of the Miguel Lillo Foundation, Tucuman, Argentina, № PVL 3827: *a* — skull, lateral view (right); *b, c* — left ramus of the lower jaw: *b* — lingual view, *c* — labial view (left). Photo by A.G. Sennikov.

Fig. 3. Heads and skulls of archosaurs, lateral view (left): *a* — crocodile Gavialis gangeticus (Gmelin, 1789) (after: Grigg, Gans, 1993, fig. 40.1, E), *b* — crocodile Crocodylus porosus Schneider, 1801 (after: Grigg, Gans, 1993, fig. 40.1, C), *c* — phytosaur Mystriosuchus planirostris (H. von Meyer, 1963) (after: Colbert, 1947, fig. 12), *d* — phytosaur Machaeroprosopus gregorii Camp, 1930 (after: Colbert, 1947, fig. 12), *e* — theropod Suchomimus tenerensis Sereno et al., 1998 (after: Sereno et al., 1998, fig. 2, d), *f* — theropod Tarbosaurus bataar (Maleev, 1955) (after: Maleev, 1974, fig. 1), *g* — proterosuchid Proterosuchus fergusi Broom, 1903 (after: Ezcurra, Butler, 2015, fig. 11, B), *h* — ornithosuchid Ornithosuchus longidens (after: Walker, 1964, fig. 5, a).

Fig. 4. Lateral view (right): *a* — crocodile Crocodylus porosus with widely open mouth (after: https://i.artfile.ru/3000x1997_823370_[www.ArtFile.ru].jpg), *b* — ornithosuchid Riojasuchus tenuisceps, Museum of Natural History of the Miguel Lillo Foundation, Tucuman, Argentina, specimen № PVL 3827, skull reconstruction with widely open mouth during prey capture (photo by A.G. Sennikov).

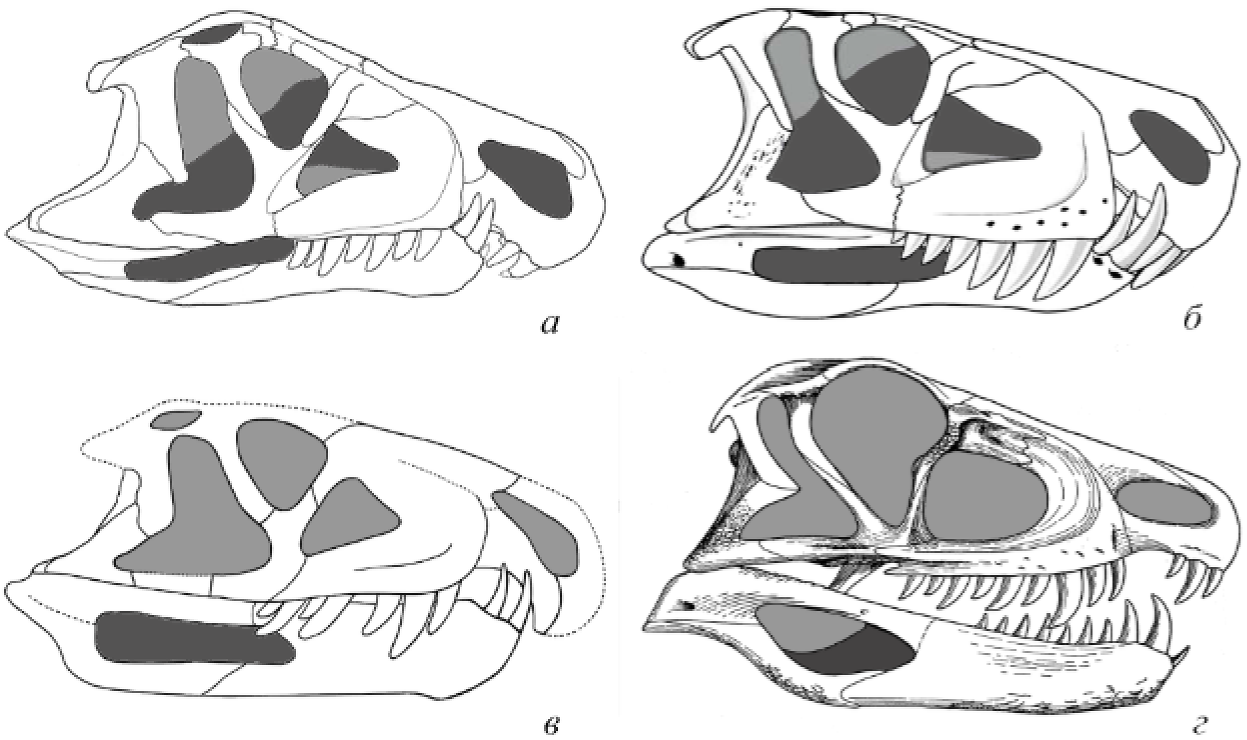
Fig. 5 . Riojasuchus tenuisceps, Museum of Natural History of the Miguel Lillo Foundation, Tucuman, Argentina, specimen № PVL 3827, cervical vertebrae in articulation from first to seventh: *a* — right view, *b* — left view, *c* — ventral view. Designations: dia — diapophyses, hyp — hypapophyses, os — osteoderms, par — parapophyses, 1-7 — vertebrae numbers. Photo by A.G. Sennikov.

Fig. 6 . Riojasuchus tenuisceps, Museum of Natural History of the Miguel Lillo Foundation, Tucuman, Argentina, specimen № PVL 3827, eighth (posterior cervical) vertebra: *a* — cranial view, *b* — lateral view (left), *c* — ventral view. Designations: dia — diapophysis, hyp — hypapophysis, par — parapophysis. Photo by A.G. Sennikov.

Fig. 7. Riojasuchus tenuisceps, Museum of Natural History of the Miguel Lillo Foundation, Tucumán, Argentina, specimen No. PVL 3827, anterior trunk vertebrae in articulation from first to fifth (ninth–thirteenth presacral), ventral view. Designations: 9–13 – vertebra numbers, others as in Fig. 6. Photo by A.G. Sennikov.

Fig. 8. Skeletons of ornithosuchids: *a* , *b* — Riojasuchus tenuisceps (after: Baczko et al., 2019, fig. 2, A, B): *a* — dorsal view, *b* — lateral view (right); *c* — Dynamosuchus collisensis, lateral view (right) (after: Müller et al., 2020, fig. 2, K).

Fig. 9. Riojasuchus tenuisceps, Museum of Natural History of the Miguel Lillo Foundation, Tucumán, Argentina, specimen No. PVL 3827, cervical vertebrae in articulation from first to seventh: *a* — dorsal view, *b* — craniolateral view (right), *c* — cranial view. Designations: Os — osteoderms, 1–7 — numbers of vertebrae and osteoderms. Photo by A.G. Sennikov.



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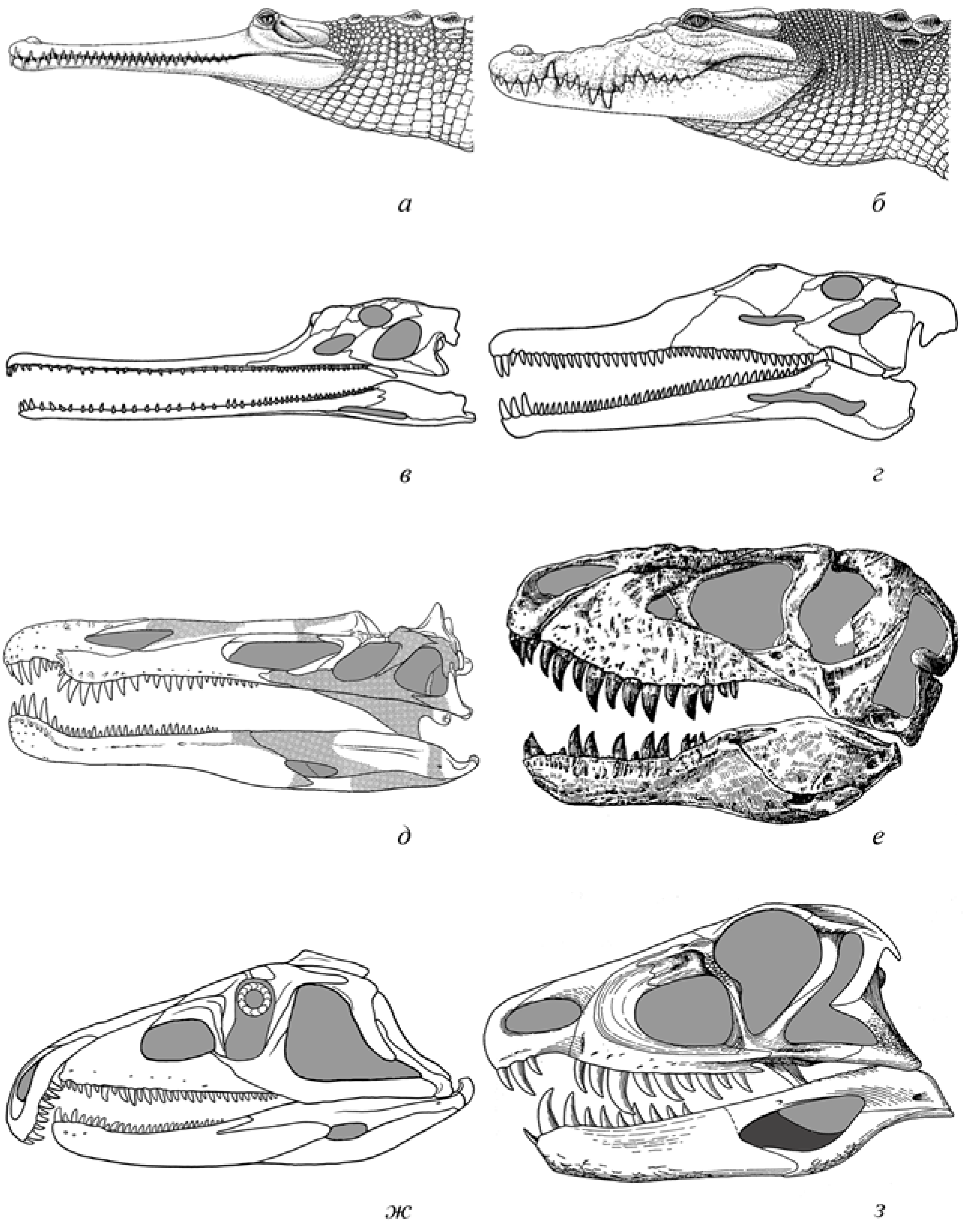

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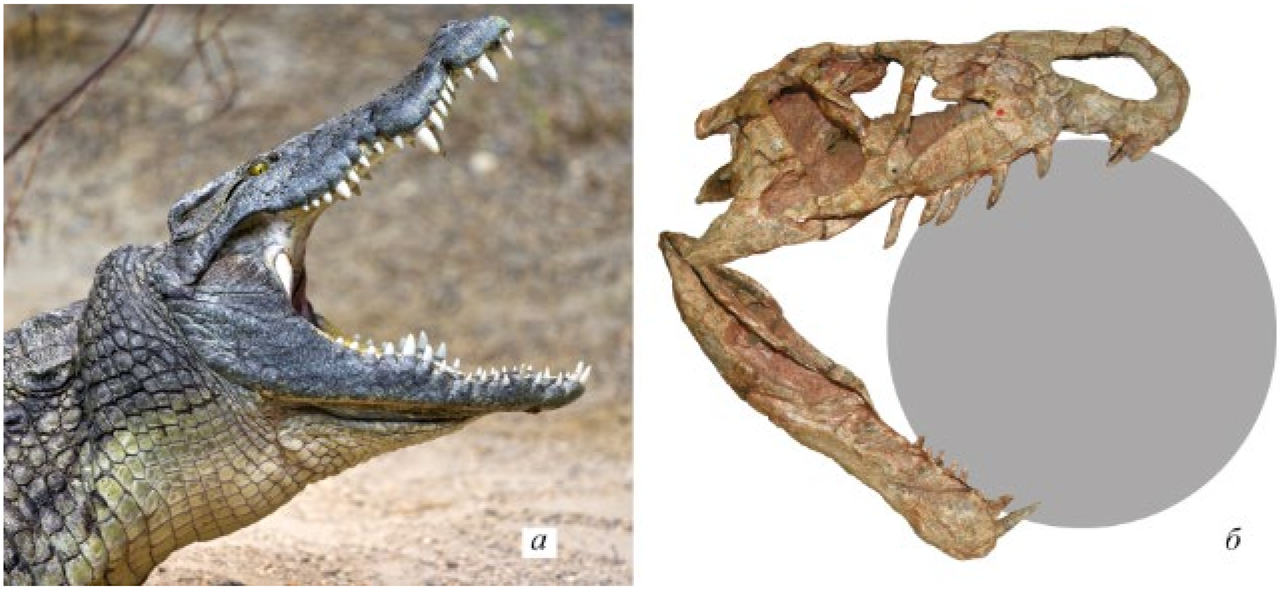
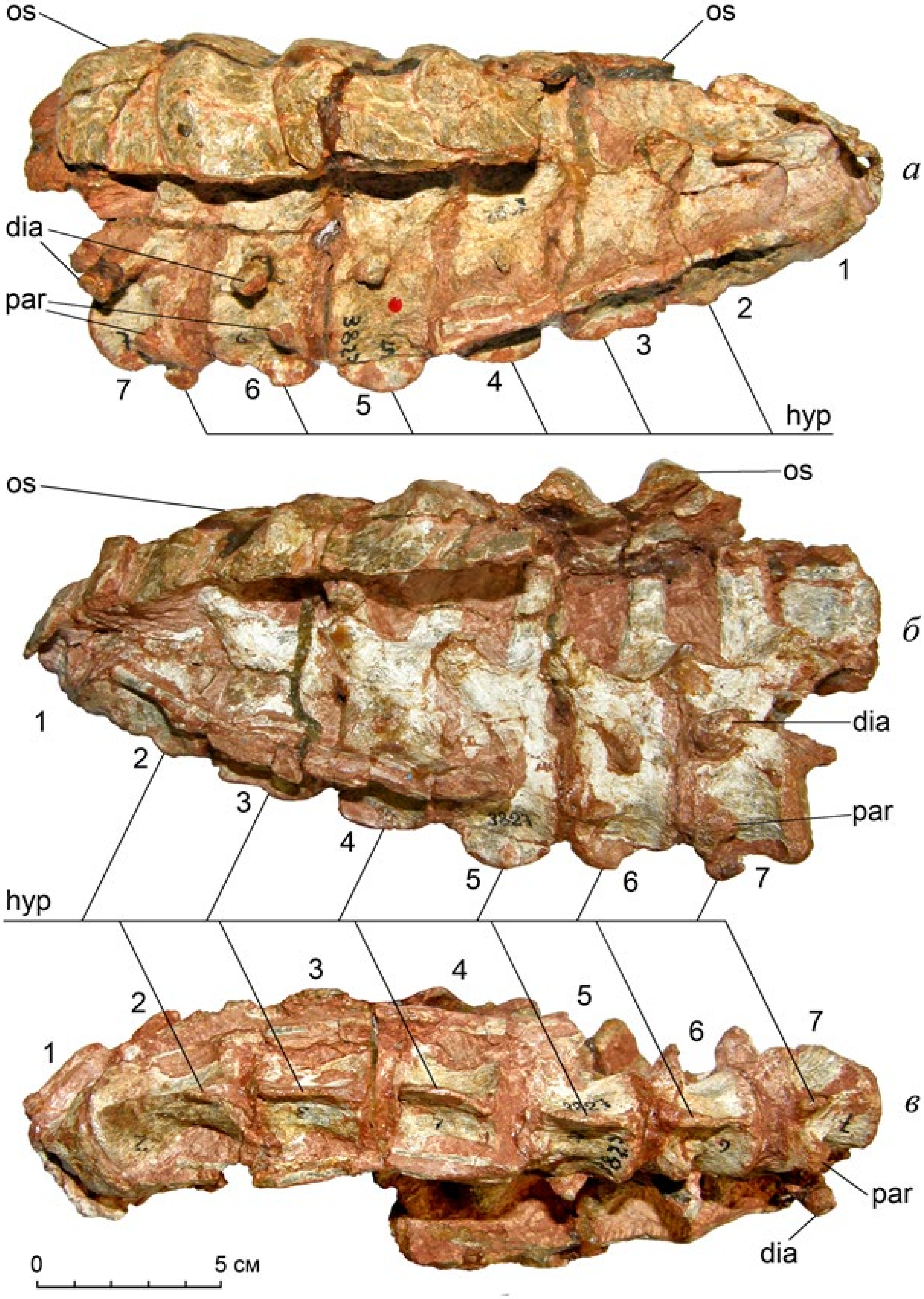


Fig. 4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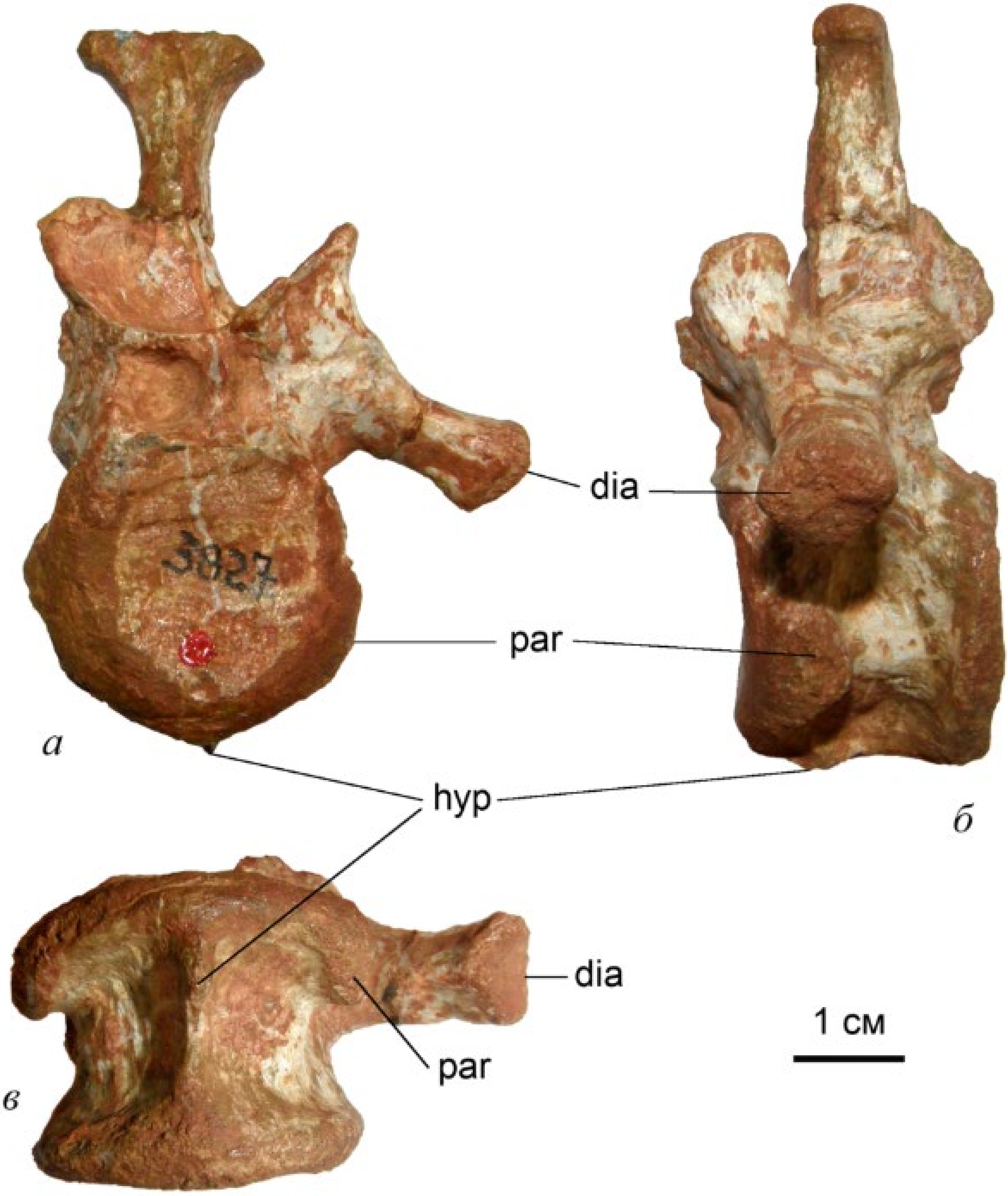

Fig. 6

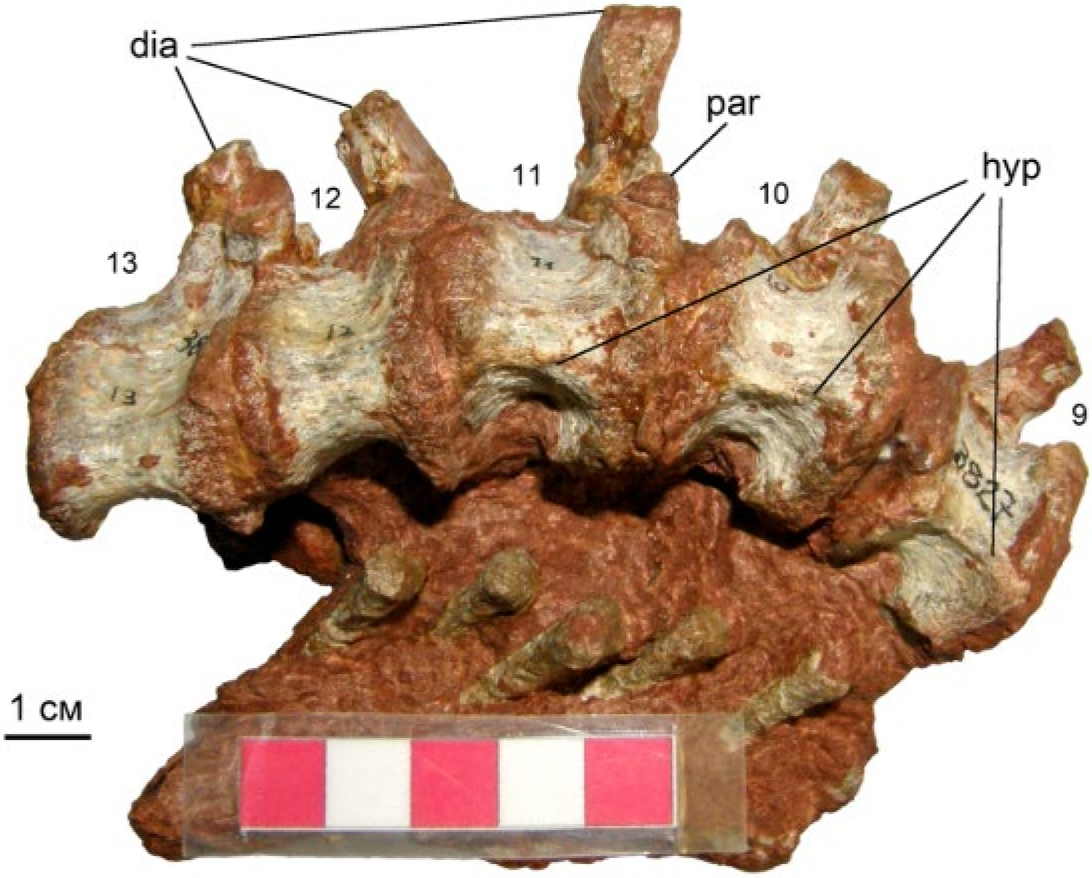

Fig. 7

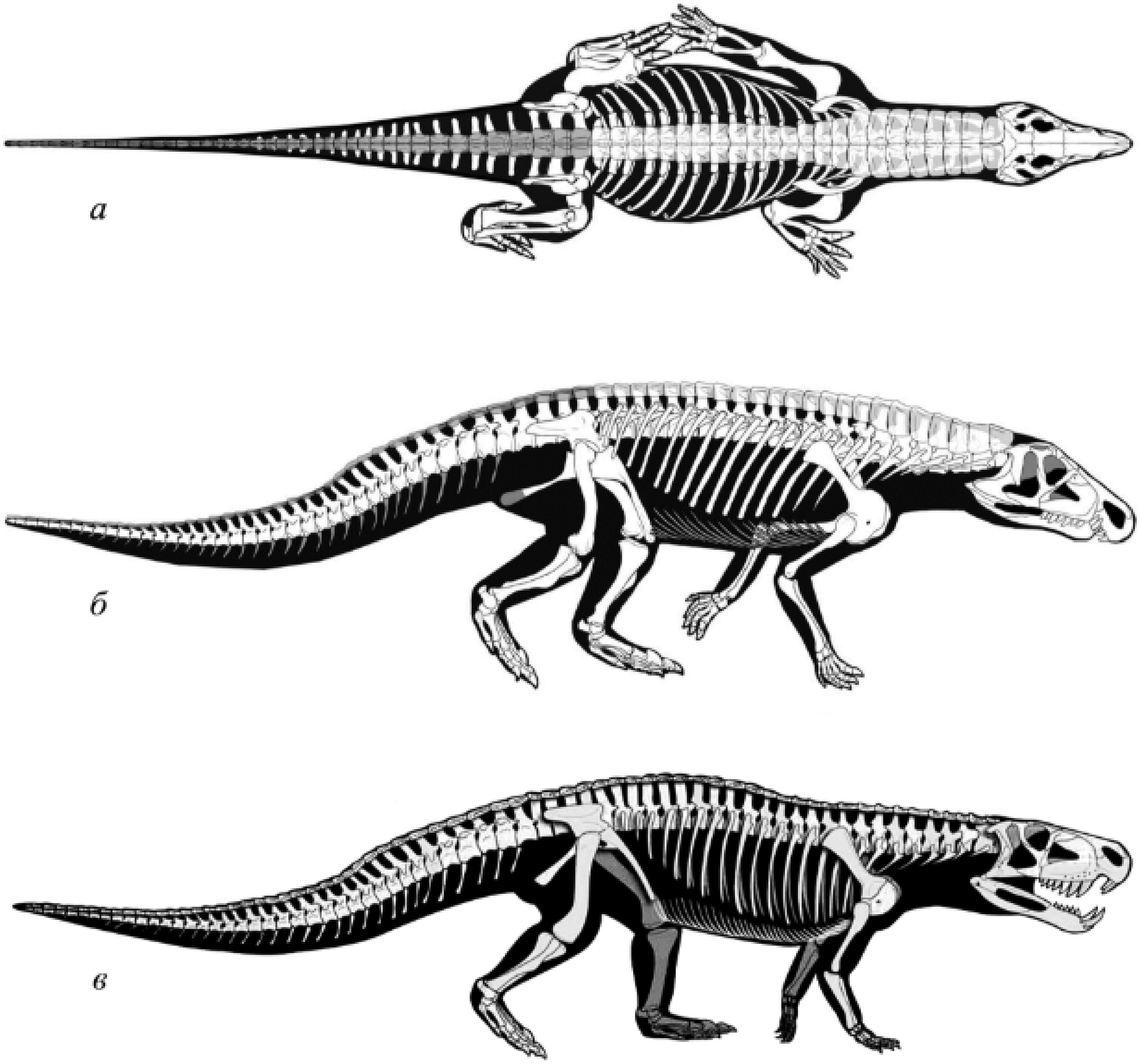

Fig. 8

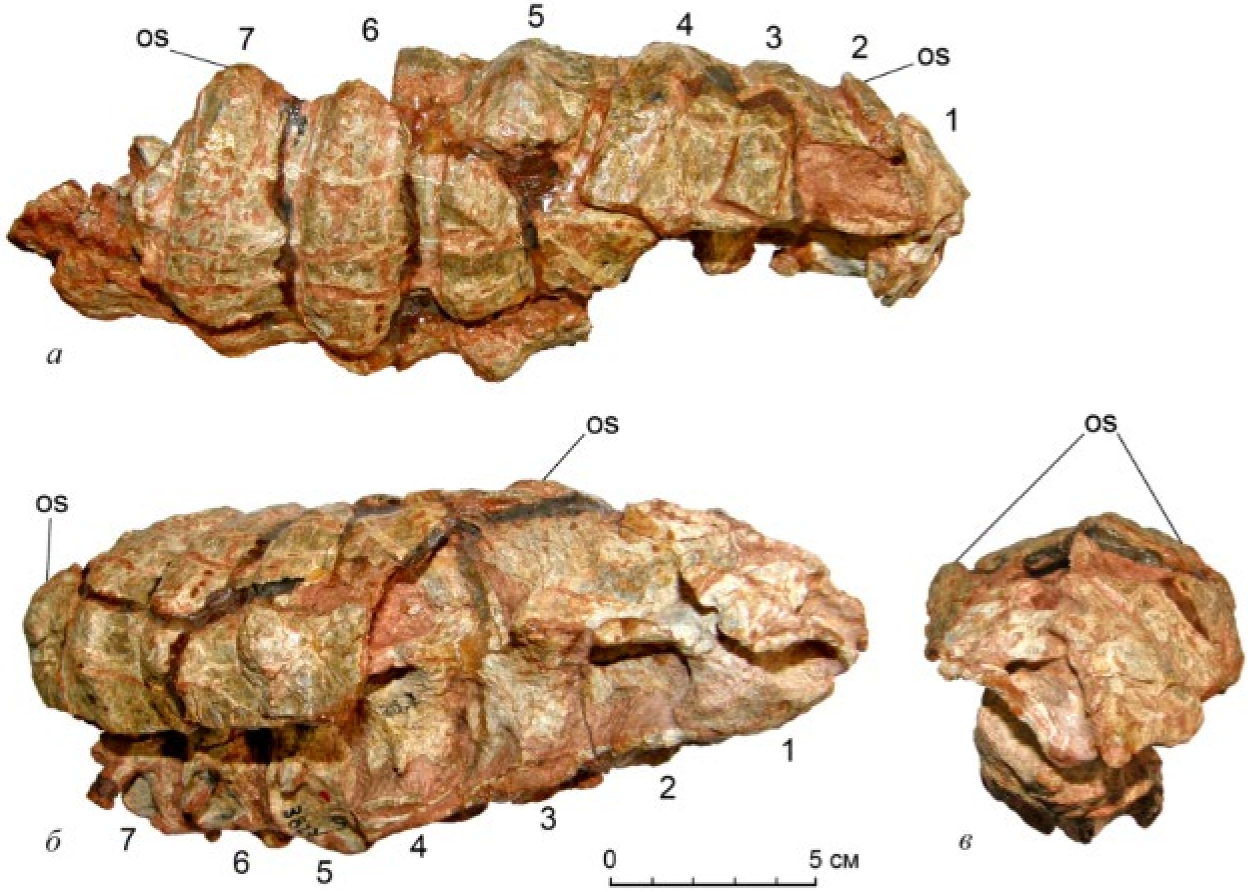

Fig. 9