A New Study of the Brain of the Predatory Dinosaur
Tarbosaurus bataar (Theropoda, Tyrannosauridae)

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Abstract—The brain morphology and the topography of the cranial nerves on an endocranial mold of the theropod dinosaur *Tarbosaurus bataar* (Tyrannosauridae) are examined. The brain of this dinosaur was constructed based on the reptile archetype, with a well-developed specialized olfactory analyzer. In terms of development, the visual centers were superseded not only by the olfactory centers, but also by the auditory centers. Comparative analysis of the brain structure of *Tarbosaurus* and *Tyrannosaurus* shows clear distinctions in the topography of roots of the accessory and trigeminal nerves.

INTRODUCTION

During the last decades, increased attention has been paid to dinosaurs, in particular, to the predatory family Tyrannosauridae. It is distinguished from other Theropoda by a unique set of skeletal characters: the massive jaws, with large dagger-shaped teeth; the short, sigmoidally curved cervical region of the vertebral column; the prepubic position of the pubis, with a craniocaudally extended symphyseal expansion; tiny forelimbs, with a reduced third digit; and the arctometatarsal structure of the foot. Tyrannosaurs are particularly interesting because they occupy the top position in the food chain at the end of the Cretaceous in Central Asia and North America, where they reached the greatest body size (more than 12 m).

The intense collection of new material, and discussions about the morphology, taxonomic composition, and relationships, have resulted in the revision of some previously accepted ideas concerning these animals. At present, they have been removed from Carnosauria sensu lato (Romer, 1956; Molnar et al., 1990) and included in the suborder Tyrannosauria (Olshevsky, 2000), or, more often, in the suborder Coelurosauria (Holtz, 1994, 2001, 2004; Sereno, 1997; Makovicky and Sues, 1998), which is probably closely related to birds.

The organizing of new and previous specimens has revealed a great diversity of tyrannosaurids. Currie (2003) divides this family into two groups. The first is characterized by large size, massive skull, and the femur longer than the shin (Tyrannosaurinae, including *Tyrannosaurus, Daspletosaurus, Nanotyrannus*, and *Tarbosaurus*). The second group has a smaller body size, relatively short femur, and relatively long tarsus (Albertosaurinae, including *Albertosaurus, Gorgosaurus*, and *Maleevosaurus*).

Relationships of some tyrannosaurid taxa (*Alectrosaurus, Shanshanosaurus, Aublysodon, Alioramus*, etc.) remain uncertain, so they possibly belong to another tyrannosaur family (sometimes named Aublysodontidae or Shanshanosauridae). In some cases, tyrannosaurids or their close relatives are thought to have existed before the Upper Cretaceous, although we regard this theory as ungrounded. These Lower Cretaceous taxa were recorded in China (Xu et al., 2004, *Dilong*), Thailand (Buffetaut et al., 1996, *Syamotyrannus*), Japan (Manabe, 1999), and England (Hutt et al., 2001, *Eotyrannus*). It was also reported that tyrannosauroid theropods were recorded in the Upper Jurassic beds, i.e., *Aviatyrannus* from Portugal (Rauhut, 2003) *Guanlong* from China (Xu et al., 2006).

As the biology of tyrannosaurids is analyzed, their feeding pattern and locomotion are usually considered. Some researchers have proposed that these dinosaurs were exclusively or predominantly carrion-eaters (Barsbold, 1983; Horner and Lessem, 1993). However, it is usually accepted that not only young tyrannosaurids but also adults were active predators. This point of view implies the development of fast locomotion (Paul, 1988; Holtz, 1995; Carrano, 1998; Currie, 2000). This conclusion is based on the arctometatarsal foot structure, as in many other theropods externally resembling cursorial birds (Ornithomimidae, Avimimidae, Troodontidae, etc.). The significantly reduced forelimbs are also evidence of a high-speed locomotion. However, the largest tyrannosaurids probably moved at most

as rapidly as a rapidly walking extant elephant (Farlow et al., 1995; Hutchinson and Garcia, 2002).

As the cerebral structures of tyrannosaurids were reconstructed, it was marked that their telencephalon was only slightly increased compared to allosauroid theropods (Larsson et al., 2000). Regarding the major sense organs, the keen sense of smell and acute vision are usually marked. The very well developed sense of smell is supported by the study of endocranial molds of *Tarbosaurus* and *Tyrannosaurus*, which show a large size of the telencephalon, olfactory tracts, and olfactory bulbs (Osborn, 1912; Maleev, 1965; Brochu, 2000), whereas the good eyesight was probably proposed based on the frontolateral position of the orbital plane of *Tyrannosaurus* (Walker, 1964; Maleev, 1965; Molnar and Farlow, 1990), although this is not typical for the majority of its relatives (Carpenter, 1999).

When the biology of tyrannosaurids is discussed, the data from the brain reconstruction are not adequately taken into account. This results primarily from the scarcity of specimens that are suitable for the production of high-quality casts of the brain cavity, reliably showing the cerebral structures. An example of this kind is specimen PIN, no. 553-3/1 (Maleev, 1974, p. 148, text-fig. 12), a braincase of a tarbosaur (*Tarbosaurus bataar* Maleev). This specimen was collected by an expedition of the Paleontological Institute of the Academy of Sciences of the USSR in 1948 in the Mongolian Altan-Ula 2 locality dated Upper Cretaceous, Nemegt Formation. This is usually correlated with the Lower Maastrichtian, although it may be earlier, correlated with the Santonian–Campanian (Alifanov, 2000). The right internal surface of the braincase is extraordinarily well preserved. A plaster cast produced using this specimen was previously used for the first brief description of some brain features of tarbosaurs (Maleev, 1965).

Taking into account recent interest in the biology of tyrannosaurids and experience gained in the study of the structure and physiology of the brain of extinct and extant reptiles, we describe the *Tarbosaurus* brain based on the endocranial cast of specimen PIN no. 553-3/1. This task is connected with the assessment of the extent of development of analyzers and motor systems of the brain of this reptile; this provides new data on the biology of tyrannosaurids.

A comparison between the tarbosaur brain reconstructed based on the endocranial cast and that of *Tyrannosaurus rex* reconstructed using tomographic scanning (Brochu, 2000) of specimen FMNH PR 2081 ("Sue," a complete skeleton including the skull) from the Upper Cretaceous (Hell Creek Formation, Upper Maastrichtian) of South Dakota, United States (Brochu, 2003) shows that the two methods complement each other. This comparison is useful not only for testing the reliability of some results but also for a better understanding of the relationships of *Tarbosaurus* and *Tyrannosaurus*. Note that, in a number of recent studies, they are regarded as closely related species of the same

genus *Tyrannosaurus* (Paul, 1988; Carpenter, 1992; Holtz, 2001). The alternative point of view is that *Tarbosaurus* and *Tyrannosaurus* belong to the Asian and North American tyrannosaurid lineages (Hurum and Sabath, 2003; Currie et al., 2003).

DESCRIPTION

The cast (Fig. 1) of the right half of the *Tarbosaurus* braincase is formed of polyurethane rubber Lasil-40; it is 23 cm long, that is, approximately one-fourth as long as the skull. The maximum width, falling on the posterior margin of the forebrain, is 6.4 cm. The brain reaches the greatest height (8.2 cm) in the region of the cerebellum. The volume of the cast was estimated as 184 cm^3, while the brain weight was approximately 200 g, taking the average density of the nervous tissue of the reptile brain as 1.087 g/cm^3. The meninges, which entirely cover the brain of this reptile during its life, are disregarded in the last calculation.

The surface structure of the endocranial cast of *Tarbosaurus* enables the recognition of the forebrain, olfactory bulbs, epiphysis, infundibulum, position of the midbrain, cerebellum, hindbrain, and medulla oblongata. In addition, the cast distinctly shows the exits of each cranial nerve and anterior cerebrospinal nerves.

The forebrain (telencephalon) of *Tarbosaurus* consisted of paired cerebral hemispheres, which were separated by longitudinal fissure (Fig. 1; Pl. 8, figs. 1, 2). Its length is equal to the width of the hemispheres, as is characteristic of extant alligators. The hemispheres compose almost 40% of the forebrain length. This is less than in the majority of extant reptiles, but coincides with the ratio in the American alligator *Alligator mississipiensis* (40.8%) (Filimonov, 1963). The lateral surface of the hemisphere has a distinct lateral sulcus (fissura lateralis cerebri), which separates the considerably increased region of the neostriatum from the archistriatum, which looks like a lateroventral tubercle (Fig. 1, *Flc, Ar, Ns*; Pl. 8, fig. 2). The dorsolateral surface of the hemispheres has one more superficial sulcus (fissura dorsolateralis cerebri). Apparently, it borders the archistriatum and the dorsal part of the forebrain of *Tarbosaurus*. This was probably represented by a primitive neocortex with transitional zones (Fig. 1, *Fdc, Nc*; Pl. 8, fig. 2). *Tarbosaurus* possibly had all the major structures of the cortical type that are characteristic of extant reptiles. No sign of the hyperstriatic organization of the dorsal part of the forebrain (which is characteristic of birds) has been recorded in *Tarbosaurus*.

Rostrally, the forebrain passes into the olfactory bulbs, which consist of two parts approximately equal in volume. The olfactory region of the bulbs is located ventrally, while the vomeronasal region is dorsally, they are separated by a sulcus (Fig. 1, *Bo, Bv*; Pl. 8, fig. 2). Each region gives rise to short roots of respective nerves, the olfactory and vomeronasal nerves. The
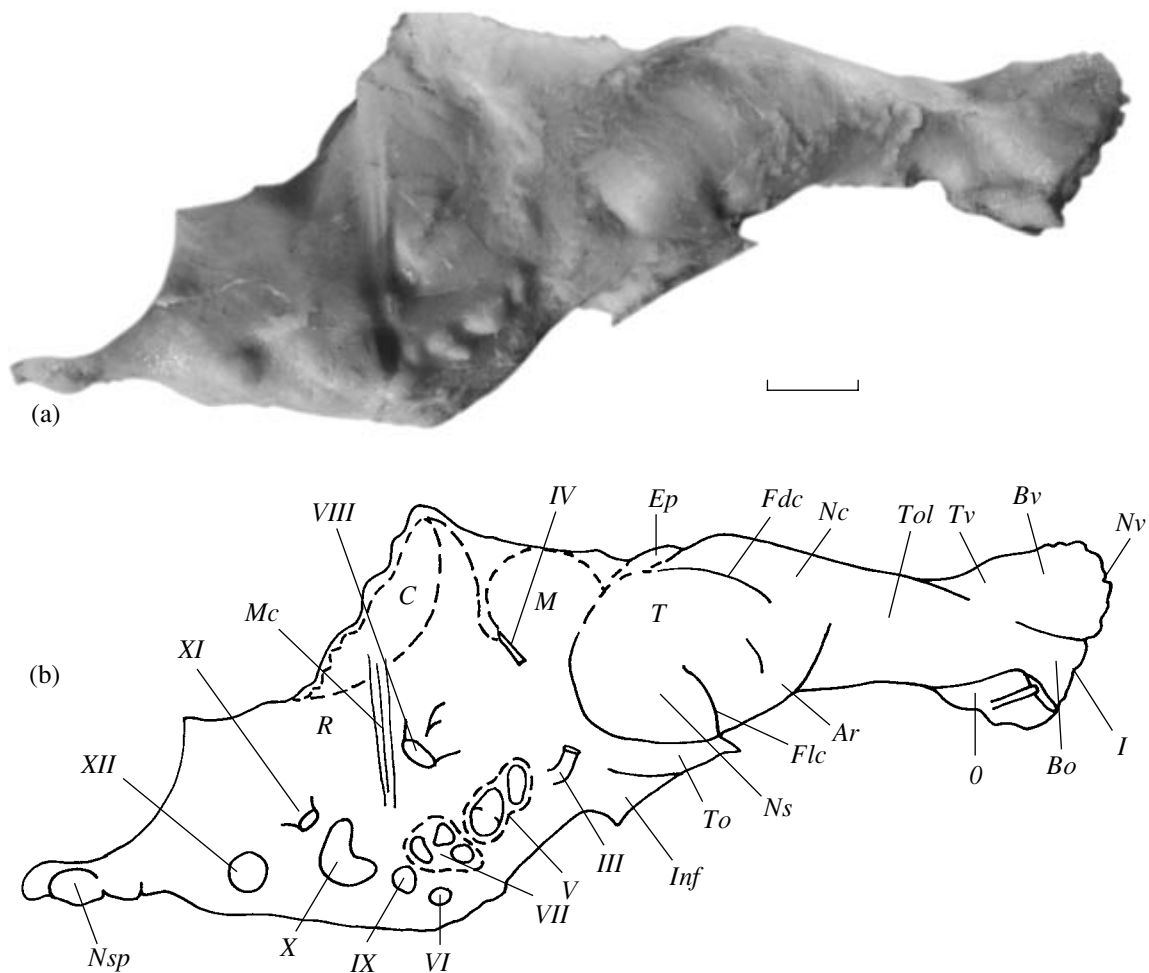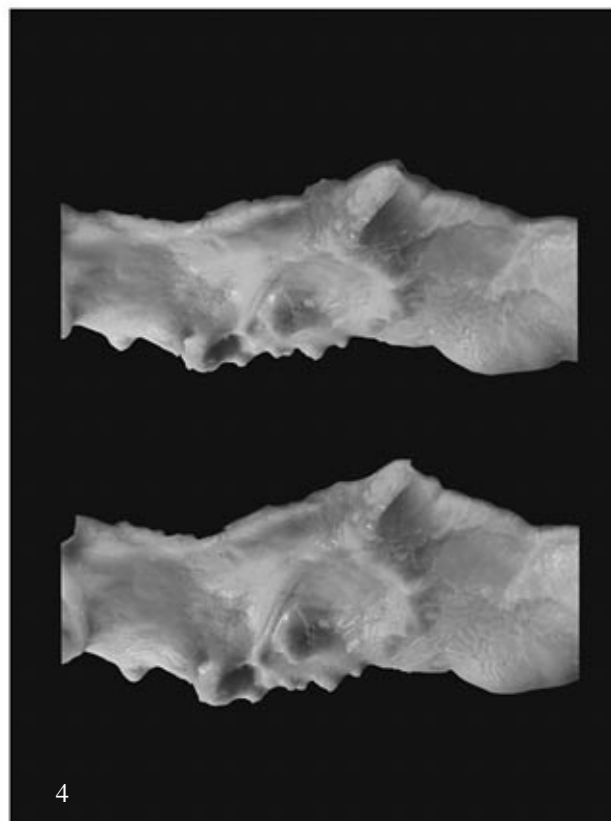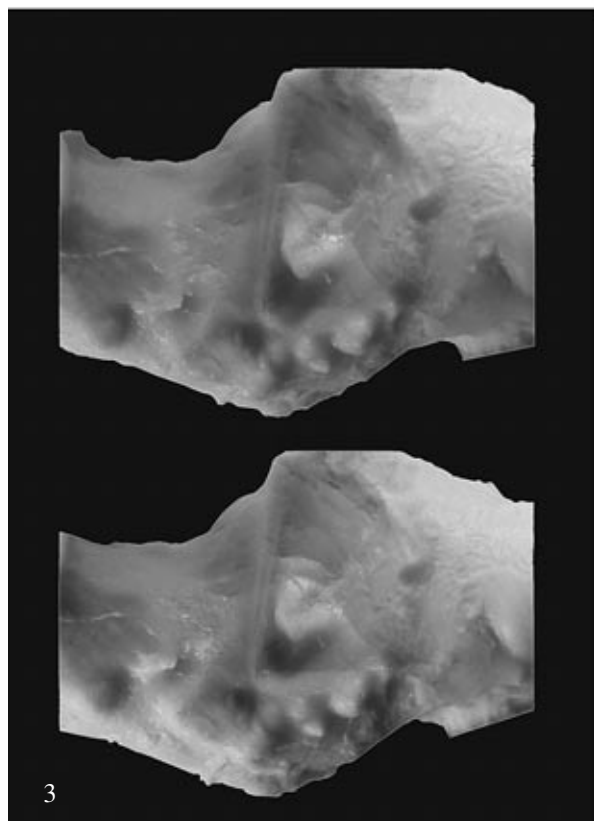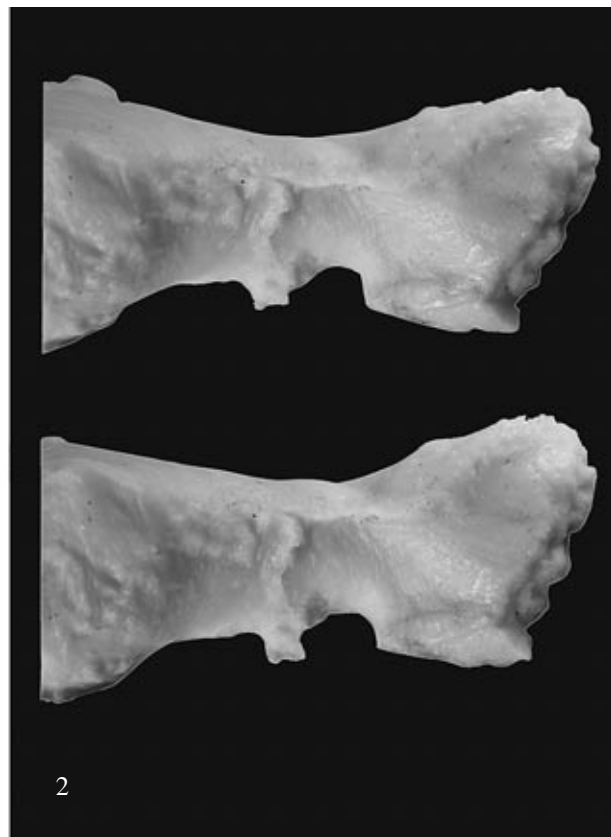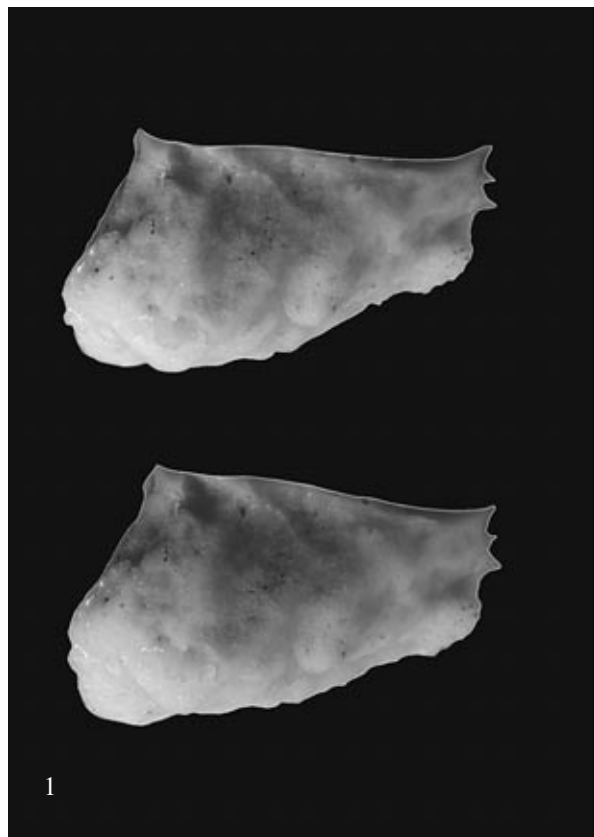
Fig. 1. A neurocranial cast (specimen PIN, no. 553-3/1) of *Tarbosaurus bataar* (Maleev): (a) lateral view and (b) scheme. Scale bar, 20 mm. Designations: (*Ar*) archistriatum, (*Bo*) olfactory bulb, (*Bv*) vomeronasal bulb, (*C*) cerebellum, (*Mc*) fibers of the cerebellar meninges, (*Ep*) epiphysis cerebri, (*Fdc*) fissura dorsolateralis cerebri, (*Flc*) fissura lateralis cerebri, (*Inf*) infundibulum, (*M*) midbrain, (*Nc*) neocortex, (*Ns*) neostriatum, (*Nsp*) root of the first spinal nerve, (*Nv*) vomeronasal nerve, (*T*) forebrain (telencephalon), (*To*) optical tract, (*Tol*) olfactory tract, (*Tv*) vomeronasal tract, (*R*) hindbrain and medulla oblongata (rhombencephalon); and nerves: (*0*) terminal, (*I*) olfactory, (*III*) oculomotor, (*IV*) trochlear, (*V*) trigeminal, (*VI*) abducent, (*VII*) facial, (*VIII*) auditory (n. vestibulocochlearis), (*IX*) glossopharyngeal, (*X*) vagus, (*XI*) accessory, and (*XII*) hypoglossal.

olfactory bulbs of vertebrates are sometimes positioned close to the organs of smell, or fused with the brain; in *Tarbosaurus*, they are connected to the forebrain by long olfactory tracts, which are occasionally mistaken for the olfactory nerves (Maleev, 1965; Brochu, 2000).

The olfactory tract of *Tarbosaurus* consists of two well-pronounced bunches separated by a fold distinctly seen in the cast. The dorsomedial bunch is the vomeronasal tract, while the ventrolateral bunch is the true olfactory tract (Fig. 1, *Tol, Tv*; Pl. 8, fig. 2). Judging from the anatomical borders of the exits of the two tracts from the forebrain, the respective receptor systems of *Tarbosaurus* were represented in the brain separately. The major olfactory system of extant animals plays a key role in the orientation and feeding behavior, while the vomeronasal system is important for sexual behavior and social communications.

The terminal (0) nerve of *Tarbosaurus* (Fig. 1; Pl. 8, fig. 2) is located under the olfactory bulb. Its medial branch is 10 mm in diameter, i.e., thicker than other nerves, except for the vagus nerve. The lateral branch is about 2 mm in diameter. It deviates from the common terminal trunk under a separate envelope and terminates in line with the anterior margin of the olfactory bulb. The terminal nerve of extant vertebrates is a sensory nerve. It innervates the epithelium of the nasal cavity and controls the air flow during breathing and recognition of odors. The large size of this nerve of *Tarbosaurus* suggests that its branches supplied the complex system of nasal cavities and partitions. Previously, the terminal nerve has not been recorded in tyrannosaurids.

The true olfactory nerve (I) is represented in *Tarbosaurus* by short roots at the anterior margin of the olfactory bulbs (Fig. 1; Pl. 8, figs. 1, 2). These are traces of

Plate 8

axons of receptor cells of the olfactory epithelium, which terminate in the olfactory bulbs. In *Tarbosaurus*, the olfactory nerves come out as separate groups of fibers; this resembles macrosmatic mammals, in which these nerves pierce the cribriform plate (lamina cribrosa) of the ethmoid.

The betweenbrain (diencephalon) is only represented in the cast by the epiphysis (epiphysis cerebri) and a fragmentary infundibulum. The epiphysis (Fig. 1, *Ep*) comes out above the longitudinal sulcus between the cerebral hemispheres. Together with the cerebral envelopes, it is 18 mm thick. The thickness of the epiphysis without envelopes is probably about 6–7 mm. The well development of the epiphysial complex suggests a major role of circadian rhythms in behavior, and archaic organization of the betweenbrain. Note that extant crocodiles lack a morphologically detached epiphysis (Nieuwenhuys et al., 1997; Saveliev, 2001).

The cast allows for only indirect judgement of hypophysial dimensions, since only traces of the infundibulum are preserved on the ventral surface of the endocranial cast (Fig. 1, *Inf*); here, it was at least 14–16 mm in diameter. As compared to the brain as a whole, the relative size of the infundibulum of *Tarbosaurus* is similar to that of extant crocodiles and turtles. In living reptiles, the hypophysial complex plays an important role in the regulation of growth, sexual differentiation, and control of hormonally determined behavior. In particular, the large size of hypophysis clearly correlates with the prevalence of instinctive–hormonal programs of sexual and everyday behavior; this is probably true of dinosaurs.

The midbrain (mesencephalon) of *Tarbosaurus* was probably enclosed in the cerebral meninges, because it is indistinct in the cast. The cast shows that the optic nerve (II), namely, the optic tract, enters the brain somewhat rostral to the infundibulum (Fig. 1, *Tol*; Pl. 8, fig. 3). Then, it ascends behind the occipital margin of the neostriatum of the forebrain and gradually disappears under the cerebral meninx. Thus, the anterior border of the midbrain is in line with the occipital margin of the neostriatum and epiphysis.

The optic nerve is a sensory nerve that extends from the ganglion cells of the retina. In reptiles, it is usually proportional in size to the diameters of the eye and optic tract. Consequently, the eyeball of *Tarbosaurus* was at most 10–12 cm in diameter. In the cast, the optic chiasm is almost indistinct; however, the small trace of the optic tract strongly suggests the absence of a complete chiasm of optic fibers.

It is possible to reconstruct the pattern of the visual system based on some features of the midbrain tectum, where its cerebral representation is accumulated. The surface of the meninges in the anterior part of the midbrain tectum has a hardly discernible prominence. The tectum was at most 24 mm long. The small size of this tectum suggests poor development of the visual analyzer. It is noteworthy that, in living birds with hyperspecialized eyesight, the optic centers (lobi optici) of the midbrain are clearly differentiated morphologically and occupy a ventral position. *Tarbosaurus* lacks these specialization characters. On the contrary, the centers of the visual system of *Tarbosaurus* are positioned as in the majority of extant reptiles.

In the cast, the cerebellum is located posterior to the midbrain (Fig. 1; Pl. 8, figs. 3, 4), without clear anatomical boundaries. However, it was probably of a pendentive structural type, as in the lizard *Tupinambis teguixin*. This conclusion is supported by the plicate cerebral meninges on the posterior surface of the cerebellum in line with the hypoglossal nerve.

The hindbrain (metencephalon) and medulla oblongata (myelencephalon) of *Tarbosaurus* compose an integrated morphological structure (rhombencephalon), as in the majority of lower tetrapods. No signs of the pons of the hindbrain are observed. Posterior to the cerebellum, the hindbrain substantially decreases in height; this is characteristic of extant reptiles, in particular, monitor lizards and crocodiles.

The oculomotor nerve (III) of *Tarbosaurus* is located near the posterior margin of the infundibulum (Fig. 1; Pl. 8, fig. 3). In living vertebrates, the size of this nerve reflects the role of orbital muscles in the rotation of the eyeball. It innervates four of six motor muscles of the eye, i.e., the inferior, superior, and medial recti and the inferior oblique muscles. The oculomotor nerve contains autonomous fibers that extend to the muscles of the ciliary body and iris, which provide the iris contraction reflex and lens accommodation. This nerve is extremely conservative in function and uniform in the topology of exit from the brain in all living vertebrates (Filimonov, 1963; Saveliev, 2001). Maleev (1965) and Brochu (2000) mistook the orbital or jaw ramus of the trigeminal nerve for the oculomotor nerve of tyrannosaurids. In actuality, these rami are located more occipitally and are much larger than the oculomotor nerve. Judging from the size of the oculomotor nerve, the eyeball was limited in mobility and, consequently, *Tarbosaurus*, with its motionless head, had a limited visual range.

The root of the trochlear nerve (IV) comes out posterior to the midbrain tectum (Fig. 1; Pl. 8, fig. 3); this is evidence that the site located anteriorly is the midbrain tectum. The trochlear nerve innervates only the

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Explanation of Plate 8

Figs. 1–4. Stereophotographs of particular sites of the cast of the neurocranial cavity (specimen PIN, no. 553-3/1) of *Tarbosaurus bataar* (Maleev): (1) olfactory bulbs, with tubercles of the olfactory nerves, frontal view; (2) olfactory tract, olfactory bulb, terminal nerve, and rostral part of the forebrain, lateral view; (3) cranial nerves of the hindbrain and medulla oblongata, lateral view; and (4) cranial nerves of the hindbrain and medulla oblongata, dorsolateral view.

superior oblique muscle of the eyeball. In reptiles, it originates from the contralateral nuclei, which are located in the ventral part of the brain, then, ascends dorsally, and forms the chiasm. Thus, the trochlear nerve marks the dorsal boundary of the hindbrain; the position of its root differs from other motor nerves, which come out of the brain ventrolaterally. This point is often overlooked. In particular, in the three-dimensional model of the endocranium of *Tyrannosaurus*, Brochu (2000) erroneously interpreted the orbital ramus of the trigeminal nerve as the trochlear nerve. In the tarbosaur endocranial cast described here, the dorsal exit of the trochlear nerve is identified with certainty; this was marked by Maleev (1965). Like the oculomotor nerve, the trochlear nerve of *Tyrannosaurus* and *Tarbosaurus* was rather small.

Thus, the visual system of *Tarbosaurus* was not the key afferent system. It is noteworthy that the idea of overlapping fields of vision of *Tyrannosaurus rex* (Walker, 1964), transformed subsequently into the concept of good and possibly stereoscopic frontal vision of tyrannosaurids (Molnar and Farlow, 1990), seems to have little force, because, based on the arrangement of bones in the orbital region, it is not always possible to judge the efficiency of the visual system. For example, the orbital structure in digging mammals, such as Spalacidae or Bathyergidae, suggests advanced stereoscopic vision; however, this is not the case. In addition, in reptiles, the coordination of images formed in the left and right halves of the midbrain tectum is performed by a small number of commissural midbrain fibers, which are insufficient for high-quality spatial analysis. Even chameleons encounter difficulties; they have to turn eyeballs in the frontal position and take aim at prey objects for several seconds (Saveliev, 2001).

The trigeminal nerve (V) is a mixed nerve. It provides somatic sensitivity of head tissues and innervates the jaw musculature. In *Tarbosaurus*, this nerve comes out of the midbrain as two rami (Fig. 1; Pl. 8, figs. 3, 4). The ophthalmic ramus (V_1) is located rostrally, while the common root of the maxillary (V_2) and mandibular rami (V_3) is caudally. The sensory fibers of the ophthalmic ramus (V_1) innervate the cover of the ethmoid part of the head. Fibers of this ramus are in the eyelids, lachrymal glands, and mucous membrane of the nasal cavity. The maxillary (V_2) and mandibular (V_3) rami include somatic sensory fibers innervating the mouth cavity and most of the head surface. Sensory fibers of the mandibular ramus (V_3) are predominantly connected with the cover tissues below the mouth and with mandibular teeth, while the fibers of the maxillary ramus (V_2) are connected with the upper facial part of the head. The mandibular branch (V_3) also contains fibers innervating the jaw musculature.

Opinions differ as to the identification of the trigeminal nerve. Brochu (2000) erroneously believed that, in *Tyrannosaurus rex*, the motor ramus of the facial nerve was the ophthalmic ramus, while the maxillary and mandibular rami were the hypoglossal nerve. When describing the brain of *Tarbosaurus*, Maleev (1965) thought that the exit of the auditory nerve was the trigeminal nerve. It is an obvious mistake, since the auditory nerve of reptiles is always located dorsal to the trigeminal nerve, because it is connected with the auditory nuclei of the dorsolateral margin of the forth ventricle. In addition, the size of the motor ramus of the trigeminal nerve correlates with the volume of muscles in the jaw apparatus; this implies that, in tyrannosaurids, it was probably better developed than the oculomotor nerve. In vertebrates, the trigeminal nerve is similar in size to the vagus or auditory nerve.

As *Tarbosaurus* and *Tyrannosaurus* are compared, it is evident that the root of the trigeminal nerve of *Tarbosaurus* is substantially displaced occipitally from the posterior margin of the infundibulum, whereas these structures of *Tyrannosaurus* are positioned closer to each other.

The abducent nerve (VI) of *Tarbosaurus* deviates from the brain rather typically for tetrapods, i.e., from the ventral surface of the hindbrain, close to the medial axis (Fig. 1; Pl. 8, figs. 3, 4). The identification of this nerve in the brain of *Tarbosaurus* is the same as in *Tyrannosaurus* (Brochu, 2000). This nerve only supplies with fibers the external rectus muscle, which controls posterior and lateral movements of the eyeball. The presence of this cranial nerve suggests that the eyeball could be turned occipitally and the field of vision apparently increased up to 270°–320°.

The facial nerve (VII) of *Tarbosaurus* is represented by three separate roots (Fig. 1; Pl. 8, figs. 3, 4). The identification of each is complicated because several combinations of sensory and motor fibers of somatic and visceral nature are known. The facial nerve of *Tarbosaurus* is well developed; this provided innervation of the extensive mucous coat of the mouth cavity, palate, and taste buds. The rami of the facial nerve innervated the dermal cover and hypodermal muscles of the head. In a recent reconstruction of cranial nerves of *Tyrannosaurus* (Brochu, 2000), the facial nerve is erroneously placed in the same stem as the auditory nerve.

The auditory tubercles (torus semicircularis) of reptiles are usually located in the posterior part of the midbrain tectum. In *Tarbosaurus*, they are hardly discernible through cerebral meninges. Possibly, they had the same arrangement as in extant birds, i.e., protruded in the cavity of ventricle 3. Thus, it is only possible to judge the auditory analyzer based on the size of the base of the auditory nerve (nervus acusticus or nervus vestibulocochlearis, VIII; Fig. 1; Pl. 8, figs. 3, 4). In the *Tarbosaurus* specimen, this nerve is represented by a large root that comes out of the dorsal part of the hindbrain rostral to the bands of the cerebellar meninges (Fig. 1, *Mc*; Pl. 8, fig. 3). This root is clearly divided by a sulcus into the auditory and vestibular components. The large auditory portion of the auditory nerve is similar in size to the complex of jaw rami of the trigeminal

nerve. In fact, the size of the auditory ramus of nerve VIII is great, so that the auditory analyzer of *Tarbosaurus* is probably the second most important sensory system, just after the sense of smell. The size of the auditory component suggests well developed hearing, which could have been used for spatial orientation, realization of the program of social behavior, and acoustic mechanisms of communication. The large vestibular component of the auditory nerve of *Tarbosaurus* strongly suggests a well developed sensory system of the receptor of angular acceleration (semicircular canals) and receptors of linear acceleration (gravitational receptors), which are also well developed in extant birds.

The glossopharyngeal nerve (IX) of *Tarbosaurus* is located directly posterior to the facial nerve (Fig. 1; Pl. 8, figs. 3, 4). This nerve contains sensory and motor visceral fibers. Judging from its size, *Tarbosaurus* had well-pronounced transversal striated muscles of the pharynx, larynx, epiglottis, and salivary glands. The sensory visceral fibers of the glossopharyngeal nerve are located in the mouth cavity and tongue, where they supply the taste buds at the base of the tongue. *Tarbosaurus* probably had well-developed taste or, at least, a perfect sense of touch in the mouth cavity. Note that, in the studies devoted to the brain of tyrannosaurids (Maleev, 1965; Brochu, 2000), the glossopharyngeal, vagus, and accessory nerves are artificially combined in one small root; however, this point of view is rejected by comparative anatomical data. The same mistakes in the description of the brain of tyrannosaurids in these studies are probably caused by the influence of the first reconstruction produced as early as the beginning of the 20th century (Osborn, 1912; Edinger, 1929).

The vagus nerve (X) of *Tarbosaurus* has the largest root (Fig. 1; Pl. 8, figs. 3, 4). This nerve usually contains all types of visceral fibers and special sensory fibers, which belong to the somatic system. It controls the heart, respiratory system, vascular system of the stomach and intestine. Judging from the size of the vagus nerve of *Tarbosaurus*, the muscles of its soft palate, larynx, and constrictors of the pharynx were well developed, and it was characterized by wide dynamic control of the major physiological functions of the organism and relatively fast mobilization in the case of changes in behavioral pattern.

The accessory nerve (XI) of *Tarbosaurus* is located dorsooccipital to the vagus nerve (Fig. 1; Pl. 8, figs. 3, 4). It contains visceral motor fibers. In vertebrates, except for mammals and some reptiles, the accessory nerve comes out of the brain within the root of the vagus nerve and is regarded as a detached motor component of this nerve. In the neurocranial cast of *Tarbosaurus*, it is possible to recognize the accessory nerve with confidence as a separate nerve, whereas, in the reconstruction of the brain of *Tyrannosaurus* (Brochu, 2000), it remains indiscernible (in our opinion). It may be that, in *Tyrannosaurus*, the accessory nerve came out of the brain within a common trunk with the vagus nerve, as is characteristic of the majority of reptiles.

The hypoglossal nerve (XII) of *Tarbosaurus* deviates from the medulla oblongata as a large medial root. Brochu (2000) mistook the first pair of spinal nerves for the hypoglossal nerve of *Tyrannosaurus*. As regards the tarbosaur cast examined by us, there is no doubt in the identification of the hypoglossal nerve. Maleev (1965) recognized it with certainty, although he examined a rough plaster cast. In the majority of amniotes, this is a somatic motor nerve that innervates the tongue and hypobrachial muscles. The well-developed hypoglossal nerve is evidence of the presence of a rather mobile tongue.

The most occipital part of the medulla oblongata has a small constriction that marks the beginning of the spinal cord. The anterior margin of the spinal cord has a thickening that is a trace of the sensory nerve ganglion of the first pair of the spinal nerves (Fig. 1, *Nsp*).

CONCLUSIONS

The study of the brain and cranial nerves based on the endocranial cast of *Tarbosaurus* displays a large forebrain and extremely well-developed olfactory tracts and bulbs. These features suggest that the tarbosaur brain was specialized according to the reptile morphological archetype. This means that behavior and physiological processes were controlled by instinctive–hormonal programs, which were chosen based on comparative data on various excitation from well-developed sense organs, while the role of individual experience was of minor importance. The arrangement of the forebrain of *Tarbosaurus* is the same as in extant crocodiles, which show a high differentiation of morphological structures. This conclusion is also supported by the superficial topology of interstructural boundaries of the olfactory centers.

Judging from the large size of the terminal nerve, the complex structure of the olfactory bulbs, and the fact that the olfactory nerves come out of the brain as separate groups of fibers, *Tarbosaurus* was a specialized macrosmatic, with a differentiated associative recognition of odors of various natures. The olfactory tract enabled *Tarbosaurus* to determine certain features of food objects and search for them using chemical traces.

The large size of the vomeronasal bulbs, which are almost as large as the bulbs of the major organ of the sense of smell, possibly implies complex sexual behavior of tarbosaurs.

The structure of the base of the auditory nerve suggests well developed hearing, which, in addition to the main functions, could have been related to social behavior. *Tarbosaurus* probably used acoustic communication, with the ability to generate amplitude and frequency modulated sound signals.

The visual system of *Tarbosaurus* was developed to a lesser extent than the olfactory or auditory systems. This, however, does not necessarily mean that it lacked

partial binocular eyesight provided by mobile eyeballs, which faced mostly laterally.

If the brain pattern of tyrannosaurids was typical for other theropods, this comes in conflict with the idea of the origin of birds from predatory dinosaurs, because the olfactory centers of birds are poorly developed, whereas the visual analyzers are usually well developed.

Comparative analysis of the brain structure of *Tarbosaurus* with the data of tomographic reconstruction of the *Tyrannosaurus* brain (Brochu, 2000) show that they are similar in the general structural pattern of the brain. Some differences are only observed in the arrangement of the root of cranial nerves. In particular, the trigeminal nerve of *Tyrannosaurus* comes out of the brain on a line with the infundibulum, whereas that of *Tarbosaurus* is located much more occipitally. In addition, the Asian genus shows a distinct large root of the accessory nerve, whereas, in *Tyrannosaurus*, despite the three-dimensional tomographic reconstruction of the brain, it is not seen and probably came out of the brain within a common trunk with the vagus nerve. Such profound differences between the two tyrannosaurids, which are usually thought to be closely related, are not typical of members of the same reptile family; they suggest at least a long independent evolution of the two taxa. This is supported by the isolation of the terrestrial vertebrate faunas of Central Asia and North America during most of the Late Cretaceous (Kalandadze and Rautian, 1992; Chinnery et al., 1998; Alifanov, 2000).

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