

Brain Structure and Neurobiology of Alvarezsaurians (Dinosauria), Exemplified by *Ceratonykus oculatus* (Parvicursoridae) from the Late Cretaceous of Mongolia

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Abstract—A natural braincase cast of the Late Cretaceous dinosaur *Ceratonykus oculatus* (Parvicursoridae, Alvarezsauria) is described. The brain of this species is constructed based on the reptilian archetype without dorsoventral curvatures. In the midbrain, the optic lobes are displaced ventrolaterally and the acoustic lobes are very large and adjoin rostrally the telencephalon. The cerebellum is bifid and transversely expanded. The complex of the metencephalon and myelencephalon narrows laterally. Some of the characters listed are not typical of the majority of extant and extinct sauropsids. It is concluded that alvarezsaurians had good eyesight and keen hearing and their ancestors were characterized by elements of an arboreal mode of life.

Keywords: Mongolia, Upper Cretaceous, Dinosauria, Alvarezsauria, brain, sense organs.

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INTRODUCTION

The Alvarezsauria are a recently established group of Late Cretaceous dinosaurs. At present, it includes several species from Argentina (*Alvarezsaurus calvoi*: Bonaparte, 1991, 1996; *Patagonykus puertai*: Novas, 1996, 1997; *Achillesaurus manazzonei*: Martinelli and Vera, 2007), Mongolia (*Mononykus olecranus*: Perle et al., 1993a, 1993b, 1994; *Parvicursor remotus*: Karhu and Rautian, 1996; *Shuvuuia deserti*: Chiappe et al., 1998; Suzuki et al., 2002; *Ceratonykus oculatus*: Alifanov and Barsbold, 2009; *Kol ghuva*: Turner et al., 2009), and Canada (*Albertonykus borealis*: Longrich and Currie, 2009). Alvarezsaurian remains undetermined to species have been recorded in Romania (distal part of the tibiotarsus: Naish and Dyke, 2004) and the United States (pubis and ischium fragment: Hutchinson and Chiappe, 1998). This group includes the families Alvarezsauridae (Bonaparte, 1991) and Parvicursoridae (Karhu and Rautian, 1996; =Mononykinae: Chiappe et al. 1998). The first has not been recorded beyond South America, while the second includes only non-South American species.

Opinions differ as to relationships of alvarezsaurians. Bonaparte (1991, 1996) assigned them to basal coelurosaurians and marked secondary similarity to Ornithomimosauria. Based on the study of *M. olecranus*, Perle et al. (1993a, 1994) concluded that it belongs to birds more advanced than *Archaeopteryx*.

This conclusion was supported in some later works (Chiappe et al., 1996, 1998; Novas, 1996, 1997; Foster et al., 1998; Suzuki et al., 2002), although certain critical remarks were also published (Ostrom, 1994; Wellnhofer, 1994; Zhou, 1995; Martin, 1997; Kurochkin, 2000), which were connected with the search for relationships of alvarezsaurians among different groups of theropod dinosaurs, including Maniraptora (Karhu and Rautian, 1996), Ornithomimosauria (Sereno, 1999, 2001), and Ornithomimidae (Martin, 1997).

Recently, some authors and followers of the hypothesis of direct relationship of alvarezsaurians and birds have abandoned the idea that this group is more advanced than *Archaeopteryx* (Chiappe et al., 2002), and assign its members to Coelurosauria (Norell et al., 2001; Novas and Pol, 2002; Chiappe and Coria, 2003), usually in a more advanced position than Tyrannosauridae and Ornithomimosauria, but within the cladistic taxon Maniraptora in the wide sense. However, there was also proposed that alvarezsaurians are a separate dinosaurian stem because their phylogenetic relationships with Theropoda are questionable (Alifanov and Barsbold, 2009).

The contradictory propositions are caused by the extraordinary structure of many skeletal elements of alvarezsaurians. Some features are characteristic of birds (fusion of the jugals and quadratojugals, the loss

of their ascending processes, the development of the keel on the unpaired sternum) and some occur in particular dinosaur groups. For example, long basipterygoid processes and procoelous caudal vertebrae have been described in some sauropods; large prefrontals, long surangular process and short angular process of dentaries, extreme proximal position of the prepubic process of the pubis, opisthopubic pelvis combined with the absence of thyroid fenestrae and strong symphyseal connection of pubes occur in Ornithischia. Unique features recorded in Parvicursoridae are connection between the quadrate and postorbital and shortened proximal end of the third metatarsals.

The most distinctive structural features are observed in the manus of alvarezsaurians. Judging from *M. olecranus* (Perle et al., 1993a, 1994), this region includes a large carpometacarpal block, which consists of fused distal carpal and flattened metacarpals, and a large digit with massive basal and ungual phalanges. One specimen of *S. deserti* has two supplementary digits which are considerably smaller than the major digit (Suzuki et al., 2002). They also have long ungual phalanges. Elements of two other spikelike digits were recorded in *C. oculatus* (Alifanov and Barsbold, 2009). In connection with the last discovery, the determination of the serial homology of previously known digits of the forelimb of alvarezsaurians is doubtful; this concerns the major digit which has been determined as the first digit because of certain structural similarity to respective manual digit of theropods. Apparently, this problem will be resolved, as more complete data are available. At the same time, it is evident now that it is impossible to compare the manus of alvarezsaurians to that of any known dinosaur group.

In this respect, the assignment of the recently described skeleton of the dinosaur *Haplocerirus sollers* from the Late Jurassic of China (Xinjiang Uygur Autonomous Region) to Alvarezsauroidea (Choiniere et al., 2010) is doubtful, because the manus of this species displays typical theropod features. Other skeleton regions show a similar picture (the presence of ascending processes of the jugals and quadratojugals, large angular process of the dentaries, serration on the cutting edges of teeth, prepubic pelvis with well-developed thyroid fenestrae, ossifying and extended symphysis of the pubes, obturator process of the ischia, etc.). Probable relationships of *H. sollers* with alvarezsaurians seem to be supported by the elongated basipterygoid processes and procoelous caudal vertebrae. However, these characters have not been figured or described in detail. At present, only a brief description of *H. sollers* is available; this, along with the incomplete data, prevents the development of alternative hypotheses for relationships of this species. Nevertheless, based on available description, it is tentatively proposed that the species in question is related to the families Coeluridae or Compsognathidae, i.e., to the basal Coelurosauria.

Alvarezsaurians also differ from birds and various dinosaur groups in paleoneurological characteristics, which appeared along with the description of *C. oculatus*. They contribute to the reconstruction of external structures of the brain of the extinct group, delineation of general features of its biology, and canalization of hypotheses concerning relationships. Taking into account the uniqueness and significance of this information, the brain of alvarezsaurians is described here in more detail than in the previous study (Alifanov and Barsbold, 2009).

MATERIAL AND METHODS

This work is based on the study of a natural braincase cast, which consists of condensed sand and lies on the base of the braincase (Figs. 1b, 1c, 1e, 1f) of *Ceratonykus oculatus* (Alifanov and Barsbold, 2009, text-figs. 1–3). This species was described based on the holotype (MPC, no. 100/124), which is a fragmentary skeleton, including an incomplete skull. The skull lacks many bones of the right side, posterior part of the roof, and upper part of the braincase (Figs. 1a, 1d).

The brain structures of *C. oculatus* were examined using a Skyscan 1172 X-ray microtomograph, with a Hamamatsu 100/250 radiating source, at 34.10/6 μm resolution. The illustrations and reconstructions obtained are shown in Figs. 2 and 3. They provided the basis for morphological description and comparative anatomical analysis, which is constructed on the comparison of the established and reconstructed structural elements of the brain of the extinct form examined and living vertebrates. The study involved wet preparations of several reptile and bird species, which are housed in the Laboratory of Development of the Nervous System of the Scientific Research Institute of Human Morphology of the Russian Academy of Medical Sciences. In particular, we examined the South African gecko *Pachydactylus turneri*, monitor lizard *Varanus exanthematicus*, reticulated python *Python reticulatus*, American alligator *Alligator mississippiensis*, hooded crow *Corvus cornix*, and tawny owl *Strix aluco*. For a better understanding we produced a plasticine model of the brain of the fossil form under study (Figs. 4a, 4e).

DESCRIPTION

The preservation of the surface structure of the natural cast of *C. oculatus* allows the recognition of the telencephalon, olfactory tracts (tracti olfactori), mesencephalon, visual (tectum mesencephali) and acoustic (torus semicircularis) regions, cerebellum and rhombencephalon, the complex of the metencephalon, and myelencephalon (Figs. 1b, 1c, 1e, 1f).

The brain of the fossil form in question is rostrocaudally extended and lacks a dorsoventral bend (Fig. 2), which is present in living lizards and snakes (Figs. 4b, 4f, 4g). The last character is evidence of the archaic brain pattern of *C. oculatus* compared to archosaurs.

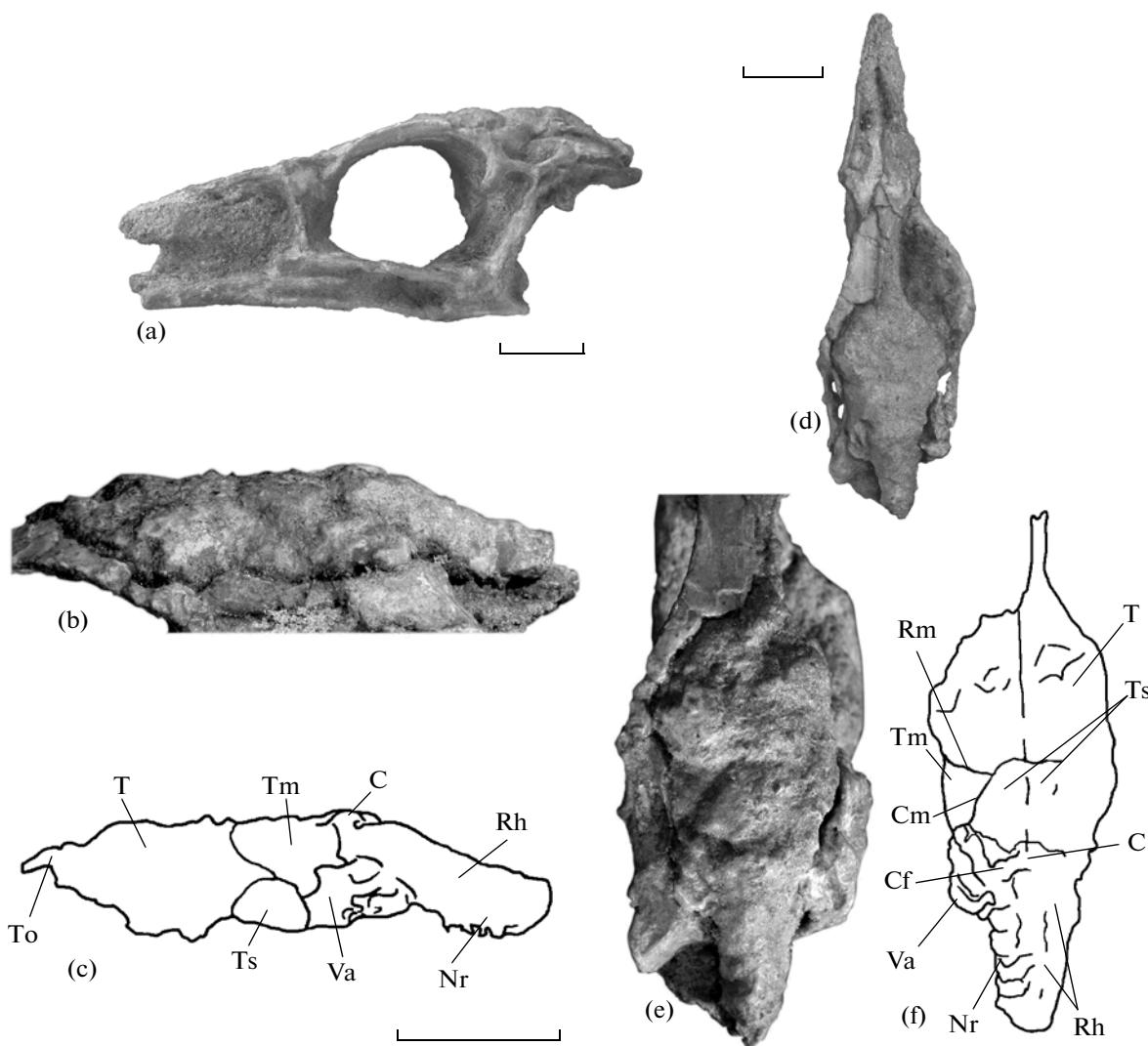


Fig. 1. *Ceratonykus oculatus*, holotype MPC, no. 100/124: (a, d) skull and (b, c, e, f) braincase cast: (b, e) magnified and (c, f) schematic; (a–c) lateral and (d–f) dorsal views. Designations: (C) cerebellum, (Cf) ?anterior cerebellar peduncle, (Cm) caudal midbrain sulcus, (Nr) nerves of the myelencephalon, (Rh) metencephalon and myelencephalon, (Rm) rostral midbrain sulcus, (T) telencephalon, (Tm) optic lobes, (To) tractus olfactorius, (Ts) acoustic lobes, (Va) acoustic and vestibular complex. Scale bar, 10 mm.

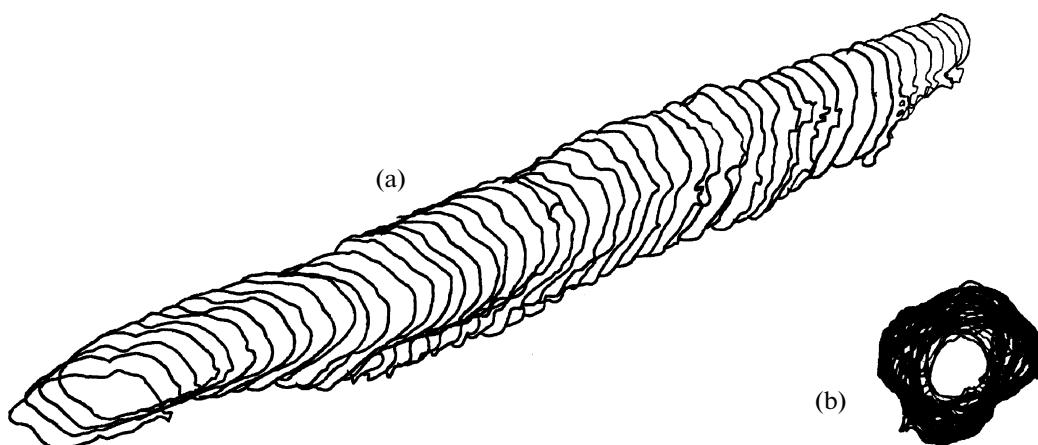


Fig. 2. Graphic reconstruction of the brain of *Ceratonykus oculatus* based on outlines of X-ray sections of different parts of the brain cast: (a) orthogonal and (b) superposition of section projections.

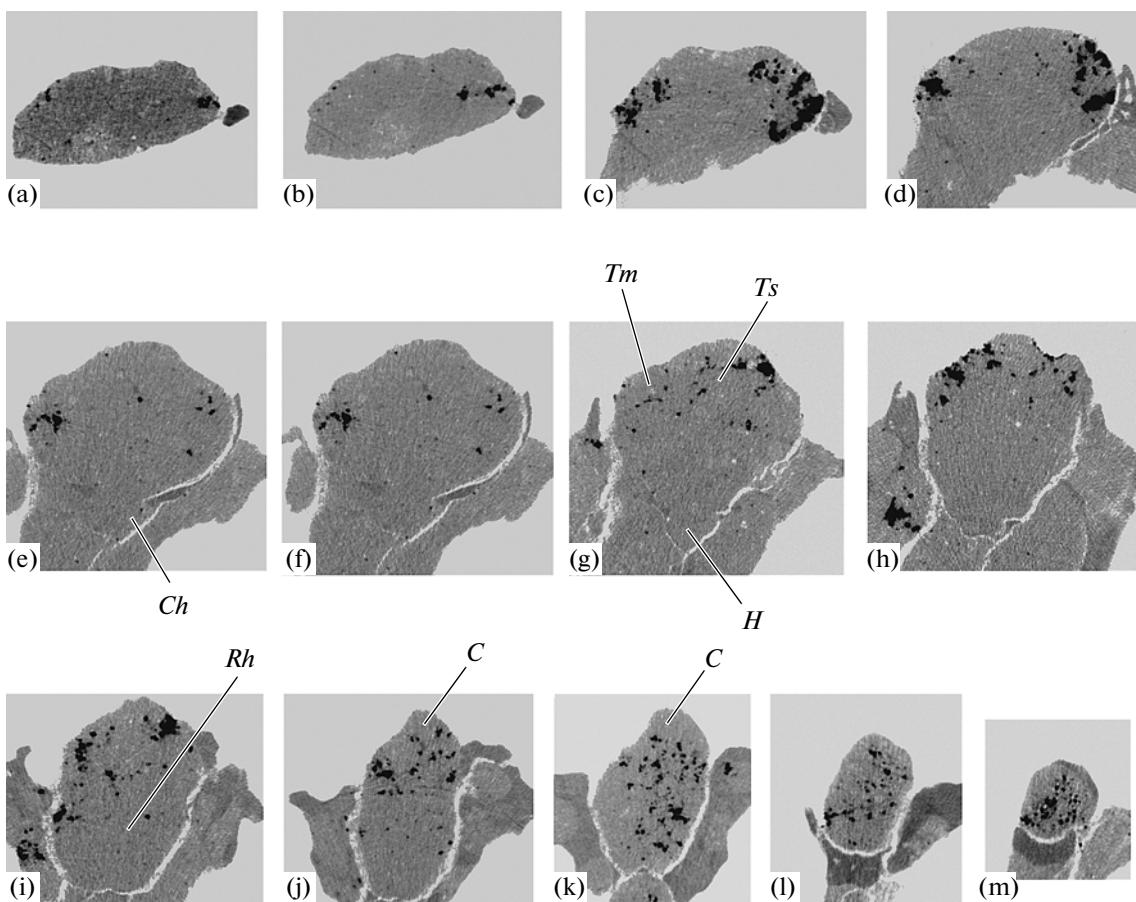


Fig. 3. X-ray sections (posteriad) of different parts of the brain cast of *Ceratonykus oculatus*: (a, b) olfactory tracts, (c, d) telencephalon, (e, f) diencephalon, (g, h) mesencephalon, (i–k) metencephalon and myelencephalon, (l, m) myelencephalon. Designations: (H) hypophysis, (Ch) optic chiasm. For other designations, see Fig. 1.

At the level of cerebral hemispheres, the brain of *C. oculatus* is 11.5 mm wide and 28.6 mm long (excluding the olfactory tracts), i.e., almost half as long as the skull (at most 60 mm). If the endocranial cast belonged to an adult, which is supported by the fusion of the tibiae and astragalus, *C. oculatus* had a very high cerebral index (weight ratio of the brain and body) compared to other reptiles. In this ratio, it approaches young crocodiles.

The telencephalon hemispheres are almost as long as wide (11.8 mm). Close to the beginning of the olfactory tracts, they are separated by the interhemispheric sulcus. The surface of the left hemisphere retains traces of the meninx. The forebrain is isolated from the midbrain by a distinct transverse sulcus, which is divided into two lateral sulci. The rostral sulcus is the boundary between the telencephalon and mesencephalon, and the occipital sulcus separates the lobes of the midbrain (Figs. 1b, 1c, 1e, 1f).

The olfactory tracts begin from the rostral margin of the telencephalon. The olfactory bulbs are indiscernible in the specimen. X-ray microtomograms do not show their features. The olfactory bulbs were prob-

ably in general the same as in the majority of extant reptiles, i.e., were separated from the telencephalon by extended olfactory tract. However, in the fossil specimen described, they are considerably smaller compared to the brain than in the reticulated python, American alligator (Figs. 4c, 4h), or monitor lizard (Figs. 4b, 4g).

Note that, in *C. oculatus*, relatively small olfactory bulbs are combined with the telencephalon (Fig. 4e) the relative size of which is not smaller than in crocodiles (Fig. 4h) and much larger than in snakes (Fig. 4f) or lizards (Fig. 4g). This fact may be connected with either a decrease in functional significance of sensory centers of the olfactory system or development of the telencephalon based on specialization of the secondary olfactory centers. Similar changes repeatedly occurred in the course of evolution of the nervous system (Saveliev, 2005). This principle gave rise to the associative apparatus of the brain of birds and mammals.

The diencephalon of *C. oculatus* is invisible on the external surface of the cast. X-ray microtomograms lack a trace of the epiphysial complex. If this is not a result of poor preservation of the diencephalon, it is

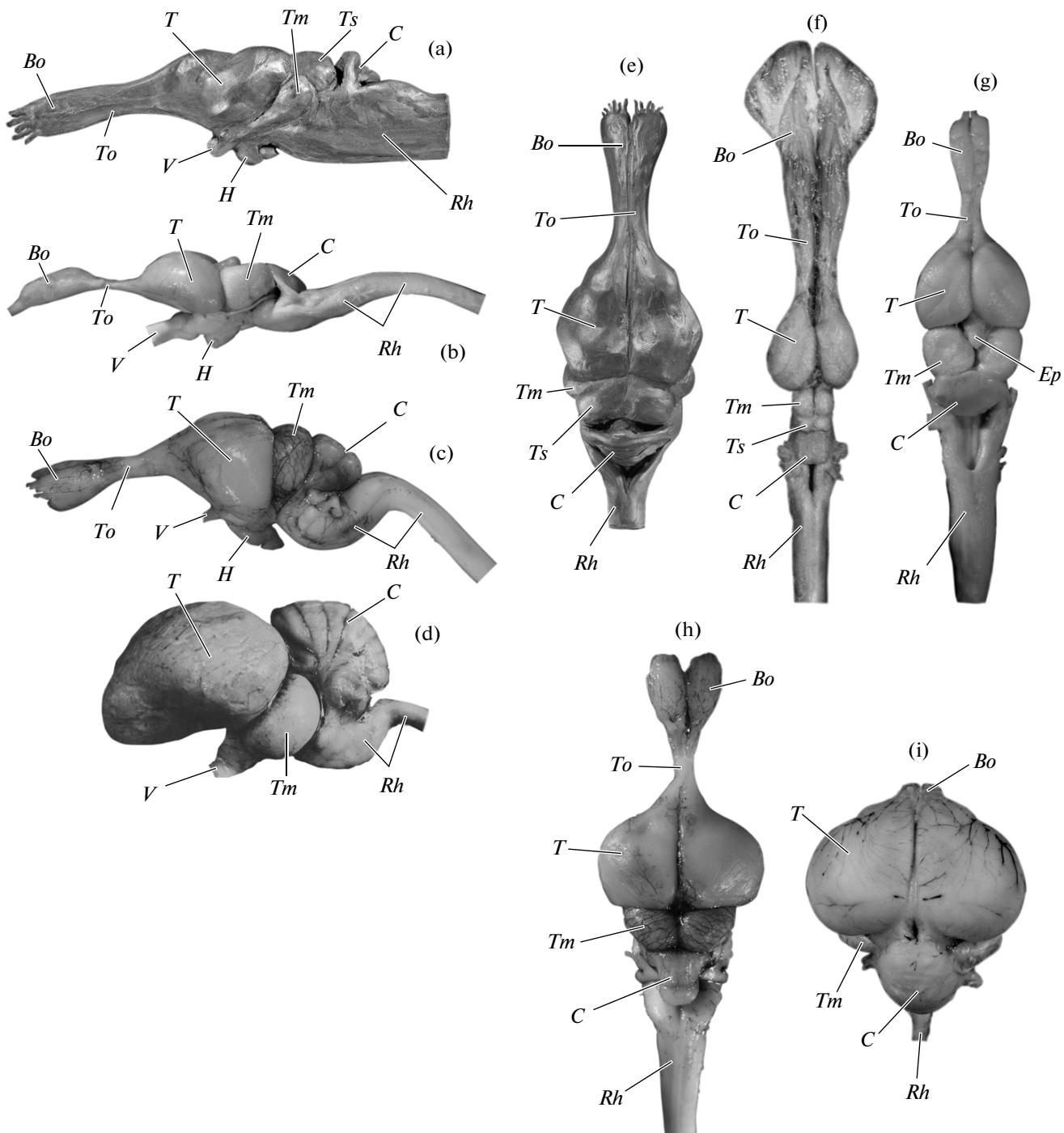


Fig. 4. Brain: (a, e) *Ceratonykus oculatus*, reconstruction; (b, c, f–h) extant reptiles; and (d, i) birds: (a–d) lateral and (e–i) dorsal views: (b, g) monitor lizard *Varanus exanthematicus*; (c, h) American alligator *Alligator mississippiensis*; (d) tawny owl *Strix aluco*; (f) reticulated python *Python reticulatus*; (i) hooded crow *Corvus cornix*. Designations: (Bo) bulbus olfactorius, (Ep) epiphysis, (IV) fourth ventricle, (V) optic nerve. For other designations, see Figs. 1 and 2.

possible to propose that, in the fossil form, the circadian rhythms were controlled by the visual system, as in crocodiles (Nieuwenhuys et al., 1997). A detailed X-ray study of the specimen shows a distinct hypophysis in the lower part of the diencephalon; this is evidence of neurohumoral regulation of growth, matura-

tion, and sexual activity, which is characteristic of many living reptiles.

The roof of the midbrain of *C. oculatus* consists of two pairs of lobes, i.e., quadrigeminal plate (lamina quadrigemina tecti). The rostral pair is homologous to the anterior part of the midbrain roof of reptiles and

the ventrally positioned optical lobes of the brain of birds. These lobes are connected by the optic tracts, with the optic chiasm and represent the cerebral center of the visual analyzer. The visual part of the quadrigeminal plate of the fossil specimen considered is large and displaced ventrolaterally relative to the telencephalon hemispheres (Figs. 1b, 1c, 1e, 1f), as in birds. Dorsorostrally, the lobes are bordered by the ventro-occipital margins of the telencephalon. The role of the visual system is estimated based on the size of the optic chiasm (Figs. 3e, 3f); in *C. oculatus*, it is relatively large, approximately as large as in the monitor lizard and larger than in alligator. Apparently, eyes of the fossil form were large; this agrees with a large size of bony orbits, which are at least 15 mm in diameter, i.e., one-fourth of the head length (judging from the narrow skull, the eyes were closely spaced). Thus, it is possible to propose that the eyesight was one of the major sense organs of alvarezsaurians.

Among reptiles, well-developed optic lobes are characteristic of snakes, in which, in addition to the initial functions, they analyze frequency fluctuations of the substrate (Nieuwenhuys et al., 1997). Like *C. oculatus*, pythons have two pairs of lobes on the midbrain roof (Fig. 4f), which are positioned successively and poorly developed compared to other regions of the brain.

Occipital to the posterior margin of the telencephalon and rostral to the cerebellum, *C. oculatus* has posterior (acoustic) lobes on the midbrain roof (torus semicircularis). These lobes are at least as large as the optic lobes, i.e., unusually large; they are positioned closely medially and separated from each other by a shallow sulcus (Figs. 1f, 4e). The acoustic lobes of *C. oculatus* do not form hemispheres, which are characteristic of mammals. Nevertheless, hearing in this species was probably developed to the same extent as eyesight. The acoustic system and vestibular apparatus are represented in the specimen by a hardly discernible fragment of the acoustic ganglion, which is partially damaged by the cast of the cavity of the gravitational receptor of the apparatus and by the rostral fragment of the semicircular duct (Figs. 1b, 1c, 1e, 1f).

The cerebellum of *C. oculatus* consists of two well-pronounced lobes outlined by the rostromedial sulcus (Figs. 1b, 1c, 1e, 1f). It also has longitudinal sulci (Fig. 1e), which differ considerably from those of birds, in which all cerebellar sulci extend transversely. The anterior part of the cerebellum cast of *C. oculatus* has a tubercle, which may be a trace of meninges of the pontocerebellar corner or tubercle produced by the cerebellar peduncle (Figs. 1e, 1f). In general, the cerebellum is similar in structure to that of living crocodiles (Figs. 4c, 4h), but with a distinct lateral expansion.

The occipital margin of the cerebellum of *C. oculatus* is followed by the myelencephalon. Its lateral surface has traces of cerebral nerves, which are not identified. The development of the complex of the myelencephalon and metencephalon, which form an

anatomically integral structure in the fossil form described, is mostly similar to that of extant reptiles, except for one important character displayed by X-ray microtomography. This is the dorsoventral extension of the complex of the myelencephalon and metencephalon over the entire extent (Figs. 3l, 3m). It is interesting that, in all extant reptiles, it expands transversely and, as a result, the cavity of ventricle IV is usually widely open under and (or) posterior to the cerebellum. In *C. oculatus*, the complex is almost twice as high as wide. The last character is usually characteristic of archaic brain of primarily aquatic vertebrates and amphibians. This circumstance suggests that *C. oculatus* had well-developed motor centers controlling the tongue, jaw apparatus, muscles of the cervical region, limbs, and vestibular apparatus. Judging from the anatomical pattern of the metencephalon and myelencephalon, the sensomotoric apparatus of *C. oculatus* was developed to a lesser extent than in all known living reptiles (Nieuwenhuys et al., 1997; Saveliev, 2001).

DISCUSSION

The study of the natural brain cast of *C. oculatus*, in particular, with the use of X-ray microtomography, provides a better understanding of evolution and biology of alvarezsaurians.

One of the most interesting features of brain anatomy of *C. oculatus* is its linear structure, i.e., the absence of bends in the parasagittal plane at the boundaries between the mesencephalon and myelencephalon and in the caudal part of the latter. The posterior cerebral and cervical bends of the brain are characteristic of crocodiles, birds (Figs. 4c, 4d), and dinosaurs; the absence of these bends in *C. oculatus* strongly suggests that they repeatedly appeared in the groups listed. The linear organization is supplemented by the unusual for terrestrial tetrapods high and laterally flattened complex of the metencephalon and myelencephalon.

The study of external structures shows that the visual and auditory analyzers are represented in the midbrain of *C. oculatus* by separate lobes (Figs. 1b, 1c). The optic lobes are displaced ventrolaterally, as that of birds (Figs. 4e, 4f). As indicated above, large acoustic lobes of *C. oculatus* are positioned between the telencephalon and cerebellum. Among extant terrestrial tetrapods, the visual and acoustic lobes of the midbrain are simultaneously well pronounced only in pythons (Fig. 4f). In dinosaurs, the roof of the midbrain has not been examined in detail. The acoustic centers of the midbrain of birds are formed by two ventricles, which open inside the brain and are indiscernible externally. It should be noted that the trend towards the formation of the acoustic lobes in a dorsal position is recorded in *Archaeopteryx* (Whetstone, 1983; Alonso et al., 2004) and recently described *Cerebavis cenomanica* (Kurochkin et al., 2006). However, in this case, the structures considered are very small.

Some features of external morphology of the midbrain supplement the picture of morphological uniqueness of alvarezsaurians, confirming the assumption of the absence of direct relationships or continuity between them and birds or known dinosaur groups.

When characterizing *Alvarezsaurus calvoi*, Bonaparte (1991, 1996) proposed that this Gondwanan taxon is analogous to Laurasian ornithomimosaurs, which are aviform in appearance and have long hind limbs, as in cursorial birds. Martin (1997) supported the general idea of reconstruction of the biology of alvarezsaurians proposed by Bonaparte that dinosaurs of the group discussed had distinct cursorial adaptations.

In the original description of *Mononykus olecranus*, a different reconstruction of the biology of alvarezsaurians was proposed, implying that this form had lost flying ability and its forelimbs became similar to the limbs of digging animals (Perle et al., 1993a, 1994). This hypothesis was supported in a number of subsequent works (for example, Ostrom, 1994; Zhou, 1995; Longrich and Currie, 2008) and even developed (Chiappe et al., 2002; Senter, 2005). In doing so, alvarezsaurians were considered to be similar in lifestyle to living anteaters and pangolins.

The cursorial specialization of alvarezsaurians is obvious, whereas the hypothesis about the use of forelimbs in feeding behavior is questionable. It is hardly probable that a considerable decrease in size of the forelimbs, which is particularly well pronounced in Parvicursoridae, was connected with a certain biological role. It is more likely that alvarezsaurians were analogous to ostrich-like birds, the tiny wings of which are a character of the loss of flight and secondary specialization towards active locomotion using the hind limbs. Alvarezsaurians probably improved cursorial adaptations after the establishment of the main morphological features of the forelimbs. However, the predisposition to active digging movements even in ancestors of this group is doubtful, since the only large digit, with distinctly restricted mobility and pointed ungual phalanx is insufficiently efficient for moving ground. Usually, digging does not result in a decrease in the number of manual elements, in contrast to, for example, climbing trees, which is often associated with reduced mobility and transformation of digits into hooklike structures. These features suggest that the major digit of ancestors of alvarezsaurians were adapted for fixing on stems, branches, or leaves of plants rather than for certain feeding acts.

For the hypothesis of climbing ancestors of alvarezsaurians, the structure of the cerebellum of *C. oculatus* is particularly important. This brain region of this form has at least one transverse sulcus, i.e., is bipartite in structure. This pattern is not typical for any living lizards, which have a sailing structural type of the cerebellum (the same type is observed in some theropods: Saveliev and Alifanov, 2007); however, it is characteristic of crocodiles. Lizards usually have a terrestrial locomotion, while crocodiles are connected with

aquatic environments and, hence, with the necessity to orient themselves in three-dimensional space. Thus, it is possible to conclude that the cerebellum of the crocodile type determines a better coordination of movements than in lizards. Based on the above reasoning, it is proposed that ancestors of alvarezsaurians had an arboreal mode of life.

The complex cerebellum could have been useful for Cretaceous and obviously terrestrial alvarezsaurians for efficient regulation of the speed and various movement patterns. Members of this group probably used not only alternate gait, which is characteristic of bipedal dinosaurs, but also jumps, which require a better muscular coordination.

Taking into account good eyesight and acute hearing, it is easy to propose that the sense of smell played a minor role in behavior of alvarezsaurians. If this is the case, the large telencephalon could have performed associative functions, which are characteristic of birds. Thus, alvarezsaurians probably had a higher level of "intelligence" than in the majority of extinct and extant reptiles. In this case, it was probably approximately as high as in bird.

Thus, the specialization of eyesight, hearing, and sense of smell suggests that, from the point of view of neurobiology, alvarezsaurians were universal predators capable of efficient search for food and hunting (mostly on arthropods and probably small vertebrates) in both open areas and thickets. As compared to other dinosaur groups, they were probably capable of a rapid response to various external factors and rapid locomotion.

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