

# On the Brain of a Primitive Bird from the Upper Cretaceous of European Russia

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**Abstract**—*Cerebavis cenomanica* gen. et sp. nov. from the Middle Cenomanian of the Volgograd Region (Russia) is described based on a brain mold. The brain of *Cerebavis* is characterized by a mosaic combination of primitive and advanced features. The brain weight is estimated as approximately 1 g. The cerebrum is relatively very large, but lacks sulci. The brain mold has long olfactory lobes with large olfactory bulbs, a well-developed epiphysis, and a parietal organ. The auditory tubercles on the dorsal surface of the midbrain are well developed. The optical lobes are located under the auditory lobes, caudoventral to the cerebral hemispheres. The cerebellum is not preserved, but its imprints just behind the midbrain suggest that it was probably relatively small and extended dorsoventrally. The brain of *Cerebavis* is similar in some features to that of *Archaeopteryx*, but is substantially more advanced and more specialized. *Cerebavis* is similar to living ornithurine birds in the large cerebral hemispheres, but differs in the absence of a well-developed neostriatum, the presence of excessively developed olfactory lobes, and in the pattern of the midbrain. Thus, senses of smell, eyesight, and hearing were well developed in *Cerebavis*. It could have been equally active in the afternoon and at night. The unique brain design demonstrated by *Cerebavis* has not been repeated in subsequent evolution. It provides evidence for a wide diversity of feathered creatures in the past. *Cerebavis* probably belongs to the Enantiornithes.

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**Key words:** Cretaceous bird, Enantiornithes, fossil brain, avian brain mold, Late Cretaceous, Cenomanian, Volgograd Region, Russia.

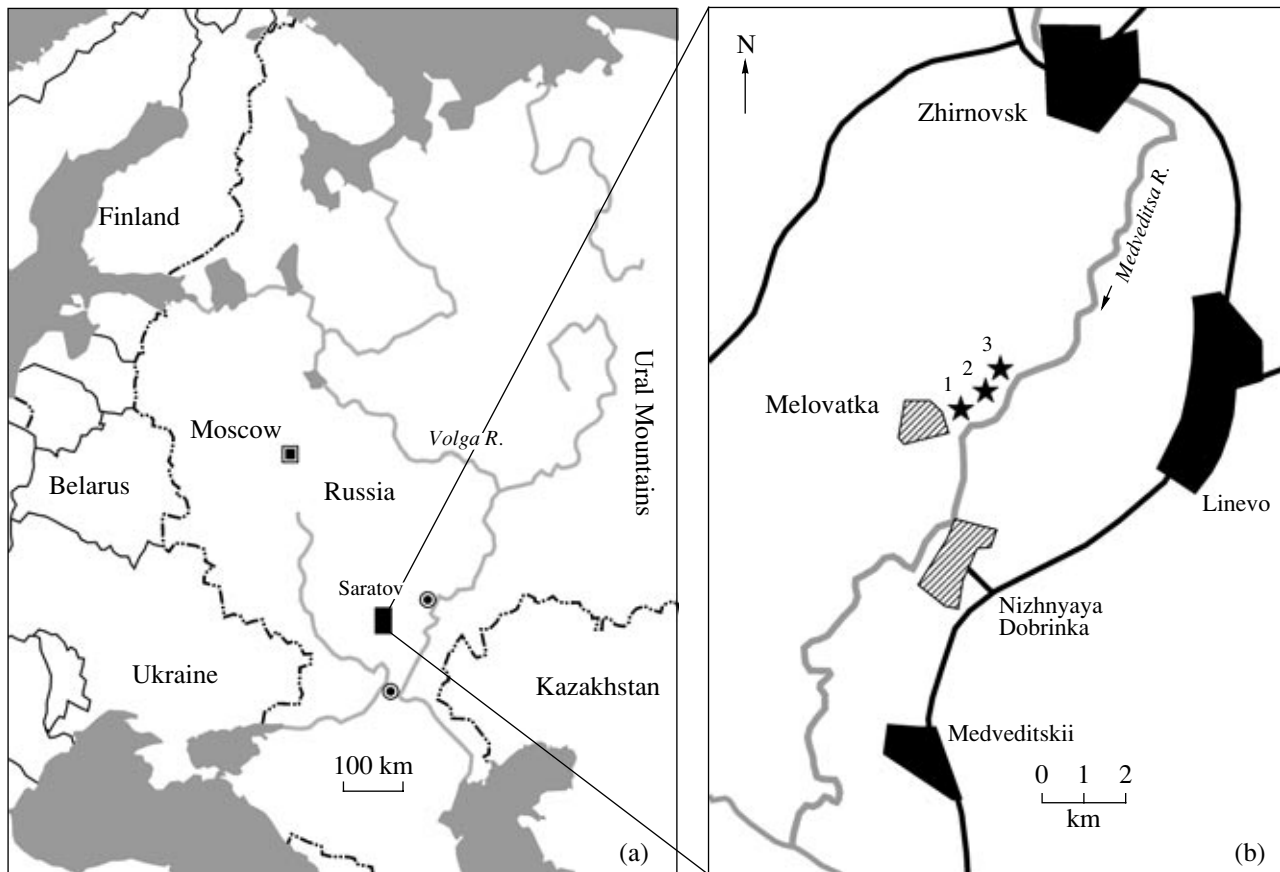
## INTRODUCTION

The nervous system of birds and dinosaurs is of special evolutionary and zoopsychological interest, since the brain of extant ornithurine birds is extremely specialized, while the data on the diversity of feathered dinosaurs and extinct birds has increased considerably during the last years (Chiappe and Witmer, 2002). Even an isolated endocranial cast provides important evidence for the reconstruction of certain stages of the complex problem of the origin of birds (Whetstone, 1983; Kurochkin, 2001, 2004; Alonso et al., 2004). For this reason, the unique endocranial cast of the London specimen of *Archaeopteryx* (BMNH, no. 37001), housed in the Natural History Museum (London), was repeatedly examined over the last 80 years (Edinger, 1926; de Beer, 1954; Jerison, 1968, 1973; Dechaseaux, 1968; Whetstone, 1983; Nieuwenhuys, 1998; Alonso et al., 2004).

The present study describes a natural mold of bird's brain of Cenomanian Age from the Melovatka-3 locality in the Zhirnovskii District of the Volgograd Region of Russia.

## LOCALITY MELOVATKA-3

The Melovatka-3 locality is situated on the right slope of ancient erosion terrace of the Medveditsa River, one of the largest tributaries of the Don River, 50°52'50.7" N, 44°44'10.9" E (WGS 84) (Fig. 1). It was repeatedly visited by the authors of this study from Saratov and by E.N. Kurochkin. The right (western) slope of the Medveditsa River valley is a high erosion terrace cut by short gullies varying in depth and extending towards the floodplain of the river. A section of marine Turonian and Cenomanian deposits more than 70 m thick outcrops in the gullies of the terrace. The Turonian beds are white and grayish yellow marls (Pervushov et al., 1999b); the Cenomanian beds are mostly white and yellowish quartz-glaucopititic and quartz sands, supplemented in the lower layers by aleurites (Pervushov et al., 1999a). The Middle and Upper Cenomanian deposits of this region are represented by the Melovatskaya Formation spreading on the right bank of the Volga Region near Penza, Saratov, and Volgograd (Olfer'ev and Alekseev, 2005). The upper part of the Cenomanian section in the Medveditsa River valley



**Fig. 1.** Geographical position of the Melovatka-3 locality: (a) large-scale and (b) small-scale maps. Asterisks designate the Melovatka-1, 2, and 3 localities.

was dated Middle Cenomanian based mostly on the mollusk and elasmobranch faunas (Pervushov et al., 1999a). This section contains several levels of phosphate concretions of different generations and various degrees of concentration. In the middle part of this interval in the Melovatka-3 section, there are one or two phosphorite horizons 0.3–0.6 m thick, which are rich in phosphate concretions and phosphatized fossils of marine invertebrates. The two phosphorite horizons are separated in places by a yellowish sand interbed up to 1 m thick; however, they sometimes merge into a single horizon. The lower interbed or part of the integrated phosphorite horizon shows in places straight diagonal bedding, which is manifested in the orientation of almost flat pellets, pebbles, and pseudomorphs on bivalve shells.

The phosphate concretions are irregular aggregates and rounded pebbles, ranging in size from several millimeters to 5–10 cm. They are dark brown or nearly black, as the molds of numerous bivalves, gastropods, and, more rarely, cephalopods (possibly *Schloenbachia* sp.). Most of them are only represented by phosphate–calcium–silica inner molds. The scarce brachiopods, including the hinged *?Rhynchonella* sp. and hingeless *Lingula* sp., initially have a phosphate shell distin-

guished by a dark purplish color and retaining its structure in detail. Skeletal remains of siliceous sponges, the Demospongiae (of the genera *Jerea*, *Siphonia*, *Seliscothon*, and *Phyllodermia*), are not numerous and usually show poor preservation and varying degrees of phosphatization; this is attributable to redeposition. The same is true of hingeless brachiopods and some mollusks from the underlying deposits and sponges substantially damaged by bioerosion, which occurred mostly before the main stage of fossilization. Bivalve molds dominate in both number and diversity. They are represented by species typical of Cenomanian seas of the southern and southeastern Russian Plate: *Amphidonte conicum* (Sow.), *A. subconicum* (Glas.), *Crano-cardium ventricosum* (Orb.), *C. constantii* (Orb.), *Protocardia hillama* (Sow.), *Hercodon aquilateralis* Sobetski, *Corbulamella elegans* (Sow.), *Panopea mandibula* (Sow.), *P. acutisulcata* (Desh.), *Neithea quinquecostata* (Sow.), *Chlamys hispida* (Goldf.), *Entonium orbicularis* (Sow.), *Flaventia plana* (Sow.) (Pervushov et al., 1999a). Carbonate shells of mollusks are almost completely dissolved and only small areas near the hinge are occasionally preserved.

Vertebrate remains also occur in these phosphorite horizons and are dominated by elasmobranch teeth.

The following elasmobranchs have been determined: *Eostriatolamia subulata* (Agassiz), *Cretolamna appendiculata* (Agassiz), *Odontaspis* sp., *Megarhizodon* cf. *macrorhiza* (Cope, 1875), *Pseudoisurus denticulatus* (Glückman), *Palaeoanacorax volgensis* Glückman, *Paraorthacodus recurvus* (Trautschold), *Synechodus dispar* (Reuss), *Squatina* sp., and *Polyacrodus* sp. In addition to shark teeth, rare dental plates of chimaeras were also found, including the edaphodontids *Edaphodon sedgwicki* Agassiz, *Ischyodus latus* Newton, *Elasmodus sinzovi* Averianov, and *Elasmodectes kiprijanoffi* (Nesov) and the rhinochimaerid *?Belgorodon* sp. The locality has also yielded vertebrae and teeth of bony fishes (including Enchodontidae), plesiosaurs (Elasmosauridae indet.), and ichthyosaurs (*?Platypterygius* sp.); large spiral coprolites of cartilaginous fishes and small elongated coprolites of bony fishes are common. Pieces of fossil wood are scarce, while pterosaurian and avian bone fragments are even less frequent (Pervushov et al., 1999a; Averianov et al., 2005; sharks were identified by V.K. Golubev and E.K. Sytchevskaya, PIN). The brain mold described below was also found in these phosphorite horizons.

#### FOSSIL BRAIN

The specimen under study was found in 1993 by an expedition of the Department of Historical Geology and Paleontology of Saratov State University and transferred to the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN). The specimen was covered in places with spots and incrustations of extremely durable phosphatized silica, which were very difficult to remove by hand and hence complicated a thorough examination. Therefore, it was initially mistaken for an avian skull. As the enclosing matrix was removed with a pneumatic needle and the specimen was prepared in the Museum of Natural History of the University of Kansas (Lawrence, United States), it became evident that we dealt with an almost complete fossil brain. However, it remained unclear as to which elements were fossilized bone structures of the skull and which were fossilized brain. These questions were resolved in the laboratory of the University of Antwerp (Belgium), using a *Skyscan* 1072 scanning x-ray microtomograph, with the resolution 6  $\mu\text{m}$ , 0.3–0.4  $\text{\AA}$ , 40–80 kV. A series of 1022 x-ray sections of the specimen was produced and recorded in the jpeg format. These sections were used in the study of neurocranial relationships of various regions of the fossil brain and bone structures of the skull.

This raises the question as to how the soft cerebral substance could be preserved in fossilized condition. It was shown that, in experiments in warm water saturated with biogenes and minerals in alkaline medium of pH 8–9, bacterial fossilization of soft tissues of animals and plants developed very quickly, in few hours or even minutes (Gerasimenko et al., 1994; Abyzov et al., 2002). Similar conditions probably existed in the nearshore shallow

water near the islands of a Cenomanian sea that occupied the southern area of the modern Russian Plain. They provided a rapid postmortem siliceous–phosphate fossilization of the brain of this bird, as was in the case with demosponges and molluscan bodies, which preserved in detail the structure of soft tissues. Subsequently, the bony phosphate–calcium elements of its skull were disrupted, while the siliceous–phosphate brain mold was preserved. Chemical analysis with the aid of a SEM in the Laboratory of Electron Microscopy of PIN has shown that the specimen consists mostly of calcium (40–50%), silicon (20–35%), and phosphorus (15–20%), which are probably included in two main minerals, i.e., calcium phosphate,  $\text{Ca}_3(\text{PO}_4)_3$ , and silica,  $\text{SiO}_2(n\text{H}_2\text{O})$ , which compose the nucleus of the brain.

#### SYSTEMATIC PALEONTOLOGY

SUBCLASS SAURIURAE HAECKEL, 1879

?INFRAClass ENANTIORNITHES WALKER, 1981

**Genus *Cerebavis* Kurochkin et Saveliev, gen. nov.**

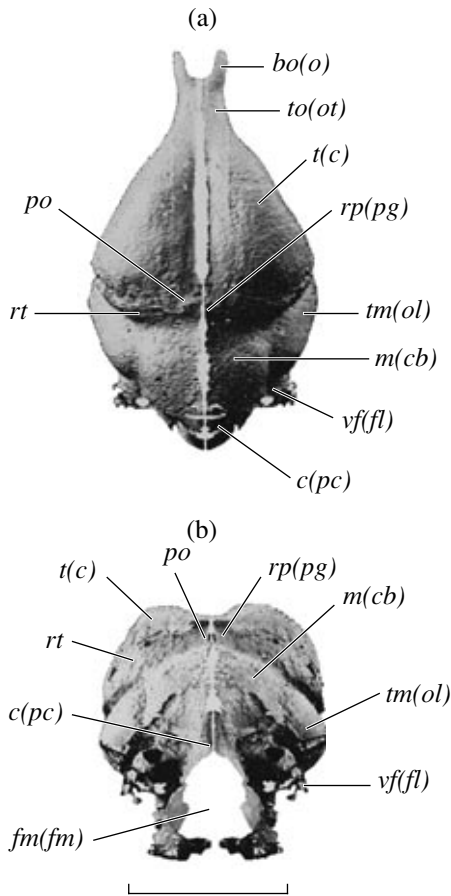
**Etymology.** From the Latin *cerebrum* (brain) and *avis* (bird, feminine gender).

**Type species.** *Cerebavis cenomanica* sp. nov.

**Diagnosis.** Cerebral hemispheres rounded oval. Olfactory tracts thick, with large olfactory bulbs. Interhemispheric fissure shallow, parietal organ well pronounced, located in pineal recess on caudal slope of interhemispheric fissure; roof of midbrain with large auditory tubercles, well-developed epiphysis (glandula pinealis) located between auditory tubercles, optic tubercles (lobi optici) located caudoventral to cerebral hemispheres, not projecting laterally beyond them. Middle part of parasphenoid rostrum swollen.

**Species composition.** Type species.

**Comparison.** It is possible and expedient to compare the brain of *Cerebavis* with that of the London specimen of *Archaeopteryx lithographica* von Meyer, 1861, which was repeatedly reconstructed and investigated (Edinger, 1926; de Beer, 1954; Jerison, 1968, 1973; Alonso et al., 2004). The brain structure of enantiornithines is not known. *Archaeopteryx* also belongs to Sauriurae (Martin, 1983; Kurochkin, 1995, 1996, 2001). In general, the brain of *Cerebavis* is shorter, higher, and wider mostly due to its large cerebral hemispheres; the olfactory tract is longer, but equally thickened (Pl. 6, figs. 1–6) compared to those of the endocast of the London specimen of *Archaeopteryx*, the brain of which is generally elongated (Figs. 2, 3). The hemispheres are separated by a shallow interhemispheric fissure, which is developed to approximately the same extent as in *Archaeopteryx*. The caudal slope of the hemispheres is substantially more abrupt than in *Archaeopteryx*. The parietal (parapineal) organ opens in the interhemispheric fissure on the caudal slope in a well-pronounced recess; it has also been recorded in *Archaeopteryx*, although a depression in this part of its



**Fig. 2.** Tomographic reconstruction of the brain of *Archaeopteryx lithographica* von Meyer, 1861 (on Alonso et al., 2004, modified; resolution no. 15055758 from Copyright Clearance Center, Inc.): (a) dorsal and (b) caudal views. Designations (in parentheses, the treatment of structures after Alonso et al., 2004): *bo(o)*—bulbus olfactorius (olfactory lobe), *c(pc)*—cerebellum (cerebellar prominence), *fm(fm)*—foramen magnum, *m(cb)*—midbrain (cerebellum), *po*—parietal organ, *rp(pg)*—pineal recess [pineal gland (epiphysis)], *rt*—telencephalon recess, *t(c)*—telencephalon [cerebrum (telencephalon)], *tm(ol)*—midbrain tectum [optic lobes (metencephalic tectum)], *to(ot)*—olfactory tract, and *vf(fl)*—vascular or lymphatic fascicle (flocular lobe of the cerebellum). Scale bar, 10 mm.

interhemispheric fissure is virtually absent. The caudo-dorsolateral surface of the hemispheres has a characteristic transverse fold (telencephalon recess), which is also present in *Archaeopteryx*, although it is shallower (Fig. 2; Pl. 6, figs. 3–5). The quadrigeminal plate (lamina quadrigemina tecti) formed by two pairs of widely spaced tubercles is clearly seen on the roof of the midbrain; the auditory (posterior) tubercles are on the dorsal surface of the midbrain, while the optic (anterior) tubercles are on the lateral sides. A well-developed epiphysis (pineal gland) is seen between the auditory tubercles (Pl. 6, figs. 2, 4, 5), while it has not been recorded on the dorsal side of the midbrain of *Archaeopteryx*; the latter also lacks auditory tubercles in this region (Fig. 2). The optic tubercles (optic lobes) are

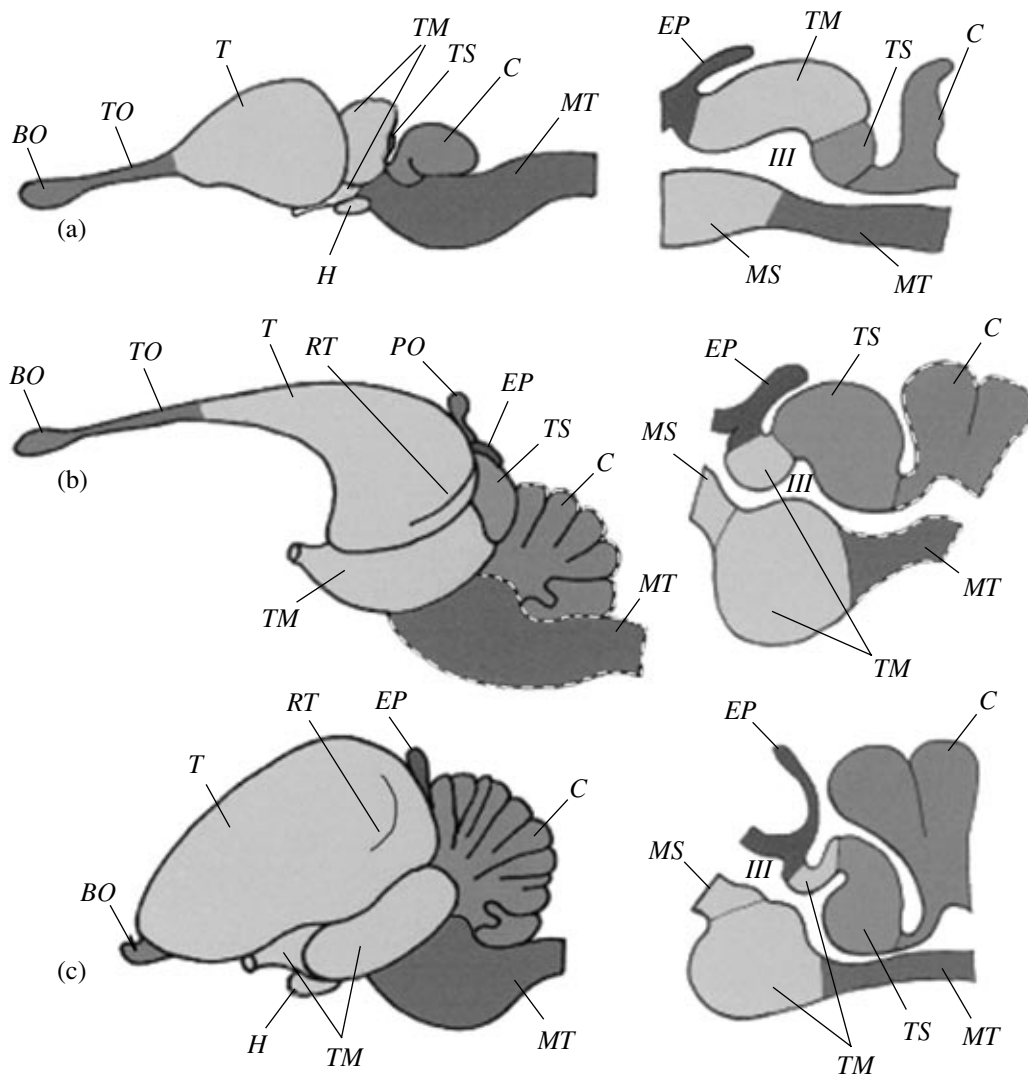
smaller in both relative and absolute dimensions than in *Archaeopteryx*, terminate short of reaching the level of the lateral surfaces of the cerebral hemispheres, and are located more caudoventrally under these hemispheres. In *Archaeopteryx*, the optic tubercles project out of the lateral sides of the hemispheres, which is connected with the smaller volume of the hemispheres, and lie under the midbrain hemispheres, more caudally with reference to the cerebral hemispheres.

Some cranial elements of *Cerebavis* are filled with phosphate–silica matrix in the shape of voluminous formations, which substantially differ from those of *Archaeopteryx*. The interorbital septum was high, extending from the ventral base of the skull to the frontals, with a small foramen in the center. The eminences in the auditory region, following the outline of the squamosal, prootic, and exoccipital are much larger in volume (Pl. 6, figs. 1, 4) than the small, narrow bones of *Archaeopteryx* (Fig. 2b). The formation following the outline of the basiparasphenoid is a broad trapezoid area (lamina parasphenoidalis), from under which an expanded base of the parasphenoid deviates, passing into the parasphenoid rostrum, which is swollen at the base. Small eminences, which most likely correspond to the bases of the basiptyergoid processes, project rostro-laterally from the base of the parasphenoid.

**Remarks.** Fossilized brain molds are extremely scarce, particularly those of birds or birdlike creatures; specimens of this kind have never been recorded in the Mesozoic. Several phosphatized cerebral molds of true Neornithes come from the Paleogene and Neogene beds of Europe, they are rather similar to the brain of extant birds (Dechaseaux, 1970; Mlíkovský, 1980). The brain of *Archaeopteryx* was examined tomographically and based on endocranial casts. The brains of Late Cretaceous *Hesperornis regalis* Marsh, 1872 and *Ichthyornis dispar* Marsh, 1872 were reconstructed based on the skull. The brain of *Enaliornis barretti* Seeley, 1876 from the Albian of England was reconstructed based on a medullary skull cavity.

Most of the fossil brain of *Cerebavis* is formed of cerebral hemispheres (Pl. 6, figs. 2, 5; Pl. 7, figs. 11, 12). The width of the hemispheres is somewhat greater than the length, and they are separated from one another by a distinct, but shallow interhemispheric fissure (Pl. 6, fig. 4; Pl. 7, figs. 12, 13, 16, 17). Due to these broad lissencephalic hemispheres and the extended trace of the cerebellum, the general structural pattern of the brain of *Cerebavis* on the dorsal surface is most similar to that of extant Neornithes. The optic lobes of *Cerebavis* are immersed under the base of the brain and are spaced laterally almost as widely as in Neornithes. However, certain essential differences are clearly pronounced.

The brain outline of *Cerebavis* is pear-shaped, extended longitudinally to a somewhat greater extent than in Neornithes, the brain of which is almost spherical, short and high (Figs. 3b, 3c). A significant distinction of *Cerebavis* from Neornithes is the position of its



**Fig. 3.** Brain structure, laterally (on the left), with sagittal sections (on the right) in line with the midbrain through ventricle III: (a) crocodile, (b) *Cerebavis cenomanica* sp. nov., and (c) pigeon. Designations: (III) third ventricle, (BO) olfactory lobe, (C) cerebellum, (EP) epiphysis, (H) hypophysis, (MS) midbrain, (MT) afterbrain (metencephalon), (PO) parietal organ, (RT) telencephalon recess, (T) cerebrum (telencephalon), (TM) midbrain tectum, (TO) olfactory tract, and (TS) torus semicircularis (auditory tubercles). Dash lines designate reconstructed regions of the brain of *C. cenomanica* sp. nov.

midbrain, which is located between the cerebral hemispheres and the trace of the cerebellum, with the roof open from the dorsal side (Pl. 6, figs. 4, 5; Pl. 7, figs. 16, 17). The midbrain is described in detail below. Another distinctive feature of *Cerebavis* is its long and thick olfactory tracts and large olfactory bulbs, which are only represented by the caudal bases; however, they clearly show large size of the entire bulbs. They are much larger in relative size of the primary olfactory centers than those of living Neornithes. This is evidence of the well-developed olfactory system of this extinct bird and its similarity to extant archosaurs (crocodiles) (Figs. 3a, 3b).

As compared to the thoroughly examined brain cast of *Archaeopteryx* housed in London (Edinger, 1926; de Beer, 1954; Dechaseaux, 1968; Jerison, 1968; Whetstone, 1983; Nieuwenhuys, 1998; Alonso et al., 2004),

the brain of *Cerebavis* has shorter and more voluminous cerebral hemispheres and longer olfactory tracts. It is similar to the brain of *Archaeopteryx* in the presence of the telencephalon recess on the dorsal surface in the caudal part of the hemispheres (Fig. 2; Pl. 6, figs. 3, 5). This fold has been recorded in a number of studies devoted to the brain of *Archaeopteryx* (but was not mentioned by Alonso et al., 2004), although its function remains uncertain (Dechaseaux, 1968; Nieuwenhuys, 1998). Apparently, this fold could have developed in *Archaeopteryx* and *Cerebavis* as a result of outstripping development of the neostriatum (Nieuwenhuys, 1998; Saveliev, 2001, 2005). The caudal topological boundary of the hemispheres of *Cerebavis* and *Archaeopteryx* is in line with the telencephalon recess, as in the majority of living birds. In living birds,

the cranial surface of the cerebrum (telencephalon) always has greater or lesser developed sulci of the cerebrum (valleculae telencephali), while *Cerebavis* and, more so, *Archaeopteryx* lack a trace of sulci. In addition, the interhemispheric fissure of *Cerebavis* is much shallower than in Neornithes. Consequently, the cerebrum of *Cerebavis* shows primitive structural characters; however, it is more similar to that of Neornithes than *Archaeopteryx*.

The design of the midbrain of *Cerebavis* is especially interesting. It essentially differs from the brain of both extant archosaurs (crocodiles) and Neornithes (Fig. 3). The midbrain roof of *Cerebavis* is formed of two pairs of widely spaced tubercles of the quadrigeminal plate. The auditory and optic tubercles are clearly visible on the surface of the neurocranial mold (Pl. 6, figs. 3–5) and in the x-ray sections through the caudal region of the specimen (Pl. 7, figs. 13, 15). The two pairs of tubercles on the midbrain roof are known in the brain of mammals (Saveliev, 2005). However, in *Cerebavis*, they occupy positions that have not been recorded in living birds or mammals. The auditory tubercles of the midbrain roof are located atypically of reptiles or mammals. They come onto the dorsal surface of the midbrain between the cerebral hemispheres and cerebellum (namely, a trace of the cerebellum in the shape of a cavity in the specimen). The auditory tubercles form two well-pronounced hemispheres, with the epiphysis between them (Pl. 6, figs. 2, 5). The midbrain of *Archaeopteryx* occupies a similar position, if it is thought to be represented by the optic tubercles and two slightly convex, bilaterally segmented hemispheres of the auditory tubercles located just behind the cerebral hemispheres, which were probably mistaken by Alonso et al. (2004) for the cerebellum (Fig. 2). The bilaterally segmented cerebellum, at least in extant reptiles and birds, has not been recorded. It is also impossible to concur with the treatment proposed by Alonso et al. (2004) for two formations that substantially project laterally and are located under the caudal bases of the optic tubercles (Fig. 2). These researchers identified them as “floccular lobes of the cerebellum.” In this case, the tomographic reconstruction probably displayed blood or lymphatic vascular fascicles. In addition, it should be noted that, in the paper cited, the optic tubercles are incorrectly assigned to the afterbrain (“metencephalic tectum”), whereas, in actual fact, they always belong to the midbrain.

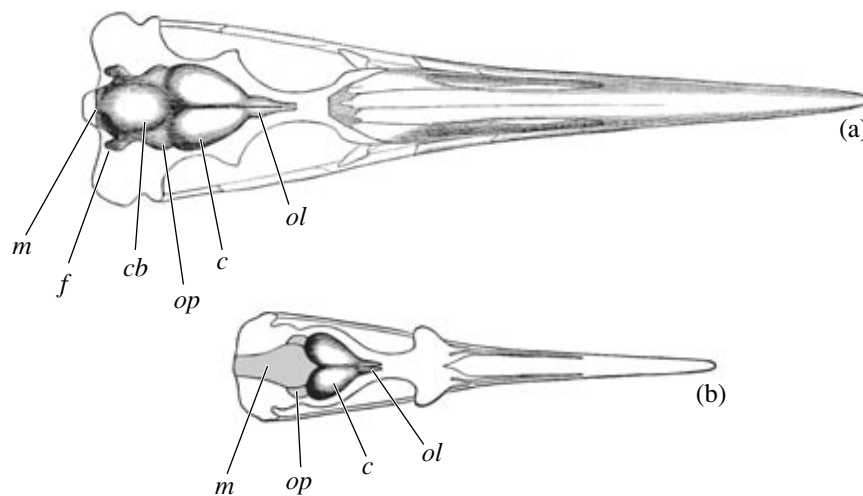
The cerebellum of *Archaeopteryx*, like that of extant reptiles, was probably represented by a very small formation that was designated by Alonso et al. (2004) as “cerebellar prominence” located between the caudal ends of the midbrain hemispheres. If our interpretation is correct, it supports the idea of some researchers that *Archaeopteryx* was only adapted for linear gliding from one landing point to another rather than for a maneuverable and active flapping flight.

The tomographic reconstruction of the brain of *Archaeopteryx* proposed by Alonso et al. (2004) lacks auditory tubercles and epiphysis. We believe these features are reconstructed correctly. The auditory tubercles of *Archaeopteryx* were most likely immersed inside the third ventricle, under the midbrain roof, as in extant reptiles (Fig. 3a). However, *Cerebavis* and *Archaeopteryx* are similar in the dorsally open midbrain.

*Cerebavis* has a well-pronounced parietal organ located rostral to the epiphysis, in the interhemispheric fissure between the cerebral hemispheres (Pl. 6, figs. 2, 4). In the reconstruction of the brain of *Archaeopteryx* (Alonso et al., 2004), it is also distinct (Fig. 2), although it was mistaken for the epiphysis [Alonso et al., 2004, p. 667, “pineal gland (epiphysis)”].

The optic tubercles of the quadrigeminal plate of *Cerebavis* are covered dorsally by the lateral margins of the cerebral hemispheres; however, the position of these tubercles is the same as in the majority of extant birds, i.e., they are located caudoventral to the hemispheres (Pl. 6, fig. 3; Pl. 7, fig. 13). They are identified with certainty based on the position, while their relative size is similar to that of the anterior tubercles of living passerines. The optic tubercles of *Archaeopteryx* are relatively and absolutely larger than those of *Cerebavis* and are shifted substantially more caudally, so that their rostral portions are only slightly covered dorsally by the cerebral hemispheres, and the lateral surfaces project somewhat out of the lateral margins of the hemispheres (Fig. 2), as was shown by Alonso et al. (2004). However, this is basically attributable to the relatively smaller cerebral hemispheres.

The position of the auditory tubercles and their size suggest that the brain of *Cerebavis* followed an unusual path of evolution, which differed from that of ornithurine birds and reptiles. In living reptiles, the midbrain roof does not form a quadrigeminal plate, while the primary bulge of the auditory tubercles is enclosed in the fold between the midbrain and cerebellum (Fig. 3a). The midbrain roof of reptiles is almost entirely occupied by the mesencephalic tectum, while the auditory tubercles are not seen. Only in rare cases, for example, in monitor lizards and crocodiles, the auditory tubercles are seen as small tori. This region of the brain of *Archaeopteryx* probably showed the same structural pattern as in reptiles, judging from the previously published brain reconstructions (de Beer, 1954; Dechaseaux, 1968; Nieuwenhuys, 1998; Alonso et al., 2004). On the other hand, some researchers believe that the cerebellum of *Archaeopteryx* adjoins the caudal edge of the cerebral hemispheres in the area where the epiphysis opens (Alonso et al., 2004); as indicated above, this point of view is in error. The possibility of such a high specialization of the brain of *Archaeopteryx* (Dechaseaux, 1968; Martin, 1995; Elzanowski and Wellnhofer, 1996; Alonso et al., 2004) or birdlike dinosaurs, such as *Ingenia yanshini* Barsbold, 1981 (Osmólska, 2004), is hardly probable. Apparently, this incorrect understand-



**Fig. 4.** Reconstruction of the brain of *Hesperornis* and *Ichthyornis* (after Marsh, 1880): (a) *Hesperornis regalis* and (b) *Ichthyornis dispar*. Designations: (c) cerebrum, (cb) cerebellum, (f) flocculi, (m) medulla oblongata, (ol) olfactory lobe, and (op) optic lobe.

ing of the brain of *Archaeopteryx* (Alonso et al., 2004) is inherited from Jerison (1968, 1973), who mistook the lobes adjoining posteriorly the cerebral hemispheres for the cerebellum. Edinger (1926) and de Beer (1954) believed that, in the London specimen, the cerebral hemispheres are followed caudally by the midbrain, without pronounced auditory tubercles; therefore, they correctly regarded the brain of *Archaeopteryx* to be closer to the reptilian than the avian brain. The cerebellum of reptiles usually lacks transverse sulci and does not approach the caudal edge of the cerebral hemispheres.

In extant ornithurine birds, the auditory tubercles are not seen on the brain surface, since they are located inside, being turned into the cavity of the third ventricle of the brain (Fig. 3c). In *Cerebavis*, the auditory tubercles are as well developed as in extant birds; however, they come onto the dorsal surface of the midbrain (Fig. 3b). As a result, the auditory tubercles are located dorsally, while the midbrain roof is located ventrally. Thus, the basic difference of the brain pattern of *Cerebavis* from extant birds, *Archaeopteryx*, and extant reptiles is the formation of the midbrain roof by the paired auditory tubercles.

The well-developed quadrigeminal plate in the midbrain roof is a distinctive feature of mammals; however, both pairs of their tubercles (auditory and optic) are positioned along the longitudinal axis of the brain. *Cerebavis* also shows both pairs of tubercles, but the auditory tubercles are located dorsally, as in mammals, while the optic tubercles are located ventrally, as in living birds; this distinguishes *Cerebavis* from mammals. A similar pattern of the midbrain roof was probably characteristic of the dromaeosaurid *Bambiraptor feinbergi* Burnham et al., 2000 (see below), but has not been recorded in any other extant or extinct vertebrates examined in this respect.

The interbrain (diencephalon) of *Cerebavis* is only represented by the epiphysis, which is clearly seen between the auditory tubercles, caudal to the parietal (parapineal) organ (Pl. 6, figs. 2, 4). The epiphysis was rather large and was probably connected to the parietal organ by an asymmetrical nerve. This pineal complex is responsible for the circadian rhythms in the activity of *Cerebavis*. Both structural elements are well developed, suggesting that *Cerebavis* was a twilight hunter. It should be emphasized that, in the majority of vertebrates, the epiphysis is located near the posterior edge of the cerebral hemispheres, rostrally or caudally above the epithalamus, or comes onto the surface of the midbrain roof. The epiphysis of *Cerebavis* is on the midbrain roof. This position is characteristic of mammals and atypical for reptiles (Saveliev, 2001).

The afterbrain (metencephalon) of *Cerebavis* is only represented by small lateral fragments and the cavity of the cerebellum, which is not preserved (Pl. 6, figs. 1, 5; Pl. 7, figs. 13–15). The outline of this cavity show that the cerebellum was extended dorsoventrally, as in the majority of extant birds.

The Cenomanian beds of Melovatka could have contained *Hesperornis* and *Ichthyornis*. Therefore, we compared the brain of *Cerebavis* and these Late Cretaceous birds. Judging from the reconstructions produced by Marsh (1880), the brain of *Cerebavis* clearly differs from that *Hesperornis regalis* and *Ichthyornis dispar* in the structure of the olfactory and optic lobes and midbrain roof. Marsh reconstructed the brain of *Hesperornis* and *Ichthyornis* based on their skulls. He concluded that the cerebral hemispheres of *Hesperornis* were extended pear-shaped in outline, with elongated olfactory lobes (Fig. 4a). The cerebellum was also elongated, the optic lobes did not project out of the lateral edges of the cerebral hemispheres. In *Ichthyornis*, the cerebral hemispheres were more rounded in outline and

the olfactory lobes were shorter than in *Hesperornis* (Fig. 4b). The cerebellum and optic lobes were similar in shape to those of *Hesperornis*. Marsh concluded that, in both toothed birds, the brain was in general more reptilian than avian. Edinger (1951), on the contrary, believed that the brain of *Hesperornis* and *Ichthyornis* was more avian than reptilian, and criticized the reconstructions proposed by Marsh, indicating that, in *Hesperornis*, only the interbrain (diencephalon) and the region of the cerebellum and, in *Ichthyornis*, only the olfactory lobes and a piece of the cerebrum could be reconstructed. Jerison (1973), on the contrary, indicated that Marsh produced outstanding reconstructions, correctly demonstrating a true brain pattern of these Cretaceous birds.

The Enaliornithidae were described from the Lower Cretaceous (Albian) beds of Great Britain. The taxonomic position of this group was the subject of considerable discussion and different solutions. Galton and Martin (2002) provided convincing arguments for their affinity to Hesperornithiformes. In addition to numerous bone fragments of the postcranial skeleton, *Enaliornis* is represented by several caudal fragments of the skull. Based on one fragment, Elzanowski and Galton (1991) reconstructed the caudal part of the brain of *Enaliornis barretti*. The caudal region of the cerebral hemispheres, optic lobes, and myelencephalon of *Enaliornis* are substantially dorsoventrally flattened. The cerebral hemispheres are substantially smaller than in extant Neornithes, while the optic lobes are displaced under the myelencephalon; this essentially differs between the brains of *Cerebavis* and *Enaliornis*.

Isolated endocranial molds of pterosaurs have also been found (Edinger, 1941); in addition, a pterosaurian brain was recently examined using computer tomography (Witmer et al., 2002). Old and new data show that the brain of pterosaurs is generally similar to that of extant birds; however, the cerebral hemispheres are only slightly larger in volume than the optic lobes, the olfactory tracts and bulbs are short and small, while the auditory tubercles of the quadrigeminal plate do not come onto the midbrain roof. These features essentially differ between the brains of *Cerebavis* and pterosaurs.

It is also expedient to compare *Cerebavis* with some theropod dinosaurs. The most thorough information is available on troodontids and the dromaeosaurid *Bambiraptor*. A brain cast of *Troodon formosus* Leidy, 1856 found in the Campanian of Canada is elongated anteroposteriorly, and its cerebrum is even smaller than the midbrain or afterbrain; it is noteworthy that the three parts of the brain are equal in height (Currie and Zhao, 1993). The basiparasphenoid and parasphenoid of *Troodon formosus* (as those of the other troodontid *Sinovenator changi* Xu et al., 2002) are narrow and project ventrally (see Xu et al., 2002). Consequently, *Cerebavis* has nothing in common with troodontids in the structure of the brain and the basal part of the skull.

Burnham (2004) reconstructed the brain of the dromaeosaurid *Bambiraptor feinbergi* from the Upper Cretaceous of the United States, and also gave us his unpublished manuscript on the brain of *Bambiraptor*. The brain cast of *Bambiraptor* was produced based on its braincase. The text is accompanied by stereophotographs of this cast and a drawing of the reconstructed brain. The brain of *C. cenomanica* is substantially smaller in absolute size than that of *B. feinbergi*. The cerebral hemispheres of *Cerebavis* differ in the more rounded outline and relatively larger volume. The olfactory tracts of *Bambiraptor* are as thick as in *Cerebavis*, but shorter, while its olfactory bulbs were probably smaller. On the caudal side of the hemispheres of *Bambiraptor*, after an abrupt ventral curvature, there is the midbrain roof, with the auditory tubercles, which occupy the same position as in *Cerebavis*. The optic tubercles lie ventrolateral to the auditory tubercles, they are relatively larger and more rounded than in *Cerebavis*. In our opinion, Burnham also mistakes the midbrain of *Bambiraptor* for the cerebellum. The brain cast of *Bambiraptor* lacks a cerebellum. Thus, *Cerebavis* and *Bambiraptor* are similar in the structure of the midbrain roof, while the cerebral hemispheres of *Bambiraptor* are less spherical and smaller in volume.

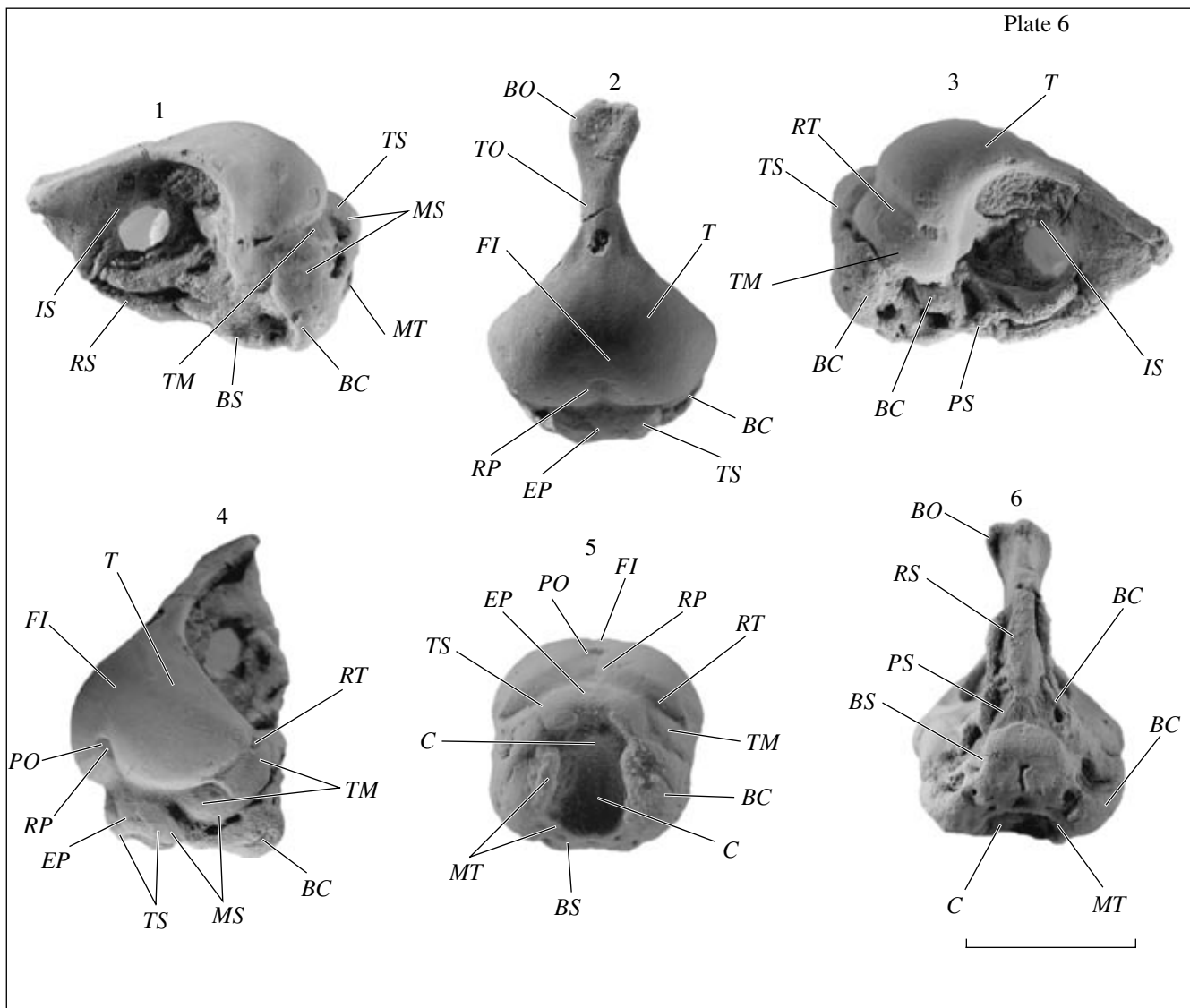
*Cerebavis cenomanica* Kurochkin et Saveliev, sp. nov.

Plate 6, figs. 1–6; Plate 7, figs. 1–17

**E t y m o l o g y.** From the Cenomanian Stage.

**H o l o t y p e.** PIN, no. 5028/2, brain mold with fragments of bony tissue and molds of bony cavities of the auditory region of the skull and sphenoids; Russia, Volgograd Region, Zhirnovskii District, 2 km east of the village of Melovatka, Melovatka-3 locality; Upper Cretaceous, Middle Cenomanian, Melovatskaya Formation, phosphorite horizon.

**D e s c r i p t i o n.** The excellent preservation of the surface structure of the fossil brain enables the recognition of the cerebral hemispheres, olfactory bulbs, parietal organ, midbrain, epiphysis, and the cavity of the cerebellum. The cerebral hemispheres are rounded oval (pear-shaped), but voluminous and large. Rostrally, they pass into thick olfactory tracts, which terminate in extended bases of large olfactory bulbs. A distinct parietal organ (pineal recess) is located on the caudal slope of the hemispheres, in the depression of the interhemispheric fissure. A voluminous midbrain is located caudal to the hemispheres, its roof has a large epiphysis between the auditory tubercles (Pl. 6, figs. 2, 4). The optic tubercles in the shape of relatively small oval prominences are located caudoventrally, under the cerebral hemispheres. The cerebellum is only represented by its cavity, which is located just caudal to the midbrain; judging from its structure, the cerebellum was extended dorsoventrally and was not large (Pl. 6, fig. 5; Pl. 7, figs. 16, 17). The x-ray sections show that the surface of the brain mold is bordered by a dark thin layer (tenths of millimeter thick), and its interior is filled with almost homogeneous fine-grained matrix



## Explanation of Plate 6

**Figs. 1–6.** *Cerebavis cenomanica* sp. nov., holotype PIN, no. 5028/2, brain mold; (1) left lateral, (2) dorsal, (3) right lateral, (4) dorsolateral, (5) caudal, and (6) ventral views. Designations: (BC) bony structures filled with matrix, (BO) olfactory lobe, (BS) basisphenoid, (C) cavity of the cerebellum, (EP) epiphysis cerebri, (FI) interhemispheric fissure, (IS) interorbital septum, (MS) mesencephalon (midbrain), (MT) metencephalon (afterbrain), (PO) parietal organ, (PS) parasphenoid, (RP) pineal recess, (RS) parasphenoid rostrum, (RT) telencephalon recess, (T) telencephalon (cerebrum), (TM) midbrain tectum (optic lobe), (TO) olfactory tract, and (TS) torus semicircularis (auditory tubercles). Scale bar, 10 mm.

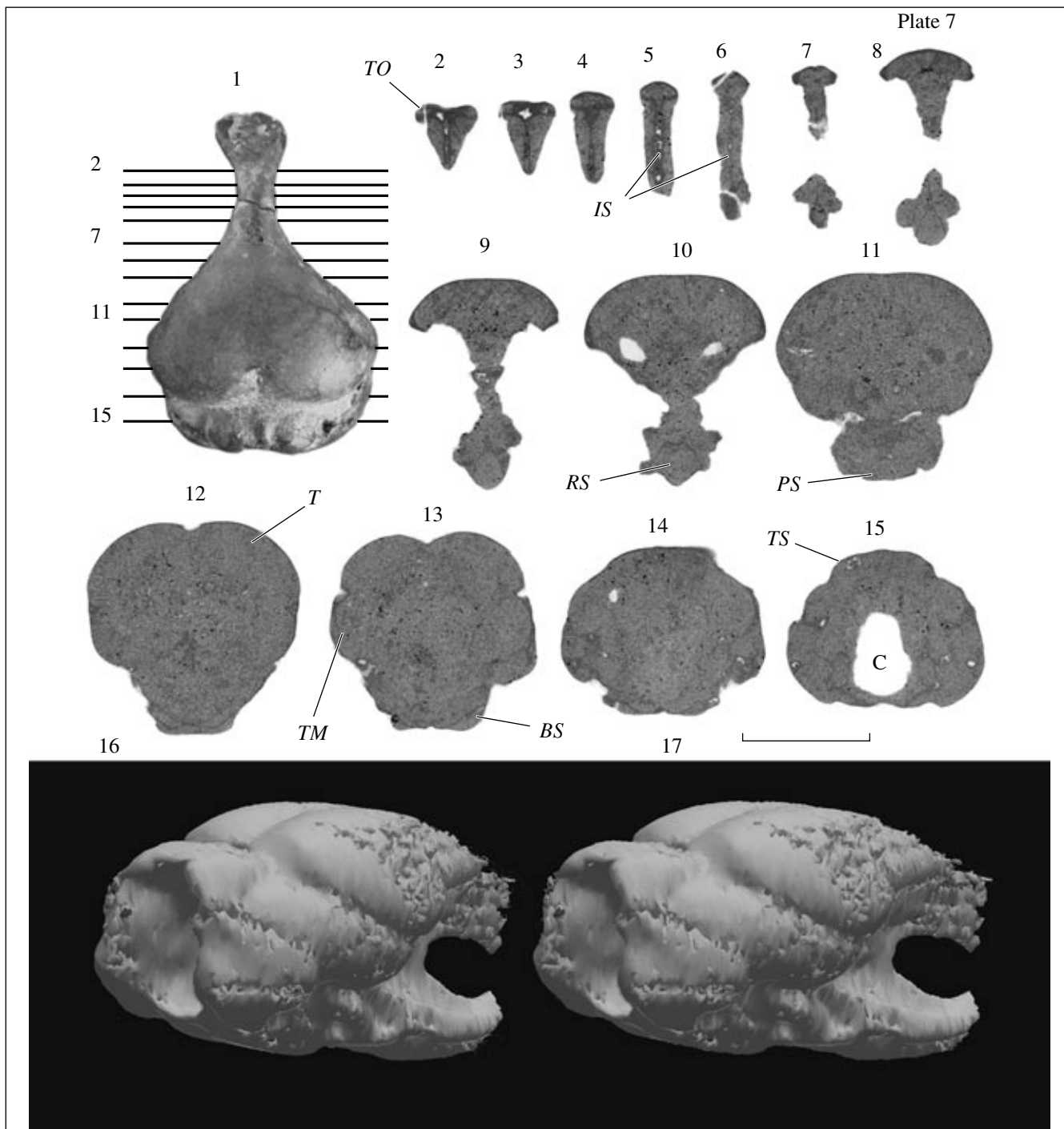
(Pl. 7, figs. 9–15). It is possible to recognize boundaries between particular brain structures and even their internal elements. Of cranial bones, only the interorbital septum and widely spaced spots of bony tissue on the external surface and inside the mold are preserved (Pl. 7, figs. 2–6, 14, 15). In addition, certain bone structures, such as the auditory region and the skull base, are represented by molds filled with calcium phosphate and silica (Pl. 6, 7).

The fossil brain enables the estimation of the general outline of the skull of *Cerebavis*, with closely spaced eyes, which are separated by a thin interorbital

septum and positioned ahead of the brain; this is characteristic of a tropibasal skull unique to birds.

The basiparasphenoid is formed of a broad trapezoid plate. The parasphenoid projects from under the basi-parasphenoid and passes into the rostrum with a peculiar swollen base. Two rostrally directed projections are located at the base of the parasphenoid, which are probably the bases of the basiptyergoid processes.

**Measurements, mm:** greatest brain width at the lateral boundaries of the cerebral hemispheres, 13.57; greatest depth of the specimen from the dorsal surface of the cerebral hemispheres to the ventral sur-



#### Explanation of Plate 7

**Figs. 1–17.** Tomography of the brain and cranial fragments of *Cerebavis cenomanica* sp. nov., holotype PIN, no. 5028/2: (1) dorsal view of the specimen, (2–15) cross sections, obtained with the aid of a Skyscan 1072 x-ray microtomograph, and (16, 17) stereophotographs of the brain, caudolateral view (without olfactory bulbs). Black transverse lines and numbers in Fig. 1 designate sections and their numbers in Figs. 2–15; for other designations, see Pl. 6. Scale bar: (1–15) 10 mm and (16, 17) out of scale.

face of the parasphenoid, 13.72; greatest length of the specimen, 20.6; length of the olfactory tracts, including the bases of the olfactory bulbs, ca. 8.5.

The volume of the fossil brain is estimated as ca. 1 cm<sup>3</sup>, i.e., it weighed ca. 1 g (Iwaniuk and Nelson,

2002). This volume includes some nonprepared pieces of matrix preserved on the specimen, interorbital septum, and small portions of other bony elements, auditory cavities, and skull base filled with phosphate–silica substrate. Therefore, the brain could have been some-

what smaller in volume and mass. However, the specimen lacks the afterbrain, medulla oblongata, and cerebellum. Thus, the estimate ca. 1 cm<sup>3</sup> is probably close to the actual volume.

**R e m a r k s.** The brain size of *Cerebavis cenomanica* is similar to that of the London specimen of *Archaeopteryx lithographica*. The greatest height of the brain of *Archaeopteryx* is 10.0 mm, the width between the lateral edges of the optic lobes is 14.5 mm (measured using the figure from Alonso et al., 2004, text-fig. 3); however, Jerison (1973) estimated the mean height of the brain of the London specimen as 7.4 mm, and its width as 7.2 mm. The volume of the brain of *C. cenomanica* is approximately 1 cm<sup>3</sup>. In the London specimen of *Archaeopteryx*, it was estimated as 1.5 cm<sup>3</sup> (after Alonso et al., 2004) or 0.92 cm<sup>3</sup> (after Jerison, 1973); the body mass was estimated as 500 g or 310–425, respectively. It is difficult to estimate the body mass of *Cerebavis*. When comparing in direct proportion the size of its skull with living birds, the estimates of body mass range from 30 g (based on passerines) to 80 g (based on nonpasserines) (Iwaniuk and Nelson, 2002; Alonso et al., 2004). However, this approach is fraught with an error, since the brain and other systems of *Cerebavis* were probably rather primitive. Nevertheless, taking into account the outline of the skull, which is similar in many respects to living ornithurines, the body mass of *Cerebavis* was probably at most twice greater than 30–80 g. Consequently, the encephalization index of *Cerebavis* is much greater than in *Archaeopteryx*.

The volume of the endocranial cast of the brain of *Bambiraptor* is 14 cm<sup>3</sup>, which corresponds to 12.6 g of weight; the length of the brain is 55.2 mm, the height is 31.3 mm, and the greatest width through the midbrain hemispheres (through the “cerebellum hemispheres” after Burnham, 2004) is 27.5 mm; the body mass of *Bambiraptor* is estimated as 1860–2240 g, with the skeleton less than 50 cm high and about 100 cm long, including the 35-cm-long tail (Burnham, 2004). Thus, the relative size of the brain of *Cerebavis* was substantially greater.

Anatomical features of the brain of *C. cenomanica* turn us to the Enantiornithes. This group of advanced feathered sauriurines developed functional adaptations for active flapping flight through the skeletal structures formed in parallel with ornithurine birds. These morphological features of enantiornithines evolved from the basis inherited from Archaeornithes; therefore, they differed from ornithurines in many structural details of the postcranial skeleton, although the general structural pattern of the skeleton was very similar (Kurochkin, 2001, 2006). The Enantiornithines also had an elongated rod-shaped coracoid, a saber-shaped scapula, V-shaped furcula, bean-shaped humeral head, consolidated carpometacarpus and metatarsus, complex vertebrae, well-developed pygostyle, sternum with a keel, etc. However, each element differed essentially in

structural details from ornithurine birds. Thus, the Enantiornithes showed a high specialization to air, ground, and aquatic locomotion, which was as profound as in ornithurine birds, although it developed on a different and relatively primitive background of their skeletal system. The same is generally true of the brain of *C. cenomanica*. We have shown that, among currently known extinct feathered diapsids, it could not belong to taxa related to theropod dinosaurs, *Archaeopteryx*, *Ichthyornis*, *Hesperornis*, *Enaliornis*, or extant Neornithes. Of all known feathered creatures, *Cerebavis* may be assigned, using indirect evidence, only to Enantiornithes. However, relationships of *Cerebavis* with primitive Early Cretaceous Ornithurae and some feathered Mesozoic groups, such as Patagopterygidae, Kuszholiidae, Zhyraornithidae, Confuciusornithidae, and others remain an open question, because their brain structure is uncertain.

**M a t e r i a l.** Holotype.

## CONCLUSIONS

*Cerebavis* had a mosaic brain structure, combining advanced characters of the central nervous system of extant ornithurine birds with nonspecialized features of reptiles. It was characterized by keen vision and excessively specialized optic tubercles of the quadrigeminal plate, which occupied the position typical for birds. It also had a large telencephalon, which is comparable in relative size to that of living birds, and a cerebellum extended dorsoventrally. These features place it close to Neornithes. However, the cerebrum of *Cerebavis* remained pear-shaped and had thickened and elongated olfactory tracts and large olfactory bulbs, which are by no means characteristic of living birds. The sense of smell was probably used for orientation, in searching for food or, possibly, for mates during the breeding season. The large olfactory analyzer and pear-shaped cerebral hemispheres suggest an archaic brain construction of *Cerebavis*.

It should be emphasized once again that the brain of *Cerebavis* is characterized by unique features, which occur neither in reptiles nor in extant birds. These are primarily the well-pronounced auditory tubercles (which are the torus semicircularis eminences) located on the dorsal surface of the midbrain. The size and shape of these tubercles suggest well developed hearing. *Cerebavis* probably even had an external ear formed of feathers. It may well have been able to equally use eyesight, sense of smell, and hearing for night hunting. The well-developed epiphysis and parietal organ are evidence of adaptation to a nocturnal mode of life. This complex controls daily hormonal activity of the epiphysis depending on illumination. The advanced control system of the circadian rhythms in activity means that it played an important role. Taking into account the small body size, it is possible that *Cerebavis* hid during the afternoon and hunted at night, as is characteristic of many living rallids. This small bird

could have been a generalist predator, feeding predominantly on various small land and aquatic invertebrates.

The unique brain design represented by *Cerebavis* has not been repeated in the subsequent evolution of vertebrates; however, it indicates the wide diversity of evolutionary routes followed by feathered creatures.

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