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Biol. Lett. 2007 **3**, 309-313
doi: 10.1098/rsbl.2006.0617

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Biol. Lett. (2007) 3, 309–313
doi:10.1098/rsbl.2006.0617
Published online 10 April 2007

Palaeontology

A fossil brain from the Cretaceous of European Russia and avian sensory evolution

Evgeny N. Kurochkin[1,*], Gareth J. Dyke[2,*], Sergei V. Saveliev[3], Evgeny M. Pervushov[4] and Evgeny V. Popov[4]

[1]*Paleontological Institute of Russian Academy of Sciences, Moscow GSP-7 117997, Russia*
[2]*School of Biology and Environmental Science, University College Dublin, Belfield Dublin 4, Republic of Ireland*
[3]*Scientific Research Institute of Human Morphology of Russian Academy of Medical Sciences, Moscow 117418, Russia*
[4]*Geological Faculty, Saratov State University, Saratov 410012, Russia*
**Authors for correspondence (gareth.dyke@ucd.ie; enkur@paleo.ru).*

Fossils preserving traces of soft anatomy are rare in the fossil record; even rarer is evidence bearing on the size and shape of sense organs that provide us with insights into mode of life. Here, we describe unique fossil preservation of an avian brain from the Volgograd region of European Russia. The brain of this Melovatka bird is similar in shape and morphology to those of known fossil ornithurines (the lineage that includes living birds), such as the marine diving birds *Hesperornis* and *Enaliornis*, but documents a new stage in avian sensory evolution: acute nocturnal vision coupled with well-developed hearing and smell, developed by the Late Cretaceous (*ca* 90 Myr ago). This fossil also provides insights into previous 'bird-like' brain reconstructions for the most basal avian *Archaeopteryx*—reduction of olfactory lobes (sense of smell) and enlargement of the hindbrain (cerebellum) occurred subsequent to *Archaeopteryx* in avian evolution, closer to the ornithurine lineage that comprises living birds. The Melovatka bird also suggests that brain enlargement in early avians was not correlated with the evolution of powered flight.

Keywords: senses; evolution; Cretaceous; avian; brain; *Archaeopteryx*

1. INTRODUCTION

Our understanding of the early evolution of birds (Aves) has undergone a renaissance in recent years. Discoveries of dozens of well-preserved Cretaceous fossils (140–65 Myr ago), particularly from the Jehol Biota in China, have revealed hitherto undocumented stages in the evolution of birds, theropod dinosaurs, avian flight, perching, diet and behaviour (Chiappe & Witmer 2002). However, with the exception of a few three-dimensionally preserved specimens, including the skull of *Archaeopteryx* (de Beer 1954; Dechaseaux 1968; Whetstone 1983; Dominguez *et al.* 2004), the evolution of the avian brain and sense organs remains poorly understood. The sequence of enlargement and modification of the brain and thus its correlation with the appearance of powered (flapping) flight remains little documented owing to inadequacies of the fossil record. We know that flight is the key morphological innovation of birds (Jerison 1968, 1973; Chatterjee 1997)—making this lineage distinct from theropod dinosaurs; *Archaeopteryx's* brain has typically been reconstructed according to a 'bird-like' model. Dominguez *et al.* (2004) recently suggested that *Archaeopteryx* had a large forebrain and cerebellum (hindbrain), indicating that this bird had 'developed senses demanded by a lifestyle involving flying ability'. We revisit these conclusions in this paper and present an interpretation of a new brain from the Late Cretaceous of European Russia (Kurochkin *et al.* 2006).

2. GEOLOGICAL SETTING

The fossil specimen presented here (PIN, Paleontological Institute of the Russian Academy of Sciences 5028/2) was discovered in a phosphate concretion at the 'Melovatka-3' site in the Volgograd region of Russia (figure 1; Kurochkin *et al.* 2006). This site is located to one side of an erosive terrace of the Medveditsa River, one of the largest inflows of the River Don, where more than 70 m of marine basal Turonian- and Cenomanian-aged sediments of the Melovatskaya Formation are exposed (Pervushov *et al.* 1999*a*,*b*). An abundant molluscan and elasmobranch fauna (Pervushov *et al.* 1999*b*) fixes the age of the Melovatka site to the Middle Cenomanian (Late Cretaceous; 95–93 Myr ago).

3. DESCRIPTION AND COMPARISONS

Preservation of the impressions of the brain surface in the Melovatka bird includes the forebrain (cerebrum or telencephalon), olfactory tracts and bulbs (associated with sense of smell), parietal organ (third eye), epiphysis (pineal gland) and midbrain (mesencephalon), and allows measurement of size and shape of the hindbrain (cerebellum or metencephalon; figure 2). Borders of brain lobes are also visible in PIN 5028/2, although the original skull bones are almost lost—only the interorbital septum, some spots of bony tissue and cavities left by the bones of the sphenoid and auditory region filled with phosphate cemented matrix remain associated with the cast (figure 2). The Melovatka bird brain is almost the same size as the endocast of the London specimen of *Archaeopteryx*—BMNH 37001 (Natural History Museum, London) is 14.5 mm wide (measured on figure 3 in Dominguez *et al.* (2004); but see 7.2 mm in Jerison 1973) compared with 13.6 mm width of the Melovatka brain (figure 3). The new fossil has an elongate and inflated rostrum and a wide parasphenoid—the eyes in the Melovatka bird were hence close together, in front of the brain and separated by the interorbital septum as in all living birds ('tropibasal' condition; Nieuwenhuys 1998; Saveliev 2001). The Melovatka bird also had long, thick and flattened olfactory tracts and large olfactory bulbs—thus may have had a well-developed sense of smell—as in living non-avian archosaurs (e.g. *Crocodylus*; figure 4) and theropod dinosaurs (figure 4); while these bulbs are comparable in size with those of *Archaeopteryx*, the olfactory tracts of the Melovatka bird were longer indicating more elongate nasal and maxillary skull regions.

Received 8 January 2007
Accepted 9 March 2007

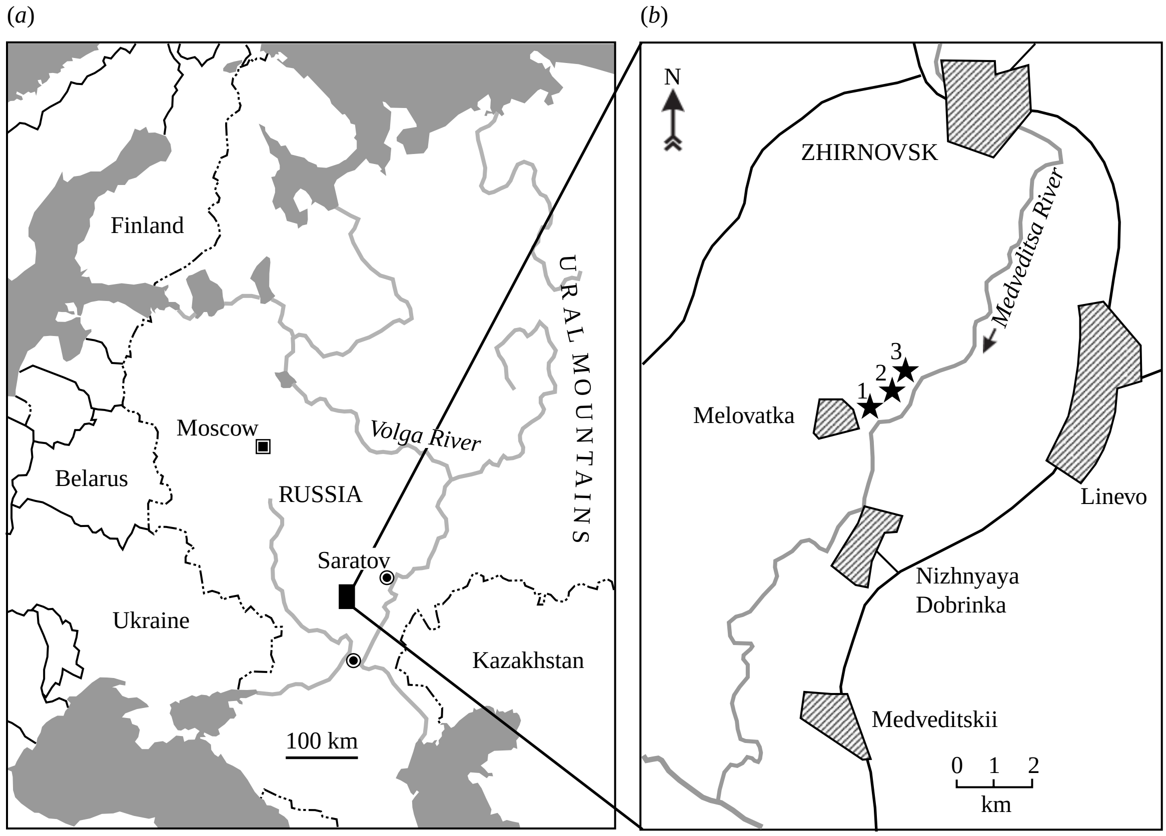

Figure 1. Geographical position of the 'Melovatka-3' locality. Asterisks designate the sequentially numbered Melovatka localities (adapted from Kurochkin *et al.* 2006).

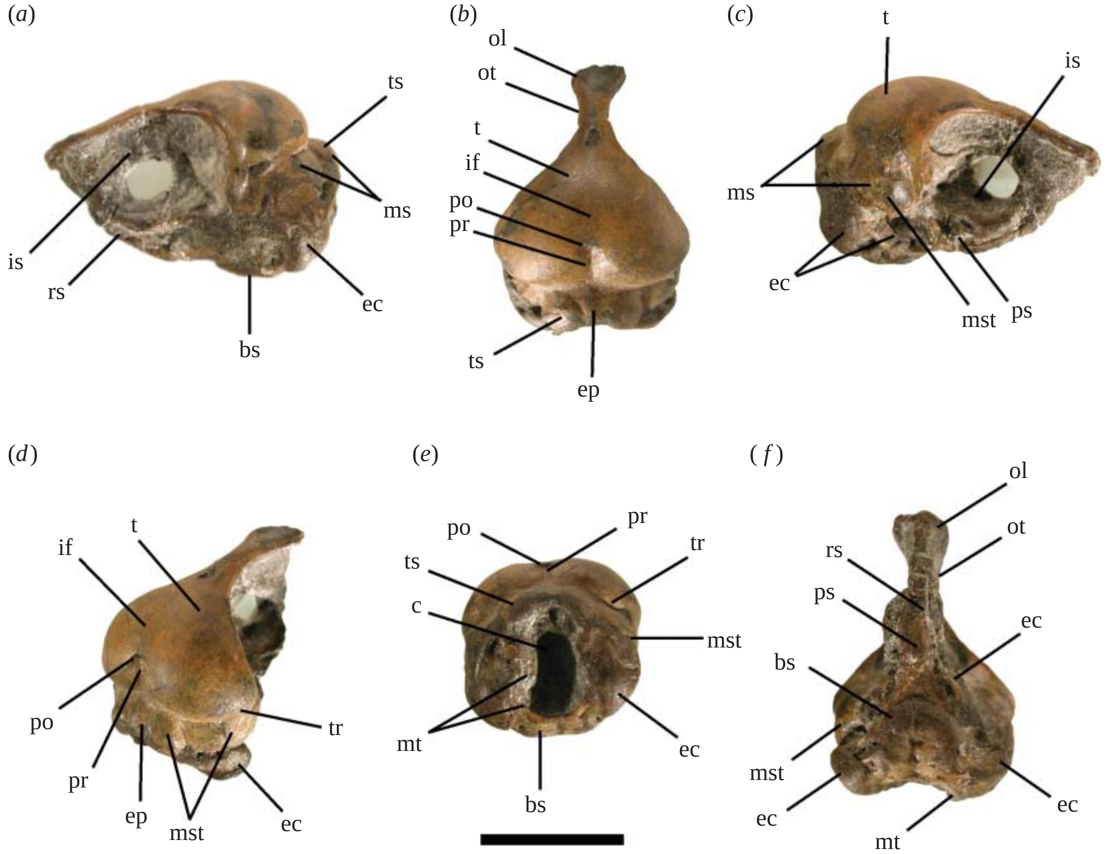

Figure 2. Endocranial cast of the Melovatka brain and associated bones (PIN 5028/2). (*a*) Left lateral view, (*b*) dorsal view, (*c*) right lateral view, (*d*) dorsocaudal view, (*e*) caudal view, (*f*) ventral view. Abbreviations: bs, basisphenoid; c, cavity of cerebellum; ec, endocasts of auditory, sphenoidal and other bone regions; ep, epiphysis; if, interhemispheric fissure; is, interorbital septum; ms, mesencephalon; mst, mesencephalon tectum (optic lobe); mt, metencephalon; ol, olfactory lobe; ot, olfactory tract; po, parietal organ; pr, pineal recess; ps, parasphenoid; t, telencephalon; tr, telencephalon recess; rs, paraspenoid rostrum and ts, torus semicircularis. Scale bar, 10 mm.

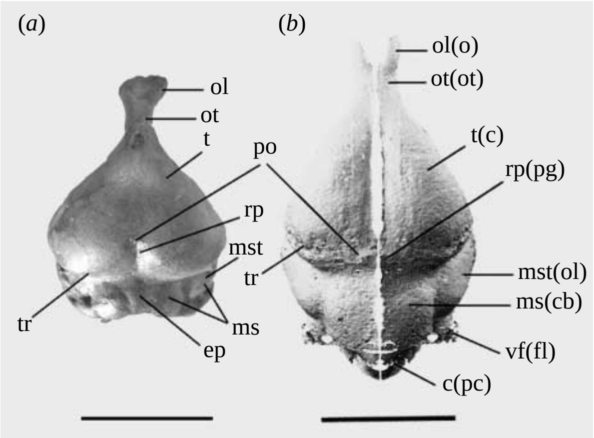

Figure 3. Reinterpretation of the brain of *Archaeopteryx*. (*a*) Melovatka brain (PIN 5028/2), (*b*) *Archaeopteryx* brain (BMNH 37001). Abbreviations (the original determinations from after Dominguez *et al.* (2004) are given in parentheses): c(pc), cerebellum (cerebellar prominence); ep, epiphysis; ms(cb), mesencephalon (cerebellum); mst(ol), mesencephalon tectum (optic lobes (metencephalic tectum)); ol(o), olfactory lobe; ot(ot), olfactory tract; po, parietal organ or third eye; rp(pg), pineal recess (pineal organ, epiphysis), t(c), telencephalon (cerebrum (telencephalon)); tr, telencephalon recess and vf(fl), vessels or lymphatic fascicle (floccular lobe of the cerebellum). Redrawn from Kurochkin *et al.* (2006). Scale bar, 10 mm.

The midbrain of PIN 5028/2 is large and bears well-developed posterior (auditory) tubercles on its roof (figure 2), differing from the archosaurian condition and from extant birds (figure 4). Between these posterior tubercles, a well-developed epiphysis is seen (pineal gland). Practically all of the dorsal midbrain in reptiles is formed by the tectum mesencephalon; the auditory tubercles are almost invisible (figure 4). The midbrain of PIN 5028/2 is much shorter than in *Archaeopteryx* (BMNH 37001; figure 3) and modern archosaurs (figure 4); in this respect, it is more similar to modern birds (Saveliev 2001). In the Melovatka brain, contact between the cerebrum and the midbrain is clearly visible (figure 2); this midbrain region was identified as the 'cerebellum' in BMNH 37001 by Dominguez *et al.* (2004; figures 3 and 4), who remarked on its large area of contact with the forebrain. The cerebrum contacts the midbrain dorsally across more than 60% of its width as in living birds, PIN 5028/2, and in *Archaeopteryx*. In PIN 5028/2, the cerebellum is represented only by a cavity; the corresponding region in *Archaeopteryx* was labelled as the 'cerebellar prominence' by Dominguez *et al.* (2004). This 'prominence' is probably the cerebellum, which is small and located posteriorly in *Archaeopteryx* (Marsh 1880; de Beer 1954; figure 3), as in extant reptiles and theropod dinosaurs (figure 3). The shape of the cerebellar cavity in PIN 5028/2 indicates that it was larger than that of *Archaeopteryx* but smaller than in modern ornithurines.

The Melovatka brain also shows that the optic lobes of some early birds were much larger than reconstructed for *Archaeopteryx* (Dominguez *et al.* 2004). We suggest that the 'floccular lobes of the cerebellum' labelled by Dominguez *et al.* (2004) are either the fascicles of cranial blood vessels or the elements of lymphatic system in this bird; this is because all reptiles, birds and mammals have tiny cerebellar floccular lobes (Saveliev 2001), much more compact in their organization than reconstructed for *Archaeopteryx* (Dominguez *et al.* 2004). In small specimens, like PIN 5028/2 and BMNH 37001, such lobes would be invisible, enclosed within the body of the avian cerebellum (Saveliev 2001).

Compared with the few other known ornithurine brains which are short and high (Marsh 1880; Elzanowski & Galton 1991), PIN 5028/2 is elongated craniocaudally with its midbrain emplaced between the pear-shaped cerebral hemispheres and the cavity of the cerebellum (figure 2). The cerebellum is extended dorsoventrally, as in ornithurines (Edinger 1951; Elzanowski & Galton 1991) including modern birds (Saveliev 2001). Since PIN 5028/2 has posterior auditory tubercles on its midbrain, pear-shaped cerebrum, and lacks marked telencephalon sulci (valleculae telencephali), visible, or reconstructed, in ornithurine brains (Marsh 1880; Edinger 1951; Elzanowski & Galton 1991), we suggest that it may not be a member of this clade (Kurochkin *et al.* 2006).

4. DISCUSSION

The remarkable preservation of the Melovatka brain and surrounding skull bones, combined with its Late Cretaceous age makes it an extremely valuable addition from the fossil record of early birds. Endocasts, brain moulds and details of internal cranial anatomy are extremely rare in the fossil record; this new fossil, *Archaeopteryx* (Dominguez *et al.* 2004) and the ornithurine *Enaliornis* (Elzanowski & Galton 1991) are the only examples from the Mesozoic. Interpretation of the early ornithurine brain is thus based largely on reconstructions from partial cranial material (Marsh 1880; Edinger 1951; Elzanowski & Galton 1991), nevertheless enough to show clear differences to PIN 5028/2. Endocasts are rare and provide us not only with evidence for the degree of sense organ development, but also allow direct inferences to be made about mode of life. The large relative sizes of the midbrain's epiphysis and parietal organ ('third eye') in PIN 5028/2 suggest that the Melovatka bird may have possessed acute nocturnal vision, while its enlarged olfactory tract and bulbs may also testify to a well-developed sense of smell. Further, the presence of tubercles on the tectum of the midbrain implies that this bird also may have had well-developed hearing—all three adaptations seen in modern avian twilight hunters (Saveliev 2001). The presence of a third eye and architecture of the midbrain tectum are unusual among modern reptiles and birds and may represent unique characteristics of this taxon, or the clade to which it belongs; this configuration of the midbrain is more often seen in mammals (Saveliev 2001).

It has long been assumed that 'remodelling of the brain towards the modern avian condition' probably began before the appearance of the flighted *Archaeopteryx* 150 Myr ago (Dominguez *et al.* 2004). However, while new data provided by the Melovatka fossil demonstrate that early

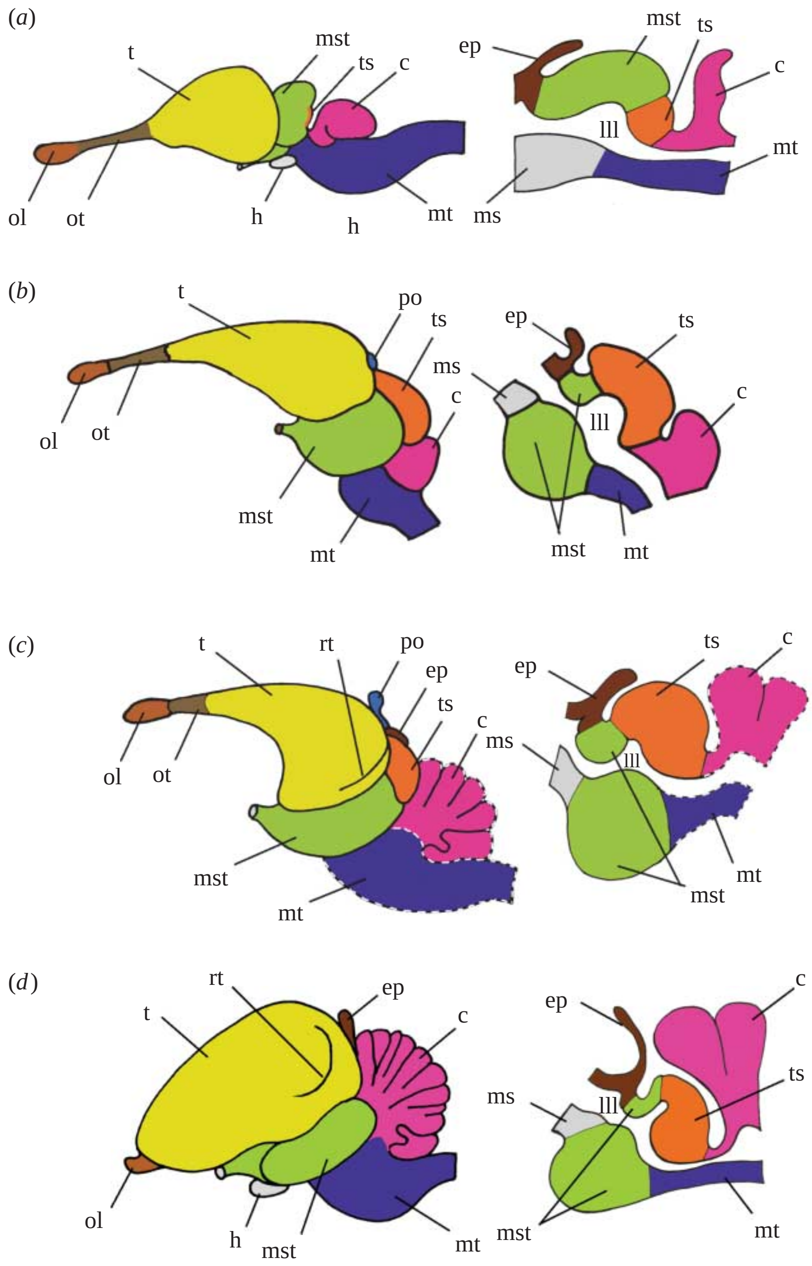

Figure 4. Brain morphology in archosaurs. (*a*) *Crocodylus*, (*b*) *Archaeopteryx*, (*c*) Melovatka brain (PIN 5028/2), (*d*) *Columba livia* (modern bird). Abbreviations: III, ventriculus tertius; c, cerebellum; ep, epiphysis; h, hypophysis; ms, mesencephalon; mst, mesencephalon tectum; mt, metencephalon; ol, olfactory lobe; ot, olfactory tract; po, parietal organ; rt, telencephalon recess; t, telencephalon and ts, torus semicircularis. The interrupted lines show the restored portions of the Melovatka brain (not to scale).

non-ornithurine birds had differently structured brains to theropod dinosaurs, anatomy of the London *Archaeopteryx* endocast does not imply any substantial 'remodelling' (particularly enlargement of the cerebellum) to 'meet the requirements of flight'. The anatomy of the brain in BMNH 37001 is not markedly different from known theropod dinosaurs (i.e. troodontids and the dromaeosaur *Bambiraptor*; Currie & Zhao 1993; Xu *et al.* 2002; Burnham 2004; Kurochkin *et al.* 2006); these taxa have elongate brains with a pear-shaped cerebrum and a small cerebellum (Edinger 1926; de Beer 1954; Chiappe & Witmer 2002). Present evidence for the sequence of avian brain evolution is not consistent with an increase in cerebellum size and a reduction of the length of the olfactory tracts—on the line to living birds—until within the phylogenetically more advanced (Chiappe & Witmer 2002) and aerially more manoeuvrable ornithurine lineage.

This work was supported by the Russian Fund for Basic Research (04-04-48829) and by a 'President of the Russian Federation to a Leading Scientific School' grant (NSh-6228.2006.4). We are grateful for the comments of two reviewers.

Burnham, D. A. 2004 Anatomy of *Bambiraptor*. In *Feathered dragons: studies on the transition from dinosaurs to birds* (eds P. J. Currie, E. B. Koppelhus, M. A. Shugar & J. L. Wright), pp. 67–111. Bloomington, IN: Indiana University Press.

Chatterjee, S. 1997 *The rise of birds: 225 million years of evolution*. Baltimore, MD: Johns Hopkins University Press.

Chiappe, L. M. & Witmer, L. M. (eds) 2002 *Mesozoic birds: above the heads of dinosaurs*, Berkeley, CA: University of California Press.

Currie, P. J. & Zhao, X.-J. 1993 A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. *Can. J. Earth Sci.* **30**, 2231–2247.

de Beer, G. 1954 *Archaeopteryx lithographica*. Watford, UK: Taylor Garnett Evans & Co. Ltd.

Dechaseaux, C. 1968 Le cerveau *d'Archaeopteryx* est-il de 'type avien' ou de 'type reptilien'? *C. R. Acad. Sci. Paris* **267**, 2108–2110.

Dominguez, P. A., Milner, A. C., Ketcham, R. A., Cookson, M. J. & Rowe, T. B. 2004 The avian nature of the brain and inner ear of *Archaeopteryx*. *Nature* **430**, 666–669. (doi:10.1038/nature02706)

Edinger, T. 1926 The brain of *Archaeopteryx*. *Ann. Mag. Nat. Hist.* **18**, 151–156.

Edinger, T. 1951 The brains of the Odontognathae. *Evolution* **5**, 6–24. (doi:10.2307/2405427)

Elzanowski, A. & Galton, P. M. 1991 Braincase of *Enaliornis*, an early Cretaceous bird from England. *J. Vertebr. Paleontol.* **11**, 90–107.

Jerison, H. J. 1968 Brain evolution and *Archaeopteryx*. *Nature* **219**, 1381–1382. (doi:10.1038/2191381a0)

Jerison, H. J. 1973 *Evolution of the brain and intelligence*. New York, NY: Academic Press.

Kurochkin, E. N., Saveliev, S. V., Postnov, A. A., Pervushov, E. M. & Popov, E. V. 2006 On the brain of a primitive Bird from the Upper Cretaceous of European Russia. *Paleontol. J.* **40**, 655–667. (doi:10.1134/S0031030106060086)

Marsh, O. C. 1880 *Odontornithes: a monograph on the extinct toothed birds of North America*. Washington, DC: Government Printing Office.

Nieuwenhuys, R. 1998 *The central nervous system of vertebrates*. Berlin, Germany: Springer.

Pervushov, E. M., Arkhangelsky, M. S. & Ivanov, A. V. 1999*a* *Catalogue of sites with remains of marine reptiles in the Jurassic and Cretaceous deposits of the lower Volga area*. Saratov, Russia: State Teaching-Scientific Center "College" Press. [In Russian.]

Pervushov, E. M., Ochev, V. G., Ivanov, A. V. & Janin, B. T. 1999*b* *Problems of biosphere study: contributions and transactions of the all-Russian scientific conference*. Saratov, Russia: State Teaching-Scientific Center "College" Press. [In Russian.]

Saveliev, S. V. 2001 *Comparative anatomy of the nervous system of vertebrates*. Moscow, Russia: Geotar-med. [In Russian.]

Whetstone, K. N. 1983 Braincase of Mesozoic birds: 1. New preparation of the 'London' *Archaeopteryx*. *J. Vertebr. Paleontol.* **2**, 439–452.

Xu, X., Norell, M. A., Wang, X., Makovicky, P. J. & Wu, X. 2002 A basal troodontid from the early Cretaceous of China. *Nature* **415**, 780–784.