

# Avian brain evolution: new data from Palaeogene birds (Lower Eocene) from England

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Investigation of how the avian brain evolved to its present state is informative for studies of the theropod–bird transition, and as a parallel to mammalian brain evolution. Neurological anatomy in fossil bird species can be inferred from endocranial casts, but such endocasts are rare. Here, we use computed tomographic analysis to determine the state of brain anatomy in two marine birds from the Lower Eocene London Clay Formation of England. The brains of *Odontopteryx* (Odontopterygiformes) and *Prophaethon* (Pelecaniformes) are remarkably similar to those of extant seabirds, and probably possessed similar somatosensory and motor capabilities. Each virtual endocast exhibits a degree of telencephalic expansion comparable to living avian species. However, the eminentia sagittalis (wulst), a feature characteristic of all living birds, is poorly developed. Our findings support the conclusion that much of the telencephalic expansion of modern birds was complete by the end of the Mesozoic, but that overall telencephalic volume has increased throughout the Cenozoic through dorsal expansion of the eminentia sagittalis. We suggest that improvements in cognition relating to telencephalic expansion may have provided neornithine avian clades with an advantage over archaic lineages at the Cretaceous–Tertiary boundary, explaining their survival and rapid diversification in the Cenozoic. © 2009 The Natural History Museum. Journal compilation © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, 155, 198–219.

**ADDITIONAL KEYWORDS:** *Archaeopteryx* – computed tomography – Neuroanatomy – *Odontopteryx* – *Prophaethon*.

## INTRODUCTION

The origin of birds has sparked heated debate among evolutionary biologists almost since the beginning of evolutionary theory (Chiappe & Dyke, 2002). Although it is now generally accepted among palaeontologists that Neornithes evolved from a common maniraptoran theropod ancestor, the details of the evolutionary pathway remain unclear. The discovery of an unprecedented number of exceptionally well-preserved specimens from the Early and Late Cretaceous of China in particular has greatly widened our understanding of avian evolution (Zhou, 2004). Elements of the Early Cretaceous dino-bird fauna from Liaoning Province have especially provided support for hypotheses of an arboreal origin of avian flight, demonstrated flight-related biomechanical capabilities,

and even allowed insight into the diet of these early birds (Zhou, 2004 and references therein). Nonetheless, *Archaeopteryx* from the latest Jurassic of Germany remains the earliest known avialan, and the only Jurassic taxon that shows direct evidence of early avian evolutionary adaptations.

By the Cretaceous, multiple avialan lineages had arisen, presumably including the ornithurine ancestor of all modern birds (Neornithes; Chiappe, 1995). No fossil evidence has been found that suggests any members of archaic lineages survived the Cretaceous–Tertiary (K–T) extinction event, but the fossil record does indicate an explosive radiation of modern bird lineages shortly afterwards. Many extant avian clades are recognisable for the first time in early Cenozoic assemblages such as the Lower Eocene London Clay. The general osteology of these early neornithine taxa is not markedly different from that of living representatives (e.g. Slack *et al.*, 2006),

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suggesting that the radiation must either have been very rapid indeed, or that the adaptations typical of modern clades were already in place by the beginning of the Cenozoic.

The timing of the neornithine radiation is uncertain. Molecular phylogenetic evidence (e.g. Cooper & Penny, 1997; Harrison *et al.*, 2004; Slack *et al.*, 2006) indicates that the divergence occurred deep in the Cretaceous, but the reliability of most Mesozoic fossils referred to extant avian clades has been questioned (Dyke, 2001; Chiappe & Dyke, 2002). Recently, however, fossil material reliably referable to stem members of extant lineages has been discovered in Late Cretaceous and early Palaeocene sediments (Clarke *et al.*, 2005; Slack *et al.*, 2006). If we accept the growing body of evidence indicating a Mesozoic origin for Neornithes, we must also acknowledge the Cretaceous as a period when Neornithes not only coexisted with other volant forms such as pterosaurs and enantiornithine birds, but were also in competition with them (Slack *et al.*, 2006). This raises an important question. What competitive advantage did neornithine clades possess that allowed them to survive the K-T boundary event when other flying forms – archaic birds and pterosaurs – did not?

The flight capabilities and adaptations for food acquisition in most known Cretaceous archaic birds were probably little different to those of Cenozoic Neornithes (Zhou, 2004), and it seems unlikely that physical adaptations allowed neornithine lineages to out-compete and replace archaic birds towards the end of the Cretaceous, as has been suggested by Slack *et al.* (2006). Alternatively, extant lineages may represent the fortunate descendants of ancestors that survived the K-T event by virtue of membership of some 'favoured' guild. This possibility would also seem unlikely, as it requires that the favoured guild was not occupied by any of the archaic avian lineages, and that each of the neornithine survivor lineages was a member of the same guild.

Another possibility is that behaviour and cognition played a significant role, as Hermon Bumpus inferred over a hundred years ago (Striedter, 2005). In extant birds the differential development of specific regions of the brain has been shown to be significantly correlated with adaptability, cognitive ability, and general behavioural factors (Eccles, 1992; Timmermans *et al.*, 2000; Madden, 2001; Beauchamp & Fernandez, 2004; Burish, Kueh & Wang, 2004; Iwaniuk, Dean & Nelson, 2004, 2005; Lefebvre, Reader & Sol, 2004; Winkler, Leisler & Bernroider, 2004). Although behaviour cannot be directly studied in fossil taxa, the evolution of avian brain size and morphology should provide a proxy measure of intelligence, as has been suggested for mammals (e.g.

Jerison, 1973; Eccles, 1992; Holloway, Broadfield & Yuan, 2004; Striedter, 2005).

Fortunately the endocranial cavity of birds and mammals represents a reasonably accurate approximation of the shape and size of the brain that it houses (Striedter, 2005). Brain morphology and volume can therefore be studied in fossil species through lithified sediment that infilled the endocranial cavity. However, such endocasts are exceedingly rare (Jerison, 1973), and those that do survive are very often damaged by mechanical processes, such that only gross morphology remains. A potentially more serious problem is that the loss of surrounding skull material generally renders even higher level taxonomic identification of isolated endocasts extremely tenuous, severely limiting the potential of any subsequent comparative morphological studies. We are aware of no more than 12 reports of endocasts from pre-Quaternary taxa, of which only three have received adequate description. Cranial endocasts from Cenozoic deposits are more numerous than those known from Mesozoic strata. A relatively complete endocast from the Upper Eocene of the Paris Basin was described by Dechaseaux (1970), and Mlíkovský provided brief descriptions of a relatively complete endocast and a fragment from the lower Miocene of Czechoslovakia (Mlíkovský, 1980), seven fragmentary endocasts from the middle Miocene of Bavaria (Mlíkovský, 1988), and a fragmentary specimen from the upper Pliocene of Hungary (Mlíkovský, 1981a). A complete endocast referable to an extinct species of penguin is also known from the late Miocene of Chile (Walsh, 2001).

Detailed anatomical data on a Mesozoic bird brain were provided by Elzanowski & Galton (1991), who described the inside of the braincase of *Enaliornis* from the Early Cretaceous of England. As only four other Mesozoic avian endocasts are known, information concerning avian brain development during this time is otherwise scarce. Reconstructions of the brains of the Late Cretaceous toothed birds *Ichthyornis* and *Hesperornis* were given by Marsh (1880), but this material was later shown by Edinger (1951) to be too incomplete to provide much evidence of the evolutionary grade at this time. However, a preliminary description of a more complete avian cranial endocast from the Late Cretaceous of Russia was given by Kurochkin (2004). This material appears to be morphologically informative, but awaits full description. The most important and best studied endocast is without doubt that associated with the holotype specimen of *Archaeopteryx* (BMNH 37001). Examination of this partially exposed endocast led early workers (e.g. Edinger, 1926; de Beer, 1954) to suggest a more reptilian form for the brain of *Archaeopteryx*, although this was later challenged by Jerison (1968).

Recent advances in imaging techniques have finally resolved this debate. Domínguez *et al.* (2004) used high resolution X-ray computed tomographic (CT) analysis to reconstruct the braincase and inner ear of *Archaeopteryx*, demonstrating beyond doubt that the brain of this basal avialan is bird-like in both shape and relative size. The results obtained by Domínguez *et al.* (2004) for *Archaeopteryx* demonstrate that CT techniques represent an important way forward in research into avian brain evolution.

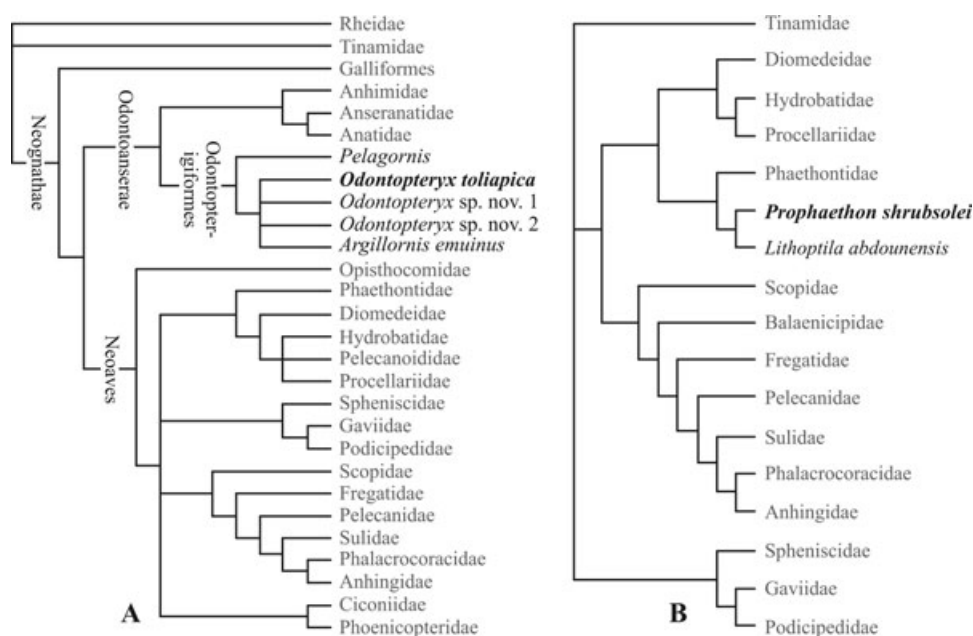
Here, we followed the analysis of the braincase of *Archaeopteryx* by applying the same techniques to two much younger fossil birds, *Odontopteryx toliapica* Owen, 1873 (BMNH 44096) and *Prophaethon shrubsolei* Andrews, 1899 (BMNH A683) from the Lower Eocene (Ypresian) London Clay Formation of south-east England. These almost complete three-dimensional (3D) holotype skulls represent excellent material through which the developmental level of the avian brain during the early Cenozoic can be studied. Although these taxa are modern in most aspects of their osteology, their occurrence only ten million years after the K-T boundary makes them particularly interesting from the aspect of their neurological development.

#### TAXONOMIC STATUS OF THE LONDON CLAY TAXA

At around the size of a medium-sized cormorant (Harrison & Walker, 1977) *Odontopteryx toliapica* is one of the smaller members of an extinct group of large (up

to 6 m wingspan) marine birds, notable for the possession of bony tooth-like projections of the premaxilla, maxilla, and dentary, and particularly thinly walled bones (Olson, 1985). Poor preservation potential because of this latter feature is perhaps one reason for the poorly resolved systematics of the group, despite a cosmopolitan fossil record spanning the Late Palaeocene (Averianov *et al.*, 1991) to the mid-Pliocene (McKee, 1985). *O. toliapica* was redescribed by Harrison & Walker (1976a) as part of a major review of the relationships of the group. Those authors considered the 'bony-toothed birds' to be closely related to Pelecaniformes (pelicans, cormorants, tropicbirds, frigatebirds, and allies) and Procellariiformes (tube noses; albatrosses, storm- and diving-petrels, and allies), but sufficiently different from each to merit their own order, Odontopterygiformes (originally proposed by Howard, 1957). Others consider the group to nest within Pelecaniformes and, following Olson (1985), most authors now regard all 'bony-toothed birds' to comprise a single pelecaniform family, the Pelagornithidae.

Recently, Bourdon (2005) included *O. toliapica* with four other 'bony-toothed' taxa in a cladistic analysis, and recovered a monophyletic Odontopterygiformes as sister group to Anseriformes (swans, ducks, and other waterfowl allies) in a new clade Odontoanserae, as sister taxon to Neoaves (Fig. 1A). It will be interesting to see if this novel result changes as more odontopterygiform taxa (e.g. *Osteodontornis*, *Caspiodontornis*, *Dasornis*) are added to the analysis.



**Figure 1.** Recent phylogenetic hypotheses of the relationships of A, *Odontopteryx toliapica* (after Bourdon, 2005) and B, *Prophaethon shrubsolei* (after Bourdon *et al.*, 2005).

Anseriformes is already known to extend into the Cretaceous (Clarke *et al.*, 2005), and if Bourdon's (2005) placement of *Odontopterygiformes* outside Neoaves (the clade containing peleciform and procellariiform taxa) is accepted, then *Odontopteryx* is potentially informative regarding brain evolution in an early aquatic neornithine radiation. Furthermore, the occurrence of the earliest fossils in the Late Palaeocene and early diversity of the order in the Eocene suggests an early radiation of the order (Harrison, 1985), potentially in the Cretaceous.

Andrews (1899) originally assigned *Prophaethon shrubsolei* to the Pelecaniformes, but in a redescription of *P. shrubsolei*, Harrison & Walker (1976b) erected a new family and order for the taxon based on the presence of a mosaic of characters that suggested *Prophaethon* might represent something of a missing link between Pelecaniformes, Procellariiformes, and Charadriiformes. Olson (1985) nevertheless regarded what was, at the time, a monotypic order as weakly supported, and referred the Prophaethontidae to the Phaethontes (Pelecaniformes) with the extant Phaethontidae (tropic birds). Since then prophaethontid remains have been recovered from the Middle Eocene of Belgium (Mayr & Smith, 2002) and late Palaeocene of Morocco (Bourdon, Baâdi & Iarochene, 2005), with possible prophaethontid remains reported from the Palaeocene of Maryland (Olson, 1994). A position for the Prophaethontidae within a monophyletic Pelecaniformes was supported by Gulas-Wroblewski (2003), but a more recent analysis by Bourdon *et al.* (2005) has recovered a relationship with Procellariiformes, albeit with Prophaethontidae as sister taxon to the Phaethontidae within a polyphyletic Pelecaniformes (Fig. 1B). Bourdon *et al.* (2005) also erected a new late Palaeocene taxon, *Lithoptila abdounensis*, based on a 3D neurocranium that was regarded as being very close to that of *Prophaethon*. Although this record brings the number of nominal prophaethontid species to two, the Belgium and Maryland unnamed taxa indicate that more species remain to be discovered. As with *Odontopteryx*, the existence of Thanetian prophaethontids similar to *Prophaethon* suggests that divergence of the family occurred lower in the Palaeocene, or earlier still.

#### INSTITUTIONAL ABBREVIATIONS

BMNH, The Natural History Museum, London;  
MNHN, Muséum national d'Histoire naturelle, Paris.

#### ANATOMICAL ABBREVIATIONS USED IN FIGURES 2–8

ac, auricula cerebelli; aic, anastomosis intercarotica; aoe, arteria ophthalmica externus; aor, ampulla ossea rostralis; bo, bulbus olfactorius; c, cochlea; cb, cere-

bellum; ch. op., chiasma opticum; com, crus osseum commune; csc, canalis semicircularis caudalis; csh, canalis semicircularis horizontalis; csr, canalis semicircularis rostralis; es, eminentia sagittalis (wulst); fc, fenestra cochlearis; fcel, fissura cerebelli; fm, foramen magnum; h, hypophysis; hpd, hypophysis pars distalis; icsr, impressio canalis semicircularis rostralis; n. acc., nervus accessorius; n. coch., nervus cochleoves-tibularis; n. fac., nervus facialis; n. glos., nervus glos-sopharyngeus; n. hypo., nervus hypoglossus; n. troch., nervus trochlearis; n. trig. V<sub>2</sub>, second branch of nervus trigeminus; n. trig. V<sub>3</sub>, third branch of nervus trigeminus; n. vagus, nervus vagus; r, rhombencephalon; ra, recessus antevestibularis; rc, ramus caroticus; sa, sacculus; so, sinus occipitalis; t, telencephalon; tm, tectum mesencephali; tr. o., tractus olfactorius; tr. op., tractus opticus; vsr, vena semicircularis rostralis.

Avian anatomical nomenclature used here follows Wingstrand (1951); Baumel *et al.* (1993) and Reiner *et al.* (2004). We have chosen to adopt the term 'eminentia sagittalis' (Baumel *et al.*, 1993) as the Latinized form of the morphological feature generally referred to as the 'wulst' (German: 'bulge'). Note that the terms 'hyperstriatum accessorium' and 'hyperstriatum apicale' (Reiner *et al.* 2004) relate more to structures that comprise the 'wulst', but are visible at the cellular level, and are therefore not strictly applicable to the description of virtual endocranial casts.

## MATERIAL AND METHODS

Both holotype skulls are preserved in-the-round with no major deformation evident, and are remarkably complete. In *O. toliapica* (BMNH 44096) there is slight damage to the caudal and dorsal margins of both orbits, and patches of the surface of the parietals are damaged where they meet the frontals. In this region the parietals and frontals appear to be unfused. Although much of the rostrum is missing, this is unimportant as the X-ray of this specimen was restricted to an area immediately caudal of the orbit mid-point. The holotype skull of *P. shrubsolei* (BMNH A683) lacks only small portions of the rostrum, parts of the dorsal margin of the right orbit, lateral margin of the quadrate, and parts of the dorsal and caudal surface of the parietals. It is externally more complete than the holotype of *O. toliapica*, and is from a slightly smaller individual.

Spirit-preserved avian brains of extant species are not widely available, so for comparative purposes descriptions and images of avian brains were taken from Stingelin (1957). Additional CT-derived 3D information for some avian species can be found at the University of Texas at Austin digital morphology website at <http://www.digimorph.org/index.phtml>.



Although this comparative data does not cover the full range of taxonomic diversity or morphological variation, it does represent the best information currently available, and provides at least some potential to highlight similarities and differences between the fossil and living taxa.

Although the endocranial surface of bird skulls provides a reasonably accurate impression of the morphology of the brain it originally housed, some brain regions leave less perfect impressions than others. For instance, the sinusoidal tissues that separate the cerebellum from the skull are so thick in many taxa that no trace is preserved of the fissura cerebelli, and the vallecule sulcus of the telencephalon in most species does not leave a trace on the internal surface of the skull roof. Similarly, the dorsum sellae that separates the hypophysis from the rhombencephalon in some species is not fully ossified, and therefore is not visible in true and virtual endocranial casts of those species. Nonetheless, apart from these differences, the morphology of virtual endocasts is so close to that of the soft tissue brain that comparisons between a brain and a virtual endocast of its endocranial impression are fully justified.

The braincases of the two fossil bird skulls were scanned at the University of Texas at Austin's High-Resolution X-ray CT facility. *Odontopteryx toliapica* was scanned at a slice distance and slice thickness of 0.102 mm producing 947 coronal slices; *P. shrubssolei* was scanned at a slice distance and thickness of 0.101 mm producing 1110 coronal slices. Parameters common to both scans: field of reconstruction 49 mm, source to object distance of 150 mm, no offset, aluminium filter used, energy 180 kV, 1000 views with two samples per view.

Reconstructions of each braincase were made using MIMICS 8.13 (Materialise NV). In order to reduce processing requirements the image stack for each specimen was reduced by half by removing every other slice, and doubling the slice thickness at the MIMICS image load prompt to compensate. We have determined from previous reconstructions of objects of similar size and slice thickness (~0.1 mm; e.g. Domínguez *et al.*, 2004) that such slice reduction does not appreciably affect resolution of the reconstruction. Variable preservation of the two fossils has resulted in differing bone density across each specimen. Consequently, the contrast of greyscale values for bone and matrix was often insufficient to allow global thresholding over the whole image stack. Instead, segmentation of the endocranial cavity and inner ear region was achieved using localized threshold values. Pyrite formation is also common in the matrix infill of both specimens, and manifests in slices as areas of white where pyrite formation is particularly dense. Although the pyrite attenuates the X-ray energy to a

high degree, it was possible to follow the trace of the original bone by experimentation with brightness and contrast value in most cases where bone had been replaced by pyrite. Where the trace was too subtle for localized thresholding to be effective, the bone trace was masked manually.

## DESCRIPTION

### *ODONTOPTERYX TOLIAPICA*

It has been possible to reconstruct almost the entire endocranial cast of *Odontopteryx*, including pathways of major efferent and afferent nerves, and the arrangement of the anastomosis intercarotica (see Table 1 for measurements). Both osseous labyrinths are largely intact, and were reconstructed fully on each side. However, no evidence of the columella was detected within the recessus antvestibularis. Using the position of the canalis semicircularis horizontalis in the skull (Pearson, 1972) it has been possible to determine the *in vivo* alert head posture of *Odontopteryx*, and this is shown in Figure 2A. A detailed description of the osteology of *O. toliapica* can be found in Harrison & Walker (1976a). As with living avian taxa, the major cranial bones of the braincase are fused. However, the CT reconstruction shows that the frontals overlap the parietals caudally, and at the posterior region of the frontals the two bones are unfused. A faint outline within the matrix covering left side of BMNH 44096 is interpreted to correspond broadly to the shape of the tractus opticus (Fig. 3C), but it was not possible to reconstruct the feature on the right side where the matrix was absent. Including cranial nerves but excluding the carotid rami the total endocranial volume of *Odontopteryx* is 9.05 mL.

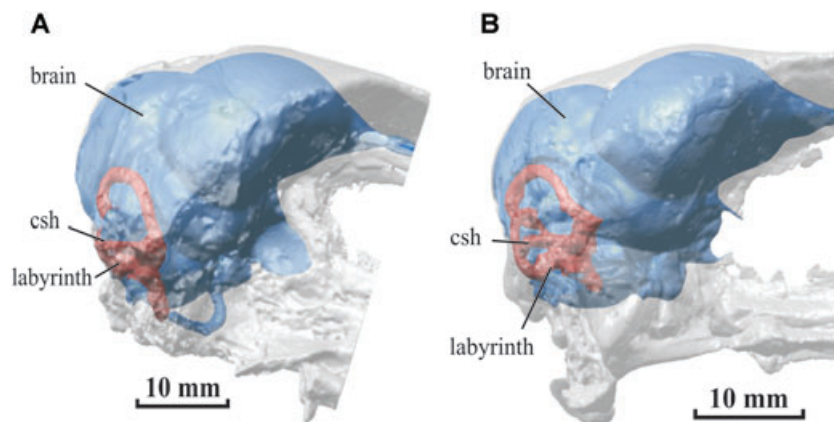
As in most living birds, the brain of *Odontopteryx* was equant in dorsal view, with the distance from the caudal-most extent of the cerebellum to the rostral-most extent of the bulbus olfactorius almost exactly equalling that measured for the telencephalic width (31.5 mm). Also as in all extant birds the tectum mesencephali (optic lobes) are largely occluded in dorsal view by the lateral expansion of the telencephalon (Fig. 3A); in *Archaeopteryx* the tectum mesencephali extend as far laterally as the telencephalon (Domínguez *et al.*, 2004).

The bulbus olfactorius is relatively large and elongate, approaching the proportions of the same region in many Anseriformes (e.g. *Branta*, *Aix*) and some Charadriiformes (e.g. *Burhinus*, *Sterna*), and far larger than in taxa with well-developed optical specializations such as Strigiformes. The bulbus apparently did not bifurcate until the nerve bundles entered the tractus olfactorius, nor is there any indication of the development of a rostrocaudally

**Table 1.** Measurements obtained from the virtual endocast and labyrinth of *Odontopteryx toliapica* using Rapidform™ 2006 (INUS Technology, Inc.)

	Length	Width	Height	Angle
Telencephalon	31.6	31.5	22.9	—
Angle between rostral telencephalon and midline	—	—	—	44°
Bulbus olfactorius	5.2	4.3	4.2	—
Cerebellum	14.5	13.4	14.0	—
Auricula cerebelli	7.6	5.2	—	—
Tectum mesencephali	11.3	6.8	6.6	—
Rhombencephalon	10.8	10.2	8.2	—
Tractus opticus	6.5	6.9	—	—
n. cochlearis/n. facialis	1.8	2.4	—	—
n. glossopharyngeus/n. vagus	4.1	2.6	—	—
n. hypoglossus	2.2	0.9	—	—
n. trochlearis	2.0	0.9	—	—
n. trigeminus	6.5	6.1	—	—
Labyrinth	9.2	6.4	16.2	—
Canalis semicircularis rostralis	8.1	1.8	—	—
Canalis semicircularis horizontalis	6.4	1.6	—	—
Canalis semicircularis caudalis	6.7	1.4	—	—
Angle between csc/csr	—	—	—	49°
Angle between csc/csh	—	—	—	82°
Angle between csr/csh	—	—	—	85°

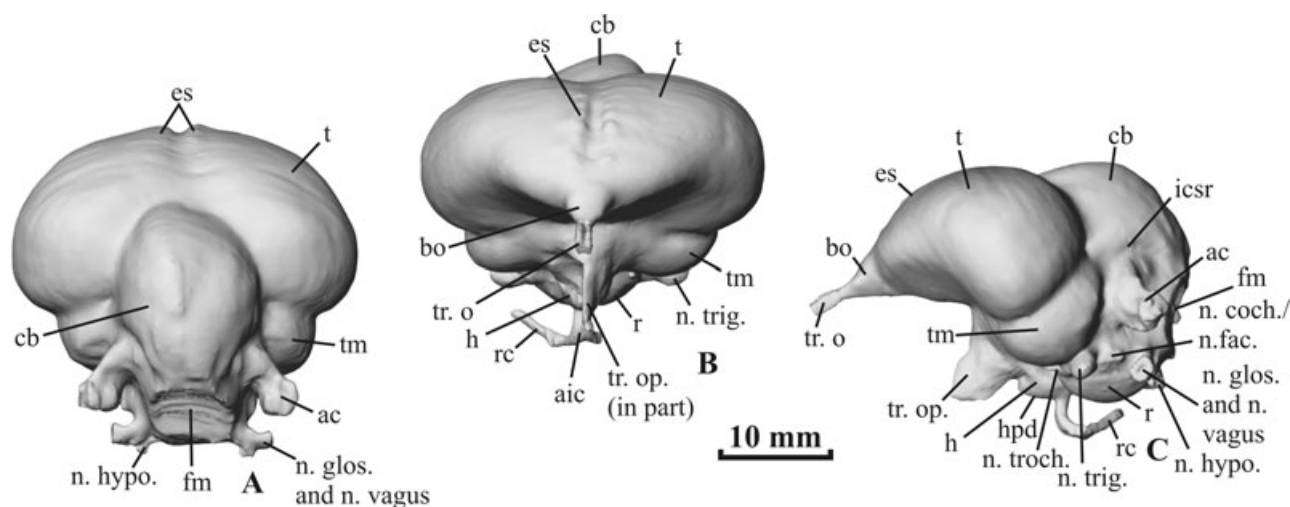
All values were measured at maximum orthogonal points, and are in millimetres. Note that semicircular canal length measurements refer to maximum dorsal (for csr) and lateral (for csh and csc) extent of canal arc; width measurements refer to maximum canal diameter. See text for abbreviations.



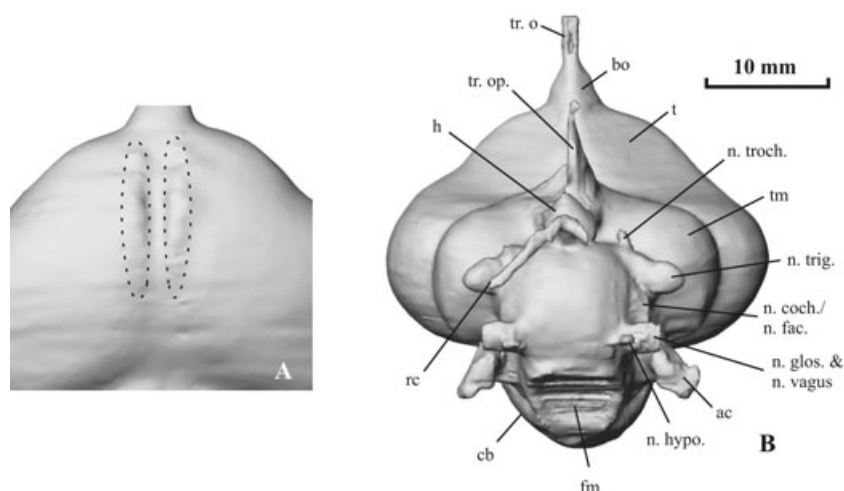
**Figure 2.** Transparent computed tomographic (CT) segmentation of two Lower Eocene skulls in right lateral views, revealing the virtual endocasts of the brain and osseous labyrinth. Compare positions of the canalis semicircularis horizontalis indicating the *in vivo* alert head positions. A, *Odontopteryx toliapica*; all sutures are fully obliterated except that between the frontals and parietals. B, *Prophaethon shrubsolei*.

directed sulcus in the dorsal surface of the bulb (Fig. 3B, C). In most Charadriiformes, Ciconiiformes, and Pelecaniformes this groove is present in the dorsal surface of the bulb, and in many Coraciiformes, Caprimulgiformes, and Psittaciformes the bifurcation occurs internally, such that the tractus olfactorius emerges as two separate branches from

the rostral region of the brain. The bulbus olfactorius also occupies a position close to the dorsal surface of the telencephalon as in Charadriiformes and Coraciiformes. In Pelecaniformes and taxa possessing a well-developed rostrally positioned eminentia sagittalis (especially Strigiformes) the bulbus is positioned far more ventrally.



**Figure 3.** Virtual endocast of *Odontopteryx toliapica* in A, dorsal; B, rostral, and C, left lateral views. See text for list of anatomical abbreviations.



**Figure 4.** Virtual endocranial cast of *Odontopteryx toliapica*. A, expanded view of the dorsal surface of the telencephalon, showing the shape and extent of the poorly developed eminentia sagittalis. B, ventral view of virtual endocast. See text for list of anatomical abbreviations.

In dorsal view, the two telencephalic hemispheres form a spade shape, with a marked expansion of the lateral regions (Fig. 3B). As a result of this expansion the rostral edge of the telencephalon is slightly notched in this view. A narrow and very poorly developed eminentia sagittalis is present in a rostral position (Figs 3A, B, 4A). The feature is only very slightly raised, and remains constant in width as it extends from a point slightly caudal of the rostral margin of the telencephalon to 8 mm rostral of the point where the telencephalon meets the cerebellum. No evidence of a vallicula is detectable. The eminentia sagittalis of *Odontopteryx* appears to be most similar to that of

some Coraciiformes, and unlike any pelecaniform for which we have comparative data.

The cerebellum is short (46% of the total brain length as measured along the interhemispheric fissure) and broad (42% of the maximum telencephalic width). The auricula cerebelli are large, expand distally and extend ventrocaudally from the ventral margin of the cerebellum (Figs 3A, C, 4B). Except for at the junction of the tectum mesencephali and cerebellum ventral of the protruberantia tentorialis on the left-hand side of the brain, there is no trace of the vena semicircularis rostralis (Fig. 3C), and the vein was apparently fully enclosed within an osseous

tunnel. There is also no evidence of a median groove for the sinus occipitalis, although slight compression of the parietal region may mask its presence.

Although the reconstruction of the left side of the tractus opticus is by no means certain, it suggests that the optic nerve extended some way from the tectum mesencephali before bifurcating (Fig. 3C). The length of the tractus opticus is apparently variable in most avian orders, but in some (e.g. *Strigiformes*, *Caprimulgiformes*, some *Psittaciformes*, *Apteryx*) the two optic nerves separate close to, or within the tectum mesencephali. This arrangement appears to be most common in taxa with high angles between the brain and bill axes, and perhaps relates to the reduced distance between the tectum mesencephali and orbits in these species (e.g. in owls and parrots).

The tectum mesencephali itself is large and globe-like, but appears distinctly lunate in lateral view because of interpenetration of the telencephalic hemispheres (Fig. 3C). In other taxa (e.g. *Columba*) the tectum mesencephali is dorsoventrally compressed into a distinct oval, which may or may not be penetrated dorsally by the telencephalon. A rounded junction with the telencephalon is seen in several species (e.g. *Larus*, *Pelecanus*, *Phalacrocorax*), although a straight or angular junction is also common (e.g. *Pluvialis*, *Sterna*).

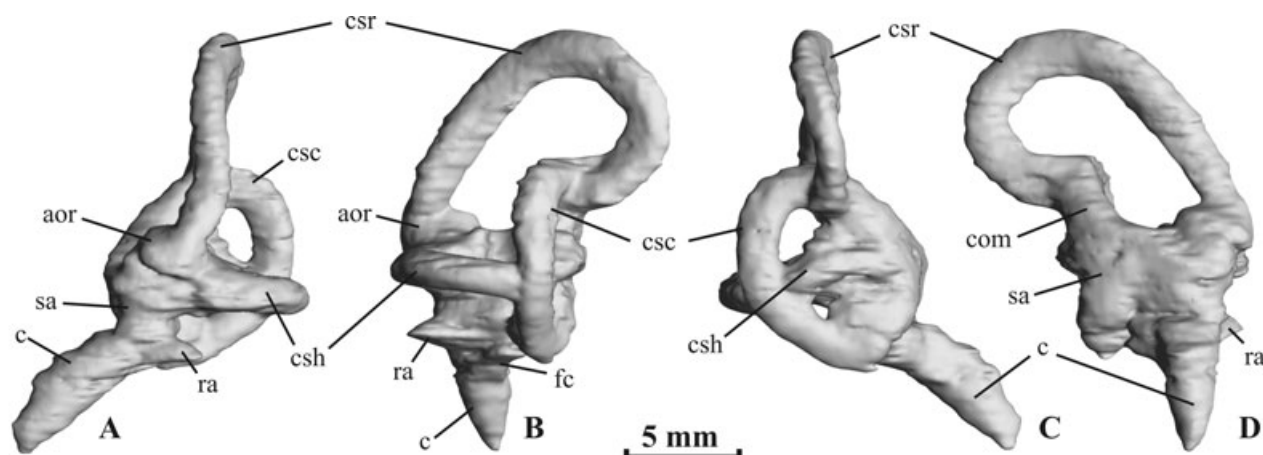
The hypophysis is rostrocaudally short and is smaller than the tractus opticus (Fig. 4B). The body of the hypophysis is only slightly laterally compressed and has a rounded ventral margin of the pars distalis that is unlike that of *Anseriformes*, where the pars distalis is flattened and elongate (Wingstrand, 1951). The rostral region of the pars distalis is markedly conical (Fig. 4B), a feature that may relate to presence of an epithelial stalk. Although our reconstruction (Fig. 4B) shows no gap between the hypophysis and rhombencephalon, a thin dorsum sellae is present that separates the regions, as in most large species of modern birds (Wingstrand, 1951). The bony tunnel that housed the ascending portion of the carotid artery terminates at the caudal-most edge of the base of the hypophysis. The tunnel is broad at this point, and widens as it extends rostroventally from the hypophysis, before bifurcating. The two separate tunnels then curve sharply and extend caudolaterally as they follow the line of the basisphenoid. The tunnel on the right-hand side can be traced caudally for 8.4 mm, but the path of the left-hand tunnel is difficult to discern as a result of replacement by pyrite. Because the bifurcation of the cranial ramus of the artery (dorsal of the hypophysis) must have occurred within the sella turcica, it is not possible to determine the exact pattern of anastomosis in *Odontopteryx*. However, the regions that can be examined are similar to those seen in *Pelecanus*, although the

enlarged sphenomaxillary and palatine arteries found in that genus (see Baumel & Gerchman, 1968) are absent.

The rhombencephalon (Fig. 4B) is globe-shaped and extends from the foramen magnum to around the midpoint of the mesencephalon. The base of the rhombencephalon shows no evidence of a ventral sulcus. On the left-hand side of the rhombencephalon a wide n. trochlearis is visible extending rostrally, but on the right-hand side only the base of the nerve can be detected. A faint trace of the n. oculomotorius is detectable on the left-hand side, extending rostrorodorsally from the dorsal region of the hypophysis to the tractus opticus. The n. trigeminus is particularly broad and its exit from the rhombencephalon is contiguous with the ventral margin of the tectum mesencephali. The n. cochlearis and n. facialis are preserved as a low dorsoventrally compressed protuberance positioned immediately caudal and slightly more ventral of the n. trigeminus. The n. vagus and n. glossopharyngeus also exit the rhombencephalon together and combined are as broad as the n. trigeminus, although slightly dorsoventrally compressed. The n. glossopharyngeus diverges from the n. vagus to exit the skull within the recessus scalae tympani slightly medial of the exit of the n. vagus. As the n. vagus/n. glossopharyngeus exit the rhombencephalon the nerve bundle is directed ventrolaterally, but curves dorsally as the smaller ventrolaterally directed n. hypoglossus branches from it. No traces of the n. accessorius are visible in this region.

An impression of the bony labyrinth of the inner ear is visible on the endocast of the cerebellum (Fig. 3C). The canals of the labyrinth itself are comparatively short and broad (Fig. 5A–C), with well-defined ampullae. The labyrinth is separated from the telencephalon by the tectum mesencephali and a protruberantia tentorialis. The rostral limb of the canalis semicircularis rostralis slopes caudally as it rises from the ampulla ossea rostralis, smoothly curving round and back until it is directed rostrally before its junction with the canalis semicircularis caudalis. The canalis semicircularis rostralis is tall, representing 50% of the total dorsoventral height of the labyrinth. The caudal limb of the canalis semicircularis rostralis frames the foramen magnum, and therefore the canalis semicircularis rostralis of each side do not come close to meeting caudally as they do in *Turdus*. The long axis of the canalis semicircularis rostralis is angled laterally at 85° (mean of rostral and caudal measurements for both sides), and in dorsal view exhibits a slight sigmoidal curvature. The canalis semicircularis rostralis et caudalis cross at a mean angle of 49° to each other. The canalis semicircularis caudalis et horizontalis meet at 82°. The ductus cochlearis is straight, directed strongly rostrally and





**Figure 5.** Reconstruction of the left osseous labyrinth of *Odontopteryx toliapica* in A, rostral; B, lateral; C, caudal, and D, medial views. See text for list of anatomical abbreviations.

slightly medially, and is approximately round in section. The fenestra cochlearis is small and faces caudolaterally, and slightly ventrally. The position of the oval window for the columella is marked by the medial extent of the small and dorsoventrally compressed recessus antivehicularis. A well-developed dorsoventrally compressed saccus is present on the lateral surface of the ductus cochlearis.

#### *PROPHAETHON SHRUBSOLEI*

As with *Odontopteryx* it has been possible to reconstruct nearly all of the cranial endocast of *Prophaethon*, with the exception of the tractus opticus, part of the left bulbus olfactorius, and the anastomosis intercarotica (see Table 2 for list of measurements). Both osseous labyrinths are complete, but no evidence of the columella was detected within the recessus antivehicularis. The *in vivo* alert head posture of *Prophaethon* based on the position of the canalis semicircularis horizontalis of the osseous labyrinth in the skull is shown in Figure 2B. As with *Odontopteryx* and extant avian taxa, the major cranial bones of the braincase are fused, but unlike *Odontopteryx* the parietal-frontal suture is fully closed. The shape of the tractus opticus is not possible to reconstruct, although some information about the lateral outline shape can be gained from the dorsal and ventral margins at the midline (Fig. 6C).

With a length of 29 mm (measured from the caudal-most extent of the cerebellum to the rostral-most extent of the bulbus olfactorius) and a maximum telencephalic width of 26 mm, the cranial endocast of *Prophaethon* is slightly more elongate than that of *Odontopteryx*. Including cranial nerves the total endocranial volume of this specimen of

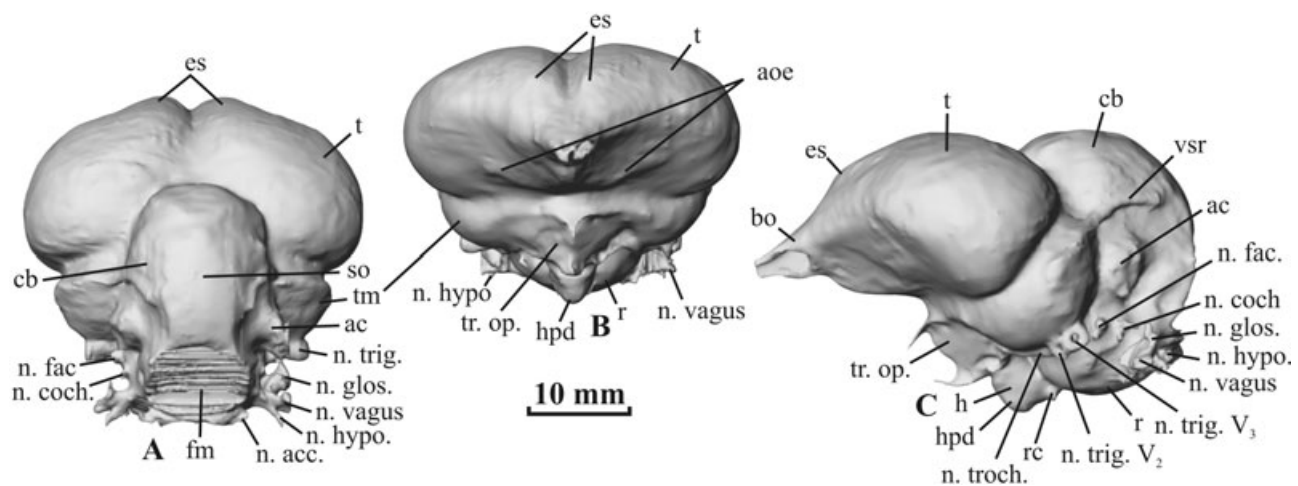
*Prophaethon* is 5.5 mL. The tectum mesencephali are entirely occluded in dorsal view by the lateral expansion of the telencephalon (Fig. 6A). The rostral margins of the telencephalic lobes are slightly concave in dorsal view, unlike *Phaethon* where the margins are approximately straight. The bulbus olfactorius is proportionately larger than in *Odontopteryx* and forms a smooth extension of the dorsal and lateral surfaces of the telencephalon, with only a slight expansion in the caudal-most region demarcating the point at which the telencephalon begins (in *Pelecanus* and *Phalacrocorax* there is a sharp angle between the bulbus olfactorius and the telencephalon). The bulbus is approximately twice as large as in *Phaethon rubricauda* (Fig. 8A) and, unlike that species, the bulbus is not overstepped dorsally by the eminentia sagittalis (Fig. 6C). As with *Odontopteryx* the bulbus olfactorius occupies a position close to the dorsal surface of the telencephalon, and a rostrocaudally directed sulcus on its dorsal surface is not present (Fig. 6B).

The eminentia sagittalis is rostrally positioned and is more prominently developed than in *Odontopteryx*. In dorsal view (Fig. 7A) its shape is very similar to *Phaethon* in that it is wider caudally (approximately triangular in shape) and is rostrally more dorsally expanded (compare Fig. 7A with Fig. 8B). It differs from *Phaethon* in that the dorsal expansion is only around half that of the living taxon (Fig. 8B), and that the eminentia does not reach the rostral-most margin of the telencephalon. In *Pelecanus* the eminentia is similar in shape, but is positioned caudally on the telencephalon. In *Phalacrocorax* the eminentia is rostrally positioned, but is oval rather than triangular. Also as in *Odontopteryx*, there is no evidence of a vallicula.

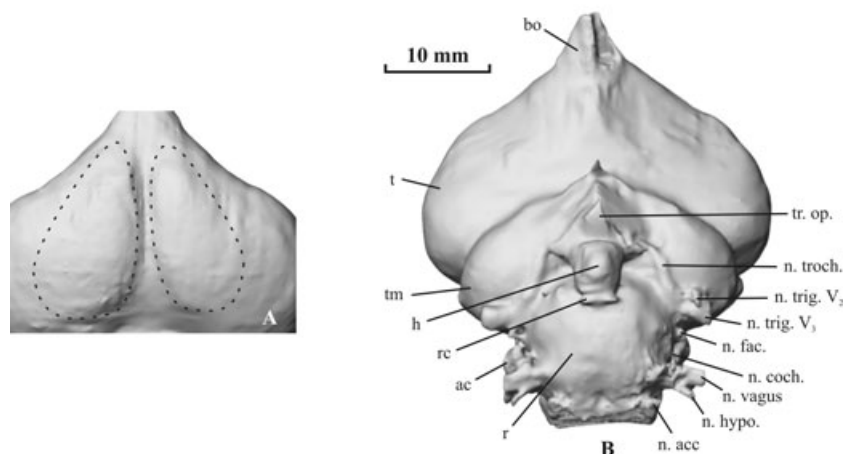
**Table 2.** Measurements obtained from the virtual endocast and labyrinth of *Prophaethon shrubsolei* using Rapidform™ 2006 (INUS Technology, Inc.)

	Length	Width	Height	Angle
Telencephalon	29.2	25.8	19.3	—
Angle between rostral telencephalon and midline	—	—	—	49°
Bulbus olfactorius	4.2	5.7	4.2	—
Cerebellum	12.9	10.4	12.0	—
Auricula cerebelli	1.8	3.7	—	—
Tectum mesencephali	10.2	5.6	6.5	—
Rhombencephalon	9.8	10.5	6.6	—
Tractus opticus	4.0	7.0	—	—
n. accessorius	0.4	1.3	—	—
n. cochlearis	1.5	1.2	—	—
n. facialis	0.9	1.3	—	—
n. glossopharyngeus	2.0	1.0	—	—
n. vagus	3.4	1.4	—	—
n. hypoglossus	1.9	1.7	—	—
n. trochlearis	4.6	0.8	—	—
n. trigeminus V <sub>2</sub>	1.2	1.4	—	—
n. trigeminus V <sub>3</sub>	3.0	1.8	—	—
Labyrinth	8.4	6.8	13.8	—
Canalis semicircularis rostralis	6.9	1.0	—	—
Canalis semicircularis horizontalis	6.5	1.3	—	—
Canalis semicircularis caudalis	5.8	0.8	—	—
Angle between csc/csr	—	—	—	62°
Angle between csc/csh	—	—	—	90°
Angle between csr/csh	—	—	—	96°

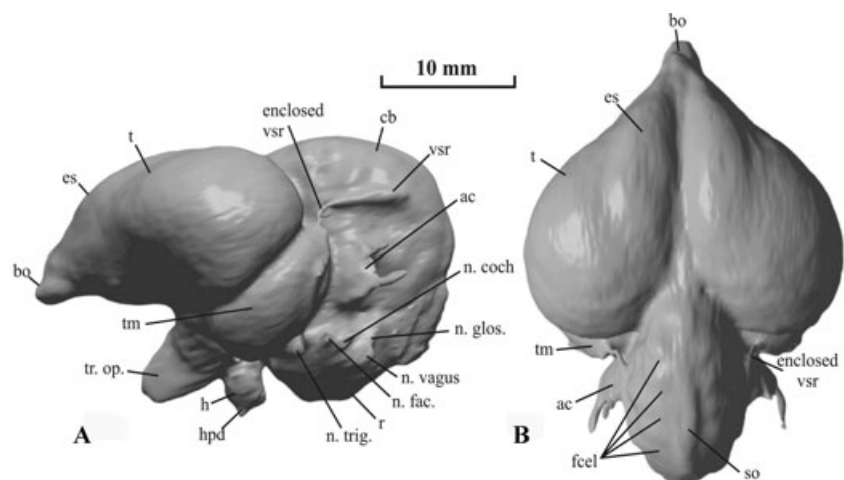
All values were measured at maximum orthogonal points, and are in millimetres. Note that semicircular canal length measurements refer to maximum dorsal (for csr) and lateral (for csh and csc) extent of canal arc; width measurements refer to maximum canal diameter.



**Figure 6.** Virtual endocast of *Prophaethon shrubsolei* in A, dorsal; B, rostral, and C, left lateral views. See text for list of anatomical abbreviations.



**Figure 7.** Virtual endocranial cast of *Prophaethon shrubsolei*. A, expanded view of the dorsal surface of the telencephalon, showing the shape and extent of the eminentia sagittalis. The eminentia sagittalis of this species is similar to living birds, but is not well developed dorsally. B, ventral view of virtual endocranial cast. See text for list of anatomical abbreviations.



**Figure 8.** Virtual endocranial cast of *Phaethon rubricauda* showing close morphological similarity to *Prophaethon shrubsolei*. A, left lateral and B, dorsal aspects. Note the absence of a vallicula and presence of well-marked impressions of the fissura cerebelli. Virtual endocranial cast reconstructed from publicly available data at [http://www.digimorph.org/specimens/Phaethon\\_rubricauda\\_melanorhynchos/](http://www.digimorph.org/specimens/Phaethon_rubricauda_melanorhynchos/) using MIMICS 8.13. See text for list of anatomical abbreviations.

The cerebellum is short (44% of the total brain length as measured along the central fissure) and broad (40% of the maximum telencephalic width); it is thus less elongate than that of *Phaethon* and does not exhibit the marked rostral narrowing in that taxon (Fig. 6A). The auricle cerebelli are caudolaterally directed but are shorter, narrower, and much less distally expanded than in *Odontopteryx*, and are also rostrocaudally compressed rather than approximately round in section. Although less rostrocaudally compressed, the feature is very similar to that seen in *Phaethon*. It is possible to detect impressions of the fissura cerebelli in *Phaethon* (Fig. 8B), but similar impressions are absent in BMNH A683 (Fig. 6A).

However, it is possible to discern a trace of the median groove for the sinus occipitalis that narrows caudally. The path of the vena semicircularis rostralis is a wide and well-marked ridge that follows the dorsal curve of the canalis semicircularis rostralis of the labyrinth before extending onto the tectum mesencephali (Fig. 6C). Unlike *Phaethon rubricauda* where the vena semicircularis rostralis arcs ventrally on the tectum mesencephali to reach the base of the n. trigeminus (Fig. 8A), the vein only extends to the midpoint of the tectum mesencephali. In *Phaethon rubricauda* the vein enters an osseous tunnel ventral of the protruberantia tentorialis; this tunnel is absent in *Prophaethon*.

The shape of the tractus opticus is difficult to estimate, but apparently extended about the same distance rostrally as in *Odontopteryx* (Fig. 7C). Unlike *Odontopteryx* and *Phaethon* the rostral surface of the telencephalon between the tractus opticus and bulbus olfactorius bears a slight wishbone-shaped ridge (Fig. 6B). The three branches of the wishbone shape terminate in an expansion. We interpret the two lateral expansions to be the exits of the arteria ophthalmica externa. In *Phaethon* the two projections are smaller and less laterally positioned, and occur more dorsally below the bulbus olfactorius.

The tectum mesencephali is larger relative to the telencephalon than in *Odontopteryx*, but proportionately similar to *Phaethon*. The region is a flattened hemisphere because of the expansion of the telencephalon, but unlike *Odontopteryx* the junction between the two is almost rectimarginate. The rostral-most ventral margin of the tectum mesencephali does, however, exhibit a slightly angular penetration by the telencephalon (Fig. 6C); in *Phaethon* this region is much more rounded.

The hypophysis is larger than in *Odontopteryx* but is still smaller than the tractus opticus (Fig. 7B). Traces of a dorsum sellae are very faint, and it appears that the feature may only have been fully ossified dorsally as in *Numenius* and *Pelecanoides* (Wingstrand, 1951). In *Phaethon* the dorsum sellae is thick (Fig. 8A). The body of the hypophysis is more laterally compressed than in *Odontopteryx*, and the rostral-most margin of the pars distalis lacks the conical development seen in *Odontopteryx*. Like *Hesperornis*, *Enaliornis*, *Procellariiformes*, and all *Pelecaniformes* except *Anhinga* (Saiff, 1978; Elzanowski & Galton, 1991), *Prophaethon* did not possess bony tunnels for the two ascending rami of the carotid artery. The preservation of their entry into the sella turcica indicates that the rami were narrow compared with those of *Odontopteryx*, and that the anastomosis intercarotica occurred at or above the level of the hypophysis, but it is not possible to determine the anastomosis pattern from our reconstruction.

The rhombencephalon exhibits a slightly flattened globe shape very similar to that of *Phaethon* (Fig. 7B). There is a slight suggestion of the presence of a ventral sulcus at its base, although this is difficult to determine. The foramen magnum is around twice the size of the same feature in *Phaethon rubricauda*, and is shaped like a rounded rectangle. The n. trochlearis is proportionately wider than that of *Odontopteryx*, and extends rostrally from the base of the n. trigeminus, but no trace of the n. oculomotorius appears to have been preserved. The n. trigeminus is proportionately as wide as in *Odontopteryx*, and its exit from the rhombencephalon partially involves the ventral margin of the tectum mesencephali (Fig. 6C). On the

left-hand side it is possible to detect two nerve bundles which, based on their position and relative width, probably correspond to the V<sub>2</sub> (maxillary) and V<sub>3</sub> (mandibular) branches. A narrow n. facialis is preserved on both sides of the rhombencephalon, and clearly bifurcates to produce two rami that are directed dorsolaterally and ventrolaterally. The n. cochlearis is the same thickness as the n. facialis, and also bifurcates to produce two dorsolaterally and ventrolaterally directed rami that are directed caudally. The n. glossopharyngeus and n. vagus exit the rhombencephalon as a single broad bundle which widens distally to produce one narrower dorsally directed ramus (n. glossopharyngeus) and a broader ventrally directed ramus (n. vagus). As in *Odontopteryx* the n. glossopharyngeus exits the skull via the recessus scalae tympani. The combined n. glossopharyngeus and n. vagus nerve bundle is around four times as broad as that of *Phaethon rubricauda*. The n. hypoglossus is as wide as the n. facialis, and originates at the base of the n. vagus, extending ventrocaudally for 1.9 mm. The n. accessorius exits caudal of the n. glossopharyngeus at the base of the foramen magnum. The ramus of the nerve extends laterally for 0.4 mm.

The canals of the bony labyrinth have well-defined ampullae, and are narrower than in *Odontopteryx* (Fig. 9A–D). The rostral limb of the canalis semicircularis rostralis strongly slopes caudally as it rises from the ampulla ossea rostralis, curving round and back with two relatively sharp changes in direction, until it is directed rostrally before its junction with the canalis semicircularis caudalis. As in *Odontopteryx* the canalis semicircularis rostralis represents 50% of the total dorsoventral height of the labyrinth. Also like *Odontopteryx* the caudal region of the canalis semicircularis rostralis frames the foramen magnum, but in contrast to *Odontopteryx* the long axis is angled medially at 96°, and the sigmoidal curvature seen in dorsal view in that taxon is negligible in *Prophaethon*. In dorsal view the canalis semicircularis rostralis et caudalis cross at an angle of 62° to each other; the canalis semicircularis caudalis et horizontalis meet at 90°. The ductus cochlearis represents only 38% of the total height of the labyrinth (in the right-hand side labyrinth the duct is shorter than the left and represents only 32% of the total height). The duct is directed rostrally and medially, and exhibits slight curvature toward the midline. The dorsal region of the duct is weakly laterally compressed but becomes more rounded ventrally. The caudally facing fenestra cochlearis is larger and more elongate than in *Odontopteryx*, the oval window of the columella is also larger, and the recessus antivistibularis extends further laterally. A well-developed dorsoventrally compressed sacculus is present on the lateral surface of the cochlear duct.



## DISCUSSION

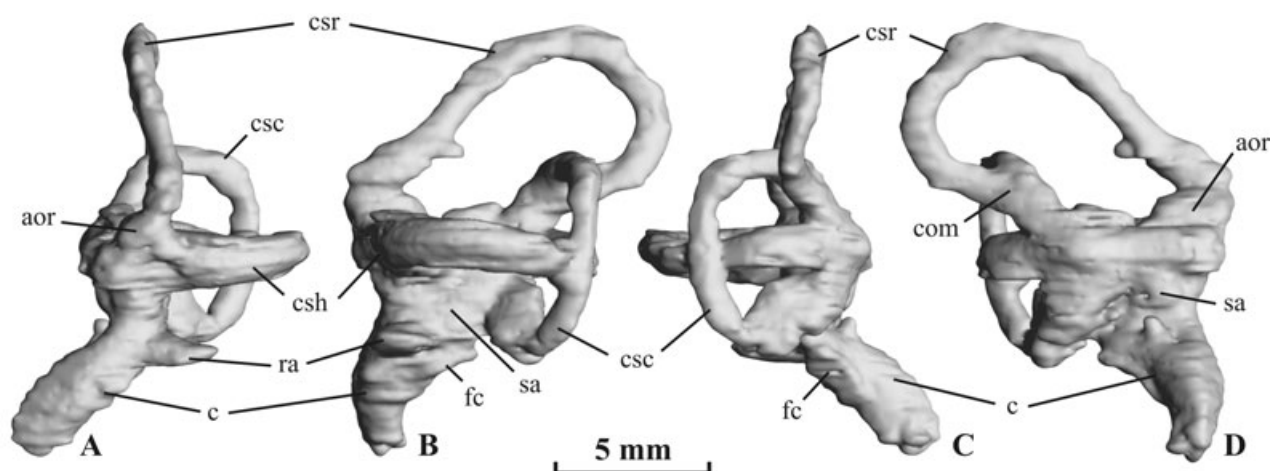
The reconstruction of the braincase of *Odontopteryx* has validated Elzanowski & Galton's (1991) interpretation of the posterior frontal-parietal suture as being unfused (c.f. Harrison & Walker, 1976a: 7). Obliteration of the cranial sutures is a characteristic of most extant birds and occurs in early ontogeny (Feduccia, 1999). However, in penguins, ratites, and some galliforms the cranial sutures often remain open after termination of growth, and in the Tinamidae the frontal-pleurospenoidal and frontal-parietal sutures remain open for life (Elzanowski & Galton, 1991). Interestingly, Elzanowski & Galton (1991) also noted that the frontal-parietal, interparietal, and parietal-supraoccipital sutures remained open in *Archaeopteryx*; in hesperornithids the interfrontal, frontal-parietal, and interparietal are unfused, in *Enaliornis* the interparietal, frontal-parietal, and possibly the parietal-supraoccipital remained open, and in extinct flying palaeognaths the frontal-pleurospenoidal and frontal-parietal sutures did not fuse. Bourdon (2005) also reported that the frontal-parietal suture of the prophaethontid *Lithoptila abdounensis* may not have been completely fused, although our reconstruction of *Prophaethon shrubsolei* demonstrates that it was in that species.

From this fossil evidence it seems likely that fusion of the frontal and parietal occurred late in the evolution of the avian skull. Although the skull bones of extinct flying palaeognaths may not have been entirely fused, the apparent restriction of late ontogenetic fusion to living nonvolant forms seems most likely to be related to the importance of possessing a light, rigid skeleton for flight, rather than evidence of retention of a plesiomorphy. The full fusion of the other sutures in BMNH 44096 and BMNH A683 and

the context of their recovery in marine sediments strongly suggest that both specimens represent flying adults, despite the incompletely ossified dorsum sellae in *Prophaethon*. The presence of an unfused frontal and parietal in *Odontopteryx* and *Lithoptila* suggests that these taxa were not as osteologically advanced as living volant birds. However, fusion of the frontal-parietal suture in *Prophaethon* indicates that this character was either variable within the Prophaethontidae, or that full fusion of the suture occurred later in life.

## TAXONOMIC IMPLICATIONS

The eminentia sagittalis of the two taxa differs in shape and relative development. Both are rostrally positioned, but whereas that of *Odontopteryx* is parallel sided, that of *Prophaethon* is broader caudally. Stingelin (1957) divided the eminentia sagittalis into two morphotypes based on its position on the dorsal telencephalon. In Type A the eminentia sagittalis is rostrally positioned, and in species where the feature is well developed (e.g. Strigiformes) it may also occlude large parts of the ventral telencephalic surface. Type B is caudally positioned, but includes intermediate forms in which the feature is situated centrally on the telencephalon. Both of the London Clay species clearly possessed Type A developments. Stingelin (1957) also hypothesized a basic ancestral type in which the eminentia sagittalis is short, rostrally positioned, but caudally separated from the fissura interhemispherica by part of the mesopallium. Although comparatively poorly developed, the eminentia sagittalis in neither *Odontopteryx* nor *Prophaethon* conformed to this pattern. Based on our observations it seems likely that the ancestral type was indeed small and rostrally



**Figure 9.** Reconstruction of the left osseous labyrinth of *Prophaethon shrubsolei* in A, rostral; B, lateral; C, caudal, and D, medial views. See text for list of anatomical abbreviations.

positioned, but perhaps extended medially to the fissura interhemispherica along much of its length. The expanded and therefore relatively derived eminentia sagittalis of *Prophaethon* could have readily developed from a basic pattern similar to that of *Odontopteryx*. The diversity of eminentia sagittalis patterns in these Lower Eocene species indicates that diversification of the ancestral eminentia sagittalis must have begun at some point earlier in time. Therefore, the pattern observed in *Odontopteryx* should not be taken as representing a true ancestral form, although its development certainly appears primitive relative to living taxa.

Stingelin's (1957) eminentia sagittalis types appear to be fairly consistent within living avian orders, suggesting that the feature may have some taxonomic utility. One obvious exception to this is within Pelecaniformes where both types are observed at the familial level. For instance, in the Phaethontidae and Phalacrocoracidae a Type A condition is observed, but in the Pelecanidae a well-developed Type B is present. The monophyly of Pelecaniformes has been questioned (e.g. Bourdon *et al.*, 2005) and the ordinal variability of this basic feature would only seem to highlight infraordinal divisions. In any case, the primitive eminentia sagittalis of *Odontopteryx* neither supports nor refutes its proposed peleciform relationships (e.g. Olson, 1985); the condition seen in this taxon could in theory have given rise to developments seen in any of the Type A peleciform taxa.

Although the anastomosis intercarotica of *Odontopteryx* is distinctive and appears to be similar to that of *Pelecanus*, the variability of this vessel within Pelecaniformes (Baumel & Gerchman, 1968) precludes its use at this taxonomic level. A similar long anastomosis intercarotica is also found in some species of *Anas* (Wingstrand, 1951; Baumel & Gerchman, 1968). The enclosure of the two carotid rami in bony tunnels in *Odontopteryx* is also informative. In Pelecaniformes this condition is found only in *Anhinga rufa*, although the rami are incompletely enclosed in the remaining two species of *Anhinga* (Saiff, 1978), and may approach closure in the Phalacrocoracidae (Bourdon, 2005). The tunnels are also absent in Procellariiformes, *Hesperornis*, and *Enaliornis* (Saiff, 1974; Elzanowski & Galton, 1991). Damage to the base of the skull in the London *Archaeopteryx* prevents the condition in that taxon from being assessed (Domínguez *et al.*, 2004). The carotid rami of Sphenisciformes (Saiff, 1976) and Anseriformes (E. Bourdon, pers. comm., 2006) are, however, fully enclosed. The long anastomosis intercarotica and enclosure of the carotid rami therefore seem to provide some support for Bourdon's (2005) hypothesis of a sister group relationship between Odontopterygiformes and Anseriformes (Odontoanserae).

However, the shape of the hypophysis is not like that of the Anseriformes (Wingstrand, 1951). Overall, the mosaic of braincase characters found in *Odontopteryx* is consistent with the situation encountered in the osteology of the bony-toothed birds as a whole, and provides no clear evidence of a closer relationship with either Pelecaniformes or Procellariiformes. Until the higher level relationships of this group can be clarified it seems wiser to retain a separate taxon Odontopterygiiformes.

Although the morphological similarities between the brain of *Prophaethon* and living *Phaethon* shed no further light on wider peleciform relationships, they at least strengthen hypotheses of a close relationship between the Phaethontidae and Prophaethontidae (e.g. Olson, 1985; Gulas-Wroblewski, 2003; Bourdon *et al.*, 2005). The main characters that unite *Prophaethon shrubsolei* and *Phaethon rubricauda* compared with *Odontopteryx toliapica* include a large bulbus olfactorius that is not strongly separated from the telencephalon, a vena semicircularis rostralis extending along the lateral surfaces of the cerebellum and tectum mesencephali in a wide sulcus, and a short auricula cerebelli. *Prophaethon* differs from *Phaethon* mainly in that the cerebellum is short and does not narrow rostrally, the osseous tunnel of the vena semicircularis rostralis between the cerebellum and tectum mesencephali is absent, the auricula cerebelli is not rostrocaudally compressed and the hypophysis makes contact with the rhombencephalon (unossified dorsum sellae).

The n. vagus and n. glossopharyngeus are not differentiated as they exit the rhombencephalon in *Prophaethon* or *Odontopteryx*. Elzanowski & Galton (1991) note that no separate foramen for the n. glossopharyngeus exists in Phaethontidae, Diomedidae, Procellariidae, and palaeognaths, in the fossil taxa *Hesperornis*, *Enaliornis*, and some of the smaller theropods (e.g. *Syntarsus* and *Stenonychosaurus*), and is therefore considered primitive within birds. However, the situation in *Archaeopteryx* remains unclear, with CT analysis indicating a possible separate n. glossopharyngeus (Domínguez *et al.*, 2004). In palaeognaths the n. glossopharyngeus exits the skull with the n. vagus (Elzanowski & Galton, 1991), but in both London Clay taxa the exit occurs within the recessus scalae tympani. In *Odontopteryx* the divergence of the n. glossopharyngeus and n. vagus is close to the exit of the n. vagus, although the significance of this (if any) is unclear.

#### FUNCTIONAL CORRELATES OF BRAIN AND LABYRINTH MORPHOLOGY

Although our knowledge of neural pathways and the function of specific brain regions in birds has

advanced enormously in recent decades, this understanding has grown from studies of cellular structures that are obviously not visible in virtual endocranial casts. The following discussion is therefore mainly based on interpretation of the relative development of specific regions, following the assumption that variations in neuronal packing should be accompanied by changes in regional volume (Striedter, 2005).

The shape and relative dimensions of the avian bony labyrinth have been compared with flying ability in modern birds (see Pearson, 1972 for a review), and it is therefore possible to use the labyrinth of *Odontopteryx* and *Prophaethon* to provide some inference of flying adaptation in these taxa. In the most adept fliers (e.g. *Falco*) the canalis semicircularis rostralis is inclined medially to produce an angle between it and the canalis semicircularis horizontalis of more than 90° (Hadžiselimović & Savković, 1964). This suggests that, with an angle of over 90° the flying ability of *Prophaethon* was probably good, but *Odontopteryx* was probably a poorer flyer with a mean angle of 85°. Nonetheless, both species possessed well-developed ampullary ends, a condition that is found in good fliers such as *Falco*, *Corvus*, and *Aquila* (Pearson, 1972).

The length and diameter of the canals themselves are also correlated with flying ability (Hadžiselimović & Savković, 1964; Pearson, 1972; Sipla, Georgi & Forster, 2003). Comparatively acrobatic fliers such as *Larus* and *Columba* have long thin canals, whereas species that tend towards more level straight line flight (e.g. *Anser*, *Anas*, and *Gallus*) have shorter and broader canals (Pearson, 1972). The short and comparatively thick semicircular canals of *Odontopteryx* therefore suggest that this taxon was not adept at rapid changes of direction, an interpretation consistent with the soaring, gliding flight mode commonly suggested for the group (e.g. Olson, 1985). Conversely the canals of *Prophaethon* are comparatively narrow, suggesting that its manoeuvring ability was somewhat greater than that of *Odontopteryx*.

Interestingly, although slightly shorter in proportion to the rest of the labyrinth, the canals of *Archaeopteryx* were proportionately narrower than those of *Odontopteryx*, and much narrower than in *Enaliornis* suggesting high manoeuvrability in that taxon. Variability in the labyrinth of living birds has been correlated with ecological niche (Hadžiselimović & Savković, 1964), and it seems likely that the apparently advanced level of flight adaptedness in the labyrinth of *Archaeopteryx* in the Jurassic compared with taxa that lived some 40 and 100 million years later, is a result of environmental pressures. If *Archaeopteryx* inhabited a forest environment as has been postulated (e.g. Jerison, 1973), acute 3D aware-

ness would have been more crucial to it than for seabirds in an open marine environment.

The minimum hearing range (see Pearson, 1972) of these taxa cannot be estimated without information on the relative size of the tympanic membrane and foot of the columella. Similarly, differences in the length of the ductus cochlearis in each species are probably not great enough to indicate an advantage in overall hearing ability between *Odontopteryx* and *Prophaethon*.

Neither of the London Clay taxa exhibit traces of fissura cerebelli, although *Prophaethon* does possess evidence of a sinus occipitalis. Elzanowski & Galton (1991) note that lack of relief on the fossa cerebellaris is characteristic of diving birds. However, the extreme pneumaticity characteristic of the skeleton of *Odontopterygiformes* would seem to make diving in *Odontopteryx* unlikely. By comparison, the diver-like pelvis of *Prophaethon* (Olson, 1985) ostensibly provides some support for diving in that taxon, particularly considering that the closely related *Phaethontidae* are plunge divers. Nonetheless, the legs of living *Phaethontidae* are reduced compared to those of *Prophaethon*, a condition characteristic of pelagic birds in which hind limbs are comparatively unimportant. Furthermore, we have observed a well-marked median sulcus and fissura cerebelli in *Phaethon rubricauda* (Fig. 9B), and the absence of fissura cerebelli in *Prophaethon* suggests that it may have been better adapted for diving than the living species. This possibility would require further corroboration from elements of the postcrania that are not preserved in the holotype of *Prophaethon* or *Lithoptila*.

Elzanowski & Galton (1991) also observed that diving birds possess large fossae auriculae cerebelli. The auricula cerebelli of *Odontopteryx* is notably large, but as stated above is unlikely to be related to diving adaptations. Witmer *et al.* (2003) suggested the remarkable enlargement of the auricula cerebelli in the pterosaurs *Anhangura* and *Rhamphorhynchus* were related to reflexes that allowed these taxa to stabilize their gaze on prey items and represented an enhancement of the gaze stability mechanism found in birds and mammals. Aerial surface capture of prey has been suggested for both *odontopterygiformes* and pterosaurs (e.g. Wellnhofer, 1991; Zusi & Warheit, 1992), with the bony pseudoteeth of the former acting as analogues of the pterosaur dentition. If this suggestion is correct, the extremely thinly walled bones of both pterosaurs and *Odontopterygiformes* would be particularly vulnerable to damage during a poorly executed surface snatch. We suggest that the comparatively well-developed auricula cerebelli of *Odontopteryx* probably represents a motor sensory adaptation to enhance surface prey capture. This



adaptation would be entirely concordant with the albatross-like gliding mode of flight generally accepted for the *Odontopterygiformes* (e.g. Olson, 1985) and level, straight line type of labyrinth described here. We note that the auricula cerebelli of *Diomedea immutabilis* (Laysan albatross) is very similar in shape and length to that of *Odontopteryx*. Future examination of comparative material will test the possible correlation between development of this region and gliding surface feeding in other seabirds. The smaller auricula cerebelli of *Prophaethon* suggests that this adaptation was less well developed than in *Odontopteryx*.

As in all living birds the n. facialis is much less well developed than the n. trigeminus. The n. trigeminus comprises both efferent (mostly jaw motor impulses) and afferent (from sensory receptors in the rostrum) fibres, and is always well developed in taxa with prominent rostra (Butler & Hodos, 1996). Consequently it is large in all living birds, and in *Odontopteryx*, *Prophaethon*, *Enaliornis*, and *Archaeopteryx*, suggesting the sensory motor capabilities of the n. trigeminus in these taxa were probably comparable with those of living birds. The external eye muscles in *Prophaethon* appear to have been better developed than in *Odontopteryx* to judge from the relative size of the n. trochlearis. However, the n. oculomotorius appears to have been better developed in *Odontopteryx* than in *Prophaethon*. This nerve is connected with both internal and external eye muscles, and its greater development in *Odontopteryx* may relate to either of these connections rather than specifically to external eye muscle innervation.

The size of the bulbus olfactorius relative to the size of the telencephalic hemispheres in both London Clay species is smaller than in *Archaeopteryx*. Thus the senses of *Odontopteryx* and *Prophaethon* appear to have been as fundamentally biased towards sight as are the senses of living birds. Results of experimental work have fuelled the debate as to whether the avian sense of smell is fundamentally important for bird species other than carrion feeders, or whether it is purely vestigial (e.g. Dubbeldam, 1998). However, no species is known to be anosmic (Pearson, 1972), and the retention of functional olfactory organs after more than 150 million years of evolution surely demonstrates that smell must fulfil some important function in birds. Nonetheless, olfactory capability is well known to vary greatly within living Aves (Pearson, 1972), and the relative importance of smell presumably also varies across species. Compared with *Prophaethon rubricauda* the bulbus olfactorius of *Prophaethon* is slightly larger, and is noticeably larger than in *Odontopteryx*. This would suggest a relatively greater reliance on smell in *Prophaethon*

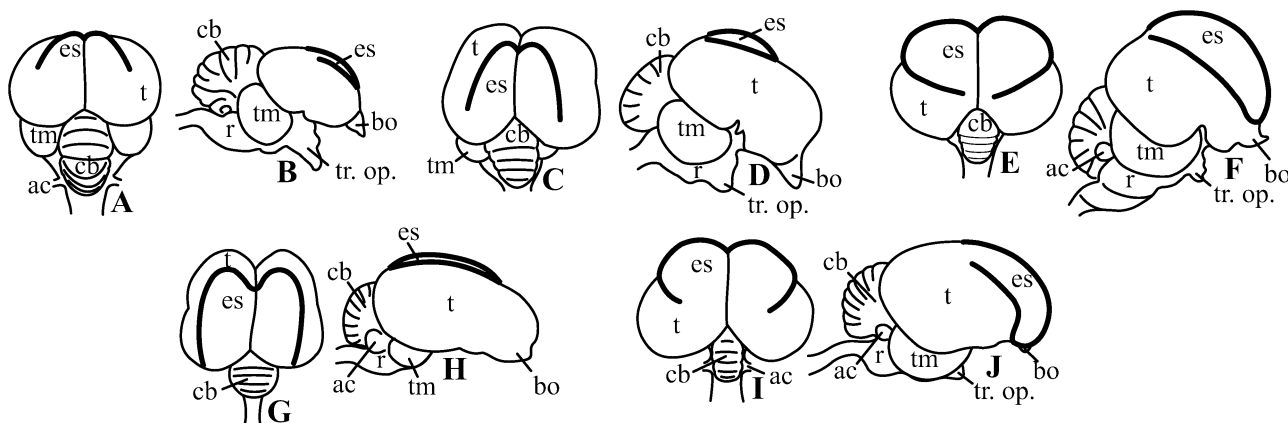
than in *Odontopterygiformes*. However, as innervation and soft tissue structure of the nasal fossae are also of major importance (see Pearson, 1972 for discussion), the size of the bulbus itself may not provide a reliable inference of olfactory capability. Our present analysis can therefore only provide evidence that the olfactory capability of *Odontopteryx* and *Prophaethon* was likely to have been similar to most other marine birds.

The size of the tectum mesencephali relative to the size of the telencephalon in *Prophaethon* also suggests a greater degree of visual acuity in that species than in *Odontopteryx*. However, much of the integration of visual and somatosensory input occurs in the eminentia sagittalis (Dubbeldam, 1998; Medina & Reiner, 2000; Mouritsen *et al.*, 2005), which is smaller in birds such as *Columba* that have more lateralized vision and larger in those with well-integrated binocular vision (e.g. Strigiformes; Dubbeldam, 1998) (Fig. 11). The structure of the eminentia sagittalis is layered to a lesser or greater degree in modern birds, with the strongest differentiation of layers again seen in species with strong visual specialization (Dubbeldam, 1998). Although we are obviously unable to determine the cellular structure of this feature in the London Clay taxa, we would not expect advanced development of the eminentia sagittalis at the microstructural level considering the relatively lateral position of the eyes in both species, and poorer macrostructural development compared with extant taxa. Nonetheless, the larger eminentia sagittalis, better development of the nerves serving the external eye musculature and relatively larger tectum mesencephali of *Prophaethon* do suggest that this species possessed a greater capacity for visual processing than *Odontopteryx*.

#### EVOLUTIONARY IMPLICATIONS OF BRAIN MORPHOLOGY

The gross structure of the brain of both *Odontopteryx* and *Prophaethon* includes caudal rotation of the tectum mesencephali and expansion of the telencephalon, and is very close to that of living birds. However, the cerebellum is small by comparison with most living species, and is notably shorter than in *Prophaethon*. Comparisons with other fossil taxa are limited by the paucity of available comparative material and the absence of living odontopterygiform and prophaethontid representatives, but the lateral expansion of the telencephalon in both taxa is obviously far greater than in *Archaeopteryx* and the Cretaceous specimen briefly described by Kurochkin (2004). The only other comparable early Cenozoic material is the geologically younger specimen from the Paris Basin described by Dechaseaux (1970)





**Figure 10.** Relative size of brain regions in selected modern bird species. A, B; pigeon (*Columbia livia*; Columbiiformes) in A, dorsal, and B, right lateral views. The wide rostrally positioned eminentia sagittalis with poor dorsal expansion is among the poorest developed in living birds. C, D; woodcock (*Scolopax rusticola*; Charadriiformes) in C, dorsal, and D, right lateral views. Note caudally positioned wide eminentia sagittalis with moderate dorsal expansion and moderate tectum mesencephali. E, F; tawny owl (*Strix aluco*; Strigiformes) in E, dorsal and F, right lateral views. Note the exceptionally well-developed (dorsally and laterally) rostral eminentia sagittalis, comparatively small cerebellum and moderately sized tectum mesencephali. G, H; macaw (*Ara* sp.; Psittaciformes) in G, dorsal and H, lateral views. Psittaciform brains are characterized by great lateral expansion of a caudally positioned eminentia sagittalis, and a very large telencephalon relative to the size of the cerebellum. The tectum mesencephali is particularly small relative to the telencephalon. I, J; raven (*Corvus corax*; Passeriformes) in I, dorsal and J, lateral views. The large, wide and dorsally well-developed rostrally positioned eminentia sagittalis of Passeriformes is exemplified in brains of Corvidae. The cerebellum is small relative to the exceptionally well-developed telencephalon. Of the species figured here, the charadriiform (*Scolopax*) (C, D) is typical in possessing the largest bulbus olfactorius. A, B adapted from Dubbeldam (1998); C, J adapted from Stingelin (1957). See text for abbreviations.

which exhibits a similar telencephalic expansion to the brains of the London Clay birds described here, although it is slightly more elongate (Fig. 10A). The Paris Basin endocast (MNHN AC7992) belonged to a fossil specimen that was originally described by Gervais (1844) as *Numenius gypsorum* (Charadriiformes, Scolopacidae), and Dechaseaux (1970) and Jerison (1973) both noted that the telencephalic expansion of the endocast was less than in living representatives of the same genus. However, the relationships of 'Numenius' are unclear. Brodkorb (1967) transferred it to the scolopacid genus *Limosa*, whereas Mlíkovský (1981b) referred the specimen to the Rallidae and erected a new genus, *Montirallus*, based primarily on endocast morphology. Whatever the true relationships of this taxon, comparisons between it and living genera should probably be regarded with caution.

Caudal and dorsal expansion of the avian telencephalon is widely regarded to have resulted from enlargement of the ancestral dorsal ventricular ridge (Dubbeldam, 1998). Although we cannot examine the internal structure in these virtual endocasts, it seems safe to assume that the observed telencephalic expansion is also related to growth of the dorsal ventricular ridge. A strong correlation between telencephalic size

and social complexity in birds was found by Burish *et al.* (2004). They noted a progressive increase in telencephalic volumes from theropods to birds, with *Archaeopteryx* occupying a transitional position. Lefebvre and others (Lefebvre *et al.*, 1997, 2004; Nicolakakis & Lefebvre, 2000; Timmermans *et al.*, 2000; Webster & Lefebvre 2001; Lefebvre, Nicolakakis & Boire, 2002; Sol, Timmermans & Lefebvre 2002) have found a positive correlation between observed number of new behaviours (innovation rate) and brain size, principally in two broad regions derived from the dorsal ventricular ridge itself; the mesopallium and parts of the hyperpallium that comprise the eminentia sagittalis. Lefebvre *et al.* (2004) also found that innovation rate was highest in species that have to deal with strong seasonal environmental changes, and have the greatest survival potential when introduced to new environments. They noted that a similar correlation exists between innovation rate and the size of the isocortex and striatum in primates. Later work by Iwaniuk & Hurd (2005) appears to support this relationship; the highest values of mesopallial volume are found in the two avian orders that are generally regarded as having the greatest cognitive and learning abilities, the Psittaciformes and Passeriformes. Both of these orders include species with

tool-using capabilities that exceed most primates (Burish *et al.*, 2004; Lefebvre *et al.*, 2004).

Our analysis of *Odontopteryx* and *Prophaethon* demonstrates that by the Lower Eocene telencephalic expansion and, presumably, mesopallial volume was very close to that of modern neornithine species (see Fig. 10). Based on these observations it appears that one major direction in the evolution of the avian brain is an overall increase in mesopallial volume accompanied by greater cognitive ability.

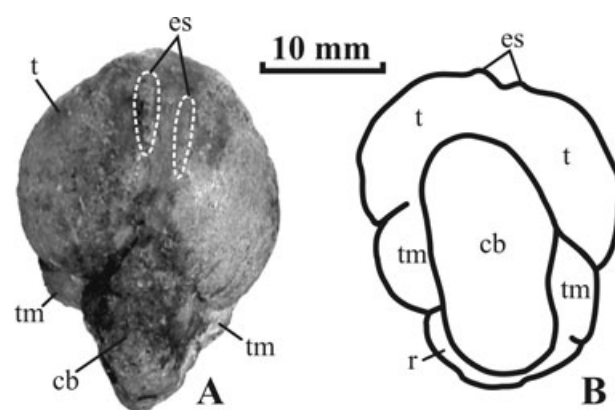
The development of the eminentia sagittalis in the two London Clay birds is also of considerable interest. This characteristic dorsal telencephalic expansion is a feature shared to a lesser or greater degree by all living birds (Dubbeldam, 1998). Neuronal connections and pseudocellular lamination in the eminentia sagittalis of extant Aves indicate that it probably represents an analogue of the mammalian neocortex (e.g. Eccles, 1992; Dubbeldam, 1998; Medina & Reiner, 2000; Lefebvre *et al.*, 2004; Reiner *et al.*, 2004; Iwaniuk & Hurd, 2005; Striedter, 2005), and the evolution of the eminentia sagittalis is therefore of importance to comparative studies as well as avian palaeontology. *Prophaethon* possessed an eminentia sagittalis that is within the size range of modern birds, albeit at the lower end of the scale. However, in *Odontopteryx* the eminentia sagittalis is negligible despite careful CT segmentation (3D reconstruction) to ensure that as much detail of the feature as possible was retained in the reconstruction; this is surprising considering its advanced lateral telencephalic expansion. The development is in fact far poorer than in any extant species for which we have comparative data.

It is notable that published figures of the only other Eocene endocast known, '*Numenius' gypsum* (Dechaseaux, 1970: fig. 1), do not appear to show any evidence of an eminentia sagittalis, but the presence or absence of this feature appear never to have been discussed in earlier accounts of the specimen. However, our recent examination of this specimen (MNHN AC7992) has revealed that it does indeed possess a rudimentary eminentia sagittalis, which is very similar in form to that of *Odontopteryx*, although slightly more dorsally expanded (Fig. 11). The next certain occurrences of an eminentia sagittalis in the fossil record come from the lower Miocene of Czechoslovakia (Mlíkovský, 1980) and upper Pliocene of Hungary (Mlíkovský, 1981a). Although Mlíkovský (1980, 1981a) provides only interpretive drawings of these specimens, it seems clear that the eminentia sagittalis was in all cases comparable in size and shape to that of living species. Chatterjee (1991) noted the presence of an eminentia sagittalis in a reconstruction of the brain of the Triassic *Protoavis texensis* Chatterjee, although this taxon has not

gained wide acceptance as closely related to birds (Dingus & Rowe, 1998; Feduccia, 1999). The London Clay specimens therefore represent the earliest reliable records of the presence of this feature in the avian brain.

These findings provide important evidence regarding the chronology of the evolution of the eminentia sagittalis in birds. At 147 Mya *Archaeopteryx* lacks this feature, as does the Russian specimen described by Kurochkin (2004) at between 99 and 93 Mya. The first species to show definite evidence of an eminentia sagittalis are *Prophaethon* and *Odontopteryx* at around 55 Mya, but it is virtually absent in the latter. '*Numenius' gypsum*, at around 40 Mya, has slightly greater dorsal expansion than *Odontopteryx*. The difference in eminentia sagittalis shape exhibited by *Odontopteryx* and *Prophaethon* would suggest that diversification of the feature had begun earlier than the Eocene, possibly within the Cretaceous. However, the similarity in position and form of the eminentia sagittalis in *O. toliapica* and '*Numenius' gypsum* suggest that this particular condition may have been widespread during the early evolution of the feature in birds. The similarity and poor development of the feature in these two Eocene taxa also suggest that the ancestral form of the eminentia sagittalis may also have been close to this form.

The absence in these reconstructions of the vallecule (a sulcus that demarcates the eminentia sagittalis from the rest of the telencephalon in modern birds) probably does not indicate that the feature was absent from the brain itself. We note that there is no trace of a vallecule in any fossil endocasts we have examined, in physical endocranial casts made from



**Figure 11.** Fossil endocast of '*Numenius' gypsum* from the Upper Eocene of the Paris Basin (MNHN AC7992). A, endocast in dorsal view showing the poor lateral development of the rostrally positioned eminentia sagittalis. B, line trace of the endocast in caudal view showing the poor dorsal development of the eminentia sagittalis. See text for abbreviations.

the skulls of modern species, or in any virtual endocast reconstructed from micro-CT data. It seems very likely that no evidence of the feature is preserved on the internal surface of the skull roof because of the presence of sinusoidal tissue between the sulcus and bone.

Overall, our findings support Jerison's (1973) hypothesis of a gradual increase in brain size throughout the Mesozoic and Cenozoic. However, it would appear that development and growth of the eminentia sagittalis were more important during the Cenozoic than telencephalic expansion which, in some taxa at least, appears to have already been more or less close to modern levels by the early Cenozoic. The eminentia sagittalis is closely related to integration of sensory input (Medina & Reiner, 2000) but, except perhaps in migrational passerines (Mouritsen *et al.*, 2005), is unlikely to be of fundamental importance to aerial locomotion. Its development may therefore be associated with an increased requirement for sensory integration in species with enhanced cognitive and learning abilities. If so, the evolution of the avian brain would closely parallel hypotheses suggested for the primate brain (e.g. Striedter, 2005), although unlike most mammals the avian brain is size-constrained by the requirements of flight.

The work of Lefebvre and others (Nicolakakis & Lefebvre, 2000; Timmermans *et al.*, 2000; Sol *et al.*, 2002, 2005; Lefebvre *et al.*, 2004) correlating innovation rate and adaptability in new environments with forebrain size in living birds, may offer insight into why Neornithes were able to survive the K-T extinction event when all other volant groups became extinct, and also provide a mechanism for their rapid radiation thereafter. For those taxa that survived the extinction, acquisition of food for niche-adapted species would have become progressively more difficult during any subsequent ecological collapse (Robertson *et al.*, 2004). However, those species capable of behavioural innovation may have been able to adapt through modified behaviour without being ecological generalists *per se*. The success of such innovative species in new environments (Lefebvre *et al.*, 2004) may have allowed them to radiate rapidly into vacant niches.

## CONCLUSIONS

The morphology of these virtual endocasts demonstrates that, by the early Eocene, the avian brain had reached a level of development very close to that of modern birds. The expansion of the telencephalon characteristic of living avian species therefore appears to have been largely complete by the close of the Mesozoic. Nevertheless the appearance during the Cenozoic of groups that today are known to have

relatively high mesopallial volumes suggest that the proportion of mesopallium (as a component of the telencephalon) has probably increased since the end of the Mesozoic. For instance, Passeriformes have comparatively high mesopallial volumes (Lefebvre *et al.*, 2004) but did not appear until the early Neogene (Olson, 1985). As this is a structural reorganization at the neuronal level it is impossible to detect in fossil material. One important feature, the eminentia sagittalis, appears to have been at an early stage of development early in the Cenozoic. Although the proportion of mesopallium may have increased without major increases in the size of the telencephalon, the dorsal expansion of the eminentia sagittalis appears to account for much of the increase in telencephalic volume during the Cenozoic. These observations suggest that, in addition to a tendency towards greater structural complexity, the avian brain is continuing a trend towards enlargement.

The London Clay birds had brains that were otherwise little different from those of seabirds today, and were almost certainly capable of similar sensory abilities. Our findings tend to confirm the widely held view that *Odontopteryx* was adapted as a gliding snatch feeder, and was probably not a particularly aerobatic flyer despite being among the smallest of *Odontopterygiformes*. *Prophaethon* was a better flyer than *Odontopteryx*, and was probably better adapted for diving than living members of the *Phaethontidae*.

Our findings provide some support for an anseriform relationship for *Odontopterygiformes* (Bourdon, 2005), and strengthen the relationship between *Prophaethontidae* and *Phaethontidae*. Characters of the brain and internal braincase have not been used in phylogenetic analysis hitherto, but we have demonstrated that the application of CT techniques will provide useful new character sets that can be coded for future analyses of avian groups.

The positive correlation between mesopallial volume and invasion success in terms of the ability of a species to survive and become established in a new environment (Sol *et al.*, 2002; Lefebvre *et al.*, 2004) may provide an explanation for the survival of Neornithes at the K-T boundary. However, this possibility can only be tested by determining the state of neurological evolution in both archaic lineages and Neornithes toward the end of the Mesozoic. The advent of CT analysis in palaeontology has at last provided the possibility to investigate this.

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## REFERENCES

- Andrews CA. 1899.** On the remains of a new bird from the London Clay of Sheppey. *Proceedings of the Zoological Society of London*, **1899**: 776–785.
- Averianov AO, Panteleyev AV, Potapova OR, Nesson LA. 1991.** Bony-toothed birds (Aves: Pelecaniformes: Odontopterygia) from the Late Paleocene and Eocene of the western margin of Ancient Asia. *Proceedings of the Zoological Institute, USSR Academy of Sciences* **239**: 3–12.
- Baumel JJ, Gerschman L. 1968.** The avian carotid anastomosis. *American Journal Of Anatomy* **122**: 1–18.
- Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC. 1993.** *Nomina anatomica avium: handbook of avian anatomy*, 2nd edn. Cambridge, MA: The Nuttall Ornithological Club.
- Beauchamp G, Fernandez JE. 2004.** Is there a relationship between forebrain size and group size in birds? *Evolutionary Ecology Research* **6**: 833–842.
- de Beer G. 1954.** *Archaeopteryx lithographica*. London: British Museum.
- Bourdon E. 2005.** Osteological evidence for sister group relationship between pseudo-toothed birds (Aves: Odontopterygiformes) and waterfowls (Anseriformes). *Naturwissenschaften* **92**: 586–591.
- Bourdon E, Baàdi B, Iarochene M. 2005.** Earliest African neornithine bird: a new species of Prophaethontidae (Aves) from the Paleocene of Morocco. *Journal of Vertebrate Paleontology* **25**: 157–170.
- Brodkorb P. 1967.** Catalogue of fossil birds. Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). *Bulletin of the Florida State Museum, Biological Sciences* **11**: 99–220.
- Burish MJ, Kueh HY, Wang SS. 2004.** Brain architecture and social complexity in birds and dinosaurs. *Brain, Behavior and Evolution* **63**: 107–124.
- Butler AB, Hodos W. 1996.** *Comparative vertebrate anatomy*. New York: Wiley-Liss.
- Chatterjee S. 1991.** Cranial anatomy and relationships of a new Triassic bird from Texas. *Philosophical Transactions of the Royal Society of London B* **332**: 277–342.
- Chiappe LM. 1995.** The first 85 million years of avian evolution. *Nature* **378**: 349–354.
- Chiappe LM, Dyke GJ. 2002.** The Mesozoic radiation of birds. *Annual Review of Ecology and Systematics* **33**: 91–124.
- Clarke JA, Tambussi CP, Noriega JI, Erickson GM, Ketcham RA. 2005.** Definitive fossil evidence for the extant avian radiation in the Cretaceous. *Nature* **433**: 305–308.
- Cooper A, Penny D. 1997.** Mass survival of birds across the Cretaceous/Tertiary boundary. *Science* **275**: 1109–1113.
- Dechaseaux C. 1970.** Moulages endocraniens d'oiseaux de l'Éocène Supérieur du Bassin de Paris. *Annales de Paléontologie* **56**: 69–72.
- Dingus L, Rowe T. 1998.** *The mistaken extinction. Dinosaur evolution and the origin of birds*. New York: W. H. Freedman and Co.
- Domínguez P, Milner AC, Ketcham RA, Cookson MJ, Rowe TB. 2004.** The avian nature of the brain and inner ear of *Archaeopteryx*. *Nature* **430**: 666–669.
- Dubbeldam JL. 1998.** Birds. In: Nieuwenhuys R, Ten Donckelaar HJ, Nicholson C, eds. *The central nervous system of vertebrates*, Vol. 3. Berlin: Springer, 1525–1636.
- Dyke GJ. 2001.** The evolutionary radiation of modern birds: systematics and patterns of diversification. *Geological Journal* **36**: 305–315.
- Eccles JC. 1992.** Evolution of consciousness. *Proceedings of the National Academy of Sciences of the United States of America* **89**: 7320–7324.
- Edinger T. 1926.** The brain of *Archaeopteryx*. *Annals and Magazine of Natural History : including Zoology, Botany and Geology* **18**: 151–156.
- Edinger T. 1951.** The brains of the Odontognathae. *Evolution* **5**: 6–24.
- Elzanowski A, Galton PM. 1991.** Braincase of *Enaliornis*, an early Cretaceous bird from England. *Journal of Vertebrate Paleontology* **11**: 90–107.
- Feduccia A. 1999.** *The origin and evolution of birds*, 2nd edn. New Haven and London: Yale University Press.
- Gervais P. 1844.** *Remarques sur les Oiseaux fossils*. Thèse de la Faculté de Sciences de l'Université de Paris. Paris.
- Gulas-Wroblewski BE. 2003.** Incorporating fossil taxa into phylogenetic analyses of modern clades: the case of Prophaethon. *Geological Society of America Abstracts with Programs* **35**: 497.
- Hadžiselimović H, Savković L. 1964.** Appearance of semi-circular canals in birds in relation to mode of life. *Acta Anatomica* **57**: 306–315.
- Harrison CJO. 1985.** A bony-toothed bird (Odontopterygiformes) from the Palaeocene of England. *Tertiary Research* **7**: 23–25.
- Harrison CJO, Walker CA. 1976a.** A review of the bony-toothed birds (Odontopterygiformes): with descriptions of some new species. *Tertiary Research Special Paper* **2**: 1–72.
- Harrison CJO, Walker CA. 1976b.** A reappraisal of *Prophaethon shrubsolei* Andrews (Aves). *Bulletin of the British Museum of Natural History (Geology)* **27**: 1–30.
- Harrison CJO, Walker CA. 1977.** Birds of the British Lower Eocene. *Tertiary Research Special Paper* **3**: 1–52.
- Harrison GL, MacLenachan PA, Phillips MJ, Slack KE, Cooper A, Penny D. 2004.** Four new avian mitochondrial genomes help get to basic evolutionary questions in the Late Cretaceous. *Molecular Biology and Evolution* **21**: 974–983.
- Holloway RL, Broadfield DC, Yuan MS. 2004.** *The human fossil record, Volume 3: brain endocasts—the paleoneurological evidence*. New Jersey: John Wiley and Sons.
- Howard H. 1957.** A gigantic 'toothed' marine bird from the



- Miocene of California. *Bulletin of the Department of Geology, Santa Barbara Museum of Natural History* **1**: 1–23.
- Iwaniuk AN, Dean KM, Nelson JE. 2004.** A mosaic pattern characterises the evolution of the avian brain. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **271** (Suppl.): S148–S151.
- Iwaniuk AN, Dean KM, Nelson JE. 2005.** Interspecific allometry of the brain and brain regions in parrots (psittaciformes): comparisons with other birds and primates. *Brain, Behavior and Evolution* **65**: 40–59.
- Iwaniuk AN, Hurd PL. 2005.** The evolution of cerebrotypes in birds. *Brain, Behavior and Evolution* **65**: 215–230.
- Jerison HJ. 1968.** Brain evolution and *Archaeopteryx*. *Nature* **219**: 1381–1382.
- Jerison HJ. 1973.** *Evolution of the brain and intelligence*. London: Academic Press.
- Kurochkin EN. 2004.** New fossil birds from the Cretaceous of Russia. *Abstracts of the Sixth International Meeting of the Society of Avian Paleontology and Evolution, Quillan* 35–36. Available at [http://nrm.museum/ve/birds/sape/SAPE\\_abstracts\\_2004.pdf](http://nrm.museum/ve/birds/sape/SAPE_abstracts_2004.pdf)
- Lefebvre L, Nicolakakis N, Boire D. 2002.** Tools and brains in birds. *Behaviour* **139**: 939–973.
- Lefebvre L, Reader SM, Sol D. 2004.** Brains, innovations and evolution in birds and primates. *Brain, Behavior and Evolution* **63**: 233–246.
- Lefebvre L, Whittle P, Lascaris E, Finkelstein A. 1997.** Feeding innovations and forebrain size in birds. *Animal Behaviour* **53**: 549–560.
- Madden J. 2001.** Sex, bowers and brains. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **268**: 833–838.
- Marsh OC. 1880.** Odontornithes: a monograph on the extinct toothed birds of North America. *U.S. Geological Exploration of the 40th Parallel*, Vol. 7.
- Mayr G, Smith R. 2002.** A new record of the Prophaethontidae (Aves: Pelecaniformes) from the Middle Eocene of Belgium. *Bulletin de l'institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre* **72**: 135–150.
- McKee JWA. 1985.** A pseudodontorn (Pelecaniformes: Pelagornithidae) from the middle Pliocene of Hawera, Taranaki, New Zealand. *New Zealand Journal of Zoology* **12**: 181–184.
- Medina L, Reiner A. 2000.** Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? *Trends in Neuroscience* **23**: 1–12.
- Mlíkovský J. 1980.** Zwei Vogelgehirne aus dem Miozän Böhmens. *Casopis pro mineralogii a geologii, roč* **25**: 409–413.
- Mlíkovský J. 1981a.** Ein fossile Vogelgehirn aus dem Oberpliozän Ungarns. *Fragmenta Mineralogica et Palaeontologica* **10**: 71–74.
- Mlíkovský J. 1981b.** Relationships of the Eocene bird 'Numenius' gypsorum Gervais. *Bulletin de la Muséum national d'Histoire naturelle, Paris, C, Sciences de la Terre, Paléontologie, Géologie Minéralogie* **4**: 341–343.
- Mlíkovský J. 1988.** Notes on the brains of the middle Miocene birds (Aves) of Hahnenberg (F.R.G.). *Casopis pro mineralogii a geologii, roč* **33**: 53–61.
- Mouritsen H, Feenders G, Liedvogel M, Wada K, Jarvis E. 2005.** Night-vision brain area in migratory songbirds. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 8339–8344.
- Nicolakakis N, Lefebvre L. 2000.** Forebrain size and innovation rate in European birds: feeding, nesting and confounding variables. *Behaviour* **137**: 1415–1429.
- Olson SL. 1985.** The fossil record of birds. In: Farner DS, King JR, Parkes C, eds. *Avian biology*, Vol. 8. New York: Academic Press, 79–252.
- Olson SL. 1994.** A giant *Presbyornis* (Aves: Anseriformes) and other birds from the Paleocene Aquia Formation of Maryland and Virginia. *Proceedings of the Biological Society of Washington* **107**: 429–435.
- Owen R. 1873.** Description of the skull of a dentigerous bird (*Odontopteryx toliapica*) from the London Clay of Sheppey. *Quarterly Journal of the Geological Society of London* **29**: 511–522.
- Pearson R. 1972.** *The avian brain*. London and New York: Academic Press.
- Reiner A, Perkel DJ, Bruce LL, Butler AB, Csillag A, Kuenzel W, Medina L, Paxinos G, Shimizu T, Streidter G, Wild M, Ball GF, Durand S, Gütürkün O, Lee DW, Mello CV, Powers A, White SA, Hough G, Kubikova L, Smulders TV, Wada K, Dugas-Ford J, Husband S, Yamamoto K, Yu J, Siang C, Jarvis ED. 2004.** Revised nomenclature for avian telencephalon and some related brainstem nuclei. *The Journal of Comparative Neurology* **473**: 377–414.
- Robertson DS, McKenna MC, Toon OB, Hope S, Lilli-graven JA. 2004.** Survival in the first hours of the Ceno-zoic. *Geological Society of America Bulletin* **116**: 760–768.
- Saiff EI. 1974.** The middle ear of the skull of birds: Procel-lariiformes. *Zoological Journal of the Linnean Society* **54**: 213–240.
- Saiff EI. 1976.** Anatomy of the middle ear region of the avian skull. *Sphenisciformes. Auk* **93**: 749–759.
- Saiff EI. 1978.** The middle ear of the skull of birds: the Pelecaniformes and Ciconiiformes. *Zoological Journal of the Linnean Society* **63**: 315–370.
- Sipla J, Georgi J, Forster C. 2003.** The semicircular canal dimensions of birds and crocodilians: implications for the origin of flight. *Journal of Vertebrate Paleontology* **23** (Suppl.): 97A.
- Slack KE, Jones CM, Ando T, Harrison GL, Fordyce RE, Arnason U, Penny D. 2006.** Early penguin fossils, plus mitochondrial genomes, calibrate avian evolution. *Molecular Biology and Evolution* **23**: 1144–1155.
- Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. 2005.** Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 5460–5465.
- Sol D, Timmermans S, Lefebvre L. 2002.** Behavioural

- flexibility and invasion success in birds. *Animal Behaviour* **63**: 495–502.
- Stingelin W. 1957.** *Vergleichend morphologische untersuchungen am vorderhirn der Vögel auf cytologischer und cytoarchitektonischer grundlage*. Basel: Verlag Helbing and Lichtenhahn.
- Striedter G. 2005.** *Principles of brain evolution*. Sunderland, MA: Sinauer Associates.
- Timmermans S, Lefebvre L, Boire D, Basu P. 2000.** Relative size of the hyperstriatum ventrale is the best predictor of feeding innovation rate in birds. *Brain, Behavior and Evolution* **56**: 196–203.
- Walsh SA. 2001.** The Bahía Inglesa Formation Bonebed: genesis and palaeontology of a Neogene Konzentrat Lagerstätte from north-central Chile. Unpublished PhD Thesis, University of Portsmouth.
- Webster SJ, Lefebvre L. 2001.** Problem solving and neophobia in a columbiform-passeriform assemblage in Barbados. *Animal Behaviour* **62**: 23–32.
- Wellnhofer P. 1991.** *The illustrated encyclopedia of pterosaurs*. London: Salamander Books Ltd.
- Wingstrand KG. 1951.** *The structure and development of the avian pituitary*. Lund: Håkan Ohlssons Boktryckeri.
- Winkler H, Leisler B, Bernroider G. 2004.** Ecological constraints on the evolution of avian brains. *Journal of Ornithology* **145**: 238–244.
- Witmer LM, Chatterjee S, Franzosa J, Rowe T. 2003.** Neuroanatomy of flying reptiles and implications for flight, posture and behaviour. *Nature* **425**: 950–953.
- Zhou Z. 2004.** The origin and early evolution of birds: discoveries, disputes, and perspectives from fossil evidence. *Naturwissenschaften* **91**: 455–471.
- Zusi RL, Warheit KI. 1992.** Evolution of the intramandibular joint of pseudodontorns. In: Campbell KE, ed. Papers in Avian Palaeontology Honoring Pierce Brodkob. *Science Series Natural History Museum of Los Angeles County* **36**: 351–360.