New evidence on brain-endocranial cavity relationships in ornithischian dinosaurs

DAVID C. EVANS

Discussions of brain morphology and relative brain size in nonavian dinosaurs have been complicated by uncertainty in the extent to which the brain filled the endocranial cavity. Recently reported vascular imprints (valleculae) on the endocranial surfaces of the braincase suggest that nonavian maniraptoriform theropods had brains that tightly fit the endocranium. Similar impressions of the intracranial vascular system are reported here in two ornithischian clades, Hadrosauridae and Pachycephalosauridae. These structures are more widespread in dinosaurs than previously thought, and suggest that the brain closely fit the endocranium in some regions of the forebrain through hindbrain in several distantly related dinosaur groups.

Key words: Dinosauria, Hadrosauridae, Pachycephalosauridae, endocranial cavity, brain, Cretaceous.

David C. Evans [devans@utm.utoronto.ca], University of Toronto, 3359 Mississauga Rd., Mississauga, ON, Canada, L5L 1C6.

Introduction

Traditionally nonavian dinosaurs have been regarded as "reptilian" in that their brains were thought to have filled a relatively small portion of the endocranial cavity in contrast with the conditions in mammals and birds (Jerison 1969, 1973; Hopson 1977, 1979; Rogers 1999; Larsson et al. 2000; Larsson 2001). The brains of dinosaurs are generally thought to have been separated from the endocranial walls by the intercession of cerebrospinal fluid between the meninges and/or venous sinuses within the dura. Many blood vessels occur between the brain and endocranium in vertebrates. The presence of complex vascular impressions (valleculae) on the endocranial surfaces of braincase bones is generally thought to indicate regions where the dural envelope was thin and that the endocranium closely reflects brain morphology in the regions where they occur (Hopson 1979; Hurlburt 1996; Jerison et al. 2001; Osmólska 2004). The density and location of vascular valleculae, together with information on endocast shape, can provide potential evidence as to the relative proportion of the endocranial cavity occupied by the brain in dinosaurs and other extinct vertebrates (Osmólska 2004).

The published record of endocranial vascular impressions in nonavian dinosaurs is scant (Osmólska 2004). The few previously reported examples of these structures occur in small, relatively large-brained theropods including dromaeosaurids (Currie 1995; Norell et al. 2004), ornithomimids (Russell 1972), oviraptorosaurs (Osmólska 2004) and troodontids (Currie 1985). The location and density of valleculae together with their phylogenetic distribution led Osmólska (2004) to suggest that enlargement of the brain relative to the endocranial cavity was a probable synapomorphy of maniraptoriform theropods, including birds. This paper presents evidence that complex endocranial vascular impressions also occur in hadrosaurid and pachycephalosaurid ornithischians, and that the brain may have been closely associated with the endocranium in some regions of the forebrain and post-cerebrum in these groups.

Institutional abbreviations (all in Canada).—CMN, Canadian Museum of Nature, Ottawa; ROM, Royal Ontario Museum, Toronto; TMP, Royal Tyrrell Museum, Drumheller.

Descriptions

Hadrosauridae.—Ramiform endocranial vascular valleculae have not been described previously in hadrosaurids, although a recent abstract by Jerison et al. (2001) mentioned evidence of meningeal blood vessels and its implications for brain size estimation in an endocast of the hadrosaurine *Edmontosaurus*. Several incomplete braincases and numerous isolated braincase bones attributable to lambeosaurine hadrosaurids from the Dinosaur Park Formation (Campanian, Alberta, Canada) show vascular structures particularly clearly (see Appendix 1).

Valleculae are particularly deep and dense on the cerebral fossa of the frontal (Fig. 1A). Numerous lambeosaurine frontals show similar but variable patterns of vessel imprint distribution. Relatively large ramiform grooves radiate from the medial aperture of a canal along the frontal-orbitosphenoid suture that passes from the orbital cavity to the endocranial cavity. These grooves extend anterodorsally and posterodorsally across the cerebral fossa, and give rise to a series of rami that subdivide into smaller branches. Posteriorly, some frontal valleculae traverse onto the parietal and laterosphenoid (Fig 1A). Vessel impressions occur on fron-

Acta Palaeontol. Pol. 50 (3): 617–622, 2005
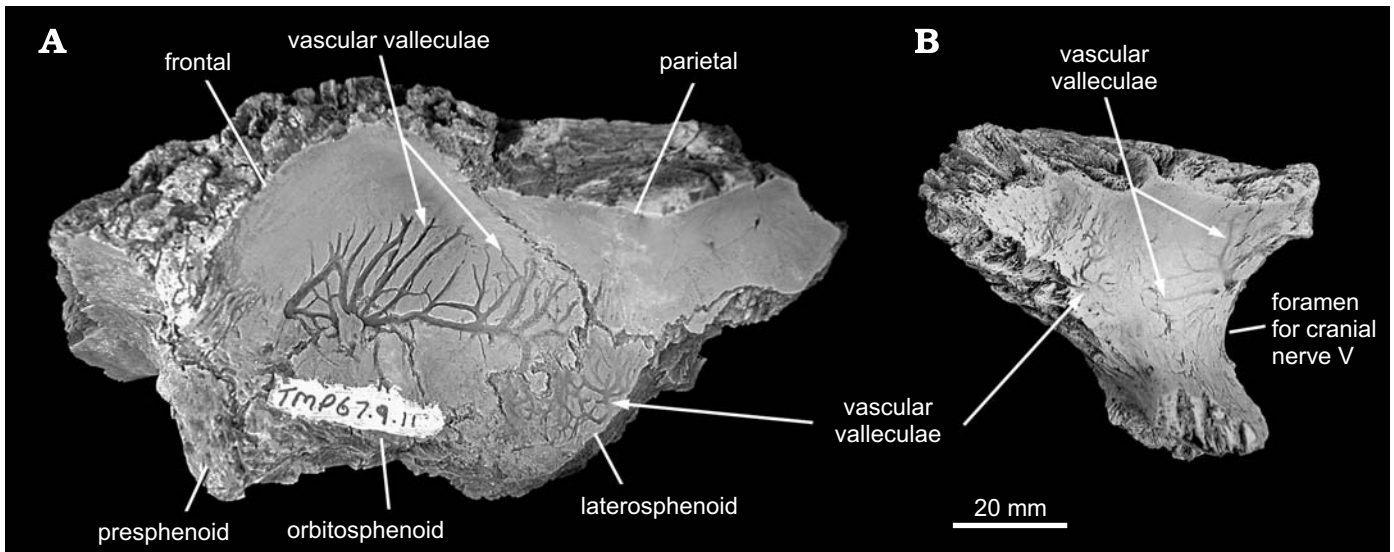
http://app.pan.pl/acta50/app50-617.pdf

Fig. 1. Endocranial vascular valleculae in Hadrosauridae, Dinosaur Park Formation, Alberta, Campanian, Cretaceous. **A**. Incomplete braincase of an indeterminate lambeosaurine (TMP 67.09.11) in medial view. **B**. Hadrosaurid laterosphenoid (TMP 1979.11.09) in medial view.

tals that span a large size range, and thus ontogenetic range, but the largest individuals are not represented in the studied sample. Parietals attributable to both hadrosaurid subfamilies (Hadrosaurinae, TMP 2000.12.179; cf. Lambeosaurinae, TMP 92.36.335) have ramiform valleculae adjacent to the frontal-parietal suture, but these structures are absent posteriorly. Dermal skull roof bones of lambeosaurines have deeper and more numerous valleculae than those of hadrosaurines.

Two endochondral braincase bones, the laterosphenoid and presphenoid, also have endocranial vascular impressions. An isolated lambeosaurine presphenoid (TMP 92.36.219) has small, transversely oriented grooves on the olfactory bulb fossa that are likely vascular in origin. Hadrosaurid laterosphenoids (e.g., TMP 1979.11.09, TMP 86.77.97, TMP 2002.12.75) of uncertain subfamily affinity have similar patterns of vallecular distribution (Fig. 1B). Valleculae are particularly dense adjacent to the orbitosphenoid and frontal. Branched grooves also extend dorsally in the region of the oculomotor foramen. More posteriorly, ramiform grooves extend anterodorsally and anteroventrally from several small foramina that surround the trigeminal foramen (Fig. 1B). Hadrosaurid prootics and exoccipitals lack vascular valleculae.

On a hadrosaurid endocast, vascular impressions extend from the forebrain through the anterior hindbrain (Fig. 2). Presphenoid valleculae correspond to the lateroventral olfactory region of the telencephalon. The extensive vessel impressions on the frontal cover almost the entire lateral surface of the cerebrum. Vessel impressions on the laterosphenoid correspond to regions of the midbrain, adjacent to the infundibulum, and the anterior medulla oblongata (hindbrain) at the base of the trigeminal nerve.

Pachycephalosauridae.—Endocranial vascular valleculae have not been reported previously in pachycephalosaurids, possibly because most cranial domes are water-worn or weathered and do not preserve sufficient detail. Ramiform

valleculae are often preserved on the endocranial surface of unmodified frontoparietals (e.g., *Stegoceras brevis* Lambe, 1918, TMP 85.36.292; *Sphaerotholus buchholtzae* Williamson and Carr, 2002, TMP 87.113.03; *Stegoceras validum* Lambe, 1902, TMP 2000.26.01). However, their presence is variable because some well-preserved specimens lack these structures (e.g., *Stegoceras brevis*, TMP 2000.12.02; *Stegoceras validum*, 99.62.01).

Valleculae, when present, can occur throughout the endocranial surface of the frontoparietal (Fig. 3). Ramiform grooves occur in the olfactory bulb fossa of the frontal in a specimen of *Stegoceras brevis* (TMP 85.36.292). The holotype cranial dome of *Sphaerotholus buchholtzae* (TMP 87.113.03) has ramiform grooves oriented posteromedially and parasagittally in the cerebral fossa of the frontal (Fig. 3). Several potential vascular imprints also occur in the parietal fossa immediately posterior to the cerebral fossa (Fig. 3).
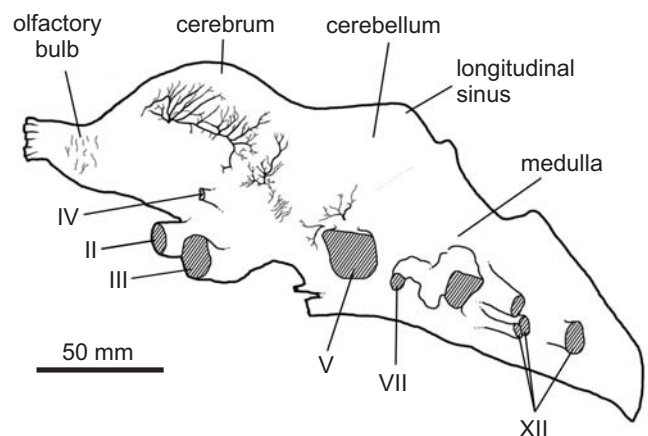

Fig. 2. Schematic diagram of a hadrosaurid endocast in lateral view showing the approximate distribution of vascular valleculae on a lambeosaurine braincase. Valleculae are dense in the lateral regions of the cerebrum, midbrain and rostral hindbrain. Roman numerals represent cranial nerves.
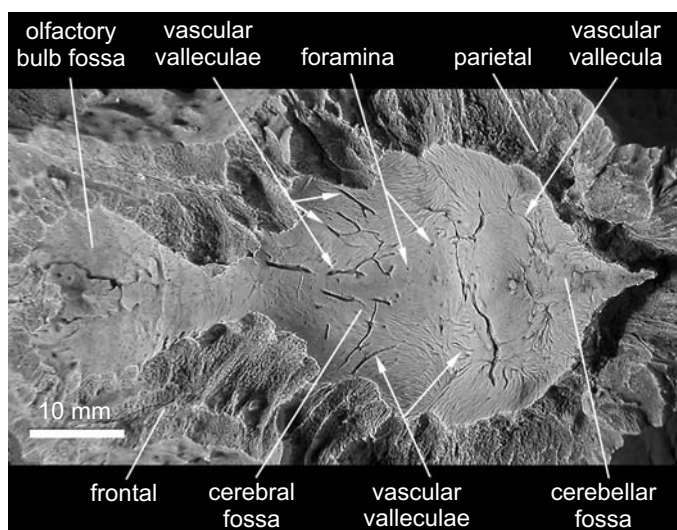
Fig. 3. Endocranial vascular valleculae in Pachycephalosauridae. *Sphaerotholus buchholtzae*, incomplete frontoparietal (TMP 87.113.03, Hell Creek Formation, Montana, Maastrichtian, Cretaceous) in ventral view. Vascular valleculae are present on the cerebral and post-cerebral fossae.

Hopson (1979) identified this as the cerebellar fossa (but see Giffin 1989). These impressions are considerably shallower and smaller than those on the frontal.

In addition to vascular impressions, the endocranial surface of the frontoparietal is often irregularly corrugated, or wrinkled (Fig. 3; TMP 85.36.292, TMP 87.113.03, TMP 99.62.01). Numerous small foramina penetrate the endocranial surface of the frontoparietal, and some foramina occur within valleculae (Fig. 3; TMP 99.62.01,TMP 2000.26.01). Superficially similar endocranial "punctures", some of which also occur within vascular grooves, have been described in oviraptorosaurs (Osmólska 2004). Whereas the "punctures" may be related to the pneumatic system in oviraptorosaurs (Osmólska 2004), the small foramina in pachycephalosaurids are likely associated with vessel development in their transiently highly vascularized cranial domes (Goodwin and Horner 2004).

Discussion

Discussions of the relative size of the brain in nonavian dinosaurs have been complicated by uncertainty in the extent to which the brain filled the endocranial cavity (Hopson 1979; Larsson 2000; Larsson et al. 2001). Dendy (1911) reported the large disparity between the size of the brain and endocranial cavity in *Sphenodon*. Jerison (1973) found a similar relationship in *Iguana*, in which the brain fills approximately 50% of the endocranial cavity. Ostrom (1961) and Starck (1979) also note a similar disparity between the brain and the endocranial cavity in extant non-dinosaurian reptiles. Most nonavian dinosaurs have been regarded as "reptilian", and their brains are typically estimated to have filled approximately 50% of the endocranial cavity (Jerison 1969, 1973; Hopson 1977, 1979; Hurlburt 1996).

Birds and crocodilians form the extant phylogenetic bracket of nonavian dinosaurs (Witmer 1995). In crocodilians, the proportion of the endocranial cavity occupied by the brain varies with body size (Hopson 1979; Rogers 1999; Hulburt and Waldorf 2002). Endocasts of juvenile crocodilians reproduce brain topography relatively accurately (Hopson 1979; Rogers 1999). The endocranial volume increases more rapidly than brain volume with increasing body size through ontogeny. Relative brain volume decreases from approximately two-thirds (66%) of the endocavity volume in small sexually mature *Alligator mississippiensis*, to approximately one third (33%) in the largest adults (Hurlburt and Waldorf 2002). The relatively large dorsal longitudinal venous sinus and its divisions account for a large part of the disparity between brain and endocranial volumes in adult crocodilians (Hopson 1979). The longitudinal sinus is largest over the cerebellum and medulla, and thinner over the forebrain. The lateral poles of the cerebral hemispheres maintain a close relationship to the endocranium throughout ontogeny (Grant Hurlburt, personal communication 2004). Not surprisingly, indications of complex vascular valleculae on the inside of the braincase are generally absent (Hopson 1979; Hurlburt 1996).

Extant birds have relatively large brains that approximately fill the endocranial cavity, as in mammals (Iwaniuk and Nelson 2002). The relationship between brain and endocranial volumes presumably remains essentially constant with increased size. Clear impressions of the intracranial vessels on the braincase are also present in avians (Zusi 1993; Sedlmayr 2002; Osmólska 2004). The meningeal branches of the profundus artery in birds, particularly ratites, leave deep vascular channels on the cerebral fossa of the braincase (Sedlmayr 2002).

Hopson (1977, 1979) suspected that the brains of some dinosaurs, including sauropods and small theropods, filled the endocranial cavity to a greater degree than in extant reptiles based on the "brain-like" shapes of their endocasts. The entire endocranial volume is typically used as an estimate of brain size in ornithomimid and troodontid theropods because of their "brain-like" endocasts (Hopson 1977; Hurlburt 1996). Branching endocranial vascular impressions are an additional line of evidence that have been used to support a close brain-endocranium relationship in these groups (Hopson 1979; Osmólska 2004).

Complex vascular impressions, such as those described here, are generally thought to indicate that the brain was pressed closely against the endocranial surface (through the enclosing meninges) in the regions where they occur (Hopson 1979; Hurlburt 1996; Jerison et al. 2001; Osmólska 2004). Valleculae that result from vessels that supplied the meninges themselves may prove to be an exception. In birds and some mammals, the arteries that supply the meninges leave deep vallecule on the endocranial surface of the braincase (e.g., Hominoidea, Falk 1993, Abrahams et al. 1998; *Canis*, Moodie 1922, Hurlburt 1982; Aves, Sedlmayr 2002). Vessels that supply the dura often occur between the dura and the endocranium, and can apparently be separated from contact with the brain by thin venous sinuses and/or thin layers of cerebro-

spinal fluid (e.g., Hominoidea, Abrahams et al. 1998; *Canis*, Hurlburt 1982). The morphology of the valleculae on the frontal in hadrosaurids and their association with a foramen linking the orbital and endocranial cavities suggests that the corresponding vessels may have supplied the meninges. The depth of the frontal valleculae in the pachycephalosaurid specimen (TMP 87.113.01) is also suggestive of epidural vessels. Precise identification of the vessels that are correlated with the impressions described here is complex, and is beyond the scope of this short report. Patterns of intracranial circulation have been described in detail in crocodilians and birds (Rathke 1866; Hochstetter 1906; Gillian 1967; West et al. 1981; Midtgard 1984; Sedlmayr 2002). Recent comparative study by Sedlmayr (2002) has laid the groundwork for the precise identification of these vessels in dinosaurs.

Until further research on intracranial blood vessels, their osteological correlates (valleculae), and their significance to brain-endocranium relationships is carried out in extant taxa, the conclusions below are somewhat tentative. Dense vascular valleculae are most distinct in taxa where the brain occupies almost the entire endocranial cavity, and they appear to be generally absent in taxa in which the brain does not. I therefore follow other authors (Hopson 1979; Hurlburt 1996; Jerison et al. 2001; Osmólska 2004) in the assumption that valleculae suggest a close brain-endocranial cavity relationship in some regions of the forebrain, midbrain and hindbrain in these ornithischian clades.

In hadrosaurids, the endocast is not particularly more "brain-like" than that of extant crocodilians (Ostrom 1961; Hurlburt 1996). The largely undefined dorsal region of the endocast posterior to the cerebrum suggests the presence of a large longitudinal venous sinus, as in crocodilians (Hopson 1979). A major lateroventral division of the longitudinal sinus, the middle cerebral vein, is clearly present on hadrosaur endocasts (e.g., ROM 1793; Hopson 1979). The lack of distinct valleculae in the dorsal post-cerebral region and on the prootic and exoccipital suggest that much of the hindbrain was not in close relationship to the endocranial wall in hadrosaurids. Therefore, the brains of hadrosaurids likely did not fill the endocranial cavity to the extent in Maniraptoriformes. However, at least in lambeosaurines, valleculae are dense and essentially continuous across the lateral regions of the brain anterior to CN VII (Fig. 2). This suggests that much of the anterior and ventral regions of the brain were closely associated with the endocranial wall in these regions.

The dense valleculate condition in hadrosaurids may affect estimates of relative brain size in the group. Relative brain size is typically measured with an encephalization quotient (EQ), although this method is problematic for fossil taxa (Larsson 2001). The EQ is an individuals actual brain size (in volume or mass) divided by the expected brain size for its particular body size, which is calculated using an allometric relationship derived from a large reference group sample (Jerison 1973; Hopson 1977; Hurlburt 1996). In extinct taxa, the brain and body sizes of an individual must be estimated. Previous EQ calculations for hadrosaurids estimate the volume of the brain under the assumption that the brain occupied 50% of the endocranial volume (Jerison 1973; Hopson 1977; Hurlburt 1996). If the extensive valleculae in hadrosaurids imply that the brain occupied a relatively larger proportion of the endocranial cavity than in other ornithischians, estimates of brain size should be adjusted. Re-calculation of the EQ for *Edmontosaurus* based on a brain size estimate of 60% endocast volume, a slight increase relative to the standard 50% used for other ornithischians that apparently lack these structures, increases its estimated EQ from 2.37 to 2.84 (using the nonavian reptile dataset of Hurlburt 1996). This value is marginally higher than EQs of *Iguanodon*, *Tyrannosaurus rex* and extant nonavian reptiles (Hurlburt 1996).

EQ has not been calculated for any pachycephalosaurid because taxa for which whole endocasts are available lack sufficiently complete skeletons for reliable body size estimates (Giffin 1989). Pachycephalosaurid endocasts are relatively "brain-like" in appearance, and show a defined cerebellum and optic lobes in some specimens (Giffin 1989). Vascular imprints and the relatively "brain-like" endocasts of pachycephalosaurids suggest that the brain may have filled a relatively larger proportion of the endocranial cavity than in most other ornithischian dinosaurs. However, the corrugated surface texture of the endocranial surface may relate to the presence of dense connective tissue between the brain and endocranium, as in some extant reptiles (Starck 1979). The factors stated above should be considered in future calculations of relative brain size in the group.
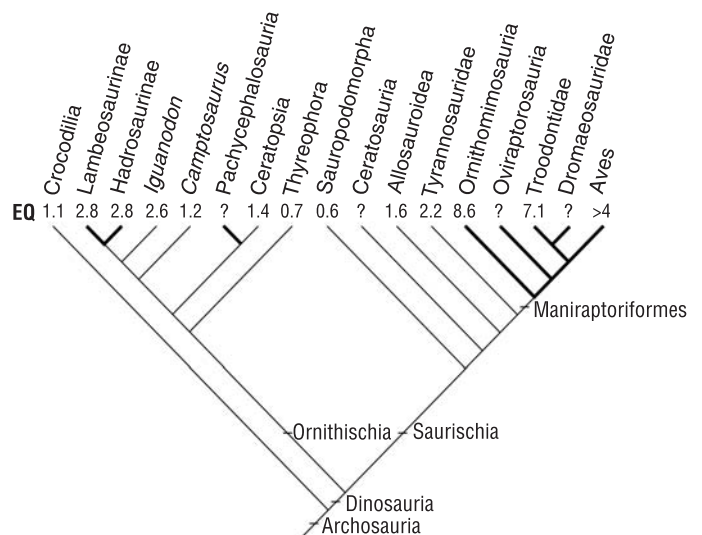

Fig. 4. Phylogenetic distribution of vascular valleculae in the forebrain region (bold lines) and Encephalization Quotients in Dinosauria. Valleculae occur in the clades with the relatively largest brains (i.e., the highest EQs). EQs are from Hurlburt (1996) and were calculated using the equation $EQ = Mbr/(0.0155 * Mbd^{0.553})$. EQ for Hadrosaurinae (*Edmontosaurus*) was recalculated using an estimate that the brain occupied 60% of the endocranial cavity. Lambeosaurine EQ is approximate and assumed to be similar to hadrosaurines. *Allosaurus* and *Tyrannosaurus* EQs were recalculated using endocast volume data from Larsson et al. (2000). When information was available for more than one taxon in a clade, an average EQ is figured. Cladogram topology after Sereno (1999), Pisani et al. (2002); theropod topology from Holtz and Osmólska (2004).

In Archosauria, the phylogenetic distribution of morphologically similar vascular impressions is uncertain at present. The known phylogenetic distribution of valleculae in dinosaurs suggests that their presence, at least in derived ornithopods and theropods, may be associated with overall enlargement of the brain relative to body size (Fig. 4). Crocodilians, along with *Sphenodon* and lepidosaurs, exhibit the presumed plesiomorphic condition for dinosaurs. The brain occupies a relatively small portion of the endocranial cavity compared to birds and mammals, and dense vascular valleculae are generally absent (Jerison 1973; Hopson 1977, 1979; Hurlburt 1996). EQs of extant crocodilians cluster around 1.0, indicating the group has an average brain size for extant non-avian reptiles (Hurlburt 1996).

Maniraptoriform theropods and hadrosauriform ornithopods have high EQs compared to crocodilians and their dinosaur outgroups, and trends toward forebrain enlargement have been noted in theropods and ornithopods (Fig. 4; Hopson 1977, 1979; Larsson et al. 2000). In theropods, endocranial vascular valleculae are known to occur in Maniraptoriformes (Osmólska 2004), and there is some evidence to suggest that they are not developed to the same degree in more basal theropods (Rogers 1998, 1999). There is an increase in the relative size of the brain, and the cerebrum in particular, in Hadrosauriformes compared to their outgroups (Hopson 1977, 1979). Presence or absence of vascular impressions in hadrosaurid outgroups is uncertain, but morphologically similar structures have not been described in the forebrain or midbrain regions of hypsilophodontid and dryosaurid ornithopods despite detailed work on their braincases and endocasts (Galton 1989; Rich and Rich 1989).

As noted above, pachycephalosaurid EQs are difficult to quantify and direct comparisons to other groups within a phylogenetic framework have not yet been made. It is notable that ceratopsians, the sister group of pachycephalosaurs, have generally small brains and correspondingly low to average EQs (Hopson 1977; Hurlburt 1996). The large-bodied ceratopsids have considerably lower EQs (EQ = 0.7 for *Triceratops*) than the smaller basal ceratopsian *Protoceratops* (EQ = 2.1) (Hurlburt 1996). Endocasts of *Protoceratops* and *Triceratops* do not show clear distinctions between the regions of the brain, and the brain likely did not closely fit the endocranial cavity in any region (Hopson 1979). Examination of 13 well-preserved ceratopsid braincases in the TMP collections suggests that vascular valleculae, if present, are not comparable in density or depth to those of the pachycephalosaurid specimens. Of the specimens examined, only one ceratopsid braincase (TMP 94.12.929) preserved three shallow, unbranched grooves on the lateral wall of the forebrain region that may represent vascular structures. In this context, brain enlargement in pachycephalosaurids relative to outgroups is a possibility that remains untested. An alternative, perhaps preferable, hypothesis is that the potential close relationship of the brain to the dorsal endocranial surface in pachycephalosaurids is related to the development of their thickened cranial domes.

Conclusions

In addition to derived theropods, ramiform endocranial vascular valleculae occur in at least two distantly related ornithischian clades: in the lateral regions of the forebrain, midbrain, and anterior hindbrain in Hadrosauridae, and in the dorsal telencephalon and anterodorsal region of the post-cerebrum in Pachycephalosauridae. Paucity of published examples of morphologically similar structures in other taxa should not necessarily imply that they are absent. Hadrosaurid braincases and endocasts have undergone detailed study (Ostrom 1961; Hopson 1979), but their presence has only recently been noted (Jerison et al. 2001). Pachycephalosaurids have also been similarly well studied (Hopson 1979; Giffin 1989). The fact that these structures are rarely described in dinosaurs may be related to a dearth of well preserved, appropriately disarticulated or partial braincase material (e.g., sauropods), or they may have been overlooked.

The presence and location of vascular valleculae on the braincase are important in the interpretation of endocasts. They provide information on the location and pathways of prominent intracranial vesssels, as well as potential evidence of a close brain-endocranium relationship in the areas they occur. Future research in this area has potential to lead to new insights into the evolution of the brain and intracranial vasculature in dinosaurs. The phylogenetic context of available data suggests that the valleculate conditions in hadrosaurids, pachycephalosaurids, and maniraptoriformes evolved independently, and that endocranial valleculae may be associated with relative brain enlargement in derived theropods and hadrosaurids.

Acknowledgements

References

Abrahams, P.H., Hutchings, R.T., and Marks, S.C. Jr. 1998. *McMinn's Color Atlas of Human Anatomy*. Fourth edition. 352 pp. Mosby, London.

Baumel, J.J. 1993. Systema Cardiovasculare. *In:* J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans, and J.C. Vanden Berge (eds.), Handbook of Avian Anatomy: Nomina Anatomica Avium. 2nd edition. *Publications of Nuttall Ornithological Club* 23: 407–475. Cambridge, Mass.

Currie, P.J. 1985. Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its bearing on the origin of birds. *Canadian Journal of Earth Sciences* 22: 1643–1658.

Currie, P.J. 1995. New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). *Journal of Vertebrate Paleontology* 15: 576–591.

Dendy, A. 1911. On the structure, development and morphological interpretation of pineal organs and adjacent parts of the brain in the Tuatara (*Sphenodon punctatus*). *Philosophical Transactions of the Royal Society, Series B* 201: 227–331.

Falk, D. 1993. Meningeal arterial patterns in great apes: implications for hominid vascular evolution. *American Journal of Physical Anthropology* 92: 81–97.

Giffin, E.B. 1989. Pachycephalosaur paleoneurology (Archosauria: Ornithischia). *Journal of Vertebrate Paleontology* 9: 67–77.

Galton, P.M. 1989. Crania and endocranial casts from ornithopod dinosaurs of the families Dryosauridae and Hypsilophodontidae (Reptilia: Ornitischia). *Geologica et Palaeontologica* 23: 217–239.

Gillian, A. 1967. A comparartive study of the extrinsic and intrinsic arterial blood supply to the brains of submammalian vertebrates. *Journal of Comparative Neurology* 130: 175–196.

Goodwin, M.B. and Horner, J.R. 2004. Cranial histology of pachycephalosaurs (Ornithischia: Marginocephalia) reveals transitory structures inconsistent with head-butting behavior. *Paleobiology* 30: 253–257.

Hochstetter, F. 1906. Beitrage zur Anatomie und Entwicklungsgeschichte des Blutgefasssystemes der Krokodile. *In*: A. Voeltzko (ed.), Reise in Afrika 4: 1–139. Stuttgart.

Holtz, T.R. Jr. and Osmólska, H. 2004. Saurischia. *In*: D. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 2nd edition, 21–24. University of California Press, Berkeley.

Hopson, J. A. 1977. Relative brain size and behavior in archosaurian reptiles. *Annual Review of Ecology and Systematics* 8: 429–448.

Hopson, J.A. 1979. Paleoneurology. *In*: C. Gans, R.G. Northcutt, and P. Ulinski (eds.), *Biology of the Reptilia (Neurology A), Vol. 9*, 39–146. Academic Press, New York.

Hurlburt, G.R. 1982. *Comparison of Endocranial Casts and Brains of the Domestic Dog Canis familiaris, Linnaeus 1758*. Unpublished M.Sc. thesis, 199 pp. Department of Zoology, University of Toronto.

Hurlburt, G. 1996. *Relative Brain Size in Recent and Fossil Amniotes: Determination and Interpretation*. 250 pp. Unpublished Ph.D. thesis, University of Toronto, Department of Zoology.

Hurlburt, G.R. and Waldorf, L. 2002. Endocast volume and brain mass in a size series of alligators. *Journal of Vertebrate Paleontology* 23 (Supplement to 3): 69A.

Iwaniuk, A.N. and Nelson, J.E. 2002. Can endocranial volume be used as an estimate of brain size in birds? *Canadian Journal of Zoology* 80: 16–23.

Jerison, H.J. 1969. Brain evolution and dinosaur brains. *American Naturalist* 103: 575–588.

Jerison, H.J. 1973. *Evolution of the Brain and Intelligence*. 482 pp. Academic Press, New York.

Jerison, H.J., Horner, J.R., and Horner, C. 2001. Dinosaur forebrains. *Journal of Vertebrate Paleontology* 21 (Supplement to No. 3): 65A.

Lambe, L.M. 1902. New genera and species from the Belly River series (Mid-Cretaceous). *Contributions to Canadian Paleontology, Geological Survey of Canada* 3: 25–81.

Lambe, L. M. 1918. The Cretaceous genus *Stegoceras*, typifying a new family referred provisionally to the Stegosauria. *Transactions of the Royal Society of Canada* 12 (4): 23–36.

Larsson, H.C.E. 2001. Endocranial anatomy of *Carcharodontosaurus saharicus* (Theropoda: Allosauroidea) and its implications for theropod brain evoluution. *In*: D. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life: New Research Inspired by the Paleontology of Philip J. Currie*, 19–33. Indiana University Press, Bloomington.

Larsson, H.C.E., Sereno, P.C., and Wilson, J.A. 2000. Forebrain enlargement among nonavian dinosaurs. *Journal of Vertebrate Paleontology* 20: 615–618.

Midtgard, U. 1984. The blood vascular system of the Herring Gull (*Larus argentatus*). *Journal of Morphology* 179:135–152.

Moodie, R.L. 1922. On the endocranial anatomy of some Oligocene and Pleistocene mammals. *Journal of Comparative Neurology* 34: 343–379.

Norell, M.A., Makovicky, P.J., and Clark, J.M. 2004. The braincase of *Velociraptor*. *In*: P.J. Currie, E. Koppelhus, M.A. Shugar, and J.L. Wright (eds.), *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds*, 133–143. Indiana University Press, Bloomington.

Osmólska, H. 2004. Evidence on relation of brain to endocranial cavity in oviraptorid dinosaurs. *Acta Palaeontologica Polonica* 49: 321–324.

Ostrom, J.H. 1961. The cranial anatomy of the hadrosaurian dinosaurs of North America. *Bulletin of the American Museum of Natural History* 122 (2): 33–186.

Pisani, D., Yates, A.M., Langer, M.C., and Benton, M.J. 2002. A genus-level supertree of the Dinosauria. *Proceedings of the Royal Society of London, Series B* 269: 915–921.

Rathke, H. 1866. *Untersuchungen über Entwinkelung und den Korperbau der Krokodile*. 275 pp. F. Vieweg und Sohn, Braunschweig.

Rich, T.H.V., and Rich, P.V. 1989. Polar dinosaurs and biotas of the Early Cretaceous of southeastern Australia. *National Geographic Research* 5 (1): 15–53.

Rogers, S.W. 1998. Exploring dinosaur neuropaleobiology: Computed tomography scanning and analysis of an *Allosaurus fragilis* endocast. *Neuron* 21: 673–679.

Rogers, S.W. 1999. *Allosaurus*, crocodiles, and birds: evolutionary clues from spiral computed tomography of an endocast. *The Anatomical Record* 257: 162–173.

Russell, D.A. 1972. Ostrich dinosaurs from the Late Cretaceous of western Canada. *Canadian Journal of Earth Sciences* 9: 375–402.

Sedlmayr, J.C. 2002. *Anatomy, Evolution, and Functional Significance of Cephalic Vasculature in Archosauria*. 398 pp. Unpublished Ph.D. thesis, Ohio University, Athens.

Sereno, P.C. 1999. The evolution of dinosaurs. *Science* 284: 2137–2147.

Starck, D. 1979. Cranio-cerebral relations in recent reptiles. *In*: C. Gans, R.G. Northcutt, and P. Ulinski (eds.), *Biology of the Reptilia (Neurology A), Vol. 9*, 1–38. Academic Press, New York.

West, N.H., Languile, B.L., and Jones, D.R. 1981. Cardiovascular system. *In*: A.S. King and J. McLelland (eds.), *Form and Function in Birds, Vol. 2A*, 385–438. Academic Press, London.

Williamson, T.E. and Carr, T.D. 2002. A new genus of derived pachycephalosaurian from western North America. *Journal of Vertebrate Paleontology* 22: 779–801.

Witmer, L.M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. *In*: J.J. Thomason (ed.), *Functional Morphology in Vertebrate Paleontology*, 19–33. Cambridge University Press, New York.

Zusi, R.L. 1993. Patterns of diversity in the avian skull. *In*: J. Hanken and B.K. Hall (eds.), *The Skull: Patterns of Structural and Systematic Diversity*, 391–437. University of Chicago Press, Chicago.

Appendix 1

Hadrosaurid specimens studied that preserve endocranial vascular valleculae.

Frontal: CMN 8502, ROM 694, TMP 67.09.11, TMP 79.06.01, TMP 79.08.127, TMP 79.08.772, TMP 80.16.310, TMP 80.16.541, TMP 80.16.1616, TMP 80.18.280, TMP 81.16.224 (?), TMP 81.23.115, TMP 1984.163.43, TMP 86.36.73, TMP 86.77.65(?), TMP 88.36.37, TMP 1991.36.27, TMP 91.36.67, TMP 93.36.276, TMP 94.12.339, TMP 94.12.953, TMP 94.12.507, TMP 94.89.03, TMP 96.12.80, TMP 96.12.227(?).

Parietal: TMP 92.36.335, TMP 2000.12.79.

Laterosphenoid: TMP 86.779,97, TMP 2002.12.75, TMP 79.11.09, TMP 80.16.1211.