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Remarkable preservation of brain tissues in an Early Cretaceous iguanodontian dinosaur

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Abstract: It has become accepted in recent years that the fossil record can preserve labile tissues. We report here the highly detailed mineralization of soft tissues associated with a naturally occurring brain endocast of an iguanodontian dinosaur found in *c.* 133 Ma fluvial sediments of the Wealden at Bexhill, Sussex, UK. Moulding of the braincase wall and the mineral replacement of the adjacent brain tissues by phosphates and carbonates allowed the direct examination of petrified brain tissues. Scanning electron microscopy (SEM) imaging and computed tomography (CT) scanning revealed preservation of the tough membranes (meninges) that enveloped and supported the brain proper. Collagen strands of the meningeal layers were preserved in collophane. The blood vessels, also preserved in collophane, were either lined by, or infilled with, microcrystalline siderite. The meninges were preserved in the hindbrain region and exhibit structural similarities with those of living archosaurs. Greater definition of the forebrain (cerebrum) than the hindbrain (cerebellar and medullary regions) is consistent with the anatomical and implied behavioural complexity previously described in iguanodontian-grade ornithopods. However, we caution that the observed proximity of probable cortical layers to the braincase walls probably resulted from the settling of brain tissues against the roof of the braincase after inversion of the skull during decay and burial.

Supplementary material: Information regarding associated fossil material, and additional images, can be found at https://doi.org/10.6084/m9.figshare.c.3519984

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The fossil record of animal soft tissues is remarkably extensive, spanning the entire Phanerozoic (Allison & Briggs 1993) and potentially the latest Neoproterozoic (cf. Budd & Jensen 2015). Discussion of whole organism biology, including the consideration of soft tissues, is now commonplace, particularly in the study of marine invertebrates. The soft tissues of vertebrates (perhaps with the exception of those from the Mesozoic) and terrestrial organisms in particular are, by comparison, rarely preserved. Brain tissues are among the least commonly preserved soft tissues in the fossil record because fossilized brains themselves are extremely rare and, more importantly, because most brain tissues are highly labile. The vast majority of our knowledge of the brains of ancient organisms comes not from preserved brain tissue (although see Pradel *et al.* 2009), but from indirect sources. These include comparative anatomical studies of closely related extant taxa, the study of fossilized endocasts (the natural internal casts of braincases; e.g. Edinger 1929, 1941; Kurochkin *et al.* 2007) and three-dimensional digital reconstructions of the space within fossilized braincases. The exceptional preservation of neural tissues is known from a range of Cambrian marine arthropods from the Chengjiang and Burgess Shale Lagerstätte (e.g. Ma *et al.* 2012, 2015; Tanaka *et al.* 2013; Ortega-Hernández 2015), providing a critical window into understanding the evolution of the nervous system during the Cambrian explosion. By contrast, although neural tissue can (rarely) be preserved in fossil vertebrates (Trinajstic *et al.* 2007), the direct replication of the soft tissue of the vertebrate brain has not previously been reported. Little information has been available (either directly or indirectly) regarding structures such as the meningeal and cortical tissues or associated brain vasculature. Fossilized brain soft tissue has never been reported for any terrestrial organism.

Perhaps unexpectedly, our knowledge of dinosaurian braincases and the structure of their endocranial cavities has a surprisingly long history. A well-preserved braincase (NHMUK R2501) was found almost 150 years ago in Wealden exposures on the Isle of Wight and was described as probably belonging to *Iguanodon* (Hulke 1871). Almost 30 years later, Andrews (1897) longitudinally sectioned the same specimen, this time unequivocally identifying it as *Iguanodon*, and prepared it so that the endocranial cavity could be cast and its principal features described (Norman & Weishampel 1990, fig. 25.8; Norman 2004, fig. 19.7). Work on this specimen was augmented by the preparation, by DBN in 1976, of a second natural iguanodontian (*Iguanodon*-like) endocast from the Weald (NHMUK R8306). The latter included better preserved details of the morphology of the intracranial vascular, neural and vestibular systems (Norman 1977, 2004; see also Norman & Weishampel 1990). The relatively smooth topography of the cranial endocast described by Hulke (1871) and Andrews (1897) suggested that dinosaurian brains, and in particular their lobes and surface convolutions, were not closely pressed against the cranial wall so as to leave detailed impressions of their shape (as is known to be the case in pterosaurs, birds and mammals; Jerison 1970, 1971, 1973). Work by Dendy (1910) on extant reptiles, and others such as Ostrom (1961) and Hopson (1979), tended to reinforce the general opinion that reptile-grade vertebrates had brains that were not packed tightly within the braincase. Romer (1956) had previously observed that the embryonic expansion of the reptile brain is rapid and far advanced before skull development begins, so, at best, the interior walls of reptile braincases reflect the shape of the brain at an early (and comparatively poorly differentiated) state of its development, rather than at a later, more differentiated state. More recently, imaging techniques such as tomography have been used to create accurate three-dimensional representations of endocranial cavities in a variety of dinosaurs (Rogers 1999; Brochu 2000; Witmer *et al.* 2008; Witmer & Ridgely 2009; Lautenschlager *et al.* 2012), as well as other fossil taxa extending back into the Palaeozoic (e.g. Pradel *et al.* 2009; Giles & Friedman 2014; Marek *et al.* 2015).

Here we report for the first time that brain tissue preservation at a microscopic scale can take place within a braincase. The fossil cranial endocast described here was salvaged by one of us (JEHH) from intertidal exposures of the Tunbridge Wells Sandstone, Hastings Group (Upper Valanginian), east of Cooden, near Bexhill in Sussex (Fig. 1). Scanning electron microscopy (SEM) revealed detailed structures, interpreted as meningeal fabrics, blood vessels (including capillaries) and potentially superficial cortical tissues, which have been replaced by calcium phosphate (collophane) or moulded by microcrystalline iron carbonate (siderite). The organism from which this endocast originates has been referred to informally as '*Iguanodon*'. The taxon *Iguanodon* has, for historical reasons, a rather tortuous history that is unfortunate given its importance as one of the founding members of Richard Owen's Dinosauria (Owen 1842). As Norman (2010, 2011, 2015) has demonstrated, a number of taxa of iguanodontian ornithopod dinosaurs have been collected from the English Wealden succession and referred to by the generic name *Iguanodon*. The type genus was first established on a range of disassociated material collected near Cuckfield in West Sussex, primarily by Mantell (1825, 1827). Following revision and re-description of *Iguanodon*-like material from the Weald of East and West Sussex by Norman (2010, 2011, 2015),

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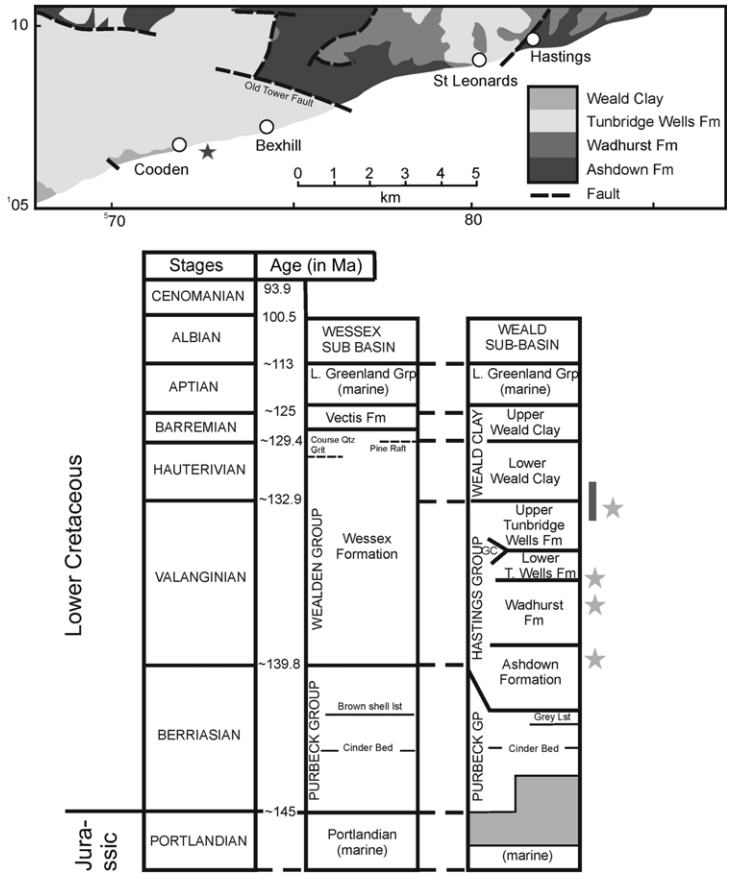


Fig. 1. Map and stratigraphic columns showing the geological context for the iguanodontian brain endocast, adapted from Brasier *et al.* (2009, fig. 1). Geological sketch map of the Bexhill area (Sussex, UK) follows that of Lake & Shephard-Thorn (1987), whereas the column and dates are updated and adapted after Allen & Wimbledon (1991) and Batten (2011). The endocast was discovered at a locality (black star) lying within the Upper Tunbridge Wells Formation. However, it was found *ex situ* and therefore may have a provenance from either the Tunbridge Wells Formation or the Lower Weald Clay (grey bar in stratigraphic columns). Grey stars indicate levels at which amber has been found (cf. Brasier *et al.* 2009, fig. 1).

two *Iguanodon*-like taxa are now recognized from the Lower Wealden outcrops of Valanginian age: *Barilium dawsoni* (Norman 2011) and *Hypselospinus fittoni* (Norman 2015). The dimensions of the new specimen indicate that it came from an individual with a body length of 4–5 m and could therefore originate from either *Barilium* (up to 8 m long) or *Hypselospinus* (up to 6 m long).

Methods

The endocast specimen was analysed using conventional photographic methods, SEM and X-ray microtomography (μCT). The uncoated surface of the entire specimen was examined using a Philips XL30S environmental scanning electron microscope in the Centre for Microscopy Characterisation and Analysis at The University of Western Australia. The analysis conditions were an accelerating voltage of 15–20 kV, a working distance of *c.* 20 mm and a chamber pressure of 0.3–0.4 Torr. Qualitative elemental and mineral analyses were undertaken on small loose fragments of the endocast. These were carbon-coated and examined using a Zeiss Supra 1555 field-emission scanning electron microscope equipped with an Oxford Instruments X-Maz 80 silicon drift energy-dispersive x-ray spectrometry (EDS) detector and Aztec analysis software at the Centre for Microscopy Characterisation and Analysis. The entire specimen was scanned using μCT at the Natural History Museum, London

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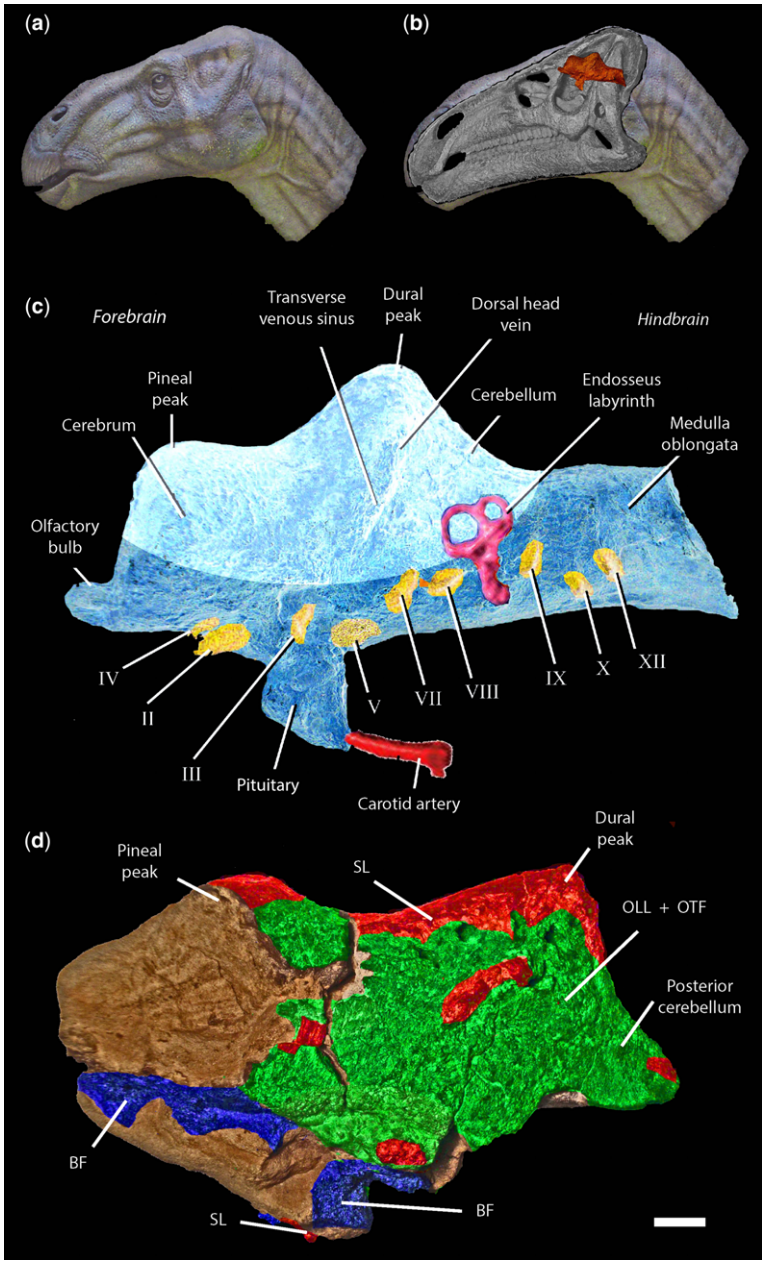


Fig. 2. Biological context for the iguanodontian endocast from Bexhill. (**a**) Life-like restoration of the head and anterior neck based on the anatomy of the iguanodontian ornithopod *Iguanodon bernissartensis* (Norman 1980; OUMNH T.127). (**b**) Semi-transparent restoration of *I. bernissartensis* head showing the position and general morphology of the endocranial cavity (orange). (**c**) Interpreted image of the plaster cast of the endocranial cavity of *Mantellisaurus* cf. *atherfieldensis* (see also Supplementary material fig. 1a). The region in pale blue indicates the approximate extent of the natural endocranial cast described herein. The principal anatomical features and positions of brain-related tissues are indicated. Roman numerals indicate the positions of the principal cranial nerve canals, which have been superimposed with reference to earlier work by Norman (2004). (**d**) Natural cranial endocast with a false-colour overlay showing bone fragments (BF) in blue, a superficial layer (SL) of crystalline siderite (red) and an outer laminar layer (OLL) and outer tubular features (OTF) preserved in calcium phosphate (collophane; green). Natural colour = silty sediment.

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(NHMUK) with a Nikon XTH-225 instrument. X-rays were generated using a tungsten target with an accelerating voltage of 225 kV, a current of 190 μA and no added filtration. To maximize resolution, two scans were undertaken to cover the length of the specimen. For each scan, 3142 projections of 0.5 s exposure were collected and then reconstructed to create volumes with 38.9 μm voxels. These were converted to two image stacks that were cropped and then aligned in SPIERSalign (Sutton *et al.* 2012), surfaced in SPIERSedit, rendered in Blender (cf. Garwood & Dunlop 2014) and volume rendered in Drishti (Limaye 2012).

The specimen is currently in the private possession of Jamie Hiscocks, but negotiations are underway to have it housed in a public museum. The loose fragments analysed using SEM-EDS (OUMNH K59010/p1–p2) are housed alongside associated post-cranial material from the same site at the Oxford University Museum of Natural History (OUMNH K.59010/1–8). Copies of the μCT scan datasets are also available as OUMNH K59010/p3–p4. All SEM and μCT images have additionally been archived on the open access server Zenodo (doi: 10.5281/zenodo. 50499).

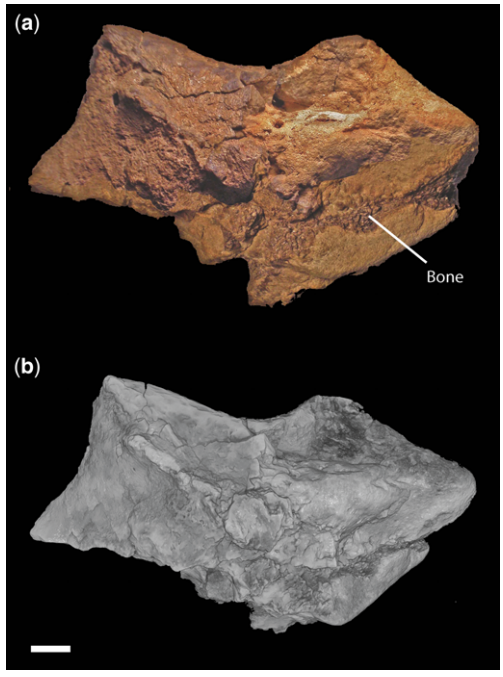


Fig. 3. Images of (**a**) the Bexhill iguanodontian natural endocast specimen and (**b**) a computed tomography volume render reconstruction of the same specimen viewed from the same orientation, made using Drishti. Scale bar = 10 mm. In the Drishti image, highly mineralized sections appear as more solid regions.

Geological context

The cranial endocast (Figs 2d & 3) was exposed by tidal erosion and found among fluvial sedimentary units of the *c.* 133 Ma Early Cretaceous Upper Tunbridge Wells Formation (Fig. 1; see also Lake & Shephard-Thorn 1987; Allen & Wimbledon 1991; Radley 2006*a*, *b*; Batten 2011). The petrified endocast had been eroded from its matrix during the winter of 2004 and was collected, *ex situ*, from a tidal pool (Ordnance Survey coordinates TQ 72498 06692). It is possible that the specimen had been transported by longshore drift and was derived from the nearby Weald Clay, which outcrops *c.* 1 km to the west. The cranial endocast was found near other ornithopod remains that included limb fragments, a tarsal bone and broken vertebrae (OUMNH K.59010/4–8). Fossilized footprints and trackways of *Iguanodon*-like ornithopods were found at a similar stratigraphic level (cf. Beckles 1854), as well as amber with probable microbial inclusions. This level lies above beds in the Ashdown Formation containing amber with the oldest known spider silk (Brasier *et al.* 2009).

All the fossil bones recovered from this location appear to originate from a fine-grained, cross-bedded siltstone that forms part of the infill of a fluvial channel. The surrounding sedimentary units consist of rippled sandstones with charcoalified wood, thin tabular ironstones with charcoal, bioturbated mudstones containing freshwater molluscs, fossil soil fabrics, lignites and amber nodules with fossil inclusions. These are consistent with a seasonal wetland depositional environment subject to occasional forest fires (cf. Brasier *et al.* 2009).

Large-scale endocast morphology and preservation

Superficial morphology

The natural cranial endocast (Figs 2d & 3) is close in both shape and size to the endocranial cavity seen within a specimen of '*Iguanodon*' on display in the OUM (OUMNH K.59015a/p-c/p; Fig. 4; see also Norman & Weishampel 1990, fig. 25.8). The latter, to judge from its size, is most likely from a fully grown individual of *Mantellisaurus atherfieldensis* (Norman 1986) and was collected from the Isle of Wight in the 1860s. As the Wealden iguanodontian taxa are closely comparable anatomically, it is not unreasonable to use one as a template for the other. Comparisons between the new specimen and other Wealden natural endocasts

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(such as NHMUK R2501 and R8306; Norman & Weishampel 1990, figs 25.11 and 25.12; Norman 2004) allow the identification of major regions occupied by the brain within the endocranial cavity, along with the cranial nerves and parts of the venous sinus drainage system (Fig. 2c).

The Bexhill endocast lacks the olfactory bulb region at the extreme anterior end of the cranial cavity, as well as most of the floor and adjacent lateral walls and the area that would have been occupied by the medulla oblongata posteriorly (Fig. 2c, the pale blue shading indicates what is actually preserved in this natural cast). The ventral surface of the endocast, which would, in life, have been supported by the floor of the braincase, is weathered and much eroded. The dorsal and lateral portions of the forebrain and hindbrain (the areas occupied by the cerebral and cerebellar expansions) exhibit the best preservation (Figs 2d & 3; Supplementary material figs 3, 4). The mid-brain region, which would have been occupied by the optic lobes in life, is completely obscured in endocasts because these lobes were overlain by the cerebral and cerebellar expansions, as well as large vascular sinuses.

Preservation

Our SEM and CT studies of the entire Bexhill endocast reveal four structurally distinct regions (Fig. 2d):

(1) Bone fragments (not in place) are located mainly in the ventral part of the endocast (Fig. 2d, blue). They consist of a coarse, dark, porous phosphate matrix with abundant Haversian canals or trabeculae (the diameter of the voids was intermediate between the two; Figs 3a & 5d, e) lined or entirely filled with iron carbonate microcrystals. The CT reconstruction revealed that the bone continues across the width of the specimen and has been eroded (Fig. 5a–d, in cream). We thus consider it likely that the bone represents either a collapsed remnant of the original braincase floor, or a fragment of bone deposited within the braincase along with the surrounding sediment.

(2) A superficial layer (SL) consisting of a very fine-grained, brown, <1 mm veneer of iron carbonate (siderite) is draped over the 'high points' along the dorsal mid-line and diagonally across the lateral margins of the endocast (Fig. 2d, red zone). This zone contains layers and patches of small reddish brown acicular iron carbonate crystals arranged parallel to the surface; these are also found coating pores and lining cavities within the outer laminar layer (OLL) (Supplementary material fig. 6a, b).

(3) The OLL flanks the mid-line SL as well as the prominent parts of the ridges on the lateral sides of the endocast, and is a more rugose textured, predominantly phosphatic area that is stained pale brown (Fig. 2d, green zone). This zone, which is 1–3 mm thick, consists of collophane in the form of layers and folds (Fig. 2d). There are large voids and irregular cavities that add to the overall three-dimensional complexity of this layer (Figs 5a–c & 6–8). Deeper within these layers the phosphate assumes an extremely fine granular texture penetrated by a network of very fine (15–30 μm) branching tubular structures, which are sometimes lined or infilled by microscopic siderite crystals (Supplementary material fig. 5b).

(4) There is an underlying zone composed of fine-grained, carbonate-cemented, quartz siltstone sedimentary infill. This zone occupies (somewhat paradoxically) the ventral portion of the endocast and also fills some of the anterior and dorsal portions of the cerebral region (Fig. 2d, natural colour). This sediment-filled zone shows weak layering and draped bedding in CT slice sections (Fig. 5h–k) and ranges from firmly cemented sediment dorsally to more friable material ventrally. The sedimentary infill also contains numerous fragments of carbonized wood (e.g. Fig. 5f), at least one plant leaf (Fig. 5g) and fragments of cortical bone (Fig. 5d).

Mineralization

Qualitative SEM-EDS shows that the phosphate-rich layers (the OLL) are dominantly calcium-rich, typical of the composition of collophane, although they also contain significant iron in places (Supplementary material fig. 6). The carbonates are mostly iron-rich (siderite), although minor calcium is sometimes present. Iron-rich carbonates are generally indicative of freshwater environments, consistent with the freshwater environment of mineralization described later in this paper. Minor iron-rich silicates are distributed throughout much of the endocast. In the following discussion, we use the terms 'collophane' and 'siderite' for the predominant mineral phases involved in the preservation of brain membranes and putative cortical tissues, but acknowledge that the mineralogy sometimes deviates from these idealized end-members.

Detailed morphology

The cortical portions of the brain in living vertebrates have a structure of such complexity, on such a small scale, that the finer details can best

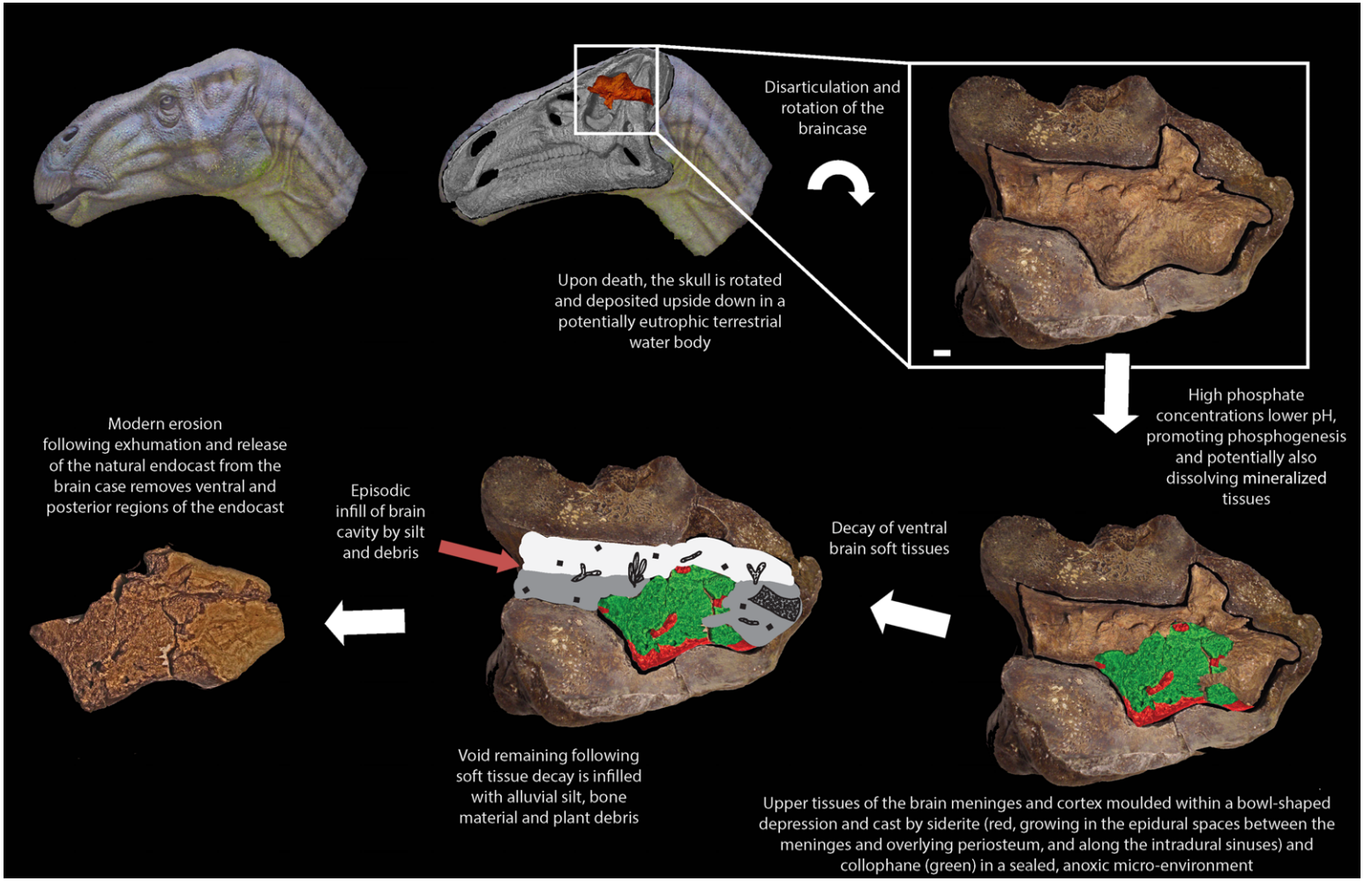


Fig. 4. A time sequence outlining the inferred taphonomic history of the iguanodontian natural endocast from Bexhill. Scale bar = 10 mm.

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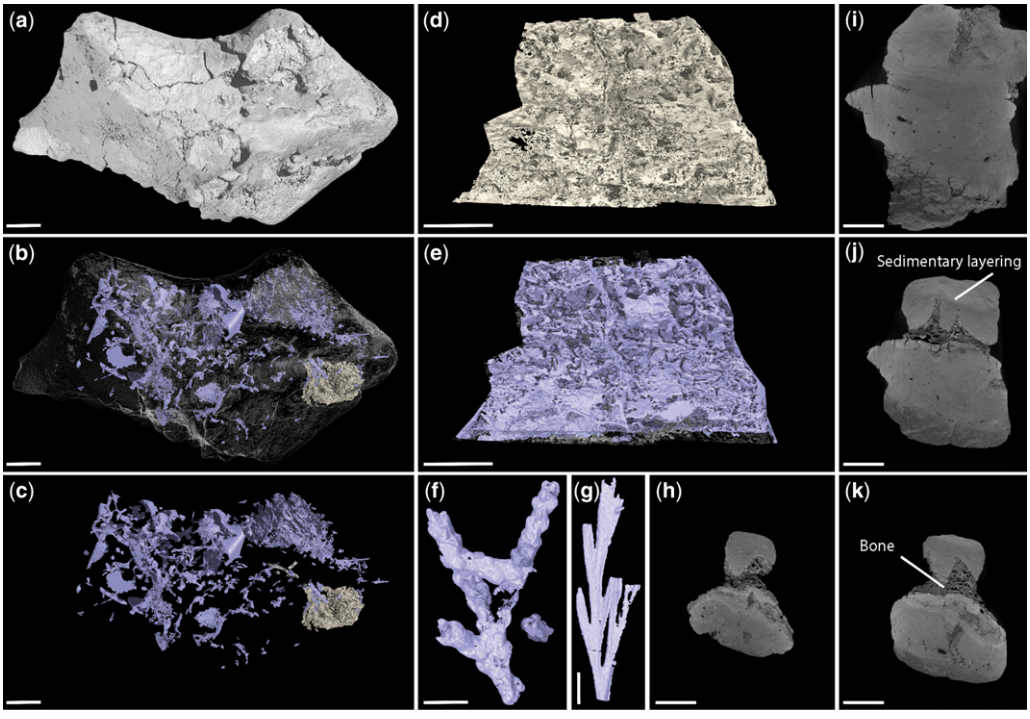


Fig. 5. Computed tomography reconstructions of: (**a**) the endocast (lateral view from the right side); (**b**, **c**) voids/regions of lower density within the endocast; (**d**) a bone fragment at the back of the endocast (dorsal view); (**e**) the voids within the bone fragment (interpreted as Haversian canals or trabeculae); (**f**) a branching twig within the sediment infill; and (**g**) a leaf within the sediment infill. (**h**–**k**) Representative computed tomography slices through the endocast revealing regions of bone and layering within the sediment infill. All reconstructions in this figure were generated using the SPIERS software suite and were rendered in Blender. Scale bars: (a–c, h–k) = 10 mm, (d, e) = 5 mm, (f, g) = 2 mm.

be examined using SEM techniques (e.g. Killer *et al.* 2003). Study of the Bexhill specimen using environmental SEM revealed structural details that appear to show features linked to brain architecture in this dinosaur (Figs 6–8). An attempt was made to identify and interpret these features in a neuroanatomical context (summarized schematically in Fig. 9).

The natural cranial endocast was unusually well-preserved along its dorsolateral flanks, corresponding to the approximate position of the cerebellum or anterior hindbrain (Fig. 2c, d); here, a SL can be traced along the dorsal surface, above the area occupied, when alive, by the superior sagittal sinus and occipital sinus (Fig. 2). This surface feature extends laterally as diagonal ridges preserved on either side of the endocast, corresponding to the area of the cranial cavity occupied by transverse venous sinuses (see also Norman & Weishampel 1990, figs 25.11, 25.12; Norman 2004, fig. 19.8). The SL was preserved as a veneer of brown, finely crystalline siderite that appears to overlie the OLL. The dorsal-most part of the SL most likely represents an early diagenetic coating of the braincase wall; it evidently lay outside the connective tissue layers that enveloped the brain itself and appears to faithfully take an impression of the inner bony lining of the braincase (Supplementary material figs 3, 4a); this layer is sporadically flecked by slivers of smooth, blackish compact cranial bone. Where the SL occupies the positions equivalent to the outer walls of the transverse venous sinuses, its presence is probably a result of the diagenetic infilling of these internal cranial spaces. We therefore infer that this moulding of the exterior surface occurred when siderite crystals began to grow in the epidural spaces located between the meninges and the overlying periosteum; this phase of mineralization would have spread into the adjacent intradural sinuses during an early phase of decay.

The OLL takes the form of a layered structure of some complexity and consists of minerals that have directly replaced the protective sheaths (the meningeal and arachnoid maters) that enveloped

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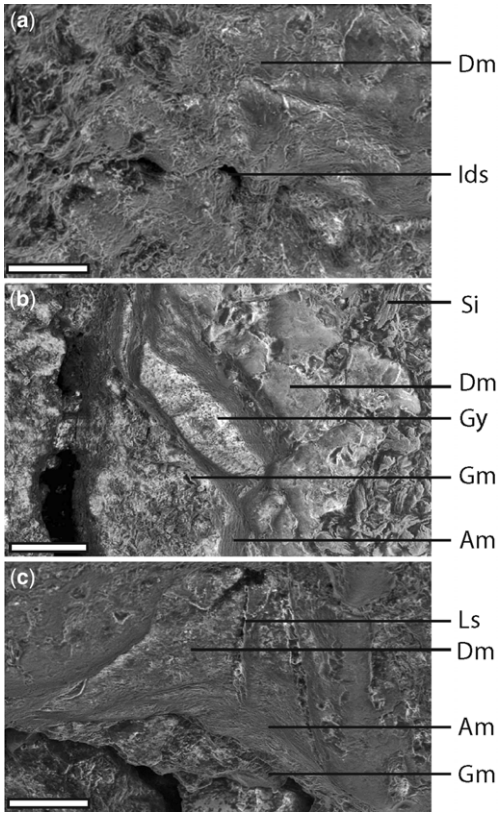


Fig. 6. Environmental scanning electron microscopy images of the iguanodontian natural cranial endocast. Images of the outer laminar layer on the flanks of the cerebellar area. (**a**) Well-preserved textures reflecting the organization of the meningeal layers lying immediately above the cortex; the pit-like structures represent intradural spaces lying between the thicker ribbons of meningeal tissue. (**b**) Features interpreted as folds and valleys of the meninges, lying above a complex fabric with recesses (Gy) possibly representing some of the superficial features of the underlying grey matter (Gm) of the cerebellar cortex. (**c**) Features interpreted as fossilized dura mater (Dm), the outermost membranes that surround the brain. Scale bars = 100 μm. All images in this figure were obtained from scans of the uncoated complete brain endocast. Am, probable arachnoid mater (traces of collagenous sheets and ribbons reinforcing the meningeal layer); Dm, probable dura mater preserved as micron-sized phosphatized filaments; Gy, potential gyri – these structures are normally associated with deeper layers in the cortex (i.e. the grey matter) and reflect some of the convolutions near the surface of the cortex; Ids, intradural spaces; Ls, lesions in the meningeal fabric; Si, lozenge-shaped siderite crystals.

the brain cortex (grey matter). The OLL is thickest on the flanks of the endocast beneath the 'dural peak' (Fig. 2). Both optical microscopy and SEM revealed this layered region to be constructed of thin, interwoven laminar sheets of phosphate (Figs 6–8) that were either planar or, more commonly, corrugated into ribbon-like folds and troughs. These structures range from microns to millimetres in diameter and are conspicuously aligned across the brain axis. SEM reveals that these ribbons were themselves composed of aligned, micrometre-sized filaments (Fig. 6, Dm). Some of the junctions between these ribbons contain small intradural spaces (Fig. 6a, Ids). Small elongate voids, infilled largely with reddish brown, rod-shaped siderite crystals 20–30 μm in length occur within and between these ribbons (Fig. 6b, Si), which also generally lie parallel to the endocast surface. This OLL fabric of fibrous ribbons with occasional voids has all the microscopic features expected of either the periosteum or meningeal mater (which together form the dura mater; see Fig. 9). These form the tough protective outer coatings seen in living vertebrate brains (cf. Runza *et al.* 1999 – as interpreted in Fig. 9). The ribbons and filaments are taken to represent the remains of bundles of fibrous collagen that have been replaced by phosphate before significant organic decay took place.

The web-like structure of phosphatized ribbons in the OLL is punctured locally by well-defined apertures (Fig. 6c, Ls); this web-like fabric closely resembles that seen in the arachnoid mater of the meninges (cf. Reina *et al.* 2002). The arachnoid mater in the dorsal hindbrain of living avian archosaurs is a thin sheet of interwoven collagen ribbons that comprises the innermost layer of the dura mater (Fig. 6b, c, Am; Fig. 8a, Am). In archosaurs, this layer directly overlies the cortex (grey matter) of the brain (Fig. 6b, Gm) without any intervening subarachnoid space and pia mater as found in the more complex brains of mammals (Runza *et al.* 1999). In this petrified natural cranial endocast, the inner, arachnoid-like layer seemingly exhibits convolutions (Fig. 6b, Gy); these structures are interpreted as 'gyri' (see also Wilson 1971), reflecting in part the topographic complexity that exists between the arachnoid mater and the underlying cerebellar cortex (=grey matter) (Fig. 6b, c, Gm; see also summary Fig. 9).

The outer tubular features within the cranial endocast mainly lie within the fabric of the OLL and are predominantly arranged parallel to the endocast surface, just above what is suggested here to be the arachnoid mater (Figs 7 & 8a, Bv). The tubular structures are either rounded or compressed in cross-section and typically range up to 100 μm in diameter (compare Figs 7 & 8). Several examples show finely layered walls (Fig. 7) and their internal spaces are either lined or infilled with microcrystalline siderite formed during early diagenesis. These tubes are very similar in size and shape to

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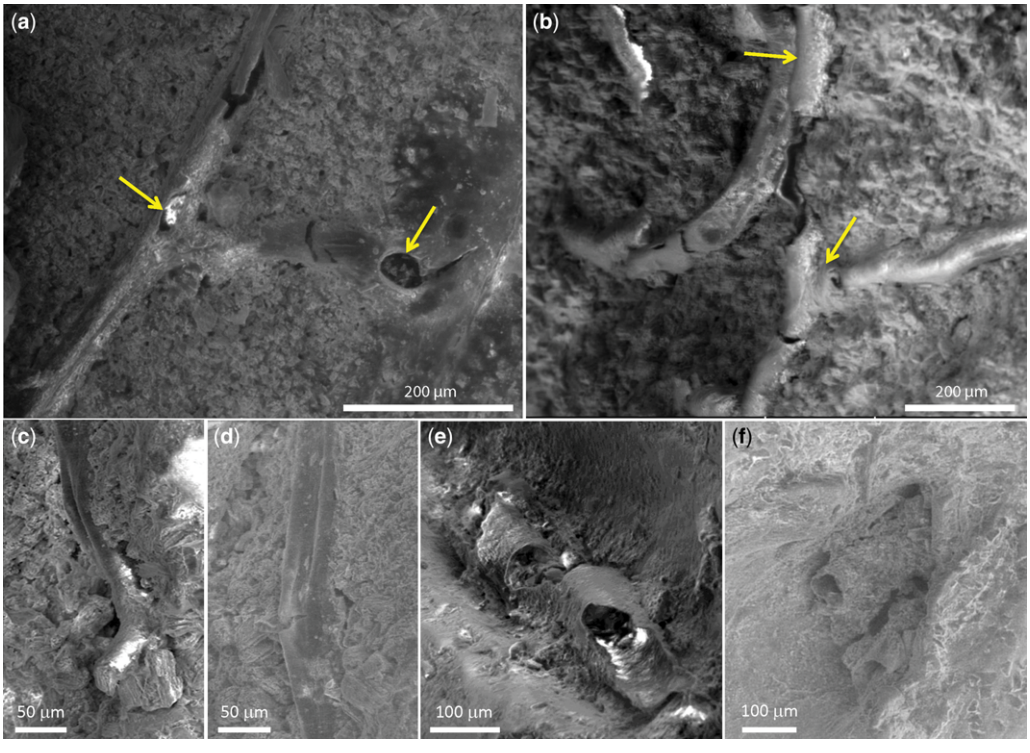


Fig. 7. Environmental scanning electron microscopy images of tubular structures on the exterior of the Bexhill iguanodontian cranial endocast and within the outer laminar layer, interpreted here as meningeal blood vessels. Arrows in (**a**) point to areas where the hollow nature of the vessels can be seen; arrows in (**b**) point to branching of the vessels; (**c–f**) additional images of hollow tubular structures within the outer laminar layer. All images in this figure were obtained from scans of the uncoated complete brain endocast.

blood vessels and form a network that extends across the surface of the meninges and, in some instances, penetrates the cortex as part of the blood supply (arterial) or drainage (venous) systems (see Fig. 9).

Immediately beneath the meninges some deeper areas of the endocast lack these laminar or ribbon-like features and exhibit a texture of considerable fine-scale complexity (Fig. 6b, c). This area could be interpreted as the mineralized remnants of cortical tissue (grey matter), representing an imperfect record of the complexity of the cerebellar cortex.

Figure 9 provides an idealized summary and interpretation of the dorsal cranium and endocranial cavity soft tissues that appear to have been preserved in the natural cranial endocast from Bexhill. Such soft tissue preservation is comparatively rare in non-avian dinosaurs and, indeed, in any terrestrial vertebrate, but this specimen clearly demonstrates that even brain-associated tissues can be preserved under exceptional taphonomic conditions.

Taphonomic history

The three zones of preservation that we recognize (carbonate, phosphate–carbonate, and siltstone), as well as their distribution on the natural endocast, are suggestive of a specific set of taphonomic conditions acting on the specimen during the period shortly after death, consistent with burial of the dinosaur braincase in an aqueous medium.

Conditions necessary for mineralization

The brain structures described here were preserved in phosphate and carbonate; however, to preserve soft tissue as phosphate, a locally anoxic environment is required to promote bacterially mediated mineralization (Briggs *et al.* 1993). In the predominantly fluvial system suggested by the sediments associated with this specimen, eutrophication (algal blooms) and/or stratification of the water column is required to result in water column anoxia. Under freshwater conditions, eutrophication adds phosphate to the water column in the form of a

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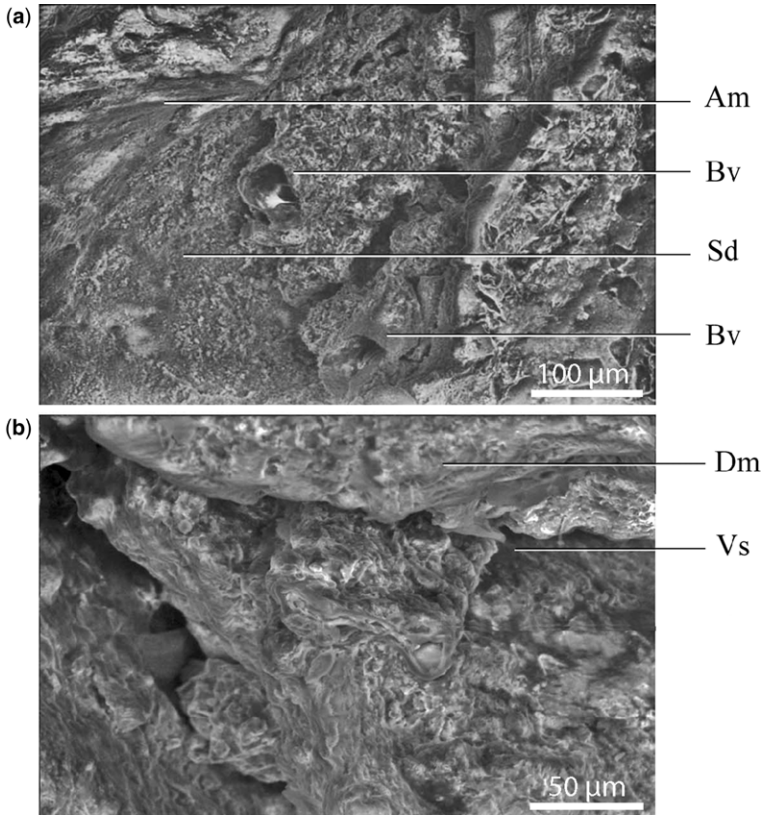


Fig. 8. Scanning electron microscopy images of small-scale tubular features and associated structures and fabrics visible on the outer laminar layer of the Bexhill iguanodontian natural cranial endocast. All images in this figure were obtained from scans of the uncoated complete brain endocast. Am, arachnoid mater-like fabric; Bv, tubular structures interpreted as blood vessels; Dm, fabric interpreted as dura mater; Sd, microcrystalline siderite fabric; Vs, groove interpreted as a venous sinus.

phosphoric acid series. Ionized phosphoric acids (hydrogen phosphate^{2-}, dihydrogen phosphate^{1-}) and orthophosphoric acid (H_3PO_4) drastically reduce the pH of the water, rapidly fixing soft tissues (the equivalent of pickling) and degrading and dissolving the surrounding mineralized tissues. Consequently, the soft tissues associated with the brain could have been preserved and cast prior to complete burial by sediment, which would complete the sealing process before the bone of the braincase had been completely dissolved away. Any phosphogenic layer is likely to have formed at the base of the water column or within the upper layer of soft sediment beneath the sediment–water interface.

Taphonomic scenario

The death of the dinosaur may have occurred adjacent to or within a temporarily eutrophic water body. The body most likely collapsed into the water column and the head came to lie, inverted and partially buried, in sediment at the bottom of the water body. With the head in the proximity of the anoxic and phosphogenic layer, the processes of soft tissue preservation (linked to decay), dissolution of the surrounding bone and phosphatization could proceed. In an inverted position the upper (dorsal) portion of the brain was, in effect, ponded, because it lay within a bowl-shaped container formed by the occipital, parietal and lateral braincase wall bones. This container was lined by the periosteum and meninges – membranes that form tough sheaths surrounding the cortical portions of the brain.

The lower parts of the braincase floor and ventral brain tissues – overturned (Fig. 4) – decayed to form a stagnant (anoxic) pool of decomposing tissue and fluid enriched in phosphate and iron. The high-fidelity replacement of durable collagen proteins and blood vessels associated with the meninges on

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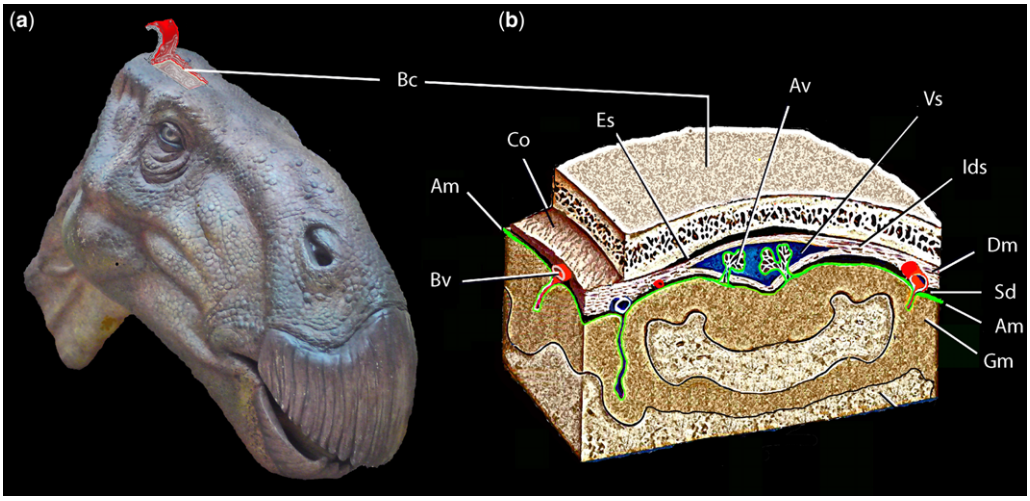


Fig. 9. An idealized reconstruction of the head of an iguanodontian dinosaur showing the dorsal braincase and associated soft tissue features as evidenced by examination of the natural endocast from Bexhill. (**a**) Reconstruction of the head of an iguanodontian (OUMNH T.127) in the oblique anterior view showing the area of the skull roof that has been 'dissected' to the right. (**b**) Partly 'exploded' restoration of the underlying braincase and brain tissues identified following detailed examination of the structures preserved in the natural cranial endocast. Am, arachnoid mater (meninge); Av, arachnoid villus (protruding into a mid-line venous sinus); Bc, braincase bone (parietal); Bv, blood vessels; Co, collagenous sheath enclosing the brain structures and lining the bones of braincase (combined periosteal and meningeal sheets); Dm, dura mater (meninge); Es, epidural space; Gm, grey matter (brain cortex); Ids, intradural space (between the meninges); Sd, subdural space; Vs, sagittal venous sinus.

the opposite, dorsal surface was facilitated by the very rapid growth of amorphous microcrystals of calcium phosphate (cf. Martill 2001). Autolithified bacteria were not observed associated with these microcrystals, suggesting that mineral replacement probably proceeded quickly. Phosphatization of the meningeal layers probably took place under conditions of low pH and low oxygen tension in fluids low in sulphate, but rich in ferrous ions (Allison & Pye 1994). Such fluids are typical of environments influenced by Fe^{3+}-reducing bacteria and with high concentrations of calcium, phosphate and ferric ions (released from the adjacent biological tissues, such as bone, brain tissue and blood cells; cf. Allison 2001). The local removal of ferrous ions by the formation of siderite may have further encouraged the rapid precipitation of calcium phosphate. Excess ferrous ions were also likely to have been incorporated into the phosphate phase in places, as suggested by our SEM-EDS analyses.

Deeper within the endocranial cavity, less refractory nervous tissues of the cerebellar cortex are presumed to have decayed away, or experienced much lower fidelity moulding via the precipitation of amorphous phosphate and carbonate microcrystals. The latter would probably have occurred under conditions that were relatively more alkaline, with more freely available bicarbonate ions. The siderite microcrystals in this region were typically rod-shaped and *c.* 30–50 μm long (Fig. 6b, Si); they were composed of nanocrystals of regular shape and size, perhaps reflecting some degree of bacterial mediation. Moulds and casts of heterotrophic bacteria are more usually coccoid (spheroidal) or bacillate (rod-shaped) in form, so the observed structures are unlikely to be bacterially derived artefacts (cf. Wilby & Briggs 1997; Liebig 2001; Martill 2001).

The ventral portion of the braincase (upper in terms of burial orientation) was evidently filled by episodic infiltrations of alluvial silt, carrying with it carbonized plant debris and broken bone. In places, phases of internal sediment deposition alternated with thin partings coated with siderite. There is a persistent, exposed suture line in iguanodontian dinosaurs between the bones that form the lateral walls and floor of the braincase (Norman 1977); this may have resulted in the floor of the braincase becoming detached from the remainder of the braincase as decay and dissolution proceeded, allowing sediment access to the floor of the endocranium. As the specimen was discovered *ex situ*, we cannot comment on the preservational processes that affected the rest of the body, or on the potential preservational fidelity they may or may not exhibit.

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How intelligent was the Bexhill iguanodontian?

Previous studies have suggested that dinosaur brains may have shared general similarities with those of modern crocodilians in having a thick outer packaging of dural tissue and extensive lymphatic and venous sinuses (Dendy 1909; Romer 1956; Ostrom 1961; Hopson 1979). It has been argued that the latter structures are very likely to obscure details of the brain tissue beneath, meaning that the topography of cranial endocasts of dinosaurs reflects (at best) an early ontogenetic stage in brain development (Romer 1956). As a consequence, dinosaur cranial endocasts typically reveal a generalized brain morphology, rather than (more desirable) fine details about the size, structure and therefore relative biological importance of the brain lobes and their bearing on probable behavioural repertoires ('intelligence') (Dendy 1909; Hopson 1979; Rogers 1999; Witmer *et al.* 2008).

Previous measurements of dinosaur endocast volumes estimate them to have contained as little as 50% of actual brain (Hopson 1979; Evans *et al.* 2009). Exceptions to this general assumption have been proposed: hadrosaurs (lambeosaurines, derived iguanodontian ornithopods) have been argued to have had brain tissues that filled rather more of the endocranial cavity (Evans 2005, cited in Evans *et al.* 2009), especially in the anterior and ventral regions of the endocasts where more detailed lobe-like structures (e.g. cerebral hemispheres and the hypothalamus) are discernible to the naked eye. More posterior regions of the endocranium in dinosaurs, adjacent to the cerebellum and medulla, are, by contrast, relatively poorly defined and may indeed have been overlain by extensive sinuses, as is the case in extant crocodilians (Ostrom 1961; Hopson 1979; Evans *et al.* 2009).

Comparison of the volume of dinosaur brains (judged from endocast volume), relative to the volume expected for a modern reptile of comparable body volume, gives what is known as the encephalization quotient (EQ) (Fig. 10). This allows for provisional estimates of intelligence (Hopson 1979; Evans 2005). In the case of iguanodontians, the EQ estimates range from 0.8 to 1.5 (Fig. 10; Hopson 1979). However, if the neural tissues in the cranial cavity of the Bexhill specimen were indeed tightly packed into the available space, then this dinosaur would have an EQ closer to 5.0, which would fall close to the base of the cited range of the largest brained dinosaurs, such as the bird-like avian theropods (Fig. 10). It has been argued on the basis of other anatomical attributes (e.g. Norman 1980, 1986, 2004) that iguanodontian dinosaurs had evolved a relatively complex range of locomotor skills and social behaviour patterns comparable with those suggested for their later Cretaceous descendants, the hadrosaurs (cf. Norman 2014, 2015). Some hadrosaurs (which are ornithopods and whose range of EQs overlap, or slightly exceed, those of the example discussed here) are known to have exhibited complex nesting and brooding behaviours (Horner & Makela 1979) and to have structures in their skulls indicating that sound production, using cranially located resonating chambers (Weishampel 1981), may have played an important role in their

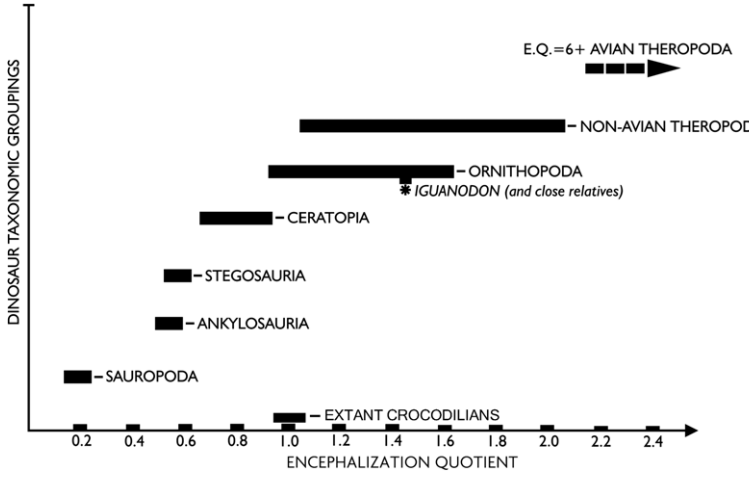


Fig. 10. Encephalization quotients (EQ) estimated across a range of dinosaur clades/groupings. Extant crocodilians represent the reference marker (EQ = 1.0) for comparison with dinosaurians more generally. Ornithopods (such as *Iguanodon* and closely related taxa) exceed the EQ of extant crocodilians and overlap the values seen in basal (non-avian) theropods. Modified from Hopson (1979).

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social interactions. However, living crocodilian archosaurs also exhibit vocalization as part of their behavioural repertoire and have complex nesting, nest-tending and brooding behaviours (Guggisberg 1972), but exhibit a relatively low EQ.

Literal interpretation of the surface features exhibited by the Bexhill fossil suggests that the meninges were not very thick and that the neural layers of the cerebellar cortex lay immediately (<1 mm) beneath the meningeal tissues. This could easily be taken as evidence that iguanodontian ornithopods had a greater volume of neural tissue than has been argued on the basis of comparison with crocodiles (Hopson 1979). In other words, iguanodontians such as *Barilium* and *Hypselospinus* were comparatively 'intelligent' dinosaurs, with a greater volume of neural tissue packed into the endocranium than previously predicted. The counter-argument to this interpretation is that the surface features on the natural endocast indicate that the meningeal tissues and decaying brain had collapsed, under gravity, into the bowl-like braincase. Consequently, the proximity of meningeal tissues to the braincase wall is here interpreted as an artefact of preservation, rather than an indication of the dense packing of neural tissue into the cranial cavity.

Conclusions

We have reported a remarkably preserved partial natural endocast of the cranial cavity of an iguanodontian ornithopod dinosaur, which, to our knowledge, is the first described example of mineralized brain soft tissues from a fossilized terrestrial vertebrate. This endocast was collected from an intertidal exposure of Valanginian (Early Cretaceous) age. The endocast topography closely reflects the morphology of the anterior and dorsal portions of known iguanodontian cranial cavities. The endocast consists of a complex of siderite, collophane and layered siltstone, the latter having accumulated within the cranial cavity after the death of the dinosaur and during later phases of organic decay and sub-aerial burial of the braincase. Superficial examination of the specimen allowed comparison with braincases and endocasts (both natural and artificial) attributable to closely related, but geologically younger (Barremian–Aptian), iguanodontians such as *Iguanodon bernissartensis* (Norman 1980) and *M. atherfieldensis* (Norman 1986). More detailed examination of the natural endocast using light microscopy, as well as SEM and μCT imaging, has revealed hitherto unexpected details about the membranous tissues lining the braincase walls and adjacent tissues that invested the brain itself. Comparisons drawn with brain-associated soft tissues in living species suggest that portions of the tissue space between the braincase wall and tough tissues (meninges) surrounding the brain itself were mineralized by siderite early in the decay process. The actual meninges (meningeal and arachnoid maters) appear to have been preserved by phosphate replacement of the original tissues (including some of the larger blood vessels that may be lined or infilled by microcrystalline siderite). The meningeal structures that could be discerned appear to show similarities with those seen in living archosaurs (crocodiles and birds). A fine-textured collophane matrix lying seemingly beneath the meningeal structures suggests the partial preservation of deeper cortical tissues of the brain itself.

As is common with many dinosaur endocasts, it appears that the anterior portion of the endocast (equivalent to the areas occupied by the forebrain lobes and hypothalamus) was well developed and moulded the developing braincase walls. More posteriorly, the mid- and hindbrain were enveloped by extensive blood and lymphatic sinuses that masked the details of brain morphology to a far greater extent. Behavioural complexity is strongly associated with forebrain development and it is reasonable to suppose that iguanodontian dinosaurs of this type were moderately complex behaviourally (no less so than modern crocodilians, for example). This suggestion is reinforced by our knowledge of iguanodontian anatomy and the complexity of their known or implied range of locomotor, social and reproductive repertoires.

JEHH found the specimen. MDB and DBN collaborated to develop this research project and co-ordinated the investigation. DW, AGL and RG conducted the analyses. DBN, MDB, JBA and AGL developed the manuscript and, following the untimely death of MDB, all the authors were involved in data interpretation and the final redrafting of the manuscript. We acknowledge the facilities, scientific and technical assistance of the Australian Microscopy & Microanalysis Research Facility at the Centre for Microscopy Characterisation and Analysis, The University of Western Australia, a facility funded by the university, state and Commonwealth governments. R. Callow undertook early petrological and SEM studies in Oxford. D. Siveter and E. Howlett kindly facilitated imaging and study of '*Iguanodon*' casts in the OUMNH collections. MDB acknowledges funds provided by V. and T. Brasier. DBN was supported by the Odell Trust Fund from Christ's College Cambridge. AGL is supported by the Natural Environment Research Council (grant number NE/L011409/1). JBA acknowledges the ongoing support of the Department of Zoology and OUMNH, University of Oxford. RG is a Scientific Associate at the Natural History Museum, London, and a member of the Interdisciplinary Centre for Ancient Life. DW acknowledges funding from the Australian Research Council and the European Commission. This is CCFS paper 861. The authors would like to thank D. Martill and A. Iwaniuk for helpful suggestions during the review process.

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