

The Frontoparietal Fossa and Dorsotemporal Fenestra of Archosaurs and Their Significance for Interpretations of Vascular and Muscular Anatomy in Dinosaurs

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ABSTRACT

The attachments of jaw muscles are typically implicated in the evolution and shape of the dorsotemporal fenestra on the skull roof of amniotes. However, the dorsotemporal fenestrae of many archosaurian reptiles

Anatomical Abbreviations: aAU = auricular artery; a,vSO = supraorbital artery and vein; a,vTO = temporoorbital artery and vein; a,vTR = trigeminal artery and vein; aFA = facial artery; aOC = occipital artery; aSO = supraorbital artery; aST = superficial temporal artery; aTO = temporoorbital artery; aTS = superficial temporal artery; ci = carunculate integument; cPO = postorbital communication; ct = cartilago transiliens; DTFen = dorsotemporal fenestra; DTFos = dorsotemporal fossa; EVS = elaborated vascular structure; FPF = frontoparietal fossa; fr = frontal; ir = integumentary region; ju = jugal; ls = laterosphenoid; mAMEM = m. adductor mandibulae externus medialis; mAMEP = M. adductor mandibulae externus profundus; mAMES = m. adductor mandibulae externus superficialis; mcr = muscular crest; mf = muscular fossa; mPSTs = M. pseudotemporalis superficialis; ncr = nuchal crest; nf = nutrient foramina; ol = ossified ligament; pa = parietal; po = postorbital; pPO = postorbital plexus; ptb = pterygoid buttress; qu = quadrate; rOP = ophthalmic rete; scr = sagittal crest; scs = supracranial sinus; sn = snood; sq = squamosal; TF = Temporal fossa; tr = trochlea; vfo = vascular foramen; vg = vascular groove; vr = vascular recess; vTO = temporoorbital vein

Institutional Abbreviations: AMNH = American Museum of Natural History, New York City, NY; CAPP/USFM = Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia/Universidade Federal de Santa Maria, Santa Maria, Brazil; CM = Carnegie Museum of Natural History, Pittsburgh, PA; CMN = Canadian Museum of Nature, Ottawa, ON, Canada; CMNH = Cleveland Museum of Natural History, Cleveland, OH; CNRST-SUNY = Centre National de la Recherche Scientifique et Technologique du Mali—Stony Brook University, NY; FMNH = Field Museum of Natural History, Chicago = IL; IGM = Institute of Paleontology and Geology, Mongolian Academy of Sciences, Ulan Bataar, People's Republic of Mongolia; MACN PV = Museo Argenino de Ciencias Naturales, "Bernadino Rivadavia", Buenos Aires, Argentina; MCZ = Museum of Comparative Zoology, Cambridge, MA; MNA = Museum of Northern Arizona, Flagstaff, AZ; MOR =

Museum of the Rockies, Bozeman, MT; NCSM = North Carolina State Museum; NHMUK = Natural History Museum, London, UK; OUVC = Ohio University Vertebrate Collections, Athens, OH; PVSJ = División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina; ROM = Royal Ontario Museum, Toronto, Canada; SGM = Ministère de l'Énergie et des Mines, Rabat, Morocco; TMP = Royal Tyrell Museum of Palaeontology, Drumheller, AB; National Museum of Natural History, Washington, DC; UCMP = University of California Museum of Paleontology, Berkeley, California; UTCT = University of Texas Computed Tomography, Austin, TX; YPM = Yale Peabody Museum, New Haven, CT

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possess smooth excavations rostral and dorsal to the dorsotemporal fossa which closely neighbors the dorsotemporal fenestra and jaw muscle attachments. Previous research has typically identified this region, here termed the frontoparietal fossa, to also have attachment surfaces for jaw-closing muscles. However, numerous observations of extant and extinct archosaurs described here suggest that other tissues are instead responsible for the size and shape of the frontoparietal fossa. This study reviewed the anatomical evidence that support soft-tissue hypotheses of the frontoparietal fossa and its phylogenetic distribution among sauropsids. Soft-tissue hypotheses (i.e., muscle, pneumatic sinus, vascular tissues) were analyzed using anatomical, imaging and *in vivo* thermography techniques within a phylogenetic framework using extant and extinct taxa to determine the inferential power underlying the reconstruction of the soft tissues in the skull roofs of dinosaurs, pseudosuchians, and other reptiles. Relevant anatomical features argue for rejection of the default hypothesis—that the fossa was muscular—due to a complete lack of osteological correlates reflective of muscle attachment. The most-supported inference of soft tissues is that the frontoparietal fossa contained a large vascular structure and adipose tissue. Despite the large sizes and diverse morphologies of these fossae found among dinosaur taxa, these data suggest that non-avian dinosaurs had the anatomical foundation to support physiologically significant vascular devices and/or vascular integumentary structures on their skull roofs. *Anat Rec*, 00:000–000, 2019. © 2019 Wiley Periodicals, Inc.

Key words: dinosaur; feeding; vasculature; crocodylian; avian; jaw muscles; integument; dorsotemporal fossa; frontoparietal fossa

Interpreting cranial structure and function in extinct taxa presents many challenges, particularly because so many important anatomical and physiological characteristics of the body's systems are lost to the fossil record. Fossilized vertebrates not only lose soft-tissue neural, sensory, and joint tissues, but also blood vessels, jaw muscles, and integumentary structures. The dorsotemporal fenestra (=supratemporal or upper temporal fenestra) is a conspicuous and evolutionarily significant feature of the skulls of amniotes (Romer, 1956). The dorsotemporal fenestra is generally thought to result from muscle forces acting upon the skull (Evans, 2008; Frazetta, 1968; Herring, 1993; Osborn, 1903; Romer, 1956; Tarsitano et al., 2001; Witzel and Preuschoft, 2005), because jaw muscles indeed fill the fossa in many vertebrates such as mammals, lizards, and turtles. However, lineages of archosaurs including crocodylomorphs and crocodyliforms, pterosaurs, and avian and non-avian dinosaurs, possessed a wide variety of dorsotemporal fenestra shapes and sizes which appear to not always directly correspond to jaw muscle attachments. Paleobiologists have revised previously hypothesized muscular features of the dinosaur skull including the ceratopsid frill (e.g., Dodson, 1996; Haas, 1955; Lull, 1908), antorbital cavity (Adams, 1919; Molnar, 2008; Witmer, 1995a, 1997), and buccal emarginations (Galton, 1973; Knoll, 2008). In a similar vein, here we present numerous lines of evidence which indicate that a sizable portion of the dorsotemporal fenestra in crocodylians, non-avian dinosaurs, and many other fossil archosaur lineages was not wholly muscular but instead likely housed vascular tissues (Figs. 1 and 2). When skull roof tissues were elaborated in fossil specimens, evidence indicates that blood

vessels found in the dorsal temporal fossa were often involved in supporting soft-tissue cranial display structures (e.g., *Aegisuchus*; Holliday and Gardner, 2012) and possibly vascular physiological devices. These findings exemplify how the interpretation of a cranial feature has complementary bearing on the inferences of surrounding soft-tissue structures, in this case integumentary structures, but also the jaw muscles and feeding apparatus.

Anatomical Background

The skull roofs and dorsotemporal fenestrae of sauropsids vary in their shape and contents, warranting a brief introduction of this article's terminology (Figs. 1 and 2). The dorsotemporal fenestra is the hole, or window, in the skull roof and forms the bony rim around the contents within it. The dorsotemporal fossa is the space and the surrounding bony surfaces immediately ventral to, or deep within, the fenestra. The fenestra and fossa are usually formed by contributions of the parietal, frontal, postorbital, squamosal, and in archosauriforms, the laterosphenoid. Ventral to the dorsotemporal fossa is the main cavity of the adductor chamber or temporal region that is located between the braincase, palate, and temporal bars. This space then transmits through the subtemporal fenestra towards the mandibular attachments of the muscles. Thus, the temporal region in general is cylindrical or funnel-shaped, bounded by the dorsotemporal fenestra (supratemporal fenestra, Osborn, 1903) and fossa dorsally and by the subtemporal fenestra and mandible ventrally (Fig. 1).

Among extant amniotes, the sizes and shapes of the dorsotemporal fossa and fenestra are relatively equal in

mammals, lepidosaurs, and turtles; adductor muscles attach to almost all of the bony surfaces of the fossa, in turn also filling the dorsotemporal fenestra (Fig. 2A,C). However, in crocodylians, the dorsotemporal fossa is smaller in circumference compared to the dorsotemporal

fenestra, forming a depression in the frontal and parietal bones, here termed the frontoparietal fossa. Vasculature and adipose tissue (i.e., fat) excavate and fill a relatively large portion of the surface of the parietal and frontal, circumscribing and capping the dorsotemporal fossa and its musculature (Figs. 2 and 3; Holliday, 2008). These nonmuscular soft tissues leave a distinct impression along the periphery of the dorsotemporal fenestra as well as a more pronounced fossa near the rostral margin of the fenestra. This additional, nonmuscular bony shelf of the dorsotemporal fossa is the frontoparietal fossa (Fig. 1). Consequently, the size and shape of the dorsotemporal fenestra is not equal to that of only the dorsotemporal fossa but instead the combined frontoparietal and dorsotemporal fossae (Figs. 1 and 2). Although Farke (2010) coined the term in his discussion of the homology of the expanded pneumatic fossae in the skull roofs of ceratopsians (i.e., supracranial sinuses), we suggest below that the ceratopsian structure may be related to the frontoparietal fossa discussed throughout this article; thus, we will retain this more general nomenclature for simplicity's sake.

Many extinct archosaurs, including crocodylomorphs, non-avian theropod dinosaurs, ceratopsians, pterosaurs, and stem taxa also possess frontoparietal fossae in the form of smooth excavations on the rostradorsal and medial margins of the dorsotemporal fossa, within the dorsotemporal fenestra. Some of these taxa possess a frontoparietal fossa that is almost larger than the dorsotemporal fossa itself (Fig. 1A). The frontoparietal fossae in these taxa often encroach upon the dorsal surfaces of the frontal and postorbital and abut the dorsotemporal fossa caudally. Consequently, the frontoparietal fossa has frequently been interpreted to be simply a part of the larger muscular region in many non-avian dinosaurs (e.g., Button et al., 2016; Carr, 1999; Coria and Currie, 2002; Currie, 1995; Currie and Zhao, 1993; Galton, 1984; Gignac and Erickson, 2017; Haas, 1955; Lautenschlager et al., 2016; Sereno and Novas, 1992) with a few exceptions (e.g., Lull, 1908; Ostrom, 1964). Although Holliday (2009) briefly refuted inferences of musculature in the frontoparietal fossa, he provided minimal explanation for this revised hypothesis. Here, we thoroughly test hypotheses of homology and soft-tissue reconstruction of the frontoparietal fossa in dinosaurs and other sauropsids.

MATERIALS AND METHODS

The morphology of the dorsotemporal fossae of sauropsids was reviewed with emphasis on non-avian dinosaurs and other archosaurs, although data from lizard and testudine taxa were also collected. Data were gathered

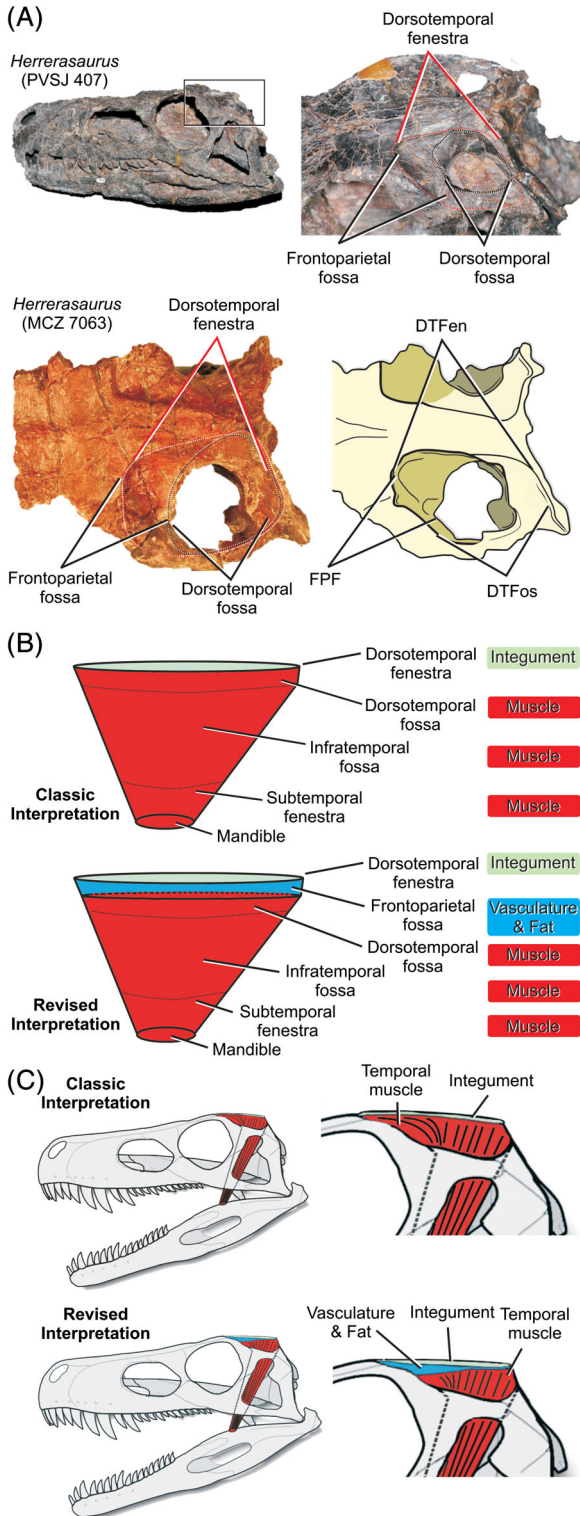


Fig. 1. This article shows evidence that the frontoparietal fossa of archosaurs houses vasculature, which impacts soft-tissue reconstruction and inferences of feeding function and physiology of dinosaurs and their relatives. **(A)** Specimens of *Herrerasaurus*, a basal dinosaur, possess well-defined differences between the dorsotemporal fossa and frontoparietal fossa, both of which are structures within the dorsotemporal fenestra. **(B)** Soft tissues sculpt the fossae of the skull roof form the upper layers of the adductor chamber. We show evidence that blood vessels and fat occupy structures previously hypothesized to be jaw muscle attachments. **(C)** Anatomical illustration of classic and revised interpretations of temporal fossa anatomy in *Herrerasaurus*.

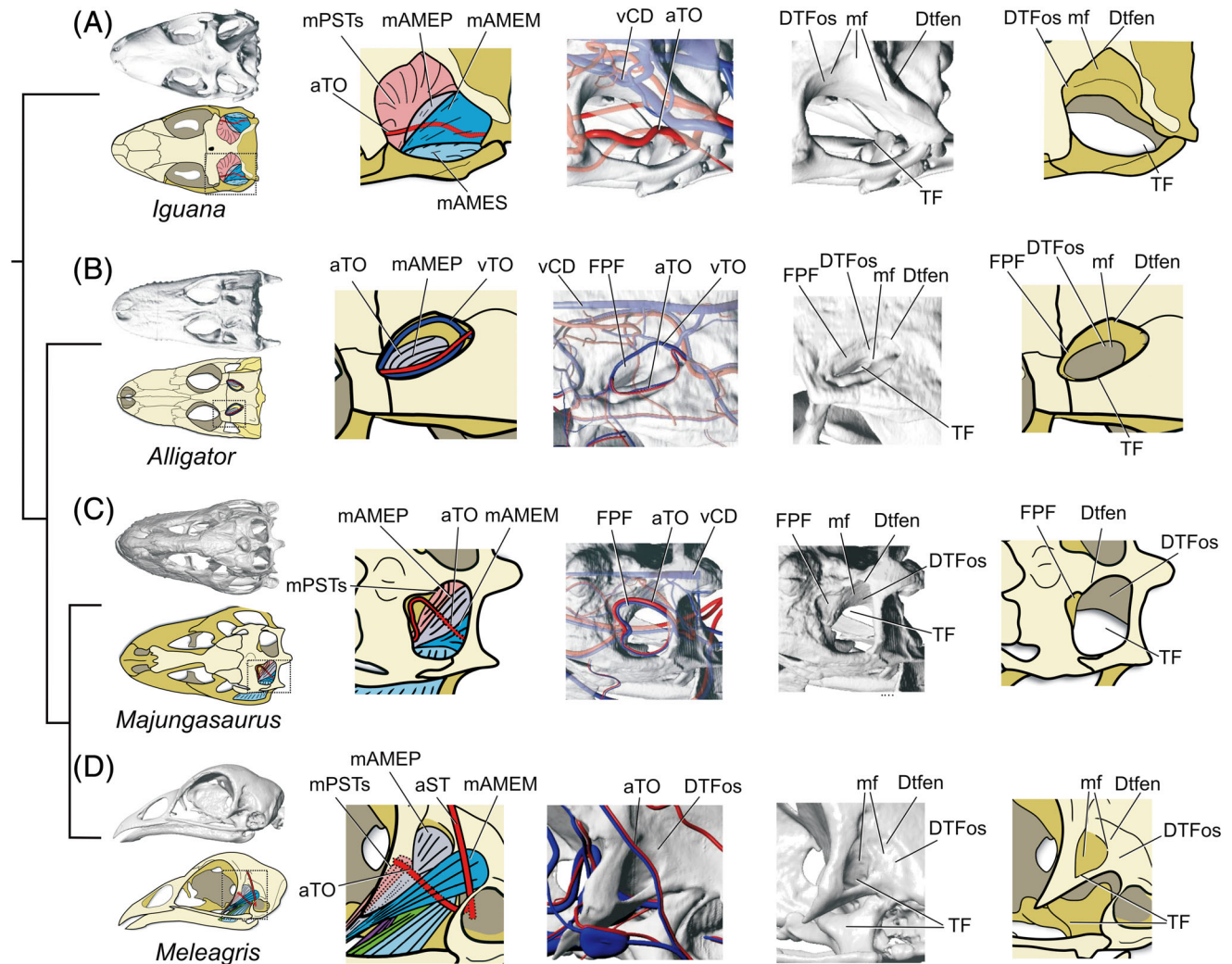


Fig. 2. Comparative anatomy of the skull roofs of reptiles illustrating bony, muscular, and vascular structures that occupy the frontoparietal and dorsotemporal fossae. **(Far Left)** Phylogeny and heads of exemplar lepidosaur and archosaur skulls showing soft tissues and bony structures of the temporal region and skull roof. **(A)**, *Iguana iguana* (OUVC 10603). **(B)**, *Alligator mississippiensis* (OUVC 10392). **(C)**, *Majungasaurus crenatissimus* (FMNH PR2100). **(D)**, *Meleagris gallopavo* (OUVC 10599). **(Left)**, Illustration of muscles and vasculature of the dorsotemporal fenestra. **(Middle)**, 3D model of vasculature and skull. **(Middle Right)**, 3D model of skull. **(Far Right)**, Illustration of osteological correlates of the skull roof.

using dissection, imaging (e.g., computed tomography [CT], magnetic resonance imaging), vascular injection (e.g., Microfil® [Flowtech Inc], barium-latex), diceCT contrast imaging (Holliday et al., 2013; Gignac et al., 2016), and other techniques from over 100 extant fresh and skeletonized crocodylian, avian, lepidosaurian, and testudine taxa (Holliday, 2009; Holliday and Witmer, 2007; Porter et al., 2016; Porter and Witmer, 2015, 2016). These data were complemented with an equally large assemblage of CT and observational data of fossil archosaur material including basal archosaurs, pseudosuchians, pterosaurs, and non-avian dinosaurs (Holliday, 2008; Holliday, 2009; Tsai and Holliday, 2011).

We reviewed the anatomical data in a systematic fashion to test which soft tissues may be responsible for excavating frontoparietal or other relevant fossae in the skull roofs of extant and fossil taxa. Because this region of the skull is an intersection of not only muscle attachments

and vasculature but also integument, glands, and pneumaticity, we carefully explored hypotheses of soft tissue reconstruction (e.g., Witmer, 1995a, 1997; Holliday and Witmer, 2007; Hieronymus et al., 2009). Ultimately, hypotheses of homology and soft-tissue reconstruction were tested using Patterson's (1982) tests for similarity and homology and the Extant Phylogenetic Bracket approach (Witmer, 1995b).

Finally, upon discovering that the frontoparietal fossae of crocodyliforms, at least, were largely vascular (see Results section), we gathered *post hoc*, pilot observational thermal imaging data from living alligators and crocodiles at the St. Augustine Alligator Farm Zoological Park, St. Augustine, Florida, to test if the fenestrae may be physiologically significant enough to warrant later study. Using an FLIR T600 thermal imaging camera with 480 × 360 30 Hz infrared detector, we captured estimates of relative surface temperatures of alligators and other

crocodilian species when possible during the day on February 12, 2014. Particular care was taken to document the dorsotemporal fossae and skull roofs of alligators early in the morning ($\sim 10^{\circ}\text{C}$) and later in the afternoon ($\sim 21^{\circ}\text{C}$) from distances within 3 m. Although

these surface data lack complementary core body temperature data, which would offer far better insight into crocodilian thermoregulatory behavior, we found them to be compelling enough to include them here (See Discussion section).

RESULTS

Anatomy of Extant Taxa

Lepidosaurs and Testudines. Among lizards and turtles, there is no structure similar to the frontal fossa. In turtles, the rostral margin of the dorsotemporal fenestra is sharp and dorsolaterally overhangs m. adductor mandibulae externus profundus and m. adductor mandibulae externus medialis, which pass caudodorsally towards the emarginated posttemporal fossa. Among most lizards, m. adductor mandibulae externus profundus, m. adductor mandibulae externus medialis, and m. pseudotemporalis superficialis occupy the dorsotemporal fossa and often form large nuchal and sagittal crests on the parietal (Haas, 1973; Wu, 2003; Holliday and Witmer, 2007; Werneburg, 2011). However, the rostral margin of the dorsotemporal fossa is smooth and vertical where m. pseudotemporalis superficialis attaches (Fig. 2).

Crocodylia. Virtually, all extant crocodylians possess clearly defined frontoparietal fossae. Although jaw muscles, namely m. adductor mandibulae externus profundus (Holliday and Witmer, 2007; Holliday, 2008), excavate the central and caudomedial portion of the dorsotemporal fossa, they do not attach rostrally in the frontoparietal fossa. Instead, the frontoparietal fossa and the rim of the dorsotemporal fossa are excavated by the temporo-orbital arteries and veins that pass along the circumference of the dorsotemporal fenestra (Fig. 3). These vessels are encapsulated by adipose and connective tissues that extend upon the frontoparietal fossa under the skin. Crocodylians and likely fossil crocodyliforms differ from other sauropsids in that the temporo-orbital artery and accompanying veins pass dorsal to m. adductor mandibulae externus profundus, rather than medial to it as found in birds, lizards, turtles, and likely non-avian dinosaurs (Holliday and Witmer, 2007; Holliday, 2008, 2009; Holliday and Witmer, 2009). The vessel's apomorphic position is likely a response to the rotation and suturing of the quadrate to the braincase during crocodylomorph evolution, which altered the position of entrance and exit of the

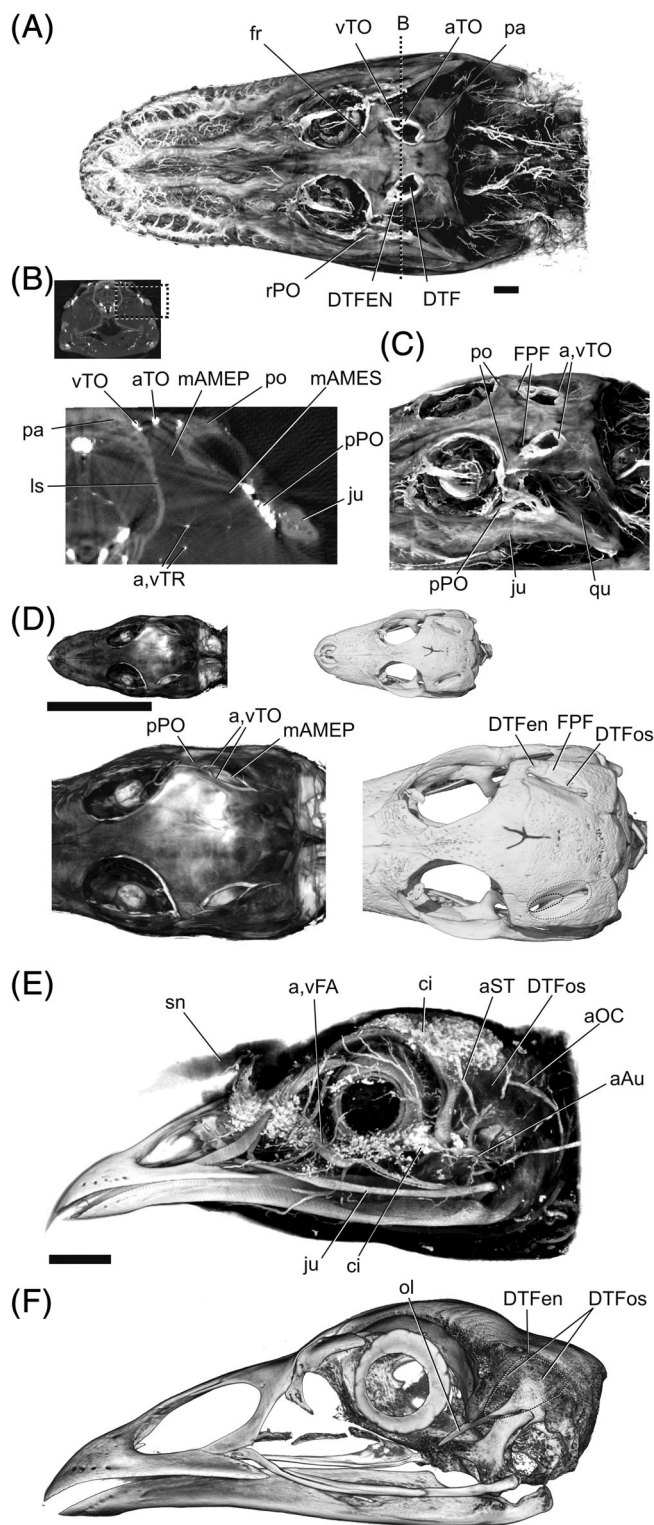


Fig. 3. Cranial vascular anatomy of *Alligator* and turkey (*Meleagris gallopavo*) showing how temporo-orbital and other vessels excavate portions of the skull roof including the frontoparietal fossa. (A), Voxel rendering of μCT data of a venous and arterial, barium and latex-injected, 3-year-old specimen of *Alligator mississippiensis* (OUVC 10395) in the dorsal view. (B), Axial section through temporal region OUVC 10395 highlighting contents of temporal region. (C), Left, oblique view highlighting vascular structures of skull roof and postorbital region of *Alligator* (OUVC 10395). (D), Dorsal views of voxel-based renderings of (Left) diceCT and (Right) skull of hatchling *A. mississippiensis* (OUVC 10606) illustrating how vasculature is the primary occupant of the dorsotemporal fenestra. (E), Left lateral view of voxel render of μCT data of an arterial Microfil[®]-injected *Meleagris gallopavo* (OUVC 10398) highlighting vascular and fleshy integumentary structures of the head. (F), Left lateral view of voxel render of μCT of skull of *Meleagris* (OUVC 10632) showing bony structures of the skull.

stapedial artery as it passes through the otic region. Consequently, the temporoorbital veins now excavate a conspicuous groove along the lateral margin of the parietal on the medial rim of the dorsotemporal fossa (see Fig. 3 for vascular pathways). In most cases, these veins then loop rostromedially between *m. adductor mandibulae externus profundus* and the overlying skin. The veins then pass across the frontal, in turn forming the frontoparietal fossa. The veins then enter the medial portion of the post-orbital to exit through a large foramen and then anastomose with the large postorbital plexus (Busbey, 1989; Sedlmayr, 2002; Porter et al., 2016), which passes across the lateral surface of the postorbital bar in eusuchians and anastomoses with the orbit and adductor chamber vasculature (Fig. 2C).

The temporoorbital vessels consistently sculpt the skull roof among crocodylians and their extinct relatives. In young individuals, the vessels leave a very prominent groove above the temporal muscles and the dorsotemporal fossa, which is merely a narrow vascular groove in the skull roof with a foramen at each end (Figs. 2 and 3). Although the relative size of the muscle increases, particularly in *Gavialis*, the vessels still leave a marked groove circumscribing the medial and rostral edges of the dorsotemporal fossa (Fig. 4). Even in taxa that have a complete bony roof over the dorsotemporal fossa (e.g., *Caiman crocodilus* [UCMP 73740] and *Paleosuchus palpebrosus* [FMNH 69872]), the vascular groove and frontoparietal fossa are still present underneath the overlying bone, and *m. adductor mandibulae externus profundus* still leaves a shallow fossa in the caudomedial corner of the dorsotemporal fossa.

Aves. The dorsotemporal fossa of birds is a wholly muscular structure, and there are no conspicuous fossae along the lateral and dorsal edges of the fossa that could be easily synonymized with the frontoparietal fossa of non-avian taxa. In palaeognaths (e.g., tinamous, ostrich), *m. pseudotemporalis superficialis* is the only muscle in the dorsotemporal fossa (Elzanowski, 1987; Holliday and Witmer, 2007). In galloanserines, bellies of *m. adductor mandibulae externus profundus*, *medialis*, and *superficialis* occupy the dorsotemporal fossa, whereas *m. pseudotemporalis superficialis* is restricted to the rostroventral (orbital) surface of the laterosphenoid. In many neoavians, *m. pseudotemporalis* is found deep to bellies of *m. adductor mandibulae externus profundus* in the rostromedial portion of dorsotemporal fossa. Galliforms do possess a moderately sized fossa on the rostrorodorsal portion of the cranium, rostral to the dorsotemporal fossa that could be interpreted as a frontoparietal fossa, but instead this fossa is the attachment for *m. cucullaris capitis*, a large, flat muscle that attaches to the integument of the head and neck. Although this muscle is likely present in all birds (Vanden Berge and Zweers, 1993), it only appears to leave a large osteological correlate in galliforms.

In birds, three parallel sets of vasculature pass through the temporal region. Laterally, the auricular rete, formed by the auricular vessels (Porter and Witmer, 2016), passes lateral to the quadrate and jaw muscles, sometimes spanning a large superficial temporal vessel dorsally over the musculature to the supraorbital region and skull roof (e.g., *Meleagris*, Fig. 3) that supplies the carunculate skin. The auricular rete also ultimately anastomoses with blood vessels of the orbit but also communicates with the

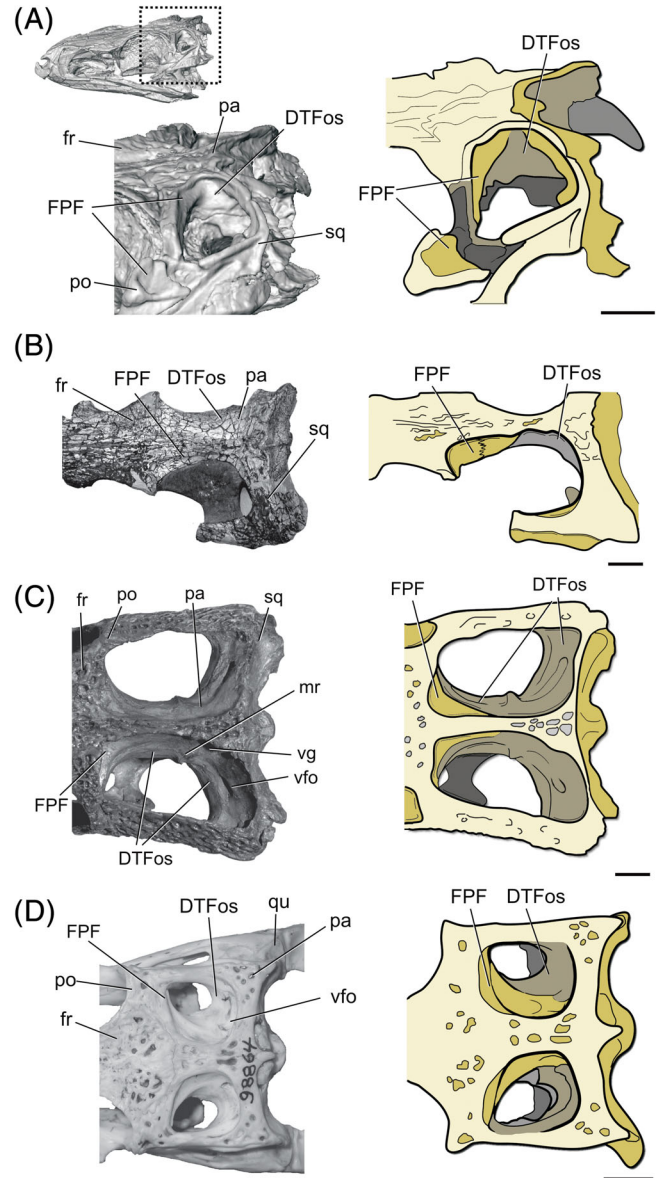


Fig. 4. Anatomy of the skull roof in exemplar pseudosuchian species illustrating the enlarged frontoparietal fossae in the lineage in the left, dorsal view. (Left) Photographs and surface renders of specimens. (Right) Schematic drawing illustrating critical features. (A) *Gracilisuchus* (MCZ 4117). (B) *Eopneumatosuchus* (MNA V2460). (C) *Pelagosaurus* (NHMUK R32599). (D) *Gavialis* (FMNH 99864).

facial artery which supplies the skin of the face and nasal regions, as well as the snood in turkeys. These vessels do not leave noticeable evidence of their presence on the skull. Internally, the ophthalmic rete (an arteriovenous vascular device derived from by the stapedial vessels; Baumel, 1993; Porter and Witmer, 2016) passes between *m. pseudotemporalis superficialis* and *m. adductor mandibulae externus profundus* in virtually all birds (Holliday and Witmer, 2007; Porter and Witmer, 2016). The rete often leaves a fossa on the ventral surface of the laterosphenoid buttress in galliforms and a small fossa on the ventral surface of the postorbital process of anseriforms. However, they

leave no evidence on the dorsotemporal fossa. Finally, dorsomedially, many avian taxa have large occipital vessels that pass caudal, dorsal, and medial to the jaw muscles that supply the skin of the skull roof. These occipital, superficial temporal, supraorbital, and facial vessels can all supply cranial display structures in birds such as wattles, combs, snoods, and carunculate skin. These vessels often leave grooves, pits, and channels near areas of specialized integument, as well as on the skull roofs of species that lack specialized structures.

Distribution of the frontoparietal fossae in fossil archosaurs.

The archosauriforms *Chanaresuchus* (MCZ 4039) and *Proterochampsa* (MCZ 3408) both possess shallow frontoparietal fossae. Phytosaurs do not possess fossae similar to these other stem taxa. Basal pseudosuchians including *Ornithosuchus* (NHMUK R2409), *Hesperosuchus* (CM 29894), and *Gracilisuchus* (MCZ 4117; Fig. 4A) also possess small, crocodylian-like frontoparietal fossae. Similar fossae are present in many fossil crocodyliforms including thalattosuchians (e.g., *Pelagosaurus* [NHMUK R32599]), notosuchians (e.g., *Araripesuchus* [AMNH 24450]; *Notosuchus* [MACN PV RN1041, MACN PV N22]), *Sebecus* (AMNH 39734), dyrosaurids (e.g., cf. *Rhabdognathus* [CNRST-SUNY-190]) (Fig. 4). Other crocodyliforms excavate relatively extreme portions of their skull roofs, further supporting the inferences of the vascular nature of the frontoparietal fossa. The basal crocodyliform *Eopneumatosuchus* (MNA V2460) has a large, shallow frontoparietal fossa which extends dorsal to the orbit (Fig. 4D). In contrast, some larger *Notosuchus* specimens have vascular correlates which form a deep sulcus caudally towards the occipital region, a reverse of the situation seen in most other crocodyliforms. The eusuchians *Aegisuchus* (Holliday and Gardner, 2012) and *Mourasuchus* (Bona et al., 2013) have deep vascular grooves that emerge from the dorsotemporal fenestra onto the skull roof. These features and their distribution suggest that vasculature significantly contributes to the morphology of the rostral borders of the dorsotemporal fossa throughout early archosaur and pseudosuchian evolution (Fig. 4).

The size and shape of the frontoparietal fossa vary considerably in different non-avian dinosaur taxa. Basal dinosaur taxa, including *Herrerasaurus* (PVSJ 407), *Eoraptor* (PVSJ 512), *Buriolestes* (CAPPA/UFMS 0035, Müller et al., 2018), *Plateosaurus* (AMNH 6810), *Scelidosaurus* (NHMUK R1111), and *Lesothosaurus* (NHMUK RU B.23), have relatively broad, flat fossae bordering the rostral boundary of the dorsotemporal fossa (Figs. 1 and 5). The basal ornithopod *Hypsilophodon* (e.g., NHMUK R197; Galton, 1974) has a very small indentation on the rostral margin of the dorsotemporal fenestra and *Hypacrosaurus* (Fig. 5F) and other derived ornithopods can possess small, paired fossae between the muscular portion of the fossa, the frontoparietal suture, and bony crests (*sensu* Ostrom 1961). The pachycephalosaur *Homalocephale* (Marynańska and Osmólska 1974; i.e., *Prenocephale sensu* Longrich et al., 2010) has small, incipient triangular frontoparietal fossae near the rostralateral corner of the dorsotemporal fenestra. However, structures clearly attributable to a frontoparietal fossa are absent in other pachycephalosaur, thyrophorans, and derived sauropods.

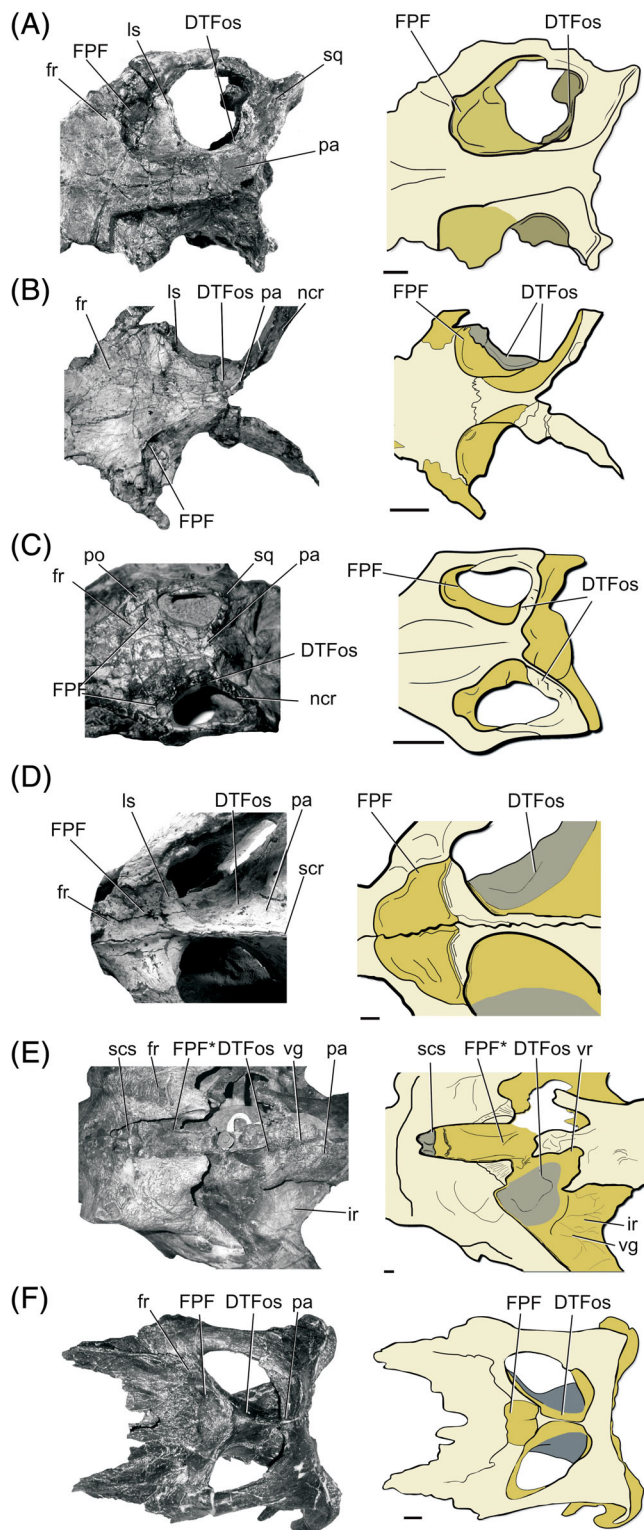


Fig. 5. Anatomy of the skull roof in exemplar basal and ornithischian dinosaur taxa in the left, dorsal view. ((Left) Photographs of specimens. ((Right) Schematic drawing illustrating critical features. (A) *Herrerasaurus* (MCZ 7063). (B) *Plateosaurus* (AMNH 6810). (C, D) *Lesothosaurus* (NHMUK RU B.23). (D) *Protoceratops* (IGM 100/1246). (E) *Styracosaurus* (CMN 344). (F) *Hypacrosaurus* (MOR 553S).

At least some ceratopsians also bear comparable frontoparietal fossae on their skull roofs. The basal ceratopsians *Yinlong* (Xu et al., 2006b), *Auroraceratops* (You et al., 2005), *Archaeoceratops* (You and Dodson, 2003), and *Leptoceratops* (NMC 8889) possess shallow frontoparietal fossae on the dorsal surface of the laterosphenoid that leave a distinct crests along the dorsal surface of the frontal similar to those found in other basal dinosaur species. In *Protoceratops* (e.g., IGM 100/1246), the fossae are larger and creep up on either side of the lateral surface of the sagittal crest where they are bounded rostrally by faint crests separating the smooth fossa caudally from the rugose, integumentary surface of the frontals dorsal to the orbits (Fig. 5D). However, this morphology does not negate the homology of these fossae with those of other basal ceratopsians and dinosaurs (Fig. 5. Although derived ceratopsians greatly elaborated and excavated the portions of their rostral dorsotemporal fossae into large supracranial cavities (i.e., supracranial sinus) (Fig. 5B,C; Hatcher et al., 1907; Forster, 1996; Sampson et al., 1997; Farke, 2006; Farke, 2010), it does not appear that the frontoparietal fossae are homologous to these sinuses (e.g., Fig. 5, FPF*). It remains unclear how the frontoparietal fossa relates to the supracranial cavity during the evolution of the lineage.

Among theropod dinosaurs, coelophysoids including *Syntarsus kayentakatae* (MNA V2623) and *Coelophysis bauri* have large, shallow frontoparietal fossae that extend onto the skull roof. Ceratosauroids including *Ceratosaurus* (NMNH 4735) and *Majungasaurus* (FMNH PR 2100) have rostrocaudally short, dorsoventrally deep, step-like fossae that extend rostral from the dorsotemporal fossa proper but do not extend onto the skull roof as in many other theropods (Fig. 7). Some allosauroids including *Allosaurus* and *Acrocanthosaurus* (NCSM 14345) have large, shallow ovate frontoparietal fossae that extend onto the skull roof (Fig. 7). On the other hand, *Carcharodontosaurus* (SGM Din-1) has a large, ovate, dorsally facing frontoparietal fossa separated from the dorsotemporal fossa by a distinct vertical ridge. Among ornithomimids, the isolated frontals of *Struthiomimus* (AMNH 5355) possess a clearly defined shallow fossa in the position of other theropods, which is fairly typical for other ornithomimids (e.g., *Dromiceiomimus*, CMN 12228; *Ornithomimus*, TMP 95.110.1; *Gallimimus*, IGM 100/1133). Tyrannosaurs have large, shallow, dorsally facing fossae separated from the dorsotemporal fossa by prominent crests (Currie, 2003; Fig. 6). The basal oviraptorosaur *Avimimus* (ROM 46144) has a small ovate frontoparietal fossa on the rostromedial corner of the dorsotemporal fenestra whereas derived species including *Citipati* (IGM 100/978) and *Conchoraptor* (IGM 100/3006) lose clear frontoparietal fossae but maintain a slight, triangular depression on the skull roof that melds with the dorsotemporal fossa. Among maniraptorans, some specimens of *Velociraptor* (e.g., IGM 100/25) have small, ovate, deep, caudodorsally facing fossae rostradorsal to the dorsotemporal fossa (Currie, 1995; Barsbold and Osmólska, 1999), whereas *Tsaagan* (IGM 100/1015) has small but identifiable frontoparietal fossae and *Deinonychus* (MOR 747) has large, shallow ovate fossae that extend onto the skull roof. Troodontids including *Latenivenatrix* (CMN 12340, TMP 82.19.23, TMP 79.8.1) have rather large, shallow fossae that extend up onto

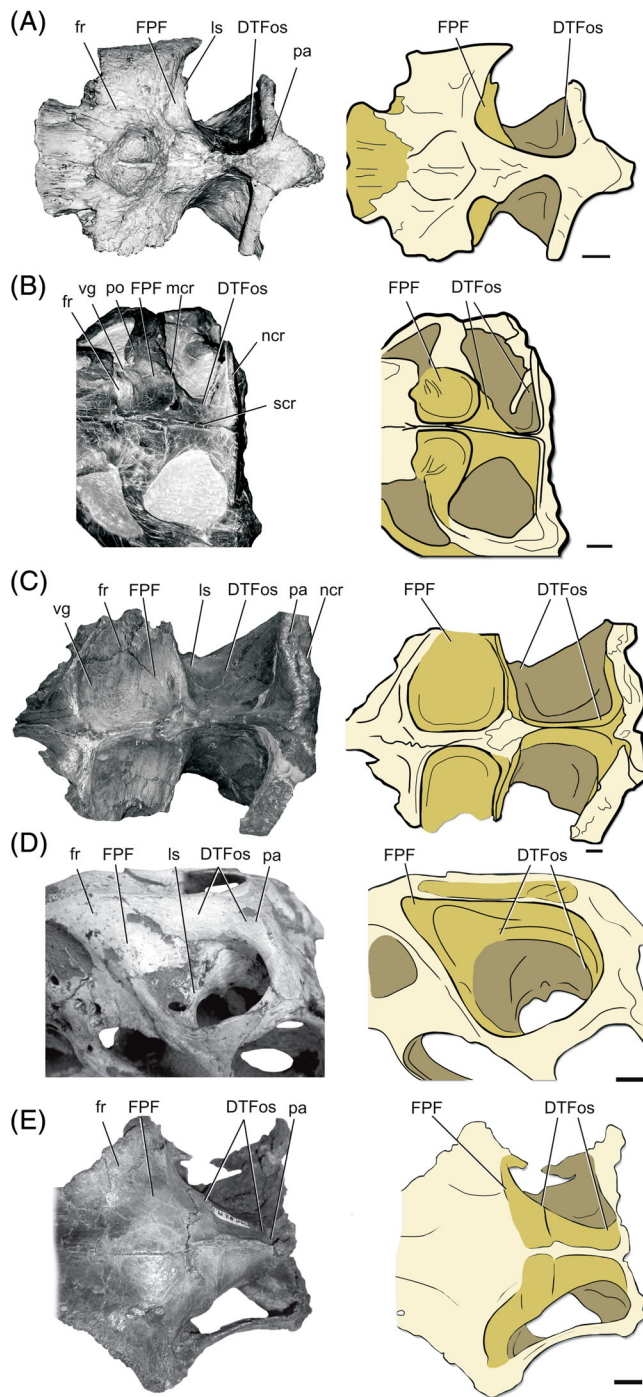


Fig. 6. Anatomy of the skull roof in exemplar non-avian theropod dinosaur taxa in the left, dorsal view. (Left) Photographs of specimens. (Right) Schematic drawing illustrating critical features. (A) *Majungasaurus* (FMNH PR2100). (B) Juvenile tyrannosaurid (CMNH 7541). (C) *Tyrannosaurus* (AMNH 5117). (D) *Citipati* (IGM 100/978). (E) *Latenivenatrix* (TMP 82.19.23).

the skull roof (Fig. 6). *Archaeopteryx* and other Avialans do not appear to possess any identifiable fossae, but preservation of many of these smaller bodied taxa impedes clear diagnosis.

DISCUSSION

Homology

The extreme diversity of morphologies present among some dinosaurs, particularly in tyrannosaurs and ceratopsids, make clear hypotheses of homology seemingly difficult to test. Regardless, evidence from crocodylomorphs, which have the most similar looking fossae and unequivocal causally associated bone-soft-tissue relationships, combined with the similarity of these structures among stem archosaurs, suggests that the frontoparietal fossae of dinosaurs are homologous and excavated by the same tissues. The consistent distribution of the frontoparietal fossa among non-avian theropods, basal sauropodomorphs, and basal ornithischians suggests that the structures are not only phylogenetically congruent but also plesiomorphic for Dinosauria (Fig. 7). Moreover, the presence of a frontoparietal fossa in basal archosauriforms including *Chaneresuchus* (MCZ 4039) and *Proterochampsa* (MCZ 3408), and then also basal pseudosuchians and dinosaurs, suggests that the structure may be plesiomorphic and ubiquitous not just for Archosauria but also for Archosauriformes as a whole.

The Frontoparietal Fossa Is Not a Site of Muscle Attachment

The proximity of the frontoparietal fossa to the dorsotemporal fossa led many paleontologists to infer that the space was occupied by temporal muscles (e.g., Molnar, 2008; Coria and Currie, 2002; Gignac and Erickson, 2017). However, the frontoparietal fossa does not bear any other osteological features that clearly identify it as a muscular attachment. First, aponeurotic attachments, which are common in sauropsid jaw muscles (Holliday and Witmer, 2007 and references therein) often leave prominent ridges or crests that are oriented toward the muscle's mandibular attachment, such as those found on crocodyliform quadrates (e.g., *m. adductor mandibulae posterior*), avian parietals (e.g., *m. adductor mandibulae externus profundus*), or on sagittal and nuchal crests in many non-avian dinosaurs, lizards, turtles, and mammals. The rostral surface of the frontoparietal fossa, however, is smooth and faces dorsally in many basal theropods (e.g., *Majungasaurus*, *Allosaurus*). In tyrannosaurs, the caudal edge of the frontoparietal fossa (or rostral edge of the dorsotemporal fossa) is angled sharply vertically creating a physical obstacle for a muscle belly to cross, rather than the excavated, concave fossa one would expect to find where a muscle belly was passing. The fossa in ceratopsids ranges from smooth excavations of the caudal edge of the frontal, medial to the dorsotemporal fossa, to expansive, smooth surfaces that depart greatly from normal muscle attachment regions which often merge at the midline of the skull and continue into the supracranial cavity (Hatcher et al., 1907; Sampson et al., 1997; Farke, 2010).

Second, there is no evidence of a tendon organ or sesamoid (Benjamin and Ralphs, 1998; Summers and Koob, 2002; Tsai and Holliday, 2011). Many animals develop sesamoids and trochleae where jaw muscles wrap over bony surfaces of the skull including elasmobranch fish (Summers et al., 2003), testudines (Gaffney, 1979; Rieppel, 1990), crocodyliforms (Schumacher, 1973; Busbey, 1989;

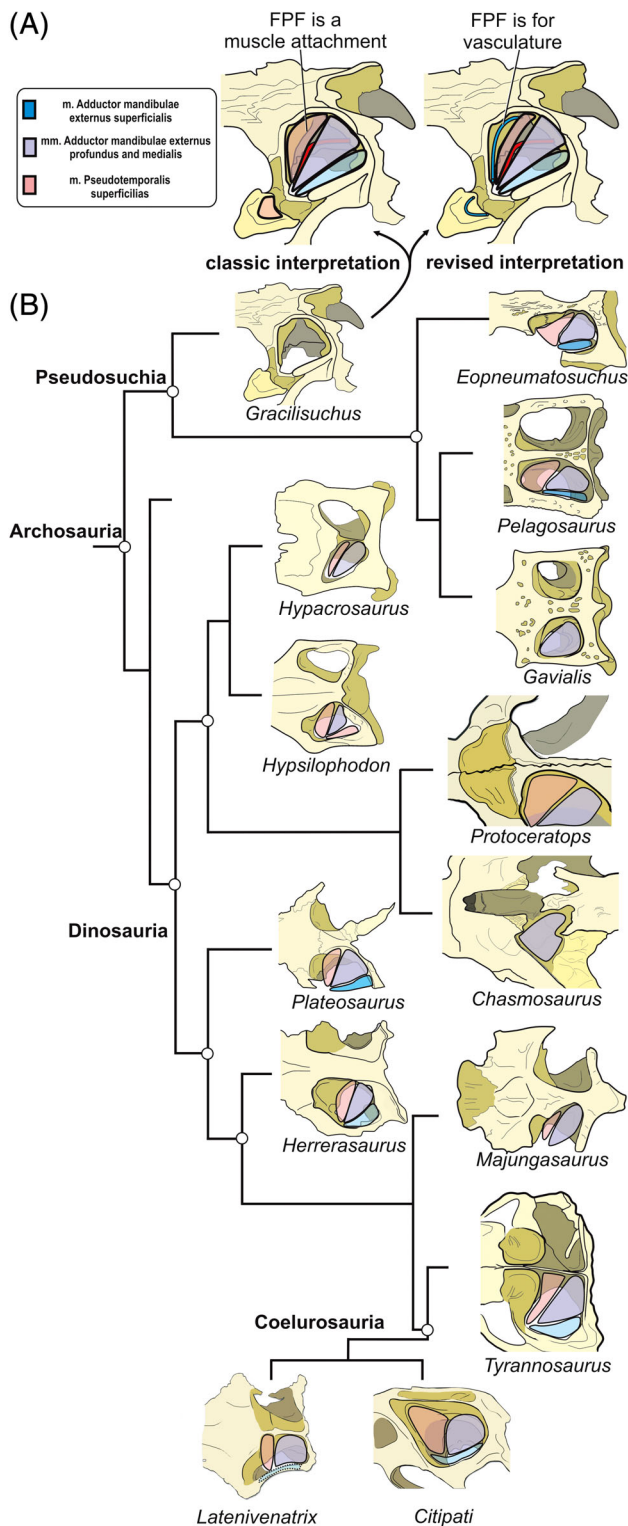


Fig. 7. Phylogenetic distribution of skull roof structures in archosaurs with hypothesized muscle anatomy of the dorsotemporal fossa. (A) Classical interpretation, or lepidosaur-like interpretation of muscles attaching to frontoparietal fossa versus revised interpretation of vasculature excavating frontoparietal fossa using the basal pseudosuchian *Gracilisuchus* (MCZ 4117) as an example. (B) Cladogram depicting general evolutionary patterns in temporal muscle attachments in archosaurs.

Tsai and Holliday, 2011), and cormorants. In each case, a fibrous or fibrocartilaginous sesamoid forms where the muscle experiences compression as it wraps around parts of the skull. The sesamoid is then complemented by a bony trochlea, such as in the pterygoid buttress in crocodyliforms, the prootic trochlea in some turtles, and the squamosal trochlea in cormorants (Fig. 8). These trochleae are common, robust osteological correlates of sesamoids and are absent in the skull roofs of fossil archosaurs.

In all the above extant examples of sesamoids, the resting angulation of the muscle belly as it wraps around the bone is obtuse, ranging between 120 degrees (*Chelydra*) to 160–170 degrees (*Alligator*; Fig. 8). During jaw opening, these angles change only minimally. A muscle attaching in the frontoparietal fossa would wrap around the dorsal surface of the laterosphenoid buttress as it passes toward the coronoid process, which is the expected attachment for *m. pseudotemporalis superficialis* or *m. adductor mandibulae externus profundus* (Fig. 8). This reconstruction requires a highly acute angle of muscle wrapping (~60–70 degrees) in *Tyrannosaurus* (Fig. 10A), *Majungasaurus*, *Velociraptor*, and *Herrerasaurus* as well as in other taxa, such as *Diplodocus*, that do not have distinct frontal fossae but still maintain highly angled dorsotemporal fossae (Fig. 8). In *Carcharodontosaurus*, the muscle would have had to have made a hairpin turn (i.e., ~180 degrees) around the ventral edge of the laterosphenoid buttress to reach its mandibular attachment. These data suggest that, were there a muscle present, there should be a tendon organ and therefore a bony trochlea. Biomechanically, even if *m. adductor mandibulae externus profundus* or *m. pseudotemporalis superficialis* muscle attached into the frontoparietal fossa (e.g., Molnar, 2008; Coria and Currie, 2002), its orientation would render it functionally equivocal if not entirely useless compared to a scenario where there was not any muscle attaching there at all.

The Frontoparietal Fossa Is Not Primarily a Pneumatic Structure

The extreme morphologies found in basal tetanurans, tyrannosaurs, dromaeosaurs, and ceratopsids clearly indicate that muscle is not the soft tissue responsible for the shape of the frontoparietal fossa. Likewise, invoking pneumaticity as a general explanation requires the identification of a likely source for the air-filled diverticulum excavating the fossa. For example, the frontoparietal fossae of large ceratopsids communicate with the supracranial sinuses, which indeed bear many of the hallmarks of pneumaticity (e.g., smooth-walled, multichambered cavities; Farke, 2010). How the frontoparietal fossa and supracranial sinuses were ventilated, however, is difficult to determine (Witmer, 1997; Sampson et al., 1997; Farke, 2010). Farke (2010) presented the most complete and honest appraisal of this problem but left the question of the source of the diverticulum open, a position with which we concur for the present. Finally, hypotheses of pneumaticity in the frontoparietal fossae of non-ceratopsid archosaurs do not bear any support, and thus, regardless of the situation with ceratopsids, pneumaticity cannot be a general explanation.

The Frontoparietal Fossa Houses Vasculature

Although hypotheses pertaining to muscles and air sinuses can be falsified by available evidence, the presence

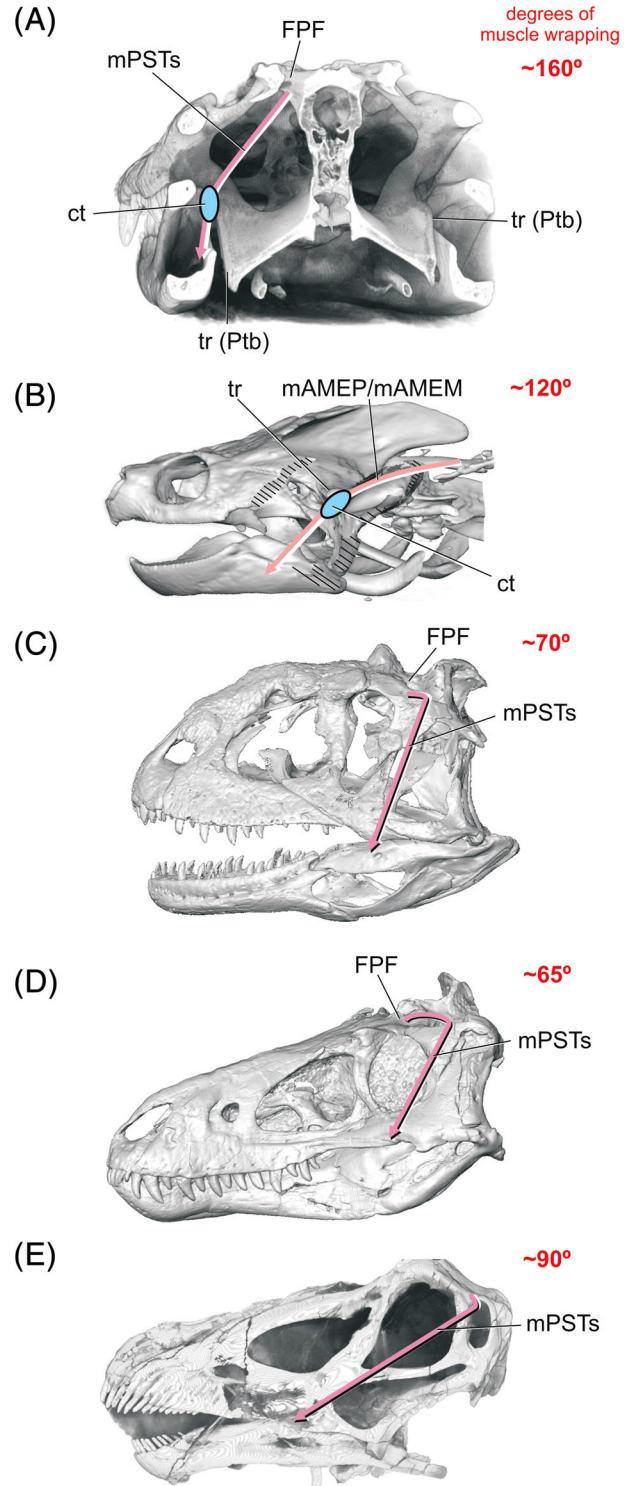


Fig. 8. Hypotheses of muscle attachments in the frontoparietal fossa require extreme angles of muscles which should produce the formation of sesamoids and trochleae. There is no evidence of sesamoids near the frontoparietal fossa supporting the inference of vasculature instead. Surface and voxel renders of skulls: (A) *Alligator*, caudal view of axial section through trigeminal foramen and dorsotemporal fenestra; (B) *Chelydra* (OUVC 10397) in the left, lateral view; (C) *Majungasaurus* (FMNH PR2100) in the left lateral view; (D) juvenile tyrannosaurid (CMNH 7541) in the left, lateral view; (E), *Diplodocus* (CM 3452) in the left, lateral view.

of vasculature is a well-supported inference of soft tissue in the frontoparietal fossa. As demonstrated above, the soft-tissue structures known to occupy the frontoparietal fossae in extant crocodylians are the temporo-orbital vessels. Likewise, although the bony temporal region is highly transformed in extant birds, these same homologous vessels are present in the homologous region. The presence of topologically similar fossae in dinosaurs as those found in extant relatives supports the hypothesis that the temporo-orbital vessels are similarly present (Fig. 9). Moreover, the elaborated morphologies of the frontoparietal fossae in many taxa suggest these structures may have also housed elaborated vascular structures necessary for the development of vascular rete or integumentary structures. Vascular devices in extant taxa, such as the postorbital venous rete in crocodylians (Fig. 2; Porter et al., 2016) or the ophthalmic rete in birds (Porter and Witmer, 2016) are complicated networks of arterioles and venules in close proximity that are encapsulated in a mass of connective and adipose tissue that is further surrounded by adipose tissue. These retia tend not to leave grooves on bones but instead occupy a large fossa on the postorbital bar in crocodylians and the ventral surface of the postorbital process in anseriforms. These morphologies are similar to that found in the frontoparietal fossae in dinosaurs (Fig. 10B), but it remains challenging to provide clear evidence for the positive inference of their presence. A key point to note with regard to vascular osteological correlates (e.g., grooves, canals, foramina) is that there is the expectation that they will be variable both interspecifically and intraspecifically as well as often discontinuous in that whether or not a blood vessel produces a bony signature depends simply on whether it is adjacent to bone (Porter and Witmer, 2015); that is, a vessel could be present, but if it were not pressed against the bone, there may be no record of it.

That caveat aside, there is ample evidence to establish broad patterns of blood flow. For example, the frontoparietal fossae in some larger tyrannosaurids (e.g., *Daspletosaurus*, TMP 2001.36.1, CMN 11594; FMNH PR2081) are perforated by numerous foramina and erosional pits in the skull roof suggesting minimally transient anastomoses with the underlying bony tissues. More significantly, the frontoparietal fossae in many tyrannosaur specimens have clear vascular grooves that communicate with the orbit through canals deep to the postorbital boss or osteoderm (e.g., *Tyrannosaurus rex*, FMNH PR 2081, AMNH FR 5027, MOR 008), directly with the orbital margin (CMNH 7541), and possibly channels through the skull roof sutures in *Albertosaurus* (TMP 81.39.08), cf. *Tyrannosaurus* (CMN 11841), and other specimens (Figs. 6 and 8). Specimens of other, more basal theropods, such as some *Allosaurus* specimens (e.g., MOR 693) show similar vascular grooves emerging from the orbit onto the skull roof near, but not clearly entering, the frontoparietal fossa; again, these vessels may have indeed entered the frontoparietal fossa region in life but simply were not close enough to the bone to leave osteological correlates. The muscular portion of the dorsotemporal fossa in ceratopsids is not only flanked by the frontoparietal fossae (i.e., frontal fontanelle) but also surrounded by vascular grooves that radiate up the frill (Fig. 5). Given the vascular pattern in extant diapsids (Porter and Witmer, 2015, 2016; Porter et al., 2016), this vascular anastomosis between the dorsotemporal and orbital regions is likely between the temporo-orbital and supraorbital vessels, respectively.

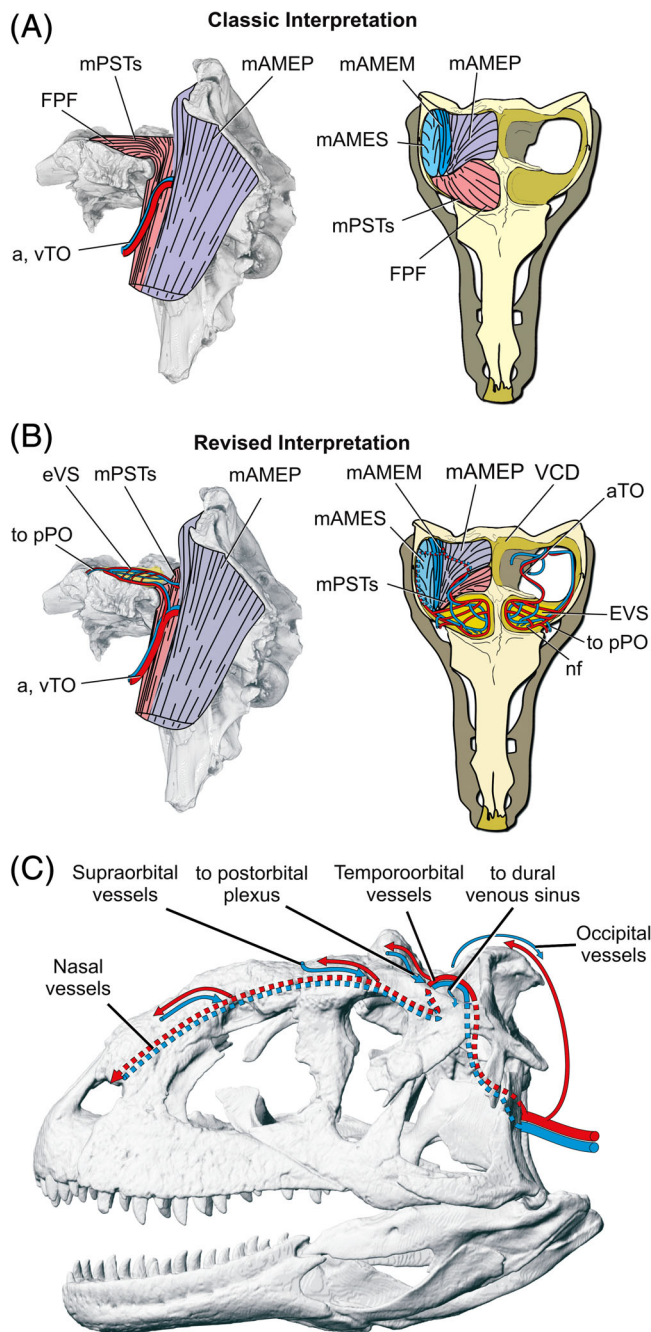


Fig. 9. Evidence presented here shows the classic interpretation that the frontoparietal fossa is a jaw muscle attachment can be rejected. Instead, the frontoparietal fossa likely housed vascular and adipose tissue. These vessels may have formed elaborated vascular structure that may have had significance for thermoregulation. (A) *Tyrannosaurus* (AMNH 5117) in the lateral and dorsal view showing classic, muscle hypothesis. (B) *Tyrannosaurus* (AMNH 5117) in the lateral and dorsal view showing revised, vascular hypothesis and communicating branches. (C) *Majungasaurus* (FMNH PR2100) in the left, lateral view illustrating skull roof vasculature and communicating branches of the frontoparietal fossa.

Thus, the vasculature within the frontoparietal fossa not only communicated with other vascular territories atop the dorsal surface of the skull but also with the orbit

through direct pathways. Moreover, there are potentially indirect routes to the endocranial region (and hence the encephalic or brain vasculature) through skull roof sutures and the vena capitis dorsalis (Sampson and Witmer, 2007; Witmer and Ridgely, 2009). In general, the temporo-orbital branches of the stapedia vessels and vena capitis dorsalis system, which are here inferred to have supplied or passed near the fossa, pass between the muscles of the dorsotemporal fossa (i.e., *mm. pseudotemporalis superficialis* and *adductor mandibulae externus profundus*) and communicate with the orbit *via* the supraorbital, infraorbital, and ophthalmotemporal vessels (and potentially any ophthalmic rete located between these branches), the brain (*via* the vena capitis dorsalis and trigeminal vessels), and the skin of the dorsal surface of the head (*via* the occipital, superficial temporal, supraorbital, and facial arteries (Figs. 3 and 8; Baumel, 1993; Sedlmayr, 2002; Holliday et al., 2006; Holliday, 2009; Porter et al., 2016; Porter and Witmer, 2016). In extant diapsids, many of these structures participate in a complicated vascular circuitry associated with regulating brain and eye temperature (e.g., Midtgård, 1984a, 1984b; Arad et al., 1987;

Sedlmayr, 2002; Porter et al., 2016; Porter and Witmer, 2016, this volume). It is likely that many dinosaur taxa also evolved similar vascular devices in this region of the head that communicated with other cephalic regions and formed a counter-current heat exchange system between the cranial integument and deeper tissues.

Significance for Thermal Physiology and Display

Having established (1) that the frontoparietal fossa likely evolved in connection with vascular specializations and (2) that these vessels anastomose with known regions of the head (orbit and potentially the brain), it is worth exploring what potential functions were at play, potentially even driving elaboration of these systems in certain clades (e.g., tyrannosaurs). One hypothesis is that these vascular pathways served a thermoregulatory function to selectively moderate eye and/or brain temperatures. We tested the hypothesis that the vessels of the dorsotemporal fossa of extant crocodylians are physiologically significant, to lend further support for our interpretations of dinosaur anatomy. Our pilot thermography data from St. Augustine Alligator Farm Zoological Park found that early in the morning ($\sim 10^{\circ}\text{C}$), the dorsotemporal fenestrae were among the warmest parts of the head. In several individuals, the circular holes of the fenestrae were conspicuously warmer than surrounding skull roof bone and the face (Fig. 11), indicating a possibility that warm blood can potentially exchange thermal energy. Later in the day, when ambient temperatures were warmer ($\sim 21^{\circ}\text{C}$), we recorded the fenestrae being conspicuously cooler than the surrounding bone and skull surface. These findings suggest that indeed the vasculature within the dorsotemporal fossa has the potential for thermoregulatory significance and could serve as a thermal window capable of heat exchange (e.g., Tattersall et al., 2009). Although more rigorous physiological data are necessary to further explore this phenomenon, we hypothesize that crocodylians could exchange thermal energy through these skull roof structures to regulate or buffer cephalic temperatures, yet other vascular devices in the orbit and palate (Porter and Witmer, 2016; Porter et al., 2016) are likely more efficient at dumping excess heat. If indeed the frontoparietal vasculature of dinosaurs, particularly giant ones like *Tyrannosaurus* (Fig. 8), were as capable of acting as thermoregulatory structures as they are in extant archosaurs, then we might expect elaborated vascular structures like those we describe here that could support thermal exchange.

Display structures also require vascular structures to grow and function properly. Many birds (e.g., various galloanserines, vultures, *Irediparra* [comb-crested jacana]) evolved elaborate vascular integumentary structures such as snoods, combs, wattles, carunculate skin, and other cavernous integumentary tissues (Lucas and Stettenheim, 1972; Stettenheim, 2000) that may carry behavioral or display significance. Moreover, the carunculate, featherless heads of turkeys have been found to aid in thermoregulatory adaptation to high-temperature environments, thereby increasing their available habitat (Buchholz, 1996). Although many of the larger, display structures (e.g., snoods, combs) are typically supplied by branches of the facial artery and vein (Fig. 3), the proximal portions of the stapedia-temporal system also supply the highly vascular, caruncular integument covering the cranium

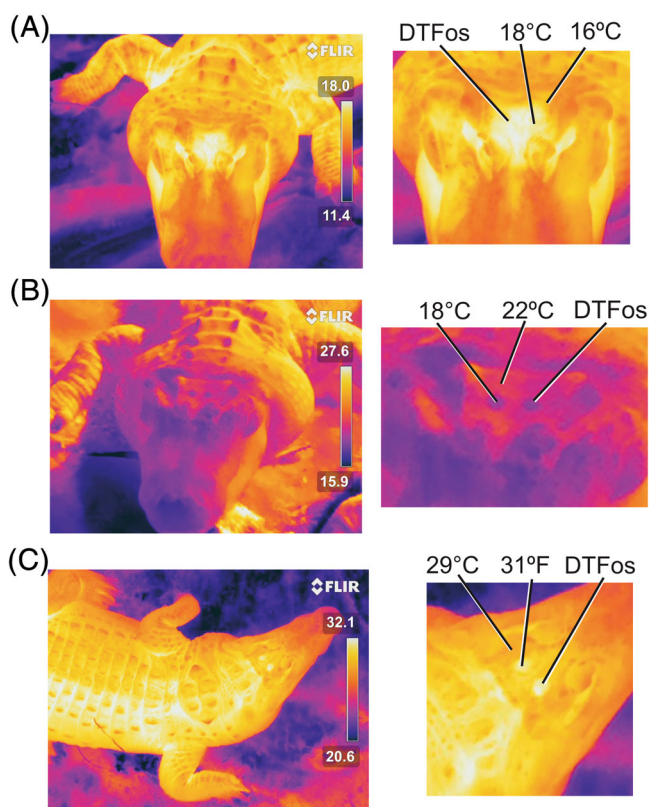


Fig. 10. Thermographic images of crocodylian skull roofs collected at St. Augustine Alligator Farm and Zoological Park suggest the dorsotemporal fossae may be physiologically significant, with blood vessels forming an elaborated vascular structure. (A) *Alligator mississippiensis*, mid-morning in sun, $\sim 15^{\circ}\text{C}$, showing warmer dorsotemporal fossae relative to head surface temperatures. (B) *Alligator mississippiensis*, later afternoon in shade, $\sim 26^{\circ}\text{C}$, showing cooler dorsotemporal fossae relative to head and body surface temperatures. (C) *Crocodylus mindorensis* showing relatively warm dorsotemporal fossae in sun, late morning, $\sim 24^{\circ}\text{C}$.

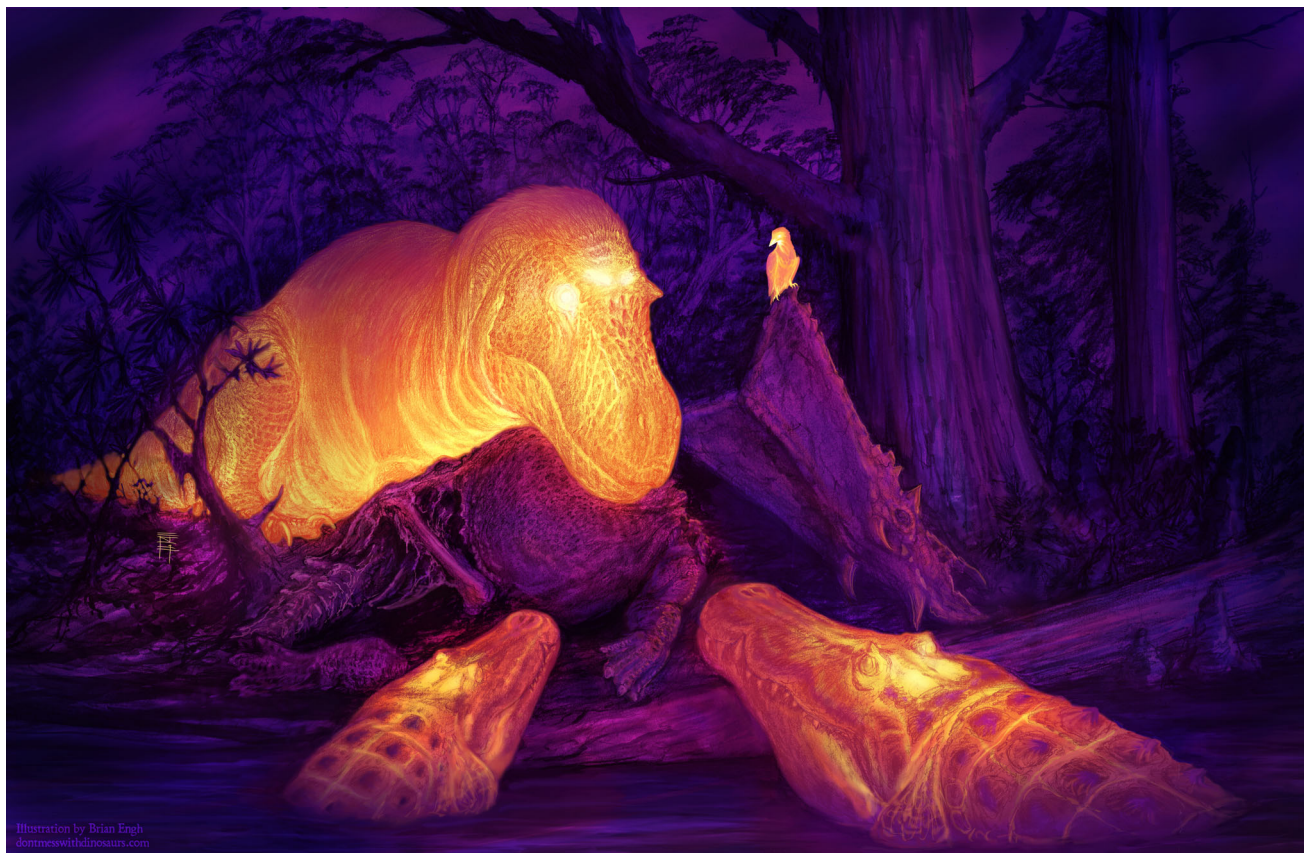


Fig. 11. *Breakfast in the Aguja* by Brian Engh. We glimpse into increasing tension about the corpse of a fallen ceratopsian, through a thermographic eye. Life reconstruction of *Daspletosaurus* and *Deinosuchus* in the early morning light of the Aguja Formation, Late Cretaceous, North America.

(Fig. 3). Among fossil archosaurs, elaborate vascular structures have been hypothesized in the skull roofs of crocodyliforms (Holliday and Gardner, 2012; Bona et al., 2013) that may have had roles in display behavior. Additionally, the crest of the pterosaur *Thalassodromeus* has vascular grooves emerging from the dorsotemporal fossa (Kellner and Campos, 2002) and the orbital region, suggesting extinct archosaurs may have been, like extant archosaurs, quite capable of supplying cranial ornamentation with vessels derived from the stapedia or temporal region. The knobby, vascularized excrescences, cornual processes, bosses, and flanges found in the supraorbital regions of theropod dinosaurs (e.g., *Allosaurus*, *Guanlong*, *Yutyrannus*, tyrannosaurids) also lend evidence that the vasculature of the frontoparietal fossa feed into ornamentation. Indeed, *Guanlong* is illustrated possessing a distinct frontoparietal fossa underlying its extravagant bony crest (Xu et al., 2006a). Thus, if the frontoparietal fossa was vascular, it is not beyond reason that non-avian dinosaurs and pterosaurs may have also possessed vascular integumentary structures supplied by the temporal vasculature.

CONCLUSION

These data suggest that the frontoparietal fossae of non-avian dinosaurs, pterosaurs, and fossil crocodyliforms are

most similar with those of extant crocodylians and most likely housed vasculature. The primitive archosaurian condition includes the presence of a modestly sized frontoparietal fossa. This hypothesis is supported by phylogenetic bracketing, several vascular osteological correlates, and a suite of characteristics that reject the prevailing hypothesis that the fossa is a muscle attachment. Although an unequivocal functional hypothesis is difficult to determine without extraordinary evidence such as a preserved soft-tissue integumentary structure, clear evidence from extant taxa indicate the necessary blood vessels were present in the temporal region to provide the foundation for a vascular physiological device or display structure.

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