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Femoral metadiaphyseal and nutrient foramen perfusion suggests similar maximal metabolic rates in a pterosaur and in a semi-aquatic maniraptoran dinosaur

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Ornithodirans represent a diverse and highly successful clade that encompasses a wide array of morphologies and ecological adaptations.This group includes volant forms such as the Jurassic long-tailed pterosaur *Rhamphorhynchus* , a derived non-pterodactyloid species. It was a medium-sized that foraged extensively in Solnhofen lagoons, piscivorous pterosaur characterized by a prow-shaped lower jaw and procumbent teeth.Additionally, it comprises theropod dinosaurs such as *Halszkaraptor escuilliei* , a dromaeosaurid from Mongolia that exhibits exhibits morphological traits suggesting a semi-aquatic lifestyle. In this study, we evaluated the aerobic performance of these two extinct ornithodirans by using femoral metadiaphyseal nutrient foramen dimensions as a proxy for maximal metabolic rate (MMR), based on an extant-amniote dataset of reference. Through the femoral artery dimensions, we estimated femoral blood flow ($\dot{Q}$) and retrodicted mass-independent MMR for both *Halszkaraptor escuilliei* and a juvenile individual of *Rhamphorhynchus* . Our findings reveal similar femoral blood flow rate and mass-independent MMR values between the taxa, despite their extreme differences in ontogeny, lifestyle, locomotory behavior and ecosystem. The juvenile *Rhamphorhynchus* displays an elevated MMR inflated due to elevated femoral perfusion associated with growth demands. While for the *Halszkaraptor escuilliei* , the predicted mass-independent MMR aligns with values observed in extant ground-dwelling emus and migratory shorebirds such as gulls and terns, but it falls below the high MMR value in ducks. Further investigation into adult specimens of *Rhamphorhynchus* is needed to refine our understanding of aerobic capacity in non-pterodactyloid pterosaurs, particularly regarding their ability to sustain powered flight and takeoff. This study advances knowledge on the physiological strategies of extinct taxa, filling gaps in paleophysiological reconstructions.

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Abstract

Ornithodirans represent a diverse and highly successful clade that encompasses a wide array of morphologies and ecological adaptations. This group includes volant forms such as the Jurassic long-tailed pterosaur *Rhamphorhynchus*, a derived non-pterodactyloid species. It was a medium-sized that foraged extensively in Solnhofen lagoons, piscivorous pterosaur characterized by a prow-shaped lower jaw and procumbent teeth. Additionally, it comprises theropod dinosaurs such as *Halszkaraptor escuilliei*, a dromaeosaurid from Mongolia that exhibits exhibits morphological traits suggesting a semi-aquatic lifestyle. In this study, we evaluated the aerobic performance of these two extinct ornithodirans by using femoral metadiaphyseal nutrient foramen dimensions as a proxy for maximal metabolic rate (MMR), based on an extant-amniote dataset of reference. Through the femoral artery dimensions, we estimated femoral blood flow ($\dot{Q}$) and retrodicted mass-independent MMR for both *Halszkaraptor escuilliei* and a juvenile individual of *Rhamphorhynchus*. Our findings reveal similar femoral blood flow rate and mass-independent MMR values between the taxa, despite their extreme differences in ontogeny, lifestyle, locomotory behavior and ecosystem. The juvenile *Rhamphorhynchus* displays an elevated MMR inflated due to elevated femoral perfusion associated with growth demands. While for the *Halszkaraptor escuilliei*, the predicted mass-independent MMR aligns with values observed in extant ground-dwelling emus and migratory shorebirds such as gulls and terns, but it falls below the high MMR value in ducks. Further investigation into adult specimens of *Rhamphorhynchus* is needed to refine our understanding of aerobic capacity in non-pterodactyloid pterosaurs, particularly regarding their ability to sustain powered flight and takeoff. This study advances knowledge on the physiological strategies of extinct taxa, filling gaps in paleophysiological reconstructions.

Keywords: aerobic performance, dinosaur, maximum oxygen consumption, metabolic rate, pterosaur.

Introduction

Maximal metabolic rate (MMR), also referred to as the maximal rate of oxygen consumption (VO2max), represents the highest aerobic metabolic rate achieved during exercise and defines the upper limit of sustained metabolic performance (Bennett & Ruben, 1979; Weibel et al., 2004). In extant amniotes, MMR can be directly measured during physical activity using a circuit respirometer. For volant taxa, this involves measurements during forced flight (Hails, 1979; Norberg, 1996), while for terrestrial species, metabolic rates are assessed using treadmill running (Fedak et al., 1974; Taylor et al., 1982; Seymour et al., 2008). For swimming amniotes such as ducks, penguins and sea turtles, MMR is measured in controlled-flow swim channels (Prange & Schmidt-Nielsen, 1970; Prange 1976; Kooyman & Ponganis, 1994).

In extinct archosaurs, reconstructing maximal aerobic capacity has posed significant challenges, leading to the development of indirect methods based on fossilized bone structures (Seymour et al., 2012; Knaus et al., 2021; Varela et al., 2024). Among various methodologies, the "foramen technique" (Seymour et al., 2012), has proven particularly effective. This approach estimates regional blood flow by measuring the size of foramina in long bones. Since long bones require blood perfusion for remodeling, which repairs microfractures induced by locomotion and weight-bearing stresses (Lieberman et al., 2003; Eriksen, 2010), nutrient foramen size provides a useful proxy for bone perfusion and aerobic capacity. A nutrient artery transpasses the femoral shaft through the nutrient foramen, typically accompanied by a vein (Currey, 2002), and the size of the foramen correlates dynamically with the size of the vessels it contains. The maximal metabolic rate is therefore tied to the size of the nutrient artery and the corresponding blood flow supplying the bone (Seymour et al., 2019). In mature terrestrial vertebrates, femoral blood flow is positively correlated with locomotor activity levels, with relatively larger nutrient foramina occurring in species with elevated metabolic rates during locomotion (Allan et al., 2014; Newham et al., 2020). According to Seymour et al. (2012), the proximate causation of this relationship would be linked to the fact that tetrapods with high activity levels undergo biomechanical constraints producing microfractures that are repaired through secondary (Haversian bone) remodelling necessitating high oxygen consumption. The application of phylogenetic eigenvector maps (PEMs; Guénard et al., 2013) to reconstruct metabolic rates in extinct amniotes has been adopted in the last decade (Legendre et al., 2016; Fleischle et al., 2018; Cubo et al., 2024). PEMs provide a framework to infer the metabolic profiles of extinct organisms by integrating phylogenetic and morphological data. When combined with the foramen technique, PEMs have been used to estimate mass-independent MMR in other archosaur group, extinct pseudosuchians (Cubo et al. 2024; Sena et al., 2023; 2025).

In this study, we used these methods by integrating a comprehensive phylogenetic amniote database with their corresponding nutrient artery blood flow measurements computed using the foramen technique and the previously measured MMR values. This combined approach is applied to retrodict the mass-independent MMR of two extinct ornithodirans with extremely different lifestyle and locomotory behaviors: a Jurassic pterosaur and a Cretaceous dromaeosaurid. Specifically, we focus on *Rhamphorhynchus*, a basal, medium-sized, piscivorous pterosaur from the Late Jurassic Plattenkalks of southern Germany. Characterized by a prow-shaped lower jaw and forward-angled (procumbent) teeth, *Rhamphorhynchus* was well-adapted for foraging extensively in aquatic environments (Voeten et al., 2018; Witton et al., 2018) and *Halszkaraptor escuilliei*, a Late Cretaceous dromaeosaurid theropod hypothesized to possess an amphibious ecomorphology, potentially relying on neck hyperelongation for predatory foraging (Cau et al., 2017; Cau, 2020). We aim to elucidate the metabolic capacities of these two ornithodirans.

Institutional Abbreviations

MdC, Musée des Confluences, Lyon, France. MPC, Institute of Paleontology and Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia.

Add your introduction here.

Materials & Methods

Material and foramen measurements

We examined the 3D models of the basal pterosaur *Rhamphorhynchus* sp. MdC 20269891 from Solnhofen Plattenkalk, Germany (Upper Jurassic) and the theropod *Halskaraptor escuilliei* MPC D-102/109 from Djadokhta Formation, Mongolia (Campanian). These fossils were imaged using propagation phase-contrast synchrotron microtomography at the European Synchrotron Radiation Facility for previous microanatomical and morphological investigations (Cau et al., 2017; Voeten et al., 2018).

Metadiaphyseal and nutrient foramina openings were measured from the 3D reconstructions of H. escuilliei and *Rhamphorhynchus* sp. The foramina areas found on the femora were measured with ImageJ/Fiji (Schindelin et al., 2012) (https://imagej.net/Fiji). For comparative purposes, we assumed that the foramen area was the same as that of a geometric circle. To estimate nutrient artery blood flow rate ($\dot{Q}$; ml s-1) in the femora we applied the curved polynomial equation:

$\log \dot{Q} = -0.20 \log r_i2 + 1.91 \log r_i + 1.82$ (Seymour et al., 2019),

where r_i is the arterial lumen radius extracted from the arterial lumen area which corresponds to about 20% of the total foramen area (Hu et al., 2022).

Maximal Metabolic rate retrodictions and recovered unit

To retrodict the mass-independent MMRs of the fossil taxa we constructed a phylogenetic inference model where the dataset of extant species was collected from published literature composed of MMRs, body masses and the nutrient artery $\dot{Q}$ values of 43 extant mammals (n=15), non-avian sauropsids (n=14), and avian sauropsids (n=14) (Supplementary files). It is well established that larger animals have greater metabolic needs in mLO2 h^{-1} but lower metabolic needs in mLO2 h^{-1} g^{-1}, metabolic rate in mLO2 h^{-1} increases with body mass following an exponential relationship, with an exponent lower than 1 (Schmidt-Nielsen, 1984). We compared three taxonomic groups according to their metabolic features and the time of evolutionary divergence. We transformed their different allometric exponents to a common value. Here, we employed the 0.87 exponent to body mass unit (expressed in grams) for all the amniotes in our dataset. This exponent corresponds to the phylogenetic mean recovered using Mesquite (Maddison & Maddison, 2014). This generates a single character matrix of distinct extant species body mass allometric exponents 0.829 for non-avian sauropsids (Seymour, 2013), 0.87 for synapsids (White & Seymour 2005) and 1.02 for avian species (Allan et al., 2014) and a question mark for fossil taxa. This approach is more aligned with evolutionary principles and was taken into consideration in an earlier study (Sena et al., 2025). In this case, the phylogenetic exponent recovered was 0.87, so mass-independent MMR data have units of mLO2 h^{-1} $g^{-0.87}$.

Phylogenetic Framework

We derived the phylogenetic relationships of Neornithes from Stiller et al. (2024), employing Zurano et al. (2019) for Cetartiodactyla, Upham et al. (2019) for other mammals, Pyron et al. (2013) and Vidal & Hedges (2005) for squamates in general and Villa et al. (2018) for varanid lizards. Branch length data for extant taxa were gathered from the Time Tree of Life (timetree.org, accessed November 29, 2024), and those for the extinct ones from the Paleobiology Database (paleobiodb.org, accessed November 29, 2024).

Phylogenetic comparative method

Paleobiology inference models for mass-independent MMR were constructed using phylogenetic eigenvector maps (PEM) from the “MPSEM” package (Guénard et al., 2013) in R (R Core Team, 2023). The model allowed us to retrodict the mass-independent MMR values, along with their 95% confidence intervals, for the two ornithodiran fossils. The normality of the residuals was checked using the Shapiro-Wilk test.

Results

The pterosaur *Rhamphorhynchus* sp. MdC 20269891 and the theropod *Halskaraptor escuilliei* MPC D-102/109 have similar calculated nutrient artery flow rate $\dot{Q}$, respectively 0.0017 ml s^{-1} and 0.0010 ml s^{-1} based on their metadiaphyseal and nutrient foramen openings (Fig. 1).

Insert Figure 1 here

The retrodicted mass-independent MMR value for the “long-tailed” pterosaur *Rhamphorhynchus* sp. was 5.55 mLO2 h^{-1} $g^{-0.87}$ (95% CI = 4.37-7.05) and the theropod *Halskaraptor escuilliei* MPC D-102/109 was 5.68 mLO2 h^{-1} $g^{-0.87}$ (95% CI = 4.44-7.26). and the “long-tailed” pterosaur *Rhamphorhynchus* sp. was The predictive model included the phylogenetic eigenvectors 1, 2, 3, 4, 5, 6, 8, 9, 20, 22, 23, 27, 28, and 41, and the estimated nutrient artery $\dot{Q}$ as the co-predictor (adjusted R2 = 0.90; AICc = 56.79; and p = 3.501e-12) (Fig. 2). Leave-one-out cross-validation tests showed no significant difference between predicted and observed values for extant species (p = 0.7788).

Insert Figure 2 here

Discussion

The dromaeosaurid *Halszkaraptor escuilliei*, estimated to have a body mass of 1.5 kg (Cau et al., 2017), represents a mallard-sized theropod that likely reached maturity. In contrast, the examined *Rhamphorhynchus* individual, weighing approximately 95 g, is identified as a juvenile based on its small size (see supplementary of Voeten et al., 2018) and its wingspan ranging from 45 to 50 cm based on Prondvai et al. (2012). Despite their distinct ecomorphologies, the two sampled ornithodirans exhibit similar mass-independent MMR and femoral nutrient artery $\dot{Q}$. This suggests a strong influence of phylogenetic constraints on the outcomes of predictive energy modeling.

The mass-independent MMR inferred for *H. escuilliei* aligns with that measured in *Varanus gouldii*, an athletic monitor lizard, and certain avian taxa, such as emus (*Dromaius novaehollandiae*), gulls (*Larus*), and terns (*Sterna*). Similarly, the aerobic capacity of *Rhamphorhynchus* also overlaps with that of *V. gouldii*, a predatory lizard known for its enhanced oxygen transport capabilities. Monitor lizards achieve aerobic scopes and sustainable running speeds more than twice those of similar size lizards due to adaptations such as increased lung surface area, blood buffers, and myoglobin-rich skeletal muscles (Bartholomew & Tucker, 1964; Bennett, 1972; 1973). These features suggest the importance of morphological investments in oxygen transport systems for achieving high aerobic performance (Bennett & Ruben, 1979).

Flightless ratites emus possess increased hindlimb muscle and heart mass compared to cursorial phasianids, enabling sustained locomotor activity (Hartman, 1961; Grubb et al., 1983). In exercising emus, the V02max is 10 times greater than their resting values (Grubb et al., 1983). Conversely, non-migratory cursorial phasianids, such as guinea fowl (*Numida meleagris*) and jungle fowl (*Gallus*), are adapted for rapid escape flights, maximizing takeoff performance for avoiding predation (Witter et al., 1994). However, they exhibit lower endurance and aerobic performance due to limited flight muscle aerobic capacity (Kiessling, 1977; Ellerby et al., 2003; Askew & Marsh, 2001; Henry et al., 2005). The contribution of flight muscles to organismal aerobic scope in these birds, even if combined with leg activity is small (Hammond et al., 2000). *Halszkaraptor*, interpreted as an amphibious dromaeosaurid, likely combined vigorous hindlimb activity for terrestrial locomotion, similar to flightless ratites with the use of its forelimbs for swimming. The plesiomorphic glenoid condition characteristic of paravians, which is also inferred for *Halszkaraptor*, may have served as a potential exaptation for a forelimb-assisted swimming style (Cau et al., 2017; Cau, 2020). However, its aerobic capacity appears to be lower than that of highly specialized swimmers, such as ducks (*Anas* spp.). This suggests that *Halszkaraptor* may have been less efficient in aquatic environments compared to these highly adapted species (e.g., mallard).

The early stage of the *Rhamphorhynchus* contributes to the overestimation of its mass-independent MMR, driven by the rapid growth rates typical of juvenile pterosaurs, as confirmed by osteohistological studies in both non-pterodactyloid and pterodactyloid pterosaurs (Prondvai et al., 2012; Araújo et al., 2023). Previous analyses of *Rhamphrorhychus* suggest the flight capability was likely achieved when individuals reached approximately 30-50% of the wingspan of an adult individual and 7-20% of the adult body mass (Prondvai et al., 2012). Recent findings indicate that the largest known specimen of *Rhamphorhynchus* had an estimated wingspan of 1.8 m and a body mass of about 3 kg (Hone and McDavid, 2025). This underscores that, despite its high mass-independdt MMR value, our specimen represents a small individual that likely did not have flight capabilities at this stage. Juveniles often exhibit relatively larger foramen areas due to the increased perfusion required for rapid growth. For example, growing kangaroos display larger femoral nutrient foramen areas compared to adults, reflecting higher energy demands for bone development (Hu et al., 2018). A similar pattern is observed in laying oviparous females, where increased femoral blood flow supports calcium mobilization for eggshell formation (Hu et al., 2021). Thus, the high MMR value found for *Rhamphorhychus* in this study is more likely linked to its growth demands rather than flight capacity. Furthermore, while this juvenile *Rhamphrorhynchus* may not have been capable of flight, it could have been able to climb trees and hunt small vertebrates and invertebrates (Prodvai et al., 2012), indicating that it maintained a sufficiently high activity rate during its early stages of life.

As the earliest archosaur group to evolve flapping flight, pterosaurs faced the energetic costs associated with aerial locomotion, in special to pterodactyloid with large body size, as *Quetzalcoatlus northropi*. The energetic advantage of larger body sizes in continuous flight, as seen in birds (Tatner & Bryant, 1986). The flight energetics of large pterosaurs, such as the *Quetzalcoatlus northropi*, probably involved anaerobic metabolism during takeoff, followed by energy-efficient soaring or high-speed flight (Marden, 1994). To sustain flight aerobically, *Quetzalcoatlus* likely required an aerobic scope comparable to migratory swans. In contrast, smaller pterosaur species like *Rhamphorhynchus* might have had different metabolic requirements during takeoff, highlighting the need for further studies on adult specimens to elucidate their flight endurance and takeoff capabilities.

In volant birds, flying is generally more energetically efficient than running or swimming over equivalent distance due to higher speeds achieved in flight (Fedak et al., 1974; Norberg, 1996; Butler, 2016). This aerodynamic efficiency is particularly pronounced in insectivore birds, which exhibit flight costs 49–73% lower than predicted for nonaerial species (Hails, 1979; Tucker, 1970). Consequently, the maximal aerobic capacity of adult *Rhamphorhynchus* is expected to be lower than of the juvenile specimen analyzed and likely lower than that of the *H. escuilliei*. Once, flight would likely be achieved in adulthood, allowing for more efficient energy use, and resulting in a lower MMR value compared to the juvenile specimen, which would have had a terrestrial and arboreal lifestyle.

The endurance flight capabilities of juvenile *Rhamphorhynchus* are comparable to migratory shorebirds, such as gulls and terns, but its flight muscles likely lacked the mass-specific power required for sustained vertical takeoff, as seen in small migratory phasianids *Coturnix coturnix* and *Coturnix chinensis* (Bishop, 1997; Askew & Marsh, 2001; Henry et al., 2005). Further investigation of adult specimens is necessary to clarify the ontogenetic influence on pterosaur flight performance.

Although *Rhamphorhynchus* and *Halszkaraptor escuilliei* belong to distinct groups and exhibit different lifestyles, parallels can be drawn regarding their metabolism and energy efficiency in locomotion. *Rhamphorhynchus*, would require a high aerobic capacity, particularly, when it would achieve greater energy efficiency for flight, although juvenile stages exhibit elevated metabolic rates due to rapid growth. On the other hand, *Halszkaraptor escuilliei*, with its semi-aquatic locomotion, would have adapted its metabolism for endurance rather than high bursts of energy, as seen in flight. Both groups demonstrate adaptations that reflect the need for metabolic efficiency, albeit in different ways: while the aerobic energy costs of flight would be high, they would be offset by the flight efficiency in adult Rhamphorhynchus individuals, whereas

Halszkaraptor's locomotion would be more balanced, with lower energy expenditure during terrestrial and aquatic activities.

Caveats

Several species of the sample of extant birds used to construct the inference model are characterized by the presence of pneumatization. The pneumatic foramina in long bones likely include arteries (in addition to the air sac), and this may have effect on the size of foramina and on the blood flow rate. As we need an extant phylogenetic bracket to construct the inference model (Witmer, 1992 unpublished data), we must include a sample of extant birds assuming that the arteries passing through the pneumatic foramina are small and do not have a significant impact on the blood flow rate through the foramina.

Conclusions

This study highlights the aerobic capacity of the theropod *Halszkaraptor escuilliei* and the pterosaur *Rhamphorhynchus*. Despite significant differences in lifestyle and ontogenetic state, both taxa exhibited similar mass-independent maximal metabolic rates (MMR) and femoral nutrient artery blood flow ($\dot{Q}$). The mass-independent MMR of H. escuilliei aligns with that of *V. gouldii* and the avian species, emus and the Charadriiformes, *Larus* and *Sterna*. However, its aerobic performance appears to fall below that of swimmers like ducks and athletic mammals. The juvenile *Rhamphorhynchus* likely displayed elevated femoral blood flow compared to mature individuals. While its endurance flight capabilities resemble those of migratory shorebirds, it is far from those seen in small migratory phasianids. In addition, adult *Rhamphorhynchus* individuals, having reduced growth-related demands, likely had lower mass-independent MMRs. The attainment of flight would have resulted in a more energetically efficient metabolism; however, further study is needed to fully understand the ontogenetic influence on their metabolic performance.

Supplementary Information

https://github.com/MAVAAS/MMR_Halszkaraptor_and_Rhamphorhynchus.git

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Figure Caption

Figure 1. 3D reconstruction of femora of *Rhamphorhynchus* sp. MdC 20269891 (voxel size of 4.24 µm) (A) and *Halszkaraptor escuilliei* MPC D-102/109 using µCT (C) (voxel size of 53.58 µm), with the identifiable foramina segmented and highlighted in red (B) and green (D). Scale bar equals 2 mm (A), 600 µm (B), and 550 µm (C and D).

Figure 2. Phylogenetic relationships including the sample of extant amniotes used to construct the mass-independent maximum metabolic rates inference model and the extinct theropod and the pterosaur for which we performed retrodictions using nutrient artery $\dot{Q}$ as co-predictor. Branch lengths are proportional to time.

Figure 1

Figure 1. 3D reconstruction of femora

3D reconstruction of femora of *Rhamphorhynchus* sp. MdC 20269891 (voxel size of 4.24 µm) (A) and *Halszkaraptor escuilliei* MPC D-102/109 using µCT (C) (voxel size of 53.58 µm), with the identifiable foramina segmented and highlighted in red (B) and green (D). Scale bar equals 2 mm (A), 600 µm (B), and 550 µm (C and D).

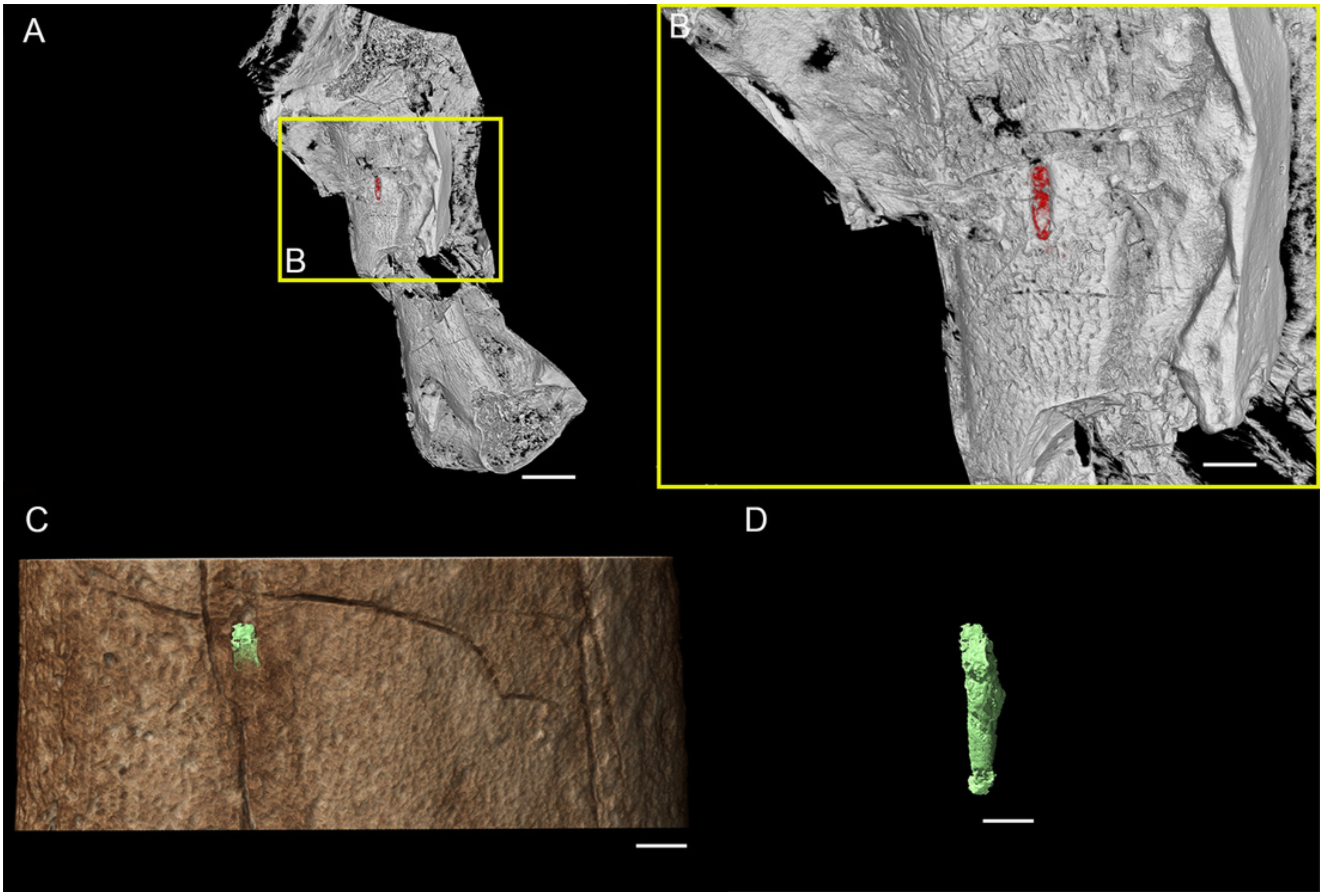

Figure 2

Figure 2. Phylogenetic + blood flow rate ($\dot{Q}$) model to estimate maximum metabolic rate

Phylogenetic relationships including the sample of extant amniotes used to construct the mass-independent maximum metabolic rates inference model and the extinct theropod and the pterosaur for which we performed retrodictions using nutrient artery $\dot{Q}$ as co-predictor. Branch lengths are proportional to time.