BIOLOGICAL REVIEWS
Cambridge Philosophical Society
Biol. Rev. (2022), pp. 000–000.
doi: 10.1111/brv.12829

Morphology and distribution of scales, dermal ossifications, and other non-feather integumentary structures in non-avialan theropod dinosaurs

Christophe Hendrickx[1†*], Phil R. Bell[2†*], Michael Pittman[3,4], Andrew R. C. Milner[5], Elena Cuesta[6], Jingmai O'Connor[7], Mark Loewen[8,9], Philip J. Currie[10], Octávio Mateus[11,12], Thomas G. Kaye[13] and Rafael Delcourt[14]

[1]*Unidad Ejecutora Lillo, CONICET-Fundación Miguel Lillo, 251 Miguel Lillo, San Miguel de Tucumán, Tucumán, 4000, Argentina*
[2]*School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia*
[3]*Vertebrate Palaeontology Laboratory, Department of Earth Sciences, The University of Hong Kong, Pokfulam, Hong Kong, SAR, China*
[4]*Department of Earth Sciences, University College London, WC1E 6BT, United Kingdom*
[5]*St. George Dinosaur Discovery Site at Johnson Farm, 2180 East Riverside Drive, St. George, UT, U.S.A.*
[6]*Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Str. 10, Munich, 80333, Germany*
[7]*Field Museum of Natural History, 1400 S Lake Shore Drive, Chicago, IL 60605, U.S.A.*
[8]*Department of Geology and Geophysics, University of Utah, Frederick Albert Sutton Building, 115 South 1460 East, Salt Lake City, UT, 84112, U.S.A.*
[9]*Natural History Museum of Utah, 301 Wakara Way, Salt Lake City, UT 84108, U.S.A.*
[10]*Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada*
[11]*GeoBioTec, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, Caparica, Portugal*
[12]*Museu da Lourinhã, 95 Rua João Luis de Moura, Lourinhã, 2530-158, Portugal*
[13]*Foundation for Scientific Advancement, 7023 Alhambra Dr., Sierra Vista, AZ 85650, U.S.A.*
[14]*Universidade Estadual de Campinas (UNICAMP), Instituto de Geociências, Cidade Universitária, Rua Carlos Gomes, 250, Campinas, SP, 13083-855, Brazil*

ABSTRACT

Modern birds are typified by the presence of feathers, complex evolutionary innovations that were already widespread in the group of theropod dinosaurs (Maniraptoriformes) that include crown Aves. Squamous or scaly reptilian-like skin is, however, considered the plesiomorphic condition for theropods and dinosaurs more broadly. Here, we review the morphology and distribution of non-feathered integumentary structures in non-avialan theropods, covering squamous skin and naked skin as well as dermal ossifications. The integumentary record of non-averostran theropods is limited to tracks, which ubiquitously show a covering of tiny reticulate scales on the plantar surface of the pes. This is consistent also with younger averostran body fossils, which confirm an arthral arrangement of the digital pads. Among averostrans, squamous skin is confirmed in Ceratosauria (*Carnotaurus*), Allosauroidea (*Allosaurus*, *Concavenator*, *Lourinhanosaurus*), Compsognathidae (*Juravenator*), and Tyrannosauroidea (*Santanaraptor*, *Albertosaurus*, *Daspletosaurus*, *Gorgosaurus*, *Tarbosaurus*, *Tyrannosaurus*), whereas dermal ossifications consisting of sagittate and mosaic osteoderms are restricted to *Ceratosaurus*. Naked, non-scale bearing skin is found in the contentious tetanuran *Sciurumimus*, ornithomimosaurians (*Ornithomimus*) and possibly tyrannosauroids (*Santanaraptor*), and also on the patagia of scansoriopterygids (*Ambopteryx*, *Yi*). Scales are surprisingly conservative among non-avialan

* Authors for correspondence (Tel.: +54.9.381.362.4528; E-mail: christophendrickx@gmail.com); (Tel.: +61.2.6773.2329; E-mail: pbell23@unne.edu.au)
†Authors contributed equally to this work.

theropods compared to some dinosaurian groups (e.g. hadrosaurids); however, the limited preservation of tegument on most specimens hinders further interrogation. Scale patterns vary among and/or within body regions in *Carnotaurus*, *Concavenator* and *Juravenator*, and include polarised, snake-like ventral scales on the tail of the latter two genera. Unusual but more uniformly distributed patterning also occurs in *Tyrannosaurus*, whereas feature scales are present only in *Albertosaurus* and *Carnotaurus*. Few theropods currently show compelling evidence for the co-occurrence of scales and feathers (e.g. *Juravenator*, *Sinornithosaurus*), although reticulate scales were probably retained on the mani and pedes of many theropods with a heavy plumage. Feathers and filamentous structures appear to have replaced widespread scaly integuments in maniraptorans. Theropod skin, and that of dinosaurs more broadly, remains a virtually untapped area of study and the appropriation of commonly used techniques in other palaeontological fields to the study of skin holds great promise for future insights into the biology, taphonomy and relationships of these extinct animals.

Key words: integument, scales, skin, Theropoda, dinosaur, footprints, trace fossils, feathers

CONTENTS

I. Introduction . . . 2
II. Historical overview of theropod integumentary discoveries (including feathers) . . . 4
III. Material and methods . . . 6
(1) Terminology . . . 7
(*a*) Scale types . . . 7
(*b*) Scale shape and ornamentation . . . 8
(*c*) Interstitial tissue . . . 10
(*d*) Dermal ossifications and osteoderm morphotypes . . . 10
IV. Results . . . 10
(1) Stem-averostran Theropoda . . . 10
(2) Indeterminate averostrans . . . 12
(3) Ceratosauria . . . 13
(4) Carnosauria . . . 13
(5) Tyrannosauroidea . . . 17
(6) Compsognathidae . . . 19
(7) Ornithomimosauria . . . 21
(8) Pennaraptora . . . 22
V. Discussion . . . 25
(1) Morphology and distribution of epidermal structures in non-avialan theropods . . . 25
(*a*) Body . . . 25
(*b*) Manus and pes . . . 31
(*c*) Scales and plumage co-occurrence . . . 31
(*d*) Excrescences . . . 32
(2) Morphological comparison of the scaly skin of theropods with other dinosaurs . . . 32
(3) Evolution of integumentary structures in non-avialan theropods . . . 34
(4) Future directions . . . 34
VI. Conclusions . . . 36
VII. Acknowledgements . . . 36
VIII. References . . . 37
IX. Supporting information . . . 45

I. INTRODUCTION

Theropods, including birds, form the most taxonomically and morphologically diverse clade of dinosaurs (Rauhut, 2003; Brusatte *et al.*, 2012; Holtz, 2012; Foth & Rauhut, 2013). Members of this clade were bipedal animals and most, if not all, carnivorous dinosaurs are included in this group (Hendrickx, Hartman & Mateus, 2015). Birds are nested within the theropod radiation, making them the only dinosaurs to survive the Cretaceous–Paleogene (K–Pg) boundary mass extinction event 66 million years ago (e.g. Gauthier & Gall, 2002; Naish, 2012; Brusatte, O'Connor & Jarvis, 2015). They are globally cosmopolitan and comprise >10000 living species, all characterised by the presence of one of the most complex integumentary appendages found in any vertebrate: the feather (Prum & Brush, 2002; Chiappe & Dyke, 2006). Although the first birds (i.e. the earliest-branching members of the clade Avialae) and their closest theropod relatives already had some form of plumage (e.g. Norell & Xu, 2005; Zhang, Zhou & Dyke, 2006; Xu

et al., 2014; Brusatte & Clark, 2015; Lefèvre *et al.*, 2020; Xu, 2020), many early-diverging clades of theropods were still covered with scales, which is considered the ancestral condition in dinosaurs [Barrett, Evans & Campione, 2015; Campione, Barrett & Evans, 2020; but see Yang *et al.* (2019) for another opinion]. Scales and feathers, like internal organs, are soft tissues that are typically rarely preserved in the fossil record (Xu & Guo, 2009; Schweitzer, 2011). Nevertheless, a particularly high number of non-avialan theropod species retain exceptionally preserved integument, revealing a wide morphological diversity of epidermal structures among this group and illuminating remarkable detail on the evolution of feathers (e.g. Prum & Brush, 2002; Norell & Xu, 2005; Xu & Guo, 2009; Xu *et al.*, 2014; Lefèvre *et al.*, 2020; Xu, 2020). The majority of non-avialan theropod specimens that include integumentary remains are from the Lagerstätte fossil sites of the Jehol Group of northeastern China, and all appear to be covered with filamentous structures, 'protofeathers' or true feathers (e.g. Zhang *et al.*, 2006; Xu *et al.*, 2014; Benton *et al.*, 2019; Lefèvre *et al.*, 2020; Xu, 2020). Yet, scales were found in many non-avialan theropods throughout the Mesozoic (Barrett *et al.*, 2015; Campione *et al.*, 2020), from the earliest-diverging forms of the Late Triassic (Gatesy, 2001) to the latest-diverging ceratosaurs and tyrannosauroids at the end of the Cretaceous (Bell *et al.*, 2017; Hendrickx & Bell, 2021b).

Because of their now-iconic connection with crown Aves, the integuments of feathered theropods have received particularly wide coverage over the past 20 years and are relatively well described in the literature. Scales, conversely, have received a surprisingly shallow treatment, despite their wider taxonomic distribution among non-avialan theropods (Barrett *et al.*, 2015; Campione *et al.*, 2020). Scaly skin has been reported in the abelisaurid *Carnotaurus* (Bonaparte, Novas & Coria, 1990; Czerkas & Czerkas, 1997), the allosauroids *Allosaurus* (Pinegar *et al.*, 2003) and *Concavenator* (Cuesta *et al.*, 2015), various tyrannosaurids (*Tarbosaurus*, *Tyrannosaurus*, *Gorgosaurus*, *Albertosaurus*, *Daspletosaurus*; Bell *et al.*, 2017), compsognathids (*Compsognathus*; Peyer, 2006), *Juravenator* (e.g. Göhlich & Chiappe, 2006; Bell & Hendrickx, 2020, 2021; Foth *et al.*, 2020), and *Sinornithosaurus* (Ji *et al.*, 2001), and the anchiornithine *Anchiornis* (Wang *et al.*, 2017b), whereas dermal ossifications have only been identified in the eponymous ceratosaurian *Ceratosaurus* (Gilmore, 1920). True skin impressions are also reported from a variety of theropod tracks and trackways (e.g. Hitchcock, 1841; Gatesy, 2001; Currie, Badamgarav & Koppelhus, 2003; Milner, Lockley & Johnson, 2006a; Milner, Lockley & Kirkland, 2006b; Kim *et al.*, 2019). Smooth or bare skin has been noted in the contentious tetanuran *Sciurumimus* (Rauhut *et al.*, 2012) and the ornithomimosaurian *Pelecanimimus* (Pérez-Moreno *et al.*, 1994; Briggs *et al.*, 1997), whereas the remarkably preserved skin (epidermis) and other soft tissues have been described in the tyrannosauroid *Santanaraptor* (Kellner, 1996; Kellner & de Campos, 1998). Scansoriopterygids, bizarre early-diverging pennaraptorans that evolved a unique airfoil formed from a membranous patagium (Xu *et al.*, 2015; Wang *et al.*, 2019), illustrate the extent to which epidermal structures played a role in forming disparate morphologies and ecologies among theropods. Despite this epidermal diversity, the relevant structures of many theropod taxa remain poorly described and often lack detailed illustrations. Consequently, this review aims to address this issue by: (*i*) providing a historical overview of the history of theropod integumentary discoveries; (*ii*) comprehensively describing and illustrating the non-feather epidermal structures (i.e. squamous skin, naked skin, dermal ossifications) of non-avialan theropods, including those known from footprints; (*iii*) exploring the distribution and morphology of squamous integument in non-avialan theropods and other dinosaurs, and; (*iv*) providing a much-needed roadmap outlining promising future directions for the study of theropod integument.

Institutional abbreviations: AC, Beneski Museum of Natural History (formerly Pratt Museum of Amherst College), Amherst, Massachusetts, USA; **AMNH**, American Museum of Natural History, New York City, USA; **BMMS**, Bürgermeister Müller Museum, Solnhofen, Germany; **BSPG**, Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany; **BYU-VP**, Brigham Young University Museum of Vertebrate Paleontology, Provo, Utah, USA; **CAGS**, Chinese Academy of Geological Sciences, Beijing, China; **CMN**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **DIP**, Dexu Institute of Paleontology, Chaozhou, China; **HMNS**, Houston Museum of Natural Science, Houston, Texas, USA; **IRSNB**, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **IVPP**, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; **JME**, Jura Museum Eichstätt, Eichstätt, Germany; KNHM, Knuthenborg Natural History Museum Collection, Knuthenborg Safaripark, Bandholm, Denmark; **LHC**, Las Hoyas Collection, Universidad Autónoma de Madrid, Madrid, Spain; **LPM**, Liaoning Paleontological Museum, Liaoning, China; **MACN**, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; **MCCM**, Museo de Ciencias de Castilla-La Mancha [now MUPA, Museo de Paleontología de Castilla-La Mancha], Cuenca, Spain; **MCF-PVPH**, Museo Municipal 'Carmen Fuñes,' Plaza Huincul, Neuquén, Argentina; **MGUH**, Geological Museum at the University of Copenhagen, Copenhagen, Denmark; **ML**, Museu da Lourinhã, Lourinhã, Portugal; **MN**, Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil; **MPC**, Institute of Paleontology and Geology (also known as the "Mongolian Palaeontology Centre"), Mongolian Academy of Sciences (formerly IGM), Ulaanbaatar, Mongolia; **MWC**, Museum of Western Colorado, Fruita, Colorado, USA; **NGMC**, National Geological Museum of China, Beijing, China; **NHMUK PV**, Natural History Museum, London, UK; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **SGDS**, St. George Dinosaur Discovery Site at Johnson Farm, St. George, Utah, USA; **SMA**, Sauriermuseum Aathal, Aathal, Switzerland; **SMF**, Senckenberg Natural History Museum, Frankfurt am Main,

Germany; **STM**, Shandong Tianyu Museum of Nature, Pingyi, Shandong, China; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP**, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta, Canada; **UAM**, Universidad Autónoma de Madrid, Madrid, Spain; **UCL**, University College London, London, England; **UMNH VP**, Natural History Museum of Utah Vertebrate Paleontology Collection, Salt Lake City, Utah, USA; **USNM**, United States National Museum Vertebrate Paleontology, National Museum of Natural History, Washington, District of Columbia, USA; **WDC**, Wyoming Dinosaur Center, Thermopolis, Wyoming, USA.

II. HISTORICAL OVERVIEW OF THEROPOD INTEGUMENTARY DISCOVERIES (INCLUDING FEATHERS)

The earliest published record of fossilised integument in a Mesozoic theropod goes back to the early nineteenth century when German palaeontologist and politician Ernst Friedrich Freiherr von Schlotheim (1820) briefly mentioned the presence of feathered fossils from limestone beds near the towns of Pappenheim and Solnhofen in Bavaria, Germany (Ostrom, 1976). Ostrom (1976, p. 97) lamented that "*the whereabouts of von Schlotheim's feathered fossils are unknown today*", yet the fact that the Late Jurassic Solnhofen deposits have since yielded numerous specimens of the early-diverging avialan *Archaeopteryx* strongly supports von Schlotheim's published record of feathered theropods. To our knowledge, the first illustrated discovery of the integument of a non-avialan theropod dinosaur appeared in 1841 when the president of Amherst College in the USA, Reverend Edward Hitchcock, reported the presence of "*an impression of the skin of the animal's foot*" (Hitchcock, 1841, p. 486, plate 36, figure 19; Fig. 1A) on a track referred to *Ornithoidichnites giganteus* (= *Eubrontes giganteus*) recovered a few years before from a fine red slate of Wethersfield, Connecticut. Interestingly, this discovery pre-dated the name Dinosauria (Davis, 2014), which was coined by Sir Richard Owen only a year later (Owen, 1842). Hitchcock (1841) did not ascribe the track to a particular animal but noted that the cross furrows producing small papillae particularly resembled those of birds. Given its morphology and stratigraphic distribution (i.e. Portland Formation, Hettangian–Sinemurian; Lower Jurassic; Gierlowski-Kordesch & Rust, 1994), the track can confidently be referred to a theropod and possibly to a non-averostran neotheropod. Edward Hitchcock later reported additional theropod tracks (all referred to the ichnogenus *Brontozoum* [= *Eubrontes*]) with skin (or 'papillary' *sensu* Hitchcock, 1865) impressions from the Connecticut Valley of New England (Hitchcock, 1858, pp. 63–64 and 178, plate X; Hitchcock, 1865, p. 24, plate XVI).

The next landmark discovery was that of an isolated feather and initial holotype of *Archaeopteryx lithographica* from the lithographic limestone of Solnhofen, Germany, in 1860 (VON MEYER, 1861; Griffiths, 1996; Carney *et al.*, 2012; Fig. 1B), although its true identity would not be recognised until the description of the so-called London specimen of *Archaeopteryx* (NHMUK OR 37001) the following year (Owen, 1863). Recent analysis, however, indicates this isolated feather may not pertain to *Archaeopteryx* after all, but to another yet-unknown feathered theropod (Kaye *et al.*, 2019). On the other side of the Atlantic, between 1876 and 1884, M. P. Felch and his brother Charles E. Felch found and collected an almost complete skeleton of *Ceratosaurus nasicornis* in Garden Park, near Canyon City, Colorado (Gilmore, 1920). Although initially reported in the literature by Marsh (1884), it was Gilmore (1920) that was the first to describe the row of dermal ossifications above the neural spines of *Ceratosaurus* – the first for any theropod. Although squamous skin of a sauropod was reported in 1852 by Gideon M. Mantell (Mantell, 1852; Czerkas, 1997; Upchurch, Mannion & Taylor, 2015; albeit incorrectly attributed to a giant crocodilian; Hooley, 1917), it would be more than a century before scaly body skin in a non-avialan theropod was discovered. In 1984, during fieldwork of the 8th Paleontological Expedition to Patagonia, Argentinian palaeontologist José Bonaparte and his team uncovered the skeleton of the abelisaurid *Carnotaurus sastrei* in Estancia Pocho Sastre at Bajada Moreno in Chubut Province (Bonaparte, 1985; Bonaparte *et al.*, 1990; Hendrickx & Bell, 2021b). The discovery was exceptional for two reasons: the specimen was almost complete and large patches of skin were preserved on its right side, revealing the detailed skin morphology of a non-avialan theropod for the first time (Bonaparte *et al.*, 1990; Fig. 1C). The importance of this discovery lead Bonaparte to launch a second expedition to the excavation site of *Carnotaurus* with paleoartists and skin experts Stephen and Sylvia Czerkas in 1988 (Czerkas & Czerkas, 1989). This expedition collected additional fragments of fossil skin from different body parts, which ultimately helped Stephen Czerkas realise an accurate life-size model of *Carnotaurus* covered with scales (Czerkas & Czerkas, 1989, 1997; Hendrickx & Bell, 2021b).

The 1990s were pivotal in the discovery of various epidermal structures in non-avialan theropods. Within 6 years, several major discoveries were announced that revolutionised our understanding of the morphological diversity of theropod integument and the evolution of feathers. Pérez-Moreno *et al.* (1994) and Kellner (1996) reported soft tissue and integumentary structures in the early-diverging ornithomimosaurian *Pelecanimimus polyodon* and the tyrannosauroid *Santanaraptor placidus* from the Early Cretaceous of Spain and Brazil, respectively. In 1997, skin morphology was revealed in tyrannosaurid theropods, with a specimen of *Gorgosaurus libratus* being described as having small rounded or hexagonal scales on the tail (Carpenter, 1997). A year before, Ji & Ji's (1996) publication *On the discovery of the earliest fossil bird in China (*Sinosauropteryx *gen. nov.) and the origin of birds* was the turning point in our understanding of the origin and evolution of birds and feathers. In August 1996, Qiang and Shu'an Ji unearthed for the first time a Mesozoic theropod covered

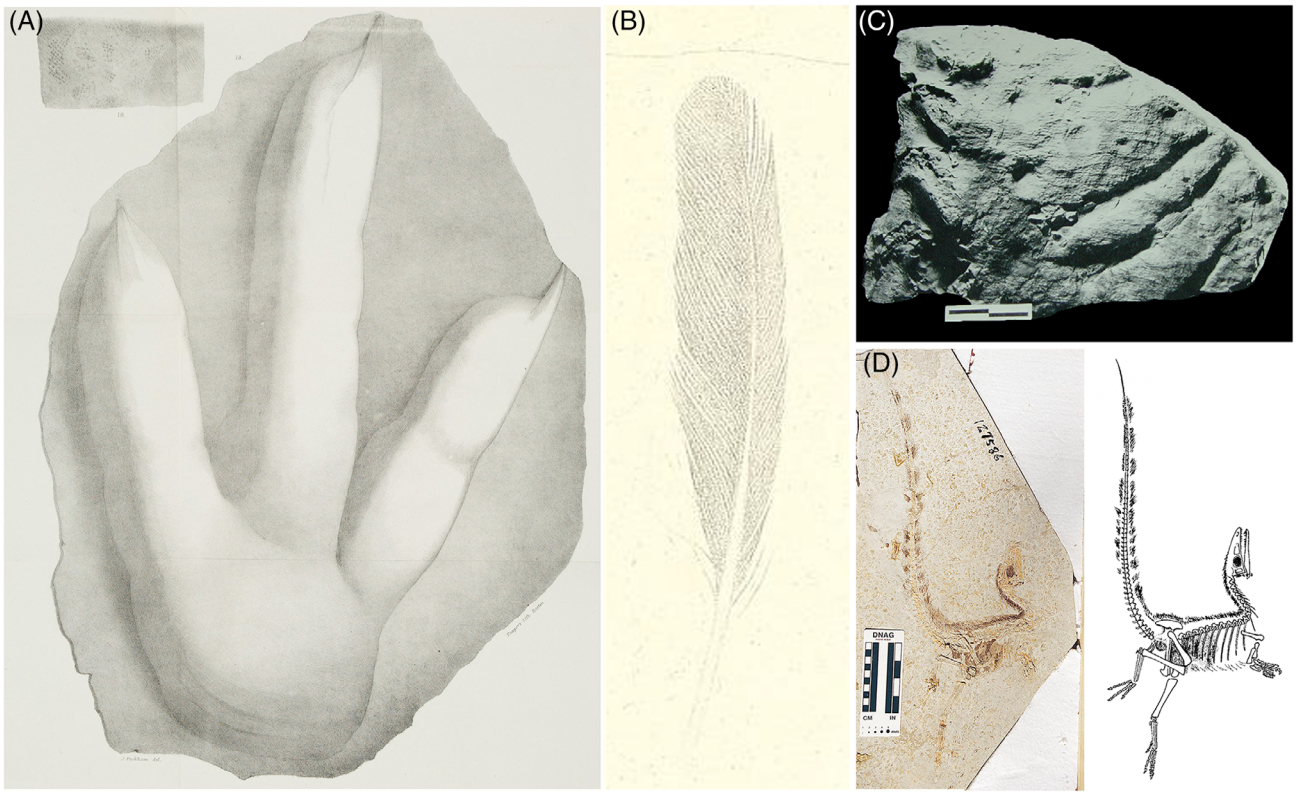


Fig. 1. Historical discoveries of integument in Mesozoic theropod dinosaurs. (A) First illustration of scaly skin in a non-avialan theropod, the reticulate scales preserved on a pedal track ascribed to *Ornithoidichnites giganteus* (= *Eubrontes giganteus*) by Reverend Edward Hitchcock (1841, plate 36) from a fine red slate of Wethersfield, Connecticut. (B) First illustration of a feather-type integument in a Mesozoic theropod, the holotype of *Archaeopteryx lithographica* described and illustrated by von Meyer (1861), consisting of an isolated pennaceous feather from the lithographic limestone of Solnhofen, Germany, belonging to an indeterminate feathered theropod. (C) First specimen with scaly integument to be described from the body of a non-avialan theropod, the skin impression of the abelisaurid *Carnotaurus sastrei* (MACN-CH 894) from the anteroventral portion of the tail, described and illustrated by Bonaparte *et al.* (1990, figure 37C, modified). (D) First non-avialan theropod to be discovered with filamentous impression, the holotype of *Sinosauropteryx prima* from the Lower Cretaceous Yixian Formation (Jehol Group) of Liaoning Province, China, described and illustrated by Ji & Ji (1996), which marks the beginning of the discoveries of non-avialan theropods with feathers.

with filamentous integument. Christened *Sinosauropteryx prima*, the specimen (Fig. 1D) was uncovered in the village of Shangyuanxiang, Beipiao, in western Liaoning Province, and initially thought to be a primitive bird (Ji & Ji, 1996) but classified as an earlier-diverging coelurosaurian two years later (Chen, Dong & Zhen, 1998). A large number of specimens from Early Cretaceous deposits of Liaoning Province were described in the two following years, exposing for the first time the presence of plumaceous feathers in early-diverging oviraptorosaurians (Ji & Ji, 1997; Ji *et al.*, 1998) and filamentous integuments in compsognathids (Chen *et al.*, 1998), therizinosaurians (Xu, Tang & Wang, 1999a) and dromaeosaurids (Xu, Wang & Wu, 1999b). Additional discoveries in the 21st century revealed that all clades of Pennaraptora, and possibly all maniraptoriforms, were likely covered with symmetrical or asymmetrical feathers (e.g. Xu, Zhou & Wang, 2000; Xu, Zheng & You, 2010; Xu *et al.*, 2011, 2017; Xu & Zhang, 2005; Zelenitsky *et al.*, 2012; Godefroit *et al.*, 2013a,b; Foth, Tischlinger & Rauhut, 2014; Han *et al.*, 2014; Lü & Brusatte, 2015; Lefèvre *et al.*, 2020; Poust *et al.*, 2020; Xu, 2020), whereas early-diverging megalosauroids (Rauhut *et al.*, 2012), early-diverging tyrannosauroids (Xu *et al.*, 2004, 2012) and compsognathids (Ji *et al.*, 2007; Chiappe & Göhlich, 2010; Foth *et al.*, 2020) bore filament-like integumentary structures.

The proliferation of feathered non-avialan theropods from China and the extremely rapid rate of discovery in this and other countries (e.g. Canada, Myanmar) has overshadowed squamous-skinned theropods found in more recent years. Despite this, there have been several exceptions, including the bull-like abelisaurid *Carnotaurus sastrei* with small non-overlapping scales surrounding larger conical studs (Hendrickx & Bell, 2021b), the diminutive *Juravenator starki* with filamentous structures and three types of scales (Chiappe & Göhlich, 2010; Bell & Hendrickx, 2020, 2021; Foth *et al.*, 2020), the bizarre hump-backed

carcharodontosaurid *Concavenator corcovatus* with feet revealing a bird-like podotheca (Cuesta *et al.*, 2015), and tyrannosaurids such as *Tyrannosaurus*, whose bodies were evidently covered with tiny polygonal scales and likely no feather structures (Bell *et al.*, 2017). One of the most unusual integumentary structures discovered in recent years pertain to the enigmatic scansoriopterygids, once again from China. At least two genera, *Yi* and *Ambopteryx*, appear to show bare-skin membranes stretched between hypertrophied manual digits and a rod-like styliform element (Xu *et al.*, 2015; Wang *et al.*, 2019), representing an entirely novel theropod flight architecture and demonstrating the role of integument in forming unprecedented structures (Dececchi *et al.*, 2020).

III. MATERIAL AND METHODS

To perform our review, we studied the non-feathered epidermal structures and dermal ossifications in 25 non-avialan theropod taxa bracketed phylogenetically between the early-diverging Theropoda *Tawa alae* (Nesbitt *et al.*, 2009) and the early-diverging avialan *Archaeopteryx lithographica* (Elzanowski, 2001; Christiansen & Bonde, 2004; Mayr, Pohl & Peters, 2005; Foth *et al.*, 2014; see online Supporting information, Appendix S1). Only postcranial osteoderms were considered in this study. With the possible exception of *Tyrannosaurus* (the epipostorbital; see Carr, 2020), the cranial dermal ossifications reported in some theropods such as abelisaurids (Carrano & Sampson, 2008) are more cornified tissues, armour-like dermis and other types of dermal ornamentations than true osteoderms (Carr *et al.*, 2017; Delcourt, 2018). Specimens belonging to 22 taxa deposited in scientific collections of France, Germany, Portugal, Spain, Argentina, Brazil, USA, Canada, and China were examined first-hand and anatomical observations were assisted with the use of a digital camera and/or a digital microscope AM411T Dino-Lite Pro. The original integument was observed in the majority of theropod taxa, but high-resolution casts of skin were also used for specimens belonging to four non-maniraptoriform avetheropods (*Allosaurus*, *Albertosaurus*, *Tarbosaurus* and *Tyrannosaurus*). Descriptions and illustrations in the literature were relied upon for three additional taxa (*Sciurumimus*, *Ornithomimus*, and *Epidendrosaurus*), including high-resolution photographs provided by two colleagues for one of them (*Sciurumimus*). Three-dimensional (3D) models of skin were generated for *Carnotaurus* (MACN-CH 894) using photogrammetric data and the software Agisoft Photoscan 1.3.4, as well as for *Allosaurus* (UMNH VP C481) using a Creaform Go! SCAN 20 surface scanner at 0.2 mm resolution. The 3D models were exported, oriented, and scaled in Meshlab version 1.3.4BETA (Cignoni *et al.*, 2008) and deposited in MorphoMuseuM (https://morphomuseum.com/) where they are freely downloadable (Hendrickx *et al.*, 2021a; Hendrickx & Bell, 2021a). Laser-stimulated fluorescence (LSF) imaging was used to describe preserved integument using standard protocols (Kaye *et al.*, 2015; Wang *et al.*, 2017b). Morphology of the non-avialan theropod skin was compared to that of other dinosaurs and living amniotes based on personal examination and high-quality photographs of the skin of ornithischian and sauropodomorph dinosaurs, living birds, crocodiles, squamates and turtles.

To review the distribution and evolution of epidermal structures and dermal ossifications in dinosaurs, we mapped 71 tegument-based characters coded for 67 archosauriform taxa, among which 40 taxa were examined first hand (Appendix S2; Hendrickx *et al.*, 2021b). Although characters on epidermal structures (i.e. smooth skin, scales, osteoderms and feathers) are incorporated in some data matrices, the majority of the integument-based characters we propose are new (Appendix S2.2). Following the best practices of recent studies dealing with integument-based characters (e.g. Holtz, Molnar & Currie, 2004; Brusatte *et al.*, 2009; Barrett *et al.*, 2015; Yang *et al.*, 2019; Campione *et al.*, 2020), we scored all integumentary structures (monofilaments, feature scales, scutate scales, etc.) that were not observed in the preserved patch (or patches) of integument as being absent (Appendix S2.1). Many dinosaur taxa preserve skin and/or feathers in a small portion of their body (e.g. *Allosaurus*, *Juravenator*, *Lourinhanosaurus*, *Tarbosaurus*) so the results of the distribution of integument-based characters should be seen as tentative since the discovery of additional specimens with more extensive body teguments or new taxa with integumentary structures could significantly change these results.

Taxa were bracketed phylogenetically between early-diverging archosauriforms [Campione *et al.* (2020) and references therein; Appendix S1 and S2.3] and the early-diverging avialan *Archaeopteryx lithographica* (e.g. Foth *et al.*, 2014). Basally branching archosauriforms such as *Proterosuchus* (Thornley, 1970) and *Longisquama* (Reisz & Sues, 2000) were chosen as the outgroup over pterosaurs because the latter already show particularly derived integuments such as a non-scaly skin forming an airfoil and complex filamentous structures (Bakhurina & Unwin, 1995; Frey *et al.*, 2003; Kellner *et al.*, 2010; Barrett *et al.*, 2015; Yang *et al.*, 2019) whereas basalmost archosauriforms show the plesiomorphic condition of having body scales (Reisz & Sues, 2000; Campione *et al.*, 2020). Sauropodomorphs and ornithischians were also excluded as the outgroups because their phylogenetic distribution among dinosaurs is unsettled (see Baron, Norman & Barrett, 2017; Langer *et al.*, 2017; Müller *et al.*, 2018; Baron, 2021) and their most-basal members preserving integument [monofilaments in the heterodontosaurid *Tianyulong*, polygonal basement scales in the sauropod *Mamenchisaurus* (Xu & Guo, 2009; Zheng *et al.*, 2009)] have very different epidermal structures.

The distribution of integument-based characters was visualised on six topological trees representative of alternative phylogenetic hypotheses for non-avian theropod evolution (Appendix S2.1; see Hendrickx *et al.*, 2021b). These informal supertrees were built using Mesquite 3.2 (Maddison & Maddison, 2017) following the results obtained by Godefroit *et al.* (2014) and Boyd (2015) for ornithischians, Müller *et al.* (2018) for non-tetanuran saurischians, Rauhut *et al.* (2012) for non-coelurosaur tetanurans, Delcourt &

Grillo (2018) for tyrannosauroids, and Pei *et al.* (2020) for maniraptoriforms (see Pittman *et al.*, 2020). Variations in the topology result from the differing placement of: (*i*) *Juravenator* as a non-avetheropod tetanuran (Tree1; Rauhut *et al.*, 2012; Foth *et al.*, 2020) or a compsognathid coelurosaur (Tree2; Pei *et al.*, 2020); (*ii*) sauropodomorphs within the clade of Saurischia (Tree1; e.g. Langer *et al.*, 2017; Müller *et al.*, 2018) or as a sister-clade of Ornithoscelida (Tree3; i.e. Theropoda + Ornithischia; Baron *et al.*, 2017); (*iii*) anchiornithines as early-branching avialans (Tree1; Pei *et al.*, 2020) or troodontids (Tree4; Brusatte *et al.*, 2014); and (*iv*) troodontids among Deinonychosauria (Tree1; Turner, Makovicky & Norell, 2012; Pei *et al.*, 2020), as the sister clade of Dromaeosauridae + Averaptora (Tree5; Motta *et al.*, 2020), or as the sister clade of Avialae (Tree6; Avialae = Anchiornithinae + *Archaeopteryx*; Cau *et al.*, 2017; Foth & Rauhut, 2017). Our preferred topology (Tree1) follows a phylogenetic tree in which Sauropodomorpha and Theropoda form the clade Saurischia, *Juravenator* and *Sciurumimus* are classified as early-branching non-avetheropod Tetanurae (N.B., the integument of *Juravenator* is, however, described in the section on Compsognathidae), anchiornithines are placed as the earliest birds, and Deinonychosauria is resolved. Although included in the data matrix for comparative purposes, a large unnamed tyrannosauroid STM 1-5 (Xu *et al.*, 2010) and the contentious maniraptoran *Yixianosaurus longimanus* (Xu & Wang, 2003) were excluded in the analyses because their phylogenetic placement among coelurosaurians is unsettled (Dececchi, Larsson & Hone, 2012; Xu, Sullivan & Wang, 2013; Lambertz, 2017). Conversely, because of its importance in our understanding of feather evolution (Xing *et al.*, 2016; Lambertz, 2017) and while its position among coelurosaurs is unsettled, the specimen DIP-V-15103 was included in the analysis and classified as a basally branching non-neocoelurosaur coelurosaur in a single tree (Tree0) using our preferred tree topology. Character distributions for integument-based features were visualised on each tree using WinClada 1.00.08 (Nixon, 2002) based on the Nexus file created with Mesquite 3.6.1. Only unambiguous changes, which include non-homoplasious (apomorphies) and homoplastic changes (represented in the figures by black and white circles, respectively), were visualised. A list of integument-based apomorphies for each clade and taxon was created using TNT 1.5 (Goloboff & Catalano, 2016) and is provided in Appendix S2.4.

An ancestral state reconstruction analysis was additionally performed in Mesquite 3.6.1 using the parsimony criterion with the integument-based data matrix and the tree topologies Tree1 to Tree6 (see Hendrickx *et al.*, 2021b). The Parsimony-Unordered model was used as it is the software's standard parsimony mapping for categorical data (Appendix S2.1). This calculates the most parsimonious ancestral states at the nodes of the tree assuming one step per state change (unordered or Fitch parsimony). In this analysis, the ichnotaxa *Grallator* and *Eubrontes* (e.g. Gatesy, 2001; Demathieu *et al.*, 2002; Milner *et al.*, 2006a) as well as the non-avialan coelurosaur DIP-V-15103 (Xing *et al.*, 2016), the oviraptorosaur *Ningyuansaurus* (Ji *et al.*, 2012) and the microraptorine IVPP V13476 (Xu & Li, 2016) were excluded as their phylogenetic affinities are insufficiently resolved. The Excel, Mesquite and TNT files used to map integument-based apomorphies and reconstruct ancestral states on different topological trees are deposited and freely available on Dryad (Hendrickx *et al.*, 2021b). The main results of the ancestral state reconstruction analysis are also summarised in Appendix S2.5.

Finally, we followed the phylogenetic definitions compiled by Hendrickx *et al.* (2015) for non-avialan theropods, with the updates provided by Hendrickx & Carrano (2016) and Pittman *et al.* (2020) for non-coelurosaur neotheropods and pennaraptorans, respectively.

(1) Terminology

The anatomical nomenclature used to describe and annotate epidermal scales (Figs 2 and 3) mostly follows the terminology provided by Lucas & Stettenheim (1972) and Bell (2012), except where noted. 'Feather' is used herein to describe a structure in which there is clear evidence of barbs and/or barbules and an inferred origin from a follicle (Campione *et al.*, 2020). Following Campione *et al.* (2020), we use the general term 'filament' to refer to all other non-squamous, non-feather epidermal structures, recognising the fact that these may or may not have differing developmental origins from one another. Plumage herein describes the widespread covering of the body with feathers and/or filaments. Terms relating to squamous integument are organised by categories and defined as follows:

(*a*) *Scale types*

Basement scales (bas) – small to large (typically 1–10 mm, but up to 30 mm) scales forming a major part of the integumentary surface (Bell, 2012; Figs 2B, D–I, 3A).

Feature scales (fes) – large (> 7 mm) and regularly or sporadically arranged scales interspersed among and often having a different morphology from that of the basement scales (Bell, 2012; Figs 2B, D, 3A).

Midline feature-scale (mfs) – feature scales present along the dorsal midline above the neural spines (Bell, 2012).

Podotheca (pod) – layer of scales covering the pes, from the tibiotarsus to the end of the toes, and variously composed of scutate, scutellate, and reticulate scales (Cuesta *et al.*, 2015; Fig. 2C).

Reticulate scales (res) – small circular-to-polygonal scales on the ventral (plantar) surface of the toes and the lateral and posterior surfaces of the metatarsus (Lucas & Stettenheim, 1972; Figs 2C, L, M, 3G, H). Reticulate scales are here divided into primary and secondary reticulate scales.

Primary reticulate scales (prs) – large reticulate scales adjacent to the scutate and scutellate scales (Figs 2L, 3H).

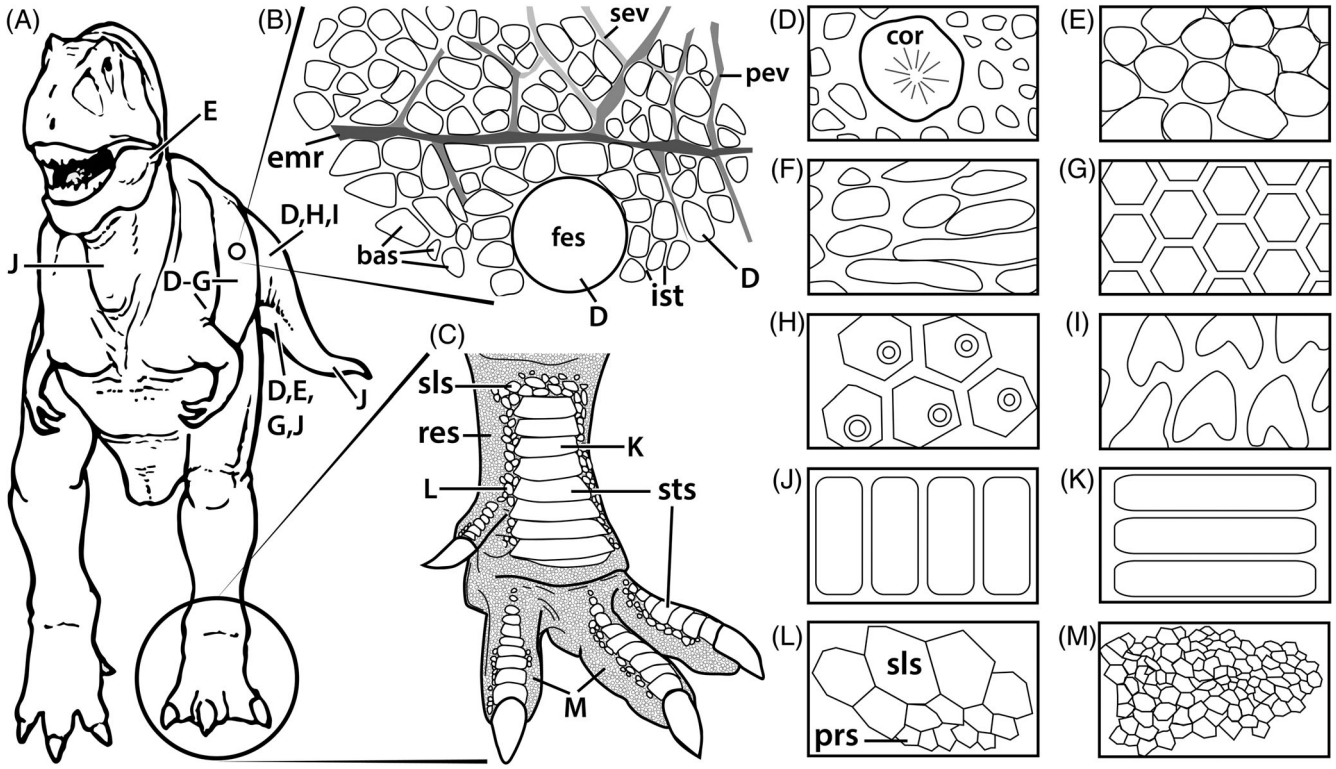


Fig. 2. Scale types and integumentary-based terminology used in this study. (A) Exemplified non-maniraptoriform theropod showing the position of each scale morphotype illustrated in B to M (courtesy of John Sibbick, used with permission). (B) Scaly integument of a non-maniraptoriform theropod from the thoracic region and showing the basement and feature scales separated by the interstitial tissues. (C) Podotheca from the pes of a theropod dinosaur and made of scutate, scutellate and reticulate scales (artwork inspired from a drawing by Arturo García). (D) Feature and irregular basement scales. (E) Pebbly basement scales. (F) Oblong basement scales. (G) Polygonal basement scales. (H) Ornamented basement scales. (I) Sagittate basement scales. (J) Scutate ventral scales. (K) Scutate scales. (L) Scutellate scales. (M) Reticulate scales. bas, basement scales; cor, corrugations; emr, epidermal midrib; fes, feature scale; ist, interstitial tissue; pev, primary epidermal vein; prs, primary reticulate scale; res, reticulate scales; sev, secondary epidermal vein; sls, scutellate scales; sts, scutate scales.

Secondary reticulate scales (srs) – small to minute reticulate scales adjacent to the larger primary reticulate scales (Figs 2M, 3H).

Scutate scales (sts) – large, rectangular or polygonal and regularly arranged scales on the anterior and caudal surfaces of the tarsometatarsus, the dorsal surface of the toes, and the ventral surface of the neck, belly and tail (Lucas & Stettenheim, 1972; Chuong *et al.*, 2000; Figs 2C, K, 3C, G). Also referred to as 'scutes' by Lucas & Stettenheim (1972).

Scutellate scales (sls) – rectangular or polygonal and regularly arranged scales smaller than the scutate scales and found adjacent to the scutate scales and on the caudal surface of the metatarsus (Lucas & Stettenheim, 1972; Figs 2C, L, 3H). Also referred as 'scutella' by Lucas & Stettenheim (1972).

Scutate ventral scales (svs) – large, rectangular or stadium-shaped scale covering the ventral surface of the body (Figs 2J, 3C); resembling the ventral scales (known as the gastrosteges) of many snakes.

Tuberculate scales (ts) – general term for any non-imbricating, non-polarised scale (Figs 2B, D, E, G, L, M, 3A–D, G, H). Tubercles can assume many of the forms mentioned here (e.g. pebbly, polygonal, reticulate, scutellate) and may form either basement and/or feature scales.

(*b*) *Scale shape and ornamentation*

Irregular (irs) – basement and/or feature scales with no obvious geometrical sides and whose surface can be smooth or corrugated (Bell, 2012; Figs 2D, 3A).

Oblong (obs) – elongated basement scales with rounded extremities, such as those forming striate-like rows in some

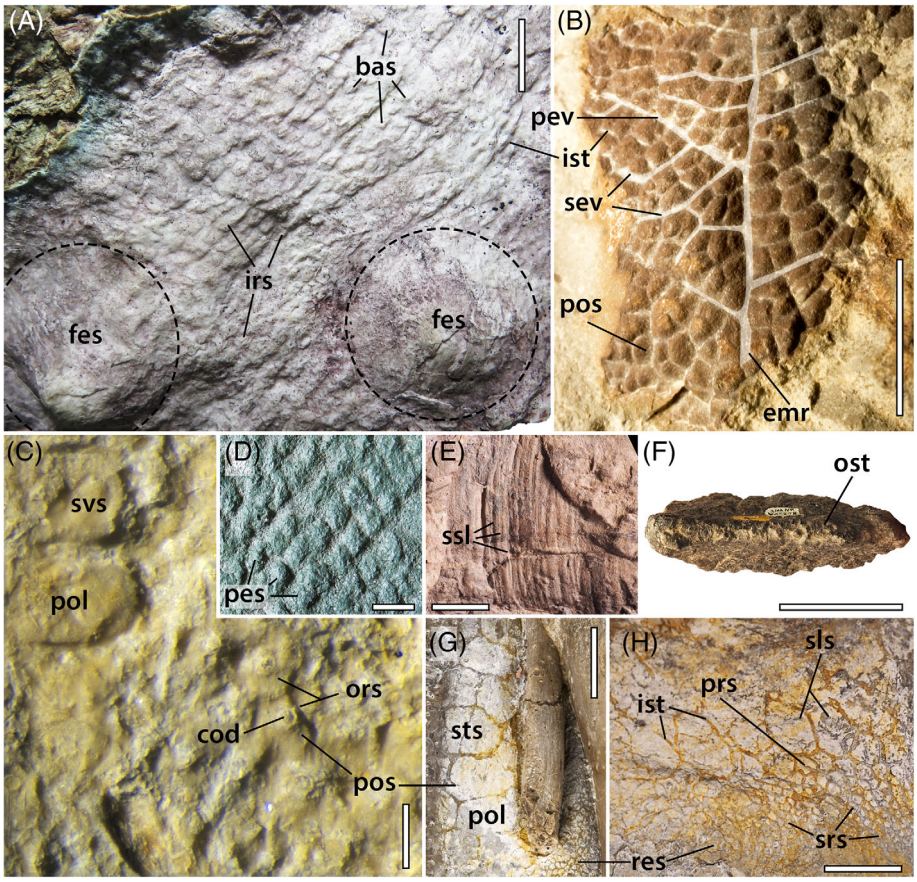


Fig. 3. Terminology used to describe the scaly integument in non-avialan theropods. (A) Mould of the skin from the anterior portion of the tail of the abelisaurid *Carnotaurus sastrei* (MACN-CH 894). (B) Natural mould of the skin from the neck region of the tyrannosaurid *Tyrannosaurus rex* (HMNS 2006.1743.01). (C) Skin impression ventral to the 10th caudal vertebra of the putative compsognathid *Juravenator starki* (JME Sch 200; taken by C. Ifrim and A. Hecker, courtesy of C. Ifrim). (D) Cast of the scaly skin of the tyrannosaurid *Albertosaurus sarcophagus* (TMP 1994.186.0001). (E) Scale scratch lines on the lateral border of the *Eubrontes* track SGDS 451. (F) Dermal ossification of the ceratosaurid *Ceratosaurus nasicornis* (UMNH VP 5278 [UUVP 80]) in dorsal view. (G, H) Skin impressions from the pes of the carcharodontosaurid *Concavenator corcovatus* (MCCM-LH-6666) associated with metatarsals IV and V (G), and over the metatarsals and tarsals (H). bas, basement scales; cod, concentric dome; emr, epidermal midrib; fes, feature scale; irs, irregular scales; ist, interstitial tissue; ors, ornamented scales; ost, osteoderm; pev, primary epidermal vein; pos, polygonal scale; pol, polarised scales; prs, primary reticulate scale; res, reticulate scales; sev, secondary epidermal vein; sls, scutellate scales; srs, secondary reticulate scales; ssl, scale scratch lines; sts, scutate scales; svs, scutate ventral scale. Scale bars = 5 cm (F), 2 cm (A), 1 cm (E, G, H), 5 mm (B, D), and 1 mm (C).

part of the skin of titanosaur embryos (Coria & Chiappe, 2007; Fig. 2F).

Ornamented (ors) – basement scales showing a ring-like circular structure adjacent to several longitudinal ridges (Bell & Hendrickx, 2020; Figs 2H, 3C).

Pebbly (pes) – small basement scale forming a pattern of closely packed, rounded nodes (Bell, 2012; Figs 2E, 3D). Pebbly scales on the plantar surface of the pes are referred to as reticulate scales in accordance with avian terminology (see above).

Polarised (pol) – scale with a distinctly elongated axis (e.g. medial–lateral axis), as in the oblong and scutate scales (Bell, 2012; Figs 2C, F, J, K, 3C, G).

Polygonal (pos) – basement and/or feature-scale with three or more geometrical sides but typically ranging from four to six sides (Bell, 2012; Figs 2G, H, L, M, 3B, C, G, H).

Sagittate (sas) – arrowhead-shaped basement scales, typically showing imbrication (Bell & Hendrickx, 2021; Fig. 2I).

Corrugation (cor) – radial striae on a scale surface (Bell, 2012; Fig. 2D).

Papillae (pap) – minute (∼1 mm diameter) dome-like protrusions on the scale surface variously described as bumps, papilliform texture, or tubercles (e.g. Foster & Hunt-Foster, 2011); commonly associated with sauropod scales.

Scale scratch lines (ssl) – parallel striations associated with vertebrate tracks and traces (Fig. 3E). They are produced by scales (usually from the pes in theropods) scratching the substrate and are often good indicators of digit and foot movement. Estimations of scale diameters can be

measured from these scratch lines (Milner *et al.*, 2006b; Milner & Lockley, 2016).

(*c*) *Interstitial tissue*

Epidermal midrib (emr) – main and/or widest band of interstitial tissue between fields of epidermal scales and from which the secondary veins arise (Figs 2B, 3B). The epidermal midrib and veins subdivide patches of scales on the skin and follow venation patterns similar to those on a leaf (Bell *et al.*, 2017).

Interstitial tissue (ist) – integument of the hinge area between the scales and affording flexibility to the skin (Bell, 2012; Figs 2B, 3A, B, H). Also referred to as the 'hinge area'.

Primary epidermal vein (pev) – accessory groove of interstitial tissue laterally arising from the epidermal midrib. Primary epidermal veins tend to be subparallel to each other and obliquely oriented from the epidermal midrib (Figs 2B, 3B).

Secondary epidermal vein (sev) – accessory groove of interstitial tissue arising laterally from the primary epidermal vein (Figs 2B, 3B).

(*d*) *Dermal ossifications and osteoderm morphotypes*

Osteoderms (ost) – dermally derived bone-rich organs, which vary widely in form and location across the body (Fig. 3F). Osteoderm morphotypes are either sagittate or mosaic in theropods.

Sagittate (sag) – elliptical osteoderm in dorsal view, which is flared ventrally and has a prominent anteroposteriorly elongated dorsal keel conferring a distinct Eiffel-tower outline in anterior and posterior views (Fig. 3F).

Mosaic (mos) – osteoderm with indistinct and variable morphologies (D'Emic, Wilson & Chatterjee, 2009).

IV. RESULTS

Below, we provide brief descriptions of the squamous integument preserved in currently known non-avialan theropods. A comprehensive description of each of these is given in Appendix S3.

(1) Stem-averostran Theropoda

Information on integumentary structure in non-averostran theropod saurischians is particularly scarce and rests only upon skin impressions from pedal tracks uncovered in Greenland, France, and the USA. To our knowledge, epidermal structure with a well-defined pattern is unknown for the rest of the body in Coelophysoidea and other stem-averostran Theropoda. Integument impressions have been described in the famous trace of a crouching theropod AC 1/7 from the Lower Jurassic Portland Formation of Massachusetts, USA (Hitchcock, 1858, 1865; Gierliński, 1994, 1997; Lockley, Matsukawa & Jianjun, 2003; Kundrát, 2004). Impressions of filamentous appearance are preserved on the ischiadic imprint and the marginal line of the pre-pubic imprint in the abdominal region of a theropod dinosaur in a resting posture (Kundrát, 2004). These filamentous imprints have been suggested to be feather impressions from semiplume-like structures (Gierliński, 1997) or branched feathers (Kundrát, 2004). If true, the specimen AC 1/7 would be the earliest-diverging theropod with evidence of feathers. Lockley *et al.* (2003) and Martin & Rainforth (2004) have, nevertheless, interpreted these fine parallel striations as the result of the motion of the scaly skin against the substrate (i.e. scale scratch lines) and pressure-release structures caused by the movement of the theropod when shifting its weight and standing up, respectively. Small trapezoid tuberculate scales are nonetheless present on the right posterior metatarsals of AC 1/7, representing a rare example of scaly skin in a body part other than the sole of the foot in a non-averostran theropod. This is further supported by the presence of scale scratch lines from the tail region of a probable theropod in one *Characichnos* swim track from the Lower Hettangian Moenave Formation of Utah (Milner *et al.*, 2006b; Appendix S3.1).

Grallator tracks from the Upper Triassic–Lower Jurassic of Greenland, Utah, and France preserve reticulate scale impressions and/or parallel scale scratch lines but vary in the arrangement of the scales (Gatesy, 2001; Demathieu *et al.*, 2002; Fig. 4; Appendix S3.1). The largest collection of these come from 19 tracks from the Norian–Rhaetian of Greenland (15–23 cm in length) in which scales are collectively found on all digital pads. Despite the variation in footprint length, scales are homogenous, consisting of polygons (1–2 mm diameter, with interstitial spacing up to 0.5 mm) arranged into roughly hexagonal clusters (Gatesy, 2001; Fig. 4A) or parallel, longitudinal rows (SGDS 642 Fig. 4B, C). Other *Grallator* tracks from the Early Jurassic of France (Fig. 4E–H) show a different pattern in which the smallest scales are found on the central part of each digital pad and increase in size centrifugally (Fig. 4F, G). This pattern is reversed on the metapodium where scales decrease in size centrifugally (Demathieu *et al.*, 2002, Plate 5, figures 6 and 8; Fig. 4H). Short ridges likely representing folds of skin on the underside of the foot are also found in at least one *Grallator* track (SGDS 1211) from the lower Hettangian St. George Dinosaur Discovery Site of Utah (Appendix S3.1).

Eubrontes tracks from North America are considered to have been produced by a relatively large theropod similar to the stem-averostran *Dilophosaurus* (Marsh & Rowe, 2020; Marsh *et al.*, 2021). Numerous *Eubrontes* tracks (23–37 cm long) from the Early Jurassic Moenave Formation include skin impressions (Milner *et al.*, 2006b; Fig. 5). Despite the range of foot sizes, scales are relatively uniform and consist of circular or ill-defined polygons (0.6–1.75 mm diameter) and arranged into longitudinal, transverse, or oblique rows on proximal digit IV, digits III and IV, and proximal digit II, respectively as seen in Fig. 5B, C, E and F (Appendix S3.1).

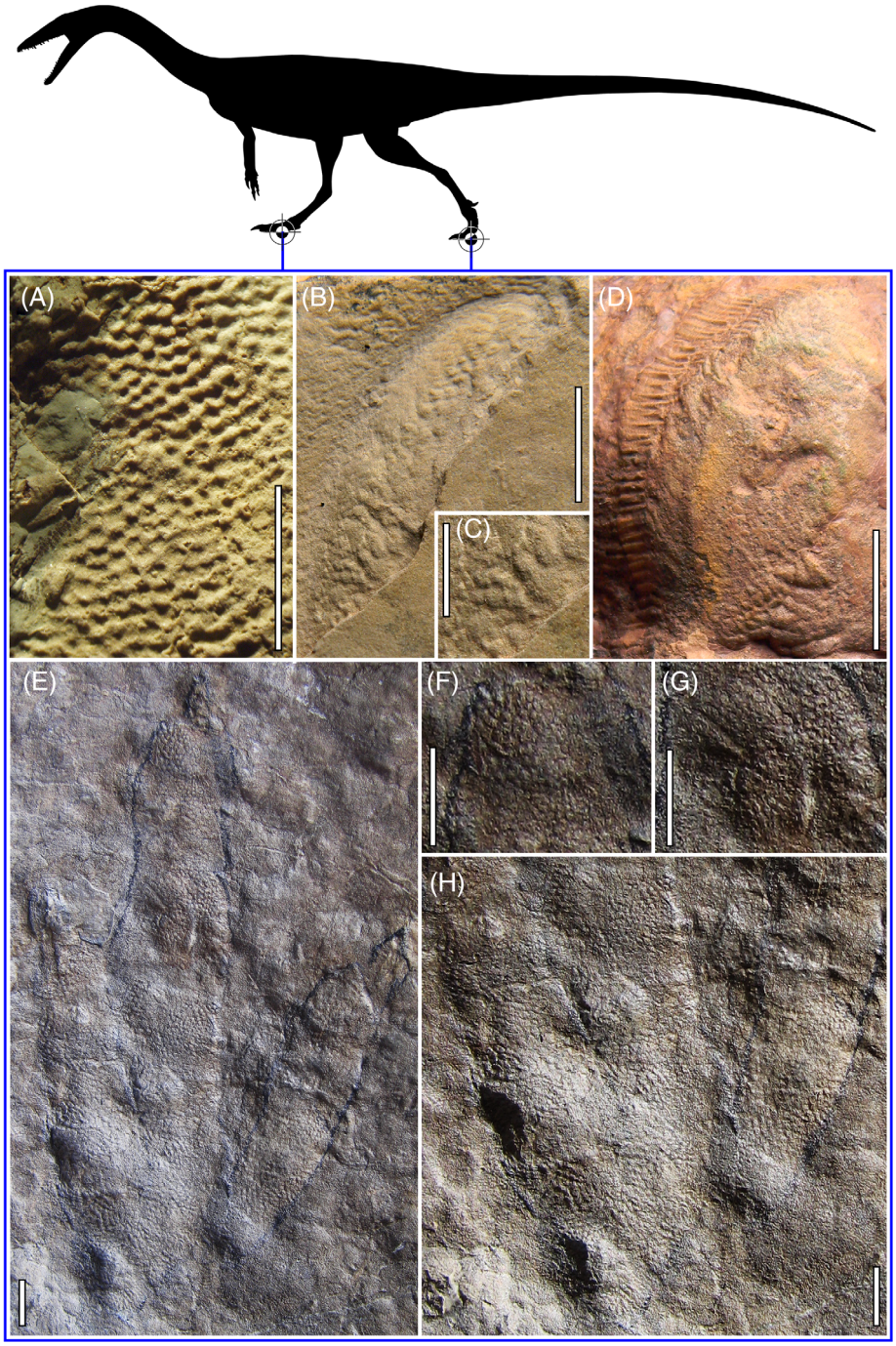


Fig. 4. Integumentary features in *Grallator* isp. (stem-averostran and possibly made by coelophysoid theropods). (A) Negative skin impression showing the reticulate scales from a *Grallator* pedal track reported by Gatesy (2001) from the Fleming Fjord Formation of Jameson Land, Greenland [from Gatesy, Shubin & Jenkins Jr (2005); used with permission]. (B–D) Natural mould of reticulate scales, and scale scratch lines from the distal pad of pedal III from the *Grallator* tracks SGDS 642 (B, C), and SGDS 1165 (D), from the Moenave Formation of St. George Dinosaur Discovery Site, Utah, USA. (C) Close up of the scales in SGDS 642. (E–H) Natural mould of a pedal track referred to *Grallator variabilis* by Demathieu *et al.* (2002) from the Grand-Causses Formation of Novis, Massif Central, France, with close up of the reticulate scales from the distal (F), and middle pads of digit II (G), as well as the posterior half of the track (H) (courtesy of Jacques Sciau, used with permission). Scale bars = 1 cm (B, D–H), and 5 mm (A, C). Black silhouette from Scott Hartman (for licence attribution, see Appendix S4).

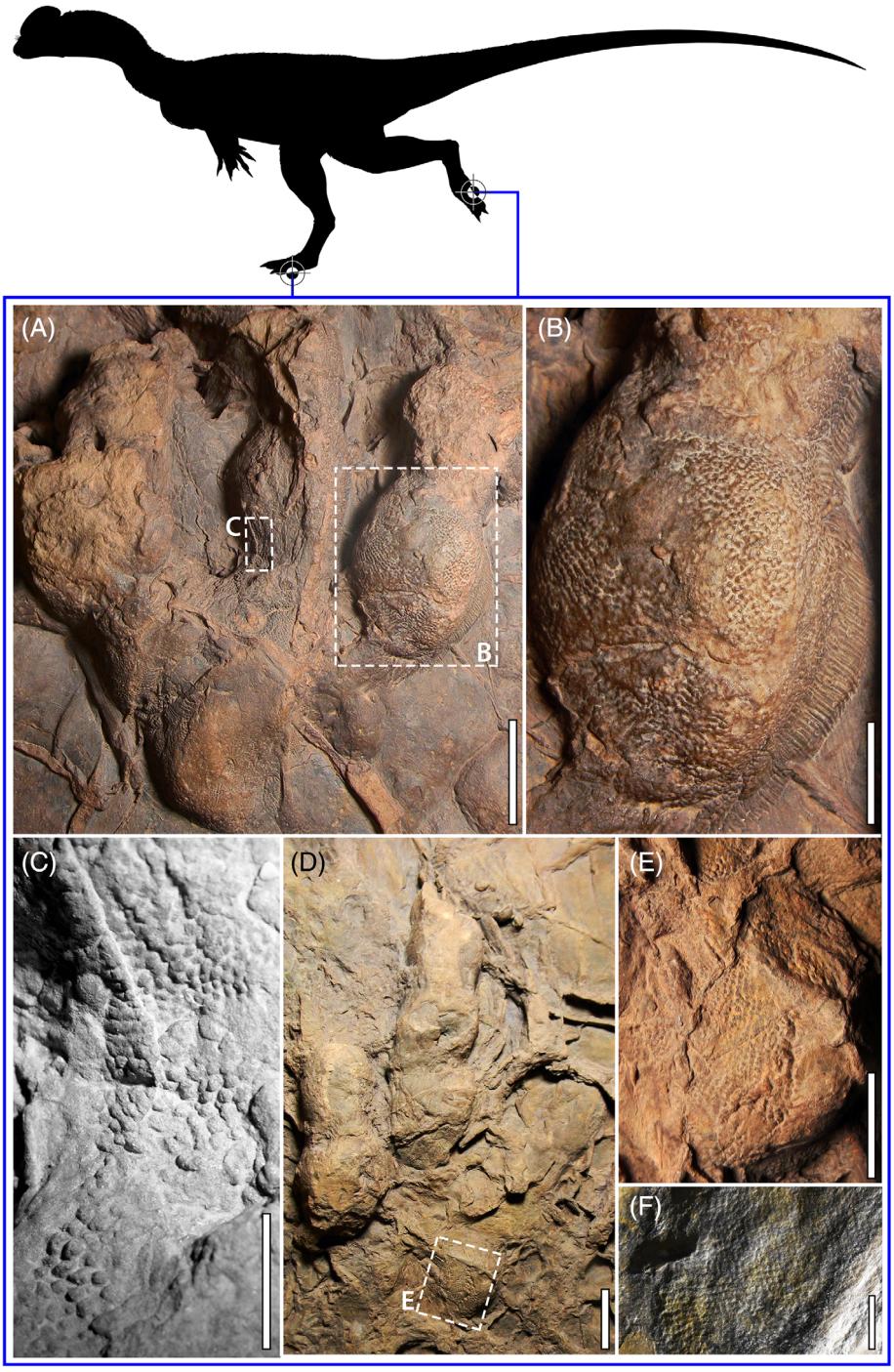


Fig. 5. Integumentary features in *Eubrontes* isp. (stem-averostran and probably made by dilophosaurid theropods), from the Moenave Formation of St. George Dinosaur Discovery Site, Utah. (A–C) Natural mould of the pedal track SGDS 15-T1, with close up of the reticulate scales from the proximal pad of pedal digit II (B), and the posterior portion of the proximal pad of pedal digit III (C). (D, E) Natural mould of the pedal track SGDS 451, with (E) close up of the reticulate scales from the posterior portion of the proximal pad of digit IV. (F) Natural mould of the reticulate scales from the proximal pad of pedal digit II of the pedal track AC 56/1. Scale bars = 5 cm (A, D), 3 cm (E), 2 cm (B), 1 cm (C, F). Black silhouette from Julio Garza (for licence attribution, see Appendix S4).

(2) Indeterminate averostrans

Skin impressions on tracks ascribed to indeterminate theropods have been reported from Cretaceous deposits of South Korea (Kim *et al.*, 2019), the USA (Noe, Lockley & Hadden, 2014), and Canada (Rylaarsdam *et al.*, 2006; Appendix S3.2). Because ceratosaurians and tetanurans are

the only clades of theropods extending to the Cretaceous (Hendrickx *et al.*, 2015), the trackmakers are assigned to indeterminate averostrans.

One of the best collections of tracks preserving true skin impressions is that of five diminutive *Minisauripus* footprints (2.38 cm in average length) from the Aptian of South Korea (Kim *et al.*, 2019; Appendix S3.2). In each of the tracks, scales are impressed across the entirety of the foot revealing minute polygonal reticulate scales (up to 0.5 mm diameter), the smallest of which are found in the posteriormost part of the footprint as well as the interdigital valleys of the metapodium. Unlike the Greenland *Grallator* tracks (Gatesy, 2001; Demathieu *et al.*, 2002), reticulate scales were also arranged into linear (not hexagonal) configurations (Kim *et al.*, 2019; Appendix S3.2). A large track (42 cm long) from the Cenomanian of Colorado assigned to the ichnogenus *Magnoavipes* preserves a small patch of circular-to-elliptical reticulate scales (1–3 mm diameter) and equivalent-sized scale scratch lines on the posterolateral portion of the heel (Noe *et al.*, 2014). Similar reticulate scales and scale scratch lines have also been reported in an indeterminate averostran track from the Turonian of western Canada (Rylaarsdam *et al.*, 2006; Appendix S3.2).

(3) Ceratosauria

Our knowledge of integumentary structures in ceratosaurian theropods is based on only two taxa, namely *Ceratosaurus nasicornis* and *Carnotaurus sastrei*, in which dermal ossifications and extensive patches of scaly skin were recovered, respectively. Traces of soft tissue were reported in the abelisaurid *Aucasaurus garridoi* by Coria, Chiappe & Dingus (2000), but those structures have since been reinterpreted as sedimentary in origin and not soft tissue of any sort (R. Coria, personal communication March 2016).

Ceratosaurus holds the distinction of being the only known theropod to have had definite postcranial osteoderms (Fig. 6). Dermal ossifications were historically described in three other theropods, namely, the abelisaurid *Lametasaurus indicus* (Matley, 1923; Chakravarti, 1935), the tyrannosaurid *Dynamosaurus imperiosus* (= *Tyrannosaurus rex*; Osborn, 1905, 1906), and *Nuthetes destructor* (Owen, 1878, 1879), originally thought to be a lizard and later classified as a dromaeosaurid theropod (Milner, 2002). However, their morphology and/or association with the material of non-theropod reptiles with dermal ossifications (e.g. titanosaurids, *Triceratops*, turtles) strongly suggest that the osteoderms do not belong to these theropods (Osborn, 1906; Barrett *et al.*, 2002; Carrano & Sampson, 2008; Appendix S3.3). The dermal ossifications of *Ceratosaurus* consist of mosaic and sagittate osteoderms of varying sizes preserved along the dorsal midline of the neck and proximal tail of the holotype (USNM 4735; Gilmore, 1920; Fig. 6A–P). The largest cervical osteoderms are sagittate, i.e. they are elliptical in dorsal view, ventrally flared, and bear a dorsal sagittal keel (Fig. 6F, G), conferring an 'Eiffel-tower' outline in posterior view. A large number of dermal ossifications with the same sagittate morphology have been found isolated with at least three additional *Ceratosaurus* individuals from Colorado (MWC 1) and Utah (BYU-VP 12893; UMNH VP 5278; Madsen & Welles, 2000; Fig. 6Q–T; Appendix S3.3, Fig. S1). Conversely, mosaic osteoderms are present above the caudal and some cervical vertebrae. They are anteroventrally elongated, transversally compressed, and irregularly shaped (Fig. 6I–P; Appendix S3.3). Whether these osteoderms originally formed a continuous midline structure or were restricted to the cervical and caudal parts is unknown.

The first body skin ever reported in a non-avialan theropod was that of the abelisaurid *Carnotaurus* from the latest Cretaceous of Argentina (Bonaparte *et al.*, 1990; Fig. 7), which remains one of the best represented non-avialan theropods in terms of preserved epidermal scales (Hendrickx & Bell, 2021b). These cover areas of the rib cage (Fig. 7A–C), shoulder (Fig. 7E, F), and base of the tail (Fig. 7G–K; Czerkas & Czerkas, 1997; Hendrickx & Bell, 2021b; Appendix S3.3). Scaly skin is thought to have been originally preserved on the skull, but was lost following mechanical preparation (Czerkas & Czerkas, 1997; Hendrickx & Bell, 2021b). Likewise, the specimen from the neck with putative integument impression does not show any scales [*contra* Czerkas (1997); Hendrickx & Bell, 2021b]. The other body regions were, however, covered with both basement and feature scales. The basement scales vary from small and oblong, large and diamond-shaped, and circular-to-lenticular in the thoracic, scapular, and tail regions, respectively. Interspersed at irregular intervals throughout the small (<14 mm) basement are unornamented, blunt, conical feature scales (20–65 mm in diameter), whose apices are variously positioned in different body parts (Hendrickx & Bell, 2021b). Contrary to previous interpretations, the feature scales are randomly distributed and neither form discrete rows nor show progressive variations in their size along parts of the body (Hendrickx & Bell, 2021b; Appendix S3.3).

(4) Carnosauria

Despite the large taxonomic diversity of carnosaurians (i.e. Megalosauridae + Spinosauridae + Allosauroidea; *sensu* Rauhut & Pol, 2019), skin is only known in the possible megalosauroid *Sciurumimus albersdoerferi* (Rauhut *et al.*, 2012; Foth *et al.*, 2020) and, among allosauroids, in the allosaurid *Allosaurus jimmadseni* (Ayer, 1999; Pinegar *et al.*, 2003), the carcharodontosaurid *Concavenator corcovatus* (Cuesta *et al.*, 2015), and an embryo referred to the putative metriacanthosaurid *Lourinhanosaurus antunesi* (ML 565-155). Epidermal structures have yet to be reported in members of the non-allosauroid clade Spinosauridae and the allosauroid clades Piatnitzkysauridae, Metriacanthosauridae, Neovenatoridae (with or without Megaraptora), and Carcharodontosaurinae.

Although best known for the bushy squirrel-like tail for which it was named, small patches of smooth featureless skin are preserved in the holotype of *Sciurumimus*. These occur dorsal to the acromion process of the left scapula; the right

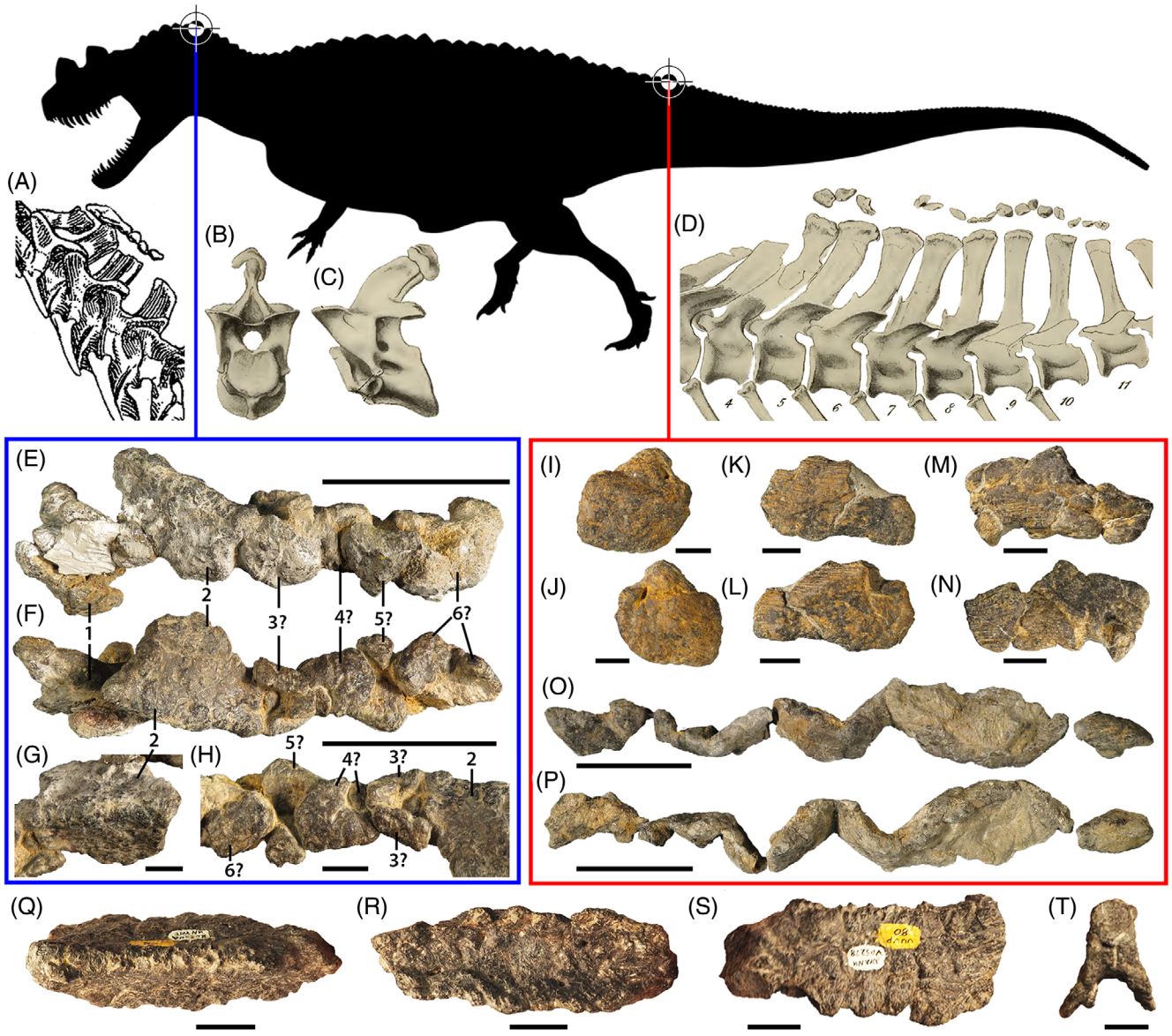


Fig. 6. Dermal ossifications in the ceratosaurid *Ceratosaurus nasicornis*. (A) Distribution of the osteoderms from cervical vertebrae 3 to 5 [from Gilmore (1920), plate 30, modified]. (B, C) Sagittate osteoderm in direct contact with the neural spine of the third cervical vertebra in (B) anterior and (C) lateral views [from Gilmore (1920), plate 20, figures 1–2, modified]. (D) Distribution of mosaic osteoderms on the caudal vertebrae 4 to 11 [from Gilmore (1920), plate 22, figure A; modified]. (E–H) Dermal ossifications from the cervical vertebrae 3 to 5 in lateral (E), and dorsal views (F–H), with close up of the second sagittate osteoderm (G) and putative third to sixth mosaic osteoderms from the set (G). (I–P) Mosaic osteoderms from caudal vertebrate 5 to 11, with close up of (I, J) the first and (K, L) second ossifications from caudal 4, the third osteoderm from caudal 5 (M, N), and the remaining osteoderms from caudal 6 to 10 (O, P). (Q–T) Isolated sagittate osteoderm (UMNH VP 5278 [UUVP 80]) "likely assigned to *Ceratosaurus dentisultacus*" by Madsen & Welles (2000), p. 32, figure 8D) in dorsal (Q), ventral (R), lateral (S), and anterior or posterior views (T). Scale bars = 5 cm (E, F; O, P), 2 cm (Q–T), and 1 cm (G–N). Black silhouette from Scott Hartman (for licence attribution, see Appendix S4).

humerus, ulna and radius; left femur and tibia, and proximal tail (Rauhut *et al.*, 2012; Foth *et al.*, 2020). An extensive plumage of monofilaments, which is preserved on the tail, is suggested to have obscured the smooth skin in life. Skin is present in the shoulder region of an embryonic specimen assigned to *Lourinhanosaurus antunesi* and reported here for the first time (Fig. 8A–C). The skin consists of tiny (~0.3 mm in diameter) subcircular basement scales separated by deep and relatively wide interstitial tissue (Fig. 8B, C). Two individuals assigned to *Allosaurus jimmadseni* preserve pebbly basement scales associated with the anterior dorsal ribs/pectoral region (WDC DMQ-A 053; Fig. 8F–J) and

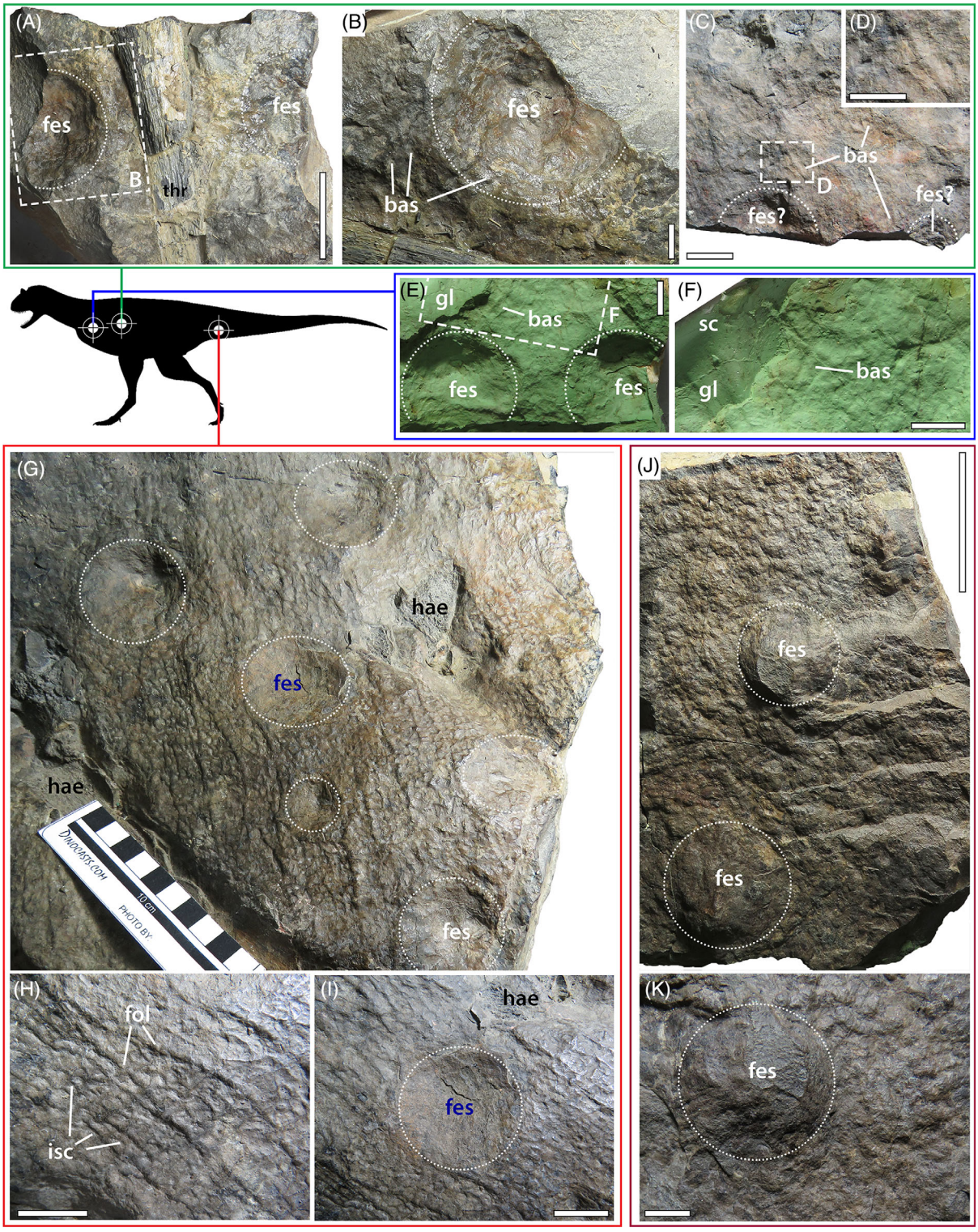


Fig. 7. Squamous skin in the abelisaurid *Carnotaurus sastrei* (MACN-CH 894). (A–D) Negative skin impression in a first (A, B) and second (C, D) specimen from the thoracic region, with close up of the feature and basement scales (B, D). (E, F) Negative skin impression on a mould of the scapular area, with close up of the glenoid area and the basement scales (F). (G–I) Negative skin impression from the anteroventral portion of the tail, with close up of the basement scales and folding (H), and a feature scale anterior to the chevron (I). (J, K) Natural mould of the scaly skin from the caudal? region, with close up of a feature scale and the surrounding basement scales (K). bas, basement scales; fes, feature scale; fol, skin folding; gl, glenoid fossa; hae, haemal arch; isc, irregular scales; thr, thoracic rib; sc, scapulocoracoid. Scale bars = 5 cm (A, J), 2 cm (C, E, F, H, I), and 1 cm (B, D, K). Black silhouette from Scott Hartman (for licence attribution, see Appendix S4).

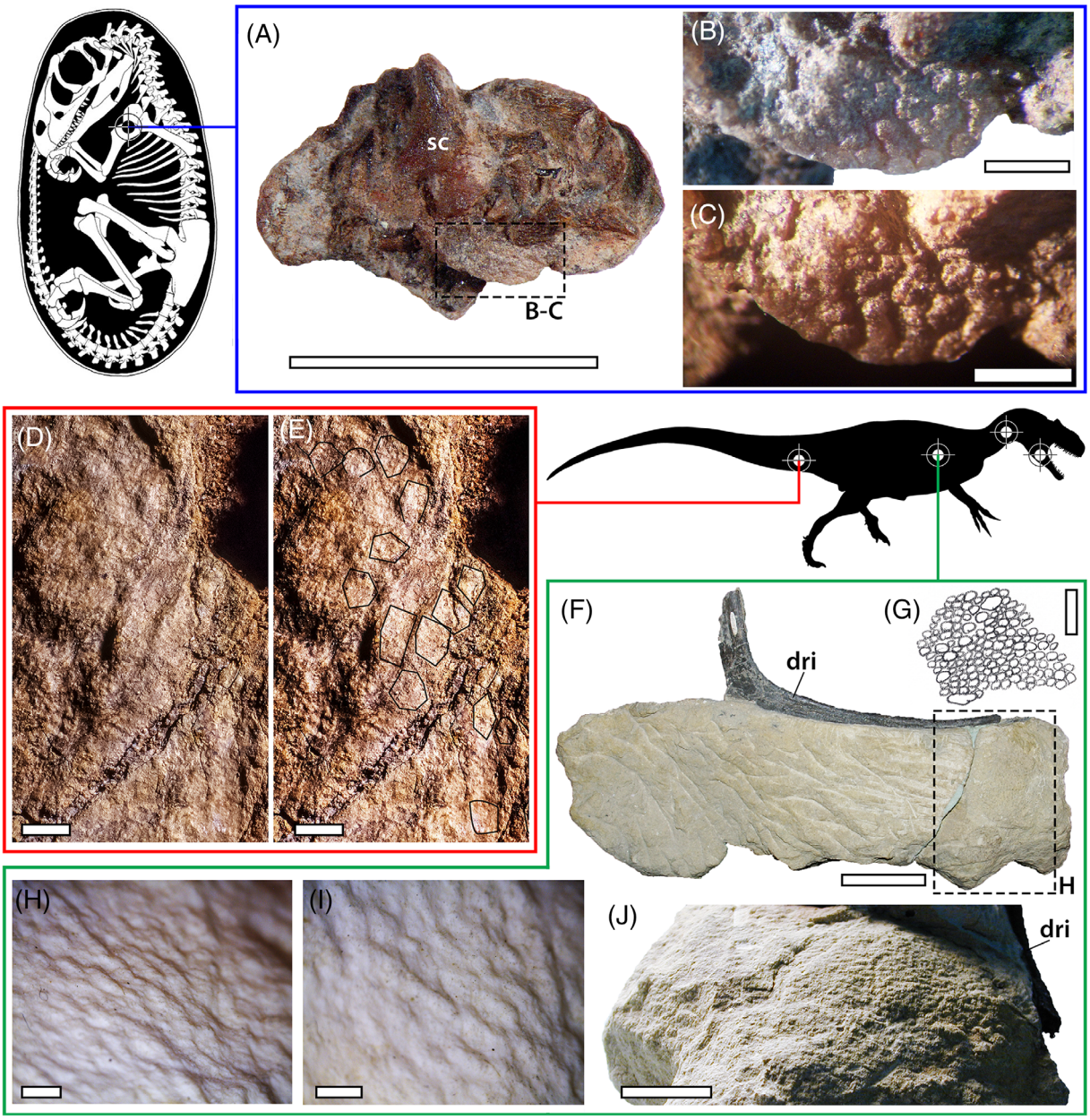


Fig. 8. Integumentary features in the non-carcharodontosaurid allosauroids cf. *Lourinhanosaurus* and *Allosaurus*. (A) Scapular region of an embryo referred to the putative metriacanthosaurid *Lourinhanosaurus antunesi* (ML 565-155). (B, C) Close up of a natural mould of the scaly skin. (D, E) Negative skin impression from the anterior tail region of an adult *Allosaurus jimmadseni* (SMA 0005), with interpretive drawing of the polygonal basement scales (E) (Sauriermuseum Aathal specimen, photograph by Urs Möckli; used with permission). [This skin specimen may also belong to a non-theropod dinosaur such as a diplodocid; see Appendix S3.4]. (F–J) Pebbly basement scales associated with a dorsal rib from the scapular region of a juvenile *Allosaurus jimmadseni* (WDC DMQ-A 053), with interpretive drawing of the basement scales (G), and close up of a plastic cast of the counterpart of the scales (UMNH VP C481, Courtesy of Natural History Museum of Utah), and of a natural mould of the scaly skin (WDC DMQ-A 053) anterior to the distal portion of a dorsal rib (H–I). dri, dorsal rib; sc, scapula. Scale bars = 5 cm (F), 2 cm (D, E, J), 1 cm (A, G), 2 mm (H, I) and 1 mm (B, C). Black silhouette from Scott Hartman (for licence attribution, see Appendix S4).

larger (∼2 cm diameter) polygonal-to-subcircular basement scales on the proximal tail (SMA 0005; Fig. 8D, E). Whether these variations are due to differences among body regions, individual variation, ontogeny, or a combination of these is unknown. We note that the dimensions of the scales associated with SMA 0005 are, however, closer to those of a sauropod (Appendix S3.4, Fig. S2), whose remains were found in abundance on the same site as SMA 0005, and

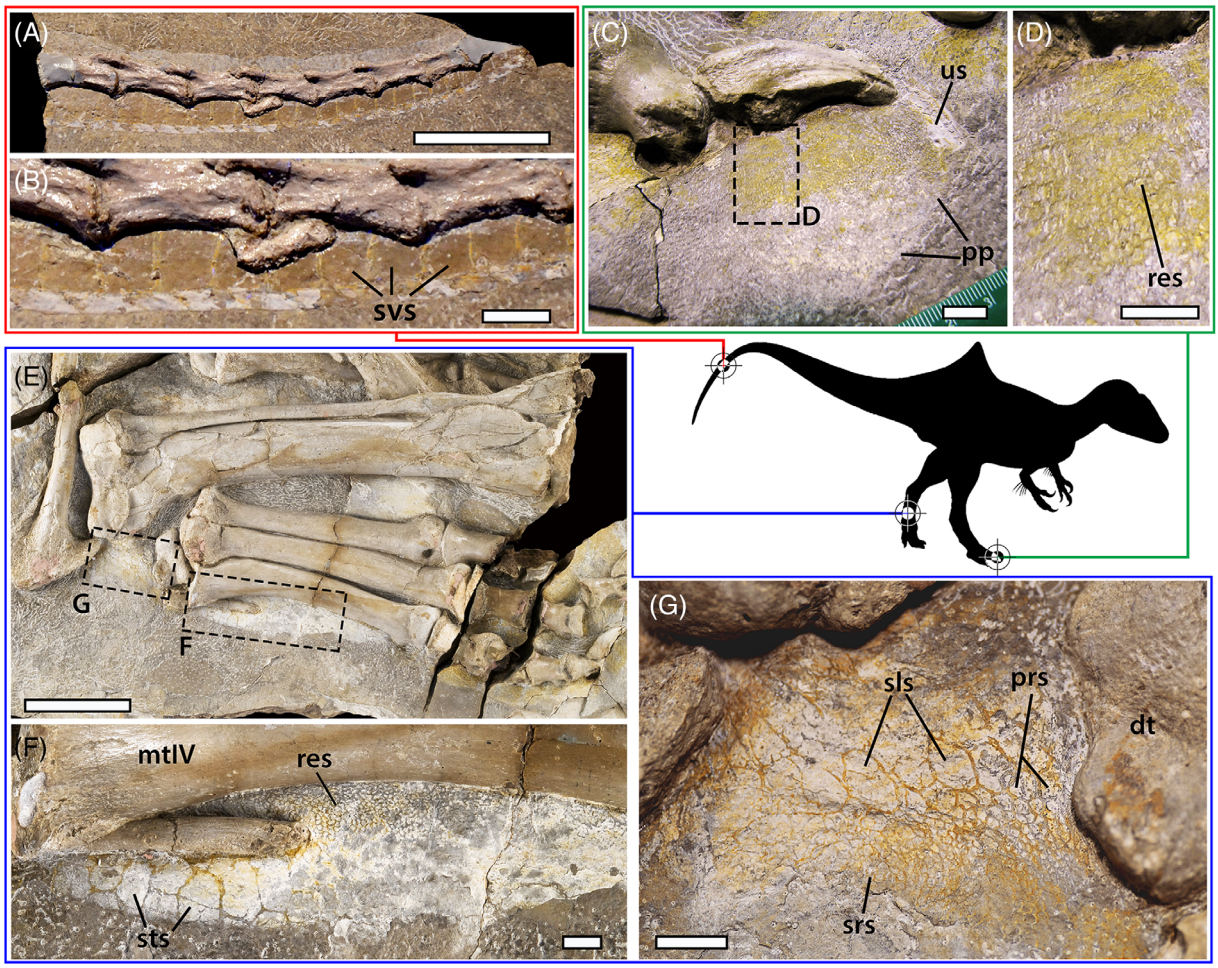


Fig. 9. Preserved integument in the carcharodontosaurid *Concavenator corcovatus* (MCCM-LH 6666). (A, B) Distal tail showing polarised ventral scales and phosphatised tissues outlining the dorsal and ventral tail margins. (C, D) Distal phalangeal pads of the right pedal digit IV with pebbly reticulate scales. (E–G) Right hindlimb showing reticulate and scutate scales associated with the metatarsals (F), and between the proximal tarsal and distal tibia (G). dt, distal tarsal; mtIV, metatarsal IV; pp, plantar pad; prs, primary reticulate scales; res, reticulate scales; sls, scutellate scales; srs, secondary reticulate scale; sts, scutate scales; svs, scutate ventral scales; us, ungual sheath. Scale bars = 10 cm (E), 5 cm (A), and 1 cm (B–D, F, G). Black silhouette modified from an illustration by R. Martín in Ortega, Escaso & Sanz (2010, figure 2a).

consequently do not reject the hypothesis that the skin instead belongs to a non-theropod dinosaur (Appendix S3.4). A third specimen of *Allosaurus jimmadseni* (KNHM 11) additionally shows that part of the mandible was covered with minute pebbly scales whereas the ventral portion of the neck appears to show broad scutate ventral scales (Appendix S3.4).

The best-preserved skin in any carnosaurian comes from the carcharodontosaurid *Concavenator* (Fig. 9), which preserves an avian-style podotheca with scutate (Fig. 9F), scutellate, and reticulate scales (Fig. 9G) combined with arthral plantar pads in which the interpad creases do not align with the interphalangeal joint (Cuesta *et al.*, 2015; Cuesta, Ortega & Sanz, 2016; Fig. 9C, D; Appendix S3.4). Rectangular ventral scales, reminiscent of those in extant snakes, also lined the underside of the tail (Bell & Hendrickx, 2021; Fig. 9A, B). Possible quill knobs on the ventral margin of the ulna hint at the presence of elongated feathers on the forearms (Ortega *et al.*, 2010), although alternative hypotheses have been proposed (Foth *et al.*, 2014; Cuesta, 2017; Appendix S3.4).

(5) Tyrannosauroidea

Tyrannosauroids are the theropod clade for which scaly integuments are best known. Whereas the non-tyrannosaurid tyrannosauroids *Dilong* (Xu *et al.*, 2004) and *Yutyrannus* (Xu *et al.*, 2012) from the Early Cretaceous of Liaoning, China, had an extensive pelage of monofilaments or branched filamentous structures, no less than six pantyrannosaurians are preserved with squamous integuments. The presence of scales of various morphology and from different locations along the body supports the hypothesis that

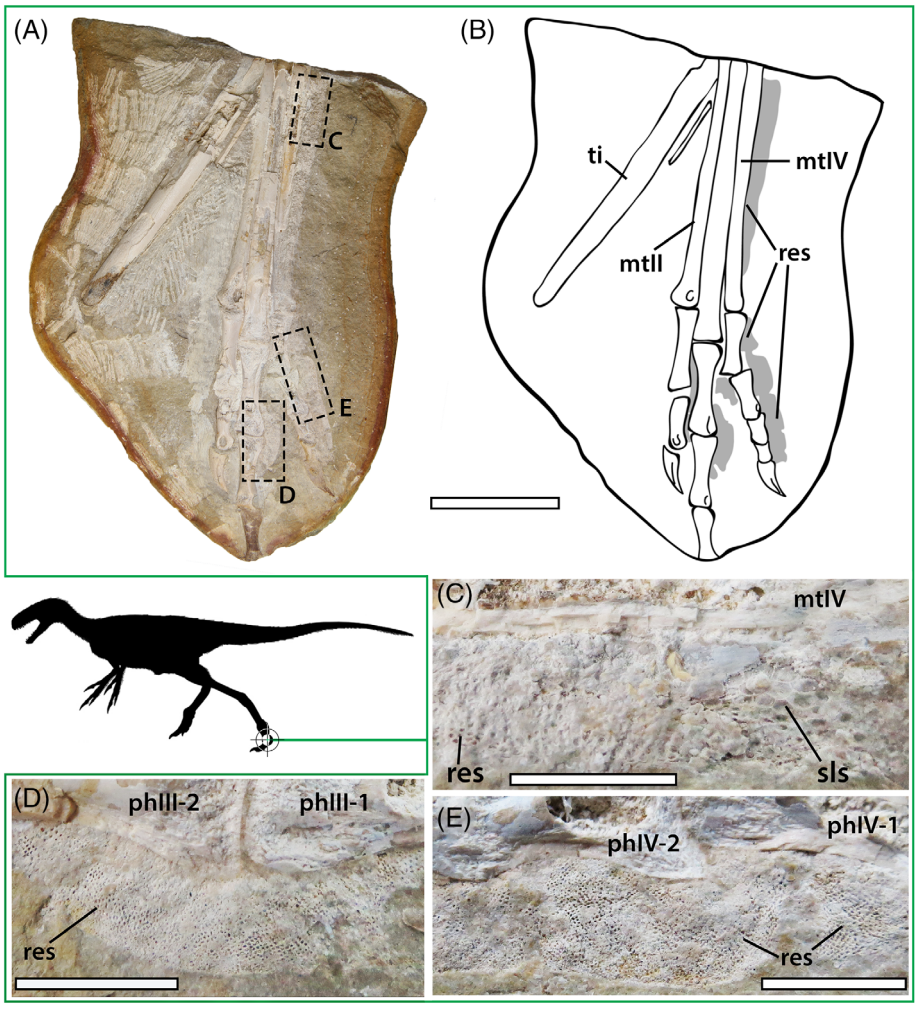


Fig. 10. Preserved integument in the non-tyrannosaurid pantyrannosaurian *Santanaraptor placidus* (MN 4802-V). (A) Tibia, metatarsals, and pedal phalanges. (B) Interpretative drawing of the hindlimb showing the preserved skin (grey zones). (C–E) Close up of the scaly skin from the proximal region of metatarsal IV (C), and the plantar pads between phalanges III-1 and III-2 (D), and phalanges IV-1 and IV-2 (E). mt, metatarsal; ph, phalanx; res, reticulate scales; sls, scutellate scales; ti, tibia. Scale bars = 5 cm (A, B), 1 cm (C–E). Black silhouette from Scott Hartman (for licence attribution, see Appendix S4).

tyrannosaurids were predominantly covered with scales (Bell *et al.*, 2017).

Santanaraptor placidus from the Albian of Brazil is the only early-diverging tyrannosauroid for which featherless skin is known (Fig. 10). Contrary to the original description, which reported "no evidence […] of dermal ossicles, scales, or feathers" (Kellner, 1996, p. 32), personal examination of the holotype shows minute reticulate scales on the plantar surfaces of the left podotheca, specifically lateral to metatarsal IV, and lateral/ventrolateral to digits III and IV (Fig. 10B–E). Larger scutellate scales are also present on a small area adjacent to metatarsal IV (Fig. 10C) suggesting that a different scalation pattern was present on the dorsal part of the foot. The well-preserved plantar pads also show the arthral condition present in other theropods (Appendix S3.5).

Skin is known from a number of later-diverging tyrannosaurids, including *Albertosaurus sarcophagus*, *Daspletosaurus torosus*, *Gorgosaurus libratus*, *Tarbosaurus baatar*, and *Tyrannosaurus rex*, all of which indicate a solely squamous integument contrary to some previous speculations (Bell *et al.*, 2017; Figs 11 and 12). These typically consist of polygonal basement scales from regions of the tail or underbelly in *Gorgosaurus libratus* (Fig. 11A), *Albertosaurus sarcophagus* (Fig. 11B–F), and *Daspletosaurus torosus* (Fig. 12A), whereas those in *Tarbosaurus* are reputedly smaller and pebbly (Currie, Badamgarav & Koppelhus, 2003; Bell *et al.*, 2017; Fig. 12B, C). Feature scales have only been described in *Albertosaurus* where they are associated with the gastral ribs, forming small (7 mm diameter), conical, and corrugated scales (Fig. 11B). Reticulate scales are also present on well preserved footprints attributed to *T. baatar* from the Nemegt

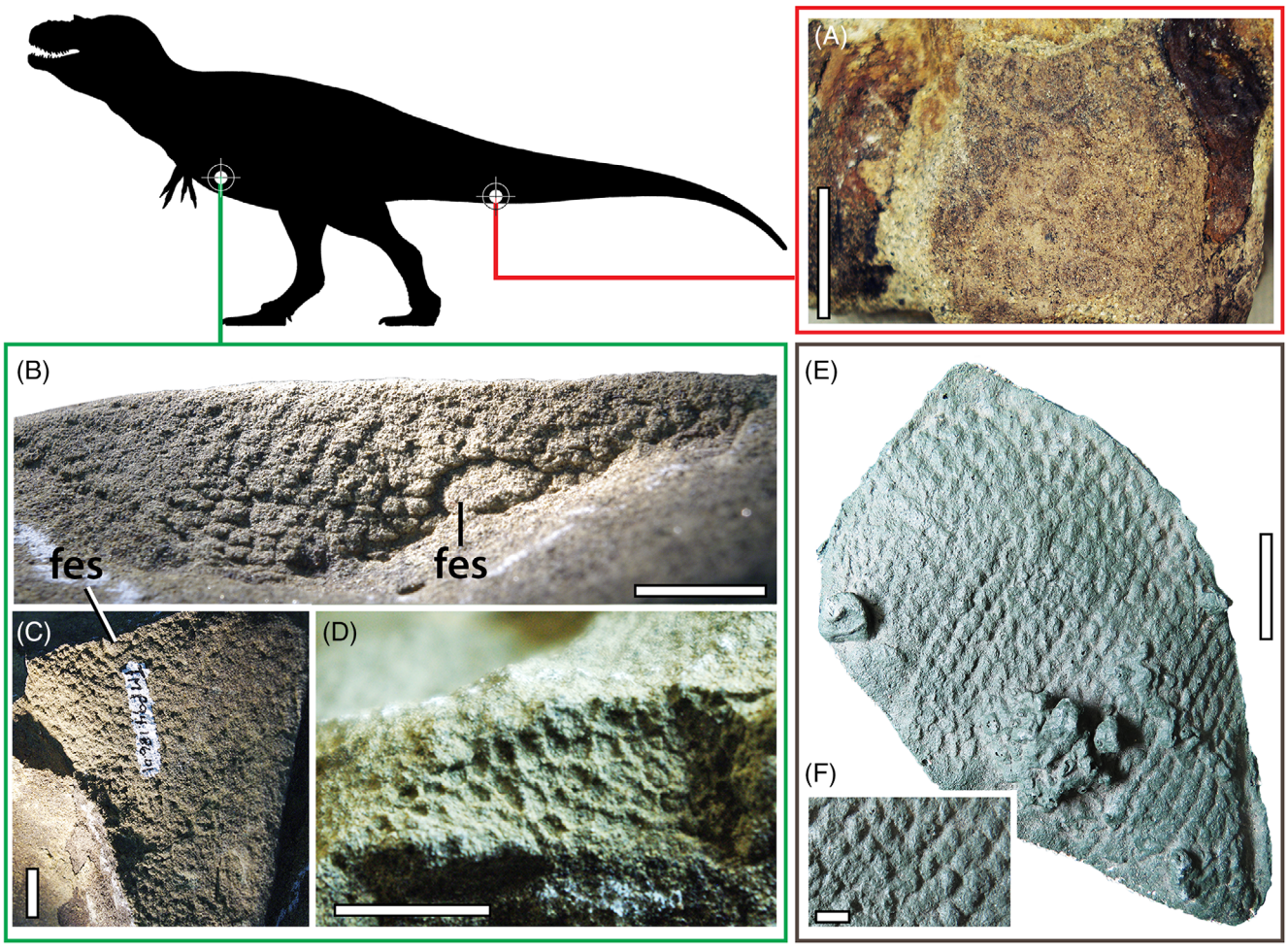


Fig. 11. Squamous skin in Albertosaurinae. (A) Faint polygonal basement scales preserved between two caudal chevrons in *Gorgosaurus libratus* (CMN 11593). (B–D) Skin patches with basement and feature scales associated with a gastral rib in *Albertosaurus sarcophagus* (TMP 1994.186.0001), with natural mould (B, C), and negative skin impression (D). (E, F) Cast of the skin from an unidentified area of the body of *Albertosaurus sarcophagus* (TMP 1994.186.0001), with close up of the polygonal basement scales (F). fes, feature scale. Scale bars = 2 cm (E), 1 cm (A–D), 5 mm (F). Black silhouette from Tasman Dixon (for licence attribution, see Appendix S4).

Formation in Mongolia (Currie, Badamgarav & Koppelhus, 2003; Fig. 12H–L), and a bag of smooth skin under the jaws was also reported in this taxon (Carpenter, 1997, 1999). *Tyrannosaurus* appears to have had a unique configuration of epidermal scales formed of tiny (≤1 mm) polygonal scales that were arranged into triangular or quadrangular clusters separated by epidermal midrib and primary and secondary epidermal veins (Bell *et al.*, 2017; Fig. 12D–G). This arrangement persists in all areas where skin is preserved, including on the neck, pelvis, and tail, suggesting that this pattern of epidermal midrib and veins was consistent across the body (Appendix S3.5).

(6) Compsognathidae

Although compsognathids such as *Sinosauropteryx prima* and *Sinocalliopteryx gigas* are well known to have had an extensive plumage of monofilaments and/or filamentous structures (Chen *et al.*, 1998; Ji *et al.*, 2007; Xing *et al.*, 2012; Smithwick *et al.*, 2017), at least one compsognathid, *Juravenator starki*, preserves diverse scaly integument in addition to short monofilaments on the tail (Göhlich & Chiappe, 2006; Chiappe & Göhlich, 2010; Foth *et al.*, 2020; Bell & Hendrickx, 2020, 2021; Fig. 13A–C). Three distinct scale types are present on the tail (Bell & Hendrickx, 2021): (*i*) sagittate and imbricating scales dorsal to the caudal vertebrae; (*ii*) ornamented polygonal basement scales ventral to the centra, and; (*iii*) mediolaterally broad, stadium-shaped scutate ventral scales that would have formed a continuous single midline row along the ventral surface of the tail (Fig. 13C; Appendix S3.6). Bell & Hendrickx (2020) also interpreted concentrically ringed features on the ornamented scales as possible integumentary sense organs (ISOs) analogous to those in extant crocodylians. If correct, this

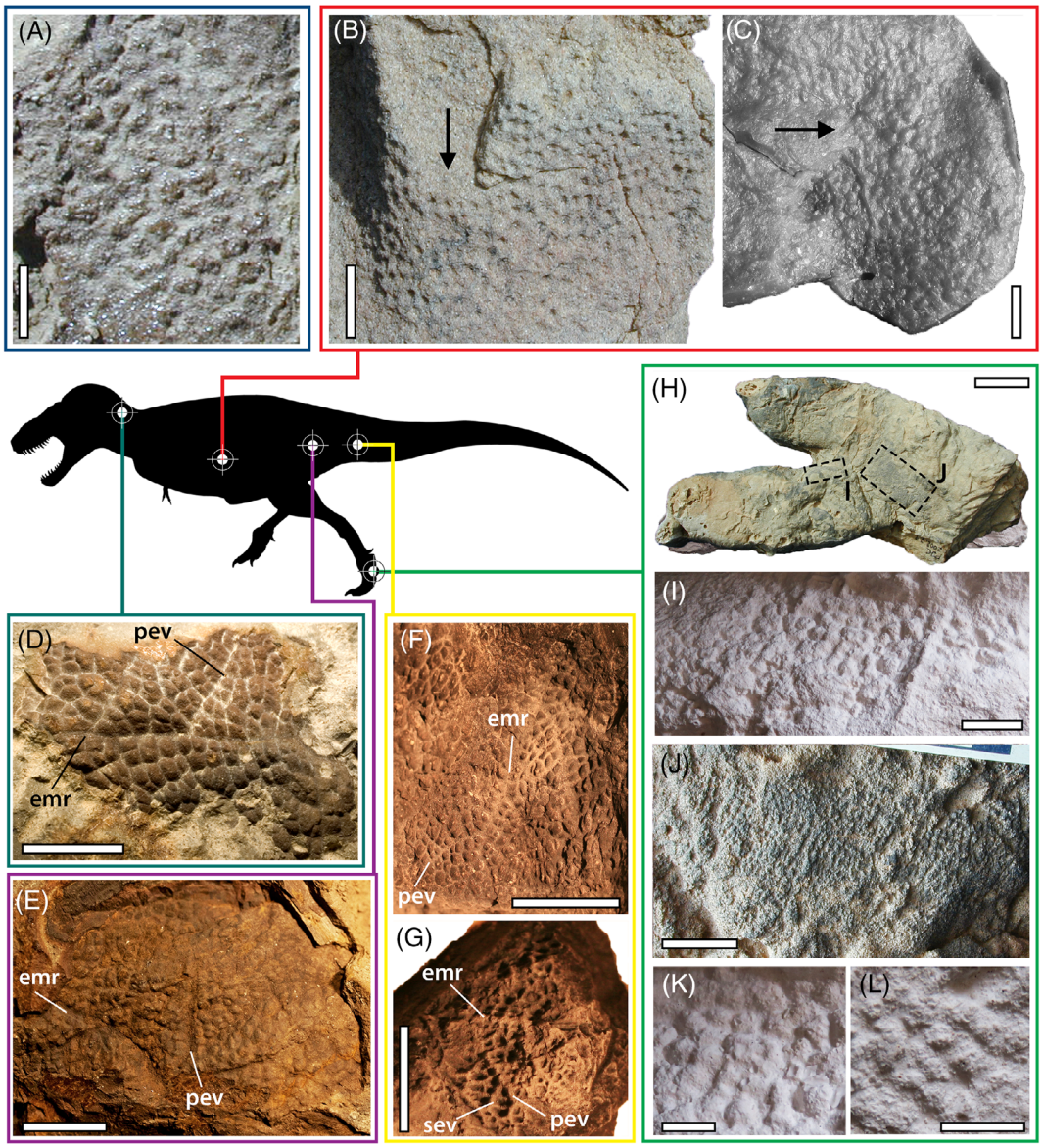


Fig. 12. Squamous skin in Tyrannosaurinae. (A) Basement scales from an unidentified area of the body of *Daspletosaurus torosus* (TMP 2001.036.0001). (B, C) Pebbly skin from the thoracic region of *Tarbosaurus baatar* (MPC 107/6A), with photographs of the negative skin impression taken in the field (B), and a positive mould (TMP 2009.141.0002) of the specimen (C). Positive (D, E) and negative (F, G) skin impression of the scaly integuments of *Tyrannosaurus rex* (HMNS 2006.1743.01) showing the polygonal basement scales and epidermal midribs from the region of the neck (D), the ilium (E), and the anterior portion of the tail (F, G). (H–L) Incomplete pedal track of *Tarbosaurus baatar* (MPC 100F/12) with close up of the skin impression of the middle pad of digit III (plaster cast; TMP 2009.141.0011) (I), the toe base (MPC 100F/12) (J), and the reticulate scales (TMP 2009.141.0011) from the pad of digit III (K), and the toe base (L). emr, epidermal midrib; pev, primary epidermal vein; sev, secondary epidermal vein. Scale bars = 10 cm (H), 2 cm (J), 1 cm (A–C, F, I), 5 mm (D, E, G, K, L). Black silhouette from Scott Hartman (for licence attribution, see Appendix S4).

would be the only direct evidence of discrete sensory receptors in the skin of any dinosaur and among the oldest direct evidence of ISOs in the fossil record (Bell & Hendrickx, 2020).

Traces of dermal bone or thickening of the skin into a swimming paddle were reported by Bidar, Demay & Thomel (1972) in the French specimen of *Compsognathus* (MNHN CNJ 79) from the Calcaires blancs de Provence Formation (early Tithonian) of Canjuers, Var Department, France. However, Peyer (2006) interpreted this putative skin impression as disturbance in the sediment. Peyer (2006, p. 895) also briefly described "uniformly seized [sic], bumpy structures" on the lateral surfaces of the caudal vertebrae in MNHN CNJ 79, drawing comparisons with the caudal integument of *Juravenator*. These 'bumps' occur either as isolated or small clusters of rounded, dome-like structures

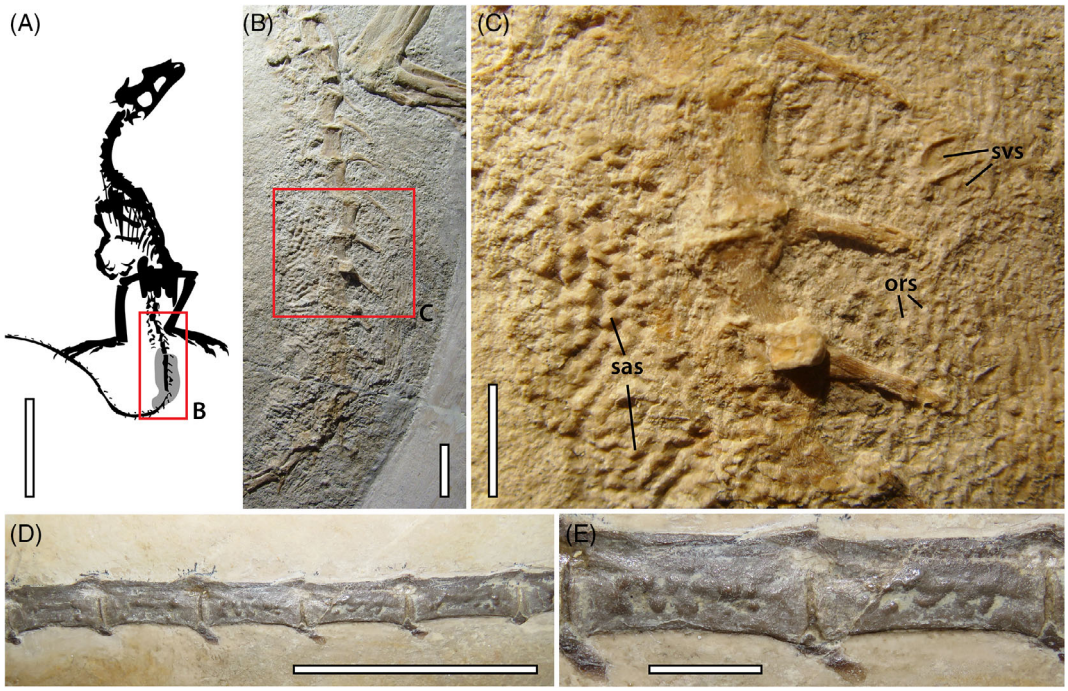


Fig. 13. Integumentary features and aberrant bony outgrowths in the tail region of two Compsognathidae. (A) Black silhouette of the preserved skeleton of *Juravenator starki* (JME Sch 200) showing the preserved skin impression (grey area) at the level of the tail. (B) Close up of the anterior caudal series with skin impression. (C) Preserved scaly skin at the level of the 10th to 12th caudal vertebrae. (D, E) 17th to 21st caudal vertebrae of *Compsognathus longipes* (MNHN CNJ79), with close up of the 19th and 20th vertebrae showing the bumpy structure interpreted as aberrant bony outgrowths (E). ors, ornamented scales; sas, sagittate scales; svs, scutate ventral scales. Scale bars = 10 cm (A), 5 cm (D), 1 cm (B, E), 5 mm (C).

on the lateral surfaces of the caudal centra from vertebra c13 to the last preserved vertebra (c29; Fig. 13D, E). Personal examination of this specimen shows unambiguously that the 'scales' are aberrant bony outgrowths that are texturally and mineralogically indistinguishable from their respective centra. The aetiology of these osseous structures is unclear; however, we disregard them as integumentary in origin.

(7) Ornithomimosauria

Whereas the vast majority of Maniraptoriformes lost an extensive squamous body covering in 'exchange' for feathers (Campione, Barrett & Evans, 2020; Bell & Hendrickx, 2021), at least two ornithomimosaurians, *Pelecanimimus polyodon* and *Ornithomimus* sp., are reported to have had smooth, scaleless skin on parts of their bodies (Briggs *et al.*, 1997; van der Reest, Wolfe & Currie, 2016), although the latter was largely covered in feathers (Zelenitsky *et al.*, 2012; van der Reest, Wolfe & Currie, 2016). Pérez-Moreno *et al.* (1994) originally described the soft tissue structures associated with the holotype of *Pelecanimimus*; however, these were later prepared off to expose the skeleton. Therefore, most evidence of the soft tissues is now missing and only a few low-resolution photographs remain (Fig. 14A, B). The holotype showed several patches of poorly defined integument, the preservation of which was attributed to phosphatisation of a microbial mat that enshrouded the carcass (Briggs *et al.*, 1997). The most salient features of the soft tissue were a small, triangular, soft occipital crest and a possible throat pouch or dewlap (Pérez-Moreno *et al.*, 1994; Briggs *et al.*, 1997; Fig. 14A, B), although the latter is certainly not an exaggerated structure and bears little resemblance to modern analogues (e.g. the dewlap in *Anolis* or the gular pouch in *Pelecanus*). The skin in general was described as smooth and covered in fine wrinkles that give it a tessellated appearance, but is otherwise lacking in scales or other integumentary structures (Briggs *et al.*, 1997; Appendix S3.7). Epidermal scales were, however, reported in the forearm of *Pelecanimimus* (Feduccia, Lingham-Soliar & Hinchliffe, 2005; Fig. 14C) although these may be non-integumentary in origin (Appendix S3.7). Whether, like *Sciurumimus* and *Anchiornis* (see below), the skin was originally covered in the same filamentous structures (and possible feathers; but see Foth, Tischlinger & Rauhut, 2014) seen in the derived ornithomimosaurid *Ornithomimus* (Zelenitsky *et al.*, 2012; van der Reest, Wolfe & Currie, 2016) is unknown but tenable given *Pelecanimimus*' position among feathered Maniraptoriformes (see Campione, Barrett & Evans, 2020).

Skin outline originating from the posterior ribs and extending ventral to the ilium and all along the legs was also

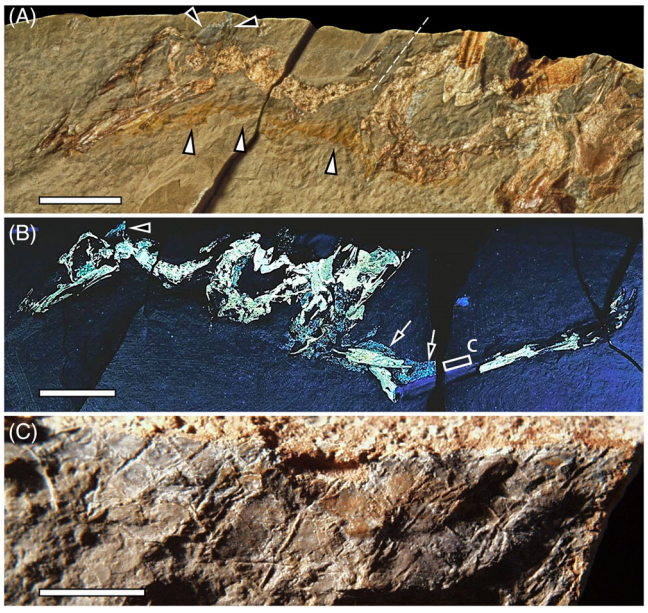


Fig. 14. Archival photographs and possible integumentary scales from the early-diverging ornithomimosaurian *Pelecanimimus polyodon* (LHC 7777). (A) Possible occipital crest (black arrowheads) and soft tissue outline of the throat and neck (white arrowheads) interpreted as a pouch or dewlap by Briggs *et al.* (1997). The dashed line indicates the point of dislocation between the anterior and posterior parts of the cervical series. (B) Entire specimen under ultraviolet (UV) light revealing the occipital crest (arrowhead) and 'drumstick' outlines associated with the forelimb (arrows). Note that the soft tissues of the neck and throat are not visible under UV. (C) Possible epidermal structures on the ventral surface of the forearm and interpreted as integumentary scales by Feduccia, Lingham-Soliar & Hinchliffe (2005). Scale bars = 10 cm (B), 5 cm (A) and 1 cm (C). Photographs by G. F. Kurtz (A, B) and Jaap Hillenius (C), used with permission.

reported in the ornithomimid *Ornithomimus* sp. by van der Reest, Wolfe & Currie. (2016). The skin appears to be scaleless and smooth, and corresponds to a thin, slightly undulating, ferruginous layer at the level of the femur. Feathers are present on the proximal half of the femur whereas the distal half of this bone and the remaining lower legs are featherless (van der Reest, Wolfe & Currie, 2016). According to those authors, the skin contour anterior to the femur (referred to as the anterior femoral web) is analogous to the skin webs of extant birds (Appendix S3.7). Besides the smooth skin of *Pelecanimimus* and *Ornithomimus*, a *Magnoavipes* track from the Cenomanian Naturita Formation of Colorado and possibly belonging to an ornithomimosaur, preserves scale scratch lines and two skin patches from the heel region (Noe, Lockley & Hadden, 2014). The anterior patch consists of small (1–2 mm), circular-to-oval reticulate scales distributed in distinct linear rows, whereas the posterior patch comprises larger (3 mm) elongated, ovoid scales oriented parallel to the scale scratch lines (Noe, Lockley & Hadden, 2014).

(8) Pennaraptora

As the theropod clade that includes the closest relatives to birds and which share pennaceous feathering (Pittman *et al.*, 2020), pennaraptoran tegument should be the most reliable to constrain and understand. This is because among theropods, non-avialan pennaraptorans benefit most from their closest proximity to the extant avian phylogenetic bracket, which includes a wealth of avian morphological and developmental data. However, this potential has yet to be realised as non-feather tegument is only known from a handful of non-avialan pennaraptorans at present, namely from certain oviraptorosaurians, troodontids, and dromaeosaurids.

In Oviraptorosauria, a propatagium has been proposed in the early-branching *Caudipteryx* based on two specimens, LPM 0005 and IVPP V12430 (Feduccia & Czerkas, 2015, figure 4). LSF imaging and first-hand observation of specimen IVPP V12430 failed to detect skin preservation. The presence of propatagial skin in LPM 0005 remains unconfirmed and should be treated tentatively. Although the leading edge of the propatagium may very well be delimited by feather extent in LPM 0005 and IVPP V12430, this cannot be reasonably validated in the absence of direct skin preservation so is seen here as speculative evidence. Skin impressions are reported on the distal forearm and manual digits of *Caudipteryx* specimen IVPP V12344 (Zhou & Wang, 2000; Fig. 15F, G). LSF imaging and first-hand observations of this specimen could not confirm this observation. Under LSF, there is a distinct area of fluorescence above the right wrist of the same individual (Fig. 15G). However, as it does not have any diagnostic information, we can only speculate that it might be soft tissue. Thus, there are currently no confirmed records of non-feather epidermal structures on the body of non-scansoriopterygid oviraptorosaurs. Scansoriopterygid theropods, which have recently been recovered among Oviraptorosauria (Brusatte *et al.*, 2014; Pei *et al.*, 2020), developed a unique airfoil consisting of a skin membrane that spanned the hyperelongated manual digits and a specialised styliform element. Although the body itself was feathered, direct evidence of the fleshy patagium is seen in *Yi qi* (Fig. 15A–C) and *Ambopteryx longibrachium* (Fig. 15D, E) where it is either smooth and devoid of surface details or has some linear features, the latter of which may or may not be related to the original form of the skin (Xu *et al.*, 2015; Wang *et al.*, 2019). Pebbly scales have also been observed along metatarsal II of the scansoriopterygid *Epidendrosaurus ningchengensis* (= *Scansoriopteryx heilmanni*; Czerkas & Feduccia, 2014). The scales are small (0.1–0.2 mm), subcircular, and relatively uniform in size and shape along the bone (Appendix S3.8). Although interpreted as feather shafts by Czerkas & Feduccia (2014), the strand-like markings on the fourth metacarpal of that specimen may be traces of scutate scales (Appendix S3.8).

Among dromaeosaurids, the microraptorine *Sinornithosaurus* was described as preserving 'tuberculate impressions' on the feet of specimen NGMC 91 (Ji *et al.*, 2001, figure 4). These are reticulate scales and, on the right foot, appear to

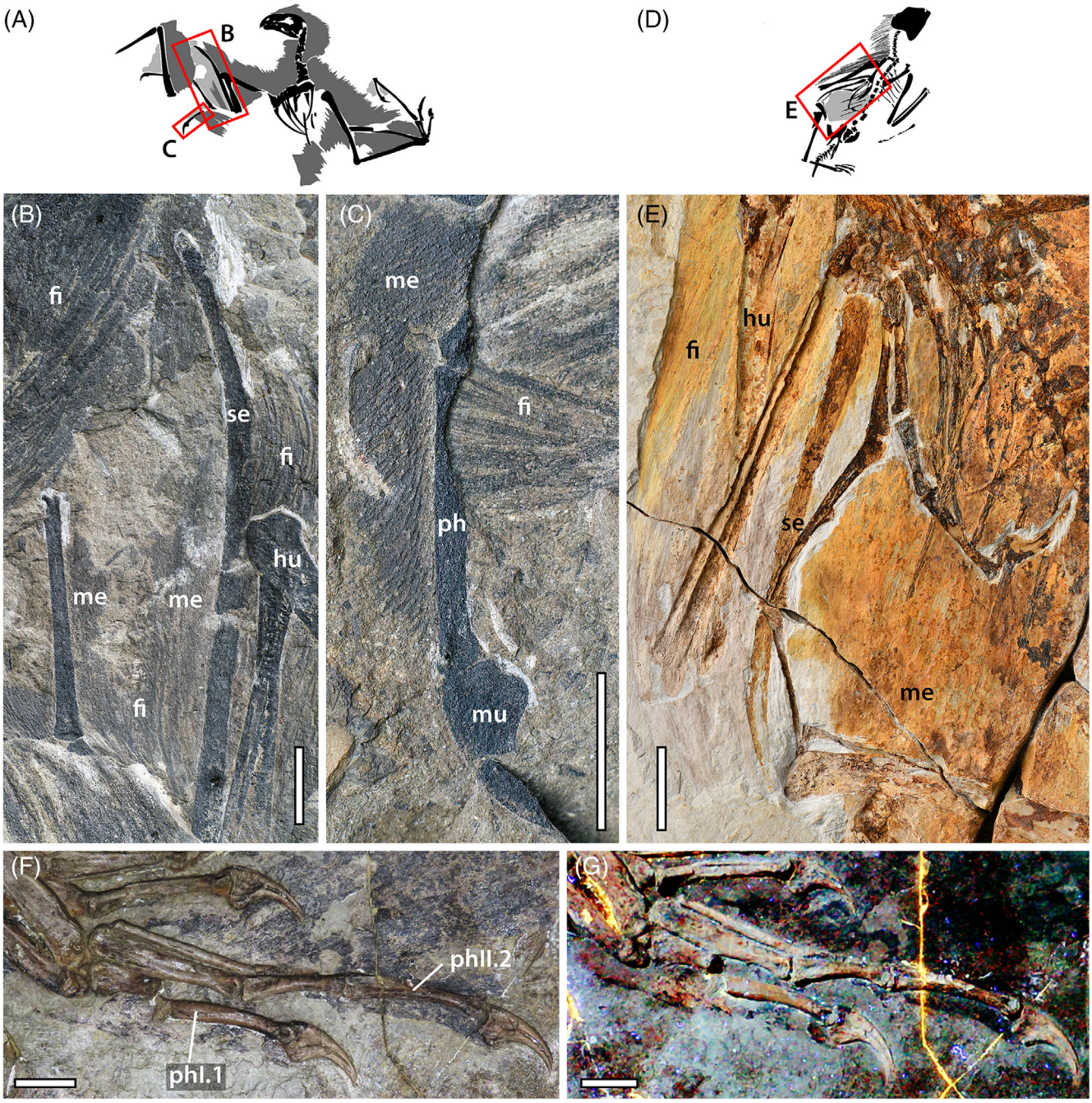


Fig. 15. Integumentary features in Oviraptorosauria. (A–E) Membranous tissues associated with the presumed airfoil in the scansoriopterygids *Yi qi* (STM 31-2) (A–C) and *Ambopteryx longibrachium* (IVPP V24192) (D–E). (A, D) Silhouettes of the holotype specimens showing distributions of filamentous plumage (dark grey) and membranous tissues (light grey). (F, G) Hand region of *Caudipteryx dongi* (IVPP V12344) with possible skin impression at the level of phalanges I and II in white light (F), and laser-stimulated fluorescence (LSF) images (G). fi, filaments; hu, humerus; me, membranous tissue; mu, manual ungual; ph, manual phalanx; se, styliform element. Scale bars = 1 cm. Photographs by M. Wang (B, C) and X. Xu (E), used with permission.

cover one digit in an arthral configuration. Soft tissues from the neck, ventrum, legs and tail base of the flying microraptorine *Microraptor* were identified under UV fluorescence in specimen IVPP V13352. We confirm these soft tissues under LSF. Whilst their spatial extent is impressive and confirms features like the comparatively narrow tail of dromaeosaurids compared to non-paravian theropods, the fidelity of these soft tissues is not high. They appear to

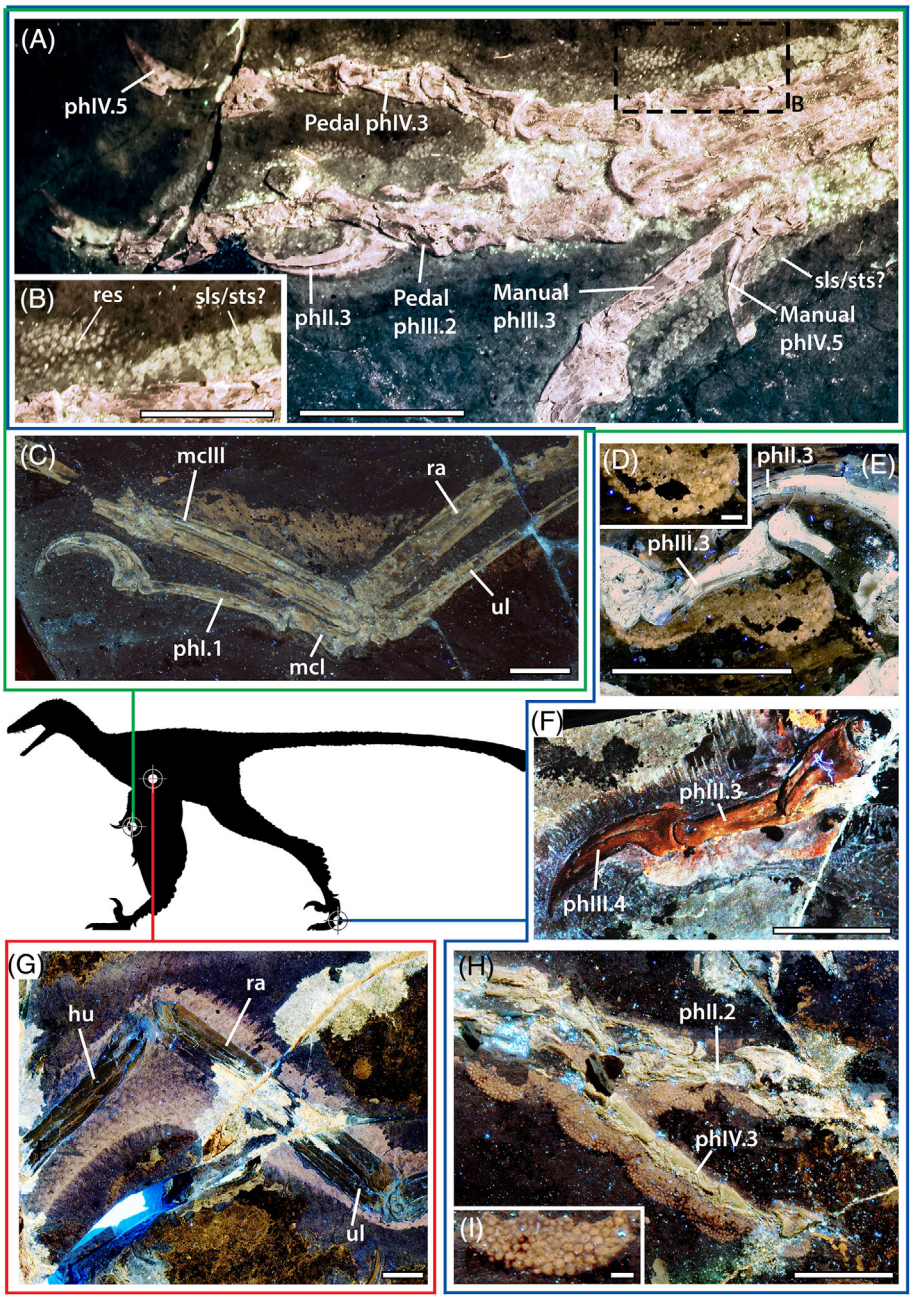


Fig. 16. Integumentary features in non-avialan Paraves. (A) Left manual digits III and IV and left? pes of the anchiornithine *Anchiornis huxleyi* (STM-0-7) under laser-stimulated fluorescence (LSF), with (B) close up of the metatarsal region, showing the reticulate scales from the digital and plantar pads, and the possible scutellate or scutate scales ventral to the manual phalanges and metatarsals. (C–E) Microraptorine dromaeosaurid *Microraptor* sp. under LSF showing (C) right postpatagium in IVPP V13320 with seemingly smooth skin, and (D, E) arthral footpad condition in STM 5-172; close up in (D) shows details of small rounded reticulate scales from the plantar pad of phalanx III-3. (F, H, I) Arthral footpad configuration of (F) the suspected anchiornithine *Pedopenna daohugouensis* (IVPP V12721) and (H, I) the anchiornithine *Anchiornis huxleyi* (STM-0-147), which also preserves details of the small rounded reticulate scales (I). (G) Forewing soft tissue outline of *Anchiornis huxleyi* (STM-0-127) showing a shallow depth and a non-regular feather follicle pattern. hu, humerus; mc, metacarpal; ph, phalanx; ra, radius; res, reticulate scale; sls, scutellate scale; sts, scutate scale; ul, ulna. Scale bars = 1 mm (D, I); 5 mm (B); 1 cm (A, C, E–H). Photographs by M. Pittman and Thomas G. Kaye (A, B), Xiaoli Wang and Xiaoting Zheng (D, E, G–I), and Xing Xu (C, F), used with permission. Black silhouette from Scott Hartman (for licence attribution, see Appendix S4).

represent naked skin, but it is not possible to comment definitively on the skin morphology within our study framework. The chemical halo around the arms of the specimen was speculated to be related to the soft tissues of the arms (Hone *et al.*, 2010; Wang *et al.*, 2017b, figure S4), but this is not substantiated by LSF study. However, in referred

specimen IVPP V13320, LSF reveals a right postpatagium with soft tissue extending away from the wrist (Fig. 16C). The postpatagium appears to have naked skin as in *Anchiornis* (Wang *et al.*, 2017b). In specimen STM 5-172, the feet preserve arthrally arranged plantar pads covered in subcircular reticulate scales (Fig. 16D, E).

Anchiornithine paravians are included in this review because, although recent studies favour their status as early-diverging avialans, several past studies have recovered them as troodontids (see discussion in Pittman *et al.*, 2020; Pei *et al.*, 2020). *Anchiornis huxleyi* retained tiny reticulate scales on the plantar surfaces of the pedal digits (Ji *et al.*, 2001; Wang *et al.*, 2017b). Wang *et al.* (2017b) further revealed the body profile of *Anchiornis* in remarkable detail using LSF (Fig. 16A, B, G–I) as well as the presence of small rounded reticulate scales in manual digit III. A closer look at the *Anchiornis* specimen STM-0-7 (Fig. 16A, B) shows that scutate or scutellate scales also covered the metatarsals (Fig. 16B) and possibly the distal manual digit III (Fig. 16A). Likewise, the manual digits of *Anchiornis* seem to lack phalangeal pads (Fig. 16A). Wang *et al.*'s (2017b) findings also demonstrated that *Anchiornis* had a functionally didactyl hand (digits III and IV were bound by soft tissues whereas digit II was free) and that the plantar pads on the feet were arranged in the arthral configuration (Fig. 16A, H, I). The latter is also observed under LSF in the suspected anchiornithine *Pedopenna* (Pittman *et al.*, 2020; Fig. 16F; Appendix S3.8).

V. DISCUSSION

(1) Morphology and distribution of epidermal structures in non-avialan theropods

(a) *Body*

Like the vast majority of ornithischian and sauropodomorph dinosaurs, the body of most non-neocoelurosaur theropods was covered with basement scales. Results of our ancestral state reconstruction analysis show that a scaly body skin is the plesiomorphic condition for theropods, regardless of their wider classification (i.e. Saurischia *versus* Ornithoscelida; see Appendix S2.5). This result was similarly obtained by Barrett, Evans & Campione (2015) and Campione, Barrett & Evans (2020) but is in contradiction to those of Yang *et al.* (2019) who consider dinosaurs and theropods as primitively feathered. Unlike these previous studies, 'early diverging Archosauriformes' [treated as a single operational taxonomic unit (OTU); Appendix S1 and S2.1] was used as the outgroup over pterosaurs [although Campione, Barrett & Evans (2020) also included living crocodylomorphs as a second outgroup] or Pseudosuchia (Yang *et al.*, 2019).

Squamous-skinned theropods are largely characterised by non-overlapping basement scales that lack distinct polarity and show a smooth surface (Figs 17–19; see Appendix S2.5). This basic configuration was not modified until the appearance of the earliest Maniraptoriformes, which coincided with an apparent shift to a predominantly filamentous integumentary covering at this node (Campione, Barrett & Evans, 2020) (see Section V.1*c*). We did not recover the latter in our reconstruction (Figs 19, 20) and instead found that scaly body skin was lost at the coelurosaurian node (Fig. 18C: character 4 state 1; Fig. 20B). The first record of plumage itself is much earlier at the tetanuran node (Fig. 18A: character 35 state 1), although some early-branching tetanuran clades like Allosauroidea possibly lost their plumage early on (Fig. 18B: character 35 state 0).

The basement scales of theropods are morphologically diverse: pebbly in the allosauroids *Lourinhanosaurus* and *Allosaurus*; irregular, polygonal and oblong in the abelisaurid *Carnotaurus*; polygonal in *Allosaurus* and the tyrannosaurids *Gorgosaurus* and *Tyrannosaurus*, and both arrow-shaped and ornamented in the compsognathid *Juravenator*. Although ontogenetic and sexual variation is currently unknown, theropods with scaly skin all seem to be covered by relatively small scales varying between 1 and 20 mm (Appendix S3.4, Fig. S2). The largest basement scales are found on the tail of an adult *Allosaurus* (∼20 mm in SMA 0005) although it is possible that the skin associated with that specimen actually pertains to a sauropod (Appendix S3.4). Basement scales are directly associated with filamentous feathers in *Juravenator* whilst a predominantly filamentous/plumulaceous feather covering is expected at the tyrannosauroid node (Fig. 18D: character 44 state 1), as found by Campione, Barrett & Evans (2020). With six non-pennaraptoran averostrans preserving scales in the tail region (*Carnotaurus*, *Allosaurus*, *Concavenator*, *Gorgosaurus*, *Tyrannosaurus*, and *Juravenator*), scale morphology is best known along the tail of theropods, particularly its anteroventral portion (Fig. 17). Polygonal scales are present in the anteroventral surface of the tail in *Allosaurus*, tyrannosaurids (*Tarbosaurus* and *Tyrannosaurus*), and *Juravenator*, suggesting that the anteroventral tail region of at least non-maniraptoriform averostrans (or tetanurans, depending on the phylogenetic affinity of *Juravenator*; see Foth *et al.*, 2020) was likely covered with polygonal scales. There is, however, strong variation in the morphology of the polygonal scales from the tail. Caudal scales are minute, strongly variable in shape and size, and separated by numerous epidermal 'veins' in *Tyrannosaurus* (Bell *et al.*, 2017), whereas they are relatively uniform in shape and size and ornamented by possible sensory organs in *Juravenator* (Bell & Hendrickx, 2020). Other than the tail, the integument of the neck is also relatively well represented (Fig. 17), being preserved in six non-avialan averostrans: the allosauroids *Allosaurus* and *Concavenator* (Appendix S3.4), the tyrannosaurid *Tyrannosaurus* (Bell *et al.*, 2017), the ornithomimosaurian *Pelecanimimus* (Pérez-Moreno *et al.*, 1994; Briggs *et al.*, 1997), the scansoriopterygid *Yi* (Dececchi *et al.*, 2020), and the dromaeosaurid *Microraptor* (Hone *et al.*, 2010). The skin appears to be scaleless at least in its ventral part in *Pelecanimimus* (Briggs *et al.*, 1997) and *Concavenator*, whereas it is made of small polygonal scales in *Tyrannosaurus* (Bell *et al.*, 2017). Skin from the thoracic region is also preserved in four non-maniraptoriform averostran taxa: the abelisaurid *Carnotaurus*, the allosauroid *Allosaurus*, and the

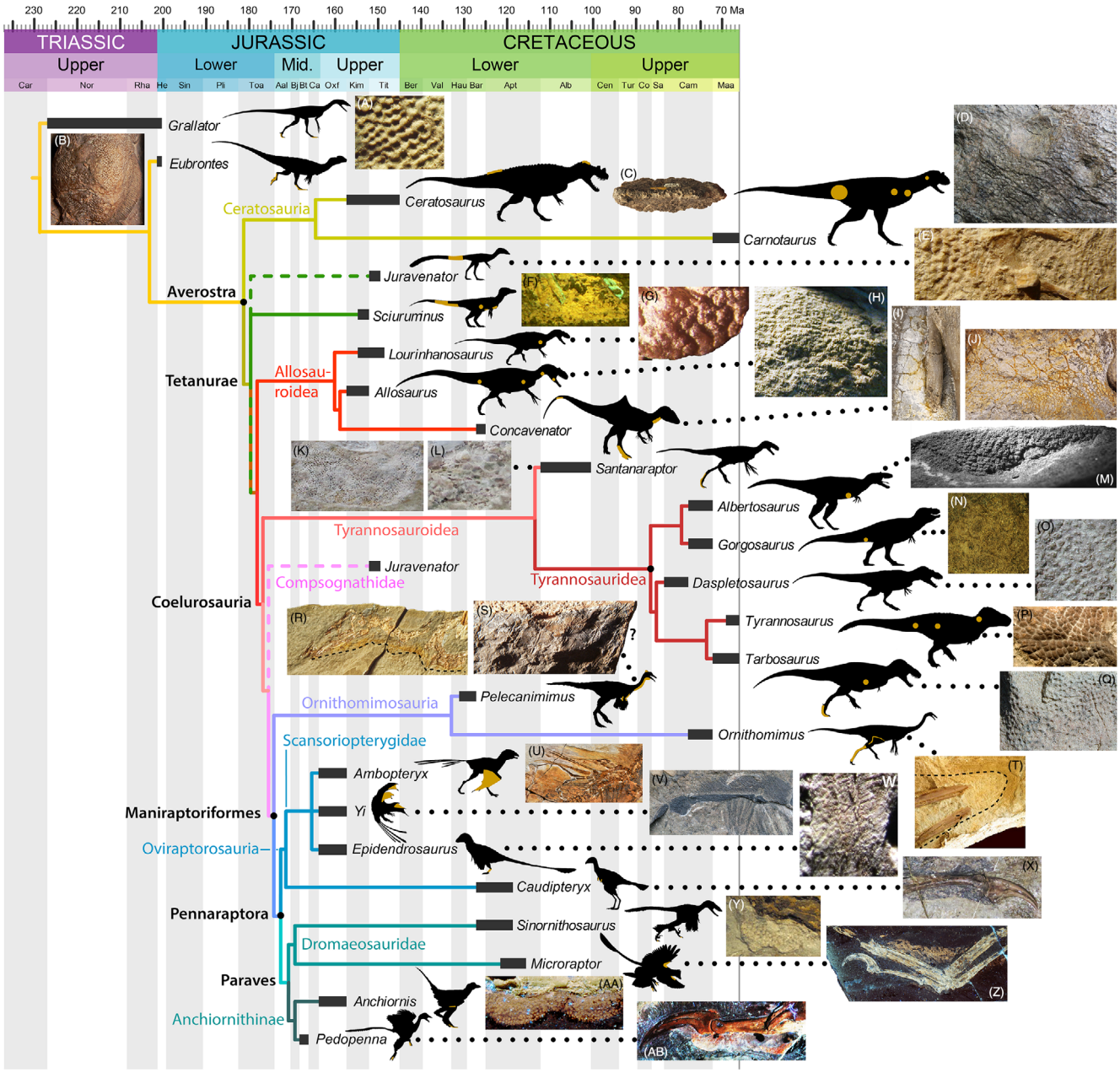


Fig. 17. Non-avialan theropod taxa known from non-feathered integuments and dermal ossifications, and their phylogenetic relationships. Orange zones within the black silhouettes represent the approximate location of the preserved integument. Colours on the tree branches and black dots represent distinct phylogenetic clades and node-based taxa, respectively. The stratigraphic ranges of *Grallator* and *Eubrontes* represents the fossil record of these two ichnotaxa known from skin impressions. Non-averostran theropods: (A) Reticulate scales in *Grallator* isp. (MGUH VP 3391) from the Upper Triassic of Greenland. (B) Reticulate scales on a pedal pad of *Eubrontes* isp. (SGDS 15-T1) from the Lower Jurassic of Utah. Non-tetanuran averostran theropods: (C) Isolated sagittate osteoderm of the ceratosaur *Ceratosaurus nasicornis* (UMNH VP 5278, Courtesy of Natural History Museum of Utah). (D) Basement and feature scales from the anteroventral portion of the tail of the ceratosaur *Carnotaurus sastrei* (MACN-CH 894). (E) Arrow-head, ornamented [integumentary sense organs (ISOs)], and scutate ventral scales from the caudal region of *Juravenator starki* (JME Sch 200). (F) Smooth skin from the ventral portion of the tail of *Sciurumimus albersdoerferi* (BMMS BK 11). (G) Pebbly basement scales from the shoulder region of an embryo referred to *Lourinhanosaurus antunesi* (ML 565-155). (H) Pebbly basement scales from the pectoral region of a juvenile *Allosaurus jimmadseni* (WDC DMQ-A 053). (I) Scutate and reticulate scales from the metatarsal region of *Concavenator corcovatus* (MCCM-LH 6666). (J) Scutellate and reticulate scales between the proximal tarsal and distal tibia of *Concavenator corcovatus* (MCCM-LH 6666). (K) Reticulate scales from a plantar pad of digit III of *Santanaraptor placidus* (MN 4802-V). (L) Scutellate scales from the proximal region of metatarsal IV of *Santanaraptor placidus* (MN 4802-V). (M) Basement

(Figure legend continues on next page.)

tyrannosaurids *Albertosaurus*, and *Tarbosaurus* (Fig. 17). Scales from the thorax are pebbly in *Allosaurus* and tyrannosaurids (*Albertosaurus* and *Tarbosaurus*), and possibly in all large-bodied averostrans with scales in this body region. Basement scales from the scapular region are known in only two allosauroid theropods: *Carnotaurus* and *Lourinhanosaurus* (Fig. 17). Such a small sample, combined with the fact that the scale impressions in *Carnotaurus* are not readily discernible, prevent us from drawing any broader conclusions on the shoulder integument. Only a single theropod, *Allosaurus*, currently preserves distinguishable scales at the level of the head (Fig. 17). Specifically, these are minute (<2 mm) and pebbly basement scales covering the posterior portion of the mandible. The scaly skin of the head of *Carnotaurus* was said to comprise feature scales (Czerkas, 1997) and likely consisted of small tuberculate basement scales (Czerkas & Czerkas, 1997; Hendrickx & Bell, 2021b), before it was lost when the skull was prepared in the field (Czerkas & Czerkas, 1997; Guillermo W. Rougier, personal communication 2020). The presence of feature scales on the skull of *Carnotaurus* should be seen as hypothetical as there is no direct evidence to support this claim (Hendrickx & Bell, 2021b). Carpenter (1997) also reported the presence of a wattle or bag of skin under the jaws of a badly weathered skull of *Tarbosaurus* from Mongolia, although such claims have not been validated (see Section V.1*d*). Dececchi *et al.* (2020) revealed soft tissues around the head of the scansoriopterygid *Yi qi* under LSF. However, these are not sufficiently well preserved to discern their textural details. Carr *et al.* (2017), however, suggested that the face of non-avialan theropods was primarily covered with flat scales and armour-like skin based on the hummocky texture of the facial bones shared between tyrannosaurids and crocodilians, and the presence of small bony papillae in some cranial bones (e.g. the premaxilla, nasal, lachrymal, jugal, and dentary), respectively.

Feature scales are currently limited to the non-maniraptoriform averostrans *Carnotaurus* (Abelisauridae) and *Albertosaurus* (Tyrannosauridae) (Fig. 18). They are reconstructed as being lost at the Tetanurae node (Fig. 18A: character 14 state 0; Fig. 20A), suggesting that the feature scales in *Albertosaurus* represent a reversal. However, at this time, it should not be ruled out that this may change as more complete tetanuran skin fossils are found. Likewise, the plesiomorphic condition of having feature scales in saurischian dinosaurs likely results from the lack of sampling (scored only in neosauropods and *Carnotaurus*; unknown in non-sauropod sauropodomorphs and non-averostran theropods; see Appendix S2.5). In *Carnotaurus*, feature scales were present on much of the body, including the shoulder, flank and tail (Czerkas, 1997; Hendrickx & Bell, 2021b; Appendix S3.3) but in neither *Carnotaurus* or *Albertosaurus* could it be confirmed that the feature scales were disposed in regular rows. Given that feature scales are relatively small in theropods (compared to overall body size) and lack a bony core, their role as possible defence structures is less tenable than as visual display structures and they thus may have been associated with colour patterns (Hendrickx & Bell, 2021b). Feature scales in both *Carnotaurus* and *Albertosaurus* are conical or dome-like, with offset apices in *Carnotaurus* (Hendrickx & Bell, 2021b; Appendix S3.3). The feature scales of *Albertosaurus* are too incomplete to reveal whether the apex was also off-centre. No peculiar structures appear to be present on the surface of the feature scales in *Carnotaurus*, whereas weak corrugations radiating from the apex, but not extended on the apex itself, are present in the feature scales of *Albertosaurus* (Bell *et al.*, 2017; Hendrickx & Bell, 2021b).

Polarised scales are widely distributed among tetanurans, being found on the ventral surface of the neck in *Allosaurus* and the tail in *Juravenator* and *Concavenator* (scutate ventral scales; Fig. 18), and associated with the metatarsus (scutate scales) of *Concavenator*, possibly the pennaraptorans

(Figure legend continued from previous page.)
and feature scales from the gastral region of *Albertosaurus sarcophagus* (TMP 1994.186.0001). (N) Polygonal basement scales from the caudoventral region of *Gorgosaurus libratus* (CMN 11593). (O) Basement scales from an unidentified location of *Daspletosaurus torosus* (TMP 2001.036.0001). (P) Polygonal basement scales from the neck region of *Tyrannosaurus rex* (HMNS 2006.1743.01). (Q) Basement scales from the thoracic region of *Tarbosaurus baatar* (MPC 107/6A). (R) Soft tissue outline from the throat and neck of *Pelecanimimus polyodon* (LHC 7777). (S) Putative integumentary scales from the forearm region of *Pelecanimimus polyodon* (LHC 7777; photograph courtesy of Jaap Hillenius). (T) Skin outline from the tibia and metatarsal IV of *Ornithomimus* sp. [UALVP 52531; from van der Reest, Wolfe & Currie (2016), modified]. (U) Membranous tissues from the forelimbs of *Ambopteryx longibrachium* (IVPP V24192). (V) Membranous tissues attached to a finger of *Yi qi* (STM 31-2). (W) Reticulate scales from the metatarsal region of *Epidendrosaurus ninchengensis* (= *Scansoriopteryx heilmanni*; CAGS-IG-02-0607). (X) Possible skin impression ventral to PhII.2 of *Caudipteryx dongi* (IVPP V12344). (Y) Reticulate scales from the digital pad of pedal phalanx II.2 of *Sinornithosaurus millenii* (NGMC 91). (Z) Seemingly smooth skin between the ulna and manual digits IV of *Microraptor zhaoianus* (IVPP V13320). (AA) Reticulate scales from the digital pad of pedal digit IV of *Anchiornis huxleyi* (STM 0-147). (AB) Distal plantar pads of pedal digit III of *Pedopenna daohugouensis* (IVPP V12721). Silhouette attribution: Emily Willoughby (*Tyrannosaurus*, *Yi*, *Microraptor*), Gareth Monger (*Sciurumimus*, *Anchiornis*), Matt Martyniuk (*Epidendrosaurus*, *Caudipteryx*), Tasman Dixon (*Eubrontes*, *Gorgosaurus*), Gregory S. Paul (*Lourinhanosaurus*), Craig Dylke (*Albertosaurus*), John Conway (*Juravenator*), T. Michael Keesey (*Pedopenna*); Stephen O'Connor (vectorised by T. Michael Keesey; *Daspletosaurus*), Nobu Tamura (*Pelecanimimus*), Audrey.m.horn (*Ambopteryx*), Raoul Martín in Ortega *et al.* (2010; *Concavenator*, modified), and Scott Hartman (all others). For licence attribution, see Appendix S4. Silhouettes not to scale. Figure inspired by a design from Henry Sharpe.

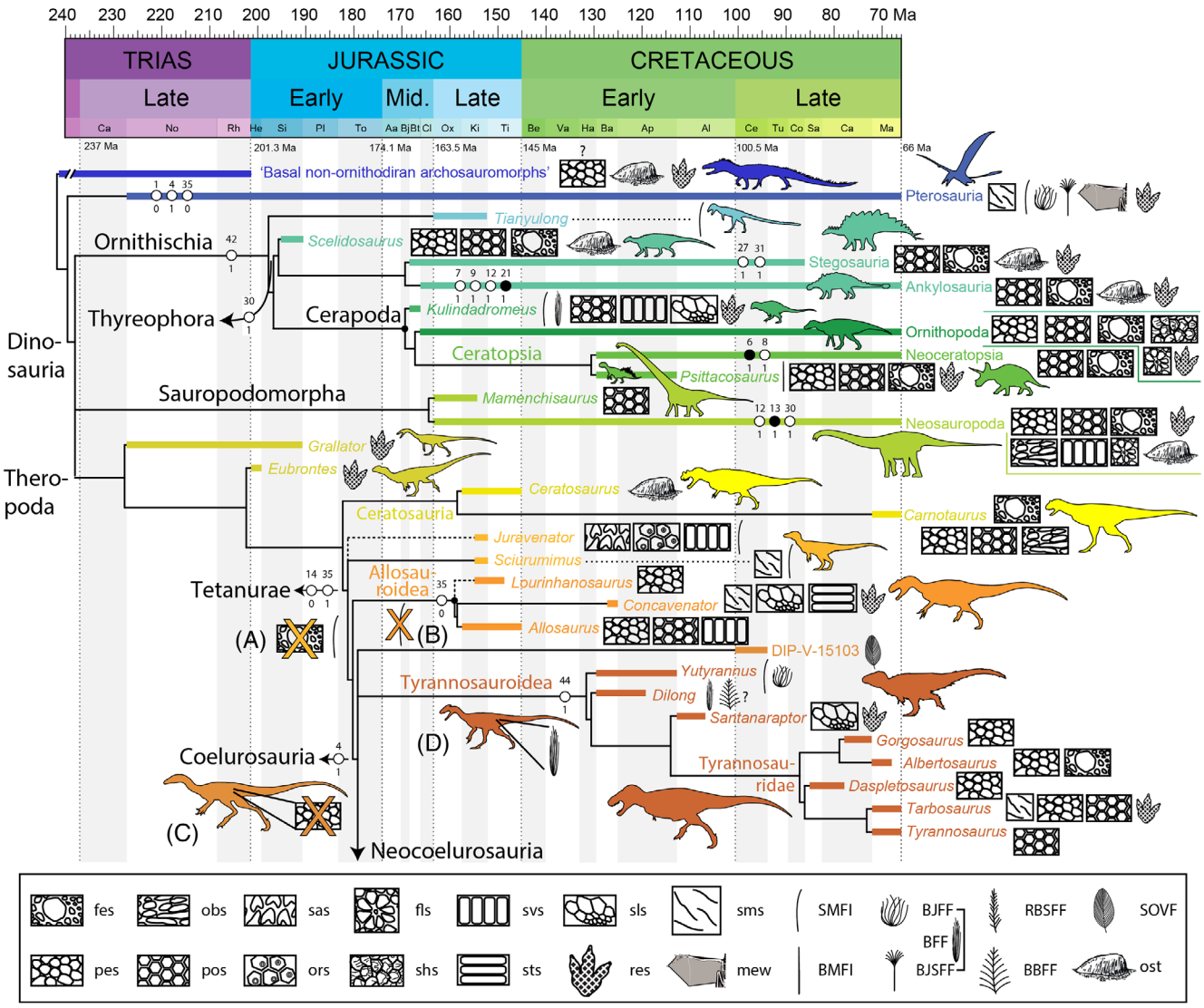


Fig. 18. Distribution of epidermal-based features among non-neocoelurosaurian archosauromorphs and major integument-based synapomorphies (Tree0). Colours of taxon names and black circles on the tree-nodes represent distinct phylogenetic clades and node-based taxa, respectively. Black and white circles on branches indicate non-homoplasious changes (apomorphies) and homoplasies, respectively. Numbers above and below black and white circles on the tree branches are integument-based characters and character states, respectively (see Appendix S2.2 for list of integument-based characters). (A) Tetanurae: loss of feature scales and development of plumage (i.e. filamentous structures). (B) Allosauroidea: loss of plumage (i.e. filamentous structures). (C) Coelurosauria: loss of scaly body skin. (D) Tyrannosauroidea: filamentous/plumulaceous feathers form the main body plumage. BBFF, bilaterally branched filamentous feather; BFF, indeterminate basally joining filamentous feather (i.e. BJFF or BJSFF); BJFF, basally joining filamentous feather; BJSFF, basally joining branched filamentous feather; BMFI, broad monofilamentous integument; fes, feature scales; fls, flowerlike arrangement of basement scales; mew, membranous wing (from Xu *et al.*, 2015), figure 3; modified); obs, oblong scales; ors, ornamented scales; ost, osteoderms (dermal ossifications); pes, pebbly scales; pos, polygonal scales; RBSFF, radially branched shafted filamentous feather; res, reticulate scales; sas, sagittate scales; shs, shell scales; sls, scutellate scales; SMFI, slender monofilamentous integument; sms; smooth skin; SOVF, symmetrical open-vaned feather; sts, scutate scales; svs, scutate ventral scales. All feather morphotypes are from Xu (2020, figure 5.4; modified). Silhouette attribution: Dmitry Bogdanov (early-diverging archosauromorphs; Pterosauria; modified), Jaime Headden (*Tianyulong*, *Psittacosaurus*; modified), Tasman Dixon (*Eubrontes*, *Yutyrannus*; modified), Gregory S. Paul [from Paul (2016); Saurischia; modified], Pete Buchholz (*Kulindadromeus*; modified), Gareth Monger (*Sciurumimus*; modified), Lucas Attwell (Coelurosauria; modified), Scott Hartman (all others). For licence attribution, see Appendix S4.

Epidendrosaurus and *Anchiornis* (Fig. 19), and more derived avialans such as *Yanornis* (Zheng *et al.*, 2013). However, these may extend to non-tetanuran averostrans as well based on possibly elongated basement scales on the thoracic region of *Carnotaurus* (Appendix S3.3). The scutate ventral scales present in *Allosaurus*, *Juravenator* and *Concavenator* appear

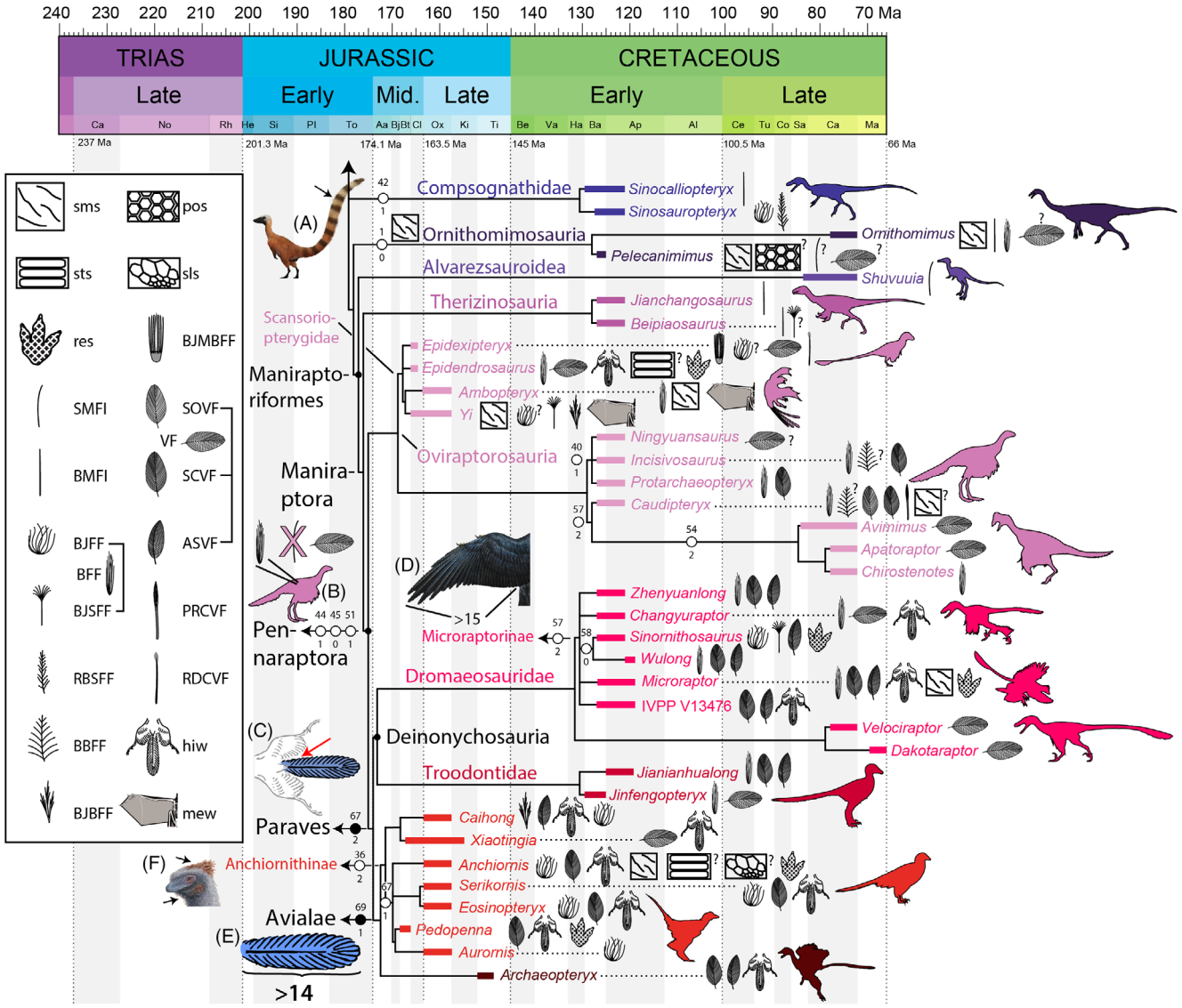


Fig. 19. Distribution of epidermal-based features among non-avialan neocoelurosaurians with major integument-based synapomorphies (Tree0). Colours of taxon names and black circles on the tree-nodes represent distinct phylogenetic clades and node-based taxa, respectively. Black and white circles on branches indicate non-homoplasious changes (apomorphies) and homoplasies, respectively. Numbers above and below black and white circles on the tree branches are integument-based characters and character states, respectively (see Appendix S2.2 for list of integument-based characters). (A) Compsognathidae: presence of a filamentous crest on the tail. (B) Pennaraptora: filamentous/plumulaceous feathers form the main body plumage, loss of monofilaments, and development of pennaceous feathers. (C) Paraves: rectrices present on most of the tail length. (D) Microraptorinae: presence of more than 15 secondary remiges on the forelimb. (E) Avialae: more than 14 pairs of rectrices on the tail. (F) Anchiornithinae: presence of plumage on both dorsal and/or ventral parts of the skull. All feather morphotypes are from Xu (2020, figure 5.4; modified). ASVF, asymmetrical close-vaned feather; BBFF, bilaterally branched filamentous feather; BFF, indeterminate basally joining filamentous feather (i.e. BJFF or BJSFF); BJBFF, basally joining branched filamentous feather; BJFF, basally joining filamentous feather; BJMBFF, basally joining membranous-based filamentous feather; BJSFF, basally joining branched filamentous feather; BMFI, broad monofilamentous integument; hiw; hindlimb wing; mew, membranous wing (from Xu *et al.* (2015), figure 3; modified); pos, polygonal scales; PRCVF, proximally ribbon-like close-vaned feather; RBSFF, radially branched shafted filamentous feather; RDCVF, rachis-dominant close-vaned feather; res, reticulate scales; SCVF, symmetrical close-vaned feather; sls, scutellate scales; SMFI, slender monofilamentous integument; sms; smooth skin; SOVF, symmetrical open-vaned feather; sts, scutate scales; VF, indeterminate vaned feather. Silhouette attribution: Matt Martyniuk (Pennaraptora; *Epidexipteryx*; *Protarchaeopteryx*, *Jinfengopteryx*; *Anchiornis*; modified), Emily Willoughby (*Yi*, *Microraptor*; modified), Julio Lacerda (coloured *Sinosauropteryx* used for Compsognathidae; modified), Jaime Headden (*Apatoraptor*/*Chirostenotes*; modified), Rebecca Gelernter (anchiornithine's head used for Anchiornithinae; modified), FunkMonk (*Shuvuuia*; modified), Pu *et al.* (2013b; *Jianchangosaurus*; modified), Gareth Monger (*Pedopenna*/*Aurornis*; modified), Li *et al.* (2012; microraptorine's forewing used for Microraptorinae; modified), Scott Hartman (all others). For licence attribution, see Appendix S4.

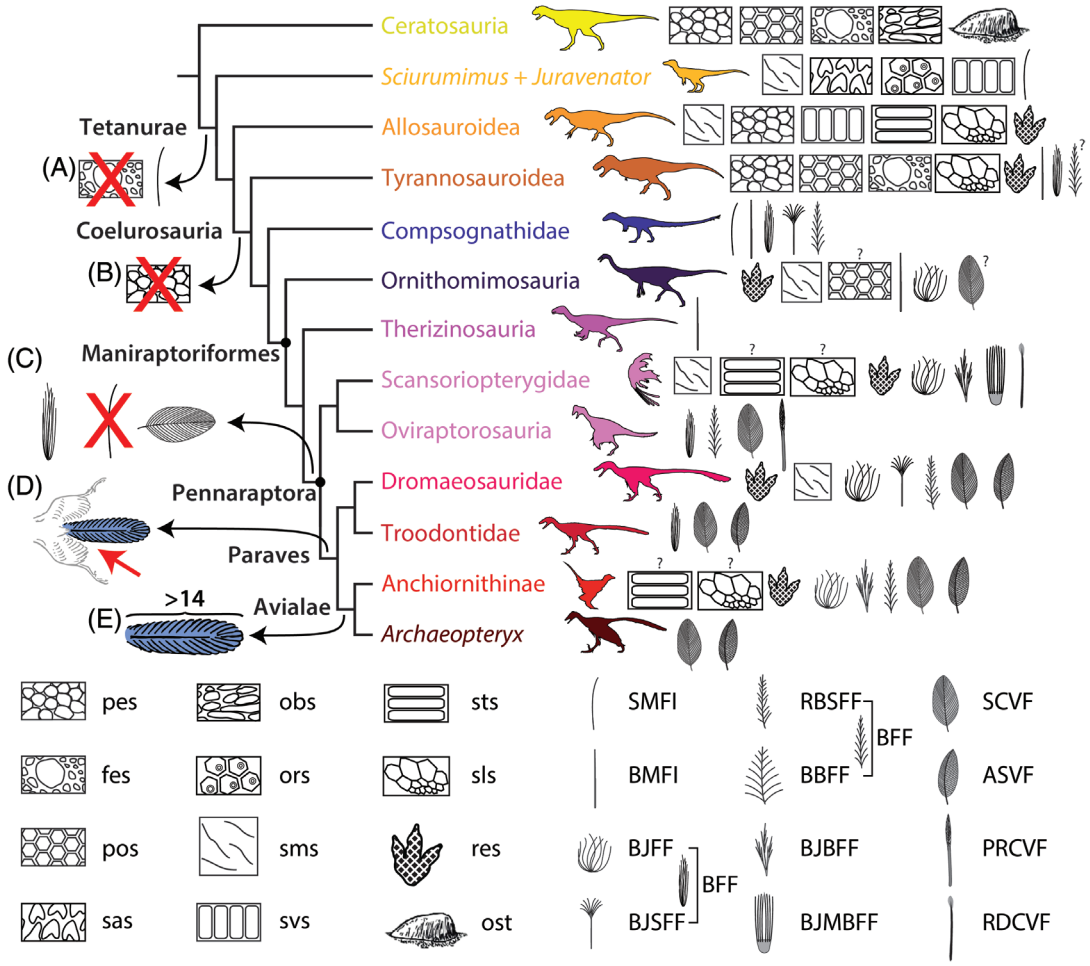


Fig. 20. Distribution of epidermal-based features in non-avian theropods showing the main integument-based evolutionary transformations. Colours of taxon names and black circles on the tree-nodes represent distinct phylogenetic clades and node-based taxa, respectively. (A) Tetanurae: loss of feature scales and development of plumage (i.e. filamentous structures). (B) Coelurosauria: loss of scaly body skin. (C) Pennaraptora: filamentous/plumulaceous feathers form the main body plumage, loss of monofilaments, and development of pennaceous feathers. (D) Paraves: rectrices present on most of the tail length. (E) Avialae: more than 14 pairs of rectrices on the tail. All feather morphotypes are from Xu (2020, figure 5.4; modified). ASVF, asymmetrical close-vaned feather; BBFF, bilaterally branched filamentous feather; BFF, indeterminate basally joining filamentous feather (i.e. BJFF or BJSFF); BJBFF, basally joining branched filamentous feather; BJFF, basally joining filamentous feather; BJMBFF, basally joining membranous-based filamentous feather; BJSFF, basally joining branched filamentous feather; BMFI, broad monofilamentous integument; fes, feature scales; obs, oblong scales; ors, ornamented scales; ost, osteoderms (dermal ossifications); pes, pebbly scales; pos, polygonal scales; PRCVF, proximally ribbon-like close-vaned feather; RBSFF, radially branched shafted filamentous feather; RDCVF, rachis-dominant close-vaned feather; res, reticulate scales; sas, sagittate scales; SCVF, symmetrical close-vaned feather; sls, scutellate scales; SMFI, slender monofilamentous integument; sms; smooth skin; sts, scutate scales; svs, scutate ventral scales. Silhouette attribution: Jaime Headden (Compsognathidae, Oviraptorosauria; modified), Emily Willoughby (Scansoriopterygidae; modified), Gareth Monger (*Sciurumimus*, Anchiornithinae; modified), Pu *et al.* (2013b, Therizinosauria; modified) and Scott Hartman (all others; modified). For licence attribution, see Appendix S4.

homologous and it is possible that the ventral part of the neck and tail in other non-feathered theropods was covered with similar polarised scales, reminiscent of the condition in modern snakes (Bell & Hendrickx, 2021). Based on their location in *Juravenator* and *Concavenator*, scutate ventral scales were restricted to the ventralmost surface of the tail anteriorly and covered the ventral half of the tail in its posteriormost region. More dorsally in the anteroventral region of the tail, at or above the level of the caudal vertebrae and chevrons, non-polarised irregular or polygonal basement scales are seen in the non-pennaraptoran averostrans *Carnotaurus*, *Allosaurus*, *Gorgosaurus*, *Tyrannosaurus*, and *Juravenator*.

Evidence of regional variations in scale architecture (i.e. between different body parts) is emerging but is limited by the few specimens in which skin is preserved on multiple parts of the body. Regional variation is best

exemplified in the tail of *Juravenator*, which comprises three longitudinal bands of morphologically distinct scales as well as dorsal monofilaments (Bell & Hendrickx, 2021). Of the four other taxa in which skin is relatively well represented along the body (the non-maniraptoriform averostrans *Carnotaurus*, *Allosaurus*, *Concavenator*, and *Tyrannosaurus*), all except *Tyrannosaurus* show some regional differences. Differences in the form of basement and feature scales between the shoulders, thorax and tail in the abelisaurid *Carnotaurus* are mainly related to the size of such structures (Czerkas & Czerkas, 1997). The basement scales of *Carnotaurus* from the thorax, shoulder and tail regions, however, appear to be different, being larger and elongated in the thorax, diamond-shaped on the shoulder and irregular with a granular surface texture on the tail (Hendrickx & Bell, 2021b).

(*b*) *Manus and pes*

Modern birds usually have scales only on their feet and hindlimbs (Lucas & Stettenheim, 1972; Stettenheim, 2000). However, in rare instances, they have scales on their manual digits like in juvenile hoatzin *Opisthocomus hoazin* (see photograph accompanying Naeem & Post, 2019). Among non-avialan theropods, manual scales are known only in *Anchiornis* and comprise pebbly reticulate scales covering the palmar surface of the manual digits, which appear to lack phalangeal pads (Fig. 16A). The palmar surface of the metacarpals also have a larger scale type which is difficult to identify, but appears to correspond to scutellate scales (Fig. 16A).

Current evidence suggests that non-theropod dinosaurs lacked a bird-like podotheca (see Appendix S2.5). The preservation of the podotheca of *Concavenator* is unique among non-avialan theropods in exhibiting scutate, scutellate, and smaller reticulate scales, similar to modern birds (Lucas & Stettenheim, 1972; Cuesta *et al.*, 2015). The absence of a similar podotheca in other well-preserved avetheropods (e.g. *Sinocalliopteryx* and *Microraptor*, which have feather-covered crura), together with the presence of scutellate and reticulate scales on the metatarsus and/or tibia of the ornithischian *Kulindadromeus* (Godefroit *et al.*, 2014, 2020) and various non-avialan theropods [*Santanaraptor*, and possibly in the scansoriopterygid *Epidendrosaurus* and the anchiornithine *Anchiornis* (Fig. 16B)], invokes a complicated history of foot scale differentiation across the Dinosauria involving multiple configurations, including some that resemble the modern bird condition.

Footprints show invariably that the plantar surface of the foot of theropods was covered in small reticulate scales (e.g. Hitchcock, 1841; Gatesy, 2001; Ji *et al.*, 2001; Demathieu *et al.*, 2002; Currie *et al.*, 2003; Rylaarsdam *et al.*, 2006; Milner *et al.*, 2006a,; Noe *et al.*, 2014; McCrea *et al.*, 2015; Milner & Lockley, 2016; Wang *et al.*, 2017b; Kim *et al.*, 2019), morphologically equivalent – but potentially not developmentally so (e.g. Stettenheim, 2000; Cooper *et al.*, 2019) – to the pebbly basement scales found elsewhere on the bodies of theropods. This is reflected in rare body fossils where the pedal integument is preserved in combination with arthral-type plantar pads in which the inter-pad creases do not correspond to the interphalangeal joints [*Anchiornis* (Wang *et al.*, 2017b); *Concavenator* (Cuesta *et al.*, 2015); *Santanaraptor*, *Microraptor*, *Pedopenna* (this study)]. Importantly, the wide distribution of the arthral condition among non-avialan theropods and early-diverging Avialae (e.g. *Sapeornis*; Pu *et al.*, 2013a) supports the hypothesis that this arrangement was plesiomorphic for Theropoda and that the mesarthral condition did not evolve until much later in crown Aves (Rainforth, 2003; Cuesta *et al.*, 2015).

(*c*) *Scales and plumage co-occurrence*

With the exception of *Juravenator* and possibly *Concavenator*, there is currently limited direct evidence for the co-occurrence of body scales (i.e. scales from the body other than the hands and feet) and plumage of any kind (i.e. monofilaments, filamentous structures or pennaceous feathers) in any non-avialan theropod. Paravians had extensive plumage characterised by the apomorphic feature of having rectrices on most of the tail length (Fig. 19C: character 67 state 2; Fig. 20D). Paravians inherited plumulaceous and pennaceous feathers and a loss of monofilamentous integument from the pennaraptoran node (Fig. 19B: character 44 state 1, character 45 state 0; Fig. 20C). Anchiornithines had feathers on their heads (Fig. 19F: character 36 state 2) and a more inclusive clade with *Anchiornis* ('Anchiornithini') had pennaceous feathers on their distal tail (Fig. 19: character 67 state 1). They also had a feather-covered podotheca; only the plantar surface retained a covering of reticulate scales on the pedal digits (Wang *et al.*, 2017b). Zheng *et al.* (2013) suggested a distal-to-proximal reduction of leg feathers in non-avian avialan evolution with extensively scaled feet appearing early in ornithuromorph evolution. Our data set only samples the very earliest non-avian avialans (anchiornithines and *Archaeopteryx*), which show the synapomorphic character of having more than 14 pair of rectrices on the tail (Fig. 19E: character 69 state 1; Fig. 20E). Avialans also had mostly or fully feathered hindlimbs (femur + tibia) (character 40 states 1 and 2). Feathered feet (metatarsals) are present in the early-diverging non-avian avialans *Xiaotingia* (Xu *et al.*, 2011), *Anchiornis* (Hu *et al.*, 2009; Zheng *et al.*, 2013), *Serikornis* (Lefèvre *et al.*, 2017), *Caihong* (Hu *et al.*, 2018), and *Pedopenna* (Xu & Zhang, 2005) suggesting this was potentially the ancestral condition in birds. This is congruent with Zheng *et al.*'s (2013) proposed distal-to-proximal reduction of leg feathers in non-avian avialan evolution. However, it would need to be evaluated further through an expanded ancestral state reconstruction analysis covering a phylogenetically broader sample of non-avian avialans. Feathered feet are poorly known in non-avialan paravian theropods but are well-preserved in the microraptorine dromaeosaurids *Microraptor* (Xu *et al.*, 2003) and *Changyuraptor* (Han *et al.*, 2014). Current evidence still suggests that feathered feet evolved multiple times in paravians (Foth *et al.*, 2014), at least twice (once in dromaeosaurids and once

in birds; this paper). As in modern birds (Lucas & Stettenheim, 1972), it seems likely that most non-avialan theropods with extensive plumage also retained reticulate scales on the pedes, an assumption also backed by ichnological and body fossil evidence (Kundrát, 2004; this study). With the exception of reticulate scales on the manus and pes, scales are unknown in any non-avialan maniraptoriform despite thousands of specimens that preserve integument. In fact, there is empirical support indicating that the ancestral state in Maniraptoriformes was primarily filamentous, reflecting a wholesale shift in integumentary covering at this node (Campione *et al.*, 2020) [although we recover this shift at the coelurosaurian node (Fig. 18D: character 4 state 1) and the first record of plumage, represented by monofilaments, was earlier at the tetanuran node (Fig. 18B: character 35 state 1)]. However, even in forms dominated by filamentous integument, the palmar and plantar surfaces of the manual and pedal digits, respectively, probably retained reticulate scales, as demonstrated by *Anchiornis*. The only maniraptoriform with non-feathery integument, *Pelecanimimus*, apparently had smooth, tessellated skin and possibly integumentary scales (Feduccia, Lingham-Soliar & Hinchliffe, 2005; Appendix S3.7). It is possible that the skin in fact bore some form of plumage as in other ornithomimosaurians (Zelenitsky *et al.*, 2012; van der Reest, Wolfe & Currie, 2016) and that this was not preserved or was shed as a result of *post mortem* decay; however, the soft tissues first reported by Pérez-Moreno *et al.* (1994) in *Pelecanimimus* were tragically prepared off after their initial description and are no longer available for study. It is notable, however, that in none of the theropods with apparently smooth skin does the skin also bear evidence of follicles (and therefore feathers). Follicles are clearly visible in the skin of a recently described penguin from the Eocene of Antarctica (Acosta Hospitaleche *et al.*, 2020) and so should, under the right conditions, be observable in older theropod fossils. *Juravenator* and possibly the carcharodontosaurid *Concavenator* are the only theropods to present an extensive squamous covering in addition to monofilaments or feather-like structures. The feathers themselves are, however, not preserved in *Concavenator* (Ortega *et al.*, 2010) but were interpreted from the presence of quill knobs along the ventral edge of the ulna, although there is another alternative hypothesis related to pathological processes (Cuesta, 2017) and both are currently hard to test. Other theropods do appear to sport filaments alongside smooth, or naked skin (e.g. *Sciurumimus*, scansoriopterygids), but reports of scaly skin in the classically filament-covered *Sinosauropteryx* (Martin & Czerkas, 2000; Lingham-Soliar, 2003) are incorrect and based on misinterpretations of sedimentary artefacts (Smithwick *et al.*, 2017). Finally, our assessment of possible scales on the caudal centra of *Compsognathus* (Peyer, 2006) suggests a possible pathological aetiology rather than an epidermal or dermal origin.

Associations between scales and feathers in non-avialan theropods are supported by the fact that both extant birds and mammals have scales that co-occur alongside other epidermal outgrowths (e.g. feathers and hair, respectively, although these structures are independently derived and non-homologous). Other epidermal elaborations are present in ornithischians ['bristles' and scales in *Psittacosaurus* and *Kulindadromeus* (Mayr *et al.*, 2002, 2016; Godefroit *et al.*, 2014)] and pterosaurs [pycnofibres (Wang *et al.*, 2002; Yang *et al.*, 2019)], which evidences the widespread experimentation with epidermal structures among ornithodirans more broadly (Barrett *et al.*, 2015). It should also be noted that despite the co-occurrence of bristle-like appendages with 'typical' squamous integument in some ornithischian dinosaurs (Mayr *et al.*, 2002; Godefroit *et al.*, 2014, 2020; Saveliev & Alifanov, 2018), whether or not such 'bristles' are homologous with the filamentous structures on non-avialan theropods is problematic (Mayr *et al.*, 2002, 2016; Barrett, Evans & Campione, 2015; Campione, Barrett & Evans, 2020).

(*d*) *Excrescences*

Soft tissue excrescences (combs, wattles, etc.) are extremely rare in any dinosaur. The proposed gular pouch in the ornithomimosaur *Pelecanimimus* appears to be based on a generous definition of the descriptive term – which relates specifically to an extension of the pharynx (Riede *et al.*, 2016) – and does not bear resemblance to related structures in living analogues (e.g. *Pelecanus* spp.). For example, the extant emu (*Dromaius novaehollandiae*) has a similarly proportioned flap of skin below the jaw that it inflates when vocalising, although it is not typically regarded as a gular pouch (e.g. Dominy & Symes, 2019). A 'wattle' of skin under the jaws was also reported in the tyrannosaurid *Tarbosaurus* by Carpenter (1997, 1999), but the specimen has not been described or figured. Consequently, we do not consider there to be sufficient evidence for a gular pouch or wattle (which have specific definitions and widely varying functions) in any theropod and urge caution in the interpretation of such structures since their anatomy cannot be determined easily from preserved soft tissues. The occipital crest in *Pelecanimimus* is more tenable than the gular pouch; however, both features are no longer visible in the holotype following over preparation of the specimen. If true, the occipital crest in *Pelecanimimus* is the only known soft tissue excrescence in a non-avialan theropod. The only other example is a 'cock's comb' in the hadrosaurid *Edmontosaurus regalis* (Bell *et al.*, 2014). These excrescences, along with other exotic structures (e.g. membranous wings in scansoriopterygids), provide rare evidence of the hidden diversity of soft tissue elaborations across the Dinosauria. It should therefore be anticipated that similar, yet equally bizarre structures will be found in many dinosaurian clades in the future.

(2) Morphological comparison of the scaly skin of theropods with other dinosaurs

The non-polarised and non-overlapping tuberculate scales of most theropods are also found in the large majority of sauropodomorphs and ornithischians (e.g. Czerkas, 1994;

Coria & Chiappe, 2007; Christiansen & Tschopp, 2010; Arbour *et al.*, 2013; Bell, 2014; Godefroit *et al.*, 2020; Gallagher, Poole & Schein, 2021). In modern reptiles, these scales are particularly present on the heads of snakes and lizards, and as isolated scales on the flanks of the green iguana *Iguana iguana* (Chang *et al.*, 2009). They are also found more broadly in other groups [e.g. Crocodylia, helodermatid lizards and some varanid lizards (Osborn, 1912; Bell, 2014)] where tuberculate scales comprise much of the body covering. In general, the tubercles of theropods form a basement of polygonal scales that are much smaller (∼2–4 mm in diameter) than is typical of other dinosaurian groups. Among non-maniraptoriform theropods at least, there is no clear relationship between body size and basement scale size ($r^2 = 0.0991$; Appendix S3.4, Fig. S2) and the smallest observed basement scales (∼1 mm) typify both the smallest (e.g. *Juravenator*) and the largest theropods (e.g. *Tyrannosaurus*) in our data set. Although considerable variation exists among all dinosaurs, iguanodontian ornithischians (including hadrosaurids) typically had moderately large basement scales (4–10 mm in diameter; Hooley, 1917, 1925; Bell, 2014), whereas the basement scales of many sauropod saurischians (Czerkas, 1994; Fondevilla *et al.*, 2017) and ceratopsid ornithischians (Brown, 1917; Lull, 1933) are even larger (up to 90 mm in diameter in the latter group; C. Hendrickx, personal observations). In addition, the scales of hadrosaurids and sauropods are often sculptured with radial corrugations and a papillate texture, respectively (Czerkas, 1994; del Giménez, 2007; Bell, 2014). Such generalisations would suggest a taxonomic (and likely functional) application to dinosaurian scale morphology (Lull & Wright, 1942; Bell, 2012) although a rigorous phylogenetic treatment of this variation has yet to be undertaken (see Section V.4).

Feature scales, restricted to the abelisaurid *Carnotaurus* and the tyrannosaurid *Albertosaurus*, are widely present on a variety of titanosaurid sauropods (Coria & Chiappe, 2007) and ceratopsian [e.g. *Psittacosaurus*, *Chasmosaurus*, *Centrosaurus* (Brown, 1917; Sternberg, 1925; Lingham-Soliar & Plodowski, 2010)], hadrosaurid [e.g. *Edmontosaurus*, *Gryposaurus*, *Maiasaura*, *Saurolophus* (Bell, 2012, 2014)], and stegosaurid [*Hesperosaurus*, *Gigantspinosaurus* (Xing, Peng & Shu, 2008; Christiansen & Tschopp, 2010)] ornithischians. This broad distribution implies that the presence of feature scales is plesiomorphic for Dinosauria. The dome-like feature scales of *Carnotaurus* and *Albertosaurus* are also present in the Auca Mahuevo titanosaur embryos (Coria & Chiappe, 2007, figure 1.6) as well as some hadrosaurs (Bell, 2012) and stegosaurs (Christiansen & Tschopp, 2010, figure 5). These domed feature scales differ from the flat feature scales covering the skin of the ceratopsids *Centrosaurus* (Brown, 1917, plate 13) and *Chasmosaurus* (Sternberg, 1925), and some hadrosaurs (Bell, 2012, 2014), as well as the feature scales with a nipple-like structure present in *Triceratops* (HMNS PV.1506). The radially corrugated feature scales of *Albertosaurus* are also seen in hadrosaurs (Bell, 2014), stegosaurs (SMA 0018), and possibly in the basally branching ceratopsian *Psittacosaurus* (SMF R 4970).

Midline feature scales, such as those found in some diplodocid sauropods (Czerkas, 1992) and hadrosaurids (Horner, 1984; Bell, 2012), have not been reported in any theropod, contrary to innumerable reconstructions flaunting such structures. Conversely, the midline osteoderms in *Ceratosaurus* would have been capped by a simple keratinous covering based on their osteological attributes (e.g. hummocky surface texture; Hieronymus *et al.*, 2009) and not as elaborate as in the aforementioned taxa. The dermal ossifications of *Ceratosaurus* also represent the sole theropod example of this form of tegument. Among saurischians, some titanosaurian sauropods also have postcranial osteoderms (D'Emic, Wilson & Chatterjee, 2009). Our analysis on integument-based characters suggests that the first saurischians had a limited distribution of undifferentiated postcranial osteoderms restricted to the midline and/or other portions of the back and tail (Appendix S2.4). However, the absence of osteoderms in particularly well preserved and often complete basally branching saurischians such as *Herrerasaurus*, *Eoraptor*, *Buriolestes*, *Plateosaurus*, *Coelophysis*, and *Dilophosaurus*, which have not been included in our integument-based data matrix, clearly indicate that osteoderms were independently derived in *Ceratosaurus* (or ceratosaurids) and derived sauropods (possibly Titanosauria; see D'Emic, Wilson & Chatterjee, 2009). Thyreophoran ornithischians had the most extensive osteodermal coverings among dinosaurs and share postcranial osteoderms ancestrally (Fig. 18: character 30 state 1). The osteoderms of *Ceratosaurus* are typically reconstructed over the neural spines of the axial column (Gilmore, 1920). Their peaked profile and foam-like internal porous structure may have offered similar fracture-limiting energy absorption and dissipation benefits to the dermal armour of modern crocodylians (Sun & Chen, 2013). This was probably true of other similarly constructed dinosaurian osteoderms. The osteoderms of modern crocodylians are part of a complex bracing system that is an integral part of their locomotory system, and which has a long evolutionary history (Salisbury & Frey, 2001). A similar role in terrestrial dinosaurs is unlikely; however, the functional significance of dinosaur osteoderms (and scales) remains understudied.

Polarised scales present as snake-like ventral scales (i.e. exhibiting mediolateral polarity) on the tails of *Juravenator* and *Concavenator* have been observed on the tail impression associated with *Anomoepus intermedius* tracks (Kundrát, 2004), an ornithischian ichnium according to Haubolt (1986). If the scale impression does indeed belong to an ornithischian, scutate ventral scales might have been widespread among dinosaurs. They are, however, distinctly absent from some clades, such as hadrosaurids, for which the tail integument is particularly well known (Bell, 2014). In extant taxa, polarised scales are best typified by the broad scutate scales on the anterior surface of the podotheca in birds or the ventral scales (known as gastrosteges) of snakes. It is also notable that in all of these groups, including dinosaurs, polarised scales form prominent compound structures arranged into longitudinal (or proximodistal, as in the case of avian

scutae) bands or rows. Polarised scales thus fulfil functional roles related to locomotion and related behaviours (e.g. perching and wading in birds; Stettenheim, 1972). Among non-theropod dinosaurs, polarised scales are also associated with embryonic titanosaurs from the Auca Mahuevo Lagerstätte of Patagonia, Argentina (Chiappe *et al.*, 1998; Coria & Chiappe, 2007) and as paired structures along the dorsal surface of the tail of the early-diverging neornithischian *Kulindadromeus* (Godefroit *et al.*, 2014, 2020). In the Auca Mahuevo titanosaurs, polarised scales are arranged into longitudinal rows, three scales wide, with the long axis of the scale oriented perpendicular to the row. Chiappe *et al.* (1998) speculated that these rows extended along the dorsal midline of the animal, although none were preserved in life position. The polarised scales of *Kulindadromeus* are unique among amniotes, being distributed in pairs along most of the length of the tail (possibly excepting the ventral surface), the long axis of the scale oriented perpendicular to the row. Each scale also bears an anterior spur that overlapped the preceding scale (Godefroit *et al.*, 2014, 2020). As an increase in scale size decreases the amount of exposed, unprotected skin (Soulé & Kerfoot, 1972), it could be speculated that polarised scales in some dinosaurs contributed to thermoregulation and water balance (as in some extant sceloporine lizards, for example; Soulé & Kerfoot, 1972) and/or added an element of protection at small body size from pests (e.g. mites, ticks, mosquitoes) and/or other animals (Bell & Hendrickx, 2020).

The regional variation seen in *Carnotaurus*, *Allosaurus*, and *Juravenator*, in particular, is not as marked as it is in the ornithischians *Psittacosaurus* (Vinther *et al.*, 2016), *Kulindadromeus* (Godefroit *et al.*, 2020), *Triceratops* (Larson *et al.*, 2007), the sauropod *Diplodocus* (Gallagher, Poole & Schein, 2021) and in some hadrosaurids (Bell, 2014). Such patterning was evidently species specific in certain hadrosaurids (Bell, 2012) and probably many other dinosaur groups [e.g. ceratopsids (Lull, 1933); ankylosaurids (Arbour *et al.*, 2014)] including theropods; however, additional specimens will be needed to characterise these differences further.

(3) Evolution of integumentary structures in non-avialan theropods

In living birds, scales are almost exclusively limited to the hindlimbs – mostly to the feet. Retention of this non-avialan theropod characteristic presumably reflects the versatility of hindlimb and foot scales in dealing with the range of substrates, mediums and predators/prey that birds interact with. This not only includes the durable material properties of the scales, but the structural characteristics provided by the arrangement of the scales in the podotheca (i.e. stiffer in some areas and more flexible in others).

Smooth skin covering the avian hand maximises the surface area available for feather attachment. Presumably this was related to the development of flapping-assisted locomotion (running speed, turning, braking and jumping) and early flight (Pei *et al.*, 2020), which would have favoured stability over a dexterous clawed hand. Non-flighted living birds simply inherited this change, which probably occurred with the fusion of the avian hand among early avialans. Juvenile hoatzin have clawed hands that help them achieve a range of beneficial locomotory behaviours (Abourachid *et al.*, 2019), suggesting that the loss of ancestral dexterous clawed hands in birds was not simply a case of loss due to functional redundancy.

Preserved soft tissues of fossil non-avialan paravians show details of patagia that are relevant to our understanding of flight development. Outline and feathering information (Fig. 16) and hints of leading edge camber tell us about the likely functional differences in different non-avialan paravian wings (Wang *et al.*, 2017b). However, internal details of the propatagial muscular complex – known only in rare early avialan fossils (Zheng *et al.*, 2017) – that can provide additional motion and control information are currently unknown in non-avialan paravians. Future finds that preserve such detail would therefore be invaluable.

The pervasion of arthrally arranged plantar and manual footpads we uncover in non-avialan theropods points to a later appearance of the mesarthral condition. The arthral condition offers good protection of the joints by fleshy pads, but at the expense of flexural capability of the digits. The later development of the mesarthral condition presumably reflects changes in the functional needs of the feet (e.g. related to the development of perching and a broadening of habitats) but its details remain unclear.

The seeming absence of feathering in non-tetanuran theropods (Fig. 18) suggests that non-tetanuran theropod scales are homologous to reptilian scales, whereas scales secondarily derived from feathers appeared among tetanurans after theropod feathers first appeared (see Wu *et al.*, 2018; Campione, Barrett & Evans, 2020). However, it is possible that secondarily derived scales may have deeper non-theropod origins given existing records of feather-like structures in non-theropod dinosaurs (e.g. Zheng *et al.*, 2009; Godefroit *et al.*, 2014) and in pterosaurs (Yang *et al.*, 2019, 2020). It is notable too that avian scutate/scutellate and reticulate scales have different developmental and evolutionary origins, the former being composed of beta-keratin and therefore apparently derived from reptilian scales (Stettenheim, 1972, 2000). Avian reticulate scales are composed of alpha-keratin and therefore have a much later origin and have been unique to the clade (Brush & Wyld, 1980; Cooper *et al.*, 2019). The avian-style podotheca seen in some non-avialan theropods (Cuesta *et al.*, 2015) and the apparent morphological similarity of the reticulate scales to those of modern birds suggests that, like many features once considered synapomorphic of crown Aves, reticulate scales were inherited from their theropod antecedents. Further systematic treatments and future discoveries will be needed to test this hypothesis further.

(4) Future directions

Theropods, as for other dinosaurs, demonstrated significant interspecific variation in their body coverings. The evolutionary significance and many fundamental questions about scale function (see Bell & Hendrickx, 2020, 2021; Hendrickx &

Bell, 2021b), and the roles of ontogeny and sex on scale architecture remain unanswered. Remarkable cases of possible sexual dimorphism have been reported in early-diverging avialans based on soft tissues [e.g. blade-like tail feathers in *Confuciusornis* (Hou *et al.*, 1996; Martin *et al.*, 1998); but see also Chiappe *et al.* (1999, 2008)], whereas convincing evidence based solely on osteology has so far been elusive (Mallon, 2017; Saitta *et al.*, 2020). Among living birds, sexual dimorphism is most commonly expressed by the males, which are larger (an osteological trait) and have more elaborate plumage (a soft-tissue trait) than the females (Møller & Cuervo, 1998). Snakes and lizards commonly possess dimorphisms in body shape (e.g. relative size of the head/trunk; Olsson *et al.*, 2002) and dichromatic skin colouration (e.g. Shine & Madsen, 1994; Stuart-Fox & Stuart-Fox & Ord, 2004). Specimen numbers of non-avialan theropods with adequate skin impressions are clearly too limited at this stage to offer any insight into potential dimorphisms. However, the current rate of discovery holds some promise for the accrual of significant numbers of specimens that will eventually be able to address some of these questions.

In spite of what was thought possible only a decade ago, dinosaurian colouration has now become an area of intense study. Melanosomes – colour-imparting organelles – preserved in fossil feathers have enabled the vivid reconstruction of colours and patterns in a variety of avialan and non-avialan theropods (Li *et al.*, 2010, 2012, 2014; Zhang *et al.*, 2010; Lindgren *et al.*, 2015; Vinther, 2015; Roy *et al.*, 2020a). Past debate regarding their interpretation (e.g. Lindgren *et al.*, 2014; Moyer *et al.*, 2014; Negro, Finlayson & Galván, 2018) now appears to be settled (Roy *et al.*, 2020b) although caution is still required in their correct interpretation. Most studies regarding palaeocolour have centred on the feathers of theropods, including birds (Roy *et al.*, 2020a). By contrast, investigations based on the scales of theropods and other dinosaurs are rare (Lingham-Soliar & Plodowski, 2010; Vinther *et al.*, 2016; Brown *et al.*, 2017). Long-considered as simple impressions (ichnofossils), chemical and micro-structural evidence indicates that dinosaur scales and other non-feather epidermal structures should in many, if not all cases, be referred to as true body fossils (e.g. Manning *et al.*, 2009; Lindgren, Kaddumi & Polcyn, 2013; Lindgren *et al.*, 2014; Barbi *et al.*, 2019). Among vertebrates, melanosomes and other colour-imparting organelles typically reside at the interface between the epidermis and dermis, and have been identified from the scales of some ornithischian dinosaurs (Vinther *et al.*, 2016; Brown *et al.*, 2017), snakes (McNamara *et al.*, 2016) and even the smooth, non-scaly skin of some marine reptiles (Lindgren *et al.*, 2014). Similar lines of inquiry will no doubt reveal novel perspectives on the colouration of squamous-skinned dinosaurs relevant to questions of sexual dichromatism, interspecific variation, and camouflage (Brown *et al.*, 2017; Vinther, 2020; Roy *et al.*, 2020a). Colour-patterned skin in non-avian avialans like *Sapeornis* (which has striped feet: STM 9-13) suggests that such studies in non-avialan theropods are within reach as more fossils become available.

Histology also has the potential to reveal additional 'cryptic' features of the scales, such as possible sensory functions and regeneration (Chang *et al.*, 2009). Histological investigation is now commonplace in dinosaur palaeobiology, but only two recent studies have employed histology to investigate scale microstructure in a dinosaur [both on hadrosaurs (Barbi *et al.*, 2019; Fabbri *et al.*, 2020)]. Considering the important role of histology in other fields of dinosaur research (e.g. Erickson, 1996, 2005, 2014; Erickson *et al.*, 2006), histology offers fertile ground for future investigations into the structure of the integument and its possible bearing on preservation potential (Davis, 2014; Fabbri *et al.*, 2020).

With few exceptions, soft-tissue characters (e.g. scale morphology/distribution) have yet to be incorporated into theropod phylogenetic data matrices. Feathers and filaments were first introduced as character states by Sereno (1999), and further characters have been elaborated on by subsequent authors (e.g. O'Connor, 2009; Cau *et al.*, 2017; Cau, 2018). These characters are particularly poorly represented in such data sets [e.g. 9/1773 characters (0.5%) in Cau *et al.*, 2017; 4/700 characters (0.57%) in Hartman *et al.*, 2019; 3/853 characters (0.35%) in Pei *et al.*, 2020] and mostly relate to the presence/absence of various integument structures. Although the distribution of different scale morphotypes has been discussed recently by Bell & Hendrickx (2021), characters based on scales have never been incorporated. Given the limited number of squamous-skinned non-avialan theropods for which the integument is (at least partially) known, this omission is unsurprising. Nevertheless, scale architecture (e.g. shape, size, count) is taxonomically informative in birds (Stettenheim, 1972) and crocodilians (Environment Canada, 1995), the two groups that phylogenetically bracket non-avialan theropods and other dinosaurs. Increasing evidence now suggests that scale architecture differed at the species level within many dinosaurian groups, including ankylosaurids (Arbour *et al.*, 2014), ceratopsids (Lull, 1933), hadrosaurids (Bell, 2014), and non-avialan theropods (this study). Yet how they stand up within the context of rigorous phylogenetic analysis – either within or between any of these groups – has yet to be determined.

Reptilian scales are considered key 'preadaptations' for adaptive radiation on land because they offer protection from abrasion, water loss, and UV irradiation (Alibardi, 2003; Chang *et al.*, 2009). Scale size, shape, and surface ornamentation varies widely among modern squamates, but the adaptive significance of such variation is poorly understood and often contradictory. In his landmark study, Soulé (1966) found that the lizard *Uta* had fewer, larger scales in warmer environments and larger numbers of smaller scales in cooler environments. He hypothesised that larger scales were better at dissipating heat than smaller ones because they tended to be more imbricated and heavily keeled (i.e. a greater surface area). Subsequent studies have, however, found a stronger correlation with aridity (precipitation) – dorsal scales tend to be larger in more arid settings, while smaller scales are found in humid environments (Soulé & Kerfoot, 1972; Calsbeek, Knouft & Smith, 2006).

Nevertheless, these 'rules' are far from firm, either among species of lizards (e.g. Calsbeek, Knouft & Smith, 2006; Oufiero *et al.*, 2011) or between squamate groups (e.g. snakes *versus* lizards). Despite these disagreements, there is no doubt that scale size plays an important role in thermoregulation and water balance (Soulé & Kerfoot, 1972), and similar roles can be inferred in theropods and other dinosaurs. Untangling the relationship between palaeoclimate and scale morphology in any dinosaur is certain to be a challenging task, but is now within reach given the large amount of climate data already amassed from fossil plants and animals as well as geological and geochemical proxies.

VI. CONCLUSIONS

(1) The importance of a squamous integument in non-avialan theropods has been overshadowed by the myriad extraordinary feathered theropods continuing to emerge, primarily from northeast China. Historic and more recent workers have advocated for greater attention to the study of squamous skin, highlighting the phylogenetic and palaeobiological relevance of these structures in other dinosaur groups (e.g. Lull & Wright, 1942; Czerkas, 1992, 1994, 1997; Bell, 2012, 2014) in addition to their importance for understanding the taphonomy and preservation of labile tissues (e.g. Manning *et al.*, 2009; Schweitzer, 2011; Barbi *et al.*, 2019). The historic dismissal of dinosaurian squamous skin may stem from the seemingly obvious connection between scales, giant, extinct reptiles, and their modern counterparts (Czerkas, 1994).

(2) A squamous covering is the likely ancestral state for all dinosaurs (Barrett, Evans & Campione, 2015) but appears to have undergone a wholesale shift towards extensive filamentous or feathered plumage in maniraptoriform theropods (Campione, Barrett & Evans, 2020).

(3) Of the >500 currently accepted species of non-avialan theropod (Starrfelt & Liow, 2016), only 23 preserve some form of integument (excluding filaments/feathers). These specimens show that non-avialan theropods, like other dinosaurs, were typified by non-imbricating scales that lack distinct polarity (i.e. tuberculate scales) and which were, in general, both proportionately and absolutely smaller and less elaborate than those of sauropod saurischians as well as hadrosaurid and ceratopsid ornithischians.

(4) Other fossilised soft tissues (e.g. feathers, melanosomes) have triggered a renaissance in dinosaur palaeontology, but the scales of dinosaurs – despite having been discovered nearly 150 years before the first feathered dinosaurs – have yet to be exploited to the same degree. The incorporation of now-standard techniques (e.g. histology, synchrotron radiation) and the deeper integration of integumentary characters into phylogenetic data sets holds great potential for the future of dinosaur scale research and promises deeper insights into the biology and relationships of these charismatic animals.

VII. ACKNOWLEDGEMENTS

We are grateful to Xu Xing (IVPP), Zheng Fang (IVPP), Corwin Sullivan (IVPP), Li Feng (IVPP), Lizhao Zhang (IVPP), Brandon Strilisky (TMP), Becky Sanchez (TMP), Don Brinkman (TMP), Donald Henderson (TMP), Stella Maris Alvarez (MACN), Martín Ezcurra (MACN), Agustín G. Martinelli (MACN), Fernando Novas (MACN), Sergio A. K. Azevedo (MN/Universidade Federal do Rio de Janeiro), Luciana B. Carvalho (MN/Universidade Federal do Rio de Janeiro), Martina Kölbl-Ebert (JME), Andreas Radecker (JME), Matthew Carrano (USNM), Amanda Millhouse (USNM), Annelise Folie (IRSNB), Pascal Godefroit (IRSNB), Oliver Rauhut (BSPG), Gertrud Rößner (BSPG), Femke Holwerda (BSPG), Carrie Levitt-Bussian (UMNH), Alyson Wilkins (UMNH), Randall B. Irmis (UMNH), Xiaoli Wang (STM), Xiaoting Zheng (STM), Dongyu Hu (Shenyang Normal University), and Arindam Roy (The Hong Kong University) for access to the integument of dinosaur specimens. We also warmly thank Jacques Sciau, Christine Ifrim (JME), Andreas Hecker (JME), Urs Möckli (SMA), Hans-Jakob Siber (SMA), Ursula Göhlich (Natural History Museum Vienna), Martín Ezcurra, Emanuel Tschopp (AMNH), Oliver Rauhut, Helmut Tischlinger, Stephen Gatesy (Brown University), Min Wang (IVPP), Darren Tanke (TMP), Patrick R. Getty (Collin College), Jose Luis Sanz (UAM), Jaap Hillenius (College of Charleston), Lida Xing (China University of Geosciences), Frederic Lacombat (Interprospekt AG) and Jakob Vinther (Bristol University) for providing specimen photographs. We are particularly indebted to Christine Ifrim and Andreas Hecker for their help in taking close-up photographs of *Juravenator* and Ryan Felice (UCL) for laser scanning a cast of the *Allosaurus* skin impression. We would also like to thank Orlando Grillo (MN), Hans-Jakob Siber (SMA), Rodolfo A. Coria (MCF-PVPH), Matthew Carrano (USNM), Fernando Novas (MACN), Agustín G. Martinelli (MACN), Martín Ezcurra, Julia McHugh (Sam Noble Museum), Sylvia Czerkas, Serjoscha Evers (University of Fribourg), Stephen Gatesy (Brown University), Guillermo W. Rougier (University of Louisville), Johan Lindgren (Lund University), Christian Foth (University of Fribourg), Julien Benoit (University of the Witwatersrand), Frederic Lacombat (Interprospekt AG), Matteo Belvedere (University of Florence), and Rhys Meyekort (University of Western Australia) for providing information on specimens with integument impressions. We thank Scott Hartman (University of Wisconsin-Madison), Matt Martyniuk, Emily Willoughby, Gareth Monger, Julio Lacerda, Dmitry Bogdanov, Jaime Headden, Tasman Dixon, FunkMonk, Rebecca Gelernter, Gregory S. Paul, Craig Dylke, Stephen O'Connor, T. Michael Keesey, John Conway, Pete Buchholz, Lucas Attwell, Nobu Tamura,

Audrey.m.horn, Julio Garza and Raoul Martín, for allowing us to use their artwork, either through Phylopic.org or with their personal permission. Henry Sharpe is thanked for sending us his artwork, whose design was used as an inspiration for one of our figures. C.H. thanks his supervisor Fernando Abdala for letting him complete this project during his postdoc in San Miguel de Tucumán. Specimen JME Sch 200 belongs to the collection of the Bischöfliche Seminar Eichstätt who kindly permitted access to the specimen and photography. This research was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Agencia Nacional de Promoción Científica y Tecnológica, Argentina to C.H. (Beca Pos-doctoral CONICET Legajo 181417). P.R.B is funded by an Australian Research Council Discover Early Career Researcher Award (DE170101325). M.P. and T.G.K.'s participation was supported by a RAE Improvement Fund of the Faculty of Science, The University of Hong Kong. E.C.'s participation was supported by a JSPS Postdoctoral Funding (PE-18034) and a DAAD Postdoctoral Funding (Ref. 91791394). C.H. dedicates this work to the memory of Juan F. Apud, Maria M. Moya de Martin, and Stephen A. Czerkas.

VIII. REFERENCES

Abourachid, A., Herrel, A., Decamps, T., Pages, F., Fabre, A.-C., Hoorebeke, L. V., Adriaens, D. & Amado, M. A. G. (2019). Hoatzin nestling locomotion: acquisition of quadrupedal limb coordination in birds. *Science Advances* **5**, eaat0787.

Acosta Hospitaleche, C., De Los Reyes, M., Santillana, S. & Reguero, M. (2020). First fossilized skin of a giant penguin from the Eocene of Antarctica. *Lethaia* **53**, 409–420.

Agnolín, F. L. & Novas, F. E. (2013). *Avian Ancestors - A Review of the Phylogenetic Relationships of the Theropods Unenlagiidae, Microraptoria, Anchiornis and Scansoriopterygidae*. SpringerBriefs South America and the Southern Hemisphere, Springer Verlag, Dordrecht, Heidelberg, New York, London.

Alcober, O. A. & Martínez, R. N. (2010). A new herrerasaurid (Dinosauria, Saurischia) from the Upper Triassic Ischigualasto Formation of northwestern Argentina. *ZooKeys* **63**, s55–s81.

Alexander, D. E., Gong, E., Martin, L. D., Burnham, D. A. & Falk, A. R. (2010). Model tests of gliding with different hindwing configurations in the four-winged dromaeosaurid *Microraptor gui*. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 2972–2976.

Alibardi, L. (2003). Adaptation to the land: the skin of reptiles in comparison to that of amphibians and endotherm amniotes. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* **298B**, 12–41.

Anderson, B. G., Barrick, R. E., Droser, M. L. & Stadtman, K. L. (1999). Hadrosaur skin impressions from the Upper Cretaceous Nelsen Formation, Book Cliffs, Utah: morphology and paleoenvironmental context. *Vertebrate Paleontology in Utah* **99**, 295.

Anderson, B. G., Lucas, S. G., Barrick, R. E., Heckert, A. B. & Basabilvazo, G. T. (1998). Dinosaur skin impressions and associated skeletal remains from the upper Campanian of southwestern New Mexico: new data on the integument morphology of hadrosaurs. *Journal of Vertebrate Paleontology* **18**, 739–745.

Arbour, V. M., Burns, M. E., Bell, P. R. & Currie, P. J. (2014). Epidermal and dermal integumentary structures of ankylosaurian dinosaurs. *Journal of Morphology* **275**, 39–50.

Arbour, V. M., Burns, M. E. & Currie, P. J. (2011). A review of pelvic shield morphology in ankylosaurs (Dinosauria: Ornithischia). *Journal of Paleontology* **85**, 298–302.

Arbour, V. M., Lech-Hernes, N. L., Guldberg, T. E., Hurum, J. H. & Currie, P. J. (2013). An ankylosaurid dinosaur from Mongolia with in situ armour and keratinous scale impressions. *Acta Palaeontologica Polonica* **58**, 55–64.

Avanzini, M. (2000). *Synaptichnium* tracks with skin impressions from the Anisian (middle Triassic) of the Southern alps (val di non - Italy). *Ichnos* **7**, 243–251.

Ayer, J. (1999). *The Howe Ranch Dinosaurs: 10Years of Dinosaur Digging in Wyoming*. Zürich, Switzerland: Sauriermuseum Aathal.

Bakhurina, N. N. & Unwin, D. M. (1995). A preliminary report on the evidence for 'hair' in Sordes pilosus, an Upper Jurassic pterosaur from Middle Asia. In Sixth Symp. Mesozoic Terrestrial Ecosystems and Biota, Short Papers 1995, pp. 79–82. Beijing, China.

Ballze, J. (2018). The Newest updated version - Tyrannosaur skinchart by Blomman87 on DeviantArt. *Deviantart*. https://www.deviantart.com/blomman87/art/The-Newest-updated-version-Tyrannosaur-skinchart-748376293 Accessed 30.07.2021.

Barbi, M., Bell, P. R., Fanti, F., Dynes, J. J., Kolaceke, A., Buttigieg, J., Coulson, I. M. & Currie, P. J. (2019). Integumentary structure and composition in an exceptionally well-preserved hadrosaur (Dinosauria: Ornithischia). *PeerJ* **7**, e7875.

Barclay, R. S., Rioux, M., Meyer, L. B., Bowring, S. A., Johnson, K. R. & Miller, I. M. (2015). High precision U–Pb zircon geochronology for Cenomanian Dakota Formation floras in Utah. *Cretaceous Research* **52**, 213–237.

Baron, M. G. (2021). Difficulties with the origin of dinosaurs: a short comment on the current debate. *Palaeovertebrata* **43**, 1–5.

Baron, M. G. & Barrett, P. M. (2017). A dinosaur missing-link? *Chilesaurus* and the early evolution of ornithischian dinosaurs. *Biology Letters* **13**, 20170220.

Baron, M. G. & Barrett, P. M. (2018). Support for the placement of *Chilesaurus* within Ornithischia: a reply to Müller *et al. Biology Letters* **14**, 20180002.

Baron, M. G., Norman, D. B. & Barrett, P. M. (2017). A new hypothesis of dinosaur relationships and early dinosaur evolution. *Nature* **543**, 501–506.

Barrett, P. M., Clarke, J. B., Brinkman, D. B., Chapman, S. D. & Ensom, P. C. (2002). Morphology, histology and identification of the 'granicones' from the Purbeck Limestone Formation (Lower Cretaceous: Berriasian) of Dorset, southern England. *Cretaceous Research* **23**, 279–295.

Barrett, P. M., Evans, D. C. & Campione, N. E. (2015). Evolution of dinosaur epidermal structures. *Biology Letters* **11**, 20150229.

Bell, P. R. (2012). Standardized terminology and potential taxonomic utility for hadrosaurid skin impressions: a case study for *Saurolophus* from Canada and Mongolia. *PLoS One* **7**, e31295.

Bell, P. R. (2014). A review of hadrosaurid skin impressions. In *Hadrosaurs* (eds D. A. Eberth and D. C. Evans), pp. 572–590. Indiana University Press, Bloomington.

Bell, P. R., Campione, N. E., Persons, W. S., Currie, P. J., Larson, P. L., Tanke, D. H. & Bakker, R. T. (2017). Tyrannosauroid integument reveals conflicting patterns of gigantism and feather evolution. *Biology Letters* **13**, 20170092.

Bell, P. R., Fanti, F., Currie, P. J. & Arbour, V. M. (2014). A mummified duck-billed dinosaur with a soft-tissue cock's comb. *Current Biology* **24**, 70–75.

Bell, P. R. & Hendrickx, C. (2020). Crocodile-like sensory scales in a Late Jurassic theropod dinosaur. *Current Biology* **30**, R1068–R1070.

Bell, P. R. & Hendrickx, C. (2021). Epidermal complexity in the theropod dinosaur *Juravenator* from the Late Jurassic of Germany. *Palaeontology* **64**, 203–223.

Benjamin, M., Evans, E. J. & Copp, L. (1986). The histology of tendon attachments to bone in man. *Journal of Anatomy* **149**, 89–100.

Benton, M. J. & Clark, J. M. (1988). Archosaur phylogeny and the relationships of the Crocodylia. In *The Phylogeny and Classification of the Tetrapods. Vol. 1. Amphibians and Reptiles* (ed. M. J. Benton), pp. 295–338. Clarendon Press, Oxford.

Benton, M. J., Dhouailly, D., Jiang, B. & McNamara, M. (2019). The early origin of feathers. *Trends in Ecology & Evolution* **34**, 856–869.

Bertozzo, F., Sasso, C. D., Fabbri, M., Manucci, F. & Maganuco, S. (2017). Redescription of a remarkably large *Gryposaurus notabilis* (Dinosauria: Hadrosauridae) from Alberta, Canada. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **43**, 1–56.

Bidar, A., Demay, L. & Thomel, G. (1972). *Compsognathus corallestris*: nouvelle espèce de dinosaurien théropode du Portlandien de Canjuers (sud-est de la France). *Annales du Muséum d'Histoire Naturelle de Nice* **1**, 9–40.

Bonaparte, J. F. (1985). A horned Cretaceous carnosaur from Patagonia. *National Geographic Research* **1**, 149–151.

Bonaparte, J. F., Novas, F. E. & Coria, R. A. (1990). *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Natural History Museum of Los Angeles County Contributions in Science* **416**, 1–42.

Boyd, C. A. (2015). The systematic relationships and biogeographic history of ornithischian dinosaurs. *PeerJ* **3**, e1523.

Briggs, D. E. G., Wilby, P. R., Pérez-Moreno, B. P., Sanz, J. L. & Fregenal-Martínez, M. (1997). The mineralization of dinosaur soft tissue in the Lower Cretaceous of Las Hoyas, Spain. *Journal of the Geological Society* **154**, 587–588.

Brown, B. (1916). *Corythosaurus casuarius*: skeleton, musculature and epidermis. *Bulletin of the American Museum of Natural History* **35**, 709–716.

Brown, B. (1917). A complete skeleton of the horned dinosaur *Monoclonius*, and description of a second skeleton showing skin impressions. *Bulletin of the American Museum of Natural History* **37**, 298–306.

Brown, B. & Schlaikjer, E. M. (1940). The structure and relationships of *Protoceratops*. *Annals of the New York Academy of Sciences* **40**, 133–266.
Brown, C. M. (2017). An exceptionally preserved armored dinosaur reveals the morphology and allometry of osteoderms and their horny epidermal coverings. *PeerJ* **5**, e4066.
Brown, C. M., Henderson, D. M., Vinther, J., Fletcher, I., Sistiaga, A., Herrera, J. & Summons, R. E. (2017). An exceptionally preserved three-dimensional armored dinosaur reveals insights into coloration and Cretaceous predator-prey dynamics. *Current Biology* **27**, 2514–2521.
Brusatte, S. L., Carr, T. D., Erickson, G. M., Bever, G. S. & Norell, M. A. (2009). A long-snouted, multihorned tyrannosaurid from the Late Cretaceous of Mongolia. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 17261–17266.
Brusatte, S. L. & Clark, N. D. L. (2015). Theropod dinosaurs from the Middle Jurassic (Bajocian–Bathonian) of Skye, Scotland. *Scottish Journal of Geology* **51**, 2014–2022.
Brusatte, S. L., Lloyd, G. T., Wang, S. C. & Norell, M. A. (2014). Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur-bird transition. *Current Biology* **24**, 2386–2392.
Brusatte, S. L., O'Connor, J. K. & Jarvis, E. D. (2015). The origin and diversification of birds. *Current Biology* **25**, R888–R898.
Brusatte, S. L., Sakamoto, M., Montanari, S. & Harcourt Smith, W. E. H. (2012). The evolution of cranial form and function in theropod dinosaurs: insights from geometric morphometrics. *Journal of Evolutionary Biology* **25**, 365–377.
Brush, A. H. & Wyld, J. A. (1980). Molecular correlates of morphological differentiation: avian scutes and scales. *Journal of Experimental Zoology* **212**, 153–157.
Buchwitz, M. & Voigt, S. (2012). The dorsal appendages of the Triassic reptile *Longisquama insignis*: reconsideration of a controversial integument type. *Paläontologische Zeitschrift* **86**, 313–331.
Buckland, W. (1837). *Geology and Mineralogy Considered with Reference to Natural Theology (the Bridgewater Treatises on the Power and Goodness of God as Manifested in the Creation, Treatise VII)*. William Pickering, London.
Burch, S. H. (2014). Complete forelimb myology of the basal theropod dinosaur *Tawa hallae* based on a novel robust muscle reconstruction method. *Journal of Anatomy* **225**, 271–297.
Cabreira, S. F., Kellner, A. W. A., Dias-da-Silva, S., da Silva, L. R., Bronzati, M., de A. Marsola, J. C., Müller, R. T., de S. Bittencourt, J., Batista, B. J., Raugust, T., Carrilho, R., Brodt, A. & Langer, M. C. (2016). A unique Late Triassic dinosauromorph assemblage reveals dinosaur ancestral anatomy and diet. *Current Biology* **26**, 3090–3095.
Calsbeek, R., Knouft, J. H. & Smith, T. B. (2006). Variation in scale numbers is consistent with ecologically based natural selection acting within and between lizard species. *Evolutionary Ecology* **20**, 377–394.
Campione, N. E., Barrett, P. M. & Evans, D. C. (2020). On the ancestry of feathers in Mesozoic dinosaurs. In *The Evolution of Feathers: From Their Origin to the Present* (eds C. Foth and O. W. M. Rauhut), pp. 213–243. Springer International Publishing, Cham.
Carney, R. M., Vinther, J., Shawkey, M. D., D'Alba, L. & Ackermann, J. (2012). New evidence on the colour and nature of the isolated *Archaeopteryx* feather. *Nature Communications* **3**, 1642.
Carpenter, K. (1997). Tyrannosauridae. In *Encyclopedia of Dinosaurs* (eds P. J. Currie and K. Padian), pp. 766–768. Academic Press, San Diego.
Carpenter, K. (1999). *Eggs, Nests, and Baby Dinosaurs: A Look at Dinosaur Reproduction*. Indiana University Press, Bloomington, Indiana.
Carpenter, K. (2014). Where the sea meets the land: the unresolved Dakota problem in Utah. In *Geology of Utah's Far South* (eds J. S. MacLean, R. F. Biek and J. E. Huntoon), pp. 357–372. Utah Geological Association Publication, Salt Lake City, Utah.
Carr, T. D. (2020). A high-resolution growth series of *Tyrannosaurus rex* obtained from multiple lines of evidence. *PeerJ* **8**, e9192.
Carr, T. D., Varricchio, D. J., Sedlmayr, J. C., Roberts, E. M. & Moore, J. R. (2017). A new tyrannosaur with evidence for anagenesis and crocodile-like facial sensory system. *Scientific Reports* **7**, 1–11.
Carrano, M. T. & Sampson, S. D. (2008). The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* **6**, 183–236.
Cau, A. (2018). The assembly of the avian body plan: a 160-million-year long process. *Bollettino della Società Paleontologica Italiana* **57**, 2.
Cau, A., Beyrand, V., Voeten, D. F. A. E., Fernandez, V., Tafforeau, P., Stein, K., Barsbold, R., Tsogtbaatar, K., Currie, P. J. & Godefroit, P. (2017). Synchrotron scanning reveals amphibious ecomorphology in a new clade of bird-like dinosaurs. *Nature* **552**, 395–399.
Cau, A., Dyke, G. J., Lee, M. S. Y. & Naish, D. (2014). Data from: sustained miniaturization and anatomical innovation in the dinosaurian ancestors of birds. Dryad Digital Repository. http://hdl.handle.net/10255/dryad.66441 Accessed 01.08.2014.
Cerda, I. A., Casal, G. A., Martinez, R. D. & Ibiricu, L. M. (2015). Histological evidence for a supraspinous ligament in sauropod dinosaurs. *Royal Society Open Science* **2**, 150369.
Chakravarti, D. K. (1935). Is *Lametasaurus* indicus an armored dinosaur? *American Journal of Science* **s5–30**, 138–141.
Chang, C., Wu, P., Baker, R. E., Maini, P. K., Alibardi, L. & Chuong, C.-M. (2009). Reptile scale paradigm: Evo-Devo, pattern formation and regeneration. *The International Journal of Developmental Biology* **53**, 813–826.
Chatterjee, S. & Templin, R. J. (2007). Biplane wing planform and flight performance of the feathered dinosaur *Microraptor gui*. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 1576–1580.
Chauveau, A. & Arloing, S. (1885). *The Comparative Anatomy of the Domesticated Animals*. D. Appleton and Company, New York.
Chen, P., Dong, Z. & Zhen, S. (1998). An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. *Nature* **391**, 147–152.
Chiappe, L. M., Coria, R. A., Dingus, L., Jackson, F., Chinsamy, A. & Fox, M. (1998). Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature* **396**, 258–261.
Chiappe, L. M. & Dyke, G. J. (2006). The early evolutionary history of birds. *Journal-Paleontological Society of Korea* **22**, 133.
Chiappe, L. M. & Göhlich, U. B. (2010). Anatomy of *Juravenator starki* (Theropoda: Coelurosauria) from the Late Jurassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **258**, 257–296.
Chiappe, L. M., Ji, S.-A., Ji, Q. & Norell, M. A. (1999). Anatomy and systematics of the Confuciusornithidae (Theropoda, Aves) from the late Mesozoic of northeastern China. *Bulletin of the American Museum of Natural History* **242**, 1–89.
Chiappe, L. M., Marugán-Lobón, J., Ji, S. & Zhou, Z. (2008). Life history of a basal bird: morphometrics of the Early Cretaceous *Confuciusornis*. *Biology Letters* **4**, 719–723.
Choiniere, J. N., Clark, J. M., Forster, C. A., Norell, M. A., Eberth, D. A., Erickson, G. M., Chu, H. & Xu, X. (2014). A juvenile specimen of a new coelurosaur (Dinosauria: Theropoda) from the Middle–Late Jurassic Shishugou Formation of Xinjiang, People's Republic of China. *Journal of Systematic Palaeontology* **12**, 177–215.
Christiansen, N. A. & Tschopp, E. (2010). Exceptional stegosaur integument impressions from the Upper Jurassic Morrison Formation of Wyoming. *Swiss Journal of Geosciences* **103**, 163–171.
Christiansen, P. & Bonde, N. (2004). Body plumage in *Archaeopteryx*: a review, and new evidence from the Berlin specimen. *Comptes Rendus Palevol* **3**, 99–118.
Chuong, C.-M., Chodankar, R., Widelitz, R. B. & Jiang, T.-X. (2000). Evo-Devo of feathers and scales: building complex epithelial appendages. *Current Opinion in Genetics & Development* **10**, 449–456.
Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F. & Ranzuglia, G. (2008). MeshLab: an open-source mesh processing tool. In *Eurographics Italian Chapter Conference* (eds V. Scarano, R. D. Chiara and U. Erra), pp. 129–136. The Eurographics Association, Salerno.
Clyde, W. C., Krause, J. M., De Benedetti, F., Ramezani, J., Cúneo, N. R., Gandolfo, M. A., Haber, P., Whelan, C. & Smith, T. (2021). New South American record of the Cretaceous–Paleogene boundary interval (La Colonia Formation, Patagonia, Argentina). *Cretaceous Research* **126**, 104889.
Cohen, S., Cruickshank, A., Joysey, K., Manning, T. & Upchurch, P. (1995). *The dinosaur egg and embryo project: exhibition guide*. Rockart.
Cooper, R. L., Lloyd, V. J., Di-Poï, N., Fletcher, A. G., Barrett, P. M. & Fraser, G. J. (2019). Conserved gene signalling and a derived patterning mechanism underlie the development of avian footpad scales. *EvoDevo* **10**, 19.
Coria, R. A. & Chiappe, L. M. (2007). Embryonic skin from Late Cretaceous sauropods (Dinosauria) of Auca Mahuevo, Patagonia, Argentina. *Journal of Paleontology* **81**, 1528–1532.
Coria, R. A., Chiappe, L. M. & Dingus, L. (2000). A new abelisaur theropod from the Upper Cretaceous of Patagonia. *Journal of Vertebrate Paleontology* **20**, 36A–37A.
Cuesta, E. (2017). *Concavenator corcovatus* (Theropoda, Dinosauria) from Las Hoyas fossil site (Early Cretaceous, Cuenca, Spain): taphonomic, phylogenetic and morphofunctional analyses. PhD Thesis, Universidad Autónoma de Madrid, Madrid.
Cuesta, E., Díaz-Martínez, I., Ortega, F. & Sanz, J. L. (2015). Did all theropods have chicken-like feet? First evidence of a non-avian dinosaur podotheca. *Cretaceous Research* **56**, 53–59.
Cuesta, E., Ortega, F. & Sanz, J. L. (2016). *Concavenator corcovatus* (Lower Cretaceous, Cuenca) under UV-light: highlighting bones and skin impressions. In *Actas de las XXXII Jornadas de la Sociedad Española de Paleontología. Cuadernos del Museo Geominero* (eds G. Meléndez, A. Núñez and M. Tomás), pp. 333–337. Instituto Geológico y Minero de España, Madrid.
Cuesta, E., Vidal, D., Ortega, F. & Sanz, J. L. (2018). The cranial osteology of *Concavenator corcovatus* (Theropoda; Carcharodontosauria) from the Lower Cretaceous of Spain. *Cretaceous Research* **91**, 176–194.
Currie, P. J., Badamgarav, D. & Koppelhus, E. (2003). The first Late Cretaceous footprints from the Nemegt Locality in the Gobi of Mongolia. *Ichnos* **10**, 1–13.

Currie, P. J. & Chen, P. (2001). Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Canadian Journal of Earth Sciences* **38**, 1705–1727.
Currie, P. J., Holmes, R. B., Ryan, M. J. & Coy, C. (2016). A juvenile chasmosaurine ceratopsid (Dinosauria, Ornithischia) from the Dinosaur Park Formation, Alberta, Canada. *Journal of Vertebrate Paleontology* **36**, e1048348.
Currie, P. J. & Koppelhus, E. B. (2010). Introduction to *Albertosaurus* Special Issue. *Canadian Journal of Earth Sciences* **47**, 1111–1114.
Currie, P. J. & Koppelhus, E. B. (2015). The significance of the theropod collections of the Royal Tyrrell Museum of Palaeontology to our understanding of Late Cretaceous theropod diversity. *Canadian Journal of Earth Sciences* **52**, 620–629.
Currie, P. J., Nadon, G. C. & Lockley, M. G. (1991). Dinosaur footprints with skin impressions from the Cretaceous of Alberta and Colorado. *Canadian Journal of Earth Sciences* **28**, 102–115.
Czerkas, S. & Czerkas, S. (1989). *My Life with the Dinosaurs*. Aladdin, New York.
Czerkas, S. A. (1992). Discovery of dermal spines reveals a new look for sauropod dinosaurs. *Geology* **20**, 1068–1070.
Czerkas, S. A. (1994). The history and interpretation of sauropod skin impressions. *Gaia* **10**, 173–182.
Czerkas, S. A. (1997). Skin. In *Encyclopedia of Dinosaurs* (eds P. J. Currie and K. Padian), pp. 669–675. Academic Press, San Diego.
Czerkas, S. A. & Czerkas, S. J. (1997). The integument and life restoration of Carnotaurus. Dinofest International, Proceedings of the Symposium at Arizona State University, 155–158.
Czerkas, S. A. & Feduccia, A. (2014). Jurassic archosaur is a non-dinosaurian bird. *Journal of Ornithology* **155**, 841–851.
Czerkas, S. A. & Yuan, C. (2002). An arboreal maniraptoran from northeast China. *Feathered Dinosaurs and the Origin of Flight. The Dinosaur Museum Journal 1. The Dinosaur Museum, Blanding, UT* **1**, 63–95.
Dal Sasso, C. & Maganuco, S. (2011). *Scipionyx samniticus* (Theropoda: Compsognathidae) from the Lower Cretaceous of Italy: osteology, ontogenetic assessment, phylogeny, soft tissue anatomy, taphonomy and palaeobiology. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **37**, 1–281.
Davis, M. (2014). Census of dinosaur skin reveals lithology may not be the most important factor in increased preservation of hadrosaurid skin. *Acta Palaeontologica Polonica* **59**, 601–605.
Dececchi, T. A., Larsson, H. C. E. & Hone, D. (2012). *Yixianosaurus longimanus* (Theropoda: Dinosauria) and its bearing on the evolution of Maniraptora and ecology of the Jehol fauna. *Vertebrata PalAsiatica* **50**, 111–139.
Dececchi, T. A., Roy, A., Pittman, M., Kaye, T. G., Xu, X., Habib, M. B., Larsson, H. C. E., Wang, X. & Zheng, X. (2020). Aerodynamics show membranous-winged theropods were a poor gliding dead-end. *iScience* **23**, 101574.
Delcourt, R. (2018). Ceratosaur palaeobiology: new insights on evolution and ecology of the southern rulers. *Scientific Reports* **8**, 1–12.
Delcourt, R. & Grillo, O. N. (2018). Tyrannosauroids from the Southern Hemisphere: implications for biogeography, evolution, and taxonomy. *Palaeogeography, Palaeoclimatology, Palaeoecology* **511**, 379–387.
Demathieu, G., Gand, G., Sciau, J., Freytet, P. & Garric, J. (2002). Les traces de pas de dinosaures et autres archosaures du Lias inférieur des Grands Causses, Sud de la France. *Palaeovertebrata* **31**, 1–143.
D'Emic, M. D., Wilson, J. A. & Chatterjee, S. (2009). The titanosaur (Dinosauria: Sauropoda) osteoderm record: review and first definitive specimen from India. *Journal of Vertebrate Paleontology* **29**, 165–177.
DePalma, R. A., Burnham, D. A., Martin, L. D., Larson, P. L. & Bakker, R. T. (2015). The first giant raptor (Theropoda: Dromaeosauridae) from the Hell Creek Formation. *Paleontological Contributions* **2015**, 1–16.
Desojo, J. B., Heckert, A. B., Martz, J. W., Parker, W. G., Schoch, R. R., Small, B. J. & Sulej, T. (2013). Aetosauria: a clade of armoured pseudosuchians from the Upper Triassic continental beds. *Geological Society, London, Special Publications* **379**, 203–239.
Dominy, N. J. & Symes, L. B. (2019). Close encounters of the bird kind. *Anthropology News* **60**, e75–e81.
Dyke, G. J. & Norell, M. A. (2005). *Caudipteryx* as a non-avialan theropod rather than a flightless bird. *Acta Palaeontologica Polonica* **50**, 101–116.
Eberth, D. A. & Currie, P. J. (2010). Stratigraphy, sedimentology, and taphonomy of the *Albertosaurus* bonebed (upper Horseshoe Canyon Formation; Maastrichtian), southern Alberta, Canada. *Canadian Journal of Earth Sciences* **47**, 1119–1143.
Elgin, R. A., Hone, D. W. E. & Frey, E. (2011). The extent of the pterosaur flight membrane. *Acta Palaeontologica Polonica* **56**, 99–111.
Elzanowski, A. (2001). A new genus and species for the largest specimen of *Archaeopteryx*. *Acta Palaeontologica Polonica* **46**, 519–532.
Elzanowski, A. (2002). Archaeopterygidae (Upper Jurassic of Germany). In *Mesozoic Birds: Above the Heads of Dinosaurs* (eds L. M. Chiappe and L. M. Witmer), pp. 129–159. University of California Press, Berkeley/Los Angeles/London.
Environment Canada (1995). *CITES Identification Guide—Crocodilians: Guide to the Identification of Crocodilian Species Controlled under the Convention on International Trade in Endangered Species of Wild Fauna and Flora*. Authority of the Minister of Environment, Ontario, Canada.
Erickson, G. M. (1996). Incremental lines of von Ebner in dinosaurs and the assessment of tooth replacement rates using growth line counts. *Proceedings of the National Academy of Sciences of the United States of America* **93**, 14623–14627.
Erickson, G. M. (2005). Assessing dinosaur growth patterns: a microscopic revolution. *Trends in Ecology & Evolution* **20**, 677–684.
Erickson, G. M. (2014). On dinosaur growth. *Annual Review of Earth and Planetary Sciences* **42**, 675–697.
Erickson, G. M., Currie, P. J., Inouye, B. D. & Winn, A. A. (2006). Tyrannosaur life tables: an example of nonavian dinosaur population biology. *Science* **313**, 213–217.
Fabbri, M., Wiemann, J., Manucci, F. & Briggs, D. E. G. (2020). Three-dimensional soft tissue preservation revealed in the skin of a non-avian dinosaur. *Palaeontology* **63**, 185–193.
Farlow, J. O. (2018). *Noah's Ravens: Interpreting the Makers of Tridactyl Dinosaur Footprints*. Indiana University Press, Bloomington.
Feduccia, A. & Czerkas, S. A. (2015). Testing the neoflightless hypothesis: propatagium reveals flying ancestry of oviraptorosaurs. *Journal of Ornithology* **156**, 1067–1074.
Feduccia, A., Lingham-Soliar, T. & Hinchliffe, J. R. (2005). Do feathered dinosaurs exist? Testing the hypothesis on neontological and paleontological evidence. *Journal of Morphology* **266**, 125–166.
Fondevilla, V., Vila, B., Oms, O. & Galobart, À. (2017). Skin impressions of the last European dinosaurs. *Geological Magazine* **154**, 393–398.
Forster, C. A., Sampson, S. D., Chiappe, L. M. & Krause, D. W. (1998). The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* **279**, 1915–1919.
Foster, J. R. & Hunt-Foster, R. K. (2011). New occurrences of dinosaur skin of two types (Sauropoda? and Dinosauria indet.) from the Late Jurassic of North America (Mygatt-Moore Quarry, Morrison Formation). *Journal of Vertebrate Paleontology* **31**, 717–721.
Foth, C., Evers, S. W., Pabst, B., Mateus, O., Flisch, A., Patthey, M. & Rauhut, O. W. M. (2015). New insights into the lifestyle of *Allosaurus* (Dinosauria: Theropoda) based on another specimen with multiple pathologies. *PeerJ* **3**, e940.
Foth, C., Haug, C., Haug, J. T., Tischlinger, H. & Rauhut, O. W. M. (2020). Two of a feather: a comparison of the preserved integument in the juvenile theropod dinosaurs *Sciurumimus* and *Juravenator* from the Kimmeridgian Torleite Formation of southern Germany. In *The Evolution of Feathers: From Their Origin to the Present* (eds C. Foth and O. W. M. Rauhut), pp. 79–101. Springer International Publishing, Cham.
Foth, C. & Rauhut, O. W. M. (2013). Macroevolutionary and morphofunctional patterns in theropod skulls: a morphometric approach. *Acta Palaeontologica Polonica* **58**, 1–16.
Foth, C. & Rauhut, O. W. M. (2017). Re-evaluation of the Haarlem *Archaeopteryx* and the radiation of maniraptoran theropod dinosaurs. *BMC Evolutionary Biology* **17**, 236.
Foth, C., Tischlinger, H. & Rauhut, O. W. M. (2014). New specimen of *Archaeopteryx* provides insights into the evolution of pennaceous feathers. *Nature* **511**, 79–82.
Frey, E. & Martill, D. M. (1998). Soft tissue preservation in a specimen of *Pterodactylus kochi* (Wagner) from the Upper Jurassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* **210**, 421–441.
Frey, E., Tischlinger, H., Buchy, M.-C. & Martill, D. M. (2003). New specimens of Pterosauria (Reptilia) with soft parts with implications for pterosaurian anatomy and locomotion. *Geological Society, London, Special Publications* **217**, 233–266.
Funston, G. F. & Currie, P. J. (2020). New material of *Chirostenotes pergracilis* (Theropoda, Oviraptorosauria) from the Campanian Dinosaur Park Formation of Alberta, Canada. *Historical Biology* **33**, 1671–1685.
Funston, G. F., Currie, P. J., Eberth, D. A., Ryan, M. J., Chinzorig, T., Badamgarav, D. & Longrich, N. R. (2016). The first oviraptorosaur (Dinosauria: Theropoda) bonebed: evidence of gregarious behaviour in a maniraptoran theropod. *Scientific Reports* **6**, 35782.
Gallagher, T., Poole, J. & Schein, J. P. (2021). Evidence of integumentary scale diversity in the late Jurassic sauropod *Diplodocus* sp. from the Mother's Day Quarry, Montana. *PeerJ* **9**, e11202.
Galton, P. M. & Upchurch, P. (2004). Stegosauria. In *The Dinosauria*, Second Edition (eds D. B. Weishampel, P. Dodson and H. Osmolska), pp. 343–362. University of California Press, Berkeley.
Gatesy, S. M. (2001). Skin impressions of Triassic theropods as records of foot movement. *Bulletin of the Museum of Comparative Zoology* **156**, 137–149.
Gatesy, S. M. & Dial, K. P. (1996). From frond to fan: *Archaeopteryx* and the evolution of short-tailed birds. *Evolution* **50**, 2037–2048.
Gatesy, S. M., Shubin, N. H. & Jenkins, F. A. Jr. (2005). Anaglyph stereo imaging of dinosaur track morphology and microtopography. *Palaeontologia Electronica* **8**, 1–12.

Gauthier, J. (1986). Saurischian monophyly and the origin of birds. In *The Origin of Birds and the Evolution of Flight* (ed. K. Padian), pp. 1–55. Memoirs of the California Academy of Sciences Number 8, San Francisco.

Gauthier, J. & Gall, L. F. (2002). *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom*. Peabody Museum of Natural History, New Haven, Connecticut.

Gierliński, G. (1994). Early Jurassic theropod tracks with the metatarsal impressions. *Przegląd Geologiczny* **42**, 280–284.

Gierliński, G. (1997). What type of feathers could nonavian dinosaurs have, according to an Early Jurassic ichnological evidence from Massachusetts. *Przegląd Geologiczny* **45**, 419–422.

Gierlowski-Kordesch, E. & Rust, B. R. (1994). The Jurassic East Berlin Formation, Hartford Basin, Newark Supergroup (Connecticut and Massachusetts): A Saline Lake Playa Alluvial Plain System. In *Sedimentology and Geochemistry of Modern and Ancient Saline Lakes Models* (eds R. W. Renaut and W. M. Last), pp. 249–265. SEPM (Society for Sedimentary Geology), Tulsa, Oklahoma.

Gilmore, C. W. (1920). Osteology of the carnivorous Dinosauria in the United State National museum: with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bulletin of the United States National Museum* **110**, 1–159.

del Giménez, O. V. (2007). Skin impressions of *Tehuelchesaurus* (Sauropoda) from the Upper Jurassic of Patagonia. *Revista del Museo Argentino de Ciencias Naturales* **9**, 119–124.

Godefroit, P., Cau, A., Dong-Yu, H., Escuillié, F., Wenhao, W. & Dyke, G. (2013a). A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds. *Nature* **498**, 359–362.

Godefroit, P., Demuynck, H., Dyke, G., Hu, D., Escuillié, F. & Claeys, P. (2013b). Reduced plumage and flight ability of a new Jurassic paravian theropod from China. *Nature Communications* **4**, 1394.

Godefroit, P., Sinitsa, S. M., Cincotta, A., McNamara, M. E., Reshetova, S. A. & Dhouailly, D. (2020). Integumentary structures in *Kulindadromeus zabaikalicus*, a basal neornithischian dinosaur from the Jurassic of Siberia. In *The Evolution of Feathers: From Their Origin to the Present* (eds C. Foth and O. W. M. Rauhut), pp. 47–65. Springer International Publishing, Cham.

Godefroit, P., Sinitsa, S. M., Dhouailly, D., Bolotsky, Y. L., Sizov, A. V., McNamara, M. E., Benton, M. J. & Spagna, P. (2014). A Jurassic ornithischian dinosaur from Siberia with both feathers and scales. *Science* **345**, 451–455.

Göhlich, U. B. & Chiappe, L. M. (2006). A new carnivorous dinosaur from the Late Jurassic Solnhofen archipelago. *Nature* **440**, 329–332.

Göhlich, U. B., Tischlinger, H. & Chiappe, L. M. (2006). *Juravenator starki* (Reptilia, Theropoda), ein neuer Raubdinosaurier aus dem oberjura der südlichen frankenalb (Süddeutschland). *Archaeopteryx: Jahreszeitschrift der Freunde des Jura-Museums in Eichstätt* **24**, 1–26.

Goloboff, P. A. & Catalano, S. A. (2016). TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* **32**, 221–238.

Gong, E.-P., Martin, L. D., Burnham, D. A., Falk, A. R. & Hou, L.-H. (2012). A new species of *Microraptor* from the Jehol Biota of northeastern China. *Palaeoworld* **21**, 81–91.

Grellet-Tinner, G., Codrea, V., Folie, A., Higa, A. & Smith, T. (2012). First evidence of reproductive adaptation to "Island Effect" of a dwarf Cretaceous Romanian titanosaur, with embryonic integument *In Ovo*. *PLoS One* **7**, e32051.

Griffiths, P. J. (1996). The isolated *Archaeopteryx* feather. *Archaeopteryx* **14**, 1–26.

Han, G., Chiappe, L. M., Ji, S.-A., Habib, M., Turner, A. H., Chinsamy, A., Liu, X. & Han, L. (2014). A new raptorial dinosaur with exceptionally long feathering provides insights into dromaeosaurid flight performance. *Nature Communications* **5**, 1–9.

Harris, J. D. & Milner, A. R. C. (2015). *Tracks in Deep Time: The St. George Dinosaur Discovery Site at Johnson Farm*. University of Utah Press, Salt Lake City, Utah.

Hartman, S., Mortimer, M., Wahl, W. R., Lomax, D. R., Lippincott, J. & Lovelace, D. M. (2019). A new paravian dinosaur from the Late Jurassic of North America supports a late acquisition of avian flight. *PeerJ* **7**, e7247.

Haubolt, H. (1986). Archosaur footprints at the terrestrial Triassic-Jurassic transition. In *The Beginning of the Age of Dinosaurs. Faunal Change across the Triassic-Jurassic Boundary* (ed. K. Padian), pp. 189–201. Cambridge University Press, Cambridge.

Hendrickx, C. & Bell, P. R. (2021a). 3D model related to the publication: the scaly skin of the abelisaurid *Carnotaurus sastrei* (Theropoda: Ceratosauria) from the Upper Cretaceous of Patagonia. *MorphoMuseuM* **7**, 1–3.

Hendrickx, C. & Bell, P. R. (2021b). The scaly skin of the abelisaurid *Carnotaurus sastrei* (Theropoda: Ceratosauria) from the Upper Cretaceous of Patagonia. *Cretaceous Research* **128**, 104994.

Hendrickx, C., Bell, P. R., Pittman, M., Milner, A. R. C., Cuesta, E., O'Connor, J., Loewen, M. A., Currie, P. J., Mateus, O., Kaye, T. G. & Delcourt, R. (2021a). 3D model related to the publication: morphology and distribution of scales, dermal ossifications, and other non-feather integumentary structures in non-avialan theropod dinosaurs. *MorphoMuseuM* **7**, 1–3.

Hendrickx, C., Bell, P. R., Pittman, M., Milner, A. R. C., Cuesta, E., O'Connor, J., Loewen, M. A., Currie, P. J., Mateus, O., Kaye, T. G. & Delcourt, R. (2021b). Data from: morphology and distribution of scales, dermal ossifications, and other non-feather integumentary structures in non-avialan theropod dinosaurs. Dryad Digital Repository. https://doi.org/10.5061/dryad.zcrjdfnck

Hendrickx, C. & Carrano, M. T. (2016). Erratum on 'An overview of non-avian theropod discoveries and classification'. *PalArch's Journal of Vertebrate Palaeontology* **13**, 1–7.

Hendrickx, C., Hartman, S. A. & Mateus, O. (2015). An overview of non-avian theropod discoveries and classification. *PalArch's Journal of Vertebrate Palaeontology* **12**, 1–73.

Herrero, L. & Farke, A. A. (2010). Hadrosaurid dinosaur skin impressions from the Upper Cretaceous Kaiparowits Formation of southern Utah, USA. *PalArch's Journal of Vertebrate Palaeontology* **7**, 1–7.

Hieronymus, T. L. (2015). Qualitative skeletal correlates of wing shape in extant birds (Aves: Neoaves). *BMC Evolutionary Biology* **15**, 30.

Hieronymus, T. L., Witmer, L. M., Tanke, D. H. & Currie, P. J. (2009). The facial integument of centrosaurine ceratopsids: morphological and histological correlates of novel skin structures. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology* **292**, 1370–1396.

Hitchcock, E. (1836). Ornithichnology—description of the foot marks of birds (*Ornithichnites*) on New Red Sandstone in Massachusetts. *The American Journal of Science and Arts* **29**, 307–340.

Hitchcock, E. (1841). *Final Report on the Geology of Massachusetts*. JS & C. Adams, Northampton.

Hitchcock, E. (1848). An attempt to discriminate and describe the animals that made the fossil footmarks of the United States, and especially of New England. *Memoirs of the American Academy of Arts and Sciences* **3**, 129–256.

Hitchcock, E. (1858). Ichnology of New England: A Report on the Sandstone of the Connecticut Valley Especially Its Fossil Footmarks, Made to the Government of the Commonwealth of Massachusetts. William White, printer.

Hitchcock, E. (1865). *Supplement to the Ichnology of New England: A Report to the Government of Massachusetts, in 1863*. Wright & Potter, Boston, Massachusetts.

Holtz, T. R. J. (2012). Theropods. In *The Complete Dinosaur*, Second Edition (eds M. K. Brett-Surman, T. R. J. Holtz and J. O. Farlow), pp. 347–378. Indiana University Press, Bloomington.

Holtz, T. R. J., Molnar, R. E. & Currie, P. J. (2004). Basal Tetanurae. In *The Dinosauria*, Second Edition (eds D. B. Weishampel, P. Dodson and H. Osmólska), pp. 71–110. University of California Press, Berkeley.

Hone, D. W. E., Tischlinger, H., Xu, X. & Zhang, F. (2010). The extent of the preserved feathers on the four-winged dinosaur *Microraptor gui* under ultraviolet light. *PLoS One* **5**, e9223.

Hooley, R. W. (1917). II.—On the integument of *Iguanodon bernissartensis*, Boulenger, and of *Morosaurus becklesii*, Mantell. *Geological Magazine* **4**, 148–150.

Hooley, R. W. (1925). On the skeleton of *Iguanodon atherfieldensis* sp. nov., from the Wealden Shales of Atherfield (Isle of Wight). *Quarterly Journal of the Geological Society* **81**, 1–61.

Horner, J. R. (1984). A "segmented" epidermal tail frill in a species of hadrosaurian dinosaur. *Journal of Paleontology* **58**, 270–271.

Hou, L., Martin, L. D., Zhou, Z. & Feduccia, A. (1996). Early adaptive radiation of birds: evidence from fossils from northeastern China. *Science* **274**, 1164–1167.

Hu, D., Clarke, J. A., Eliason, C. M., Qiu, R., Li, Q., Shawkey, M. D., Zhao, C., D'Alba, L., Jiang, J. & Xu, X. (2018). A bony-crested Jurassic dinosaur with evidence of iridescent plumage highlights complexity in early paravian evolution. *Nature Communications* **9**, 217.

Hu, D., Hou, L., Zhang, L. & Xu, X. (2009). A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* **461**, 640–643.

Irmis, R.B., Hutchison, J.H., Sertich, J.J.W. & Titus, A.L. (2013). Crocodyliforms from the Late Cretaceous of Grand Staircase-Escalante National Monument and vicinity, southern Utah, USA. At the Top of the Grand Staircase, The Late Cretaceous of Southern Utah. Indiana University Press, Bloomington, Indiana, 424–444.

Jain, S. L. & Bandyopadhyay, S. (1997). New titanosaurid (Dinosauria: Sauropoda) from the Late Cretaceous of Central India. *Journal of Vertebrate Paleontology* **17**, 114–136.

Jenkins, F. J., Shubin, N. H., Amarel, W. W., Gatesy, S. M., Schaff, C. R., Clemmensen, L. B., Downs, W. R., Davidson, A. R., Bonde, N. C. & Osbaeck, F. (1994). Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, east Greenland. Meddelelser om Grønland, Geoscience, 1–25.

Ji, Q., Currie, P. J., Norell, M. A. & Shu-An, J. (1998). Two feathered dinosaurs from northeastern China. *Nature* **393**, 753–761.

Ji, Q. & Ji, S. (1996). On the discovery of the earliest fossil bird in China (*Sinosauropteryx* gen. nov.) and the origin of birds. *Chinese Geology* **233**, 30–33.

Ji, Q. & Ji, S. (1997). A Chinese archaeopterygian, *Protarchaeopteryx* gen. nov. *Geological Science and Technology* **238**, 38–41.

Ji, Q., Ji, S.-A. & Yuan, C.-X. (2002). Restudy on a small dromaeosaurid dinosaur with feathers over its entire body. *Earth Science Frontiers* **9**, 57–64.

Ji, Q., Ji, S., Lü, J., You, H., Chen, W., Liu, Y. & Liu, Y. (2005). First avialian bird from China. *Geological Bulletin of China* **24**, 197–210.

Ji, Q., Ji, S., Lü, J. & Yuan, C. (2007). A new giant compsognathid dinosaur with long filamentous integuments from lower Cretaceous of Northeastern China. *Acta Geologica Sinica* **81**, 8–15.

Ji, Q., Lü, J., Wei, X. F. & Wang, X. R. (2012). A new oviraptorosaur from the Yixian Formation of Jianchang, western Liaoning Province, China. *Geological Bulletin of China* **31**, 2102–2107.

Ji, Q., Norell, M. A., Gao, K.-Q., Ji, S.-A. & Ren, D. (2001). The distribution of integumentary structures in a feathered dinosaur. *Nature* **410**, 1084–1088.

Ji, S. (1999). Initial report of fossil psittacosaurid skin impression from the uppermost Jurassic of Sihetun, northeastern China. *Earth Science (Chikyu Kagaku)* **53**, 314–316.

Ji, S. (2002). New Data of Early Cretaceous dromaeosaurs from Western Liaoning, with Comments on the Origin of Feathers. Ph.D. Dissertation, Beijing University, Beijing, China, Beijing, China.

Ji, S. & Ji, Q. (2007). *Jinfengopteryx* compared to *Archaeopteryx*, with comments on the mosaic evolution of long-tailed avialan birds. *Acta Geologica Sinica* **81**, 337–343.

Kaye, T. G., Falk, A. R., Pittman, M., Sereno, P. C., Martin, L. D., Burnham, D. A., Gong, E., Xu, X. & Wang, Y. (2015). Laser-stimulated fluorescence in paleontology. *PLoS One* **10**, e0125923.

Kaye, T. G., Pittman, M., Mayr, G., Schwarz, D. & Xu, X. (2019). Detection of lost calamus challenges identity of isolated *Archaeopteryx* feather. *Scientific Reports* **9**, 1182.

Kellner, A. W. & de Campos, D. A. (1998). *Archosaur Soft Tissue from the Cretaceous of the Araripe Basin, Northeastern Brazil*. Museu Nacional, Rio de Janeiro, Brazil.

Kellner, A. W. A. (1996). Fossilized theropod soft tissue. *Nature* **379**, 32–32.

Kellner, A. W. A. (1999). Short note on a new dinosaur (Theropoda, Coelurosauria) from the Santana Formation (Romualdo Member, Albian), Northeastern Brazil. *Boletim do Museu Nacional, N.S.* **49**, 1–8.

Kellner, A. W. A., Wang, X., Tischlinger, H., de Campos, D. A., Hone, D. W. E. & Meng, X. (2010). The soft tissue of *Jeholopterus* (Pterosauria, Anurognathidae, Batrachognathinae) and the structure of the pterosaur wing membrane. *Proceedings of the Royal Society of London B: Biological Sciences* **277**, 321–329.

Kim, K. S., Lockley, M. G., Lim, J. D. & Xing, L. (2019). Exquisitely-preserved, high-definition skin traces in diminutive theropod tracks from the Cretaceous of Korea. *Scientific Reports* **9**, 1–10.

Kirkland, J. I., Milner, A. R. C., Olsen, P. E. & Hargrave, J. E. (2014). The Whitmore Point Member of the Moenave Formation in its type area in Northern Arizona and its age and correlation with the section in St. George, Utah: evidence for two major lacustrine sequences. *Geology of Utah's Far South: Utah Geological Association Publication* **43**, 321–356.

Kowallis, B. J., Christiansen, E. H., Deino, A. L., Peterson, F., Turner, C. E., Kunk, M. J. & Obradovich, J. D. (1998). The age of the Morrison Formation. *Modern Geology* **22**, 235–260.

Kundrát, M. (2004). When did theropods become feathered?—evidence for pre-archaeopteryx feathery appendages. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* **302B**, 355–364.

Kundrát, M., Cruickshank, A. R. I., Manning, T. W. & Nudds, J. (2008). Embryos of therizinosauroid theropods from the Upper Cretaceous of China: diagnosis and analysis of ossification patterns. *Acta Zoologica* **89**, 231–251.

Kurzanov, S. M. (1982). Structural characteristics of the fore limbs of *Avimimus*. *Paleontological Journal* **1982**, 108–112.

Kurzanov, S. M. (1987). Avimimidae and the problem of the origin of birds. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition* **31**, 5–92.

Lambertz, M. (2017). Phylogenetic placement, developmental trajectories and evolutionary implications of a feathered dinosaur tail in Mid-Cretaceous amber. *Current Biology* **27**, R215–R216.

Langer, M. C. (2014). The origins of Dinosauria: much ado about nothing. *Palaeontology* **57**, 469–478.

Langer, M. C., Ezcurra, M. D., Rauhut, O. W. M., Benton, M. J., Knoll, F., McPhee, B. W., Novas, F. E., Pol, D. & Brusatte, S. L. (2017). Untangling the dinosaur family tree. *Nature* **551**, 24011.

Larson, N. L. (2008). One hundred years of *Tyrannosaurus rex*: the skeletons. *Tyrannosaurus rex, The Tyrant King* **1**, 56.

Larson, P., Larson, M., Ott, C. & Robert, B. (2007). Skinning a *triceratops*. *Journal of Vertebrate Paleontology* **27**, 104A.

Lefèvre, U., Cau, A., Cincotta, A., Hu, D., Chinsamy, A., Escuillié, F. & Godefroit, P. (2017). A new Jurassic theropod from China documents a transitional step in the macrostructure of feathers. *The Science of Nature* **104**, 74.

Lefèvre, U., Cau, A., Hu, D. & Godefroit, P. (2020). Feather evolution in Pennaraptora. In *The Evolution of Feathers: From Their Origin to the Present* (eds C. Foth and O. W. M. Rauhut), pp. 103–118. Springer International Publishing, Cham.

Lessem, D. (1989). Skinning the Dinosaur. *Discover* **10**, 38–44.

Li, Q., Clarke, J. A., Gao, K.-Q., Zhou, C.-F., Meng, Q., Li, D., D'Alba, L. & Shawkey, M. D. (2014). Melanosome evolution indicates a key physiological shift within feathered dinosaurs. *Nature* **507**, 350–353.

Li, Q., Gao, K.-Q., Meng, Q., Clarke, J. A., Shawkey, M. D., D'Alba, L., Pei, R., Ellison, M., Norell, M. A. & Vinther, J. (2012). Reconstruction of *Microraptor* and the evolution of iridescent plumage. *Science* **335**, 1215–1219.

Li, Q., Gao, K.-Q., Vinther, J., Shawkey, M. D., Clarke, J. A., D'Alba, L., Meng, Q., Briggs, D. E. G. & Prum, R. O. (2010). Plumage color patterns of an extinct dinosaur. *Science* **327**, 1369–1372.

Lindgren, J., Kaddumi, H. F. & Polcyn, M. J. (2013). Soft tissue preservation in a fossil marine lizard with a bilobed tail fin. *Nature Communications* **4**, 2423.

Lindgren, J., Sjövall, P., Carney, R. M., Cincotta, A., Uvdal, P., Hutcheson, S. W., Gustafsson, O., Lefèvre, U., Escuillié, F., Heimdal, J., Engdahl, A., Gren, J. A., Kear, B. P., Wakamatsu, K., Yans, J., et al. (2015). Molecular composition and ultrastructure of Jurassic paravian feathers. *Scientific Reports* **5**, 13520.

Lindgren, J., Sjövall, P., Carney, R. M., Uvdal, P., Gren, J. A., Dyke, G., Schultz, B. P., Shawkey, M. D., Barnes, K. R. & Polcyn, M. J. (2014). Skin pigmentation provides evidence of convergent melanism in extinct marine reptiles. *Nature* **506**, 484–488.

Lingham-Soliar, T. (2003). Evolution of birds: ichthyosaur integumental fibers conform to dromaeosaur protofeathers. *Naturwissenschaften* **90**, 428–432.

Lingham-Soliar, T. & Plodowski, G. (2010). The integument of *Psittacosaurus* from Liaoning Province, China: taphonomy, epidermal patterns and color of a ceratopsian dinosaur. *Naturwissenschaften* **97**, 479–486.

Lockley, M., Matsukawa, M. & Jianjun, L. (2003). Crouching theropods in taxonomic jungles: ichnological and ichnotaxonomic investigations of footprints with metatarsal and ischial impressions. *Ichnos* **10**, 169–177.

Lockley, M. G., Cart, K., Martin, J. & Milner, A. R. C. (2011). New theropod tracksites from the Upper Cretaceous "Mesaverde" Group, western Colorado: implications for ornithomimosaur track morphology. *New Mexico Museum of Natural History & Sciences Bulletin* **53**, 321–329.

Lockley, M. G., Nadon, G. & Currie, P. J. (2004). A diverse dinosaur-bird footprint assemblage from the Lance Formation, Upper Cretaceous, Eastern Wyoming: implications for ichnotaxonomy. *Ichnos* **11**, 229–249.

Loewen, M. A. (2010). Variation in the Late Jurassic theropod dinosaur Allosaurus: ontogenetic, functional, and taxonomic implications. Ph.D. Dissertation, The University of Utah, Texas, Utah.

Longrich, N. R., Tischlinger, H. & Foth, C. (2020). The feathers of the Jurassic urvogel *Archaeopteryx*. In *The Evolution of Feathers: From Their Origin to the Present* (eds C. Foth and O. W. M. Rauhut), pp. 119–146. Springer International Publishing, Cham.

Longrich, N. R., Vinther, J., Meng, Q., Li, Q. & Russell, A. P. (2012). Primitive wing feather arrangement in *Archaeopteryx lithographica* and *Anchiornis huxleyi*. *Current Biology* **22**, 2262–2267.

Lü, J. & Brusatte, S. L. (2015). A large, short-armed, winged dromaeosaurid (Dinosauria: Theropoda) from the Early Cretaceous of China and its implications for feather evolution. *Scientific Reports* **5**, 11775.

Lucas, A. M. & Stettenheim, P. R. (1972). *Avian Anatomy: Integument*, First Edition. U.S. Department of Agriculture, Washington, D.C.

Lucas, S. G., Klein, H., Lockley, M. G., Spielmann, J. A., Gierlinski, G. D., Hunt, A. P. & Tanner, L. H. (2006). Triassic-Jurassic stratigraphic distribution of the theropod footprint ichnogenus *Eubrontes*. *New Mexico Museum of Natural History and Science Bulletin* **37**, 86–93.

Lull, R. S. (1933). A revision of the Ceratopsia or horned dinosaurs. *Peabody Museum of Natural History Bulletin* **3**, 1–175.

Lull, R. S. & Wright, N. E. (1942). *Hadrosaurian Dinosaurs of North America*. Geological Society of America, Boulder, Colorado.

Lund, E. K. (2010). Nasutuceratops titusi, a new basal centrosaurine dinosaur (Ornithischia: Ceratopsidae) from the Upper Cretaceous Kaiparowits Formation, southern Utah. MSc. Dissertation, The University of Utah, Salt Lake City, Utah, USA.

Maddison, W. P. & Maddison, D. R. (2017). Mesquite: a modular system for evolutionary analysis. Version 3.2. Mesquite. http://mesquiteproject.org Accessed 16.06.2017.

Madsen, J. H. & Welles, S. P. (2000). *Ceratosaurus* (Dinosauria, Theropoda): a revised osteology. *Utah Geological Survey, Miscellaneous Publication* **2**, 1–89.

Mallon, J. C. (2017). Recognizing sexual dimorphism in the fossil record: lessons from nonavian dinosaurs. *Paleobiology* **43**, 495–507.

Manning, P. L., Morris, P. M., McMahon, A., Jones, E., Gize, A., Macquaker, J. H. S., Wolff, G., Thompson, A., Marshall, J., Taylor, K. G., Lyson, T., Gaskell, S., Reamtong, O., Sellers, W. I., Dongen, B. E., et al. (2009). Mineralized soft-tissue structure and chemistry in a mummified hadrosaur from the Hell Creek Formation, North Dakota (USA). *Proceedings of the Royal Society B: Biological Sciences* **276**, 3429–3437.

Mantell, G. A. (1852). On the structure of the Iguanodon, and on the fauna and flora of the Wealden Formation. *Notice Proceedings, Royal Institute of Great Britain* **1**, 141–146.
Marsh, A. D. & Rowe, T. B. (2020). A comprehensive anatomical and phylogenetic evaluation of *Dilophosaurus wetherilli* (Dinosauria, Theropoda) with descriptions of new specimens from the Kayenta Formation of northern Arizona. *Journal of Paleontology* **94**, 1–103.
Marsh, A. D., Milner, A. R. C., Harris, J. D., De Blieux, D. D. & Kirkland, J. I. (2021). A non-averostran neotheropod vertebra (Dinosauria: Theropoda) from the earliest Jurassic Whitmore Point Member (Moenave Formation) in southwestern Utah. *Journal of Vertebrate Paleontology* **41**, e1897604.
Marsh, O. C. (1884). Principal characters of the American Jurassic dinosaurs. Part VIII. The order Theropoda. *American Journal of Science, Series 3* **27**, 329–340.
Martill, D. M., Batten, D. J. & Loydell, D. K. (2000). A new specimen of the thyreophoran dinosaur cf. *Scelidosaurus* with soft tissue preservation. *Palaeontology* **43**, 549–559.
Martin, A. J. & Rainforth, E. C. (2004). A theropod resting trace that is also a locomotion trace: case study of Hitchcock's specimen AC1/7. In Geological Society of America, Abstracts with Programs p. 96.
Martin, L. D. & Czerkas, S. A. (2000). The fossil record of feather evolution in the Mesozoic. *Integrative and Comparative Biology* **40**, 687–694.
Martin, L. D., Zhou, Z., Hou, L. & Feduccia, A. (1998). *Confuciusornis sanctus* compared to *Archaeopteryx lithographica*. *Naturwissenschaften* **85**, 286–289.
Martz, J. W., Kirkland, J. I., Milner, A. R. C., Parker, W. G. & Santucci, V. L. (2017). Upper Triassic lithostratigraphy, depositional systems, and vertebrate paleontology across southern Utah. *Geology of the Intermountain West* **4**, 99–180.
Mateus, I., Mateus, H., Antunes, M. T., Mateus, O., Taquet, P., Ribeiro, V. & Manuppella, G. (1997). Couvée, œufs et embryons d'un dinosaure théropode du Jurassique supérieur de Lourinha (Portugal). *Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science* **325**, 71–78.
Mateus, I., Mateus, H., Antunes, M. T., Mateus, O., Taquet, P., Ribeiro, V. & Manuppella, G. (1998). Upper Jurassic theropod dinosaur embryos from Lourinhã (Portugal). *Memórias da Academia das Ciências de Lisboa* **37**, 101–110.
Mateus, O., Antunes, M. T. & Taquet, P. (2001). Dinosaur ontogeny: the case of *Lourinhanosaurus* (Late Jurassic, Portugal). *Journal of Vertebrate Paleontology* **21**, 78A.
Mateus, O., Milàn, J., Romano, M. & Whyte, M. A. (2011). New finds of stegosaur tracks from the Upper Jurassic Lourinhã Formation, Portugal. *Acta Palaeontologica Polonica* **56**, 651–658.
Matley, C. A. (1923). Note on an armoured dinosaur from the Lameta beds of Jubbulpore. *Records of the Geological Survey of India* **55**, 105–109.
Mayr, G., Peters, S. D., Plodowski, G. & Vogel, O. (2002). Bristle-like integumentary structures at the tail of the horned dinosaur *Psittacosaurus*. *Naturwissenschaften* **89**, 361–365.
Mayr, G., Pittman, M., Saitta, E., Kaye, T. G. & Vinther, J. (2016). Structure and homology of *Psittacosaurus* tail bristles. *Palaeontology* **59**, 793–802.
Mayr, G., Pohl, B. & Peters, D. S. (2005). A well-preserved *Archaeopteryx* specimen with theropod features. *Science* **310**, 1483–1486.
McCrea, R. T., Buckley, L. G., Plint, A. G., Lockley, M. G., Matthews, N. A., Noble, T. A., Xing, L. & Krawetz, J. R. (2015). Vertebrate ichnites from the Boulder Creek Formation (Lower Cretaceous: middle to ? upper Albian) of northeastern British Columbia, with a description of a new avian ichnotaxon, *Paxavipes babcockensis* ichnogen. et isp. nov. *Cretaceous Research* **55**, 1–18.
McCrea, R. T., Lockley, M. G. & Meyer, C. A. (2001). Global distribution of purported ankylosaur track occurrences. In *The Armored Dinosaurs* (ed. K. Carpenter), pp. 413–454. Indiana University Press, Bloomington.
McNamara, M. E., van Dongen, B. E., Lockyer, N. P., Bull, I. D. & Orr, P. J. (2016). Fossilization of melanosomes via sulfurization. *Palaeontology* **59**, 337–350.
Meyekort, R. (2019). The life appearance of T. rex by Paleonerd01 on DeviantArt. https://www.deviantart.com/paleonerd01/art/The-Life-Appearance-of-T-rex-781791931 Accessed 9.10.2020.
von Von Meyer, H. (1861). *Archaeopteryx lithographica* (Vogel-Feder) und *Pterodactylus* von Solnhofen. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde* **1861**, 678–679.
Milàn, J., Christiansen, P. & Mateus, O. (2005). A three-dimensionally preserved sauropod manus impression from the Upper Jurassic of Portugal: implications for sauropod manus shape and locomotor mechanics. *Kaupia* **14**, 47–52.
Milner, A. C. (2002). Theropod dinosaurs of the Purbeck limestone group, Southern England. *Special Papers in Palaeontology* **68**, 191–202.
Milner, A. R. C. & Lockley, M. G. (2006). History, Geology and Paleontology: St. George Dinosaur Discovery Site at Johnson Farm, Utah. Making Tracks Across the Southwest.
Milner, A. R. C., Birthisel, T. A., Kirkland, J. I., Breithaupt, B. H., Matthews, N. A., Lockley, M. G., Santucci, V. L., Gibson, S. Z., DeBlieux, D. D., Hurlbut, M., Harris, J. D. & Olsen, P. E. (2012). Tracking Early Jurassic dinosaurs across southwestern Utah and the Triassic–Jurassic transition. In Field Trip Guide Book for the 71st Annual Meeting of the Society of Vertebrate Paleontology: Nevada State Museum Paleontological Papers pp. 1–107.
Milner, A. R. C. & Lockley, M. G. (2016). Dinosaur swim track assemblages: characteristics, contexts, and ichnofacies implications. In *Dinosaur Tracks: The Next Steps* (eds P. L. Falkingham, D. Marty and A. Richter), pp. 152–181. Indiana University Press, Bloomington.
Milner, A. R. C., Lockley, M. G. & Johnson, S. (2006a). The story of the St. George Dinosaur Discovery Site at Johnson Farm: an important new Lower Jurassic dinosaur tracksite from the Moenave Formation of southwestern Utah. *The Triassic-Jurassic Terrestrial Transition, New Mexico Museum of Natural History and Science Bulletin* **37**, 329–345.
Milner, A. R. C., Lockley, M. G. & Kirkland, J. I. (2006b). A large collection of well-preserved theropod dinosaur swim tracks from the Lower Jurassic Moenave Formation, St. George, Utah. In *The Triassic-Jurassic Terrestrial Transition*, pp. 315–328. New Mexico Museum of Natural History, Albuquerque, New Mexico.
Møller, A. P. & Cuervo, J. J. (1998). Speciation and feather ornamentation in birds. *Evolution* **52**, 859–869.
Motta, M. J., Agnolín, F. L., Brissón Egli, F. & Novas, F. E. (2020). New theropod dinosaur from the Upper Cretaceous of Patagonia sheds light on the paravian radiation in Gondwana. *The Science of Nature* **107**, 24.
Moyer, A. E., Zheng, W., Johnson, E. A., Lamanna, M. C., Li, D., Lacovara, K. J. & Schweitzer, M. H. (2014). Melanosomes or microbes: testing an alternative hypothesis for the origin of microbodies in fossil feathers. *Scientific Reports* **4**, 4233.
Müller, R. T., Langer, M. C., Bronzati, M., Pacheco, C. P., Cabreira, S. F. & Dias-Da-Silva, S. (2018). Early evolution of sauropodomorphs: anatomy and phylogenetic relationships of a remarkably well-preserved dinosaur from the Upper Triassic of southern Brazil. *Zoological Journal of the Linnean Society* **184**, 1187–1248.
Naeem, S. & Post, K. (2019). How wings lost their claws. *Science* **364**, 746–746.
Naish, D. (2012). Birds. In *The Complete Dinosaur*, Second Edition (eds M. K. Brett-Surman, T. R. J. Holtz and J. O. Farlow), pp. 379–423. Indiana University Press, Bloomington.
Negro, J. J., Finlayson, C. & Galván, I. (2018). Melanins in fossil animals: is it possible to infer life history traits from the coloration of extinct species? *International Journal of Molecular Sciences* **19**, 230.
Nesbitt, S. J. (2011). The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History* **352**, 1–292.
Nesbitt, S. J., Smith, N. D., Irmis, R. B., Turner, A. H., Downs, A. & Norell, M. A. (2009). A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. *Science* **326**, 1530–1533.
Nixon, K.C. (2002). WinClada, version 1.00.08. *Published by the author*, Ithaca, New York.
Noe, D., Lockley, M. & Hadden, G. (2014). Vertebrate tracks from the Cretaceous Dakota Group, Gunnison Gorge National Conservation Area, Delta County, Colorado. *New Mexico Museum of Natural History and Science, Bulletin* **62**, 385–391.
Norell, M. A. & Xu, X. (2005). Feathered dinosaurs. *Annual Review of Earth and Planetary Sciences* **33**, 277–299.
Norman, D. B. (2020). *Scelidosaurus harrisonii* from the Early Jurassic of Dorset, England: the dermal skeleton. *Zoological Journal of the Linnean Society* **190**, 1–53.
Novas, F. E. (1994). New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *Journal of Vertebrate Paleontology* **13**, 400–423.
O'Connor, J. K. (2009). A systematic review of Enantiornithes (Aves: Ornithothoraces). PhD Thesis, University of Southern California, Los Angeles, California, USA.
Olsen, P. E., Smith, J. B. & McDonald, N. G. (1998). Type material of the type species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, USA). *Journal of Vertebrate Paleontology* **18**, 586–601.
Olsson, M., Shine, R., Wapstra, E., Ujvari, B. & Madsen, T. (2002). Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* **56**, 1538–1542.
Ortega, F., Escaso, F. & Sanz, J. L. (2010). A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. *Nature* **467**, 203–206.
Osborn, H. F. (1905). *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bulletin of the American Museum of Natural History* **21**, 259–265.
Osborn, H. F. (1906). *Tyrannosaurus*, Upper Cretaceous Carnivorous Dinosaur: (second communication). *Bulletin of the American Museum of Natural History* **22**, 281–296.
Osborn, H. F. (1912). Part II. Integument of the iguanodont dinosaur *Trachodon*. In *Memoirs of the American Museum of Natural History*, pp. 33–54.
Ostrom, J. H. (1976). *Archaeopteryx* and the origin of birds. *Biological Journal of the Linnean Society* **8**, 91–182.

Oufiero, C. E., Gartner, G. E. A., Adolph, S. C. & Garland, T. (2011). Latitudinal and climatic variation in body size and dorsal scale counts in *Sceloporus* lizards: a phylogenetic perspective. *Evolution* **65**, 3590–3607.

Ouyang, H. & Ye, Y. (2002). The first mamenchisaurian skeleton with complete skull, Mamenchisaurus youngi. Sichuan Publishing House of Science and Technology, Chengdu, China.

Owen, P. (1863). On the *Archeopteryx* of von Meyer, with a description of the fossil remains of a long-tailed species, from the lithographic stone of Solenhofen. *Philosophical Transactions of the Royal Society of London* **153**, 33–47.

Owen, R. (1842). Report on British fossil reptiles. *Report of the British Association for the Advancement of Science* **11**, 60–294.

Owen, R. (1878). On the fossils called "Granicones": being a contribution to the histology of the exoskeleton in "Reptilia". *Journal of the Royal Microscopical Society* **1**, 233–236.

Owen, R. (1879). Monograph on the fossil Reptilia of the Wealden and Purbeck formations. Supplement IX. Crocodilia (*Goniopholis*, *Brachydectes*, *Nannosuchus*, *Theriosuchus* and *Nuthetes*). *Monographs of the Palaeontographical Society* **33**, 1–19.

Pacheco, C., Müller, R. T., Langer, M., Pretto, F. A., Kerber, L. & da Silva, S. D. (2019). *Gnathovorax cabreirai*: a new early dinosaur and the origin and initial radiation of predatory dinosaurs. *PeerJ* **7**, e7963.

Paik, I. S., Kim, H. J., Lee, H. & Kim, S. (2017). A large and distinct skin impression on the cast of a sauropod dinosaur footprint from Early Cretaceous floodplain deposits, Korea. *Scientific Reports* **7**, 16339.

Parrish, J. M. (1993). Phylogeny of the Crocodylotarsi, with Reference to Archosaurian and Crurotarsan Monophyly. *Journal of Vertebrate Paleontology* **13**, 287–308.

Paul, G. S. (2016). *The Princeton Field Guide to Dinosaurs*. Princeton University Press, Princeton, NJ.

Pei, R., Li, Q., Meng, Q., Gao, K.-Q. & Norell, M. A. (2014). A new specimen of *Microraptor* (Theropoda: Dromaeosauridae) from the Lower Cretaceous of western Liaoning, China. *American Museum Novitates* **3821**, 1–28.

Pei, R., Li, Q., Meng, Q., Norell, M. & Gao, K. (2017). New specimens of *Anchiornis huxleyi* (Theropoda, Paraves) from the late Jurassic of northeastern China. *Bulletin of the American Museum of Natural History* **411**, 1–66.

Pei, R., Pittman, M., Goloboff, P. A., Dececchi, T. A., Habib, M. B., Kaye, T. G., Larsson, H. C. E., Norell, M. A., Brusatte, S. L. & Xu, X. (2020). Potential for powered flight neared by most close avialan relatives, but few crossed its thresholds. *Current Biology* **30**, 4033–4046.

Pérez-Moreno, B. P., Sanz, J. L., Buscalioni, A. D., Moratalla, J. J., Ortega, F. & Rasskin-Gutman, D. (1994). A unique multitoothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature* **370**, 363–367.

Peyer, K. (2006). A reconsideration of *Compsognathus* from the upper Tithonian of Canjuers, southeastern France. *Journal of Vertebrate Paleontology* **26**, 879–896.

Pinegar, R. T., Loewen, M. A., Cloward, K. C., Hunter, R. J. & Weege, C. J. (2003). A juvenile allosaur with preserved integument from the basal Morrison Formation of Central Wyoming. *Journal of Vertebrate Paleontology* **23**, 87A–88A.

Pittman, M., O'Connor, J., Field, D. J., Turner, A. H., Ma, W., Makovicky, P. J. & Xu, X. (2020). Pennaraptoran systematics. In *Pennaraptoran Theropod Dinosaurs Past Progress and New Frontiers Bulletin of the American Museum of Natural History* (eds M. Pittman and X. Xu), pp. 7–36. American Museum of Natural History, New York.

Platt, B. F. & Hasiotis, S. T. (2006). Newly discovered sauropod dinosaur tracks with skin and foot-pad impressions from the Upper Jurassic Morrison Formation, Bighorn Basin, Wyoming, U.S.A. *PALAIOS* **21**, 249–261.

Poust, A. W. (2014). Description and ontogenetic assessment of a new Jehol microraptorine. MSc. Dissertation, Montana State University-Bozeman, College of Letters & Science, Bozeman, Montana, USA.

Poust, A. W., Gao, C., Varricchio, D. J., Wu, J. & Zhang, F. (2020). A new microraptorine theropod from the Jehol Biota and growth in early dromaeosaurids. *The Anatomical Record* **303**, 963–987.

Powell, J. E. (2003). *Revision of South American Titanosaurid Dinosaurs: Palaeobiological, Palaeobiogeographical and Phylogenetic Aspects*. Queen Victoria Museum and Art Gallery, Launceston, Australia.

Prum, R. O. (2010). Moulting tail feathers in a juvenile oviraptorisaur. *Nature* **468**, E1–E1.

Prum, R. O. & Brush, A. H. (2002). The evolutionary origin and diversification of feathers. *The Quarterly Review of Biology* **77**, 261–295.

Pu, H., Chang, H., Lü, J., Wu, Y., Xu, L., Zhang, J. & Jia, S. (2013a). A new juvenile specimen of *Sapeornis* (Pygostylia: Aves) from the Lower Cretaceous of Northeast China and allometric scaling of this basal bird. *Paleontological Research* **17**, 27–38.

Pu, H., Kobayashi, Y., Lü, J., Xu, L., Wu, Y., Chang, H., Zhang, J. & Jia, S. (2013b). An unusual basal therizinosaur dinosaur with an ornithischian dental arrangement from Northeastern China. *PLoS One* **8**, e63423.

Rainforth, E. C. (2003). Revision and re-evaluation of the Early Jurassic dinosaurian ichnogenus *Otozoum*. *Palaeontology* **46**, 803–838.

Rainforth, E. C. (2005). Ichnotaxonomy of the fossil footprints of the Connecticut Valley (Early Jurassic, Newark Supergroup, Connecticut and Massachusetts). Ph. D. dissertation, Columbia University, New York, USA.

Rauhut, O. W. M. (2003). The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology* **69**, 1–213.

Rauhut, O. W. M., Foth, C., Tischlinger, H. & Norell, M. A. (2012). Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the Late Jurassic of Germany. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 11746–11751.

Rauhut, O. W. M. & Pol, D. (2019). Probable basal allosauroid from the early Middle Jurassic Cañadón Asfalto Formation of Argentina highlights phylogenetic uncertainty in tetanuran theropod dinosaurs. *Scientific Reports* **9**, 1–9.

Reisz, R. R. & Sues, H.-D. (2000). The 'feathers' of *Longisquama*. *Nature* **408**, 428–428.

Renne, P. R., Mundil, R., Balco, G., Min, K. & Ludwig, K. R. (2010). Joint determination of 40K decay constants and 40Ar*/40K for the Fish Canyon sanidine standard, and improved accuracy for 40Ar/39Ar geochronology. *Geochimica et Cosmochimica Acta* **74**, 5349–5367.

Riede, T., Eliason, C. M., Miller, E. H., Goller, F. & Clarke, J. A. (2016). Coos, booms, and hoots: the evolution of closed-mouth vocal behavior in birds. *Evolution* **70**, 1734–1746.

Romano, M. & Whyte, M. A. (2012). Information on the foot morphology, pedal skin texture and limb dynamics of sauropods: evidence from the ichnological record of the Middle Jurassic of the Cleveland Basin, Yorkshire, UK. *Zubia* **30**, 45–92.

Rothschild, B. M. & Depalma, R. (2013). Skin pathology in the Cretaceous: evidence for probable failed predation in a dinosaur. *Cretaceous Research* **42**, 44–47.

Roy, A., Pittman, M., Saitta, E. T., Kaye, T. G. & Xu, X. (2020a). Recent advances in amniote palaeocolour reconstruction and a framework for future research. *Biological Reviews* **95**, 22–50.

Roy, A., Rogers, C. S., Clement, T., Pittman, M., Habimana, O., Martin, P. & Vinther, J. (2020b). Fossil microbodies are melanosomes: evaluating and rejecting the 'fossilised decay-associated microbes' hypothesis. In *Pennaraptoran Theropod Dinosaurs Past Progress and New Frontiers*. *Bulletin of the American Museum of Natural History* (eds M. Pittman and X. Xu), pp. 251–276. American Museum of Natural History, New York.

Rylaarsdam, J. R., Varban, B. L., Plint, A. G., Buckley, L. G. & McCrea, R. T. (2006). Middle Turonian dinosaur paleoenvironments in the Upper Cretaceous Kaskapau Formation, northeast British Columbia. *Canadian Journal of Earth Sciences* **43**, 631–652.

Saitta, E. T., Fletcher, I., Martin, P., Pittman, M., Kaye, T. G., True, L. D., Norell, M. A., Abbott, G. D., Summons, R. E., Penkman, K. & Vinther, J. (2018a). Preservation of feather fibers from the Late Cretaceous dinosaur *Shuvuuia deserti* raises concern about immunohistochemical analyses on fossils. *Organic Geochemistry* **125**, 142–151.

Saitta, E. T., Gelernter, R. & Vinther, J. (2018b). Additional information on the primitive contour and wing feathering of paravian dinosaurs. *Palaeontology* **61**, 273–288.

Saitta, E. T., Stockdale, M. T., Longrich, N. R., Bonhomme, V., Benton, M. J., Cuthill, I. C. & Makovicky, P. J. (2020). An effect size statistical framework for investigating sexual dimorphism in non-avian dinosaurs and other extinct taxa. *Biological Journal of the Linnean Society* **131**, 231–273.

Salgado, L. (2003). Considerations on the bony plates assigned to titanosaurs (Dinosauria, Sauropoda). *Ameghiniana* **40**, 441–456.

Salisbury, S. W. & Frey, E. (2001). A biomechanical transformation model for the evolution of semi-spheroidal articulations between adjoining vertebral bodies in crocodilians. In *Crocodilian Biology and Evolution* (eds G. C. Grigg, F. Seebacher and C. E. Franklin), pp. 85–134. Surrey Beatty & Sons, Chipping Norton.

Saveliev, S. V. & Alifanov, V. R. (2018). Bristle scale as a predecessor of protofeather and feather. *Paleontological Journal* **52**, 1436–1439.

Von Schlotheim E. F. F.(1820). Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung: Seiner Sammlung versteinerter und fossiler überreste des thier-und pflanzenreichs. In der Becker'schen Buchandlung.

Schweitzer, M. H., Watt, J. A., Avci, R., Knapp, L., Chiappe, L., Norell, M. & Marshall, M. (1999). Beta-keratin specific immunological reactivity in feather-like structures of the Cretaceous alvarezsaurid, *Shuvuuia deserti*. *Journal of Experimental Zoology* **285**, 146–157.

Schweitzer, M. H. (2011). Soft tissue preservation in terrestrial Mesozoic vertebrates. *Annual Review of Earth and Planetary Sciences* **39**, 187–216.

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

Shine, R. & Madsen, T. (1994). Sexual dichromatism in snakes of the genus *Vipera*: a review and a new evolutionary hypothesis. *Journal of Herpetology* **28**, 114–117.

Smithwick, F. M., Nicholls, R., Cuthill, I. C. & Vinther, J. (2017). Countershading and stripes in the theropod dinosaur *Sinosauropteryx* reveal heterogeneous habitats in the Early Cretaceous Jehol Biota. *Current Biology* **27**, 3337–3343.

Soulé, M. (1966). Trends in the insular radiation of a lizard. *The American Naturalist* **100**, 47–64.
Soulé, M. & Kerfoot, W. C. (1972). On the climatic determination of scale size in a lizard. *Systematic Biology* **21**, 97–105.
Starrfelt, J. & Liow, L. H. (2016). How many dinosaur species were there? Fossil bias and true richness estimated using a Poisson sampling model. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**, 20150219.
Sternberg, C. M. (1925). Integument of *Chasmosaurus belli*. *Canadian Field Naturalist* **39**, 108–110.
Stettenheim, P. R. (1972). The integument of birds. *Avian Biology* **2**, 1–63.
Stettenheim, P. R. (2000). The integumentary morphology of modern birds—an overview. *Integrative and Comparative Biology* **40**, 461–477.
Storrs, G. W., Oser, S. E. & Aull, M. (2013). Further analysis of a Late Jurassic dinosaur bone-bed from the Morrison Formation of Montana, USA, with a computed three-dimensional reconstruction. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **103**, 443–458.
Stuart-Fox, D. M. & Ord, T. J. (2004). Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **271**, 2249–2255.
Sun, C.-Y. & Chen, P.-Y. (2013). Structural design and mechanical behavior of alligator (*Alligator mississippiensis*) osteoderms. *Acta Biomaterialia* **9**, 9049–9064.
Tanke, D. H. & Currie, P. J. (2010). A history of *Albertosaurus* discoveries in Alberta, Canada. *Canadian Journal of Earth Sciences* **47**, 1197–1211.
Thornley, A. L. (1970). Epidermal remnants of *Proterosuchus vanhoepeni*. *Palaeontologia Africana* **13**, 57–60.
Tischlinger, H. & Arratia, G. (2013). Ultraviolet light as a tool for investigating Mesozoic fishes, with a focus on the ichthyofauna of the Solnhofen archipelago. *Mesozoic Fishes* **5**, 549–560.
Trujillo, K. C., Foster, J. R., Hunt-Foster, R. K. & Chamberlain, K. R. (2014). AU/Pb age for the Mygatt-Moore Quarry, Upper Jurassic Morrison Formation, Mesa County, Colorado. *Volumina Jurassica* **12**, 107–114.
Tschopp, E. D., Oliver, W. & Thomas, F. (2015). Articulated bone sets of manus and pedes of *Camarasaurus* (Sauropoda, Dinosauria). *Palaeontologia Electronica* **18.2.44A**, 1–65.
Turner, A. H., Makovicky, P. J. & Norell, M. (2012). A review of dromaeosaurid systematics and paravian phylogeny. *Bulletin of the American Museum of Natural History* **371**, 1–206.
Turner, A. H., Makovicky, P. J. & Norell, M. A. (2007). Feather quill knobs in the dinosaur *Velociraptor*. *Science* **317**, 1721–1721.
Unwin, D. M. & Bakhurina, N. N. (1994). *Sordes pilosus* and the nature of the pterosaur flight apparatus. *Nature* **371**, 62–64.
Upchurch, P., Mannion, P. D. & Taylor, M. P. (2015). The anatomy and phylogenetic relationships of "*Pelorosaurus*" *becklesii* (Neosauropoda, Macronaria) from the Early Cretaceous of England. *PLoS One* **10**, e0125819.
van der Reest, A. J., Wolfe, A. P. & Currie, P. J. (2016). A densely feathered ornithomimid (Dinosauria: Theropoda) from the Upper Cretaceous Dinosaur Park Formation, Alberta, Canada. *Cretaceous Research* **58**, 108–117.
Vera, E. I., Perez Loinaze, V. S., Llorens, M., Paez, M. & Passalia, M. G. (2019). Fossil woods with coniferalean affinities from the Upper Cretaceous (Campanian–Maastrichtian) Puntudo Chico Formation, Chubut Province, Argentina. *Cretaceous Research* **99**, 321–333.
Vidal, D., Ortega, F. & Sanz, J. L. (2014). Titanosaur osteoderms from the Upper Cretaceous of Lo Hueco (Spain) and their implications on the armor of Laurasian titanosaurs. *PLoS One* **9**, e102488.
Vinther, J. (2015). A guide to the field of palaeo colour. *BioEssays* **37**, 643–656.
Vinther, J. (2020). Reconstructing vertebrate paleocolor. *Annual Review of Earth and Planetary Sciences* **48**, 345–375.
Vinther, J., Nicholls, R. & Kelly, D. A. (2021). A cloacal opening in a non-avian dinosaur. *Current Biology* **31**, R182–R183.
Vinther, J., Nicholls, R., Lautenschlager, S., Pittman, M., Kaye, T. G., Rayfield, E., Mayr, G. & Cuthill, I. C. (2016). 3D camouflage in an ornithischian dinosaur. *Current Biology* **26**, 2456–2462.
Walker, J. D., Geissman, J. W., Bowring, S. A. & Babcock, L. E. (2012). Geologic time scale v. 4.0. *Geological Society of America* **10**, 2012.
Wang, M., O'Connor, J. K., Xu, X. & Zhou, Z. (2019). A new Jurassic scansoriopterygid and the loss of membranous wings in theropod dinosaurs. *Nature* **569**, 256–259.
Wang, S., Stiegler, J., Amiot, R., Wang, X., Du, G., Clark, J. M. & Xu, X. (2017a). Extreme ontogenetic changes in a ceratosaurian theropod. *Current Biology* **27**, 144–148.
Wang, X., Pittman, M., Zheng, X., Kaye, T. G., Falk, A. R., Hartman, S. A. & Xu, X. (2017b). Basal paravian functional anatomy illuminated by high-detail body outline. *Nature Communications* **8**, 14576.
Wang, X., Zhou, Z., Zhang, F. & Xu, X. (2002). A nearly completely articulated rhamphorhynchoid pterosaur with exceptionally well-preserved wing membranes and "hairs" from Inner Mongolia, northeast China. *Chinese Science Bulletin* **47**, 226–230.
Wegweiser, M. D., Breithaupt, B. H., Matthews, N. A., Sheffield, J. W. & Skinner, E. S. (2004). Paleoenvironmental and diagenetic constraints on Late Cretaceous dinosaur skin from western North America. *The Sedimentary Record* **2**, 4–8.
Wegweiser, M. D., Hartman, S. & Lovelace, D. (2006). Duckbill dinosaur chin skin scales: ups, downs and arounds of surficial morphology of Upper Cretaceous Lance Formation dinosaur skin. *New Mexico Museum of Natural History and Science Bulletin* **35**, 119–125.
Whyte, M. A. & Romano, M. (2001). Probable stegosaurian dinosaur tracks from the Saltwick Formation (Middle Jurassic) of Yorkshire, England. *Proceedings of the Geologists' Association* **112**, 45–54.
Wiersma, K. & Sander, P. M. (2017). The dentition of a well-preserved specimen of *Camarasaurus* sp.: implications for function, tooth replacement, soft part reconstruction, and food intake. *PalZ* **91**, 145–161.
Wilson, J., D'Emic, M., Rogers, C. A. C., Mohabey, D. M. & Sen, S. (2009). Reassessment of the sauropod dinosaur *Jainosaurus* (= "*Antarctosaurus*") septentrionalis from the Upper Cretaceous of India. *Contributions from the Museum of Paleontology, University of Michigan* **32**, 17–40.
Witton, M. P. (2013). *Pterosaurs: Natural History, Evolution, Anatomy*. Princeton University Press, Princeton, NJ.
Wu, P., Lai, Y.-C., Widelitz, R. & Chuong, C.-M. (2018). Comprehensive molecular and cellular studies suggest avian scutate scales are secondarily derived from feathers, and more distant from reptilian scales. *Scientific Reports* **8**, 16766.
Xing, L., Bell, P. R., Persons, W. S., Ji, S., Miyashita, T., Burns, M. E., Ji, Q. & Currie, P. J. (2012). Abdominal contents from two large Early Cretaceous compsognathids (Dinosauria: Theropoda) demonstrate feeding on confuciusornithids and dromaeosaurids. *PLoS One* **7**, e44012.
Xing, L., McKellar, R. C., Xu, X., Li, G., Bai, M., Persons, W. S., Miyashita, T., Benton, M. J., Zhang, J., Wolfe, A. P., Yi, Q., Tseng, K., Ran, H. & Currie, P. J. (2016). A feathered dinosaur tail with primitive plumage trapped in Mid-Cretaceous amber. *Current Biology* **26**, 3352–3360.
Xing, L. D., Peng, G. Z. & Shu, C. K. (2008). Stegosaurian skin impressions from the Upper Jurassic Shangshaximiao Formation, Zigong, Sichuan, China: A new observation. *Geological Bulletin of China* **27**, 1049–1053.
Xu, X. (2002). Deinonychosaurian fossils from the Jehol Group of western Liaoning and the coelurosaurian evolution. Ph. D. dissertation, The Chinese Academy of Sciences, Beijing, China.
Xu, X. (2020). Filamentous integuments in nonavialan theropods and their kin: advances and future perspectives for understanding the evolution of feathers. In *The Evolution of Feathers: From Their Origin to the Present* (eds C. Foth and O. W. M. Rauhut), pp. 67–78. Springer International Publishing, Cham.
Xu, X., Currie, P., Pittman, M., Xing, L., Meng, Q., Lü, J., Hu, D. & Yu, C. (2017). Mosaic evolution in an asymmetrically feathered troodontid dinosaur with transitional features. *Nature Communications* **8**, 14972.
Xu, X. & Guo, Y. (2009). The origin and early evolution of feathers: insights from recent paleontological and neontological data. *Vertebrata PalAsiatica* **47**, 311–329.
Xu, X. & Li, F. (2016). A new microraptorine specimen (Theropoda: Dromaeosauridae) with a brief comment on the evolution of compound bones in theropods. *Vertebrata PalAsiatica* **54**, 269–285.
Xu, X., Norell, M. A., Kuang, X., Wang, X., Zhao, Q. & Jia, C. (2004). Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* **431**, 680–684.
Xu, X., Sullivan, C. & Wang, S. (2013). The systematic position of the enigmatic theropod dinosaur *Yixianosaurus longimanus*. *Vertebrata PalAsiatica* **51**, 169–183.
Xu, X., Tang, Z. & Wang, X. (1999a). A therizinosauroid dinosaur with integumentary structures from China. *Nature* **399**, 350–354.
Xu, X., Wang, K., Zhang, K., Ma, Q., Xing, L., Sullivan, C., Hu, D., Cheng, S. & Wang, S. (2012). A gigantic feathered dinosaur from the Lower Cretaceous of China. *Nature* **484**, 92–95.
Xu, X. & Wang, X. (2003). A new maniraptoran dinosaur from the Early Cretaceous Yixian Formation of western Liaoning. *Vertebrata PalAsiatica* **41**, 195–202.
Xu, X., Wang, X.-L. & Wu, X.-C. (1999b). A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. *Nature* **401**, 262–266.
Xu, X., You, H., Du, K. & Han, F. (2011). An *Archaeopteryx*-like theropod from China and the origin of Avialae. *Nature* **475**, 465–470.
Xu, X. & Zhang, F. (2005). A new maniraptoran dinosaur from China with long feathers on the metatarsus. *Naturwissenschaften* **92**, 173–177.
Xu, X., Zheng, X., Sullivan, C., Wang, X., Xing, L., Wang, Y., Zhang, X., O'Connor, J. K., Zhang, F. & Pan, Y. (2015). A bizarre Jurassic maniraptoran theropod with preserved evidence of membranous wings. *Nature* **521**, 70–73.
Xu, X., Zheng, X. & You, H. (2009). A new feather type in a nonavian theropod and the early evolution of feathers. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 832–834.
Xu, X., Zheng, X. & You, H. (2010). Exceptional dinosaur fossils show ontogenetic development of early feathers. *Nature* **464**, 1338–1341.

Xu, X., Zhou, Z., Dudley, R., Mackem, S., Chuong, C.-M., Erickson, G. M. & Varricchio, D. J. (2014). An integrative approach to understanding bird origins. *Science* **346**, 1253293.
Xu, X., Zhou, Z. & Prum, R. O. (2001). Branched integumental structures in *Sinornithosaurus* and the origin of feathers. *Nature* **410**, 200–204.
Xu, X., Zhou, Z. & Wang, X. (2000). The smallest known non-avian theropod dinosaur. *Nature* **408**, 705–708.
Xu, X., Zhou, Z., Wang, X., Kuang, X., Zhang, F. & Du, X. (2003). Four-winged dinosaurs from China. *Nature* **421**, 335–340.
Yang, Z., Jiang, B., McNamara, M. E., Kearns, S. L., Pittman, M., Kaye, T. G., Orr, P. J., Xu, X. & Benton, M. J. (2019). Pterosaur integumentary structures with complex feather-like branching. *Nature Ecology & Evolution* **3**, 24–30.
Yang, Z., Jiang, B., McNamara, M. E., Kearns, S. L., Pittman, M., Kaye, T. G., Orr, P. J., Xu, X. & Benton, M. J. (2020). Reply to: no protofeathers on pterosaurs. *Nature Ecology & Evolution* **4**, 1–2.
Young, J. (2011). Dino Gangs: Dr. Philip J. Currie's New Science of Dinosaurs.
Zelenitsky, D. K., Therrien, F., Erickson, G. M., DeBuhr, C. L., Kobayashi, Y., Eberth, D. A. & Hadfield, F. (2012). Feathered non-avian dinosaurs from North America provide insight into wing origins. *Science* **338**, 510–514.
Zhang, F., Kearns, S. L., Orr, P. J., Benton, M. J., Zhou, Z., Johnson, D., Xu, X. & Wang, X. (2010). Fossilized melanosomes and the colour of Cretaceous dinosaurs and birds. *Nature* **463**, 1075–1078.
Zhang, F., Zhou, Z. & Dyke, G. (2006). Feathers and 'feather-like' integumentary structures in Liaoning birds and dinosaurs. *Geological Journal* **41**, 395–404.
Zhang, F., Zhou, Z., Xu, X. & Wang, X. (2002). A juvenile coelurosaurian theropod from China indicates arboreal habits. *Naturwissenschaften* **89**, 394–398.
Zhang, F., Zhou, Z., Xu, X., Wang, X. & Sullivan, C. (2008). A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. *Nature* **455**, 1105–1108.
Zheng, X., O'Connor, J. K., Wang, X., Pan, Y., Wang, Y., Wang, M. & Zhou, Z. (2017). Exceptional preservation of soft tissue in a new specimen of *Eoconfuciusornis* and its biological implications. *National Science Review* **4**, 441–452.
Zheng, X., Zhou, Z., Wang, X., Zhang, F., Zhang, X., Wang, Y., Wei, G., Wang, S. & Xu, X. (2013). Hind wings in basal birds and the evolution of leg feathers. *Science* **339**, 1309–1312.
Zheng, X.-T., You, H.-L., Xu, X. & Dong, Z.-M. (2009). An Early Cretaceous heterodontosaurid dinosaur with filamentous integumentary structures. *Nature* **458**, 333–336.
Zhou, Z.-H. & Wang, X. L. (2000). A new species of *Caudipteryx* from the Yixian Formation of Liaoning, northeast China. *Vertebrata PalAsiatica* **38**, 113–130.
Zhou, Z.-H., Wang, X.-L., Zhang, F.-C. & Xu, X. (2000). Important features of *Caudipteryx*-evidence from two nearly complete new specimens. *Vertebrata PalAsiatica* **38**, 243–265.

IX. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.
Appendix S1. List of taxa studied.
Appendix S2. Mapping integument-based characters and ancestral state reconstruction analysis.
2.1. Methodology
2.2. Integument-based characters
2.3. Integument-based data matrix
2.4. List of non-ambiguous integument-based synapomorphies
2.5. Results of the ancestral state reconstruction analysis
Appendix S3. Systematic description of non-avialan theropod integument (excluding feathers)
3.1. Stem-averostran Theropoda
3.2. Averostra
3.3. Ceratosauria
3.4. Carnosauria
3.5. Tyrannosauroidea
3.6. Compsognathidae
3.7. Ornithomimosauria
3.8. Pennaraptora
Appendix S4. Licence attribution for the silhouettes
Appendix S5. References used in the supporting information

(*Received 3 December 2020; revised 10 December 2021; accepted 14 December 2021*)