Did all theropods have chicken-like feet? First evidence of a non-avian dinosaur podotheca

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ABSTRACT

The podotheca is the structure of scales covering the foot in extant birds. It is usually assumed that this structure is present in the whole clade of theropod dinosaurs; however, the knowledge of the origin of the podotheca is based on scarce direct evidence and its point of emergence within Theropoda is ambiguous. Here we discuss the relatively complete and well preserved podotheca of the basal tetanurae *Concavenator corcovatus*, which allows the description of its structure and its osteological correlation. We describe the skin pattern around the autopod of *Concavenator* and we compare it with available fossil skin impressions and the skin of extant crocodiles and birds. These scale impressions present a similar pattern to those observed in the autopod of avian theropods, so our results suggest that *Concavenator* have a bird-like podotheca. On the other hand, there is a current debate about the ichnological—osteological correlation in dinosaurs, derived from the lack of knowledge about the position of the phalanges in relation to the plantar pads of the podotheca. We describe, in *Concavenator*, an arthral condition of the position of the plantar pads. This condition would be the basal condition in the tetanurans and, thus, the ichnological record could be interpreted with an additional criterion. The autopod of *Concavenator* provides the first evidence of this type of structure in a non-avian theropod and it sheds light on the origin and distribution of this structure in the theropod large lineage.

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1. Introduction

The pes of extant birds is covered, from the tibiotarsus to the end of the toes, by an integumentary structure that is a layer of scales known as podotheca. This structure is composed of three distinct types of scales (Stettenheim, 2000) showing a characteristic pattern of arrangement. Scutate and scutellate scales are the largest; mostly rectangular, and regularly arranged, situated on the anterior surface of the tarsometatarsus and the dorsal surface of the toes. In contrast, the smallest and irregular reticulate scales are located on the underside of toes and the posterior surface of the tarsus (Stettenheim, 2000). Traditionally, the presence of an avian podotheca has been inferred for the whole Theropoda clade (Hitchcock, 1836; Lull, 1904; Heilmann, 1926); however, the knowledge of the origin of this structure in non-avian theropods is conditioned by the limited fossil record of the skin covering the pes (Ji et al., 2001;

Pu et al., 2013). In Dinosauria, skin impressions around the foot have been described in the hadrosaurids *Saurolophus osborni*, *Saurolophus angustirostris* and *Corythosaurus casuaris* (Brown, 1916; Bell, 2012; Bell, 2014). The anterior surface of the metatarsus of *S. osborni* is covered with scales like pebbles of 2 mm in diameter (Bell, 2012). Skin impressions over the digits are composed of slightly elongated hexagons of 7 mm and other smaller scales, randomly positioned (Bell, 2012; Bell, 2014). *Saurolophus angustirostris* present skin around the ankle joint and the dorsal surface of the pes. This skin is comparatively simpler than the skin of *S. osborni*, consisting of uniform pebbles 1—2 mm in diameter devoid of variation (Bell, 2012). *Corythosaurus casuaris* presents a similar pattern of the scales to other hadrosaurian (Brown, 1916; Bell, 2014). Moreover, skin impressions associated to pedal bones are also preserved in the basal ceratopsian *Psittacosaurus* (Mayr et al., 2002), with small (1—2 mm) and irregular tuberculate scales arranged in rosettes around and over metatarsals. Scales preserved over the metatarsal IV lack variation in size or shape. All of these impressions show a different pattern of size and arrangement from those observed in the avian podotheca. However, the

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recently described *Kulindadromeus*, a basal neornithischian, shows a skin patch around the tibia and the metatarsal area (Godefroit et al., 2014) that presents scales similar to those of birds.

Crocodiles, the extant sister group of birds, do not exhibit a bird-like podotheca. The pes is only covered by rectangular and ellipsoidal scales, presenting an oblique arrangement with respect to the axis of the toes (Alibardi and Thompson, 2000). The absence of a podotheca in the closest extant out-group of dinosaurs does not provide a strong support to the presence of this structure in non-avian theropod. Therefore, using the Extant Phylogenetic Bracketing (EPB: Witmer, 1995), the skin coverage of the autopod in Theropoda clade is reconstructed as Level II of inference.

Ichnological evidence is an alternative source of information about the skin coverage of the pes of dinosaurs. Based on this evidence, it is known that the skin pattern on the pes of some sauropods is different from the crocodilian-like structure and from the avian podotheca. Preserved scale impressions in sauropod footprints have a polygonal contour and are arranged in rosettes, where each polygon is separated by grooves (Platt and Hasiotis, 2006). These data are also consistent with the distribution of scales interpreted on sauropod embryos (Coria and Chiappe, 2007). Furthermore, a similar pattern of scale impressions in rosettes is also observed in footprints attributed to *Stegosaurus* and *Ankylosaurus* (McCrea et al., 2001; Mateus et al., 2011). Available ornithopods footprints show a unique large pad beneath the digits (Langston, 1960; Currie et al., 1991), unlike the multipads of the avian podotheca. This isolated digital pad is observed in a preserved foot of *Mantellisaurus* from Las Hoyas (Llandres-Serrano et al., 2013). Furthermore, the paleoichnological records of other archosauriforms have been also compared. The footprints of ichnofamily Chirotheriidae were associated to several members of the crurotarsi (Avanzini, 2000; Avanzini et al., 2007). In the skin impressions of its digits some of them show millimetre-sized ellipsoidal and rectangular scales. These scales are arranged in irregular rows crossing obliquely the digit axis and forming a checkerboard pattern (Avanzini, 2000; Avanzini and Mietto, 2008; Avanzini et al., 2011; Díaz-Martínez and Pérez-García, 2012).

Therefore, neither direct nor indirect evidence provided by out-groups of Theropoda provide unambiguous information on the coverage of skin neither on the feet of basal theropod groups nor on the origin of extant bird podotheca.

We test herein the presence of an avian podotheca in the Tetanurae clade, analyzing the holotype specimen of *Concavenator corcovatus* Ortega et al., 2010 (MCCM-LH 6666). This specimen partially preserves the skin covering the pes. The analysis of its integumentary impressions enables a description of the first evidence of this structure in non-avian theropods.

2. Material and methods

The integumentary impressions analysed belong to MCCM-LH 6666, the holotype of *Concavenator corcovatus* (Ortega et al., 2010), a well-preserved, nearly complete and articulated skeleton from the Lower Cretaceous (Barremian stage) in Las Hoyas fossil site (Cuenca, Spain). The current study focus on the delicate integumentary structures located under the pedal digits and in the metatarsal area of the right pes of *Concavenator*. This autopod is almost complete and the metatarsals and phalanges are arranged in dorsal view, except the distal phalanges of digit III and IV that are placed on lateral position. It is difficult to make observations in the left pes because it is situated below the right tibia, and the only visible elements are the phalanx II-1 and part of the bone of metatarsal II in lateral view. The sample analysed here belongs to the collections of the Museo de las Ciencias de Castilla-La Mancha (Cuenca, Spain).

2.1. Description of the fossil sample under visible light

Soft tissues and skin impressions data were analysed under visible light following standard procedures and using the descriptive terms defined by Kim et al. (2010). They were separately described according to their location on the foot, differentiating between skin impressions from the ankle region and from the phalangeal region. The patches were measured on pictures using ImageJ 1.47 (Rasband, 1997).

2.2. UV-induced visible fluorescence photographs

The pedal soft-tissues impressions of the specimen MCCM- LH-6666 were examined and photographed under UV-A light in order to recognize and establish essential details of the impressions. UV-A lamps with a wavelength of 365 nm were used for this purpose. The photographic protocol was carried out based on previous studies (Tischlinger, 2005; Hone et al., 2010; Tischlinger and Arratia, 2013). The exposure time was a few seconds, in accordance to the features of the light and the fossil.

3. Geological setting

Las Hoyas fossil site (Fig. 1) is situated 30 Km NE from the city of Cuenca, in the Cuenca Province (Spain), within Las Hoyas subbasin in the Serranía de Cuenca. The latter is part of the Iberian Ranges, which runs NW-SE in the East Central part of the Iberian Peninsula.

Las Hoyas subbasin was filled mainly with deposits of the La Huérguina Fm, with almost 400 m of distal alluvial and palustrine-lacustrine deposits from Barremian age (Fregenal-Martínez and Meléndez, 2000). Las Hoyas fossil site is considered as a Konsevart-lagerstätte, given the widely diversity of the fossil remains and their quality of preservation (Buscalioni and Fregenal-Martínez, 2010).

4. Results

4.1. Skin impressions of metatarsal area

The preserved skin impressions are located in the lateral side of metatarsal IV and around metatarsal V (Fig. 2). The soft-tissue mainly consists of skin impressions with different rate of preservation, resulting from the distinct mineralization associated to the authigenic early mineralization (Briggs et al., 1993; Briggs et al., 1997). This differentiation has been also observed in *Pelecanimimus polyodon* (Briggs et al., 1997), where the outlines of the tissues are associated to the phosphatized microbial mats and a three-dimensional detail was preserved in an iron carbonate (Briggs et al., 1997). Therefore, the variation on the preservation is not randomly arranged. On the one hand, there are distinctive scales on the proximal end of the patch. These impressions have a well-defined structure but do not present a recognizable relief. On the other hand, there are poorly preserved impressions on the distal end, where the scales are unrecognizable.

The scale impressions present a diameter range of few millimetres to centimetres (Fig. 2B, C). The shape is variable and it is hardly related to the size. Therefore, the outline of smaller scales is commonly irregular, although some of them seem to have a sub-regular pentagonal shape. In contrast, the medium-sized scales have a well-defined elongated hexagonal outline. Despite the fact that the shape and size of the scales are not uniform, they have the pattern of a honeycomb with a progressive variation in size, where the smallest scales are situated in the closest area to the lateral surface of metatarsal IV and the largest scales appear distal to this surface. The scales are separated by 1–2 mm from the
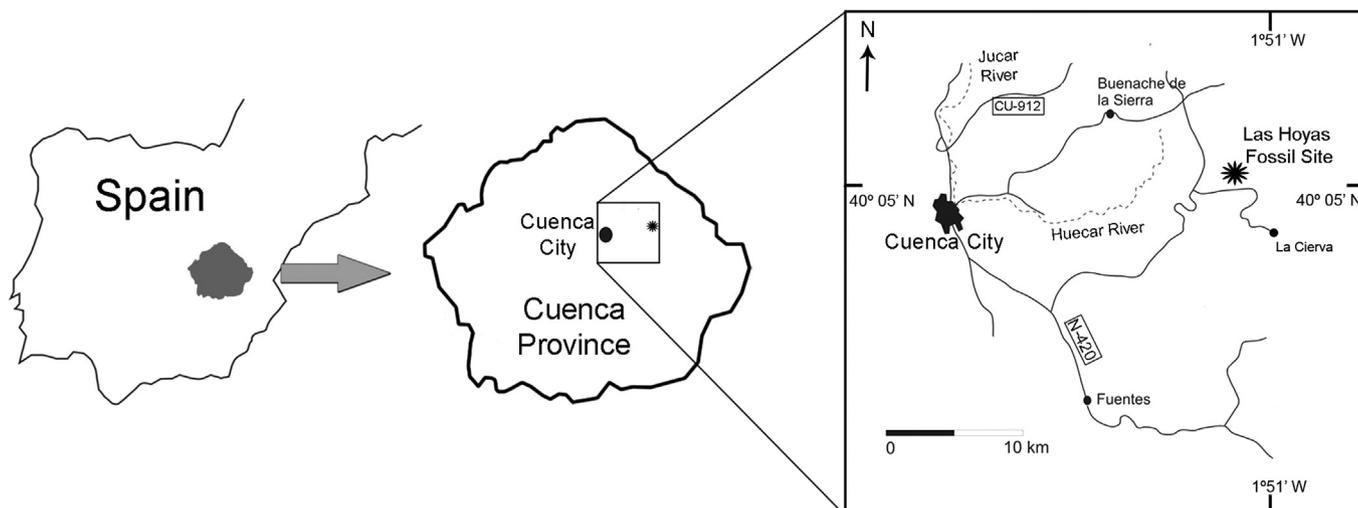
Fig. 1. Locality where the holotype MCCM-LH 6666, here studied, was found, at the Las Hoyas fossil site (indicated with a star), 30 km NE from the city of Cuenca, Cuenca Province, Spain.
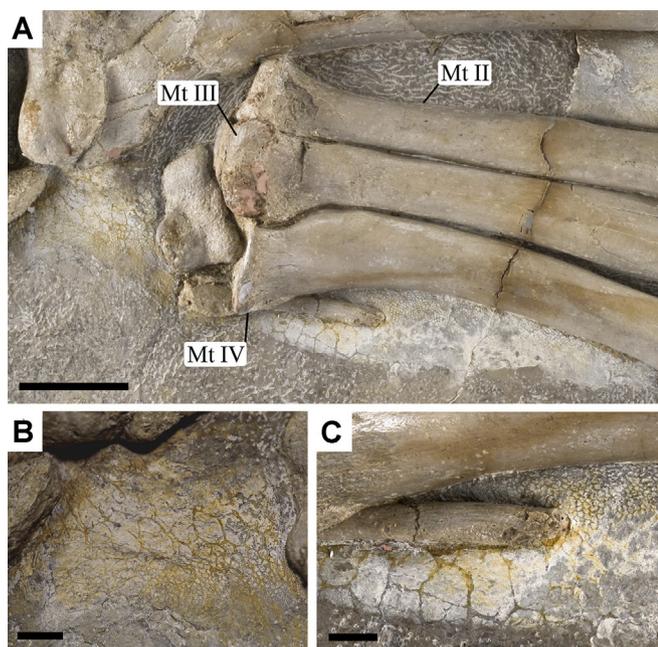

Fig. 2. Photographs of the ankle region of the right pes of MCCLM-6666 under visible light. A, Dorsal view of the ankle region showing two skin-impression patches. Scale bar, 5 cm. B, Detail of the area over tarsal and metatarsal showing the most proximal patch showing three different kinds of scales. Scale bar, 1 cm. C, Detail of the patch around metatarsal IV and V. Note the pattern of arrangement of the three kinds of scales. Scale bar, 1 cm. Abbreviations: Mt II, Metatarsal II; Mt III, Metatarsal III; Mt IV, Metatarsal IV.

neighbouring impressions, but these boundaries do not present a notable relief. The surface of the impressions is also flattened and lacks ornamentation.

A similar pattern is observed in a patch located proximal to the distal tarsal and metatarsals (Fig. 2B). In general, its scales are quite similar to those described above, although they show some differences, such as an intermediate size of the scales (5 mm) and an inverse pattern of arrangement (smaller external scales and medium-sized central scales).

4.2. Skin impressions of the phalangeal area

The skin impressions around the pedal phalanges are preserved in several areas such as: (1) along the lateral side of digit IV, from proximal end of phalanx IV-1 to beyond the ventral surface of ungual phalanx IV-5; (2) in lateral side of phalanx III-1 and proximal end of phalanx III-2; (3) from the distal end of phalanx III-2 to beyond the distal end of phalanx III-4; (4) in dorsomedial side of distal digit III and in distal position to phalanx II-1 (Fig. 2A).

In digit III and IV, the limit of the outline of the impression of soft tissues is parallel to the edge of bones with approximately 20 mm wide. In the distal end of both digits, the outline of the impressions shows an oval shape and its width increases, reaching 39.5 mm in digit IV and 55.21 mm in digit III. In digit II, only the oval shaped outline is visible. The boundary between the skin impression and the sedimentary matrix is well determined by different changes of colour. There are several constrictions marked on these boundary outlines (Fig. 3A, B).

Preservation range varies in different areas. For most of them, the scale impressions are poorly defined, even becoming unrecognizable. In this case, the scales present irregular form, very small sizes (<1 mm−2 mm) and their arrangement seems to be random. Contrary to those areas of poor preservation, the impressions on the ventral side to phalanges IV-4 and IV-5 show well-preserved scales, with a slightly negative epirelief (Fig. 3C, D). These scales are closely spaced, with a raised boundary, less than 1 mm wide, separating them. A nearly linear pattern of the scales can be observed perpendicularly oriented to the long axis of the phalanx. A colour pattern is associated to the scales with different range of preservation: the better-preserved scales show some kind of reddish colours in contrast to the light colour observed in the areas of poor preservation.

In addition to the integumentary structures previously described, there is another type of soft-tissues preserved which is located on the distal end of the ungual phalanges of digit III and IV (Fig. 3A, B). Their length is 61.83 mm and 48.77 mm respectively. This impression protruded beyond the tip of the ungual phalanx by 41.27% of the total claw length for the digit III and 31.78% for the digit IV. The shape of the outline is slightly curved. The impressions lack ornamentation and show a white colour. There is a curved line on the centre of the impression associated to digit III (Fig. 3A). The
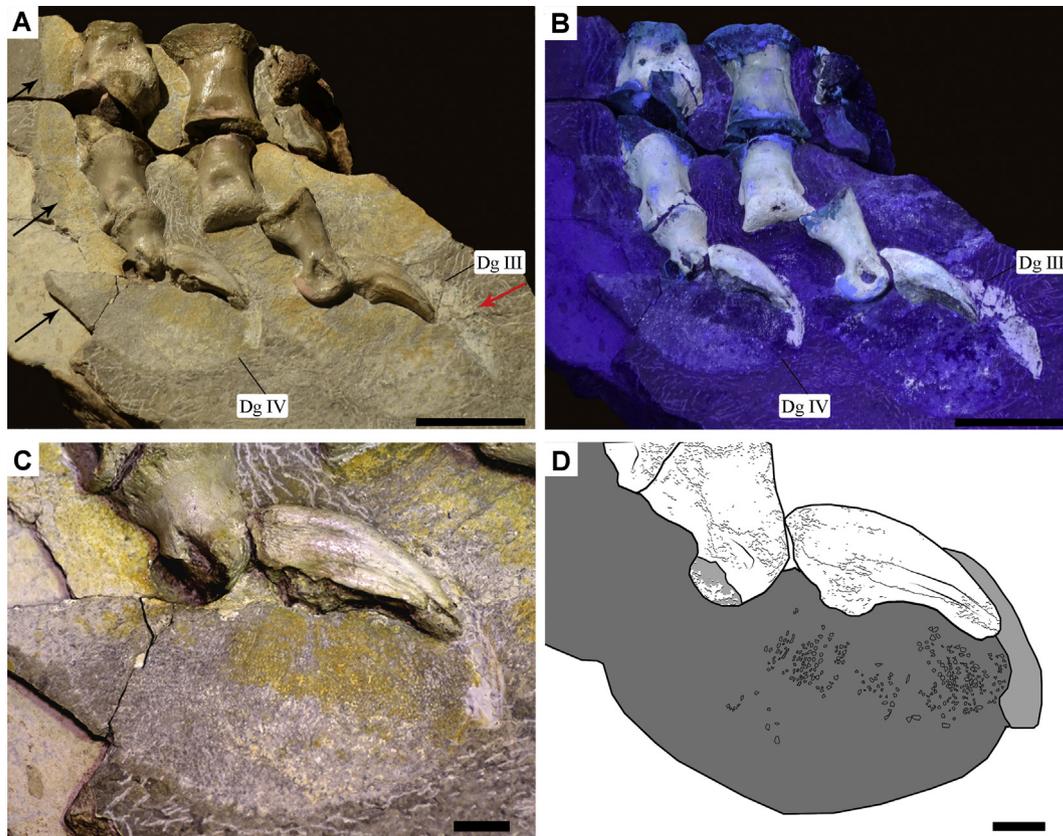
Fig. 3. Photographs of the digital region of the right pes of MCCM-LH 6666 under visible and UV light. A, Dorsal view of the digital region showing the skin impressions around the digits. Note the constrictions marked on the outline of the impressions (black arrows) and the curved mark in the sheath impressions (red arrow). Scale bar, 5 cm. B, Dorsal view of the digital area under UV light. Scale bar, 5 cm. C, Detail of the impressions associated to the distal digit. Note the linear pattern of arrangement in the reticulate scales. Scale bar, 1 cm. D, Drawing of the detail of the scale impressions associated to the distal digit showing in C. Scale bar, 1 cm. Abbreviations: Dg III, Digit III; Dg IV, Digit IV. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

impression of the digit IV is incomplete and, thus, the same line is not observable.

4.3. UV-induced visible fluorescence photographs

The images obtained under UV radiation show different colour patterns over the fossil and sediment matrix (Fig. 3B). The most evident difference is the boundary between the sediment matrix and the patches of skin impressions. This differentiation is possible due to the darker tone of the sediment matrix, in contrast to the impressions that present a more fluorescent response. The striking fluorescent patches are the tissues associated to the ungual phalanx.

5. Discussion

Due to their location, arrangement and shape, the impressions observed around the autopod of MCCM-LH 6666 are interpreted as the skin around the ankle area, the plantar pads and the ungual sheaths; as suggested by Ortega et al. (2010).

The scale impressions have been compared with the skin of the pes in certain taxa (eg *Alligator mississippiensis, Struthio camelus, Gallus gallus domestic*). *Concavenator* has the same arrangement of the integumentary structure as the podotheca of extant birds (reticulate, scutate and scutellate scales) differing from those of extant crocodiles and sauropod dinosaurs.

Accordingly, the arrangement can be interpreted in function of the podotheca structure of extant birds, as explained below. The

largest scales prints around the proximal ends of metatarsals IV and V would correspond to those of the anterior and anterolateral surfaces of these ones, and the surrounding smallest scales would be those situated on the posterior surface. The scales preserved from the digits are similar to those irregular and small from the ankle. These impressions would correspond to the papillae forming the pads. These papillae resemble to those observed on the toepads from ostriches (El-Gendy et al., 2012).

We interpret the impressions associated to ungual phalanges as the evidence of the corneous sheath. These claw sheaths protrude from the tip of the ungual phalanx by 41.27% (digit III) and 31.78% (digit IV) of the total claw length. We observe that these percentages differ from those of modern birds (Manning et al., 2009; El-Gendy et al., 2012) and extinct avian theropods (Pu et al., 2013), which show a variability ranging from 12% to 30%. It is possible to explain the sheath overcoming based on taphonomic processes. We propose that the sheath and the rest of the skin are displaced from their anatomical position due to the detachment of the skin from the bone because of the taphonomic process affecting the carcass of *Concavenator*. *Concavenator* suffered a subaerial exposition in subtropical conditions (Cuesta and Fregenal-Martínez, 2012) that could explain the detachment of the soft tissues from the bone, as it has been observed in actuotaphonomic experiments (Cambra-Moo, 2006) and in the fossil record (Hone et al., 2010; Bell, 2012). This hypothesis is supported by the presence of the lateral groove of claws for the phalanx (Stettenheim, 2000) in digit III. The distal tip of this groove in the sheath is separated 25 mm from the tip of the vascular groove in the phalanx, indicating the total length of the
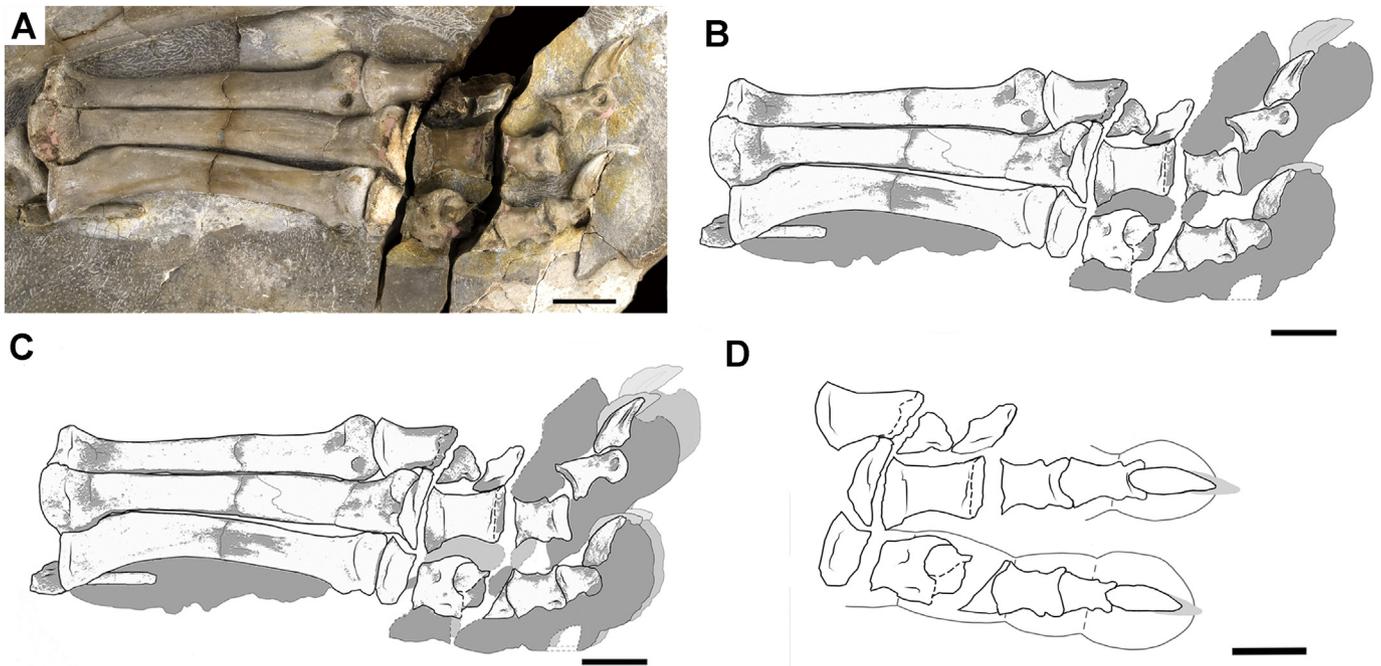
Fig. 4. Reconstruction of the relationships between skin and bone. A, Photography of the whole right pes under visible light. B, Line drawing of the whole right pes showing the impressions in their position on the fossil. Bone tissues in white, pedal pads in dark grey and corneous sheath in light grey. C, Line drawings of the whole right pes showing the correct position of the impressions relative to the bone. Bone tissues in white, pedal pads with modified position in dark grey, corneous sheath with modified position in light grey and impressions in the fossil position in a lighter grey. D, Reconstruction in dorsal view of the whole pes in function of the known skin, showing the hypothetical track of the *Concavenator corcovatus* and its osteological correlation. The discontinuous lines indicate incomplete areas. Scale bar, 5 cm.

displacement. We have established the anatomical position through retrodeformation of this known displacement (Fig. 4).

Since the beginning of dinosaur ichnology (e.g. Hitchcock, 1858; Lull, 1904), it has been discussed the location of the interpad grooves with respect to the phalanges. There are two relative positions in the present-day avian podotheca: arthral (Lull, 1904, 1915) (the interpad groove does not fit the joint between two phalanges); and mesarthral (Peabody, 1956; Baird, 1957) (the interpad groove fits the joint between two phalanges). Rainforth (2003) proposed that the arthral condition is primitive in non-avian dinosaurs and the variability between both character states is due to evolution in more derived taxa. In basal birds, as in *Sapeornis*, the arthral condition is present (Pu et al., 2013). We interpret the constrictions on the outline of digital impressions in *Concavenator* as derived from the interpad grooves like those observed in extant birds (Bock and Miller, 1959; Stettenheim, 2000; Milan, 2006; El-Gendy et al., 2012). We determine the presence of an arthral condition in this specimen based on the retrodeformed autopod of *Concavenator* (Fig. 4C, D), supporting the hypothesis that this state is primitive for non-avian dinosaurs (Rainforth, 2003) as occurs in basal birds (Milan, 2006; El-Gendy et al., 2012; Pu et al., 2013). Nevertheless, as Smith and Farlow suggested (2003), the strict assumption of one condition or another is an oversimplification because they have a broad variability among individuals and species in extant birds.

Moreover, the ichnological evidence proposes that digit IV of theropods presents four pads (Thulborn, 1990; Farlow et al., 2000) as occurs in *Concavenator* (Fig. 4C, D). The commonly accepted ichnological–osteological correlation suggests that the phalanx IV-4 is completely covered by the distal pad (Smith and Farlow, 2003; Xing et al., 2014) while the remaining phalanges present an arthral condition. Nevertheless, the pads in *Concavenator* show a different distribution. Its second pad completely covers the phalanx IV-2 while the phalanx IV-4 exhibits the arthral condition (Fig. 4C,

D). Therefore, the foot of *Concavenator* would refuse this hypothesis or, at least, the traditional interpretation would not be applicable to forms with the same condition as *Concavenator*.

The arrangement of the scales, the pedal pads and the corneous sheath described in *Concavenator* confirm the presence of an avian podotheca in a non-coelurosaurian theropod. As commented before, the origin of this structure was ambiguous within the theropoda lineage because it is present in extant birds but not in extant crocodiles. Taking into account the autopod of *Concavenator*, the presence of the avian podotheca would be unambiguously positioned in the common ancestor of Avetheropoda (clade comprising Allosauroidea and Coelurosauria: Carrano et al., 2012) (Fig. 5). However, Godefroit et al. (2014) have recently published a paper about the skin patch around the tibia and metatarsal of *Kulindadromeus*, an ornithischian dinosaur, which presents two types of scales similar to the scutella and the reticula in birds. It is possible to pose that the pedal scales of *Kulindadromeus* may be homologous to those of *Concavenator*. If this hypothesis is supported by further research, the origin of this structure would be situated on the Dinosauria node, forcing us to interpret the loss of the podotheca in sauropods as a reversion to the primitive condition. In any case, the podotheca of *Concavenator* provides key evidence for the evolutionary history of this structure.

6. Conclusion

Historically, the reconstruction of the pes of theropod dinosaurs was based on an accelerated optimization of the ambiguous rise of the avian podotheca in the evolution of the group. *Concavenator* provides evidence of the presence of an avian podotheca structure in a non-avian theropod, supporting the presence of this condition for, at least, the Avetheropoda clade. Moreover, the reconstruction of the complete structure allows the establishment of the arthral disposition of the plantar pads as the basal condition in Tetanurae.
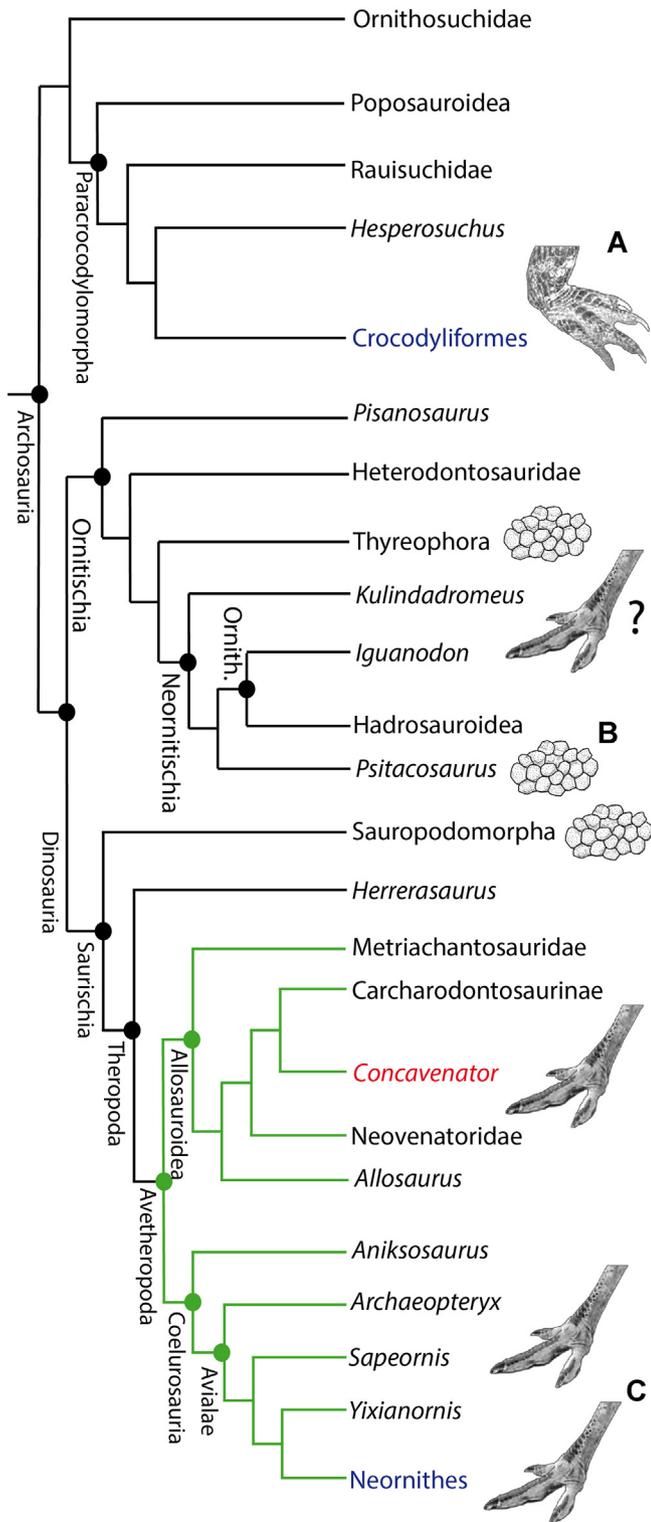
Fig. 5. Phylogenetic relationships of archosaurs and distribution of the skin morphology of the autopod. A, The autopod of the crocodilians (blue). B, Scale with rosette pattern. C, The podotheca of the Neornithes clade (blue) and some well-preserved fossils of taxa as *Sapeornis*. This structure is present in the autopod of *Concavenator* (red), suggesting the presence of this structure in the base of the clade Avetheropoda (green). Archosaurs phylogeny is modified from Nesbitt, 2011; Carrano et al., 2012 and Godefroit et al., 2014. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

In addition, we propose a different correlation between the phalanges and plantar pads from those observed in modern birds and from what had been assumed in the reconstruction of the track records. Therefore, this correlation might be taken into account when establishing the relationship between ichnological and osteological evidence in non-avian theropods.

Acknowledgments

References

Alibardi, L., Thompson, M.B., 2000. Scale morphogenesis and ultrastructure of dermis during embryonic development in the alligator (*Alligator mississippiensis*, Crocodilia, Reptilia). Acta Zoologica 81, 325–338. http://dx.doi.org/10.1046/j.1463-6395.2000.00063.x.

Avanzini, M., 2000. Synaptichnium tracks with skin impressions from the Anisian (middle Triassic) of the Southern Alps (val di non-Italy). Ichnos International Journal for Plant and Animal 7, 243–251.

Avanzini, M., Dalla Vecchia, F.M., Mietto, P., Piubelli, D., Preto, N., Rigo, M., Roghi, G., 2007. A vertebrate nesting site in northeastern Italy reveals unexpectedly complex behavior for late Carnian reptiles. Palaios 22, 465–475.

Avanzini, M., Mietto, P., 2008. Lower and Middle Triassic footprint-based biochronology in the Italian Southern Alps. Oryctos 8, 3–13.

Avanzini, M., Bernardi, M., Nicosia, U., 2011. The Permo-Triassic tetrapod faunal diversity in the Italian Southern Alps. In: Ahmad Dar, I. (Ed.), Earth and Environmental Sciences. INTECH Open Access, pp. 591–608.

Baird, D., 1957. Triassic reptile footprint Faunules from Milford, New Jersey. Bulletin of The Museum of Comparative Zoology 117, 447–520.

Bell, P.R., 2012. Standardized terminology and potential taxonomic utility of hadrosaurid skin impressions: a case study for Saurolophus from Canada and Mongolia. PLoS One 7 (2), e31295. http://dx.doi.org/10.1371/journal.pone.0031295.

Bell, P.R., 2014. A review of hadrosaurid skin impressions. In: Eberth, D.A., Evans, D.C. (Eds.), The Hadrosaurs: Proceedings of the International Hadrosaur Symposium. Indiana University Press, Bloomington and Indianapolis, pp. 572–590.

Bock, W.J., Miller, W.D., 1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. American Museum Novitates 1931, 42–43.

Briggs, D.E.G., Kear, A.J., Martill, D.M., Wilby, P.R., 1993. Phosphatization of soft-tissue in experiments and fossils. Journal of the Geological Society 150, 1035–1038.

Briggs, D.E., 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, 709–723.

Buscalioni, A.D., Fregenal-Martínez, M.A., 2010. A holistic approach to the palaeoecology os Las Hoyas Konservat-Lagerstätte (La Huérguina Formation, Lower Cretaceous, Iberian Ranges, Spain). Journal of Iberian Geology 36 (2), 297–326. http://dx.doi.org/10.5209/rev_JIGE.2010.v36.n2.13.

Cambra-Moo, O., 2006. Bioestratinomía y Fosildiagénesis de Arcosaurios: Aplicación de la Actuotafonomía al Estudio de la Influencia Paleobiológica en el Proceso Tafonómico. Universidad Autónoma de Madrid, Madrid, p. 330.

Carrano, M.T., Benson, R.B.J., Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). Journal of Systematic Palaeontology 10, 211–300. http://dx.doi.org/10.1080/14772019.2011.630927.

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.

Cuesta, E., Fregenal-Martínez, M.A., 2012. Taphonomic study of *Concavenator corcovatus* (Theropoda: Carcharodontosauria) from Las Hoyas fossil site (Lower Cretaceous, Serranía de Cuenca, Spain). Fundamental 20, 57–58.

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 (1), 102–115. http://dx.doi.org/10.1139/e91-009.

Díaz-Martínez, I., Pérez-García, A., 2012. Historical and comparative study of the first spanish vertebrate paleoichnological record and bibliographic review of the spanish Chirotheriid footprints. Ichnos 19, 141–149. http://dx.doi.org/10.1080/10420940.2012.685565.

El-Gendy, S.A.A., Derbalah, A., El-Magd, M.A., 2012. Macro-microscopic study on the toepad of ostrich (Struthio camelus). Veterinary Research Communications 36, 129–138. http://dx.doi.org/10.1007/s11259-012-9522-1.

Farlow, J.O., Gatesy, S.M., Holtz, T.R., Hutchinson, J.R., Robinson, J.M., 2000. Theropod locomotion. American Zoologist 40 (4), 640–663. http://dx.doi.org/10.1093/icb/40.4.640.

Fregenal-Martínez, M.A., Meléndez, N., 2000. The lacustrine fossiliferous deposits of the Las Hoyas sub-basin (Lower Cretaceous, Serranía de Cuenca, Iberian Ranges, Spain). AAPG Studies in Geology, 46. In: Gierlowski-Kordesch, E.H., Kelts, K. (Eds.), Lake basins through space and time, pp. 303–314.

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. http://dx.doi.org/10.1126/science.1253351.

Heilmann, G., 1926. The origin of birds. Witherby, London, p. 208.

Hitchcock, E., 1836. Ornithichnology. Description of the footmarks of birds (Ornithichnites) on New Red Sandstone in Massachusetts. American Journal of Science 29, 307–340.

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. W. White, Boston.

Hone, D.W., 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. http://dx.doi.org/10.1371/journal.pone.0009223.

Ji, Q., Norell, M.A., Gao, K., Ji, S., Ren, D., 2001. The distribution of integumentary structures in a feathered dinosaur. Nature 410, 1084–1088. http://dx.doi.org/10.1038/35074079.

Kim, J.Y., Kim, K.S., Lockley, M.G., Seo, S.J., 2010. Dinosaur skin impressions from the Cretaceous of Korea: New insights into modes of preservation. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 167–174. http://dx.doi.org/10.1016/j.palaeo.2010.05.012.

Langston, W.J.R., 1960. A hadrosaurian ichnite (Alberta). National Museum of Canada, Natural History Papers 4, 1–9.

Llandrés-Serrano, M., Vullo, R., Marugan-Lobon, J., Ortega, F., Buscalioni, A.D., 2013. An articulated hindlimb of a basal iguanodont (Dinosauria, Ornithopoda) from the Early Cretaceous Las Hoyas Lagerstätte (Spain). Geological Magazine 150 (03), 572–576. http://dx.doi.org/10.1017/S0016756813000095.

Lull, R.S., 1904. Fossil footprints of the Jura-Trias of North America. The Society, Boston, p. 557.

Lull, R.S., 1915. Triassic life of the Connecticut Valley. State geological and Natural history survey, Hartford, p. 334.

Manning, P.L., Margetts, L., Johnson, M.R., Withers, P.J., Sellers, W.I., Falkingham, P.L., Mummery, P.M., Barrett, P.M., Raymont, D.R., 2009. Biomechanics of Dromaeosaurid Dinosaur Claws: Application of X-Ray Microtomography, Nanoindentation, and Finite Element Analysis. Anatomical Record 292, 1397–1405. http://dx.doi.org/10.1002/ar.20986.

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 (3), 651–658. http://dx.doi.org/10.4202/app.2009.0055.

Mayr, G., Peters, D.S., Plodowski, G., Vogel, O., 2002. Bristle-like integumentary structures at the tail of the horned dinosaur *Psittacosaurus*. Naturwissenschaften 89, 361–365. http://dx.doi.org/10.1007/s00114-002-0339-6.

McCrea, R.T., Lockley, M.G., Meyer, C.A., 2001. Global distribution of purported ankylosaur track occurrences. In: Carpenter, K. (Ed.), The Armored Dinosaurs. Indiana University Press, Bloomington, pp. 413–454.

Milàn, J., 2006. Variations in the morphology of emu (*Dromaius novaehollandiae*) tracks reflecting differences in walking pattern and substrate consistency: ichnotaxonomic implications. Palaeontology 49, 405–420. http://dx.doi.org/10.1111/j.1475-4983.2006.00543.x.

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. http://dx.doi.org/10.1206/352.1.

Ortega, F., Escaso, F., Sanz, J.L., 2010. A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. Nature 467, 203–206. http://dx.doi.org/10.1038/nature09181.

Peabody, F.E., 1956. Ichnites from the Triassic Moenkopi Formation of Arizona and Utah. Journal of Paleontology 30 (3), 731–740.

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. http://dx.doi.org/10.2110/palo.2004.p04-69.

Pu, H., Chang, H., Lü, J., Wu, Y., Xu, L., Zhang, J., Jia, S., 2013. 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. http://dx.doi.org/10.2517/1342-8144-17.1.27.

Rainforth, E.C., 2003. Revision and re-evaluation of the Early Jurassic dinosaurian ichnogenus *Otozoum*. Palaeontology 46, 803–838. http://dx.doi.org/10.1111/1475-4983.00320.

Rasband, W.S., 1997. ImageJ. US National Institutes of Health, Bethesda, Maryland, USA.

Smith, J.B., Farlow, J.O., 2003. Osteometric approaches to trackmaker assignment for the Newark supergroup ichnogenera *Grallator*, *Anchisauripus*, and *Eubrontes*. In: LeTourneau, P.M., Olsen, P.E. (Eds.), The Great Rift Valleys of Pangea in Eastern North American: Volume 2: Sedimentology, Stratigraphy, and Paleontology. Columbia University Press, pp. 273–292.

Stettenheim, P.R., 2000. The integumentary morphology of modern birds—an overview. American Zoologist 40, 461–477. http://dx.doi.org/10.1093/icb/40.4.461.

Thulborn, T., 1990. Dinosaur tracks. Chapman and Hall, London, p. 410.

Tischlinger, H., 2005. Ultraviolet light investigations of fossils from the Upper Jurassic Plattenkalks of Southern Frankonia. Zitteliana B 26, 26.

Tischlinger, H., Arratia, G., 2013. Ultraviolet light as a tool of investigating Mesozoic fishes with a focus on the ichthyofauna of the Solnhofen Limestone. In: Arratia, G., Schultze, H., Wilson, M.V.H. (Eds.), Mesozoic Fishes 5 – Global Diversity and Evolution, pp. 549–562. München.

Witmer, L.M., 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Thomason, J.J. (Ed.), Functional Morphology in Vertebrate Paleontoly. Cambridge University Press, Cambridge, pp. 9–33.

Xing, L.D., Peng, G.Z., Ye, Y., Lockley, M.,G., Mccrea, R.T., Currie, P.J., Zhang, J.P., Burns, M.E., 2014. Large theropod trackway from the Lower Jurassic Zhenzhuchong Formation of Weiyuan County, Sichuan Province, China: Review, new observations and special preservation. Palaeoworld 23, 285–293. http://dx.doi.org/10.1016/j.palwor.2014.10.010.