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Soft tissue anatomy of pterosaur hands and feet – new information from Solnhofen region pterodactyloid specimens

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The pterosaur fossil record is known for a large number of complete and articulated specimens, including those with soft tissues, that predominantly come from a number of key localities. However, isolated elements or body parts can still provide important information. Here we describe a leg of a ctenochasmatid pterosaur from the Solnhofen region of southern Germany which shows exceptional preservation of the scales of the foot pad and webbing between the toes. A second specimen shows details of the hand and foot. We show that the soft tissues are remarkably consistent with those of other very distantly related pterosaurs. It is likely that the structure of the surfaces of the hands and feet that contacted the substrate were largely uniform across the clade, despite the enormous differences in habitats, body sizes and temporal differences between the various lineages. *Pterosauria, Pterodactyloidea, integument, soft tissue, taphonomy.*

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Pterosaurs are an extinct group of archosaurian reptiles that were the first vertebrate clade to evolve powered flight. Their fossil record is extensive, with records from the Late Triassic to the End Cretaceous and covering every continent (Barrett *et al.* 2008). However, the record is heavily skewed with a very high number of specimens and taxa that are well-preserved coming from a very small number of localities that are sites of exceptional preservation (Dean *et al.* 2016). Despite the dominance of these sites in terms of specimens that are often largely complete and well-preserved, they also produce lots of fragmentary and incomplete pterosaur parts that can be important for understanding their biology.

The Late Jurassic lithographic limestones of the Solnhofen region of southern Germany have long been one of the most important sites for pterosaur fossils and research. These have produced numerous fossils (e.g. Wellnhofer 1970, 1975) and both new specimens (e.g. Augustin *et al.* 2022) and new taxa continue to be found (e.g. Hone *et al.* 2024). However, partial specimens, especially those of unusually large individuals are often important as these can provide upper estimates of the sizes of animals that are present, and some may also represent new taxa (e.g. Elgin & Hone 2020). In particular, there are a number of large legs and feet of pterosaurs known from the Solnhofen area which have generally been overlooked in discussions of the local faunas.

Although pterosaur soft tissues are generally rarely preserved (Witton, 2013), there remains some exceptional examples (e.g. Frey *et al.* 2003; Bennett 2007) and important details are often revealed or enhanced through illumination with UV light (e.g. Kellner *et al.* 2010; Jäger *et al.* 2018). This includes wing membranes and internal structures (Unwin & Bakhurina 1994; Frey *et al.* 2003), muscles (Bennett 2007), head crests (Beccari *et al.* 2021), tail vanes (Wellnhofer 1975) and integumentary structures (Kellner *et al.* 2010). For the legs and feet, preserved soft tissues include claw sheaths, scales on the feet (Frey *et al.* 2003) and foot webbing between the toes (Wellnhofer 1978). Understandably, much of the focus on pterosaur research has been on their ability to fly, but in recent years there has been more focus on their terrestrial abilities and the accompanying anatomical adaptations that facilitated this (e.g. Witton 2015; Smyth *et al.* 2024). This absence of information is therefore unfortunate given the potential importance for such data from the hands and feet in terms of terrestrial locomotion, ecosystem occupation and foraging, and even potentially the ability to take off (Pittman *et al.* 2022).

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Here we add significant new data on this area of pterosaur biology with a description of a new large pterodactyloid pterosaur leg and foot that preserves the soft tissue of the foot pad scales and webbing between the toes. Notably, these are not visible under natural light but are superbly preserved when seen under UV light. We compare this specimen to other known 'big legs' from the Solnhofen region, and well-preserved soft tissues from the hindlimbs. A second specimen of a wing and foot provides some additional details of the hand and foot soft tissues.

Locality information

LF 2314P and the counterpart LF 3398N (Fig. 1) are described as coming from the Eichstätt general area, Eichstätt, Bavaria, Germany which would make them mostly likely from the Solnhofen Formation. Specimens LF 2314P and LF 3398N were acquired by the Lauer Foundation for Paleontology, Science and Education in January 2016 and February 2019, respectively.

More details are known for LF 547. This was found in 1996 in the Sappenfeld Quarry, Sappenffeld which is near Eichstätt (Fig. 2). It was found in the lower layers of the quarry, Malm zeta 2a, below the 'Tsunami layer' (or 'crooked layer', for example see Arratia *et al.* 2015, fig. 138) and so is also from the Solnhofen Formation and Tithonian in age. The specimen was first acquired by Stefan Schäfer and sold to an unknown American, who sold it to the commercial dealer Paleosearch. Bruce Lauer and René Lauer acquired the specimen in April 2011 and this was formally donated to the Lauer Foundation in December 2021.

Material and methods

Photography of the specimen was taken with a Nikon Z9 mirrorless digital camera using a Nikkor 60 mm macro lens and a Nikon FTZ II adapter. Visible light images were taken using a pair of Raleno video LED panels, set at 5600K colour temperature, with built in diffuser and a sheet of polarizing film over the LED screen and a linear circular polarizing filter on the lens. UV light images were taken with illumination from a Way Too Cool, 'triple lamp' equipped with appropriate filters and three 95-watt bulbs which include UV A, UV B and UV C wavelengths, which were used together. An orange colour correction filter was used on the lens for UV photography as this counteracts the purple tone of the UV lights to provide clearer recognition of ultraviolet induced fluorescence (UVIF) expressed in the visible light spectrum. All images were stacked using HeliconFocus Software.

The specimens are permanently held with the Lauer Foundation for Paleontology, Science and Education, Wheaton, Illinois, USA. The mission of the Lauer Foundation is to curate its fossil collection providing the scientific community and other museums with permanent access for the purposes of exhibition, study and education. Public access to specimens listed or cited in publications is guaranteed.

Institutional abbreviations: BSPG, Bavarian State Collection for Palaeontology and Geology, Munich, Germany; JME-SOS, Jura-Museum, Eichstätt, Bavaria, Germany; LF, Lauer Foundation for Paleontology, Science and Education, Wheaton, Illinois, USA; NHM-UK, Natural History Museum, London, UK; SMNK, Staatliches Museum fur Naturkunde, Karlsruhe, Germany.

Results

Under UV light, a number of important details of the soft tissues of the foot of LF 2314P and its counterplate LF 3398N are revealed. This includes individual scales of the foot pad, webbing between the toes, and ungual sheaths. Specimen LF 547 also shows some details of the hand and foot soft tissues, including scales and well-preserved unguals.

Description

LF 2314P is a small irregularly shaped slab (c. 30 by 25 cm) of cream coloured lithographic limestone that is typical for the region and preserves the right leg of a pterosaur. The bones of the limb are generally quite well-preserved, though various parts have suffered damage (e.g. the head and part of the shaft of the femur) and some bone has been lost. As is seen in a number of Solnhofen region pterosaurs, there are large build-ups of calcite crystals on the joints that obscure these to a degree, and especially the distal end of the tibia through to the tarsals to the proximal ends of the metatarsals. Dark coloured dendrites are present as a halo around the fossil and lie along a crack that bisects the slab. There is a larger counterplate slab (LF 3398N) to the main plate which clearly preserves a natural mould of the bones and some chips of bone, but otherwise contains no useful information under natural light. All subsequent description and

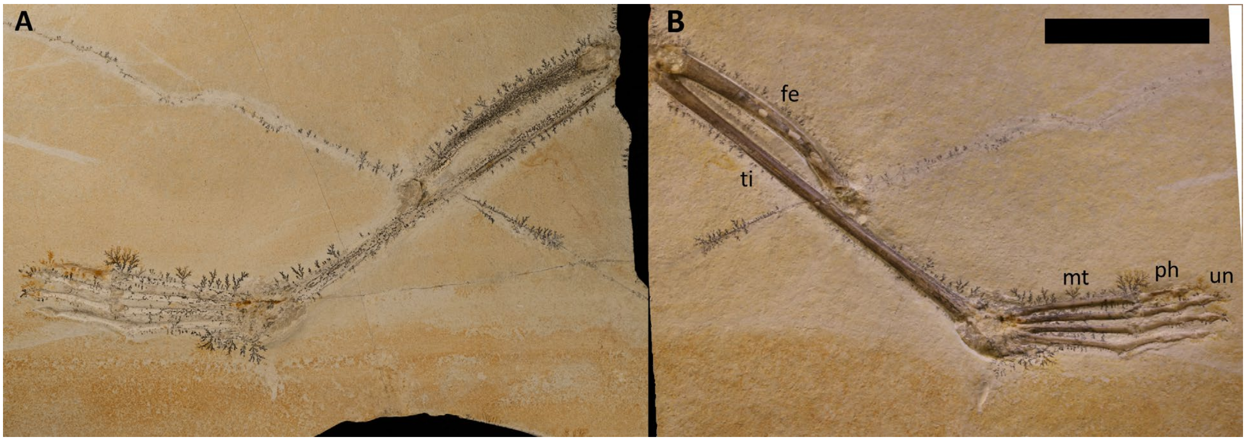

Fig. 1. Pterodactyloid leg, LF 3398N (A) and LF 2314P (B) under natural light. Abbreviations as follows here and in subsequent fig.s: fe, femur; fi, fibula; hu, humerus; mt, metatarsal; ph, phalanges; ppb, prepubes; pt, pteroid; pv, pelvis; sc, scales; sh, ungual sheaths; st, soft tissues; ta, tarsals; ti, tibia; ul, ulna; un, ungual; wpx, wing phalanges; wmc, wing metacarpal. Scale bar 5 cm.

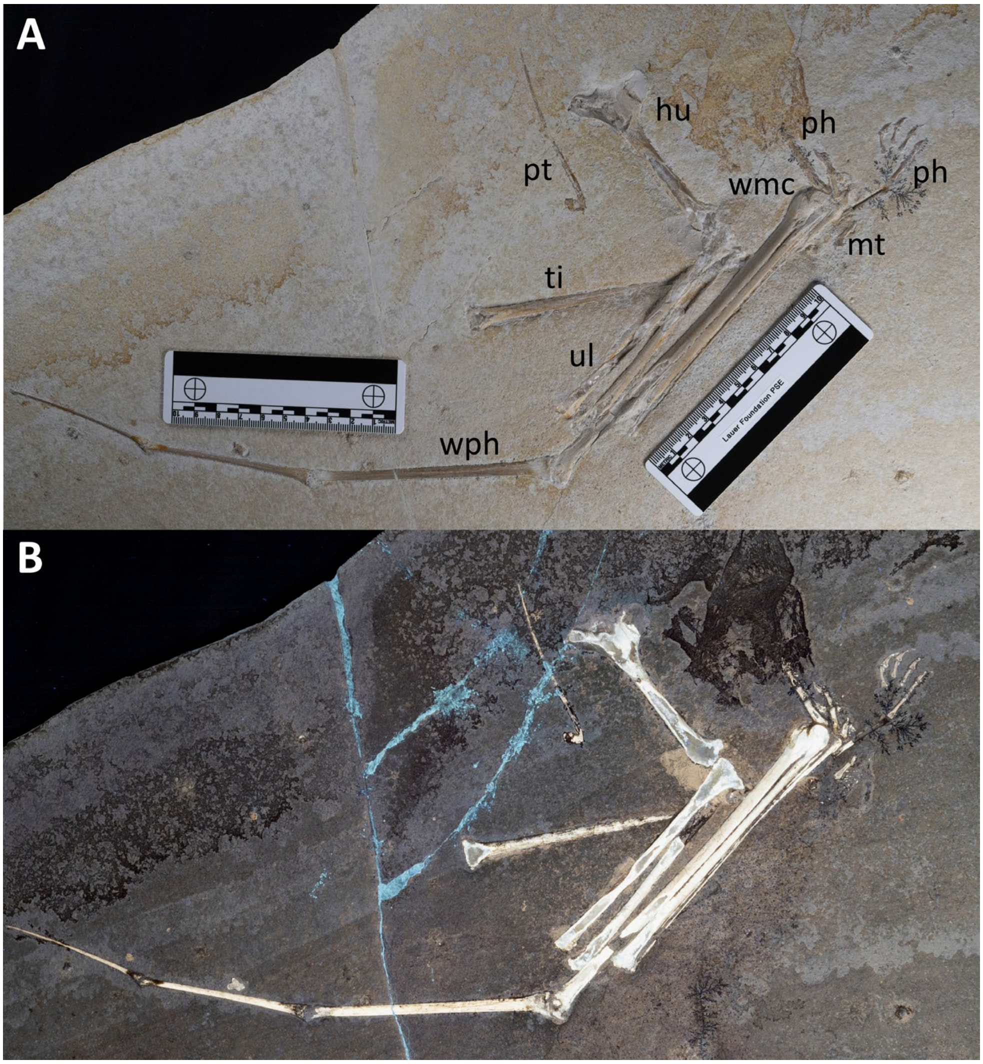

Fig. 2. LF 547, a pterodactyloid pterosaur forelimb and hindlimb under natural and UV light. Pictured scale bars are 10 cm.

discussion of the bones therefore relate to the main plate alone (Fig. 1).

The femur is 81 mm long with a midshaft diameter of 4.5 mm. The head of the femur is all but lost and so this and the trochanters cannot be made out. The shaft is distinctly curved anteriorly along its length. Part of the midshaft is missing and this shows that the core of the bone is also filled with calcite crystals. The bone wall thickness in the middle of the femur is c. 0.6–0.9 mm. The distal end of the femur is somewhat expanded such that the distal half of the femoral shaft gradually widens along its length.

The tibia is a simple long and straight element that is around 131 mm long (this is difficult to measure exactly because of calcite build-up). The proximal end appears to be nearly complete though it is damaged and is slightly wider than the shaft. The shaft of the tibia is close to 4.5 mm in diameter for almost its entire length, but only slightly wider proximally and distally the last 20 mm are a little wider such that the distal end of the bone is around 6 mm wide where it becomes covered in calcite. The fibula cannot be seen.

The tarsals cannot be made out as the entire joint section is a large and robust nodule of calcite crystals, as is common in Solnhofen area pterosaurs. All of the elements of the pes are present, though the smaller phalanges are not well preserved and difficult to make out and the proximal parts of the metatarsals are covered by calcite. There are five metatarsals present, with 1–4 being subequal in length, and the longest of which is 40 mm long and 2 mm in diameter, with the fifth being greatly reduced and is only c. 7 mm long. The foot as preserved is relatively narrow, with metatarsals 1–4 being spread a total of 11 mm proximally but only 18 mm by their distal ends. Digits 1–4 are also subequal in length, though digit 1 is around five millimeters shorter than the others which are up to 25 mm long, with 2 being slightly longer than 3 and 4. Digit 5 is greatly reduced and is a short and simple nub of bone around 3 mm long. Digits 1–4 bear short (5.5 mm long) and slightly curved unguals, with a tapered and needle-like point and a well-defined, curved groove on the lateral surface.

Under natural light, there is no visible soft tissue on the specimen. The following description is based on observation under UV light, both direct observation and, primarily, from the resulting UVIF photographs (Fig. 3). The former is limited for safety reasons.

There are clear scales present along the ventral part of the foot from the base of the tarsals to the end of the penultimate (i.e. last non-ungual) phalanx of digit 4. These are generally small with the largest scales being around 0.75 mm across below the middle of metatarsal IV, around 0.4 mm across around the distal end of the metatarsal and proximal phalanx, and the smallest ones are 0.15 mm and appear towards the later phalanges. These are not too well preserved around their margins on LF 2314P, but on the counterplate (3398N) it is clear that, proximally, the scales are larger and polygonal, and then are smaller and more simple (perhaps even circular) distally. This is similar to what is seen in the feet of crocodylians (Grigg & Kirschner 2015, p. 84 fig. 3.5).

Webbing is present between digits 1 and 4 and is preserved as a series of fibres. This tissue type starts deep in the crux of the metatarsals at their proximal end, and extend to the base on the bony unguals (seen most clearly ventral to digit 3). The fibres are very thin, circa. 0.15 mm in diameter and although not entirely clear, these appear to be continuous and would be a single fiber running the entire length of the space between the metatarsals and toes. The longest of these that is clear and can be measured is 11 mm long before it is broken and sits between metatarsals III and IV. There are at least 11 bands present between digits 3 and 4, but given how they are spaced the true count could be rather higher.

Claw sheaths are present on digits 1–4, but not well preserved. These are short and slightly curved. The longest preserved sheath is on digit 4 and is about 2.5 mm long, but part of this overlaps with the bony ungual and so extends the length of the claw by less than 2 mm, on a bony ungual that is 5 mm long.

There are also some indeterminate phosphatized tissues between the tibia and metatarsals and between the elements of the tarsals. This includes some tissue that is on the medial face of the tibia and tarsals. It has a spotted appearance, but is distinct from that seen on the ventral face of the foot and it is not clear what its composition or appearance would have been.

LF 547 is preserved as a near complete wing (missing only the carpus), a partial tibia and a pes (Fig. 2). Some of the elements are not preserved well and broken open and infilled with calcite, or are present as impressions in the matrix. The wing is mostly articulated but a number of the joints are highly flexed. The humerus is straight, with a total length of 86 mm and proximally has a large subcircular deltopectoral crest and a similarly large medial crest, that is more triangular in shape though rounded. The distal end is slightly expanded, but the shape is unclear due to the poor preservation. The radius and ulna are long and straight and subequal in length (115 mm) and are similar in width. The carpus is not preserved, though this may be hidden behind the wing metacarpal and first wing phalanx, but a poorly preserved and faint pteroid is present. This is long (79 mm), thin, and

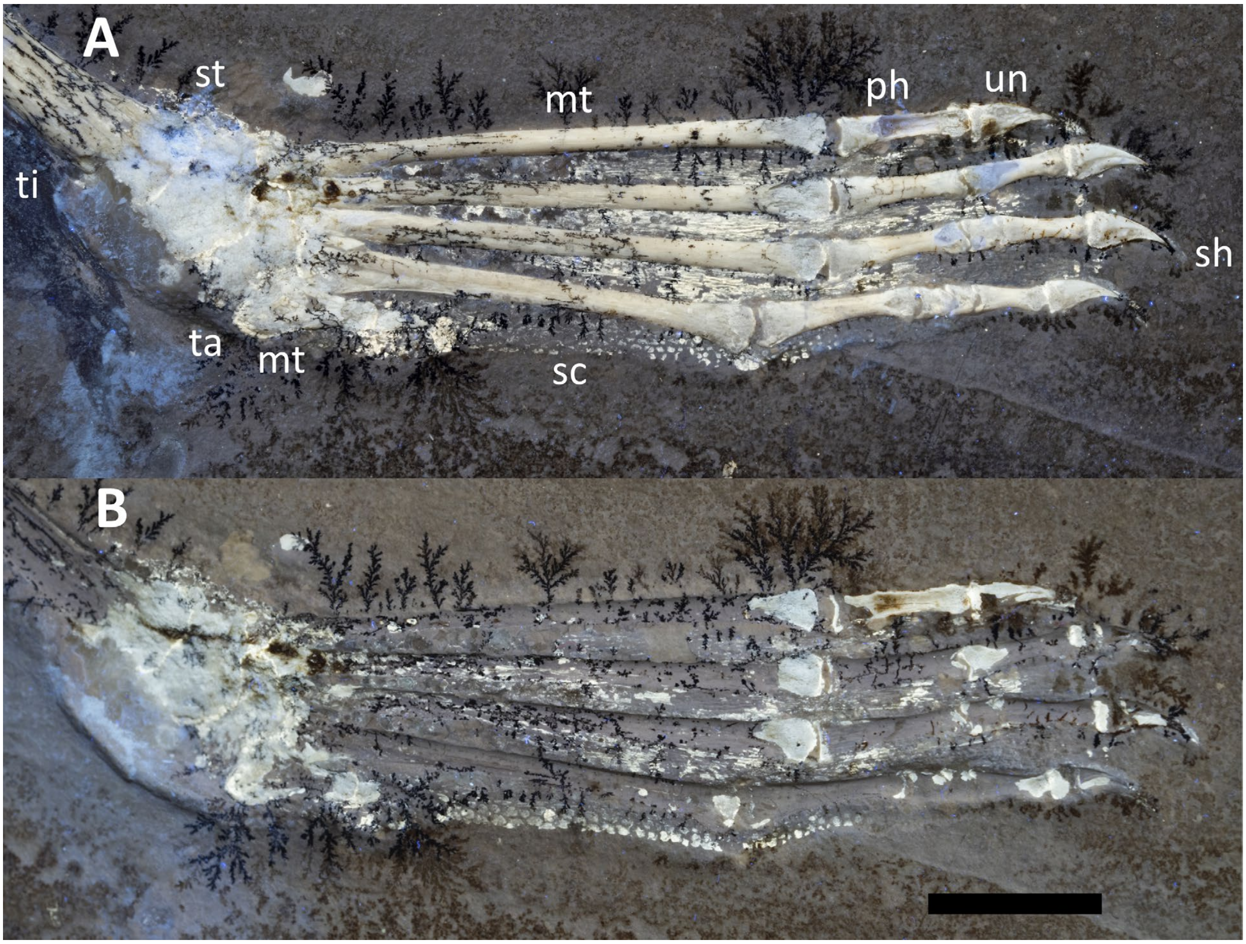

Fig. 3. Close ups of foot of LF 2314P (A), and 3398N (B) under UV light. The latter image has been reversed so that it matches the plate and they can be more easily compared. The webbing between the toes and metatarsals is not labelled, but can be clearly seen. Scale bar is 10 mm.

curved along its length. It is L-shaped with a large expansion to articulate with the wrist.

The four metacarpals are present, with metacarpals I-III being subequal in length to each other and the large fourth wing metacarpal which is 148 mm long. The manual phalanges for the free fingers are present, as is normal for pterosaurs, the manual formula is 2–3–4. The manual phalanges are generally short, and the unguals are also rather short and not strongly curved. The phalanges of the wing finger are all present and articulated and decrease in length successively. These respectively measure 138, 112, 79, 67 mm in length. The extensor tendon process on wing phalanx one is fully fused suggesting a relatively late ontogenetic stage for the individual. Wing phalanges 1–3 are all straight, but phalanx four is slightly curved as is seen in many pterosaurs (Hone *et al.* 2015).

The tibia is partially preserved and the midsection is missing and hard to see, but the distal end aligns with the proximal part suggesting that this is a single and continuous element, which can therefore be measured and is 169 mm long in total. The tibia is long and straight and tapers slightly along its length, and the fibula is not seen, although it may be hidden behind the tibia. The ankle is not seen, but part of the metatarsals and the pedal phalanges are present. This shows relatively short and robust metatarsals (32 mm) with toes that are longer than the metatarsals to which they are attached. The pedal phalanges are robust. The pedalunguals are short and only moderately curved, and so are similar in form to the manual unguals.

Under UV light, soft tissues of both the hand and foot are visible on LF 547 (Fig. 4) though neither set of tissues are extensive or as well-preserved as those of LF 2314P. There are several pieces of largely indeterminate phosphatised tissues around the manual digits. These are all on the ventral faces of the free digits (1–3), the largest of these is around 2.5 mm across

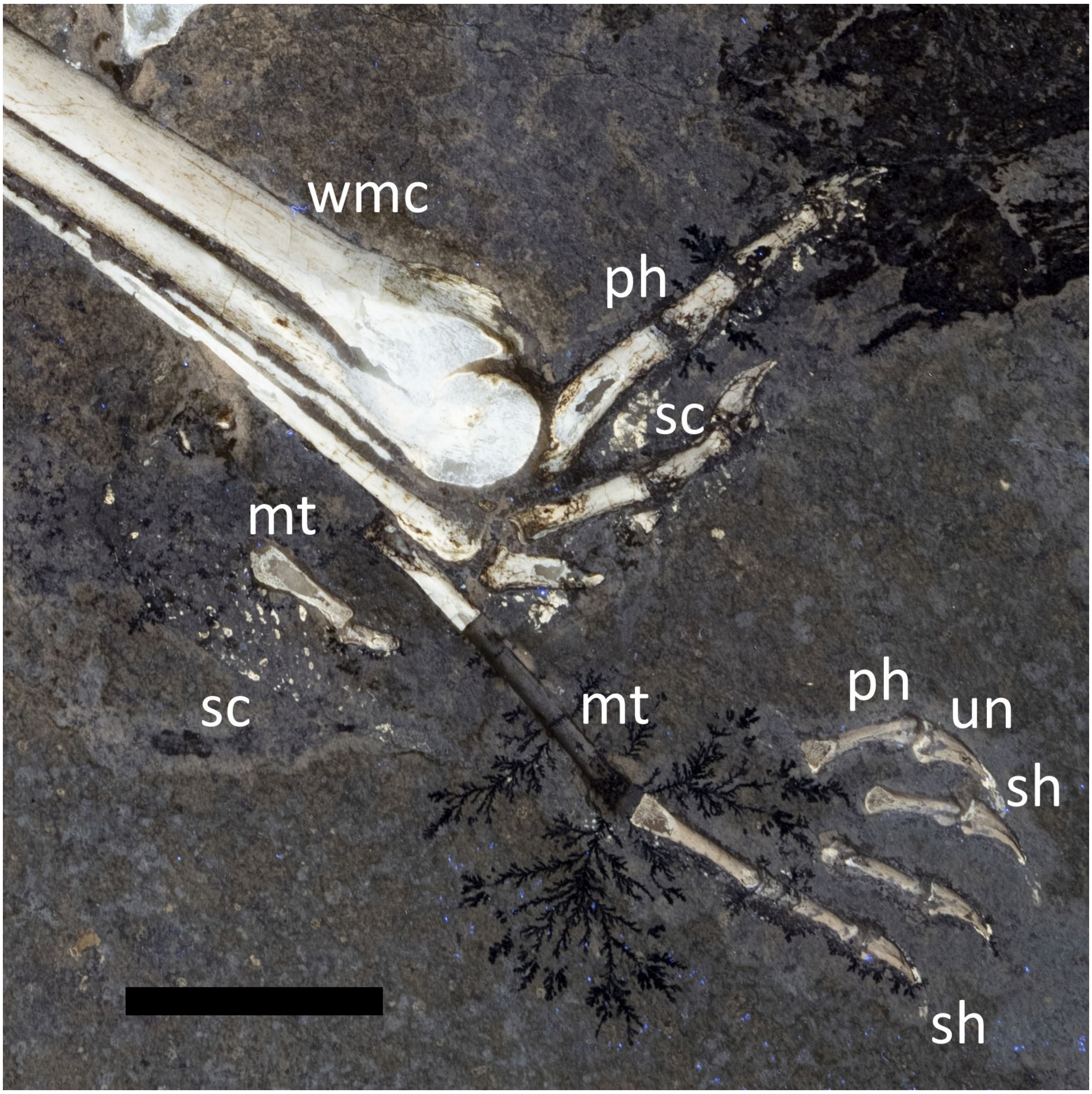

Fig. 4. Close of up of the manus and pes of LF 547 under UV light showing various preserved soft tissues. Scale bar is 20 mm.

and is ventral to the middle part of the first phalanx of digit 3. There is something of a spotted pattern to these, and based on the tissues of the foot here, and as seen in other pterosaurs, these are interpreted as a series of small scales where the edges are rather indeterminate and have blurred together. There are some apparently distinct single dots and these are c. 2 mm in diameter.

There is some faint staining around the unguals of manual digits 2 and 3, showing that claw sheaths were present. These are not well-preserved and only digit 2 shows some staining both dorsal and ventral to the ungual, but it is not clear how far this would extend distally.

On the pes, the scales are clearer. There are some tiny dots (between 0.1 and 0.2 mm across) of scales around the distal end of metatarsal IV and then around the ventral side of the joints of the phalanges of the 4th digit. There are one or two dots on the dorsal side of digit 4, and a large indeterminate patch of tissue around the base of the tibia and ventral to digit 5 is presumably part of a large heel pad of tissue. This patch extends as much as 6 mm ventral to the 5th toe. Some larger dots and streaks that are in subparallel lines are also present, the largest of these is just over 1 mm long, so small in absolute terms, but much larger than the tiny scales seen on the pes.

Claw sheaths are clearly present on digits 1–4. All of them increase the curvature of the ungual such that the tips would finish ventral to the slight proximal expansion at the proximal end of the ungual. These are thin and pointed and extend at the tip and over the distal and dorsal parts of the unguals. The sheaths significantly extend the length of the claws. On digit 2, the longest preserved sheath is 3 mm longer than the bony ungual which is 5 mm long.

Discussion

Taxonomic identity

LF 2314P belongs to a pterodactyloid pterosaur based on the greatly reduced 5th toe, which is not seen even in the nearest sibling taxa to this clade (e.g. *Propterodactylus* – Spindler 2024). There are a large number of genera and species of pterodactyloid pterosaurs from the Solnhofen region, all of which belong to the Ctenochasmatoidea. This matches what is seen here with the foot bearing long metatarsals that are commonplace in the Ctenochasmatidae (Witton, 2013) at least. Of the taxa known, most are a very modest in size and although there could be anomalously large individuals that would be the size of LF 2314P. For example, the largest specimens of *Pterodactylus* have a femoral length of c. 45 mm (Bennett 1996), barely half what is seen here. Nevertheless, a number of taxa can be ruled out given the differences they present to the specimen here (see Table 1) based on a recent comprehensive phylogenetic matrix (Hone *et al.* 2024).

Cycnorhamphus has very short metatarsals that are less than one fifth of the length of the tibia, which is in contrast to the proportions here where they are a third of the tibia (Table 1). *Ardeadactylus* has very straight femora which contrast to the clear curvature seen in LF 2314P. *Auroroazhdarcho* (Frey *et al.* 2011) and *Altmuehlopterus* (BSP AS.I.745) both have a proportionally rather shorter tibia (ratio of 1.47 and 1.37 respectively compared to 1.62), and show a much straighter femur. Finally, *Petrodactyle* also has much shorter metatarsals (nearly one fifth of the length of the tibia), and is from the younger Mörnsheim Formation (Hone *et al.* 2023). *Ctenochasma elegans* is a fairly close match here, but is a much smaller animal with a straight femur which is typically only 35 mm (BSPG 1935 I 24) and we are not aware of femoral curvature increasing with increasing size in other taxa so this overall a poor match here. Although *Gallodactylus* has a similarly curved femur to LF 2314P, the tibia is proportionally much shorter, and the metatarsals are also only slightly less than one quarter of the length of the tibia which makes them rather short (see Bennett 2013, fig. 5).

The closest match anatomically from the coding data is *Germanodactylus cristatus*. This species is not known from any material as large as LF 2314P with the holotype bearing a femur of 56.5 mm (BSPG 1892 IV 1) and a slightly larger specimen (SMNK PAL 6592) one of 61.6 mm. SMNK PAL 6592 has a femur to tibia ratio of 1.5, which is a close match for the ratio seen here (1.6), and they also have similarly proportioned metatarsals, toes and ungual shapes. The holotype specimen BSPG 1892 IV 1, does not have a complete foot to compare, but has a still closer ratio of femur to tibia lengths (1.6). Given the similarities here in coding and proportions, we therefore provisionally assign LF 2314P / 3398N to *Germanodactylus cristatus.*

LF 547 is also a pterodactyloid, based on the very elongate wing metacarpal and reduced fifth toe. Determining which clade this may belong to is difficult since there are few diagnostic traits based on the available elements that can be observed beyond the moderately elongate metatarsals. However, given the complete domination of ctenochasmatoids of the pterodactyloid fauna in the Solnhofen region, we here compare it to these local species and assume that this represents a ctenochasmatoid or allied taxon. Of the hindlimb, LF 547 only has an incomplete tibia and a foot, though this has long pedal digits which suggests that this is different to most of the other taxa discussed above (see Table 1). It is also a large animal which eliminates a number of smaller taxa from consideration (*Aerodactylus, Pterodactylus, Ctenochasma*).

Simple comparisons to the larger Solnhofern ctenochasmatoids also shows some clear differences. The humerus to wing phalanx 1 ratio is unusually high in LF 547 at 0.62, but is 0.5 or even 0.4 in *Ardeadactylus* in the two largest specimens that can be measured (Wellnhofer 1970, specimen 59, and an unnumbered SMS specimen respectively), and *Cycnorhamphus* gives a ratio 0.45 for the largest measurable specimen (GPIT 80). This ratio is much closer in *Germanodactylus cristatus* that has a ratio of 0.67 (BSPG 1892 IV 1), though this it a proportionally much shorter tibia (tibia:humerus 1.56, vs 1.97 for LF 547) which rules this out. *Petrodactyle* has a short humerus to wing metacarpal ratio of 0.46, which is considerably shorter than the ratio of 0.58 seen here in LF 457, although the two do have similarly short metatarsals compared to the tibia seen here (c. one fifth of the length). Other differences are present compared to these taxa, with, for example *Ardeadactylus* (SMNS 56003) and bears a much more robust humerus and a straight fourth wing

TABLE 1. Phylogenetic characters taken from the matrix of Hone *et al.* (2024) on anatomy of the hindlimbs of pterodactyloid pterosaurs from the Solnhofen region that can be compared to LF 2314P. The table does not include the species *Ctenochasma roemeri* or C. *taqueti*, or *Gnathosaurus subulatus* as there is no coding for these traits. *Gallodactylus* was coded based on figures in Bennett (2013) and the unnamed specimens were coded from direct observations.

Taxon or Specimen	Femur curvature (493)	Distal expansion of femur (499)	Ratio of femur to tibia lengths (503)	Pedal digits shorter than metatarsals (512)
LF 2314P	Strong	Present	1.5–1.7	Shorter
Germanodactylus cristatus	Strong		1.5–1.7	Shorter
Almuehlopterus rhamphistinus	Slight		<1.5	
Pterodactylus antiquus	Slight	Absent	<1.5	Shorter
Diopecephalus kochi	Slight		<1.5	Shorter
Petrodactyle wellnhoferi		Absent		
Cycnorhamphus suevicus	Straight		<1.5	
Gallodactylus canjuersensis	Strong	Absent	<1.5	
Aerodactylus scolopaciceps	Slight		<1.5	As long or longer
Ardeadactylus longicollum	Slight		<1.5	
Auroroazhdarcho micronyx	Slight		<1.5	As long or longer
Ctenochasma elegans	Slight		1.5–1.7	Shorter
NHM UK PV OR 42737				Shorter
BSPG 1977 XIX 39		Present	1.5–1.7	
LF 547				Longer

phalanx than seen here. *Cycnorhamphus* (GPIT 80) has a similarly most robust humerus, while its first wing phalanx is rather longer than the metacarpal which contrasts with the shorter one seen in LF 547). *Altmuehlopterus* (BSP AS.I.745) has a wing metacarpal that is similar in length to the humerus and so is quite unlike the condition seen here, despite the generally similar shape of the humerus to that of LF 547. *Germanodactylus* (BSPG 1892 IV 1) bears a somewhat curved humerus and lacks the greatly elongate tibia seen here. *Gallodactylus* has similar proportions for the known wing phalanges, but a much shorter tibia than here (data from Bennett 2013).

LF 547 has a rather proportionally short wing metacarpal and wing phalanges (humerus, ulna and wing metacarpal are 0.88 of the length of the wing finger) compared to the 'Type 1' big-winged specimens (ratio of 0.71) of Elgin and Hone (2020). The one specimen assigned as a 'Type 2' configuration of Elgin and Hone, is rather incomplete but the humerus and ulna ratio can be compared, and in LF 547 it is 0.75, but 0.87 in the Type 2 specimen. Therefore, this animal is not a good match for any of the known taxa from the Solnhofen region currently, or even these putative unnamed forms.

As noted earlier, several other remains of isolated legs and feet are known for some Solnhofen area pterodactyloids (see Fig. 5). NHM UK PV OR 42737 is a specimen of a tibia and pes that is slightly larger than LF 2314P (tibia length 143 mm vs 131 mm) and has extraordinarily long metatarsals compared to the phalanges. BSPG 1977 XIX 39 (given as '*Pterodactylus grandipelvis*' on the label though we do not think this name has appeared in the literature) is a complete pelvic girdle and sacrum articulated with one leg. It is also very large for the Solnhofen area pterosaurs, with a femur length of 100 mm, and a tibia of 165 mm. The specimen has proportionally long tibia therefore, and the femur is notably robust compared to other Solnhofen area pterodactyloids. We do not make any detailed comparisons here, but given that at least some of these differences between these specimens shown here and the traits given in Table 1, it is possible that they represent additional currently unknown taxa. At the least, they are unusually large animals and would represent some of the largest known elements recovered from the Solnhofen region. For reference, *Petrodactyle* (Hone *et al.* 2023) is one of the largest pterodactyloid specimens known from the area and has a femur that is 134 mm in length with the next largest being a specimen of *Gallodactylus* having a femur of 102 mm and tibia of 144 mm showing that these isolated legs are at the upper end of sizes seen.

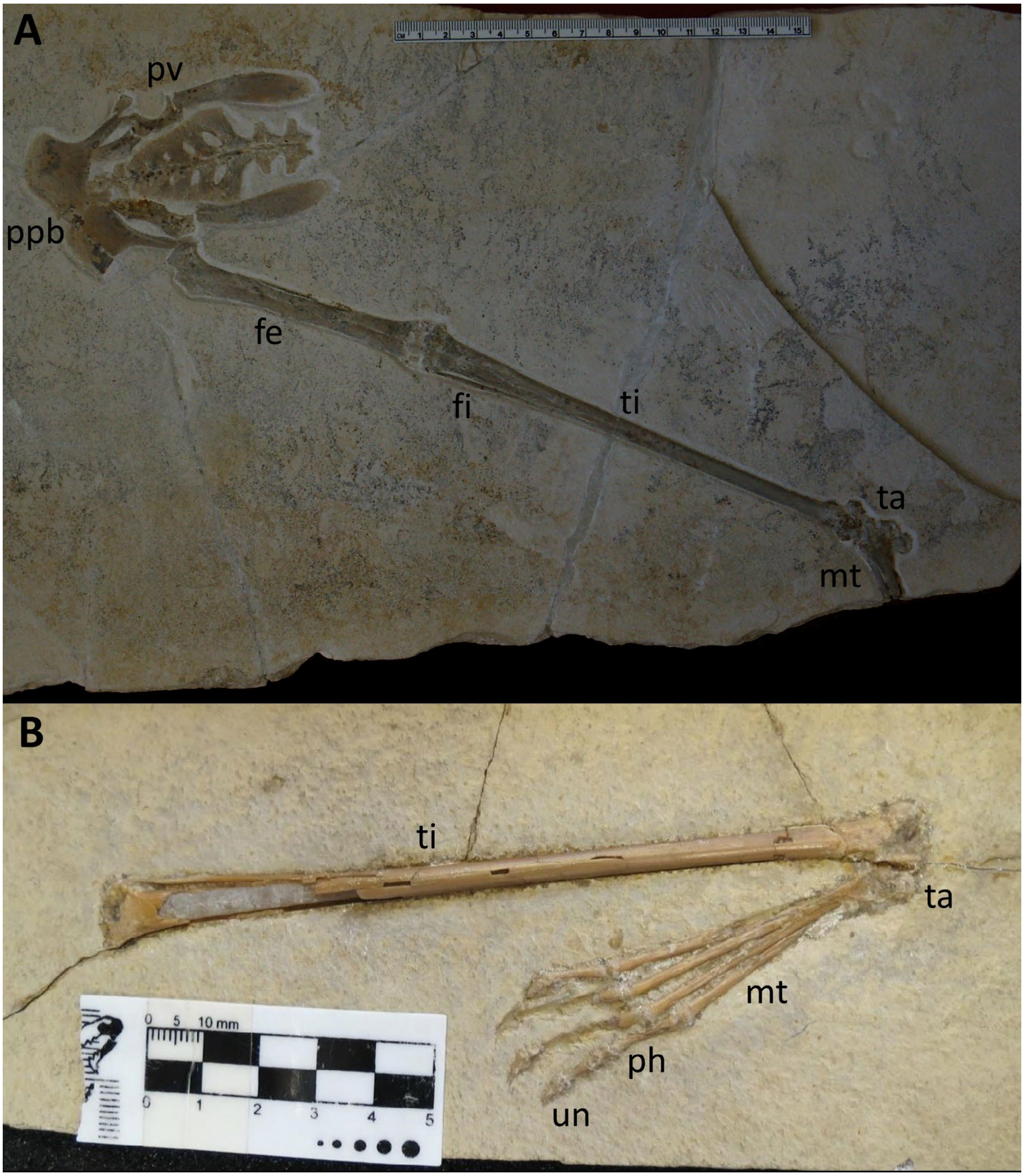

Fig. 5. Other 'big leg' specimens of Solnhofen region pterodactyloids. A, BSPG 1977 XIX represented by a pelvis and hindlimb, scale bar 150 mm. B, NHM UK PV OR 42737 a lower leg, scale bar 50 mm.

Soft tissues

The soft tissues of the foot seen here are generally very similar for those that have been described from a number of pterosaurs. The scales of pterosaur feet are generally small, round and pebble-like (Frey *et al.* 2003). Given the ancestry of pterosaurs, these scales are presumably archosaurian in nature, and therefore not squamous as in squamates (e.g. see Chang *et al.* 2009). Although a variety of apparent scale morphologies are seen in some archosaurs (Milinkovitch *et al.* 2013; Bell & Hendricx 2021) those seen in pterosaurs to date are very consistent with one another.

Some descriptions are available for details of the feet of a *Rhamphorhynchus* and *Pterodactylus* from the Solnhofen area, and an indeterminate azhdarchid from the Crato Formation (Frey *et al.* 2003) which show various scales, webbing and claw sheaths.

Better preserved, and described in more detail, are the soft tissues of a pes of a similarly unnumbered and privately held specimen of *Pterodactylus* (Frey *et al.* 2003). This clearly possessed circular scales around the heel which are clear under UV light (Frey *et al.* 2003, fig. 2), though difficult to make out under natural light (DWEH, pers. obs.). The scales are 0.2 mm across, round and slightly 'vaulted' (i.e. domed) with a row of scales twice this size at distal end of digit 5. The scales are present around the distal tibia, around the ankle and along the fifth metatarsal and fifth digit (Frey *et al.* 2003). Between the distal part of the toes there are subparallel fibres that make up the webbing. These are up to 5 mm long as seen, and c 0.01 mm in diameter (measured from Frey *et al.* 2003, fig 2). There are 24 fibres that are around 0.2 mm apart, in a 4.3 mm gap between two toes (Frey *et al.* 2003). In addition, very long claw sheaths are present on the pedal unguals. These are approximately double the length of the underlying bony unguals and are curved and terminate in sharp point (Frey *et al.* 2003, fig 2). Similar webbing is also seen between the toes of one specimen of *Pterodactylus* under UV light (JME-SOS 4008, Smyth & Unwin 2024, fig. 10).

An indeterminate azhdarchid SMNK PAL 3830 (Frey *et al.* 2003) has scales preserved on the foot. These are mostly 1 mm across, although these are larger around digit 5. These are much larger than other taxa, although on a much larger animal (metatarsal length of 62 mm, vs 18 mm in the *Pterodactylus*). There are also scales seen on the distal tibia, on an extensive heel pad, and along ventral margin of the foot. There are swollen patches of these around joints. There is the stain of apparent webbing between the toes, but no details were given (Frey *et al.* 2003). Webbing between the toes is also seen in the privately held specimen of *Rhamphorhynchus muensteri* known as the 'Dark Wing', but these are not described or illustrated in detail by Frey *et al.* (2003).

Soft tissue in the feet have also been mentioned in Chinese pterosaurs, for the holotype of *Jeholopterus* (Wang et al. 2002) and an indeterminate pterodactyloid (Lü 2002 – though based on the elongate cervicals and large pes, this is likely a ctenochasmatid). In both cases, little detail was given, though Wang *et al.* (2002) states that there are fibres between the toes and that the foot was webbed in *Jeholopterus*. In the pterodactyloid, Lü (2002, fig. 5b) illustrates web tissue between the pedal digits, but no striations are seen, and no description was given.

All of these features are very congruent with the features seen here on the feet. The scales are generally of a similar size and shape with a similar distribution on the foot, being thicker at the joints and with a large heel pad. The webbing similarly is composed of long and thin fibres that run parallel between the toes, and the claw sheaths extend both the length and also the curvature of the claws. There are though, still some important novelties seen in these specimens.

The polygonal scales of LF 2314P / 3398N have not been described before, with other previous pterosaur scales having always been described as being round. Such a shape is new for pterosaurs, but similar scalation in non-avian dinosaurs (e.g. see Hendrickx *et al.* 2022, fig. 2) as well as extant crocodylians (Grigg & Kirschner 2015, p. 84) means that these are consistent with other archosaurs and are not unexpected. Some of the scales seen here are also rather larger than those previously reported for Solnhofen area taxa, though as these animals are large compared to most other Solnhofen area specimens (but smaller than the Crato azhdarchid, which does have larger scales) again this is expected.

The presence of the webbing, not just between the toes, but between the metatarsals has not been seen clearly before. Wellnhofer (1991, p. 159) does illustrate both a *Pterodactylus* and *Rhamphorhynchus* pes as having webbing extending between the metatarsals and a photo of a the former apparently showing this (though the image is small, and the details are not clear). However, these are shown as being generic soft tissue rather than with any supporting fibres or similar structures, so exactly what was seen and how it was interpreted is not clear. This is definitive here in LF 3398N and we interpret this as the metatarsals not being bound together with extensive interstitial tissue but were sufficiently spaced that the webbing was needed to fill in the space. Although this has not been described before in pterosaurs, the separation of the metatarsals is seen in numerous *Rhamphorhynchus* specimens from the Solnhofen region, even in specimens that are otherwise well articulated. This does therefore suggest that pterosaurs had not just separate digits but also separate metatarsals, in earlier forms and that this persisted until the ctenochasmatids at least.

Finally, this is the first probable scales that have been reported for the pterosaur manus as these have only otherwise been reported for the pes (Witton 2013). Some indeterminate tissue around the hand is seen in one azhdarchoid specimen (SMNK PAL 3803) which also may have had webbing between the fingers (Frey *et al.* 2003), and has been inferred for others based on some tracks (Hwang *et al.* 2002). Claw sheaths are known in some others, (e.g. Frey *et al.* 2003) but otherwise the details of manual soft tissues are almost unknown. This is true even in specimens with otherwise superb soft tissue preservation (e.g. Kellner *et al.* 2010) or where pedal scales are seen (SMNK PAL 3830). As such the preservation here in LF 547 is important, even if the details are also limited.

Trackways are informative here. Numerous pterosaur tracks known from the fossil record, with wide distribution in time and space and referred taxa (e.g. see Lockely *et al.* 1995, 2008; Elgh *et al.* 2019; Li *et al.* 2021). However, few preserve more than general morphology of the hands and feet – details are rare, although some very-well preserved traces from small pterosaurs are known (e.g. Mazin *et al.* 1995). Bumps correlating to the pads around the joints of the digits are seen in pes tracks for pterosaurs but not that of the manus (Mazin *et al.* 1995; Hwang *et al.* 2002; Elgh *et al.* 2019). This suggests that the hands may have lacked such large expansions around the manus and that this would have had a much thinner covering than the pes. Coupled with very small scales, these might be all but impossible to see in most tracks.

Given the very small size of the scales seen in various feet noted above (as little as 0.2 mm), these could be so small that they would not show up unless the sediment was very fine-grained and very well-preserved. This cannot be true in every case though, as for example very small scales are present in traces for small theropods in conditions where pterosaur tracks are also present, but do not show traces of scales (e.g. Kim *et al.* 2019). In this case the pterosaur traces are only of the hands, but if these also bear scales then these could be visible.

There would likely be variation in manual morphology, but the general rarity of manual tissues compared to the relatively common pedal ones, does suggest a genuine difference between the two. Less tissue with smaller or more indistinct scaling would explain why this is rarely preserved, and little information is available even here. Such a pattern would be unusual. Pterosaurs were obligate quadrupeds (Witton 2013) and would have walked with both hands and feet on the substrate (as seen in trackways). Although pterosaurs tracks are known where the manus prints are much less clear or less deep than the pes (Mazin *et al.* 2003, fig. 1 e-g), the fingers were still taking weight and the muscular forelimbs of pterosaurs would have produced much of the locomotory power during walking but especially during the launch to takeoff (Habib 2008). As such, contact with the substrate would have been important and a constant part of terrestrial locomotion, but the reduction or perhaps even absence, of scales and covering here is therefore most notable.

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