Interpreting the autopodia of tetrapods: interphalangeal lines hinge on too many assumptions

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Recently Peters proposed the concept of 'interphalangeal lines', defined as sub-parallel lines that could supposedly be drawn across the joints of the digits of all tetrapods. The lines were viewed as potential axes of rotation, and it was suggested that they could be used to determine the resting position of the digits, reconstruct missing digital elements of fossil tetrapods, and provide information on systematic relationships. Evidence was adduced from the skeletons of recent and fossil vertebrates and from footprints. However, detailed analysis shows that these claims are largely unfounded. Linear alignments of joints on neighbouring digits are not consistently present in tetrapods, especially across locomotor cycles. Even if present, interphalangeal (IP) lines would rarely be in an appropriate orientation to facilitate joint movements during locomotion. There is no reason to believe that IP lines would be homologous across different taxa, so they cannot be used to infer systematic relationships. Finally, the alleged support from the ichnological record is undermined by the uncertain relationship between the joint structure of the skeleton and the form of the print. We conclude that IP lines cannot be consistently constructed on tetrapod extremities, and would have minimal functional relevance or predictive power in any case.

Keywords: pterosaurs; tetrapods; phalanges; hinge lines; footprints; ichnology

Introduction

The manual and pedal digits of tetrapods have an obvious functional role in contacting the substrate during locomotion, and may be used secondarily in a wide range of behaviours such as digging, prey capture and self-defense. The proportions of the metapodials and phalanges can therefore provide a basis for drawing functional inferences in extinct taxa (e.g. Hopson 2001) or matching fossil tracks to potential trackmakers (Farlow and Lockley 1993). Manual and pedal features also play an important role in phylogenetic analysis, as in the recognition of reduced lateral manual digits as a theropod synapomorphy (e.g. Rauhut 2003). Accordingly, patterns of variation in digital structure are of wide interest from the perspectives of systematics, functional morphology and ichnology.

Some years ago Peters (2000a) proposed that tetrapod digits display structural and functional regularities that can be demonstrated by superimposing straight 'interphalangeal lines' on the skeleton of the manus or pes, or even on a track impression. These lines were considered to represent 'a previously unnoticed geometric pattern . . . present in the extremities of all tetrapods' (Peters 2000a, p. 11). As the name implies, such interphalangeal (IP) lines connect sets of adjacent metatarsophalangeal (MP) or IP joints, and/or the tips of ungual phalanges. Peters (2000a) suggested that IP lines act as 'hinge lines' about which flexion and extension of the manus or pes can occur, that the lines

might be helpful in matching fossil tracks to trackmakers and elucidating phylogenetic relationships, and that they might represent a powerful tool for vertebrate palaeontologists because the lines could be used to predict the lengths of missing phalanges. IP lines have not met with widespread acceptance – Peters (2000b) used them to reconstruct the manus of *Longisquama* and Padian (2003) reproduced Peters' (2000a, Figure 19(a)) figure of the ichnite *Purbeckopus* with superimposed IP lines but did not comment on them. However, the idea that hinge lines might represent a widespread pattern and a powerful predictive tool is an intriguing possibility that requires analysis and testing. If the validity and predictive utility of IP lines could be upheld, they would represent a significant addition to the range of available tools for reconstructing incomplete fossils and analysing digit function.

Peters (2000a) advanced four specific claims about IP lines that deserve scrutiny: (1) IP lines are present in all tetrapods, and can be recognised objectively; (2) IP lines represent axes of flexion and extension within the manus or pes; (3) IP lines are present in footprints; and (4) IP lines have predictive power. In this paper, we examine both the primary issue of whether IP lines can be consistently recognised in tetrapod mani and pedes at all (Claim 1) and the secondary issue of whether the lines have the properties attributed to them (Claims 2–4). For the sake of brevity, we omit the year when citing Peters (2000a)

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hereafter, but all citations to Peters refer specifically to the 2000a paper unless stated otherwise.

Peters used the terms 'interphalangeal hinge lines', 'interphalangeal lines' and 'hinge lines' interchangeably, but because the notion that they represent axes of flexion and extension is integral to Peters' concept we refer to them in the remainder of this paper as either hinge lines or IP hinge lines. We refer to Peters' conception of hinge lines and their properties as the 'hinge line hypothesis' (HLH).

Discussion

Claim 1: universality and objectivity of IP hinge lines

The HLH postulates that IP hinge lines can be constructed (i.e. recognised and illustrated) in virtually all tetrapods according to a simple methodology. Beginning with a mounted skeleton, a drawing of a manus or pes, or a cineradiographic image, straight lines are drawn to connect sets of adjacent joints and/or ungual tips. Regarding the robustness of this procedure, Peters stated that (p. 12) 'when continuous lines could be drawn through neighboring joints, a high degree of confidence was placed on their validity', though he later cautioned that (p. 36) '[c]are must be exercised to arrange the digits in their natural pose' in order to recognise IP hinge lines in at least some cases. However, the objectivity and consistency of this procedure are highly questionable. Peters in fact noted (p. 12) that some reviewers (including SCB) of his study had found the construction of hinge lines 'problematic, subjective or controversial' and conceded that '[t]o a certain extent, this is true'. Indeed, for many of his illustrations of autopodia with superimposed hinge lines (Peters, Figures 2, 11(a), (e), 12(c), 13(f), 14(d) and 15(a)) he drew an alternative partial set of dashed lines in addition to the primary set of solid lines, as these were cases in which 'the choice of where to draw the line seem[ed] arbitrary' (pp. 12, 14). Even where hinge lines were presented without alternative possibilities, it could be argued that they remained subjective because the points at which they passed through the digits (the middle of joints or ungual tips) often varied among lines or even along a single line. In some cases, hinge lines passed though the mediolateral centres of MP or IP joints, but in other cases they were significantly displaced towards either the medial or the lateral side of the joint. It is not clear how the 'natural' position of a pes or manus was ascertained, and in any case positional changes would be inevitable during locomotion.

Peters (p. 14) stated explicitly that 'intersections [of hinge lines] with certain IP joints may only approximate a direct intersection or tangentially graze [the articular surfaces]' (Figure 1). The word 'approximate' calls into question the validity of the method, particularly given that no indication of the maximum acceptable distance between an intersection point and the centre of the
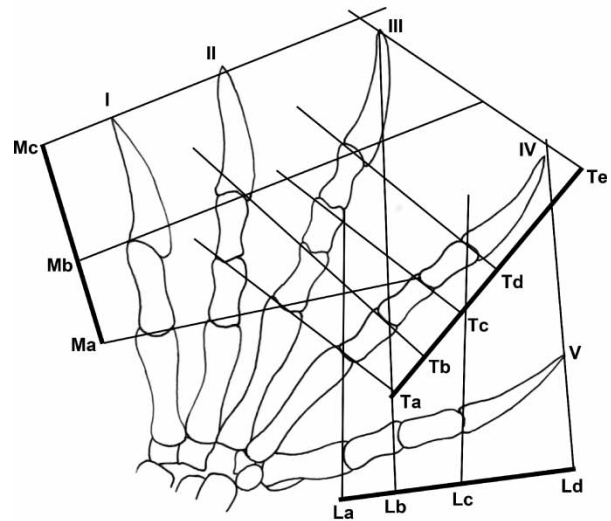

Figure 1. Redrawn from Peters (Figure 2(a)) including the IP hinge lines with their original labels. 'Alternate' sets of hinge lines proposed by Peters are omitted for clarity. Various inconsistencies can be observed here: hinge line Mb intersects with the medial part of a joint on digit I, the lateral part of a joint on digit II, and the central part of a joint on digit III; hinge line Ta passes through the medial parts of three joints, but then has to be terminated before it collides with the ungual of digit I (see also Tc and Td); and hinge line Te crosses a single ungual and nothing else.

articular surface in question was provided. In Figures 1 and 2, we present redrawn versions of Peters' own illustrations of pedes with superimposed hinge lines, including cases in which the putative hinge lines fall substantially medial or lateral to an articular centre, or even miss a joint entirely. This looseness of construction implies that the figures presented cannot serve as a rigorous demonstration of the presence of hinge lines in the species Peters investigated, let alone in all tetrapods. Furthermore, substantial displacement of a hinge line medially or laterally from the middle of a joint obviates the possibility that the hinge line might act as an axis of rotation for the joint, as postulated by the HLH. A valid hinge (i.e. axis of rotation) must pass through the instantaneous centre of rotation of the joint in question (Zatsiorsky 1998), not merely graze the joint surface.

According to the rules of construction presented as part of the HLH, an IP hinge line was regarded as valid if it passed through three or more adjacent joints or ungual tips. However, hinge lines passing through only two points were acceptable if they were 'approximately parallel to more extensive hinge lines in the same set, or if they [were] derived from known primitive patterns' (Peters, p. 12). A set was defined simply as a series of sub-parallel hinge lines. Typically Peters presented a 'medial set' of hinge lines extending from proximomedial to distolateral across the medial side of the manus or pes, a 'lateral set' extending from proximolateral to distomedial across the

lateral side, and a 'transverse set' extending transversely across the middle digits. The three sets were designated by the letters M, L and T, respectively.

In practice, many of these reconstructed hinge lines connected only two points (see Figures 1 and 2), and were presumably considered to fulfill the criteria of sub-parallel orientation with respect to more extensive hinge lines and/or congruence with a primitive pattern. However, neither criterion is particularly rigorous. Sub-parallel orientation is a geometric certainty provided that the adjacent digits do not suddenly diverge or converge partway along their lengths, and provided that the length of a given phalanx in one digit is not grossly dissimilar to that

of its counterpart in the other digit. A hinge line that connects the joints between phalanges 1 and 2 on digits IV and V, for example, is very likely to be sub-parallel to a hinge line connecting the joints between phalanges 2 and 3 on the same digits. The alternative criterion of congruence with a primitive pattern requires only that the phalangeal proportions of basal and derived members of a clade not be too different from one another. That hinge lines can be drawn according to these criteria is at best extremely weak evidence for the validity of IP hinge lines as conceived in the framework of the HLH. Furthermore, many of the hinge lines constructed by Peters also appear arbitrary in that they could just as easily have been drawn across a different pair or series of adjacent joints. The problem is not simply that some joints and ungual tips have no hinge lines passing through them, a circumstance that is inevitable when the digits of the manus or pes have unequal numbers of phalanges (see Figure 2). Rather, some of Peters' illustrations include cases in which two adjacent digits have equal numbers of phalanges, and yet not all of the joints are connected by hinge lines (e.g. his Figures 7(c) and 12(b)).

Figure 2 (of the present paper) depicts a clear example. Digits IV and V both have joints that are not encompassed by the line sets constructed by Peters (proximally in digit V and distally in digit IV). The whole system of hinge lines could be shifted distally along digit IV, and an extra hinge line added proximally, in order to connect equivalent joints all the way along both digits. However, there seems to be no *a priori* reason to prefer this configuration to the one illustrated in Figure 2, or vice versa. Shifts between alternative configurations or sets of hinge points, resulting
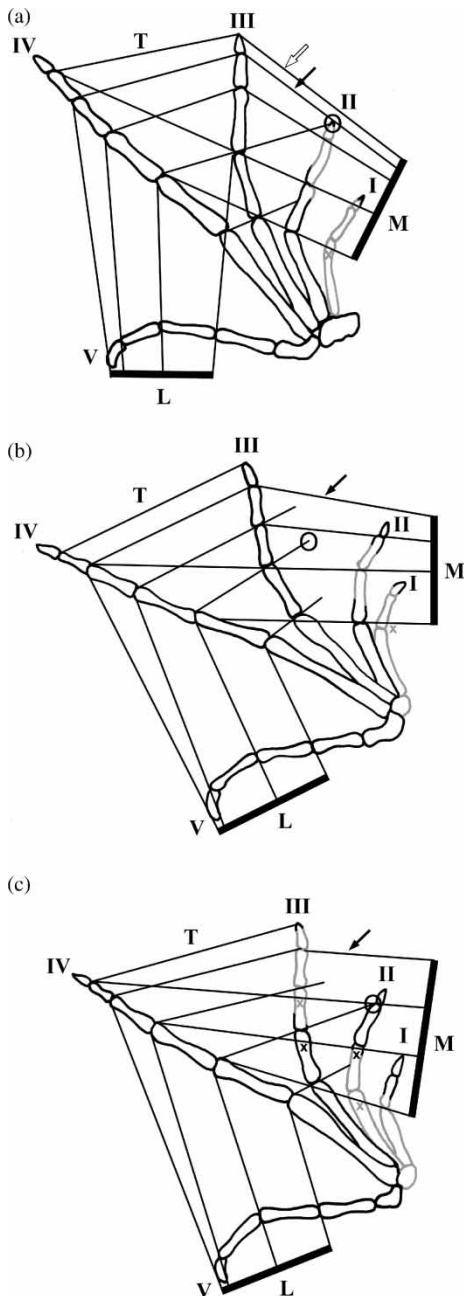

Figure 2. Redrawn from Peters (Figure 1(b)–(d)) and Brinkman (1981, Figure 4(b)–(d)) where our (a) = their (b), etc. The IP hinge lines are taken from Peters and the bones of the foot from Brinkman (the original source). Parts of the bones of digits I and II were reconstructed (in grey) based on parts (a) and (b) of the original figure, as they were obscured by the crus. Hinge lines are added as in Peters, with M, T and L denoting the Medial, Transverse and Lateral line sets. However, the heavy black line associated with the Transverse set is omitted for clarity. Several inconsistencies of the hinge lines are marked. Outline arrow indicates a line that only contacts the ungual of digit III in (a) and is missing in both (b) and (c). Solid arrow denotes a line that joins two points in (a) but only contacts a single ungual in (b) and (c), even though the pattern seen in (a) could have been repeated. *X* indicates points where the hinge lines cross bones and not joints. Grey *X* indicates hinge lines crossing bones that we have interpolated into the figure; while this was not done by Peters, our reconstructions are tightly constrained by the proportions of the pedal bones and the positions of the distal and proximal parts of the digits. Circles track the termination point of a particular Transverse hinge line. In (a) the line terminates at the tip of the ungual of digit IV, in (b) the line does not contact this digit, and in (c) it terminates at the distalmost IP joint.

in the disappearance of some hinge lines, even occur among the three panels of Figure 2, which are intended to represent successive positions of a pes passing through a step cycle.

The HLH proposes that hinge lines represent axes about which the joints of the manus or pes can rotate (see Claim 2). In this context, the procedure of drawing hinge lines across the tips of ungual phalanges, as well as across MP and IP joints, is meaningful only if the ungual tips act as points of rotation as the foot rolls off the substrate. However, even this relies on the false assumption that the bony unguals would be in direct contact with the surface. In the case of amniotes, each ungual would be sheathed in a keratinous covering that might markedly change the shape and length of the ungual (Maddin and Reisz 2007). The tip of the keratinous claw would not coincide with the bony tip of the ungual, and it is the former that would contact the substrate and would therefore be functionally relevant. The distance between the bony tip and the keratinous tip would be substantial in many cases, such as that illustrated in Figure 3, and the keratinous tip would be displaced in more than one dimension if the claw were significantly curved. Furthermore, in several cases (e.g. digit III in Figure 1) the hinge lines constructed by Peters do not even pass though the tip of the bony ungual, but instead pass through the ungual more proximally.

Finally, Peters generally drew IP hinge lines on a 2-D illustration of the manus or pes, so there is no guarantee that the points connected by a given line were appropriately positioned in the third dimension. For instance, a straight hinge line could not pass through the middle of each MP joint of an arched metatarsus even if the joints appeared perfectly aligned in dorsal or plantar view. Although Peters presented some Figures (e.g. his Figure 14(b)) as stylised 3-D renderings of autopodia, the vast majority were presented in a 'flat' dorsal view.

Figure 3.   The discrepancy in size and curvature between the bony ungual (termination point marked with black arrow) and the keratin sheath that surrounds it (white arrow) in the pes of a fossil azhdarchoid pterosaur. Note also that the fleshy pads lie over the IP joints rather than the individual phalanges.

It is hard to be confident that any given hinge line really passes through each joint or ungual tip in the third dimension, even when it appears to do so in the two dimensions illustrated. Relying on 2-D illustrations also prevents many aspects of joint surface geometry from being taken into account when constructing IP lines.

In summary, there is no convincing evidence for the consistent occurrence of meaningful linear alignments among the joints and ungual tips of tetrapod digits. Some hinge lines clearly are valid, in the sense that straight lines can indeed be drawn precisely through three or more joint centres or ungual tips for some tetrapod digits in some positions. However, it has not been demonstrated that these cases are anything other than isolated, uncommon geometrical coincidences. The creation of more extensive hinge line sets is a largely subjective exercise, since the rules governing their construction are loose enough to permit hinge line sets to be superimposed upon almost any reasonably generalised tetrapod pes or manus. The possibility of sub-parallel lines connecting only two points is especially permissive. Nevertheless, the method gives peculiar results when applied to more specialised forms. For example, Figure 4 shows an ornithomimid pes upon which we have constructed hinge lines in accordance with the HLH criteria. The few lines that can be drawn are highly implausible as axes of rotation, and multiple alternative lines could be arbitrarily drawn from one particular joint (asterisk in Figure 4).

The fact that hinge lines can be drawn under the rules of the HLH does point to regularities in tetrapod digital structure, but the regularities are essentially trivial: digits are unlikely to suddenly be medially or laterally deflected partway along their lengths, and the length of a particular phalanx in one digit is unlikely to be grossly different from that of the same phalanx in the adjacent digit. These structural regularities certainly do not amount to '[a] previously unnoticed geometric pattern...present in the extremities of all tetrapods' (Peters, p. 11).

Claim 2: IP hinge lines represent axes of flexion and extension

The HLH postulates that IP hinge lines are effectively axes of flexion and extension, about which multiple digits can move in a coordinated fashion in order to achieve 'strength through union' and obviate the possibility that 'excess pressure might be placed upon a single digit' (Peters, p. 36). Unless adjacent digits are tightly linked by soft tissues and not mere webbing, it seems likely that each digit would flex and extend as necessary to conform to the substrate and would not be directly strengthened or supported by union with adjacent digits. However, the theoretical advantages of such a mechanism may be demonstrated by the case of a weight-bearing plantigrade foot lifting off the substrate. As long as all metatarsals
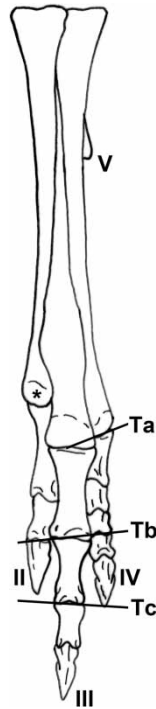
Figure 4. The pes of the theropod dinosaur *Ornithomimus*, redrawn from Romer (1956, Figure 191(d)). Despite claims by Peters that numerous line sets can be drawn for any tetrapod, only three possible hinge lines can be drawn in this case. Ta crosses two joints but then must terminate in order to avoid passing through the proximal phalanx of digit II. Therefore Ta probably does not represent a real line of possible flexure as proposed by Peters. Tc includes only a single joint and an ungual, and this can also be discounted (see Figure 3). Therefore only a single functional hinge line (Tb) can be reconstructed for a taxon that has three well developed pedal digits, and a phalangeal formula of 0–3–4–5–0. This strongly implies that the hinge line itself is meaningless and represents an incidental alignment of joints rather than a manifestation of a broader 'geometric pattern'. Several possible alternate hinge lines could conceivably extend from the point marked with an asterisk (*), and each hinge line could cross three joints (the start point, the metatarsophalangeal joint of digit III and then any interphalangeal joint in digit IV). However, there is no non-arbitrary basis for preferring any one of these possible hinge lines to the others.

remain distally in contact with the ground, and are held at the same angle, the risk that any one metatarsal will be exposed to undue stress is minimised. Such coordinated movement of the metatarsus is only possible if the metatarsus is rotating about an axis that passes through all of the MP joints, which would represent an IP hinge line as conceived under the HLH.

Metatarsals I–III of *Iguana* have been demonstrated to approach this pattern of movement early in the stance phase of the stride cycle (Brinkman 1980). With the foot diverging laterally from the direction of travel, the foot is lifted off the substrate by rotation about an axis connecting the MP joints of the first three digits. However, this pattern

of movement is not present in most tetrapods, and is possible in *Iguana* only because the first three metatarsals increase monotonically in length from first to third and are held at a divergent angle that permits the hinge line drawn across the MP joints to lie roughly transverse to the direction of travel (Brinkman 1980). Furthermore, the MP joints in *Iguana* do not have a ginglymoidal structure that would constrain their movement to flexion and extension about a single, approximately transverse axis. Were this the case, rotation about the hinge line defined by the MP joints would not be possible, since the hinge line is oblique to the metatarsals themselves.

Lateral divergence of the metatarsus during the stance phase is almost certainly a normal phenomenon in lizards, because retraction of the femur in a non-parasagittal plane imposes a tendency for outward pivoting of the crus on the substrate (Rewcastle 1983). Accordingly, initial elevation of the metatarsus about an axis defined by the MP joints may be a general phenomenon in lizards as well, so that the concept of a functional IP hinge line may be valid in this specific case. However, functionality of the hinge line depends on its meeting three criteria, which are not likely to be fulfilled in the vast majority of tetrapod manual and pedal movements. Firstly, the hinge line must cross all joints involved in the motion. Secondly, each individual joint must be anatomically capable of rotating about the axis defined by the hinge line. Thirdly, the hinge line must be perpendicular to the plane in which motion will occur.

The pes of the saber-toothed felid *Smilodon* (Figure 5), with superimposed IP hinge lines as reconstructed by Peters, demonstrates the consequences of violating all three criteria. Following Peters, the pes is illustrated in a plantigrade, fully extended position, even though *Smilodon* was almost certainly digitigrade to some degree (Carrano 1997). There are two hinge line sets, medial and transverse-lateral, but only two hinge lines (TLbc and TLd in Figure 5) cross all four functional digits. As a large, relatively cursorial mammal, *Smilodon* may be presumed to have moved its limbs in an essentially parasagittal fashion (Jenkins 1971), as is also true of modern felids.

The animation program Maya 7.0 was used to explore the possible movements of this reconstruction of the pes, with the metatarsals and phalanges represented by simple cylinders that matched the proportions of the illustrated bones (Figure 5; see also animations available from: http://www.fhsu.edu/biology/cbennett/IHL-Animations.html). For this plantigrade version of the pes to move parasagittally, all four metatarsals would have to lift off the substrate simultaneously, about an axis perpendicular to the trend of the metatarsus as a whole. However, no hinge line exists in this orientation, since the transverse-lateral hinge lines are markedly oblique. Flexion and extension about any of the medial hinge lines will cause the proximal end of the metatarsus to move medially, as well as in the desired dorsal and anterior directions
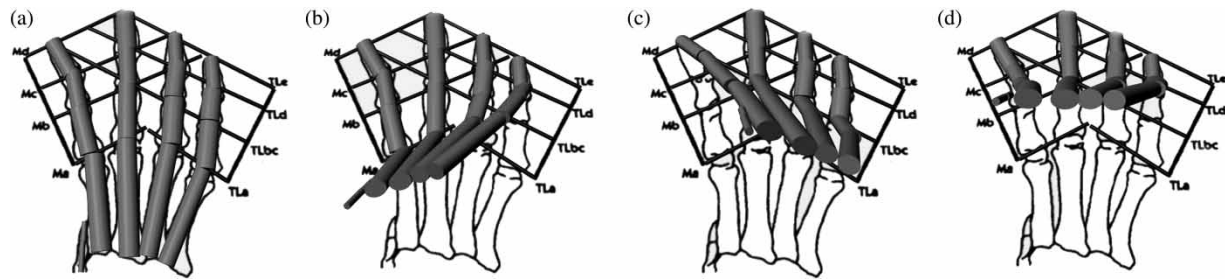
Figure 5.   Stills from a digital Maya 7.0 animation of the pes of the extinct saber-toothed cat *Smilodon* superimposed on a drawing by Peters (Figure 12(b)) with his reconstructed IP hinge lines. Figure 5(a) shows cylindrical models of the metatarsals and phalanges overlying the original drawing of the pes in a plantigrade position (although *Smilodon* was at least somewhat digitigrade). In (b), the pes is dorsiflexed along hinge line Ma. Note how this rotates the metatarsus out of the parasagittal plane in which the pes would be expected to move. Similarly, in (c) the foot is dorsiflexed along hinge line TLbc, and is correspondingly rotated out of the parasagittal plane in the opposite direction. In (d) the foot is dorsiflexed in the correct parasagittal plane, by rotation about a true transverse axis that does not correspond with any proposed hinge line. See also the accompanying animations available from: http://www.fhsu.edu/biology/cbennett/IHL-Animations.html.

(Figure 5(b); see 'Medmovie' animation). Similarly, flexion and extension about any of the transverse-lateral hinge lines will cause the proximal end of the metatarsus to move laterally (Figure 5(c): see 'Latmovie' animation). Either outcome would violate the assumption of parasagittal movement. Furthermore, the hinge line Ma (for example) crosses only the medial two functional digits (II and III), so that rotation about this hinge line would cause metatarsals IV and V to lift off the substrate prematurely (Figure 5(b)). Flexion and extension about the hinge line Ma would therefore fail to achieve the 'strength through union' postulated by Peters (p. 36). Finally, most of the hinge lines are at least slightly oblique to the axes of the MP and IP joints, which would lie approximately transverse to the shafts of the bones. Therefore, the majority of the joints would probably be incapable of flexing and extending about the hinge lines without damage or dislocation.

Parasagittal motion of the reconstructed pes about a true transverse axis is shown in Figure 5(d) (see also 'Tranmovie' animation). This axis clearly does not coincide with any of the putative hinge lines, which indicates that the hinge lines have no relationship to the motion of the reconstructed pes in this instance. It will be noted that the point chosen as the centre of pedal rotation in this simulation (the joint between the second and third phalanges of digit III) lies at the intersection of the hinge lines Mb and TLbc, and by definition remains at the intersection as motion occurs. However, all other joints initially falling on these hinge lines move away from them as soon as motion begins, because rotation is taking place about a transverse axis rather than an axis coinciding with either hinge line.

Rotation about a transverse axis does cause the digits to fall slightly out of register as they are lifted off the substrate (Figure 5(d)), so in this respect 'strength through union' is not maintained. While this might not apply

to a real *Smilodon* foot, which would have been held in a digitigrade posture during locomotion, the example demonstrates that 'union' in the sense of the HLH is geometrically impossible in a plantigrade foot if the four MP joints do not fall on a straight line. The 'union' among the metatarsals will inevitably be compromised as soon as the foot begins to lift off the substrate by rotating about any one MP joint. Furthermore, it is clear that the lines reconstructed by Peters on the pes of *Smilodon* could not function as meaningful axes of rotation, even under the unrealistic assumption that the pes was held in a plantigrade stance.

In general, there are likely to be a number of specific cases in which an IP hinge line does indeed operate as an axis of rotation, as in the metatarsus of *Iguana* during initial elevation of the metatarsus (Brinkman 1980). In such cases, the concept of a hinge line is useful from a functional perspective, and likely to be helpful in describing the observed motion. However, this occurs only under very specific circumstances, and is clearly not a general phenomenon, as the example of a plantigrade pes rising parasagittally off the substrate demonstrates. The mere existence of an approximate linear alignment among a set of adjacent joints should not be taken as evidence that the joints actually flex and extend about the hinge line in question. This is only possible if the joints are anatomically capable of flexing and extending about the axis defined by the line, and only probable if the postulated motion would be useful to the animal.

In passing, it should be noted that incidental comparison of the *Smilodon* pes as figured by Peters (Figure 12(b)) with the cited source of the illustration (Coombs 1978, Figure 3) revealed that the orientations of the phalanges of digits III and IV had been altered slightly, presumably in order to facilitate the drawing of hinge lines. This apparently represents a case in which 'manipulation [of a figure from the literature] was necessary to produce sets of continuous

interphalangeal hinge lines' (Peters, p. 12). However, the fact that such manipulation was necessary appears to undermine the force of the statement on the same page that none of the specimens or images used by Peters, including 'figures from the literature', were 'originally reconstructed, illustrated or photographed with a bias toward presenting hinge lines'. It is irrelevant that the *Smilodon* foot was not originally drawn with a bias toward presenting hinge lines if such a bias was imposed when the drawing was modified!

Claim 3: IP hinge lines are present in footprints

A major component of the HLH is the claim that IP hinge lines occur 'in a wide variety of living tetrapods and in their footprints' (Peters, p. 11). This idea was supported by several examples of tetrapod footprints, both recent and fossil, upon which IP hinge lines had been traced. Well-preserved fossil footprints often show impressions of individual pads of tissue along the digits. These pad impressions have sometimes been interpreted in the ichnological literature as having a consistent relationship to the MP and IP joints; for example, Olsen et al. (1998) assumed that the centre of each pad impression in the tracks of small theropod dinosaurs corresponded to the location of a joint. Accordingly, Peters suggested that supporting evidence for the consistent presence of hinge lines could be found in the ichnological record, although he implicitly took pad impressions to coincide with the phalanges themselves rather than the intervening joints. Peters (p. 15) asserted that 'linear divisions between fleshy pads and pad impressions typically coincide with hinge lines at interphalangeal joints' in order to justify the procedure of superimposing hinge lines on drawings of footprints. However, this procedure can only be regarded as valid if divisions between fleshy pads on the foot do indeed correspond to joints, and if the fleshy pads are clearly and consistently impressed in the substrate when a track is formed. Both assumptions are open to question.

The relationship of fleshy pads to MP and IP joints

Contrary to the HLH assumption that fleshy pads along tetrapod digits almost invariably coincide with the phalanges, a great deal of inconsistency is present in the relationship between the pads and the underlying skeleton. In the human hand, a pad exists for each phalanx of each digit, with each division between successive pads corresponding to an IP joint. However, in ratites (at least) the fleshy pads generally have a precisely opposite relationship to the joints (Padian and Olsen 1989; Milan 2006), with each pad lying across two phalanges so that the centre of each pad corresponds to an IP joint rather than the midpoint
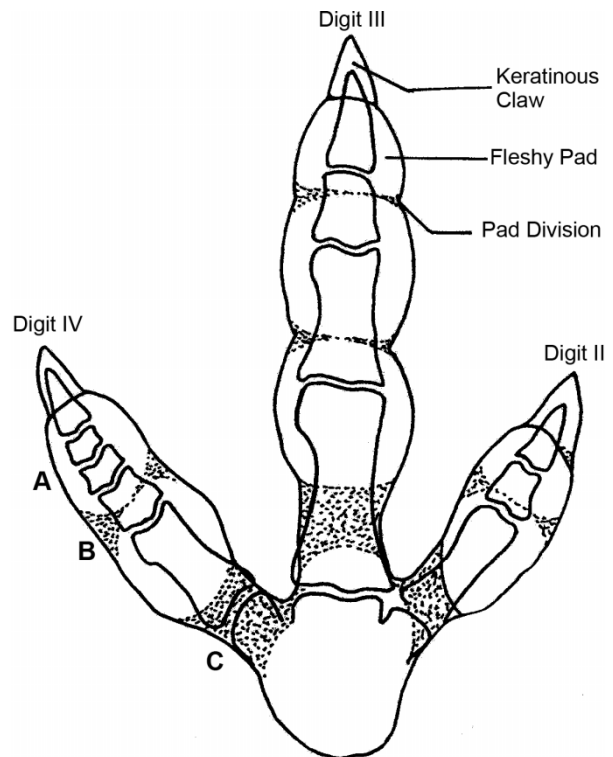

Figure 6. The inconsistent relationships between fleshy pads and the underlying phalanges and unguals in the pes of an emu (*Dromaius novaehollandiae*), redrawn from Milan (2006). 'A' indicates two phalanges that are completely surrounded by a pad. 'B' indicates a pad division line that corresponds to the midpoint of a phalanx, so that two different pads contact the phalanx. 'C' indicates a pad division that corresponds to a joint.

of a phalanx (Figure 6). However, there is some variability among conspecific individuals, and along the digits of a given individual, in the placement of the pads relative to the joints (Smith and Farlow 2003). Pads may even be enlarged to the point where they extend across multiple joints, covering the intervening phalanx completely (Milan 2006).

The lack of any consistent correspondence between the bones of tetrapod digits and the overlying fleshy pads implies that drawing hinge lines upon footprints is a futile exercise unless it is guided by intimate knowledge of the way the shape and extent of the pads relate to the structure of the skeleton in the taxon in question. Without this knowledge, there is no way of knowing whether hinge lines should be drawn through pad divisions (Peters, Figures 8 and 9) or through the centres of the pads. In extant taxa, the necessary data about the relationship between pads and phalanges could be collected by dissection or radiography, but in extinct taxa the nature of the relationship will always be a matter of inference using techniques such as the Extant Phylogenetic Bracket (Witmer 1995), and therefore subject to considerable uncertainty.

The preservation potential of fleshy pads during track formation

Even if the relationship between fleshy digital pads and phalanges were known for a particular taxon, the confidence with which IP hinge lines could be super-imposed on a footprint would depend on the fidelity of the track with respect to the pad impressions. If the pads were not clearly impressed into the substrate during formation of the track, they could not be used to guide the construction of hinge lines. Experiments with live animals (especially ratites: Milan 2006) indeed show that pad impressions vary with the substrate they are impressed into, so that they cannot be treated as a reliable record of the fleshy pads on the foot of the trackmaker. Various pads can appear, disappear or merge between tracks and entire digits may even be missing from a particular track (e.g. dromaeosaurs have three functional toes, yet their prints contain full traces only of digits III and IV; see Li et al. 2008). In a palaeontological context, Olsen and Baird (1986) reported changing pad numbers in successive footprints within individual trackways of the ichnogenus *Atreipus*, and a similar phenomenon was illustrated by Demathieu and Haubold (1974, Figure 8.5).

Because tracks may not faithfully record fleshy pads on the digits of a hand or foot, and because the pads may have an uncertain relationship to the MP and IP joints of the skeleton in any case, the use of footprints as a basis for constructing hinge lines is plagued by two levels of uncertainty. There is no guarantee that hinge lines superimposed on a track will have any precise relationship to the joints of the trackmaker. Therefore, illustrations of tetrapod footprints with hinge lines drawn across the digits can hardly be regarded as supporting evidence for the HLH proposal that linear arrangements consistently occur among the digital joints and ungual tips of tetrapods (see Claim 1).

Claim 4: IP hinge lines have predictive power

The HLH presents hinge lines as a powerful analytical and predictive tool for vertebrate palaeontologists. Peters (p. 11), claimed that '[h]inge lines...have predictive value in that missing phalanges, including unguals, can be reconstructed with confidence using hinge lines as size guides' and that '[c]orrect digit spread and metapodial configuration can also be determined in extinct taxa by seeking the appearance of continuous IP hinge lines in tested reconstructions'. He also suggested that hinge lines could be used to identify trackmakers provided that the characteristic pattern of hinge lines in the clade in question was known, which implies that particular hinge line patterns are sufficiently characteristic of clades to form a valid basis for inferring phylogenetic relationships. The utility of hinge lines in each of these four separate areas of inference – anatomical, postural, ichnological and phylogenetic – is evaluated in turn below.

Reconstructing missing phalanges

Peters asserted that hinge lines could be used to reconstruct missing phalanges in fossil taxa with incompletely preserved mani or pedes. The procedure was not described in detail, but presumably hinge lines would be constructed as usual on the basis of whatever joints and unguals were intact, and missing phalanges would then be restored on the assumption that the hinge lines would define their lengths (because the hinge lines would be presumed to pass through the intervening joints). However, the fact that Peters allowed hinge lines to pass through the medial and lateral edges of the joint surfaces, as well as the articular centres, implies that uncertainty about the length of any recon-structed phalanx would be large. Furthermore, the procedure would give variable results depending on the manus or pes posture used to carry out the reconstruction, and depending on what orientation was considered probable for the reconstructed phalanx. Between a given pair of hinge lines, one could choose to restore either a short phalanx extending straight from one line to the other, or a longer phalanx deviating from this orientation.

The figures provided by Peters include examples in which, if part of a digit were lost, it could not be accurately reconstructed on the basis of the hinge lines. Peters (Figure 14(b)) illustrated the pes of *Rhea* with only two hinge lines (designated Lb and Lc) crossing the fourth digit, even though the digit has five phalanges. Three short phalanges fall between Lb and Lc, but if they were unknown, then Lb and Lc would provide a basis for reconstructing only a single long phalanx in their place. Incidentally, it is doubtful that Lc could even be constructed unless the fourth toe were completely known, since Lc passes through only digits III and IV and crosses both at relatively distal points. Similarly, some illustrations (e.g. Peters, Figure 13(e) and (g)) include a digit that is not contacted by any hinge lines, and these digits could not be reconstructed at all.

These uncertainties could perhaps be obviated by using the pattern of hinge lines of a closely related species with a more completely known hand or foot to guide the reconstruction. However, it is not clear why this procedure would be preferable to traditional reconstructions, in which the manual or pedal morphology of related taxa is used directly to inform the restoration of missing parts. Constructing a set of hinge lines as an intermediate step would merely complicate the process and introduce an unnecessary level of uncertainty. Morphological infor-mation would effectively have to be translated into a set of hinge lines, and back again, with some fidelity being lost at each stage because of the uncertainties associated with hinge lines.

Determining manual and pedal posture

In well-preserved fossil vertebrates, the articular surfaces of the metapodials and phalanges can often be aligned

in order to determine the range of motion of each MP and IP joint, and hence the range of feasible postures for the pes or manus as a whole (e.g. Senter 2006). Peters (p. 36) suggested that, in cases where the articular surfaces are insufficiently well-defined for this procedure, 'manipulation of the specimen until continuous hinge lines appear can be a secondary method for approximating correct configuration and digit radiation'. The assumption is apparently that linear alignments will be present only in the 'correct configuration' of the digits, implying that the presence of such alignments can be used as a criterion for determining which configuration is correct.

As noted previously (see Claim 1), the rules for constructing hinge lines are so permissive that some hinge lines could be superimposed upon almost any biomechanically reasonable arrangement of tetrapod digits. Accordingly, IP hinge lines are hardly a stringent criterion for choosing among possible postures. Furthermore, the very idea that there is a single correct configuration ignores the fact that a tetrapod foot or hand will assume a range of positions in the course of its normal activities (Peters 2000a, Figure 1). The variability in digital divarication and other parameters among fossil and recent trackways (even from a single individual) confirms this. At best, it might be possible to use the hinge line criterion to identify a broad envelope of possible configurations for a given foot or hand, and to exclude as implausible the inverse set of configurations on which hinge lines could not be drawn. However, the set of possible configurations would almost certainly be so large as to be virtually meaningless, and would include many postures that the manus or pes rarely or never assumed. The practice of using 2-D renderings of the manus and pes to construct hinge lines is also relevant in this context, in that it is difficult to understand how the hinge line criterion could be applied to a putative posture in which the manus or pes did not lie approximately in a single plane.

As a demonstration of the predictive power of hinge lines in regard to pedal posture, Peters attempted to construct them on pterosaur pedes and trackways. He was unable to construct hinge lines on the pedes of a broad range of pterosaurs including *Rhamphorhynchus*, *Pterodactylus* and *Pteranodon* when the pes was in a plantigrade posture, but could construct hinge lines after reconstructing the pes in a digitigrade posture. Only in ctenochasmatid pterosaurs could he reconstruct hinge lines on plantigrade pedes, and on that basis he argued that ctenochasmatid pedes were plantigrade, whereas those of the other pterosaurs were digitigrade. Hinge lines constructed on pes tracks of the probable plantigrade pterosaur ichnite *Pteraichnus* appeared to match those of ctenochasmatids, suggesting that *Pteraichnus* was attributable to a ctenochasmatid and potentially supporting the conclusion that members of this clade were plantigrade.

However, these inferences regarding pterosaur foot posture are problematic for several reasons. The hinge lines constructed for *Pteraichnus* were based on the assumption that the lines between digital pads necessarily coincided with joint positions, which has been shown not to be the case (see Claim 3), and indeed an azhdarchoid pterosaur specimen with soft tissue preservation seems to show fleshy pads aligned with its MP and IP joints rather than with its phalanges (Frey et al. 2003; Figure 3). Therefore, there is no reason to think that all *Pteraichnus* trackways were made by ctenochasmatids, or even that any *Pteraichnus* trackways were necessarily made by ctenochasmatids. Moreover, the morphology of the MP joints is remarkably consistent across a broad range of pterosaurs including *Rhamphorhynchus*, *Pterodactylus*, *Ctenochasma* and *Pteranodon*, and this morphological pattern is consistent with plantigrady and inconsistent with digitigrady (Wellnhofer 1970, 1975; Bennett 1997, 2001; Clark et al. 1998). Thus, we can reject Peters' (2000a, 2000b) suggestion that most pterosaurs were digitigrade, and the case of pterosaurs certainly provides little support for the idea that hinge lines can be used to infer pedal posture.

Identifying trackmakers

The HLH asserts that IP hinge lines can be used to identify the trackmakers responsible for particular ichnotaxa. While providing little explicit elaboration of the methods to be used, Peters (p. 31) matched the foot of the prolacertiform *Cosesaurus* to the ichnite *Rotodactylus* partly because '[p]ad division lines on *Rotodactylus* align with hinge lines in *Cosesaurus*'. The expectation was clearly that hinge lines constructed on the hand or foot of the trackmaker should be approximately congruent with pad division lines constructed on the ichnite, as was supposedly the case for *Pteraichnus* tracks and the pedes of ctenochasmatid pterosaurs.

In practice, however, the construction of both sets of hinge lines is inevitably subject to considerable uncertainties. The variability of track impressions on different substrates, or even among successive prints within a single trackway (see Claim 3), implies that the pattern of pad division lines may not be consistent across multiple specimens of a single ichnotaxon. Even ignoring this preservational factor, congruence between the pad division lines and the hinge lines would be expected only for those taxa in which pad impressions correspond to bony phalanges, rather than to MP and IP joints. Finally, the essential subjectivity involved in constructing hinge lines upon a tetrapod hand or foot skeleton opens up the possibility that a set of hinge lines could be produced in order to justify an *a priori* judgement in favour of a candidate trackmaker, even if the fit between the skeleton and the ichnite according to traditional criteria was not particularly convincing.

As with the problem of reconstructing missing phalanges, it is highly unlikely that the hinge line procedure will prove to be a more reliable technique for identifying trackmakers than standard ichnological methods, such as morphometric comparisons between tracks and the hands or feet of potential trackmakers (Farlow and Lockley 1993). The use of hinge lines merely achieves a similar comparison by an indirect route that is liable to introduce additional subjectivity and inaccuracy into the process.

Taxonomy and pterosaur relationships

Peters (p. 11) asserted that 'hinge line patterns appear to identify clades so that they may, to a limited extent, be used taxonomically'. This implies that hinge line patterns could potentially be codified as synapomorphies of particular clades, or even used as characters in phylogenetic analyses. However, the uncertainties in the construction of hinge lines described in previous sections (see especially Claim 1) make it difficult to see how the hinge lines could act as a reliable guide to taxonomic or systematic relationships. Even if hinge lines could be traced consistently and reproducibly, they would be as likely to correlate with posture and ecomorphology as with evolutionary descent. All digitigrade or unguligrade species, for example, would presumably have similar hinge line patterns irrespective of their phylogenetic histories. Digital loss within a clade, as in the famous example of equids (Benton 2000), would make it difficult even to compare hinge line patterns between primitive and derived species (ornithomimid theropods are another example: see Figure 4).

To some extent, of course, problems of functionally driven convergence and character inapplicability also affect traditionally defined phylogenetic characters that are based on skeletal morphology. However, the use of morphological characters at least avoids the ambiguities inherent in the construction of hinge lines, as well as potentially incorporating phalangeal shape and other morphological data that hinge line patterns capture only indirectly or not at all. Changes in digital count or phalangeal formula are frequently used in phylogenetic analyses, and an attempt to formulate characters based on hinge line patterns would merely convey the same information in a less explicit manner. The fact that hinge line patterns can apparently change substantially as an appendage moves through a locomotor cycle (see Figure 2) makes it especially difficult to conceive of the line sets as stable phenomena displaying homologies that can be traced through evolutionary time and used to build cladograms. Phylogenetic analysis is simply another area in which hinge lines amount to little more than a time consuming and rather imprecise method for elucidating data that are already available in a more convenient form.

By stating that '[to] a limited extent hinge lines can be used to differentiate, but not determine, taxonomic groups',

Peters (p. 38) conceded that hinge lines are only partly effective as a means of inferring systematic relationships. Nevertheless, he identified an 'apparent hinge line clade comprised of pterosaurs and *Cosesaurus*' (p. 27), implying once again that hinge line patterns can serve as identifiable synapomorphies. However, in addition to the methodological problems discussed above, hinge lines would at best be a derivative of the actual morphology, and this suggests that actual measurements of metapodials and phalanges and ratios thereof would be more reliable characters for use in phylogenetic analyses. Moreover, the suggestion of a close relationship between pterosaurs and prolacertiforms such as *Cosesaurus* is contradicted by a considerable weight of opposing evidence. Although the phylogenetic position of the Pterosauria within the Diapsida is controversial, all cladistic analyses to date have suggested that pterosaurs are not closely related to prolacertiforms (e.g. Benton 1985, 1990, 1999; Gauthier 1986; Sereno 1991; Bennett 1996; Hone and Benton 2008), with the single exception of Peters (2000b) and an unsual analysis by Renesto and Binelli (2006). Peters' (2000b) analysis includes characters and codings that cannot be corroborated by independent observers (e.g. pedal posture reconstructions based on the pattern of hinge lines, presence of three antorbital fenestrae in *Cosesaurus*) and has been strongly criticised on methodological grounds (Hone and Benton 2007). Thus, it is unlikely that comparisons of hinge line patterns will be of use in reconstructing phylogenetic relationships.

Conclusions

IP hinge lines, as conceived by Peters (2000a), can often be superimposed on 2-D drawings of tetrapod mani or pedes but have little or no value as a tool in palaeontological and biological research. The rules given for constructing the lines are so permissive as to be almost arbitrary, and the putative supporting evidence from ichnology for the widespread occurrence of hinge lines is obviated by preservational problems and variability in the relationship between soft tissue pads and underlying skeletal structures. IP hinge lines have functional significance only in rare cases, and cannot be reliably utilised to predict autopodial postures of extinct animals or to infer the proportions of missing phalanges or metapodials. We would therefore strongly advise against the use of hinge lines as a guide to functional analysis, a source of phylogenetic information, or a basis for identifying trackmakers in the ichnological record. It is difficult to envision circumstances in which the concept of IP hinge lines would be helpful to researchers.

Acknowledgements

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