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Ankle structure of the Tokay gecko (*Gekko gekko*) and its role in the deployment of the subdigital adhesive system

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Abstract

The remarkable ability of geckos to adhere to smooth surfaces is often thought of in terms of external structures, including the branching setae that make contact with the surface producing van der Waals forces. Some geckos also exhibit unique movements of the distal segments of the limbs during locomotion and static clinging, including active digital hyperextension and considerable pedal rotation. During static clinging, geckos can exhibit considerable adduction/abduction of the pes while the crus and thigh remain firmly adpressed to the substratum. This decoupling of pedal adduction/abduction from ankle flexion/extension and pedal long-axis rotation is a significant departure from pedal displacements of a typical lizard lacking adhesive ability. The structure of the ankle is likely key to this decoupling, although no detailed comparison of this complex joint between pad-bearing geckos and other lizards is available. Here we compare the configuration of the mesotarsal joint of nongeckotan lizards (*Iguana* and *Pristidactylus*) with that of the Tokay gecko (*Gekko gekko*) using prepared skeletons, scanning electron microscopy, and micro-computed tomographic (μ CT) scans. We focus on the structure of the astragalocalcaneum and the fourth distal tarsal. The mesotarsal joint exhibits a suite of modifications that are likely associated with the secondarily symmetrical pes of pad-bearing geckos. For example, the lateral process of the astragalocalcaneum is much more extensive in *G. gekko* compared with other lizards. The mesotarsal joint exhibits several other differences permitting dissociation of long-axis rotation of the pes from flexion–extension movement, including a reduced ventral peg on the fourth distal tarsal, an articular pattern dominated by a well-defined, expansive distomesial notch of the astragalocalcaneum, and an associated broad proximodorsal articular facet of the fourth distal tarsal. Pad-bearing geckos are capable of effectively deploying their intricate adhesive system across a broad array of body angles because of this highly modified ankle. Future research should determine whether the differences encountered in *G. gekko* (and their extent) apply to the Gekkota as a whole and should examine how the elements of the ankle move dynamically during locomotion across a range of taxa.

KEYWORDS

adhesion, astragalocalcaneum, CT scanning, Gekkota, locomotion, mesotarsal joint, morphology

1 | INTRODUCTION

Geckos are well known for their ability to adhere strongly to smooth surfaces. Among lizards, some anoles have comparable adhesive ability, although with lower adhesive performance (Higham et al., 2017; Irschick et al., 1996). Numerous morphological changes, both internally and externally, have accompanied this specialized ability in geckos (Russell et al., 1997). For example, in addition to being secondarily symmetrical, the foot exhibits modified tendons and muscles as well as a series of blood sinuses that likely aid in adhesion (Russell, 2002). Pad-bearing geckos also exhibit the ability to rotate their secondarily symmetrical pes considerably during static clinging (Russell & Oetelaar, 2016) and locomotion (Birn-Jeffery & Higham, 2014, 2016). The significant changes in the structure of the pes and its orientation and function during locomotion in pad-bearing geckos suggest that the anatomy and function of the ankle joint is likely highly modified compared with that of “typical” lizards.

The ankle joint of lizards is architecturally intricate (Rewcastle, 1980; Russell & Bauer, 2008), with its highly sculpted juxtaposing surfaces (Rewcastle, 1980) rendering it arguably the most complex of all lacertilian diarthrotic joints. The ankle joint is situated between the proximal and distal tarsal rows, rendering it mesotarsal (Rewcastle, 1980) rather than crurotarsal (in which the joint is located between the crus and proximal tarsal row). The skeletal elements comprising the lacertilian ankle are the astragalocalcaneum, which constitutes the proximal tarsal row, and the fourth distal tarsal, which is the largest element of the distal tarsal row (Rewcastle, 1980; Russell & Bauer, 2008). The astragalocalcaneum is essentially immovably fixed to the elements of the crus (Landsmeer, 1990), and the fourth distal tarsal is closely associated with the other distal tarsals and the metatarsals (see below), which collectively have been recognized as a tarsometatarsus (Rewcastle, 1980; Russell & Bauer, 2008). As a result of the complexly sculpted articulating faces of the astragalocalcaneum and fourth distal tarsal, the latter can translate and rotate about the sellar tarsal facet of the astragalocalcaneum. The reciprocal geometry of these facets conjointly entrains flexion/extension and long-axis rotation of the pes in lizards that ancestrally lack adhesive toepads (Brinkman, 1980; Rewcastle, 1980).

Evolution of the configuration of the mesotarsal ankle joint in lacertilians (Romer, 1956) was accompanied by a reduction in the number of distal tarsals, with only the third and fourth remaining as independent units (Russell & Bauer, 2008). The pes is thus rendered asymmetrical (Rewcastle, 1980; Russell et al., 1997), the tarsus being narrower medially than laterally. As a result, the proximal end of the first metatarsal closely approaches the distomesial border of the astragalocalcaneum and forms a joint with it via a meniscus (Rewcastle, 1980; Russell & Bauer, 2008). The fourth distal tarsal is linked to the third and this couplet carries the articular facets for the metatarsals, thereby constituting a composite functional unit, the tarsometatarsus (Rewcastle, 1980; Russell & Bauer, 2008).

The fourth distal tarsal articulates with the fifth metatarsal, the latter receiving the insertions of the major pedal plantar flexor muscles (Brinkman, 1980; Rewcastle, 1980; Russell & Bauer, 2008)

that drive conjoint pedal plantar flexion and long-axis rotation (Rewcastle, 1980). Due to these indissociable motions at the ankle joint, adduction, and abduction of the pes on the crus cannot occur independently of flexion and extension. In nongeckotan lizards, even those that climb (Arnold, 1998), considerable pedal plantarflexion occurs during the stance phase of locomotion prior to pedal rotation that pivots the pes onto its shorter mesial border (Brinkman, 1980; Rewcastle, 1980; Russell & Bauer, 2008), raising the first to fourth metatarsals, and ultimately their associated digits, onto their distal tips.

As noted above, gekkotan lizards (except for the limbless pygopodids) depart from the typical morphology of the lacertilian pes (Russell et al., 1997), the foot instead being secondarily symmetrical (Figure 1), with digits of subequal length arrayed over a broad arc (often in excess of 180°) (Russell & Oetelaar, 2016) carried on foreshortened metatarsals that are subequal in length (Powell et al., 2018; Russell et al., 1997). The secondarily symmetrical configuration of the pes is most evidently expressed in geckos that bear subdigital adhesive pads (Russell et al., 1997; Zhuang et al., 2019). Biomechanically, pad-bearing geckos have a specialized pattern of digit motion, with the distal portions leaving the surface first at the end of stance when on an inclined surface (Supplementary Video; Russell & Higham, 2009). This alters the application of forces to the ground. When moving on horizontal surfaces the adhesive pads are held in a permanently hyperextended configuration (Figure 1a) (Russell & Higham, 2009), with those phalanges lying proximal to the pads operating, in a functional sense, as the most distal region of the autopodium, delivering thrust to the substratum (Russell & Higham, 2009). When climbing, however, the subdigital pads are deployed, engaging the adhesive apparatus. Even in these circumstances, the pads are hyperextended away from the surface prior to pedal plantar flexion at the ankle, and the more proximal regions of the digits impart the final phases of locomotor thrust (Russell, 2002, figure 3; Higham et al., 2015).

Additionally, pad-bearing geckos exhibit specific patterns of digit orientation when particular body orientations (head up, head down, and intervening stations between these—Russell & Oetelaar, 2016; Song et al., 2020) are adopted while clinging to vertical surfaces via adhesive attachment. Such postures (Russell & Oetelaar, 2016, figure 4; tables 2, 3) are accompanied by a broad range of abduction and adduction of the pes while the crus and thigh remain firmly adpressed to the substratum (Figure 1b,c). Such adjustments of digit orientation allow the optimization of clinging performance (Imburgia et al., 2019; Russell & Oetelaar, 2016; Song et al., 2020) regardless of body orientation or direction of travel. The ability to reorient the manus on the antebrachium is much more restricted (Russell & Oetelaar, 2016). The data presented by Russell and Oetelaar (2016, figure 4) indicate that, while clinging to a vertical surface, the pes long axis relative to that of the crus (representing adduction/abduction of the pes) describes an arc in excess of 50° as different orientations of the body are adopted, whereas the equivalent displacement of the long axis of the manus versus that of the antebrachium barely exceeds 20° of adduction/abduction. The difference between the

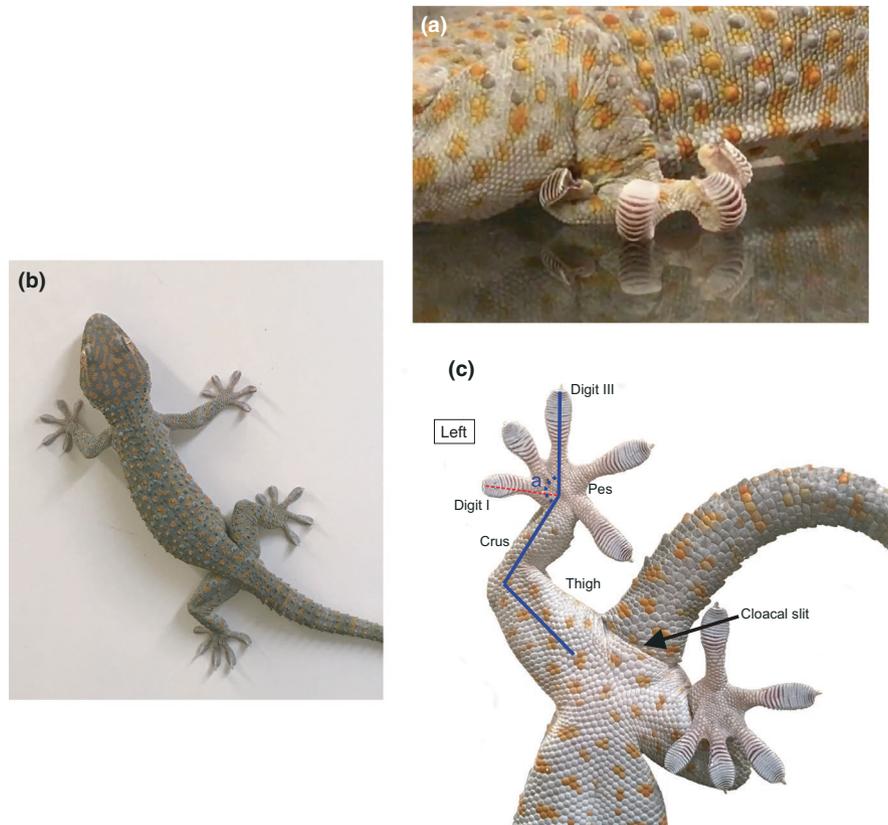


FIGURE 1 A still image from a video of *Gekko gecko* walking on a level glass surface, showing the hyperextended distal sectors of the digits that persist throughout the entire step cycle (a; also see Supplementary Video). Dorsal view of an individual of *G. gecko* holding position on a vertical surface (b). Ventral view of an individual of *G. gecko* adhering to the vertical wall of a glass terrarium (c). The gecko's head is pointing down. The image shows the different orientations taken up by the right and left hind feet even though the venter and hind limbs are firmly addressed to the terrarium wall and the long axes of the thighs are oriented essentially equally relative to the long axis of the cloacal slit. The ankle angle (148°), indicated as "a," measured between the long axis of the crus and that of digit III, is obtuse for the left pes, and the foot is abducted away from the long axis of the crus. When assessed against the transverse axis of the cloacal slit the long axis of digit III makes an angle of 119° and that of digit I (dashed yellow line) makes an angle of -30° . For the right pes, the ankle angle is acute (29°), and the right pes is adducted such that its long axis (as depicted by digit III) makes an angle of -14° with the cloacal slit, and the long axis of digit I makes an angle of -90° with that slit

left and right pes of a single individual clinging to vertical support by its adhesive apparatus can be extensive, as shown in Figure 1b,c, wherein it is 66° . Furthermore, during the descent of steep inclines, the pedal adhesive apparatus can assume a braking role by the digits being turned posteriorly (Birn-Jeffery & Higham, 2014) through pedal abduction in the absence of plantar flexion, further indicating the potential for decoupling of flexion/extension and long-axis rotation of the pes. These functional/behavioral observations are important as they likely indicate morphological changes that facilitate such abilities.

The above-mentioned observations suggest that in pad-bearing geckos, the conjoint flexion/extension and rotatory motions of the pes typical of lizards, in general, are less evident and that mesotarsal joint structure may depart from the condition documented for other lizards (Rewcastle, 1980; Russell & Bauer, 2008), permitting adduction and abduction of the pes somewhat independently of ankle flexion/extension and pedal long-axis rotation. We, therefore, predict that the structure of the mesotarsal joint of pad-bearing geckos will exhibit structural characteristics associated with the enhancement

(compared with that joint in non-gekkotan lizards) of mediolateral translation. To explore this, we compare the configuration of the mesotarsal joint of nongekkotan lizards (Rewcastle, 1980, 1983) with that of *Gekko gecko*, the species of gecko most extensively employed (from a wide variety of perspectives) in investigations of the structure and function of a seta-based adhesive system (Autumn, 2006; Autumn et al., 2000; Hansen & Autumn, 2005; Maderson, 1964; Rizzo et al., 2006; Ruibal & Ernst, 1965; Russell, 1975, 2002; Russell et al., 2019; Russell & Garner, 2021; Song et al., 2020; Stork, 1983; Xu et al., 2015; Yao & Gao, 2007).

2 | MATERIALS AND METHODS

To confirm the general aspects of the configuration of the lacertilian mesotarsal joint and its contributing elements we re-examined its structure in *Iguana iguana* and added *Pristidactylus achalensis* as another representative of the nongekkotan condition. These taxa were selected to be representative of what is currently known of

the structure of the mesotarsal joint of lizards in general (Rewcastle, 1980, 1983; Russell & Bauer, 2008). Rewcastle (1980) examined several genera of nongekkotans and found relatively minimal differences in mesotarsal joint structure. Therefore, the two species in our study represent the condition found across most lizards. The ankle joint of *Iguana iguana* was examined by observation of prepared skeletons (Russell & Bauer, 2008) and micro-computed tomographic (μ CT) scans employing the Scanco 35 and Scanco 40 (at a minimum of 5 μ m resolution) in the MicroCT Laboratory, Cumming School of Medicine, University of Calgary. Scanned specimens were juveniles. Specimens for μ CT were wrapped in cheesecloth moistened with ethanol and encased in Styrofoam to prevent movement and rotation of the specimen and ethanol evaporation from the sample chamber during long scanning periods (about 1 h per foot). Following processing of the scans, the foot was volumized and the astragalocalcaneum and fourth distal tarsal segmented in 3D Slicer, enabling 3D reconstructions.

The ankle of *Pristidactylus achalensis* was examined via scanning electron microscopy (SEM) because it is sufficiently small to permit SEM exploration and imaging of its fully articulated ankle. To achieve this, the crus and pes were excised from formalin-fixed, ethanol-preserved specimens (from the collection of APR) and the integument and musculature removed by dissection (with care being taken to retain ligaments that bind the skeletal elements together). The resulting preparations were dehydrated by immersion in a sequential series of ethanol baths (70%, 90%, 96%, 100%), air dried,

coated with high purity silver paint, and sputter coated with gold to a thickness of ~ 20 nm using a Sempreg2 sputter coater. The specimens were viewed with a Hitachi S-450 SEM in the Microscopy and Imaging Facility, Cumming School of Medicine, University of Calgary. Photomicrographs of appropriate regions of the preparations were amalgamated into composite images.

To establish the equivalent structural reference for the Tokay, *Gekko gecko*, similar μ CT scans and ligamentous preparations were made, employing identical preparatory and imaging methods to those outlined above. Tokay specimens were from the collections of APR. Additionally, the crura and pedes of previously frozen, thawed specimens were excised and positioned at five angles of opening of the ankle joint (0° , 45° , 90° , 135° , 180°) and subjected to μ CT scanning and 3D image reconstruction to enable assessment of displacement patterns at the mesotarsal joint.

3 | RESULTS

3.1 | Iguana and Pristidactylus

The structure of the ankle joint in *Iguana iguana* is illustrated in Figure 2 and the articulated ankle of *Pristidactylus* in Figure 3. The following descriptions are based upon information gained from both species and from the various methods of preparation and observation outlined above.

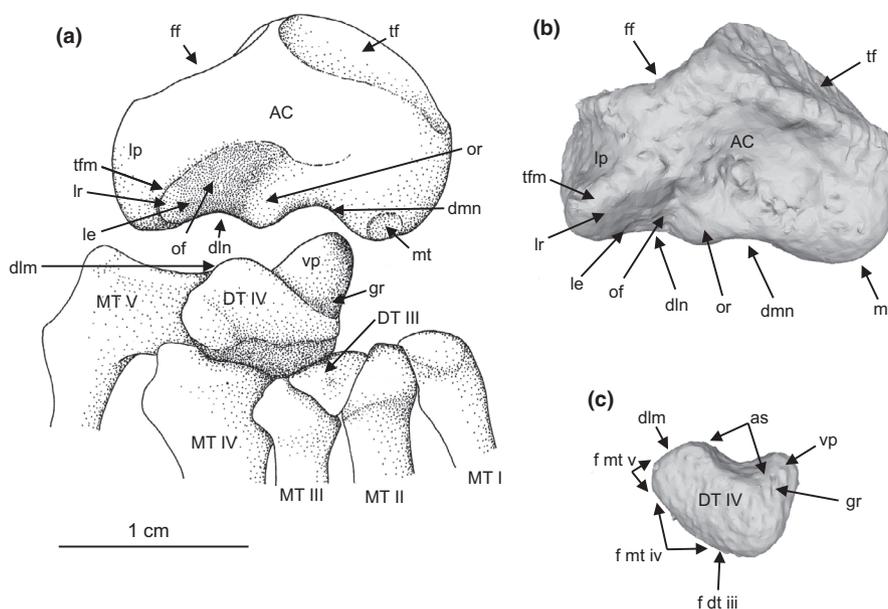


FIGURE 2 (a) Dorsal view of the right astragalocalcaneum and distal tarsal-metatarsal functional complex of *Iguana iguana* (redrawn from Rewcastle, 1980). The major features of the astragalocalcaneum (AC) and fourth distal tarsal (DT IV) are indicated. (b) Micro-computed tomographic scan reconstruction of the right astragalocalcaneum and (c) DT IV of a juvenile *Iguana iguana* in dorsal view. Abbreviations. Upper case abbreviations for skeletal elements. AC: astragalocalcaneum; DT III: third distal tarsal; DT IV: fourth distal tarsal; MT I-V: first to fifth metatarsals. Lower case abbreviations for structural components of skeletal elements: Features of the astragalocalcaneum: dln, distolateral notch; dmn, distomesial notch; ff, fibular facet; le, lateral expansion; lp, lateral process; lr, lateral rim of tarsal facet; mt, mesial tubercle; of, oblique furrow; or, oblique ridge; tf, tibial facet; tfrm, tarsal facet margin. Features of the fourth distal tarsal: dlm, dorsolateral margin; gr, groove; vp, ventral peg

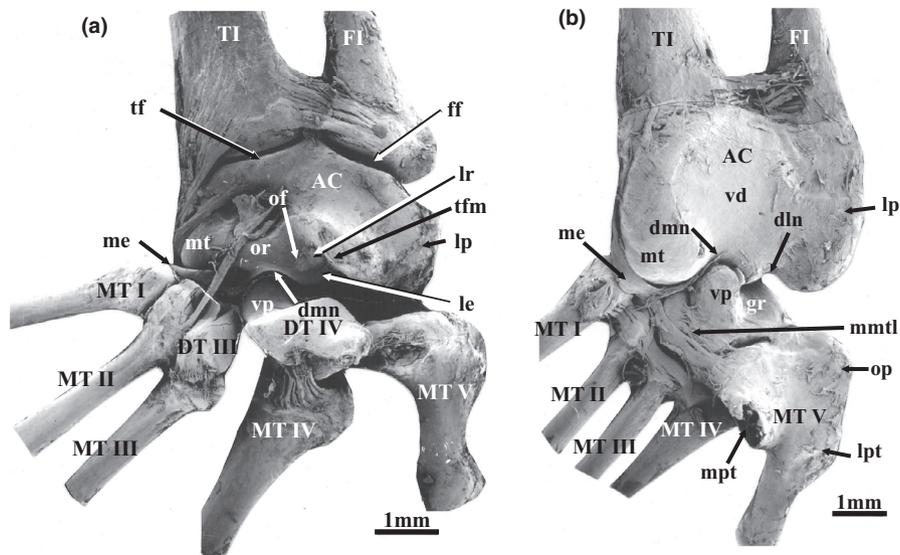


FIGURE 3 (a) Dorsal and (b) ventral view of ligamentous preparations of the skeleton of the left and right (respectively) ankle region of the iguanoid *Pristidactylus achalensis* (as assembled from composite scanning electron micrograph [SEM] images) showing the form and configuration of the mesotarsal joint. Abbreviations: Upper case abbreviations for skeletal elements. AC: astragalocalcaneum; DT III: third distal tarsal; DT IV: fourth distal tarsal; FI: fibula; MT I–V: first to fifth metatarsals; TI: tibia. Lower case abbreviations for structural components of skeletal elements and associated soft tissues: Features of the astragalocalcaneum: dln, distolateral notch; dmn, distomesial notch; ff, fibular facet; le, lateral expansion; lp, lateral process; lr, lateral rim of tarsal facet; mt, mesial tubercle; of, oblique furrow; or, oblique ridge; tf, tibial facet; tfm, tarsal facet margin; vd, ventral depression. Features of the fourth distal tarsal: vp, ventral peg. Features of the fifth metatarsal, lpt, lateral plantar tubercle; mpt, mesial plantar tubercle; op, outer process. Soft tissue features: me, meniscus; mmtl, meniscometatarsal ligament

The astragalocalcaneum (AC) is a depressed element (Figure 2a,b). Ventrally, it bears a large suboval depression (Figure 3b) that extends to the distal margin of the element where it becomes the tarsal facet (Figure 2a), forming the proximal face of the mesotarsal joint. The tarsal facet (tf) is complexly sculpted into a series of ridges and grooves (Figure 2a,b) and is divided by an oblique furrow (of) into a lateral expansion and a mesial oblique ridge (or; Figures 2, 3a). The lateral expansion (le; Figure 2) is suboval in outline on its lateral face, with a subtly convex surface that curves from the distal margin of the bone to its dorsal surface (Figure 2). The lateral rim (lr; Figures 2a,b, 3a) of this expansion bears a slightly convex lip that diminishes dorsally and ventrally. The lateral expansion is separated from the mesial oblique ridge by a rounded oblique groove (Figure 2) that crosses the distal margin of the astragalocalcaneum in a distolateral to proximomedial direction. The mesial oblique ridge (Figures 2a,b, 3a) is rounded, parallels the oblique groove, and projects somewhat distally, thereby forming the protruding margin between the distomesial (dmn) and distolateral (dln) notches (Figures 2a,b, 3a,b) on the distal border of the astragalocalcaneum. The former of these notches is the largest and receives the ventral peg (vp) of the fourth distal tarsal (DT IV; Figures 2a, 3a,b). The articulating surfaces between the astragalocalcaneum and the fourth distal tarsal form an interlocking system of ridges and grooves (Figure 2a) that dictate the movements at the mesotarsal joint (Rewcastle, 1980). With reference to the ventral peg of the fourth distal tarsal (Figures 2a,b, 3a), the ridge and groove (gr) on its proximal aspect are arranged essentially concentrically, crossing from ventrolateral to dorsomesial

(Figure 2a,b). The form of the articulation between the astragalocalcaneum and fourth distal tarsal necessitates that during the latter stages of ankle flexion/extension, this movement of the pes is accompanied by its conjunct long-axis rotation. Details of the mechanics of the lacertilian mesotarsal joint, as exemplified by *Iguana* and *Pristidactylus*, are provided by Rewcastle (1980) and Russell & Bauer (2008: 177–178).

The distomesial margin of the astragalocalcaneum is thickened, rounded, and bears the mesial tubercle (mt; Figures 2a,b, 3a,b) which forms the articular surface for the proximal extremity of the first metatarsal via an intervening meniscus (me) (Russell & Bauer, 2008). Its lateral margin extends ventrolaterally as the flange-like lateral process (lp; Figures 2a,b, 3a,b), around which pass, dorsally and ventrally, respectively, the tendons of the peroneus brevis and peroneus longus muscles (Russell & Bauer, 2008).

The fourth distal tarsal is irregularly shaped (Figure 2a,c). It is broadest proximally and narrows distally, but the difference in width between the proximal and distal margins is not great (Figures 2a,c, 3a). Proximally, it bears a complex facet for articulation with the astragalocalcaneum. Its proximoventral margin is produced into a prominent conical ventral peg (Figures 2a,c, 3a,b) that interdigitates with the distomesial notch (Figures 2a,b, 3a,b) of the astragalocalcaneum. The dorsolateral margin (dlm) of the proximal surface of the fourth distal tarsal (Figure 2a) is expanded into a complexly contoured surface that mirrors the surface of the lateral expansion of the tarsal facet of the astragalocalcaneum, along which it is displaced during flexion and extension of the ankle joint.

The facet for the fifth metatarsal (Figures 2a,c, 3a) lies on the ventrolateral margin of the fourth distal tarsal, and the facet for the fourth metatarsal lies dorsal and somewhat distal to the latter (Figures 2a,c, 3a). The facet for the third distal tarsal (Figure 2a,c) is a broad concavity on the ventral aspect of the distomesial surface of the fourth distal tarsal. The proximal head of the second metatarsal does not contact, or only marginally contacts, the third distal tarsal (Figures 2a, 3a) and shares, with the proximal head of the first metatarsal, a meniscally mediated articulation with the distomesial border of the astragalocalcaneum (Figure 3a,b).

3.2 | Gekko

The astragalocalcaneum of *Gekko* (Figure 4) is a depressed element, but less so than that of *Iguana* and *Pristidactylus*, and is much more intensely sculpted. Its fibular facet (ff) is similarly more deeply incised than the tibial facet (Figure 4a,b) and, as in *Iguana* and *Pristidactylus* (Figure 2a,b), these two facets meet at a sharp crest separating them proximally. The ventral depression of the astragalocalcaneum of *Gekko* is suboval in outline, sharply set off from the raised

ventromesial border of this element (Figure 4b, d) and opens onto the distal face of the astragalocalcaneum (Figure 4b,d). At its lateral side the ventral depression blends with the built-up tarsal facet, which is demarcated by a conspicuous margin (Figures 4a,b, 5a). Like the tarsal facet of *Iguana* and *Pristidactylus*, that of *Gekko* is molded into a series of ridges and grooves (Figure 4a,c,d). It is divided by an oblique furrow (which parallels the lateral expansion from distolateral to proximomesial) (Figure 4a) into a suboval, elongate lateral expansion, and a more mesial oblique ridge (Figures 4a,c, 5a), the latter being less pronounced than that of *Iguana*. The lateral expansion is sharply demarcated from the lateral rim of the tarsal facet and bears a steep face at its distal extremity (Figure 4a). Distally, it lies adjacent to a very small, shallow distolateral notch (Figure 4a). The distomesial notch (Figures 4a–d, 5a), in contrast, is markedly enlarged, semicircular in outline, deeply incised compared with that of *Iguana* and *Pristidactylus* (Figures 2, 3) and demarcated by a distinct rim on its dorsal perimeter (Figure 4a,d). It merges with the tarsal facet margin (tfm) laterally, extending more broadly across the lateromedial width of the astragalocalcaneum and is essentially contiguous with the small posterodistal notch (Figure 4a), there being no noticeable protuberance between them. The entirety of the distal

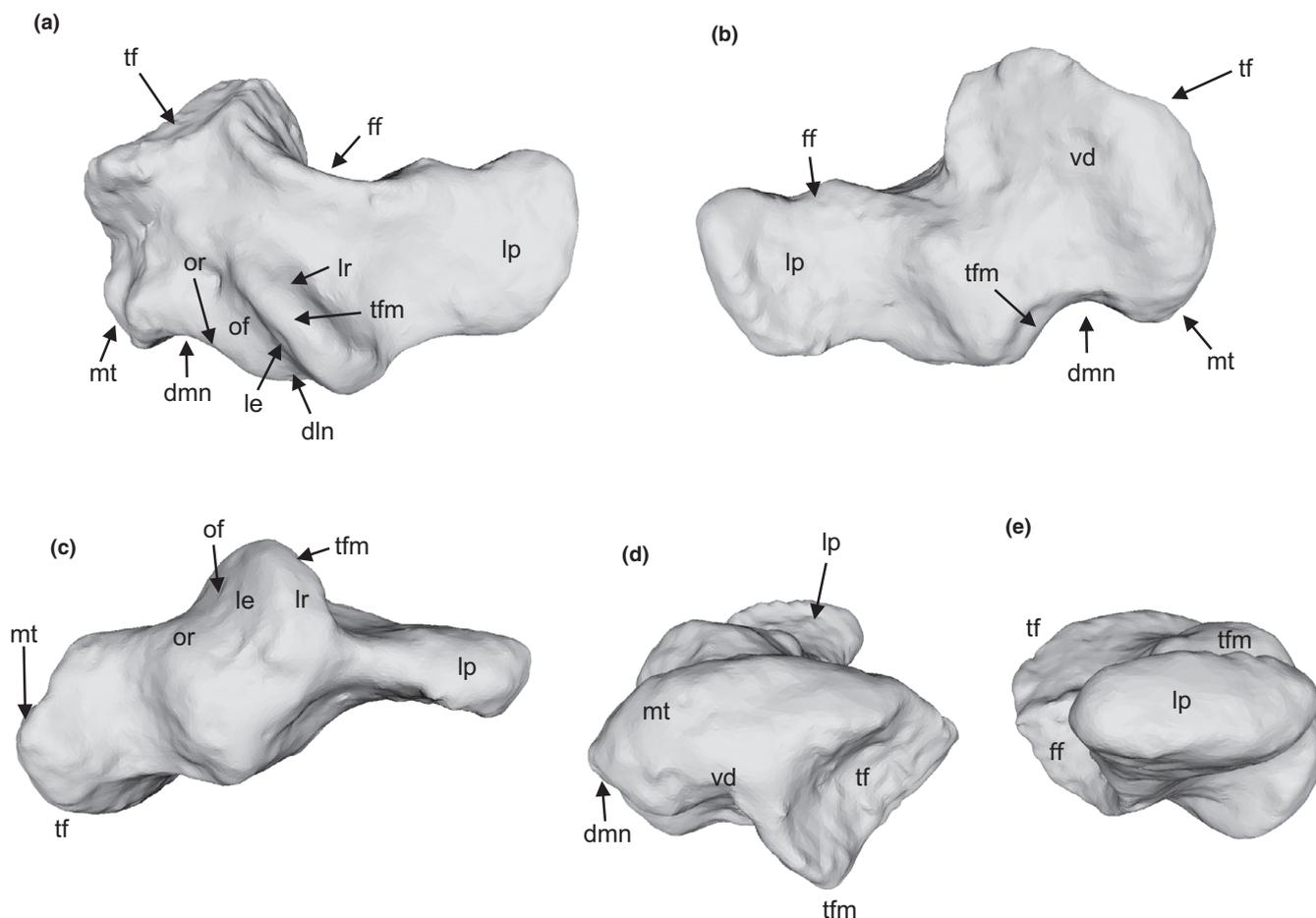


FIGURE 4 Micro-computed tomographic scan reconstruction of the left astragalocalcaneum of *Gekko gekko* in (a) dorsal, (b) ventral, (c) distal, (d) mesial, and (e) lateral views. Abbreviations, dln, distolateral notch; dmn, distomesial notch; ff, fibular facet; le, lateral expansion; lp, lateral process; lr, lateral rim of tarsal facet; mt, mesial tubercle; of, oblique furrow; or, oblique ridge; tf, tibial facet; tfm, tarsal facet margin; vd, ventral depression

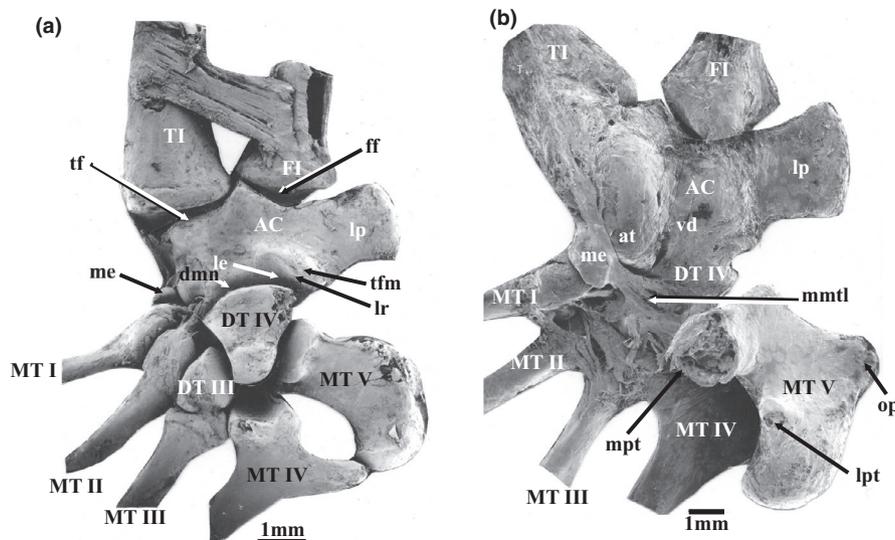


FIGURE 5 (a) Dorsal and (b) ventral view of ligamentous preparations of the skeleton of the left and right (respectively) ankle region of *Gekko gecko* (as assembled from composite scanning electron micrograph [SEM] images), showing the form and configuration of the mesotarsal joint. Abbreviations: Upper case abbreviations for skeletal elements. AC: astragalocalcaneum; DT III: third distal tarsal; DT IV: fourth distal tarsal; FI: fibula; MT I–V: first to fifth metatarsals; TI: tibia. Lower case abbreviations for structural components of skeletal elements and associated soft tissues: Features of the astragalocalcaneum: dm, distomesial notch; ff, fibular facet; le, lateral expansion; lp, lateral process; lr, lateral rim of tarsal facet; tf, tibial facet; tfm, tarsal facet margin; vd, ventral depression. Features of the fifth metatarsal: lpt, lateral plantar tubercle; mpt, mesial plantar tubercle; op, outer process. Soft tissue features, me, meniscus; mmtl, meniscometatarsal ligament

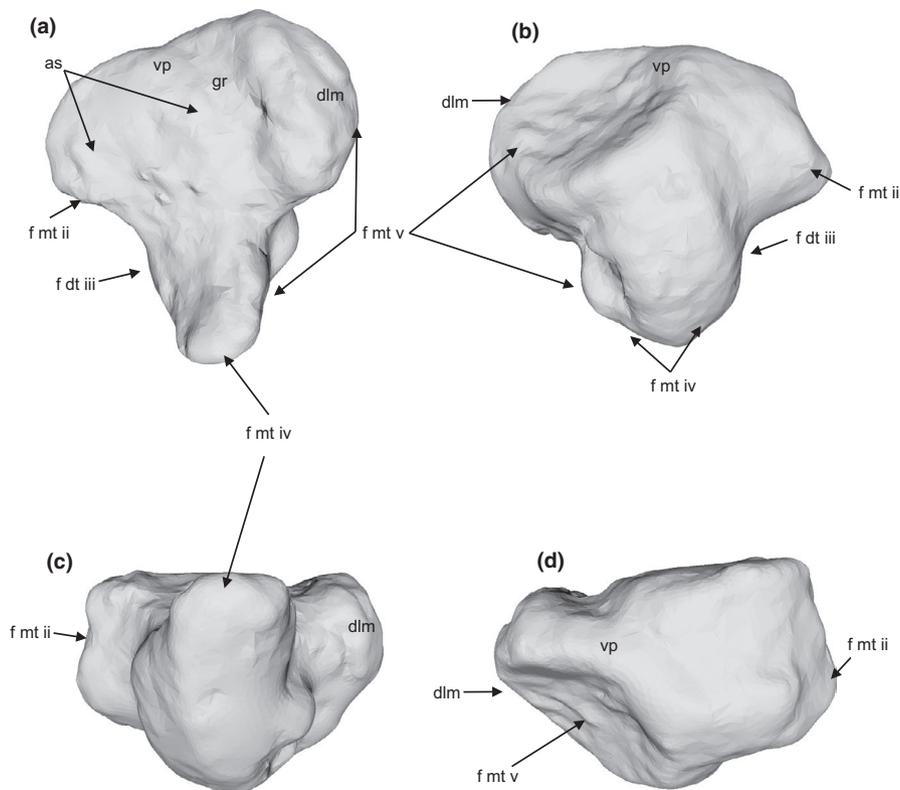


FIGURE 6 Micro-computed tomographic scan reconstruction of the right fourth distal tarsal of *Gekko gecko* in (a) dorsal, (b) ventral, (c) distal, (d) proximal views. Abbreviations: as, articular surface for contact with the distomesial notch of the astragalocalcaneum; dlm, distolateral margin; gr, groove; f dt iii, facet for the third distal tarsal; f mt III–V, m facets for the third, fourth, and fifth metatarsals; vp, ventral peg

articular face of the astragalocalcaneum thus constitutes an essentially continuous, undivided, expansive surface (Figure 4a–c) for receipt of the large proximal articular facet of the fourth distal tarsal. The large distomesial notch extends relatively much closer to the mesial border of the astragalocalcaneum (Figure 4a) than is the case in *Iguana* and *Pristidactylus* (Figures 2, 3). Overall, there is a much greater definition of the features of the astragalocalcaneal surfaces of the mesotarsal joint than is the case in *Iguana* and *Pristidactylus* (Figures 2, 4). In the latter, two taxa those surfaces flow more gently into one another and blend more gradually with the dorsal and ventral surfaces of the element (Figure 2).

In *Iguana*, *Pristidactylus*, and *Gekko* the distomesial notch of the astragalocalcaneum interdigitates with the ventral peg of the fourth distal tarsal (Figures 2a, 3a,b, 5a), and in all three, there is a matching of the articular surfaces of these two elements. In *Gekko*, however, the broad proximodorsal articular surface of the fourth distal tarsal (Figures 5a, 6a) is accommodated by the much more expansive distomesial notch (Figures 4a–c, 5a). The essentially semicircular proximodorsal articular surface of the fourth distal tarsal (Figure 5a) matches the anterodorsal outline of the distomesial notch of the astragalocalcaneum, permitting mediolateral displacement of the fourth distal tarsal on the astragalocalcaneum, ostensibly independently of pedal plantar flexion and the associated long-axis rotation of the former, which are inextricably entrained displacements in *Iguana* and *Pristidactylus*. The mesotarsal joint of *Gekko* thus exhibits a morphology that indicates greater independence of long-axis rotation and abduction/adduction than is evident in *Iguana* and *Pristidactylus*.

Although the width to length ratio of the astragalocalcaneum is similar in *Iguana* and *Gekko* (1.5× mediolaterally wider than proximodistally long in the former and 1.4× in the latter) (Figures 2a,b, 4a,b), the relative position and proportion of key features are notably different. In *Gekko*, the relatively truncated mesial portion (the distance between the mesialmost extent of the distomesial notch and the mesial boundary of the element) results in the distomesial margin of the distomesial notch being positioned almost at the distomesial edge of the astragalocalcaneum (Figures 4a,b, 5a). In *Iguana* and *Pristidactylus*, the mesialmost extent of the anterodistal notch is situated considerably further laterally (Figures 2, 3) and the distance between the lateralmost point of the fourth distal tarsal and the proximal head of the first metatarsal is relatively much greater (Figures 3a,b, 5a). On the lateral aspect of the astragalocalcaneum, the lateral process of *Gekko* (Figures 4a,b, 5a,b) is much more blade-like than that of *Iguana* and *Pristidactylus* (Figures 2a,b, 3a,b), and projects relatively much further laterally with reference to the lateral expansion of the tarsal facet and the lateralmost extent of the fibular facet (Figures 2, 4a,b). This has a direct relationship to the positional relationships and form of the fifth metatarsal, fourth distal tarsal, and astragalocalcaneum (see below).

The fourth distal tarsal of *Gekko* (Figure 6), like that of *Iguana* and *Pristidactylus*, is irregularly and complexly shaped. In dorsal view, its body is broadest proximally, with its proximal articular margin being gently curved (Figures 5a, 6a), mirroring the distal

curved margin of the anterodistal notch of the astragalocalcaneum (Figure 4a). In contrast, the proximal articular margin of the fourth distal tarsal of *Iguana* and *Pristidactylus*, when seen in dorsal view (Figures 2a, 3a), is diamond-shaped and its mediolateral width is considerably greater than its proximodistal length. The angular nature of its proximal border (Figures 2a, 3a) provides interlocking contact with the anterodistal notch of the astragalocalcaneum and reduces the facility for mediolateral translation in this notch independent of movement about the flexion–extension arc at the ankle joint. Distally, the fourth distal tarsal of *Gekko* narrows to a blunt-tipped wedge (Figures 5a, 6a) which is slotted into an extensive v-shaped facet on the proximomesial aspect of the proximal head of the fourth metatarsal (Figure 5a), effectively locking these two elements together. On its distomesial face, the fourth distal tarsal carries articular facets for the third distal tarsal and the proximal head of the second metatarsal (Figure 6a,b,d). Distolaterally, the articular facet for the fifth metatarsal is extensive and heavily excavated (Figure 6b). The expansive proximal articular facet of the fifth metatarsal (Figure 5a,b) undercuts the proximolateral aspect of the ventral face of the fourth distal tarsal (Figure 6b) such that there is extensive overlap between these two elements.

Laterally, the fourth distal tarsal of *Iguana* and *Pristidactylus* articulates relatively narrowly with the proximal head of the fifth metatarsal (Figures 2a, 3a), distally with the relatively narrow proximal head of the fourth metatarsal by way of an interdigitation (Figures 2a, 3a) and distomesially with the third distal tarsal (Figures 2a, 3a). There is no, or only a very limited, articular contact between the proximal head of the second metatarsal and the fourth distal tarsal, and the proximal heads of the third, fourth, and fifth metatarsals are much less closely integrated with each other than they are in *Gekko* (Figures 2a, 3a, 5a).

Proximally, ventral to the smoothly curved articular surface of the main body of the fourth distal tarsal of *Gekko*, this element extends posteriorly as a ventral peg set off by a transverse groove (Figure 6a), as is the case in *Iguana*. In *Gekko*, however, this ventral peg is relatively very short (Figure 6a). The dorsolateral margin of the fourth distal tarsal (Figure 6a–d) is built up into a more prominent process than is the case in *Iguana* (Figure 2a) and *Pristidactylus*, making up the dorsolateral margin of the element and standing proud of its broad, smooth proximal articular surface (Figure 6a). The lateral face of this dorsolateral margin articulates with the lateral expansion of the tarsal facet of the astragalocalcaneum (Figures 4a, 5a, 6a) and its ventral surface is accommodated by the oblique furrow of the latter (Figure 4a,c). The anterodistal notch courses posteroventrally (Figure 4b,d) and provides a narrowing channel toward which the short ventral peg of the fourth distal tarsal (Figure 6a) is displaced as the pes plantarflexes upon ankle extension (Figure 7).

As noted above, the fourth distal tarsal of *Gekko* articulates broadly with the proximal head of the fifth metatarsal via an extensive articular facet that encroaches far ventrally (Figure 5a). The greatly expanded proximal head of the fourth metatarsal articulates via a wedge-like articulation with the distal end of the fourth distal tarsal and with both the proximomedial and distomedial extremities

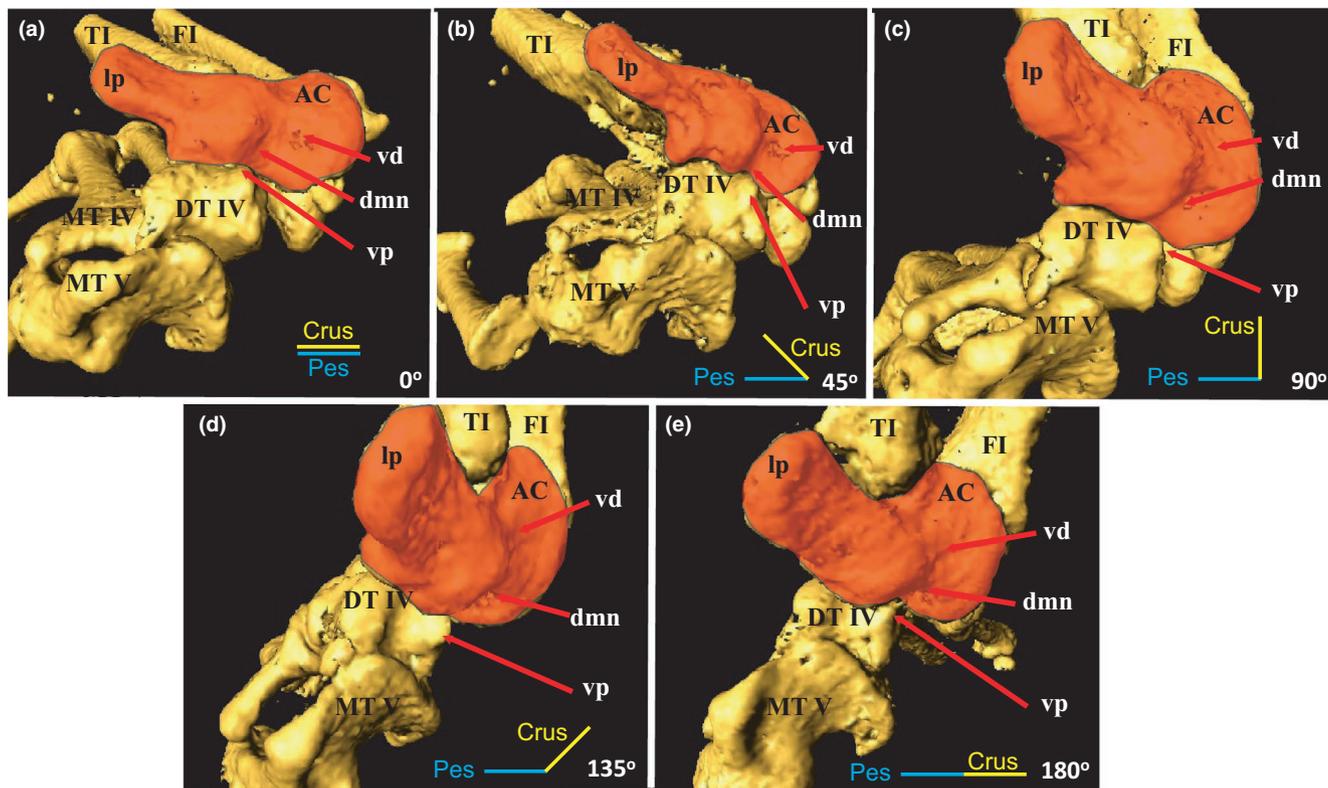


FIGURE 7 Micro-computed tomographic scan reconstruction of the left ankle of *Gekko gecko* in posterior view at different stages of ankle extension (simulating the stages of pedal plantar flexion) (a) 0°, (b) 45°, (c) 90°, (d) 135°, (e) 180°. The small insets below the images depict the relative positions of the pes (in blue) and crus (in yellow) at different stages of ankle extension. The astragalocalcaneum (AC) is highlighted in orange for visibility. Panels (a) and (b) depict positions of the pes and crus when the animal is clinging to a surface via its adhesive apparatus, with the crus flexed over the fixed foot (as depicted in Figure 1). Panels (c) and (d) depict displacements of the skeletal elements as pedal plantar flexion occurs and the ankle opens. Panel (e) represents full ankle extension. Throughout this series of images, the ventral peg (vp) of the fourth distal tarsal transitions from being unconstrained by the ventral extension of the distomesial notch (dmn) of the AC to being further enveloped by its walls. In panels (a) and (b), the broad articular facet of the fourth distal tarsal (DT IV; see Figure 6a) is free to translate mediolaterally in the distal aspect of the distomesial notch of the AC. As further opening of the ankle joint occurs (during pedal plantar flexion), the vp of the DT IV becomes more closely applied to the walls of the distomesial notch of the AC, which entrains long-axis rotation of the DT IV (and thus the entire pes) along with increased opening of the ankle. Abbreviations: Upper case abbreviations for skeletal elements. FI, fibula; MT IV–V, fourth and fifth metatarsals; TI, tibia. Lower case abbreviations for structural components of skeletal elements: lp, lateral process; vd, ventral depression

of the fifth metatarsal (Figure 5a). The third distal tarsal articulates with the distomesial face of the fourth distal tarsal and the proximal heads of all five metatarsals are closely interlinked (Figure 5a). This arrangement of the fourth and third distal tarsals and their intimate connections with the proximal heads of all five metatarsals creates a linked set of elements able to be displaced as a unit on the smooth, rounded articulation between the broad proximodorsal articular facet of the fourth distal tarsal (Figure 6a) and the commodious anterodistal notch of the astragalocalcaneum (Figure 4a,b,d). The blade-like lateral process of the astragalocalcaneum and the broadly expanded proximolateral head of the fifth metatarsal (Figure 5a,b), its outer process (op; Figure 5b), respectively, provides for the origin and insertion of the adductor digiti quinti muscle that abducts the pes. The equivalent aspects of *Iguana* and *Pristidactylus* are relatively much less prominent (Figures 2a, 3).

Figure 7 depicts the pattern of displacement of the fourth distal tarsal on the astragalocalcaneum in *Gekko* as the ankle goes from

being fully flexed to fully extended, simulating the motions that occur during pedal plantar flexion. Pad-bearing geckos, however, also have the ability to flatten the thigh and crus against the substratum when adhering to a vertical surface (Figure 1), meaning that the pes can be extended on the crus and the pes still be abducted and adducted relative to the crus in such situations (Figure 1). Only by dissociation of adduction/abduction from long-axis rotation of the pes are such postures possible. The relatively small amount of long-axis rotation that occurs at the mesotarsal joint upon pedal plantar flexion in *Gekko* (Russell, 2002: figure 3), results only modestly of the raising the pes onto its mesial border as the foot plantar flexes. Instead, the pad-bearing distal zones of the digits are hyperextended away from the substratum, sequentially from digit V to digit I, prior to the commencement of pedal plantar flexion, with the proximal part of the pes then being raised from the substratum without pivoting onto its mesial border. Thus, the displacement patterns of the pes during pedal plantar flexion typical of lizards with asymmetrical

pedes (Brinkman, 1980; Rewcastle, 1980, 1983) are not prominent in pad-bearing geckos, and adduction/abduction of the pes predominates over long-axis rotation. The short ventral peg of the fourth distal tarsal does not engage deeply with the distomesial notch of the astragalocalcaneum and its ventral, channel-like extension (Figure 7), thus enabling adduction/abduction of the pes to be largely dissociated from pedal long-axis rotation. As the ankle of *Gekko* opens (Figure 7) the short ventral peg of the fourth distal tarsal becomes driven toward the ventral extension of the distomesial notch of the astragalocalcaneum, but the entrainment of the displacement of the former by the latter is modest.

4 | DISCUSSION

Our prediction that we would discover structural changes in the ankle joint of *Gekko gekko* compared with the anatomical configuration documented for non-gekkotan lizards (Rewcastle, 1980, 1983) was borne out, the differences being substantial. They are consistent with enhancement of mediolateral translation at this joint. Indeed, differences go beyond changes to the mesotarsal joint and are also encountered in the overall structure of the astragalocalcaneum, fourth distal tarsal, and the entire tarsometatarsus. *Gekko gekko* is the gekkotan species most extensively employed in investigations of the functional and structural features associated with a seta-based adhesive system (Autumn, 2006; Autumn et al., 2000; Hansen & Autumn, 2005; Maderson, 1964; Rizzo et al., 2006; Ruibal & Ernst, 1965; Russell, 1975, 2002; Russell et al., 2019; Russell & Garner, 2021; Song et al., 2020; Stork, 1983; Xu et al., 2015; Yao & Gao, 2007). We predict, however, that similar features will be found across pad-bearing geckos, although configurations may vary because adhesive toe pads have arisen multiple times within the Gekkota (Gamble et al., 2012, 2017; Russell & Gamble, 2019).

4.1 | General aspects of lacertilian ankle form and function

Distal tarsals III and IV and metatarsals I–IV of lizards comprise a distinct functional unit, the tarsometatarsus (Rewcastle, 1980; Russell & Bauer, 2008). Its constituent elements are bound together by their mutual articulations and by distinct sets of ligaments (Rewcastle, 1980; Russell & Bauer, 2008) that collectively greatly constrain movement between them. Metatarsal V is functionally and morphologically a distinct entity that is linked to the tarsometatarsus (Robinson, 1975) but able to move independently of it. The peroneus complex is responsible for moving the fifth metatarsal on the fourth distal tarsal. The peroneus brevis inserts onto the dorsal aspect of the outer process of the fifth metatarsal (Figure 3) and abducts this element (Brinkman, 1980; Rewcastle, 1980), whereas the peroneus longus inserts onto the dorsal aspect of the shaft of the fifth metatarsal and adducts it (and its associated digit). The shafts of

metatarsals I–IV are arranged essentially parallel to each other and are of differential lengths such that their distal tips lie in a straight line (the metatarsophalangeal line) that is oriented perpendicular to the body long axis when the pes is placed onto the substratum during locomotion (Rewcastle, 1980, 1983). The patterns of displacement of the pes throughout the locomotor cycle are governed by the opposing faces of the mesotarsal joint, whereby the fourth distal tarsal (the freely articulating part of the tarsometatarsus) displaces relative to the astragalocalcaneum (Rewcastle, 1980). During the later stages of the stance phase of locomotion, the pes moves relative to the crus (of which the astragalocalcaneum, although developmentally a part of the tarsus, makes up its distalmost component), with the pes being raised onto the distal tips of metatarsals I–IV (and the ventral surfaces of their associated digits) during pedal plantar flexion. Displacement of distal tarsal IV relative to the astragalocalcaneum results in conjunct rotation and extension (= plantarflexion) due to the interlocking, interdigitating ridge, and groove system of the mesotarsal joint, with the amount of rotation at the ankle being directly and indissociably related to a given amount of extension (Rewcastle, 1980, 1983; Russell & Bauer, 2008).

4.2 | Variation in ankle morphology among nongekkotan lizards

Although details about the form and mechanics of the lizard mesotarsal joint are not plentiful (Russell & Bauer, 2008), Rewcastle's (1980) comparative survey indicates that its morphology, as seen in *Iguana*, pertains broadly across the lacertilian phylogeny. Rewcastle's examination of *Basiliscus* (Corytophanidae), *Uromastix* (Agamidae), *Tupinambis* (Teiidae), *Timon* (= *Lacerta*) (Lacertidae), *Heloderma* (Helodermatidae), and *Varanus* (Varanidae) revealed no major differences (Rewcastle, 1980). Of these taxa, *Varanus* was found to be the most deviant in that movement at this joint is more restricted than in the others (Rewcastle, 1980). Both *Varanus* and *Heloderma* exhibit a lateral process of the astragalocalcaneum that is laterally more extensive than that of the other genera examined (Rewcastle, 1980), but no functional explanation relating to this difference has been proffered (Russell & Bauer, 2008). The unitary nature of the tarsometatarsus and the relative independence of the fifth metatarsal was found to be common to all of the genera investigated by Rewcastle (1980). The fifth metatarsal, with its proximal end lying ventral to the unitary tarsometatarsus, takes on a heel bone role in this arrangement, with the femoral gastrocnemius muscle, inserting on its mesial and lateral plantar tubercles (lpt) (Figure 3), extending the pes on the crus when stimulated (Rewcastle, 1980). This raises the proximolateral border of the pes and presses its distomesial border against the substrate, these displacements being mediated through the mesotarsal joint. As a result, the pes rises onto the distal tips of the first to fourth metatarsals (Rewcastle, 1980; Vialleton, 1924). These findings indicate that a mesotarsal joint that simultaneously entrains rotation and extension at the ankle is ancestral for lizards (Russell & Bauer, 2008).

4.3 | The ankle of *Gekko gekko* in relation to locomotion

The astragalocalcaneum and fourth distal tarsal of *Pristidactylus achalensis* (Figures 3a, 4a) display great similarity to those of *Iguana iguana* (Figure 1) but differ markedly from those of the Tokay, *Gekko gekko* (Figures 3b, 4b). In the latter, the lateral process of the astragalocalcaneum is much more extensive (Figure 3b); the tarsal facet is extended more broadly across the lateromedial width of the astragalocalcaneum (Figure 3b); the dorsolateral margin of the fourth distal tarsal is less extensive and less sharply deviant from the remainder of its proximal border (Figure 3b); the fourth distal tarsal is proximodistally relatively longer and articulates broadly with the second metatarsal as well as the third, fourth, and fifth (Figure 3b); the articular facet between the fourth distal tarsal and the fifth metatarsal is relatively much more extensive (Figure 3b); the mesial tubercle of the astragalocalcaneum is more distinctively set off from the ventral depression (Figure 4b); and the expanded lateral region of the proximal head of the fourth metatarsal articulates directly with the medial aspect of the distal end of the fifth metatarsal (Figures 3b, 4b).

All of the above-mentioned differences in *Gekko gekko* are expressed in association with modifications of the metatarsus and digits that render the pes of pad-bearing geckos secondarily symmetrical (Russell et al., 1997). The digits are of subequal length, rather than becoming progressively longer from the first to the fourth, this resulting from changes in the proportions of the metatarsals and the phalanges (Russell et al., 1997). The digits are arrayed about a broad arc (Russell et al., 1997; Russell & Oetelaar, 2016), rather than the first four being subparallel and the fifth being highly deviant from these. The digits exhibit the ability to be abducted and adducted with reference to each other (Russell & Oetelaar, 2016) such that the arc over which they are spread can be increased or decreased in association with body orientation (Russell & Oetelaar, 2016). These changes in digit proportions, orientation, and relative placement are associated with changes in the way in which the digits are deployed during locomotion. The relatively small amount of long-axis rotation that occurs at the mesotarsal joint upon pedal plantar flexion in *Gekko* (Russell, 2002: Figure 3), results in a marked diminution of the raising the pes onto its mesial border as the foot plantarflexes. Instead, the pad-bearing distal zones of the digits are hyperextended away from the substratum, sequentially from digit V to digit I, prior to pedal plantar flexion commencing, with the proximal part of the pes then being raised from the substratum without conspicuous pivoting onto its mesial border. Thus, the displacement patterns of the pes during pedal plantar flexion that is typical of lizards with asymmetrical pedes (Brinkman, 1980; Rewcastle, 1980, 1983) are not prominent in pad-bearing geckos, and adduction/abduction of the pes predominates over long-axis rotation.

The enhancement of abduction and adduction of the pes and the dissociation of these displacements from flexion and extension at the ankle joint are related to skeletal modifications. The mesotarsal joint exhibits a modified structure, with a reduced ventral peg

on the fourth distal tarsal, an articular pattern dominated by a well-defined, expansive distomesial notch of the astragalocalcaneum, and an associated broad proximodorsal articular facet of the fourth distal tarsal. This configuration permits dissociation of long-axis rotation of the pes from flexion to extension movements and provides a broad surface for translation of the proximodorsal articular facet of the fourth distal tarsal across the essentially semicircular distomesial notch of the astragalocalcaneum. Increased consolidation of the tarsometatarsus is evident in the following ways (Figure 5): close connectivity of the proximal heads of the metatarsals; broad expansion of the proximal head of the fourth metatarsal and its wedge-like interlocking with the distal extremity of the fourth distal tarsal; extensive connectivity (at two locations) between the proximal head of the fourth metatarsal and the fifth metatarsal (also noted by Mitchell, 1965 in the pad-bearing gekkonid gecko *Gehyra*); and extensive overlapping articulation between the fourth distal tarsal and the proximal head of the fifth metatarsal. These changes, relative to the condition exhibited by *Iguana* and *Pristidactylus* (Figure 3), integrate the fifth metatarsal much more fully into the unified tarsometatarsus.

The fifth metatarsal and its relationship to the mesotarsal joint is critical to the movements that occur at this articulation (Rewcastle, 1980, 1983; Robinson, 1975; Russell & Bauer, 2008; Schaeffer, 1941). In *Gekko gekko*, input from the peroneus muscle complex is able to abduct the entire pes through insertion onto the enlarged mesial and lateral plantar tubercles of the fifth metatarsal (Figure 5), the resultant displacement is transferred to the fourth distal tarsal via the greater connectivity between, and integration of, the fourth and fifth metatarsals. Abduction of the entire pes, by way of the fully integrated tarsometatarsus, is further enhanced by the greatly extended lateral process of the astragalocalcaneum (Figure 5), this being associated with the increased prominence of the outer process of the fifth metatarsal (Figure 5). The extension of the lateral process of the astragalocalcaneum provides the origin for pedal abductors, chief among which is the abductor digiti quinti (Russell, 1975; Russell & Bauer, 2008). This inserts on the outer process of the fifth metatarsal. The increased displacement of the origin of this muscle from the mesotarsal joint (at the distomesial notch) and the closer proximity of this articulation to the mesial border of the astragalocalcaneum (compare Figures 3 and 5) enhance the mechanical advantage of the abductors, as does the relatively increased size and subdivision into two parts (seemingly uniquely among lizards) of the abductor digiti quinti (Russell, 1975; Russell & Bauer, 2008).

4.4 | Future directions

Our study focuses on *Gekko gekko*, given the extensive body of research employing this species in investigations of the adhesive system. Future research should examine whether such differences (and their extent) apply to the Gekkotans as a whole, or more restrictively to those gekkotans that bear a subdigital adhesive apparatus (including, possibly, those that have secondarily reduced or lost this). This

will require a more comprehensive survey. The structure of the ankle joint and the associated tarsometatarsus may provide insights into interpretations of whether particular lineages of geckos are ancestrally padless or have secondarily attained this condition (Gamble et al., 2012, 2017; Russell & Gamble, 2019).

We have identified extensive structural differences in ankle joint structure between *Gekko gekko* and what is known of other lizards, but functional studies examining how the elements of the ankle move dynamically (Figure 7) during locomotion across a range of taxa will help solidify the link between form and function. Such information will then allow us to address questions such as whether the observed ankle structure in *Gekko gekko* is ideal for deploying an adhesive system.

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DATA AVAILABILITY STATEMENT

The bulk of our manuscript involves qualitative descriptions of ankle structure. Therefore, there are no quantitative data to share. However, our CT scans are available from the corresponding author upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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