



OPEN Forelimb biomechanics in the derived therizinosaur *Nothronychus* and its relation to the origin of the avian wing

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Therizinosauria is a clade of extinct unusual maniraptoran theropods. *Nothronychus* is a derived representative of the clade from the upper Cretaceous Moreno Hill Formation, west-central New Mexico and Tropic Shale, southern Utah. It represents an ideal taxon to establish basal function in maniraptoran theropods. This project models the function of a maniraptoran arm and establishes a good starting point to test the hypothesis that there will be significant muscular and functional changes leading to the avian forelimb. A model of *Nothronychus* forelimb function is presented including thirty-five muscles. It assumes a fairly conventional maniraptoran forelimb with typical ranges of motion in comparison with *Allosaurus*. Therefore, abduction/adduction, protraction/retraction, and long-axis rotation are modelled for the shoulder. In keeping with other maniraptorans, the elbow is modelled as a simple hinge. Little functional difference was observed between the forelimbs of *Allosaurus* and *Nothronychus*, so much muscular modification associated with flight had yet to evolve, even with the enlargement of the forelimbs. However, *M. supracoracoideus* and *M. pectoralis* had already developed antagonistic moment arms. Abduction in *M. supracoracoideus* was weaker than *M. pectoralis* adduction in *Nothronychus* and *Allosaurus*, so this relation evolved prior to flight.

Abbreviations

AzMNH Arizona Museum of Natural History, Mesa, Arizona
UMNH Utah Museum of Natural History, Salt Lake City, Utah

Therizinosaurids were a rapidly evolving lineage of omnivorous to herbivorous maniraptoran theropods related to oviraptorosaurs, alvarezsaurids, and deinonychosaurs from the Upper Cretaceous of Asia and North America¹. Therefore, they were phylogenetically close to those dinosaurs that gave rise to birds². *Nothronychus graffami* was a highly derived therizinosaurid from the Upper Cretaceous Tropic Shale of southern Utah known from a nearly complete postcranial skeleton^{3–5} (Fig. 1). Derived therizinosaurids, including *Nothronychus*, possessed some axial and hindlimb characters convergent with Neornithes⁵. The forelimb of most therizinosaurids, including *Nothronychus*, was nearly plesiomorphic for non-avian theropods (Fig. 2), whereas that of birds is highly modified as a flight organ⁶.

Moment arms about any joint are related to muscular force⁷. Increased moments reduce the absolute force required and result in changes in muscle contraction distances. Normally, they are defined as the shortest distance between the line of action of a muscle and the center of rotation of a joint. However, the path of a muscle can be altered with muscle contraction and concurrent changes in limb orientation^{8–13}.

Explicit three dimensional biomechanical analyses on the hindlimb have lately been published for a number of bipedal carnivorous theropods, including *Coelophysis*¹⁴ and *Tyrannosaurus*⁷, clarifying limb and mechanical function, and locomotion in these animals. Notably, *Coelophysis* was determined to have been far more cursorial than *Tyrannosaurus*. In neither case, however, can locomotion be directly analyzed using living analogues. In the case of *Coelophysis*, the degree of tail development was found to be important¹⁴, but this structure was generally reduced over maniraptoran evolution, ultimately to an abbreviated pygostyle in extant theropods. Allen et al. recently presented a biomechanical transformation series of non-avian theropod hindlimbs leading to neornithine birds¹⁵.

A number of forelimb muscular reconstructions, often with some functional consideration have been published, for non-avian theropods including groundbreaking work by Jasinoski et al. for dromaeosaurs¹⁶, and

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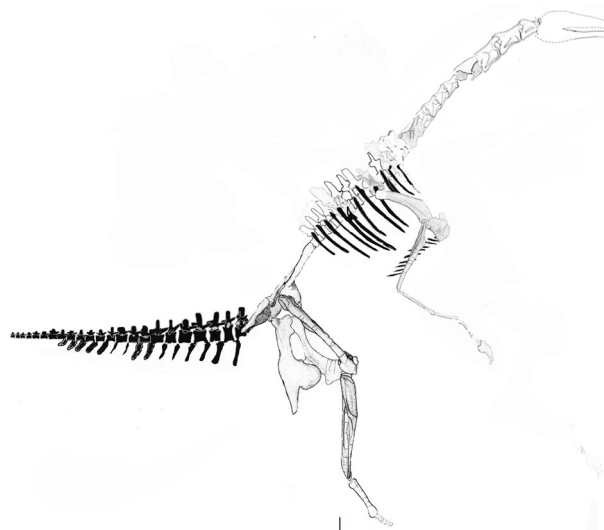


Fig. 1. Skeletal reconstruction of *Nothronychus* based mainly on *N. graffami* (UMNH 16,420) Turonian Tropic Shale, near Big Water, southern Utah. Scale equals 10 cm.

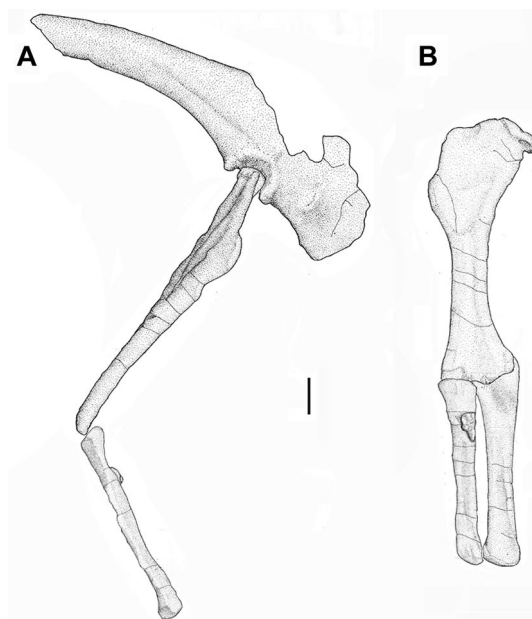


Fig. 2. *Nothronychus graffami* forelimb (UMNH 16,420) Turonian Tropic Shale, near Big Water, southern Utah. (A) lateral, (B) anterior views, Scale equals 5 cm.

Burch on *Tawa*¹⁷ and *Majungasaurus*¹⁸. The reduced forelimbs of *Tyrannosaurus* have been studied from several perspectives in an attempt to determine general function^{19–21}. Senter, with other authors, studied range of motion based on a bare-bones approach using soft-tissue scars without reconstructing muscles in *Mononykus*²², *Deinonychus*²³, *Ornitholestes*²⁴, *Acrocanthosaurus*²⁵, *Dilophosaurus*²⁶, *Carnotaurus*²⁷ and *Australovenator*²⁸. In all cases, range of motion was estimated by manipulating articulated bones and limiting motion based on margins of articular surfaces. In *Australovenator*, as in most non-avian maniraptoran theropods, the forelimbs were considered incapable of abducting beyond a sub-horizontal orientation or retracting past a vertical pose. White et al. report a reduction in digit flexibility in coelurosaurs compared with more basal forms²⁸ and this trend appears to hold for the therizinosaurian *Nothronychus*.

Therizinosaurids are often noted for their development of enlarged to exaggerated manual unguals^{29–31}. Qin et al. used finite element analysis to propose that variety in ungual function was greatest in early, small to medium therizinosaurids, but decreased in larger ones³⁰. They suggested that the basal taxa possessed generalized unguals and were most proficient at pulling. *Alxasaurus* and *Erliansaurus* were determined to possess especially generalized unguals^{29,30}. Lautenschlager inferred a digging function for *Nothronychus*, but a pulling function

for *Beipiaosaurus* and *Erliaosaurus*. This latter model was supported by Kobayashi et al. in the description of *Paralitherizinosaurus*³². The unguals were quite fragile and unable to resist significant stress in *Therizinosaurus*, so Qin et al. proposed a decorative function³⁰.

A model for forelimb function based on an earlier muscular reconstruction³³ is presented here for *Nothronychus graffami*. It is intended to provide estimates of dynamic moment arm changes with changes in forelimb position based on a purely geometric argument, so is derived from previous work on the hindlimb of *Tyrannosaurus*⁷. Dynamic moment arm models for *Nothronychus* and *Allosaurus* presented here expand on the static analysis for the forelimb of *Tyrannosaurus* by Carpenter and Smith that assumes a perpendicular elbow²⁰. Their discussion focusses solely on flexion induced by M. biceps brachii and they calculated considerable force at the elbow. The results generated here should contribute to understanding the plesiomorphic functional condition for the non-avian maniraptoran theropod forelimb in the lineage leading to birds, setting a baseline on the development of the avian wing. An additional goal of this work is to determine if function of the derived therizinosaurian forelimb of *Nothronychus* is significantly different from the more basal theropod *Allosaurus*. A second model of the forelimb of *Allosaurus fragilis*, based on disarticulated Cleveland-Lloyd material, was created to estimate the more primitive condition in non-avian tetanuran theropods.

Methods and materials

Permission to CT scan the appendicular material of *Nothronychus* was requested and received from representatives of the Utah Museum of Natural History. The left forelimb material of *Nothronychus graffami* (UMNH 16,420) was scanned at a 0.4 mm slice thickness. Some taphonomic distortion is apparent in some elements, but was not considered to have major impact on the final model. The right scapulocoracoid was mirrored for inclusion in the model. Unfortunately, phalanx III-3 was not preserved for *N. graffami*, so this element was included using laser scanned data from a corresponding phalanx from the closely related *N. mckinleyi* (AzMNH P2117). A comparison of phalanx III-3 in the manus of *Falcarius*³⁴, *Erliaosaurus*³⁵, and *Beipiaosaurus*^{36,37} indicates a similar relative length to the other phalanges in digits II and III. In all cases, it is the longest phalanx of digit III. Both specimens of *Nothronychus* are mature and a similar size^{5,38}. The morphology is very similar to that of the corresponding element III-3 in *N. graffami*, so its substitution should not be significant.

Moderate-sized *Allosaurus fragilis* forelimb material was CT scanned at the same resolution (UMNH-VP 8151, 8146, 8144, 11,033, 20,230, 9973, 7834, 9708, 9949, 11,461, 9831, 9718, 6074, 6636, 7018, and 5443) to minimize allometric effects. Missing elements and scaling sizes were estimated based on published descriptions^{39,40}. The right ulna was mirrored to simulate a left element.

In contrast to the plesiomorphic horizontal orientation of the ilium and dorsal vertebrae of *Allosaurus*, the major orientation of *Nothronychus* is nearly vertical⁵. This re-orientation of the ilium is based on ossification of the pre-acetabular labrum and associated ligaments due to a marked increase in compressive stress in that area associated with Wolff's Law. As a result, the pectoral girdle is nearly horizontal despite an acute angle relative to the vertebral column. Therefore, protraction of the forelimb would an increase in vertical reach without requiring elevation of the arm above the vertebral column. Jasinoski et al. follow previous work⁴¹ in reconstructing dromaeosaurs with a horizontal scapular orientation. If this is followed for *Nothronychus*, the scapula would approach a similar orientation.

One trait that would affect the results is the presence of a functional semilunate carpal. This development would permit passive abduction/adduction at the wrist with flexion of the antebrachium^{42,43}. Functional semilunate carpals are widely distributed in maniraptoran theropods and described for some therizinosaur⁴⁴. Chure regarded the semilunate also present in *Allosaurus*⁴⁵. Apparently, *Allosaurus* possessed a functional semilunate carpal mostly composed of distal carpal I with a trochlea and covering the proximal end of the first metacarpal. He suggested that the lack of a fused semilunate carpal in therizinosaur could either be the result of a reversal or multiple originations. Both scenarios were considered equally parsimonious. Xu et al. implied the presence of an unfused semilunate carpal in *Allosaurus*⁴⁴. However, recently presented embryological data combined with paleontology were used to argue that the avian semilunate is not homologous with that of maniraptoran dinosaurs and that its origin and distribution are complex⁴⁶. No carpals are preserved for either specimen of *Nothronychus*, so the presence of a functional, unfused semilunate carpal, making its presence an inference based on phylogenetic bracketing⁴⁷. Semilunate carpals are known for *Falcarius*⁴⁴, *Alxasaurus*⁴⁸, *Therizinosaurus*⁴⁹, and *Beipiaosaurus*³⁷. If the trochlear surface facet of the carpometacarpus of extant birds is homologous with the semilunate carpal of non-avian theropods, *Archaeopteryx*⁵⁰, and *Sapeornis*⁵¹, as is commonly accepted⁴⁴, its presence in *Nothronychus* could be bracketed with one extinct group and an extant group⁴⁶.

The presence of soft tissue associated with the joints can have a significant effect on movement and there can be a substantial amount in archosaurs⁵². The presence of thick epiphyseal caps can introduce considerable shape change and articular congruence in crocodylians. This issue is also present in neognath birds, but less so. Ostriches exhibit an intermediate condition⁵². The presence of the epiphyseal cartilage has caused an underestimate of range of motion in the crocodylian and avian forelimb^{53–55}. The presence of a thick cartilage cap prevents precise placement of the humeral head within the glenoid in *Dilophosaurus*, as in extant archosaurs⁵⁶, and this trait is apparent in *Nothronychus*, as well.

Virtual three dimensional DICOM images were imported into 3d Slicer for segmentation and the creation of object files. The scapulocoracoid, humerus, and radius/ulna were each considered discrete objects for both taxa. Metacarpals and phalanges were included as separate objects for each element. Object files for *Allosaurus* and *Nothronychus* models were created the same way. All files were decimated in Blender to reduce them to a manageable size. Estimated space for the carpals is provided in the models.

Nothronychus and *Allosaurus* files were imported into Opensim Creator⁵⁷ for independent analyses for the two taxa. For both, the virtual pectoral girdle and forelimb were assembled and articulated within the same

program. Individual ranges of motion at each articulation were estimated using joint morphology (Fig. 3). Two joint types were included in the model to exhibit degrees of freedom.

Pin joints were placed at the elbow, metacarpophalangeal, and interphalangeal joints to model a 2-dimensional hinge-like extension/flexion motion. Flexion/extension at the elbow was limited to 90–180°, close to results published for other maniraptoran theropods²³. Limits to the range of motion were manually defined in OpenSim Creator, but default settings altered the angles away from those relative to perpendicular in all cases. Some hyperextension was permitted at the interphalangeal joints, based on condylar morphology²³. Three dimensional motion was modelled at the shoulder and wrist, including protraction/retraction (PR), abduction/adduction (ABAD), and long axis rotation (LAR) of the humerus. The joint orientations were adjusted so that axes of motion were the same in *Nothronychus* and *Allosaurus* models. No active rotation or flexion/extension/hyperextension was considered possible at the wrist.

Moment of inertia is defined as the resistance to rotation. It is a function of mass and its distribution about the joint axis⁵⁸. As the center of mass approaches the axis of rotation, the moment of inertia is reduced and the easier the structure is to rotate. Many variables, including segmental muscle mass, remain unknown so the center of mass and segmental inertia⁵⁹ were visually estimated as the center of each bone. Bone masses for *Nothronychus* and *Allosaurus* were estimated using scaled up values reported for extant birds⁶⁰.

The orientation of the scapula is important in reconstruction of some muscles⁶¹. A nearly horizontal orientation is suggested here, as proposed for other maniraptorans^{16,61}. Some degree of long-axis rotation was modelled for the humerus as in *Deinonychus*⁶², but the amount portrayed is only limited by the head within the glenoid fossa. The muscles modelled here permitted protraction/retraction and adduction/abduction at the shoulder and flexion/extension at the elbow. The ability of dinosaurs to pronate/supinate the antebrachium is more controversial, with a number ROM studies indicating they could not^{22–27}, whereas Ostrom proposed that it was possible in some maniraptorans such as *Deinonychus*⁶². Recent muscle reconstructions of *Tawa*¹⁷ and *Majungasaurus*¹⁸ conclude that this capability was present. Rotation of the antebrachium is not included in the current models, though it may have been possible.

Points of interest were identified corresponding to muscle attachments (Figs. 4, 5)³³. Some muscles, such as Mm. pectoralis and deltoideus scapularis with broad attachments, required multiple attachment points to reflect aponeuroses or division into separate tendons. Thirty five muscles are included in the *Nothronychus* forelimb

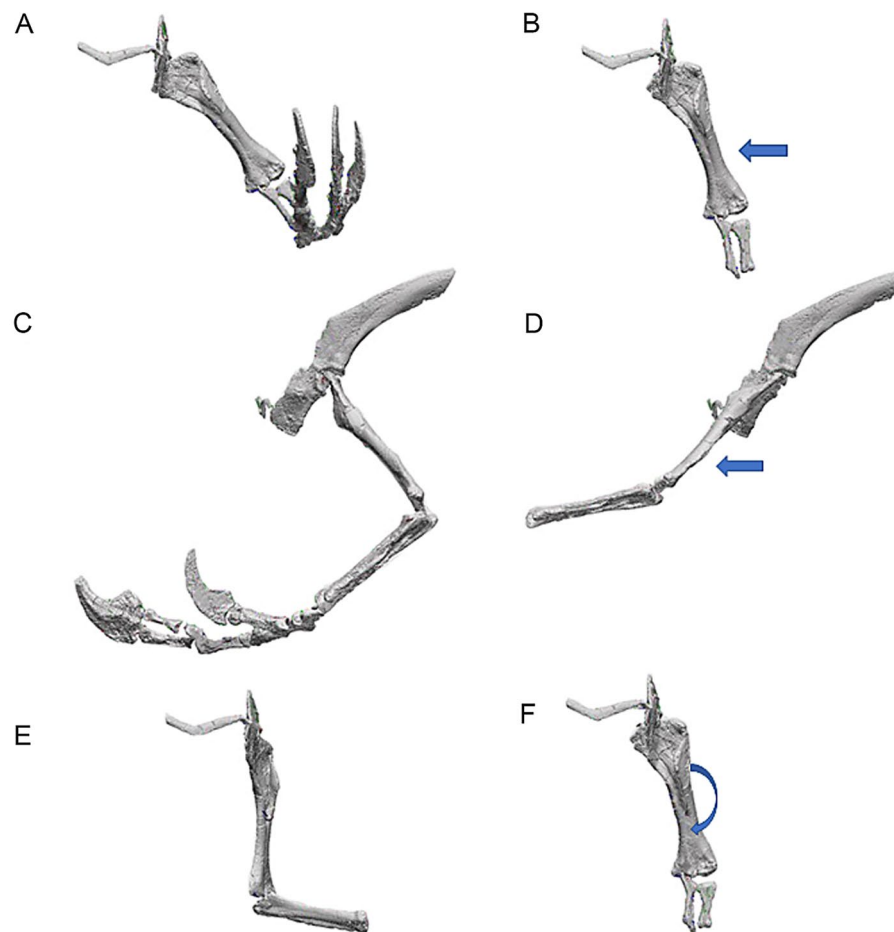


Fig. 3. *Nothronychus* forelimb movement. (A), (B) abduction, adduction; (C), (D) flexion, extension; (E), (F) external, internal rotation. Arrows represent planes of displacement.

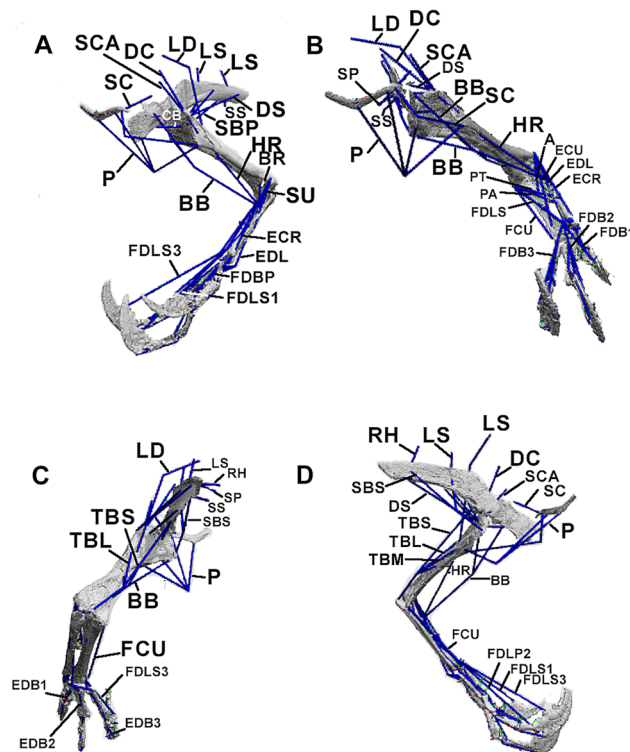


Fig. 4. *Nothronychus* left forelimb with muscle topology modelled. Manual phalanx III-3 is *N. mckinleyi*. Blue lines represent major muscle vectors.

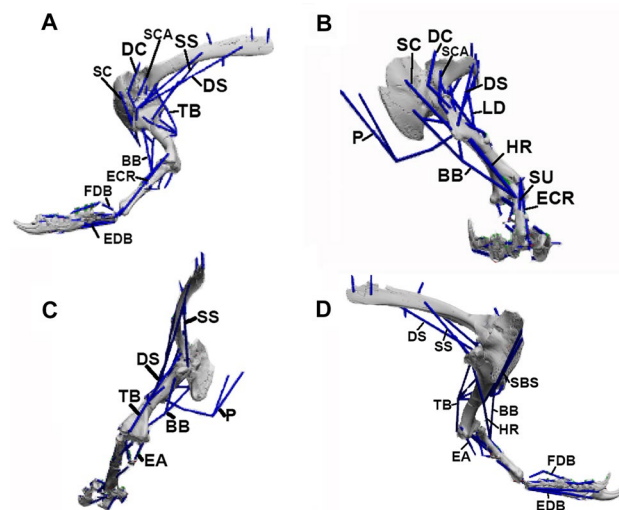


Fig. 5. *Allosaurus* left forelimb with muscle topology modelled. Blue lines represent major muscle vectors.

model (Table 1) to estimate moment arms (Figs. 6–8, S1–S10). Muscles spanning the shoulder, elbow, wrist and interphalangeal joints are all incorporated. Any muscles exhibiting variable, non-zero moment arms were considered loaded at the joint as it moved. Three degrees of freedom are possible in motion at the shoulder in *Nothronychus*. The humerus is subject to abduction/adduction (ABAD), protraction/retraction (PR), and long axis rotation (LAR). Key muscles and function in avian flight are *M. pectoralis* and *M. supracoracoideus*. In non-flying animals, such as *Allosaurus* and *Nothronychus*, abduction of the forelimb is considered roughly equivalent to elevation of the wing in birds.

Many muscles change direction to go around bones along their pathways, so changes in force vector direction were modelled with multiple points of interest within the models. Some muscles merged together along their trajectories, possibly, though not necessarily, through a retinaculum. These were subdivided and modelled

	<i>Nothronychus</i>	<i>Allosaurus</i>	Crocodilians	Function	
				<i>Nothronychus</i>	
Abductor Pollicis Longus (APL)	x	x	E	Ab	Ab
Anconeus (AN)	x	x	E	F→E	F
Biceps Brachii (BB)	x	x	F, P	F	F
Brachialis (BR)	x	x		F	F
Coracobrachialis (CB)	x	x	P	Ab, P, LAR	Ad, LAR
Deltoideus Coracoideus (DC)	x	x	P	Ab, P, LAR	Modified
Deltoideus Scapularis (DS)	x	x	Ab, P	Ab, R, LAR	Ab, R
Epitrochleoanconeus (EA)	x		-	F	F
Extensor Carpi Radialis (ECR)	x	x	E	E	E
Extensor Carpi Ulnaris (ECU)	x	x	E	E	E
Extensor Digitorum Brevis (EDB)	x		E	E	E
Extensor Digitorum Longus (EDL)	x	x	E	E	E
Flexor Digitorum Brevis (FDB)	x	x	F	F	F
Flexor Digitorum Longus (FDL)	x		F	F	F
Humeroradialis (HR)	x	x	F	F	F?
Latissimus Dorsi (LD)	x	x	Ab, LAR	Ab, P, LAR	Ab, R
Levator Scapulae (LS)	x	x			
Pectoralis (P)	x	x	P	Ad, P, LAR	Ad
Pronator Accessorius (PA)	x	x	-	F	F, LAR
Pronator Teres (PT)	x	x	F, LAR	F	F, LAR
Rhomboideus (R)	x	x	Ad	Not included	P
Scapulohumeralis Anterior (SHA)	x	x	R	Ad, R, LAR	Ad, R
Scapulohumeralis Posterior (SHP)	x	x	Ad, R	Ad, R, LAR	R
Serratus Profundus (SP)	x	x	Ad	Not included	Ad, P
Serratus Superficialis (SS)	x	x	R	Not included	R
Subcoracoideus (SBC)	x	x	with SBS	Ab, P, LAR	Ad, LAR
Subscapularis Anterior (SCA)	x	x	Ad, R	Ad, P, LAR	Ad, LAR
Subscapularis Posterior (SSP)	x	x	Ad, R	Not included	LAR
Supinator (SU)	x	x	F, LAR	F→E	F
Supracoracoideus (SC)	x	x	P	Ab, P, LAR	Ab
Supracoracoideus Anterior (SCA)	x	x			
Triceps Brachii Lateralis (TBL)	x	x	E	E	E
Triceps Brachii Mediale (TBM)	x	x	E	E	E
Triceps Brachii Scapularis (TBS)	x	x	E	E	E

Table 1. Muscles with abbreviations included in models for both taxa. Functions for crocodilians and neornithines are taken from Chiasson^{81–83}; Jasinoski et al.¹⁶; and Burch¹⁷.

separately. Muscles were placed extending from origins to insertions, but constrained to go around surfaces, so as to not go through bones. All muscles were entered into Opensim Creator using a Rigid Tendon paradigm. Other related parameters, including pennation angle and tendon length, were based on values published for *Tyrannosaurus*⁷ using a geometric argument based on skeletal proportions. Many of these parameters are important, but the precise values remain unknown. For instance, muscle fiber length in biological modelling ranges is closest to the fascicle length is relevant, but must be estimated in an extinct species^{59,63}. Extending from this, muscle force varies as a function of the degree and speed of contraction, complicating the model. Therefore, the models provided here are simplified. A sensitivity analysis was performed at selected points by altering muscle attachments and pathways⁶⁴. The generated model was moved into OpenSim software to produce bivariate plots of moment arms vs. joint angle for each muscle to confirm torque changes with changes in joint configuration.

Forelimb motion and musculature in *Nothronychus*

Initial estimation of minimal forelimb motion based on a bare-bones method in *Nothronychus* reveals typical maniraptoran range of motion²³ (Fig. 3). A thick cartilage epiphyseal pad and substantial synovial capsule is considered present on the humeral head as the surface of the glenoid is markedly rugose and birds are characterized by similar development. Attachment points for a number of forelimb muscles in *Nothronychus* were published previously³³ and are used for these models (Figs. 4, 5). Shoulder motion is extremely complex in extant birds^{65,66}, but is reduced here to simplify the model, permitting only abduction/adduction, protraction/retraction, and long-axis rotation of the humerus, without translation²⁷. This inferred motion is in contrast to

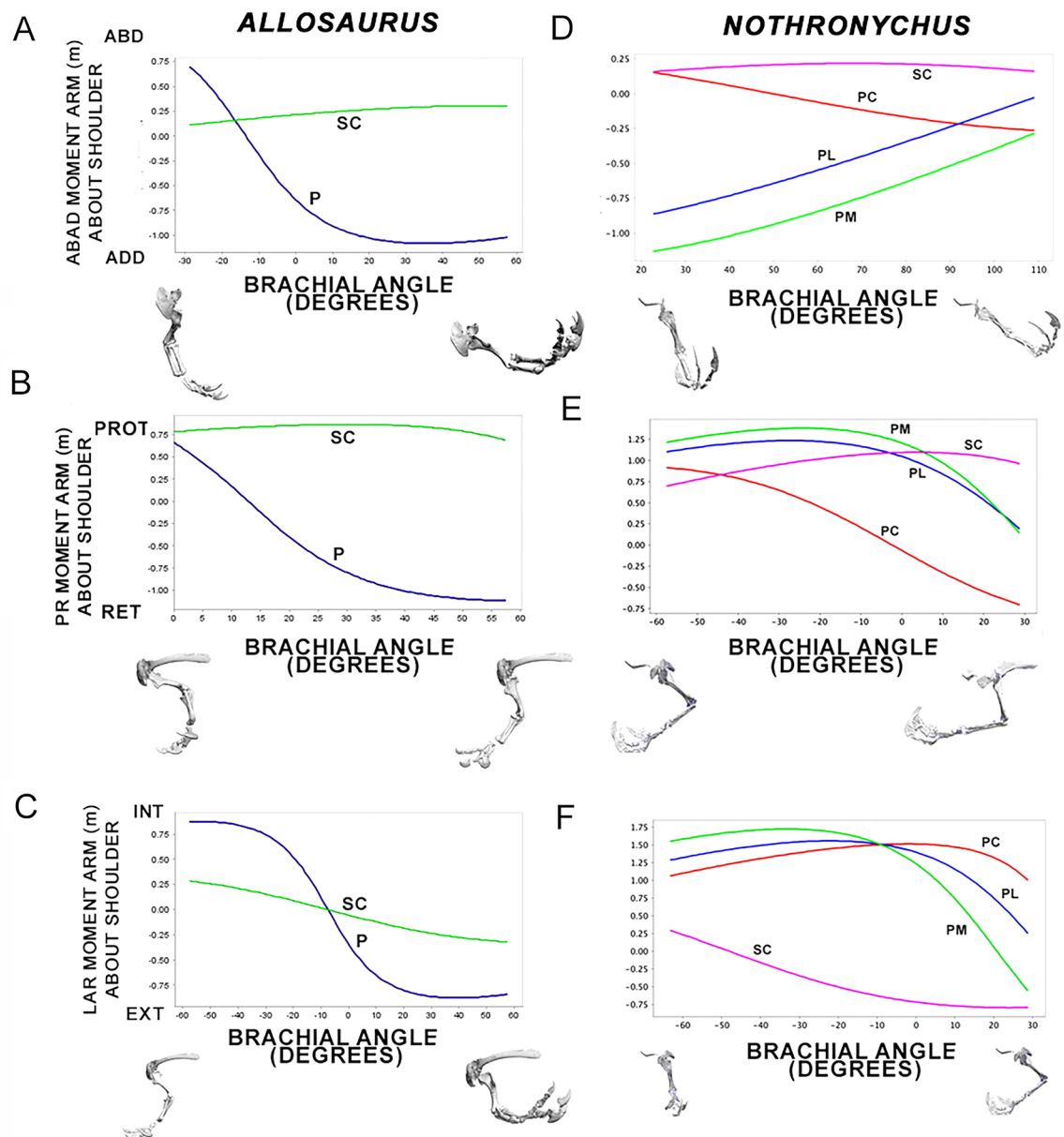


Fig. 6. *Nothronychus* (A, B, C) and *Allosaurus* (D, E, F) shoulder long axis rotation (A, D), abduction/adduction (B, E), protraction/retraction (C, F) plots of M. supracoracoideus and M. pectoralis. Negative angles and moment arms represent adduction, flexion, and internal rotation. Positive angles and moment arms represent abduction, extension, and external rotation. Crossing 0 reflects a change in function (Hutchinson et al., 2005).

non-maniraptoran theropods, which show reduced abduction and long axis rotation²³. Most muscle originating at the trunk and neck⁶⁷ were not included, as a complete vertebral column is not available for *Nothronychus*. Multiple muscles spanning the shoulder are involved in movement in all three axes, including M. biceps brachii, M. pectoralis, M. supracoracoideus, M. supracoracoideus anterior, M. triceps brachii pars scapularis, M. deltoideus coracoideus and scapularis, and M. latissimus dorsi⁶⁸.

Maximum protraction of the humerus to horizontal was manually set in OpenSim Creator, but maximum retraction was limited to a vertical orientation, as in other non-avian theropods^{22–27}. Abduction to roughly 90°, resulting in a nearly horizontal humerus, was modelled as is typical for non-avian maniraptorans²³, limiting movement to below the vertebral column. This motion may have been driven by M. supracoracoideus elevating the arm as in birds, if indeed, it passed through a structure analogous to a tri-osseal canal⁵. This function might be predicted for *Nothronychus*, but not *Allosaurus* if an analogous structure defined the muscle trajectory in the former. The same muscle also functions in long axis rotation in European starlings^{69–71}. The M. deltoideus heads, including M. deltoideus pars cranialis inserting on the deltopectoral crest, are at least synergistic with M. supracoracoideus in birds^{70,71}. Other heads insert more distally. M. deltoideus pars coracoideus is reconstructed

as inserting in the same place as pars cranialis, presumably an additional important antebrachial elevator. The moment of this head would increase with lengthening of the deltopectoral crest. A major variable is the orientation of the pectoral girdle, modified from a ventrally-oriented glenoid in non-avian theropods to a laterally oriented glenoid in extant birds^{41,72}. *M. deltoideus* pars caudalis inserts distally on the posterior face of the humerus in birds, but there is no corresponding attachment in *Nothronychus*. Therefore, a partial arm elevator mechanism with an intermediate glenoid orientation is inferred in the therizinosaur. However, it is absent in *Archaeopteryx*, suggesting a complex evolution within the maniraptoran lineage⁵⁰.

Elbow range of motion in *Nothronychus* is considered more extensive than in more basal forms, including *Herrerasaurus*⁷³. The antebrachium is modelled to flex to about 50° as inferred for derived maniraptorans such as *Deinonychus*²³. Extension was limited to less than 180°. The radius and ulna are parallel. The distal humerus is marked by a larger radial condyle than ulnar, resulting in the radius sliding distally past the ulna with flexion of the lower arm. This movement will cause the radiale to extend into the wrist and posterior rotation of the manus accompanying lower arm flexion, as in birds^{42,43}. Carpenter, however, presented an alternative range of movement model, with no avian-like folding at the elbow⁷⁴, based on the development of the glenoid and shape of the scapula to limit motion in a bare-bones reconstruction. The labra at the glenoid would have limited protraction/retraction, but permitted more extensive abduction/adduction.

The distal end of the ulna in *Nothronychus* is strongly compressed as compared to the radius⁵. The distal radius is somewhat ventrally expanded, presumably similar to caenagnathoids including the oviraptorid *Heyuannia*⁷⁵. Since the shapes of the semilunate carpal and radiale are unknown in *Nothronychus*, the radiale angle and the degree of wrist abduction are also unclear for *Nothronychus*, but the flattened ulna and ventrally expanded radius indicate that such movement would have been significant.

Initial inferred wrist motion includes flexion/extension/hyperextension at the distal carpals as modelled in *Herrerasaurus*⁷³. However, theropod wrist flexion/extension/hyperextension is considered reduced or lost^{25,74}, so such motion may well be limited to the interphalangeal joints in *Nothronychus*, as in *Deinonychus*. Inversion/eversion at a semilunate carpal should be permitted, as the one described for the related *Alxasaurus*⁴⁸. Digit I could abduct from digit II, as is primitive for archosaurs^{24,76,77}. Phalangeal motion is limited to flexion/extension/hyperextension, but this is probably an oversimplification, as digits I-III converged with flexion and hyperextension as in *Herrerasaurus*⁷³ and theropods including *Megapnosaurus*⁷⁷ and *Dilophosaurus*⁵⁶.

Results

Shoulder

Two important flight muscles in birds are *m. pectoralis*, mainly an adductor, and *m. supracoracoideus*, mainly an abductor. Shoulder motion is complex in birds, with loading in multiple planes. Here, adduction is regarded as functionally related to depression and abductor related to elevation⁷¹. Either is possible for non-avian theropods and *Archaeopteryx*. Two hypotheses affecting *M. supracoracoideus* are modelled. One hypothesis is that the supracoracoideus tendon is deflected around the pectoral girdle, possibly through a tri-osseal foramen analog. *M. pectoralis* exhibits a large adductor (depressor) moment arm presumably also related to increased muscle mass relative to *M. supracoracoideus*, but the latter muscle is a weaker abductor (elevator) in both *Allosaurus* and *Nothronychus*, as in flying birds^{65,66,69–71}. The model reveals a moment arm difference in the two muscles in the ABAD plane. This result, however, contradicts the prediction that moment arms of the two muscles in a non-flying animal would be similar. This relation assumes an avian-like topology⁷¹, with the *M. supracoracoideus* tendon permitting recovery during flight travelling through a structure functionally analogous to the tri-osseal foramen in birds in *Nothronychus*, but not *Allosaurus*, so a similar function would be expected. It may be related to accommodation of *M. supracoracoideus* around the coracoid in *Allosaurus* resulting in a similar muscle topology for both, so such a tri-osseal analogous structure would not be completely necessary for such ABAD loading in non-avian theropods. A tri-osseal foramen was notably absent in *Archaeopteryx*, so it was not necessary for at least weak flight⁷⁸.

ABAD dominates function for *M. supracoracoideus* and *M. pectoralis* in both taxa. In *Nothronychus*, *M. supracoracoideus* exhibits a smaller abductor moment arm in the ABAD plane than *M. supracoracoideus* accessorius, but this relationship flips in *Allosaurus*, so SC is larger (Figure S4). Loading is also observed in the other two planes. All these muscles showed similar functions in *Nothronychus* and *Allosaurus* during the long axis rotation. *M. subcoracoideus* shifts from an adductor to an abductor at high ABAD angles in *Nothronychus*, while is a consistent adductor in *Allosaurus*.

For protraction/retraction in both *Nothronychus* and *Allosaurus*, all three muscles are protractors, but *Mm. supracoracoideus* accessorius and subcoracoideus exhibit smaller moment arms than SC. A clear difference in moment arms is observed in the protraction/retraction plot (Fig. 6) for *M. supracoracoideus* and *M. pectoralis* in the forelimb of *Allosaurus*, with the former exhibiting protraction and the latter acquiring an increasing moment arm with increasing extension. The two muscles are functionally similar in *Nothronychus*, with a large protraction moment arm.

Long axis rotation (Fig. 6) also exhibits a major change for *M. supracoracoideus* and *M. pectoralis*⁶³. In *Allosaurus*, *M. pectoralis* shows an exaggerated shift in the moment arms as the angle changes from external to internal rotation. Changes in moment arm are reduced, along with the LAR magnitudes in *Allosaurus*. Clear separation is observed between *M. pectoralis* and *M. supracoracoideus* in *Nothronychus*. *M. pectoralis* is characterized by large external rotation moment arms, whereas *M. supracoracoideus* exhibits smaller internal rotation moment arms.

An alternative hypothesis infers *M. supracoracoideus* travelled directly, with no deflection, to the insertion on the humerus from the coracoid. This model changed the moment arm results in all planes. In the ABAD plane, *M. supracoracoideus* shows a larger abductor moment arm than when the muscle was deflected around the pectoral girdle. The muscle remains antagonistic to *M. pectoralis*. *M. supracoracoideus* continues to show a

retractor moment arm, but remains synergistic with *M. pectoralis*. In the LAR plane, it remains antagonistic to *M. pectoralis*.

With long axis rotation and abduction/adduction, *Mm. scapulohumeralis anterior* (SHA) and posterior (SHP) have similar functions in *Allosaurus* and *Nothronychus*, but this changes in the PR plane (Fig. 7). In *Nothronychus*, SHA exhibits a smaller retractor moment arm than SHP in any position, but in *Allosaurus*, they become antagonistic, so SHA is a retractor and SHP a protractor. Therefore, these inferences are sensitive to assumptions about muscle pathways and attachment points⁶⁶.

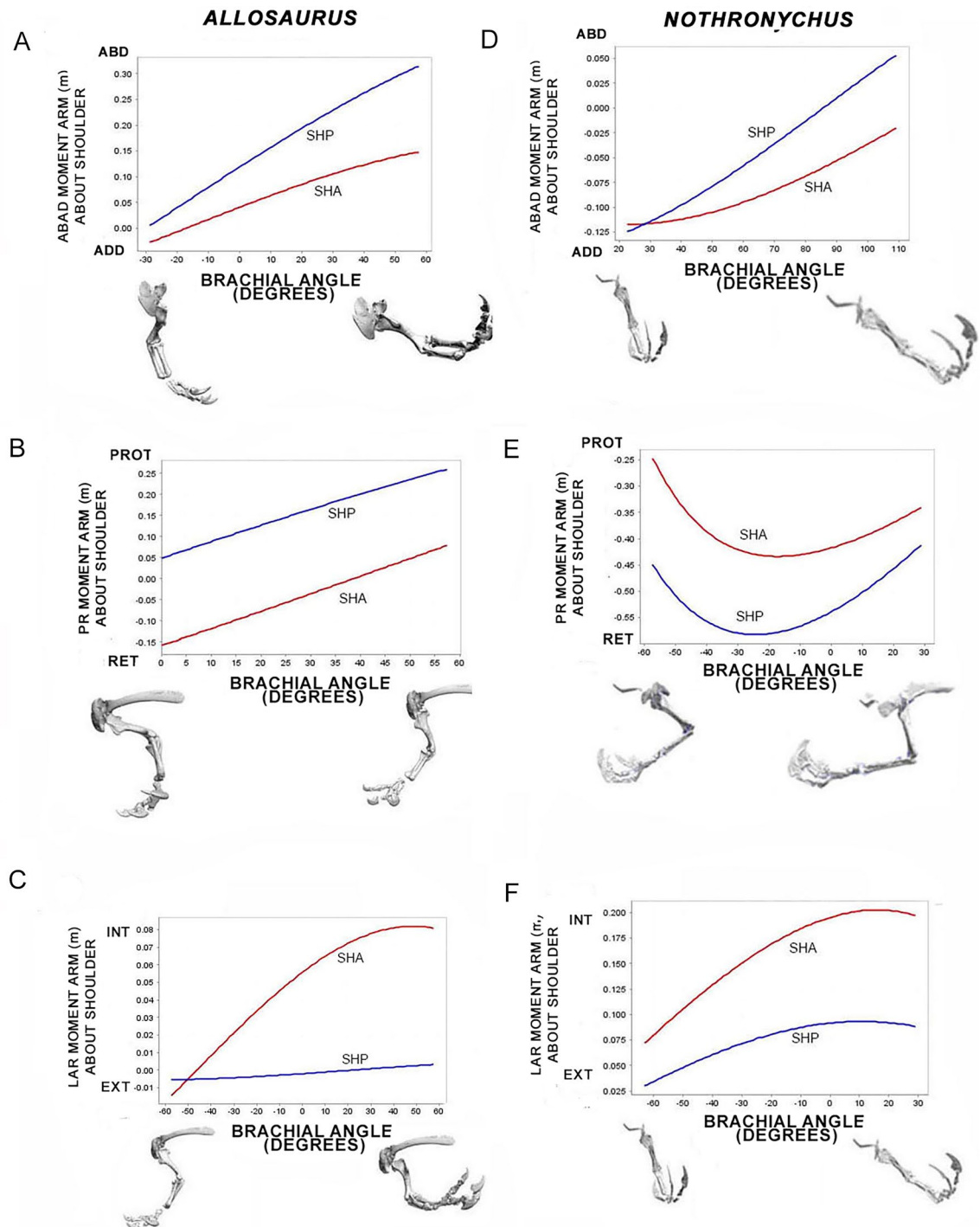


Fig. 7. *Nothronychus* (A, B, C) and *Allosaurus* (D, E, F) abduction/adduction, flexion/extension and long axis rotation plots at the shoulder of *M. scapulohumeralis anterior* and *M. scapulohumeralis posterior*. Negative angles and moment arms represent adduction, flexion, and internal rotation. Positive angles and moment arms represent abduction, extension, and external rotation. Crossing 0 reflects a change in function (Hutchinson et al., 2005). Crossing 0 reflects a change in function (Hutchinson et al. 2005).

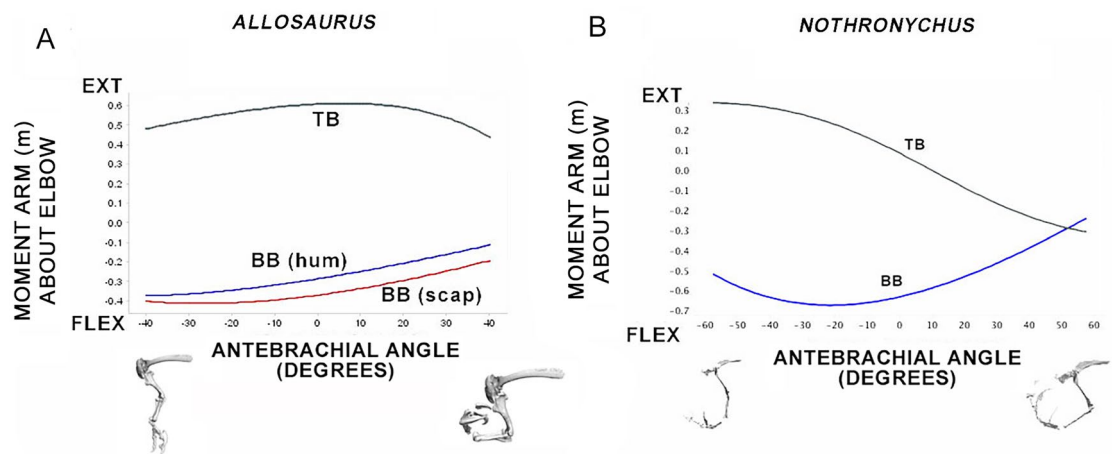


Fig. 8. *Nothronychus* (A, B, C) and *Allosaurus* (D, E, F) flexion/extension plots at the elbow of *M. biceps brachii* and *M. triceps brachii*. Negative angles and moment arms represent flexion. Positive angles and moment arms represent extension. Crossing 0 reflects a change in function (Hutchinson et al., 2005).

Mm. deltoideus clavicularis and *scapularis* also contribute to motion of the humerus in all three planes in *Allosaurus* and *Nothronychus*. The former muscle is homologous with *M. propatagialis* in birds¹⁷. Both heads of *M. deltoideus* have similar ABAD characteristics. *M. deltoideus clavicularis* (DC) exhibits a larger moment arm for abduction than *M. deltoideus pars scapularis* (DS), which is a small adductor. The former muscle exhibits an increase with increasing abduction in both animals. DC is a protractor, whereas DS exhibits a retractor moment arm in *Allosaurus* and *Nothronychus*. Both heads participate in long axis rotation, but in *Nothronychus*, DC has a much smaller external rotator moment arm than DS. This is not the case in *Allosaurus*, where DC shifts from an external to an internal rotator with increasing abduction. LAR is not modelled for this muscle in birds. This interpretation is more complex than that presented for dromaeosaurs, where only protraction and abduction were proposed¹⁶.

In crocodylians, CB protracts the humerus, whereas LD is an adductor, but in birds, both are adductors. CB is regarded as a protractor¹⁷. Jasinoski et al.¹⁶, considered LD a humeral retractor in dromaeosaurs. CB was considered an adductor with some LAR in that clade. *Mm. coracobrachialis* and *latissimus dorsi* function is more complex in the two non-avian theropods than what has been modelled^{16,17}. In *Nothronychus*, *M. coracobrachialis* (CB) changes its relation to *M. latissimus dorsi* (LD) in different planes. In the ABAD plane, the two are synergistic in *Nothronychus*, but CB exhibits smaller adductor moment arms than LD in any angle. However, in *Allosaurus*, CB shifts from an abductor to an adductor along with the increasing abduction angle. At low abduction angles, CB is antagonistic to LD, but this relationship becomes synergistic at higher angles, where CB has a larger adductor moment arm than LD. *M. coracobrachialis* exhibits a protractor moment arm, but *M. latissimus dorsi* has a larger retractor moment arm in *Nothronychus*, as in dromaeosaurs. This relationship is similar in *Allosaurus*, but CB exhibits larger moment arm for protraction. During long axis rotation in *Nothronychus*, CB is antagonistic to LD, whereas they are synergistic in *Allosaurus*.

Elbow

Important muscles at the elbow include *M. triceps* and *M. biceps* as is typical for vertebrates (Fig. 8). Muscles in both *Allosaurus* and *Nothronychus* exhibit the expected results in both taxa, with *M. biceps* as an important flexor and *M. triceps* an important extensor. *M. biceps brachii* (BB) is synergistic with *M. brachialis* (BR), but exhibits a larger moment arm in *Nothronychus*. In all cases, flexion is characterized by a larger moment arm than extension at the elbow.

Wrist

No reconstructed major muscles changed load during abduction/adduction at the wrist in either taxon, suggesting ABAD may be passive, or nearly so, occurring only with antebrachium flexion/extension. Small interphalangeal muscle control, however, may have been possible.

Manus

Moment arms of manual extensors and flexors in *Nothronychus* do not show any unusual patterns during interphalangeal joint extension and flexion, as inferred from muscle topology. The flexor moment arm exceeds the extensor moment arm in the phalanges. The digital flexors and extensors also behaved as expected in both genera. In digit I of *Allosaurus*, flexors attained maximum moment arms at an intermediate finger position, as expected. For both taxa, digit II extensor moment arm magnitude and changes were similar for the unguals. Flexor ungual moment arms in digit III are also similar in both taxa (Figures S7–S10).

Discussion

In both *Allosaurus* and *Nothronychus*, there are significant changes in forelimb muscle moment arms (Figs. 6–8). The changes may be related to changes in arm function associated with trophic level. This hypothesis would have to be tested against patterns in other non-avian theropods.

The forelimb muscles of *Allosaurus* and *Nothronychus* frequently exhibit similar moment arm characteristics, but not always. Some muscles alter moment arms or functional relationships at certain ranges of joint angles. Therefore, a shift in forelimb muscle function from basal tetanurans to more derived maniraptorans is becoming apparent. However, this result would need to be explored by looking at more taxa.

Theropod forelimb muscles, along with associated osteology, underwent extensive functional alteration associated with the development of flight⁷⁸. Two critical muscles are *M. pectoralis* and *M. supracoracoideus*^{65,66}. The current model reveals a separation of the two in the ABAD plane. *M. pectoralis* exhibits a large adductor (depressor) moment arm, but displays complex function with additional activation during forelimb motion in birds⁷⁰. It is often described with increased mass relative to *M. supracoracoideus*. *M. pectoralis* participates, but SC is interpreted as the main abductor (elevator) in both *Allosaurus* and *Nothronychus*, as in flying birds^{70,79}. In extant archosaurs, *M. supracoracoideus* has variable functions. Novas⁷⁹ described a protractive motion for *M. supracoracoideus* in rheas and ostriches. It is an humeral elevator in neognaths and tinamous. He implied a long axis rotation in neognaths, but not tinamous. In crocodilians, *M. supracoracoideus* protracts the humerus, but in neognaths and probably enantiornithines, it shifts to mainly elevate the humerus. In adult birds, but not juveniles, *M. pectoralis* is enlarged, with an extensive origin along the furcula extending onto the ribs and increased fiber length, both of which increase power associated with active downstroke⁷⁹. Downstroke may be related to adduction of the humerus in a non-flying animal. Increased power of *M. pectoralis* is likely related to increased origin and strain on the furcula and development of the increasingly enlarged hypocleidium in *Velociraptor*⁷⁹, *Falcarius*³³, and *Nothronychus*⁵, but not *Archaeopteryx*⁵⁰. The current model reveals a functional separation of *M. pectoralis* and *M. supracoracoideus* in the ABAD plane and that this distinction evolved prior to the origin of allosaurids.

Function in some muscles, including *M. supracoracoideus*, associated with flight developed early in theropod evolution with increase of an acrocoracoid process⁷⁹ and prior to the shift onto the clavicle and alteration of the forelimb into a flight organ, so were not strictly related to the development of a tri-osseal canal and the acquisition of flight⁷¹ as their functional relations evolved beforehand. In both *Allosaurus* and *Nothronychus*, *M. pectoralis* would have been large with long fibers and a large moment arm. Forelimb elevation and external rotation are functions of the smaller, antagonistic *M. supracoracoideus*, but in birds, upstroke is mainly produced passively by aerodynamic force⁶⁵. The latter muscle also originates from the sternum, and may extend through a structure formed by a deflected epicleidium in *Nothronychus*; functionally analogous to the tri-osseal foramen in birds⁵. In a completely volant animal, *M. supracoracoideus* would terminate in a long tendon extending through the foramen and a somewhat smaller abductor moment arm. In some extant, non-flying birds, however, this muscle also protracts the humerus⁶⁶. This additional function was possible in *Nothronychus*. This morphology, however, is not seen in *Archaeopteryx*, widely considered a weak flier⁸⁰. Wing elevation is related to humeral abduction in a non-flying animal. Upstroke duration in most birds is much shorter than downstroke, leading to prolonged, powerful contraction of *M. pectoralis* and shorter contraction times for the smaller *M. supracoracoideus*⁶⁵. However, it might be predicted that in the non-flying, bipedal *Nothronychus*, prior to the evolution of birds, *M. pectoralis* and *M. supracoracoideus* would have similar functional characteristics, but morphology and moment arms in both *Allosaurus* and *Nothronychus* are distinct. This observation may result from elongation of the two muscles around the coracoid. In both, abduction associated with *M. supracoracoideus* is expected to be weaker than adduction of *M. pectoralis*. Therefore, this functional separation of moment arms would have long evolved prior to flight and prior to the evolution of allosaurids.

Given the similarity with *Allosaurus*, there is nothing unexpected within the manus of most therizinosaurs. Some therizinosaurs (eg. *Therizinosaurus*), however, are characterized by the development of 80 cm long, laterally compressed, slightly recurved manual unguals^{31,32}. The biophysics of such a forelimb are not currently modelled, so no elaboration of previous hypotheses for a *Therizinosaurus* forelimb can be presented, but it would be of interest to describe functional diversity in therizinosaurs. Novas listed a number of hypotheses to explain osteological and muscular shifts that would be required for flight prior to the evolution of a fully flying animal, including, but not limited to, grasping, hunting, or fighting⁷⁹. An alternative could be the use of these mechanisms in the forelimb to aid in locomotion as in Wing Assisted Incline Running of extant birds⁸¹. It would be of interest to describe forelimb functional changes in basal birds.

Data availability

All CT data are available at Utah Museum of Natural History and Northland Pioneer College.

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Author contributions

D.K.S. conducted all aspects of the project and manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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