MUSCULATURE OF THE BIZARRE FORELIMB OF THE ALVAREZSAURID *MONONYKUS OLECRANUS* (DINOSAURIA: THEROPODA) AND ITS IMPLICATIONS FOR DIGGING

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BACKGROUND

Mononykus olecranus, from the Late Cretaceous of Mongolia, was a small, nonavian theropod dinosaur belonging to the clade Alvarezsauria (Perle et al., 1993). Like other derived Alvarezsaurids, the forelimbs of *Mononykus* are distinctly stunted in size with only one digit and claw on each hand, and the perplexity of this morphology has prompted hypotheses that derived members of this clade may have had an insectivorous diet, and in particular might be specialized as ant or termite eaters (Perle et al., 1993, 1994; Zhou, 1995; Longrich, 2000; Senter, 2005; Longrich & Currie, 2010). The only explicit analysis of the function of these forelimbs found that the functional morphology of *Mononykus* deviated substantially from that of typical theropods (Senter, 2005). This study focused on the orientation and range of motion (Senter, 2005), but did not consider the modifications of the musculature or its implications for the function of the forelimb. In this study, we chose to focus on the specific muscle attachment sites in order to assess how the musculature has been modified from the primitive morphology. To investigate the hypotheses that these forelimbs were used in digging, we completed the first muscular reconstruction of the forelimb of *Mononykus*. Previous reconstructions of the musculature of *Tyrannosaurus rex* (Burch, in prep) and the early theropod *Tawa hallae* (Burch, 2014), both representing a primitive condition, the ceratosaur *Majungasaurus crenatissimus*, which also displays extreme forelimb reduction (Burch, 2017), and other Alvarezsaurids were used as a foundation and combined with an analysis of homologous osteological correlates found in *Mononykus* to develop a phylogenetically-informed muscle reconstruction and help us better understand its forelimb function. Comparisons with the myology of more basal taxa allowed us to identify extreme modifications in the forelimb that greatly improve the leverage of a number of muscles acting on the shoulder, elbow, and wrist.

MATERIALS AND METHODS

This reconstruction is based on the myology of early theropod dinosaurs *Tawa hallae* (Burch, 2014), *Majungasaurus crenatissimus* (Burch, 2017), and *Tyrannosaurus rex* (Burch, in prep) along with a close evaluation of superficial evidence present on the bones of the forelimb such as crests, ridges, and tubercles. The holotype of *Mononykus olecranus* (MPC 107/6; Perle et al., 1994) preserves a complete forelimb including a scapulocoracoid, humerus, radius, ulna, and manus.
Our reconstruction of the musculature utilizes phylogenetic muscle reconstruction methods (e.g., Bryant & Russell, 1992; Witmer, 1995) for the muscle attachment sites in *Mononykus olecranus*. In conjunction with the comparisons to other alvarezsaurids and phylogenetic muscle reconstruction methods, Adobe Illustrator was used to accurately trace a photo of the bone which was further employed to identify potential muscle attachment sites via critical examination of any and all muscle scars and osteological correlates. The reconstructed musculature of *Mononykus* was further compared to that of *Tawa*, *Majungasaurus*, *Tyrannosaurus* and other Alvarezsaurids along with the entire structure of the forelimb to allow for proper assessment of the attachment sites.

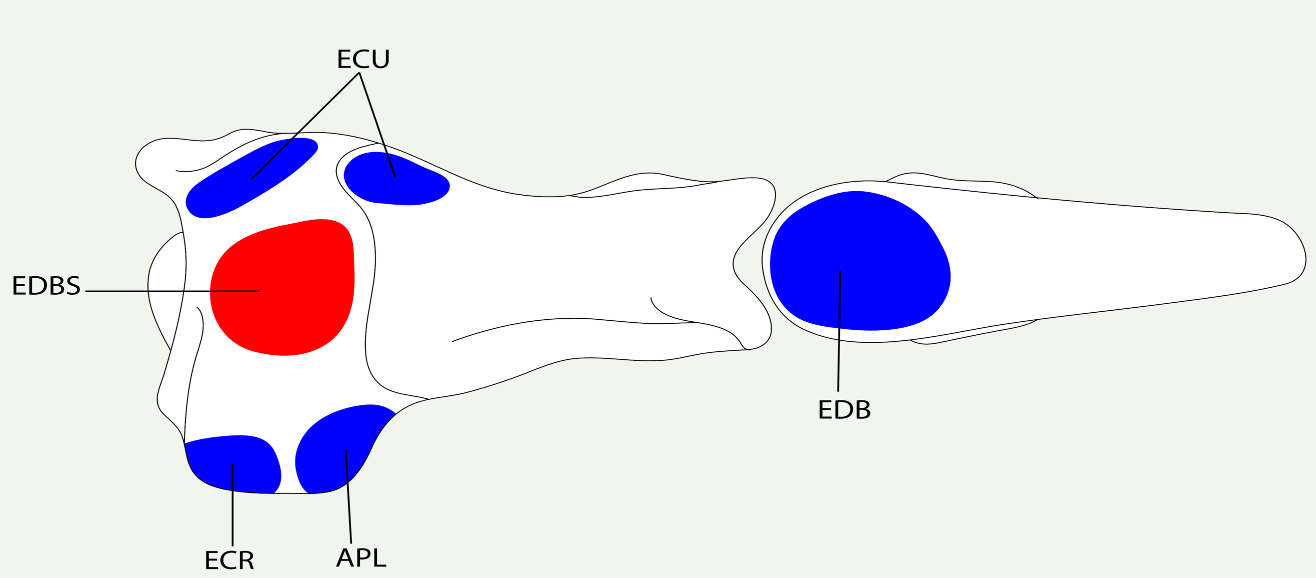

Figure 1. The left manus showing proposed muscle origins (red) and insertions (blue) in the dorsal view. APL, Abductor pollicis longus; ECR, Extensor carpi radialis; EDBS, Extensor digitorum brevis superficialis; ECU, Extensor carpi ulnaris; EDB, Extensor digitorum brevis.

RESULTS

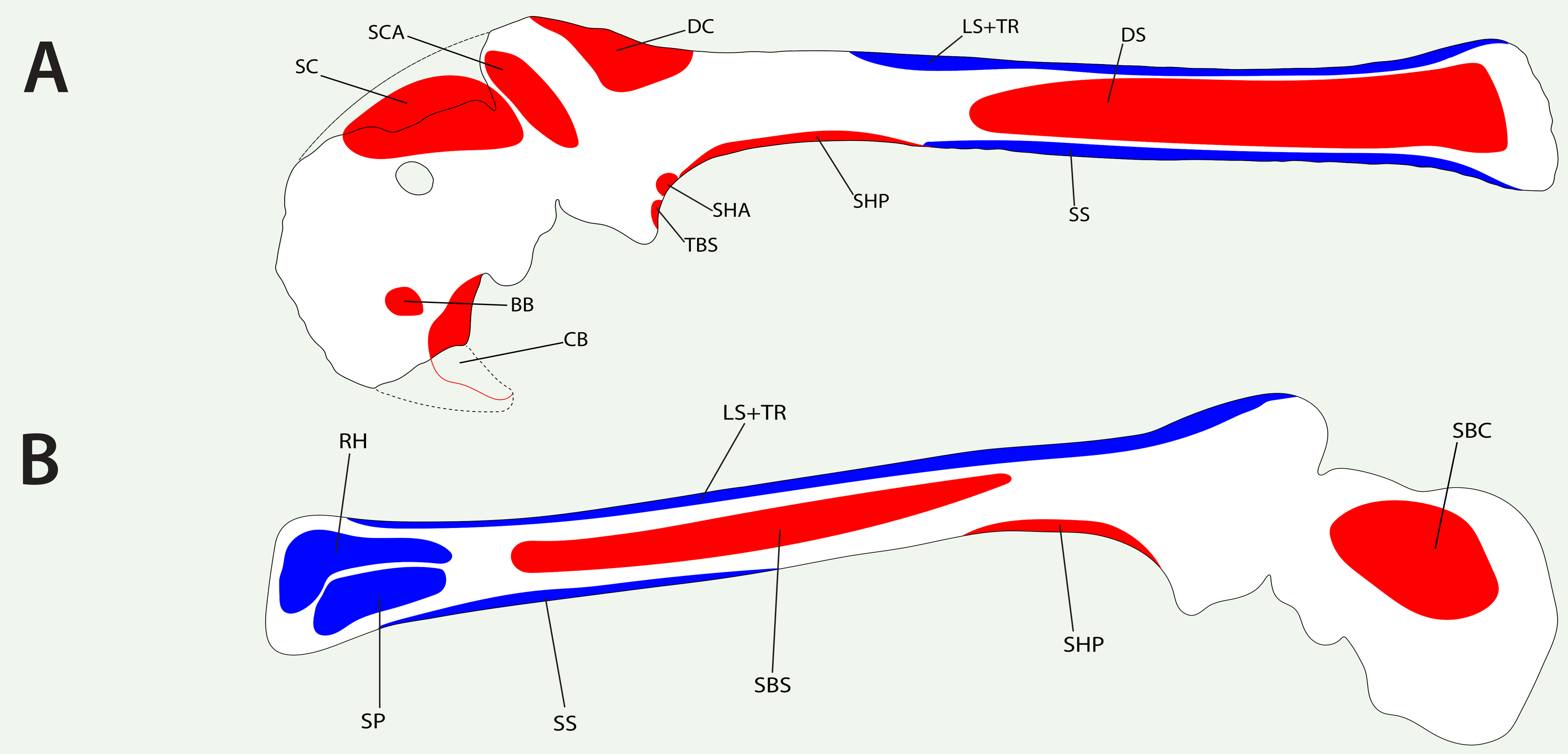

Figure 2. The left scapulocoracoid showing proposed muscle origins (red) and insertions (blue) in the lateral (A) and medial (B) views. BB, Biceps brachii; CB, Coracobrachialis; DS, Deltoideus scapularis; DC, Deltoideus clavicularis; LS, Levator scapulae; RH, Rhomboideus; SC, Supracoracoideus; SCA, Supracoracoideus accessorius; SS, Serratus superficialis; SHP, Scapulohumeralis posterior; SHA, Scapulohumeralis anterior; SP, Serratus profundus; SBS, Subscapularis; SBC, Subcoracoideus; TR, Trapezius; TBS, Triceps brachii scapularis.

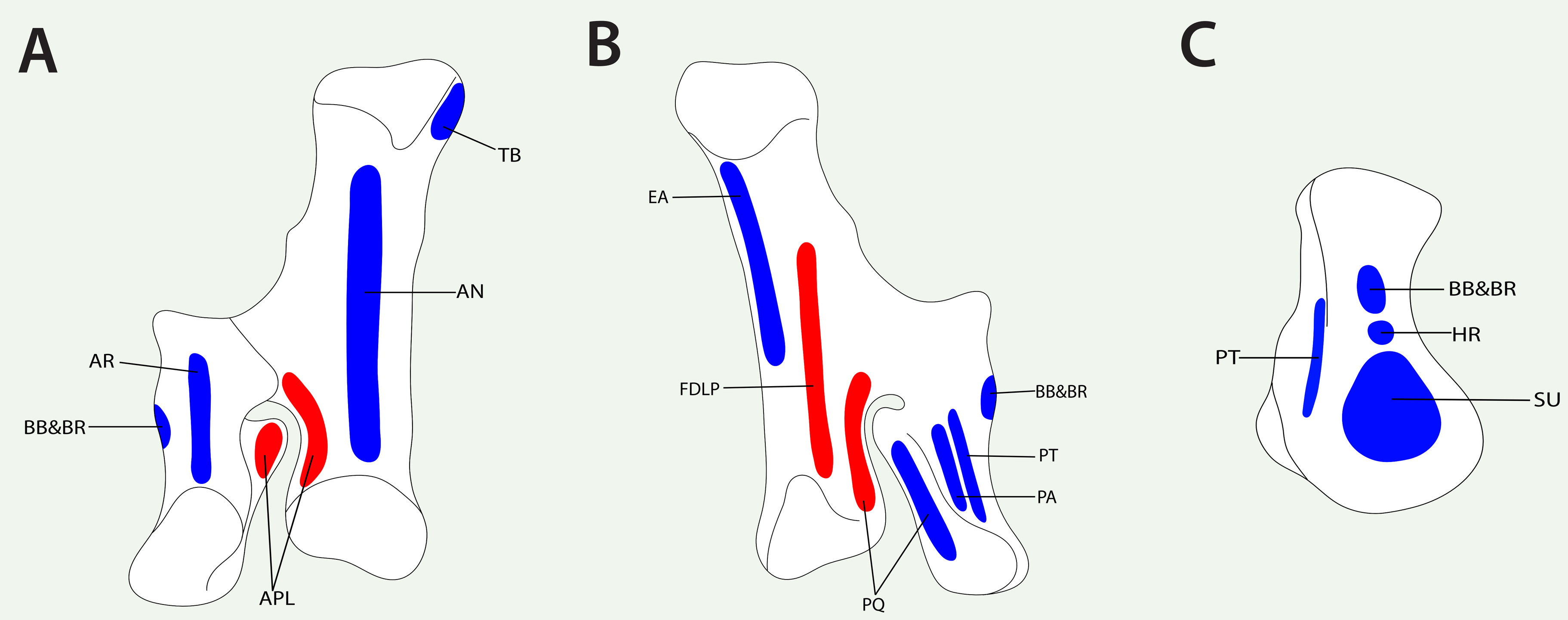

Figure 3. The left antebrachium (A and B) and radius (C) showing proposed muscle origins (red) and insertions (blue) in the lateral (A), medial (B), and anterior (C) views. AN, Anconeus; APL, Abductor pollicis longus; AR, Abductor Radialis; BB, Biceps brachii; BR, Brachialis; ECR, Extensor carpi radialis; EDBS, Extensor digitorum brevis superficialis; ECU, Extensor carpi ulnaris; EDB, Extensor digitorum brevis; EA, Epitrochleoanconeus; FDLP, Flexor digitorum longus profundus; HR, Humeroradialis; PT, Pronator teres; PA, Pronator accessorius; SU, Supinator; PQ, Pronator quadratus; TB, Triceps brachii.

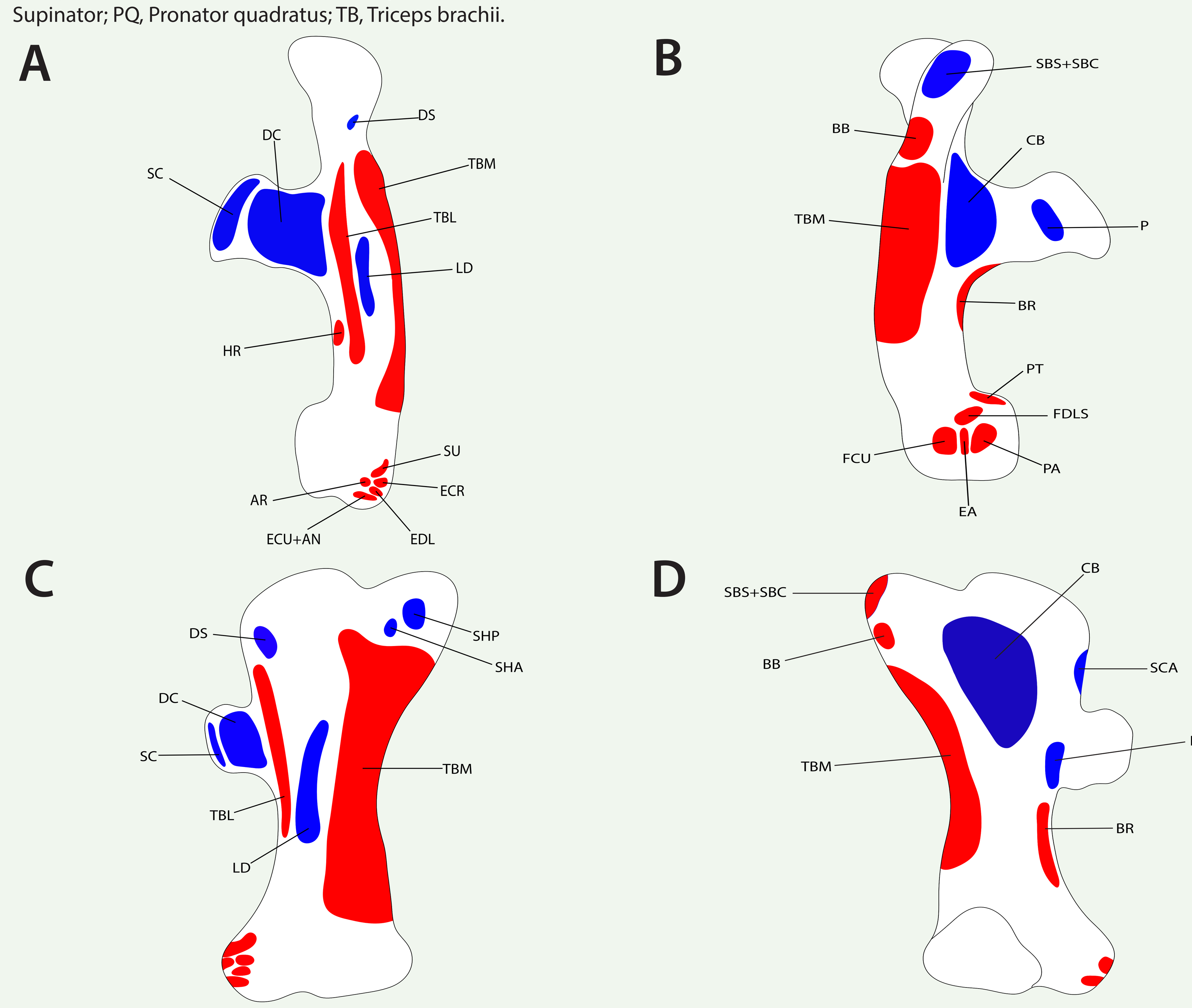

Figure 4. The left humerus showing proposed muscle origins (red) and insertions (blue) in the lateral (A), medial (B), posterior (C), and anterior (D) views. AN, Anconeus; AR, Abductor radialis; BR, Brachialis; BB, Biceps brachii; CB, Coracobrachialis; DC, Deltoideus clavicularis; DS, Deltoideus scapularis; ECR, Extensor carpi radialis; EDL, Extensor digitorum longus; ECU, Extensor carpi ulnaris; EA, Epitrochleoanconeus; FDLS, Flexor digitorum longus superficialis; FCU, Flexor carpi ulnaris; HR, Humeroradialis; LD, Latissimus dorsi; PT, Pronator teres; P, Pectoralis; PA, Pronator accessorius; SC, Supracoracoideus; SU, Supinator; SBS, Subscapularis; SBC, Subcoracoideus; SCA, Supracoracoideus accessorius; SHA, Scapulohumeralis anterior; SHP, Scapulohumeralis posterior; TBM, Triceps brachii medialis; TBL, Triceps brachii longus.

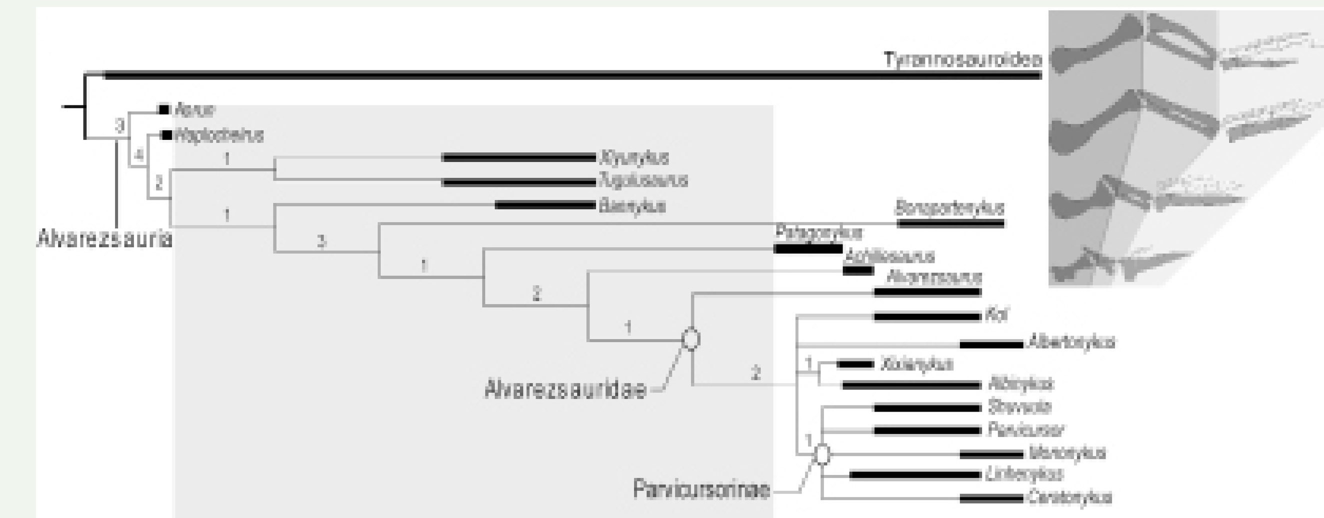

Figure 5. Time-calibrated simplified theropod phylogeny showing evolution of alvarezsaurian forelimb. (Modified from Xu et al., 2018)

CONCLUSIONS

- Compared to the more basal theropods *Tawa hallae* (Burch, 2014) and the basal alvarezsaurids *Haplocheirus sollers* (Choiniere et al., 2010), *Xiyunykus pengi* (Xu et al., 2018), and *Bannykus wulatensis* (Xu et al., 2018), the enlarged posteroventral process of the scapulocoracoid, massive internal tuberosity, and projecting deltopectoral crest suggest substantial development of muscles that provide an increase in leverage of shoulder flexion and adduction.
- The massive olecranon process of the ulna (also present in *Haplocheirus*) indicates improved leverage of elbow extensors, and the expansion of the ectepicondyle of the humerus (present in both *Haplocheirus* and *Bannykus*) suggests improvement of extension and flexion at the elbow along with extension of the wrist and digit.
- The massive internal tuberosity that is exhibited by *Mononykus* is not found in *Tyrannosaurus* (Burch, in prep) nor *Majungasaurus* (Burch, 2017) which suggests that *Mononykus* required greater power in the forelimb to perform its hypothesized scratch-digging.
- Compared to modern digging animals, pangolins have an overall forelimb morphology that is most similar to alvarezsaurs as opposed to some moles that exhibit incredibly unusual and different forelimb morphology.
- The enlarged ungual found in both pangolins and *Mononykus* allows for an increase in leverage to effectively scratch dig. Pangolins, along with *Mononykus*, also exhibit "bony stops" that increase the stability of the joints and decrease the possibility of dislocation (Hildebrand, 1985) which provides evidence that *Mononykus* performed an action similar to that of the pangolin.
- The enlarged deltopectoral crest and internal tuberosity typical of *Mononykus* are not found in the pangolin or similar modern digging animals, which suggests that *Mononykus* perhaps performed more intense shoulder and forelimb movement than modern digging animals.
- The modifications and comparisons identified in the forelimb musculature in this taxon suggest enhanced movement of the arm and claw along with increased stabilization of the joints, which is consistent with the hypothesis that *Mononykus* used its remarkably reduced forelimbs for digging or scratching when foraging for insects, similar to extant insectivorous diggers like the pangolin. Further studies and reconstructions on the forelimbs of theropods similar to *Mononykus* will add more data that may help resolve some ambiguity found within this reconstruction.

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LITERATURE CITED

Bryant H. N. et al. *Philosophical Transactions: Biological Sciences* 337, 405-418 (1992).

Burch S. H. *Journal of Anatomy* 225, 271-297 (2014).

Burch S. H. *Journal of Anatomy* 231, 1-17 (2017).

Burch S. H. *Manuscript in preparation*.

Choiniere J. N. et al. *Science* 327, 571 (2010).

Hildebrand M. In: *Functional Vertebrate Morphology*, pp. 89-109 (1985).

Longrich N. *Journal of Vertebrate Paleontology* 20, 54A (2000).

Longrich N. et al. *Cretaceous Research* 30, 239-252 (2010).

Perle A. et al. *Nature* 362, 623-626 (1993).

Perle A. et al. *American Museum Novitates* 3105, 1-29 (1994).

Senter P. *Paleobiology* 31(3), 373-381 (2005).

Witmer L. M. In: *Functional Morphology in Vertebrate Paleontology*, pp. 9-33 (1995).

Xu X. et al. *Current Biology* 28, 2853-2860 (2018).

Zhou Z. *auk* 112, 958-963 (1995).