



Figure 1. The Laysan Albatross (*Phoebastria immutabilis*) (<https://ebird.org/species/layalb>)

The Embryogenesis of the Manus of the Laysan Albatross (*Phoebastria immutabilis*)

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Introduction

The basic structure of the avian forelimb consists of 3 digits supported by corresponding metacarpals, the carpals os carpi radiale and os carpi ulnare, the radius, and the ulna. (Baumel and Wittmer, 1993). The conversion of a 5-digit hand to a 3-digit hand occurred in their dinosaur ancestors and was passed down to modern birds. (Barta et al., 2017).

Discrepancies in forelimb identity and homology are long debated topics between dinosaur paleontologists and bird embryologists. (Burke and Fedducia, 1997). Dinosaur paleontologist believe the numeration of the digits to be I-II-III while Bird embryologists believe it to be II-III-IV. (Bothelo et al. 2014: Baumels and Wittmer, 1993). Dinosaur paleontologist believe the homology of the carpals to be a radiale and an ulnare while bird embryologists believe it to be a scapholunare and a pisiform for the os carpi radiale and the os carpi ulnare respectively. (Bothelo et al. 2014: Baumels and Wittmer, 1993)

The Laysan albatross is a large pelagic bird with a long incubation period of 65 days (Prum, 2002). The embryos exhibit transient primitive features in their elongated development which could help give insight into the evolution and homologies of the avian hand (Rehorek et al., 2016).

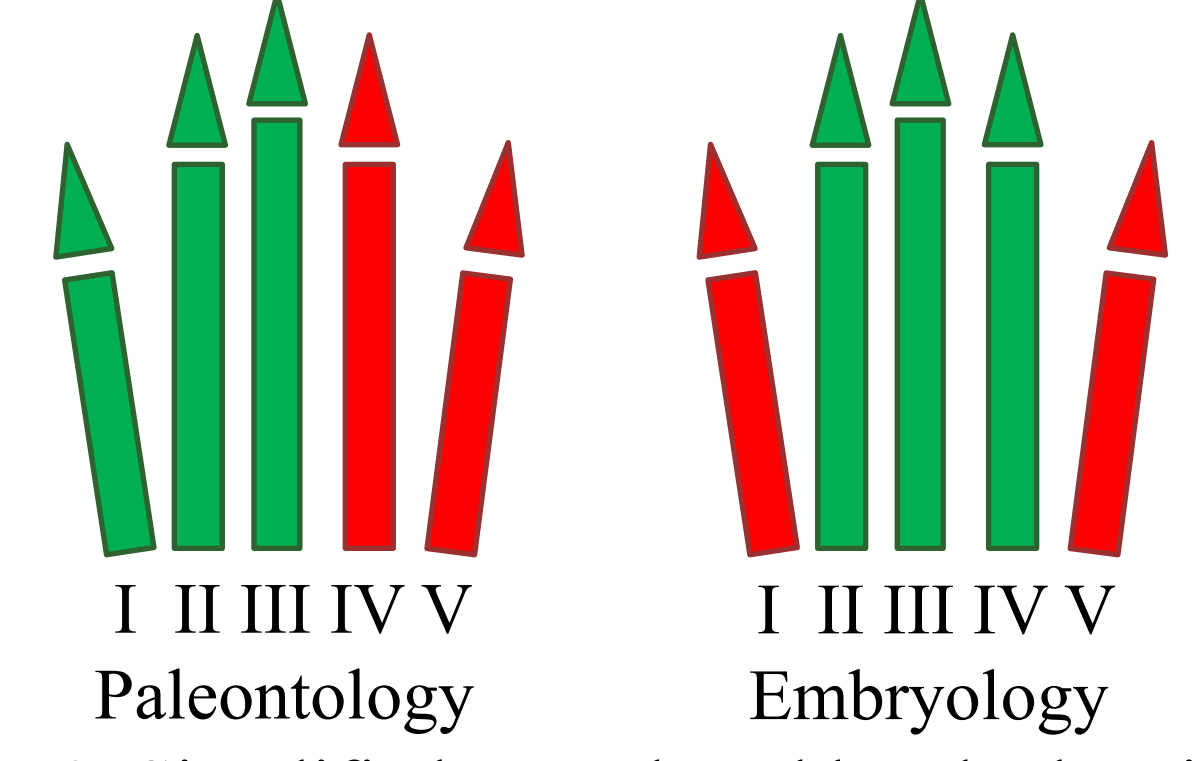


Figure 2. Simplified pentadactyl hands showing believed finger conservation from the standpoints of paleontologists and embryologists. Conserved fingers are depicted in green while fingers lost in evolution are depicted in red.

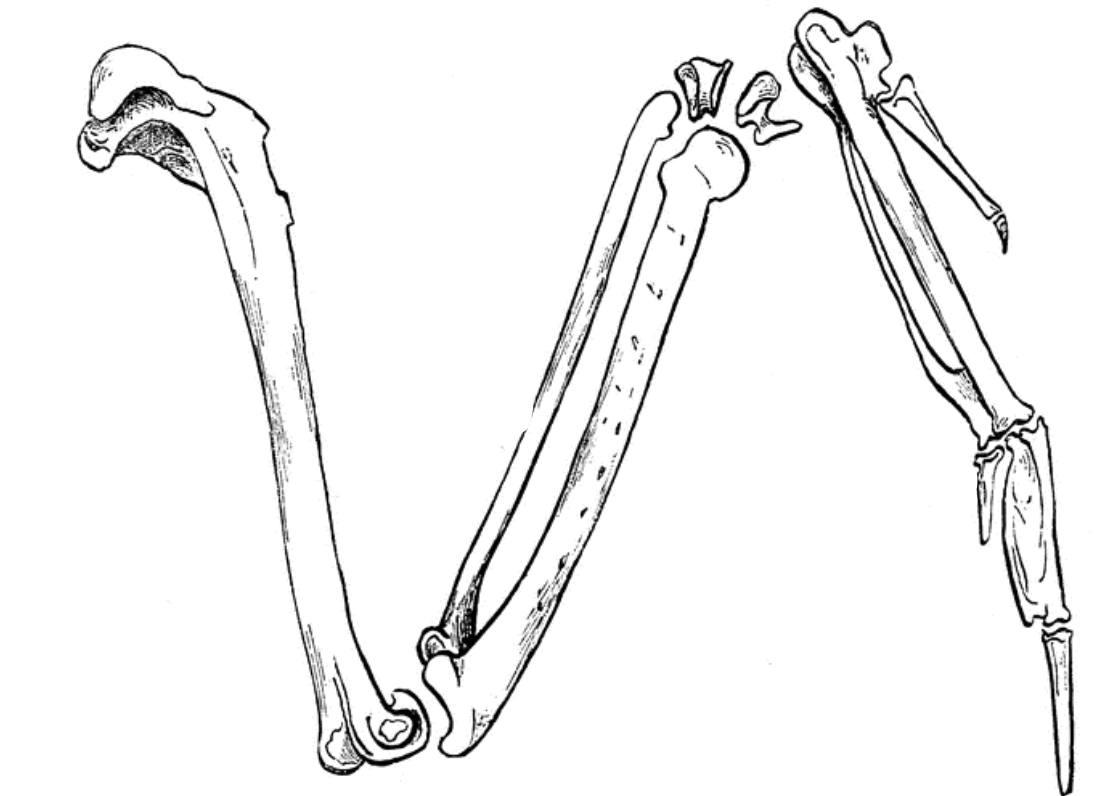


Figure 3. the structure of the forelimb in birds which correlates with the that of the Laysan Albatross. (etc.usf.edu)

Materials & Methods

The forelimbs of albatrosses from days 15, 19, 21, 23, 25, and 28 of development (embryonic stages 29, 31, 32, 34, 36, and 37) were prepared for paraffin histology and serially sectioned at a 10-micron thickness. The sections were stained with a Masson's trichrome stain and photographed using a Zeiss microscope at 25x magnification with digital imaging capabilities.

Using Adobe photoshop 2021 the sections for each day were digitally aligned. Each cartilage condensation, which is a precursor for bone generation, was outlined and filled in on separate layers from the original photos. The layers containing the filled in outlines were then exported as individual tiff format images.

Results and Discussion

Abbreviations: H:Humerus; R:Radius; U:Ulna; RL: Radiale; UL: Ulnare; P:Pisiform; C1: Embryonic carpal 1; C2: Embryonic carpal 2; C3: Embryonic carpal 3; I/II/III/IV/V: Digits I/II/III/IV/V respectively

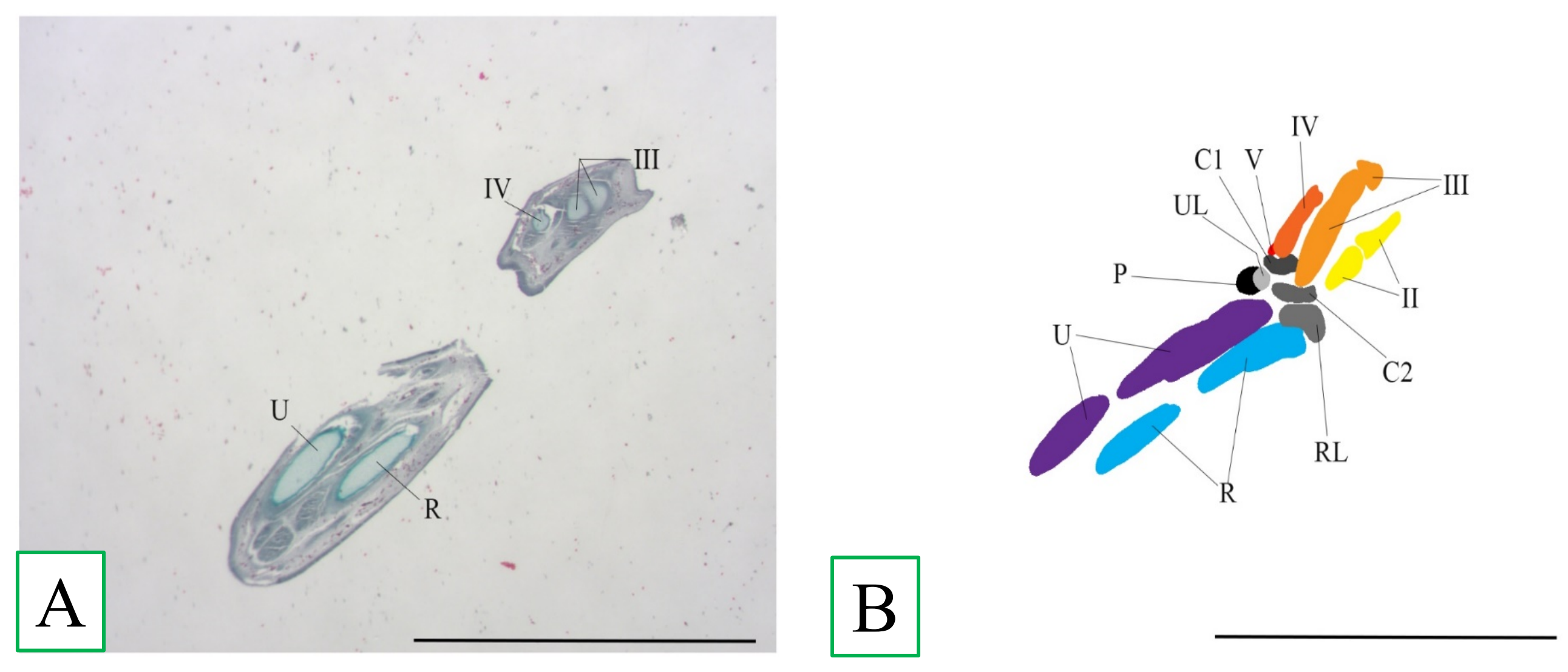


Plate 1. A palmar view of the albatross manus at day 19 (stage 31). B depicts an overlay of the outlines giving a dorsal view for full context of the manus. The carpals are still in development and a transient fifth metacarpal (V) is present starting at this stage. Scale Bar = 4mm

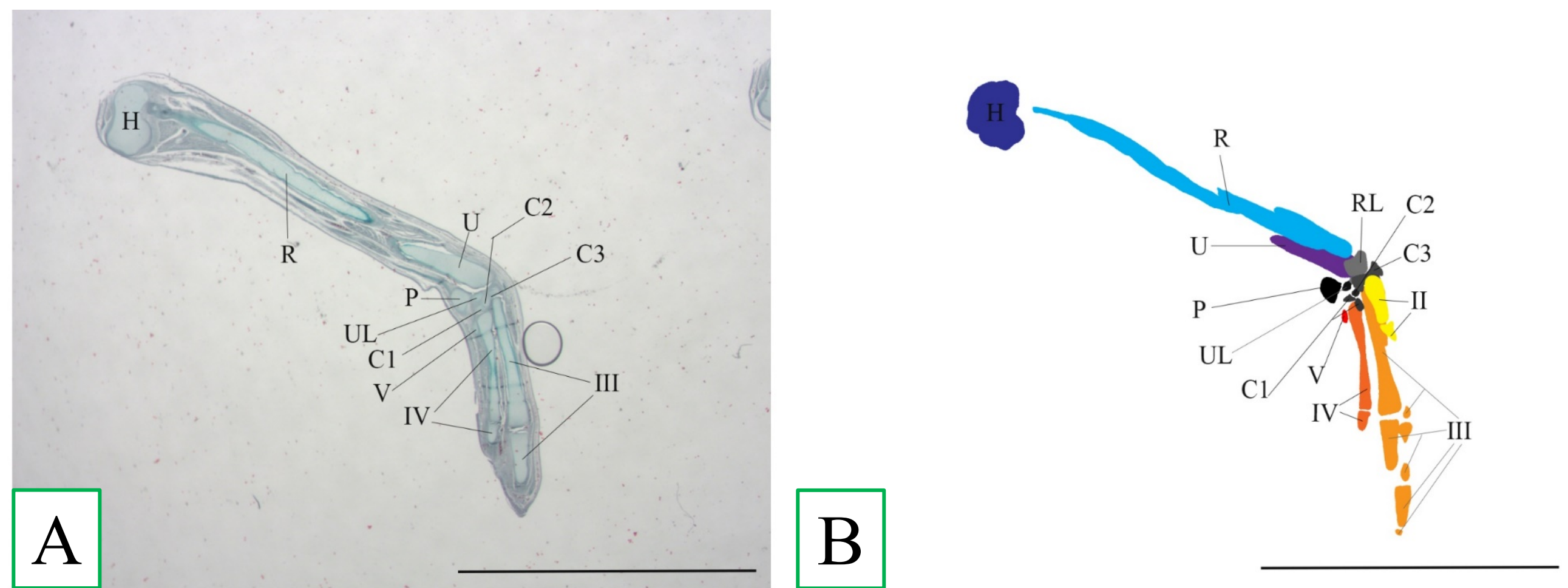


Plate 2. A medial view of the albatross manus at day 21 (stage 32). B depicts an overlay of the outlines giving a full context to the manus. The maximum number of embryonic carpals are present, metacarpal V is still visible, and the embryonic ulnare is starting to degenerate. Scale Bar = 5mm

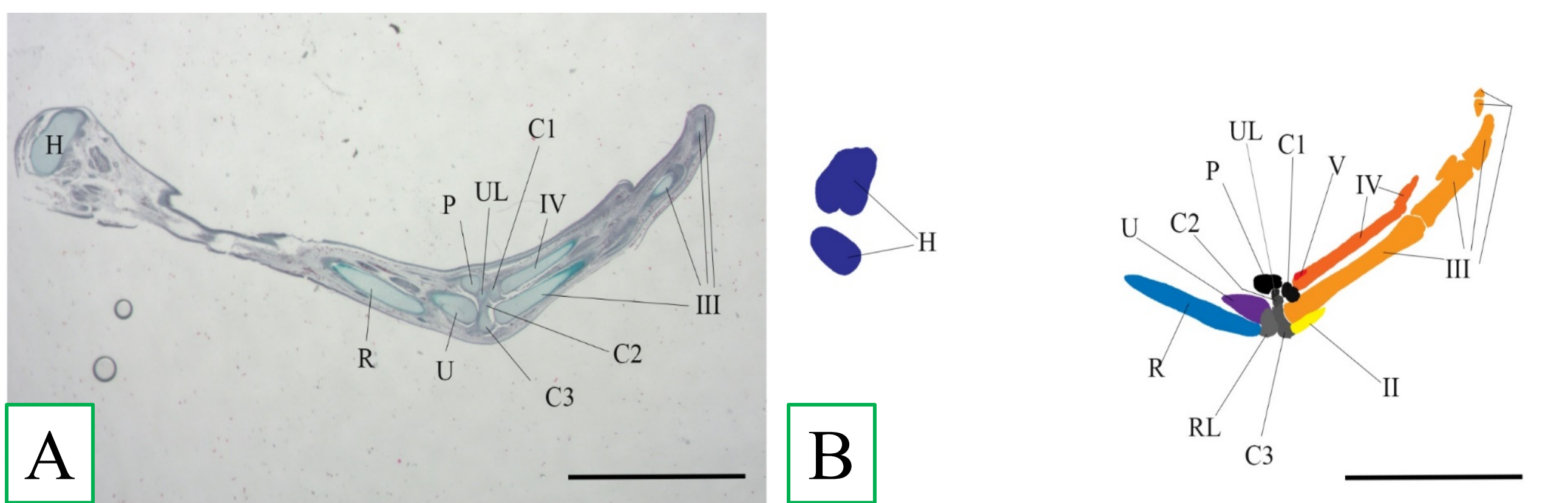


Plate 3. A medial view of the albatross manus at day 23 (stage 34). B depicts an overlay of the outlines giving a full context to the manus. C1, C2, and C3 are lined up and, C2 and C3 begin to fuse into a semilunate carpal. Metacarpal V is still present at this stage. Scale Bar = 3mm

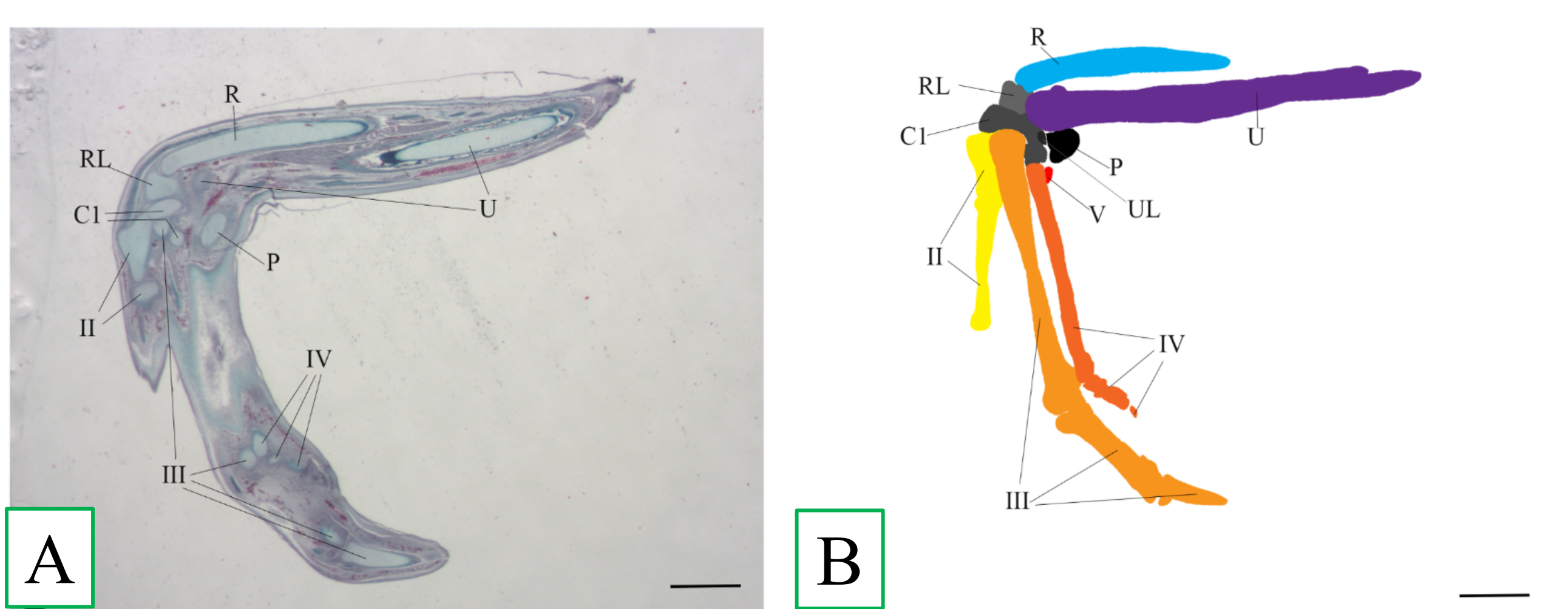


Plate 4. A palmar view of the albatross manus at day 25 (stage 36). B depicts an overlay of the outlines giving a full context to the manus. Fusion into a singular carpal proximal to metacarpals shows that a semilunate carpal had formed before C1 will fuse with the metacarpals of III and IV. Metacarpal V is still present at this stage. Scale Bar = 1mm

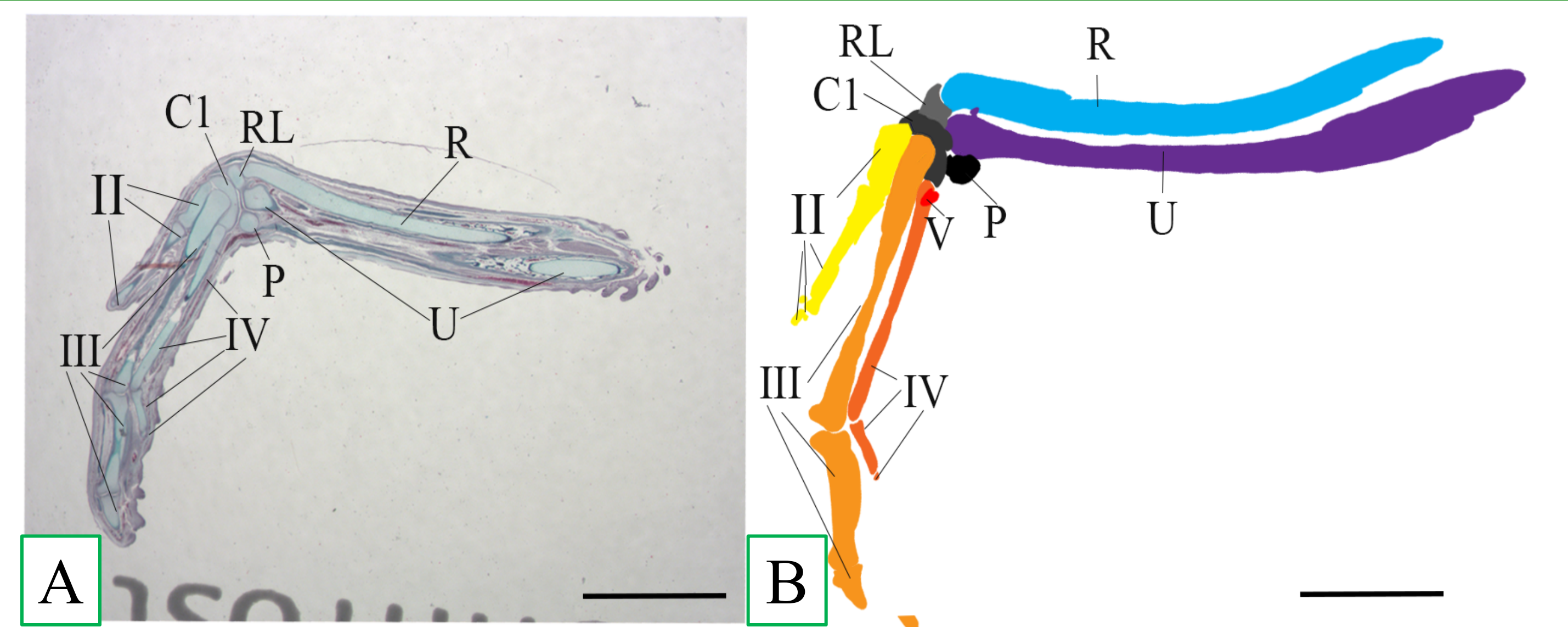


Plate 5. A palmar view of the albatross manus at day 28 (stage 37). B depicts an overlay of the outlines giving a full context to the manus. Complete degeneration of the ulnare leaves the pisiform as the primary center for ossification on the lateral side of the manus showing that it will become the os carpi ulnare. Metacarpal V is still present at this stage. Scale Bar = 3mm

Conclusion

- A study showing that ostriches contain precursors for digits I and V in early embryogenesis supports the proper identification of digit V in the Albatross (Feduccia and Nowicki, 2002)
- The presence of a transient metacarpal V supports the numbering of digits as II-III-IV.
- Degeneration of the embryonic radiale supports that the os carpi ulnare is a pisiform, supporting homologies proposed by bird embryologists and also seen in Bothelo et al. (2014).
- Formation of an embryonic semilunate from embryonic carpals 2 & 3 support a Bird-theropod link. (Xu et al., 2014)
- Studies involving chicken embryos and immunofluorescent staining for type II and IX collagen expression showed distinct foci in the semilunate and radiale suggesting the fusion of embryonic carpals for formation (Bothelo et al., 2014).
- Future investigation using florescent immunohistochemistry in earlier embryonic stages could help clarify homologies of the carpals or reveal other possible primitive features.
- Future investigations using birds with longer incubation periods, like the Kiwi (74-84 days) could be used to investigate the possibility of other primitive features (Reid and Williams, 1975)

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