Supplementary Information

Retention of the flight-adapted avian finger-joint complex in the Ostrich helps identify when wings began evolving in dinosaurs

Joel D Hutson and Kelda N Hutson

Ostrich 2018, 89(2): 173–186. https://doi.org/10.2989/00306525.2017.1422566

Extended Finger-joint Descriptions

First interphalangeal (IP1) joint of *digitus alularis*. Despite a bony I_2 ungual core, with the convex proximal articular surface reported in birds with jointed phalangeal claws rather than horny spurs (Gadow and Selenka 1891: 75; Vialleton 1916; cf. Banzhaf 1929: 137), the *S. camelus* IP1 joint was found to be almost completely immobilised by integument and interphalangeal fascia throughout the ROM1–ROM3 levels of dissection treatment. This meant that the I_2 claw was not diarthrotic, as was reported by Banzhaf (1929: 135) for *Opisthocomus cristatus* (Hoatzin) I_2, but resisted ROM1–ROM3 flexion/extension and adduction/abduction. Furthermore, Banzhaf (1929) noted that the musculature to *digitus alularis* in *O. cristatus* chicks could not affect IP1 joint movement. Finally, in ROM4 and ROM5 the distal and proximal I_2 articular surfaces of *S. camelus* were both convex (Figure 2; a type of joint predicted to not exist in nature by Stolpe 1932: 173), making it impossible to ascertain the extent of mobility. Therefore, ROM degree data were not gathered for the IP1 joint.

***Digitus alularis* metacarpophalangeal (MCP1) joint**. The *S. camelus digitus alularis* is not a serviceable alula (little wing), meaning that it does not function aerodynamically in flight as with volant birds (Lee et al. 2014). It has long been reported in the literature that many volant birds are capable of actively abducting *digitus alularis* away from the rest of the manus. Although it's overall morphology is unlike those reported for various volant neognathous birds, the *S. camelus digitus alularis* exhibits similar joint morphologies. For example, the morphology of the *S. camelus* MCP1 joint matches that described for *O. cristatus* by Banzhaf (1929: 135). It

has a concave proximal articular surface, and a triangular, concave distal articular surface (Figure 2). Thus, the MCP1 joint of *S. camelus* is a saddle joint, as stated in general for most birds by Sy (1936), who fully described its functional morphology in neognathous birds. In general, the ulnar edge, or flange, of the proximal concavity of the *S. camelus* MCP1 joint is larger than the radial (Figures 1 and 2). However, the distal articular surface of FMNH 489294 had a more prominent radial bony flange, which did not change the pattern of mobility. In contrast with the IP1 joint, the *S. camelus* MCP1 joint could be manipulated at all dissection treatment levels. The ROM1–ROM3 replicate-measurement data for *digitus alularis* were taken from the MCP1 joint by grasping the immobilised I_2 claw with tweezers.

Concerning *S. camelus* MCP1 joint mobility that could be tested with a ROM study, Prechtl (1846: 26, 27) reported that the movements of abduction and adduction (presumably forced *ex vivo*) are possible, while Gadow and Selenka (1891: 75) added that slight amounts of pronation and supination may also be possible. Sy (1936) agreed with the latter assessment, but argued that the avian MCP1-joint morphology should result in passively forced supination during the downstroke, and passively forced pronation during the upstroke. Banzhaf (1929) inferred that the *S. camelus digitus alularis* could be slightly flexed *in vivo* by the *flexor digitorum profundus*. Alix (1874) reported that all three *S. camelus* digits are capable of slight *ex vivo* adduction/abduction and long-axis rotation. Moreover, Alix (1874: 413) claimed that, unlike with other birds, *S. camelus* finger extensors were capable of a “trace” of extension.

Here, we could not easily force flexion/extension at the *S. camelus* MCP1 joint until ROM4. Namely, throughout treatment levels ROM1–ROM3 each *S. camelus digitus alularis* firmly resisted *ex vivo* flexion/extension, and long-axis rotations into pronation or supination at the MCP1 joint. The resistance of the *S. camelus digitus alularis* to flexion/extension (and

concomitantly forced long-axis rotation during these movements; Sy, 1936), may be due to the observation that the saddle-shaped MCP1 joint in *S. camelus* has even more restrictive surrounding soft tissue (ligaments) than is reported for volant neognathous birds (Banzhaf 1929). Moreover, as noted by Hultkrantz (1897), it is highly unlikely that an animal can naturally perform movements at a joint *in vivo* that have to be moved with extreme force in fresh specimens *ex vivo*. Thus, even though slight displacements were observed during ROM1 for MCP1 joint flexion/extension and pronation/supination, they were not consistently measurable, and it is assumed here that these movements could not have occurred *in vivo* in *S. camelus*. By contrast, Vazquez (1995), in an *in situ* ROM study that electrically stimulated manual musculature in anesthetized rock doves (*Columba livia*), observed abduction/adduction and flexion/extension at their MCP1 joints, but pronation/supination were restricted. Finally, Raikow et al. (1988) did not report on ROM at this joint, presumably due to its loss in penguins, their primary focus of comparison with other birds.

In ROM1 initial resistance was immediate for MCP1 joint adduction, due to impaction against the fleshy radial edge of *digitus major*. As such, although both adduction and abduction were possible at this joint, the majority of movement was abduction away from *digitus major*. The inclinometer was used to gather ROM data in degrees in a vertical plane for ROM1. One observer would press the inclinometer flush to the radial edge of *digitus alularis*, while the other observer recorded degree data that were blind to the manipulating observer. For ROM2–ROM5 data gathering, the same method of data recording was followed, but with the finger goniometer. During ROM2–ROM5 measurements, the *S. camelus* manus was placed horizontally, palmar side up following the standardized position shown in figure 1b of Vazquez (1995). For all replicate measurements any differences between abduction and adduction were subtracted for a

total ROM movement in degrees.

Common *digiti major* and *minor* MCP2/MCP3 joint. The overall morphology of *digitus minor* (i.e. III_1 + III_2) in *S. camelus* bears some resemblance to those of volant neognathous birds (Gilbert et al. 1981), while the morphology of II_1 in *S. camelus* was observed to be wholly unlike that of volant neognathous birds (Figures 1 and 2). Nonetheless (as with *digitus alularis*) the *S. camelus* MCP1 and MCP2 joint surfaces were found to be functionally equivalent to those reported for volant neognathous birds. Specifically, they are of the ball and socket type, albeit with somewhat flattened proximal convexities and distal concavities (Prechtl 1846; Banzhaf 1929; cf. Sy 1936). Notably, as documented previously by Prechtl (1846) and Vazquez (1995), due to the tightly appressed nature of the avian II_1 and III_1 phalanges at their proximal epiphyses, it is difficult to initiate isolated movements of either *digitus major* or *minor* at their MCP joints. Moreover, as described and illustrated by Sy (1936: Figure 47), the presence and orientation of fibers within the II_1/III_1 interosseous ligament restrict and control ROM in this area. Consequently these workers functionally treated the avian MCP2 and MCP3 joints as a common MCP2/MCP3 joint, a condition observed here as well for *S. camelus* (Figure 2).

Despite the ball and socket nature of the avian MCP2/MCP3 joint, the compressed proximal epiphyses, a restrictive common synovial capsule, and a stiff II_1/III_1 interosseous ligament limit pronation/supination and flexion/extension out of the plane of the semi-pronated manus. For example, Prechtl (1846: 29) and Alix (1874: 323–324, 335–336) observed in various birds that the MCP2/MCP3 joint allows *ex vivo* abduction/adduction, with some pronation/supination enabled by an additional joint (see below). By comparison, while observing that isolated movements of II_1 and III_1 were not possible, Banzhaf (1929: 136) stated that limited amounts of pronation/supination and perhaps a slim amount of flexion can be forced at the

MCP2 joint in *O. cristatus*. By contrast, Banzhaf (1929) was only able to measure the ROM of the MCP3 joint of *O. cristatus* using abduction/adduction. It is important to note here that Banzhaf (1929) used *ex vivo* manipulations of preserved specimens. Like Banzhaf (1929), Sy (1936: Figure 44) claimed via *ex vivo* manipulations that (unlike the MCP1 joint) the MCP2 half of the avian MCP2/MCP3 joint is adapted primarily for active long-axis rotations. Sy (1936: Figures 45 and 46) also reported that extensive abduction/adduction is possible at the MCP2-joint area, along with slight flexion/extension via soft-tissue displacement. However, Sy (1936: 278–279) also proposed that the MCP3 portion of the avian MCP2/MCP3 joint is more adapted for hinge-like abduction/adduction than long-axis rotations. Using this reasoning, Sy (1936) suggested that movements between II_1 and III_1 were more independent than prior researchers had proposed (see below). Vazquez (1995) may have provided some empirical tests of Sy's (1936) claims. Although he also noted that isolated movements were not possible at the MCP2 and MCP3 joints, Vazquez (1995) reported abduction/adduction as well as pronation/supination at the MCP2 joint of *C. livia* via electrical stimulations, but only flexion at the MCP3-joint area. Raikow et al. (1988) did not discuss or measure any MCP2/MCP3 movements out of the plane of the manus (but see Bannasch 1986).

Common *digiti major* and *minor* II_1/III_1 fulcrum joint. Alix (1874: 323) reported that another joint that is intrinsically linked with the avian MCP2/MCP3 joint is also found in *S. camelus*; Prechtl's (1846: 29, 50) II_1/III_1 "hypomochlion" or "fulcrum joint" (see also Gadow and Selenka 1891: 281, 283; Sy 1936). This joint occupies the area where the proximal epiphyses of II_1 and III_1 are firmly pressed together (Figures 1 and 2G). As was mentioned above, although the II_1/III_1 fulcrum joint is a flattened gliding joint, soft tissues surrounding the ball and socket MCP2/MCP3 joint have been argued to inhibit isolated flexion/extension of II_1or

III_1, supposedly causing long-axis rotations instead due to pivoting at the II_1/III_1 fulcrum joint. Thus, Prechtl (1846: 29, 50) predicted that phalanges II_1 and III_1 exhibit slight amounts of shared *ex vivo* pronation during downstroke, and supination during upstroke at the II_1/III_1 fulcrum joint. Prechtl (1846) postulated that these movements are adaptations to allow the manus to displace during flight or wing folding, or to adjust nearby feathers. Sy (1936) agreed with Prechtl's (1846) assessment of II_1/III_1 fulcrum joint mobility, but with the addendum that rotatory movements were only allowed at the MCP2 portion of the MCP2/MCP3 joint, because: i) the axis of long-axis rotation passed between II_1 and III_1 at the fulcrum joint, and; ii) the MCP3 portion of the avian MCP2/MCP3 joint only allows abduction/adduction to be forced *ex vivo*. Unfortunately, this disagreement in avian II_1/III_1 fulcrum-joint function has not been tested by later studies. Raikow et al. (1988) neither measured rotational ROM in their *ex vivo* ROM study of MCP2/MCP3 joints, nor mentioned the II_1/III_1 fulcrum joint. Likewise, Vazquez (1995) did not mention the II_1/III_1 fulcrum joint in a ROM study of *C. livia* finger-joint movements. However, Vazquez (1995) did find, in contrast to the forced *ex vivo* pronation observed in prior studies, that pronation could not be forced past the plane of the manus in *C. livia* finger joints via *in situ* electrical stimuli of manual musculature.

Here, despite possessing MCP2/MCP3 and II_1/III_1 fulcrum joints, due to soft tissue connections that appeared to be more restrictive than those previously reported for volant neognathous birds, we found in ROM1–ROM3 that it was not possible to force isolated, and therefore reliably measurable *ex vivo* pronative/supinative or flexor/extensor movements at these two joints in *S. camelus*. Moreover, graphically portraying movement at these and the other vestigial joints of *S. camelus* would not be accurate models for how homologous joints behave during flapping/gliding in volant birds. This information explains why ROM degree data for the

II_1/III_1 fulcrum joint were not collected by us, and its purported flight-related motions in volant birds were not illustrated here. Finally, no flexion/extension articular edges could be found on the cartilaginous articular surfaces of the MCP2/MCP3 joints in practice dissection specimens, which is another reason why flexion/extension measurements were not attempted. Thus, only the movements of abduction and adduction of *digiti major* and *minor* as one unit at the *S. camelus* MCP2/MCP3 joint were repeatedly measured in this study.

Replicate measurements in degrees for the MCP2/MCP3 joint were recorded with the finger goniometer throughout the ROM1–ROM5 stages of dissection treatment. The manus was held firmly and horizontally against the stationary goniometer with one hand by an observer, while the other hand moved the combined *digiti major* and *minor* distal to the MCP2/MCP3 joint. The other observer pressed the mobile edge of the goniometer to the radial edge of II_1 while gathering degree data blind to the other observer. In ROM1, initial resistance was immediate for ulnar deviation, due to the stiffened, quill-filled trailing edge of the manus.

During ROM4 replicate-measurement gathering at the MCP2/MCP3 joint, neither the MCP2, nor the MCP3 articular surfaces were observed to be ginglymoid (i.e. adapted for uniplanar, hinge-like movements; cf. Sy 1936), but there were fine lines on complimentary cartilaginous articular surfaces that demarcated where ulnar and radial deviation stopped at their extreme ROM. Due to foreknowledge of the restrictive influence of the surrounding soft tissues that had been removed before ROM4, these lines were used as guides during ROM4 data gathering to move both II_1 and III_1. The finger goniometer was used during this level of dissection treatment in a manner similar to dissection treatment levels ROM1–ROM3. However, because the II_1/III_1 interosseous ligament had been severed at the ROM4 level of dissection treatment, one observer would press and move phalanges II_1 and III_1 together (i.e. pressed firmly

together at their shared fulcrum joint), while the other observer gathered degree data that were unknown to the manipulating observer. Phalanges II_1 and III_1 were moved radially into abduction until II_1 met the edge of the marked predetermined articular surface (i.e. edge of the synovial capsule). Similarly, the same bones were then moved together ulnarily in to adduction until disarticulation of III_1 occurred. A similar procedure was used during ROM5 data gathering. This methodology was analogous to that used for the carpal elements in the EPB study of wrist joints using these specimens (Hutson and Hutson 2014), and unlike the impaction methodology used in the EPB studies of the finger, elbow, and shoulder joints (Hutson and Hutson 2012, 2013, 2015a).

***Digitus major* proximal interphalangeal (PIP2) joint**. Regarding possible *ex vivo* manipulations of the PIP2 joint between II_1 and II_2, Sy (1936) disregarded the avian PIP2 joint as rudimentary and meaningless. By contrast, Banzhaf (1929: 138) assumed that flexor musculature could affect abduction at this joint in juvenile *O. cristatus*, but did not report any attempted ROM measurements in degrees. Banzhaf (1929) also noted that the avian PIP2 joint is of the ball and socket type (elongated in the plane of the manus in *S. camelus*; Figure 2d), with a proximal convexity and distal concavity. In *S. camelus*, Alix (1874: 324) stated that II_2 can perform adduction/abduction and long-axis rotation. In partial support of Alix (1874) and Banzhaf (1929), Vazquez (1995) used *in situ* electrical stimulations of anesthetized *C. livia* to induce abduction/adduction, flexion/extension, and pronation at this taxon's PIP2 joint. Finally, Raikow et al. (1988) did not measure ROM at the PIP2 joints in their study, likely because this joint (like the MCP2/MCP3) is reported to have become immobilised throughout the evolution of underwater flapping in penguins (Bannasch 1986).

Here, as with the *S. camelus* MCP1 and MCP2/MCP2 joints, we were unable to reliably

force PIP2-joint long-axis rotations or flexion/extension, due to surrounding soft tissues that are presumably more restrictive than those reported for volant neognathous birds. Thus, only the movements of abduction/adduction within the plane of the manus were used to gather degree data. The tools and methodology for gathering degree data were the same as those discussed above for the MCP2/MCP3 joint, except that II_2 + II_3 was grasped and manipulated with tweezers rather than with fingers.

***Digitus major* distal interphalangeal (DIP2) joint**. Neither Alix (1874) nor Banzhaf (1929) reported any attempt to induce or measure *ex vivo* movement at the DIP2 joint between II_2 and the II_3 claw in adult *S. camelus* or juvenile *O. cristatus* specimens, respectively. Here, as with the IP1 joint mentioned above, the *S. camelus* DIP2 joint was observed to be completely immobilised by interphalangeal fascia throughout the ROM1–ROM3 stages of dissection treatment. Likewise, the II_2 and II_3 articular surfaces were both convex, precluding accurate ROM4 and ROM5 replicate measurements. Thus, repeated-measures data were not gathered from this joint.

***Digitus minor* interphalangeal (IP3) joint**. Although it is reported that some *S. camelus* specimens possess a free III_2 claw at an IP3 joint, all specimens examined for this study exhibited completely fused IP3 joints (Figure 1). Likewise, reports of an III_2 claw in rheas are difficult to substantiate (Friant 1959). According to some authors, reports of free IP3 joints may reflect observations of embryos with unfused elements rather than the adult condition (Alix 1874: 323; Gadow and Selenka 1891: 76).