ON THE SPURS ON BIRDS' WINGS

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In handling specimens of birds bearing spurs on their wings, two points emerged which seem to be little known or new: (a) the horny covering of the wing spur, in some species, undergoes molt, and (b) the spur in some birds is a modification of a process already in existence for another purpose. In presenting these points, a summary of our knowledge regarding wing spurs is presented.

In early writings spurs and claws were confused until Jefferies (1881) pointed out that they are quite different: claws are horny sheaths on the tips of terminal phalanges (for a review of their occurrence see Fisher, 1940); spurs are projecting bony cores with an outer layer of horn, similar to the horns of cattle. Between the bone core and horn covering is a layer of tissue, the outer part of which produces new horn material. The horn must obviously increase in length from the base, the tip being the oldest (Gadow, 1891).

Well developed spurs occur on the tarsi of many gallinaceous birds, but wing spurs, all borne on the forward edge of the wing in the neighborhood of the carpal joint, are found only as follows.

ANSERIFORMES

Anhimidae (Screamers).—All three species of this family have two conspicuous, stout, smoothly tapering, sharp spurs with a slight radial curve on each wing; the proximal spur is much the larger. They are both on the fused metacarpals; the proximal spur on the process of metacarpal I which is for the attachment of the extensor muscles; the distal spur on the distal end of metacarpal II (as figured by Sclater, 1886:150). Specimens examined show fine lines about the base of the spurs indicating growth in layers, and one specimen had three separate bands of these lines suggesting annual growth. The molt that occurs complicates this idea, however. Following are descriptions of the spurs in the three species, as seen in specimens in the Chicago Natural History Museum:

Anhima cornuta: the spur is triangular in cross section, with the side of the spur facing proximally, somewhat concave, and all the corners as well as the tip sharp; length of proximal spur, males, 58–61; females, 50–55; distal spur, males, 15, 16; females, 11–17 mm.

Chauna torquata: spur nearly oval in cross section but with a sharp-edged flange near the proximal edge, recalling the triangular, sharp-edged spur of the previous species; length of proximal spur, males, 30–47; females, 35–45; distal spur, males, 13–20; females, 15–17 mm.

Chauna chavaria (Fig. 1C): spur smoothly oval in section, sharp only at tip; length of proximal spur, male, 28; female, 30; distal spur, male, 18; female, 18 mm.

Anatidae (Ducks, Geese, etc.).—The ducks and their relatives number some 144 species. A number of genera have a projection near the carpal joint. This projection is conspicuous as a knob especially in *Sarkidiornis* and *Chloephaga* in which it projects beyond the feathering and bears a horny covering. This seems to be the process of metacarpal I. However, only two genera of the Anatidae, both monotypic, have a single well-developed spur on each wing. In the two species the spurs differ in position and some details; descriptions follow.

Plectropterus gambensis (Fig. 1D): the spur is borne on the radial carpal bone (skeleton, C.N.H.M.) as shown by Sclater (1886, p. 300). The spur is stout, strong, with a gradual taper, nearly oval in cross section, but with a tendency toward flanges giving small sharp edges. There is an area about 5 mm. from the base that suggests a growth ring in all specimens. Length of the spur in males is 20–25 mm., in females, 18–22 mm. In one specimen there is a small pad of horn on an auxiliary spur that appears to be the tip of the process of metacarpal I.

Merganetta armata (Fig. 1E): the spur is borne on the basal anterior edge of the metacarpal on the process of metacarpal I (specimen C.N.H.M.). The spurs are stout at the base, oval in section, and taper abruptly, but with an attenuated, very sharp tip. They differ from the spurs of *Plectropterus* also in that the horny sheath ends abruptly basally with an abruptly rounded edge indicating thickness of the horny covering to the base. No suggestion of growth rings is evident. Length of the spur in males is 9–17 mm.; in females, 6–13 mm. The spur of the female usually has a less attenuated and less sharp point.

CHARADRIIFORMES

Jacanidae (Jacanas).—Of the seven species in six genera in this family, only two species have well developed spurs:

Jacana spinosa (Fig. 1G) has a long conspicuous spur, borne on the process of metacarpal I (skeleton, C.N.H.M.), as figured by Sclater (1886:301). The spur is almost conical, with a slightly attenuated and very sharp tip. Faint lines suggesting growth rings are somewhat evident. The spurs of males measure 7–10; of females, 8–10 mm.

In *Hydrophasianus chirurgus* the spur is apparently similarly located and is short and very sharp; in males it measures 3–5; in females, 4–7 mm.

Another aspect of wing armature in this group is noteworthy in this connection. In *Actophilornis africana* (Fig. 1F), *A. albinucha*, *Metopidius indicus*, and *Irediparra gallinacea*, the radius is flattened and heavy, much heavier than the ulna (Forbes, 1881:646). In these species, spurs are absent, being represented only by the knob of the process of metacarpal I. *Jacana spinosa* and *H. chirurgus*, both with sharp spurs, have "normal" radii (Forbes, 1881:646–7).

Charadriidae, subfamily Vanellinae (Wattled Plovers and Lapwings).—Of the 25 species in 19 genera belonging to this subfamily I have examined 24[1] species in 18 genera and find a conspicuous spur in 10 species in 7 genera, a very small but distinct sharp spur in 4 species in 4 genera, and a condition in which a spur is represented only by the knob formed by the process of metacarpal I in 7 genera (see list below).

The following species have conspicuous, well developed spurs:

Species	*Length of Spur*	
	Male	*Female*
Belonopterus chilensis (Fig. 1H)	8–14 mm.	8–12
Xiphidiopterus albiceps	18–23	16–22
Rogibyx tricolor	15	no specimen
Lobibyx novae-hollandiae	16, 17	13–14
Lobibyx miles	15	no specimen
Afribyx senegallus	3–11	2–5
Hoplopterus spinosus	5–11	4–7
Hoplopterus armatus	9–12	7–12
Hoplopterus duvaucelii	11–13	6–15
Hoploxypterus cayanus	4–9	4–5

[1] I have not seen *Tylibyx melanocephalus* which is said to have no spur.

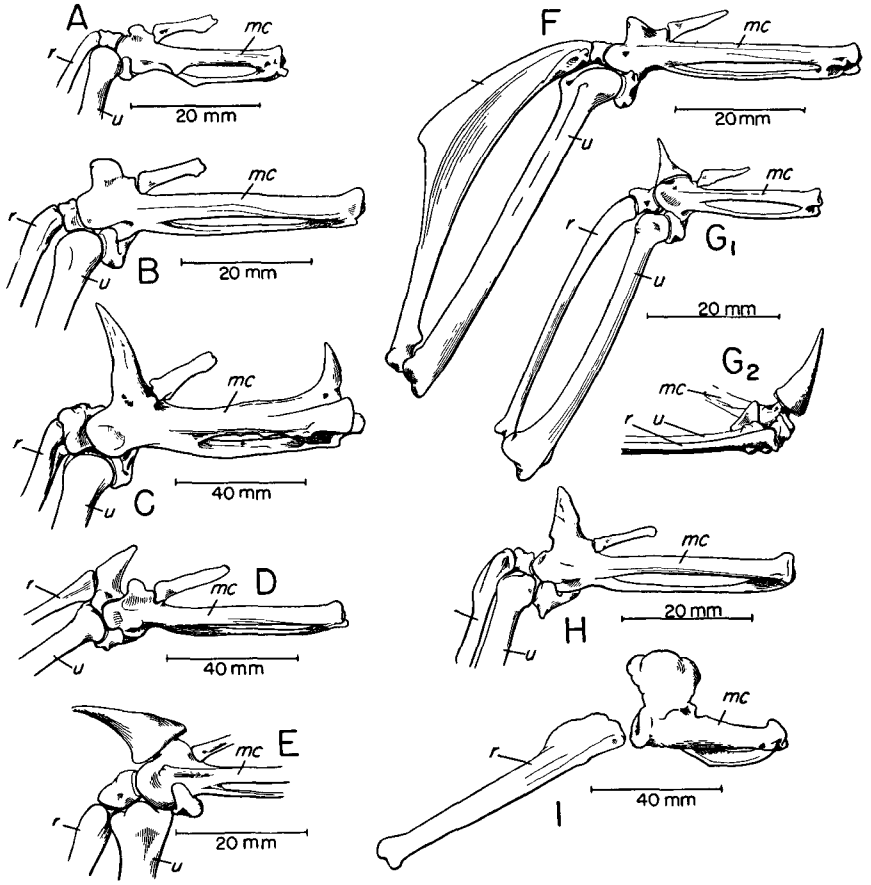

FIG. 1. Bony structures in the region of the wrist of birds. Species figured are: A, *Alectoris rufa;* B, *Haematopus ostralegus;* C, *Chauna chavaria;* D, *Plectropterus gambensis;* E, *Merganetta armata;* F, *Actophilornis africana;* G 1, *Jacana spinosa;* G 2, *Jacana spinosa,* another view, showing curve of spur; H, *Belonopterus chilensis;* I, *Pezophaps solitaria* (from Newton and Newton, 1868). A and B show "normal" process of metacarpal I; in C, E, G, and H, this process is elongated into a spur (drawn with horny sheath in E and G); C has an extra spur; D has the spur on a carpal; F has a thickened radius; I has a swollen knob on metacarpal and on radius. Abbreviations: *r*=radius; *u*=ulna; *mc*=metacarpal.

The following species, all in different genera from those listed above, have short spurs only a few millimeters long at most, but usually pointed and apparently horn covered: *Hemiparra crassirostris, Microsarcops cinereus, Lobivanellus indicus, Ptiloscelys resplendens.*

In the three species of *Stephanibyx;* the single species of *Zonifer, Lobipluvia, Sarciophorus, Anomalophrys,* and *Vanellus;* and two species of *Chettusia,* the knob formed by

the process of metacarpal I can scarcely be called a spur. *Tylibyx* is said also to lack a spur.

I have examined skeletons of but two genera of the plovers with conspicuous spurs, *Hoplopterus* and *Belonopterus*, and in these the spur is on the process of metacarpal I (Fig. 1H) as in jacanas and screamers (main spur). In the other genera the spur appears to be in a similar location and presumably is also on the process of metacarpal I.

In these plovers with well developed spur, the spurs are usually more or less oval in cross section, somewhat flattened in *Lobibyx*, rather slender, sharply pointed, and more or less distinctly curved radially. Frequently there are faint, wavy lines running around the spurs which are suggestive of growth rings (see under molt), but otherwise the spurs are smooth at the base. Usually the spurs of the female are slightly smaller than those of the male.

Columbiformes

Raphidae (Dodos, Solitaires.—No pigeons have a wing spur as such, but the wing armature of the extinct solitaire, *Pezophaps solitaria* (Fig. 1 I) of Rodriguez (Newton and Newton, 1868), should be mentioned. In this species large examples, presumably males, have a considerable enlargement of the distal end of the radius, especially at the base of the fused carpometacarpus. While apparently not sharp pointed, it may well have been horn covered and certainly could have increased the wing's effectiveness as a weapon.

Other Groups.—The older literature sometimes mentions spurs on such birds as a thrush (*Turdus*), the knob-winged pigeon (*Didunculus*) of Samoa, and the mound-builders (*Megapodius*) (Jefferies, 1881). Examination of specimens in the Chicago Natural History Museum showed no wing spurs on any of our specimens of these groups. However, the rather pronounced projection of the process of metacarpal I might be considered a rudimentary spur, as it could in most flying birds (see Fig. 1 A and B). Also, as Gadow (1891:501, 502) points out, cornification can occur sporadically on the skin of various parts of the bird's body, producing horny spurs, and to have this happen occasionally on the wings of birds which normally lack spurs is probable.

In summary, well developed wing spurs occur in: Anhimidae—2 spurs, in all 3 species; Anatidae—1 spur, in 2 of the 144 species; Jacanidae—1 spur, in 2 of the 7 species (rudimentary in all others); Charadriidae, subfamily Vanellinae—1 spur in 10 of the 25 species (present, small and sharp in a number of others).

The location of the spurs is as follows (Thomson, 1923:219), lists spurs as occurring on digits but none of his examples show this condition):

A. On radial carpal: *Plectropterus*.

B. On carpometacarpus: all others

a. on process of metacarpal I: all except the distal spur of screamers.

b. on distal end of metacarpal II near articulation of digit II: distal spur of screamers.

Functionally related structures are the enlarged radii of jacanas of the genera *Actophilornis, Metopidius* and *Irediparra* and the enlargement of the distal end of the radius and also of the proximal end of the carpometacarpus of a solitaire, *Pezophaps*.

Uses of Wing Armature

Spurs probably have their use in fighting. In many gallinaceous birds the tarsal spurs, worn only by the male, are definitely secondary sexual characters used in intraspecific fighting at mating time. Wing-spurs are well developed in both sexes of species in which they occur but those of the female are usual-

ly slightly smaller. This might imply they were not used primarily in courtship and mating. However, the jacana (*J. spinosa*) is said to have displays at mating time when with spread wings the birds act as though they were attempting to strike each other with their sharp spurs.

Some birds use their wings in fighting off enemies or intruders of other species. The swans (*Cygnus*), without spurs, make such effective use of their wings as weapons that they can be dangerous to children. The spur-winged goose (*Plectropterus*), with its formidable spurs, is said to be extremely aggressive and sometimes to injure other waterfowl with its spurs (Delacour and Mayr, 1945:28). Both male and female screamer (*Chauna torquata*) defend their nest with strong wing blows in which the spur is brought into play (Stoner, 1939:48).

One can assume that the bony enlargement of the carpal area of the solitaire and the thickened radius of certain jacanas serve to render blows more effective.

Origin of Wing Armature

Well developed wing spurs occur in only two families of each of two orders, Anseriformes and Charadriiformes. In one small family (Anhimidae) all the species have wing spurs, while in the related large family (Anatidae) about two per cent have spurs.

The diversity of the armature of birds' wings is apparent from the preceding summary. Two main effects are achieved: a club effect in two ways; a knife effect in one main and two less frequent ways.

It is interesting to note here that both club and knife or spear motive are present in one group, the jacanas, but no species has both. Those species with spurs do not have thickened radii.

Though wing armature is varied, the spur is the most common and in all but one species the spur (only the proximal spur in screamers) appears to be a continuation and modification of the process of metacarpal I, a process that in birds serves for the attachment of the extensor muscles. This process is easily felt through the skin of specimens of many, perhaps most, flying birds as a distinct point or knob. It gives the impression of a rudimentary spur. The size, shape, and position of this process apparently varies with the type of flight of the bird, as Fisher (1946:559) has demonstrated for some hawks and their relatives. Almost surely this process arose in connection with the attachment of extensor muscles. But once present, it made the wing more effective as a weapon when dealing a blow, as do some birds without spurs. Already useful as a weapon, a new set of selection factors, connected with fighting ability, could have operated to elongate the process and give it a horny coating to add to its effectiveness as a weapon. Presumably the process can maintain its first func-

tion as a point of muscle attachment and take over its new function as a weapon. This seems to be a good example of a structure arising for one purpose through the action of one set of selective factors becoming useful in quite another way when a certain point of development was reached. At this point the structure comes under the influence of another set of selective factors, and the direction of its evolution is changed. The present-day structure is the result of two sets of selective processes acting at different times.

Assuming that the process of metacarpal I is a ready made knob capable of being turned into a spur, it seems strange that this knob has been ignored, so to speak, in some species in which wing armature was achieved in other ways, as, for example, the spur on the radial carpal of the spur-winged goose (*Plectropterus*). It seems just as strange that in the jacanas certain species developed spurs while in certain other species a heavy radius was developed suitable for use as a club. No species has both.

It seems that wing armature originated separately a number of times; in the majority of cases a bony process already in existence was modified into a spur, but in some cases this process was not used and a weapon evolved along other lines.

Spur Molt

Molt of feathers usually occurs at least once a year. Molt of other epidermal structures is well known, but its occurrence is less general. Molt has been recorded for such structures as: the nails of the red grouse, *Lagopus scoticus* (Witherby, et al, 1941:227); the pectinations on each side of the toes that serve for "snowshoes" for the ruffed grouse, *Bonasa umbellus* (figured, Forbush, 1927:27); the outer sheath of the puffin's (*Fratercula arctica*) bill that serves as a nuptial adornment (Witherby, et al, 1941:172); and the "knob" on the bill of the white pelican, *Pelecanus erythrorhynchos*, that is worn during the breeding season (Baird, 1869). Apparently the spurs of domestic fowl at least do not molt, and I find only one mention of wing spur molt. Chapin (1939:86), writing of the plover *Xiphidiopterus albiceps*, says of a pair that were molting their remiges and rectrices, "Their wing-spurs were likewise about to shed the outer sheath, which could be lifted off, leaving a perfect new horny point beneath."

I have found further evidence of molt of wing spurs in three species:

(a) Screamer. *Chauna chavaria*.—In screamers there is characteristically a series of fine lines near the base of the spur which I assume are growth lines due to horn being laid down in layers. In one specimen there were three such series of lines separated by intervals. These lines I assumed to be annual growth lines. Hence it came as a surprise in handling a specimen of *C. chavaria* that an outer layer of one spur separated at the "growth ring" and slipped off as a cap, leaving the spur about 3 mm. shorter but in ap-

pearance much as it was before. This bird showed molt of flight feathers.

(b) Jacana. *Jacana spinosa.*—A specimen had long, pointed spurs (13 mm.) that showed irregular growth lines and a scaly appearance about the base. A gentle pull on each spur caused an outer layer of the horn of the spurs to slip off like a cap, leaving a pair of clean, pointed, shorter spurs (9 mm.) with less attenuated points. This specimen was also molting its remiges.

(c) Spur-winged Plover. *Hoplopterus armatus.*—A specimen had clean, fresh looking spurs 12 mm. long. A gentle tug on each spur caused the outer layer to slip off like a cap, leaving a pair of spurs similar to the old ones but about two mm. shorter. This specimen also showed molt of its remiges.

The data are scanty for generalization. The similarity of the spur before and after shedding makes it necessary to see the shed cap to realize what has happened. But from the three examples described above it appears that molt of the outer layer of the horn covering of spurs takes place in at least one species of screamer, one jacana, and two species of plovers. The correlation of this spur cover molt with wing molt indicates the former may be a regular part of the annual molt.

The structure of the spurs of birds has been compared to that of horns of cattle by Gadow. It is interesting to compare the molt of the covering of the spurs on wings of birds with the annual molt of the covering of the bony core of the horns of the Pronghorn, *Antilocapra,* which is similar.

Summary

The occurrence of wing spurs is noted for all species of screamers, some plovers, two jacanas, and two ducks. Additionally, knob or club-like wing armature is listed for several jacanas and a pigeon. These specialized structures occur on different parts of the wing and involve the radius, the radial carpal, or the fused metacarpals depending on the species. The structures are apparently used in fighting.

The process of metacarpal I (for the attachment of the extensor muscles) has been modified into the spur in a great majority of cases. This process presumably arose in connection with the insertion of muscles, and its size and location are influenced by the type of flight. But another result was that this knob made the wing more effective as a striking organ. This knob was then acted on by a new set of selective factors, those involved in providing the bird with better weapons, and a spur was produced. However, in a few cases wing armature developed independently from other parts of the wing.

Molt of an outer cap-like layer of the horny covering of the spur in a single piece is recorded in four species. In each case this molt was correlated with wing molt. It is possible that the annual molt may regularly include the outer covering of the spur.

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