

ACCESSORY PYGOSTYLE BONES OF FALCONIDAE

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OCCURRENCE

A conspicuous and constant pair of bones, presumably of sesamoid origin, is attached at the base of the pygostyle apparently throughout the Falconidae. The bones appear to be undescribed and unillustrated in the literature, perhaps primarily because of their small size and frequent separation and loss even in skeletons prepared by dermestid beetles. Sufficient complete specimens have been found in this study to know that the bones occur at least in *Herpetotheres* and *Micrastur* of the Herpetotherinae (laughing and forest falcons); *Caracara* of the Polyborinae (caracaras); and 10 species of *Falco* in the Falconinae (falcons and kestrels). Specimens were not available to determine the occurrence of the bones in the Polihieracinae (pigmy falcons). No trace of the bones was found in other families of Falconiformes.

A partially comparable pair of bones occurs in Trochilidae. I have Dr. Jean W. Cohn to thank for calling them to my attention and commenting on their condition and possible function. The bones occur in at least *Calypte*, *Stellula*, and *Patagona*.

DESCRIPTION

As typified by *Falco sparverius* (fig. 1), the accessory pygostyle bones articulate with each other in the mid-ventral line and are closely bound to the base of the pygostyle and to the lateral edges of its disk. The actual size of the bones (combined maximum width from side to side) averaged 7.5 mm for four specimens of this species. The bones are curved and flattened yet not thin, for they have a diploic structure, smooth on the surfaces but cancellous or strutted within.

Relationships of muscles to the accessory pygostyle bones in the Prairie Falcon are partly shown in figure 2, the main feature being that all three major tail depressors (Mm. caudofemoralis, depressor coccygis, and lateralis coccygis) insert or act on the pygostyle and closely bound rectrices almost entirely through their insertions on the accessory bones. The caudofemoralis inserts by its single strong tendon on the anterior medial edge of each accessory bone, the depressor coccygis inserts over much of the ventral surface, and the large lateralis coccygis, along the anterior edge and anterior ventral surface of each bone.

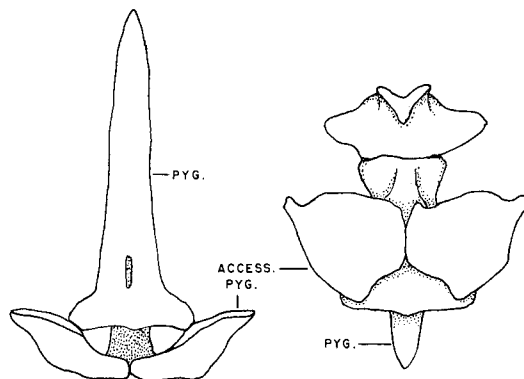


FIGURE 1. Posterior (left) and ventral (right) views of pygostyle and accessory pygostyle bones in *Falco sparverius*, $\times 4.35$. The last free caudal vertebra is also shown in the ventral view.

I have followed the nomenclature of Fisher and Goodman (*The Myology of the Whooping Crane, *Grus americana**; Univ. of Illinois Press, 1955), but the separation and naming of the complex of tail depressor muscles of falcons are not entirely clear. The Prairie Falcon and Sparrow Hawk have, for instance, a well-developed muscle originating partly with the lateralis coccygis from the transverse processes of caudal vertebrae but with a distinct insertion of the median ventral surface of the accessory pygostyle bone. Perhaps this clearly separable falcon tail depressor (marked with an \times in fig. 2) has been derived from the lateralis coccygis.

In hummingbirds, the partly comparable pair of accessory pygostyle bones is a pair of very thin sesamoids attaching separately to the ventral lateral protuberances of the pygostyle disk. Based on dissection of *Stellula calliope*, these relatively long (1.8 mm) bones form the insertion almost exclusively of the caudofemoralis muscles.

VARIATION

Inadequate series of accessory bones were available for quantitative treatment but a relative constancy in size and shape was clear even with small series. Four *Falco sparverius* paired bones were 8.0, 8.0, 7.1, and 6.8 mm in width. Four male *Falco mexicanus* paired accessory bones showed a similar constancy, but the fifth pair, of a female, was markedly larger and divergent in shape (fig. 3). In three of five *Falco berigora* specimens, the accessory bones were fused in the mid-ventral line, but in two they were not. This species also showed the most variation in shape.

Interspecific variation observed is further illustrated by the outline drawings of six additional species in

TABLE 1. Ratios of length of one accessory pygostyle bone to length of femur (in parentheses). Arranged by subfamilies but with species of *Falco* ordered by increasing length of femur.

<i>Herpetotheres cachinans</i>	10.6% (60.5 mm)	<i>Falco timunculus</i>	13.4 (44.9)
<i>Micrastur semitorquatus</i>	8.0 (68.5)	<i>Falco berigora</i>	11.4 (61.4)
<i>Caracara cheriway</i>	8.6 (70.0)	<i>Falco mexicanus</i>	10.1 (61.5)
<i>Falco sparverius</i>	11.0 (37.2)	<i>Falco pelegrinoides</i>	11.6 (62.7)
<i>Falco albicularis</i>	10.3 (39.0)	<i>Falco peregrinus</i>	10.9 (69.5)
<i>Falco cenchroides</i>	14.5 (42.0)	<i>Falco rusticolus</i>	11.0 (80.0)
<i>Falco columbarius</i>	12.6 (44.6)		

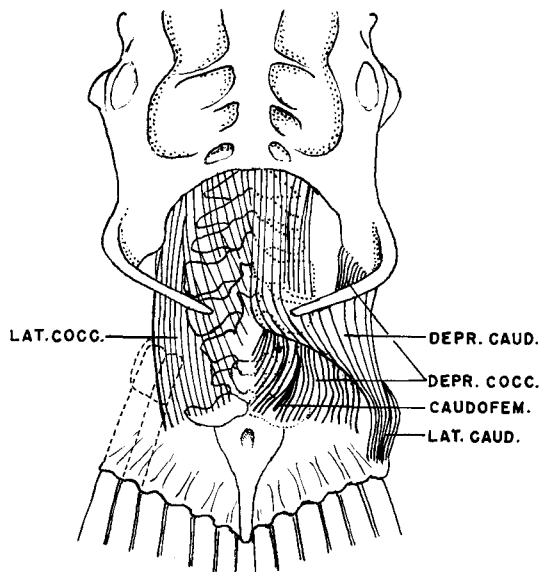


FIGURE 2. Ventral view of *Falco mexicanus* caudal skeletal region and muscles, $\times 1.3$. The bases of the rectrices are shown at the bottom. Abdominal muscles and viscera are removed and the superficial caudal muscles removed at the left. Muscles represented: lateralis coccygis, depressor caudae, depressor coccygis, caudofemoralis (tendon of insertion only shown), and lateralis caudae.

figure 4, representing three subfamilies of the Falconidae. Relative sizes are not shown here, but in Table I the accessory pygostyle bones of all species observed are compared relative to femoral length. Femur length, even though probably subject to slight adaptive or other changes in the Falconidae, was considered the most accurate, available, and relatively stable measurement for this comparison. Plotting of the data shows that all but three of the 13 species show a significant negative correlation between the length of the accessory bone and the femur, that is, the smallest birds tend to have relatively the longest accessory bones.

FUNCTION

The accessory pygostyle bones of falcons have probably evolved as sesamoid bones although they no longer are enclosed in tendons in typical sesamoid

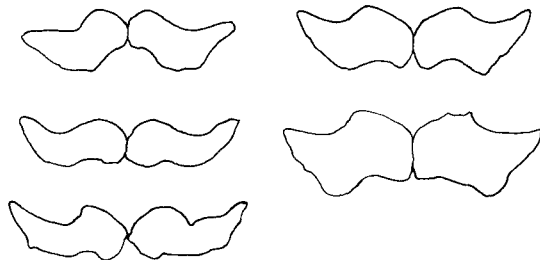


FIGURE 3. Ventral views of accessory pygostyle bones to show variation in *Falco mexicanus*, $\times 2.28$. The first four paired bones are from males but the fifth pair (lower right) is from a female.

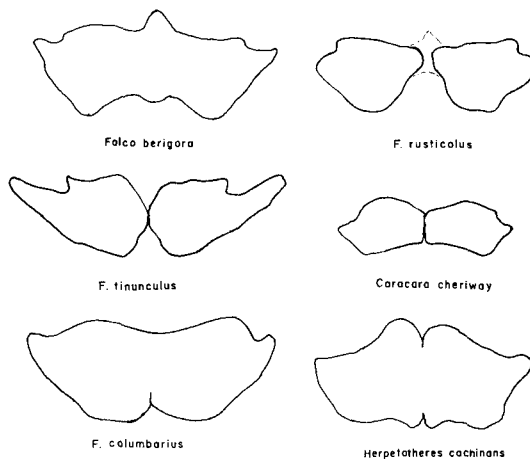


FIGURE 4. Ventral views of accessory pygostyle bones in different Falconidae. Magnification variable.

fashion. Stained microscopic sections of the bones showed their strong bone, muscle, and tendon relationships but could not prove their sesamoid origin as might embryological studies. The function of the accessory bones appears to be to concentrate and transmit the force of several major tail depressor and abductor muscles to the pygostyle and its closely bound complex of rectrices.

The adaptive significance of the accessory pygostyle bones would seem to be to afford a greater area for the insertion of the powerful tail depressor muscles or their tendons than is possible by direct attachment to the more limited surfaces of the pygostyle. These muscles may well be larger and stronger in falcons, and their action in unison on the tail more forceful as indicated by their combined insertion on a newly evolved expanded and rigid structure. The occurrence of such accessory bones in falcons only implies more powerful use of or greater stress on the tail in the notably rapid maneuvering and forceful braking flight of these birds. The occurrence of somewhat similar bones in at least some hummingbirds, where again the maneuvering and braking action of the tail is striking and the tail area is relatively very large, would appear to confirm this importance of the accessory bones in falcons.

ACKNOWLEDGMENTS

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DEDICATION

I am honored to dedicate this article to Dr. Loye Holmes Miller and his son, Dr. Alden Holmes Miller. My several decades of association with these great men, first as their student and later as their friend, were and remain a deep source of inspiration.

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