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The Morphological Basis of Folded-Wing Posture in the American Kestrel, *Falco sparverius*

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ABSTRACT Gross dissection and histochemical analysis of the shoulder musculature of the American kestrel, *Falco sparverius,* revealed that four muscles are specialized for slow contraction and may function in the postural control of the folded wing. Mm. latissimus dorsi pars cranialis, scapulohumeralis cranialis, and brachialis were found to contain >95% tonic fibers, whereas M. deltoideus minor was found to possess a relatively even mix of fast-twitch and tonic muscle fibers. M. latissimus dorsi pars cranialis, M. scapulohumeralis cranialis, and M. deltoideus minor all cross the shoulder joint caudally to the articulation, and M. brachialis crosses the elbow joint on the ventral surface of the forearm. This paper suggests postural muscles have largely been ignored in studies of avian musculature, and the need to consider a variety of possible muscle functions when analyzing locomotor muscle functions.

Studies on the forelimb musculature of birds have concentrated on functional aspects of that limb as it relates to flight (e.g., Fisher, 1946; Dial et al., 1991) or on the taxonomic aspects of muscle variations (e.g., Raikow, 1978). Few studies, however, have examined the role of postural muscles in the avian forelimb. The avian forelimb does not normally bear any body weight when at rest, but the wing does need to be held in a folded position against the body. The wings are generally believed to assume a flexed (folded) position due to elasticity of the connective tissue elements in the forelimb (Raikow, 1985). Goldspink (1981) suggested that the tonic M. latissimus dorsi pars cranialis functions to hold the wings against the body. Simpson (1979) found "slow" fibers in several shoulder muscles of the pigeon, and presumed that they function in some postural role. Studies on the mammalian hindlimb (e.g., Ariano et al., 1973; Sickels and Pinkstaff, 1981) and avian hindlimb (e.g., Cracraft, 1971; Suzuki and Tamate, 1979; Maier, 1983) have found "slow" contracting muscle fibers within locomotory muscles and have suggested that these muscles play a role in posture.

Most studies investigating posture make use of muscle histochemistry to assess the relative contractile speed of the muscle fibers. This technique involves assaying the muscle for adenosine triphosphatase (ATPase) activity and permits one to identify slow-twitch, fast-twitch, and slow-tonic muscle fibers. It is believed that those muscles involved in posture are generally "slow" in contraction time, and should be relatively unfatigable (Goldspink, 1981). Hence, these muscles are metabolically specialized for the sustained contraction necessary for posture.

Recently, Hikida (1987) has shown that birds possess three types of muscle fibers discernible via histochemistry and ultrastructure: slow-twitch, fast-twitch, and slow-tonic fibers.

Avian tonic fibers have long been known to be present in the latissimus dorsi pars cranialis muscle of many species (see Hikida and Bock, 1971). The tonic nature of this muscle has been demonstrated physiologically in chickens (Ginsborg, 1960a; Hess, 1961), and many studies have used this muscle as a model of "tonic" muscle (see Ginsborg, 1960b; Fedde, 1969; Page, 1969; Toutant et al., 1980; Rouand and Toutant, 1982).

Apart from the many studies on the avian M. latissimus dorsi pars cranialis, and a whole series of papers on the pectoralis muscles of various taxa (Rosser and George, 1984, 1985a, 1986a,b), the 40-odd other muscles of the avian forelimb have received little attention.

This study examines the gross morphology and histochemical profile of a select number of shoulder muscles of the kestrel (*Falco sparverius*) as part of a larger investigation on the functional morphology of flapping and gliding flight in this species.

MATERIALS AND METHODS

Preserved material for dissection was obtained from the American Museum of Natural History. Dissections of two specimens were performed under a Wild M5 stereomicroscope with a camera lucida attachment. An iodine solution (Bock and Shear, 1972) was added to the specimen to help distinguish muscle from connective tissue. Anatomical nomenclature is from *Nomina Anatomica Avium* (Baumel et al., 1979). Live kestrels were obtained from the Macdonald Raptor Research Centre of Macdonald College in Ste-Anne-de-Bellevue, Québec. They were housed at Brown University in a flight room and fed mice daily. Three birds were used for this study.

Birds were sacrificed with an overdose of sodium

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pentobarbitol and the muscles subsequently removed. Muscles were attached to the end of a tongue depressor with a drop of OTC (Tissue Tek II) embedding compound, were frozen in isopentane cooled to about −150°C in liquid nitrogen, and stored in an ultracold freezer at −70°C. Serial sections (10–12 μm) were cut on an AO Reichert cryostat at −20°C. ATPase procedure is from Staron et al. (1983), using pHs of 4.2 and 10.4 for acid and alkaline preincubations. At a pH of 4.2, slow-twitch fibers have high activity, whereas fast-twitch fibers have low activity. At a pH of 10.4 there is a reversal of staining, such that the slow-twitch fibers now show low activity, and the fast-twitch fibers show high activity. Slow-tonic fibers have moderate activity at both acid and alkaline preincubations. To eliminate any possible variation, all muscle sections of a specific preincubation were processed in a single coplin jar. Hikida (1987) has shown that Mm. latissimus dorsi pars cranialis, biventer cervicis, and pectoralis of the pigeon consist of slow-tonic, mixed slow-twitch/fast-twitch, and fast-twitch muscle fibers, respectively. Samples of these muscles from a pigeon were assayed concurrently with the kestrel tissue as examples of the three fiber types. Although the current literature on histochemistry is filled with many classification schemes and fiber type nomenclature (see Gollnick and Hodgson, 1986), that of Hikida (1987) is used here: slow-twitch, fast-twitch, and slow-tonic.

In addition, standard histochemical techniques for glycogen (periodic acid-Schiff's) and nicotinamide adenine dinucleotide diaphorase (NADH-D) activity (Novikoff et al., 1961) were also used.

Observations

A histochemical survey of approximately 20 shoulder and brachial muscles of the American kestrel revealed that four muscles are specialized for "slow" contraction. The remaining muscles consisted of fast-twitch fibers. The "slow" muscles are: M. deltoideus minor, M. latissimus dorsi pars cranialis, M. scapulohumeralis cranialis, and M. brachialis, and their gross morphology is briefly described below. All four muscles were found to be relatively low in their glycogen content.

M. deltoideus minor (DM)

The M. deltoideus minor is a narrow, parallel-fibered muscle which lies deep to the origins of the caudal head of M. deltoideus major and M. propatagialis pars brevis. It extends from the cranial scapula to the proximal humerus and crosses the scapulohumeral joint dorsally. DM arises fleshily from a small area on the cranial portion of the scapula adjacent to the origin of the caudal head of M. deltoideus major, and also from the adjacent dorsal scapuloclavicular ligament (Fig. 1). It crosses the shoulder joint cranially to Os scapulohumerale, and caudally to M. supracoracoideus (Fig. 1). DM has a fleshy insertion onto the proximal aspect of a small process (Tuberculum dorsale) on the cranial edge of the proximal part of the deltopectoral crest of the humerus, just distal to the tendon of insertion of M. supracoracoideus (Fig. 1).

DM is a histochemically mixed muscle, consisting of relatively even percentages of slow-tonic and fast-twitch fibers (45%–55%, respectively) at mid-belly (Fig. 2). The majority of fast-twitch fibers lie along the periphery of the muscle. DM showed moderate NADH activity. Although it is a relatively small muscle, it is in an anatomical position to assist in shoulder flexion.

M. latissimus dorsi pars cranialis (LDCr)

The M. latissimus dorsi pars cranialis is a superficial muscle of the back which spans the gap between the axial skeleton and the forelimb. LDCr is a thin, narrow, parallel-fibered muscle which arises from the spinous process of the 13th cervical vertebra and from the connective tissue between C13 and C14 (Fig. 1). Its fibers run laterally, tapering slightly before passing dorsally to M. latissimus dorsi pars caudalis. LDCr has a fleshy insertion on a narrow area on the dorsal aspect (margo caudalis) of the humerus, caudally to the insertion of M. latissimus dorsi pars caudalis.

LDCr is oriented to hold the humerus against the body. It is composed exclusively of slow tonic fibers (Fig. 3), and exhibited moderate NADH activity.

M. scapulohumeralis cranialis (SHCr)

The M. scapulohumeralis cranialis is a narrow, parallel-fibered muscle extending from the scapula to the humerus caudally to the shoulder joint. SHCr takes its origin from a narrow area on the dorsal surface of the cranial part of the scapula, cranial to the origin of M. subscapularis pars externa (Fig. 1). It extends caudolaterally from its origin, passing deep to the origin of both parts of M. triceps. SHCr inserts along a narrow area on the proximal aspect of the pneumatic fossa of the humerus (Fig. 1).

SHCr is in a position to adduct/retract the humerus. Histochemically it is comprised of >95% slow-tonic muscle fibers (see Fig. 3). A few (<5%) fast-twitch fibers were found. SHCr showed moderate to strong NADH activity.

M. brachialis (Br)

The M. brachialis is a short, parallel-fibered muscle located ventrally at the elbow joint. It extends from the distal humerus to the proximal ulna (Fig. 1), where it is covered by Mm. pronator superficialis and pronator profundus. Br originates fleshily from a depression on the lateral aspect of the distal humerus. It inserts fleshily onto the proximal ulna.

Br is histochemically an exclusively tonic muscle

Abbreviations

Br	M. brachialis
BB	M. biceps brachii
C	Coracoid
CBC	M. coracobrachialis cranialis
DM	M. deltoideus minor
F	Furcula
H	Humerus
LDCa	M. latissimus dorsi pars caudalis
LDCr	M. latissimus dorsi pars cranialis
RP	M. rhomboideus profundus
RS	M. rhomboideus superficialis
PB	M. propatagialis pars brevis
S	Scapula
SC	M. supracoracoideus
SHCa	M. scapulohumeralis caudalis
SHCr	M. scapulohumeralis cranialis
SS	M. subscapularis pars externa
U	Ulna

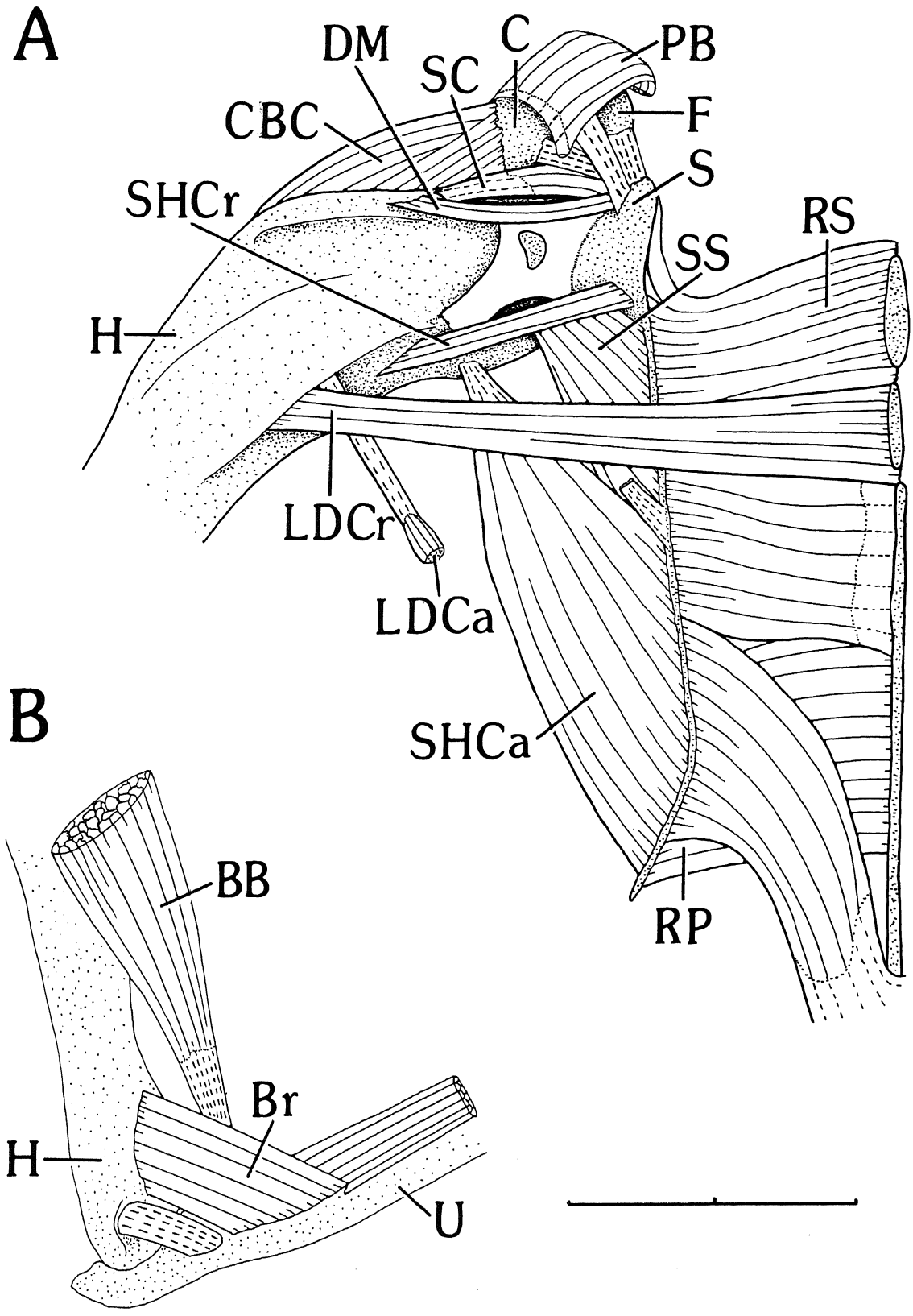

Fig. 1. **A:** Deep dorsal view of left shoulder of *F. sparverius,* illustrating postural muscles. M. deltoideus major and M. triceps removed; M. propatagialis pars brevis reflected; M. latissimus dorsi pars caudalis cut. **B:** Ventral view of left elbow of *F. sparverius,* showing M. brachialis. Overlying muscles have been removed. Scale: 1 cm.

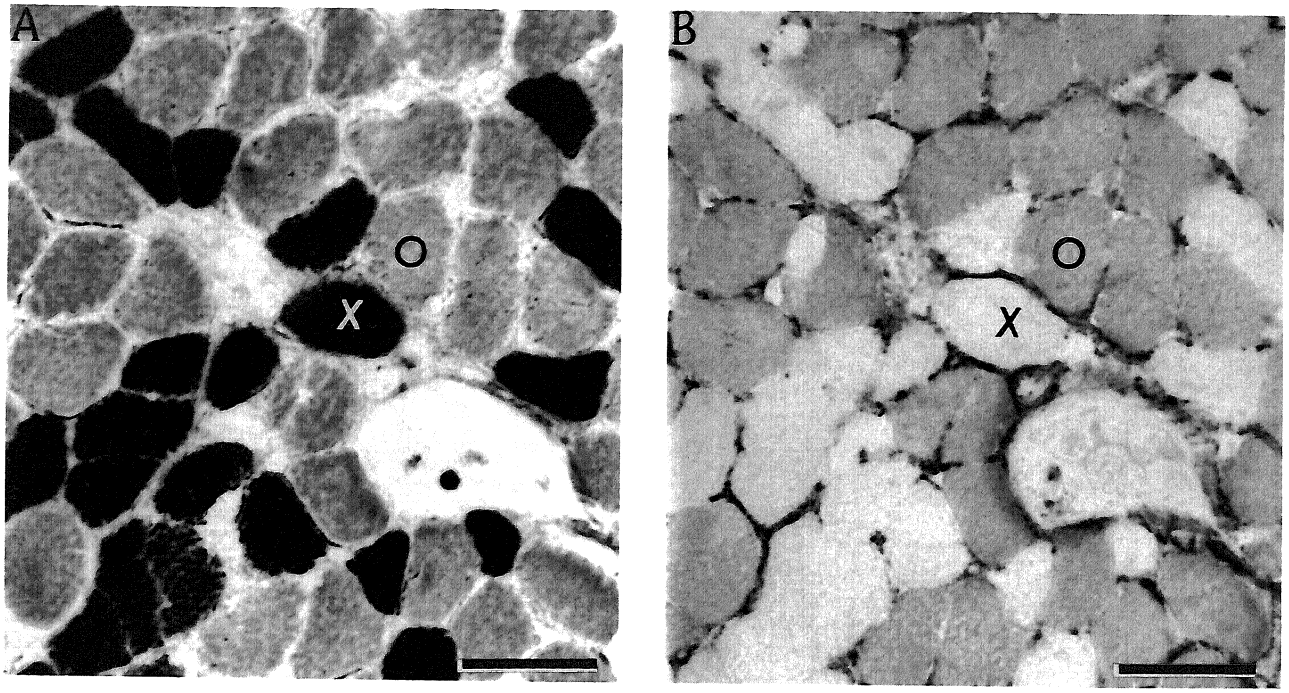

Fig. 2. Serial sections (12 μm) of M. deltoideus minor of *F. sparverius*. Both slow-tonic and fast-twitch fibers are represented. **A:** Alkaline preincubation: fast-twitch fibers stain darkly for ATPase (x), and slow-tonic fibers stain moderately (○). **B:** Acid preincubation: fast-twitch fibers (x) stain weakly for ATPase, whereas slow-tonic fibers (○) stain moderately. Scale: 50 μm.

(see Fig. 3), and is in a position to assist in wing flexion and maintain the closed wing. It stained weakly for NADH activity.

DISCUSSION

The results of this study suggest that four muscles of the forelimb of *F. sparverius*, Mm. latissimus dorsi pars cranialis, deltoideus minor, scapulohumeralis cranialis and brachialis maintain postural integrity of the folded wing. Gross anatomy of these muscles indicates that they lie across forearm joints in appropriate positions to facilitate keeping the wings folded against the body. The uniformly tonic histochemical profile of three of the muscles, and the mixed fast-twitch/slow-tonic nature of M. deltoideus minor is a specialization for slow contracture and maintenance of isometric contraction, used for postural control. Although other muscles are in a mechanical position to assist in wing posture (e.g., M. biceps brachii, M. propatagialis pars brevis), in *Falco* they contain neither slow-tonic nor slow-twitch muscle fibers. Thus, they may be able to assist in the positioning of the folded wing, but probably do not contribute significantly to maintenance of the posture.

Previous histochemical studies of avian muscles have neglected the majority of muscles of the forelimb. Maier (1983) and Rosser and George (1985b) examined the histochemical characteristics of different forelimb muscles, but both studies examined muscle spindles within pigeon muscles. Studies on ostriches and emus (Rosser and George, 1984, 1985a) and kiwis (McGowan, 1982) suggest that slow-tonic fibers found in the pectoralis muscle are responsible for wing posture in these flightless birds. The existence of tonic fibers in the pectoralis muscles of red-tailed hawks (*Buteo jamaicensis*), turkey vultures (*Cathartes aura*) (Rosser and George, 1986a,b), and herring gulls (*Larus argentatus*) (Talesara and Goldspink, 1978) suggests a function in postural control of the wings during gliding in these species. Rosser and George (1986a) suggest that tonic fibers in the pectoralis of chickens may function in wing posture but then question that postural role since these fibers are not found in the pectoralis of most birds. Undoubtedly, tonic fibers contribute to wing posture in soaring species such as vultures and gulls. Simpson (1979) identified Mm. deltoideus minor, coracobrachialis cranialis, and latissimus dorsi pars cranialis as containing various percentages of tonic fibers in the pigeon, and suggested that they functioned in posture. Of these muscles, M. coracobrachialis cranialis may not function in the postural control of wing folding, as it crosses the shoulder joint cranially to the articulation (see Fig. 1). Its anatomy suggests that it functions in protraction of the humerus, a movement associated with gliding posture (see Stegmann, 1964), and may function posturally during that behavior. In *F. sparverius*, M. coracobrachialis cranialis consists entirely of fast-twitch fibers.

Of all the myological variations seen across avian taxa, one may predict that there should always be postural muscles present in appropriate anatomical positions. Many avian taxa lack M. latissimus dorsi pars caudalis (e.g., *Columba livia, Agelaius phoeniceus, Gallicolumba luzonica, Eugenes fulgens, Indicator variegus, Artamella viridis, Fregilupus varius, Dendroica kirtlandii, Otis, Pterocles*, the Pleoceidae, Fringillidae and Picidae; George and Berger, 1966), yet as far as is

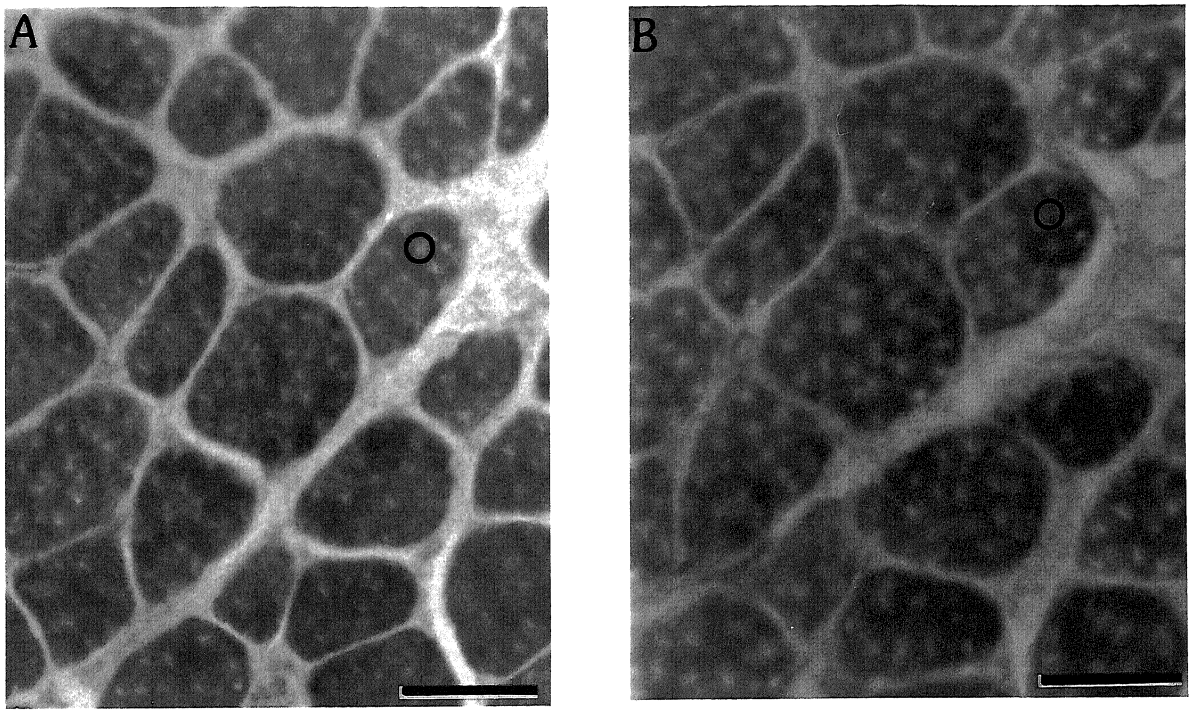

Fig. 3. Serial sections (12 μm) of M. latissimus dorsi cranialis of *F. sparverius* illustrating typical staining of tonic muscles based on ATPase activity. **A:** Alkaline preincubation. **B:** Acid preincubation. Note the fiber (○) and that both preincubations result in equivalent staining. Scale: 25 μm.

known, only *Apteryx* and *Alcedo bengalensis* lack pars cranialis (Beddard, 1898). One explanation for this may be that if the caudal part is not necessary for posture, it can be more variable in its existence. The cranial part, however, intrinsic to the postural mechanism, is present in most taxa. Loss of the pars cranialis in *Apteryx* may be due to flightlessness in this species and its associated modifications (see McGowan, 1982). Loss of this muscle in *A. bengalensis* is functionally problematic, since congeners possess this muscle (George and Berger, 1966). Individual variation may account for the absence of pars cranialis in the specimen examined by Beddard. Postural muscles, usually ignored in studies on the avian forelimb, may be an integral part of wing form, and may be intrinsic to wing design.

Two observations provide areas for future research. First, Jirmanová and Zelená (1970) and Hikida and Bock (1972) described a drooping of the wing following denervation of the cranial latissimus dorsi alone. Experimental studies utilizing denervation of these muscles in isolation and in various combinations are needed to assess and quantify the relative role of each muscle in maintaining wing posture. Second, Rosser and George (1985b) showed that the tonic M. coracotriceps of the pigeon contained an unusually high number of muscle spindles. Examination of the tonic muscles of *F. sparverius* also revealed a greater number of muscle spindles per area than in a similar sized area of fast muscle (e.g., pectoralis). Further quantification of spindle density within these muscles is warranted.

Finally, care must be taken when evaluating the function of muscles from gross dissection alone. Although a muscle may have an anatomical orientation to perform a particular action (i.e., wing elevation), in many species it may be too small to facilitate the function described. Such muscles may be used primarily for posture and not in the locomotor activity often the focus of the particular study.

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