PECTORAL APPENDAGE MYOLOGY OF THE HAWAIIAN HONEYCREEPERS (DREPANIDIDAE)

ROBERT J. RAIKOW

ABSTRACT.—Describes variations in the forelimb muscles of the Drepanididae. These are few in number and generally minor in terms of structural variation. This basic uniformity is remarkable in view of the great adaptive radiation of feeding mechanisms in the family. The lack of significant variation in the locomotor apparatus attests the unity of the Drepanididae and supports the premise that the family evolved from a single ancestral species.—*Department of Life Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15260.* Accepted 4 November 1975.

THIS is the second in a series of studies of the appendicular myology and relationships of passerine birds. In the first paper (Raikow 1976, Auk 93: 774–792) I presented detailed descriptions of the hind limb muscles of the Drepanididae; the present paper similarly describes the forelimb muscles. Together these reports give a detailed account of the myology of a reference species, *Loxops virens,* and comparisons with other members of the family. They thus provide for the Drepanididae the information that George and Berger (1966, Avian myology, New York and London Academic Press) listed as one of the types of avian myological studies currently needed, in order to characterize the nature of intergeneric variation in circumscribed groups of birds. This type of study is important because many previous workers have tried to characterize large groups, such as families, on the basis of one or two genera, without determining how much and what kind of variation might occur in such taxa.

This study has an additional function. The muscle descriptions for *L. virens* will be used as the basis of comparison in a comprehensive study of the phylogenetic relationships of the New World nine-primaried oscines, and in a study of the origin and evolution of the Drepanididae, both of which will be presented elsewhere.

MATERIALS AND METHODS

These are the same as in the first paper (Raikow ibid.) and need not be repeated in detail. The species in the present study are *Hemignathus procerus, H. wilsoni, Loxops virens wilsoni, L. maculata bairdi, Psittirostra c. cantans, P. c. ultima, P. psittacea, Himatione sanguinea, Vestiaria coccinea,* and *Palmeria dolei. Ciridops anna* was not included because the forelimbs are lacking in the only existing specimen. The names of muscles used herein are those tentatively selected for the forthcoming Nomina Anatomica Avium at the time this is written. Where these names differ from those of Berger (George and Berger ibid.) the older name is given in parentheses following the name adopted. Also following the N.A.A., *cranial* replaces *anterior,* and *caudal* replaces *posterior* as terms of direction. The primary muscle description is for *L. virens wilsoni.* Unless comments to the contrary are given, the same applies to all species studied.

MUSCLE DESCRIPTIONS

M. latissimus dorsi.—Pars cranialis (pars anterior), a strap-shaped muscle, is nearly parallel-fibered except that it is slightly wider at the origin than at the insertion, and hence converges slightly toward the latter. It arises by a short aponeurosis from the neural spines of the last cervical and first dorsal vertebrae. The belly enters the forearm between the bellies of M. triceps brachii caput scapulotricipitale and caput humerotricipitale, and has a fleshy insertion on a small ridge on the dorsal surface of the humerus. The distal end of the insertion is level with the distal end of the deltoid crest. No variations were noted except that in *Psittirostra* the origin is a

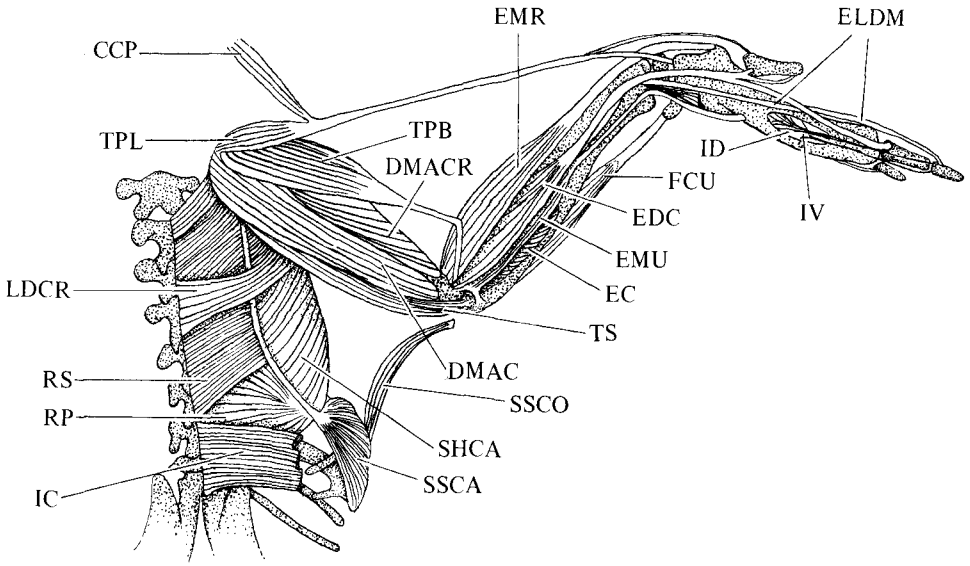

Fig. 1. Superficial dorsal muscles of the forelimb of *Loxops virens wilsoni*. Abbreviations for Figs. 1–5; ABA, M. abductor allulae; ADA, M. adductor allulae; ADM, M. abductor digiti majoris; B, M. brachialis; BB, M. biceps brachii; CC, M. coracobrachialis caudalis; CCP, M. cucullaris capitis pars propatagialis; DMAC, M. deltoideus major caudalis; DMACR, M. deltoideus major cranialis; DMI, M. deltoideus minor; EC, M. ectepicondyloulnaris; EDC, M. extensor digitorum communis; ELA, M. extensor longus allulae; ELDM, M. extensor longus digiti majoris; EMR, M. extensor metacarpi radialis; EMU, M. extensor metacarpi ulnaris; ES, M. expansor secondariorum; FCU, M. flexor carpi ulnaris; FDM, M. flexor digiti minoris; FDP, M. flexor digitorum profundus; FDS, M. flexor digitorum superficialis; IC, M. iliotibialis cranialis; ID, M. interosseus dorsalis; IV, M. interosseus ventralis; LDCR, M. latissimus dorsi pars cranialis; P, M. pectoralis; PP, M. pronator profundus; PPB, M. pectoralis pars propatagialis brevis; PPL, M. pectoralis pars propatagialis longus; PS, M. pronator superficialis; RP, M. rhomboideus profundus; RS, M. rhomboideus superficialis; SBC, M. subcoracoideus; SBC D.Hd., M. subcoracoideus dorsal head; SBC V.Hd., M. subcoracoideus ventral head; SBS, M. subscapularis; SBS MED, M. subscapularis medial head; SC, M. supracoracoideus; SHCA, M. scapulohumeralis caudalis; SHCR, M. scapulohumeralis cranialis; SP, M. serratus profundus; SSCA, M. serratus superficialis pars caudalis; SSCO, M. serratus superficialis pars costohumeralis; SSCR, M. serratus superficialis pars cranialis; ST, M. sternocoracoideus; SU, M. supinator; TH, M. triceps brachii caput humerotricipitale; TPB, M. tensor propatagialis pars brevis; TPL, M. tensor propatagialis pars longa; TS, M. triceps brachii caput scapulotricipitale; UD, M. ulnometacarpalis dorsalis; UV, M. ulnometacarpalis ventralis.

bit wider, just reaching the tip of the second dorsal spine. Pars caudalis (pars posterior) is absent (Fig. 1).

M. rhomboideus superficialis.—This thin, flat muscle lies deep to M. latissimus dorsi pars cranialis and superficial to M. rhomboideus profundus. It arises by a narrow aponeurosis from the neural spines and interspinous ligaments of the last two cervical vertebrae, the first three dorsal vertebrae, and the cranial tip of the neural spine of the fourth dorsal vertebra. The fibers pass craniolaterally to insert on the dorsomedial margin of the cranial two-thirds of the scapula. The most cranial fibers insert immediately caudal to the articulation with the head of the clavicle, but do not insert on that bone. These fibers form a somewhat distinct belly about 1 mm wide slightly separated at their insertion from the rest of the muscle (Fig. 1).

M. rhomboideus profundus.—This flat, fan-shaped muscle arises from the neural spines and interspinous ligaments of the first four dorsal vertebrae and the caudal tip

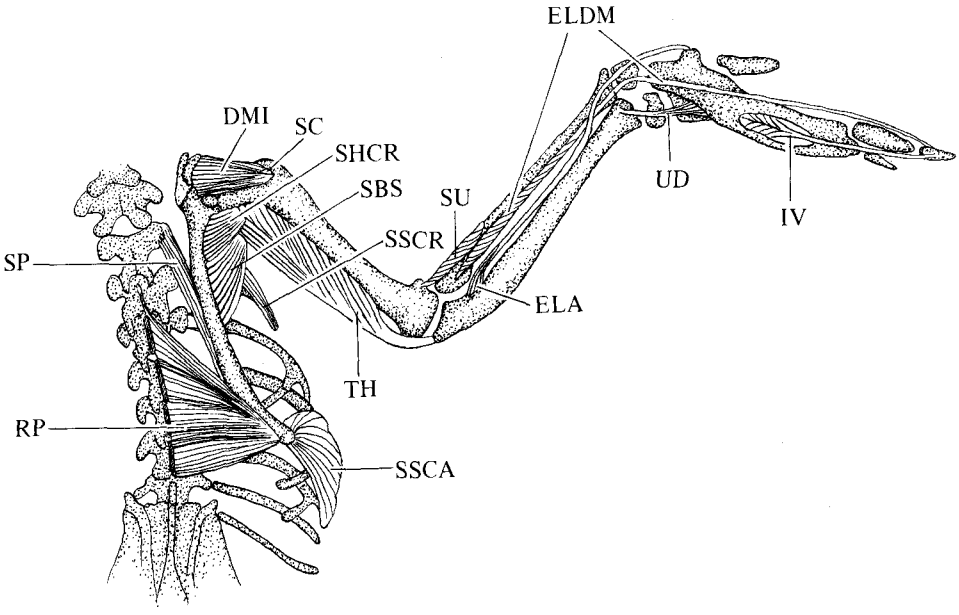

Fig. 2. Deep dorsal muscles of the forelimb of *Loxops virens wilsoni*. Abbreviations under Fig. 1.

of the neural spine of the last cervical vertebra. It inserts fleshy on the dorsomedial margin of the caudal one-third of the scapula. In *Hemignathus* and *Psittirostra* the origin begins more cranially, from the last cervical vertebra's neural spine (Figs. 1, 2).

M. serratus profundus.—This muscle arises by three separate heads that fuse at their insertion. The most caudal and smallest belly arises fleshy from the lateral surface of the first true rib near its proximal end. The middle, somewhat larger belly arises at the same level from the last cervical rib. The cranial and largest belly arises from the transverse process of the penultimate cervical vertebra. All three bellies are approximately strap-shaped and parallel-fibered, being slightly wider at their origins in the case of the two more caudally located bellies (Fig. 2). The three bellies insert in sequence (and slightly fused together) on the medial surface of the blade of the scapula just cranial to the insertion of M. rhomboideus profundus.

In *Himatione* the muscle is as described above. This also appears to be true in *L. maculata,* but because of the poor condition of the specimen I am not certain of this. In the other forms studied the cranial head is in two parts instead of one. There is a second head from the transverse process of the antepenultimate cervical vertebra.

M. serratus superficialis.—Pars cranialis (M. serratus anterior) has two parallel-fibered bellies with separate origins and a common insertion. The larger caudal head arises from the lateral surface of the first true rib at the level of its uncinate process. The cranial head arises from the lateral surface of the last cervical rib. The two heads extend craniodorsally, the caudal head lying superficial to the cranial head. The two fuse distally and give rise to a flat tendon that inserts on the ventral margin of the scapula slightly cranial to its midpoint. The insertion lies between the two heads of M. subscapularis (Figs. 2, 5). In *Vestiaria* the origin of the caudal head is wider than usual, arising in part from the proximal half of the uncinate process of the first true rib. In *Hemignathus* the cranial head is wider than usual and lies more cranial than medial to the caudal head.

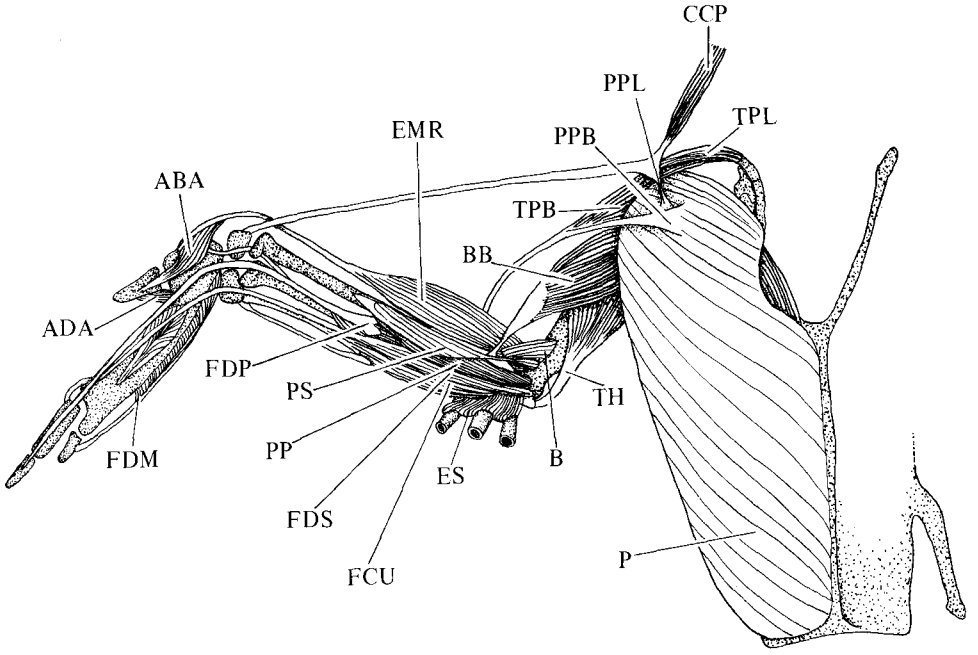

Fig. 3. Superficial ventral muscles of the forelimb of *Loxops virens wilsoni*. Abbreviations under Fig. 1.

Pars caudalis (*M. serratus posterior*), a fan-shaped muscle, arises by three fleshy fasciculi from the lateral surfaces of true ribs 2, 3, and 4 ventral to their uncinate processes. The fasciculi pass dorsally, fusing into a single belly that inserts fleshy on the caudal tip of the scapula, and by an aponeurosis for about 2 mm cranial to this. In *P. cantans* the muscle is wider, spanning the distance at its origin from true ribs 2 through 5. In *Himatione* the muscle is of normal size, but shifted caudally, arising from ribs 3, 4, and 5. (Figs. 1, 2).

Pars costohumeralis (*M. serratus metapatagialis*), a narrow, parallel-fibered muscle, arises fleshy from the lateral surface of the third true rib just ventral to the origin of pars caudalis. It inserts under the caudal patagium skin near the elbow (Fig. 1).

M. scapulohumeralis cranialis (M. proscapulohumeralis).—This muscle has a fleshy, 2-mm-wide origin from the dorsal surface of the scapula just caudal to the glenoid lip. It passes laterally to insert on the caudoproximal surface of the humerus at the distal end of the pneumatic fossa as far cranially as the median bar separating the pneumatic fossa from the second pneumatic fossa. The fleshy insertion lies between the two heads of M. triceps brachii caput humerotricipitale. The muscle is slightly fan-shaped, but nearly parallel-fibered in structure, the origin being slightly wider than the insertion (Fig. 2).

M. scapulohumeralis caudalis (M. dorsalis scapulae).—The origin is fleshy from the lateral surface of the caudal two–thirds of the scapula and by a weak aponeurosis from the ventral margin of the scapula. The muscle is mainly fan-shaped, but the fibers of the dorsal and ventral parts converge rather sharply toward the insertion so that the muscle approaches a bipennate condition at that point. The insertion is on the anconal surface of the bicipital crest of the humerus by fleshy fibers enclosed in a

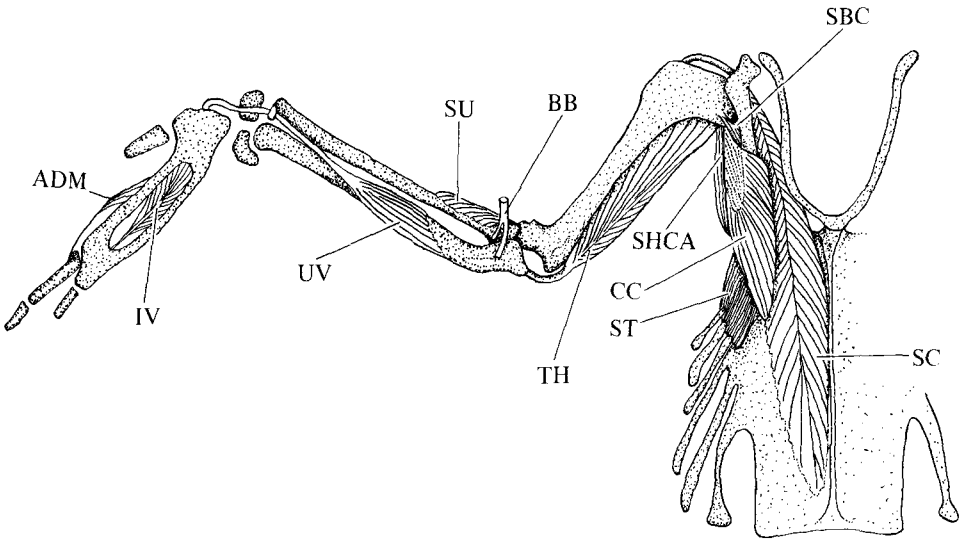

Fig. 4. Deep ventral muscles of the forelimb of *Loxops virens wilsoni*. Abbreviations under Fig. 1.

dense tendinous envelope. At its cranial margin the muscle lies deep to M. latissimus dorsi pars cranialis and superficial to the caudal part of M. subscapularis. It lies caudal to M. scapulohumeralis cranialis (Figs. 1, 4).

M. subscapularis.—The lateral head or caput laterale (pars externa) arises from the lateral and ventrolateral surfaces of the scapula. The fleshy origin begins at the caudal margin of the glenoid lip. The medial head or caput mediale (pars interna) arises fleshy from the medial scapular surface. The two heads are separated by the insertion of M. serratus superficialis pars cranialis on the scapula. They fuse to form a single tendon that inserts on the internal tuberosity of the humerus, adjacent to the insertion of M. subcoracoideus (Figs. 2, 5).

M. subcoracoideus.—This arises by two heads from the medial surface of the pectoral girdle. The larger, slightly bipennate ventral head has a fleshy origin from the ventral half of the medial surface of the coracoid, and by a very small aponeurosis from the medial sternocoracoidal process of the coracoid. The smaller dorsal head has a fleshy origin from the ventromedial surface of the cranial end of the scapula just caudal to its articulation with the head of the clavicle, and cranial to the medial head of M. subscapularis. The two heads join in forming a short tendon that passes distally across the caudal surface of the coracoid just ventral to the glenoid, and inserts on the lesser tuberosity of the humerus. (Figs. 4, 5).

M. pectoralis.—The belly, pars thoracicus, has a fleshy origin from the ventral half of the sternal carina, the sternal plate caudal to the origin of M. supracoracoideus, the posterior lateral process of the sternum and the membrane joining this to the sternal plate, a membrane overlying the last three sternal ribs, the craniolateral and caudolateral surfaces of the clavicle and lateral surface of the hypocleideum, and the coracoclavicular membrane. The muscle inserts on the deltoid crest of the humerus. The insertion is partly fleshy and partly by a dense tendon that arises deep within the belly, as well as from the dorsal and ventral surfaces of the belly near the insertion. The fiber arrangement is not readily described by the usual terms. It is an asymmetrical, curved, fan-shaped belly, with the fibers arising from a

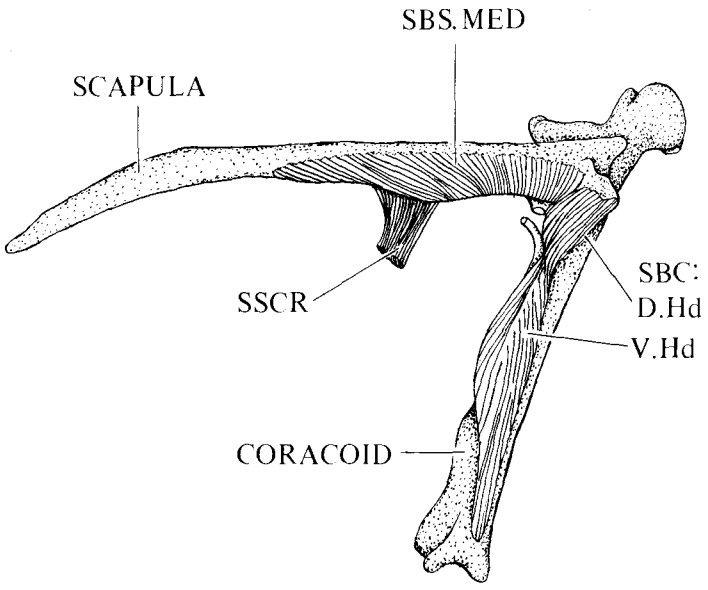

Fig. 5. Muscles on the medial side of the scapula and coracoid of *Psittirostra c. cantans*. Abbreviations under Fig. 1.

very wide area and converging on a comparatively small area of insertion. Pars propatagialis longus is a flat tendon arising from the craniomedial surface of pars thoracicus near the latter's insertion. It passes craniolaterally to insert on the tendon of M. tensor propatagialis pars longa at the latter's origin. There are no muscle fibers at its base. Pars propatagialis brevis is a tendon arising from the cranial surface of pars thoracicus slightly caudolateral to the origin of pars propatagialis longus. It passes to the distal end of the belly of M. tensor propatagialis pars brevis where it contributes to the formation of the tendon of that muscle (Fig. 3).

M. supracoracoideus.—This large, bipennate muscle lies deep to M. pectoralis pars thoracicus. It arises fleshy from the dorsal half of the sternal carina, the craniomedial aspect of the sternal plate, the craniolateral surface of the distal half of the coracoid, and the distolateral surface of the coracoclavicular membrane. The fibers converge on a stout tendon that passes through the triosseal canal and then proceeds craniolaterally through a fibrous canal arising from the craniomedial anchorage of the os humeroscapulare. The tendon inserts on the craniomedial surface of the head of the humerus at the proximal margin of the deltoid crest. Distal to the foramen triosseum this tendon is covered by M. deltoideus minor (Figs. 2, 4).

M. coracobrachialis caudalis (M. coracobrachialis posterior).—This muscle lies lateral to M. supracoracoideus and deep to M. pectoralis pars thoracicus. It is intermediate between being fan-shaped and bipennate, the fibers converging on a tendon that arises as an aponeurosis on the ventral surface. The origin is fleshy from the craniolateral surface of the basal two-thirds of the coracoid. It inserts by a short tendon on the internal tuberosity of the humerus (Fig. 4).

M. sternocoracoideus.—This short, broad, parallel-fibered muscle has a fleshy origin from the sternocoracoidal process of the sternum and from the distal ends of the sternal ribs. It inserts on the sternocoracoidal impression on the caudal surface of the basal half of the coracoid. The insertion is mainly fleshy but by an aponeurosis superficially (Fig. 4).

M. cucullaris capitis pars propatagialis (M. cucullaris pars propatagialis).—This is a cutaneous muscle on the undersurface of the skin of the side of the neck. Pars propatagialis has a narrow muscular belly about 5 mm long and 1 mm wide. It gives rise to a tendon that passes distally to fuse with the tendon of M. tensor propatagialis pars longa just beyond the belly of that muscle (Figs. 1, 3).

M. tensor propatagialis (Mm. tensor patagii longus and tensor patagii brevis).—This muscle has two separate parts in passerines. *Pars longa* (M. tensor patagii longus) is a small, parallel-fibered muscle that arises from the apex of the clavicle medial and adjacent to the origin of pars brevis. It passes distally giving rise to a tendon, tendo longa, which forms the leading edge of the cranial (anterior) patagium. This tendon is joined by those of M. cucullaris capitis pars propatagialis and M. pectoralis pars propatagialis longus just beyond the belly of M. tensor propatagialis pars longa. The tendon divides into three branches. Two, perforated by the tendon of M. extensor metacarpi radialis, insert on the os radiale on either side of the tendon of M. extensor metacarpi radialis. The third, a very fine tendon, inserts on the first digit. A scapular tendon, from the dorsal surface of the scapula, contributes to the origin of this muscle and that of M. tensor propatagialis pars brevis (Figs. 1, 3).

As in Passeriformes generally, *pars brevis* (M. tensor patagii brevis) is much larger than pars longa. It is a spindle-shaped, nearly parallel-fibered muscle that arises by a 1-mm-long tendon from the apex of the clavicle and extends distally superficial to M. deltoideus major pars cranialis. In addition a scapular tendon passes from the craniodorsal surface of the scapular blade diagonally across M. deltoideus major pars caudalis and ends as part of the tendon of origin of both tensor propatagialis muscles, at their common origin. At about the midpoint of the humerus the belly of M. tensor propatagialis pars brevis gives rise to a thin, flat tendon that continues distally. Just beyond the belly of the muscle this tendon is joined by the pectoralis pars propatagialis brevis tendon. The common tendon then attaches to the surface of M. extensor metacarpi radialis about 4 mm from its origin on the humerus. The tendon then passes proximally along the surface of this muscle. Some fibers of M. extensor metacarpi radialis arise from the tendon for about 2 mm proximal to where it joins the muscle; from here to the humerus the humerus tendon is attached to the muscle only by loose connective tissue. It inserts on the ectepicondylar process (Figs. 1, 3).

M. deltoideus major.—There are two separate bellies. The caudal belly, M. deltoideus major caudalis, arises fleshy from the medial surface of the apex of the clavicle and the anterior coracoclavicular ligament. It passes distad along the dorsocaudal surface of the upper arm superficial to M. triceps brachii caput scapulotricipitale and caudal to the cranial belly. It inserts by fleshy fibers on the distal end of the humerus just proximal and caudal to the ectepicondylar process. The scapular anchor, a flat tendon, arises from the deep caudal margin and is attached to the scapula just cranial to the origin of M. latissimus dorsi pars cranialis. The cranial belly, M. deltoideus major cranialis, is a large, triangular muscle lying just cranial to the caudal belly. It originates primarily fleshy from the os humeroscapulare, but the caudal part of the belly arises by a tendon from the ventrolateral surface of the acromion. This flat tendon passes out of the triosseal canal superficial to the supracoracoideus tendon and passes caudal to the os humeroscapulare, to which it is attached by an aponeurosis, before giving rise to the caudal portion of the belly. The muscle is fan-shaped. It inserts by a fine tendon on the ectepicondylar process of the humerus, and by a fleshy insertion on the deltoid crest and shaft of the humerus distal to the deltoid crest for about two-thirds the length of the humerus (Fig. 1).

M. deltoideus minor.—This muscle lies on the dorsal surface of the shoulder deep to M. tensor propatagialis pars brevis. It arises from the lateral surface of the acromion process of the scapula and the apex of the coracoid. The muscle is slightly fan-shaped, narrowing toward its insertion. The belly passes distad cranial to the os humeroscapulare and inserts on the head of the humerus mainly just cranial to the insertion of the supracoracoideus tendon. The more caudal part of the muscle inserts around the end of the supracoracoideus tendon at its insertion (Fig. 2).

M. biceps brachii.—The primary origin, caput coracoideum, is by a broad, flat tendon from the craniolateral face of the head of the coracoid. A smaller branch, the caput humerale, arises from the bicipital crest of the humerus at the level of the insertion of M. scapulohumeralis caudalis. The wide, spindle-shaped belly arises distal to the fusion of the two tendons. It passes into the forearm between the bellies of M. extensor metacarpi radialis and M. pronator superficialis, and forms a tendon that divides immediately into two unequal branches. The larger branch inserts on the proximal end of the ulna, while the smaller branch inserts on the proximal end of the radius. There is no pars propatagialis (biceps slip) (Figs. 3, 4).

M. triceps brachii.—Caput scapulotricipitale (M. scapulotriceps) arises by two fairly distinct heads from the cranial end of the scapula. Except for a slight convergence toward the insertion it is nearly parallel-fibered. The larger, caudal head has a fleshy origin from the dorsolateral surface of the acromion and the scapular surface proximal to the glenoid fossa, while the smaller cranial head arises by fleshy and tendinous fibers from the caudal margin of the glenoid lip and associated ligaments. The two heads merge at about the level of the insertion of M. latissimus dorsi pars cranialis. The muscle passes distad to the elbow where it forms a stout tendon containing a sesamoid at the distal end of the humerus, and inserts at the base of the coronoid process of the ulna. A few fibers of caput humerotricipitale may insert on it proximal to the sesamoid (Fig. 1).

Caput humerotricipitale (M. humerotriceps) arises by two distinct fleshy heads. The dorsal head arises from the second pneumatic fossa and the ventral head from the pneumatic fossa. The two heads are separated by the insertion of M. scapulohumeralis cranialis, beyond which they fuse into a single, bipennate belly. Part of each also arises from the humeral shaft. The muscle inserts by a short tendon on the olecranon process. The tendon lacks a sesamoid (Figs. 2, 3, 4).

In *Psittirostra cantans cantans* and *P. c. ultima* caput humerotricipitale is somewhat reduced in size, the two heads being separated by a greater distance than in the other forms studied owing to their more restricted areas of origin. *P. psittacea* is normal in this respect.

M. expansor secondariorum.—This small, triangular muscle arises from the distal, superficial surface of the humeroulnar pulley in the ventral region of the elbow, and fans out to insert on the bases of the innermost three secondaries (Fig. 3).

M. brachialis.—This short, wide, parallel-fibered muscle has a fleshy origin in the brachial impression on the distal end of the humerus. It passes across the elbow joint superficial to the tendon of insertion of M. biceps brachii and inserts fleshy on the ulna's proximal end between the two heads of M. flexor digitorum profundus (Fig. 3).

M. pronator superficialis.—This muscle arises by a tendon from the ventral surface of the distal end of the shaft of the humerus adjacent to the origin of M. brachialis. The belly fans out to insert mainly fleshy on the caudoventral surface of the middle of the shaft of the radius. The distal end of the insertion is tendinous and is fused with the insertion of M. pronator profundus (Fig. 3).

M. pronator profundus.—This fan-shaped muscle has a dual origin. There is a tendinous origin from the distomedial surface of the humerus, and just distal to this a largely fleshy origin from the humeroulnar pulley. The muscle passes distally, fanning out to insert on the radius by an aponeurosis in common with M. pronator superficialis distally, and by an aponeurosis on the radius distal to the insertion of M. brachialis (Fig. 3).

M. flexor digitorum superficialis.—This muscle arises by a tendon from the median epicondyle of the humerus distal to the origin of M. pronator profundus. The tendon of origin fans out to form a complex sheet of connective tissue, the humerocarpal band, which is described below. The narrow, spindle-shaped belly of M. flexor digitorum superficialis arises from the cranial surface of the tendon of origin and the humerocarpal band and extends distally cranial to the belly of M. flexor carpi ulnaris and closely applied to it, but is shorter than that muscle. It gives rise to a tendon that passes distally in common with that of M. flexor carpi ulnaris, and passes across the surface of the os ulnare, where it is held in place by a fine retinaculum. The tendon then passes craniodistally across the manus and deep to the tendon of M. flexor digitorum profundus, and inserts on the cranioproximal surface of the first phalanx of digit II (Fig. 3).

The humerocarpal band arises from the median epicondyle of the humerus as part of the origin of M. flexor digitorum superficialis. It fans out to envelop the bellies of M. flexor digitorum superficialis and most of the distal half of the belly of M. flexor carpi ulnaris, as well as the tendons of insertion of these two muscles, which pass distally side by side enclosed in a common sheath. Caudally it is associated with the tendinous bands arising from the belly of M. flexor carpi ulnaris proximally, and its accessory tendon distally, and passes to the bases of all but the proximal 3 secondaries. Distally the humerocarpal band passes across the os ulnare and is associated with the aponeurotic sheets in the palmar surface of the manus, sending tendons to (1) the base of the first digit, (2) a short branch ensheathing the tendon of M. flexor digitorum profundus, and (3) to metacarpal 3 and the bases of the inner 4 primaries.

M. flexor digitorum profundus.—This spindle-shaped muscle occupies the ventral surface of the ulna superficial to M. ulnometacarpalis ventralis. It arises fleshy from near the proximal end of the ulna at the level of the insertion of the biceps tendon, and extends distally for slightly over one-half the length of the ulna. At its proximal end the origin is by two heads between which M. brachialis inserts on the ulna, but distal to this the two heads fuse to form a single belly. The muscle gives rise to a tendon that passes distally around the pisiform process of the carpometacarpus and then proceeds distally along the cranioventral margin of the manus to its insertion on the cranioventral surface of the proximal end of phalanx 2 of digit II (Fig. 3).

M. flexor carpi ulnaris.—This is the most caudal muscle on the ventral surface of the forearm. It arises by a stout tendon from the distal end of the median epicondyle of the humerus. The tendon passes through the humeroulnar pulley and gives rise to a stout, spindle-shaped belly. This extends distally and forms a strong tendon that inserts on the proximal face of the os ulnare. From the caudal surface of the main belly there arises a small secondary belly that forms an accessory tendon that passes distally to insert on the os ulnare deep to the main insertion. As it proceeds distally, this tendon sends branches to the bases of the outermost 6 secondaries (Figs. 1, 3).

M. ulnometacarpalis ventralis (M. ulnimetacarpalis ventralis).—This elongate, fan-shaped muscle lies on the ventral surface of the ulna deep to M. flexor digitorum profundus. It has a fleshy origin from the cranioventral and caudoventral surface of

the middle third of the ulna, the caudal portion arising farther proximal than the cranial portion. The proximal edge of the caudal margin begins at the level of the distal edge of the brachialis insertion on the ulna, but the two do not overlap. The muscle gives rise to a flat tendon that passes distad to the end of the ulna where it passes through a tendinous sling arising from the distal end of the radius. It then turns caudally, passes over a groove on the os radiale, and turns craniad to insert on the cranial margin of the base of the carpometacarpus (Fig. 4).

The point of origin of the proximal end of the caudal portion on the ulna varies somewhat in relation to the area of insertion of M. brachialis. In some forms, as described above, the origin does not extend proximal to the distal edge of M. brachialis. In *Hemignathus wilsoni* the muscle begins slightly proximal to this point. In *Himatione* the muscle arises much more proximally, completely overlapping the area of insertion of M. brachialis. In *Vestiaria* it overlaps about the distal two-thirds of this area, and in *Palmeria* it overlaps the distal one-half of this insertion.

M. extensor metacarpi radialis.—This large muscle forms the cranial margin of the forearm. It arises from the distal end of the humerus by 2 adjacent heads. Pars anconalis arises from the lateral epicondyle of the humerus just proximal to the origin of M. extensor digitorum communis. Pars palmaris arises by fleshy and tendinous fibers from the distal end of the humerus deep to the origin of pars anconalis and lateral to the brachial depresssion. The fibers of the two heads converge on a central tendon that continues as the tendon of insertion and inserts on the extensor process of the carpometacarpus. The belly is thus bipennate (Figs. 1, 3).

M. extensor metacarpi ulnaris.—This elongate, bipennate muscle arises by two tendons. One arises from the distal end of the humerus distal to that of M. extensor digitorum communis, and proximal to that of M. ectepicondyloulnaris. The second, broader tendon arises from the proximal end of the ulna (ulnar anchor). The two join to form a common origin for the belly, which extends distally about half the length of the forearm. It gives rise to a tendon that passes around a tubercle on the craniodorsal surface of the ulna and proceeds caudodistally to insert on the proximal end of the carpometacarpus at the base of metacarpal III (Fig. 1).

M. extensor digitorum communis.—This muscle lies caudal to M. extensor metacarpi radialis and cranial to M. extensor metacarpi ulnaris on the dorsal side of the forearm. It arises by a tendon from the lateral epicondyle of the humerus just distal to the origin of M. extensor metacarpi radialis. The belly extends slightly more than half the length of the forearm. The tendon passes distally around the end of the ulna and into the manus. At the base of the first digit it bifurcates. The smaller branch passes to the first digit and bifurcates, a short branch inserting on the base of digit I and a thinner, longer branch inserting on the tip of the digit. The main branch of the tendon continues distad along the craniodorsal margin of the carpometacarpus, and passes through a bony canal near the distal end of the carpometacarpus, then turns craniad to insert on the craniodorsal corner of phalanx 1 of digit II (Fig. 1).

M. ectepicondyloulnaris (M. anconeus).—This muscle arises by a flat tendon from the lateral supracondylar ridge on the distal end of the humerus, distal to the tendon of M. extensor metacarpi ulnaris. It crosses the elbow joint and gives rise to a narrow, asymmetrically fan-shaped belly, which spreads over the proximal half of the craniodorsal surface of the ulna, onto which it has a fleshy insertion. In *Hemignathus* and *Psittirostra* the muscle is somewhat longer, extending about two-thirds the length of the ulna (Fig. 1).

M. supinator.—This small muscle arises by a fine tendon from the lateral epicon-

dyle of the humerus just proximal to the origin of M. ectepicondyloulnaris, and spreads out to a fleshy insertion on the proximal third of the craniodorsal surface of the radius (Figs. 2, 4).

M. extensor longus digiti majoris (M. extensor indicus longus).—The long, narrow bipennate belly of this muscle extends about two-thirds the length of the forearm. It arises fleshy from the proximal two-thirds of the caudodorsal surface of the radius. The belly ends in a flat tendon that passes distally around the external ulnar condyle and proceeds diagonally across the carpometacarpus superficial to the tendon of M. extensor digitorum communis. It proceeds along the cranial edge of phalanx 1 of digit II, and inserts on the proximal end of the cranial margin of phalanx 2 of digit II. In *Hemignathus procerus* the belly extends about four-fifths the length of the forearm (Fig. 2).

M. extensor longus allulae (M. extensor pollicis longus).—This small muscle arises fleshy from the cranioproximal surface of the ulna at the base of the coronoid process. There is no radial head. The long, slender belly passes distally caudal to M. extensor longus digiti majoris, to which it is bound by a loose fascia, and gives rise to a fine tendon that continues distad across the caudodorsal surface of the distal end of the radius and along the dorsal margin of the tendon of insertion of M. extensor metacarpi radialis to insert on the extensor process of the carpometacarpus just caudal and adjacent to the insertion of the latter muscle. It is separate from that tendon for its entire length (Fig. 2).

M. ulnometacarpalis dorsalis (M. ulnimetacarpalis dorsalis).—This small muscle arises by a narrow tendon from the craniodorsal surface of the distal end of the ulna. The tendon gives rise to a fan-shaped belly that inserts fleshy on the proximal end of metacarpal III of the carpometacarpus (Fig. 2).

M. abductor allulae (M. abductor pollicis).—This small, spindle-shaped muscle (about 2 mm long) has a fleshy origin from the caudoventral surface of the tendon of M. extensor metacarpi radialis about 1 mm proximal to the latter's insertion on the extensor process of the carpometacarpus. The belly passes across the ventral surface of the extensor process and narrows to a fine tendon that inserts on the caudoventral edge of the first digit about one-third of the distance from its proximal end (Fig. 3).

M. abductor allulae (M. abductor pollicis).—This small, spindle-shaped muscle mm long and 0.5 mm wide. It arises fleshy from the carpometacarpus at the base of the extensor process and inserts partly on the first digit and partly on a branch of the tendon of M. extensor digitorum communis (which see for details) (Fig. 3).

M. abductor digiti majoris (M. abductor indicis).—This small, elongate, fan-shaped muscle arises fleshy from the cranioventral margin of the second metacarpal. Its fine tendon passes distally and inserts on the cranioproximal end of phalanx 1 of digit II (Fig. 4).

M. interosseus dorsalis.—This is a tiny bipennate muscle occupying the proximal half of the intermetacarpal space of the carpometacarpus. It has a fleshy origin from the proximal margin of the intermetacarpal space and the facing surfaces of metacarpals II and III. The muscle lies dorsal to M. interosseus ventralis, and is about half the length of the latter. The fibers converge on a fine tendon that passes across the distal end of the carpometacarpus and the craniodorsal surface of phalanx 1 of digit II. It inserts on the craniodorsal corner of phalanx 2 of digit II (Fig. 1).

M. interosseus ventralis (M. interosseus palmaris).—This tiny, bipennate muscle arises from the proximal margins of the intermetacarpal space deep to M. interosseus

TABLE 1
VARIATIONS IN THE FORELIMB MUSCLES OF THE DREPANIDIDAE

Muscle	Variation compared to *Loxops virens*
Latissimus dorsi pars cranialis	In *Psittirostra* the origin is slightly wider, arising caudally from the tip of the neural spine of the second dorsal vertebra rather than ending at the first dorsal.
Rhomboideus profundus	In *Hemignathus* and *Psittirostra* the origin begins more cranially, on the neural spine of the last cervical vertebra rather than just on its caudal tip.
Serratus profundus	In *Loxops virens* and *Himatione* the cranial head arises only from the penultimate cervical vertebra; in the other forms there is also a head from the antepenultimate cervical.
Serratus superficialis pars cranialis	In *Vestiaria* the origin of the caudal head is wider; in *Hemignathus* the cranial head is wider.
Triceps brachii	In *Psittirostra cantans* the caput humerotricipitale is reduced.
Ulnometacarpalis ventralis	There is variation in the point of origin of the proximal end of the muscle relative to M. brachialis. See text for details.
M. ectepicondyloulnaris	In *Hemignathus* and *Psittirostra* the belly is somewhat elongated.
M. extensor longus digiti majoris	In *Hemignathus procerus* the belly is slightly elongated.

dorsalis. Its fine tendon passes distally over the caudodorsal surface of the distal end of the carpometacarpus, the proximal corner of digit III, and the caudodorsal margin of phalanx 1 of digit II to insert at the caudodorsal margin of the second phalanx of digit II. Just proximal to its insertion the tendon is anchored to the caudodistal end of phalanx 1 by a broad band of fibers of unknown composition (Figs. 1, 2, 4).

M. flexor digiti minoris (M. flexor digiti III).—This small muscle arises on the proximocaudal surface of metacarpal III and extends about two-thirds the length of the carpometacarpus. At its proximal end it is bipennate, but for most of its length it is unipennate, with fibers passing to the tendon from the dorsal side. Its hairlike tendon extends distally to insert on the caudal surface of digit III halfway to its tip.

DISCUSSION

The variations in the forelimb muscles of the Drepanididae are summarized in Table 1. They are few in number and largely minor in terms of structural variation. In general, the forelimb myology of the Drepanididae is marked by great uniformity, a characteristic that was found to almost the same degree in the hind limb muscles (Raikow ibid). This basic uniformity is remarkable in view of the adaptive radiation of the feeding mechanism seen in the Drepanididae, and indicates that no great adaptive modifications were needed in the locomotor apparatus in conjunction with the evolution of the feeding mechanism. This lack of significant variation again attests to the unity of the Drepanididae, and supports the theory that the family evolved from a single ancestral species.

ACKNOWLEDGMENTS

I am grateful to A. J. Berger, University of Hawaii, Honolulu; R. L. Zusi, National Museum of Natural History, Washington D. C.; A. C. Ziegler, Bernice P. Bishop Museum, Honolulu; and P. J. K. Burton, British Museum (Natural History), Tring, for providing the specimens used in this investigation. This study was supported by N.S.F. grant no. BMS74-18079 and N.I.H. grant no. 1-FO2-GM-36, 212-01. Lee Ambrose prepared the figures.