PELVIC APPENDAGE MYOLOGY OF THE
HAWAIIAN HONEYCREEPERS (DREPANIDIDAE)

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THIS is the first in a series of studies on the appendicular myology and relationships of passerine birds. Despite the many studies that have been done to clarify relationships within the largest order of birds, the interrelationships of passeriform families are still a matter of great confusion. Relatively few anatomical studies have been done on passerines as compared to nonpasserine orders, and most of these (such as Beecher 1953, Tordoff 1954, Bock 1960) have dealt with the structure of the head or the pterylosis (Clench 1970). Few studies have been carried out on the appendicular muscles of passerine birds, and most of these (e.g. Berger 1968, Gaunt 1969) have been limited to single species or families. Hudson (1937) compared a few passerine species with various nonpasserine forms, and Stallcup (1954) and Swinebroad (1954) made limited interfamilial comparisons. Berger (1969) reviewed the present state of knowledge of the subject and emphasized how little still is known about the appendicular myology of passerines. The need for new studies of passerine relationships using previously unutilized sources of data has been pointed out by a number of authors in recent years, including Mayr and Amadon (1951), Beecher (1953), Stresemann (1959), and George and Berger (1966: 229).

The New World nine-primaried oscines (Fringillidae and related families) constitute a large segment of oscine forms and encompass a number of interrelated taxonomic problems. The present study includes a largely descriptive account of the myology of the hind limb in a representative family, the Drepanididae, and a subsequent paper will present a similar account of the muscles of the forelimb. Following this, hopefully, a comparative study of the entire New World nine-primaried oscine assemblage will be presented, utilizing an analysis of variations from the basis of comparison provided in the first two studies.

The Drepanididae or Hawaiian honeycreepers are endemic to the Hawaiian Islands and have been the subject of much discussion regarding their origin and subsequent evolution. Nothing has been previously written about their appendicular myology. The only detailed anatomical study of this family is an analysis of the feeding mechanism in the genus *Loxops* (Richards and Bock 1973). Amadon (1950) reviewed the earlier and more limited studies of their structure. In the following account each muscle is described in detail and illustrated in a representative species,

Loxops virens wilsoni. This is followed by a comparison with the other species studied. Finally the significance of these data to the problems of the Drepanididae relationships is discussed.

MATERIALS AND METHODS

The following forms were studied (the number in parenthesis shows the number of specimens dissected): *Hemignathus procerus* (1), *H. wilsoni* (1), *Loxops maculata bairdi* (1), *L. virens wilsoni* (3), *Psittirostra c. cantans* (2), *P. c. ultima* (2), *P. psittacea* (1), *Himatione sanguinea* (2), *Vestiaria coccinea* (2), *Palmeria dolei* (1), *Ciridops anna* (1). The *Ciridops* specimen was very incomplete and contained only a few muscles. Except where specific reference is made to *Ciridops*, statements referring to a general condition in the Drepanididae do not include this form.

Dissection was done under a stereomicroscope at magnifications of 6× to 25×, and the muscles were made more visible with an iodine stain (Bock and Shear 1972) that emphasizes details of fiber arrangement.

Berger (George and Berger 1966) presented a standardized nomenclature for avian muscles, which I followed in my previous work (Raikow 1970). In the present study I have introduced some changes from this system in accordance with a new nomenclature of avian anatomy that the International Committee of Avian Anatomical Nomenclature is now developing. This will eventually be published as *Nomina Anatomica Avium* (N.A.A.), which it is hoped will stabilize the nomenclature of avian anatomy. The names chosen are intended to avoid unsupported implications of homology with the muscles of mammals, and to be accurate descriptively. The names for muscles used herein have been tentatively adopted for the N.A.A. at the time of this writing. If a name differs from that given by Berger (George and Berger 1966), then the older name is given in parentheses following that currently adopted. Terms of direction have also been modified. *Cranial* means toward the head and replaces *anterior*, while *caudal* means toward the tail and replaces *posterior*. After each muscle is described in *Loxops virens*, any variations in other Drepanididae are given. If no such variations are listed, then it may be assumed that the description fits all the species studied.

MUSCLE DESCRIPTIONS

M. iliotibialis cranialis (M. sartorius).—This is the most cranial muscle of the thigh. It arises by an aponeurosis from the caudal part of the neural spine of the fourth dorsal vertebra and the neural spine of the fifth dorsal vertebra, and is fleshy from the anterior iliac process of the ilium. It inserts by fleshy fibers on the craniomedial surface of the head of the tibiotarsus and the medial margin of the patellar tendon. The insertion is covered by the patellar band of M. gastrocnemius pars interna. The muscle is basically parallel-fibered, but as the origin is slightly wider than the insertion, the fibers converge slightly toward the insertion (Figs. 1, 4).

M. iliotibialis lateralis (M. iliotibialis).—This flat triangular muscle covers the lateral surface of the thigh caudal to M. iliotibialis cranialis and cranial to M. flexor cruris lateralis. It includes well-developed preacetabular, acetabular, and postacetabular portions, which are continuous with one another as in most passerines. The muscle originates over most of its length by a broad aponeurosis from the cranial and caudal iliac crests of the ilium. This aponeurosis covers the
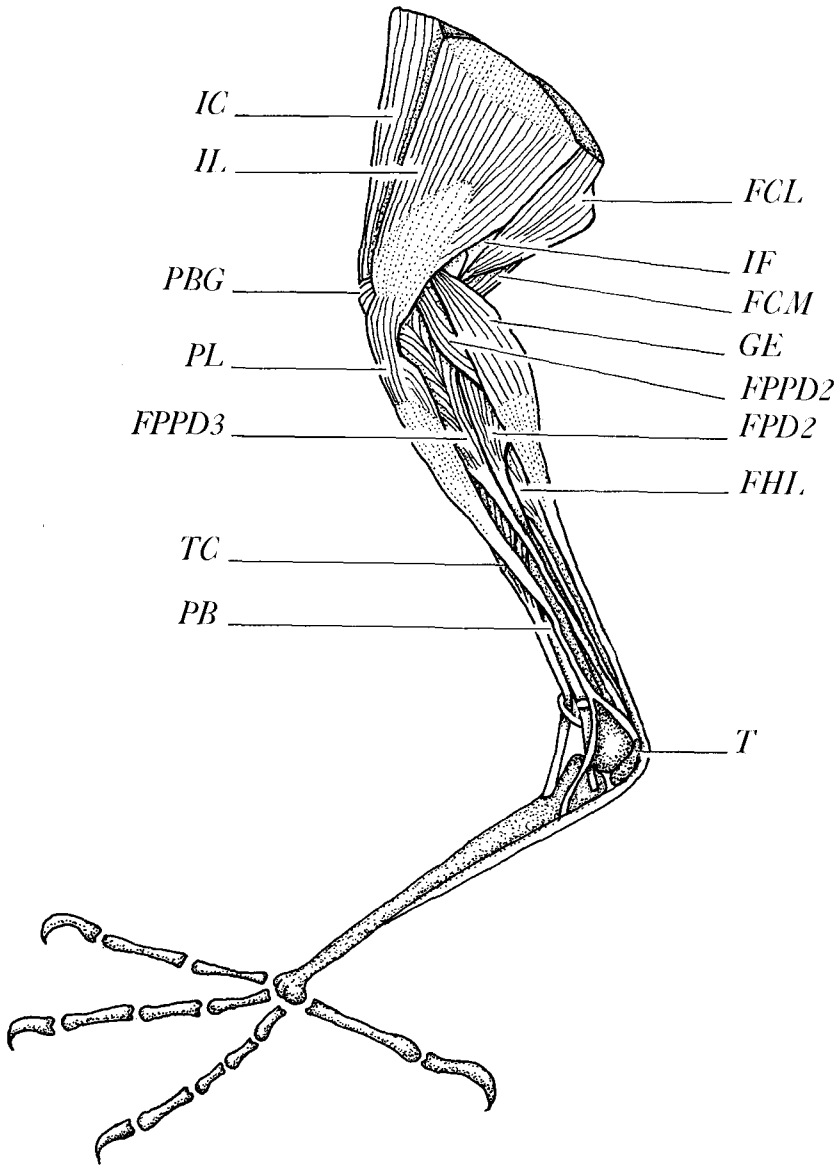
Fig. 1. Lateral view of the hind limb of *Loxops virens wilsoni* showing the superficial muscles. Abbreviations for Figs. 1–4: CF, M. caudiliofemoralis pars caudofemoralis; EDL, M. extensor digitorum longus; FCL, M. flexor cruris lateralis pars pelvina; FCLA, M. flexor cruris lateralis pars accessorius; FCM, M. flexor cruris medialis; FDL, M. flexor digitorum longus; FHL, M. flexor hallucis longus; FPD2, M. flexor perforatus digiti II; FPD3, M. flexor perforatus digiti III; FPD4, M. flexor perforatus digiti IV; FPPD2, M. flexor perforans et perforatus digiti II; FPPD3,

underlying iliotrochantericus muscles and extends distally to just beyond the head of the femur. The origin is fleshy for its caudal 1–2 mm. Distally the central part of the muscle is formed by a large aponeurosis closely applied to the underlying M. femorotibialis externus, but fleshy fibers extend nearly to the insertion at the cranial and caudal margins of the muscle. These fasciculi give rise to tendinous fibers that together with the central aponeurosis form the superficial layer of the patellar ligament that finally inserts on the head of the tibiotarsus (Fig. 1).

M. iliotrochantericus caudalis (M. iliotrochantericus posterior).—This large, roughly oval-shaped muscle occupies the iliac fossa of the ilium, lying deep to the aponeurotic origin of the preacetabular portion of M. iliotibialis lateralis. Its origin is fleshy from the concave surface of the iliac fossa and the cranial iliac crest. The fibers converge on a short, broad tendon that inserts on the lateral surface of the head of the femur just distal to the trochanter, and proximal to the insertion of M. iliotrochantericus medius. The fiber arrangement is fan-shaped, with the longest fibers passing from the cranial margin of the cranial iliac crest, and progressively shorter fibers arising along the dorsal and ventral margins of the muscle belly from the cranial toward the caudal aspect of the fossa (Fig. 2).

M. iliotrochantericus cranialis (M. iliotrochantericus anterior).—The origin is from the lateroventral margin of the preacetabular ilium, cranial to that of M. iliotrochantericus medius and deep to M. iliotrochantericus caudalis. The muscle inserts on the craniolateral surface of the femur distal to the insertion of M. iliotrochantericus medius and between the heads of Mm. femorotibialis externus and femorotibialis medius. Although superficially the muscle appears parallel-fibered, it is actually unipennate. Most of the fibers arise not directly from the ilium, but from an aponeurosis that extends over the proximal one-third of the lateral surface of the muscle belly. Most of the fibers do not insert directly onto the femur, but via an aponeurosis that extends over the distal one-third of the medial surface of the belly (Figs. 2, 3, 4).

M. iliotrochantericus medius.—This tiny muscle has a fleshy origin from the ventralateral edge of the ilium caudal to the origin of M. iliotrochantericus cranialis. It inserts by means of a short, flat tendon on the craniolateral surface of the femur proximal to the insertion of M. iliotrochantericus cranialis and

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M. flexor perforans et perforatus digiti III; FTED, M. femorotibialis externus pars distalis; FTEP, M. femorotibialis externus pars proximalis; FTI, M. femorotibialis itnernus; FTM, M. femorotibialis medius; GE, M. gastrocnemius pars externa; GI, M. gastrocnemius pars interna; GM, M. gastrocnemius pars intermedia; IC, M. iliotibialis cranialis; IF, M. iliofibularis; II, M. iliofemoralis internus; IL, M. iliotibialis lateralis; ISF, M. ischiofemoralis; ITC, M. iliotrochantericus caudalis; ITCR, M. iliotrochantericus cranialis; ITM, M. iliotrochantericus medius; OM, M. obturatorius medialis; PB, M. peroneus brevis; PBG, patellar band of M. gastrocnemius; PIFC, M. pubischiofemoralis pars cranialis; PIFCD, M. pubischiofemoralis pars caudalis; PL, M. peroneus longus; T, tibial cartilage; TC, M. tibialis cranialis.
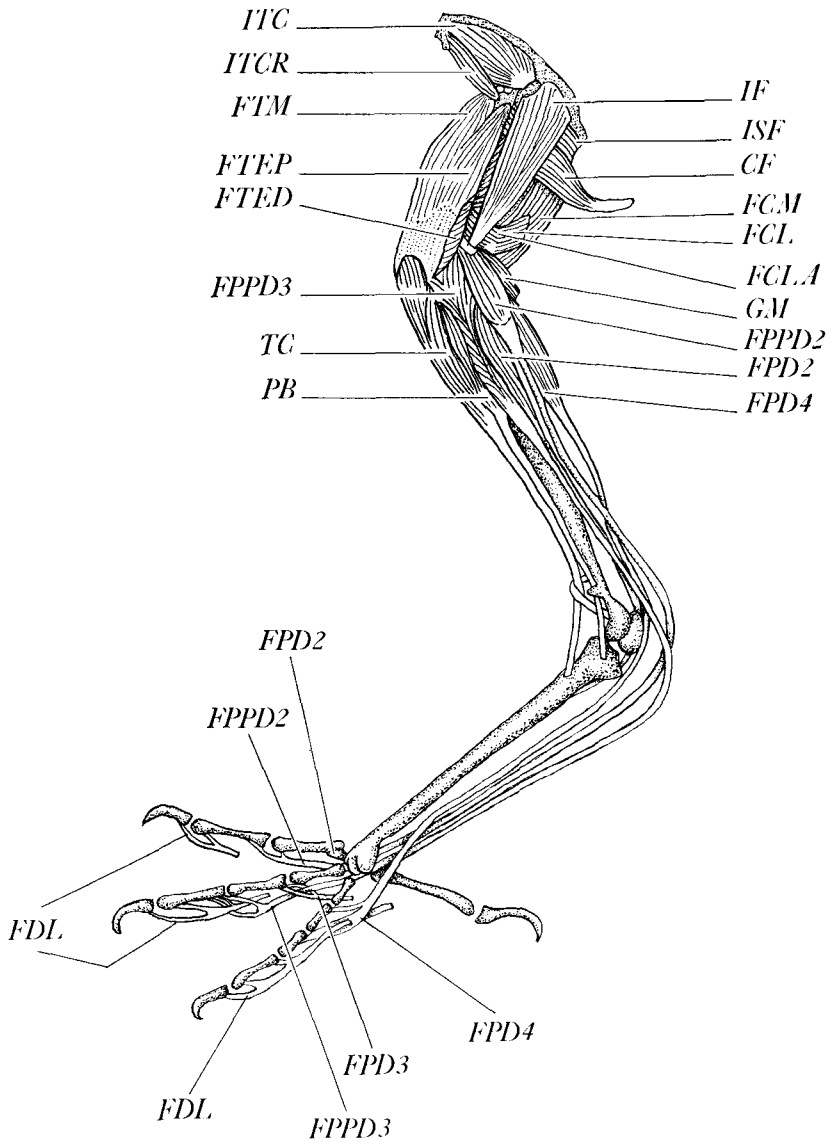
Fig. 2. Lateral view of the hind limb of *Loxops virens wilsoni* showing a second layer of muscles. The following muscles, shown in Fig. 1, have been removed: M. iliotibialis cranialis, M. iliotibialis lateralis, M. flexor cruris lateralis, proximal portion, M. peroneus longus, M. gastrocnemius pars externa. Abbreviations under Fig. 1.
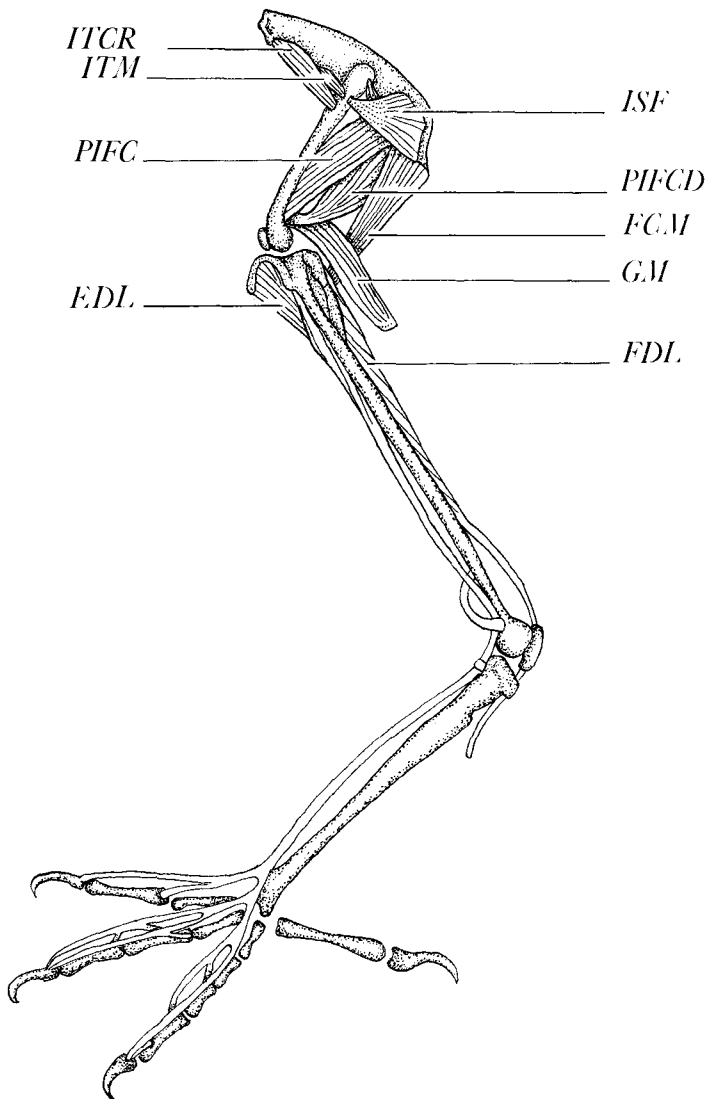
Fig. 3. Lateral view of the hind limb of *Loxops virens wilsoni* showing a third layer of muscles. The following muscles, shown in Fig. 2, have been removed: M. iliotrochantericus caudalis, M. femorotibialis externus, M. femorotibialis medius, M. iliofibularis, M. caudiliofemoralis pars caudofemoralis, M. flexor cruris lateralis, M. flexor perforans et perforatus digiti II, M. flexor perforans et perforatus digiti III, M. flexor perforatus digiti IV, M. tibialis cranialis, M. peroneus brevis. Abbreviations under Fig. 1.

distal to the insertion of M. iliotrochantericus caudalis. It is nearly parallel-fibered, but is slightly wider at the origin than at the insertion (Figs. 3, 4).

M. femorotibialis externus.—The main part of this muscle (pars proximalis) has a fleshy origin from the lateral and craniolateral surfaces of the femur, beginning proximally at the level of the insertion of M. ischiofemoralis. Some-what distal to the insertion of M. iliotrochantericus cranialis it is fused for its entire length with M. femorotibialis medius. A strong tendinous sheet arises on the distal half of the muscle's surface and continues distally as the lateral part of the patellar tendon, which inserts on the head of the tibiotarsus. A deep distal head (pars distalis) arises from the caudolateral surface of the distal half of the femur and joins the proximal head, forming a deeper layer of the patellar tendon (Fig. 2).

M. femorotibialis medius.—This is the central and cranial portion of the femorotibialis complex. It arises fleshy from the cranial surface of nearly the entire length of the femoral shaft. It is fused with M. femorotibialis externus along this lateral margin for its entire length except the proximal 2–3 mm. The insertion is on the proximal face of the patella by both fleshy and tendinous fibers (Figs. 2, 4).

M. femorotibialis internus.—This arises from the medial surface of the femur, primarily by fleshy fibers, but also by a weak aponeurosis along its caudal border. It has two heads. The proximal head arises from the proximal one-half of the femoral shaft, beginning slightly distal to the insertion of M. iliofemoralis internus. The distal head arises from the distal half of the femur just proximal to the median condyle. The two heads are not clearly separate at their origins, but insert by adjacent flat tendons on the medial side of the head of the tibiotarsus, and are unipennate in fiber arrangement (Fig. 4).

M. iliofibularis (M. biceps femoris).—This large, roughly triangular muscle lies on the caudolateral surface of the thigh deep to M. iliotibialis lateralis. It arises by an aponeurosis from the cranial iliac crest dorsal to the acetabulum and from the cranial 3 mm of the caudal iliac crest, the latter part of the origin being fleshy. The muscle narrows distally to form a stout tendon that passes through the biceps loop, continues medial to the tendon of origin of the lateral head of M. flexor hallucis longus and M. flexor perforatus digiti II, and inserts on the caudolateral surface of the fibular shaft. In superficial appearance the fiber architecture of the muscle appears largely fan-shaped, but dissection of the belly shows that it actually approaches a bipennate condition as the tendon of insertion extends some way into the belly, with fibers inserting on it cranially and caudally.

The biceps loop has three arms. The proximal femoral arm arises on the craniolateral surface of the femur about 2 mm from the distal end of the bone. The distal femoral arm arises on the caudolateral surface of the femur together with the tendinous origin of M. gastrocnemius pars externa. The fibular arm arises from the craniolateral surface of the fibula 2 mm from the proximal end of the fibula (Fig. 2).

M. flexor cruris lateralis (M. semitendinosus).—This strap-shaped, parallel-fibered muscle arises fleshy from the caudal end of the caudal iliac crest and
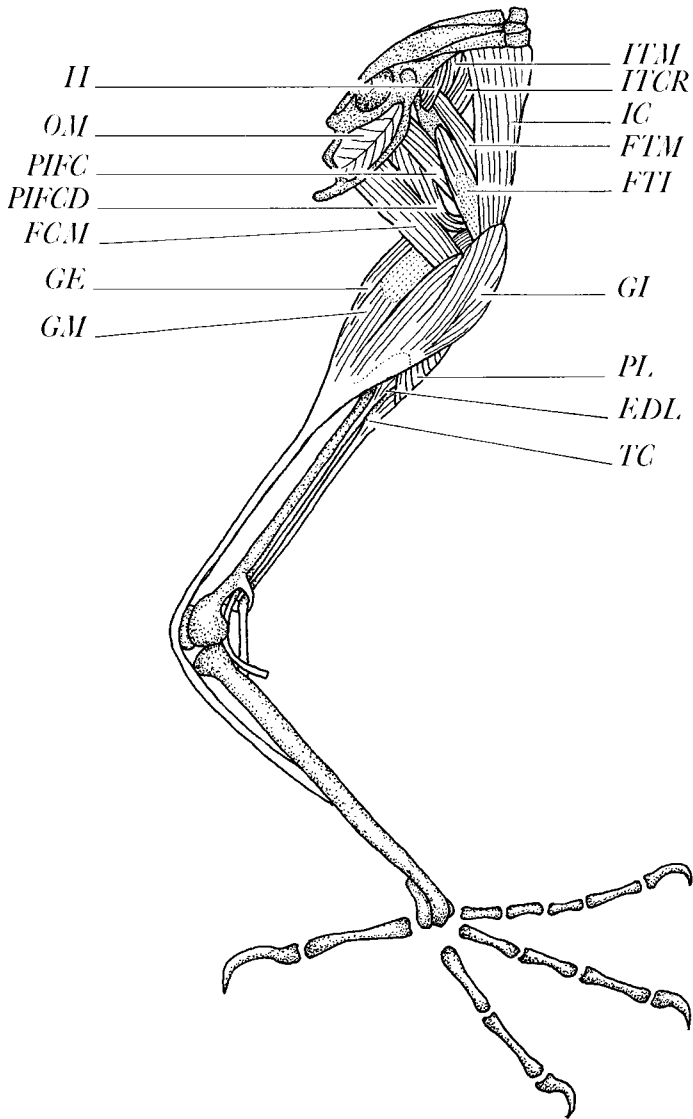
Fig. 4. Medial view of the hind limb of *Loxops virens wilsoni*. Abbreviations under Fig. 1.

tendinously from the first several caudal vertebrae. Distally the belly is bisected by a tendinous raphe that separates the main part (pars pelvina) from pars accessorius (accessory semitendinosus). The raphe extends beyond the muscle in two branches. One branch binds M. flexor cruris lateralis to the middle of M.

gastrocnemius pars intremedius, while the other joins the tendon of insertion of M. flexor cruris medialis. Pars accessorius extends cranioventrally from the raphe and inserts fleshy on the distal one-fourth of the shaft of the femur proximal to the external condyle and superficial to M. pubischiofemoralis, and medially in the popliteal area of the femur (Figs. 1, 2).

M. caudiliofemoralis (M. piriformis).—This muscle has two parts in many birds, pars caudofemoralis and pars iliofemoralis, but only the former normally occurs in passerines. It is a flat, spindle-shaped muscle that arsies by a short (2 mm) tendon from the caudolateral margin of the pygostyle. It passes craniad deep to M. iliofibularis and superficial to Mm. flexor cruris medialis, ischiofemoralis, and pubischiofemoralis. It inserts by a short, flat tendon on the caudal surface of the femur distal to the insertion of M. ischiofemoralis (Fig. 2).

M. ischiofemoralis.—This large, fan-shaped muscle has a fleshy origin from the lateral surface of the ischium caudal to the ilioischiadic fenestra and from the ventral surface of the laterally projecting caudal iliac crest. At its caudoventral margin the origin borders the cranial half of the origin of M. flexor cruris medialis, and the main part of the belly lies superficial to the origin of M. pubischiofemoralis pars cranialis. The aponeurosis of insertion arises on the lateral surface of the distal half of the belly; the muscle is thus unipennate. The aponeurosis converges to a flat tendon 0.5 mm wide that inserts on the lateral surface of the femur distal to the insertion of M. iliotrochantericus medius (Figs. 2, 3).

M. flexor cruris medialis (M. semimembranosus).—This parallel-fibered, strap-shaped muscle lies deep in the caudal region of the thigh. It arises fleshy from the caudolateral surface of the ischium caudal to the origin of M. pubischiofemoralis pars cranialis and dorsal to the ischiopubic fenestra. The muscle passes distally to insert on the proximomedial surface of the tibiotarsus by a broad, flat tendon. This tendon is joined by that of M. flexor cruris lateralis, as described above under the discussion of that muscle (Figs. 1, 2, 3, 4).

M. pubischiofemoralis (M. adductor longus et brevis).—As in passerines generally, this has two distinct parts, pars cranialis and pars caudalis, which apparently correspond to pars lateralis and pars medialis respectively in nonpasserines.

Pars cranialis (pars anterior) is the larger of the two muscles. It has a semitendinous origin from the ventrolateral margin of the ischium beginning at the caudal edge of the obturator foramen and extending caudally about half the length of the ischium. It is a parallel-fibered, strap-shaped muscle and has a fleshy insertion on the caudal face of the distal half of the femoral shaft. The area of insertion extends from about the level of the insertion of M. caudiliofemoralis proximally, to the proximal end of the internal condyle distally. Along its caudal margin, especially in the proximal half of the belly, this muscle lies superficial to the cranial margin of pars caudalis.

Pars caudalis (pars posterior) arises by a flat aponeurosis from the ventrolateral surface of the ischium between the origins of M. pubischiofemoralis pars cranialis and M. flexor cruris lateralis. This aponeurosis passes distally superficial to the membrane occupying the ischiopubic fenestra, and the belly

of the muscle arises at about the level of the pubis. The parallel-fibered belly extends distally and fuses loosely to the craniodorsal surface of the cranial half of the belly of M. gastrocnemius pars intermedia. It then turns cranially and has a largely tendinous insertion on a tubercle on the proximal side of the internal condyle of the femur in common with the origin of M. gastrocnemius pars intermedia (Figs. 3, 4).

The area of insertion of pars cranialis extends about two-thirds the length of the femoral shaft in *Psittirostra*.

M. obturatorius lateralis (M. obturator externus).—This muscle has separate dorsal and ventral bellies. Pars dorsalis is a short (3 mm × 1 mm) parallel-fibered muscle. The origin is fleshy from a small area on the lateral surface of the ischium just caudodorsal to the obturator foramen and on the ventral margin of the ilioischiadic fenestra. The muscle passes cranially superficial to the tendon of M. obturatorius medialis and has a fleshy insertion on the femur just cranial to the insertion of the obturatorius medialis tendon, onto which a few fibers also insert. Pars dorsalis was present in all forms studied, including *Ciridops anna*. Pars ventralis is a compact mass of short, parallel fibers that arise fleshy from the lateral surface of the ischium along the cranioventral border of the obturator foramen and have a fleshy insertion on the caudomedial surface of the femur just distal to the insertion of M. obturatorius medialis.

M. obturatorius medialis (M. obturator internus).—This flat, leaf-shaped, bipennate muscle occupies the ischiopubic fenestra medial to the ischiopubic membrane. It has a fleshy origin from the ischium and pubis forming the rim of the fenestra. The fibers converge on two central tendons that fuse near the obturator foramen. The single tendon thus formed passes out through the obturator foramen and inserts on the caudolateral surface of the head of the femur in conjunction with M. obturatorius lateralis as described above (Fig. 4).

M. iliofemoralis internus (M. iliacus).—This tiny, strap-shaped, parallel-fibered muscle has a fleshy origin from the ventral edge of the ilium caudo-medial to the origin of M. iliotrochantericus medius. It passes caudoventrally to a fleshy insertion on the medial side of the femur proximal to the origin of M. femorotibialis internus (Fig. 4).

M. gastrocnemius.—This muscle is composed of three separate bellies with a common tendon of insertion. Pars externa arises by a broad, flat tendon from the caudolateral surface of the distal end of the femur just proximal to the external condyle. This tendon is fused to the lateral arm of the underlying biceps loop. The muscle extends about one-half the length of the crus and ends in a tendon that is joined medially by that of pars intermedia and pars interna to form the common tendon of insertion. The tendon of origin spreads to form the medial surface of the muscle, while the tendon of insertion arises as an aponeurosis over the lateral surface. The fibers pass from the former to the latter, so the muscle is essentially unipennate in construction.

Pars intermedia is the smallest part of M. gastrocnemius, extending less than one-third the length of the crus. It is a flattened, parallel-fibered muscle that

arises tendinously from the proximocaudal surface of the internal femoral condyle, where it is closely associated with the insertion of M. pubischiofemoralis pars caudalis. Distally it ends in an aponeurosis that joins with the tendons of the other two bellies to form one tendon of insertion. On its lateral surface it is joined by the tendon separating the two parts of M. flexor cruris lateralis.

Pars interna is the most superficial muscle on the medial surface of the crus. It arises by two distinct heads. The anterior head arises in part from the inner cnemial crest, while a band of fibers (the patellar band) extends around the cranial surface of the knee, arising from the patellar tendon. This portion overlies the insertion of M. iliotibialis cranialis. A small part of pars interna was retained in the incomplete specimen of *Ciridops anna*, showing that a patellar band is present as in the other forms studied. Both parts of the origin are fleshy. The posterior head of pars interna arises from the medial surface of the head of the tibiotarsus. The two heads fuse and the common belly extends distally. It gives rise to a tendon that joins with those of pars intermedia and pars externa to form the tendon of insertion. This passes over the tibial cartilage, is lightly bound to the hypotarsus, and then has a long insertion along the plantar ridge of the tarsometatarsus. It is also bound into the fascial covering overlying the flexor tendons on the plantar surface of the tarsometatarsus (Figs. 1, 2, 3, 4).

M. tibialis cranialis (M. tibialis anterior).—This lies on the cranial surface of the crus deep to M. peroneus longus. It has two bipennate heads. The tibial head has a fleshy origin from the lateral surface of the inner cnemial crest, the medial surface of the outer cnemial crest, and the rotular crest superficial and cranial to the origin of M. extensor digitorum longus. The femoral head arises by a short, stout tendon from the apex of the external condyle of the femur. The two heads fuse just proximal to the formation of the common tendon of insertion and extend slightly more than half the length of the crus. The tendon passes distally along the cranial surface of the tibiotarsus, passes beneath the ligamentum transversum, and inserts on the dorsal surface of the tarsometatarsus (Figs. 1, 2, 4).

M. extensor digitorum longus.—This muscle occupies the craniomedial surface of the tibiotarsus deep to M. tibialis cranialis. The belly extends about half the length of the crus. The origin is fleshy from the medial side of the inner cnemial crest, the base of the outer cnemial crest, and the rotular crest and head of the tibiotarsus between the two cnemial crests, as well as from the shaft of the proximal one-fourth of the tibiotarsus. The muscle is fan-shaped and unipennate, the fibers converging on a strong tendon that arises along the cranial surface of the belly. The tendon passes beneath the ligamentum transversum deep to the tendon of M. tibialis cranialis, beneath a bony bridge, and then crosses the intertarsal joint. At the proximal end of the tarsometatarsus it passes through a thin bony canal and then proceeds distally along the dorsal surface of the tarsometatarsus, at the distal end of which it divides into three branches, one to each of the cranial digits.

The branch to digit II bifurcates, the medail branch inserting on the dorsal surface of the proximal end of the second phalanx, while the lateral branch

inserts on the proximodorsal surface of the ungual phalanx. There are small sesamoids at both insertions. The branch to digit III divides into lateral and medial tendons that interconnect in a complex way (see Fig. 3) with insertions on the proximal ends of the second, third, and ungual phalanges. The branch to digit IV bifurcates, the lateral branch inserting on the ungual phalanx in association with an automatic extensor ligament. The medial branch bifurcates and inserts on the bases of the third and fourth phalanges.

In *Loxops maculata, Psittirostra cantans, Himatione sanguinea, Palmeria dolei,* and *Vestiaria coccinea* the belly is the same length as in *Loxops virens*, while in the other forms it is about two-thirds the length of the crus (Figs. 3, 4).

M. peroneus longus.—M. peroneus longus occupies the craniolateral surface of the crus superficial to M. tibialis cranialis, which it almost completely covers. It has a fleshy origin from the inner cnemial crest, the rotular crest, and the outer cnemial crest of the tibiotarsus, and an aponeurotic origin from the medial surface of the head of the tibiotarsus. Some fibers are also associated with the fascial covering of the underlying M. tibialis cranialis. The bipennate muscle extends less than half the length of the crus and gives rise to a tendon that passes along the lateral surface of the tibiotarsus and bifurcates about 3 mm proximal to the external condyle. One branch inserts on the proximolateral corner of the tibial cartilage. The other passes across the intertarsal joint superficial to the peroneus brevis tendon and passes to the lateroplantar surface of the tarsometatarsus, where it joins the tendon of M. flexor perforatus digiti III (Figs. 1, 4).

M. peroneus brevis.—This muscle lies on the lateral surface of the crus just caudal to the tibial head of M. tibialis cranialis. It has a fleshy origin from the caudal margin of the outer cnemial crest, just caudal to the origin of the tibial head of M. tibialis cranialis. This tibial head passes distally superficial to the femoral head of M. tibialis cranialis and joins a fibular head, which arises from the craniolateral surface of the fibular shaft beginning just distal to the point of insertion of M. iliofibularis. The belly extends a little more than half the length of the tibiotarsus and gives rise to a tendon that passes distally lateral to the tendon of M. tibialis cranialis. It passes beneath a fibrous loop just proximal to the lateral condyle of the tibiotarsus, then widens and passes laterally of the lateral condyle to insert on the proximal end of the tarsometatarsus.

The muscle was identical in all Drepanididae examined, but it was not seen in *Ciridops*. A tibial head has apparently never been described in birds, and is not mentioned in George and Berger (1966). It is an important taxonomic character in the New World nine-primaried oscines, and will be considered more fully in a later paper on the relationships of this assemblage (Figs. 1, 2).

M. flexor perforans et perforatus digiti III.—This muscle lies on the lateral surface of the crus caudal to M. peroneus longus and cranial to M. flexor perforatus digiti II. Its origin is partly concealed beneath M. flexor perforans et perforatus digiti II. The belly is formed by fibers converging from two distinct heads. The cranial head arises primarily fleshy from the outer cnemial crest of the tibiotarsus and the adjacent patellar tendon. The caudal head arises by an aponeurosis from the proximal part of the lateral femoral condyle, together

with M. flexor perforatus digiti II and M. flexor perforans et perforatus digiti II. The proximal half of the muscle is bipennate, as fibers from the two points of origin converge on a central tendon. Distally the muscle narrows as the component from the caudal head ends, and only the cranial head continues. This part is thus unipennate.

The muscle extends distally about half the length of the tibiotarsus. It gives rise to a tendon that passes through a canal in the medial part of the tibial cartilage and then through the posteromedial canal of the hypotarsus. It continues distally along the plantar surface of the tarsometatarsus to the plantar side of digit III. Here it ensheathes the tendon of M. flexor digitorum longus, and these two tendons perforate the tendon of M. flexor perforatus digiti III. The tendon of M. flexor perforans et perforatus digiti III then bifurcates, the tendon of M. flexor digitorum longus continuing distally between the branches. The two branches insert on the lateral and medial sides, respectively, of the proximoplantar end of the third phalanx of digit III (Figs. 1, 2).

M. flexor perforans et perforatus digiti II.—This small (7 mm) muscle lies on the lateral surface of the crus just caudal to M. flexor perforans et perforatus digiti III. It has a fleshy origin from the caudoproximal corner of the lateral femoral condyle, just distal to the origin of M. gastrocnemius pars externa. The fiber arrangement is nearly parallel, but approaches being unipennate as the fibers insert into the tendon of insertion which arises on the caudolateral surface of the belly. The fine tendon passes distally through the median part of the tibial cartilage and the posteromedial canal of the hypotarsus. It proceeds along the plantar surface of the tarsometatarsus to digit II, where it bifurcates. The main insertion is on the medial surface of the base of phalanx 2, while an elastic ligament inserts subterminally on the distoplantar surface of phalanx 1 of digit II. The belly appears slightly elongated in *Psittirostra c. cantans* (Figs. 1, 2).

M. flexor perforatus digiti IV.—This long, spindle-shaped muscle lies on the caudal surface of the crus caudomedial to M. flexor hallucis longus and lateral to M. flexor perforatus digiti III. It has a partly fleshy origin from the intercondyloid region of the femur in common with the medial head of M. flexor hallucis longus and M. flexor perforatus digiti III. In addition, some fibers arise directly from the tendinous origin in common with the latter muscle. The belly extends distally about half the length of the crus. The tendon of insertion arises as an aponeurosis on the caudolateral surface of the belly. The fibers insert into this aponeurosis from beneath so the fiber arrangement is essentially unipennate. The tendon proceeds distally through the tibial cartilage loosely ensheathed by the tendon of M. flexor perforatus digiti III. The two tendons continue through the posterolateral canal of the hypotarsus and along the plantar surface of the tarsometatarsus. At the base of digit IV the tendon of M. flexor perforatus digiti IV bifurcates and is perforated by the tendon of M. flexor digitorum longus. The lateral branch of the tendon inserts at the base of phalanx 2 of digit IV, while the larger median branch inserts at the base of phalanx 3. The belly extends about three-fourths the length of the crus in *Psittirostra* and *Hemignathus* (Fig. 2).

M. flexor perforatus digiti III.—This muscle arises from the intercondyloid region of the femur by a tendon in common with M. flexor perforatus digiti IV and M. flexor hallucis longus. It lies medial to M. flexor perforatus digiti IV and extends about half the length of the crus. The fibers pass from the tendon of origin on its lateral surface to an aponeurosis on the medial surface from which the tendon of insertion arises; it is therefore basically unipennate in form. The tendon proceeds through the tibial cartilage and the posterolateral canal of the hypotarsus cranial to and loosely ensheathing the tendon of M. flexor perforatus digiti IV. Beyond the hypotarsus the two tendons diverge, the tendon of M. flexor perforatus digiti III being joined by the long branch of the tendon of M. peroneus longus. At the base of digit III the tendon bifurcates to allow passage of the tendons of M. flexor perforans et perforatus digiti III and M. flexor digitorum longus. The two branches insert on the medial and lateral corners respectively, of the base of phalanx 1 of digit III. In *Hemignathus* and *Psittirostra* the belly extends about three-fourths the length of the crus (Fig. 2).

M. flexor perforatus digiti II.—This small, spindle-shaped muscle arises by an aponeurosis from the caudal surface of the external femoral condyle distal to the origin of M. gastrocnemius pars externa, sharing an aponeurosis of origin with the lateral head of M. flexor hallucis longus, and also by a short aponeurosis from the neck of the fibula. The belly extends about half the length of the crus and gives rise to a tendon that passes through the lateral part of the tibial cartilage, through the middle canal of the hypotarsus, and continues along the plantar surface of the tarsometatarsus. It then passes through a canal in the ligaments at the base of digit II and inserts on the proximomedial corner of the base of phalanx 1 of digit II. It is not perforated by the tendons of either M. flexor perforans et perforatus digiti II or M. flexor digitorum longus as in some birds (Figs. 1, 2).

M. plantaris.—This is absent in *Loxops virens wilsoni.* The following description is for *Psittirostra c. cantans.* This tiny (4 mm) triangular muscle arises fleshy from the caudomedial surface of the head of the tibiotarsus just medial to the medial head of M. flexor digitorum longus. The fine tendon passes distally and inserts on the proximomedial corner of the tibial cartilage.

M. plantaris is also absent in *Himatione sanguinea, Palmeria dolei,* and *Vestiaria coccinea,* but is present in the other forms studied, though it is poorly developed in *Loxops maculata.*

M. flexor hallucis longus.—This muscle has three heads. The small lateral head arises from the caudolateral surface of the proximal end of the lateral femoral condyle by means of an aponeurosis closely connected to the aponeurosis of origin of the intermediate head and M. flexor perforatus digiti II. This aponeurosis passes lateral to the iliofibularis tendon, at which point the belly of the lateral head arises. This belly fuses with the intermediate head near the end of the muscle. The intermediate head arises by an aponeurosis from the distal end of the femur, partly fuses with the origin of the lateral head, but passes medial to the iliofibularis tendon. The medial head arises fleshy from the intercondyloid region of the femur. Some fibers also arise from the medial

side of the cranial end of the aponeurosis of origin of the intermediate head. Otherwise the two heads are separate for most of their length, but fuse near the distal end of the muscle.

The muscle is bipennate. The fibers of the medial head converge laterally, and those of the other two heads converge medially onto the tendon of insertion. The muscle extends about half the length of the crus, giving rise to a tendon that passes through a deep canal in the tibial cartilage, and then through the anterolateral canal of the hypotarsus. The tendon passes distally along the plantar surface of the tarsometatarsus, crossing to the medial side superficial to the tendon of M. flexor digitorum longus. No vinculum connects these tendons. The tendon then passes between the tarsometatarsus and metatarsal I. Passing around the trochlea of metatarsal I it is ensheathed in a pulley arising from the tendon of M. flexor hallucis brevis. The tendon inserts on the base of the ungual phalanx of the hallux. An elastic vinculum arises from the inner surface of the tendon at about the level of the middle of the first phalanx and inserts on the plantar surface of the first phalanx just proximal to its distal articular surface. Before doing so it gives rise to a thin branch that inserts on the cartilaginous pad between the two phalanges of the hallux. In *Psittirostra* the belly is slightly elongated (Fig. 1).

M. flexor digitorum longus.—This is the deepest muscle on the caudal surface of the crus. It arises fleshy by two heads, the lateral one from the caudal surface of the head of the fibula and the medial one from the caudal surface of the head of the tibiotarsus. No femoral head is present as has been found in a few passerines (George and Berger 1966: 450–451). The two heads fuse distally into a single belly, from which a strong tendon arises. The muscle is thus bipennate. The belly extends nearly two-thirds the length of the crus. The tendon proceeds distally through a deep, medial portion of the tibial cartilage and then through the anteromedial canal of the hypotarsus. It passes along the plantar surface of the tarsometatarsus, passing deep to the tendon of M. flexor hallucis longus. The distal two-thirds of the tendon is rigid, presumably ossified. At the level of metatarsal I the tendon divides into three branches, one passing along the plantar surface of digits II, III, and IV respectively. The branch to digit II inserts at the base of the ungual phlanx and, by an elastic vinculum, near the distal end of the second phalanx. The branch to digit III inserts on the ungual phalanx and by elastic bands on the distal end of phalanx 3 and on the cartilaginous pad at the proximal end of phalanx 3. The branch to digit IV inserts on the ungual phalanx and by elastic bands on the distal end of phalanx 4 and on the pad at the base of phalanx 4.

The muscle is generally similar in all species except that in both races of *Psittirostra cantans* and in *Palmeria dolei* the elastic band to the cartilaginous pad at the base of phalanx 4 of digit IV is absent (Figs. 2, 3).

M. flexor hallucis brevis.—This fine strand of muscular tissue arises from the medial surface of the hypotarsus and extends distally along the medioplantar surface of the tarsometatarsus. A fine tendon is formed that passes distally and ends by being incorporated into the connective tissue sheathing the tendon of M. flexor hallucis longus as this passes over the trochlea of metatarsal I. I

could not demonstrate the existence of this muscle in *Loxops maculata*, perhaps because it is so small and the specimen was poorly fixed. In *Psittirostra psittacea* the muscle arises by a tendon 5 mm long rather than by the typical fleshy origin.

M. extensor hallucis longus.—This muscle includes proximal and distal heads. The proximal head is a tiny, parallel-fibered muscle arising on the craniomedial surface of the tarsometatarsus about 1 mm distal to its proximal articular surface. It passes distally medial to the tendons of M. tibialis cranialis and M. extensor digitorum longus. About halfway along the tarsometatarsal shaft the 10 mm long belly gives rise to a fine, hairlike tendon that curves caudomedially and passes to the dorsal surface of the hallux. It continues along the dorsal surface of the proximal phalanx, passes between the arms of an automatic extensor ligament, and inserts with the latter at the base of the ungual phalanx.

A distal head has been described in a few nonpasserine birds (George and Berger 1966: 454–455), but apparently has not previously been found in any passerine. It is exceedingly tiny and I discovered it only after staining with iodine (Bock and Shear 1972). This distal head is a fan-shaped muscle about 3 mm long. It arises from the medial surface of the distal end of the shaft of the tarsometatarsus just proximal to the first metatarsal. It passes distally alongside the tendon of the proximal head and inserts into the joint capsule between metatarsal I and the proximal phalanx of the hallux.

M. lumbricalis.—This small, strap-shaped muscle lies deep in the plantar surface of the foot. It arises from the tendon of M. flexor digitorum longus just proximal to the point where that tendon divides, and inserts on the joint pulleys of digits III and IV.

DISCUSSION

The outstanding feature evident from the muscle descriptions given above is the general uniformity of the hind limb muscles in the Drepanididae. The differences are relatively minor considering the great diversity in the feeding apparatus in these species. *Loxops, Himatione,* and *Palmeria* have short, slightly decurved or straight bills and feed by gleaning insects from tree surfaces, as well as on nectar. *Vestiaria* and *Hemignathus* have long, crescent-shaped bills for probing, and *Psittirostra* has a short, conical, finchlike bill. The evolution of the feeding apparatus in the Drepanididae is a classic example of adaptive radiation (Bock 1970, Richards and Bock 1973), and it is noteworthy that this radiation in the feeding mechanism was not accompanied by a comparable evolution in the hind limb musculature. Nevertheless some variations may be noted (Table 1).

The extensor of the digits (M. extensor digitorum longus) and several flexors are significantly enlarged in *Psittirostra* and *Hemignathus* as compared to *Loxops, Himatione, Palmeria,* and *Vestiaria.* While a precise analysis of the biomechanical characteristics is not possible with the

TABLE 1

MAJOR VARIATIONS IN THE HIND LIMB MYOLOGY OF DREPANIDIDAE[1]

Species	Muscles				
	EDL	FPD3	FPD4	FHL	Plantaris
Loxops virens wilsoni					−
L. maculata bairdi					+
Psittirostra c. cantans		*	*	*	+
P. c. ultima		*	*	*	+
P. psittacea	*	*	*	*	+
Hemignathus wilsoni	*	*	*		+
H. procerus	*	*	*		+
Himatione sanguinea					−
Palmeria dolei					−
Vestiaria coccinea					−

[1] * means that the muscle belly is significantly longer relative to the length of the crus than in *L. virens*; + means that the muscle is present; − means that the muscle is absent. Abbreviations: EDL, M. extensor digitorum longus; FPD3, M. flexor perforatus digiti III; FPD4, M. flexor perforatus digiti IV; FHL, M. flexor hallucis longus.

limited material available, probably the strength of the grip of the foot is increased by these enlarged flexor muscles; the enlargement of the extensor may be correlated with this in some way. This change may be functionally related to differences in feeding habits. *Loxops, Himatione,* and apparently also *Palmeria* and *Vestiaria* feed by moving rapidly through the foliage and gleaning insects from exposed leaf and bark surfaces. *Psittirostra* and *Hemignathus* are more sedentary, respectively eating seeds and probing forcefully into bark crevices for insects. For the latter behavior a stronger grip might well be advantageous in helping the bird maintain its position on the branch. In a comprehensive study of the hind limb muscles of the New World nine-primaried oscines to be published later, I have found this general relationship to hold true. For example, the shank muscles of the insectivorous Parulidae are generally less robust than those of the closely related seed-eating Emberizine finches. Some of this variation may be attributable to allometric changes in muscle size, as the forms with larger muscles are generally of slightly larger body size.

The loss of M. plantaris in a few forms (Table 1) is of unknown significance. This tiny muscle is not infrequently lost in passerines. Gaunt (1969) found that it is absent in most Hirundinidae, and I have found a tendency for its loss in other groups, especially the Cardueline finches.

The tibial head of M. peroneus brevis, present in all forms studied, has not been described in birds before. The general uniformity of the pelvic myology, including the condition of M. peroneus brevis, strongly supports the belief that the Depanididae are a monophyletic group descended from a single common ancestor. The similarity of *Himatione,*

Palmeria, and *Vestiaria* (subfamily Drepanidinae) to the other forms studied (subfamily Psittirostrinae) further argues that these two divisions of the family arose by an early splitting of a single ancestral group rather than from two different founding species. Finally, the hind limb myology of the Drepanididae confirms that this family is correctly placed within the New World nine-primaried oscine assemblage, and that its closest relatives are among the fringillid subfamily Carduelinae. A full account of the basis of these conclusions will be presented later.

SUMMARY

The hind limb myology of the Hawaiian honeycreepers (Drepanididae) is described in detail. In the 11 forms in 10 species and 7 genera studied, little variation occurs, attesting to the unity of this insular family. The spectacular adaptive radiation in the feeding apparatus of the Drepanididae is not reflected to any great extent in the hind limb musculature.

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