

ON THE ANATOMY AND  
RELATIONSHIPS OF  
*FREGILUPUS VARIUS*,  
AN EXTINCT STARLING  
FROM THE  
MASCARENE ISLANDS

ANDREW J. BERGER

BULLETIN  
OF THE  
AMERICAN MUSEUM OF NATURAL HISTORY  
VOLUME 113 : ARTICLE 3      NEW YORK : 1957







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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 113, article 3, pages 225-272,  
figures 1-12, tables 1-5

*Issued October 7, 1957*

*Price: \$1.00 a copy*



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## INTRODUCTION

*Fregilupus*, THE BOURBON CRESTED STARLING, was a monotypic genus endemic on the Mascarene Islands, perhaps only on Réunion. It probably has been extinct since about 1854 (Murie, 1874, p. 474). Murie summarized available information on this genus as of 1874, Milne-Edwards and Oustalet (1893, p. 205) discussed certain anatomical features, Amadon (1943) commented on its relationships, and Hachisuka (1953, pp. 213–221) presented a colored plate of the bird and discussed extant specimens. Hachisuka listed two alcoholic specimens and 21 or 22 skins, some of which may have been destroyed in France during World War II. Both spirit specimens are in the United States: one (incomplete and partly dissected; M. R. Miller, 1941) is in the Museum of Comparative Zoölogy of Harvard College, Cambridge, Massachusetts, and one is in the American Museum of Natural History in New York. It is the latter specimen, collected by Desjardins in 1839, and received from Paris as an exchange, which served as the basis for the present paper. Though the plumage was badly discolored and most of the remiges and rectrices were broken, the muscles were, surprisingly, in excellent condition.

That the genus *Fregilupus* presents an interesting taxonomic problem is attested by the fact that it has been variously thought to show affinities with the Coraciidae, Upupidae, Paradisaeidae, Corvidae, Vangidae, and Sturnidae. In recent years, however, the only families seriously considered for *Fregilupus* have been the Sturnidae and the Vangidae. Murie (1874) illustrated and discussed the skeleton of *Fregilupus* and concluded that it was not closely related to the "Hoopoes, nor to the Fregiline section of the Crows," but that it "hails close proximity to *Pastor*" and is less closely related to *Sturnus* (see also Murie, 1873, p. 200). Sclater (1930, p. 669) and Amadon (1943) placed *Fregilupus* in the Sturnidae.

The genus *Aplonis* contains 19 species and ranges widely through coastal Bengal, the Malay Peninsula, East Indies, northern Australia, the Philippines, and most of Polynesia (Amadon, 1943, p. 8). *Artamella* is one of nine or 10 genera assigned to the family

Vangidae, which is endemic to Madagascar. Unfortunately, little is known about the life history of the Vangidae, and there are apparently no reliable data on the breeding biology of *Fregilupus*.

## ACKNOWLEDGMENTS

I am indebted to the American Museum of Natural History and to Dr. Dean Amadon for allowing me to dissect the specimen of *Fregilupus* and for sending alcoholic specimens of *Aplonis tabuensis* (Sturnidae) and *Artamella v. viridis* (Vangidae). I also dissected three Michigan specimens of *Sturnus vulgaris*.

I wish to express my appreciation to Drs. Dean Amadon and Ernst Mayr, and the late Dr. Josselyn Van Tyne and to Mr. Walter Bock for reading the manuscript; to Mr. Peter Stettenheim for taking the pictures of the feather tracts of *Fregilupus*; and to Dr. Norman E. Hartweg for identifying the chameleon. I am especially indebted to Mr. David R. Sterrett for preparing the final ink drawings that illustrate the present paper.

## ABBREVIATIONS FOR TEXT FIGURES OF WING MUSCLES

Abd. ind., abductor indicis  
Abd. poll., abductor pollicis  
Add. poll., adductor pollicis  
Anc., anconeus  
Biceps, biceps brachii  
Brach., brachialis  
Cor. bra. ant., coracobrachialis anterior  
Cor. bra. post., coracobrachialis posterior  
Cuc., cucullaris, pars propatagialis  
Delt. ant., deltoideus major, anterior head  
Delt. min., deltoideus minor  
Delt. post., deltoideus major, posterior head  
Dor. scap., dorsalis scapulae  
Exp. sec., expansor secundariorum  
Ext. dig. comm., extensor digitorum communis  
Ext. ind. long., extensor indicis longus  
Ext. meta. rad., extensor metacarpi radialis  
Ext. poll. long., extensor pollicis longus  
F. d. III, flexor digiti III  
Flex. carp. uln., flexor carpi ulnaris  
Flex. carp. uln. brev., flexor carpi ulnaris brevis  
Flex. dig. prof., flexor digitorum profundus  
Flex. dig. sup., flexor digitorum superficialis  
Flex. meta. post., flexor metacarpi posterior  
Flex. meta. rad., flexor metacarpi radialis  
Hum.-ul. pul., humero-ulnar pulley



Int. dor., interosseus dorsalis	Serr. ant., serratus anterior
Int. palm., interosseus palmaris	Serr. meta., serratus metapatagialis
Lat. dor. ant., latissimus dorsi, pars anterior	Serr. post., serratus posterior
Lat. dor. post., latissimus dorsi, pars posterior	Serr. prof., serratus profundus
Pect., pectoralis, pars thoracicus	Ster. cor., sternocoracoideus
Pect. pro. long., pectoralis, pars proapatagialis longus	Subcor., subcoracoideus
Pro. prof., pronator profundus	Subscap., subscapularis, pars externa
Pro. sup., pronator superficialis	Sup., supinator
Proscap., proscapulohumeralis	Supracor., supracoracoideus
Rhomb. prof., rhomboideus profundus	T. hum., humerotriceps
Rhomb. sup., rhomboideus superficialis	T. pat. brev., tensor patagii brevis
Sar., sartorius	T. pat. long., tensor patagii longus
	T. scap., scapulotriceps

## PTERYLOSIS, OSTEOLOGY, AND MYOLOGY OF *FREGILUPUS*

### PTERYLOSIS

PICTURES WERE TAKEN of the feather tracts of *Fregilupus varius*. Kodachrome transparencies of these have been deposited with the American Museum of Natural History and with the Bird Division of the University of Michigan Museum of Zoology.

#### VENTRAL FEATHER TRACTS

The inter-ramal region is completely feathered, containing six rows of feathers anteriorly. There is a single, midline, ventral cervical feather tract, which bifurcates, at about the level of the shoulder joint, to form the bilateral sternal tracts. The sternal tract and its lateral expansion, the axillary tract, form a solid feathered area, eight to 10 rows wide. A single, bilateral, ventral abdominal tract leads posteriorly from the sternal tract to within 1 cm. of the anus. The abdominal tract contains three to four rows of closely spaced feathers throughout most of its extent, but ends posteriorly as a single row of feathers. Medial to the sternal and abdominal tracts, there are four rows of small, filamentous, more widely spaced feathers, which extend to the furculum and the base (dorsal part) of the carina; these rows continue to the caudal end of the sternum. There is an anal circlet, composed of two rows of feathers.

#### DORSAL FEATHER TRACTS

There is a solid capital tract, without apertures in the frontal, coronal, or occipital regions, but there is a large apterium in the post-ocular and temporal regions. The spinal cervical tract is broad just caudal to the occipital region, but it narrows at the level of cervical vertebra number 4 or 5; throughout most of its length, the spinal cervical tract contains four rows of closely spaced feathers. This tract continues into the dorsal spinal tract in the interscapular region. There are small, widely spaced feathers on each side of the dorsal spinal tract (see fig. 2), and this tract has two arms which extend laterally over the anterior end of the pelvis; there is no central apterium in this tract. The median pelvic tract, a caudal extension of the dorsal spinal tract, contains two main central rows

of feathers, the shafts of which project upward and backward, and a row on each side of the central tract, in which the small feathers project laterally. There is a slight dilatation (five to six rows) of the median pelvic tract over the posterior end of the pelvis.

There is a well-developed humeral feather tract (scapulars), composed of four rows of closely spaced feathers. This tract is continuous anteriorly with the dorsal marginal coverts. There is no after shaft on the contour feathers.

The bilobed oil gland is nude. It measured 4 mm. in width, 2.5 mm. in anteroposterior direction, and 3.5 to 4.0 mm. in height.

#### LATERAL FEATHER TRACTS

There is a small superciliary apterium, and there is a large apterium in the post-ocular and temporal regions. The lateral cervical apterium is well developed only in the caudal half of the neck, the anterior half being almost completely feathered. Approximately five rows of small, filamentous feathers are widely spaced on the lateral thoracic and abdominal regions. There is a strong femoral tract, paralleling the plane of the os pubis, composed of four rows of closely spaced feathers. Dorsal to the femoral tract there are widely spaced, small feathers, which extend dorsad almost to the level of the posterior iliac crest of the pelvis. There is an extensive crural tract (on the lateral, medial, anterior, and posterior surfaces), extending from the knee to the distal end of the crus, so that feathers pass distad over the proximal end of the tarsometatarsus.

#### REMIGES AND RECTRICES

There are 10 primaries, the outermost (no. 10) being much smaller than the others. The tips of many of the primaries (including the tenth bilaterally) had been broken. Nevertheless, it seems important to preserve all possible information about the present specimen. Table 1 presents certain information which may prove useful in future studies and gives a fairly accurate indication of the length of the tenth primary relative to the other nine. Furthermore, the diameter at the base



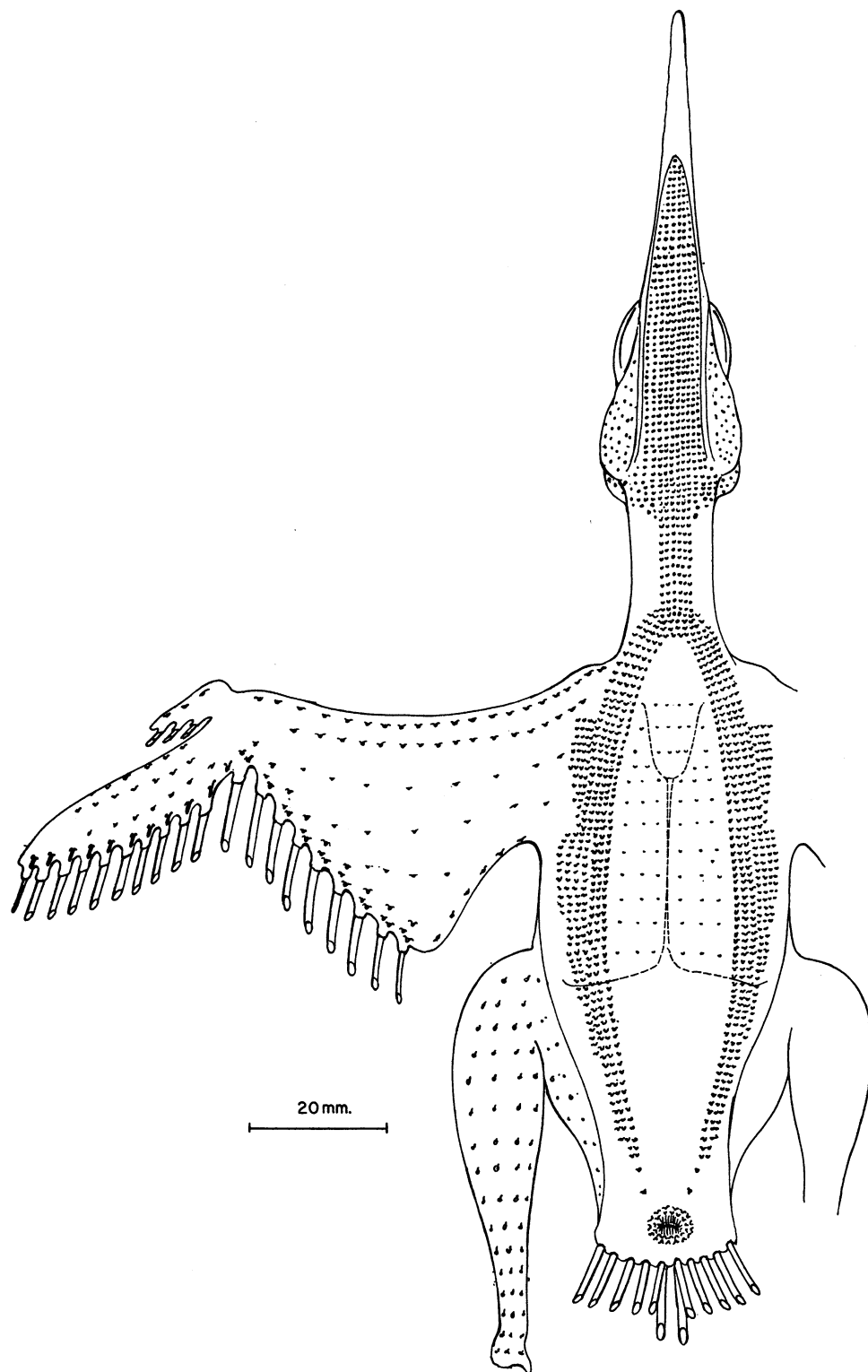


FIG. 1. *Fregilupus*. Ventral feather tracts.

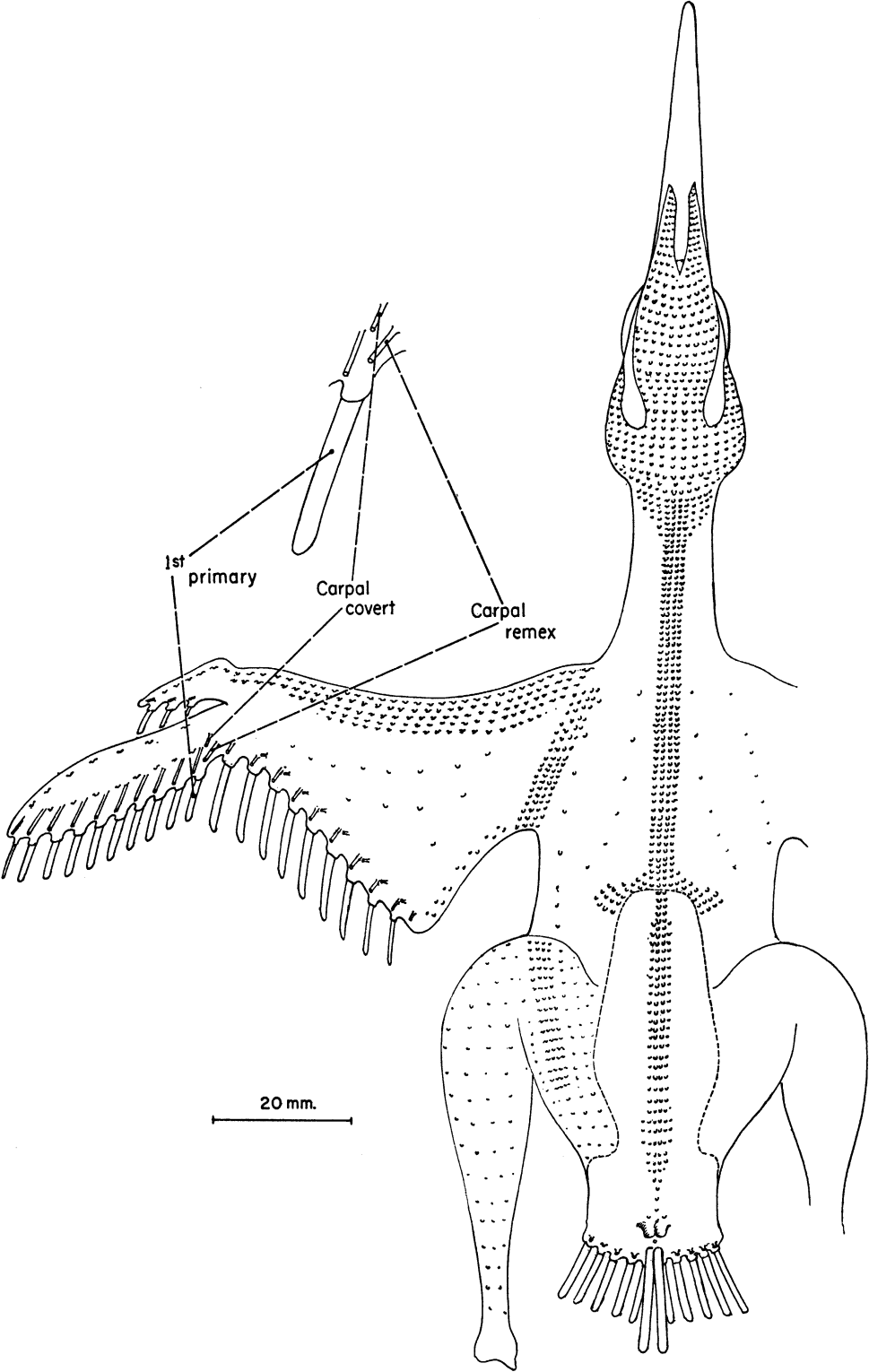


FIG. 2. *Fregilupus*. Dorsal feather tracts.

TABLE 1  
LENGTH (IN MILLIMETERS) OF PRIMARIES OF *Fregilupus*

Number	Left Wing	Right Wing	Comments
1 <sup>a</sup>	110	111	Feathers intact, tips not broken
2	112	114	
3	111	112	
4	90	101	Recently molted bilaterally; basal sheaths present
5	Missing	3.5	Only an unopened basal sheath
6	95	71	Tip broken off of each feather, bilaterally
7	78	95	
8	59	86	
9	77	79	Probably 1 or 2 mm. broken off of left feather
10	16	11	

<sup>a</sup> First primary is the innermost primary.

of the ninth primary was 2 mm., whereas the diameter at the base of the tenth primary was less than 0.1 mm.

The carpal remex (23 mm. long bilaterally) arises from the dorsal surface of the basal sheath of the first primary, just 4 mm. distal to the proximal end of that feather. The carpal covert (12 mm. long, left wing; 10 mm. long, right wing) arises in the skin a short distance proximal to the base of the first primary; the carpal covert conceals the basal 6 mm. of the carpal remex. In *Coua caerulea* (Berger, 1953; Berger and Lunk, 1954) both the carpal remex and its covert are inserted on the dorsal surface of the basal sheath of the first primary. In the present species, the carpal covert (if, indeed, it be properly identified) is inserted in the skin proximal to the primary. This relationship also has been reported in *Troglodytes* (Boulton, 1927, p. 396), *Lanius* (A. H. Miller, 1928, p. 398; 1931, p.

127), and *Aphelocoma* (Pitelka, 1945, p. 232). There is an urgent need for a reinvestigation of the development and comparative anatomy of the carpal remex and its covert. The carpal remex is said sometimes to be absent (see Degen, 1894, especially the footnotes on pp. ix, x).

There are three alula quills, the innermost being the shortest. All three were broken on the right wing; measurements of those of the left wing are given in table 2.

There are nine secondaries. The wing is eutaxic. The innermost secondary (no. 9) is the shortest. Secondaries numbers 8 and 9 were the only intact feathers; number 8 measured 75 and 77 mm., respectively, on the left and right wing; number 9, 54 and 51 mm. The outermost (no. 1) secondary measured 110 mm. (tip broken) on the left wing and 93 mm. (recently molted) on the right wing. The greater and middle secondary coverts are well

TABLE 2  
MEASUREMENTS (IN MILLIMETERS) OF CERTAIN FEATHERS

	<i>Sturnus</i>	<i>Fregilupus</i>	<i>Aplonis</i>	<i>Artamella</i>
Ninth primary	96	79 <sup>a</sup>	70	70
Tenth primary	13	16 <sup>b</sup>	14	37
Third alula <sup>c</sup>	30	39 <sup>d</sup>	—	27
Second alula	22	30	—	23
First alula	14	23	—	16

<sup>a</sup> An unknown amount broken off tip of feather.

<sup>b</sup> Plus 1 or 2 mm., probably.

<sup>c</sup> Outermost feather.

<sup>d</sup> Tip broken.



developed; the lesser secondary coverts are filamentous, poorly developed, and scattered.

There are 12 rectrices. The innermost pair is raised above the level of the others, owing to their place of attachment to the pygostyle. I could find only eight upper tail coverts.

#### COMPARATIVE PTERYLOSIS

Each of the genera studied for this paper has 10 primaries, and in each the outermost is the shortest, but in *Artamella* the outermost is half of the length of the ninth primary (see table 2). *Sturnus*, *Aplonis*, and *Fregilupus* each have nine secondaries; *Artamella* has 10. All these genera have 12 rectrices.

A carpal remex and carpal covert are present in these genera and exhibit the same relationships as illustrated and described for *Fregilupus*. The wing is eutaxic in each genus and each has three alula quills, of which the innermost (no. 1) is the shortest. The oil gland is nude in all.

The inter-ramal region is completely feathered in *Fregilupus*. In *Artamella* and *Aplonis*, there are well-developed marginal apteria on each side of the midline inter-ramal feather tract. These apteria are minute or completely absent in *Sturnus*, so that it is like *Fregilupus* in this character. There are several (minor?) differences in the ventral feather tracts among the four genera, though all are similar to *Fregilupus*. The sterno-axillary tract is more extensive in *Sturnus* than in *Fregilupus*. In *Sturnus* this tract does not become narrowed until it reaches the posterior margin of the sternum. In *Artamella*, on the other hand, the single (bilateral) ventral abdominal tract exhibits its best development. The tract is wide (six to eight rows of feathers) anteriorly; it decreases to two or three rows just before it ends a short distance anterolateral to the anal aperture. *Artamella* also possesses a discrete lateral thoracic tract (two to three rows wide), which extends dorsocephalad from the posterodorsal margin of the sternal tract to the axilla; this tract is not found in the other genera.

The dorsum of the head is completely feathered in *Sturnus* and *Aplonis*. *Artamella* has a small post-ocular apterium (as in *Fregilupus*), but it is concealed by adjacent feathers, and there is neither a distinct super-

ciliary apterium nor an apterium in the temporal region.

The most conspicuous difference between *Fregilupus* and the other three genera is found in the dorsal spinal tract. In *Fregilupus* this tract is forked just anterior to the pelvis (fig. 2). This tract differs from that in other passerine genera having a forked dorsal spinal tract (*Eurylaimus* and *Hirundo*, Nitzsch, 1867, pl. 3; *Garrulus* and *Corvus frugilegus*, Lowe, 1938, pl. 6) in that there is no central apterium, nor is there a gap between the dorsal tract and the median pelvic tract. *Sturnus*, *Aplonis*, and *Artamella* differ from *Fregilupus* in that the dorsal spinal tract is roughly diamond-shaped and is similar to that in *Motacilla alba* (Nitzsch, 1867, pl. 3) and in *Aphelocoma coerulescens* (Pitelka, 1945, fig. 35).

In *Sturnus*, the single median pelvic tract is composed of three rows of feathers anteriorly, but of eight rows posteriorly. From the posterior end of the diamond-shaped dorsal spinal tract in *Artamella*, a single row of large feathers, flanked on either side by a single row of smaller feathers, passes caudad towards the tail. Posteriorly, this median pelvic tract broadens out into a triangular-shaped tract, the base of which, just anterior to the oil gland, is a row five feathers wide. In general, the median pelvic tract in *Artamella* is similar to that found in *Lanius ludovicianus*, as illustrated by A. H. Miller (1931, fig. 39).

Stonor (1937, p. 484) pointed out that it is difficult to know how far pterylosis can be depended on to show exact interrelationships because the comparative pterylosis has not been reported for any passerine family. The dorsal spinal tract seems to have a constant pattern in those members of the Picidae thus far studied (Burt, 1929, p. 431; Lowe, 1946, p. 123). Judging, however, from published illustrations of the dorsal spinal tract in the Corvidae (Lowe, 1938, pl. 6; Pitelka, 1945, fig. 35), one might conclude that it is of little value in determining closeness of relationship. One can hardly imagine two patterns more different than those illustrated by Lowe for *Corvus frugilegus* and for *C. corone*. One would say that there should not be a difference of such magnitude between the species of one genus. At the same time, one could conceive a graded series (in feather pattern) leading

from *Aphelocoma* to *Garrulus* to *Corvus frugilegus* on the one hand and from *Garrulus* to *Pica pica* and *Corvus corone* on the other. An investigation of all members of the Corvidae, as well as of other passerine families, is badly needed.

In the Broadbills (Eurylaimidae), also, there is variation in the dorsal spinal tract. There is a diamond-shaped tract without a central apterium in *Smithornis*, although Lowe (1924, p. 281) found one in the embryo. There is a central apterium in *Eurylaimus* and *Pseudocalyptomena* (Nitzsch, 1867, pl. 3; Lowe, 1931, p. 448), but the patterns in these two genera differ considerably from each other.

In the Birds of Paradise (Paradisaeidae) studied by Stonor (1938, p. 469; see also 1937, pp. 481-483, figs. 6 and 8 reversed), the dorsal spinal tract has "the same general shape" in all, "the tract possessing a solid saddle of rhombic shape." Nevertheless, there is a considerable difference between the pattern found in *Loria* and that found in *Cicinnurus* (Stonor, 1938, figs. 12 and 21). In fact, the pattern in the latter genus resembles that in *Fregilupus varius* more closely than does the pattern illustrated for any other passerine bird.

### OSTEOLOGY

Murie (1874) presented an excellent series of illustrations of the bones of *Fregilupus*, including a lateral view of the articulated skeleton. It seems likely that he did not have a completely articulated skeleton, however, and certain additional information about it should be recorded.

There are 14 cervical, five dorsal, and seven free caudal vertebrae, plus a pygostyle. As nearly as I could determine, there are 12 fused vertebrae in the synsacrum, which make a total of 38 vertebrae, plus the pygostyle, in the vertebral column. Murie listed a total of 34 or 35. I found only one cervicodorsal rib, as did Murie, which articulates dorsally with the last (no. 14) cervical vertebra. There are five dorsal or true ribs, all of which possess uncinate processes and all of which articulate ventrally with the sternum. There are two thoracic ribs, neither of which possesses uncinate processes; these two ribs articulate dorsally with the first two segments of the

synsacrum. The first (anteriormost) thoracic rib is well developed; it fuses with the sternal part of the last true rib, about 4 mm. before it articulates with the sternum. The second thoracic rib is a mere sliver of bone less than 0.5 mm. wide; it fuses with the ventral portion of the first thoracic rib. The atlas is perforated by the odontoid process of the axis.

Table 3 gives the length of the appendicular bones of two specimens of *Fregilupus* and of one each of *Artamella* and *Sturnus*. For purposes of comparison, I converted Murie's measurements (in inches) to millimeters. None of the bones of the American Museum specimen of *Fregilupus* was broken. All the long bones of the specimen of *Aplonis* were broken except for the two humeri and one carpometacarpus: the humeri measured 23.8 mm. bilaterally; the right manus, 25.0 mm.

The wing of *Fregilupus* is 86.1 per cent of the length of the "leg" (exclusive of digit III); the wing of *Sturnus vulgaris* is 92.5 per cent, that of *Paradisaea rubra* 92.9 per cent, of the length of the leg.

Table 4 presents additional information on the proportion of the individual bony elements of the appendages.

The sternum is 32.7 mm. long; it is 13.3 mm. wide at the sternocoracoidal processes; and it has a maximum width (at the caudal end of the bone) of 24.5 mm. The carina is about 30.1 mm. in length; it has a maximum height (anteriorly) of 9.1 mm.

The synsacrum is 30.5 mm. long. The pelvis is 9.9 mm. wide at its anterior end; its intertrochanteric width is 13.7 mm.; and its maximum width (at the posterior iliac crests) is 20.0 mm. The ischia are well developed and project ventrocaudad; the pelvis is 14.3 mm. high, measured along a vertical line, which extends from the posterior iliac crest ventrad to the inferior margin of the pubis, where the latter articulates with the ventrocaudal end of the ischium. There is no pectineal process; the absence of this process is presumably correlated with the absence of *M. ambiens*.

The large pygostyle has a well-developed basal disc. The pygostyle is 11.8 mm. high; the disc is 4.3 mm. in width.

### COMPARATIVE OSTEOLOGY

*Sturnus*, *Aplonis*, and *Artamella* also have 14 cervical and five dorsal vertebrae and five

TABLE 3  
MEASUREMENTS (IN MILLIMETERS) OF APPENDICULAR BONES

	<i>Fregilupus</i> (A.M.N.H. Specimen)		<i>Fregilupus</i> (Murie)	<i>Artamella</i>		<i>Sturnus</i>	
	Right	Left		Right	Left	Right	Left
Humerus	35.6	35.6	37.5	Broken	Broken	Broken	26.4
Ulna	41.8	41.4	45.0	33.6	33.6	33.1	32.8
Radius	37.3	37.2	—	30.3	30.1	—	—
Manus <sup>a</sup>	36.1	36.2	40.0	27.7	27.7	34.0	33.9
Total wing	113.4		122.5	—		93.3	
Femur	31.6	31.6	35.0	22.5	22.3	25.6	25.6
Tibiotarsus	58.5	58.5	65.0	35.8 <sup>b</sup>	Broken	Broken	45.2
Tarsometatarsus	41.9	41.7	45.0	25.4	25.4	30.0	29.9
Hallux <sup>c</sup>	27.8	28.1	—	17.6	17.6	21.4	20.9
Digit II	26.7	24.2	—	14.9	14.7	19.5	19.3
Digit III	35.1	35.9	36.3	21.3	20.8	29.1	28.3
Digit IV	28.5	26.9	—	17.2 <sup>d</sup>	16.3	19.6	19.5
Total Leg <sup>e</sup>	167.4		181.3	104.7		129.5	

<sup>a</sup> Carpometacarpus plus digit II, articulated.

<sup>b</sup> Bone broken, but the measurement is fairly accurate.

<sup>c</sup> Measurements were made of articulated digits.

<sup>d</sup> The length of the digits varies considerably owing to variation in the curvature of the claws.

<sup>e</sup> Average of bones; includes digit III.

true ribs, which articulate with the sternum and which possess uncinate processes. I was able to find only one pair of cervicodorsal ribs in these genera. There are two pairs of thoracic ribs in *Fregilupus* and *Artamella*, but I found only one pair in *Sturnus* and *Aplonis*. In the specimens I had for study, *Artamella* had six free caudal vertebrae, *Fregilupus* and *Aplonis* each had seven, and of three specimens of *Sturnus* two had six free caudal vertebrae and one specimen had seven. All genera have a well-developed os humero-scapulare. All have five bony canals in the

hypotarsus. The sternum is single-notched in all genera considered here.

Shufeldt (1888, p. 332) mentioned the presence of "ilioneural canals" in the Corvidae. The ilioneural canals, located in the anterior one-third to one-half of the pelvis in various families, result from the failure of the dorsomedial edges of the ilium to fuse with the median dorsal ridge (i.e., the neural spines) of the synsacrum. The space between these bony structures is occupied by deep back muscles. In all passerine, and some non-passerine, genera that I have examined, these

TABLE 4  
PROPORTION OF BONY ELEMENTS TO TOTAL LENGTH OF APPENDAGE<sup>a</sup>

	Humerus	Ulna	Manus	Femur	Tibio-tarsus	Tarso-metatarsus
<i>Artamella</i>	—	—	—	26.7	42.8	30.4
<i>Sturnus</i>	28.3	35.3	36.4	25.4	44.8	29.7
<i>Fregilupus</i>	31.3	36.8	31.7	23.9	44.3	31.7
<i>Paradisaea</i>	30.5	39.1	30.3	24.8	44.2	30.9
<i>Cyanocitta</i>	31.2	37.9	30.8	25.8	43.5	30.5
<i>Corvus</i>	28.5	35.2	36.2	25.3	44.7	30.0

<sup>a</sup> Digit III was excluded in the computation of the length of the pelvic appendage.



are actually grooves rather than canals, in that the space is completed dorsally by a dense membrane rather than by bone. Such is the situation in all genera compared in this paper. In some non-passerine genera, there is a canal, completely arched over by bone, which houses the posterior segments of the deep back muscles.

Many years ago, Shufeldt (1888, pp. 340, 347) called attention to the fact that the pneumatic fossa at the proximal end of the humerus is single in certain families of passerine birds (Corvidae), double in others (Icteridae, Fringillidae). Later, Ashley (1941) discussed this character in his analysis of the corvid humerus. In *Fregilupus varius* there is a well-developed double pneumatic fossa (see Murie, 1874, fig. 7; Milne-Edwards and Oustalet, 1893, p. 213). A strong bony partition divides the fossa into a dorsal and a ventral portion. The ventral head of *M. humerotriiceps* arises from the entire ventral bony wall of the ventral fossa. *M. proscapulohumeralis* inserts at the distal end of the ventral fossa and between the two heads (dorsal and ventral) of *M. humerotriiceps*. *Sturnus* also has a double pneumatic fossa, though the accessory fossa, located dorsally, is smaller than the similar fossa in *Fregilupus*. In *Aplonis* and *Artamella* there is a rudimentary dorsal fossa (see p. 267).

There is little similarity among the four genera in the form of the bill. It is long and slightly decurved in *Fregilupus*; long, straight, and chisel-shaped in *Sturnus*; relatively short and robust in *Aplonis*; strong and high in *Artamella*. The nostrils are imperforate, naked, and oval (*Artamella* and *Sturnus*) to rounded (*Aplonis*), more elliptical in *Fregilupus*, though long years in preservative may have altered somewhat the shape in *Aplonis* and *Fregilupus*. There is a very prominent horizontal shelf in the narial cavity of *Fregilupus*, *Artamella*, and *Sturnus*; the shelf appears to be placed more diagonally in *Aplonis*.

There is a conspicuous operculum arching over the nostril dorsally in *Sturnus*; in life, the operculum was apparently very similar in *Fregilupus*. The operculum is absent in *Artamella*, much reduced in *Aplonis*.

The os opticus of *Artamella* is quite different from that bone in the other genera. The

os opticus is crescent-shaped (similar to that in *Syrnaticus*, as illustrated by Tiemeier, 1950, p. 35) in *Artamella*, whereas in *Fregilupus*, *Aplonis*, and *Sturnus*, it is U- or V-shaped. Further comparison seems unwarranted in view of Tiemeier's conclusion that the os opticus is "too variable in size and shape within a species" to be useful as a taxonomic character.

The ectethmoidal plate in *Sturnus* is "winged" (Beecher, 1953, figs. 1 and 4), and there are two ectethmoidal foramina, the medial being the larger. In *Aplonis* the lacrimal is also fused with the anterior wall of the orbit, but the ectethmoidal plate is much closer to being "truncate" in shape rather than being winged. There are three foramina. The largest is located on the dorsomedial corner of the ectethmoidal plate; a second, on the dorsolateral edge; and a third, on the ventrolateral projection of the plate. Variation in the number of foramina is, in all probability, not significant.

The ectethmoidal plate in *Fregilupus* is best described as being "moderately winged," in that it is intermediate in shape between that in *Sturnus* and in *Aplonis*. I found only two ectethmoidal foramina. The major foramen is that one located along the dorsomedial corner of the bone; the secondary, much smaller, foramen is situated on the ventrolateral projection of the bone.

*Artamella* differs from the preceding three genera in that the lacrimal bone is free and the ectethmoidal foramen is a single, large opening (Beecher, 1953, fig. 11).

I would suppose that the presence of a free lacrimal bone might be a fairly constant (but not invariable) character within a family (for variation in this bone, see Beecher, 1953, p. 288). When the lacrimal bone is fused with the anterior wall of the orbit, however, I would expect considerable variation in the shape of the ectethmoidal plate (i.e., winged or truncate) within a family. But here, as with other anatomical characters, we do not know how much variation occurs within any one passerine family.

In discussing the anatomy and relationships of the Broadbill, *Pseudocalyptomena*, Lowe (1931, p. 449 and fig. 2) said that "the plantar surface of the tarso-metatarsus differs from the normal Passerine arrangement

in presenting small somewhat conical papillomatous scales. . . . This is a very important feature, and entirely in accordance with the Eurylaemid characters of the bird generally." *Artamella* differs from the other genera discussed in the present paper in that it presents what is apparently the identical configuration to that illustrated for *Pseudocalyptomena*. There is a continuous series of these papillomatous scales extending from the plantar surface of the foot proximad to the "heel" joint and covering the posterior surface of the hypotarsal region of the tarsometatarsus (see fig. 3).

### WING MYOLOGY

Of *M. latissimus dorsi*, pars anterior is a thin fleshy band 9 mm. wide at its origin by an aponeurosis from the neural spines of the last cervical and the first dorsal vertebrae. The muscle has a fleshy insertion (5 mm. wide) on a ridge on the anterodorsal surface of the humeral shaft, beginning about 5 mm. distal to the junction of the articular head and the deltoid crest. Pars posterior was absent bilaterally. Pars metapatagialis was absent on the right side. On the left side there was a rudimentary belly, which consisted primarily of a sheet of fascia containing a thin layer of striated muscle fibers. In gross dissection, one could not determine whether or not muscle fibers were present, but these were readily demonstrated in microscopic sections. Posteriorly, the fascia covered *M. rhomboideus profundus*, but a discrete origin could not be determined. Nor could I trace any tendon to an insertion into the skin or elsewhere; the fascia simply lost its identity in the fascia posterior to the arm. There is no way of knowing whether this was a remnant of pars metapatagialis, pars posterior, or neither. When both are present, the dermal component is but a specialization of pars posterior.

*M. latissimus dorsi dorsocutaneous* is a flat band (about 1.5 mm. wide), which arises by fleshy fibers from the anterior end of the ilium. The belly runs cephalad on the deep surface of the skin, just lateral to the dorsal spinal and cervical feather tracts. At about the midlength of the neck, the fleshy fibers lose their identity by intermingling with the fibers of *M. cucullaris*.

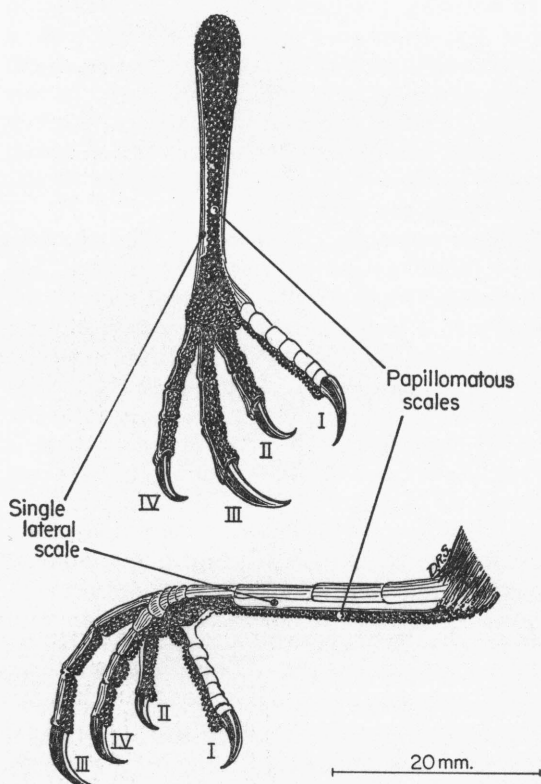


FIG. 3. *Artamella viridis*. Posterior and lateral views of tarsal scutellation.

*M. rhomboideus superficialis* arises from the neural spines of the last two cervical and the first three dorsal vertebrae (from the anterior part only of dorsal vertebra number 3). The fleshy fibers insert on the anterior 22 mm. of the dorsomedial edge of the scapula and on the medial surface of the posterior extension of the clavicle.

*M. rhomboideus profundus* arises from the neural spines of the last cervical and the five dorsal vertebrae. The origin from dorsal vertebra number 5 is shared with *M. sartorius*. The fleshy fibers insert on the caudal 10 to 11 mm. of the dorsomedial edge of the blade of the scapula.

*M. cucullaris pars proapatagialis* is well developed. The fleshy fibers give rise to a small tendon, which inserts on the tendon of *M. tensor patagii longus*.

*M. serratus profundus* arises by several fleshy fasciculi from the lateral surface of the cervicodorsal rib and the first true rib and

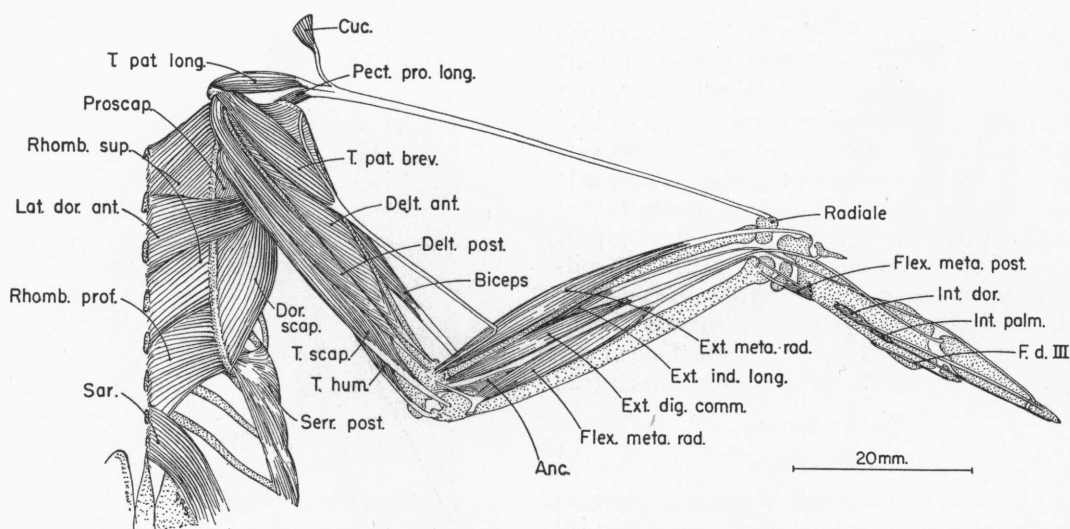


FIG. 4. *Fregilupus*. Dorsal view of wing muscles.

from the transverse process of the penultimate cervical vertebra. The slip arising from the first true rib is much larger than that arising from the cervicodorsal rib. The muscle inserts by fleshy fibers on the medial surface of the scapula for a distance of 10 mm., beginning 17 mm. from the caudal tip of the bone.

*M. serratus anterior* arises by two fleshy slips, one each from the lateral surface of the cervicodorsal rib and the first true rib. The two slips fuse to form a single belly, which passes upward between the two heads of *M. subscapularis* to insert by an aponeurosis on the ventral edge of the scapula, beginning about 5 mm. caudal to the glenoid fossa.

*M. serratus posterior*, a well-developed complex, arises by fleshy fasciculi from the lateral surface of true ribs numbers 2, 3, 4, and 5, ventral to their uncinate processes. The muscle inserts by fleshy fibers on the ventral edge of the scapula in its caudal 5 mm., and by an aponeurosis anterior to the fleshy insertion.

*M. serratus metapatagialis* is a single fleshy slip (2 mm. wide), which arises from the lateral surface of the third true rib just inferior to the uncinate process. The fleshy fibers end in the skin at the posterior border of the humeral feather tract. From this area, a fibrous tendon passes distad in the metapatagium to the elbow, but I could not trace the

tendon to a bony attachment.

*M. proscapulohumeralis* is a well-developed muscle, which arises from the lateral surface of the scapula (for a distance of 10 mm.), between the areas of origin of *Mm. scapulotriceps* and *dorsalis scapulae*. The belly tapers to a width of 2 mm. at its insertion at the distal end of the ventral pneumatic fossa of the humerus (see Osteology), between the two heads of *M. humerotriceps*.

*M. dorsalis scapulae* arises from the lateral surface of the caudal 18 mm. of the blade of the scapula. It inserts, by fleshy fibers surrounded by a dense tendinous envelope, on the dorsodistal surface of the bicapital crest of the humerus, just distal to the humeral origin of *M. biceps brachii*. The insertion is opposite that of *M. proscapulohumeralis*.

*M. subscapularis* has the usual two heads of origin. The two heads fuse and give rise to a single tendon, which inserts on the internal humeral tubercle located on the posteroventral surface of the humerus just distal to its articular head. *Pars externa* arises from an area about 8 mm. long on the lateral surface of the scapula, caudal and ventral to the origin of *M. proscapulohumeralis*. *Pars interna* arises from the medial surface of the scapula for a distance of about 17 mm. (i.e., about the proximal half), beginning on the acromion process and extending caudad to the area of insertion of *M. serratus profundus*.

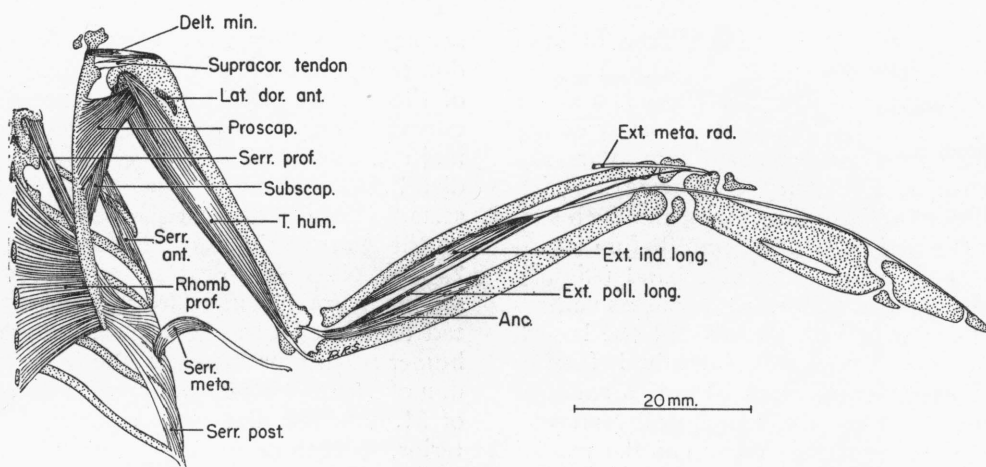


FIG. 5. *Fregilupus*. Dorsal view of wing muscles, deep layer.

*M. subcoracoideus* arises by two heads, which fuse on a common tendon. It inserts on the proximal end of the bicipital crest of the humerus, proximal to the origin of the biceps muscle and posterior to the insertion of the subscapularis tendon. *Pars ventralis* arises by fleshy fibers from the posterior surface of the coracoid, at the junction of its basal and middle thirds, and from the adjacent area on the coracoclavicular membrane. It is a small, flat band of fleshy fibers, less than 1 mm. in width. *Pars dorsalis* is a roughly triangular-shaped muscle, 4 mm. wide at its origin from the medial surface of the shaft of the clavicle, just inferior to its head. The belly tapers to the common tendon.

*M. coracobrachialis anterior* is a poorly developed muscle, partly embedded in the anteroventral surface of the capsule of the shoulder joint. It arises by a tendon from the apex of the coracoid, dorsal to the tendon of the biceps muscle. The belly is 8 mm. long and 2 mm. in maximum width. It inserts by fleshy fibers on the anteroventral surface of the humerus, just distal to the articular head.

*M. coracobrachialis posterior* is a well-developed muscle, typical in all respects. It arises from the anterior and lateral surfaces of the coracoid in its basal 15 mm. The strong tendon passes upward and forward, dorsal to the tendons of *Mm. subcoracoideus* and *subscapularis*, to insert on the bony partition which separates the two pneumatic fossae of the humerus.

*M. supracoracoideus* has an extensive origin from the anterior and medial portions of the body of the sternum, from the dorsal two-thirds of the carina, from the antero-medial surface of the coracoid, and from the lateral two-thirds of the coracoclavicular membrane. The fibers converge onto a central tendon, which passes dorsad through the triosseal canal. As in *Paradisaea rubra*, the Corvidae, *Artamella*, *Aplonis*, and *Sturnus*, the tendon passes through a fibrocartilaginous pulley after emerging from the triosseal canal. This pulley, a part of the joint capsule, is firmly attached to the base of the os humeroscapulare. The tendon, partly concealed by *M. deltoideus minor*, inserts on the humerus at the junction of the deltoid crest and the articular head.

*M. sternocoracoideus* arises by fleshy fibers from the ventral surface of the sternocoracoid process of the sternum. The muscle passes mesiad to insert in the sternocoracoid fossa on the posterior surface of the base of the coracoid.

Of *M. pectoralis*, *pars thoracicus*, the major portion of *M. pectoralis*, has an extensive origin from the ventral third of the carina and from the anterolateral and posterior regions of the body of the sternum, including the xiphoid process and membrane; from an aponeurosis attached to the dorsolateral border of the xiphoid process and which extends as high as the five sternal ribs; and from all but the dorsal 6 mm. of the lateral surface of



the clavicle and the adjacent area (3 mm. wide, i.e., about the medial one-third) on the coracoclavicular membrane. There is a single belly. It inserts on the pectoral crest of the humerus for a distance of 9 mm. Pars abdominalis is a dermal component, which arises from the lateral region of the deep surface of the belly, about 12 mm. before its insertion. It is a flat, muscular band (slightly more than 1 mm. wide), which passes ventro-caudad to insert into the skin at the lateral margin of the ventral abdominal feather tract. Pars propatagialis longus is a small (2 mm. wide and 15 mm. long), fleshy muscle, which arises from the surface of the medial or furcular portion of pars thoracicus. Its fleshy fibers fuse with the distal end of the belly of *M. tensor patagii longus*. Pars propatagialis brevis is a dense aponeurotic band, derived from the tendinous envelope which surrounds the insertion of pars thoracicus. The propatagialis brevis fuses with the tendon of *M. tensor patagii brevis* near the distal end of its belly.

*M. deltoideus major* has two well-developed parts. Pars anterior has its major origin from the very large os humeroscapulare. These fibers insert on the deltoid crest, thus forming the most proximal portion of insertion of *M. deltoideus major*. Longer fibers arise from a strong, flat tendon, which has its origin on the lateral surface of the tip of the

acromion process of the scapula. As this tendon passes around the posteromedial surface of the os humeroscapulare, a strong tendon extends from that sesamoid to reinforce the main tendon; the fleshy fibers begin at the distal end of this junction. Pars anterior inserts by fleshy fibers on the deltoid crest and on the shaft of the humerus for a distance of 25 mm. Near the distal end of the fleshy insertion, a small tendon forms and passes distad to insert on the lateral epicondyle of the humerus, just proximal to the inserting tendon of *M. tensor patagii brevis* and the origin of *M. extensor metacarpi radialis*. Pars posterior, smaller than pars anterior, has a deep fleshy origin from the acromion process of the scapula and a semitendinous origin from the apex of the head of the coracoid and from the dorsal and medial surfaces of the posterior extension of the clavicle, the latter origin extending anteriorly to the area of origin of *Mm. tensores patagii longus et brevis*. I was unable to demonstrate a secondary tendinous origin from the blade of the scapula dorsal to the proscapulohumeralis muscle (see p. 249). Pars posterior inserts on the shaft of the humerus in about its middle third, but the superficial portion of the belly gives rise to a tendon which inserts at the base of the lateral epicondyle, posterior to and separate from the tendon of insertion of pars anterior.

*M. deltoideus minor* is a thin, fleshy band

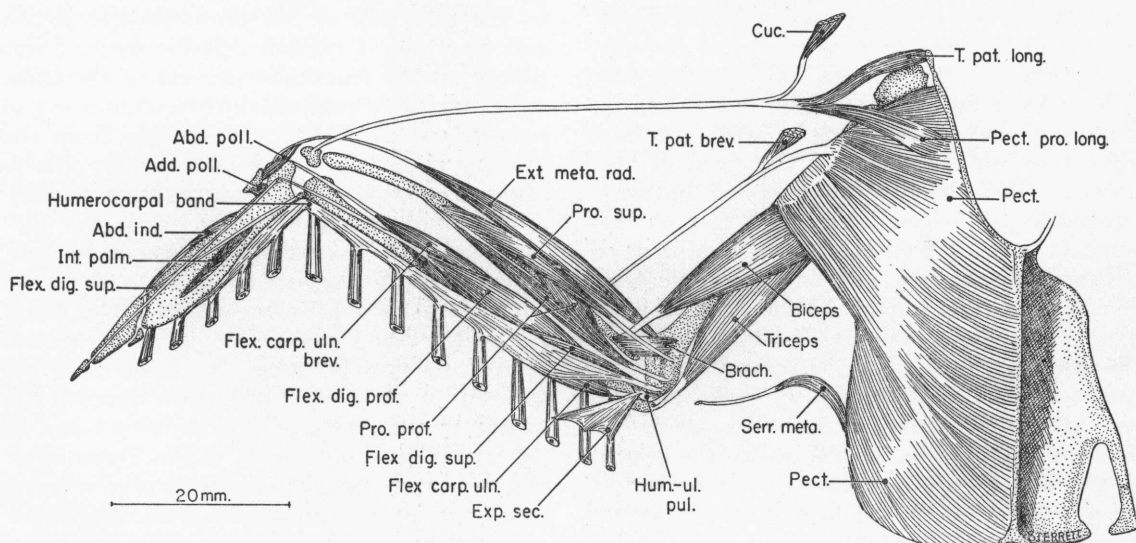


FIG. 6. *Fregilupus*. Ventral view of wing muscles.



about 10 mm. long but less than 1 mm. wide. It arises from the acromion process of the scapula, dorsal and anterior to the tendon of origin of pars anterior of the *deltoideus major*. The belly passes outward, superficial to the tendon of *M. supracoracoideus*, to insert on the head of the humerus, between the areas of insertion of *Mm. supracoracoideus* and *pectoralis*. *M. deltoideus minor* conceals the distal part and the insertion of the *supracoracoideus* tendon, but not its proximal portion.

*M. tensor patagii longus*, a small muscle with a belly about 7 mm. long and 2.5 mm. wide, arises primarily from the superficial surface of a common tendon, shared with *M. tensor patagii brevis*, from the dorsal surface of the apex of the clavicle. The bellies of the two muscles, however, are entirely separate. The fleshy fibers of *M. pectoralis*, pars *propatagialis longus*, fuse with the distal end of the belly of the *tensor patagii longus* muscle, after which the tendon of insertion is formed. The tendon is further reinforced by the tendon of *M. cucullaris*, pars *propatagialis*. The tendon has a typical course along the leading edge of the *propatagium*. Near the distal end of the forearm, the wide, elastic portion of the *tensor patagii longus* tendon gives rise to two tendons. The smaller, anterior tendon passes into the manus to fuse with the deep fascia over the base of the pollex and the extensor process, but there seems to be no direct insertion on the extensor process itself. The larger, posterior tendon passes over the distal end of the radius to insert on the *os radiale*.

*M. tensor patagii brevis* has a well-developed belly about 20 mm. long and 4 mm. in maximum width. It arises by a flat tendon from the dorsal surface of the apex of the clavicle. The belly extends about halfway down the arm. Near the distal end of the belly, it is reinforced by *M. pectoralis*, pars *propatagialis brevis*. The strong, single tendon of *M. tensor patagii brevis* fuses in part with the belly of *M. extensor metacarpi radialis*, but the main part of the *brevis* tendon passes proximad, diagonally, superficial to the *extensor metacarpi radialis* muscle to insert on the humerus, just distal to the origin of the latter muscle. There is no posterior fascial extension of the *brevis* tendon as in many non-passerine birds.

*M. biceps brachii* has a belly about 24 mm. long; it is 6 mm. in maximum width, inferior to the origin of fleshy fibers from the Y-shaped tendon of origin. This tendon has the two usual attachments: the anterior surface of the head of the coracoid and the bicipital crest of the humerus. The tendon of insertion bifurcates, both tendons inserting about 1 mm. from the proximal articular surfaces of the radius and ulna. The larger tendon inserts in a fossa on the ulna; the smaller tendon inserts on the bicipital tubercle of the radius.

*M. triceps brachii*. *M. scapulotriceps* arises by fleshy and tendinous fibers from the lateral surface of the scapula for a distance of 4 mm., beginning on the posterior glenoid lip, and by a strong tendon from the postero-inferior margin of the glenoid lip. There is no humeral anchor. The tendon of insertion, containing a large sesamoid where it crosses the distal end of the humerus, inserts on the dorsal surface of the ulna, about midway between the olecranon process and the anterior edge of the condyle. *M. humerotriceps* has two heads proximally. The fleshy fibers of the dorsal or internal head arise from the dorsal wall of the dorsal pneumatic fossa and extend nearly to the distal end of the humerus. The fleshy fibers of the ventral or external head arise from a large area on the ventral wall of the ventral pneumatic fossa and for a distance of about two-thirds of the length of the humeral shaft. The two heads fuse distal to the insertion of *M. proscapulohumeralis* and insert by a tendon and by fleshy fibers (deep) on the olecranon process of the ulna.

*M. expansor secundariorum*, composed of smooth muscle fibers, arises solely from the humero-ulnar pulley. It inserts by fleshy fibers on the calami of the inner three secondaries (nos. 7, 8, and 9).

*M. anconaeus coracoideus* was not present.

*M. brachialis*, typical in all respects, arises from the brachial impression near the distal end of the humerus. The belly passes distad in the interval between the flexor and extensor muscles of the forearm to insert in the brachial impression on the proximal end of the ulna. The two heads of *M. flexor digitorum profundus* arise, respectively, anterior and posterior to the insertion of *M. brachialis*.

*M. pronator superficialis* has a typical

origin by a strong, flat tendon (5 mm. long) from the distal end of the humerus. The belly is about 19 mm. long, extending to within 14 mm. of the distal end of the radius.

*M. pronator profundus* also arises by a stout tendon from the humerus, but distal to the origin of the *pronator superficialis*. Flethy fibers form almost at once, and the belly (about 17 mm. long) is much larger proximally than distally. A deep fasciculus, proximally, inserts by a dense aponeurosis on the radius, posterior to and in contact with the insertion of *M. pronator superficialis*. The belly decreases in size distally, to give rise to a flat tendon, which, in part, fuses with the posterior surface of the *superficialis*, but, in part, continues distad to insert on a small tubercle on the radius. The tubercle is located just distal to the terminal fibers of the *pronator superficialis* and is about 12 mm. from the distal end of the radius.

*M. flexor digitorum superficialis* has a typical origin by a tendon from the distal end of the humerus. The tendon fans out almost immediately into a tough aponeurotic sheet (the humerocarpal band of Gadow), which almost completely ensheathes the belly and tendon of *M. flexor carpi ulnaris* and which sends discrete tendinous slips to attach to the calami of secondaries 2 through 5. At the distal end of the forearm, there is a strong attachment to the os ulnare, anterior to the insertion of the *flexor carpi ulnaris*, but most of the humerocarpal band passes into the manus to attach to the posteroventral edge of metacarpal III and to the calami of the four proximal primaries. The small belly of *M. flexor digitorum superficialis* (12 mm. long and 1 mm. in maximum width) arises from the anterior and deep side of the humerocarpal band, about 2 to 3 mm. from its humeral attachment. The belly gives rise to a small tendon, which passes distad on the deep surface of the humerocarpal band. At the wrist, the tendon passes through a groove on the anterior surface of the os ulnare and into the hand. Here the tendon passes forward diagonally, deep to the tendon of *M. flexor digitorum profundus*, to insert on the anterobasal corner of the proximal phalanx of digit II.

*M. flexor digitorum profundus* has a V-shaped origin on either side of the area of

insertion of *M. brachialis*. The posterior head arises from the posterior surface of the ulna, beginning at the base of the olecranon process; this head then winds around the ulna to the ventral surface of the bone. The anterior head arises just distal to the insertion of the biceps muscle. The total length of the fleshy belly is 22 mm.; it lies in slightly more than the proximal half of the forearm. In the manus, the tendon passes around the anterior surface of the pisiform process and along the anteroventral edge of the carpometacarpus, superficial to the tendon of *M. flexor digitorum superficialis*, to insert on the anteroventral edge of the base of the distal phalanx, digit II.

*M. flexor carpi ulnaris* arises by a stout tendon from the distal end of the humerus. The tendon passes through a humero-ulnar pulley. The relatively small pars anterior is about 20 mm. long and 1 mm. in diameter. A large tendon forms distally and inserts on the proximal face of the os ulnare. There is a small (about 10 mm. long, but less than 1 mm. wide), flat pars posterior. From the dorsal surface of this belly and its tendon, fascial bands extend to the calami of all but the proximal three secondaries. The small tendon of pars posterior also inserts on the ulnare, but dorsal to the insertion of pars anterior.

*M. flexor carpi ulnaris brevis* is a well-developed muscle (17 mm. in length), which arises from a little less than the middle half of the ventral surface of the ulna. The fleshy fibers begin 13 mm. distal to the proximal tip of the olecranon process; they extend to within 10 mm. of the distal end of the ulna. The tendon passes over the ventral surface of the distal end of the ulna, deep to the tendons of *Mm. extensor metacarpi radialis* and *extensor pollicis longus*, to insert on the anteroventral edge of metacarpal I, just proximal to the base of the extensor process. As the tendon crosses the carpal region, it is held in place by a series of ligaments.

*M. extensor metacarpi radialis* arises by a stout tendon and by fleshy fibers from the lateral epicondyle of the humerus. Eight millimeters distal to this origin, the tendon of *M. tensor patagii brevis* is strongly anchored to the belly (24 mm. long) of *M. extensor metacarpi radialis*. Its tendon passes over the distal end of the radius and the os

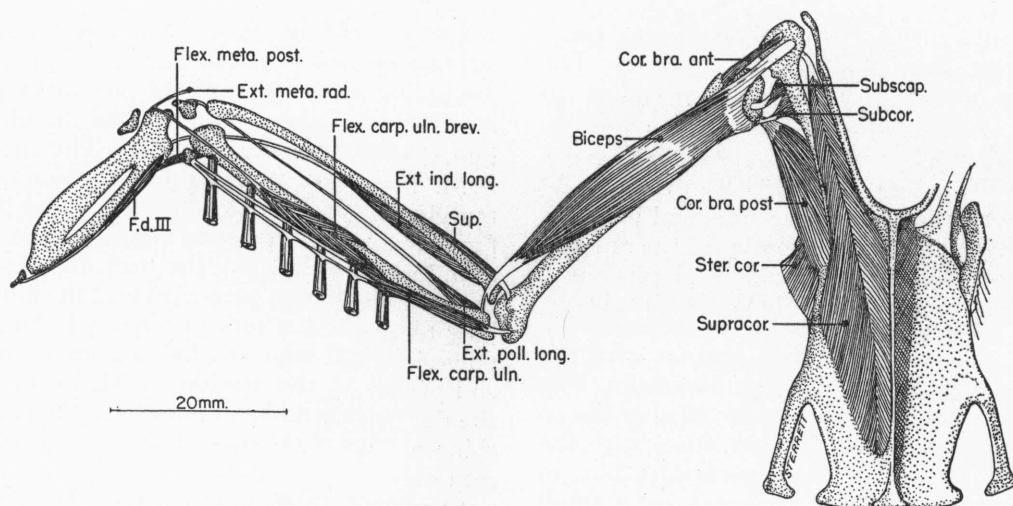


FIG. 7. *Fregilupus*. Ventral view of wing muscles, deep layer.

radiale to insert on the extensor process of the carpometacarpus. *M. abductor pollicis* arises from the ventral edge of this tendon a short distance before its insertion, and the tendon of *M. extensor pollicis longus* fuses with its dorsal side near the insertion.

*M. flexor metacarpi radialis* arises by a tendon from the lateral epicondyle of the humerus, proximal to the origin of *Mm. extensor digitorum communis* and *anconeus*. The tendon passes distad superficial to the tendons of both of those muscles. There is a wide (1 mm.), tendinous, ulnar anchor. Flethy fibers begin 5 mm. distal to the humeral origin of the tendon. The belly (25 mm. long) conceals all but the most proximal part of *M. anconeus*. The tendon of insertion passes anterior to a bony process near the distal end of the ulna and then crosses the dorsal surface of the condyle and the os ulnare to insert on the posterodorsal corner of metacarpal III.

*M. extensor digitorum communis* arises by a tendon from the distal end of the humerus, between the areas of origin of *Mm. extensor metacarpi radialis* and *anconeus*. Flethy fibers form at once. The belly (23 mm. long) tapers to a small tendon, which passes around the anterior surface of the dorsal condyle and into the manus. Opposite the base of the pollex, the tendon bifurcates. The shorter branch inserts on the posterodorsal corner of the pollex. The longer branch passes

distad in a groove on metacarpal II, first on its anterior surface, but then on its antero-dorsal surface. At the distal end of the carpometacarpus, the tendon turns around a bony process to insert on the anterodorsal surface of the base of phalanx 1, digit II.

*M. anconeus* is a small muscle (about 18 mm. in length), which is limited to the proximal half of the forearm. It has the most distal origin of those muscles arising from the lateral epicondyle of the humerus. The tendon and belly lie deep to *M. flexor metacarpi radialis*. It inserts on the anterior surface, dorsal to the interosseous membrane, of the ulna in its proximal half.

*M. supinator* is a small muscle with a rounded belly 8 mm. long and about 0.5 mm. in diameter. It arises by a tendon from the lateral epicondyle, distal to the origin of *M. extensor digitorum communis* and anterior to the origin of *M. anconeus*. It inserts by flethy fibers on the anterior edge of the radius on a little more than its proximal quarter.

*M. extensor indicis longus* is a very long (23 mm.), small (less than 1 mm. wide), thin muscle, which arises only from the radius. The flethy fibers begin at the proximal end of that bone at the distal end of the area of insertion of *M. biceps brachii*. The belly lies ventral to the interosseous membrane proximally, but distally the tendon passes through a groove near the dorsal surface of the ulnar condyle and into the manus. There the ten-

don passes distad, diagonally along the dorsal surface of metacarpal II. In the distal third of that bone, the tendon passes superficial to the tendon of *M. extensor digitorum communis* and against a bony process on the metacarpal. This tubercle improves the angle of pull of the tendon, which then runs along the anterior surface of the proximal phalanx of digit II. The tendon inserts on the antero-basal corner of phalanx 2 (distal phalanx).

*M. flexor metacarpi brevis* was absent bilaterally.

*M. extensor pollicis longus* is a very small, almost rudimentary muscle, the belly of which is 13 mm. in length. It arises from an area about 4 mm. long on the proximal end of the ulna, beginning just distal to the articular surface. The muscle is separated from the insertion of *M. anconeus* by the interosseous membrane. The belly extends through the proximal third of the forearm and tapers to a minute, hair-like tendon, which fuses with the tendon of *M. extensor metacarpi radialis* near its insertion.

*M. extensor pollicis brevis* was absent bilaterally.

*M. abductor pollicis* is a small (4 mm. long and less than 1 mm. wide), fleshy muscle, which arises by fleshy fibers from the tendon of insertion of *M. extensor metacarpi radialis*. It inserts by a tendon on a ridge on the posteroventral surface of the pollex, about 1 mm. from the proximal end of that bone.

*M. adductor pollicis* is also a small muscle; it arises from the anteroventral edge of metacarpal II, anterodistal to the pisiform process. It inserts by fleshy fibers on nearly the entire posterior surface of the pollex and on the bases of the alula quills.

*M. flexor pollicis* was absent bilaterally.

*M. abductor indicis* is a minute, rudimentary muscle, about 3 mm. long and 0.4 mm. in maximum width at its origin from a small area on the anteroventral edge of metacarpal II, in the second third of that bone. The fine tendon fuses with the deep surface of the tendon of *M. flexor digitorum superficialis*, just before that tendon inserts on the anterior edge of the base of phalanx 1, digit II.

*M. flexor metacarpi posterior* is a very poorly developed muscle (4 mm. long and less than 1 mm. in maximum width), which arises by a tendon from the distal end of the

ulna. This tendon is intimately fused with the joint capsule. The belly lies ventral to the tendon of *M. flexor metacarpi radialis* and inserts by fleshy fibers on the posterodorsal corner of metacarpal III, just distal to the insertion of *M. flexor metacarpi radialis*.

*M. flexor digiti III* is a small, but long muscle, lying in a groove on the posterior surface of metacarpal III. The belly, about 10 mm. long and 2 mm. in maximum width, lies in the proximal half of the metacarpal. The long tendon passes distad in a groove on the posterior side of the bone, but near the distal end of metacarpal III the tendon passes to the dorsal surface. It inserts on the posterior spine of digit III. The entire muscle can be seen only from a posterior view and the belly not at all from the dorsal side.

*M. interosseus dorsalis* has a typical origin from the facing surfaces of metacarpals II and III. The tendon forms as a midline raphe, passes diagonally from posterior to anterior along the dorsal surface of the distal end of the carpometacarpus and the proximal phalanx of digit II, and inserts on the anterior surface of the distal phalanx, near its mid-length.

*M. interosseus palmaris* also has a typical origin. The tendon passes distad, posterior to the tendon of *M. interosseus dorsalis*, to insert on the posterior edge of the distal phalanx, digit II, near the tip of that phalanx.

#### COMPARATIVE MYOLOGY OF THE WING

The muscles of the specimen of *Aplonis* were poorly preserved, and bones of both wings had been broken by shot so that it was not possible to work out the complete relationships of many of the muscles. The following wing muscles, however, are absent in *Fregilupus*, *Sturnus*, *Aplonis*, and *Artamella*: latissimus dorsi metapatagialis, biceps pars propatagialis, anconeus coracoideus, entepicondylo-ulnaris, flexor metacarpi brevis (=a distal head of *M. extensor indicis longus* of Hudson), extensor pollicis brevis, and flexor pollicis. *M. abductor indicis* is rudimentary in all genera, and *Mm. coracobrachialis anterior* and *flexor metacarpi posterior* are poorly developed in all.

Certain similarities in development of the wing muscles are worthy of note. *M. proscapulohumeralis* is present in all genera and has a typical origin and insertion, but it is

relatively much better developed in *Fregilupus* than in the other genera. Mm. latissimus dorsi dorsocutaneous and pectoralis pars abdominalis are present in each genus and are similar in origin and relationships. M. pectoralis propatagialis brevis is a tendinous band, rather than a fleshy slip, in each genus. In each genus, the tendon of insertion of M. tensor patagii longus is similar to that described for *Fregilupus* (p. 245). M. biceps brachii is similar in the four genera; the bulk of the tendon inserts in a pit on the proximal end of the ulna, but a small branch inserts on the proximal end of the radius. Mm. scapulotriceps and humerotriceps are independent throughout most of their extent; a few fleshy fasciculi of M. humerotriceps insert on the tendon of M. scapulotriceps at the elbow, but the areas of insertion of the two muscles on the ulna are separate. M. extensor indicis longus arises from a small area on the proximal end of the radius, though in one out of six wings of *Sturnus* there was a small, accessory origin from the ulna also.

M. latissimus dorsi pars posterior is present in *Sturnus* and *Aplonis*, but it is absent in *Fregilupus* and *Artamella*. The pattern of insertion of the two parts of M. latissimus dorsi differs in the two starlings. In *Aplonis* pars posterior inserts immediately posterior to and in contact with pars anterior; in *Sturnus* there is, relatively, a wide gap between the areas of insertion of the two parts of this muscle. M. cucullaris pars propatagialis in *Artamella* differs from that in the other genera in that it inserts by fleshy fibers, rather than by a tendon, on the tendon of M. tensor patagii longus. Pars interna of M. subscapularis has an origin which begins on the medial surface of the acromion process of the scapula in all genera except for *Artamella*, in which genus it begins just caudal to the acromion process. M. subcoracoideus is composed of two parts (pars ventralis and pars dorsalis) in each genus, but there are differences in the origins. In *Fregilupus* and *Artamella*, pars ventralis is a small head, which arises from the posterior face of the coracoid dorsal to the insertion of M. sternocoracoideus, i.e., roughly at about the junction of the middle and lower thirds of the coracoid; in *Sturnus* and *Aplonis*, pars ventralis is unusually well developed and arises from the ventral third of the coracoid and medial

to the area of insertion of M. sternocoracoideus. In *Fregilupus*, pars dorsalis arises from the medial surface of the shaft of the clavicle, just ventral to the apex; in *Sturnus* and *Aplonis*, it arises from the medial surface of the clavicle and from the acromion process of the scapula; in *Artamella*, pars dorsalis arises primarily from the medial surface of the acromion process, but it has a small origin from the adjacent area of the coracoid (pars dorsalis arises from the coracoid and the scapula in the Corvidae, from the acromion process in *Paradisaea rubra*).

M. coracobrachialis posterior in *Fregilupus* and *Sturnus* inserts on the bony partition which separates the two pneumatic fossae of the humerus; in *Artamella* and *Aplonis*, it inserts on the internal tuberosity of the humerus. M. pectoralis pars thoracicus is similar in most respects in the four genera, except that in *Artamella* it arises from the ventral half of the carina; in the other genera, it arises from the ventral third of the carina. M. pectoralis propatagialis longus is a well-developed fleshy slip in all except *Artamella*, in which it is entirely tendinous.

M. deltoideus major is similar in the four genera, each having two well-developed heads, pars anterior and pars posterior. In *Sturnus vulgaris*, pars posterior arises from the scapula dorsal to the glenoid fossa and from the acromion process, from the medial surface of the head of the clavicle, ventral to the origin of Mm. tensores patagii longus et brevis, and from the coracoclavicular ligament. Pars posterior also has a thin fascial connection with the scapula, dorsal to the origin of M. proscapulohumeralis. The other genera are similar, but I was unable to demonstrate in *Fregilupus* the latter fascial connection with the scapula, dorsal to the origin of M. proscapulohumeralis; it very likely is present. M. deltoideus minor exhibits its best development in *Artamella*, in which it arises from the acromion process of the scapula, as in the other genera, but also has a small origin from the posterior extension of the clavicle and the coracoscapular ligament. The belly of M. tensor patagii brevis is relatively and absolutely larger in *Sturnus* than in the other genera.

In each genus, M. expansor secundariorum arises from the humero-ulnar pulley; in *Fregilupus*, *Sturnus*, and *Aplonis*, it inserts



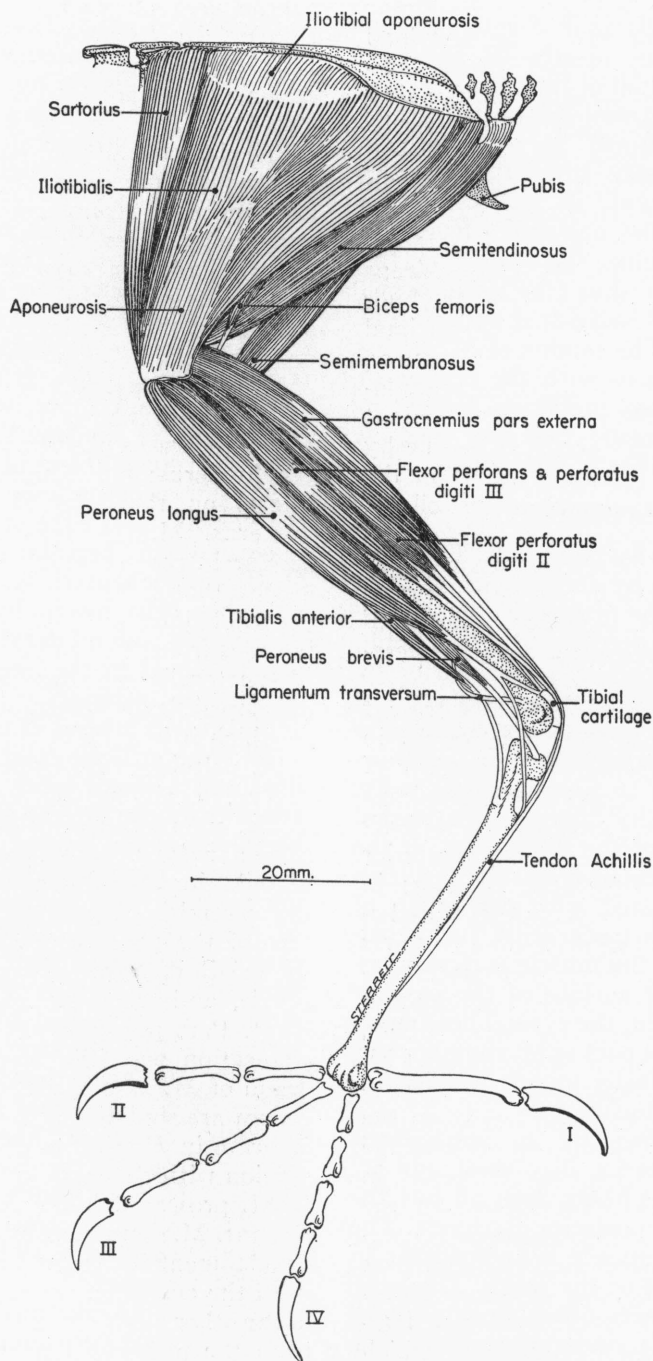


FIG. 8. *Fregilupus*. Superficial muscles of left leg, lateral view.

on the inner three secondaries (nos. 7, 8, and 9); in *Artamella*, it inserts on the inner four secondaries (nos. 7, 8, 9, and 10). Mm.

pronator superficialis and pronator profundus are similar in the four genera, though the two separate insertions of the profundus are not

so distinct in *Artamella* as in *Fregilupus* and *Sturnus*. *M. anconeus* inserts on approximately the proximal half of the ulna in *Fregilupus*, *Aplonis*, and *Artamella*; on the proximal two-thirds in *Sturnus*. *M. extensor pollicis longus* arises only from the ulna in *Fregilupus* and *Sturnus*; in *Artamella*, the muscle has two heads: one arises from the proximal end of the ulna, the other from the proximal end of the radius (the latter origin might be a matter of individual variation in this one specimen). The tendon of *M. extensor pollicis longus* fuses with the tendon of insertion of *M. extensor metacarpi radialis* in *Fregilupus* and *Sturnus*; the two tendons have separate insertions in *Artamella*.

#### "LEG" MYOLOGY

*M. sartorius* arises by two heads. The typical head takes origin by an aponeurosis from the neural spine of the fifth (last) dorsal vertebra and from the anterior end of the ilium. A second, deeper head arises primarily by fleshy fibers from the ventrolateral edge of the anterolateral end of the ilium, anterior to the origin of *M. iliotrochantericus anterior*. The two heads fuse to form a single belly, which inserts by fleshy fibers on the medial surface of the head of the tibiotarsus, at the base of the inner cnemial crest; the insertion is intimately associated with the origin of pars interna of *M. gastrocnemius*. Just proximal to its insertion, the muscle is closely applied to the anterior surface of the patellar ligament. At its origin, the typical head overlies the posteriormost part of *M. rhomboideus profundus*, i.e., the latter muscle lies deep to the origin of *M. sartorius*.

*M. iliotibialis* arises by an aponeurosis from the entire anterior iliac crest and by fleshy and tendinous fibers from all but the caudal 3 mm. of the posterior iliac crest. The central part of the muscle is aponeurotic in the distal two-thirds of the thigh. The belly is a thin sheet of fleshy fibers, both anterior and posterior to the aponeurotic portion. The tendon takes part in the formation of the patellar tendon (by tradition called the patellar ligament).

*M. iliotrochantericus posterior* is a well-developed muscle, which arises from the entire anterior iliac fossa, including an area dorsal to the acetabulum. The anterior half

of the belly is partly fused laterally with *M. iliotrochantericus anterior*. *M. iliotrochantericus posterior* inserts by a strong, wide (3.5 mm.) tendon along a curved line on the dorsolateral and anterolateral edge of the femur, beginning on the proximal end of the trochanter.

*M. iliotrochantericus anterior* has a fleshy and tendinous origin from the anterolateral tip of the anterior iliac crest and from the ventrolateral edge of the ilium for a distance of about 7 mm. The distal half of the muscle is flat and strap-like. It has a tendinous insertion (about 1.5 mm. wide) on the anterolateral edge of the femur, beginning 5.5 mm. from the proximal end of that bone.

*M. iliotrochantericus medius* arises from the ventrolateral edge of the ilium for a distance of 3 mm., beginning caudal to the origin of *M. iliotrochantericus anterior*. The small, strap-like belly inserts by a 1 mm.-wide tendon on the anterolateral edge of the femur, just proximal to the insertion of the *iliotrochantericus anterior*.

*M. gluteus medius et minimus* was absent.

*M. femorotibialis externus* has both a proximal and a distal head. The proximal head arises from the lateral surface of the femur, beginning at the level of insertion of the tendon of *M. iliotrochantericus medius* and lying between that tendon and the tendon of *M. ischiofemorialis*. Throughout most of its extent, this head is fused with the belly of *M. femorotibialis medius*. Proximally, the two muscles are separated by the tendons of insertion of *Mm. iliotrochanterici anterior et medius*. The distal head lies deep and posterior to the proximal head and arises by tendinous and fleshy fibers from the posterolateral surface of the distal half (15 mm.) of the femur. Both heads, but especially the proximal head, become tendinous near the knee and contribute to the formation of the patellar ligament.

*M. femorotibialis medius* arises by fleshy and tendinous (proximally) fibers from the anterior surface of the femur, beginning just distal to the trochanter and medial to the areas of insertion of the three *iliotrochanterici* muscles. The belly inserts on the proximal surface of the patella and contributes to the patellar ligament.

*M. femorotibialis internus* has two inde-

pendent bellies. The proximal ("typical") belly arises by fleshy fibers from the posteromedial surface of the femur, beginning at the level of insertion of *M. iliacus*, i.e., about 6 mm. from the proximal end of the bone. The belly is very narrow proximally, but increases in width distally. It inserts by a tendon on the posteromedial corner of the head of the tibiotarsus. The distal belly lies deep to the above-described belly and arises from the distal 11 mm. of the femur, including the medial surface of the medial femoral condyle. It inserts by a large, flat tendon on the tibiotarsus, just posterior to the insertion of the proximal belly.

*M. biceps femoris* arises by an aponeurosis from the posterior 10 mm. of the anterior iliac crest and by fleshy fibers from the anterior 7 mm. of the posterior iliac crest. The belly (about 25 mm. long) reaches the musculature of the posterior aspect of the crus. The strong, round tendon passes through a ligamentous biceps loop and inserts on the posterior surface of the fibular shaft about 11 mm. distal to the proximal end of that bone.

*M. ischiofemoralis* is a well-developed mass, arising primarily by fleshy fibers from nearly the entire lateral surface of the ischium, beginning at the posterior margin of the obturator foramen. The muscle inserts by a large (1.5 mm. wide), flat tendon on a ridge on the lateral surface of the femur, beginning 3 mm. from the proximal end of the bone.

Of *M. piriformis*, *pars caudofemoralis* arises by a strong, flat tendon (about 6 mm. long) from the anterolateral corner of the base of the pygostyle. The well-developed belly is about 25 mm. long and 5.5 mm. in maximum width. About 4 mm. caudal to the femur, the belly gives rise to a flat tendinous band, which is about 1 mm. wide at its insertion on the posterolateral surface of the femur, beginning 12 mm. distal to the proximal end of the bone. The deep head of *M. femorotibialis externus* begins at the level of insertion of the caudofemoralis tendon.

*Pars iliofemoralis* was absent.

*Mm. semitendinosus* and *accessorius semitendinosi*. The semitendinosus muscle is a relatively thin sheet, which arises by fleshy and tendinous fibers from the ventral surface of the projecting posterior iliac crest in its caudal 4 mm. and by an aponeurosis from

the ventrolateral edge of free caudal vertebrae numbers 2, 3, and 4 (though the posterior limit of the aponeurosis is indistinct owing to its fusion with the caudal fascia). An indistinct raphe separates the distal end of the belly from *M. accessorius semitendinosi*. On the deep surface of the belly, however, a 2.5 mm.-wide aponeurosis arises and passes distad to fuse with the upper part of the superficial surface of the tendon of *M. semimembranosus*; there is also a strong fascial connection with the belly of *pars media* of *M. gastrocnemius*. The accessory semitendinosus muscle is a relatively small fleshy mass, which inserts on the posterolateral surface of the femoral shaft for a distance of about 4 mm., beginning posterior to the attachment of the proximal arm of the biceps loop and extending to the lateral femoral condyle. Parts of the belly are intimately fused with *Mm. adductor longus et brevis* (*pars posterior*) and *gastrocnemius* (*pars media*).

*M. semimembranosus* is a flat band of fleshy fibers, about 4 mm. wide except at its origin from the ventrolateral surface of the caudal end of the ischium, where it is about 6 mm. in width. The origin lies dorsal to the large ischiopubic fenestra and ventral to the posteriormost origin of *M. ischiofemoralis*. When the belly of *M. semimembranosus* reaches the musculature of the crus, a flat, 4 mm.-wide aponeurosis forms; it inserts on the tibiotarsus, beginning about 7 mm. from the proximal end of the bone.

*M. iliacus* is well developed, with a fleshy belly about 6 mm. long and 1 mm. wide. It has a 3 mm.-wide fleshy origin from the ventral margin of the ilium, just caudal to the origin of *M. iliotrochantericus medius* and anterior to the acetabulum. It inserts primarily by fleshy fibers on the medial surface of the femur, beginning 6 mm. from the proximal end of the bone, i.e., at about the level of insertion of *M. iliotrochantericus* anterior on the lateral surface of the bone.

*M. ambiens* was absent bilaterally.

*M. obturator internus*, roughly triangular in shape, arises from the inner surface of the ischium and pubis. The strong tendon emerges from the obturator foramen and inserts on the lateral surface of the femur, less than 1 mm. from its proximal end.

*M. obturator externus* has two well-

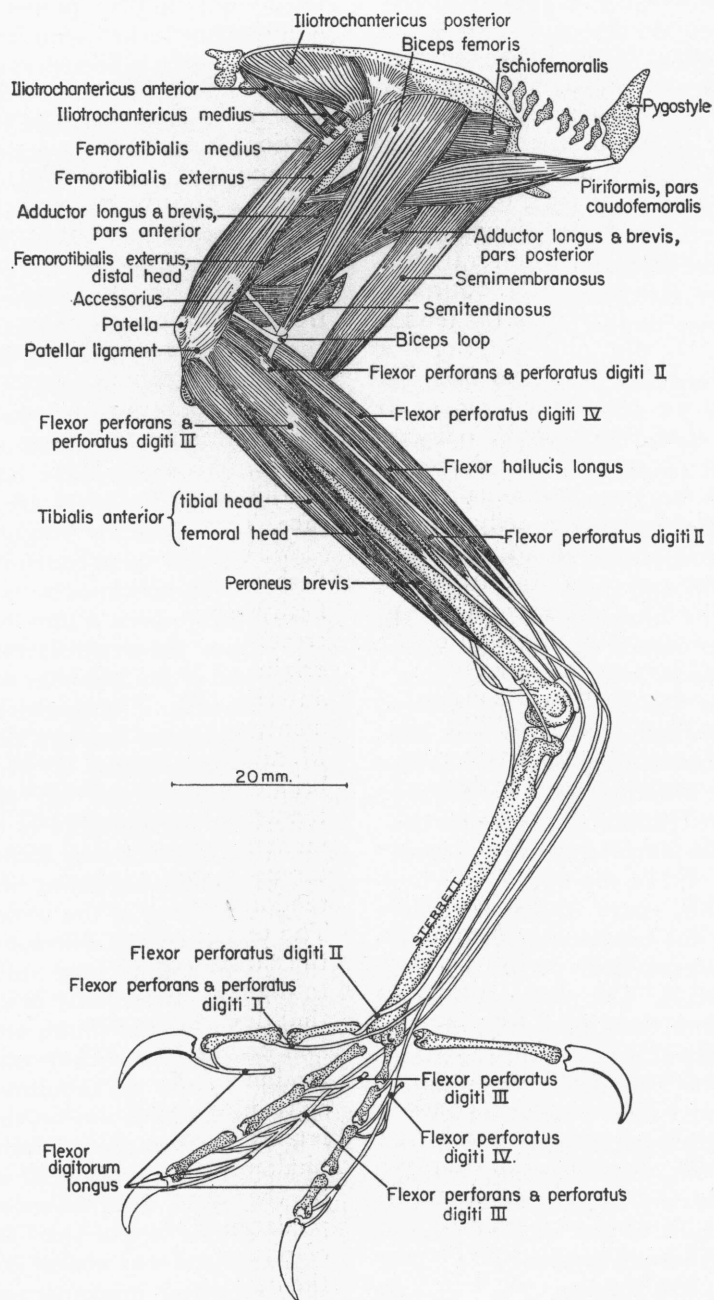


FIG. 9. *Fregilupus*. Lateral view of left leg to show a second layer of muscles. The following muscles have been wholly or partly removed: sartorius, iliotibialis, semitendinosus, gastrocnemius (pars externa), and peroneus longus.

developed heads, which are independent throughout. The dorsal and posterior head arises from the ventral bony margin of the ilio-ischiatic fenestra, lateral to the ilio-ischiatic membrane. The somewhat rounded belly passes forward and outward, superficial to the tendon of *M. obturator internus*, to insert, in part, by fleshy fibers on the tendon of the latter muscle and, in part, to insert by tendinous fibers on the femur, immediately anterior to the insertion of *M. obturator internus*. The belly and tendon of *M. obturator externus* thus overlap nearly all of the tendon of *M. obturator internus*. The anterior and ventral head arises by fleshy fibers from the anterior border of the obturator foramen. It is a large fleshy mass, which passes outward to insert on the posterior surface of the femur over an area 3 mm. long, beginning at the proximal end of the bone. The belly and insertion lie deep to the tendon of insertion of *M. obturator internus* and are not visible in a lateral view. Hence *M. obturator internus* inserts between the areas of insertion of the two heads of *M. obturator externus*.

*M. adductor longus et brevis* consists of two mostly independent, flat, band-like muscles. Pars anterior arises by fleshy fibers laterally but by an aponeurosis on the deep surface from the ventrolateral edge of the ischium for a distance of 8 mm., beginning at the posterior margin of the obturator foramen. It inserts by fleshy fibers on the posterolateral surface of the femur, beginning medial to, and on the level of, the insertion of *M. piriformis* pars caudofemoralis (i.e., about 12 mm. from the proximal end of the femur), and extending distad to the lateral condyle. Distally, the area of insertion curves mesiad just proximal to the insertion of the accessory semitendinosus. Pars posterior arises by an aponeurosis for a distance of 6 mm. from the ventrolateral edge of the ischium, immediately caudal to the origin of pars anterior; the two muscles are, in fact, partially fused at the origin. Posterior to the knee, the belly, in part, inserts on a raphe shared with pars media of *M. gastrocnemius* and, in part, inserts on the posteromedial face of the medial femoral condyle, just distal to the insertion of pars anterior. It is not possible in a lateral approach to separate the insertion of pars posterior from the origin of pars media of *M. gastrocnemius*.

*M. tibialis anterior* has a well-developed belly about 45 mm. in total length, extending almost to the ligamentum transversum, near the distal end of the tibiotarsus. The belly is formed by the fusion of two heads about half-way down the crus. The single tendon of insertion passes deep to the ligamentum transversum, but superficial to the tendon of *M. extensor digitorum longus*, and inserts on the anterior surface of the tarsometatarsus about 5 mm. from the proximal articular surface of the bone. The tibial head has a small origin from the inner and outer cnemial crests and the rotular crest of the tibiotarsus. The muscle is broad (8 mm.) at its origin, but tapers to the tendon of insertion. The femoral head arises by a large tendon from the anterior surface of the distal end of the lateral condyle, at the proximal margin of the articular surface. This head is about 42 mm. in length.

*M. extensor digitorum longus* has a small fleshy belly about 30 mm. in length. It has a fleshy origin from the inner and outer cnemial crests and the rotular crest, inferior to the origin of *Mm. peroneus longus* and *tibialis anterior*. The tendon passes under the ligamentum transversum, deep to the tendon of *M. tibialis anterior*, and then under a bony bridge just above the condyles of the tibiotarsus. The tendon is held in place by a ligament on the proximal end of the tarsometatarsus and then passes distad medial to the tendon of insertion of *M. tibialis anterior*. The tendon trifurcates near the distal end of the tarsometatarsus. A single tendon is sent to digit II; it passes along the dorsal side of that digit and inserts on the base of phalanx 2 and on the base of the ungual phalanx. The tendon to digit III is more complicated. It splits into a medial and a lateral branch. The lateral branch bifurcates again, opposite phalanx 2: the lateral slip inserts on the base of the third phalanx and on the ungual phalanx; the medial slip inserts on the base of phalanx 3. The medial branch inserts on the base of the ungual phalanx, but also gives off slips to insert on the bases of phalanges 2 and 3. A single, small tendon passes along the dorsal surface of digit IV. This tendon bifurcates at about the middle of the second phalanx. The lateral branch continues distad to insert on the base of the ungual phalanx. The medial branch gives off a slip which inserts on the proximal end of phalanx 3, but the

main tendon inserts on the proximal end of phalanx 4. An automatic extensor of the claw is present on digits II and IV; it arises from the dorsal surface of the penultimate phalanx and inserts on the dorsal surface of the ungual phalanx, proximal to the insertion of the tendons of *M. extensor digitorum longus*.

*M. peroneus longus* is a large muscle, covering all the other muscles on the antero-lateral aspect of the proximal two-thirds of the crus. It arises by fleshy and tendinous fibers from the inner and outer cnemial crests and the rotular crest at the proximal end of the tibiotarsus and by a strong aponeurosis, which is attached to the anteroventral tip of the inner cnemial crest, deep to the origin of pars interna of *M. gastrocnemius*. The belly (40 mm. in length) extends two-thirds of the way down the crus and gives rise to a strong tendon. The tendon bifurcates 9 mm. from the distal end of the tibiotarsus. The shorter branch continues distad in the same direction as the common tendon and inserts into the proximolateral corner of the tibial cartilage. The longer branch crosses the intertarsal joint and inserts on the tendon of *M. flexor perforatus digiti III*, about 7 mm. inferior to the proximal end of the tarsometatarsus.

*M. peroneus brevis* has a fleshy and tendinous origin from the anterior surface of the fibula, beginning a short distance proximal to the biceps insertion, and from the shaft of the tibiotarsus, anterior to the fibula, for a total distance of about 28 mm. A short distance (6.5 mm.) from the distal end of the tibiotarsus, the large, round tendon passes through a bony groove and is held in place by a ligament. The tendon then passes deep to the long branch of the peroneus longus tendon and inserts on the posterolateral corner of the head of the tarsometatarsus, just proximal to the base of the hypotarsus.

*M. gastrocnemius* arises by the usual three heads. Pars externa has a belly about 32 mm. long, extending over halfway down the crus. It has a tendinous origin from the patellar ligament and associated fascia and ligaments of the knee-joint capsule and a mixed fleshy and tendinous origin from the posterolateral surface of the lateral femoral condyle and the shaft of the femur just proximal to the condyle. The latter origin is intimately associated with the distal arm of the biceps loop, and, in part, is fused with its superficial

surface. The biceps tendon enters the musculature of the crus by passing between pars externa and pars media. Pars media, a flat, band-shaped muscle, about 17 mm. long, arises by fleshy fibers from the popliteal fossa of the femur. The origin is, in part, fused with the distal fibers of insertion of the accessory semitendinosus muscle and with those of pars posterior of *M. adductor longus et brevis*. There is also a strong fascial connection between pars media and *M. semitendinosus*. Pars interna is separated from pars media by the tendon of insertion of *M. semimembranosus*. The belly (about 35 mm. long) arises from the entire medial surface of the large inner cnemial crest. A small part arises from the anterior edge of that crest and wraps around the anterior surface of the crus in the region of the inner cnemial crest and can be seen from a lateral view. The aponeurosis-like tendons of the three parts of *M. gastrocnemius* fuse to form a common tendon Achilles, which inserts on the posterior surface of the hypotarsus and on the posterolateral and posteromedial edges of the tarsometatarsus throughout most of its length, though the insertion is stronger in the proximal third of that bone. The tendon forms a complete investment for the flexor tendons on the posterior surface of the tarsometatarsus.

*M. plantaris* is a small muscle with a belly about 10 mm. long and 3 mm. in maximum width where it arises from the posteromedial corner of the head of the tibiotarsus. The belly tapers to a small, flat tendon, which inserts on the proximomedial corner of the tibial cartilage.

*M. popliteus* was absent bilaterally.

*M. flexor perforatus digiti II* has a spindle-shaped belly about 25 mm. long. It arises by a strong tendon (shared with *M. flexor hallucis longus*) from the posterolateral face of the lateral femoral condyle. The tendon of origin is fused with the capsule of the knee joint and the distal and third arms of the biceps loop and thus has an indirect origin from the head of the fibula. The belly passes distad lateral to the biceps tendon, and inferior to it the belly is fused with the anterior surface of *M. flexor hallucis longus*. The tendon enters the lateral side of the tibial cartilage but crosses to its medial side, deep to all tendons except for those of *Mm. flexor digitorum longus* and *flexor hallucis longus*.



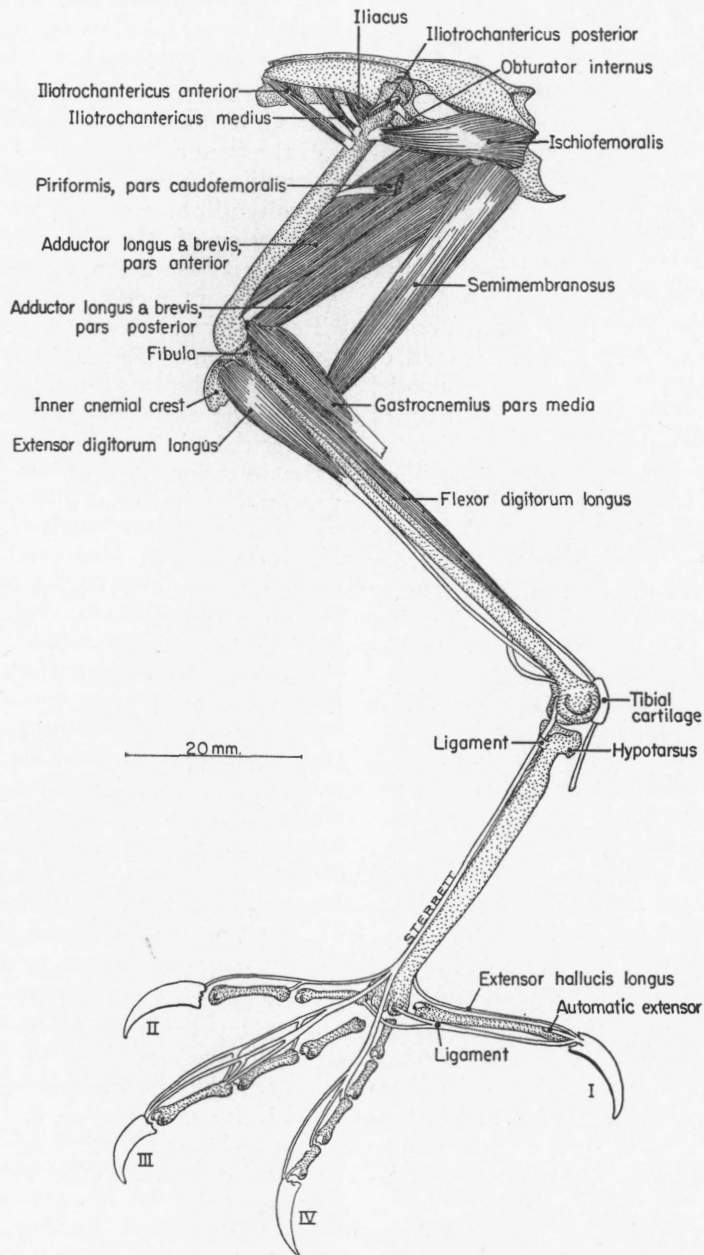


FIG. 10. *Fregilupus*. Lateral view of left leg to show a third layer of muscles.

The tendon then passes through its own bony canal, deep to that of *M. flexor perforans et perforatus digiti II*, on the medial side of the hypotarsus, and thence distad along the posteromedial aspect of the tarsometatarsus. The tendon passes around a fibrous pulley in the

intertrochlear space and inserts on the medial side of the base of the proximal phalanx, digit II. The tendon does not ensheath either of the deep flexor tendons.

*M. flexor perforatus digiti III* (belly about 25 mm. long) lies on the posteromedial aspect

of the crus immediately deep to *M. gastrocnemius*. It arises in the popliteal fossa of the femur from the common tendon shared with *Mm. flexor perforatus digiti IV* and *flexor hallucis longus*. The fleshy fibers form about 6 mm. distal to the head of the tibiotarsus, and the belly is fused with the deep surface of *M. flexor hallucis longus*. The tendon passes through the middle of three compartments on the posterior (superficial) surface of the tibial cartilage and partly envelops the more superficially located tendon of *M. flexor perforatus digiti IV*. These two tendons retain this relationship as they pass through the most superficial bony canal on the lateral side of the hypotarsus. At about midlength of the tarsometatarsus, the tendon of the *flexor perforatus digiti III* passes diagonally mesiad, deep to the tendon of *M. flexor perforans et perforatus digiti III*, but at the distal end of that bone the tendon of the latter muscle passes deep to the tendon of the *flexor perforatus digiti III*. The tendon of the latter muscle expands and ensheathes both of the deep flexor tendons (*flexor perforans et perforatus digiti III* and *flexor digitorum longus*) and then splits to permit their passage distad. The two slips of the tendon insert on each side of the base of the proximal phalanx and on the joint capsule at the distal end of that phalanx. There is no vinculum between the tendons of *Mm. flexor perforatus digiti III* and *flexor perforans et perforatus digiti III*. The tendons of these two muscles are about five times as large (diameter) as the similar tendons to digit II. The *peroneus longus* tendon inserts on the tendon of *M. flexor perforatus digiti III* about 7 mm. inferior to the proximal surface of the tarsometatarsus.

*M. flexor perforatus digiti IV* has a semi-tendinous origin from the intercondylar area (popliteal fossa) of the femur, just distal to the insertion of the accessory semitendinosus muscle; the origin is shared with *Mm. flexor perforatus digiti III* and *flexor hallucis longus*. The belly extends about two-thirds of the length of the crus. The tendon passes through the superficial surface of the tibial cartilage, lateral to the other tendons in that layer, and is in contact with the subjacent tendon of *M. flexor perforatus digiti III*. The two tendons pass through the most superficial (posterior) bony compartment on the lateral

side of the hypotarsus. Opposite the base of the proximal phalanx of digit IV, the tendon completely ensheathes the tendon of *M. flexor digitorum longus*. Just distal to this area, a strong branch is given off and inserts on the lateral side of the base of the second phalanx, but the main tendon continues distad to insert on the plantar surface of the fibrocartilaginous pad between the second and third phalanges. The tendon of the *flexor digitorum longus* muscle emerges from its ensheathement at about midlength of the proximal phalanx.

*M. flexor perforans et perforatus digiti II* has a small, flat belly about 18 mm. long and less than 2 mm. in maximum width. It has a fleshy and tendinous origin from the posterolateral edge of the femur, between the condyle and the attachment of the distal arm of the biceps loop. This origin is immediately posterior and deep to the origin of *M. flexor perforans et perforatus digiti III*. The muscle is fused on its deep surface with the tendon of origin of *M. flexor perforatus digiti II*. The belly and tendon are concealed by *pars externa* of *M. gastrocnemius*. The tendon passes through the most medial of three compartments in the superficial surface of the tibial cartilage and then through the middle one of three bony canals on the medial side of the hypotarsus. The tendon does not perforate the tendon of *M. flexor perforatus digiti II*, nor does it ensheath the branch of *M. flexor digitorum longus* to digit II. The tendon of *M. flexor perforans et perforatus digiti II* passes through a large fibrocartilaginous mass in the intertrochlear space and inserts on the medial corner of the base of phalanx 2, digit II.

*M. flexor perforans et perforatus digiti III* has a belly about 30 mm. long, and it is visible just posterior to *M. peroneus longus* in a superficial view of the crus. It arises by tendinous and fleshy fibers from a small area on the lateral femoral condyle primarily, but has some origin from the head of the fibula. The belly is fused anteriorly with the proximal part of the *peroneus longus* muscle and posteriorly with *flexor perforans et perforatus digiti II*. The tendon passes through the middle compartment in the superficial surface of the tibial cartilage and through the most superficial bony canal on the medial side of

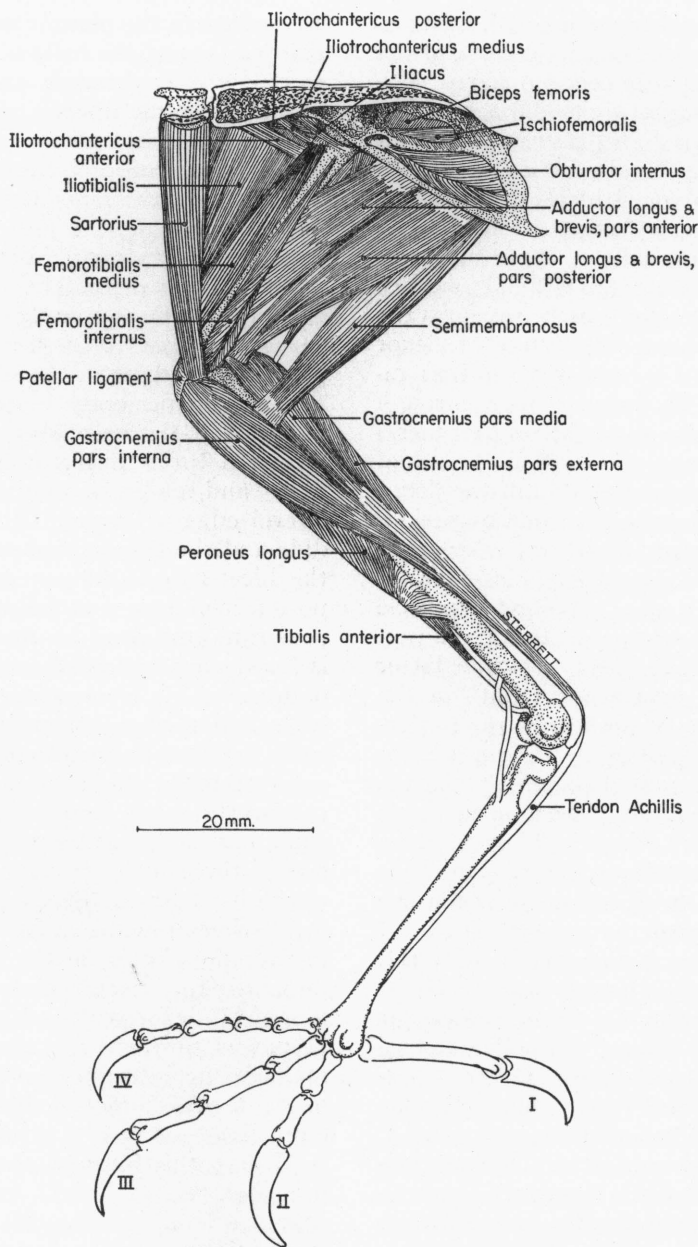


FIG. 11. *Fregilupus*. Medial view of muscles of right leg.

the hypotarsus. At the distal end of the tarso-metatarsus, the tendon passes deep to and is ensheathed by the tendon of *M. flexor perforatus digiti III*. The tendon expands and ensheathes the tendon of *M. flexor digitorum longus*. The combined mass perforates the tendon of *M. flexor perforatus digiti III*. The tendon of *M. flexor perforans et perforatus*

digiti III then splits to permit passage of the longus tendon and then inserts on the medial and lateral sides of the base of the fibrocartilaginous pad between the second and third phalanges of digit III.

*M. flexor digitorum longus* arises from the posterior surface of the tibiotarsus and the posterior face of the fibula in about their

proximal half; there is no femoral head. The belly, about 40 mm. long, extends about three-fourths of the way down the crus. The tendon passes through the medial side of the deep surface of the tibial cartilage and through the deepest bony canal on the medial side of the hypotarsus, and then diagonally downward and laterad, deep to the tendon of *M. flexor hallucis longus*. The tendon is calcified in about the middle half of the tarso-metatarsus. The tendon trifurcates near the distal end of that bone. The branch to digit II is not ensheathed by either *M. flexor perforatus digiti II* or *M. flexor perforans et perforatus digiti II*, but passes distad to insert on the base of the unguis phalanx. A vinculum is sent to the distal end of phalanx 2. The branch to digit III perforates the tendons of *Mm. flexor perforatus digiti III* and *flexor perforans et perforatus digiti III* and inserts on the base of the unguis phalanx. Two vinculae arise from the deep surface of the tendon and insert, respectively, on the fibrous pads between phalanges 2 and 3 and 3 and 4. The branch to digit IV perforates the tendon of *M. flexor perforatus digiti IV* and inserts on the base of the unguis phalanx. A single vinculum is given off and inserts on the distal end of phalanx 4.

*M. flexor hallucis longus* has two separate heads. The medial head arises by tendinous and fleshy fibers from the popliteal fossa of the femur. This head passes distad medial to the biceps tendon. The lateral head arises by a tendon, shared with *M. flexor perforatus digiti II*, from the lateral femoral condyle. This head passes distad lateral to the biceps tendon. The two heads fuse a short distance inferior to the insertion of the biceps tendon. The belly is about 42 mm. in total length. The tendon passes through the deep surface of the lateral side of the tibial cartilage and through the deepest (anterior) bony canal on the lateral side of the hypotarsus. Just inferior to that structure, the tendon crosses superficial to the tendon of *M. flexor digitorum longus* to the medial side of the tarsometatarsus. The two tendons are not connected by a vinculum. The very large tendon (not calcified) of the flexor hallucis longus muscle passes distad through a groove on the proximal end of metatarsal I, but then winds around that bone to pass over its distal articu-

lar surface to the plantar surface of the proximal phalanx of the hallux. In this course, the tendon passes through, and is held in place by, a very large fibrous pad. The tendon inserts on the base of the unguis phalanx. A strong vinculum, given off the deep surface of the tendon, inserts on the distal end of the proximal phalanx.

*M. flexor hallucis brevis* was absent. I found a sheet of fascia located in the distal third of the tarsometatarsus, but there were no muscle fibers present (determined microscopically). Lying in the intertrochlear space between metatarsals I and II, however, I found a minute, hair-like tendon, which ended on the massive fibrous pulley, at the base of the hallux, which transmits the tendon of *M. flexor hallucis longus*. This fibrous mass replaces the enlarged tendon of *M. flexor hallucis brevis* in those genera that possess this muscle. In some non-passerine genera, however, the tendon of *M. flexor hallucis longus* is not ensheathed by the tendon of the flexor hallucis brevis, even when the latter muscle is present and well developed.

*M. extensor hallucis longus* has a poorly developed belly about 20 mm. long but less than 0.5 mm. in maximum width. It arises from the anteromedial surface of the tarsometatarsus, medial to the tendon of *M. extensor digitorum longus*, and beginning at the proximal end of the bone. The minute, hair-like tendon inserts on the base of the unguis phalanx. The automatic extensor of the claw is unusually large. It arises from the dorsal surface, near the distal end, of the proximal phalanx; it inserts on the base of the unguis phalanx. The small tendon of *M. extensor hallucis longus* inserts into the automatic extensor at the base of the unguis phalanx (see also Hudson, 1937, p. 51 and fig. 17). A strong ligament (fig. 10) extends from the wing of the trochlea for digit IV and from the proximal phalanx of digit II to the unguis phalanx of the hallux. This ligament occupies the position of an automatic flexor found in some birds, but in *Fregilupus* it attaches distally to the automatic extensor. Hence it may serve to compensate for the weak extensor hallucis longus and for the large flexor hallucis longus muscles.

*M. abductor digiti IV* is a rudimentary muscle, consisting of a thin layer of striated

muscle fibers in a sheet of fascia about 2 mm. long, lying at the distal end of the tarsometatarsus. In order to demonstrate that muscle fibers were present, however, it was necessary to use the staining technique described by Berger (1956, p. 140). I could not find any definite tendon of insertion.

The following "short toe" muscles are absent in *Fregilupus*: extensor proprius digiti III, extensor brevis digiti III (reported in only a few ratites and may represent a second head of the preceding muscle), extensor brevis digiti IV, abductor digiti II, adductor digiti II, lumbricalis, and adductor digiti IV (thus far reported in only a few non-passerine genera). Some of these may be represented by a rudimentary or vestigial belly such as described for M. abductor digiti IV above, in which gross dissection does not enable one to determine whether or not muscle fibers are actually present.

#### COMPARATIVE MYOLOGY OF THE "LEG"

The following muscles are absent in *Fregilupus*, *Sturnus*, *Aplonis*, and *Artamella*: gluteus medius et minimus, ambiens, pars iliofemoralis of M. piriformis, popliteus, extensor proprius digiti III, extensor brevis digiti III, extensor brevis digiti IV, abductor digiti II, adductor digiti II, lumbricalis, and adductor digiti IV. M. abductor digiti IV is rudimentary in each genus. The muscle formula for each genus is ACXY. There is no vinculum between the tendons of Mm. flexor perforatus digiti III and flexor perforans et perforatus digiti III, nor is there a vinculum connecting the tendons of Mm. flexor digitorum longus and flexor hallucis longus.

The following comments pertain to all four genera; for details one may refer to the descriptions of *Fregilupus*. M. femorotibialis externus has both a proximal and a distal head. M. semitendinosus arises from the caudal part of the posterior iliac crest and from three free caudal vertebrae. M. obturator externus has two separate heads. The tendon of M. flexor perforatus digiti II is not perforated by either of the deep flexor tendons, but the tendon of M. flexor perforatus digiti III is perforated by both of the deep flexor tendons. The tendon of M. flexor perforatus digiti IV is perforated by the tendon of M. flexor digitorum longus. The tendon of

M. flexor perforatus digiti IV has a double insertion: the larger part of the tendon inserts on the fibrocartilaginous pad between phalanges 2 and 3, digit IV; the smaller part inserts on the lateral side of the base of the proximal phalanx in *Fregilupus*, but on the pad between phalanges 1 and 2 in *Sturnus* and *Artamella*. The tendon of the flexor perforans et perforatus digiti II does not perforate the tendon of M. flexor perforatus digiti II, nor is the tendon of the former muscle perforated by the tendon to digit II of M. flexor digitorum longus. The tendon of M. flexor perforans et perforatus digiti III perforates the tendon of the flexor perforatus digiti III and itself is perforated by the tendon of the flexor digitorum longus. M. flexor hallucis longus has two heads, both of which arise from the femur; one head passes distad medial to the biceps tendon, the other lateral to the biceps tendon. A very large vinculum is given off from the deep surface of the tendon of M. flexor hallucis longus; it inserts on the ungual phalanx.

Hudson (1937, pp. 47, 76) described two heads (one from the femur, the other from the tibiotarsus) of origin for M. flexor digitorum longus in *Tyrannus* and *Corvus*, and stated that "this condition is apparently peculiar to the Passeriformes." I did not, however, find a femoral head of this muscle in the genera reported on in the present paper. The tendon of M. flexor digitorum longus was calcified in its course down the tarsometatarsus in *Fregilupus* and *Artamella*, but not in *Sturnus* and *Aplonis*.

The muscles of the pelvic appendage differ among the four genera as discussed below. M. sartorius has two separate heads in *Fregilupus*, one head in the other genera. M. iliotibialis is similar in the four genera, but in *Artamella*, the posterior fleshy part is thicker than the anterior part; in the other genera, the two parts have about the same thickness. M. iliotrochantericus anterior is relatively and absolutely largest in *Sturnus*, in which genus it overlaps the insertion of M. iliotrochantericus medius. In *Artamella*, these two muscles are more like those of *Sturnus* than those of *Fregilupus*. In *Aplonis*, Mm. iliotrochantericus anterior and medius are fused throughout much of their extent. M. femorotibialis internus has two independ-

ent bellies in *Fregilupus*, a single belly in the other genera. The origin begins at the level of insertion of *M. iliacus* in *Fregilupus* and *Sturnus*, but distal to that area in *Artamella* and *Aplonis*. *M. femorotibialis internus* is unusually small proximally in *Aplonis*. *M. biceps femoris* has a relatively large aponeurotic origin from the caudal part of the anterior iliac crest in *Fregilupus*, *Sturnus*, and *Aplonis*, but only a small aponeurotic origin there in *Artamella*. Pars caudofemoralis of *M. piriiformis* has a more proximal insertion in *Artamella* than in the other genera. *M. semi-membranosus* has a well-developed belly in *Sturnus*; it is thin and sheet-like in *Fregilupus* and *Artamella*. *M. obturator internus* is roughly triangular in shape in *Fregilupus* and in *Artamella*; it is more oval-shaped or rectangular in *Sturnus* and *Aplonis*. The origin of *M. peroneus longus* is more extensive in *Fregilupus* and *Sturnus* than in *Artamella*; there is a very strong tendon of insertion in *Fregilupus*, but a small one in *Sturnus* and *Artamella*. The tendon of *M. peroneus brevis*, on the other hand, is well developed in each genus; however, the peroneus longus muscle is much larger than the peroneus brevis in each genus. *M. extensor digitorum longus* is poorly developed in *Fregilupus* and *Sturnus*, somewhat better developed (though not strong) in *Aplonis* and *Artamella*. The tendon of *M. extensor digitorum longus* is held in place by a ligament on the proximal end of the tarsometatarsus in *Fregilupus*, *Sturnus*, and *Aplonis*, but the tendon passes under a bony bridge in *Artamella* (this small point needs to be checked throughout the Passeriformes; see Hudson, 1937, p. 32).

*M. flexor hallucis brevis* is absent in *Fregilupus*, *Sturnus*, and *Aplonis*, but it is present in *Artamella*. In the last-named genus, this muscle arises from the proximal end of the tarsometatarsus; the belly is 10 mm. long and about 2 mm. in maximum width. The belly tapers to the small, long tendon, which passes distad with the tendon of *M. flexor hallucis longus* and through the interval between metatarsals I and II and then winds around the distal articular surface of metatarsal I. At this point, the tendon of flexor hallucis brevis expands into, or inserts on, a very large fibrous pad, which completely ensheathes the tendon of *M. flexor hallucis*

longus; the pad is attached to most of the basal surface of the proximal phalanx of the hallux.

### JAW MUSCLES

At least two authors have mentioned the relative development of the digastric muscle (= *M. depressor mandibulae*) in different birds. Garrod (1872, p. 646) compared its development in *Heteralocha* [= *Neomorpha*] *gouldi* with certain icterine, corvine, and sturnine genera. That his analysis, based on an

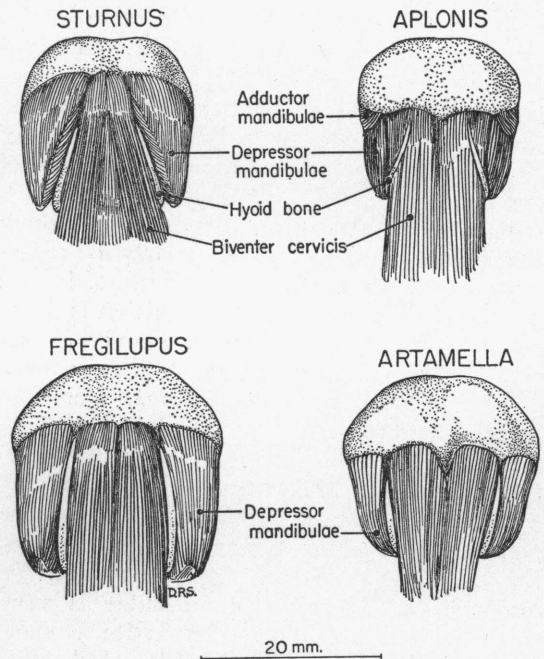


FIG. 12. Posterior view of heads of *Fregilupus*, *Sturnus*, *Aplonis*, and *Artamella* to show relative development of *M. depressor mandibulae* (= digastricus).

examination of the skulls alone, was accurate may be judged by a comparison of the illustrations of *Sturnella* and *Molothrus* in Beecher (1951b, figs. 4, 5). Lowe (1938, p. 262) also discussed the relative development of the digastric muscle in his attempt to determine the systematic position of *Picathartes*. This muscle is unusually well developed in *Sturnus vulgaris* and some other starlings (fig. 12), but in still other sturnine genera the digastric muscle is relatively poorly developed, approaching the "corvine condition." There



can be no doubt that the development of this muscle is directly related to feeding habits, as Lowe (1938, p. 263) correctly stated: "The great development of this muscle is evidently correlated with a long, slender, and more or less pointed bill which is designed for digging into the ground." The relative development of *M. depressor mandibulae* alone, therefore, would be a poor criterion in an attempt to place a genus into one family or another.

Beecher (1953, fig. 4) illustrated the jaw musculature of *Sturnus vulgaris*. Although it is impossible to illustrate all the interrelationships of the various parts of certain of the jaw muscle complexes (e.g., *M. adductor mandibulae*, Beecher's M7), my dissections confirm the general relationships of all the jaw muscles as shown in Beecher's figure of *Sturnus*. Two points, perhaps, are worthy of comment here. *M. depressor mandibulae* is tripartite (as shown by Beecher), although the boundary between the parts is represented by little more than a plane of fascia; nevertheless, the tripartite condition is obvious as soon as one removes the covering fascia. The hypertrophy of *M. depressor mandibulae* in *Sturnus* is reflected in the increased length of the processus retroarticularis of the mandible. The second noteworthy feature is the large size of *M. protractor quadrati*.

*Mm. depressor mandibulae* and *protractor quadrati* in *Aplonis tabuensis* exhibit an entirely different pattern from that seen in *Sturnus*. *M. depressor mandibulae* is very small (fig. 12), and it is not tripartite. In fact, a lateral view of the jaw muscles of *Aplonis* would be nearly identical to Beecher's (1953, fig. 11) illustration of *Lanius ludovicianus*. Further, *M. protractor quadrati* in *Aplonis* is a small, inconspicuous muscle unlike that in *Sturnus*, in which genus the muscle is a very large, conspicuous mass on the posteroventral wall of the orbit. Beecher (1953, p. 284) dissected several species of *Aplonis*, but not *tabuensis*. Nevertheless, I see little in the pattern of the jaw muscles, nostril (operculate or non-operculate), palate (vaulted or flat), or bill—all characters used by Beecher—that would indicate that *Sturnus* and *Aplonis* belong in the same family. I suggest, therefore, that the relative development of these muscles is not indicative of closeness of relationship but rather of feeding habits.

Beecher (1953, p. 298) also dissected representatives of the Vanga Shrikes but not the genus *Artamella*. I found that the pattern of all the jaw muscles in *Artamella* seems to be identical to the pattern in *Shetba rufa* (Beecher, 1953, fig. 11).

*M. depressor mandibulae* in *Fregilupus* (fig. 12) is well developed, but it is reduced from that in *Sturnus*, and the muscle is not tripartite. Aside from these minor differences, however, the remaining jaw muscles are nearly identical in pattern to those found in *Sturnus*. At the same time, it would be very difficult, if possible at all, in a lateral view of *Mm. depressor mandibulae* (M1) and *adductor mandibulae pars externus superficialis* (M7a), to distinguish between illustrations of these muscles in *Fregilupus* from those in *Aethorhynchus lafresnayei* (Aegithinidae; Beecher, 1953, fig. 12).

#### TRACHEAL MUSCLES

In my effort to describe and illustrate the appendicular myology of *Fregilupus* and to preserve the skeleton intact, I found it impossible also to determine the relationships of all the muscles associated with the trachea. Further, these muscles are small, partial fusion is common, and frequently they are not well preserved, so that one needs a series of syringes in order to be sure that all relationships have been determined accurately. Consequently, the descriptions presented here should be checked on the other extant specimen of *Fregilupus*, preferably by some other investigator.

The intrinsic tracheal muscles, all of which occur in pairs, arise and insert on some part of the tracheal system. Following is a description of these muscles in *Fregilupus*. For ease of reference, I have adopted the terminology used by Miskimen (1951), who followed Shufeldt (compare with Köditz, 1925, and Mayr, 1931).

*M. tracheolateralis* arises from the ventrolateral surface of the cricoid cartilage. It is a 2 mm.-wide, thin band of fleshy fibers which passes caudad along the lateral surface of the trachea. At about the level of the third or fourth tracheal ring (no. 1 being the caudalmost ring; see Miskimen, 1951, fig. 1), the muscle divides into a large anterior fasciculus (= *M. bronchotrachealis anticus*) and a

much smaller posterior fasciculus (=M. bronchotrachealis posticus). Thus M. tracheolateralis has a double insertion, but each portion of the muscle has been given a separate name.

M. bronchotrachealis anticus passes caudad along the lateral surface of M. bronchialis anticus and overlaps part of that muscle, especially near its insertion. The bronchotrachealis anticus inserts primarily on the ventral end of the first intermediary bar (Miskimen, 1951, fig. 1), but also has some fascial connection with the adjacent area on the second bar.

M. bronchotrachealis posticus inserts on the dorsal end of the second intermediary bar. This muscle is much smaller than the preceding muscle.

M. bronchotrachealis brevis is a thin sheet of muscle located on the dorsal surface of the caudal four tracheal rings. It arises by semitendinous fibers primarily from the fourth tracheal ring. It seems to insert on the dorsal ends of both the second and the third intermediary bars.

M. bronchialis anticus is well developed. It arises from the ventral surface of the first tracheal ring. Its fibers pass caudad to insert on the ventral end of the second intermediary bar.

M. bronchialis posticus arises from the lateral surface of the first tracheal ring, immediately caudal to the insertion of M. sternotrachealis. It inserts on the dorsal ends of the second and third intermediary bars, just lateral to the insertion of M. bronchotrachealis brevis, and on the caudal end of the dorsal surface of the "drum" (Miskimen, 1951, fig. 1).

The extrinsic tracheal muscles have one attachment to a non-tracheal structure; this attachment differs considerably in the several groups of birds. Of these muscles I am able to report very little; others may be present.

M. sternotrachealis presumably arises from the anterior edge of the sternum. It inserts on the lateral surface of the first or the first and second tracheal rings, immediately cephalad to the origin of M. bronchialis posticus. It is a very small band of muscle (as illustrated by Shufeldt, 1890, fig. 14).

M. ypsilotrachealis (=cleidotrachealis).

The anterior portion of this muscle was destroyed in the working out of other relationships. Apparently the muscles from the two sides fuse at their insertion on the anterior end of the carina of the sternum; this seems to be an unusual area of insertion for this muscle.

A comparison of the descriptions given above with those by Miskimen (1951, pp. 498–500) for *Sturnus vulgaris*, the Catbird (*Dumetella carolinensis*), and the Crow (*Corvus brachyrhynchos*) reveals that some of the muscles do not have so discrete and limited an origin or insertion in *Fregilupus*, i.e., they arise or insert on the adjacent areas of two rings or two intermediary bars. However, I found a similar situation in *Sturnus*; unfortunately, it was not possible to determine relationships of what remained of these poorly preserved muscles in the specimens of *Aplonis* and *Artamella*. Both Mm. sternotrachealis and bronchotrachealis posticus are much smaller in *Fregilupus* than in the crow (Miskimen, 1951, figs. 2 and 3). Nevertheless, Miskimen's figures for the tracheal muscles in the Crow would serve almost equally well for the same muscles in *Fregilupus*. The pattern is the same in *Fregilupus* and in *Sturnus*, but all the muscles seem to be better developed in *Sturnus*, and Mm. bronchotrachealis anticus and posticus are nearly equal in size. M. R. Miller (1941, pp. 586–587) also stated that the muscles of the syrinx of *Fregilupus varius* "revealed an almost exact similarity in form" to those of *Sturnus vulgaris*.

## VISCERA

The American Museum specimen of *Fregilupus* was a male: the right testis measured 1.0 by 2.5 mm.; the left testis, 1.5 by 3.0. The right lobe of the liver was approximately three times as large as the left lobe. There was a large, saccular gall bladder, which measured about 15 mm. in length and 7 mm. in diameter. The stomach was empty. The spleen was 10 mm. long and 2.5 mm. in maximum diameter; it was a cylindrical mass, drawn to a point at each end. The pancreas, about 33 mm. long, apparently is a single structure, i.e., it did not appear to be bilobed. There was a pair of caecae. Each was 5 mm. in length and about 1.5 mm. in diameter at

its attachment to the side of the intestine about 20 mm. anterior to the anal opening of the tube.

An interesting fact is that the stomach and

esophagus of *Artamella* contained a chameleon (*Chamaeleo*) approximately 80 mm. in length, plus some insect fragments (primarily Coleoptera).

## DISCUSSION

I THINK THAT THE DATA presented above, as well as those in recent papers on passerine anatomy by other authors, clearly demonstrate that the anatomy of the passerines is not so uniform as commonly believed. To be sure, there is a close similarity, but not an identical pattern, in the formulas or pattern of the muscles of both appendages. This does not obviate the necessity for investigating this musculature (e.g., see the excellent analysis by Stallcup, 1954, pp. 175–185). The analysis of the differences found constitutes an exceedingly difficult problem. One must have, as Beecher (1951a, p. 274) stated, "sound criteria for clearly distinguishing between adaptation and phylogeny." When one begins to analyze small differences in structure or relationships, however, one begins to think of the possibility expressed by Tordoff (1954, p. 19) who said: "As the number of similarities which must be assigned to 'adaptive convergence' increases, however, one wonders if perhaps there is not a real phyletic relationship involved." The problem is intensified because, as mentioned above, we do not know how much variation in structure is found in the osteology, feather pattern, or muscle pattern in any circumscribed or well-defined passerine family. The following problems arise in any attempt to analyze data from the several systems discussed in this paper. Each of these features which involves degree of development is worthy of a separate investigation; the information to be obtained would do much towards the clarifying of relationships among passerine genera.

The outermost (no. 10) primary is much shorter than the ninth primary in each genus examined here (see p. 236), but, as Amadon (1943, p. 3) has pointed out, there is a considerable range in the relative length of the tenth primary in the family Sturnidae, and in *Lamprotorornis caudatus* the tenth primary "is at least two-thirds as long as the ninth and as long as in many species of the Corvidae." Hence the fact that the tenth primary is about one-half of the length of the ninth in *Artamella* is of little significance by itself in a comparison with *Sturnus*, *Aplonis*, and *Fregilupus*. Similarly, there are well-developed marginal apteria on each side of the

midline inter-ramal feather tract in *Artamella* and *Aplonis*. These apteria are so small in *Sturnus* that it is a question whether they should be considered to be present at all. In *Fregilupus* the inter-ramal area is completely feathered. Further, there are minor differences in extent and degree of development of other ventral feather tracts. If one knew the pattern of these tracts in all members of the Sturnidae, it is possible that one would find differences of equal or greater magnitude within that family. Until such information is available, one can only guess at the probable significance of the differences alluded to in the discussion of pterylosis. The presence of a discrete lateral thoracic feather tract in *Artamella*, for example, might be a characteristic feature of the Vangidae. The presence of 10 secondaries in *Artamella* and of nine in the other genera suggests that *Artamella* is not closely related to them. The pattern of the dorsal spinal feather tract in *Fregilupus* should set it apart from the starlings and the Vanga Shrikes. However, as discussed at some length above (pp. 237–238), such a decision must be considered tentative until the comparative pterylosis of the Sturnidae, Corvidae, and related families has been investigated. A study of the feather tracts in the genus *Corvus* alone is needed. One would like to see Lowe's (1938, pl. 6) work corroborated. It is difficult to believe that the pattern of the dorsal spinal tract varies so much in two species of the same genus.

The following discussion of osteological differences could be prefaced by the same comments made above with reference to pterylosis. There is a single pair of thoracic ribs in *Sturnus* and *Aplonis*; there are two pairs in *Fregilupus* and *Artamella*. The second pair of thoracic ribs, however, is so small that these ribs might be considered rudimentary. At any rate, I have found no data on the occurrence of two pairs of thoracic ribs in passerine birds. The development of an operculum (covering the nostril) is variable within the Sturnidae; hence it is of little use in the present instance. The configuration of the scales on the tarsometatarsus and the presence of a free lacrimal bone, however, set *Artamella* apart from the other genera. The

shape of the ectethmoidal plate exhibits a graded series from *Sturnus* ("winged" plate), to *Fregilupus*, to *Aplonis* (plate nearly "truncate").

So little has been written about the so-called double "pneumatic fossa" of the humerus that it is difficult to determine its taxonomic significance. Shufeldt (1888, pp. 340 and 347) implied that the pneumatic fossa is divided throughout the families Icteridae and Fringillidae. His statement undoubtedly was made after his examining a few representatives of these families, so that we do not know whether the character is constant within a family. In order to obtain more information, I examined the humeri of the following species of the family Fringillidae in the University of Michigan Museum of Zoology:

*Caryothraustes polioaster*  
*Cyanocompsa parellina*  
*Guiraca caerulea*  
*Passerina amoena*  
*Passerina ciris*  
*Passerina cyanea*  
*Pheucticus ludovicianus*  
*Pheucticus melanocephalus*  
*Richmondia cardinalis*  
*Saltator atriceps*  
*Spiza americana*  
*Aimophila acuminata*  
*Aimophila aestivalis*  
*Aimophila cassini*  
*Aimophila humeralis*  
*Aimophila rufescens*  
*Aimophila ruficauda*  
*Aimophila ruficeps*  
*Ammodramus savannarum*  
*Amphispiza bellii*  
*Amphispiza bilineata*  
*Arremon aurantirostris*  
*Arremonops conirostris*  
*Arremonops rufivirgatus*  
*Arremonops verticalis*  
*Ammodramus maritima*  
*Brachyspiza capensis*  
*Calamospiza melanocorys*  
*Calcarius lapponicus*  
*Calcarius ornatus*  
*Chlorura chlorura*  
*Chondestes grammacus*  
*Coryphospingus pileatus*  
*Emberiza calandra*  
*Emberiza citrenella*  
*Fringilla coelebs*  
*Junco aikenii*

*Junco caniceps*  
*Junco hyemalis*  
*Junco oreganus*  
*Junco phaeonotus*  
*Loxia violacea*  
*Melanodera melanodera*  
*Melospiza georgiana*  
*Melospiza lincolni*  
*Melospiza melodia*  
*Melospiza kieneri*  
*Paroaria cristata*  
*Paroaria dominicana*  
*Passerculus sandwichensis*  
*Passerella iliaca*  
*Passerherbulus caudacutus*  
*Passerherbulus henslowii*  
*Pezopetes capitalis*  
*Pipilo aberti*  
*Pipilo erythrophthalmus*  
*Pipilo fuscus*  
*Pipilo maculatus*  
*Plectrophenax nivalis*  
*Poocetes grammacus*  
*Pselliophorus tibialis*  
*Rhynchophanes mccownii*  
*Spizella arborea*  
*Spizella breweri*  
*Spizella pallida*  
*Spizella passerina*  
*Spizella pusilla*  
*Sporophila aurita*  
*Tiaris bicolor*  
*Tiaris olivacea*  
*Volatinia jacarini*  
*Zonotrichia albicollis*  
*Zonotrichia coronata*  
*Zonotrichia leucophrys*  
*Zonotrichia querula*  
*Acanthis flammea*  
*Carduelis carduelis*  
*Carpodacus cassinii*  
*Carpodacus mexicanus*  
*Carpodacus purpureus*  
*Chloris chloris*  
*Coccothraustes coccothraustes*  
*Hesperiphona vespertina*  
*Leucosticte tephrocotis*  
*Loxia curvirostra*  
*Loxia leucoptera*  
*Pinicola enucleator*  
*Pyrrhula pyrrhula*  
*Serinus canarius*  
*Spinus pinus*  
*Spinus psaltria*  
*Spinus tristis*

The divided pneumatic fossa is found in each of the 54 genera and 92 species listed above. The configuration of the fossa is similar

within this large group, but there are some differences. The dorsal fossa is smallest in *Passerherbulus* and *Ammospiza*; in these genera it is reduced so much that it approaches the undivided condition as seen in the Corvidae. The humeri of *Passerherbulus* and *Ammospiza* probably could be distinguished from the humerus of any of the other genera on the basis of the pneumatic fossa alone. There is less difference in this character between the Carduelinae and the Fringillinae than between most genera of the Fringillinae and *Passerherbulus* and *Ammospiza*.

The dorsal fossa is formed by an excavation of the humerus proximad into the articular head and by the development of an overhanging lip at the distal margin of the articular head. The internal humeral tuberosity tends to be less prominent when the bony partition that separates the two fossae is strongly developed. Usually there is an increase in width of the humerus just distal to the articular head, although this feature is seen in some genera that have an undivided fossa. Finally, the dorsal fossa in one sense may not be a "pneumatic" fossa at all but may serve primarily as an area of origin for part of the dorsal head of *M. humerotriceps*.

I examined the humeri of 15 genera of tanagers and found a divided fossa in all. I then examined a few representatives of other families and found a well-developed divided fossa in the following: Paridae, Mimidae, Turdidae, Muscicapidae, Prunellidae, "Coerebidae," Parulidae, Ploceidae, Icteridae (but not in *Gymnostinops*), Thraupidae, and Fringillidae. Both fossae are present in the following families but the dorsal fossa is very small: Aegithinidae (*Chloropsis*), Sittidae, Certhiidae, Cinclidae, Troglodytidae, and Vangidae. There is a single or undivided fossa in the following: Alaudidae, Hirundinidae, Corvidae, Paradisaeidae, Timaliidae, Pycnonotidae, Sylviidae, Bombycillidae, Laniidae, Cyclarhidae, and Vireonidae (except *Vireo flavifrons*). *Vireo gilvus*, *olivaceus*, *philadelphicus*, and *hypochryseus* have a single fossa. *Vireo griseus* and *V. solitarius* have essentially a single fossa, but there is a slight depression dorsally for the origin of *M. humerotriceps*. Among four specimens of *V. flavifrons*, I found a graded series from the undivided to the distinctly divided condition. Whether or

not this represents an age difference I do not know. An investigation of this feature is desirable.

Both *Fregilupus* and *Sturnus vulgaris* (and four other species of *Sturnus*) exhibit two very prominent fossae on the proximal end of the humerus. Although there is a suggestion of a dorsal fossa in *Artamella* and *Aplonis*, it amounts only to a slight depression in the bone for the origin of *M. humerotriceps*; the humerus in these genera is intermediate in configuration between the undivided and the divided condition of the pneumatic fossa.

Hudson and Lanzillotti (1955) have published the only thorough and accurate comparative study of the wing myology of a passerine family (14 genera of the Corvidae). They decided that "the small differences noted do not suggest any taxonomic groupings." That they found a "remarkable uniformity" in the wing muscles of corvine genera suggests that certain types of differences in the wing myology of passerine birds can be used with some degree of confidence in a determination of closeness of relationship. We must at any rate proceed on this assumption until more is known about passerine myology.

*M. latissimus dorsi*, pars posterior, is found in some passerine families but not in others. I know of no instance in which pars posterior is present in some genera and absent in other genera of the same passerine family. *M. latissimus dorsi*, pars posterior, is present in *Sturnus* and *Aplonis*, though it is not strongly developed; it is absent in *Fregilupus* and *Artamella*. My opinion is that the absence of pars posterior represents a more specialized condition than does the presence of the muscle.

An unusual difference exists between *Sturnus* and *Aplonis* in the pattern of insertion exhibited by pars anterior and pars posterior of *M. latissimus dorsi*. Pars posterior inserts immediately posterior to, and in contact with, pars anterior in *Aplonis*. In *Sturnus*, on the other hand, pars anterior inserts on the anterolateral edge of the humerus, whereas pars posterior inserts on the posterolateral edge of the bone, so that there is a space about 3 mm. wide between the two areas of insertion; pars posterior inserts lateral to the dorsal head of *M. humerotriceps*. I have seen a similar pattern only in *Geococcyx californianus*. In *Geococcyx*, however, pars posterior inserts medial



to the dorsal head of *M. humerotriceps*.

Hudson and Lanzillotti (1955, p. 17) apparently found no variation, among the corvid genera they examined, in the areas of origin of the two heads of *M. subcoracoideus*. The ventral head in *Fregilupus* and *Artamella* is similar in that it is small and in that it arises from the coracoid at about the junction of its middle and lower thirds, which places the origin dorsal to the insertion of *M. sternocoracoideus*. In *Sturnus* and *Aplonis*, *pars ventralis* is a large muscle, and it arises medial to the area of insertion of *M. sternocoracoideus*, i.e., from the lower end of the coracoid. *Pars dorsalis* of *M. subcoracoideus* arises from the clavicle and the acromion process (scapula) in *Sturnus* and *Aplonis*; in *Fregilupus*, it arises only from the clavicle; in *Artamella*, the primary origin is from the acromion process, but there is a small origin from an adjacent area on the coracoid also.

The apparent difference (p. 249) in the area of insertion of *M. coracobrachialis posterior* is significant only in that it reflects the difference in development of the pneumatic fossa of the humerus. The insertion is slightly more

anterior and distal in cases in which the tendon inserts on the proximal end of the bony partition, which probably is important from a functional viewpoint alone.

If *M. pectoralis*, *pars propatagialis longus*, is tendinous in all specimens of *Artamella*, this feature would set *Artamella* apart from the other genera discussed here. The more extensive insertion of *M. anconeus* in *Sturnus* is in all probability related to function rather than to phylogeny. A similar conclusion must be reached in any consideration of other differences in development of some of the wing muscles.

With respect to the myology of the pelvic appendage, *M. sartorius* has two heads in *Fregilupus*, one head in the other genera. *M. femorotibialis internus* has two independent bellies in *Fregilupus*, a single belly in the other genera. A ligament holds the tendon of *M. extensor digitorum longus* in place on the proximal end of the tarsometatarsus in *Fregilupus*, *Sturnus*, and *Aplonis*, but in *Artamella* the tendon passes through a bony canal. *M. flexor hallucis brevis* is present in *Artamella*, absent in the other genera.

## CONCLUSIONS

THE FOLLOWING ANATOMICAL FEATURES separate *Artamella* from *Fregilupus*, *Sturnus*, and *Aplonis*. *Artamella* has 10 secondaries, a lateral thoracic feather tract, a free lacrimal bone, and a peculiar pattern of scales on the posterior surface of the tarsometatarsus; *M. subcoracoideus*, pars dorsalis, arises from the acromion process of the scapula and from the coracoid; *M. pectoralis*, pars proptagialis longus, is tendinous, rather than fleshy; the tendon of *M. extensor digitorum longus* passes through a bony canal on the proximal end of the tarsometatarsus; *M. flexor hallucis brevis* is present.

*Sturnus* differs from *Aplonis* as outlined here. Marginal apteria in the inter-ramal region are well developed in *Aplonis*; they are very small or absent in *Sturnus*. There is a large nasal operculum in *Sturnus*, a small one in *Aplonis*. The ectethmoidal plate is "winged" in *Sturnus*, nearly "truncate" in *Aplonis*. There is a large double pneumatic fossa on the humerus of *Sturnus*; a distinct dorsal fossa is absent in *Aplonis*. There is a striking difference in the pattern of insertion

of the two parts of *M. latissimus dorsi* between the two genera. The jaw muscles were discussed above (p. 261); further comment here does not seem warranted. These differences suggest that further investigation of the Sturnidae might reveal the presence of two separate but closely related groups (subfamilies) in this family (see also Lowe, 1938).

The characters listed for *Artamella* indicate that *Fregilupus* does not belong in the Vangidae. Thus it is desirable to compare *Fregilupus* with *Sturnus* and *Aplonis*. The pattern of the dorsal spinal feather tract in *Fregilupus* is unlike that in the two starlings. *Fregilupus* possesses two pairs of thoracic ribs; *Sturnus* and *Aplonis* possess one pair. *M. latissimus dorsi*, pars posterior, is present in *Sturnus* and *Aplonis*; it is absent in *Fregilupus*. The ventral head of *M. subcoracoideus* in *Fregilupus* is small, and it has an origin from the coracoid, dorsal to the insertion of *M. sternocoracoideus*; in *Sturnus* and *Aplonis*, this head is large, and it has an origin medial to the insertion of *M. sternocoracoideus*. *M. sartorius* has two heads in *Fregilupus*, one head in the

TABLE 5  
COMPARATIVE DATA ON CERTAIN PASSERINE BIRDS

	<i>Fregilupus</i>	<i>Sturnus</i>	Corvidae	<i>Paradisaea</i>	<i>Artamella</i>
Number of secondaries	9	9	10	10	10
Cervicodorsal ribs	1	1	2	2	1
Thoracic ribs	2	1	1	1	2
Pneumatic fossa	Divided	Divided <sup>a</sup>	Single	Single	Divided <sup>a</sup>
Free lacrimal	0 <sup>b</sup>	0	+ <sup>c</sup>	+0 <sup>d</sup>	+
Latissimus dorsi pars posterior	0	+	+	+	0
Pectoralis pars proptagialis longus	Fleshy	Fleshy	Tendinous	Tendinous	Tendinous
Abductor indicis	Rudimentary	Rudimentary	+	Rudimentary	Rudimentary
Sartorius	2 heads	Single	Single	2 heads	Single
Flexor perforatus digiti II <sup>e</sup>	0	0	+	0	0
Femoral head of flexor digitorum longus	0	0	+	+	0
Flexor hallucis brevis	0	0	+	+	+

<sup>a</sup> The dorsal fossa is rudimentary in *Aplonis* and *Artamella*.

<sup>b</sup> 0, absent.

<sup>c</sup> +, present.

<sup>d</sup> Variable in the Paradisaeidae (see Beecher, 1953, p. 288).

<sup>e</sup> 0 indicates that the tendon of insertion of this muscle is not perforated by the tendons of *Mm. flexor perforans et perforatus digiti II* and *flexor digitorum longus*; + indicates that the tendon is perforated by both of the deep flexor tendons.

other genera. *M. femorotibialis internus* is composed of two independent bellies in *Fregilupus*; it is a single muscle in *Sturnus* and *Aplonis*. *M. obturator internus* is roughly triangular in shape in *Fregilupus*; it is more oval or rectangular in *Sturnus* and *Aplonis*. The tendon of insertion of *M. peroneus longus* is very large in *Fregilupus*, relatively small in *Sturnus* and *Aplonis*, though the belly is well developed in each of the genera. I have not encountered this type of difference in working with other families of birds.

If one may judge from our meager knowledge of the comparative anatomy of the Passeriformes, these differences suggest that

*Fregilupus varius* is not a starling. Such a tentative conclusion, however, is made primarily on the assumption that two characters listed above do not vary within a well-defined phylogenetic assemblage of genera. These two characters are the pattern of the dorsal spinal feather tract and the absence of *M. latissimus dorsi*, pars posterior, in *Fregilupus*. Furthermore, data presented in table 5 suggest that *Fregilupus* is even further removed from the Corvidae and the Paradisaeidae. Drs. Dean Amadon and Ernst Mayr have both suggested a possible relationship between *Fregilupus* and the Prionopidae.

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