

## Systematic and Functional Aspects of the Locomotor System of the Scrub-birds, *Atrichornis*, and Lyrebirds, *Menura* (Passeriformes: Atrichornithidae and Menuridae)

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**ABSTRACT.** The forelimb and hindlimb musculature was dissected in the Noisy Scrub-bird, *Atrichornis clamosus* (Atrichornithidae), and the Superb Lyrebird, *Menura novaehollandiae* (Menuridae). The purposes of the study were to test certain phylogenetic hypotheses and to examine the locomotor specializations of the Menurae. The two families share derived myological traits and are sister groups. The structure of *M. flexor perforatus digiti IV* confirms that their affinities are with the oscines and not with the suboscines. The scrub-birds have the more highly derived limb morphology. The Menurae exhibit several myological conditions not shared with the Ptilonorhynchidae, other members of the 'corvid assemblage' or other passerines. They are, therefore, not similar to the bowerbirds in their limb musculature. A sister-group relationship with bowerbirds is not ruled out, however, because the peculiarities of the Menurae could have evolved after separation from a common ancestor with the bowerbirds, but the same is true for any suggested sister group.

Both scrub-birds and lyrebirds are nearly flightless. *Atrichornis* has reduced clavicles and greater forelimb reduction than does *Menura*. In contrast, *Menura* shows greater specialization in the hindlimb, which is elongated and has enlarged claws specialized for digging and grasping.

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**KEYWORDS:** Atrichornithidae, forelimb, hindlimb, Menuridae, Menurae, morphology, myology.

Two families of Australian passerines, the Menuridae (lyrebirds) and Atrichornithidae (scrub-birds), have puzzled systematists for over a century. While generally considered closely related to each other, their affinities to other birds have remained unclear. Although they bear little resemblance to suboscines, they have been classified as a suborder Menurae within the order Passeriformes (Wetmore, 1960). The question of their relationships was reopened by Sibley (1974) who studied the electrophoretic patterns of the egg-white proteins of *Menura* and reviewed other data, especially relating to anatomy and behaviour. He concluded that the Menuridae are oscine and are most closely related to the bowerbirds (Ptilonorhynchidae) and birds-of-paradise (Paradisaeidae) within a radiation of Australasian 'corvine' families. Because of the presumed

relationship of the Atrichornithidae to the Menuridae, Sibley also suggested that the former family be placed next to the Menuridae in the suborder Passeres (oscines), although he did not study the proteins of the scrub-birds. Sibley (1974, 1976) reviewed the history of the problem.

More recently, Sibley & Ahlquist (ms.) reinvestigated this problem using the technique of DNA-DNA hybridization. Their study supported the sister-group relationship of the Atrichornithidae and Menuridae, and also indicated that these families are in turn most closely related to the Ptilonorhynchidae. Surprisingly, however, the Ptilonorhynchidae and Paradisaeidae were found to be widely separated on the basis of the DNA analysis, so Sibley no longer hypothesizes a close relationship of the birds-of-paradise with the lyrebirds and scrub-birds.

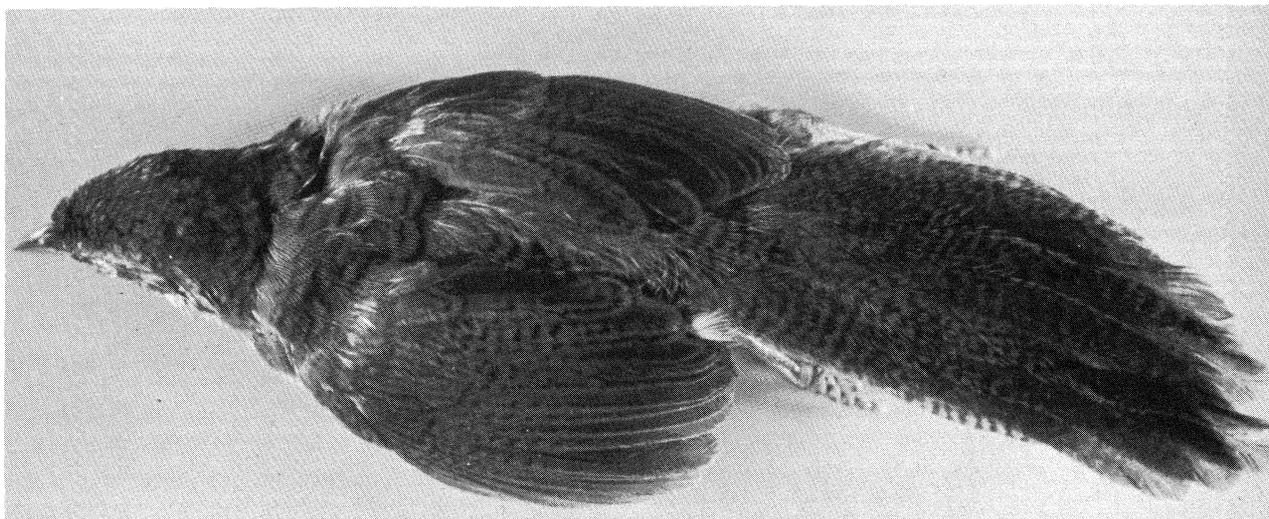


Fig. 1. Dorsal view of female Noisy Scrub-bird, *Atrichornis clamosus*, preserved specimen with feathers air-dried. Note the long, broad tail and the short, rounded wings.

The behaviour of the Menuræ is likewise poorly known. Only brief observations on the locomotion of scrub-birds and lyrebirds have been reported. Both groups are ground-dwelling, forest inhabitants and forage for invertebrates in the leaf litter. Smith (1976) reported that the Noisy Scrub-bird (*Atrichornis clamosus*) does not use its feet when foraging, but Serventy (1966) cited a report that the Rufous Scrub-bird (*A. rufescens*) does scratch on the ground with its feet. This single report appears to be exceptional given the experience of other observers. The Superb Lyrebird (*Menura novaehollandiae*) actively uses its feet in foraging by raking the litter with its large claws and picking up branches to move them aside with its feet (Smith, 1968), and Albert's Lyrebird (*M. alberti*) forages in a similar manner (Robinson, 1976:333).

Both genera of the Menuræ are nearly flightless. The Superb Lyrebird nests and roosts above the ground, climbing up through the trees by leaping zig-zag fashion from branch to branch, then gliding down to the nest (Smith, 1968). Mary H. Clench (pers. comm.) reported that a Superb Lyrebird flew from the ground to a branch about six feet high by leaping upward and flapping its wings strongly. Lyrebirds return to the ground by gliding downward and using the wings for braking (Smith, 1968). Little has been written about the flight of scrub-birds, but Jackson (1921) observed a Rufous Scrub-bird that he was pursuing fly (or at least flutter) for a distance of about ten feet at an altitude of one foot. Smith & Robinson (1976), however, reported that, although scrub-birds are primarily terrestrial, "they spend far more time in short flights in thick scrub than has previously been reported. . .". The wings of scrub-birds are very short and rounded, hardly reaching past the base of the long tail (Fig. 1).

In this paper I provide new information on the anatomy of the Menuræ and comment on its relevance to the taxonomic and behavioural matters noted above. My study involved a dissection of the forelimb and hindlimb muscles of a lyrebird and a scrub-bird. The results are analyzed in relation to Sibley's hypotheses

and also in comparison to other studies of passerine appendicular myology. Specifically, I address the following questions. (1) Are the Atrichornithidae and Menuridae most closely related to each other? (2) Are they oscine? (3) Are they closely related to the Ptilonorhynchidae or Paradisaeidae? (4) What are the morphological correlates of their locomotor specializations?

#### MATERIALS AND METHODS

The specimens dissected included an adult female Noisy Scrub-bird, *Atrichornis clamosus*, and an adult female Superb Lyrebird, *Menura novaehollandiae*. Some additional observations were made on an adult male Superb Lyrebird. Dissection was done with the aid of a stereomicroscope, the muscles being stained with iodine to enhance the clarity of the fibre arrangements. Comparisons with the myology of the Ptilonorhynchidae and Paradisaeidae are based on the work of Borecky (1977), who also provided helpful personal consultations. The drawings were made directly from specimens with the aid of a camera lucida microscope attachment. Anatomical nomenclature is based largely on the *Nomina Anatomica Avium* (Baumel *et al.*, 1979).

A functional comparison of the locomotor system may profitably include a study of the relative proportions of various parts. In order to make direct comparisons of birds of different sizes, ratios were calculated of various measurements relative to body weight. Linear measurements were compared to the cube root of weight in order to minimize the effect of different weights. These simple comparisons provide only a rough estimate of the relationship between linear dimensions and weight, but they are adequate to illustrate the deviation that the Menuræ show from some 'typical' oscine bodily proportions.

In order to assess changes associated with the near loss of flight, a group of five species of oscines was chosen as a basis for comparison. These are all strong

fliers but are not highly specialized for any particular mode of flight, e.g., prolonged aerial hawking. The mean values of measurements of five species provide a rough model of a 'typical' oscine for comparison with the Menuræ. *Atrichornis* lies within the range of weights of these five species, but *Menura* is much larger (Table 4).

The arcs of curvature of the claws were measured by the method used by Engels (1940) in measuring bill curvature.

The following abbreviations are used in the figure legends:

BB:	M. biceps brachii
CC:	M. coracobrachialis caudalis
CCR:	M. coracobrachialis cranialis
CF:	M. caudofemoralis
CL:	clavicle
CO:	coracoid
DM:	a dermal muscle
DMA:	M. deltoideus major
DMAC:	M. deltoideus major pars caudalis
DMACR:	M. deltoideus major pars cranialis
DMAP:	M. deltoideus major proximal head
DMI:	M. deltoideus minor
DP:	deep dermal component of M. pectoralis
EMR:	M. extensor metacarpi radialis
FCL:	M. flexor cruris lateralis pars pelvica
FCLA:	M. flexor cruris lateralis pars accessoria
FCM:	M. flexor cruris medialis
FTED:	M. femorotibialis externus pars distalis
FTEP:	M. femorotibialis externus pars proximalis
FTI:	M. femorotibialis internus
FTM:	M. femorotibialis medius
GM:	M. gastrocnemius pars intermedia
H:	humerus
IC:	M. iliotibialis cranialis
II:	M. iliofemoralis internus
IL:	M. iliotibialis lateralis
ISF:	M. ischiofemoralis
ITC:	M. iliotrochantericus caudalis
ITCR:	M. iliotrochantericus cranialis
ITM:	M. iliotrochantericus medius
LDC:	M. latissimus dorsi pars caudalis
LDCR:	M. latissimus dorsi pars cranialis
LDD:	M. latissimus dorsi pars dorsocutaneous
OH:	os humeroscapulare
OM:	M. obturatorius medialis
P:	M. pectoralis
PIF:	M. pubo-ischio-femoralis
PIFC:	M. pubo-ischio-femoralis pars cranialis
PIFCD:	M. pubo-ischio-femoralis pars caudalis
RS:	M. rhomboideus superficialis
S:	scapula (Fig. 4), sternal carina (Fig. 9)
SBC:	M. subcoracoideus
SC:	M. supracoracoideus
ST:	sternum
TB:	M. triceps brachii
TH:	M. humerotriceps

TPB:	M. tensor propatagialis pars brevis
TPL:	M. tensor propatagialis pars longa
TS:	M. scapulotriceps.

### MYOLOGY OF THE FORELIMB

A fully detailed description will not be given for each muscle because much of this would be a repetition of previous studies. Instead, I will compare each muscle with the descriptions for other passerines, especially the New World nine-primaried oscines (Raikow, 1977, 1978), the 'corvid assemblage' (Borecky, 1978) and the general review by Berger (1969), and will only comment on aspects in which the muscles of the Menuræ differ from those descriptions, or on other points considered noteworthy. If no other comments are given, it may be assumed that the condition in the Menuræ is similar to that in *Loxops virens* (Raikow, 1977) which is the reference species for comparison. If no distinctions are noted between them, then the condition is the same in *Menura* and *Atrichornis*.

The following muscles do not differ significantly from those in *Loxops virens* (Raikow, 1977) and require no discussion: Mm. rhomboideus profundus, scapulohumeralis cranialis, scapulohumeralis caudalis, subscapularis, coracobrachialis caudalis, sternocoracoideus, biceps brachii, brachialis, flexor digitorum superficialis, flexor carpi ulnaris, extensor metacarpi radialis, extensor metacarpi ulnaris, extensor longus digiti majoris, ulnometacarpalis dorsalis, abductor alulae, adductor alulae, abductor digiti majoris, interosseus dorsalis, interosseus ventralis and flexor digiti minoris.

**M. latissimus dorsi** (Figs 2, 4). Both parts are present and entirely separate. Pars cranialis, a narrow, parallel-fibred muscle, arises from the dorsal midline superficial to M. rhomboideus superficialis and cranial to pars caudalis. It inserts fleshy on the proximodorsal surface of the humeral shaft caudal to the deltoid crest.

Pars caudalis is extremely large; a wide, flat, fan-shaped muscle arising fleshy from most of the dorsal midline of the thorax and also by a wide aponeurosis from the midline, which gives rise to three distinct caudal heads whose fleshy portions begin more distally. The entire muscle converges on a stout tendon of insertion that arises along its lateral border. It inserts on the caudodorsal surface of the humerus at the level of M. scapulohumeralis cranialis, the tendon inserting between fascicles of the humerotriceps. In *Menura*, pars caudalis is not as distinctly divided into heads caudally as it is in *Atrichornis*. A cutaneous component, M. latissimus dorsi interscapularis (dorsocutaneous), is also present (Fig. 2).

The form of pars caudalis, greatly enlarged and with an extensive area of origin, appears to be unique among passerines as far as known. It does not occur in the Paradisaeidae or Ptilonorhynchidae (Borecky, 1977). This condition is apparently a specialization of the Menuræ, that is, a synapomorphy linking the two families.

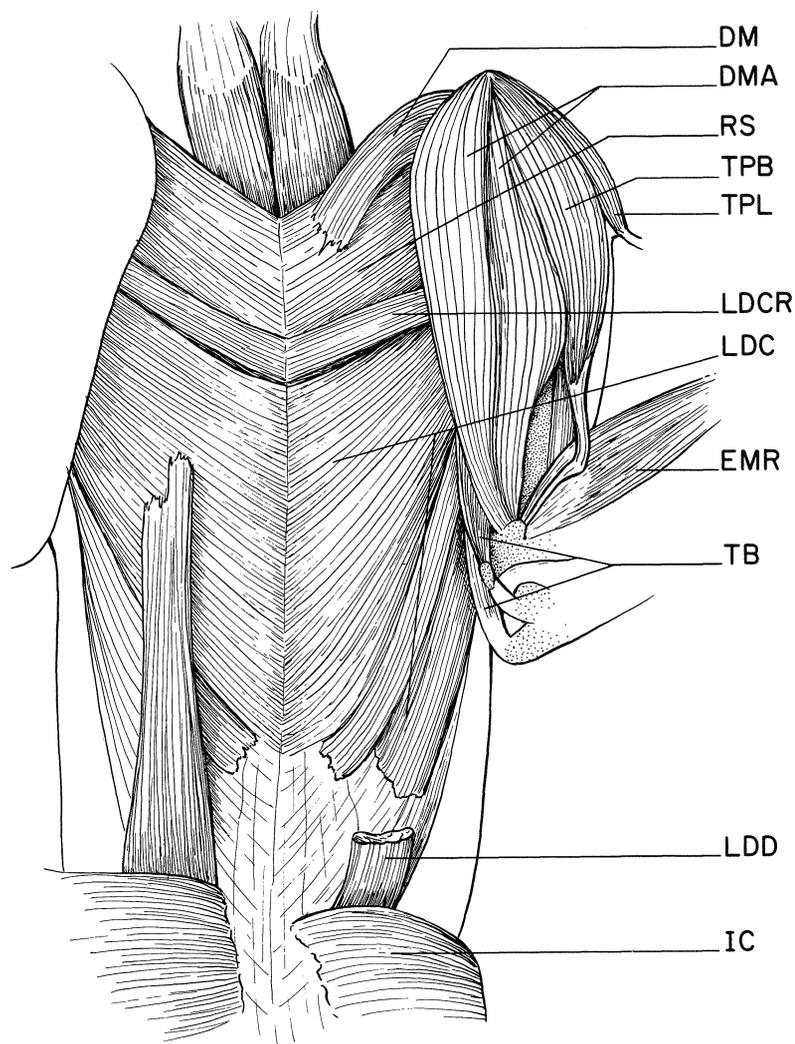


Fig. 2. Dorsal view of the muscles of the back and upper arm of *Atrichornis clamosus*. The greatly enlarged *M. latissimus dorsi pars caudalis* (LDC) is a synapomorphy of the Menuridae. For abbreviations see Materials and Methods.

**M. rhomboideus superficialis** (Figs 2, 4). This muscle arises from the dorsal midline and converges slightly toward a fleshy insertion on the dorsomedial surface of the cranial half of the scapula; a few fascicles just reach the medial surface of the head of the clavicle.

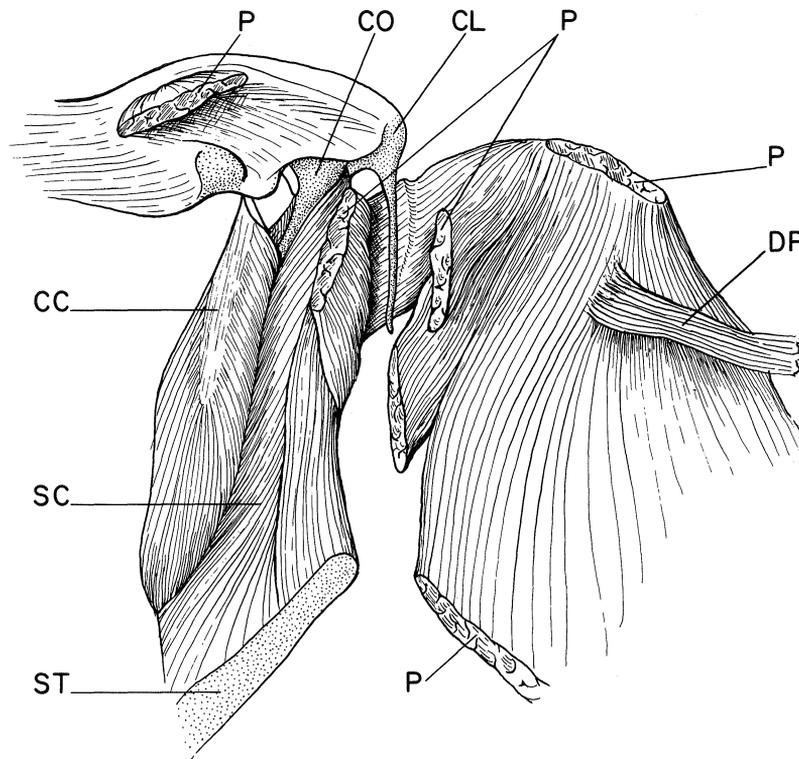
**M. serratus profundus**. The two large cranial bellies are entirely separate.

**M. serratus superficialis**. This is of normal passerine form. I did not find pars costohumeralis in *Atrichornis*, but it was probably removed during prior skinning. Pars costohumeralis was present in *Menura*.

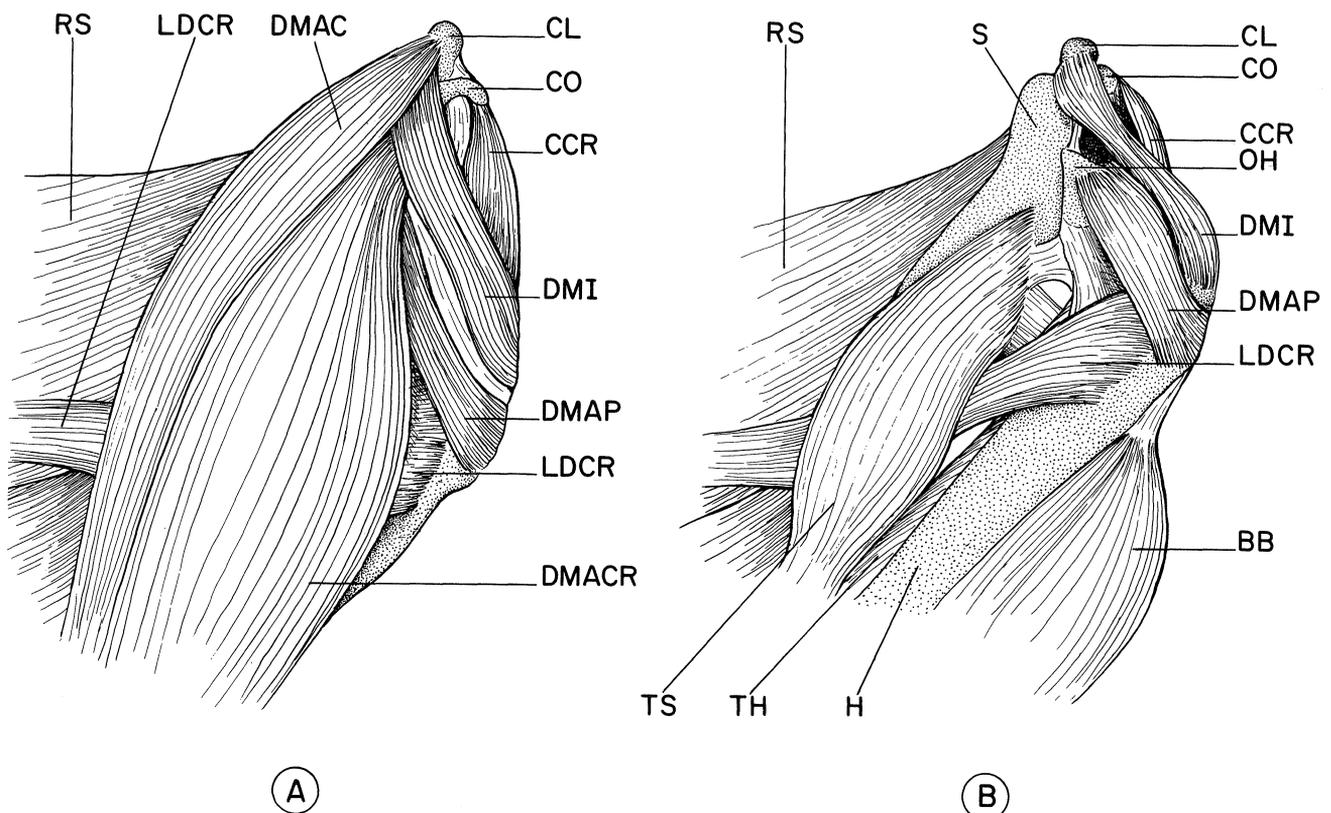
**M. subcoracoideus** (Fig. 5) In *Menura*, the dorsal head arises only from the scapula, while in *Atrichornis* a few fascicles also arise from the adjacent ventral margin of the head of the clavicle.

**M. pectoralis** (Figs 3, 5, 8, 9). In *Atrichornis*, the belly (pars thoracicus) is relatively small in association with reduced flying ability. It has a normal area of origin from the sternal plate and carina, and the membrane

overlying the sternal ribs. As discovered by Garrod (1876) in *Atrichornis rufescens*, the distal 60% of the clavicle is absent, only the head and a short shaft remaining. Only a few fibres of the pectoralis arise from the clavicle; the muscle mainly attaches around the bone, arising from both the cranial and caudal surfaces of the coracoclavicular membrane. A dermal component arises from the deep surface. In *Menura*, pars thoracicus is also reduced in size but retains a normal origin from the areas noted above and also from the ventral, caudal and dorsal surfaces of the clavicle (which is complete) in the usual manner. Near the insertion there is a wide tendinous connection from the deep surface of the muscle to the origin of the *M. biceps brachii*. Pars propatagialis longus is fleshy in *Loria* and *Semioptera* (Paradisaeidae) and *Amblyornis* (Ptilonorhynchidae). In the other bowerbirds and birds-of-paradise, and in the Corvidae, Callaeidae, Grallinidae and Cracticidae, it is tendinous (Borecky, 1977), as in the Menuridae and Atrichornithidae.



**Fig. 3.** Ventrolateral view of the deep muscles of the shoulder region in *Atrichornis clamosus*. The *M. pectoralis* has been cut free in several places (P) and reflected to the right, showing how the vestigial shaft of the clavicle lies essentially free within the belly of the muscle. For abbreviations see Materials and Methods.



**Fig. 4.** Dorsal views of the shoulder muscles in *Atrichornis clamosus*. A, Superficial muscles. B, Deeper muscles after removal of *M. deltoideus major*, and rotated somewhat to the left. For abbreviations see Materials and Methods.

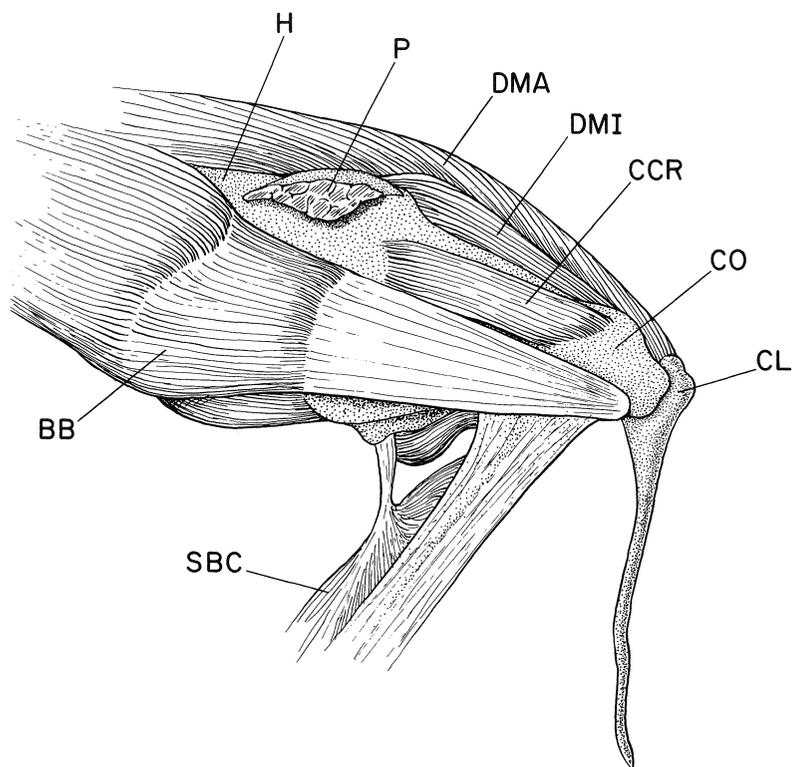


Fig. 5. Craniolateral view of the deep shoulder muscles in *Atrichornis clamosus*, also showing the vestigial form of the clavicle, with a well developed head but a short and attenuated shaft. For abbreviations see Materials and Methods.

**M. supracoracoideus** (Figs 3, 9). This bipennate muscle is reduced in size from that expected in a bird of comparable size but normal flying ability. In *Menura*, it arises fleshy from the dorsolateral surface of the cranial  $\frac{2}{3}$  of the sternal carina, the adjacent sternal plate, the cranioventral surface of the sternum, a small area on the cranioventral surface of the coracoid and cranioventrally from a midsagittal sternoclavicular membrane and the coracoclavicular membrane, all deep to the *M. pectoralis*. The origin of the muscle in *Atrichornis* is similar, but the muscle is relatively more reduced than in *Menura* and arises only from the cranial  $\frac{1}{2}$  of the sternal carina (compared to  $\frac{2}{3}$  in *Menura*). Also, in *Atrichornis*, the origin of the muscle does not extend cranially beyond the end of the sternum, as in *Menura*, because there is no discernible sternoclavicular membrane in *Atrichornis*.

**M. coracobrachialis cranialis** (Figs 4, 5). This is a small but fully developed muscle with normal muscle tissue; it has not degenerated to connective tissue as in many passerines. The parallel-fibred belly arises by a short tendon from the lateral surface of the head of the coracoid and passes across the shoulder joint to insert fleshy on the proximal end of the humerus, just ventral to the proximal end of the pectoral crest, between the latter and the coracoidal tendon of *M. biceps brachii*, and along its edge deep to the latter.

**M. cucullaris capitis pars propatagialis**. I did not find this muscle in either of the *Menurae* examined.

However, it may have been removed during prior skinning and so should not necessarily be considered absent.

**M. tensor propatagialis** (Fig. 2). Pars longa and pars brevis are separate as in other passerines. Garrod (1876) reported that in *Menura superba* (= *novaehollandiae*) and *Atrichia* (= *Atrichornis*) *rufescens* the tendon of insertion of pars brevis differs from that in most passerines. Typically, this tendon passes to the dorsal surface of the belly of *M. extensor metacarpi radialis* is attached there, and then turns to run parallel to the long axis of the muscle to an insertion on the ectepicondylar process of the humerus, near the elbow. In doing so, it runs roughly parallel to the tendinous origin of the *M. extensor metacarpi radialis*, but is separate from it. Garrod reported that in the *Menurae* he dissected, the tendons of the two muscles were fused together for their entire length, as also occurs in some Piciformes. My dissection confirms this for *Menura*, but in *Atrichornis clamosus* I found the two tendons to be separate in the usual passerine manner.

**M. deltoideus major** (Figs 2, 4, 5). This muscle occupies the dorsal surface of the forearm. At its proximal end it lies deep to *M. tensor propatagialis* pars longa. It is divided into two separate bellies, pars cranialis and pars caudalis, which are of normal form in most respects. However, pars cranialis in *Menura* has an unusual proximal head that is continuous with the main part of the belly, but demarcated from it by a fairly

distinct plane of separation, and arising from the os humeroscapulare. In *Atrichornis*, this proximal portion has become clearly separated from the main part of pars cranialis, a distinct gap separating the insertions of the two parts. In this characteristic, then, *Atrichornis* is more highly derived than is *Menura*. This separate proximal head does not occur in other passerine birds so far as known.

**M. deltoideus minor** (Figs 4, 5). In *Atrichornis*, this small, strap-shaped, parallel-fibred muscle lies cranioproximal to M. deltoideus major and caudal to M. coracobrachialis cranialis. It arises fleshy from the apex of the coracoid and slightly from the coracoclavicular ligament, a few fascicles perhaps also arising from the acromion of the scapula. The muscle passes distally, superficial to the supracoracoideus tendon to insert fleshy on the pectoral crest of the humerus just distal to the insertion of the supracoracoideus tendon. *Menura* is like *Atrichornis*, but it is more apparent that a few fascicles do arise from the acromion. This muscle is unusual in the Menurae in that it arises almost exclusively from the coracoid, with hardly any origin from the scapula. In the New World nine-primaried oscines, it arises either from the scapula alone, or from the scapula and coracoid (Raikow, 1978). The muscle arises from the scapula alone in the Sturnidae, Callaeidae, Cracticidae, Corvidae, Paradisaeidae (except *Loria*), and *Grallina* and *Struthidia* (Grallinidae). It arises from both the scapula and coracoid in *Corcorax* (Grallinidae), *Loria* and the Ptilonorhynchidae (Borecky, 1977). In the latter case there is an extensive origin from the scapula, unlike the very small origin in the Menurae. Thus, the peculiar form of this muscle does not support a relationship of the Menurae with the Ptilonorhynchidae or Paradisaeidae.

**M. triceps brachii** (Figs 2, 4). The scapulotriceps cannot be divided into two parts as in some passerines (Raikow, 1978). Distally, several fascicles of the humerotriceps contribute to the insertion of the scapulotriceps.

**M. expansor secundariorum**. This muscle is of normal passerine form in *Atrichornis*, including its insertion onto three secondaries. In *Menura*, however, it inserts onto the innermost four secondaries.

**M. pronator superficialis**. The belly extends for most of the length of the radius, inserting near the wrist.

**M. pronator profundus**. This muscle originates from the distal end of the humerus and from the adjacent humeroulnar pulley. It is the same in both genera. It spreads out to an extensive line of attachment along the shaft of the radius. Two distinct forms have been described in passerines. In one, the muscle is fan-shaped and single, with a continuous line of insertion. In the second, the muscle is divided into two distinct bellies, one inserting proximally and one distally on the radius; the two insertions are separated by a clear gap. Intermediate conditions sometimes occur. The undivided form is considered primitive in passerines and

the divided form derived (Raikow, 1978; Bentz, 1979). The condition in the Menurae is single and undivided, as it is in the 'corvid assemblage'.

**M. flexor digitorum profundus**. This muscle is of normal form in the Menurae. The two heads originate adjacent to the entire length of the area of insertion of the M. brachialis.

**M. ulnometacarpalis ventralis**. This is of normal form in the Menurae. It arises by a shallow V-shaped origin, the caudal arm being longer than the cranial arm.

**M. extensor digitorum communis**. The belly extends almost the entire length of the forearm, but is slightly shorter than the underlying M. extensor longus digiti majoris and M. extensor metacarpi ulnaris. The proximal branch of the tendon of insertion inserts on the base of the dorsal surface of the alular digit; it does not branch as in the New World nine-primaried oscines (Raikow, 1977).

**M. ectepicondylo-ulnaris**. The belly extends about  $\frac{2}{3}$  the length of the ulna, compared to about  $\frac{1}{3}$  in the 'corvid assemblage' (Borecky, 1977).

**M. supinator**. This muscle inserts along the proximal  $\frac{1}{2}$  of the radius, whereas in the 'corvid assemblage' it inserts on the proximal  $\frac{1}{4}$  (Borecky, 1977).

**M. extensor longus alulae**. As in other passerines there is only an ulnar head, no radial head occurs. The tendon of insertion fuses with that of the M. extensor metacarpi radialis a short distance before their common insertion.

## MYOLOGY OF THE HINDLIMB

The format of the muscle descriptions is the same as that used for the forelimb. The basis of comparison is with the hindlimb muscles of *Loxops virens* (Raikow, 1976). Mm. femorotibialis medius, extensor digitorum longus, fibularis longus and lumbricalis are present in normal form and require no discussion.

**M. iliotibialis cranialis** (Figs 2, 7). In *Atrichornis*, this muscle arises from the median dorsal ridge of the cranial end of the pelvis, mainly fleshy but by a short aponeurosis at its caudal end. There is one head, lying superficial to the M. iliotrochantericus caudalis, and entirely cranial to the M. iliotibialis lateralis. The cranial end of the M. iliotrochantericus caudalis lies medial to this muscle. In *Menura*, the origin is quite different: slightly from the median dorsal ridge cranially, but mainly from the cranial edge of the ilium, partly medial to the M. iliotibialis lateralis and M. iliotrochantericus caudalis; the latter does not extend over the medial surface of the muscle as in *Atrichornis*. The origin in *Menura* is thus longer than in *Atrichornis*, the muscle as a whole being relatively larger. This origin is of typical passerine form, that of *Atrichornis* being rather more restricted in area. In both genera, the insertion lies deep to the patellar band of M. gastrocnemius.

**M. iliotibialis lateralis**. There are complete preacetabular, acetabular and postacetabular portions; no reduction of this muscle occurs as in some

passerines. The origin extends caudally slightly farther in *Menura* than in *Atrichornis*. In the former it lies superficial to the caudal edge of the *M. flexor cruris lateralis*, while in the latter it reaches only the cranial edge of that muscle. *M. iliotibialis lateralis* is well developed in both genera, and especially in *Menura* is quite massive and thick. The proximal and distal aponeurotic regions are of normal passerine form.

**M. iliofemorales externus.** This muscle is absent in *Atrichornis* and *Menura*. In many nonpasserine birds it arises from the cranial iliac crest just caudal to *M. iliotrochantericus caudalis*, and in some cases is fused in part to the latter muscle. Its tendon passes distally over the lateral surface of the trochanter of the femur and inserts in some cases distal, but more commonly proximal, to the tendon of insertion of *M. ischiofemorales* (references in George & Berger, 1966: 393). Until recently, this muscle was considered lacking in passerines, though it has been found as a developmental anomaly (Raikow, 1975; Raikow *et al.*, 1979). However, Borecky (1977) found the *M. iliofemorales externus* to be present in the Callaeidae and Ptilonorhynchidae, where its belly is partly fused to that of the *M. iliotrochantericus caudalis*, but partly free and with an entirely separate tendon of insertion. In *Turnagra* (now considered to be a paradisaeid by Olson *et al.*, 1983) and in the primitive bird-of-paradise *Loria*, the muscle is also present, its belly fully fused to that of the *M. iliotrochantericus caudalis*, but still with a separate tendon. Among the Paradisaeidae, *Epimachus* had a condition like that in the Ptilonorhynchidae, while in seven other genera the situation is difficult to interpret. There is no apparent *M. iliofemorales externus*, but the *M. iliotrochantericus caudalis* extends caudally slightly farther than in most passerines, and Borecky (1977) suggested that this might represent a complete fusion of the *M. iliotrochantericus caudalis* and the *M. iliofemorales externus*.

The condition in the *Menurae* is like that in most paradisaeids, that is, there is no *M. iliofemorales externus*, but the *M. iliotrochantericus caudalis* is extensive. Thus, the condition in the *Menurae* is unlike that in the Ptilonorhynchidae or in *Loria* or *Epimachus*, but is similar to that in most birds-of-paradise. At my request, Dr Borecky examined the specimens of the *Menurae*, and felt that the caudal extent of the *M. iliotrochantericus caudalis* was not as pronounced as in the birds-of-paradise, although this is admittedly a subjective judgement. The problem is that the resemblance could be due either to a shared primitive condition or to a shared derived condition, but we lack the information necessary to choose between these possibilities. Considering the condition in the Ptilonorhynchidae, *Loria* and *Epimachus*, however, we may at least conclude that this character fails to support a relationship between the *Menurae* and the bowerbirds and primitive birds of paradise, and perhaps also the typical birds of paradise.

**M. iliotrochantericus caudalis** (Fig 6). This muscle is

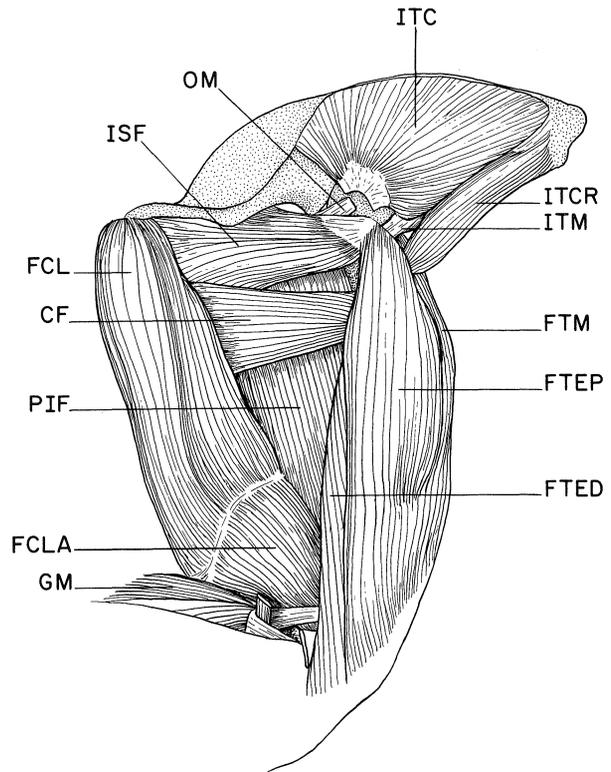


Fig. 6. Lateral view of the thigh muscles in *Atrichornis clamosus* after removal of the more superficial muscles *M. iliotibialis cranialis*, *M. iliotibialis lateralis* and *M. iliofibularis*. For abbreviations see Materials and Methods.

of normal form in the *Menurae*, but quite well developed with a full cranial margin that curves ventrally and then back up to the tendon of insertion. Caudally, in *Menura* a part of the belly is partially separate, which could be interpreted as a fused belly of the *M. iliofemorales externus*, but is actually due to a fascial plane accompanying the point of entry of a nerve, and commonly seen as an artifact of dissection. See discussion under *M. iliofemorales externus*.

**M. iliotrochantericus cranialis** (Figs 6, 7). This is of normal form. It inserts on the cranio-lateral surface of the femur, on a raised tubercle in *Atrichornis* and on a well developed ridge (iliotrochanteric tuberosity) in *Menura*.

**M. iliotrochantericus medialis** (Fig. 6). This is of normal form and quite well developed. It arises on the lateroventral surface of the pelvis, cranial to the acetabulum, and lies lateral to *M. iliofemorales internus*.

**M. femorotibialis externus** (Fig. 6). A deep distal head (pars distalis) is present, arising proximally at the level of insertion of the *M. caudofemorales* on the femur. It is almost entirely separate from pars proximalis. The *M. femorotibialis externus* is much more distinctly separate from the adjacent *M. femorotibialis medialis* than in the Paradisaeidae, Ptilonorhynchidae or other passerines studied. The two muscles are separated by a deep cleft in the proximal half of the thigh. Distally,

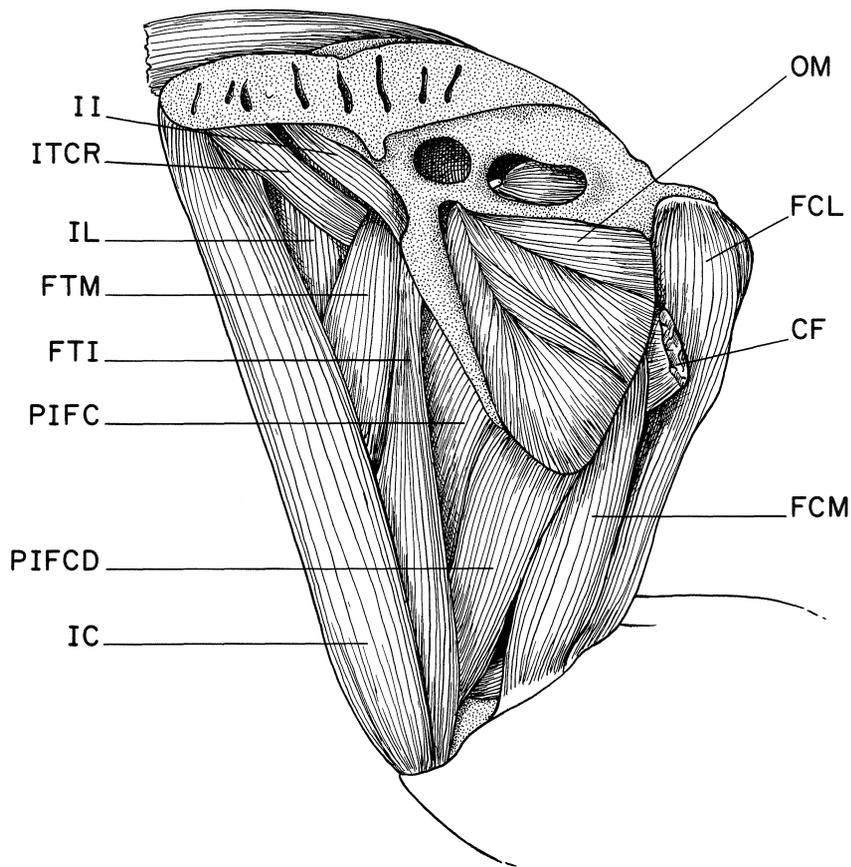


Fig. 7. Muscles on the medial surface of the thigh in *Atrichornis clamosus*. The expanded, doubly bipennate form of the *M. obturatorius medialis* (OM) is a synapomorphy of the Menuræ. For abbreviations see Materials and Methods.

however, they merge in a way that makes separation arbitrary.

**M. femorotibialis internus** (Fig. 7). In many passerines, including the Ptilonorhynchidae, Paradisaeidae and Corvidae (Borecky, 1977), this muscle is divided into two heads with separate tendons of insertion. In the Menuræ, however, there is only a single head and tendon.

**M. iliofibularis**. This muscle is generally of normal form, but more narrow than usual. It arises mainly fleshy along the dorsolateral iliac crest, and by a narrow aponeurosis at its cranial end from the deep surface of the overlying *M. iliotibialis lateralis*. The dorsolateral iliac crest projects laterally to an unusual degree, with the muscle arising fleshy from its ventral surface. The muscle then is fairly thick, and thus relatively massive despite its narrowness in the cranial-caudal dimension. Because the belly is narrow, the line of origin does not extend caudally as far as the cranial margin of the *M. flexor cruris lateralis*, but instead a small gap separates the two muscles at their origins.

**M. flexor cruris lateralis** (Figs 6, 7). This muscle is massively developed in the Menuræ. It arises mainly fleshy from the caudal end of the ilium which projects caudally as a bony projection, a continuation of the caudolateral iliac crest. The muscle arises from the lateral, caudal and medial surfaces of this projection. This origin is different from that in the

Ptilonorhynchidae, Paradisaeidae and most other passerine birds described, in that there is no aponeurotic origin from the caudal vertebrae. A similar condition exists, however, in many of the furnarioid or 'tracheophone' passerines (Raikow, unpubl. obs.). The belly passes distally to a raphe separating the proximal portion just described, *pars pelvica*, from the distal portion, *pars accessoria*. The raphe extends medially to fuse with the lateral surface of the distal end of *M. flexor cruris medialis*, contributing to the latter's tendon of insertion. It is also rather loosely joined to the adjacent *M. gastrocnemius pars intermedia*. *Pars accessoria* inserts fleshy on the femur in the popliteal area and on the shaft proximal to this and lateral to *M. pubo-ischio-femoralis pars cranialis* and medial to the biceps loop (*ansa M. iliofibularis*).

**M. caudofemoralis** (Figs 6, 7). The attachment to the femur and form of the belly are normal. The attachment to the pygostyle was not observed. The belly is relatively wider in *Atrichornis* than in *Menura*.

**M. ischiofemoralis** (Fig. 6). This is of normal form in the Menuræ. The area of origin is more extensive in *Atrichornis*, beginning dorsally just under the caudolateral iliac crest, while in *Menura* it arises only from the lateral surface of the ischium, its dorsal margin beginning even with the dorsal margin of the ilioischiatric fenestra.

**M. flexor cruris medialis** (Fig. 7). In *Atrichornis*, the

origin begins just caudal to that of the *M. pubo-ischio-femoralis* pars cranialis, while in *Menura* it is separated from that muscle by a gap of about 1 cm.

**M. pubo-ischio-femoralis** (Figs 6, 7). Pars cranialis is normal. In other passerines, the insertion of pars caudalis fuses with the origin of *M. gastrocnemius* pars intermedia, but in *Menura* these muscles are entirely separate, while in *Atrichornis* they are only slightly fused.

**M. obturatorius lateralis**. Pars ventralis is of normal form. Pars dorsalis is exceedingly small. It arises from the ischium just dorsal to the obturator foramen, passes cranio-laterally dorsal to the tendon of *M. obturatorius medialis* and inserts on the head of the femur just distal to that tendon, which it overlies slightly. The muscle has no origin from the ventral edge of the ilioischiatric fenestra. In *Atrichornis*, it consists of only a few fascicles, being practically absent. This is in great contrast to the condition in the Paradisaeidae, Ptilonorhynchidae and their allies (Borecky, 1977), where the muscle is very large, arising along nearly the entire ventral margin of the ilioischiatric fenestra. Furthermore, in those groups, the muscle inserts in part on the tendon of the *M. obturatorius medialis* and in part on the femur, rather than just on the femur as in the *Menurae*.

**M. obturatorius medialis** (Figs 6, 7). This triangular muscle is of unusual form in the *Menurae*. It is distinctly wider in dorsoventral dimension than is typical for passerines, including the bird-of-paradise assemblage (Borecky, 1977; pers. comm). From the medial aspect, its fibre arrangement is divided into two bipennate portions converging on the tendon of insertion, one dorsal and one ventral. Although this muscle is often divided into two bipennate regions, this is usually not visible from the medial surface. In the Paradisaeidae and allies, the medial aspect shows a simple bipennate pattern.

**M. iliofemoralis internus** (Fig. 7). This muscle arises fleshy from the ventrolateral surface of the ilium, just cranial to the acetabulum and caudal to the origin of *M. ilioprochantericus cranialis*. It inserts fleshy on the caudomedial surface of the femur. The muscle lies medial to *M. ilioprochantericus medius*. In *Atrichornis*, the cranial edge of the muscle is even with that of *M. ilioprochantericus medius*, while in *Menura* it originates slightly cranial to the cranial edge of that muscle. This is in contrast to the Paradisaeidae and Ptilonorhynchidae, in which *M. iliofemoralis internus* arises caudal to *M. ilioprochantericus medius* (Borecky, 1977).

**M. gastrocnemius**. Pars lateralis is of normal form in both genera and extends about  $\frac{2}{3}$  the length of the shank. Pars intermedia is of normal form. It extends about half the length of the crus in *Menura* and about  $\frac{1}{3}$  this distance in *Atrichornis*. Pars medialis has a well developed superficial head and a patellar band in both species, and is therefore Type 1 (Raikow, 1978). In *Atrichornis*, the patellar band does not quite reach the

patella, covering 0.80 of the patellar ligament, while in *Menura* it does reach the ventral edge of the patella (1.00). This is like the condition in the Ptilonorhynchidae, Paradisaeidae and most of the 'corvid assemblage' (Borecky, 1977), but as it is probably a primitive state in the oscines it is of little taxonomic significance.

**M. tibialis cranialis**. This is of normal form in the *Menurae* and extends about  $\frac{3}{4}$  the length of the crus.

**M. fibularis brevis**. This is of normal passerine form in *Menura*. In *Atrichornis*, the origin extends slightly proximal to the level of the *M. iliofibularis* tendon, but there is no tibial head as in the Drepanididae (Raikow, 1976).

**M. flexor perforans et perforatus digiti III**. This muscle extends about  $\frac{2}{3}$  the length of the crus. It is bipennate for its entire length, unlike the condition in the New World nine-primaried oscines (Raikow, 1976, 1978) and the bowerbird group (Borecky, 1977), where the proximal part is bipennate and the distal part is unipennate.

**M. flexor perforans et perforatus digiti II**. This muscle is of normal form, including a partial origin from the adjacent *M. flexor perforans et perforatus digiti III*. It extends  $\frac{1}{2}$  the length of the crus in *Atrichornis* and  $\frac{3}{4}$  in *Menura*. At its insertion, the tendon ensheathes that of the *M. flexor digitorum longus*, which is the primitive state (Borecky, 1977).

**M. flexor perforatus digit IV**. In *Menura*, this arises by a tendon from the intercondyloid region in common with *M. flexor perforatus digiti III* and the medial head of *M. flexor hallucis longus*. In *Atrichornis*, the origin is similar but is partly fleshy. The structure of this muscle corroborates Sibley's hypothesis of oscine affinities for the *Menurae*. In dissections of many oscine and suboscine groups, I have found that this muscle has three distinctively different forms among the passerine birds. In Type 1, the muscle has two separate bellies: a lateral belly arising near the proximal end of the crus mainly from the head of the fibula, and a medial belly arising from the intercondyloid region of the femur. These bellies give rise to separate tendons that pass distally, fusing into a single tendon just before entering the tibial cartilage at the intertarsal joint. This type was found in the Pittidae, Philepittidae, Furnariidae, Formicariidae, Dendrocolaptidae, Rhinocryptidae and some species of Eurylaimidae. Because this condition is similar to that in most nonpasserine birds, and because the order Passeriformes is monophyletic (Raikow, 1982), outgroup comparison indicates that Type 1 is primitive among passerines. Type 2 is different, having two bellies but with a single tendon. Variants of this type occur in the Tyrannidae, Cotingidae and Pipridae, and in some Eurylaimidae. These are derived states in the passerines. The third major variation in *M. flexor perforatus digiti IV* is Type 3, in which only the medial belly is present, and no lateral component of any sort occurs. This is a derived state that helps to define the oscines as a clade. The

Menuræ have this condition, which confirms that they are part of a clade with the oscines, but does not itself indicate anything about their relationship to any particular oscine group.

**M. flexor perforatus digiti III.** This muscle is of normal passerine form; as in other birds its tendon is joined by the long branch of the tendon of insertion of *M. fibularis longus*. The muscle arises by a long tendon from the intercondyloid region of the femur in common with *M. flexor perforatus digiti IV*; this tendon is separate from the origin of *M. flexor hallucis longus*. In *Menura* the belly does not extend as far caudally as does that of *M. flexor perforatus digiti IV*, while in *Atrichornis* it extends farther caudally than the latter.

**M. flexor perforatus digiti II.** This muscle is of normal passerine form. At its insertion, the tendon is not bifurcate and is not perforated by the tendons of *Mm. flexor perforans et perforatus digiti II* and *flexor digitorum longus*. In the Paradisæidae and most Ptilonorhynchidae (Borecky, 1977), it is bifurcate and perforated.

**M. plantaris.** This is of normal form in the Menuræ. It extends about  $\frac{1}{4}$  the length of the crus in *Menura* and slightly less in *Atrichornis*.

**M. flexor hallucis longus.** This muscle arises by three heads, as in passerines generally. The lateral head arises from the lateral femoral condyle by a tendon shared with *M. flexor perforatus digiti II*, as in other passerines. The intermediate head has a fleshy origin from the medial intercondyloid region of the femur, just lateral to the tendon of origin of the medial head. It is large in *Menura* and smaller in *Atrichornis*. In contrast, this head arises by a tendon in the Paradisæidae and relatives (Borecky, 1977) and other passerines (Raikow, 1978). The medial head arises by a tendon in common with *M. flexor perforatus digiti III* and *M. flexor perforatus digiti IV* in the Menuræ, while in other passerines this origin is fleshy.

**M. flexor digitorum longus.** In the Menuræ, this muscle arises by two heads, one from the fibula and one from the tibiotarsus, as in most birds. In the Corvidæ and Paradisæidae (except *Loria*), there is a third head from the intercondyloid region of the femur. This is lacking in the Ptilonorhynchidae.

**M. flexor hallucis brevis.** This small muscle of the foot is of normal size in the Menuræ, while in the Paradisæidae and Ptilonorhynchidae it is enlarged compared to most passerines (Borecky, 1977).

**M. extensor hallucis longus.** This is of normal form, though quite slender. A distal head was observed in *Atrichornis*, but could not be discerned in *Menura*.

### SYSTEMATIC CONCLUSIONS

Most of the forelimb muscles of the Menuræ are of typical oscine form. Where unusual conditions occur, the two genera are usually similar, so that the forelimb myology confirms their close relationship. The major differences between the Menuræ and the

Ptilonorhynchidae and Paradisæidae are summarized in Table 1. Some of the peculiarities of the Menuræ are clearly correlated with their near loss of flight; certainly this is the explanation for the reduced size of the *M. pectoralis* and *M. supracoracoideus*, and for the reduction of the clavicle in *Atrichornis*. In these respects *Atrichornis* is more highly derived than is *Menura*. The forearm muscles of the Menuræ are relatively longer than those of the bowerbirds and birds-of-paradise, mostly reaching nearly the whole length of the forearm. However, in the Menuræ, the forelimb skeleton is shortened relative to strongly flying birds (see below).

Other peculiarities of the forelimb muscles in the Menuræ are more difficult to explain. The enlarged *M. latissimus dorsi pars caudalis* and the development of a proximal head in the *M. deltoideus major* differ from the condition in passerines generally. Thus, it is difficult to assess their significance relative to the Sibley and Ahlquist hypothesis. They are probably synapomorphies of the Menuræ that developed after separation from their common ancestor with their closest relatives, whether these are the bowerbirds or some other group. The presence of a well developed *M. coracobrachialis cranialis* is not an indication of affinity between the Menuræ and the bowerbirds as it is a primitive character state in the Passeriformes.

The hindlimb muscles give a similar picture (Table 2). Several muscles are distinctly different, not only from the bowerbird group, but from passerines generally; these include the *M. femorotibialis externus*, *M. flexor cruris lateralis*, *M. obturatorius medialis*, *M. flexor perforans et perforatus digiti III* and *M. flexor hallucis longus*. Other muscles show character states found in some other passerines, but differing significantly from the bowerbirds and birds-of-paradise; these include the *M. femorotibialis internus*, *M. obturatorius lateralis pars dorsalis*, *M. iliofemoralis internus*, *M. flexor perforatus digiti II*, *M. flexor digitorum longus* (in part) and *M. flexor hallucis brevis*. Again, these are not readily explained by reference to the near loss of flight in the Menuræ.

Based on the preceding discussion and the differences noted in Tables 1 and 2, it is clear that the appendicular myology does not support the hypotheses (Sibley, 1974, 1976; Sibley & Ahlquist, ms.) that the Menuræ are closely allied to the Ptilonorhynchidae or Paradisæidae, but shows that they are structurally quite different. It is important here to clarify the possible meaning of 'relationship'. Phenetically, the two groups are quite dissimilar, but in cladistic or historical terms the problem is not degree of similarity, but recency of common ancestry. Sibley & Ahlquist hypothesize that the Menuræ and Ptilonorhynchidae are sister groups, that is, that they share a more recent common ancestry with each other than with any other group. The Menuræ possess a number of distinctive myological conditions not otherwise known in passerines, and therefore it is impossible to suggest another group with which they might share a more recent common ancestry than with the bowerbirds. It is possible that the

peculiarities of the Menuræ arose after their separation from a common ancestry with the bowerbirds, but this could also be suggested for other possible sister groups. Thus, the limb muscle characters of the Menuræ neither corroborate nor refute the hypothesis that the Menuræ are most closely related to the Ptilonorhynchidae. Other systems may provide data showing such a relationship; such similarities will be most convincing if they constitute shared derived character states.

The appendicular myology strongly corroborates the close affinity of the Atrichornithidae and Menuridae. Some muscles differ slightly in size or proportions, generally those of the Menuridae being relatively larger in association with the lyrebirds' greater body size. Several differences may be noted (Table 3). These are minor compared to the distinctive and apparently synapomorphous similarities shared with no other known taxa. In addition, the *M. flexor perforatus* digiti IV, as discussed above, clearly confirms the affinity of the scrub-birds and lyrebirds with the oscines.

Considering their large size and specialized plumages, the Menuridae might be regarded as more highly derived than the Atrichornithidae, with their more typical passerine body size and nondescript plumage. In terms of limb morphology, however, the scrub-birds are the more advanced of the two families. This is seen in their more greatly reduced flight muscles (see below), the reduction of the clavicle and loss of the clavicular origin of the *M. pectoralis*, the greater separation of the proximal head of the *M. deltoideus major pars cranialis*, and the reduced extent of the origin of the *M. iliobtibialis cranialis*.

#### FUNCTIONAL ANATOMY OF THE FORELIMB

**Pectoral muscles.** Reduction in the size of the pectoral muscles commonly accompanies the loss of flight in birds. I divided the wet weight of the paired muscles by the weight of the bird recorded before preservation. This value is the percent-weight of the muscle. The *M. pectoralis* provides the force for the downstroke or power stroke in flight, while *M. supracoracoideus* provides the upstroke or recovery stroke. Detailed descriptions of these muscles are given above. Table 4 shows that these muscles are reduced to less than half their 'normal' size in the Menuræ, and are more reduced in *Atrichornis* than in *Menura*. The extent of the area of origin of both muscles is also reduced in *Atrichornis* compared to *Menura*. The reduction in *Atrichornis* especially is very evident from observation of the intact specimen (Fig. 8). Associated with the extreme reduction of *M. pectoralis* in *Atrichornis* is the loss of the distal part of the clavicular shaft (Figs 3, 5, 9). A similar phenomenon was reported in a few other species by Glenny & Friedmann (1954) who noted that the distal part of the clavicle sometimes remains as an unossified ligament (Ligamentum corpus claviculi). In *Atrichornis*, however, there was no sign of such a ligament, and the short clavicular shaft merely ended within the belly of the *M. pectoralis* (Fig. 3). In

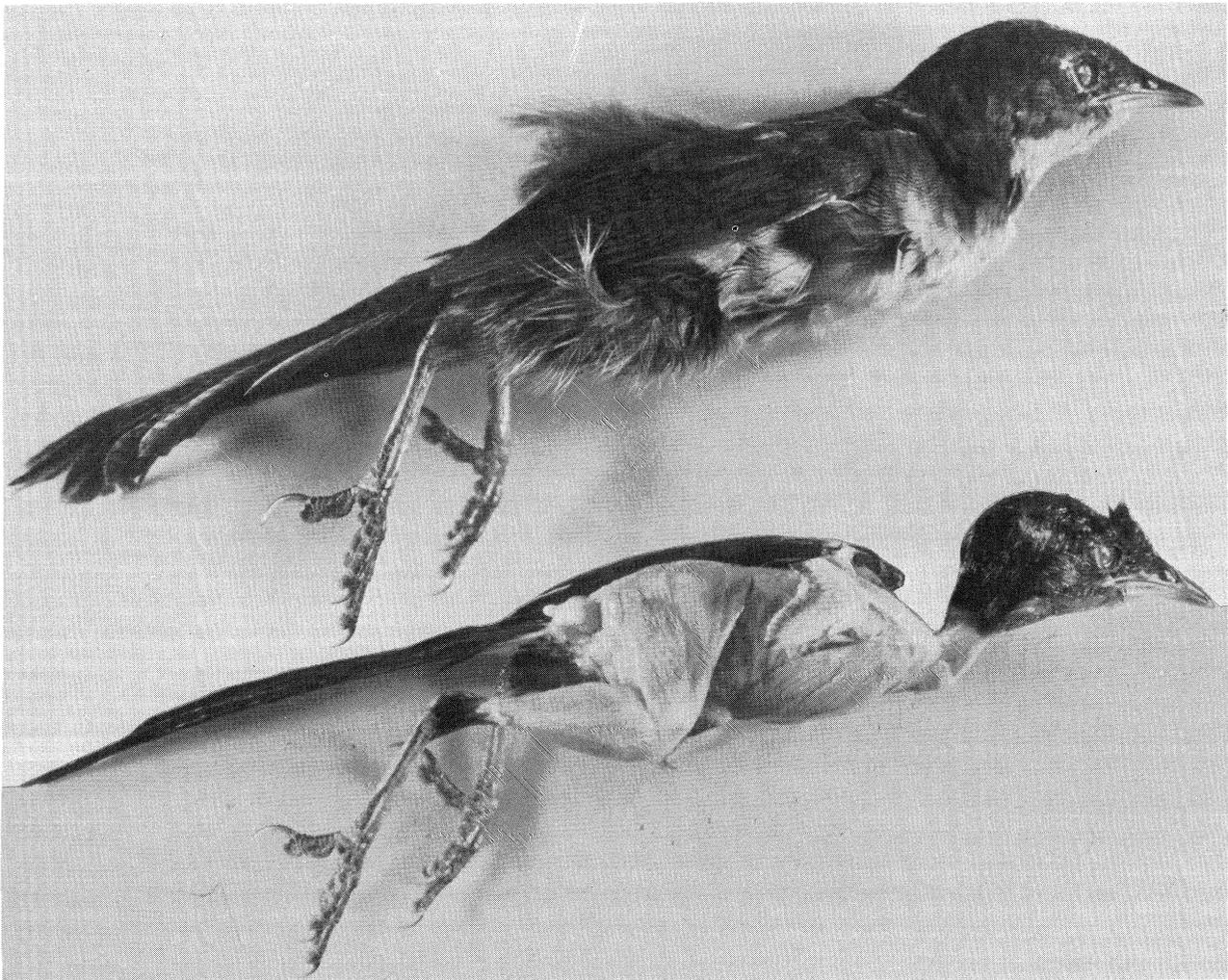
both forms, the sternal carina is correspondingly shallow.

**Forelimb length.** The lengths of the upper arm, forearm and manus were measured in the intact specimens after skinning; their sum is the total forelimb length. These values, divided by the cube root of body weight, give a measure of the lengths of the parts, relative to body size, corrected for differences in weight so that the species may be compared directly (Table 5). Compared to the reference species, *Atrichornis* shows about a 25% reduction in forelimb length. This reduction is not proportional in the three segments. Compared to the mean reference values, the upper arm is reduced about 5%, the forearm about 41% and the manus about 30%. The comparison with *Menura* is difficult because of the great difference in body size, but it is probably valid to assume that the relationship of wing length to body size holds across this range, as Greenewalt (1962) found this to be generally true with other wing length measurements across a much greater size range. Compared to the mean reference value, *Menura* shows a total forelimb length reduction of about 7%, with reduction in the individual segments being about 3% in the upper arm, 14% in the forearm and 5% in the manus. As in *Atrichornis*, the greatest reduction is in the forearm and the least in the upper arm. Although the values for *Menura* are below the means for the reference species, only the length of the forearm lies below the range of reference values. Thus, although *Menura* undoubtedly has a relatively short forelimb, it is uncertain to what extent this is biologically significant in relation to the reduction of flight. These values, though only rough estimates, do provide the means to compare the deviation of values in the Menuræ from approximate expected values. In association with the nearly complete loss of the ability to fly, *Atrichornis* shows a clear reduction in forelimb length, and *Menura* a lesser but probably real reduction, both species having a similar pattern of relative reduction in the upper arm, forearm and manus.

Some brief comments on the reduction of flight in the Menuræ, with additional specimen photographs, are presented elsewhere (Raikow, 1985: 85-86).

#### FUNCTIONAL ANATOMY OF THE HINDLIMB

**Hindlimb length.** The lengths of the thigh, crus and tarsus were measured, their sum being the total hindlimb length. As with the forelimb, these values were divided by the cube root of body weight to give comparative values. In this limb, both genera show relative elongation compared to the oscine 'standard' (Table 6). *Atrichornis* has a hindlimb 8.4% longer than the mean value, but not the highest value of the forms examined. *Menura* has a relatively longer hindlimb than any form examined (about 27% above the mean reference value). *Atrichornis* has its greatest elongation in the thigh (15% elongated), but less in the crus (8%) and tarsus (3%). *Menura* has less relative elongation in the thigh (6%), but a greatly elongated crus (32%) and tarsus (38%).



**Fig. 8.** Noisy Scrub-bird, *Atrichornis clamosus*, preserved specimen, photographed intact (above) and after skinning (below). Note the dorsoventral flattening of the body due to the greatly reduced pectoral muscles, and the relative proportions of the large hind limbs and reduced forelimbs.

Just as the forelimb shows reduction in length in the Menuræ, the hindlimb shows relative elongation, especially in *Menura*. This is presumably correlated with these species' terrestrial habits, and probably also with the use of the legs for digging by *Menura*.

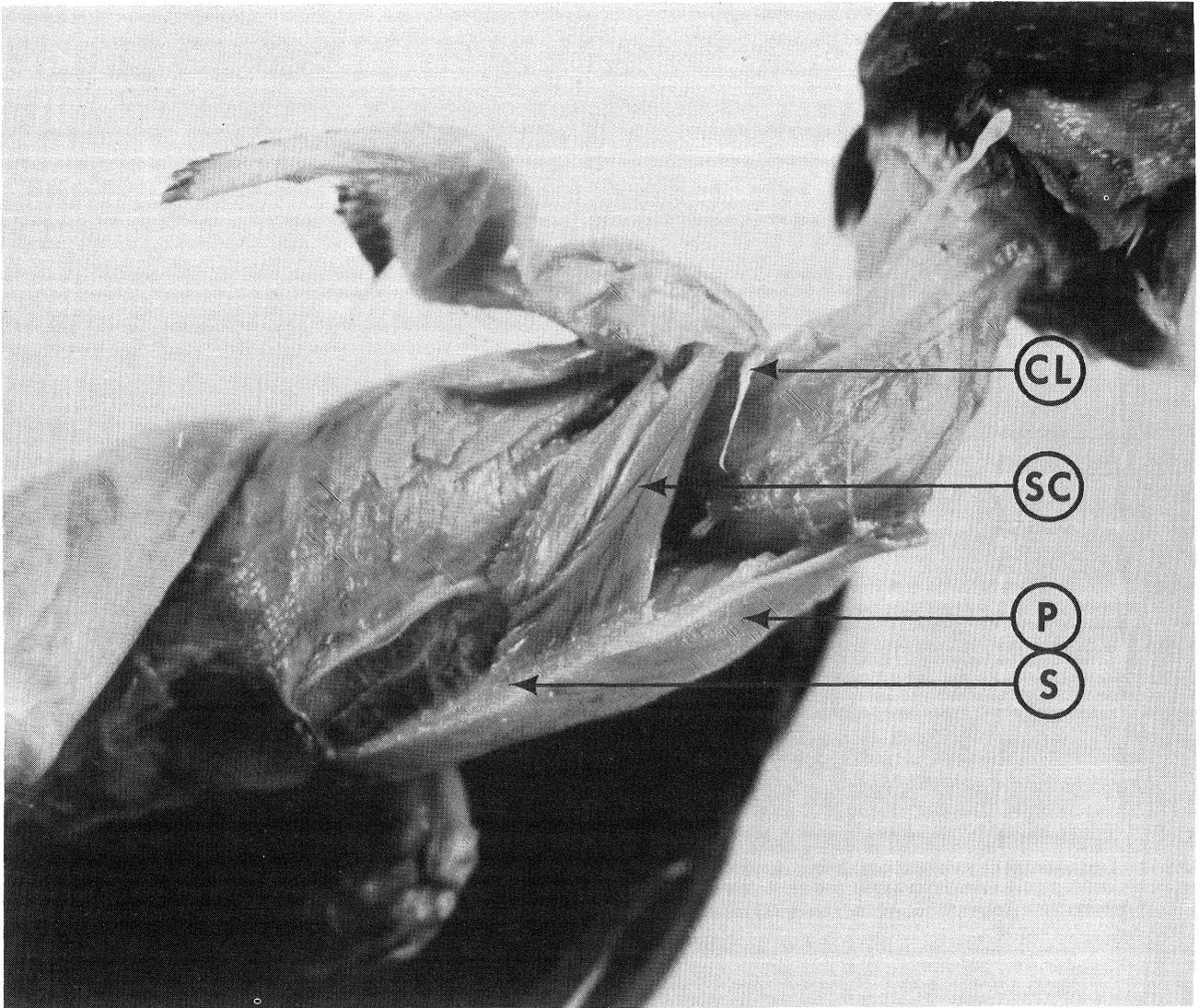
The preceding discussion has shown that the Menuræ have rather short forelimbs and long hindlimbs. This is most clearly demonstrated by the ratio of total forelimb length to total hindlimb length (Table 6, last column). Despite differences in intramembral proportions, both genera are remarkably similar in this value, and distinctly separated from the other species studied.

**Claws.** In *Atrichornis* (Table 7), the claw of digit I is moderately longer than in the standard, while that of *Menura* is considerably longer. This may be related to their terrestrial habits, as an elongated first claw is not uncommon in passerines like longspurs and larks. However, in such cases this claw is usually rather straight, that is, having a small degree of curvature,

which presumably helps to spread the bird's base of support on the ground. In the Menuræ, however, the curvature is not drastically reduced (Table 9) and in the male *Menura* was quite high. Probably this is related to the use of the foot in grasping by *Menura*.

In *Atrichornis*, the claws of digits II, III and IV are relatively short and only moderately curved (Tables 7, 9), which is probably correlated with the fact that *Atrichornis* seldom, if ever, uses its feet either for perching or for grasping objects. Combined with the well developed claw of digit I, this gives the foot of *Atrichornis* a distinctive appearance (Fig. 10).

In *Menura*, the claws of digits II, III and IV are much elongated (Table 7), though not too sharply curved (Table 9). They are heavy and wide, and the tips are rounded off, perhaps by abrasion during digging. In typical passerines, the third digit is considerably longer than digits II and IV, and the same is true in *Atrichornis*. In *Menura*, however, these digits are almost as long as digit III. In addition, *Menura* is unique in that the claws



**Fig. 9.** Noisy Scrub-bird, *Atrichornis clamosus*, in ventrolateral aspect, following removal of the *M. pectoralis* on the right side of the body. Note the vestigial clavicle (CL) and the shallow sternal carina (S). Other abbreviations are as in Materials and Methods.

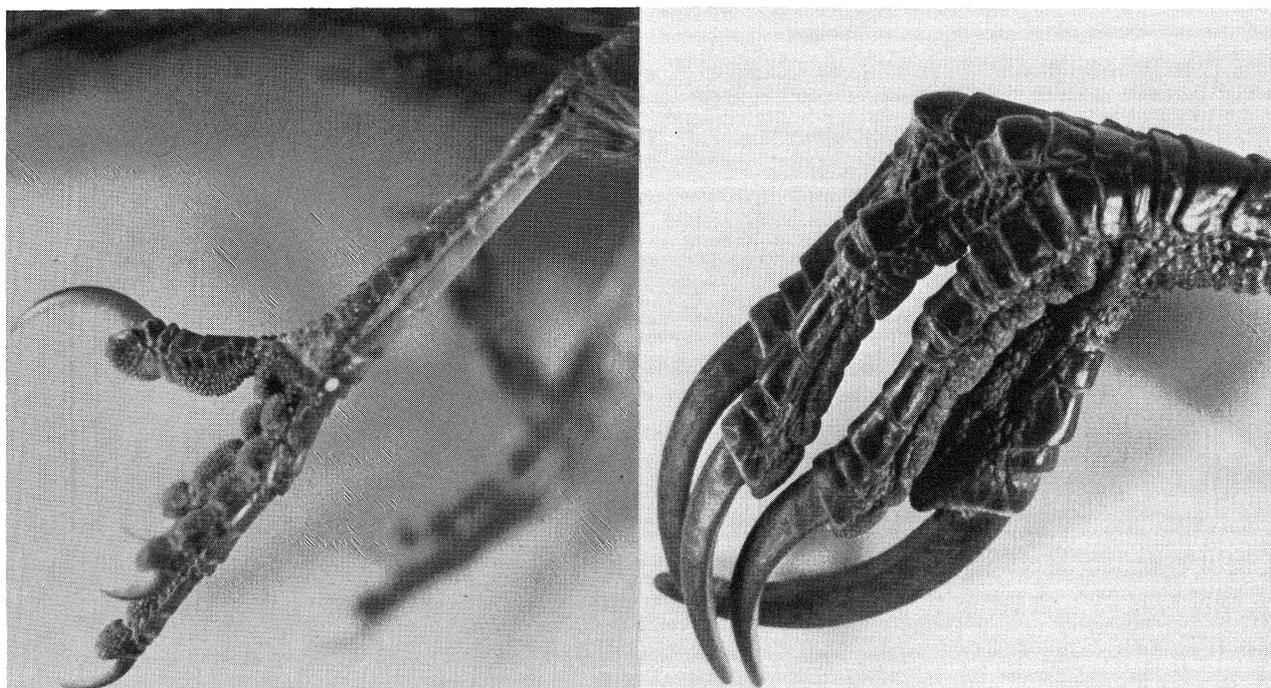
of digits II and IV are essentially equal in length to that of digit III, while in the other species, including *Atrichornis* (Fig. 10), they are shorter (Table 8). As a result, when the three anterior toes are held together the tips of the claws are nearly in line, rather than claw III extending beyond claws II and IV as is typical. This is perhaps an adaptation for digging, giving a cutting surface three times as wide as would otherwise be the case.

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**Fig. 10.** Foot of *Atrichornis clamosus* (left) and *Menura novaehollandiae* (right). Not to scale. Note that in the scrub-bird the claws of the anterior digits are relatively small and pointed, and that digit III extends well beyond digits II and IV. In *Menura*, however, the claws are extremely heavy, with rounded tips, and extend to nearly the same level. See text for discussion.

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Muscle	Menurae	Ptilonorhynchidae/Paradisaeidae
M. latissimus dorsi pars caudalis	Extremely enlarged with extensive area of origin	Narrow in usual passerine condition
M. pectoralis	Reduced in size	Normal size
M. supracoracoideus	Reduced in size	Normal size
M. tensor propatagialis pars brevis	Tendon of insertion fused with tendon of origin of M. extensor metacarpi radialis in <i>Menura</i> , separate in <i>Atrichornis</i>	Tendons separate in normal passerine manner
M. deltoideus major	Pars cranialis with proximal head	Proximal head lacking
M. deltoideus minor	Origin from apex of coracoid, slightly from scapula	Origin extensive from scapula alone in most Paradisaeidae, from coracoid and extensively from scapula in <i>Loria</i> and Ptilonorhynchidae
Forearm muscles	Relatively long	Relatively short

**Table 1.** Major differences in the forelimb muscles of the Menurae, the bowerbirds and the birds-of-paradise.

Muscle	Menurae	Ptilonorhynchidae/Paradisaeidae
M. iliofemoralis externus	Absent in both genera	Present in Ptilonorhynchidae and some Paradisaeidae
M. femorotibialis externus	More separate from M. femorotibialis medius	More fused to M. femorotibialis medius
M. femorotibialis internus	Single head and tendon	Two heads and tendons
M. flexor cruris lateralis	Origin from ilium only	Origin from ilium and caudal vertebrae
M. obturatorius lateralis pars dorsalis	Extremely small	Extremely large
	No origin from ventral edge of ilioischiatric fenestra	Originates from ventral edge of ilioischiatric fenestra
	Inserts on femur only	Inserts on femur and on tendon of M. obturatorius medialis
M. obturatorius medialis	Wider; doubly bipennate in medial aspect	Narrower; singly bipennate in medial aspect
M. iliofemoralis internus	Arises medial to M. iliotrochantericus medius	Arises caudal to M. iliotrochantericus medius
M. flexor perforans et perforatus digiti III	Bipennate for entire length	Bipennate proximally, unipennate distally
M. flexor perforatus digiti II	Tendon not bifurcate or perforated	Tendon bifurcate and perforated (most)
M. flexor hallucis longus	Origin of intermediate head fleshy	Origin tendinous
	Origin of medial head tendinous	Origin fleshy
M. flexor digitorum longus	Femoral head absent	Femoral head present in most Paradisaeidae
M. flexor hallucis brevis	Relatively small	Relatively large

**Table 2.** Major differences in the hindlimb muscles of the Menurae, the bowerbirds and the birds-of-paradise.

Muscle	<i>Menura</i>	<i>Atrichornis</i>
FORELIMB		
M. pectoralis	Normal origin from clavicle	Origin from clavicle almost completely lost
M. supracoracoideus	Origin more extensive, including sternoclavicular membrane	Origin less extensive, not including sternoclavicular membrane
M. tensor propatagialis pars brevis	Tendon of insertion fused to M. extensor metacarpi radialis for entire length	Tendon of insertion separate except distally
M. deltoideus major	Proximal head of pars cranialis not distinctly separate	Proximal head distinctly separate
HINDLIMB		
M. iliotibialis cranialis	Origin from median dorsal ridge of synsacrum and cranial edge of ilium	Origin from median dorsal ridge only
M. ischiofemorialis	Origin from lateral surface of ilium	Origin from lateral surface of ilium and caudolateral iliac crest
M. gastrocnemius	Patellar band wider	Patellar band narrower

**Table 3.** Major differences in the limb muscles of *Menura* and *Atrichornis*.

Species	Weight (g)	Percent-Weight of M. pectoralis	Percent-Weight of M. supracoracoideus
<i>Menura novaehollandiae</i>	921.4	5.64	0.64
<i>Atrichornis clamosus</i>	34.0	3.71	0.38
<i>Zonotrichia leucophrys</i>	31.9	11.29	1.48
<i>Chondestes grammacus</i>	27.8	13.60	1.59
<i>Carpodacus purpureus</i>	30.0	14.80	1.27
<i>Cardinalis cardinalis</i>	40.0	12.05	1.38
<i>Dumetella carolinensis</i>	34.9	11.46	1.37
Mean of non-Menuræ species		12.64	1.42

**Table 4.** Relative weights of the pectoral muscles.

Species	Upper Arm	Forearm	Manus	Total Forelimb Length
<i>Menura novaehollandiae</i>	7.31	6.61	6.53	20.45
<i>Atrichornis clamosus</i>	7.13	4.51	4.85	16.49
<i>Zonotrichia leucophrys</i>	7.03	6.72	6.06	19.81
<i>Chondestes grammacus</i>	7.52	7.92	7.33	22.77
<i>Carpodacus purpureus</i>	7.20	7.72	6.82	21.74
<i>Cardinalis cardinalis</i>	7.84	7.95	6.81	22.60
<i>Dumetella carolinensis</i>	7.95	7.98	7.37	23.30
Mean of non-Menuræ species	7.51	7.66	6.88	22.04

**Table 5.** Forelimb measurements/cube root of weight.

Species	Thigh	Crus	Tarsus	Total Hindlimb Length	Forelimb length/Hindlimb length
<i>Menura novaehollandiae</i>	6.80	14.65	8.86	30.31	0.67
<i>Atrichornis clamosus</i>	7.35	11.91	6.64	25.90	0.64
<i>Zonotrichia leucophrys</i>	6.78	11.29	6.69	24.76	0.80
<i>Chondestes grammacus</i>	6.01	10.36	6.11	22.48	1.01
<i>Carpodacus purpureus</i>	5.59	9.77	5.21	20.57	1.06
<i>Cardinalis cardinalis</i>	6.37	11.05	6.49	23.91	0.95
<i>Dumetella carolinensis</i>	7.31	12.84	7.61	27.76	0.84
Mean of non-Menuræ species	6.41	11.06	6.42	23.90	0.92

**Table 6.** Hindlimb measurements/cube root of weight.

Species	Digit I	II	III	IV
<i>Menura novaehollandiae</i> (male)	3.26	2.52	2.50	2.44
<i>Menura novaehollandiae</i> (female)	3.06	2.57	2.45	2.32
<i>Atrichornis clamosus</i>	2.17	1.02	1.25	0.94
<i>Zonotrichia leucophrys</i>	2.04	1.18	1.46	1.09
<i>Chondestes grammacus</i>	1.56	0.92	1.31	0.97
<i>Carpodacus purpureus</i>	1.38	0.85	1.45	0.95
<i>Cardinalis cardinalis</i>	1.94	1.14	1.82	1.13
<i>Dumetella carolinensis</i>	2.07	1.27	1.83	1.25
Mean of non-Menuræ species	1.80	1.07	1.57	1.08

**Table 7.** Claw length/cube root of weight.

Species	Digit II	Digit IV
<i>Menura novaehollandiae</i> (male)	1.00	0.98
<i>Menura novaehollandiae</i> (female)	1.09	0.98
<i>Atrichornis clamosus</i>	0.81	0.76
<i>Zonotrichia leucophrys</i>	0.80	0.76
<i>Chondestes grammacus</i>	0.72	0.74
<i>Carpodacus purpureus</i>	0.60	0.72
<i>Cardinalis cardinalis</i>	0.59	0.62
<i>Dumetella carolinensis</i>	0.71	0.71
Mean of non-Menuræ species	0.68	0.71

**Table 8.** Lengths of claws II and IV/length of claw III.

Species	Digit I	II	III	IV
<i>Menura novaehollandiae</i> (male)	48.5	38.6	35.3	44.6
<i>Menura novaehollandiae</i> (female)	42.4	36.0	35.1	38.0
<i>Atrichornis clamosus</i>	41.5	34.4	37.8	37.5
<i>Zonotrichia leucophrys</i>	37.6	30.5	31.8	32.7
<i>Chondestes grammacus</i>	42.3	40.5	44.7	46.3
<i>Carpodacus purpureus</i>	51.2	42.6	42.7	42.3
<i>Cardinalis cardinalis</i>	45.9	46.1	45.0	43.4
<i>Dumetella carolinensis</i>	48.3	45.5	44.4	46.2
Mean of non-Menuræ species	45.1	41.0	41.7	42.2

**Table 9.** Arcs of claws (degrees).