Muscles of the Neck, Trunk and Tail in the Noisy Scrub-bird, *Atrichornis clamosus*, and Superb Lyrebird, *Menura novaehollandiae* (Passeriformes: Atrichornithidae and Menuridae)

R. L. ZUSI

National Museum of Natural History, Smithsonian Institution,
Washington, DC 20560, U.S.A.

ABSTRACT. Muscles of the neck, trunk and tail of the Noisy Scrub-bird, *Atrichornis clamosus*, are described, illustrated and compared with those of the Superb Lyrebird, *Menura novaehollandiae*. It is proposed that hypertrophy of various neck muscles in *Atrichornis* is related to use of the head in penetrating litter and undergrowth. *Atrichornis* and *Menura* are shown to have qualitative differences in myology and in morphology of the uropygial glands, but taxonomic interpretation of these differences is judged to be premature without broader comparisons.

The Noisy Scrub-bird, *Atrichornis clamosus* (Gould), is an endangered species of passerine bird restricted to Western Australia. The only other species in the genus, *Atrichornis rufescens* (Ramsay), occurs in eastern Australia. Until recently, little was known of the internal anatomy of either species, except for the structure of the syrinx, some peculiarities of the skeleton and notes on the myology of the shoulder (Fürbringer, 1888). In this paper I describe the skeletal myology of the neck, trunk and tail, from a single specimen of *Atrichornis clamosus* (adult female, Western Australian Museum A15926). Muscles of the tongue, jaws and appendages of that specimen have been described elsewhere (Bock, 1985; Raikow, 1985). In addition, I present comparative comments on the Superb Lyrebird, *Menura novaehollandiae* Latham, based on my dissection of a single specimen (adult female, Carnegie Museum Alc1834).

My primary purpose is to place the myological data from these specimens on record for comparison with other species. It is beyond the scope of this paper to make a critical appraisal of the phylogenetic relationships of *Atrichornis* because there is no existing body of data on these muscles for comparison. Such a study would require dissection of species from many oscine and suboscine families and subfamilies.

It is ironic that *Atrichornis* should be the subject of the first exposition of the trunk and tail muscles in a passerine bird since that of Shufeldt (1890) who described most of these muscles for the Common Raven, *Corvus corax* Linnaeus. Unfortunately his work is not always adequate for comparison with other species. Muscles of the trunk of the American Crow, *Corvus brachyrhynchus* Brehm, were illustrated but not described by Hudson & Lanzillotti (1955). Several studies have dealt with passerine neck muscles: Shufeldt (1890) described the Common Raven (Corvidae); Palmgren (1949) compared a few species from the Paridae, Certhiidae, Sylviinae, Turdinae and Carduelinae; and Burton (1974) described the Callaeidae. Boas (1929) and Kuroda (1962) treated passerines only incidentally.

Palmgren (1949) interpreted most differences among the several families he dissected as adaptations for foraging. The differences are mainly in the relative sizes of muscles, in the numbers of slips of complicated muscles and in the vertebrae on which they attach. I have drawn tentative conclusions about the adaptations of *Atrichornis* based on limited comparisons of such differences.

MATERIALS AND METHODS

Dissection was done entirely under a dissecting

microscope and all drawings, except those labelled 'diagrammatic', were made by me in pencil with a camera lucida. No skeletal specimen of *Atrichornis* was available, and drawings of bony elements are therefore somewhat crude because of the presence of connective tissue or parts of muscles. The abdominal muscles had been cut and were shrunken and contorted, making camera lucida drawings impossible.

Terminology of muscles and bones generally follows that of Baumel *et al.* (1979). Myological differences between *Atrichornis clamosus* and *Menura novaehollandiae*, as well as some other passerines, are noted after the descriptions of *Atrichornis*, and when no difference is given, similarity between the two species is implied. Information on families other than Menuridae came from Palmgren (1949) and Burton (1974).

Throughout this paper the use of a numeral in a muscle description indicates a particular vertebra. Cervical vertebrae are numbered 1–14 beginning with the atlas, and the thoracic vertebrae, 15–19.

The following list identifies abbreviations that appear in the figures:

b c	M. (musculus) biventer cervicis
b r	M. bulbi rectricium
c	M. complexus
c a	M. cervicalis ascendens
cf	M. caudofemoralis
csp	M. costoseptalis
cst	M. costosternalis
cst ma	M. costosternalis, pars major
cst mi	M. costosternalis, pars minor
d c	M. depressor caudae
f c l	M. flexor colli lateralis
f c m	M. flexor colli medialis
ic	Mm. (musculi) intercristales
i e	Mm. intercostales externi
i i	Mm. intercostales interni
ilc	M. iliocostalis
in i	Mm. inclusi inferior
in s	Mm. inclusi superior
it	Mm. intertransversarii
la c	M. lateralis caudae
l c d ca	M. longus colli dorsalis, pars caudalis
l c d cr	M. longus colli dorsalis, pars cranialis
l c d p	M. longus colli dorsalis, pars profunda
l c d t	M. longus colli dorsalis, pars thoracica
l cl	M. levator cloacae
l co	Mm. levatores costarum
l c v	M. longus colli ventralis
l d d	M. latissimus dorsi dorsocutaneous
le c	M. levator caudae
o e a	M. obliquus externus abdominis
o i a	M. obliquus internus abdominis
p	Pygostylus
p e	M. pubocaudalis externus
p i	M. pubocaudalis internus
p s a	M. pectoralis, pars subcutanea abdominalis
r a	M. rectus abdominis

r c d	M. rectus capitis dorsalis
r c l	M. rectus capitis lateralis
r c v	M. rectus capitis ventralis
s	M. scalenus
s ca	M. splenius capitis
s cl	M. sphincter cloacae
se	M. serpihyoideus
t ab	M. transversus abdominis
t as	M. thoracicus ascendens
t c	M. transversus cloacae
u	Glandula uropygialis

OSTEOLOGY

Commonly used synonyms for some of the osteological terms in this paper are as follows:

This paper	Synonym
VERTEBRAE	
vertebral arch	neural arch
vertebral body	centrum
cranial articular process	prezygapophysis
caudal articular process	postzygapophysis
dorsal process	anapophysis
costal spine	cervical rib
costal process	'ansa' (Boas 1929)
carotid process	sublateral process
spinous process	neural spine
ventral process	hypapophysis
STERNUM	
trabecula lateralis	posterior lateral process
craniolateral process	sternocoracoidal process

The following comments are based on my observations on the skeletons of the spirit specimens of *Atrichornis clamosus* and *Menura novaehollandiae*, and skeletons of species from various other passerine families.

Both Palmgren (1949) and Burton (1974) stated that the neck in the passerine families they studied was subdivided into functional sections as follows: Section I, vertebrae 1–4; Section II, vertebrae 5–9; Section III, vertebrae 10–14 (Palmgren omitted the two cervical vertebrae that bear floating ribs from his count). My interpretation of the limits of Section II differs slightly from theirs. Boas (1929) defined the second section primarily on its capacity to bend upward, but not downward beyond a straight line. Nevertheless, he also included only vertebrae 5–8 or 5–9 in this section for various passerine families. I include vertebrae 5–10 in the second neck section of *Atrichornis*, *Menura* and the species studied by Palmgren and Boas, on the basis of the bending capability of that section and the associated morphology of the vertebrae. Vertebra 10 is intermediate in form between typical vertebrae of the second and third sections, but it more closely resembles the former. Thus, in my opinion, the neck sections of *Atrichornis* and *Menura*, as in many other passerines, are constituted as follows: I, 1–4; II, 5–10; III, 11–14.

Atrichornis and *Menura* have five free thoracic vertebrae and five ribs that attach on the sternum. Each

thoracic rib consists of a dorsal vertebral rib and a ventral sternal rib. In the sixth, or accessory rib, the vertebral rib articulates with the synsacrum and the associated sternal rib fails to reach the sternum. In addition, there are two floating cervical ribs — a small one from 13, and a larger one from 14 that bears an uncinate process. Spinous processes are borne on vertebrae 2-5, 6 (small), 13, 14 and the five thoracic vertebrae. Ventral processes occur on 2, 3, 4 and 10-15. Costal spines occur on vertebrae 3-12. The terms cranial, caudal, dorsal and ventral apply to the bird when its vertebral column is extended horizontally.

NECK MUSCLES

M. biventer cervicis (b c; Fig. 1A,B,C,D,E). This muscle consists of a long tendon interrupted by two fleshy bellies. The muscle lies superficial to M. longus colli dorsalis and partly deep to M. complexus. It originates from the spinous processes of 14, 15 and 16, and by an aponeurosis that is fused caudally with the underlying aponeurosis of M. longus colli dorsalis, pars caudalis. The aponeurosis of origin broadens as it passes craniad to the stout, strap-like caudal belly overlying vertebrae 13-18. From this belly, a broad tendon passes craniad through a connective tissue sheath enclosing the dorsal neck muscles over vertebrae 7, 8 and 9. The cranial belly begins at the level of 4 and ends on a short, broad aponeurosis that attaches on the occipital wall of the cranium between the insertions of M. complexus and M. splenius capitis.

In *Menura*, the muscle is proportionately weaker. It has tendons that are relatively more slender, thinner bellies and a shorter caudal belly covering only 12-10. It originates from 15.

M. complexus (c; Fig. 1A,B,C,D). This is a broad, flat muscle that lies superficially on the craniodorsolateral portion of the neck. The cranial portion of the belly is partially segmented by three tendinous intersections. Caudally, the belly is partially separated longitudinally into four major slips of origin. The most caudal arises by an aponeurosis, from the transverse process of 8, that fuses with an aponeurosis from 7 serving the second slip. The third slip arises from the lateral surface of the aponeurosis of origin of M. cervicalis ascendens, attaching on transverse process 6; the fourth slip arises similarly from 5. Fibres of these slips terminate on the caudalmost tendinous intersection. In addition, small slips arise from transverse processes 4 and 3, and terminate on the second tendinous intersection. The muscle inserts by fleshy fibres along a narrow line on the occipital wall of the cranium just dorsal to the insertions of M. biventer cervicis and M. splenius capitis. Laterally, the insertion is adjacent to the dorsal portion of M. rectus capitis lateralis.

In several passerine families, including Menuridae, this muscle arises only from 5 and 4 (small), or 6-5 (Certhiidae). *Heteralocha* has slips from 6, 5 and 4. This muscle is thus unusually well developed in *Atrichornis*.

M. splenius capitis (s ca; Figs 1A,B,C,D,E; 2A). This is a stout, fan-shaped muscle that lies deep to M. biventer cervicis, M. complexus and M. rectus capitis lateralis. It arises semitendinous from the tip of the spinous process of the axis, and fans out to its insertion. The insertion is along a narrow line on the occipital wall of the cranium, from the dorsal midline ventrally to the attachment of M. serpihyoideus (Fig. 1B) on the basitemporal plate. A small, flat slip arises separately from the tip of the dorsal process of the axis and joins the main belly at its ventrolateral area of insertion.

M. rectus capitis dorsalis (r c d; Fig. 1A,B,D,E). This muscle consists of two portions — a larger superficial part and a smaller deep part. The superficial part originates from the lateral surface of the vertebral arch of the atlas, the lateral edge of the axis ventral to the dorsal process, semitendinous from the dorsal process of 3, from a prominence on the lateral bar of 4, and by a narrow tendon from the craniolateral tip of the transverse process of 5. The third of these slips is the largest and the last very small. These slips partially coalesce as they converge cranioventrally on parallel tendons that form a bundle before inserting, along with fleshy fibres, on the basitemporal plate just medial to the cranial attachment of M. serpihyoideus.

The deep portion originates from the lateral edge of the vertebral arch of the axis, the lateral bar and the craniolateral surface of the transverse process of 3, and the prominence of the lateral bar of 4 deep to the attachment of the superficial slip. These slips converge on a short tendon that inserts on the basitemporal plate medial to the main insertion and just anterior to the lateral margin of the occipital condyle.

Menura is similar except that both the deep and superficial portions have their caudal attachment on 5. The caudal attachment in *Heteralocha* is from 5 or 6 (males), and in several other passerine families from 4.

M. rectus capitis lateralis (r c l; Fig. 1A,B,C,D,E). This is a superficial muscle of the craniolateral portion of the neck. It originates by flat tendons from the ventral processes of 3, 4 and 5, and by a slender tendon from the transverse process of 6 in company with M. rectus capitis ventralis. These tendons form a single, flat sheet that gives rise to the parallel fibres of the strap-like belly. The belly curves around those of M. longus colli ventralis and M. rectus capitis dorsalis to its insertion along the lateral portion of the occipital wall of the cranium lateral to M. splenius capitis. About midway along the line of insertion, fibres share the caudalmost portion of the aponeurosis of origin of M. depressor mandibulae. Ventrally, the insertion is deep to the hyoid horns and is semitendinous along the caudal edge of the attachment of the depressor mandibulae.

In *Menura*, this muscle arises by flat tendons from the ventral processes of 2-5; in *Parus*, 4-6; *Certhia*, 3-5; *Pyrrhula* and *Phoenicurus*, 1-4; and *Heteralocha*, 2-4.

M. rectus capitis ventralis (r c v; Figs 1A,E; 2C). This muscle lies on the cranioventral surface of the neck, medial to M. rectus capitis lateralis. It originates fleshy
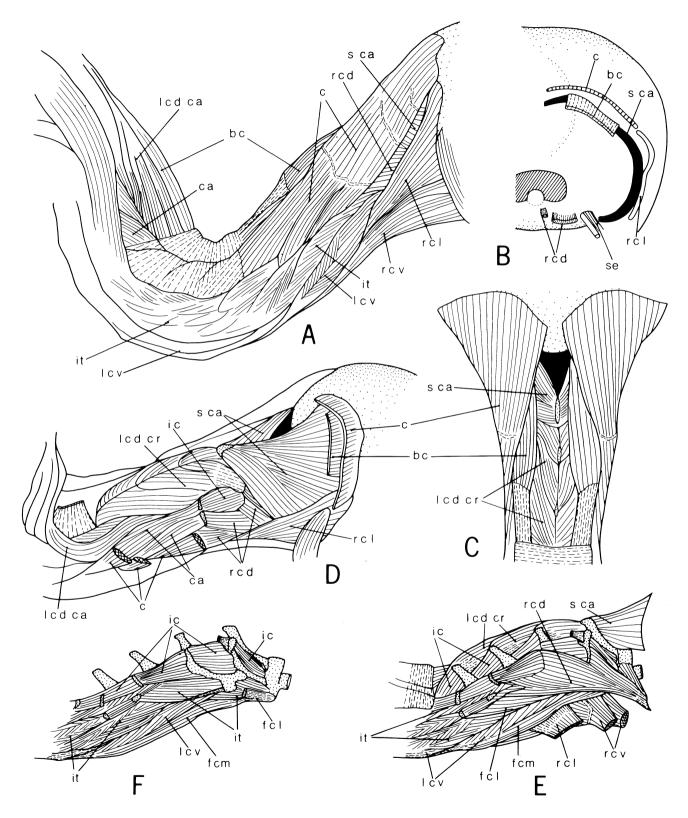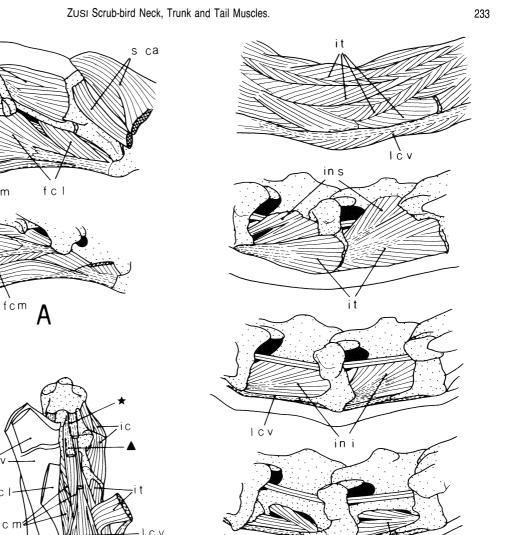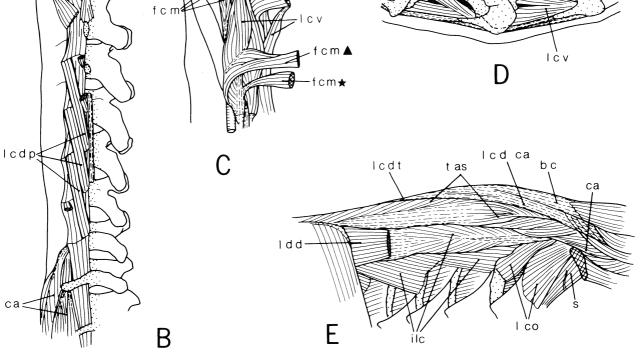
Fig. 1. Neck muscles of *Atrichornis clamosus*. **A**, superficial muscles, right side. **B**, insertions on occipital surface of skull (diagrammatic). **C**, dorsal view of anterior muscles. **D**, dorsolateral view of anterior muscles; M. complexus and M. biventer cervicis removed. **E**, lateral view of second layer of anterior muscles, right side; M. rectus capitis lateralis and M. rectus capitis ventralis cut and reflected. **F**, lateral view of deep anterior muscles. Abbreviations see Materials and Methods.

Fig. 2. Neck and trunk muscles of *Atrichornis clamosus*. **A**, lateral views of deep anterior muscles, right side; above, M. rectus capitis dorsalis removed; below, M. flexor colli lateralis removed. **B**, dorsal view (all unlabelled muscles are Mm. intercristales). **C**, ventral view of deep anterior muscles; M. rectus capitis ventralis and M. rectus capitis lateralis cut and reflected to opposite side. **D**, lateral musculature of vertebrae 7 and 8, right side. Top to bottom shows superficial to deep layers. Outline of l c v deep to costal process shown by dashed line in bottom figure. **E**, lateral view of dorsal trunk muscles, right side. Abbreviations see Materials and Methods. Stars and triangles identify different bisected portions of M. flexor colli medialis.

from the ventromedial surfaces of vertebrae 2, 3, 4 and 5, and by short, flat tendons from the ventral processes of those vertebrae. The caudalmost slip arises by a short tendon from the transverse process of 6, just lateral to the carotid artery. A separate dorsal slip of this muscle arises from the ventral process of 2 and from a narrow aponeurosis. This aponeurosis passes laterally and joins an intersection that crosses the dorsal surface of the main belly. Insertion of the entire muscle is fleshy on the basitemporal plate of the cranium, anterior to the insertions of M. rectus capitis dorsalis.

The caudal limit of this muscle differs within passerines: vertebra 4 in *Carduelis* and *Phoenicurus*; 5 in *Pyrrhula* and *Regulus*; 6 in *Menura*, *Parus*, *Acrocephalus* and *Heteralocha*; and 7 in *Certhia*. None of these genera exhibits the extra slip from 2 found in *Atrichornis*.

M. cervicalis ascendens (c a: Figs 1A,D; 2B,E). This muscle consists of a series of overlapping bellies lying along the dorsolateral portion of the neck. Each belly contains several slips that originate from the transverse processes of two or more vertebrae and pass cranially to converge on a common insertion on the dorsal process of a single vertebra. Bellies inserting on 5, 6 and 7 have two slips each, a slender one from the second vertebra caudal to that of insertion, and a larger one from the third vertebra caudal to that of insertion. The larger slip inserts on the medial side of an aponeurosis that is shared by the smaller slip and by a slip of M. longus colli dorsalis. Bellies inserting on 8–12 have three, and sometimes four, slips of origin. The additional slips arise from successively more caudal vertebrae and are typically weak. The belly to 13 has two slips. Its insertion on the caudal articular process is deep to the tendon of insertion of the first slip of M. thoracicus ascendens. The bellies inserting on the dorsal processes of 3 and 4 also have three slips each, originating from 5, 6, 7, and 6, 7, 8, respectively.

In *Menura*, this muscle differs in having only two slips of origin for the cranial five bellies as follows: 3(insertion)–6,7(origins); 4–6,7; 5–7,8; 6–8,9; 7–9,10.

M. longus colli dorsalis, pars cranialis (l c d cr; Fig. 1C,D,E). This muscle consists of five stout slips arising from the dorsal surface of the vertebral arch of 6 and 7, and from the lateral and cranial surfaces of the spinous processes of 3, 4 and 5. These slips insert sequentially on the medial, dorsal and ventral surfaces of the tendon of insertion of pars caudalis, attaching on the dorsal process of the axis. The fleshy belly of pars caudalis of this muscle attaches on this tendon between the fourth and fifth slips of pars cranialis.

Menura is similar. Origins of slips in some other forms are: 6–4, *Acrocephalus*; 7–4, *Parus*; 6–4 or 7–4, *Heteralocha*; 9–4 (not 8), *Pyrrhula*.

M. longus colli dorsalis, pars caudalis (l c d ca; Figs 1A,D; 2E). This is the major dorsal muscle of the neck, acting in opposition to M. longus colli ventralis. It consists of a series of overlapping, flattened slips that insert on the dorsal process of the axis and on 6–13. The

slip to the axis is the largest and its insertion is by a stout tendon that also serves as insertion for pars cranialis. Attachments on 6–13 are semitendinous, each sharing an aponeurosis of insertion with a belly of M. ascendens cervicis. The slips arise in succession from the ventral surface of a common aponeurosis that extends forward and fans out from the tips of the spinous processes of 14 through 18. The origins of slips 1, 4 and 5 attach across the full breadth of the aponeurosis of origin, 2 and 3 only on the lateral portion, 6 and 7 on the medial portion, and 8 and 9 on all but the medialmost part. Origins of these slips occupy the aponeurosis from the level of 12–15.

Menura differs in that the origins of all slips occupy almost the full breadth of the aponeurosis that originates from 14–17. The insertions to 6–9 are by tendons that are buried in the inserting slips of M. cervicis ascendens. A separate insertion by short tendon attaching medial to the dorsal process is present on 8 and 9. Insertions on 10–14 are broad and fleshy on the transverse-oblique crest.

M. longus colli dorsalis, pars profunda (l c d p; Fig. 2B). This muscle is largely confined to the second neck section. It consists of a series of strap-like bellies that extend from the midline of the vertebral arch of one vertebra to the dorsal process of the second vertebra cranial to it. On the left side I found only three bellies (8 to 6, 9 to 7, 10 to 8), all with fleshy attachments on both ends, whereas on the right side two additional bellies connected vertebrae 11 and 9, and 12 and 10. The caudal attachment of each of these additional bellies was by a short, flat tendon.

Menura has three developed bellies (8 to 6, 9 to 7 and 10 to 8). *Heteralocha* has four or five — the first between 8 and 6, and the last between 11 and 9 or 12 and 11. Some passerines have two bellies, some only one and others none.

Mm. intercristales (ic; Figs 1D,E,F; 2A,B,C). These muscles include the Mm. interspinales and Mm. splenii accessorii of other authors. The interspinales portion consists of those fibres that interconnect successive spinous processes: 2–3, 3–4, 4–5, 12–13, 13–14, 14–15.

Most of these muscles are flat bellies connecting successive vertebrae at their transverse-oblique crests and dorsal processes. They lie deep to M. longus colli dorsalis profundus and caudalis, and medial to Mm. ascendens cervicis. Bellies of this description begin at 13–12 and end at 6–5, and are broadest at 10–9, 9–8, 8–7. The insertion on 5 is atypical, attaching at the base of the spinous process and on a prominence craniolateral to it.

In neck section I these muscles abruptly become larger and more complex. In addition to the interspinales, bellies between 5 and 4, 4 and 3, 3 and 2, and 2 and 1 consist of a lateral portion from one dorsal process to the next, and a dorsal portion passing craniolaterally from the lateral surface of the spinous process (this portion not present between 5 and 4) and

the dorsal surface of the vertebral arch to the adjacent vertebra. Three additional slips lie superficially and pass from the base of the spinous process to the dorsal process as follows: 5 to 3, 4 to 2, 2 to 1. The caudal slip arises semitendinously and inserts, in part, on an aponeurosis from the dorsal process that also receives fibres from the vertebral arch of 4. The middle slip is entirely fleshy, whereas the cranial slip arises semitendinously and inserts by a slender tendon.

Menura is similar except for the pattern of superficial slips just described. I found only two slips, both fleshy, as follows: 5 to 3, 4 to 3.

Mm. intertransversarii (it; Figs 1A,E,F; 2A,C,D). These bellies interconnect the transverse processes and costal processes of successive vertebrae. The caudalmost belly originates from 13 and the cranialmost inserts on the axis. Bellies from 10 through 6 are similar in structure. Laterally, they consist of interdigitating aponeuroses from origin and insertion with short fibres arranged in multipennate fashion. Deep to this portion, a stout aponeurosis passes forward from its origin on the ventral portion of the costal process and gives rise to fibres that fan out and insert on the ventrolateral and caudal surfaces of the adjacent costal process. Dorsal to this portion lies M. inclusi superior and deep to it, M. inclusi inferior. Cranial to vertebra 6 this series becomes simplified and reduced to two major slips in each belly. One joins successive transverse processes and the other passes forward from the costal process to the medial surface of the adjacent costal spine, costal process and vertebral body. Only a single slip is present between 3 and the ventrolateral surface of 2. The belly of the main series of this muscle between 11 and 12 is reduced to a dorsal and a ventral slip, and that between 12 and 13 to a single dorsal slip.

In the first neck section, an additional series of slips passes craniad from the costal process to the tip of the costal spine as follows: a stout slip from costal process 5 and a cylindrical slip from 7 attach on an aponeurosis to costal spine 3; a stout slip from 6 and a slender one from 7 attach on an aponeurosis to costal spine 4; a fleshy slip extends from the costal process of 6 to the lateral surface of costal spine 5. The aponeuroses of insertion of the slips to costal spines 3 and 4 are fused ventrally with the aponeuroses of insertion of M. longus colli ventralis.

Menura is similar but I found that the tendon to costal spine 3 received fibres from costal processes 4, 5 and 6, and that to 4 received a few fibres from 6.

Mm. inclusi (in; Fig. 2D). This series of bellies extends craniad from the craniomedial surface of the costal process to the lateral surface of the body of the adjacent vertebra. Most bellies are divided into a superior and an inferior slip, separated longitudinally by the vertebral artery. The superior slip (in s) inserts on the lateral surface of the vertebral arch, and the inferior slip (in i) on the lateral surface of the vertebral body. Both slips arise from the medial surface of a fan-shaped aponeurosis whose lateral surface is occupied

by fibres of Mm. intertransversarii. The inclusi are thus closely associated with those muscles, and the cranial and caudal bellies are scarcely separable from them. The most cranial of the typical bellies connects 6 and 5; superior slips are lacking between 5 and 4, and 4 and 3. Caudally, the last complete belly is between 12 and 11; the last belly (13 to 12) contains only the inferior slip.

In *Menura*, the first small belly lies between 4 and 5, and consists of only the inferior slip. The last two bellies (10 to 11, 11 to 12) also contain only the inferior slip. The five intervening bellies are two-parted and typical.

M. longus colli ventralis (l c v; Figs 1A,E,F; 2A,C,D). This is the major ventral muscle of the neck, acting in opposition to M. longus colli dorsalis. It consists of a series of parallel overlapping bellies originating from the carotid processes or ventral processes, and inserting by tendons on the tips of the costal spines. These bellies inserting on the first neck section originate from 7; all others originate from the third neck section and first thoracic vertebra.

The cranial bellies insert on the ventral portions of aponeuroses shared by Mm. intertransversarii and attaching as short tendons on the costal spines of 3 and 4. Most of the ventral portion of the tendon or origin of these cranial bellies serves as origin for parts of M. flexor colli medialis.

The first and ventralmost of the long bellies to neck section II inserts by a flat tendon on costal spine 5. A series of fleshy slips arising from the carotid processes, ventral surfaces of the vertebral bodies, and the ventral processes of vertebrae 8–12 joins the long aponeurosis of this belly. Each of the bellies inserting on successive vertebrae (6–12) receives a slip from the vertebral body of the adjacent vertebra, and slips from the ventral processes or carotid processes of all succeeding vertebrae. The belly to 6 extends caudally as far as ventral process 14; those to 7–11 extend back to a common aponeurosis arising from ventral process 15. A belly from 12 originates on 13 and 14.

In the pattern of bellies and slips of *Menura*, the belly inserting on 5 originates from 7–11; those to 6 through 12 all extend back to 15. *Menura* lacks a slip from the body of the vertebra adjacent to that of insertion, as found in all but the first of the long slips of *Atrichornis*. Space occupied by that slip in *Atrichornis* is taken by the intertransversarii and inclusi muscles in *Menura*. The belly to 4 receives slips from 6 and 7.

M. flexor colli lateralis (f c l; Figs 1E,F; 2A). This is a fan-shaped muscle of the anterior portion of the neck, lying mostly deep to M. rectus capitis dorsalis. It originates from the lateral surface of the costal spine of 3, the cranial articular process and the edge of the lateral bar of 4 caudally to its prominence, from the costal processes of 5 and 6, and from an aponeurosis shared by the intertransversarii between those vertebrae. The fibres converge onto the dorsal surface of a tendon that inserts on the ventral process of the atlas. This tendon is shared by a belly of M. flexor colli medialis.

In *Heteralocha* (females), *Menura* and *Regulus* the origin is from 3, 4 and 5. An additional slip from 6 is present in males of *Heteralocha*.

M. flexor colli medialis (f c m; Figs 1E,F; 2A,C). This is the deepest muscle of the cranioventral portion of the neck. It consists of a series of cylindrical slips that interconnect the vertebrae of the cranial half of the neck. The cranialmost slip is stout and cylindrical. It originates from the lateral surface of a flat aponeurosis from the carotid process of 7 that is shared by the cranialmost slip of M. longus colli ventralis. It inserts by a stout tendon on the ventral process of the atlas. Two slips insert by an aponeurosis on the ventral process of the axis — a major slip from the medial portion of the aponeurosis from 7, and a stout slip from the lateral surface of an aponeurosis from the ventromedial portion of transverse process 5. The ventral portion of the vertebral body of 3 receives fleshy fibres from the medial surface of an aponeurosis from 5 and from an aponeurosis arising on the carotid process of 6. Similarly, the centra of 4 and 5 receive fibres from the carotid processes of 5 and 6, and 6 and 7, respectively.

In *Menura* I found slips from the carotid processes of 7, 6 and 5 to the ventral process of the axis. From 6, slips also go to 3 and 4. In *Heteralocha* and some other oscines the insertions are on 2, 3 and 4.

TRUNK MUSCLES

Muscles of the trunk vertebrae are complicated, interconnected and not always clearly related to the neck muscles. Their nomenclature also is confusing. In birds, the name 'M. longissimus dorsi' has been applied to different portions of the vertebral musculature of the thorax (compare Shufeldt, 1890, and Vanden Berge, 1975). Consequently, I shall not use the term 'longissimus dorsi', but instead describe all the muscles of the thoracic vertebrae under the names M. iliocostalis, M. thoracicus ascendens and M. longus colli dorsalis, pars thoracica. I tentatively regard these muscles as continuations and elaborations of Mm. intertransversarii, M. cervicalis ascendens and M. longus colli dorsalis, pars caudalis, respectively. Development of a more meaningful terminology for these muscles must await further comparative studies within birds, and between birds and reptiles.

M. longus colli dorsalis, pars thoracica (l c d t; Fig. 2E). This muscle constitutes the medialmost portion of the muscle mass that occupies the trough formed by the transverse processes and the spinous processes of the thoracic vertebrae. The slips of this muscle interconnect the spinous processes, and also extend from spinous processes to the caudal articular processes of the thoracic vertebrae.

There are two sets of aponeuroses of origin and two sets for insertion. Superficially, the long, narrow aponeuroses of origin of M. longus colli dorsalis, pars caudalis, send a few muscle fibres cranioventrad to a series of strong, underlying aponeuroses of insertion

that extend caudolaterally from the dorsocaudal tips of the spinous processes of 14–18. Most of the lateral surface of these aponeuroses is occupied by fibres of M. thoracicus ascendens. Zusi & Bentz (1984) referred these aponeuroses to M. thoracicus ascendens, but I prefer now to follow Boas (1929) in treating them as part of M. longus colli dorsalis, pars thoracica, because of their intimate relation to its aponeuroses of origin. Deep to these aponeuroses of insertion, another set of flattened aponeuroses of origin extends cranioventrolaterally from the dorsocranial edge of the spinous processes of 17–19 and from the cranial edge of the fused synsacral spinous processes. Fibres from the lateral surface of these aponeuroses insert on the medial surface of the aponeuroses of insertion described above, and fleshy and by aponeuroses on the caudal articular processes of 13, 14 and the thoracic vertebrae. Fibres from their medial surface insert fleshy on the spinous processes and vertebral arches of the first or second vertebrae cranial to that of origin; fibres to aponeuroses from the spinous processes insert on the third, fourth and fifth vertebrae cranial to that of origin.
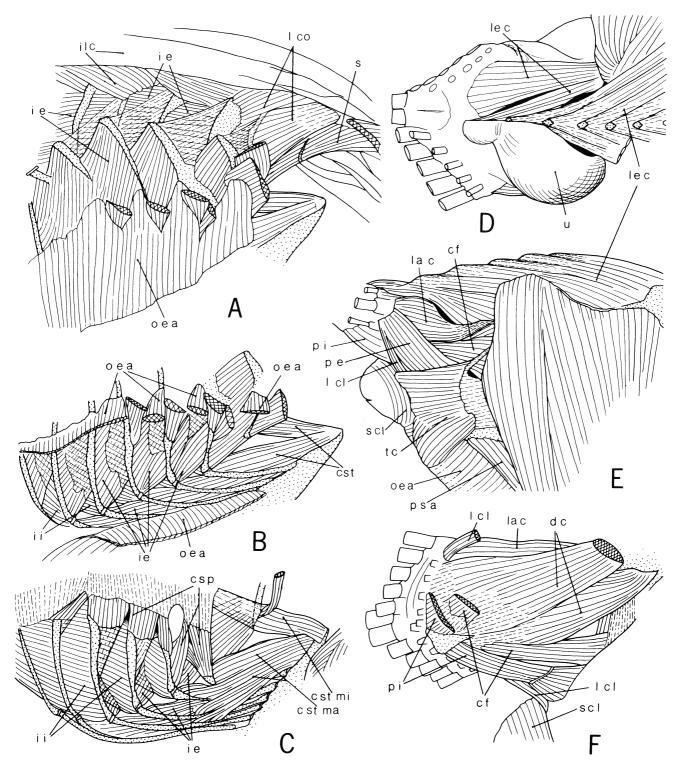
In *Menura*, the aponeuroses of origin of the deep part of the muscle attach on spinous processes 16 (small), 17, 18 and 19.

M. thoracicus ascendens (t as; Fig. 2E). This muscle constitutes a major portion of the musculature of the thoracic vertebrae. It lies between M. longus colli dorsalis, pars thoracica and M. iliocostalis, and shares aponeuroses with both. The limits of these three muscles are clear only at their origins and insertions.

The superficial fibres of this muscle originate from both walls of the synsacral trough, and from the ventral and ventromedial surfaces of a long, partially superficial aponeurosis that extends craniad over most of the muscle from the craniodorsal edge of the ilium. The lateral surface of the deep portion of this aponeurosis is occupied by M. iliocostalis. The fibres of the superficial portion of M. thoracicus ascendens are compacted and only partially separable into slips. The more dorsal fibres insert on the almost continuous surface formed by the series of flat aponeuroses of insertion from the caudal tips of the spinous processes of 14–18 described under M. longus colli dorsalis, pars thoracica.

The deeper fibres of this muscle arise from the medial surface of the aponeurosis shared by M. iliocostalis, and from the transverse processes and their aponeuroses (described under M. iliocostalis). The fibres extend craniomedially to the aponeuroses from the caudal articular processes of 13, 14, and of the thoracic vertebrae which they share with M. longus colli dorsalis, pars thoracica.

M. iliocostalis (ilc; Figs 2E, 3A). This is the lateralmost of the thoracic muscles of the vertebral column. It lies lateral to M. thoracicus ascendens and dorsal to the dorsomedial portion of the thoracic ribs. The origin consists of a series of long, flattened, parallel and overlapping aponeuroses from the craniolateral tips

Fig. 3. Trunk and tail muscles of *Atrichornis clamosus*. **A**, superficial muscles of thorax, right side (cut muscles are serratus group). **B**, right lateral view of lower rib cage (M. obliquus externus abdominis cut and reflected). **C**, medial surface of lower left thoracic wall. **D**, dorsal view of tail; left uropygial gland removed. **E**, superficial muscles of the tail and abdomen, right side. **F**, ventrolateral surface of tail muscles, right side; M. pubocaudalis externus removed; cloaca reflected downward toward left side. Abbreviations see Materials and Methods.

of transverse processes 19–16, and from the cranial edge of the ilium. These aponeuroses are largest caudally. In the caudal half of the muscle, an additional large area of origin is from the lateral surface of a long aponeurosis from the ilium shared by M. thoracicus ascendens. Insertion is on a series of overlapping aponeuroses attaching on the caudolateral tips of the transverse processes of 13–18. These aponeuroses pass caudolaterally and cross those of origin dorsally. Fibres converge on the tendons of insertion in pennate fashion, and the bulk of the muscle inserts on the tendons to 13 and 14.

The lateralmost fibres of this muscle originate from the ventral portion of the long aponeurosis from the cranioventral edge of the ilium, and from the aponeuroses of origin from 19–16. These fibres pass craniolaterally to insert fleshy on the dorsolateral surfaces of the thoracic ribs.The cranialmost fibres to the first attached rib have a separate origin from rib 3.

That this muscle may be a thoracic continuation of Mm. intertransversarii is suggested by its interconnections with transverse processes of the thoracic vertebrae, and the close association of its major insertion on 13 with the caudalmost belly of the intertransversarii. Its attachments on the thoracic ribs may be homologous with those of the intertransversarii on the costal spines in the first neck section.

In *Menura*, the slips attaching on the ribs also attach on aponeurotic sheets extending back from their dorsocaudal edges. The slip to the first rib inserts by a narrow, flat tendon. These slips, except for the caudalmost, are mostly deep to the main belly.

Mm. levatores costarum (l co; Figs 2E, 3A). This series of muscles connects the transverse processes with the thoracic ribs and the second floating rib. All but the two cranial bellies lie deep to the lateral portion of M. iliocostalis. The cranialmost levator is the largest. It arises from the ventrolateral surface of the transverse process of 13, and from a superficial aponeurosis. Fibres fan out caudoventrally to insert on the lateral and cranial surfaces of the uncinate aponeurosis, and on an adjoining aponeurosis. The three caudal bellies originate by an aponeurotic sheet from the ventral edge of the preacetabular wing of the ilium and insert on the 4th, 5th and 6th (accessory) thoracic ribs. Each insertion is on a flattened depression of the thoracic rib from the tuberculum, laterally to the ventral curvature of the rib. The insertion is aponeurotic distally and lies between the intercostales externi and interni muscles.

In *Menura*, the first belly (from 13) is less developed than that of *Atrichornis*, inserting only on the upper lateral surface of the second floating rib. The third belly is largely superficial rather than covered by a slip of M. iliocostalis.

M. scalenus (s; Figs 2E, 3A). This muscle is probably serially homologous with the levatores costarum. It arises fleshy from the ventrolateral surface of the transverse process of 12, and inserts on the entire cranial and lateral surfaces of the first floating rib.

Mm. intercostales externi (i e; Fig. 3A,B,C). These muscles consist of a series of flat bellies interconnecting successive thoracic ribs and floating ribs. Each muscle of the thoracic ribs has three separate portions — two associated only with the vertebral ribs and one only with the sternal ribs. I shall call these the vertebral portion, the uncinate portion and the sternal portion.

The vertebral portion is a thin sheet of fibres extending from one rib to the next, from the lateral surface of the iliocostalis muscle to the attachment of the uncinate process. The fibres attach on the opposing edges of the two ribs and, to varying degrees, on their lateral surfaces. The fibres pass mainly cranially, but somewhat dorsally as well, from the caudal to the cranial attachment. The cranialmost of these bellies connects the two floating ribs.

The uncinate portion is a thin sheet connecting the cranial half of each uncinate process with the entire process cranial to it. Ventral to the uncinate process, the sheet connects adjacent ribs ventrad as far as their articulations with the sternal ribs. The uncinate portion lies superficial to the vertebral portion where they overlap. Fibres are oriented dorsally or craniodorsally from their caudal attachment to the next rib. Ventral to the uncinate process, the fibres extend only about half way to the more cranial rib; there they give way to a thin aponeurotic sheet, with the following exceptions: fibres extend from one rib to the other ventrally between thoracic ribs 3 and 2, 2 and 1, and between 1 and the second floating rib.

From the craniodorsdal edge of each uncinate process, an aponeurosis (uncinate aponeurosis) extends craniodorsally to the caudal edge of its rib. This aponeurosis stabilizes the uncinate process against the pull of the uncinate portion of this muscle.

The sternal portion is thicker than the other portions and it passes between successive sternal ribs (1 and 2, 2 and 3, and 3 and 4). The muscles become smaller caudally and the connection between 4 and 5 is largely aponeurotic, containing only a few short fibres dorsally.

Mm. intercostales interni (i i; Fig. 3B,C). This is a series of thin sheets of muscle interconnecting successive thoracic vertebral ribs. The muscles lie deep to the intercostales externi and pass cranioventrally from the edge of one rib to the edge of the adjacent rib. The cranialmost belly connects the first and second floating ribs; the caudalmost connects the fifth thoracic and sixth (accessory) ribs. Fleshy fibres connect successive ribs only in the ventral portions of the three caudal bellies; elsewhere the fibres are restricted to the cranial half of the muscle and attach caudally on an aponeurotic sheet.

M. costosternalis (cst; Fig. 3B,C). Pars major (cst ma) of this muscle extends from the caudal and lateral surfaces of the craniolateral process of the sternum to the ventral end of the first thoracic vertebral rib and to all the attached sternal ribs, deep to M. intercostalis externus. The sternal attachment is both fleshy and by a superficial ventral aponeurosis, whereas costal attachments are mainly fleshy. The slips become

progressively smaller caudally, with that to the fifth rib attaching only by a slender aponeurosis.

Pars minor (cst mi) is a stout slip that attaches fleshy on the tip of the craniolateral process of the sternum and passes dorsocaudally where it is bound to the tip of the second floating rib. It continues onto its insertion on the cranial edge of the first attached rib by a flat aponeurosis.

Pars minor in *Menura* has no binding to the second floating rib and it passes directly to a fleshy attachment on the first attached rib.

M. costoseptalis (csp; Fig. 3C). This is a series of muscle sheets inside the thoracic cavity that connect the lateral portion of the horizontal septum with the vertebral portions of the five attached ribs. Attachments on the first two ribs are fleshy; those on ribs 3, 4 and 5 partly fleshy and partly aoneurotic. The muscles lie deep to the intercostales interni.

M. obliquus externus abdominis (o e a; Fig. 3A,B,E). This is an extensive sheet of muscle covering the ventral portion of the rib cage and the abdomen. It originates fleshy from the ventral angles of the uncinate processes of the first floating rib and first three thoracic ribs, and by an aponeurotic sheet from the fifth and sixth uncinate processes. Cranially, the uncinate attachments interdigitate with the costal attachments of M. serratus superficialis. The sheet also attaches fleshy on the lateral surfaces of the third and fourth thoracic ribs, and by an aponeurotic sheet on the fifth and sixth (accessory) ribs. The line of origin of this muscle sheet continues caudally across an aponeurosis covering the dorsolateral abdominal wall to the ventral edge of the pubis. Fibres originate along the edge of the pubis as far as its distal tip.

The sternal insertion is by a short, broad aponeurosis attaching along the entire lateral border of the trabecula lateralis of the sternum. The abdominal insertion is on the linea alba. This muscle is crossed superficially by M. pectoralis subcutaneous abdominis.

M. rectus abdominis (r a; Fig. 4). This sheet of muscle passes from the caudal edge of the sternum to the distal portion of the pubis and the linea alba. The long lateral fibres pass primarily caudad to the pubis, but those from more medial portions of the sternal border become progressively shorter as their direction becomes more medial. The muscle is superficial to the ventral portion of M. obliquus internus and to much of M. transversus abdominis, and is covered laterally by M. obliquus externus abdominis.

M. obliquus internus abdominis (o i a; Fig. 4). This is a flat sheet of fibres extending between the last thoracic rib and the proximal half of the pubis. The dorsal border of the muscle is aponeurotic and curves to accommodate passage of blood vessels to the thigh.

M. transversus abdominis (t ab; Fig. 4). This muscle passes mainly transversely from the cranial edge of the distal portion of the pubis to the linea alba. Craniodorsally its attachment on the pubis is by an
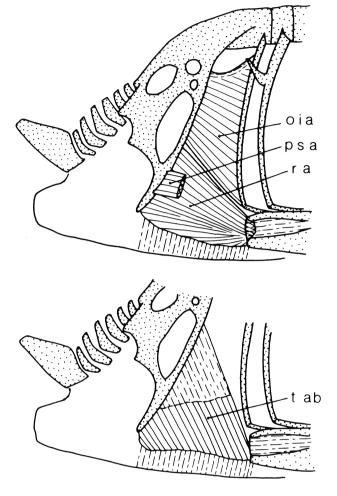

Fig. 4. Abdominal muscles of *Atrichornis clamosus*. Right side; diagrammatic. Above, M. obliquus externus abdominis removed. Below, M. obliquus internus abdominis and M. rectus abdominis removed. Abbreviations see Materials and Methods.

aponeurotic sheet. Its dorsolateral fibres are overlapped by the ventral portion of M. obliquus internus abdominis.

M. transversus cloacae (t c; Fig. 3E) This muscle lies largely superficially on the caudolateral surface of the trunk. It arises by an aponeurotic sheet from the caudal edge of the terminal process of the ischium and the adjacent dorsal edge of the pubis. Its origin parallels and is lateral to that of M. pubocaudalis internus and is separated from it by the belly of M. pubocaudalis externus. Additional origin is by a narrow aponeurosis from the terminal process of the ilium and the tip of the transverse process of the third free caudal vertebra. This aponeurosis extends caudoventrally to meet the dorsal edge of the main aponeurosis, thus forming a loop that is penetrated by M. caudofemoralis. Fleshy fibres arise from the entire conjoined aponeurosis, caudal to the loop, and form a sheet that attaches on the surface of the sphincter cloacae and on the linea alba caudal to the limit of M. transversus abdominis.

M. sphincter cloacae (s cl; Fig. 3E,F). This is a broad band of muscle that encircles the cloaca just

cranial to the vent.

This muscle was not available for comparison in *Menura* because the cloaca had been removed from the specimen.

M. levator cloacae (l cl; Fig. 3E,F). This is a slender band of muscle that arises from the caudoventrolateral corner of the retricial bulb, medial to the attachment of M. pubocaudalis externus. It passes ventrally to insert on the dorsolateral wall of the cloaca, cranial to M. sphincter cloacae and medial to the dorsal attachment of M. transversus cloacae.

The muscle was not available for comparison in *Menura*.

M. pectoralis, pars subcutanea abdominalis (p s a; Figs 3E, 4). This strap-like, fleshy muscle originates from the cranial border of the distal portion of the pubis and passes forward, superficial to M. obliquus externus abdominis, to insert on the inner surface of the lateral skin of the breast.

In *Menura* the muscle originates as a flat aponeurosis from the distal portion of the pubis. Fleshy fibres begin at about the level of the caudal end of the rib cage and continue onto the skin of the breast.

TAIL MUSCLES

Baumel (1971) pointed out that rectrices of the pigeon (*Columba livia* Gmelin) have little direct fibrous attachment to the tail skeleton, and that all but the central pair are implanted into a fibro-adipose mass that he called the 'retricial bulb'. This structure articulates in a shiny connective tissue socket supported by the tail skeleton and musculature (see also Vanden Berge, 1975:1813). In *Atrichornis*, all retrices are included in the bulb, but the central pair is closely bound by connective tissue to the caudal portion of the pygostyle; cranially the bulb has a looser connective tissue connection with the pygostyle. Thus, motions of the tail are effected by muscular action on the free caudal vertebrae and pygostyle, on the right and left retricial bulbs, and on the individual feathers within the bulb.

M. levator caudae (le c; Fig. 3D,E). This muscle is partially separable into dorsal and ventral portions. The dorsal portion consists of a series of parallel and contiguous slips that originate from the entire dorsal surface of the postacetabular wing of the ilium, the adjacent surface of the fused synsacral vertebrae and the vertebral arches of the free caudal vertebrae. These slips pass caudomedially to insert fleshy, and by superficial aponeuroses, on the tips of the dorsal processes of the free caudal vertebrae. The ventral portion lies deep to the uropygial gland (Fig. 3D). It originates fleshy from the dorsal surfaces of the transverse processes of the free caudal ventebrae and fans out to insert on the tendinous surface of the rectrical bulb.

In *Menura* the dorsal fibres of insertion of the ventral portion of this muscle attach on the aponeurotic cranial surface of the uropygial gland. Unlike those of

Atrichornis (see Fig. 3D), the two glands are fused cranially, forming a continuous surface across the caudal vertebrae.

M. lateralis caudae (la c; Fig. 3E,F). This muscle is largely superficial on the lateral surface of the tail musculature. Ventrally, its fibres are scarcely separable from those of the depressor caudae. It originates from the tips of the transverse processes of free caudal vertebrae 3-6. The fibres fan out over the surface of the rectricial bulb where they insert deep to M. levator caudae. The major bulk of the belly arises from 3 and 4, and attaches on the lateral edge of the retricial bulb between the levator and the depressor caudae.

M. depressor caudae (d c; Fig. 3F). This is the major ventral muscle of the tail. It arises from the caudal edge of the fused synsacral vertebrae and from the ventral surfaces of the transverse processes of the free caudal vertebrae. The fibres pass caudoventrally to insert on the tips of the ventral processes of the free caudal vertebrae and on aponeuroses that extend cranially from them. A major part of the insertion is on an extensive superficial aponeurosis that attaches on the ventral edges of the pygostyle, whereas the more caudolateral fibres insert on that portion of the aponeurosis that attaches on the rectricial bulb and the bases of the caudal retrices. Aponeuroses passing caudally from the caudal edges of the transverse processes of the ultimate and penultimate free caudal vertebrae, send fibres in pennate fashion to the ventrolateral surface of the pygostyle.

M. pubocaudalis externus (p e; Fig. 3E). This lateral muscle of the tail lies superficial to M. transversus cloacae caudally, and deep to it cranially. The strap-like belly originates from the caudodorsal edge of the pubis and passes dorsally to its insertion on the caudolateral corner of the rectricial bulb and the base of the lateral rectrix.

In *Menura*, this muscle is broader at its insertion, meeting the lateral edge of pubocaudalis internus about halfway across the retricial bulb.

M. pubocaudalis internus (p i; Fig. 3E,F). This muscle lies mainly deep to M. pubocaudalis externus. It originates from the caudal edge of the terminal process of the ischium and the adjacent dorsal edge of the pubis. The pubic origin is immediately deep to that of pubocaudalis externus but it extends less far caudally. The muscle passes dorsocaudally to its insertion on the superficial aponeurosis of M. depressor caudae along the caudolateral edge of the pygostyle, and laterally along the bases of all but the lateral two major undertail coverts. A tendinous, transverse intersection divides the belly into a shorter cranial portion and a longer caudal portion.

In *Menura*, this muscle meets the medial edge of pubocaudalis externus about half way across the retricial bulb.

M. caudofemoralis (cf; Fig. 3E,F). This is a large muscle that originates on the femur, passes caudally through a loop in the aponeurosis of M. transversus

cloacae, and continues caudally, ventral to M. lateralis caudae and deep to the two pubocaudalis muscles. Its insertion is on the superficial aponeurosis of M. depressor caudae cranial to (and deep to) the insertion of M. pubocaudalis internus. Through that aponeurosis its force is directed to the ventrolateral edge of the pygostyle.

The caudofemoralis of *Menura* inserts by a rounded tendon. The tendon fuses with that of the opposite caudofemoralis muscle to form a single median tendon that attaches on the caudoventral surface of the pygostyle. This common tendon separates the right and left pubocaudalis internus muscles.
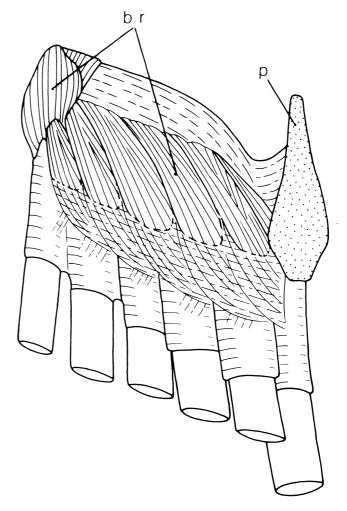
M. bulbi rectricium (b r; Fig. 5). This muscle consists of a series of stout slips on the ventral side of the rectricial bulb deep to M. depressor caudae. The slips originate in sequence from the aponeurotic cranioventral surface of the bulb and pass caudomedially to aponeurotic attachments on the under tail coverts and on the rectrices between the stout tendons of insertion of M. depressor caudae. A slip supplies each of the retrices except the lateral one in each rectricial bulb. The medialmost slip also includes fibres from the craniomedial surface of the bulb that converge on a tendinous sheet attaching on the medial surface of the follicle of the inner rectrix and on the adjacent caudal surface of the pygostyle. The lateral rectrix receives fibres on the dorsal, lateral and ventral surfaces of the base of its follicle from a muscular sheet that curves around the craniolateral corner of the bulb from its origin on the aponeurotic dorsal surface of the bulb. This slip is deep to M. lateralis caudae. A small sheet of fibres from the centrolateral surface of the bulb passes over the cranial edge to the dorsolateral surface. Most of the dorsal surface of the bulb is aponeurotic.

In *Menura*, this muscle is somewhat more complex. Its description is not included here as it might better accompany a detailed study of the rectricial bulb in relation to the use of the tail for display.

I did not find M. adductor retricium in *Atrichornis*.

DISCUSSION

Individual variation in avian muscles, even of different sides of the same bird, is of common occurrence. Comparisons drawn between species from single specimens must thus be made with caution because differences may have no taxonomic or adaptive significance. Variations in the number of slips of a muscle or in the vertebrae on which they attach are particularly frequent. Nevertheless, the occurrence of additional slips or relatively larger muscles or stouter tendons in seven muscles of the anterior portion of the neck of *Atrichornis*, when compared to *Menura*, strongly suggests an adaptation for unusually forceful movements of the head, and neck section I, in *Atrichornis clamosus* (see Mm. biventer cervicis, complexus, cervicalis ascendens (cranial part), longus colli dorsalis profundus, flexor colli lateralis, flexor colli medialis, rectus capitis ventralis). A basis for these

Fig. 5. M. bulbi retricium of *Atrichornis clamosus*. Ventral view of retricial bulb, right side. M. depressor caudae and M. lateralis caudae removed. Abbreviations see Materials and Methods.

modifications is suggested by an account of the habits of *Atrichornis rufescens* that appeared in Mathews (1919-1920:27). Speaking of birds foraging on the ground in undergrowth, he quoted Ramsay's comment that "They moved by a series of short hops, putting their heads under the loose, dead leaves and forcing themselves along in such a manner that the leaves passed over their backs, so that at times they were completely hidden, and could only be detected by the slight movement of the leaves over them." Of *A. clamosus*, Smith (1976) stated that "It spends most of its time feeding on the ground. It searches for food by poking its head under the litter, or flicking leaves aside with the bill. The feet are not used" (p. 130). Use of the head and neck as a 'ploughshare' in litter and dense vegetation, and use of the bill rather than the feet for clearing the ground could account for hypertrophy of the neck muscles. Unfortunately, because of the extreme difficulty of seeing scrub-birds, there is no detailed account of the use of the bill in foraging.

Several qualitative differences between *Atrichornis* and *Menura* may have taxonomic significance. These

are the presence of an extra slip and tendinous intersection of M. rectus capitis ventralis in *Atrichornis*, the presence of a slip to the centrum of the vertebra adjacent to that of insertion in bellies of the longus colli ventralis of *Atrichornis*, the different configurations of the uropygial gland and their relation to M. levator caudae in the two genera, and the differences in the insertion of M. caudofemoralis. The taxonomic significance of these differences cannot be properly evaluated without broader comparison of these and other features.

References

Baumel, J.J., 1971. Morphology of the tail apparatus in the pigeon (*Columba livia*). In 'XIX World Veterinary Congress (Mexico City)' 3: 849 (abstract).

Baumel, J.J., A.S. King, A.M. Lucas, J.E. Breazile & H.E. Evans (eds), 1979. Nomina anatomica avium. Academic Press, London, pp. xxv + 637.

Boas, J.E.V., 1929. Biologisch-anatomische Studien über den Hals der Vögel. Det Kongelige Danske Videnskabernes Selskabs Skrifter, Naturvidenskabelig og Mathematisk, Ser. 9, 1: 102-222.

Bock, W.J., 1985. The skeletomuscular system of the feeding apparatus of the Noisy Scrub-bird, *Atrichornis clamosus* (Passeriformes: Atrichornithidae). Records of the Australian Museum 37(4): 193-210.

Burton, P.J.K., 1974. Anatomy of head and neck in the Huia (*Heteralocha acutirostris*) with comparative notes on other Callaeidae. Bulletin of the British Museum (Natural History), Zoology 27 (1): 1-48.

Fürbringer, M., 1888. Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz-und Bewegungsorgane, Vol. 1. Van Holkema, Amsterdam, pp. xliv + 834.

Hudson, G.E. & P.J. Lanzillotti, 1955. Gross anatomy of the wing muscles in the family Corvidae. American Midland Naturalist 53 (1): 1-44.

Kuroda, N., 1962. On the cervical muscles of birds. Miscellaneous Reports of the Yamashina's Institute for Ornithology and Zoology 3 (3): 189-211.

Mathews, G.M., 1919-1920. The birds of Australia, Vol. 8. H.F. & G. Witherby, London, pp. xiv + 316.

Palmgren, P., 1949. Zur biologischen Anatomie der Halsmuskulatur der Singvögel. In 'Ornithologie als biologische Wissenschaft' (eds E. Mayr & E. Schuz): 192-203. Carl Winter Universitatsverlag, Heidelberg.

Raikow, J.R., 1985. Systematic and functional aspects of the locomotor system of the scrub-birds, *Atrichornis*, and lyrebirds, *Menura* (Passeriformes: Atrichornithidae and Menuridae). Records of the Australian Museum 37(4): 211-228.

Shufeldt, R.W., 1890. The myology of the Raven (*Corvus corax sinuatus*). Macmillan, London, pp. xix + 343.

Smith, G.T., 1976. Ecological and behavioural comparisons between the Atrichornithidae and Menuridae. Proceedings of the 16th International Ornithological Congress: 125-136. Australian Academy of Science, Canberra.

Venden Berge, J.C., 1975. Aves myology. In 'Sisson and Grossman's The anatomy of the domestic animals' (ed. R. Getty), 5th edition: 1802-1848. W.B. Saunders, Philadelphia.

Zusi, R.L. & G.D. Bentz, 1984. Myology of the Purple-throated Carib (*Eulampis jugularis*) and other hummingbirds (Aves: Trochilidae). Smithsonian Contributions to Zoology 385, pp. iii + 70.