Osteological Comparison of the Scrub-birds, *Atrichornis*, and Lyrebirds, *Menura* (Passeriformes: Atrichornithidae and Menuridae)

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ABSTRACT. Within *Atrichornis* the two species *A. clamosus* and *A. rufescens* are very similar overall, differing only in characters related to flightlessness, with *A. clamosus* appearing more volant than *A. rufescens*. Similarly, the two species within *Menura* are very similar overall, although *M. novaehollandiae* may be a stronger flyer than *M. alberti*. There are many differences between the genera *Atrichornis* and *Menura*, but the distribution of these character states across the order Passeriformes remains unstudied. What has been noted is that a suite of characters shared by *Menura* and *Atrichornis*, hitherto used to relate the Menurae to the Rhinocryptidae, are also shared by several other genera of birds from a variety of families. We suggest that these characters indicate convergence towards a terrestrial lifestyle and should not be used to indicate phylogenetic proximity.

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Until comparatively recently, the relationships of the Australian scrub-birds (*Atrichornis*) and lyrebirds (*Menura*) seemed clear: both genera were closely allied and appeared to form a primitive group, sometimes given subordinal status (Menurae) within the order Passeriformes (Wetmore, 1960; Mayr & Amadon, 1951; Schodde, 1975, amongst others). Sibley (1974) reviewed the taxonomic history of this group and broke with tradition in suggesting that the lyrebirds and scrub-birds should be closely allied to the bowerbird/bird-of-paradise assemblage based on his studies of egg-white proteins. More recent work by Feduccia & Olson (1982) has challenged this view, by pointing out a significant number of osteological differences between the ptilonorhynchids and *Menura*. Work by Raikow (1985) on the appendicular myology of the Menurae and Ptilonorhynchidae/Paradisaeidae assemblage illustrates a number of other differences. Even though Sibley and Ahlquist's most recent work (in press), utilizing DNA × DNA hybridization technique, again closely allies the Menurae and the Ptilonorhynchidae (but no longer the Paradisaeidae), the diversity of opinions clearly indicates that a clear understanding of *Menura* and *Atrichornis* relationships to other songbirds is in the future.

What is also clear from a survey of past and current literature on *Menura* and *Atrichornis* is that their close affinity, although claimed by many authors, is not as well documented as one might believe. Both *Atrichornis* and *Menura* have a relatively simple syrinx that lacks the complexity of muscles present in the oscines. Ames (1971) has suggested this condition is primitive within the Passeriformes. Both *Menura* and *Atrichornis* have, however, an oscine stapes with a flat footplate and a straight bony shaft, a condition also thought to be primitive within the Passeriformes (Feduccia, 1975a, b; Feduccia & Olson, 1982).

Feduccia & Olson (1982) further point out that, besides *Menura* and *Atrichornis*, only members of two other groups, the New Zealand 'wrens' (Acanthisittidae) and some tapaculos (Rhinocryptidae), lack the derived suboscine stapes and the derived oscine syrinx. Their comparisons of members of all these groups led them to conclude that the Menurae (including both *Atrichornis* and *Menura*) were more similar to the Rhinocryptidae than to any other passerine group that they examined, and that both retained a large number of primitive passeriform characteristics. From this, they suggested a close relationship between these two groups and assumed a close relationship of *Menura* and *Atrichornis* based on a variety of osteological, myological and syringeal characteristics.

In considering those characters that ally *Menura* and *Atrichornis*, and they in turn to the Rhinocryptidae, one of us (RFB) noted a high degree of correlation between such characters and a ground-dwelling, terrestrial mode of life. Examination of birds in the order Passeriformes made it clear that a number of terrestrially adapted species (e.g. *Dasyornis, Orthonyx, Amytornis*, amongst others) also possessed many of those characters that Feduccia and Olson had used to ally the Menurae with the Rhinocryptidae. Thus, we now wonder how many of the shared characters used to ally *Menura* and *Atrichornis* and the Rhinocryptidae are due to convergence towards a common terrestrial lifestyle; and how many are, in fact, due to derivation from a common ancestor. Such a statement applies to all the above taxa, not just the Menurae. Both possibilities need, at this point, to be entertained and tested through well documented studies on a variety of characters across the Passeriformes as a whole, many of which are underway. Until such studies are completed, however, the relationship of such forms as *Menura* and *Atrichornis* will probably remain uncertain.

The purpose of the following study is to document and extensively illustrate the osteology of all the species of *Menura* and *Atrichornis*, which we hope will serve to point out a number of differences that exist between these forms. We also hope that in providing extensive information on these rare forms it will enable workers on passeriform taxonomy and phylogeny access to previously unavailable data that can be used in broad-based comparative studies of this avian order. We further point out that those characters used by Feduccia & Olson (1982) to ally the Menurae and the Rhinocryptidae might have been produced by a similar mode of life and not necessarily by close relationship. We hope such a study will stimulate and encourage further detailed comparative studies of the Passeriformes.

Abbreviations

AMS: Australian Museum, Sydney
ANWC: Australian National Wildlife Collections, CSIRO Division of Wildlife and Rangelands Research, Lyneham
DM: National Museum of New Zealand, Wellington
NMV: Museum of Victoria, Melbourne

Methods and Materials

Traditional classifications which recognized the Menurae utilized plumage, syringeal and osteological characters to delimit this primitive passeriform group. Among the osteological characters were (Sibley, 1974): 1) presence of a curved posterior margin of the sternum, 2) lack of hypocleideum in *Menura*, and 3) presence of only a rudimentary clavicle in *Atrichornis*.

With so few characters forming the osteological evidence, it is obvious that a thorough review of the skeletal system is warranted. In the following study, comparisons of the skeletons of *Atrichornis rufescens, A. clamosus, Menura novaehollandiae* and *M. alberti* are made, as are comparisons of the genera *Menura* and *Atrichornis*.

Comparative material available included: *Atrichornis clamosus*, a skeleton (NMV R11354 ?♀); *A. rufescens*, two partial skeletons (NMV B12407 ♀ + NMV B55794 ♂); *Menura alberti*, two skeletons (AMS 5593 + NMV W10916); and *M. novaehollandiae*, ten skeletons (NMV W Nos. 9655, 8713 and B Nos. 8857, 10398 ♂, 10728, 10729, 10730 ♀, 10731 ♂, 11391, 12391 ♂).

Skeletons were disarticulated and compared on the basis of limb and girdle elements, but comparisons did not include vertebrae, ribs or phalanges. Comparisons between the two species in each genus were made after those of the two genera, using *Menura novaehollandiae* and *Atrichornis clamosus*, the best represented in our sample, as morphotypes.

Osteological Comparison of *Menura* and *Atrichornis*

Fig. 1, Table 1, Plates I–XIX

Comments that follow are based on *Atrichornis clamosus* and *Menura novaehollandiae*.

Cranium. Proportionally, *Menura* is broader and shorter. *Atrichornis* lacks an interorbital septum, *Menura* has partial interorbital septum. Viewed laterally the tympanic wing of the exoccipital extends futher anteriorly in *Atrichornis* but does not extend as far posteriorly as in *Menura*, viewed laterally. Thus, the auditory meatus, in lateral view, is proportionally larger in *Menura*, and not partially closed by bone posteriorly as in *Atrichornis*. The internal mandibular articulation surface of the quadrate is elongate in *Menura* and rounded in *Atrichornis*. The opisthotic of *Menura* is not as inflated as in *Atrichornis*. The foramen magnum of *Menura* is broad and dorsoventrally compressed, whereas in *Atrichornis* it is deeper and mediolaterally compressed. *Menura* has two small openings into the brain case through the posterior wall of the orbit; *Atrichornis* has a single, large fonticulus above a smaller opening.

Rostrum. *Menura* lacks the ossified crest on the culmen that *Atrichornis* displays. The external nares are proportionally more elongated in *Menura*.

Mandible. The medial mandibular process extends further internally and slightly ventral in *Menura*. In *Atrichornis* this process is relatively shorter and curves slightly anteriorly.

Sternum. Note: Only half of the *Atrichornis* sternum (right half) is preserved in NMV R11354 (*A. clamosus*), and thus more information on this element is desired. Shapes of the sterna of *Atrichornis* and *Menura* differ radically, with that of *Atrichornis* being

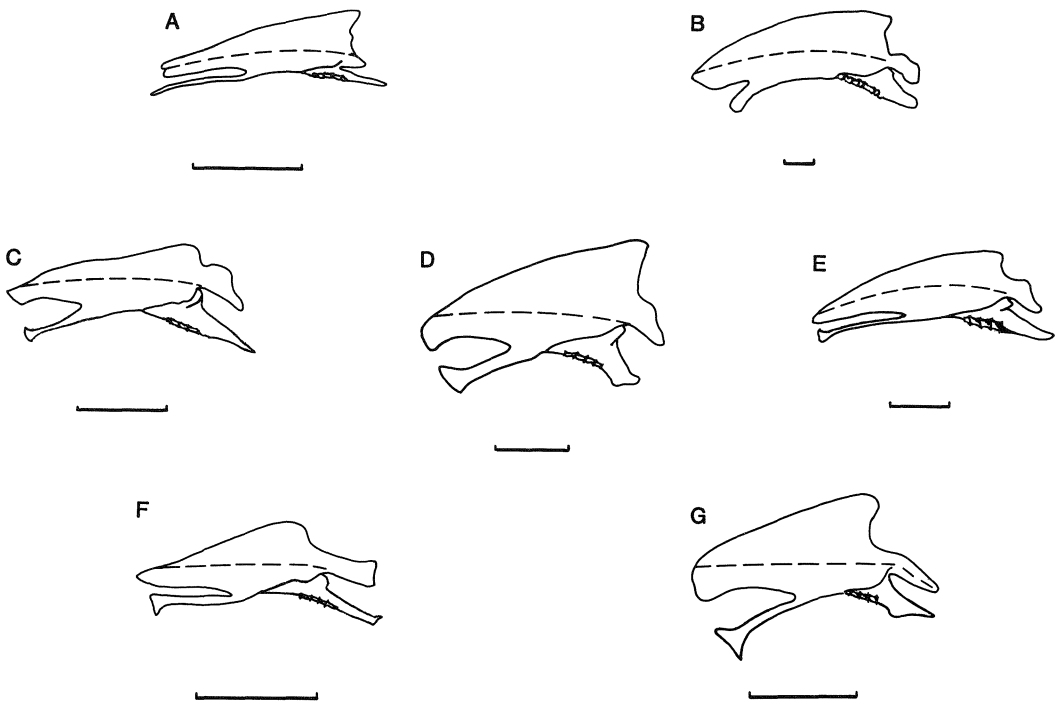

Fig. 1. Lateral views of sterna demonstrating the decreased depth of the sternal keel in non volant birds vs. volant birds: **A** = *Atrichornis clamosus* (NMV R11354); **B** = *Menura novaehollandiae* (NMV W8713); **C** = *Dasyornis broadbenti* (NMV B6839); **D** = *Philemon argenticeps* (ANWC BS101); **E** = *Callaeus cinerea wilsoni* (DM 8637); **F** = *Amytornis woodwardi* (ANWC BS2419); **G** = *Malurus cyaneus* (NMV B10515). Scales = 10 mm.

decidedly more reduced than that of *Menura*. Further differences, some of which are probably related to this whole reduction of the forelimb in *Atrichornis* are as follows. The ventral manubrial spine in *Atrichornis* and *Menura* (viewed ventrally or dorsally) is a narrow spike that bifurcates only slightly at its anterior-most point; in *Menura* this spine broadens into two wings that protrude dorsolaterally at the anterior end of the projection, and the lateral sides of this spine are highly concave, rather than only slightly concave, as they are in *Atrichornis*. The sternum of *Atrichornis*, especially when the posterior lateral processes are excluded, narrows posteriorly, whereas in *Menura* it is about the same width at both its anterior and posterior ends. In *Atrichornis*, the sternocoracoidal processes project far anterior to the ventral manubrial spine and are slender, V-shaped processes; in *Menura* these processes are U-shaped, blunted, and do not project as far forward as the ventral manubrial spine.

In *Atrichornis*, attachments for the costal margins extend half way out onto the sternocoracoidal processes, to the level of the anterior-most projection of the ventral manubrial spine; in *Menura*, the costal margin extends only to the base of the sternocoracoidal process. *Atrichornis* has six costal ribs including, at least in *A. clamosus*, the sixth, which is slender and elongated, appearing to course backwards on the dorsal surface of the sternum, looping down through the deep sternal notch and then curving upward on the outside of the posterior lateral process (more specimens are needed to confirm this, as it may be an artifact of preparation); *Menura* has five well defined intercostal spaces that indicate at least five costal ribs are present, but the sternal notch is so small and so far posterior to the last intercostal space, that it is doubtful whether a sixth costal rib would loop through that notch as it does in *Atrichornis*. *Atrichornis* has a single, deep sternal notch on either side of the sternum and an elongate, slender posterior lateral process that is convex laterally and somewhat flattened and rounded at its posterior tip; the notch is about half the length of the sternum. In *Menura* the notch is an insignificant incision in the outer part of the posterior margin of the sternum, and the resultant posterior process is short and broad. Dorsally, the sternum of *Atrichornis* is distinctly less concave than that of *Menura*, especially near the anterior end where pronounced basins are formed in *Menura*, one at the base of either sternocoracoidal process and a third median one at the anterior end just posterior to the medial margin of the coracoidal sulcus. Ventrally, the coracoidal sulci in *Atrichornis* are oriented to form an angle of about 75–80° with the carina, whereas in *Menura* they form an angle of about 40° with the carina. In lateral view, the carina in *Atrichornis* extends as far forward as, perhaps slightly farther than, the ventral manubrial spine; in *Menura* the ventral manubrial spine extends decidely beyond the carina. In overall proportions, the sternum of *Menura* is more than twice as long as it is wide; in *Atrichornis* it is only slightly longer than it is wide.

Table 1. Measurements (in mm) of osteological material of *Atrichornis* and *Menura*: A, *Atrichornis clamosus*; B, *A. rufescens*; C, *Menura novaehollandiae*: D, *M. alberti*. > greater than; ~ approximately.

CRANIUM

WIDTH AT THE THE ORBITS

	A	B	C	D
Mean	4.2	0	18.9	20.1
Maximum value	4.2	0	21.6	20.1
Minimum value	4.2	0	16.2	20.0
Variance	0	0	3.3	0
Standard deviation	0	0	1.8	0.1
Total number	1	0	9	2

GREATEST WIDTH

	A	B	C	D
Mean	22.2	0	34.8	34.2
Maximum value	22.2	0	36.7	35.3
Minimum value	22.2	0	32.0	33.0
Variance	0	0	3.0	2.6
Standard deviation	0	0	1.7	1.6
Total number	1	0	8	2

GREATEST LENGTH

	A	B	C	D
Mean	17.2	0	49.4	48.5
Maximum value	17.2	0	52.0	48.8
Minimum value	17.2	0	47.0	48.2
Variance	0	0	2.8	0.2
Standard deviation	0	0	1.7	0.4
Total number	1	0	9	2

ROSTRUM

TOTAL LENGTH

	A	B	C	D
Mean	0	0	38.7	40.2
Maximum value	0	0	42.5	40.9
Minimum value	0	0	36.7	39.4
Variance	0	0	3.6	1.1
Standard deviation	0	0	1.9	1.1
Total number	0	0	8	2

LENGTH OF EXTERNAL NARES

	A	B	C	D
Mean	0	0	19.8	21.0
Maximum value	0	0	21.3	21.3
Minimum value	0	0	18.9	20.6
Variance	0	0	0.7	0.2
Standard deviation	0	0	0.8	0.5
Total number	0	0	9	2

MANDIBLE

GREATEST LENGTH

	A	B	C	D
Mean	0	0	69.1	69.6
Maximum value	0	0	71.5	69.7
Minimum value	0	0	65.5	69.5
Variance	0	0	4.6	0
Standard deviation	0	0	2.2	0.1
Total number	0	0	8	2

GREATEST DEPTH

	A	B	C	D
Mean	2.4	0	4.4	5.2
Maximum value	2.4	0	4.8	5.2
Minimum value	2.4	0	3.8	5.1
Variance	0	0	0.1	0
Standard deviation	0	0	0.3	0.1
Total number	1	0	9	2

WIDTH ACROSS PROC. MAND. MEDIALIS

	A	B	C	D
Mean	3.6	0	10.3	11.2
Maximum value	3.6	0	10.8	11.5
Minimum value	3.6	0	10.1	10.9
Variance	0	0	0.1	0.2
Standard deviation	0	0	0.3	0.4
Total number	1	0	9	2

STERNUM

MAXIMUM LENGTH ALONG MIDLINE

	A	B	C	D
Mean	>17.8	>12.3	80.4	72.5
Maximum value	>17.8	>12.3	86.8	72.5
Minimum value	>17.8	>12.3	70.2	72.5
Variance	0	0	41.6	0
Standard deviation	0	0	6.4	0
Total number	1	1	7	1

WIDTH ACROSS STERNOCORACOIDIAL PROC.

	A	B	C	D
Mean	~11.6	9.6	31.6	30.3
Maximum value	~11.6	9.6	34.6	30.3
Minimum value	~11.6	9.6	28.4	30.3
Variance	0	0	4.9	0
Standard deviation	0	0	2.2	0
Total number	1	1	8	1

DISTANCE BETWEEN ANTERIOR END OF STERNOCORACOIDAL PROC. AND POSTERIOR END OF COSTAL AREA

	A	B	C	D
Mean	11	7.9	28.2	29.5
Maximum value	11	7.9	30.5	29.5
Minimum value	11	7.9	24.1	29.5
Variance	0	0	4.3	0
Standard deviation	0	0	2.1	0
Total number	1	1	8	1

DISTANCE FROM DORSAL TIP OF VENTRAL MANUBRIAL SPINE TO CARINAL APEX

	A	B	C	D
Mean	5.3	3.4	21.9	23.6
Maximum value	5.3	~3.4	23.4	25.2
Minimum value	5.3	~3.4	20.3	22.0
Variance	0	0	1	5.1
Standard deviation	0	0	1	2.3
Total number	1	1	7	2

PELVIS

MAXIMUM LENGTH (NOT INCLUDING PUBIS)

	A	B	C	D
Mean	23.3	18.3	73.1	72.9
Maximum value	23.3	18.3	78.7	76.3
Minimum value	23.3	18.3	69.2	69.4
Variance	0	0	14.1	23.8
Standard deviation	0	0	3.7	4.9
Total number	1	1	6	2

MAXIMUM WIDTH ACROSS ANTITROCHANTER

	A	B	C	D
Mean	13.9	12.2	45.2	41.8
Maximum value	13.9	12.2	49.3	41.8
Minimum value	13.9	12.2	42.2	41.8
Variance	0	0	8.2	0
Standard deviation	0	0	2.9	0
Total number	1	1	5	1

MAXIMUM WIDTH OF ANTERIOR END

	A	B	C	D
Mean	7.2	6.2	31.3	27.5
Maximum value	7.2	6.2	34.6	31.7
Minimum value	7.2	6.2	29.0	23.2
Variance	0	0	3.3	36.1
Standard deviation	0	0	1.8	6.0
Total number	1	1	6	2

MAXIMUM WIDTH OF POSTERIOR END MEASURED ON DORSAL SURFACE

	A	B	C	D
Mean	8.6	7.8	44.3	42.2
Maximum value	8.6	7.8	48.7	42.2
Minimum value	8.6	7.8	40.0	42.2
Variance	0	0	10.9	0
Standard deviation	0	0	3.3	0
Total number	1	1	6	1

LENGTH FROM POSTERIOR END OF ANTITROCHANTER TO ANTERIOR END OF ELEMENT

	A	B	C	D
Mean	15.1	12.9	45.1	44.6
Maximum value	15.1	12.9	49.8	46.0
Minimum value	15.1	12.9	42.5	43.2
Variance	0	0	7.8	3.9
Standard deviation	0	0	2.8	2.0
Total number	1	1	6	1

LENGTH OF SYNSACRUM FROM POSTERIOR END OF ANTITROCHANTER TO POSTERIOR END OF ELEMENT

	A	B	C	D
Mean	9.9	7.4	29.9	31.7
Maximum value	9.9	7.4	32.1	33.5
Minimum value	9.9	7.4	28.2	29.8
Variance	0	0	2.2	6.8
Standard deviation	0	0	1.5	2.6
Total number	1	1	7	2

DEPTH OF PELVIS AT POSTERIOR END FROM DORSALMOST PART OF ILIUM TO BASE OF ISCHIUM

	A	B	C	D
Mean	10.5	8.8	32.4	29.7
Maximum value	10.5	~8.8	36.0	31.4
Minimum value	10.5	~8.8	28.6	27.9
Variance	0	0	7.8	6.1
Standard deviation	0	0	2.8	2.5
Total number	1	1	5	2

SCAPULA

MAXIMUM MEASUREMENT ACROSS ACROMION TO DISTAL PART OF GLENOID FACET

	A	B	C	D
Mean	4.2	3.0	11.7	11.3
Maximum value	4.2	3.0	13.4	11.3
Minimum value	4.2	3.0	9.9	11.3
Variance	0	0	1.0	0
Standard deviation	0	0	1.0	0
Total number	1	1	9	1

MAXIMUM DEPTH ACROSS ACROMION

	A	B	C	D
Mean	2.6	1.3	6.5	6.5
Maximum value	2.6	1.3	7.2	6.5
Minimum value	2.6	1.3	5.9	6.5
Variance	0	0	0.2	0
Standard deviation	0	0	0.5	0
Total number	1	1	8	1

MAXIMUM LENGTH

	A	B	C	D
Mean	21.6	16.5	59.9	59.5
Maximum value	21.6	16.5	63.3	61.5
Minimum value	21.6	16.5	54.6	57.5
Variance	0	0	8.9	8.0
Standard deviation	0	0	3	2.8
Total number	1	1	9	2

WIDTH OF SHAFT AT DISTAL END OF GLENOID FACET

	A	B	C	D
Mean	1.6	2.0	5.7	5.5
Maximum value	1.6	2.0	6.6	5.8
Minimum value	1.6	2.0	4.5	5.2
Variance	0	0	0.5	0.2
Standard deviation	0	0	0.7	0.4
Total number	1	1	7	2

CORACOID

TOTAL LENGTH FROM DORSALMOST END TO TIP OF STERNOCORACOIDAL PROCESS

	A	B	C	D
Mean	19.6	15.2	42.8	42.9
Maximum value	19.6	15.2	44.7	43.9
Minimum value	19.6	15.2	38.8	41.8
Variance	0	0	3.5	2.2
Standard deviation	0	0	1.9	1.5
Total number	1	1	8	2

DORSAL WIDTH FROM BRACHIAL TUBEROSITY EXTENSION ACROSS GLENOID FACET

	A	B	C	D
Mean	2.6	1.2	8.9	9.1
Maximum value	2.6	~1.2	9.6	9.2
Minimum value	2.6	~1.2	7.7	9.0
Variance	0	0	0.4	0
Standard deviation	0	0	0.6	0.1
Total number	1	1	8	2

MAXIMUM WIDTH OF VENTRAL END

	A	B	C	D
Mean	3.2	2.5	12.5	11.6
Maximum value	3.2	2.5	15.0	12.6
Minimum value	3.2	2.5	10.2	10.5
Variance	0	0	3.0	2.2
Standard deviation	0	0	1.7	1.5
Total number	1	1	8	2

LENGTH FROM DORSALMOST EXTENSION OF CORACOHUMERAL SURFACE TO VENTRAL PART OF SCAPULAR FACET

	A	B	C	D
Mean	3.8	2.6	12.1	11.4
Maximum value	3.8	2.6	12.7	12.0
Minimum value	3.8	2.6	11.4	10.8
Variance	0	0	0.2	0.7
Standard deviation	0	0	0.4	0.8
Total number	1	1	7	2

CLAVICLES

MAXIMUM LENGTH FROM SCAPULAR TUBEROSITY TO SYMPHYSIS

	A	B	C	D
Mean	7.6	0	40.2	36.6
Maximum value	>7.6	0	44.3	36.6
Minimum value	>7.6	0	37.9	36.6
Variance	0	0	6.2	0
Standard deviation	0	0	2.5	0
Total number	1	0	8	1

MAXIMUM WIDTH ACROSS SCAPULAR TUBEROSITY AND CORACOIDAL FACET

	A	B	C	D
Mean	2.6	0	8.1	7.1
Maximum value	2.6	0	9.4	7.1
Minimum value	2.6	0	7.0	7.1
Variance	0	0	0.7	0
Standard deviation	0	0	0.8	0
Total number	1	0	8	1

HUMERUS

TOTAL LENGTH

	A	B	C	D
Mean	5.0	3.4	63.3	61.7
Maximum value	5.0	3.4	66.5	61.7
Minimum value	5.0	3.4	59.5	61.7
Variance	0	0	6.1	0
Standard deviation	0	0	2.5	0
Total number	1	1	7	1

MAXIMUM WIDTH ACROSS PROXIMAL END

	A	B	C	D
Mean	5.0	3.4	17.7	16.9
Maximum value	5.0	3.4	19.9	17.6
Minimum value	5.0	3.4	15.1	16.1
Variance	0	0	1.9	1.1
Standard deviation	0	0	1.4	1.1
Total number	1	1	9	2

DEPTH OF INTERNAL TUBEROSITY

	A	B	C	D
Mean	2.1	2.2	6.1	5.7
Maximum value	2.1	2.2	6.7	5.9
Minimum value	2.1	2.2	5.5	5.5
Variance	0	0	0.2	0.1
Standard deviation	0	0	0.4	0.3
Total number	1	1	9	2

MAXIMUM DEPTH OF HEAD

	A	B	C	D
Mean	1.4	1.1	5.3	5.2
Maximum value	1.4	1.1	5.9	5.3
Minimum value	1.4	1.1	4.8	5.0
Variance	0	0	0.1	0
Standard deviation	0	0	0.4	0.2
Total number	1	1	9	2

MAXIMUM WIDTH OF DISTAL END

	A	B	C	D
Mean	4.5	0	15.4	15.5
Maximum value	4.5	0	16.8	15.5
Minimum value	4.5	0	14.0	15.5
Variance	0	0	0.8	0
Standard deviation	0	0	0.9	0
Total number	1	0	9	1

MAXIMUM DEPTH OF EXTERNAL CONDYLE

	A	B	C	D
Mean	2.1	0	6.8	7
Maximum value	2.1	0	7.9	7.2
Minimum value	2.1	0	5.9	6.7
Variance	0	0	0.4	0.1
Standard deviation	0	0	0.7	0.4
Total number	1	0	9	2

MAXIMUM DEPTH OF INTERNAL CONDYLE

	A	B	C	D
Mean	1.1	0	3.8	4.1
Maximum value	1.1	0	4.4	4.3
Minimum value	1.1	0	3.0	3.9
Variance	0	0	0.3	0.1
Standard deviation	0	0	0.5	0.3
Total number	1	0	9	2

LENGTH OF INTERNAL CONDYLE

	A	B	C	D
Mean	1.2	0	5.4	4.0
Maximum value	1.2	0	6.6	4.0
Minimum value	1.2	0	4.0	4.0
Variance	0	0	1.0	0
Standard deviation	0	0	1.0	0
Total number	1	0	8	1

LENGTH OF EXTERNAL CONDYLE

	A	B	C	D
Mean	1.4	0	5.0	5.2
Maximum value	1.4	0	6.2	5.2
Minimum value	1.4	0	4.0	5.2
Variance	0	0	0.6	0
Standard deviation	0	0	0.7	0
Total number	1	0	8	1

RADIUS

TOTAL LENGTH

	A	B	C	D
Mean	14.8	0	58.8	56.8
Maximum value	~14.8	0	62.5	57.8
Minimum value	~14.8	0	55.2	55.8
Variance	0	0	5.3	2.0
Standard deviation	0	0	2.3	1.4
Total number	1	0	9	2

MAXIMUM MEASUREMENT ACROSS PROXIMAL END

	A	B	C	D
Mean	1.3	0	4.9	5.1
Maximum value	1.3	0	5.6	5.4
Minimum value	1.3	0	3.6	4.7
Variance	0	0	0.4	0.2
Standard deviation	0	0	0.6	0.5
Total number	1	0	9	2

MAXIMUM MEASUREMENT ACROSS DISTAL END

	A	B	C	D
Mean	1.6	0	6.2	6.2
Maximum value	1.6	0	7.0	6.6
Minimum value	1.6	0	5.5	5.8
Variance	0	0	0.2	0.3
Standard deviation	0	0	0.5	0.6
Total number	1	0	9	2

MEASUREMENT OF DISTAL END ACROSS LIGAMENTAL PROMINENCE

	A	B	C	D
Mean	0.9	0	3.4	3.1
Maximum value	0.9	0	3.7	3.4
Minimum value	0.9	0	3.0	2.7
Variance	0	0	0.1	0.2
Standard deviation	0	0	0.2	0.5
Total number	1	0	8	2

ULNA

MAXIMUM LENGTH

	A	B	C	D
Mean	16.4	0	65.8	63.7
Maximum value	16.4	0	69.9	65.1
Minimum value	16.4	0	60.1	62.3
Variance	0	0	9.9	3.9
Standard deviation	0	0	3.1	2.0
Total number	1	0	9	2

MAXIMUM WIDTH OF PROXIMAL END

	A	B	C	D
Mean	2.8	0	10.3	9.7
Maximum value	2.8	0	11.2	10.5
Minimum value	2.8	0	9.4	8.9
Variance	0	0	0.3	1.3
Standard deviation	0	0	0.5	1.1
Total number	1	0	9	2

MAXIMUM WIDTH OF DISTAL END

	A	B	C	D
Mean	2.6	0	8.3	8.8
Maximum value	2.6	0	9.0	9.3
Minimum value	2.6	0	8.0	8.3
Variance	0	0	0.1	0.5
Standard deviation	0	0	0.3	0.7
Total number	1	0	9	2

DEPTH OF EXTERNAL CONDYLE

	A	B	C	D
Mean	2.1	0	7.7	7.3
Maximum value	2.1	0	8.5	7.6
Minimum value	2.1	0	6.8	6.9
Variance	0	0	0.3	0.2
Standard deviation	0	0	0.5	0.5
Total number	1	0	9	2

LENGTH OF INTERNAL COTYLA

	A	B	C	D
Mean	1.9	0	6.3	5.9
Maximum value	1.9	0	7.0	6.0
Minimum value	1.9	0	5.5	5.7
Variance	0	0	0.2	0
Standard deviation	0	0	0.5	0.2
Total number	1	0	9	2

LENGTH FROM DISTAL END OF INTERNAL COTYLA TO PROXIMAL END OF OLECRANON

	A	B	C	D
Mean	2.9	0	9.8	9.5
Maximum value	2.9	0	10.5	9.7
Minimum value	2.9	0	8.5	9.3
Variance	0	0	0.4	0.1
Standard deviation	0	0	0.6	0.3
Total number	1	0	9	2

CARPOMETACARPUS

MAXIMUM LENGTH

	A	B	C	D
Mean	10	0	38.3	36.3
Maximum value	10	0	41.3	38.1
Minimum value	10	0	35.3	34.5
Variance	0	0	3.9	6.5
Standard deviation	0	0	2.0	2.5
Total number	1	0	9	2

MAXIMUM WIDTH ACROSS TROCHLEAE

	A	B	C	D
Mean	1.7	0	5.4	5.1
Maximum value	1.7	0	5.7	5.4
Minimum value	1.7	0	5.0	4.8
Variance	0	0	0.1	0.2
Standard deviation	0	0	0.3	0.4
Total number	1	0	9	2

MAXIMUM DEPTH (TROCHLEAE TO METACARPAL I)

	A	B	C	D
Mean	3.5	0	12.2	11.4
Maximum value	3.5	0	13.3	11.6
Minimum value	3.5	0	11.2	11.1
Variance	0	0	0.4	0.1
Standard deviation	0	0	0.6	0.4
Total number	1	0	9	2

LENGTH OF INTERMETACARPAL SPACE

	A	B	C	D
Mean	2.9	0	14.8	14.1
Maximum value	2.9	0	17.2	14.5
Minimum value	2.9	0	14.3	13.6
Variance	0	0	0.8	0.4
Standard deviation	0	0	0.9	0.6
Total number	1	0	9	2

DEPTH ACROSS FACETS FOR DIGITS II AND III

	A	B	C	D
Mean	2.2	0	8.1	7.9
Maximum value	2.2	0	8.9	8.0
Minimum value	2.2	0	7.3	7.8
Variance	0	0	0.2	0
Standard deviation	0	0	0.5	0.1
Total number	1	0	9	2

FEMUR

TOTAL LENGTH

	A	B	C	D
Mean	27.1	20.4	71.2	68.3
Maximum value	27.1	>20.4	75.9	69.2
Minimum value	27.1	>20.4	67.8	67.3
Variance	0	0	8.4	1.8
Standard deviation	0	0	2.9	1.3
Total number	1	1	9	2

MAXIMUM WIDTH OF PROXIMAL END

	A	B	C	D
Mean	4.7	4.3	18.4	17.2
Maximum value	4.7	4.3	20.8	17.7
Minimum value	4.7	4.3	16.0	16.7
Variance	0	0	1.8	0.5
Standard deviation	0	0	1.3	0.7
Total number	1	1	9	2

DEPTH OF HEAD

	A	B	C	D
Mean	1.8	1.4	8.4	8.3
Maximum value	1.8	1.4	9.1	8.7
Minimum value	1.8	1.4	7.7	7.9
Variance	0	0	0.2	0.3
Standard deviation	0	0	0.5	0.6
Total number	1	1	9	2

DEPTH OF TROCHANTER

	A	B	C	D
Mean	3.6	2.6	12.1	11.5
Maximum value	3.6	2.6	14.2	11.9
Minimum value	3.6	2.6	10.9	11.0
Variance	0	0	1.0	0.4
Standard deviation	0	0	1.0	0.6
Total number	1	1	9	2

MAXIMUM LENGTH OF TROCHANTERIC RIDGE

	A	B	C	D
Mean	5.5	3.0	22.3	21.8
Maximum value	5.5	3.0	25.8	22.1
Minimum value	5.5	3.0	20.4	21.4
Variance	0	0	4.3	0.2
Standard deviation	0	0	2.1	0.5
Total number	1	1	9	2

MAXIMUM WIDTH OF DISTAL END

	A	B	C	D
Mean	4.6	0	18.4	17.6
Maximum value	4.6	0	20.0	18.4
Minimum value	4.6	0	16.4	16.8
Variance	0	0	1.2	1.3
Standard deviation	0	0	1.1	1.1
Total number	1	0	9	2

MAXIMUM DEPTH OF INTERNAL CONDYLE

	A	B	C	D
Mean	3.7	0	9.9	9.4
Maximum value	3.7	0	11.0	10.1
Minimum value	3.7	0	8.7	8.6
Variance	0	0	0.5	1.1
Standard deviation	0	0	0.7	1.1
Total number	1	0	9	2

MAXIMUM DEPTH OF EXTERNAL CONDYLE

	A	B	C	D
Mean	3.7	0	13.5	13.1
Maximum value	3.7	0	14.8	13.4
Minimum value	3.7	0	11.9	12.8
Variance	0	0	0.7	0.2
Standard deviation	0	0	0.8	0.4
Total number	1	0	9	2

TIBIOTARSUS

TOTAL LENGTH

	A	B	C	D
Mean	40.2	35.6	136.2	137.4
Maximum value	40.2	35.6	144.0	143.4
Minimum value	40.2	35.6	127.2	131.3
Variance	0	0	26.4	73.2
Standard deviation	0	0	5.1	8.6
Total number	1	1	8	2

LENGTH OF FIBULAR CREST

	A	B	C	D
Mean	6.3	4.4	20.0	22.2
Maximum value	6.3	~4.4	23.5	23.1
Minimum value	6.3	~4.4	16.3	21.2
Variance	0	0	4.5	1.8
Standard deviation	0	0	2.1	1.3
Total number	1	1	9	2

ANTERIOR WIDTH OF PROXIMAL END

	A	B	C	D
Mean	5.4	0	23.1	23.0
Maximum value	5.4	0	24.6	24.4
Minimum value	5.4	0	21.1	21.5
Variance	0	0	1.4	4.2
Standard deviation	0	0	1.2	2.1
Total number	1	0	9	2

POSTERIOR WIDTH OF PROXIMAL END

	A	B	C	D
Mean	4.5	0	15.6	15.1
Maximum value	4.5	0	17.0	15.9
Minimum value	4.5	0	13.6	14.2
Variance	0	0	0.8	1.4
Standard deviation	0	0	0.9	1.2
Total number	1	0	9	2

MAXIMUM WIDTH OF DISTAL END

	A	B	C	D
Mean	3.7	3.0	13.9	14.2
Maximum value	3.7	3.0	14.9	15.5
Minimum value	3.7	3.0	12.5	12.8
Variance	0	0	0.6	3.6
Standard deviation	0	0	0.8	1.9
Total number	1	1	9	2

DEPTH OF INTERNAL CONDYLE

	A	B	C	D
Mean	3.5	2.9	12.2	12.1
Maximum value	3.5	2.9	13.3	12.9
Minimum value	3.5	2.9	10.8	11.2
Variance	0	0	0.5	1.4
Standard deviation	0	0	0.7	1.2
Total number	1	1	9	2

DEPTH OF EXTERNAL CONDYLE

	A	B	C	D
Mean	0	2.6	11.5	11.4
Maximum value	0	2.6	12.9	12.3
Minimum value	0	2.6	10.3	10.5
Variance	0	0	0.6	1.6
Standard deviation	0	0	0.8	1.3
Total number	0	1	9	2

TARSOMETATARSUS

TOTAL LENGTH

	A	B	C	D
Mean	26.1	22.1	112.3	108.8
Maximum value	26.1	22.1	121.2	112.6
Minimum value	26.1	22.1	100.7	104.9
Variance	0	0	53.0	29.6
Standard deviation	0	0	7.3	5.4
Total number	1	1	9	2

WIDTH OF PROXIMAL END

	A	B	C	D
Mean	4.0	3.3	14.9	12.7
Maximum value	4.0	3.3	15.9	13.8
Minimum value	4.0	3.3	13.5	11.5
Variance	0	0	0.8	2.6
Standard deviation	0	0	0.9	1.6
Total number	1	1	9	2

DEPTH OF PROXIMAL END

	A	B	C	D
Mean	3.5	0	13.7	13.8
Maximum value	3.5	0	14.5	14.2
Minimum value	3.5	0	11.9	13.3
Variance	0	0	0.7	0.4
Standard deviation	0	0	0.8	0.6
Total number	1	0	9	2

WIDTH OF DISTAL END

	A	B	C	D
Mean	3.6	3.3	13.3	14.6
Maximum value	3.6	3.3	14.5	14.6
Minimum value	3.6	3.3	11.9	14.6
Variance	0	0	0.6	0
Standard deviation	0	0	0.8	0
Total number	1	1	9	1

MAXIMUM DEPTH OF DISTAL END

	A	B	C	D
Mean	1.7	1.5	6.3	6.1
Maximum value	1.7	1.5	7.2	6.4
Minimum value	1.7	1.5	5.6	~5.7
Variance	0	0	0.2	0.2
Standard deviation	0	0	0.5	0.5
Total number	1	1	9	2

Synsacrum. In dorsal view, the sacral area between the posterior iliac crests is flattened in *Menura*, but curved in an arch from anterior to posterior in *Atrichornis*. The synsacrum of *Menura*, in dorsal view, has two distinct lateral processes, one on either side, that protrude beyond the contours of the anterior iliac crest; *Atrichornis* lacks these. In dorsal view, the contours of the anterior iliac crest in *Menura* are curved over the entire length, markedly concave laterally; in *Atrichornis*, although slightly concave, the crest is straight over much of its length. In *Menura*, the anterior part of the iliac crest grades into the posterior iliac crest without interruption; a distinct crest exists over the entire length, whereas in *Atrichornis* a distinct break occurs where no definable ridge is present. In dorsal view, the lateral border of the ilium in *Menura* is slightly convex laterally, then slightly concave near the posterior end, smoothly grading into distinct posterior projections. In *Atrichornis* the lateral border is strongly flexed and L-shaped, producing an elongate, slender projection. In dorsal view, in *Menura*, the anterior iliac crest terminates dorsal to, and at the same level as, the antitrochanter; in *Atrichornis* the crest ends distinctly posterior to the antitrochanter. The dorsal border of the synsacrum, in lateral view, is more highly curved in *Atrichornis* than in *Menura* where it is nearly a straight, rather than a curved line, convex dorsally. In lateral view, the angle formed between the anterior part of the ilium and pubis in the area round the acetabulum is a small obtuse one in *Atrichornis* and a large obtuse angle in *Menura*, thus giving *Atrichornis* a much more highly arched appearance. The ischiopublic fenestra, in lateral view, is decidedly larger with respect to overall size of the synsacrum in *Atrichornis* than in *Menura*, thus rendering the posteroventral process of the ischium much more slender than that in *Menura*. In lateral view, the posterior border of ilium and ischium is more deeply incised (concave posteriorly) dorsally in *Menura* than in *Atrichornis*. The posterior process of ilium just dorsal to this area is directed posterodorsally in *Atrichornis*, but posteroventrally in *Menura*. In lateral view, the ischial angle forms a short process extending only a short distance ventral to the obturator foramen in *Menura*; in *Atrichornis* this angle forms an elongate process that extends far ventral to the obturator foramen. In lateral view, the ilioischiatic fenestra is large in *Menura*, but very large in *Atrichornis*. In ventral view, the ventral border of synsacral vertebrae is planar, flat in *Menura*, whereas in *Atrichornis* it is highly concave ventrally near the posterior end; this results in the posterior decurvature of the *Atrichornis* synsacrum. In ventral view, the posterior end of synsacrum is more inflated in *Menura* with the result that two deep fossae are present, one on either side of the midline extending back into the ilium in *Menura*. No such fossae occur in *Atrichornis*.

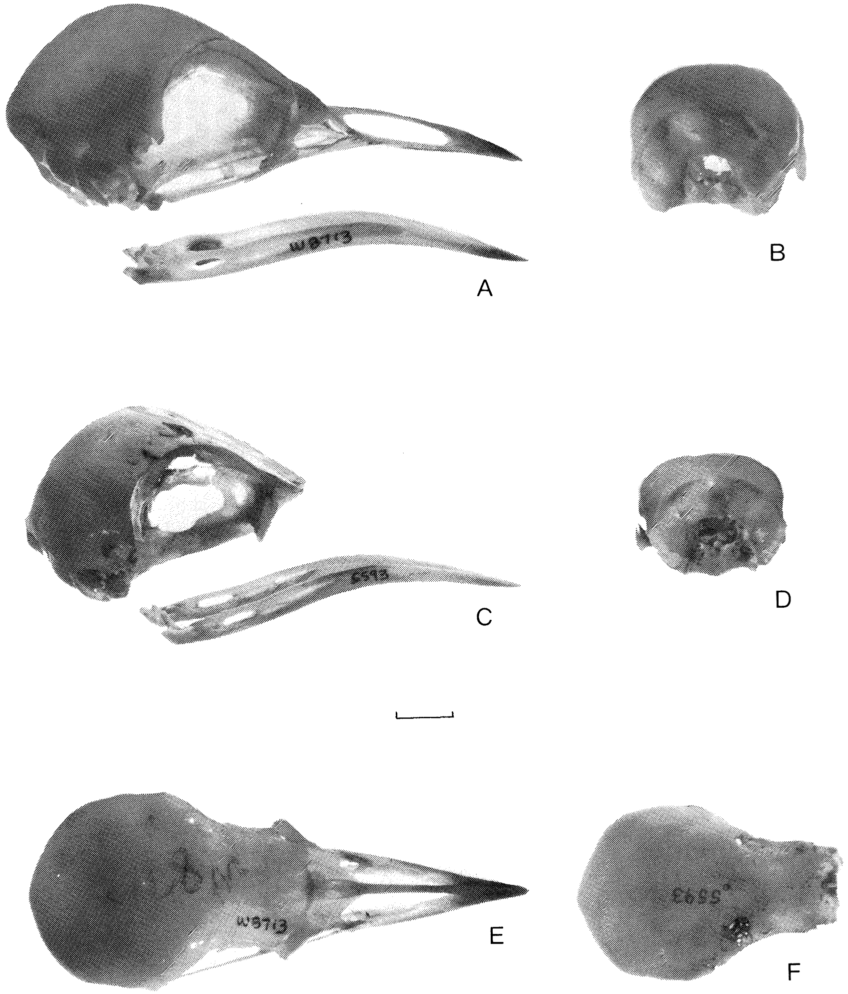

Plate I. Skulls of *Menura*. A, B, E: *M. novaehollandiae* (NMV W8713); C, D, F: *M. alberti* (AM S593). A, C: lateral; B, D: posterior; E, F: dorsal views. Scale = 10 mm.

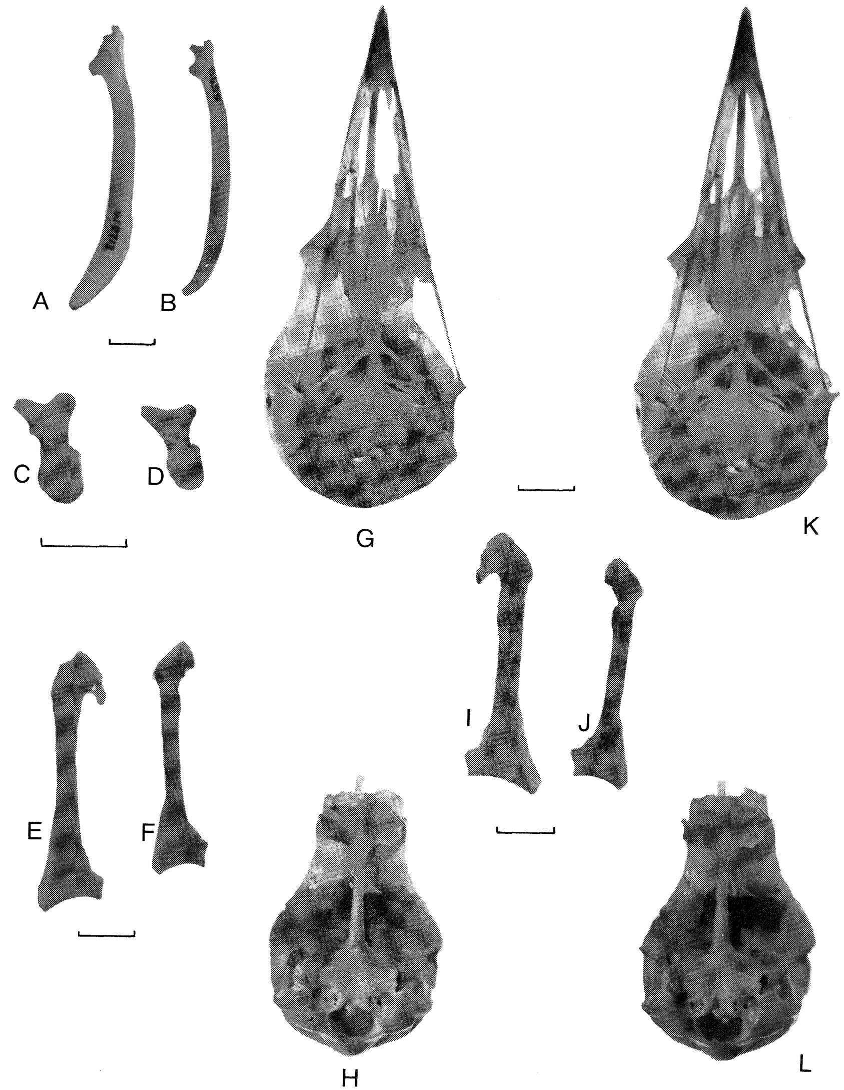

Plate II. Skulls and shoulder girdle elements of *Menura*. A, C, E, G, I, K: *M. novaehollandiae* (NMV W8713); B, D, F, H, J, L: *M. alberti* (AM S593). A, B: scapulae, dorsal view; C, D: scapulae, distal or articular view; E, F: coracoids, internal view; I, J: coracoids, external view; G, H, K, L: skulls, ventral view. Scales = 10 mm. Single scale applies to G, K; single scale applies to H, I, J, L.

Scapula. In both *Menura* and *Atrichornis* the acromion bifurcates into two blunt, knob-like processes. In *Menura*, these two are nearly equal in size, whereas in *Atrichornis* the dorsal-most is distinctly more elongate and more bulky than the second. Also in *Menura*, both processes extend about an equal distance anteriorly, whereas in *Atrichornis* the ventral process extends farther anteriorly.

Coracoid. The following observations are viewed dorsally (distally). *Menura* has an elongate, blunt process that extends ventrally from the brachial tuberosity, whereas *Atrichornis* lacks any process in this area. In *Menura*, the area beneath the brachial tuberosity is deeply excavated with a pneumatic fossa accompanying this; in *Atrichornis* this area is rather flattened or only slightly curved and has no fossa. In *Menura*, when the distal (dorsal) end of the coracoid is viewed, the coracohumeral surface is twisted only slightly away from a plane defined by the dorsal surface of the coracoidal shaft; in *Atrichornis*, the coracohumeral surface is twisted anteriorly to a much greater degree, forming a large acute angle with the coracoidal shaft plane. In both *Menura* and *Atrichornis*, coracoids are elongate and slender, and the (dorsal) ends, when viewed anteriorly, are rather similar, except that *Atrichornis* lacks a process from the brachial tuberosity; the coracoid of *Atrichornis* is relatively more slender than that of *Menura*.

The following observations are viewed anteriorly (ventrally). *Menura* has a distinct, well-defined ridge for muscle attachment bordering the proximolateral side of coracoidal shaft; in *Atrichornis* the ridge is only slightly indicated. In *Menura*, the coracoid shaft expands more broadly ventrally with development of a reduced sternocoracoidal process, whereas this process flares only slightly in *Atrichornis*, and no distinct sternocoracoidal process is developed. In *Menura* a distinct process courses dorsally from the internal distal angle; *Atrichornis* lacks this process. The lateral end of the sternal face in *Menura* extends further ventrally than the medial part of the facet; in *Atrichornis* both medial and lateral parts of the sternal facet extend about the same distance ventrally. In *Menura*, a distinct notch is present along the internal border of the shaft just dorsal to a point where the shaft begins to flare for the ventral end; no notch is present in *Atrichornis*. As viewed proximally: in *Menura* the coracoid is slightly arched, and concave posteriorly; (dorsally) *Atrichornis* is more highly arched.

Clavicles. The clavicles in *Atrichornis* are extremely reduced (they are somewhat reminiscent of a rib in shape), not even fusing along the midline as they do in *Menura*. In *Atrichornis*, the individual clavicle is nearly T-shaped, with the scapular tuberosity being slightly more elongate than the process extending in the opposite direction bearing the coracoidal facet. In *Menura*, the expansion at the dorsal end of the shaft for the scapular tuberosity and coracoidal facet is more bulbous, and the angle between one line joining the scapular tuberosity and the coracoidal facet, and another line following the shaft of the clavicle, is distinctly less than 90°.

Humerus. In anconal view, the pneumatic fossa is more deeply excavated in *Menura*, the excavation leading far into the interior of the bone. In *Atrichornis*, the fossa is closed off at the bottom of a considerable excavation with no indication of connection with the interior parts of the bone. In *Atrichornis*, the proximal part of the shaft just distal to the pneumatic fossa is deeply excavated, and this excavation leads directly into the pneumatic fossa. This excavation does not occur in *Menura*. The deltoid crest extends relatively further palmad (or, in other words, it is better developed) in *Menura* than in *Atrichornis* where it is generally low and rounded. When viewed proximally, the deltoid crest simply extends further from the shaft in *Menura*. In proximal view, the palmar and anconal margins of the head are straight and parallel at right angles to the internal tuberosity in *Atrichornis*, whereas in *Menura*, the external and internal margins converge and are concave palmarly. *Atrichornis* differs from *Menura* in having a deep excavation along the internal border of the shaft (viewed palmarly) just proximal to the entepicondyle; a distinct, much shallower depression is indicated in this region in *Menura*. In *Atrichornis*, the entepicondyle extends farther distally beyond the internal and external condyles than in *Menura*. In *Atrichornis*, the internal and external condyles are more nearly the same proximodistal length, the external slightly exceeding the internal, whereas the disparity between those of *Menura* is much greater. In *Atrichornis*, the area between the entepicondylar prominence and the more lateral and prominent anterior articular ligament is depressed (concave palmarly), whereas in *Menura* it is not excavated at all, but flat. In ventral view, *Atrichornis* has a slight depression for the *pronator brevis*, not a relatively marked one, as in *Menura*, just anconal to the entepicondylar prominence. In dorsal view, the proximal end of the ectepicondylar prominence is located about twice the length of the external condyle away from the distal end of the humerus in *Atrichornis*, whereas in *Menura* it is situated only slightly proximal to the proximal end of the external condyle. In distal view, the entepicondyle in *Atrichornis* is relatively more inflated than in *Menura*.

Radius. There are very few differences between the radii of *Menura* and *Atrichornis*. The only major difference noted was that, relative to the thickness of the ulna, the radius in *Atrichornis* is much slighter than in *Menura*.

Ulna. The feather papillae are much more prominent in *Menura* than in *Atrichornis*. The shaft of the ulna in *Menura* is slightly curved, concave palmarly, but not as highly curved as in *Atrichornis*. In proximal view, the palmar border of the proximal articular surface is much more deeply incised between the internal and external cotylae in *Menura* than in *Atrichornis*. The olecranon in *Menura* is displaced farther internally than

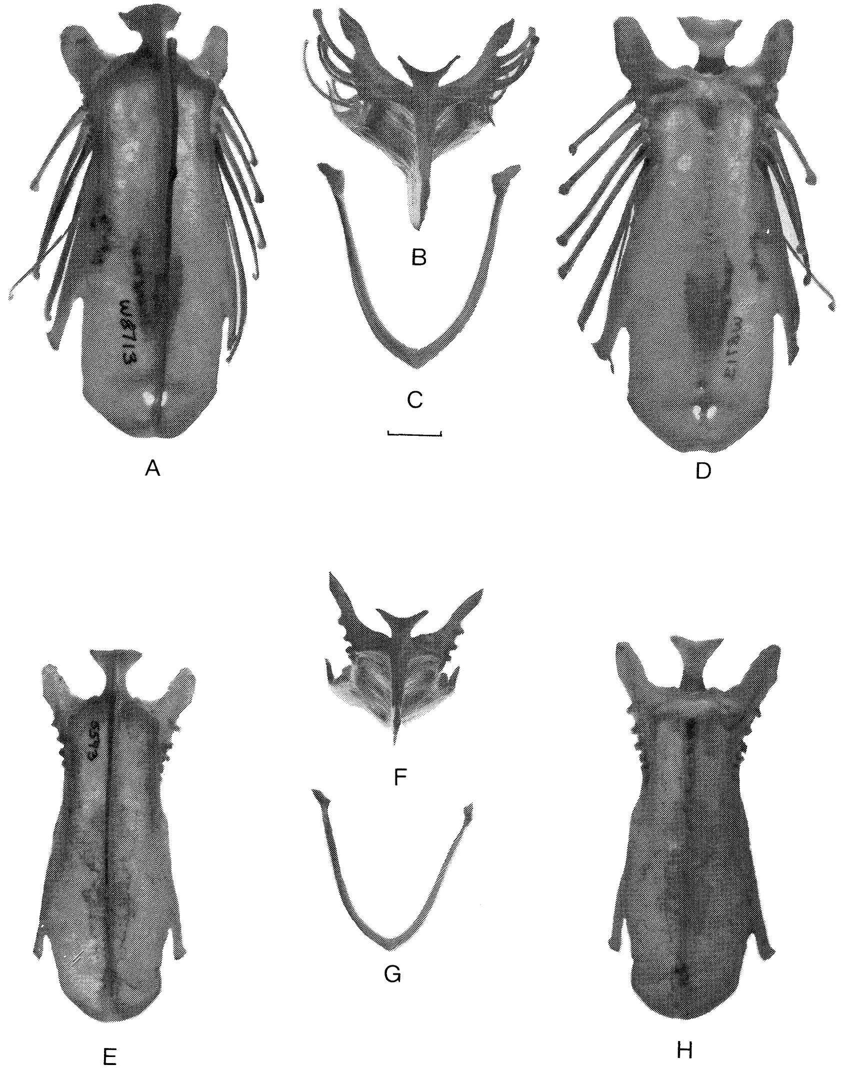

Plate III. Sterna and furcula of *Menura*. A–D: *M. novaehollandiae* (NMV W8713); E–H: *M. alberti* (AM S593). A, E: sterna, ventral view; B, F: sterna, anterior view; D, H: sterna, dorsal view; C, G: furcula, posterior view. Scale = 10 mm.

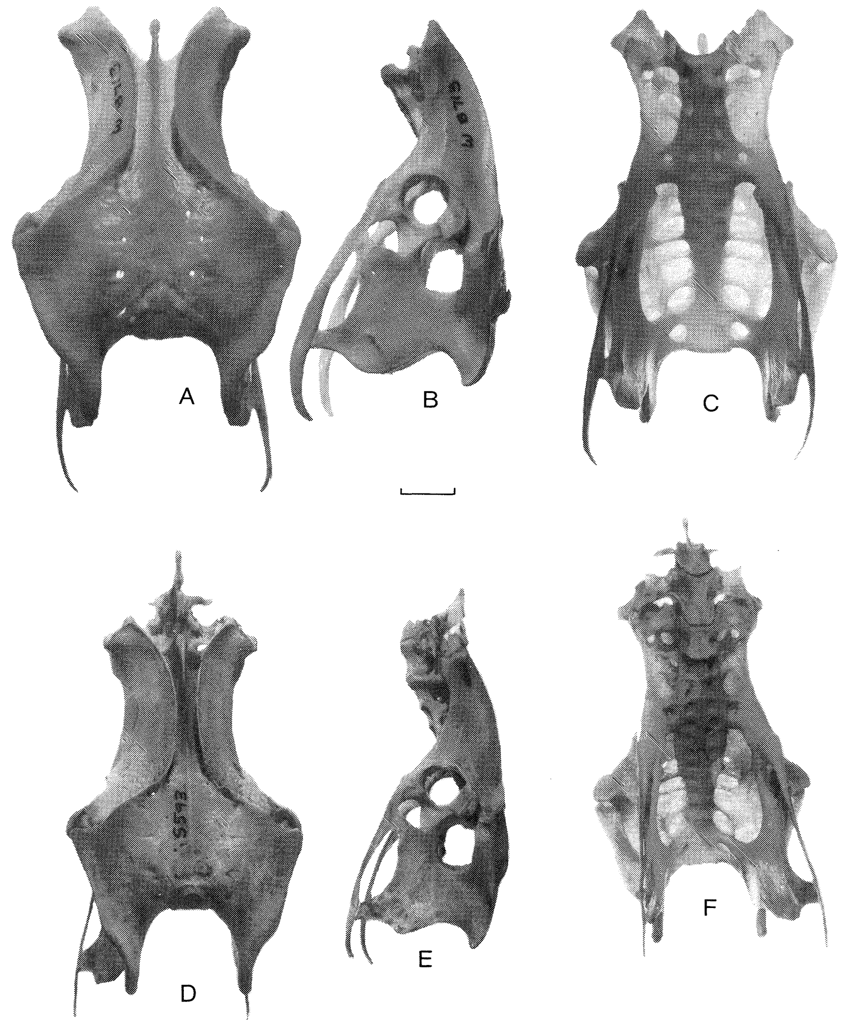

Plate IV. Synsacra of *Menura*. A–C: *M. novaehollandiae* (NMV W8713); D–F: *M. alberti* (AM S593). A, D: dorsal view; B, E: lateral view; C, F: ventral view. Scale = 10 mm.

it is in *Atrichornis*.

Carpometacarpus. The ligamental attachment of the pisiform process is much more prominent in *Menura* than in *Atrichornis*. In *Menura* the process is a single prominence, whereas in *Atrichornis* two low prominences are present. In *Menura*, the external ligamental attachment is much more prominent than in *Atrichornis*. The carpometacarpus is proportionally stouter in *Atrichornis* than it is in *Menura*. A prominence that is represented only by a slight swelling in *Atrichornis* is present on metacarpal II about midway between proximal and distal ends on the external border in *Menura*. The external carpal trochlea in *Atrichornis* extends relatively farther proximally than the internal trochlea, whereas in *Menura* this difference is less pronounced. The intermetacarpal tuberosity has a narrower base in *Atrichornis* than it has in *Menura*, when viewed externally. The ligamental groove on the external surface of the distal half of the carpometacarpus is deep and well defined in *Menura*, but is shallow and broad in *Atrichornis*.

Femur. In proximal view, *Menura* has a femoral head whose anteroposterior depth is more than one-half of the depth of the trochanter, whereas in *Atrichornis* the depth of the head is no more than half the depth of the trochanter. The neck (viewed proximally) in *Menura* is more emphasized than in *Atrichornis*, mainly because the anterior margin of the proximal end, just lateral to the head, in *Menura* is broadly concave anteriorly, and not narrowly notched as in *Atrichornis*. In medial view, the shaft of the femur in *Atrichornis* is markedly curved, being concave posteriorly, whereas in *Menura* it is quite straight. In *Atrichornis*, the main flexure occurs distal to the proximodistal midpoint of the shaft. In medial view, the internal condyle of *Menura* is more anteroposteriorly compressed than in *Atrichornis*, where the outline of the internal condyle approximates a half circle. In *Atrichornis*, the mediodistal corner of the posterior shaft surface is excavated, concave posteriorly, whereas this area is not excavated in *Menura*. In posterior view, *Atrichornis* has a small, short obturator ridge on the lateral side of the posterior shaft surface that is a continuation of the proximal articular surface. *Menura* has nothing comparable to this, with only a distinct process on the lateral side of the trochanter for muscle attachment, which is also present in *Atrichornis*. In anterior view, the trochanteric ridge of *Menura* is bifurcated with a short ridge medial (that continues into the anterior intermuscular line) to a second ridge, which occurs along the border of the shaft. *Atrichornis* has a single, laterally placed ridge. The lateral trochanteric ridge in *Menura* is basically divided into two parts, a proximal, more massive, and a distal, more delicate section, both separated by a swail. In *Atrichornis*, the two parts of the ridge are developed, but the distal segment is not at all prominent. In *Atrichornis*, the anterior intermuscular line joins the trochanteric ridge along the lateral shaft border, about one-third the shaft's length from the proximal end, and continued as a very slight ridge down the midline of the shaft; in *Menura*, the anterior intermuscular line originates from the medial branch of the trochanteric ridge, in the middle of the shaft near the proximal end, and continues as a prominent ridge angling across the shaft towards the internal border. In lateral view, the most proximal projection occurs at the anterior part of the trochanter in *Atrichornis*. In *Menura*, the proximal-most projection occurs at a point between the anteroposterior midpoint and the border of the shaft. Thus, the shape of the trochanter is different in the two genera. In distal view, the fibular condyle and the external condyle in *Menura* appear to be more inflated and more massive, relative to the internal condyle, than in *Atrichornis*. The rotular groove in *Atrichornis* is nearly bilaterally symmetrical, whereas in *Menura* it is assymmetrical with the deepest part being displaced medially from the mediolateral midpoint. In distal view, the medial margin of the internal condyle in *Atrichornis* is straight and nearly perpendicular to the mediolateral axis of the distal end. In *Menura*, although also straight, the medial margin of the internal condyle forms an obtuse angle with the distal ends of the axis; thus, the posterior edge of the internal condyle extends further, medially, than the anterior edge.

Tibiotarsus. In proximal view, the inner cnemial crest of *Atrichornis* is near the internal side of the proximal end, while in *Menura* the crest is displaced externally nearing the midline. In *Atrichornis*, the inner cnemial crest protrudes only slightly beyond the anterior border of the proximal end, whereas in *Menura* the crest extends far anteriorly. The inner cnemial crest in *Menura* also extends far beyond the proximal articular surface. In *Atrichornis*, the crest does not extend far proximally. In proximal view, the interarticular area at the base of the cnemial crest is marked by two moderately deep depressions in *Atrichornis*. In *Menura* these are relatively shallower. The ligamental attachment distal to the inner cnemial crest originates at the base of the crest in *Atrichornis*, whereas in *Menura* it is further displaced, extending distally to the level at which the fibular crest begins. In *Atrichornis*, the ligamental crest terminates before the fibular crest originates on the opposite side of the shaft. Thus, the ligamental crest is separated by a gap from the inner cnemial crest in *Menura*, whereas it merges with that crest in *Atrichornis*. The fibula in some *Menura* is more elongate with respect to the shaft than in the *Atrichornis* studied, where the fibula extends slightly beyond the fibular crest. This character, however, seems to be a most variable one even on opposite sides within the same bird. On NMV B10730, the left fibula, which appears to be complete, extends only 16.5 mm beyond the distal end of the fibular crest, whereas the right fibula is elongate, extending 40.5 mm beyond the fibular crest (in *Menura*). In anterior view, the shaft surface medial to the fibular crest is marked by a distinct ridge running distomedially from the lateral margin in *Menura*. This

Plate V. Wing elements of *Menura*. B, C, E, G, I, K, N, O, Q: *M. novaehollandiae* (NMV W8713); A, D, F, H, J, L, M, P, R, *M. alberti* (AM S593). A, B: humeri, proximal view; C, D: humeri, distal view; E–F, I–J: humeri, anconal view, stereo pair; G, H: radii, palmar view; K, L: radii, anconal view; M, N: humeri, ventral view; O–R: humeri, palmar view, stereo pairs. Scales = 10 mm; single scale applies to E–R .

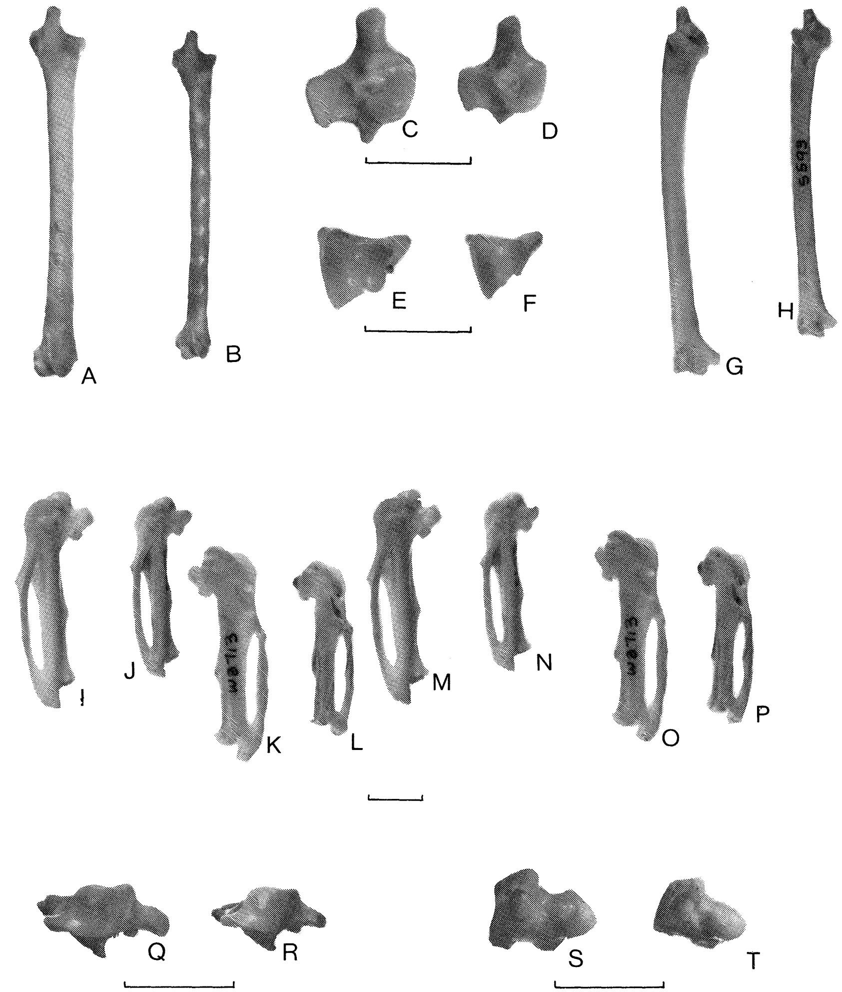

Plate VI. Wing elements of *Menura*. A, C, E, G, I, K, M, O, Q, S: *M. novaehollandiae* (NMV W8713); B, D, F, H, J, L, N, P, R, T: *M. alberti* (AM S593). A, B: ulnae, anconal view; C, D: ulnae proximal view; E, F: ulnae, distal view; G, H: ulnae, palmar view; I–J, M–N: carpometacarpi, internal view, stereo pairs; K–L, O–P: carpometacarpi, external view, stereo pairs; Q, R: carpometacarpi, proximal view; S, T: carpometacarpi, distal view. Scales = 10 mm; same scale applies to A–B, G–H, I–P.

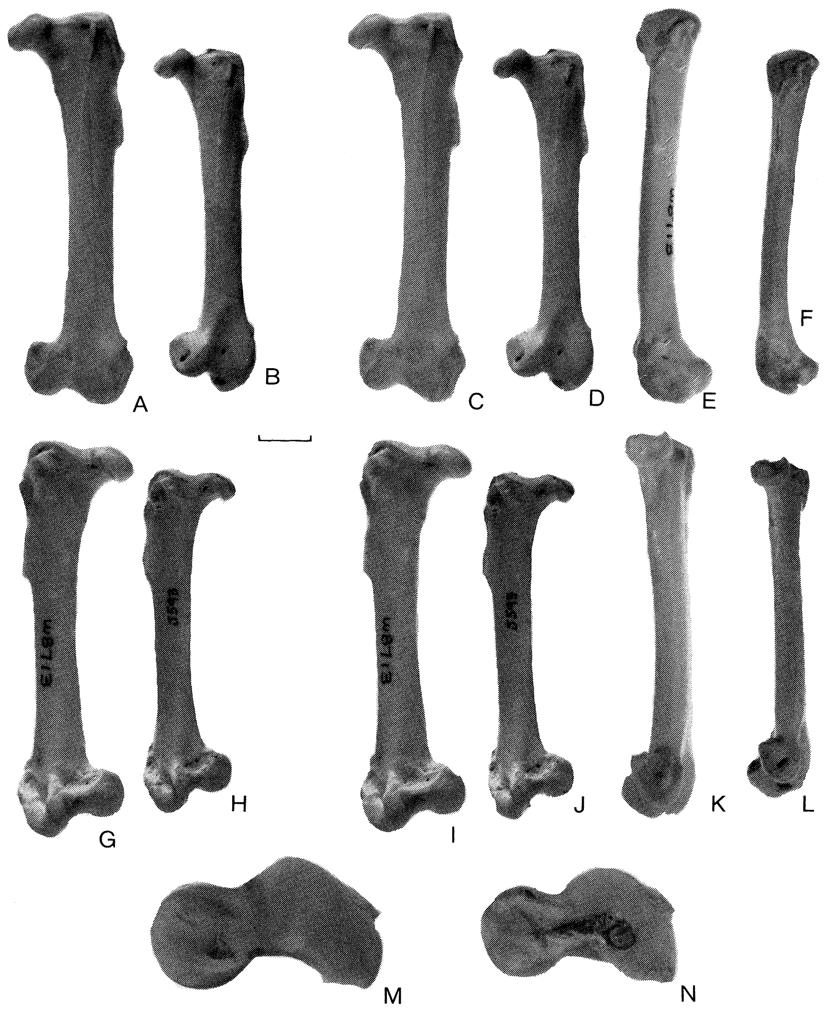

Plate VIII. Femora of *Menura*. A, C, E, G, I, K, M: *M. novaehollandiae* (NMV W8713); B, D, F, H, J, L, N: *M. alberti* (AM S593). A–D: anterior view, stereo pairs; E, F: lateral view; G–J: posterior view, stereo pairs; K, L: medial view; M, N: proximal view. Scales = 10 mm. Single scale applies to A–L; single scale applies to M–N.

Plate IX. Hind limb elements of *Menura*. A, C, E, G: *M. novaehollandiae* (NMV W8713); B, D, F, H: *M. alberti*. A–D: anterior view, including metatarsal I, stereo pairs; E, F: internal view; G–H: distal view. Scales = 10 mm. Single scale applies to A–F; single scale applies to G–H.

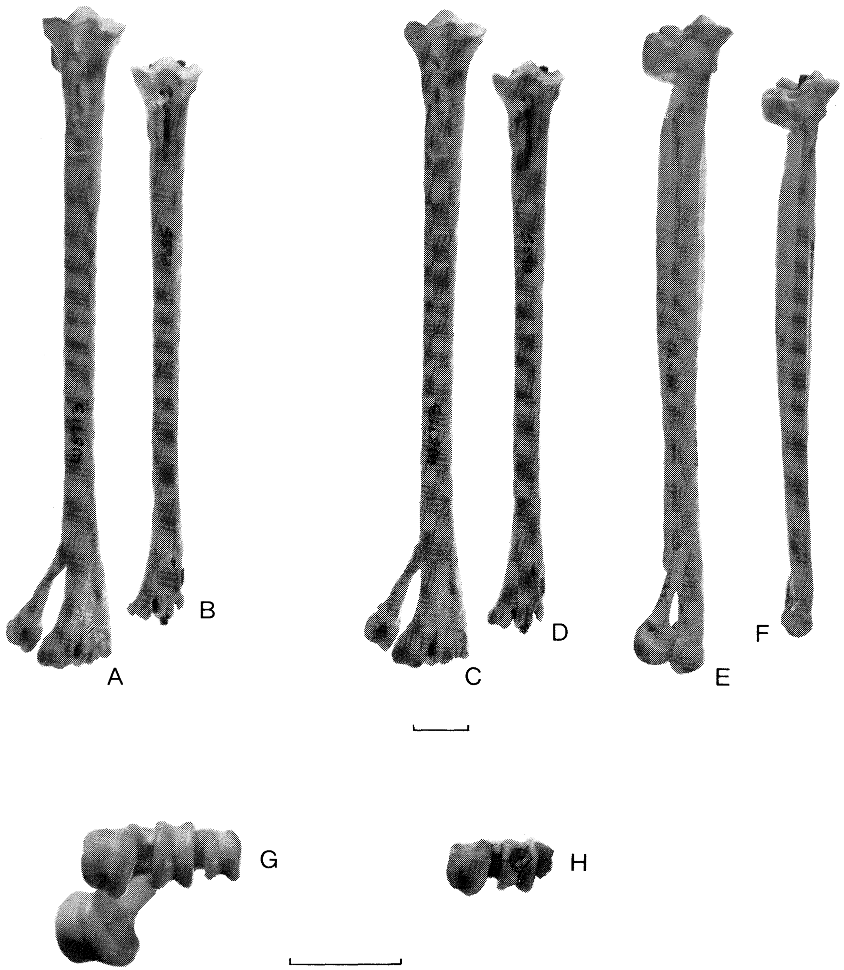

Plate X. Tarsometatarsi of *Menura*. A, C, E, G: *M. novaehollandiae* (NMV W8713); B, D, F, H: *M. alberti* (AM S593). A–D: anterior view, including metatarsal I, stereo pairs; E, F: internal view; G, H: distal view. Scales = 10 mm. Single scale applies to A–F; single scale applies to G–H.

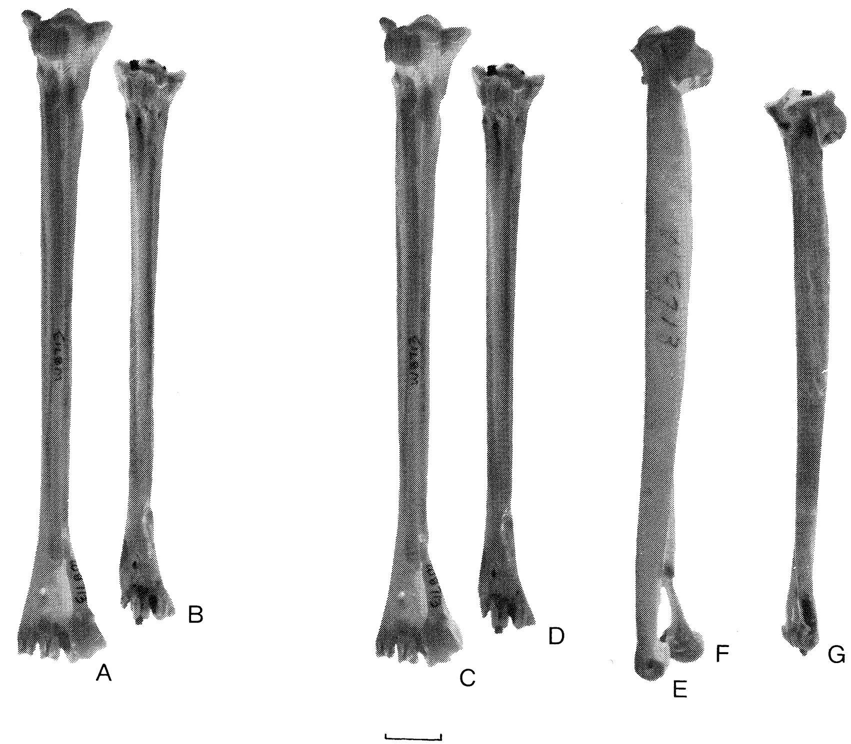

Plate XI. Tarsometatarsi of *Menura*. A, C, E: *M. novaehollandiae*; B, D, G: *M. alberti*. A–D: posterior view, including metatarsal I, stereo pairs; E–G: lateral view. Scale = 10 mm.

ridge is totally lacking in *Atrichornis*. In *Atrichornis*, the shaft surface is gently rounded. The posterior intercondylar sulcus is deeply excavated in *Menura* — only shallowing so in *Atrichornis*. In *Menura*, when viewed distally, a distinct ridge is present within the intercondylar sulcus, located slightly lateral of the midpoint, and this is much less pronounced in *Atrichornis*. In medial view, the rim of the internal condyle in *Atrichornis* is flattened distally, not rounded as in *Menura*. In external view, in *Menura* the ridge along the distal part of the shaft leads into the external ligamental prominence, which is quite distinct. In *Atrichornis* neither ridge nor prominence is present.

Fibula. In lateral view, the proximal end of the fibula of *Menura*, on the anterior half of the shaft, rises more abruptly from the fibular shaft and presents a better defined surface of ligamental attachment than in *Atrichornis*, where this area is relatively smoother. In side view, the fibula of *Atrichornis* tapers gradually toward its distal end; but in *Menura* this bone tapers abruptly about midway along the fibular attachment to the tibiotarsus to produce a flattened, splint-like, knife-edged bone over the remainder of its length. In proximal view, the head of the fibula is concave on the internal side in *Menura* and is nearly straight in *Atrichornis*.

Tarsometatarsus. *Atrichornis* has three tendinal canals; *Menura* has five. The shapes of the proximal articular surfaces differ in the two genera, *Menura* being more expanded anteroposteriorly on the external and internal margins, thus being dumbell-shaped; *Atrichornis* has a more rectangular-shaped surface. In both genera a ridge or process, perhaps more properly termed a calcaneal ridge, extends far posterior to the external cotyla, ending between the first and second calcaneal canals. In *Atrichornis* the ridge is decidely shorter than that in *Menura* with respect to width of the proximal end. In *Menura*, the intercotylar prominence occupies all of the space between the anterior and posterior margins of the proximal end, whereas in *Atrichornis* the prominence is restricted to the anterior half of the proximal end. The internal cotyla is more deeply excavated in *Atrichornis* than in *Menura*. In *Atrichornis* the internal margin of the internal cotyla extends farther proximally than the external margin of the external cotyla, yet not as far as the tip of the intercotyla prominence; in *Menura* the margins of the cotylae extend about an equal distance proximally, while the intercotylar prominence extends farther than both. The posterior metatarsal groove is fairly shallow, if present at all in *Atrichornis*. It is located along the more proximal points of the posterior shaft in *Atrichornis*, whereas in *Menura* it is always well developed over most of the shaft. The external ligamental ridge that courses along the posterior surface of the shaft expands relatively farther posteriorly in *Menura* than in *Atrichornis*. Although lower, the ridge extends farther along the shaft in *Atrichornis* than in *Menura*, coarsing well beyond the midpoint in the former and about to the midpoint in the latter. The distal end of the tarsometatarsus in *Menura* tends to expand and broaden more, particularly externally, than in *Atrichornis*; in fact, in *Atrichornis*, the external shaft margin continues nearly as a straight line right into the distal end, not curving laterally. In distal view, the trochlea for digit II in *Menura* is the largest (in surface area) of all the trochleae, followed by III and IV. In *Atrichornis*, trochleae II and III are equal in area, both being distinctly larger than IV. In anterior view of the distal end, the marked depressions occurring at the bases of the trochleae for digits II, III and IV vary as follows: *Atrichornis* — II, a deep depression occurs on the external half of the base; III, the groove ends in a depression; IV, no depression is present. *Menura* — II, a slight depression lies external to centre of the base; III, the groove ends in a deep, central depression at its base; IV, the groove ends in a deep, central depression. In *Menura*, a well developed ossified tendon lies closely apposed to the tarsometatarsus over most of the length of the posterior metatarsal groove; it is flattened over much of its length, but swells to a bulbous distal end that lies external to the proximal end of metatarsal I. We have not observed this in any of the *Atrichornis* specimens available to us.

Osteological Comparisons of *Menura novaehollandiae* and *Menura alberti*

Plates I–XI

Menura novaehollandiae differs from *M. alberti* in having: **Cranium:** greater inflation of the region dorsal to the foramen for the greater mandibular nerve (for n. max. mand.). **Rostrum:** the palantines more proximodistally elongate and laterally compressed. **Sternum:** a marked ventral bulge in the ventral manubrial spine, which is totally lacking in *M. alberti*; deep excavations in the ventral surface on either side of the midline that are quite shallow in *M. alberti*. **Synsacrum:** a proportionally much broader, shorter synsacrum; a relatively larger surface area of the antitrochanter; a relatively shorter ilioischiatic fenestra that is more approaching a circle than ellipsoid in shape; posterior projections of ilium that are relatively wider. **Scapula:** the blade of the scapula more broadly expanded distally (in *M. alberti* the blade tapers to a narrow end gradually, not abruptly); the area between the furcular articulation and the coracoidal atriculation relatively broader in proximal view (this area is more constricted in *M. alberti*), and the furcular articulation relatively shallower in *M. novaehollandiae*. **Coracoid:** better developed sternocoracoidal processes — the lateral border of the shaft abruptly turns externally near the distal end, forming a distinct, well defined process (in *M. alberti* the lateral border grades evenly to the distal end); a brachial tuberosity that forms a smaller acute angle with a long axis of the coracoid in posterior view; the sternal facet not as anteroposteriorly expanded, particularly medial to the mediolateral midpoint; a less deeply excavated dorsal end particularly

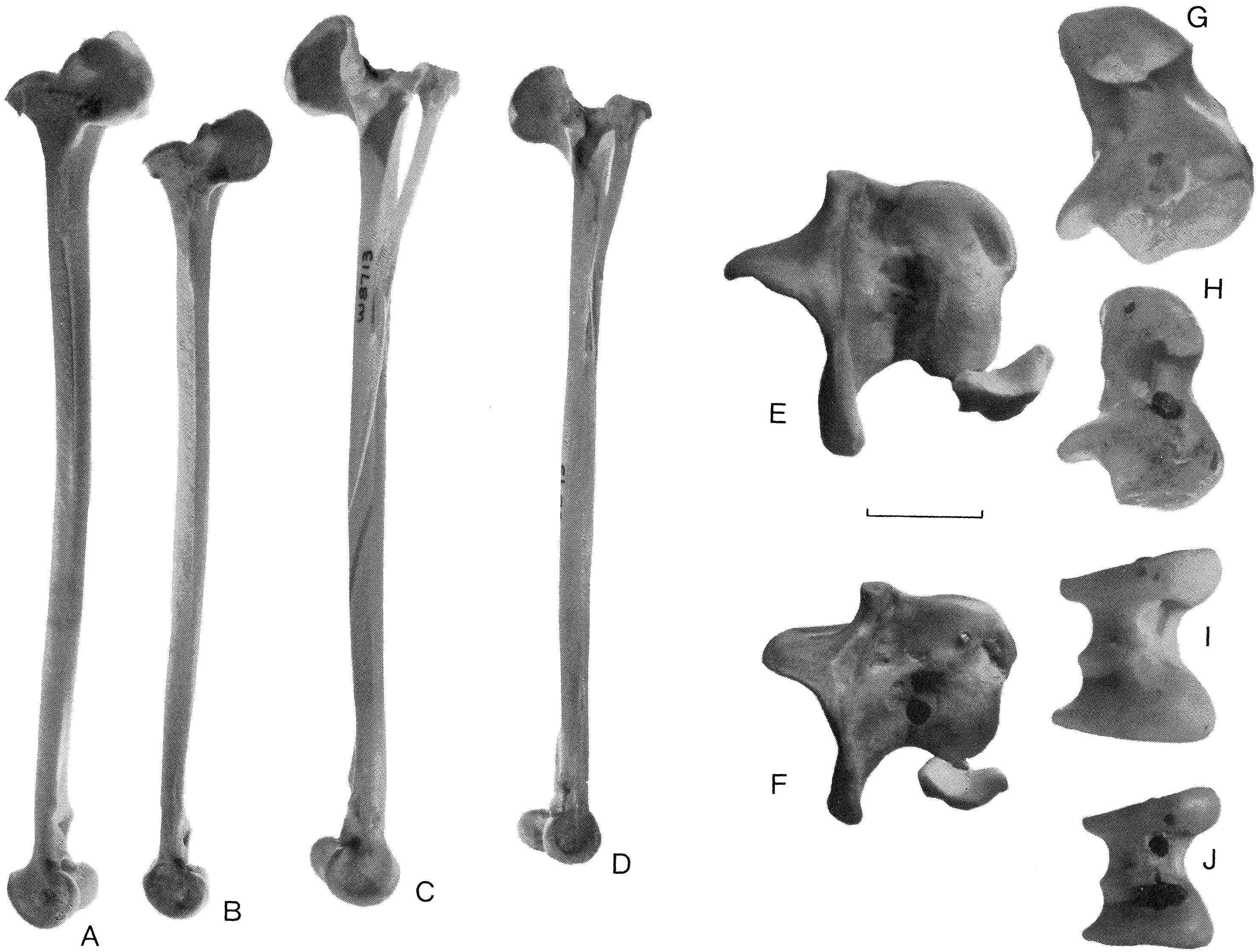

Plate VII. Hind limb elements of *Menura*. A, C, E, G, I: *M. novaehollandiae* (NMV W8713); B, D, F, H, J: *M. alberti* (AM S593). A, B: tibiotarsi, medial view; C, D: tibiotarsi, lateral view; E, F: tibiotarsi, proximal view; G, H: femora, distal view; I, J: tibiotarsi, distal view. Scales = 10 mm. Single scale applies to A–D; single scale applies to E–J.

beneath the furcular facet in posterior view. **Clavicles:** the dorsal end of the clavicles, in side view, more broadly expanded; the coracoidal facet with a greater surface area relative to the size of the entire clavicle. **Humerus:** the deltoid crest better developed and extending distinctly further palmarly; a bicipital surface more inflated, extending relatively further anconally. **Radius:** the distal end somewhat more inflated. **Ulna:** the secondary papillae more prominent. **Carpometacarpus:** the facet for digit III not as squared off but more pointed in internal view; the excavation at the base of the carpal trochleae on the external surface relatively shallower with only a slight impression present; the facet for digit II with an internally directed process that is lacking in *M. alberti* — the facet is also broader, not so mediolaterally compressed in distal view. **Femur:** the internal condyle more anteroposteriorly compressed and proximodistally elongate; the internal condyle more deeply excavated. **Tibiotarsus:** the fibular crest less elongate relative to the total length of the tibiotarsus (13.4–13.5% vs 16.1%), as is the ligamental attachment along the internal side of the bone; the inner cnemial crest extending relatively further proximally; the external ligamental prominence pronounced, not inconspicuous. **Fibula:** the variability between individuals of *M. novaehollandiae* is quite marked and sufficient to account for differences seen between specimens of *M. novaehollandiae* and *M. alberti*. **Tarsometatarsus:** the anterior border of the proximal end not as deeply incised, thus making the cotylae project less abruptly forward in proximal view; five tendinal canals (*M. alberti* has six); the medial border of the outer calcaneal ridge not straight, but notched, unlike that in *M. alberti*; there are no apparent differences in the distal ends of the tarsometatarsi in the above two species. Note: The internal edge of the bone (upper region) is more decidedly flattened in *M. alberti*.

Osteological Comparisons of *Atrichornis clamosus* and *Atrichornis rufescens*

Plates XII-XIX

Atrichornis clamosus differs from *A. rufescens* in being: **Sternum:** more elongate with respect to width, i.e., more slender; in having: a relatively narrow ventral manubrial spine that is only slightly, not broadly, bifurcated; a more anteroposteriorly elongated ventral manubrial spine that extends anteriorly from the main body of the sternum nearly half of the length of the sterno-coracoidal process, instead of about ⅓ the length; a carina that is, although shallow, still deeper than that in *A. rufescens*, and that grades into the main body of the sternum posteriorly, not expanding abruptly ventral near its anterior end; a sternum that is more highly concave dorsally, not flattened.

Atrichornis clamosus differs from *A. rufescens* in having: **Synsacrum:** a somewhat narrower anterior half with the bony surface of the ilium either side of the median ridge more vertically oriented; more flexure between the front and back halves of the synsacrum (when viewed laterally); a relatively narrower and more elongate ishiopubic fenestra; a more anteroposteriorly elongated ischium that narrows abruptly, rather than gradually, near the connection with the pubis; a relatively large obturator foramen, nearly the size of the acetabulum, instead of decidedly smaller; pubes that don't flare broadly, thus making the entire synsacrum narrower posteriorly. **Scapula:** a slender and elongate process along the dorsal border of the proximal end between the furcular articulation and the glenoid facet (in *A. rufescens* this process is short and broad); a very distinct and well defined furcular articulation instead of one that merges gradually with the rest of the proximal articular surface; a furcular facet that is well defined and separate from the rest of the proximal end, and does not evenly grade into it in proximal view; a furcular articulation whose lateral margin forms a smaller obtuse angle with the glenoid facet than in *A. rufescens*, when viewed dorsally; a more rounded apex. **Coracoid:** a proportionally shorter internal surface of the shaft, just distal to the procoracoid groove; a slightly more prominent procoracoid; a sternal facet only moderately concave, not highly concave ventrally in anterior or posterior view; a straight, rather than convex, lateral margin of the coracoid near the distal end. **Humerus:** (Only proximal ends available for comparison) a distinctly larger humerus; a deep excavation at the base of the capital groove that is lacking in *A. rufescens*, in anconal view; a relatively more prominent internal tuberosity; a much more deeply excavated pneumatic fossa; a better developed, more elongate, deltoid crest; a proximal end that is broadly, not just slightly, splayed, where the bicipital surface extends relatively further internally; a distinct ridge on the external surface of the shaft at the base of the deltoid crest that is totally lacking in *A. rufescens*. No more distal wing elements are preserved in our collections of *A. rufescens*.

Femur: the most proximal extension of the trochanter occurring near its anterior end rather than near the anteroposterior midpoint; a shallow, not deep, excavation on the proximal end of the shaft's posterior surface near the base of the trochanter; when viewed laterally, it lacks a deep notch in the posterior shaft border near the proximal end; when viewed proximally, the head shifted further posteriorly with respect to the trochanter, extending further posteriorly than the trochanter itself, and with the head extending relatively further internally, possessing a more elongate neck; a much more highly curved shaft (concave posteriorly); a relatively more deeply excavated anterior shaft surface at its proximal end. **Tibiotarsus:** a rotular crest that is both lower and rises more gradually from the articular surface; an outer cnemial crest (in anterior view) that ends in an apex rather than being blunt and rounded; a very prominent ligamental attachment on the posterointernal surface of the shaft near the proximal

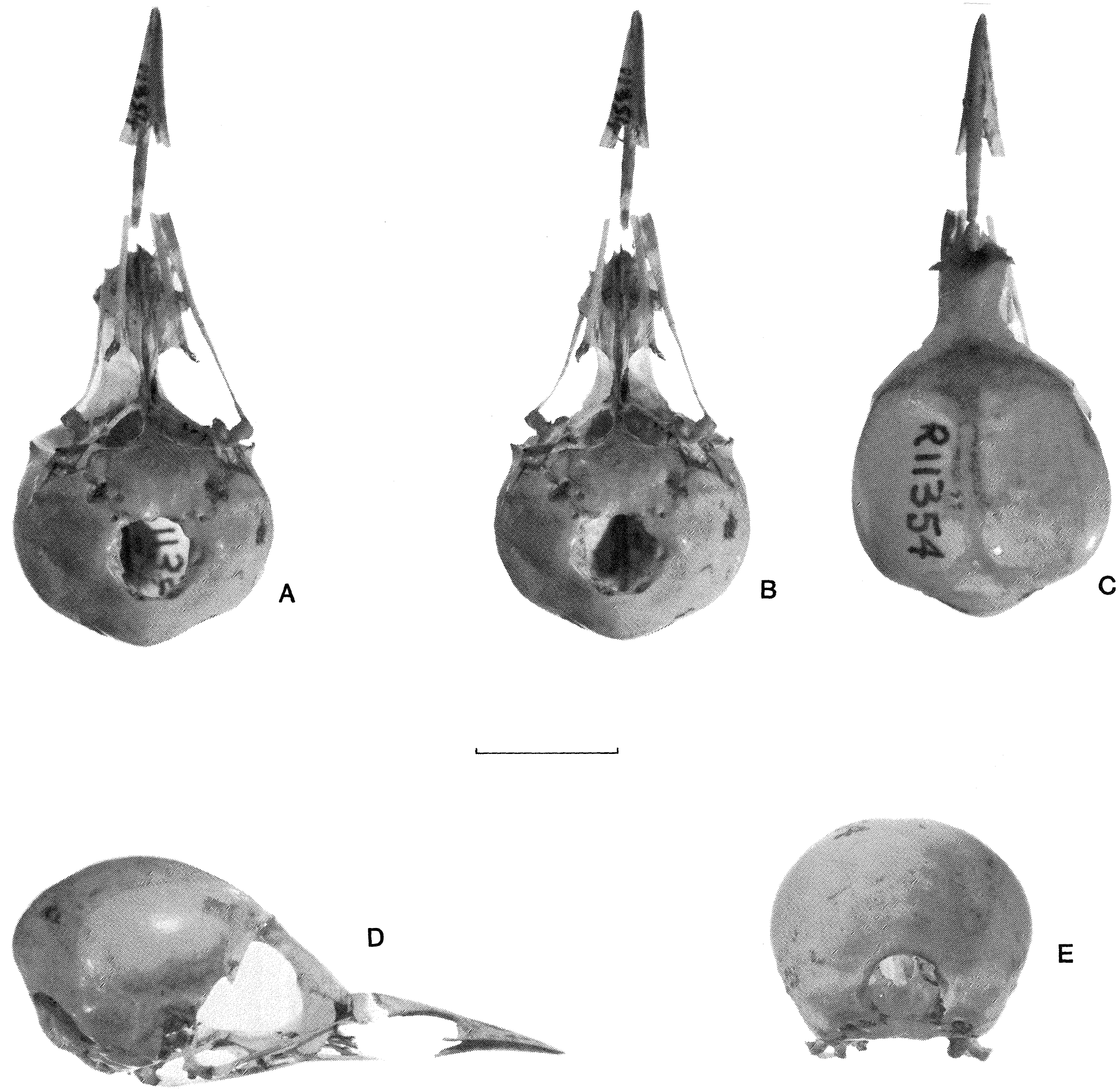

Plate XII. Skull of *Atrichornis clamosus* (NMV R11354). A–B: ventral view, stereo pairs; C: dorsal; D: lateral; E: posterior views. Scale = 10 mm.

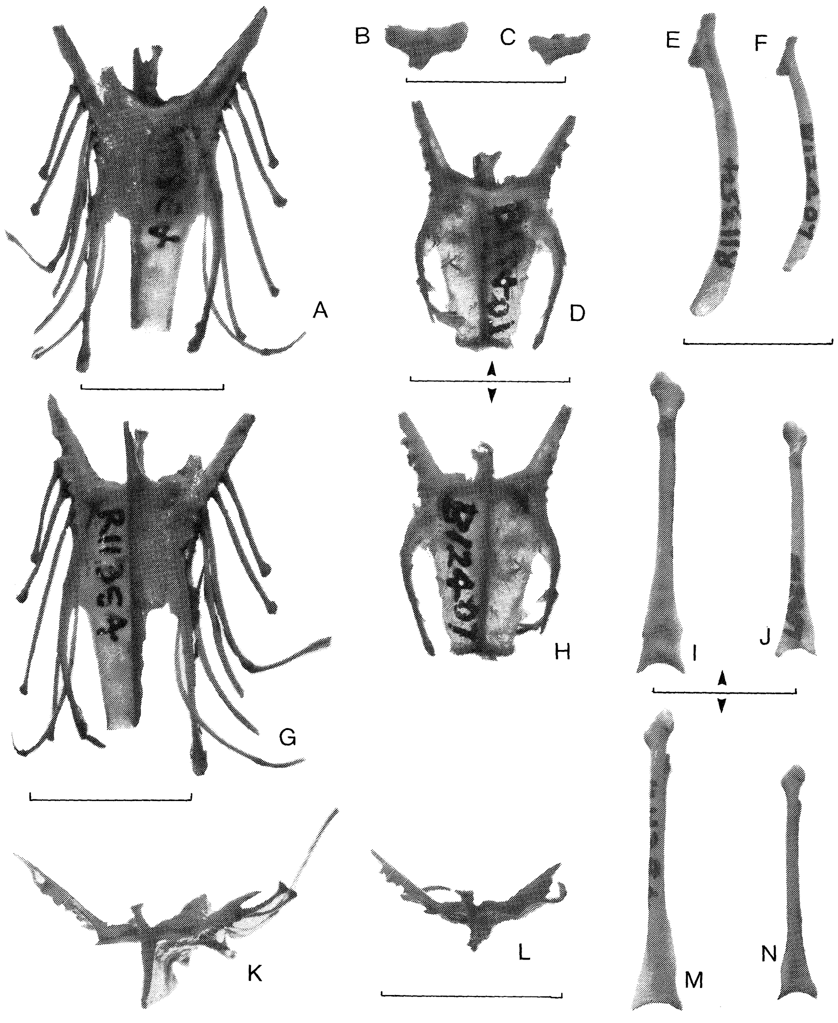

Plate XIII. Sterna and shoulder girdle elements of *Atrichornis*. A, B, E, G, I, K, M: *A. clamosus* (NMV R11354); C, D, F, H, J, L, N: *A. rufescens* (NMV B12407). A, D: sterna, dorsal view; B, C: scapulae, distal or articular view; E, F: scapulae, dorsal view; G, H: sterna, ventral view; I, J: coracoids, internal view; K, L: sterna, anterior view; M, N: coracoids, external view. Scales = 10 mm.

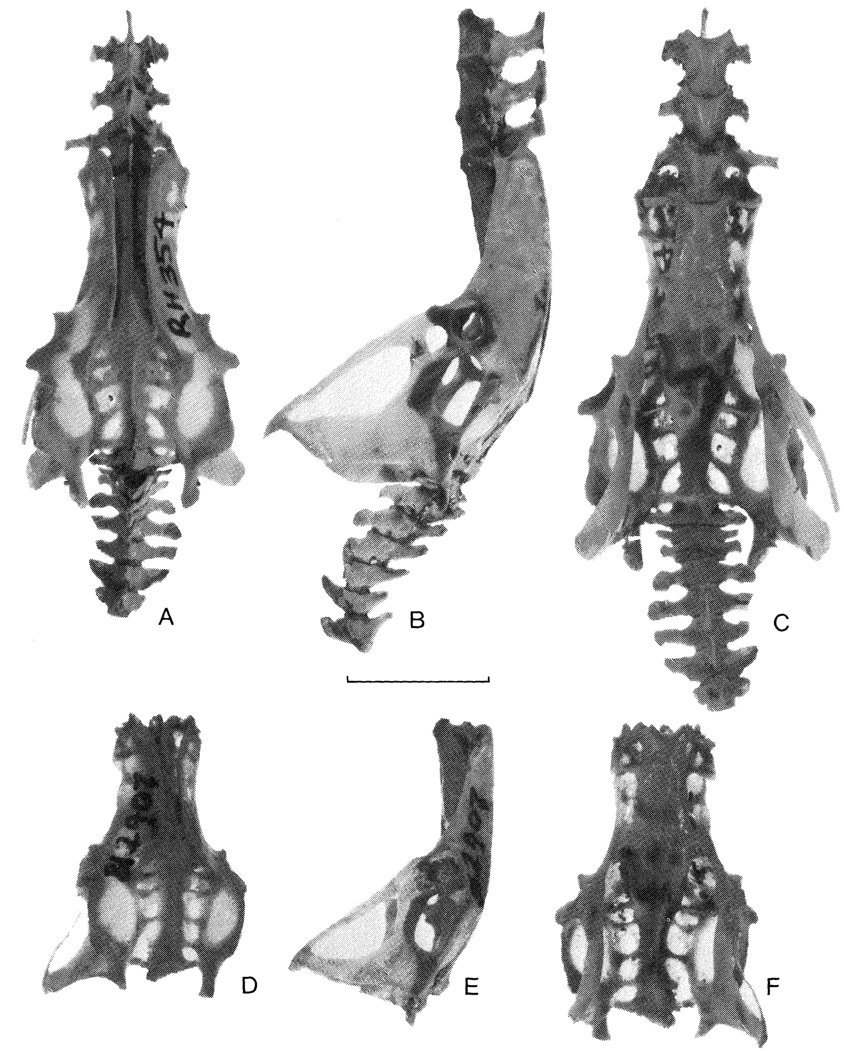

Plate XIV. Synsacra of *Atrichornis*. A–C: *A. clamosus* (NMV R11354) D–F: *A. rufescens* (NMV B12407). A, D: dorsal; B, E: lateral; C, F: ventral views. Scale = 10 mm.

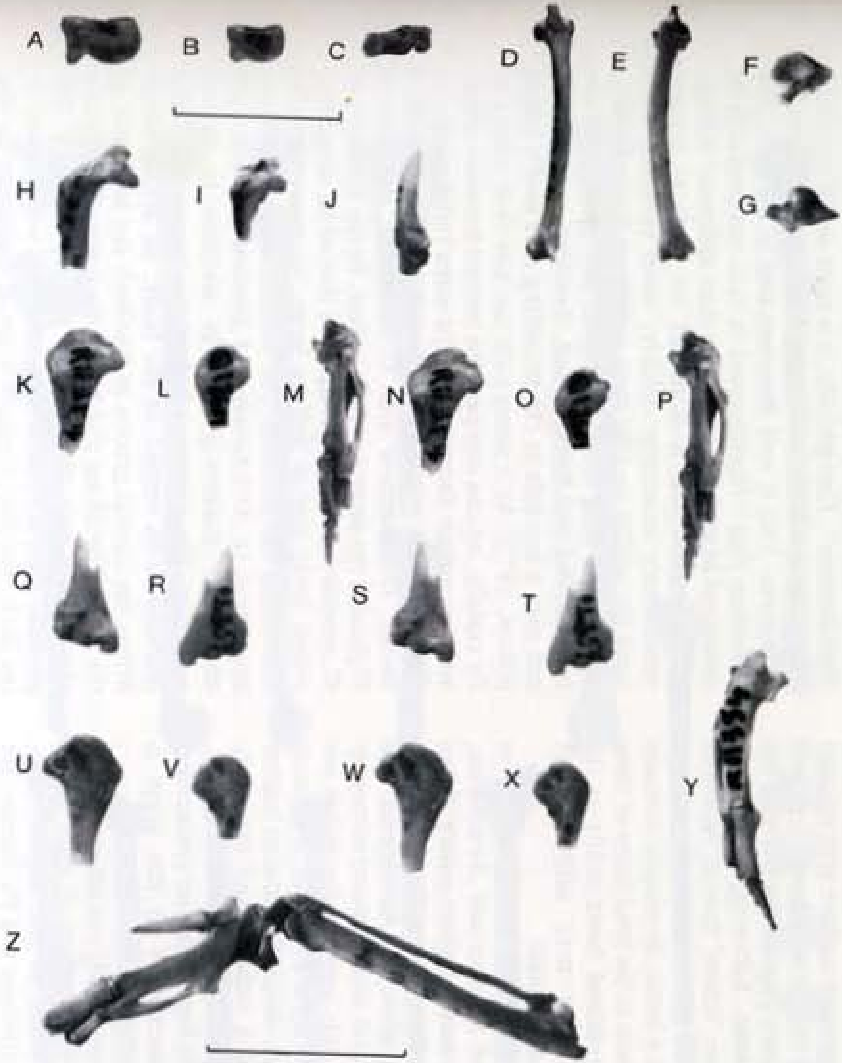

Plate XV. Wing elements of *Atrichornis*. A, C, D–H, J, K, M, N, P–U, W, Y, Z: *A. clamosus* (NMV R11354); B, I, L, O, V, X: *A. rufescens* (NMV B12407). A, B: humeri, proximal view; C: humerus, distal view; D: ulna, anconal view; E, ulna, palmar view; F: ulna, proximal view; G: carpometacarpus, proximal view; H, I: proximal humeri, ventral view; J: distal humerus, external view; K–L, N–O: proximal humeri, palmar view, stereo pairs; M, P: carpometacarpi with attached phalanges, internal view, stereo pair; Q, S: distal humerus, palmar view, stereo pair; R, T: distal humerus, anconal view, stereo pair; U–X: proximal humeri, anconal view, stereo pairs; Y: carpometacarpus, external view; Z: articulated ulna, radius, carpometacarpus and phalanges, external view. Scales = 10 mm. Single scale applies to A–Y; single scale applies to Z.

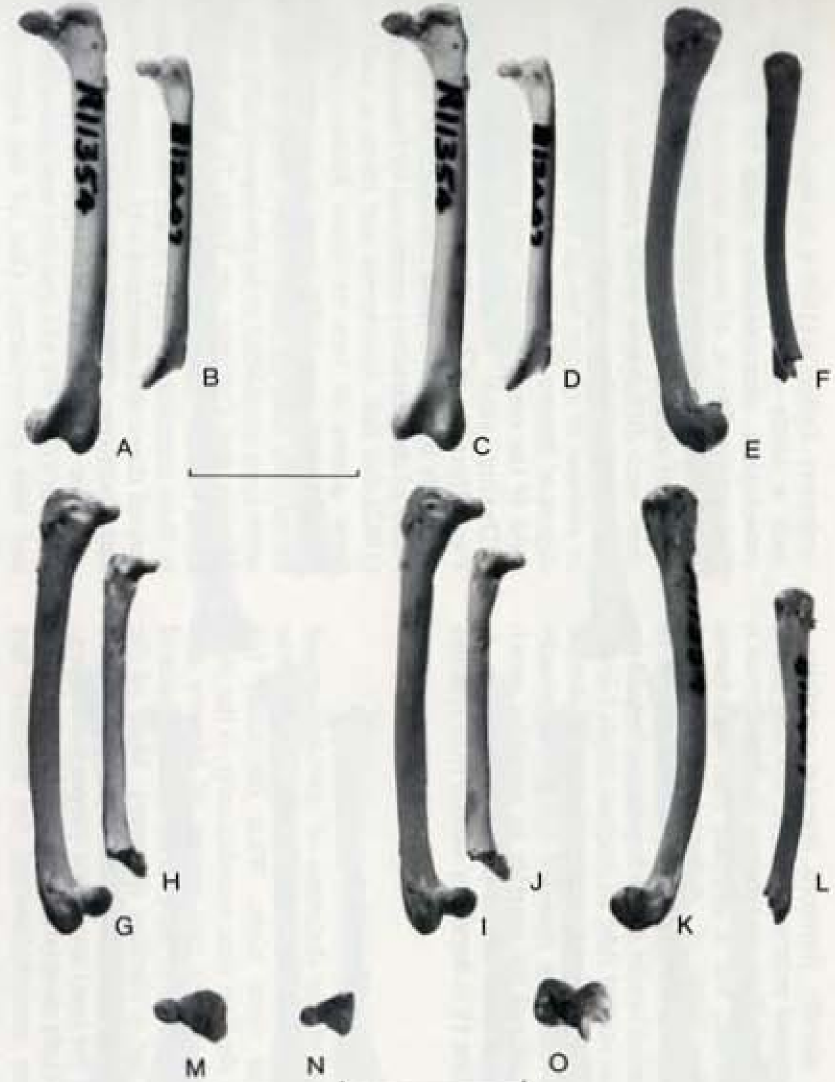

Plate XVI. Femora of *Atrichornis*. A, C, E, G, I, K, M, O: *A. clamosus* (NMV R11354); B, D, F, H, J, L, N: *A. rufescens* (NMV B12407). A–D: anterior view, stereo pairs; E, F: lateral view; G–J: posterior view, stereo pairs; K, L: internal view; M, N: proximal view; O: distal view. Scales = 10 mm. Single scale applies to A–L; single scale applies to M–O.

end; a more distally flattened internal condyle; a posteriorly flattened external condyle, not one that is smoothly rounded. **Tarsometatarus:** the hypotarsus is not well preserved, but it appears that *Atrichornis clamosus* differs from *A. rufescens* in having: 3 hypotarsal canals rather than 1; no distinct groove on the posteroexternal border of the hypotarsus behind the hypotarsal canal on that side; an external cotyla (viewed proximally) with a flattened, straight, anterior/external corner, not a smoothly rounded margin; a broadly splayed proximal end (in anterior or posterior view); trochleae that are more nearly the same length (in *A. rufescens* trochlea IV is decidedly shorter than trochlea II and III).

Discussion

In our study of the skeletons of *Atrichornis* and *Menura*, comparisons have not clearly resolved the relationships of these birds. What the study has illustrated, for the first time osteologically, is the close similarities between the two species of *Menura* and between the two species of *Atrichornis* clearly illustrated in the plates, not a startling discovery. Most of the differences between each species in the pairs (which are enumerated in the text) are minor proportional ones, and many are likely correlated with reduction in flying ability. *Menura novaehollandiae*, for instance, has osteological characteristics that would suggest it is a stronger flier than *M. alberti* in having a better developed deltoid crest on the humerus and a better developed sternum with a greater surface area per unit length (both areas of flight muscle attachment), as well as better developed secondary papillae on the ulna for secondary feather attachment. Likewise, *Atrichornis clamosus* appears to be more 'volant' than *A. rufescens* in having a better developed deltoid crest (= pectoral crest) on the humerus and a better developed sternum with a deeper keel. Differences in the hind limbs of these species pairs remain unexplained functionally at the moment until field studies may allow better understanding of behavioural traits.

On the other hand, as illustrated in the section on osteological comparison of *Menura* and *Atrichornis*, there are many differences between these genera. Some differences, again, can be directly correlated with the greater reduction of flying ability in *Atrichornis*: this species has a reduced coracoid and sternum; extremely reduced clavicles, so that only two slender spikes are retained that do not fuse to form a furcula; a reduced deltoid crest on the humerus; decidedly reduced feather papillae on the ulna; and a reduced and extremely shortened and broadened carpometacarpus. Differences, too, exist in the hind limb and synsacrum, but what these mean functionally at this stage is uncertain.

In order to complete the taxonomic evaluation of their osteology, comparisons with members of each of the passeriform families and those in the 'higher' non-passeriforms, such as Coraciiformes and Piciformes, are underway. Feduccia (1975 a, b) has already carried out such a study on the columella, but many other osteological characteristics need to have similar evaluations. This is, of course, necessary if any attempt is to be made to determine the primitive or advanced nature of each of these individual characteristics. Only then, such differences as the presence of three or five hypotarsal canals on the tarsometatarsus, the presence or absence of a bony bridge on the tibiotarsus, or the degree of flexure of the synsacrum can be evaluated in light of the entire passeriform assemblage.

During such evaluations across the order Passeriformes, the possibility of convergence due to similarity of lifestyle must constantly be kept in mind. Many of the characters mentioned by Feduccia & Olson (1982) that link *Atrichornis* and *Menura*, and both of these genera in turn to some Rhinocryptidae, are features that repeatedly occur in a wide variety of terrestrially adapted passeriforms, many of which have never been considered to be phylogenetically close (e.g. *Menura* and *Callaeus*; see Table 2). So the question arises whether these characters were derived only once in their common ancestry or are merely a complex of derived characters associated with increased cursoriality and, therefore, convergent.

Let us take specific examples from Table 2 to exemplify this. We will consider non-passeriforms first and then passeriforms. One of the elements most affected by decreased volancy is the humerus. As Olson (1973) states: "In my opinion, the energy factor is the overriding consideration in the evolution of flightlessness". Energetically, it is most useful to remove appendages which no longer function as necessary structures. This is well demonstrated in the rails. The statement that "flightlessness in rails can probably be measured in generations rather than millenia" (Olson, 1973) implies that it is useful for birds to remove unnecessary structures quickly, when possible. Rails have the ability to lose their power of flight rapidly, because the long bones, sternum, and girdles are not fully ossified post-hatching and, therefore, environment can play a key role in the moulding of a bird's habits (Olson, 1973). As it seems rails can lose their ability to fly rapidly, we can compare the humeri between volant and non-volant forms within the same rallid genus. In *Gallinula*, for example, there are two closely allied forms, *G. mortierii* and *G. ventralis*: the first is flightless, the second is fully volant. In the humerus of *G. mortierii* the length is equal to that of its congenor, whose body size is half as large, so a comparative shortening has occured. The reduction in the pectoral appendage in *Atrichornis* and *Menura* has also been noticed by Raikow (1985). In addition to overall reduction, the proximal end of the humerus is tilted medially, with respect to the body, an action which brings the capital groove in line with the long axis of the shaft. The tilting also brings the internal tuberosity almost level with the proximal part of the head. The pectoral crest is rotated dorsomedially with respect to the shaft, but this character is not as diagnostic for the

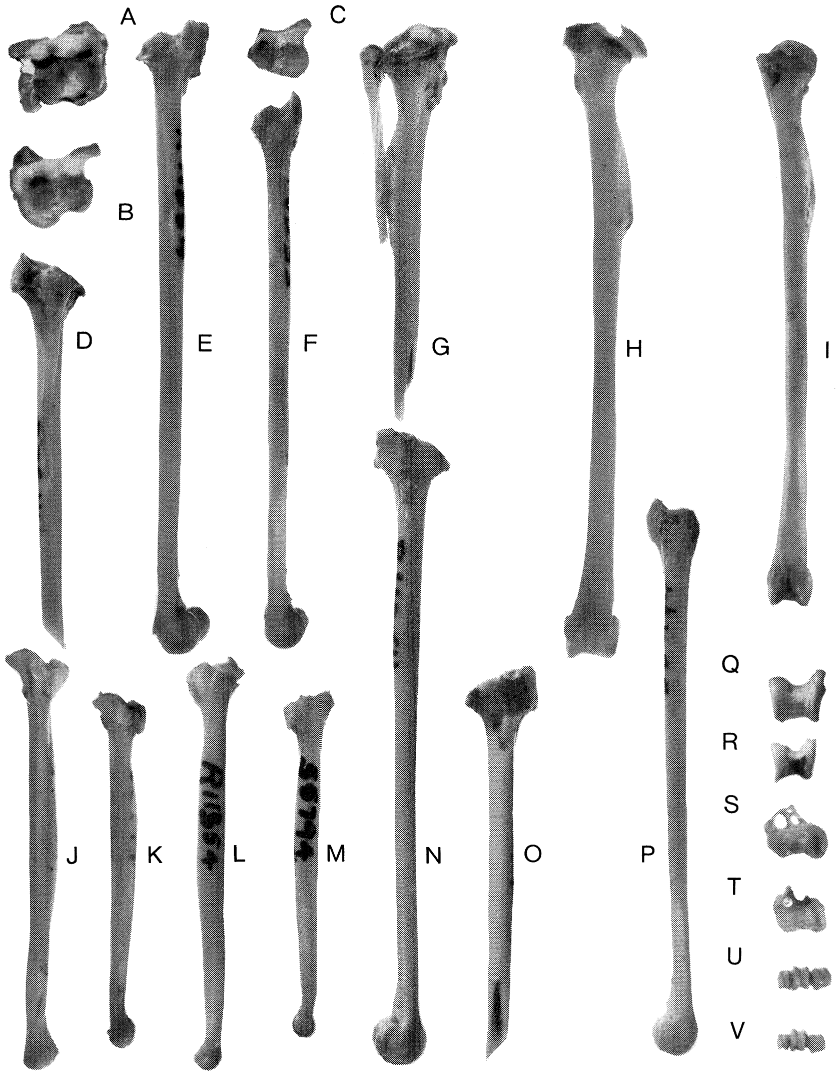

Plate XVII. Hindlimb elements of *Atrichornis*. A, B, D, E, G, H, J, L, N, O, Q, S, U: *A. clamosus* (NMV R11354); C, F, I, K, M, P, R, T, V: *A. rufescens* (NMV B55794). A–C: tibiotarsi, proximal view; D: tibiotarsus, external view; E, F: tibiotarsi, internal or medial view; G–I: tibiotarsi, posterior view; J, K: tarsometatarsi, internal view; L, M: tarsometatarsi, lateral or external view; N–P: tibiotarsi, internal view; Q, R: tibiotarsi, distal view; S, T: tarsometatarsi, proximal view; U, V: tarsometatarsi, distal view. Scale = 10 mm.

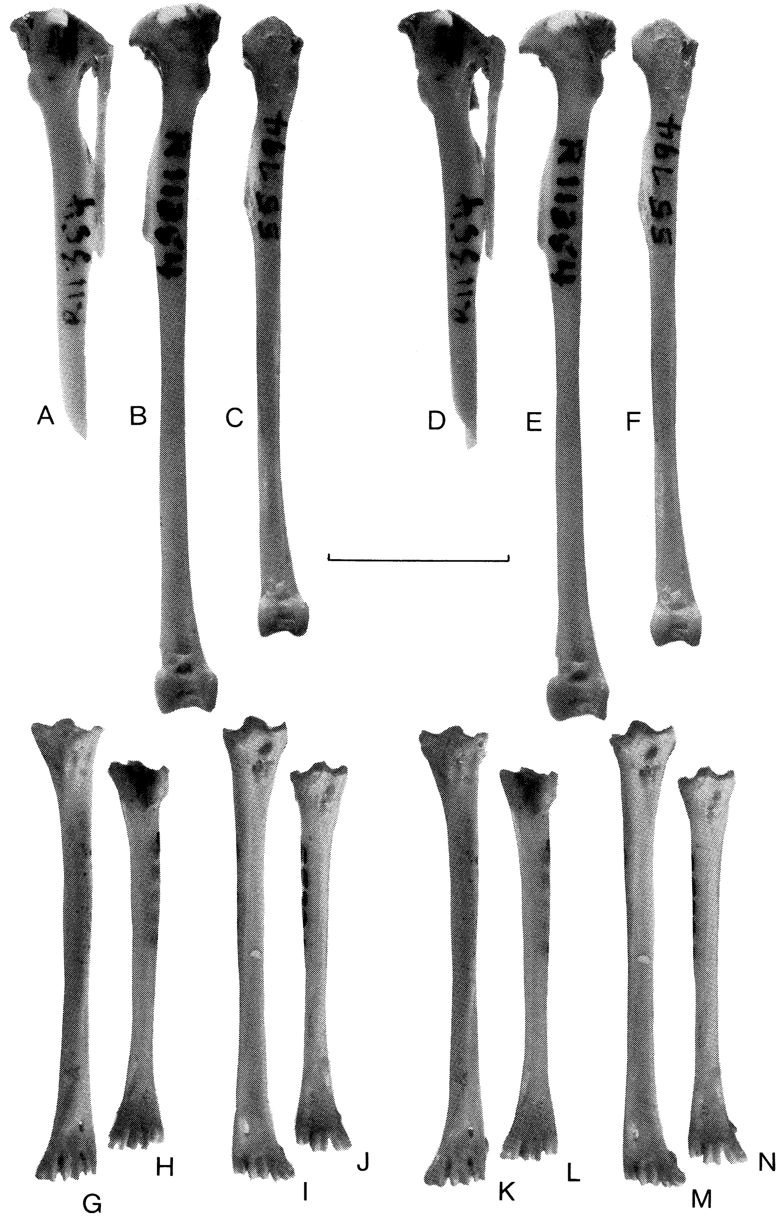

Plate XVIII. Hindlimb elements of *Atrichornis*. A, B, D, E, G, I, K, M: *A. clamosus* (NMV R11354); C, F, H, J, L, N: *A. rufescens* (NMV B55794). A–F, tibiotarsi, anterior view, stereo pairs; G–J, tarsometatarsi, anterior view, stereo pairs; K–N, tarsometatarsi, posterior view, stereo pairs. Scale = 10 mm.

Rallidae. The shaft is curved and stout with respect to that of *G. ventralis*. The same description was given by Olson (1973) for the humerus of flightless rails of the Atlantic, and by Olson & Wetmore (1976) and Olson & Steadman (1979) for two species of flightless ibises. Olson & Steadman (1979) mentioned that the humerus is useless for taxonomic characters, and yet in Feduccia & Olson (1982) this same shaped humerus is used for the alliance of Menurae and rhinocryptids. So, why aren't the same criteria producing the same conclusions for the Passeriformes? The abovementioned characters can be explained by a decreased use of the wings, as can be seen in modern songbirds (e.g. *Dasyornis, Amytornis, Callaeas*), and so use of such characters in determining phylogenetic similarity is rather unwise unless supported by other data.

The sternum may also be considered to be a good measure of the bird's flight capabilities. Figure 1 shows the sternal outlines of the passeriforms *Menura, Atrichornis, Dasyornis, Amytornis* and *Callaeas* in lateral view, as compared with volant forms, *Malurus* and *Philemon*. The sternal keel can be seen as to be much reduced in the first group as compared with the second, a character which Olson (1973) also pointed out as being a measure of flightlessness.

With a decreased use of the wings the emphasis on the legs occurs. This is reflected in the clambering arboreal existence of *Callaeas* (Falla, Sibson & Turbott, 1981) or a terrestrial/cursorial mode of life in *Dasyornis* and *Amytornis* (Pizzey, 1980; Schodde, 1982). The increased use of the hindlimb in a terrestrial sense is reflected by corresponding changes in each of the three long bones composing this limb (e.g. increased size of the trochanteric ridge of the femur; emphasis of a ridge between the distal trochlea on the tibiotarsus; and lateral expansion of the trochlea on the tarsometatarsus, among others.) All of these characters can be seen on the aforementioned genera. The presence of the sulcus on the third (outer) trochlea on the tarsometatarsus is related to the degree of use of the feet in foraging, as well as in locomotion. This condition is well developed in the genus *Menura* (Smith, 1968).

Special structures mentioned by Feduccia & Olson (1982) not correlated with terrestriality could be used in phylogenetic reconstructions, but, unfortunately, like the ossified ridge of the culmen of *Atrichornis* and some rhinocryptids, many of these can also be found in other taxa. At least two species of friarbirds (*Philemon argenticeps* and *P. corniculatus*) bear an ossified ridge on the culmen, although admittedly, it is swollen as compared with *Atrichornis*. In *Philemon*, a genus of meliphagid, the culmen ridge is present in these two species, but lacking in a third, *P. citreogularis*. Another special structure is the notch and knob arrangement of the two outer basal tarsal phalanges. But this, once again, is a character probably associated with cursoriality and found also in *Cinclosoma*, a genus presently placed in the Orthonychidae, most probably a polyphyletic group. According to Sibley & Ahlquist (in press), *Cinclosoma* probably belongs within the superfamily Corvi.

Why haven't many of these characters previously been associated with terrestriality in passeriforms? The problem is twofold: first, many of the non-volant or semi-volant birds relying on laboured flight or gliding occur in the Southern Hemisphere and are rare in museum collections. Often they occur only in their respective countries of origin, where only a few, if any, workers might have an interest in classical taxonomy. Secondly, within their respective groups, each of the genera exhibiting characters of 'semi-flightlessness' are the extreme of a range of morphologies within the family. For example, the genus *Amytornis*, according to Schodde (1982), belongs in the family Maluridae with four other genera, *Stipiturus, Malurus, Clytomyias* and *Sipodotus*.

Malurus is a genus characterised by its bright array of brilliant blues, reds and purples and spends most of its time moving in closely knit family groups in the scrub layer. The postcranial elements of these birds are of volant birds, with large, straight pectoral crests, humeral heads posterodistally projecting, etc. *Amytornis*, in contrast, consists of generally drab brown or black birds that also move about in closeknit family groups but are mostly confined to the arid inland, spending much of their time either on the ground or in clumps of Porcupine Grass (*Triodia* sp.). The flight of *Amytornis* is laboured and rarely observed (Schodde, 1982). Therefore, it would be expected to have just the type of humerus that it indeed has, that of a non-volant or semi-volant bird. Thus, the range of volant vs. semi-volant forms within a family can be quite extreme. Although a good series of rhinocryptids is not available to us, it appears that it may be a group with both cursorial and volant forms with varied stages in between. Into a sequence such as this, the stages attained by *Atrichornis* and *Menura* can be slotted quite easily. The fact that these two genera have forms intermediate between them in the rhinocryptids, based on the characters discussed by Feduccia & Olson (1982), however, does not yet support close relationship of any of these groups. More information is needed before that decision can be made.

Summary and Conclusions

Detailed comparisons of the postcranial skeleton of all species of *Atrichornis* and *Menura* confirm that the two species of *Menura* are indeed closely related, as are the two species of *Atrichornis*. Not so clear, however, are the relationships of *Menura* to *Atrichornis*. Although they share simple syringes, they also show a number of differences in detail of the syringeal muscles (e.g. *Atrichornis* has short ventral muscles, while *Menura* has none) and in morphology and degree of fusion of the tracheal rings. Both genera possess a primitive avian stapes and lack the expanded bulbous footplate that characterizes the derived suboscines.

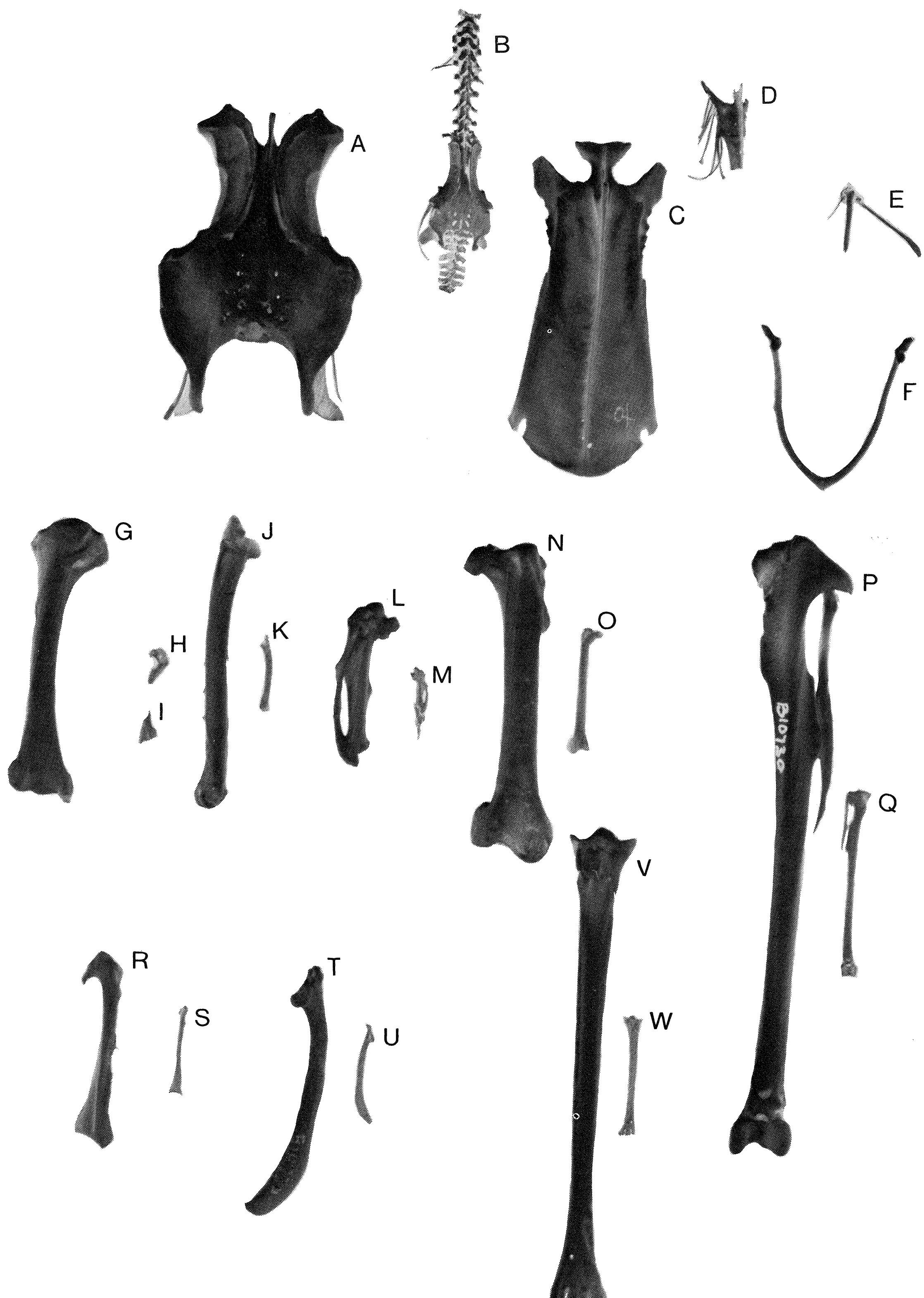

Plate XIX. A comparison of the skeletons of *Menura novaehollandiae* (NMV B10730) and *Atrichornis clamosus* (NMV R11345). A, C, F, G, J, L, N, P, R, T, V: *M. novaehollandiae*; B, D, E, H, I, K, M, O, Q, S, U, W: *A. clamosus*. A, pelves and synsacra; C, D: sterna; E, F: shoulder girdles (E, includes silver-like clavicle, coracoid and scapula; F, clavicles only); G, H, I: humeri; J, K: ulnae; L, M: carpometacarpi; N, O: femora; P, Q: tibiotarsi; R, S: coracoids; T, U: scupulae; and V, W: tarsometatarsi. Scale = 10 mm.

		Rhynochetos (Rhynochetidae)	Rhinocryptidae	*Pitta brachyura* (Pittidae)	*Menura novaehollandiae* (Menuridae)	*Atrichornis* (Atrichornithidae)	*Orthonyx temminckii* (Orthonychidae)	*Cinclosoma* (Orthonychidae)	*Philemon argenticeps* (Meliphagidae)	*Amytornis* (Maluridae)	*Dasyornis* (Acanthizidae)	*Callaeas* (Callaeidae)	Meliphagidae
	Volancy	NV	SV	V	V	SV	V	V	V	SV	V	—	V
	External Resemblances												
1.	long, strong front and hind claws	—	✓	✓	✓	✓	✓	—	—	—	—	—	—
2.	external nasal operculum	✓	✓	—	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Comparative Osteology												
3.	osseus ridge of the culmen	—	✓	—	—	✓	—	—	✓	—	—	—	✓
4.	sternal notches deep; sternocoracoidal processes very long, attenuate and anteriorly directed	—	✓	—	—	✓	—	—	—	—	—	—	— (some)
5.	clavicles unfused	—	✓	—	—	✓	—	—	—	—	—	—	—
6.	(A) humerus with a slender, curved shaft, (B) proximal end with distinctive reduced curved deltoid crest, etc. (✓ = A & B)	✓	✓	—	B	✓	—	—	—	B	B	B	—
7.	carpii short and stout with broad intermetacarpal tubercle and exceptionally large carpometacarpal process	—	✓	—	✓	✓	✓	—	—	✓	✓	✓	—
8.	pelvis with most posterior part of ilium overhanging distally	—	✓	✓	✓	✓	—	✓	✓	—	✓	✓	✓
9.	femur with strongly developed lateral trochanteric ridge	—	✓	—	✓	—	✓	—	—	✓	✓	—	—
10.	tibia with proximal end offset from line of shaft, and well developed, blade-like crest on internal side of proximal end of shaft	—	✓	—	✓	✓	✓	—	✓	✓	✓	✓	✓ (some)
11.	tibia distally with deep intercondylar excavation and particularly well defined ridge within the excavation	—	✓	✓	✓	—	✓	—	✓	✓	✓	✓	✓
12.	tarsi with inner and outer trochlea very broad and distinctly grooved	✓	✓	✓	✓	✓	—	—	—	—	—	—	—
13.	toes with basal phalanx of digit IV distinctly notched to accommodate knob protruding from basal phalanx of digit III	—	✓	—	✓	✓	—	✓	—	—	—	—	—

Table 2. Distribution, in a select group of non-passerines and passerines, of characters used by Feduccia & Olson (1984) to suggest phylogenetic closeness of the Menurae and Rhinocryptidae. ✓ = character present, — = character absent; v = volant, sv = semi-volant, nv = non-volant.

Primitive character states, however, give little information about relationship, and in this case simply indicate what groups neither *Menura* nor *Atrichornis* belong to. Many of the osteological similarities discussed by Feduccia & Olson (1982) and Raikow (1985) can be explained by convergence towards a terrestrial lifestyle and should be used very cautiously when seeking to determine relationships. Although Raikow (1985) points out that *Atrichornis* and *Menura* possess "a number of distinctive myological conditions not found in any passerine group whose appendicular myology has yet been studied", a study that incorporates a number of representatives of each of the endemic Australasian forms, as well as the whole spectum of passeriform families and a thorough analysis of the effects of flightlessness on myology in different passeriform families, needs to be carried out. The results need to be tabularized and presented so the reader can decide the value of these characters relative to passeriforms as a whole. Once characters that could have resulted from functional convergence can be recognized, then perhaps a better estimate of the relationship of *Menura* and *Atrichornis* can be made. At present we do not believe there is sufficient comparative evidence to support any one hypothesis of relationship, even though the possibilities of relationship posed by Feduccia & Olson are intriguing.

Whether the original passerines were terrestrial forms, a possibility raised by Feduccia & Olson (1982), must also remain a moot point until more information is at hand. It would seem difficult to rederive a volant form from terrestrial birds like *Atrichornis*, because element reduction and alteration have been extreme. But perhaps forms that had not proceeded so far could provide the ancestral terrestrial stock for the perching passerines. Another possibility, however, is that the passeriforms developed in an area of the world where the 'perching bird' niches were not so heavily utilized by coraciiforms and piciforms, such as perhaps Australia, and spread from there into areas, e.g. North America, where they met with competition in the trees, and thus moved into the more terrestrial mode of life. Thus, terrestriality, although perhaps developed early in passeriform history, could have been secondarily and even multiply derived. If ever there is a better early Cainozoic record on the Southern Continents, perhaps a choice of hypotheses can be made, but for now we do not think a single choice is obvious.

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A female Noisy Scrub-bird *Atrichornis clamosus* at nest (photo G. Chapman, CSIRO Wildlife Research).