Morphology of the Noisy Scrub-bird, *Atrichornis clamosus* (Passeriformes: Atrichornithidae): Systematic Relationships and Summary

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ABSTRACT. Evidence provided in this monograph supports the conclusion that the genera *Atrichornis* and *Menura* are sufficiently distinct for each to be placed in a monotypic family, viz. the Atrichornithidae and the Menuridae. The suborder Menurae, in which these two families are usually placed, should be merged with the suborder Oscines of the Passeriformes as the differences between them are not sufficiently large to justify continued recognition of these two suborders. The Atrichornithidae and the Menuridae are each other's closest relatives, but the evidence available in this monograph does not suggest an especially close relationship to the Ptilonorhynchidae. It is recommended that the Atrichornithidae and the Menuridae be placed in a superfamily, the Menuroidea, of unknown affinities within the Oscines. The Menuroidea do not appear to be primitive within the Oscines. They are not closely related phylogenetically to the Rhinocryptidae of the Tyranni. Reduction in flying ability of the Menuroidea is presumably advanced in the Oscines and is reflected in a number of morphological features of the skeletomuscular system. The extreme terrestrial habits of the species of the Menuroidea, together with the long incubation and fledgling periods of the single annual chick (two in *A. rufescens*), may be contributing to their decline. Moreover, the scrub-birds and lyrebirds may be relict remnants of an earlier larger radiation, and are unable to compete successfully with other avian species and/or to cope with recent changes in the environment, such as the introduction of foxes and feral cats. Conservation efforts for the scrub-birds and lyrebirds should consider the morphological and systematic findings presented in this monograph in addition to ecological data, with the suggestion that the undertakings for the Two Peoples Bay population of *Atrichornis clamosus* serve as a model for future actions.

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In the concluding paper to this monograph on *Atrichornis clamosus*, we would like to cover several points that are general to all of the individual contributed studies, as well as to provide an overview of the major findings. In particular, we wish to present a full discussion, including an historical summary, of the systematic relationships of the Atrichornithidae and of the suborder Menurae in which they have usually been placed. This analysis must include, of course, the Menuridae. We emphasize at the onset that the views expressed herein are our own and do not represent a consensus of the authors of the individual contributions. We do not wish to supercede these individual opinions, but we will use freely the evidence presented in the several papers, although we may sometimes reach different conclusions.

Three technical points must be made about the results of studies based on the 'Upper Coffin' specimen of

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Atrichornis clamosus which formed the foundation of this monograph. The bony stapes was sent to Alan Feduccia. He chose not to present his results with the other authors in this monograph, but published his ideas separately (see Feduccia & Olson, 1982). The syrinx was sent to Peter Ames. Upon dissecting it, he found that its morphology corresponded to that described earlier in his monograph on the passeriform syrinx (Ames, 1971:86–87) and felt that an additional description was not justified. Ames kindly provided an informal report to the organizers of this project for which we express our appreciation. Blood and other tissues were taken in Australia and sent separately to Professor Charles G. Sibley of Yale University to use in his comparative studies of DNA–DNA hybridization of birds. Because of the schedule of Professor Sibley's research program it would not have been possible for him to provide a contribution to this monograph. He has, however, kindly made available to us manuscripts of his findings (Sibley & Ahlquist, 1985, in press) and has given us permission to use this information for our summary.

Summary of the Monograph and Associated Studies

The first three papers deal with the plumage. Using the flat skin technique, Clench (1985) provided a detailed description of the body pterylosis of *Atrichornis* and *Menura*, and compared it with the pterylosis of a large number of Australasian and other birds suggested as possible relatives of the Menurae. She found that *Atrichornis* and *Menura* have extremely dense feathering, both dorsally and ventrally. The pattern of feathering, however, showed no close similarity to that of any other group of passerines. Using the clipping method, Morlion (1985) described the pterylosis of the wing and tail of these two genera, but was unable to undertake any further comparative analysis. She reported that *Menura* has 11 primaries and 14 secondaries. The wing and tail feathers of *Atrichornis* are not greatly different from those of other passerine birds. Smith (1985) described the natal downs and the feather development in wild and captive chicks of *Atrichornis clamosus*. Chicks have a dense line of grey down from the crown to the rump, with small thin patches on the shoulders and thighs. Fledglings have a plumage similar to that of the female but with bright rufous patches on the forehead, chin and throat. These bright patches may provide easier location by the female of her young lurking in dark vegetation.

Rich, McEvey & Baird (1985) described and compared the postcranial skeleton of both species of *Atrichornis* and the two species of *Menura*, but were unable to carry out a detailed comparison with other groups that might be allied to these genera. They discussed those osteological features cited by Feduccia and Olson (1982) as being similar in the Menurae and in the Rhinocryptidae, and alluded to by these authors as suggesting a close relationship between the groups. Rich *et al.* (1985) argued that a number of these features were found in other terrestrial passerines and suggested that the similarities in the Menurae and the Rhinocryptidae were the result of convergent adaptation for terrestrial life.

Bock (1985) described the skeletomuscular system of the jaw and tongue apparatus in *Atrichornis clamosus* and made some comparisons with the skull of *Menura*. Both genera possess a large, free lacrymal — largest in *Menura*. No special features were found in the jaw muscles of *Atrichornis*, but this bird has five features of its tongue musculature and one of its tongue skeleton which are advanced for passerine birds, and one feature of the tongue musculature which may be primitive. These attributes of the tongue suggest that the Atrichornithidae may not be primitive among the passerine birds, as is usually believed.

In a short preliminary report to the monograph authors, Feduccia showed that *Atrichornis* has a stapes similar to that seen in the Oscines. In a separate paper, Feduccia & Olson (1982) argued that *Atrichornis* and *Menura* share many osteological similarities with the Rhinocryptidae of South America, and hinted at a relationship between these groups.

Raikow (1985) described the appendicular myology of *Atrichornis* and *Menura* and, based on his work and that of his students, compared it with the myology of many other passerine groups. He discussed, in detail, modifications seen in these two families that are associated with the reduction of flight and with increased terrestrial locomotion.

Zusi (1985) described the trunk and axial muscles, including those of the tail, in *Atrichornis* and *Menura*. As he stated, it is ironic that the first study of the trunk and tail muscles for a passerine bird since that of Shufeldt (1890) should be for an endangered species. Zusi was unable to make comparisons with other passerine birds. *Atrichornis* has strongly developed cervical muscles, compared with those of *Menura*. Zusi suggested that the larger size of these muscles may be associated with the use of the head, by *Atrichornis*, to clear leaf litter when feeding.

Ames reported (in litt) that his study of the syrinx from the 'Upper Coffin' specimen simply confirmed the information gained from the earlier (c. 1889) specimen on which he had already published (1971:86–87).

Sibley & Ahlquist (1985, in press) compared *Atrichornis* with *Menura* and a large number of other passerine birds in their extensive survey of DNA–DNA hybridization in birds. They argued that these comparisons show that *Atrichornis* and *Menura* are sister groups and are most closely related to the Ptilonorhynchidae within the corvine complex.

The result of the studies in this monograph is that we now have an excellent knowledge of the morphology of *Atrichornis clamosus*, as good as that for any other passerine bird — and better than for most. A problem does exist in that only one specimen was available for dissection and hence nothing is known about individual variation. But this is true for most anatomical studies of avian species. Except in the case where they were

already engaged in a broad-based, comparative-systematic analysis (Clench; Raikow; Sibley & Ahlquist), the authors were unable to undertake a comparison of their findings from *Atrichornis* with those from passerine birds other than *Menura*. This situation resulted from the fact that several authors interrupted their research program to take part in this cooperative venture, and were unable to conduct an extensive comparative study at the time. Thus, we are left with a detailed knowledge of *Atrichornis* and *Menura*, but lack information on other passerine groups to permit those comparative analyses necessary for detailed taxonomic conclusions. As repeatedly expressed by the authors of the individual papers, a broad-based, detailed survey of these morphological systems is needed, especially for Australasian and other relevant passerine families. We believe, however, that the present monograph permits a few conclusions and we hope it will stimulate further work in this area.

Taxonomic Relationships of *Atrichornis* and *Menura*

Historical survey. The taxonomic position of *Atrichornis* and *Menura* has attracted the attention of ornithologists ever since these birds were discovered. *Menura* was believed to be a gallinaceous bird when it was first described (e.g. Vigors, 1825:486–7). Chisholm (1951) has reviewed the taxonomic history of *Atrichornis*, and Sibley (1974) that of *Menura*. Because of a number of errors and differences in interpretations, and the need to bring the literature review up to date, we will present a historical overview of the systematics of these birds. To avoid confusion between similarly appearing, but actually different conclusions, we took pains to check all original sources cited herein. Although *Atrichornis* is the subject of this monograph, a discussion of its taxonomic history is not possible without that of *Menura*. Unless otherwise stated, our comments refer equally to *Atrichornis* and *Menura* — the Menurae.

Although Vieillot (1816:12–13,48) had earlier suggested that *Menura* is a passerine bird, Nitzsch (1840; see 1867:82–83) was the first ornithologist to provide solid morphological evidence supporting placement of this bird in the Passeres. Contrary to Sibley (1974:66), Nitzsch did not ally *Menura* with the Clamatores, the New World non-oscines, but placed it in a group "Subulirostres *seu* Canorae" which included most of the insect-eating oscines as well as a few non-oscines such as *Pteroptochos*. In his monograph, Nitzsch did not have a concept of oscine versus non-oscine passerines. When *Atrichornis* was discovered, it was thought to be related to genera such as *Dasyornis* (the bristlebirds), *Psophodes* (the whipbirds) and *Orthonyx* (the logrunners or chowchillas); all reasonable suggestions (Chisholm, 1951). Relationship of *Menura* to the Rhinocryptidae (the tapaculos of the Neotropics) was suggested by Eyton (1841:52; **not** Eyton, 1841, Notes on Birds, No. II (sic), Ann. Mag. Nat. Hist. 7:177–179 as cited by Ames, 1971:165 and followed by Sibley, 1974:78 — this paper deals with *Biziura lobata*!). Eyton's conclusions on the possible relationships of *Menura* are difficult to unravel. He stated (1841:52) that it may belong to the Pteroptochidae (= Rhinocryptidae) or perhaps to the Megapodiidae (Galliformes); quite different conclusions. Cabanis (1847:201–202, 337) concluded that *Menura* cannot belong to the songbirds because of its large number of wing and tail feathers and placed it as a subfamily Menurinae in the Eriodoridae (Clamatores). Cabanis's family Eriodoridae included mainly the Formicariidae, but also the Pittidae, the Rhinocryptidae and the former Conopophagidae. Contrary to Sibley (1974:66), Cabanis did not follow Nitzsch and did not place *Menura* in the Pteroptochidae. Later, Sclater (1874:191) said "there seems to be no doubt that the *Menura* represents a distinct family, 'Menuridae', quite different from all other Passeres, and to be referred to the division Oscines", but in a footnote he suggested that *Atrichornis* may be a member of the Pteroptochidae (= Rhinocryptidae) on the mistaken information that its sternum has two emarginations on each side of the posterior border. In recent years, Feduccia & Olson (1982) have resurrected the idea of a close relationship between the Menurae and the Rhinocryptidae.

Müller (1847:330) did not dissect the syrinx of *Menura* in his monograph on the syringeal muscles of passerine birds, but relied on the description of Eyton (1841). He stated that *Menura* possesses the oscine type of syrinx (Müller, 1847:367) and discussed similarities between the lyrebird and the larks. Müller placed (p. 384) the Menuridae between the Certhiidae at the end of the oscine series and the Myiotheridae (= Formicariidae) at the beginning of the tracheophone series. In his final remarks (p. 385) Müller stated that *Menura* has an oscine syrinx and implied that he believed it is allied to the songbirds. Unfortunately, Müller hedged on his ideas on the affinities of *Menura*, probably because he was unable to dissect its syrinx himself.

Wallace (1874:413) placed the Menuridae in the formicarioid Passeres (non-oscines) based strictly on the structure of the 10th primary (= his 1st primary). He did not realize that *Menura* has 11 primaries (see Morlion, 1985). Wallace argued that the Menuridae are closely related to the Pteroptochidae (= Rhinocryptidae). He did not mention *Atrichornis*.

Newton (1896:524) claimed to be the first ornithologist, in 1875, to suggest a close affinity between *Atrichornis* and *Menura*. His statement (Newton, 1875:741) in the section on 'Geographic distribution of birds' in his article 'Birds' is: "Australia, however, possesses two extraordinary families of abnormal *Passeres* — the Lyre-birds (*Menuridae*) and the Scrub-birds (*Atrichiidae*) — which, so far as is at present known, stand by themselves, though it is possible that the latter have a somewhat distant ally in the genus *Orthonyx* or even in the South American family *Pteroptochidae* [= Rhinocryptidae]." Although

suggestive, this statement is too vague to be considered a sufficient claim of close relationship between *Menura* and *Atrichornis*. Newton (1875) could not have adopted Garrod's classification for these birds, which was first published in 1876, contrary to Sibley's statement (1974:66). Much confusion also exists on the citation to Newton's two major articles on birds in the famous 9th edition of the Encyclopedia Britannica (see Sibley, 1974:79). These articles are not both 'Ornithology', in two different editions — the 9th in 1875 and the 18th in 1885 (not 1884 as cited by Sibley). Rather they are on 'Birds', in volume 3 in 1875 and on 'Ornithology', in volume 18 in 1885, both in the 9th edition of this encyclopedia. The second article (Newton, 1885), updated, was used by Newton as the introduction to his 'Dictionary of Birds' (1896).

The first conclusion with strong morphological support for a close relationship between *Atrichornis* and *Menura* was that of Garrod (1876). He argued on the basis of a number of features — the M. tensor patagii brevis, the femoral artery and the syrinx — that *Menura* and *Atrichornis* are closely related and, further, that they should be considered as Acromyodi Abnormales (= abnormal Oscines). It is not clear whether Garrod regarded his Menurinae (= *Menura* and *Atrichornis*, the Acromyodi Abnormales) as a separate suborder of the Passeres — most likely he did not. Contrary to Feduccia & Olson (1982:3), Garrod did not state that his Menurinae represented a distinct suborder, nor did he isolate them from the rest of Passeriformes. It is very clear that Garrod regarded the Menurinae as most closely allied to the normal Oscines. He placed both groups under the heading of Acromyodi (= Oscines), a group of equal rank with the Mesomyodi which contain all non-oscine passerines (Garrod, 1876:518). This arrangement differs from that proposed earlier by Garrod (1873:463) in which he included *Menura* in the Tracheophone Passeres on the basis of its carotid artery. Sibley (1974:66) was unclear in his reference to Garrod (1873 = 1873–4) in which he stated that Garrod united *Menura* and *Atrichornis* for the first time as the Acromyodi Abnormales. We find no mention of either genus in Garrod (1873–4) and suggest that Sibley confused reference to this paper either with Garrod (1873) or Garrod (1876). Sibley's discussion (1974:66) greatly confuses the whole issue, not only because it is unclear whether he referred to Garrod (1873) or Garrod (1876), but because Garrod's conclusions on the systematic position of the Menurae differ in these two papers, and because Newton (1875) could not have adopted Garrod's (1876) conclusion. To our knowledge, Garrod did not publish on the Menurae after 1876. Forbes (1881) summarized Garrod's contributions to the anatomy and systematics of birds.

Sclater (1880:345), in a vague, unsupported and undocumented statement, claimed that the Menurae are "the most anomalous forms of Passerine birds yet known" and placed them in the Pseudoscines as a separate group (= suborder) at the end of the passerine series. Sclater's conclusion is the basis for the separation of the Menurae as a suborder of the passerine birds, which was followed for the next century.

Forbes (1880:391) agreed with Garrod's system, and later (1881:26–27) disagreed strongly with Wallace's (1874) and Sclater's (1880) opinions that the Menurae should be separated from the Oscines and placed in their own suborder. It is not correct, as claimed by Sibley (1974:67), that Forbes (1881) did not argue for inclusion of *Menura* and *Atrichornis* in the Oscines. The group Acromyodi of Garrod and of Forbes are the Oscines (Garrod, 1876:518), and *Menura* and *Atrichornis* were regarded as abnormal Oscines by these two workers. In any review of the systematic history of birds, one must be most careful in noting the exact concept of taxonomic groups of earlier workers, especially when the same name is used for taxa of differing concepts. The Oscines of most modern authors are not the same as the Oscines of Garrod and Forbes. Subsequently, Forbes showed (1882a:544) that *Orthonyx* had a typical oscine syrinx (in his sense of the term) and, therefore, could not be closely allied to the Menurae. Forbes (1882b:571) reported on the syrinx of *Xenicus* and *Acanthisitta*, showing that they are Mesomyodian Passeres, and stated that, aside from the Pittidae, no additional member of the Mesomyodian Passeres is found in the Australasian region, thereby excluding the Menurae from this group. To our knowledge, this paper is the last published comment by Forbes on the affinities of these birds.

Until recently, the studies of Garrod and of Forbes have been the most important ones on the morphology and systematics of the Menurae. The subsequent history is complex and provides almost no new evidence supporting the different taxonomic conclusions until recent decades. Two major schools of opinion developed, one following the position of Garrod–Forbes and the other that of Wallace–Sclater. These differences appear to be rooted in a dispute between British morphologists (= prosectors of the Zoological Society of London) on the one side and systematists–biogeographers on the other.

The minority school of morphologists accepted the position of Garrod–Forbes. This included Beddard (1898:176–183), successor to Forbes as prosector of the Zoological Society of London, and Gadow in his volume on morphology and classification of birds (1893:270–282, see 277), but not in a shorter paper published the previous year (Gadow, 1892). Gadow (1893) quite clearly accepted the Garrod system, in which the Suboscines (= *Menura* and *Atrichornis*) are placed as a group under 'Passeres diacromyodals Oscines'. Gadow did not state why his arrangement of the Menurae differed in his paper of 1892 and in his volume of 1893. Nor is it clear which of these works represented his final ideas. An even greater problem exists for the classifications advocated by Sharpe who, in his major review of avian classifications (Sharpe, 1891a:84), placed the Menuridae in a monotypic order, the Menurae, and separated it from the Atrichiidae (= Atrichornithidae) which was placed in a distinct section

(= suborder ?) of the Passeriformes (Sharpe, 1891a:88). But in a catalogue of avian anatomical specimens, he (Sharpe, 1891b:xx) placed the Menuridae and the Atrichiidae in the Passeres Acromyodi or Oscines as a separate subdivision, the Passeres Abnormales, this being the Garrod-Forbes system. In 1901, Sharpe advocated yet another system in which he placed *Menura* in a separate order, the Menuriformes (Sharpe, 1901:3), and *Atrichornis* as the only family, the Atrichornithidae, in the Passeres Abnormales of the suborder Acromyodi, Passeriformes (p. 187). No comment is ever given by Sharpe for the changes in his placement of *Atrichornis* and *Menura*. The only possible summary of Sharpe's treatments of these genera is that he did not accept the Wallace-Sclater system. The major ornithologists of this century to accept the Garrod-Forbes arrangement are Evans (1900:491-493), Stresemann (1927-34:845) and Berlioz (1950:988-990). Evans and Stresemann placed the Suboscines (= Menurae) as a group, together with the Oscines in the division Diacromyodae which is of equal rank with the Mesomyodae. Thus, Stresemann accepted the arrangement of Gadow (1893), but it is a misrepresentation to state that he retained the 'isolated' position of the Menurae, as claimed by Sibley (1974:67). Berlioz placed the Menuridae and the Atrichornithidae in the suborder Oscines with the comment that these families are aberrant and constitute a connecting link between the Oscines (Acromyodae) and the Mesomyodae.

The majority school of thought started with Huxley (1867:472) who concluded that *Menura* stands apart from all other passerine birds. On the basis of skull morphology, he divided the Coracomorphae (= Passeriformes) into two groups, one containing *Menura* and the other the rest of the order. Parker (1875:306-309) agreed that *Menura* is primitive and isolated among the aegithognathous birds but was vague on the reasons supporting his conclusion. As mentioned earlier, Newton (1875:741) considered *Atrichornis* and *Menura* to be isolated within the passerine birds. Sclater (1880:345) concluded that these genera are the most anomalous passerines and placed them in a separate suborder, but with no support for his action. Newton (1885:41,47) did not accept the system of Garrod, contrary to Sibley (1974:66); instead, Newton adopted that of Sclater in which *Atrichornis* and *Menura* are placed in an isolated suborder. Stejneger (1885:459-461) agreed, claiming that the Menurae possess a number of characters of the Pici and arguing that they should be placed in a suborder separated from all other passerine birds. Fürbringer (1888:1538,1556) agreed with this position (see also the review by Gadow, 1888:181). As mentioned earlier, Gadow (1892:254) placed the Menurae in a separate order from the oscines and other non-oscines (except the Eurylaimidae which were placed in their own suborder). The only difference he cited between the Menurae and the oscines was the type of intestinal convolutions.

In his classic 'Dictionary of Birds', Newton (1896:524) supported his earlier position. Sharpe (1891a:84-88) took a somewhat unusual position by placing *Menura* in a separate order between the orders Eurylaimi and Passeriformes, which parallels the system of Gadow (1892), but he placed *Atrichornis* in a separate section (= suborder) at the end of the Passeriformes, separated from the Oscines by the Oligomyodae and the Tracheophonae.

As stressed by Sibley (1974:67-68), the influence of Newton, Sclater, Fürbringer and Stejneger was overwhelming, and most avian systematists thereafter followed the system in which *Menura* and *Atrichornis* are placed in a separate suborder of the Passeriformes. This is the arrangement advocated by Wetmore in the several editions of his influential classification (e.g., Wetmore, 1960; Wetmore followed Stejneger, 1885, closely in many details of his classification of birds which was originally developed and first published in 1929, following the earlier request of the Checklist Committee of the American Ornithologists' Union, see Wetmore & Miller, 1926), and by Mayr & Amadon (1951). It is also the system used in Peters's 'Check-list' (Traylor, 1979). Sibley (1974:67) erred, however, when he stated that no objection to the Newton-Sclater system has been raised since Forbes (1881). Sharpe (1891b), Gadow (1893), Evans (1900), Stresemann (1927-34:845), Berlioz (1950:988-990) and Bock (1972) accepted the Garrod-Forbes arrangement which constitutes a strong objection to the generally accepted Wallace-Sclater system.

No major advances were made until the 1970's when Ames (1971) published his major review of the syrinx and syringeal muscles in the Passeriformes. Ames gave less attention to the Menurae than to the other non-oscine groups, and said little about the taxonomic history of this suborder. On the basis of his morphological survey, Ames (1971:163-164) concluded that sufficient differences exist to maintain recognition of the suborder Menurae. He stated that the structure of the syringeal musculature and cartilages of the Menurae lies outside the range of variation shown by the Oscines. In his review of Ames, Bock (1972:902) concluded: "Instead of recognizing five suborders as does Ames (pp. 153-164), I would prefer to recognize only three — the Furnarii, the Tyranni and the Oscines (his Passeres and Menurae). I cannot find any strong reason to maintain the Menurae as a distinct suborder, as its syringeal morphology is basically that of the Oscines." Bock pointed out (p. 901) that Ames never discussed the syringeal aponeurosis which is present only in his Menurae and his Passeres (= the Oscines) and may be responsible for both the basic similarities of the syringes of these groups and their differences from the syringes of other passeriform groups.

Sibley (1974) provided the first new evidence in almost a century to support the oscine relationships of *Menura*; his work was based on isoelectric focusing of egg-white proteins. Sibley's paper is significant in that it focused attention on the Menurae, and argued for oscine relationships of these birds. He concluded that

Menura is probably most closely related to the Ptilonorhynchidae-Paradisaeidae complex. These conclusions were reinforced by Sibley (1976). Subsequently, using DNA–DNA hybridization, Sibley & Ahlquist (1985, in press) were able to compare *Menura* and *Atrichornis* with other passerine birds. They concluded that these two genera are closely allied, and that the Ptilonorhynchidae, but not the Paradisaeidae, are the closest relatives of the Menuridae-Atrichornithidae complex. They do not discuss the reasons for the differences between their conclusions and the earlier ones of Sibley (1974, 1976).

In a complex series of papers, Feduccia (1975a, 1975b, 1976, 1977, 1979) described the morphology of the bony stapes in passerine and other birds, and discussed its value for classifying birds. The results of these studies are difficult to assess because of major modifications of his conclusions without new factual information. More recently, Feduccia & Olson (1982) compared the Menurae to the Rhinocryptidae of the Neotropics. In this paper, they were most concerned with the question of whether the Menurae are related to the Ptilonorhynchidae, and they showed that these groups are not especially similar osteologically. Their paper is interesting because it puts forth, once again, a strong suggestion for relationships between the Menurae and the Rhinocryptidae, an idea that had become dormant about 100 years ago.

Taxonomic Analysis

Because *Atrichornis* (Atrichornithidae) and *Menura* (Menuridae) are currently placed in Peters's 'Check-list' in a separate suborder, Menurae, listed just before the Oscines (Mayr, 1979), we will use this arrangement as the basis of our taxonomic analysis.

Group hypotheses. Based on earlier ideas on the relationships of *Atrichornis* and *Menura*, a series of group hypotheses (Bock, 1981) about these birds can be offered. We accept the conclusion that these birds are members of the Passeriformes, although several workers at the end of the last century placed one or both genera in a separate order. The group hypotheses are:

(1) *Atrichornis* and *Menura* are each other's closest relatives (sibling groups) and hence constitute a monophyletic group.

(2) *Atrichornis* and *Menura* are members of the suborder Oscines (Acromyodi), as recognized in Peters's 'Check-list'.

(3) *Atrichornis* and *Menura* are members of the suborder Tyranni (Mesomyodi), as recognized in Peters's 'Check-list'. (We are not here concerned with the question of whether this suborder actually consists of two distinct groups, the Furnarii and the Tyranni, as recognized by Ames, 1971. If one regards both of these groups as suborders, then the hypothesis can be rephrased to ask whether the Menurae are members of the Furnarii.)

(4) *Atrichornis*, *Menura* and the Ptilonorhynchidae form a monophyletic group within the Oscines.

(5) *Atrichornis*, *Menura* and the Rhinocryptidae form a monophyletic group within the Tyranni.

(6) *Atrichornis* and *Menura* constitute a monophyletic group of unknown affinities within the Oscines.

(7) *Atrichornis* and *Menura* are sufficiently distinct to be placed in monotypic families, the Atrichornithidae and the Menuridae.

(8) *Atrichornis* and *Menura* are primitive within the Oscines.

(9) *Atrichornis*, *Menura* and the Rhinocryptidae are all primitive groups within the Passeriformes and are closely related phylogenetically, *Atrichornis* and *Menura* being the most primitive members of the Oscines and the Rhinocryptidae being the most primitive members of the Tyranni.

The first seven are classificatory hypotheses about groups, and the last two are phylogenetic hypotheses about groups and must be tested somewhat differently (Bock, 1981).

Character analyses. The evidence presented by the several authors in this monograph and by other workers (Ames; Sibley; Feduccia & Olson) will be summarized.

THE SYRINX. As soon as the syringes of *Atrichornis* and *Menura* were described by Garrod (1876), it was clear that these birds agreed most closely with the Oscines in syringeal morphology. This conclusion was further strengthened by the monograph of Ames (1971) on the passerine syrinx. *Atrichornis* has a weakly fused syringeal drum but *Menura* has unfused syringeal cartilages. Both *Atrichornis* and *Menura* possess a syringeal aponeurosis which appears to be homologous with that of the Oscines. This aponeurosis is lacking in all other passerine groups. Although the syringeal aponeurosis appears to be fundamental to the morphological organization and to the function of the syrinx, Ames scarcely mentioned it. The syringeal muscles present in *Atrichornis* and *Menura* appear to be homologous to those present in the Oscines. We agree with Sibley (1974:72) that the medial fibres of the M. bronchotrachealis anticus in *Atrichornis* are homologous with the M. bronchialis anticus, pars medialis of the Oscines. Basically, we agree with the analysis of syringeal morphology and evolution presented by Sibley (1974:69–73); this is not special pleading, as characterized by Feduccia & Olson (1982:4). Little is known about how sound is produced by the avian syrinx, and nothing is known about the correlation between variation in syringeal structure as seen in passerine birds and the sounds produced by these birds (Gaunt & Gaunt, 1985). Therefore, we do not believe that it is possible to determine, at this time, whether the menurine syrinx is primitive or advanced, compared with the typical oscine syrinx. We find no structural features or arguments precluding the conclusion that the menurine syrinx is advanced, having reduced the musculature slightly and decreased considerably the degree of fusion of the tracheal rings comprising the oscine drum. As Ames stated (in Sibley 1974:73–74): "no syringeal data that says that they [*Menura* and

Atrichornis] can't [be derived from the Oscines]", and "Virtually any oscine syrinx can be derived from almost any other, and without too much change in muscles."

Sibley (1974:72–73) made a most important point when he stressed that the amount of observed variation in syringeal musculature in passerine birds depends very largely on the detail in description. As description becomes less detailed, the amount of variation in a feature within a taxonomic group decreases. For example, variation in syringeal muscles in the Passeriformes would disappear completely if the level of description were limited to statements of the presence or absence of syringeal muscles. A major difficulty in assessing the significance of differences in syringeal morphology between the Menurae and the Oscines is that we still lack a detailed survey of syringeal morphology in the Oscines, a point stressed by Sibley.

BONY STAPES. In a series of papers, Feduccia described the bony stapes of a number of avian groups and argued that this feature is a useful taxonomic character. Among passerine birds, the stapes has two basic morphologies. One is a flat footplate with a straight, central bony shaft, and the other is an expanded bulbous footplate extending well along the shaft with one or more large fenestrae and an offset bony shaft. The first morphology is found in many avian groups and in reptiles; it is presumed to be primitive. The second morphology is one of the few advanced avian conditions. Nothing is known about the functional properties and possible adaptive significances of the major stapedial morphologies in birds.

Feduccia (1975a), agreeing with Sibley (1974), concluded that the lyrebirds are oscine and are likely to be close to the bowerbird/bird-of-paradise group. He also concluded that the Acanthisittidae are probably members of the Oscines.

In his major review, Feduccia (1975b) repeated these conclusions in a somewhat different form. He argued that the stapes found in the Tyranni plus Eurylaimidae and that found in the Alcediniformes (Meropidae, Alcedinidae, Todidae, Momotidae and Trogonidae) are homologous as a bulbous stapes with a marginal membrane. The alcediniform stapes differs from the tyranniform stapes in the shape of the base and position of the shaft (Feduccia, 1975b:26). Feduccia concluded that the Passeriformes (as usually recognized) are polyphyletic, with the suboscines (Tyranniformes = Tyranni plus Eurylaimi) related to the Alcediniformes and not to the Passeriformes. Further, he concluded (Feduccia, 1975b:33) that it was improbable that *Menura* and *Acanthisitta* are suboscines, backing off somewhat from his earlier conclusion. Subsequently, Feduccia (1977:19) reaffirmed that the Menurae and the Acanthisittidae are Oscines (= his Passeriformes) but this conclusion was not based on stapedial morphology. He stated only that possession of the primitive stapes in these groups shows that they are not suboscines (= his Tyranniformes).

In a later paper, Feduccia (1979:691) reversed his opinion on the homology of the suboscine and the alcediniform stapes as one with a rounded, bulbous, fenestrated footplate. He now concluded that these are two distinct types of stapes which are not homologous, but are similar only through convergence. The minor difference in the shape of the footplate and position of the shaft mentioned in his earlier paper (Feduccia, 1975b:26) was now considered to be a major difference, showing that these stapes cannot be homologous. This conclusion appears to be based on the finding that sperm of the oscines and that of the suboscines are morphologically similar enough to be homologous as bundled sperm with a tripartite structure of its undulating membrane (Henley, Feduccia & Costello, 1978; see also McFarlane, 1963).

Feduccia & Olson (1982) showed that the Menurae and the Acanthisittidae both possess the typical primitive avian stapedial morphology. Yet they assume *Acanthisitta* and *Xenicus* to be oscines, but that *Atrichornis* and *Menura* are either not allied to other suboscines or that these genera evolved before the advent of the derived suboscine type of stapes. No additional evidence is presented to support either interpretation of the homology of the stapes of the Acanthisittidae and the stapes of the Menurae with that of the Oscines. It appears that the conclusion of Feduccia & Olson (1982) on the homology of the stapes of the Menurae and of the Oscines, which is directly opposite to the conclusion reached by Feduccia (1975a), is based strictly on their argument that the Menurae are not related to the Ptilonorhynchidae, but may be related to the Rhinocryptidae. We hold their conclusions on the homology of the stapes to be based on special pleading.

It is difficult to reach conclusions on the homologies of the various morphologies of the stapes and their taxonomic value. Clearly, the stapedial condition with a flat footplate and straight, thin stem has little taxonomic value because it is found without significant variation in many groups of birds and in reptiles. We would agree with Feduccia that this shape appears to be primitive.The stapedial morphology with a bulbous, fenestrated footplate appears to be advanced. But we do not believe that a strong argument has been presented showing a lack of homology between the stapes with a bulbous, fenestrated footplate in the suboscines (Tyranniformes) and that in the Alcediniformes. Whether these groups have evolved the rather similar bulbous condition of the stapes independently must remain an open question at this time.

PTERYLOSIS. Details of the body pterylosis are reported by Clench (1985), and of the wing and tail pterylosis by Morlion (1985). Although it is possible to determine homologies of many of the attributes of the pterylosis between the Menurae and other passerine birds, it is not easy to establish ancestral-descendant sequences. No basis exists on which to conclude that the large number of remiges and rectrices in *Menura* is primitive. And it is difficult to evaluate the pecularities seen in the wing and tail pterylosis of *Atrichornis* and *Menura* because of the absence of sufficient comparative studies.

OSTEOLOGY. Comparisons of the skeleton have been used traditionally in avian systematics because many characteristics can be examined readily and because the skeletons of many avian groups have been examined, thereby providing a broad comparative foundation. The major problem is that homologies between attributes of the skeleton are far more difficult to establish that usually believed, and primitive or advanced conditions are usually impossible to ascertain. This is especially true for the skeleton of passerine birds, in which parallel evolution and reversal of evolutionary changes run rampant.

Sibley (1974:68) claimed that skeletons of *Menura novaehollandiae* and of *Chlamydera lauterbachi* "are virtually identical except for the shape of the posterior margin of the sternum, the absence of an ossified hypocleideum in *Menura* and the difference in size of all elements." Bock (1985) stated that, aside from the similarity of the free lacrymal bone of the Menurae and of the Ptilonorhynchidae, the cranial osteology of these groups differs markedly within the range of variation seen in passerine birds. Feduccia & Olson (1982:16) concluded that the "osteology of these two birds [= *Menura* and *Chlamydera*] is actually extraordinarily divergent, especially in light of the relative osteological homogeneity of the vast majority of Passeriformes."

Further, Feduccia & Olson (1982:16) stated that, in many features of the skeleton, "the Menurae are much more similar to the Rhinocryptidae than to any other passerine group. Most of the characters shared by these two groups are not found elsewhere in the Passeriformes." Many of the similarities cited are in the structure of the wing and the leg. Feduccia & Olson did not discuss the possibility that these similarities may be parallelisms related to reduction of flight and increased terrestriality of both groups. Rich, McEvey & Baird (1985) discussed this possibility in detail and concluded that the observed skeletal similarities in the Menurae and the Rhinocryptidae may be convergent adaptations to a terrestrial way of life. We would agree. Even the keel on the dorsal edge of the upper jaw of *Atrichornis* and of some rhinocryptids may be convergent to terrestrial feeding. Smith (1976:130) reported that *Atrichornis* searches for food by flicking the ground litter aside, using its bill. The dorsal ridge on the upper jaw could be an adaptation for this feeding behaviour.

CRANIAL MYOLOGY. The tongue muscles provide some interesting clues to the phylogenetic position of *Atrichornis* (Bock, 1985). Five aspects of the tongue musculature and one of the hyoid skeleton appear to be advanced, compared with those seen in other passerine birds. None of these are unique. One feature of the tongue musculature is still somewhat primitive. Although little is known about the food and feeding behaviour of *Atrichornis* (Smith, 1976), the scrub-bird presumably feeds on insects and other small invertebrates living in the forest floor litter (Smith & Calver, 1984). Most of the advanced attributes of the tongue musculature are not obviously correlated with feeding on invertebrates in the forest floor litter.

APPENDICULAR MYOLOGY. The musculature of the wings and legs of the Menurae possess a number of features not found in other passerine groups (Raikow, 1985). The structure of the M. flexor perforatus digiti IV is homologous with that of the oscines and not with that of the suboscines. The appendicular myology of the Menurae does not show any particular homologies with that of the Ptilonorhynchidae, nor to any other oscine group.

The reduction in flying ability is correlated with a number of features in the pectoral morphology, such as decrease in the size of the flight muscles, reduction of the clavicles, and shortened wing length. Specializations are found in the pelvic myology associated with increased terrestrial habits. These pelvic changes are especially developed in *Menura*. Although a thorough functional-adaptive analysis is not available for the changes in the skeletomuscular systems of the forelimb and the hindlimb, the most reasonable conclusion is that these features are advanced in the Menurae compared to other passerine birds. No one would doubt that primitive passerine birds flew and that development toward flightlessness is derived. Feduccia & Olson (1982:18), however, argued for "the interesting possibility that the original passerine adaptations were for life on the ground and that this order as a whole, the epitome of 'perching' birds, is only secondarily adapted for an arboreal existence." Rich, McEvey & Baird (1985) provided a strong counterargument. We find this latter discussion far more convincing, especially in view of the evolution of many diverse terrestrial groups among the passerine birds.

BIOCHEMICAL CHARACTERS. Sibley (1974) provided the first new evidence in recent years indicating a relationship between *Menura* and the Oscines. Using isoelectric focusing of egg-white proteins, he concluded that these proteins in *Menura* agreed closely with those in the Paradisaeidae and the Ptilonorhynchidae. In later works, Sibley & Ahlquist (1985, in press), using the technique of DNA–DNA hybridization, stated that the Menurae were closely related to the Ptilonorhynchidae, but not to the Paradisaeidae. Unfortunately, they did not discuss why the earlier studies using egg-white proteins indicated a close relationship between the Paradisaeidae and the Ptilonorhynchidae and, hence, between both of these groups and the Menurae.

LIFE HISTORY. Aspects of the life history of *Atrichornis* and *Menura* have been reviewed by Smith (1976). Information on the diet of *Atrichornis clamosus* is provided by Smith & Calver (1984). *Menura novaehollandiae* is reasonably well known, and most of our knowledge about the life history of *Atrichornis* comes from recent studies on the Two Peoples Bay population of *A. clamosus*. These genera agree in many aspects of breeding, courtship displays, song and terrestrial way of life. Some of the similarities are striking in view of the great difference in body size of the two genera, and considering the courtship

specializations of *Menura*.

Conclusions. Using the information available in the several studies of this monograph and the above summary, we would like to examine the nine group hypotheses presented earlier.

(1) We accept the hypothesis that *Atrichornis* and *Menura* are each other's closest relatives and constitute a monophyletic taxon. All of the evidence in this monograph supports this hypothesis, as do Sibley & Ahlquist (1985, in press) and Feduccia & Olson (1982). Most earlier workers, following Garrod (1876), accepted this conclusion although Sharpe (1891a; 1901) placed *Menura* in a different order from the Passeriformes.

(2) We accept the hypothesis that *Atrichornis* and *Menura* are members of the suborder Oscines as recognized in Peters's 'Check-list'. This is supported by the structure of the syrinx, as first pointed out by Garrod (1876) and commented on by Bock (1972). We believe that the detailed homologies of the syringeal musculature, as well as that of the syringeal aponeurosis of the former Menurae and of the normal Oscines, provide strong support for this hypothesis. Raikow (1985) showed that the structure of the M. flexor perforatus digiti IV is homologous in the former Menurae and the normal Oscines (see also Raikow, 1982, when he discussed the monophyly of the Passeriformes). Sibley (1974, 1976) and Sibley & Ahlquist (1985, in press) demonstrated close similarity among the egg-white proteins and DNA–DNA hybridization of the former Menurae and the normal Oscines. Most of the earlier conclusions for a very isolated taxonomic position of the Menurae in the Passeriformes, or even their placement in a separate order, were based on peculiar features of *Menura* which reflect its large size, terrestrial habits and courtship displays.

(3) We reject the hypothesis that *Atrichornis* and *Menura* are members of the suborder Tyranni (= suboscines of Feduccia & Olson, 1982), as recognized in Peters's 'Check-list'. Such a relationship was advocated by Feduccia & Olson (1982), following up on the old suggestion by Sclater (1874) and Wallace (1874) that *Atrichornis* and *Menura* may be members of the Rhinocryptidae. We believe that the similarities between the Menurae and the Rhinocryptidae cited by Feduccia & Olson (1982) are most likely the results of convergence (see Rich, McEvey & Baird, 1985). No convincing set of homologous features supports this hypothesis, and many oppose it strongly, e.g., those homologues supporting the hypothesis that the Menurae are members of the suborder Oscines.

(4) We cannot accept the hypothesis that *Atrichornis*, *Menura* and the Ptilonorhynchidae form a monophyletic taxon within the Oscines. The only evidence that seems to support this hypothesis comes from the biochemical studies by Sibley (1974, 1976) and by Sibley & Ahlquist (1985, in press). The bulk of the evidence from the pterylosis, osteology and myology of these birds presented in this monograph and by Feduccia & Olson (1982) does not support this hypothesis or, at best, is only suggestive. However, none of the morphological evidence serves to falsify this hypothesis at this time, so that it cannot be rejected.

(5) We reject the hypothesis that *Atrichornis*, *Menura* and the Rhinocryptidae form a monophyletic group within the Tyranni for the same reasons given above in rejecting hypothesis 3.

(6) We accept the hypothesis that *Atrichornis* and *Menura* form a monophyletic group of unknown affinities within the Oscines. These two genera possess a number of unique features that separate them from other Oscines. Moreover, they do not possess any features that indicate strongly a relationship with any other oscine group, except, of course, the biochemical evidence suggesting an affinity with the Ptilonorhynchidae (see hypothesis 4). This lack of evidence may simply be the result of insufficient comparative studies and it may change in the future. It is not clear whether the suite of features unique to *Atrichornis* and *Menura* are largely the result of terrestrial habits and decreased flight abilities or are also strongly indicative of a close relationship. And it is not known whether a number of these features will be found in other specialized terrestrial passerine birds.

(7) We accept the hypothesis that *Atrichornis* and *Menura* are sufficiently distinct to be placed in monotypic families, the Atrichornithidae and the Menuridae. The differences in size, feeding habits, courtship displays and numerous morphological features support this hypothesis strongly. These differences are compatible with differences among many other families of passerine birds. It should be noted that Sibley & Ahlquist (1985, in press) place *Atrichornis* and *Menura* in the same family, the Menuridae, based strictly on the size of the delta $T_{50}H$ value for the DNA–DNA hybridization between the two genera.

(8) We do not accept the hypothesis that *Atrichornis* and *Menura* are primitive within the Oscines. These two genera possess a number of derived specializations such as decreased flying ability, terrestrial habits, morphological features of the tongue musculature, etc. At this time, it is not possible to establish the particular syringeal features of these genera as primitive or advanced. Analysis of the evolutionary history of the Oscines, and determination of presumed primitive groups, cannot be accomplished with certainty at the present state of our knowledge.

(9) We reject the hypothesis that *Atrichornis*, *Menura* and the Rhinocryptidae are all primitive groups within the Passeriformes and are closely related phylogenetically. We cannot speak about the phylogenetic position of the Rhinocryptidae within the suboscines, but not accepting hypothesis 8 determines our decision on the current hypothesis. We would add that we would reject the hypothesis suggested by Feduccia & Olson (1982:17–18) that the original passerine adaptations were for life on the ground.

In conclusion, we would place the Atrichornithidae

and the Menuridae in a superfamily, the Menuroidea, of unknown affinities within the suborder Oscines. The Menuroidea, as we delimit them, differ from the concept of the Menuroidea advocated by Sibley & Ahlquist (1985), which includes the Climacteridae and the Ptilonorhynchidae, as well as the lyrebirds and the scrub-birds. The Menuroidea, as we delimit them, appear to be specialized for a semivolant, terrestrial mode of life. It seems reasonable to suggest that the Atrichornithidae and the Menuridae are relict members of an earlier, more diverse radiation of Australasian oscine birds. The Ptilonorhynchidae and others may also be part of this early radiation, but we do not feel that the available evidence is sufficient to resolve the detailed relationships within the major early radiations of Australasian oscine birds. This idea of an early radiation is not new, but has been postulated by a number of other workers. We believe that the contributions to this monograph have provided considerable evidence supporting this conclusion. We consider, however, that it is premature to speculate on possible causes for the reduction of the presumed earlier radiation of menurine birds.

Conservation Efforts

The species of *Menura*, and especially of *Atrichornis*, are endangered or threatened throughout much of their range. *Atrichornis clamosus*, believed for many decades to be extinct, survives in only one small locality at Two Peoples Bay, east of Albany, Western Australia. Scrub-birds and lyrebirds are very secretive birds, specialized for ground dwelling in thick growth. They are easy to hear because of the loud songs of the males but difficult to see because of their shy habits and the dense habitat in which they live. These habits are not unique for Australian birds; they are also found in the chowchillas (*Orthonyx*), whipbirds (*Psophodes*), fairy wrens (*Malurus*), grass wrens (*Amytornis*), bristlebirds (*Dasyornis*) and the pilotbird (*Pycnoptilus floccosus*). The menurines are not necessarily driven out by human contact, as demonstrated by the long-studied Superb Lyrebirds of Sherbrooke Forest east of Melbourne (Pratt, 1974; Smith, 1951). The slow reproductive rate (one or two eggs per year) and long incubation and fledgling periods of chicks of *Atrichornis* and *Menura* may be important factors contributing to their decline. These extreme terrestrial habits may also make these birds easy prey for feral cats and introduced foxes.

It is quite possible that the scrub-birds and lyrebirds are evolutionary relicts and, as remnants of an earlier larger radiation, are facing extinction because of competition from other avian species and/or because of modified environmental conditions. These possibilities would make conservation efforts far more difficult. Special efforts would be required to preserve large tracts of habitat suitable for these species. More studies should be undertaken without delay to learn the ecological requirements of each species because this information is essential for further conservation actions. The undertakings at Two Peoples Bay for the population of *Atrichornis clamosus* appear to be an excellent model for similar efforts with the other three species of the Menuroidea.

Scientific Cooperation

When the *Atrichornis* project was in its initial planning stages, the problem to be addressed was having an anatomical specimen of an endangered species, *Atrichornis clamosus*, for which very little was known about its morphology and systematic position. The question was, how should studies be arranged so that maximum information could be obtained from a single specimen. Clearly, the answer was to seek out the needed expertise and to arrange the sequence of study in a suitable way. It was necessary to obtain cooperation among enforcement officers and scientific researchers in Australia and abroad, mainly in the United States. After individual workers agreed to take part in the study, they had to stop other work and turn to the *Atrichornis* specimen when it arrived. Dr Morlion travelled to the United States to do her investigations because of the dangers and difficulties in shipping the specimen to Europe and back again to North America.

The resulting monograph is proof of the success of this cooperative effort. The results will benefit Australians interested in the evolutionary biology and preservation of their avifauna. These results are also of importance to international ornithologists interested in avian morphology and systematics. This study served to bring together a number of ornithologists from Australia, Belgium and the United States who may have never met or only rarely see each other at International Ornithological Congresses. We hope that the *Atrichornis* study will serve as a role model for future cooperative investigations on the morphology and systematics of little-known species of birds.

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