OSTEOLOGY AND SYSTEMATICS OF THE FERNBIRDS (*BOWDLERIA*: SYLVIIDAE)

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ABSTRACT

Although the New Zealand fernbirds were long maintained in their own genus *Bowdleria*, some authors have recently submerged them in the Australasian genus *Megalurus*. The osteology of the fernbirds shows them to be very distinct, however, so that the genus *Bowdleria* is fully justified. The skull of *Bowdleria* is most similar to that of *Amphilais* ("*Dromaeocercus*") *seebohmi* of Madagascar and these two species are similar in plumage and tail structure as well. A particularly close relationship between *Bowdleria* and *Megalurus* may thus be doubted. *Bowdleria* is characterized by reduced elements of the wing and pectoral girdle, and a strikingly modified pelvis combined with very robust hindlimb elements. This functional complex of the hindlimb is quite unlike any of the presumed close relatives of *Bowdleria*, but convergent similarities are identified in several other passerine groups. On the basis of plumage and osteology, *Bowdleria rufescens* of the Chatham Islands is a very distinct species from *B. punctata*.

INTRODUCTION

The fernbirds of New Zealand, Snares, and Chatham Islands have most frequently been recognized in their own genus, *Bowdleria*, in the Old World warbler family Sylviidae. Before Rothschild's (1896) parenthetical creation of the genus *Bowdleria*, the fernbirds were often placed in the African genus *Sphenoeacus*. Even before this, Gray (1848) had tentatively referred them to the Australasian genus *Megalurus*. An association between *Bowdleria* and *Megalurus* was later revived and continued to be suggested until eventually *Bowdleria* was synonymized with *Megalurus* (see the taxonomic review of Sibley & Ahlquist 1987). This treatment was sanctified by Mayr (1986), in accordance with his frequently voiced desire to reduce the number of avian genera. Yet no morphological studies of *Bowdleria* have ever appeared in support of such a taxonomic treatment. On the basis of DNA-DNA hybridization experiments Sibley & Ahlquist (1987:65) concluded that *Bowdleria punctata* and *Megalurus gramineus* had "a congeneric relationship". Recent criticisms of Sibley & Ahlquist's methods, however, indicate that their studies are seriously flawed, so that their results should not be accepted without verification (see Houde 1987, Lewin 1988a,b, Sarich *et al.* 1989, and references cited therein).

On obtaining an incomplete skeleton of *Bowdleria* in exchange from the National Museum of New Zealand, I was immediately struck by the bizarre morphology of the pelvis, in addition to the extremely robust hindlimb and much reduced sternum and wing elements. Never having seen a similar condition in any other passerine, I at first even entertained the possibility that *Bowdleria* might be a suboscine. This idea was not without precedent, because the fernbird was originally described by Quoy & Gaimard (1830) in *Synallaxis*, a Neotropical genus in the suboscine family Furnariidae. *Bowdleria* is not a suboscine, as it turns out, but further investigation into its morphology yielded some most interesting results.

Here I will deal with osteology and to a limited extent with external morphology. The myology of *Bowdleria* has been investigated in detail by G. D. Bentz (MS), whose results will appear separately. Bentz found that, concomitant with its osteology, the myology of *Bowdleria* is highly peculiar. In the course of these dissections, the syrinx of *Bowdleria* was examined by P. L. Ames (pers. comm.), who found it to possess the morphology typical of the oscine passerines (Ames 1971). Boles (1985) reported that the nestlings of *Bowdleria* have the mouthspots that are characteristic of the Sylviidae, the pattern in *Bowdleria* being similar to that in *Megalurus*. As discussed beyond, the cranial osteology of *Bowdleria*, although differing considerably from that of *Megalurus*, is consistent with its placement in the Sylviidae, so that at this point the familial relationships of the genus are not in doubt.

MATERIAL EXAMINED

Skeletons: *Bowdleria p. punctata* NMNZ 22848; *Bowdleria p. stewartiana* NMNZ 8699/1 (body skeleton only); *Bowdleria punctata* subsp. NMNZ 1398 (pelvis only); NMNZ 1512 (sternum, coracoid, scapula); *Bowdleria rufescens* USNM 554710 (incomplete postcranial); *Dromaeocercus brunneus* MRAC 50616; *Amphilais* (*Dromaeocercus* auct.) *seebohmi* USNM 432211; *Megalurus timoriensis* USNM 561990, YPM 7089; *Eremiornis carteri* UMMZ 214261; *Cincloramphus cruralis* UMMZ 214264; *C. mathewsi* UMMZ 214265; *Calamanthus* (*fuliginosus*) *isabellinus* AMNH 9478, AMNH 9611; *Sphenoeacus afer* USNM 558701; *Melocichla mentalis* UMMZ 208325, UMMZ 218573; *Achaetops pycnopygius* TM 32629.

COMPARISONS WITH *MEGALURUS*

Because *Bowdleria* has repeatedly been suggested as being most closely related to, or congeneric with, the Australasian genus *Megalurus*, I have made the following comparisons with *M. timoriensis*, one of the geographically closest species to *Bowdleria*, in order to point up the great differences between these two genera.

In dorsal view, the overall configuration of the skull in *Bowdleria* is markedly narrower (Figure 1). The sides of the bill, instead of diverging widely, become constricted posteriorly, being drawn together and more in parallel in the vicinity of the naso-frontal hinge. The frontals are conspicuously narrower at the hinge than in *Megalurus*, in which the ectethmoid plates are much larger and greatly inflated by comparison with *Bowdleria*. In *Bowdleria*, the dorsal bar of the nasals (the ridge of the culmen) is narrower and laterally compressed, and in lateral view is rather strongly arched, in this respect actually being more like the African Grassbird (*Sphenoeacus afer*) than *Megalurus*. The interorbital septum is less ossified and the anterior cranial fenestra larger in *Bowdleria*. The mandible in *Megalurus* is wider, with the rami deeper and much more laterally flared at the posterior end of the dentary.

The wing and pectoral girdle of *Bowdleria* appear to be proportionately reduced in size compared to *Megalurus* (Figure 2), this being most evident in the shallower keel on the sternum. Reduced flight capability is not unexpected in an insular endemic, however, and is not an important taxonomic character at the generic level.
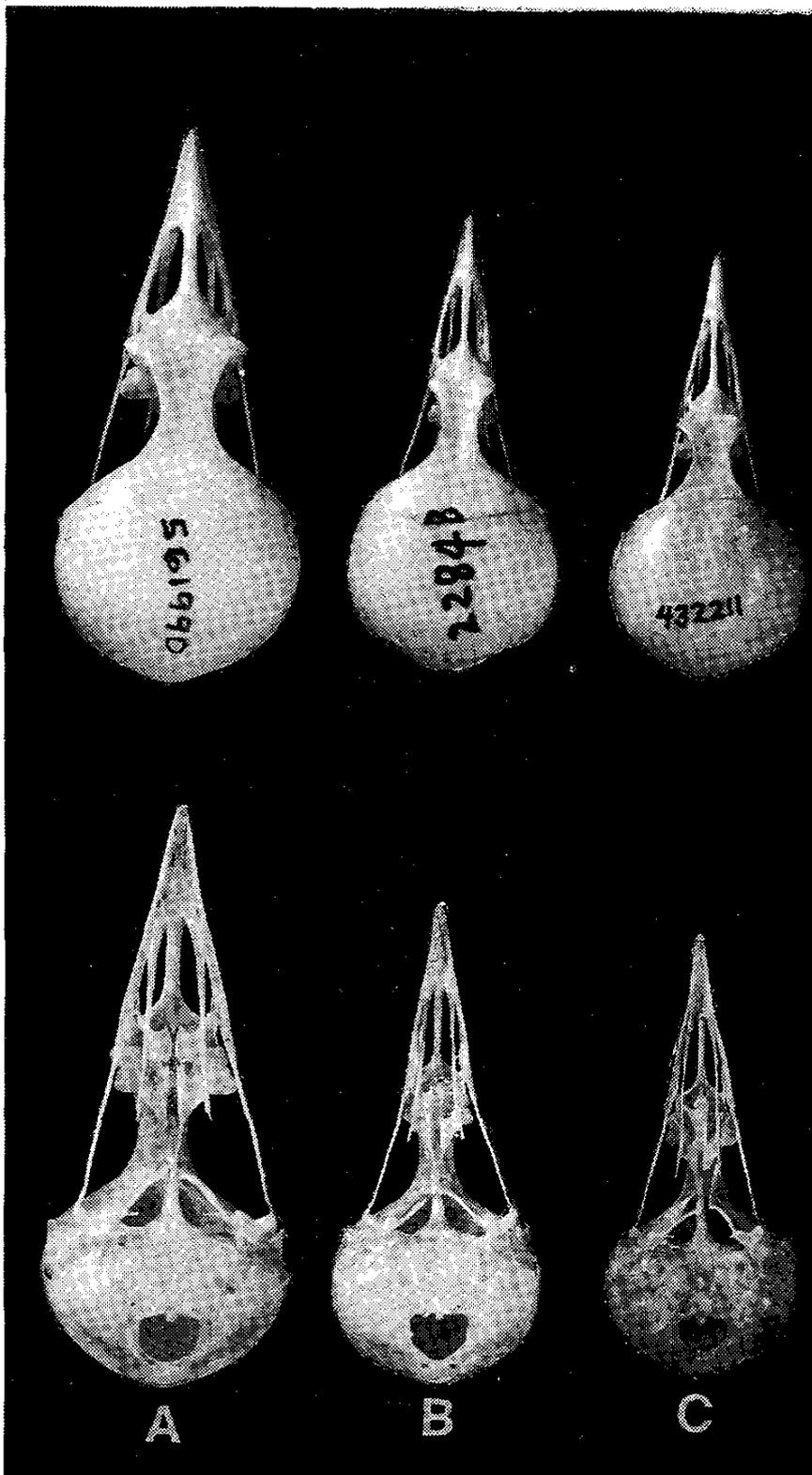
FIGURE 1 — Comparison of the skulls of warblers (top row, dorsal view; bottom row,
ventral view). A, *Megalurus timoriensis* (USNM 561990); B. *Bowdleria
p. punctata* (NMNZ 22848); C. *Amphilais* (*Dromaeocercus* auct.)
seebohmi (USNM 432211). Note the much narrower, constricted bill
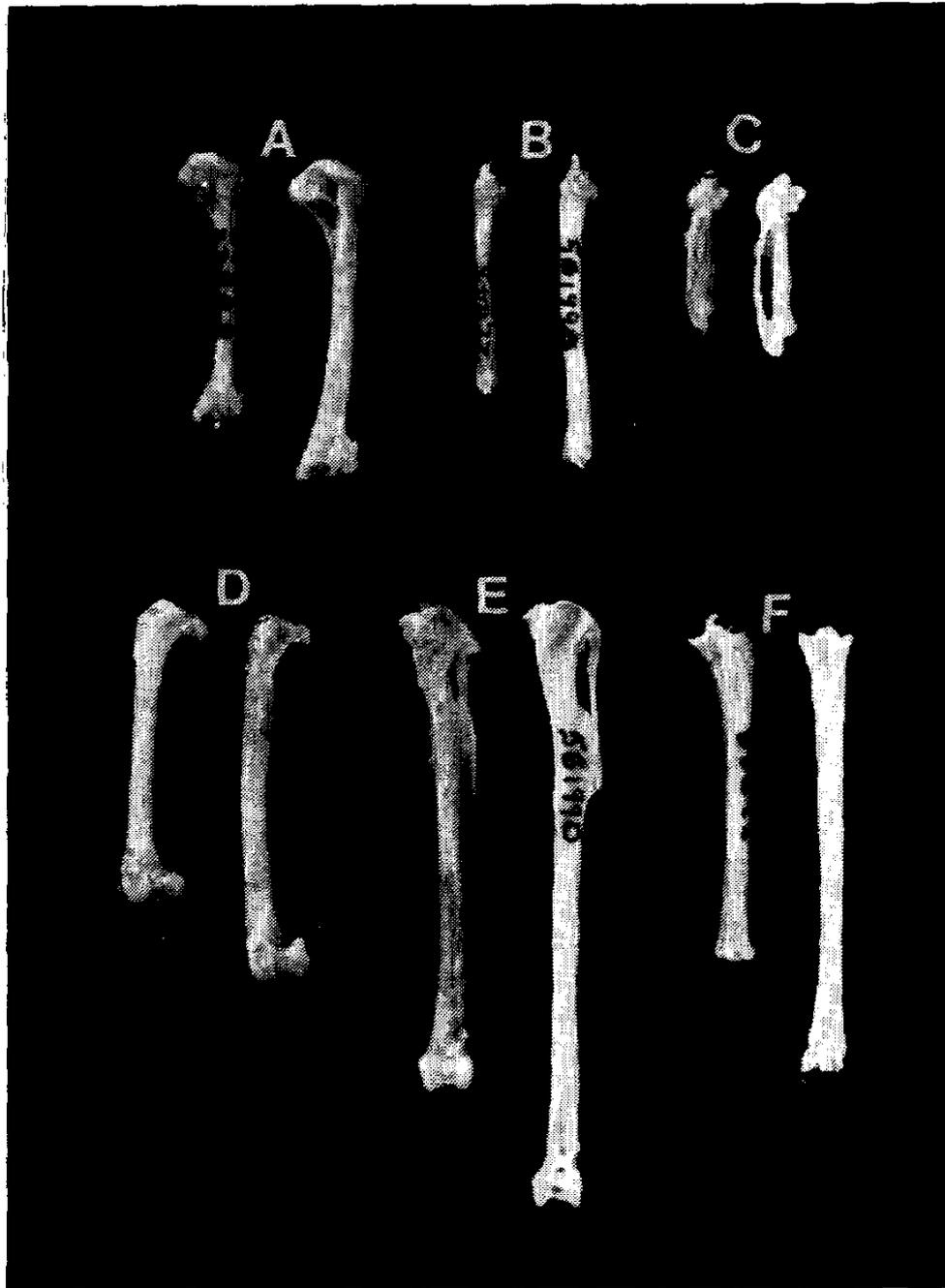and frontal area (arrow) in *Bowdleria* and *Amphilais* as opposed to
Megalurus.

FIGURE 2 — Comparison of wing bones (top row) and leg bones (bottom row) of
Bowdleria p. punctata (NMNZ 22848), on the left in each pair, with
Megalurus timoriensis (USNM 561990), on the right in each pair. A,
humeri; B, ulnae; C, carpometacarpi; D, femora; E, tibiotarsi; F,
tarsometatarsi. Note the more reduced wing bones and much more
robust leg bones of *Bowdleria*.

By far the most startling difference between *Bowdleria* and *Megalurus*
is in the pelvis (Figure 3). That of *Megalurus* is unexceptional among
passerines but in *Bowdleria* the anterior iliac shields are grotesquely expanded
both medially and posteriorly, so that they meet at the midline and are
separated only by a thin lamina of bone. In dorsal view they appear to occupy
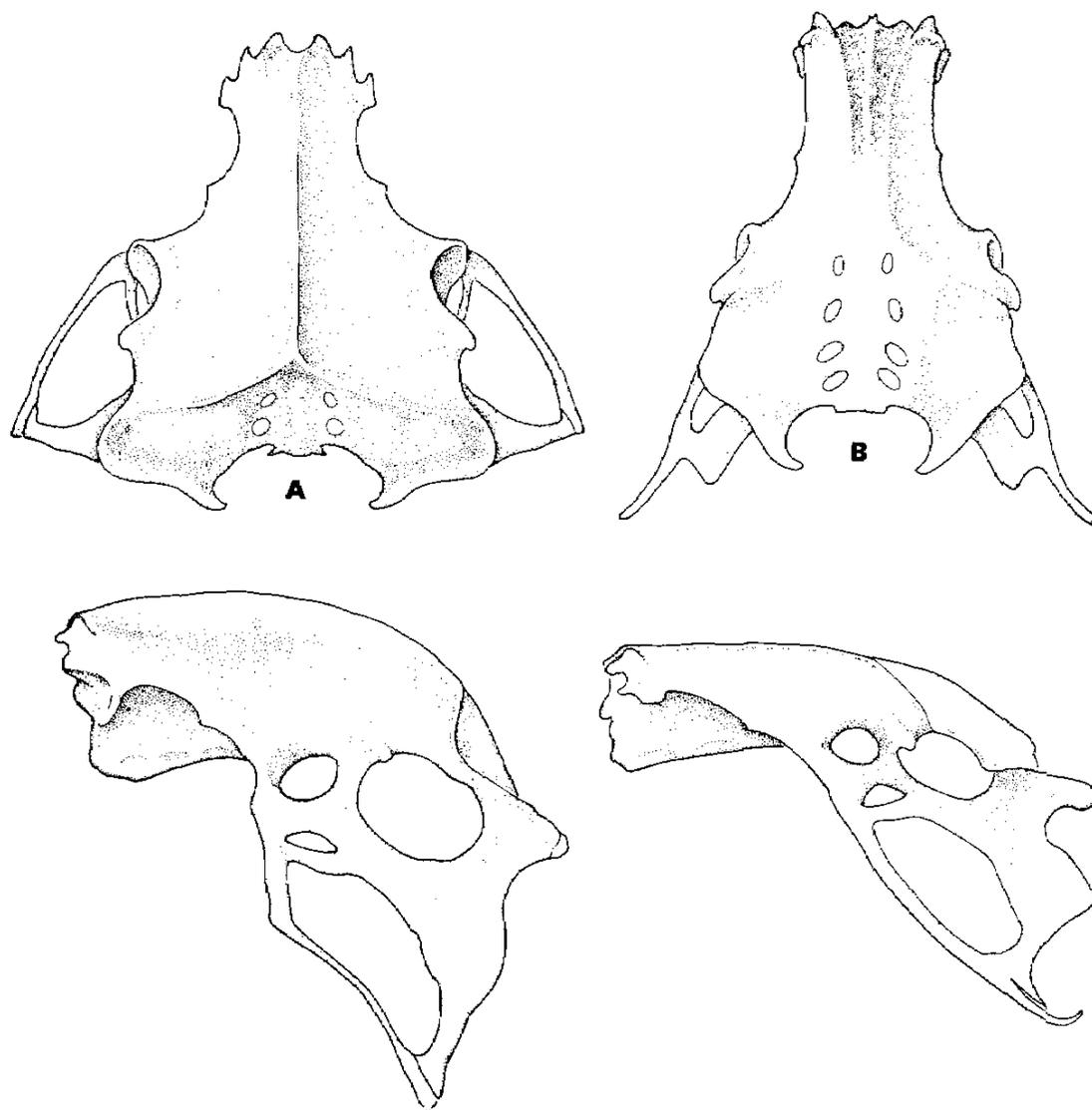almost the whole of the pelvis, so that the posterior portion of the ilium

FIGURE 3 — Comparison of the pelvis of (A) *Bowdleria rufescens* (USNM 554710) and (B) *Megalurus timoriensis* (YPM 7089) (top row, dorsal view; bottom row, lateral view).

is greatly compressed and reduced. This stems in part from the whole posterior portion of the pelvis being rotated ventrally. In lateral view, the postacetabular portion of the pelvis is seen to be much deeper in *Bowdleria*, partly as a result of the greater expansion of the ischium.

Concomitant with the bizarre morphology of the pelvis, the hindlimb elements in *Bowdleria* are much more robust than in *Megalurus* (Figure 2). The femur is much shorter and stouter, with the trochanteric crest and distal end more expanded. The tibiotarsus is likewise much heavier, with the inner cnemial crest extending farther dorsally and the distal end expanded.

FUNCTIONAL CORRELATES OF THE HINDLIMB OF *BOWDLERIA*

For what activity is the hindlimb of *Bowdleria* adapted, and are there any other passerines that are similarly adapted? Although *Bowdleria* at first seemed unique among passerines in its strange pelvis and extremely robust hindlimb, apparently similar adaptations have come to light in some unrelated taxa. Baird (1985) has described and illustrated the pelvis in the Australian logrunners, or chowchillas, of the genus *Orthonyx*, which are quite similar in overall morphology to *Bowdleria*. In *Orthonyx*, the femur is extremely short and stout, appearing almost like that of a foot-propelled diving bird such as a loon (fossil specimen examined with W. Boles). A similarly modified pelvis, though less extreme, is found in the New Zealand genus *Mohoua*, again accompanied by very robust hindlimb elements, most pronounced in *M. ochrocephala* (see Olson 1990a).

This functional complex appears to be strongly correlated with the use of the feet in foraging, particularly in moving vegetation and detritus to expose prey. This activity has been well described by Best (1979: 484) for the Snares Fernbird *Bowdleria punctata caudata*.

> Parts of the forest floor were covered by accumulations of dead *Olearia* leaves up to 20 cm deep. The *Olearia* leaves were leathery-textured and measured *c.* 12 x 18 cm, compared to a fernbird's 15-18 cm length. The edge of a leaf was grasped with a foot and raised laterally. The uncovered area was scrutinised rapidly, and the underlying material was probed and pecked at to disturb prey. If nothing attracted the hunter's attention, the leaf was released. This behaviour was repeated frequently, first with one foot, then the other, raising and dropping leaves in rapid succession.
>
> If something of interest was detected, leaves, twigs, and other debris were flicked or thrown aside with strokes of one or both legs. Peat clods, small stones, or semi-decomposed vegetation were either pushed away or raked over systematically with the feet. During such activity a bird sometimes cleared a path down to bare peat or tunnelled completely under the leaves. The concealed bird's position was marked by a small, trembling hummock of leaves from out of which material was ejected vigorously.

Best (1979:485) noted similar use of the feet in fernbirds foraging in tussocks, in various other ground vegetation, and in penguin nests made of twigs, dead leaves, and stones. Birds also used this foraging technique in *Olearia-Senecio* forest "in crevices and under loose pieces of bark on the trunk and branches, but less often around the bases of tightly packed leaf axils and exposed root systems."

Zusi (1978) described somewhat similar but even more extreme use of the feet in foraging in *Orthonyx*, which sweep away vegetation and litter with one foot and then scratch the ground beneath and in front of them while supporting themselves on the full length of the other tarsus and with the spine-tipped tail.

Despite its mainly arboreal habits, the Yellowhead (*Mohoua ochrocephala*) exhibits similar foraging behaviour, according to Soper (1976:50).

> Though Yellowheads feed mostly in the tops of the trees they also have a
> fondness for rooting through the accumulations of rubbish that fall down
> and collect in the forks. To do this a bird will grip the bark with one foot
> (and they have relatively huge feet), dig its tail, which is supplied with spines,
> into the trunk, and scratch vigorously with the other foot, sending down
> a shower of debris. The action is very much that of a domestic fowl – a
> vigorous scratch, a look, then another vigorous scratch, and so on.

It is actually rather curious that this functional complex and its correlated behaviour have not previously been identified as another passerine adaptive shift. It must certainly have arisen independently in the three lineages mentioned above, particularly as the condition is scarcely developed in the most primitive of the *Mohoua* group (see Olson 1990a). It is difficult to believe that this adaptation evolved only in Australasian passerines and it should be sought in other taxa. A similarly robust hindlimb and somewhat modified pelvis occur in the Hawaiian genus *Ciridops* (Fringillidae, Drepanidini), but unfortunately nothing is known about the behaviour of this extinct genus (Olson and H. F. James, MS).

SYSTEMATICS AND RELATIONSHIPS OF *BOWDLERIA*

The postcranial morphology of *Bowdleria* is so radically different from that of *Megalurus* that even if a convincing case could be made for a derivation of one from the other there would still be sufficient grounds for retaining a separate genus for *Bowdleria*. One would not expect cranial morphology to be affected by increasing specialization of the hindlimb, however, so that the marked differences in the skulls of *Megalurus* and *Bowdleria* may be taken as an indication that these genera are not as closely related as has generally been assumed.

Of the various genera of Sylviidae I examined, the greatest similarity to the narrowed skull, bill and frontal area of *Bowdleria* was in the Madagascan warbler *Amphilais* (= *Dromaeocercus* auct.) *seebohmi*. The skull in this species, incidentally, differs from that in its assumed congener *Dromaeocercus brunneus* in much the same way that *Bowdleria* differs from *Megalurus*, thus supporting Parker's (1984) separation of these species into different genera (Olson 1990b). Interestingly enough, *Amphilais seebohmi* has the same spiny, decomposed rectrices that *Bowdleria* has, so that there is a strong resemblance in external appearance between these two species as well (Figure 4). Although this may well be attributable to convergence, a possible relationship between *Bowdleria* and *Amphilais* should not be considered improbable solely on geographical grounds. These might well be relict forms, much as the Madagascan Vangidae and the Australasian Cracticidae appear to be closely related groups with relictual distributions.

If Sibley & Alquist (1987) were correct that the genetic divergence between *Bowdleria* and *Megalurus* is no greater than between congeneric species, then this would seem to mean that the genome does not necessarily track profound structural reorganization and major adaptive shifts within lineages. The morphological differences between *Bowdleria* and *Megalurus* are greater than between almost any two families of passerines. If this is not reflected in Sibley & Ahlquist's data, then we might fairly ask whether DNA hybridization studies are capable of accurately determining the divergence points of major lineages.
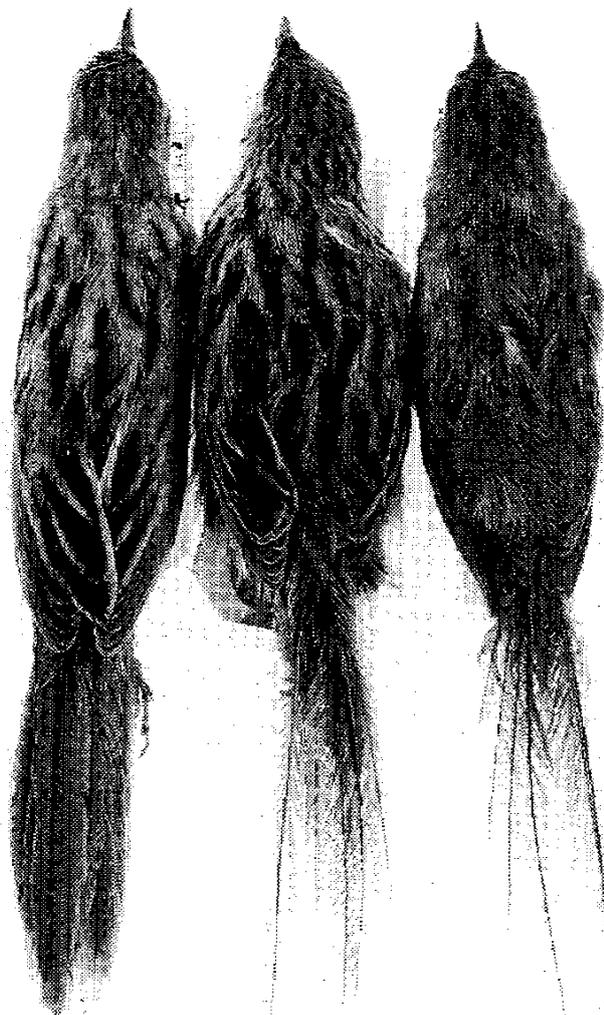
FIGURE 4 — Dorsal aspect of study skins of warblers: (left to right) *Megalurus timoriensis* (USNM 406080), *Bowdleria p. punctata* (USNM 124643), *Amphilais* (*Dromaeocercus* auct.) *seebohmi* (USNM 484181). Note the greater similarity of the decomposed tail of *Bowdleria* to that of the Madagascan genus *Amphilais* than to the Australasian *Megalurus*.

In summary, *Bowdleria* is a very distinct genus of Sylviidae with the pelvis and hindlimb highly specialized for moving vegetation and litter while foraging. Nothing in its osteology or external morphology substantiates a close relationship to *Megalurus* and its closest relative within the family remains to be determined, although *Amphilais seebohmi* of Madagascar remains a possiblity.

DISTINCTNESS OF *BOWDLERIA RUFESCENS* OF THE CHATHAM ISLANDS

In the earlier literature and continuing up at least through the second edition of Oliver (1955), the Chatham Island Fernbird was recognized as a full species, *Bowdleria rufescens*, distinct from the various other populations of fernbirds included as subspecies of *B. punctatus*. However, following the

modern trend of lumping allopatric insular forms no matter how distinct, it has lately been carried as simply one more subspecies of *B. punctatus* (e.g. OSNZ Checklist Committee 1970; Mayr 1986).

Nevertheless, on plumage alone the Chatham Island birds, now unfortunately extinct, stand quite apart, being particularly remarkable for the white, unspotted underparts.

> In the Chatham Fernbird the absence of spots on the under surface . . .
> and bright rufous colouring of the upper surface, contrast with the spotted
> under surface and more or less brownish upper surface of the other forms
> of *Bowdleria*. Its separation as a species consequently makes a natural division
> of the genus. (Oliver 1955:468)

Osteology now lends weight to this argument. The skeletal specimen cited above as *B. rufescens* (USNM 554710) was received in exchange from the National Museum of New Zealand (formerly #1397), unfortunately with no data of any sort, which doubtless explains why it was exchanged away. The specimen lacks the skull and left wing, and both femora and tibiotarsi were broken, having evidently been wired, so that the skeleton had probably once been mounted. This specimen is so distinctive by comparison with a skeleton of *B. p. punctata* that I conclude that it can only be an example of *B. rufescens* (Figure 5). The pelvis and hindlimb elements are larger and very much more robust, whereas the wing elements and pectoral girdle are markedly more reduced. This accords with the measurements from skins given by Oliver (1955) and with visual inspection of the relative robustness of the tarsometatarsus in skins of both forms.

The measurements (mm) of the skeleton of *B. rufescens* are as follows, with those of *B. p. punctata* in parentheses for comparison: sternum, length from the base of manubrium 12.2 (13.0), width at base of sternocoracoidal processes 10.8 (7.4), depth of carina 2.2 (3.3); humerus, length 17.3 (17.7), width of shaft at midpoint 1.4 (1.2); ulna, length 13.9 (15.1), width of shaft at midpoint 1.9 (1.0); carpometacarpus, length 9.6 (10.0), proximal depth 2.7 (2.6); pelvis length of synsacrum 13.6 (13.8), width across antitrochanters 14.2 (11.3), width across posterior iliac shields 14.9 (10.9); femur, proximal width 5.1 (4.2), width of shaft at midpoint 2.0 (1.5); tibiotarsus, length 36.4 (31.6), proximal width through cnemial crests 6.3 (5.2), width of shaft at midpoint 2.0 (1.6); distal width 4.0 (3.6); tarsometatarsus, length 25.9 (22.2), proximal width 4.1 (3.6), width of shaft at midpoint 1.6 (1.4); distal width 3.2 (2.7).

There are qualitative differences in the skeleton as well (Figure 5), particularly in the pelvis, which in *B. rufescens* has the posterior iliac shield in dorsal view more laterally expanded, with the margins rounded rather than truncate. Although the wing elements are shorter than in *B. punctata*, like the bones of the hindlimb they have much heavier shafts. The sternum is quite different in shape, being much wider, with a shorter manubrium and much shallower keel. After writing the above, I was informed by P. R. Millener (*in litt.* 23 May 1989) that he had found the same differences between *B. punctata* and subfossil pelves and sterna of *Bowdleria* from the Chatham Islands, thus confirming that the specimen in question (USNM 554710) is correctly identified as *B. rufescens*.
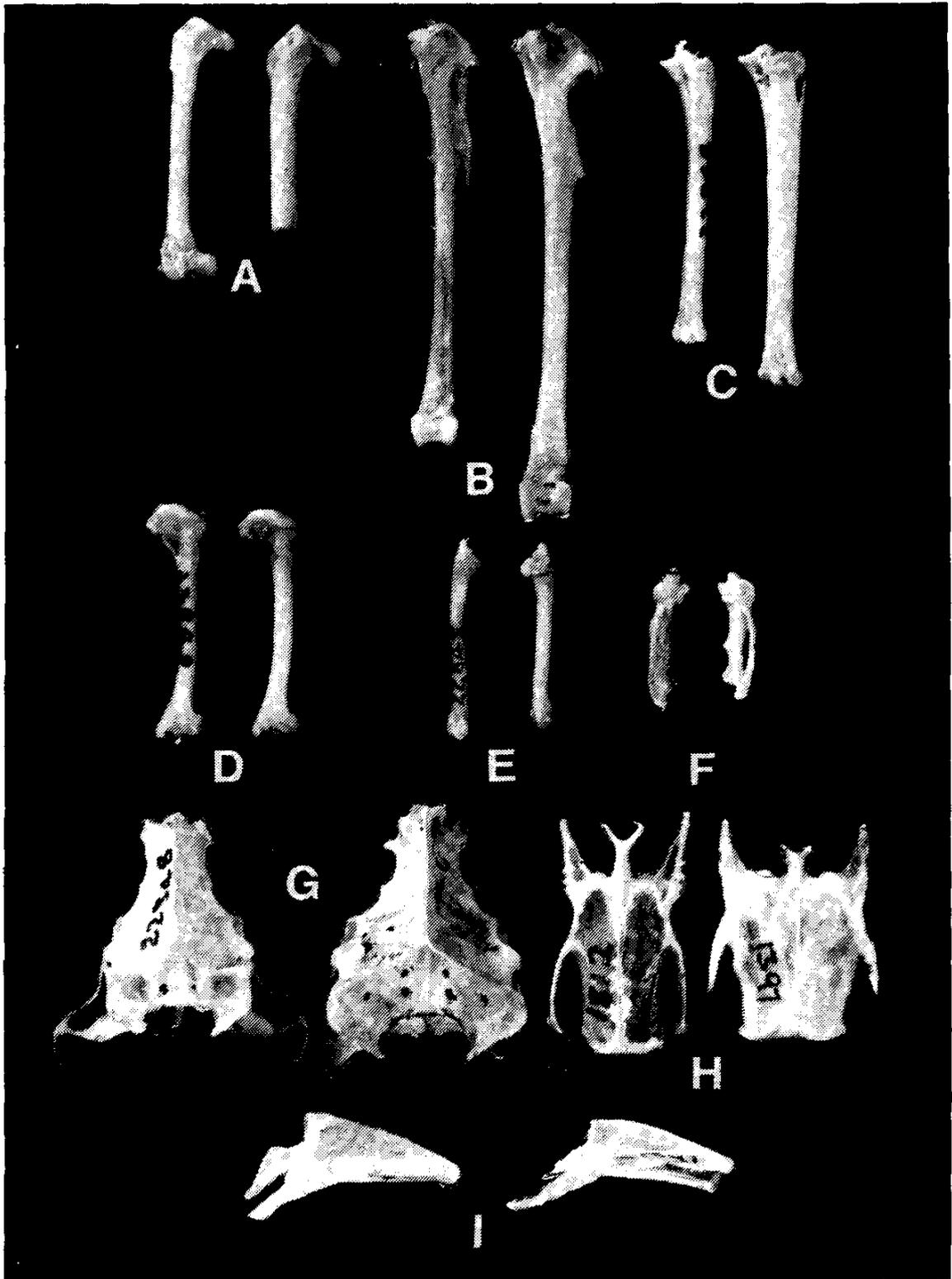
FIGURE 5 — Comparison of the bones of *Bowdleria p. punctata* (NMNZ 22848 except in H, which is from NMNZ 1512), on the left in each pair, with the Chatham Island species *B. rufescens* (USNM 554710). A, femora; B, tibiotarsi; C, tarsometatarsi; D, humeri; E, ulnae; F, carpometacarpi; G, pelves in dorsal view; H, sterna in ventral view; I, sterna in lateral view. Note the very much larger and more robust pelvis and leg bones but more reduced wing bones and sternum of *B. rufescens*.

The osteological and plumage differences shown by the Chatham Island birds are of such a magnitude that *Bowdleria rufescens* should be re-elevated to the rank of a full species.

ACKNOWLEDGEMENTS

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