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VARIATION IN THE STERNAL NOTCHES OF SUBOSCINE PASSERIFORM BIRDS

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ABSTRACT

The present study was undertaken to record the variations of the posterior border of the sternum of the New World suboscines, in an attempt to determine the reliability of this area of the sternum as a taxonomic character. The conclusions drawn from this survey (of 993 specimens) are that, within a broad range of variants, two basic kinds of sternal configuration are found: two-notched (Types 2-3-4, as defined), and four-notched (Types 5-6). The four-notched sternum is not confined to genera in the Rhinocryptidae and *Conopophaga*, as previously believed. Variations within the two- and four-notched sterna may not be considered taxonomically significant unless they can be shown to be consistent in a large series of specimens. In no case should a single specimen of a species be assumed to show the only sternal configuration of the species. The possible adaptive significance of the observed range of variation is briefly discussed, but no conclusions may be drawn until a functional analysis of the passerine sternum can be made.

INTRODUCTION

The shape of the posterior border of the sternum has long been accepted as a useful character in the classification of birds. Within the Passeriformes it has been employed particularly to

distinguish between several of the families of the superfamily Furnarioidea. It was once believed that the only passerines possessing four (rather than two) notches in the posterior border of the sternum were the tapaculos (Rhinocryptidae) and the tendency of taxonomists was to include any "four-notcher" passerine within that family. Sclater (1874, p. 191) stated: "The only other known Passerine form in which two emarginations are present on each side [i.e. a total of four notches] of the posterior margin of the sternum is the Australian genus *Atrichia* [= *Atrichornis*]. Whether this form certainly belongs to the Pteroptochidae [= Rhinocryptidae], cannot be positively ascertained until the structure of its larynx is known; but I have little doubt that such is the case." In diagnosing the family Atrichiidae (= Atrichornithidae) Sharpe (1890, p. 659) remarked: "Dr. Sclater . . . refers to the double-notched sternum of *Atrichia rufescens*, but Garrod [1876] figures the sternum of *A. rufescens* with only a single indentation . . ., and only one notch exists in the sternum of *A. clamosa* in the Museum of the Royal College of Surgeons." Sharpe must have considered Sclater to be in error, for his diagnosis for Atrichiidae in the Catalogue reads (loc. cit.): "sternum with a single deep lateral indentation on its hinder margin; . . ."

In 1881 Forbes noted that the antpipits (*Conopophaga*) also possessed two pairs of notches, and he used this and other evidence to erect the family Conopophagidae for the genera *Conopophaga* and *Corythopsis*, although the sternum of *Corythopsis* had not been examined.

The tendency has remained, however, to place in the family Rhinocryptidae any passerine found to have a four-notched sternum. For example, Shufeldt (1913) described *Hebe schucherti* as a new genus and species of passerine from the Lower Eocene, Green River Formation, Wyoming; he tentatively placed the form in the Rhinocryptidae on the basis of its four-notched sternum, and Brodkorb (1965) has concurred, at the same time substituting the new generic name *Neanis* for *Hebe*, preoccupied. W. D. Miller and A. Wetmore (in Wetmore, 1926, p. 292) moved *Melanopareia* from the Formicariidae to the Rhinocryptidae after it was found to have four sternal notches. Plótnick (1958) placed the antwren *Psilorhamphus* in the Rhinocryptidae primarily on the basis of its tracheal syrinx and four-notched sternum. All of these

actions imply a heavy reliance upon sternal notches as a taxonomic character in this group of passerines.

The configuration of the posterior border of the sternum has also appeared in most of the technical diagnoses of passerine families. It should be mentioned here that the key to mesomyodian passerines in Cory and Hellmayr (1924, p. 1) contains at least two errors. The Formicariidae are incorrectly characterized by: "Sternum with two pairs of posterior notches; nares schizorhinal" in contrast to the Conopophagidae and Pteroptochidae (=Rhinocryptidae) with: "Sternum with one pair of posterior notches; nares holorhinal." This key was adapted from Ridgway (1907, pp. 331-332) who correctly lists the two-notched sternum for the Formicariidae and the four-notched for the Conopophagidae and Rhinocryptidae. Both keys are in error in stating that the Formicariidae have schizorhinal nares; in passerines schizorhinal nares are found only in the Furnariidae (Garrod, 1877).

PROCEDURES

In the course of an anatomical study of the Conopophagidae we examined the sterna of several species of *Conopophaga* and *Corythopsis*. We were surprised to find two-notched sterna in the first specimens studied, not four-notched as Forbes' work had led us to expect. We therefore undertook a survey of the sterna of a large number of suboscines in an attempt to determine the range of variation in this structure, and its consequent reliability as a taxonomic character. We were able to examine at least the majority of the skeletons of the Furnarioidea available in this country. In addition, we studied a sample of other suboscine families, concentrating on the New World forms, and we also included a few oscines and non-passerines for comparison. In most cases we were working with skeletons that had been prepared by maceration, dermestid beetles, or both. In a very few instances, genera of particular interest were not available as skeletons, so their sterna were examined in specimens preserved in alcohol. In the alcoholic specimens, the notches of the sternum were noted from the inner (dorsal) surface, in order to minimize damage to the thoracic area.

In all, we examined 993 specimens representing 276 species and 146 genera of suboscines; we were unable to obtain a specimen of *Atrichornis*, but otherwise at least one genus of each of the sub-

oscine families was seen. (An unsuccessful search was made for the British specimens of *Atrichornis* mentioned in the Introduction; apparently they have been lost or destroyed during wartime.) The full list of specimens examined is presented in Table I.

NOMENCLATURE

Fortunately the nomenclature of sternal anatomy is not quite so confused as it is in most anatomical fields of study. The sternum is almost universally agreed to consist, at least topographically, of two areas: the "costal sternum" which refers to the anterior half, associated with the ribs; and the "metasternum" which refers to the posterior half, caudal to the ribs. In this paper we are dealing solely with the metasternal area. The metasternum usually shows a variably thin process, directed posteriorly, on the lateral edge: the "posterior lateral process" (see fig. 1, on Type 6). Although admittedly this process is part of the metasternal area, the word "metasternum" as traditionally used in descriptions excludes the process. Conforming to this traditional usage, "metasternum" in the remainder of this paper will refer *only* to the central bony plate of the posterior sternum (see fig. 1, Type 2). A few species have an additional process between the posterior lateral process and the medial metasternum: the "lateral metasternal process" (see fig. 1, Type 6). We have coined this new term for the structure because we feel that the others ("internal lateral process," "intermediate lateral process," "internal lateral xiphoid process," etc.) which have been used, are unsatisfactory. Our work and several embryological studies indicate that this process is derived from the metasternum, not from adventitious growth or from subdivision of the posterior lateral process. Forbes used "internal xiphoid process" but Lindsay (1885), who did the basic embryological study on the structure, used "xiphoid" to refer just to the *ends* of *both* processes. We believe, therefore, that "lateral metasternal process" is less confusing, more descriptive, and that it reflects the metasternal origin of the structure.

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RESULTS

The 993 specimens of suboscines examined represent a structural continuum from an unperforated sternum to one with two processes and two notches on each side. In order to evaluate the distribution of the various configurations, the following categories were set up (see fig. 1):

- Type 1. Sternum entire: no notches or perforations.
- Type 2. Sternum with a lateral fenestra on each side: the posterior lateral process bears a wide terminal flange which either touches or is continuous with the metasternum, enclosing a fenestra or window.
- Type 3. Sternum with a lateral notch on each side (the "two-notched" sternum): the flange of the posterior lateral process, if present, does not touch the metasternum. The opening (notch) may be wide or very narrow.

- Type 4. Sternum with a lateral notch and small medial fenestra or fenestrae on each side: this condition is the same as Type 3 except that the metasternum is perforated by at least one small hole, whose diameter is not larger than one-fifth the width of its side of the metasternum.
- Type 5. Sternum with a lateral notch and a large medial fenestra on each side: this condition is like Type 4 except that the fenestra is wider than one-fifth the width of its side of the metasternum. (Experience later showed that this fenestra is always wider than one-half the width of its side of the metasternum.)
- Type 6. Sternum with a lateral and a medial notch on each side (the "four-notched" sternum): the flange on the lateral metasternal process, if present, does not touch the medial metasternum.

Although the categories were established in advance simply as a means of recording the variations in the sternum, we found that nearly all of the specimens fell clearly into one of the six categories. We anticipated difficulties in distinguishing between Types 4 and 5 because they were based on arbitrary size differences of the fenestrae. We found, however, that the fenestrae occurred in two distinct size classes. Type 4 characteristically had many small fenestrae, asymmetrically placed; Type 5 had a single pair of large, more or less symmetrical, fenestrae. Some individuals of some species were bilaterally asymmetrical in the entire metasternum, but with only four exceptions, the two sides fell into categories consecutive on the above list. The system of sternal types established for this study, therefore, seems to represent a natural rather than an artificial morphological sequence.

Artifacts

Some of the "fenestrae" observed in the sterna were clearly either artifacts resulting from collection or preparation, or the products of the physiological state of the bird when it died; these were discounted in the classification into sternal types. Natural fenestrae have a smooth, finished-looking rim, usually with a

slight thickening or lip; artificial holes (such as those caused by shot or by dermestids) are jagged and/or thin-edged.

A serious problem occurs, however, in young or incompletely ossified specimens in which the cartilage or cartilage-bone interface has been lost in preparation. Klíma (1964) and others have shown that during embryological development and post-hatching maturation of passerines, ossification of the sternum begins in the costal sternum and gradually extends posteriorly. The last area to ossify is the posterior edge of the metasternum and the posterior lateral processes. It is important, therefore, to know the age of a specimen in order to be sure it has completed its bone deposition. Unfortunately very few of the available specimens had age data. The extent of the skull ossification was recorded for many individuals to indicate probable age, but this is not an entirely reliable character as some suboscines, notably the Rhinocryptidae, never complete skull ossification. Being aware of this general age effect on skeletal material, we have attempted to take possible incomplete sternal ossification into consideration in the analysis of our data. It is likely, however, that some individuals classified as having open notches would actually have had closed notches (fenestrae) if the bridges of cartilage had had time to ossify. Nevertheless, for consistency we have recorded only the condition of the bone, not the cartilage. Artifacts in bone can be seen clearly, but cartilage varies too greatly to be dependable. Much of the cartilage undoubtedly has been removed by dermestids or maceration, but on some poorly cleaned specimens it is still present and often impossible to distinguish from other dried soft tissue, particularly at the ends of the processes.

The effects of the general physiological condition of adult birds on sternal morphology are also difficult to assess. To our knowledge, studies have never been made on the impact of such processes as egg formation, molt, etc., upon the general skeletal ossification of adult passerines. (For a discussion of these effects on some non-passerines, see Hanson, 1962.) The observations made in this study have led us to believe that, at least in some species, there are periods in adult life during which the bone loses and later regains some of its substance. Unfortunately most of the specimens lack sufficient data on breeding condition, molt, cause of death, etc., for us to be able to pursue this line of investigation.

Experience with many hundreds of sterna, however, gradually led us to believe that a metasternum riddled with many tiny holes is the result of a general lack of ossification, and is of no phylogenetic significance. These "pinholes" were not included in the final classification of specimens into sternal types.

No attempt has been made to distinguish between the various shapes observed in the metasternum and processes. Several genera or groups of genera appear to be distinguishable by the shape of the sternum itself, as well as the shape of the flanges on the sternum and processes, the depth of the notches, relative differences in length between the sternum and processes, etc. It is probable that these variations have phylogenetic significance in some groups, but this is difficult to determine with the available material. Artifacts of preparation, especially the warping that results from maceration or bleaching, render it almost impossible to obtain an accurate outline of the sternum in some specimens. Sterna suitable for study of general shape would represent only a small fraction of the sample we examined for notching.

Age, Sex, and Population Effects

In a few genera it was possible to obtain enough material with data to determine the possible effects of age, sex, and geographical population upon sternal notching. Comparison of 61 specimens of *Tyrannus tyrannus* showed almost no variation in sternal type, and none that could be attributed to a peculiarity within a small gene pool or a particular sex or age class (other than the extent of ossification mentioned above). A sample of 60 specimens of *Xiphorhynchus* spp., on the other hand, showed wide variation (see Table I) but again no correlation within age, sex, or population groups. Of this genus, the best sample from a single locality was a series of six *X. triangularis* collected at El Sauce, Cartago Province, Costa Rica, in less than a month, and including both males and females with fully ossified skulls. Of these, five (3 ♂♂, 2 ♀♀) had Type 3 sterna and one (sex unknown) had a Type 2 sternum. In the latter the sternum was asymmetrical, with the left posterior lateral process fused to the metasternum with a wide bridge of bone, and the right with a broad flange touching (not fused with) the equally broad flange extending from the metasternum. Two other specimens of *X. triangularis*, one from another

province in Costa Rica, and one from Colombia, had Type 3 sterna. Similar variation was seen in smaller samples of other species of *Xiphorhynchus*, but never in this or any other genus was the type of any one sex, age, or population seen to be consistently different from the type of any other. We believe, therefore, that (allowing for possible error caused by scoring incompletely ossified specimens) the range of variation observed in the sterna represents that of the species itself, unaffected by age, sex, or population.

Variation within Taxa

Table I lists the series of specimens examined and the sternal types found in each. The Table is arranged in the taxonomic order followed by Peters (1951) for the Eurylaimidae through the Rhinocryptidae, and by Hellmayr (1929) and Cory and Hellmayr (1927) for the remainder of the New World families. The specimens are recorded by sternal types, in columns, each "x" representing one specimen.

Dendrocolaptidae: 173 specimens of 29 species in 9 genera were examined. It was found that the woodcreepers varied widely in sternal type. The only passerine (aside from *Menura*) in the entire study that had a solid sternum, without notches or fenestrae (Type 1), was one specimen of *Xiphocolaptes promeropirhynchus*; two additional specimens of the species, however, had Type 2 sterna, and two others had Type 3. Many other genera and species of woodcreepers also showed wide variability. For instance, in *Xiphorhynchus flavigaster* three specimens had Type 2 sterna, two had Type 2 on one side and Type 3 on the other (Type 2-3 asymmetry), fifteen had Type 3 on both sides, two had Type 3-4 asymmetry, and two had Type 4 sterna. Within the family as a whole, the Type 3 sternum was the most common (128 of the 173 specimens examined), Type 2 occurred fairly often (20 specimens), Type 4 less so (7), and Type 1 only once. Of asymmetrical sterna, five specimens were of Type 2-3 and nine of Type 3-4. The only individuals in the entire study (again, aside from *Menura*) that showed non-consecutive sternal types were two *Dendrocolaptes certhia* and one *Xiphorhynchus lachrymosus* which had small (Type 4) medial fenestrae in Type 2 sterna; other specimens of these species had Type 3, Type 4 or Type 3-4 sterna.

Furnariidae: 199 specimens of 71 species in 33 genera were examined. Considerably more consistency was seen in this family than in the woodcreepers; every ovenbird studied had a single pair of notches in the sternum, and some individuals had additional medial fenestrae. The great majority of the specimens (166) had Type 3 sterna, 18 had Type 4, and 5 had Type 5. There was also a limited amount of asymmetry, with nine Type 3-4 and one of Type 4-5. Some intraspecific variation was seen, for example, in *Cinclodes fuscus*, with three specimens of Type 3, one of Type 3-4, two of Type 4 and one of Type 4-5. The genera usually placed at the end of the family (*Xenops*, *Pygarrhichas* and *Sclerurus*) were the only ones examined that had large symmetrical medial fenestrae (Type 5).

Formicariidae: 194 specimens of 54 species in 32 genera were examined. Although wide variation in sternal types was observed in this series of antbirds, there appears to be less intraspecific and more interspecific and intergeneric variation than in the previous families. The only species found to have more than two types was *Dysithamnus mentalis*, a specimen of which was the only antbird examined that had a Type 2 sternum. Of a series of 15 individuals 1 had Type 2, 12 had Type 3, 1 had Type 3-4, and 1 had Type 4. In the family as a whole, 171 specimens had Type 3 sterna, 1 had Type 2, 9 had Type 4, 2 had Type 5 and 7 had Type 6. Very little asymmetry was seen, with only four individuals having Type 3-4 asymmetry.

The great majority of antbirds were found to have two-notched sterna, and a few had small medial fenestrae. One group of genera (*Pittasoma*, *Grallaricula* and *Grallaria*), however, was markedly different from the rest of the family. A single specimen of *Pittasoma michleri* had a Type 6 sternum and one of *Grallaricula nana* had a Type 5. The species of *Grallaria* separated into two distinct groups: *G. guatemalensis* (2 specimens), *varia* (3), *haplonota* (1), *quitensis* (1), *ruficapilla* (1) and *rufula* (1) had Type 3 sterna; *G. fulviventris* (1 specimen), *perspicillata* (5), and *ochroleuca* (1) had Type 6 sterna, except for one specimen of *perspicillata* in which the lateral metasternal process was fused to the metasternum, forming a Type 5 configuration. [Ridgway (1909, p. 71) erected *Hylopezus* for *Grallaria perspicillata* and later (1911) added *G. (fulviventris) dives* and *macularius* to the

new genus; he did not have *G. ochroleuca* available for study. *Hylopezus* was separated from *Grallaria* by differences in the nasal fossae, nostrils, bill, etc., and by the lack of rictal bristles.] In view of their sternal disparity with the rest of the Formicariidae, it will be important to reexamine the taxonomic status of *Pittasoma*, *Grallaricula*, and *Grallaria*, and particularly to review the relationships of the species currently placed in the latter genus. Available anatomical material (9 out of 27 species) is not sufficient for a thorough study of the genus *Grallaria*, but these preliminary findings suggest that its division into two genera may well be justified.

Conopophagidae: 28 specimens of this family were examined, 20 in 4 species of gnateaters (*Conopophaga*) and 8 in the 2 species of antpipits (*Corythopsis*). The two genera were found to differ strongly and consistently. Nineteen specimens of *Conopophaga* had Type 5 sterna, the remaining individual being Type 5-6. All 8 specimens of *Corythopsis* had Type 3 sterna. These and other anatomical findings have led us to believe that this is an artificial family, and that *Conopophaga* should be placed in the Formicariidae and *Corythopsis* in the Tyrannidae.

Rhinocryptidae: 25 specimens of 9 species in 5 genera were examined. The tapaculos were found to be quite consistent in sternal type; all but one specimen had the Type 6 sternum. In the exception, one of two individuals of *Pteroptochos tarnii* examined, only the left side of the sternum was Type 6; on the right, the medial notch was replaced by two large fenestrae, side by side.

Cotingidae: 79 specimens of 22 species in 15 genera were examined. A certain amount of variation was found in the cotingas, but only four genera showed individuals with sterna other than Type 3. Some specimens of *Lipaugus*, *Procnias*, and *Rupicola* had Type 2 sterna, but others had Type 3; one specimen of *Tityra semifasciata* had Type 3-4 asymmetry, but thirteen others had symmetrical Type 3. The family totals were: 6 specimens with Type 2; 1 with Type 2-3; 71 with Type 3; and 1 with Type 3-4.

Pipridae: 42 specimens of 10 species in 6 genera were examined. Almost no variation was observed in the manakins; two specimens (one *Pipra coronata* and one *Manacus manacus*) had

Type 2-3 asymmetry, but at least four other specimens of each species, and all of the rest of the family were found to have Type 3 sterna.

Tyrannidae: 220 specimens of 55 species in 33 genera were examined. Within this sample of tyrant flycatchers, 203 individuals had Type 3 sterna, 5 had Type 2, 4 had Type 2-3, 5 had Type 3-4, and 3 had Type 4. All but three of the individuals that were not Type 3 were of species which also included Type 3 specimens in their series; the three exceptions were species of which only single specimens were examined (*Myiobius barbatus* and *M. sulphureipygius*, Type 2, and *Capsiempis flaveola*, Type 4).

Oxyruncidae and Phytotomidae: 1 specimen of *Oxyruncus cristatus*, 4 specimens of *Phytotoma rara* and 2 of *P. rutila* were examined. The sharpbill and the plantcutters all showed Type 3 sterna.

Eurylaimidae, Pittidae, Philepittidae, and Acanthisittidae: In these Old World families, the following limited series was examined: 8 specimens of 5 species in 4 genera of broadbills; 11 specimens of 8 species in the single genus of pittas; 1 specimen of the asity, *Philepitta castanea*; and 1 specimen of each of the two genera of New Zealand Wrens. All were found to have Type 3 sterna, except for one individual of *Pitta moluccensis*, which had Type 4.

Menuridae: The four specimens of lyrebirds (*Menura superba*) examined were consistent in having a basic sternal shape different from that of any other passerine examined. The sternum was unusually long and narrow, and the bone was comparatively thick and solid. In the two Type 3 individuals the notches were very shallow and narrow. In the Type 1-4 asymmetrical individual, the notch, which was on the left side, was covered by a thin sheet of cartilage and there were two small fenestrae in the metasternum, close to the keel. On the right side a shallow notch was indicated by thinner bone where the cartilage had evidently ossified, leaving the filled "notch" plainly visible. The fourth individual was completely Type 1, showing no suggestion of notches. Because of the unusual nature of its whole sternum, *Menura* will be largely omitted from the following discussion of the suboscine sternum.

DISCUSSION

The posterior border of the sternum of suboscines has been found to be much more variable than had been previously suspected. Most passerine anatomical features that have been examined for variability (e.g. pterylosis [Heimerdinger, M.A. 1964. A study of morphological variation in the dorsal and ventral pterylae of Passeriformes. Ph.D. Diss., Yale Univ. 241 p.], syrinx [Ames, P.L. 1965. The morphology of the syrinx in passerine birds: its application to the classification of the order Passeriformes. Ph.D. Diss., Yale Univ. 315 p.], etc.) exhibit only a very limited amount of individual variation and in studying these features the anatomist can fairly safely depend on a single specimen of a species to be typical of that species. This is not true of the sternum. The present study has shown that, aside from possible ossification effects, there is probably no variation correlated with sex, age, or infraspecific populations; on the other hand, wide individual variation may exist in sternal types, in the size of notches and fenestrae, and in bilateral symmetry. Of the 150 New World suboscine species represented in this study by two or more specimens, 24 per cent (36 species) contained individuals of two or more sternal types, and an additional 26 species contained asymmetrical specimens. Some families were more variable than others. Ten species of woodcreepers were represented by series of five or more specimens. Of these species, six had specimens of two sternal types, and two had specimens of three types. Comparable figures for the tyrant flycatchers were much lower: two out of twelve species contained two types and none was found to contain three.

In addition to the simple presence or absence of notches and fenestrae recorded in this study, many other variations were observed. For example, the following characters were seen to vary within a genus or species, or even from side to side of a single sternum: the size and shape of notches, fenestrae, metasterna, and processes; the width of the bridge of bone connecting the lateral processes to the metasternum in Types 2 and 5; and the number, size, and position of the small fenestrae in Type 4. In the case of the small fenestrae, asymmetry was more common than symmetry.

Analysis of the variations in type, however, shows two fundamental kinds of sternal condition. Types 2, 3, and 4 all contain

an essentially solid metasternum with a pair of posterior lateral processes. The observed intraspecific variations make it difficult at this time to see any taxonomic significance in whether the end of the posterior lateral process is free from (Type 3) or touches or fuses with (Type 2) the metasternum, or in the presence of small asymmetrical fenestrae in the metasternum (Type 4). This general connection between Types 2-3-4 is clearly shown by the large number of instances of occurrence of more than one of these configurations within a single species, or on the two sides of a single specimen. Even the apparent significance of the difference between solid and perforated sterna in suboscines is weakened by the finding of a specimen with a Type 1 sternum in a genus (*Xiphocolaptes*) of which all others seen were Type 2 or Type 3. This, of course, is not meant to imply that a solid versus a perforated sternum (or any other sternal variation) may not have taxonomic significance in any group of birds, but differences must be shown to be *consistent*, and not just to be two or three out of a wide range of individual variations.

Type 5 and Type 6 also demonstrated a fundamental similarity to each other, both in morphology and in occurrence. From the specimens examined, it appears that the bridge between the lateral metasternal process and the metasternum is almost as "easily" formed or lost as that between the posterior lateral process and the metasternum in Types 2-3-4. The sample of sterna of Types 5 and 6 was small, as taxa which possess these types are unfortunately rather rare in anatomical collections. Nevertheless, single individuals of two unrelated species, *Conopophaga lineata* and *Pteropotochos tarnii*, were bilaterally asymmetrical Type 5-6, and *Grallaria perspicillata* showed both Type 5 and Type 6 specimens.

Examination of Table I will show a strong tendency of suboscines to vary only within one of the two fundamental kinds of sterna; this tendency suggests some type of basic separation between them. In no instance was a species found to vary between the two-notched (Types 2-3-4) and the full, four-notched, Type 6 sternum. The only intermediates found were between Types 3 and 5, or Types 4 and 5. These exceptions were in three genera of ovenbirds: one specimen of *Cinclodes fuscus*, Type 4-5 (compared to six others of the species which were Types 3, 3-4, or 4), and

several specimens of *Xenops* and *Pygarrhichas*, which showed Type 5 (with additional specimens of Type 3 or 4).

The evolutionary significance of this segregation into Types 2-3-4 or Types 5-6 is not understood. Logically the intermediate morphological steps between two and four notches should be, first, a formation of one or more small fenestrae, which may then enlarge and or merge to form a single large fenestra, which in turn may lose its posterior border and open to form a notch. The process can, of course, be reversed, in that the notch closes, and the fenestra ossifies to form a solid metasternum. A remarkably small number of the examined specimens appeared to be intermediate in these respects. Most of the Type 4 specimens had small, irregularly and asymmetrically placed fenestrae; in none was it clear that several small fenestrae had merged to form a larger, irregularly shaped fenestra, approximately symmetrical with one on the opposite side of the sternum. An occasional Type 4 specimen had a symmetrical pair of small fenestrae in the posterolateral corners of the metasternum; these fenestrae showed some variation in size, but none reached the size originally designated as the dividing line between Types 4 and 5. The only specimen in the study that showed some indication of a morphological progression between the two- and four-notched sternum was the single individual of *Cinclodes fuscus*, in which there was a large fenestra on one side opposite a small fenestra on the other. This individual seems to indicate that the progression between Type 4 and Type 5 is possible, but the fact that it was the only one out of 993 specimens that bridged the two- and four-notched sterna, argues for a fairly strong barrier between them.

Other rare conditions found in the study were four instances of small metasternal fenestrae in association with Type 1 or 2 sterna. Two specimens of *Dendrocolaptes certhia* and one of *Xiphorhynchus lachrymosus* had these Type 4 fenestrae in otherwise Type 2 sterna, and one specimen of *Menura superba* had an asymmetrical Type 1-4 sternum. Although all three genera showed generally wide variability (Types 2, 2-3, 3, 3-4, and 4 in the two woodhewers, and Types 1 and 3 in the lyrebird) these specimens also serve to demonstrate that the postulated sequence of phylogenetic development of the two Type 4 characters (lateral notches and small medial fenestrae) might occasionally be reversed.

The functional and adaptive significance of the observed variations in the sternum is not evident from the material that we have examined. Previous studies by others indicate that strength of flight and the consequent development of the pectoral and abdominal muscles influence the shape and heaviness of the sternum. In a basic embryological study of the non-passerine sternum, Lindsay (1885, p. 707) stated: "... since the posterior border of the sternum affords attachment to two opposite sets of muscles, (a) the pectoral, (b) the abdominal, the resultant of their forces must be to some extent expressed in its shape, for in general the outline of a bone tends to express the direction and strength of the mechanical forces acting on it. In other words, we should expect to find the posterior border of the sternum varying with the habits of the bird, whether it is a good flyer, and uses its pectoral muscles most, or is accustomed to run or hop, and thus makes a greater proportional use of its abdominal muscles." Lindsay found that in non-passerines, birds with strong flight (e.g. gulls) had long, broad and solid sterna with short processes, but ground-living species (e.g. tinamous and galliforms) had short sterna with long thin processes for the attachment of the enlarged abdominal muscles.

This generalization seems reasonable, and it appears to be largely (but not invariably) true for passerines as well as for more primitive birds. The taxa examined in the present study in which the sternum is relatively short with long thin processes (Types 5 and 6: Rhinocryptidae, *Grallaria* spp., *Conopophaga*, etc.) are generally ground-dwelling, weak-flying birds. Those with relatively longer and heavier sterna with fewer and shorter processes (Types 1 through 4: the majority of suboscines and all known oscines) are largely arboreal and have good powers of flight. Many exceptions to this generalization, however, may be found: for example, *Cinclodes* (of which one specimen was Type 4-5) is an unusually strong flyer for its family, yet the majority of the ovenbirds are Type 3; and a great many basically terrestrial forms (e.g. *Geositta*, *Formicarius*, *Chamaeza*, *Pitta*, etc.) have Type 3 or 4 sterna. Perhaps the greatest contradiction to this "rule of thumb" for an interrelationship between sternal shape and power of flight is *Menura superba*. The lyrebird, a markedly aberrant passerine in almost all aspects of its morphology, has a uniquely long and heavy sternum, with very short if any processes, yet it might be

considered to be the most terrestrial of all passerines. It may be, of course, that this solid sternum is a specialization for terrestrial life, but in an entirely different way from the rest of the passerines.

Oscines which have a specialized form of locomotion such as creeping on vertical surfaces (*Certhia*, *Sitta*), or which are partially terrestrial (*Eremophila*, *Cinclus*), have exactly the same sternal characters as the more typical oscines. It is also true, however, that many of these specialized species are migratory; the importance of certain regular, but short-time, activities during the life span may override a tendency toward adaptation for the daily type of locomotion. Unfortunately, the behavior and life histories of most of the sternally exceptional suboscines are poorly known.

An alternative explanation for why certain forms do not possess the sternal type "expected" for the mode of life involved, is that some groups, such as oscines, have not had the time or the genetic latitude to produce sternal variation. This seems unlikely because the marked variation in some of the relatively closely related suboscines shows that the genetic potential is present in the order, and that it can be extremely active in some families.

The final answer as to why the New World suboscines show a high degree of variability cannot be given until a thorough functional analysis can be made of the sternum, its processes, and attached muscles. Once the function of this complex is known, then the adaptive significance of the various configurations can be studied and understood as well.

Previous investigators who have studied the posterior border of the sternum have all concluded that it is an extraordinarily plastic structure. Klíma (1962, p. 151) summarized his and earlier embryological studies on passerine and non-passerine sterna by stating: "The results obtained suggest that the avian sternum is a very young, still considerably plastic, element which, during phylogenesis, has undergone progressive evolution." The results of the present study, derived from the adult sternum, confirm the conclusions drawn from embryological material.

Garrod (1877) was probably the first to suggest that the ancestral passerines possessed a two-notched sternum. Forbes (1881, p. 438) apparently agreed with this, for in his discussion of the four-notched sternum of *Conopophaga* and the Rhinocryp-

tidae, he stated: ". . . I am not inclined to consider it in any way a primitive character, but rather as an instance of a simple modification having been independently acquired in different groups of birds. . . ." The present study has shown that the great majority of modern passerines have basically two-notched sterna (Types 2-3-4). All the variants observed may be morphologically achieved through a structural progression from Type 3: Types 1 and 2 by fusion and ossification between the posterior lateral process and the metasternum, and Types 4, 5, and 6 by fenestration and separation of the lateral metasternal process from the metasternum. Because the entire variation can be arranged sequentially (Types 1 through 6), however, it is impossible to state definitely which is the basic structural type, and which are the derivations. Unfortunately, there are no clues to the basic type, either from the fossil record or from related modern taxa. Many of the Piciformes, believed to be the order most closely related to the Passeriformes, have a very specialized form of pedal locomotion. The woodpeckers and toucans examined for comparison in this study had Type 6 sterna, but the processes were relatively much shorter and broader than those in the passerine Type 6 sternum; four genera of barbets and one jacamar had longer thinner processes, more like the passerine type, but all four processes had very wide posterior flanges which were rarely found in the Type 6 suboscines. If any of the above theorizing on function affecting the shape of the sternum is correct, then we cannot expect evolutionary indicators in this case from such a highly specialized group as the Piciformes.

CONCLUSIONS

The main conclusion of this study is that the suboscine sternum is an exceptionally variable anatomical structure. We recommend caution, therefore, in the taxonomic use of sternal configurations until their range of variation has been determined, and their functional and adaptive significance can be understood. The present investigation was designed only to sample the range of variation, and although the evolutionary significance of this variation is not yet known, we hope our purely observational results can have some immediate utility for the taxonomist.

In order to use the posterior border of the sternum as a taxonomic character, reasonably large series must be examined and differences must be shown to be consistent before they can be

considered significant. If, however, only a few specimens are available and they all show either Types 2-3-4 or Types 5-6, then we feel it is relatively safe to conclude that the species is basically either two- or four-notched. Basing one's conclusions on these sternal criteria (rather than on Types) in small series also avoids most of the errors possible with incompletely ossified specimens, particularly in confusing Type 2 with 3 and Type 5 with 6. As an example, if only single specimens of Species A and Species B were available, and one had a Type 2 sternum and the other a Type 3, then these would not be considered significantly different. If, on the other hand, Species C were found to have a Type 3 sternum and Species D a Type 6, then this could be considered important as the separation between the two- and four-notched sterna has been shown to be quite consistent.

The present study has also indicated that certain families or groups of genera have general types of sternal characters which may be useful in taxonomic decisions. The woodcreepers (*Dendrocolaptidae*) show a tendency toward Type 2 sterna, and they also possess a striking sternal diversity which is interesting in view of the rather strong ecological and behavioral homogeneity of the family. In contrast, the ovenbirds (*Furnariidae*) show considerable homogeneity in the sternum, but a broad range of ecological and behavioral diversity. Certain sternally aberrant ovenbird genera (*Cinclodes*, *Xenops*, etc.) may warrant additional anatomical study. The majority of the antbirds (*Formicariidae*) have two-notched sterna, but certain genera possess four-notched sterna (*Pittasoma*, *Grallaricula*, and *Grallaria*). It will be important to study further this subdivision of the family, and also to investigate *Grallaria* in which the presence of both two- and four-notched sterna strongly suggests that the genus as presently defined is a composite. The Conopophagidae, as shown elsewhere (Ames, P. L., M.A. Heimerdinger, and S. L. Warter, unpublished. The anatomy and systematic position of the antpipits *Conopophaga* and *Corythopis*.), are an artificial family; we advocate returning the gnateaters (*Conopophaga*: four-notched) to the Formicariidae, and including the antpipits (*Corythopis*: two-notched) in the Tyrannidae. The tapaculos (*Rhinocryptidae*) are characterized by having a four-notched sternum, but contrary to previous belief, the four-notched sternum is not unique to the rhinocryptids and *Conopophaga*.

The New World Tyrannoidea (Cotingidae, Pipridae, Tyrannidae, Oxyruncidae, and Phytotomidae) and the Old World suboscines, with the exception of *Menura*, all show a consistent two-notched sternum, with only limited variation away from the Type 3 configuration. The sternum of *Menura* is unique among all other passerines studied.

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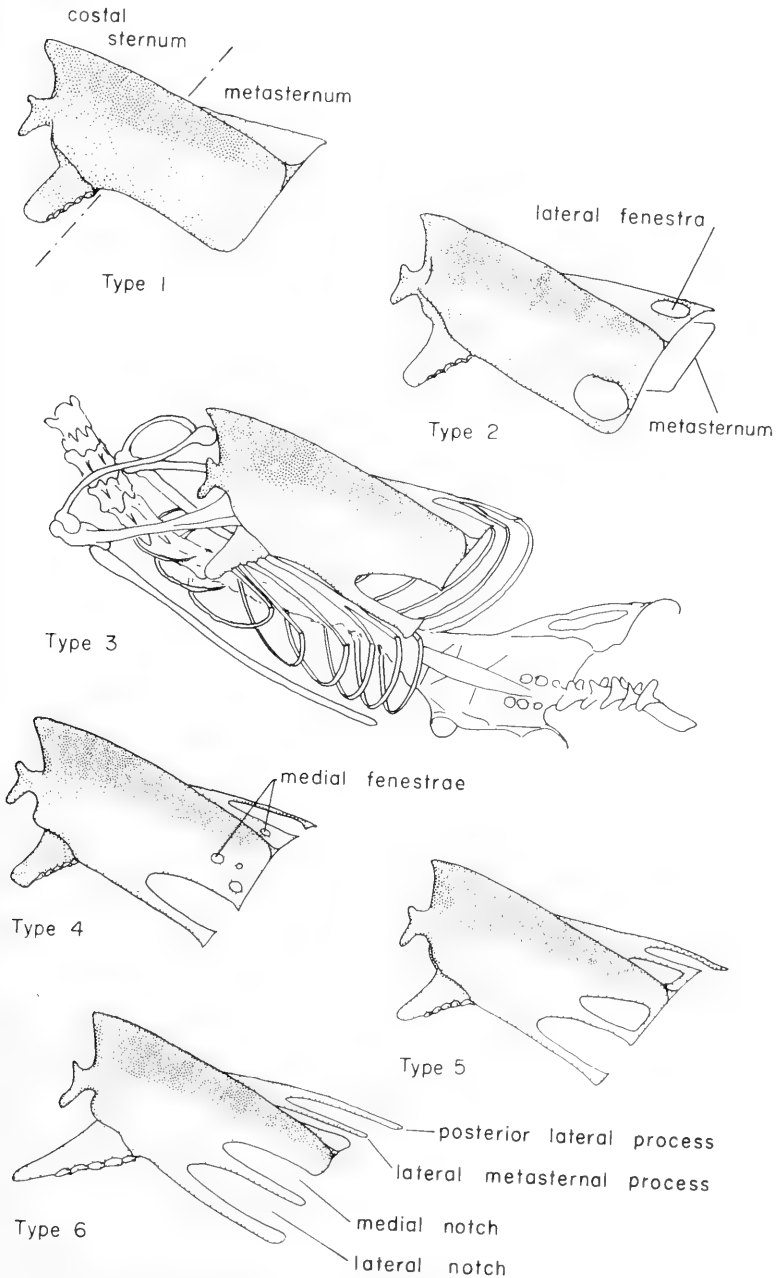


Fig. 1. Passerine sternal types. Generalized representations, not drawn from specific specimens. Type 3 shown in place on the trunk skeleton.

TABLE I
Distribution of sternal types in the suboscine passerines.

Species	Type 2	Type 2-3	Type 3	Sternal Notch Types						
				Type 3-4	Type 4	Type 4-5	Type 5	Type 5-6	Type 6	
Family Eurylaimidae: 8 specimens, 4 genera.										
<i>Smithornis</i>										
<i>capensis</i>			X							
<i>sharpei</i>			XXX							
<i>Cymbirhynchus</i>										
<i>macrorhynchus</i>			XX							
<i>Eurylaimus</i>										
<i>javanicus</i>			X							
<i>Psarismus</i>										
<i>dalhousiae</i>			X							
Family Dendrocolaptidae: 173 specimens, 9 genera.										
<i>Dendrocincla</i>										
<i>fuliginosa</i>			XXX							
<i>anabatina</i>			XXXX							
<i>homochroa</i>			X						X	

Species	Sternal Notch Types					
	Type 2	Type 2-3	Type 3	Type 3-4	Type 4-5	Type 5-6
<i>Deconychura longicauda</i>			xxx			
<i>Sittasomus griseicapillus</i>			xxxxxxxxxxxxxxxxxxx xxx	x		
<i>Glyphorhynchus spirurus</i>			xxxxxxxxxxx			
<i>Xiphocolaptes promeropyrhynchus</i> ¹ <i>major</i>	xx		xx x			
<i>sp.</i>	x	x	xx			
<i>Dendrocolaptes certhia</i>	x ²	x ²	xxx xxxx	xxx	x	
<i>picumnus platyrostris</i>			x			
<i>Xiphorhynchus pictus</i>			xxx x		x	
<i>obsoletus spixii</i>			x			
<i>pardalotus guttatus</i>	x		xx			
<i>flavigaster lachrymosus</i>	xxxxx xxx	x xx	xxx xxxxxxxxxxxxxxxxxxx	xx xx	xx	
<i>erythropygius triangularis</i>	x	x ²	xxxxx xxxxxx	x		

Species	Sternal Notch Types								
	Type 2	Type 2-3	Type 3	Type 3-4	Type 4	Type 4-5	Type 5	Type 5-6	Type 6
<i>Ochetorhynchus</i>									
<i>ruficaudus</i>		xx							
<i>certhioides</i>							x		
<i>Eremobius</i>									
<i>phoenicurus</i>		x							
<i>Cinclodes</i>									
<i>antarcticus</i>		xx							
<i>patagonicus</i>		x					xx		
<i>fuscus</i>		xxx					xx		x
<i>atacamensis</i>						x			
<i>taczanowskii</i>						x			
<i>nigrofumosus</i>		x							
<i>Furnarius</i>									
<i>rufus</i>			xxxxxxxxxxxxxx						
<i>leucopus</i>			xx						
<i>Sylvioorthorhynchus</i>									
<i>desmursii</i>		x							
<i>Aphrastura</i>									
<i>spinicauda</i>			xxx						xx
<i>Phleocryptes</i>									
<i>melanops</i>		x							x

TABLE 1 (cont'd)
Distribution of sternal types in the suboscine passerines.

Species	Type 2	Type 2-3	Type 3	Sternal Notch Types				
				Type 3-4	Type 4	Type 4-5	Type 5-6	Type 6
<i>Leptasthenura</i>								
<i>andicola</i>			x					
<i>striata</i>			x					
<i>aegithaloides</i>			xxxx					
<i>Schizocaca</i>								
<i>fuliginosa</i>			x					
<i>Schoeniophylax</i>								
<i>phryganophila</i>			xx					
<i>Synallaxis</i>								
<i>frontalis</i>			x					
<i>subpudica</i>			x					
<i>albescens</i>			xxxxxxx					
<i>brachyura</i>			xxxxxxx					
<i>albigularis</i>			x					
<i>guyanensis</i>			xxx					
<i>rutilans</i>			x					
<i>erythrothorax</i>			xxxxxxxxxxxx				x	
<i>Certhiaxis</i>								
<i>cinnamomea</i>			xx					
<i>Cranioleuca</i>								
<i>pyrrhophia</i>			xxx					
<i>erythrops</i>			xx					

Species	Sternal Notch Types								
	Type 2	Type 2-3	Type 3	Type 3-4	Type 4	Type 4-5	Type 5	Type 5-6	Type 6
<i>Asthenes</i>									
<i>pyrrholeuca</i>			xx						
<i>dorbignyi</i>			x						
<i>baeri</i>			xx						
<i>humicola</i>			x						
<i>modesta</i>			xx						
<i>humilis</i>			x						
<i>hudsoni</i>			x						
<i>flammulata</i>			x						
<i>Phacellodomus</i>									
<i>rufifrons</i>			x						
<i>striaticollis</i>			xx						
<i>Coryphistera</i>									
<i>alaudina</i>			xxx						
<i>Anumbius</i>									
<i>annumbi</i>			xx						
<i>Margarornis</i>									
<i>squamiger</i>			xxxx						
<i>rubiginosus</i>			xxx				x		
<i>Premnoplex</i>									
<i>brunnescens</i>			xx				x		
<i>Pseudocolaptes</i>									
<i>boissonneaui</i>			xxx						

Species	Sternal Notch Types								
	Type 2	Type 2-3	Type 3	Type 3-4	Type 4	Type 4-5	Type 5	Type 5-6	Type 6
<i>Hylocryptus rectirostris</i>		xx							
<i>Xenops rutilans minutus</i>		x xxxxxx					x		
<i>Pygarrhichas albogularis</i>				xx			x		
<i>Sclerurus rufigularis guatemalensis</i>							x	xx	
<i>Lochmias nematura</i>							x		
Family Formicariidae: 194 specimens, 32 genera.									
<i>Cymbilaimus lineatus</i>		xxxx							
<i>Hypoedaleus guttatus</i>		x							
<i>Batara cinerea</i>		x							
<i>Mackenziaena severa</i>		x							

TABLE 1 (cont'd)
Distribution of sternal types in the suboscine passerines.

Species	Type 2	Type 2-3	Type 3	Sternal Notch Types						
				Type 3-4	Type 4	Type 4-5	Type 5	Type 5-6	Type 6	
<i>Taraba major</i> sp.			xxxx	x						
<i>Sakesphorus canadensis</i>			xxxxxxx	x	x					
<i>Thamnophilus doliatus</i>			xxxxxxxxxxxxxxxxx xxx		x					
<i>multistriatus</i>			x							
<i>bridgesi</i>			xx		x					
<i>unicolor</i>			x							
<i>punctatus</i>			xxxxxxxxxxxxxxxxx							
<i>caerulescens</i>			xxx							
<i>Dysithamnus mentalis</i>	x		xxxxxxxxxxxxxxxxx	x						
<i>straticiceps</i>			xxx							
<i>puncticeps</i>			x							
<i>Thamnomanes caesius</i>			xx							

Species	Sternal Notch Types								
	Type 2	Type 2-3	Type 3	Type 3-4	Type 4	Type 4-5	Type 5	Type 5-6	Type 6
<i>Myrmotherula</i>									
<i>surinamensis</i>			xxx						
<i>fulviventris</i>			xxxxxxx				x		
<i>axillaris</i>			xxxx						
<i>schisticolor</i>			xx				x		
<i>Herpsilochmus</i>									
<i>rufimarginatus</i>			x						
<i>Microorhopias</i>									
<i>quixensis</i>			xxxxxxx						
<i>Formicivora</i>									
<i>grisea</i>			xxxx						
<i>rufa</i>									x
<i>Drymophila</i>									
<i>caudata</i>			x						
<i>Cercomacra</i>									
<i>tyrannina</i>			xxxxxxxxx						
<i>nigricans</i>			x						
<i>Myrmoborus</i>									
<i>leucoplrys</i>			x						
<i>Hypocnemis</i>									
<i>cantator</i>			xxxx						
<i>Hypocnemoides</i>									
<i>melanopogon</i>			x						

TABLE 1 (cont'd)
 Distribution of sternal types in the suboscine passerines.

Species	Type 2	Type 2-3	Type 3	Sternal Notch Types						
				Type 3-4	Type 4	Type 4-5	Type 5	Type 5-6	Type 6	
<i>Gymnocichla nudiceps</i>			xxxx							
<i>Scelateria naevia</i>			xx							
<i>Pernostola rufifrons</i>			xx							
<i>Myrmeciza exsil ferruginea</i>			xxxx xx			xx				
<i>Myrmophylax atrothorax</i>			xx							
<i>Formicarius analis</i>			xxxxxxxxxxxxx				x			
<i>Chamaeza campanisona</i>			xxxxx							
<i>Pithys albifrons</i>			x							

TABLE I (cont'd)
Distribution of sternal types in the suboscine passerines.

Species	Type 2	Type 2-3	Type 3	Sternal Notch Types						
				Type 3-4	Type 4	Type 4-5	Type 5	Type 5-6	Type 6	
<i>Laniocera hypopyrrha</i>			x							
<i>Rhytipterna holerythra</i>			xx							
<i>Lipaugus subalaris uniuifus</i>		x								
<i>Pachyramphus polychopterus major</i>			xx							
<i>Platyparis aglaiae</i>			x							
<i>Tityra semifasciata inquisitor</i>			xxxx							
<i>Querula purpurata</i>			xxxx							
<i>Cephalopterus ornatus</i>			x							

Species	Sternal Notch Types								
	Type 2	Type 2-3	Type 3	Type 3-4	Type 4	Type 4-5	Type 5	Type 5-6	Type 6
<i>Muscivora forficata</i>			XXXXX						x
<i>Tyrannus tyrannus</i>	xx		XXXXXXXXXXXXXXXXXXXX XXXXXXXXXXXXXXXXXXXX XXXXXXXXXXXXXXXXXXXX XXXXXXXXXXXXXXXXXXXX XX						XX
<i>vociferans</i>			XXXX						
<i>verticalis</i>			XXXXXXXXXXXXX						
<i>melancholicus</i>			XXXXXXXXXXXXX						
<i>dominicensis</i>			XXXXXXXXXXXXX						
<i>Empidonomus varius</i>			x						
<i>Myiodynastes luteiventris</i>			xxx						
<i>maculatus</i>			x						
<i>Megarynchus pitangua</i>		x	xxxx						
<i>Myiozetetes similis</i>			xxxxx						
<i>granadensis</i>			xxx						
<i>Pitangus sulphuratus</i>			xxxxxxx						

TABLE 1 (cont'd)
Distribution of sternal types in the suboscine passerines.

Species	Sternal Notch Types					
	Type 2	Type 2-3	Type 3	Type 3-4	Type 4-5	Type 5-6
<i>Myiarchus</i>						
<i>crinitus</i>			xxxxxxxxxxx		x	
<i>cinerascens</i>			xxxxxxxxxxx			
<i>tyrannulus</i>	xx		x			
<i>ferox</i>			xx			
<i>tuberculifer</i>			x			
			x			
<i>Nuttallornis</i>						
<i>borealis</i> [= <i>mesoleuctus</i>]			xxxx		x	
<i>Empidonax</i>						
<i>flaviventris</i>			x			
<i>virescens</i>			x			
<i>trailli</i>			x			
<i>minimus</i>			x			
<i>wrightii</i>			x			
<i>Mitrephanes</i>						
<i>phacocercus</i>						xx
<i>Myiobites</i>						
<i>barbatus</i>	x					
<i>sulphuriceps</i>	x					

Species	Sternal Notch Types								
	Type 2	Type 2-3	Type 3	Type 3-4	Type 4	Type 4-5	Type 5	Type 5-6	Type 6
<i>Myiophobus fasciatus</i>			x						
<i>Onychorhynchus coronatus</i>			xx						
<i>Platyrinchus mystaceus</i>			x						
<i>cancrominus</i>			x						
<i>Tolmomyias sulphurescens</i>			xx						
<i>Rhynchochocylus brevirostris</i>			x						
<i>Todirostrum cinereum</i>			x						x
<i>maculatum</i>			x						
<i>Oncostoma cinereigulare</i>			x						
<i>Lophotriccus pileatus</i>			x						
<i>Capsiempis flaveola</i>									x
<i>Mecocerculus leucophrys</i>			x						

TABLE 1 (cont'd)
Distribution of sternal types in the suboscine passerines.

Species	Sternal Notch Types								
	Type 2	Type 2-3	Type 3	Type 3-4	Type 4	Type 4-5	Type 5	Type 5-6	Type 6
<i>Elaenia</i>									
<i>flavogaster</i>			xxxxxx						
<i>albiceps</i>			x						
<i>gaimardii</i>			x						
<i>viridicata</i>			xxxx						
<i>Phaeomyias</i>									
<i>murina</i>			x						
<i>Camptostoma</i>									
<i>obsoletum</i>			xxxx						
<i>Tyranniscus</i>									
<i>vilissimus</i>			x						
<i>acer</i>			x						
<i>Pipromorpha</i>									
<i>oleaginea</i>			xx						
Family Oxyruncidae:									
1 specimen, 1 genus.									
<i>Oxyruncus</i>									
<i>cristatus</i>			x						

Species	Sternal Notch Types					
	Type 2	Type 3	Type 3-4	Type 4	Type 4-5	Type 5-6
Family Phytotomidae: 6 specimens, 1 genus.						
<i>Phytotoma</i>						
<i>rara</i>		XXXX				
<i>rutila</i>		XX				
Family Pittidae: 11 specimens, 1 genus.						
<i>Pitta</i>						
<i>brachyura</i>		XXX				
<i>baudi</i>		X				
<i>erythrogaster</i>		X				
<i>guajana</i>		XX				
<i>moluccensis</i>					X	
<i>reichenowi</i>		X				
<i>sordida</i>		X				
<i>versicolor</i>		X				
Family Philepittidae: 1 specimen, 1 genus.						
<i>Philepitta</i>						
<i>castanea</i>						X

TABLE I (cont'd)
Distribution of sternal types in the suboscine passerines.

Species	Type 2	Type 2-3	Type 3	Sternal Notch Types						
				Type 3-4	Type 4	Type 4-5	Type 5	Type 5-6	Type 6	
Family Acanthisittidae: 2 specimens, 2 genera.										
<i>Acanthisitta</i> <i>chloris</i>										x
<i>Xenicus</i> <i>longipes</i>										x
Family Menuridae: 4 specimens, 1 genus.										
<i>Menura</i> <i>superba</i>										xx ⁴

¹Additional specimen, Type 1; see text, p. 9.

²With a small fenestra on one side.

³See text, p. 11.

⁴One specimen, Type 1; the other, Type 1-4; see text, p. 12.

