

## TAXONOMIC COMMENTS ON THE EURYLAIMIDAE

STORRS L. OLSON

Received on 10 January 1971

### INTRODUCTION

The broadbills (Eurylaimidae) are a group of eight genera and 14 species of suboscine passerines confined to the Old World tropics. Newton (1896) credits Baron de Selys-Longchamps with first recognising the eurylaimids as a distinct family in 1842. However, the passerine affinities of the group were not immediately appreciated and in early works it was variously placed near the Caprimulgidae, in or near the Coraciidae, in the Todidae, Muscicapidae, Pipridae or Cotingidae (cf. Sclater 1872). Nitzsch (1867), on the basis of their pterylography, considered the eurylaimids as passerines and put them near the Cotingidae. Sclater (1872), Garrod (1877, 1878) and Forbes (1880a) further established the passerine characteristics of the eurylaimids. To Pycraft (1905) they were osteologically passerine and my own observations confirm that the skeleton in this group agrees well with the basic passerine conformation. In all modern classifications the Eurylaimidae are included in the Passeriformes and there is little doubt that this is their correct ordinal allocation. But their classification within the order is another question altogether.

### THE SUPPOSED SUBORDINAL STATUS OF THE EURYLAIMIDAE

The Swedish ornithologist Sundevall (1889) was the first to use the disposition of the deep plantar tendons in birds as a taxonomic character. He found in all the passerines he examined that the tendons of *M. flexor hallucis longus* and *M. flexor digitorum longus* were separate for their entire length with no intercommunication via a vinculum as he found in most of the lower orders. Garrod (1877) noted that the broadbills differed from other Passeriformes when he found a vinculum between the deep plantar tendons of three species, and he stated (p. 449) that "The order Passeres falls, therefore, into two sections to start with:—those with the hallux not free, the Eurylaemidae; and those with the hallux independently movable. This latter suborder may again be divided up . . ." Thus, the first reference to subordinal status for the Eurylaimidae was by inference and no formal names were proposed. This task was left to Garrod's successor, Forbes (1880b), who used the terms *Desmodactyli* for a suborder containing the Eurylaimidae, and *Eleutherodactyli* for the remaining passerines. Stejneger (1885) put the broadbills in a superfamily *Eurylaimoideae* equivalent to Forbes' *Desmodactyli*. Seebohm (1890) used the term *Eurylaemi* (amended later to *Eurylaimi*) for the suborder. This latter terminology and separate subordinal rank for the Eurylaimidae has been adopted by subsequent authors and is the one used in such modern systems of classification as Mayr & Amadon (1951), Wetmore (1960), Sibley (1970), and Ames (1971).

Ridgway (1901), in a key to the suborders of passerines, used four characters to distinguish the *Desmodactyli* (=Eurylaimi) from the remaining passerine groups. These supposed distinctions were echoed recently by Brodkorb (1968) and most were relied heavily upon by Sibley (1970). I will treat each separately here and make comparisons with the Cotingidae.

### DEEP PLANTAR TENDONS

I have already made reference to Garrod's original disclosure of a vinculum between the deep plantar tendons in the Eurylaimidae; specifically in *Cymbirhynchus macrorhynchus*, *Eurylaimus ochromelas*, and *Calypdomena viridis*. It was not until 1914 that Bates

demonstrated that the African genus *Smithornis*, formerly placed in the Muscicapidae, possesses a deep plantar vinculum, thereby giving the first indication that eurylaimids were present outside of Asia. Lowe (1924) confirmed Bates' observations and later (1931) showed that the excessively rare *Pseudocalyptomena*, of very restricted distribution in Africa, was also a broadbill and had the plantar vinculum present.

I dissected specimens of *Eurylaimus javanicus*, *E. steerei*, *Serilophus lunatus*, *Psarisomus dalhousiae* and *Calyptomena whiteheadi*, and found a vinculum between the deep plantar tendons in all of them. Bates (1914), in his observations on *Smithornis*, remarked that the vinculum was weak in all his specimens and may have been absent in one of them. I examined one specimen each of *S. capensis* and *S. rufolateralis* and found a narrow, weak vinculum in both. The tendon of *M. flexor hallucis longus* was not as well developed in this genus as in the other genera of broadbills.

I found no vinculum present in the following species of Cotingidae: *Pachyramphus cinnamomeus*, *Querula purpurata*, *Cephalopterus ornatus*, *Gymnoderus foetidus*, *Procnias nudicollis* (3 specimens) and *P. tricarunculata*. Berger (George & Berger 1966) also found no vinculum in *P. nudicollis*. Garrod (1877 : 447) reported the lack of a vinculum in *Rupicola*, although he added the comment that this genus was "thought by some to be intimately related to the Eurylaemidae." The above is a small sample of the large and exceedingly heterogeneous conglomeration of species placed in the Cotingidae and does not preclude the possibility that some species may yet be discovered to have the deep plantar tendons united. Anatomical specimens of some of the more peculiar forms (e.g. *Phoenicircus*) should be examined for this character as they become available.

What is the taxonomic significance of the deep plantar tendons in this case? Pycraft (1905) disparaged the usefulness of this character in the systematics of the Eurylaimidae. Beddard (1898) calls to our attention that the plantar vinculum is occasionally lacking in *Calyptomena viridis*. As we have seen, this vinculum is weak and possibly lacking at times in *Smithornis*. Its presence in any instance, however, may attest to the primitiveness of the broadbills. Because of its occasional absence and because, as I will show below, it is the *only* distinctive character of the family not known to be shared with some other suboscine group, I do not believe that the presence of a plantar vinculum merits retention of subordinal rank for the Eurylaimidae.

#### SPINA EXTERNA OF THE STERNUM

Sclater (1872) figured the sternum of *Cymbirhynchus macrorhynchus* (under the name *Eurylaemus javanicus*; cf. Forbes 1880a : 381) and noted that the spina externa (=manubrium) was a simple rod and not forked as in other passerines. The same condition was found in *Psarisomus* (Garrod 1878). Forbes (1880a) reported an unforked spina externa in *Eurylaimus ochromelas* and *Cymbirhynchus*, as did Lowe (1931) for *Pseudocalyptomena*. My own observations showed this condition to obtain in *Serilophus lunatus*, *Calyptomena viridis*, *C. whiteheadi*, and *Corydon sumatranus*. However, in *Smithornis* the spina externa is well forked as has been previously reported (Bates 1914, Lowe 1924) and as I can confirm from examination of skeletons of *S. capensis* and *S. sharpei*. Lowe (1924) described a slight tendency towards forking in certain specimens of *Cymbirhynchus*. Despite these reports, subsequent treatments have considered all the broadbills as possessing a simple spina externa (Mayr & Amadon 1951, Wetmore 1960, Brodkorb 1968, Sibley 1970, Ames 1971).

To check further on this character I looked at skeletons of other passerines, especially the cotingas. In the following species of Cotingidae the spina externa was typically forked (nomenclature after Meyer de Schauensee 1966; number of specimens follows the name): *Cotinga ridgwayi*, 1; *C. cayana*, 3; *Xipholena punicea*, 1; *Ampelion rubrocristatus*, 2; *Pipreola riefferii*, 2; *P. aureopectus*, 1; *P. formosa*, 1; *Attila spadiceus*, 1; *A. bolivianus*, 1; *Casiornis rufa*, 1; *Rhytipterna simplex*, 2; *R. holerythra*, 1; *Lipaugus vociferans*, 1;

*L. unirufus*, 1; *Pachyramphus rufus*, 1; *P. homochrous*, 1; *P. niger*, 1; *Tityra cayana*, 7; *T. semifasciata*, 11; *T. inquisitor*, 8; *Querula purpurata*, 2; *Pyroderus scutatus*, 1; *Cephalopterus ornatus*, 4; *Perissocephalus tricolor*, 1; *Gymmoderus foetidus*, 2; *Rupicola rupicola*, 9; *R. peruviana*, 7. (Of the closely related Pipridae, all the genera I examined had a forked spina externa. These were: *Pipra*, *Antilophia*, *Chiroxiphia*, *Corapipo*, *Manacus*, *Machaeropterus*, *Neopelma*, *Tyranneutes*, *Sapayoa*.)

The four species of cotingas in the genus *Procnias* present a different case. In the two specimens of *P. tricarunculata* that I examined the spina externa was well forked as in the species above (Fig. 1 (a) and (c)), but in one specimen of *P. averano* the spina was only slightly notched (Fig. 1 (d)) and two specimens of *P. alba* and 14 of *P. nudicollis* varied from very slightly notched to totally simple (Fig. 1 (b) and (e)). So within one genus of cotingas is found the same variation in the spina externa as has been used to define suborders of passerines. The spina externa is also unforked in the Philepittidae (Ames 1971). The forked versus simple spina externa is variable in other orders as well. In the Piciformes either conformation may be found in the Picidae, Capitonidae, Bucconidae and Galbulidae. The character is also variable in the Coraciiformes and Trogoniformes.

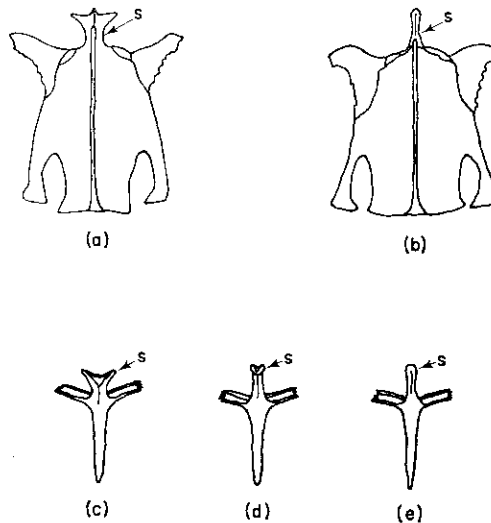


FIGURE 1. Upper: Ventral view of sternum; (a) *Procnias tricarunculata* showing forked spina externa; (b) *P. nudicollis* with simple spina externa. Lower: Anterior view of spina externa and carina of sternum; (c) *P. tricarunculata* (forked); (d) *P. averano* (slightly notched); (e) *P. nudicollis* (simple). s = spina externa.

Lowe (1924) regarded the taxonomic value of the spina externa as dubious. Since the character is variable within the Eurylaimidae and intragenerically variable in *Procnias*, it can hardly be of value in maintaining a separate suborder for the eurylaimids. At least in passerines, the unforked spina externa probably represents a primitive condition. If so, the fact that this character is shared by both broadbills and cotingas may be interpreted as demonstrating the relatively primitive nature of these families and supports the possibility that they may be related.

#### CERVICAL VERTEBRAE

The cervical vertebrae, by definition, are those vertebrae anterior to the first vertebrae attached by ribs to the sternum. As far as known, all passerines have 14 cervical vertebrae except the eurylaimids, all of which have been thought to have 15. Lowe (1924) in his

discussion of the anatomy of *Smithornis* does not mention the number of cervicals, although he notes (1931) that *Pseudocalyptomena* has 15. In two specimens of *Smithornis capensis* and two of *S. sharpei* I found that there were only 14 cervical vertebrae, the typical passerine condition. Actually this difference in the number of cervicals does not represent a decrease in the total number of vertebrae but rather the acquisition of a single pair of sternal ribs, thus converting what was the posteriormost cervical vertebrae into the anteriormost thoracic vertebra. The number of cervical vertebrae cannot be used to distinguish the Eurylaimidae from other passerines, even on the familial level, much less subordinally. That most species have 15 again reflects the primitiveness of the eurylaimids.

#### HALLUX

Ridgway (1901 : 14), in his key to the suborders of Passeriformes, gives as a distinguishing character of the Desmodactyli (=Eurylaimi), "hallux weak" as opposed to "hallux strongest toe" in the Eleutherodactyli. This is repeated by Brodkorb (1968) in his diagnosis of the subgroupings of passerines. The basis for making this distinction is not at all clear to me and it would seem to be a very subjective one at best. I have examined specimens of all the species of broadbills and cannot detect any consistent difference between their halluces and those, for instance, of most cotingas. "As regards position, structure and size, the hallux is the most variable of all the toes, and its taxonomic value is very limited" (Newton 1896 : 404). It is not a sound basis for attributing subordinal rank to any group even if a difference were detectable.

#### QUADRATO-JUGAL ARTICULATION

The following statement by Lowe (1931 : 460) implies that the quadrato-jugal articulation of the Eurylaimidae is distinctive: "In the Eurylaemids the quadrato-jugal makes junction with the outwardly projecting spur at the lower end of the quadrate by means of what is nearly a symphysis; whereas in such forms as the crows, starlings, etc. there is a cup-and-ball joint." No mention is made of other suboscine forms, however. In a quick survey of skeletons, I found the "eurylaimid-type" articulation in the Cotingidae, Pipridae, Tyrannidae, Phytotomidae, Rhinocryptidae, Furnariidae, Dendrocolaptidae, Formicariidae and Pittidae (I was not able to examine skeletons of the Acanthisittidae or Philepittidae), and a ball-and-socket articulation in the Menuridae and all oscine families examined. This is an interesting character, worthy of further study, and may provide a demarcation between oscines and suboscines; but it cannot be used to distinguish the broadbills from other suboscines.

To recapitulate, all the characteristics that have been used to isolate the Eurylaimidae from the remaining suboscine passerines in a suborder of their own have been shown to be variable intrafamiliarily or shared with other families. I therefore recommend that the subordinal designation "Eurylaimi" be abandoned and that the Eurylaimidae be included in the suborder Tyranni.

#### THE RELATIONSHIPS OF THE EURYLAIMIDAE

Sclater (1872 : 179) long ago stated: "I believe, however, that Mr Wallace [1856] will probably be found to be correct in considering the Eurylaemidae the paleogean representatives of the neotropical Cotingidae." Stejneger (1885) was of the same persuasion. Sundevall (1889 : 130) felt that the Eurylaimidae were "scarcely to be distinguished from the American ones [of his Rupicolinae, which included *Laniisoma*, *Phoenicircus*, and *Rupicola*] in any general way." Ridgway (1901 : 15), in speaking of the eurylaimids, said that they were a small group "confined to the Indo-Malayan region [the African species were not known to be eurylaimids at the time], where it takes the

place of the rather closely related haploophone Clamatores (especially the family Cotingidae) of the Neotropical region." Shortly after this, Pycraft (1905) published his paper on the osteology of the Eurylaimidae wherein he was much impressed with the resemblance of the skeletons of eurylaimids and cotingas. He repeatedly emphasised the similarity of the skulls of *Calypomena* and "*Chasmorhynchus*" (= *Procnias*)\*, especially of the lacrimals, premaxillaries, and maxillopalatine processes. These shared skeletal characters and resemblances of the musculature, syrinx, and pterylography led him so far as to say that "It is quite possible that further investigation will show that the Eurylaimidae are entitled to rank no higher than a subfamily of the Cotingidae" (p. 55). Later (1907), he recognised four suborders of passerines and included the Cotingidae, Pipridae, and Philepittidae along with the Eurylaimidae in his suborder Eurylaimi. For some reason, these opinions have been ignored or overlooked by subsequent authors who have preferred to recognise the differences that were perhaps overemphasised by Garrod and Forbes.

There are other points of similarity between the broadbills and cotingas. The great width of the bill that gives rise to the vernacular name of the Eurylaimidae (and which reaches the extreme for passerines in *Corydon*) is not found throughout the family. The three species of *Calypomena* possess bills of normal passerine proportions. In Fig. 2 the skull of *C. viridis* is contrasted with *Procnias nudicollis* and it can be seen that not only is there little difference in bill proportions, but also the overall likeness of the skulls is apparent, as Pycraft noted. The similarity of the tuft of feathers that cloaks the bill of *Calypomena* to the crown of *Rupicola*, which also envelops the bill, while perhaps not significant, is certainly suggestive.



FIGURE 2. Dorsal view of skull: (a) *Procnias nudicollis*; (b) *Calypomena viridis*.

Broadbills are uniformly described as building large, bulky, pendant nests with an opening on the side. While the nesting habits of cotingas are exceedingly diverse (cf. Skutch 1969) the nests built by *Pachyramphus* and *Platypsaris* are strikingly like those of eurylaimids. Little seems to be known about the ethology of broadbills but Bates (1914) has described behaviour of *Smithornis* and Chapin (1953) has described display behaviour in *Smithornis rufolateralis*. Males of this genus perform a darting circular flight while emitting a croaking noise that is believed to be made by the wings. This whole procedure is reminiscent of certain of the Pipridae, a family intimately related to the cotingas, and some species of which perform similar displays using the wings most effectively as organs of sound production. Both the Eurylaimidae and Cotingidae contain strikingly coloured species clothed in various shades of green, violet,

\*I should point out here that Sibley (1970:36) is entirely in error in making the statement that Lucas "recommended the establishment of a separate family, the Procnidae, for the bellbirds based upon palatal characters." Lucas' (1895) paper concerns the Swallow-tanager *Tersina viridis* and no mention is made of bellbirds. *Procnias* and Procnidae were synonyms for *Tersina* and Tersinidae, respectively, that were in use in Lucas' time.

red and yellow. Both families consist of insectivorous and frugivorous birds of the treetops and do not seem to have evolved terrestrial or creeping forms. Certain members of both families have concealed white patches in the shoulder area that are revealed at times in displays, e.g. *Smithornis* (Bates 1914) and *Platypsaris* (Skutch 1969).

Sibley (1970) has presented a detailed review of the taxonomy of the Passeriformes, including his new information derived from egg-white protein analyses. Of the Eurylaimidae he says (p. 33), "The broadbill [egg-white protein electrophoretic] patterns resemble those of the cotingas (*Platypsaris*) and tyrannids but not any more closely than those of several other groups." And he continues—"... because of ample anatomical evidence to the contrary the resemblances to the New World groups cannot be considered important". However, I think that I have shown that such ample contrary evidence is not available and therefore the egg-white protein data can at least be regarded as not contradicting a relationship between the eurylaimids and the New World suboscines, if not actually supporting such a view. I agree with Sibley that the broadbills are not closely related to the Pittidae, Mackworth-Praed (1964) and others to the contrary. Sibley gives evidence that neither the Pittidae nor Acanthisittidae are closely related to the other suboscine families and suggests an alternative that they may be derivatives of oscines. But as I have mentioned, the quadrato-jugal articulation, at least in *Pitta*, is typically suboscine.

From their present distribution the eurylaimids evidently represent a scattered remnant of rather specialised species from an ancient passerine lineage of once wider distribution. There are eight genera, five of which are monotypic. None of these genera seems to me to be particularly closely related to any of the others. In Africa, where there are only two genera, even these two are not at all closely related. *Pseudocalyptomena graueri* is found only in a small area of forest in the Congo and Uganda (Friedmann 1970). *Calyptomena hosei* and *C. whiteheadi* are restricted to a few mountaintops in Borneo. *Eurylaimus steerei*, found only in the Philippines, was once put in a separate genus (*Sarcophanops*) and is quite distinct from the other two species of *Eurylaimus*. Ballman (1969) reports a fossil eurylaimid of undetermined relationships from Lower Miocene deposits in Bavaria. All this suggests that the family is a retreating one. Modern eurylaimids probably represent the oldest remaining passerine stock. Their ancestors very likely arose in the Old World tropics early in the Tertiary and distributed themselves widely throughout the world in suitable habitat. With the rise of the more advanced oscines (also probably in the Old World tropics) at some later point in the Tertiary, this ancestral suboscine stock would have been largely replaced everywhere except in South America, which was isolated through the Tertiary until the end of the Pliocene. This isolation allowed for the persistence and radiation of the suboscines that characterise the South American passerine fauna today, in comparative freedom from the oscine onslaught taking place in the rest of the world. Only a few specialised remnants of this original primitive passerine stock survived the takeover in the Old World, these being the existing Eurylaimidae. This is consistent with a general picture of animal distribution presented by Darlington (1957) wherein many vertebrate groups appear to have arisen in the Old World tropics and a number of groups became isolated and diversified in South America. (After writing the above, I find that Amadon (1957) has proposed a nearly identical theoretical history of the suboscines.)

To get an impression of how diverse the genera of eurylaimids probably are, let us imagine widespread replacement and extinction among the Cotingidae. Suppose we were left with only the eight genera *Phibalura*, *Querula*, *Conioptilon*, *Iodopleura*, *Cephalopterus*, *Procnias*, *Phoenicircus*, and *Xipholena*; an exceedingly heterogeneous group of species. It is quite conceivable that taxonomists might have separated such an assemblage into a number of subfamilies or even families (as some do now for *Rupicola*). Such a vast extinction probably took place among the Eurylaimidae, leaving a hodgepodge of more or

TABLE 1  
Recent classifications of the subsocial passerines with a suggested rearrangement

Wetmore 1960	Mayr & Amadon 1951	Suggested rearrangement
Order Passeriformes	Order Passeres	Order Passeriformes
Suborder Eurylaimi	Suborder Eurylaimi	Suborder Tyranni
Family Eurylaimidae	Family Eurylaimidae	Superfamily Tyrannoidea
Suborder Tyranni	Suborder Tyranni	Family Eurylaimidae
Superfamily Furnarioidea	Superfamily Furnarioidea	Philepittidae
Family Dendrocolaptidae	Family Rhinocryptidae	Cotingidae
Furnariidae	Conopophagidae	Pipridae
Formicariidae	Fornicariidae	Phytotomidae
Conopophagidae	Furnariidae	Tyrannidae
Rhinocryptidae	Subfamily Furnariinae	Oxyruncidae
Superfamily Tyrannoidea	Subfamily Dendrocolaptinae	Superfamily Furnarioidea
Family Cotingidae	Superfamily Tyrannoidea	Family Formicariidae
Pipridae	Family Pittidae	Rhinocryptidae
Tyrannidae	Philepittidae	Furnariidae
Oxyruncidae	Xenicidae	Dendrocolaptidae
Phytotomidae	Tyrannidae	
Pittidae	Subfamily Tyranninae	
Acanthisittidae	Oxyruncinae	
Philepittidae	Family Pipridae	Pittidae } <i>incertae</i>
Suborder Menurae	Family Cotingidae	Acanthisittidae } <i>sedis</i>
Family Menuridae	Phytotomidae	
Suborder Passeres	Suborder Menurae	Suborder Menurae
etc.	Family Menuridae	Family Menuridae
	Atrichornithidae	Atrichornithidae
	Suborder Oscines	Suborder Oscines
	etc.	etc.

less unrelated genera. For this reason I do not think that it is useful to maintain a separate subfamily of the Eurylaimidae for *Calyptomena* (Calyptomeninae) as was done by Sclater (1888) and subsequently by Ames (1971). *Smithornis*, for instance, is at least as divergent as *Calyptomena*. It is appropriate here to bring up another point concerning *Smithornis*. This genus was listed first by Peters (1951) in his treatment of the Eurylaimidae, thereby presumably indicating it to be the most primitive of the family. What his reasoning was for this I do not know; perhaps he was influenced by the rather plain colours of *Smithornis* as compared to the rest of the broadbills, although Amadon (1957) suggests that subdued colour may be an advanced character in passerines. However, by virtue of possessing a weak plantar vinculum, a forked spina externa, and 14 cervical vertebrae, *Smithornis* certainly may be considered to be the most advanced genus in its family and therefore should be placed at the end of any listing of the Eurylaimidae.

#### THE SEQUENCE OF SUBOSCINE FAMILIES

We may now discuss some aspects of the phylogeny of the entire group of suboscines. For this purpose, I have included a list (Table 1) with two of the most widely followed systems of classification to which I have appended a suggested rearrangement. The higher categories of passerines have usually been defined on the basis of the structure of the syrinx. To previous studies we may now add the monumental work of Ames (1971) who has greatly augmented and clarified our understanding of this subject.

In the Eurylaimidae, the syrinx is very simple and unspecialised, a condition once again indicating the primitiveness of the family. But this structure is not sufficiently distinct from that of certain other suboscines, especially some of the cotingas, to differentiate the broadbills from them. For these reasons as well as those given previously, I place the Eurylaimidae at the beginning of the suborder Tyranni.

The syrinx in the Philepittidae is very similar to that of the Eurylaimidae and the family also possesses an unforked spina externa. These birds probably represent a specialised offshoot of the ancestral Old World suboscine lineage, long isolated on the ancient Madagascar land-mass. I place them therefore, after the Eurylaimidae.

The Pittidae and Acanthisittidae do not as yet present any obvious affinities to other passerine families but it does seem fairly certain that they do not belong with the distinctive and relatively homogeneous oscine group. In our present state of knowledge they are best treated as Tyranni *incertae sedis* as I have done here, meaning to imply no relationships by their terminal position.

The remaining suboscine families have been divided into two groups, usually at the superfamily level. In the Tyrannoidea the syrinx is exceedingly variable, some forms being quite primitive. In the Furnarioidea the syrinx, although more variable than in the oscines, presents elaborate and specialised structures that are shared by all the families of the group and that are found in no other passerines. For this reason and because "there are no characters to ally them particularly to the Tyranni," Ames (p. 153) elevates the Furnarioidea to the rank of suborder. What may be said of their relationships, however, is that they are *not* oscines. While it is possible that such a negative approach to classification may have drawbacks, I prefer to retain the Furnarioidea as a superfamily within the suborder Tyranni. It appears likely that this group has been derived from the more primitive suboscine types in South America and that in their specialisation of the syrinx and subdued colours they have somewhat paralleled the development of the oscines. Assuming the Furnarioidea to be more advanced, I place them after the Tyrannoidea, a position in which, strangely, they have not appeared in any recent classification although they may be found there in the lists of Stejneger (1885), Sharpe (1891) and others. Within the Furnarioidea, as within the Tyrannoidea, family limits are often difficult to discern. The relationships of the Furnariidae and Dendrocolaptidae may be more complicated than is reflected by most treatments (cf. Sibley 1970 : 33) but as currently conceived, the Dendrocolaptidae with their more specialised habits and syringes should probably be placed after the Furnariidae. I follow Ames *et al.* (1968) in relegating the two genera of the Conopophagidae to the Formicariidae and Tyrannidae.

In the Tyrannoidea, the Cotingidae contain the most primitive Neotropical forms. With the Pipridae and Phytotomidae they form a fairly close group (Sibley; Ames) followed by the diverse Tyrannidae. As has been pointed out, the family limits here are by no means always clear.

The Menurae of Australia are an anomalous group well deserving of their subordinal status. While their relationships remain uncertain, it is my present opinion that they will ultimately be found to be closer to the Oscines than the Tyranni.

#### ACKNOWLEDGMENTS

I am grateful for being given access to examine specimens in the collections of Pierce Brodtkorb, the United States National Museum, and the American Museum of Natural History. R. L. Zusi made it possible for me to perform the necessary dissections. G. E. Watson read a draft of the manuscript and an earlier preliminary draft was read by R. K. Godfrey, R. B. Short, H. M. Stevenson and R. W. Yerger.



## SUMMARY

On the basis of supposed differences in the shape of the spina externa of the sternum, the number of cervical vertebrae, the deep plantar tendons, the quadrato-jugal articulation, and the size of the hallux, the Eurylaimidae were put in a separate suborder, the Eurylaimi. All of these characters are now shown to be variable within the family or shared with other suboscine families. It is recommended that the subordinal designation "Eurylaimi" be abandoned and that the family be included in the suborder Tyranni. A number of characters point to the Cotingidae as the nearest possible extant relatives of the Eurylaimidae. The Eurylaimidae consist of a number of unrelated genera with several relict species, and probably represent the remains of an ancient, once more widespread group that became isolated and gave rise to the suboscine fauna in South America while being largely replaced by oscines in the Old World. Recognition of subfamilies within the Eurylaimidae is discouraged. *Smithornis* should be considered the most advanced of the eurylaimids. The sequence of suboscine families is discussed and a rearrangement is suggested.

## REFERENCES

- AMADON, D. 1957. Remarks on the classification of the perching birds (order Passeriformes). Proc. zool. Soc. Calcutta, Mookerjee Memorial Volume : 259-268.
- AMES, P. L. 1971. The morphology of the syrinx in passerine birds. Bull. Peabody Mus. nat. Hist. 37 : 1-194.
- AMES, P. L., HEIMERDINGER, M. A. & WARTER, S. L. 1968. The anatomy and systematic position of the antipits *Conopophaga* and *Corythopsis*. Postilla 114 : 1-32.
- BALLMAN, P. 1969. Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstätt in Bayern. Zitteliana 1 : 5-60.
- BATES, G. L. 1914. Some facts bearing on the affinities of *Smithornis*. Ibis (10) 2 : 495-502.
- BEDDARD, F. E. 1898. The structure and classification of birds. London: Longmans, Green & Co.
- BRODKORB, P. 1968. Birds. In Blair *et al.*, Vertebrates of the United States, 2nd ed. New York: McGraw-Hill.
- CHAPIN, J. 1953. The birds of the Belgian Congo. Part 3. Bull. Am. Mus. nat. Hist. 75A.
- DARLINGTON, P. J. 1957. Zoogeography: The geographical distribution of animals. New York: John Wiley & Sons.
- FORBES, W. A. 1880a. Contributions to the anatomy of passerine birds. Part II. On the syrinx and other points in the anatomy of the Eurylaimidae. Proc. zool. Soc. Lond.: 380-386.
- FORBES, W. A. 1880b. Contributions to the anatomy of passerine birds. Part III. On some points in the structure of *Philepitta* and its position amongst the passerines. Proc. zool. Soc. Lond.: 387-391.
- FRIEDMANN, H. 1970. The status and habits of Grauer's Broadbill in Uganda (Aves: Eurylaimidae). Los Angeles Co. Mus. Contr. Sci. 176 : 1-4.
- GARROD, A. H. 1877. Notes on the anatomy of passerine birds. Part II. Proc. zool. Soc. Lond.: 447-453.
- GARROD, A. H. 1878. Notes on the anatomy of passerine birds. Part IV. Proc. zool. Soc. Lond.: 143.
- GEORGE, J. C. & BERGER, A. 1966. Avian myology. New York: Academic Press.
- LOWE, P. R. 1924. On the presence of broadbills (Eurylaimidae) in Africa. Proc. zool. Soc. Lond.: 279-291.
- LOWE, P. R. 1931. On the anatomy of *Pseudocalyptomena* and the occurrence of broadbills (Eurylaimidae) in Africa. Proc. zool. Soc. Lond.: 445-461.
- LUCAS, F. A. 1895. Osteological and pterylographical characters of the Procnatiidae. Proc. U.S. nat. Mus. 18 : 505-507.
- MACKWORTH-PRAED, C. W. 1964. Broadbill. In A. L. Thompson (Ed.), New dictionary of birds. London: Nelson.
- MAYR, E. & AMADON, D. 1951. A classification of recent birds. Am. Mus. Novit. 1496 : 1-42.
- MEYER DE SCHAUENSEE, R. 1966. The species of birds of South America and their distribution. Narberth, Pennsylvania: Livingston.
- NEWTON, A. 1896. A dictionary of birds. London: Adam & Charles Black.
- NITZSCH, C. L. 1867. Nitzsch's Pterylography. Translated from the German. London: Ray Society.
- PETERS, J. L. 1951. Checklist of birds of the world, Vol. VII. Cambridge, Massachusetts: Mus. Comp. Zool.
- PYCRAFT, W. P. 1905. Contributions to the osteology of birds, Part VII. Eurylaimidae: with remarks on the systematic position of the group. Proc. zool. Soc. Lond. (2) : 30-56.
- PYCRAFT, W. P. 1907. Contributions to the osteology of birds, Part IX. Tyranni; Hirundines; Muscicapae; Lani; and Gymnorhines. Proc. zool. Soc. Lond.: 352-379.
- RIDGWAY, R. 1901. The birds of North and Middle America. Part 1. Bull. U.S. nat. Mus. 50 : 1-715.
- SCLATER, P. L. 1872. Observations on the systematic position of *Peltops*, *Eurylaimus*, and *Todus*. Ibis (3) 2 : 177-180.
- SCLATER, P. L. 1888. Catalogue of the birds in the British Museum, Vol. XIV. London.
- SEEBOHM, H. 1890. Classification of birds; an attempt to diagnose the subclasses, orders, suborders and some of the families of existing birds. London: R. H. Porter.

- SHARPE, R. B. 1891. A review of recent attempts to classify birds. Proc. Int. orn. Congr. 2 (Budapest).
- SIBLEY, C. G. 1970. A comparative study of the egg-white proteins of passerine birds. Bull. Peabody Mus. nat. Hist. 32 : 1-131.
- SKUTCH, A. F. 1969. Life histories of Central American birds III. Pacific Coast Avifauna 35.
- STEJNEGER, L. 1885. Birds. In J. S. Kingsley (Ed.), The standard natural history. Boston: Cassino & Co.
- SUNDEVALL, C. J. 1889. Methodi naturalis avium dispondendarum tentamen. English transl. of 1872 ed. by F. Nicolson. London: R. H. Porter.
- WALLACE, A. R. 1856. Attempts at a natural arrangement of birds. Ann. Mag. nat. Hist. (2) 18 : 193-216.
- WETMORE, A. 1960. A classification for the birds of the world. Smithson. misc. Collns. 139 (11): 1-37.

*Storrs L. Olson, Dept. of Pathobiology, The Johns Hopkins University, School of Hygiene and Public Health, 615 North Wolfe Street, Baltimore, Maryland 21205, U.S.A.*