MONOPHYLY OF THE PASSERIFORMES: TEST OF A PHYLOGENETIC HYPOTHESIS

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ABSTRACT.—The order Passeriformes was largely defined by 19th century anatomists on the basis of phenetic similarities. The purpose of this study was to determine whether the group is monophyletic in the strict contemporary sense. Similarities used by previous workers were reanalyzed to determine whether or not they could be shown to be derived character states corroborating the hypothesis of passeriform monophyly. Of 18 traditional taxonomic characters analyzed, none refuted the hypothesis of passeriform monophyly, 13 failed to corroborate the hypothesis, and 5 did corroborate it. These are the aegithognathous palate, the "passerine" tensor propatagialis brevis, the bundled spermatozoa with coiled head and large acrosome, the enlarged hallux, and the type VII deep plantar tendons.

To this analysis is added new information from the hind limb musculature. Previous knowledge of oscine musculature is augmented by new information from representative suboscines. The division of M. pubo-ischio-femoralis into Pars cranialis and Pars caudalis is confirmed for suboscines, distinguishing the entire order Passeriformes from nonpasserine birds. In the foot, the loss of a set of intrinsic muscles of the forward digits, previously known from oscines, is also confirmed for suboscines. These limb-muscle characters supplement the analysis of traditional characters in corroborating the hypothesis that the order Passeriformes is monophyletic.

A functional analysis of the passerine foot shows that it is a derived mechanism specialized for perching, but with a reduction in the subtlety and variety of certain other movements. *Received 9 March 1981, accepted 3 August 1981.*

IN this paper I address the question of whether or not the avian order Passeriformes is monophyletic, using the concept of monophyly in its strict contemporary sense. I would define as monophyletic a group whose characteristics support most strongly the hypothesis that it consists of all the known descendents of a single common ancestor, that is, a group all of whose members share a more recent common ancestor with each other than with any other taxa. In other words, the question is whether the order Passeriformes is a clade.

There are four reasons why this question is important in the context of my research. First, passeriform monophyly has long been a tacit assumption based on a century-old definition of the assemblage as being "natural" or monophyletic in an old and vague sense at best. It is a phenetic cluster of groups traditionally united by various "similarities" without consideration of the nature of those similarities or of the sorts of information that different kinds of similarity can or cannot provide about phylogenetic relationships. In recent years our concepts of monophyly and our methods of character analysis have been sufficiently re-

fined that it is desirable now to reconsider the nature of the largest order of living birds.

Eldredge and Cracraft (1980: 158) have noted that a recurrent theme in the history of classification has been the elimination of nonmonophyletic taxa. The fact that such apparently nonmonophyletic groups as "Pisces," "Reptilia," and "Carduelinae" have long persisted in classifications warns us not to assume that a group is monophyletic just because it has traditionally been formally classified as a taxon. In our previous studies of the appendicular muscles, my students and I have questioned the monophyly of various traditional groups and have found that such hypotheses are supported to different degrees. The family Drepanididae is hardly definable as monophyletic except by a geographic argument (Raikow 1977b, 1978). Monophyly of the ploceid/estrildid complex remains uncertain, because no synapomorphies were found in the limb muscles to reinforce previous arguments (Bentz 1979). The shrikes (Laniidae) are only weakly defined as monophyletic (Raikow et al. 1980). Some support for monophyly of the Coraciiformes was found (Maurer and Raikow 1981),

but it is not unequivocal. On the other hand, monophyly of the Piciformes is strongly corroborated (Swierczewski and Raikow 1981), as is that of the New World nine-primaried oscine assemblage when the Vireonidae are excluded (Raikow 1978). The evidence is likewise strong that the Atrichornithidae and Menuridae form a clade (Raikow MS).

A second reason for reexamining passeriform monophyly is that Feduccia (1975, 1977) recently proposed that the suboscines and oscines together do not form a clade, but that the suboscines are instead part of a clade with several coraciiform families, which he termed the Alcediniformes. This conclusion followed from a study of the stapes or middle ear ossicle. Feduccia argued that oscines have a primitive stapes, while suboscines and Alcediniformes share a distinctive derived condition. Later Feduccia (1979) recanted this heresy and decided that the suboscines and Alcediniformes do not form the clade originally postulated, but evolved their derived stapes independently. Feduccia (1979) also provided evidence from spermatozoan morphology that supports the idea of passeriform monophyly. Nevertheless, inasmuch as Feduccia did raise a serious question about passerine monophyly, and because his hypothesis and its subsequent retraction were based on a limited range of data, the matter remains worthy of reconsideration.

Third, the long-term goal of my research is to work out the phylogenetic relationships among passerine birds, using a cladistic analysis mostly of the limb muscles as the method. Before undertaking such an analysis, I consider it prudent to determine with reasonable confidence that the order is monophyletic, because, if it is not, then any hypothesis about its genealogy will be wrong.

Fourth, there is a practical problem related to the previous point. In analyzing cladistic relationships among passerines, I expect to do outgroup comparisons between passerines and nonpasserines in order to cluster clades within the Passeriformes. The logical validity of this procedure requires that the monophyly of the order be established before attempts are made to determine the polarity of character transformations within the order (see below).

METHODS

In order to demonstrate passeriform monophyly it is not enough just to list similarities, because not all

similarities will support such a hypothesis. Monophyly can be shown by the possession of characters that are best interpreted as being derived at the level of the group in question. I looked for such synapomorphies in two places: (1) traditional taxonomic characters from the literature and (2) new information from my dissections of the limb muscles.

I reexamined the phenetic similarities used by previous workers as evidences for grouping. Such similarities could be shared primitive characters (symplesiomorphies), or they could be derived states shared with nonpasserines and not demonstrable as having evolved independently in passerines. Such characters would not corroborate a hypothesis of monophyly. Alternatively, traditional characters found to be most reasonably interpreted as uniquely or independently derived by the Passeriformes would indicate monophyly. In addition, I searched for new synapomorphies in the structure of the limb muscles. Most of the literature on avian limb muscles deals either with oscines or with nonpasserines, and little work has previously been done on the muscles of suboscines. To date I have completed only a limited survey of suboscine muscles, but it includes representatives of all the suborders and major families, and is adequate for the purposes of this paper. Following the classification of Wetmore (1960), the suboscine species dissected include the following: Suborder EURYLAIMI: *Calyptomena viridis* (Eurylaimidae); Suborder TYRANNI: *Dendrocolaptes certhia* (Dendrocolaptidae); *Certhiaxis cinnamomea* (Furnariidae); *Thamnophilus doliatus* (Formicariidae); *Acropternis orthonyx* (Rhinocryptidae); *Procnias nudicollis* (Cotingidae); *Pipra erythrocephala* (Pipridae); *Tyrannus tyrannus*, *Pachyramphus rufus* (Tyrannidae); *Pitta guajana* (Pittidae); Suborder MENURAE: *Menura novaehollandiae* (Menuridae); *Atrichornis clamosus* (Atrichornithidae).

Comparative data on oscines and nonpasserines from our laboratory include numerous families as reported in the following works: Raikow 1973, 1975, 1976, 1977a, 1977b, 1978; Bentz 1976, 1979; Maurer 1977; Swierczewski 1977; Raikow et al. 1979; Raikow et al. 1980; Swierczewski and Raikow 1981; Berman and Raikow 1981; Borecky 1977, 1978; Maurer and Raikow 1981. Additional avian myological data were taken from the summaries by Hudson (1937) and George and Berger (1966).

OUTGROUP COMPARISON

The traditional taxon Passeriformes is a phenetic cluster. In order to demonstrate that it is monophyletic, we must show that its members possess character states that are derived within the class of birds, that is, conditions for which nonpasserine birds are primitive. This requires a method for determining the polarity (primitive-derived directionality) of the characters in question. The most widely used method of character analysis is the *outgroup comparison*.

Often in papers in which this method is used, it is cited without an adequate explanation of how it works. Perhaps the most detailed explanations of the method are given by Ross (1974: 152) who calls it "ex-group comparison," Eldredge and Cracraft (1980: 26, 63), and Watrous and Wheeler (1981).

As usually explained, outgroup comparison works as follows. If a certain character shows variations among the members of a group of organisms (which will be called the *ingroup*), and if one of these variations also occurs in other organisms (the *outgroup*), then the variant that occurs only within the ingroup is considered a derived state in that group, the other being primitive within the group. Here is an example. Some Hawaiian honeycreepers (Drepanididae) have a particular type of tubular tongue (used for nectar-feeding), while others have a simple nontubular tongue. Which is the derived condition in the family? If we look at the other New World nine-primaried oscines we see that such a tubular tongue is never present. Therefore, we may conclude that in the Drepanididae a nontubular tongue is primitive and a tubular tongue is derived. We may further conclude that the species having the tubular tongue form a monophyletic subgroup of the Drepanididae (Raikow 1977b, 1978).

There is a potential problem with this analysis, however. As given above, it contains the unstated assumption that the Hawaiian honeycreepers themselves are a monophyletic group, being more closely related to each other genealogically than to any of the other New World nine-primaried oscines. This assumption is necessary for the outgroup comparison to be logically valid, because character variations arise through the process of evolutionary change in an evolving lineage; there is a temporal polarity to the process. If we say that some Hawaiian honeycreepers have the primitive condition and others the derived condition, we mean that the character underwent a change in one lineage and that all of the tubular-tongued species are descended from the ancestral form that first had this changed character. All of this requires the existence of a monophyletic group of species within which this character transformation took place in one lineage. If we do not have reason to believe that the Hawaiian honeycreepers form a monophyletic group, then we cannot logically make a comparison between this group and an outgroup, because we do not know that some Hawaiian honeycreepers are not members of that outgroup.

Explanations of the outgroup comparison do not always mention this point. For example Ross (1974: 153) illustrates the procedure by describing two variations in the form of the male genitalia of the leaf-hopper genus *Exitianus*: triangular with setae or circular without setae. In related genera the form is triangular with setae. Ross concludes that the triangular, setose condition is primitive. Here, the unstated assumption is that *Exitianus* is monophyletic,

that the ancestral species giving rise to the members of this genus had the primitive state, and that the circular nonsetose condition arose within a lineage of this group. It is not uncommon for a writer to assume that a familiar taxon is monophyletic, but one of the points of this paper is that such assumptions should not be made.

MONOPHYLY OF AVES

In order to demonstrate passeriform monophyly we require derived states that define the order as a clade within some larger group, of which the practical choice is the class Aves. As discussed above, this requires that Aves be considered monophyletic, so that the appropriate outgroup comparisons can be made. We must therefore argue for the monophyly of Aves, but to do this by an outgroup comparison would require the prior assumption that some still larger group, e.g. the amniotes, is monophyletic. That would also have to be demonstrated, requiring yet another hypothesis, such as the monophyly of the tetrapods. This series of dilemmas is not infinite; eventually one comes to a hypothesis of the monophyly of all life, and then there is no outgroup. The solution to this problem is to use a method other than outgroup comparison to demonstrate the monophyly of *some* group so that the study can begin. Gaffney (1979: 95) suggests that ". . . in practice one usually assumes the correctness of a higher-level (more inclusive or more general) hypothesis and makes comparisons within it." In the present case, I believe that one can do better than this and provide an independent argument for the monophyly of Aves. Then, it will be possible to do valid outgroup comparisons between Aves and non-Aves in order to test the monophyly of the Passeriformes within Aves, which is the real purpose of this exercise.

Here is an argument, not based on an outgroup comparison, that the class Aves is monophyletic. Feathers are considered to be homologous with reptilian epidermal scales based on their similar composition of keratinized epidermal tissues and their similar development through the interaction of the ectoderm with a dermal papilla. Epidermal scales occur throughout the "reptilia," which predate birds in the fossil record. Epidermal scales are themselves regarded as a derived specialization of the stratum corneum, a universal tetrapod character first appearing in the "amphibia," which appear in the fossil record even

earlier. Not only are feathers clearly derived in vertebrates, but they are no doubt uniquely derived. The structural complexity of feathers, and their several diverse but often intergrading types, makes it appear highly unlikely that they evolved more than once.

Similar arguments may be made regarding other avian characters, such as the specialization of the forelimb as a wing. This involves a complex of losses and fusions of elements, which first appear separately in the embryo, to produce the specialized structure of the wrist and hand. Likewise derived is the avian forelimb musculature, with its enormously enlarged wing depressor M. pectoralis and the elevator M. supracoracoideus, situated ventral to the wing but inserting dorsally via the pulley provided by the foramen triosseum. The evolution of this flight mechanism from the reptilian condition via an intermediate stage in *Archaeopteryx* has been described by Ostrom (1976a).

Again, the respiratory system, with its complicated system of air sacs and its unique organization of air capillaries, is seen to be derived in birds through its functional correlation with flight and endothermy, which are also derived in comparison with more ancient tetrapod groups.

The preceding argument for avian monophyly is based on the temporal (stratigraphic) sequence of fossil vertebrates correlated with the distribution of characters associated with the evolution of adaptive specializations, some aspects also being corroborated by embryological information. Any of these features alone is convincing evidence of avian monophyly; their co-occurrence in birds reinforces the argument.

ANALYSIS OF TRADITIONAL CHARACTERS

The characters on which the order Passeriformes is based are mostly anatomical features discovered during the nineteenth century and summarized by Beddard (1898) and Ridgway (1901), though some were described more recently. The number and diversity of these characters suggests at first glance that the order Passeriformes is firmly established by a thorough technical diagnosis. As presented, however, these are *phenetic* characters, similarities recorded without consideration of their nature. The purpose of the following analysis is to see

which of these characters may be considered to be derived at the level of the Passeriformes and which will, therefore, corroborate the hypothesis of passeriform monophyly.

The analysis was performed by asking a series of questions about each character, as outlined in Fig. 1. First, is the character *valid* or *invalid*; that is, was the character described correctly in the first place? If not valid, I rejected it as possible evidence for passeriform monophyly. The validity of most characters was not checked by reexamination of specimens, so in general validity was assumed, and the analysis began with the second question: *Is the character primitive or derived within Aves?* If primitive within Aves, a character cannot be derived for passeriforms and was rejected. If the question could not be answered, then the character was also rejected, as it is preferable to reject potentially corroborative evidence than to chance accepting false evidence. If the character is derived within Aves, the next question is whether it is *unique to Passeriformes*. If it is, then it strongly corroborates the hypothesis of monophyly. If it is derived within Aves but is not unique to Passeriformes, there are two possible explanations: it may or may not have been independently evolved in the Passeriformes. If it was *not independently evolved* by the Passeriformes, then it is a derived state shared by the passerines and some other group(s), was presumably present in the common ancestor of the passerines and those other groups, and cannot be used to argue monophyly of the Passeriformes. On the other hand, if the state is derived within Aves, is not unique to passerines, but is *independently evolved in Passeriformes* from its origin in other groups (convergence or parallelism), then it does support passerine monophyly. Again, if the question could not be decided, then the character was rejected so as to avoid the chance of error.

The most convincing argument for monophyly would be given by characters that are derived within Aves and unique to Passeriformes. Characters derived within Aves, not unique to Passeriformes, but thought to have been independently evolved by them are somewhat less certain, because they require one more decision in their analysis and hence involve one more potential source of error.

In the following analysis the polarity of some traditional characters will be tested by out-
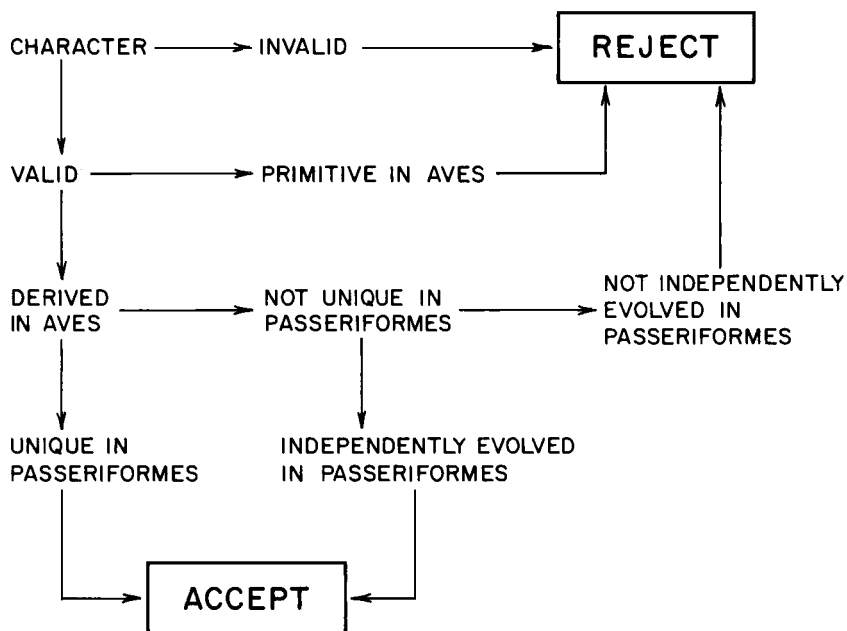
Fig. 1.   A scheme for determining whether traditional phenetic characters are derived within Aves at the level of Passeriformes and whether they will therefore corroborate the hypothesis of passeriform monophyly. Characters that are *accepted* do corroborate the hypothesis; those that are *rejected* do not. See text for discussion.

group comparisons with "reptiles" on the assumption, discussed above, that the class Aves is monophyletic. In the case of characters for which such comparisons cannot be made because they occur only among birds, other methods of analysis will be used where possible.

(1) *Palate aegithognathous.*—Huxley (1867) defined several palatal types on the arrangement of the bones. I examined the descriptions and illustrations of the palate in archosaurs given by Romer (1956, 1966). Often the palate is poorly known, but it appears clear that aegithognathism is not present in the Thecodontia, Crocodilia, Saurischia, Ornithischia, or Pterosauria. Generally, the vomers, if known, are paired and do not show the characteristic form of aegithognathous birds. In addition, the maxillopalatines are lacking, unless McDowell (1978) is correct in his assumption that the avian maxillopalatines are homologous with the reptilian palatines, in which case they are still dissimilar. I conclude that the aegithognathous palate is a derived condition within Aves.

It is not unique to passerines, however. Bock and McEvey (1969: 205) point out that Huxley (1867) used a complex of characters in defining his palatal types but that more recent workers often simplified the definitions, with a resulting loss of precision. On the basis of the full set of characters, these authors determined that the palate in the Pedionomidae and Turnicidae is schizognathous and not aegithognathous, as is sometimes stated (e.g. Beddard 1898: 321). In the Capitonidae (Piciformes), the skull is "aegithognathous with a desmognathous tendency" (Beddard 1898: 195), meaning that the maxillopalatines may blend with the nasal septum or with each other across the midline. The vomer is truncated caudal to the line of the palatines, instead of rostral to it as in passerines (Beddard 1898: 196). There are other differences. Collectively, these suggest that the capitonid condition is not directly comparable to the passerine condition. Also among Piciformes, *Indicator* is reported as being aegithognathous (Beddard 1898: 197). Swierczewski and Raikow (1981) studied the limb musculature of the Piciformes and found that the Capitonidae are a fairly derived family within the order and that the Indicatoridae are even more

highly derived. Synapomorphy of the questionable piciform aegithognathism with the passerine condition would involve extensive conflicts with myological features that clearly place both barbets and honeyguides in the monophyletic order Piciformes.

The swifts (Apodidae) also have an aegithognathous palate. Beddard (1898: 229) notes that, while in passerines the vomer is truncated in front of a line joining the maxillopalatines, in swifts this truncation is at the level of this line, though the significance of this difference is obscure. At the turn of the century the close relationship of the swifts to the passerine swallows (Hirundinidae) was hotly debated, but their similarities have now been dismissed as convergence associated with aerial insect hawking. Beddard (1898: 224) points out many differences between swifts and passerines, including several in the limb musculature that seem highly significant to me, as they depart greatly from the usual passerine conditions. Sibley and Ahlquist (1972: 198) review the problem thoroughly. Although a connection to the Passeriformes is possible, the question of the swifts' relationships to the Trochilidae, Caprimulgiformes, Coliiformes, and Trogonidae appears at least as important. I agree with Sibley and Ahlquist (1972: 206) that this problem is one of the most interesting in nonpasserine systematics. Meanwhile, however, I see little evidence that the swifts are particularly close to the passerines and think it more likely that their palatal similarities are due to convergence than to immediate common ancestry.

In general, then, the aegithognathous palate appears to be a character of some structural complexity that is probably independently derived in the Passeriformes and therefore corroborates the hypothesis that the order is monophyletic.

(2) *Atlas perforated.*—The atlas and axis are the first two cervical vertebrae. The atlas articulates within the odontoid process of the axis. The opening in the atlas into which the odontoid process fits may be fully enclosed (perforated atlas), or it may be open dorsally (notched atlas). It is perforated in the Passeriformes. I cannot determine the polarity of this character, but it does not matter. If primitive, it is of no value. If derived, it is far from unique in the Passeriformes, being present in various other groups, including many piciforms and

coraciiforms (Beddard 1898). There is no indication in the literature that the passerine condition is in any way distinctive; hence, this character will not corroborate the hypothesis of passeriform monophyly.

(3) *Only left carotid artery present.*—Both Beddard (1898) and Ridgway (1901) cite the presence of only the left carotid artery as a passerine character. More recently, Glenny (1955) studied the patterns of avian carotid arteries in some detail. He proposed that the primitive condition in birds is the presence of both left and right arteries and that various patterns of reduction and loss could be recognized, which he identified by a coding system. "All birds, insofar as presently known, develop a complete aortic arch system, and this system undergoes a series of developmental (atrophic) deletions and other modifications which result in the adult arterial arrangement-patterns . . ." (Glenny 1955: 609). In current terms, Glenny proposes that loss patterns are derived states, as indicated by a developmental criterion. Passeriforms share a derived arterial condition, termed B-4-s by Glenny, but this also occurs in most piciforms, in trogons, in colies, and in several other orders and families of birds. Thus, the characteristic is derived in passerines but is far from unique. There is no apparent method to determine whether it is autapomorphic for the Passeriformes or shared with other groups. Therefore, this traditional character cannot corroborate the hypothesis of passeriform monophyly.

(4) *Oil gland nude.*—In some birds, the orifice of the uropygial gland is surrounded by a circle of feathers forming a tuft that acts like a wick; this condition is called *tufted.* In others, including passerines, the circlet is lacking, giving the *nude* condition. Both conditions are so wide-spread among birds that the character cannot be shown to be derived for the Passeriformes and therefore does not corroborate the hypothesis of passerine monophyly.

(5) *Wing eutaxic.*—In many birds there is a gap in the row of secondary remiges, the fifth secondary appearing to be absent while its covert remains in place. The condition in which the gap occurs is called *diastataxy,* while that in which the gap is absent is called *eutaxy.* Passeriformes are eutaxic. I cannot determine the polarity of this character by outgroup comparison, because "reptiles" lack feathers, so both possibilities must be considered. If it is

primitive within Aves, then it is not derived for the Passeriformes. If it is derived, however, it is not unique to Passeriformes; on the contrary, there are many groups that show each condition, and occasionally both conditions occur in a single order or family. Because of this widespread occurrence of both conditions, I can see no basis for suggesting that the eutaxic condition in passerines, even if derived, was derived independently from its origin in any other eutaxic groups. Therefore, the condition of eutaxic feathering cannot be used as evidence for monophyly of the order Passeriformes.

(6) *Intestinal ceca small.*—Beddard (1898) and Ridgway (1901) both report that the intestinal ceca are small in passerines. This character appears to be of no value; "The caeca are among the most variable organs of birds" (Beddard 1898: 30). Van Tyne and Berger (1976: 576) also discuss this character. The ceca are often vestigial as in the Passeriformes and may vary considerably in closely related birds with different feeding habits. Small ceca are not unique to the Passeriformes, nor is there a basis for determining the polarity of this character; hence, it cannot be cited as evidence of passeriform monophyly.

(7) *Expansor secundariorum lacking.*—Both Beddard (1898) and Ridgway (1901) state that this small forelimb muscle is absent in passerine birds. Berger (1956) reported it in 23 families of both oscine and suboscine passerines, however, including the Eurylaimidae, Furnariidae, Formicariidae, Cotingidae, and Tyrannidae among the latter. Berger also refered to earlier papers reporting its presence in passerines. We have also found this muscle to be present in passerine birds, including the Menuridae and Atrichornithidae (Raikow MS). Clearly, the early anatomists overlooked this muscle in the passerines that they dissected, probably because it is small and requires staining to be clearly visible. This character is therefore invalid and does not support the hypothesis of passeriform monophyly.

(8) *Biceps slip lacking.*—Passeriform birds are characterized by the absence of the biceps slip, a muscular branch that arises from the belly of the biceps brachii and passes through the patagium to join the tendon of the propatagialis pars longa. This structure occurs in many groups of birds. It is also absent in the Coraciiformes, however (neither Beddard 1898 nor Maurer 1977 mentions it). It is also lacking in at least some piciforms and in hummingbirds, swifts, owls, parrots, cuckoos, turacos, and some caprimulgiformes (Beddard 1898). It is therefore unnecessary to worry about the polarity of this character; the absence of the biceps slip is so widespread that it cannot be proposed as a uniquely derived state of the Passeriformes.

(9) *Tensor propatagialis brevis tendon "passerine".*—This muscle arises in the shoulder and sends its tendon through the patagium to an insertion on the surface of the extensor metacarpi radialis, a forearm muscle. The tendon does not end there, however. After making its attachment, it turns proximad and passes to an insertion on the humerus. Garrod (1876) considered this to be a good character for defining the passerine birds. The condition as described does appear to be characteristic of passerines generally, including suboscines, though Garrod did note some minor variations, as I have also. These seem insignificant, however, compared to the great diversity that the muscle shows in other groups. It is not possible to do outgroup comparisons with "reptiles" in analyzing this character, as it is an avian specialization associated with the patagium of the wing. Because this condition appears to be unique to the Passeriformes, it is tempting to suggest that, if the Passeriformes are shown to be monophyletic by other characters, then by correlation this character is also presumably derived at the level of the order. Then to use this as an evidence of passerine monophyly, however, verges on circular reasoning. Because the determination of its polarity is not independent of other characters, I would hesitate to argue passerine monophyly on this character alone, were that possible.

(10) *Iliofemoralis externus absent.*—The absence of this hindlimb muscle (under the name gluteus medius et minimus) was noted by Hudson (1937) on the basis of limited dissections. It is also absent in various other groups, including the Piciformes (Swierczewski 1977, Hudson 1937) and Coraciiformes (Maurer and Raikow 1981). The muscle tends to reappear as a developmental anomaly in passerine birds and is even thought to have become reestablished in some groups (Raikow 1975; Raikow et al. 1979, 1980). The arguments for the concept that the muscle became reestablished in some passerine groups indicate that its ab-

sence is a derived state within Aves. Because it is also absent in groups generally considered close to the passerines, however, one cannot argue that its apparently primitive absence within the Passeriformes is a unique, derived condition within Aves; hence, this character cannot support the concept of passeriform monophyly.

(11) *Ambiens lacking.*—This is the most superficial muscle on the medial surface of the thigh. According to Lance Jones (1979), it is homologous with the muscle of the same name in "reptiles"; therefore, its absence in birds is a derived state. It is absent in Passeriformes but also in Piciformes, Coraciiformes, Trogoniformes, Apodiformes, and many other groups (George and Berger 1966: 421). Because there is no reason to suppose that it was lost in Passeriformes independently of its loss in any other group, it cannot be used as an argument for passeriform monophyly.

(12) *Iliofemoralis lacking.*—Also known as M. piriformis pars iliofemoralis, this muscle passes from the ilium to the femur. It is present in many groups of birds and absent in many others, including the Passeriformes (George and Berger 1966: 407). Because its homology with reptilian muscles is uncertain, its polarity cannot be determined by outgroup comparisons. This muscle has been found as an occasional developmental anomaly of an apparently atavistic nature in passerine birds, including a Fox Sparrow (*Passerella iliaca*, Raikow 1975) and a White-breasted Wood-swallow (*Artamus leucorhynchus*, Raikow et al. 1979). This indicates that the absence of the muscle in passerines is derived. As there is no reason to believe that the muscle was lost in passerines separately from its loss in other birds, however, this character will not serve as an argument for the monophyly of the Passeriformes.

(13) *Spermatozoa bundled, with coiled head and large acrosome.*—McFarlane (1963) explored the use of spermatozoan structure as a taxonomic tool, reviewing earlier work and reporting new observations. In nonpasserines, the sperm cells are relatively simple in structure, being straight and having a small acrosome. In contrast, the spermatozoa of passerines are coiled in the head region and have a large acrosome. The nonpasserine type is similar to the reptilian condition and hence may be considered primitive within Aves, the passerine form thus being derived. This condition occurs both in

oscines and suboscines. Henley et al. (1978) noted that oscine spermatozoa occur in bundles and are nonmotile under certain experimental conditions. Feduccia (1979) reported that in two suboscine species the spermatozoa are also bundled. The use of this character complex at present is limited because of the relatively small number of species yet examined and because proper outgroup comparisons will require the observation of a diversity of oscine, suboscine, nonpasserine, and nonavian spermatozoa under identical laboratory conditions. The distinctions are sufficiently great, however, and the range of taxa already examined sufficiently broad, that it is a reasonable conclusion that sperm morphology does corroborate the hypothesis of passerine monophyly.

(14) *Foot anisodactyl.*—There are various arrangements of the toes among birds. In the Passeriformes the condition is anisodactyl, meaning that the first toe (hallux) is directed backward, while the second through fourth toes are directed forward. This condition occurs in the majority of birds, including forms with widely divergent locomotor habits, while other toe arrangements are clearly associated with one or another functional specialization. For this reason, it appears probable that anisodactyly is primitive among birds. In addition, this arrangement occurs in *Archaeopteryx* and in the theropod dinosaurs from which birds are believed by some to have evolved (Ostrom 1976b). Therefore, this character does not constitute an argument for passeriform monophyly.

(15) *Phalangeal formula 2-3-4-5.*—This refers to the number of phalanges in digits I, II, III, and IV of the hind limb. The same considerations apply here as for anisodactyly; hence, this character does not corroborate the hypothesis that the order Passeriformes is monophyletic.

(16) *Hallux incumbent.*—This means that the hallux in Passeriformes is at the same level as the forward three toes, rather than being elevated. The polarity of this character is uncertain, but, because an incumbent hallux is a common characteristic among birds, no argument for its being uniquely derived in passerines is possible; hence, it does not corroborate passerine monophyly.

(17) *Hallux and its claw large.*—Among passerines, the hallux and its claw are relatively

large in relation to the other toes, as compared
to the condition in most other birds, including
the Piciformes and Coraciiformes. The large
size of the hallux and its claw may be func-
tionally related to the degree of independent
action permitted the hallux in passerines (ex-
cept Eurylaimidae) by the absence of a con-
nection between their major flexors. Ridgway
(1901) considered the hallux in the Eurylaimi-
dae to be relatively weak, but Olson (1971) dis-
counted this. The enlarged hallux appears to
be a derived component of the specialized pas-
serine perching foot, which will be discussed
in more detail below. Therefore, it apparently
does corroborate the idea of passeriform
monophyly.

(18) *Type VII deep plantar tendons.*—Birds
have two deep flexor muscles of the toes, the
flexor digitorum longus (FDL) and flexor hal-
lucis longus (FHL) (Fig. 2A). In most birds the
FDL tendon trifurcates and supplies digits II,
III, and IV, so that the muscle flexes these three
digits simultaneously. The hallux is flexed by
FHL. There are exceptions to this, however. In
addition, most bird groups have an intercon-
nection between the FHL and FDL tendons,
either by a tendinous slip (vinculum) passing
from the FHL tendon to the FDL tendon or
by complete fusion of the two tendons. These
variations in the deep plantar tendons have
long been used as taxonomic characters, es-
pecially following Garrod (1875) and Gadow
(1893–1896). Most passerines have the Type VII
arrangement of Gadow's system, with no con-
nection between the FDL and FHL tendons.
Garrod (1875) confirmed earlier observations
by Sundevall on this, and later (Garrod 1876)
included this character as part of his diagnosis
of the Passeriformes. Subsequently, Garrod
(1877) reported an exception to this condition,
namely the presence of a vinculum in the
broadbills, Eurylaimidae. He concluded that
either the character must be abandoned or that
the Eurylaimidae are not passerine and chose
the first alternative. Subsequent workers have
minimized the importance of this character
and have shown that the vinculum is occasion-
ally absent in broadbills (see Olson 1971 for a
review). The assumption has been that the
presence of a vinculum is a primitive state and
its absence derived.

It does appear probable that the lack of a
connection between the deep plantar tendons
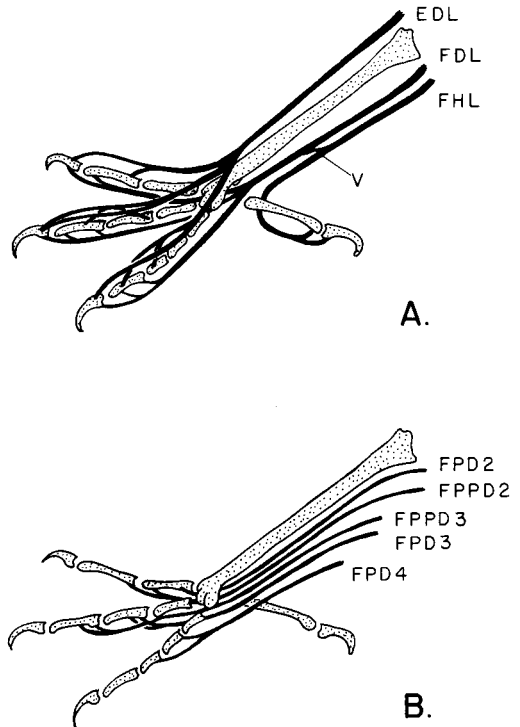is a derived state in birds. At least in some

Fig. 2. Diagrammatic representation of the ten-
dons of insertion of the extrinsic digital muscles of
passerine birds, the bellies of which, not shown
here, lie in the shank. **A.** extensor digitorum longus
(EDL); flexor digitorum longus (FDL); and flexor hal-
lucis longus (FHL). A vinculum (v) connects the FDL
and FHL tendons only in the Eurylaimidae (Broad-
bills). **B.** flexor perforatus digiti II (FPD2); flexor per-
forans et perforatus digiti II (FPPD2); flexor perforans
et perforatus digiti III (FPPD3); flexor perforatus dig-
iti III (FPD3); and flexor perforatus digiti IV (FPD4).

"reptiles" there is one deep flexor muscle that
supplies all five digits, and the FHL-FDL di-
vision may have arisen in birds or their direct
reptilian ancestors along with the movement
of the hallux into its opposing position. Also,
the character (except for the Eurylaimidae) oc-
curs in correlation with other derived states
shown by the Passeriformes. Finally, the sep-
aration of the two tendons appears to be cor-
related with the enlarged hallux as part of a
functional specialization of the passerine foot
(see below).

The problem of the Eurylaimidae would dis-
appear if the presence of the vinculum in that
group could be considered a derived (second-
arily primitive) condition. I do not know of any

previous suggestion of this hypothesis, but there is good reason to consider it. The Eurylaimidae possess a derived stapes morphology (Feduccia 1975) that clusters them together with most other suboscines as a subclade of the Passeriformes. If the vinculum is primitive, then the derived stapes of the Eurylaimidae must have evolved independently of that in other suboscines. Compared to the stapes, the vinculum is a relatively simple structure. Variations in the plantar tendons of birds are numerous and diverse; members of a single order often show considerable diversity. It appears more likely that the vinculum of broadbills evolved within that group than that the stapes is convergent. The feeble vinculum of the Eurylaimidae, in my opinion, is not strong enough to exclude the Type VII deep plantar tendon arrangement from being considered a probable synapomorphy of the Passeriformes.

For each character analyzed there are three possible outcomes: it may corroborate the hypothesis of passeriform monophyly, it may fail to corroborate the hypothesis, or it may refute the hypothesis. In order to refute the hypothesis a character would have to be shown to be derived once in a group containing *some* passerines plus some nonpasserines, but primitive in other passerines. The alcediniform stapes was originally argued by Feduccia (1975, 1977) to be a character of this type. None of the 18 traditional characters analyzed above was found to refute the hypothesis. Five of these characters (numbers 1, 9, 13, 17, and 18) corroborate the hypothesis, while the remaining 13 simply fail to do so. On this basis two conclusions may be made. First, passeriform monophyly is corroborated by some traditional characters with sufficient force that it appears to be a reasonably viable hypothesis, certainly one worthy of further investigation. Second, the large number of traditional characters that fail to support the hypothesis underscores the importance of not assuming that long recognized taxa are monophyletic in the contemporary sense, merely because they share some similarities.

THE HIND LIMB MUSCLES

My preliminary study of some of the hind limb muscles of representative suboscines has yielded results that contribute to the analysis of passeriform monophyly. As already noted,

previous to this study our knowledge of passerine limb muscles was mostly limited to the oscines, so that it was difficult to generalize about the order Passeriformes as a whole. The species of suboscines dissected, and references to previous studies pertinent to the following discussion, are listed above under Methods.

M. pubo-ischio-femoralis.—This large muscle of the thigh passes from the postacetabular pelvis to the femur. In most birds it has two separate bellies, although sometimes these are partly or completely fused. In nonpasserines the bellies are arranged so that one lies more or less completely superficially to the other, the superficial belly being called Pars lateralis and the deep belly Pars medialis. In passerine birds, however, one belly lies mostly cranially to the other, with only slight overlap. Here, they are termed Pars cranialis and Pars caudalis (Baumel et al. 1979). For illustrations of this point compare Figs. IX 52, IX 53, and IX 54 in George and Berger (1966), where this muscle is labeled with its old name M. adductor longus et brevis. It is probable, based on details of their attachments, that the passerine Pars cranialis is the homologue of the nonpasserine Pars lateralis, while Pars caudalis corresponds to Pars medialis. In any case, the difference between passerines and nonpasserines is distinctive.

The polarity of this difference must be determined by comparisons within Aves, because I lack information to do outgroup comparisons with "reptiles." If we accept the above discussion of the characters as evidence that the order Passeriformes is monophyletic, then this character must also be derived by correlation with its common occurrence with those characters.

In all of the suboscines dissected, this muscle had the distinctive passerine conditions rather than the nonpasserine form. This confirms the description given by Hudson (1937) for *Corvus* and *Tyrannus*. Thus, the form of M. pubo-ischio-femoralis appears to corroborate the hypothesis of passeriform monophyly, although I would give it greater weight if its polarity had been determined by a more independent method than correlation with other characters.

Intrinsic foot muscles.—Birds in general have a set of intrinsic foot muscles that arise from the tarsometatarsus and insert on the base of one or another of the digits. A list of these muscles and the digits on which they insert is

TABLE 1. Avian digital muscles. The distributions shown here are those found in the Passeriformes and various other groups.

	Intrinsic muscles	Extrinsic muscles[a]
Digit I	flexor hallucis brevis extensor hallucis longus	flexor hallucis longus
Digit II	adductor digiti II[b] abductor digiti II[b]	flexor perforatus digiti II flexor perforans et perforatus digiti II [flexor digitorum longus] [extensor digitorum longus]
Digit III	extensor proprius digiti III[b] extensor brevis digiti III[b]	flexor perforatus digiti III flexor perforans et perforatus digiti III [flexor digitorum longus] [extensor digitorum longus]
Digit IV	extensor brevis digiti IV[c] adductor digiti IV[b] abductor digiti IV[b]	flexor perforatus digiti IV [flexor digitorum longus] [extensor digitorum longus]

[a] Bracketed muscles have multiple insertions on different digits in different groups of birds.
[b] Absent in passerine birds.
[c] Absent (occasionally vestigial) in passerine birds.

given in Table 1, and the function of each is given by its name. The number of these muscles varies in different groups of birds, but nonpasserines generally have fairly complete sets. George and Berger (1966) and Hudson (1937) record the occurrence of these muscles and give illustrations of them. It was previously known that oscines lack most of these muscles (summary in George and Berger 1966), and our dissections of oscines have confirmed this, but little was previously known about suboscines. My dissections of the representative suboscines listed above confirm the similar absence of these muscles.

The intrinsic muscles of the hallux are generally present in passerines. Except for the occasional presence of extensor brevis digiti IV in a very reduced (essentially vestigial) state, however, all of the intrinsic foot muscles of digits II, III, and IV are lacking in the Passeriformes, including both oscines and suboscines. This set of muscles as a group is homologous to the intrinsic foot muscles of other tetrapods. Because the class Aves is monophyletic and because these muscles occur both in nonpasserine birds and in nonavian tetrapods, outgroup comparison clearly indicates that this absence is a derived state and thereby corroborates the hypothesis of passeriform monophyly.

It must be noted, however, that the loss of *all* of these muscles may not have occurred at one time or at the level of the passeriform clade. In the Coraciiformes and Piciformes,

which are widely regarded as being closely related to the Passeriformes, there are also trends toward the loss of intrinsic foot muscles. In each of these nonpasserine orders, however, some families retain at least one of the muscles for each toe, and no families lack the entire set. Furthermore, the three orders show the evolution of quite different foot adaptations for perching: zygodactyly in Piciformes, anisodactyly leading to syndactyly in Coraciiformes, and a specialized form of anisodactyly in Passeriformes (discussed below). The greatest losses of intrinsic foot muscles in the Coraciiformes and Piciformes occur in the most derived groups (data from Maurer 1977 and Swierczewski 1977). I conclude, therefore, that most of the losses of intrinsic foot muscles in the Passeriformes occurred independently of their loss in the other two groups.

ADAPTIVE SIGNIFICANCE OF THE
PASSERINE FOOT

In this section I will accept the conclusion that the order Passeriformes is monophyletic and will speculate briefly on the functional and adaptive significance of the passerine foot. The hypothesis of monophyly does not depend upon the validity of these speculations, but they may help to give some insight into the biological significance of certain passeriform characteristics.

As a functional mechanism, the passerine foot is distinctively specialized and is probably a factor in the success of the order in radiating

into a variety of niches. Basically the foot is adapted for perching but in such a way that the development of terrestrial habits has not been precluded. Perching adaptations have arisen in a number of ways among birds (see Bock and Miller 1959 for a general discussion). The primitive anisodactyl foot has been modified by rearranging the digits into zygodactyl or heterodactyl configurations, or by joining some of the forward toes at their bases in syndactyly. In different ways these modifications enhance the use of the foot as a grasping mechanism. Among passerines, one modification of the retained primitive anisodactyl foot is the enlargement of the hallux, which presumably provides a more evenly balanced distribution of strength between the numerically unequal opposing sets of toes and permits the hallux to encircle the perch effectively in opposition to the other toes.

The most striking aspect of the evolution of the passerine foot is the loss of the intrinsic muscles of the forward toes as described above. The pattern of losses and their functional consequences may be understood by considering the general structure of the limb.

Extrinsic muscles.—There are a number of muscles activating the toes, the bellies of which lie in the shank and that may therefore be termed *extrinsic* foot muscles. The three forward toes have a common extensor, M. extensor digitorum longus (EDL), the tendon of which passes across the intertarsal joint and down the dorsal surface of the tarsometatarsus (Fig. 2A). Near the distal end of that bone, the tendon trifurcates, the branches inserting on the dorsal surfaces of the three forward toes. Thus, the EDL provides for simultaneous extension of these digits. There is also a common flexor, M. flexor digitorum longus (FDL), the tendon of which passes down the plantar surface of the tarsometatarsus, trifurcating distally to insert on the plantar surfaces of the three forward toes (Fig. 2A). This provides simultaneous flexion of these digits. Thus, these two muscles produce *simultaneous* extension and flexion of the forward three toes. The hallux is likewise provided with an extrinsic flexor muscle, the flexor hallucis longus (FHL), but it has no extrinsic extensor in birds (Fig. 2A). In most passerine birds the tendons of the FHL and FDL have no interconnection as they pass down the plantar surface of the tarsus, as noted above. The absence of this connection (except

in the Eurylaimidae, which have a feeble vinculum) presumably allows independent flexion of the forward toes and of the hallux, which may aid in the versatility of movement in adjusting the foot to perches of varying sizes and shapes. This functional separation of the flexion of the forward toes from that of the hallux is probably associated with the enlarged size of the hallux as part of the passerine perching specialization. These extrinsic muscles EDL, FDL, and FHL are always present.

Each forward toe also has one or two individual extrinsic flexor muscles that insert at one or more points along the plantar surface of the digit, flexing it around one or another interphalangeal joint. These muscles, together with the FDL, permit varying patterns of flexion, so that the toes can conform to perches of different sizes and shapes. These muscles are the flexor perforatus digiti II (FPD2), flexor perforans et perforatus digiti II (FPPD2), flexor perforatus digiti III (FPD3), flexor perforans et perforatus digiti III (FPPD3), and flexor perforatus digiti IV (FPD4) (see Table 1 and Fig. 2B). Again, these muscles are always present in passerine birds.

Thus, the extrinsic flexor system consists of one muscle that provides simultaneous flexion of the forward three toes, plus individual flexors of each forward toe, and an independent flexor of the hallux. The extrinsic extensor system is simpler, as there are no individual extensors, only the common extensor of the forward three toes. This entire extrinsic muscle system is always present in passerines, apparently representing a necessary minimum of complexity.

Intrinsic muscles.—As discussed earlier, nonpasserine birds have intrinsic foot muscles that arise on the tarsometatarsus and insert at the bases of the forward three toes, while in passerines this entire set is lost except for one occasional vestige. The order Passeriformes is therefore characterized by a major simplification of the foot mechanism.

The hallux opposes the forward toes and, as noted above, has a single extrinsic flexor, FHL. It also has two intrinsic muscles (Fig. 3). The intrinsic extensor, M. extensor hallucis longus (EHL), is the *only* extensor of the hallux, as there is no extrinsic extensor in birds, and it is never lost. The intrinsic flexor, M. flexor hallucis brevis (FHB), is a synergist of the much larger FHL.

The forward toes have the capacity for simultaneous extension and for simultaneous or individual flexion, including variation in shaping the flexed digits to fit the perch. The loss of the intrinsic forward toe muscles, however, eliminates a repertoire of individual abduction, adduction, and extension movements. Passerines have thus retained a variable mechanism for grasping but have simplified the range of movements not associated directly with the grip. This presumably limits the functional capabilities of the foot where such subtle movements might be useful, such as in walking or climbing over irregular surfaces or grasping variously and irregularly shaped objects. The passerine condition is in striking contrast, for example, to the complexity of the intrinsic foot musculature of mousebirds (Coliiformes), which hold food with their feet and have an astonishing variety of movements and postures (Berman and Raikow 1981). Clearly, passerines do not depend upon these capabilities; the bill is the usual manipulative organ, and passerines are prone to fly even short distances rather than clamber over difficult terrain.

The loss or major reduction of foot muscles in passerine birds tends to occur in certain patterns not unlike those described by Stegmann (1978) in the avian forelimb: muscles that are reduced or lost tend to be those that (1) are initially small in size; (2) are complementary to others in their actions, so that their loss may reduce the subtlety or variety of some movements but will not eliminate an action entirely; and (3) are usually smaller in size and simpler in structure (e.g. crossing fewer joints) than their synergists that are retained.

Adaptive potential.—Nevertheless, although passerines have a limb muscle system greatly simplified in many respects, it does retain the capability of some adaptive variation. There is much variety in the two intrinsic muscles of the hallux. The EHL is never lost, presumably because it has no synergist and its loss would eliminate the necessary ability to extend the hallux. In the Ocellated Tapaculo (*Acropternis orthonyx*: Rhinocryptidae), however, it is reduced to a vestige, probably in association with the terrestrial habits of this species. The intrinsic flexor, FHB, is lost entirely in this species and is often reduced to a vestige in passerines. Presumably this muscle is dispensable, because it is a small synergist of the much
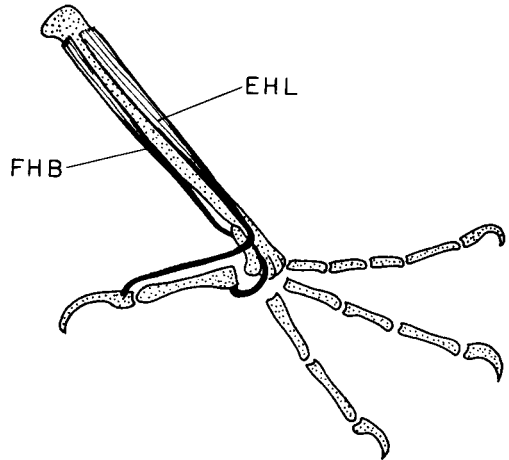

Fig. 3. Diagrammatic representation of the two intrinsic foot muscles generally found in passerine birds, M. extensor hallucis longus (EHL) and M. flexor hallucis brevis (FHB).

larger FHL. On the other hand, passerines with a strong grip may have considerable enlargement of the intrinsic hallux muscles along with other modifications, such as were discussed previously in the shrikes (Laniidae) (Raikow et al. 1980).

CONCLUSIONS

Some readers of an earlier version of this paper suggested that this analysis is hardly necessary, because the order Passeriformes is almost universally recognized as being monophyletic. One found my arguments quite unconvincing but agreed with my conclusions. To this I have two responses. First, the concept of monophyly often employed is vague and imprecise. Second, previous studies have amply demonstrated that many traditionally recognized taxa are *not* monophyletic in the strict and meaningful sense, and therefore I urge that such assumptions should not be made. I mention these points because they illustrate a common tendency for biologists to assume that traditional taxa are monophyletic, perhaps because that which is familiar tends to appear "natural" in some sense.

The task of systematic biology is to produce hypotheses of phylogenetic relationships among organisms, and the key to doing this is the ability to recognize monophyletic groups. The chief virtue of the cladistic school in con-

trast to others is not that it accomplishes this goal more satisfactorily, although it does, but that its methodology permits the full exposure of every facet of an analysis for maximum ease of criticism. As a result, a hypothesis, like the one of passerine monophyly discussed herein, may be seen to rest on individual arguments that vary in their strength, weakness, and degree of ambiguity.

On the basis of the arguments presented in this paper I conclude that the order Passeriformes, originally defined as a phenetic cluster, is a clade or monophyletic group in the specific contemporary sense.

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