

COMMENTS ON THE PHYLOGENY AND SKULL OF THE PASSERIFORMES

BY M. JOLLIE

The publications of Beecher and Tordoff have stirred discussion relative to the classification of the oscines, particularly the nine-primaried ones of the New World. Comments on the phylogeny of this group have been limited to those who are primarily systematists and not comparative anatomists. As a representative of the latter group I would like to call attention to certain aspects of skull structure and to express certain views which may help to refine our knowledge of the phylogeny of the oscines and suboscines.

COMMENTS ON RECENT PAPERS

Tordoff (1954 a and b) has described the palates of the oscines and has placed considerable weight on the occurrence of the "palato-maxillaries." It is noteworthy that there is no mention of the development of the bones of the palate as observed in nestlings, nor is there any attempt to relate bony configuration to muscle form. Tordoff (1954a: 25; 1954b: 275) hypothesizes that the palato-maxillaries are an adaptation for feeding on seeds and fruits. Other species with a similar diet appear to lack this structure, yet this has not been taken into consideration. A study of functional anatomy should require more than a survey of the adult structure and a more positive kind of correlation.

Beecher's (1950 to 1953) studies of the jaw musculature of oscines is open to criticism. The illustrations, which have been cited as a major contribution to anatomy, only support the conclusions in part. One wonders why, for example, the shrikes were not placed closer to the corvids and Old World orioles, which from his drawings they resemble in their myology. The assumption that parallel fibers are the primitive style and various grades of pinnate the advanced state has already been discussed by Tordoff (1954). Supplementing his remarks is the point that the development of a muscle is a functional response. Pinnate and parallel fibers are adaptations; the one enables greater tension to be produced, the other has greater contractility. There is doubt that one is more primitive than the other since both were probably present in the reptilian ancestors of birds. I must agree with Tordoff (1954b: 282) that "Perhaps all that can be said is that both parallel and pinnate jaw muscles occur, in various groups throughout the world."

Beecher's (1953: 272) assumption that muscles "are more conservative than bones," disregards a great deal of comparative study, including that of the jaw muscles (*see* Starck and Barnikol, 1954). The anatomist

can only accept the proposition that sometimes myology will yield valuable features, while elsewhere bone characteristics will be more useful.

As to the taxonomic value of the jaw muscles described by Beecher, it is not surprising that they should have limited use in such a closely related array as the oscines, since the bill form and the use of the bill, with which they are associated, already indicate the same relationships in most cases.

The search for the restricted group of anatomical features on which to base a phylogeny must end in disappointment. This comment might lead one to return to the safe attitude that an anatomical solution to the classification of birds is next to the impossible. To the contrary, both of these contributors have helped clarify relationships within the oscines. What is needed, in the words of Tordoff, are "more studies of both bones and muscles." We need more facts concerning both developmental and adult anatomy. Facts from experimental manipulation during development would also be desirable. It is also clear at this time that we need to know how to interpret information (i.e., to discern the phylogenetic lines) as much as we need new information.

As a step in this direction, I would like to discuss certain aspects of the skull structure. This discussion is based on an examination of the materials in the osteological collections at the Museum of Comparative Zoology at Harvard University, the American Museum, and the United States National Museum. A list of the species examined was not kept although notes were taken on representative specimens of many passeriform families (Appendix 1). It was largely from these notes that the views expressed here were derived. Developmental stages (Appendix 2) for a restricted number of passeriform families were collected, along with adult examples. These are in the writer's possession. This study is a part of a more general one supported by National Science Foundation Grants (G-1737, G-3861).

FEATURES OF THE SKULL HAVING POSSIBLE PHYLOGENETIC VALUE

The "palato-maxillaries". The development of the passerine skull has been described at length by Parker (1874-77), yet the true nature of the "palato-maxillaries" has been lost (see Amadon, 1950; Tordoff, 1954a; and Mayr, 1955). It should be stated at the start that the palato-maxillary, as it occurs in the Emberizidae, is a remnant of the palatine process of the premaxilla, not a new bone (fig. 2). A palatine process is characteristic of all birds (about 15 orders examined—figs. 1-4). In the families Accipitridae (fig. 1A) and Falconidae these processes are most reduced (vestigial).

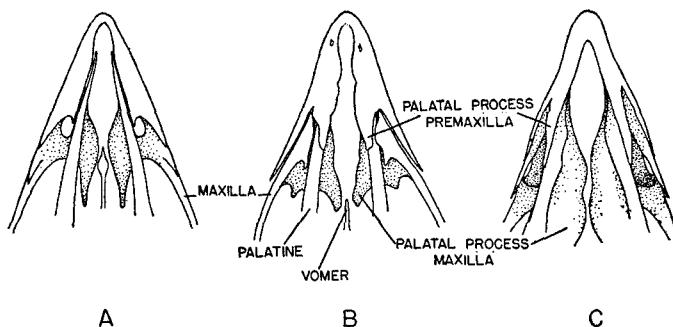


FIGURE 1. Ventral view of anterior tip of palate showing the palatal process of the premaxilla. A. Cooper's Hawk (*Accipiter cooperii*) just before hatching; B. White Leghorn Chicken (*Gallus gallus*) just after hatching; C. Great Horned Owl (*Bubo virginianus*) four week old nestling.

The fate of these processes varies: generally they fuse to the palatine (prepalatine process of above authors), though they may fuse with the maxilla or remain free. A free palatine process may be large or small, or it may be cut off from its basal attachment by movement in this palatine hinge area (as in *Junco*, fig. 2). The palatine process of *Acanthorhynchus tenuirostris* (Meliphagidae—as illustrated by Parker, 1877–79, pl. XLVII) is unique in that it lies medial to the anterior end of the palatine, not lateral or ventral to it as in most birds. Details of the development and fate of the palatine process of the premaxilla may contribute evidence as to the phylogeny of the oscines.

The pterygoid. Recent discussion of the palaeognathous palate by

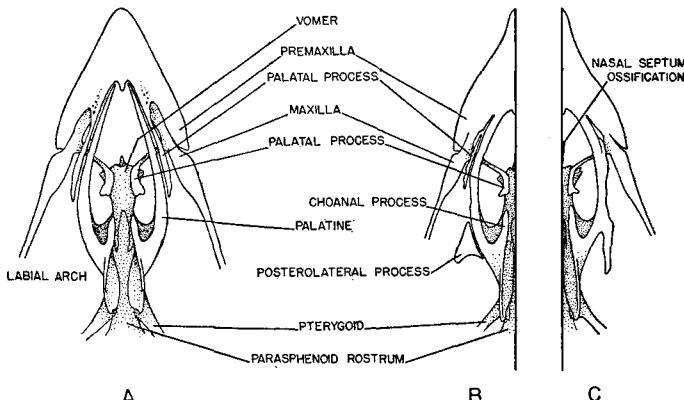


FIGURE 2. Palates of three stages of Oregon Junco (*Junco oreganus*), Family Emberizidae. A. Juvenile at time of nest leaving; B. Fully fledged juvenile; C. Adult.

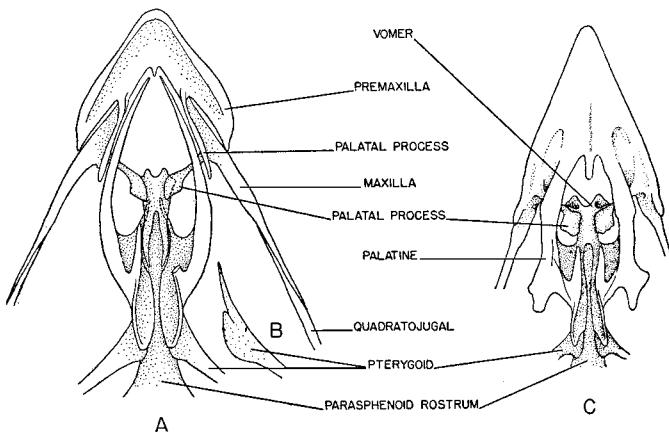


FIGURE 3. Palates of two stages of the House Sparrow (*Passer domesticus*), Family Ploceidae. A. Nestling about half grown; B. Pterygoid moved to the right to show anterior part; C. Adult.

McDowell (1948) and Hofer (1955) give reason for reviewing the relationship between the vomer and the pterygoid. Figures 3A, 3B and 5 show that in the nestling passerine the pterygoid is a unit structure as in the palaeognath and its anterior end is associated with the vomer (fig. 5). Later in development this association is confused. We must adopt new terminology in order to describe more clearly this area. In the passerine what has been called the "pterygoid" is actually only the posterior part of that bone; the term posteropterygoid would be a more useful name. The anterior part, the anteropterygoid (= hemipterygoid,

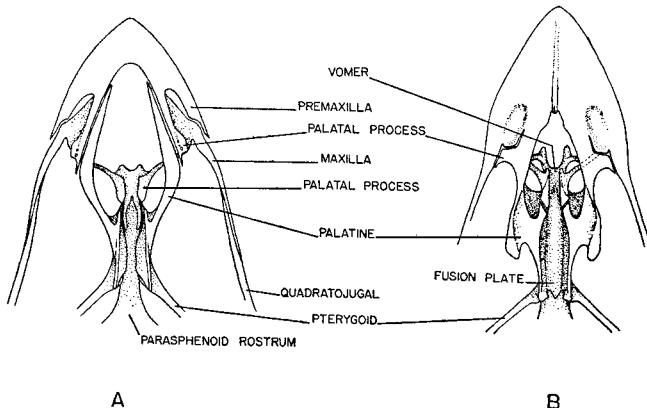


FIGURE 4. Palates of two stages of House Finch (*Carpodacus mexicanus*), Family Fringillidae. A. Nestling about half grown; B. Adult.

mesopterygoid of many authors, *see* Pycraft, 1900-03), fuses to the palatine, thus creating a compound bone which can be called the pala-topterygoid.

The pterygoid is not subdivided into two parts in all passerine birds. In *Taraba sp?* (American Museum 5342—Formicariidae), *Xiphorhynchus guttatus* (American Museum 5753—Dendrocolaptidae), and *Glyphorynchus sp?* (American Museum 5077—Dendrocolaptidae) the pterygoid is like that of the woodpecker and its anterior end is incompletely fused to the palatine (just as in most palaeognaths). Among the Piciformes there may be a joint between the parts as in *Indicator variegatus* (U.S. National Museum 428639). From this it follows that the palaeognath palate is present and hardly modified in some of the neognathous birds. Thus the passerine is more primitive in this feature

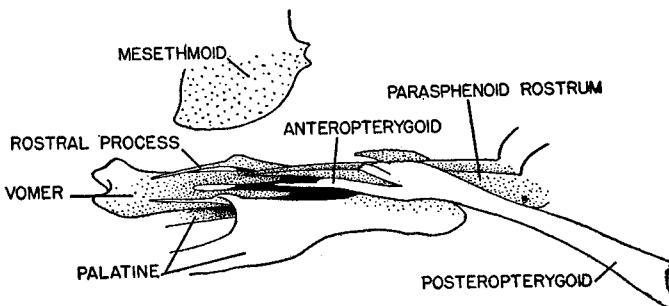


FIGURE 5. Dorsolateral view into orbit of nestling House Sparrow about half grown.

than many of the so-called "lower orders of birds" (i.e., the chicken, in which the anterior end of the pterygoid arises separate from the posterior part and fuses immediately with the palatine).

The posteropterygoid is fairly constant in its form and relationships with the exception of the development of an epipterygoid process in the woodpeckers (fig. 6A, *see* Verheyen, 1955: 14) and in *Sitta* (Sittidae). This process may be related to the wood-pecking habit of these two groups of birds. The passerine posteropterygoid (fig. 6B) has a small, dorsal projecting, *quadrate process* on its posterior, outer end. This small process is fairly characteristic of the group but it also occurs in the Coraciidae, Meropidae, and the Momotidae.

The vomer. The passerine vomer is extremely modified in that it fuses with chondral ossifications of the nasal capsule; Parker (1872: 224; 1875-79: 108, 109) has stressed this compound nature. He also described as "septomaxillaries" separate nasal capsule ossifications which I have observed only in the non-passерine species *Monias benschi* (U.S. National

Museum, 290927). The compound nature of the passerine vomer can be identified by the term vomeroturbinal. A vomeroturbinal perhaps is limited to the passerines—observed (?) elsewhere only in a specimen of *Nyctibius aethereus* (U.S. National Museum 321588).

The prefrontal (=lacrimal of most present authors). In the passerines this bone may be large or absent (see Beecher, 1953, figures); in the group as a whole it tends to be reduced in size. It may be present (well developed or vestigial) or absent within a family (Icteridae). In some species it does not appear even in the early stages of development. Because of this variation it may be an indicator of the phylogenetic position of different families, subfamilies and genera, since it

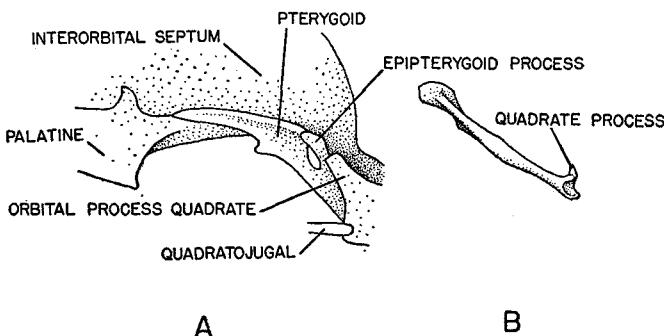


FIGURE 6. A. Dorsolateral view into orbit of Pileated Woodpecker (*Dryocopus pileatus*). B. Posteropterygoid of Common Raven (*Corvus corax*) as seen from same angle as in A.

can be assumed that in this case a well developed bone is more primitive than a small one or the total absence of this structure.

There is no evident adaptive value to reduction in size of the prefrontal, although it may be related to body size. Reduction in size of the body has usually been greater than that of the eye with the result that this bone may have been crowded out by the relative expansion of the orbit. This, however, is not the whole story since the passerine skull features an increase in size of the lateral ethmoid plate which lies in front of the eyeball. This plate has displaced the prefrontal forward so that it no longer forms the anterior margin of the orbit. This type of orbital modification is shared with the Caprimulgiformes and Apodiformes. Also not all small species lack the prefrontal; for example, *Troglodytes* has it.

The same pattern of reduction of the prefrontal appears in the suboscines and supports the supposition that the primitive bird was of medium size and less narrowly adapted to food source or environmental niche. Thus very large species and very small ones represent specializa-

tions in response to abundant or limited food niches—limited meaning food sources which offer a small volume of matter for each unit ingested, as well as limitation in the number of units available.

Absence of jugal. The jugal bone is missing from the labial arch of the upper jaw (zygomatic arch, quadratojugal arch) in the nestlings of passerines examined (Appendix 2). This lack is shared with the genus *Falco* and possibly with other groups and might be correlated with increase in relative size of the orbit. In this feature the passerine may be considered a specialized type. The labial arches of many more species will need to be investigated before any conclusions can be reached.

"Ectopterygoid" ossification. In the development of the oscine, the posterolateral angle of the palatine ossifies separately (seen only in *Junco oregonus* and *Pica pica*—observed also by Parker, 1875–79: 109, and called the transpalatine bone). This ossification appears about the time the juvenal is fully fledged; within a week it has fused to the palatine. That this bone is not a true part of the skull assemblage is shown by its association with the palatine muscle and its late appearance.

Holorhiny versus schizorhiny. This problem (Hofer, 1955) presents the difficult question, of which came first. It can only be assumed that holorhiny was primitive since this is the condition of the reptile, but the type of holorhiny is open to question, and it could in fact have been the style which Hofer has termed, "atypical schizorhiny" (better identified as incisorhiny?). In the passerines the situation is not as complex as in the Class Aves as a whole. Here the primitive, holorhinal opening has a nicely rounded posterior angle. Modification of form toward schizorhiny is correlated with elongation and narrowing of the upper jaw and changes in the relationships of the nasal capsule to the outer bones; these changes accompany retention of movement in the fronto-nasal hinge. A schizorhinal condition is approached by some dendrocolaptids and furnariids. A more rounded nasal margin (superholorhiny!) has developed in many short, thick-billed types. Thus, in the passeres, both extremes appear to be specializations.

The same sequence probably occurred in the Class as a whole but the pattern cannot be followed for the simple reason that both styles occur in closely related groups, indicating independent variations. This seems to be a functional characteristic related to several variables and probably modification has gone independently in either direction. I am inclined to agree with Hofer that the incisorhinal type appears to be the primitive form.

DISCUSSION AND CONCLUSIONS

The skull of the passerine does not differ markedly in any feature from types found in "lower groups" but it does differ on the basis of a combination of features. This skull cannot be considered as more specialized than that of other groups; to the contrary it must be considered less specialized than many. Reduction in the size of the prefrontal of passerines suggests that, as in other orders, the families consisting mainly of medium-sized species (in terms of all kinds of birds) are the primitive. Since the medium-sized species are actually the largest passerines, evolution in this group has tended toward small species fitting into restricted habitats where small food units are available. From this we can assume that the crows and the several Australian families of large "blackbirds" (Callaeidae, Grallinidae, Cracticidae—including *Pityriasis*, Ptilonorhynchidae, Paradisaeidae) are remnants of the ancestral oscine population—showing specialization, it is true, for various ways of life. Close to these would be the starlings, and in the nine-primaried assemblage the American blackbirds (Icteridae).

Where, or how, the small groups arose is not clear, since in their extreme specialization their origin has been obscured and can only be determined through detailed study (which as yet has not been carried out). It does not seem out of place to say that a recent approach (Mayr and Greenway, 1956), which lists the families with small species as if they were the more primitive and those with the large as if they were the more advanced (apparently on the basis of brain development), has reversed the real order of things. Admittedly the contemporary species, whether large or small, have been separated from their common ancestor for the same length of time, but the larger ones have probably retained more of the ancestral features in a recognizable form.

SUMMARY

Recent contributions to the phylogeny of the oscines are discussed and certain features of the anatomy of the skull reviewed. It is suggested that the form of the prefrontal is of value in determining the direction of evolution in the oscine. The development of this bone indicates that the large species of this suborder, as represented by the crows, are the more primitive while the small species are the more specialized. Other features of the skull suggest that the passerines may not be the most advanced birds.

APPENDIX 1

Representative species of passeriform families on which much of the comparative study is based. For convenience in reference (and not as an indication of the writer's opinion) the order is basically that of Wetmore (1951). The association of *Pithecates* with the Sturnidae and *Pityriasis* with the Cracticidae represents the writer's views.

Suborder Eurylaimi. Eurylaimidae: *Calyptomena viridis*, *Smithornis capensis*, *Corydon sumatranaus*.

Suborder Tyranni. Dendrocolaptidae: *Xiphorhynchus guttatus*, *Glyphorynchus sp.*, *Dendrocolaptes picumnus*. Furnariidae: *Upucerthia dumetaria*, *Automolus sp.* Formicariidae: *Taraba sp.* Rhinocryptidae: *Pteroptochus albicollis*. Cotingidae: *Pipreola riefferii*, *Rupicola peruviana*, *Cephalopterus ornatus*. Pipridae: *Pipra mentalis*. Tyrannidae: *Pipromorpha oleaginea*, *Tyrannus tyrannus*. Oxyruncidae: *Oxyruncus cristatus*. Phytotomidae: *Phytotoma rara*.

Suborder Menurae. Menuridae: *Menura superba*.

Suborder Oscines. Oriolidae: *Sphecotheres vieilloti*. Corvidae: *Pyrrhocorax pyrrhocorax*, *Podoces panderi*, *Corvus corax*. Cracticidae: *Pityriasis gymnocephala*, *Strepera graculina*, *Gymnorhina tibicen*, *Cracticus torquatus leucopterus*. Grallinidae: *Struthidea cinerea*, *Corcorax melanorhamphos*. Ptilonorhynchidae: *Ptilonorhynchus violaceus*, *Loria loriae*. Paradisaeidae: *Astrapia stephaniae*, *Paradisaea apoda*. Sittidae: *Sitta carolinensis*. Timaliidae: *Garrulax canorum*, *Garrulax striatus*. Pycnonotidae: *Microscelis virescens*. Troglodytidae: *Troglodytes aedon*. Laniidae: *Lanius collurio*. Callaeidae: *Callaeas cinerea*, *Heteralocha acutirostris*. Sturnidae: *Gracula religiosa*, *Scissirostrum dubium*, *Pithecates oreas*. Meliphagidae: *Foulehaio carunculata*, *Anthornis melanura*. Zosteropidae: *Zosterops montana*. Parulidae: *Mniotilla varia*, *Seiurus aurocapillus*. Icteridae: *Ostinops decumanus*, *Cassicus sp.*, *Sturnella magna*.

APPENDIX 2

Developmental stages, in the possession of the writer, used in the preparation of this account. Adult specimens of each were also available. The arrangement of families is modified from Wetmore (1951).

Hirudinidae. *Hirundo rustica*: 1 specimen, nearly fledged.

Corvidae. *Pica pica hudsonia*: 20 specimens of fifteen stages, half incubated to fully fledged.

Mimidae. *Dumetella carolinensis*: 1 specimen, half fledged.

Turdidae. *Turdus migratorius*: 1 specimen of each of two stages, half fledged and nearly fledged.

Sturnidae. *Sturnus vulgaris*: 8 specimens of four stages, half to fully fledged.

Icteridae. *Quiscalus quiscula versicolor*: 1 specimen nearly fledged.

Ploceidae. *Passer domesticus*: 5 specimens of four stages, half to fully fledged.

Emberizidae. *Junco oreganus*: 1 specimen of each of three stages, half to fully fledged.

Fringillidae. *Carpodacus mexicanus*: 1 specimen of each of three stages, just hatched to nearly fledged.

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