THE EMU

THE PHYLOGENY AND CLASSIFICATION OF THE AUSTRALO-PAPUAN PASSERINE BIRDS

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SUMMARY

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In a series of studies the technique of DNA-DNA hybridization has been used to compare the single-copy nuclear DNAs of all but three of the *ca* 70 traditional "families" of the order Passeriformes. The comparisons have included representatives of all of the suprageneric groups of Australo-Papuan passerines recognized by the authors of recent publications.

The DNA data show that the Australo-Papuan oscines (Passeres) consist primarily of an old endemic group, the parvorder Corvi, which began its radiation *ca* 55-60 million years ago (MYA) and today consists of three superfamilies and ten families. The superfamily Menuroidea includes the Climacteridae, Menuridae, and Ptilonorhynchidae. The Meliphagoidea is composed of the Maluridae, the Meliphagidae, and the Acanthizidae, and the Corvoidea includes the families Eopsaltriidae, Orthonychidae, Pomatostomidae and Corvidae. Many of the groups previously recognized as "families" are reduced to subfamilies or tribes.

The Corvi apparently originated in Australia and their sister group, the parvorder Muscicapae, may have originated in Africa, although an origin from an Asian ancestor is not ruled out. Since the Corvi are ten-primaried oscines it is clear that they did not diverge from a South American group. The Muscicapae includes all of the oscine groups not members of the Corvi.

As Australia drifted closer to Asia during the late Tertiary, representatives of some of the groups of Corvi dispersed to Asia and radiated there and in other parts of the world. In a reciprocal movement members of the Muscicapae have colonized Australia and New Guinea from Asia.

INTRODUCTION

The order Passeriformes contains 5247 (= 58%) of the 9021 species of Recent birds (Bock & Farrand 1980). Schodde (1975) listed 324 species of Australian passerines, of which 16 were introduced. Many of the 308 species occurring naturally may be defined as endemic, and *ca* 242 (79%) qualify as "old endemics." These 242 species belong to lineages that almost certainly originated and radiated in Australia and New Guinea. In Schodde's list (1975) they are members of the Menuridae, Atrichornithidae, Muscicapidae, Orthonychidae, Timaliidae, Maluridae, Acanthizidae, Neosittidae, Climacteridae, Meliphagidae, Ephthianuridae, Pardalotidae, Paradiseaeidae, Corcoracidae, Grallinidae, Artamidae, and Cracticidae.

There are *ca* 433 species of passerines recorded from Papua New Guinea (Peckover & Filewood 1976) and at least 221 (51%) qualify as old endemics. There is some overlap between the species of Australia and New Guinea but at least 400 (57%) of the more than 700 species of Australo-Papuan passerines are old endemics.

The determination of the taxonomic relationships of these birds, and their arrangement in a classification reflecting their phylogeny, has proved to be especially difficult. Convergent morphological characters have resulted in the clustering of Australo-Papuan species with groups based upon European, Asian, and African types, thus obscuring the true relationships of the old endemic taxa. This problem has long been recognized (e.g., Storr 1958; Mayr 1963; Sibley 1970, 1974, 1976; Schodde 1975; Schodde & McKean 1976; Boles 1979) but the available methods were often unsuccessful in differentiating between similarities due to common ancestry and those due to convergence.

During the past thirty years the development of techniques based upon the discoveries in molecular

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genetics and the biochemistry of nucleic acids have made it possible to compare the genomes of different species and to obtain measurements of the degrees of similarity between them. Since 1973 we have been using the technique of DNA-DNA hybridization to compare the nuclear DNAs of birds. We have prepared and studied more than 20,000 DNA-DNA hybrids involving more than 1,500 species in over 1,000 experimental sets. Approximately 10,000 of these DNA hybrids have been between species of passerine birds. All but three of the *ca* 70 traditional "families" of Passeriformes (e.g., Wetmore 1960) have been examined. The missing groups are the Philepittidae and Vangidae of Madagascar, and the Callaeidae of New Zealand. Thus we have compared species representing all of the suprageneric groups of Australo-Papuan passerines, as well as nearly all of the other passerine taxa above the generic level. The DNA hybridization evidence pertaining to the phylogeny and classification of the passerines has been presented in Sibley & Ahlquist (1980, 1981b, c, 1982a-i, in press a-d,) Sibley *et al.* (1982, in press a, b,) and Ahlquist *et al.* (in press).

In this paper we present a synopsis of our DNA hybridization studies of the Australo-Papuan passerines and a classification based upon the phylogeny revealed by the DNA-DNA measurements.

METHODS

Our DNA-DNA hybridization procedures have been described in Sibley & Ahlquist (1981a-c, 1982a-e, and in press a. See 1982e and in press d for descriptions in The Emu, and 1981a and 1983 for the most complete descriptions of the technique).

As described in the cited papers, we use a single number statistic, $T_{50}H$, to compare the genetic similarity between taxa. The $T_{50}H$ is the temperature in degrees Celsius at which 50% of all actual or potential DNA duplex molecules have dissociated when exposed to a controlled temperature gradient. The $T_{50}H$ is thus the median temperature of the DNA-DNA hybrid melting curve and the delta $T_{50}H$ measures the average amount of genetic divergence between the two species forming a DNA-DNA hybrid.

It has also become apparent that the *average* rate of DNA evolution (= nucleotide substitution) is the same in all avian lineages. Thus the delta T_{50} values are measures of the *relative* times of divergence between the lineages represented by the species composing a DNA-DNA hybrid. We have determined an approximate calibration of the delta $T_{50}H$ values in terms of *absolute* time which indicates that each delta $T_{50}H$ 1.0 = *ca* 4.5 million years (MY) since the two lineages diverged. For example, a delta $T_{50}H$ of 5.0 means that the two lineages diverged *ca* 22-23 MYA. The calibration in absolute time is tentative, preliminary, and subject to correction but the delta $T_{50}H$ values are valid indices of relative time and may, therefore, be used to reconstruct the branching pattern of the phylogeny.

CLASSIFICATION

The new classification presented in this paper is based

upon the phylogeny revealed by the DNA-DNA comparisons and it departs in many respects from previous classifications. However, it is the first to be based upon objective, quantitative data that measure genealogical distances, rather than upon subjective evaluations of morphological similarities and differences. We have found no reason to doubt the validity of the distance measurements and therefore we believe that the branching pattern of the phylogeny is essentially correct. However, the derivation of a classification from a phylogeny depends to some extent upon the taxonomic philosophy of the classifier. The DNA hybridization data show that the evolution of birds proceeds as a series of dichotomous branchings, beginning as speciation events, and resulting in adaptive radiations through time. This is, of course, standard evolutionary theory, based on many lines of evidence.

The genealogical distance measurements provided by the DNA hybridization technique produce a phylogeny which is independent of morphological characters. This removes the risk of circularity inherent in using morphology to deduce phylogeny, then using that phylogeny to document adaptive radiation and convergent evolution. A classification based upon morphological characters cannot entirely avoid this trap and it accounts for the difficulties that afflict the process of translating morphological characters into classifications.

The DNA-based phylogeny usually agrees quite well with evidence of relationships from morphology, but it is the exceptions to such congruencies that are of special interest because they identify convergences and reveal adaptive radiations, often previously unsuspected.

The Australo-Papuan passerines have proved to be one of the most fascinating and illuminating assemblages in the world because the old endemic elements were derived from a single ancestral source and their present diversity is the result of adaptive radiation within the continent. Under such circumstances convergence was bound to be frequent, as the marsupials also demonstrate so dramatically.

Because the phylogeny revealed by the DNA hybridization data is cladistic, and because it reconstructs the history of the avifauna, we agree with Hennig (1966) and his many disciples, that a classification should reflect only the branching pattern of the phylogeny. We also accept Hennig's principles that categorical rank should be determined by the age of origin of lineages, and that sister groups should be of coordinate rank. To make it practical to reflect most, if not all, of the cladistic details revealed by the DNA data we also accept the principles of "subordination and sequencing" of categories proposed by Nelson (1973).

Subordination concerns the division of taxa into sub-taxa, which is accomplished by grouping together the descendants of the same ancestral taxon. For example, the division of a family into two or more subfamilies. The problem is to use a consistent criterion to determine the number of subtaxa. We use the delta $T_{50}H$ values to determine the number and rank of taxa and subtaxa. All taxa that branched from a sister group within the range of delta values assigned to a given categorical rank are assigned to that rank. For example, all groups that branched from one another between delta $T_{50}H$ 9 and 11 are considered to be families. See below for the definitions of categories.

Sequencing concerns how subgroups of equivalent rank may be listed in a specific order. We use the branching order of the phylogeny to determine the linear order of taxa in the classification, i.e., the taxon that branched first within a group is listed first, etc. This produces a classification from which it is possible to reconstruct the phylogeny.

We reject the argument that a classification should reflect the degrees of morphological specialization as judged by the human eye. We agree with Griffiths (1973: 340) that it is neither possible nor important to attempt to express "evolutionary grades" of morphological characters. We also believe that the DNA hybridization data provide the "satisfactory general measure of evolutionary differentiation" which Griffiths (1973: 338) considered to be "the central problem of evolutionary classification."

Because the delta $T_{50}H$ values are measures of the divergence times between lineages it has been possible to apply Hennig's (1966) principle that categorical rank should reflect the time of origin. However, we cannot apply the Hennigian principle that every dichotomy should result in new categorical names for the resultant sister groups because the DNA phylogenies are too complex and would proliferate names beyond reason or practicality. We have compromised by assigning categories to segments of the delta $T_{50}H$ scale, which also reflects the time scale, as follows: Up to delta $T_{50}H$ 4.0 (ca 18 MY) = congeners or closely related genera; delta 4-7 (ca 18-30 MY) = tribes; delta 7-9 (ca 30-40 MY) = subfamilies; delta 9-11 (ca 40-50 MY) = families; delta 11-13 (ca 50-60 MY) = superfamilies; delta 13-15 (ca 60-70 MY) = parvorders; delta 15-18 (ca 70-80 MY) = infraorders; delta 18-20 (ca 80-90 MY) = suborders; delta 20-22 (ca 90-100 MY) = orders. We have had to be flexible about the boundaries of categories, allowing a variation of ± 1.0 delta $T_{50}H$ or ca 4.5 MY. Thus our classification reflects the DNA-based phylogeny, but only the actual measurements and the phylograms reveal all the details in the branching patterns.

Our classification is also a step toward the ideal of "categorical equivalence" among all groups of organisms, which Hennig (1966) advocated, and which we have discussed elsewhere (Sibley & Ahlquist 1982d).

The following discussion will concentrate on the Australo-Papuan passerines with minimal attention to other groups. Figures 1-4 present the phylograms and Table I the classification. The phylograms were developed by the average linkage method from a matrix of delta $T_{50}H$ values. Space limitations preclude the publication of the entire data set but some of the tables of data have been published in our papers listed in the References.

THE SUBORDERS OF THE PASSERIFORMES

Müller (1847) discovered the morphological complexity of the passerine syrinx and since then the major subdivisions have been based, in part, upon syringeal differences. Sibley (1970: 23-31) and Ames (1971: 127-129, 153-164) have reviewed this subject.

Mayr & Amadon (1951) and Wetmore (1960) recognized four suborders: Eurylaimi for the broadbills; Tyranni for the New World suboscines plus the pittas, New Zealand wrens, and philepittas; Menurae for the lyrebirds and scrub-birds, and Oscines or Passeres for the "songbirds." Olson (1971) placed the broadbills in the Tyranni because of their convergent similarities to cotingas, and suggested that the lyrebirds *Menura* might be "closer to the Oscines than to the Tyranni." Sibley (1974) and Feduccia (1975) concluded that the lyrebirds and scrub-birds are oscines and should not be placed in a separate suborder.

The DNA hybridization data show that the broadbills and pittas are sister groups, not closely related to the New World suboscines, and that *Menura* is an oscine, most closely related to the scrub-birds and the bowerbirds.

Thus we recognize only two suborders, the Oligomyodi for the suboscines and the Passeres for the oscines. These two groups diverged ca 85-90 MYA, as indicated by the delta $T_{50}H$ value of 19.8. Sibley et al. (1982) and Sibley & Ahlquist (in press b) present additional information.

THE SUBORDER OLIGOMYODI

The Oligomyodi are represented in Australia and New Guinea by the pittas *Pitta*, presumably recent arrivals in both areas. The infraorder Eurylaimides (broadbills, pittas) branched from the lineage leading to the infraorder Tyrannides (New World suboscines) at delta $T_{50}H$ 17.0, ca 75-80 MYA. The Pittidae and Eurylaimidae diverged ca 55-57 MYA (delta $T_{50}H$ 12.3).

The New Zealand wrens (infraorder Acanthisittides) are the only living descendants of the oldest branch in the Oligomyodi at delta $T_{50}H$ 17.7, *ca* 80 MYA (Sibley *et al.* 1982).

THE SUBORDER PASSERES

The DNA data reveal two major groups of Passeres which we designate as the parvorders Corvi and Muscicapae, each divided into three superfamilies. The Corvi and Muscicapae diverged *ca* 58–60 MYA (delta 13) in the Palaeocene. Most of the living Corvi are confined to Australasia and it seems highly probable that the group originated in Australia because the oldest lineages are still confined to Australia and New Guinea. These are the lyrebirds, scrub-birds, bowerbirds, and treecreepers of the superfamily Menuroidea; the fairy-wrens, honey-eaters, and Australian warblers of the superfamily Meliphagoidea; and most of the many groups forming the superfamily Corvoidea. See the figures and Table I for the names of these taxa.

TABLE I

Classification of the Australo-Papuan passerine birds

Order Passeriformes
  Suborder Oligomyodi (Suboscines)
    Infraorder Eurylaimides
      Superfamily Pittoidea, Pittas and Broadbills
        Family Pittidae, Pittas
  Suborder Passeres (Oscines)
    Parvorder Corvi
      Superfamily Menuroidea
        Family Climacteridae, Treecreepers
        Family Menuridae
          Subfamily Menurinae, Lyrebirds
          Subfamily Atrichornithinae, Scrub-birds
        Family Ptilonorhynchidae, Bowerbirds
      Superfamily Meliphagoidea
        Family Maluridae
          Subfamily Malurinae
            Tribe Malurini, Fairy-wrens
            Tribe Stipiturini, Emu-wrens
          Subfamily Amytornithinae, Grasswrens
        Family Meliphagidae, Honeyeaters, incl.
               Ephthianura and Ashbyia
      Family Acanthizidae
        Subfamily Pardalotinae, Pardalotes
        Subfamily Dasyornithinae, Bristlebirds
        Subfamily Acanthizinae
          Tribe Sericornithini, Scrub-wrens
          Tribe Acanthizini, Thornbills, Whitefaces, etc.
      Superfamily Corvoidea
        Family Eopsaltriidae, Australo-Papuan robins
        Family Orthonychidae, Log-runners or
               Chowchillas
        Family Pomatostomidae, Australian Pseudo-
               babblers
       Family Corvidae
        Subfamily Cinclosomatinae, Quail-thrushes, etc.

TABLE I *Continued*

        Subfamily Corcoracinae, White-winged Chough,
                   Apostlebird
        Subfamily Pachycephalinae
          Tribe Neosittini, Sittellas
          Tribe Falcunculini, Shrike-tits
          Tribe Oreoicini, Crested Bellbird
          Tribe Pachycephalini, Whistlers, Shrike-
                   thrushes, etc.
        Subfamily Monarchinae
          Tribe Rhipidurini, Fantails
          Tribe Dicrurini, Drongos
          Tribe Monarchini, Monarchs, Magpie-larks
        Subfamily Corvinae
          Tribe Corvini, Crows, Ravens, etc.
          Tribe Paradisaeini, Birds-of-Paradise
          Tribe Cracticini, Currawongs, Butcherbirds,
                 Australian magpies,
                 Peltops, Artamus
        Tribe Oriolini, Orioles, Figbirds, Cuckoo-
                shrikes, Trillers
      Family Laniidae, True Shrikes: *Lanius*
               (+ *Corvinella* and *Eurocephalus*
               of Africa).
  Parvorder Muscicapae
    Superfamily Turdoidea
      Family Turdidae
        Subfamily Turdinae, *Zoothera, Turdus*
        Subfamily Muscicapinae
          Tribe Muscicapini, *Muscicapa*
          Tribe Erithacini, *Saxicola*
      Family Sturnidae
        Tribe Sturnini, Starlings
    Superfamily Sylvioidea
      Family Hirundinidae, Swallows
      Family Pycnonotidae, Bulbuls
      Family Cisticolidae, African Warblers, *Cisticola*
      Family Zosteropidae, White-eyes
      Family Sylviidae
        Subfamily Phylloscopinae, Leaf Warblers
        Subfamily Megalurinae, Grass Warblers,
                  Megalurus, Eremiornis,
                  Cincloramphus
        Subfamily Sylviinae
          Tribe Sylviini, Old World Warblers,
                Locustella, Acrocephalus
    Superfamily Fringilloidea
      Family Alaudidae, Larks
      Family Nectariniidae
        Subfamily Melanocharitinae, Papuan Sunbirds,
                   Berrypeckers,
                   Melanocharis, incl.
                   Toxorhampus
        Subfamily Nectariniinae
          Tribe Dicaeini, Flowerpeckers
          Tribe Nectariniini, Sunbirds
      Family Ploceidae
        Subfamily Passerinae, Sparrows, incl. *Passer*
        Subfamily Estrildinae, Waxbills, Grassfinches
        Subfamily Motacillinae, Pipits and Wagtails
        Subfamily Ploceinae, Weaverbirds, incl. *Euplectes*
      Family Fringillidae
        Tribe Carduelini, Cardueline Finches

(Genera *incertae sedis: Rhamphocharis, Oreocharis, Paramythia, Ifrita, Melampitta, Androphobus, Amalocichla*).
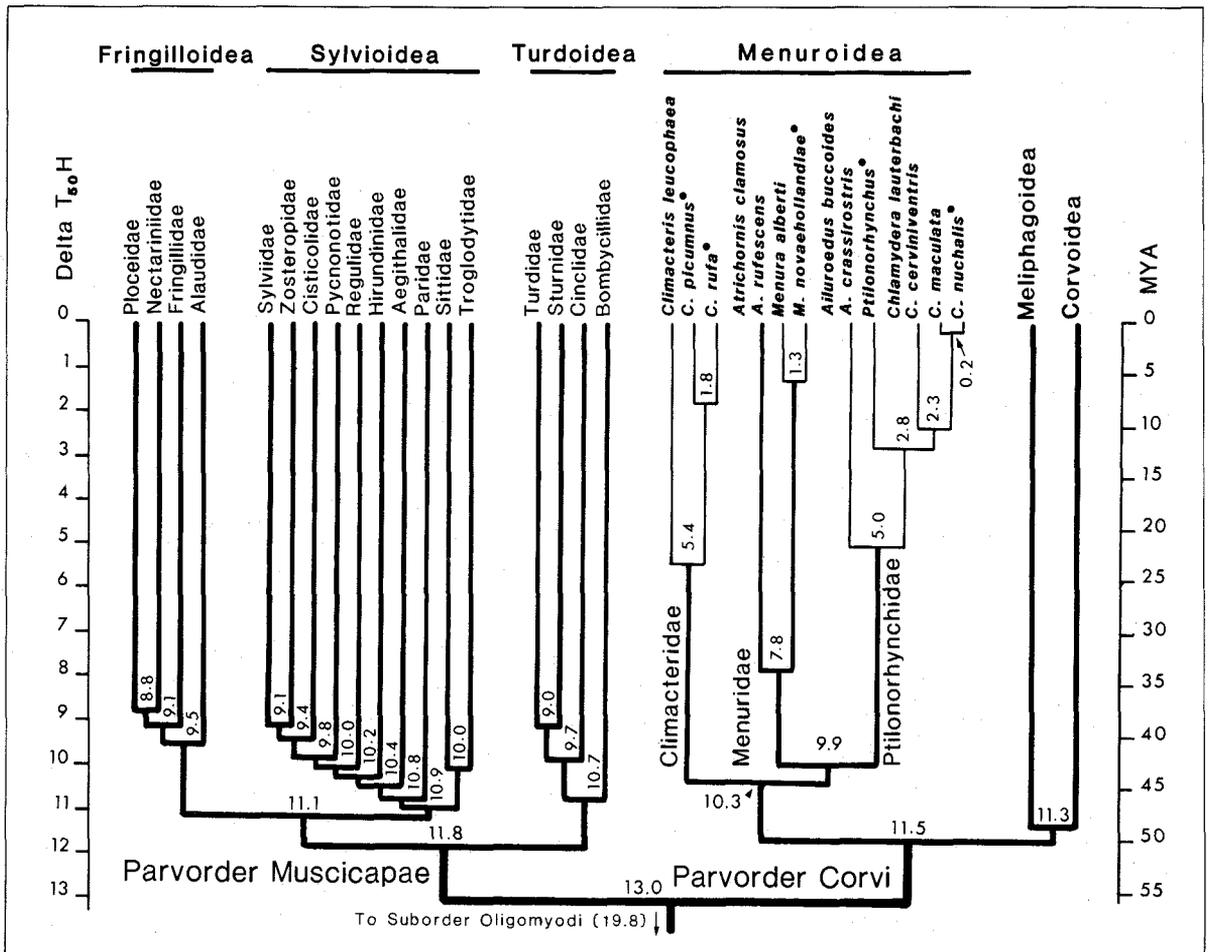
Figure 1. Phylogeny of the major subgroups of the suborder Passeres. The DNAs of the taxa followed by black dots, e.g., *C. rufa*, were used as radio-labelled "tracers." Numbers on divergence nodes, e.g., 11.5, are average Delta $T_{50}H$ values. See text for definition of Delta $T_{50}H$. MYA = millions of years ago.

The Muscicapae includes all of the Passeres that are not members of the Corvi. All of the Muscicapae in Australia and New Guinea are relatively recent colonists, migrants, vagrants, or introductions.

THE SUPERFAMILY MENUROIDEA

One of the major surprises revealed by the DNA comparisons is that the bowerbirds are not closely related to the birds-of-paradise. Instead, the bowerbirds are the sister group of the lyrebirds and scrub-birds. The birds-of-paradise are members of the Corvoidea and are most closely related to the Australo-Papuan magpies and butcherbirds (Cracticini).

Sibley (1974) suggested a close relationship between *Menura* and the bowerbirds based on the similar electrophoretic patterns of their egg white proteins and shared behavioural and other characters, and the DNA data reveal many more details about the relationships of all of these taxa.

Feduccia & Olson (1982) interpreted certain similiar anatomical characters as evidence of a relationship between the New World suboscine family Rhinocryptidae and the lyrebirds. They also suggested that skeletal differences between *Menura* and the bowerbirds proved that the two groups are unrelated. The DNA hybridization measurements show that these proposals were incorrect.

The relationships of the treecreepers *Climacteris* have been uncertain. The honeyeaters were favoured as their closest relatives by Harrison (1969) and Parker (1982); they were viewed as a "distinct branch of a major Australian radiation" by Orenstein (1977); allied with the Northern creepers *Certhia* by Wetmore (1960) and others, or placed in a monotypic family (e.g. Schodde 1975).

The DNA data produced an answer more surprising than any of these for they show that the treecreepers are the descendants of the oldest known branch in the Menuroidea at delta $T_{50}H$ 10.4, *ca* 45–48 MYA (Sibley *et al.* in press b). Although *Climacteris* is morphologically distinct from the lyrebirds and bowerbirds it is similar to *Atrichornis* in size, coloration, bill shape, and nasal

opercula. These superficial characters may mean little but they suggest that a search for additional anatomical evidence might be fruitful.

THE SUPERFAMILY MELIPHAGOIDEA

The fairy-wrens *Malurus*, emu-wrens *Stipiturus*, and grasswrens *Amytornis* of the Maluridae have often been included in the Sylviidae but the DNA data show that they are the sister group of the Australian warblers (Acanthizidae) and honeyeaters (Meliphagidae) from which they branched *ca* 47–50 MYA = delta $T_{50}H$ 10.7 (Sibley & Ahlquist 1982h).

The Meliphagidae includes the Australian chats *Ephthianura* and *Ashbyia* which, the DNA data indicate,
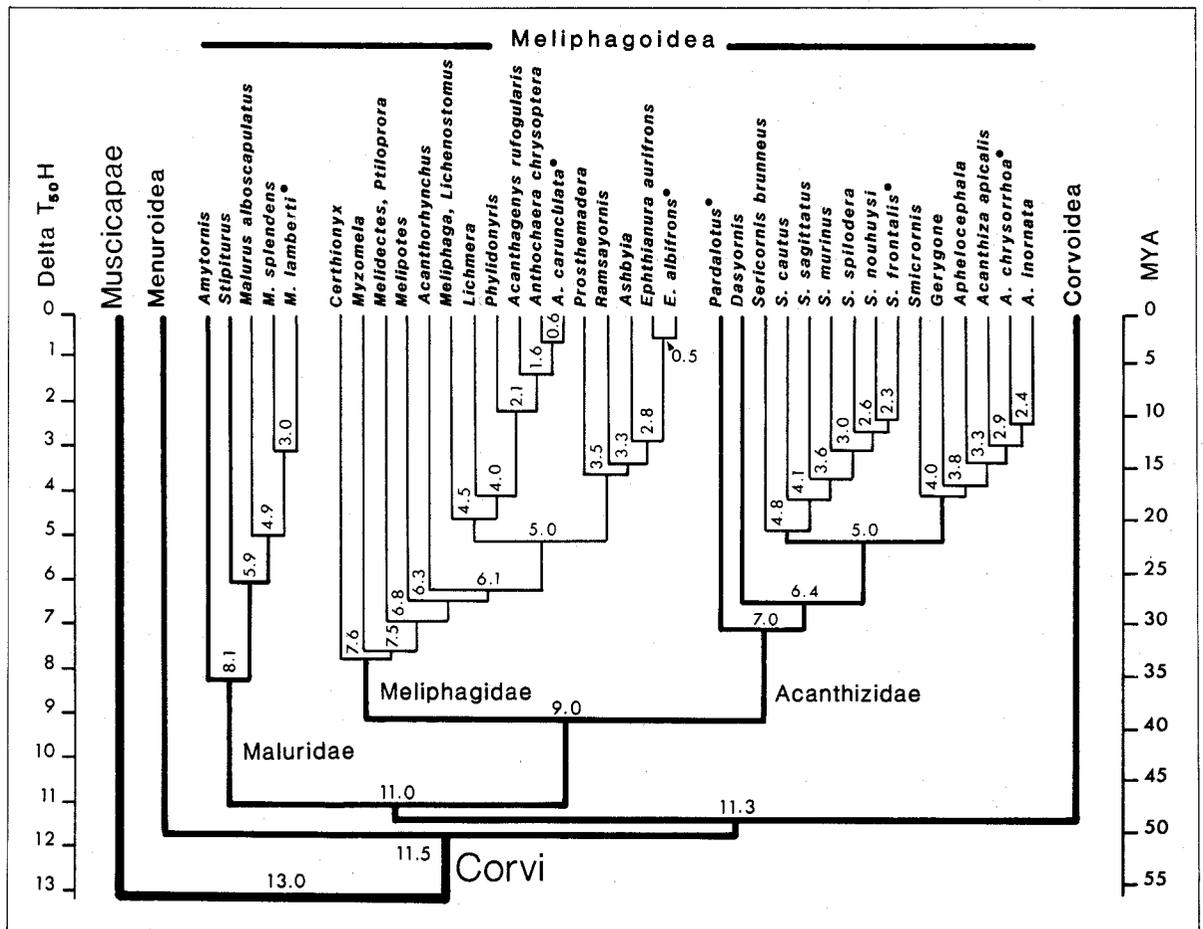

Figure 2. Phylogeny of the superfamily Meliphagoidea. See caption of Figure 1 for explanation of abbreviations and symbols.

are actually more closely related to such typical honey-eaters as *Anthochaera, Phylidonyris,* and *Entomyzon* than are such unquestionable meliphagids as *Certhionyx* and *Myzomela.* Evidence that *Ephthianura* and *Ashbyia* are honeyeaters has also been reported by Sibley (1970: 73, 1976: 566) and Parker (1973).

The Australo-Papuan warblers (Acanthizidae) are not related to the Sylviidae, but are members of an old endemic group that includes the genera *Acanthiza, Sericornis, Crateroscelis, Dasyornis, Smicrornis, Gerygone, Aphelocephala, Origma,* and *Pycnoptilus* of Schodde (1975).

The pardalotes *Pardalotus* are also members of the Acanthizidae, not relatives of the flowerpeckers *Dicaeum,*

which are closely related to the sunbirds (Nectariniidae). These relationships were also suggested by the electro-phoretic patterns of the egg-white proteins (Sibley 1976: 567).

THE SUPERFAMILY CORVOIDEA

The Corvoidea includes the remaining old endemics, plus the crows and ravens *Corvus,* magpies *Pica,* jays *Garrulus, Cyanocitta,* etc (Corvini), the orioles and cuckoo-shrikes (Oriolini), the true shrikes (*Lanius,* etc.) the vireos (Vireoninae, Sibley & Ahlquist 1982c), the fairy-bluebirds *Irena,* the ioras *Aegithina,* and the leaf-birds *Chloropsis.* These groups presumably were derived from corvoid ancestors that "escaped" from Australia and radiated elsewhere.
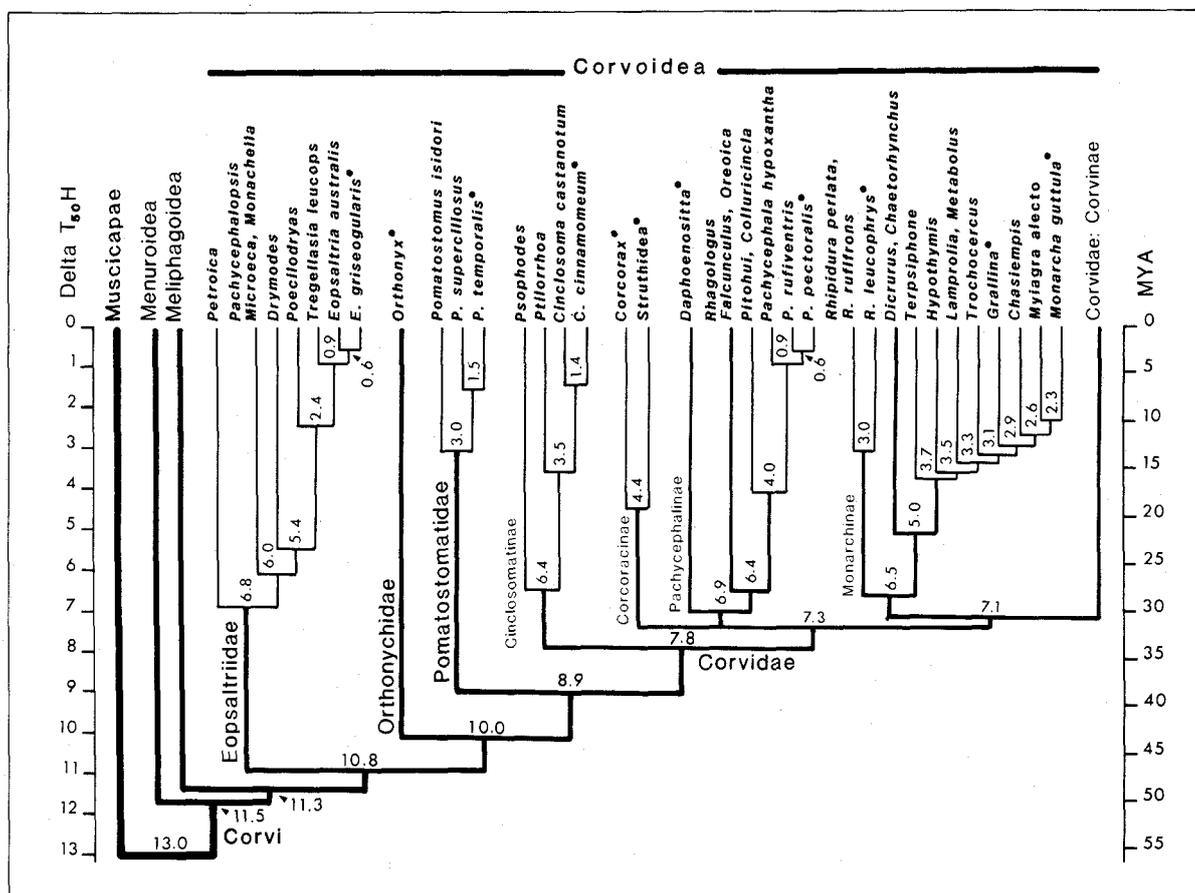

Figure 3. Phylogeny of the superfamily Corvoidea, in part. See caption of Figure 1 for explanation of abbreviations and symbols. Note: The correct spelling of the family name based on *Pomatostomus* is Pomatostomidae.

The first branch in the corvoid phylogeny separated the ancestor of the Australo-Papuan robins and fly-catchers (Eopsaltriidae) from that of the other corvoid groups. The scrub-robins *Drymodes*, often thought to be turdine thrushes or timaliine babblers, are members of the Eopsaltriidae (Sibley & Ahlquist 1982e). Other genera are *Eopsaltria, Petroica, Melanodryas, Microeca, Tregellasia, Poecilodryas, Heteromyias, Monachella, Peneothello*, and *Pachycephalopsis*. Other Papuan genera may also be members of the Eopsaltriidae, but we lack their DNAs. These genera are not related to the true thrushes (Turdinae), the Old World flycatchers (Muscicapinae), or the true babblers (Timaliini) (Sibley & Ahlquist 1980; 1982b).

The genus *Orthonyx* (logrunners) is so distant from other corvoids that we place it in a monotypic family.

Similarly, the pseudo-babbler genus *Pomatostomus*, often thought to be a timaliine babbler, is also the descendant of an early branch in the Corvoidea and is therefore given family rank. It is not related to the Sylviidae, which includes the true babblers (Timaliini).

The remaining corvoids must be included in the family Corvidae if we are to preserve the structure of a cladistic classification. Even so, we are forced to violate the principle of coordinate ranking for sister groups to avoid an excessive number of categorical ranks. To accommodate to this compromise we have used the principles of "subordination and sequencing" proposed by Nelson (1973), and discussed above under Classification. The resulting classification reduces several morphologically distinctive groups to subfamilies and tribes but it is a reasonably accurate reflection of the phylogeny.
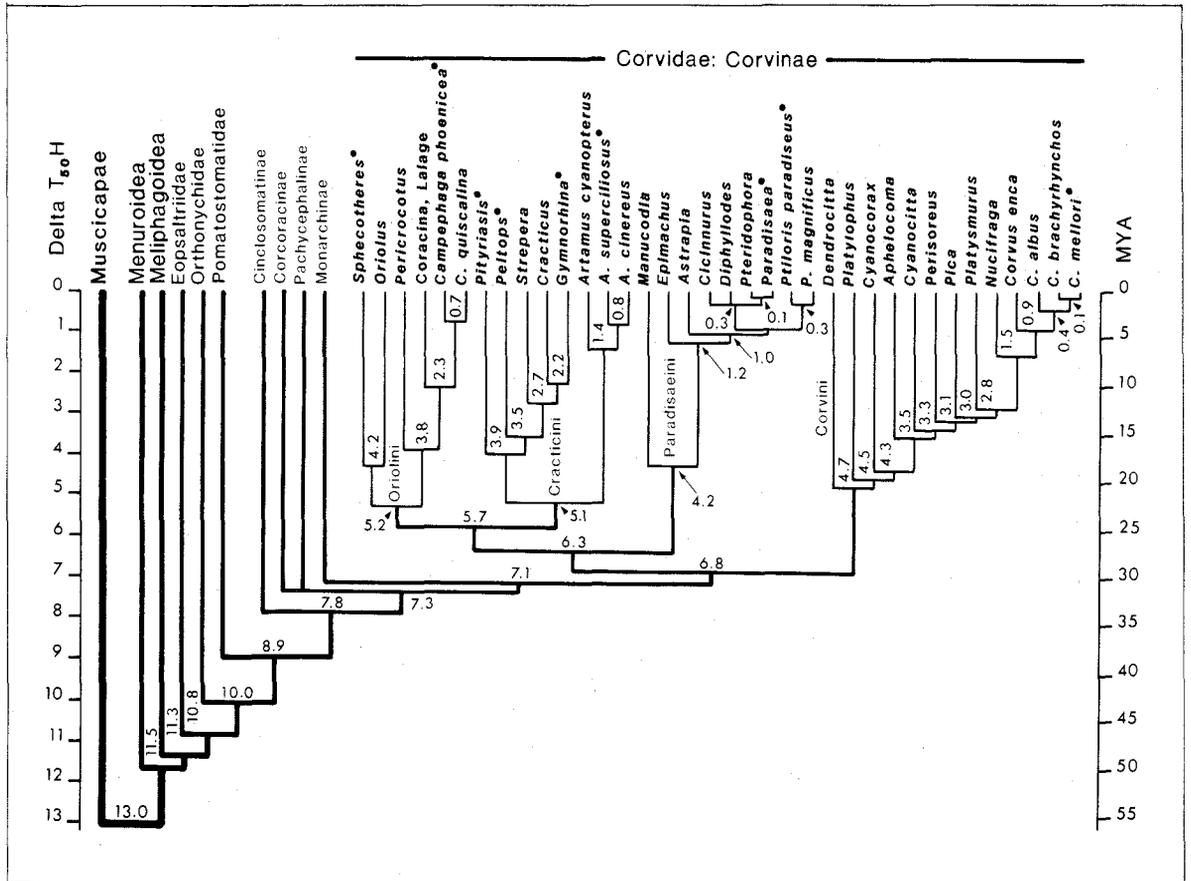

Figure 4. Phylogeny of the family Corvidae, in part. See caption of Figure 1 for explanation of abbreviations and symbols.

If we were to inflate the ranks so that tribes became families the entire hierarchy would have to shift so much that the groups traditionally recognized as orders would, in some cases, become classes.

The subfamily Cinclosomatinae includes the quail-thrushes *Cinclosoma*, the three species of Papuan "rail-babblers" *Ptilorrhoa (Eupetes)*, and the whipbirds and wedgebills *Psophodes*. Peckover & Filewood (1976) list *Melampitta, Orthonyx, Androphobus*, and *Ifrita* in the "Cinclosomatidae". Although we can be certain that *Orthonyx* does not belong in this group, we lack DNAs of the other genera.

The White-winged Chough *Corcorax* and the Apostle-bird *Struthidea* are closely related genera which we place in the Corcoracinae. The Magpie-lark *Grallina*, often considered to be related to *Corcorax* and *Struthidea* because all three build mud nests, is actually a large monarch, closely related to *Monarcha*.

The Pachycephalinae includes the whistlers *Pachycephala*, shrike-thrushes *Colluricincla*, Crested Bellbird *Oreoica*, the shrike-tits *Falcunculus*, the pitohuis *Pitohui*, and the Mottled Whistler *Rhagologus. Pachycare* of New Guinea is, presumably, also a member of this subfamily, but we lack its DNA.

The nuthatch-like sittellas *Daphoenositta* are the descendants of the earliest branch in the Pachycephalinae and we place them in the tribe Neosittini. Their nests, eggs, and immature plumages are similar to those of the whistlers *Pachycephala*, which caused Parker (1982) to suggest that the sittellas "may have arisen...from the ancestors of the Pachycephalidae." Thus the DNA evidence is congruent with the characters noted by Parker. The convergently similar nuthatches *Sitta* are members of the parvorder Muscicapae, superfamily Sylvioidea (Sibley & Ahlquist 1982f, g).

The monarch flycatchers (Monarchinae) occur in Australia, New Guinea, many Pacific islands, southern Asia, and Africa. We have DNA hybridization data for *Monarcha, Myiagra, Arses, Hypothymis, Philentoma, Metabolus, Terpsiphone, Trochocercus, Lamprolia,* and *Chasiempis*, showing that all are monarchs. The only muscicapine flycatcher occurring in either Australia or New Guinea is *Muscicapa griseisticta* which is a winter visitant to New Guinea from eastern Asia.

The magpie-larks *Grallina cyanoleuca* and *G. bruijni* are also monarchs. *G. cyanoleuca*, at an average delta $T_{50}H$ 2.9 from *Monarcha*, is barely in a separate genus and is as close to *Monarcha* as are *Lamprolia* (3.3), *Trochocercus* (3.1), or *Chasiempis* (2.6).

The drongos, *Dicrurus* and *Chaetorhynchus*, are also

monarchines with an average delta $T_{50}H$ of 5.0 from *Monarcha* and *Grallina*. We place the drongos in the tribe Dicrurini.

The fantails *Rhipidura* are the descendants of the earliest branch in the monarchine cluster and the sister group of the other monarchines. We recognize a tribe Rhipidurini and list the fantails first in the Monarchinae in accordance with the rules of subordination and sequencing.

The other corvoids are placed in the subfamily Corvinae which thus includes at least six groups traditionally ranked as families: Corvidae, Paradisaeidae, Artamidae, Cracticidae, Oriolidae, and Campephagidae. That these groups should be so closely related is surprising but their most recent common ancestors began to diverge *ca* 30–32 MYA as indicated by the average delta $T_{50}H$ of 6.8 for the branch between the Corvini and the other groups. We believe that it may be desirable to revise the categorical assignments in the future when we have a complete set of data for the entire Class Aves, which could be raised to the level of a superclass and thus permit the entire hierarchy to move upward. For now it seems preferable to use the system we have proposed so that a reasonable degree of categorical equivalence can be maintained.

The tribe Corvini includes the same taxa as the traditional Corvidae, namely, the crows, jays, magpies, nutcrackers, choughs, etc. Of these only the genus *Corvus* occurs in Australia and the close relationship between the Australian *C. mellori* and other species outside of Australia (Fig. 4) indicates that the Australian species of *Corvus* are the descendants of recent colonists.

The Paradisaeini includes only the birds-of-paradise. The sexually monomorphic manucodes branched from the lineage that produced the dimorphic taxa *ca* 18–20 MYA (delta 4.2) and the dimorphic taxa are closely related to one another. Between the Paradise Riflebird *Ptiloris paradiseus* and six other dimorphic genera we obtained delta $T_{50}H$ values from 0.9 to 1.2. (See Fig. 4). These values indicate that these "genera" diverged from one another within the past 4–5 MY. All could be contained in a single genus and it is not surprising that at least ten of the dimorphic genera have hybridized and produced viable offspring (Mayr 1942: 260). The distinctive male plumages and displays evolved in response to sexual selection and selection against hybridization and are thus additional evidence of their close relationships, not of phylogenetic diversity (Sibley 1957). Diamond (1972) proposed that the 20 genera of birds-of-paradise usually recognized could be reduced to ten. The DNA data suggest that even more "lumping" may be justified.

The Cracticini includes the woodswallows *Artamus*,

the currawongs *Strepera*, Australian magpies *Gymnorhina*, butcherbirds *Cracticus*, the genus *Peltops* of New Guinea, and the Bornean Bristlehead *Pityriasis gymnocephala*. *Artamus* branched from the lineage leading to the other genera *ca* 22-24 MYA and the Artamidae have been recognized as a monotypic family in all recent classifications. *Pityriasis* was placed with *Cracticus* and *Gymnorhina* from its discovery in 1835 until recent years when some authors have placed it in the "Prionopidae." It is only delta 3.9 from the other cracticines (Ahlquist *et al.* in press). The Papuan genus *Peltops* is also a cracticine at delta 3.5 from the typical genera. It has usually been thought to be a monarch (Sibley & Ahlquist in press d).

The Oriolini includes the Old World orioles ("Oriolidae") and the cuckoo-shrikes ("Campephagidae"). It was another surprise to discover that these two morphologically distinctive groups are so closely related. They diverged from one another at delta $T_{50}H$ 5.2, *ca* 23-24 MYA. The *Oriolus* in Australia and New Guinea are probably recent immigrants.

The true shrikes (Laniidae) are the sister group of the Corvidae. The two lineages diverged *ca* 40 MYA. The Laniidae includes only *Lanius* and the African genera *Corvinella* and *Eurocephalus*. The other African "shrikes" are members of the monarchine radiation and we place them in the tribe Malaconotini, subfamily Monarchinae, of the Corvidae. The Laniidae are not represented in Figure 4.

There are at least seven Papuan genera of uncertain affinities: *Rhamphocharis, Oreocharis, Paramythia, Ifrita, Melampitta, Androphobus,* and *Amalocichla*. Some of these may be members of the Corvi, but we lack their DNAs. *Melanocharis* and *Toxorhamphus* are nectariniids and are treated below.

THE PARVORDER MUSCICAPAE

The remaining oscines are members of the parvorder Muscicapae, which we subdivide into three superfamilies: Turdoidea, Sylvioidea, and Fringilloidea.

THE SUPERFAMILY TURDOIDEA

The Turdoidea includes the waxwings, silky flycatchers, and palm chats (Bombycillidae), dippers (Cinclidae), thrushes, Old World flycatchers and chats (Turdidae), and the starlings and mockingbirds (Sturnidae). In Australia and New Guinea the only unquestionable native members of the Turdoidea are three species of Turdidae and two genera of the Sturnidae.

The native turdids are the Scaly Thrush *Zoothera*

dauma, the Island Thrush *Turdus poliocephalus*, and the Pied Chat *Saxicola caprata*. All occur widely outside of Australia and/or New Guinea and they are obviously recent colonists, not old endemics. The Papuan genus *Amalocichla* may or may not be turdine, but we lack its DNA. As noted above, *Drymodes* is not a thrush, but a member of the corvoid family Eopsaltriidae, and an old endemic.

The muscicapine flycatchers (Turdidae: Muscicapinae: Muscicapini) do not occur in Australia or New Guinea as breeding birds and the only representative of the group is the Grey-streaked Flycatcher *Muscicapa griseisticta* which is a winter visitant to New Guinea from eastern Asia.

The convergent similarities between the muscicapine flycatchers and the monarchs, whistlers, Australo-Papuan "robins" and "flycatchers", have caused one of the most troublesome problems in determining the relationships of the passerines of Australia and New Guinea. This problem can be traced back to early attempts to classify birds, but it was the influence of Hartert (1910) that caused many subsequent authors to recognize a large family "Muscicapidae" that included the muscicapines, monarchines, sylviine warblers, timaliine babblers, and turdine thrushes. Hartert's "Muscicapidae" was adopted by Mayr & Amadon (1951) and it formed part of the widely used "Basel sequence" which was adopted for the Peters check-list by Mayr & Greenway (1956). The publication of this paper stimulated a series of other proposals concerning the classification of the oscines (Delacour & Vaurie 1957; Amadon 1957; Wetmore 1957; Mayr 1958; Storer 1959). From these debates there developed a consensus that an assemblage of "primitive insect eaters" should be recognized, composed of the muscicapine flycatchers, the monarchs and other Australo-Papuan "flycatchers", the thrushes, sylviine warblers, Australo-Papuan "warblers" and the babblers, with included or adjacent groups being the mockingbirds *Mimus, Toxostoma*, etc, wrens *Troglodytes*, etc, dippers *Cinclus*, accentors *Prunella*, and the wagtails and pipits *Motacilla, Anthus*. Many classifications have included all or part of these groups in a family "Muscicapidae" (e.g., Vaurie 1959; Rand & Gilliard 1960; Berndt & Meise 1962; Storer 1971; Schodde 1975; Voous 1977; American Ornithologists' Union Check-list 1983).

The DNA hybridization data have revealed that the "Muscicapidae", as defined above, is a polyphyletic assemblage that has included members of both parvorders and of all of the six superfamilies of the Passeres! It is a classical example of the difficulties encountered by taxonomists when trying to determine the boundaries of monophyletic clusters from morphological characters.

(See Sibley & Ahlquist 1980; 1981b, c; 1982e, g, h; in press a, c for the evidence supporting the foregoing analysis).

We urge the abandonment of the "Muscicapidae" as a family name to terminate the confusion that will be caused by its continued use. We have used Muscicapinae for the subfamily of the Turdidae that includes the muscicapine flycatchers (Muscicapini) and the chat-like thrushes (Erithacini).

The starlings *Sturnus, Aplonis,* etc have usually been thought to be related to the crows, orioles, drongos, weaverbirds, or New World troupials (Icterini). DNA comparisons show that the starlings are related most closely (delta $T_{50}H$ 5.7) to the New World mockingbirds and thrashers *Mimus, Toxostoma,* etc and we treat the two groups as sister tribes (Sturnini, Mimini) in the Sturnidae. The Sturnidae is the sister group of the Turdidae (Sibley & Ahlquist 1980; in press a, c). The genera *Aplonis* and *Mino* are the only starlings native to Australia and New Guinea. *Sturnus* and *Acridotheres* have been introduced.

THE SUPERFAMILY SYLVIOIDEA

In our classification the Sylvioidea includes the nuthatches and wallcreepers (Sittidae), the wrens, gnatcatchers, and Northern creepers (Troglodytidae), titmice (Paridae), long-tailed tits and bushtits (Aegithalidae), swallows (Hirundinidae), kinglets (Regulidae), bulbuls (Pycnonotidae), African warblers (Cisticolidae), white-eyes (Zosteropidae), and the Old World warblers and babblers (Sylviidae). Of these groups the Hirundinidae, Pycnonotidae, Cisticolidae, Zosteropidae, and Sylviidae are represented in Australo-Papuasia.

The cosmospolitan swallows are poor indicators of zoogeographical history and we have no DNA data for the endemic genus *Cheramoeca* of Australia.

The swallows have been viewed as "primitive" and distinct from other oscines because of their unique syringes and tarsi, and they usually have been placed at or near the beginning of the sequence of oscine taxa in classifications. The DNA evidence shows that they are the descendants of a lineage that branched from other sylvioid groups *ca* 45–47 MYA. Their specialized characters evolved after this divergence and are therefore derived, not primitive (Sibley & Ahlquist 1982i; in press a).

The two species of bulbuls *Pycnonotus* were introduced into Australia and none occurs in New Guinea.

The DNA data revealed the existence of a cluster of African "warbler" genera, including *Cisticola,* that are well separated from the other sylvioids by an average delta $T_{50}H$ of 9.3, indicating a divergence time *ca* 40–43 MYA. Of the six genera so far identified as members of the Cisticolidae, only *Cisticola* occurs in Australia and New Guinea.

Most classifications have viewed the white-eyes as a distinct family, Zosteropidae, but their affinities have been unclear. Their brush-tipped tongue has been the basis for placing them near the nectarivorous groups (sunbirds, honeyeaters), but the DNA data show them to be a sylvioid lineage that diverged *ca* 40–42 MYA.

The relationships of the "Old World warblers" to one another and to other groups of small, ten-primaried oscines have been debated for more than a century without producing a consensus about their classification. Sibley (1970: 68–74) reviewed the problem and Sibley & Ahlquist (1980: 1982b, h; in press a) have presented DNA evidence concerning the group. The following statements summarize our present understanding of the Sylviidae.

1. The Maluridae and Acanthizidae are members of the parvorder Corvi, therefore they are not sylviids, which are members of the parvorder Muscicapae.

2. The only sylviid genera in Australia are the reed warblers *Acrocephalus,* the Spinfexbird *Eremiornis,* the grassbirds *Megalurus,* and the songlarks *Cincloramphus,* as indicated by Schodde (1975). The sylviids *Locustella, Acrocephalus, Megalurus,* and *Phylloscopus* have been recorded from New Guinea.

3. The true babblers (Timaliini) are closely related to *Sylvia* and are members of the Sylviidae. There are no true babblers in Australia. *Pomatostomus* (pseudo-babblers) is a member of the superfamily Corvoidea.

THE SUPERFAMILY FRINGILLOIDEA

The Fringilloidea includes four families: the larks (Alaudidae), sunbirds and flowerpeckers (Nectariniidae), weaverbirds and allies (Ploceidae), and the chaffinches, carduelines, and New World nine-primaried groups (Fringillidae).

The larks differ from other oscines by lacking an ossified syringeal pessulus and having a reticulate pattern of tarsal scutes. Apparently these are derived conditions that evolved after the lark lineage diverged from the other fringilloids, *ca* 42–44 MYA (delta 9.5). The Singing Bushlark *Mirafra javanica* occurs in Australia and New Guinea and the Skylark *Alauda arvensis* has been

introduced in Australia.

The sunbirds and flowerpeckers are not related to the honeyeaters or to the pardalotes, with which they have often been associated because of their convergent similarities. The family Nectariniidae includes the sunbirds, the flowerpeckers, and the Papuan genera *Melanocharis* and *Toxorhampus*. We recognize the subfamily Melanocharitinae for these latter two genera. The melanocharine lineage branched from the nectariniine lineage *ca* 35–40 MYA, thus before the divergence of the sunbirds and flowerpeckers *ca* 30–32 MYA. As noted above, we lack the DNAs of *Rhamphocharis, Oreocharis,* and *Paramythia* which have been thought to be related to *Dicaeum*.

The Ploceidae includes the sparrows (Passerinae), the waxbills (Estrildinae), wagtails and pipits (Motacillinae), accentors (Prunellinae), and the weaverbirds (Ploceinae) (Sibley & Ahlquist 1981b, c).

Two species of the ploceine genus *Euplectes* have been introduced into Australia and the native grassfinches of Australia and New Guinea are estrildines. Introduced sparrows *Passer* represent the Passerinae, and the resident pipit *Anthus novaeseelandiae* and wintering or vagrant species of wagtails *Motacilla*, are members of the Motacillinae.

The Fringillidae is composed of two subfamilies; the Fringillinae includes the chaffinches (Fringillini), the goldfinches, greenfinches, etc. (Carduelini), and the Hawaiian honeycreepers (Drepanidini) (Sibley & Ahlquist 1982a). Of these, only the carduelines are represented in Australia by two introduced species of *Carduelis*. The Emberizinae are the "New World nine-primaried oscines", some of which occur in the Old World (e.g., *Emberiza*). None occurs in Australo-Papuasia.

THE HISTORY OF THE AUSTRALO-PAPUAN PASSERINES

The earliest branch in the passerine genealogy, *ca* 80–90 MYA, gave rise to the lineages leading to the living Oligomyodi and Passeres. The Australo-Papuan Passeres are ten-primaried oscines, thus they must have originated from either African or Asian ancestors. A South American origin is improbable because the passerines of that continent are suboscines and nine-primaried oscines.

The divergence between the ancestors of the Corvi and the Muscicapae occurred *ca* 55–60 MYA (delta 13.0) when Australia was far south of its present position and connected to Antarctica. This connection persisted until *ca* 50 MYA, when Australia began its northward drift

(Keast 1981).

"Sixty million years ago Australia lay much further south, attached to East Antarctica....Only during the Eocene (40–50 m.y.B.P.) did break-up occur between East Antarctica and Australia, and Australia began drifting north....an equable climate prevailed in both East and West Antarctica during the late Mesozoic and early Tertiary..." (Rich 1976: 60). Antarctica extended westward from Australia and may have provided part of a connection to Africa, although there was a considerable water gap between Africa and Antarctica by the late Cretaceous. However, there may have been emergent "stepping-stone" islands which today are represented by the numerous seamounts and submarine ridges in the southern Indian Ocean.

An Asian origin for the Corvi also faces difficulties. At the time that the Corvi and Muscicapae diverged, Australia was *ca* 3000 km south of Asia. There may have been "stepping-stones" between, but if there were why do we not see evidence in the DNA data of a series of colonizations, as proposed by Mayr (1944) when it was assumed that the continents had always been in their present positions. Instead, we see clear evidence of a single divergence, followed by radiation within the continent. There were no invasions from any source and no "escapes" of the endemic groups, until *ca* 40 MYA, when the ancestor of the Laniidae apparently was able to emigrate to Asia or Africa.

The Corvi must have originated in Australia because the oldest elements in the group, the Menuroidea and Meliphagoidea, obviously evolved there and the Corvi radiated during the Tertiary when Australia was isolated from other large land masses. The parallel with the marsupials and the eucalypts is apparent. When Australia drifted closer to Asia in the late Oligocene-Miocene, *ca* 20–30 MYA, the ancestor of the Corvini (crows, jays, etc.) was able to disperse to Asia and the group radiated in Asia and Europe. This is indicated by the delta $T_{50}H$ value of 6.8 between *Corvus* and the other members of the Corvinae (= Paradisaeini, Cracticini, Oriolini) and the lower values, delta 4.7 or less, between *Corvus* and such corvine genera as *Dendrocitta, Platylophus, Cyanocorax, Aphelocoma, Cyanocitta, Perisoreus, Pica, Platysmurus,* and *Nucifraga* (see Fig. 4). Sixteen genera of the Corvini evolved in Eurasia and twelve occur in the New World, but only two genera reached South America and only three genera occur in Africa. The native species of *Corvus* and *Gymnocorvus* of Australia and New Guinea are presumably the descendants of recent immigrants from Asia.

The Australo-Papuan orioles and cuckoo-shrikes (Oriolini) are also probably recent colonists whose

ancestor came from Australia and radiated in Eurasia and Africa. The monarchs, drongos, and fantails (Monarchinae) have dispersed far from Australasia, some reaching Africa (e.g., *Terpsiphone, Dicrurus*, the Malaconotini) and distant Pacific islands (*Chasiempis* to Hawaii, *Lamprolia* to Fiji), as well as radiating within Australasia. Among the cracticines the wood-swallows have colonized southeast Asia and *Pityriasis* reached Borneo. The Pachycephalines have colonized many Pacific islands and southeast Asia.

Thus Australia was the nursery of the Corvi, a group that includes half of the six superfamilies of oscines. Their sister group, the Muscicapae, originated in Africa or Asia and dispersed throughout Eurasia and the Americas. The long isolation of the two groups from one another provided the opportunities for convergence to produce the morphologically similar ecological counterparts that have generated so much taxonomic confusion.

ACKNOWLEDGEMENTS

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Added Note: Readers may note small discrepancies between some delta $T_{50}H$ values in the text and the figures, e.g., 10.3 vs 10.4, 10.7 vs 11.0. These are the result of calculations made at different times during the study; the branching pattern is not changed.