THE RELATIONSHIPS OF THE STARLINGS (STURNIDAE: STURNINI) AND THE MOCKINGBIRDS (STURNIDAE: MIMINI)

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ABSTRACT.—Old World starlings have been thought to be related to crows and their allies, to weaverbirds, or to New World troupials. New World mockingbirds and thrashers have usually been placed near the thrushes and/or wrens. DNA-DNA hybridization data indicated that starlings and mockingbirds are more closely related to each other than either is to any other living taxon. Some avian systematists doubted this conclusion. Therefore, a more extensive DNA hybridization study was conducted, and a successful search was made for other evidence of the relationship between starlings and mockingbirds. The results support our original conclusion that the two groups diverged from a common ancestor in the late Oligocene or early Miocene, about 23–28 million years ago, and that their relationship may be expressed in our passerine classification, based on DNA comparisons, by placing them as sister tribes in the Family Sturnidae, Superfamily Turdoidea, Parvorder Muscicapae, Suborder Passeres. Their next nearest relatives are the members of the Turdidae, including the typical thrushes, erithacine chats, and muscicapine flycatchers. *Received 15 March 1983, accepted 1 November 1983.*

STARLINGS are confined to the Old World, mockingbirds and thrashers to the New World. Starlings usually have been thought to be related to crows and other members of the corvoid assemblage, or to New World troupials (Icterini) and/or Old World weaverbirds (Ploceinae). Mockingbirds and thrashers have been viewed as relatives of thrushes (Turdidae) and/or wrens (Troglodytidae).

Evidence of a relationship between starlings and mockingbirds had been reported at least twice (Beecher 1953, Stallcup 1961) before we published the results of a comparison of their DNAs (Sibley and Ahlquist 1980). The 1980 study was based on 153 DNA-DNA hybrids among 18 oscine genera used as radio-labeled single-copy "tracers." Among our conclusions was the following statement. (DNAs of the cited genera were used in the 1980 study).

"The thrushes, muscicapine flycatchers, mockingbirds, starlings, and dippers are members of a monophyletic assemblage. a) Within this group the muscicapine flycatchers (*Muscicapa, Melaenornis, Niltava, Rhinomyias*) are closely related to the chat-like thrushes (*Erithacus, Erythropygia, Phoenicurus, Luscinia, Cossypha, Pogonocichla, Myrmecocichla, Copsychus*). b) The starlings (*Sturnus, Onychognathus, Spreo, Ampeliceps, Aplonis*) are closest to the mockingbirds and thrashers (*Mimus, Dumetella, Toxostoma, Oreoscoptes*. c) The tur-

dine thrushes include *Turdus, Catharus, Hylocichla, Zoothera* and *Myadestes*. d) *Cinclus* is closer to the thrushes, flycatchers, starlings and mockingbirds than to the wrens."

A Distance Wagner tree (Farris 1972) based on the DNA hybridization data showed *Mimus* and *Sturnus* to be more closely related to each other than to any other taxon, and they clustered with the thrushes, muscicapine flycatchers, erithacine chats, and dippers.

The same pattern emerged from a more extensive study of the passerines (Sibley and Ahlquist in press a) in which the mimine-sturnine relationship was based on the same data as in the 1980 paper, but many additional data pertaining to other passerine groups were included. In the classification derived from this study, we treated the tribes Sturnini and Mimini as sister groups in the family Sturnidae. The following is a partial outline of this classification to indicate the relative positions and the names we have assigned to the taxa mentioned in the present paper. Details for most groups have been omitted.

Order Passeriformes
  Suborder Oligomyodi, the suboscines
  Suborder Passeres, the oscines
    Parvorder Corvi
      Superfamily Corvoidea

Family Corvidae
  Subfamily Corvinae, crows, jays,
      magpies, birds-of-paradise,
      Australian magpies, etc.
Parvorder Muscicapae
  Superfamily Turdoidea
  Family Bombycillidae, waxwings
  Family Cinclidae, dippers
  Family Turdidae
      Subfamily Turdinae, typical
          thrushes
      Subfamily Muscicapinae
          Tribe Muscicapini, muscicapine
              flycatchers
          Tribe Erithacini, chats
  Family Sturnidae
          Tribe Sturnini, starlings
          Tribe Mimini, mockingbirds
              and thrashers
  Superfamily Sylvioidea, Old World
      warblers, wrens, titmice, nut-
      hatches, swallows, etc.
  Superfamily Fringilloidea, larks, sun-
      birds, weavers, fringillines, trou-
      pials, etc.

Although this classification contains depar-
tures from previous arrangements, most of the
changes were received with approval or mild
doubts, but the inclusion of the starlings and
mockingbirds in the same family elicited vig-
orous dissent from several colleagues. We have
therefore made a new study, using different
taxa for the "tracers," several additional species,
and many more comparisons. Our original con-
clusions have been confirmed by these new
data, and we have also found several congruent
morphological characters. We have been un-
able to find hard evidence that precludes a close
relationship between starlings and mocking-
birds.

In this paper we review the taxonomic his-
tories of the two groups, note evidence from
other sources, and present the results of the
new DNA hybridization study.

DIVERSITY AND DISTRIBUTION

Amadon (1962) recognized 111 species of
starlings in 26 genera, approximately evenly
divided between Africa and Asia. Three species
of *Sturnus* occur in Europe, and *Aplonis* reaches
Australia and many southwest Pacific islands.
Most starlings nest in cavities, but *Aplonis me-*

tallica builds a pendant, globular nest with a
side entrance, and *Acridotheres ginginianus* digs
a nest hole in an earthen bank. The color of
starling eggs varies from white to green or blue-
green; some are unmarked, and others have
reddish or brownish markings.

Davis and Miller (1960) recognized 31 species
in 13 genera in the "family Mimidae," includ-
ing *Donacobius atricapillus*, which Miller (1964)
noted as having the voice and habits of a wren
(Troglodytidae). Clench et al. (1982) concluded
that *Donacobius* actually *is* a wren, which is con-
sistent with several DNA comparisons. In Ta-
bles 1 and 3, *Donacobius* clusters with the Syl-
vioidea, including the wrens, not with the
mimines in the Turdoidea.

Most mockingbirds and thrashers occur from
southern Canada and the United States to the
West Indies and Central America. With the ex-
clusion of *Donacobius*, only *Mimus* occurs in
South America.

All mimines build open, cup-shaped nests,
usually placed in bushes or trees. The Pearly-
eyed Thrasher (*Margarops fuscatus*) places its
"bulky, cup-shaped nest . . . in a bush or tree,
cavity of a tree, or on the side of cave or cliff"
and the Trembler (*Cinclocerthia ruficauda*) builds
its nest "in a cavity of a tree or tree fern, or at
the base of a palm frond" (Bond 1971: 169). Egg
colors are blue or green with various amounts
of spotting or streaking. Thus, the eggs and
nests, although variable, are somewhat similar
and do not oppose a relationship between the
two groups.

TAXONOMIC HISTORY

Opinions about the relationships of starlings
have ranged widely, but most of the classifi-
cations of the past 130 yr have placed starlings
close to crows and their allies, including birds-
of-paradise, Old World orioles, and drongos. A
relationship to the corvoid groups was advo-
cated by Sharpe (1890, 1891), Reichenow (1914),
Stresemann (1934), Stonor (1938), Delacour and
Vaurie (1957), and Bock (1963). A relationship
to the corvoids and the New World troupials
(Icterini) was indicated in the classifications of
Bonaparte (1850), Gray (1870), Sundevall (1872),
Sclater (1880), the early A.O.U. Check-lists
(1886, 1895, 1910), Shufeldt (1889), and Coues
(1896). Sharpe (1890: 1) declared that the star-
lings are "undoubtedly allied" to the Corvidae
and repeated this emphatic opinion in his ex-

tensive review of avian classification in 1891 (p. 85). The corvoids and ploceines were viewed as starling relatives by Reichenow (1882), von Boetticher (1931), Amadon (1943, 1956), Mayr and Amadon (1951), Mayr and Greenway (1956, 1962), Storer (1971), and Voous (1977).

Wallace (1874) associated starlings with weaverbirds, woodswallows, and larks as "Sturnoid Passeres." Parker (1875) reported similarities between the skulls of the Celebean Myna (*Enodes*) and that of a Song Thrush (*Turdus philomelos*) but decided that the myna was more shrike-like and possibly related to the birds-of-paradise and the drongos (*Dicrurus*).

Stejneger (1885) placed starlings with corvids and meliphagids, which may have influenced Wetmore (1930, 1951, 1960), who listed starlings near meliphagids, although far from Corvidae. Wetmore (1960) also placed New Zealand wattlebirds (Callaeidae), shrike-vireos (*Vireolanius*), and shrikes (Laniidae) near starlings. His influence on the A.O.U. Check-lists of 1931, 1957, and 1983 is apparent. In the 1983 list, the Sturnidae are between the Laniidae and Meliphagidae, far from the Corvidae.

Amadon (1943, 1956) reviewed the genera of starlings and, as possible relatives (1956: 9), suggested the Oriolidae, Vangidae, and Dicruridae, with the Prionopidae, Cracticidae, Paradisaeidae, and Corvidae as less likely relatives. He also noted that the Ploceidae might be related to the starlings, as von Boetticher (1931) had suggested. Mayr and Amadon (1951) assigned the Sturnidae to a group of "Weaverbirds, Starlings and Associated Families," which included the Ploceidae, Oriolidae, and Dicruridae, followed by the Corvidae and their allies. This arrangement was also used by Mayr and Greenway (1956, 1962).

Berndt and Meise (1962) placed starlings between the Ploceidae and Fringillidae, and Bock (1963) suggested that birds-of-paradise and bowerbirds may have been derived from starlings. Voous (1977: 382) placed the Sturnidae between the Corvidae and Passeridae and noted that "the Ploceidae may probably be their closest relatives."

Thus, there has been no consensus about the relationships of starlings, right up to the present. Among the groups that have been suggested as their closest relatives are members of both parvorders and three of the six superfamilies that we recognize in our DNA-based classification. The alleged relationship between

starlings and corvids seems to have been based on the similar shape of the bill in starlings, some corvines, and Old World orioles and the fact that some starlings and some corvines are black. It appears that the most influential "character" has been tradition, with most authors following the opinions of previous authors.

The taxonomic history of the mockingbird-thrasher group has been relatively simple. Most authors have placed them with or near the thrushes; some have allied them to the wrens. They were considered to be thrushes by Bonaparte (1850), Gray (1869), Coues (1896), Ridgway (1907), Beecher (1953, 1978), Morioka (1967), and Gulledge (1975). Of these authors, only Beecher (1953) compared mockingbirds and thrushes with starlings, and he found several similarities, as noted below.

Baird (1858), following Cabanis (1850), removed the Miminae from the Turdidae and placed them with the babblers, wrens, and Wrentit (*Chamaea*) in the "Liotrichidae" (= Timaliidae). He noted that "the Miminae . . . have a Thrush-like appearance, which has caused them to be placed by most authors among the *Turdidae*." He concluded, however, that "it is very difficult to draw the line between this sub-family and the wrens; the chief difference lies in the larger size and bristled gape." In 1864 Baird reversed himself and reinstated the mimines as a subfamily of the Turdidae.

Stejneger (1883) was the principal proponent of the view that mockingbirds are closely related to wrens. This opinion was adopted by the A.O.U. Check-list Committees of 1886 and 1895, which treated the mockingbirds as a subfamily of the Troglodytidae, and the Check-list Committee of 1910, which listed the wrens and mockingbirds as adjacent families. Lucas (1888) forged a compromise when he suggested that "the Miminae hold a somewhat intermediate position between the Wrens and the Thrushes" and thus provided the basis for one of the most frequent arrangements in lists, *viz.*, Troglodytidae, Mimidae, Turdidae. This pattern was followed by Wetmore (1930, 1951, 1960), Stresemann (1934), Mayr and Amadon (1951), Mayr and Greenway (1956, 1960), Amadon (1957), Delacour and Vaurie (1957), Berndt and Meise (1962), Storer (1971), and Voous (1977). The A.O.U. Check-list Committee of 1983 placed the "Mimidae" between the poly-

phyletic family "Muscicapidae" (which includes the thrushes) and the "Prunellidae."

Thus, as for starlings, there has been no consensus about the relationships of mockingbirds, although an alliance to the thrushes has been a reasonably consistent suggestion.

MORPHOLOGICAL EVIDENCE

Beecher (1953) compared the jaw musculature, the ectethmoid plate, and other characters of the head region in a quest for evidence of phylogenetic relationships among the oscines. In starlings, he found the jaw-muscle pattern to be "similar to that of the Turdinae in complex M3b . . ." and the palate to resemble that of the Turdinae. In mockingbirds, the jaw-muscle pattern and the bill, palate, and tongue are similar to those of the thrushes. Starlings, mockingbirds, and thrushes have a double ectethmoid foramen, thus differing from the corvoid groups, in which it is single. Beecher (p. 282) noted that "the double ectethmoid foramen and the muscle differences suggest that the supposed affinity of the Miminae to the babblers and wrens is the result of convergence. The Miminae may stem from the Turdinae . . . ." Thus, Beecher was the first to suggest a fairly close relationship among thrushes, mockingbirds, and starlings.

In suboscines and most of the corvoid groups (crows, birds-of-paradise, Old World orioles, drongos, woodswallows, etc.), there is one pneumatic fossa in the head of the humerus. In most of the other oscines (= our parvorder Muscicapae), there are two fossae, as described and reviewed by Bock (1962). Starlings have two complete fossae or, in *Eulabes* (= *Gracula*), the beginning of a second fossa. *Sturnus* has two fossae, as in mockingbirds and thrushes. This character is not consistent in its development among non-corvoid oscines, but the double condition in starlings at least suggests that they are not closely related to corvoids.

W. E. Lanyon (pers. comm.) found syringeal characters that unite mimines, sturnines, and turdines and distinguish them from corvines. Lanyon examined the stained cartilaginous syringeal elements in these groups, as follows: Mimines (*Dumetella, Mimus, Cinclocerthia, Margarops*); Turdines (*Catharus, Turdus, Copsychus*); Sturnines (*Sturnus, Aplonis, Scissirostrum, Cinnyricinclus*); and Corvines (*Dendrocitta, Crypsirina, Cyanocorax, Cyanocitta, Perisoreus, Pica, Calocitta,*

Corvus). Lanyon noted that "The only character complex that varies in any significant way among these four samples is the size of the pessulus . . . and the positional relationship of the ventral ends of the A3 elements to the pessulus. In *Dumetella, Catharus,* and *Sturnus,* the ventral ends of the left and right A3's do not meet but rather are separated by the comparatively wide pessulus, which is continuous with the fused A4's. But in *Dendrocitta* the pessulus is so narrow that the ventral ends of the A3's nearly touch each other medially. I can separate all eight of the corvid specimens on the basis of this character complex. I would not be able, with certainty, to distinguish between turdids, mimids, and sturnids, however." Lanyon noted that Warner (1972: 385) also observed these differences between corvoids and the starlings and thrushes.

Although these morphological characters do not prove that mockingbirds and starlings are each other's closest living relatives, they do suggest that it is unlikely that starlings are more closely related to corvoids than to mimines and turdines.

SEROLOGICAL EVIDENCE

Stallcup (1961) used the precipitin technique to compare the saline-soluble tissue proteins of 17 genera representing 15 of the families of oscines recognized in the 1957 A.O.U. Checklist. Among the taxa in this study were the Corvidae, represented by the Blue Jay (*Cyanocitta cristata*); Troglodytidae, Carolina Wren (*Thryothorus ludovicianus*); Mimidae, Northern Mockingbird (*Mimus polyglottos*) and Brown Thrasher (*Toxostoma rufum*); Turdidae, American Robin (*Turdus migratorius*); and Sturnidae, European Starling (*Sturnus vulgaris*).

Antisera were prepared against tissue extracts from these species and comparisons were made between them and representatives of 11 or 12 other oscine families. The results were presented in two tables and a series of diagrams, and Stallcup offered the following interpretations of the precipitin measurements:

1. "Members of several families are more like *Cyanocitta* than is *Sturnus* . . . ." (p. 51).
2. "*Thryothorus* does not resemble closely the members tested of the families Mimidae, Turdidae, and Regulidae." (p. 52).
3. "On the basis of the serological data, there is some justification for assuming relationship

between the mimids and thrushes, although the serological resemblance of . . . these two families is not as great as that between *Toxostoma* and *Sturnus*." (p. 52).

4. "The serological data present no clear idea as to the species most like . . . *Turdus* . . . . The species that show greatest serological correspondence to *Turdus* are *Sturnus*, *Dendroica*, *Parus*, and *Mimus*. It would seem, therefore . . . that the turdids and mimids are related. There are other species . . . that show greater serological correspondence to *Turdus* than does *Mimus*. *Sturnus* is a notable example." (pp. 52–53).

[Note: Stallcup was considering only the question of the relationship between mimines and turdines in these comments. Thus, he did not attempt to explain the reactions between the antiserum against *Turdus* with *Dendroica* and *Parus*. In other tests *Dendroica* was most like *Spiza* and *Agelaius*, and *Parus* was most like *Cyanocitta* and *Turdus*. The degrees of relationship indicated in these comparisons with *Parus* were lower (82%, 79%) than those between *Turdus* and *Sturnus* (92%, 86%).]

5. "Serologically, *Sturnus* seems to be most like *Toxostoma*." (p. 54). The *Sturnus-Toxostoma* reactions were 92% and 91% and, thus, among the higher values in the experiments.

There are some internal discrepancies in Stallcup's data that are characteristic of serological comparisons in which several rabbits are used to produce antisera. As Stallcup noted (1961: 49), this explains the unequal reciprocals in some of the tests. Stallcup's data clearly reveal a close relationship between starlings and mimines, however, with the thrushes nearby and the corvids and wrens at a considerable distance away.

METHODS

Our procedures are based primarily on those of Britten and Kohne (1968), Kohne (1970), and Britten et al. (1974). A brief description of our methods was published in *The Auk* (Sibley and Ahlquist 1982) and more complete versions in Sibley and Ahlquist (1981, 1983).

The two strands of a DNA-DNA duplex molecule are held together by hydrogen bonds between the complementary base pairs in homologous nucleotide sequences. The DNA hybridization technique determines the similarity between the two base sequences by measuring the temperature required to melt the hydrogen bonds and thereby to convert double-stranded DNA into single-stranded DNA.

The thermal dissociation curve of a DNA-DNA hybrid is a plot of the different rates of nucleotide substitution that have occurred in different sequences (Grula et al. 1982). Those hybrid duplexes composed of homologous sequences that have diverged most rapidly, and hence are most different, will contain the largest number of mismatched base pairs and will therefore melt at the lower temperatures. The DNA hybrids that do not melt until exposed to the highest temperatures are composed of sequences that have evolved slowly and contain few, or no, mismatched bases. Figure 1 shows the relationship between temperature and percentage of counts eluted, which measures the percentage of base pairs that have melted.

To obtain a measure of genealogical divergence between taxa we calculate the $T_{50}H$ statistic, which is the temperature in degrees Celsius at which 50% of the DNA duplexes in a given hybrid have melted into single strands. Thus, the delta $T_{50}H$ measures the average *amount* of divergence, which is a product of the average *rate* of divergence. The delta $T_{50}H$ is the average (or median) difference between the two genomes composing a DNA-DNA hybrid. In the calculation of delta $T_{50}H$, it is assumed that all of the nucleotide sequences in the genomes of the two species being compared have homologs in the other species, that all sequences potentially can hybridize with their homologs, and that all degrees of divergence can be detected. The percentage of hybridization declines, however, as the amount of divergence increases, and the thermal-stability curve is progressively truncated by the effects of the experimental conditions. Figure 1 illustrates this by the intercepts between the 60°C temperature and the percentage of counts eluted values. For the curves in Fig. 1 this is not a problem, because all of the curves cross the 50% hybridization level, and the delta $T_{50}H$ values can be calculated easily. For more divergent taxa, whose melting curves are entirely above the 50% level, it is necessary to extrapolate the most nearly linear portion of the curve to its intercept with the 50% level. This is done by fitting a cumulative distribution function to the data to find the intercept. Thus, the $T_{50}H$ values incorporate the percentage of hybridization and the measure of thermal stability in a single number.

To convert the delta $T_{50}H$ values into a phylogeny requires a procedure to obtain a hierarchical clustering of taxa. We use the "average linkage," unweighted-pair-group method, which begins by clustering the closest pair or pairs of taxa. The next step links the taxa that have the smallest average distance to any existing cluster. This procedure continues until all taxa are linked. The underlying idea is that the only reason for "closeness" is true homology of characters, while "distance" may result from the failure to identify existing homologies. The DNA hybridization data are especially compatible with this view,
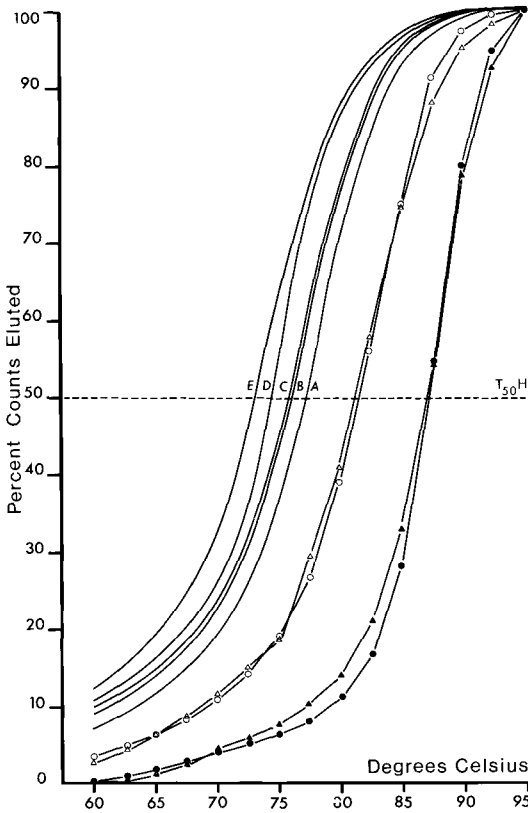
Fig. 1. Cumulative thermal dissociation curves of hybrids involving the radio-labeled DNAs of the Long-billed Thrasher (*Toxostoma longirostre*) and the Red-shouldered Glossy Starling (*Lamprotornis nitens*). Solid circles are the average data points of three homologous hybrids of *Toxostoma longirostre*; solid triangles are the average data points of three homologous hybrids of *Lamprotornis nitens*. Open circles are the average data points of 20 hybrids between *Toxostoma* and various starlings; open triangles are the average data points of 16 hybrids between *Lamprotornis* and various mimines. Smooth curves identified by letters are averages of hybrids between both labeled *Toxostoma* and labeled *Lamprotornis* and other passerine groups as follows: (A) Turdidae, $n = 18$; (B) Cinclus, $n = 2$; (C) Bombycillidae, $n = 6$; (D) Superfamilies Sylvioidea and Fringilloidea, $n = 30$; and (E) Parvorder Corvi, $n = 15$.

because there is no known reason, other than nucleotide-sequence homology, for the thermal stabilities of DNA-DNA hybrids.

The experimental error in our data has been measured, and a single delta $T_{50}H$ value should be assumed to have a possible error of ± 1.0 (Sibley and Ahlquist 1983: 270). We have found it possible to

compensate for all sources of experimental error by using five or more species and/or replicates for each pairwise comparison between taxa so that an average delta $T_{50}H$, its standard error (SE), and standard deviation (SD) can be calculated for each branch node in a phylogeny. Because of the incremental summation of values in the average linkage procedure, the older nodes in the phylogenies are often the averages of 10, 20, or more delta $T_{50}H$ measurements.

THE UNIFORM AVERAGE RATE OF DNA EVOLUTION

The time dimension of the DNA hybridization data derives from the observed evidence that the same *average* rate of sequence evolution occurs in all lineages of birds. We also have some evidence that the same average rate occurs in mammals (Sibley and Ahlquist in press b). This should not be surprising, because the Uniform Average Rate (UAR) is nothing more (or less) than the inevitable statistical result of averaging over billions of nucleotides and millions of years. Different DNA sequences evolve at many different rates, as the melting curves demonstrate, but the *average* rate is the same in all lineages, because the genome is so large compared with the range in the rates of different sequences. Sibley and Ahlquist (1983: 270) provide additional details about the UAR. Our DNA hybridization data fit the definitions of Farris (1981: 6, 13) for "metric" and "ultrametric" distance measures, i.e. the data never violate the "triangle inequality" and they are "clocklike."

Because all avian genomes evolve at the same average rate, the delta $T_{50}H$ values are measures of *relative* time. They may be used, therefore, to reconstruct the branching pattern of a phylogeny. To convert the delta values into *absolute* time, it is necessary to calibrate them against an external dating source, *viz.*, fossils or geological events that have caused phyletic dichotomies. Using this procedure, we have obtained an estimate of the calibration such that delta $T_{50}H$ 1.0 = about 4.3–4.6 million years (my) (Sibley and Ahlquist 1981, 1983, in press b; Sibley et al. 1982; Diamond 1983). These constants of proportionality are tentative and subject to correction, but we will use them to provide approximate dates for divergence nodes.

RESULTS AND DISCUSSION

Tables 1–5 and Figs. 1 and 2 present the data from nine experimental sets in which the Long-billed Thrasher (*Toxostoma longirostre*), the Northern Mockingbird (*Mimus polyglottos*), the Red-shouldered Glossy Starling (*Lamprotornis nitens*), and the European Starling (*Sturnus vulgaris*) were the radio-labeled taxa. In Table 1 the delta $T_{50}H$ values between the Long-billed

TABLE 1.   DNA-DNA hybridization values between the radioiodine-labeled single-copy DNA of the Long-billed Thrasher (*Toxostoma longirostre*) and the DNAs of other oscine passerine birds. Under "Group index" M = Mimini, S = Sturnini, T = Turdidae, B = Bombycillidae, C = Cinclidae, Sy = Sylvioidea, F = Fringilloidea, and Co = Corvoidea. Numbers in parentheses, e.g. (2) = more than one hybrid averaged.

Common name	Scientific name	Delta $T_{50}H$	Group index
Long-billed Thrasher	*Toxostoma longirostre*	0.0	M
Brown Thrasher	*Toxostoma rufum*	0.9	M
Curve-billed Thrasher	*Toxostoma curvirostre*	1.0	M
Crissal Thrasher	*Toxostoma dorsale* (2)	1.3	M
California Thrasher	*Toxostoma redivivum*	1.3	M
Sage Thrasher	*Oreoscoptes montanus* (2)	2.0	M
Long-tailed Mockingbird	*Mimus longicaudatus*	2.0	M
Northern Mockingbird	*Mimus polyglottos* (3)	2.1	M
Tropical Mockingbird	*Mimus gilvus*	2.1	M
Gray Catbird	*Dumetella carolinensis* (2)	2.6	M
Red-shouldered Glossy Starling	*Lamprotornis nitens* (3)	5.0	S
Greater Glossy Starling	*Lamprotornis australis*	5.2	S
Singing Starling	*Aplonis cantoroides*	5.4	S
Micronesian Starling	*Aplonis opaca*	5.6	S
Philippine Glossy Starling	*Aplonis panayensis* (2)	5.7	S
Wattled Starling	*Creatophora cinerea* (2)	5.7	S
Violet Starling	*Cinnyricinclus leucogaster*	5.7	S
Hill Myna	*Gracula religiosa* (2)	5.8	S
Spotless Starling	*Sturnus unicolor* (2)	5.9	S
European Starling	*Sturnus vulgaris*	6.0	S
Red-winged Starling	*Onychognathus morio*	6.0	S
African Pied Starling	*Spreo bicolor*	6.1	S
Common Myna	*Acridotheres tristis*	6.2	S
Golden-crested Myna	*Ampeliceps coronatus*	6.4	S
Rufous-tailed Rock Thrush	*Monticola saxatilis*	8.2	T
Veery	*Catharus fuscescens*	8.3	T
White-throated Jungle Flycatcher	*Rhinomyias umbratilis*	8.3	T
Townsend's Solitaire	*Myadestes townsendi*	8.7	T
Black Solitaire	*Entomodestes coracinus*	8.8	T
Western Bluebird	*Sialia mexicana*	8.8	T
Orange-breasted Flycatcher	*Ficedula dumetoria*	8.8	T
American Robin	*Turdus migratorius*	9.0	T
Common Nightingale	*Erithacus megarhynchos*	9.3	T
Palm Chat	*Dulus dominicus*	9.9	B
American Dipper	*Cinclus mexicanus*	10.0	C
Phainopepla	*Phainopepla nitens*	10.3	B
Cedar Waxwing	*Bombycilla cedrorum*	10.5	B
Black-capped Chickadee	*Parus atricapillus*	10.5	Sy
Yellow-vented Bulbul	*Pycnonotus goiavier*	10.5	Sy
House Sparrow	*Passer domesticus*	10.5	F
Village Weaver	*Ploceus cucullatus*	10.6	F
Black-tailed Gnatcatcher	*Polioptila melanura*	10.6	Sy
Red-breasted Nuthatch	*Sitta canadensis*	10.7	Sy
Orphean Warbler	*Sylvia hortensis*	10.7	Sy
Verdin	*Auriparus flaviceps*	10.9	Sy
Carolina Wren	*Thryothorus ludovicianus*	10.9	Sy
Red-billed Leiothrix	*Leiothrix lutea*	11.0	Sy
Bushtit	*Psaltriparus minimus*	11.0	Sy
Swamp Sparrow	*Melospiza georgiana*	11.0	F
Bank Swallow	*Riparia riparia*	11.1	Sy
Green-headed Sunbird	*Nectarinia verticalis*	11.2	F
Horned Lark	*Eremophila alpestris*	11.2	F
Black-capped Wren	*Donacobius atricapillus*	11.3	Sy
Dusky Munia	*Lonchura fuscans*	11.3	F
Musician Wren	*Cyphorhinus aradus*	11.4	Sy
White-eyed Vireo	*Vireo griseus*	12.1	Co
White-bellied Oriole	*Oriolus sagittatus*	12.1	Co
Northern Shrike	*Lanius excubitor*	12.2	Co
Shining Monarch	*Myiagra alecto*	12.7	Co
Red-shouldered Cuckoo-shrike	*Campephaga phoenicea*	12.9	Co
Little Raven	*Corvus mellori*	13.5	Co

TABLE 2. DNA-DNA hybridization values between the radioiodine-labeled single-copy DNA of the North-
ern Mockingbird (*Mimus polyglottos*) and the DNAs of other oscine passerine birds. Under "Group index"
M = Mimini, S = Sturnini, T = Turdidae, C = Cinclidae, B = Bombycillidae, Sy = Sylvioidea, Co = Cor-
voidea.

Common name	Scientific name	Delta $T_{50}H$	Group index
Northern Mockingbird	*Mimus polyglottos*	0.0	M
Sage Thrasher	*Oreoscoptes montanus*	1.9	M
Curve-billed Thrasher	*Toxostoma curvirostre*	2.5	M
Gray Catbird	*Dumetella carolinensis*	2.7	M
European Starling	*Sturnus vulgaris*	6.2	S
Natal Chat	*Cossypha natalensis*	8.0	T
Northern Black Flycatcher	*Melaenornis edolioides*	8.2	T
Eurasian Robin	*Erithacus rubecula*	8.9	T
American Robin	*Turdus migratorius*	9.0	T
Black Solitaire	*Entomodestes coracinus*	9.3	T
American Dipper	*Cinclus mexicanus*	9.7	C
Cedar Waxwing	*Bombycilla cedrorum*	10.0	B
Phainopepla	*Phainopepla nitens*	10.4	B
Palm Chat	*Dulus dominicus*	10.4	B
Bewick's Wren	*Thryomanes bewickii*	11.4	Sy
Musician Wren	*Cyphorhinus aradus*	11.6	Sy
Garden Warbler	*Sylvia borin*	11.6	Sy
House Wren	*Troglodytes aedon*	11.7	Sy
Black-capped Wren	*Donacobius atricapillus*	11.8	Sy
Asian Paradise Flycatcher	*Terpsiphone paradisi*	12.1	Co
American Crow	*Corvus brachyrhynchos*	13.1	Co

Thrasher and the nine other mimines (14 hy-
brids) range from 0.9 to 2.6, indicating that these
species are closely related. The 14 species (20
hybrids) of starlings have delta $T_{50}H$ values from
5.0 to 6.4, and the average is 5.7 ± 0.1 SE,
±0.4 SD. In Tables 1 and 2 the 21 hybrids be-
tween *Toxostoma* plus *Mimus* vs. the starlings
range from 5.0 to 6.4 and have an average delta
$T_{50}H$ of 5.7 ± 0.1 SE, ±0.4 SD, as summarized
in Table 5.

Tables 3 and 4 present the delta $T_{50}H$ values
between the two labeled starlings and the
mimines. In Table 3 there are 15 hybrids be-
tween *Lamprotornis* and the 10 species of mi-
mines, and in Table 4 there are three hybrids
between *Sturnus* and two species of mimines.
These 18 hybrids range from 5.3 to 6.4 and av-
erage 5.7 ± 0.1 SE, ±0.4 SD. The reciprocals
(5.7:5.7) are identical. Thus, the average delta
$T_{50}H$ of 5.7 measures the branch node between
the Sturnini and the Mimini and indicates that
their divergence began about 23–28 million
years before the present (mybp), in the late Oli-
gocene or early Miocene.

Note that the delta $T_{50}H$ values for *Donacobius
atricapillus* in Tables 1–3 are 11.3, 11.8, and 10.9,
which average 11.3. The six delta values for
typical wrens in these tables average 11.4; thus

Donacobius and the wrens are the same genea-
logical distance from the mimines.

Because of the uniform average rate of DNA
evolution, the delta $T_{50}H$ values between all
sturnids and the members of other monophy-
letic groups should be equal, within the limits
of experimental error. Therefore, using the
clustering method of "average linkage," we can
combine the delta $T_{50}H$ values for hybrids be-
tween the members of the Sturnidae and mem-
bers of the next nearest cluster, the Turdidae.
These 28 values range from 8.0 to 9.8, and the
average is 8.9 ± 0.1, ±0.4 (see Table 5). From
other data sets, we have 10 DNA hybrids in
which the labeled taxa are turdids (*Turdus,
Myadestes, Melaenornis, Erithacus*). These 10 val-
ues range from 8.7 to 10.1 and average 9.4 ±
0.1, ±0.5. The reciprocal discrepancy is 0.5, and
the average for all 38 sturnid × turdid values
is 9.0 ± 0.1, ±0.5. The divergence between the
Sturnidae and the Turdidae thus occurred about
38–42 mybp, in the late Eocene. In our study
of the passerines (in press a) we obtained an
average of 9.5 for this node, based on the 10
turdid × sturnid values noted above plus the
data in our 1980 study.

The dippers (*Cinclus*) represent the next old-
er branch from the Sturnidae. By combining all

TABLE 3. DNA-DNA hybridization values between the radioiodine-labeled single-copy DNA of the Red-shouldered Glossy Starling (*Lamprotornis nitens*) and the DNAs of other oscine passerine birds. Under "Group index" S = Sturnini, M = Mimini, T = Turdidae, C = Cinclidae, B = Bombycillidae, F = Fringilloidea, Sy = Sylvioidea, and Co = Corvoidea. Numbers in parentheses, e.g. (2) = more than one hybrid averaged.

Common name	Scientific name	Delta $T_{50}H$	Group index
Red-shouldered Glossy Starling	*Lamprotornis nitens*	0.0	S
African Pied Starling	*Spreo bicolor*	1.0	S
Red-winged Starling	*Onychognathus morio*	2.2	S
Violet Starling	*Cinnyricinclus leucogaster*	2.5	S
Common Myna	*Acridotheres tristis*	3.6	S
Wattled Starling	*Creatophora cinerea* (2)	3.7	S
Spotless Starling	*Sturnus unicolor* (3)	3.7	S
European Starling	*Sturnus vulgaris*	3.8	S
Golden-crested Myna	*Ampeliceps coronatus*	4.6	S
Singing Starling	*Aplonis cantoroides* (3)	4.8	S
Micronesian Starling	*Aplonis opaca*	4.9	S
Hill Myna	*Gracula religiosa*	4.9	S
Philippine Glossy Starling	*Aplonis panayensis*	5.1	S
Long-billed Thrasher	*Toxostoma longirostre* (3)	5.3	M
Sage Thrasher	*Oreoscoptes montanus*	5.4	M
Crissal Thrasher	*Toxostoma dorsale* (2)	5.5	M
Northern Mockingbird	*Mimus polyglottos* (2)	5.5	M
Gray Catbird	*Dumetella carolinensis* (2)	5.6	M
Curve-billed Thrasher	*Toxostoma curvirostre*	5.7	M
California Thrasher	*Toxostoma redivivum*	5.7	M
Long-tailed Mockingbird	*Mimus longicaudatus*	5.9	M
Brown Thrasher	*Toxostoma rufum*	6.0	M
Tropical Mockingbird	*Mimus gilvus*	6.1	M
Townsend's Solitaire	*Myadestes townsendi*	8.4	T
Rufous-tailed Rock-Thrush	*Monticola saxatilis*	8.6	T
White-throated Jungle Flycatcher	*Rhinomyias umbratilis*	8.9	T
Veery	*Catharus fuscescens*	9.1	T
Common Nightingale	*Erithacus megarhynchos*	9.1	T
Sunda Whistling-Thrush	*Myiophoneus glaucinus*	9.4	T
Orange-breasted Flycatcher	*Ficedula dumetoria*	9.4	T
Western Bluebird	*Sialia mexicana*	9.6	T
American Robin	*Turdus migratorius*	9.8	T
Palm Chat	*Dulus dominicus*	9.9	B
American Dipper	*Cinclus mexicanus*	10.2	C
Cedar Waxwing	*Bombycilla cedrorum*	10.6	B
Phainopepla	*Phainopepla nitens*	10.6	B
Village Weaver	*Ploceus cucullatus*	10.6	F
Yellow-vented Bulbul	*Pycnonotus goiavier*	10.8	Sy
Black-capped Chickadee	*Parus atricapillus*	10.9	Sy
Black-capped Wren	*Donacobius atricapillus*	10.9	Sy
Red-billed Leiothrix	*Leiothrix lutea*	11.0	Sy
Orphean Warbler	*Sylvia hortensis*	11.2	Sy
House Sparrow	*Passer domesticus*	11.4	F
Horned Lark	*Eremophila alpestris*	11.4	F
Swamp Sparrow	*Melospiza georgiana*	11.6	F
Carolina Wren	*Thryothorus ludovicianus*	11.6	Sy
Green-headed Sunbird	*Nectarinia verticalis*	11.8	F
Bank Swallow	*Riparia riparia*	12.0	Sy
Red-breasted Nuthatch	*Sitta canadensis*	12.2	Sy
Dusky Munia	*Lonchura fuscans*	12.2	F
Little Raven	*Corvus mellori*	12.3	Co
Northern Shrike	*Lanius excubitor*	12.3	Co
White-eyed Vireo	*Vireo griseus*	12.3	Co
Red Wattlebird	*Anthochaera carunculata*	12.4	Co
White-bellied Oriole	*Oriolus sagittatus*	12.5	Co
White-browed Woodswallow	*Artamus superciliosus*	12.8	Co
African Drongo	*Dicrurus adsimilis*	13.1	Co
Red-shouldered Cuckoo-shrike	*Campephaga phoenicea*	13.2	Co
Shining Monarch	*Myiagra alecto*	13.2	Co

TABLE 4. DNA-DNA hybridization values between the radioiodine-labeled single-copy DNA of the European Starling (*Sturnus vulgaris*) and the DNAs of other oscine passerine birds. Under "Group index" S = Sturnini, M = Mimini, T = Turdidae, C = Cinclidae, B = Bombycillidae, F = Fringilloidea, Sy = Sylvioidea, and Co = Corvoidea. The number in parentheses (2) = two DNA hybrids were averaged.

Common name	Scientific name	Delta $T_{50}H$	Group index
European Starling	*Sturnus vulgaris*	0.0	S
African Pied Starling	*Spreo bicolor*	3.9	S
Singing Starling	*Aplonis cantoroides*	5.9	S
Gray Catbird	*Dumetella carolinensis* (2)	6.3	M
Northern Mockingbird	*Mimus polyglottos*	6.4	M
Eurasian Robin	*Erithacus rubecula*	8.6	T
American Robin	*Turdus migratorius*	8.7	T
Large-billed Blue Flycatcher	*Niltava caerulata*	8.8	T
Northern Black Flycatcher	*Melaenornis edolioides*	8.8	T
Ant-eating Chat	*Myrmecocichla formicivora*	9.1	T
American Dipper	*Cinclus mexicanus*	9.7	C
Cedar Waxwing	*Bombycilla cedrorum*	10.7	B
Cape Weaver	*Ploceus capensis*	10.8	F
Red-backed Mannikin	*Lonchura bicolor*	10.9	F
Pale White-eye	*Zosterops pallida*	11.4	Sy
Garden Warbler	*Sylvia borin*	11.5	Sy
Short-tailed Babbler	*Trichastoma malaccense*	11.7	Sy
Black-naped Oriole	*Oriolus chinensis*	11.9	Co
Black Butcherbird	*Cracticus quoyi*	12.0	Co
Black-faced Woodswallow	*Artamus cinereus*	12.0	Co
Spot-winged Monarch	*Monarcha guttula*	12.0	Co
American Crow	*Corvus brachyrhynchos*	12.1	Co
Rufous Shrike-thrush	*Colluricincla megarhyncha*	12.3	Co
Brown Whistler	*Pachycephala simplex*	12.3	Co
Willie Wagtail	*Rhipidura leucophrys*	12.6	Co
Common Wood-shrike	*Tephrodornis pondicerianus*	12.7	Co
Red-eyed Vireo	*Vireo olivaceus*	13.0	Co
Asian Paradise Flycatcher	*Terpsiphone paradisi*	13.3	Co
Red-backed Shrike	*Lanius collurio*	13.5	Co
Large Cuckoo-shrike	*Coracina novaehollandiae*	13.9	Co
Lauterbach's Bowerbird	*Chlamydera lauterbachi*	14.0	Co

available delta values for the Sturnidae and Turdidae, to and from *Cinclus*, we have 15 measurements with an average of 9.8 ± 0.1, ±0.5 for the divergence of the Cinclidae from the sturnid-turdid lineage. This branch probably occurred about 42–45 mybp, in the Eocene.

The oldest branch in the Turdoidea led to the living members of the Bombycillidae, which includes waxwings (*Bombycilla*), silky flycatchers (*Phainopepla, Phainoptila, Ptilogonys*), and the Palm Chat (*Dulus dominicus*). We have 52 delta $T_{50}H$ values between the bombycillids and the other turdoids, which average 10.7 ± 0.1, ±0.4. This indicates that the ancestor of the Bombycillidae branched from the lineage leading to the other turdoids about 46–50 mybp, in the mid-Eocene.

The sylvioid-fringilloid clade (11.3) branched from the turdoid clade about 50 mybp, and the parvorders Muscicapae and Corvi (12.7) diverged about 60 mybp.

Figure 1 presents a series of thermal dissociation curves between the tracer DNAs of *Toxostoma* and *Lamprotornis* and other oscine taxa. It is apparent from these melting curves that *Toxostoma* and *Lamprotornis* are the most closely related taxa in this set, that the other turdoids are progressively more distant, that the Sylvioidea and Fringilloidea are still more distant, and that the Corvi are the most distant from the Sturnidae.

Figure 2 is based on the data in Tables 1–5 and the additional data noted in the text. All DNA-DNA distance measurements are between a radio-labeled species and the unlabeled species, not between the unlabeled species. Thus, the delta values between *Lamprotornis* and *Spreo, Onychognathus*, and other
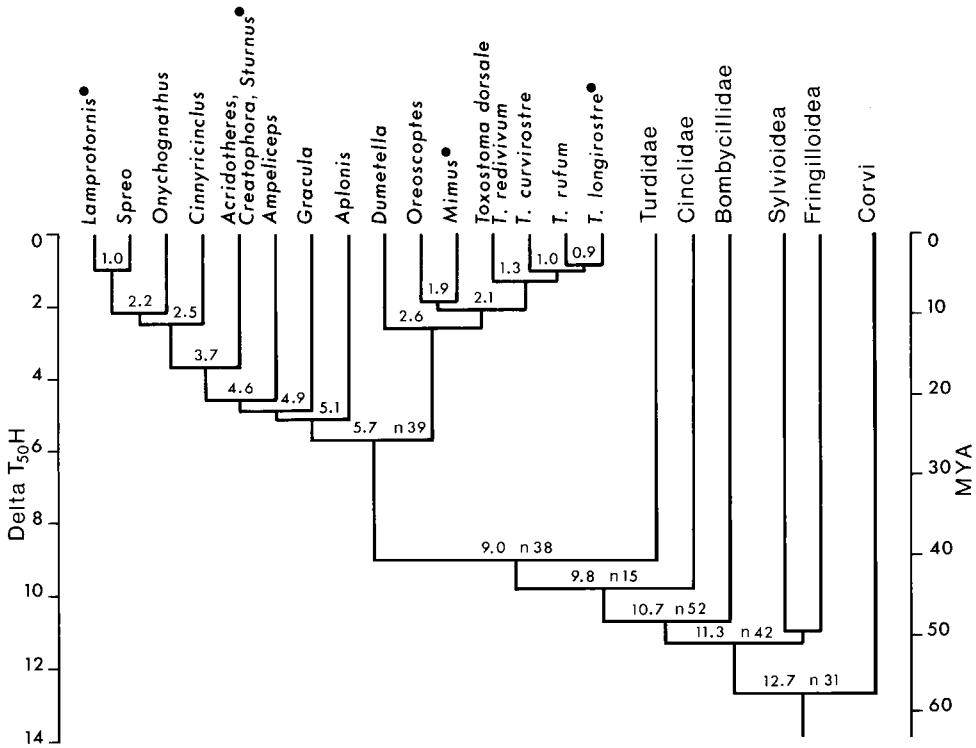
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Fig. 2.   Diagram of relationships of and among the Sturnidae. Branch lengths at nodes are taken from the delta $T_{50}H$ values given in Tables 1–5. Solid circles indicate radio-labeled taxa. MYA = millions of years ago.

unlabeled taxa do not indicate how these taxa are related to one another, except that they are no more distant from one another than they are from the tracer species. A delta value between two labeled taxa (e.g. the 5.7 average between the sturnines and mimines), however, is a valid measurement of the genealogical distance between them. Note that the Sage Thrasher (*Oreoscoptes montanus*) is closer to *Mimus* than to the true thrashers (*Toxostoma*). Gulledge (1975) came to the same conclusion.

We have suggested that the sturnine-mimine dichotomy occurred in the late Oligocene or early Miocene, about 23–28 mybp. This implies that their common ancestral population was divided into two separate populations at that time. The present breeding distributions of the Mimini are far south of the Bering Strait and the north Atlantic, and among the Sturnini only *Sturnus vulgaris* breeds in northern Europe and Iceland (Voous 1960). In North America the introduced *S. vulgaris* rarely breeds as far north

as central Alaska (Kessel and Gibson 1978). During the late Oligocene and early Miocene, however, there were emergent land connections between Europe and North America, and the climate in the northern hemisphere was considerably milder than today. Eldholm and Thiede (1980) concluded that "connections by shallow water and possibly emerged, or locally emerged, continent existed to the Middle Oligocene between Greenland and Svalbard [= Spitsbergen] and to the Pliocene on the Faeroe-Iceland Ridge." Gradstein and Srivastava (1980) noted that relatively warm Atlantic waters occurred in the Labrador Sea in the Eocene and that "less warm Atlantic water influence prevailed in Oligocene and Miocene time but it was not until late Miocene time that there is evidence of a cold Labrador Current hugging the Canadian shelves." Similarly, Wolfe (1980) found evidence of a mixed broad-leaved deciduous forest at high latitudes in the northern hemisphere during the Oligocene and Mio-

TABLE 5. Summary of the data in Tables 1–4. The numbers are the group averages, standard error, and standard deviation, e.g. 5.7 ± 0.1, ±0.4, and the number of DNA-DNA hybrids, e.g. n = 20.

Labeled taxa	Sturnini	Mimini	Turdidae	Cinclidae	Bombycillidae	Sylvioidea	Fringilloidea	Corvoidea
Toxostoma longirostre	5.7 ± 0.1, ±0.4 (n = 20)	See Table 1	8.7 ± 0.1, ±0.4 (n = 9)	10.0 (n = 1)	10.2 ± 0.2, ±0.3 (n = 3)	10.9 ± 0.1, ±0.3 (n = 12)	11.0 ± 0.1, ±0.3 (n = 6)	12.6 ± 0.2, ±0.6 (n = 6)
Mimus polyglottos	6.2 (n = 1)	See Table 2	8.7 ± 0.2, ±0.5 (n= 5)	9.7 (n = 1)	10.3 ± 0.1, ±0.2 (n = 3)	11.6 ± 0.1, ±0.1 (n = 5)	—	12.6 ± 0.5, ±0.7 (n = 2)
Lamprotornis nitens	See Table 3	5.6 ± 0.1, ±0.2 (n = 15)	9.1 ± 0.1, ±0.5 (n = 9)	10.2 (n = 1)	10.4 ± 0.2, ±0.4 (n = 3)	11.3 ± 0.2, ±0.6 (n = 7)	11.7 ± 0.3, ±0.7 (n = 7)	12.7 ± 0.1, ±0.4 (n = 9)
Sturnus vulgaris	See Table 4	6.3 ± 0.05, ±0.1 (n = 3)	8.8 ± 0.1, ±0.2 (n = 5)	9.7 (n = 1)	10.7 (n = 1)	11.5 ± 0.1, ±0.1 (n = 3)	10.8 ± 0.05, ±0.1 (n = 2)	12.7 ± 0.2, ±0.7 (n = 14)
Total n per column	21	18	28	4	10	28	14	31
Range	5.0–6.4 (1.4)	5.3–6.4 (1.1)	8.0–9.8 (1.8)	9.7–10.2 (0.5)	9.9–10.7 (0.8)	10.5–12.2 (1.7)	10.5–12.2 (1.7)	11.9–14.0 (2.1)
Average delta $T_{50}H$	5.7	5.7	8.9	9.9	10.3	11.2	11.2	12.7
Standard error	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Standard deviation	0.4	0.4	0.4	0.2	0.3	0.5	0.5	0.6

cene, with no evidence of glaciation until "late in the Neogene." It thus seems probable that the common ancestor of the starlings and mockingbirds was able to spread over the northern hemisphere in the Eocene and that the increasingly severe boreal climate in the late Oligocene-Miocene pushed the two populations southward and out of contact.

CONCLUSIONS

The DNA-DNA hybridization measurements indicate that the starlings and mockingbirds are each other's closest living relatives. Comparisons of their DNAs with those of all other living groups of oscine passerine birds show that there is no other group that is more closely related to one of them than they are to each other.

The morphological characters known to be shared by the Sturnini and the Mimini would not, alone, make it possible to recognize the close genealogical relationship between the two groups, but, in conjunction with Stallcup's (1961) serological evidence, they support the DNA hybridization data. No other proposal about the relationships of the starlings and mockingbirds has been based on evidence of equal or greater competence, and we suggest that additional congruencies will be discovered, now that the DNA comparisons have made it possible to reconstruct the phylogeny of these taxa.

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