THE RELATIONSHIPS OF THE SILKY FLYCATCHERS

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THE silky flycatchers include the genera *Ptilogonys*, *Phainopepla*, and *Phainoptila*, which are usually treated either as a family, Ptilogonatidae (e.g. Wetmore 1960), or as a subfamily of the waxwing family Bombycillidae (e.g. Greenway 1960). Some authors have included the Palm Chat (*Dulus dominicus*) of Hispaniola and the Grey Hypocolius (*Hypocolius ampelinus*) of Iraq and Iran in the Bombycillidae (Arvey 1951, Mayr and Amadon 1951). Others have considered some of these allocations to be tentative or unproved and have recognized separate families for some or all of these groups (e.g. Wetmore 1960, Greenway 1960).

The silky flycatchers are confined to North and Central America. The Phainopepla (*Phainopepla nitens*) occurs in the arid and semiarid regions of the southwestern United States and in Mexico south to Puebla and Vera Cruz. The Gray Silky Flycatcher (*Ptilogonys cinereus*) is a montane species ranging from northwestern and eastern Mexico to Guatemala. The Long-tailed Silky Flycatcher (*P. caudatus*) and the Black-and-yellow Silky Flycatcher (*Phainoptila melanoxantha*) are each endemic to the highlands of Costa Rica and western Panama.

This paper reviews some of the taxonomic history and characters of the silky flycatchers and presents new evidence from studies of the egg-white proteins indicating that they are closely related to the genus *Myadestes*, the solitaires, of the thrush family Turdidae. The two species of the genus *Entomodestes* of northwestern South America may be part of this natural cluster, but their egg whites have not been available for comparison.

TAXONOMIC HISTORY OF THE SILKY FLYCATCHERS AND ALLIES

Ptilogonys cinereus, the first of the group to be discovered, was described by Swainson in 1824. Swainson also described the Phainopepla (1837), which he placed in *Ptilogonys*. From the time of their discovery these birds were considered to be closely related to the waxwings. Gray (1846) placed them near the waxwings because of similarities in bill shape, tarsal scutellation, plumage texture, and the possession of a crest. But there also are differences. *Phainopepla* differs from *Bombycilla* in having a long tenth primary (vs. a rudimentary one), a rounded wing (vs. a long, pointed wing), long rictal bristles (vs. the obsolete condition), unfeathered nasal fossae (vs. densely feathered), downy nestlings (vs. naked), and unstreaked juvenal plumage (vs. streaked). Thus those who advocated placement in separate taxa also had a basis for their opinion.

Baird (1858) proposed the genus *Phainopepla* for Swainson's *Ptilogonys nitens*, an arrangement that has since been accepted without debate.

The association of *Myadestes* with the waxwings and silky flycatchers was apparently first challenged by Baird (1864–72: 417–433) who advocated the tranfer of *Myadestes* from its "usual association with *Ptilogonys*, among Ampelidae [= Bombycillidae], to, or at least very near, the Turdidae." Although Baird noted the "close resemblance in general appearance" between *Myadestes* and *Ptilogonys* he traced a series of links that showed the alliance of *Myadestes* to the typical thrushes. Baird proposed the subfamily "Myiadestinae" to include "*Myiadestes*. . . *Cichlopsis*. . .*Platycichla*. . .the latter genus is so closely related to *Cichlopsis* as almost to be the same; *Platycichla* forming the link with with *Turdinae* through *Planesticus*, while such species as *Myiadestes unicolor* show the affinities of *Cichlopsis* to *Myiadestes*."

Coues' treatment of the problem provides an indication of the transition of taxonomic opinion from the older view of *Myadestes* as a relative of *Phainopepla* to the new alliance with the thrushes. In the first edition of his "Key" Coues (1872) included *Phainopepla* and *Myadestes* in the waxwing family (Ampelidae), but noted that Baird had separated them and that this course was possibly correct. In the "Birds of the Colorado Valley" (1878) Coues adopted Baird's arrangement and placed *Myadestes* with the thrushes. Then, in later editions of the "Key" (e.g. 1887), he recognized the subfamily "Myiadestinae" but placed it in the "Ampelidae," following the Ptilogonatinae, and stated that although *Myadestes townsendi* "was formerly called 'Ptilogonys', it has nothing to do with the foregoing subfamily. The Myiadestinae are in fact nearly related to the Turdidae."

Seebohm (1881) left *Myadestes* completely out of the Turdidae and Sharpe (1883) included the genus in the Timaliidae, noting (p. 368) that this was an unsatisfactory arrangement but that he "placed them near the Mocking-Thrushes [= Mimidae], which they resemble in the power of song." Seebohm defined the Turdinae primarily on the basis of the booted tarsus and spotted juvenal plumage, a definition relied upon to the present day.

Stejneger (1883) praised Seebohm's definition of the Turdinae, but was "provoked by the arrangement proposed." As a reply Stejneger presented a review of the systematics of the American thrushes in which he adopted Baird's proposal concerning *Myadestes*. But one species did not fit the definition and Stejneger decided that "the group will not, however, be naturally limited or clearly defined without removing the species *Myadestes leucotis* (Tschudi), which is widely different, from the Myadestinae, being a true member of the Ptilogonatidae." Stejneger then

proposed the new genus *Entomodestes* for *M. leucotis* and assigned it to the silky flycatchers. An important factor in this decision seems to have been that Stejneger had found the tarsus of *leucotis* to be faintly scutellate anteriorly whereas Baird had thought that it was "without distinct scutellar divisions anteriorly, except below" (Stejneger 1883: 457). Thus by applying Seebohm's definition, Stejneger felt obliged to separate *leucotis* from the thrushes.

Although *Entomodestes* later was replaced in the thrushes (Ridgway 1904, Ripley 1964), *Myadestes* was not again considered to be a relative of the silky flycatchers. The Seebohm definition, supported by Baird, Coues, Stejneger and others, precluded the association with the thrushes of a species with a scutellate tarsus. But that a relationship existed between the waxwings and silky flycatchers was not challenged, and they continued to be placed together.

Lucas (1894) noted that *Phainopepla* and *Ampelis* (= *Bombycilla*) are alike "in the palatal region and both possess a large, free, swollen lachrymal, this last being a point of much importance, since such a lachrymal is of rare occurrence among birds." According to Beecher (1953) free lachrymals are also present in (at least) some corvids (*Cissa*), *Oriolus*, *Paradisaea*, *Ailuroedus*, *Callaeus*, *Pericrocotus*, *Cracticus*, *Artamus*, *Laniarius*, *Vanga*, *Prionops*, *Aegithina*, and *Sitta*.

Lucas (1894) also found that "the quadrates of *Ampelis* and *Phainopepla* agree with each other in minute as well as general characters, as do also the pneumatic maxillo palatines." This last point is of special interest because the thrushes, including *Myadestes*, also have maxillo-palatines with inflated ("pneumatic") tips. Lucas noted further that *Phainopepla* and the waxwings agree in the general contour of the dorsal feather tract, but this has little or no taxonomic significance for Mary H. Clench tells me that nothing in their pteryloses distinguishes between thrushes, waxwings, silky flycatchers, and several other passerine groups.

Lucas (1894: 310) also stated that "the skull of *Myadestes* is rather short, and on its superior aspect bears a considerable resemblance to that of *Ampelis*." It follows that the skulls of *Myadestes* and *Phainopepla* should be similar, and examination shows that they are. It is curious that Lucas stated (p. 311) that "*Myadestes* . . . has a flat non-pneumatic maxillo-palatine." This is certainly incorrect for I have examined these bones in *Myadestes*, *Phainopepla*, and *Bombycilla* and all three have an inflated, hollow, i.e. "pneumatic" tip. Those of *Myadestes* and *Phainopepla* are more alike than either is like that of *Bombycilla*. It is possible that Lucas' specimen of *Myadestes* was damaged and that this similarity therefore escaped his notice. His Figure 10 (p. 311) shows the palatal region

of *Myadestes* with the tip of one of the maxillo-palatines missing, but the other seems to be intact. Lucas concluded (p. 311) that although *Myadestes* "has some leanings toward the Ampelidae it seems to have more decided affinities with the thrushes, although it is by no means a typical thrush."

Ridgway (1904) recognized the families Ampelidae, Ptilogonatidae, and Dulidae and considered them allied to one another. Concerning the silky flycatchers he stated (pp. 113–114) that "they are related to the Waxwings (family Ampelidae), and have usually been placed with them; but they differ in their rounded wings, with well-developed tenth and shortened ninth primaries, their well-developed rictal bristles and different character of the frontal feathers. Their habits, however, are said to be very similar." The statement about similar "habits" presumably referred to the fact that both groups eat fruit and insects and have somewhat similar nests.

In his diagnosis of the Ptilogonatidae Ridgway (1904: 113) noted that in adults of *Phainoptila* (Salvin 1877) the acrotarsium is not distinctly scutellate and that "the genus *Phainoptila* is doubtfully a member of this group, and as far as the adult is concerned might easily be referred to the Turdidae without materially affecting the diagnosis of the latter family; but the young have the plumage absolutely plain-colored and the acrotarsium distinctly scutellate."

Ridgway was not consistent in his application of the Seebohm definition of the Turdidae, for he brought *Entomodestes* back into that family, in spite of its having the "acrotarsium divided ("scutellate") on inner side" (1907: 7) and contrary to Stejneger's argument that it is a ptilogonatid. Ridgway placed *Entomodestes* next to *Myadestes* in his key to the genera of American Turdidae and distinguished between them on the basis of bill length and tarsal scutellation.

Ridgway (1907: 1) also expressed doubt about the taxonomic value of the spotting in the juvenal plumage of thrushes, citing several examples of species in which the spotting is indistinct or nearly absent. One of his examples was *Zeledonia*, which has no trace of spotting in the juvenal plumage, but in this he was not citing an exception within the Turdidae for as I have shown (Sibley 1968) *Zeledonia* is actually a wood warbler (Parulini) that had been mistakenly assigned to the Turdidae. Ridgway's point was that the diagnostic value of the spotting in the juvenal plumage of thrushes is less than had been supposed. He also referred to his earlier (1904) remarks about *Phainoptila* (quoted above) as an example of a bird that "might easily be referred to the Turdidae" but which has unspotted young.

Since 1907 the taxonomic discussions of the silky flycatchers have con-

cerned themselves almost exclusively with the question of their relationships to *Bombycilla* and *Dulus*. The possibility that they might be related to the thrushes via *Myadestes* and *Entomodestes* appears to have been mentioned only by Hellmayr (1934: 444) who noted that *Entomodestes* "seems to be well differentiated from *Myadestes* by longer bill and scutellate inner side of the acrotarsium, and may even prove to belong to the Ptilogonatidae." He thus followed Ridgway but appeased Stejneger with this neutral footnote.

Stresemann (1927–34) placed the silky flycatchers in the Bombycillidae but recognized the Dulidae as a separate, but adjacent, family. Wetmore (1930) followed Ridgway by recognizing three separate families and has done so consistently through the years (1960). He noted (1951: 1, 1960: 20) that "suggestions for the union of the Bombycillidae, Ptilogonatidae, and the Dulidae in one family are not substantiated by examination of the skeleton. *Dulus*, the palmchat, is widely different from the other two, a structural distinction that is further emphasized by its curious communal nesting habits. The first two seem more closely related but are separated clearly by characters found in the ectethmoid region of the skull, and in the manubrium, to mention only two points that are easily apparent."

Arvey (1951) made a comparative study of *Bombycilla*, the silky flycatchers, and *Dulus*, based upon coloration, nesting, food habits, skeleton, and certain soft parts. Arvey tended to explain the differences between the three groups as due to specialization and concluded that they are related and should be placed in a single family. He made no comparisons with *Myadestes* except in tables of ratios of the relative lengths of certain bones.

Delacour and Amadon (1949) considered the relationships of *Hypocolius* and concluded that it should be assigned to the Bombycillidae as a subfamily, with the Ptilogonatinae, and possibly the Dulinae as additional subfamilies. Mayr and Amadon (1951) adopted this arrangement but noted (p. 23) that "*Hypocolius* shares with *Eurocephalus*, and to a lesser extent with *Prionops*, the peculiar feature of having the normally unbroken plates comprising the rear half of the oscinine tarsus divided weakly into a number of shields or scutes. This might mean that the resemblance of *Hypocolius* to other bombycillids is superficial. Another possibility is that the Bombycillidae belong in the general vicinity of the Prionopidae and related families. We here tentatively follow the latter alternative." In a later paper Amadon (1956) expressed uncertainty about the relationship of *Hypocolius* to the waxwings.

Ripley (1952) included the two species of *Entomodestes* in *Myiadestes*

[*sic*] but in a later (1964) treatment recognized both genera and placed them next to one another.

Beecher (1953) interpreted the patterns of the jaw muscles as supporting a relationship among the waxwings, silky flycatchers, palm chat, and *Hypocolius*, and between them and the Campephagidae and Pycnonotidae.

Greenway (1960) expressed doubt about an alliance between *Bombycilla* and the silky flycatchers by noting (p. 371, footnote) that "actual relationship of this group to *Bombycilla* has not been proved." Similar skeptical footnotes about *Hypocolius* and *Dulus* also were expressed (p. 373).

Skutch (1965) studied the nesting of *Ptilogonys caudatus* in Costa Rica and presented a useful comparative summary of the life histories of *Ptilogonys*, *Phainopepla*, *Bombycilla*, and *Hypocolius*, with some notes on *Phainoptila*, the nest of which was then unknown. All of these species feed on small fruits and flying insects. Only *Phainopepla* has a conspicuous, melodious song, but voice seems to play a minor role in the biology of the group. The nest in all species is an open cup placed in a tree or bush. The male helps to build, but his participation varies. The eggs of all are generally similar, being mostly grayish with darker markings of lilac, brown, and black.

The young hatch naked in *Bombycilla* and have pinkish skin. In *Phainopepla* and *Ptilogonys* the young have white down (especially long in *Phainopepla*) and dusky skin. Skutch notes (p. 424) that "a peculiarity of both *Ptilogonys* and *Phainopepla* is that feathered nestlings make excursions through nearby branches and return to the nest, before they finally sever contact with it."

Skutch concluded that the resemblances between these birds are more numerous than the differences, and that (p. 425) "so far as their life histories are now known, they provide no reason for classifying these birds in separate families."

Skutch notes (p. 425) that *Phainoptila* contrasts with the others in "its lack of a crest, thrush-like aspect, slight sociability, and forest habitat. . .one who has watched this bird in the field feels the strength of Ridgway's (1904: 113) remark that 'the genus *Phainoptila* is doubtfully a member of this group. . .and might easily be referred to the Turdidae' " (see complete quotation above).

In 1972 Lloyd F. Kiff found the first known eggs of *Phainoptila* in Costa Rica. He reports (in litt.) that the nest and the egg colors and markings are "like those of *Phainopepla* and *Ptilogonys*."

The adult plumage coloration of *Phainopepla* seems to differ from that of *Myadestes*, but the female plumage of *Phainopepla* is similar to that

of *M. townsendi*. Furthermore the plumage of the black solitaire, *Entomodestes coracinus*, is similar to that of the male of *Phainopepla* being lustrous jet black with areas of white in the wings, tail, cheeks and breast. The shape and proportions of the bills in *Myadestes* and *Phainopepla* are essentially identical.

The juvenal plumage of *Myadestes* is like that of the typical thrushes in having buff spots on the body feathers and wing coverts, but *Phainopepla* has an unspotted juvenal plumage. In both genera the postjuvenal body molt tends to be complete, but in *Phainopepla* about 50 percent of the individuals also replace all or most of the remiges and rectrices (Miller 1933).

Ames (MS) has found that most of the genera currently placed in the Turdinae and Muscicapinae share a pattern of the syringeal musculature that he calls the "turdine," as opposed to the "generalized oscine" pattern found in most other members of the Passeres. Among the exceptions Ames found is *Myadestes* which, like *Phainopepla*, has the generalized oscine pattern, not the turdine arrangement. *Entomodestes*, however, has the turdine syringeal pattern. Ames further informs me (in litt.) that the syringes of *Phainopepla* and *Bombycilla* are much alike and that the syrinx of *Myadestes* is more like that of *Phainopepla* than that of *Turdus*. The syrinx of *Ptilogonys* is like that of *Phainopepla*, but *Phainoptila* is "more robust in the syrinx than are the other ptilogonatids." Ames' findings thus suggest an alliance among the ptilogonatids, *Myadestes* and *Bombycilla*, but not between these and *Entomodestes*.

The syringeal characters provide an interesting comparison with the tarsal scutellation patterns. *Myadestes*, which has a booted tarsus, agrees in its general syringeal characters with *Phainopepla*, which has a scutellate tarsus, and *Entomodestes*, which resembles both *Myadestes* and *Phainopepla* in several ways, has a typical thrush syrinx but also has faintly scutellate tarsi. And *Phainoptila*, which is closely related to *Phainopepla*, has a booted tarsus and a thrushlike appearance but a "generalized oscine" syrinx.

The significance of the syringeal patterns is not yet clear but the taxonomic value of tarsal scutellation patterns is certainly low and has been questioned many times, notably by Pycraft (1906), Blaszyk (1935), Plotnick and Pergolani de Costa (1955), Rand (1959), and Ames et al. (1968).

In summary: From 1824 until 1866 the silky flycatchers and solitaires (*Myadestes*) were often considered to be related because of their external similarities. Following Baird's transfer of *Myadestes* to the Turdidae, the silky flycatchers, waxwings and, sometimes, the Palm Chat (*Dulus*) and

the genus *Hypocolius* have been placed together or in separate but adjacent families. A possible relationship between the silky flycatchers and *Myadestes* has been forgotten or ignored because of reliance upon the combination of booted tarsi and spotted juvenal plumage to define the Turdidae. The two species of the South American genus *Entomodestes*, placed in the Ptilogonatidae by Stejneger because of having faintly scutellate tarsi, were returned to the Turdidae, next to *Myadestes*, by Ridgway and later authors. Ripley (1952) merged the two genera, later (1964) separated them again. In external appearance and skeletal characters *Phainopepla* and *Myadestes* are extremely similar and also similar to *Bombycilla*. *Phainopepla* and *Myadestes* have similar syringes and similar food habits. *Phainopepla* and *Myadestes* differ in tarsal scutellation and juvenal plumage spotting, but *Phainoptila*, which seems closely related to *Phainopepla* and *Ptilogonys*, has a booted tarsus and has been considered to be thrush-like in appearance and behavior. *Entomodestes* shares characters with both the thrushes and the silky flycatchers.

The Egg-White Protein Evidence

In a comparative study of passerine egg-white proteins using starch gel electrophoresis (Sibley 1970) I found that *Phainopepla* and *Bombycilla* had similar patterns, but that *Dulus* differed enough to cast doubt on a close relationship between it and the other two genera. Although *Phainopepla* was not made the subject of a special comparison with the thrushes, it clearly shares a common pattern with them. *Myadestes* was not illustrated in this paper but its starch gel pattern agrees with that of the thrushes and with *Phainopepla*.

The limitations of the starch gel technique did not provide sufficient resolution of the egg-white proteins to make detailed comparisons, but I am now able to present data based upon the electrophoretic method of isoelectric focusing in acrylamide gel (abbreviated IFAG). The technique was described by Sibley and Frelin (1972) and used in a study of *Opisthocomus* by Sibley and Ahlquist (1973). With IFAG it is possible to resolve from 20 to 30 protein bands in most passerine egg-white specimens, compared with fewer than 10 in starch gel. The IFAG technique separates proteins on the basis of their isoelectric properties and it is possible to examine limited portions of the pH spectrum, thus achieving a "magnified" view of those proteins that are isoelectric within the chosen pH range. This has been done for the pH ranges of 6–4 and 8–3 in the present study, as well as for the complete range of pH 3–10. The numerical direction in each case indicates that the sample was applied at the pH indicated by the first value, and thus the movement of proteins took place from

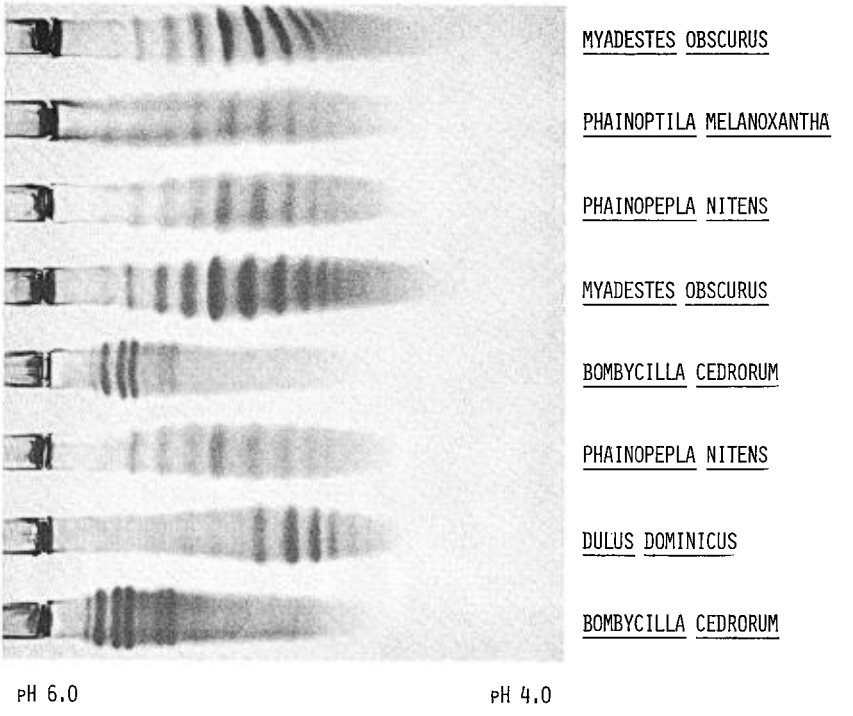

Figure 1. The egg-white proteins of the silky flycatchers *Myadestes*, *Bombycilla*, and *Dulus* compared using the technique of isoelectric focusing in acrylamide gel with an Ampholine range of pH 6–4, gel A-1202. See text for description.

that point toward the second pH value during the period of migration to the isoelectric point of each protein. The reason for using a limited pH range is to examine a particular set of proteins in greater detail. For example pH 6–4 (or 4–6) covers the region in which the ovalbumin fraction or fractions occur. This region tends to contain a large percentage of the proteins in avian egg white and experience with some 10,000 samples has shown them to be especially informative for taxonomic comparisons. The direction of migration (i.e. 6–4 or 4–6) is dictated by technical considerations that make the 6–4 direction preferable. All critical comparisons are made only among the eight samples in a given gel, thus insuring that all have been exposed to identical conditions during analysis.

In all comparisons using pH ranges of 3–10, 6–4, and 8–3, *Phainopepla* agrees in detail with *Myadestes*. The 6–4 patterns are the most informative and are the only ones illustrated in this paper (Figures 1–3). At least 15 protein bands can be seen in the original gels (some may be lost in the

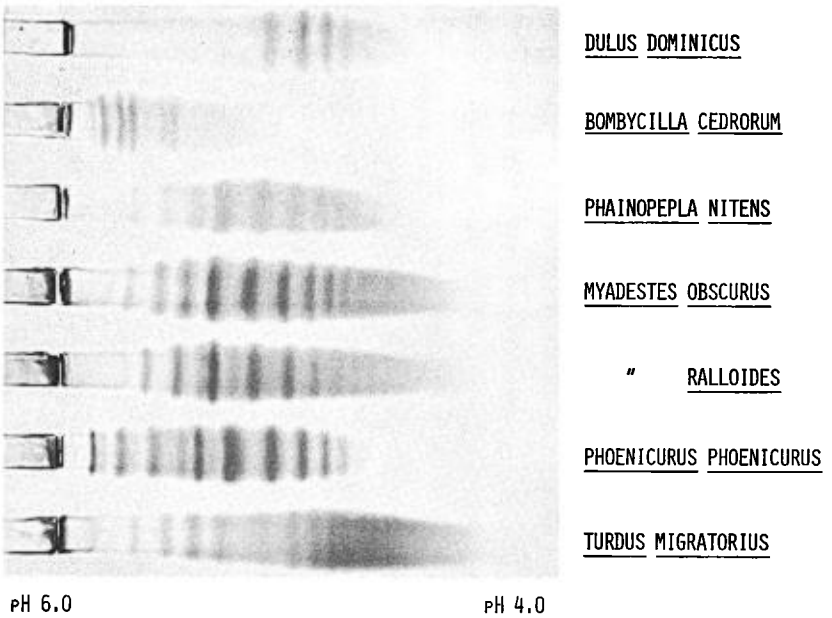

Figure 2. The egg-white proteins of *Dulus*, *Bombycilla*, *Phainopepla*, *Myadestes*, and two thrushes. Conditions as in Figure 1. Gel A-1203. See text for description.

photographic reproduction) and the two genera agree in the positions of all of them. *Phainoptila* also agrees with *Phainopepla* and *Myadestes* although one protein near pH 6.5 has a slightly different position. When the comparisons are extended to various thrushes both similarities and differences are apparent. It should be noted that all passerines seem to possess certain of the proteins in this region, that is, all have homologs of the same basic set. Thus it is usually possible to identify the homologous proteins when comparing different species. The differences among a closely related group of species thus take the form of differing degrees of agreement in isoelectric points, which presumably reflect structural differences in amino acid sequence and, hence, genetic differences. At the magnification achieved with the pH 6–4 range it is reasonable to assume that even the smallest difference in the isoelectric points of two homologous proteins is due to a difference of at least one amino acid and, therefore, of at least one nucleotide at the DNA level. Thus when two species are identical in the isoelectric points of 15 proteins it is reasonable to assume that they are closely related, providing there is no important conflicting evidence.

More detailed comparisons of the pH 6–4 IFAG patterns follow: In

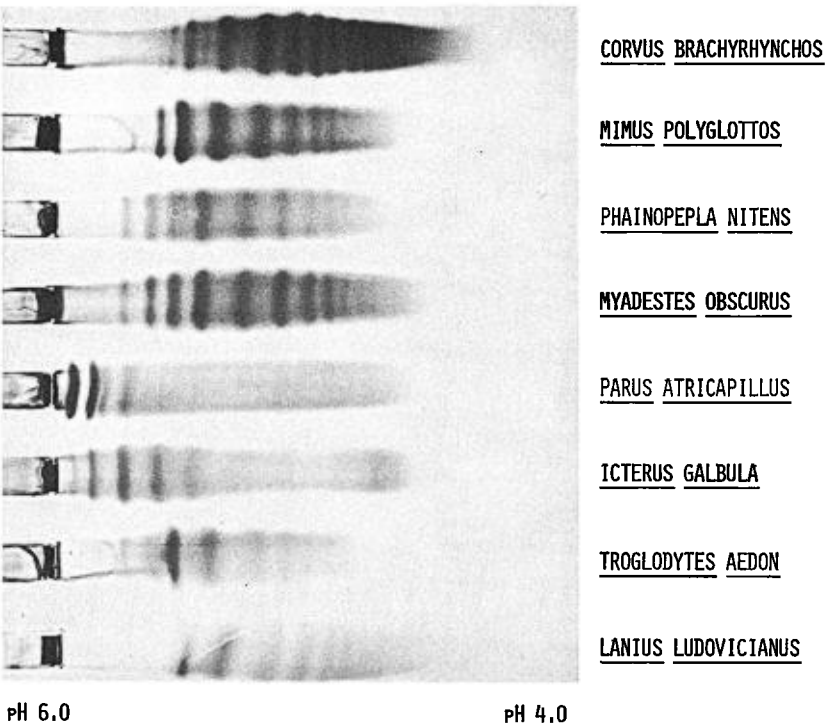

Figure 3. The egg-white proteins of several passerine genera compared with those of *Phainopepla* and *Myadestes*. Conditions as in Figure 1. Gel A-1204. See text for description.

Figure 1 at least nine protein bands can be seen in *Phainopepla* and *Myadestes obscurus* and they are essentially identical. In gel A-803 (not illustrated) 13 protein bands can be seen in the pH 6–4 region and the two genera are identical in all of them, that is, the isoelectric points and quantities of each pair of homologous proteins correspond in the two genera. *Phainoptila*, in Figure 1, shows close agreement with *Phainopepla*, although at least two proteins seem to have slightly different isoelectric points from their homologs in *Phainopepla*.

The pattern of *Bombycilla* differs strikingly from those of *Phainopepla*, *Phainoptila*, and *Myadestes*. The well-resolved proteins near pH 6 do not have obvious counterparts in *Phainopepla* and the remainder of the pattern in the pH 5–4 region lacks well-defined bands in all of the many gels that have been studied. In gel A-757, pH 3–10 (not illustrated), *Bombycilla* and *Phainopepla* differ in the way reflected in the pH 6–4

patterns, that is, the major bands in *Phainopepla* occur near pH 5 but in *Bombycilla* they are near pH 6. These differences are real, but in some gels (A-755, A-803, A-814) it is possible to see that the two genera do have several proteins with identical or similar isoelectric points in the pH 5–4 region. I conclude that *Phainopepla* and *Myadestes* are more alike than *Phainopepla* and *Bombycilla*.

The pattern of *Dulus* is similar to that of *Phainopepla* in the pH 5–4 region, but less so near pH 6, although some faint bands in the *Dulus* pattern do have strong counterparts in *Phainopepla*. In pH 3–10 gels (e.g. A-757) *Dulus* has a cluster of strong bands near pH 4, *Phainopepla* near pH 5, and *Bombycilla* near pH 6, thus reflecting the situations in their pH 6–4 patterns. All three genera have the same set of homologous proteins in the pH 5–6 region but so also do certain other passerines, as illustrated in Figure 3. In this gel, *Corvus*, *Mimus*, *Troglodytes*, *Lanius*, *Phainopepla*, and *Myadestes* are similar or identical in the pH 5–4 region, but only the latter two also agree in the pH 6–5 section of the gel. *Parus* and *Icterus* differ from the others and from one another. In Figure 2 the patterns of the two species of *Myadestes* are more like that of *Phainopepla* than like those of *Phoenicurus* and *Turdus*. It is also clear that the two species of *Myadestes* differ slightly from one another in the isoelectric points of some proteins. The faint bands next to strong ones in two positions in the *M. ralloides* and *Phoenicurus* patterns may be due to genetic polymorphisms and may be ignored for our present considerations. I conclude that *Myadestes* is more like *Phainopepla* than it is like *Turdus* or *Phoenicurus*. The patterns of other thrushes, including *Erithacus rubecula*, *Cossypha caffra*, *C. heuglini*, *P. phoenicurus*, *Saxicola caprata*, *S. torquata*, *Myiophoneus horsfieldii*, *Zoothera citrina*, *Catharus fuscescens*, *Hylocichla mustelina*, *Platycichla flavipes*, *Turdus pilaris*, and *Turdus leucomelas* also have been used in the comparisons. All show some similarities to *Myadestes*, but none is as similar to it as is *Phainopepla*.

Conclusions

From these comparisons, and in the light of the other evidence cited above, I conclude as follows:

1. The silky flycatchers, *Phainopepla*, *Ptilogonys*, and *Phainoptila*, are more closely related to *Myadestes* than to any other genus (or genera).

2. The relationship between the silky flycatchers and the waxwings is unclear and more evidence is needed before any conclusion is made.

3. Similarly the relationships of *Dulus* and *Hypocolius* remain to be determined beyond question.

DISCUSSION

The results of this study are several. That the silky flycatchers are closely related to the solitaires seems clear. But the implications of the discovery that the silky flycatchers are more closely allied to *Myadestes* than *Myadestes* is to most (or all?) typical thrushes, is the most significant result for it forces a reevaluation of certain taxonomic characters and of the definition of the boundaries of one or more passerine groups. For nearly a century the Turdidae have been defined on the basis of the combination of characters first clearly enunciated by Seebohm (1881). Stejneger (1883: 450) expressed his approval in words that have been considered acceptable to the present day. "The definition of the group *Turdidae*. . . given by Mr. Seebohm, seems to be a very proper one, and I think he has therein expressed the only chief character which really indicates the relationship of the birds to be included in this family. The peculiar spotted first plumage of the *Turdidae* is a very striking feature, and its coincidence with booted tarsi very remarkable. A careful comparison with forms, which, without showing these characters, have at different times been referred to the *Turdidae*, will convince us that the limits traced by Mr. Seebohm are the only reliable ones, and that the family thus defined is a very natural group, and, indeed, one of the best among the Passeres. . . . It is not difficult to foresee that his definition of the family will be heartily accepted by ornithologists."

Stejneger proved to be a good prophet for Seebohm's definition was "heartily accepted." Ridgway (1907: 3) gave it his approval and the definition has been used to include or exclude species from the thrushes ever since. But was it ever *precisely* definitive? It was not. Seebohm himself noted that the "very young birds of one or two species" might show evidence of tarsal scutellation and Ridgway (1907: 1) called attention to some species in which the spotting of the juvenal plumage is indistinct or almost absent. The definition held up because it includes over 300 species and the correlation between plumage and tarsal characters is remarkably constant for such a large group.

But each of these characters is found in other groups. A booted tarsus, or a tendency toward that condition, occurs in *Pitta*, in some genera of the Formicariidae (*Gymnopithys*, *Phaenostictus*, *Hylophylax*), and in the Acanthisittidae, Cracticidae, Grallinidae, Ptilonorhynchidae, Paradiseidae, some Corvidae, Callaeidae, and some Dicaeidae. The booted tarsus in *Cinclus*, some sylviids, and a tendency toward the condition in *Prunella* have been used as evidence of a relationship between these birds and the thrushes.

A spotted juvenal plumage is usually present in the Muscicapidae and

has been used as evidence of a relationship to the thrushes, although the muscicapids have scutellate tarsi. The members of the thrush genus *Myiophoneus* are only slightly spotted or unspotted as juveniles and the Sylviidae, often considered to be close relatives of the Turdidae, are unspotted in the juvenal plumage.

The adaptive significance of booted tarsi is not easy to discern because species with a great variety of habits possess the condition. It is this apparent lack of a clear functional relationship that has made this character so resistant to criticism. If there is a single adaptive correlation between a smooth tarsus and some environmental or behavioral selective pressure it has not yet been identified. A detailed study of the question may reveal that there are actually several types of booted tarsi, each correlated with a different source of selection, or that all are the result of a single selective force and thus similar by convergence.

Somewhat the same argument can be presented in relation to the spotted juvenal plumages of thrushes and Old World flycatchers. Presumably juvenal plumage coloration performs at least two functions. It is protective by being concealing, and it relieves the young birds from the attacks of territory-holding adults by lacking the "signal" characters that elicit hostile responses. In some sexually dimorphic groups (but not in the thrushes) it is convergently similar to the adult female plumage for these same reasons. Any pattern that will satisfy these or additional requirements of selection will serve, and a variety of plumage patterns have evolved in different groups. The particular type of spotting shared by most thrushes and many muscicapids is a significant character because such spotting is rare outside these groups. They are therefore often believed to be related, whereas species with streaked juvenal plumages, which occur in many groups of passerines, are not.

The resolution of these questions lies outside the present paper, but Seebohm's definition of the thrushes must either be modified to include the silky flycatchers or to exclude the genus *Myadestes*. Either solution breaches the definition and casts doubt on the validity of the Turdidae as presently understood.

Recommendations

At least two taxonomic treatments might be employed to reflect the relationships revealed by this study. *Myadestes* could be included in the Ptilogonatidae, or the silky flycatchers plus *Myadestes* (and perhaps *Entomodestes*) could be placed in a subfamily (Ptilogoatinae) in the Turdidae.

Because so many facets of the larger problems involving the thrushes,

muscicapids, and their real or assumed allies remain unclear I prefer a treatment that, for the moment, disturbs the present classification least and yet expresses the close relationship between *Myadestes* and the silky flycatchers. I therefore recommend that Wetmore's (1960) arrangement be modified by including *Myadestes*, and perhaps *Entomodestes*, in the Ptilogonatidae and that this family be placed next to the Turdidae. At this time I prefer to reserve judgment on the relationships of *Bombycilla*, *Hypocolius* and *Dulus*.

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SUMMARY

From the time of the discovery of *Ptilogonys cinereus* in 1824 until 1866, the silky flycatchers (Ptilogonatidae) and the genus *Myadestes* were considered to be related to one another and to the waxwings (*Bombycilla*). Since 1866 *Myadestes* has been placed in the Turdidae and the other genera have been placed together or in adjacent taxa. Data from comparative studies of the egg-white proteins, using the electrophoretic technique of isoelectric focusing in acrylamide gel, indicate that *Myadestes* and the silky flycatchers actually are closely related. Evidence from other sources also supports this conclusion. It is recommended that *Myadestes* and, perhaps, *Entomodestes*, be transferred to the Ptilogonatidae and that this family be placed next to the Turdidae.

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