## Reflections

**Reflections** are short contributions ( $\leq 2$ printed pages, about 1200–1500 words) in which an editor and/or a reviewer comments on, and provides a perspective on one of the published papers in the same issue. An abstract is not required.

JOURNAL OF AVIAN BIOLOGY 00: 1–3, 2003

# *The "Coerebidae": a polyphyletic taxon that dramatizes historical over-emphasis on bill shape as a taxonomic character*

*J. V. Remsen, Jr., Museum of Natural Science, Foster Hall 119, Louisiana State University, Baton Rouge, Louisiana 70803, USA. E-mail: najames@lsu.edu*

Because the core body shapes of birds are relatively conservative (Hafner et al. 1984), differences in bill shape and size account for much of the variation among birds that we humans perceive. Although tail and leg size and shape may vary almost as much, the bill may exert more influence on our cognitive perception because of its proximity to the bird's face. The close association of bill size and shape with food type and feeding behavior adds additional weight to the ornithologist's perception of their "importance." For these reasons, it is perhaps no surprise that bird bills have played a prominent role in their classification.

For the Passeriformes known as nine-primaried oscines, bill characters historically have been used frequently in determining family boundaries. For example, Ridgway's (1901) classic treatment used bill characters in virtually every line of his dichotomous key for the six New World families that he recognized: Fringillidae for finches (all the conical-billed species), "Tanagridae" ( = Thraupidae) for tanagers, "Mniotiltidae" ( = Parulidae) for warblers, Icteridae for blackbirds, Catamblyrhynchidae for one species, the plushcap *Catamblyrhynchus diadema*, with an unusual bill, and Coerebidae for honeycreepers, which were those species that had bill shapes or tongues associated with flower-feeding. Yet Ridgway himself recognized that his key didn't work for some species, especially some of the honeycreepers, and his accompanying text was sprinkled with cautionary sentences and pleas for additional data. He astutely noted that some species that he placed in the Coerebidae might actually be warblers or tanagers.

A century later, Kevin Burns, Shannon Hackett and the late Nedra Klein (2003, see pp. xx-yy in this issue) have hammered the final nail into the coffin of the "Coerebidae". The importance of the dismantling of the "Coerebidae", which actually began more than 50 years ago with Beecher's anatomical studies, reaches beyond the boundaries of phylogenetic classification. Darwin, for whom plasticity of bill shape in Galapagos "finches" catalyzed his famous ideas, would presumably have warned ornithologists against using bill shape as a character, but many bird families were and continue to be defined, at least in part, by bill shape. This criterion "works" well for some groups with unique bills, such as ducks, flamingos, parrots, and woodpeckers. In many other cases, however, over-emphasis on bill shape, or skeletal and muscle characters that co-vary with bill shape (Bock 1964), has produced taxa that are either not monophyletic or if so, merely arbitrary breaks inflicted on continuous variation (Storer 1969). Burns et al.'s research is the most recent of several studies that indicate that perhaps the worst case of over-emphasis on bill shape is in the group known as the New World nine-primaried oscines, the ones included in Ridgway's key.

Burns et al.'s analysis of mitochondrial sequences shows beyond a doubt that the "Coerebidae" actually consists of multiple independent lineages. In fact, of the 10 original genera in that family, the new genetic data can confirm that only three pairs are each others' closest relatives (*Chlorophanes* and *Iridophanes*, *Conirostrum* and *Oreomanes*, and *Dacnis* and *Cyanerpes*), and that the "honeycreeper" ecotype evolved a minimum of six times within the tanager-finch lineage. In three of those cases, the sister genera are not of the omnivore "tanager" ecotype but rather of the "finch" ecotype, e.g., *Coereba* and a *Tiaris* grassquit. Burns et al. did not data from enough species of *Diglossa* to determine whether that genus is polyphyletic, as is strongly suggested by morphological data (Bock 1985).

All this reflects the ongoing overhaul of family boundaries within the New World nine-primaried oscines. Long-suspected of taxon boundary problems (Sclater 1886, Storer 1969), the tanagers (Thraupidae) and sparrows (Emberizidae) were identified as paraphyletic taxa by DNA hybridization studies of Bledsoe (1988) and Sibley and Ahlquist (1990). Although DNA

hybridization data have often been harshly criticized, the results from such studies often have been vindicated by subsequent, different genetic techniques, and this would now include the results of Burns et al. (2003). Currently, the delimitation of monophyletic groups in the New World nine-primaried oscines is undergoing systematic and thorough investigation, with at least four research teams actively working together on this group, each with a different taxon focus. With the probable exception of the Icteridae, the other four "families" contain multiple genera that actually belong in other groups. For example, the "tanager" genera *Euphonia* and *Chlorophonia* have already been excised from the Thraupidae and deported to the Fringillidae (Burns 1997, Klicka et al. 2000, Yuri and Mindell 2002, Banks et al. 2003). The eventual taxonomic realignments will have important effects on research on these taxa, which are frequently studied by bird biologists because of their abundance and ubiquity. By now, all avian biologists recognize that controlling for phylogenetic effects is critical to the interpretation of all comparative data (e.g., Lanyon 1993).

The contrast between the fates of the Coerebidae and the Icteridae are striking and are worth exploring. The Icteridae has included species with somewhat curved bills used for flower-probing (some *Icterus* orioles) as well as some taxa with conical, seed-crushing bills (*Molothrus ater*, *Dolichonyx*), yet with one exception (below), the monophyly has never been seriously questioned. The Icteridae as defined by Ridgway (1901) and Hellmayr (1937) remains 100% intact, whereas the Coerebidae, as defined by Ridgway (1901), Hellmayr (1935), Wetmore (1960), and Meyer de Schauensee (1966), no longer exists. Assuming that further investigations continue to show that the Icteridae is a monophyletic, the reasons for the "resiliency" of the Icteridae are presumably: (1) plumage patterns in the Icteridae are relatively conservative (e.g., Omland and Lanyon 2000) and are unlike those of most other New World nine-primaried oscines; (2) most species in the Icteridae are above the range in body size shown in the other families; and (3) within the genera that deviate from the straight, pointed bill with elevated culmen (often with associated with "gaping" feeding behavior) that typifies most Icteridae, intermediates between the typical and atypical shapes exist so that the extremes are not isolated but seem part of a continuum. The one exception, the bobolink *D. oryzivorus* in the monotypic genus *Dolichonyx*, has produced the only challenge to the family's monophyly and often has been placed in a separate subfamily within the Icteridae, mainly because of lack of intermediates between it and more typical Icteridae. Recent genetic results (Lanyon and Omland 1999), however, clearly show that it is embedded deep within the Icteridae and does not warrant subfamily status.

As Burns and others firm up the branching pattern within the species-rich and morphologically diverse tanagers and relatives, it will be possible to analyze these lineages to quantify and identify where morphology has masked phylogeny. Such analyses so far in birds have shown that plasticity and convergence in characters associated with feeding, namely the head and bill in herons (McCracken and Sheldon 1998) and the legs in diving ducks (McCracken et al. 1999), are largely responsible for the differences in phylogenies based on morphology versus genetics. Convergence among lineages that are obviously distantly related has been recognized for more than a century. For example, the extreme "honeycreeper" ecotype, namely small birds with strongly decurved bills and bright plumage, has evolved at least five times in the Passeriformes: *Cyanerpes* in the Thraupidae, *Myzomela* and perhaps others in the Meliphagidae, *Vestiaria* and *Drepanis* in the Fringillidae, *Neodrepanis* in the Philepittidae, and almost all Nectariniidae. However, many cases of polyphyly as a consequence of past taxonomic over-emphasis on bill shape and other plastic morphological characters doubtless remain to be discovered.

## References


Banks, R. C., Cicero, C., Dunn, J. L., Kratter, A. W., Rasmussen, P. C., Remsen, J. V., Jr., Rising, J. A. and Stotz, D. F. 2003. Forty-fourth supplement to the American Ornithologists' Union Check-list of North American Birds. – Auk 120: 923–931.

Bledsoe, A. H. 1988. Nuclear DNA evolution and phylogeny of the New World nine-primaried oscines. – Auk 105: 504–515.

Bock, W. J. 1964. Bill shape as a generic character in the cardinals. – Wilson Bulletin 76: 50–61.

Bock, W. J. 1985. Is *Diglossa* (?Thraupinae) monophyletic? – In: Buckley, P. A., Foster, M. S., Morton, E. S., Ridgely, F. G. and Buckley, F. G. (eds), Neotropical Ornithology. Ornithological Monographs no. 36, pp. 319–332.

Burns, K. J. 1997. Molecular systematics of tanagers (Thraupinae): Evolution and biogeography of a diverse radiation of Neotropical birds. – Mol. Phyl. Evol. 8: 334–348.

Burns, K. J., Hackett, S. J. and Klein, N. J. 2003. Phylogenetic relationships of Neotropical honeycreepers and the evolution of feeding morphology. – J. Avian Biol. 34: xx–yy.

Hafner, M. S., Remsen, J. V., Jr. and Lanyon, S. M. 1984. Bird versus mammal morphological differentiation. – Evolution 38: 1154–1156.

Hellmayr, C. E. 1935. Catalogue of birds of the Americas. Alaudidae to Compsothlypidae. – Field Mus. Nat. Hist. Publ., Zool. Ser., vol. 13., pt. 8. 541 pp.

Hellmayr, C. E. 1937. Catalogue of birds of the Americas. Icteridae. – Field Mus. Nat. Hist. Publ., Zool. Ser., vol. 13., pt. 10. 228 pp.

Klicka, J., Johnson, K. P. and Lanyon, S. M. 2000. New World nine-primaried oscine relationships: constructing a mitochondrial DNA framework. – Auk 117: 321–326.

Lanyon, S. M. 1993. Phylogenetic frameworks-towards a firmer foundation for the comparative approach. – Biol. J. Linnean Soc. 49: 45–61.

Lanyon, S. M. and Omland, K. E. 1999. A molecular phylogeny of the blackbirds (Icteridae): five lineages revealed by cytochrome-b sequence data. – Auk 116: 629–639.

McCracken, K. G., Harshman, J., McClellan, D. and Afton, A. D. 1999. Data set incongruence and correlated character

evolution: an example of functional convergence in the hindlimbs of stifftail diving ducks. – Syst. Biol. 48: 683–714.
McCracken, K. G. and Sheldon, F. H. 1998. Molecular and osteological heron phylogenies: sources of incongruence. – Auk 115: 127–141.
Meyer de Schauensee, R. 1966. The species of birds of South America and their distribution. – Livingston Publ. Co., Narberth, Pennsylvania.
Omland, K. E. and Lanyon, S. M. 2000. Reconstructing plumage evolution in orioles (*Icterus*): repeated convergence and reversal in patterns. – Evolution 54: 2119–2133.
Ridgway, R. 1901. The birds of North and Middle America. – Bull. U. S. Nat. Mus., no. 50, pt. 1.
Sclater, P. L. 1886. – Catalogue of the birds of the British Museum 11: 1–431.
Sibley, C. G. and Ahlquist, J. E. 1990. Phylogeny and classification of birds. – Yale Univ. Press, New Haven, Connecticut.
Storer, R. W. 1969. What is a tanager? – Living Bird 8: 127–136.
Wetmore, A. 1960. A classification of the birds of the world. - Smithsonian Misc. – Coll. 139: 1–37.
Yuri, T. and Mindell, D. P. 2002. Molecular phylogenetic analysis of Fringillidae, ''New World nine-primaried oscines'' (Aves: Passeriformes). – Mol. Phyl. Evol. 23: 229–243.