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Nomenclatural solution for a polyphyletic *Agelaius*

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One function of taxonomy is to reflect phylogeny and evolutionary relatedness. Indeed, for many researchers, taxonomy represents a simple tool for introducing assumptions of phylogenetic relationships into comparative studies of extant taxa. The difficulty is that our understanding of avian phylogeny is improving very rapidly and taxonomy, which changes very slowly, is increasingly in conflict with this new information. If taxonomy is to be a useful tool for biologists, we must balance our desire for stability in nomenclature with the need for taxonomy to reflect accurately our knowledge of evolutionary relationships. Consequently,

evolutionary relationships and overlying taxonomy need to be re-affirmed on a regular basis. In the light of significant advances in our understanding of the evolutionary relationships of the species classified in the genus *Agelaius*, we believe it is time to propose formal changes to blackbird taxonomy.

The New World blackbird genus *Agelaius* presently consists of a group of ten morphologically and ecologically similar species (Hellmayr 1937, Blake 1968, Sibley & Monroe 1990). Males have black plumage with some species having yellow or chestnut on the head and others with yellow or red epaulets; females of this group have either a duller version of the male plumage or are brown and streaked. Most species are marsh-nesters. However, the group has been shown to be polyphyletic based on cladistic analyses of 879 base-pairs of cytochrome-*b* and 1035 bases of ND2 mtDNA sequence data. Species traditionally placed in the genus *Agelaius* actually form three separate clades (Lanyon 1994, Lanyon & Omland 1999, Johnson & Lanyon 1999; see also Freeman & Zink 1995). Taxonomic recommendations to describe this new understanding of the relationships of these taxa have not yet been made. We suggest a solution here.

Among the ten species *Agelaius*, three monophyletic groups have been defined by genetic analyses and are identified as follows:

Group 1 (five species in two clusters—[a] *humeralis* of Cuba and Haiti, and *xanthomus* of Puerto Rico; and [b] *phoeniceus* of North America, *tricolor* of California, USA, and *assimilis* of western Cuba). In genetic analyses, Group 1 species form a sister-taxon to the brood parasitic cowbirds (*Molothrus* [encompassing *Scaphidura*]).

Group 2 (two species—*icterocephalus* of northern South America and *ruficapillus* of Brazil to northern Argentina). In genetic analyses, Group 2 species form a cluster with sister-taxa *Xanthopsar* and *Pseudoleistes* and then joining with *Agelaioides*.

Group 3 (three species—*cyanopus* of southern Brazil to northern Argentina, *xanthophthalmus* of Peru and Ecuador, and *thilius* of temperate South America; *thilius* appears slightly more distant from the other two species). In genetic analyses, Group 3 species form a sister-group to the cluster described above (i.e., the taxa *Agelaioides*, Group 2, *Xanthopsar* and *Pseudoleistes*).

The marsh blackbirds of Group 1 are distinctly separated from other '*Agelaius*' in genetic analyses, in geography, and somewhat in skeletal morphology (Webster 2003). These five species have distributions in North America and the Caribbean; all species in both Groups 2 and 3 are limited to South America. Group 1 species show clumped breeding behaviours, either in true colonies or as packed clusters of normal territories. In addition, these species are often polygynous, and all five nest in marshes, which is different from the breeding habitats occupied by most members of their sister group (i.e., *Quiscalus* and *Euphagus*; see Searcy *et al.* 1999, Johnson & Lanyon 2000). We view it as appropriate to unite the species of Group

1 in a single genus. As *phoeniceus* is the type species of the genus *Agelaius* Vieillot, these five species are retained as members of *Agelaius*.

The question of how best to allow taxonomy to reflect phylogeny in the case of Groups 2 and 3 is more complicated. To some extent the number of genera to recognise is subjective and a matter of taste. Recognition of anything from a single genus (including all members of Groups 2 and 3 as well as all species of *Pseudoleistes*, *Xanthopsar*, *Agelaioides*, *Amblyramphus*, *Curaeus* and *Gnorimopsar*) to as many as nine genera (separate genera for all of the six other genera currently recognized in this clade, as listed above, and one genus for Group 2 and 2 genera for species of Group 3) is consistent with the known phylogeny of these species. Recognition of a single genus, however, would obscure a great deal of ecological diversity.

Some differences exist between members of Groups 2 and 3 with respect to feeding ecology and aspects of their breeding biology. Arthropods (mostly insects) seem to comprise 50% or more of the diet of the 'thin-billed' (Group 3) species. Detailed studies are available for *thilius* in Argentina (Darrieu *et al.* 2001). Stomach contents of 85 adults from northern Buenos Aires province (all seasons combined) comprised 78% animal food and 22% seeds. Among insects ingested (66% of all food items), weevils (Curculionidae: Coleoptera), aquatic midges (Stratiomyidae: Diptera) and caterpillars (Lepidoptera) were numerically important. Ingested seeds were mostly of native grasses, particularly *Panicum* sp. According to Orians (1980), *thilius* also feeds on emerging aquatic insects, including dragonflies and damselflies (Odonata). Less extensive data on stomach contents also are available for *cyanopus* (Beltzer & Paporello 1983). This blackbird is more aquatic than *thilius*, and commonly picks prey from the underside of floating plants (*Pistia*, *Azolla*, etc.) or from the water surface. Stomach contents contained c.50% of insect prey, including beetles (Curculionidae, Dysticidae: Coleoptera) and flies (Chironomidae, Stratiomyiidae: Diptera). This species also feeds on small cichlid fishes up to 3 cm long. Data on *xanthophthalmus* food are scant, but habitat choice in this icterid (floating meadows of *Panicum* grass, Orians & Orians 2000) suggests aquatic adaptations similar to those of *cyanopus*.

The two species in Group 2 contrast with the 'thin-billed' group. Both *icterocephalus* and *ruficapillus* consume large amounts of seeds even in the breeding season and both species, particularly *ruficapillus*, are regarded as important pests of cultivated rice (e.g. French 1991, Bello Falavena 1988, Bruggers & Zaccagnini 1994). Stomach contents of *ruficapillus* may contain up to 62% of rice seeds (Vieira *et al.* 2000). In addition, males of these species have similar pattern of 'display colours' in their plumage—the head is yellow (*icterocephalus*) or chestnut (*ruficapillus*)—while 'display colours' in all other '*Agelaius*' is either lacking or limited to epaulets (wing-coverts) only.

Differences in mating system and parental behaviour also occur. In Group 2, *icterocephalus* is usually polygynous (Wiley & Wiley 1980). The mating system of *ruficapillus* was described as monogamous (Bello Falavena 1988) but more recent

data indicate that polygyny is common (Lyon 1997, C. Feare pers. comm.). In *icterocephalus*, nests are started and built mostly by males (Wiley & Wiley 1980, Naranjo 1995), who attract females to the structure by singing and displaying. Females that accept a nest add a nest lining of fine grass. Comparable data for *ruficapillus* seem more controversial. Klimaitis (1973) mentioned nest building only by females in one Argentinian *ruficapillus* population, but all other studies for the species contradict his statement. Nest building mostly by males has been found elsewhere in Argentina (Lyon 1997, unpublished data of R. Fraga for five nests in Buenos Aires, Entre Ríos and Chaco provinces, unpublished data of C. Feare in Santa Fe Province), and is the standard behaviour in Brazilian populations as well (Belton 1985, Bello Falavena 1988, Cirne *et al.* 2000). Therefore, the account by Klimaitis (1973) probably is erroneous; his paper mentions that he did not visit his colony during a critical 15-day period that included most of the nest-building phase. According to Lyon (1997), males of *ruficapillus* build nests during the courtship phase while singing and displaying; nests not occupied by females quickly become disheveled and deteriorate. This suggests that females finish or complete the nest structure.

In some bird families (e.g., Ploceidae [Collias & Collias 1964]) males commonly attract females by building a nest, but this courtship pattern in *icterocephalus* and *ruficapillus* seems unique for icterids (Orians 1985) and represents good evidence of a close phylogenetic relationship between both species of Group 2. Within the 'thin-billed' Group 3, monogamy seems to be the rule (Borshchein *et al.* 1994 for *cyanopus*; Orians 1980 for *thilius*, and Orians & Orians 2000 for *xanthophthalmus*). According to these sources the nest is built by the female in *thilius* and *cyanopus*; data for *xanthophthalmus* are lacking.

We believe that this ecological diversity warrants recognition at the generic level and, therefore, reject the idea of creating a single large genus for Group 2, Group 3, and their close relatives. Instead we prefer a more conservative change in taxonomy that recognises these three groups at the generic level. We note also that *Xanthopsar flavus*—sister-taxon of Group 2—has been lumped sometimes into '*Agelaius*' (see Sclater 1886, Short 1975, Ridgely & Tudor 1989, Sibley & Monroe 1990), but this species' behaviour and ecology (Jaramillo & Burke 1999) and its genetics (Lanyon 1994, Lanyon & Omland 1999) indicate *Xanthopsar* to be closer to *Pseudoleistes* rather than to Group 2 species. We do not consider *Xanthopsar flavus* to be '*Agelaius*'.

We considered the placement of *thilius* in its own genus to reflect certain ecological, vocal, and plumage differences from the other Group 3 species, as detailed above. If this were done, however, then *Agelasticus* would be limited to *thilius* and a new name would be needed for the two remaining Group 3 species.

Our preference is for a taxonomy that is consistent with phylogeny, that introduces the fewest necessary taxonomic changes to reflect phylogeny, and that recognises the natural history differences between Groups 2 and 3. Therefore, we propose resurrection of *Chrysomus* Swainson for Group 2 and *Agelasticus* Cabanis

for Group 3. Our proposed nomenclatural solution for *Agelaius*, as indicated below, identifies 3 genera:

Group 1: AGELAIUS Vieillot 1816 (type *Oriolus phoeniceus* Linnaeus 1766)

***Agelaius humeralis* (Vigors 1827)**

Leistes humeralis Vigors 1827, Zool. J. 3: 442 [Tawny-shouldered Blackbird]

***Agelaius xanthomus* (Sclater 1862)**

Icterus xanthomus P. L. Sclater 1862, Catalogue Coll. Amer. Birds, p. 131 [Yellow-shouldered Blackbird]

***Agelaius phoeniceus* (Linnaeus 1766)**

Oriolus phoeniceus Linnaeus 1766, Syst. Nat., 12 ed., p. 161 [Red-winged Blackbird]

***Agelaius tricolor* (Audubon 1837)**

Icterus tricolor Audubon 1837, Birds Amer. vol. 4, pl. 388, fig. 1 [Tricolored Blackbird]

***Agelaius assimilis* Lembeye 1850**

Agelaius assimilis Lembeye 1850, Aves Isla Cuba, p. 64, pl. 9, fig. 3 [Red-shouldered Blackbird]

Group 2: CHRYSOMUS Swainson 1837 (type *Oriolus icterocephalus* Linnaeus 1766)

***Chrysomus icterocephalus* (Linnaeus 1766)**

Oriolus icterocephalus Linnaeus 1766, Syst. Nat. 12 ed., p. 163 [Yellow-hooded Blackbird]

***Chrysomus ruficapillus* (Vieillot 1819)**

Agelaius ruficapillus Vieillot 1819, Nouv. Dict. Hist. Nat. 34: 556 [= 536], [Chestnut-capped Blackbird]

Group 3: AGELASTICUS Cabanis 1851 (type *Turdus thilius* Molina 1782)

***Agelasticus cyanopus* (Vieillot 1819)**

Agelaius cyanopus Vieillot 1819, Nouv. Dict. Hist. Nat. 34: 552 [Unicoloured Blackbird]

***Agelasticus xanthophthalmus* (Short 1969)**

Agelaius xanthophthalmus Short 1969, Occ. Pap. Mus. Zool. Louisiana State Univ. no. 37 [Pale-eyed Blackbird]

***Agelasticus thilius* (Molina 1782)**

Turdus thilius Molina 1782, Saggio Storia Nat. Chile, p. 250, 345 [Yellow-winged Blackbird]

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Range extension for Grey-headed Tanager *Eucometis penicillata* in south-east Brazil

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Large areas in South America have still never been visited by ornithologists (Silva 1995a). This is particularly true for the Cerrado region of central Brazil, which encompasses 1.8 million km² (Silva 1995b), and the semi-arid region of Caatinga in north-east Brazil, extending to 0.9 million km² (Sampaio 1995, Pacheco 2000). This paper describes the geographic distribution of a forest bird of South America, Grey-headed Tanager *Eucometis penicillata*. Although common, the species has been systematically overlooked in south-east Brazil by all bird compilations published so far.

Grey-headed Tanager is an Oscine passerine member of the Thraupini tribe of the Emberizinae subfamily Fringillidae (Sibley & Monroe 1990). This tribe encompasses 413 species distributed mainly in the Neotropical region (Sibley & Monroe 1990). *Eucometis* is a monotypic genus occurring from southern Mexico to



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