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REPEATED EVOLUTION OF FUSED THORACIC VERTEBRAE IN SONGBIRDS

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Abstract.—The fusion of two or more thoracic vertebrae, independent of the synsacrum, is more widespread in the Passeriformes than has previously been reported. The bone thus formed is known as a "notarium." I surveyed oscine passerine skeletons and found a notarium with fully fused vertebrae in Chabert's Vanga (*Leptopterus chabert*), certain woodswallows (Artamidae) and shrikes (Laniidae), the Willie Wagtail (Rhipiduridae, *Rhipidura leucophrys*), the Phainopepla (Bombycillidae, *Phainopepla nitens*), the penduline tits (Remizidae) including the Verdin (*Auriparus flaviceps*), various larks (Alaudidae), the Common Starling (*Sturnus vulgaris*), the sickle-billed thrashers (*Toxostoma* spp.), and the crossbills (*Loxia* spp.). Mapping of character evolution on a supertree suggests that a fully fused notarium has evolved independently at least 12 times in the oscine passerines and that notaria with less extensive fusion of the vertebrae (only the spinous processes fused, for example) are even more widespread phylogenetically. Phenotypic expression of a notarium is fixed in some species and higher taxonomic groups but varies within the species in others. Ontogenetically, the fully fused notarium forms when the bird is immature. The evolutionary development of notaria probably depends on mutations that alter expression patterns of transcription genes (Pax and Hox genes are likely candidates) that control embryological differentiation of the vertebrae. Among the systematic implications of this study are additional support for placement of the Verdin in the Remizidae and for the monophyly of a group of western thrashers (*Toxostoma* spp.) with strongly decurved bills. *Received 2 October 2008, accepted 3 May 2009.*

Key words: convergent evolution, notarium, oscine, osteology, Passeri, synsacrum.

Evolución Repetida de Vértebras Torácicas Fusionadas en Aves Canoras

Resumen.—La fusión de dos o más vértebras torácicas, independientemente del sinsacro, es un fenómeno que está más ampliamente distribuido entre los paseriformes que lo que se había documentado previamente. El hueso que se forma de este modo se llama notario. Hice una evaluación de esqueletos de aves paserinas y observé la presencia de un notario con vértebras completamente fusionadas en *Leptopterus chabert*, algunos Artamidae y Laniidae, *Rhipidura leucophrys*, *Phainopepla nitens*, los Remizidae incluyendo a *Auriparus flaviceps*, varios Alaudidae, *Sturnus vulgaris* y las especies de los géneros *Toxostoma* y *Loxia*. El mapeo de la evolución de este rasgo sobre un superárbol sugiere que un notario completamente fusionado ha evolucionado independientemente al menos 12 veces en los paseriformes oscinos y que notarios con fusión menos completa de las vértebras (por ejemplo, con sólo los procesos espinosos fusionados) están aún más ampliamente distribuidos filogenéticamente. La expresión fenotípica de un notario está fija en algunas especies y grupos taxonómicos mayores, pero varía entre individuos en otras especies. Ontogenéticamente, el notario completamente fusionado se forma cuando el ave es inmadura. El desarrollo evolutivo de los notarios probablemente depende de mutaciones que alteran los patrones de expresión de genes de transición (los genes Pax y Hox son candidatos probables) que controlan la diferenciación embriológica de las vértebras. Entre las implicaciones sistemáticas de este estudio se encuentran el apoyo adicional para la ubicación de *Auriparus* en la familia Remizidae y para la monofilia de un grupo de mímidos occidentales (*Toxostoma* spp.) con picos fuertemente decurvados.

All birds dating back at least to *Archaeopteryx* have a series of vertebrae adjacent to the ilium that are fused together, forming a bone called the "synsacrum"; all modern birds also have several fused terminal caudal vertebrae that form the pygostyle. Some birds have a third series of fused vertebrae, the notarium, defined as any group of thoracic vertebrae that are fused to each other but not to the synsacrum (Baumel and Witmer 1993). Although notaria principally involve fusion of thoracic vertebrae, the definition should be amended to include the caudal-most cervical vertebra, which sometimes participates. Notaria occur in an ecologically disparate assortment of nonpasserine birds, including ground-dwelling birds (e.g., Galliformes, Tinamiformes, Columbiformes, and various Gruiformes), waders (e.g., Threskiornithidae, Phoenicopteridae, and Gruidae), divers (e.g., Podicipediformes

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and some Phalacrocoracidae), certain arboreal types (*Steatornis*, *Opisthocomus*, and *Forpus*), and in the falcons (Falconidae). Fused vertebrae are of interest because they are a clearly definable osteological trait, useful in systematics, for the identification of fossils, and for studies of patterns in evolution of the avian skeleton.

Three previous surveys of the distribution of notaria in birds gave scant attention to the Passeriformes. Rydzewski (1935) reported finding fused vertebrae in three species of larks; Storer (1982) found the trait to be absent in his family-level survey of the Passeriformes; and Samejima and Otsuka (1984) found it present only in a species of weaver finch. Being familiar with Storer's paper, I was surprised to find a fully fused notarium involving three to four thoracic vertebrae in the penduline tits (Remizidae), including the Verdin (*Auriparus flaviceps*). I incorporated my observations in the data matrix for a previous paper without further elaboration (James et al. 2003: character 41). The discovery inspired me to undertake a more thorough survey of oscine skeletons, with the aim of documenting the distribution of notaria and laying the foundation for study of their evolutionary history.

Methods

I examined >500 skeletons of oscine passerines, most of them in the collection of the National Museum of Natural History (USNM, Washington, D.C.). The taxonomic sample included ~250 genera and ~350 species, encompassing 80% of the 82 oscine families recognized by Dickinson (2003). For each species, I examined one or a few adult skeletons, and if fused vertebrae were found, I then examined a broader sample of that species (including immatures) and related species, provided that skeletons were available. I recorded whether the braincase was double-walled (pneumatic) as in adult birds or partly single-walled as in immatures and described any fusion of thoracic (and caudal cervical) vertebrae. Vertebral columns of smaller birds were examined under 6–50× magnification using a dissecting microscope. Birds that died in captivity were excluded from the sample except where noted. Dickinson (2003) was followed as a taxonomic authority for scientific names, and Gill and Wright (2006) for common names. However, for North American Paridae, the generic names follow the AOU Check-list (American Ornithologists' Union 1998).

Some skeletons in the USNM collection are preserved with the vertebrae articulated, and in others they are disarticulated. A limitation of my observations is that, for specimens with articulated vertebral columns, I may have overlooked some instances of lightly fused vertebrae when the fusion affected only the interior part of the articular surfaces that is concealed from view. I consider this an unimportant source of error because, in specimens with disarticulated vertebrae, I found that fusion of the bodies is almost always accompanied by visible bone remodeling.

There is as yet no comprehensive molecular-sequence data set from which a phylogenetic hypothesis for all the taxa in the present study could be derived. Jønsson and Fjeldså (2006) recently created a supertree for the oscines that summarizes the results of 99 separate molecular phylogenetic studies, encompassing 1,724 species. I used the supertree as the best available phylogenetic hypothesis for reconstructing the evolutionary history of notaria in the taxa examined, but I expanded the tree for the Mimidae and Sturnidae on the basis of a more recent, comprehensive paper for that clade (Lovette and Rubenstein 2007).

Based on the supertree, a phylogenetic tree covering as many of the taxa examined as possible was constructed using MACCLADE, version 4.08 (Maddison and Maddison 2005). In cases in which the genus but not the species examined was present in the supertree, I substituted the species I examined or added it in a polytomy with other members of the genus. This was not done if there was ambiguity about where to add the species. Ambiguity would occur if the genus was depicted as polyphyletic in the supertree or if there was a resolved branching pattern within the genus that would need to be collapsed in order to add the species in a polytomy.

My observations of patterns of fusion were coded as a simple character with three states. Instances of intraspecific polymorphism were recorded as multistate taxa; the few cases in which the state could not be determined were coded as "uncertainty." Character-state changes were then mapped on the phylogeny using MESQUITE (see Acknowledgments), with the parsimony criterion.

Results

For reference, Figure 1K shows the vertebral column and articulating postcranial bones of the Black-capped Chickadee (*Poecile atricapillus*), a species that lacks a notarium. As is typical of passerine birds, there are five free thoracic (also called "dorsal") vertebrae, all of which connect to the sternum via a vertebral and a sternal rib. The last cervical vertebra has a floating vertebral rib attached to it, with no corresponding sternal rib. The sixth complete pair of ribs in the sequence articulates with the first vertebra in the synsacrum dorsally and with the fifth sternal rib (rather than directly with the sternum) ventrally; thus, it is not associated with a thoracic vertebra. There are three places where the vertebrae contact each other and, therefore, can potentially fuse: the articular surfaces of the corpus vertebrae (vertebral bodies), the articular surfaces of the zygapophyses, and the expansive spinous processes that project dorsad and help to stiffen the thoracic column of vertebrae. Some passerines have ventral crests on the caudal cervical and the cranial thoracic vertebrae (although Black-capped Chickadee does not), which provide a fourth potential point of contact and fusion.

I found a notarium with fully fused vertebrae in Chabert's Vanga (*Leptopterus chabert*), certain woodswallows (Artamidae) and shrikes (Laniidae), the Willie Wagtail (Rhipiduridae, *Rhipidura leucophrys*), the Phainopepla (Bombycillidae, *Phainopepla nitens*), the penduline tits (Remizidae) including the Verdin, various larks (Alaudidae), the Common Starling (*Sturnus vulgaris*), various thrashers (*Toxostoma* spp.), and the crossbills (*Loxia* spp.) (Fig. 1). Vertebrae with a lesser extent of fusion, involving only one or two of the four structures, were found to be more widespread in the oscines. The text below mentions only the families of birds in which I found at least one species with fused vertebrae; a complete list of the taxa in which I observed the absence of fused vertebrae is presented in an online Appendix (see Acknowledgments).

Systematic Osteology

Artamidae.—A fully fused notarium was present in two of the three species and six of the seven specimens of woodswallows (Artamidae: *Artamus*) examined. In all instances, the spinous

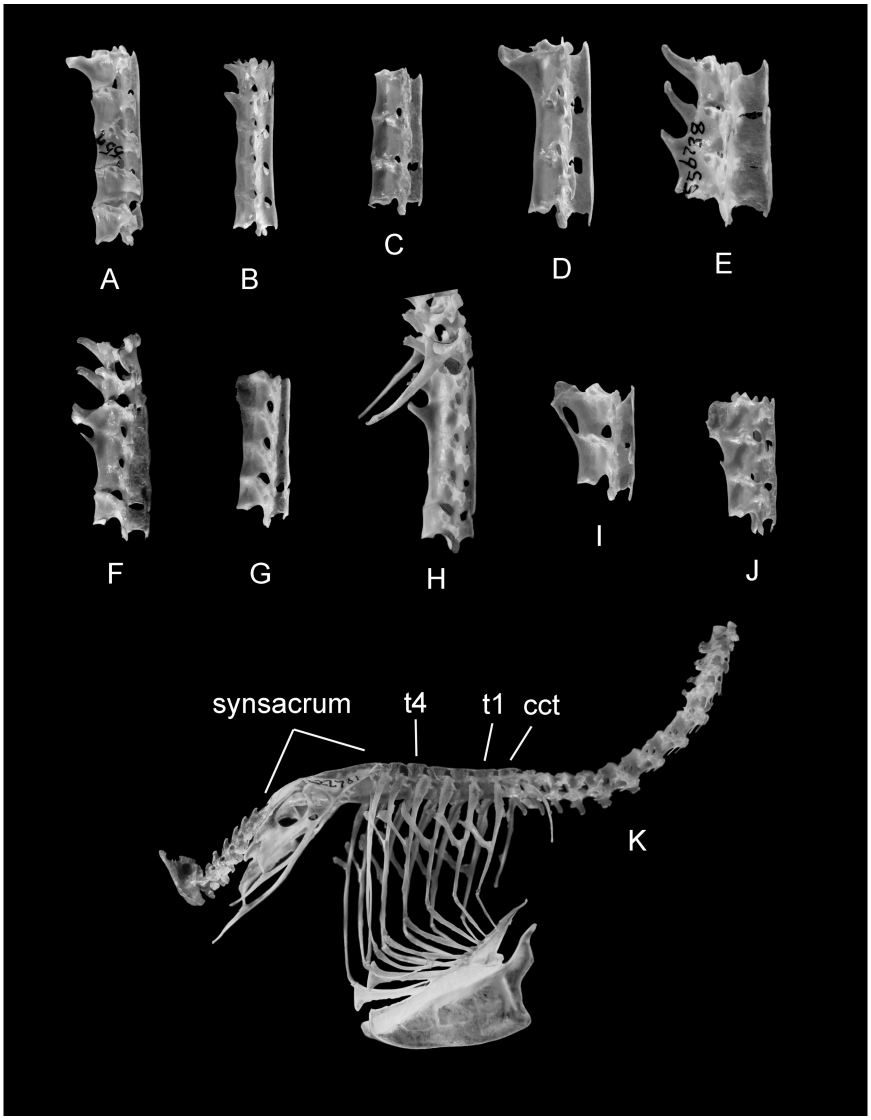

Fig. 1. (A–J) Examples of fused vertebrae in the Passeriformes in lateral view, with (K) the vertebral column and articulating postcranial bones of Black-capped Chickadee (*Poecile atricapillus*), a species that lacks a notarium, shown for reference. The last cervical (or cervicothoracic) vertebra (cct) and the first through fourth thoracic vertebrae (t1–t4) are variably fused in some songbirds to form a notarium. Notaria are shown in (A) Ashy Woodswallow (*Artamus fuscus*), (B) Chabert's Vanga (*Leptopterus chabert*), (C) Phainopepla (*Phainopepla nitens*), (D) Common Starling (*Sturnus vulgaris*), (E) California Thrasher (*Toxostoma redivivum*), (F) Cape Penduline Tit (*Anthoscopus minutus*), (G) Eurasian Penduline Tit (*Remiz pendulinus*), (H) Verdin (*Auriparus flaviceps*), (I) Red Crossbill (*Loxia curvirostra*), and (J) Two-barred or White-winged Crossbill (*L. leucoptera*).

processes of thoracic vertebrae one through three and the zygapophyses of thoracic vertebrae two and three were fused. In two of four White-breasted Woodswallows (*Artamus leucorynchus*), the third and fourth thoracic vertebrae were also fully fused. In one individual, the ventral processes of the last cervical and first thoracic vertebrae were also fused.

Vangidae.—One Chabert's Vanga (Fig. 1B) had a fully fused notarium similar to that of the woodswallows. Three other species of vangas had no fusion.

Cracticidae.—An Australian Magpie (*Gymnorhina tibicen*) had the spinous processes of the first and second thoracic vertebrae fused. Two other species in the family had no fusion.

Rhipiduridae.—Two Willie Wagtails had fully developed notaria involving fusion of the bodies and zygapophyses of one or two thoracic vertebrae and the spinous processes of four thoracic vertebrae. Two Blue Fantails (*Rhipidura superciliaris*) had no fusion.

Laniidae.—Both species of the genus *Eurocephalus*, Northern White-crowned Shrike (*E. rueppelli*) and Southern White-crowned Shrike (*E. anguitimens*), have fully fused thoracic vertebrae. Of three Loggerhead Shrikes (*Lanius ludovicianus*) examined, one had the spinous processes and zygapophyses of thoracics two and three fused, one had the spinous processes of thoracics two and three fused, and one had no fusion. Four skeletons representing four other species of *Lanius* had no fusion, nor did a skeleton of Magpie Shrike (*Urolestes melanoleucus*).

Petroicidae.—In notes taken in 2001, I recorded fusion of the spinous processes of thoracic vertebrae one and two in the Tomtit (*Petroica macrocephala*) and New Zealand Robin (*P. australis*). In the present study, I found fusion of spinous processes and zygapophyses of thoracic vertebrae two and three in the Eastern Yellow Robin (*Eopsaltria australis*) but no fusion in another skeleton of the same species.

Ploceidae.—Samejima and Otsuka (1984: figure 10) figured a notarium consisting of three fully fused thoracic vertebrae in a male Little Weaver (*Ploceus luteolus*) but found no fusion in a female of the same species. I found no fusion in nine skeletons representing eight other species of Ploceidae.

Estrildidae.—One wild-caught and two captive male Crimson Finches (*Neochmia phaeton*) had the spinous processes and zygapophyses of thoracic vertebrae two and three fused, whereas another captive male and a wild-caught female had no fusion. A male White-bellied Munia (*Lonchura leucogastra*) had the bodies of thoracics one and two fused. A male Java Sparrow (*L. oryzivora*) may also have the bodies of thoracics one and two fused (coded as "uncertainty"). Thirteen skeletons representing nine other species of Estrildidae, including four other *Lonchura* spp., had no fusion.

Fringillidae: Drepanidinae.—A tendency toward fusion was found in two closely related Hawaiian honeycreepers with finch-like bills, *Loxioides* and *Telespiza*. Two Palilas (*Loxioides bailleui*) had the spinous processes of thoracic vertebrae one and two fused. One of them had some fusion of the bodies of thoracic vertebrae three and four, but the fusion was asymmetrical and accompanied by lipping; hence, it may have developed later in life because of inflammation. One Laysan Finch (*Telespiza cantans*) had the spinous processes of thoracic vertebrae three and four fused, whereas two other individuals of this species had no fusion. It was unclear whether an individual Akiapolaau (*Hemignathus munroi*) had some fusion of spinous processes (coded as "uncertainty"). No fusion was found in nine other skeletons representing eight species of Hawaiian honeycreepers.

Fringillidae: Fringillinae and Carduelinae.—The crossbills have a fully fused notarium that is distinctive because of the fusion of the prominent ventral crests. The form of the notarium differs between Red Crossbill (*Loxia curvirostra*, as traditionally composed) and Two-barred or White-winged Crossbill (*L. leucoptera*). In all five Red Crossbills examined, only thoracic vertebrae one and two participated in the notarium, and the bodies of the vertebrae appeared to be unfused, although the vertebrae were firmly connected by the ventral crests, spinous processes, and zygapophyses (Fig. 1I). (One individual had the zygapophyses unfused.) Five White-winged Crossbills had thoracic vertebrae one through three joined in a notarium, with the ventral crests, zygapophyses, and bodies fused (Fig. 1J). (In one of those individuals, the bodies of thoracics two and three appeared to be unfused.) In both these species, the spinous processes of only the first two thoracic vertebrae were fused. Among other Fringillidae, I found no fused vertebrae in either species in the genus *Fringilla* nor in eight species selected to broadly sample the cardueline finches.

Bombycillidae and Dulidae.—A notarium is variably present in the Phainopepla. Of three skeletons examined, one had thoracic vertebrae two through four fully fused (Fig. 1C), one had at least three and four fused and possibly two as well, and the third had no fusion. No fully fused vertebrae were found in eight other skeletons of this group, representing four species, although one of three skeletons of Palmchat (*Dulus dominicus*) and one of two skeletons of Long-tailed Silky-flycatcher (*Ptilogonys caudatus*) had a pair of vertebrae lightly fused at the spinous processes.

Sturnidae.—A fully fused notarium was observed in only one species of Sturnidae, the Common Starling (Fig. 1D). Two adult males, three adult females, and one juvenile female had the bodies, zygapophyses, and spinous processes of thoracic vertebrae one through three fused. Variants observed were an adult male with the fourth thoracic vertebra also fused and an adult female with clear fusion only of the spinous processes of thoracic vertebrae one and two (I was unable to ascertain whether the bodies of thoracics one through three were fused in this individual). Four other species in the genus *Sturnus* had fusion limited to the spinous processes (usually of only two vertebrae), and one lacked fusion. Nine other skeletons of the Sturnidae, representing nine genera other than *Sturnus*, had no fusion, or—in the case of the Common Myna (*Acridotheres tristis*)—had fusion of the spinous processes of thoracics one and two only.

Two very immature skeletons of Common Starling (USNM 611224, 611225), with the sutures still open between the cranial bones, had no fusion of thoracic vertebrae one through five, despite having a fully fused synsacrum. Ontogenetically, fusion of the notarium, therefore, occurs after the synsacrum forms but before the cranium has fully ankylosed and before the dorsal wall of the braincase has become pneumatic (see also observations of fused vertebrae in immature Remizidae).

Mimidae.—A notarium involving at least the second and third thoracic vertebrae is shared by the thrashers of western North America that have long, strongly curved bills. In the California Thrasher (*Toxostoma redivivum*; Fig. 1E), the bodies, zygapophyses, and ventral crests, and usually the spinous processes, of vertebrae two and three are joined. The bodies of vertebrae one and two sometimes also fuse. In the Crissal Thrasher (*T. crissale*), the bodies, zygapophyses, and sometimes the ventral crests and spinous processes of vertebrae two, three, and usually four are fused. In Le Conte's Thrasher (*T. lecontei*), one individual had only the bodies of vertebrae two and three fused, and a second had the bodies, zygapophyses, and spinous processes of the same vertebrae fused. Six skeletons representing three other species in the genus *Toxostoma* had no fusion, nor did seven skeletons representing *Mimus*, *Dumetella*, and *Cinclocerthia*.

Turdidae.—No fully fused vertebrae were found in the Turdidae. The spinous processes of two or three thoracic vertebrae were lightly fused in Red-legged Thrush (*Turdus plumbeus*), Hermit Thrush (*Catharus guttatus*), and Townsend's Solitaire (*Myadestes townsendi*). In two instances, two vertebrae were also joined at the zygapophyses. There may have been light fusion of two spinous processes in one of two examples of American Robin (*T. migratorius*) examined. In addition, the absence of fusion was observed in five skeletons representing five other species of the Turdidae.

Muscicapidae.—No fully fused vertebrae were found in this family. A skeleton of Whinchat (*Saxicola rubetra*) and one of Blue Rock Thrush (*Monticola solitarius*) each had a pair of thoracic vertebrae lightly fused at the apices of the spinous processes. A skeleton of Black-eared Wheatear (*Oenanthe hispanica*) had light fusion of both spinous processes and zygapophyses. The absence of fusion was observed in nine skeletons representing eight genera and species of Muscicapidae.

Polioptilidae.—I found fusion of the spinous processes and zygapophyses in some Blue-gray Gnatcatchers (*Polioptila caerulea*). Of seven individuals examined, two had the spinous processes and zygapophyses of thoracic vertebrae two and three fused, and one had the same structures of thoracic vertebrae two, three, and four fused, although three birds had no fusion. No fusion was observed in three other species of *Polioptila*.

Remizidae.—In all skeletons of the Remizidae examined, the first three and sometimes the fourth thoracic vertebrae were fused (Fig. 1F–H). The vertebrae were fused across all surfaces that contact each other: the bodies, zygapophyses, and spinous processes. In most skeletons examined, fusion of the vertebrae was more advanced than in typical oscine notaria in that the seams between the first three vertebrae were obliterated. I found this type of notarium in two skeletons of Eurasian Penduline Tit (*Remiz pendulinus*), one of Cape Penduline Tit (*Anthoscopus minutus*), and two of Yellow Penduline Tit (*A. parvulus*, from the University of Michigan Museum of Zoology), and in 19 adult and immature Verdin skeletons.

Intraspecific variation in the notarium was observed in the series of Verdin skeletons. There was no apparent association of the variants with age or sex of the birds. Of the 16 adult birds (judged by skull ossification), 10 had the basic form of the remizid notarium, with complete ankylosis of thoracic vertebrae one through three and no seams visible between the vertebrae. One also had the ventral processes of the first thoracic and last cervical vertebra fused. Five had complete fusion of thoracics one and two, with no seams visible, but less advanced fusion of thoracics two and three, because either the vertebrae were only partly fused or seams were visible in places. All three immature skeletons had a fully fused, seamless notarium. Two had the typical form with three fused thoracic vertebrae, and one had four.

Alaudidae.—Rydzewski (1935) reported finding fused thoracic vertebrae in Eurasian Skylark (*Alauda arvensis*), Greater Hoopoe-Lark (*Alaemon alaudipes*), and Desert Lark (*Ammomanes deserti*). I found full fusion of thoracic vertebrae one through three, and sometimes four, in Desert Lark, and full fusion of one through four in Greater Hoopoe-Lark. Eurasian Skylark had only the spinous processes of one through three fused. I also found a fully fused notarium in a skeleton of Agulhas Long-billed Lark (*Certhilauda brevirostris*; thoracic vertebrae one through three) and two skeletons of Spike-heeled Lark (*Chersomanes albofasciata*; thoracic vertebrae two and three). However, there was no fusion in a third skeleton of Spike-heeled Lark. A skeleton of Crested Lark (*Galerida cristata*; spinous processes and zygapophyses) and one of Calandra Lark (*Melanocorypha calandra*; spinous processes only) had partial fusion of thoracic vertebrae one and two, yet a second skeleton of Crested Lark lacked fusion. In one of two skeletons of Gray-backed Sparrow-Lark (*Eremopterix verticalis*) and one of Lesser Short-toed Lark (*Calandrella refescens*), it was unclear whether the spinous processes of two thoracic vertebrae were lightly fused.

Hirundinidae.—Limited fusion of two vertebrae was found in one of two skeletons of Tree Swallow (*Tachycineta bicolor*; spinous processes of thoracics one and two only) and one skeleton of Cave Swallow (*Petrochelidon fulva*; spinous processes and possibly the bodies of thoracics two and three). No fusion was found in six skeletons representing four other species of Hirundinidae.

Cisticolidae.—Five skeletons representing *Cisticola*, *Prinia*, and *Apalis* were examined. Fusion was found only in one Zitting Cisticola (*Cisticola juncidis*), in which the spinous processes and zygapophyses of thoracic vertebrae two and three were joined. There may have been some fusion of the bodies of these two vertebrae without obliteration of the suture between them. A second skeleton of the same species had no fusion.

"Sylviidae" (sensu *Dickinson 2003*).—The Striated Grassbird (*Megalurus palustris*) had fusion of the apices of the spinous processes of two thoracic vertebrae. No fusion was found in six other species representing *Megalurus*, *Hippolais*, and *Acrocephalus*.

Evolutionary Context

Fully fused vertebrae, with the spinous processes, zygapophyses, vertebral bodies, and sometimes the ventral spines connected, were found in species in seven of the major clades of oscine passerines in the supertree, although in no instance were fused vertebrae present in all members of the clade. To visualize phylogenetic patterns in the evolution of notaria, I coded my observations as a simple character with three states: (0) fusion absent; (1) limited fusion involving one or two of the four structures that can potentially fuse; and (2) full fusion involving the vertebral bodies, zygapophyses, and spinous processes (or, in one case, ventral processes, zygapophyses, and spinous processes). As shown in Figures 2–5, the reconstructed state changes for this character suggest that fully fused notaria (state 2) have evolved at least 12 times in the oscines: 3 times in the Corvoidea ("crown Corvida"), twice in the Passeroidea, 3 times in the Muscicapoidea, and 3 times in the Sylvioidea. Lightly fused vertebrae, with one or two of the four structures joined (state 1), also have evolved frequently (perhaps 17 instances identified in Figs. 2–5). These numbers assume no evolutionary reversals from fused to unfused vertebrae, an assumption that appears to be reasonable in most cases. Additional instances of lightly fused vertebrae, in taxa that are not part of the supertree, are listed in Table 1 (online supplementary material; see Acknowledgments).

The character that is mapped in Figures 2–5 encodes the extent of the fusion of vertebrae but ignores patterns among taxa in the structures and the specific vertebrae that fuse. These patterns are summarized in Table 1 (online) and Figure 6. The most common vertebrae to fuse are thoracics two and three, the two vertebrae that also tend to have the most extensive connection between them. Lightly fused vertebrae are often joined at the spinous processes only, a condition that is particularly common between thoracics one and two. Several taxa have diagnostic patterns of fusion. For example, the sickle-billed species in the genus *Toxostoma* have only thoracics three and four fused, whereas notaria in other taxa are fused higher in the column. Fusion in the Remizidae involves up to four vertebrae and is so complete that the seams between the vertebrae are usually obliterated. In *Loxia*, the ventral crests tend to fuse before the bodies of the vertebrae, unlike in any other taxon. This is most clearly expressed in members of the superspecies *L. curvirostra*, which share (in the skeletons examined) a unique form of the notarium in which only two vertebrae fuse and the ventral processes, spinous processes, and zygapophyses are firmly connected, whereas the bodies are unfused.

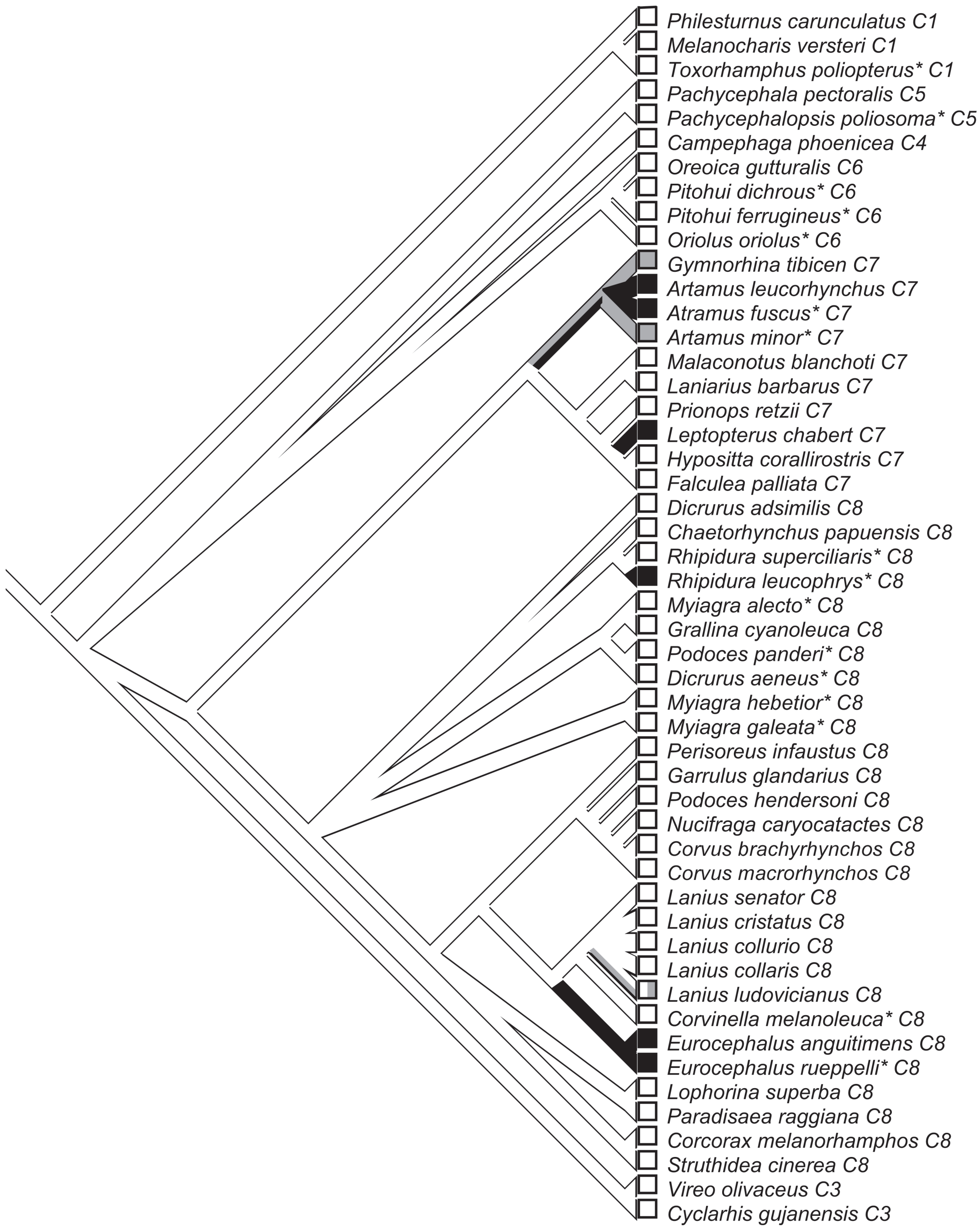

Fig. 2. Reconstructed character-state changes in the fusion of thoracic vertebrae for the Corvoidea. Species names are followed by clade numbers from the supertree (i.e., C1 = Corvoidea or "crown Corvida," clade 1). Dark lines indicate presence of fully fused vertebrae, and light lines indicate partly fused vertebrae. Bicolored lines indicate polymorphism. Asterisks indicate species added to the supertree.

Within species, I observed polymorphism in the presence and extent of fusion as well as in the vertebrae and structures that fuse. Intraspecific variants among adults include individuals with fully fused notaria versus no fused vertebrae (in *Phainopepla nitens*, *Ploceus luteolus*, and *Chersomanes albofasciata*), individuals with fully fused notaria versus lightly fused vertebrae (*Sturnus vulgaris*, *Toxostoma lecontei*, and possibly *Phainopepla nitens*), and individuals with no fusion versus light fusion (in *Eopsaltria australis*, *Lanius ludovicianus*, *Dulus dominicus*, *Ptilogonys caudatus*, *Neochmia phaeton*, *Cisticola juncidis*, *Polioptila caerulea*, *Telespiza cantans*, *Galerida cristata*, *Tachycineta bicolor*, and possibly *Phainopepla nitens*). Intraspecific variation in the vertebrae and structures that fuse is graphed in Table 1 (online).

In large sections of the supertree, I found no fused vertebrae (full tree not shown, but information given in the online Appendix). For example, no fusion was found in any of the basal oscine clades ("Basal Corvida" in the supertree, *Menura* through

Fig. 3. Reconstructed character-state changes in the fusion of thoracic vertebrae in the Muscicapoidea. Species names are followed by clade numbers from the supertree (i.e., M4 = Muscicapoidea, clade 4). See Figure 2 for explanation of line shading. Asterisks indicate species added to the supertree.

Orthonyx) nor in most clades of nine-primaried oscines, *Loxia* being the striking exception.

Discussion

The notarium is a distinctive osteological trait that has evolved repeatedly in the oscine passerines. The precise number of independent derivations is uncertain, because future systematic revisions may lower the total somewhat or the examination of additional skeletons may raise it. Traits that evolve repeatedly present an opportunity for comparative study of the evolutionary process, and by documenting the systematic distribution and intraspecific variability in this trait I aim to encourage such study. Aspects of the notarium that may facilitate further study include that, ontogenetically, the vertebrae fuse well before adulthood (at least in the case of fully fused vertebrae), that phenotypic expression of the

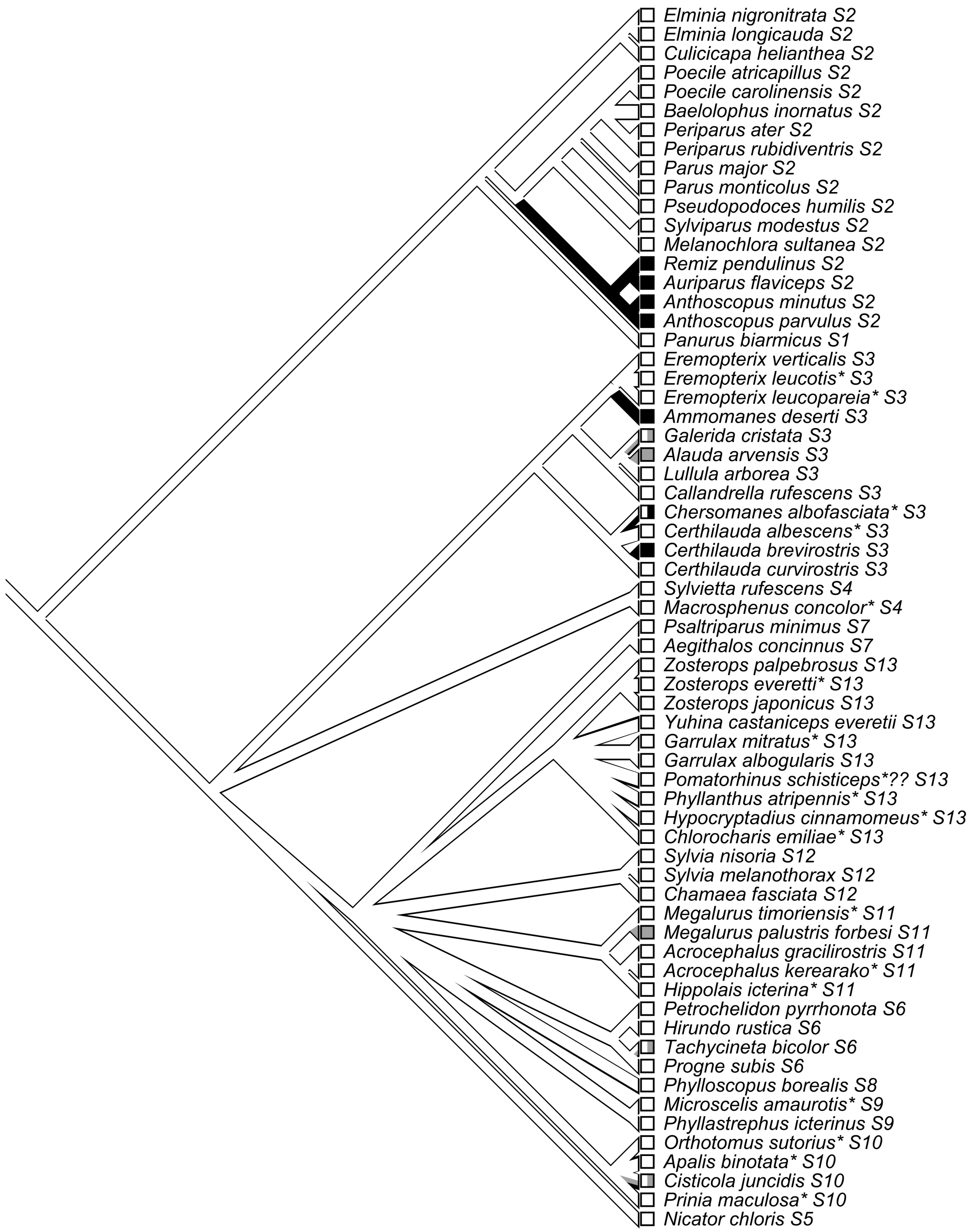

Fig. 4. Reconstructed character-state changes in the fusion of thoracic vertebrae for the Sylvioidea. Species names are followed by clade numbers from the supertree (i.e., S2 = Sylvioidea, clade 2). See Figure 2 for explanation of line shading. Asterisks indicate species added to the supertree.

trait is fixed in some species but not others, and that it would be possible to observe its expression in living birds using x-rays.

Future study of the notarium can also take advantage of evidence from gene-expression studies on the role of transcription genes, especially Pax and Hox genes, in producing differentiation and segmentation of the vertebral column during embryological development (Wallin et al. 1994, Wellik 2007). Now that the pattern of repeated evolution of notaria in birds is more thoroughly documented, there is an opportunity to apply phylogenetically based comparative methods to ask whether the independent

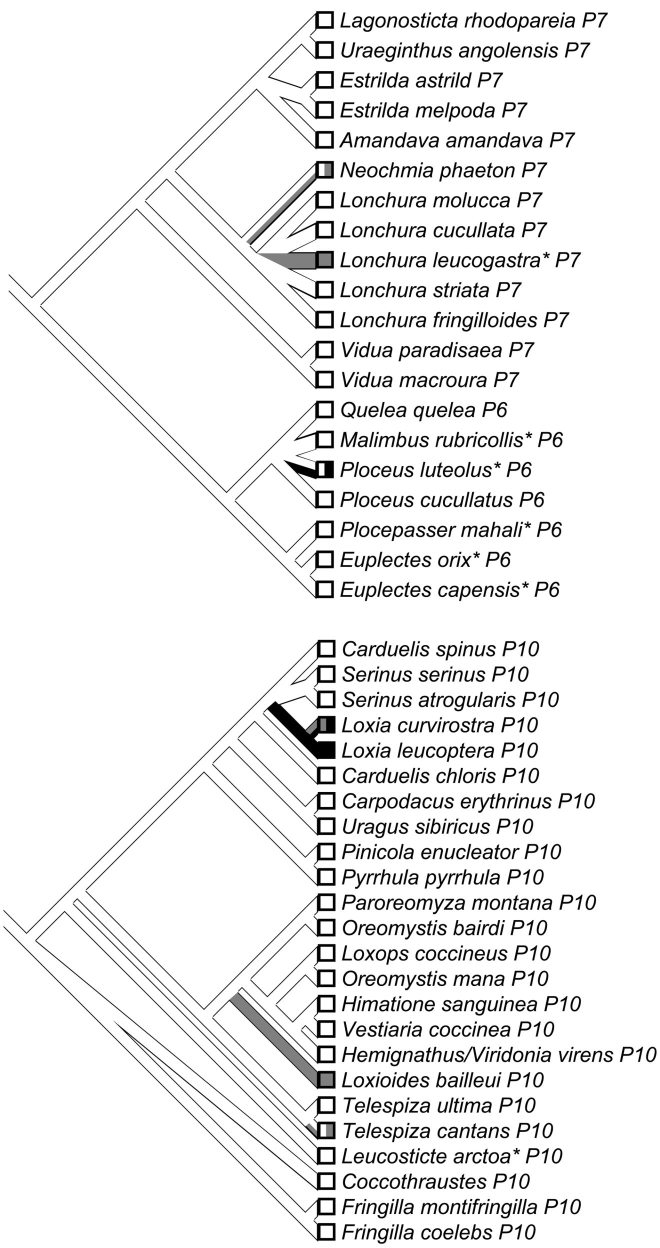

Fig. 5. Reconstructed character-state changes in the fusion of thoracic vertebrae in the Passeroidea. Only the clades with presence of fusion are shown. Species names are followed by clade numbers from the supertree (i.e., P7 = Passeroidea, clade 7). See Figure 2 for explanation of line shading. Asterisks indicate species added to the supertree.

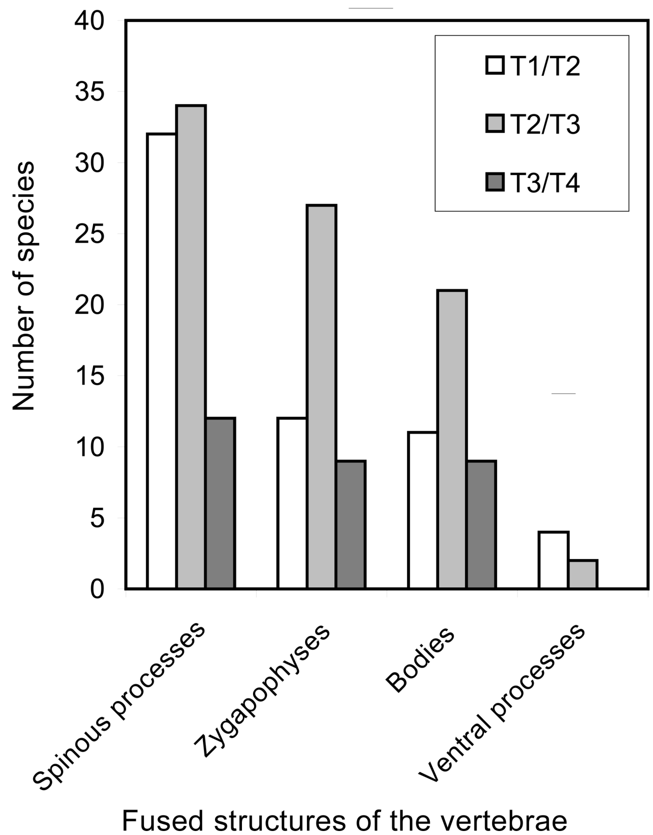

Fig. 6. Observations of fused vertebrae in songbirds. The legend identifies the vertebrae that were fused to each other (thoracic vertebrae one through four). If several individuals of a species were examined, the modal condition per species was counted; if only two individuals were examined, the individual with the most extensive fusion was counted. In two species, the ventral process of the caudal-most cervical vertebra was also fused (data not shown in this figure but given in Table 1 in the supplemental material; see Acknowledgments).

evolutionary origins of notaria are accomplished via the same or different genetic mutations and patterns of gene expression. Although identifying the genetic mutations involved is a difficult problem, recent advances have been made toward relating gene-expression patterns to beak morphology in Darwin's finches (Abzhanov et al. 2004, 2006). The studies of Darwin's finches addressed quantitative traits like bill depth and length; however, presence–absence traits like the notarium may prove even more amenable in such studies. In addition, the recognition that some species exhibit intraspecific variability in expression of a fully fused notarium opens the possibility that family-pedigree studies could help identify the genes involved.

The notarium functions to eliminate motion between vertebrae. Previous authors sought to account for its systematic distribution by identifying a functional context that would favor stiffening of thoracic vertebrae in some groups of birds and not others. The realization that a variety of songbirds also have evolved notaria broadens the already wide range of functional contexts in which the trait has developed or been maintained in birds. Notaria form at the back of the thoracic cavity, a functional nexus where the vertebrae participate in several important aspects of body function: breathing, flight, bipedal posture, and hindlimb locomotion have been mentioned by previous authors. Muscles that help control motion of the neck also originate on these vertebrae (m. longus colli pars caudalis and thoracica, m. biventer cervicis; Vanden Berge and Zweers 1993). Considering that natural selection for stiffening of the thoracic column of vertebrae could arise from each of these functions, we may need to ask: Why is it that not all birds possess a notarium (as they do a synsacrum and pygostyle)?

Part of the answer may be that there are several possible design solutions to the problem of limiting movement between thoracic vertebrae. Thoracic vertebrae in all birds possess expanded spinous processes, and their vertebral bodies have relatively extensive and planar articular surfaces, which limit motion between the vertebrae in comparison with the cervical column (Fig. 1K). Further expanding the spinous processes until they are firmly in contact with each other and tightly articulating the vertebral bodies so that motion between them is more restricted are two design solutions to the problem that tend to occur in tandem (e.g., in the Bananaquit [*Coereba flaveola*]). A third solution, more common in nonpasserine birds, is to develop a series of overlapping ossified tendons along the dorsal side of the vertebrae (e.g., in the Canada Goose [*Branta canadensis*]). A fourth, seen in a variety of nonpasserine and passerine birds, is to interlock the spinous processes to each other via a tongue-and-groove articulation (e.g., in the Rufous Wren [*Cinnycerthia unirufa*]). We might then view the notarium as a fifth possible solution. For species in which there is no advantage in allowing any motion between the vertebrae, it could be energetically the least expensive and physically the most effectual.

Although the present study has not addressed the function of the notarium in a rigorous way, I speculate below on the source of natural selection that may have led to establishment of a notarium in several passerine taxa. My speculation suggests a new hypothesis, that in most instances, fully fused notaria have evolved to provide a rigid platform for attachment of neck muscles. This is based on the observation that notaria tend to occur in birds that engage in unusually intricate, repetitious, or vigorous motions of the head and neck in the course of food getting, nest building, or display. The hypothesis may have explanatory power in both passerine and nonpasserine birds.

A trait that has evolved repeatedly may appear to have little utility in systematics; however, in a variety of taxa the notarium has a diagnostic form, and in some major clades it has evolved only once. In these taxa, notaria can be helpful in delimiting clades and, potentially, in identifying fossils. Comments on the systematic importance of notaria in selected taxa follow.

Verdin.—The Verdin and penduline tits were originally associated with each other because they are small, acrobatic passerines that build elaborate covered nests and have short conical bills rather like those of chickadees, but the relationship was long held in doubt. Taylor (1970) proposed that the Verdin is instead related to Bananaquits, and Sibley and Ahlquist (1990) placed it near gnatcatchers (*Polioptila*). A more thorough genetic study (but with limited outgroups) and two osteological studies have since supported the placement of the Verdin in the Remizidae (Webster 2000, James et al. 2003, Gill et al. 2005), a family clearly related to and often subsumed within the tits and chickadees (Paridae; James et al. 2003, Barker et al. 2004, Alström et al. 2006, Johansson et al. 2008). Besides the Paridae, the family has been thought to be related to the long-tailed tits (Aegithalidae) and a group including flowerpeckers, sunbirds, white-eyes, and honeyeaters (Dicaeidae, Nectariniidae, Zosteropidae, and Meliphagidae; Delacour and Vaurie 1957). Representatives of all the above groups were included in the present survey, and only in *Remiz*, *Auriparus*, and *Anthoscopus* is there a fully fused notarium. Thus, the tiny and seamless notarium in the Remizidae provides strong evidence that the Verdin of southwestern North America truly is a member of this otherwise Old World group. Motions of the head and neck needed for constructing elaborate nests may be the source of natural selection that enabled the trait to become established in this group. It is not known, however, whether the Fire-capped Tit (*Cephalopyrus flammiceps*), also sometimes assigned to the Remizidae, has a notarium.

Thrashers.—Engels (1940) and Zink et al. (1999) recognized three species of thrashers with relatively long, decurved bills as a related species group within the genus *Toxostoma*. Engels found that members of the group composed of *T. lecontei*, *T. redivivum*, and *T. crissale* forage by excavating in soil (using the bill, not the feet) to a greater extent than other thrashers and share an adaptive complex in the skeletomuscular system of the head for this behavior. They also are the only three thrashers with a notarium, a trait that is probably part of the same adaptive complex for digging and whose evolution in the ancestor of these species may have enabled the lineage to inhabit drier habitats compared with other thrashers.

Crossbills.—The crossbills stand out among nine-primaried oscines for the unusual motions that they make with the head and neck when foraging. The occurrence of a notarium in *Loxia* could be related to the forces exerted on the thoracic vertebrae by the neck muscles when making these motions. The notarium in *Loxia* has a unique developmental pattern in which the vertebral bodies fuse late or not at all, and in addition the notarium in the *L. curvirostra* species group is distinct from that in *L. leucoptera*. Further survey of the form of the notarium in this group could assist with understanding the complex pattern of population segregation and speciation in crossbills (e.g., Benkman 1993, Groth 1993, Summers et al. 2007, Edelaar 2008).

Larks.—The Alaudidae show the most complex pattern of gains and losses of the notarium of any family examined, which may indicate that the systematics of the family needs a revision. Fully fused notaria were found in four genera in this family (one of which does not appear in the supertree); lightly fused vertebrae and polymorphic species were also found. Among the species in the long-billed lark complex that were formerly classified as a single polymorphic species (see Ryan and Bloomer 1999), one has a fully fused notarium and another lacks fusion. Thus, the notarium may prove useful as a taxonomic character in future revisions of the family.

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