Two spinal cords in birds: novel insights into early avian evolution

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Birds can be subdivided into two large superordinal assemblages based on differences in the dorsal horn of the spinal grey matter. Palaeognaths (i.e. ratites and tinamous), along with a few other orders of neognathous birds, exhibit the primitive dorsal horn state characteristic of other amniotes wherein cutaneous nerves form a single map of the body surface across the dorsal horn. In contrast, the vast majority of neognaths exhibit a novel, distinctly bifid dorsal horn wherein cutaneous nerves form not one, but two separate maps of the skin, each lying side-by-side. This unusual dorsal horn organization, which has been highly conserved and represents the derived state in birds, may identify a novel, major avian clade. These findings shed new light on historically problematic taxa and the early evolutionary branching sequence among living birds. Most notably, they reveal that the traditional orders Gruiformes, Columbiformes, Cuculiformes and Piciformes are unnatural assemblages. Further, in addition to palaeognaths, these findings suggest that most gruiforms, including buttonquails and mesites, as well as pigeons, cuckoos, woodpeckers and songbirds, represent ancient lineages whose ancestry predates the majority of 'modern' birds. The phylogeny of living birds may thus be likened more to a dense bush than the traditional tree, with more than half of all living species arising from a basal side branch.

Keywords: systematics; phylogeny; birds; spinal cord; dorsal horn; evolution

1. INTRODUCTION

The dorsal horn of the spinal grey matter plays a major role in processing sensory information from the skin. This highly laminated structure receives the central projections of a myriad of types of cutaneous sensory fibres, all of which become organized within specific laminae in a highly ordered, stereotypical manner (reviewed in Willis & Coggeshall (1991)). Recently, the dorsal horn of chickens has been shown to be unique among the vertebrates described to date (Brinkman & Martin 1973; Woodbury & Scott 1991; Woodbury 1992). Unlike the dorsal horn of other amniotes, which is characterized by a smooth, rounded outline and radially stacked cellular laminae (Rexed 1952; Kusuma *et al.* 1979), this structure in chickens is split along its length by a pronounced apical inflection which separates lamina II from lamina III across the mediolateral plane (Brinkman & Martin 1973). Pivotal support for this distinction is provided through analyses of the central projections of cutaneous nerves. Thus, in striking contrast to the radially aligned projections of cutaneous nerves typical of most vertebrates (e.g. Koerber & Brown 1982), these same nerves in chickens form not one, but two separate projections, giving rise to dual maps of the body surface, lying side-by-side, across the dorsal horn (Woodbury & Scott 1991).

Here I report that most avian orders share this unusual bifid dorsal horn with chickens, whereas relatively few exhibit the dorsal horn seen in other amniotes. Both types have been highly conserved throughout avian evolution. Importantly, as the typical amniote dorsal horn is present in palaeognathous birds (i.e. ratites and tinamous), generally considered the earliest lineage of 'modern' birds (Cracraft 1988), the unusual bifid dorsal horn is derived and may therefore identify a novel, major avian clade. These novel findings have significant consequences for our current understanding of the phylogenetic history of higher avian taxa. Among the most notable, this robust difference in the central nervous system (CNS) of birds suggests that the traditional orders Gruiformes, Columbiformes, Cuculiformes, and Piciformes (*sensu* Wetmore 1960) are unnatural. In addition, these findings suggest that the most successful group of birds, songbirds of the order Passeriformes, arose far earlier than is generally believed, well before the origin of most non-passerines.

2. MATERIALS AND METHODS

The dorsal horn of birds spanning a broad spectrum of higher taxa was surveyed using normal histological techniques. These findings were independently confirmed in select taxa through analyses of the dorsal horn projection patterns of cutaneous nerves, using experimental neuroanatomical tract-tracing techniques; the latter were successfully performed in 43 individuals from 33 species, representing 27 families from 19 orders of birds. All species successfully examined for this study are listed in Appendix A.

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Spinal cords from alcohol-preserved museum specimens were dissected from their surrounding bone, embedded in paraffin, and cut into 10 µm thick transverse sections. In freshly fixed specimens, spinal cords were dissected, cryoprotected, mounted on the stage of a freezing microtome and cut into 50 µm sections. When possible, comparisons were confined to rostral synsacral segments (SS1–SS3), although thoracic, brachial, and cervical levels were also examined in many cases. Optimal visualization of these dorsal horn characters was obtained in unstained hydrated sections viewed under dark-field illumination; many sections were also stained with Nissl substance to allow examination of cytoarchitectonic detail.

The procedures used to label the central projections of cutaneous nerves have been described in detail (Woodbury & Scott 1991). Briefly, a concentrated solution of horseradish peroxidase (HRP) was applied to hindlimb cutaneous nerves in birds anaesthetized with ketamine and xylazine. Following the transport of HRP into the central terminals of labelled cutaneous fibres (1–6 d, depending on size and metabolic rate), the animals were euthanized with an overdose of anaesthetic and perfused with saline followed by fixative. The spinal cord was dissected free, cryoprotected, and frozen-sectioned at 50 µm; field-collected tissues were cryoprotected and stored in liquid nitrogen prior to histological processing. Serial transverse sections (50 µm) from mid-thoracic to mid-synsacral segments were reacted histochemically to visualize transported HRP, counterstained with neutral red, and drawn with the aid of a camera lucida.

3. RESULTS

On the basis of normal histology, birds could be subdivided into two discrete groups, one characterized by a markedly inflected dorsal horn, the other by a smooth, rounded dorsal horn (see figure 1). These two conditions, here termed *schizocerate* ('split-horned') and *leiocerate* ('smooth-horned'), respectively, extended the length of the spinal cord and could generally be discerned macroscopically in all but the smallest cords.

The results of experimental nerve-tracing studies were entirely concordant with predictions based upon normal histology (see figure 2). In *schizocerate* taxa, cutaneous nerves gave rise to two distinct projections, each on opposite sides of the inflection, as in chickens. In contrast, these same nerves in *leiocerate* taxa formed a single, radially aligned projection, as in mammals. Despite these differences, the overall somatotopic organization of nerve inputs was conserved. Thus, two maps of the body surface lie side-by-side across the superficial dorsal horn of *schizocerates*, as detailed previously (Woodbury & Scott 1991), in contrast to the single map in *leiocerates*.

Extensive surveys across a variety of lower- and higher-level taxa revealed a striking taxonomic stability in both dorsal horn conditions. While many taxa were represented by a single specimen, multiple individuals (2–5) were examined in over 40 species; multiple species (2–4) were examined in 20 genera; and multiple genera (2–13) were examined in 28 families, in many cases covering a broad spectrum of subfamilial diversity (e.g. eight species of tinamous examined, representing seven of the eight genera in this family; Woodbury 1998a). While both conditions exhibited minor variation between both closely and more distantly related taxa (e.g. figure 1),

Figure 1. Dark-field photomicrographs of hydrated transverse sections through the dorsal horn of (a) the sandhill crane (*Grus canadensis*; family Gruidae) and (b) the red-backed buttonquail (*Turnix maculosa*; family Turnicidae), both in the order Gruiformes. They reveal a smooth, rounded dorsal horn typifying the *leiocerate* condition. Dorsoventral lamination of gelatinous laminae (II and III) in the head of the dorsal horn is readily apparent in (a) as well as in Nissl-stained sections (not shown). By contrast, sections through the dorsal horn of (c) the rainbow bee-eater (*Merops ornatus*; family Meropidae) and (d) the short-legged ground roller (*Brachypteracias leptosomus*; family Brachypteraciidae), both in the order Coraciiformes, reveal the pronounced dorsal inflection (arrow) typifying the *schizocerate* condition. These dorsal horn types accurately predict cutaneous nerve projection patterns (e.g. figure 2) and the localization of neuropeptides (e.g. substance P and calcitonin gene-related peptide) associated with unmyelinated afferent terminals in laminae I/II (not shown). All sections in this and the following figure show the right dorsal horn (midline to the left) at the level of the second synsacral segment. Scale bars = 100 µm.

each was completely stable within families. Indeed, no polymorphism was observed within the majority of traditional avian orders, some of which were sampled intensively (e.g. 39 passerine families). Such stability underscores the fact that these character states have been highly conserved throughout avian evolution.

Interestingly, most orders of birds were found to be *schizocerate*. To date, only ratites and tinamous (i.e. palaeognaths), cranes and their allies, as well as doves, cuckoos, woodpecker-like birds, and songbirds have been found to be *leiocerate* (table 1). Importantly, four of these orders were polymorphic (see (a)–(d) below), highlighting some of the most problematic taxa among living birds.

(a) *Gruiformes*

Most families traditionally grouped with cranes were found to be *leiocerate*, including the 'core' gruiforms, i.e. cranes (Gruidae), rails (Rallidae), trumpeters (Psophiidae), and sungrebes (Heliornithidae), as well as the mesites (Mesitornithidae) and buttonquails (Turnicidae). By contrast, both bustards (Otididae) and the sunbittern (Eurypygidae) were found to be *schizocerate*. Specimens examined from other possible allies (Rhynchotidae, Cariamidae, Pedionomidae) were frozen previously and thus inadequately preserved to assess dorsal horn state.

Figure 2. Dark-field photomicrographs (left column) and camera lucida tracings of dorsal horn projections (stippling in the right column) from the lateral femoral cutaneous nerve (CFL) in the Japanese quail (*Coturnix coturnix*; order Galliformes) (a and b) and the blue-throated hummingbird (*Lampornis clemenciae*; order Apodiformes) (c and d). They reveal the unusual, derived schizocerate condition with two discrete projections separated across the mediolateral plane of the superficial dorsal horn, each on either side of a pronounced inflection (arrow). By contrast, the same nerve in the mourning dove (*Zenaida macroura*; family Columbidae; order Columbiformes) (e and f) and the American crow (*Corvus brachyrhynchos*; order Passeriformes) (g and h), reveals the primitive leiocerate condition, with radially aligned projections in a smooth, rounded dorsal horn. Note that somatotopy is conserved throughout all taxa, with the CFL projecting laterally within laminae II and III as in other vertebrates. Scale bars = 100 μ m.

(b) Columbiformes

While pigeons and doves (Columbidae—18 species from 12 diverse genera) were consistently found to be leiocerate, sandgrouse (Pteroclididae) were found to be schizocerate. Interestingly, sandgrouse shared this condition with shorebirds (Charadriiformes), often considered to be the closest allies of columbiforms.

(c) Cuculiformes

Whereas cuckoos (Cuculidae—16 species from 10 genera, representing all subfamilies) were consistently seen to be leiocerate, tauracos (Musophagidae) were found to be schizocerate. Moreover, the hoatzin

(Opisthocomidae), recently proposed to belong within the Cuculidae, was also found to be schizocerate, verified in five individuals.

(d) Piciformes

All families within the suborder Pici, including woodpeckers (Picidae), honeyguides (Indicatoridae), toucans (Ramphastidae) and barbets (Capitonidae), were found to be leiocerate. However, the suborder Galbulae was found to be polymorphic; puffbirds (Bucconidae), like typical piciforms, are leiocerate (7 genera examined), whereas jacamars (Galbulidae) are schizocerate (3 genera examined). Interestingly, the schizocerate condition was also found to characterize the roller-kingfisher group (Coraciiformes), to which the suborder Galbulae has often been allied.

4. DISCUSSION

These studies reveal a novel character in the spinal cord of birds which separates higher taxa into two large superordinal assemblages, herein termed leiocerates and schizocerates, respectively. Although macroscopically visible, and plainly evident in some of the earliest figures of the avian spinal cord (e.g. Clarke 1859; Steida 1869; Gadow & Selenka 1891; Ramón Y Cajal 1891, 1909; von Kölliker 1902), this major distinction between birds has been overlooked.

As evidenced by the robust congruence with family and ordinal-level assemblages, both the leiocerate and schizocerate character states have been highly conserved throughout avian evolution. This is set against the backdrop of seemingly complete stasis of the leiocerate condition throughout mammalian evolution (see Rexed 1952, p. 459; see also Martin & Fisher 1968; Marsh 1972; Ralston 1979; Molander *et al.* 1989). These findings, coupled with similar analyses across all major reptilian taxa (Cruce 1979; Kusuma *et al.* 1979; Pritz & Stritzel 1994), suggest that the leiocerate arrangement of radially stacked laminae represents the generalized amniote condition. Ultimately, a complete understanding of homology will require knowledge of the termination patterns of single, physiologically identified cutaneous fibres on the one hand, and comparative developmental studies on the other, neither of which is yet available in birds or reptiles.

The factors responsible for the evolution of the unusual schizocerate condition are not clear. Despite such obvious differences in dorsal horn organization between birds, no obvious functional differences are apparent (Woodbury 1992). This finding is reinforced by the many extremes (e.g. ecological, behavioural, morphological, developmental, metabolic, etc.) exhibited within both leiocerate and schizocerate assemblages. Hence, the selective advantages initially conferred by this novel condition on the ancestral schizocerate, if any, remain elusive. From a phylogenetic perspective, however, it is clear from the rarity of polymorphic taxa that character transformation has been severely constrained throughout avian evolution; furthermore, the orders shown to be polymorphic are by no means secure taxa, as they have posed some of the most recalcitrant questions in the history of avian systematics.

Table 1. *Higher level taxonomic distribution of dorsal horn type in birds*

(Orders and families from which representative species were examined: bold indicates taxa on which neuroanatomical studies were conducted; unnatural orders are underlined.)

Leioceratae	Schizoceratae		
Struthioniformes*	Gaviiformes	<u>Gruiformes</u>	Caprimulgiformes
Rheiformes*	Podicipediformes* †	Otididae†	Steatornithidae
Casuariiformes	Procellariiformes	Eurypygidae*	Podargidae*
Casuariidae	Pelecanoididae†	Charadriiformes	Nyctibiidae
Dromiceidae*	Pelecaniformes	Jacaniidae†	Aegothelidae
Tinamiformes†	Phaethontidae	Rostratulidae	Caprimulgidae*
<u>Gruiformes</u>	Pelecanidae*	Charadriidae†	Apodiformes
Mesitornithidae†	Sulidae	Scolopacidae†	Apodidae
Turnicidae*†	Phalacrocoracidae	Recurvirostridae	Trochilidae†
Gruidae	Ciconiiformes	Burnhinidae	Coliiformes
Psophiidae	Ardeidae* †	Glareolidae	Trogoniformes*
Rallidae*†	Threskiornithidae	Thinocoridae	Coraciiformes
Helionithidae	Anseriformes	Laridae*	Alcedinidae*†
<u>Columbiformes</u>	Anatidae*	<u>Columbiformes</u>	Momotidae†
Columbidae*†	Falconiformes	Pteroclididae†	Meropidae
<u>Cuculiformes</u>	Cathartidae	Psittaciformes*†	Coraciidae
Cuculidae*†	Falconidae	<u>Cuculiformes</u>	Brachypteraciidae
<u>Piciformes</u>	Galliformes	Musophagidae†	Leptosomatidae
Bucconidae*†	Megapodiidae	Strigiformes	<u>Piciformes</u>
Capitonidae†	Cracidae	Tytonidae	Galbulidae†
Indicatoridae	Phasianidae*†	Strigidae†	
Ramphastidae†	Meleagridae		
Picidae†	Opisthocomidae*		
Passeriformes*†‡			

* Multiple individuals examined from a single species.

† Multiple species examined in a family (different genera in most cases).

‡ Suboscine families examined were the Pittidae, Eurylaimidae, Dendrocolaptidae, Furnariidae, Thamnophilidae, Rhinocryptidae, Cotingidae†, Pipridae, Tyrannidae*†, and the Phytotomidae.

Neuroanatomical studies were conducted in 5 (Hirundinidae, Corvidae, Turdidae, Emberizidae, and Estrildidae) out of 29 oscine families examined (see Appendix A).

If palaeognaths represent the sister-group to all other living birds (e.g. Cracraft 1988), then the leiocerate condition is the ancestral state among neognaths, and hence the derived, schizocerate condition may identify a novel, major neognath clade (figure 3). The consequences of this phylogenetic hypothesis for avian higher-level systematics are far-reaching and bear upon some of the most vexing problems in avian phylogeny. While largely congruent with traditional theories of higher-level relationships (Wetmore 1960), this marked CNS difference argues against the monophyly of the orders Gruiformes, Columbiformes, Cuculiformes, and Piciformes.

(a) *Polymorphic orders*

(i) *Gruiformes*

With regard to the heterogeneous order Gruiformes, these findings are consistent with the inclusion of button-quails and mesites with the 'core' group of crane-like birds, but exclude bustards and the sunbittern (*contra* Sibley & Ahlquist 1990). Hence, these results are concordant with earlier views that bustards are derived shorebirds (Parker 1868a; Fürbringer 1888; Beddard 1898; Olson 1985), and that the sunbittern is more closely related to other schizocerates, including herons (Nitzsch 1867; Parker 1868b; Beddard 1898; Chandler 1916; Olson 1979), than to true gruiforms. Given the isolated, basal position of buttonquails and mesites relative to core

gruiforms (see below), the present findings are also largely congruent with molecular findings (Houde *et al.* 1997; see also Hendrickson 1969).

(ii) *Columbiformes*

Regarding the order Columbiformes, these findings clearly exclude sandgrouse, and thus are congruent with DNA–DNA hybridization studies (Sibley & Ahlquist 1990) which place sandgrouse, but not pigeons and doves, with shorebirds (Woodbury 1998b). Moreover, these findings indicate that parrots share a more recent common ancestor with other schizocerates, including mousebirds (Gilliard 1958; Berman & Raikow 1982) and tauracos (Gadow 1892), than with pigeons (Burton 1974; Stegmann 1978).

(iii) *Cuculiformes*

With regard to the traditional order Cuculiformes, these findings exclude tauracos; this is in agreement with previous morphological studies (Moreau 1938; Lowe 1943; Verheyen 1956; Berger 1960) and has been corroborated by DNA–DNA hybridization studies (Sibley & Ahlquist 1990). Importantly, however, these results reveal that the hoatzin is clearly not a cuckoo, as formerly proposed (Sibley & Ahlquist 1972, 1973); instead, it shares a more recent common ancestor with other schizocerates (including tauracos; Nitzsch 1867; Verheyen 1956;

Figure 3. Basal lineages of living birds. Identified taxa exhibit the primitive leiocerate spinal cord of palaeognaths, while all other avian taxa are united by the shared possession of the derived schizocerate spinal cord (bar). As represented here, the orders Gruiformes and Piciformes include all traditional families except the Eurypygidae, Otididae and Galbulidae, respectively (see text for explanation).

Stegmann 1978; and galliforms; Gadow 1892), than with any cuckoo (Woodbury 1998c). Previous attempts to resolve this issue through analyses of molecular evolution have been problematic (see Hackett *et al.* (1995) and references therein). Indeed, recent arguments emphasizing a hoatzin–cuckoo alliance belie striking internal inconsistencies (cf. figs 8.5 and 8.6 of Mindell *et al.* (1997)) and critical dependence on method of analysis and restricted sampling; more inclusive sampling, by contrast, contradicts such an alliance (Mindell *et al.* 1997; see also Adachi & Hasegawa 1996).

(iv) *Piciformes*

Perhaps most significantly, this spinal cord trait helps resolve long-standing uncertainty surrounding the monophyly and interordinal affinities of woodpeckers and their allies in the order Piciformes. While typical piciforms (i.e. suborder Pici) constitute a well-corroborated clade, sharing considerable similarities with songbirds, inclusion of the jacamars and puffbirds (i.e. suborder Galbulae) within Piciformes remains highly controversial due to similarities shared between the Galbulae and members of the roller–kingfisher group (Coraciiformes) (Simpson & Cracraft 1981; Swierczewski & Raikow 1981; Olson 1983; Raikow & Cracraft 1983; Burton 1984; Brom 1990). The remarkable finding that jacamars share the derived schizocerate condition with Coraciiformes, whereas puffbirds share the leiocerate condition with the Pici and passerines, indicates that the suborder ‘Galbulae’ is unnatural: jacamars share a more recent common ancestor with coraciiforms than with puffbirds. Indeed, these new findings about the spinal cord, in combination with characters previously used to support opposing arguments of piciform affinities (from the references just quoted), generate a single, most parsimonious solution whereby the Pici, puffbirds, and jacamars constitute successively closer sister-groups to the diverse coraciiform assemblage (tree length=30 steps; consistency index

(CI)=0.80). The hypothesis of piciform diphyly (e.g. Olson 1983) requires 37 steps (CI=0.65), whereas strict monophyly of Piciformes requires a length of 43 steps (CI=0.56) to explain the distribution of these characters (Woodbury 1998d).

(b) *Leiocerate affinities*

With the possible exception of Pici and passerines, the evolutionary relationships of leiocerates have long generated considerable uncertainty. As a shared primitive state, the leiocerate condition stops short of providing positive evidence of affinity. It is noteworthy, nevertheless, that these independent findings precisely mirror the underpinnings of traditional avian systematics (Fürbringer 1888), that cuckoos’ closest relatives may lie among the woodpecker–songbird assemblage (see also Huxley 1867; Beddard 1898; Pycraft 1903; Shufeldt 1901; Adachi & Hasegawa 1996), and perhaps more significantly, that buttonquails (and through them, the mesites and core gruiforms) may be close to the lineage that has given rise to tinamous (see also Parker 1875; Lowe 1923). The present findings are clearly consistent with earlier views that buttonquails, as well as the songbird-like mesites, are relicts of archaic, basal groups (Huxley 1868; Parker 1875; Fürbringer 1888; Lowe 1923; Stresemann 1934; Verheyen 1958), neither of which are closely related to galliforms. Furthermore, these findings may help to explain numerous paradoxical similarities between, on the one hand, these basal gruiforms and pigeons, and on the other, passerines (Parker 1875; Beddard 1898, 1911; Lowe 1923, 1924, 1926), along with the early classification of mesites with both pigeons and passerines (Milne-Edwards 1878). That is, pigeons and passerines may each represent independent derivations from basal gruiform stock (see also Sibley & Ahlquist 1990). In consideration of earlier work, future investigations into possible songbird–buttonquail, pigeon–mesite sister relationships may prove fruitful.

(c) Basal avian lineages

The cryptic nature of leiocerate affinities has frequently been attributed to the profound antiquity of these groups (reviewed in Sibley & Ahlquist 1990). Indeed, the present findings suggest that leiocerates represent the earliest lineages among extant birds. As a close relationship between tinamous and chickens (or ducks) is contra-indicated by these findings, the position of galliforms and anseriforms, recently hypothesized to constitute the most basal clade (i.e. Galloanserae) among neognaths (Cracraft 1988; Cracraft & Mindell 1989), warrants consideration. In this regard, morphological evidence previously marshalled in support of 'Galloanserae' is exceedingly problematic (Ericson 1996), and since no characters unite remaining neognaths to the exclusion of chickens and ducks (Cracraft 1988), the 'basal Galloanserae' hypothesis is in essence a molecular argument. As for the molecular evidence, no single data set provides direct support for Galloanserae, whereas some directly contradict it (Laskowski & Fitch 1989; Cooper & Penny 1997). Many agree, however, on a high degree of molecular divergence in chickens and ducks. Indeed, reanalyses of the published DNA–DNA hybridization melting curves in Sibley & Ahlquist (1990), reveal that galliforms and anseriforms are as distant from each other as they are from other neognaths (Pettigrew & Woodbury 1998). Further, basal groups (e.g. megapodes, screamers) are closer to other neognaths than are derived groups (e.g. chickens, ducks), yet they differ with respect to which group each comes closest to. Finally, both neognath and schizocerate monophyly are supported by the finding that basal 'Galloanserae' are significantly closer to other schizocerates than to leiocerates, including palaeognaths. Relative rate tests of these data, using palaeognaths as the outgroup, reveal that galliforms and anseriforms exhibit some of the highest rates of genomic change among birds, suggesting that evolutionary-rate artefacts (e.g. long-branch attraction) underlie the basal placement of galliforms and anseriforms in molecular studies. Close inspection of other molecular data sets provides additional evidence for this (Woodbury & Pettigrew 1998).

In retrospect, the seemingly intractable nature of avian relationships over the past century appears to reflect the fact that the earlier *scala naturae* of avian classification was erected upon its head. Long-perched at the crown of the avian tree, the unparalleled radiation of songbirds appears instead to be an offshoot from one of the lowermost branches. While the fossil record is 'silent' on this issue (Olson 1985; Feduccia 1996), some signal to this effect appears to be emerging from analyses of molecular evolution (Mindell *et al.* 1997; see also Prager *et al.* 1974; Adachi & Hasegawa 1996).

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APPENDIX A

Orders, families, and species of birds in which dorsal horn character state was verified. Specimens were examined from the following institutions: the American Museum of Natural History (AMNH), the US National Museum of Natural History (USNM), the Queensland Museum (QM), the Colección Phelps, Caracas, Venezuela (COP), the University of Michigan Museum of Zoology (UMMZ), and the Universidad Central de Venezuela (UCV). C.J.W. denotes the author's holdings; bracketed values indicate the number of individuals examined. Bold type indicates specimens used in experimental neuroanatomical studies.

LEIOCERATAE:

STRUTHIONIFORMES: Struthionidae; *Struthio camelus* (C.J.W. (4)).

RHEIFORMES: Rheidae; ***Rhea americana*** (C.J.W. (1 of 4)).

CASUARIIFORMES: Casuariidae; *Casuarius* sp. (AMNH 10768). Dromiceidae; ***Dromaius novaehollandiae*** (C.J.W. (5), AMNH 7849).

TINAMIFORMES: Tinamidae; *Tinamus major* (UCV uncat.), *Crypturellus variegatus* (AMNH 10414), ***Eudromia elegans*** (AMNH 10557), ***Nothoprocta perdicaria*** (AMNH 10558), *N. cinerascens* (AMNH 10770), *Rhynchotus rufescens* (AMNH 8645), *Nothura darwinii* (AMNH 10771), *Tinamotis pentlandii* (AMNH 8646).

GRUIFORMES: Mesitornithidae; *Mesitornis variegata* (USNM 289725), *M. unicolor* (AMNH 5830), *Monias benschi* (AMNH 5860). Turnicidae; *Turnix maculosa* (QM 26136, 26141), *T. varia* (QM 25532), *T. pyrrhorothea* (QM 26091, 26093), *T. velox* (QM 21546, 21632). Gruidae; *Grus canadensis* (C.J.W.). Psophiidae; *Psophia crepitans* (AMNH 9108). Rallidae; *Gallirallus torquatus* (AMNH 10774), *Fulica americana* (AMNH 10507, 10567), *Porzana pusilla* (QM 26157). Heliornithidae; *Heliopais personata* (USNM 509508).

COLUMBIFORMES: Columbidae; *Columba livia* (C.J.W.), *Macropygia amboinensis* (AMNH 2606), *Phaps chalcoptera* (AMNH 10530), *Geophaps lophotes* (AMNH 10531), *G. plumifera* (QM 22556), *G. ferruginea* (AMNH 4066), *G. scripta* (QM 24295), *Geopelia placida* (QM 23146), ***Zenaidura macroura*** (C.J.W. (1)), *Otidiphaps nobilis* (AMNH 10810), *Treron vernans* (AMNH 10807), *Ptilinopus magnificus* (QM 17181), *P. superbus* (QM 71264), *Ducula aenea* (AMNH 10808), *D. spilorrhoa* (QM 17087), *Goura cristata* (AMNH 7790, 10812), *G. victoria* (AMNH 10809), *Didunculus strigirostris* (AMNH 7531).

CUCULIFORMES: Cuculidae; *Cuculus saturatus* (QM 16457), *C. pallidus* (QM 23144), *Cacomantis variolosus* (QM 26166), *C. flabelliformis* (QM 14288), *Chrysococcyx lucidus* *plagosus* (QM 17041, 22814), *C. basalis* (QM 23426, 21631), *Eudynamis scolopacea* (QM 24259), *Coua cristata* (AMNH 2203), *Centropus phasianinus* (QM 17065), *C. viridis* (AMNH 10777), *C. unicolor* (AMNH 10775), *Piaya cayana* (COP 76678), *Crotophaga ani* (COP 76680), *Guiraca guiraca* (AMNH 7323), ***Geococcyx californianus*** (AMNH 10510, 10527).

PICIFORMES: Bucconidae; *Monasa atra* (AMNH 10388, 10389), *Bucco tamatia* (AMNH 10430), *Nystalus maculatus* (AMNH 8506), *Nonnula rubecula* (AMNH 9177), *Hypnelus ruficollis* (AMNH 8520), *Malacoptila panamensis* (AMNH 8438), *Chelidoptera tenebrosa* (AMNH 10432). Indicatoridae; *Melichneutes robustus* (AMNH 5342). Capitonidae; *Lybius guifso-balito* (AMNH 5067), *Capito niger* (AMNH 9188). Ramphastidae; *Pteroglossus aracari* (AMNH 10391), *P. viridis* (AMNH 5384). Picidae; *Melanerpes carolinus* (AMNH 10363), *M. formicivorus* (AMNH 10519), *Picoides pubescens* (AMNH 8205), *P. villosus* (C.J.W.), *Colaptes (auratus) cafer* (AMNH 10518).

PASSERIFORMES:

(Suboscines): Pittidae; *Pitta erythrogaster* (AMNH 10780). Eurylaimidae; *Smithornis rufolateralis* (AMNH 2232). Dendrocolaptidae; *Dendrocolaptes picumnus* (AMNH 10393). Furnariidae; *Philydor pyrrhodes* (AMNH 10395). Thamnophilidae; *Gymnophis rufigula* (AMNH 10401). Rhinocryptidae; *Rhinocrypta lanceolata* (AMNH 2310). Cotingidae; *Procnias alba* (AMNH 10375), *Rupicola rupicola* (AMNH 7682), *Perissocephalus tricolor* (AMNH 10403). Pipridae; *Pipra pipra* (AMNH 10450). Tyrannidae; *Sayornis nigricans* (AMNH 4158), *Empidonax occidentalis* (AMNH 10520, C.J.W.). Phytotomidae; *Phytotoma rara* (AMNH 4314).

(Oscines): Climacteridae; *Climacteris picumnus* (QM 22965). Ptilonorhynchidae; *Chlamydera maculata* (QM 25701). Meliphagidae; *Meliphaga lewinii* (QM 24402). Epthianuridae; *Ashbyia lovensis* (QM 24009). Pardalotidae; *Pardalotus punctatus* (QM 23589, 25760). Acanthizidae; *Smicronis brevirostris* (QM 24465). Eopsaltriidae; *Microeca leucophaea* (QM 22973). Pomatostomidae; *Pomatostomus superciliosus* (QM 21630). Neositidae; *Daphoenositta chrysoptera* (QM 24277). Corvidae; *Corvus brachyrhynchos* (C.J.W.). Artamidae; *Artamus superciliosus* (QM 24342). Campephagidae; *Coracina papuensis* (QM 23205). Grallinidae; *Grallina cyanoleuca* (QM 26728). Turdidae; *Turdus migratorius* (AMNH 10522), *Catharus guttatus* (AMNH 10524). Muscipidae; *Oreoica gutturalis* (QM 24198). Sturnidae; *Sturnus vulgaris* (C.J.W.). Mimidae; *Mimus polyglottos* (C.J.W.). Sittidae; *Sitta canadensis* (C.J.W.). Certhiidae; *Certhia americana* (C.J.W.). Paridae; *Parus palustris* (C.J.W.). Hirundinidae; *Hirundo rustica* (AMNH 10364). Zosteropidae; *Zosterops lateralis* (QM 24425). Sylviidae; *Regulus satrapa* (C.J.W.). Dicaeidae; *Dicaeum hirundinaceum* (QM 23161). Passeridae; *Passer domesticus* (C.J.W.). Motacillidae; *Anthus novaeseelandiae* (QM 22851). Estrildidae; *Taeniopygia guttata* (C.J.W. (2)). Emberizidae; *Melospiza melodia* (C.J.W.), *M. lincolni* (AMNH 10526). Parulidae; *Geothlypis trichas* (AMNH 10046), *Dendroica coronata* (C.J.W.).

SCHIZOCERATAE:

GAVIIFORMES: Gaviidae; *Gavia immer* (C.J.W.).

PODICIPEDIFORMES: Podicipedidae; *Podilymbus podiceps* (AMNH 10506), *Aechmophorus occidentalis* (AMNH 10563–10566), *Podiceps nigricollis* (AMNH 10559–10562, C.J.W.).

PROCELLARIIFORMES: Pelecanoididae; *Pelecanoides garnotii* (AMNH 10781), *P. urinatrix* (AMNH 10782).

PELECANIFORMES: Phaethontidae; *Phaethon aethereus* (AMNH 10788). Pelecanidae; *Pelecanus erythrorhynchos* (AMNH 10624, C.J.W.). Sulidae; *Sula leucogaster* (AMNH 10792). Phalarocoracidae; *Phalacrocorax auritus* (AMNH 10357).

CICONIIFORMES: Ardeidae; *Egretta thula* (AMNH 10359–10360), *Butorides striatus* (AMNH 10415). Threskiornithidae; *Plegadis chihi* (AMNH 10508).

ANSERIFORMES: Anatidae; *Anas platyrhynchos* (C.J.W. (3)).

FALCONIFORMES: Cathartidae; *Cathartes aura* (C.J.W.). Falconidae; *Falco sparverius* (AMNH 10511).

GALLIFORMES: Megapodiidae; *Megapodius freycinet* (AMNH 9825). Cracidae; *Mitu tomentosa* (UCV uncat.). Phasianidae; *Coturnix coturnix* (C.J.W. (3)), *Gallus gallus* (C.J.W. (>100)). Meleagridae; *Meleagris gallopavo* (C.J.W.). Opisthocomidae; *Opisthocomus hoazin* (AMNH 2217–2218, 2221, 10793–10794).

GRUIFORMES: Otididae; *Eupodotis afra* (AMNH 7789, USNM 507603), *Chlamydotis undulata* (USNM 503832). Eurypygidae; *Eurypyga helias* (AMNH 4168, USNM 504067, USNM 616106).

CHARADRIIFORMES: Jacanidae; *Hydrophasianus chirurgus* (USNM 615477), *Jacana spinosa* (AMNH 10795, 10797), *J. jacana* (AMNH 10799). Rostratulidae; *Rostratula benghalensis* (AMNH 10801). Charadriidae; *Vanellus miles* (AMNH 10528), *V. cayanus* (AMNH 10416). Scolopacidae; *Calidris minutilla* (AMNH 10509), *Tringa flavipes* (AMNH 10811). Recurvirostridae; *Recurvirostra avosetta* (AMNH 7788). Burhinidae; *Burhinus grallarius* (QM 16005). Glareolidae; *Glareola nuchalis* (AMNH 5057). Thinocoridae; *Thinocorus rumicivorus* (AMNH 10800). Laridae; *Larus argentatus* (AMNH 10361–10362).

COLUMBIFORMES: Pteroclididae; *Pterocles coronatus* (UMMZ 225643), *P. lichtensteinii* (USNM 540003).

PSITTACIFORMES: Psittacidae; *Melopsittacus undulatus* (C.J.W. (2)), *Poicephalus senegalus* (AMNH 8564), *Bolbopsittacus lunulatus* (AMNH 10803).

CUCULIFORMES: Musophagidae; *Tauraco persa* (AMNH 10568), *T. corythaix* (AMNH 8699).

STRIGIFORMES: Tytonidae; *Tyto alba* (AMNH 10512). Strigidae; *Otus choliba* (AMNH 10468), *O. asio* (AMNH 7429).

CAPRIMULGIFORMES: Steatornithidae; *Steatornis caripensis* (AMNH 7677). Podargidae; *Podargus strigoides* (AMNH 10533–10534). Nyctibiidae; *Nyctibius griseus* (AMNH 9127). Aegothelidae; *Aegothales cristatus* (QM 22734). Caprimulgidae; *Chordeiles minor* (AMNH 10513, C.J.W.).

APODIFORMES: Apodidae; *Streptoprocne zonaris* (AMNH 10386). Trochilidae; *Thalaurania furcata* (AMNH 7683), *Campylopterus duidae guaiquinimiae* (AMNH 10474), *Lampornis clemenciae* (AMNH 10515).

COLIIFORMES: Coliidae; *Urocolius macrourus* (AMNH 8481).

TROGONIFORMES: Trogonidae; *Trogon viridis* (AMNH 10424–10425).

CORACIIFORMES: Alcedinidae; *Megaceryle alcyon* (AMNH 8648, 10261), *Chloroceryle amazona* (AMNH 10428). Momotidae; *Eumomota superciliosa* (AMNH 8293), *Momotus momota* (AMNH 9172). Meropidae; *Merops ornatus* (AMNH 7578). Coraciidae; *Eurystomus orientalis* (AMNH 10806). Brachypteraciidae; *Brachypteracias leptosomus* (AMNH 8419). Leptosomatidae; *Leptosomus discolor* (AMNH 2209).

PICIFORMES: Galbulidae; *Brachygalba lugubris* (AMNH 9173), *Galbula albirostris* (AMNH 10387), *G. galbula* (AMNH 7687), *Jacamerops aurea* (AMNH 10390).

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