REGULAR PAPER

COMPARATIVE ANATOMY OF THE SYRINX IN THE TRIBE ARINI (AVES: PSITTACIDAE)

Renato Gaban-Lima and Elizabeth Höfling

Department of Zoology, Institute of Biosciences, University of São Paulo (USP), São Paulo, SP, Brazil.

ABSTRACT

The syrinx is the organ responsible for producing the vast majority of bird sounds. Because its anatomy varies greatly among bird taxa, prior knowledge of variations is extremely important to studies of functional anatomy and phylogenetic systematics. With the aim of accessing and describing morphological variation in birds of the tribe Arini, this paper presents the findings of a comparative analysis of the syrinxes of 156 specimens belonging to 47 species in 22 genera of the tribe. A number of hitherto unknown variations are highlighted and confronted with the knowledge produced to date on the morphology of the syrinx in Psittaciformes. Some of the variations detected occurred in structures probably involved in sound production and this should be taken into consideration in future studies of functional anatomy. Several characters suggest the presence of a phylogenetic signal, given the congruence between their distribution among taxa and the hypotheses regarding monophyletic groupings proposed in the literature. Some of the variations found, including those suggesting a phylogenetic signal, are intraspecifically polymorphic, which reinforces the importance of using series of specimens in studies of syrinx anatomy.

Key words: Comparative-anatomy, Psittacidae, syrinx, trachea, variations

INTRODUCTION

The members of the tribe Arini are neotropical representatives of the order Psittaciformes, which includes cockatoos, cockatiels, parakeets, macaws, parrots, Amazons and related birds. The distribution of Psittaciformes is typically Gondwanian, covering the Neotropical, Ethiopian, Oriental and Australian regions. The tribe Arini includes some 151 species in 31 genera, out of about 355 species in 79 genera comprising the order Psittaciformes [6,18].

The syrinx is the organ of voice in birds and is probably present in all avian species. The anatomy of the syrinx varies widely, even across relatively small groups [1,3,10,11,15], and studies of the organ's comparative anatomy have therefore helped both to establish the mechanisms involved in sound production and modulation [*e.g.* 9,10,11], and to assist in the proposition of phylogenetic and classificatory hypotheses regarding bird taxa [*e.g.* 1,3,15].

The syrinx is supported by a modified skeletal structure at the base of the windpipe. These modifications frequently provide support for the membranes (which vibrate to produce sounds) and muscles (which control air flow as well as tension and position of the membranes and the entire windpipe).

The syrinx is traditionally classified as tracheal, bronchial or tracheobronchial in accordance with its position relative to the tracheal bifurcation [10,11]. This approach to classification is demonstrably subjective, however, since the syrinx can be located near the tracheal bifurcation and its borders may not be very clear-cut. Thus exclusive attribution to any of the above categories is difficult and often controversial. For example, the syrinx in Psittacidae is tracheobronchial for Nottebohm [14] and tracheal for Gaunt and Gaunt [9,10].

In most groups of Aves, the syrinx is delimited cranially by the *tympanum*, a rigid cylinder formed by the firm opposition or fusion of certain skeletal elements [12]. Other modifications to skeletal elements giving support to the membranes and musculature are also observed.

In most cases, the membranes consist of a thin elastic lamina positioned on the wall of the windpipe between the skeletal elements or in the space formed by

---

Correspondence to: Dr. Elizabeth Höfling
Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo (USP), Rua do Matão,Travessa 14, 101, CEP: 05508-900, São Paulo, SP, Brasil. Tel: (55) (11) 3091-7622. E-mail: ehofling@usp.br

reduction of portions of one or more of these elements.

Sound production is controlled in the vast majority of birds solely by the tracheal or extrinsic muscles of the syrinx, which configure the syrinx and trachea appropriately for sound production [4,10]. The *M. sternotrachealis* in most birds originates in the sternum and inserts on the trachea. The *M. tracheolateralis* originates from the glottis, extends laterally along the trachea and inserts on the caudal portion of the trachea or the cranial portion of the bronchi in the region of the syrinx [4,11,12]. Because this muscle often inserts on the syrinx, Beddard [2] and Beddard and Parson [3] consider it as intrinsic to the syrinx. Some avian groups (*e.g.* Passeriformes, Psittaciformes and Steatornithidae) have an independent set of muscles restricted to the syrinx and known as syringeal muscles or intrinsic muscles of the syrinx. The musculature of the trachea and syrinx is innervated by the tracheal branches of the hypoglossocervical nerves (XII cranial nerve) [5].

The purpose of this study was to extend existing knowledge of morphological variations in the syrinx of birds of the tribe Arini and provide information of importance for future research in both functional anatomy and phylogeny.

MATERIAL AND METHODS

The study used 156 specimens belonging to 47 species in 22 of the 31 genera recognised as members of the tribe [6,8,16]. The specimens came from the ornithological collections of Museu Paraense Emílio Goeldi (MPEGA), Museu Nacional do Rio de Janeiro (MN), Museu de História Natural de Taubaté (MHNT), Museu de Zoologia da Universidade de São Paulo (MZUSP), and the Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo (AZUSP). The taxonomic order and nomenclature follow Collar [6], except for adoption of the genus *Gypopsitta* [16], since the genus *Pionopsitta* as mentioned by Collar [6] is not monophyletic [7,16], as well as recognition of the species *G. aurantiocephala* [8] described more recently. Table 1 presents the list of specimens with their respective registration numbers in the collections from which they came, and the common English name.

The windpipe region containing the syrinx was removed for later observation. The musculature and innervation of the syrinx were observed in the material preserved in 70% ethanol (v/v). The skeletal support was observed in material cleared, stained with alizarin red (which dyes calcified structures) and alcian blue (which stains cartilage), and preserved in 80% glycerine (v/v). The syrinxes were observed, described and photographed using a stereomicroscope (Opton TIM 2T) fitted with a digital camera (DCE-01).

The nomenclature used follows *Nomina Anatomica Avium* [12] except for the identification of series of skeletal elements and their individualisation, where the nomenclature is that proposed by Ames [1], considered most suitable when formulating hypotheses of homology between elements. The proposal adopted here separates elements into two series, "A" and "B", according to certain criteria and individualises them by enumeration based on contact between the series. The criteria used for this purpose are as follows: (1) position relative to the *Mem. tympaniformis lateralis* – A elements are cranial, B elements caudal; (2) general composition of the element – A elements are mainly calcified, B elements mainly cartilaginous; and (3) position relative to insertion of the syringeal musculature – B elements are directly under the influence of the *M. syringealis superficialis*, A elements are cranially positioned to the insertion point of the *M. syringealis profundus*.

The main difficulty experienced was in the individualisation of elements and the establishment of hypotheses regarding homologies in character states. Because skeletal elements were numbered according to contact between series A and B, complete reduction, fusion or emergence of a new element led to loss of relations of homology with adjacent elements. Thus, evidence such as fragments, unusual spaces between elements and relations between their general shapes in different species had to be taken into consideration when individualising skeletal parts.

To introduce the terminology used in the study and facilitate comprehension of the text, the first section outlines syrinx morphology in Arini, generally followed by a detailed description of the main variations detected in this study.

RESULTS

General description

The syrinx in Arini is delimited cranially by the *tympanum* (Fig. 1), a cylinder formed by partial or total fusion of several complete A elements creating a ring shape. The ventral and dorsal processes of the *tympanum* extend out from the caudal edge in a roughly triangular shape (Fig. 1).

Caudally to the *tympanum* and attached to it is a pair of roughly flat skeletal pieces positioned laterally to the trachea and supporting the cranial portion of the *Mem. tympaniformis lateralis*, here termed tympanic plates (Fig. 1) (synonymy: paired

Table 1. List of species and specimens analyzed. Ornithological Collections: AZUSP - Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo; MHNT – Museu de História Natural de Taubaté; MZUSP –Museu de Zoologia, Universidade de São Paulo; MNA –Museu Nacional do Rio de Janeiro; MPEGA – Museu Paraense Emílio Goeldi.

Species	Common English names	Specimens
Anodorhynchus hyacinthinus	Hyacinth Macaw	AZUSP1326
Ara ararauna	Blue-and-yellow Macaw	AZUSP664, AZUSP105, AZUSP106, MNA unnum. (3 specimens)
Ara macao	Scarlet Macaw	AZUSP607
Ara severa	Chestnut-fronted Macaw	AZUSP192, AZUSP280, AZUSP281
Orthopsittaca manilata	Red-bellied Macaw	MPEGA7469, MPEGA7470, MPEGA7474, MPEGA7475
Propyrrhura maracana	Blue-winged Macaw	MNA unnum. 46
Propyrrhura auricollis	Yellow-collared Macaw	MNA unnum.30
Diopsittaca nobilis	Red-sholdered Macaw	MNA unnum. (4 specimens)
Guarouba guarouba	Golden Parakeet	AZUSP1316, AZUSP1317, AZUSP1321, MNA unnum. (4 specimens)
Aratinga acuticaudata	Blue-crowned Parakeet	AZUSP502, AZUSP552
Aratinga leucophthalmus	White-eyed Parakeet	AZUSP107, AZUSP108, AZUSP278, AZUSP290
Aratinga solstitialis	Sun Parakeet	AZUSP114
Aratinga auricapilla	Golden-capped Parakeet	MNA unnum.8, MNA unnum.9
Aratinga jandaya	Jandaya Parakeet	MPEGA6125, MPEGA4008, MPEGA3768, MPEGA6381, AZUSP485
Aratinga aurea	Peach-fronted Parakeet	AZUSP500, MPEGA 449, MPEGA6413, MPEGA6414, MPEGA6415, MPEGA6416, MZUSP unnum.(PI297), MZUSP unnum.(PI285), MZUSP unnum.(PI289); AZUSP1310 AZUSP1311
Aratinga pertinax	Brown-throated Parakeet	AZUSP473, AZUSP471
Aratinga cactorum	Cactus Parakeet	AZUSP362
Nandayus nenday	Nanday Parakeet	AZUSP1314, MNA unnum.10
Cyanoliseus patagonus	Burrowing Parakeet	MNA unnum. (1 specimen)
Pyrrhura cruentata	Blue-throated Parakeet	MNA unnum.32
Pyrrhura perlata	Crimson-bellied Parakeet	AZUSP313, AZUSP483, AZUSP347, AZUSP82
Pyrrhura lepida	Pearly Parakeet	MNA unnum, AZUSP1313, AZUSP1325, MPEGA6418, MPEGA6417, MPEGA6419, MPEGA5911, AZUSP81
Pyrrhura picta	Paited Parakeet	AZUSP185, AZUSP187, AZUSP268, AZUSP272, AZUSP186, AZUSP198, AZUSP255
Myiopsitta monachus	Monk Parakeet	AZUSP476, AZUSP480
Forpus passerinus	Green-rumped Parrotlet	AZUSP877
Forpus crassirostris	Blue-winged Parrotlet	AZUSP unnum., AZUSP679, AZUSP671
Brotogeris tirica	Plain Parrotlet	AZUSP557
Brotogeris chiriri	Yellow-chevroned Parakeet	AZUSP1312, AZUSP482
Brotogeris chrysopterus	Golden-winged Parakeet	AZUSP253, AZUSP254
Brotogeris versicolorus	Canary-winged Parakeet	AZUSP873, MPEGA409, MPEGA410, MPEGA411, MPEGA412
Touit huetii	Scarlet-shouldered Parrotlet	MPEGA7467, MPEGA7468, MPEGA7473
Pionites leucogaster	White-bellied Parrot	AZUSP1315, AZUSP241, AZUSP247, MPEGA prov. num. AMZ350
Pionites melanocephala	Black-crowned Parrot	AZUSP88, AZUSP89, AZUSP118, MNA unnum. (1 specimen)
Pionopsitta pileata	Pileated Parrot	AZUSP499, AZUSP689, AZUSP131919, AZUSP85, AZUSP84, AZUSP484, MNA unnum. (1 specimen)
Gypopsitta barrabandi	Orange-cheeked Parrot	MNA unnum.43, MNA unnum.44
Gypopsitta vulturina	Vulturine Parrot	MPEGA4959, MPEGA4955, MPEGA4958, MPEGA4957
Gypopsitta aurantiocephala	Bald Parrot	AZUSP199, AZUSP221, AZUSP256, AZUSP383
Graydidascalus brachyurus	Short-tailled Parrot	MPEGA439, MNA unnum. (2 specimens)
Pionus menstruus	Blue-headed Parrot	MPEGA6780, MPEGA4003, MPEGA453, MPEGA454, AZUSP189, AZUSP271
Amazona pretrei	Red-spectacled Amazon	MHNT unnum.
Amazona brasiliensis	Red-tailed Amazon	AZUSP692
Amazona xanthops	Yellow-faced Amazon	MNA unnum.29
Amazona aestiva	Blue-fronted Amazon	AZUSP360
Amazona ochrocephala	Yellow-crowned Amazon	AZUSP70
Amazona amazonica	Orange-wing Amazon	AZUSP123, AZUSP661, MZUSPs/no, MNA unnum. (4 specimens)
Deroptyus accipitrinus	Red-fan Parrot	AZUSP595, MPEGA6779, MNA unnum. (1 specimen), MZUSP unnum.
Triclaria malachitacea	Blue-bellied Parrot	AZUSP1318, AZUSP90, AZUSP687, AZUSP178, AZUSP875, MNA unnum. (1 specimen)

protrusions [13]; *tympanum* [14]; element T1 [9,10]; tracheosyringeal elements 5 and 6 in *Ara ararauna*, 7 and 8 in *Myopsitta monachus*, and 6 in *Melopsittacus undulatus* – [11,12]). The tympanic plates are interpreted for present purposes as being element A1 (Fig. 1) medially divided both ventrally and dorsally. The ventral and dorsal processes of the tympanic plates extend out from their caudal edge, one at the ventral vertex and the other at the dorsal (Fig. 1). Two regions are delimited in these plates (Fig. 2): (1) thick and spongy, similar to the A elements constituting the *tympanum*, occupying the most cranial portion including the caudal processes and their ventral, dorsal and cranial edges; (2) thin membranous calcified tissue, occupying the caudal portion of the plates as far as the caudal edge.

B elements are always pairs and medially incomplete (Fig. 1). The most cranial B elements are generally concave cranially and have a flat lateral region that varies considerably in length. In a caudal direction these regions taper, together with the cranial concavity, until they disappear. The most caudal elements are positioned more dorsally and are more slender (Fig. 1).

The *Mem. tympaniformis laterales* (Fig. 1) are supported cranially by the tympanic plates and caudally by element B1. Besides the *Mem. tympaniformis laterales*, some authors note the presence of another pair of membranes in Psittacidae, the *Mem. tracheosiringeales*, occupying the space bounded by the extremities of certain B elements, by the ventral and dorsal edges of the tympanic plates, and by the extremities of the ventral and dorsal processes of the *tympanum*.

The Arini have two pairs of tracheal muscles, the *M. tracheolateralis* and the *M. sternotrachealis*.

The *M. tracheolateralis* was present in all the specimens analysed. Its origin was not observed in all species, since the cranial portion of the trachea and the region of the larynx was preserved only in some specimens. Where observed, the origin was always the cricoid cartilage (*cartilago cricoidea*). From there it extended laterally and inserted laterally on the *tympanum* (Fig. 3). In all species analysed here, the *M. tracheolateralis* inserted under the *M. syringealis superficialis* as far as the *M. syringealis profundus*. Fibres of the *M. tracheolateralis* were frequently observed adjoining fibres of the syringeal muscles. Muscle fibres were often seen extending out from one *M. tracheolateralis* towards the other. This was more frequently observed on the ventral face than the dorsal.

In all specimens analysed the *M. sternotrachealis* originated through fibrous connective tissue close to the point where the bronchi cross the peritoneum between the cavity containing the syrinx and the cavity containing the heart and lungs. This peritoneum was identified as the *septum obliquum* according to Gaunt and Gaunt [9]. In all specimens this muscle inserted laterally and ventrally on the trachea and was attached lateroventrally by a narrow flat aponeurosis, continuing in a caudal direction as a tendon (Fig. 3). It was laterally attached by fasciae to the *M. syringealis superficialis*, where it formed a groove (Fig. 3) that varied in width and depth. Cranially the pair of *M. sternotrachealis* was attached to the trachea by fasciae and was ventrally positioned relative to it until they joined the trachea medially (Fig. 3). This junction was slightly skewed to the left in all specimens.

In addition to these tracheal muscles, the Arini have two pairs of syringeal muscles: the *M. syringealis superficialis* (Figs. 1 and 3) originates laterally from the *tympanum* and inserts laterally on the bronchi, while the *M. syringealis profundus* (Figs. 1 and 3) originates laterally from the *tympanum* and inserts on the caudal portion of the tympanic plates and the cranial portion of the *Mem. tympaniformis lateralis*.

Main Variations

Skeletal elements

The number of A elements fused in the *tympanum* varied both intraspecifically and interspecifically (Figs. 4 and 5). Pieces were observed with as few as two fused A elements and as many as six. Even with this degree of intraspecific variation, a certain pattern of variation was detected among the species studied. The *tympanum* was formed by only two or three A elements in *Anodorhynchus*, *Ara*, *Propyrrhura*, *Orthopsittaca*, *Diopsittaca* (except one specimen), *Aratinga acuticaudata*, *A. pertinax* and *Guarouba*, whereas three, four or five A elements were involved in *Aratinga leucophthalmus, A. solstitialis, A. auricapilla, A. jandaya, A. aurea, Cyanoliseus, Pyrrhura* (for which a larger proportion of specimens had only two elements in the tympanum) and *Pionites*. All specimens of *Triclaria* and *Deroptyus* had four fused elements. In *Brotogeris*, *Forpus*, *Touit*, *Gypopsitta*, *Pionopsitta*, *Pionus*, *Graydidascalus* and *Amazona*, the tympanum varied in size and had four or five fused elements.

In some cases (*Ara, Propyrrhura, Orthopsittaca, Aratinga acuticaudata, A. aurea, A. pertinax,*

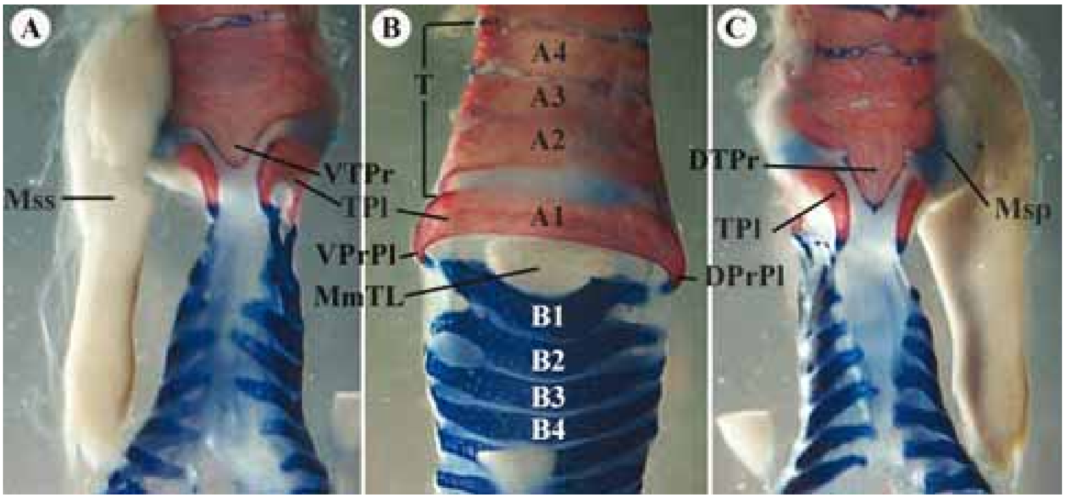

Figure 1. Ventral (**A**), left lateral (**B**) and dorsal (**C**) views of syrinx in *Aratinga aurea* (specimen AZ500). A_1, A_2, A_3, A_4 – cranial skeletal elements B_1, B_2, B_3, B_4 – caudal skeletal elements. **Mss** – *M. syringealis superficialis*, **Msp** – *M. syringealis profundus*, **MmTL** – *Mem. tympaniformis lateralis*, **T** – *tympanum*, **VTPr** – ventral tympanic process, **DTPr** – dorsal tympanic process, **TPl** – tympanic plate, **VPrPl** – ventral process of the tympanic plate, **DPrPl** – dorsal process of the tympanic plate. Bar: 1 mm.

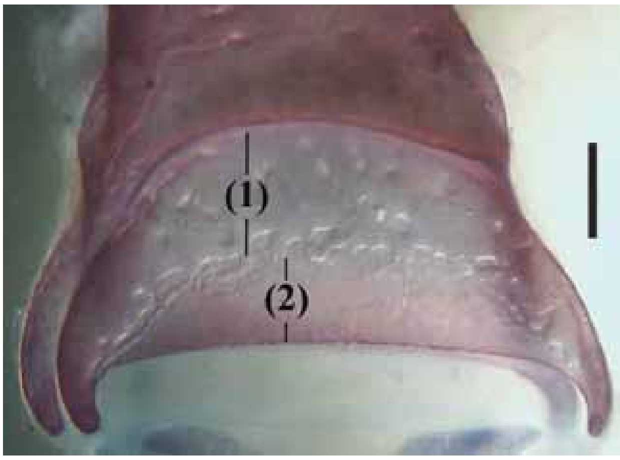

Figure 2. Lateral view of syrinx showing spongy (**1**) and membranous (**2**) areas of tympanic plate (*Pionus menstruus* – MPEGA6780). Bar: 1 mm.

Guarouba, Pyrrhura and *Deroptyus*), the external diameter of the *tympanum*, seen ventrally or dorsally, was uniform (Fig. 4). In *Nandayus, Aratinga solstitialis, A. jandaya, A. auricapilla* and *Cyanoliseus*, the diameter of the *tympanum* tapered caudally (Fig. 4). The external diameter of the tympanum increased in the region of element A2 in *Diopsittaca* and *Aratinga leucophthalmus* (Fig. 4). The diameter increased in the region of A3 in *Myiopsitta, Brotogeris, Forpus, Touit, Pionopsitta, Gypopsitta, Graydidascalus, Pionus* and *Amazona* (Fig. 4). In *Anodorhynchus* and *Pionites*, the external diameter of the *tympanum* seen ventrally increased from element A4 (Fig. 4).

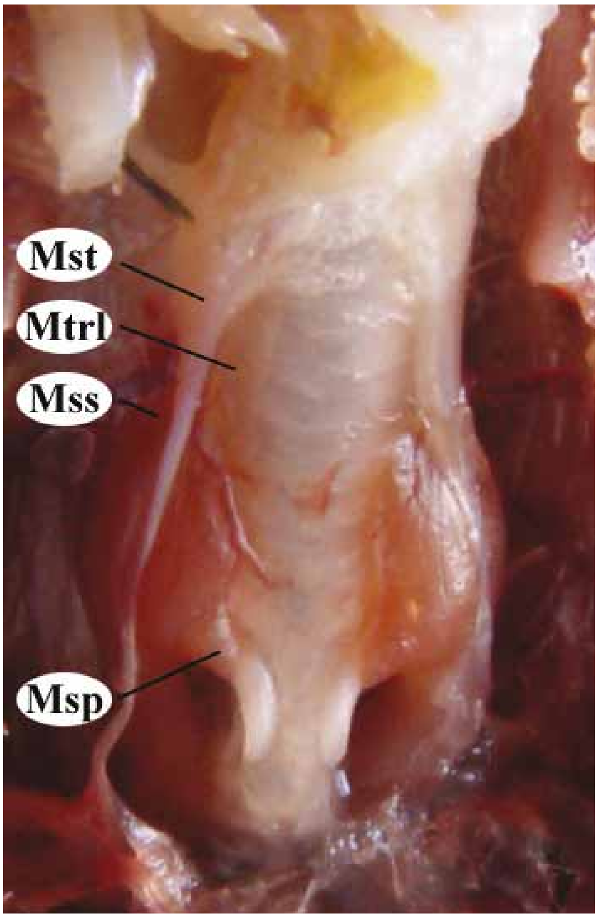

Figure 3. Ventral view of the syrinx showing the tracheal and syringeal muscles (*Pionites leucogaster*, MPEGA prov.num. AMZ350). **Mst** - *M. sternotrachealis*, **Mtrl** – *M. tracheolateralis*, **Mss** – *M. syringealis superficialis*, **Msp** – *M. syringealis profundus*.

At the caudolateral edge of the *tympanum*, where it joins the tympanic plates, a cotyloid articular surface holding these plates was frequently observed. This cotyloid joint formed by a thickening of the *tympanum* wall was present in *A. aurea*, *Pyrrhura*, *Myiopsitta*, *Brotogeris*, *Forpus*, *Touit*, *Pionites*, *Pionopsitta*, *Gypopsitta*, *Graydidascalus*, *Pionus*, *Amazona*, *Deroptyus* and *Triclaria*. The overall shape of the ventral and dorsal processes of the *tympanum* also varied. In some cases, *e.g. Brotogeris*, *Forpus*, *Touit*, *Pionopsitta*, *Gypopsitta*, *Graydidascalus*, *Pionus*, *Amazona* and *Triclaria* (Fig. 4), they were acute and narrow, with the base corresponding to 70% of the height. In others, conversely, they were obtuse and broad, with the base corresponding to more than 100% of the height: examples included *Anodorhynchus, Ara, Propyrrhura, Orthopsittaca, Aratinga, Guarouba, Cyanoliseus, Pyrrhura, Myiopsitta* and *Amazona xanthops* (Fig. 4). Intermediate categories with the base corresponding to between 70% and 100% of the height included *Diopsittaca* and *Pionites* (Fig. 4). In *Deroptyus* this character was polymorphic. The lateral edges of the ventral processes (Fig. 4) and dorsal processes of the *tympanum* were straight, slightly concave or convex. This character presented extreme intraspecific variation. The size of the base and the height of the ventral process of the *tympanum* were often different from those of the dorsal process, the one being larger or smaller than the other, or both being equal. These characters also displayed considerable intraspecific variation.

The shape of the tympanic plate in a lateral view displayed significant variation in the specimens analysed. It was roughly rectangular with the ventral edges parallel to the dorsal and the cranial edges parallel to the caudal, or roughly trapezoidal with cranially converging ventral and dorsal edges. In *Amazona*, *Brotogeris*, *Deroptyus*, *Touit*, *Forpus*, *Graydidascalus*, *Myiopsitta*, *Pionites*, *Gypopsitta*, *Pionopsitta*, *Pionus* and *Triclaria*, the tympanic plate was trapezoidal, with the ventral and dorsal edges clearly converging cranially (Fig. 5). In *Anodorhynchus*, *Ara*, *Orthopsittaca*, *Aratinga*, *Guarouba*, *Propyrrhura* and *Pyrrhura*, it was more rectangular or square (Fig. 5). The height of this piece (in the craniocaudal direction) also varied in proportion to the base (ventrodorsal). *Propyrrhura, Ara, Orthopsittaca, Aratinga, Brotogeris, Myiopsitta, Pionites* and *Pyrrhura* had clearly shorter tympanic plates than *Touit, Amazona, Forpus, Graydidascalus, Pionopsitta Gypopsitta, Pionus* and *Triclaria* (Fig. 5). In *Guarouba* this character was polymorphic.

The shapes of the cranial, caudal, ventral and dorsal edges of the tympanic plates also varied. The cranial edge was straight, slightly convex or extremely convex, in this latter case assuming a semicircular shape (Fig. 5). The caudal edge varied from concave in some cases to straight in others (Fig. 5). The ventral and dorsal edges varied between straight and convex (Fig. 5). These characters were highly plastic in the specimens analysed.

The proportion occupied by the membranous region of the tympanic plates also varied. In some cases the plate consisted only of spongy tissue, while in others it was made up solely of an arc corresponding to the entire ventral, cranial and dorsal edge. A range of intermediate conditions were observed between these two extremes (Fig. 5). The membranous region occupied a large area in *Aratinga pertinax*, *Pyrrhura*, *Myiopsitta*, *Forpus*, *Touit* and *Pionites.*

The caudal processes of the tympanic plates were partially cartilaginous in most taxa. However, in *Pionopsitta*, *Gypopsitta*, *Graydidascalus*, *Pionus*, *Amazona* and *Triclaria* these processes were completely calcified in most specimens (Fig. 5). In *Deroptyus* they were completely cartilaginous (Fig. 5).

The ventral processes of the tympanic plates were often thinner than the dorsal processes. However, in several specimens of *Pionopsitta*, *Gypopsitta*, *Graydidascalus*, *Pionus*, *Amazona* and *Triclaria*, both had the same thickness (Fig. 5).

The size of the caudal processes of the tympanic plates was another feature that varied in the specimens analysed. These processes were evidently smaller in *Aratinga solstitialis*, *A. auricapilla*, *A. jandaya* and *Nandayus* (Fig. 5).

In some cases, both the ventral and dorsal processes of the tympanic plates pointed entirely in a caudal direction; in others they pointed slightly or entirely toward the frontal plane. This feature also displayed intraspecific variation. These processes were completely curved in most specimens of *Anodorhynchus*, *Ara ararauna*, *A. macao*, *Propyrrhura*, *Orthopsittaca*, *A. leucophthalmus*, *Nandayus*, *A. solstitialis*, *A. auricapilla* and *A. aurea* (Fig. 5). The curvature was slight in most specimens of *Ara severa*, *Aratinga acuticaudata, A. pertinax, A. cactorum, Guarouba, Pyrrhura, Myiopsitta, Brotogeris, Forpus, Touit* and *Pionites* (Fig. 5). In most specimens of *Pionopsitta, Gypopsitta, Graydidascalus, Pionus, Amazona,*

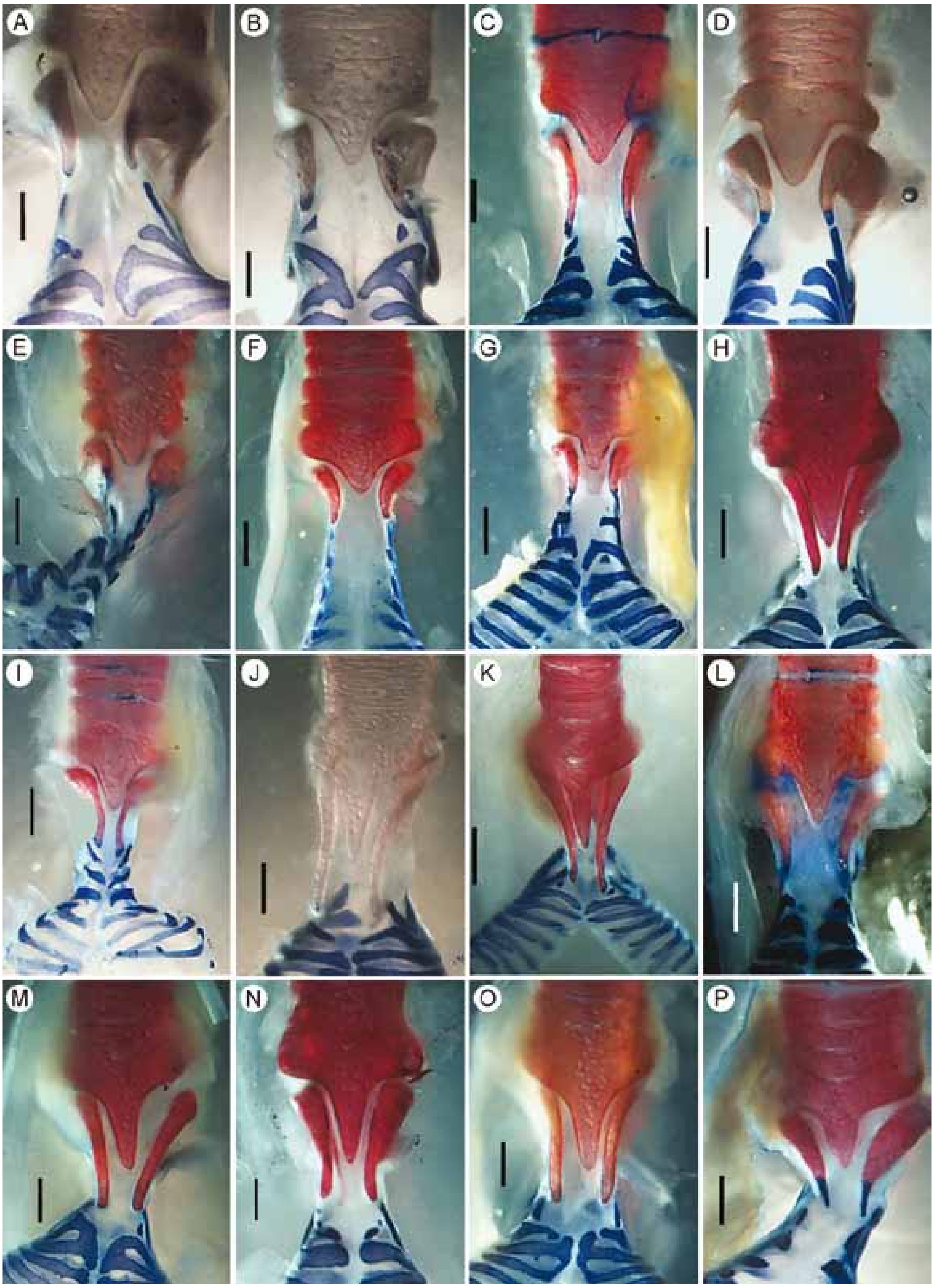

Figure 4. Ventral view of syrinx in Arini: (**A**) AZUSP192 - *Ara severa*; (**B**) MPEGA7474 - *Orthopsittaca manilata*; (**C**) AZUSP1321 **-** *Guarouba guarouba*; (**D**) AZUSP108 - *Aratinga leucophthalmus*; (**E**) AZUSP114 - *Aratinga solstitialis*; (**F**) AZUSP1310 - *Aratinga aurea*; (**G**) MNA unnum. - *Phyrrhura lepida*; (**H**) MPEGA 409 - *Brotogeris versicolorus*; (**I**) AZUSP476 - *Myiopsitta monachus*; (**J**) MPEGA7473 - *Touit huetii*; (**K**) AZ670 - *Forpus crassirostris*; (L) AZUSP1315 - *Pionites leucogaster*; (**M**) AZUSP686 - *Pionopsitta pileata*; (**N**) AZUSP256 - *Pionopsitta aurantiocephala*; (**O**) AZUSP687 - *Triclaria malachitacea*; (**P**) AZUSP595 - *Deroptyus accipitrinus*. Bar: 1 mm.

Deroptyus and *Triclaria*, they pointed completely in a caudal direction (Fig. 5).

Only in *Orthopsittaca manilata* was a cartilaginous piece found to be aligned with the caudal processes of the tympanic plates, positioned medially to the ventral extremities of the first B elements (Fig. 5B).

The region of the windpipe supported by paired and medially incomplete B elements corresponds to the bronchi. A laterally flat area was frequently observed in the cranial portion of this region (Figs. 1, 3 and 4), but in some cases (*Myiopsitta* and *Brotogeris*) the area included a slight depression close to the frontal plane.

Although the B elements were entirely cartilaginous in most cases, a certain amount of calcification was observed in some cases, often only in the lateral portion of some elements (*Amazona, Pionus* and *Graydidascalus*), or only at the dorsal extremities (*Gypopsitta*).

The cranial edge of element B1 was strongly concave in most cases. However, the concavity was slight in *Brotogeris* (Fig. 5H) and absent in *Nandayus*, *Aratinga sostitialis, A. jandaya, A. auricapilla* and *Myiopsitta* (Fig. 5). In species of the genus *Gypopsitta* the concavity was present but irregular (Fig. 5K).

The space between the caudal edge of the tympanic plate and the first B element, occupied by the *Mem. tympaniformis lateralis*, was extremely reduced in *Nandayus, Aratinga solstitialis, A. auricapilla* and *A. jandaya* (Fig. 5E).

In most cases the thickness of element B1 was roughly the same as that of element B2. However, in *Aratinga aurea* and *A. cactorum* the thickness of element B1 was usually twice that of B2, and its terminal portions were narrower than the medial portions (Fig. 5F). In *Orthopsittaca* the thickness of element B1 was roughly three times that of the adjoining element, and its medial portions were broader than the terminal regions (Fig. 5B).

In several cases, the first cartilaginous piece in a caudal position relative to the membrane appeared to have been formed by fusion of the first two B elements, as it was distinctly broader than the following element (probably B3) and the extremities of elements B1 and B2 were observed dorsally and/or ventrally, sometimes as vestiges. In some cases, this piece was reduced at the ventral extremity of element B2 and had a tendency to fusion at the dorsal extremities; the lateral dimension of the piece was no larger than that of the B element that followed caudally (*Pyrrhura*) (Fig. 5G). In other cases, the lateral dimension of the piece was about twice that of the adjoining element, the ventral extremity of element B2 was always reduced and the dorsal element was often apparent (*e.g.* in *Pionites*) (Fig. 5J) or fused with the ventral extremity of element B1 (*e.g.* in *Forpus* and *Touit*) (Fig. 5M-N). There were also cases where this piece was broader, reaching at least three times the breadth of element B3, and usually with the dorsal terminal portion of element B2 detectable but not the ventral (*Pionopsitta*, *Gypopsitta*, *Graydidascalus*, *Pionus*, *Amazona* and *Triclaria*) (Fig. 5K, 5O-P). The ventral terminal portion was reduced by varying amounts and was frequently replaced by a cartilaginous fragment (Fig. 5).

The ventral and dorsal terminal portions of the most cranial B elements varied considerably in shape, without a clear pattern of variation among the taxa studied. In other words, they appeared to vary randomly. In some cases, these terminal regions were dilated; in others, they curved caudally with varying intensity and the extremities of the B elements were sometimes even fused on either side (Fig. 4). In some cases, there were cranial and caudal projections from these extremities (Fig. 5).

Musculature

In *Aratinga jandaya* the *M. tracheolateralis* were highly developed. In two extreme cases (specimens MPEGA 3768 and AZUSP 485) they were fused ventromedially. No such condition was observed in any other species analysed.

Insertion of the *M. syringealis superficialis* was fleshy in most cases, while in some cases it was tendinous (*Diopsittaca, Aratinga acuticaudata, Guarouba, Nandayus, Aratinga solstitialis, A. jandaya* and *A. auricapilla*) or intermediate, with muscle fibres not quite touching the B elements but connected to them and sheathed in fibrous connective tissue that did not assume the form of a tendon (*Propyrrhura, Aratinga pertinax* and *A. cactorum*).

In most cases, the *M. syringealis profundus* was visible under the *M. syringealis superficialis*. However, in species of the genus *Pyrrhura* (except *P. perlata*) the *M. syringealis profundus* was completely covered dorsally by the *M. syringealis superficialis*.

Both the *M. syringealis superficialis* and *M. syringealis profundus* displayed varying degrees of development. In *Nandayus, Aratinga auricapilla, A. solstitialis* and *A. jandaya*, the caudal half of the *M.*

syringealis superficialis consisted almost exclusively of a tendon. The *M. syringealis profundus* varied from low development (restricted to the lateral portion of the *tympanum* in *Anodorhynchus, Ara ararauna, A. macao, Orthopsittaca, Diopsittaca, Aratinga cactorum, A. leucophthalmus, A. aurea* and *Pyrrhura*) to intermediate development (occupying about half the *tympanum* in *Ara severa, Aratinga pertinax, Cyanoliseus, Touit, Pionites, Pionopsitta, Gypopsitta, Pionus, Amazona, Deroptyus* and *Triclaria*) or high development (when the muscle pairs almost met medially, as in *Propyrrhura, Guarouba, Nandayus, A. solstitialis, A. auricapilla, A. jandaya, Myiopsitta, Brotogeris* and *Forpus*).

The position of syringeal muscle origin varied relative to the A elements. The reference for this position was the point of contact between the *M. syringealis superficialis* and the *M. syringealis profundus* in the lateral portion of the *tympanum*. This point was found to vary from contact between

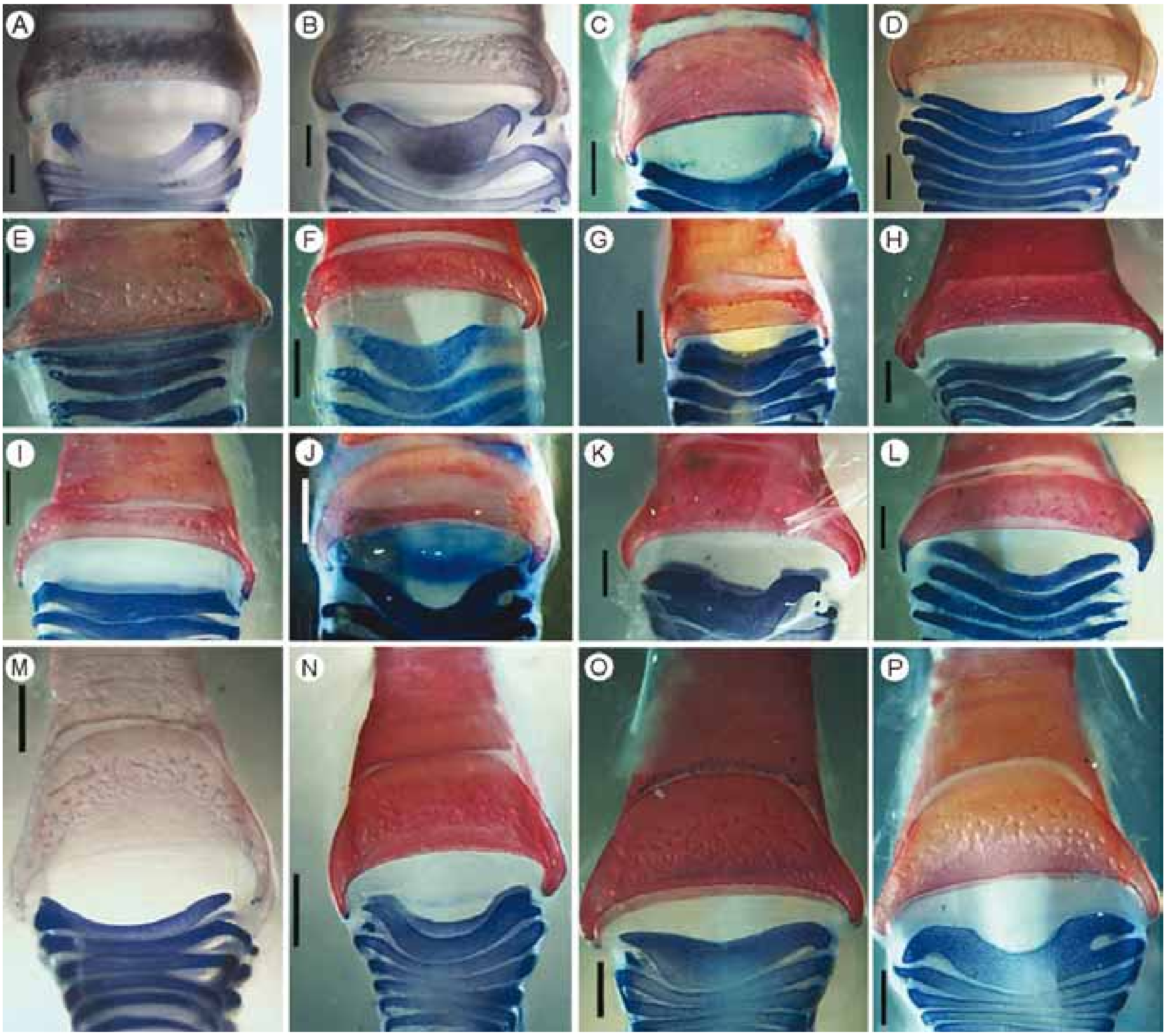

Figure 5. Lateral view of syrinx in some Arini: (**A**) AZUSP192 - *Ara severa*; (**B**) MPEGA7474 - *Orthopsittaca manilata*; (**C**) AZUSP1321**-** *Guarouba guarouba*; (**D**) AZUSP108 - *Aratinga leucophthalmus*; (**E**) AZUSP114 - *Aratinga solstitialis*; (**F**) AZUSP1310 - *Aratinga aurea*; (**G**) MNA unnum. - *Phyrrhura lepida*; (**H**) MPEGA 409 - *Brotogeris versicolorus*; (**I**) AZUSP476 - *Myiopsitta monachus*; (**J**) AZUSP1315. - *Pionites leucogaster*; (**K**) AZUSP256 - *Pionopsitta aurantiocephala*; (**L**) AZUSP595 - *Deroptyus accipitrinus;* (**M**) MPEGA7473 - *Touit huetii*; (N) AZUSP670 - *Forpus crassirostris*; (**O**) AZUSP686 - *Pionopsitta pileata*; (**P**) AZUSP687 - *Triclaria malachitacea*. Bar: 1 mm.

elements A2 and A3 to contact between elements A5 and A6. This character also displayed considerable intraspecific variation.

The length of syringeal muscle origin also varied intraspecifically to a significant extent, with no detectable pattern among the taxa analysed. *M. syringealis superficialis* origin varied from one A element to four A elements. *M. syringealis profundus* origin varied from one to three elements.

The length of *M. syringealis superficialis* insertion also varied considerably, from one B element to as many as seven.

Innervation

It was not possible to verify syrinx innervation in all specimens. What could be observed was that the tracheosyringeal branches (*R. tracheossyringealis*) of the hypoglossocervical nerve (*N. hypoglossocervicalis*) extended laterally along the cranial portion of the trachea in a caudal direction up to a certain point, where the right-hand branch turned ventrally to the left, sometimes being fused in this region, or proceeded parallel to each other in a caudal direction and fused in a more caudal position. The presence and dimensions of this plexus varied intraspecifically. The branches separated caudally and each then extended to either half of the syrinx. Only two branches left the plexus in most cases, but some specimens had three or even four branches in a caudal direction. On reaching the windpipe region corresponding to the syrinx, each branch divided into two: the lateral portion innervated the *M. syringealis superficialis*, while the medial portion crossed the *M. syringealis superficialis* and innervated the *M. syringealis profundus*.

DISCUSSION

The morphology of the syrinx in Psittaciformes and the great many variations observed make it possible to recognise the main homologous structures for the species analysed, i.e. muscles, membranes, tympanic plates, processes, etc.

The nomenclature proposed by Ames [1] for the skeletal support was found appropriate to assure more precise recognition of the two series of skeletal elements in the different species, thanks to the use of distinct criteria for this purpose, rather than one as nomenclature proposed by King [12] based solely on the element's position relative to the site of tracheal bifurcation. The criteria used here (topographical relations: positions of elements relative to membranes and muscles; and ontogenetic relations: via indirect evidence such as calcification and consistency of elements) proved more adequate than the single criterion adopted by King [12]. The latter is too imprecise for observation of the syrinx in Psittacidae, since in this case tracheal bifurcation is not due to a skeletal piece as it is in other avians. The inadequacy of *Nomina Anatomica Avium* [12] for individualisation of skeletal elements in Psittacidae is evidenced in the literature [11], where the first element caudal to the *Mem. tympaniformis lateralis* – B1 in the present paper – is recognised as 7 in *Ara ararauna* and 9 in *Myopsitta monachus*.

A comparison of the descriptions presented here with those found in the literature [3,10-13] shows the existence of a general pattern for the syrinx in Psittaciformes not found in any other group of birds and involving the existence of several diagnostic characteristics for the order (*e.g.* the *M. sternotrachealis* originating from the *septum obliquum*, the *M. syringealis superficialis* and *M. syringealis profundus*, the tympanic plates, and the caudal processes of the *tympanum*). In a phylogenetic context where the order is clearly monophyletic, these characteristics must be seen as synapomorphies of the order.

According to King [11], the number of elements in the *tympanum* of Psittacidae varies from four to six. The present study shows that there are species which may have specimens with only two elements forming this piece.

Nottebohm [14] assumes that the tympanic plates (which he calls the *tympanum*) are formed by the fusion of certain skeletal elements, while King [11] interprets them as being formed by two elements. Gaunt and Gaunt [9] recognise that because this piece is divided medially it may possibly derive from the broadening (or fusion) and calcification of bronchial half-rings. However, none of the above-mentioned authors presents the evidence on which such interpretations are based. Our analysis of specimens from the tribe Arini did not bring to light any evidence that this piece is formed by more than one skeletal element or by modification of a B element (according to composition and consistency, both identical to those of A elements). Beddard and Parson [3] state that the bronchial elements (B) are ossified in *Chrysotis* (=*Amazona*), *Pyrrhulopsis* (=*Touit*), *Pionus, Trichoglossus*, *Lorius*, *Psittacus*, *Tanygnathus*, *Eos*, *Polyteles*, *Platycercus* and *Poicephalus*. However, in species of the genera *Amazona*, *Touit* and *Pionus* the B elements are mainly cartilaginous, which agrees with observations of the species dissected by Gaunt and Gaunt [9]. Beddard and Parson [3] were probably mistaken because at the time there were no specific dyes for cartilaginous and calcified structures as there are today.

Although Beddard and Parson [3] recognise the first piece caudal to the *Mem. tympaniformis lateralis* in *Amazona* and *Pionus* as being formed by the fusion of two bronchial elements (here recognised as B1 and B2), Nottebohm [14] recognises this piece in *Amazona amazonica* as a single skeletal element. The present study shows that this fusion also occurs in other genera. The flimsy cartilage on which the *M. syringealis profundus* inserts, observed by Nottebohm [14] to be positioned over the tympanic plates, has not been observed by any other authors and was not found in any of the specimens analysed here.

According to Gaunt and Gaunt [9], the *M. tracheolateralis* is usually underdeveloped, when present at all, and they say they did not study its role in vocalisation for that reason. In all species studied here, however, the *M. tracheolateralis* was easily delimited, and it was especially well-developed in *Aratinga jandaya*. The constant presence of this muscle could indicate its contribution in vocalisation and/or in ventilation (maintaining a tension in trachea and keeping the syringeal lumen opened during respiration) in Psittacidae, as well as in many other groups of Aves [4,10].

The presence of *M. tracheolateralis* fibres close to syringeal muscle fibres, as in some Passeriformes [1,15], may be evidence that the syringeal muscles develop out of the caudal portion of the *M. tracheolateralis*.

Asymmetry similar to that found in the position of the *M. sternotrachealis* relative to the trachea has been observed in other birds. According to Ames [1] and Prum [15], this asymmetry is due to the fact that the trachea is to the right of the spinal column in the cervical region and due to the oval cross-section of the windpipe, which is ventrodorsally compressed and rotated to the right. The anatomy of the syrinx in the sample universe displayed several hitherto unknown characteristics. Recognition of these variations provides an array of new information that is important both for studies of the functional anatomy of the syrinx in Psittaciformes and for researchers who use differences among taxa for phylogenetic reconstruction.

There is no consensus on the number of functional membranes in the syrinx of Psittacidae. King [11] recognises the *Mem. tracheosyringeales*, positioned medially to the windpipe and supported by the tympanic plates and first B elements; the *Mem. tympaniformis laterales*, situated laterally between two concave skeletal elements (one cranially, the other caudally); and the *Mem. tympaniformis mediales*, positioned medially in the cranial portion of the bronchi. Nottebohm [14] found, through histological sections, that the internal epithelium of the *Mem. tympaniformis lateralis* differed from the epithelium lining the rest of the syrinx and trachea (including the *Mem tracheosyringealis* and *Mem. tympaniformis medialis*), while Gaunt and Gaunt [9] concluded that the only functional membranes in Psittacidae were the *Mem. tympaniformis laterales*. Two mechanisms of sound production by the syrinx in Psittaciformes are recognised in the literature [9,10,14]. One involves vibration of the *Mem. tympaniformis lateralis*. The other involves the formation of a slit in the region of this membrane, generating a whistle-like sound. The two mechanisms may interact. The variations detected here in the size and shape of the *Mem. tympaniformis lateralis* and in the shapes of the structures that contribute to the formation of the slit – the caudal edges of the tympanic plates and their processes, and the cranial edge of the first B element – furnish new information to be taken into consideration in future research on sound production by these birds.

Experiments involving the sectioning of the right and left tracheal branches of the hypoglossocervical nerves cranially and caudally to the plexus in *Amazona amazonica* [14] suggest an exchange of nerve fibres between the two branches in this region, enabling either brain hemisphere to control the syrinx [14]. However, because this plexus was not found in all the specimens analysed, it is possible that normal vocalisation in those specimens without the plexus is produced with the contribution of the two tracheal branches of the hypoglossocervical nerves. Some of the variations detected were distributed among the taxa studied in a manner congruent with the hypotheses on phylogenetic relationships found in the literature [7,16,17,19]. This congruence can be interpreted as evidence of a phylogenetic signal in some of these variations, reinforcing the relevance of syrinx anatomy as a source of characters for studies in phylogenetic systematics.

The descriptions of the variations detected show that some characters are intraspecifically polymorphic while other are not. The evidence of a phylogenetic signal in the intraspecifically polymorphic characters suggests their usefulness for research on systematics provided such polymorphisms are recognised and the pattern of variation is detected, as is feasible only when the investigation comprises a series of individuals.

ACKNOWLEDGMENTS

This article is dedicated to Professor Carminda da Cruz Landim, who was an outstanding example as both teacher and scientist in the life of one of the authors (EH). The authors would like to thank the following institutions and collection curators responsible for lending the specimens used: Museu Paraense Emílio Goeldi (MPEGA), Museu Nacional do Rio de Janeiro (MN), Museu de História Natural de Taubaté (MHNT), Museu de Zoologia da Universidade de São Paulo (MZUSP). We are also grateful to CAPES and FAPESP (98. 12672-1) for research grants to RGL and to CNPq for a research grant to EH; to Valquiria Badini Tronoloni for her helps with the figures, Kevin Mundy for the English version and Dr. Grabriël J.L. Beckers and one of anonimous reviewers for suggesting improvements to the manuscript.

REFERENCES

1. Ames PL (1971) The morphology of the syrinx in passerine birds. *Peabody Mus. Nat. Hist. Yale Univ.* **37**, 1-194.
2. Beddard FE (1898) *Structure and Classification of Birds.* Longsman, Green and Co.: London.
3. Beddard FE, Parson FG (1893) On certain points in the anatomy of parrots bearing their classification. *Proc. Zool. Lond.* **1893,** 506-514.
4. Brackenbury JH (1989) Functions of the syrinx and the control of sound production. In: *Form and Function in Birds.* Vol. 4. (King AS, McLelland J, eds) pp. 193-220. Academic Press: London.
5. Bubién-Waluszewska A (1981) The cranial nerves. In: *Form and Function in Birds.* Vol. 2. (King AS, McLelland J, eds) pp. 385-438. Academic Press: London.
6. Collar NJ (1997) Family Psittacidae (Parrots). In: *Handbook of the Birds of the World***.** Vol. 4 (del Hoyo J, Elliot AE, Sargatal J, eds). pp. 280-477. Lynx Edition: Barcelona.
7. Gaban-Lima R, Ribas CC, Höfling E, Miyaki CY (2003) O gênero *Pionopsitta* (Aves; Psittacidae) como um grupo não monofilético: evidências baseadas em caracteres morfológicos e moleculares. *Resumos do XI Congresso Brasileiro de Ornitologia.* Feira de Santana (BA), Brazil, 23-28 de novembro de 2003.
8. Gaban-Lima R, Raposo M, Höfling E (2002) Description of a new species of *Pionopsitta* (Aves, Psittacidae) endemic to Brazil. *Auk* **119**, 815-819.
9. Gaunt AS, Gaunt SLL (1985) Electromyographic studies of the syrinx in parrots (Aves, Psittacidae). *Zoomorphology* **105,** 1-11.
10. Gaunt AS, Gaunt SLL (1985) Syringeal structure and avian phonation. In: *Current Ornithology.* Vol. 2. (Johnston RF, ed). pp. 213-245. Plenum Press: New York.
11. King AS (1989) Functional anatomy of the sirynx. In: *Form and Function in Birds.* Vol. 4. (King AS, McLelland J, eds) pp. 105-192. Academic Press: London.
12. King AS (1993) Apparatus Respiratorius. In: *Handbook of Avian Anatomy: Nomina Anatomica Avium.* 2nd edn. (Baumel JJ, King AS, Breazile JE, Evans HE, Berge JC, eds). pp. 257-299. Nuttall Ornithological Society: Cambridge.
13. Larsen ON, Goller F (2002) Direct observation of syringeal muscle function in songbirds and parrot. *J. Exp. Biol.* **205**, 25-35.
14. Nottebohm F (1976) Phonation in the Orange-winghed Amazon parrot (*Amazona amazonica*). *J. Comp. Physiology* **108**, 157-170.
15. Prum RO (1992) Syringeal morphology, phylogeny, and evolution of Neotropical manakins (Aves: Pipridae). *Am. Mus. Novit.* **3043,** 1-65.
16. Ribas CC, Gaban-Lima R, Miyakil CY, Cracraft J (2005) Historical biogeography and diversification within the Neotropical parrot genus "*Pionopsitta*" (Aves; Psittacidae). *J. Biogeog.* **32,** 1409-1427.
17. Ribas CC, Miyaki CY (2004) Molecular systematic in *Aratinga* parakeet: species limits and historical biogeography in the '*soltitialis*' group, and the systematic position of *Nandayus nenday. Mol. Phylogenet. Evol.* **30**, 663-675.
18. Rowley I (1997) Family Cacatuidae (cockatoos). In: *Handbook of the Birds of the World.* Vol. 4. (del Hoyo J, Elliot AE, Sargatal J, eds). pp. 280-477. Lynx Edition: Barcelona.
19. Tavares ES, Yamashita C, Miyaki CY (2004) Phylogenetic relationships among neotropical parrot genera (Psittacidae) based on mitochondrial sequences. *Auk* **121**, 230-442.

Received: February 1, 2006
Accepted: May 10, 2006