■ ORIGINAL ARTICLE

The Avian Middle Ear (*Struthio camelus*). Data for the Physiology of Sound Transmission in Systems With a Single Ossicle in the Chain

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Introduction and objetives: The columella of birds, often cited in the literature, has yet to be adequately described. We aim to give an account of this transmission element, describing its anchoring systems and detailing the muscle associated to it.
Material and method: We performed microscopic dissection and obtained images of ostrich specimens (*Struthio camelus*), chosen because it is the bird with the largest head.
Results: We describe the columella: the osseous tripod formed on its external section (extracolumella), the conic shape of its inner section (stapedial), and links to the tympanic membrane and the oval window. We describe its anchoring system: posterior ligament and annular ligament. We conclude by describing the characteristics of the columella muscle, its insertions and the fibrous vein surrounding it.
Conclusions: The avian middle ear is a valid model for understanding the mechanical characteristics of the human ear repaired with total ossicular replacement prosthesis, ie replacement of the ossicular chain by a single element. We highlight an apparent contradiction: the existing muscle is inserted into the columella in an area close to the tympanic membrane rather than adjacent to the oval window.

Key words: Middle ear. Columella. Muscle. *Struthio camelus*.

Del oído medio de las aves *(Struthio camelus)*. Datos para la fisiología de la transmisión en sistemas de un único osículo en la cadena
Introducción y objetivos: La columela de las aves, citada frecuentemente en la literatura, no aparece descrita convenientemente. Pretendemos mostrar este elemento de transmisión sonora precisando sus sistemas de anclaje y fijación y detallando el músculo de que dispone.
Material y método: Realizamos una disección microscópica de especímenes de avestruz *(Struthio camelus)*, y obtuvimos y procesamos imágenes de éstos. Escogimos este animal por ser el ave con mayor tamaño cefálico.
Resultados: Se describe la columela: el trípode óseo que se forma en su porción externa (extracolumela), la forma cónica de su porción interna (estapedial), sus relaciones con la membrana timpánica y con la ventana oval. Mostramos sus medios de anclaje: ligamento posterior y ligamento anular. Relatamos las características del músculo de la columela, sus inserciones y la potente vaina fibrosa que lo rodea.
Conclusiones: El oído medio de las aves es un modelo válido para la comprensión de las características mecánicas del oído humano, en el que se sustituye la cadena osicular por un solo elemento de transmisión sonora. Denotamos una aparente paradoja: el músculo existente se inserta en la columela en un lugar próximo a la membrana timpánica, en vez de en la proximidad de la ventana oval.

Palabras clave: Oído medio. Columela. Músculo. *Struthio camelus.*

INTRODUCTION

In amphibians and *Sauropsidae* (reptiles and birds), communication between the tympanic membrane and the oval window is established due to a single bone or osteocartilaginous element called the columella. The classic treatises distinguish between 2 areas in the columella, the medial area, which is bone (stapedial portion), and the lateral area, which is cartilaginous (extracolumella)[1,2]; both are found together in an articulation with synchrondosis to form an elastic concatenation to protect against trauma. The insertion area of the columella in the tympanum is always wide, with various forms, plate, fan, arch, etc.[2]

In 2002, a dynamic three-dimensional computerized model was published, using the finite element method,[3] which sought to realize a revision of the physiology of the middle ear. Recently the remodelling of the middle ear

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was published, and the outer ear and its relationship with the tympanic membrane was modelled, keeping in mind a characteristic not considered in previous tools, such as the buffer coefficient of the elements making up the middle ear.[4,5] With these computerized systems some apparently surprising results were obtained, such as that the efficiency of the middle ear, when faced with certain frequencies and intensities, is greater when a single ossicle is present (with lower mass), as happens in birds, than when 3 ossicular elements exist to link the tympanum to the oval window, as happens in mammals. With sounds of low intensity and low frequency, the negative effect of the mass of the 3 small bones is greater than the benefit obtained by having 3 elements. Hence, if in certain circumstances possessing 3 small bones results in a reduction of the efficiency of the system than if we had 1 alone, what is the functional performance gain of having 3 ossicular elements?

Having 2 muscles capable of synchronously or sequentially contracting, even with various strengths, would not make sense in a middle ear with just 1 small bone. For the function of the 2 muscles to be appropriate, there has to be another element between the bones on which they are based (malleus and stapes) to serve as a pivot and make the actions and the movements of both muscular elements independent or complementary. From this point of view, having 3 small bones is in reality a epiphenomenon, since 3 is the minimum number of elements to have 2 articulations between them; in other words, the incus can be interpreted simply as the need to have a new bone to ensure there are 2 joint unions. As a general starting hypothesis, we posit that we possibly have 3 small bones to be able to have 2 articulations, with a muscle acting on each one; the implications of this assumption in the physiology of hearing are still to be determined.

The specific hypothesis of this article is to describe why birds have a single ossicle and why that is the reason its motor system comprises a single muscle.

The present work is justified by various necessities. A first objective is to obtain specific data on the columella of birds; this structure is known and cited by many, but its characteristics are not published or are poorly outlined in terms of specific details. The fundamental goal is to describe the transmission element found specifying the anchoring and fixation systems of said columella and, principally, detailing the muscular element found. The information we seek will allow the design of the geometry and physical properties of the elements involved in the sound transmission physiology of this bird, indispensable for creating a three-dimensional computerized model of an ossicular system comprising a single element.

MATERIAL AND METHOD

The middle ear is studied, and, concretely, the tympano-ossicular system with its muscular element and fixation ligaments. We used 4 specimens of ostrich (*Struthio camelus*), a bird which is the only species in the order of the Struthioniformes. The ostrich was selected as the bird with greatest cephalic size, thus facilitating the study undertaken.

All the specimens were obtained by acquiring the head of animals intended for human consumption, recently sacrificed in an officially authorized slaughterhouse. The authors possess the recently obligatory national permission to conduct investigation with experimentation animals.

To carry out the dissection of the temporal, we used a Zeiss surgical microscope and the diverse conventional material in otological microsurgery that was considered useful. We used the temporal milling laboratory Bien-Air motor to carry out the carving and resections necessary in the tissue bone of the specimens.

For the capture of images we used a reflex analogue camera with macro lens and 3 integrated illumination elements (Yashica dental-eye II) and the surgical Zeiss microscope cited above, adapted to a Storz image scanning system.

RESULTS

The transcranial approach, penetrating into the middle ear through the upper faces of the petrous bone, is difficult in this animal, as it requires significant milling due to the hardness of the bone wall. We found no bibliographical data on the best way of accessing the middle ear of birds by dissection. Taking advantage of the canal's wide dimensions and of the tympanic membrane, we decided to approach the tympanic cavity through an incision similar to that designed by Rosen to carry out a replacement of the stapes in humans.

We observed in the first place that the ostrich does not have an outer ear, but an operculum with an anterior hinge covered by feathers, a structure to close the entrance to the external auditory canal. The canal is some 15 mm deep; at the bottom lays the tympanic membrane, which is circular, with a dark grey aspect. It is thick and its maximum diameter is 18-20 mm.

This tympanic membrane is flat, and lacks the conical aspect typical in mammals and in humans. The membrane, seen from the external auditory canal, presents a clearer tract or thickening that comes up in its median zone by way of linear elevation (Figure 1); this tract is solid, tense, and horizontal and could be compared to the aspect characterizing the sleeve of the malleus in the membrane of mammals, but in an anomalous position, even though, as we shall see, it does not originate from the direct pressure of a bone formation.

By raising the tympanic membrane, we find a cavity covered by a very thickened mucosa lined with numerous folds and difficult-to-recognize bone structures without equivalence in humans. With a careful revision, a calcified pillared structure is located, thin, perpendicular to the tympanum, to which it is firmly attached. We identified this structure as the columella classically described in birds. This ossicle, in its portion closest to the tympanic membrane (extracolumella), folds at obtuse angles dividing into three more or less rectilinear bone segments that conform to a

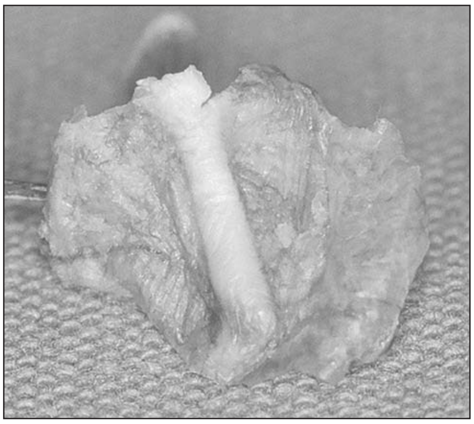

Figure 1. Aspect of the tympanic membrane seen from the external auditory canal. Observe the powerful thickened and whitened tract running through it.

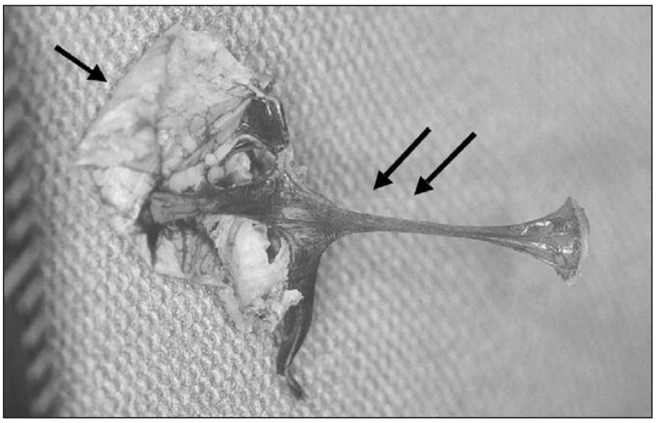

Figure 2. Tympano-ossicular complex of *Struthio camelus*. The tympanic membrane (arrow) and the columella (double arrow). Observe the tripod with which the columella is supported in the tympanic membrane and the conical formation that inserts itself in the oval window.

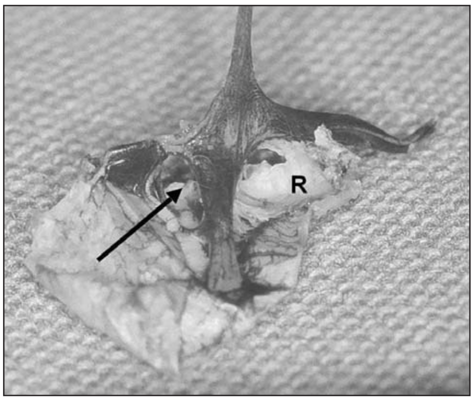

Figure 3. Between 2 segments of the support tripod, an orifice is formed in the shape of an arch (arrow). A fibrous raphe extends from the third segment to the tympanic membrane (R).

tripod (Figure 2). Two of them create a kind of arch with its feet supported on the tympanic membrane; this arched structure is separated from the membrane, constituting an arciform orifice (Figure 3). Between the feet or tips of these 2 bone segments a fold extends by way of thickening, that gives way to the tract seen in the tympanic membrane of the animal when viewed from the external auditory canal.

The third bone segment is separated equidistantly from the previous 2; it is directed towards the periphery of the tympanic membrane and is attached to it by a fibrous raphe (Figure 3). In short, these 3 bone segments are going to end in 3 peripheral points of the tympanic membrane to form a kind of tripod.

The columella, through a fine rod, is directed from the tympanic membrane to a space in the heart of the tympanic cavity, as we describe further on. The total length of the columella is 12 mm (Figure 2).

Vision and manipulation is facilitated by sectioning the tympanic membrane around the points at which the bone segments of the tripod of the extracolumella are inserted.

Despite separating it from the margins of the tympanic membrane, the columella does not lose stability, but maintains its position and, like a spring, "bounces back" at the slightest pressure movement.

From the anterior and external part of the tympanic cavity ceiling, a thick structure with a progressively thinning fibrous aspect unfolds away from its origin, moving down and back to insert itself in the columella by a fine tendon at a point close to the bifurcation of the arch formed by 2 of the bone segments in the areas of the tympanic membrane (Figure 4A). At the ceiling, this tendinous structure becomes wider and inserts itself into the bone. In the interior of this fibrous cone is the muscle of the middle ear of the animal; this muscle, which splays out like an open fan, has a maximum width of 3 mm (Figure 4B).

In the lower part, a nacre-like uncalcified ligamentous structure rises up from the cavity floor, the same width as the columella rod, to insert itself in the end of the third segment of the tripod; it is a ligament that limits the upward displacement of this structure (Figure 5).

By sectioning muscle and ligament, the columella, without tympanic support, maintains itself in its position without losing stability and with the same spring capacity it had initially, despite the fact that we did not observe any other ligaments or muscular union to fixate it.

Finally we reached the medial wall of the cavity. There we observed the stapedial or medial portion of the columella; it has a conical shape with the vertex towards the rod of the small bone and the circular base directed towards the deep end. This base is introduced in the equivalence of the oval fossa of mammals, anchoring itself firmly to the oval window by a strong ring-shaped ligament, giving it the spring capacity described for the columella. This stapedial portion is not pillared like the rest, but, as we said, widens like a cone, in which 4-5 linear digitations were observed (Figure 2) linked together by thinner bone.

DISCUSSION

Recent bibliography on the head and neck of *Struthio camelus* is scant, save for articles on ophthalmology, which are somewhat more numerous[6-8]; in the sphere of otorhinolaryngology we find only 1 work on the ostrich[9] syrinx and another on the sensitive innervation of the nasal mucosa.[10]

A first point to discuss is the number of specimens necessary to be able to extract reliable conclusions; in morphological-descriptive works, where the results are repetitive, only a small number of animals is used, estimated at between 3 and 6; this also occurs in the articles on ostriches in the sphere of otorhinolaryngology cited here.

The surgical approach to the middle ear of guinea pigs was studied in a work published in 2000, and 2 ways were described to approach the tympanic cavity in that animal.[11] Its authors describe a retromandibular or infrasternal route reaching the tympanic ampulla through the upper part of the neck, and a suprameatal or superoexternal route reaching the bone plate existing on top of the external auditory canal, in other words, what would be the attic wall in humans. For the reasons expressed, we thought the ostrich a suitable animal for the study of the middle ear with transmission through a single ossicle; in addition, we believed that the approach described in the "Results" section is the most useful in birds, at least in the species studied by us.

In the works by Lavinsky et al[12-14] and Ayres et al,[15] due to the great similarity of their specimens to the human ear, the sheep is designated as a preferred model for surgical training, experimental surgery and designing research on the middle ear. We propose the ostrich as a model for the study of the middle ear with single ossicle transmission systems; this investigation does not suppose a banal curiosity, but can bring fundamental data to the design of surgical prostheses for chain substitution, mainly to tilt the tendency towards conventional total ossicular replacement prostheses (TORP) or prostheses for malleo-vestibulopexy.

The middle ear, in animals that have 1, is the part of the hearing organ that transmits the sound energy from the air to the liquid in the inner ear. This arises with terrestrial life; its development can be extremely varied if we consider different animals, even if they belong to the same group (as happens with amphibians).

The morphology of the ossicular transmission in the middle ear shows extreme differences against which various stages of the phylogenetic scale are considered and are observed, to a lower extent, even between animals in the same genus. The bones making up the middle ear in the various species of the animal kingdom have been phylogenetic acquisitions generated over millions of years, in such a way that what were gills in fish came to be part of the jaw (articular and quadrate bones) in reptiles, and the malleus and incus in mammals. The stapes of mammals comes from the hyomandibular bone of fish, which would later become the columella of reptiles and birds. Some species of salamander possess another small bone situated on the oval window (opercular bone); the importance of this bone lies in the fact that fibres of the elevator muscle of the scapula are anchored to it, so enabling vibrations to be transmitted to the ear, disseminated through the floor, and reach the cochlea directly through the anterior legs, missing out the middle ear. We believe that it is not by chance that the muscle system of the middle ear in birds, which only possess a columella, consists of a single element, while in the chain of mammals, with 3 elements, there are 2 muscles.

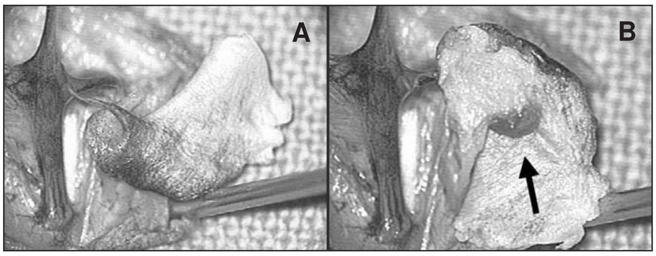

Figure 4. A: the muscle of the middle ear of *Struthio camelus* inserts itself in the point at which the 2 segments of the tripod unite to form an arch. B: separating the fibrous structure enveloping it allows the muscle to be observed (arrow).

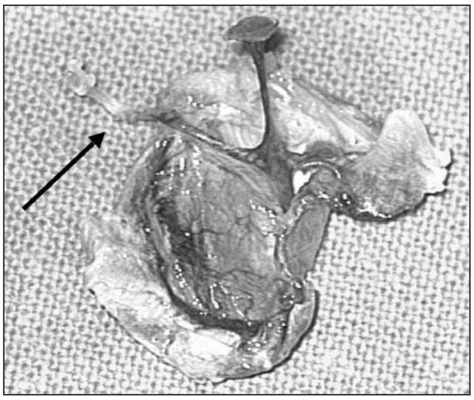

Figure 5. The arrow points to the tendon that inserts itself in the end of the third segment of the tripod.

The external auditory canal is inserted gradually into the tympanic bone (derived from the angular bone of fish and reptiles) to create a protective element for the tympanic membrane. Birds already possess a small external auditory canal, much more marked than that of reptiles, but it does not reach its definitive development until we consider mammals. Some birds, as happens with the ostrich specimens in our study, possess a structure similar to an anteriorly hinged door to protect the entrance to a well-constituted external auditory canal.

In contrast with what happens in the kind of animal studied here, which is apparently simple, the middle ear in reptiles is found to be better developed and shows a columella oriented externally downwards and supported on small articular and quadrate bones, an arrangement announcing the inclusion of these small bones in the middle ear.[16]

In birds, the columellar bone is situated between the tympanic membrane and the oval window. The medial extremity of this columella, in the shape of a cone, is always ossified in our preparations, while its base adopts a circular shape and plugs the oval window, carrying out the function of the stapes in mammals. This medial portion of the columella has always been described in the literature as ossified, but sometimes with a semicircular aspect.

The published works on the middle ear of birds state that the most external portion of the columella (called the extracolumella) may stay definitively cartilaginous.[1,2] In our specimens of *Struthio camelus*, taken from adult animals, the entire extension of the columella is bony, both through

Some Animal Species and Their Spectrum of Audible Frequencies, Hz*

Human	64-23 000
Dog	67-45 000
Cat	45-64 000
Cow	23-35 000
Horse	55-33 500
Sheep	100-30 000
Rabbit	250-45 000
Rat	200-76 000
Mouse	1000-91 000
Gerbil	100-60 000
Guinea pig	54-50 000
Porcupine	360-42 000
Raccoon	100-40 000
Ferret	16-44 000
Weasel	500-64 000
Chinchilla	90-22 800
Mouse	2000-110 000
Beluga	1000-123 000
Elephant	16-12 000
Porpoise	75-150 000
Goldfish	20-3000
Catfish	50-4000
Tuna	50-1100
Bullfrog	100-3000
Tree frog	50-4000
Canary	250-8000
Parakeet	200-8500
Cockatoo	250-8000
Owl	200-12 000
Chicken	125-2000

*Modified from Fay[20] and Fay et al.[21]

observation with the surgical microscope and through fracture of the structure.

In our study, we locate 2 important formations in relation with the columellar bone, which may be fundamental for passing comment on the physiology of the middle ear: a tendon (anchored inferiorly) and a muscle enveloped in a fibrous raphe (anchored anterosuperiorly). We believe, and the evolution of species seems to corroborate this, that more than 1 muscle is not efficient with a single bone element. The rationale for the existence of 3 ossicles in mammals lies in the need to individualize the actions of the 2 muscles they possess.

As we know, the columella (which corresponds with the hyomandibular bone in fish) appears in reptiles and birds. This structure communicates the tympanic membrane with the oval window and is suspended in the middle ear in different ways. In the description of our dissections we see that the columella is very firmly maintained, helped by the muscle cited, the long ligament inserted in the third supporting segment of the columella's tripod in the tympanic membrane, and the ring-shaped ligament linking the periphery of the medial end of the columella to the oval window. Even if we dissect the first ones, the structure stays well-sustained due to its anchoring in the oval window by the ring-shaped ligament, which permits the springing movement described.

The entire evolutionary process affecting the middle ear requires associated modifications in the bones of the cranium situated in proximity, basically those used for chewing. This occurs in order to give this process greater mechanical efficiency.[16] Hotton supports the idea of a dual evolution of the middle ear in amphibians: one for reptiles and another for mammals.[16] If this phylogenetic possibility is accepted, the middle ear of birds would be included in the first possibility.

If we consider its position on the taxonomic scale, an ostrich is: cellular organism, *Eukaryote, Amniote, Sauropsid, Sauria, Archosauria, Aves, Palaeognathae, Struthioniformes, Struthionidae, Struthio*. In birds there are different types of cranial movement as the upper beak moves in conjunction with the cranium[17]; this movement of the upper beak results from the mobility of the quadrate bone and from the pterygopalatine complex. The *Palaeognathae* (to which the ostrich belongs) are characterized by the possession of a different pterygopalatine complex and a special type of cranial mobility (different from that found in Neognathae). The morphology of the middle ear has been related to cranial kinesis, in that the middle ear would present differentiations depending on the degree of movement of the cranial bones (depending on whether it is akinetic or metakinetic).[16] The precise relationships between kinesis and the tympanic cavity do not seem to have been clarified yet and our data are not related with these possibilities.

The histological characteristics of the muscles in the middle ear have been studied by Hirayama et al[18,19] in rabbits. Due to the peculiarities found, those authors conclude that these muscles possess the specific capacity of rapid contraction and the possibility of anaerobic metabolism. They note the possibility that, because of their characteristics, the muscles of the middle ear can be considered a different histological type of normal striated muscle. The histological study of the muscle in the middle ear of the ostrich may be a model for investigating this possibility in birds.

It is important to point out the absence of muscles inserted in the stapedial portion of the columella in the middle ear of our specimens. As we have seen in the ostrich, the muscle is anchored in the proximity of the tympanic membrane. However, phylogenetically, the more medial portion of the columella, the stapedial section, is the forerunner of what will become the stapes in mammals, so the muscle should be inserted there. Therefore, rather than the formation of a vestige of more or less developed muscle that would later, in subsequent phylogenetic stages, give rise to the stapedial muscle, we should be thinking of a progressive modification in the morphology of the columella and the site of the muscle's insertion.

Most of the animal species studied possess a greater hearing range than humans (Table). We have not found in the bibliography[20,21] the range of frequencies for birds in the order *Struthioniformes*. As can be seen, those of the 5 species of birds shown in Table 1 are more reduced than that of humans, although this is not related to having a theoretically simpler middle ear. We consider that the greater or lesser development of the middle ear does not participate in having a greater hearing spectrum, but rather the middle ear, mostly by the capacity of its muscles, has to do with the selection of frequencies in sound function stages prior to the cochlea.

The conclusion drawn is that the tympanic membrane in birds is already anchored in a sinking of the tympanic bone equivalent to the external auditory canal of mammals. In ostriches, this canal outline is well developed, as the tympanic membrane is protected from exterior aggression. In the majority of mammals, the tympanic membrane has a conical aspect similar to that of humans, while in the ostrich the tympanic membrane is flat. In the *Struthio camelus*, both the external or myringeal portion of the columella (extracolumella), and the medial or stapedial portion possess a specific morphology. The external portion is supported on the tympanic membrane through a tripod bone and the internal portion is conical in shape. The specimens studied have a single muscle, wrapped in a powerful fibrous fascia, and it is inserted in the columella between the 2 segments of the tripod forming an arch. A long, fine ligament is inserted in the third bone segment of the tripod. The medial or stapedial portion of the columella has a conical shape and is housed in the equivalent of the oval window, to the perimeter of which it is attached by a ring-shaped ligament. The apparent paradox is noted that the existing muscle is inserted in the extracolumella in a place close to the tympanic membrane, instead of attaching to the medial or stapedial portion in the area surrounding the oval window.

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REFERENCES

1. Gil-Carcedo LM, Vallejo LA, Gil-Carcedo E. Ontogenia y filogenia del oído. In: Otología. Madrid: Médica Panamericana; 2004. p. 1-12.
2. Beck C. Anatomía comparada del oído. In: Berendes J, Link R, Zöllner F, editors. Tratado de Otorrinolaringología. Barcelona: Cientifico-Médica; 1969. p. 33-45.
3. Gil-Carcedo E, Pérez López B, Vallejo LA, Gil-Carcedo LM, Montoya F. Modelo computarizado 3D para el estudio de la biomecánica del oído medio con el método de los elementos finitos (MEF). Acta Otorrinolaringol Esp. 2002;53:527-37.
4. Vallejo Valdezate LA, Gil-Carcedo Sañudo E, Gil-Carcedo García LM. Modeling the auditory canal by finite element method. Otolaryngol Head Neck Surg. 2006;135 Suppl 2:256.
5. Vallejo LA, Delgado VM, Hidalgo A, Gil-Carcedo E, Gil-Carcedo LM, Montoya F. Modelado de la geometría del conducto auditivo externo mediante el método de los elementos finitos. Acta Otorrinolaringol Esp. 2006;57:82-9.
6. Wright MW, Bowmaker JK. Retinal photoreceptors of paleognathous birds: the ostrich (Struthio camelus) and rhea (Rhea americana). Vision Res. 2001;41:1-12.
7. Kiama SG, Maina JN, Bhattachariee J, Mwangi DK, Macharia RG, Weyrauch KD. The morphology of the pectin oculi of the ostrich, Struthio camelus. Ann Anat. 2006;188:519-28.
8. Altunav H. Fine structure of the retinal pigment epithelium, Bruch's membrane and choriocapillaris in the ostrich (Struthio camelus). Anat Histol Embryol. 2004;33:38-41.
9. Yildiz H, Bahadir A, Akkoc A. A study on the morphological structure of syrinx in ostriches (Struthio camelus). Anat Histol Embryol. 2003;32:187-91.
10. Palmieri G, Dessole AA, Minelli LB, Botti M, Gazza F, Corriero A. The sensitive innervation of the ostrich nasal mucosa. Ital J Anat Embryol. 2004;109:239-48.
11. Martín MC, Gil-Carcedo E, Vallejo LA, Gutiérrez V, Gil-Carcedo LM, Vaquero C. Abordaje quirúrgico del oído medio del cobaya. Rev Esp Invest Quir. 2000;3:3-6.
12. Lavinsky L, Goycolea M. In search of a teaching, training and experimental model for otological surgery. In: Tos M, Thompson J, editores. Otitis media today. Copenhagen: Prosper Meniere Society; 1997. p. 1-8.
13. Lavinsky L, Goycolea M. Study of sheep's middle ear to be applied in surgical training and experimental otological surgery. Aspen: Annals of the 4th International Symposium and Workshops in inner ear medicine and surgery; 1997. p. 16-23.
14. Lavinsky L, Goycolea M, Ganança MM, Zwetsch I. Surgical treatment of vertigo by utriculostomy: an experimental study in sheep. Acta Otolaryngol (Stockh). 1999;119:522-7.
15. Ayres VA, Lavinsky L, Preto de Oliveira JA. Morphometric study of the external and middle ear anatomy in sheep: A possible model for ear experiments. Clin Anat. 2006;19:503-9.
16. Pirlot P. Morfología evolutiva de los cordados. Barcelona: Omega; 1984.
17. Gussekloo SW, Vosselman MG, Bout RG. Three dimensional kinematics of skeletal elements in avian prokinetic and rhynchokinetic skulls determined by Roentgen stereophotogrammetry. J Exp Biol. 2001;204:1735-44.
18. Hirayama M, Davidowitz J, Daly JF. Ultrastructure of middle ear muscle in the rabbit. I. Stapedius muscle. Acta Otolaryngol. 1974;77:171-5.
19. Hirayama M, Davidowitz J, Daly JF. Ultrastructure of middle ear muscle in the rabbit. II. Tensor tympani. Acta Otolaryngol. 1974;77:175-9.
20. Fay RR. Hearing in vertebrates: a psychophysics databook. Winnetka: Hill-Fay; 1988.
21. Fay RR, Popper AN. Comparative hearing: Mammals. New York: Springer-Verlag; 1994.