Resumen por el autor, Augustus G. Pohlman.
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La posición e interpretación funcional de los ligamentos elásticos
de la región del oído medio de Gallus.

El presente trabajo trata de la anatomía aplicada de la región del oído medio, basada en Gallus. El autor describe con detalle la posición de los ligamentos elásticos y su relación con el aparato transmisor del sonido, cuando se consideran en conjunto con un sistema de articulaciones que se encuentra en el complejo columelar. Mientras que el músculo stapedio y el tensor del tímpano del mamífero se consideran como sinergistas, el músculo tensor del tímpano del gallo parece desempeñar la función de ambos músculos citados, y su existencia puede atribuirse a un doble desplazamiento en el mamífero, que tiene lugar en relación con la cadena osicular, mientras que en las aves existe un solo desplazamiento. El autor mantiene que el músculo y el aparato columelar están adaptados a una topografía variable de la membrana timpánica, debida a las presiones relativas del aire en el oído externo y medio.

Los ajustes no están probablemente asociados directamente con la agudeza del oído y la tensión del tímpano es probablemente un resultado y no una causa. El autor compara las necesidades mecánicas en las aves y mamíferos, y cree que las vibraciones moleculares del aire que llegan al tímpano son proyectadas sobre la ventana vestibular, y que las necesidades generales, según se establecen primeramente en los anuros terrestres, persisten en todas las formas superiores de los vertebrados terrestres.

Translation by José F. Nonidez
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THE POSITION AND FUNCTIONAL INTERPRETATION OF THE ELASTIC LIGAMENTS IN THE MIDDLE-EAR REGION OF GALLUS

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TWELVE FIGURES

HISTORICAL

Little work has been done on the applied anatomy of the middle-ear region in birds, and it was thought that a detailed study of the structures and mechanics of this region might lead to a better understanding of its function. The great difficulty in determining the function of the middle ear in mammals comes about through inability to find a suitable form in which the definite relation of structure to function may be experimentally established.

It may be well to state that Denker's ('07) excellent monograph on the inner-ear region of the parrot, undertaken with a somewhat similar point in mind, was not productive of interpretation because of the dissimilarity of the structures in birds and mammals. However, this does not militate against a comparative consideration of the middle-ear mechanics, because birds hear as acutely as or more acutely than mammals; the sound transmitting apparatus is of more simple construction and open to as little variation as the ossicular chain in mammals, and, finally, because of the differences in this region in birds and mammals, some conclusions may be attained bearing on the variable factor which calls for muscular adjustment in both forms. If one must go as far back as the amphibians for an explanation of the ear-cough reflex and class it as a phylogenetic reflex associated with the respiratory function of the middle ear, it is probably safe to assume that the general functional

requirements of this region are about the same in all forms. Here again we find inadequate explanation of the significance of the opercular muscle and the functional interpretation of a movable skeletal element applied to the perilymphatic space of the anurans.

The bibliography on the function of the middle-ear region in birds is not surprisingly large. Krause's ('01) monograph on the form of the columella and the relation of its form to acuteness of hearing is not productive of definite results or convictions. He concludes that, while the form of the sound-transmitting apparatus has something to do with the acuteness of hearing, much must be referred to the development of the end organs and to the central nervous system. His excellent figures demonstrate that the columella in birds is not subject to wide variations in form. It is impossible in the limited scope of this paper to go into any great amount of comparative detail, and the discussion will be limited practically to the conditions as found in the chicken. A general description of the relations of the structures in the middle-ear region of birds is, however, essential because only one article presents anything like a comprehensive account and none is adequately illustrated.

The best general description of the middle-ear region in birds is to be found in the account of Breuer ('08), whose abstracts and deductions read about as follows:

The drum membrane of birds presents a marked inversion in its relations to that found in mammals. The drum membrane in mammals is drawn inward toward the cavum tympani, while in birds, it is pushed outward. The manubrium mallei extends from the upper border of the drum toward its mid-area (in man, from above ventrally); in birds, the corresponding cartilage apparatus extends downward and backward from the central area of the drum toward its periphery. In mammals, the uppermost portion of the drum is flaccid; in birds, the relaxed portion is below. If one imagine a human ear drum turned through 180° on an axis represented by a diagonal line drawn across its surface from the postero-superior to the antero-inferior margin the resulting relations would represent roughly the position of the structures found in birds.

The drum membrane in birds, including the entire sound-transmitting apparatus, has but a single muscle attached to it and corresponding with the above mentioned inverted relations, the *M. tensor tympani*

Breschet) is not an intrinsic muscle of the tympanum, but arises from and is applied to the outer surface of the skull.

Breschet ('36) describes the muscle in the following manner: The malleus (by which Breschet means the cartilaginous portion of the columella attached to the drum) has strictly speaking a single muscle, *M. externus* (laxator) memb. tympani. This muscle attaches to the malleus at the union of the body of the bone with the stalk of the columella. Its tendon, at first fused to the drum, loses its connection at the drum margin; passes into a bony canal; emerges from the tympanum; becomes fleshy; and attaches to the lower border of this cavity. It is here covered by the *Nn. glossopharyngeus* and *vagus*. (There is undoubtedly some error in the translation of the French into German. The text itself was not available.)

The inner muscle of the malleus (*M. tensor tympani*) is present only as a rudiment. It is a delicate strand of connective tissue, particularly prominent in the turkey where it is well separated from the drum membrane. I have investigated it in other forms and have found it constant and united with the drum as a glistening pearly streak. This attaches to the malleus and runs forward and medialward; follows the general direction of the Eustachian tube and merges with the fibro-cartilaginous lining of the tube itself. The action of the muscle is naturally a very limited one because it can propagate to the drum only those movements imparted to it by the motion of the tubal walls to which stout muscles are attached. It is hardly necessary to state that, if one pulls upon this strand or upon the tubal walls to which it is attached, the drum membrane becomes more tense. Traction upon the tendon of the *M. externus* causes a relaxation of the drum; an experiment which demonstrates the respective function of each.

Gadow ('93) describes the muscle in the following manner: The muscle is relatively stout; arises by fleshy fibres from the lower surface of the *os occipitalis basilaris*; and passes through a large opening into the *cavum tympani*. The muscle renders the drum more tense and draws it outward. The muscle corresponds to the *M. tensor tympani* of the mammals, and is innervated by a fine twig of the *ramus III* of the *N. trigeminus*. A *M. stapedius*, innervated by the *N. facialis*, is wanting in birds.

Gaupp ('98) remarks: It is difficult to believe that this description is correct. It is in direct opposition to what is known of the middle ear muscle of the *Sauropsidans* and above all is contrary to Killian's positive statements. Furthermore, the innervation of a muscle attached to the posterior border of the drum through the *N. trigeminus* would be a remarkable thing. The notations of Killian, ('90) who undoubtedly worked on this same muscle, give its nerve supply through a separate branch of the *N. facialis*. Killian found this to be true in duck, goose, and chicken, and describes the embryonic attachments of the muscle first to the extrastapedial and later into the margin of the drum membrane proper.

According to Geoffry Smith ('04): The columella is provided with a single muscle. The *M. tensor tympani*, which attaches to the infra-stapedial and the drum margin between the infra- and extrastapedial cartilages. The muscle passes out of the ear through a wide opening, close to the foramen stylo-mastoideum, bends to the posterior surface of the skull, and attaches to the basioccipitale in a gentle depression which extends almost as far as the condylus occipitalis.

I will confine the description of this questioned muscle for the most part to its relations in the pigeon and chick which I have compared with a few other forms. Inspection of the figures given by Breschet shows that here, as well as in the relations of the organ of hearing itself, a very great similarity exists in the various classes of birds.

The sound-transmitting apparatus, which lies between the drum and the labyrinth, is formed by the columella. This resembles a mammalian stapes provided with a long stalk and attached laterally to a cartilaginous apparatus which has been homologized in part with the malleus and incus. This cartilage may be called the cartilage-head of the columella (extra-stapedial of Huxley). Its figure is that of an obtuse angle triangle with one point and the baseline attached to the drum. The latter is placed radially in the posterior-inferior quadrant of the drum membrane which is thickened between the head of the columella and the drum margin by tendinous fibres. Cartilaginous processes arise from either side of this structure posteriorly and inferiorly, somewhat raised on the inner surface of the drum and attached to the borders of this membrane. Just as the struts support the canvas of a tent, so the head of the columella together with its cartilaginous processes press the drum outward, and indeed even after the columellar stalk has been severed, the elasticity of the cartilage-head and its processes is sufficient to maintain the drum convexity.

If one divides the drum by two diagonal lines, four quadrants result which are somewhat different in structure. The ventral upper quadrant forms a regularly stretched conical mantle; the lower is flaccid; while the posterior quadrant is thickened by tendinous fibres particularly near its margin. The *M. tensor tympani* arises, as described by Gadow, from the outer surface of the skull close to the condyle; is directed horizontally forward and lateralward toward the bony border attaching the drum membrane. The *Nn. glossopharyngeus* and *vagus* emerge from the skull at its lower border. The muscle passes through an opening in the bony border of the external auditory canal and sends its tendinous fibres to attach to the drum margin medially below the columellar head. It therefore never enters the tympanic cavity as described by Breschet. The tendon breaks up in a sort of *pes anserinus* which unites with the drum; the upper portion however coming from below and behind unites to the manubrium-like process of the head of the columella.

The muscle is innervated by the *N. facialis* and may be stimulated with ease and certainty through the trunk of this nerve. This may be accomplished through a dissection exposing the semicircular canals and

by introducing a protected electrode into the foramen communicans just posterior to posterior canal. Here the electrode is in contact with the N. facialis and the other electrode may be placed on an indifferent part of the bird's body. When the circuit is closed, the head of the columella is drawn backward and downward; the upper and anterior quadrants of the drum are rendered tense and the concavity of the conical surface is decreased. The lower quadrant is rendered more tense from before backward but because the head of the columella slips downward, it is relaxed in this direction. (This makes it simple to understand why Breschet called the muscle a laxator memb. tympani because one would assume, unless it was demonstrated to him, that a M. tensor tympani would not under any circumstances be an extrinsic muscle of the middle ear.)

The columella returns to its original position when the stimulation of the N. facialis ceases. This comes about through the elasticity of the cartilaginous processes which were bent through muscular contraction. Particularly the lower process, which Breschet homologizes with the proc. gracil. mallei, seems to react because of its spring-like form; while the upper cartilage process seems to prevent too great a backward displacement by pressing against the drum border. When the head of the columella is pulled backward, the plate closing the oval window must also be influenced. In what manner is this accomplished and how is the cochlea affected by this displacement?

In the experiments on the stimulation of the N. facialis in the pigeon, the cochlear area was necessarily thoroughly exposed. Fine droplets of perilymph appeared on the surface through the small crevices in the bone occasioned by the dissection. These tiny holes were also intentionally produced by boring into the bony wall of the cochlea with a needle, and with the same result. When the N. facialis trunk was stimulated the small drops of perilymph were immediately sucked into the cochlea and would reappear as soon as the stimulation ceased. The contraction of the M. tensor tympani therefore tends to reduce the pressure within the perilymphatic space.

If one opens the cochlea from its cranial aspect and removes the membranous labyrinth, one may readily observe the columellar foot-plate. If the tendon of the M. tensor tympani is pulled on, one may see that the proximal anterior border of the columellar plate appears to be displaced. I have used the word 'appears' because the traction upon the tendon of the muscle in the manner described is, after all, a rough experiment but the displacement is quite probable from the anatomical relation of the parts themselves.

It does not appear possible to homologize this muscle with the intrinsic ear muscles of the mammals. A comparison with the M. retractor auriculæ is more readily accomplished. A functional comparison is however readily made. It seems certain that a muscle which attaches to the head of the columella; draws it backwards; displaces the stapedial plate out of the fenestra vestibuli; and reduces the pressure within the labyrinth—is a complete functional analogue of the mam-

malian *M. stapedius*. But this muscle is, at the same time, one which increases the tension of the drum membrane. Functions, which in mammals, are divided between two antagonistic muscles, are therefore accomplished in birds by a single muscle which not only renders the drum more tense but also decreases the intra-labyrinthine pressure. If both of these functions may be merged in the bird, the *M. tensor tympani* and *M. stapedius* of the mammals cannot properly be classed as muscles of opposition.

Breuer's conclusions on the function of the *M. tensor tympani* in birds are:

That it combines the action of the mammalian *M. tensor tympani* and *M. stapedius* in that it increases the drum tension and at the same time decreases intra-labyrinthine pressure; second, because the single muscle in birds replaces the double muscle in mammals, the two muscles in the mammal cannot well be regarded as opponents but rather as synergists; third, the *M. tensor tympani* possesses no muscle of opposition, and its contractions therefore have to do with preserving its tonus, with maintaining the pliability of the columella and in particular, the annular ligament attaching the columellar foot-plate to the margin of the fenestra vestibuli; fourth, to compensate for minor mechanical errors in the sound-transmitting apparatus (the nature of which he does not suggest).

Beyer ('07) describes the drum membrane in greater detail and particularly in the matter of its attachments. An annulus is not found in birds and the membrane is therefore attached to the adjacent borders of the surrounding bones; the pars basilaris of the sphenoid, the os occipitale laterale and basale, the squamosum, and the tympanic process of the quadratum. The last-named bone is movable, and may therefore influence the drum.

STATEMENT OF THE PROBLEM

Little work, apart from the notation in Bronn ('93), has been done on the tuba auditiva. Here the common tubal orifice is described as occupying a median position in the occipitosphe-noidal suture. The right and left tubae fuse into a short common tube or duct which opens into the posterior part of the oral cavity.

It occurred to the writer ('14) that little work had been done on the mechanical factors involved in the middle-ear region of

birds, and attention was then called to the position of certain elastic ligaments which are practically constant in all birds examined. More detailed investigation has been undertaken to ascertain the functional relation of these elastic ligaments to the action of the M. tensor tympani, to the drum membrane, and to the columellar apparatus. Breuer has undoubtedly described the muscle correctly as one without an opponent, and the structure should be of interest to the physiologist in determining the possibility of a dual nerve supply; an excitor-inhibitor system as found in involuntary muscles or in the voluntary muscles with opponents as proposed in Sherrington's reciprocal innervation.

The scope of this paper, based almost entirely on Gallus, will be limited, first, to the description of the elastic elements of this region and to the mechanical features in the columellar system; second, to an interpretation of the mechanism of the bird's middle ear.

The material used consists of newborn and semiadult chickens, fixed in Bouin's fluid or in formalin, decalcified in hydrochloric acid-alcohol and sectioned in collodion or paraffin. The sections were stained in Weigert's resorcin-fuchsin or in orcein, and for the most part differentiated in acid alcohol. The collodion sections were all cut at 50μ , the paraffin sections at 25μ .

ELASTIC TISSUE OF THE EXTERNAL AUDITORY CANAL

The external auditory canal in the chicken leads obliquely downward and backward from its oval external opening which is protected by the upward projection of the lower bordering feathers. The orifice lies well in front of the short bony external canal and is situated in a plane at right angles to the position of the drum membrane. The canal has a distinct kink in it and particularly the ventral-median wall is bent upon itself so that the most external part is applied to the side of the head. The dorsal wall of the canal is longer than the ventral, because of the oblique position of the drum membrane, and is reinforced by a heavy fibrous plate which is attached to the edges of the bones surrounding the region, with the exception of the quadratum.

This fibrous plate, bent to conform to the outline of the canal, affords origin to the heavy *M. digastricus*. The lateral portion of the canal is freely movable, so that the bird may shear off communication from the surface to the drum at the point of the kinking. The skin of the canal is loosely applied, particularly over the fibrous plate which attaches the *M. digastricus*, where a bursa-like slit occurs which continues to the region of the drum. Traction upon the skin of the external canal does not affect the drum membrane, and it may be assumed that the contraction of the *M. digastricus* or the closing of the external auditory canal in no way influences the middle ear or its contents.

The drum membrane occupies the upper wall of the canal and looks downward and somewhat backward. It is well hidden from inspection by the kinking in the canal and the convexity of the fibrous plate. This is further accentuated by the presence of the erectile auditory pad — a semicircular worm-like elevation following the dorsal drum margin and located about 2 mm. lateral to it. The erectile pad is firmly attached at the upper and lower bony borders of the external canal, but its semicircular base is separated from the canal by the bursa-like slit. In section this pad (fig. 1) is a rugous structure, largely composed of connective-tissue elements and some venous spaces. It is limited at its base by stout elastic fibers which are attached to the periosteum near the drum margin, but are not continuous with the drum membrane (fig. 2). The structure was first described by Wurm ('85) as responsible for the deafness in *Tetrao urogallus* during the period of sexual excitement in that it plugs the external auditory canal through turgescence. This was substantiated by von Graaf ('85), who, however, questions the additional contributing factor suggested by Wurm in a pressure exerted by the processus angularis mandibulae against the external canal. The pad itself partakes of the age and sex differences displayed in the comb and wattles, and is larger in the adult than the young bird, and better developed in males than in females. The bursa-like slit separates the pad from the tendinous fibers of the *M. tensor tympani* which crosses its base at right angles near the drum margin.

Turgescence of the pad might readily displace it forward and outward and seal the external auditory canal, as Wurm has suggested, but the position of its elastic fibers would indicate that they are related to a pressure against the medial surface of the pad and might therefore afford support to the drum mem-

Fig. 1 Section through the dorsal limit of the drum membrane and external auditory canal of an adult chicken; orcein stain. *B*, bursa; *DM*, drum marginal elastic tissue; *E*, extrastapedial; *EC*, external auditory canal; *EP*, erectile pad; *I*, infrastapedial.

The stippled figures are drawn by Miss Gertrude Hance of St. Louis.

Fig. 2 Oblique section through the dorsal region of an adult chicken; resorcin-fuchsin stain. *B*, bursa; *DM*, drum marginal elastic tissue; *E*, extrastapedial; *MTS*, membrana tympani secundaria; *T*, tympanum.

brane or columella against a too-marked lateral excursion. The elastic fibers would tend to draw the pad inward and backward and assist in returning the blood into the jugular vein, or would tend to bring the pad back to the normal position when the drum membrane returns to its usual location. The glands of the external auditory canal probably secrete a defensive mate-

rial against the intrusion of vermin, and because of the shearing mechanism and the erectile pad, the bird undoubtedly possesses a more adequate protection against violence from without than does the mammal.

While the fibrous elements of the ventral wall of the external auditory canal swing around the prominence indicating the position of the tympanic process of the quadratum, to terminate in close relation to the drum attachment, this is not the case at the dorsal drum margin, which is separated from the fibrous plate by a bony lip which contributes to a rudimentary external osseous canal. This lip is perforated by a foramen which transmits the tendon of the *M. tensor tympani* from the external surface of the skull to the dorsal-inferior drum margin. The muscle has been correctly described by Killian, figured correctly by Breschet, and is clearly innervated through the *N. facialis* as the experiments of Breuer substantiate. The relation of the tendon of this muscle to the drum membrane and the function of the *M. tensor tympani* will be considered later. The pull of the muscle, judging from its attachments and structure, is probably limited and feeble.

The drum is attached to the margins of the bones surrounding the external canal, but in the case of the quadratum this does not appear to be the case, although Beyer has noted it explicitly. The attachment of the drum, at this region, is to a stout fibrous ligament which rides over the rounded surface of the tympanic process of the quadratum near its articulation with the squamosum, and at this portion of the drum circumference, a diverticulum of the middle ear appears to afford a sort of cushion which insulates the drum membrane from the small movements in the quadratum.

ELASTIC ELEMENTS OF THE DRUM MEMBRANE

The drum membrane has been well described by Breuer and by Beyer. It consists of a delicate oval membrane attached to the bones limiting the tympanic cavity, with the exception of the quadratum anteriorly. The movements of the tympanic

process of the quadratum, which is directed upward in front of the drum membrane to articulate with the squamosum, are mainly a fore-and-back hinge motion and very limited near the joint. It must be remembered that the quadratum is intermediate in position between the mandible and the squamosum, and because of its attachments through the zygomatic also participates in movement of the upper bill. However, the bone is limited in motion through attachment to the pterygoideum, and in birds with a freely movable upper bill, as in the parrot, the quadratosquamosal articulation is even more pronouncedly a hinge than in birds with little upper bill movement, as in the chicken. A stout ligament usually bridges the tympanic process of the quadratum at the drum margin. In any event when the quadratum is freed below, it may be violently wrenched out of its socket without any visible influence on drum tension or columellar position, even when the performance is observed under binocular magnifier. The drum attachments are therefore probably as stable as if an annulus were present, and the movement of the quadratum in reference to the tympanum may be quite disregarded, as far as the chicken is concerned.

The drum margin is thickened by intrinsic elastic fibers, and in the ventral attachment area, includes a rudimentary air sinus which was at first mistaken for a vein. It is possibly a rudiment of a siphonium canal which connects the air sinuses of the mandible, when they are present, with the cavity of the middle ear just inferior to the foramen pneumaticum for the quadratum and pterygoideum. The marginal sinus, indicated in the semischematic figure 4, in so far as the writer is aware, has not been described, and the result of its position in relation to insulating the drum margin from movement of the quadratum has already been mentioned.

The margin of the drum is thickened postero-inferiorly, where the tendinous fibers of the M. tensor tympani pass to their attachment to the extra- and infrastapedial cartilages. Additional elastic elements are related to the tendinous portion of this muscle, and the drum margin and membrana tympani secundaria appear to be more or less continuous at this point.

The drum, in addition, receives strengthening fibers from definite elastic ligaments which may well be named the drum-tubal ligaments; these will be discussed after the general structure of the columella has been considered, because they are definitely related to the columella, both in position and in function.

Fig. 3 Section through the length of the columellar recess of a twenty-day chick; resorcin-fuchsin stain. *C*, columella; *CSL*, columellar-squamosal ligament; *F*, fibrous tube of external canal; *LA*, ligamentum annulare; *MD*, musculus digastricus; *MT*, membrana tympani; *MTS*, membrana tympani secundaria; *T*, tympanum; *TT*, tendon of tensor tympani.

COLUMELLAR APPARATUS

The strut responsible for the prominence of the drum in the external auditory canal is the columellar apparatus, which demands a careful consideration and which may be divided into two segments, a medial bony columella proper and a lateral cartilaginous extracolumella.

The bony columella has been likened to the mammalian stapes with a long stalk attached to it. It begins medially at the margin of the fenestra vestibuli as a flattened bony plate, the columellar foot-plate, which rapidly decreases in size to form a

slender spicule of bone which is directed laterally and somewhat downward to terminate in the extracolumella. It is flattened from before backward as it approaches its lateral extremity. The columella occupies a recess formed by a diverticulum of the

Fig. 4 Dissection of the middle ear of an adult chicken, somewhat schematized. 1, columella; 2, columellar foot-plate; 3, infrastapedial; 4, suprastapedial; 5, extrastapedial; 6, middle drum-tubal ligament; 7, drum-marginal air sinus; 8, columellar-squamosal ligament; 9, ligamentum annulare; 10, membrana tympani secundaria; 11, M. tensor tympani.

tympanic cavity under the carotid canal, ossifies early, and, in the young bird, is relative plump and better developed than the extracolumella (fig. 3).

The description of the extracolumella is more difficult because it consists of a cartilage tripod with the three processes set at right angles to each other. Figure 4, drawn from the actual dissection, gives the general form of the structure fairly well in

an adult bird. The three processes have received many names of which, perhaps, infrastapedial, suprastapedial, and extrastapedial are as good as any. We may refer to the common origin of these processes as the common cartilage stalk of the extracolumella. The infrastapedial (3) leaves the common cartilage stalk at its union with the columella and extends downward, at a right angle to the position of the columella, to terminate in a somewhat sharpened extremity close to the drum margin. The attachment of the columella to the extracolumella is somewhat flattened in the axis of the infrastapedial, and results in a movable member in this axis, which may be termed 'the columellar hinge.' The suprastapedial (4) is a spatulate process with its pointed extremity downward and forward, where it attaches to the common cartilage stalk, and its widened area correspondingly upward and backward where it attains the postero-superior drum margin. The flattened surface is at right angles to the columellar axis and the plane of its position is about the same as that of the infrastapedial. This process is not only the largest and most firmly attached portion of the extracolumella, but its base, attached to the drum margin, constitutes another hinge member which may be called the 'suprastapedial hinge.' The movement of this hinge is necessarily accompanied by drum displacement, and, in a general way, is outward-downward and inward-upward. The extrastapedial process (5) arises from the cartilage stalk, nearly in the axis of the bony columella, and lateral to the confluence of the infra- and suprastapedials. This process acts like the center pole of a tent and gives the drum membrane its curious inverted umbo to which attention has already been called. The extrastapedial receives most of the fibers of the *M. tensor tympani*, the drum course of which can readily be identified by inspection; sometimes the extrastapedial cartilage is particularly well developed out along the drum in the direction of the tendinous fibers. This process varies markedly in different ages and in different species of birds. Its greatest movement occurs at the union of the three cartilage processes and is a hinge, practically in the plane of the action of the *M. tensor tympani*. These hinge areas in

the columella are of some little importance in interpreting the mechanics of the columellar system, and will be referred to later.

DRUM-TUBAL LIGAMENTS

Medial inspection of the drum membrane, particularly in a specimen stained in toto with orcein and differentiated in alcohol, reveals a series of elastic ligaments which were pictured by Breschet and rediscovered by Smith, although neither investigator apparently understood their nature or function. These ligaments may well be named the drum-tubal ligaments and described in drum and tubal segments. The superior and middle drum-tubal ligaments arise from a common strand of elastic tissue in the lateral wall of the tuba auditiva and in close relation to the drum margin. The superior ligament joins the drum margin and runs upward, contributing to the medial elastic wall of the drum marginal sinus. It may be traced to the quadratosquamosal joint or to the foramen pneumaticum for the quadratum.

The smaller segment, the middle drum-tubal ligament (fig. 4), is the pearly streak of Breschet, and is readily observed in most birds, and in all instances is distinctly fused to the drum tissue and not independent in the turkey, as Breschet described it. It terminates in the tip of the extrastapedial and forms a very obtuse angle with the line of the pull of the *M. tensor tympani* on this process. It seems to become less markedly developed as it passes across the drum surface.

The inferior drum-tubal ligament arises from the floor of the tuba auditiva, and while it contributes some fibers to the inferior drum margin, the major portion passes across the edge of the drum to terminate in the tip of the infrastapedial which, it will be recalled, does not quite reach the edge of the drum. This ligament is ordinarily better developed than the other two combined (not shown in figure 4).

The tuba auditiva therefore presents two elastic strands near the drum margin, the inferior drum-tubal ligament and the fused superior and middle drum-tubal ligaments. These two join to form a common elastic bundle before the tuba has crossed

Figs. 5 to 10 CC, carotid canal; DTL, common drum-tubal ligament; IDTL, inferior drum-tubal ligament; O, projecting lip of the occipitale; PM, pharyngeal membrane; SDTL, fused superior and middle drum-tubal ligaments; SS, sphenoidal sinus; TD, common tubal duct; TA, tuba auditiva.

the plane of the carotid canal and lie in the lateral tubal wall. The tube becomes rapidly smaller as it proceeds medially, and when the tube fuses with its fellow to form the common duct already mentioned, the right and left elastic strands also fuse to

form the floor of the common opening in the occipitospheoidal suture. Here the amount of elastic tissue is increased by fusion with the stout elastic pharyngeal membrane which is projected upward into the tubal recess between the palatal muscles. This may be followed upward from the recess in figures 5 to 10, inclusive. It may be interesting to note that in certain birds (goose,

duck) the tubal course of these ligaments is replaced largely with involuntary muscle which becomes continuous with the involuntary muscle at the common tubal orifice. Breschet pictures the ligaments, but his account of the influence of traction upon these ligaments or the indirect traction through the mus-

Fig. 11 Section through the length of the columellar-squamosal ligament of an adult chicken; orcein stain.

Fig. 12 Section through the quadrato-squamosal articulation of an adult chicken, showing the relation of the head of the quadrate (Q) to the fibers of the columellar-squamosal ligament; resorcin stain.

cles of the mandible attached to the tubal wall must be denied. The bird does not possess the cartilaginous tuba auditiva of the mammal. The function of the drum-tubal ligaments is clearly one of limiting the amount of excursion in the extra-stapedial, in particular the infrastapedial process, and will be considered later.

While birds undoubtedly close the tubal recess during the act of swallowing, a direct relation of what corresponds to the raising of the soft palate and its effect on the cartilaginous tuba auditiva in the mammals cannot obtain. This region demands further study. It is interesting to note the relatively small tubae auditivae of the bird, when compared with the relatively large air-sinus system, and in figure 6 the confluence of the air-sinus system may be noted in a twenty-day chick, which would tend to show that air sinuses are a result of bone absorption rather than a causal factor.

COLUMELLAR-SQUAMOSAL LIGAMENT

This ligament was also pictured by Breschet and described by Platner ('39), hence commonly known as Platner's ligament. It is a well-developed elastic band somewhat conical in form. Its apex is attached to the suprapedial and the common cartilage stalk. It is directed forward, at right angles to the columella, to become attached by a broad conical base at the region of the quadratosquamosal articulation (fig. 11). While it is usually described as attached to the quadratum, its strong attachment appears to be to the squamosum, and it seems to ride over the quadratosquamosal joint to become continuous with the elastic tissue of the drum margin and with the elastic ligaments of this articulation. It is sometimes well separated from its bony attachment by an air-sinus opening. In very young birds the ligament appears to be placed almost at right angles to the position of the middle drum-tubal ligament, and while the ligament is in part set in opposition to the pull of the *M. tensor tympani*, its chief function seems to be to afford support to the extracolumella, so it may be considered a third member of extracolumellar stability; the other two being formed by the supra- and infrapedials. All three of these members are attached just medial to the drum margin and the three form a somewhat elastic support to the extrapedial which projects beyond the plane of the drum margin and is therefore responsible for the convexity of that membrane outward. This also accounts for the fact that drum convexity is maintained when the bony

columella has been severed. While the columellar-squamosal ligament resists the pull of the M. tensor tympani, and therefore is a passive agent in preventing outward displacement of the drum, it also affords certain resistance to medial displacement in the same manner that three toothpicks may be placed over the opening of an ordinary drinking glass. This ligament is indicated in figure 4 and is shown in figure 3.

The columellar processes have, therefore, definite elastic ligaments associated with them. The infrastapedial attaches the inferior drum-tubal ligament; the suprastapedial, the columellar-squamosal ligament, and the extrastapedial, the middle drum-tubal ligament. All of these ligaments are seen in a gross dissection and the forces which bring about an increase in tension may readily be demonstrated.

Occasionally additional ligaments occur. Sometimes a delicate elastic strand extends directly across the tympanum, from the quadratosquamosal articulation to the drum proper, and this may be regarded as an aberrant portion of the columellar-squamosal ligament; more often the fibers of the inferior drum-tubal ligament are projected up the length of the infrastapedial. In spite of the close relation of the columellar-squamosal ligament to the quadratosquamosal articulation, there does not appear to be a transfer of motion from the quadratum to the columella. With the exception of the middle drum-tubal ligament, which is wanting or poorly developed in the pigeon, the ligaments as described seem to hold for all birds examined—chicken, duck, goose, turkey, and hawk.

ELASTIC LIGAMENTS OF THE FENESTRA VESTIBULI AND FENESTRA COCHLEAE

The perilymphatic space of the inner ear is separated from the cavum tympani at the fenestra vestibuli by the columellar footplate which is held in place by an annular ligament, much in the same manner as the basis of the stapes is attached by the ligamentum annulare in the mammal. The margin of the footplate practically fits the fenestra vestibuli, and the interval is bridged by short stout elastic fibers, which permit a limited

inward and outward movement. It is perfectly obvious that the motions in the columellar foot-plate must be accompanied by corresponding mass displacement of the perilymph and that the plus or minus pressure developed would be in direct proportion to the elasticity of the tissues which limit that space. Breuer has called attention to the possible function of the *M. tensor tympani* in maintaining a pliability of the annular ligament, but from the elastic nature of its structure it may be safely assumed that exercise in no way contributes to this property. Whether the foot-plate motion is a direct tilting, after the manner of the basis of the stapes, or whether it is a direct in-and-out displacement is not germane at this point. The position of the elastic fibers are indicated in figures 3 and 4.

The fenestra cochleae in birds is relatively larger in proportion to the size of the perilymphatic space and of the fenestra vestibuli than in mammals. It is placed on the posterior aspect of the columellar recess in the chicken, and extends almost from the margin of the fenestra vestibuli to the drum attachment in baby chicks, although in older birds the growth of bone separates it more and more from the drum membrane. The membrane which closes in this opening, the *membrana tympani secundaria*, is composed of long, interlacing elastic fibers, which attach for the most part directly to the lip of the fenestra. This membrane is undoubtedly an adaptation for compensative displacements in the perilymphatic fluid, due to the direct application of a movable skeletal element to this space. This same mechanical requirement would hold for the operculum in the amphibians; the columellar foot-plate in the birds, and the basis of the stapes in the mammals, and would imply that somewhat similar functional requirements might obtain in these widely separated forms. It is interesting to note that the *membrana tympani secundaria* in the amphibians seems to be composed of elastic tissue, although the membrane occupies a dehiscence at the base of the otic capsule (as H. S. Harrison ('03) has shown) and is applied to a lymph sinus in this situation. The *membrana tympani secundaria* in the amphibians therefore has no direct relation to the tympanic cavity. Similarly, the

operculum is fixed in place, partly by a hinge in the cartilage and also by a stout elastic ligament which appears to have a functional relation to the *M. opercularis* as determined by Ahearn in an unpublished thesis on the anuran ear.

MECHANICS OF THE COLUMELLA AND EXTRACOLUMELLA

The results of the contraction of the *M. tensor tympani* are apparently in accord with Breuer's statement—downward, backward, outward displacement of the extrastapedial and an increase in tension of the anterior-superior drum quadrants. The changes in the drum membrane can naturally only come about through displacement of the extracolumella. The mechanics of this displacement and its effect upon the columella demand a more detailed description. The writer does not feel that drum tension itself has any very important relation to the problem, but rather that it is a result of adjustment of drum position.

Close inspection of the columellar apparatus *in situ* reveals four distinct kinds of movement. The first of these is a more or less typical plunger motion of the columellar foot-plate in and out of the fenestra vestibuli. The other three are hinge-like in character and are dependent either on the displacement of the extracolumella as a whole or upon bendings which take place in the extracolumella itself. These three movements will be described under the terms columellar hinge, suprastapedial hinge, and extrastapedial hinge. It must of course be remembered that the hinges in the cartilage are much of the same character as the operculum hinge in amphibians—merely weakened areas which permit a bending and not true joints.

The movement of the columellar foot-plate in the fenestra vestibuli is more or less an in-and-out motion probably combined with a slight tilting as found in the mammalian stapes. Unlike the condition in the mammal, however, where the force is directly applied to the bony stapes, the movement is imparted to the columellar foot-plate through the bony columellar lever by a tilting of the elastic extracolumella. The result of this is a final direct push and pull of the relatively long bony columella upon its foot-plate, or a resultant limitation of the tilting which

is so characteristic in the mammal. The amount of medial and lateral excursion of the columellar foot-plate is limited by a number of factors: 1) The shortness of the stout elastic fibers of the ligamentum annulare which is quite evenly developed about the circumference of the foot-plate, with the possible exception of the extension of fibers toward the drum margin; 2) by a compensating tension of the *membrana tympani secundaria* which allows a mass displacement of inner-ear fluid as an adjustment to movements of the foot-plate; 3) by limitations in a medial and lateral excursion because of the position of the columella in its attachment to the extracolumella and the restrictions in the tilting of the latter. Breuer's experiments on the living pigeon substantiate, what appears obvious from dissections, that contractions of the *M. tensor tympani* result in displacement of the extracolumella and a slight lateral excursion of the columellar foot plate. The result of this movement will be discussed later.

The second point of motion is in what may be termed the columellar hinge, located at the point of union of the lateral tip of the columella with the extracolumella, immediately medial to the point where the *infrastapedial* process is given off. Here the form of the columella changes from a rounded to a flattened spicule—the flattening being in the axis of the *infrastapedial* process. This hinge represents the spot where the tilting action of the extracolumella is translated to a prunner action of the columella proper and is accompanied by certain resisting forces; the twisting of the *infrastapedial* and the tension on the elastic columellar-squamosal ligament. It will be recalled that the *infrastapedial* has attached at its tip, or inferior end, not only the tendinous fibers of the *M. tensor tympani*, but the inferior drum-tubal ligament as well. The twist in the *infrastapedial* is one of the factors which tends to return the columella to a position of rest on muscular relaxation, as noted by Breschet.

The third point of motion occurs when the extracolumella, as a whole, swings upon a hinge formed by the attachment of the *suprastapedial* to the drum margin. This hinge is reinforced by the tip of the *infrastapedial* and perhaps also by a long drum process of the *extrastapedial*. The movement consists in an out-

ward, backward, and downward tilting of the entire extracolumella and is limited, as far as the downward movement is concerned, by the infrastapedial and the direction of the force exerted by the M. tensor tympani. The outward and downward motion is controlled through the attachment of the columellar squamosal ligament, plus the indirect pull of the M. tensor tympani on the extrastapedial, and the thickness of the adjacent drum quadrant.

The fourth hinge member is formed at the point of attachment of the extrastapedial to the common cartilage stalk, just lateral to the confluence of the supra- and infrastapedial processes. This process is directed laterally and is responsible for the drum prominence, because it acts like a strut which is supported by the supra- and infrastapedial and the columellar squamosal ligament. The cartilage bends downward and backward as it touches the drum, and may continue in the direction of the attached tendinous fibers of the M. tensor tympani as far as the drum margin. The pull of the muscle is directed mainly on the extrastapedial, and when stability is attained in the plane of the three members—supra- and infrastapedial and columellar squamosal ligament—further displacement may occur by a tilting of the extrastapedial at its basal attachment. This motion is limited, in part, by the form of the extrastapedial and by the middle drum-tubal ligament. The movement is pronounced in the chick, but poorly developed in the turkey, where the extrastapedial is relatively heavy and the middle drum-tubal ligament well developed.

FUNCTIONAL RELATION OF COLUMELLAR APPARATUS AND M. TENSOR TYMPANI TO THE INNER EAR

The entire elastic-ligament system is directly related to the movements in these four areas, and must therefore be set in opposition to the forces which bring about these movements. The mechanism is one which allows for marked alterations in drum position, and therefore in the sound-transmitting apparatus, without materially influencing the pressure within the perilymphatic space. It would appear these bending areas are

compensatory to drum movements and are probably not primarily associated with acuteness in hearing. The variable factor which allows the single voluntary *M. tensor tympani* to remain in tonus against the constant pull of elastic ligaments is logically, therefore, a function associated with the middle ear. This factor is necessarily a variable one and must involve a change in the topography of the middle-ear region which requires adjustment.

This attempt to look upon the *M. tensor tympani* and the columellar system as adjustment factors to a variable middle-ear topography calls for a short account of the adjustment necessarily involving inner-ear mechanism. It is not my purpose to consider the inner-ear function except as it pertains to middle-ear mechanics.

Keith dismisses the mechanical factors in the middle-ear region of birds in a few words. His work deals mainly with the problem of the inner-ear adjustments to columellar movements, and his evidence was obtained largely from the sparrow.

In the case of the bird, a single bone—the columella—connects the drum with the oval window. While the outer end, of the columella is fixed to the drum, its inner end extends into a foot-plate which is fixed into the margin of the oval window by a ligamentous membrane. The lower and hinder borders of the foot-plate are more tightly fixed in the window than the upper and anterior margin, not unlike the manner in which the stapes is attached in the fenestra ovalis of the mammalian ear. The movements of the columella are more like those of a lever than of a piston; it is hinged to the lower margin of the oval window. Internal to the foot-plate is the cavity of the vestibule, filled with fluid. The horizontal partition is drawn across the floor of the vestibule, stretching from the lower margin of the oval window which is occupied by the foot-plate to the opposite or inner wall of the vestibule (p. 222).

It will be noted that the middle passage (*scala media*) of the cochlea is separated from the cavity of the vestibule by a thick folded membrane containing many blood vessels—the *tegmentum vasculosum*. It represents a combination of the Reissner's membrane and the vascular body (*stria vascularis*) of the mammalian ear.

The horizontal partition just described forms the floor of the vestibule and the roof of the lower or tympanic passage of the cochlea—at least the terminal part of that passage. The round window lies immediately below the oval window. It is closed by a strong but loose membrane which is placed between the lower end of the tympanic

passage and the cavity of the middle ear or tympanum. Now, in considering the mechanism of the bird's ear, we may omit from our calculations the movements of the tegmentum vasculosum; it is a slack membrane and may be regarded for our present purposes as forming part of the fluid which fills the vestibule. When, then, the outer end of the columella is set into vibration by the drum, its foot-plate will carry the impulses of the drum to the fluid filling the vestibule. As in the mammalian ear, we may distinguish four phases in each vibrational cycle. In phase I the foot-plate, starting from its point of rest, moves or rotates inwards, displacing a minute quantity of the vestibular fluid. The vestibule has firm walls everywhere except that part of its floor formed by the basilar membrane. The membrane yields, displacing the fluid contents of the lower passage and forcing out the round membrane. In phase II, the foot-plate returns to its starting point, and the basilar membrane and organ of Corti rise to their equatorial level. In phase III, the outward excursion of the foot-plate continues and the basilar membrane rises so as to become convex upwards; the round membrane is drawn in. In phase IV all these parts return to rest.

Both Wrightson ('18) and Keith ('18) in their discussion have attempted to make the anatomy and physiology conform to the theory rather than analyze the theory on the basis of structure and function. It would appear from Wrightson's account that the pressure of the fluid in the perilymphatic and endolymphatic spaces is atmospheric and that the opposed action of the *M. tensor tympani* and *M. stapedius* preserves this condition. It has already been pointed out that the most recent investigations declare for a synergistic action (Kato, '13) of the muscles named. Keith, in any event, makes no suggestion as to the opponent for the single *M. tensor tympani* in birds, nor does he even mention the unusual mammals in which only one muscle is found. It must be conceded that the intralabyrinthine pressure is probably controlled by secretion and by blood pressure, and that the control exerted by the muscles of the middle ear is merely transient and secondary.

This again brings up several points which have been disregarded by Keith: The bony labyrinth is not a closed container, but communicates freely to the outside through the ductus endolymphaticus and through blood-vessels, with which the region is richly supplied, with the general venous system. Many bird forms show no direct relation of the *membrana tympani secundaria* to the tympanic cavity, but to the vena jugularis.

While Keith notes the dehiscence in the otic capsule in the amphibians, as established by H. S. Harrison, he does not emphasize the fact that the *membrana tympani secundaria* in this form is applied to the base of the skull, outside of the territory of the *tuba auditiva* or that the middle-ear region of the anurans is distinctly respiratory in function, dilating with the injection of air into the lungs. While Keith suggests that we regard the *tegmen vasculosum* in birds and the *stria vascularis* in mammals as merely contributing to the fluid contents of the space, the writer feels they afford a most delicate adjustment to slight variations in pressure, owing to the fact the pressure within the labyrinth and the venous pressure is practically equal. Certainly, this regulation is more delicate than the bending of the *membrana tympani secundaria*, even granting this force to be less than the friction head against a mass displacement through the *helicotrema*.

It has been mentioned that a plane of stability is formed by the *suprastapedial* and *infrastapedial* processes and the *columellar-squamosal* ligament which attach on a line medial to the drum margin. This plane is responsible, in part, for the support to the *columella* proper. Breuer's experiments on the cochlea have demonstrated that when the cochlear wall is perforated, the *perilymph* tends to ooze out in the form of surface droplets and these droplets disappear on a stimulation of the *M. tensor tympani* through the *N. facialis*. The interpretation, however, that the resulting contraction of the muscle is designed to reduce *intralabyrinthine* pressure is, however, open to objection. The *perilymphatic* fluid undoubtedly has a pressure, as has been stated, which is about that of the capillary blood-vessels of this region, and the moment a hole is made in the bony canal; the fluid will naturally ooze out in the form of droplets, due also in part to the tendency of the *columellar* apparatus to be displaced inward on loss of tone in the *M. tensor tympani*. In fixed specimens the *membrana tympani secundaria* normally appears to bulge slightly into the *cavum tympani*, and is undoubtedly an artifact. The function of the muscle can be more properly associated with a push factor which tends to

press the columella into the fenestra vestibuli and thereby to beget increased perilymphatic pressure.

COMPARISON OF THE EAR REGION IN BIRDS AND MAMMALS

The region of the external and middle ear in birds differs in certain particulars from the corresponding regions in mammals. The external auditory canal in the bird may be closed to afford a direct protection against violence and pressure from without, whereas in mammals this is not possible. The drum membrane in birds, as indicated in the dead or anesthetized bird, appears to be displaced medially on relaxation of the *M. tensor tympani*, while in mammals relaxation of the muscle of the same name is accompanied by lateral displacement of the drum, carrying with it the malleus, probably on a rotation of the incus, the nature of which has not been clearly defined. The tympanic cavity and the large air-sinus system associated with it and the tuba auditiva, afford a relatively greater surface for air absorption in the bird than in the mammal. The two middle-ear cavities stand in open communication in the bird, while in the mammal they are distinct. The tubae auditivae in birds open directly, by a small common canal, into the posterior oral cavity, while in mammals the separate orifices lie above the level of the soft palate in relation to the posterior nasopharynx. In mammals the opening and closing of the tubal orifices is controlled by voluntary muscles associated with the muscles of the soft palate, while the shearing off of the common tubal recess is probably brought about by approximation of the bordering palatal folds. The *M. tensor tympani* and its closely associated *M. tensor veli palati* of the mammal are wanting in the bird, although the position of these muscles is occupied by the drum-tubal and columellar-squamosal ligaments. The *M. tensor tympani* of the bird corresponds to the *M. stapedius*, both in action and in nerve supply, except that the *M. stapedius* acts directly on the stapes, while the *M. tensor tympani* acts indirectly on the columella through a tilting of the extracolumella. Finally, in spite of the quadratosquamosal articulation and its close relation to the ventral drum margin and the tympanic cavity, the bird's middle

ear is probably as stable in the matter of fixed boundaries as is that of the mammals. Both groups have an arrangement in the sound-transmitting apparatus, which decreases the amount of drum excursion in the propagation of this motion to the perilymphatic space. The two joints in the mammalian ossicular chain are therefore replaced by a series of intrinsic columellar movements which have been spoken of as hinges. The lever action in the ear bones of the mammal finds a functional analogue in the columellar system in birds, and in neither instance is this movement probably associated with an attempt to transform the character of the sound wave. Recent evidence seems to point to the sound wave transmission as a molecular quantity.

While there can be little doubt that some changes in acuteness in hearing result from the contractions of the *M. tensor tympani* and *M. stapedius*, it is hardly fair to assume at this time that this is their prime function. A similar result is obtained in the eyes. Narrowing the palpebral fissure is accompanied by contraction of the pupil and therefore increase in sharpness of vision. This is, however, the normal sleep reflex and can scarcely be classed as a function of the lids.

If the bird and the mammal both enjoy a middle-ear region of relatively stable nature, there is at least one major factor which calls for muscular adjustment, and that is the variable topography of the drum in reference to the inner ear. It might therefore be well to review briefly some of the theories of the muscle function in the mammal. Wales ('09) has suggested the possibility of a plus pressure phase in the air content of the middle ear, which he holds is due to a forcible injection, caused by the method of tubal closure. This result is, however, the same as Mangold's ('13) observation in voluntary relaxation of the *M. tensor tympani*, apparently not accompanied by palatal motion, although, as has been suggested, it might be that the *M. tensor veli palati* might operate independently from the *M. levator palati* in these cases. In any event, the drum membrane undergoes a lateral displacement on relaxation of the *M. tensor tympani*, which has not been satisfactorily explained. The *M. stapedius*, according to Wales, would prevent a pressure of the

ossicular chain on the perilymph during the minus pressure phase (air absorption) in that it would hold the weight of the displacing incus from the stapes by transferring some of its thrust to the M. stapedius. The writer feels that, while Wales may have speculated on the changes in the pressure of the middle ear, the deductions in his article are both clever and suggestive.

The apparent double displacement factor in the mammalian middle ear makes difficult an actual observation of what takes place, under relatively normal conditions, although the cat seems to afford a material in which this may be done. The displacement of the drum membrane in the bird does not offer this objection, because the active muscular contraction operates in only one direction. The assumed plus pressure phase in the middle-ear region may therefore be constructed by creating a minus pressure in the external auditory canal, while the minus pressure phase may be imitated by increasing the pressure in the external canal. In either instance the middle ear may be thoroughly exposed without disturbing the drum or columellar apparatus, although the push-and-pull element on the columellar foot-plate and the membrana tympani secundaria is naturally diminished. This factor of error may be entirely eliminated by a simple change in technique in constructing a transparent roof for the tympanum and creating the pressure directly through the tuba auditiva. However, the conditions are fairly well reproduced in a gross dissection and are easily studied.

EVIDENCES OF ADJUSTMENTS TO DRUM MEMBRANE DISPLACEMENTS

By placing a carefully dissected specimen of a bird's middle-ear under binocular magnifier and gently aspirating the air from the external auditory canal, the following changes may be observed: The lateral displacement of the drum membrane is accompanied by a tilting outward and downward of the extracolumella on the suprastapedial hinge, supported in part by the infrastapedial, which is held from backward displacement by the tension on the

inferior drum-tubal ligament; the tilting action of the extracolumella is transformed into a plunger action of the columella at the columellar hinge, accompanied by a twisting of the infrastapedial on its long axis; the columellar-squamosal ligament becomes tense; the columellar foot-plate moves laterally at the fenestra vestibuli and the membrana tympani secundaria becomes concave to allow for displacement of the perilymph. If the aspiration be increased, the supra- and infrastapedials and columellar squamosal ligament apparently create a stability in the extracolumella, so that further lateral displacement of the entire apparatus is eliminated, and the extrastapedial is drawn downward and backward in the direction of the tendinous fibers of the M. tensor tympani, until the middle drum-tubal ligament is under marked tension. At this time the extrastapedial is supported by the erectile auditory pad and the thin portion of the drum membrane applied to the anterior wall of the external auditory canal. This entire result implies that the amount of movement in the columellar foot-plate does not correspond to the amount of movement in the lateral displacement of the drum membrane, partly because of the hinge system in the columellar apparatus and partly because the extracolumella lies obliquely behind the midarea of the drum. Release of suction returns the parts to their former position.

Reversing the conditions by increasing the pressure in the external auditory canal, the drum moves medially, carrying with it the entire extracolumella on the suprastapedial hinge; the columella is displaced medially at the fenestra vestibuli and the membrana tympani secundaria becomes correspondingly convex. The medial displacement of the extracolumella is, however, limited by the close relation of the suprastapedial to the medial bony wall of the tympanum, and by the position of the intrastapedial and the columellar-squamosal ligament, so that further medial displacement of the drum occurs at the extrastapedial hinge. The extrastapedial buckles forward and inward, so that it may come to lie parallel to the columellar-squamosal ligament and, in the living bird, this is probably not so marked unless the M. tensor tympani relaxes to the utmost.

The delicate part of the drum is then applied to the medial wall of the tympanum. In other words, after a limited motion of the drum medially and laterally, all further movements are compensated for in the extracolumella itself, and therefore displacement of the drum does not give rise to corresponding displacement at the columellar foot-plate. It may be that the lever action ascribed to the three ear ossicles has the same purpose, rather than to function as transformers, because, in the bird, a similar arrangement is present and because, in the bird, the course from the tip of the extastapedial to the columellar foot-plate is practically a straight line.

The displacement which comes about through a minus pressure in the external auditory canal is practically equivalent to the action of the *M. tensor tympani*, while the plus pressure corresponds with its exaggerated relaxation. Therefore, the muscle might function to combat plus pressures in the external auditory canal, while the elastic-ligament system would passively counteract a plus pressure in the middle ear. It must be admitted, because of the relatively small tubal orifice and the large air content of the tympanum and its related sinuses, that birds are subject to as great, if not greater, displacements in the drum membrane as a result of barometric variations and altitudinal fluctuations. Relative increases in pressure against the drum would be shunted from the extracolumella through the contraction of the *M. tensor tympani*, while the reverse would be taken care of by the elastic ligaments. Therefore, because the drum membrane in birds normally tends to displace medially and press the columellar system against the perilymphatic space, a single muscle may operate. While in the mammal, according to Wales and Mangold, there is normally a tendency for the drum to be displaced outward which is controlled by the *M. tensor tympani*, while a medial displacement of the drum, carrying with it the ossicular chain, would press the stapes into the fenestra vestibuli and would be counteracted by the *M. stapedius*. It would appear, therefore, that the bird affords an excellent material for proving or disproving the importance of the columellar movements, the contraction of the *M. tensor*

tympani, and the displacement of the elastic ligaments against a variable topography in the middle-ear, which is due to drum displacements as a result of fluctuations in air pressure. This part of the problem clearly falls in the province of the physiologist.

CONCLUSIONS

The minor mechanical errors suggested by Breuer may prove to be the major factors calling for an adjustment, and in any event, the bird's middle-ear, with its relatively stable surroundings, its simple columellar apparatus, its single muscle, its elastic ligaments, and the possibility of shearing off its external auditory canal, is remarkably well adapted to varying conditions of air pressure. It would appear that the M. tensor tympani primarily compensates for variable drum positions in the columellar apparatus, rather than adapting the sound-transmitting mechanism to greater acuteness in hearing. The resulting drum tension would, therefore, be an incident to the contraction of the muscle, and in comparing conditions in bird and mammal, the greater the drum tension in the former, the more convex the drum; the greater the drum tension in the latter, the more concave the drum.

The prime function of the entire mechanism in birds would be represented by a function of the middle-ear, and compensatory to drum displacement, due to air absorption, on the one hand, and to fluctuations in barometric pressures on the other. The bendings in the columellar apparatus, while they are quite similar to the behavior of the ossicles in the mammal, probably do not have any effect upon the character of the sound wave. The sound wave, impinging upon the drum, would be focused, as it were, upon the stapedial or columellar foot-plate and beget vibrations of a molecular rather than of a molar character in the perilymph. The tension of the drum, like the shifting of the columellar foot-plate, is probably only a result of the variable topography of the drum in its relation to the inner ear and have little to do with acuteness in hearing.

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