

UNIVERSITY OF MANITOBA ANTHROPOLOGY PAPERS NUMBER 20

ENTOTYMPANIC ONTOGENY AND THE TRUE CONSTRUCTION
OF THE PRIMATE TYMPANIC FLOOR

R. D. E. MacPHEE
Department of Anthropology
The University of Winnipeg
Winnipeg, Canada

MAY 1978

DEPARTMENT OF ANTHROPOLOGY
THE UNIVERSITY OF MANITOBA
WINNIPEG, MANITOBA
CANADA R3T 2N2

Key Words. Auditory region . Tympanic floor . Entotympanics .
Embryology . Primordial suppression .

Abstract. Ontogenetic investigations confirm that independent entotympanics are absent in living primates. Although cartilage occurs in the petrosal tympanic processes of some primates, the assumption that a suppressed entotympanic is thereby indicated can be adequately refuted according to embryological canons of interpretation. Problems regarding the homologies of different entotympanics, largely ignored by paleontologists and systematists, reduce or negate their taxonomic valency for all but closely-related groups. Until such puzzles are resolved, the possible but doubtful existence of entotympanics in plesiadapoids and inferred pre-primate ancestors cannot buttress claims for alleged ties between primates and certain entotympanic-bearing eutherians (principally bats, colugos and tree shrews).

Short Title. Entotympanics, Ontogeny and Primates

INTRODUCTION

The entotympanics are a medley of enigmatic skeletal elements which occupy the floor of the tympanic cavity in some but not all mammals. Majority opinion holds that extant primates lack these elements, and that their tympanic floors are instead formed by outgrowths of the petrosal (and the ectotympanic, a constant constituent of the mammalian auditory region). However, this view has been occasionally challenged by authors who assert that entotympanics may exist in certain primate groups or in their putative ancestors [e.g., VAN KAMPEN, 1905; GREGORY, 1910; LEGROS CLARK, 1926; VAN DER KLAUW, 1931; BOWN and GINGERICH, 1973; HERSHKOVITZ, 1977]. If it were not for the heavy weight given to otic characters in primate taxonomy, this discordance in opinion would be a minor issue. As matters stand, however, it is a rather significant one; according to one argument, the presumed absence of an entotympanic is one of the few skeletal traits which bind together all likely members of the primate phylum [SZALAY, 1972].

A conspicuous feature of the recent literature on the primate basicranium is that nearly all of it has been written by paleontologists and systematists. Several of the interpretative obstacles faced by these workers could be at least partially overcome if due attention were paid to the development of taxonomically-significant basicranial structures in modern groups [MACPHEE, 1977a,b]. However, with a few prominent exceptions [e.g., SPATZ, 1966; STARCK, 1975],

comparative embryologists have contributed little to the resolution of such problems. This paper will attempt to reveal the advantages of employing ontogenetic perspectives in addressing the vexed question of the true construction of the primate tympanic floor.

MATERIALS

This paper is based on the results of a comprehensive study of the development of the auditory region in strepsirhine primates, tree shrews, elephant shrews and lipotyphlous insectivores, as well as a thorough survey of the literature pertinent to entotympanic ontogeny [MACPHEE, 1977b]. I was extremely fortunate in having access to sectioned, stained specimens during the course of my research, instead of having to rely on macerated materials (which give little or no insight into the complexities of middle ear development).

Intensively-studied sectioned specimens, most of which were fetal or perinatal, were distributed in the following manner (numbers identify the quantity of specimens per species):

Primates: Lemur catta (1), Microcebus murinus (4), Propithecus sp. (1), Loris tardigradus (1), Galago (Galago) senegalensis (2), Galago (Galagoides) demidovii (4).

Scandentia: Tupaia glis (5).

Macroscelidea: Elephantulus fuscipes (2).

Lipotyphla: Erinaceus europaeus (4), Solenodon sp. (1), Microgale (Nesogale) dobsoni (1), Hemicentetes semispinosus (3), Setifer setosus (1).

These were supplemented by adult skulls and partial slide sets of other species belonging to the four orders.

All of the sectioned specimens are housed within the embryological collections of the Neurobiologische Abteilung, Max-Planck-Institut für Hirnforschung, Frankfurt/M. (FRG), with the exception of the fetus of Propithecus sp. (which is located in the Anatomisches Institut, J.-W.-Goethe-Universität, Frankfurt/M.). A complete catalogue of the specimens and species used in the original study may be found in MACPHEE [1977b].

RESULTS

Development of the Tympanic Floor in Living Primates

In a previous paper [MACPHEE, 1977a], I briefly outlined the development of the bony tympanic floor in representative lemurs and lorises. In the course of my descriptions I noted that the strepsirhine bulla incorporates rostral and caudal tympanic processes of the petrosal (plus the ectotympanic, in lorises). Left undescribed or unevaluated, however, were certain aspects of bullar ontogeny which are of the utmost importance to the present topic.

The first of these is the earliest condition of the tympanic floor. In adults, this floor is actually a complex of soft and hard tissues that ventrally enclose the middle ear and separate its spaces and contents from surrounding structures. But in the young of all mammals, the tympanic floor is initially composed of membrane alone. The development of this primordial floor is first signalled in the fetus by the appearance of a sheet-like formation within the mesenchyme

surrounding the expanding cavum tympani (fig. 6A). Since this sheet gradually assumes the character of dense connective tissue as a result of a progressive increase in fiber content, it is appropriate to identify it as the fibrous membrane of the tympanic cavity. It usually takes the form of an irregular, flattened hemisphere ('membranous bulla' of some authors) which ventrally cloaks the entire presumptive middle ear. Medially, the fibrous membrane is continuous with other dense connective tissues lining the basicranium (chiefly perichondria and fasciae); laterally, it extends beneath the developing ectotympanic, without meeting the tympanic membrane at any point, to the position of the cartilage of the auricle (fig. 5A). The fibrous membrane constitutes all there is of the nascent tympanic floor in early fetal strepsirhines, prior to the development of tympanic processes (fig. 1). The fibrous membrane also serves as a medial uniting layer for the later ectotympanic-petrosal plate suture, as noted previously [MACPHEE, 1977a].

The second matter requiring discussion is the relationship between the fibrous membrane and tympanic processes of the petrosal. In strepsirhines, as in most mammals, the fibrous membrane is functionally replaced during ontogeny by skeletal elements (i.e., cartilaginous or bony constituents of the tympanic floor). Particularly important for subsequent analysis is the fact that both the rostral and caudal tympanic processes of the petrosal (which unite early in ontogeny to form the petrosal plate) arise adjacent to and expand along the intratympanic surface of the fibrous membrane, which thus directs their initial growth along predetermined planes (figs. 1, 4B). My personal observations indicate that petrosal processes are not

unique in this regard; with respect to the fibrous membrane, all tympanic processes of the constant bones of the basicranium (e.g., basisphenoid, alisphenoid) grossly develop in the same manner (fig. 2B).

A final point concerns the individual styles of development of these petrosal processes; certain features of their ontogeny are not completely in line with STARCK's [1975] view that such outgrowths always develop periosteally. The caudal process arises as a cartilaginous excrescence on the presumptive mastoid well before the auditory capsule is significantly ossified (fig. 3). When the process begins to ossify, it does so from a center located in the pars canalicularis (and not autonomously). Except where secondarily reduced, the caudal tympanic process of the petrosal is a characteristic feature of the therian auditory region [CARTMILL and MACPHEE, in press], and seems to follow the same method of development in every known case. The situation with the rostral tympanic process is more complicated. When present in a mammal, it begins to develop only after the promontorium (from which it arises) is substantially ossified, and has no precursor in primary cartilage. In this its development corresponds to STARCK's [1975] general concept of tympanic process ontogeny. However, in fetal Microcebus, but perhaps not in lorises¹ or other mammals possessing a rostral tympanic

¹Secondary cartilage is found within the ectotympanic-petrosal plate suture in young postnatal Galago senegalensis [MACPHEE, 1977a]; it also occurs in other cranio-facial sutures. This type of secondary cartilage is not relevant to the present discussion.

process, a strip of cartilage-like material develops on the process' rim (fig. 4).

In my view [MACPHEE, 1977a], this material is 'secondary cartilage,' a poorly-understood tissue that is consistently found at certain times and places in several rapidly-growing intramembranous bones of the cranium. Like secondary cartilage found elsewhere, the material in the rostral tympanic process of prenatal Microcebus is composed of large, darkly-nucleated cells embedded in a sparse, honeycombed matrix. Characteristically, staining qualities of cells and matrix conform to those of cartilage rather than bone. Also evident within the zone of secondary cartilage are numerous empty lacunae associated with giant cells reminiscent of chondroclasts. Nothing in its morphology or histology suggests that it originates separately and then coalesces with the petrosal plate. Nor is there any indication that the secondary cartilage is pathological or abnormally formed, despite the fact that I found it in only one of two mouse lemur fetuses with the same crown-rump length.

This tissue was not found in a young postnatal Lemur catta used in the same study, indicating that it either does not form in this species at all or is rapidly replaced around the time of birth. I know of no other published instance in which secondary cartilage, correctly identified, definitely occurs within a growing tympanic process.

Having also seen sectioned specimens of prenatal ceboids, Gorilla gorilla and Homo sapiens in the embryological collections of the MPIH, I am convinced that there can no longer be any doubt that the only elements involved in the tympanic floors of living

primates are petrosal processes and the ectotympanic. However, the term 'petrosal processes' refers to conditions which visibly obtain in extant forms. There is a theory, appearing in various guises in the works of a number of authors [e.g., VAN KAMPEN, 1905; SPATZ, 1966; SZALAY, 1977], which holds that during the previous evolution of some mammals (including primates), entotympanics were present but underwent embryonic suppression. That is, although initially independent structures in ancestral forms, in descendants they began to fuse earlier and earlier in ontogeny with the petrosal, and now appear to arise directly from that bone as its tympanic processes. This hypothesis cannot be directly assailed from an embryological standpoint without introducing recapitulationist fallacies [MACPHEE, 1977a]. Currently-available ontogenetic evidence and parsimony nonetheless imply that it is almost certainly false. Before showing this, however, it is vital to set out what is known or suspected about the entotympanics themselves.

Development of the Entotympanics

It is well known that VAN DER KLAUW [1922] presented conclusive evidence for the existence of two different types of entotympanics, the rostral and the caudal. The rostral entotympanic, normally the smaller of the two when both are present, develops in the anteromedial corner of the membranous tympanic floor and grows posteriorly. The caudal entotympanic, on the other hand, develops in the middle or rear of this floor and grows anteriorly. VAN DER KLAUW [1922] took pains, however, to emphasize that their identification and

ontogeny are not nearly so simple as these positional definitions insinuate. Subsequent studies of entotympanic development have amply confirmed his point. Since many students of the mammalian auditory region are unaware of the literature on entotympanic embryogeny, it is useful to summarize a few of the more important findings made in the last several decades. This is most easily accomplished by providing replies to a series of questions.

(1) Where do entotympanics originate in the tympanic floor?

It is virtually certain that all entotympanics, unlike tympanic processes, develop and grow within the fibrous membrane of the tympanic cavity. Documentation for this proposition abounds, although its implications have not been adequately pursued in the past [e.g., FAWCETT, 1919, Miniopterus; VAN DER KLAUW, 1922, 1929, Dasypus and macroscelideans; REINBACH, 1952, Dasypus; FRICK, 1954, Myotis; SPATZ, 1966, Tupaia; MACPHEE, 1977b, Tupaia, Elephantulus]. One might object that the difference between 'within' and 'adjacent to' is either trivial or incapable of proof. In tracing the development of individual tympanic processes in a number of unrelated eutherians, I found that these outgrowths were always enclosed in periosteal tissues derived from those surrounding their parent bones (fig. 1, 2B). Conversely, similar tracing of entotympanic elements revealed that they always expand within the fibrous membrane, which serves as their perichondrium or periosteum (fig. 5B). The difference, then, is not only real but fundamental.

(2) From what skeletal tissues are entotympanic rudiments formed?

While it is often assumed that entotympanics can only develop

endochondrally, this is not universally the case. The entotympanic of the sloth Bradypus is apparently not preceded by a cartilaginous model, and instead develops like an intramembranous bone [SCHNEIDER, 1955]. In Elephantulus, [MACPHEE, 1977b] the caudal entotympanic (fig. 6C) develops neither like an endochondral bone nor like a typical intramembranous bone, but rather more like the heterotopic ossifications that regularly appear within certain dense connective tissues in some mammals (e.g., penis bones, heart bones, tracheal bones; WEIDENREICH [1930]). Entotympanic anlagen found in other species have also been compared to young elastic cartilage, chondroid tissue, and a form of metaplastic osseous tissue. Whether this baffling diversity in primordial tissues actually exists, or is the result of mistaken observation, is still an open question without a suitable answer at present. It may well be that entotympanics which now arise intramembranously are true homologues of those which arise endochondrally; differences are then due to the suppression of the cartilaginous matrix or acceleration of the time of appearance of the ossification center. Certainly, there are instances of membrane-bones having become cartilage-bones during evolution, and vice versa [DE BEER, 1937]. However, most of these cases are restricted to fish, and such reversals are almost unknown in mammals.

- (3) What is the nature and significance of associations formed between entotympanics and other elements of the auditory region?

This question is one of the most troublesome of any that can be asked about the entotympanics.

Studies of the rostral entotympanic indicate that it can follow two, apparently distinct, methods of development. Observations on

Procavia [VAN DER KLAAUW, 1922], Dasypus [REINBACH, 1952] and Tupaia [SPATZ, 1966], for example, suggest that the rostral entotympanic of these forms is continuous ab initio with the rear of the cartilage of the auditory tube (the structure that conducts the auditory or eustachian tube from the pharynx to the cavum tympani). But in Myotis [FRICK, 1954], Rousettus, Cynocephalus and macroscelideans [VAN DER KLAAUW, 1922, 1929], its primordium arises independently, although in many instances it later fuses with the tubal cartilage. Fusion may be secondary in the first selection of examples as well, but occurs so rapidly after initial differentiation that it has so far been missed by investigators. This would make interpretation easier, but I am not convinced that this conjecture is warranted on present evidence.

Whether this difference in the style of origin of the rostral entotympanic (if it exists) should be given any weight depends on one's attitude towards the significance of so-called primary vs. secondary fusions in general. There is, after all, a strong tendency for unrelated cartilages to fuse into a solid mass during chondrocranial development [STARCK, 1967]. Yet there are also several cranial cartilages that develop from more than one center of chondrification in the young of modern mammals, despite the fact that they could not have arisen through the fusion of phylogenetically separate structures during evolution [DE BEER, 1937].

Considerations similar to these led VAN DER KLAAUW [1922] to conclude that there are at least two plausible explanations for the origin of the rostral entotympanic (given that all elements identified by this term share a common origin in the first place). The

first is that during the evolution of mammals, the cartilage of the tube underwent subdivision into a tubal cartilage proper and a rostral entotympanic (the latter presently showing varying degrees of developmental independence from its parent element). The second is that the rostral entotympanic evolved as a completely separate entity (but now exhibits varying degrees of fusion with the tubal cartilage). Existing data do not permit an informed choice between these alternatives. For this reason, there is no point in doing away with the term 'rostral entotympanic' and replacing it with some other, such as 'tubotympanic' (for the tubal cartilage + rostral entotympanic; REINBACH [1952]). The use of REINBACH's term involves a prior decision about the derivative nature of this entotympanic which we are really in no position to make.

Fortunately, it is possible to be somewhat more definitive about the significance of the association which occasionally forms between the caudal entotympanic and the visceral bar of the second branchial arch. On the basis of a very limited set of observations on young stages of Pteropus and Dasypus, VAN KAMPEN [1915] proposed that the entotympanic (by which he meant the caudal entotympanic of VAN DER KLAAUW) was a derivative of second-arch material. Although he claimed that in these forms the caudal entotympanic was primordially continuous with Reichert's cartilage, almost every worker who has investigated entotympanic ontogeny since VAN KAMPEN's time has found that this association occurs very late in development, if at all. On the whole, it seems very likely that the caudal entotympanic is properly an independent development of the tympanic floor that does not owe its origin to the second arch, either phylogenetically or

ontogenetically (contra HUNT, 1974).

Entotympanics also fuse with other elements of the auditory region in many mammals, which often makes it difficult to determine the true constitution of the tympanic floor in adults [VAN DER KLAUW, 1930]. Examples of this include a frequent tendency for fusion with the caudal tympanic process of the petrosal and the rim of the ectotympanic. Although some authors have attributed great importance to unions like these, all of the well-documented ones occur late in entotympanic ontogeny and, in my view, are devoid of evolutionary or morphological significance.

Incidence of Entotympanics in Extinct and Extant Mammals

VAN KAMPEN [1905] claimed that the entotympanic(s) were mammalian neomorphs, on the footing that no homologue for them could be found in lower vertebrates. This interpretation has been followed by all later authors [e.g., VAN DER KLAUW, 1922, 1931; STADTMÜLLER, 1936; REINBACH, 1952; STARCK, 1967; NOVACEK, in press]. However, consensus on this issue might be regarded as inevitable, since no one other than VAN KAMPEN [1905] has made a systematic study of this facet of the homology problem.

While VAN KAMPEN's mammalian innovation theory remains unchallenged, it is important to be clear about the quality of its substantiating data. To be blunt, there is no evidence, other than negative or indirect evidence, which touches upon the phylogenetic origins of the entotympanics. We cannot identify with any degree of precision the group in which they first appeared, or when. Although

it appears deductively likely that one or the other of the entotympanics existed in several eutherian lineages by the late Paleocene-early Eocene [NOVACEK, in press], the time of their origin must have been much earlier, barring multiple independent inventions. Elucidation of this matter must await further relevant fossil discoveries.

Since the course of mammalian evolution was not well understood at the time of VAN KAMPEN's researches, he could not be specific about the breadth of forms to be included under the term 'ancient mammals.' Further, it is clear from other contexts that he would have expected the origin of the entotympanic(s) to have antedated the marsupial-placental dichotomy. Some supplementary remarks need to be made here.

Entotympanics have yet to be identified in members of any of the wholly-extinct, non-therian groups of mammals (multituberculates, docodonts, triconodonts, symmetrodonts and pantotheres). There are no more than a dozen known basicrania or isolated petrosals of these predominantly-Mesozoic forms [KERMACK and KIELAN-JAWOROWSKA, 1971]; yet even the marvelously preserved skulls of the multituberculate species Kamptobaatar kuczynskii and Sloanbaatar mirabilis [KIELAN-JAWOROWSKA, 1970] display no indication of having possessed entotympanics, or, for that matter, any sort of bony tympanic floor. Although it is impossible to provide proof, the ventral wall of the middle ear was probably closed by membrane alone (plus the ectotympanic) in all of the ancient non-therian mammals. Entotympanics are almost certainly absent in extant monotremes [cf. KÜHN, 1971].

An entotympanic has not been incontrovertibly identified in a fossil marsupial; NOVACEK [in press], however, believes that one may

exist in a few of the living metatherians. I know of no convincing embryological evidence for the oft-repeated assumption that entotympanics participate in the marsupial tympanic floor [e.g., SEGALL, 1969]. Recent authors have failed to note that the foundation for this conjecture was VAN KAMPEN's [1905] acceptance of suspect observations garnered from the writings of HYRTL and PARKER, rather than original investigations based on suitable young material. Until a study employing the proper techniques is made, the claim that an entotympanic exists in metatherians should be met with a Scottish verdict of 'unproven.'

Although the negative evidence cited above cannot be regarded as decisive, most indications point toward the conclusion that entotympanics may be specifically eutherian innovations. There is abundant evidence to show that they develop in a large number of living placentals (see incidence lists in CARTMILL and MACPHEE [in press] and in NOVACEK [in press]). Among those orders which have been directly or indirectly linked with primates, several conditions obtain.

For scandentians and macroscelideans, there is conclusive proof of entotympanic participation in the ventral wall of the tympanic cavity. The entotympanic of Tupaia appears to be a rostral one [SPATZ, 1966; CARTMILL and MACPHEE, in press]; there is no ontogenetic evidence for a second entotympanic [contra NOVACEK, in press]. Conditions in Ptilocercus have not been adequately investigated; an entotympanic is present [LEGROS CLARK, 1926], but whether it is the homologue of the one in Tupaiinae remains to be seen [cf. CARTMILL and MACPHEE, in press]. If Anagale (?Oligocene, Asia) is not related to tree

shrews [MCKENNA, 1963], there is no evidence for the ancestral condition of the scandentian tympanic floor. The same is true for macroscelideans, although all investigated Recent elephant shrews definitely possess two independent entotympanics [contra ROUX, 1947]. The rostral entotympanic is minute and may not ossify [MACPHEE, 1977b]; the caudal entotympanic has been compared to the tupaine entotympanic [e.g., VAN KAMPEN, 1905; EVANS, 1942], but its development is utterly different and these elements are surely non-homologous.

An entotympanic exists in a handful of extinct eutherians often assigned to the insectivore dustbin, such as Leptictidae [NOVACEK, in press]. However, I confirm the generally-held assumption that entotympanics are undoubtedly absent in most or all living lipotyphlans. In none of the specimens investigated by me was there any instance of a separate rudiment within the fibrous membrane, or of pronounced elongation or apparent subdivision of the tubal cartilage.

One doubtful case still demands a careful investigation. FORSTER COOPER [1928] mentions that a small ossicle (?), the 'eustachian cover,' conceals the pharyngeal aperture of the bullar tubal canal in species of the golden mole Chrysochloris. I have seen an equivalent structure in adults of Carpitalpa stuhlmanni; it may simply represent a highly-calcified tubal cartilage, although it appears to be bony. This element is not identified in any of the studies dealing with chrysochlorid cranial development [BROOM, 1916; ROUX, 1947; SIMONETTA, 1957], and its status remains uncertain. If the 'eustachian cover' is an entotympanic, and not part of the hyoid apparatus as I suspect, its position is unusual in that it lies exterior to the bullar wall rather than within it.

MCKENNA [1975] places bats and colugos along with primates and tree shrews in the supposedly monophyletic taxon Archonta. Despite the implication contained in his telegraphic summary of the archontan tympanic floor, available ontogenetic data suggest that entotympanics are probably formed in all non-primate archontans [CARTMILL and MACPHEE, in press]. Ossification of entotympanic cartilages does not always occur in megachiropterans [VAN KAMPEN, 1905; NOVACEK, in press], however, and VAN DER KLAUW's [1922, 1930] identification of independent elements in the tympanic floors of young colugos has not yet been corroborated by other workers.

Conclusions

The following arguments are securely established or strongly buttressed by available data:

- (1) Entotympanics develop within the fibrous membrane of the tympanic cavity.
- (2) At least two categories of entotympanics can be defined by positional criteria. Whether this categorization obscures more than it reveals is moot. Observed variation in anlagen, course of development and primary associations may have no meaning; or, they may indicate that the term 'entotympanics' encompasses an assortment of non-homologous entities unified only by their tendency to develop independently.
- (3) There is some evidence to support the conclusion that entotympanics, whatever their nature, are eutherian neomorphs. Their existence in other mammalian groups, although possible, remains

undemonstrated.

(4) Modern primates lack independent entotympanics, but modern representatives of most of the orders with alleged primate ties possess at least one of these elements.

With these considerations in mind, it is necessary to come to some final conclusions about the entotympanic problem as it relates to primates.

DISCUSSION

The components of the primate petrosal plate develop like other tympanic processes and not like any known entotympanic. This is primary evidence against the one being derived from the other. But there is one aspect of petrosal plate development which may suggest a contrary conclusion to some, and that is the formation of secondary cartilage in young Microcebus. Under one interpretation, the secondary cartilage found in the anterior part of the plate in this lemur could represent the nearly, but not completely, suppressed rudiment of an entotympanic that has undergone primordial fusion with the petrosal.

The roots of the suppression theory extend back to the earliest phases of the debate over the supposed affinities of tree shrews and lemurs. Had this debate never arisen, the attempts to view the bullae of these mammals as homologous or mutually derived might not have been made. Among the features employed to bolster the homology argument were the shared presence in these mammals of an anular, enclosed ectotympanic [LEGROS CLARK, 1925, 1926, 1971] and a caudal tympanic

process of the petrosal [SPATZ, 1966]. CARTMILL and MACPHEE [in press] show that (1) the condition of the ectotympanic is achieved by different ontogenetic means in the two groups, and that (2), in addition to the fact that the caudal tympanic process is merely a general therian sympleiomorphy, its architecture in primates displays unique derived states not found in tupaiids. All that remains of the 'very significant' [LEGROS CLARK, 1925] otic evidence for special tupaiid-primate ties is the nature of the primate petrosal plate itself: can it be regarded, in whole or in part, as a suppressed entotympanic?

Secondary cartilages have sometimes been regarded as vestiges of phylogenetically-independent skeletal elements. The best known example of this is DE BEER's [1929] argument that the therian pterygoid is a compound bone. The therian pterygoid nearly always displays, at some ontogenetic stage, two morphological areas. The one is composed of typical intramembranous bone and is attached to the other, which is composed of secondary cartilage. After making a number of comparisons, DE BEER decided that the intramembranous part is the basitemporal or detached lateral wing of the parasphenoid, while the secondary cartilage represents the reptilian pterygoid.

Nonetheless, in the overwhelming majority of therians in which this point has been carefully investigated, the cartilaginous and intramembranous parts of the pterygoid are never separate, and there is no a priori reason to believe that they ever were [ELOFF, 1950]. DE BEER's appeal to primordial fusion is not convincing, however justified his interpretation of the therian pterygoid might be on other grounds. As he himself noted in a later work [DE BEER, 1937,

p. 505], primordial fusion is 'a dangerous precedent to go on, for there would be no check to speculative assumptions of fusion in order to explain all difficulties.' To my mind, recognition of secondary cartilage formations as the rudiments of phylogenetically independent bones can only lead to absurdities. Secondary cartilage is commonly found in fetu in the postglenoid area of the squamosal, the medial margins of the palatines, and the condyles of the dentary, but no morphologist or paleontologist would regard these as compound bones.

Furthermore, the term 'secondary cartilage' has been used to cover an extraordinary variety of tissues which appear under very different circumstances and at very different stages of development [WEIDENREICH, 1930; DURKIN, 1972]. Modern studies support the idea that the main function of secondary cartilage is to promote rapid growth [WEINMANN and SICHER, 1955; YUODELIS, 1966]. Mechanical stress may also play a role in its evocation, at least in birds [MURRAY, 1957]. As a final note, cells which produce secondary cartilage in the mandible of Mus are capable of forming either cartilage or bone, depending on local tissue conditions [HALL, 1968]. Economy of hypotheses leads one to the conclusion that embryonic secondary cartilage, whatever its function or functions, is an ontogenetic adaptation that provides no concrete evidence of supposed instances of primordial fusion. Also, it will not be surprising if future investigators find that secondary cartilage often forms in relation to rapidly-growing tympanic processes in other mammals.

Secondary cartilage develops only in the part of the petrosal plate originally derived from the rostral tympanic process in fetal

Microcebus. On the other hand, the caudal process is the only known tympanic wing which develops endochondrally. One might therefore ask, as VAN KAMPEN [1905] does for the caudal process of marsupials and lipotyphlans, whether this outgrowth (rather than the rostral process) was originally an independent element. Again, nothing in its development in insectivores or other mammals supports such an interpretation; it neither chondrifies nor ossifies independently of the auditory capsule. In order for VAN KAMPEN's notion to have any foundation, it must be demonstrated that an entotympanic does, in fact, exist in some marsupials or lipotyphlans or their immediate ancestors. Otherwise, there is no reason to believe that this hypothesis is particularly likely. Such a demonstration has not been and probably cannot be made. Also, there is the consideration that the caudal process and both entotympanics exist in some groups (e.g., elephant shrews; VAN DER KLAUW, 1929, 1931). I conclude that the caudal tympanic process, like the rostral, is just what it appears to be--a true derivative of the petrosal.

Accordingly, it is difficult to accept STARCK's [1975] supposition that an entotympanic may be present in modern Tarsius because cartilage occurs in the petrosal plate of young tarsiers. Although the cartilage is identified as 'enchondral,' it is not clear from STARCK's notes (or those of WÜNSCH [1975], who studied the same material) whether reference is being made to secondary cartilage like that found in fetal Microcebus or to the rudiment of the caudal tympanic process of the petrosal. It is evident from the discussion above that the actual situation, if it corresponds to one of these alternatives, makes no difference to interpretation. All lines of evidence are heavily in

favor of the view that entotympanics are absent in Recent primates.

I cannot evaluate with authority the fossil evidence for the construction of the primate tympanic floor, since I have not personally examined any of the relevant specimens. However, SZALAY's [1975, 1976] data strongly indicate that a petrosal (or compound petrosal-ectotympanic) bulla can still be regarded as diagnostic for all primates of modern aspect. Opinions regarding the plesiadapoid tympanic floor seem to undergo a regular fluctuation; HERSHKOVITZ [1977, p. 8 and fig. I.5] is the most recent author to resuscitate the proposition that an entotympanic is present in Plesiadapis [cf. RUSSELL, 1964]. If there is one, it is not clearly evident in HERSHKOVITZ' illustration of the CR 125 specimen. In any event, the possible presence of entotympanics in plesiadapoids and microsyopids [BOWN and GINGERICH, 1973; but see NOVACEK, in press], and their indisputable presence in non-primate archontans, only assumes significance if one believes that the lineages of these mammals and that of undoubted primates converge in something other than a basal eutherian [CARTMILL and MACPHEE, in press]. Even then, one must still ask what, in fact, entotympanics are and whether they have any utility for broad systematic purposes, given the present state of knowledge. Use of the terms 'rostral entotympanic' and 'caudal entotympanic' gives the impression that the homologies of these elements in different mammals are somehow clear and incontestible. To say the least, the bewildering contrasts they display, along all important embryological and morphological vectors, indicates that entotympanics may have evolved on several separate occasions. HUNT's [1974] recent demonstration that as many as three entotympanics can be found in some carnivores is one

more piece of evidence that promotes this idea.

In sum, I see no reason to believe that entotympanics exist in any living primate, either as independent entities or in the suppressed state. Nor do I believe that they have figured in primate ancestry, to the extent that this is known. Incidence data for fossil and Recent mammals reveal only that independent chondro-osseous elements of some sort have long been associated with the tympanic floor of many eutherians, including those with putative ties to primates. Frequency counts and cladistic considerations aside, assignation of one or any of the entotympanics to the pre-primate morphotype can mean nothing until and unless the homologies of different types of entotympanics are determined.

Therefore, with regard to the constitution of the primate ventral wall, and with some necessary violence to NEWTON's famous quip, non fingo ossa--I posit no bones.

SUMMARY

Entotympanics occur in most of the eutherian groups believed (by some authors) to have evolutionary ties with primates. A question which has often been asked, but never satisfactorily answered, is whether there are grounds for thinking that an entotympanic exists in primates or primate ancestors. Ontogenetic investigations reveal that no independent entotympanic is incorporated into the tympanic floors of Recent primates. However, the presence of both primary and secondary cartilage in the petrosal plate of young Microcebus might be taken as evidence for a suppressed entotympanic which no

longer develops separately.

A review of what is known about the rostral and caudal entotympanics shows that there is extraordinary variety in their development and associations with other structures of the auditory region. However, they can be unilaterally distinguished from true tympanic processes by reference to their developmental relations with the fibrous membrane of the tympanic cavity.

Constituents of the primate tympanic floor develop like other tympanic processes and not like any known entotympanic; this is primary evidence that they are not of the same nature. The evocation of secondary cartilage in the rostral tympanic process of the petrosal of prenatal Microcebus can be reasonably interpreted as an embryonic adaptation that has nothing to do with the primordial fusion of once-separate entities. Further, the fact that the caudal tympanic process of the petrosal develops endochondrally in all known cases is not good evidence for the thesis that this outgrowth represents a suppressed entotympanic.

An entotympanic may or may not have been present in plesiadapoids. However, even if one existed, the significance of its presence would depend on one's conception of the relationships between these archaic eutherians and undoubted primates. Likewise, the presence of entotympanics in non-primate archontans could imply that an entotympanic was present in pre-primates and subsequently lost--but only if it is assumed that the last common ancestor of archontans possessed one (which is wholly unproven, if not wholly unlikely).

ACKNOWLEDGEMENTS

I am indebted to Prof. Dr. R. HASSLER and Dr. H. STEPHAN (both of the Neurobiologische Abteilung, MPIH) and Prof. Dr. D. STARCK (then of the Anatomisches Institut, J.-W.-Goethe-Universität) for permission to study materials in their care. Dr. M. CARTMILL (Departments of Anatomy and Anthropology, Duke University) read and improved a draft of this paper; my errors are not his. I also thank Dr. D. G. STEELE (Department of Anthropology, University of Alberta) and Prof. Dr. W. B. SPATZ (Arbeitsgruppe für Morphologische Hirnforschung, Universität Freiburg im Breisgau) for various favors, and Mr. S. Saylor (Department of Anthropology, University of Winnipeg) for photographic assistance. Some phases of the research for this paper were made possible by a doctoral fellowship from the Canada Council and a grant from the Research Committee, University of Winnipeg.

REFERENCES

- BOWN, T.M. and GINGERICH, P.D.: The Paleocene primate Plesiolestes and the origin of Microsyopidae. *Folia primatol.* 19: 1-8 (1973).
- BROOM, R.: On the structure of the skull in Chrysochloris. *Proc. zool. Soc., Lond.* 1916: 449-459 (1916).
- CARTMILL, M. and MACPHEE, R.D.E.: Tupaiid affinities: the evidence of the carotid arteries and cranial skeleton; in LUCKETT Comparative biology and evolutionary relationships of tree shrews (Plenum, New York, in press).
- CLARK, W.E. LEGROS: On the skull of Tupaia. *Proc. zool. Soc., Lond.* 1925: 559-567 (1925).
- CLARK, W.E. LEGROS: On the anatomy of the pentailed tree shrew (Ptilocercus lowii). *Proc. zool. Soc., Lond.* 1926: 1179-1309 (1926).
- CLARK, W.E. LEGROS: The antecedents of man, an introduction to the evolution of the primates; 3rd ed. (Quadrangle Books, Chicago 1971).
- COOPER, C. FORSTER: On the ear region of certain of the Chrysochloridae. *Phil. Trans. R. Soc. Lond.* B216: 265-281 (1928).
- DEBEER, G.R.: The development of the skull of the shrew. *Phil. Trans. R. Soc. Lond.* B217: 411-480 (1929).

- DEBEER, G.R.: The development of the vertebrate skull (Clarendon, Oxford 1937).
- DURKIN, J.F.: Secondary cartilage: a misnomer? Amer. J. Orthod. 62: 15-41 (1972).
- ELOFF, F.C.: The homology of the mammalian pterygoid in the light of some new evidence. Proc. Linn. Soc. Lond. 162: 56-63 (1950).
- EVANS, F.G.: The osteology and relationships of the elephant shrews (Macroscelididae). Bull. amer. Mus. nat. Hist. 80: 85-125 (1942).
- FAWCETT, E.: The primordial cranium of Erinaceus europaeus. J. Anat., Lond. 53: 315-350 (1919).
- FRICK, H.: Die Entwicklung und Morphologie des Chondrokraniums von Myotis Kaup (Beitrag zur Kenntnis der Morphologie und Entwicklung des Chiropterkraniums III) (Georg Thieme, Stuttgart 1954).
- GREGORY, W.K.: The orders of mammals. Bull. amer. Mus. nat. Hist. 27: 3-524 (1910).
- HALL, B.K.: A histochemical study of the condylar secondary cartilage of the mouse, Mus musculus (Mammalia: Rodentia). Austr. J. Zool. 16: 807-813 (1968).
- HERSHKOVITZ, P.: The living new world monkeys (Platyrrhini), with an introduction to the primates, vol. 1 (University of Chicago Press, 1977).

- HUNT, R.M.: The auditory bulla in Carnivora: an anatomical basis for reappraisal of carnivore evolution. J. Morphol. 143: 21-76 (1974).
- KAMPEN, P.N. VAN: Die Tympanalgegend des Säugetierschädels. Morph. Jb. 34: 321-722 (1905).
- KAMPEN, P.N. VAN: De phylogenie van het entotympanicum. T. nederl. dierk. Ver. 14: xxiv (1915).
- KERMACK, K.A. and KIELAN-JAWOROWSKA, Z.: Therian and non-therian mammals; in KERMACK and KERMACK Early mammals, pp. 103-115 (Academic Press, London 1971).
- KIELAN-JAWOROWSKA, Z.: Unknown structures in multituberculate skull. Nature, Lond. 226: 974-976 (1970).
- KLAAUW, C.J. VAN DER: Über die Entwicklung des Entotympanicums. T. nederl. dierk. Ver. 18: 135-174 (1922).
- KLAAUW, C.J. VAN DER: On the development of the tympanic region of the skull in the Macroscelididae. Proc. zool. Soc., Lond. 1929: 491-560 (1929).
- KLAAUW, C.J. VAN DER: On mammalian auditory bullae showing an indistinctly complex structure in the adult. J. Mammal. 11: 55-60 (1930).
- KLAAUW, C.J. VAN DER: The auditory bulla in some fossil mammals, with a general introduction to this region of the skull. Bull. amer. Mus. nat. Hist. 62: 1-352 (1931).

- KÜHN, H.-J.: Die Entwicklung und Morphologie des Schädels von Tachyglossus aculateus. Abh. Senckenb. Naturforsch. Ges. 528: 1-224 (1971).
- MACPHEE, R.D.E.: Ontogeny of the ectotympanic-petrosal plate relationship in strepsirhine prosimians. Folia primatol. 27: 245-283 (1977a).
- MACPHEE, R.D.E.: Auditory regions of strepsirhine primates, tree shrews, elephant shrews and lipotyphlous insectivores: an ontogenetic perspective on character analysis; Ph.D. diss., Univ. of Alberta (1977b).
- MCKENNA, M.C.: New evidence against the tupaoid affinities of the mammalian family Anagalidae. Amer. Mus. Novit. 2158: 1-16 (1963).
- MCKENNA, M.C.: Toward a phylogenetic classification of the Mammalia; in LUCKETT and SZALAY Phylogeny of the primates, a multidisciplinary approach, pp. 21-46 (Plenum, New York 1975).
- MURRAY, P.D.F.: Cartilage and bone: a problem in tissue differentiation. Austr. J. Sci. 14: 65-73 (1957).
- NOVACEK, M.J.: Aspects of the problem of variation, origin and evolution of the eutherian auditory bulla. Mammal Rev. (in press)
- REINBACH, W.: Zur Entwicklung des Primordialcraniums von Dasypus novemcinctus Linné (Tatusia novemcincta Lesson) II. Z. Morph. Anthropol. 45: 1-72 (1952).

- ROUX, G.H.: The cranial development of certain Ethiopian 'insectivores' and its bearing on the mutual affinities of the group. Acta. zool., Stockh. 28: 165-397 (1947).
- RUSSELL, D.E.: Les mammifères paléocènes d'Europe. Mém. Mus. natl Hist. nat., Paris, sér. C 13: 1-324 (1964).
- SCHNEIDER, R.: Zur Entwicklung des Chondrocraniums der Gattung Bradypus. Morph. Jb. 95: 210-301 (1955).
- SEGALL, W.: The middle ear region of Dromiciops. Acta anat. 72: 489-501 (1969).
- SIMONETTA, A.: Condrocranio e dermascheletro di 'Chrysochloris asiatica' (Linnaeus). Monit. zool. ital. 65: 28-47 (1957).
- SPATZ, W.B.: Zur Ontogenese der Bulla tympanica von Tupaia glis Diard 1820 (Prosimiae, Tupaiiformes). Folia primatol. 4: 26-50 (1966).
- STADTMÜLLER, F.: Krania und Visceralskelett der Säugetiere; in BOLK, GÖPPERT, KALLIUS and LUBOSCH Handbuch der vergleichenden Anatomie der Wirbeltiere, vol. 4, pp. 839-1016 (Urban & Schwartzburg, Berlin 1936).
- STARCK, D.: Le crâne des mammifères; in GRASSÉ Traité de zoologie, vol. 16 (1), pp. 405-549, 1095-1102 (Masson, Paris 1967).
- STARCK, D.: The development of the chondrocranium in primates; in LUCKETT and SZALAY Phylogeny of primates, a multidisciplinary approach, pp. 127-155 (Plenum, New York 1975).

- SZALAY, F.S.: The paleobiology of the earliest primates; in TUTTLE The functional and evolutionary biology of primates, pp. 3-35 (Aldine, Chicago 1972).
- SZALAY, F.S.: Phylogeny of primate higher taxa: the basicranial evidence; in LUCKETT and SZALAY Phylogeny of primates, a multidisciplinary approach, pp. 91-125 (Plenum, New York 1975).
- SZALAY, F.S.: Systematics of the Omomyidae (Tarsiiformes, Primates), taxonomy, phylogeny and adaptations. Bull. amer. Mus. nat. Hist. 156: 157-450 (1976).
- SZALAY, F.S.: Phylogenetic relationships and a classification of the eutherian Mammalia; in HECHT, GOODY, and HECHT Major patterns in vertebrate evolution, pp. 315-374 (Plenum, New York 1977).
- WEIDENREICH, F.: Das Knochengewebe; in VON MOLLENDORFF Handbuch der mikroskopischen Anatomie des Menschen, vol. 2, pp. 391-508 (Springer, Berlin 1930).
- WEINMANN, J.P. and SICHER, H.: Bone and bones, fundamentals of bone biology; 2nd ed. (Mosby, Saint Louis 1955).
- WÜNSCH, D.: Zur Kenntnis der Entwicklung des Craniums des Koboldmaki, Tarsius bancanus borneanus, Horsfield, 1821 (Beiträge zur Kenntnis des Primaten-Craniums IV) (Selbstvlg. Senckenb. Anat. Inst., J.-W.-Goethe-Univ., Frankfurt/M. 1975).

YUODELIS, R.H.: The morphogenesis of the human temporomandibular joint and its associated structures. J. den. Res. 45: 182-191 (1966).

R.D.E. MacPhee, Department of Anthropology, The University of Winnipeg,
Winnipeg, Manitoba R3B 2E9 (Canada)

FIGURE 1. Relationship of the fibrous membrane and the rostral tympanic process of the petrosal in a prenatal specimen of the mouse lemur, Microcebus murinus (MPIH 1964/41, CRL 34.5 mm; s. 905, Azan). The rostral tympanic process (or anterior part of the petrosal plate) has just begun development in this specimen. Its trabeculae are entirely enclosed within the periosteal tissues (asterisks) of the promontorium. Note that the process clearly arises adjacent to rather than within the fibrous membrane. Scale represents 0.1 mm.

(In this and all succeeding figures, frontal sections of the apparent left-hand side of the skull are illustrated. For abbreviations used in figs. 1-6, see p. 38.)

FIGURE 2. Relationship of the fibrous membrane and the tympanic process of the basisphenoid in a near-term fetus of the streaked tenrec, Hemicentetes semispinosus (MPIH 1964/45, CRL 40.0 mm; s. 1352, Azan). A illustrates major otic structures; B, an enlarged view of the same section, shows that the tympanic process of the basisphenoid grows along the intratympanic surface of the fibrous membrane (identified by arrows). Thus petrosal tympanic processes (cf. fig. 1) are not unique in their relationship to this membrane. Scale represents 0.2 mm in A and 0.1 mm in B.

FIGURE 3. Caudal tympanic process of the petrosal (posterior part of the petrosal plate) in a young fetus of the dwarf galago, Galago (Galagoides) demidovii (MPIH 102, CRL 26.0 mm; s. 563, Cresyl Violet). Although the cartilaginous caudal process of galagine fetuses is rather large compared to that of many other mammals, its development is identical. Note that it is continuous with the sidewall of the auditory capsule in the area beneath the lateral semicircular canal. Scale represents 0.2 mm.

FIGURE 4. Secondary cartilage in the part of the petrosal plate derived from the rostral tympanic process in a fetus of Microcebus murinus (MPIH 1964/42, CRL 41.0 mm). A Major otic structures (s. 1120, Azan). B Enlarged view of secondary cartilage (s. 1126, Heidenhain-Woelke). With the latter stain, bone matrix and cartilage cells stain black, while cartilage matrix is colorless (or slightly darkened, if calcified). The secondary cartilage (asterisk in fig. 4A) of the petrosal plate is less organized in appearance than the (primary) cartilage of Reichert's cartilage (lower right). Arrows identify apparent chondroclasts. Scale represents 0.2 mm in A and 0.1 mm in B.

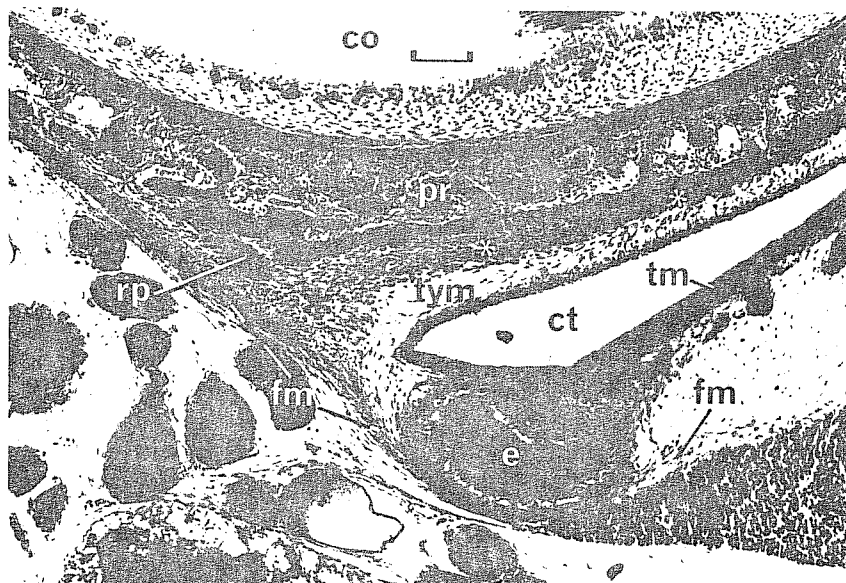
FIGURE 5. Development of the entotympanic in a near-term fetus (A) and neonate (B) of the common tree shrew, Tupaia glis. A Major otic structures (MPIH 1960/82a, CRL 54.0 mm; s. 1020, Azan). B Enlarged view of the entotympanic cartilage at an early stage of development (MPIH 1959/4, CRL 59.0 mm; s. 322/1, Azan). In A, the fibrous membrane is well developed, but the entotympanic has not yet appeared. In B, the nascent entotympanic cartilage is clearly contained within the fibrous membrane. Further rostrally, the entotympanic cartilage is continuous with the tubal cartilage. The fibrous membrane is not fused with the tympanic membrane in B, despite its close approach to the latter. Scale represents 0.2 mm in A and 0.1 mm in B.

FIGURE 6. Development of the fibrous membrane, tubal cartilage and entotympanics in fetuses of the Congolese long-eared elephant shrew, Elephantulus fuscipes. A Magnified view of the fibrous membrane (MPIH 311/E1, CRL 31.0 mm; s. 1190, Azan). B Major otic features (MPIH 305/E, CRL 43.0 mm; s. 1581, Azan). C Enlarged view of the entotympanics in latter specimen (s. 1570, Cresyl Violet). Neither of the entotympanics is represented in the younger fetus, MPIH 311/E1; the cartilaginous structure embedded in the fibrous membrane in A is the posterior end of the tubal cartilage. The fibrous membrane is not evident medially in B and C because the entotympanics have already attained large size. Note that the histological characteristics of the rostral entotympanic cartilage differ only slightly from those of the upper part of the caudal entotympanic (with which it is seemingly fused). The ventral part of the caudal entotympanic, however, is composed of typical woven bone (asterisk). The apparently-isolated piece of bone above the rostral entotympanic is actually part of the basisphenoid. The arrow in C identifies the location of the ectotympanic-caudal entotympanic suture. Scale represents 0.1 mm in A and C and 0.2 mm in B

Abbreviations used in figures 1-6

ac	cartilage of the auricle
al	alisphenoid bone
b	basisphenoid bone
bp	tympanic process of the basisphenoid
cat	cartilage of the auditory tube
cen	caudal entotympanic
co	cochlea
CRL	crown-rump length
cs	central stem
ct	cavum tympani
cp	caudal tympanic process of the petrosal
e	ectotympanic
eam	external acoustic meatus
fm	fibrous membrane of the tympanic cavity
g	gonial
lsc	lateral semicircular canal
MPIH	Max-Planck-Institut für Hirnforschung (Neurobiologische Abteilung)
m	malleus
mc	Meckel's cartilage
pa	promontory artery
pp	petrosal plate (rp + cp)
pr	promontorium of the petrosal
rc	Reichert's cartilage
ren	rostral entotympanic
rp	rostral tympanic process of the petrosal

s	stapedius muscle
sq	squamosal
tm	tympanic membrane
tt	tegmen tympani
tym	tympanic myxomatous tissue
ut	utricle
v	trigeminal nerve



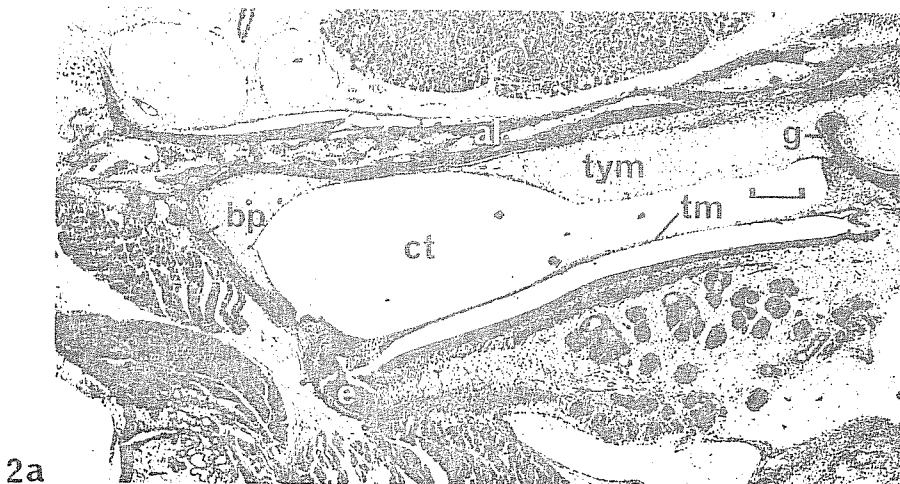
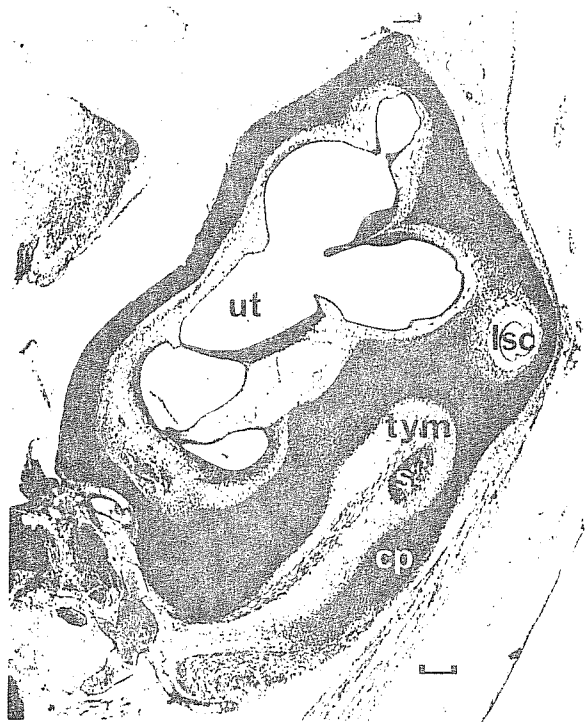
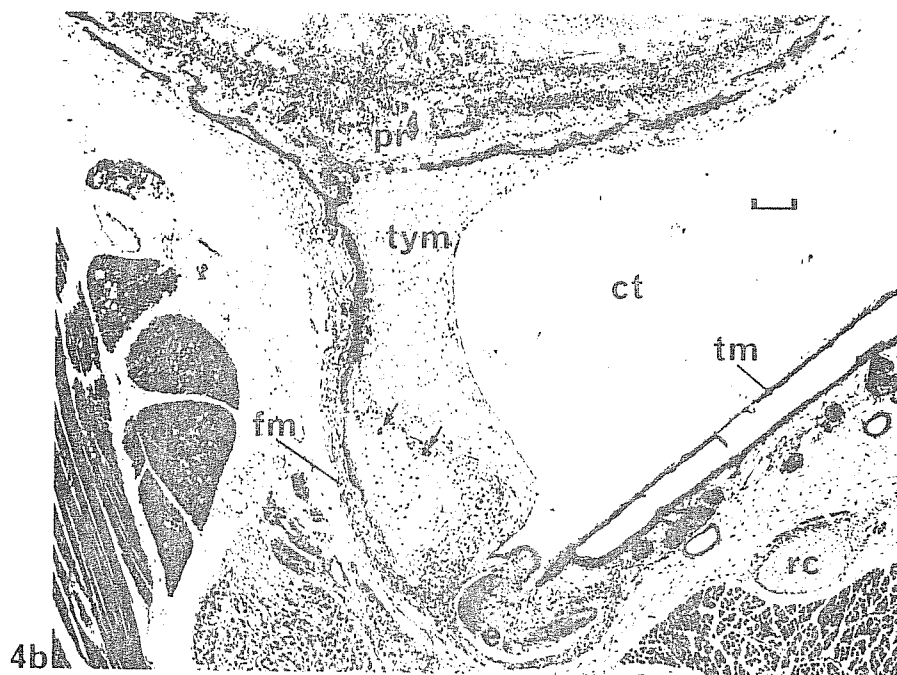
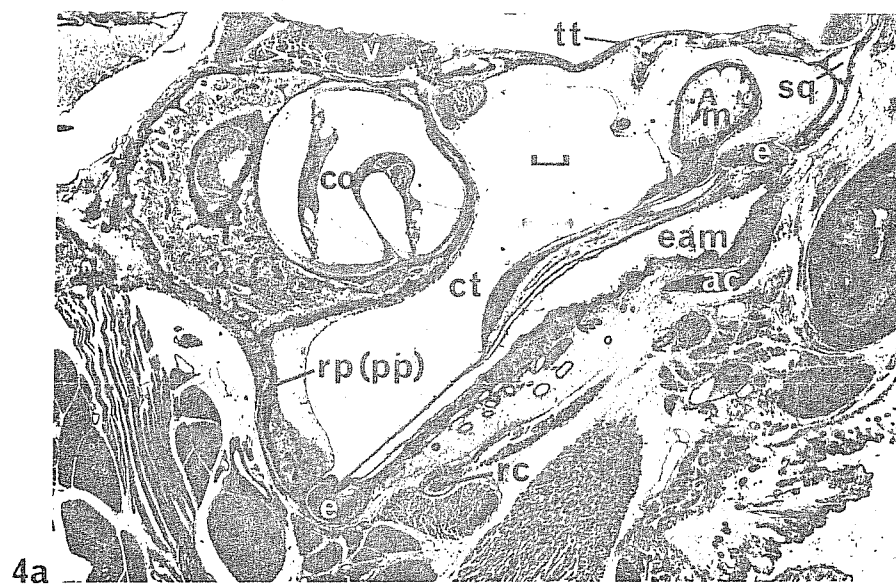
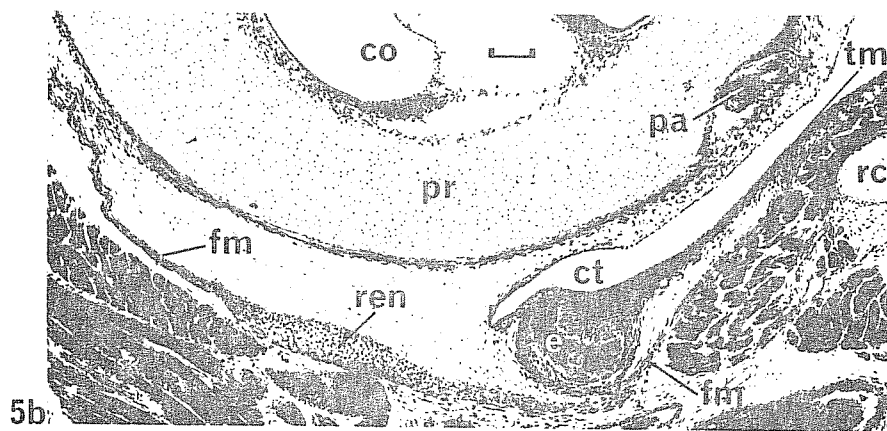
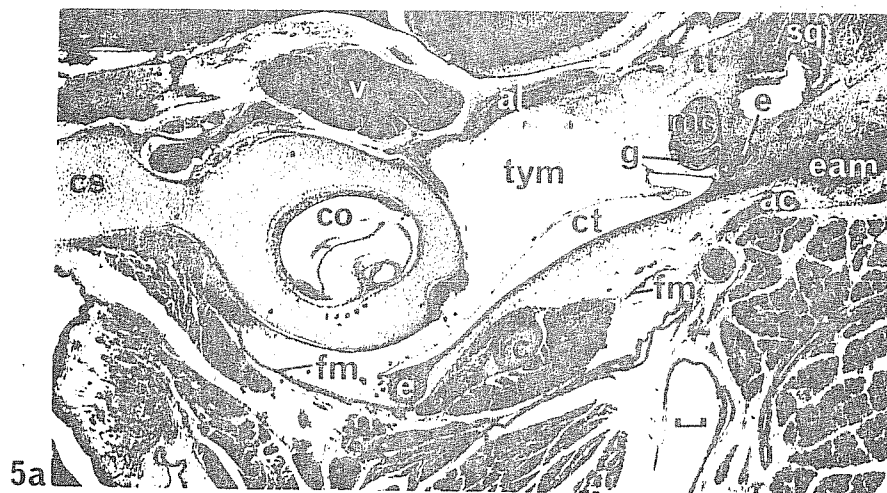


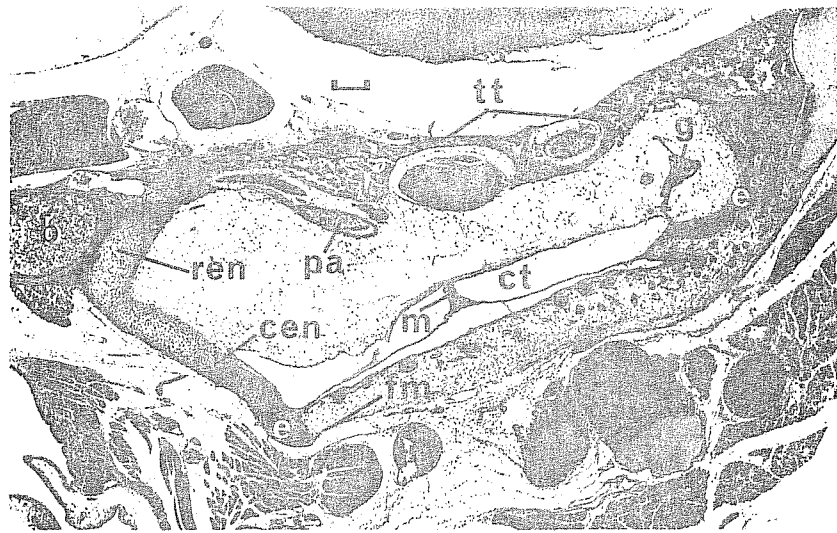
Fig. 1 (b)



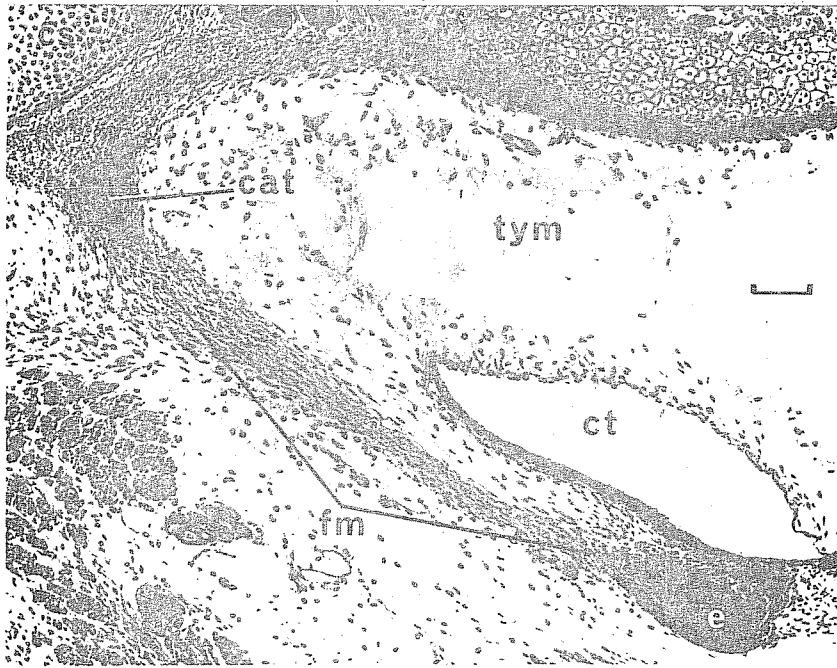
3







6b



6a

