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Development of the auditory organ in terrestrial, semi-aquatic, and aquatic mammals

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Abstract

This is an extensive comparative study of prenatal development of the peripheral auditory system in mammals. A wide range of ecologically different species were studied, including terrestrial, semi-aquatic, and aquatic species with auditory systems that perceive low, middle, and high frequencies. Structural peculiarities of the development of the auditory system were determined for each species studied in relation to its frequency range and to the acoustic properties of the medium. The stages of morphological adaptations found in terrestrial, semi-aquatic, and aquatic species are described. The data reveal general principles of development of the peripheral auditory system in mammals with different ecological specializations.

Key words: peripheral auditory system, outer, middle, inner ears, middle ear ossicles, tympanic membrane, prenatal development, Organ of Corti, terrestrial, semi-aquatic, aquatic species, external auditory meatus.

Introduction

The mammalian auditory system is characterized by great anatomical complexity. Studies on the peripheral auditory system have a long history. Over the years, studies of auditory structure in terrestrial mammals of different evolutionary lines produced many publications on morphology, physiology and biomechanics (Hensen, 1863; Doran, 1878; Denker, 1901; Bekesy, 1936; Pye, 1973).

Investigations into the auditory system of marine mammals (Cetacea, Pinnipedia), which have a distinctive trend in the evolution of placental animals, began over three centuries ago. These works were largely anatomical (Denker, 1902; Eschricht, 1849; Huber, 1934; Clarke, 1948; Reysenbach de Haan, 1957; Fraser & Purves, 1960; Fleischer, 1973; Ramprashad, 1975; Ketten, 1992). This approach made understanding the operation of the echolocation apparatus more difficult and led inevitably to misinterpretation of reception mechanisms for acoustic signals underwater.

We previously studied the postnatal ontogenetic structure of the outer, middle, and inner ear in representatives of different ecological groups (Bogoslovskaya & Solntseva, 1979), but we felt the need to conduct a comparative embryological analysis of prenatal development of all components of the peripheral auditory system in terrestrial, semi-aquatic, and aquatic mammals with high, middle, and low frequency hearing. Thus, we have been able to study in more detail the structural features of the auditory organ in the species under study, to understand how characteristic features of its formation account for some structural adaptations in aquatic species, and to determine their formation stages.

Prenatal development of the ear in laboratory animals and in humans has been described in a number of papers (Kölliker, 1861; Alexander, 1900; Brunner, 1934; Cooper, 1948, Titova, 1968).

There are abundant data on the development of the auditory system in terrestrial forms, but information on embryos of Cetacea and Pinnipedia is scarce. Developmental studies on marine mammals were primarily concerned with the anatomy of single auditory structures at one of the stages of later embryogenesis or fetal period (Kükenthal, 1889–1893). The complete absence of data on the development of the auditory system of Cetacea and Pinnipedia in early developmental stages made it difficult to establish the development of the peripheral auditory system in mammals.

We have performed a comparative embryological study of the auditory system in the terrestrial, subterranean, semi-aquatic, and aquatic species in the early embryogenesis (as defined by Schmidt, 1968); i.e., beginning at the formation of the auditory vesicle (the stage of the forelimb bud) to the complete formation of primary auditory structures. This study showed certain differences and similarities at developmental stages.

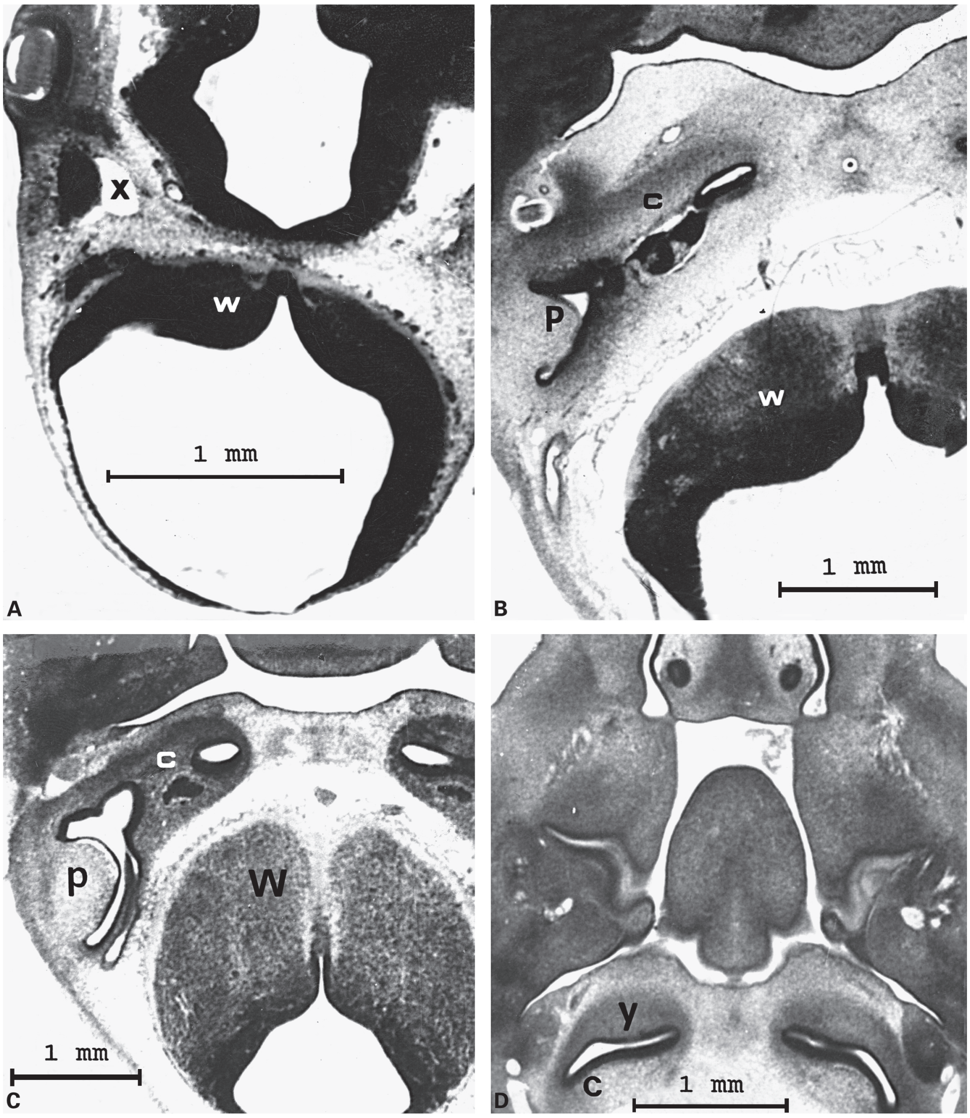

Figure 1. Dorso-ventral sections of the head showing the auditory organ of embryos: A- *Balaenoptera acutorostrata*, stage 13. Development of the acoustic vesicle (the forelimb bud); B- *Balaenoptera acutorostrata*, stage 14–15; C- *Rattus norvegicus*, stage 14–15. The division of the acoustic vesicle into lower (cochlear canal) and upper (vestibular apparatus) parts. The rudiments of the auditory ossicles are seen as independent formations; D- *Cavia porcellus*, stage 16. Formation of the basal turn of the cochlea. Labels for all figures: W- cerebrum; X- acoustic vesicle; C- cochlea; P- vestibular apparatus; Y- auditory capsula; B- pinna; A- external auditory meatus; m- malleus; i- incus; s-stapes; venous sinus; f- tympanum; g- basal turn; e- middle turn; n- apical turn; F- acoustic nerve; U-cochlear nerve; Z- vestibular nerve; k- m. stapedius; h- m. tensor tympani; q- cavernous plexus; J- fibrous ligament; T- tympanic membrane; N- vestibular scala; G- tympanic scala; d- cochlear canal; r- Reissner's membrane; H- tympanic bulla; R- peribullar sinus; Sk- stria vascularis; Q- spiral ligament; 1s- primary osseous spiral lamina; 2s- secondary osseous spiral lamina; we- inner hair cells; ne- outer hair cells; D- columnar cells; E- cuboidal epithelium.

It should be noted that in developmental studies of various organs, auditory organs included, most investigators rely on the length of the different embryos, which is a poor basis for comparison in a comparative series. The term of pregnancy and length of embryos at similar stages vary greatly among different species. However, in experimental embryology there is a widely used concept of equivalent stages of an animal's development (Otis & Brent, 1954).

To compare embryos of different species, several investigators (Dyban, Puchkov, Baranov, Samoshina & Chebotar, 1975) have studied the normal development of some laboratory animals. These authors categorized developmental stages according to characters common to different species.

In order to compare formation of the peripheral auditory system in different mammal species, we compared outer, middle, and inner ear structures at similar developmental stages using tables of normal development for laboratory animals (Dyban *et al*., 1975). Most mammals follow a similar sequence of development of outer, middle, and inner ear structures. Therefore, for the sake of description, we used known developmental stages for some terrestrial forms (as defined by Dyban *et al*., 1975).

A comparison was made also of the developmental level of outer, middle, and inner ear structures with stages at which the mesenchymous tissue is replaced by embryonic cartilage.

Material and methods

The following species of mammals were used in the study: Insectivora—mole (*Talpa europaea*); Microchiroptera—lesser horseshoe bat (*Rhinolophus hipposideros*), greater horseshoe (*Rhinolophus ferrumequinum*), great (*Nyctalis noctula*), mouse-eared bat (*Myotis myotis*); Rodentia—rat (*Rattus norvegicus*), guinea pig (*Cavia porcellus*); Cetacea—Odontoceti: spotted dolphin (*Stenella attenuata*), common dolphin, (*Delphinus delphis*), bottle-nosed dolphin (*Tursiops truncatus*); harbor porpoise (*Phocaena phocaena*); beluga (*Delphinapterus leucas*); Mysticeti: Minke whale (*Balaenoptera acutorostrata*); Artiodactyla—pig (*Sus scrofa domestica*); Pinnipedia-Otariidae: eared seal (*Eumetopias jubatus*); Phocidae: ringed seal (*Pusa hispida*), bearded seal (*Erignathus barbatus*); Odobenidae: walrus (*Odobenus rosmarus divergens*).

Specimens were fixed in 10% buffered formalin and Wittmaak fixative then dehydrated and treated in an increasing series of ethanols, embedded in celloidin and sectioned at 10–15 micron thickness in a dorso-ventral plane. The sections were stained with hematoxylin-eosin according to the methods of Mallory and Kulchitsky, and impregnated with silver nitrate.

Results

The results of the comparative embryological study show that in all the species studied the peripheral auditory system develops in the early embryogenesis; i.e., in the period from the formation of the auditory vesicle (stage 13) to the completion of the main structures of the peripheral auditory system (stage 20) during the formation of the cartilaginous skeleton (Solntseva, 1983; 1985*a*; 1985*b*; 1986; 1987; 1988*a*; 1988*b*; 1990; 1992; 1993).

Figure 2. Dorso-ventral sections of the head showing the auditory organ of *Erignathus barbatus*, stage 16. The basals turn of the cochlea is formed. Labels as in Fig. 1.

In the early embryogenesis (stages 13–16) a similarity was found in the formation of the outer, middle, and inner ear structures. The paired rudiments of the membranous labyrinth are observed at the stage of 2–3 pairs of somites (Wilson, 1914). Later, at the stage of 6–9 pairs of somites, the auditory placode is formed (Kappers, 1941). At the stage of 14–15 pairs of somites, the auditory pit is visible, from which the auditory vesicle develops later at the stage of 20 somite pairs (forelimb bud, stage 13) (Titova, 1968) (Fig. 1A). In all species studied, at stage 13, the rudiment of the ossicles (in the form of condensed mesenchyme) is found. Subdivision of the auditory vesicle into the upper and lower parts is noted at stages 14–15 (Figs. 1B and C). The cochlear canal is formed from the lower part and from the upper part, the vestibular apparatus. The basal cochlea canal is formed by the columnar epithelium and consist of cuboidal epithelium are differentiated (stage 16). At this stage, the cochlea canal begins twisting into a spiral shape to form the basal turn of the cochlea (Fig. 1D). The capsule surrounding the cochlea consists of condensed mesenchyme.

At stage 16, a depression surrounded by small tuberculae is formed from the first branchial cleft. In the early embryogenesis the auditory meatus is

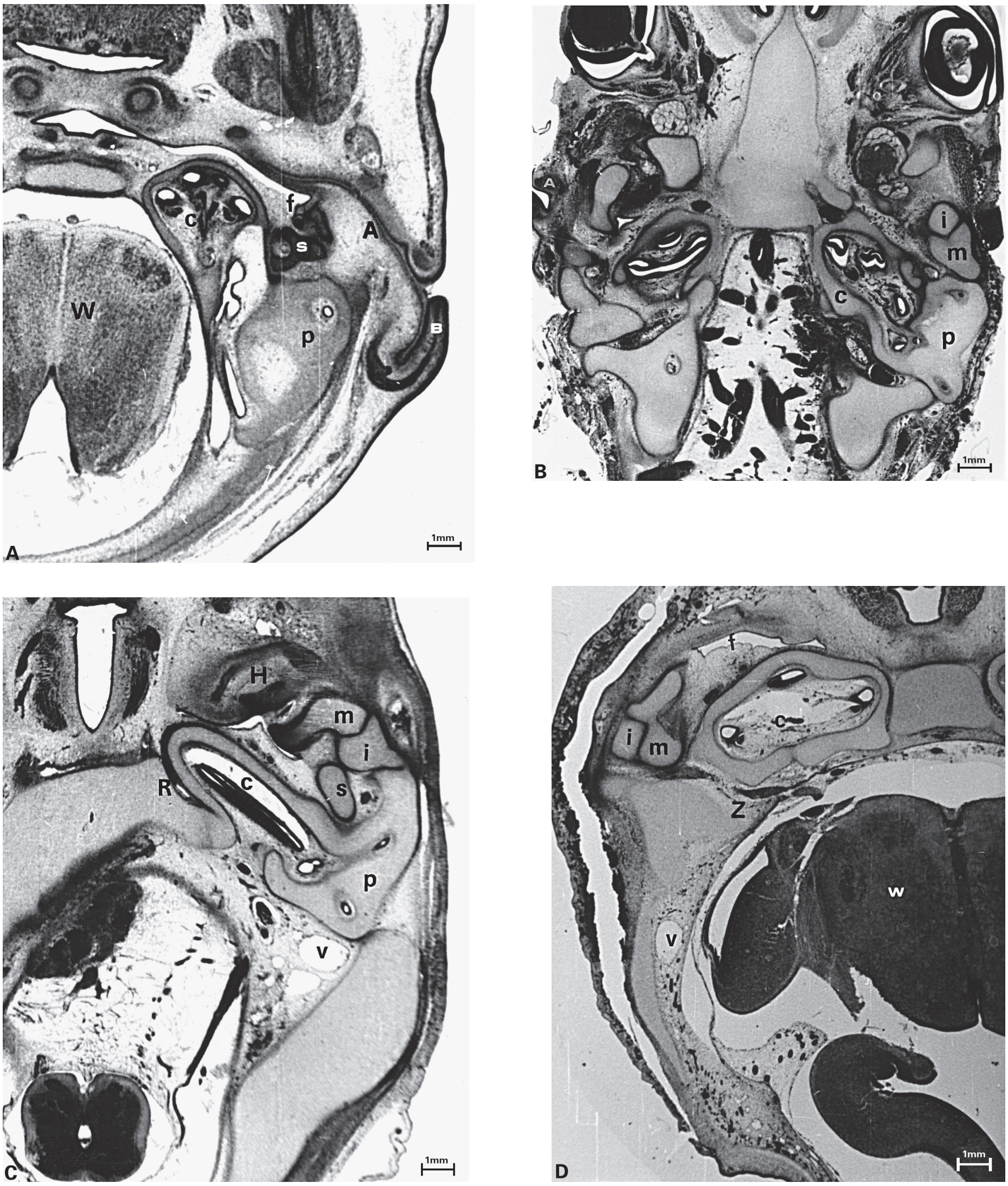

Figure 3. Dorso-ventral sections of the head showing the auditory organ in embryos. stage 17. A- *Rattus norvegicus*. Clear contours of the pinna are shown; B- *Erignathus barbatus*; C- *Balaenoptera acutorostrata*; D- *Stenella attenuata*. Rigid joint between the malleus and incus (at right angles) is shown. The middle turn of the cochlea is formed. Labels as in Fig. 1.

patent in all species. The middle ear is formed as a protrusion of the first pharyngeal pouch. As already mentioned, the rudiment of the ossicles in all species studied appears at stage 13 as a condensed mesenchyme. At stage 16, the contours of the rudiment of the auditory ossicles are clearly distinguished, appearing as separate components (Fig. 2). At this stage the middle ear cavity is a narrow blind

Figure 4. Dorso-ventral sections of the head showing the auditory organ of *Balaenoptera acutorostrata*, stage 18. The external auditory meatus has been formed, but is open. Labels as in Fig. 1.

canal running under the rudiment of the auditory ossicles. The rudiment of the tympanic membrane is visible.

At stage 17, in the inner ear, the middle turn of the cochlea is formed (Figs. 3A, B, C and D). In the outer ear, a single mesenchymal rudiment of the pinna is formed as a result of fusion of the tuberculae surrounding the poroid (Fig. 3A). In the middle ear each of the rudiments of the auditory ossicles is an independent formation consisting mainly of immature cartilaginous tissue. In all species, the tympanic membrane is thick and soft. The middle ear cavity is enlarged. The distal part of the auditory meatus is filled with epithelial cells (Fig. 4).

At stage 18, formation of the cochlea is complete in most of the species. The apical turn is complete (Figs. 5A, B, C. D and E). The ear capsule becomes cartilaginous. The cell elements of the Organ of Corti are at the same stage of cell differentiation in all cochlea turns. At this stage the columnar epithelium looks as if it has been drawn apart, with two thickenings, axial and lateral. In the outer ear, the Pinna acquires more distinct contours and a small curl appears. At this stage, in some Phocidae (*Pusa hispida*) (Solntseva, 1988), the pinna does not develop in the fetal period and is absent in adults (Fig. 6). The cartilaginous part of the external auditory meatus in all species studied is a straight, short canal. Its osseous part is formed later. The osseous part of the external auditory meatus is formed early in the mature born species (Cetacea, Pinnipedia, Artiodactyla), before birth. In the immature born species (rats, bats) its osseous part is formed in the early postnatal ontogenesis. In the middle ear, the structural elements of the auditory ossicles are formed within the middle ear cavity (Figs. 7A and B). The malleal head, neck and manubrium are clear, as are the body and two arms (short and long) of the incus. The stapes is subdivided into footplate and crus. The auditory ossicles consist mainly of the mature cartilaginous tissue by embryonic hyaline cartilage. This process is uneven, it begins in the centre of each rudiment of the auditory ossicles and gradually extends to the periphery. The ossicles are surrounded by mesenchyme consisting of small, flat cells, or chondroblasts. Owing to the presence of mesenchyme,

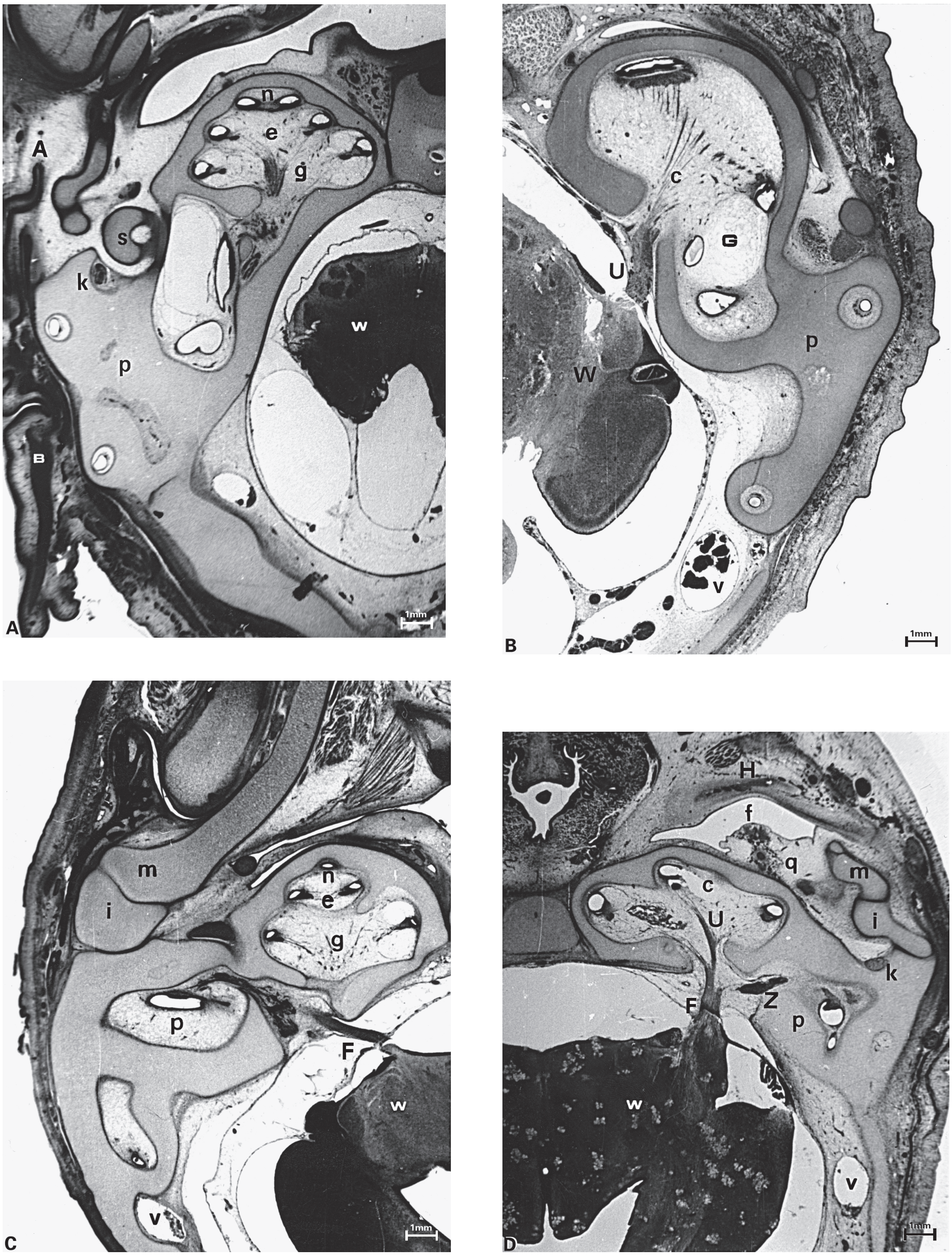
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Figure 5 A–D.

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Figure 5. Dorso-ventral sections of the head showing the auditory organ in embryos, stage 18. A- *Sus scrofa*. Number of the cochlear turns-3, 0; B- *Erignathus barbatus*. Number of the cochlear turns- 2, 5; C- *Odobenus rosmarus*. Number of the cochlear turns-2, 5; D- *Stenella attenuata*. Number of cochlear turns-2, 0; formation of the cavernous plexus; E- *Balaenoptera acutorostrata*. Number of the cochlear turns- 2, 5. Anatomical formation of the cochlea is completed. The formed structures of the outer, middle and inner ears are shown. Labels as in Fig. 1.

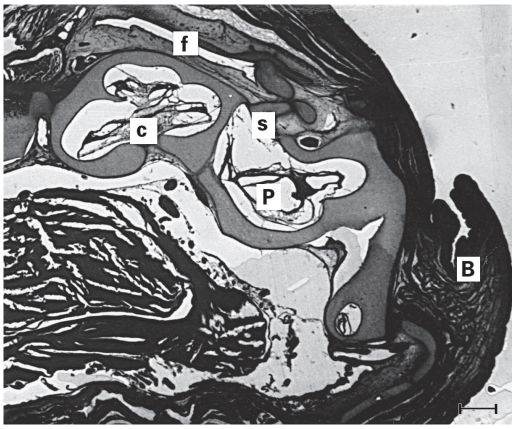


Figure 6. Dorso-ventral sections of the head showing the auditory organ of *Pusa hispida*, stage 18–19. The rudimentary pinna, which does not develop in the fetal period and is absent in adults. Labels as in Fig. 1.

the junctures of the auditory ossicles are clearly distinguishable. At stage 18, the features appear which are determined by relative positions of the auditory ossicles. The ossicles have changed their position and turned around the sagittal and frontal body axes (Fig. 7C). The stapes is caudal relative to the malleus and incus. After the turn, the footplate stapes is found caudal. The tympanic membrane is thin, consists of three layers, and rests on the lateral side of the middle ear cavity. In Odontoceti and Mysticeti the tympanic membrane follows similar developmental stages (Figs. 8A, B and C); in the fetal period their structure acquires species-specific features.

At stage 19, the elements of the cochlear canal and the cells of the Organ of Corti are differentiated. Differentiation of the elements of the cochlear canal and cells of the Organ of Corti begins in the basal turn of the cochlea. Then the process gradually extends to the higher turns (Fig. 9A, B, C and D). As a result, one observes different stages of the anatomical and cell differentiation in the turns of the cochlea. The cuboidal epithelial cells flatten and the adjacent connective tissue loosens. Here begins formation of the vestibular and tympanic scalae. The cells of the Organ of Corti are differentiated from the columnar cells, which look as if they were forced apart. By the end of the stage 19, the lateral part of the external auditory meatus is filled with epithelial cells. In Cetacea and Pinnipedia, species-specific features are formed in the outer ear. In Pinnipedia, the cartilaginous part of the external auditory meatus is noticeably narrowed in the distal part. In Odontoceti, Phocidae and Odobenidae the auditory meatus is considerably elongated, and assumes an S-shape. The cartilage is formed around the auditory meatus. In the middle ear formation of the middle ear cavity continues and the auditory ossicles become cartilaginous. The substitution of the immature cartilaginous tissue by the primary cartilaginous tissue one does not occur simultaneously in the various species. For example, in *Rattus norvegicus*, the auditory ossicles at this stage still consist mainly of precartilaginous tissue. In *Cavia porcellus*, the malleus is wholly cartilaginous, whereas in the incus and stapes, the substitution process is only beginning. In *Sus scrofa* only the malleus is cartilaginous. In bats, just as in rats, the ossicles consist of the precartilaginous tissue. In Pinnipedia, the maturation of auditory ossicles occurs at different times. The first to mature are the malleus and the body of the incus, whereas, the lenticular arm of the incus and stapes consists of mature cartilaginous tissue. Conversely, in Cetacea, the incus and stapes are the first to become cartilaginous; in the malleus formation of cartilage has only begun. However, in the mature born species, replacement of the precartilaginous tissue by embryonic cartilage is completed by stage 20.

At stage 20, in the inner ear of cetaceans and bats, the cochlea is greatly enlarged as compared to the vestibular apparatus (almost two-fold). In all the species studied, in the cochlear canal, differentiation of the spiral limbus, stria vascularis and Reissner's membrane begins (Fig. 9D). The

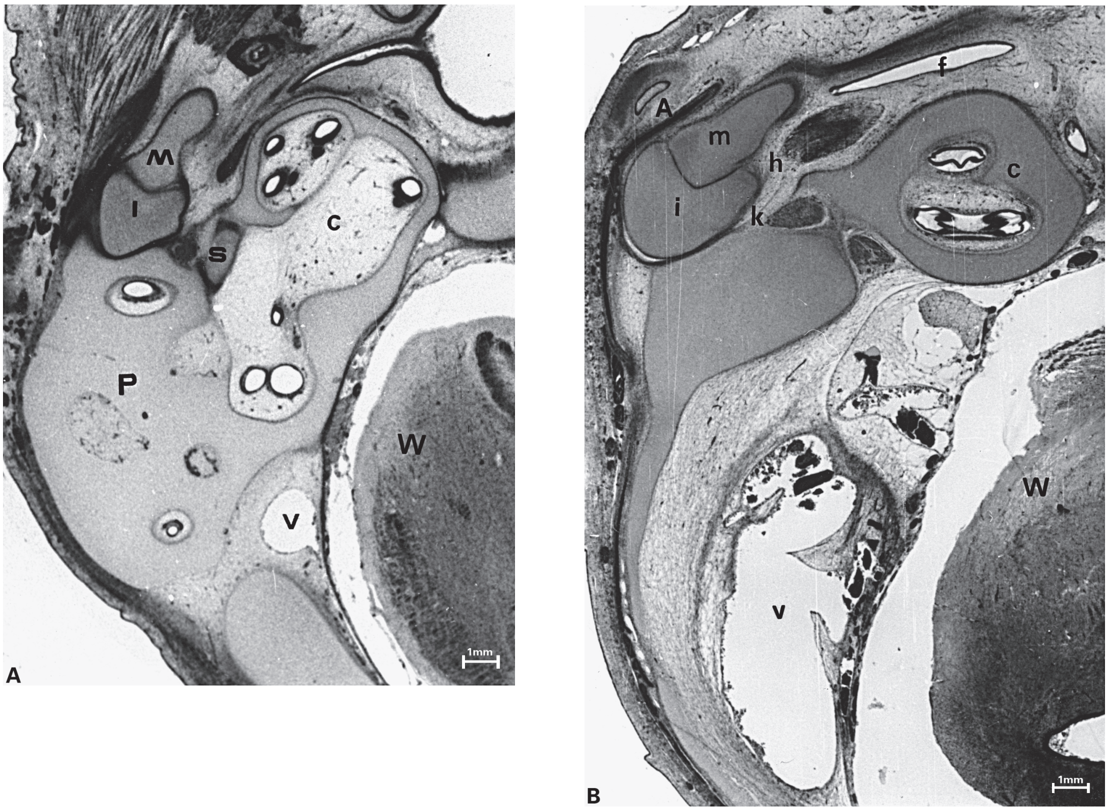
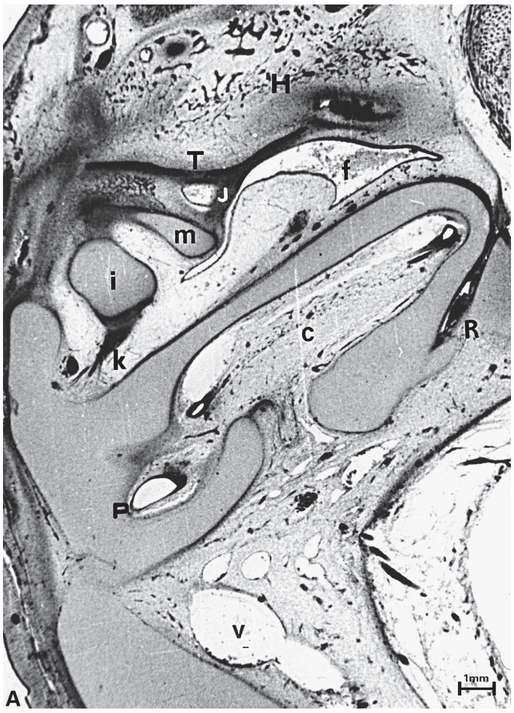


Figure 7. Dorso-ventral sections of the head showing the auditory organ in embryos, stage 18. A- *Eumetopias jubatus*; B- *Erignathus barbatus*; C- *Balaenoptera acuto-rostrata*. The tympanum and auditory ossicles in the middle ear already have turned around the sagittal and frontal axes of the early embryogenesis body; the long arm of the malleus is grown together with tympanic bulla. The auditory ossicles have been formed, and connections between them and location in respect of one another acquire features characteristic of adult animals. Labels as in Fig. 1.

stria vascularis is formed by undifferentiated epithelium. The prospective spiral notch consists of stratified tall columnar epithelium. The cochlear and vestibular branches of the auditory nerve are well distinguished. Differentiation of the elements of the cochlear canal and of the Organ of Corti continues. In Odontoceti, Phocidae, and Odobenidae, in the outer ear, the auditory meatus widens proximally. Increase of the size of the auditory meatus in mature born mammals is proportional to the growth of the embryos. At this stage the main formation process in the outer ear is completed. In the middle ear of the Odontoceti, the cavernous plexus is formed (Fig. 5D). In the osseous part of the auditory meatus the venous sinuses are formed (in the Cetacea and Pinnipedia) (Fig. 3D, 5B, D and 7A) and peribullar sinuses are found between the cranial wall and the



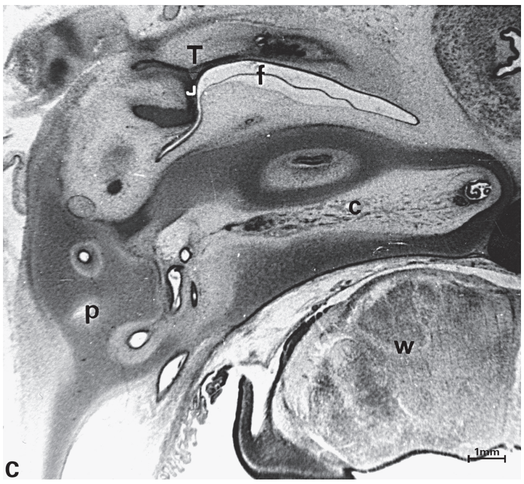
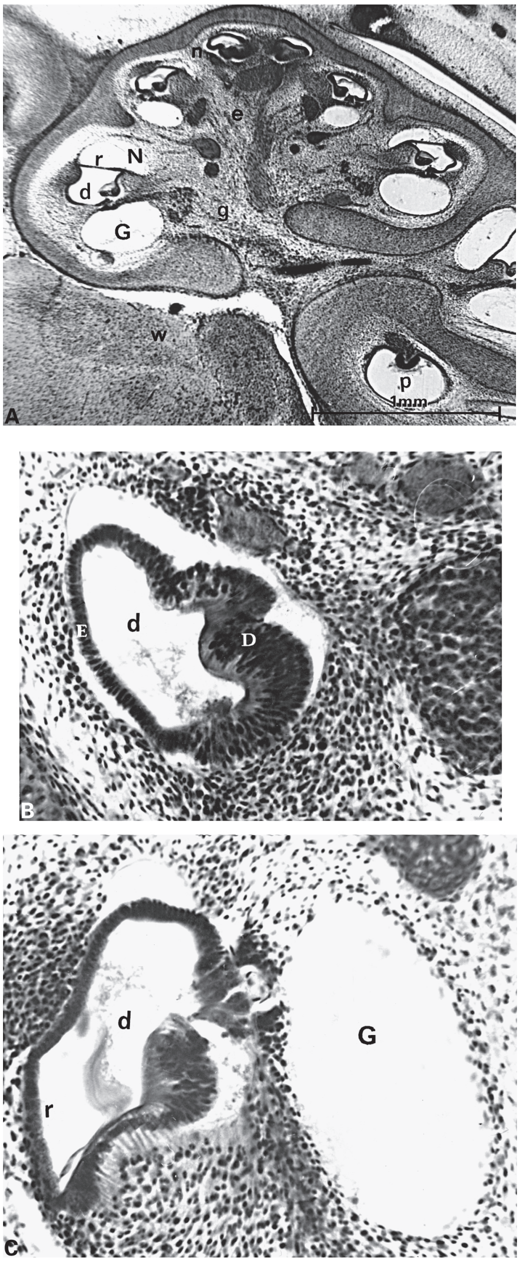


Figure 8. Dorso-ventral sections of the head showing the auditory organ in embryos, stage 18. A- *Balaenoptera acutorostrata*; B- *Stenella attenuata*; C- *Delphinapterus leucas*. Similarity is observed in the structure and formation of the tympanic membrane which already in the fetal period acquires species-specific features. Labels as in Fig. 1.

cochlear capsule (only in Cetacea) (Figs. 3C, 4 and 7C). In Odontoceti, the tympanic bulla is separated from the cranium. Stage 20 marks the end of the early embryogenesis of the peripheral auditory system. The main process of the formation of the outer, middle, and inner ears of completed. The auditory meatus is filled with epithelial cells (Fig. 10). These epithelial cells are known to resorb in the mature born species by the moment of the birth, whereas in the immature born mammals the resorbtion is delayed until early postnatal development.

For the first time, we have ascertained the source of the epithelium filling in the distal part of the auditory meatus in some Delphinidae. In Odontoceti, the structure of the auditory meatus differs from that of all other mammalian species studied. In Odontoceti, the auditory meatus has a distinct S-shape. At some distance from the opening, the cavity of the auditory meatus gets filled, so



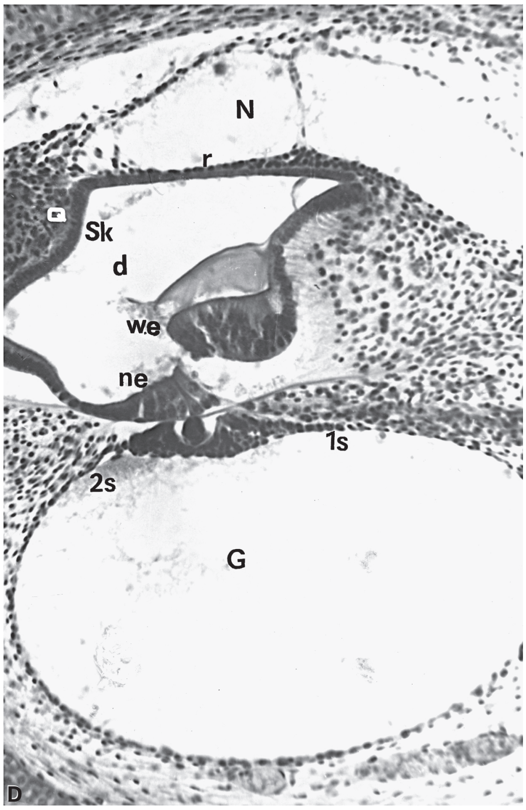


Figure 9. Dorso-ventral sections of the head showing the auditory organ of *Rhinolophus hipposideros*, stage 19–20. A- Cochlea. Differentiation of the elements of the Organ of Corti begins in the basal turn of the cochlea, and then the process gradually extends to the higher turns; B- The apical turn of the cochlea. The base of the cochlear canal formed by the columnar cells and the roof consisting of the cuboidal epithelial are distinguished; C- The middle turn of the cochlea. The columnar cells looks as if it has been drawn apart, with two thickenings, axial and lateral, being formed; formation of the tympanic scala; D- The basal turn of the cochlea. Differentiation of the vestibular scala, Reissner's membrane, spiral ligament, stria vascularris, outer and inner hair cells. Labels as in Fig. 1.

that two parts (distal and proximal) are formed. As it has been already mentioned, at stage 20 the auditory meatus is filled with epithelial cells throughout. In Odontoceti, the epithelial cells in the proximal part are completely resorbed before birth, whereas in the distal part, a part of this embryonic plug persists and later serves as a basis for the formation of the epthelial tissue of an adult canal which was reported earlier (Belkovich & Solntseva, 1970).

Discussion and conclusions

The results of the comparative study have shown that in different ecological groups, the formation of the outer, middle, and inner ear structures in the

Figure 10. Dorso-ventral sections of the head showing the auditory organ of *Sus scrofa*, stage 19–20. The external auditory meatus is filled with epithelial cells. Labels as in Fig. 1.

early developmental stages proceeds with a similar sequence and roughly at the same developmental stages. The greatest similarity in the formation of the peripheral auditory system is noted in the first half of the early embryogenesis. The species-specific features of the structural organization of the auditory organ appear in the second half of the early embryogenesis. The process of the cell differentiation of the Organ of Corti and resorption of the epithelial cells of the auditory meatus in the mature born species is practically completed by the moment of the birth. In the immature born species differentiation of the elements of the cochlear canal, of the cells of the Organ of Corti, and resorption of the epthelial cells of the aiditory meatus is not completed until the 20th day of early postnatal ontogenesis. In bats it is completed by the 25–30th day (Airapetyants & Konstantinov, 1974). In echolocating forms (bats, dolphins), belonging to different taxonomic and ecological groups, common features in the development of the middle and inner ears appeared through parallel evolution in the course of which conditions were created for intraspecific acoustic communication in specific habitat unfavorable for eyesight.

The results obtained revealed the following general regularities in the development of the peripheral auditory system in the representatives of the different ecological groups:

1. In the first half of the early embryogenesis of the peripheral auditory system (stages 13–16) most mammals share common structural features;
2. In the structural organization or the peripheral aiditory system, species-specific features are formed in the second half of the early embryogenesis (stages 18–20), depending on ecological specialization of the species;
3. The morphological features of the periphearal auditory system in mammals, which are formed in the early developmental stages, continue to develop in the later embryogenesis, fetal, and early postnatal periods.

One of the aims of the comparative embryological study of the peripheral auditory system in Cetacea and Pinnipedia was to reveal their phylogeny. From the viewpoint of the proponents of monophyletic origins, the present-day groups of Cetacea and Pinnipedia, each had a common ancestor (Kellogg, 1922; Romer, 1933; Slijper, 1936; Tomilin, 1957; Van Valen, 1968; Borisov, 1969*a*). According to the adherents of diphyletic origin of Cetacea, evolution of two suborders proceeded by convergence rather than by divergence and it would be more correct to consider them as two independent orders (Gregori, 1910; Kleinenberg, 1958; Andersen, 1967; Rice & Scheffer, 1968).

The idea of monophyletic origin of Pinnipedia was the outcome of ecological-climatological (Weber, 1928; Matthew, 1939; Davies, 1958; Scheffer, 1958) and biochemical studies (Borisov, 1969*b*; Sarich, 1969; Seak, Erikson, Siniff & Hofman, 1970), of the comparative analysis of Karyotypes (Fay, Fausch & Felts, 1967; Duffield Kulu, 1972; Anbinder, 1980) and of the comparative embryological study of the formation pattern of the external adaptive features in Otariidae and Phocidae in the prenatal period (Kuzin, 1970).

The hypothesis of a polyphyletic origin was advanced after the discovery of serious morphological differences among Otariidae, Phocidae and Odobenidae and in view of the pecularities of their areas (Chapsky, 1970; Howell, 1929; McLaren, 1960; Ray, 1976; Repenning, 1979).

Our comparative morphological and comparative embryological study of the peripheral auditory system revealed differences in ear structure between representatives of two suborders of Cetacea and within the order Pinnipedia—between Otariidae, on the one hand, Phocidae and Odobenidae, on the other. The results seem to favor the hypothesis of diphyletic rather than monophyletic origin of these divisions. However, in the developmental study of the ear it was shown that in Mysticeti and Odontoceti at similar developmental stages in the early prenatal period there is a similarity in the structure of the tympanic membrane, whereas in the fetal period it acquires species-specific features.

It can be inferred from the structure of the peripheral auditory system in adult cetaceans, that Mysticeti are the most ancient group of cetaceans and retain the same structural features typical for terrestrial forms (Bogoslovskaya & Solntseva, 1979). This is especially clearly seen in the structure of the auditory meatus, in the growing together of the tympanic bulla and cranial bones, and in the number of turns in the cochlea.

Odontoceti should be considered an evolutionary more advanced group, their auditory organ having acquired new adaptations related to the appearance of a special means of orientation, namely echolocation.

Among Pinnipedia, Otariidae have the most similar peripheral auditory system in comparison to terrestrial forms, whereas Phocidae and Odobenidae are more advanced groups of mammals, with the auditory organ better adapted for functioning underwater (Ramprashad, 1975; Bogoslovskaya & Solntseva, 1979).

In the developmental study of the auditory organ of Pinnipedia certain similarities have been found in its structure betweens the representatives of Otariidae and those of Phocidae (*Pusa hispida*). They are seen in the formation of the pinna which in *Pusa hispida* does not develop in the fetal period and is absent in adults.

From the data obtained, it can be supposed that the most ancient group of Pinnipedia is the Otariidae which later gave rise to Phocidae and Odobenidae, and this is a further indication in favor of the monophyletic origin of Pinnipedia.

Thus, our data favor the earlier advanced hypothesis of the monophyletic origin of Cetacea. This hypothesis is also supported by the results of immunological study (Borisov, 1969*a*), by the method of molecular DNA-DNA hybridization (Mednikov & Shubina, 1977) and by the comparative analysis of karyotypes (Anbinder, 1980). Our results also support the hypothesis of the monophyletic origin of Pinnipedia and are confirmed by the evidence of immunological study (Borisov, 1969*b*) and by the comparative analysis of karyotypes (Anbinder, 1980).

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