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HOMOLOGIES OF THE CYCLOSTOME EAR.

BY H. W. NORRIS.

The ear of the Cyclostomata has until recently been considered so peculiar as to render it difficult to explain its relations to the typical Vertebrate ear. Then again, the diversity of structure in the auditory organ of the Cyclostomes themselves renders the task of homologizing the various parts somewhat uninviting.

Our exact knowledge of the structure and relations of the ear of the Cyclostomata begins with the researches of Ketel¹, in 1872. His predecessors had assumed that the auditory organ of the Cyclostomata was a thing *sui generis*, hence most of their observations were defective. Ketel was the first to attempt to find a fundamental type of the vertebrate ear. While the results of his studies in that direction did not find ready acceptance, nevertheless, in the light of most recent investigations, we see that his conclusions were essentially correct. In the light of zoological knowledge twenty years later, his opinions would have seemed not only reasonable, but they would have been considerably modified from their original form. Johannes Müller² in 1836 discovered the semicircular canals in the ear of Petromyzon, and that they were only two in number. Dumeril³ in 1800 claimed to have found the canals, but his statements are extremely vague. Other observers, Pohl⁴, Weber⁵, Blainville⁶, Rathke⁷ and Breschet⁸, had denied the existence of the

¹ Ueber das Gehororgan der Cyclostomen.—Hasse *Anat. Studien*, 1872.

² Ueber den eigenthümlichen Bau des Gehororgans bei den Cyclostomen. *Fortsetz d. Vergl. Anat. d. Myxinoïden in Abh. d. K. Akad. d. Wissen.* Berlin, 1836.

³ Anatomie des Lamproles *Memoires d'anatomie comparee.* Paris, 1800.

⁴ Expositio generalis anatomica organi auditus per classes animalium. Vindobonae, 1818.

⁵ De aure et auditu hominis et animalium. Leipzig, 1820.

⁶ De l'organisation des animaux ou Principes d'anatomie comparee. Paris, 1822.

⁷ Bemerkungen über den Inneren Bau der Pricke. Danzig, 1826.

⁸ Recherches anatomiques et physiologiques sur l'organe de l'ouïe des poissons. *Acad. des Sci. Savans Etrangers.* 1838.

canals, or at least any more than as rudiments. It was very early recognized that two distinct forms of ear were to be found in the group of Cyclostomata, the one found in the Myxine and the other in the Lampreys. Müller⁹ first gave any adequate description of the ear of Myxine. Previously Anders Retzius¹⁰ had given a very meager description. Ketel attempted to show that the ear of Myxine is genetically related to that of higher vertebrates through the ear of Petromyzon as a connecting link. Unfortunately he failed to recognize the existence of semicircular canals in the ear of Myxine, considering the membranous vestibule as merely a ring. Ibsen¹¹ had in 1846 recognized a semicircular canal in Myxine and two ampullae.

Ketel considered the Cyclostome ear as in an arrested stage of evolution, and that it really represented an ancestral condition of the Vertebrate ear. He sought for traces of the third or horizontal canal in Petromyzon, and believed he found it in a sense organ connected with the *crista acustica* of the anterior canal. The cochlea he found represented in the "sackartiger Anhang" of the membranous labyrinth. Ketel failed to completely homologize the Cyclostome ear with that of the Vertebrate type, because he did not recognize the existence of semicircular canals in Myxine, and further, because, working from the higher types downward, he had not grasped the idea of the fundamental form of the auditory organ. Gustav Retzius¹² in 1881 recognized the existence of a single semicircular canal in Myxine; but he did not agree with Ketel as to the relationships of the ear of the Cyclostomata. It remained for Ayers¹³ in 1892 to establish beyond question the rank of the Cyclostome ear. Starting with the idea that the Vertebrate auditory organ is composed of modified sense organs of the lateral line system, he shows almost beyond question that the Cyclostome ear is not a degenerate structure, but rather represents an ancestral type. According to this interpretation, we recognize in the Vertebrate ear two originally distinct parts, an anterior utriculus and a posterior sacculus, with which, and forming a part of, are a number of canals. The ear of Myxine

⁹ Loc. cit.

¹⁰ Ytterligare Bidrag till anatomen af Myxine glutinosa. *Kongl. Vet.-Akad. Handl.* Stockholm, 1824.

¹¹ Anatomiske Undersogelser over Orets Labyrinth, afsluttet af Forgatteren i 1846.

¹² Das Gehororgan der Wirbelthiere I, Stockholm, 1881.

¹³ Vertebrate Cephalogenesis, II. A Contribution to the Morphology of the Vertebrate Ear, with a Reconsideration of its Functions. *Journal of Morphology*, Vol. VI, Nos. 1 and 2. 1892.

is seen to consist of a utriculo-sacculus, imperfectly divided into two parts, into which open two canals, each with an ampulla containing a sense organ. Unlike the condition in the Lampreys, or higher Vertebrates, the two canals unite with each other without an unpaired connection, or commissure, with the vestibule. Hence the failure heretofore to recognize more than one canal. The ear of *Petromyzon* differs from that of *Myxine* chiefly in the fact that the two canals are connected with the membranous labyrinth at their point of union by an unpaired commissure. The two semicircular canals of the Cyclostome ear correspond to the anterior and posterior canals of higher Vertebrates.

The anterior is connected with the utriculus, and the posterior with the sacculus, at their ampullar ends. In other vertebrates the connection of the posterior canal with the sacculus is lost at an early stage of development, so that the three canals in the adult are connected only with the utriculus. This, however, is not the ancestral nor the early embryonic condition. Embryology¹⁴ indicates that the vertebrate ear early consists of two parts, an anterior utricular and a posterior saccular region. This is the adult condition in the cyclostomes. Ayers calls particular attention to the fact, which Ketel, Hasse, and Retzius had already noticed, that in *Petromyzon* there are two distinct endolymphatic ducts, a further striking indication that the vertebrate ear is a two fold structure in origin. Ayers, however, gave the first explanation of their presence. That the existence of these two ducts is a fundamental characteristic, is indicated by the fact that they are distinct from a very early stage of development.

Unfortunately the material at my disposal does not give a complete series of the development of the ear, but the stages studied by me indicate that Ayers is correct in his interpretation of their presence. Thus we see that recent investigation confirms the opinion of Ketel that the auditory organ of the Cyclostomata is not an aberrant structure. Ayers may be said to be the first and only one who has given a coherent explanation of the structure and origin of the Vertebrate ear.

¹⁴H. W. Norris. Studies on the ear of *Amblystoma*. Part I. *Journal of Morphology*, 1892.