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An Observation on the Development of the Mammalian Vomer

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WITH TWO FIGURES.

The name "vomer," given to the unpaired plowshare-shaped bone of the human cranium, has been applied in the works on comparative anatomy to a pair of bones in the skulls of the Sauropsida and Ichthyopsida. This homology, maintained by the earlier writers and by most osteologists up to the present time, is founded largely on the relations of parts in the adult skull. The unpaired vomer of the mammals was explained by assuming it to be the equivalent of a pair fused together, a theory supported by observations on the origin and development of the single vomer in certain teleosts and birds and in man. According to Gaupp¹ true paired Anlagen of the vomer have not, however, been seen in the lower mammals.

In 1884 Sutton² proposed a new homology for the mammalian vomer by claiming its presence in the lower animals in the parasphenoid, an unpaired bone in the base of the cranium which exists in all classes from the fishes on, except the mammals. The parts in the mammalian cranium which, according to the theory, should correspond with the ichthyopsidan paired vomers, were found in the palatine

³Gaupp, E. Die Entwickelung des Kopfskelettes. Hertwig's Handbuch der Entwickelungslehre der Wirbeltiere. 1906, Bd. III, Zweiter Teil, p. 850.

²Sutton, J. B. Observations on the Parasphenoid, the Vomer and the Palato-pterygoid Arcade. Proc. Zool. Soc., 1884, p. 566.

processes of the premaxillaries. These processes have been observed by Albrecht, Sutton and others to arise independently of, and subsequently to fuse with, the tooth-bearing portions of the premaxillaries.

In later years, Broom³ has contributed much to our knowledge of the comparative anatomy of the vomer, and with evidence adduced from the investigations of Turner, W. K. Parker, Wilson and Symington, he strongly supports the homology of the mammalian vomer and parasphenoid. As to the comparison of the paired vomers of the lower forms with the palatine processes of the premaxillaries, he does not agree entirely with Sutton. Broom has suggested the term "prevomer" for the category of bones represented by the paired vomers (of other authors) in the lizard, and finds its homologues in the paired vomers of the Ichthyopsida. But in the great majority of the higher mammals the prevomer does not exist, its place being taken by invasion of the palatine processes of the premaxillaries. These are regarded as true portions of the premaxillaries and not independent elements which Sutton considered them to be. In the dumbbell-shaped bone of Ornithorhynchus and in a median ossification in the nasal region of Miniopterus, Broom identifies the prevomer. These bones, although azygos in the adult, are both derived from a fusion of a pair of splints underlying the cartilages of the vomeronasal organs.

An objection to the comparison of the mammalian vomer and the non-mammalian parasphenoid lies in the fact that the latter presents in the series of animals a history of retrogression; in the lowest forms the parasphenoid reaches forward to the ethmoidal region, whereas in most reptiles and birds its anterior end is far back and away from this region. A more serious obstacle to the new homology is the circumstance, already mentioned, of the single vomer developing from a pair of centers. The one instance in mammals might well be taken to be an exception to the rule of single origin, if

⁸Broom, R. On the Homology of the Palatine Process of the Mammalian Premaxillary. Proc. Linn. Soc. N. S. W., 1895, Vol. X, p. 477-485.

On the Occurrence of an Apparently Distinct Prevomer in Gomphognathus. Jour. Anat. and Physiol., 1896, Vol. XXXI.

On the Mammalian and Reptilian Vomerine Bones. Proc. Linn. Soc. N. S. W., 1902, Vol. XXVII, part 4, p. 545-560.

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single origin were known to be the rule. But how many studies have been made by modern methods to determine this matter?

During the reconstruction of the cranium of a cat embryo there was observed a tendency to bilateral formation of the vomer, and my attention was thereby directed to the question of the origin of this bone in the mammals. A review of the series in the Harvard Embryological Collection resulted in finding one instance of paired origin of the vomer, and that in a marsupial. The discovery by Fuchs⁴ of the remains of the parasphenoid in a Didelphys embryo and



FIGS. 1 and 2.—Transverse sections through the nasal region of a 17 mm. specimen of *Caluromys philander*; 1, through the anterior ends of the vomers; 2, through the middle of the vomers. Harvard Emb. Coll., Series 707, Sections 245 and 228. \times 39 diam.

A, cartilaginous nasal septum; B, palate; C, vomer; D, palate process of premaxilla; E, vomeronasal organ of Jacobson.

its bearing on the homology of the mammalian vomer, induced me at this time to communicate the observation. Through the courtesy of Professor Minot I have been enabled recently to review the sections of the heads of three pouch-specimens of *Caluromys* (*Didelphys*) philander in which the paired origin of the vomer had been noted.

⁴Fuchs, Hugo. Ueber einen Rest des Parasphenoids bei einem rezenten Säugetiere. Anat. Anz., 1908, Bd. 32, p. 584-590.

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In a specimen 18 mm. in length there is present a pair of vomers. These elongate ossifications lie approximately parallel with the ventral edge of the cartilaginous nasal septum and extend from its caudal end forward as far as the middle of the vomero-nasal cartilages of Jacobson. Here the septum is continuous ventrally with the palate, and in this region the vomers are connected with one another across the median line. The connection is a feeble one, consisting of a few delicate bony trabeculæ which are present in only three of the sections. Beyond this place in the caudal direction, the septum and palate are separated by a space, so that the nasal cavities are in communication with each other from side to side. In this region the two vomers are seen to diverge as they are followed backward. Each bone for the most part is compressed, with sharp edges and surfaces directed more or less obliquely-ventrally toward its anterior end, ventrolaterally in the middle of its extent. Anterior to the vomers lie the paired palatine processes of the premaxillaries, adapted to the convex surfaces of the vomero-nasal cartilages. A parasphenoid ossification center was not observed.

The conditions here described were found to be essentially the same in the two other specimens examined which were from the same pouch.

The study of younger specimens may decide whether or not the bony bridges are secondary connections between a pair of independent vomerine ossifications. The large size and advanced state of ossification of the lateral parts is indicative of an earlier origin for them than for the insignificant median ossification. The osteogenetic tissue in which the vomers are developing is disposed in two lateral masses of mesenchyma, connected here and there by strands of the same tissue stretching across the middle line ventrad of the nasal septum. In sections passing through its anterior end, the vomerine ossification tract is found to be unpaired and to be situated beneath the nasal septum, from the perichondrium of which it is well separated. This median mass of osteogenetic tissue is, however, of small extent in comparison with the lateral masses of the tissue, and, except anteriorly, presents itself in strands and not as a continuous bed of mesenchyma.

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Relics of the pair of plates which fuse to form the vomer in man are to be found in the alæ, projecting conspicuously at the caudal end of the bone. This suggests the probability of the alæ of the cat's vomer and of the vomers of other mammals having an origin from paired parts of the developing bone. The dumbbell-shaped bone of Ornithorhynchus is bifid caudally, a condition which seems to follow from the original paired state of this element. It is not, however, my intention at this time to enter into the question of the phylogeny of the vomer. The object of this communication is to record the paired origin of the vomer in a low mammal, in which class generally it must be insisted that further study of the development is necessary before the bone can be regarded as azygos in its beginning.

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