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THE ORIGIN OF THE VERTEBRATE SKELETON.

By J. S. Kingsley.

Until a very recent date, not a doubt existed that any part of the vertebrate skeleton was of other than mesodermal origin. The cartilages were mesoderm, and in their further development the cartilages were transformed into bone by means of the cells from the same parent layer. The membrane bones of the skull were also believed to mesodermal, since the researches of Oscar Hertwig ('74) had shown that in the Batrachia especially, as well as in other forms, they arose from the layer which formed the dentine of the teeth, and which was homologous with that which formed the dentine of the placoid scale. The details of this need not be given here, as they will be found in every text-book; the point to be emphasized is that dentine and its homologue membrane bone were assumed to be, and even thought to be proved to be, of mesodermal origin.

One of the first papers to lay a foundation for a different view was one by Kastschenko ('88), which, while saying nothing of the origin of the skeleton, pointed out that certain parts of the mesenchyme were of ectodermal origin. Next, another Russian, Goronowitsch ('92), showed that in the formation of the "ganglionic folds" into the head, not all the tissues proliferated from the ectoderm into the "ganglienleisten" was used up in
the formation of nervous matter, but that some of it became mesenchymatous and was possibly utilized in the development of the skeleton. Other authors at about the same time confirmed more or less clearly this view that all mesenchyme was not of entodermal, but that at least some of it was ectodermal, in origin.

In 1893, Miss Julia B. Platt, in a preliminary paper, made the noteworthy statement that the embryology of Necturus showed that, at least in the head, the cartilages were derived from the ectoderm. Necturus was especially favorable in this respect, for its cells are larger and pigment is absent. At about the stage of the formation of the ganglienleisten, the differences between the entoderm and mesothelial tissues on the one hand, and the ectoderm on the other, were very great, the former being loaded with yolk granules, the latter containing comparatively few. Further, the layers readily differentiated by staining with the Erlich-Biondi mixture. With the formation of the ganglienleisten from the ectoderm, its cells could be distinguished in the same way, and it was found that only the dorsal portion of ridge becomes nervous, the lower contributing its cells to the mesenchyme, while between the two regions there was a portion which contributed to both tissues. These ectodermal mesenchymal parts (mesectoderm, as Miss Platt calls them) can readily be distinguished after their separation from the parent layer by the peculiarities already mentioned. From these proliferations tissue arises which later forms the gill cartilages, while further in front, near the eyes and the nose, similar ingrowths are seen, and especially in the region where the mouth is to break through. From these last arise at least the trabecular cartilages; the origin of the parachordals and otic capsule is not given.

In a second paper ('93*), Miss Platt further elaborates some of her earlier statements, illustrating the parts with three figures, one of which shows the downward growth of the mesectoderm, to use her extremely convenient term, between the gill clefts and in the region of eye and nose.

Before the appearance of Miss Platt's second paper, Goronowitsch published his detailed account ('93), fully confirming
the statements of his preliminary, and showing that ectodermal ingrowths occur in the birds in just such positions as to justify the view that they gave rise to skeletal structures. Some of these, according to Goronowitsch, found their destiny in the cutis, a fact to be remembered while considering the work of Klaatsch, outlined below. A little later (93°) Goronowitsch published a short note in which, among other points, he claimed that Miss Platt had not made good her thesis that these mesectoderm cells gave rise to the cartilage. Miss Platt's final paper will, we understand, soon appear.

The most important and most detailed paper of all is that of Klaatsch, which appeared in April of this year. Its title—"On the Origin of the Scleroblasts. A Contribution to the Knowledge of Osteogenesis"—shows its scope. We can give but the merest outline of the points detailed in the 90 pages of the paper.

The first point considered is the development of the placoid scale. This, as is well-known, consists of two portions, a harder outer portion, the enamel secreted by the basal ends of cells of undoubted ectodermal origin; and a deeper dentine which, up to now, has been universally regarded as of true mesodermal nature. Klaatsch studied the development of the placoid organ in several species of Acanthias, Mustelus and Heptanchus. These presented various differences, but in general, they agreed in the following features. In the earlier stages the ectoderm is two cells in thickness, a flattened superficial layer and a deeper cubical or columnar layer. Between this last and the corium is a clear space, and there is no continuous basal membrane. A little later this deeper layer begins to undergo modifications, cells being budded from it into the clear space. These cells are readily seen to belong to the ectoderm, not only from the directions of the mitotic spindles, but from the fact that their nuclei are greatly larger than those of the corium, the only other layers from which they could arise. These cells are the scleroblasts. They are not scattered irregularly through the clear space, but are more abundant in some places than in others, thus early marking out the positions of the later placoid organs. With the modi-
fications of the ectoderm described by Klaatsch, we have nothing to do here further than is concerned in the scale development. It is to be noticed that along with the formation of the little patches of scleroblasts the overlying cells of the basal layer become elongated, the first step in the development of an enamel organ. The later stages in their general features are much as described by Oscar Hertwig in his classic paper of twenty years ago, and yet there are important differences to be noted. The heaping up of the scleroblasts continues, the result being the formation of the dentine organs, carrying with it the superposed enamel cells in the form of a pyramid. The enamel organ is terminated on all sides by a groove, and even at this stage the cells at the bottom of this groove are actively engaged in proliferating additional scleroblasts which are pushed into the still-growing dentine organ. The necessary conclusion is not only is the enamel of the placoid scale an ectodermal derivation, but such is the nature of the dentine as well.

Now placoid scales and teeth have long been regarded as homologous structures, and so Klaatsch studies the history of the latter. In the sharks he finds that the conditions of the development of the scales are paralleled in the ontogeny of the teeth. There is the same early proliferation of scleroblasts into the clear layer, and later, when the enamel cap is formed, its limiting groove is the seat of additional ingrowth of dentine-forming cells. In short, we must no longer regard the teeth as structures derived from two germ layers—ectoderm and mesoderm—but as purely ectodermal products.¹

In the fin of the shark are numerous horny rays, and their history is followed. Earlier workers had universally regarded them as belonging to the connective-tissue series, although in 1885 Krukenberg had shown that their organic base was different from the chemical standpoint from the other connective tissues. Klaatsch finds that here there is a similar inwander-

¹It is to be noted that in the recent meeting of the Anatomische Gesellschaft at Strassburg, May 13–16, Professor Rahl had a paper “Ueber die Herkunft des Dentinkeims in den Placoidschuppen und den Zähnen der Selachier (gegen Klaatsch).” The publication of this will be waited with interest.
ing of ectoderm cells into the region between the basal epithelium and the corium. From these cells are produced at first extremely minute horny rods, and these, later, together with their parent cells, sink through the corium into the position they finally occupy, where no one, not tracing their history in detail, would suspect their ectodermal origin. Even in Torpedo, where no horny rays occur in the paired fins of the adult ingrowths of ectoderm into the axial portions of the fin exist. At this point one author supports Rabl in his view that the unpaired fins are not derived from the fusion of paired rudiments. The opposite view is fastened upon Dohrn, regardless of the fact that it was first shown to be probable by J. K. Thacher and later supported by Balfour. Dohrn's special contention was that the fins, paired and unpaired, were derivatives of the parapodia of the worms, and later, Paul Mayer claimed to have found structures—"parapodoids"—which represented these. These "parapodoids" are, according to Klaatsch's view, the early placoid organs.

In studying the development of true bone, Klaatsch studied Salmo salar. Here the earliest to appear were the opercular bones, and but little later those of the shoulder girdle and those arising in connection with the teeth, later those of the cranium. The details of the formation of the scleroblasts for a few of these bones is given, including the squamosal, operculum, clavícula, dentary, and the osseous fin-rays. In the case of each, the osteoblasts are derivatives of the ectoderm. The squamosal is especially interesting, since it begins from outgrowths at the point of the infolding of the mucous canals, and is developed in connection with these organs. At first it is connected solely with them, and is plainly a membrane bone; later it comes into contact with the otic capsule. Klaatsch sides with those who would make no sharp distinction between cartilage- and membrane-bones, and regards not only the squamosal but the cranial roof and the ossifications which appear in the cranial roof and on the primordial cranium as having their origin in bones developed, like the squamosal, for protection of the cutaneous sense-organs.
After discussing these, Klaatsch passes to the bony fin-rays of the Teleosts and then to their scales, giving details which our space will not allow us to repeat, but in each case he comes back to the conclusion that in each and every case the so-called mesodermal element is of ectodermal origin. Then a few instances are taken from other groups—Salamandra and Lepus. In the Batrachia he finds the same conditions as in sharks and Teleosts. In the Mammals he fails to trace the history of his scleroblasts, but he finds here, as elsewhere, proliferations of ectodermal cells into the subadjacent tissues, which, it is possible, may later form the skeletogenous cells.

It needs hardly be said that these various contributions thus superficially summarized are most important, since, if they be confirmed, they will tend to an overthrow of many ideas long believed to be firmly grounded. The questions concerned are far from settled, but we venture to predict that the subject will occupy a prominent place in the morphological literature of the immediate future.

**Literature Cited.**

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