

IV. "On the Anatomy and Physiology of *Protopterus annectens*."

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(Abstract.)

The work which has resulted in the present paper was begun in Freiburg in the summer of 1888, when the author was fortunate enough, owing to the generosity of Professor Wiedersheim, to obtain a number of fresh specimens for examination. As so many interesting points presented themselves at an early stage in the research, a short preliminary notice, without illustrations, was published in the following autumn ('Berichte d. Naturforsch. Gesellschaft zu Freiburg i.Br.,' vol. 4, 1888).*

This notice merely forms the basis of the present paper, in which the whole subject has been worked out in greater detail. A number of new facts are recorded, some of the author's earlier conclusions modified, and the paper illustrated with 11 plates containing 71 figures.

With the exception of certain special details, the structure of the skeleton and of the nervous and muscular systems is not described, the paper consisting mainly of an account of other organs which have not received so much attention from previous observers, and of a comparison of *Protopterus* with the other genera of Dipnoi, so far as their structure is known, as well as with other Ichthyopsida.

The author returns his sincere thanks to the Council of the Royal Society for the grant out of which various expenses connected with the investigation were defrayed, as well as to Professor Wiedersheim, not only for the gift of abundant fresh and preserved material, but also for his continued help and advice during the progress of the work. To Professor Howes the author is indebted for many valuable suggestions.

A number of details with regard to the habits of *Protopterus* in captivity are given, and reference is made to Stuhlmann's observations with regard to its mode of life under natural conditions.

The paired extremities, the movements of which are more like those of limbs than of fins, show no connexion with the cheiropterygium, and, in spite of their considerable nerve supply, are evidently greatly degenerated structures as regards their free portions. Sensory organs are not present on them, and they therefore cannot have a tactile function. Their distal ends, like the apex of the tail, are very variable, and can undoubtedly be reproduced when lost by

* See also 'Nature,' vol. 39, p. 19.

accident. The tail is almost certainly not primarily diphycercal, and shows signs of a possible origin from a heterocercal form.

The epidermis on the whole most nearly resembles that of Perenni-branchiate Amphibians, and gives rise to simple multicellular glands (which are most numerous on the snout), as well as to very numerous closely-packed goblet-cells, which produce the gluey secretion as well as the main substance of the capsule which surrounds the animal during the torpid state. The epidermis forms a regular and continuous layer over the derma, in which the cycloid imbricating scales are imbedded. Pigment cells are present in both layers of the integument, and the derma encloses nests of leucocytes here and there, small cells, apparently migratory leucocytes, being seen in places amongst the ordinary epidermic cells.

Integumentary sense organs, similar to those of Fishes and larval Amphibians, are present not only on the head and lateral line, but in various other regions of the trunk also; they are most numerous on the head. In young animals they are all superficial, and do not project below the general level of the epidermis, and this condition is retained in those situated on the trunk. On the head, the epidermis becomes involuted along certain lines to form grooves, which then become converted into sub-epidermic tubes, in which the sensory organs are situated, and which communicate with the exterior by an aperture at one end. The relations of the sensory organs of the trunk are therefore similar to those seen in young stages of Fishes and in Amphibian larvæ, while in the case of the head, they resemble those which are typical for adult Fishes. End-buds, similar in structure to the taste-buds of Fishes and Amphibians, are present on the tongue and oral epithelium, but are absent on the lips, and, as in Amphibians, do not occur on the surface of the body.

As regards its general structure, the olfactory organ most nearly resembles that of Elasmobranchs, but the presence of posterior nostrils raises it to a higher level. The position of the anterior nostrils beneath the upper lip is probably to be accounted for as an adaptation in connexion with the torpid state (*vide infra*). The space between the eyeball and its muscles and the orbit is filled with a delicate connective tissue; there are no orbital glands or eyelids. Four straight and two oblique muscles are present. The cornea is continuous with the derma on the one hand, and the sclerotic on the other; the latter is fibrous in young animals, and islands of cartilage first appear at the points of insertion of eye-muscles, and then gradually extend so as to chondrify the whole sclerotic. The eye resembles that of Amphibians; a *processus falciformis* and *campanula Halleri* are absent, and no ciliary muscles were observed, though possibly present; almost all the pigment of the eye is ectodermic.

No specialised glands are present in connexion with the greatly

folded epithelium of the oral cavity. The lips contain no muscles. The tongue, as well as the palate, is covered with blunt conical papillæ, on which the taste-buds are situated. Beneath the epithelium the tongue is composed anteriorly to the hyoid of a simple connective tissue, while posteriorly to the hyoid it is made up of extrinsic muscles, the main mass of which is continuous with the ventral musculature of the trunk. A horny cap is developed over each tooth from the overlying epithelium, which apparently becomes cut through by the sharp edges and points of the teeth, and which probably corresponds to the *cuticula dentis*. The thyroid is a small bilobed organ imbedded in the tongue just above the hyoid symphysis, and has the characteristic structure. The thymus consists of lymphoid tissue, and is situated dorsally and posterior to the branchial arches, surrounding the blood-vessels of the external gills.

The alimentary canal extends almost in a straight line from the mouth to the vent. A ventral, as well as a fenestrated dorsal, mesentery is present supporting the intestine. The so-called urinary bladder ("cloacal cæcum") opens into the cloaca dorsally to the intestine; the author compares it with the "processus digitiformis" of Elasmobranchs. A spleen and pancreas are present, imbedded in the thin walls of the stomach, and extending on to the proximal part of the intestine; they are covered externally by sparse muscular fibres as well as by the peritoneum. The relations of the pancreas therefore most nearly resemble those met with in Ganoids and certain Teleosteans. The pancreas is deeply pigmented, and its ducts open into the bile-duct. The pigmented walls of the intestine and the spiral valve are very thick, owing to the abundance of lymphoid tissue contained within them. With the exception of the bursa entiana, the internal walls of which are raised up into a number of deeply pigmented oblique folds, the whole of the mucous membrane of the stomach and intestine is perfectly smooth, and there is no indication of any differentiated gastric or intestinal glands.

Cilia are present on the epithelium throughout the stomach and intestine. The epithelium is columnar and stratified, and branched pigment cells extend into it in the greater part of the intestine. Small leucocytes can be recognised among the epithelial cells here and there. A layer of small-celled lymphoid tissue directly underlies the epithelium. In the spleen and lymphoid organs of the intestine two kinds of tissue are present: (1) a large-celled tissue, which forms the greater part of these organs, and which somewhat resembles embryonic connective tissue; and (2) a smaller-celled tissue, similar to that lying directly beneath the epithelium, and resembling that of ordinary lymphoid follicles. Large migratory cells are present in both kinds of tissue, many of which enclose

yellowish granules. Gradations between these and rounded cells of a deeper yellow or brown colour can apparently be made out; the latter are arranged in larger or smaller groups, and cells appearing to be intermediate forms between these and the ordinary black branched pigment cells can also be seen. The lymphoid tissue is penetrated by networks of blood-vessels, and it seems probable that the yellow granules mentioned above are due to the disintegration of red corpuscles, which are ingested by leucocytes, and then undergo some change, whereby the latter gradually pass into the condition of black pigment cells, which migrate through the epithelium, and are so got rid of. The muscular layers are very thin. A muscularis mucosæ is present, and the circular and longitudinal layers are represented, but the direction of the fibres is in many regions difficult to trace. Strands, only a few cells in thickness, extend throughout the lymphoid tissue of the intestine, and some of these unite to form a longitudinal band passing down the axis of the spiral valve.

An analysis of the contents of the gut, for which the author is indebted to Professor Baumann, while yielding negative results as regards the stomach, proves the presence of peptones, in small quantities, in the intestine. The question as to the mode of digestion and absorption of the food in *Protopterus* is discussed.

The branchial apparatus shows signs of considerable reduction. Internal gills are present on the posterior face of the hyoid, on both faces of the third and fourth branchial arches, and on the anterior face of the fifth. Three pairs of external gills were present in all specimens, even the largest, examined. The pulmonary apparatus, on the whole, more nearly resembles the air-bladder and its duct of certain Ganoids than the lungs and laryngo-tracheal chamber of Amphibians. The pulmonary branches of the vagus cross one another at the base of the lungs.

The blood is remarkable for the large size of its elements, which is only exceeded in the case of *Proteus* and *Siren*, as well as for the large proportion of white corpuscles in comparison with the red ones. Two forms of the former are described, in one of which fine radiating pseudopodia can be protruded, and different stages in the degeneration of the nucleus and cell-body could be observed. The chief points of interest with regard to the blood-vessels are as follows:—(1) the presence of a paired pulmonary artery, the left supplying the ventral, and the right the dorsal, aspect of the lungs; (2) the presence of a single true post-caval, along with a persistent left posterior cardinal vein; and (3) the single caudal vein, giving rise to a right and a left renal portal.

No external sexual differences could be observed, and amongst the specimens examined, females were the more abundant. The urino-genital organs are surrounded by masses of tissue resembling the

large-celled lymphoid tissue of the gut, but differing from the latter in becoming largely converted into adipose tissue. The kidneys probably represent the mesonephros, and their duct the Wolffian duct; nephrostomes are absent.

In unripe males, delicate Müllerian ducts are present. The sperm is conducted to the exterior by a duct, which is probably formed in connexion with the testis, quite independently of the excretory apparatus. The seminal tubules are directly connected with it, and it opens into the base of the Müllerian duct, the rest of which apparently aborts completely. Unlike most of the tissue elements, which are very large, and closely resemble those of the Amphibia, the spermatozoa are very minute, and are remarkable in possessing *two* vibratile flagella attached to the carrot-shaped "head." The generative organs of the female bear a striking resemblance to those of Amphibians. The oviduct corresponds to the Müllerian duct; the epithelium covering its internal folds shows signs of degeneration similar to those which have recently been described amongst Urodeles.

No traces of a sympathetic were found.

An account of the mode of life of *Protopterus* during the torpid period is given. The cocoon is provided with a "lid," perforated by a hollow funnel-shaped tube, which passes between the lips of the animal, and thus forms a passage for the respiratory current. The source of nutriment during the summer sleep lies in the adipose tissue in connexion with the gonads and kidneys and alongside the notochord in the tail, as well as in the lateral muscles, some of which, especially in the caudal region, undergo a granular degeneration. Very probably the latter is the precursor of the fatty degeneration, and, in all probability, leucocytes are the active transporting agents of the degenerated material. This assumption would help to explain the large development of lymphoid tissue in the body of the animal.

An analysis of the muscles, by Professor Baumann, shows that they do not retain quantities of the products of nitrogenous waste, as is the case in Elasmobranchs.

The systematic position of the Dipnoi is briefly discussed in the light of the new facts brought forward in the present paper. Although the Dipnoi present many points of resemblance to Fishes on the one hand, and to the lower Amphibians on the other, their connexion with any living forms of either class is probably a very distant one, and it is inadvisable to classify them amongst the Fishes. Owing to the absence of ontological evidence, and to the incompleteness of our knowledge of the palæontological history of the Dipnoi, it is impossible to construct a genealogical tree which will show, with any approach to accuracy, the probable connexion between them and other

Ichthyopsidan types. The most that can be said at present, with anything like certainty, is that the Dipnoi are the isolated survivors of an exceedingly ancient group, which was probably related to the ancestors of existing Fishes and Amphibians. Amongst the former, the connexion seems to be closest to the Elasmobranchs, more particularly to the Chimæroids on the one hand, and to such an ancient Selachian type as *Chlamydoselache* on the other; but at the same time, the Ganoids probably arose from the common ancestral stock not very far off. Though retaining many primitive characters, the Dipnoi, and more especially *Protopterus* and *Lepidosiren*, are in some respects highly specialised, the specialisation being largely due to a change of habit.

- V. "On the Constitution of the Terpenes, Camphors, and Camphor Acids." By J. NORMAN COLLIE, M.D. Communicated by Professor RAMSAY, F.R.S. Received April 29, 1891.

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