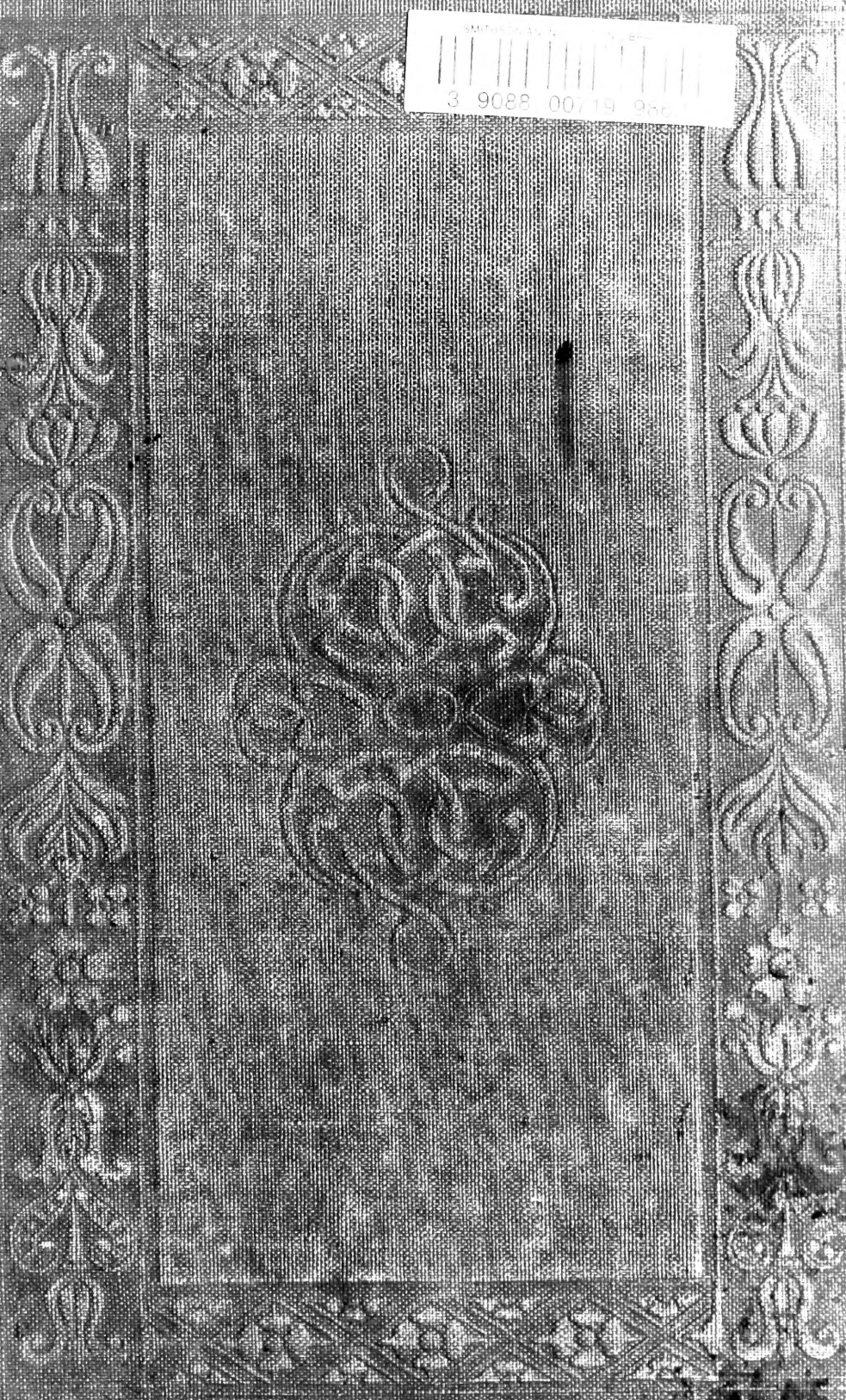


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light of peculiar brilliancy. The Claudian policy in Gaul, the disintegration of the British hierarchy, the subjugation of Britain, the insurrection of Boadicea and the form, as preliminaries to the operation of that great curse which gave the Romans to Nero during fourteen infamous and miserable years. After his fall, the stormy reign of Galba, the brief struggle of Otho, raised from voluntariness to empire, the supremacy of the glutton Vitellius, the civil war led by Vespasian, the provincial revolts, the Flavian conspiracies, and the concentration of the Roman power against Jerusalem, fill many pages; but the moral of the narrative is a whole conveyed in a form so important as to be read at Nero. The scene of his death is described in one of the most remarkable descriptions we have read for many years. A century of imperialism rendered it impossible that Rome should not adopt the best historical position; and hence the lesson of the Rev. Mr. Merivale, whose masterly narration, written with singular strength and polish of style, is a work which the youth of England may study with confidence and with admiration."

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HUNTERIAN LECTURES.

VOL. II.

Class p. 47.

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LECTURES

ON THE

COMPARATIVE ANATOMY AND PHYSIOLOGY

OF THE

VERTEBRATE ANIMALS,

DELIVERED AT

THE ROYAL COLLEGE OF SURGEONS OF ENGLAND,

IN 1844 AND 1846.

BY

Deposit of S. F. BAIRD.

RICHARD OWEN, F.R.S.

HUNTERIAN PROFESSOR, AND CONSERVATOR OF THE MUSEUM OF THE COLLEGE.

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“ But ask now the beasts, and they shall teach thee ; and the fowls of the air, and they shall tell thee :

“ Or speak to the earth, and it shall teach thee ; and the fishes of the sea shall declare unto thee.

“ Who knoweth not in all these that the hand of the LORD hath wrought this ? ”

JOB, xii. 7, 8, 9.

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## ADVERTISEMENT.

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THE increasing professional avocations of my friend Mr. W. White Cooper having prevented his rendering the kind aid which led to the publication of the "Lectures on the Invertebrata" so speedily after their delivery, a longer delay has occurred in the preparation for the press of those on the Vertebrate Animals than was originally contemplated. Such notes of these Lectures as Mr. Cooper had leisure to take he has kindly placed at my disposal, and they have served to recal characteristic expressions and ideas which suggested themselves in the course of the oral demonstrations. The desire to verify some of the propositions then enunciated, by repeating the observations on which they were founded, has led to many new dissections and examinations of numerous specimens, and reference is made to all those that form part of the Hunterian Museum. I have, also, reconsulted most of the original authorities from which the great bulk of the information imparted in the Lecture-room had been derived: and a list is given of the Works referred to in the text.

The utility of the present Volume has been further regarded, by ingrafting into the text some remarkable discoveries with

which the Science of Comparative Anatomy has been enriched since 1844, and by adding details which the time allotted to the Hunterian course compelled me to omit in the theatre: but I have been careful to preserve the scope and opinions of the original Lectures, and, as far as possible, the very words in which they were delivered.

The Volume concluding the Course will, I hope, appear in the earlier half of the ensuing year.

London, 1846.

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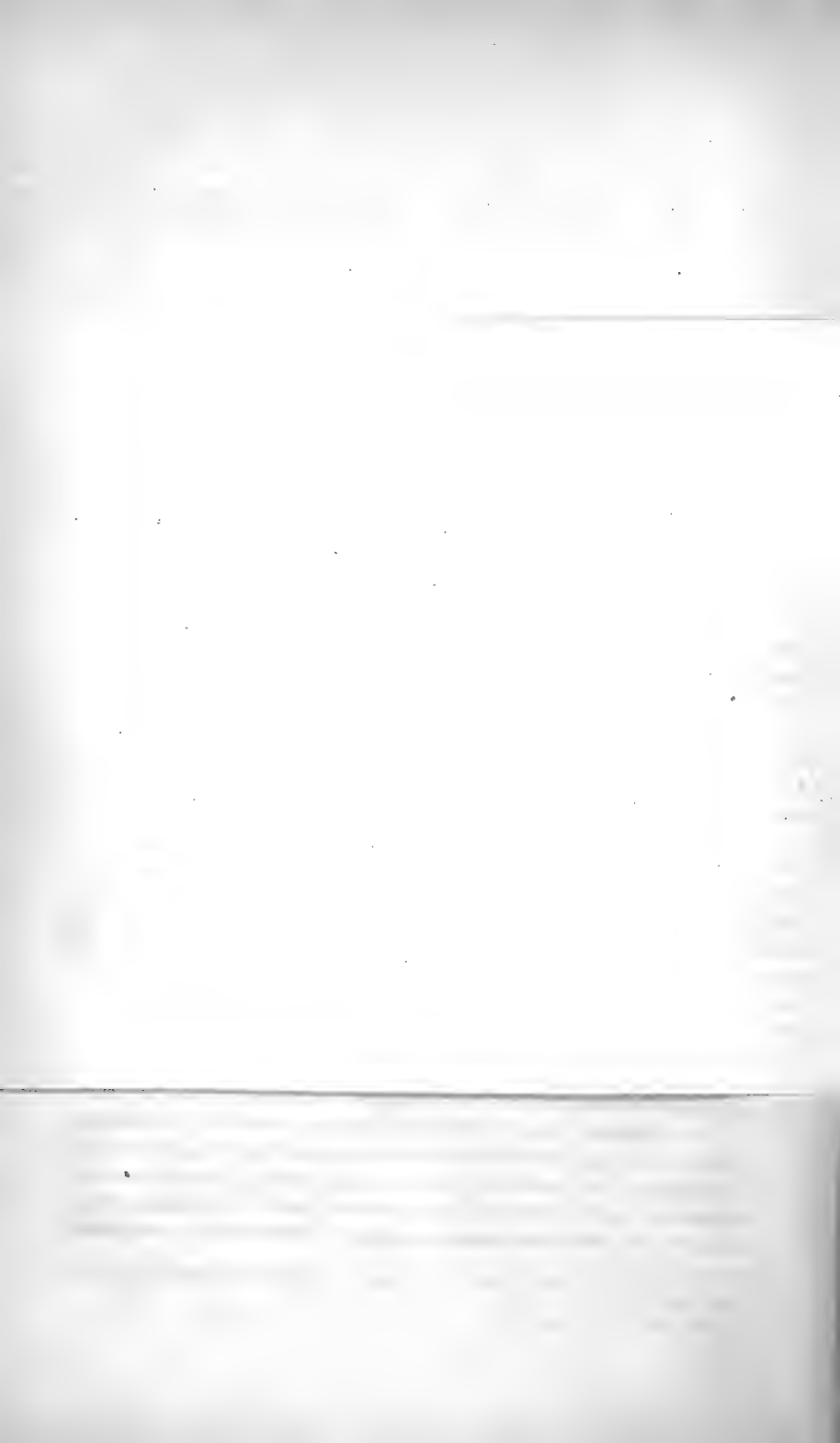
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## ERRATA.

- Page 17. line 9. from bottom, for "only the aquatic," read "only the struthions and aquatic."
36. — 20. from bottom, for "XIII," read "XII."
40. — 13. from top, for "XIII," read "XII."
40. — 22. from top, for "spinal," read "special."
42. — 12. from top, for "XIII," read "XII."
52. — 12. from top, for "came," read "come."
64. — 16. from top, for "vertebra," read "vertebræ."
115. end of note, for "p. 64.," read "p. 43."
138. line 12. of note, for "p. 523.," read "p. 543."
158. 160, 161, 162. after "GEOFFROY," for "xiv.," read "xiv. ii."
158. line 13. from bottom, for "5. Sphenöide principale," read "6. Sphenöide principal."
173. cut 47. has been reversed in printing.
178. note †, for "LVIII.," read "LVII."
198. for note "\* LXXVII. ii. p. 479." read "\* LIV. pl. x." and fo. "† LIV. pl. x." read "† LXXVIII. ii. p. 479."
210. note \*, for "LX.," read "LXX." and in note † for "LXXIX.," read "XXXIX."
211. note \*, for "LXXIII.," read "LXXIV."
238. note \*, for "XXXIII.," read "XXIII."



# HUNTERIAN LECTURES,

1844.

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## INTRODUCTORY LECTURE.

### CHARACTERS OF THE CLASSES OF VERTEBRATE ANIMALS.

Mr. President and Gentlemen,

IN appearing before you on the present occasion, again honoured by the Council with the arduous and responsible duties of the Hunterian Professorship, it might be expected that time, and the repetition of their performance, would have abated much of that anxiety and diffidence which naturally oppress whoever undertakes to expound from this place, and before this audience, the principles of Comparative Anatomy and Physiology. Seven successive annual deliveries of the Hunterian Lectures have, indeed, in some measure familiarised me with this department of the expository labours of the Museum; but they have also tended to impress me with the necessity for increased exertion in order to their successful fulfilment. And now, more than on any previous occasion, when we have assembled in the Theatre of the College under the auspices of a new Charter, honoured, for the second time, by a special mark of the Royal condescension and favour\*, it more especially behoves us, each in his respective sphere, and according to his capacity, to redouble our efforts to maintain, and, if possible, to raise, the high character of British Surgery.

Called by the fruitful principle of the division of labour to the duties of the conservation, extension, and exposition of the preparations which enrich the Museum,—impressed by a sense of the intimate connection of the present estimation of Surgical Science with the labours in Comparative Anatomy of that immortal Physiologist by whom the Museum was founded,—convinced that what has before reflected lustre on the name of SURGEON must continue to have the same influence,—I have felt it especially

\* The present Charter of the Royal College of Surgeons was granted September 4th, 1843.

incumbent on me to labour in the acquisition of that knowledge of the science of Animal Organisation, and of its varied and daily extending applications, which may enable me so to discharge my present duties that the valuable time, which you are not unwilling to spare for attendance on these Lectures, may be not unprofitably bestowed.

And, first, permit me to dwell a little on the inestimable privilege which we enjoy, in entering upon our Professional studies by the portal of Anatomy.

How vast and diversified a field of knowledge opens out before us as we gaze from that portal! Consider what it is that forms the subject of our essential introductory study; nothing less than the organic mechanism of the last and highest created product which has been introduced into this planet. Contrast this, which both Sage and Poet have called the "noblest study of mankind," with the dry and unattractive preliminary exercises of the Lawyer or the Divine.

Every new term which the Anatomical student has to commit to memory is associated with a recognisable object, with some part which may be vibrating, contracting, or pulsating, in his own frame.

First, we enter upon the study of Human Anatomy that we may know with what we have to deal as Operative Surgeons; and, as Physicians, may recognise the seat of disease. Then, that we may learn, by the structure and connections of the parts of the Human body, their office in the vital economy. We next test the physiological ideas, so acquired, by experiments on the lower animals, which we are thus led to dissect in order to find the amount of resemblance with the Human structure which must guide the operation, influence the judgment as to the result, and indicate the conditions for new experiments.

We cannot advance far into the lower region of Anatomy without appreciating the same admirable adjustment of means to ends which pervades the Human frame: thus the field of Physiology expands before us, and we are enabled to bear a part with a RAY or a PALEY in illustrating the doctrine of final causes, and demonstrating the "Wisdom of God in the Creation."

In extending our Anatomical comparisons, we cannot fail to be struck with the close general resemblance of the structure of the lower animals with that of Man: almost every part of the Human frame has its homologue in some inferior animal; and we at length begin to perceive that Man's organisation is a special modification of a more general type. From analysis, the philosophic mind is irresistibly led on to comparison and synthetic combination of the multitude of particulars observed. In grasping the abstract idea of the general type, we appreciate the precise nature of the charac-

eristic modifications of the Human frame ; and then only can we be said to know properly our own structure, and, from Anthropotomists, to become Anatomists in the true sense of the word.

As such we begin to feel ourselves in possession of an instrument which can be brought to operate successfully in the solution of deep and difficult problems of more general interest in the commonwealth of knowledge, and which renders us indispensable auxiliaries in the advancement of Sciences which might at first appear to have but a remote relationship with Anatomy. I need not expatiate on the light which Anatomy lends to the Zoologist, in threading the intricate mazes of the natural affinities of animals : it is, by universal consent, admitted to be the essential basis of a sound system of classification. I need not dwell on the importance of the Comparative Anatomy of the minute and low organised Invertebrata in establishing true theories, and eradicating false notions, of the origin of living species ; of which different hypothetical secondary causes have been from time to time offered for the acceptance or speculation of the thinking public.

But I would allude to the power which the appreciation of the correlations and interdependencies of the several parts of each organic machine gives us to interpret the nature of the whole from the observation of a part.

By this principle its discoverer, the immortal CUVIER, and his successors in this application of Anatomy, have been enabled to restore and reconstruct many species that have been blotted out of the book of life. By this we determine from fossil bones or fragments, submitted to us by the Geologist, the species which are characteristic of different strata. By physiological deductions we can prove that such species, now extinct, have lived and died, generation after generation, through the period when those additions were made to the earth's crust which their remains characterise.

Thus, and thus only, can we obtain a clear idea of the lapse of time in which these formations have taken place. The order of superposition of strata indicates, indeed, their successive formation, but the determination of their organic remains proves that each formation was gradual and progressive.

One of the results of this application of Anatomy has been no less than the discovery of the law of succession of animal life on this planet, or the determination of the relative periods at which the different classes were successively called into being.

Another result may be expected, and is in progress, as a corollary of the preceding, viz. the determination of the true Chronology of the Earth.

We know that it has pleased God to grant us faculties, by the right use of which we may obtain a true knowledge of His works; and it seems part of His providence to permit certain parcels of knowledge to be thus introduced from time to time, to the dissipation of the erroneous notions which previously prevailed. By the exercise of these faculties, the true shape of our Spheroid was determined, and, after some opposition\*, accepted: next, its true relation to the sun, as respects its motion. It has been reserved for the present generation to acquire more just ideas of the age of the world, and Anatomy has been, and must be, the chief and most essential means of establishing this important element in the earth's history.

But Anatomy aids not only the Geologist, but the Geographer: by comparing the local distribution of restored extinct species from coeval geological strata over all the earth, with the geographical distribution of existing animals, we obtain an insight into the past conditions of continents and islands; we determine that our own island, for example, once formed part of the continent, and obtain data for tracing out much greater mutations and alternations of land and sea.†

Thus, upon Anatomy depends the safe and successful practice of Medicine and Surgery: the knowledge of the uses of parts, and of their essential nature in Man, viewed as modifications of a general type. Anatomy is the basis of right classification and philosophical Zoology: it unfolds the law of the introduction of animal life on this planet; it is essential to the right progress of Geology, and gives an insight into the true chronology and ancient geography of the globe.

Almost every day brings some new proof of the importance of the knowledge of Animal Organisation, which bids fair to take rank as the first of all sciences; and it is to Anatomy, that we have the high privilege to be introduced at the very outset of our professional studies.

More might be said, and better, in praise of our peculiar science; but when I reflect on that department which I propose to treat of in the present Lectures, viz. the Comparative Anatomy of the Vertebrate Classes of Animals, its great extent, and the diversity of details which it embraces, I feel it incumbent to enter, without further preface, upon the proper subject of this Course.

\* See Lactantius, *Instit.* lib. iii. c. 24, against the earth's rotundity: and Augustine, *De Cirit. Dei*, lib. xvi. c. 9. against Antipodes.

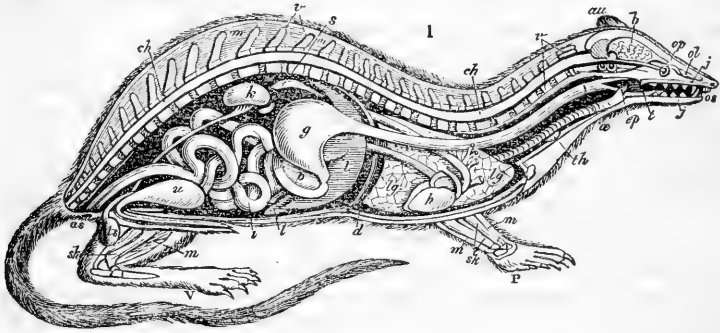
† Report of British Association for the Advancement of Science, 1844; and "History of British Fossil Mammalia," 8vo. 1845, pp. xxvii. xlvi.

IN the numerous classes of animals which constituted that inferior, more extensive, and diversified group, linked together by the single negative character of the absence of a vertebral column, and thence termed "Invertebrata," we saw that, as the several series became elevated in the scale of organisation, they diverged from one another by reason of the preponderating development of some particular class of organs, and culminated in species, inferior either in their general form, or their powers of motion and perception, to some of the antecedent forms, through which the series had passed.\* The spider and the crab are not the kinds of animals in which one should have anticipated that the type of organisation, so richly varied in the Insect class, would have ended, had that class been a step in the direct progress to the vertebrate series. The loss of wings, and the abrogation of the power of flight, would indicate a retrograde course of development. In the insect, the animal organs, more particularly those of locomotion, preponderate over the vegetative or plastic organs, and in the attempt, as it were, to restore the balance, by establishing, as in the Crustacea and Arachnida, a better defined system of circulation, and a more vigorous and concentrated heart, the general plan of the articulate structure appears not to be such as to bear this adjustment without a sacrifice of some of the faculties enjoyed by Insects. So likewise the route of organisation traceable through the molluscous type seems, on the other hand, to lead to an extreme subordination of the motive and sensitive to the vegetative systems. And in those species which make the nearest approach to the Vertebrata, we find the viscera of organic life occupying so large a proportion of the body, that no room is left for the development of nervous or muscular organs, except by what seems an undue expansion and overloading of the head, as, for example, in the Cephalopoda. In fact, the nervous system, the essence and prime distinction of the animal, had not, so to speak, any proper or defined abode in the bodies of the invertebrated animals. Its centres were sometimes dispersed irregularly through the general cavity of the body, sometimes aggregated around the gullet, sometimes arranged with more symmetry along the abdomen; yet seldom better cared for or protected than the neighbouring viscera.

The grand modification, by which a higher type of organisation is established, and one which becomes finally equal to all the contingencies, powers, and offices of animated beings, in relation to this Planet, is the allocation of the mysterious albuminous electric pulp in a special cylindrical cavity, of which the firm walls rest upon a basal

\* Hunterian Lectures, Invertebrata, Svo. 1843.

axis, forming the centre of support to the whole frame, and from which all the motive powers radiate, and this axial cylinder (*fig. 1. v*) is called the "Vertebral Column;" *vertebral*, as consisting of segments of the skeleton, which turn one upon the other, and as being the centre on which the whole body can bend and rotate; from the Latin "*verto, vertere,*" to turn.



Ideal section of a Vertebrate (Mammalian) animal.

The vertebrated animals have the nervous matter concentrated in this vertebral case, which expands at certain parts, where the largest currents of sensation enter, and those of volition go out; and more especially at the anterior or upper extremity, where the impressions to be appreciated by the nervous centre are the most varied and the most distinct. The expanded mass of nervous matter, at this part, is called the *brain* (*fig. 1. b*), the rest of the nervous axis, the *spinal chord*, (*ch, ch*); whence the highest primary group of animals is called "Myelencephala," from the Greek words signifying brain and spinal marrow. The prolongations and ramifications from these centres, forming the internuntiate channels of sensation and the will, are the *nerves*.

There are five special modifications of sensation in the vertebrated animals, three of which have special nerves, viz. smell (*ol*), sight (*op*), and hearing (*au*). Taste (*t*) appears to be less generally enjoyed by the Vertebrata, and its nerve is a large branch of an ordinary nerve, the fifth pair. Feeling, which, in its more exquisite degree, constitutes touch, seems a common property of all those nervous filaments, which, passing into the posterior columns of the central axis, are continued to the brain. Speaking generally, such are the attributes of the recipient or sensitive portion of the nervous axis in the Vertebrated animals. They can take cognisance of all the impressing powers which surround them; as the character and resistance of the surface which supports them, the flavour and fitness of the substances which nourish them, the purity of the atmosphere which they breathe,



the delicate vibrations of that atmosphere which follow the mutual contact or percussion of sonorous bodies, and the finer vibrations of a more subtle æther, the appreciation of which produces the sense of sight.

With these means of perceiving, knowing, and investigating the world around them, the Vertebrated animals possess a proportionate power of acting upon and subduing it. Not any species is fixed to the earth; all can move, and every variety and power of animal locomotion is manifested in the vertebrated sub-kingdom. Yet some permanently retain the worm-like figure, which all primarily manifest in common with the embryos of the articulate series; but always with the grand difference of the dorsal nervous column. Such vermiform species glide by undulatory inflections of the entire body through the waters, or on the surface of the ground. But in most Vertebrata special instruments of locomotion are developed; some single from the median line, some in pairs; the latter never exceed four in number, two before or above, called arms, or pectoral extremities (*P*), and two below or behind, called legs, or pelvic extremities (*V*): thus, the vertebrated type is essentially tetrapodal.\* The solid mechanical supporting and resisting axis, framework, or leverage (*sk*) of these members is internal, vascular, and commonly ossified. It is covered, and, as it were, clothed by the muscles (*m*), which are attached to its outer surface. The elementary contractile fibre of the voluntary muscular system is transversely striated.

The internal position of the skeleton seems to be the chief condition of the attainment, by certain Vertebrata, of a bulk far surpassing that of the largest of the Invertebrata: and the division of the skeleton into numerous pieces diversely articulated, gives great variety and precision to the movements of the Vertebrate animals.

The forms and proportions of the Vertebrata are as varied as their kinds of locomotion, and the elements in which these are exercised. With very few exceptions the body is laterally symmetrical, the right and left sides corresponding. We may likewise discern a general characteristic of the Vertebrata in the tendency to a symmetrical development, or a repetition of parts in the vertical direction; that is, in the dorsal and ventral regions. Each vertebral segment of the internal skeleton, for example, forms typically a dorsal and a ventral arch; the one protecting the nervous axis, the other the vascular trunks and organs of plastic life. The nervous trunk itself

\* The homologues of these special instruments of locomotion may exist in greater numbers, more or less developed and modified, in subserviency to other functions; as, for example, the opercular and branchiostegal flaps of fishes, the simple appendages of the ribs in fishes and in birds. The arms and legs commence in Lepidosiren, for example, as simple unbranched filamentary appendages diverging from inferior vertebral arches.

consists of dorsal and ventral columns. Whilst the Invertebrata manifest a general tendency to development in breadth, the Vertebrata rather gain in height by this doubling or repetition of parts in the vertical or dorso-ventral direction: and in this we may discern the tendency to rise above the surface of the earth, until in man the entire body is uplifted; and what is *below* and *above* in all other Vertebrata, in him becomes *before* and *behind*.

The general external integument in the Vertebrata is rarely burthened and clogged by large and massive calcareous plates, but is usually defended by light, and sometimes exquisitely organised and singularly complex developments of the epidermal covering; modified according to the spheres of existence, the habitual temperature and movements, and therefore eminently characteristic of the different classes of Vertebrated animals.

The actions of the unusually developed nervous element, — whether the vibrating filament conveys to the sentient centre impressions from without, or, obedient to the inward intelligence, imparts from within the stimulus of volition to the moving fibre, — are essentially productive of change. It is most probable that the same nervous fibre is not equally fit for two successive actions; but needs, after each, a certain amount of restoration. The same may be predicated of the action of the muscular fibre; viz., that some change, no matter how small, but to that extent unfitting it for the due repetition of the act, is the consequence of its stimulated contraction: and thus the continued existence of the living animal requires the presence of organs of renewal and repair in intimate, but harmonious combination, with those of sensation and motion.

The raw material of this restoration is derived from without: the alimentary canal, in which the conversion and animalisation of the food take place, is provided, in the Vertebrata, with two apertures, an entry or mouth (*os*), and an excremental outlet (*as*). The jaws (*j*) are two in number, and placed one below or behind the other, working vertically or in the axis of trunk; the principal part of the alimentary canal is contained in an abdominal cavity, and is supported by a reflection of the serous membrane upon the walls of that cavity; and the canal is divided into œsophagus (*æ*), stomach (*g*), and intestine (*i*). All Vertebrata have a liver (*l*) which is usually a very complicated gland, with a special venous or portal system of vessels; and the biliary secretion is conveyed into the commencement of the intestine. The pancreas (*p*), which in most Vertebrata presents the form of a compact and conglomerate gland, adds its secretion to the bile in the duodenum. The spleen (*s*), a cellulovascular ganglion, or gland without a duct, makes its first appearance coincidentally with that of the portal vein, and manifests a progressive

development closely corresponding with that of the pancreas. Lacteal vessels convey the nutrient fluid to the veins, and thus it reaches the heart.

The central organ of circulation, always present, and of a compact muscular character, always below or anterior in position to the alimentary tube and nervous axis, is situated towards the fore-part of the body, most commonly in a compartment distinct from the abdomen, where it is suspended in a special bag or pericardium (*fig. 1. h*). The blood is red in all the Vertebrated animals, and the colouring matter is contained in microscopic discoid cells, of an oval or circular form (*fig. 4*). The whole or part of the circulating fluid is transmitted directly from the heart to the respiratory organ (*fig. 1. l**g*). The respiratory medium, whether air or water, is admitted to the respiratory organ by the mouth. From this organ the arterial blood is sent, sometimes directly, sometimes after a second return to the heart, or in both ways, to the rest of the system; but the breathing organs are never developed, as we saw in many of the Invertebrata, from the returning venous channels.

The venous blood in the lower Vertebrata is submitted to the depurating influence of the kidneys; but in the higher Vertebrata these de-azotising glands (*k*) are supplied exclusively by arteries. A part of the venous blood in all Vertebrata circulates through the liver, as through a second and subordinate lung, before it finally reaches the heart.

The system for perpetuating the species is not complete in any Vertebrated animal; that is, the generative organs are divided between two individuals, there being no natural Hermaphrodite in this sub-kingdom. Every Vertebrate embryo soon takes on its special and determinate sexual character, and ends a perfect male or perfect female—a fertiliser or a producer.

The instinctive sense of dependence upon another, manifested by the impulse to seek out a mate,—which impulse, even in fishes, is sometimes so irresistible that they throw themselves on shore in the pursuit,—this first step in the supercession of the lower and more general law of individual or self preservation, although not first introduced at the Vertebrate stage of the animal series, is never departed from after that stage has been gained. To this sexual relation is next added a self-sacrificing impulse of a higher kind, viz. the parental instinct. As we rise in the survey of Vertebrate phenomena, we see the entire devotion of self to offspring in the patient incubation of the bird, in the unwearied exertions of the Swift or the Hawk to obtain food for their callow brood when hatched; in the bold demonstration which the Hen, at other times so timid, will make to repel threatened attacks against her cowering young.

Still closer becomes the link between the parent and offspring in the Mammalian class, by the substitution, for the exclusion of a passive irresponsive ovum, of the birth of a living young, making instinctive irresistible appeal, as soon as born, to maternal sympathy; deriving nutriment immediately from the parent's body, and both giving and receiving pleasure by that act.

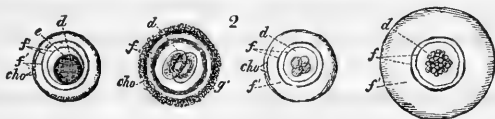
These beautiful foreshadowings of higher attributes are, however, transitory in the brute creation, and the relations cease, as soon as the young quadruped can provide for itself. Preservation of offspring has been superinduced on self-preservation, but there is as yet no self-improvement: this is the peculiar attribute of mankind. The human species is characterised by the prolonged dependence of a slowly maturing offspring on parental cares and affections, in which are laid the foundations of the social system, and time given for instilling those principles on which Man's best wisdom and truest happiness are based, and by which he is prepared for another and a higher sphere of existence. In this destination alone may we discern an adequate end and purpose in the great organic scheme developed upon our planet.

In ascending to Man, we trace a very extensive and varied, but progressive course of development, through the great Vertebrated Series, which commences at a very low point.

It might, perhaps, be imagined that the lowest Vertebrated form began where the highest Invertebrated form ended, and made a direct step in advance in the scale of Animal Organisation. Such, indeed, ought necessarily to follow on the hypothesis of the development of species by progressive transmutation, and of the arrangement of animal life in a single and uninterrupted chain of being.

But truer views of the nature and direction of Zoological affinities, and a deeper insight into the laws of Development and of Unity of Organisation in the Animal Kingdom, concur to disprove those once favourite and recently-revived hypotheses. We have seen that the Invertebrata resemble each other only at the earliest and most transitory periods of their development, diverging thence, in special directions, to the manifestation of very distinct types of animal structure. So likewise we must look to the very beginning of the development of the Vertebrate animal before we shall discover that amount of concordance which will justify us in predicating "Unity of Organisation" between it and any of the Invertebrated forms. And when, with infinite care and minutest scrutiny, availing ourselves of all the aids and appliances of optical art, we have arrived at clear and satisfactory demonstration of the greatest amount of resemblance, in constitution and properties, between the Vertebrate

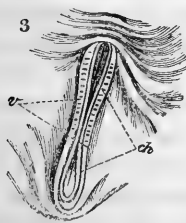
embryo and the Invertebrate adult,—it is not with any of the higher forms of Invertebrata,—with neither the Cephalopod, the Arachnidan, nor the Insect,—that such organic correspondence is found to exist; but it is with the lowest forms and simplest beginnings of animal life,—with the infusorial monads. Only, in fact, during that period of the ovum-life of the Vertebrated being, in which the mysterious properties of the impregnated germ-vesicle are diffused and distributed by fissiparous multiplication amongst countless nucleated cells—the progeny of the primary germinal vesicle and coils of



Ova of the Rabbit, at four early stages of development (Barry).

the seminal virtue—do we find such a form and such properties of the Vertebrated animal as justify us in affirming that there is “Unity of Organisation” between it and an Invertebrate animal. (Compare *fig. 2.* with *cut 14.*, p. 24., Lectures on Invertebrata.)

The next step in the development of the ovum—and it is so speedy a one, that those which precede it long escaped observation—impresses upon the nascent being its Vertebrated type. Certain nucleated cells lose their individuality and powers of propagation; they coalesce and fill the fine tubes so formed with albumen, as the final act of their assimilative power, and thus become converted into nervous tissue, in the form of a double chord (*fig. 3. ch*), which, from its first beginning, marks the dorsal aspect of the embryonic trace: other nucleated cells lay the foundation of the vertebral column (*v*) around the spinal chord; others again change into the softer tissues, and the rest, circulating with the nutrient fluid, as blood discs, through channels which sketch out the sanguiferous system, maintain life, and furnish materials by their powers of assimilation and spontaneous fission to the growing body.\*



Germ of a Rabbit (Barry).

All vertebrated animals, during a greater or less extent of these developmental processes, float in a liquid of similar specific gravity to themselves. A vast proportion, constituting the lowest and fun-

\* “The blood [*damo*, *Hebr.*] is the life.”—Deut. xii. 23. “*αἷμα . . . ἐν τούτῳ γὰρ ἐστὶ ἡ ψυχὴ.*”—Josephus, *Antiq.* 1. 3. 8. “Empedocles,” says Plutarch, “considers the soul to be the blood poured into the heart.” Homer (*Odyssey*, xi. 36. 97. 147.) says, “The shades thirst after blood, for by its influence they escape from Erebus, and regain speech.” See also Sprengel, “*Beiträge zur Geschichte der Medizin*,” i. 3, for the belief by the ancients in the vitality of the blood.

damental group of Vertebrated animals, are never destined to quit the watery medium; these constitute the class of Fishes. A few species retain the primitive vermiform type, and have no distinct locomotive members; and these members, in the rest of the Piscine class, are small and simple, rarely adapted for any other function than the propulsion or guidance of the body through the water. The form of the body is, for the most part, such as mechanical principles teach to be best adapted for moving with least resistance through a liquid medium. The surface of the body is either smooth and lubricous, or is covered by closely imbricated scales, rarely defended by bony plates or roughened by hard tubercles; still more rarely armed with spines.

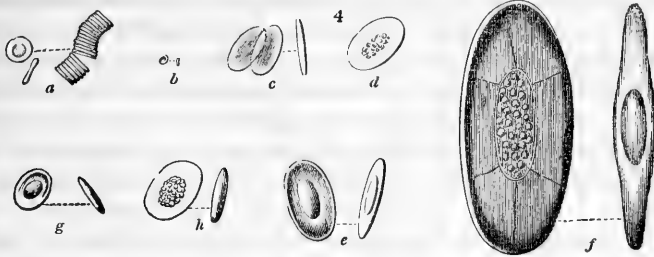
The central axis of the nervous system presents but one partial enlargement, and that of comparatively small size, at its anterior extremity, forming the brain, which consists of a succession of simple ganglionic masses (*fig. 46.*), most of them exclusively appropriated to the function of a nerve of special sense. The power of touch can be but feebly developed in fishes. The organ of taste is a very inconspicuous one, the chief function of the framework supporting it, or the hyoidean apparatus, relating to the mechanism of swallowing and breathing.

Of the organ of hearing there is no outward sign; but the essential part, the acoustic labyrinth, is present, and the semicircular canals largely developed within. The labyrinth is without cochlea, and is rarely provided with a special chamber, but is lodged, in common with the brain, in the cranial cavity. The eyes are usually large, but are seldom defended by eyelids, and never served by a lachrymal organ. The alimentary canal is commonly short and simple, with its divisions not always clearly marked, the short and wide gullet being hardly distinguishable from the stomach. The pancreas, for the most part, retains its primitive condition of separate cæcal appendages to the duodenum. The heart consists essentially of one auricle and one ventricle, receiving the venous blood, and propelling it to the gills; whence the circulation is continued over the entire body in vessels only, which are aided by the contraction of the surrounding muscular fibres.

The blood of fishes is cold; its temperature being rarely elevated above that of the surrounding medium. The coloured discs are sometimes subcircular (*fig. 4. g.*), sometimes subelliptical (*h*) or elliptic: comparatively large, but not the largest amongst vertebrate animals.

The primordial elongated renal glands are persistent, and secrete the urine from venous blood.

Procreation is rarely attended with a coitus or intromission, the requisite accessory organs being wanting in the majority of the class: and the product still more rarely receives, after exclusion, any parental attention or care.



Blood-discs, each magnified 300 diameters linear. *a*, Man; *b*, Musk-deer; *c*, Goose; *d*, Crocodile; *e*, Frog; *f*, Siren; *g*, Cod-fish; *h*, Skate.

In many respects Fishes typify the embryonic stages of development of the higher animals: they were the first created Myelencephala; and, through a series of vast geological periods, as the Silurian, Devonian, and, perhaps, the Carboniferous, the sole representatives of the Vertebrated sub-kingdom in this planet.

The second class of Vertebrated animals, called *Reptilia*, by no means presents so uniform a type as that of Fishes. Reptiles have more varied spheres of action. Some retain the form and breathe the element of fishes, living and moving in water during the whole or a part of their existence. The transition, indeed, from Fishes to these lowest Amphibian or *Batrachian* forms is so close and gradual, that whilst some true Reptiles\* have passed for Fishes, the higher Fishes† have been classed with Amphibia, and even at the present day, a true Fish—the Protopterus or Lepidosiren—has been described, and by some naturalists is still regarded, as a Reptile. But no Reptile has dorsal parapophyses or the scapular arch articulated to the occiput, and every Reptile has two auricles to the heart, and the nasal canal communicating with the mouth. The Tortoises (*Chelonia*) and Lizards (*Sauria*) have locomotive members adapted for progression on dry land; but they can only raise the body a little way, if at all, above the ground, and creep rather than walk: the Serpents (*Ophidia*) have no visible members, but move by the reaction of the entire trunk upon the ground, and so drag their belly through the dust of the earth: whence the name "*Reptilia*" (*repto*, to creep), given to this class of Vertebrate animals.

\* Larvæ of *Rana Paradoxa*, called Frog-fish.

† Sharks and Rays, called "*Amphibia nantes*" by Linnæus.

Reptiles are cold-blooded, like Fishes; but all of them possess lungs, or organs for breathing atmospheric air. Most of the class exercise the function of these organs; but some, retaining gills, chiefly breathe water; and those with lungs alone are less dependent on respiration than the higher *Vertebrata*. Hence the Reptiles were defined by Linnæus as “arbitrary breathers,”—“*Pulmones spirantes arbitrarie*,”—and were called by him “*Amphibia*.” The blood is remarkable for the large relative size and constant elliptical form of its red particles (*fig. 4. d, e*), which, as in Fishes, have a distinct granular nucleus. And, what is more remarkable, the size increases in the ratio of the persistence of the branchial organs. You may, for example, discern the blood-discs with the naked eye in the *Siren lacertina* (*fig. 4. f*). The typical condition of the heart in Reptiles is three-chambered; having two auricles and one ventricle; one auricle receives the venous blood from the general system, the other that which has undergone chemical change in the lungs: both kinds of blood are mixed in the ventricle, and distributed in that state, partly to the lungs again, partly to the general system. The breathing apparatus is so far inferior to that of fishes, as that the whole mass of circulating fluid is not distributed through it; but this apparently retrograde step in development seems as if preparatory to the establishment of a more perfect respiratory system, adapted to the exigencies of higher classes of animals. Always, however, in using or hearing this metaphorical language, it is to be borne in mind, that each condition, which represents a step in progress as regards the series of species, is complete and perfect in relation to the particular species in which it is manifested.

The nervous system of Reptiles presents an advance in the larger proportional size of the cerebral lobes; but the whole brain is still a mere linear series of smooth ganglionic masses, and the cerebellum is often inferior, in size and complexity, to that in Fishes.

The eyes are smaller than in Fishes, but generally more perfect and defended by eyelids: the ears are provided with a vibratory membrane and chamber, called the “tympanum:” but the most characteristic feature of Reptiles in contrast with Fishes, which the organs of the senses present, is the establishment of a communication from the eye, the ear, and the nose respectively, with the respiratory tract or mouth; the eye by the lachrymal duct, the ear by the Eustachian tube, and the nose by its prolongation into a meatus, with a posterior opening into the mouth, or fauces. This latter character the *Siren* manifests, but not the *Lepidosiren*, nor any true Fish. The sense of touch must be enjoyed by the naked



Batrachians and the thin-skinned Lizards in a degree much superior to any of the scaly class of Fishes: but the integument in many of the *Reptilia* is covered or studded with horny or bony scutes.

The generation of Reptiles has certain analogies with that of Fishes. It is still effected in some species, as the Frogs and Toads, without intromission, and in the same species we perceive a simultaneous development of very numerous ova; but the Batrachia form the exception instead of the rule. The intromittent organ which exists in the great majority of the class is also double in most of these, as in Serpents and many Lizards. There are in the *Reptilia* both viviparous and oviparous species; but the fœtus in the former has no attachment to the womb, and the eggs in the latter are hatched by extraneous warmth: the young, after exclusion, receive no parental care or tuition in any species of the class.

In investigating the various strata of the Earth, which form, as it were, the grave-yards of as many successive generations of species and classes, we meet with the earliest remains of air-breathing Vertebrate animals in the triassic or Permian series, subsequent to the deposition of the coal\*, and we consequently infer that the date of their existence, in this planet, is much later than that of Fishes. But the Reptilian class seems soon to have acquired a vast extension, and to have flourished under a variety of forms, developed also to an enormous bulk, with powers for the acquisition and assimilation of both animal and vegetable substances, of which the present state of the class can afford no adequate idea. The deposition of the chalk-formation seems to have been the date of the decline of the *Reptilia*, when they gave way to as varied and colossal forms of animals of a higher type of organisation. Amongst the numerous species, genera, and even orders of the *Reptilia*, which at that period became extinct, was one in which the anterior members of the animal were developed into wings: these veritable "Flying-Dragons," the "Pterodactyles," as they are termed, seem to have perished when true winged Birds made their appearance.

The present is scarcely a suitable occasion for speculating, even if time permitted, on the probable changes in the atmosphere of our planet which accompanied those undoubted revolutions in its crust, by the investigation of which we obtain the evidence of this successive introduction of organic forms; otherwise we might discuss the reasonableness of the surmise that the atmosphere was unfit to be breathed by lungs during that vast lapse of time when fishes reigned supreme upon earth; or we might enquire if the atmosphere of the

\* The less conclusive evidence of foot-prints would carry back the date of the Salamandroid Cheirotheria to the coal formation.—*Lyell, in Silliman's Journal*, vol. ii. p. 25.

later secondary periods was so dank and dense, and overloaded with irrespirable elements, as to need the precipitation of so much carbon as has been consolidated in our coal-fields and chalk-hills, before it was fitted for the full development and vital enjoyment of the warm-blooded and quick-breathing classes? But these and other considerations suggested by the successive introduction of water-breathing and slow air-breathing Vertebrates, would lead us too far away from the proper subject of the present elementary discourse. Suffice it to say, that the oviparous class of animals which next makes its appearance in the order of Creation, is remarkably characterised by the energy of the circulating and respiratory functions, and by the high temperature of the body. I allude to the class *Aves*, characterised as accurately, as briefly, by the name of "feathered bipeds:" bipeds, because the anterior members are exclusively organised for flight; feathered, because the body which is to soar in air must be lightly clad, and yet warmly clad,—must be covered by most efficient non-conductors, so as to retain that elevated temperature which is the necessary consequence of the organic combustion of so much muscular and nervous fibre in the energetic actions of flight. But Birds enjoy almost every kind of locomotion: a few (*Apteryx*) burrow in the earth: some (*Ostrich*, *Rhea*) traverse its surface as swiftly as the most rapid courser: many climb trees: an entire Order is aquatic, swimming or diving with facility. The legs and feet of Birds are accordingly variously modified for these different powers, and furnish the Naturalist with excellent characters for the primary divisions of the class. The lungs are now divided into very minute cells, producing a vast extent of the vascular respiratory membrane; they also communicate with larger cells, forming capacious reservoirs of air, which are continued through every part of the body, even into the substance and cavities of the bones. The heart is divided into four chambers, two muscular ventricles and two auricles; a single artery arises from each ventricle, and a complete double circulation is established,—the left auricle and ventricle circulating the arterial blood, the right auricle and ventricle the venous, transmitting to the lungs the entire mass of the carbonized blood. The blood is of a deep but bright vermilion red, and richly laden with the discoid cells, which are elliptical, but smaller than in the *Reptilia* (*fig. 4. c*).

The jaws of Birds are always edentulous and sheathed with horn, of divers configurations, adapted to their different modes of life and kinds of food. The head is small, and supported upon a long neck; the mandibles performing most of those purposes for which the anterior members, by their conversion into wings, are unfitted; so that the beak combines the functions of hand and mouth. The

gullet, being co-extensive with the neck, is of great length; the stomach is always divided into two cavities, the first glandular, the second muscular; and the distinction between small and large intestines is usually marked by the presence of two cæca. The intestine terminates, as in the Reptiles, in a common cloaca.

The cerebral hemispheres have acquired a large proportional size in Birds as compared with Reptiles, and the cerebellum is complicated by many transverse folds: but Birds are peculiarly distinguished by the inferior and lateral position of the optic lobes; and the whole brain presents a more compact form and larger size, in proportion to the spinal cord and nerves, than in Reptiles. The partial enlargements of the spinal marrow, corresponding to the brachial and lumbar nervous plexuses, are more marked than in Reptiles, and the lumbar enlargement is distinguished by a ventricle. The sense of sight is peculiarly keen and perfect in the class of Birds, and the eye has some structures which are not found in other Vertebrata. The organisation of the ear has likewise advanced, a cochlea, though of simple form, being added to the semicircular canals. A circle of feathers radiates from the outer aperture of the ear, forming a concave disc or conch, to catch and concentrate the vibrations of sound; and such an advance is in harmony with the varied power of expressing the feelings and the passions with which Birds are gifted. We may still, indeed, hear in the aquatic members of the class the hiss of the serpent or the croak of the frog; but as Birds rise in the scale their vocal powers rapidly develop: the cock "with shrill clarion sounds the silent hours," and the nightingale, bursting forth in song, fills all the grove with her varied melody. With regard to the sense of smell we estimate its improvement by observing the more extensive and complex turbinated cartilages in the present Class. But taste must still be dull; there is no true gustatory nerve, and the tongue is commonly sheathed with horn. The beak is in some birds modified to communicate a delicate faculty of touch, but elsewhere this sense is very limited, the general surface of the body being defended by the dense, imbricated, insensible plumage.

All birds are oviparous: only the aquatic birds enjoy intromission. The female constructs a nest and incubates her eggs, and, after exclusion, cherishes, feeds, and educates her young.

The class *Mammalia*, which crowns the vertebrated series and the animal kingdom, is characterised by a double circulation, a quick respiration by lungs subdivided into minute cells, warm blood, and, with few exceptions, a covering of hair. But the lungs are not fixed in the interspaces of the ribs, as in birds; nor do they communicate with abdominal air-cells; but are confined, with the heart, and freely

suspended in a particular compartment of the general cavity of the body, called "thorax," which is partitioned off from the abdomen by a transverse vaulted muscular floor, called the "diaphragm," (*fig. 1. d*). Neither the circulation nor the respiration are quite so active, nor is the animal heat so high, as in the class of Birds: few, indeed, of the Mammalia enjoy the power of flight: most of the class are quadrupeds, as they are commonly called *par excellence*, and support themselves and move by the action of four feet upon the ground. Some burrow: most can swim, and a few are exclusively adapted for living in water, and have the form of fishes; in these the hinder limbs are wanting, and the anterior ones present the shape of fins: but all Mammalia breathe the air directly. The colouring particles of the blood are more minute than in birds, and for the most part of a circular form, (*fig. 4, a, b*).

With a few exceptions the jaws of the Mammalia are armed with teeth, variously modified in subserviency to the habits and food of the different species. In like manner the stomach is simple or complex, in relation to the amount of change to be effected in the assimilation of the food: the small intestine is usually divided from the large by the presence of a single cœcum, and the rectum, with very few exceptions, has its outlet distinct from that of the genital and urinary systems. The kidneys are supplied with blood from the renal arteries exclusively; but the liver continues to receive the superadded system of the vena portæ. The secretion of the kidneys is always conveyed to a urinary bladder (*fig. 1. u*), and the penis is traversed by the urethral canal.

All Mammalia intromit in fecundation, and all are viviparous: in most the ovum, after quitting the ovary, becomes a second time attached to the parent, through a variously modified cellulo-vascular organ called "placenta." The young are nourished after birth by the secretion of glands, called mammary — whence the name of the class. Perhaps the peculiar and constant existence of a well-developed epiglottis, which Aristotle in one of his surprising generalisations states to be present in all hairy viviparous quadrupeds, may have its true relation of physiological co-existence with the mammary glands, being most essential as a defence of the glottis during the act of sucking.

The bodies of the vertebræ are united to each other by concentric ligaments, attached commonly to flattened surfaces, forming the intervertebral substance. The cervical vertebræ are seven, not varying in number according to the length or shortness of the neck. Hair is the characteristic clothing of the body; but almost all the modifications of the epidermal system which we meet with in the inferior vertebrated classes are repeated in the present: thus we have quills

in the "fretful porcupine," spines in the hedgehog, scales in the manis, bony scutes in the armadillo; whilst a few species at the two extremes of the series are naked, for example, the whale and the man.

Thus far the review of the general anatomical characteristics of the Mammalian class seems not to indicate a very marked superiority: in the energetic contraction of the muscular fibre, in the rapidity of the actions of the heart and lungs, Mammals are surpassed by Birds: but the functions which attain their highest development in the Mammalian class are of far nobler character than those which are more immediately connected with the maintenance of animal life. The progressive expansion of the brain is greatest, and the final predominance of reason over instinct is achieved, in the present class: sensation is its characteristic rather than muscular energy or irritability; the instincts become more varied, they are also less mechanical and more educable. In Mammalia we first find the cerebral hemispheres acquiring an additional extent of the grey and vascular surface by convolutions, which increase in number and depth as the species approximate Man: a fornix first, and then a corpus callosum, are introduced into the Mammalian brain, to bring into mutual communication the various parts of the hemispheres. A new cranial bone, the squamosal, developed from the proximal piece of the mandibular arch, now, for the first time, takes a share in the formation of the walls of the cranial cavity. The organs of the senses attain their most complex structures in the present class. The ear has a perfect spiral cochlea, and the distinct appendage called outer ear. No bony plates are ever developed in the sclerotic coat of the eye. The turbinated bones and pituitary membrane of the nose present in most Mammalia a great, and in some a prodigious extent of surface. The tongue is large, soft, and papillose, and is supplied with a gustatory as well as a motor and respiratory nerve.

We see the locomotive extremities progressively endowed with more varied and complicated powers. At first retaining, in the Cetacea for example, their primitive embryonic form of simple flattened fins; they next, with ampler proportions, acquire the full development of the normal joints and segments, and have their extremities enveloped in dense hoofs: next we find the digits liberated, and armed with claws confined to the upper surface, leaving the under surface of the toes free for the exercise of touch: then we have certain digits endowed with special offices, and, by a particular position, enabled to oppose the others, so as to seize, retain, and grasp: lastly, in Man, the offices of support and locomotion are assigned to a single pair of members, so organised as to sustain the body erect; leaving the

anterior, and now the upper, limbs free to execute the various purposes of the will, and terminated by a hand, which, in the matchless harmony and adjustment of its organisation, is made the suitable instrument of a rational intelligence.

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## LECTURE II.

### THE SKELETON.

DESCRIPTIVE Anatomy usually commences with the bones, and the consideration of the passive organs of motion before the active ones is conformable to the sequence of development, since the fixed points are formed before the muscular fibres.

The branch of anatomy which treats of the Skeleton of Vertebrate animals is designated "Osteology," because in anthropotomy it relates exclusively to the bones and teeth. But the skeleton, according to its etymological signification of hard and dry parts, might apply to the hair and nails, and, indeed, the entire epidermal system. When, also, in a general survey of the Vertebrata, we see the spinal column gristly in some fishes, and the tendons bony in some birds; and when we call to mind such homological relations as that of the fibro-membranous sclerotic of the human eye with the cartilaginous sclerotic of the turtle and the osseous sclerotic of the cod-fish, it will be obvious that the present branch of anatomy ought naturally to embrace the aponeuroses, ligaments, and cartilages, since these are so many arrested stages in the histological development of the internal skeleton.

In the Invertebrata we saw that the skeleton, or parts analogous,\* to the bones of the Vertebrata, commonly consisted of large, strong, thick, often unjointed plates, developed in or upon the skin, hardened principally by carbonate of lime, protecting the whole body, and having the muscles attached to the inner surface.

In the Vertebrata the skeleton chiefly consists of diversely configured, but most commonly cylindrical and articulated pieces, hardened chiefly by phosphate of lime, developed from fibrous and cartilaginous tissue in the interior of the body, of which it forms the internal framework, giving attachment to the muscles by the outer surface, and subserving their action as levers and fulcra.

The exterior calcified shells and crusts of the Invertebrata are un-

\* For the sense in which the terms homologous and analogous are used in the present Lectures, see the Glossary appended to the "Lectures on Invertebrata," 8vo. 1843.

vascular; they grow by the addition of layers to their circumference, or they may be cast off when too small for the growing body, and be reproduced of a more conformable size; but they have no inherent power of repair.

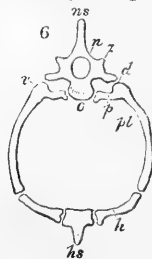
The internal bones of the Vertebrata are vascular; they grow by internal molecular addition and change, and have the power of repairing fracture or other injury.

Such are the broad and obvious distinctive characters of the skeletons of the Invertebrate and Vertebrate animals; the contrasts having relation chiefly to the difference in the development of the nervous system. Thus, when the powers of discerning and avoiding lethal or hurtful agencies are dull and contracted, the entire animal is protected by a hard insensible dermal armour, or exo-skeleton; but, as those powers become expanded and quickened, the body is disencumbered of its coat of mail, the skeleton is put inside, and made subservient to the activities, and the skin becomes proportionally more susceptible of outward impressions of pleasure and pain.

Some estimable anatomists, who have more especially devoted their attention to the detection of the corresponding parts in different animals, have supposed that these different functions were performed by modifications of essentially the same or homologous parts of the skeleton.



Segment of exo-skeleton, *Astacus*.



Segment of endo-skeleton, *Mammal*.

Observing that a segment of the outer skeleton of an articulate animal, the thoracic ring of a lobster for example (*fig. 5.*), formed a small canal (*es*) for the nervous trunks, and a larger one (*h*) for the vascular trunks and plastic organs; and that a thoracic segment of the skeleton of a Vertebrate animal (*fig. 6.*) also formed a small protecting canal for the spinal chord (*c, ns*), and a larger hoop (*c, hs*) about the vascular and other viscera of that cavity,—they have concluded that both were modifications of the same elements or primary segment of the skeleton. Carus, for instance (No. 1. p. 73.), calls both rings “vertebræ;” and Geoffroy St. Hilaire (II. p. 119. pl. 7.) thought it needed but to reverse the position of the Crustaccan,—to turn what had been wrongly deemed the belly upwards,—in order

to demonstrate the unity of organisation between the Articulate and Vertebrate animal. But the position of the brain is thereby reversed, and the alimentary canal still intervenes in the Invertebrate between the aortic trunk and the neural canal.

The outer and the inner skeletons do agree in certain relations: neither of them are primitive parts of the organism, but are modifications or metamorphoses of other pre-existing systems: both serve as fixed points of attachment to the muscles, aid their action as levers, and determine the kind of movements by particular joints: both are organs of protection and support.

But, besides the differences of tissue, mode of growth and vital properties, already noticed, the exo- and the endo-skeletons differ in the one being developed from the skin, the other from the internal cellular and fibrous systems. The exo-skeleton defends or surrounds the periphery of the animal; the endo-skeleton the internal parts. The exo-skeleton is related to the muscles by its inner surface, the endo-skeleton by its outer surface. The exo-skeleton is the reflex of the circumambient medium and relations of the animal: the endo-skeleton is the index of its motive energies and its intelligence.

Even the neural canal itself is differently constructed in the segments of the exo- and endo-skeletons selected for comparison: in the Vertebrate it is an arch developed from a central column (*c*, *fig.* 6.), which, in like manner, gives origin to the opposite or hæmal arch; in the Articulate the neural canal is formed by processes, apodemata, or entapophyses (*e*, *fig.* 5.) sent off from the great peripheral arch. Moreover, the development of these processes relates rather to that of the muscular than of the nervous systems. We saw\* how greatly the ganglions vary in number and position upon the abdominal nerve-trunks of insects. Now, if the entapophyses of the dermo-skeleton—the secondary vertebræ of Carus—were developed, like the neural arches of the vertebræ of the endo-skeleton, in special relation to the protection of the nervous centres, and conformable in number with the pairs of nerves thence sent off†, we ought to find them governed by the existence and position of the ganglions; but it is not so. In the Myriapoda, as Von Baer well objects (III.), entapophyses are entirely absent; and in winged insects they are confined to the thorax or locomotive segment, although there may be two, three, or four ganglions in the abdomen. And, what is further to be remarked, the thoracic entapophyses are not developed over the thoracic ganglions, but over the inter-communicating chords. In fact, their relation to

\* Lectures on Invertebrata, 8vo, 1843, p. 205.

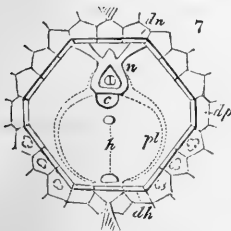
† "Numerus vertebrarum semper cum numero nervorum spinalium intime hæret."—Otto Heer, *De Ossium Concretionem normali*, &c., 4to. 1836, p. 6.



the nerve-trunks seems to be accidental, depending upon the position of the muscular masses to which they give attachment, and which office is the essential condition of their existence. For this purpose the processes of the exo-skeleton of Insecta and Crustacea must go inwards, and thus they happen to protect certain parts of the nervous system.

Only the highest of the Mollusca possess a true homologue of the endo-skeleton, developed in relation to the defence of the nervous centres: but it is a feeble cartilaginous rudiment in the best organised Cephalopods; and, in the cuttle-fish, is far outweighed by the calcareous dorsal plate which still represents the exo-skeleton of the testaceous mollusks. Thus a cartilaginous cranial vertebra co-exists in the highest Invertebrata with a calcareous dermal skeleton; and there is no abrupt contrast in passing thence to the consideration of the skeleton in the Vertebrata.

The exo-skeleton is by no means indeed dispensed with in the Vertebrate series, although the endo-skeleton is constant, and here attains its full development. In the lowest class, most fishes, for example, present an imbricated outer covering of scales, developed like shells, between the derm and epiderm: other fishes have hard ossaceous plates or spines scattered over their exterior, or are entirely surrounded by a connected armour of dense enamelled bony scales, as in the Lepidosteus and the Ostracion, which latter fish offers an instructive example of the co-existence of an exo- with an endo-skeleton, and a convincing refutation of the idea of the homology of the annular segment of the crust of the lobster with a true typical vertebra. In the subjoined diagram, (*fig. 7.*) *n* is the cartilaginous neural canal;



Segment of endo- and exo-skeletons, *Ostracion*.

*pl*, the membranous pleurapophysial wall of the abdomen; *h*, the arterial and venous trunks of the abdomen; *dn*, *dp*, *dh*, the dermal ganoid plates. The ossified scutes of the Crocodiles and the tessellated armour of the Armadillos are examples of the exo-skeleton co-existing with a well-developed and ossified endo-skeleton; and wherever the exo-skeleton of a Vertebrate animal is calcified, it presents the same organised vascular structure and

vital properties as the bones within. Most commonly the exo-skeleton of the air-breathing Vertebrata is epidermal, as where it forms the scales of the serpent or lizard, the large plates of the tortoise, the imbricated pointed scales of the manis, the spines of the hedgehog, the quills of the porcupine, the feathers of the bird, or the hair of the ordinary mammal.

The skeleton is not entirely external or dermal in the Invertebrata. Independently of the true cartilaginous endo-skeleton of the Cephalopods, and of the entapophyses, sometimes also cartilaginous, of the annular segments of the exo-skeleton of Insects and Crustacea, there are parts, as the calcified framework supporting the gastric teeth, and giving attachment to the muscles which work them, in the lobster, and the calcareous gastric plates of the *Bulla*, which relate more particularly to the functions of the internal organs, or contained viscera; and we find a corresponding group of parts of the general skeleton in most Vertebrate animals. The cartilages or bones of the larynx, trachea, and bronchia of the air-breathing Vertebrates, the bones and cartilages supporting the branchiæ in fishes and batrachians, the bones in the hearts of certain birds and mammals, are examples of the visceral series of hard parts, or the "splanchno skeleton," as it has been termed by Carus; and very nearly and naturally connected with this primary division of hard and dry parts are those bones and gristles which form capsules, or support the appendages of the special organs of the senses; as, for example, the sclerotic osseous cups or plates of the eye, the petrous capsule of the labyrinth, the ossicles and cartilages of the tympanum and external ear, the turbinate bones and gristles of the nose. But some of these "sense capsules" are connected and intercalated with the true bones of the endo-skeleton, and subservient to similar functions, besides their own special uses, so that they are generally described as ordinary bones of the skull. As in all arrangements of natural objects, where nature is followed in selecting their characters, so in classifying the parts of the general skeleton of the Vertebrata, the primary groups blend into one another at their extremes, and make it difficult to draw a well-defined boundary line between them. Thus the hyoid and branchial arches closely resemble each other in fishes. Bones of the dermo-skeleton combine with those of the endo-skeleton to form the opercular and the single median fins. But we must not on that account abandon the advantage of arrangement and classification in acquiring an intelligible and tenable knowledge of a complex system of organs, when typical characters clearly indicate the general primary groups. Clearly appreciating the existence of such characters in the very numerous and diversified parts of the general skeleton of the Vertebrate animals, I, therefore, adopt the primary division of those parts into endo-skeleton, exo-skeleton, and splanchno-skeleton.

The endo-skeleton may present itself to our observation under three histological conditions, the fibrous, the cartilaginous, and the

osseous: the exo- and splanchno-skeletons may offer also another, or fourth condition, viz. the albuminous, or epidermal.

The most common tissue of the endo-skeleton of the Vertebrata is that called "bone," and it is peculiar to this primary division of the Animal Kingdom.

Bone consists of animal, chiefly gelatinous, matter, hardened by a general but regulated diffusion of earthy molecules; the proportion of organic to inorganic matter varies in different classes. Fishes have the least, Birds the largest proportion of earthy matter; and of the two, in this respect, intermediate classes, the Mammalia, especially the active predatory species, have more earth, or harder bones, than Reptiles. This difference depends chiefly upon the quantity of fluid, or evaporable matter, in the cells and tubes of the animal basis, but not wholly, as some have supposed; at least the apparently exact, certainly most carefully and scientifically conducted experiments of M. Bibra (iv.) on thoroughly dried portions of bone, show the following differences:—

PROPORTIONS OF EARTHY AND ANIMAL MATTER IN THE BONES OF VERTEBRATE ANIMALS.

FISHES.

	SALMON. <i>Salmo Salar.</i>	CARP. <i>Cyprinus Carpio.</i>	COD. <i>Gadus Morrhua.</i>
Organic -	60·62	40·40	34·30
Inorganic -	39·38	59·60	65·70
	<hr/> 100·00	<hr/> 100·00	<hr/> 100·00

REPTILES.

	FROG. <i>Rana esculenta.</i>	SNAKE. <i>Coluber Natrix.</i>	LIZARD. <i>Lacerta agilis.</i>
Organic -	35·50	31·04	46·67
Inorganic -	64·50	68·96	53·33
	<hr/> 100·00	<hr/> 100·00	<hr/> 100·00

MAMMALS.

	DOLPHIN. <i>Delphinus Delphis.</i>	OX. <i>Bos Taurus.</i> (Femur.)	WILD-CAT. <i>Felis Catus.</i> (Femur.)	MAN. <i>Homo.</i> (Femur.)
Organic -	35·90	31·00	27·77	31·03
Inorganic -	64·10	69·00	72·23	68·97
	<hr/> 100·00	<hr/> 100·00	<hr/> 100·00	<hr/> 100·00

## BIRDS.

	GOOSE.	TURKEY.	HAWK.
	<i>Anser</i> (femur.)	<i>Gallopavo</i> (femur.)	<i>Falco Gallinarius.</i>
Organic -	32·91	30·49	26·72
Inorganic -	67·09	69·51	73·28
	100·00	100·00	100·00

In the above table it will be observed that the bones of the fresh-water fishes are lighter and retain more animal matter than those of the fish which swims in the denser sea, and that the Mammalian marine species, *Delphinus*, differs little from the sea-fish in this respect. The Batrachian Reptile has more animal matter in its bones than the Ophidian or Saurian, and thus more resembles the Fish. Serpents almost approach Birds in the great proportion of the earthy salts, and hence the density and ivory-like whiteness of their bones. The typical bones of Birds are the whitest and most compact of all bones, by reason of their large proportion of earthy matter, and also of the absence of marrow from their capacious pneumatic cavities, on which their lightness depends: in those bones of Birds from which air is excluded, the oily marrow deadens the whiteness of the tissue, and it is often difficult to get rid of the greasy surface in skeletons.

The nature of the inorganic or hardening particles, and of the organic basis, according to the analysis by Bibra of completely dried portions of bone, is exemplified in the subjoined table, including a species of each of the four classes of Vertebrata.

## CHEMICAL COMPOSITION OF BONES.

	HAWK.	MAN.	TORTOISE.	COD.
Phosphate of Lime, with trace of Fluat - - -	64·39	59·63	52·66	57·29
Carbonate of Lime - - -	7·03	7·33	12·53	4·90
Phosphate of Magnesia - -	0·94	1·32	0·82	2·40
Sulphate, Carbonate, and Chlorate of Soda - - -	0·92	0·69	0·90	1·10
Glutin and Chondrin - - -	25·73	29·70	31·75	32·31
Oil - - - - -	0·99	1·33	1·34	2·00
	100·00	100·00	100·00	100·00

In addition to the differences already noted in the proportions of earthy and animal matter, it is interesting to observe that the propor-

tion of soluble salts to the less soluble phosphates of lime is greatest in the fish, and that there is most carbonate of lime in the bones of the tortoise. The quantity of evaporable fluid is greatest in the bones of Fishes, especially in those of the semi-osseous sharks and rays, in the skeletons of which also the salts of soda are in larger proportion than in the osseous fishes. The animal part of the shark's skeleton differs from the glutin of ordinary bones, and from the ossifiable cartilage of higher animals; it has more analogy with mucus, requiring 1000 times its weight of boiling water for its solution; and this is neither precipitated by infusion of galls, nor yields any gelatine upon evaporation. In the entirely unossified skeleton of the lamprey *Bibra* found only  $1\frac{1}{2}$  per cent. of earthy salts.

How, we may next ask, are the inorganic earthy particles diffused through the animal basis, and whence are they obtained? Bones are not a primitive formation, but the result of a transmutation of pre-existing tissues. The inorganic salts defined in the foregoing tables pre-exist in the albumen of the egg, in the milk which nourishes the new-born mammal, in the plasma or "liquor sanguinis" of the circulating fluids.

The blastema or primitive basis of bone is not originally cartilage, but more resembles mucus in its chemical characters: it appears at first to be a sub-transparent glairy fluid, but contains a multitude of minute corpuscles. Its assumption of the cartilaginous character and consistency is attended with the appearance in it of numerous small, sub-elliptic, nucleated cells. As the cartilage hardens, these cells increase in number and size, and begin to accumulate, and to be arranged in linear series at the part where ossification is about to commence. These series in the cartilage of long bones are usually vertical to its ends, and in flat bones are vertical to the peripheral edge; *i. e.* they are parallel to the axis of the long bone, and are radiated in the flat one, but not with mathematical exactness.

The nucleated cells are the instruments by which the earthy particles are arranged in order; and, in bone, as in tooth, there may be discerned in this predetermined arrangement, the same relation to the acquisition of strength and power of resistance, with the greatest economy of the building material, as in the disposition of the beams and columns of a work of human architecture. (v. p. vi.)

The power of the cells so to operate upon the salts of the plasma, which percolates the intervening tissue, seems to reside chiefly in the repellent property of their nuclei: I have been led by observation of

some of the phenomena of osteogeny to surmise that the walls and the nucleus of the cell were in opposite electric or magnetic states, one attracting, the other repelling, the surrounding earthy particles.

Certain of the columnar series of nucleated cells become more aggregated or pressed together; their nuclei become more concentrated, and, according to Miescher and Gerber, they coalesce and become dissolved, leaving a cylindrical tube, parallel with the long axis of the future bone. First, a reddish lymph, and then a capillary vessel is prolonged into each of these cylinders, which is converted into a "Haversian," or vascular canal: before, however, the direct influence of the circulation has penetrated so far, the nucleated cartilaginous cells have arranged or propagated themselves in concentric series round the cylinder, and the intervening layers of the molecular blastema begin to be impregnated with the hardening salts, which, being repelled by the nuclei of the cells, are forced into the concentric laminated arrangement around the Haversian canal. The establishment of the capillary circulation in these canals accelerates the progress of ossification by the rapid import of new material: the resisting nuclei of the surrounding concentric cells, pressed on all sides, undergo a remarkable change, and the nucleolar matter is forced out in rays, but chiefly in the direction where the resistance is least, viz. towards the Haversian canal. The remaining central nuclear matter and that of the diverging rays finally become dissolved, and establish permanent bone-cells and minute tubes, which tubes, traversing the concentric lamellæ, open into the Haversian canal, and receive the transuded plasma from the blood-capillary. The tubes branch and anastomose, and form the medium of the transmission of the plasma through the densest osseous tissue. This system of cells and tubes, in fact, perform the same important function in the nutrition of the osseous tissue, which I ascribed in 1838 to the corresponding cells and tubes of the cemental tissue of the teeth of the *Megatherium* (vi. p. 104.): and they might be appropriately termed the "Plasmatic system." They correspond with one of the series of the "vasa lymphatica" of the older physiologists; the first kind, for example, specified in Noquez's edition of Kiel, quoted by Hunter: "Les premiers naissent des extrémités artérielles; on les nomme 'artères lymphatiques,' qui peut-être ne sont autre chose que les conduits excrétoires d'une lympe très subtile, ou de la matière qui respire" (vii. vol. ii. p. 11.). The dentinal tubes of teeth and the plasmatic tubes of bone are not, indeed, prolonged from attenuated ends of arterial capillaries, but they receive the plasma transuded or transpired from the parietal pores of the capillary system, and thus

they agree in their main physiological relations with the first class of Noquez's Lymphatics: and the solid tissues of tooth and bone manifest under the microscope a system of nutrient vessels, which were only hypothetically known to the older physiologists. I have detected a similar system of plasmatic tubes in tendon; and they probably exist, under characteristic modifications, in all tissues, constituting the essential nutritive system of such.

The remains of the metamorphosed cartilaginous cells in bone were first discovered by Purkinje and Deutsch, (VIII.), arranged in concentric series around the Haversian canals: they believed them to be solid, and called them "corpuscula ossea." Treviranus (IX.) first described them as cavities or "lacunæ," in the intervals of the concentric ossified lamellæ, and he believed them to be filled with fluid. Professor Müller (X.) was led by the whiteness of the radiated corpuscles when viewed by reflected light, and by its disappearance, accompanied with evolution of gas, when acted upon by dilute acid, to regard them as containing, either in their parietes or cavity, calcareous salts. Serres and Doyere and others have reproduced the idea of Treviranus, which is true to a certain extent, but have erred in denying that the radiated cells contain any calcareous salts, and have objected to the term "calci-gerous" applied to those cells. But the effects of reaction of dilute acid in removing the opacity of the cell when viewed by transmitted light, and in removing its whiteness when viewed by reflected light, show that these optical phenomena are not due to the mere depth of empty cells: aggregated particles of the earthly salts become deposited after the solution of the resisting nuclear matter upon their parietes; but the cavities are preserved by the slow but constant percolation of the plasmatic fluids. Thus bone, like dentine, "presents a two-fold arrangement of its hardening particles, which are either blended with the animal matter of the interspaces and parietes of the tubes and cells, or are contained in a minute and irregular granular state in their cavities;" and "the density of bone, as of dentine, arises principally from the proportion of earth in the first of these states of combination." (v. p. iii.)

The primitive arrangement of the osseous tissue, so composed, is lamellar, the lamellæ being arranged either concentrically around the Haversian canal, or around the entire circumference of the bone, or in interrupted plates connecting together the Haversian cylinders, and those with the generally surrounding peripheral lamellæ.

The Haversian canals usually contain, in addition to the capillary vessel, some oil, and this is the seat of the green colour in the bones of the Belone and Lepidosiren.

In most osseous fishes the nucleus of the cartilage-cell quite disappears in the process of ossification, and only the tubular prolongations of the nuclear matter leave permanent traces, as plasmatic tubes, which traverse the osseous lamellæ in the intervals of the vascular canal, and freely open into the latter, which are unusually numerous. In the bones of Reptiles there is more diversity in the number of the Haversian canals, which is less in Ophidians and Saurians than in the fish-like Batrachian. The radiated cells are always present, but are less regular in form and rather larger than in Mammals; they are rounder in Birds, with less conspicuous radiating plasmatic tubes; they are usually more elliptic and compressed in Mammals, in the osseous tissue of which class the more appreciable difference in microscopic structure obtains in the relative size of the Haversian canals to the plasmatic, calcigerous, radiated cells.

These cells vary little in diameter in different Mammalia; but the Haversian canals which average  $\frac{1}{800}$ th of an inch in diameter in the mouse are  $\frac{1}{300}$ th of an inch in diameter in the ox, and  $\frac{1}{400}$ th of an inch in the human subject.

The Haversian canals are fewer in the dense osseous tissue of Birds than in that of Mammals: in the bones of Chelonia and Batrachia they are more numerous, larger, and more reticularly disposed; the radiated cells are also larger.

In my treatise on the teeth (v. pp. xvi—xxii.), I have shown that the osseous tissue corresponds in microscopic structure with that of the dentine in many fishes. In no class is the structure of the teeth more varied, and in none do we find such extreme modifications in that of the bones.

Throughout a great part of the skeleton of the pike the osseous, like the dental, tissue is characterised by “a reticulo-medullary tubular structure:” the meshes or interspaces being traversed by the rich series of plasmatic tubes communicating with the vascular or Haversian canals; and there are few central dilatations radiating plasmatic tubes, in other words, few purkingian cells.

In this section of the lower jaw of a *Muræna* (Prep. 2560 a.) we perceive, on the contrary, an abundance of radiated cells, but no Haversian canals. The cells, divided lengthwise, present a long, thin ellipse, with the ends prolonged into plasmatic tubes, larger than those which radiate from the sides; and, as the terminal prolongations communicate with each other, a series of cells may often be traced resembling a moniliform or alternately dilated and contracted canal. In a section of a jaw of the common eel, large, irregular vascular canals are seen, combined with radiated cells like those in the *Muræna*. In a section taken from the second thin longitudinal crest of the cranium of an



*Ehippus*, there are no radiated cells; the dense tissue is traversed by parallel undulating plasmatic tubes, which here and there present slight dilatations, divide, and give off minuter tubes which anastomose in their interspaces. The medullary canals, from which the tube derive their plasma, are few and large.

Almost endless are the minor modifications of the structure of the osseous tissue of the Vertebrate animals, chiefly produced by varieties in size, course, and number of the vascular canals and the radiated cells and tubes: both vascular canals and radiated cells may be absent in the portion of bone examined; but the plasmatic tubes are always present. In the dermal bone-plates of the sturgeon, they become, in the dense exterior layer, as minute as in the so-called enamel of the shark's teeth.\*

The growth of bone presents some modifications in the different classes of Vertebrate animals.

In Fishes the bones continue to increase in dimension almost throughout life: this is best seen in the cranium, where the periphery of the bones, both of those which overlap by squamous sutures, and those which interlock by broad dentated surfaces, is cartilaginous, and, in the thin bones, sub-transparent. Here the development, serial arrangement and metamorphoses of the cartilaginous cells, in other words, the growth of temporary cartilage, are always to be seen in progress.

The long bones of most Reptiles retain a layer of ossifying cartilage beneath the terminal articulating cartilage, and growth continues at their extremities throughout life. Few of the long bones of Birds have separate terminal pieces or epiphyses: the distal epiphysis of the tibia is an exception to this rule; but the distinct single piece which forms the upper end of the ankle-bone in the young bird represents the tarsal segment, and rests, not on a single diaphysis, but on the still separate proximal ends of the three metatarsals. In tail-less Batrachians and in most of the Mammalian class, the ends of the long cylindrical bones, which support the articular cartilages, are distinct in the growing bone from the shaft, and are termed "epiphyses," the shaft being the "diaphysis:" the seat of the active growth of the bone is in a cartilaginous crust at the ends of the diaphysis. When the epiphyses finally coalesce with the diaphysis, growth in the direction of the bone's axis is at an end: but in the Mammalian bones, as in those of Birds and Reptiles, there is a slower growth going on over the entire periphery of the bone, which is covered by the periosteum: the

\* The work of Bibra (iv.) contains good observations and illustrations of the comparative microscopic anatomy of the osseous tissue in the different classes of Vertebrata.

periosteum is that membrane in which the vascular system of a bone undergoes the amount of subdivision which reduces its capillaries to the dimensions suited for penetrating the pores leading to the vascular and Haversian canals.

These preparations of the bones of young pigs fed with madder (Nos. 190—201. Phys. Series), and those of young birds, showing artificial perforations (Nos. 188, 189.), illustrate some experiments by Hunter on the growth of bone.

The strong affinity of phosphate of lime for the colouring matter of the *Rubia tinctorum*, which, when taken as food, passes into the plasma of the circulating fluids and combines with the phosphates of lime with which that fluid comes in contact, has been supposed to throw some clear light upon the growth of bone. All the phosphate of lime which is deposited in tooth or bone, whilst the madder is in the system, is deeply tinged by it, and Hunter found that the exterior layers of the growing bone of a young pig which had been fed a fortnight on madder were most strongly coloured. But he observed also in another young pig similarly fed, but killed a fortnight after the madder had been omitted from its food, that "the exterior of the bones was of the natural colour, but the interior red." (xi. p. 75.) The inference deduced was, that a new layer of bone, during the absence of madder from the circulating system, had been formed, uncoloured, on the exterior surface.

Mr. Gibson endeavoured to invalidate the conclusion, by hinting that the colouring matter might have been removed from the previously stained bone by the serum of the blood, which fluid he believed to have a greater affinity for the dye than phosphate of lime had; but Mr. Paget has proved by experiment that the phosphates have actually the stronger affinity for the dye.

The well-known fact that the phosphates on every internal or external surface of the bone, which is exposed to the current of the dye-charged plasma, attract the dye, by no means invalidates the conclusions from the ingenious experiments of Hunter; for the quantity of colour so imbibed by the previously and completely formed bone is always much less than that which the growing bone receives from the phosphates deposited during the presence of madder in the circulating system.

Hunter's experiments, therefore, coincide with those of Du Hamel, made by encompassing shafts of growing bones with rings of wire, in proving that the increase in circumference is due to growth at the periphery beneath the periosteum, such rings having been found, after a certain period of growth, in the cavity of the enlarged bone. The growth in length is, however, much more active; and this, in

the long bones of Mammalia, takes place chiefly at the cartilaginous ends beneath the epiphyses. This is proved by boring holes, or introducing shots, at definite distances in the diaphyses of growing bones, and examining the perforations a week or a fortnight after the experiments. The interval between the holes next the ends of the bone is found much increased, whilst that between those nearer the middle is but little, if at all, changed. All these experiments concur to prove that the growth of a bone is not by uniform and general extension, but by accelerated increase at particular parts.

But extension of parts is not the sole process which takes place in the growth of bone: to adapt the bone to its specific office changes are wrought in it by the absorption of parts previously formed, especially in the higher classes of Vertebrata. In fishes we observe a simple unmodified increase; but in some species, ossification commences at the periphery of the animal mould or basis, and is always limited to a thin outer crust of the bone, the rest remaining cartilaginous or gelatinous. In some of the higher cartilaginous fishes, for example, an osseous crust is formed upon the periphery of certain cartilages, in the form of prisms, which contain oval calcigerous cells, but without conspicuous radiated tubes. Such bones in a dried or fossil state seem to have had large internal or medullary cavities; but they were filled by the unossified animal basis. To whatever extent the bone of a fish is originally ossified, such it remains, and consequently most of the bones of fishes are solid or spongy in their interior.

The bones of the Chelonia are likewise solid; a coarse diploë fills the interior of the long bones of the extremities; and we find a similar structure in the bones of the Cetacea and of the Seal tribe. Among terrestrial mammals the inactive Sloths and their great extinct congeners, the Megatherium and Mylodon (xii. p. 83.), have the long bones of the extremities solid; whilst the agile Ruminant shows each diaphysis in the condition of the hollow column, both the strength and lightness of the bones being increased by the progressive absorption of the first-formed substance, as new bone is deposited from without. The condition which is illustrated by this section of the femur of the Nilghau (Prep. 856 *c*), is common, in fact, to the long bones of all land mammals, except the Tardigrades above specified. The Saurian and most of the Batrachian reptiles have likewise the cavity in each long bone, called "medullary," from its containing a cellular tissue filled by a fine, light, oily matter or marrow. Even the ribs of the large Ophidians have their medullary cavities: and the bodies of the vertebræ of some lizards and of the great extinct Poikilopleuron are similarly excavated. The medullary cavities of the

long bones of the extremities of the colossal Iguanodons and Megalosaurs are as capacious as in any mammalian quadruped, and the white crystallised spar with which these petrified bones are often filled, is called, not unaptly, "fossil marrow" by the quarry-men. In the ordinary marrow-bones of quadrupeds the walls of the cavity are thickest and strongest at the middle, and become thin towards the ends, where the peripheral concentric lamellæ are separated by wider interspaces, and are broken up into a fine lattice or lace work. All the cavity and the cells are lined by a delicate membrane, less vascular than the external periosteum, which secretes and immediately contains the marrow; this fine oily fluid diminishes the brittleness of the bones. A special artery called the "medullary," supplies the lining membrane of the medullary cavity; and the foramen and canal have the same relative position and course in most Mammalia as in Man; to wit, the canal in the humerus and tibia inclines *distad*, in the femur and anti-brachial bones *proximad*, as it approaches the medullary cavity: the true Ruminants, however, present an exception as regards the femur, in which the medullary artery, instead of penetrating the back part of the shaft and running upwards, enters the fore part of the shaft at its upper third, and inclines downwards.

The flat bones of Mammalia, *e. g.* those of the cranium, the scapulæ, and ilia, have a spongy texture, called diploë, included between two compact plates; the internal one in the cranial bones is called the "vitreous table" from its density and brittleness. But the most compact example of the osseous tissue is the bone containing the organ of hearing, thence called "petrous," which, with the tympanic bone, reaches the maximum of density in the Cetacea.

The bones of birds, especially those of flight, present the opposite extreme of lightness; not but that the osseous tissue itself is more compact than in most Mammalia, but its quantity in any given bone is much less, the most admirable economy being traceable throughout the skeleton of birds in the advantageous arrangement of the weighty material for the office it is destined to perform. Thus, in the long bones, the cavities, analogous to the medullary in mammals, are more extensive, and the solid walls of the bone much thinner; a large aperture called the "foramen pneumaticum," near one or both ends of the bone, communicates with its interior, and an air-cell or prolongation of the lung is continued into and lines the cavity of the bone, which is thus filled with rarefied air instead of marrow. The extremities of the bone, instead of being occupied by a spongy diploë, present a light open network, slender columns shooting across in different directions from wall to wall, and these columns are likewise hollow. The vastly expanded beak, with its hornlike process, in the Hornbill

forms one great air-cell, with thin bony parietes; and in this bird, in the Swifts, and the Humming-birds, every bone of the skeleton, down to the phalanges of the claws, is pneumatic.

The extent to which the skeleton is permeated by air, varies in different birds, in relation chiefly to their different kinds and powers of flight. The opposite extreme to the Swift is met with in the terrestrial Apteryx and aquatic Penguin, in which not any bone of the skeleton receives air.

In the mammalian class the air-cells of bone are confined to the head, and are filled from the nasal or tympanic cavities, never from the lungs. The frontal, sphenoidal, and maxillary sinuses, and the mastoid cells, are examples of pneumatic bones in the human subject. The frontal sinuses extend backwards over the calvarium in most Ruminants, and penetrate the cores of the horns in oxen, sheep, and a few antilopes.

The whole diploë of the upper, back, and side walls of the cranium was inflated, as it were, with air in the great extinct Sloths; the outer table was raised considerably above the vitreous, and the brain thus seemingly defended by a double skull; the advantage of which modification to these leaf-devouring animals, in the event of blows from the falling trees which they uprooted, is well displayed in the healed fractures of the skull of the Mylodon, in the museum of the College (xii. p. 157.). The outer table of the entire epicranium is similarly raised above the inner one by intervening large air-cells, and their sinuous septa, in the Giraffe; the short horns are solid, but are sustained by the vaulted roof of the skull; and, as the animal can deal heavy blows with these simple weapons, the concussion is diminished by the interposition of these air-chambers between the outer table and the immediate covering of the brain.

The most remarkable development of air-cells in the mammalian class is, however, presented by the Elephant; the intellectual physiognomy of this great Pachyderm being caused, as in the Owl, not by actual capacity of the brain-case, but by the enormous extent of the pneumatic cellular diploë between the two tables of the skull.

In each of these modifications the vacuities of the osseous tissue, whether mere cancelli as in the Tortoise, or small medullary cavities as in the Crocodile, or larger medullary cavities as in Mammals, or pneumatic cavities and sinuses, are the result of secondary changes by absorption, and not of the primitive constitution of the bones. These are in all air-breathing animals solid at their first commencement, and the vacuities are formed by the removal of osseous matter previously formed, whilst fresh bone is added to the exterior surface.

The thinnest-walled and hollowest pneumatic bone of the bird of flight was first solid, next a marrow-bone, and finally the case of an air-cell. The solid bones of the Penguin, and the medullary femur of the Apteryx and Dinornis, are arrested stages of that course of development through which the pneumatic wing-bone of the soaring Eagle had previously passed.

In proceeding after the foregoing survey of the general nature, chemical constitution, development, growth, and structure of the osseous system, to the description of the skeleton in the vertebrate animals, there next remains to define *a bone*; and the endeavour to do this has not been the least difficult part of my task, with reference to the applicability of the definition to the vertebrate series in general.

To the human anatomist the question—what is *a bone*?—may appear a very simple, if not a needless one: he will most probably reply that *a bone is any single piece of osseous matter entering into the composition of the adult skeleton*; and, agreeably with this definition, he will enumerate about 260 bones in the human skeleton.

Soemmering, who includes the thirty-two teeth in his enumeration, reckons from 259 to 264 bones; but he counts the os sphenoccipitale as a single bone, and also regards, with previous anthropotomists, the os temporis, the os sacrum, and the os innominatum, as individual bones; the sternum, he says, may include two or three bones, &c. (XIII. p. 6.): but, in Birds, the os occipitale is not only ankylosed to the sphenoid, but these early coalesce with the parietals and frontals; and, in short, the entire cranium proper consists, according to the above definition, of a single bone. Blumenbach, however, applying the human standard, describes it as composed of the proper bones of the cranium consolidated, as it were, into a single piece (XIV. p. 56.). And in the same spirit most modern anthropotomists, influenced by the comparatively late period at which the sphenoid becomes ankylosed to the occipital in Man, regard them as two essentially distinct bones. In directing our survey downwards in the mammalian scale, we speedily meet with examples of persistent divisions of bones which are single in Man. Thus it is rare to find the basi-occipital confluent with the basi-sphenoid in mammalian quadrupeds; and before we quit that class we meet with adults in some of the marsupial and monotrematous species, for example, in which the supra-occipital, “pars occipitalis propriè sic dicta,” of Soemmering, is distinct from the condyloid parts, and these from the basilar or cuneiform process of the os occipitis: in short, the single occipital bone in Man is four bones in the Opossum or Echidna; and just as the human cranial bones lose their individuality in the Bird, so do those of the Marsupial lose their

individuality in the ordinary mammalian and human skull. In many Mammalia we find the pterygoid processes of anthropotomy permanently distinct bones; even in Birds, where the progress of ossific confluence is so general and rapid, the pterygoids and tympanics, which are subordinate processes in Man, are always independent bones.

In many Mammalia the styloid, the auditory, the petrous, and the mastoid processes remain distinct from the squamous or main part of the temporal, throughout life; and some of these claim the more to be regarded as distinct bones, since they obviously belong to different natural groups of bones in the skeleton; as the styloid process, for example, to the series of bones forming the hyoidean arch.

The artificial character of that view of the os sacrum, in which this obviously more or less confluent congeries of modified vertebræ is counted as a single component bone of the skeleton, is sufficiently obvious. The os innominatum is represented throughout life in most reptiles by three distinct bones, answering to the iliac, ischial, and pubic portions in anthropotomy. The sternum in most quadrupeds consists of one more bone than the number of pairs of ribs which join it; thus it includes as many as thirteen distinct bones in the *Bradypus didactylus*.

The arbitrary character of the above cited definition of a bone, and the essentially complex nature of many of the single bones and independency of the processes of bone in anthropotomy, are taught by anatomy, properly so called, which reveals the true natural groups of bones, and the modifications of these which peculiarly characterise the human subject.

It will occur to those who have studied human osteogeny, that the parts of the single bones of anthropotomy which have been adduced as continuing permanently distinct in lower animals, are originally distinct in the human fœtus: the occipital bone, for example, is ossified from four separate centres; the pterygoid processes have distinct centres of ossification; the styloid, and the mastoid processes, and the tympanic ring, are separate parts in the fœtus. The constituent vertebræ of the sacrum remain longer distinct; and the ilium, ischium, and pubes are still later in anchylosing together, to form the 'nameless bone.'

These and the like correspondencies between the points of ossification of the human fœtal skeleton, and the separate bones of the adult skeletons of inferior animals, are pregnant with interest, and rank among the most striking illustrations of unity of plan in the vertebrate organisation.

Cuvier, commenting on the arbitrary character of some of the

definitions of single bones in anthropotomy, goes so far as to state that, in order to ascertain the true number of bones in each species, we must descend to the primitive osseous centres as they are manifested in the fœtus.\*

According to this rule we ought to count the humerus as three bones, and the femur as four bones instead of one; for the ossification of the latter begins at four distinct points, one for the shaft, one for the head, one for the great trochanter, and one for the distal condyles. But who will be induced to regard these parts and processes as distinct bones? No such distinction is kept up in any of the lower classes. In both Birds and Reptiles the femur is developed from a single centre.

The rule laid down by the great French anatomist fails in its application to the difficult point under consideration, because he did not distinguish between those centres of ossification that have homological relations, and those that have only teleological ones: *i. e.* between the separate points of ossification of a human bone which typify permanently distinct bones in the lower animals, and the separate points which, without such signification, facilitate ossification, and have for their final cause the well-being of the growing animal. The young lamb or foal, for example, can stand on its four legs as soon as it is born; it lifts its body well above the ground, and quickly begins to run and bound. The shock to the limbs themselves is broken and diminished at this tender age, by the divisions of the supporting long bones, — by the interposition of the cushions of cartilage between the diaphyses and the epiphyses. And the jar that might affect the pulpy and largely developed brain of the immature animal is further diffused and intercepted by the epiphysial articular extremities of the bodies of the vertebræ.

We thus readily discern a final purpose in the distinct centres of ossification of the vertebral bodies, long bones, and the limbs of mammals, which would not apply to the condition of the crawling reptiles. The diminutive brain in these low and slow cold-blooded animals does not demand such protection against concussion; neither does the mode of locomotion in the quadruped reptiles render such concussion likely; their limbs sprawl outwards, and push along the body, which commonly trails upon the ground; therefore we find no epiphyses with interposed cartilage at the ends of a distinct shaft in the long bones of Saurians and Tortoises. But when the reptile moves by leaps, then the principle of ossifying the long bone by distinct centres again

\* "Mais ces distinctions sont arbitraires, et pour avoir le véritable nombre des os de chaque espèce, il faut remonter jusqu'aux premiers noyaux osseux tels qu'ils se montrent dans le fœtus." (XIII. tom. i. p. 120.)



prevails, and the extremities of the humeri and femora long remain epiphyses in the frog.

A final purpose is no doubt, also, subserved in most of the separate centres of ossification which relate homologically to permanently distinct bones in the general vertebrate series; it has long been recognised in relation to facilitating birth in the human fetus; but some facts will occur to the human osteogenist, of which no teleological explanation can be given.

One sees not, for example, why the process of the scapula which gives attachment to the pectoralis minor, the coraco-brachialis, and the short head of the biceps should not be developed by continuous ossification from the body of the blade-bone, like that which forms the spinous process of the same bone. It is a well-known fact, however, that not only in Man, but in all Mammalia, the coracoid process is ossified from a separate centre. In the Monotremes it is not only a distinct, but is as large a bone as in Birds and Reptiles, in which it continues a distinct bone throughout life. Here, then, we have the homological, without a teleological explanation of the separate centre for the coracoid process in the ossification of the human blade-bone.

This distinction in the nature and relations of such centres, which is indispensable in the right application of the facts of osteogeny to the determination of the number of essentially distinct bones in any given skeleton, has never been considered, so far as I know, in that application. Some homologists (II. xiv.) have gone beyond Cuvier, and still more beyond nature, in arguing the number of individual bones, as indicated by the number of separate centres of ossification in the embryo, to be the same in all vertebrate animals; and that they afterwards differed, or seemed to differ, only by reason of the greater or less rapidity or extent of the confluence of those ossific centres or essentially distinct bones.

This primitive conformity of separate osseous pieces in the vertebrate series holds good, however, only in regard to the separate centres of ossification of those bones of higher animals which have homological relations to the permanently distinct bones of lower species; it by no means applies to those which have merely teleological relations to the species in which they exist.

But, besides the epiphyses of the long bones of Mammalia, which enter into the latter category, and cannot, therefore, be properly viewed in the light of distinct bones; what are we to say to the intercalated, inconstant "ossa wormiana," or to the ossified tendons of birds, or to those developed in the tendons of the vertebral muscles of the musk-deer? Are these to be reckoned equally distinct and in-

dividual bones of the skeleton, with the occipital and parietal bones, with the dorsal vertebræ, or the tibiæ ?

In considering this and other questions previously discussed, you will begin to appreciate the difficulties in defining or determining what shall be considered a distinct and an individual bone in the skeleton.

If we apply to each species the anthropotomical definition of a bone, as "any single osseous piece of which the skeleton of the mature animal is composed," we must qualify it by subordinate definitions of the different natures of such separate pieces of the skeleton. Hitherto bones have been primarily classified according to their form, as long and cylindrical, broad and flat, thick and squab, symmetrical, or unsymmetrical (XIII. xi. pp. 9, 10.); or, according to their position, into median\* and lateral (XVI. p. xviii.), or into endo-skeletal, exo-skeletal, and splanchno-skeletal bones (I. p. 113. 115.). But, besides these, the above discussed deeper and more essential differences of the bones require that they should be divided into *simple*, as being developed from a single centre, and *compound*, as developed from separate centres; and the compound bones, in the human subject, for example, may be subdivided into the *teleologically compound*, as the *ossa cylindrica*, which are originally developed from separate centres in relation to a spinal final purpose; and the *homologically compound*, as most of the *ossa lata* (occiput, scapula), and many *ossa mixta* (vertebræ, sacrum), which are developed from separate centres, representing permanently distinct simple bones in other Vertebrata.

The teleologically compound bones have their relations limited to the particular exigencies of particular classes, but the homologically compound bones have relations extending over the whole vertebrate series.

The great aim of the philosophical osteologist is to determine, by natural characters, the natural groups of bones of which a vertebrate skeleton typically consists; and, next, the relations of individual simple bones to each other in those primary groups, and to define the general, serial, and special homologies of each bone throughout the vertebrate series.

By general homology I mean the relation in which a bone stands to the primary segment of the skeleton of which it is a part; thus, when the basi-occipital bone (basilar process of the os occipitis in anthropo-

\* These are mostly symmetrical; but the youngest anthropotomist must have met with instances of a curved vomer, and an unsymmetrical sternum; and, on the other hand, most of the phalanges among the *ossa paria, seu lateralia*, are symmetrical.

tomy) is said to be the centrum or body of the occipital or posterior cranial vertebra, its *general* homology is enunciated. When it is said to repeat in its vertebra, or to answer to the basi-sphenoid in the parietal vertebra, or to the body or centrum in the atlas, dentata, or any other of the vertebral segments of the skeleton, its *serial* homology is indicated: when the essential correspondence of the basilar process of the occipital bone in Man with the distinct bone called "basi-occipital" in a Crocodile or Fish is shown, its *special* homology is determined.

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### LECTURE III.

#### THE VERTEBRA, AND VERTEBRAL COLUMN IN FISHES.

To understand the fundamental type of the vertebrate skeleton its study must be commenced, not in the highest species, — not in that skeleton where irrelative repetition is least, and where modification of each part in mutual subserviency to another is greatest, — but in the lowest Class where, conformably with the law enunciated in the previous Course \*, vegetative uniformity most prevails, and the primitive type is least obscured by teleological adaptations.

Such conditions are best displayed in the skeletons of fishes: fishes form, however, but one branch of the vertebrate stem, which, like other primary branches, ramifies in diverging from the common trunk. We should miss our aim, therefore, and be led astray from the detection of the true general type of the vertebrate skeleton, were we to confine our observations to fishes only. A comparison of their skeletons with those of the higher classes teaches that the natural arrangements of the parts of the endo-skeleton in Vertebrata, like that of the exo-skeleton in Articulata, is in a series of segments succeeding each other in the axis of the body. I do not find these successive segments composed of precisely the same number of bones in all Vertebrata; rarely, indeed, in the same animal. Yet certain constituent parts of each segment do preserve such constancy in their existence, relative position, and offices throughout the body, as to enforce a conviction that they are homologous parts, both in the consecutive series of the same individual skeleton, and throughout the entire series of vertebrate animals.

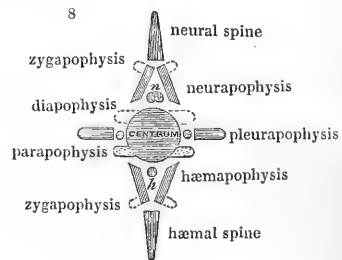
\* Lectures on Invertebrata, 8vo. 1843, p. 364.

To each of these primary segments of the skeleton I shall, with Geoffroy St. Hilaire (xiv. ii.), apply the term "vertebra": the word may seem to the anthropotomist to be used in a different or more extended sense than it is usually understood; yet he is himself, unconsciously perhaps, in the habit of including in certain vertebræ of the human body, elements which he excludes from the idea in other natural segments of the same kind; influenced by differences of proportion and coalescence, which are the most variable characters of a bone. Thus the rib of a cervical vertebra is the "processus transversus perforatus," or the "radix anticus processus transversus vertebræ colli:" whilst in the chest, it is "costa," or "pars ossea costæ." (xiii. 239. 250.) But the ulna is not the less an ulna in the horse, because it is small and anchylosed to the radius.

The osteology of Man, therefore, cannot be fully or rightly understood until the type of which it is a modification is known, and the first step to this knowledge is the determination of the vertebral segments, or natural groups of bones, of which the myelencephalous skeleton consists.

I define a vertebra, as *one of those segments of the endo-skeleton which constitute the axis of the body, and the protecting canals of the nervous and vascular trunks*: such a segment may also support *diverging appendages*. Exclusive of these, it consists in its typical completeness, of the following parts or elements:—

- c.* A body or *centrum*. \*  
*n.* Two *neurapophyses*. †  
*p.* Two *parapophyses*. ‡  
*pl.* Two *pleurapophyses*. §  
*h.* Two *hæmapophyses*. ||  
*ns.* A *neural spine*. ¶  
*hs.* A *hæmal spine*. \*\*



Ideal typical vertebra.

\* Greek, *kentron*, centre. Syn. *Corpus vertebræ*<sup>1</sup>, *Corps de vertèbre*, Cuvier; *Tertiar-wirbel*, Carus; *Wirbel-körper*, German<sup>2</sup>; *Cycléal*, Geoffroy; *Cyclo-vertebral element*, Grant.

† Gr. *neuron*, nerve; and *apophysis*, a process of bone. Syn. *Arcus posterior vertebræ*, seu *radices arcus posterioris*. *Deckplatten* and *Grundplatten*, Carus. *Bogenstücke des Rückenwirbels*, Carus. *Obere Wirbelbogen*, Germ. *Partie annulaire*, Cuv. *Perial*, Geof. *Peri-vertebral elements*, Grant.

‡ Gr. *para*, trans, across; and *apophysis*. Syn. *Radix prior seu antica processus*.

<sup>1</sup> The Latin synonyms are from Soemmerring's Classical Anthropotomy, "De corporis humani fabricâ," 1794.

<sup>2</sup> The German synonyms are those of John Müller, Wagner, and most German Zootomists, unless otherwise specified.

These, being usually developed from distinct and independent centres, I have termed "autogenous" elements (XIX. p. 518.). Other parts, more properly called processes, which shoot out as continuations from some of the preceding elements, are termed "exogenous:" *e. g.* (*t*) the diapophyses, or upper "transverse processes,"\* and (*z*) the zygapophyses, or the "oblique" or "articular processes" † of human anatomy.

The autogenous processes generally circumscribe holes about the centrum, which, in the chain of vertebræ, form canals. The most constant and extensive canal is that (*fig. 8. n*) ‡ formed above the centrum, for the lodgment of the trunk of the nervous system (neural axis) by the parts thence termed "neurapophyses." The second canal (*fig. 8. h*) ††, below the centrum, is in its entire extent more irregular and interrupted; it lodges the central organ and large trunks of the vascular system (hæmal axis), and is usually formed by the laminæ, thence termed "hæmapophyses." At the sides of the centrum, most commonly in the cervical region, a canal (*fig. 9. v*) is circumscribed by the pleurapophysis or costal process (*ib. pl*), and by the diapophysis or upper transverse process (*ib. t*), which canal includes a vessel, and often also a nerve.

Thus a typical or perfect vertebra, with all its elements, presents four canals or perforations about a common centre; such a vertebra we find in the thorax of man, and most of the higher classes of Vertebrata (*fig. 6.*), also in the neck of many birds. In the example from the latter class (*fig. 9.*), the hæmapophyses (*h, s*) are anchy-

*transversi vertebræ; Querforsatz, Carus; Untere Querforsatz, Germ.; Apophyse transverse, Cuv.; Paraal, Geof.; Para-vertebral elements, Grant.*

§ *Gr. pleura, a rib; and apophysis. Syn. Processus transversus vertebræ cervicalis, Costa seu, pars vertebralis, seu ossea, costæ. Ruckentheil and Ober-sternal-theil des Urwirbelbogens, Carus; Côtes vertébrales, Cuv.; Paraal, Geof.; Cata-vertebral elements, Grant.*

|| By Syncope for hæmatoapophyses, from *Gr. haima, blood; and apophysis. Syn. Cartilago costæ, seu pars sternalis costæ: in the abdomen, inscriptions tendineæ musculi recti; Unter-sternal-theil des Urwirbelbogens, Carus; Bogenstücke des Bauchwirbel, Carus; Untere Wirbelbogen, Ger.; Côtes sternales, Cuv.; Os ployé en chevron, Cuv.; Cataal, Geof.; Cata-vertebral elements, Grant.*

¶ *Syn. Processus spinosus vertebræ. Its base is the Oberer Tertiar-wirbel, Carus; its apex is the Oberer Dorn-forsatz, Carus; Apophyse épincuse, Cuv.; Epial, Geof.; Epi-vertebral elements, Grant*

\* *Syn. Ossa sterni et processus ensiformis; in the abdomen, "linea alba." Sternal-wirbel Körper, Carus; Unterer Dorn-forsatz, Carus.*

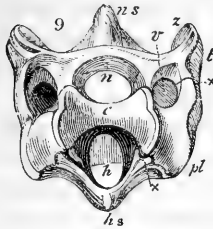
\* *Diapophysis, from Gr. dia, trans, across; and apophysis. Syn. Radix posticus processus transversus vertebræ, and processus transversus. Querforsatz, Carus; Obere Querforsatz, Germ.; Apophyse transverse, Cuv.*

† *Zygapophysis, from Gr. zugos, junction; and apophysis. Syn. Processus obliquus vertebræ; Seitlicher Tertiar-wirbel, Carus; Gelenk-forsatz, Germ.; Apophyse articulaire, Cuvier.*

‡ *Rückenmarks-kanal, Carus.*

†† *Aortenkanal, Carus.*

losed to the under part of the centrum, to which part they are moveably articulated in the tails of most reptiles and mammals; space



Natural typical Vertebra,  
from the neck of a Pelican.

being needed only for the protection of the carotids in the one case, and for the caudal artery and vein in the other. In the chest, where the central organ of circulation is to be lodged, an expansion of the hæmal arch takes place, analogous to that which the neural arches of the cranial vertebræ present for the lodgment of the brain. Accordingly in the thorax, the pleurapophyses (*fig. 6. pl*) are much elongated, and the hæmapophyses (*fig. 6. h*) are removed from

the centrum, and are articulated to the distant ends of the pleurapophyses; the bony hoop being completed by the intercalation of the hæmal spine (*fig. 6. hs*) between the ends of the hæmapophyses. And this spine is here sometimes as widely expanded (in the thorax of Birds and Chelonians, for example) as is the neural spine (parietal bone or bones) of the middle cranial vertebra in Mammals. In both cases, also, it may be developed from two lateral halves, and a bony intermuscular crust may be extended from the mid-line, as in the skull of the Hyæna, and the breast bone of the Hawk.

The vertebræ of the trunk present essentially their most simple, though often apparently the most complete, condition in Fishes, in which class a typical vertebra can only be obtained from the head; in the rest of the column, the hæmapophyses, for example, are always absent or unossified. It is by no means true that the several elements of a vertebra are found most isolated and distinct in the lowest classes; the neurapophyses are commonly ankylosed to the centrum in fishes, but commonly remain isolated and distinct in reptiles; the hæmal canal is formed by modified parapophyses in fishes, but by isolated and distinct hæmapophyses co-existing with transverse processes in reptiles and mammals.

The number of vertebræ, or at least of neural arches, is governed by the number of segments of the cerebro-spinal axis. These segments in the spinal chord are chiefly indicated by the pairs of spinal nerves. In the brain, the centres are more definitely indicated by the ganglionic form under which they first make their appearance; but here, by the superaddition of fasciculi of nerve-fibres for the special functions of the brain, the origins of essentially single nerves become separated, and the motor roots divided from the sensitive, as we see in the nerves of the eyeball. Hence, the cranial vertebræ do not correspond with the number of seemingly distinct

cranial nerves; and they undergo, in their neural arches, as extreme modifications as we perceive in the hæmal portions of those vertebræ that protect the great centres of the vascular system. We may learn how much the development of the neurapophyses and vertebral bodies depends, in the trunk, upon the conjunction of nerves with the spinal chord, by the fact that, in the regenerated tails of lizards, the vertebral axis remains continuous and unjointed, because there is no co-extensive spinal chord giving off pairs of nerves.

An extremely delicate fibrous band, with successively accumulated gelatinous cells, compacted in the form of a cylindrical column, and inclosed by a membranous sheath, is the primitive basis, called 'chorda dorsalis,' in and around which are developed the cartilaginous or osseous elements, by which the vertebral column is established in every class of *Myelencephala* (III. p. 340.).

The earlier stages of vertebral development are permanently represented, with individual peculiarities superinduced, in the lower forms of the class of fishes. In the anencephalous Lancelet (*Bran-chiostoma*) the lowest of all, the entire vertebral column consists of the gelatino-cellular chord and its membranous sheath. In the Lamprey cartilaginous arches and spines are added above the chorda dorsalis, in the membranous wall of the neural canal, and in the tail, also beneath it. In the Sturgeon and Chimæra, the bases of the cartilaginous arches inclose the 'chorda.' In the Lepidosiren the neural and hæmal arches and their spines are ossified, but the centrums are still confluent as a dorsal membrano-gelatinous chord. In many Sharks and Rays the 'chorda' is encroached upon by osseous or cartilaginous convergent laminae, and by concentric, successively shorter, centripetally developed cylinders, and is thus reduced to a string of gelatinous beads, each bead occupying the interspace between the opposed concave surfaces of the vertebral bodies. This moniliform state of the chorda dorsalis is persistent in most osseous fishes, the biconcave bodies of the vertebræ being perforated in the centre; whilst, in some other osseous fishes, the gelatinous biconical segments of the 'chorda' are insulated by the completed centripetal progress of ossification; and in one exception (*Lepidosteus*), they are converted into osseous balls, fixed to the fore part of each vertebral body, which plays in the concavity or cup of the next vertebra in advance.

The neural and hæmal arches and spines are bony in all osseous fishes; and in all fishes chondrification and ossification of the vertebral column commences in these arches. In reptiles, birds, and mammals, the vertebræ are bony throughout.

Development diverges from the membrano-gelatinous stage, so as

to establish three types of vertebræ, which may be characterised by the form of the articular ends of the centrum, as the "biconcave," the "concavo-convex," and the "flattened" types, respectively distinguishing, as a general rule, Fishes, air-breathing Ovipara, and Mammals.

The least perfect form of a vertebra is that in fishes, though it often seems the most complex, from the intercalation of bones of the dermal system, and Geoffroy (II. p. 119.)\* was unfortunate in taking a fish's vertebra, with this extrinsic complication, as the perfect type of that primary segment of the myelencephalous skeleton. Two of the autogenous elements, the "hæmapophyses," for example, are not developed till we reach the Reptilia: in fishes they are represented by the "parapophyses" or lower transverse processes.

Before entering, however, upon the special osteology of the class *Pisces*, it will be necessary to explain the sense in which the terms of groups or divisions of the class are used in these Lectures, in reference to their anatomical characters. Cuvier (xxiv. ii. p. 128.) primarily divides the class, according to the nature of their endo-skeleton, into *Pisces ossei*, and *Pisces cartilaginei*; but the latter group includes species of widely different grades of organisation, and in the "Tables of Classification" exhibited in my first course of Lectures in this Theatre in 1837, I separated the Lampreys, Myxinoids, and Lancelets, under the name "*Dermopteri*," from the rest of the *Chondropterygii* of Cuvier, making these the highest, and those the lowest order of fishes.†

M. Agassiz, with views enlarged by a survey of the extinct members of the class, divided the *Pisces*, by characters taken from the exo-skeleton, into four primary groups; viz. *Placoidi*, *Ganoidei*, *Cycloidei*, and *Ctenoidei*.

The fishes of the *Placoid* order are characterised by having the skin covered irregularly with plates of hard osseous matter, sometimes of large size, and sometimes reduced to small points, as where they form the shagreen on the skin of many sharks and the prickly tubercles on the skin of most rays. This order comprehends all the

\* This ingenious anatomist was thus driven to as arbitrary assumptions of mutations of place, and to as far-fetched analogies, in reference to the supposed elementary parts of the vertebra, as in his attempt to exemplify the homologies of the cephalic division of the endo-skeleton of the higher Vertebrata, by the combined bones of the exo- and endo-skeleton, which constitute the complex skull in Fishes.

† The distinguished naturalist, C. L. Bonaparte, Prince of Canino, has also founded a distinct order for the Cyclostomous Chondropterygians of Cuvier, under the name of "*Marsipo-branchii*," which well applies to the Lampreys and Myxinoids. — *Selachorum Tabula Analytica*, 1838.



cartilaginous fishes of Cuvier, except the Sturgeons and Chimæræ (*Sturioniens*). It is as necessary, however, for the expression of general anatomical propositions, to separate the *Dermopteri* from the *Placoidei* of Agassiz as from the *Chondropterygii* of Cuvier; and it is with this restriction that the Placoids will be referred to in these Lectures, as answering namely to the Plagiostomes of Cuvier.

The *Ganoid* fishes are defended by plates or scales covered with a thick coat of enamel; some of considerable dimensions and irregular form, as in the Sturgeon; more commonly angular and imbricated, as in the Bony Pike (*Lepidosteus*). Most of the species and genera of this order have become extinct. The recent species included in it by Agassiz differ materially in their anatomical characters.

The *Ctenoid* fishes have scales formed of laminae of horn, or of unenamelled bone, with the posterior margin pectinated, like a comb; *e. g.*, the Perch, and most of the *Acanthopterygii* of Cuvier.

The *Cycloid* fishes have their scales composed of laminae of horn or unenamelled bone, of a rounded form, with smooth and simple margins. The Carp, the Salmon, the Herring, and many other *Malacopterygii* of Cuvier, are examples of this order.

Linnaeus divided the bony fishes into the orders *Jugulares*, *Thoracici*, *Abdominales*, and *Apodes*, according to the position or the absence of the ventral fins. Cuvier divided the bony fishes, according to the structure of the fins, into *Acanthopterygii* and *Malacopterygii*. Not many general anatomical propositions, however, can be expressed with regard to these orders. A more natural arrangement has been founded upon a consideration of both external and internal anatomical characters by Prof. J. Müller (xxv.), which, with some modifications, I here adopt; arranging the class of Fishes, as follows, in the ascending series:—

## CLASSIS PISCES.

### Ordo I. DERMOPTERI.

Endo-skeleton unossified; exo-skeleton and vertical fins mucodermoid; vermiform, or abrachial and apodal; no pancreas; no air-bladder.

#### Suborder I. PHARYNGOBRANCHII, seu *Cirrhostomi*.

Gills free, pharyngeal, inoperculate; no heart.

Fam. *Amphioxidae*. Example \*, Lancelet.

\* These are cited under their common English names, where such exists.

Suborder 2. *MARSIPOBRANCHII* (*Cyclostomi*, Cuvier).

Gills fixed, bursiform, inoperculate, receiving the respiratory streams by apertures usually numerous and lateral, distinct from the mouth; a heart.

Fam. *Myxinoidei*,           Examples, Myxine, or Hag.  
*Petromyzontidæ*,           Lamprey.

Ordo II. MALACOPTERI (*Physostomi*, Müller).

Endo-skeleton ossified; exo-skeleton, in most, as cycloid, in a few as ganoid, scales; fins supported by rays, all, save the first sometimes in the dorsal and pectoral, soft or jointed; abdominal or apodal; gills free, operculate; a swim-bladder and air-duct.

Suborder 1. *APODES*.

Fam. *Symbranchidæ*,   Example, Cuchia.  
*Murænidæ*,           Eel.  
*Gymnotidæ*,           Gymnotus.

Suborder 2. *ABDOMINALES*.

Fam. *Heteropygii*,   Example, Amblyopsis.  
*Clupeidæ*,           Herring.  
*Salmonidæ*,           Salmon.  
*Scopelidæ*,           Saurus.  
*Characini*,           Myletes.  
*Galaxidæ*,           Galaxias.  
*Esocidæ*,           Pike.  
*Mormyridæ*,         Mormyrus.  
*Cyprinodontidæ*,   Umber.  
*Cyprinidæ*,         Carp.  
*Siluridæ*,           Sheat-fish.

## Ordo III. PHARYNGOGNATHI (Müller).

Endo-skeleton ossified; exo-skeleton in some as cycloid, in others as ctenoid, scales; inferior pharyngeal bones coalesced; swim-bladder without duct.

Suborder 1. *MALACOPTERYGII*.

Fam. *Scomber-esocidæ*, Example, Saury-pike.

Suborder 2. *ACANTHOPTERYGII*.

Fam. *Chromidæ*,       Example, Chromis.  
*Cyclo-Labridæ*,     Wrasse.  
*Cteno-Labridæ*,     Pomacentrus.

Ordo IV. ANACANTHINI (Müller).

Endo-skeleton ossified ; exo-skeleton in some as cycloid, in others as ctenoid scales ; fins supported by flexible or jointed rays ; ventrals beneath the pectorals, or none ; swim-bladder without air-duct.

Suborder 1. *APODES.*

Fam. *Ophididæ*, Example, Ophidium.

Suborder 2. *THORACICI.*

Fam. *Gadidæ*, Example, Cod.  
*Pleuronectidæ*, Plaice.

Ordo V. ACANTHOPTERI (Müller).

Endo-skeleton ossified ; exo-skeleton as ctenoid scales ; fins with one or more of the first rays unjointed or inflexible spines ; ventrals in most beneath or in advance of the pectorals ; swim-bladder without air-duct.

Fam. <i>Percidæ</i> ,	Example, Perch.
<i>Sclerogenidæ</i> ,	Gurnard.
<i>Sciænidæ</i> ,	Maigre.
<i>Labyrinthibranchii</i> ,	Anabas.
<i>Mugilidæ</i> ,	Mullet.
<i>Notacanthidæ</i> ,	Notacanth.
<i>Scomberidæ</i> ,	Mackerel.
<i>Squamipennes</i> ,	Chætodon.
<i>Tænioidei</i> ,	Riband-fish.
<i>Theutyidæ</i> ,	Acanthurus, or Lancet-fish.
<i>Fistularidæ</i> ,	Pipe-mouth- and Snipe-fish.
<i>Gobiidæ</i> ,	Goby, Remora, and Lumpfish.
<i>Blenniidæ</i> ,	Blenny and Wolf-fish.
<i>Lophiidæ</i> ,	Angler.

Ordo VI. — PLECTOGNATHI (Cuvier).

Endo-skeleton partially ossified ; exo-skeleton as ganoid scales or spines ; maxillaries and pre-maxillaries fixed together ; swim-bladder without air-duct.

Fam. <i>Balistinæ</i> ,	Example, File-fish.
<i>Ostraciones</i> ,	Trunk-fish.
<i>Gymnodontes</i> ,	Globe-fish.

## Ordo VII. — LOPHOBRANCHII (Cuvier).

Endo-skeleton partially ossified ; exo-skeleton ganoid ; gills tufted, opercular aperture small ; swim-bladder without air-duct.

Fam. *Hippocampidae*, Example, Sea-horse.  
*Syngnathidae*, Pipe-fish.

## Ordo VIII. — GANOIDEI.\*

Endo-skeleton in some osseous, in some cartilaginous, in some partly osseous partly cartilaginous ; exo-skeleton ganoid ; fins usually with the first ray a strong spine ; a swim-bladder and air-duct.

Fam. <i>Salamandroidei</i> ,	Example,	{ <i>Lepidosteus</i> ,
		{ <i>Polypterus</i> .
<i>Pycnodontidae</i> ,		<i>Pycnodus</i> .
<i>Lepidoidei</i> ,		<i>Dapedius</i> .
<i>Sturionidae</i> ,		{ <i>Sturgeon</i> .
		{ <i>Paddle-fish</i> .
<i>Acanthodei</i> ,		<i>Acanthodes</i> .
<i>Dipteridae</i> ,		<i>Dipterus</i> .
<i>Cephalaspidae</i> ,		<i>Cephalaspis</i> .

## Ordo IX. — PROTOPTERI.

Endo-skeleton partly osseous partly cartilaginous ; exo-skeleton as cycloid scales ; pectorals and ventrals as flexible filaments ; gills filamentary, free ; no pancreas ; swim-bladder as a double lung, with an air-duct ; intestine with a spiral valve.

Fam. *Sirenoidei*, Example, *Lepidosiren*.

## Ordo X. — HOLOCEPHALI.

Endo-skeleton cartilaginous ; exo-skeleton as placoid granules ; most of the fins with a strong spine for the first ray, ventrals abdominal ; gills laminated, attached by their margins ; a single external gill aperture ; no swim-bladder ; intestine with spiral valve. *Copula gaudent*.

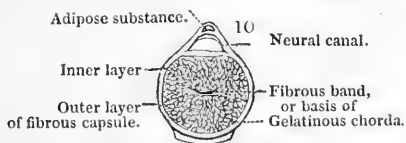
\* I use this ordinal term of M. Agassiz in the sense in which it is restricted by Professor J. Müller.

Fam. <i>Chimæroidei</i> ,	Example, Chimæra.
<i>Edaphodontidæ</i> ,	{ Edaphodon. { Passalodon.

Ordo XI.— PLAGIOSTOMI.

Endo-skeleton cartilaginous or partially ossified ; exo-skeleton placoid ; gills fixed with five or more gill-apertures ; no swim-bladder ; scapular arch detached from the head ; ventrals abdominal ; intestine with spiral valve. *Copula gaudent.*

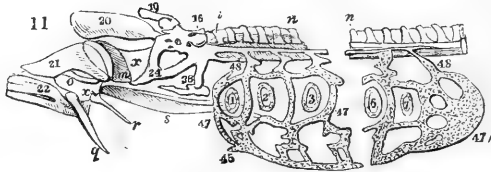
Fam. <i>Hybodontidæ</i> ,	Example, Hybodus.
<i>Cestraciontidæ</i> ,	Cestracion.
<i>Notodanidæ</i> ,	Gray-shark.
<i>Spinacidæ</i> ,	Piked Dog-fish.
<i>Scylliidæ</i> ,	Spotted Dog-fish.
<i>Nictitantes</i> ,	Tope.
<i>Lamnidæ</i> ,	Porbeagle.
<i>Alopeciidæ</i> ,	Fox-shark.
<i>Scymniidæ</i> ,	Greenland-shark.
<i>Squatina</i> ,	Monk-fish.
<i>Zygænidæ</i> ,	Hammerhead-shark.
<i>Pristidæ</i> ,	Saw-fish.
<i>Rhinobatidæ</i> ,	Rhinobates.
<i>Torpedinidæ</i> ,	Electric-ray.
<i>Raidæ</i> ,	Ray or Skate.
<i>Trygonidæ</i> ,	Sting-ray or Fireflaire.
<i>Myliobatidæ</i> ,	Eagle-ray.
<i>Cephalopteridæ</i> ,	Cephaloptera.



Transverse vertical section of vertebral column of *Myxine*.

In the Myxinoid fishes the neural and hæmal canals are formed by a separation of the layers of the outer division of the fibro-membranous sheath of the gelatinous chorda (*fig. 10.*) ; the neural canal extending the whole length of the upper part of the chorda, the hæmal canal being confined to the caudal region, where it contains the prolongation of the aorta and the vena cava (*xxi. p. 25.*). In the Lamprey (*Petromyzon*) cartilaginous laminae (*fig. 11. n*) are developed in the fibrous sheath (*i*), and give the first indication of neural arches. We should hardly expect to find the unity of the vertebral

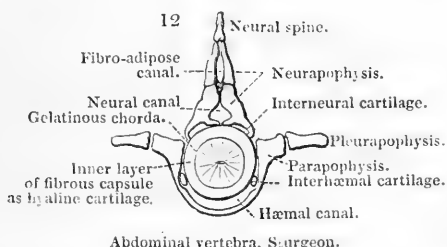
type to be further exemplified at this low step in the series, but rather be prepared for a divergence into individual peculiarities; and this is illustrated by the complex development of the visceral arches for the support of the heart and gills, which are homologous to the branchial arches in higher fishes. Yet the analogy of these parts in the Lamprey, which Müller has termed the cartilaginous basket of the branchiæ (xxi. p. 254.) to the modifications of the pleurapophyses, hæmapophyses and their spines, constituting the ribs and sternum in the air-breathing Vertebrates, is so close that we may be justified in describing them in connexion with the vertebral column.



Fore part of skeleton, Lamprey (*Petromyzon*).

Seven cartilaginous processes, analogous to pleurapophyses, but homologous with epibranchials (*fig.* 11. 48, 48), came off from a cartilaginous tract on both sides of the chorda dorsalis, one below each alternate neuropophysis (*ib.* *n*): after a short course outwards and downwards the process divides into three branches, one passing forwards, one backwards, and the intermediate process (cerato-branchial, 47), or continuation of the quasi-rib, downwards: the anterior and posterior processes of contiguous ribs coalesce and form arches above the branchial apertures (1, 2, to 7), which are circumscribed by similar arches, formed below by analogous branches there given off from the cerato-branchial; this then descends, bends inwards, dilates, and is perforated; then contracts and joins a broad and long cartilaginous hypo-branchial (45), or quasi-sternum, typifying by its double row of perforations that complex bone in birds. The anterior branches of the first cerato-branchial unite to form a vertical arch, convex forwards; the posterior pair (47') expand and unite to form the perforated cartilaginous case, lined by the pericardium, which contains the heart: pursuing the analogy of this complex cartilaginous branchial and cardiac skeleton with the thorax of higher Vertebrata, we might regard the posterior processes of the ribs as foreshadowing the costal appendages of birds. Homologically, the entire apparatus answers to the branchial skeleton of higher fishes, a part which Geoffroy St. Hilaire regards as a repetition of the thorax of air-breathing Vertebrata, but which the metamorphoses of the Batrachia prove to be a development of the visceral skeleton in immediate connexion with the hyoidean arch.

Returning, then, to what may be called the high road of vertebral development, we find in the Sturgeons (*Sturio*, *Polyodon*), that the inner layer of the fibrous capsule of the gelatinous 'chorda' has increased in thickness, and assumed the texture of tough hyaline cartilage. In the outer layer are developed distinct, firm, and opaque cartilages, the neurapophyses, which, in the young sturgeon (*fig.* 12.), are two superimposed pieces on each side, the basal portion bounding the neural canal, the apical portion the parallel canal filled by fibrous elastic ligament and adipose tissue\*; above this is the single cartilaginous neural spine. The parapophyses are now distinctly developed, and joined together by a continuous expanded base, forming an inverted arch beneath the 'chorda' for the vascular trunks, even in



the abdomen. Short and simple pleurapophyses are articulated by ligament to the ends of the laterally projecting parapophyses in the first twelve or twenty abdominal vertebræ; the parapophyses themselves gradually disappear, or bend down to form hæmal arches in the tail, at the end of which we find hæmal cartilaginous spines corresponding to the neural spines above. The first five or six neural arches are confluent with each other in the sturgeon, and, with the parapophyses, enclose the fore part of the 'chorda' in a firm, continuous, cartilaginous sheath, perforated for the exit of the nerves. The tapering anterior end of the 'chorda' is continued forwards into the basal elements of the cranial vertebræ.

Vegetative repetition of perivertebral parts not only manifests itself in the double neurapophysis on each side, but in a small accessory (interneural) cartilage, at the fore and back part of the base of the neurapophysis; and by a similar (interhæmal) one at the fore and back part of most of the parapophyses. The peripheral cartilages are more feebly developed in the *Polyodon*. †

\* I long ago pointed out, in a preparation of Hunter's (No. 234.), the "space above the canal of the spinal chord formed by the divarication of the cartilaginous pieces which constitute the support of the spinous processes of the vertebræ. This is filled by fibro-cartilaginous substance, connecting the processes in question." (xx. vol. i.)

† Cuvier, Mémoires du Muséum, tom. i. 1815, p. 130.

In the southern Chimæra (*Callorhynchus*) a greater proportion of the chorda dorsalis is composed of the dense fibrous capsule, but it shows no trace of annular structure. In the northern Chimæra, according to Müller (xxi. p. 68.), another stage towards the formation of vertebral bodies begins to manifest itself by slender sub-ossified rings in the cartilaginous sheath of the chorda dorsalis, which, however, are more numerous than the neural arches. The neurapophyses and the bases of the transverse processes of about ten of the anterior vertebræ coalesce, in all the Chimæra, to form a continuous accessory covering of the fore part of the chorda; and the confluent neural spines here form a broad and high compressed cartilaginous plate. In the remainder of the vertebral column the neural arches are distinct from the transverse processes (parapophyses), and from the hæmal arches, which these constitute in the tail. Between each neurapophysis an accessory cartilaginous interneurapophysis\* is wedged.

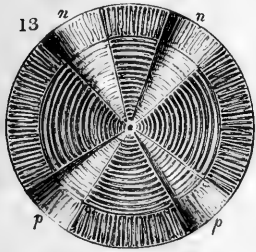
Amongst the Sharks (*Squalidæ*) a beautiful progression in the further development of a vertebra has been traced out, chiefly by J. Müller (xxi. p. 64.). In *Heptanchus* (*Squalus cinereus*) the vertebral centres are still feebly and vegetatively marked out by numerous slender rings of hard cartilage in the capsule, the number of vertebræ being more definitively indicated by the neurapophyses and parapophyses; but these remain cartilaginous. Interneural pieces are wedged between the neural arches, and close them above; the pleurapophyses are similarly wedged into the interspaces of the parapophyses, and articulate directly with the vertebral bodies.† In the Piked Dog-fish (*Acanthias*) the vertebral centres coincide in number with the neural arches, and are defined by a thin layer of bone, which forms the conical cavity at each end, but the rest of the vertebra remains cartilaginous. In the Spotted Dog-fish (*Scyllium*) the whole exterior of the centrum is covered by soft cartilage, except at the concave ends, where the two thin funnel-shaped plates of osseous matter coalesce at their perforated apices, and form a basis of the vertebral body like an hour-glass; the series of these centruns protecting a continuous moniliform chorda dorsalis. In the great Basking Shark (*Selache*) the vertebral bodies are chiefly established by the terminal bony cones, the thick margins of which give attachment to the elastic capsules containing the fluid remains of the gelatinous chorda, which now tensely fills the interver-

\* "*Ossa intercalaria crurum*," "*Lamine intererurales*" (Müller).

† Traces of the vegetative repetition of vertebral elements may be seen in the higher animals; the interparietal bone of the Rodents is the '*os intercalare spinale*' of the second cranial vertebra, and the *ossa Wormiana* are '*ossa intercalaria*,' as John Müller has well remarked in his memoir on Myxinoïds, p. 92.



tebral biconical spaces.\* The rest of the centrum is strengthened by a beautiful arrangement of osseous plates, with intervening layers of cartilage (*fig. 13.*). Four sub-compressed conical cavities extend, two from the bases of the neuropophyses (*n, n*), and two from those of the parapophyses (*p, p*) towards the centre of the vertebral body, contracting as they penetrate it. These cavities always remain filled by a clear cartilage: the central two-thirds of the vertebral body contain concentric and minutely perforated rings or cylinders of bone, interrupted by the four depressions: the peripheral third contains longitudinal bony laminae, which radiate, perpendicularly to the plane of the outermost cylinder, toward the periphery of the vertebra: these outer laminae lie, therefore, parallel with the axis of the vertebra, and the intervening fissures, like those between the concentric cylinders within, are filled by clear cartilage, which shrinks and leaves them open in the dry vertebra. There is a transition from the cylindrical to the longitudinal lamellar structure; the outer cylinder being broken up, and sending out processes which join the irregular inner edges of the outer lamellae.



Vertical transverse section of centrum of *Selache maxima*.

There are few examples in the animal economy in which the smallest possible quantity of earthy matter is arranged according to such beautiful and clearly manifested mechanical principles, for affording the greatest amount of strength, and that degree of resistance which the necessarily light, semi-ossified vertebra of a gigantic Shark, maintaining itself near the surface by muscular exertion, without help from a swim-bladder, must have to sustain during the vigorous inflexions of the vertebral column, producing the violent compressions of their interposed elastic balls.

I have been induced to enter into the details of the condition of the vertebræ of the Selache, both on account of the large scale on which the beautiful structure is shown, and because of the meagre notice of it in Home's "Anatomy of the Basking Shark (*Squalus maximus* †)," of which John Müller justly complains. Müller's inference that the vertebræ of Selache resemble those of Lamna is correct: but in *Lamna cornubica* the outer longitudinal plates are fewer, and are bent so as to intercept long elliptical spaces filled with cartilage.

\* Mr. Clift found, on piercing the capsule with a knife, that the contained fluid was spirted out to a considerable distance, by the contraction or recoil of the tensely filled elastic bag. See Prep. Nos. 237 A. and 237 B. and xx. vol. i. 1832.

† Phil. Trans. 1809, p. 177.

Cuvier appears to have overlooked the peripheral longitudinal lamellæ: he says, "dans certains grands squales, le *maximus*, par exemple, ce sont des lames cylindriques, toutes concentriques, toutes séparées par des couches d'un cartilage tendre," &c. (*Leçons d'Anat. Comp.* 1835, i. p. 127.) Our compilers have copied this description, and, as usual, have applied it to the vertebræ of Fishes in general. In the *Squatina*, the part of the vertebral body included by the terminal cones is, indeed, composed of concentric layers, decreasing in breadth as they approach the centre; but, in the *Cestracion*, there are no concentric layers, but only longitudinal lamellæ, radiating from the centre to the circumference, and giving off short lateral plates as they diverge: the most common disposition of the osseous matter in the vertebral bodies of the *Plagiostomes* is a combination of longitudinal and cylindrical plates, as in the *Selache*.

In the *Tope* (*Galeus communis*), as well as in most Sharks which possess the nictitating eyelid, may be seen the highest stage of vertebral ossification in the *Chondropterygian* Fishes: the external surface, as well as the terminal concavities, of the centrum, are covered by a smooth osseous crust, except at the openings of the four conical cavities, which, as in *Selache*, correspond with the bases of the neur- and par-apophyses. In most Sharks the principle of vegetative repetition is manifested in the numerous centres of ossification in the cartilaginous neural and hæmal arches: four stellate points, for example, represent the neurapophysis in *Galeus*, and as many smaller points the neural spine: in most other *Squalian* genera the centrum supports two osseous pieces on each side of the spinal canal: one of these, by its position above the neural canal of the centrum, claims to be regarded as the neurapophysis; the other by its position, usually over the intervertebral space, and by its shape as an inverted cone, indicates an intercalary interneural piece. It is worthy of remark that the nerve-foramen is usually not a "trou de conjugaison" between these cartilages, but a direct perforation of either the neurapophysis, or of both this and the interneurapophysis, when both roots of the spinal nerve escape separately. The ribs (pleurapophyses) are short and simple semi-osseous styles attached to the ends of the parapophyses, in this skeleton of the *Tope*, [Prep. 369.] along the twenty-six anterior vertebræ, decreasing in length posteriorly. In the *Piked Dog-fish* the ribs are quite cartilaginous, and I have counted forty pairs: in a few Sharks, as in *Carcharias*, *Heptanchus*, and *Alopias*, the ribs are connected to the centrum at the base of the parapophyses.

In the *Monk-fish* (*Squatina*), a transitional form between Rays and Sharks, the vertebral bodies are very numerous, and manifest ex-

ternally a thin layer of hyaline cartilage, internally a thin layer of bone, and, between these, two alternate layers of semi-osseous and hyaline cartilages.

In the flat Plagiostomes (Skates, Rays, Torpedos) vegetative repetition manifests itself still more strongly in the multiplication of vertebræ, and especially of the central elements; which, as indicated by their rudimentary primary ossification in *Chimæra* and *Heptanchus*, are commonly more numerous than the more constant neural arches; nor are interneural and interhæmal pieces altogether wanting in the Rays. Müller (xxi. p. 92.) rightly states that in *Raia clavata* these ossa intercalaria constitute the chief part of the neural arch, at the anterior part of the vertebral column; whilst the neurapophyses resume their ordinary share in its formation at the posterior part of the column. In the *Zygæna* we perceive, also, interspinal cartilages. In *Rhinobatus* a single spine answers to two vertebral bodies (xxi. p. 93.), and we may well suppose this multiplication of central pieces to have been carried still farther in the primæval fossil Ray (*Spinachorhinus*) from the Dorsetshire Lias.\*

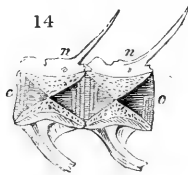
In the anchylosed cervical vertebræ of the Skate the short centrans are indicated by transverse bars along the middle of the under part. The parapophyses in most Rays pass forwards, and are then bent backwards, the angle of one fitting, like an articular process, into the notch of the parapophysis in advance: they do not support pleurapophyses; they gradually bend down behind the pelvic arch, and complete the hæmal canal about six vertebræ beyond it; the hæmal spines become flattened in the tail of some Rays.

In the 'Pisces ossei' of the Cuvierian system, which include the great majority and typical members of the class, it might be expected that ossification, of the vertebral axis at least, would be a constant condition: yet I have already had occasion to allude to a fish, viz. *Lepidosiren*, in which the embryonic state of the bodies of the vertebræ, as a continuous chondro-gelatinous chord, remains; although the neur- and par-apophyses, many cranial bones, and the maxillary, mandibular, hyoidean and scapular arches, are well ossified. The fact of many fossil Ganoid fishes showing the same parts of the skeleton petrified and undisturbed, but without a trace of the central elements of the vertebræ, shows that the transitional condition of the *Lepidosiren's* skeleton was not uncommon in the primæval

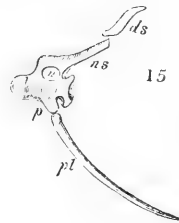
\* *Squaloraia* of Riley and Stutchbury (Geol. Trans. 2d ser. vol. v. p. 83. pl. 4.), regarded as a fossil reptile by Dr. Grant (Lectures, Lancet, Jan. 1834, p. 576.): 170 vertebral bodies are included in the abdominal part of the column; and the part extending beyond the pelvic arch, if equal to that in most Rays, probably did not contain less than four times the above number of abdominal vertebræ.

members of the class. So far as the observations of M. Agassiz have extended, not one of the fossil fishes hitherto discovered in the Silurian and Devonian rocks, the most ancient in which remains of that class have been found, manifest a vertebral centrum; and not many have shown neural and hæmal arches and spines.\*

As a rule we find that the existing bony fishes have well ossified vertebræ, but retain a greater proportion, than in higher classes, of the primitive gelatinous basis, which fills up the deep concavity of each articular end of the centrum (*fig. 14. c*). Only in the salamandroid *Lepidosteus*, with its lung-like air-bladder, does ossification encroach upon these cavities, so as to render the anterior end of the centrum convex, the posterior end concave (*fig. 15.*), and thus unite



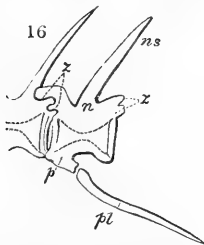
*Scarus.*



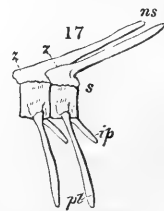
*Lepidosteus.*

the vertebræ together by ball and socket joints. (XXVI. p. 59.) In the rest of the class, the vertebral bodies are connected together by a strong elastic capsule, attached to the border of the base of each terminal hollow cone, and enclosing the gelatinous fluid, which tensely fills the biconcave space and renders the entire column light and elastic.

The vertebra of a bony fish consists essentially of a biconcave body, of two neurapophyses (*fig. 16. n*) completing the canal



Abdominal vertebræ, *Mugil.*



Abdominal vertebræ, Pike (*Esor*).

of the spinal chord, and usually supporting a spinous process (*ns*); of two parapophyses (*p*) usually projecting from the lower part of the sides of the body, or bent down to form the canal for the aorta (*fig. 20.*):

\* Agassiz, Poissons Fossiles du Système Devonien, 4to. p. xxvi.

to which are added in the abdominal region of most fishes two pleuropophyses (*pl*), or vertebral floating ribs.

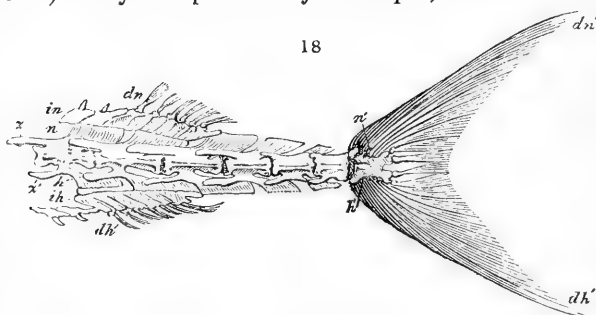
Ossification commences in the bases of the two neurapophyses and the two parapophyses, and in the terminal concave plates of the centrum; the intermediate part of the centrum is sometimes completely ossified, when it is filled by a coarse cancellous texture. More commonly a communicating aperture is left between the two terminal concavities, (as indicated by the dotted line in *fig. 16.*); and, in many cases, the plates by which calcification attains the periphery of the body leave interspaces permanently occupied by cartilage, forming cavities in the dried vertebræ, especially at their under part, or giving a reticulate surface to the sides of the centrum. The expanded bases of the neur- and par-apophyses usually soon become confluent with the bony centrum: sometimes first expanding so as wholly to enclose it, as, for example, in the Tunny, where the line of demarcation may always be seen at the border of the articular concavity, though it be quite obliterated at the centre, as a section through that part demonstrates.

In the Pike the neurapophyses seldom, in the Polypterus never, coalesce with the centrum: the letter *s* shows the neurapophysial suture in *fig. 17.* In the *Salmonidæ* the parapophyses remain, for some time, distinct from the body of the vertebra as well as from the ribs. In the anterior vertebræ of the Carp the neurapophyses remain distinct, as they do in the atlas of many other fishes, and a suture is observable between the parapophyses and centrum in embryo Cyprinoids.\* In each vertebra the summits of the two neurapophyses usually become ankylosed together, and to their spine; but in the *Lepidosiren* (*fig. 27.*) the spine retains its character as a distinct element, and is always attached by ligament to the tops of the neurapophyses, as it is in the Sturgeon (*fig. 12.*). In the anterior abdominal vertebræ of the Tetrodon, each of the neurapophyses, though they coalesce in the interspace of the two spines to form the roof of the neural canal, sends up its own broad truncated spine, and these are not, as might at first sight be supposed, enormously developed oblique processes, for they gradually approximate and blend together, to form the single normal spine at the sixth abdominal vertebra: in the Barbel the neural arches also support two spines, but one is placed behind the other.

The interspaces of the neural arches are occupied by a fibrous aponeurosis—the remains of the primitive essential covering of the neural axis: but in most fishes the arches are additionally connected together by articular or oblique processes (zygapophyses), which are developed from the base of each neurapophysis; sometimes

\* First noticed by Von Baer.

four, two anterior, two posterior, as in the Mullet (*Mugil*, *fig. 16. z*); sometimes two, as in the Perch, the posterior in this and most other fishes being overlapped by the anterior articulating process of the succeeding vertebra: commonly only the anterior zygapophysis is developed (*fig. 17. z*), which touches, but rarely overlaps, as in the Polypterus, the neural arch in advance. It is peculiar to fishes to have articular processes developed from the parapophyses; we have noticed these already in the abdominal region in the Ray; in the osseous fishes, when present, they are confined to the caudal vertebræ (*fig. 18. z'*): they are particularly developed, sometimes branched,

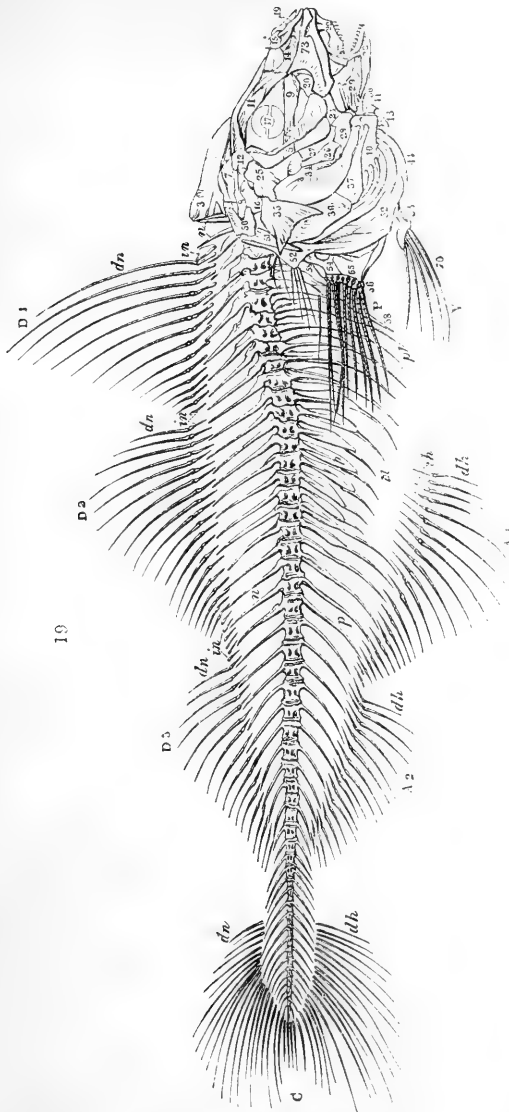


Terminal caudal vertebræ, Sword-fish (*Xiphias*).

forming a network about the hæmal canal in certain species of Tunny (*Thynnus*, XXIII. i. p. 265.). In *Loricaria* peculiar accessory processes are sent out from the neural arch of the seven anterior vertebræ which abut against the osseous lateral shields of the dermal skeleton.

The parapophyses are very short in some fishes (*Salmo*, *Clupea*): they are longest and most expanded in the abdominal region of the Cod tribe (*fig. 19. p*), where they support the air-bladder, which intimately adheres to their under surface, and, in one species of *Gadus*, sends processes into expanded cavities of the parapophyses, thus foreshowing the pneumatic bones of birds. They gradually bend down near the tail, where they form, as in all fishes, the hæmal canal.

The pleurapophyses of fishes correspond to what are usually termed in Comparative Anatomy 'vertebral ribs,' and in Human Anatomy 'false' or 'floating ribs': for, with few exceptions, of which the Herring is one (*fig. 23.*), their distal ends are not connected with any bones analogous to sternal ribs or sternum; *i. e.* the abdomen is unclosed below by the crura and spines completing the hæmal arch. The true homologues of sternal ribs or abdominal hæmapophyses retain the primitive aponeurotic tissue, and may be well seen in the Bream, extending from the ends of the vertebral ribs. These elements,



Skeleton of the Haddock (*Gadus aeglefinus*).

or pleurapophyses (*fig. 19. pl, pl*) are usually appended to the extremities of the parapophyses, the articulation frequently presenting a reciprocal notch in each. But, in some bony fishes, as *Platax*, the ribs articulate with the bodies of the vertebrae, in depressions behind the parapophyses; and in *Polypterus* beneath the para-

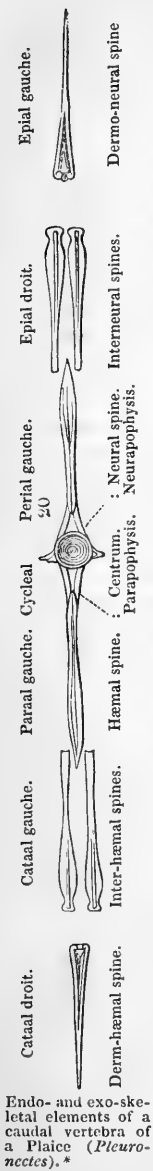
pophyses, as in the cartilaginous *Heptanchus*, *Carcharias*, and *Alopias*.

Between the floating ribs extends an aponeurosis, the remains or homologue of the primitive fibrous investment of the abdomen in the Lancelet and Lamprey. In the Salmon and Dory the ribs continue to be attached to some of the parapophyses after they are bent down to form the hæmal canal and spine in the tail; and we derive the same striking evidence of the true nature of these inferior arches from the skeleton of the Tunny, the Dory, and some other fishes. The costal appendages of the first vertebra of the trunk are usually larger than the rest, and detached from the centrum; at least if we regard as such the styli-form bones (*fig. 19. 58*) which project from the inner side of the scapulæ, and which have been described as coracoids (Cuvier) and sometimes as displaced iliac bones (Carus). By the muscles attached to these styli-form bones the succeeding ribs are drawn forwards and the abdomen expanded in the Cyprinoids. Pleurapophyses are entirely absent in the Sun-fish, Globe-fish (*Diodon*), the Tetradon, the Pipe-fish (*Fistularia* and *Syngnathus*), the Lump-fish and the Angler. This of all osseous, or rather semi-osseous, fishes presents the simplest vertebral column: the abdominal vertebræ are not only devoid of ribs, but have the feeblest rudiments of parapophyses. The bodies of these vertebræ interlock at their lower and lateral parts by a short angular process fitting into a notch in the next vertebra; the lower border of this notch represents the lower transverse process in other fishes: it is obsolete in the anterior abdominal vertebræ; begins to appear about the middle ones; shows its true character in the tenth; and elongates, bending downwards, backwards, and inwards, to coalesce with its fellow, and form the hæmal arch at the twelfth or thirteenth vertebra, from which the hæmal spine is developed. The interlocking process of the anterior vertebra disappears as the true inferior transverse process is increased. The side of the neural arch is perforated for the nerve, and that of the hæmal arch for the blood-vessel.\* The anterior abdominal vertebræ of the Tetradon are more firmly clamped together by the parapophyses than in the Angler.

A vegetative sameness of form prevails in Fishes throughout the vertebral column of the trunk, which is made up of only two kinds of vertebræ, characterised by the direction of the parapophyses:

\* The gelatino-cartilaginous basis is progressively but continuously ossified around these foramina, which form part of a vast series of exceptions to the so-called "loi de conjugaison" of M. Serres; who, by this phrase, expresses his notion that every foramen is formed, like those that give passage to the spinal nerves in Mammalia, by the approximation of two notches of two distinct bones or bony elements.





these in the abdominal region are lateral, usually stand out and support ribs; but in the caudal region they bend down and coalesce at their extremities. The caudal vertebræ of some flat-fishes (*Pleuronectidæ*, fig. 20.), the *Polypterus* and the *Muraenæ*, would seem to disprove this homology of the hæmal arches, since transverse processes from the sides of the body co-exist with them, as they do in the *Cetacea*. But, if we trace the vertebral modifications throughout the entire column in any of these fishes, we shall find that the hæmal arches are actually parts of the transverse processes; not independent elements, as in the *Cetacea*; but due to a progressive bifurcation: this, in *Muraena Helena*, for example, begins at the end of the transverse processes of about the twenty-fifth vertebra, the forks diverging as the fissure deepens, until, at about the seventy-third, the lower fork descends at a right angle to the upper one (which remains to represent the transverse process), and, meeting its fellow, forms the hæmal arch, and supports the antero-posteriorly expanded hæmal spine. In the *Plaice* a small process is given off from the expanded base of the descending parapophysis of the first caudal vertebra, which increases in length in the second, rises upon the side of the body in the third, becomes distinct from the parapophysis in the fourth, and gradually diminishes to the ninth or tenth caudal vertebra, when it disappears. These false transverse processes never support ribs.

The atlas may usually be distinguished by some slight modification of the anterior articular end of the body, by the persistent suture of the neural arch, or by the absence or detachment of its pleurapophyses: but none of these characters are constant. Peculiar processes are sometimes sent off from the under part of the centrum: two very long and strong processes from this part are articulated with the basi-occipital in the great *Sudis* (*Arapaima gigas*). The second vertebra is never characterised by an odontoid process; but the absence of this is not to be accounted

\* Compare this figure with nature, and with the figures of a corresponding vertebra in II. pl. 5., and in XXVIII. p. 58. The names assigned by Geoffroy St. Hilaire

for by the characteristically well-developed body of the atlas in fishes, since the atlas has a small centrum in crocodiles and birds, where the odontoid process likewise exists.

The number of vertebræ varies greatly in the different osseous fishes: the Plectognathi (*Diodon*, *Tetrodon*,) have the fewest and largest: the apodal fishes (Eels, Gymnotes,) have the most and smallest, in proportion to their size. It is not often easy to determine the precise number, on account of the coalescence of some of the vertebræ, or at least of their central elements, in particular parts of the column. Instances of anchylosis of some of the anterior vertebra, analogous to that noticed in the cartilaginous Sturgeons, Chimæræ, Rhinobates, and some Sharks, occur also amongst the osseous fishes, as in many Siluroid and Cyprinoid species; in the Loricaria and Fistularia: here is an example (*fig. 21.*) of the four



21  
1  
2  
3  
4  
Anchylosed anterior vertebra, Pipe-fish (*Fistularia*).

singularly elongated anchylosed anterior abdominal vertebra, in the Tobacco-pipe fish (*Fistularia tabaccaria*). A coalescence of several vertebræ is more constant at the opposite end of the column in osseous fishes, in order to form the base of the caudal fin. The bodies at least of the vertebræ situated here, at the part most remote from the centre of life, do not emerge separately from the primitive embryonic condition of the gelatinous 'chorda,' but are continuously ossified to form a common, compressed, vertically extended, and often bifurcated bony plate (*fig. 18. n'h'*), from which the neural and hæmal arches and their spines radiate: from these elements alone can the number of vertebræ of the caudal fin be estimated; normal development proceeding here in the peripheral elements, as throughout the vertebral column in Lepidosiren, whilst it is arrested in the central parts of the vertebræ. In the Sun-fish (*Orthogoriscus mola*) it would seem as if a row of rudimental vertebræ had been blended together at right angles to the rest of the column, in order to support the rays of the short, but very deep caudal fin, which terminates the suddenly truncated body of this oddly shaped fish. Our common Pike affords a simple and intelligible

view of this modified base of the tail-fin: in the Eels, the Polypterus, the Lepidosiren, the Trichiurus, and Pipe-fishes, the vertebræ always remain distinct to the end of the tail.

Cuvier, in the tables of the number of vertebræ in various species

to the several parts of this combined segment of endo- and exo-skeleton are opposite the left hand of the reader; those applied to them in the present work are placed opposite the right hand.

of fishes contained in the "Leçons d'Anatomie Comparée,"\* counts the anchylosed vertebræ of the caudal fin as one, and so assigns seventeen vertebræ to the Sun-fish. I find but sixteen according to the vertebral centres, eight abdominal, and eight caudal: but if we count the neural spines, we have then twelve caudal vertebræ; the spines of the last five being driven, as it were, by the extreme contraction of their anchylosed bodies, to rest their bases upon the back part of the seventh or last upright neural spine. In the Conger there are 162 vertebræ, in the Ophidium 204, and in the Gymnotus 236 vertebræ; but even this number is surpassed by some of the plagiostomous fishes. Nor are the extremities of the vertebral column the only regions where anchylosis of the vertebræ takes place. Hunter had preserved this specimen of confluence of the first two vertebræ of the post-abdominal or caudal region in a large flat-fish (probably *Rhombus*, fig. 22.), forming a true sacrum. In the Halibut (*Hippoglossus*) the parapophyses of the corresponding vertebræ, with those of the last abdominal, are similarly united, though the bodies remain distinct. In Loricaria both the upper and lower arches of a considerable part of the caudal region are blended together into an inflexible sacrum; but, as a general rule, there exists no such impediment to the lateral inflections of the tail in the present class.



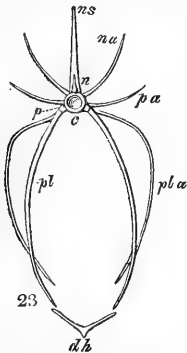
Anchylosed anterior caudal vertebræ, or sacrum, of a Flat-fish.

Although the vertebræ maintain a considerable sameness of form in the same fish, they vary much in different species. The bodies are commonly subcylindrical; as deep, but not so broad, as they are long; more or less constricted in the middle, in some to such a degree as to present an hour-glass figure. In the Spinachorhinus they are extremely short; in the Fistularia extremely long; in the Tetrodon they are much compressed; in the Platycephalus they are more depressed; in the tail of the Tunny the entire vertebra is cubical, with the ends hollowed as usual, but the four other sides flat, the upper and lower ones being formed, in the connected series, by the neural and hæmal arches of the vertebra in advance, flattened down and, as it were, pressed into cavities on the upper and under surfaces, of the centrum of the next vertebra; so that the series is naturally locked together in the dried skeleton; and these arches cover not the neural and hæmal canals of their own, but of the succeeding, centrum.

The principle of vegetative repetition is manifested, in osseous

\* Ed. 1836, tom. i. p. 229.

fishes, by the numerous centres of ossification, from which shoot out bony rays affording additional strength to many of the intermuscular aponeuroses: some of these supernumerary or intercalary ossicles belong to the endo-skeleton, but most of them to the exo-skeleton. In the former system of bones may be ranked those spines which are attached to, or near to, the heads of the ribs, and extend upwards, outwards, and backwards, between the dorsal and lateral masses of muscles: these are the 'diverging appendages' of the abdominal ribs (*fig. 17. ip, fig. 23. pl a*), and may be termed 'epipleural spines;' though they sometimes pass gradually, as the vertebræ approach



Abdominal vertebra,  
Herring (*Clupea*).

the tail, from the rib upon the parapophysis, and even in the posterior abdominal vertebræ (e. g. *Holocentrum*), upon the bodies and neural arches. They are the "obere rippe" of Meckel, and at the fore-part of the abdomen, in *Polypterus*, the epipleural spines are stronger than the ribs themselves. The spinous appendages are remarkably developed in the Halecoid fishes, (Salmon and Herring,) in the Mackerel-tribe, and the Dolphin (*Coryphæna*). In our common herring you will find them attached not only to the ribs (*fig. 23. pl, a*), but also diverging from the parapophyses (*pa*), and the neuropophyses (*na*), and the vertebra is further complicated by dermal bones, those on the under surface of the abdomen (*dh*) being connected, like the scutes of serpents, with the lower ends of the ribs (*pl*).

The very distinct histological condition of the endo- and exo-skeleton of the Sturgeon (*fig. 43.*), shows clearly the nature of those spines (*fig. 19. dn, dn*), which form, in osseous fishes, a second row, of greater or less extent, above the true neural spines, and support the dorsal fins. Thus, in *Accipenser Ratzburgii*, twelve of the hard enamelled calcareous plates (ganoid scales) along the mid-line of the back, send upwards and backwards a moderately long spine: the series is then continued in a cartilaginous state to support the dorsal fin.

In the *Polypterus* sixteen accessory bones, in the form of longer and sharper spines, are extended over thrice as many vertebræ: and each dermal spine supports a membrane, strengthened at its upper part by four or five branched and jointed rays. From the base of the dermal spines, other spines (*fig. 19. in, in*) usually shoot downwards, into the intervals of the neural spines: these inverted spines may be the homologues of the wedge-shaped interneural pieces before noticed in the vertebræ of Sharks, and may well retain that name in the osseous fishes. Sometimes they are double, as in the Flat-fish

(Plaice, Sole, &c., *fig. 20.*), and in some parts of the vertebral column of the Deep-fish, as the Dory, the Chæton, the Sun-fish, &c. But whatever modifications these dermal and intercalary spines present above, the same are usually repeated below, in connection with the hæmal arches and spines, for the support of the anal fin: and just as in the framework of the dorsal fin we find interneural spines and dermoneural spines, so in that of the anal fin we recognise interhæmal spines (*fig. 19. ih*), and dermohæmal spines (*ib. dh*), with the, sometimes, expanded base from which they diverge. Both interneural and interhæmal spines are, in the osseous fishes, commonly shaped like little daggers, plunged in the flesh up to the hilt, which is represented by the part to which the true fin-ray (dermoneural or dermohæmal spine) is attached. These parts of the dermal skeleton, developed in the primitive continuous fold of skin which forms the groundwork of the vertical fins in the embryo fish, manifest the vegetative character, which is the usual concomitant of peripheral position, by the partial spontaneous fission which each ray has undergone in the progress of its development; this is shown by the longitudinal raphé or suture along which each dermal spine or ray may commonly be divided into two lateral moieties. The framework of the caudal fin is composed of the same intercalary and dermal spines, superadded to the proper neural and hæmal spines, of those caudal vertebræ which have coalesced and been shortened by absorption, in the progress of embryonic development, to form the base of the terminal fin (*fig. 18, 19. c, dn, dh*).

In the Sharks and Sturgeons this fin is not symmetrical as in most osseous fishes, but is formed chiefly by the hæmal spines and their intercalary and dermal spinous appendages; the progressively decreasing bodies of the caudal vertebræ are continued along the upper border or lobe of the fin, sending off short neural spinous processes to increase the height of that border.

M. Agassiz calls those fishes in which, from the peculiar development of the lower lobe of the caudal fin, the vertebræ seem to be prolonged into the upper lobe, "heterocercal;" and those with the lobes of the caudal fin equal or symmetrical, he calls "homocercal." The preponderance of heterocercal fishes in the seas of the ancient geological epochs of our planet is very remarkable: the prolongation of the superior lobe characterises every fossil fish of the strata anterior to, and including, the Magnesian limestone. The homocercal fishes first appear above that formation, and gradually predominate, until, as in the present period, the heterocercal bony fishes are almost limited to a single ganoid genus, e. g. *Lepidosteus*.

The shape, size, and number of the median azygous dorsal and

anal fins, depend on the development and grouping of the accessory and intercalary spines: the true vertebral, neural, and hæmal spines give scarcely more indication of the nature or existence of those fins, than the neural spines in the Porpoise or Fin-whales do of their not less essentially though more histologically dermal dorsal fin; but the development of the dermo-skeleton, in the fish's fin, and its intercalation with the spines of the endo-skeleton, and consequently its retention in our prepared skeletons, lead me to notice it in connection with the vertebral column, as I shall subsequently, for similar reasons, have to describe parts of the dermo-skeleton which are intercalated with, or appended to, the vertebræ and bony arches of the head.

In the *Dermopteri* (Lampreys, Lancelet), the dorsal, anal and caudal fins are simply cutaneous folds, with scarcely distinguishable soft fibres for rays, and they are continuous, as in the embryos of higher fish. In the *Gymnotus*, a very long but shallow anal is continued into the caudal fin; but, as the name of this fish implies\*, there is no dorsal fin. In many, both cartilaginous and osseous fishes, a single group of dermal spines supports a single dorsal fin, as in the Sturgeon, the Grey Shark (*Heptanchus*), and the Shad: in others, as the Dog-fish (*Spinax*), and the Mullet, there are two groups of dermo-neural spines and two dorsal fins; in the Cod and its congeners there are three dorsals (*fig. 19. D*); in the *Polypterus* there are, as its name implies, numerous (as many as sixteen) dorsal fins; and many accessory vertical finlets, both dorsal and anal, may be seen in the *Caranx*, or Mailed Mackerel.

Cuvier called those bony fishes "Malacopterygian," whose vertical fins were supported by soft, jointed, and branched dermal spines, and he called those "Acanthopterygian," which had the fin-rays or some of the anterior ones in the form of simple, unjointed, and unbranched bony spines: but we have seen that these variable parts of the dermo-skeleton form unsafe and artificial grounds for the larger groups of the class.

Very rarely do the interneural and dermal spines coincide in number with the neural spines: they are often more numerous, as in *Acanthurus* and *Pleuronectes*; more frequently less numerous, as in the *Lepidosteus* or *Trachinus*. The *Lophius* has only three long detached dermal rays, projecting from above the abdominal region of the spine, and two or three above the cranial vertebræ; the base of these dermal spines expands, bifurcates, and the extremities curve inwards, to be inserted into lateral depressions, or a transverse perforation, of the summit of the interneural spine, represented in *Lophius* by a small semi-osseous disc. Those dermal spines that sustain the caudal fin offer the lowest condition, as might be expected

\* Gr. *γυμνος*, naked; *νοτος*, back.

from their terminal position ; they are almost always bifurcated, or dichotomously subdivided, as the effect of the continued spontaneous fission of their embryonic elements, or of the activity of the vegetative force of irrelative repetition. This part is accordingly subject to monstrosity by excess, as is manifested by the double and triple tails of Gold-fish in confinement, where nutriment is not expended by the due action of muscular force. The singular sucking-apparatus upon the head of the Remora is an assemblage of peculiarly modified and connected dermal spines. The more common modification is the excessive development of one or more of the dermal spines, to form peculiar weapons of defence.

The Chimæra, the Cestracions, and the Piked Dog-fish, show such a stout bony spine, sometimes, as in the last-named shark, sheathed with horn, at the front border of each dorsal fin, which it also serves to strengthen. The Fire-flares (*Trygon*) and Eagle Rays (*Myliobates*) have one or more strong, detached, barbed or serrated spines, on the upper part of the tail. Agassiz has pointed out the close resemblance of the microscopic structure of the bone of these spines and the dentine of the teeth of the same kind of fishes ; they are both hardened by an outer layer of modified dentine, but as hard as enamel. Many large fossil spines, called in Palæontology "Ichthyodorulites," have been determined by their form and structure to have belonged to extinct cartilaginous fishes, allied to the above-cited existing genera, of which they are sometimes the sole indications left by the wreck of former worlds. Amongst bony fishes, the Siluroids (Sheat-fish) and Balistes (File-fish) are most remarkable for these dermal weapons. In our rare *Balistes capriscus* the anterior dorsal is sustained by three such spines ; the first much the strongest, and the second subservient to the use of the first as a weapon, rather than for the support of the fin. The first spine is articulated by a very remarkable joint to the broad interneural osseous plate : its base is expanded and perforated, and a bony bolt passes freely through the ring. When this spine is raised, a depression at the back part of its base receives a corresponding projection from the contiguous base of the second ray, which fixes it like the hammer of the gun-lock at full-cock, and it cannot be forced down till the small spine has been depressed, as by pulling the trigger : it is then received into a groove on the supporting plate, and offers no impediment to the progress of the fish through the water. The name of the genus (*Balistes*) and the common Italian name of the species in question (*Pesce balestra*) refer to this structure : the spine of the Balistes is also roughened with ganoid or enamel grains like a file, whence our English name for it, 'File-fish.' The margins of the ana-

logous but stronger weapon of the Siluroids is usually beset with denticles of the same hard substance, sometimes ankylosed to the spine, sometimes movably articulated with it. M. Agassiz has found that the fixed denticles have the same osseous texture, characterised by radiated corpuscles in concentric layers, as the spine itself; whilst the movable denticles present a simpler structure, being permeated by calcigerous tubes, radiating from a central vascular pulp cavity, like teeth; but the comparative anatomist who has extended his observations beyond the class of Fishes, will pause before he admits the sweeping conclusion which the celebrated ichthyologist draws from his interesting microscopical observations.\*

The distinction between the internal or splanchnic and external skeletons does not rest upon the microscopic character of their tissues; if it did, and if every calcified plate or spine that presented the characteristic radiated cells of bone, were to be classed with the pieces of the internal skeleton, we must cease to regard the scales of the Crocodile, and the tessellated carapace of the Armadillo, as parts of the external or dermal skeleton.

## LECTURE IV.

### THE SKULL OF FISHES.

PASSING from the trunk to the head, we find in the Lancelet (*Branchiostoma*, xxx.), at the lowest step of the Vertebrate series, that the cranium is not indicated by difference of size or structure of the rudimental vertebral column, but consists of that gradually contracting anterior termination of the neural canal, which retains its primitive fibro-membranous wall, (*fig. 46. n*), without any superaddition of parts, and is supported by the tapering end of the gelatinous 'chorda dorsalis' (*ib. ch*). This part, in the Lancelet, even extends farther forwards than the cranial end of the neural canal, indicating the non-development of the prosencephalon and corresponding part of the cranial cavity. In fact, there is no ganglionic cerebral expansion whatever in this vermiform fish: the epencephalon or medulla oblongata is indicated by the origin of the trigeminal nerve (*ib. ob*), in advance of which the mesencephalic segment sends off the short optic nerve to the dark ocellus (*op*), and there terminates, somewhat obtusely, beneath what Dr. Kölliker (xxxii. p. 32.) has described as a ciliated olfactory capsule (*ib. ol*). The cranium of the Lancelet,

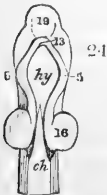
\* Les genres *Hypostoma* et *Callichthys* présentent cette singulière structure, et prouvent par là même que les différences qu'on a voulu établir, entre un squelette paucier ou externe, et un squelette intérieur ou intestinal, sont dénuées de tout fondement."—*Poissons Fossiles*, tom. iii. p. 213.



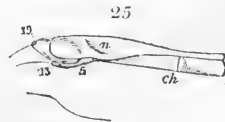
therefore, may be said to be composed of the primitive continuous fibro-gelatinous basis of the vertebral bodies, and of the membrane which is represented by our 'dura mater,' without the superaddition of cartilaginous or osseous coverings.

But if we were to limit our view of the skull of the *Branchiostoma* by this primitive embryonic condition of the cranium proper, we should have an incomplete idea of it. A large, jointed, cartilaginous hæmal arch (*fig. 46. h*) extends on each side, from below the cranial end of the chorda dorsalis, downwards and backwards to the orifice of the pharynx; this represents the labial arch of higher Myxinoids, and it supports the jointed slender oral filaments, which may be regarded as a continued representation, in the Vertebrate series, of the cephalic tentacula of the Cephalopods. It is the sole chondrified part of the skeleton in the *Branchiostoma*, a fact which must be borne in mind if we would avoid the common error of supposing the neural vertebral column to be the first and only rudiment of an internal skeleton in the lower Vertebrata.

Before proceeding to the next stage at which cranial development is arrested in the ascending series of Vertebrata, I may briefly describe the form under which the cartilaginous tissue is superinduced upon the fibrous brain-sac in osseous fishes, according to the observation of M. Vogt on the embryo of one of the Salmonidæ (*Coregonus*, xxii. tom. i. p. 3.). The chorda dorsalis advances as far as the pituitary sac, or 'hypophysis cerebri,' where it terminates in a point; cartilage is developed on each side of the chorda, forming a thick *occipito-sphenoidal* mass\*, which extends outwards, and envelops the sac of the internal ear, forming the ear-ball or acoustic capsule. The cartilage rises a little way upon the lateral walls of the cranium, and is there insensibly lost in the primitive cranial membrane. At the end of the chorda, the basal cartilages diverge, surround the pituitary vesicle, and meet, in front of it, to join or be expanded in the *presphenoid* plate †: these arches I term "*sphenoidal*." ‡ (*fig. 24.*)



Base of skull, *Ammocete*, Müller.



Side view of skull, *Ammocete*, Müller.

\* *Plaque nuchale*, Vogt; *Knöcherner basis cranii*, Müller, xxi.

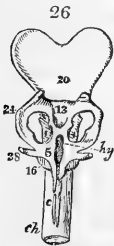
† *Plaque faciale*, Vogt; *Gaumenplatte*, Müller.

‡ *Ansés latérales*, Vogt; *Flügel-forsätze basis cranii*, Müller.

The Sand-lance (*Ammocetes*) presents a condition of the skull which corresponds with this first appearance of the cartilages in the embryo of higher fishes (*fig. 24*). The occipital cartilages extend from the sides of the pointed end of the chorda (*ib. ch*), and expand into the acoustic capsules (*ib. 16*): the sphenoidal arches (*ib. 5*), encompass the pituitary or hypophysial space (*hy*), now closed by a membrano-cartilaginous plate, and unite anteriorly to form a small vomerine plate (*ib. 13*), in front of which is the single undivided nasal capsule (*ib. 19*). The now expanded cerebral end of the neural canal (*fig. 25. n*) is still defended by fibrous membrane only: but is divided from the vomerine plate (*ib. 13*), by a backward extension of the nasal sac (*ib. 19*) to the pituitary vesicle.

In the Myxine the acoustic capsules are approximated at the base of the skull, near the end of the chorda: the sphenoidal arches are longer, and unite with the palatine plate and arches, from which are sent off the labial cartilaginous processes supporting the buccal tentacles, answering to those in the Lancelet. In the long hypophysial interspace of the sphenoidal arches a more or less firm cartilaginous plate is developed, from which a slender median process is continued forward to the vomerine or palatine plate, which supports the nasal capsule; another process extends backwards to the occipital cartilage. Other processes are also sent off from the sides, which form a complex system of peculiarly Myxinoid cartilages.\*

In the Lamprey (*Petromyzon*, *fig. 26*.) the occipital cartilage is continued backwards, in the form of two slender processes (*c*), upon the under part of the chorda dorsalis (*ch*) into the cervical region. The hypophysial space (*hy*) in front of the occipital cartilage remains permanently open, but has been converted into the posterior aperture of the naso-palatine canal.† The sphenoidal arches (*5*) are very short, approximated towards the middle line; and the presphenoid and vomerine cartilage (*13*) is brought back closer to the sphenoidal arches. Two cartilaginous arches (*24*) circumscribe elliptical spaces outside the presphenoid plate: these appear to represent the pterygoid arches; but, as in the embryo of higher fishes, are not separated from the base of the skull by distinct joints. The basal cartilages, after forming the ear-capsules (*16*) extend upwards upon the sides of the cranium (*fig. 11*.), arch over its back part, and leave



Base of skull,  
*Lamprey*  
(Müller).

\* See Müller's masterly Memoir, "Ueber die Myxinoiden," Abhandlung. der Berlin. Akad. 1835, p. 105. tab. iii.

† Agassiz (xxxii.) describes this aperture as "un très petit espèce presque circulaire (E) dans laquelle est logée l'hypophyse du cerveau." The figure to which his letter (E) refers is copied, like mine, from Müller.

only its upper and middle part membranous, as in the human embryo when ossification of the cranium commences. Two broad cartilages (*ib.* 20, 21) may represent, upon the roof of the infundibular suctorial mouth, the palatine and maxillary bones, and anterior to these there is a labial cartilage (*ib.* 22): there are likewise cartilaginous processes (*ib.* *r*, *s*) for the support of the large dentigerous tongue, and the attachment of its muscles; besides the cartilaginous basket, before described, which supports the modified and perforated homologue of the large respiratory pharynx in the Branchiostoma (*fig.* 46.).

As regards the development of the skull, properly so called, the ordinary course is pursued with very little deviation in the Dermopterous fishes; but is arrested at more or less early embryonic stages: yet at each of these, even the earliest, development proceeds in a special direction, to stamp the species with its own distinctive and peculiar character: in the Branchiostoma by the articulated cartilaginous labial arch and its numerous filaments; and in the proper Myxinoids and Lampreys by the formation of the complex system of lateral and labial cartilages; or by the modification of the palatine, maxillary, and hyoid rudiments, in relation to the suctorial function of the mouth.

The more or less cartilaginous skull of the Plagiostomous fishes might be histologically regarded as the transitional step from the Cyclostomous to the Osseous fishes; but, morphologically, it offers a very different type, apparently a simpler one, if compared with the Myxine or Lamprey, but one which in consequence of the progress of development in the direct vertebrate route, more nearly approximates to the type of cranial organisation in the lower forms of Reptilia. The Monk-fish (*Squatina*, — an intermediate form between the Sharks and Rays) affords a good and typical example of the essential characters of the plagiostomous skull. The cranial end of the chorda dorsalis and its capsule are converted into firm granular cartilage; and this cartilage extends from the prominent median basal ridge, indicative of the primitive place of the chorda, on each side and forwards so as to constitute an oblong flattened plate forming the whole basis cranii. The posterior margin of this 'occipito-sphenoidal' plate supports two convex condyles, as in most of the Rays, for articulation with the body and parapophyses of the axis.\* The lateral margins of the basal cartilage have two notches, the intervening prominence representing the primitive sphenoidal arch, here filled up and sending off a rudimental pterygoid process outwards. Just an-

\* The body of the atlas has coalesced with the basi-occipital, as is indicated by its slender but separate neural arch. The condyloid foramen is just above the outer end of the condyle.

terior to the median ridge there is a small fossa, (in the young *Squatina* a foramen,) the last trace of the pituitary canal: the basal cartilage then expands to form the lower border of the groove which receives the palatine process or point of suspension of the palato-maxillary arch, and the cartilage then suddenly contracts, and is continued forwards to form the vomerine anterior base of the cranial cavity. The fibro-membranous parietes of this cavity are every where covered with, or converted into, the same firm granular cartilage as the base, save at the anterior and upper end, where a large fontanelle, closed by the primitive membrane, remains: the cartilaginous walls are perforated by the exit of the cerebral nerves, and the spinal chord.

The cranial cavity is not moulded upon the brain, but is of larger size; it communicates merely by the nervous and vascular foramina with the acoustic labyrinth, which is buried in the thick lateral cranial cartilage. This insulation of the ear-capsules from the brain-case is a high grade of development common to all the typical Plagiostomes: in the *Chimæra* the separation is only partial. The large pituitary depression, or 'sella,' marked by a ridge across the floor of the cavity, indicates the compartment between the orbits for the mesencephalon, and in front of this is the wide prosencephalic, or cerebral, compartment, which communicates by the two large foramina with the nasal cavities, and, in the dry skull, opens forwards by the wide persistent fontanelle. In the vertical lateral cartilaginous walls of the cranium we recognise the part representing the great ala of the sphenoid by the two perforations answering to the foramina oralia and rotunda for the exit of branches of the fifth pair of nerves. The orbital alæ of the sphenoid are indicated by the foramina optica; the part corresponding to the bones in osseous fishes, called by Cuvier "frontaux antérieures," by the olfactory foramina, and by their articulation with the palatine process of the maxillary arch. Two broad and thin cartilaginous plates, from the upper and anterior walls of the cranium, support anteriorly the nasal sacs, and thence extend backwards and outwards over the sides of the anterior half of the cranium forming the roof of the orbits. Two longitudinal and vertical ridges, which rise from the posterior and lateral cranial parietes, extend outwards at both extremities in the form of strong triedral conical transverse processes. The anterior one forms the post-orbital process; the posterior answers to the mastoid; between these is a long cavity lodging the temporal muscle, and beneath this the parallel articular cavity for the tympanic pedicle. The extreme point of the mastoid is perforated by a mucous canal extending to the upper surface of the back part of the skull. The post-orbital processes touch, and some-

times blend with, the supra-orbital plates, and circumscribe vacuities at the sides of the parietal region of the cranium. But the exterior of the skull is variously and singularly modified in the different Plagiostomous genera, development proceeding from the advanced cartilaginous stage just described, to establish peculiar plagiostomous characters, and to adapt the individual to its special sphere of existence.

The same general confluence of cartilage, which pervades the protecting walls of the brain-case, characterises the appended arches of the cranium. A single strong suspensory pedicle, articulated to the side of the skull beneath the posterior angular (mastoid) process, has the hyoidean, and partly the mandibular\*, arches attached to its lower end, the former by a close joint, the latter by two ligaments. The maxillary arch, in *Squatina*, is suspended by a ligament from its ascending or palatal process, to the notch between the vomerine and the anterior supra-cranial cartilaginous plate. From this point the jaw is continued in one direction forwards and inwards, completing the arch by meeting its fellow, to which it has a close ligamentous junction; and in the opposite direction, backwards and outwards, as a coalesced diverging appendage to the outer side of the tympanic pedicle, where it forms the more immediate articulation for the lower jaw, or mandibular arch, like the hypo-tympanic continuation of the upper maxillary bone in the Batrachia. Each lateral half or ramus consists of a single cartilage, the two being united together at the symphysis by ligament.

Two slender labial cartilages are developed on each side the maxillary, and one on each side the mandibular arch; which complete the sides of the mouth. These cartilages Cuvier regarded as rudiments, respectively, of the intermaxillary, maxillary, and dentary bones; the dentigerous maxillary arch being his palatine bones, and the mandibular arch the articular piece of the lower jaw; but both palatines and articulators co-exist with labial cartilages, like those of the *Squatina*, in a Brazilian Torpedo (*Narcine*), and at the same time with distinct pterygoid cartilages. (xxi. 1835, pl. v. *fig.* 3. & 4.) †

Four or five short cartilaginous rays, in *Squatina*, diverge from the posterior margin of the tympanic pedicle, and support a membrane answering to the opercular flap in Osseous fishes; in their ultimate homology these rays are the skeleton of the diverging appendage or limb of the tympano-mandibular arch.

\* Throughout these Lectures the term "mandible" is applied to the lower jaw, and the inverted cranial arch which that jaw completes is called "mandibular:" the arch formed by the upper jaw is called "maxillary."

† It may be questioned whether the detached plate, called palatine by Dr. Henle, be not rather the ento-pterygoid.

The hyoid arch in the *Squatina*, as in most other Plagiostomes, consists of two long and strong lateral pieces or cerato-hyoids (*cornua* of Anthropotomy), and a median flattened symmetrical piece, the basi-hyoid, (*corpus ossis hyoidei*) below. Short cartilaginous rays extend outwards from the back part of the cornua, supporting the outer membranous wall of the branchial sac: these answer to the branchiostegal rays in osseous fishes, and support the diverging appendage or limb of the hyoidean arch. But the fold of integument in which they project is not liberated, and is continuous with that supported by the opercular rays from the tympanic pedicle. Five branchial arches succeed the hyoidean; but are suspended, as in the Lamprey, from the sides of the anterior vertebræ of the trunk.

The *Cestracion*, so interesting from its early introduction into the seas of this planet, is not so far advanced in cranial development as is the more modern *Squatina*. In the existing species of the Australian seas (*Cestracion Phillipi*, v. pl. 10.), the cartilaginous basi-occipital retains a deep conical excavation, adapted to a corresponding one in the atlas, which cavity is consolidated by cartilage in the *Squatina*; the original place of the extended anterior end of the chorda, along the middle of the posterior half of the basi-cranial cartilage, continues membranous, and the pituitary perforation is permanently closed by membrane only; the basal cartilage expands anterior to this, and comes into close connection with the maxillary arch, and is thence continued forwards, contracting to a point between the nasal capsules, which meet at the middle line above the symphysis of the upper jaw. The proper cranial cartilage is thinner than in the *Squatina*; the anterior or pineal fontanelle forms an extended membranous tract on the upper part of the cranium; the vertical ridges, which rise from the sides of this tract, extend forwards and outwards to support the nasal sacs, and are continued backwards, interrupted by a notch filled by membrane, to the posterior angular processes, which overhang the joint of the maxillo-hyoidean pedicle. The maxillary and mandibular arches are as simple as in the *Squatina*, but much stronger, since they support a series of massive grinding teeth, as well as pointed ones or laniaries. The rami of the lower jaw are confluent at the symphysis.

The Skates and Rays have the skull movably articulated, as in *Squatina*, by two basilar condyles and an intervening space, to the axis.\* The skull is flat and broad; the upper wall membranous for a greater or less extent, except in *Narcine*, where it is closed by

\* The basi-occipital also affords a small but distinct intermediate surface between the two large condyles in the *Zygana*.

cartilage. The anterior or vomerine part forms a long pyramidal rostrum, to which are articulated cartilages connecting its extremities with the radial or anterior angles of the enormously developed hand (pectoral fin): in the space between the skull and those fins, the *Torpedo* carries its electric batteries. The tympanic pedicles are short and thick; the maxillary and mandibular arches long and wide, stretching transversely across the under part of the head.

In the ordinary Sharks the anterior prolongation of the cranial cavity gives a quite anterior position, and almost vertical plane, to the fontanelle: three columnar rostral cartilages are produced, two from above, and one from between the nasal cavities, which processes converge and coalesce to form the framework of a kind of cut-water, at the fore-part of the skull. In the place of articular condyles, processes extend backwards from each side of the occipital foramen and clasp, as it were, the bodies of three or four anterior vertebræ of the trunk. The pterygoidean arches extend outwards, in *Carcharias*, from the base of the cranium, but, as in embryo osseous fishes, are confluent therewith at both ends. The maxillary arch, suspended near its closed anterior extremity to the vomerine part of the base of the skull, is thence extended backwards to the articulation of the lower jaw. A simple cartilaginous pedicle forms the upper part (pleurapophysis) of the mandibular arch, which is completed below by the lower jaw. A few cartilaginous rays diverge outwards and backwards from the pedicle, and support a small opercular flap or fin. The hyoid arch consists of a basi-hyoid and two simple cerato-hyoid cartilages; the stylo-hyoid is ligamentous, as in the *Squatina*. Short cartilaginous rays diverge from the cerato-hyoid to support the branchiostegal membrane, or hyoid fin. The scapular arch, which we shall find normally articulated with the occiput in osseous fishes, is attached thereto, at a little distance behind the head, by ligament and muscles in the sharks: from this arch, also, cartilaginous rays immediately diverge for the support of a radiated appendage or fin; the third in the series counting backwards from the tympanic or opercular fin.

The capsules of the special organs of sense are all cartilaginous: that of the ear is involved in the lateral walls of the cranium; that of the eye is articulated by a cartilaginous pedicle with the orbit; and the olfactory sacs are over-arched by the nasal processes of the epicranial cartilage.

Amongst the stranger forms in which special development radiates, in diverging from that stage of the common vertebrate route attained by the Plagiostomes, may be noticed the lateral transverse elongations of the orbital processes, supporting the eye-balls at their extremity,

and giving the peculiar form to the skull of certain Sharks, thence called "Hammer-headed" (*Zygæna*). In the Eagle-ray (*Myliobates*) a cartilage is attached to the anterior prolonged angle of the great pectoral fin, and connects it with the fore-part of the cranial (internasal) cartilage; it supports a number of branched and jointed cartilaginous rays, which project forwards, and are connected at the middle line with a like series from the opposite side of the head; they may be regarded as partial dismemberments of the great pectorals; and in *Rhinoptera Braziliensis* their supporting cartilage is directly continued from that of the pectoral fins, though it is closely attached to the fore-part of the head. These form what Müller has termed "cranial fins;" but the parts more properly meriting that name are the opercular and branchiostegal appendages of the tympanic and hyoidean arches.

Having traced in the examples of cartilaginous fishes selected for demonstration, the progressive steps by which the typical features of the ichthyic skull are modelled, as by the hand of the sculptor, in the yielding gristle, we have next to consider them with their leading varieties, as they are permanently wrought out in hard bone.

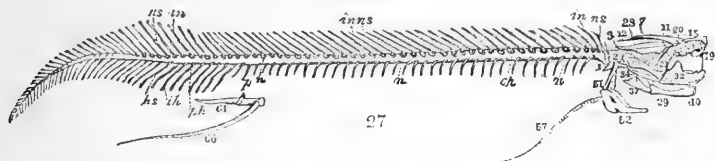
We saw that the base of the skull was first formed by the anterior prolongation of the gelatinous chorda dorsalis, and that the cranial cavity resulted from the extension of the membrane from the fibrous sheath of the gelatinous chorda over the anterior end of the nervous axis. We saw next the superaddition of special capsules for the organs of sense; and then the cartilaginous tissue developed from the basis cranii, according to a pattern common to the lowest forms of the class, and to the embryos of the higher forms which the Cyclostomes permanently represent. We saw the cartilaginous tissue acquiring a firmer texture, hardened by superficial osseous grains, or tesseræ, mounting higher upon the lateral and upper walls of the cranium, and at length entirely defending it: and we then also recognised the maxillary, mandibular, and hyoidean arches, established in a firm cartilaginous material, and on a recognisable ichthyic type.

We have next to trace the course and the forms under which the osseous material is superadded to, or substituted for, the primitive cartilaginous material of the skull in osseous fishes; and the remarkable transitional genus *Lepidosiren*, whose organisation I first made known under the name of *Protopterus* (xxxiii.), offers the most natural and instructive passage in the shape and structure of its skull, between the gristly and the bony fishes.

In the *Lepidosiren* ossification of the cranial end of the chorda dorsalis extends along the under and lateral part of its sheath, backwards to beneath the atlas and axis (*fig. 27. 1*), the posterior slightly



expanded end of this ossified part supporting, as in the *Squatina*, the neurapophyses of the atlas (*fig. 28. n*), the bases of which expand and meet above that end of the ossified chorda and below the spinal



Skeleton of *Lepidosiren annectens*.

canal. Ossification of the fibrous sheath of the chorda, commencing posteriorly at its under part (*ib. b*), ascends upon the sides as it advances forwards, and incloses it above, where it supports the medulla oblongata, and the lateral bony plates (neurapophyses) called ex-occipitals (*ib. 2*); leaving behind a wide oblique concavity lodging the anterior unossified end of the 'chorda,' which does not extend further upon the 'basis cranii.' The ex-occipitals (*fig. 27, 28. 2, 2*), expand as they ascend and converge to meet above the 'foramen magnum' which they complete. A small mass of cartilage connects their upper ends with each other, and with the overhanging backward projecting point of the fronto-occipital spine (*ib. 3*). This cartilaginous mass answers to the base of the supra-occipital in better ossified fishes: a similar cartilage connects the ex-occipitals with the occipital spine in the *Tetrodon*.



Atlas and occipital vertebra, *Lepidosiren*.

We clearly perceive in the *Lepidosiren* that ossification, advancing on the common cartilaginous mould of the plagiostomous skull, has marked out the posterior cranial vertebra, and not only its neurapophyses but also its centrum; the neural spine being left in a less completely ossified state than in the vertebræ of the trunk. The occipital pleurapophyses (scapulae, *fig. 27. 51*) are much more developed, and appear as two strong, bony, styliform appendages, articulated by a synovial capsule and joint, one on each side, to the persistent cartilaginous base of the neurapophyses (ex-occipitals), and partly to the centrum or basi-occipital. To the lower and less expanded ends of the pleurapophyses are attached the extremities of the hæmapophyses (coracoids, *fig. 27. 52*); and thus is completed the hæmal arch of the occipital vertebra, here unusually developed in relation to its office of protecting the heart and pericardium: the hæmapophyses or coracoids belong to the same category of vertebral elements as the sternal ribs which protect the heart in higher Vertebrata. The costal or hæmal arch of the occipital vertebra of the *Lepidosiren* supports an appendage (*fig. 27. 57*), projecting outwards and backwards like

the simple diverging appendages to the abdominal pleurapophyses of better ossified fishes, and like the costal appendages in the thorax of birds; but it is here cartilaginous, and consists of many segments. It forms in fact the rudiment (a solitary ray) of the pectoral fin; it is the key to the homology of the anterior or upper limbs of the higher Vertebrata, showing them to be appendages of the hæmal arch (usually called scapular) of the occipital or posterior cranial vertebra.

In the second (parietal) and third (frontal) cranial vertebrae, ossification extends along the basal and along the spinal elements, but not into the neural or lateral elements; these remain cartilaginous in continuation with the cartilage surrounding the large capsule of the internal ear. The basal ossification, representing at its posterior end the body of the atlas and the basi-occipital, expands as it advances along the base of the skull in the situation of the sphenoids, constituting the floor of the cerebral chamber, supporting the medulla oblongata, the hypophysis, the crura and lobes of the cerebrum, and terminating a little in advance of the olfactory lobes by a broad transverse margin, bounding a triangular space left between it and the converging palatine arches, which space is filled by cartilage representing the vomer. The occipital part of this basi-cranial bone may be defined by a slight transverse depression, where also terminates a median longitudinal groove, traversing the under part of the thus defined occipital portion of the bone; and indicating, like the corresponding membranous fissure in Cestracion, the primitive place of the cranial end of the chorda. The expanded sides, originally arches of the cartilaginous portion, bend down to abut against the bases of the pterygoid plates. In this expansion of the basi-sphenoid the Lepidosiren resembles the Plagiostomes and also the Batrachian Reptiles.

Two ridges rise from the upper surface of the occipito-sphenoidal plate, near its outer margin, and support the cartilaginous lateral walls of the cranium. The cranial cavity is defended above by a longitudinal bony roof (*fig. 27. 3, 7, 11*), nearly co-extensive with the bony floor beneath; the roof commences behind by the spine or point which overhangs the ex-occipitals, gradually expands as it advances, resting upon the cartilaginous walls of the cranium, is then suddenly contracted, and is united anteriorly by fibrous ligament to the ascending process of the palato-maxillary arch, and to the base of the nasal plate. A strong sharp crest or spine rises from above the whole of the middle line of the cranial roof-bone, which may be regarded as representing the mid-frontal, the parietal, and supra-occipital bones, or, in more general terms, the neural spines of the three cranial vertebrae: but this supra-cranial bone not only covers the medulla

oblongata, cerebellum, optic lobes, pineal sac, and cerebral hemispheres, but also the olfactory lobes. The lateral cartilaginous walls of the cranium are continued forwards from the acoustic capsule between the basal and superior osseous plates: the part perforated by the fifth pair of nerves, and protecting the side of the optic lobes, represents the great ala of the sphenoid: the next portion in advance, protecting the sides of the cerebral hemispheres and perforated by the optic nerve, answers to the orbital ala of the anterior sphenoid: and the cartilage terminates by a part which is perforated by the olfactory nerve, and which abuts laterally against the ascending or palatine process of the maxillary arch.

The outward extension of the lateral cartilages of the cranium downwards, in the form of a broad triangular plate, the apex of which forms the articulation for the lower jaw, is like that which we see in the Chimæra; but ossification has extended along two tracts, which converge as they descend, one (*fig. 26. 28*) from behind to the outer, the other (*ib. 23*) from before to the inner side of the cartilaginous maxillary joint, which these bony plates strengthen and support like the backs of a book. The posterior of these bony arches is obviously the homologue of the tympanic pedicle in the Squatina: the anterior bony arch as plainly answers to the pterygoid buttress in osseous fishes; but it is here confluent with the coalesced palatine and superior maxillary bones, the dentigerous part of which extends outwards, downwards, and backwards (*fig. 29. 21*), but does not reach, as in the Sharks and Rays, the mandibular joint. From the upper part of the palato-maxillary portion a compressed sharp process (*ib. 20*) ascends obliquely backwards, and terminates in a point: the inner side of this process is closely attached by ligament to the fore and outer part of the frontal portion of the epicranial bone (*ib. 11*); the outer side of the process is excavated for the reception of the outer and anterior process of the remarkable bone, which in my Memoir (xxxiii. p. 334.) I have compared with the post-frontal bone. This bone (*fig. 27. 12*), in connection with the ascending process of the maxillary (*ib. 20*), forms the upper part of the orbit, and behind this connection it sends out the post-orbital process, beyond which it extends backwards, freely overhanging the fronto-occipital, and gradually decreasing to a point, which terminates just above the occipital spine, in the position of the mastoid, in bony fishes, and giving attachment to the anterior end of the great dorso-lateral muscles of the trunk. This bone is flat above like a scale, and from its superficial position might be classed, like the similar



29. Cranial spines and upper jaw of *Lepidosiren*.

reach, as in the Sharks and Rays, the mandibular joint. From the upper part of the palato-maxillary portion a compressed sharp process (*ib. 20*) ascends obliquely backwards, and terminates in a point: the inner side of this process is closely attached by ligament to the fore and outer part of the frontal portion of the epicranial bone (*ib. 11*); the outer side of the process is excavated for the reception of the outer and anterior process of the remarkable bone, which in my Memoir (xxxiii. p. 334.) I have compared with the post-frontal bone. This bone (*fig. 27. 12*), in connection with the ascending process of the maxillary (*ib. 20*), forms the upper part of the orbit, and behind this connection it sends out the post-orbital process, beyond which it extends backwards, freely overhanging the fronto-occipital, and gradually decreasing to a point, which terminates just above the occipital spine, in the position of the mastoid, in bony fishes, and giving attachment to the anterior end of the great dorso-lateral muscles of the trunk. This bone is flat above like a scale, and from its superficial position might be classed, like the similar

bones which project freely backwards from the occiput of the *Fistularia*, with the dermal skeleton: the strong temporal muscle is attached to the two surfaces, divided by the ridge on its inferior part: it is movable up and down upon its anterior ligamentous union. In its relative position and functions, it combines the characters of post-frontal and mastoid; and, since the basilar elements of these cranial vertebræ are confluent, and their spinal elements also form one piece, (*fig. 29. 4, 11*), we may here also have an example of a similar confluence of the parapophyses of two distinct vertebræ. The mid-frontal (*ib. 11*) constitutes the anterior part of the epicranial bone, which is connected with the post-frontal and the cartilage perforated by the olfactory nerves and representing the pre-frontals.

A more remarkable and less easily determinable bone is that triangular horizontal plate (*ib. 15*), the broad posterior base of which is attached by ligament to the mid-frontal, to the post-frontal, and to the pre-frontal processes of the palato-maxillary arch; whilst the apex forms the anterior extremity of the cranium, and supports at its under part two vertical sharp-pointed teeth. I originally compared it to the combined nasal and intermaxillary bones; but I now regard the cranial structure of the *Muraenidæ*, in which the intermaxillaries are absent, and the nasal bone dentigerous, as giving the true key to the special homology of the bone in question. This nasal bone is movable, up and down, upon its basal joint, and reminds one of the similarly movable and attached appendage in the *Callorhynchus*, the free end or apex of which is beset at its under part with several small teeth.

The triangular vomerine, or prefronto-vomerine, cartilage closes the anterior and under part of the cranial cavity, and supports the origins of the olfactory nerves, which perforate it in their passage to the cartilaginous nasal capsules.

Each ramus of the lower jaw (*fig. 27. 32*) is composed of an articular and a dentary piece, the latter ankylosed together at the symphysis, and completing the inverted tympano-mandibular arch. The articular piece is a simple slender plate, strengthening the outer part of the articular concavity of the jaw, and closing the outer groove of the dentary, along which it is continued forwards to near the symphysis, where it ends in a point. The articular trochlea is formed by a persistent cartilage, which penetrates the cavity in the dentary, escapes from the fore-part of the groove on the outer surface of the dentary, and joins its fellow, in a small cartilaginous mass, which fills the hollow in front of the symphysis. The dentary piece has the notched and trenchant dentinal plate ankylosed to it, and sends up a strong coronoid process.

Behind the tympanic pedicle is the pre-opercular bone (*fig. 27. 34*), elongated, pointed at both ends, triedral, with the outer surface concave: its lower two-thirds is attached by ligament to the mandibular or tympanic pedicle. Behind and below this is an inequilateral triangular bone (*ib. 37*) closely attached by ligament to the expanded cranial end of the hyoidean arch: this I originally described as the styloid bone; it may be the homologue of the inter-opercular.\*

Only a single 'cerato-hyoid' (*ib. 40*) is ossified on each side: they complete the arch by the ligamentous junction of their lower extremities, having no intervening basi-hyal: their upper expanded ends are suspended by a short ligamentous mass to the cartilage immediately behind the tympanic pedicle.

The capsules of the organs of sense are of nearly equal size; the eye is the smallest; the nose the largest. The acoustic capsules are principally buried in the lateral cartilages of the skull; but one of the otoliths protrudes through a moderately wide hole into the cranial cavity. The eye-ball occupies the space between the pre- and post-frontals above, and the outward prolongation of the maxillary below; its capsule, the sclerotic, is cartilaginous. The nasal capsules (*ib. 19*) are also cartilaginous, with vertical slits closed by membrane; they are situated on each side and below the nasal plate.

You may perhaps think that I have been biased by the extrinsic interest of personal discovery, in dwelling so long upon the cranial structure of the *Lepidosiren*; but I persuade myself that the actual value and intrinsic importance of this remarkable type of Ichthyic organisation, will justify the time and attention we have been bestowing upon it. The skeleton of the *Lepidosiren* affords the right key to the complexities of those of the typical and better ossified fishes. I believe it to manifest, upon the whole, the highest grade which is attained in the class of Fishes, in the direct progress to perfection, or, in what may be termed the Vertebrate high road.

The true or typical osseous fishes deviate from this road into by-paths of their own, and superadd endless complexities of which we shall seek in vain for homologous parts in Reptiles, Birds, or Mammals. Therefore it is, that, on the whole, the *Lepidosiren*'s skeleton presents the closest resemblance to that of the lowest class of Reptiles, though it differs therefrom both by a little less and a little more development: the vertebral centres of the trunk, for example, have not risen above the embryonic state of soft confluence; but secondary spines have been superadded to the neural and hamal

\* Agassiz regards the pre-opercular in fishes as the homologue of the styloid.

spines; a post-frontal extends, like a bony scale, above the roof of the cranium, and over the strong temporal muscles, which are attached to the *inner* surface of that bone, as to an exo-skeleton; and one or two opercular bones are superadded behind the simple pedicle of the jaw. But the single concave surface presented by the basi-occipital to the vertebræ of the trunk, the lower transverse processes (*parapophyses*) of the abdominal vertebræ, and the articulation of the scapulo-coracoid arch to its proper cranial vertebra, afford unequivocal evidence that the *Lepidosiren* is a true Fish.

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## LECTURE V.

### THE SKULL OF OSSEOUS FISHES.

HAVING noticed the principal facts in the development of the skull in the embryo of an Osseous Fish, and the several stages at which that development is arrested, or diverted to acquire special modifications, in the Cartilaginous Fishes; and having dwelt more particularly on the instructive semiosseous, semicartilaginous skull of the *Lepidosiren*, I proceed, in the present Lecture, to the demonstration of the complex skull of the Osseous Fishes, which constitute the great bulk and the typical members of the class; and, for that purpose, I shall take one of our largest and most common species—the Cod-fish (*Gadus Morrhua*)—in which you may easily repeat the observations and test the conclusions about to be submitted to you. In describing the general form and composition of this skull, according to my views of the homologies of its constituent bones, I shall also indicate the most instructive and remarkable modifications of the skull in other Osseous Fishes, and notice those which, stopping short of the acquisition of the most characteristic features of the fish's skull, lead more directly to the cranial type of higher Vertebrata.

The head is larger in proportion to the trunk in Fishes than in any other class of animals; it forms a cone whose base is vertical, directed backwards and joined to the trunk without an intervening neck, and the sides three in number, one superior and two lateral and converging downwards: the cone is shorter or longer, more or less compressed, more or less depressed, with a sharper or blunter apex, in different species. The base of the skull is perforated by the foramen

magnum; the apex is more or less widely and deeply cleft transversely by the aperture of the mouth; the orbits are lateral, large, and usually communicating freely with one another; and there are also two lateral fissures behind, called gill-apertures, with a mechanism for opening and closing them. The mouth receives not only the food, but also the streams of water for respiration, which escape by the opercular or gill-apertures. The head contains not only the brain and organs of sense, but likewise the heart and the whole respiratory apparatus. The inferior, inverted, hæmal protecting arches are greatly developed accordingly, and their diverging or radiated appendages support membranes re-acting upon the surrounding fluid, and more or less employed in locomotion: one pair, in fact, is the homologue of the pectoral extremities in higher Vertebrata, and the sustaining (scapular) arch frequently also supports the homologues of the pelvic extremities. Thus jaws and tongue, heart and gills, arms and legs, may all belong to the head; and the disproportionate size of the skull, and its firm attachment to the trunk, required by these functions, are precisely the conditions most favourable for facilitating the movements of the fish through its native element.

It may well be conceived, then, that more numerous bones enter into the formation of the skeleton of the head of Fishes, than of any other animals. Most of these bones present the squamous character and mode of union, being flattened, thinned off, and overlapping one another like scales; and although the skull, as a whole, has less mobility on the trunk than in higher animals, more of the component bones enjoy independent movements.

The principal cavities, which are formed by this assemblage of bones, are, the 'cranium,' lodging the brain and organs of hearing; the 'orbital' and the 'nasal' fossæ; the 'buccal' and the 'branchial' canals. Few of these cavities are well defined, and in no class of animals is the exterior of the skull so broken by irregular depressions and prominent spines and protuberances. The upper surface of the cranium is commonly traversed by five longitudinal crests, intercepting four channels: the principal crest is the median one, formed by the frontal and occipital bones (*fig.* 19. 3); next to this is the pair formed by the parietals (*ib.* 7) and par-occipitals; and the lateral pair of crests is formed by the post-frontals and mastoids (*ib.* 12, 8): the intervening depressions lodge the anterior origins of the great muscles of the back and of the scapular arch: very rarely do the temporal muscles extend their attachments (as in the Conger, *Lepidosiren* and *Symbranchus*) to the upper surface of the cranium. The upper border of the orbit sometimes sends off strong

angular processes; the lower border of the orbit, when present, projects freely downwards; and the posterior border of the bony operculum is often produced backwards in the form of spines.

It would seem an almost hopeless task to attempt to arrange naturally and determine satisfactorily the numerous bones of this most complex part of the skeleton of Fishes, so as to convey as clear and tenable a knowledge of them as the Anthropotomist does of the human skull: we need but glance, indeed, at the labours which Comparative Anatomists of the highest merit have bestowed on the craniology of Fishes, in order to appreciate its difficulty, and at the same time its importance. By these labours, however, of which the best summary will be found in Cuvier's great work on Recent Fishes (XXIII. t. i.), and in Agassiz's most valuable and original History of Fossil Fishes\* (XXII.), not only has the descriptive osteology of the head of Fishes been rendered as complete and minute as that of the human skull, but it may be truly averred to be more intelligible, more philosophical, more agreeable with the natural arrangement and true signification of the series of bones of which that complex part of the skeleton is composed. It must be confessed that, in this respect, Ichthyotomy, as true anatomical science, is at present in advance of Anthropotomy.

After an attentive study of the original authors in this field of Anatomy, testing their extensive series of comparisons of the permanent forms of the skull in the higher Vertebrate classes, and the transitory foetal conditions of each, with the results of my own observations, I have been led to the following view of the craniology of Fishes.

The bones of the skull are primarily divided, in Anthropotomy, into those of the cranium and those of the face; but the proportions which these divisions bear to each other in Man are reversed in Fishes. According to this binary classification, the facial series in Fishes includes an extensive system of bones—the hyoid—of which part only, viz. the 'styloid element,' is admitted into the skull by the Anthropotomist, who describes it as a process of the 'temporal bone.' This very 'temporal,' moreover, is originally and essentially an assemblage of bones, which are always distinct in Fishes and Reptiles; and the squamous part, which enters so largely into the

\* The general results of the study of the skull of Fishes are briefly but clearly given in the recent compendiums of Comparative Anatomy, by Dr. Carus (xxxiv.), Prof. Grant (xxviii.), Prof. Rymer Jones (xxix.), and Dr. Köstlin (xxxv.). The generally accepted views of the classification and homologies of the cranial bones are those adopted in the very useful "Elements of the Comparative Anatomy of the Vertebrate Animals," by the learned Göttingen Professor (Wagner), ably translated by Mr. Tulk (Longmans, 8vo. 1845).



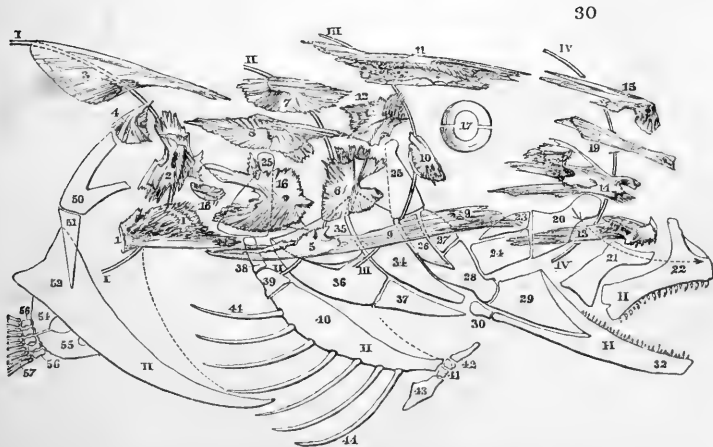
formation of the cranial cavity of man and most Mammals, has no share in its formation in the lower Vertebrata.

The two classes of cranial and facial bones, having been originally founded upon the exclusive study of the most peculiarly and extremely modified skull in the whole Vertebrate series — that of Man, — their characters, as might be expected, are artificial, and applicable to the same bones in only a small proportion of the Vertebrata; the unity of the plan pervading the organisation of which it is the business of the Anatomist, properly so called, to demonstrate.

The bones of the skull of Fishes are primarily divisible into those of

- A. Neuro-skeleton;
- B. Splanchno-skeleton;
- c. Dermo-skeleton.

A. The bones of the neuro- or proper endo-skeleton are arranged here, as in the rest of the body, in a series of horizontally succeeding segments; each segment consisting of an upper (neural) and a lower (hæmal) arch, with a common centre, and with diverging appendages. As the bones, respectively entering into the formation of these segments, are the same in relative position, and nearly the same in number, as in the typical vertebræ of the trunk — the excess arising from subdivision of peripheral elements — the same term ought to be extended to those cranial segments which has been usually restricted



Disarticulated bones of the cranial vertebrae and sense-capsules, [the hæmal arches (H, H) and appendages in diagrammatic outline,] Cod-fish, *Gadus Morrhua*.

to their neural arches, in which the typical characters of the vertebra are least departed from.

The vertebræ of the head are usually enumerated in a direction contrary to those of the trunk, because, like the vertebræ of the tail, they lose their typical character as they recede from the common centre.\* The names of the cranial vertebræ are taken from those applied in Anthropotomy to the bones composing their neural spines, and the names of the neural arches from the significant terms lately given (XXII. t. i. p. 145.), to the primary segments of the brain, which they respectively protect.

Each cranial vertebra, or natural segment of the skull, is divided into a *neural arch*, with which the centrum and parapophyses are always more immediately connected, and a *hæmal arch* with its *appendages*.

The neural arches are:—

Nos. of component bones in the Cuts.

- I. Epencephalic arch (1, 2, 3, 4);
- II. Mesencephalic arch (5 to 8);
- III. Prosencephalic arch (9—12);
- IV. Rhinencephalic arch (13—15).

The hæmal arches are:—

- i. Scapular, or scapulo-coracoid (50 to 52);
- ii. Hyoid, or stylo-hyoid (25, 38 to 43);
- iii. Mandibular, or tympano-mandibular (25—32);
- iv. Maxillary, or palato-maxillary (20—22).

The appendages of the hæmal arches are:—

1. The Pectoral (54 to 57);
2. The Branchiostegal (44);
3. The Opercular (34—37);
4. The Pterygoid (23, 24).

b. The bones of the splanchno-skeleton constitute:—

- The ear-capsule or petrosal, and otolite (16, 16'');
- The eye-capsule or sclerotic, and pedicle (17);
- The nose-capsule or æthmoid, and turbinal (18, 19);
- The branchial arches (45—49).

\* We find the leading condition of these terminal modifications of the vertebral column in the fact, that the contained nervous axis shrinks and recedes centripetally at both ends.

c. The bones of the dermo-skeleton are:—

	Nos. of bones.			
Supra-temporals	-	-	-	71
Supra-orbitals	-	-	-	72
Sub-orbitals	-	-	-	73, 73'
Labials	-	-	-	74*

#### SUPERIOR (NEURAL) ARCHES OF THE CRANIAL VERTEBRÆ.

The first series of endo-skeletal bones constitutes the axis or backbone of the skull, as the rest of the vertebral neural arches do that of the trunk; and it includes and protects the encephalon or anterior expanded extremity of the great nervous axis. The under and upper parts of the annular segments are commonly formed by single and symmetrical bones, as in the vertebral axis of the trunk; but sometimes, even in the present low class, the expansion of the cranial cavity is accompanied, not only by a transverse development, but also by a median division of the upper piece or key-bone of one or more of the protecting arches.

Though subject to various degrees of ankylosis, the cranial vertebræ always accord in number with the primary ganglions or divisions of the encephalon in Fishes. For the better understanding of this important relation, I may premise that the brain of Fishes consists of four primary divisions succeeding each other in a linear series horizontally, which, viewed from behind forwards, are:—

1. The medulla oblongata, with the superimposed cerebellum, or the 'epencephalon.'

2. The third ventricle, with its upper (pineal) and lower (hypophysial) prolongations, and the superimposed optic lobes, or the 'mesencephalon.'

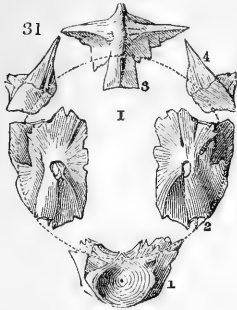
3. The cerebrum proper, or 'prosencephalon.'

4. The olfactory ganglionic or chord-like prolongation of the cerebrum, or 'rhinencephalon.'

In most osseous fishes, as in this disarticulated skull of the Cod (*Gadus Morrhua*), the bones encompassing, or in vertebral relation with, the epencephalon are six in number (*fig. 30.* and *fig. 31. 1.*).

\* In the human skull the only bones that can, with any probability, be referred to the dermal system are the 'lachrymal.' The splanchnic system is reduced to the capsules of the organs of sense, of which only those of the ear and nose are ossified. The endo-skeletal bones form the same number of neural and hæmal arches as in the fish, but that of the occipital vertebra is far removed from its centrum, and neither the mandibular nor hyoidean arches retain diverging appendages.

The first and lowest, called *basi-occipital* (*ib. 1*)\*, is a short, strong, sub-rhomboidal bone, sub-cylindrical and truncate posteriorly, where it is excavated to form the articular cavity, united by a jelly-filled capsule with the corresponding hollow cone on the fore-part of the body of the atlas; the anterior pointed end of the basi-occipital is wedged into the basi-sphenoid, fitting and filling up the deep posterior cleft of that bone. The basi-occipital supports the 'oblong prolongation,' of the spinal chord in the skull; and on each side offers a rough articular surface for sutural union with two lateral bones, the ex-occipitals (*ib. 2, 2*); behind which the basi-occipital, also, sometimes receives the



Disarticulated epencephalic arch, viewed from behind: *Gadus Morrhuua*.

anteriorly projecting base of the neural arch of the atlas, which, in the Cod, is wedged into the posterior angle between the basi- and ex-occipitals, and is firmly united to them by broad sutural surfaces.

The articular cup for the atlas varies from the deep conical excavation seen in the Carp, to the almost flat surface in the Holibut; it is extremely rare to find, as in the *Fistularia*, the basi-occipital presenting a convex surface for articulation with the body of the atlas. In many fishes the under part of the basi-occipital is expanded and excavated; in the Carp the under surface of this part forms a broad triangular plate, which supports the large upper pharyngeal grinding tooth †; in the bony Gar-fish (*Lepidosteus*) the basi-occipital develops two plates from its upper and outer angles, which complete the foramen magnum and support the ex-occipitals above.

The *ex-occipitals* (neurapophyses of the occipital vertebra, *ib. 2, 2*) present, in the Cod, the form of oblong, sub-quadrate bones, thick, and with two rough deeply indented articular surfaces below, but expanded and produced outwards above; they encircle the epencephalon, over-arching and often meeting above it, and completing the contour of the foramen magnum. They are perforated for the passage of the *nervi vagi*, sometimes for the first spinal or hypoglossal nerve; the foramina being unusually large in the Carp-

\* The synonymes and corresponding numbers and letters of the bones of the skull are given in the tabular conspectus appended to this Lecture; the numbers of the bones in the text correspond in each of the figures.

† Dentigerous processes are developed from the under part of the cervical vertebral centres in the *Coluber scaber* of Linnaeus.

tribe (*fig. 35. 2*), where they relate also to the connection of the air-bladder with the organ of hearing, by means of the ossicles *a, b, c, d,* and *e*. The ex-occipitals are immovably articulated in the Cod, below with the basi-occipital, behind with the neurapophyses of the atlas, above with the supra-occipital and the par-occipitals, and in front with the petrous bones, or acoustic capsules, intercalated between them and the alisphenoids. In a few fishes (e.g. *Fistularia*) the ex-occipitals send backwards articular processes modified to allow a slight movement upon the corresponding anterior articular processes of the neurapophyses of the atlas. Like these elements of the ordinary vertebræ of some fishes (e.g. *Lepidosiren, Thynnus, Xyphias*), the bases of the ex-occipitals expand, approximate, and in most osseous fishes, meet upon the upper surface of the basi-occipital, and immediately support the medulla oblongata; but sometimes a space is left between them, which is filled up by the basi-occipital\*, and in *Lepidosteus*, as I have just observed, the basi-occipital protects the whole epencephalon.

The *supra-occipital* (spine of the occipital vertebra, *fig. 30 & 31. 3*), of an elongated rhomboidal form in the Cod, triangular in the Carp, is articulated by an inferior cellulo-sutural surface, with the summits of the ex-occipitals and the mesial angles of the par-occipitals, completing the circle or forming the key-stone of the neural arch: it usually sends upwards and backwards a strong compressed spine from the whole extent of the middle line, and a transverse 'supra-occipital' ridge outwards from each side of the base of the spine, to the external angles of the bone. In most fishes this bone advances forwards and joins the frontal, pushing aside as it were the parietals: in *Balistes*, the produced part of the supra-occipital is even wedged into the hinder half of the frontal suture. In the Carp, on the contrary, the anterior angle of the supra-occipital is truncated, forming the base of the triangle, and is articulated by a lambdoidal suture to the parietal bones, (*fig. 35. 7*), which here meet at the mid-line of the skull, and the upper part of the occipital spine is low and flattened. The supra-occipital is also separated from the frontal by the parietals, in the Salmonoid, Clupeoid, Murænoïd, and Salamandroid fishes (*Lepidosteus, Polypterus*), and is itself divided, in *Lepidosteus*, by a median suture; these modifications tell strongly against extending the homo-

\* M. Agassiz, who has noticed a similar interspace between the summits of the ex-occipitals, as well as between the par-occipitals and sur-occipital above, observes, "On dirait alors qu'une large fente médiane entame tout l'occiput." (*Poissons Fossiles*, i. p. 118.) But this could only be affirmed correctly, if the basi-occipital were likewise divided, and separated along the median line, of which I know not any example.

logy of the supra-occipital with the supernumerary 'interparietal' bone of Mammals, beyond the anteriorly produced portion, which, however, is not developed from a separate centre in Fishes.

When the skull is much compressed, the occipital spine is usually very lofty, and in the Light-horse-man fish (*Ephippus*), expands above its origin into a thick crest of bone, giving the skull the appearance of a helmet; but in low flattened skulls the spine is much reduced, projecting merely backwards in the Pike and Salmon, and being sometimes obsolete, as in the *Remora*; in a few instances the broad posterior part of the supra-occipital articulates with the neural arch and spine of the atlas, and sometimes on the other hand, *e. g.* in the Holibut, the entire bone is pushed by the par-occipitals upon the upper surface of the skull, where it manifests the loss of symmetry by the absence of the expanded plate on the left side of the spine, which immediately articulates with the left parietal.

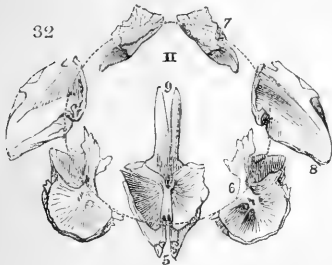
The *par-occipitals* (par-apophyses of the occipital vertebra, *fig.* 30 and 31. 4, 4), are always wedged into the angles between the ex- and supra-occipitals: they are of a sub-rhomboidal or conical form, with the base towards the cranial cavity and the apex turned outwards and backwards. The outer surface, in the Cod, is traversed obliquely by a prominent ridge, ending at the lower and hinder projecting angle: in the Carp the process is short, and comes from the middle of the outer surface.

In broad and depressed skulls the par-occipital forms a strong crest, and exceeds the ex-occipital in size: in narrow and deep skulls the proportions of these bones are commonly reversed, and the par-occipitals sometimes disappear; but in *Ephippus*, they are as large as the ex-occipitals. In the Shad the par-occipitals unite with the mastoids almost as in the *Chelonia*: and in the *Polypterus* they become anchylosed to the ex-occipitals, as in *Batrachian* Reptiles.

In *Synodus*, *Callichthys*, and *Heterobranchus*, the par-occipital is visible only at the back part, not at the upper part of the skull. The inner surface of the par-occipital, like that of the ex-occipital, is excavated for the lodgment of part of the posterior and external semicircular canal of the enormous internal organ of hearing in Fishes. The outer projecting process supports the upper fork of the first piece of the scapular arch, sometimes, as in *Ephippus*, by a distinct articular cavity. The parts of the occipital vertebra are those which are commonly in Fishes the most completely ossified at the expense of their primitive cartilaginous basis, and, in the *Polypterus*, they become anchylosed into one piece, like the occipital

bone of Anthropotomy. All the parts of the occipital vertebra are developed from or ossified in the pre-existing cartilaginous cranium.

The second ring of bones, or that which encircles the mesencephalon, includes the 'basi-sphenoid,' the 'ali-sphenoids,' the 'parietals,' and the 'mastoids' (*fig. 30. II. & fig. 32.*). The *basi-sphenoid* (centrum of mesencephalic vertebra, *ib. 5*), is always connate with the pre-sphenoid, (*ib. 9*), forming with it a long subtriedal



Disarticulated neural arch of parietal vertebra, viewed from behind: *Gadus Morrhua*.

bone (basi-pre-sphenoid\*), usually bifurcate posteriorly, and more or less expanded beneath the cranial cavity; it is then continued forwards (sometimes after sending out a pair of lateral processes, as in the Perch, more commonly without such processes) along the base of the inter-orbital space to near the fore-part of the roof of the mouth: its posterior extremity is joined by a squamous suture, as in *Diodon*, to the basi-occipital; or more commonly, as in the Cod, is firmly wedged by a kind of double gomphosis into the basi-occipital: its expanded part supports the petrosals and ali-sphenoids: the pre-sphenoidal prolongation (9) articulates with the orbito-sphenoids and the ethmoid, when this is ossified, and it terminates forwards by a cavity receiving the pointed end of the vomer. It is this portion of the basi-pre-sphenoid which manifests the loss of symmetry in the flat fishes (*Pleuronectidæ*), being twisted up to one side of the skull. The basi-pre-sphenoid varies in form with that of the head in general, being longest and narrowest in long and narrow skulls, and the converse; the whole of its upper surface is commonly rough for articulation with the petrosals and ali sphenoids; rarely does any portion enter into the direct formation of the cranial cavity, and then, perhaps, *e. g.* in the Cod, a small surface may support the pituitary sac. When it enters more largely into the formation of the floor of

\* The ossification of the basi-pre-sphenoid proceeds from a common centre; but this does not invalidate its general homology with the bodies of the second and third cranial vertebrae, as manifested by their neurapophyses (alisphenoids and orbito-sphenoids) and spines (parietal and frontal), any more than the ossification from a single centre of the common supporting bifurcate bone of the neural and hæmal spines of the caudal fin disproves the inference that that single bone represents the coalesced bodies of the terminal vertebrae to which those spines belong. The partially united radius and ulna of the frog are ossified from a common centre at their coalesced proximal ends.

the cranial cavity, it usually sends upwards a little process on each side; or, as in *Fistularia*, a transverse ridge. The basi-sphenoid is smooth below, where it is usually flattened or convex, but sometimes is produced downwards in the form of a median ridge, and sometimes is perforated for the lodgment of certain muscles of the eye-ball. In the *Polypterus* both the ali-sphenoids and orbito-sphenoids are anchylosed to the basi-sphenoid, and the result is a bone that answers to the major part of the 'os sphenoides' in Anthropotomy. As two large and important hæmal arches of the head are suspended from the parapophyses of the second and third cranial vertebræ, this seems to be the condition of the fixation and coalescence of the bodies of those vertebræ in all Fishes.

The *ali-sphenoids* (neurapophyses of the parietal vertebra, *ib.* 6. 6.) are firmly articulated by broad sutural surfaces to the expanded sides of the basi-sphenoid, above which their bases usually meet and immediately support the third ventricle or mesencephalon, or leave an interspace for its pituitary prolongation, which then rests in a cavity or 'sella' of the basi-sphenoid. In some fishes, *e. g.* Perch and Carp, the base of each ali-sphenoid rises some way above the basi-sphenoid, and then sends inwards a horizontal plate, which, meeting that of the opposite ali-sphenoid, forms the immediate support of the mesencephalon, and at the same time the roof of a canal, excavated in the basi-sphenoid, and which traverses the base of the skull, below the cranial cavity from before backwards, opening behind at the under part of the basi-occipital; this subcranial canal exists in the Salmonoids, Sparoids, Scomberoids, and is very remarkable in most fishes with lofty compressed skulls, as the *Ephippus*: it exists in some Clupeoids, as the Herring, but not in the Salamandroid Fishes. The subcranial canal resembles, but is not homologous with, being differently formed from, the posterior prolongation of the nasal passages in the Crocodiles, and it lodges some of the muscles of the eye-ball. The form of the ali-sphenoids is influenced by that of the skull: when this is low and flat, their antero-posterior exceeds their vertical extent; in deep and compressed skulls they are narrow and high plates; in ordinary shaped skulls they present either a sub-circular form, and are perforated as in the Carp (*fig.* 35. 6), or are reniform, the anterior border being deeply notched, as in the Cod (*fig.* 30. 6): they form a more definite and fixed proportion of the lateral parietes of the skull than do the petrosals (*ib.* 16), which are interposed between them and the ex-occipitals; and they have their essential function in sustaining and protecting the sides of the mesencephalon, and in affording exit to the second and third divisions of the fifth pair of



nerves. The ali-sphenoid articulates in the Cod with the petrosal posteriorly, with the orbito-sphenoid anteriorly, and with the mastoid and post-frontal above. Where the ali-sphenoids have a greater relative size, as in the Perch, and where the less constant petrosal decreases or disappears, their connections are more extensive; they then reach the ex-occipitals, and sometimes even join a small part of the basi-occipital. In the incompletely ossified skulls of some fishes, *e. g.* the Pike and the Salmon tribe, the basal and lateral cranial bones are lined by cartilage, which forms the medium of union between them, especially the lateral ones: in better ossified fishes, *e. g.* the Cod, the union of the ali-sphenoids is by suture, partly dentated, partly squamous. In the Cod the second and third divisions of the trigeminal nerve pass out of the cranium by the anterior notch; in some other fishes they escape by foramina in the ali-sphenoid: a part of the vestibule and the anterior semicircular canal of the acoustic labyrinth usually encroach upon its inner concavity, whence some have deemed it to be the petrous bone.\*

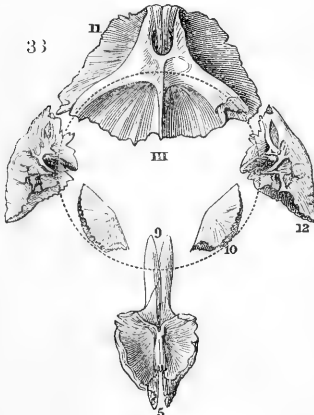
The *parietals* (spine of mesencephalic arch, *figs.* 30. 32. 7), which complete above the osseous cincture of the most expanded segment of the brain in fishes, are most commonly two in number: in the Cyprinoid (*fig.* 35. 7) and Salamandroid fishes they meet and unite by a sagittal suture; in the Salmonoids they soon coalesce; and in some Siluroids not only with each other but also with the supra-occipital: in the Pike, the Perch, the Cod, and most osseous fishes, the parietals are separated from one another by the anterior prolongation of the supra-occipital. They are always flat, and present much smaller proportions than in the higher classes of Vertebrata. They are commonly articulated to the mastoids outwardly and below, to the supra-occipital above, to the frontal before, and to the par-occipital behind; sometimes, but rarely to the ali-sphenoids, and in a few fishes, as the Pike and Gurnard, where the parietals are more than usually developed, they appear upon the hinder as well as the upper surface of the skull. In some fishes they are perforated by the *nervus lateralis* which supplies the vertical fins. The left parietal is broader than the right in the Holibut and some other flat fishes (*Pleuronectidae*). The parietals are ossified in and from the perichondrium and continuous membrane closing the great fontanelle of the primitive cartilaginous cranium.

The *mastoids* (parapophyses of the parietal vertebra, *ib.* 8) bear

\* As, *e. g.* Meckel, Wagner and Hallman (*Vergleichende Osteologie des Schläfenbeines*, p. 55.). Köstlin, who approves of this view, gives, however, the name of posterior ali-sphenoid (*hintern schläfen-flugel*, xxxv, p. 315.) to the petrosal.

the same relation to the mesencephalic bony girdle, which the par-occipitals do to the epencephalic one behind: and they project outwards and backwards further than the par-occipitals, forming the second strong transverse process at each side of the cranium. This process is developed from the outer margin of the mastoid; the inner side of the bone is expanded, and enters slightly into the formation of the walls of the cranial or rather the acoustic cavity, its inner, usually cartilaginous, surface lodging part of one of the semicircular canals.\* It is wedged into the interspace of the ex- and par-occipitals, the petrosal, the ali-sphenoid, the parietal, the frontal and post-frontal bones. The projecting process lodges above, the chief mucous canal of the head, and below affords attachment to the epitympanic, or upper, piece of the bony pedicle from which the mandibular, hyoid, and opercular bones are suspended: its extremity gives attachment to the strong tendon of the dorso-lateral muscles of the trunk. The mastoid is ossified in and from the primitive cartilaginous wall of the cranium.

The basal piece of the third cranial cincture, which defends the prosencephalon, is formed by the *pre-sphenoid* (centrum of the frontal vertebra, *figs.* 30. 33. 9) already described as connate with or produced from the basi-sphenoid. The sides of the prosencephalon are defended by the *orbito-sphenoids* (neurapophyses of the frontal vertebra, *ib.* 10): these are osseous plates, usually of a square shape, sometimes semicircular or semi-elliptic, as in the Cod; larger in the Malacopteri (*fig.* 35. 10) but very small, usually, in Acanthopteri, and sometimes represented by a descending plate of the frontal, as in the Garpike, or by unossified cartilage, as in Mail-cheeked fishes. They are occasionally separated from the pre-sphenoid by the ali-sphenoid, to which they are articulated below and behind, whilst above they are joined to the frontal and post-frontal, completing the anterior part of the lateral walls of the cranium.



Disarticulated neural arch of frontal vertebra, viewed from behind: *Gadus Morrhuæ*.

\* The great cavity, 'otocrane,' which the ex-occipital, par-occipital, ali-sphenoid, mastoid, and sometimes the parietal and supra-occipital form for the lodgment of the cartilaginous or osseous proper acoustic capsule, 'petrosal,' of the great labyrinth of fishes, may be compared to the accessory cavity or orbit, which lodges the cartilaginous or bony capsule, 'sclerotic,' of the organ of vision.

in the Carp their bases meet, like those of the ali-sphenoids, above the sphenoid: when osseous matter is developed in the interorbital septum the orbito-sphenoids are articulated by their under and anterior part to that bone or bones.\* The olfactory nerves pass out of the skull by the superior interspace of the orbito-sphenoids, and the optic nerves by their inferior interspace, or by a direct perforation; and the essential functions of the orbito-sphenoids relate to the protection of the sides of the cerebrum or prosencephalon, and to the transmission of the optic nerves. The orbito-sphenoids frequently bound or complete the foramen ovale.

The *frontal* or mid-frontal bone, (spine of the prosencephalic arch, *ib.* 11), completes the prosencephalic arch above, as the supra-occipital does that of the epencephalon; but it always enters into the formation of the cranial cavity, though its major part forms the roof of the orbits, which accessory function is the chief condition of the great expanse of this neural spine in fishes. Single, and sending up a median crest in the Cod, the Ephippus, and some other fishes, the frontal is more commonly divided along the median line, the divisions having the form of long and broad sub-triangular plates; narrower in the lofty compressed skulls, smaller in those with large orbits, and becoming greatly expanded in the fishes with small and deep-set eyes. The frontals rest in a small part of their extent upon the orbito-sphenoids, but are more constantly articulated anteriorly, to the nasal and pre-frontals, and posteriorly, with the post-frontals, the parietals, the mastoids, and frequently also with the supra-occipitals: each frontal sends up its own crest in the Tunny †, the interspace leading to a foramen, penetrating the cranial cavity in front of the single occipital spine: a larger fontanelle exists in the Cobitis and some Siluroids between the frontal and parietal bones. In the Salamandroid fishes (e.g. *Polypterus*) each frontal sends down a vertical longitudinal plate, which rests directly upon the anterior prolongation of the sphenoid, and intercepts a canal along which the olfactory nerves are continued forwards to the prefrontals: the lateral parietes of this canal thus form not only a complete, but a double bony partition between the orbits. ‡ In the Shad a corresponding descending plate takes the place of the orbito-sphenoid. In most Acanthopteri an olfactory groove is formed by shorter vertical descending plates from the under surface of the frontal. The mid-frontal is single in the *Pleuronctide*, but

\* The specially developed interorbital septum or cranial æthmoid of Cuvier in the Bream and Carp misled Bojanus into the belief that it was the body of the prosencephalic vertebra (vertebra optica).—*Isis*, 1818, p. 502.

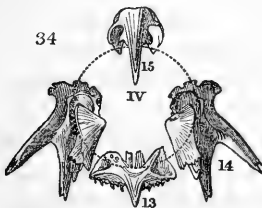
† Reminding one of the double spine of the neural arch of the atlas in *Tetradon*.

‡ xxii., t. iv. p. 122.

has undergone more modification than any of the preceding bones in connection with the general distortion and loss of symmetry of the head: in the *Holibut* the right posterior angle is truncated, and the rest of that side scooped out, as it were, to form the large orbit of the right side: the left side of the bone retains its normal form: a median crest, a continuation of that upon the supra-occipital, divides the two sides. The frontal is developed in and from the perichondrium and the membrane closing the upper fontanelle in the primitive cartilaginous cranium.

The *post-frontals* (parapophyses\* of the frontal vertebra, *figs.* 30. 33. 12, 12) obviously belong to the same category of vertebral pieces as the mastoids, whose prominent crest they partly underlie and complete, lending their aid in the formation of the single (*e. g.* Cod, Salmon), or double (*e. g.* Pike) articular cavities for the tympanic pedicle: like the mastoids they are ossified in and from the primitive cranial cartilage; and their inner surface is expanded, but this less frequently enters into the formation of the cranial cavity: they form the posterior boundary of the orbit; are articulated below to the orbito-sphenoid and ali-sphenoid, above to the frontal, and by their posterior and upper surfaces to the mastoid. The area included by the prosencephalic cincture is widely open anteriorly, corresponding with the great anterior membranous fontanelle in the Sharks, but this relates more essentially to the fact of the true cranial or neural canal not being terminated by the frontal vertebra.

The circle of bones† which completes the axis of the skull anteriorly, and protects the olfactory chords or ganglions, consists of the 'vomere' below, the 'pre-frontals' laterally, and the 'nasal' above (*fig.* 34.).



Disarticulated neural arch of nasal vertebra: viewed from behind. (*Gadus Morrhua*.)

The *vomer* (centrum of nasal vertebra, *figs.* 30. and 34. 13) is thick and expanded anteriorly, slender, and terminating in a point posteriorly, where it is wedged into the under part of the pre-sphenoid; its antero-lateral angles are articulated to the pre-frontals; its upper surface supports the nasal bone, sometimes immediately, sometimes by an intervening ethmoidal cartilage.

\* The position of the transverse processes [par-occipitals, mastoids, and post-frontals] of the foregoing cranial vertebræ, would seem to indicate them to be upper ones (diapophyses) rather than lower ones (parapophyses); but I know not any example of diapophyses developed as independent, autogenous, vertebral elements; and we see the parapophyses of the trunk gradually ascending in position, as they advance towards the head, in fishes.

† The "vertebra olfactoria" of Bojanus, who, however, regards the spine as the "lamina media ethmoidei."

The palatine bones abut against the expanded anterior part of the vomer, the under side of which commonly supports teeth. The left ala of the anterior end of the vomer is chiefly developed in the Holibut and other flat fishes. In the *Lepidosteus*, the vomer is divided into two by a median cleft. Although its posterior end joins obliquely to the under part of the pre-sphenoid, it is not, therefore, less a continuation of the basi-cranial series than is the post-sphenoid, which joins in a similar manner with the basi-occipital.\* In the *Lepidosiren*, we have seen the basi-sphenoid confluent with the basi-occipital; in the *Polypterus* it is confluent with the vomer.

The *prefrontals* (neurapophyses of the nasal vertebra, *ib.* 14) defend and support the olfactory prolongations of the cerebral axis, give passage to these so-called 'olfactory nerves,' bound the orbits anteriorly, form the surface of attachment or suspension for the palatine bones, and through these for the palato-maxillary arch: they rest below upon the pre-sphenoid and vomer, support above the fore part of the frontal and the back part of the nasal bones, and give attachment to the large antorbital or lachrymal scale-bone, when this exists: they are always ossified in and from pre-existing cranial cartilage.

Such are the essential characters of the bones which Cuvier has called 'frontaux antérieures'† in Fishes, and to which I shall apply the name of 'prefrontal' in all classes of Vertebrate animals. In the Cyprinoids, and most Halecoids, the prefrontals form part of an interorbital septum. When ankylosis begins to prevail in the cranial bones of Fishes, the prefrontals manifest their essential relationship to the vomerine and nasal bones by becoming confluent with them: thus we recognise the prefrontals in the confluent parts of the nasal vertebra of the Conger, by the external groove conducting the olfactory nerves to the nasal capsules, and by the inferior process

\* Straus, however, argues it to be an appendage from that mode of union (xxxvi. t. i. p. 333.).

† "Deux frontaux antérieures, qui donnent passage aux nerfs olfactifs, ferment les orbites en avant, s'appuyent sur le sphénoïde et le vomer, et donnent attache par une facette de leur borde inférieure aux palatins." (*Leçons d'Anat. Comp.* ii. 1837, p. 606.) Compare this enunciation of the essential characters of the anterior frontals with Cuvier's descriptions of the bones to which he applies that name in other classes, and with the variable determinations of the same bones by other anatomists — *le lacrymal*, Geoffroy and Spix; *lamina cribrosa ossis ethmoïdei* of Bojanus; *seitliche reichheine*, Meckel, Wagner. Without at present entering into the respective merits or demerits of these determinations, I shall only state that the prefrontals, under whatever names they are described, are essentially the neurapophyses of the nasal vertebra, and that the failure in the attempt to determine the special homologies of these bones may, in every case, be traced to the non-appreciation of their true general homology.

from which the palatine bone is suspended.\* In the *Muraena*, also, the prefrontals are plainly confluent with the nasal bone, and form the well-marked articular surfaces for the palato-maxillary bone. In some fishes a process of the prefrontal circumscribes the foramen by which the olfactory nerve finally emerges from the anterior prolongation of the cranio-vertebral canal. In the Carp the olfactory nerve traverses a deep notch on the inner side of the prefrontal (*fig. 35. 14*). In the Cod the palatine arch is chiefly but not wholly suspended to the prefrontals. The right prefrontal is the smallest in the unsymmetrical skulls of the flat-fishes.

The *nasal bone* (spine of the rhinencephalic arch, *figs. 30. and 34. 15*) is usually single, and terminates forwards in a thick obtuse extremity. In some fishes, as the *Salmonidae*, the nasal is broad, but not deep: in *Istiophorus* it is long and narrow: in the *Discoboles* and *Lophobranchii* it is a short vertical compressed plate: it is altogether absent in the *Lophius*, or is represented here, as in the *Diodon*, by a fibrous membrane, retaining the primitive histological condition of the skeleton. It is articulated above and behind to the frontal and prefrontals, and below either directly or by a vertical cartilage, as in the Cod, to the vomer. In the Flying Gurnard the nasal has no immediate connection with the vomer; but this is a rare exception. In most fishes the nasal cavity is more completely divided by the nasal bone into two distinct lateral fossæ than in any other class of Vertebrates.

The backward prolongation of the usually cartilaginous, sometimes membranous interorbital septum, in which one (*Cyprinus*, *Gadus*) or more (*Perca*) osseous plates may be present, intervenes between and more immediately supports the olfactory nerves. In the Salamandroid Fishes the nasal is divided by a median suture. The horn-like projection from the fore part of the skull of the *Naseus unicornis* is formed chiefly by a process of the frontal bone, to the under part of which a small nasal is articulated with a trifid anterior end, the lateral divisions of which articulate with the premaxillaries, as in *Citharinus*. The anterior end of the nasal is deepest in those Fishes which have a small maxillary arch suspended from the cranial axis by vertical palatines, and which have a large basi-cranial canal.

The turbinate bones (*fig. 30. 19*), or osseous capsules of the nose, are situated at the sides or above the nasal: the pre-maxillary and the maxillary bones are usually attached to its extremity through the

\* In the Conger, Cuvier<sup>1</sup> recognises the prefrontals as persistent cartilages.

<sup>1</sup> Op. cit. p. 255.

medium of a symmetrical cartilage\*, which is articulated with the fore part of the nasal bone, and extends forwards to the interspace of the upper ends of the pre-maxillaries. This 'pre-nasal' cartilage often forms a septum between the two 'ossa turbinata': it is partially ossified in the Carp.

In the *Muraenida* the normal elements of the fourth or rhinencephalic vertebra coalesce into a single bone: the pre-frontals or neurapophysial elements are plainly manifested, as has been already observed, by the articular surfaces which stand out in front of the orbits for the suspension of the palato-maxillary arches: the spine or nasal bone forms the usual obtuse expansion at its anterior extremity, immediately beneath the skin of the upper part of the snout, and it supports teeth, as in the *Lepidosiren*: it is intimately confluent anteriorly with the centrum or vomer, the limits being indicated by the interruption of the median series of vomerine and nasal teeth.

#### SENSE-CAPSULES.

The sense-capsules are so intercalated with the neural arches, which are modified to form cavities or orbits for their reception, that the demonstration of the skull will be best facilitated by describing them before we proceed to the hæmal arches of the cranial vertebra.

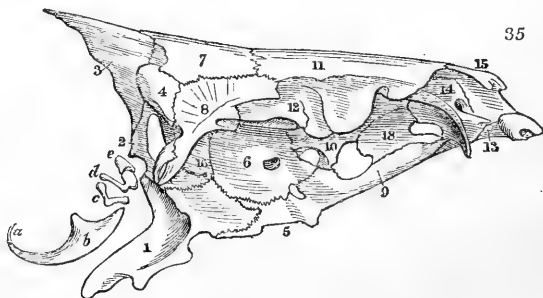
Acoustic capsule, or *Petrosal*† (*fig.* 30. 16).

We have seen that the first developed cartilage upon the primitive membranous walls of the skull forms a special protecting envelope for the labyrinth, which alone constitutes the organ of hearing in Fishes (*Ammocetes*, *fig.* 24. 16). In the progressive accumulation of cartilaginous tissue upon the base and sides of the cranium, the ear-capsule loses its individuality, and becomes buried in the common thick basi-lateral parietes of the cranium. It is blended with that persistent cartilaginous part of the skull in the *Lepidosiren*; but, in the better ossified Fishes, when the osseous centres of the neurapophyses of the cranial vertebrae begin to be established in that cartilaginous basis, a distinct bone is likewise, in most cases, developed for the more express defence of the labyrinth. Since, however,

\* This is regarded by some homologists as the body of a fifth cranial vertebra; but from its relations to the nasal bone it would have better claims to be considered the spine of such, if there were sufficient grounds for admitting vertebral segments beyond the nasal one: and the cephalic region of the skeleton might well differ, like the cervical and other regions, in the number of its vertebral segments; but I have not found good evidence of such variation.

† *Rocher*, Cuvier; *rupéal*, Geoffroy; *pars petrosa ossis temporis* of Anthropotomy. The nature of the 'os petrosum' as an envelope of the acoustic bulb, and its serial homology with the sclerotic capsule of the optic bulb, are clearly enunciated by Professor de Blainville, in the first part of his great "Ostéographie," 4to. 1839, pp. 13. 22.

functions are less specialised, less confined to the particular organ ultimately destined for their performance in the lower than in the higher classes, we find in Fishes several bones taking part with the special acoustic capsule in the lodgment of the labyrinth; and it is only in the higher Vertebrata that the capsule, under the name of the 'petrous bone,' entirely and exclusively envelopes the labyrinth. Its ossification commences later than that of the cranial neurapophyses, in the series of Osseous Fishes: there are species (*e. g.* Pike) in which, after the ex-occipitals, ali-sphenoids, and orbito-sphenoids have received their destined amount of ossification, the petrosal still remains in the cartilaginous state: it is very small, yet nevertheless exists in the Carp (*fig. 35. 16*) and Bream, where Cuvier and Bojanus\* describe it as a dismemberment of the mastoid: in the Perch, however, where the petrosal is a little better developed than in the Carp, Cuvier recognises its true homology: it is somewhat larger in the flat-fish (*e. g.* Holibut), and in the Cod tribe attains an equal size with the ali-sphenoid, which it resembles in form, except that the notched margin is posterior (*fig. 30. 16*). Here it forms the posterior lateral wall of the cranium; articulates below with the basi-occipital and basi-sphenoid, above with the mastoid and par-occipital, behind with the ex-occipital, and before with the ali-sphenoid: it supports the cochlear division of the labyrinth containing the otolites. The cavities (otocranes) lodging the petrosals and organs of hearing are completely separated from each other, and are formed, on each side, by the ex-occipital, par-occipital, ali-sphenoid, mastoid, and post-frontal: they are sometimes closed externally, but open widely into the cranial cavity.



Cranium of a Carp.

The optic capsule, or sclerotic, (*fig. 30. 17*) like the acoustic capsule, is cartilaginous in all Chondropterygians, and also in the semi-ossaceous fishes, as the *Lepidosiren*, the *Lophius*, the *Lophobranchs* and *Plectognathes*. In most osseous fishes it is bony, and commonly

\* xxxvi. p. 504. tab. 7. figs. 1. and 5. 16.



consists of two hollow hemispheroid pieces, each with two opposite emarginations; the inner ones circumscribing the hole, (analogous to the meatus internus of the petrosal,) for the entry of the nerves and vessels to the essential parts of the organ of vision; and the outer or anterior emarginations supporting the cornea. As this part of the skeleton of the head retains its primitive fibro-membranous condition in Man and Mammalia, it is called the sclerotic coat of the eye; and the osseous plates developed in it in Birds, many Reptiles, and Fishes, are termed 'sclerotic bones.' It bears, however, the same essential relation to the vascular and nervous parts of the organ of sight, which the petrous bone does to the organ of hearing, and which the turbinate bones do to the organ of smell: the persistent independence of the eye-capsule, which has led to its being commonly overlooked as part of the skeleton, relates to the requisite mobility and free suspension of the organ of vision. In the Cartilaginous Fishes, however, it is articulated by means of a pedicle with the orbito-sphenoid. The osseous cavity or 'orbit' lodging the eye-ball is formed by the pre-sphenoid, orbito-sphenoid, frontal, post-frontal, pre-frontal, and palatine bones: it opens widely outwards, where it is, often, further circumscribed by the chain of 'sub-orbital' scale-bones below, and, but less frequently, by a supra-orbital bone above. The bony orbits in most fishes communicate freely together, or rather with that narrow prolongation of the cranial cavity lodging the olfactory nerves: but, in many *Malacopteri*, e. g. the Shads and *Erythrinus*, the *Citharinus* and *Hydrocyon*, the *Synbranchus*, and the genus *Cyprinus* (fig. 35. 18), an osseous septum divides the orbits. In the *Lepidosteus* and *Polypterus* the orbits are divided by a double septum, forming the proper walls of the olfactory prolongation of the cranium, as we shall find to be the case in the Batrachia.

The bony capsules of the organ of smell present the same division into cranial and nasal (*ethmoidal*, fig. 35. 18, *turbinal*, fig. 30. 19) portions, in Fishes as in Man, and, as in Man likewise, other bones, the vomer and nasal, for example, contribute an accessory protective function. All the parts of the proper capsule are cartilaginous in cartilaginous and semi-osseous fishes; the ethmoidal part continues cartilaginous in many osseous fishes, closing the fore part of the cranium, assisting to form the interorbital septum, and contributing to support the olfactory nerves in their exit from the skull. When ossification is established in the ethmoidal cartilage, it is usually confined in fishes to the cranial end, forming there a single symmetrical, slender, bifurcate or sub-quadrate piece, usually perforated by the olfactory nerves; but never in two distinct pieces corresponding to the two

nerves. The ethmoid forms a slender vertical compressed plate, expanded and bifurcate above, in the Perch: it is a broader and larger plate, bent upon itself, with the concavity upwards, in the Cyprinoid (*fig. 35. 18*) and Siluroid Fishes, where it articulates below to the pre-sphenoid, behind and above to the orbito-sphenoids, and above and before to the frontals and prefrontals, and forming the chief part of the interorbital septum.\*

The cartilaginous capsules of the terminal or pituitary expansions of the organ of smell are, proportionally, large in the Chondropterygians and the Lepidosiren. They form a single tube, with interrupted cartilaginous parietes, like a trachea, in several of the Cyclostomes; and the interposed membranous slits are present in the Lepidosiren (*fig. 27. 19*), where, as in all the higher fishes, the olfactory capsules cease to be confluent, as the ethmoid is, but form a pair.

The *turbinals* (*fig. 30. 19*), or bones which are developed for the more immediate support of each olfactory capsule, in osseous fishes, are generally thin, more or less elongated, and turbinated scales, situated at the sides of the nasal bone and of the ascending processes of the premaxillaries; usually free, but in the Gurnards articulated with the prefrontals and nasal, and in the Cock-fish (*Argyrciosus*) suspended above the nasal bone, from the anterior prominence of the frontal spine.

#### INFERIOR (HEMAL) ARCHES OF THE CRANIAL VERTEBRÆ.

These, though apparently more numerous than the vertebral centres,

\* Oken and Bojanus regarded the ethmoid as the body or centrum of their third (anterior) cranial vertebra; and M. Agassiz, combating the vertebral theory of the skull, says—“Ainsi que serait dans cette hypothèse, le sphénoïde principal, les grandes ailes du sphénoïde, et l'ethmoïde, qui forment pourtant le plancher de la cavité cérébrale? Des apophyses? Mais, les apophyses ne protègent les centres nerveux que du côté et d'en haut. Des corps des vertèbres? Mais ils se sont formés sans le concours de la corde dorsale; ils ne peuvent donc pas être des corps des vertèbres.” (*Poissons Fossiles*, t. i. p. 229.) The ethmoid, however, forms the anterior wall, rather than the floor of the cranium; and since it is related in all Vertebrata to the support and protection of the olfactory organ, it enters into the category of the ‘Capsules of the organs of special sense,’ with the petrous and sclerotic bones, and not into that of the neural arches or vertebral coverings of the cerebro-spinal axis. The argument of M. Agassiz would be good, if change of position involved an essential distinction of a bone, *i. e.* a different homology, and a consequent change of name; but M. Agassiz finds no difficulty in determining the frontal and the parietal bones in all bony fishes, notwithstanding their variety of proportion and position. Therefore, in determining and expressing their special homology, by the arbitrary names borrowed from Anthropotomy, why should not their general homology as spines of the prosencephalic and mesencephalic vertebræ respectively be recognised? If M. Agassiz could show modifications of the relations of the frontal and parietal bones, so that they thereby ceased to be recognisable as such, then also their more essential and general characters might be so obscured as to afford grounds for rejecting their vertebral homologies.

correspond with them and the neural arches, and are essentially four in number in the osseous fishes; viz. the 'palato-maxillary,' the 'tympano-mandibular,' the 'hyoidean,' and the 'scapular.' Most fishes have, likewise, appendages, which diverge or radiate from these arches. A special (visceral) system of bony arches, called 'branchial,' also persists in fishes, for the support and movements of the gills.

*Palato-maxillary Arch* (*fig. 30. H, IV, 20, 21, 22*).

I am induced to regard this as essentially one arch, from its condition in the *Lepidosiren* and *Plagiostomous* fishes, and from the circumstance of its being completed or closed at one point only, viz. where the premaxillaries meet or coalesce. The palatine bones are the piers of this inverted arch, and their points of suspension are their attachments to the prefrontals, the vomerine and the nasal bones. The arch is completed by the maxillary and premaxillary bones, the symphysis of the latter forming its apex; and it is inclined forwards, nearly or quite parallel with the base of the skull; which, in most fishes, extends to the apex of the arch, and in some far beyond it, being usually more or less closely attached to it. In air-breathing Vertebrates the arch is more dependent, circumscribing below the nasal or respiratory canal. The pterygoid bones project backwards and outwards as the appendages of the palato-maxillary arch. Both maxillary and intermaxillary bones tend by their peculiar development and independent movement in bony fishes to project freely outwards, downwards, and backwards. We find, at least, that the general form, position, and attachments of the single and simple palato-maxillary arch, in the *Lepidosiren* or *Cestracion*, are represented in most osseous fishes, by their several detached bones, the names of which have been just mentioned, and which I shall now proceed to point out and describe as they recede from the parts of the vertebra to which they are suspended; taking as before the Cod-fish as the type.

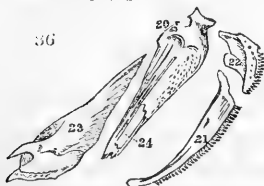
The *palatine* (pleurapophysis of nasal vertebra\*, *fig. 30. 20*) is an inequilateral triangular bone, thick and strong at its upper part, which sends off two processes; one is the essential point of suspension of the palato-maxillary arch, and articulates with the prefrontal and vomer at their point of union; the other is convex, and passes forwards to be articulated to a concavity in the superior maxillary, to which, in all Fishes, it affords a more or less movable

\* To Bojanus belongs the merit of having first enunciated this general homological relation, in his description of tab. xii. fig. † 4. of his famous monograph. "Os palatinum, seu costa corpori hujus vertebrae (æthmoidalis seu capitis quartæ) appensa." (*Anatome Testudinis Europææ*, p. 44.)

joint. In the Parrot-fishes and Diodons the articulation is quite analogous to that of the mandible below with the tympanic pedicle. In the Salamandroid fishes it is a fixed suture. In the Shad the palatine articulates with the premaxillary as well as the maxillary. In the Mormyrus the palatines meet, and unite together at the median line. The posterior angle of the base of the palatine is attached, in the Cod, by short and strong ligaments to the prefrontal. The thin posterior and inner border of the bone is joined by ligament to the ento-pterygoid, and its outer angle is dovetailed into the pterygoid. The palatine contributes to form the floor of the orbit and the roof of the mouth; in many fishes it supports teeth, but is edentulous in the Cod. It varies much in form in different species; is slender and elongated in the wide-mouthed voracious fishes, as the Pike, and is short and broad in the broad-headed, small-mouthed fishes.

The *maxillary* (hæmapophysis of nasal vertebra, *fig. 30. 21*) is usually a small edentulous bone\*, concealed in a fold of the skin between the palatine and premaxillary: it lies, in the Cod, posterior to and parallel with the premaxillary, which it resembles in form, but is longer and thinner in most osseous fishes: the expanded and bifurcate end of the maxillary is produced inwards rather than upwards, and forms a socket on which the ascending or nasal process of the premaxillary glides; a posterior tubercle at this end is attached to the palatine, and ligaments connect the same expanded end to the nasal, the turbinal, the vomer, and the premaxillary: the lower and hinder expanded end of the bone is attached by strong elastic ligament, in which a labial gristle is developed, to the coronoid process of the lower jaw.

In the Salmon tribe the maxillary is joined to the hinder and lower end of the short premaxillary, forming with it a continuous arch, and it supports teeth; this normal and higher character of the maxillary † prevails also in the Clupeoid fishes, and is here illustrated in the great *Sudis* (*fig. 36*). In the *Plectognathi* (Globe-fish and File-fish), the maxillaries coalesce wholly or in part with the premaxillaries. In the *Lepidosteus* the contrary condition prevails: the premaxillary and maxillary bones constitute, indeed, a single dentigerous arch or border of the upper jaw, but are subdivided



Disarticulated bones of palato-maxillary arch (*Arapaima gigas*).

\* The *Os mystaceum* of ichthyotomists.

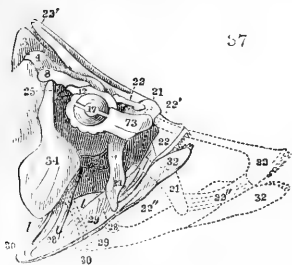
† Cuvier first recognised the special homology of the 'os mystaceum' by observing its modifications in the salmon.

into many bony pieces, a condition which seems to have prevailed in some of the ancient extinct Salamandroid fishes; for example, the genus of the Old-Red-Sandstone, which I have called *Dendrodus*. In the *Polypterus* the maxillary is large and undivided on each side; it supports teeth, and sends inwards a broad palatine plate to join the vomer and the palatine bone; thus acquiring a fixed position and all the normal features of the bone in higher animals. The maxillary bone is very diminutive in the Siluroid fishes, and appears, with the premaxillary, to be entirely wanting in certain Eels (*Muraenidae*).

The *premaxillary*, or intermaxillary bone (hæmal spine of nasal vertebra, *fig.* 30, 22), one of a symmetrical pair in the Cod and most other osseous fishes, is moderately long and slender, slightly curved, expanded and notched at both extremities: the anterior end is bent upwards, forming the nasal process, and is attached by lax ligaments to the nasal bone and prenasal cartilage, to the palatine, and to the anterior ends of the maxillary bones. The premaxillaries are movably connected to each other by their anterior ends; the nasal processes are separated by the prenasal cartilage, the lower or outer branches project freely downwards and outwards: the labial border of each premaxillary is beset with teeth, whilst the maxillary bone is quite edentulous in most osseous fishes, as in the Cod. By those who may regard the prenasal cartilage as a vestige of a fifth cranial vertebra the premaxillaries may be viewed as its inferior arch: but such an arch would be incomplete, widely open; the piers or crura diverging, instead of converging, to unite, like other inferior or hæmal arches. In the *Diodon* the premaxillaries and their lamellated dental apparatus coalesce and constitute a single symmetrical beak-shaped bone: Müller also found a single premaxillary in the *Mormyrus*. The confluent premaxillaries constitute the sword-like anterior prolongation of the snout in *Xiphias*, and are firmly and immovably articulated with the pre-nasal and maxillary bones, in both the Sword-fish and the Garpike. The premaxillaries are commonly more extended in the transverse than in the vertical direction, which latter most prevails in Mammals: but there are many examples in Fishes where their development is equal in both directions. The vertical extension, which forms the nasal branch of the premaxillary, is of unusual length in the fishes with protractile snouts, as, for example, in the Picarels (*Menidae*), the Dorics (*Zeus*), and in certain Wrasses, as *Coricus*, and especially the *Epibulus*, or *Sparus insidiator* of Pallas (*fig.* 37, 22).\*

\* See Cuvier and Valenciennes, *Hist. des Poissons*, t. xiv. p. 92. The hypotympanic or suspensory pedicle of the lower jaw is there called the 'malar' bone.

the intermaxillary (*ib.* 22') plays in a groove on the upper surface of the skull, and reaches as far back as the occiput when the mouth is retracted.



Mechanism of protraction and retraction of the mouth (*Epibulus insidiator*).

The descending or maxillary branch is attached by a ligament (*ib.* 22''), longer than itself, to the lower end of the maxillary bone (*ib.* 21.), and consequently draws forwards that bone, together with the lower jaw, to which the same end of the maxillary is attached by ligament, when the long nasal branch of the premaxillary glides forwards out of the epicranial groove in which it usually lies.

The protractile action is further favoured by a peculiar modification of the hypo-tympanic (*ib.* 28), which, by its great length and movable articulation at both ends, co-operates with the long premaxillary in the sudden projection of the mouth, by which this fish seizes the small, agile, aquatic insects that constitute its prey. In the *Lophius* the nasal processes of the premaxillaries enter a groove in the frontal: in the *Uranoscopus* they also reach the frontal, playing upon the small nasal bone and pressing it down, as it were, upon the vomer. In the *Dactylopterus* they penetrate between the nasal and the vomer, and play in the cavity of the rhinencephalic arch.

The small bony piece situated above the maxillary in some Halecoids (Trout, Herring) and Lucicoids (Pike) seems to belong to the series of mucous or scale bones: the Flying Gurnard (*Dactylopterus*) has two delicate cartilages in a similar position, and the *Sciæna aquila* a large labial cartilage in the angle of the mouth, attached to the lower jaw.

The *Diverging Appendage* of the palato-maxillary arch consists, in Fishes, of the pterygoid and entopterygoid bones, which, as they are the least important parts of the arch, so are they the least constant: they are wanting, for example, in the *Synodon*, *Platystacus*, *Hydrocyon*, and *Lophius*; are connate with, or indistinguishable from, the palatine in most Salmonoids and Eels; whilst in the *Muraena* a single bone, the pterygoid, exists, but is disconnected with the maxillary arch. Most Fishes, however, present, as in the Cod, the two bones above named.

The *ento-pterygoid* (*fig.* 30. 23) is an oblong, thin, scale-like bone, attached to the inner border of the co-adapted halves of the palatine and true pterygoid, and increasing the bony roof of the mouth in

the direction towards the median line. It is edentulous in the Cod and most other fishes, but is richly beset with teeth in the *Arapaima gigas*. It principally constitutes the floor of the orbit, its breadth depending much upon the depth of that cavity; it sometimes is joined by its median margin to the vomer and pre-sphenoid, as in the Cod-tribe, Carp-tribe, and Flat-fishes; and to the basi-sphenoid in *Lepidosteus*, *Erythrinus*, and *Polypterus*, and then divides the orbit from the mouth; but more commonly a vacuity here exists in the bony skull, filled up only by mucous membrane in the recent fish: in *Upeneus*, *Polyprion*, and *Cheilinis*, for example, the ento-pterygoid does not join the basi-sphenoid; and in *Lophius* it appears to be wanting.

The *pterygoid*\* (*fig. 30. 24*) forms in the Cod an inequilateral triangular plate, but more elongated than the palatine, with which it is dovetailed anteriorly; it becomes thicker towards its posterior end, which is truncated and firmly ingrained with the anterior border of the hypo-tympanic and pre-tympanic bones; its lower border is smooth, thickened and concave; edentulous in the Cod, but more frequently supporting teeth, as in the Perch. The pterygoid and palatine appear to form one bone in the great Sudis (*Arapaima gigas*, *fig. 36. 20, 24*): and they are confluent in the Eel tribe. In the Conger the compound bone is articulated anteriorly to a short lateral process of the vomer, and posteriorly with the hypo-tympanic: it is very large in the Gymnotus. In the *Muraena* the palatine processes of the vomer do not exist, and the fore part of the long pterygoid is attached by ligament to the sides of the vomer, behind its expanded denticerous part.

The ten bones of which the palato-maxillary arch is composed in Osseous Fishes are, in the Cod and most other species, so dispersed, in relation to the peculiar movements of the mouth, as to appear like three parallel and independent arches, successively attached behind one another, by their keystones, to the fore part of the axis of the skull, and with their piers or crura suspended freely downwards and outwards, except those of the last or pterygo-palatine arch, which abut against the tympanic pedicles. The simplification or confluence of the two first of these spurious arches is effected in the Salmonoid Fishes, by the shortening of the premaxillary, and by the mode of its attachment to the maxillary, which now forms the larger part of the border of the mouth and supports teeth: the maxillaries are brought

\* Well argued by Dr. Küstlin not to be, as Cuvier supposed, the homologue of the 'os transversum' of Reptiles.—xxxv. pp. 328, 329.

into close articulation with the palatines in the Plectognathes, and the consolidation of the whole series into its normal unity is effected in the Lepidosiren. The palatines form the true bases of the inverted arch at their points of attachment to the prefrontals; the intermaxillaries constitute the true apex, at their mutual junction or symphysis; the approximation of which to the anterior end of the axis of the skull is rendered possible in fishes, by the absence of any air-passage or nasal canal; the pterygoids are the diverging appendages of the arch\*; but are attached posteriorly to strengthen the pedicle supporting the lower jaw, and combine its movements with those of the upper jaw; just as the bony appendages of one costal arch in Birds associate its movements with those of the next.

*Tympano-mandibular Arch* (*fig. 30. II, III, 25—32*).

This presents its true inverted or hæmal character; its apex or key-stone formed by the symphysial junction of the lower jaw hanging downwards freely, below the vertebral axis of the skull. The piers, or points of suspension of the arch, are formed by the *epi-tympanics* (*fig. 30. 25*), or upper pieces of the tympanic pedicles (pleurapophyses of the prosencephalic vertebra): each epi-tympanic is articulated to both the post-frontals and the mastoids, and is divided artificially accordingly in *fig. 30.*; its articular surface is formed in the Cod by a single elongated condyle; in many other fishes by a double condyle, one for each of the above named cranial parapophyses. In the Diodon the upper border of the epi-tympanic is articulated by a deeply indented suture to the frontal, the post-frontal and mastoid bones; its posterior margin supports, as in many other fishes, a circular articular surface for the opercular bone. Below the condyle, the epi-tympanic in the Cod becomes compressed laterally, but is much expanded from before backwards. The almost constant bifurcation of both ends of the epi-tympanic in osseous fishes, for articulation with two cranial parapophyses above, and suspending two inverted arches below, make it appear like a coalescence of the uppermost pieces of both those arches. In most fishes the lower end is bifid, and supports two inverted arches, the mandibular and the hyoidean; the stylo-hyoid being attached near the junction of the epi-tympanic with the meso-tympanic. The contiguous ribs of the Chelonia are immovably connected together to ensure fixity and

\* By Bojanus they were regarded as the ribs of the second (parietal) vertebra of the head. (*Anatome Testudinis Europææ*, p. 44.)



strength to the carapace: the bulky apparatus suspended from the parietal and frontal vertebræ demanded the additional strength to the supporting axis which is gained by the confluence of their bodies, and apparently by the confluence of the proximal pieces of the pleurapophyses by which the two hæmal arches are suspended from those vertebræ. The anterior division of the epi-tympanic piece articulates with the pre-opercular (34), the meso-tympanic (26), and pre-tympanic (27); the posterior division is again bifurcate in the Cod, supporting part of the pre-opercular and part of the opercular bone. A strong crest projects from its outer surface in this and many other fishes. The epi-tympanic is simple at both ends in the Carp tribe.

The *meso-tympanic* (*fig. 30. 26*), or 'symplectic' of Cuvier, is a slender, compressed, slightly curved, elongated, triangular bone, articulated by its upper part or base to the epi-tympanic and pre-opercular; by its lower end to the inner side of the hypo-tympanic, reaching almost to the mandibular trochlea; and by its anterior border to the pre-tympanic. The upper part of its posterior border is free, and gives attachment to the membrane that fills up the vacuity between it, the pre-opercular and hypo-tympanic bones. The meso-tympanic is confluent with the epi-tympanic in the Siluroid, the Murænoïd, and some other fishes; but does not join the epi-tympanic in the *Lepidosteus*, being in that fish supported by the pre-opercular.

The *pre-tympanic* (*fig. 30. 27*), to which part of the suspensory pedicle of the jaw Cuvier restricts the name 'caisse' or 'os tympanicum\*', is an oblong bony scale, with the posterior margin thickened and grooved for the reception of the fore part of the meso-tympanic and the upper and fore part of the hypo-tympanic. It is confluent with the hypo-tympanic in the Conger and *Muræna*: it does not join either this or the meso-tympanic in the *Lepidosteus*.

The *hypo-tympanic* (*fig. 30. 28*) is a triangular plate of bone, like the epi-tympanic reversed, bearing the articular convex trochlea for the lower jaw upon its inferior apex, and having its upper side or base more even than the opposite base of the epi-tympanic. The

\* This is perhaps one of the best examples of the extent to which Cuvier was influenced by the idea or principle of homology, when a determination had originated from his own comparisons; few of the names imposed by Geoffroy St. Hilaire, in conformity with his peculiar views, seem more overstrained than the transference of the name and signification of the little process supporting the ear-drum in man to a small segment of a strong pedicle, wholly deprived of the proper tympanic function, and with which the homology of the human tympanic process of the temporal bone can only be established by taking the pedicle of the lower jaw in Fishes as a whole.

posterior margin of the hypo-tympanic is grooved for the reception of the part of the pre-opercular (34), its inner side is excavated for the insertion of the pointed end of the meso-tympanic (26), and the anterior angle is wedged between the pre-tympanic (27) and the pterygoid (24), and is firmly united to the latter; the trochlea is slightly concave transversely, convex in a greater degree from before backwards. The *Sparus insidiator*, or Sly-bream (*Epibulus*, Cuv.), presents the most remarkable modification of the hypo-tympanic (*fig. 37. 28*); it is much elongated and slender, carrying the lower jaw at an unusual distance from the base of the skull, and it is itself movably connected at its upper end with the meso-tympanic. Thus, in the extensive protractile and retractile movements of the mouth, the under jaw swings backwards and forwards on its long pedicle, as on a pendulum; the lower jaw being further supported or steadied in those movements by a long ligament, extending from the pre-operculum to its angular piece (*fig. 37. l, 30*).

By the confluence of the meso-tympanic with the epi-tympanic, and of the pre-tympanic with the hypo-tympanic, in the Eel tribe, the suspensory pedicle of the lower jaw is reduced to two pieces, as it is in the *Batrachia*. In the *Lepidosiren* it is represented, as we have seen, by a single osseous piece; but this I regard as the homologue of only the lower half of the pedicle in the *Muraena*, viz. the confluent pre-tympanic and hypo-tympanic pieces. This progressive simplification, or diminution of the multiplied centres of ossification of the tympanic pedicle of Fishes, even within the limits of the class, has mainly weighed with me in rejecting the Cuvierian view of its special homologies; according to which, not only the squamo-temporal bone and the malar bone of higher animals, but also the 'symplectic'—a peculiar ichthyic bone—are superadded to the 'tympanic' or quadrate bone of Reptiles and Birds, in the formation of the suspensory pedicle of the under jaw of Fishes. Ascending to the higher generalisations of homology, we see in the tympanic pedicle a serial repetition of the palatine bone; and, in both, the ribs or pleurapophyses of contiguous vertebræ specially modified for the masticatory functions of the arches they support.\*

The *mandible*, or lower jaw (hæmapophysis of the frontal vertebra (*fig. 30. 29, 32*), is the lower portion of the arch, being articulated to the hypo-tympanics above, and closed by a ligamentous union or bony symphysis with its fellow at its lower end. The term

\* The division of the pleurapophysis of the frontal vertebra into four tympanic pieces no more destroys its individuality than does the division of the maxillary bone in *Lepidosteus* the individuality of that bone.

'ramus' is applied in anthropotomy to each half of the mandible, and each ramus consists of two, three, or more pieces in different fishes. Most commonly it consists of two pieces, one (hæmapophysis proper), articulated to the suspensory pedicle, and edentulous, analogous to the maxillary; and the other (hæmal spine) completing the arch, and commonly supporting teeth, like the premaxillary. In the Cod, and some other fishes, a third small piece is superadded, at the angle of the posterior piece. That (*ib.* 29) which forms the sigmoid concavity adapted to the tympanic trochlea is termed the 'articular piece;'<sup>\*</sup> it sends upwards a pointed coronoid process, to which the ligament from the maxillary bone, and the masticatory muscles are attached; one short square plate downwards, to join with the angular (*ib.* 30); and a long pointed process forwards, to be sheathed in the deep notch of the anterior piece. This (32) is characterised by the teeth, which, when present in the lower jaw, are always supported by it; whence its name of the 'dentary piece.' The dentary is always deeply excavated, and receives a cylindrical cartilage\* from the inner side of the hypo-tympanic, and the vessels and nerves of the teeth. The great Sudis (*fig.* 38.) and the Polypterus have the splint-like plate



Lower jaw (*Arapaima gigas*).

along the inner surface of the ramus, answering to that which Camper and Cuvier have unfortunately called 'operculaire,' in the mandible of Reptiles, but to which I have given the name of '*splenia*' to prevent the confusion from the synonymy with the true opercular bones of Fishes: and in both Sudis and Lepidosteus there is superadded a small bony piece (*ib.* 29 *a*), answering to that which Cuvier calls the 'sur-angulaire' in Reptiles. These modifications, co-existing with the true opercular bones, demonstrate the fallacy of the idea that those bones are much developed homologues of the posterior pieces of the lower jaw of Reptiles; an idea which could never have been entertained by its propounders, had they appreciated the general homology of the opercular pieces, as the diverging appendage of the hæmal arch of a cranial vertebra.

The *Diverging Appendage* of the tympano-mandibular arch consists of the bones which support the gill-cover, a kind of short and broad fin, the movements of which regulate the passage of the currents through the branchial cavity, opening and closing the branchial aperture on each side of the head. The first of these opercular bones, which forms the chief medium of the attachment of the

\* M. Agassiz observes that this cartilage is the "reste de l'ancien arc embryonal, autour duquel les pièces osseuses se sont développées." (XXII. i. p. 138.)

appendage to the supporting arch, is the *pre-opercular* (*fig. 30. 34*), which is usually the longest in the vertical direction, if not the largest of the bones: it commonly presents a crescentic or an angular form; it is sometimes bifurcate above, as in the Cod, and with the lower slender angle continued downwards and forwards to beneath the hypo-tympanic. In the Gurnards, or 'mailed-cheeked' Fishes, the pre-opercular is articulated with the enormously developed sub-orbital scale-bones.

Three bones usually constitute the second series of this appendage: the upper one is commonly the largest and of a triangular form, thin and with radiated lines like a scale: it is the *opercular* (*fig. 30. 35*): in the Cod it is principally connected with the posterior margin of the pre-opercular, and below with the *sub-opercular* (*ib. 36*); but it has usually, also, a partial attachment to the outer angle of the epi-tympanic, and is sometimes (*Diodon, Lophius, Anguilla*) exclusively suspended therefrom. In the *Lophius piscatorius* the opercular is a long and strong bone suspended vertically from the convex epi-tympanic condyle, and with a long and slender fin-ray proceeding from the back part of that joint. The sub-opercular forms the chief part of the opercular fin by its long backwardly produced lower angle. The sub-opercular bone in the Conger is soon reduced to a mere ray, which curves backwards and upwards like one of the branchiostegals. The opercular itself, though shorter and retaining more of its laminated form, also shows plainly, by its length and curvature in the Eels, its essential nature as a metamorphosed ray of the tympanic fin. We have seen that all the framework of this fin had the form of rays in the Plagiostomes. In *Muræna* the small opercular bones articulate only to the under half of the tympanic pedicle. The sub-opercular is wanting in the *Shad*. The lowermost bone, called the *inter-opercular* (*fig. 30. 37*) is articulated to the pre-opercular above, to the sub-opercular behind, and usually to the back part of the mandible; it is attached, also, in the Cod by ligament to the cerato-hyoid in front. The interopercular and preopercular are the parts of the appendage which are most elongated in the peculiarly lengthened head of the *Fistularia*.

#### *Hyoidean Arch* (*fig. 30. H, II, 38—43*).

The third inverted arch of the skull is the 'hyoidean,' and is suspended, in Osseous Fishes, through the medium of the epi-tympanic bone to the mastoid; and I regard it as the costal or hæmal arch of the parietal segment or vertebra of the skull.\* The first portion of

\* Bojanus, studying the vertebral homologies of the head in the fresh-water tortoise, deemed the cornua of the hyoid to be the last costal arch of the skull, and

the arch, *stylo-hyal* (pleurapophysis, in part, of the mesencephalic vertebra, *fig.* 30. 38) is a slender styloform bone, which is attached at the upper end by ligament to the inner side of the epi-tympanic, close to its junction with the meso-tympanic, and at the lower end to the apex of a triangular plate of bone, which forms the upper portion of the great cornu, or hæmapophysial part of the arch. I apply to this second piece, which is pretty constant in fishes, the name of *epi-hyal* (*ib.* 39): the third longer and stronger piece is the *cerato-hyal* (*ib.* 40).

The keystone or body of the inverted hyoid arch is formed by two small sub-cubical bones on each side, the *basi-hyals* (*ib.* 41). These complete the bony arch in some fishes: in most others there is a median styloform ossicle, extended forwards from the basi-hyal symphysis into the substance of the tongue, called the *glosso-hyal* (*ib.* 42), or 'os linguale;' and another symmetrical, but usually triangular, flattened bone, which expands as it extends backwards, in the middle line, from the basi-hyals; this is the *uro-hyal* (*ib.* 43). It is connected with the symphysis of the coracoids, which closes below the fourth of the cranial inverted arches, and it thus forms the isthmus which separates below the two branchial apertures. In the Conger the hyoidean arch is simplified by the persistent ligamentous state of the stylo-hyal, and by the confluence of the basi-hyals with the cerato-hyals: a long glosso-hyal is articulated to the upper part of the ligamentous symphysis, and a long compressed uro-hyal to the under part of the same junction of the hyoid arch. The glosso-hyal is wanting in the *Muraenophis*.

The *Diverging Appendage* of the hyoidean arch retains the form of simple, elongated, slender, slightly curved rays, articulated to depressions in the outer and posterior margins of the epi- and cerato-hyals: they are called 'branchiostegals,' or gill-cover rays, because they support the membrane which closes externally the branchial chamber. The number of these rays varies, and their presence is not constant even in the bony fishes: there are but three broad and flat rays in the Carp; whilst the clupeoid *Elops* has more than thirty rays in each gill-cover: the most common number is seven, as in the Cod (*fig.* 30. 44). They are of enormous length in the Angler,

adds a dotted outline of it to complete his *Vertebra occipitalis*, in xxxviii. tab. xii. *fig.* 32. 31. He had not been prepared by the normal position of the true hæmal arch of the occiput in fishes, and by the example of the extreme displacement to which a hæmal arch and its appendages may be subject, as in the case of the pelvis and pelvic fin in fishes, to recognise the true hæmapophyses of the occiput in the displaced scapular arch. Bojanus considered the "pterygoids" as the ribs (*costæ*) of the parietal vertebra (*ib.* p. 64.).

and serve to support the membrane which is developed to form a great receptacle on each side of the head of that singular fish.

### *Branchial Arches.*

Certain bony arches, which appertain to the system of the visceral skeleton, succeed the hyoidean arch, with the keystone of which they are more or less closely connected. Six of these arches are primarily developed, and five usually retained; the first four of these supporting the gills (*fig. 39. 4<sup>r</sup>, 47*), the fifth (*ib. 47'*) beset with teeth and guarding the opening of the gullet: this latter is termed the pharyngeal arch, the rest the branchial arches.

The lower extremities of these arches adhere to the sides of a median chain of ossicles, which is continued from the posterior angle of the basi-hyal, or from above the uro-hyal, when this is ossified: the arches curve as they ascend; and their upper extremities, which are usually distinct pieces, bend inwards and almost meet beneath the base of the cranium, to which they are attached by ligamentous and cellular tissue.

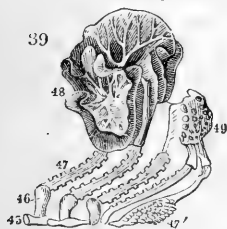
The inferior median symmetrical piece is commonly divided into three ossicles, (the *basi-branchials*, *ib. 45*), following each other in a linear series along the median line: the first rests upon the uro-hyal, when this is present; or it is attached to the posterior interspace of the cerato-hyals: the second gives attachment to the first pair of branchial arches, and the third to the second pair of arches: the third pair of arches is attached to the extremity of the second pair and to a ligament continued from the third basi-branchial: the fourth pair of arches adheres to the same ligament in the angle of the third pair: and the pharyngeal arches, forming the fifth pair, are attached to the angle of the fourth.

Each branchial arch, independently of the basal key-bones, consists of three or four pieces, enjoying a certain elastic, flexible movement on each other. The first three arches consist each of a short piece below, the *hypo-branchial* (*fig. 39. 46*), which, in the Halibut, sends a ridge or process downwards and inwards beneath the basi-branchials: next, of a long bent portion, the *cerato-branchial* (*ib. 47*), grooved on its outer convex side; usually supporting dentigerous processes, tubercles, or fine plates on its concave side: and, above, of a shorter, similarly formed piece, bent inwards and forwards, the *epi-branchial* (*ib. 48*). To the epi-branchial of the second and third arches is commonly attached a shorter and broader bone beset with teeth, the *pharyngo-branchial*.

The fourth arch consists of the cerato-branchial, the epi-branchial, and the pharyngo-branchial pieces. The fifth arch (*ib. 47'*) usually

consists simply of the cerato-branchial element; but in *Anabas* supports a pharyngo-branchial (*ib.* 49). It is often expanded, and usually more or less beset with teeth: it has been termed the inferior pharyngeal bone (*os pharyngien inférieure*, Cuvier), as if it were homologically distinct from the gill-bearing arches; and in the same insulated sense the upper expanded dentigerous portions of these arches are termed by Cuvier the “*os pharyngiens supérieures* :” they are sometimes blended together into one piece, as in the *Cottus*.

The peculiar cribriform or labyrinthic cavities, lined by vascular membrane, and subservient to the continuance of respiration in certain fishes, which can live long out of water, the Climbing Perch (*Anabas*) for example, and other genera of the Order called by Cuvier “*Pharyngiens labyrinthiformes*,” are due to a peculiar development of the epi-branchial and pharyngo-branchial pieces of the first, second, and sometimes the third branchial arches (*fig.* 39. 48).



Branchial arch, with labyrinthic pharyngo-branchials (*Anabas*).

All these gill- and tooth-bearing arches appertain to the splanchno-skeleton, or to that category of bones to which the hard jaw-like pieces supporting the teeth of the stomach of the Lobster belong. The branchial arches are sometimes cartilaginous when the true endo-skeleton is ossified: they are never ossified in

the perenni-branchiate Batrachians, and are the first to disappear in the larvæ of the caduci-branchiate species; and both their place and mode of attachment to the skull demonstrate that they have no essential homological relation to its vertebral structure. All the primitive six pairs of branchial arches are present, but cartilaginous in the *Lepidosiren*; and the last, which answer to the inferior pharyngeal bones in normal Osseous Fishes, supports gills, and not teeth, whilst the second and third arches have no gills in this remarkable fish: they offer a striking contrast in tissue, connections, and development with the strong, bony, persistent hyoidean arch of the true endo-skeleton.

#### *Scapular Arch* (*fig.* 30. II, I, 50, 51, 52).

The fourth cranial inverted arch is that which is attached to the par-occipital; or to the par-occipital and mastoid; or, as in the Cod, to the par-occipital and petrosal; or, as in the Shad, to the par-occipital and basi-occipital: thus either wholly or in part to the par-apophysis of the occipital vertebra, of which it is essentially the hæmal arch; it is usually termed the ‘scapular arch.’ In the Eel tribe, where it is very feebly developed, and sometimes devoid of any diverging appendage, it is loosely suspended behind the skull; and in

the Plagiostome Cartilaginous Fishes it is not directly attached to its proper vertebra, the occiput, but is removed further back, where we shall usually find it displaced in the higher Myelencephala, in order to allow of greater freedom to the movements of the head.

The superior piece of the arch (*supra-scapula*, *fig. 30. 50*) is bifurcate in the Cod, or consists of two short columnar bones, attached anteriorly, the one to the par-occipital, the other and shorter piece to the petrosal, and coalescing posteriorly at an acute angle, to form a slightly expanded disk, from which the second piece of the arch is suspended vertically.

This second piece, called "*scapula*" (*ib. 51*) is a slender, straight, styliform bone terminating in a point below, and morticed into a groove on the upper and outer side of the lower and principal bone of the scapular arch. The supra-scapula and scapula together represent the rib or pleurapophysis of the occipital vertebra; they are always confluent in the Siluroids.

The lower bone, or hæmapophysis (*coracoid*, *ib. 52*), which completes the arch below, is commonly termed the 'clavicle' (as by Spix, Geoffroy, Meckel and Agassiz); but I am induced to regard it as homologous with that bone, the coracoid, which progressively acquires a more constant and larger development in descending from Mammals down to Fishes, and which is manifestly a more essential part of the arch than the clavicle, since it contributes more or less of the surface of attachment for the radiated appendage, which the clavicle never does. By Cuvier the hæmapophysial portion of the occipital inverted arch in fishes is termed the 'humerus;' but it is unquestionably a part of the arch, and the most important part in the present class, in no member of which does it present the slightest approach to the character of a diverging appendage, such as the humerus essentially is, whenever it has an independent existence. By some Ichthyotomists the bone in question has received the special name of 'cœnosteon.'

Whether viewed insulated, *i. e.* merely ichthyotomically, or by the light of the modifications of the sustaining arch of the pectoral member in higher Vertebrata, the essential nature of the bone in question was little likely to be understood: its general homology can only be appreciated by studying its relations to the general vertebrate skeleton in the lowest class, where vegetative repetition most prevails, and the fundamental type is least departed from. The relation to the primary constituent segment of the skeleton being thus ascertained, the special homology of the bone is to be determined by tracing the modifications of the scapular arch in the ascending direction. The serial homologies of the hæmapophyses of the scapular arch are obviously with the cerato-hyoids, the mandible, the cartilages



of the ribs, or sternal ribs, &c. The modification of the coracoids, most characteristic of fishes, is the symphysial union of their lower extremities, like the hæmapophyses of the maxillary and mandibular arches, either by ligament, or dentated suture; or, as in Plagiostomes, by cartilaginous confluence. But this mode of closing the inverted arch seems inevitable in a class in which a true sternum 'hæmal spine' is absent; and we shall find the same symphysis of the coracoids in those fish-like Reptiles, the *Enaliosauria*, which are now extinct.

In the Cod-tribe the pointed upper extremity of the *coracoid* (*figs.* 19. and 30. 52), projects behind the scapula and almost touches the supra-scapular bone; below this part a broad angular plate of the coracoid projects backwards and gives attachment to the radiated appendage of the arch: the rest of the coracoid bends inwards and forwards, gradually decreasing to a point, which is connected by ligament to its fellow, and to the uro-hyal bone. The inner side of the coracoid is excavated, and its anterior margin folded inwards and backwards; it is continued above into the posterior angular process, but in the rest of the coracoid it is simply bent upon the inner concavity of the bone, which lodges the origin to the great lateral muscle of the trunk.

In most fishes the lower end of the arch is completed, as in the Cod, by the ligamentous symphysis of the coracoids; but in the Siluri and Platycephali the coracoids expand below, and are firmly joined together by a dentated suture. In all fishes they support and defend the heart, and form the frame, or sill, against which the opercular and branchiostegal doors shut in closing the great branchial cavity; they also give attachment to the aponeurotic diaphragm dividing the pericardial from the abdominal cavity.

Like the tympano-mandibular and hyoidean arches the scapular arch supports, in most fishes, a *Diverging or radiated Appendage* on each side.

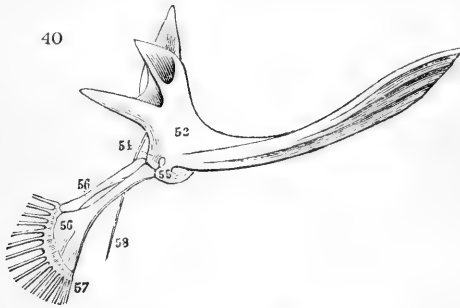
This appendage consists in Lepidosiren of a single ray: but in Osseous Fishes it is composed usually, first, of two rarely of three bones immediately articulated with the coracoid; next, of a series of from two to six smaller bones; which, lastly, support a series of spines or jointed rays. These rays in the scapular appendage, or 'pectoral fin,' are a repetition of the branchiostegal rays in the hyoidean appendage, and of the opercular rays in the tympanic appendage. Of the special homology of the pectoral fin-rays with the digits of the pectoral extremity in higher animals, there has been no question. The vegetative repetition of digits and joints, and the vegetative sameness of form in those multiplied peripheral parts of the fins of

fishes, accord with the characters of all other organs on their first introduction into the animal series. The single row of fewer ossicles supporting the rays, obviously represents the double carpal series in Mammals; and the bones of the brachium and anti-brachium seem in like manner to be reduced to a single series, unless the humeral segment be confluent with the arch. In the ventral fin no segment is developed between the arch and the digital rays: it is in this respect like the branchiostegal fin.

The pectoral fin is directed backwards, and being applied, prone, to the lateral surface of the trunk, the ray or digit answering to the thumb is towards the ventral surface. The lowest of the bones supporting the carpus should, therefore, be regarded as the *radius* (*figs.* 19. and 30. 55), holding the position which that bone unquestionably does in the similarly disposed pectoral fin of the Whales and Enaliosaurs. The upper bone, which commonly affords support to a smaller proportion of the carpal row, may be compared to the *ulna* (*ib.* 54). As a third small bone is articulated to the coracoid, in some Osseous Fishes, at least in their immature state, the name of *humerus* may be confined to that bone: but in these it is generally above and on the inner side of the ulna, and seems to be rather a dismemberment of it. In the young Tench, however, the humerus is a small ossicle, firmly attached to the inner surface of the coracoid, and articulated at the other end to both the ulna and the radius, but not reaching to the carpus. The ulna is beneath it, and of an annular form; the radius is much larger, and of a triangular form, articulated by its smallest side with the humerus and ulna, by its anterior and outer border with the coracoid, and by its upper and hinder border with the carpus. In the Cod, Haddock, and most other fishes, there is no separate representative of the humerus: in these the *ulna* is a short and broad plate of bone, deeply emarginate anteriorly, attached by suture to the coracoid, and by the opposite expanded end to the radius, and to one or two of the carpal ossicles, and directly to the upper or ulnar ray of the fin.

The *radius* (*ib.* 55) is a crescentic or sub-triangular plate with an upper emargination completing an interosseous foramen with that of the ulna; articulated by a small part of its upper and anterior angle and by its produced lower and anterior angle with the coracoid, so as to permit a slight movement, and having its upper and hinder border equally divided between the ulna and the carpus. In the Bull-head and Sea-scorpion (*Cottus*), the radius and ulna are widely separated, and two of the large square carpal plates in their interspace articulate directly with the coracoid. A similar arrangement obtains in the Gurnards and the Wolf-fish; but the carpals in the

interspace of the radius and ulna are separated from the coracoids by a space occupied by an aponeurosis; and in the Wolf-fish the intermediate carpals are almost divided by two opposite notches. The ulna is perforated in all these fishes. The radius is of enormous size in the Opal (*Lampris*) and in the Flying-fish; it is ankylosed with the coracoid in the *Silurus*, to give firmer support to its strong serrated pectoral spine. I find both radius and ulna, which are extremely small, connate with the coracoid in a large *Lophius* (*fig.* 40. 54, 55). This condition probably occasioned them to be overlooked by Geoffroy, whose figure of the bones of the pectoral extremity of this fish\* moreover represents the two long bones of the carpus, (*ib.* 56, 56), which he calls 'radius' and 'ulna' upside down.



Bones of pectoral fin, Angler (*Lophius*).

The ossicles called *carpals* are usually four or five in number, as in the Cod tribe (*fig.* 19. 30. 56); they progressively increase in length from the ulnar to the radial side of the carpus, especially in the Parrot-fish (*Scarus*) and the Mulletts (*Mugil*). They are three in number and elongated in the Polypterus (*fig.* 41. 56), but are reduced to two in number, and more elongated in the *Lophius* (*fig.* 40. 56); thus they retain in this species and in the Sharks their primitive form of 'rays,' but change to broad flat bones in the Wolf-fish, just as the rays of the opercular fin exchange that form in the Plagiostomes for broad and flat plates in ordinary Osseous Fishes.

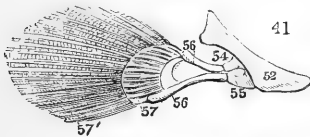
The rays representing the *metacarpal* and *phalangeal* bones (*fig.* 30. 40. 57) are in the Cod twenty in number, and all soft, jointed, and sometimes bifurcate at the distal end. Their proximal ends are slightly expanded and overlap each other, but are so articulated as to permit an oblique divarication of the rays to the extent permitted by the uniting fin-membrane, the combined effect being a movement of the fin, like that called the 'feathering of an oar.' Each soft and

\* Annales du Muséum, 1807, pl. 29.

jointed ray splits easily into two halves as far as its base, and appears to be essentially a conjoined pair.

In the series of Osseous Fishes the rays of the pectoral and ventral fins offer the same modifications as those of the median fins, on which have been founded the division into "Malacopterygians" and "Acanthopterygians:" in the former the last or ulnar fin-ray is usually thicker than the rest; in the latter it is always a hard, unjointed spine: in some fishes it forms a strong pointed or serrated weapon (*Silurus*). In the Gurnards the three lowest rays are detached and free, like true fingers; and are soft, multi-articulated, and larger than the rest; they are supplied by special nerves, which come from the peculiar ganglionic enlargements of the spinal chord, and they appear to be organs of exploration. In all the Gurnards the locomotive part of the pectoral member is of large size; but in one species (*Dactylopterus*) it presents an unusual expanse, and is able by its stroke to raise and sustain for a brief period the body of the fish in the air. The pectoral fins present a still greater development in the true Flying-fish (*Exocætus*).

Only in the Polypterus can any segment analogous to a metacarpus be distinguished by modification of structure from the phalangeal portion of the fin-rays: there are seventeen simple cylindrical metacarpal bones (*fig. 41. 57*), the middle ones being the longest: they are supported on two carpal bones (*ib. 56*), almost as remarkable for their length as in the *Lophius*; a third shorter and broader carpal is wedged into the interspace of the two longer ones, but does not directly join the



Bones of pectoral fin of *Polypterus*.

metacarpus. The carpus is supported by a small radius (54) and ulna (55), which articulate directly with the coracoid. A further approach to the higher conditions of the pectoral member is made by the same Salamandroid Fish in the carpal portion projecting freely from the side of the body, as in the Lophioid Fishes. In the Lepidosiren the diverging appendage of the scapular arch is reduced to the condition of a single jointed ray (*fig. 27. 57*). From this elementary form, development may be traced in one direction, through osseous and cartilaginous fishes, in the progressive manifestation of irrelative repetition of parts, until the number of jointed rays exceeds a hundred, as in the fishes thence called "Rays"; and in another direction, through the didactyle and tridactyle Perenni-branchiate Reptiles, to the perfection of the more normal type of the anterior member in higher Vertebrata; in each class diverging in special directions, more or less, from that

common undivided embryonal bud, which is permanently typified in the *Lepidosiren*. Since, however, in all its modifications, the anterior or pectoral member is essentially, in its widest homological relations, but the diverging or radiated appendage of the hæmal arch of the occipital vertebra, we must not be surprised to find that arch retained, as in the *Synbranchi* and *Muræna*, where no vestige of its appendage is developed.

To the inner side of the upper end of the coracoid there is attached, in the Cod and Carp, a bony appendage in the form of a single styli-form rib; but in other fishes this is more frequently composed of two pieces, as in the Perch. This single or double bone, here called *epi-coracoid* (*figs.* 19. 40. 5s), is slightly expanded at its upper end in the Cod-tribe, where it is attached by ligament to the inner side of the angular process of the coracoid: its slender pointed portion extends downwards and backwards, and terminates freely in the lateral mass of muscles. In its mode of attachment to the coracoid it resembles that of the hyoidean arch to the tympanic pedicle: but in the *Batrachus* its upper extremity rises above the coracoid, and is directly attached to the spinous process of the atlas. In some fishes, as the Snipe-fish (*Centriscus Scolopax*), the Cock-fish (*Argyreiosus Vomer*), the Lancet-fish (*Siganus*), it is joined by the lower end to the corresponding bone of the opposite side, thus completing an independent inverted arch, behind the scapular arch. There is some reason, therefore, for viewing the epi-coracoids as representing the inverted arch of the atlas, or its hæmapophysial portion, and not as parts or appendages of a cranial vertebra.

The usually free lower extremities of the epi-coracoids, together with their taking no share in the direct support of the pectoral fin, and their inconstant existence, oppose more strongly the view of their special homology with the coracoids of higher Vertebrates. They have been regarded as advanced 'ossa innominata' by Carus (xxxiv. p. 125.). To their special homology with the 'clavicles' of higher classes it has been objected that these bones are always situated in those classes in advance of the coracoids; but this inverted position may be a consequence of the backward displacement of the scapulo-coracoid arch in the air-breathing Vertebrata; and if, notwithstanding such displacement, we are able to discern the general homological relations of that arch as the hæmal one of the occipital vertebra, we may, in like manner, discern in the clavicle a less displaced hæmal arch of the atlantal vertebra.

The epi-coracoids are either absent or are very slender spines in the Wolf-fish (*Anarhichas*), the Mullet, the Goby, the Stickleback,

the Remora, the Ribband-fish (*Cepola*), the *Uranoscopus scaber*, the Blennies, the Siluroids, and the Apodal Fishes, with the exception of the Sand-lance, which differs from the Eels in having the epi-coracoids.

That they belong to the system of hæmal or inferior vertebrate arches, and make a transition from the enormously developed arch of the occipital to the ordinary costal arches of the second and subsequent abdominal vertebrae, is indicated by their functions arising out of their muscular attachments. In the Carp two ‘musculi quadrati,’ arising from the coracoid, are inserted into the epi-coracoid; one entirely, the other partially, and this latter is continued backwards, to be similarly implanted into the rib of the second abdominal vertebra; similar but more delicate muscular bands, degenerating into aponeuroses, pass to the succeeding ribs, which are thus drawn forward by the protraction of the epi-coracoids, or hæmapophyses of the atlas. By this action an effect analogous to the expansion of the thorax in Mammalia is produced, the air-bladder being permitted to dilate by the augmented capacity of the abdomen.

As the terminal segment (hand or foot) of a locomotive member is the essential part, or the great aim, so to speak, of the development of such radiated appendage, it is the first part to appear and the last to disappear. It exists without intermediate segment in the ventral fins of all fishes, and in the pectorals of some, *e. g.* the Rays, and the Lepidosiren (*fig. 27.*): in others there may be a carpal segment, as in the Lophius (*fig. 40. 56*), the anti-brachial segment being confluent with the arch: in most fishes both a carpal (*56*) and an anti-brachial segment exist, as in the Cod (*fig. 19. 54, 55*); in Polypterus a metacarpus makes its appearance: but in none is there a distinct brachial segment or humerus, interposed between the anti-brachium and the arch; it is at best represented by some small, supplemental third bone manifesting that relation very dubiously.

The special homology of the pectoral fins of fishes with the fore limbs of quadrupeds was indicated by Aristotle, and first definitely pointed out in later times by Artedi, in 1735, who says,—“Ossa pectoris et ventris in piscibus reperiuntur; suntque in piscibus spinosis: 1. Claviculæ; 2. Sternum; 3. Scapulæ, seu ossa quibus pinnæ pectorales ad radicem affiguntur.” (*Partes Piscium*, p. 39.) Geoffroy St. Hilaire, who has devoted special Memoirs to the determination of the bones of the pectoral fin, had no knowledge of the primary homology of the pectoral fin as the radiated appendage of the inferior arch of a cranial vertebra, or of its serial homology with the branchiostegal and opercular fins. He consequently speaks of the junction of the basis of the fin to the cranium as something very strange:—“Disposition

véritablement très singulière, et que le manque absolu de cou, et une combinaison des pièces du sternum avec celles de la tête pouvoient seuls rendre possible." (*Annales du Muséum*, IX. p. 361.)

Oken's latest idea of the essential nature of the arms and legs is, that they are no other than 'liberated ribs:': "Freye Bewegungsorgane können nichts anderes als frey gewordene Rippen seyn." (*Lehrbuch der Natur Philosophie*, p. 330. 8vo. 1843.)

Carus (I.), in his ingenious endeavours to gain a view of the primary homologies of the locomotive members, sees in their several joints repetitions of vertebral bodies (*tertiar-wirbel*)—vertebræ of the third degree—a result of an ultimate analysis of a skeleton pushed to the extent of the term 'vertebra' being made to signify little more than what an ordinary anatomist would call a 'bone.'

But these transcendental analyses sublimate all differences, and definite knowledge of a part escapes through the unwarrantable extension of the meaning of terms. We have seen, however, that a vertebra is a natural group of bones, that it may be recognised as a primary division or segment of the endo-skeleton, and that the parts of that group are definable and recognisable under all their teleological modifications, their essential relations and characters appearing through every adaptive mask.

According to the definition of which a vertebra has seemed to me to be susceptible, we recognise the centrum, the upper (neural) arch, the lower (hæmal) arch, and the appendages, diverging or radiating from the hæmal arch. The centrum, though the basis, is not less a part of a vertebra, than are the neurapophyses, hæmapophyses, pleurapophyses, &c.; and each of these parts is a different part from the other: to call all these parts 'vertebræ' is in effect to deny their differential and subordinate characters, and to voluntarily abdicate the power of appreciating and expressing them. The terms 'secondary' or 'tertiary vertebra' cannot, therefore, be correctly applied to the appendages of that natural segment of the endo-skeleton to which the term 'vertebra' ought to be restricted.

So likewise the term 'rib' may be given to each moiety of the hæmal arch of a vertebra; although I would restrict it to that part of such arch to which the term 'vertebral rib' is applied in Comparative Anatomy and the term 'pars ossea costæ' in Anthropotomy: but, admitting the wider application of the term 'rib' to the whole hæmal arch, yet the bony diverging and backward projecting appendage of such rib or arch is something different from the part supporting it. Arms and legs may be developments of costal appendages, but cannot be ribs themselves liberated: although liberated ribs may perform analogous functions, as in the Serpents and Dragons.

A series of developments may be traced from the primitive form of the appendage, as a simple plate, spine, or ray, through the many-jointed single ray in the *Lepidosiren* and the bifurcate jointed ray in the *Amphiuma didactylum*, up to the wing of the Bird and the arm of the Man, without the essential nature of the part being lost sight of; for all these forms of the pectoral member are, in their ultimate or general homology, 'diverging' or 'radiated appendages' of a hæmal arch; but not 'ribs,' nor 'vertebræ.' We may further define the fore-limb, wing, or pectoral fin to be the radiated appendage of the arch called 'scapular,' and this to be the 'hæmal arch of the occipital vertebra.'

There remain to complete the analysis of the skeleton of the Cod, here taken as a type of Osseous Fishes, the bones of the ventral pair of fins and the cranial parts of the dermal skeleton. The rays of the ventral fin are supported by two bones, which represent the lower portion of an imperfect inverted or hæmal arch; each bone is a sub-triangular bifurcate plate in the Cod tribe, with its apex anterior and superior, joined by ligament to the same part of the corresponding bone, and suspended beneath the coracoid arch. To the outer part of the base of each suspending bone the rays of the ventral fin are attached without the intermedium of any series of short ossicles; in fact, the representatives of tarsal, tibial, and femoral bones are wanting in all fishes, and the lower half of the pelvic arch, (or the *pubic bones*, *fig.* 19. 63), and the peripheral and essential parts of the fin, the *metatarso-phalangeal* jointed rays (*ib.* 70), alone represent the hinder or lower locomotive member in fishes. In Acanthopterygian Fishes one or more of the anterior rays of the ventral fin may be hard unjointed spines, as in the other fins; in the Malacopterygians all the ventral rays are soft, multi-articulate, and bifurcate.\*

In no fish is this incomplete pelvic arch directly attached to the vertebral column. If we may judge from the position in which the ventral fin appears, in the development of the embryo fish, as a little bud attached to the skin of the belly, and from the fact that all the

\* Ichthyologists avail themselves of the number and kind of rays in the several single and parial fins to characterise the species of fishes, and adopt an abbreviated formula to express those characters; thus Mr. Yarrell (xxxix. i. p. 4.) uses the following with reference to the Perch:—*d.* 15, 1 + 13 : *p.* 14 : *v.* 1 + 5 : *a.* 2 + 8 ; *c.* 17 : which signifies that *d.*, the dorsal fin, has in the first fin 15 rays, all spinous; in the second fin, 1 spinous + (plus) 13 rays that are soft. *p.*, the pectoral fin, 14 rays, all soft. *v.*, the ventral fin, with 1 spinous ray + 5 that are soft. *a.*, the anal fin, with 2 spinous rays + 8 that are soft. *c.*, the caudal fin, 17 rays. The formula of the fin-rays in the Haddock is: *d.* 15, 21, 19 : *p.* 18 : *v.* 6 : *a.* 24, 18 : *c.* 44. : *i. e.* all the rays are soft, and there are 15 rays in the first dorsal, 21 in the second dorsal, and 19 in the third dorsal; 18 rays in the pectoral fin; 6 rays in the ventral fin; 24 rays in the first anal, and 18 in the second anal fins; and 44 rays in the caudal fin.

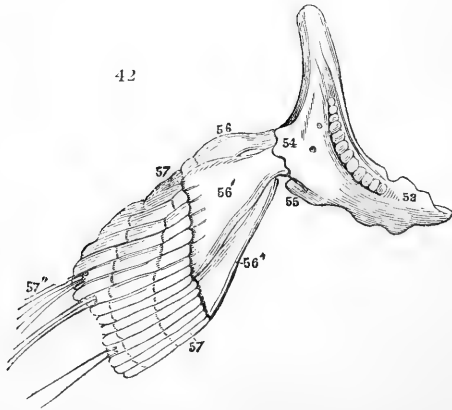


fishes in the geological formations anterior to the chalk are abdominal, that is, have the ventral fins near the posterior end of the abdomen\*, we may conclude that the supporting bones are, essentially, the hæmapophyses of the last rib-bearing (or pelvic) abdominal vertebra; and that the rays are the diverging appendage, but are attached, like the branchiostegal rays of the hyoidean (parietal hæmal) arch, without the intervention of fewer short and broad bones, homologous with femoral, tibial, tarsal bones, &c. The hæmapophysial portion (pubis) of the pelvic arch is never joined to the pleurapophysial portion (ilium) of the same arch in fishes; but is suspended more or less freely to other parts, always projecting from the under or ventral part of the body, but subject to great diversity of position in relation to the two extremes of the abdomen. On these differences Linnæus based his primary classification of fishes: he united together, for example, those fishes which have the pelvic or ventral fins near the anus, to form the order called "*Pisces Abdominales*;" those with the ventral fins beneath the pectorals, into an order called "*Pisces Thoracici*;" and those with the ventrals in advance of the pectorals, into an order called "*Pisces Jugulares*;" lastly, those fishes in which the ventral fins are absent formed the order called "*Pisces Apodes*." And by this name it will be observed that Linnæus recognised the special homology of the radiated appendages of the pelvic arch of fishes with the hinder or lower extremities of the higher classes of animals.

In the Angler (*Lophius piscatorius*) each pelvic bone is attached to the under and near the fore part of the long coracoid, expands at the opposite end, and bends inwards to meet its fellow at a kind of symphysis pubis; the fin, supported by six rays with expanded imbricated bases, diverges from the angle; and the suspending branch above this seems to represent an iliac bone. The pubic bones are detached from the coracoid arch in *Abdominal* Fishes; the *Thoracic* character depends upon the peculiar length of those bones, which carries back the ventral fins to beneath the pectorals. As the ventral fins are always the last to be developed in the embryo abdominal, thoracic, and jugular fishes, so the apodals may be regarded as analogous to permanent embryo forms of these fishes, in which development has been arrested before arriving at the abdominal stage, and growth has proceeded, in most cases, to excess in the linear direction; as is exemplified in the Eel tribe, where vegetative repetition of a vast number of incomplete vertebræ has taken the place of the perfection of part of a fewer number of vertebræ.

\* Agassiz, *Hist. des Poissons*, t. i. p. 105.

There are neither pectoral nor ventral fins in the Cyclostomous Fishes. In the Plagiostomes there are both: but the scapular arch is detached from the occiput, the condition of its displacement being the more posterior position of the heart in these fishes. In the Sharks and Chimæra it is loosely suspended by ligaments from the vertebral column: in the Rays the point of resistance of their enormous pectoral fins has a firmer, but somewhat anomalous attachment, by the medium of the coalesced upper ends of the supra-scapular pieces to the summits of the spines of the confluent anterior portion of the thoracic abdominal vertebræ. In the Sharks the scapular arch consists chiefly of the coracoid portions (*fig. 42. 52*), which are confluent together beneath the pericardium which they support and defend; the scapular ends of the arch, connected to the coracoids by ligament, project freely upwards, backwards, and outwards. To a posterior prominence of the coracoid cartilage corresponding with the ankylosed radius and ulna (*ib. 54, 55*) in the Lophius, there are attached, in the Dog-fish and most other Sharks, three sub-compressed, sub-elongated carpal cartilages, the uppermost (*ib. 56*) the smallest, and styliform; it supports the upper or outer phalangeal ray. The next bone (*ib. 56'*) is the largest and triangular, attached by its apex to the arch, and supporting by its base the majority of the phalanges.



Cartilages of the pectoral fin and arch of the Dog-fish (*Spinax acanthias*).

The third carpal (*ib. 56''*) is a smaller but triangular cartilage, and supports six of the lower or radial phalanges. Three joints (metacarpal and digital) complete each cartilaginous ray or representative of the finger (*ib. 57*); and into the outer surface of the last are inserted the fine horny rays or filaments (*ib. 57''*), the homologues of

the claws and nails of higher Vertebrata, but which on their first appearance, in the present highly organised class of fishes, manifest, like other newly introduced organs, the principle of vegetative repetition, there being three or four horny filaments to each cartilaginous unguis phalanx.

On the fore part of the coracoid arch, near to the prominence supporting the fin, there are developed a vertical series of small bony cylindrical nuclei in the substance of the cartilage in most Sharks. In the Rays the coraco-scapular arch forms an entire circle or girdle attached to the dorsal spines: it consists of one continuous cartilage in the *Rhinobates*, but in other Rays is divided into coracoid, scapular, and suprascapular portions, the latter united together by ligament. The scapula and coracoid expand at their outer ends, where they join each other by three points, to each of which a cartilage is articulated homologous with the three above described in the Shark, and which immediately sustain the fin-rays. The posterior cartilage answering to the upper one in the Shark curves backwards and reaches the ventral fin: the anterior cartilage curves forwards, and its extremity is joined by the ant-orbital process as it proceeds to be attached to the end of the rostral cartilage; the middle proximal cartilage is comparatively short and crescentic, and sustains about a sixth part of the fin-rays, which are the longest, the rest being supported by the anterior and posterior carpals, and gradually diminishing in length as they approach the extremities of those cartilages. In the common Ray there are upwards of a hundred metacarpo-phalangeal rays in each great pectoral fin. The longest rays begin after the tenth or eleventh joint to bifurcate; the shorter ones bifurcate progressively nearer their origin.

The ventral fin is better developed in the Plagiostomes than in any other fishes. The supporting arch consists indeed of the same simple pubic elements, united together by ligament in the middle line, and loosely suspended in the abdominal walls, but they do not immediately support the fin-rays. Two intermediate cartilages are articulated to the expanded outer end of each pubis; the anterior is the shortest in the Dog-fish, and supports three or four rays; the posterior one is much longer, and supports the remainder of the rays, fifteen or sixteen in number. To the end of this cartilage likewise is attached, in the male Plagiostomes and *Chimæra*, the peculiar accessory generative organ or clasper.

In the *Torpedo* the pubic arch sends forwards two processes like marsupial bones; these processes are longer in an extinct Ray to which its discoverer Sir P. de M. Grey Egerton has given the name of *Cyclobates oligodactylus* (XL. p. 225. pl. 5.).

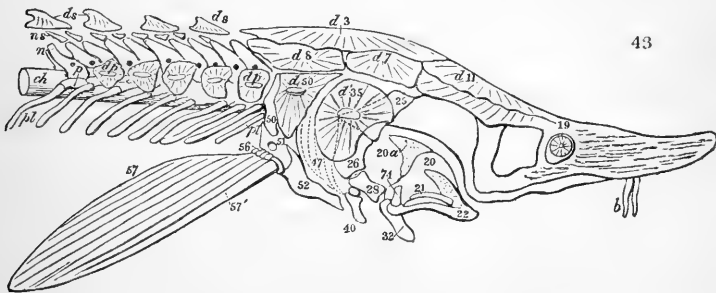
## LECTURE VI.

DERMAL BONES AND TELEOLOGY OF THE SKELETON OF  
FISHES.

THE Sturgeon is one of the transitional steps from the Cartilaginous to the Osseous Fishes; but as its skeleton more especially elucidates those bones of the Osseous Fishes which have been superadded to the proper cranial and other bones of the endo-skeleton to form the dermal system or exo-skeleton, I have deferred a notice of it to this place. All the parts of the skull of the Sturgeon which belong to the endo-skeleton are, with the exception of the appended arches, one continuous mass of cartilage, which is defended by a crust of shagreened, ganoid bones of the dermal system. It seems, as Agassiz well says, as if the space between the outer bony crust and the cerebral membranes within had formed a mould into which the liquid gristle had been thrown at a single jet, and there hardened. There is no membranous fontanelle in this cartilaginous cranium. The base of the skull shows the embryonic character of the prolongation of the pointed end of the 'chorda dorsalis' as far forwards as the pituitary depression, which is persistent in the Sturgeons. The occipito-sphenoidal cartilaginous plate is developed around the 'chorda,' and extends upon the base and sides of the skull, whence it is continued backwards, without an intervening joint, into the cartilage of the coalesced anterior vertebræ of the trunk. The upper surface of the cartilaginous skull is gently convex; it extends outwards at its middle part between the large orbital and branchial cavities, and to the under part of this prominence the tympanic pedicle is articulated. The cartilaginous cranial mass contracts in front of the orbits, is deeply excavated on each side for the nasal cavities, and thence is continued forwards into a rostral process, which gradually tapers to a more or less obtuse point. A thin continuous crust of bone covers the lower surface of the occipito-sphenoidal cartilage, except at the middle line, beneath the cranial end of the chorda, where we saw the cartilage arrested in the Cestracion; this crust extends backwards into the cervical region. The pituitary sella pierces the basal cartilage, but not the subjacent osseous crust. This crust seems analogous to the basi-sphenoid plate in the Lepidosiren; but its extension upon the neck, the absence of the articular concavity, and the persistence of the

cartilaginous basis of the skull oppose the view of its homology with the basal elements of the cranial vertebræ. With regard to the upper and lateral osseous plates of the head, they are, as Von Baer has indicated (III.), the continuation of the series of dermal osseous plates upon the upper mid-line and sides of the trunk.

Before, however, applying this instructive condition of the cranium of the Sturgeon to the elucidation of the nature and homologies of the bones which still remain to be noticed in the skull of the Cod, I shall briefly describe the maxillary, mandibular, hyoid, and scapular hæmal arches of the coalesced cranial vertebræ of the Sturgeon. The first three of these arches are suspended from the tympanic pedicle; but this, instead of being a single piece, as in the Plagiostomes and Lepidosiren, consists of three cartilages, articulated in *Accipenser Ruthenus*, according to Müller, by a small accessory or interarticular cartilage, with the under part of the mastoid process. The three principal bones describe a semicircle, concave forwards, and answer respectively to the epi-tympanic (*fig. 43. 25*), the meso-tympanic (*ib. 26*), and hypo-tympanic (*ib. 28*) bones of Osseous Fishes.



Fore-part of endo- and exo-skeleton of Sturgeon.

The upper jaw, or maxillary arch of Plagiostomes and Lepidosiren, is represented in the Sturgeon by a partly osseous, partly cartilaginous, broad arch, in which the centres of ossification have been three in number on each side, and indicate both by their relative position, and by the direction in, and extent to, which the bony fibres have diverged from them, the pre-maxillary, maxillary, and palatal bones of the Osseous Fishes. The pre-maxillaries (*ib. 22*) form the anterior and inferior border of the arch: each bone is a sub-triangular plate, joined by ligament to its fellow at the middle line, trenchant anteriorly, contracted and thickened posteriorly, whence it rises and extends in the form of an arched process, outwards and downwards to the outer side of the joint for the lower

jaw. This process corresponds with the outward and downward prolongation of the transversely developed pre-maxillary in Osseous Fishes.

The maxillary bone (*ib.* 21) is a small and simple oblong plate, articulated to the under part of the base of the outer process of the pre-maxillary, and attached by the whole of its inner and posterior side to the palatine. Only the gradual transmutation of the similarly insignificant 'os mystaceum' in the Osseous Fishes to its higher form and functions in the Salmonoid and Salamandroid species, could have made the homology of this separate bone appreciable in the Sturgeon.

The os palati (*ib.* 20) articulates by its anterior angle with both maxillary and pre-maxillary; expands posteriorly in one direction towards the median line, along which a slender pointed process is directed forwards; and in the opposite direction outwards and downwards to the inner side of the cartilaginous joint of the lower jaw; like the pterygoid extension of the same part of the arch in the *Lepidosiren*. A slender ossicle (*ib.* 74) extends along the outer side of the cartilaginous joint, from the end of the premaxillary process to the posterior ridge of the palatine bone; homologous with the angulo-labial cartilage in the *Squatina*. In the cartilaginous interspace between the anterior notch of the palatines and the premaxillary synchondrosis, I have found a small separate ossification in a very large and old *Accipenser Sturio*.

The roof of the mouth is extended posteriorly by three cartilaginous plates: one single (*ib.* 20 *a*) and extending backwards, from the posterior interspace of the palatines; this seems to be the homologue of the two median cartilages, called 'palatal' by Dr. Henle, on the roof of the broader mouth of the *Narcine*\*: the two outer cartilages correspond with those called 'pterygoid' by the same author in the same Brazilian *Torpedo*. †

The lower jaw (*ib.* 32), which is joined by a concavity to the trochlear cartilage supported by the pterygoid process of the palatine and the premaxillary, consists principally of a single bony ramus on each side, joined by ligament to its fellow at the symphysis, with a posterior excavation filled by cartilage, in which there is a small detached ossification in the old *Accipenser Sturio* above adverted to. ‡

The whole of the above apparatus of the jaws is suspended to

\* Müller's *Myxinoiden*, tab. v. fig. 3 and 4. *e e*.

† *Ib. d d*.

‡ The bones and gristles of the Sturgeon's mouth are well described by J. Müller (xxi.); but ichthyotomically, *i. e.* without determination of homologies, and accordingly under special names.

the hypo-tympanics (*ib.* 28), which are attached principally to the pterygoid processes and the back part of the cartilaginous joint of the lower jaw. The mouth of the Sturgeon opens, as in Sharks, upon the under surface of the head, and is protruded and retracted chiefly by the movements of the tympanic pedicle, which swings, like a pendulum, from its point of suspension to the post-orbital process.

The hyoid arch is also small and simple in the Sturgeon. The epi-hyal is short and attached to near the upper end of the hypo-tympanic. The cerato-hyal (*ib.* 40) of thrice the length, is expanded above, and is attached by ligament extending from that part to near the joint of the lower jaw. The basi-hyal is a short sub-cubical piece: it gives attachment anteriorly to cerato-hyals, and posteriorly to the anterior basi-branchial and hypo-branchial cartilages.

The three first branchial arches consist of hypo-branchials, progressively decreasing in size, of cerato-branchials, epi-branchials, and pharyngo-branchials: the fourth arch consists of cerato-branchials and epi-branchials: the fifth arch of cerato-branchials only.

In an old *Accipenser Sturio* I found the tympanic pedicle in two pieces, and partly ossified. The epi-tympanic was cartilaginous where it articulated with the post-frontal and mastoid, the osseous part commencing at a definite transverse plane. This, as it descended, expanded, and reverted to the cartilaginous state, forming a broad triangular flattened plate, which supported the large opercular dermal bone: the hypo-tympanic was a simple strong cylindrical cartilage, giving attachment to the hyoid near its upper end, and to the ligaments suspending the palatine and mandibular arches at its lower end.

The cartilaginous representation of the par-occipital projects boldly backwards from each angle of the occiput. A triangular supra-scapular cartilage (*ib.* 50) has the angles of its base slightly produced, one being articulated to the end of the par-occipital, the other to the ex-occipital region. To the apex is attached the scapulo-coracoid arch (*ib.* 51, 52), which is completed below, as in *Lepidosiren*, by ligamentous union, not, as in Sharks, by cartilaginous confluence. The scapulo-coracoid cartilage expands as it descends, sends inwards and forwards a broad wedge-shaped plate, and presents a large perforation at its thick posterior part, answering probably to the perforated ulna of Osseous Fishes, here confluent with the arch. The pectoral fin is articulated to the under part of this perforated projection: the coracoid terminates below by sending inwards and forwards a broad and thin plate beneath the pericardium, which is joined by strong aponeurosis to that of the opposite coracoid. There

are no separate homologues in the Sturgeon's fin of the bones called ulna and radius in Osseous Fishes: the carpal bones (*ib.* 56) immediately articulate with the coracoid, and support about thirty rays (*ib.* 57), two or three of which seem to have coalesced to form the strong bony spine (*ib.* 57') on the outer border of the fin.

The ventral fins are small and are suspended each by a simple cartilaginous pubis to the abdominal muscles a little in advance of the anus.

The osseous scales on the upper surface of the skull are so arranged as, at first sight, to suggest certain analogies with the epicranial bones. Thus, the scale marked *a* (*ib.* *d* 3) in Brandt and Ratzburgh's figure of the head of the *Accipenser Sturio*\* might be compared with the supra-occipital bone; the pair in advance (*ib.* *d* 7), marked *e* (*loc. cit.*), with the parietals; and the pair (*d* 11) marked *g* (*loc. cit.*), with the frontals; but then these are separated by an interfrontal osseous plate, and in *Accipenser Scypha* by two or three such plates; the supra-occipital plate is divided in the *A. brevirostris* and in the *A. sturio* of Pallas†, and other varieties occur which render the attempt to illustrate the homology of the true epicranial bones in Osseous Fishes by these dermal ganoid plates in the Sturgeons difficult and unsatisfactory. The median plates are more obviously and essentially a continuation forwards of the dermal spinous plates (*ib.* *ds*), from the mid-line of the back; and we may see their more veritable repetition amongst the Osseous Fishes in the dermal epicranial spines, for example, of the Angler (*Lophius*), which support the long fishing filaments upon the head, or in those modified ones forming the sucking disk on the head of the *Remora*. They are more obviously homologous with the dermal bones forming the helmet of the Armadillo, and bear the same relation in the Sturgeon to the cartilaginous skull as those bones do in the Armadillo to the osseous skull beneath.

The lateral series of dermal bony plates (*ib.* *dp*) are also continued upon the head, and seem to represent in the Sturgeons the supra-scapular (*ib.* *d* 50) and the opercular bones (*d* 35) in osseous Fishes. Other constant series of cranial scale-bones, in the Sturgeon, circumscribe the orbits below and the temporal spaces above. But before applying the well-contrasted states of the endo- and exo-skeleton of the Sturgeon to the determination of the bones of the skull in the Cod, I may advert to the reversed conditions of the endo- and exo-skeletons in the Lepidosiren, which lends another valuable aid in the solution of this difficult and much discussed subject. The

\* Medizin Zoologie, band. ii. tab. iii.

† Fauna Rosso-Asiatica, iii. p. 91.



supra-cranial movable plates (*fig. 27. 12*) are the only bones of the head of the *Lepidosiren* which can be referred, with any probability, to the dermal system. It is plain that the subjacent epicranial plate (*fig. 27. 11*) in close connection with the cartilage of the cranium, is a true part of the endo-skeleton, and is as certainly the homologue of the mid-frontal, parietal, and supra-occipital bones. In the development of the skull of Osseous Fishes it is found, however, that, whilst the central or basilar, the neurapophysial, and the parapophysial elements of the cranial vertebræ are developed out of a pre-existing cartilaginous basis, the modified spinous elements, with the exception of that of the occipital vertebra, are formed by the deposition of the calcareous salts in the epicranial membrane; and Dr. Reichert, apparently not remembering that the cartilaginous, or intermediate histological, change between the primitive membranous and ultimate osseous stage has been as little recognised in the development of the epicranial bones of Man, would reject the parietal and frontal bones from the system of the endo-skeleton.

To those who may be inclined to support this view, by reference to the epicranial dermal plates in the species of Sturgeon where their correspondence with the mid-frontal and parietal bones may be most easily recognised, it may be replied, that the pre-frontals, post-frontals, mastoids, and supra-occipitals, might also be referred to the exo-skeleton, by a like reference to dermal plates holding the corresponding positions in the Sturgeon's head: but the skeleton of the *Lepidosiren*, with the known relations of the pre-frontals, post-frontals, mastoids, and supra-occipitals to the primitive cartilaginous basis of the skull in Osseous Fishes, demonstrate the fallacy of the conclusions as to the dermal origin of the frontals and parietals, based upon the deceptive analogies of the dermo-cranial plates in the Sturgeon, and upon the absence or brief duration of the cartilaginous stage in the ossification of certain expanded spines of the cranial vertebræ. That the homologues of some of the dermal plates in the Sturgeon are retained in the skull of Osseous Fishes is, however, rendered extremely probable by the constancy of their relative position, by their development in a dermal basis, and by their relation to the dermal mucous canals.

The accessory bones of the skull in Osseous Fishes, which I regard, on the above grounds, as appertaining to the exo-skeleton, and which are more especially connected with the mucous organs of the skin, are the *sub-orbital*, the *supra-orbital*, and the *supra-temporal* ossicles. The first sub-orbital bone (*fig. 19. 73*) is always the largest: it is triangular in the Cod, and covers the side of the muzzle, extending from the fore part of the orbit to the anterior end of

the turbinate bone, to which it is attached by ligament, and it is articulated by its upper and posterior angle with the pre-frontal: from its position it might be termed the pre-orbital bone. The second sub-orbital, a much smaller and sub-quadrate bone, is attached to the lower and posterior angle of the first; and the rest, four in number, of similar form, and gradually smaller in size, complete the chain extending to the post-orbital angle of the os frontis. There are no supra-orbitals in the Cod: the Carp has a single one on each side; the *Lepidosteus* has three supra-orbitals, which quite exclude the frontal from entering into the formation of the orbit. The supra-temporal scale bones are three in number on each side in the Cod, extending backwards from the outer and hinder part of the mastoid: they are very thin, transparent scales, folded on themselves to form a prolongation of the mucous channel, which extends from above the mastoid and frontal bones. The large pre-orbital scale-bone is similarly folded upon itself, from above downwards, forming a mucous channel, extending from the orbit to the nasal sac, and analogous to the muco-lachrymal groove and canal in the lachrymal bone of higher Vertebrata, which always presents a similar position and connections. The smaller sub-orbitals are subservient, chiefly, to the formation of similar mucous ducts, which are completed in these, as in the supra-temporals, by aponeurotic processes of the corium, and are lined by mucous membrane continued from many small and numerous excretory pores on the outer surface of the skin, and forming, in the Cod, ramified secreting follicles in the interior of the bony canals. The bony canals themselves are ramified in the corresponding dermal ossicles of the Herring. The turbinate bones, from their intimate relation with the olfactory sacs, appertain by their form and structure to the same category as the sub-orbitals, and are, with the anterior of these mucigerous ossicles, the only bones of the dermal system constantly retained in the higher Vertebrata, even to Man, under the names of 'lachrymal' and 'spongy' bones. The turbinate bones are very small in the Conger; and both these and the sub-orbital bones are wanting in the rest of the Eel tribe. The sub-orbital bones present their maximum of development in the Mailed-checked (*Trigla*) and Sciaenoid Fishes; in the Star-gazer (*Uranoscopus*) and the *Lepidoleprus*: in the *Sciaena gangetica* they extend over the tympanic pedicle almost to the pre-opercular, and have a bold reticulate exterior, like that bone, the mastoid, and the supra-scapular bone.

In the skull of the Cod you may observe many bones which send a scale-like process from their outer surface, which process forms a more or less complete canal for the ducts of mucous glands. The frontal, the

parietal, the mastoid, and the pre-opercular, as well as the turbinate, the sub-orbital, and the supra-temporal bones, offer this modification of their outer surface. The same correspondence in the pattern of the exterior markings usually prevails in all these bones, and is very conspicuous in some fishes; as in the bold net-work and deep depressions of the surface, observable in the *Pristipoma* and some Sciaenoids; and in the entirely exposed, enamelled, and shagreened surface of the same bones, together with the maxillary arches, in the *Polypterus*. This correspondence of exterior character, though it diminishes the contrast between the endo- and exo-skeleton bones of the skull, does not destroy their distinction. In certain parts of fishes the endo- and exo-skeletons are so connected together that we can scarcely find the boundary line in nature; yet the advantage to the Osteologist of classifying the multiform subjects of his study according to their typical characters must not, therefore, be abandoned.

Guided by the skull of the *Lepidosiren*, and by the light of the general homology of the opercular bones as diverging appendages of the tympano-mandibular arch, I consider the pre-opercular, sub-opercular, and inter-opercular bones to be parts of the endo-skeleton. The opercular bone is very constantly represented by the large dermal plate in the Sturgeon, which M. Agassiz regards as being, with the supra-scapular dermal plate, an anterior continuation of the lateral series of dermal scales. There is also a small dermal plate upon the opercular flap, below the large opercular plate, and which small plate might be regarded as the homologue of the sub-opercular bone. All the four opercular bones forming the diverging appendage of the tympano-mandibular arch were deemed by Cuvier to be peculiar ichthyic super-additions to the ordinary vertebrate skeleton; whilst by Spix, Geoffroy, and De Blainville they are held to be modifications of parts which exist in the endo-skeleton of other Vertebrata. The learned Professor of Comparative Anatomy in King's College, who regards this as "the more philosophical mode of considering them,"\* has briefly stated the homologies proposed by the supporters of this view, viz. that the opercular bones are gigantic representatives of the ossicles of the ear (Spix, Geoffroy, Dr. Grant †): or that they are dismemberments of the lower jaw (De Blainville, Bojanus),—a view refuted by the discovery of the complicated structure of the lower jaw in certain fishes, *e. g.* *Sudis*, (*fig.* 38.), which likewise possess the opercular bones: thirdly, that they are parts of the dermal skeleton; in short, scales modified

\* Professor Rymer Jones, *General Outline of the Animal Kingdom*, 8vo. 1811, p. 509.

† Lectures, *Lancet*, Jan. 11. 1834, p. 573.; *Outlines of Comp. Anat.* p. 64.

in subserviency to the breathing function ; an opinion which Professor Jones acknowledges that he derived from my Lectures on Comparative Anatomy, delivered at St. Bartholomew's Hospital in 1835, and which he adopts. I have subsequently seen reason to modify that view, although it has received the sanction of the greatest Ichthyologist of the present day, M. Agassiz ; and although I find that, so early as 1826, it had presented itself under a peculiar aspect to the philosophical mind of Von Baer. In his admirable paper on the endo- and exo-skeleton he expresses his opinion, that the opercular bones are (dermal) ribs or lateral portions of the external cincture of the head.\* The idea of the relationship of the opercular flaps to locomotive organs is presented by Carus, under the fanciful view of their homology with the wing-covers of beetles and the valves of a bivalve shell (i. p. 122.). In 1836, M. Agassiz propounded his idea of the relation of the opercular bones to scales in a very precise and definite manner ; though, as I shall presently show, the chief ground of his opinion is erroneous. He says, — “ Les pièces operculaires des poissons ne croissent pas, comme les os des vertébrés en général, par irradiation d'un ou de plusieurs points d'ossification ; ce sont, au contraire, des véritables écailles, formées, comme celles qui recouvrent le tronc, de lames déposées successivement les unes sous les autres, et dont les bords sont souvent même dentelés comme ceux des écailles du corps. Tels sont l'opercule, le sub-opercule, et l'inter-opercule. Le supra-scapulaire même peut-être envisagé comme la première écaille de la ligne latérale, dont le bord est également dentelé. On pourrait

\* “ In mancher Beziehung gehören die Kiemendeckel zu ihr, und ich halte sie um so mehr für (Haut) Rippen, d. h. für Seitentheile der äussern Ringe des Kopfes, da ich sie auch in den gewöhnlichen Knochenfischen für nichts anderes ansehen kann. Hat bei diesen auch der oberste Knochen des Kiemendeckels wenig Aehnlichkeit mit Rippen, so geht dagegen der unterste so unverkennbar in die strahlender Kiemenhaut über, das der Uebergang gar nicht zu verkennen ist.” (*Meckel's Archiv*. 1826, 3 heft, p. 369.)

An analogous idea of the relation of the opercular bones to the inferior or costal arches is expressed by the learned Professor of Comparative Anatomy in University College, who, speaking of the occipital vertebræ, says — “ The two external and the two lateral occipitals form the upper arch, and the two opercular and two sub-opercular bones constitute the lower arch.” (*Lectures, Lancet*, 1834, p. 523.) He subsequently, however, adopts and illustrates (p. 573.) the homology of the opercular bones with the “*ossicula auditûs*” of Mammalia ; and in the “*Outlines*” (xxviii.) cites only the Spixian and Blainvillian hypotheses (pp. 64, 65.). I have adduced the grounds which have led me to the conclusion that the opercular bones are neither ribs of the exo-skeleton, nor inferior arches of the endo-skeleton, but persistent radiating appendages of an inferior (hæmal) arch ; not, however, of the occipital vertebra, but of the frontal ; just as the branchiostegal rays are the appendages of the hæmal arch of the parietal, and the pectoral fins of that of the occipital vertebræ. That parts of both endo- and exo-skeleton may combine to constitute the opercular fin is the more probable, inasmuch as we see the same combination of cartilaginous and dermal rays in the pectoral fins of the Plagiostomes, and in the median fins of most Fishes.

dire aussi que le scapulaire n'est qu'une très grande écaille de la partie antérieure des flancs" (XXII. livraison 6me, 1836, tom. iv. p. 69.). And he adds, "L'opinion que j'ai émise à leur égard prouve que je suis loin d'admettre les rapports que l'on a cru trouver entre les pièces operculaires et les osselets de l'oreille interne" (*Ib.* p. 73.).

I apprehend that the idea of the development of the opercular bones by the successive excretion or deposition of layers, one beneath the other, according to the mode in which M. Agassiz supposes scales to be formed, was derived merely from the appearance of the concentric lines on the opercular, sub-opercular, and inter-opercular bones in many Fishes. I have examined the development of the opercular bone in young Gold-fish and Carp, and I find that it is effected in precisely the same manner as that of the frontal and parietal bones. The cells which regulate the intus-susception and deposition of the earthy particles make their appearance in the primitive blastema in successive concentric layers, according to the same law which presides over the concentric arrangements of the radiated cells around the medullary canals in the bones of the higher Vertebrata: and the term "successive deposition," in the sense of excretion, is inapplicable to the formation of the opercular bones.

The inter-opercular as well as the pre-opercular bones exist in the *Lepidosiren annectens* with all the characters, even to the green colour, of the rest of the ossified parts of the endo-skeleton: the pre-opercular as an appendage to the tympanic arch, the inter-opercular being partly attached to the hyoid arch. Of the supra-scapular there is no trace in the *Lepidosiren*; but in the Sturgeon it plainly exists (*fig.* 43. 50) as part of the cartilaginous endo-skeleton, under the same bifurcate form, and double connection with the cartilaginous skull, as we have seen it to present in most Osseous Fishes. The large triangular bony scale (*ib.* *d.* 50) firmly adheres to its broad, triangular, flat, outer surface. The epi- and meso-tympanic cartilages (*ib.* 25, 26) in like manner expand posteriorly, and give a similar support to the large opercular scale. Were the supporting cartilages of the opercular and supra-scapular scales to become ossified in the Sturgeon, they could doubtless become anchylosed to the dermal bony plates, and bones, truly homologous with the opercular and supra-scapular in ordinary Osseous Fishes, would thus be composed of parts of the endo- and exo-skeleton blended together. I cannot, therefore, concur with Von Baer in the opinion that the opercular bones are ribs of the exo-skeleton, nor with Agassiz that both the opercular and supra-scapular bones are merely modified scales. The supra-scapular bone is the pleurapophysial element of the occipital arch, *i. e.* the upper or first part of the hæmal arch of that vertebra, and corresponds in

serial homology with the epi-tympanic portion of the mandibular arch, and with the palatine portion of the maxillary arch. The opercular bones are the diverging appendages of the tympano-mandibular arch, and correspond, in serial homology, with the branchiostegal appendages of the hyoid and the pectoral appendages of the scapular arches, and have the same title to be regarded as cephalic fins, and as parts of the normal system of the vertebrate endo-skeleton; but neither opercular bones nor branchiostegal rays are retained in the skeletons of higher Vertebrata. All diverging appendages of vertebral segments make their first appearance in the vertebrate series as 'rays;' and the opercular bones are actually represented by cartilaginous rays, retaining their primitive form in the Plagiostomes. In the Conger the sub-opercular still presents the form of a long and slender fin-ray.

The opercular and sub-opercular may, in ordinary Osseous Fishes, frequently coalesce, like the supra-scapular, with their representative scales of the dermal system; but they are essentially something more than peculiarly developed representatives of those scales. M. Agassiz, indeed, excepts the pre-opercular bone from the category of "*pièces cutanées*," believing it to be the homologue of the styloid process of the temporal bone in Anthropotomy, or the 'stylo-hyal' of Vertebrate Anatomy, as the piece, viz. which completes the hyoid arch above. "*C'est en effet*," he says, "*cet os à la face interne duquel l'os hyoïde des poissons est suspendu, qui s'articule en haut avec le mastoïdien et très souvent même sur l'écaïlle du temporal.*" So far as my observation has gone, it is a rare exception to find the hyoid arch suspended to the pre-operculum; the rule in Osseous Fishes is to find the upper styloform piece of the hyoid arch attached to the epi-tympanic (*mastoïdien* of Agassiz), close to its junction with the meso-tympanic bone. It is equally the rule to find the pre-opercular articulated with the epi-, meso-, and hypo-tympanics; and it is an exception, when it rises so high as to be connected with the mastoid (*écaïlle du temporal* of Agassiz). If the stylo-hyal be not the upper piece of the hyoid arch displaced, and if the upper piece connecting that arch with the mastoid is to be sought for in Osseous Fishes, I should rather view it in the posterior half of the epi-tympanic, which is usually bifurcate below and very commonly also above, when the posterior upper fork articulates with the mastoid, and the posterior lower fork with the hyoid arch.

The normal position, form, and connections of the pre-operculum clearly bespeak it to be the first or proximal segment of the radiated appendage of the tympano-mandibular arch: the opercular, sub-opercular, and inter-opercular bones form the distal segment of the

same appendage. In some of the earliest introduced fishes on our planet, *e.g.* the Cephalaspids of the Old Red Sandstone, the opercular appendages were functionally as well as homologically cephalic fins, and the only pair of radiated appendages so developed from the hæmal arches.

Returning to the consideration of the dermo-skeleton, we find in the Sturgeon that, besides the cephalic plates, it is represented by five longitudinal rows of dermal bones, one extending along the mid-line of the back (*fig.* 43. *ds*) already noticed in the elucidation of the skeleton of the trunk, one along each side of the body (*ib.* *dp*), and two along the lower part of the abdomen, between the pectoral and ventral fins. The upper lateral series of scale bones is pretty constant in the exo-skeleton of fishes, and is usually closely related to the mucous tube and its conduits, which form the so-called 'lateral line' in this class. The systematic Ichthyologist finds in the varieties of this line characters for the distinction of genera or species. The lateral bones, which are either perforated or grooved by its ducts, are modified scales, and the scales of fishes are more or less modified dermal bones: they do not belong to the horny or epidermal system, but lie between the cuticle and cutis, their fore margin directed inwards and lodged somewhat loosely in depressions of the cutis, and their hind margin outwards, and firmly adherent to the cuticle, when the development of the scales renders its existence possible. The scales of the lateral line are commonly more ossified than those of the rest of the trunk: in the Eel tribe the lateral mucous ossicles are tubular and concealed by the epiderm. In the Sole and Plaice the mucous scale bones of the lateral line are quite superficial. There are many circular radiated ossicles scattered over the dark or upper side of the skin of the Turbot. A row of small chevron-shaped dermal bones extends along the median line of the belly of the Herring, and the extremity of each lateral process (*fig.* 23. *dh*) is connected with that of the long and slender vertebral rib, completing the inferior arch, like a sternum and sternal ribs. The Dory has two rows of thick osseous plates along the under part of the abdomen; and both this fish and the Herring have been cited as exceptional examples of fishes with a true sternum.\* But the superficial position of the ventral ossicles indicates their essentially dermal character, and we may regard this as another instance of the connection of the endo- and exo-skeletons in the class of fishes. Parts analogous to a sternum are thus supplied from the exo-skeleton in the Herring, as they are from the splanchno-skeleton in the Lamprey

\* Gorce's translation of Carus' *Comp. Anat.* vol. i. p. 117.

(fig. 11.); but the true homologues of the sternum are first seen in the endo-skeleton of the Batrachia. In the Trunk-fishes (*Ostracion*), and Pipe-fishes (*Syngnathus*) the dermal scale bones form a continuous coat of mail, like a tessellated quincuncial pavement, over the entire body. In the *Lepidosteus* the scales defend the body in close-set oblique rows, are thick, completely ossified, and with an exterior hard, shining, enamel-like layer, having the microscopic structure of the hard dentine of Shark's teeth; the subjacent osseous part exhibits the radiated corpuscles. I described the organic structure of these so-called 'ganoid' scale bones in 1840, in both recent and extinct fishes, showing that it militated against the theory of development by successive deposition of layers being applied, at least, to ganoid scales.\* A like organisation prevails in the tri-radiate dermal bones which support the strong spines of the Diodon; and in the usually unenamelled, less regularly formed and arranged, dermal 'placoid' ossicles of Sharks and Rays. The thinner subtransparent scales of ordinary Osseous Fishes are either sub-circular and with entire margins as in the Carp, when they are called 'cycloid,' or have the outer and hinder margin dentated or spined, as in the Perch, when they are called 'ctenoid.' We have seen that the primary classification of fishes in the system of M. Agassiz, is based on these various modifications of the dermal skeleton.

One of the interesting generalisations which has risen out of the vast series of researches on Fossil Fishes to which this eminent Naturalist has devoted himself, is the discovery of the progressive predominance of the exo-skeleton over the endo-skeleton as we descend into the strata of the earth, or, in other words, penetrate into past time in quest of the species that have been successively blotted out in the revolutions of the globe. At the present day the Placoids or Plagiostomous cartilaginous fishes form a small minority of the class; and amongst the existing majority of fishes called, from the advanced development of their internal skeleton, 'Osseous,' only two genera exhibit that kind of scale called 'ganoid:' one of these, the *Lepidosteus*, is peculiar to North America; the other, the *Polypterus*, to Africa: both are fresh-water fishes. As we descend to the older tertiary deposits the number of Ganoid Fishes increases, their geographical relations expand, and their sphere of life was extended to the salt waters of the ocean.

Thus Ichthyolites with a dense imbricated armour of polished bony scales occur in the marine deposits of the eocene age in our own

\* Odontography, part i. p. 15.



island. In the chalk formations the members of both Ganoids and Placoids multiply rapidly, and in all the older fossiliferous strata they exclusively represent the class of fishes. The predominance of osseous matter deposited in the tegumentary system in these ancient extinct fishes is not unfrequently accompanied by indications of a semi-cartilaginous state of the endo-skeleton, like that in the *Lepidosiren* of the present day; the total absence of any trace of vertebral centres in this fossilised skeleton of the *Microdon radiatus* (No. 70. Fossil Fishes, Mus. Coll. Chirurg.), and the vacant tract, where they should have been, between the bases of the neur- and hæma-pophyses which have been little disturbed; together with the remains of the ganoid scale-armour which has kept all the fossilisable parts of the extinct fish together, show plainly enough that the primitive gelatinous chorda dorsalis has been persistent. In not one of the numerous extinct fishes of the Devonian and Silurian systems has a vertebral centrum been discovered; but the enamelled dermal osseous scales and plates are richly developed, and most remarkable for their beautiful and varied external sculpturing, and often for their great size. In the *Coccosteus* they form a broad helmet upon the head, and a back-plate and breast-plate for the fore part of the trunk, and have been mistaken for the scutes of a *Tryonyx* or *Mud-tortoise*; whilst only the peripheral arches and spines of the vertebræ of this fish were ossified, and a great proportion of the cranial vertebræ was cartilaginous. In the still better defended *Pterichthys* and *Pamphractus*\*, which have been mistaken for extinct Crustacea, all the internal skeleton was soft and perishable, and the earthy salts were exclusively developed in that peripheral skeleton, which forms the sole calcified defence of the invertebrate classes of animals. It is a striking and suggestive fact this prevalence of a low and rudimental state of the endo-skeleton, with an excessive development of the exo-skeleton, in the fishes of the old Silurian and Devonian strata—the earliest periods at which Geology teaches that fishes were introduced into this planet. At the present day the *Lepidosiren* repeats the low condition of the endo-skeleton, but without the compensating ganoid or placoid developments of the skin; and the Siluroids combine the large tuberculated osseous dermal plates with a well ossified internal skeleton. The existing Sturgeons alone manifest contrasted conditions of the endo- and exo-skeletons, like those in the ancient Cephalaspids; but what is now a rare and exceptional instance of analogy to the

\* See M. Agassiz' admirable, philosophical, and splendidly illustrated monograph, "Sur les Poissons Fossiles du Système Devonien," 4to. tab. 24—31.

testaceous and crustaceous Invertebrates appears to have been the rule in the first-born fishes of our globe.

These primæval members of the vertebrate sub-kingdom manifest other remarkable traits of embryonic life. The Cephalaspids of the Old Red Sandstone were shaped like the tadpoles of Batrachia; the breathing organs and chief part of the alimentary apparatus were aggregated with the proper viscera of the cranial cavity, in an enormous cephalic enlargement; the rest of the trunk was for locomotion, and dwindled away to a point. The cephalic abdominal enlargement was defended by large bony scutes; the muscular tail-part was, in the higher species (*Coccosteus*), strengthened by an incompletely developed vertebral axis, with intercalary and dermal spines, supporting a dorsal and an anal fin. The position of the anal fin proves the anus to have been situated, as in tadpoles, immediately behind the cephalic abdominal expansion. In the lowest forms, as *Pterichthys*, the mouth was small and inferior, as in the young tadpole, and the post-cephalic or abdominal part of the enlargement very short and ill-defined. In the *Coccosteus* it nearly equals the cranial part of the enlargement; the scutes are fewer, larger, and show the progress of coalescence; the mouth is anterior, large, and formed by well developed dentigerous upper and lower jaws. In this genus the cephalic or opercular appendages are inconspicuous or reduced to the normal proportions; in *Pamphractus* and *Pterichthys* they form long fin-like appendages, projecting from the sides of the cephalic enlargement, like the external gills of the Batrachian and Selachian larvæ, and they may have supported external fringed gills in the ancient Cephalaspids.

*Genesis of Fins.*—In the order of succession of Fishes the development of locomotive organs is first restricted, as in most Cephalaspids, to the region of the head: in *Pterichthys* and *Pamphractus* they project like pectoral fins (which M. Agassiz describes them to be) from the sides of the head just anterior to the division between the facial and nuchal plates, and from the place corresponding to that occupied by the pedicle of the lower jaw, from which the opercular fin projects in the Sturgeon. There is no trace of true pectoral, ventral, or of vertical fins in these Cephalaspids. In the *Coccosteus* these cephalic fins are reduced to ordinary opercular proportions (they appear to be represented by the plate *b* in the restored side view, given by M. Agassiz, *Op. cit.* tab. xxiv.); but here we have the earliest manifestation of dorsal and anal fins, without, however, any modification of the terminal vertebræ to form a caudal fin, either heterocercal or homocercal, and without the slightest trace of true pectoral or ventral fins. In the *Dipterus* and *Glyptolepis* there are two closely approximated dorsal and two anal

fins, and both are situated near the end of the tail, which runs into the upper lobe of an unsymmetrical caudal fin. Now in the embryos of existing Osseous Fishes these vertical fins are developed from a single continuous fold of integument, which is extended round the tail from the dorsal to the ventral surface; a condition which we shall see in the tadpoles of Batrachia, and which is persistent in the Eel and Lepidosiren. The growth of this fold is progressive at certain parts and checked at others; and where development is active the supporting dermal rays make their appearance, and the transformation into dorsal, anal, and caudal fins is thus effected. At first the caudal fin is unequally lobed and the terminal vertebræ extend into the upper and longer lobe; the dorsals and anals are also, at first, closely approximated to each other and to the caudal fin. M. Agassiz has shown that all these embryonic characters were retained in many of the extinct fishes of the Old Red Sandstone; and the development of the caudal fin did not extend in any fish beyond the heterocercal stage until the preparation of the earth's surface\* had advanced to that stage which is called jurassic or oolitic in geology. (xxxii. fasc. *Sur le Système Devonien.*)

*Teleology of the Skeleton of Fishes.*—Thus far the osteology of Fishes has been considered chiefly from a homological point of view, and I have aimed at relieving the dryness of descriptive detail, and at connecting the multifarious particulars of this difficult part of Comparative Anatomy in natural order, so as to be easily retained in the memory, by referring to the relations which the skeletons of Fishes bear to the general plan of Vertebrate organisation, and by indicating their analogies to transitory states of the embryo skeleton in higher animals, and to those answerable conditions of the mature skeleton which, in longer lapse of time, have successively prevailed and passed away in the generations of species that have left their remains in the superimposed strata of the earth's crust.

To determine the parts of the Vertebrate skeleton which are most constant; to trace their general, serial, and special homologies, under all the various modifications by which they are adapted to the several modes and spheres and grades of existence of the different species, should be the great aim of osteological science; as being that which will reduce its facts to the most natural order, and their exposition to the simplest expressions. It is impossible, in pursuing the requisite comparisons upwards through the higher organised classes, not to recognise the close and interesting analogies between the mature states and forms of ichthyic organs, and the embryonic condi-

\* "The sea is His, and He made it, and His hands prepared the dry land."—Ps. xcv.

tion of the same parts, in the higher species. But these analogies have been frequently overstated, or presented under unqualified metaphorical expressions, calculated to mislead the student and to obstruct the attainment of true conceptions of their nature. We should lose some most valuable fruits of anatomical study were we to limit the application of its facts to the elucidation of the unity of the Vertebrate type of organisation, or if we were to rest satisfied with the detection of the analogies between the embryos of higher and the adults of lower species in the scale of being. We must go further, and in a different direction, to gain a view of the beautiful and fruitful physiological principle of the relation of each adaptation to its appropriate function, and if we would avoid the danger of mistaking analogy for homology or identity, and of attributing to inadequate hypothetical secondary causes the manifestations of Design, of supreme Wisdom and Beneficence, which the various forms of the Animal Creation offer to our contemplation.

To revert, then, to the skeleton of Fishes, with a view to the teleological application of the facts determined by the study of this complex modification of the animal framework. No doubt there is analogy between the cartilaginous state of the endo-skeleton of Cuvier's Chondropterygians, and that of the same part in the embryos of air-breathing Vertebrates; but why the gristly skeleton should be, as it commonly has been pronounced to be, absolutely inferior to the bony one is not so obvious. The ordinary course of age and decrepitude, or of what may be called the decay of the living body, is associated with a progressive accumulation of earthy and inorganic particles, gradually impeding and stiffening the movements, and finally stopping the play of the vital machine. And I know not why a flexible vascular animal substance should be supposed to be raised in the histological scale because it has become impregnated, and as it were petrified, by the abundant intus-susception of earthy salts in its areolar tissue. It is perfectly intelligible that this accelerated progress to the inorganic state may be requisite for some special office of such calcified parts in the individual economy; but not, therefore, that it is an absolute elevation of such parts in the series of animal tissues.

It has been deemed no mean result of Comparative Anatomy to have pointed out the analogy between the shark's skeleton and that of the human embryo, in their histological conditions; and no doubt it is a very interesting one. But can no insight be gained into the purpose of the all-wise Creator, in so arresting the ordinary course of osteogeny in the highly organised fish? Are we to entertain no other view of it than as an unfinished, incomplete stage of an hypothetical serial development of organic forms?

The predaceous Sharks are the most active and vigorous of fishes ; like the birds of prey they soar, as it were, in the upper regions of their atmosphere, and, without any aid from a modified respiratory apparatus, devoid of an air-bladder, they habitually maintain themselves near the surface of the sea, by the actions of their large and muscular fins. The gristly skeleton is in prospective harmony with this mode and sphere of life, and we shall subsequently find as well marked modifications of the digestive and other systems of the shark, by which the body is rendered as light, and the space which encroaches on the muscular system as small, as might be compatible with those actions. Besides, lightness, toughness and elasticity are the qualities of the skeleton most essential to the shark : to yield to the contraction of the lateral inflectors, and aid in the recoil, are the functions which the spine is mainly required to fulfil in the act of locomotion, and to which its alternating elastic balls of fluid, and semi-ossified bi-concave vertebræ, so admirably adapt it. To have had their entire skeleton consolidated and loaded with earthy matter would have been an encumbrance altogether at variance with the offices which the sharks are appointed to fulfil in the economy of the great deep.

Yet there are some who would shut out by easily comprehended but quite gratuitous systems of progressive transmutation and self-creative forces, the soul-expanding appreciations of the final purposes of the fecund varieties of the animal structures by which we are drawn nearer to the great First Cause. They see nothing more in this modification of the skeleton, which is so beautifully adapted to the exigencies of the highest organised of fishes, than a foreshowing of the cartilaginous condition of the reptilian embryo in an enormous tadpole, arrested at an incomplete stage of typical development. But they have been deceived by the common name given to the Plagiostomous fishes : the animal basis of the shark's skeleton is not cartilage ; it is not that consolidated jelly which forms the basis of the bones of higher Vertebrates : it has more resemblance to mucus ; it requires 1000 times its weight of boiling water for its solution, and is neither precipitated by infusion of galls, nor yields any gelatine upon evaporation.

In like manner the modifications of the dermal skeleton of fishes have been viewed too exclusively in a retrospective relation with the prevalent character of the skeleton of the Invertebrate animals. Doubtless it is in the lowest class of Vertebrata that the examples of great and exclusive development of the exo-skeleton are most numerous ; but some anatomists, in their zeal to trace the serial progression of animal forms, seem to have lost sight of all the vertebrate instances

of the bony dermal skeleton except those presented by the Ganoid and Placoid fishes. He must have sunk to the low conception that nature had been limited to a certain allowance of the salts of lime in the formation of each animal's skeleton, who could affirm that in the higher Vertebrata "the internal articulated skeleton takes all the earthy matter for its consolidation" (xxvii. p. 537.), forgetting that the bulky Glyptodon and its diminutive congeners the Armadillos have their internal skeleton as fully developed and as completely ossified as in any other mammals. The organising energies which perfect and strengthen the osseous internal skeleton do not destroy nor in any degree diminish the tendency to calcareous depositions on the surface, when the habits and sphere of life of the warm-blooded quadruped require a strong defensive covering from that source.

The moment that the observations of the naturalist bring to light the mode of life of any of those fishes which are said to retain an unusual proportion of the external shell of the Invertebrata, we are in a condition to appreciate the adaptation of that external defensive covering to such mode of life. The Sturgeons, for example, were designed to be the scavengers of the great rivers; they swim low, grovel along the bottom, feeding, in shoals, on the decomposing animal and vegetable substances which are hurried down with the debris of the continents drained by those rapid currents: thus they are ever busied re-converting the substances, which otherwise would tend to corrupt the ocean, into living organised matter. These fishes are, therefore, duly weighted by a ballast of dense dermal osseous plates, not scattered at random over their surface, but regularly arranged, as the seaman knows how ballast should be, in orderly series along the middle and at the sides of the body. The protection against the water-logged timber and stones hurried along their feeding grounds, which the Sturgeons derive from their scale-armour, renders needless the ossification of the cartilaginous case of the brain or other parts of the endo-skeleton: and the weight of the armour requires that endo-skeleton to be kept as light as may be compatible with its elastic property and other functions. The Sturgeons are further adjusted to their place in the liquid element, and endowed with the power of changing their level and rising with their defensive load to the surface, by a large expansive air-bladder.

These teleological interpretations of the dermal bony plates may give some insight into the habits and conditions of existence of those Ganoid and heavily protected Placoid fishes which so predominated in the earlier periods of animal life in our planet; whereas these Ganoids and Placoids have hitherto been viewed almost exclusively by the light of the analogy of an embryonic "Age of Fishes," or explained

by the hypothesis of transmuted Crustacea. Some have gone so far as to affirm, that in all those solid parts that cover and shield the exterior of the body of the sturgeon and analogous fishes, "there is nothing in the least analogous to any part of the internal articulated skeleton of Vertebrata," but that "it is entirely a remnant of the superficial shells of Invertebrata." (XXVII. p. 337.) You would hardly suppose from these exaggerated expressions, that both ganoid and placoid plates are as richly organised and permeated by nutrient vessels as the bones within; and that they present the same microscopic structure as the ossified parts of the endo-skeleton, which they serve to protect. I have proved this with regard to the existing *Lepidosteus*, and the extinct *Lepidotus*. (v. p. 14.) Drs. Peters and Müller have shown the osseous rayed corpuscles in the scales of *Polypterus* and other Ganoids. Nay, many of the ganoid fishes have these modified bony scales articulated in regular series by a kind of gomphosis, like the pegs and sockets by which the tiles of a roof are linked together. The dermal bones which form the carapace of the Armadillo have the same cellulo-reticulate interior structure as the carpal, tarsal, or other bones of the endo-skeleton not excavated by a medullary cavity. This is well demonstrated in the dermal bones of the great extinct *Glyptodons*. \*

The great proportion of the primitive cartilage which is retained in the skull of many of the Osseous Fishes, the Salmon and Pike, for example, and the greater proportion of the animal to the earthy matter in all the bones, their coarse texture, the radiating fibres of the flat cranial bones, and the general absence of dentated sutures, are all persistent characters in Osseous Fishes, which remind the Anthropotomist of transitional ones in the human fœtus; but the light of teleology demonstrates the perfection of such, so termed embryonic conditions, in relation to the atmosphere and movements of the Fish. It is generally in fresh-water abdominal Fishes that the semi-osseous condition of the skull is found, and the diminution of the quantity of heavy earthy particles may be connected with the less dense quality of their medium, as compared with sea-water, and with the usually more posterior position of the ventral fins.

In reference to the analogies to the form of a fish, we may be reminded that the head of the human embryo is disproportionately large. True: but the head of a fish must needs be large to meet and overcome the resistance of the fluid, in the mode most favourable for rapid progression: it must therefore grow with the growth of the fish.

\* M. de Blainville, in the "Généralités Ostéologiques," prefixed to his great "Ostéographie," admits that the structure of the dermal bones has a certain resemblance with that of true bones; but errs in stating, "avec cette différence importante, qu'elle n'est jamais celluleuse et reticulée." 4to. 1839, p. 12.

Hence the large cranial bones always show the radiating osseous spiculae in their clear circumference, which is the active seat of growth; hence the number of overlapping squamous sutures, which least oppose the progressive extension of the bones. The cranial cavity expands with the expansion of the head: the absorbents remove from within as the arteries are extending the osseous walls without; but the brain undergoes no corresponding increase; it lies at the bottom of its capacious chamber, which is principally occupied by a loose cellular tissue, situated, like the arachnoid, between the pia mater and the dura mater, and having its cells filled with an oily fluid, or sometimes, as in the Sturgeon, by a compact fat. (xxiii. t. i. p. 309.) Now, this condition of the envelopes of the brain is not only, like the fibrous tissue and squamous sutures of the ever-growing cranial bones, related to the requisite proportions of the fore-part of the fish for facilitating its progressive motion, but it is one which no embryo of a higher animal ever presents: it is as peculiarly ichthyic, as it is expressly adapted to the exigencies of the fish.

It has been held that confluence of distinct bones is a consequence of high circulating and respiratory energies; yet the anchyloses of the supra-occipital, parietal, and frontal above the cranium, and of the basi-occipital, basi-sphenoid, and pre-sphenoid below the cranium in *Lepidosiren*, and the constant confluence of the posterior and anterior basi-sphenoids in all bony fishes, disprove the constancy of the supposed relationship, and lead us to look for other explanations of such coalescence of primitively or essentially distinct bones. We shall find a final cause for the rapid consolidation and union of the elongated bodies of the two middle cranial vertebræ of Fishes in the necessity for strength in the basis of that part of the skull, from the sides of which the large and heavy mandibular and hyoid arches and their appendages are to be suspended, and to swing freely to and fro. The posterior and anterior sphenoids continue distinct bones in all Mammalia during a period of life at which they form one continuous bone in Fishes.

The flattened form of the frontal and parietal bones in Osseous Fishes has been associated with the small development of the brain which they protect; but observe how they would have impeded the progress of the fish, had they been expanded into the dome-shaped vault which arches over the skull of Birds and Mammals. There was no need of that development in Fishes; but we must not overlook the fact that its very absence is a perfection in their structure, — an adaptation to their sphere and mode of locomotion.

The loose connections of most of the bones of the face may likewise



remind the homologist of their condition in the imperfectly developed skull of the embryos of higher animals; but this condition is especially subservient to the peculiar and extensive movements of the jaws, and of the bones connected with the hyoid and branchial apparatus.

Not any of the limbs, properly so called, of Fishes, are prehensile; the mouth may be propelled and guided by them to the food, but the act of prehension must be performed entirely by the jaws. Hence in many fishes both upper and lower maxillary bones enjoy movements of protraction and retraction, as well as of opening and shutting. The firm connections of the upper jaw, and wedged fixity of the bone suspending the under jaw, which characterise the higher Reptiles and Mammals, would be imperfections in the Fish; in which, therefore, such characters are not only absent, but special development in the opposite direction, not unfrequently, goes so far as to produce the most admirable mechanical adjustments of the maxillary apparatus, compensating for the absence of hands and arms like those which have been exemplified in the instance of the *Epibulus insidiator* (p. 108. *fig.* 37.).

We must guard ourselves, however, from inferring absolute superiority of structure from apparent complexity. The lower jaw of fishes might at first view seem more complex than that of man, because it consists of a greater number of pieces, each ramus being composed of two or three, and sometimes more separate bones. But, by parity of reasoning, the dental system of that jaw might be regarded as more complex, because it supports often three times, or ten times, perhaps fifty times the number of teeth which are found in the human jaw. We here perceive, however, only an illustration of the law of vegetative repetition as the character of inferior organisms; and we may view in the same light the multiplication of pieces of which the supporting pedicle of the jaw is composed in Fishes. But the great size and the double glenoid or trochlear articulation of that pedicle, are developments beyond, and in advance of the condition of the bones supporting the lower jaw in Mammalia, and relate both to the increase of the capacity of the mouth in Fishes for the lodgment of the great hyoid and branchial apparatus, and to the support of the opercula or doors which open and close the branchial chambers. The division of the long tympanic pedicle of Osseous Fishes into several partly overlapping pieces adds to its strength, and by permitting a slight elastic bending of the whole diminishes the liability to fracture. The enormous size, moreover, of the tympano-mandibular arch, and of its diverging appendages, contributes to ensure that proportion of the head to the trunk which is best adapted for the progressive motion of the fish through the water. But without the

admission and appreciation of these pre-ordained adaptations to special exigencies in the skeleton of Fishes, the superior strength and complex development of the tympanic pedicle and its appendages would be inexplicable and unintelligible in this lowest and first-born class of Vertebrate animals.

In contrasting the skeletons of the Fish and Mammal, with reference to hypothetical secondary origins of organic species; such, for example, as that of transmutation and progressive ascent of specific forms; the vast disparity of the hyoidean arch, in point of size, complexity, and strength, both intrinsic, and as due to its connections, must not be overlooked. Its small size, simple structure, and loose suspension in the flesh, have led to its being reckoned in Anthropotomy as a single bone; and it is rarely preserved in the artificial skeletons of man or beast: whilst if absolute and relative magnitude, complexity of structure, and importance of function, are tests of the grade of organisation of a part, the progress of development must be held to have been reversed in respect of the hyoid arch; which, with its appendages, offers the highest grade in Fish and the lowest in Man. And why this great difference — this striking exception to the general condition of the ichthyic organisation? It is explicable only on teleological principles. It is true the Fish tastes not with its tongue, neither does it speak: the sole function of the human tongue-bone, which is performed by that of the fish, is that which is in subserviency to deglutition. But this function is not in relation to food alone; all the mechanical part of breathing in the fish is a modified act of swallowing. The hyoid arch is the chief point of suspension of the visceral arches which support the gills; and the branchiostegal membranes, stretched out upon the diverging rays of the hyoid arch, regulate the course and exit of the respiratory currents: thus the mechanical functions of the thorax of the air-breathing classes are transferred to the hyoid arch and its appendages in Fishes.

By the retraction of the hyoid arch the opercular doors are forced open, and the branchial cavity is widened; whilst all entry from behind is prevented by the branchiostegal membranes, which close the posterior branchial slits: the water, therefore, enters by the gaping mouth, and rushes through the sieve-like interspaces of the branchial arches into the branchial cavity: the mouth then shuts, the opercular doors press upon the branchial and hyoid arches, which again advance forwards, and the branchiostegal membranes being withdrawn, the currents rush out at the open posterior branchial orifices. These functions are the true condition of the high development of the os hyoides in fishes.

I have noticed the great development, the persistence, and ossifi-

cation of the branchial arches in connection with the transitory manifestation of cartilaginous branchial arches in the larvæ of the Batrachia: this is one of those similarities that has led to the metaphorical expressions of "gigantic tadpoles," as applied to fishes. But we see how admirably the branchial arches are adapted to the aquatic respiration of the fish, by their advance to a grade of development, which they are never destined to attain in the frog. Observe their firm ossification, their elastic joints, the sieve-like valves developed from the side next to the mouth, pre-arranged with the utmost complexity and nicety of adjustment to prevent the entry of any particles of food or other irritating matters into the interspace of the tender, highly vascular, and sensitive gills. Observe, also, how the last pair of these arches is reduced to the capacity of the pharynx which it surrounds, how it is thickened in order to support teeth of multiform character, according to the nature of the food; in short, converted into an accessory pair of jaws, and the most important of the two. In no other Vertebrate Animals is the mouth provided with maxillary instruments at both fore and hind apertures: in no other part of the ichthyic organisation is the special divergence from any conceivable progressive scale of ascending structure culminating in Man so plainly marked as in this.

All writers on Animal Mechanics have shown how admirably the whole form of the fish is adapted to the element in which it lives and moves: the viscera are packed in a small compass, in a cavity brought forwards close to the head; and whilst the consequent abrogation of the neck gives the advantage of a more fixed and resisting connection of the head to the trunk, a greater proportion of the trunk behind is left free for the development and allocation of the muscular masses which are to move the tail. In the caudal, which is usually the longest, portion of the trunk, transverse processes cease to be developed, whilst dermal and intercalary spines shoot out from the middle line above and below, and give the vertically extended, compressed form, most efficient for the lateral strokes, by the rapid alternation of which the fish is propelled forwards in the diagonal, between the direction of those forces. The advantage of the bi-concave form of vertebra with intervening elastic capsules of gelatinous fluid, in effecting a combination of the resilient with the muscular power, is still more obvious in the Bony Fishes than in the Shark.

You may be reminded that all the vertebrae of the trunk are distinct from one another at one stage of the quadruped's development, as in the fish throughout life; and you might suppose that the absence of that development and confluence of certain vertebrae near the tail, to form a sacrum, was a mark of inferiority in fishes.

But note what a hindrance such a fettering of the movements of the caudal vertebræ would be to creatures which progress by alternate vigorous inflections of a muscular tail. A sacrum is a consolidation of a greater or less proportion of the vertebral axis of the body, for the transference of more or less of the weight of the body upon limbs organised for its support on dry land; such a modification would have been useless to the fish, and not only useless, but a hindrance and a defect.

The pectoral fins, those curtailed prototypes of the fore-limbs of other Vertebrata, with the last segment, or hand, alone projecting freely from the trunk, and swathed in a common undivided tegumentary sheath, present a condition analogous to that of the embryo buds of the homologous members in the higher Vertebrata. But what would have been the effect if both arm and fore-arm had also extended freely from the side of the fish, and dangled as a long flexible many-jointed appendage in the water? This higher development, as it is termed, in relation to the prehensile limb of the denizen of dry land, would have been an imperfection in the structure of the creature which is to cleave the liquid element: in it, therefore, the fore limb is reduced to the smallest proportions consistent with its required functions: the brachial and antibrachial segments are abrogated, or hidden in the trunk: the hand alone projects and can be applied, when the fish darts forwards, prone and flat, by flexion of the wrist, to the side of the trunk; or it may be extended at right angles, with its flat surfaces turned forwards and backwards, so as to check and arrest more or less suddenly, according to its degree of extension, the progress of the fish; its breadth may also be diminished or increased by approximating or divaricating the rays. In the act of flexion, the fin slightly rotates and gives an oblique stroke to the water. For these functions, however, the hand requires as much extra development in breadth, as reduction in length and thickness; and mark how this is given to the so-called embryo or rudimental fore-limb: it is gained by the addition of ten, twenty, or it may be even a hundred digital rays, beyond the number to which the fingers are restricted, in the hand of the higher classes of Vertebrata. We find, moreover, as numerous and striking modifications of the pectoral fins, in adjustment to the peculiar habits of the species in Fishes, as we do of the fore limbs in any of the higher classes. This fin may wield a formidable and special weapon of offence, as in many Siluroïd fishes. But the modified hands have a more constant secondary office, that of touch, and are applied to ascertain the nature of surrounding objects, and particularly the character of the bottom of the water in which the fish

may live. You may witness the tactile action of the pectoral fins when gold fish are transferred to a strange vessel: their eyes are so placed as to prevent their seeing what is below them; so they compress their air-bladder, and allow themselves to sink near the bottom, which they sweep as it were, by rapid and delicate vibrations of the pectoral fins, apparently ascertaining that no sharp stone or stick projects upwards, which might injure them in their rapid movements round their prison. If the pectorals are to perform a special office of exploration certain digits are liberated from the web, and are specially endowed with nervous power for a finer sense of touch, as we see in the gurnards, where they compensate for the loss of the tactile property consequent on the hard covering of the exterior of the mouth in these mailed-cheeked fishes (*Joues cuirassées*, Cuv.)

Certain Lophioids living on sand-banks that are left dry at low water, are enabled to hop after the retreating tide by a special prolongation of the carpal joint of the pectoral fin, which fin in these 'frog-fishes' projects like the limb of a terrestrial quadruped and presents two distinct segments clear of the trunk.

The sharks, whose form of body and strength of tail enable them to swim near the surface of the ocean, are further adapted for this sphere of activity and compensated for the absence of an air-bladder by the large proportional size and strength of their pectoral fins, which take a greater share in their active and varied evolutions than they can do in ordinary fishes.

The flat-bodied Rays, equally devoid of an air-bladder, and with a long and slender tail, deprived of its ordinary propelling powers, grovel at the bottom; but have a still greater development of the hands, which surpass in breadth the whole trunk, and react with greater force upon it in raising it from the bottom, by virtue of a special modification of the scapular arch, which is directly attached to the dorsal vertebrae.

Nor is the pectoral member restricted in length where its office, in subserviency to the special exigencies of the fish, demands a development in that direction; the fingers of the *Exocetus* or *Dactylopterus*, are as long, and the web which they sustain as broad, as in the expanded wing of the flying mammal. Everywhere, whatever resemblance or analogy we may perceive in the ichthyic modifications of the Vertebrate skeleton to the lower forms or the embryos of the higher classes, we shall find such analogies to be the result of special adaptations for the purpose or function for which that part of the fish is designed.

The ventral fins or homologues of the hind-legs are still more rudimental — still more embryonic, having in view the compari-

son with the stages of development in a land animal — than the pectoral fins; and their small proportional size reminds the homöologist of the later appearance of the hind limbs, in the development of the land Vertebrate. But the hind limbs more immediately relate to the support and progression of an animal on dry land than the fore limbs: the legs are the sole terrestrial locomotive organs in Birds, whose fore-limbs are exclusively modified, as wings, for motion in another element. The legs are the sole organ of support and progression in Man, whose pectoral members or arms are liberated from that office, and made entirely subservient to the varied purposes to which an inventive faculty and an intelligent will would apply them. To what purpose, then, encumber a creature, always floating in a medium of nearly the same specific gravity as itself, with hind limbs? They could be of no use: nay, to creatures that can only attain their prey, or escape their enemy, by vigorous alternate strokes of the hind part of the trunk, the attachment there of long flexible limbs would be a grievous hindrance, a very monstrosity. So, therefore, we find the All-wise Creator has restricted the development and connections of the hind limbs of Fishes to the dimensions and to the form which, whilst suited to the limited functions they are capable of in this class, would prevent their interfering with the action of more important parts of the locomotive machinery.

In most fishes the ventral fins merely combine with the pectoral fins in raising, and in preventing as outriggers, the rolling of the body; but some very interesting modifications of the ventral fins, in relation to particular habits of certain species, may be noticed. In the Blennies, the Forked Hake (*Phycis*), the Forked Beard (*Raniceps*), and some other fishes, the ventral fins are reduced to filamentary feelers. In the Lump-suckers (*Cyclopterus*), the ventrals unite together, and combine with part of the pectorals to form a sucking disc or organ of adhesion, below the head, just as the opercular and branchiostegal fins are united together to form the gill-cover. In the long-bodied and small-headed abdominal fishes, the ventrals are situated near the anus, where they best subserve the office of accessory balancers; in the large-headed thoracic and jugular fishes, the loose suspension of these fins, and the absence of any connection with a sacral part of the vertebral column, permits their transference forwards, to aid the pectoral fins in raising the head.

The following short account of some experiments upon fish, made for the purpose of ascertaining the use of their fins, I give in the words of their gifted describer, PALEY, to whom Comparative Physiology owes many beautiful accessions to its teleological applications.

“In most fish, beside the great fin — the tail, we find two pairs of

fins upon the sides, two single fins upon the back, and one upon the belly, or rather between the belly and the tail. The balancing use of these organs is proved in this manner. Of the large-headed fish, if you cut off the pectoral fins, that is the pair which lies close behind the gills, the head falls prone to the bottom; if the right pectoral fin only be cut off, the fish leans to that side; if the ventral fin on the same side be cut away then it loses its equilibrium entirely; if the dorsal and anal fins be cut off, the fish reels to the right and left: when the fish dies, that is, when the fins cease to play, the belly turns upwards. The use of the same parts for motion is seen in the following observation upon them when put into action. The pectoral, and more particularly the ventral fins, serve to raise and depress the fish; when the fish desires to have a retrograde motion, a stroke forward with the pectoral fin effectually produces it; if the fish desire to turn either way, a single blow with the tail the opposite way sends it round at once; if the tail strike both ways, the motion produced by the double lash is progressive, and enables the fish to dart forwards with an astonishing velocity. The result is not only in some cases the most rapid, but in all cases the most gentle, pliant, easy, animal motion with which we are acquainted. However, when the tail is cut off, the fish loses all motion, and it gives itself up to where the water impels it. The rest of the fins, therefore, so far as respects motion, seem to be merely subsidiary to this. In their mechanical use the anal fin may be reckoned the keel; the ventral fins outriggers; the pectoral fins the oars; and if there be any similitude between these parts of a boat and a fish, observe that it is not the resemblance of imitation, but the likeness which arises from applying similar mechanical means to the same purpose." (XLI. p. 257.)\*

\* See also Carlisle Phil. Trans. 1806, p. 3.

## SYNONYMS OF THE BONES OF THE HEAD OF FISHES, ACCORDING TO THEIR SPECIAL HOMOLOGIES.

OWEN (xlv. 1843).		CUVIER (xxiii. 1828).		AGASSIZ (xxii. 1843).		GEOFFROY (xiv. 1824).		HALLEMANN (xlv. 1837).		MECKEL (xvii. 1844); WAGNER (xvii. 1844).	
Nos. <sup>1</sup>	Names.	Nos. <sup>2</sup>	Names.	Ib.	Names.	Names.	Names.	Names.	Names.	Names.	Names.
1.	Basioccipital.	5.	Basilaire.	Ib.	Basisphénal and otosphénal.	Corpus ossis occipitis.	Hinterhauptbeinkörper.				
2.	Exoccipital.	10.	Occipital latéral.	Ib.	Suroccipital.	Oecipitale laterale.	Gelenktheil, oder Seitlichen untern Hinterhauptbene.				
3.	Supraoccipital.	9.	Interpariétal.	Ib.	Interpariétal.	Squama occipitalis.	Hinterhauptschuppe.				
4.	Paroccipital.	8.	Occipital externe.	Ib.	Exoccipital.	Os mastoideum (c).	Seitlichen obern Hinterhauptbeine.				
5.	Basisphenoid.	6.	Sphénoïde postérieur.		Hyposphénal.	Sphenoideum basilare and progressus ascendens piscium.	Keilbeinkörper.				
6.	Alisphenoid.	11.	Grande aile du sphénoïde.	Ib.	Ptéreal.	Petrosum.	Felsenbein. <sup>3</sup>				
7.	Parietal.	7.	Pariétal.	Ib.	Pariétal.	Parietale.	Schielbein				
8.	Mastoid.	12.	Mastoïdien.		Ex-rupéal.	Squama temporis.	Zitsenbein. <sup>4</sup>				
9.	Presphenoid.	5.	Sphénoïde principale.	Ib.	Hyposphénal.	Sphenoideum basilare.	Keilbeinkörper.				
10.	Orbitsphenoid.	14.	Aile orbitaire.	Ib.	Ingrassial.	Ala magna sphenoidci.	Grosse Keilbeinflügel. <sup>5</sup>				
11.	Frontal.	1.	Frontal principal.	Ib.	Frontal.	Frontale.	Stirnbein.				
12.	Postfrontal.	4.	Frontal postérieur.	Ib.	Temporal.	Frontale posterior.	Schläfbeinschuppen (Bojanus).				
13.	Vomer.	16.	Vomer.	Ib.	Rhinosphenal.	Vomer.	Pflugschar.				
14.	Prefrontal.	2.	Frontal antérieur.	Ib.	Lacrymal.	Frontale anterior. <sup>6</sup>	Seitlichen Riechbeine.				
15.	Nasal.	3.	Ethmoïde.	Nasal.	Nasal.	Ethmoideum. <sup>7</sup>	Riechbeinkörper. <sup>8</sup>				
16.	Petrosal.	13.	Rocher.		In-rupéal.	Os innominatum.	Felsenbein (Oken.) <sup>9</sup>				
17.	Sclerotol.	10									
18.	Ethmoid.	15.	Sphénoïde antérieur.		Entosphenal.	Os innominatum (in Perch), Ala parva sphenoidci (in Carp).	Vordere oder kleiner Keilbeinflügel.				
19.	Turbinal.	20.	Nasal.		Ethmophysal.	Nasale.	Nasenbein.				
20.	Palatine.	22.	Palatin.	Ib.	Ib.	Palatinum.	Gaumenbein.				
21.	Maxillary.	18.	Maxillaire supérieur.	Ib.	Accidental.	Maxilla superior.	Oberkieferbein.				
22.	Premaxillary.	17.	Intermaxillaire. <sup>11</sup>	Ib.	Adnasal.	Intermaxillare.	Zwischenkieferbein.				



23.	Entopterygoid.	Pterygoidien interne.	Ib.	Herissal.	Pterygoideum internum.	Untere Keilbeinflügel. <sup>12</sup>
24.	Pterygoid.	Transverse.	Ib.	Adgustal.	Pterygoideum externum.	Keilbeinflügel (Köstlin.)
25.	Eptympanic.	Temporal.	Mastöidien.	Serrial.	Os quadratum s. tympanicum.	Obere Gelenkbein. <sup>13</sup>
26.	Mesotympanic.	Symplectique.	Tympanomalléal.	Uro-serrial.	Os symplecticum.	Griffelförmig Knoche.
27.	Pretympnic.	Tympanal.	Caisse, or os tympani.	Epicotyéal.	Pterygoideum posterius.	Scheibenförmig Knoche. <sup>14</sup>
28.	Hypotympanic.	Jugal.	Os carré, or os quadratum.	Hypocotyéal.	Os quadrato-jugale.	Unter Gelenkbein. <sup>15</sup>
29.	Articular.	Articulaire.	Ib.	Submalléal.	Os articulare.	Gelenkstück des Unterkiefers. <sup>16</sup>
29. <sup>a</sup>	Surangular.	Súrangularaire.	Ib.	Subcotyéal.	Os dentale.	Zahnstück des Unterkiefers.
30.	Angular.	Angularaire.	Ib.	Subvomerál.	Præoperculum.	Vorkiemendeckelstück.
31.	Spöñtal.	Operculaire.	Ib.	Subdental.	Os dentale.	Zahnstück des Unterkiefers.
32.	Dentary.	Dentaire.	Ib.	Tympanal.	Præoperculum.	Vorkiemendeckelstück.
33.	Præopercular.	Pré-opercule.	Apophyse styloïde du temporal.	Stapéal.	Opereulum.	Engentlich Kiemendeckelstück.
35.	Opercular.	Operculaire.	Ib.	Stapéal.	Opereulum.	Engentlich Kiemendeckelstück.
36.	Subopercular.	Sous-opercule.	Ib.	Inéal.	Suboperculum.	Unterkiemendeckelstück.
37.	Interopercular.	Inter-opercule.	Ib.	Malléal.	Interoperculum.	Zwischenkiemendeckelstück.
38.	Stylohyal.	Styloïde.	Styloïde de l'os hyoïde.	Stylo-hyal.	-	Griffelforsatz des Schläfensbein.
39.	Epiphyal.	Grande pièce latérale.	{ Branche } { latérale. }	Hyo-sternal.	-	{ Zungenhorn oder
40.	Ceratohyal.	Grande pièce latérale.	{ Branche } { latérale. }	Hyposternal.	-	{ Zungenbogen.
41.	Basi-hyal.	Petites pièces latérales.	Tête glénoïdale.	Apo-hyal and Ceratohyal.	-	
42.	Glosso-hyal.	Os lingual.	-	Côtes sternales.	-	
43.	Urohyal.	Queue de l'os hyoïde.	Corps de l'hyoïde.	Episternal.	-	Zungenbein.
44.	Branchiostegal.	Rayon branchiostège.	Ib.	Glosso-hyal.	-	Kiemenhautstrahlen.

<sup>1</sup> These are the numbers by which the bones of the head are indicated in the figures throughout the present work.

<sup>2</sup> These are the numbers by which the bones of the head of the Perch are indicated in the plates of the great 'Histoire des Poissons' of Cuvier and Valenciennes. In the 'Régne Animal,' the bones of the head of the Cod are indicated by letters.

<sup>3</sup> 'Hinterer Schläfenflügel,' of Köstlin. (xxxv.)

<sup>4</sup> 'Schuppentheil des Schläfenbein,' Köstlin. 'Felsenheit' desselben (os petrosum), Bojanus. (xxxvii.)

<sup>5</sup> 'Kleine Flügel des Keilbeins,' Bojanus. 'Vordere Schläfenflügel,' Köstlin.

<sup>6</sup> 'Ethmoideum cribrosum,' Bojanus.

<sup>7</sup> 'Sitzbein,' Köstlin.

<sup>8</sup> Not reckoned as part of the skull.

<sup>9</sup> The term 'intermaxillaire' had previously been applied, by Schneider, to the bone called 'os quadratum' in Birds, or 'os tympanicum.'

<sup>10</sup> 'Os transversum,' Köstlin.

<sup>11</sup> Gelenktheil des Schläfensbein, Köstlin. 'Paukering-knochen,' Bojanus.

<sup>12</sup> 'Gaumenflügel des Keilbein,' Bojanus. <sup>13</sup> 'Jochforsatz,' Köstlin. 'Flügelbein,' Bojanus.

<sup>14</sup> 'Gaumenflügel des Keilbein,' Bojanus. <sup>15</sup> 'Jochforsatz,' Köstlin. 'Flügelbein,' Bojanus.

<sup>16</sup> 'Gaumenflügel des Keilbein,' Bojanus. <sup>17</sup> 'Jochforsatz,' Köstlin. 'Flügelbein,' Bojanus.

## SYNONYMS OF THE BONES OF THE HEAD OF FISHES, ACCORDING TO THEIR SPECIAL HOMOLOGIES: — continued.

Nos.	OWEN (Xliv. 1843).	CUVIER (XXiii. 1828).	AGASSIZ (XXii. 1843).	GEOFFROY (Xiv. 1824).	HALLMANN (Xiv. 1837).	MECKEL (Xiv. 1824) ; WAGNER (XVii.).
45.	<i>Names.</i> Basibranchial.	<i>Names.</i> Chaîne intermédiaire d'osselets.	<i>Names.</i> Queue de l'os hyoïde.	<i>Names.</i> Basi-hyal.	<i>Names.</i> Ento-hyal, Uro-hyal.	<i>Names.</i> Kiemenbogen.
46.	Hypobranchial.	Pièce interne de partie inférieure de l'arcéau branchiale.	Pièce articulaire.	Thyréal.	- - -	- - -
47.	Ceratobranchial.	Pièce externe de la partie inférieure de l'arcéau branchiale.	Pièce branchiale.	Pluréal inférieur.	- - -	- - -
48.	Epibranchial.	Partie supérieure de l'arcéau branchiale.	Pièce branchiale.	Pluréal supérieur.	- - -	- - -
49.	Pharyngo-branchial.	Os pharyngien supérieur.	Pharyngien supérieur.	Pharyngeal.	- - -	Obere schlundknochen.
50.	Suprascapula.	Surscapulaire. <sup>2</sup>	Ib. <sup>2</sup>	Omolite. <sup>2</sup>	- - -	Schulterblatt. <sup>2</sup>
51.	Scapula.	Scapulaire. <sup>2</sup>	Ib. <sup>2</sup>	Omoplate. <sup>2</sup>	- - -	Vordere Schlüsselbein. <sup>2</sup>
52.	Coracoid.	Huméral. <sup>2</sup>	Clavicule. <sup>2</sup>	Clavicule. <sup>2</sup>	- - -	- - -
53.	Humerus.	Troisième os de l'avant bras qui porte la nageoire pectorale.	Huméral.	- - -	- - -	- - -
54.	Ulna.	Radial. <sup>2</sup>	Radial. <sup>2</sup>	Radial. <sup>2?</sup>	- - -	Vorderarmknochen.
55.	Radius.	Cubital. <sup>2</sup>	Cubital. <sup>2</sup>	Humérus. <sup>2</sup>	- - -	- - -
56.	Carpal.	Os du carpe. <sup>2</sup>	Carpe and metacarpe. <sup>2</sup>	Radius and Cubitus. <sup>2</sup>	- - -	- - -
57.	Metacarpo-phalanges.	Rayons de la pectorale. <sup>2</sup>	Ib.	Carpe and phalanges. <sup>2</sup>	- - -	Brustflossenstrahle.
58.	Epitoracoid. <sup>1</sup>	Os coracoïdien.	Coracoïde.	Os coracoïdiens.	- - -	Hintere Schlüsselbein
71.	Supraorbital.	Sur-orbitaire.	Ib.	- - -	- - -	Oberaugenhöhlenbein.
72.	Supratemporal.	Sur-temporal.	Ib.	- - -	- - -	Augenbogenschuppe (Boj.)
73 <sup>1</sup> .	Suborbital.	Sous-orbitaire.	Jugal.	Jugal	Ossa jugalia, <i>Bojanus</i> .	Unteraugenhöhlenbein. <sup>3</sup>
73.	Lachrymal.	Lachrymal.	Jugal.	Adorbital.	- - -	Thänenbein.
74.	Labial.	Labial.	Labial.	- - -	- - -	Lippenbein.

<sup>1</sup> This forms no part of a cranial segment of the endo-skeleton: it probably belongs, in general homology, to the hernal arch of the atlas.

<sup>2</sup> Not reckoned as parts of the skull.

<sup>3</sup> Jochbein, Meckel.

SYNONYMS OF THE BONES OF THE HEAD OF FISHES, ACCORDING TO THEIR GENERAL HOMOLOGIES.

Nos.*	OWEN (xlv. 1843).	BOJANUS (xxxvii. 1818). †	SMK (li. 1815).	GEOFFROY (xiv. 1824).	CARUS (i. 1828). §
1.	Occip. centrum.	<i>Ohrwirbel (Vertebra acustica)</i> . Ohr-Grundstück.	<i>Vertebra prima, seu occipitalis</i> . Corpus vertebrae prima.	Cycléaux des VIème et VIIème vertèbres. †	Grundbein oder Wirbelkörper (Unterer parallerer Tertiarwirbel) des I. Schädelwirbels.
2.	neurapophyses. spine.	Bogenstücke. Dornfortsatz.	Processus transversi vert. Iae. Pars inferior processus spinosi vert. Iae.	Périaux du VIème vertèbre. Epiaul du VIème vertèbre.	Bogenstücke oder Grund-platten des I. S. W. Obere deckplatten des I. S. W.
3.	parapophyses.	Undetermined.	Pars inferiores processus spinosi vert. Iae.	Epiaux du VIIème vertèbre.	Untere deckplatten des I. S. W.
50, 51.	hamapophyses. diverging appendages.	} Not recognised as bones of the head.	Ossa extremitatis thoracica.	} Not recognised as bones of the head.	} Obere Sternalthheil } des Halsrippen. Untere Sternalthheil } Glieder der Brustflosse.
52.	parietal Vertebra.		<i>Schmectwirbel (Vertebra gastatoria)</i> . Schmect-Grundstück. Bogenstücke. Dornfortsatz.		
53—57.	Par. centrum. neurapophyses. spine.				
5.	parapophyses.	Costae vertebrae Iae. seu occipitalis (xxxviii. p. 44.).	Os faciei iliacum.		Wirbelkörper des II. Schädelwirbels. Bogenstücke des II. S. W. Deckplatten des II. S. W.
38.	hamapophyses. haemal spine. diverging appendage.				Obere bogenstücke des Ites. Zwischenwirbels. Rückenheil der Eingeweide-rippe. Sternalthheil der Eingeweide-rippe. Eingeweide-wirbelkörper. Auswärts gekehrte Ausstrahlungen des Kopfs-eingeweidekettes.
39, 40.					
41—43.	Frontal Vertebra.	<i>Sch-wirbel (Vertebra optica)</i> . Undetermined. Sch-Bogenstücke. Dornfortsatz. Undetermined.	<i>Vertebra tertia, seu frontalis</i> . Corpus vertebrae tertia. Processus transversi vert. 3tae. Processus spinosus vert. 3tae. Os faciei scapulare.	Cycléal du IVème vertèbre. † Périaux du IVème vertèbre. Epiaul du IIIème vertèbre. Périaux du Vème vertèbre.	Wirbelkörper des III. Schädelwirbels. Bogenstücke des III. S. W. Deckplatten des III. S. W. Vordere abtheilungen d. obern grundplatten des I. S. W.
9.	Front. centrum. neurapophyses. spine.		Os faciei ischiale.		} 25. Obere rückenstücke der I. zwischen-rippe. 26. Untere-rückenheil der I. zwischenrippe. 27. Rudiment der I. Schädelrippe. 28. Obere sternal-theil der I. zwischenrippe. 29. Hintertheil des untern kopf-gliedmaasses.
10.	parapophyses.		Femur, tibia, fibula, tarsus, faciei.	Anneau inférieure du Vème vertèbre.	
11.	hamapophyses.			Undetermined.	
12.					
25—28.					
29, 30.					

\* These are the numbers by which the bones of the head are indicated throughout the present work.  
 † The determinations of Bojanus closely agree with those propounded by Oken, in 1807, in his original exposition of the vertebral homologues of the cranial bones, exemplified by the skull of the sheep. (lxix.)  
 § I have been induced to subjoin the synonyms from this work on the fundamental type of animal structures on account of the zeal and pains manifested in the attempt, and the artistic talent of the illustrations, rather than from the intrinsic merit of the results.  
 || Carus views the modified centrum of the occipital vertebra of the carp as including, also, the whole hernal arch of that vertebra.

Nos.	OWEN (xliv. 1843).	BOJANUS (xxxvii. 1818).	SPIX (li. 1815).	GEOFFROY (xiv. 1824).*	CARUS (i. 1828).
32.	<i>Frontal Vertebra.</i> Front, hæmal spine, diverging appendage.	Undetermined. Undetermined.	<i>Vertebra tertia, seu frontalis.</i> Phalanges pedis faciei. Os pubis faciei.	Undetermined. 31. 37. Anneau inférieure du Vième vertèbre. 35, 36. Anneau inférieure du VIIème vertèbre.	32. Vordertheil des untern kopf-gliedmaasses. Obere-hintere kopf-gliedmaasse.
13. 14. 15. 20.	<i>Nasal Vertebra.</i> Nasal centrum. neurapophyses. spine. pleurapophyses.	<i>Riech-wirbel (Vertebra olfactoria).</i> Riech-Grundstück. Bogenstücke. Dornfortsatz. Costa vertebrae 4te, seu æthmoidalis (xxxviii. p. 44). Undetermined. Undetermined.	Os mediastino-faciale. Ossa thyreoideo-facialia. Os faciei sternale. Os secundum hyoideo-faciale.	Cyclod du IIde vertèbre. † Périaux du IIde vertèbre. Epiäl du IIde vertèbre. Cataaux du IIIème vertèbre.	Wirbel-körper des IV. Schädelwirbels. Grundplatten des III. Zwischenwirbels. Deckplatten des IV. S. W. Ite. Antlitz-rippenpaar.
21. 22.	hemapophyses. hæmal spine.	Os ulnare faciei. Os radiale faciei.	Cataaux du Ière vertèbre. Périaux and Paraux du Ière vertèbre.	2te. Antlitz-rippenpaar. 3te. Antlitz-rippenpaar.	
23, 24.	diverging appendage.	Costæ vertebrae, 2dæ, et 3tiæ, seu sphenoidales (xxxviii. p. 44.).	Os hyoideo-faciale.	23. Cataaux du IVème vert. 24. Paraux du IIde. vert.	23. Schädel-rippenpaar des III. S. W. 24. Untere sternalthcil der Ite. Zwischen- rippe.
16. 17. 18. 19. 45. 46, 47. 48, 49.	<i>Splanchno-skeleton.</i> Capsules of organs of sense. Branchial arches.	Undetermined. Undetermined. Grundstück der Seh-wirbel.	Undetermined. Os crico-arytenoideo-faciale. Os coracoideo faciale. Undetermined.	Undetermined. Epiäux du Ière. vertèbre. Pleureaux, ou Côtes de la poitrine. †	Untere bogenstücke der Ites Zwischenwirbels. Wirbel-körper des 3tes Zwischenwirbels. Grund-platten des V. Schädelwirbels. 45. Bauchwirbelkörper. Untere theil des Eingeweiderippe.
71.	<i>Dermo-skeleton.</i> Supra-orbital scælebone.	Processus zygomaticus ossis frontis.	Undetermined.	Paraux du IIIème. vertèbre. Paraux du IVème. vertèbre.	Obere theil des Eingeweiderippe.
72. 73. 79. 74.	Supra-temporal do. First suborbital do. Suborbital do. Labial do.	Undetermined. Ossa jugalia.	Os claviculare faciei. Os humerale faciei.		3te Zwischenrippe. 2te Zwischenrippe.

\* "The number of distinct osseous pieces in the composition of the skull is greatest in fishes, and they correspond nearly with the theory of this part of the skeleton being composed of seven vertebrae, each consisting, as usual, of a body with four elements above, and four elements below. . . . The arches, which hang down from the sides of the vertebral column, are more like ribs in fishes than in higher classes, as the lower jaw, the os hyoides, the scapular arch, and that of the pelvis." (*Graaf*, xxviii. pp. 63, 65.) It does not appear that the scapular arch is recognised as essentially a part of a cranial vertebra. In xviii. the lower jaw is described as "the first of these inferior arches; the hyoid as "the second arch," (p. 572.) And, with regard to the posterior cranial vertebra, "the two external and two lateral occipitals form the upper arch, and the two occipital and two suboccipital bones constitute the lower arch." (xxviii. p. 543.) This is the view taken by Geoffroy of the posterior, his 7th, cranial vertebra.

† Body of cranial vertebra. (*Graaf*, xxviii. p. 62.)

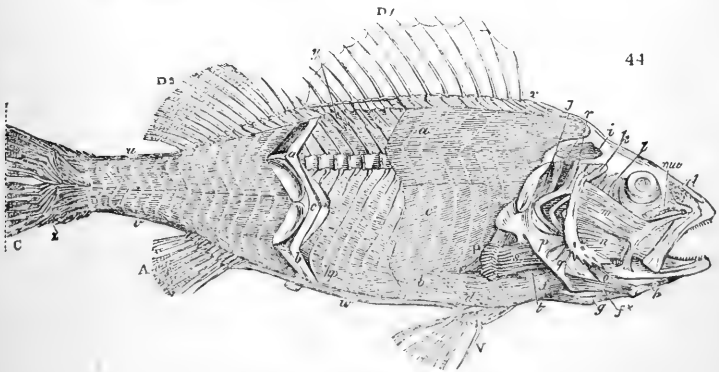
‡ LII. p. 217. "The branchial arches are connected with the os hyoides, which, by extending backwards behind these arches, produces a true thoracic sternum, considering the branchial apparatus as analogous to ribs for respiration." (xxvii. p. 573.) In xxviii. p. 65. the branchial arches are stated to be "the analogues of tracheal rings," which is likewise a view propounded by Geoffroy.

## LECTURE VII.

## MUSCULAR SYSTEM OF FISHES.

THE modification of the muscles, or active organs of motion, and their deviation from the fundamental vertebrate type, proceed concomitantly with the metamorphosis of the passive organs of motion, as the Myelencephala rise in the scale and gain higher and more varied endowments: therefore, as the segments of the skeleton preserve the greatest amount of uniformity in the lowest class, so does the principle of vegetative repetition most prevail in the corresponding segments of the muscular system.

The chief masses of this system in ordinary Osseous Fishes are disposed on each side of the trunk, in a series of vertical flakes or segments, corresponding in number with the vertebræ. Each lateral flake (*Myocomma*, *fig. 44. a, b, c*) is attached by its inner border to

Muscular system, *Perca fluviatilis*.

the osseous and aponeurotic parts of the corresponding vertically extended segment of the endo-skeleton, by its outer border to the skin, and by its fore and hind surfaces to an aponeurotic septum common to it and the contiguous myocommata. The gelatinous tissue of these septa is dissolved by boiling, and the muscular seg-

ments or flakes are then easily separated, as we find in carving a cod or salmon at table. The vegetative similarity of the myocommata of the trunk has led to their being described, by an abuse of synthesis, as parts of one individual 'great side-muscle'\*, extending from the occiput and scapular arch to the bases of the caudal fin-rays. The modifications of the cranial vertebræ impress corresponding changes on their muscular segments, and the essential individuality of these segments has, on the other hand, been lost sight of, through the opposite excess of analytic separation: special names are, however, conveniently applied to their constituent, and in fact often separated and independently acting, fasciculi.

The fibres of each myocomma of the trunk run straight and nearly horizontally from one septum to the next; but they are peculiarly grouped, so as usually to form semi-conical masses, of which the upper (*a*), and lower (*b*), have their apices turned backwards; whilst a middle cone (*c*), formed by the contiguous parts of the preceding, has its apex directed forwards; this fits into the interspace between the antecedent upper and lower cones, the apices of which reciprocally enter the depressions in the succeeding segment, and thus all the segments are firmly locked together, their general direction being from without obliquely inwards and backwards, and their peripheral borders describing the zig-zag course represented in *fig. 44*, in which one myocomma is represented partly detached, and others quite removed from the side of the abdomen. Thus, guided by the fundamental segmental type of the vertebrate structure, we come to recognise the 'grand muscle latéral' of Cuvier, as a group of essentially distinct vertical masses or segments. A superficial view of these segments, or an artificial analysis, has led to their being regarded as forming a series of horizontal muscles extending lengthwise from the head to the tail: the upper portions (*a*) of the myocommata being grouped together, and described as a dorsal longitudinal muscle with tendinous intersections directed downwards and backwards; the lower portions (*b*) as a ventral longitudinal muscle, with tendinous intersections directed downwards and forwards, whilst the margins of the middle portions of the myocommata (*c*) being curved, and usually bisected by the lateral mucous line, have been taken as indications of two intermediate longitudinal muscles. In the Sharks, indeed, instead of a curve the margins of the middle portions of the myocommata form an angle with the apex turned forwards; and in the Rays the dorsal segments of the myocommata have actually

\* "*Des grands muscles latéraux du tronc.* Il n'y en a essentiellement qu'un de chaque côté." (XXIII. i. p. 287.)

become insulated from the middle ones, and metamorphosed into a continuous longitudinal muscle (*fig. 45. a*); the change being essentially the same as that which the bony segments themselves undergo, when by anchylosis the sacral or cranial vertebræ



Caudal muscles, Mackerel. rel.

are blended into a continuous longitudinal piece.\* In the Mackerel Professor Müller found the middle fibres of the caudal myocommata disposed in two entire cones: *fig. 44. a*, is a transverse section of the tail to show the two concentric series of cut segments of the sheathed

cones, on each side the spine. †

In ordinary osseous Fishes the myocommata of one side are separated from those of the opposite side of the body by the vertebræ, by the interneural and interhæmal aponeuroses, and by the abdominal cavity and its proper walls (44, *h p*). The ventral portions recede from each other to give passage to the ventral fins (*v*), and the ventral and lateral tracts separate to give passage to the pectoral fins (*p*).

From this part forwards, portions of the myocommata undergo that change, analogous to anchylosis, which justifies their being regarded as distinct longitudinal muscles: here the separated ventral tract (subcoracoideus, *d, f*) derives a firmer origin from the ossified, though slender hæmapophysis of the atlas (epicoracoid), when it exists; and, in consequence of the peculiar forward curve of the strong hæmapophysis of the occiput (coracoid), it is not only expanded but unusually elongated, in order to be inserted there. But the serial homology of this fasciculus with the more normal ventral portions of the succeeding myocommata, the hæmapophysial attachments of which have not risen above the aponeurotic state, is unmistakable. The lateral portion of the anterior myocomma is attached to the upper end of the coracoid and to the scapula; the dorsal portion to the supra-scapula, par-occipital and supra-occipital. We recognise the dorsal portion of the posterior cranial myocomma in the fasciculus called 'protractor scapulæ' (*i*), which extends from the supra-scapula forwards to the parietal and frontal cristæ; and the middle portion in that which is exposed by the removal of the operculum, and which extends from the scapula to the mastoid in the

\* The continuators of Cuvier group the portions of the myocommata above the lateral line into three longitudinal muscles, compared respectively to the 'spinalis dorsi,' 'longissimus dorsi,' and 'sacro-lumbalis;' and the portions below the line into two muscles, viz. 'obliquus abdominis,' and 'rectus abdominis.' (XIII. i. pp. 305. 327.): but Professor Müller has well shown that the homologues of the obliquus abdominis do not exist in Fishes. (XXI. p. 223.)

† See XXI. tab. IX. fig. 14.

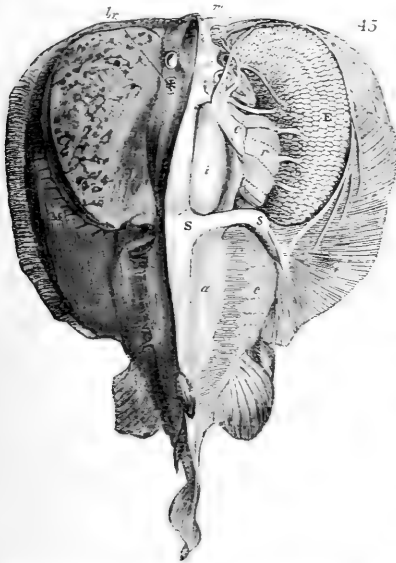
Perch (*j*); and, in some fishes, also, from the aponeurotic septum between the branchial and abdominal cavity, to the lateral and lower parts of the cranium. The protractor scapulæ in the Skate and Torpedo (45. *i*) is of considerable length, in consequence of the backward displacement of the scapular arch (*s*), and of great strength, by reason of the enormous pectoral appendage which the arch sustains. The representatives of dorsal and middle portions of a second cranial myocomma, in the Perch, are seen in the protractor tympani (44. *k*) and in the retractor maxillæ (*m*): a lower parallel subquadrate portion of the same segment passes from the preoperculum and tympanic pedicle to the coronoid process of the lower jaw, and forms the 'levator mandibulæ' (*n*). A cephalic continuation of the ventral segments of the myocommata is recognisable in the fasciculus which passes forwards in part (*g*) directly from the subcoracoideus (*d, f*), in part (*f'*) from the coracoid itself, to the basi- and uro-hyals, and which, if it does not perform, as Cuvier states, all the functions of the sterno-hyoid, represents the muscle to which that name is given in higher vertebrata, and proves it to be, in its general homology, the ventral segment of a cranial myocomma.

Other dismemberments of the cranial myocommata are modified to act specially upon the branchial arches: one of these fasciculi is the branchi-depressor (*o*): it rises from the basi-hyal, and passes obliquely backwards to be inserted into the pharyngeal or last branchial arch: two other fasciculi rise from the coracoid, and converge to be similarly inserted, forming the branchi-retractores (*p, q*). Several small fasciculi from the sides of the cranium are inserted into the epibranchials and the first two pharyngo-branchials, forming the branchi-levatores (*r*). There are also several transverse and oblique muscles, peculiar to the branchial arches. The ventral portion of the most anterior of the myocommata extends between the apex of the hyoidean and that of the mandibular arches: Cuvier recognises its special homology with the genio-hyoideus (*h*): it protracts the hyoid arch; it retracts the mandibular arch; and, when the lower jaw is left free to move upon the tympanic pedicle, it depresses the jaw. There is no digastricus or proper depressor of the mandible in Fishes. A strong muscle (*l*) from the postfrontal is inserted into the pterygoid; and partly through that, and partly by direct insertion into the pre-tympanic, it raises and protracts the tympanic pedicle. The operculum, or fin of the tympanic pedicle, has a levator or extensor (*k*) and a depressor muscle; the one rises from the mastoid, the other from the petrosal or alisphenoid.

In the Angler each of the long rays of the branchiostegal fin has



its proper muscles, which rise from the sustaining hyoidean arch. A more constant and important muscle rises from the operculum and suboperculum, and attaches itself to the inner surface of the branchiostegal rays, expanding over the whole membrane of the branchial chamber, and the more completely as the chamber becomes more circumscribed, and its outlet smaller. In the *Lepidosiren* the homologous muscle rises not only from the suboperculum but from the ramus of the jaw, and, meeting its fellow along a median raphé beneath the head and hyoid arch, represents the 'mylo-hyoideus'\* The muscular investment of the branchial chamber of the *Torpedo*



Muscles and Electric Batteries of the *Torpedo*. Carus.

(45. *r*) receives a fasciculus from the scapula, and sends another (*ib. o*) forwards to the cranium, from which the constrictor of the electric battery is continued.

In most osseous fishes there is a decussating pair of muscles (*depressores branchiostegorum*) which rise from the base of one ceratohyal, and are inserted into the lower branchiostegals of the opposite side.

The levator and abductor muscle (44, *s*) of the pectoral fin rises from the coracoid, and descends obliquely to its insertion by distinct fasciculi into the bases of the fin-rays: the depressor and abductor (*t*)

of the pectoral is deeper seated, and usually rises from the radius; it ascends to its insertion. There are two posterior or adductor muscles, whose fibres are oblique and decussate, but in opposite directions to the abductors, and tending also, in separate action, to raise or depress the fin. There are small special muscles in most fishes for divaricating the fin rays. The muscles of the pectoral fin are well developed in sharks; enormously so in the skate and torpedo, where the horizontal position of the fin involves further modifications. In *fig. 45.* the letter *s* shows the 'levator pectoralis,' and *t* the upper radiated muscle of the digits.

\* xxxiii. p. 358. pl. 24. fig. 4. a.

The pubic arch supporting the ventral fins, is attached in the Perch by a pair of slender longitudinal muscles (*w*) to the prolonged hæmal arch, sometimes called 'pelvis,' of the first caudal, and which, in its course to the pubic arch, surrounds the anus: the length of these muscles is moderate in the ventral fishes, considerable in the thoracic, and extreme in the jugular fishes, in which they simulate the 'recti abdominis.' It is probable that the external 'sphincter ani' of Mammals is the reduced homologue of these muscles. In general homology they must be viewed as the lowest ventral strip of a single myocomma, more or less developed in accommodation to the varying distance between the last abdominal and first caudal, its proper, hæmal arches, which variation relates to the office required to be performed by the ventral fins, or appendages of the last abdominal hæmal arch, in the different species of fishes. The protractors of the pubic arch are attached, when present, to the apex of the coracoid arch. Transverse muscles extend from one pubic bone to the other; and similarly disposed special muscles serve to contract the span of the mandibular and hyoidean arches. The levators and depressors of the ventral fin are inserted, as in the pectorals, by as many fasciculi as there are digital rays.

The deeper seated fibres of the segments, which together constitute the great lateral muscular masses of the trunk, alter slightly their direction, and, in the abdomen, represent the 'intercostals,' passing from one vertebral rib to another, and from one aponeurotic representative of the sternal rib (*inscriptio tendineâ, h, p.*) to another.

The myocommata answering to the neural and hæmal spines of the suppressed centres of the terminal caudal vertebræ, change their direction like those spines, slightly diverging from the axis of the trunk to be inserted into them: these modified terminal segments (*z*), by their connection with the interlocked myocommata of the great lateral masses, concentrate the chief force of those muscles upon the caudal fin. Special series of small dermal muscles are inserted into the rays of the dorsal, anal, and caudal fins: the dorsal and anal rays have each six fasciculi, two superficial (*x*) and four deep-seated (*y*), which rise from the expanded dagger-shaped interneural and interhæmal spines. Beneath the muscles of the tail-fin which terminate the lateral series of myocommata, there are long and slender fasciculi which rise directly from the compressed coalesced bodies of the terminal caudal vertebræ, and are inserted into the bases of the diverging rays. Other small muscles pass from the bases to act upon the more distant parts of the rays. Slender longitudinal muscles, 'supra carinales,' extend along the midline of the back from the occiput to the first dorsal, and

along the interspaces of the dorsal fins in the Cod: similar muscles extend from the last dorsal to the caudal fin (*u*) in the Perch; and 'infra-carinales' (*v*) extend from the anal to the caudal along the keel of the tail. In the *Gymnotus* the supra-carinales form a single pair, which extends from the occiput to the end of the tail. The modified cranio-dermal spines, which constitute the oval sucking-disc of the *Remora*, have a complex series of minute muscles, which raise or depress the transverse lattice-work; and thus become the means of giving the little feeble fish all the advantage of the rapid course of the whale or the ship to which it may have attached itself. The muscular and membranous webs of the coalesced pectorals and ventrals of the Lump-fish, form a sucker on the opposite surface of the body, by which it may safely anchor itself to the rock, in the midst of the turbulent surf or storm-tossed breaker.

The muscles of the gills, the eyeball, the air-bladder, and other special organs will be described with the parts they move.

The muscular tissue (myonine) of fishes is usually colourless, often opaline, or yellowish; white when boiled: the muscles of the pectoral fins of the Sturgeon and Shark are, however, deeper coloured than the others; and most of the muscles of the Tunny are red, like those of the warm-blooded classes. The want of colour relates to the comparatively small proportion of red blood circulated through the muscular system\*; and to the smaller proportion of red-particles in the blood of fishes: the exceptions cited seem to depend on increased circulation with great energy of action; and, in the Bonito and Tunny, with a greater quantity of blood and a higher temperature † than in other fishes. The deep orange colour of the flesh of the Salmon and Char depends on a peculiar oil diffused through the cellular sheaths of the fibres. The muscular fasciculi of Fishes are usually short and simple: and very rarely converge to be inserted by tendinous chords.‡ The proportion of myonine is greater in fishes than in other Vertebrata; the irritability of its fibres is considerable, and is long retained. Fishermen take advantage of this property, and induce rigid muscular contraction, long after the usual signs of life have disappeared, by transverse cuts and immersion of the muscles in cold water: this operation, by which the firmness and specific gravity of the muscular tissue are increased, is called 'crimping.'

There are many and great modifications of the muscular system of Fishes, especially in the aberrant orders at the two extremes of the class: Carus has illustrated some of these in the Plagiostomes (XLIII.

\* XLVIII, pp. 4. 16.

† L.

‡ XLIX, p. 3.

tab. iv.): a full and accurate detail of the myology of the Myxinoids, together with a philosophical comparison of the muscular system of Fishes generally with that of the higher Vertebrata, will be found in XXI. pp. 179-246. But the determination of the special, serial, and general homologies, and the recognition of the various individual adaptive modifications, of the muscles of Fishes, still remain a rich and little-explored field for the labours of the myologist.

The normal character of Ichthyic myology shows itself in the vast proportion of the vegetatively repeated myocommata, corresponding with the vertebral arches, as compared with the superadded system of muscles subservient to the action of their diverging appendages: but this condition, which, inasmuch as it deviates so little from the fundamental type, throws so much light upon the essential nature and homologies of the muscles of the Vertebrata, is not less admirably and expressly adapted to the habits and medium of existence of the Fish. The interlocked myocommata of the trunk constitute, physiologically, two great lateral muscular masses, adapted by their attachments, and especially by those of the anterior and posterior ends, to bend vigorously from side to side, with the whole force of their alternating antagonistic contractions, the caudal moiety of the trunk; producing that double lash of the tail by which the fish darts forwards with such velocity. When the lateral muscles are more violently contracted, so as to bend the whole trunk, the recoil may even raise and propel the fish some distance from its native element: thus the salmon overleaps the roaring cataract which opposes its migration to the shallow sources whither an irresistible instinct impels it to the business of spawning; and thus the flying-fish, in the extremity of danger, baffles its pursuer by springing aloft, and prolongs its oblique course through the air by the rapid fluttering of its outspread pectorals. When the anterior portions of the great lateral masses act from the trunk as a fixed point upon the head, they move it rapidly and forcibly from side to side: in this way the Siluri deal severe blows with their outstretched serrated pectoral spines; thus the Percoid and Cottoid Fishes strike with their opercular spines; and so likewise may the Saw-fish (*Pristis*), and Sword-fish (*Xiphias*), wield their formidable weapons, although their deadly cut or thrust is commonly delivered with the whole impetus of the onward course, the head being rigidly fixed upon the trunk.

The supra-carinales, combining with the dorsal portions of the myocommata, give tension to the region of the back, slightly raise the tail, and depress the dorsal fins. The infra-carinales, in combi-

nation with the retractores pubis, tend to compress the abdomen, to constrict the anus, and to depress the tail.

The muscles of the pectoral fins, though, compared with those of the homologous members in higher vertebrates, they are very small, few, and simple, yet suffice for all the requisite movements of the fins; elevating, depressing, advancing, and again laying them prone and flat, by an oblique stroke, upon the sides of the body. The rays or digits of both pectorals and ventrals, as well as those of the median fins, can be divaricated and approximated, the intervening webs spread out or folded up, and the extent of surface required to react upon the ambient medium in each change and degree of motion, can be duly regulated at pleasure.

LECTURE VIII.

NERVOUS SYSTEM OF FISHES.

THE neural axis is a simple continuous chord in the Lancelet (*Branchiostoma*, fig. 46, *md.*), of opaline sub-transparency, ductile

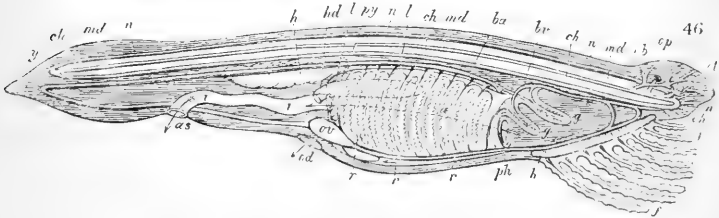


Diagram of Anatomy of the Lancelet, *Branchiostoma*.

and elastic, flattened, composed entirely of nucleated cells <sup>o</sup> showing a feeble indication of a median linear arrangement, which becomes more general and distinct at the anterior end, where the axis becomes cylindrical and terminates obtusely: the nerves, trigeminal (*ob*), and optic (*op*), in connection with this slightly modified part of the axis, indicate it to be the brain. This is the most simple persistent condition of the central organs of the nervous system known in the vertebrate sub-kingdom: it is typified by that of the Entozoa in the articulate sub-kingdom. In all other Fishes the fore part of the neural axis receives the vagal, trigeminal, and special-sense nerves.

\* Prof. Goodsir, lxxxix.

and develops and supports ganglionic masses, principally disposed in a linear series parallel with the axis: this part is called the 'brain' or encephalon: the rest of the axis I term the 'myelon'\*; retaining its columnar or chord-character, and, being lodged in the canal of the spinal column, it is usually defined as the medulla spinalis, spinal marrow, or spinal chord.

In the Lamprey the myelon is flattened, opaline, ductile, and elastic, as in the Lancelet and other *Dermopteri*: in typical Fishes it is inelastic and opaque, cylindrical or sub-depressed, of nearly uniform diameter, gradually tapering in the caudal region to a point in heterocercal Fishes, but swelling again into a small terminal ganglion † in most homocercal Fishes.

The Hunterian preparation of the skate (*Raia Batis*, No. 1347.) shows a slight (brachial or pectoral) enlargement of the myelon where the numerous large nerves are sent off to the great pectoral fins ‡: a feebler brachial enlargement may be noticed in the Sharks. I have not recognised it in osseous Fishes; not even in those with enormous pectorals adapted for flight, e. g. *Exocetus* and *Dactylopterus*: in the latter the small ganglionic risings upon the dorsal columns of the cervical region of the myelon receive nerves of sensation from the free soft rays of the pectorals, and the homologous ganglions are more marked in other Gurnards (*Trigla*), which have from three to five and sometimes six pairs, e. g. in *Trigla Adriatica*. § Similar myelonal cervical ganglions are present, also, in *Polyænemus*. In the heterocercal Sturgeon there is a feeble expansion of the myelon at the beginning of the caudal region, whence it is continued, gradually diminishing to a point along the neural canal in the upper lobe of the tail. In some bony fishes (Trout, Blenny), the caudal ganglion is not quite terminal, and is less marked than in the Cod or Bream, in which it is of a hard texture, but receives the last

\* Gr. *μυελος*, marrow. As an apology for proposing a name, capable of being inflected adjectively, for a most important part of the body which has hitherto received none, I may observe that, so long as the brief definitions, 'marrow of the spine,' 'chord of the spine,' are substituted for a proper name, all propositions respecting it must continue to be periphrastic, e. g. 'diseases of the spinal marrow,' 'functions of the spinal chord,' instead of 'myelonal diseases,' 'myelonal functions:' or, if the pathologist speaks of 'spinal disease,' meaning disease of the spinal marrow, he is liable to be misunderstood as referring to disease of the spinal or vertebral column. But, were the Anatomist to speak of the canal in the spinal marrow of Fishes as the 'myelonal canal,' he would at once distinguish it from the canal of the spinal column. The generally accepted term 'chorda,' or 'chorda dorsalis,' for the embryonic gelatinous basis of the spine, adds another source of confusion likely to arise from the use of the term 'spinal chord,' applied to the myelon, or albuminous contents of the spinal canal.

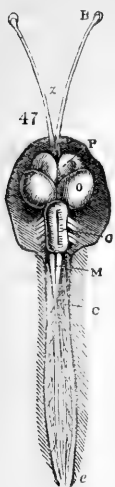
† LIII. p. 6.; LIV. p. 26. (in the Cod).

‡ This structure is accurately figured by Mr. Swan in LIV. pl. xi.

§ LIII. pl. 2. fig. 4. p. 106.; and LIII. p. 6., pl. 2. fig. 24, 25.

pair of spinal nerves. The absence of this ganglion in the Shark shows that it relates not to the strength of the tail but to its form, as depending on the concentration and coalescence of the terminal vertebræ; except, indeed, where such metamorphosis is extreme, as, e. g. in *Orthogoriscus mola*, and where it affects the entire condition of the myelon, which has shrunk into a short, conical, and, according to Arsaki (LIII. tab. iii. *fig.* 10.), gangliated appendage to the encephalon. A like singular modification, but without the ganglionic structure, obtains in *Tetrodon* and *Diodon*, in a species of which latter genus I found the myelon (*fig.* 47. M.) only four lines long in a fish of seven inches in length, and measuring three inches across the head. The neural canal in these Plecognathic fishes is chiefly occupied by a long 'cauda equina' (*ib.* c. e.). But, insignificant as the myelon here seems, it is something more than merely unresolved nerve fibres: transverse white striæ are discernible in it, with grey matter, showing it to be a centre of nervous force, not a mere conductor. In the *Lophius* a long cauda equina partly conceals a short myelon which terminates in a point at about the twelfth vertebra: in other fishes the myelon is very nearly or quite co-extensive with the neural canal, and there is no cauda equina, or bundle of nerve roots, in the canal: a tendinous thread sometimes ties the terminal ganglion to the end of the canal.

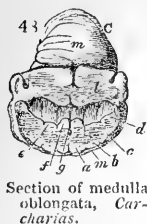
Brain and Myelon, *Diodon*.  
nat. size.



A shallow longitudinal fissure divides the ventral surface, and a deeper one the dorsal surface, of the myelon, into equal moieties: a feeble longitudinal lateral impression (*Sturgeon*) subdivides these into dorsal and ventral columns: in other fishes (*Cod*, *Herring*) these are separated by a lateral tract, and six columns or chords may be distinguished in the myelon; two dorsal or sensory, two ventral or motory; and two lateral or restiform tracts. A minute cylindrical canal extends from the fourth ventricle, beneath (ventrad of) the bottom of the dorsal fissure, along the entire myelon; this canal is not exposed in the recent fish by merely divaricating the dorsal columns. Both lateral halves of the myelon have grey matter in their interior, and white transverse striæ. Although many fishes (*Bream*, *Dorsk*) show a slight enlargement at each junction of the nerve roots with the myelon, the anatomical student will look in vain in the recent *Eel*, or *Lump-fish*, for that ganglionic structure of the myelon which the descriptions of *Cuvier*\* might lead him to expect.

\* XXIII. i. p. 323.; XIII. iii. p. 176.

As the myelon approaches the encephalon it expands, and the following changes may be here observed, in the Cod and Shark: in the ventral columns a short longitudinal groove divides a narrower median 'pre-pyramidal' tract (*fig. 48. a*), from a broader lateral 'olivary' tract (*ib. b*): in the dorsal columns a median 'funicular' tract (*ib. e*), is similarly marked off from a lateral 'post-pyramidal' tract (*d*); this is now, also, distinguished by a deeper fissure from the true lateral or 'restiform' tract (*c*), at the inferior part of which a distinct slender portion is also sometimes defined. The post-pyramidal



Section of medulla oblongata, *Caracharias*.

tracts diverge, expand and blend anteriorly with the similarly bulging restiform tracts, forming the side-walls of a triangular or rhomboidal cavity, called the 'fourth ventricle': the pre-pyramidal and olivary tracts forming the floor of the ventricle, are covered below by a thin superficial layer of transverse 'arciform fibres'\* (*ib. m*) concealing their boundary fissures. At the bottom of the ventricle the myelonal canal is exposed, and its sides swell and rise as rounded or 'teretial' tracts (*ib. f*) † from the floor of the ventricle, diverging slightly as they advance, and exposing an intermediate 'nodular' tract; this structure is well seen in the Sturgeon and Selache: two lateral prominent 'vagal' columns, also, project inwards into the ventricle, from the conjoined restiform and post-pyramidal tracts; these vagal columns present a series of nodules, corresponding with the fasciculi of the roots of the great vagal nerve in Selache: (Prep. 1311 *A*).

In the Cyprinoid fishes the median inferior tract rises into the ventricle, and is developed into a smooth hemispheric mass, the 'nodulus' (*fig. 51. h*): the conjoined post-pyramidal and restiform walls swell outwards, and form large lateral 'vagal' lobes (*fig. 51. h*): these are remarkably developed, and are nodulated in the Carp, which is so tenacious of life. The vagal lobes are enormously developed in the *Torpedo*; they join the trigeminal lobes, and present a yellowish colour in the recent fish: many non-nucleated cells are present in their substance; they give origin to the nerves of the electric organs, and have been called 'lobi electrici'; but the vagal lobes are scarcely less remarkable for their size in the Gymnotus, where they have no direct connection with any of the nerves of the electric organs. In the Cod the vagal ganglions are obsolete, and

\* Homologous with the "filamenti arciformi" of Rolando, LVIII. p. 170. t. i. fig. 2.

† Three are called "vordere pyramiden" by Dr. Stannius, LVI. p. 43.

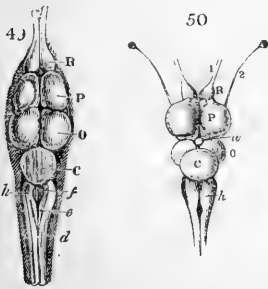


the nodulus slightly swells above, and obliterates the 'calamus scriptorius.' In the Luciopeca the vagal lobes are not very distinct, but they mark the commencement, and form the broadest part, of the very long medulla oblongata, the restiform tracts diminishing in size as they advance. In no other Vertebrata save fishes are the vagal lobes and the nodulus present.

The posterior pyramids, which are the encephalic continuation of the posterior myelonal columns, diverging as they are pushed aside by the deeper-seated tracts that form the floor of the fourth ventricle, and combining with the lateral columns to form the corpus restiforme and the basis of the vagal lobes, quit those columns to converge, ascend, and unite together above the anterior opening of the fourth ventricle: they there form either a simple bridge or commissure (*fig. 54. c*), or are developed upwards and backwards into a ganglionic mass, over-arching the ventricle; this mass is the 'cerebellum' (*figs. 47—53. c*). It is formed chiefly by the post-pyramidal columns, but doubtless derives some share of the proper lateral or restiform fibres, as the result of the previous confluence of these with the post-pyramids.

The cerebellum retains its earliest embryonic form of a simple commissural bridge or fold in the parasitic suctorial Cyclostomes, in the heavily laden ganoid Polypterus\*, and in the almost finless Lepidosiren (*fig. 54. c*) †; it attains its highest development, in the present class, in the Sharks, where it not only covers the fourth ventricle, but advances over the optic lobes, and in the Sawfish extends beyond them to rest upon the cerebrum: its surface is further extended in these active predaceous fishes by numerous transverse folds (*fig. 55. c*). In most osseous fishes the cerebellum is

a smooth convex body; hemispheroid (*pl. 50. c*), or transversely subelliptic (Eel), or longitudinally subelliptic (Lepidosteus, *fig. 49. c*), or an oblong body (Diodon, *fig. 47. c*), or it is depressed and tongue-shaped (Cod), or oval, or pyramidal (Perch): it is very rarely found extending forwards, as in *Echineis* and *Amblyopsis speleus* ‡ (*fig. 50. c*), over any part of the optic lobes; but often backwards over the whole fourth ventricle, as in the Cod, the Diodon; or over the major part of the ventricle, as in the Herring, the Eel; but sometimes covering only a small portion, as in the Lump-fish, the Lepidosteus,



Lepidosteus; nat. size.

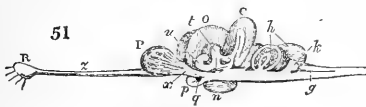
Amblyopsis; magnified.

\* xxv. p. 24. pl. ii. figs 5. 7.

† xxxiii. p. 339. pl. 27.

‡ See Dr. Wyman's excellent description of this fish, in LXXXVI.

and the Sturgeon. The relative size of the cerebellum, accordingly, varies greatly in different bony fishes: it is very small in the lazy Lump-fish, and extremely large in the active and warm-blooded Tunny, where also its surface shows transverse groovings. The cerebellum is unsymmetrically placed in the Pike and Flatfish (*Pleuronectidæ*), and is unsymmetrically shaped in the Sharks; it presents a posterior notch in the Herring, a transverse notch dividing it into an anterior and posterior lobe in the Lophius, and a crucial impression in the Skate. The cerebellum presents in many fishes a small cavity or fossa at its under part, continued from the fourth ventricle (*fig. 51. c*); it is solid in the Tench, the Gar-Pike, and the common Eel; some grey matter is usually found in its interior, with feeble indications of white striæ, but there is no 'arbor vitæ,' except in the Tunny and the Sharks.



Section of Brain, Carp.

The posterior 'crura cerebelli' are formed, as we have seen, by the posterior pyramids in conjunction with part of the restiform tracts: vertical fibres from

the side of the cerebellum continue to attach it to the sides of the restiform or trigeminal lobes, and some of these are continued, as arciform filaments, upon the under surface of the medulla oblongata: they answer to the 'crura cerebelli ad pontem' of mammalia; but, as there are no lateral lobes to the cerebellum in Fishes, these crura are rudimentary, and the 'pons' is absent. In the Shark they connect the sides of the base of the cerebellum with the 'restiform commissure' (*figs. 48 and 55. l.*). In most Fishes two fasciculi of medullary fibres proceed, as 'anterior crura,' from the under and fore part of the cerebellum, or converge from the lateral and fore part forwards, to form the inner wall or septum (*fig. 52. r*) of the optic lobes: these answer to the 'processus à cerebello ad testes' of the human brain: they are connected below their origin at the under part of the cerebellum by one or two transverse fasciculi of white fibres, forming the 'commissura ansulata,' which crosses the prepyramids just behind the 'hypocoria' (*fig. 53. n*). The inferior white surface of the cerebellum which forms the roof of the fourth ventricle is called 'discus cerebelli,' and from this part small tubercles project in a few fishes (*e. g. Blennius*).

The restiform columns, quitting the postpyramidal crura of the cerebellum, and having effected by their previous confluence therewith some interchange of filaments, swell out at the anterior lateral parts of the medulla oblongata, and give origin to the great trigeminal nerve. They here form considerable 'trigeminal lobes' in the

Loach and Herring (*fig. 52. i*), and also in the Sturgeon and Chimæra, where they are closely connected with a thick vascular mass of pia mater and arachnoid. The trigeminal lobes are large in the Skate; enormous and blended with the vagal lobes in the Torpedo: but in most Osseous Fishes (*Lepidosteus*, *Cod*,) they are not developed so as to merit the name of lobes. In the *Cod* the inner surfaces of the restiform bodies project into the fourth ventricle, and obliterate the fore part of the 'calamus' by meeting above it; this commissure, which is beneath the cerebellum, I call the 'commissura restiformis;'<sup>\*</sup> it is remarkably developed in the *Carcharias*, where it seems to form a small supplemental cerebellum beneath the large normal one, (*fig. 55. l*).<sup>\*</sup> In figure 48. the medulla oblongata is cut across, the fourth ventricle exposed from behind, and the restiform commissure, *l*, is raised: it has an anterior and posterior median notch.

The primary division of the brain, which consists of the medulla oblongata with the cerebellum and other less constant appendages in Fishes, is called the 'encephalon:' it is relatively larger, occupies a greater proportion of the cranium, and is more complex and diversified in this than in any of the higher classes of Vertebrata.

The next succeeding primary division of the brain, is called the 'mesencephalon:' it is usually the largest division in Osseous Fishes, and consists of two upper spheroidal bodies, called 'optic lobes' † (*o*), of two lower subspherical bodies, called 'hypoaria' ‡ (*n*), with intervening connecting walls enclosing a cavity, called the 'third ventricle,' which is prolonged downwards into the pedicle of the 'hypophysis' or pituitary gland (*p*), and upwards into that of the 'conarium' or pineal gland (*w*). The prepyramidal columns are continued forwards, along the floor of the fourth ventricle, where they are covered by a thin layer of medullary fibres, to the hypoaria and prosencephalon; some fibres blending with the wall of the third ventricle and the base of the optic lobes. The transverse 'ansulate' commissure, which unites or crosses the prepyramids before they penetrate the hypoaria, is very obvious in the Sturgeon and Perch, where it is figured by Gottsche (LVII. pl. iv., *fig. 7. l*): it may be regarded as the most anterior of the arciform filaments, which feebly represent the pons Varolii in fishes. The restiform columns are expended chiefly in forming the walls of the third ventricle and the base and exterior

\* The medullary lamina which Valentin describes as crossing the posterior point of the calamus in the Chimæra, may be the homologue of the restiform commissure. Müller's Archiv. 28. tab. 2. fig. 8, 9.

† 'Lobes creux,' Cuvier, xxiii. i. p. 310. But the cerebellum and hypoaria are likewise 'hollow lobes,' and the prosencephala are hollow in the *Lepidosiren* and Sharks.

‡ 'Lobes inférieurs,' ib.

walls of the optic lobes, a small part only being continued forwards to the cerebrum in most Osseous Fishes. The anterior cerebellar crura are chiefly lost in the inner walls, septum, or longitudinal commissure of the optic lobes.

These lobes are commonly of a subspherical figure, and larger than the cerebral lobes (as in *figs.* 47. 49. 51, 52. o.); they are often larger than the cerebellum, (*ib. ib.*); they are of equal size with the cerebellum in the Eel; are smaller than the cerebral lobes, but larger than the cerebellum, in the Polypterus and Lepidosiren (*fig.* 54. o.); they are smaller than either the cerebrum or cerebellum in the *Amblyopsis spelæus* (*fig.* 50. o.), and in the Sharks (*fig.* 55. o.). In the latter they bear the same proportion to the optic nerves and eyes as in other fishes, their small relative size depending on the advanced development of both cerebellum and cerebrum: in the blind *Amblyopsis* of the subterraneous waters, the diminution of the optic lobes relates to the almost total abrogation of the visual organ: but since both in the *Amblyopsis* and the equally blind *Myxine* these lobes are present, they cannot be exclusively the central ganglion of the optic nerve, nor their sole function that of receiving the impressions of the sense of sight, giving them form, and making them perceptible and tenable as ideas by the animal.

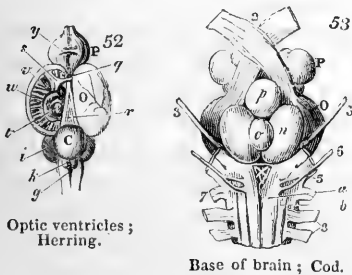
The optic lobes are hollow in most fishes. The exterior surface shows blended grey and white matter, the white fibres converging to the optic nerves on the outer side of the lobes, and passing transversely from one lobe to the other from their inner sides across the ventricle.\* Some of these fibres unite with the anterior crura of the cerebellum to form the 'longitudinal commissure' (*fig.* 52. r), which consists of two or four medullary fasciculi, decreasing in the Tench, increasing in the Cod, as they pass forwards.† On divaricating the optic lobes from above, their cavity or ventricle is exposed: its floor is variously configured in different fishes. There are one or two small white tubercles ('tuberculi optici,' *fig.* 51, 52. t) on each side of the back part of the septum: the Pike and Perch show four of these bodies, the Carp and Herring two; in the Carp they are oblong, juxtaposed, and were called 'tuberculum cordiforme' by Haller‡; they are not present in the Polypterus, Lepidosiren, Sturgeon,

\* These transverse fibres are analogous to the 'corpus callosum,' but not homologous with it, as Carus (xciv.), Cuvier (xxiii.), and Gottsche (lvii.) supposed.

† Analogous to the 'fornix,' but not homologous with it, as Gottsche contends (lviii. p. 266.)

‡ LIX. In the *Salmo Umbla*, where they are four in number, Haller called them 'corpora quadrigemina:' Cuvier, also, regards them as answering to the 'corpora quadrigemina' of Mammals (xxiii. i. p. 317.), mistaking a relation of analogy for one of homology.

or Plagiostome fishes. External to these tubercles the floor of the ventricle usually rises into a curved eminence with its convexity outwards; this is the 'torus semicircularis' of Haller\* (*fig. 52. w.*) In the Carp, where the great physiologist first described and named them, they are large, and much curved: in general the 'tori' describe only a small portion of a circle; and in some bony fish, as the Garpike, Loach, and Lump-fish, they are scarcely raised above the level of the floor of the ventricle. They are not developed in the Polypterus, the Lepidosiren or the higher Plagiostomes; and both tori and globuli are peculiar ichthyic developments in the ventricles of the optic lobes. The bottom of the optic ventricle anterior and external to the tori, is grey, and usually prominent (*fig. 52. v*), with white fibres radiating through it to rise and expand upon the walls of the lobes. The optic lobes have almost coalesced in the Polypterus, Lepidosiren, Amblyopsis, Eel, and Loach (*Cobitis*). Where they appear distinct externally, as in most osseous fishes, they are brought into mutual communication by one or two commissures, besides the so-called 'corpus callosum;' the anterior 'commissura transversa' is shown in the Herring (*fig. 52. s*); it crosses in front of the entry to the third ventricle. †



Optic ventricles; Herring.

Base of brain; Cod.

In the Myxine and Lepidosiren the prepyramidal fibres curve suddenly forwards and upwards before expanding into the floor and sides of the third ventricle, and they thus form a small protuberance beneath the basis of the optic lobes (*fig. 54. n*). In the Shark the same columns swell out laterally and form two small

protuberances (*fig. 55. n*), separated below by the vascular (hypophysial) floor of the third ventricle. In most osseous fishes the corresponding fibres of the prepyramidal tracts swell out suddenly, beneath the optic lobes, into two protuberant well-defined oval

\* LIX. t. iii. p. 201. It is analogous to, but not, as Gottsche supposes, homologous with, the 'thalamus opticus' of the Mammalian brain. It is neither analogous to nor homologous with the 'corpus striatum.'

† Cuvier affirms (xxiii. t. i. p. 316.) that this "necessarily answers to the anterior commissure of the cerebrum;" but it has only a remote analogy with it, in so far as the mechanism of the whole mesencephalon of Osseous Fishes resembles that of the cerebrum in Mammals, whilst the true homology of the mesencephalon does not extend beyond the parts immediately surrounding the third ventricle and the 'iter' to the fourth in the Mammalian cerebrum.

ganglions ('*hypoaria*,' *fig. 53. n*)\*: their bulk is increased by added grey matter, which variegates their outer surface; they are well developed in the common Cod, in which, as in some other fishes, they contain a cavity called '*hypoarian ventricle*.' In some *Salmonidæ* their surface is striated; in some *Cyprinidæ* (Tench) they are confluent; but commonly they are distinct, and have in their inferior interspace a vascular medullary depressed sac (the '*hæmatosac*,' *fig. 53. o*), usually oblong, as in the Cod, rarely bifid or cordiform, as in the Lump-fish. These prominences from the floor of the mesencephalon, posterior to the infundibulum and hypophysis, are peculiar to the brain of fishes, and, in their full development, are restricted to the typical osseous member of the class; they are absent in the lowest, and disappear in the highest orders; they are mere rudiments, or are wanting, in the Polypterus, as in the still more amphibioïd *Lepidosiren*.

The true vasculo-membranous infundibular downward prolongation of the third ventricle exists in all osseous Fishes, and extends from the anterior angle of the *hypoaria* where these exist: the infundibulum is commonly short and thick, so that the hypophysis is almost sessile, as in the Cod; but in the *Lophius*, the infundibulum is longer than the entire brain, and the hypophysis lies at the fore-part of the cranial cavity, far in advance of the cerebral lobes. † In the Cod the hypophysis (*fig. 53. p*) is a sub-spherical mass with an irregular or slightly nodulated surface, almost half the size of the human, so called, '*pituitary gland*,' and well exemplifies the vast proportional size of this constant appendage to the brain of Fishes. In the *Lepidosiren* the infundibulum is wide, and the hypophysis a white flattened discoid body (*fig. 54. p*). ‡ In all fishes it is richly supplied with vessels, and is closely attached to the floor of the cranium; but, although its early development checks or modifies that of the cranial vertebræ, it is not provided with a special chamber or '*sella*.' The prolongations of the fibres from the mesencephalon which expand into the prosencephalic or proper cerebral lobes rarely show any preliminary development of '*thalami*;' but the parts homologous with those recruiting ganglia are constantly indicated by the attachment of the conarium, or upper prolongation of the third ventricle.

The conarium (*figs. 50. 54, 55. w*) is as constant an appendage of the encephalon in Fishes, as the hypophysis; but is commonly only a vasculo-membranous pyramidal sac continued from the third ven-

\* Analogous to the '*corpora mammillaria*' of the human brain, but not homologous with them, as Arasaki (LIII.), and Desmoulins (LXXVIII.) supposed. Cuvier defines them as the '*lobes inférieurs*,' xxiii. i. p. 318.

† *Lx.* p. 56. t. ii. *fig. 1.*

‡ The hypophysis is marked *g* in xxxiii. pl. 27. *fig. 4.*, and is called '*mammillary body*' in *Lepidosiren annectens*, *ib.* p. 361.

tricle; the base expanding from between the anterior interspace of the optic lobes, and the apex directed forwards and attached to the roof of the cranium. Some medullary matter mingles with the membranous walls of the conarium in the Clupeoid and Cyprinoid Fishes: in some fishes there is grey matter in the conarium: in most it is membranous only, as in the Lepidosiren, Sturgeon, and Shark: in all it is highly vascular. In the Bream the conarium shows an analogous peculiarity to that of the hypophysis in the Angler, viz., in the length and tenuity of its attachment; but this consists of two distinct crura. The value of the constancy of the hypophysis and conarium consists chiefly in their marking the boundary line between the mes- and pros-encephala, although they belong to the mesencephalon and are both essentially vertical prolongations of the third ventricle through an interspace produced by the divarication of the main lateral columns of the encephalon.\*

The fasciculi continued forwards from the parietes of the third ventricle or mesencephalic basis, are principally those which may be traced back through the epencephalon to the anterior and lateral myelonal tracts, augmented by fibres from the grey centres or lobes through which they have passed, and retaining a small admixture of post-pyramidal fibres from the optic septum (*fig. 53, r.*). In Osseous Fishes the two cerebral crura, so constituted, rarely undergo any enlargement, homologous with the 'thalami,' where they form the anterior boundary of the third ventricle; but after a very brief course, as 'crura cerebri,' radiate into two small subspherical 'prosencephalic' masses † of grey matter (*fig. 53, r.*), situated anterior to the optic lobes, and there in great part terminate. A few of the medullary fibres extend along the base of the prosencephalon, receive a small tract of its grey matter, converge to the anterior interspace of its lobes, and either expand there into 'rhinencephala' (*figs. 49, 50, r.*), or are continued forwards and outwards, as 'rhinencephalic crura' (*figs. 47.*

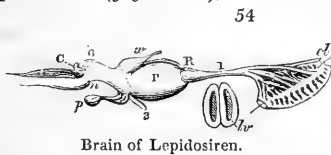
\* Is this vertical slit homologous with the encephalic ring perforated by the œsophagus in Invertebrata?

† Influenced by the inapplicability of the term 'hemispheres' to parts which are more commonly spheres or spheroids, and to avoid misconception by those who attach to the word 'cerebrum' the idea of the whole brain minus 'cerebellum' and 'medulla oblongata,' or who may restrict the term 'cerebral hemispheres' to the super-imposed masses of the lateral ventricles in higher Vertebrata, I shall apply the term 'prosencephalon' to the constant division of the brain in question, and prosencephalic lobes or prosencephala to its commonly distinct moieties. It is unfortunate for the student of anatomy that, in his introduction to the science by the human structure, he should become acquainted with these parts of the brain under the name of 'hemispheres,' as if they were two halves of an essentially spherical whole or single organ. In most Vertebrata the homologous parts are presented to our view under a form more agreeable to their true duplex nature.

51. 55. *z*), to form the olfactory lobes, or ganglia (*ib.* *R*), at some distance from the brain. Although the prosencephalic lobes are commonly in contact with the optic lobes, yet something analogous to the displacement of the rhinencephala may be seen in the prosencephala of the Polypterus and Lepidosiren, in which the procensephalic crura advance some way before they expand into the prosencephala: in the Plagiostomes, also, the prosencephalic crura (*fig.* 55. *x*) have a short independent course in advance of the optic lobes.

The prosencephala are distinguished from the optic lobes by their grey pinkish exterior, and, generally, also by their fissured or nodulated surface. The first of these characters must be looked for in recent fish: the second is more permanent, and may be seen in the preparations of the brain of the Eel (*Anguilla acutirostris*, No. 1309, *B.*); of the Lump-fish (*Cyclopterus*, No. 1309, *C.*); of the Gurnard (*Trigla lyra*, No. 1309, *D.*); and especially in the specimen of the brain of the Cod (No. 1309), which Hunter truly, though briefly, describes as follows:—“The *cerebrum* fissured; the *cerebellum* a long projecting body, also fissured in a less degree; the *nates* two projecting bodies: the optic nerves decussate one another.” This is the earliest recognition of the homology of the optic lobes with the anterior of the bigeminal bodies of the human brain. With regard to the ‘*cerebrum*’ of the Cod, a median tract or convolution is marked off by a longitudinal fissure, which extends along the back of each prosencephalon, defining also a posterior and inferior convolution; the median convolution is vertically fissured on its inner side. In the Amblyopsis (*fig.* 50. *P*) it is cleft anteriorly; and here, as in most fishes, the median longitudinal tract is the most constant subdivision of the prosencephalic superficies.

The large elongated prosencephala are smooth in Polypterus and Lepidosiren (*fig.* 54. *P*), and in the still more developed confluent mass



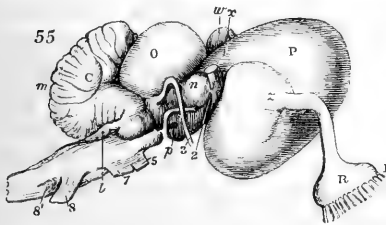
in the Sharks (*fig.* 55. *P*); the prosencephala are, also, smooth in the Myxines, where they are relatively smallest. The comparative anatomists, who have failed to recognise the true homology of the pro-

sencephalon in Osseous Fishes, appear to have been misled chiefly by its small proportional size, which is commonly that exhibited in these preparations of the brain of the Cod (*fig.* 53, *P*), the Carp, and the Globe-fish\*; in some species the prosencephalon is still smaller, as in the Gar-fish, the Herring (*fig.* 52, *P*), or the Lump-fish. The prosencephalon

\* The preparations exhibited and here alluded to are those numbered 1309, 1309 *k*, 1309 *m*.



equals the cerebellum in size, but is less than the optic lobes in the Perch and Bream ; it equals the optic lobes, but is less than the cerebellum in the Eel ; in the Stickleback and Gurnard the prosencephalon exceeds the cerebellum ; still more so in the *Lepidosteus*, but is less than the optic lobes ; in the *Lucioperca*, the *Amblyopsis*, and the Skate, neither the cerebellum nor the optic lobes are so large as the prosencephalon ; in the large Sharks their united size scarcely equals that of the prosencephalon ; and in the Salamandroid *Polypterus* and the *Lepidosiren* the prosencephalic lobes surpass all the rest of the brain, and manifest their true cerebral character and importance. In the *Amblyopsis* the relative magnitude of the prosencephalon is due to the diminution of the optic lobes in that blind fish ; in the *Plagiostomes* it is due to absolute development ; as it is, also, in the *Polypterus* and *Lepidosiren*, where the prosencephalon presents the closest similarity in form and structure to that division of the brain in the *Batrachian Reptiles* ; each lobe, for example, is elongated in the axis of the skull, and is of a subcompressed oval form, and has a large 'lateral ventricle' in its interior in the *Lepidosiren* (*fig. 54. lv.*) In the Skate the prosencephala coalesce into a subdepressed transversely elongated mass, their essential distinction being indicated by a mere superficial



Brain of Shark, *Carcharias*.

median fissure ; in the *Carcharias* (*fig. 55. P.*), the prosencephalon forms an almost globular mass, with scarcely a trace of a median fissure. Amongst bony fishes the prosencephalic lobes are more or less confluent in *Lucioperca sandra*, *Trachinus draco*, *Sargus*, *Mullus*, *Scomber tra-*

*chinus*, *Belone*, *Clupea harengus*, and *Clupea sprattus* ; they appear as distinct symmetrical spheroids in most other fishes, their union being reduced to a small transverse medullary band (prosencephalic commissure, *fig. 52. y\**). The symmetrical character of the prosencephala, as of the optic lobes, is wanting in most *Pleuronectidæ*.

The grey vascular neurine forms the greatest part of the prosencephalon in most osseous fishes ; the white fibres radiate into this substance, and rarely appear on any part of the exterior surface ; the white neurine, however, predominates in the *Plagiostomes* and *Lepidosiren*. As a rule, the prosencephalic lobes are solid ; but the preparation of the brain of *Carcharias* (No. 1310, A.) shows a deep ventricular fissure at the anterior and under part of the prosencephalon, with a vascular

\* Carus well recognises the homology of this commissure with that of the corpus striatum, called 'anterior commissure' in the human brain (i. p. 24.).

fold of membrane or 'choroid plexus' penetrating the fissure, which is continued forward into the crus of the olfactory lobe. The lateral ventricle is more extensive in the Lepidosiren, and is continued directly into the olfactory lobe.

The 'rhinencephalon' (*figs.* 47. 49. 50. 54. 55. *r*) consists of two lobes of grey matter, which receive the prolongations of chiefly white fibres from the prosencephalon and its crura, and give off the nerves to the olfactory capsule, whence they are termed 'olfactory lobes,' 'tubera,' or 'ganglia.' The rhinencephala are solid bodies, always distinct, wide apart from each other when remote from, and in mutual contact when near to, the rest of the brain, but never united by a commissure. The rhinencephalic crura (*figs.* 47. 51. 55. *z*) vary exceedingly in length. In the Lepidosiren (*fig.* 54.) they are feebly indicated by a continuous indentation circumscribing the base of each rhinencephalon (*r*), and defining it from the anterior end of each prosencephalon (*p*.) in Polypterus and Lepidosteus (*fig.* 49.), the indentation is deeper, and the attachment of the base of the now pyriform rhinencephalon sinks to the prolonged crus or basis of the prosencephalon. It is from this substratum that the rhinencephalic crura are prolonged in all osseous fishes; in some they are so short that the rhinencephala are partly overlapped by the prosencephala (*Trigla*), or rise into view immediately in front of them (*Amblyopsis*, *Anguilla*, *Cottus*, *Cyclopterus*); but in many fishes the rhinencephala are developed far in advance of the rest of the brain, and their crura are prolonged close to the olfactory capsules: this has led some excellent observers to deny the existence of olfactory lobes in such fishes; but the rhinencephala are truly present in both the Tetrodon\*, the Cod and Carp; they are merely removed to juxta-position with the olfactory capsules, with a concomitant prolongation of their crura. These crura, so prolonged, have been called 'olfactory nerves' by those who, failing to appreciate the true homology of the remote 'rhinencephala,' have described them as ganglionic swellings of the ends of the olfactory nerves.† These ganglions, wherever situated, consist of proper nervous matter over and above the mere radiation or expansion of the fibres of the so-called 'olfactory nerves.' The true olfactory nerve quits the rhinencephalon as a plexiform chord, or as a group of distinct fibres. If the thick olfactory nerve of the Gurnard be compared with the thick rhinencephalic crus of the Skate, or if the long olfactory nerve of the Eel be compared with the long rhinencephalic crus of the Cod, their

\* Dr. Desmoulins (*LXXVIII.* t. i. p. 169.), has erroneously denied the existence of the 'lobes olfactifs' in the Diodon; but in other fishes both he and Mr. Solly (*LXII.* p. 78.), have taken a correct view of the rhinencephala or 'olfactory tubercles.'

† Camper, *LXI.* p. 95.; Cuvier, *XXIII.* p. 321.

respective differences of structure will be readily appreciated: the crus is a compact tract of medullary with a small proportion of grey matter; the nerve is a bundle of nerve filaments: the medullary tract of the crus is fibrous, but the fibres are as fine as in the crus cerebri, and much more numerous and less easily separable than in the true olfactory nerve: in this there is no grey tract; it consists wholly of comparatively large and readily separable white fibres, which radiate at once upon the olfactory capsule: the divergence and radiation of the true end of the olfactory nerve is well seen in the *Lepidosiren* (*fig. 54. 1. ol.*). In the Sharks a ventricle is continued to each rhinencephalon along its crus from the prosencephalon. The olfactory nerve never forms a ganglion before spreading upon the olfactory capsule: the rhinencephalic crus, when prolonged to the capsule, always expands into a 'tuberculum olfactorium,' or rhinencephalon, before it transmits the true olfactory nerves to the capsule. In other words, the olfactory nerve conveys impressions to a proper centre or lobe, which in fishes may be situated close to the capsule, or close to the rest of the brain, and the length of its crus will be inversely as that of the nerve. To say, with Cuvier, that "the ganglion of the olfactory nerve is sometimes at its beginning, and sometimes at its end" (t. iii. xxiii. p. 146.), or that it occurs "in the course of the olfactory nerve, at a greater or less distance from the hemispheres" (xxvii. p. 227.), is, in fact, to deny the marked anatomical difference between the crus and the nerve proper; and to overlook the serial homology of the rhinencephalic crura with those of the prosencephalon. The olfactory lobes or rhinencephala themselves are serially homologous with the optic lobes. As to the prosencephalon, since this does not immediately receive or transmit any nerve, it resembles in this important character the cerebellum, and proceeds, even in the present class, to be developed to a degree beyond that of the ganglions of any nerves or organs of sense.

The more special homology of the prosencephalic lobes, under their normal proportions and solid structure in Osseous Fishes, with the parts of the complex and fully developed prosencephalon in Mammalia, will be made manifest as we trace the progress of that complication synthetically. Cuvier had already, by the opposite course of analysis, reduced the hemispheres in birds to the 'corpora striata,' with their commissures and a thin supra-ventricular covering. "Le corps cannelé," he says, "forme à lui seul presque tout l'hémisphère." (*Leçons d'Anat. Comp.* t. ii. 1799, p. 162.) But he failed altogether to recognise the homology of the prosencephala in Fishes. Since Arasaki's time their homology with the cerebral lobes of Reptiles, Birds, and Mammals has been generally recognised.

Girgensohn (LXIII. p. 155.) says they may well be compared with the 'corpora striata;' but he recognises the important difference, that, whereas these 'transmission ganglia' (durchgangsknoten) give passage to the radiating fibres of the cerebral crura in their course to other parts of the cerebrum in Mammals, those fibres terminate in the solid prosencephala of Fishes. The establishment of the lateral ventricles in the prosencephala of the Plagiostomes and Lepidosiren also show them to be something more than 'corpora striata.'

It now becomes highly important to note the mode of establishment of these cerebral ventricles: they are not formed by the super-addition of a layer or film of neurine overlapping parts answerable to the solid hemispheres in other Fishes, but are either central excavations, as you perceive in these elongated prosencephala of the Lepidosiren (*fig. 54. lv*), or they are deep fissures towards the under part, as in the coalesced hemispheres of the Shark; whence I conclude that the solid prosencephalon of Osseous Fishes is not a mere representative of a basal ganglion forming the floor of the ventricle of the hemispheres in the higher Vertebrata, where such ganglion is a medium of transmission or source of accession to the cerebral fibres; but that the fish's prosencephalon is the seat of the terminal expansion of the radiating medullary fibres of the cerebral crura. Dissection of the recent brain shows (as in *fig. 51. p*) that these fibres, besides being blended with grey matter, as in the corpora striata, are thickly covered with a layer of the same grey and highly vascular neurine of which the hemispheric convolutions in Mammals are chiefly formed; and it is most interesting to perceive on the superficies of the solid prosencephalon in many fishes the foreshadowing of the convolutions, which are not fully established until the Mammalian type is attained. The prosencephalon of the fish is far, indeed, from being a miniature model, but it may be regarded as representing the potential germ, of the complex cerebral hemispheres of man.

The average proportional weight of the brain to the rest of the body in Fishes is as 1 to 3000. A certain size seems to be essential to the performance of its functions, as a recipient of the impressions from the organs of sense; and it does not, therefore, vary in different species so as to accord precisely with the general bulk of the body. The size of the optic lobes, *e. g.* has a more constant and direct relation to that of the eyes, which soon acquire their full development. We find the entire brain proportionally greater in young than in old fishes: it acquires its full size long before the termination of the growth of the fish, if this has a fixed period. But as the head must grow with the growth of the fish, provision for occupying the in-

creasing capacity of the cranium is made by a concomitant development of the light cellular arachnoid, which has the further advantage of regulating the specific gravity of the head.

As the branchial respiration is a peculiarly active and important function in Fishes, and is served by an extraordinary apparatus of bony or gristly arches with their muscles, we may associate therewith the peculiar development and complexity of the medulla oblongata, as the centre of the vagal or respiratory nerves. The Carp and other cyprinoid Fishes, which have not the mechanical modifications for retaining water in contact with the gills, so characteristic of the Apodal, the Lophioid, and Labyrinthibranch fishes, are remarkable, nevertheless, for their tenacity of life out of water; and the peculiarly developed vagal lobes in them may relate to this maintenance of the power of the respiratory organs during a suspension of their natural actions.

The extensive gradation of the cerebellum between the extremes of structure presented by the Myxine and the Shark throws, as might be expected, more direct light upon its function. With regard to this, two views have been taken. According to one it is the organ of amativeness; according to the other it is the seat of the muscular sense, or the regulator of voluntary motion. Many experiments in which the cerebellum has been mutilated or removed in warm-blooded animals support the idea of its intimate relation with the locomotive powers. But to the conclusions from these experiments has been objected the possibility of the convulsive muscular phenomena having arisen from the stimulus on the remaining centres, occasioned by the mutilation or destruction of the one in question; and it may well be doubted whether Nature ever answers so truly when put to the torture, as she does when speaking voluntarily through her own experiments, if we may so call the ablation and addition of parts which comparative anatomy offers to our contemplation.

If, in reference to the sexual hypothesis of the cerebellum, we contrast the Lamprey with the Shark, we shall be led, by the much larger proportional size of the generative organs in the lower cartilaginous Fish, and by the observed fact of the male and female Lampreys entwining or wreathing themselves entirely about each other, mutually aiding in the expulsion of their respective generative products and so absorbed in the passion as to permit themselves to be taken out of the water and replaced there without interruption of the act, to expect a larger cerebellum in the Lamprey than in the Shark. But the reverse of this is the fact: the Lamprey has the smallest, and the Shark the largest, cerebellum in the class of

Fishes. If, on the other hand, we compare the Cyclostome and Plagiostome Cartilaginous Fishes, in reference to their modes and powers of locomotion, we shall find a contrast which directly accords with that in their cerebellar development. The Myxine commonly passes its life as the internal parasite of some higher organised fish: the Lamprey adheres by its suctorial mouth to a stone, and seldom moves far from its place: neither fish possesses pectoral or ventral fins. The Shark, on the contrary, unaided by an air-bladder, by vigorous muscular exertion of well-developed pectoral and caudal fins, sustains itself at the surface of the sea, soars, as it were, in the upper regions of its atmosphere, is proverbial for the rapidity of its course, and subsists, like the Eagle, by pursuing and devouring a living prey: it is the fish in which the instruments of voluntary motion are best developed, and in which the cerebellum presents its largest size and most complex structure. And this structure cannot be the mere concomitant of a general advance of the organisation to a higher type, for the sluggish Rays, that grovel at the bottom, though they copulate, and have in most other respects the same grade and type of structure as the more active Squaloid Plagiostomes, yet have a much smaller cerebellum, with a mere crucial indentation instead of transverse laminae. A more decisive instance of the relation of the cerebellum to the power of locomotion is given by the Lepidosiren, in which, with a more marked general advance of organisation than in the Ray or Shark, the cerebellum has not risen above the simple commissural condition which it presents in the Lamprey; the generative system, however, of the Lepidosiren is as complex as in the Plagiostomes, and is more extensive: but the fins are reduced to mere filaments, and the fish is known to pass half the year in a state of torpid inactivity. In the heavy-laden ganoid fishes the cerebellum is smaller than in the ordinary osseous fishes: the imbricated armour of dense enamelled bony scales must limit the lateral inflections of the tail; so we find in the Polypterus the cerebellum hardly more developed than in the Lepidosiren, whilst in the somewhat more active and predacious Lepidosteus it is the smallest of all the segments of the brain. In the grovelling Sturgeons the cerebellum offers an intermediate grade of development between those that characterise the above-cited Ganoids. Finally, amongst the normal Osseous Fishes, the largest and highest organised cerebellum has been found in the Tunny, whose muscular system approaches, in some of its physical characters, most nearly to that of the warm-blooded classes.

If we could enter the sensorium of the fish, and experience the kind of sensations and ideas derived from the inlet of their peculiarly

developed and enormous eyes, we might, perhaps, gain some insight into the office of the peculiar complexities of their large optic lobes : without such experience, we can at best only indulge in vague conjecture from the analogy of our own sensations. We find, when Nature reduces the organs of sight to such minute specks as can give but a feeble idea of the presence of light, sufficient, perhaps, to warn the Amblyopsis to retreat to the darker recesses of its subterranean abode, that the optic lobes are not reduced in the same proportion, but retain a form and size, which, as compared with their homologues in other animals, are sufficiently remarkable to suggest a function over and above that of receiving the impressions of visual spectra, and forming the ideas consequent thereon.

The anatomical condition of the prosencephalon, and its homology with the hemispheres of the bird's brain experimented on by M. Flourens (LXIV.), would lead to the belief that it was in this division of the fish's brain that impressions become sensations, and that here was the seat of distinct and tenable ideas : of such, for example, as teach the fish its safest lurking-places, and give it that degree of caution and discernment which requires the skill of the practised angler to overmatch. If different parts of the prosencephalon were special seats or organs of different psychical phenomena, such phenomena are sufficiently diversified in the class of Fishes, and are so energetically and exclusively manifested, as to justify the expectation, on that physiological hypothesis, of corresponding modifications in the form and development of the homologues of the cerebral hemispheres. Some species as, for example, the Shark and Pike, are predatory and ferocious : some, as the Angler and the Skate, are crafty : some, as the Sword-fish and Stickleback, are combative : some, as the Carp and Barbel, are peaceful, timid browsers : many fishes are social, especially at the season of oviposition : a few are monogamous and copulate ; still fewer nidificate and incubate their ova.

Now, if we compare the prosencephala of the Shark and Pike, fishes equally sanguinary and insatiable, alike unsociable, the tyrants respectively of the sea and lake, we find that those parts of the brain can hardly differ more in shape, in relative size, or in structure, in any two fishes. The prosencephalon of the Pike is less than the cerebellum, much less than the optic lobes ; in the Shark it exceeds in size all the rest of the brain ; in the Pike, the prosencephalon consists of two distinct lobes brought into communication only by a slender transverse commissure ; in the Shark, the hemispheres are indistinguishably blended into one large subglobular mass. If we compare the prosencephala of the Pike with those of the Carp, we find them narrow in the devourer, broad in the prey.

The Lophius lurks at the bottom, hidden in the sand, waiting, like the Skate, for its prey to come within the reach of its jaws: the difference in the shape, size, and structure of their prosencephala is hardly less than that between the Shark and Pike. The combative Stickleback has longer and narrower prosencephala than the cowardly Gudgeon. The nidificative and philo-progenitive *Callichthys* \* has neither the antero-lateral nor the posterior regions of the cerebrum more developed than in bony fishes generally.

#### MEMBRANES OF THE NEURAL AXIS.

Both brain and myelon are immediately invested by a thin but firm fibro-cellular and highly vascular membrane, the outer surface of which is usually covered by a stratum of pigment-cells, belonging properly to the central layer of the arachnoid, which has here coalesced with the proper vascular pia mater. This vascular membrane seems, therefore, to be coloured with dark points, and sometimes to be minutely speckled upon a silvery ground; and the pigmental stratum often accompanies the processes of the pia mater in the ventricles of the brain. There is commonly a remarkable development of the vascular and pigmental membrane over the fourth, or open-cephalic ventricle. I found such a mass concealing the rudimental cerebellum in the Lepidosiren; it is largely developed in the Sturgeon and Paddle-fish, where it is posterior to the cerebellum. The commonly considerable space between the brain and cranial walls is occupied by a peculiar loose cellular structure, filled by gelatinous or albuminous fluid, and by oily matter: in the Perch and Bream it seems to consist of an aggregate of minute spherical cells filled with fine colourless oil, the mass being traversed by blood-vessels. Cuvier † found the cells, which he compares to a kind of arachnoid, filled by a pretty compact adipose matter in the Tunny and Sturgeon. This modified arachnoid exists, but in less quantity, in the spinal canal, and even accompanies the cerebral nerves in their exit from the skull in some fishes with large nerve-foramina. The quantity of the cellular arachnoid above the cerebral lobes of Lepidosiren is a striking example of the piscine nature of that genus.

The primitive fibrous capsule of the neural axis, the unossified or unchondrified remains of which, or of its inner layer, form the so-called 'dura mater,' is most distinct in the low-organised *Dermopteri*;

\* *Callichthys littoralis*, or Hassar-fish of Demerara. See the specimen of its brain, No. 1309, *b*, and that of its nest and eggs, No. 3787, *b*. Phys. Series, and an account of its habits in the Zoological Journal, vol. iv. p. 244.

† xxiii. i. p. 309.



in the *Plagiostomi* it is reduced to a few thin shining aponeurotic bands closely adherent to the inner surface of the cartilaginous walls of the cranium and spinal canal; such traces of dura mater are more feeble and indistinct in Osseous Fishes, in which no proper continuous fibrous membrane can be distinguished from the inner periosteum of the walls of the cerebro-spinal cavity: no curtains of dura mater divide the cerebral from the acoustic compartments of the cranium in the Osseous Fishes.

#### NERVES.

The head is short and obtuse in the embryo fish; the ganglionic centres of the *olfactory nerves* are always originally developed in close contiguity with the prosencephalon; they govern the development of the rhinencephalic arch; and, as this advances in the elongation of the skull, and recedes from the prosencephalic arch, either the brain is co-elongated, the rhinencephalon retaining its primitive relation with its vertebra, and the prolonged crura occupying the narrow interorbital tract of the cranial cavity; or, the rhinencephalon retains its primitive juxtaposition with the prosencephalon, and the olfactory nerves are prolonged through the interorbital space, perforate or traverse a notch in the prefrontals, and expand, as a resolved plexus, upon the pituitary plicated sac.

The rhinencephalon accompanies its vertebra and recedes from the rest of the brain in *Salmo*, *Cyprinus* proper, *Brama*, *Tinca*, *Gadus*, *Lota*, *Hippoglossus*, *Clupea*, *Belone*, *Lucioperca*, *Cobitis*, the *Plectognathi*, and *Plagiostomi*; it retains its primitive contiguity with the prosencephalon in *Perca*, *Scomber*, *Esox*, *Pleuronectes*, *Blennius*, *Anguilla*, *Cyclopterus*, *Gasterosteus*, *Eperlanus*, *Leuciscus*, *Cottus*, *Trigla*, *Amblyopsis*, *Echeneis*, the *Ganoidei* and *Lepidosiren*. The condition of this difference would be an interesting subject of enquiry.

As the crus of the rhinencephalon is formed not only of fibres continued from the prosencephalon, but also, and in some fishes chiefly, of distinct white and grey tracts traceable along the base of the mesencephalon, in part as far back as the prepyramidal bodies, so the origin of the olfactory nerve has been described as characterised by the same complexity and extent; and it is true that in some instances, where the rhinencephalon is in contact with the prosencephalon, a small portion of the true olfactory nerve may be distinctly traced, *e. g.* in the Perch, backwards as far as the mesencephalon: just as we find in some fishes, Sturgeon, *e. g.*, a portion of the optic nerve traceable as far back as the cerebellum, and in the Eel to the hypoparia, and not exclusively terminating in the optic lobe. Most of the characteristics of origin and course attributed in works of Comparative

Anatomy to the olfactory nerves are to be understood of the *crura rhinencephali*. In the Lancelet the little ciliated olfactory sac (*fig. 46. ol.*) is brought into close contact with the rhinencephalic extremity of the neural axis. When the olfactory lobe or ganglion, in other fishes, is near the organ of smell, it sends off the nerves by numerous very short fasciculi: this characteristic multiplicity of virtual origins of the proper nerve is less conspicuous where the rhinencephalon is near the rest of the brain; but a careful analysis of the long olfactory nerve in the Eel, the Ide, or the Roach, shows that it is a fasciculus of filaments distinct from their origin.

The *optic nerves*, like the eyes, are of large relative size in most fishes: but where the organs of sight are small, the nerves are slender, as in the Silurus: they are still more slender in the Myxinoids, and they are scarcely discernible filaments in the Amblyopsis. In the Plagiostomes, the Sturgeon, the Polypterus, and the Lepidosiren, the optic nerves, traceable in part from the optic lobes, closely adhere to the basis of the mesencephalon, from which they seem to rise, anterior to the infundibulum, and are there connected together by a short transverse commissure; but they do not cross each other. In ordinary Osseous Fishes the exterior white fibres of the optic lobes converge to their under and anterior part, to form the chief part of the origin of the optic nerves; but a portion of the origin may be traced through the septum opticum to the cerebellum; and in the Eel, the Gar-pike, and the Lump-fish, a portion may be traced to the hypoaria: in the Cod some fibres of the optic nerve are derived from both the hypoaria and the wall of the third ventricle. The nerves are connected together at their origins by a commissure; but afterwards they cross one another without interchange of fibres (*fig. 53. 2*): sometimes the right nerve in its passage to the left eye passes under, sometimes over, the left nerve\*: rarely does one nerve perforate the other, as, *e. g.* in the Herring. The nerves are flattened where they decussate. In most Osseous Fishes the structure of the optic nerve is peculiar; it consists of a folded plate of membrane and neurine (*fig. 57. a*). The retina is formed by the unfolding of the nerve; and it would be a forced and overstrained analogy to compare it with the ganglion of the olfactory nerve (rhinencephalon), because this happens in some fishes to be close to the nasal capsule. The optic nerve escapes, in Osseous Fishes, either through the anterior fibrous wall of the cranium beneath the orbito-sphenoid, or through a notch or a foramen in that bone. In the Flounder one optic nerve is usually shorter than the other. In

\* I have seen both varieties in different individuals of *Gadus morrhua*. See also LXXV. ii. p. 203.

the Eel the nerves form, after decussation, a very acute angle in the axis of the body : in the Lump-fish they form an obtuse open angle.

Since there are no muscles of the eyeball in the Lancelet, the Myxinoids, the Amblyopsis, and the Lepidosiren, there are no motory nerves of the orbit. In the Lamprey a small third nerve and a fourth nerve, which are closely connected where they quit the cranium, again separate, the one to supply the rectus superior and rectus internus, the other the obliquus superior ; the filaments supplying the other muscles of the eyeball cannot be separated from the fifth pair. In all other fishes the sixth or *abducent* nerve has its proper origin, as well as the fourth and third. The third, or *oculo-motorius*, (*fig. 53. 55. 3.*) rises from the base of the mesencephalon, behind the hypoaria, or from the commissura ansulata ; it escapes through the orbito-sphenoid (Carp), or the unossified membrane beneath it (Cod), and is distributed constantly to the recti superior, inferior, and internus, and to the obliquus inferior : it also sends filaments into the eyeball ; the ciliary stem, or a branch of it, usually uniting with a branch of the fifth nerve, and sometimes, as in the Mackerel, Gar-pike, and Lump-fish, developing a small ciliary ganglion at the point of communication.

The fourth nerve, or *trochlearis*, rises from the back of the base of the optic lobes, between these and the cerebellum : it escapes either through the orbito-sphenoid (Carp), or the contiguous membrane (Cod), and is constantly and exclusively distributed to the superior oblique eye-muscle.

The sixth, or *abducent*, nerve (*fig. 53. 6*) rises from the prepyramidal tracts of the medulla oblongata, beneath the fifth, and, in most Osseous Fishes, by two roots, as figured by Mr. Swan (*LIV. pl. viii. fig. 2*), in the Cod. It usually closely adheres to the ganglionic origin of the fifth ; in the Carp and Lump-fish it receives a filament from the sympathetic, before its final distribution to the rectus externus : it escapes by the foramen or anterior notch of the alisphenoid, in advance of the fifth nerve.

This nerve, the *trigeminal* (*fig. 53. 55. 5*), enormous in all Fishes, from the Lancelet to the Lepidosiren, rises, often by two or more roots, from the restiform, or from the anterior angle between the olivary and restiform tracts ; in some fishes (*Clupeidæ, 52, i. Cyprinidæ*) from a special ganglion or enlargement of that part of the medulla oblongata : in a few (Conger, Lump-fish) by a smaller origin resolved into several roots. The trigeminus shows well its spinal (myelonal) character in Fishes, but its double root is more deeply buried in the medulla oblongata. In *Cottus, Blennius, Cobitis*, and *Leuciscus*, the

dorsal roots may be traced receding from the ventral ones, as they penetrate the medullary substance. The hinder roots in the Blenny join the facial and glosso-pharyngeal. Of the five roots of the trigeminal in the Sturgeon, the first, second, and fourth form a ganglion Gasserianum. In most Osseous Fishes the first branch is sent backwards, to form, in conjunction with a branch of the nervus vagus, the so-called 'nervus lateralis,' which escapes by a foramen in the parietal bone; the rest of the fifth emerges from the skull by a hole (Carp), or a notch (Cod), of the alisphenoid. The lateral nerve in the Cod receives only a slender filament of the vagus: it sends off a branch which runs along the sides of the interneural spines (*fig. 56. l.*), receiving branches from all the spinal nerves: it then curves down along the scapular arch, gives branches to the pectoral and ventral fins, supplies the great lateral muscular masses and the mucous canal, and sends a nerve along the interhæmal spines, which communicates with filaments from the corresponding spinal nerves: both interneural and interhæmal branches terminate in the spinal plexus supplying the caudal fin: thus all the locomotive members are associated in action by means of the nervi laterales.\* The mandibular division of the fifth (*r. mandibularis, seu maxilla inferioris*), consists chiefly of motory filaments which supply the muscles of the hyoid and mandibular arches, and send the '*ramus opercularis seu facialis*,' to those of the gill-cover: the sensory filaments supply the teguments of the sides of the head and under jaw, enter the dental canal, supply the teeth, and, in the Cod, the symphysial tentacle. The maxillary division (*r. maxillaris*) bifurcates behind the orbit, one branch passes outwards to supply the suborbital mucous canals and integuments on the sides of the head; the other, after sending a branch obliquely outwards, curves forwards along the floor of the orbit, gives off a palatine nerve (*r. pterygo-palatinus*), and supplies the integuments, mucous tubes, and teeth of the upper jaw: the supra-orbital division gives off the two ciliary nerves, one of which joins the ciliary branch of the third: it then supplies the olfactory sacs, and the integuments of the upper and fore part of the head.

In the Skate the large sensory branches of the fifth, sent to the integuments and to the singularly developed mucous canals, have ganglionic enlargements near their origins where they leave the main trunk. The first electric nerve is given off by the non-ganglionic part of the fifth in the Torpedo (*fig. 45. 5*), and many of the terminal filaments of the tegumentary branches of the fifth swell into peculiar

\* See the beautiful figure given by Mr. Swan of this nerve in *LIV. pl. vii.*

muco-ganglionic corpuscles.\* In the Sturgeon the snout and its tentacula are supplied by branches of the infra-orbital, not from the supra-orbital division of the fifth: the opercular or facial branch supplies, in addition to the gill-cover, the integuments and lips of the protractile mouth, and the pseudo-branchia: it communicates with the glosso-pharyngeal.

In the Lancelet the fifth nerve (*fig. 46. ob*) distributes many filaments to the expanded sensitive integument which represents the head, and forms the sides of the wide oral opening; it also supplies the oral tentacula. In the Myxinoids the same nerve supplies both the muscles and the integuments of the head, the tentacula, the nasal tube, the mucous membrane of the mouth and tongue, the hyoid and palatal teeth, and the pharynx. The trigeminus supplies the same parts in the Lamprey, but in a more compact manner as it were, *i. e.* by fewer primary branches: it also sends filaments to the rectus externus and r. inferior of the eyeball: the nerves to the muscular parts of the jaws and tongue arise in the Lamprey distinct from the fifth, and their trunk may be regarded as a *facial* nerve; one of the filaments of this joins a branch of the vagus to form a short 'nervus lateralis.'

Thus in reference to the motor filaments of the trigeminus or great spinal nerve of the head, those that form the portio dura or facial nerve in higher Vertebrata are not distinct from the rest of the trigeminus at its apparent origin, except in the Lamprey; in which, on the other hand, the motory filaments of the rectus externus, forming the sixth nerve of higher Fishes and Vertebrata, retain an associated origin with the trigeminal. The opercular or facial division of the fifth forms the hindmost portion of its apparent origin in the Perch †, it supplies the mandibular, opercular, and branchiostegal muscles; and sends off the branch to form, with a branch of the vagus, the dorsal division of the 'nervus lateralis.' In the elongated 'medulla oblongata' of the Sander (*Lucioperca*) the facial nerve has a distinct origin between the trigeminal and acoustic.

The *acoustic* nerve rises so close to the fifth, in the Skate, as to appear to be a primary branch of that great nerve; its distribution on the labyrinth is beautifully shown by Mr. Swan in LIV. pl. x. fig. 2. It communicates on the great otolithic sac with a motor branch from the vagus, which, after giving filaments to the posterior semicircular canal, passes out to supply the first and the adjacent surface of the second gill, and the faucial membrane. Mr. Swan calls this branch

\* LXXVI.

† XXIII. tom. i. p. 325. pl. vi. fig. v.  $\mu$ .

the glosso-pharyngeal; and says, "this nerve, on being touched near its origin in a recently dead animal, immediately produces a contraction of the muscular appendages of the gills." (ib. p. 41.) In the Cod the acoustic nerve (fig. 53. 7), which here, as in all fishes above the *Dermopteri*, is of large size, rises close behind, but distinct from the fifth pair, between it and the vagus: the acoustic nerve receives a filament from the vagus, extends in a crescentic form upon the labyrinth, expands upon the large sac of the otolite, and sends filaments to the ampulliform ends of the semicircular canals. In other Osseous Fishes (Pike, Blenny), the acoustic blends at its origin with the back part of that of the fifth: it sometimes communicates with the opercular branch of the fifth as well as with the glosso-pharyngeal of the vagus.

The *nervus vagus* has a development proportional to the extent and complexity of the branchial apparatus in Fishes, and is usually larger than the trigeminal; it rises (fig. 53. 55. 8) from the restiform tract forming the side of the medulla oblongata, and commonly from a specially developed lobe; and is distributed to the branchial apparatus, the pharynx and pharyngeal arches, the œsophagus and stomach; it sends also filaments to the heart, and to the air bladder when this exists (fig. 58. *t*). In the Lamprey a portion of the vagus combines with branches of the facial and hypoglossal nerves to form a *ramus lateralis vagi*, which extends to the middle third part of the body, where it terminates. In the Cod we saw that the 'lateral nerve' was formed chiefly by the trigeminal; but in many Osseous Fishes (*Cyprinus*, *Belone*, and *Cottus*) the proportions are reversed, and the lateral nerve is formed by a branch of the vagus, which receives filaments from the trigeminal nerve: in a few genera (*Salmo*, *Clupea*, *Acipenser*) it is formed exclusively by the vagus. In all these fishes it is continued very far back along the lateral or dorso-lateral region of the body; sometimes lodged deeply in the lateral mass of muscles, ex. gr. *Belone*, *Clupea*, and *Scomber* (Prep. 1384 of the Mackerel): but more commonly the nerve or a main branch lies just under the skin, and in the course of the lateral mucous line, as in the Salmon, and Sturgeon: in the Flat fish and Bull-heads (*Cottus*) it has both a deep-seated and a superficial branch. In the Carp and Herring the vagal 'ramus lateralis' sends off a strong branch to the dorsal fin: in the Gar-pike it sends, as in the Cod, large branches to the pectoral and ventral fins: it distributes its smaller branches to the skin and mucous ducts; and those in the Cod and Lump-fish anastomose with branches of the spinal nerves. In the Perch there are two 'nervi laterales' on each side; the dorsal one, which escapes through the

parietal bone, is formed by the union of a branch from the facial portion of the fifth with a branch of the vagus: the proper lateral nerve is formed exclusively by the vagus, and divides into a superficial branch supplying the lateral line, and a deep-seated branch, communicating with the spinal nerves, and supplying the myocommatal aponeuroses and the skin.\* Whether the vagus forms the whole or a part of the 'nervus lateralis' it transmits it from the fore part of its origin: the 'nervus accessorius' when present, which is rare in fishes, forms the hindmost part of the vagus, as in higher Vertebrata. The nervus lateralis chiefly supplies the myocommata, vertical fins and mucous line, peculiarly ichthyic parts either by their preponderating development, or their very existence: the nervus accessorius in mammalia, sends no branch to the 'spinalis,' 'semispinalis,' or 'longissimus, dorsi' — the reduced homologues of the dorso-lateral myocommata of fishes, but exclusively supplies the 'cleido-mastoideus' and 'cucullaris,' associating them with the respiratory actions of the thorax. The nervus lateralis may be in some respects analogous to the accessorius; it is not homologous with it.

The vagus sends supra-temporal branches to the head, and opercular branches to the gill covers. The usually double roots of the nervus vagus pass out, in most fishes, by a single foramen in the exoccipital bone. The fore part of the root is the largest, and is ganglionic: it is the true pneumo-gastric, supplying the gills and stomach; in the Tunny the branchial nerves are remarkable for their size and their radical ganglions. The hinder second origin is usually non-ganglionic, and is the source of the supra-temporal, glosso-pharyngeal and lateral nerves. Some filaments rising behind the vagus have been traced to the parts surrounding the brain within the cranial cavity. The intestinal terminal filaments of the vagus in Osseous Fishes communicate freely with the sympathetic. Each vagal nerve of the Sturgeon equals the spinal chord in size and rises by numerous roots. The vagal nerve has numerous roots, and an extensive tract of origin in the Sharks, in which a posterior fasciculus (*fig. 55. 8'*), representing the 'nervus accessorius,' can be best demonstrated.

There is no 'nervus lateralis' in the Myxinoids, but the gastric branches of the vagus are continued, united as a single nerve, along the intestine to the anus. The proportion of clear (organic) filaments to the opaque (animal) filaments in the vagus of fishes is much greater

\* xxiii. tom. i. pp. 325—327.

than in that nerve in higher Vertebrata, according to Bidder and Volkmann : which illustrates the progressive character of the individualisation (selbstständigkeit) of the great sympathetic.

The vagus is represented in the Branchiostoma by a branch sent from the fifth to the pharynx. In the Myxine its origin is close to that of the fifth. The peculiar erectile palatal organ of the Cyprinoids is wholly, and the peculiar electric organs of the Torpedo are, in great part, supplied by the very remarkable and characteristic vagal nerve of fishes.

The *first spinal* nerve rises usually by two roots, the dorsal one having a ganglion, rarely by non-ganglionic roots exclusively from the prepyramidal tracts: it usually emerges between the ex-occipital and the atlas, and divides into a small dorsal and a larger ventral branch: this communicates with the ventral branch of the next spinal nerve, and supplies the pectoral fin-muscles, the subcoradoideus, and the sterno-hyoideus (44. *f, f'*); it is called 'hypoglossal nerve' by some Ichthyotomists.

Each of the true spinal nerves has a dorsal or sensory, and a ventral or motory origin: sometimes each rises by a single root; sometimes, as in the Cod, by two or more roots. Both sensory and motory roots are long in most fishes: the sensory root is the largest, arises by more filaments, and further back than the motory roots in the Sturgeon.

In most Osseous Fishes one dorsal root goes to form the dorsal branch of the spinal nerve, and the other dorsal root joins the ventral branch of the same nerve: sometimes the ganglion is formed on the dorsal root of the dorsal branch, as in the Cod; more commonly upon the whole sensory origin of the nerve, where it emerges from the neural canal. In some fishes (Bream and Gar-pike) the ganglions on the dorsal root are situated in the spinal canal: more commonly (as in the Cod, the Ling, the Sander) the ganglions are external to the spinal canal. In both cases the nerve is increased in size beyond the ganglion and the union of the ventral root. This is well seen in the Skate, in which the ganglions are situated beyond the holes of emergence, and the junction of the two roots takes place quite exterior to the neural canal.\*

The connection of the nerve-roots with the myelon is weaker in fishes than in air-breathing animals: it is so easily broken in the *Dermopteri*, as to have led to a denial of its existence. † The best illustration of the peculiar combination of the dorsal and ventral

\* LXXVII. ii. p. 479.

† LIV. pl. x.



roots of the spinal nerves in Osseous Fishes, is that given by Mr. Swan from the Cod.\* The dorsal root sends a filament (*fig. 56. a*) upwards, which joins a ventral filament (*b*) from the preceding nerve,



56  
Connections of spinal and lateral nerves, Cod. (Mr. Swan.)

and forms the 'ramus dorsalis' (*d*): the dorsal root sends two filaments (*c*) downwards, which unite together, and with a ventral filament (*e*) of the same nerve to form the 'ramus ventralis' (*v*). The filament of the ventral root sent to the ramus dorsalis of the succeeding nerve perforates the lower division of the dorsal root of its own nerve. Thus each spinal nerve forms a dorsal and a ventral branch; the ramus dorsalis includes a sensory filament of its own nerve, and a motory filament of the antecedent nerve: the ramus ventralis is formed by a motory and a sensory filament of its own nerve; both rami 'ventrales' and 'dorsales' are associated together, and with the vagal and trigeminal nerves through the medium of the great 'nervus lateralis.'

The roots of the nerves distributed to the free, exploratory, pectoral rays of the Gurnards, rise from special ganglionic swellings of the cervical portion of the dorsal myelonal columns.

*Sympathetic.*—In the Myxinoid Fishes this nerve, or system of nerves, is represented by the intestinal branch continued from the confluence of the two nervi vagi. The best illustrations of the sympathetic in ordinary Osseous and Plagiostomous Fishes are those given by Mr. Swan, from the Cod† and the Skate.‡ Each trunk of the nerve extends in Osseous Fishes, from the side of the basis cranii (not entering the cranial cavity) to the tail, accompanying the aorta along the hæmal canal. Its first or anterior communication is with a branch of the fifth, and a filament is sent forward to the ciliary ganglion; and, in the Carp a filament joins the abducent nerve, to which Cuvier thought he had also traced a filament of the sympathetic in the Cod: the sympathetic next communicates with that anterior portion of the vagus (the glosso-pharyngeal?) which joins part of the acoustic nerve, and supplies the first partition of the gills: the sympathetic trunks also receive accessions from the trunks of the vagus; and, converging, intercommunicate by a cross branch: they then send nerves which join the gastric branches of the vagi, in order to form or join a splanchnic ganglion and plexus on the mesenteric artery from which plexus branches are sent to the intestines, pancreas, and spleen. The sympathetic trunks are continued on each side of the

\* Liv. pl. viii.

† Ib. pl. vi.

‡ Ib. pl. ix.

aorta, along the back of the abdomen, into the hæmal canal; communicate, in their course, with the ventral branches of each of the spinal nerves; supply the kidneys, the generative glands, and the urinary bladder, where this exists; and often, finally, blend together into a common trunk beneath the tail. Ganglions are sometimes found at the junction of the sympathetic with the fifth, as well as at that with the glosso-pharyngeal and with the vagus, before the great splanchnic is formed: small ganglions are more rarely discernible at the junction of the sympathetic with the spinal nerves.

The splanchnic ganglion of the Skate is a large fusiform body, of an ash-red colour; the succeeding ganglia on the trunks of the sympathetic are larger and more constant than in Osseous Fishes; but the intervening chords are semi-transparent.\*

#### SPECIAL ORGANS OF SENSES.

The essential character of the *Organ of Smell* in fishes is, that the pituitary membrane lines the concave wall of a sac with one or more apertures upon the external surface, and that, in the few exceptions in which it is extended into a canal communicating with the mouth or fauces, such naso-palatine canal is never traversed by the respiratory medium in its course to the respiratory organs.

The extremities of the olfactory nerves (*fig. 54, 55. 1*) expand upon the pituitary membrane, which is highly vascular, and is covered by ciliated epithelium: its extensive surface is packed into the small compass of the olfactory capsule by numerous folds. The capsule is formed by a fibrous membrane, which is sometimes supported by a cartilaginous, and more frequently by an osseous, basis, called the 'turbinal bone' (*fig. 30. 19*).

In the Dermopteri the olfactory organ is single: Dr. Kolliker † regards as such a small, blind, tegumentary depression (*fig. 46. ol*), beset with vibratile cilia, and connected with the anterior end of the quasi-brain of the *Branchiostoma*. The more obvious and satisfactorily determined olfactory organ of the Ammocete is in the median line, opening above the mouth in front of the brain-sac (*fig. 25. 19*), whence a narrow canal is produced backwards from the bottom of the sac to the base of the skull. In the Myxine the parietes of the olfactory canal are similarly situated, lined by a longitudinally-plicated pituitary membrane, and are strengthened by cartilaginous rings, like a trachea. The naso-palatine tube opens backwards upon the roof of the mouth; and this opening is provided

\* LIV.

† XXXII. p. 32. pl. ii. fig. 5 A: it should be looked for over the left eye-speck.

with a valve. In the Lamprey the flask-shaped nasal sac opens upon the top of the head: a simple membranous tube is continued from the expanded bottom of the sac, which dilates as it descends, but terminates in a blind end at the hypophysial vacuity (*fig. 26. hy*) of the base of the skull, where the mucous membrane of the palate passes over it entire and imperforate.\*

In all Fishes, save the Dermopteri, the olfactory organs are double: and they have no communication with the mouth. In Osseous Fishes they are situated on the sides of the snout, and are covered by the skin, which is usually pierced by two openings for each sac: the Chromides, and all the Wrasses with ctenoid scales, have a single opening for each nose sac; the anterior aperture in the biperforate sacs is often produced into a tubular process, which acts either by muscular power, or some modification of form, as a valve. It is provided with a moveable cartilage in the Conger; and the tubular nostrils of the Cyclopterus are in perpetual motion in the living fish. Both apertures in some Lophioid fishes are bell-shaped and pedunculate. In some Siluri a tentacle is continued from the external nasal tube. When the nasal sac is round, the pituitary plicæ radiate from its centre: when the sac is elongated, it is usually traversed by an axial partition with a row of transverse folds on each side. In a few Fishes these folds are further complicated by secondary processes. The Sturgeon presents the radiated type of the olfactory organ with secondary folds (*fig. 43. 19*); but, like the Polypterus and *Lepidosteus*, each nasal sac has a double aperture. The *Lepidosiren* has an elongated nasal sac, with the bi-serial arrangement of pituitary folds, and with a double aperture (*fig. 54. ol*); but neither of these communicate with the mouth: the peculiar position of the nasal sacs on the under part of the thick upper lip, may have deceived the German naturalists who have affirmed the reptilian nature of this animal on the erroneous supposition that the posterior aperture of the nasal sac communicated with the mouth: the cartilaginous capsule of the sac is fissured, or barred, reminding one of the more complex nasal cartilage in the *Myxine*.† In the *Plagiostomes* the nasal cavities are situated beneath the snout, near the angles of the mouth, especially in the Rays: each cavity has a single and commonly wide opening, defended by valvular processes,

\* *xxi. p. 43.*; *figs. ii. and iv.*

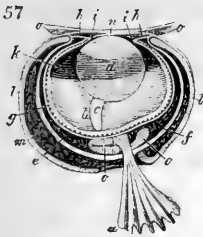
† In the first specimen of *Lepidosiren annectens* which served for my description of its anatomy in 1839, partial decomposition of the upper lip had destroyed the soft membrane extended over the mouth of the olfactory sac, which led me to the belief that it had but one opening; the second, or posterior opening, is outside the maxillary teeth.

with special muscles; these processes are supported by peculiar cartilages more or less intimately connected with the proper olfactory cartilaginous sacs, and representing the superadded cartilages of the 'alæ nasi' in higher Vertebrata.\* They have their proper muscles; whence we must conclude that these Fishes scent as well as smell: *i. e.* actively search for odoriferous impressions by rapidly changing the current of water through the olfactory sac.

The *Organ of Sight* makes its appearance in the lowest of Fishes, *e. g.* the Lancelet and Myxine, under as simple a form as in the Leech: a minute tegumentary follicle is coated by dark pigment, which receives the end of a special cerebral nerve. This simple eyespeck, the first mechanism for the appreciation of light, is repeated in the *Amblyopsis spelæus* (*fig.* 50. 2). Rudimental eyeballs covered by the skin exist in the *Apterichthys cæcus*: the small, but more complex eyes of the Lepidosiren, with crystalline and vitreous humours, choroid and sclerotic tunics, are also covered by the skin; but this becomes transparent where it passes over them, and, adhering to the sclerotic, forms a 'cornea.' The eyes of the Eel-tribe and the Siluroid Fishes are small: they are of moderate size in the Plagiostomes and Ganoids; but in most Osseous Fishes the eyes are remarkable for their large size, which becomes enormous in some, *e. g.* *Orthogoriscus* (Prep. 1665. A), *Myripristis*, *Priacanthus*. The eyes are usually placed in orbital cavities, one on each side of the head; only in the unsymmetrical Flat-fish are they both placed on the same side: in the Star-gazer (*Uranoscopus*) the eyes are approximated on the upper surface of a nearly cubical head, and are directed towards the heavens: in the Hammer-headed Sharks they are supported on long outward projecting pedicles.

The optic nerve (unfolded in *fig.* 57. *a*) usually perforates the eyeball obliquely out of its axis; but sometimes directly in its axis. In Osseous Fishes it is compressed where it passes through the sclerotic and choroid, and then forms the retina by unfolding itself like a fan spread out and bent into the form of a cone, leaving a fissure (*b*) where the free lateral borders meet after lining about two-thirds of the hollow globe. This fissure extends, of course, from the entry of the nerve to the anterior margin of the retina, and through it a fold of the innermost layer of the choroid extends into the vitreous humour, sometimes accompanied by the dark pigmental Ruyschian layer, as is shown in the preparation of the eye of the Bonito (No. 1651.). The fold of the vascular choroid, whether accompanied

\* See the description of these 'nasenflügelknorpel' in *xxi.* p. 171.



Eye of Sword-fish;  
one-third natural size.

by the pigmental layer or not, is called the falciform process' (*e*); it carries before it a fold of the proper tunic of the vitreous humour ('*membrana hyaloidea*'), and usually extends to the capsule of the lens (*d*), to which it is attached by means of a clear but firm substance, called the '*campanula Halleri*.'

The posterior or outer layer of the retina consists of the cellular basis, supporting the stratum of cylindricules, standing vertically upon its concave surface, with the interblended twin-fusiform corpuscles, both of which microscopic structures are more easily demonstrated in the present than in the higher classes of Vertebrata. Each twin-corpuscle is surrounded by a circle of cylindricules. The primitive nerve-fibres radiate over the cylindricules, without anastomosing, and terminate in free ends, not by loops, at the basis of the ciliary zone. A delicate but well-defined raised rim or 'bead' runs along both the anterior margins of the retina, and along those which form the falciform slit.

The crystalline lens (*d*) is spherical, large, firm, with a dense nucleus: it is almost buried in the vitreous humour, where it is steadied by the attachment of the falciform ligament to its thin capsule: the fore part projects through the pupil against the flat cornea, and so nearly fills the anterior chamber, that but a very small space is left for 'aqueous humour.'

The radiating fibres and elongated cells of the hyaloid tissue\*, with the interstitial 'vitreous humour,' present a firmer consistency than in the human eye, and show their intimate structure and arrangement more clearly under the microscope than in Mammalia.

The membranes situated between the retina and sclerotica, called collectively '*choroid tunic*,' are three in number: the external layer in Osseous Fishes, called '*membrana argentea*' (*e*), is composed chiefly of microscopical acicular crystals reflecting a silvery, or sometimes a golden lustre, with a delicate cellular basis, which assumes more firmness where it is continued upon the 'iris.' The second or middle layer is the '*membrana vasculosa*,' seu '*Halleri*,' (*f*), and, as its name implies, is the chief seat of the ramifications of the choroid vessels: it also supports the ciliary nerves. The innermost layer is the '*membrana picta*,' seu '*Ruysehiana*,' (*g*), also called '*uvea*,' which is composed of hexagonal pigment-cells, usually of a deep brown or black colour. In the Grey Shark (*Galeus*) the silvery layer

\* LXV.

is laid upon the central surface, not the periphery, of the choroid : (Prep. No. 1669.)

The formation of the iris by the production of all these membranes is well shown in this preparation of the eye of the Sword-fish (*Xiphias*, No. 1661.), where its thick base or 'ciliary ligament' (*h*) overlaps the convex border of the bony sclerotic. The pupil (*i*) is large and usually round: in many Plagiostomes it is elliptic: in the flat-bodied Skates and Pleuronectidæ, that grovel at the bottom and receive the rays of light from above, a fringed process descends from the upper margin of the pupil, and regulates the quantities of admitted light by being let down or drawn up like a blind. The muscular structure of the iris is very feebly developed in most fishes: it is best seen in the pupillary curtain of the Skate. The preparations of the Sword-fish's eye (Nos. 1661 and 1662.), and these of the eyes of the Grey-Shark (*Galeus*, No. 1670), and the Basking-Shark (*Selache*, No. 1670. *A.*), demonstrate the plicated anterior border of the uvea, forming the so-called 'ciliary zone, or processes' (*k*): they are the most complicated in the great Shark, where each process "consists of two or three minute folds, which, as they run forward, unite into one, and terminate in a point at the circumference of the iris\*:" but they do not, as yet, project freely inwards and forwards from the surface of the uvea.

The subordinate and accessory character of the sclerotic capsule (*l, l*) is illustrated in most Osseous Fishes by its deviation from the sub-spherical form of the true eyeball which it protects, and by the great quantity of cellular, and often also of adipose tissue (*m*), which fills the wide interspace between the sclerotic and the choroid. In the fibrous tissue of the sclerotic are usually developed the two cartilaginous or osseous hemispheroid cups already described (p. 103. *fig.* 30. 17); but in place of these, in the *Orthogoriscus*, as in the Plagiostomes, the capsule is strengthened by a single hollow, cartilaginous, perforated spheroidal globe. The anterior aperture is closed by the cornea (*n*), which is essentially a modified portion of the corium (*o*), adhering to, as it passes over, the usually thickened borders of that aperture. In this specimen of the eye of the *Xiphias* (No. 1661.) you may trace an accession to the cornea from the outer fibrous layer of the sclerotic, which undergoes the same change of tissue, and forms the posterior layer of the cornea. This transparent window of the eye-capsule is quite flat: its laminated structure is well displayed in the preparation of the cornea of the *Orthogoriscus* (No. 1665.), and a dark-

\* LXVI. iii. p. 147.

brown pigment here stains the soft integument or 'conjunctive membrane' (*o*), continued from the periphery of the cornea. In the preparation of the eye of the same fish (No. 1649.), a very delicate layer or lining membrane is reflected from the posterior surface of the cornea, answering to the 'membrane of the aqueous humour' of land animals: this humour exists in very small quantity, just enough to lubricate the iris in the eyes of Fishes: the medium through which the rays of light reach the eye needs no refractive aid from an aqueous fluid interposed before the lens in the globe itself.

Amongst the most characteristic peculiarities of the eye in the typical or Osseous Fishes is the so called 'choroid gland' (*o*): this is of the class of bodies called vascular- or vaso-ganglions: it usually presents a dark red colour, and lies between the 'silvery' and 'vascular' layers of the choroid, more or less encompassing, in the shape of a horse-shoe or bent magnet, the entry of the optic nerve. Dr. Albers\* discovered the rich marginal plexuses of vessels, whose trunks ('stämme') have their origin in this body, which he believed to consist also of a convolution of blood-vessels. Ordinary dissection, however, shows its compact substance to be arranged in parallel straight lines running between the convex and concave borders, and it has been called a 'muscle;' but I found that the supposed "fibres consisted, in reality, of minute, parallel, and closely disposed vessels," both arteries and veins. † Professor Müller has detected an unexpected relation of co-existence between the choroid vaso-ganglion and the pseudo-branchia, to which the Sturgeon, Lepidosiren, and the Plagiostomes are amongst the few exceptions having the pseudo-branchiæ, but not the vaso-ganglia. The genera *Silurus*, *Pimelodus*, *Synodon*, *Cobitis*, and all the Eel-tribe, have neither pseudo-branchiæ nor choroid vaso-ganglia. The most remarkable exceptional peculiarity in the structure of the eye in the present class is presented by the Anableps, the cornea of which is bisected by an opaque horizontal line, and the iris perforated by two pupils.

The general form of the eyeball, or rather its capsule, in Fishes, is a spheroid, flattened anteriorly, around which part the integuments commonly form a circular fold, yielding to the movements of the globe. In *Orthogoriscus* the circular palpebral fold is deeper, and is provided with a sphincter: in most Scomberoid and Clupeoid Fishes there is an anterior and a posterior vertical transparent fold or eyelid. In the eye of the *Galeus* (Prep. 1762.), you may see a nictitating membrane superadded to a well-developed circular palpebral fold of

\* LXXVI.

† LXVI. vol. iii. (1836); p. 145. prep. 1656. : and LXVII.

the skin. A conjunctive membrane is reflected from the circular eyelid over the third eyelid, which is placed at the nasal side of the orbit, and then passes over the anterior half of the eyeball. A strong 'nictitator' muscle rises from the temporal side of the orbit, and passing through a muscular and ligamentous loop, descends obliquely to be inserted into the lower margin of the third lid. The trochlear muscle has an insertion into the upper part of the circular lid, and depresses that part simultaneously with the raising of the third lid.\*

The proper muscles of the eyeball exist in all fishes except the Myxinoidea and Lepidosiren, and consist of the four *recti* and two *obliqui*: the latter rise from the nasal side of the orbit, and are inserted most favourably for effecting the rotatory movements of the eyeball: but the superior oblique has not its direction changed by a trochlea in the present class. In the *Galeus* there is a special protuberance of the upper part of the cartilaginous sclerotic for the common insertion of the *rectus superior* and *obliquus superior*; and a second protuberance below for the common insertion of the *obliquus inferior* and *rectus inferior*. The *recti* muscles rise in many Osseous Fishes from the sub-cranial canal †; the origin of the *rectus externus* being prolonged furthest back. But the *recti* muscles are most remarkable for their length in the Hammer-headed Sharks, since they rise from the basis cranii, and extend along the lateral processes or peduncles, at the free extremities of which the eyeballs are situated. In all Plagiostomes the eyeball is supported on a cartilaginous peduncle: this is short and broad in the Rays; longer and cylindrical in the Sharks; in the Selache it is articulated by a ball and socket synovial joint to a tubercle above and external to the entry of the optic nerve. A fibrous ligament attaches the sclerotic to the wall of the orbit in the Sturgeon and the Salmon.

The space between the eyeball and the orbit contains a soft bed of gelatinous and adipose substance: but there is no lachrymal gland in fishes. An apparatus to moisten the cornea was, of course, unnecessary in animals perpetually moving in a liquid medium. The cornea, which in most fishes is always exposed to that medium, is flat; it is, therefore, less liable to injury in the rapid movements of the fish, and being

\* Prof. Müller has established the family 'Nictitantes' for the Sharks, including the *Galeus*, *Carcharias*, and a few other genera, with the third eyelid.

† If, therefore, we regard this canal as part of the orbits, we must add the alisphenoid, basi-sphenoid, and even the basi-occipital to the bones enumerated at p. 103., as forming the chambers for the eyeballs and their appendages in Fishes; and this multiplicity of orbital bones interestingly repeats or parallels the characteristic formation of the otocranes or ear-chambers in the present class.



level with the side of the head, offers no impediment to those movements. This form of cornea diminishes the capacity of the aqueous chamber; but the aqueous humour is needed only to float the free border of the iris; and to make up for the small quantity of that humour, the convexity and refractive power of the lens are increased. To compensate for the deviation from the spherical form of the eyeball produced by the flattening of its fore-part, and the consequent weakening of the power to resist external pressure, the sclerotic capsule is cartilaginous or bony.

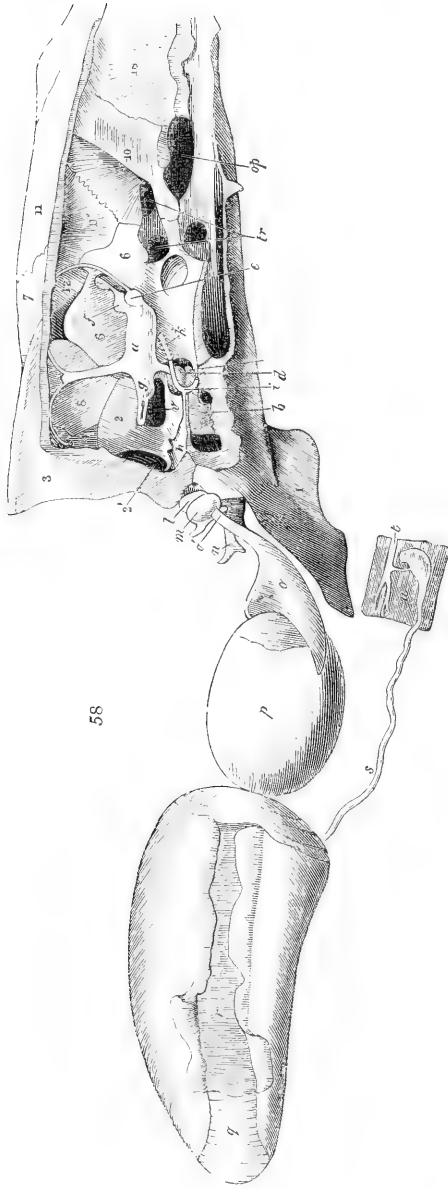
This beautiful chain of adjustments and interdependencies cannot but raise the rightly constituted mind to the contemplation of the attributes of that Creative Intelligence herein so strikingly displayed.

*Organ of Hearing.* — The cartilaginous capsules of the acoustic organs are precociously developed in all fishes: in the Myxinoids and Ammocetes they retain their primitive exterior position at the sides of the base of the proper cranium (*fig. 24. 16*); they are less conspicuous in the Lamprey (*fig. 26. 16*); they become involved in the thick cartilaginous walls of the cranium in the Plagiostomes; and, in Osseous Fishes, are walled up externally either by the surrounding cranial bones, or by a special ossification of the exterior part of the capsule itself, forming an ‘os petrosum,’ as, *e. g.* in the Cod (*fig. 30. 16*). In the dry-skull the ear-chamber appears as a large lateral compartment of the cranial cavity, and is formed as described in p. 102.

In the Myxinoids the membranous labyrinth is a simple annular tube, lined by vibratile cilia, filled with fluid, and supporting the ramifications of the acoustic nerve. In the Ammocete and Lamprey the labyrinth is specially attached to its cartilaginous capsule, and consists of a ‘vestibule’ and two ‘semicircular canals,’ each of which dilates, at its origin, into an ‘ampulla,’ which has some processes from its inner surface. The two canals again communicate with the vestibule, where they cross each other: the two divisions of the acoustic nerve first surround the ampullæ before they spread over the rest of the labyrinth.

In all other Fishes the membranous labyrinth consists of a vestibule and three semicircular canals; the vestibule dilating into one or more ‘sacculi,’ separated by a constriction, or by a narrow canal from the ‘alveus communis,’ and containing, besides the fluid called ‘endolymph,’ two or more masses of carbonate of lime, called ‘otoliths.’\* These are compact and crystalline in Osseous Fishes.

\* Figures of these bodies will be found in LXVI. iii. pl. 35.; in LXXI. LXVIII. and in LXXII., with microscopic figures of the crystals.



Organ of Hearing in situ, with air-bladder and ossicles, Carp (after Weber).

The largest (*fig. 30. 16''*) is an oval or round flattened body, striated and indented at the margins; convex, and sometimes grooved (*Ephippus*), on one side, more or less excavated on the other. The smaller otolite is less regular in its shape: there are often two of these. Each semicircular canal rises by an ampulliform end (*fig. 58. e, f, g*) from the 'alveus communis,' (*a*) and communicates, by the opposite end, either with another canal, or with the vestibule separately, without previous dilatation: two of the canals are sub-vertical in their course, and are anterior (*e*) and posterior (*g*) in relative position: the third canal (*f*) is external and horizontal. A septum is continued across the ampulla from the line where the division of the acoustic nerve enters: a large proportion of the nerve expands upon the sac of the otolites. All the parts of the labyrinth are of large size; yet the compartments of the otocrane which the semicircular canals traverse "are much too wide for them, and they are supported in these passages by a very fine cellular membrane."\*

The Chimæra and Sturgeons resemble the bony fishes in the form and position of the labyrinth. The otolites are a hard chalky substance in the *Lepidosiren*; in which fish, as well as in the *Plagiostomes*, the whole labyrinth is buried in the thick basi-lateral walls of the cranium: in both the cartilaginous capsule conforms more closely in size and configuration to the membranous labyrinth; its passages and compartments are lined by a delicate perichondrium, from which filaments are detached to support the semicircular canals. The vestibule is divided in the *Skate* and *Tope* into three compartments,—the 'alveus communis' (*fig. 59. a*); the sac (*ib. b*) and the cysticule (*ib. c*), and it has also a small cæcal appendage, called the 'utricule' (*ib. d*): the otolitic contents are like soft chalk, and are disposed in two masses; one very large, occupying the sac and the cysticule, the other small, and lodged in the utricule. A canal extends in *Sharks* from the vesti-



Organ of Hearing, Skate  
(Breschet).

bulbar capsule to a foramen at the upper part of the occiput, which is closed by the skin. In the *Rays*, besides this 'fenestra capsulæ' (*ib. v*), a membranous canal (*ib. o, p*) is produced from the vestibule itself, and, as *Hunter* well describes, "from the union of the two perpendicular canals (*fig. 59. p*); which is the case with all the *Ray* kind, the external orifice being small, and placed on the upper flat surface of the head." So minute and approximated are these 'outer ears,'† that

\* *Hunter*, vii. iii. p. 101.

† *Ib.* p. 389. pl. xxxiii. *fig. 1.* *Hunter's* original memoir "On the Organ of

Scarpa may be pardoned for overlooking them, though scarcely for the warmth with which he repudiates their existence.\* The 'meatus vestibuli' (*fig. 59, p*) is provided at its bent extremity with a special muscle (*ib. w*).

A true tympanic cavity and membrane, together with a cochlea, are absent in all Fishes. But in many Osseous species a communication is established, either by tubular prolongations, or by chains of ossicles between the acoustic labyrinth and the air-bladder. Weber† discovered the latter interesting structure in the Carp, Loach, and Sheat-fish. A canal is sent from the sac of each vestibule (*fig. 58, b*), to a common 'sinus impar' (*ib. h*) in the substance of the basi-occipital: this communicates on each side by a small orifice with two subspherical 'atria,' on the body of the atlas, close to the foramen magnum, which 'atria' are supported externally by the ossicles *l* and *m*, and, by means of the large ossicle *o*, are brought into communication with the fore part of the air-bladder (*p*). Both the atria and common sinus are filled by the endolymph, and from the fore part of the sinus a 'canalis furcatus' (*ib. i*) is produced, the blind ends of which penetrate the alisphenoids. In the groveling Loach (*Cobitis barbatula*), the air-bladder would seem to exist chiefly in subserviency to the organ of hearing. It is so small as to be wholly included within the singularly modified parapophyses of the second and third cervical vertebræ, which are expanded and coalesced so as to form a large 'bulla ossea' beneath their centruns.‡ The three ossicles on each side, which bring the air-bladder into communication with the 'atria' of the labyrinth, are also concealed by the fore part of the parapophysial bullæ: it is plain, therefore, that they are not dismemberments of those lateral or transverse apophyses of the vertebræ; and, with regard to their relation to the 'ossicula auditûs' of the tympanic cavity in Mammalia, Weber mistook a relation of analogy for one of homology, when he called them 'malleus,' 'incus,' and 'stapes.' They belong, like the capsules of the special organs of sense, to the 'splanchnoskeleton.' And since the vestibule is prolonged by the 'atria' into the neural canal of the atlas, this vertebra must be added, in the Cyprinoid and Siluroid Fishes, to the parts of the cranial verte-

Hearing in Fishes" was printed in the volume of the Philosophical Transactions for 1782, not, as Breschet states, in the year 1786. (LVIII. p. 58.)

\* "Hunterum autem atque Monroum vehementer super hac re sibi hallucinatos fuisse." (LX. pp. 1, 2.)

† LXXIII.

‡ Mr. Yarrell, who has given a figure of these singularly modified parapophyses of the Loach (LXXIX. i. p. 380.) compares them to 'scapulæ;' but I find the pectoral fins attached to the true scapular arch, and this suspended as usual to the paroccipitals, in the *Cobitis barbatula*.

brae enumerated at p. 102., as entering into the formation of the chamber of the acoustic organ. In the Herring a tubular prolongation of the fore part of the air-bladder advances to the basi-occipital, and bifurcates; each branch penetrates the side of the base of the skull, again bifurcates, and terminates in two blind sacs, which are in contact with similar cæcal processes of the labyrinth. In the *Holocentrum* and *Sargus*, cæcal processes of the swim-bladder also diverge, to attach themselves to the membrane closing the part of the otocrane containing the sac of the great otolite.

In Osseous Fishes the sonorous vibrations of their liquid element is communicated by the medium of the solid parts of their body, and in some species, also, through the vibrations of the air in the air-bladder, to the liquid contents of the labyrinth. In the Plagiostomous Fishes the resonance in the walls of their cartilaginous cranium is less than in the bony skull of ordinary fishes; but the labyrinth is wholly inclosed in the cartilage; and a further compensation is made by the prolongation of its chamber to the surface of the body in some, and by a similar prolongation of the membranous labyrinth itself in others. The position of the external orifices on the top of the head in the Skate tribe, may relate to the commonly prone position of these flat fishes at the bottom of the sea. Professor Müller concludes, from his experiments, "that the air-bladder in fishes, in addition to other uses, serves the purpose of increasing by resonance the intensity of the sonorous undulations communicated from water to the body of the fish."\* The vibrations thus communicated to the peri- and endo-lymph of the labyrinth are doubtless made to beat more strongly upon the delicate extremities of the acoustic nerve, in osseous fishes, by their effect upon the suspended otolites: and it will be observed, that the chief portions of the nerve expand upon those chambers of the vestibule, which contain the otolites. The large size of the organ of hearing, and especially that of the hard otolites, also relate to the medium through which the sonorous vibrations are propagated to the fish, and to the mode in which they are transmitted to the organ; in like manner as the eyeballs are expanded, in order to take in the utmost possible amount of light. The contracted encephalon harmonises with and suffices for the sensations and volitions, and the simple series of ideas daily repeated in the monotonous existence of the scaled inhabitants of the waters. To say that the fish's ears and eyes were made enormous in order to strike strongly on its dull brain — that the development of the organs of sense has been exaggerated to compensate for the defective size of their nervous centres — implies a want of due appreciation of the beautiful adjustment of the

\* LXXIII. p. 1245.

proportions of the labyrinth and eyeball to the conditions under which the fish receives its impressions of the sonorous and luminous undulations.

### ELECTRIC ORGANS.

Extraordinary as are the modifications and appendages of the peripheral extremities of the nerves of smell, sight, and hearing, other nerves in fishes are subject to still stranger combinations, and constitute organs quite unknown in any other class of Vertebrate Animals; those, viz., which endow a fish with the wonderful property of accumulating, concentrating, and applying in its own behoof an imponderable agent of a purely physical nature, which gives it the power to communicate electric shocks,—to wield at will the artillery of the skies.

But few fishes are known to possess this faculty, and I shall limit the demonstration of the electric organs to the two genera which possess them in the highest state of development, and which are most dreaded for the force of the shocks they impart; these are the *Torpedo* and the *Gymnotus*.

In the *Torpedo Galvani*\* the organs are two in number, are large, flattened, reniform bodies, lodged on each side the head and gills, and encompassed by these and by the anterior borders of the pectoral fins (*fig. 45. E*), and they consist of a mass of vertical, for the most part hexagonal, prisms, the ends of which are covered by the dorsal and ventral integuments. When you reflect these, you find the organs immediately coated by a thin glistening aponeurosis, which sends down partitions forming the chambers of the prismatic columns. Each column, when insulated in the recent fish, seems like a mass of clear trembling jelly; but consists of a series of delicate membranous plates inclosed by, or adherent by their margins to a proper capsule, and separated from each other by a small quantity of a limpid albuminous fluid. Each flattened cell thus formed, is lined by an epithelium of nucleated corpuscles: the fibrous tissue of the plates and common capsule presents the microscopic characters of elastic tissue; between it and the epithelium is a clear unorganised layer, the seat of the ultimate ramifications of the vessels and nerves. The proper capsule adheres to the aponeurotic partition-walls which support the columns and the larger branches of the nerves and vessels of the organ.† The transverse plates of the vertical columns are

\* The electric organs in the *Torp. Narce* and *Torp. Nobiliana* do not materially differ from those above described and illustrated by the dissections of Hunter.—See Nos. 2167—2179., and LXXX.

† Some of the vertical columns do not extend through the entire thickness of the organ. I have found them interrupted where the deep-seated nerves traverse the substance of the battery, but have not, in any instance, succeeded in finding a natural division of the organ into two strata of dorsal and ventral columns.—See XCI. p. 60.

conspicuous in Preparations 2176 and 2177. Hunter, who counted 470 columns in each organ, describes the partitions as being very vascular:—"The arteries," he says, "are branches from the vessels of the gills, which convey the blood that has received the influence of respiration." But the most characteristic feature of the organisation of the electric battery is, as Hunter also demonstrates, its enormous supply of nervous matter. Each organ derives this supply from one branch of the trigeminal (*fig. 45, 5*), and from four branches of the vagal nerves (*ibid.* 8, 8), and the four anterior nerves are each as thick as the spinal chord: the last nerve is a feeble branch of the vagus. The trigeminal and vagal enlargements of the olivary and restiform tracts coalesce on each side, forming the so-called 'electric lobes' of the medulla oblongata. The electric branch of the fifth nerve may be defined, even at its origin, from the true ganglionic part of that nerve; and Professor Savi\* affirms that both this and the vagal branches consist entirely of the primitive nerve-fibres of animal life, or "à double contour;" and that they are distributed by successive resolution into smaller and smaller fasciculi, until they finally penetrate the septa of the columns, and terminate thereon by meshes formed by loops, or by the return and anastomosis of the terminal elementary nerve-fibres. †

In the eel-like *Gymnotus* the electric organs are four in number, and are situated two on each side the body, extending from behind the pectoral fins to near the end of the tail (see Preps. 2186, 2187). They occupy and almost constitute the whole lower half of the trunk; the upper organ is much larger than the lower one, from which it is separated by a thin muscular and aponeurotic stratum. The organs of one side are separated from those of the other, above by the vertebral column and its muscles, then by the air-bladder, and below this by an aponeurotic septum. From this septum, and from that covering the air-bladder, there extend outwards, to be attached to the skin, a series of horizontal, or nearly horizontal, membranes, arranged in the longitudinal axis of the body nearly parallel to one another; they are of great but varying length, some being co-extensive with the whole organ; their breadth is almost that of the semidiameter of the plane of the body in which they are situated. These membranes are about half a line apart at their outer borders; but, as they pass from the skin towards their inner attachments, they approach one another. They are intersected transversely by more delicate vertical plates, extending from the skin to the median aponeurosis, and co-extensive in length with the breadth of the septa between which they are

\* LXXVI. p. 318.

† Savi. "Actes du Congrès Scientifique, à Florence," 1840.

placed. Hunter counted about 240 of these plates in a single inch of length of the horizontal membrane. He rightly compares those stronger membranes to the aponeurotic walls of the prisms of the Torpedo, and the intersecting delicate plates, to the partitions of the prisms: a pellucid liquid intervenes between the plates of the Gymnotus; and, if we admit the analogy of these plates, and of those of the Torpedo, to the plates of the voltaic pile, we perceive that, in the Gymnotus, the batteries are horizontal and the plates vertical, whilst in the Torpedo the batteries are vertical and their plates horizontal. The situation of the organs is also very different in the two fishes; they extend from before the pectoral fins to the anterior part of the head in the one, and from behind the pectoral fins to near the end of the tail in the other. But a more important difference exists in the source of the nervous supply. In the Gymnotus the electric organs are supplied by the 'rami ventrales' of all the spinal nerves, about 200 pairs, that issue in the course of their extent; some of the filaments ramify upon the horizontal membranes from their cutaneous margins; but the greater part of the nerves come from the deeper-seated branches which descend upon the median aponeurotic partition-wall, and spread upon the septa of the organ from within outwards. Yet the nervus lateralis, which is derived from the same cerebral nerves as those which, in the Torpedo, supply the electric batteries, and which is formed by similar proportions of the trigeminal and vagus, extends the whole length of the electric organs in the Gymnotus without rendering them a filament; it is situated nearer the spine, and is of larger size than usual, but Hunter\* "was not able to trace any nerves going from it to join those of the medulla spinalis, which run to the organ."

The proportional size of the electric organs is much greater in the Gymnotus than in the Torpedo: indeed, the proper body of the Gymnotus is, as it were, a mere appendage tacked on to the fore part of the enormous batteries; for the digestive and generative viscera, with the respiratory and circulating organs, the brain and organs of sense,—all, in fact, that constitute the proper animal,—are confined to that small segment of the entire body which is anterior to the electrical apparatus. The vent even opens beneath the head, in advance of the pectoral fins.

The electric organs of the *Malapterurus electricus* are described as forming on each side the body, between the skin and the lateral muscles, two thin strata, one consisting of minute lozenge-shaped cells, the other of six or more fine longitudinal membranes, with a delicate intervening cellular structure: they thus combine the cha-

\* LXXX.



acters both of those of the *Torpedo* and the *Gymnotus*, and not only in structure, but in some degree, likewise, in regard to the source of their nervous energy, the outer organs being supplied by the 'nervus lateralis' from the vagus; the laminated inner one receiving branches from the 'rami ventrales' of the spinal nerves.\* The shock communicated by the *Malapterurus electricus* is comparatively feeble.

When the Neapolitan fishermen pull their nets to shore, their first act usually is to wash the fishes by dashing over them bucketfuls of sea-water; and if a *Torpedo* be amongst the captured shoal, it makes its presence instantly felt by the shock transmitted to the arm, which is in the act of discharging the bucket. If the fish be handled, the shock is too strong and painful to be willingly encountered a second time, and the arm remains benumbed for some time. Each repetition of the discharge, however, enfeebles its force, and the surface of the fish capable of communicating the shock progressively contracts, as life departs, to the region of the organs themselves.

An animal must be in communication with the *Torpedo* by two distinct points, in order to receive the shock. If an insulated and prepared frog † touches the torpedo by the end of a nerve only, no muscular contractions ensue on the discharge of the battery; but a second contact by the end of another nerve, or by a portion of muscle, or any other part of the body, immediately produces them. When the fisherman dashes the stream of water over the *Torpedo*, the electric current passes up from the dorsal surface of the batteries against the stream to the man's hand, and the circle is completed by the earth extending from the man's feet to the ventral surface of the prone fish.

The dorsal surface of the electric organ is always positive, the ventral surface negative. ‡ The *Torpedo* has no power of otherwise directing the electric currents; but Matteucci found that wounding the electric lobes of the brain sometimes reversed the direction. These currents, besides their effects on the living body, exercise all the other known powers of electricity: they render the needle magnetic §, decompose chemical compounds, and emit the spark. || The discharge of strong currents is usually accompanied by visible contraction of parts of the body, usually by a retraction of the eyes of the *Torpedo*, and one muscle (*fig. 45. o*) is arranged so as to constrict part of the circumference of each battery; but such consentaneous muscular action, though it may add to the force of the discharge, is not essential to its production. The numbing effect seems to be produced by the rapid succession of shocks delivered by

\* XCI.  
§ LXXXI.

† LXXVI. p. 148.  
|| LXXVI.

‡ LXXXIII.

the recent and vigorous fish. Matteucci ascertained that, during the discharge, the nerves of the organ were not traversed by any electric current.

Humboldt has given a lively narrative of the mode of capture of the *Gymnoti*, employed by the Indians of South America.

They rouse the *Gymnoti* by driving horses and mules into the ponds which those fish inhabit, and harpoon them when they have exhausted their electricity upon the unhappy quadrupeds; "I wished," says Humboldt, "that a clever artist could have depicted the most animated period of the attack: the groups of Indians surrounding the pond, the horses with their manes erect and eyeballs wild with pain and fright, striving to escape from the electric storm which they had roused, and driven back by the shouts and long whips of the excited Indians: the livid yellow eels, like great water-snakes, swimming near the surface and pursuing their enemy: all these objects presented a most picturesque and exciting 'ensemble.' In less than five minutes two horses were killed: the eel, being more than five feet in length, glides beneath the body of the horse and discharges the whole length of its electric organ: it attacks at the same time the heart, the digestive viscera, and, above all, the gastric plexus of nerves. I thought the scene would have a tragic termination, and expected to see most of the quadrupeds killed; but the Indians assured me the fishing would soon be finished, and that only the first attack of the *Gymnoti* was really formidable. In fact, after the conflict had lasted a quarter of an hour, the mules and horses appeared less alarmed; they no longer erected their manes, and their eyes expressed less pain and terror: One no longer saw them struck down in the water; and the eels, instead of swimming to the attack, retreated from their assailants and approached the shore." The Indians now began to use their missiles; and by means of the long cord attached to the harpoon, jerked the fish out of the water without receiving any shock so long as the cord was dry.\*

All the circumstances narrated by the celebrated philosopher, establish the close analogy between the *Gymnotus* and *Torpedo* in the vital phenomena attending the exercise of their extraordinary means of offence. The exercise is voluntary and exhaustive of the nervous energy; like voluntary muscular effort, it needs repose and nourishment to produce a fresh accumulation.

I was so fortunate as to witness the experiments performed by Professor Faraday on the large *Gymnotus* which was so long preserved alive at the 'Adelaide Gallery' in London. That the most

\* *cv.* p. 55.

powerful shocks were received when one hand grasped the head and the other hand the tail of the *Gymnotus*, I had painful experience ; especially at the wrists, the elbows and across the back. But our distinguished experimenter showed us that the nearer the hands were together within certain limits, the less powerful was the shock. He demonstrated by the galvanometer that the direction of the electric current was always from the anterior parts of the animal to the posterior parts, and that the person touching the fish with both hands received only the discharge of the parts of the organs included between the points of contact. Needles were converted into magnets : iodine was obtained by polar decomposition of iodide of potassium ; and, availing himself of this test, Professor Faraday showed that any given part of the organ is negative to other parts before it, and positive to such as are behind it. Finally, heat was evolved, and the electric spark obtained. Referring to the admirable Memoir \*, in which these and other experiments on the *Gymnotus* are described, I shall only revert to the relation which exists between the comparative anatomy of the organs of the *Torpedo* and *Gymnotus*, and the difference in the direction of their electric currents, as determined by the physical experiments. The delicate plates sustaining the terminal meshes of the nerves and vessels are horizontal in the *Torpedo* ; the course of the electric current is from above downwards. The corresponding plates in the *Gymnotus* are vertical ; the direction of the electric current is from before backwards : *i. e.* it is vertical to the planes of the plates of the organised voltaic piles in both cases.

There is another analogy which the row of compressed cells constituting the electric prism of the *Torpedo* suggests, viz. to the striated fibre of voluntary muscle, or to the row of microscopic discoid cells of which the elementary muscular filament appears to consist. The looped termination of the exciting nerve is common to muscular tissue and that of the electric organ. The electric, like the motory nerves, rise from the anterior myelonal tracts ; and, though they have a special lobe at their origin, beyond that origin they have no ganglion. An impression on any part of the body of the *Torpedo* is carried by the sensory nerves either directly, or through the posterior myelonal tracts, to the brain, excites there the act of volition, which is conveyed along the electric nerves to the organs and produces the shock : in muscular contraction, the impression and volition take the same course to the muscular fibres. If the electric nerves are divided at their origin from the brain the course of the stimulus is interrupted,

\* LXXXII.

and no irritant to the body has any effect on the electric organs any more than it would have under the like circumstances on the muscles. But, if the ends of the nerves in connection with the organ be irritated, the discharge of electricity takes place, just as irritating the end of the divided motor nerve in connection with muscle would induce its contraction. If part of the electric nerves be left in connection with the brain, the stimulus of volition cannot, through these, excite the discharge of the whole organ, but only of that part of the organ to which the undivided nerves are distributed. So, likewise, the irritation of the end of a divided nerve in connection with the electric apparatus, excites the discharge of only that part to which such nerve is distributed. We have seen that the power of exciting the electric action, like that of exciting the muscular contraction, is exhausted by exercise and recovered by repose: it is also augmented by energetic circulation and respiration; and what is more significative of their close analogy, both powers are exalted by the direct action, on the nervous centres, of the drug 'strychnine:' its application causes simultaneously a tetanic state of the muscles of the fish, and a rapid succession of involuntary electric discharges.\*

The survey of the nervous system of fishes cannot be concluded without a notice of two systems of mucous organs in intimate connection with the nerves of sensation; one system is common to the Torpedo with other Plagiostomes; the other system is peculiar to the Torpedo, in which it was discovered by Prof. Savi.

The first or muciferous system consists of the long slender mucous tubes (*fig. 45. m*), which, commencing by groups of globular vesicles (*ib. m.*) situated in the Torpedo, symmetrically at the forepart of the head and outside the electric organs, run in parallel fasciculi from which the tubes, successively detaching themselves, perforate the skin, and terminate by orifices, some at the dorsal, some at the ventral surface, between the outer border of the electric organs and that of the body of the animal. A considerable filament of the ganglionic portion of the trigeminal nerve expands upon the ampulliform commencement of each of the muciferous tubes: the nerve may receive impressions conveyed to it by the tube and its clear jelly-like contents, or it may preside over the secretion of those contents, or combine both functions.

The second or follicular system consists of linear series of minute subcutaneous subspherical cells, situated at the anterior part of the head of the Torpedo, chiefly on the under surface: each cell has a double membranous tunic, and contains a grey cerebriform matter;

\* LXXVI. p. 162.

a branch of the anterior division of the fifth nerve enters each follicle, makes a coil there, and quits it to join another filament, or to return to its own stem.\*

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## LECTURE IX.

### DIGESTIVE SYSTEM OF FISHES.

#### *Dentition.*

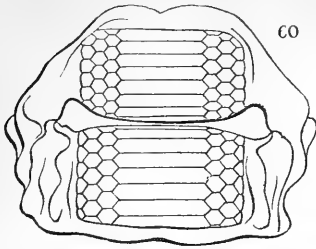
THE teeth of fishes, whether we study them in regard to their number, form, substance, structure, situation, or mode of attachment, offer a greater and more striking series of varieties than do those of any other class of animals.

As to number, they range from zero to countless quantities. The Lancelet, the Ammocete, the Sturgeon, the Paddle-fish (*fig. 61. a. b.*), and the whole order of Lophobranchii, are edentulous. The Myxinoids have a single pointed tooth on the roof of the mouth, and two serrated dental plates on the tongue. The Carp has a single grinding tooth on the occiput, opposed to two dentigerous pharyngeal jaws below. In the Lepidosiren a single maxillary dental plate is opposed to a single mandibular one, and there are two small denticles on the nasal bone. In the extinct Sharks with crushing teeth, called *Ceratodus* and *Ctenodus*, the jaws were armed with four teeth, two above and two below. In the Chimæra two mandibular teeth are opposed to four maxillary teeth. From this low point the number in different fishes is progressively multiplied until, in the Pike, the Silurus, and many other fishes, the mouth becomes crowded with innumerable teeth.

With respect to form, I may first observe, that as organised beings withdraw themselves more and more, in their ascent in the scale of life, from the influence of common physical agents, so their parts progressively deviate from geometrical figures: it is only, therefore, in the lowest vertebrated class that we find teeth in the form of perfect cubes, and of prisms or plates with three (*Myletes*), four (*Scarus*),

\* LXXVI. p. 332. pl. iii. figs. 10. 12.

five, or six sides, *Myliobates*, *fig. 60*.\* The cone is the most common form in fishes: such teeth may be slender, sharp-pointed, and so minute, numerous, and closely aggregated, as to resemble the plush or pile of velvet; these are called 'villiform teeth (*dentes villiformes*, *dents en velours*†); all the teeth of the Perch are of this kind: when the teeth are equally fine and numerous, but longer, they are called



Jaws and teeth; *Myliobates*.

'ciliiform' (*dentes ciliiformes*): when the teeth are similar to, but rather stronger than these, they are called 'setiform (*dentes setiformes*, *dents en brosse*): conical teeth, as close set and sharp pointed as the villiform teeth, but of larger size, are called 'rasp-teeth' (*dentes raduliformes*; *dents en rape* or *en cardes*); the Pike presents such teeth on the back part of the vomer: the teeth of the Sheat-fish (*Silurus glanis*) present all the gradations between the villiform and raduliform types. Setiform teeth are common in the fishes thence called Chætodonts‡; in the genus *Citharina* they bifurcate at their free extremities; in the genus *Platax* they end there in three diverging points (V, pl. 1), and the cone here merges into the long and slender cylinder. Sometimes the cone is compressed into a slender trenchant blade: and this may be pointed and recurved, as in *Muræna* (V, pl. 56, *fig. 4*.); or barbed, as in *Trichiurus* (V, pl. 1, *fig. 8*.), and some other Scomberoids; or it may be bent upon itself, like a tenterhook, as in the fishes thence called Goniodonts.§ In the Bonito may be perceived a progressive thickening of the base of the conical teeth; and this being combined in other predatory fishes with increased size and recurved direction, they then resemble the laniary or canine teeth of carnivorous quadrupeds, as we see in the large teeth of the Pike.

The anterior diverging grappling teeth of the wolf-fish (V, pl. 60.) form stronger cones; and by progressive blunting, flattening, and expansion of the apex, observable in different fishes, the cone by degrees changes to the thick and short cylinder, such as is seen in the back teeth of the wolf-fish (V, pl. 61.), and in similar grinding and crushing teeth in other genera, whether phytiphagous, or feeders on crustaceous and testaceous animals. The grinding surface of these short cylindrical teeth may be convex, as in the Sheep's-head Fish (*Sargus*, V, pl. 1. *fig. 13*.); or flattened, as in the pharyngeal teeth of

\* See v. pl. 25. 49.

† The French terms are those used by Cuvier and Valenciennes in xxiii. *passim*.

‡ *Χαίτη*, bristle; *ὀδὸς*, tooth.

§ *Γωνία*, an angle; *ὀδὸς*, a tooth.

the *Wrasse* (*Labrus*, V, pl. 45. *fig.* 4.). Sometimes the hemispheric teeth are so numerous, and spread over so broad a surface, as to resemble a pavement (*Chrysophrys*, V, pl. 45. *figs.* 3, 6; and *Pisodus*, pl. 47. *fig.* 3.); or they may be so small, as well as numerous (*dentēs graniformes*), as to give a granulated surface to the part of the mouth to which they are attached (premaxillaries of *Labrus*, V, pl. 45. *fig.* 1.). A progressive increase of the transverse over the vertical diameter may be traced in the molar teeth of different fishes, and sometimes in those of the same individual, as in *Labrus* (V, pl. 45. *fig.* 4) and *Placodus* (V, pl. 30.), until the cylindrical form is exchanged for that of the depressed plate. Such dental plates (*dentēs lamelliformes*) may be found, not only circular, but elliptical, oval, semilunar, sigmoid, oblong, and even, as above-mentioned, square, hexagonal, pentagonal, or triangular; and the grinding surface presents as various and beautiful kinds of sculpturing. The broadest and thinnest lamelliform teeth are those that form the complex grinding tubercle of the *Diodon* (V, pl. 38. *fig.* 2.). The front teeth of the Flounder and *Sargus* present the form of compressed plates, at least in the crown, and are true '*dentēs incisivi*.' Numerous wedge-shaped dental plates (*dentēs cuneati*) are set vertically in the pharyngeal bones of the Parrot-fish (*Scarus*, V, pl. 51.). A thin lamella, slightly curved like a finger-nail, is the singular form of tooth in an extinct genus of fishes, which I have thence called *Petalodus* (V, pl. 22. *figs.* 3, 4, 5.) Sometimes the incisive form of tooth is notched in the middle of the cutting edge, as in *Sargus unimaculatus* (V, pl. 1. *fig.* 9.). Sometimes the edge of the crown is trilobate (*Aplodactylus*, *ib.* *fig.* 10.). Sometimes it is made quincelobate by a double notch on each side of the large middle lobe (*Boops*, *ib.* *fig.* 11.). In the formidable Sea-pike (*Sphyræna Barracuda*, V, pl. 53.) the crown of each tooth, large and small, is produced into a compressed and sharp point, and resembles a lancet. Sometimes the edges of such lancet-shaped teeth are finely serrated, as in *Priodon* (V, pl. 1. *fig.* 12.), and the great Sharks of the genus *Carcharias*, the fossil teeth of which indicate a species (*Carch. Megalodon*) sixty or seventy feet in length.

The lancet is changed for the stronger spear-shaped tooth in the Sharks of the genus *Lamna*, and in the allied great extinct *Otodus*, as in the small Porbeagle, similarly shaped, but stronger, piercing and cutting teeth were accompanied by one or more accessory compressed cusps on each side their base, like the Malay crease.

With respect to situation, the teeth, in Sharks and Rays, are limited to the bones (maxillary and mandibular), which form the anterior aperture of the mouth: in the Carp and other Cyprinoids the teeth are confined to the bones which circumscribe the posterior aperture of the mouth, viz. the pharyngeals and basi-occipital. The Wrasses

(*Labrus*), and the Parrot-fishes (*Scarus*), have teeth on the pre-maxillary and pre-mandibular, as well as on the upper and lower pharyngeals; both the anterior and posterior apertures of the mouth being thus provided with instruments for seizing, dividing, or comminuting the food, the grinders being situated at the pharynx. In most fishes teeth are developed also in the intermediate parts of the oral cavity, as on the palatines, the vomer, the hyoid bones, the branchial arches; and, though less commonly, on the pterygoids, the entopterygoids, the basi-pre-sphenoid, and even on the nasal bone. It is very rare to find teeth developed on the true superior maxillary bones; but the Herring and Salmon tribes, some of the Ganoid Fishes and the great *Sudis* (*fig. 36.*), are examples of this approach to the higher Vertebrata. Among the anomalous positions of teeth may be cited, besides the occipital alveolus of the Carp (*V. pl. 57. fig. 6.*), the marginal alveoli of the prolonged, depressed, well ossified rostrum of the Saw-fish (*Pristis, V. pl. 8.*) In the Lampreys and in *Helostomus* (an osseous fish), most of the teeth are attached to the lips. Lastly, it is peculiar to the class *Pisces*, amongst Vertebrata, to offer examples of teeth developed in the median line of the mouth, as in the palate of the Myxines; or crossing the symphysis of the jaw, as in *Notidanus, Scymnus* and *Myliobates*.

Nor is the mode less varied than the place of attachment: some teeth, as those of *Lophius, Pécilia, Anableps*, are always moveable: in most fishes they are anchylosed to the jaws by continuous ossification from the base of the dental pulp; the histological transition being more or less gradual from the structure of the tooth to that of the bone. Sometimes we find, not the base, but one side of the tooth anchylosed to the alveolar border of the jaw: and the teeth oppose each other by their sides instead of their summits (*Scarus, V. pl. 49.*): in *Pimelodus*, however, where the teeth are thus attached, the crown is bent down in the upper teeth, and bent up in the lower ones, at right angles to the fang, so that they oppose each other in the normal way. The base of anchylosed teeth is, at first, attached to the jaw-bone by ligament; and in the Cod-fish, Wolf-fish, and some other species, as calcification of the tooth progresses towards its base, the subjacent portion of the jaw-bone receives a stimulus, and develops a process corresponding in size and form with the base of the tooth: for some time a thin layer of ligamentous substance intervenes, but ankylosis usually takes place to a greater or less extent before the tooth is shed. Most of the teeth of the *Lophius* retain the primitive ligamentous connection: the ligaments of the large internal or posterior teeth of the upper and lower jaws, radiate on the corresponding sides of the bone, the base of the tooth resting on a conformable alveolar process. The ligaments do not permit the



tooth to be bent outwards beyond the vertical position, but yield to pressure in the contrary direction, by which the point of the tooth may be directed towards the back of the mouth: the instant, however, that the pressure is remitted, the tooth returns through the elasticity of the bent ligaments, as by the action of a spring, into its usual erect position: the deglutition of the prey of this voracious fish is thus facilitated, and its escape prevented. The broad and generally bifurcate bony base of the teeth of Sharks is attached by ligament to the semi-ossified crust of the cartilaginous jaws; but they have no power of erecting or depressing the teeth at will. The small and closely crowded teeth of Rays are also connected by ligaments to the subjacent maxillary and mandibular membranes. The broad tessellated teeth of the *Myliobates* have their attached surface longitudinally grooved to afford them better hold-fast, and the sides of the contiguous teeth are articulated together by serrated or finely undulating sutures (V, *pl.* 27.), a structure unique in dental organisation. The teeth of the *Sphyrana* are examples of the ordinary implantation in sockets, with the addition of a slight ankylosis of the base of the fully-formed tooth with the alveolar parietes; and the compressed rostral teeth of the Saw-fish are deeply implanted in sockets: the hind margin of their base is grooved, and a corresponding ridge from the back part of the socket fits into the groove, and gives additional fixation to the tooth. Some implanted teeth in the present class have their hollow base further supported, like the claws of the feline tribe, upon a bony process arising from the base of the socket: the incisors of the *Balistes*, *e. g.*, afford an example of this double or reciprocal gomphosis. In fact, the whole of this part of the organisation of fishes is replete with beautiful instances of design, and instructive illustrations of animal mechanics. The vertical section of a pharyngeal jaw and teeth of the Wrasse (*Labrus*) would afford the architect a model of a dome of unusual strength, and so supported as to relieve from pressure the floor of a vaulted chamber beneath. The base of the domeshaped tooth is slightly contracted, and is implanted in a shallow circular cavity; the rounded margin of which is adapted to a circular groove in the contracted part of the base; the margin of the tooth which immediately transmits the pressure of the bone is strengthened by an inwardly projecting convex ridge. The masonry of this inner buttress, and of the dome itself, is composed of hollow columns, every one of which is placed so as best to resist or transmit in the due direction the external pressure. The floor of the alveolus is thus relieved from the office of sustaining the tooth: it forms, in fact, the roof of a lower vault, in which the germ of a successional tooth is in course of development: had the crushing tooth in use, rested, as in the Wolf-fish, by the whole of its base upon the alveolus, the sup-

porting plate gradually undermined by the growth of the new tooth must have given way and been forced upon the subjacent delicate and highly vascular and sensitive matrix of the half-formed tooth. But the superincumbent pressure being exclusively sustained by the border of the alveolus, whence it is transferred to the walls dividing the vaulted cavities containing the germs of the new teeth, the roofs of these cavities yield to the absorbent process consequent on the growth of the new teeth without materially weakening the attachment of the old teeth, and without the new teeth being subjected to any pressure until their growth is sufficiently advanced to enable them to bear it with safety ; by this time the sustaining borders of the old alveolus are undermined, and the old worn-down tooth is shed.

With regard to the substance of the teeth of fishes, the modifications of dentine, called vaso-dentine, and osteo-dentine\*, predominate much more than in the higher Vertebrata ; and they thus more closely resemble the bones which support them. There is, however, great diversity in respect of substance. The teeth of most of the Chatodonts are flexible, elastic, and composed of a yellowish subtransparent albuminous tissue ; such, likewise, are the labial teeth of the Helostome, the premaxillary and mandibular teeth of the Goniodonts, and of that percoid genus thence called *Trichodon*. In the Cyclostomes the teeth consist of a denser albuminous substance. The upper pharyngeal molar of the Carp consists of a peculiar brown and semitransparent tissue, hardened by salts of lime and magnesia. The teeth of the Flying-fish (*Exocætus*), and Sucking-fish (*Remora*), consist of osteodentine. In many fishes, *e. g.* the Acanthurus (V, pl. 44. *fig.* 1.), Sphyræna (V, pl. 53.), and certain Sharks (*Lamna*, V, pl. 6.), a base, or body of osteodentine is coated by a layer of true dentine, but of unusual hardness, like enamel: in *Prionodon* this hard tissue predominates. In the Diodon the dental plates consist wholly of hard or unvascular dentine. In *Sargus* and *Balistes* the body of the tooth consists of true dentine, and the crown is covered by a thick layer of a denser tissue, developed by a distinct organ, and differing from the 'enamel' of higher animals only in the more complicated and organised mode of deposition of the earthy salts. The ossification of the capsule of the complex matrix of these teeth covers the enamel with a thin coating of 'cement.' In the pharyngeal teeth of the *Scarus* a fourth substance is added by the ossification of the base of the pulp after its summit and periphery have been converted into hard dentine ; and the teeth, thus composed of cement, enamel, dentine, and osteodentine (V, pl. 52.), are the most complex in regard to their substance that have yet been discovered in the animal kingdom.

\* V. Introduction, p. lxxii.

The true teeth of all Vertebrates consist, like bone, of an animal gelatinous basis, hardened by salts of lime, magnesia, and soda; the phosphates of lime predominating. Analyses of the teeth of the Pike, Carp, and Shark, will be found in V. pp. lxiv. and 9.; and in LXXXV.

The tubes which convey the capillary vessels through the substance of the osteo- and vaso-dentine of the teeth of fishes\* were early recognised, on account of their comparatively large size; as by André *e. g.*, in the teeth of *Acanthurus*, and by Cuvier and Von Born in the teeth of the Wolf-fish and other species.† Leeuwenhoek had, also, detected the much finer tubes of the peripheral dentine of the teeth of the Haddock. These 'dental tubuli' are given off from the parietes of the vascular canals, and bend, divide, and subdivide rapidly in the hard basis-tissue of the interspaces of those canals in osteo-dentine (V. pl. 7.); the dental tubuli alone are found in true dentine, and they have a straighter and more parallel course, usually at right angles to the outer surface of the dentine (V. pl. 7. and pl. 52. *b*).

I give the name 'vaso-dentine' to that modification of the tissue in which the vascular canals run nearly parallel with, and equidistant from, each other, through the major part of the extent of such modified dentine; it is exemplified in the rostral teeth of the Saw-fish, the maxillary dental plates of the *Chimæra*, *Psammodonts*, and *Myliobates*: in the latter each medullary canal and its system of dental tubes represents a slender subcylindrical denticle, being separated from the contiguous denticles by a thin coat of bone or 'cement.' The dense covering of the jaws of the Scari consists of a stratum of quite distinct prismatic denticles, standing vertically to the surface of the bone.

'Osteo-dentine' is that tissue in which the medullary canals are wavy, irregular, and anastomotic; in Mammalia it contains the Purkingian cells; in fishes it usually is covered more or less thickly by hard dentine. Those conical teeth which, when fully formed, consist wholly or in great part of osteodentine or vasodentine, always first appear with an apex of true dentine. In some fishes the simple central basal pulp-cavity of such teeth, instead of breaking up into irregular or parallel canals, sends out a series of vertical plates from its periphery, which, when calcified, give a fluted character to the base of the tooth; (*Lepidosteus oxyurus*, LXXXVI. pl. v. fig. 1.) Sometimes such radiating vertical basal plates of dentine are wavy in their course, and send off narrow processes from their sides; and, as a thin layer of the outer capsule interdigitates with the outstanding

\* The vaso-dentine of *Pristis* and *Myliobates* is like that of the teeth of the Cape Anteater (*Orycteropus*): the vaso-dentine of the *Psammodonts* resembles that which forms the base of the tooth of the Sloth and Megatherium: the vaso-dentine of Mammals differs from the osteo-dentine in the absence of the radiated 'Purkingian' cells.

† See v. p. 10.

plates of the dentinal pulp, and becomes co-calcified with them, a transverse section of such a tooth presents a series of interblended wavy or labyrinthic tracts of thick dentine radiating from the centre, and of thin cement converging towards the centre of the tooth.\* An analogous but more complicated structure obtains when the radiating, wavy, vertical plates of dentine dichotomise, and give off from their sides, throughout their course, numerous branch plates and processes, which are traversed by medullary sinuses and canals with their peripheral terminations dilated, and becoming the centres of lobes or columns of hard dentine. The transverse section of such teeth gives the appearance of branches of a tree, with leaf-stalks and leaves, radiating from the central pulp-cavity to the circumference of the tooth; and I have called the fossil Fish in which this structure was first detected, *Dendrodus* †. Thus, with reference to the main and fundamental tissue of tooth, we find not fewer than six leading modifications in Fishes: hard or true dentine (*Sparoids*, *Labroids*, *Lophius*, *Balistes*, *Pycnodonts*, *Prionodon*, *Sphyrna*, *Megalichthys*, *Rhizodus*, *Diodon*; *Scarus*); osteo-dentine (*Cestracion*, *Acrodus*, *Lepidosiren*, *Ctenodus*, *Hybodus*, *Percoids*, *Sciænoïds*, *Cottoids*, *Gobioids*, and many others); vaso-dentine (*Psammodus*, *Chimæroids*, *Pristis*, *Myliobates*); plici-dentine (*Lophius*, *Holoptychius*, *Lepidosteus oxyurus*, at the base of the teeth); labyrintho-dentine (*Lepidosteus platyrhinus*, *Bothriolepis*); and dendro-dentine (*Dendrodus*); besides the compound teeth of the *Scarus* and *Diodon*.

One structural modification may prevail in some teeth, another in other teeth of the same fish; and two or more modifications may be present in the same tooth, arising from changes in the process of calcification and a persistency of portions or processes of the primitive vascular pulp or matrix of the dentine.

As might have been anticipated from the discovery of the varied and predominating vascular organisation in the teeth of fishes, and the passage from non-vascular dentine to vascular dentine in the same tooth, the true law of the development of dentine "by centripetal metamorphosis and calcification of the cells of the pulp," was first definitely enunciated and illustrated from observations made on the development of the teeth of fishes. ‡

\* This remarkable structure attains its highest complication and forms the largest proportion of the tooth in the gigantic extinct Batrachia, which I have thence called Labyrinthodonts, and from which, therefore, I have taken the illustrations of that complex modification of dental structure in my "Odontography" (pls. 63 b, 64, 64 a, 64 b). I had discovered in 1841 (LXXXVII.) the more simple modification of this structure "at the base of the tooth in a few Fishes," but had not then seen so complex an example in that class as Dr. Wyman (LXXXVI. pl. v. fig. 4.) and M. Assassiz (XXII. 'Sauroides,' 1843) subsequently described and figured, in teeth of the genus *Lepidosteus*. † cxxvi. pl. b.

‡ In my Hunterian Lectures, delivered at the Royal College of Surgeons, May, 1839. See also LXXXVIII. r. 784.; and v. Introduction, and part i. *passim*.

It is interesting to observe in this class the process arrested at each of the well-marked stages through which the development of a mammalian tooth passes. In all fishes the first step is the simple production of a soft vascular papilla from the free surface of the buccal membrane: in Sharks and Rays these papillæ do not proceed to sink into the substance of the gum, but are covered by caps of an opposite free fold of the buccal membrane; these caps do not contract any organic connection with the papilliform matrix, but, as this is converted into dental tissue, the tooth is gradually withdrawn from the extraneous protecting cap, to take its place and assume the erect position on the margin of the jaw (v. pl. 5. *fig.* 1.) Here, therefore, is represented the first and transitory 'papillary' stage of dental development in mammals; and the simple crescentic cartilaginous maxillary plate, with the open groove behind containing the germinal papillæ of the teeth, offers in the Shark a magnified representation of the earliest condition of the jaws and teeth in the human embryo.

In many Fishes, *e. g.*, *Lophius*, *Esox*, the dental papillæ become buried in the membrane from which they rise, and the surface to which their basis is attached becomes the bottom of a closed sac: but this sac does not become inclosed in the substance of the jaw; so that teeth at different stages of growth are brought away with the thick and soft gum, when it is stripped from the jaw-bone. The final fixation of teeth, so formed, is effected by the development of ligamentous fibres in the submucous tissue between the jaw and the base of the tooth, which fibres become the medium of connection between those parts, either as elastic ligaments, or by continuous ossification. Here, therefore, is represented the 'follicular' stage of the development of a mammalian tooth; but the 'eruptive' stage takes place without previous inclosure of the follicle and matrix in the substance of the jaw-bone.

In *Balistes*, *Scarus*, *Sphyræna*, the Sparoids, and many other Fishes, the formation of the teeth presents all the usual stages which have been observed to succeed each other in the dentition of the higher vertebrata: the papilla sinks into a follicle, becomes surrounded by a capsule, and is then included within a closed alveolus of the growing jaw, where the development of the tooth takes place and is followed by the usual eruptive stages. A distinct enamel-pulp is developed from the inner surface of the capsule in *Balistes*, *Scarus*, *Sargus*, and *Chrysophrys*.

In all Fishes the teeth are shed and renewed, not once only, as in Mammals, but frequently, during the whole course of their lives. The maxillary dental plates of *Lepidosiren*, and the rostral teeth of *Priotis* (if these modified dermal spines may be so called) are, per-

haps, the sole examples of 'permanent teeth' to be met with in the whole class.

When the teeth are developed in alveolar cavities, they are succeeded by others in the vertical direction (V. *pl.* 46. *fig.* 1.): these owe the origin of their matrix to the budding out from the capsule of their predecessors of a cæcal process, in which the papillary rudiment of the dentinal pulp is developed according to the laws explained in V (Introduction). But, in the great majority of Fishes, the germs of the new teeth are developed, like those of the old, from the free surface of the buccal membrane throughout the entire period of succession; a circumstance peculiar to the present class. The Angler, the Pike, and most of our common Fishes, illustrate this mode of dental reproduction: it is very conspicuous in the Cartilaginous Fishes (V. *pl.* 5, *fig.* 1.), in which the whole phalanx of their numerous teeth is ever moving slowly forwards in rotatory progress over the alveolar border of the jaw, the teeth being successively cast off as they reach the outer margin, and new teeth rising from the mucous membrane behind the rear rank of the phalanx.

This endless succession and decadence of the teeth, together with the vast numbers in which they often coexist in the same Fish, illustrate the law of Vegetative or Irrelative Repetition, as it manifests itself on the first introduction of new organs in the Animal Kingdom, under which light we must view the above-described organised and calcified preparatory instruments of digestion in the lowest class of the Vertebrate series.

#### ALIMENTARY CANAL.

The mouth of Fishes is the common entry and vestibule to both the digestive (*fig.* 61. *d* to *n*) and the respiratory (ib. *t*, *u*) organs; it is, therefore, of great capacity: and, as the transmission of the food to the stomach, and of the respiratory currents to the gills, is performed by similar acts of deglutition, the bony arches which surround the mouth are not only large, but are complicated by a mechanism for regulating the transit of the nutritious and oxygenating media, each to their respective localities. The branchial slits are provided with denticles and sieve-like plates or processes to prevent the entry of food into the interspaces of the gills, and the branchial outlets are guarded by valves which reciprocally prevent the regurgitation of the respiratory streams back into the mouth.

The necessary co-operation of the jaws with the hyoid arch in the rythmical movements of respiration is incompatible with protracted maxillary mastication; and, accordingly, the branchial apparatus renders a compensatory return by giving up, as it were, the last pair of its arches to the completion of the work which the proper or

anterior jaws were compelled by their services to respiration to leave unfinished: and thus the mouth of typical fishes is closed at both ends by dentigerous jaws.

The first portal to the alimentary tract is usually formed by the upper and lower jaws (*fig. 61. a, b*), and their teeth; the Gymnodonts\*, are so called on account of their conspicuous manifestation of this character. But in some Fishes the arched and fortified barrier is preceded by a fosse inclosed by fleshy lips: the whole genus *Labrus* owes its name to this peculiarity; the Carp-tribe (*Cyprinidae*) also have it; and, in some of them, the labial organs are developed to excess, as, for example, in the genus thence termed *Labeobarbus*, in which the lips are not only unusually thick and fleshy, but the lower one is produced downwards like a pointed beard. The labiated Fishes have not, however, so distinct a 'sphincter oris' as Mammals. Many Fishes, especially those of the Cyprinoid and Siluroid families, have fleshy and sensitive barbs or tentacles in the vicinity of the mouth, and subservient to its functions; those of the Siluroids being supported by bony or gristly stems. Tentacles depend from the rostral prolongation of the Sturgeon, and from the mandibular symphysis of the Cod. The Lepidosiren and Cod have fringed processes or filaments between the teeth and lips, which seem designed to assist in testing and selecting the food. Mr. Couch † narrates an instance of a large Cod, in good condition, taken on a line at Polperro, Cornwall, in which the orbits contained no eyeballs, but were covered with an opaque reticulated skin. So that he felt convinced that "eyes never had existed;" yet the fish was in good condition, and must have depended on the tactile organs about the mouth for the discovery of its food.

The edentulous Sturgeon is compensated by a produced cartilaginous snout, with which it upturns the mud in quest of food at the bottom of the rivers it frequents. The allied *Spatularia*, in which a minutely shagreened surface on the jaws represents the whole dental system, has had the force of development of subsidiary organs of alimentation expended in the production of the still more remarkable rostrum (*fig. 61. y.*), which is broad and flat, like the mandible of a spoonbill, and is more than half the length of the entire body.

The conical lip of the suctorial Myxinoids sends off from its anterior expanded border six or eight long tentacula: the inner surface of the lips is beset with short branched tentacles in the Ammocete: the Lancelet has more simple, but highly vascular intra-buccal processes (*fig. 46. g g*), and the vertically fissured aperture of its mouth is provided on each side with a series of long slender jointed

\* *Gr. gymnos*, uncovered; *odonts*, tooth.

† *xcviii. p. 72.*

and ciliated tentacula, (*ib. f, f*), which mainly tend, by the perpetual vortex they cause in the surrounding water, to bring the animalcular nutriment within the grasp of the pharynx (*ph*). There is no tongue in this rudimentary fish; that organ is often absent or very small in the typical members of the Class; its basis, the glossohyal, when it projects at all into the mouth, as in *fig. 61. c*, is rarely covered by integuments so organised as to suggest their being endowed with the sense of taste; they are generally callous, and either smooth and devoid of papillæ, or, if the representatives of these be present, they are calcified and the tongue is beset with teeth. The integuments of the palate, however, not unfrequently present that degree of vascularity and supply of nerves which indicate some selective sense, analogous to taste. In the Cyprinoids the palate is cushioned with a thick soft vascular substance, exuding mucus by numerous minute pores, but more remarkable for its irritable erectile or contractile property\*: if you prick any part of this in a live Carp, the part rises immediately into a cone, which slowly subsides; this peculiar tissue is richly supplied by branches of the glosso-pharyngeal nerves: it may assist in the requisite movements of the vegetable food, as well as add to it an animalising and solvent mucus, whilst it is undergoing mastication by the pharyngeal teeth. In the Gymnotus there are four series of branched fleshy processes in the mouth, one upon the dorsum of the tongue, a second depending from the palate, and one along each side of the mouth. The reddish vascular body, discovered by Retzius† between the basi-branchials and the sterno-hyoid muscles in Cartilaginous Fishes, and which exists also in *Gadus*, *Salmo*, and some other Osseous Fishes, has been compared to a sublingual salivary gland: but it is a ‘vaso-ganglion;’ and its homology with the thyroid, indicated by Mr. Simon‡, is a truer view of its nature. The only other representatives of a salivary system in Fishes are the mucous follicles that communicate with the mouth. There are neither tonsils nor velum palati in Fishes: the folds of membrane behind the upper and lower jaws, of which ‘internal lips’ the Sword-fish and Dory afford good examples, seem intended to prevent the reflux of the respiratory streams of water rather than the escape of food from the mouth. In the Lepidosiren these folds or inner lips are papillose and glandular.

In the aberrant *Dermopteri* and *Plagiostomi*, at the two extremes of the Class, in which there are numerous branchial apertures on each side, and the respiratory streams do not necessarily enter by the mouth, the last pair of branchial arches are not metamorphosed into pharyngeal jaws, and the entry to the gullet is simply constricted

\* XCIX.

† CXIX.

‡ CXVI. p. 300.



by a sphincter; in the *Lepidosiren* it is further defended by a soft valvular fold like an epiglottis.\*

The alimentary canal is usually short, simple, but capacious in fishes; in a few instances, *e. g.* *Branchiostoma* (*fig. 46. ph, as*), Myzinoids (xxi. Neurologie, tab. iii. *fig. 6.*), *Exocetus*, *Lepidosiren* (xxxiii. *pl. 25.*), it extends in almost a straight line from the pharynx to the anus: but it is generally disposed in folds and sometimes in numerous convolutions. It is primarily divided into a gastric and an intestinal portion by the constriction called 'pylorus.' The gastric portion is subdivided into 'œsophagus' and 'stomach,' the boundary line being more commonly indicated by a change of structure of the lining membrane than by a cardiac constriction; the intestinal portion is subdivided into a 'small' and a 'large intestine;' the latter usually answering to the 'intestinum rectum,' and the boundary, when well defined, being a constriction and an internal valvular fold; but very rarely marked by an external cæcum.

The alimentary canal is situated wholly or in part in the abdominal cavity, to the walls of which it is usually suspended by mesogastric and mesenteric duplicatures of the peritoneal lining membrane of the abdomen. When not wholly so situated, the extra-abdominal part is not contained in a thoracic division of the cavity, but extends beyond the peritoneal region into the muscular mass of the tail; a portion of the intestines, for example, lies between the right myocommata and the hæmal spines in the Sole. The peritoneal serous membrane, which defines the abdominal cavity, extends anteriorly to the pericardium, from which it is separated by a double aponeurotic septum (*fig. 61. o*): it is continued along the back over the ventral surface of the kidneys and the air-bladder, when this exists, a little way beyond the anus, and is reflected upon the alimentary canal, (*ib. d. i*), the liver (*ll*), the spleen (*n*), the pancreas (*k*), or its cæcal rudiments, the ovaria or testes, and the urinary bladder, if this be present. In many fishes the peritoneum does not form a shut sac, but communicates with the external surface, by one (*Branchiostoma, fig. 46. od, Lepidosiren, xxxiii. pl. 25. fig. 1. a*), or two (*Lamprey, fig. 74. l, Eel, Salmon, Sturgeon, Planirostra, Chimæra, and Plagiostomes, figs. 73. and 75. l*), orifices, situated, except in the Lancelet, in or near the cloaca. The peritoneal orifices give exit to the generative products (milt or roe) in the Lancelet, Myxinoids, Lampreys, Murænidæ, and Salmonidæ, but not in the *Lepidosiren* and *Plagiostomes*. In the Myxinoids, the Ammocetes, the Sturgeon, the Chimæra and the *Plagiostomes*, the peritoneum communicates also with the pericardium. †

\* xxxiii. p. 342. *fig. j. d.*

† lxix. pl. 8.

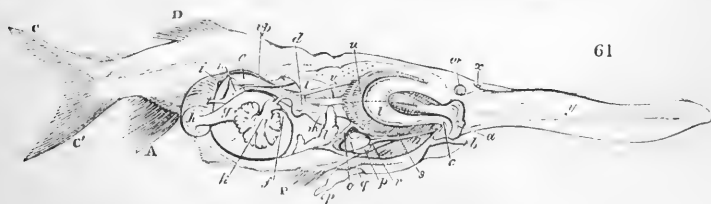
We have seen that the jaws and mouth are subservient to the respiratory as well as the digestive functions: but in the lowest of fishes, viz. the Lancelet, this community of offices extends through the whole œsophageal and seemingly gastric part of the alimentary canal, which is dilated into a capacious sac, and is richly provided with branchial vessels and vibratile cilia arranged in transverse linear series, like those in the respiratory pharynx of Ascidians (the arrow *a* extends from the pharynx into the intestine in *fig. 46.*): the œsophageal portion of the alimentary canal is here seen to be longer than the whole gastric and intestinal portions. In the Myxinioids lateral diverticula are derived from the œsophagus and metamorphosed into special respiratory sacs, communicating by narrow canals both with the œsophagus and with the external surface (*fig. 66, f, m.*): in other fishes the respiratory apparatus is more concentrated and brought more forwards, so as to communicate with the pharynx, and to leave the œsophagus free for the exclusive transmission of food to the stomach.

The œsophagus (*fig. 61. d*) is usually a short and wide funnel-shaped canal with a thick muscular coat and a smooth epithelial lining, more or less longitudinally folded to admit of increased capacity for the deglutition of the often un-masticated or undivided food. The muscular fibres are arranged in different fasciculi, the outer ones being usually circular, the inner ones longitudinal. Some fasciculi from the abdominal vertebræ are attached to the œsophagus in the *Cottus scorpius* (XCIX.). The cardiac half of the œsophagus is characterised by increasing width in most *Cyprinidæ*, and by a more vascular or otherwise modified texture in the *Pharyngognathi*, *Lopho-branchii*, the Gobioids, Blennies, Flying-fish, Garfish, and some others. The inner surface of the œsophagus sends off short processes, papilliform in *Box* and *Cæcio*, obtuse in *Acipenser*, (prep. 463.), hard and almost tooth-like in *Rhombus xanthurus*, *Stromateus fiatola*, and *Tetragonurus* or the keel-tailed Mullet. The inner surface of the gullet presents longitudinal papillose ridges in *Planirostræ*. But the most striking peculiarities of the œsophagus are met with in the Plagiostomes. A layer of grey parenchymatous substance is interposed between the muscular and inner coats at the cardiac half of the œsophagus in the *Torpedo*. Numerous pyramidal retroverted processes, jagged or fringed at their extremity, project from the inner surface of the œsophagus in the Dog-fish (*Spinax acanthias* (prep. 664.)). In the great Basking Shark (*Selache*) the homologous processes, near the cardia, acquire unusual length, dividing and subdividing as they extend inwards, so that the cardiac opening is surrounded by ramified tufts directed towards the stomach. This valvular mechanism (prep. 464. A), seems intended to prevent

the return of such fishes or mollusks as may have been swallowed alive and uninjured by the small obtuse teeth of this great Shark. In many Osseous Fishes we may, finally, notice the communication of the 'ductus pneumaticus' with the œsophagus, usually by a small simple foramen; but provided with special muscles in the *Lepidosteus*, where it opens upon the dorsal aspect of the œsophagus, and with a sphincter and cartilage in the *Polypterus*, and *Lepidosiren*, where it communicates like a true glottis with the ventral surface of the beginning of the œsophagus. In the Globe-fishes (*Diodon*, *Tetrodon*) the great air-sac seems to be a more direct development, as a cul de sac, of the œsophagus (prep. 2095.). These singular fishes blow themselves up by swallowing the air, which escapes through a large anterior oblique orifice into the sac: and this again communicates with the fore-part of the œsophagus by a second orifice much smaller than the first, and having a tumid valvular margin.\*

The cardiac orifice of the stomach is occasionally defined by a constriction, as in the *Planirostra* (*fig. 61. e*), and *Mormyrus* (*fig. 63. e*): but an increased expansion with increased vascularity and a more delicate epithelial lining of the mucous membrane more usually indicate, in Fishes, the beginning of the digestive cavity. The stomach is a simple and commonly an ample cavity, with a great disproportion in the diameters of the cardiac and pyloric orifices; in the Cornish Porbeagle-Shark, for example, the cardiac entry will readily admit a child's head, whilst the pyloric outlet will barely allow of the passage of a crow-quill.

There are two predominant forms of the stomach in Fishes, viz. the 'siphonal' and the 'cæcal;' in the first it presents the form of a bent tube or canal, as in the specimens† from the Turbot, Flounder, Sole, Cod, Haddock, Salmon, Carp, Tench, Ide, Lump-fish, *Lepidosteus*, Sturgeon, Paddle-fish (*fig. 61. e, f*), and most Plagiostomes; in the



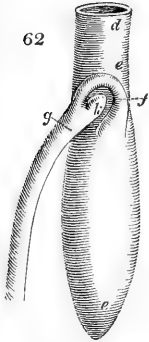
Digestive Organs *in situ*. *Planirostra*.

second form the cardiac division of the stomach terminates in a blind

\* LXVI. t. iii. p. 271. pl. 47.

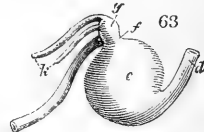
† Reference was made to preparations or recent dissections on the lecture-table.

sac and the short pyloric portion is continued from its right side, as in the Perch, the Scorpcœna, the Gurnards, the Bull-heads, the Smelts, the Angler, the Pike, the Lucio-perca, the Sword-fish, the Silurus, the Herring, and Pilchard, the Conger, the Muræna, and the Polyp-terus (*fig. 62*). A transitional form, in which the pyloric end is



Stomach and pancreas ;  
Polypterus.

bent so abruptly upon the cardiac as to make the cœcal character of the latter doubtful, is presented by the short and capacious stomach of the Burbot, the Blenny, and the Gymnotus. In the Mormyrus the stomach presents the rare form of a globular sac (*fig. 63. e*). Where the cœcal character is well marked the length of the blind end of the cardia varies considerably ; in the Polypterus, Conger, and Swordfish it forms almost the whole of the elongated stomach, the



Stomach and pancreas ;  
Mormyrus.

short pyloric portion being continued from near its commencement ; in the equally elongated stomach of the Pike, the pyloric portion is continued from the cardiac sac at a little distance from its blind end ; the Herring, Gurnard, and Scorpcœna show an intermediate position of the pyloric portion, and this is usually attended with a shorter and wider form of the cardiac cœcum. The pyloric portion is usually slender and conical ; but it dilates into a wide sac in *Sargus* and *Lophius* ; and forms a small oval pouch in *Trachypterus*. In certain fishes the stomach deviates from the typical forms either into the extreme of simplicity or the converse, without, however, attaining in any species that degree of complexity which we shall find in the higher organised Vertebrata. A proper gastric compartment of the alimentary canal cannot be said to exist in the Lancelet ; the long cœcum (*fig. 46. hd, l*) continued from it just beyond the cardia appears to be a simple form of liver. In the higher *Dermopteri*, as the Sand-prides, the Myxines, and the Lampreys, as also in *Cobitis* and *Lepidosiren*, the stomach is continued straight from the œsophagus to the intestine. I have found the capacious cardiac division of the stomach of the *Lophius* partially divided into two sacs ; the unusually wide and short pyloric portion forming a third sac : there may also be observed a few obtuse processes from the inner side of the cardia in this fish. In the Gillaroo Trout the ascending or pyloric half of the bent or siphonal stomach has its muscular parietes unusually thickened, by which it is enabled to bruise the shells of the small fluviatile testaceans that abound in the streams in which this variety of trout is

peculiar.\* The pyloric portion of the stomach is very muscular in the Indian Whiting (*Johnius*), and in some species of *Scomber*: but the modification which gives the stomach the true character of a gizzard is best seen in the Mulletts (*Mugil*). The cardiac portion here forms a long cul de sac; the pyloric part is continued from the cardiac end of this at right angles, and is of a conical figure externally; but the cavity within is reduced almost to a linear fissure by the great development of the muscular parietes, which are an inch thick at the base of the cone; and this part is lined by a thick horny epithelium (prep. 502). In the Herring the ductus pneumaticus of the swim-bladder is continued from the attenuated extremity of the cardiac end of the stomach. In the Basking-shark the contracted pyloric division of the stomach (*fig. 65. f*) communicates by a narrow aperture with a second small rounded cavity (*f'*), which opens by a narrow pylorus into the short and capacious duodenum (*g*).

These are the observed extremes of the modifications of the stomach in Fishes, which it will be seen, therefore, are far from according or parallellising those of the dental system. There is often, indeed, no essential difference of form in the stomach of a fish with exclusively laniary teeth, *e. g.* the carnivorous Salmon, and in that of one with exclusively molar teeth, *e. g.* the herbivorous Carp. The *Ætobates*, whose teeth form a crushing pavement, has a stomach similar in shape and size to that in the common Ray, in which every tooth is conical and sharp pointed.

The inner surface of the stomach presents few modifications in Fishes; it is usually smooth; rarely reticulate, as in the *Gymnotus* (prep. 500.); still more rarely papillose. The lining membrane is thrown into wavy longitudinal rugæ in the cardiac portion of the stomach of most Sharks. The gastric follicles are conspicuous, especially in the pyloric portion of the stomach in many Fishes, as, *e. g.*, the Gurnards, Blennies, and Lump-suckers. The circular pyloric valve is commonly well developed and has sometimes a fimbriated margin. The solvent power of the gastric secretion is conspicuously exemplified in Fishes: if a voracious species be captured after having swallowed its prey, the part lodged in the stomach is usually found more or less dissolved, whilst that which is in the œsophagus is entire; and, in specimens dissected some hours after death, one may observe, what Hunter so well describes, "the digesting part of the stomach itself reduced to the same dissolved state as the digested part of the food."† This surrender of the dead membranes of the stomach to the solvent power of the previously secreted gastric juice is well exemplified in the preparation of the Shark's stomach, N. 507. B.

\* J. Hunter, xcii. p. 126.

† xcii. p. 120.

The muscular action of a fish's stomach consists of vermicular contractions, creeping slowly in continuous succession from the cardia to the pylorus; and impressing a two-fold gyratory motion on the contents: so that, while some portions are proceeding to the pylorus, other portions are returning towards the cardia. More direct constrictive and dilative movements occur, with intervals of repose, at both the orifices, the vital contraction being antagonised by pressure from within. The pylorus has the power, very evidently, of controlling that pressure, and only portions of completely comminuted and digested food (chyme) are permitted to pass into the intestine. The cardiac orifice appears to have less control over the contents of the stomach; coarser portions of the food from time to time return into the œsophagus, and are brought again within the sphere of the pharyngeal jaws, and subjected to their masticatory and comminuting operations. The fishes which afford the best evidence of this ruminating action are the Cyprinoids, (Carp, Tench, Bream,) caught after they have fed voraciously on the ground-bait previously laid in their feeding haunts to ensure the angler good sport. A Carp in this predicament, laid open, shows well and long the peristaltic movements of the alimentary canal; and the successive regurgitations of the gastric contents produce actions of the pharyngeal jaws as the half-bruised grains come into contact with them, and excite the singular tumefaction and subsidence of the irritable palate, as portions of the regurgitated food are pressed upon it. The Eel is, also, a good subject for studying the movements of the stomach; and, besides at the cardiac and pyloric orifices, the direct constrictive action of the circular fibres may be seen in this fish at the beginning of the short pyloric division; regulating the passage of the food from the long cardiac sac. These observations throw light on the functions of the pharyngeal teeth in the predatory Fishes, (the Pike, for example,) in which one sometimes finds a recently swallowed fish in the stomach: it may show, for example, a few marks of the large mandibular canine teeth; but it has undergone no sub-division by the pharyngeal rasp-teeth. It would seem, at first sight, that these took no other part in the mechanical operations of digestion, than to aid in the act of swallowing: the analogy, however, of the ruminant or regurgitant function of the stomach of the Carp, suggests that the pharyngeal teeth take a more important share in digestion, and indicates the nature of their operations. As the gelatinous integuments and intermuscular aponeuroses of the swallowed fish are dissolved by the gastric juice, masses of the myocommata become detached, and these fibrous portions are most probably carried by the regurgitating power of the stomach to the pharyngeal teeth,

are there carded and comminuted, and again swallowed, to be reduced to chymous pulp by the solvent power of the secretions and by the continuous grinding pressure of the spiral movements of the gastric parietes. It is highly probable, therefore, that the shortness and width of the œsophagus, the masticatory mechanism at its commencement, and its direct terminal continuation with the cardiac portion of the stomach, relate to the combination of an act analogous to rumination, with the ordinary processes of digestion, in all Fishes possessing those concatenated and peculiar structures. For it will be seen that the Fishes, as, for example, the Sturgeon, the Paddle-fish, the Dog-fish, and the Selache, whose œsophagus is best organised to prevent regurgitation from the stomach, are devoid of the pharyngeal jaws and teeth.

Fishes disgorge the shells and other indigestible parts of their food : and it is known to practised anglers that Fishes, when hooked or netted, often empty their stomach by an instinctive act of fear, or to facilitate escape by lightening their load.\*

The intestinal canal is shorter in Fishes generally than in the higher Vertebrata : in the Dermopteri, Plagiostomes, Holocephali, Sturionidæ (see the Paddle-fish, *fig.* 61. *f* to *i*), the Lepidosiren (xxxiii. pl. 25. *figs.* 1 and 2.), the Flying-fish, the Loach, the Gar-pike, the Wolf-fish, the Salmon, the Herring, and the apodal fishes, it is shorter than the body itself : in some of the above-cited examples, the intestine extends in a straight line from the pylorus to the anus (*fig.* 46. *i*) ; in most fishes it presents two or three folds ; it is sinuous in the Sword-fish ; concentrically and subspirally wound in the Mullet, in which the convolutions are numerous and form a triangular mass ; and it is in this fucivorous fish, in the Chætodonts, and the Carp-tribe, that the intestinal canal attains its greatest length in the present class.

With a few exceptions, of which the Dermopteri and the Lepidosiren are examples, the intestines are divided into ‘small’ and ‘large.’ The beginning of the small intestine, to which is arbitrarily given the name of ‘duodenum’ (*fig.* 61. *i*) is usually wider than the rest of that division of the canal : it receives the ducts of the liver and pancreas, the latter accessory organ presenting, in most Osseous Fishes, the elementary form of simple cæca (*fig.* 63. *k*), which are usually termed, from their communication with, or development from, the commencement of the small intestine, ‘appendices pyloricæ.’ The termination of the small intestine is commonly marked by a circular

\* A netted Salmon is generally found with an empty stomach ; whence it has been supposed, notwithstanding its extraordinary array of teeth, that its staple food consisted of such animalcules as are alone, under those circumstances, discoverable in the gastric mucus.

valve. In the Bogue-bream (*Box vulgaris*) and the Flounder there is a small cæcal process at the commencement of the large intestine; there are two short cæca at the same part in *Box Salpa*.\* The large intestine is usually short and straight in Fishes, answering to the rectum of higher animals. In some Fishes, *e. g.*, *Salmo*, *Clupea*, *Esox*, *Anableps*, *Anarrichas*, and the Gymnodonts, it preserves the same diameter as the small intestine, and the term 'large,' becomes arbitrary: in some fishes, *e. g.*, *Gasterosteus*, *Centriscus*, *Ostracion*, *Balistes*, and *Syngnathus*, it is even narrower than the 'small intestine;' but most commonly it is wider, as in the Percoid family, the Gurnards (*Triglidæ*), the Breems (*Sparidæ*), *Sciæna*, *Scomber*, *Cottus*, *Labrus*, *Pleuronectes*, *Gadus*, *Lophius*, *Cyclopterus*, the *Siluridæ*, the *Plagiostomi*, and the *Planirostra* (*ib. h.*).

The tunics of the intestinal canal consist in Fishes, as in other Vertebrates, of the peritoneal or serous, the muscular, and the mucous coats, with their intervening cellular connecting layers, and the epithelial lining; the muscular and mucous coats are commonly thicker and of a coarser character than in the warm-blooded classes; pigmental cells are not unfrequently developed in the serous coat; the epithelial scales of the intestine of the Lancelet support vibratile cilia.

The muscular fibres are arranged in a thin outer longitudinal and a thick inner circular stratum (see preps. 637. 639. from the Sturgeon); the elementary fibres in general present the smooth character of those of the involuntary system; but Reichert† has detected the transversely striated fibre in the muscular tunic of the whole tract of the intestine in the Tench.

The mucous membrane presents numerous modifications, some of them more complex and remarkable than in any of the higher Vertebrates. It is commonly thick and glandular, and always highly vascular. In the small intestines it presents, in some Fishes (Cod, prep. 633.), a smooth and even surface; in some it is produced into obliquely longitudinal or wavy folds (Turbot, prep. 634., Salmon, prep. 635.); in the Herring it presents feeble transverse rugæ; in many Fishes it is reticulate, as in the Wolf-fish (prep. 631.) and *Muræna* (prep. 630.); this character is present in the peculiarly thick and parenchymatoid mucous tunic of the small intestine of the Sturgeon, where the larger meshes include irregular spaces, subdivided into smaller cells (prep. 638.). In a few Fishes the mucous membrane is coarsely villose or papillose. There is often a well-marked difference in the character of the lining membrane of the small and large intestine: thus, in the Salmon, the rugæ become fewer, larger,

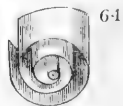
\* xxxiii. t. vi. pp. 624. 270.

† xciii. p. 26.



and less oblique as they approach the rectum; the commencement of this intestine is marked by a large transverse fold or circular valve, which is succeeded by several others less produced, and resembling the *valvulæ conniventes* in the human jejunum. The straight 'large intestine,' which is relatively longer in the *Amia*, *Polypterus*, *Paddle-fish* (*fig. 61.*), *Sturgeon*, and *Chimæra*, is characterised by the continuity of such transverse folds as those in the *Salmon*, producing an uninterrupted spiral valve of the mucous membrane. In the *Lepidosiren* the entire tract of the straight and short intestine is traversed by this peculiarly piscine extension of the inner coat.\* The spiral valve characterises the large intestine in all the *Plagiostomes*, and establishes the essential difference between the short and apparently simple intestinal canal of these cartilaginous fishes, and that of the low-organised *Myxinoid* species.

The true homologue of the small intestine is extremely short in the *Plagiostomes*; it is narrow in the *Rays*, expanded and sometimes sacciform (*fig. 65. g*) in the *Sharks*, where it seems to form the commencement of the suddenly expanded large intestine: this is straight, and though constituting the chief extent of the intestinal canal, it is very short in proportion to the body; not exceeding, for example, one eighth of the entire length of the body in the *Alopias* or *Fox-shark*. The economy of space in the abdominal cavity † is, however, effected at the expense of the serous and muscular coats, not of the mucous membrane. The required extent of secreting and absorbing superficies is gained by raising or drawing inwards, from the intestinal parietes, the mucous membrane in a broad fold at the beginning of the large intestine, and continuing it in spiral volutions to near the anus. The coils may be either longitudinal and wound vertically about the axis of the intestinal cylinder, or they may be transverse to that axis. In the first case, when the gut is slit open lengthwise, the whole extent of the fold may be uncoiled and spread out as a broad sheet; and, if the gut be divided transversely, the cut edges of the valve present a spiral disposition, as in *fig. 64.* The *Hunterian* preparation (No. 645.) shows the longitudinal form of the spiral valve; as it may be seen, also, in the squaloid genera *Carcharias*, *Scoliodon*, *Galeocerdo*, *Thalassorhinus*, and *Zygæna*.‡ In the second and more common modification, the fold of mucous membrane is disposed in close transverse coils, as shown in the longitudinal section of the *Selache's* gut (*fig. 65. h.*); and a transverse section exposes only the flat surface of one of the coils. Prep.



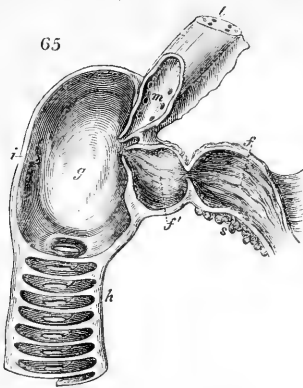
Spiral valve. *Zygæna*;  
Duvernoy.

\* XXXIII. p. 343. pl. 25. fig. 2.

† Roget, c. ii. p. 205.

‡ XLVI. t. iv. p. 314.; t. xcvi. p. 277. pl. 2 and 3.

652. A, shows a typical example of this disposition of the mucous



Spiral valve, *Selache*; Clift.

membrane in the Fox-shark (*Alopias Vulpes*); the valve describes thirty-four circumgyrations within seven inches extent of the intestine; the mucous membrane is minutely honey-combed: a few scattered fibres of elastic or involuntary muscular tissue may be traced in the vasculo-cellular layer included within the mucous fold, and they form a slender band within the free border of the valve, retaining much elasticity in the dead intestine, and drawing that border into festoons.

Besides *Selache* and *Alopias*, the spiral valve is transverse in *Galeus*, *Lamna*, and all the Dog-fishes (*Scylliidae* and *Spinacidae*). The trunk of the veins of the longitudinally convoluted valve runs along its free thickened border, and quits its commencement to join the vena portæ\*: that of the transversely spiral valve is external to the gut.

One may connect the peculiarity of the spiral valve with the necessity for reducing the mass and weight of the abdominal contents in the active high-swimming Sharks, which have no swim-bladder; the essential part of an intestine being its discerning and absorbing surface, we see in them the requisite extent of the vasculo-mucous membrane packed in the smallest compass and associated with the least possible quantity of accessory muscular and serous tunics by the modifications above described. Analogous ones exist, however, in other Plagiostomes, and in the Lamprey, to which the above physiological explanation will not apply; and the spiral valve is associated with the air-bladder in some of the highly organised Ganoids, and in the *Lepidosiren*. Nevertheless, it is to be remarked that the intestinal canal is shortest, and the spiral valve most complex and extensive, in the Sharks. In both these, and the Rays, the valve subsides at a short distance from the anus; and into the back part of this terminal portion of the rectum an elongated cæcal process with a glandular inner surface opens (*fig. 75. i*). The anus itself communicates with the fore-part of a large cloacal cavity in the Plagiostomes. In other Fishes, where it opens distinctly upon or near the external surface, it is anterior in position to the orifices of oviducts, or sperm-ducts, and

\* Duvernoy, xcvi. p. 274. pl. 10.

of the uterus or urinary bladder; the *Lepidosiren* has the peculiarly ichthyic arrangement of the anal, genital, and urinal outlets.\*

In the *Dermopteri* the intestinal canal is pretty closely attached to the back of the abdomen, though the primitively continuous mesenteric fold becomes reduced in the Lampreys to filamentary processes accompanying the mesenteric vessels. Rathké has observed a similar metamorphosis of the mesentery in the *Syngnathi* and *Cyprinidae* into detached membranous bands. The mesentery is entire in the *Lepidosiren*, the *Plagiostomes*, and many other fishes: it is usually single and continuous from the stomach to the end of the intestine: there are two parallel mesogastrics in the Eel, and a kind of omental accumulation of adipose matter is sometimes found along the ventral surface of the intestines: a second mesentery is continued from this part of the intestine to the ventral parietes of the abdomen in the *Muraena*.

The position of the cloacal outlet varies much in fishes: in some of the jugular species it follows the ventral fins to the region of the throat; and, in the apodal *Gymnotus*, it is placed so far forwards as to remind us of the position of the excretory outlet in the *Cephalopods*. It is beneath the pectorals in the *Amblyopsis spelæus*: but the more normal posterior position of the vent obtains in most abdominal and all cartilaginous fishes.

Petrified faeces or 'coprolites' give some insight into the structure of the intestinal canal in extinct species of fishes: some that have been found in the skeleton of the abdomen of the great *Macropoma* of the Kentish Chalk, and detached coprolites associated with the scales and bones of the more ancient *Megalichthys*, indicate by their exterior spiral grooves that these ancient Ganoids, like their modern representative, the *Polypterus*, possessed the spiral valve.

The *liver* makes its first appearance in the lowest vertebrated, as in the lowest articulated species, under the form of a simple caecal production from the common alimentary canal: commencing in the Lancelet (*fig. 46. hd*), a little beyond the orifice *py*, the hepatic caecum (*l*) extends forwards by the side of the ciliated respiratory sac, which appears to be the homologue of the long œsophagus with the attached marsipo-branchial organs of the Lampreys, but which some may view as representing the stomach of higher fishes. As the true digestive function, however, cannot be supposed to begin until the food has entered the canal *ii*, the place of communication of the rudimental liver corresponds in the Lancelet with that in the

\* xxxiii. pl. 25. fig. '1, m, n, o, l. The *Branchiostoma* offers no exception to this rule; the opening, by which the ova and semen are expelled, is a common peritoneal outlet.

lower organised Mollusks: other members of the Piscine class do not show by permanent structures the gradational steps in the development of the hepatic, as in that of the pancreatic gland. Passing to the Myxinoids we find the liver to be, as in all higher fishes, a well-defined conglomerate, or acinous parenchymatoid organ, with a portal and an arterial circulation, with hepatic ducts, and generally a gall-bladder and cystic duct, by which the bile is conveyed to the duodenum, from which the stomach is divided by a pyloric valvular orifice.\*

The texture of the liver is soft and lacerable; its colour usually lighter than in higher Vertebrata, being whitish in the Lophius, in many other fishes of a yellowish-gray or yellowish-brown: it is, however, reddish in the Bream; of a bright red in the *Holocentrum orientale*, orange in *Holocentrum hastatum*, yellow in *Atherina presbyter*, green in *Petromyzon marinus*, reddish-brown in the Tunny, dark brown in the Lepidosiren; almost black in the Paddle-fish. In most fishes the liver is remarkable for the quantity of fine oil in its substance, under which form almost the whole of the adipose tissue is there concentrated in the Cod-tribe, the Rays, and the Sharks.† Fishes which, like the Salmon and Wolf-fish, have oil more diffused through the body have comparatively little oil in the liver.

The liver is generally of large proportional size: it is attached at the fore-part of the abdomen to the aponeurotic wall partitioning off the pericardium (*fig. 61. l, o*), and extends backwards, with a few exceptions, further on the left than on the right side: in the Carp, the Bream, and the Stickleback, the right lobe is longest. Its shape varies with that of the body or of the abdominal cavity: it is broadest, for example, in the Rays, longest in the Eels; not, however, elongated in the Gymnotus, in which apodal fish, by reason of the peculiar aggregation of the organs of vegetative life in the region of the head, the liver is divided into two short and broad lobes connected by a transverse lobule. The liver consists of one lobe in most Salmonoid and Luciid Fishes, in the Gymnodonts and Lophobranchs, in the Mulletts, Loaches, and Bullheads. It is long and simple in the Lamprey and Lepidosiren; long and bilobed in the Conger. The Lump-fish has a lobulus besides the chief lobe, which is round and flat. There is a short thick convex lobe to the right of the long left lobe in the Lophius. In many fishes the two lobes are subequal: they are rarely quite distinct, as in the Myxinoids; but commonly confluent at their base, as in the Wolf-fish; or connected by a short transverse portion, as in most Sharks, the Siluroids, the

\* The Bream is the only fish in which I have found the cystic duct terminating directly in the stomach.

† The myriads of Dog-fish captured and commonly rejected on our coasts show that the fishermen have not yet taken full advantage of this anatomical fact, which exposes to them an abundant source of a pure and valuable oil.

Polypterus, the Dory, the Coryphene, the Chætodonts, and the Cod-tribe. In the Whiting the two chief lobes extend the whole length of the abdomen. The liver is trilobed in the Corvina, the Clupeoid and the Cyprinoid fishes: in many of the latter family it almost conceals the convoluted intestinal canal. The broad and flat liver of the Raiidæ is trilobed. The liver is much subdivided in the Sand-lance and in the Tunny, in which latter fish it presents remarkable modifications of the vascular system.\* There are few well-established exceptions to the general rule of the presence of a gall-bladder in the class of Fishes. My dissections confirm the statement of its absence in the Lump-fish by Cuvier† and Wagner.‡ Cuvier did not detect a gall-bladder in *Lates niloticus*, *Holocentrum Sogho*, *Sphyræna Barracuda*, *Trigla Lyra*, *Tr. Cuculus*, *Corvina dentex*, *Glyphisodon saxatilis*, *Lepidopus argenteus*, *Labrus turdus*, *Ammodytes*, and *Echineis remora*. The gall-bladder is wanting in the Ammocete and Lamprey, but exists in the Myxinoids; it is absent in the *Pristis*, *Zygæna*, and *Selache*, but is present in *Galeus*, and others of the Shark-tribe. I have studied the rich series of observations recorded by Cuvier§ and his able Editors|| on the gall-bladder and gall-ducts in fishes without obtaining a clue to the law of the development of the special receptacle of the biliary secretion in fishes. The pouch in which the aggregated hepatic ducts terminate in the *Selache maxima* may compensate for the absence of the gall-bladder in that Shark; these ducts are enclosed in a broad flat band of dense cellular tissue (*fig. 65, l.*), which passes obliquely down in front of the stomach as far as the duodenum, when each of the ducts opens by a separate oblique orifice into a common cavity (*ib. m.*) of an oval form, communicating with the duodenum by a single opening.

The gall-bladder is usually situated towards the fore-part of the liver, and attached to the right lobe when this exists (as in *fig. 61. m.*). In some Cyprinoids and Rays, and in the Sturgeon, it is imbedded in the substance of the liver. In many Chætodonts and Salmonoids, in the Sword-fish, in the Eel and the Muræna, it hangs freely at some distance from the liver. I found the gall-bladder three inches from the liver in a Lophius of two feet in length. The size of the gall-bladder varies in different fishes: it is very small in most Rays; in Osseous Fishes it usually bears a direct relation to that of the liver itself. It is pyriform in the Lophius, Mullet, Sea-perch (*Sebastes*), Pike, Sturgeon, Planirostra, and most other Fishes: it is subspherical in the Gray-shark (*Galeus*), and in the Wolf-fish: it is like a long-necked flask in Polypterus; is bent like a retort in Xiphias, and is

\* Eschricht, ci.  
§ xxiii. passim.

† XIII. t. iv. p. 551.  
|| XIII. t. iv. pt. ii. p. 559—569.

‡ XLVII.

remarkably long and slender in *Sciæna*, *Upeneus*, *Lates nobilis*, and in the Bonito, the Tunny, and other *Scombridæ*. The bile is sometimes conveyed directly into the gall-bladder by hepato-cystic ducts, and thence by a cystic duct into the duodenum (Wolf-fish, *Erythrinus*, *Lepidosiren*): or it is conveyed by a single hepatic duct, formed by the union of several branches from the liver (*Zygæna*, where the duct is very long): or by two hepatic ducts opening separately into the intestine, as in *Pristis*: or an hepatic duct from the left lobe joins a cystic duct from the bladder, receiving the gall from the right lobe, and the secretion is conveyed by a 'ductus communis choledochus' into the duodenum, as in *Pimelodus*: or the bile is conveyed to the duodenum partly by a cystic duct and partly by a distinct hepatic duct, as in the Salmon, in which the latter dilates before it terminates. In the *Lophius* three hepatic ducts join the very long cystic, which duct sometimes dilates where it receives them. In the Turbot I found numerous hepatic ducts, some of which communicated with different parts of the cystic duct, and four opened into the dilated termination of the ductus communis. (Prep. 811. A.) In the *Galeus* the cystic duct runs some way through the substance of the liver, and sometimes between the tunics of the pyloric canal of the stomach, before it enters the commencement of the wide intestine, near the beginning of the spiral valve. The gall-duct in the Sturgeon and *Planirostra* (*fig.* 61.) terminates at a greater distance above the valvular intestine. The ordinary position of the entry of the bile into the alimentary canal in Osseous Fishes is at the commencement of the small intestine near the pylorus. The terminal orifice of the gall-duct is often supported on a papilla, as in the Sturgeon, the Skate, and the *Labrax lupus*. In the Bream I found the short cystic duct opening into the fore-part of the cardiac portion of the stomach.

In most Osseous Fishes the intestine buds out at its commencement into long and slender pouches, or cæca, into which it appears that the food never enters, and which, therefore, increase the direct secreting surface of the alimentary tract, over and above the extent of the mechanism for pounding and propelling the chyme, or of the vascular surface which selects and absorbs the chyle. By a very gradual series of changes of these cæcal processes, within the limits of the class of Fishes, we are led to recognise them as homologous with the conglomerate gland called 'pancreas' in Man. The secretion of the rudimental representatives of this gland is so like the fluid which the ordinary mucous surface of the intestine eliminates and sets free from its capillary system, that conditions of the ordinary alimentary tract exist in some fishes which render needless the development of the special accessory surfaces. The *Dermopteri* show no trace of pancreas: their whole digestive canal is simple; the whole

organisation for which that canal is the commissariat is the most simple in the Piscine class. The Lamprey, at the head of the Dermopterous order, derives from the slight spiral extension of its intestinal mucous coat the required concomitant complexity of the digestive canal. The torpid Lepidosiren, which, though of a much more advanced type of ichthyic organisation, can have but little expenditure of nervous and muscular force to repair, seems, in like manner, to derive from a spiral extension of its thick and glandular intestinal mucous membrane the equivalent of a pancreas, and no rudiment of that gland exists in this fish. In several Osseous Fishes either the inactive nature of the species, or the extent or special modifications (as the long intestine and glandular palate of the Carp, for example,) of the mucous membrane in the ordinary tract of the alimentary canal, render unnecessary the presence of a pancreas. Thus there is no cæcal production of the duodenum in the Ambassis, the Wolf-fish, nor the Warty Agriope, nor in most Labroids, Cyprinoids, Lucioids, Siluroids, nor in the Lophobranchs and Plectognats; nor in the genera *Antennarius*, *Malthæus*, and *Batrachus*. The pancreas is represented by a single pyloric cæcum in the Sandlance and Polypterus (*fig. 62. k*); by two cæca in most Labyrinthibranchs, in many species of Amphiprion, in the Lophius, the Turbot, and the Mormyrus (*fig. 63. k*); by three cæca in the Perch, the percoid Popes (*Acerina*), the Asprodes, and Diploprions; of from four to nine cæca in the genus *Cottus*; of from five to nine cæca in the genus *Trigla*; of six cæca and upwards in *Scorpena* and *Holocentrum*; and so on, increasing to a numerous group of pendent pyloric pouches, as we find in the Scomberoids, Chætodonts, Gadoids, Halecoids, Cyclopterus, and Lepidosteus. There is a difference, however, worthy of note, in the mode and extent of attachment of these numerous cæca: in the Salmon (*prep. 773.*), the Herring, and Haddock, they rank almost in a line along the whole duodenum: in the Gymnotus and Lump-fish they form a circular cluster around the distal side of the pylorus. Even in the longitudinally arranged cæca the principle of concentration dawns: thus the fifty pancreatic cæca of the Pilchard communicate with the duodenum by thirty orifices; but the fifty attenuated terminal blind sacs in the pancreas of the Lump-fish unite, reunite, and discharge their secretion by a circle of six orifices around the duodenal side of the pyloric valve. In the Tunny a more subdivided bunch of pancreatic cæca empty themselves by five orifices; in the Sword-fish by two orifices; and, finally, in the Sturgeon and Paddle-fish (*fig. 61. k*) by a single opening of what now becomes the short and wide duct of a pancreas. The interposition of cellular tissue binding together longer, more slender and

more ramified cæca, with a concomitant increase of the vascular supply, and a common covering or capsule, finally converts the accessory intestinal growths into a true parenchymatous conglomerate gland; as we see in the Holocephali and Plagiostomes, (preps. 776, 777.): the papilliform termination of the duct of such a pancreas is shown in the Selache at *fig. 64. i.*

The existence of this highly developed form of pancreas over and above the spiral intestinal valve may relate to the high organisation of these Cartilaginous Fishes, and to the great development of the organs of locomotion, occasioning the necessity for rapid and complete digestion. But if we compare the few existing species of heavily-laden Ganoid fishes, we shall again find good evidence of the compensation for a pancreas by the extension of the intestinal mucous membrane within the canal, the circumstances calling for a more complete development of the digestive system in the predatory Sharks and large-finned Rays not being present. Thus the Polypterus, which has a spiral intestinal valve, has only one short pyloric cæcum (*fig. 62. k*); whilst the Lepidosteus, which has no spiral valve, has a compact group of above a hundred small cæca, which unite and reunite to communicate by a few apertures with the commencement of the duodenum.

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## LECTURE X.

### VASCULAR SYSTEM OF FISHES.

#### THE ABSORBENTS.

THE assimilation of food in an animal body has a close analogy to a chemical operation, the general result being the obtaining from a combination of two substances a third distinct from both. If the chemist operates on a solid substance, he first triturates and reduces it to powder, then digests it in a solvent menstruum, next adds the reagent, and if the result of the admixture be a precipitate, the supernatant fluid is drawn or filtered off. So it is with the food: it first undergoes the process of mastication in the mouth, next that of solution in the stomach, then the chyme is mixed with the intestinal, biliary, and pancreatic secretions, and lastly the chyle is filtered off from the fæcal precipitate. The instruments of this separation and conveyance of the chyle to the circulating organs are the 'lacteals:' analogous vessels which take up the effete parts of the body are called the 'lymphatics;' both together constitute the 'absorbent



system.' This system exists as a separate organic vascular apparatus only in the Vertebrate subkingdom: it was first observed in Man and Mammalia; was discovered by John Hunter in Birds\* and Reptiles †, and afterwards described by Mr. Hewson and Dr. Monro in Fishes. The most systematic and detailed descriptions of the absorbent system of the Oviparous animals, published in the last century, are those of Hewson. ‡

The lacteal system in Fishes commences by a reticulate or plexiform layer of vessels attached to the cellular side of the mucous coat of the stomach and intestines: in the Skate § the network is so coarse that, when inflated, dried, and cut open, it appears like a subdivided cellular receptacle. The chyle is conveyed thence in all fishes by more vasiform lacteals situated immediately beneath the serous covering of the intestines to large reticulate receptacles, one in the mesenteric angle along the junction of the small and large intestines, the other extending along the duodenum, its pancreatic appendages, and the pyloric part of the stomach; and often also surrounding the spleen. The presence of the mesentery in the Myxinoids, and its absence in the Lampreys, involve corresponding differences in their lacteal systems: in the Myxinoids the lacteals are supported and conveyed by the mesentery to the dorsal region of the abdomen, and empty themselves into a receptacle above the aorta and the cardinal veins, between these and the vertebral chord: in the Lamprey the lacteals pass forwards, and enter the abdominal cavernous sinus beneath the aorta.

The lymphatic system is best demonstrated by injecting the large absorbent trunk which runs upon the inner surface of the ventral parietes of the abdomen, along the median line from the vent for-

\* "It is but doing justice to the ingenious Mr. John Hunter to mention here, that these lymphatics in the necks of fowls were first discovered by him many years ago." (Hewson, *cit.* 1768, p. 220.)

† Hunter's account of this discovery, in a manuscript copied by Mr. Clift, is as follows:—"In the beginning of the winter 1764-5, I got a crocodile, which had been in a show for several years in London before it died. It was, at the time of its death, perhaps the largest ever seen in this country, having grown, to my knowledge, above three feet in length, and was above five feet long when it died. I sent to Mr. Hewson, and, before I opened it, I read over to him my former descriptions of the dissections of this animal relative to the absorbing system, both of some of the larger lymphatics and of the lacteals, with a view to see how far these descriptions would agree with the appearances in the animal now before us; and, on comparing them, they exactly corresponded. This was the crocodile from which Mr. Hewson took his observations of the colour of the chyle." Hunter here alludes to the note appended to Mr. Hewson's paper on the "Lymphatic System in Amphibious Animals," *Philosophical Transactions*, vol. lix. 1769, p. 199. *a*: "In a crocodile which I lately saw by favour of Mr. JOHN HUNTER, the chyle was white."

‡ *cit.* 1768, 1769.

§ In this and other Plagiostomes the gastric lacteals are confined chiefly to the contracted pyloric canal.

wards to the interspace of the pectoral fins, where the size of the vessel best favours the insertion of the injecting pipe. It receives the lymphatics of the pectorals, and (in thoracic and jugular fishes) of the ventral fins; then, advancing forwards through the coracoid arch, it spreads out into a rich network, which almost surrounds the pericardium. The lymphatic plexus which covers the heart of the Sturgeon and Paddle-fish presents a spongy and almost glandular appearance when uninjected: large lymphatic trunks from the upper (dorsal) part of this plexus receive the lymphatics of the myocommata by a deep-seated trunk which runs along the ribs, and the lymphatics of the mucous ducts and integuments by a superficial trunk, which extends along the lateral line, and gets a penniform character by the regular mode in which its tributary lymphatics join it. The lymphatics of the head form minor plexuses at the bases of the orbits, and in the Carp they extend into the basi-cranial canal; those from the cellular arachnoid pass through the occipital foramen to join the lymphatics of the spinal canal, and terminate in the cervical and sub-occipital trunks, which receive the lymphatics from the upper extremities of the gills: these, with the deep-seated lymphatics from the kidneys, join the single or double trunks at the under part of the vertebral column, which combine with the lacteal plexiform trunks continued forwards along each side of the stomach and œsophagus, to form a large, short, common lacteo-lymphatic trunk on each side, which terminates in the jugular vein near its junction with the short precaval vein. The lymphatic system of the caudal portion of the body is chiefly received by two caudal sinuses, intercommunicating by a transverse canal, which sometimes perforates the base of the anchylosed compressed terminal tail-vertebra, and, converging to enter the hæmal canal, terminates there in the commencement of the 'vena caudalis.' Dr. M. Hall discovered that the caudal lymphatic sinus, in the Eel, possessed a contractile pulsating power.\* Folman† describes other and minor communications between the absorbent and venous system of Fishes.

The lymphatics of Fishes consist generally of a single tunic; a most delicate epithelial lining may be distinguished in the larger trunks. The only situations where valves have been seen in these vessels are at the terminations of the trunks in the caudal and the jugular veins. There are no lymphatic glands: these are represented by the large and numerous plexuses; and the whole absorbent system presents, as might be expected in Fishes, the first step beyond the primitive condition of the common areolar or cellular receptacle of the lymph in the Invertebrata. The chyle, as well as the

\* xxxix. ii. p. 217.

† ciii.

lymph, of Fishes is colourless and transparent: both contain corpuscles, or centres of assimilative force, five or six times smaller than the blood-discs, and manifesting an inherent power of development and change, some being granular, others with a capsule and in the condition of nucleated cells.

Professor Stannius\* has described ash-coloured bodies, lying near the pylorus and spleen, which contain a whitish fluid laden with microscopic granules, much smaller than the blood-discs: he regards them, apparently with justice, as a residuum of the fœtal vitellicle or yolk-bag.

#### THE VEINS.

As the blood moves in a circle, it signifies little at what point we commence the description of the parts concerned in the circulation, since there also we must end. But as, in tracing the progress of the nutriment through the organs concerned in its chylicification and sanguification, we were led by the absorbents to the veins, we may begin with them the account of the circulating system.

The tunics of the veins of fishes are unusually thin, and their valves few: though commonly in the form of tubes, yet they more frequently dilate into sinuses than in the higher classes, and traces of the diffused condition of the venous receptacles, so common in the Invertebrata, are not wanting in Fishes; as, for example, in the fissures of the renal organs, where the veins seem to lose their proper tunics, or to blend them with the common cellular tissue of the part; and in the great cavernous sinus beneath the abdominal aorta, receiving the renal and genital veins in the Lamprey. The jugular veins of Osseous Fishes and the hepatic veins of the Rays form remarkable sinuses.

The veins of fishes constitute two well-defined systems; viz. the 'vertebral' and the 'visceral,' answering to the division of the nerves and muscles into those of 'animal' and 'organic' life: the portal system is a subdivision of the visceral one, but also frequently includes part of the vertebral system of veins, especially in the Myxines, in which the portal sinus forms a common meeting-point between portions of both systems.†

The vertebral system of veins commences by a series of capillary roots‡ in the integuments and muscles, which unite to form branches

\* CIV. p. 39.

† Retzius, in XXI. "Gefasssystem," 1841, p. 16.

‡ The capillary system of vessels consists in Fishes, as in other Vertebrata, of minute but similar-sized tubules, capable of carrying a single file of blood-discs, and connecting the termination of the arteries with the commencement of the veins.

corresponding with the muscular and osseous segments of the body: these 'segmental' veins consist, in the tail, of superior or neural, and inferior or hæmatal branches; in the abdomen, of superior and of lateral branches; in the head, where the vertebral segments are more modified, the veins manifest a less regular and appreciable correspondence with these segments. The cephalic veins, returning the blood from the cranial vertebræ, their appendages and surrounding soft parts, from the brain, the organs of special sense and their orbits or proper cavities, from the mouth and pharynx, and, receiving also the whole or part of the 'venæ nutritiæ' from the branchial arches, unite together on each side to form a pair of 'jugular' veins, each of which usually dilates into a large sinus, and again contracts and resumes the vasiform character, as it descends to beneath the parapophyses of the atlas and axis, in order to join the corresponding trunk of the vertebral veins of the body.\* This great trunk, called 'vena cardinalis' by Rathké†, commences at the base of the tail-fin, where it receives the lymph from the pulsating sac in the Eel-tribe. The 'vena cardinalis' is double, there being one for each side of the body, and both right and left 'venæ cardinales' extend forwards, in close contact, along the hæmal canal in the tail, then through the abdomen, and in both regions immediately beneath the aorta and vertebral bodies, to near the 'axis,' where each trunk diverges and descends to join its corresponding 'vena jugularis,' forming the short 'pre-caval' vein‡ (*fig. 79, e*), which empties itself in the great auricular sinus between the aponeurotic layers of the pericardial and abdominal septum. In the Lamprey the 'vena cardinalis' is single along the tail, but it bifurcates on entering the abdomen into two veins, each of which is six times as large as the aorta. The left cardinal vein is larger than the right in the Myxinoids: but the symmetrical disposition of the vertebral venous system is more disturbed in many osseous fishes, at the expense of the right side; the right cardinal vein, after some transverse connecting channels with the left, finally terminating or losing itself therein anteriorly: part of the right jugular vein, also, in this

\* In the Lamprey the corresponding jugular trunks lie above the aponeurotic representatives of the vertebral parapophyses.

† 'La veine cave' of Cuvier; but it is not homologous with either the 'inferior' or 'superior venæ cavæ' of Man.

‡ *Ductus Cuvieri*, Rathké; *querverenstämme*, Müller. The precaval veins are the homologues of the two 'superior cavæ' in Reptiles and Birds, which receive the so-called 'azygos' veins or reduced homologues of the 'venæ cardinales' of Fishes: in the higher Mammals and in Man they are concentrated into a single 'superior vena cava,' receiving the 'venæ cardinales' by a common trunk, thence called 'azygos' in Anthropotomy. The anatomical student is usually introduced to the cardinal veins, or, to speak more strictly, their single homologue in the human subject, where their normal symmetrical character becomes masked by an extreme modification, and where their name is applicable only to so rare and exceptional a condition.

case enters the left or common cardinal vein.\* In the Tunny the two 'venæ jugulares' unite and form a common trunk, which enters the auricular sinus independently.† The Shad, the Pike, and the *Lucioperca* are examples where the jugular veins are symmetrical, and terminate distinctly in the precaval veins. With regard to the vertebro-venal system of the trunk, not all the segmental branches terminate in the 'vena cardinalis;' the 'neural' or superior twigs form with the 'myelonal' veins a trunk which runs parallel with the cardinal veins, but above the vertebral bodies in the neural canal. This trunk, which I call the 'vena neuralis,' communicates by short lateral and vertical canals with the 'venæ cardinales, and in the region of the abdomen these short anastomosing veins perforate the substance of the kidneys, and receive the 'renal veins' before terminating in the abdominal cardinal veins. The 'neural vein' gradually exhausts itself by these descending branches, and does not extend to or terminate anteriorly in the precaval trunk. Jacobson, observing that the abdominal anastomotic branches of the neural vein, in transferring its contents to the cardinal veins, perforated the kidneys, thought that those branches ramified in the renal tissue, like the portal veins in the liver; but my observations concur with those of Meckel and Cuvier‡ in showing that they rather receive or communicate with the renal veins *in transitu* in Osseous Fishes. In the Lamprey the renal vein assumes the form of a cellular or cavernous sinus, of a very dark colour, extending along the mesial margin of the kidney, uniting with its fellow posteriorly, and communicating by small orifices with the contiguous cardinal vein.

The visceral system of veins commences in Osseous Fishes by the capillaries of the stomach and intestines, of the pancreatic cæca and spleen, of the generative organs and air-bladder: these, by progressive union and reunion, constitute either a single trunk which forms the portal arterial vein of the liver; or, as in the Perch, a second trunk, the true homologue of the 'inferior vena cava' which returns the blood from the genital organs and air-bladder to the auricular sinus, without previous ramification in the liver; the portal trunk being formed only by the veins of the alimentary canal and its appendages. The portal trunk is single in the Ling, the Burbot, the Pope, the Eel, the Lamprey, and the Plagiostomes: but, in the Carp, where the lobes of the liver interlace with the convolutions of the intestine, the veins of this canal pass directly into the liver by several small branches, which ramify therein without forming a portal trunk.

\* XXI. ib. p. 38.

† Ib. p. 37.

‡ XXIII. p. 381.

In the Plagiostomes with the longitudinal spiral valve the main root of the portal vein is concealed in the free, thickened, muscular margin of that valve\* : the trunk of the intestinal vein is lodged also in an internal fold of the mucous coat in the Lamprey : in the Plagiostomes and Ganoids with transverse coils of the spiral valve, the venous blood is collected into an external intestinal vein. In the Paddle-fish this vein joins the vein of the spleen (*fig. 61. n*), and then, with the duodenal, pancreatic, and gastric veins, forms the portal trunk.

Professors Eschricht and Muller † found, in the Tunny, that the veins of the stomach, intestine, pyloric appendages, and spleen, respectively subdivided into numerous minute venules, which interlaced with corresponding 'retia mirabilia' of the arterial branches sent from the cæliac axis to the same viscera, and formed pyriform masses of vessels before entering the liver.

In a few Osseous Fishes, as the Shad, some of the caudal branches of the vertebral system of veins anastomose with the veins of the rectum, and thus form part of the roots of the portal system. But the most interesting modification of the portal system of Fishes is that discovered by Retzius in the Glutinous Hag. In this and also in other Myxinoids, the genital and intestinal veins form a common trunk along the line of attachment of the mesentery : all the gastric veins that do not empty themselves into the cardinal vein also join the great mesenteric vein. This vein advances to the space between the pericardium and the right suprarenal body, receives the anterior vein of that body (its posterior one joining the cardinal vein), and dilates into an elongated sinus, which is said to contract, as if it were a portal heart. The anterior part of this sinus receives a vein from the right anterior parietes of the body, which is formed by the union of all those veins of the muscular parts there which do not join the right jugular vein : the portal arterial vein is sent off from the posterior end of the pulsating sac, near the entry of the mesenteric vein, and goes backwards to beneath the two livers, and there divides, enters, and ramifies in each. The hepatic vein of the hinder and larger liver enters the common trunk or sinus formed by the union of the two cardinal veins with the left jugular : the hepatic vein of the smaller liver joins the termination of the left jugular vein, and they together end in the opposite side of the same common sinus.

In the Plagiostomes the right jugular and cardinal veins unite, and, receiving the vein of the pectoral fin (brachial vein), and a superficial vein from the head (external jugular), form a short transverse

\* Duvernoy, *xcvi.* p. 274.

† *ci.*

'precaval' trunk. A corresponding precaval trunk is formed in the same way on the left side, and the great auricular sinus is constituted by these and by the wide hepatic veins, which contract before they terminate. In many Osseous Fishes, as *Salmo*, *Silurus*, *Belone*, *Anguilla*, *Ammodytes*, and *Accipenser*, the hepatic veins terminate in the common sinus by a single trunk; in others, as *Thynnus*, *Gadus*, *Esox*, and *Pleuronectes*, by two trunks; and in a few Fishes, as *Clupea*, *Cottus*, and certain Cyprinoids, by three or more trunks.

Thus in Fishes the chyle, having already begun to manifest its independent life by the development of distinct microscopic granular corpuscles, as primitive centres of assimilative force, before it enters the lacteals, undergoes in those vessels and their receptacles a further stage of conversion into blood by the reaction and, as it were, impregnation of the lymph, and by the interchange of properties therewith: the vitalising stimulus of which interchange and reaction is manifested by the repeated spontaneous fission of the corpuscles, many of which now acquire a capsule, and thus become nuclei of cells. Then the mixed chyle and chyme enter the veins, where a further interchange of properties with the venous blood and a new course of action and reaction take place. The primitive pale chyle-corpuscles are here few in number; they have a capsule, and the granular character of their contents shows them to be in the course of change: a centre of superior assimilating force has already begun to establish itself amongst them, and to grow at their expense.\*

#### THE HEART.

The venous blood undergoes some change, probably, in its passage through the kidneys, by virtue of the anastomoses of the renal vascular system: it undergoes further change in its circulation through the liver, in so far as the bile, a fluid highly charged with carbon and hydrogen, is eliminated from it: it is said that in some fishes (*Myxine*, *Bdellostoma*) a contractile receptacle accelerates its course through the portal circulation. The venous blood has finally to be submitted to the influence of the atmosphere, and especially to the

\* Most of the stages analogous to those demonstrated by Dr. Martin Barry (cvii.), in the first periods of development of the mammiferous ovum, have been recognised in the corpuscles of chyle, lymph, and blood. The powers of one series of granules, the progeny of a primary centre, are concentrated in a secondary nucleus, which absorbs them as they liquefy; develops itself at their expense, generates a second series of granules, which, in their turn, give way to subserve a third regeneration of aggregated but distinct spherular centres of force; the final purpose of the successive development, liquefaction, and assimilation of the independent granular centres, being apparently to concentrate their vital energy in the form ultimately assumed, as coloured blood-discs. The shape and relative size of these particles are shown in *fig. 4. p. 13*, in a plagiostomous fish at *h*, in a typical osseous fish at *g*; the blood-discs of the Lamprey are circular. — See the admirable Memoir on the Development of Blood-discs. cxxvii.

reaction of the oxygenous element; and for this, the most important and efficient cause of its conversion into arterial blood, a contractile cavity, with strong muscular walls, is provided, in order to impel the blood to the organs especially destined to effect its decarbonisation and oxygenation. The propelling organ is called the 'heart' (*fig.* 61. *p, q*); the respiratory organs the 'gills' or branchiæ (*ib. t, u*), since they submit the blood to the influence of the air through the medium of the water in which it is suspended or dissolved.

There is only one known fish, viz. the Lancelet, in which a venous or branchial heart is not developed as a compact and predominant muscular organ of circulation: a great vein answering to the 'vena cardinalis' extends forwards along the caudal region, beneath the chorda dorsalis, above the kidney (*fig.* 46. *h*); and as it extends along the branchial œsophageal sac gives vessels to or receives them from the ciliated vertical bands or divisions of that sac, which vessels communicate with a vascular trunk along the inferior part of that sac. This trunk at its posterior end dilates into a small sinus (*ov*), which pulsates rhythmically, and represents rudimentally the branchial heart of the Myxinoids: the cardinal vein (*ba*) divides anteriorly, and supplies the short vascular processes (*gg*), which project above the pharyngeal orifice (*ph*) into the wide buccal cavity: the blood oxygenized in these processes is transmitted to the cerebral portion of the neural axis, to the organs of sense, especially the sensitive integument of the head, and to the jointed labial tentacula, (*f, f*), whence it returns to the pharynx by the labial vessels which there unite together, and with the inferior trunk of the vascular system, or arches, of the branchial pharynx. The free vascular processes (*gg*) seem to me to perform most distinctly the function of gills, and they are so referred to in the characters of the suborder *Pharyngo-branchii* (p. 47.): but they may be homologous with the supralabial tentacles of the Ammocete.

In the Myxinoids a heart consisting of an auricle and a ventricle is situated, like the pulsating tube or sinus of the Lancelet, far back from the head, in the beginning of the abdomen, where it is inclosed by a fold or duplicature of the peritoneum, extending between the cardiac end of the œsophagus above, and the anterior liver below, and forming the homologue of the pericardium, which sac communicates freely by a wide opening with the common peritoneal cavity. The auricle is much longer than the ventricle: it receives the blood from the common sinus by an orifice defended by a double valve. The auricle communicates with the left side of the rounded ventricle, the 'ostium venosum' having also a double valve. There are no 'columnæ carneæ' or 'chordæ tendineæ.' The artery, single here as in all Fishes, rises from the fore-part of the ventricle with a pair of



semilunar valves at the 'ostium arteriosum' behind its origin, beyond which it slightly dilates, but has no muscular parietes constituting a 'bulbus arteriosus.' In this Hunterian preparation of a large Myxinoid fish (No. 1018.) the artery divides at once into two branchial trunks, reminding one of the separate branchial arteries of the Cephalopods. In other species of *Bdellostoma* the artery extends beyond two or three pairs of gills before it bifurcates; and Müller\* saw one instance in the *Myxine glutinosa*, where the branchial artery continued single as far as the anterior gills.

The pericardium of the Ammocete communicates by one wide orifice with the peritoneum: that of the Lamprey is a shut sac, and is supported by a perforated case of cartilage, formed by the last modified pair of branchial arches (*fig. 11. 47'*, p. 52.). Not any of the Dermopteri possess the 'bulbus arteriosus:' this is present, and forms, as it were, a third compartment of the heart, beyond the ventricle and auricle in all other Fishes (*fig. 61. r. fig. 70. c*): nay, if we include the great 'sinus communis' as part of the heart, then we may reckon four chambers in that of Fishes; but the student will observe that these succeed each other in a linear series, like the centres of the brain, and their valves are so disposed as to impress one course upon the same current of blood from behind forwards, driving it exclusively into the branchial artery and its ramifications. This is very different from the arrangement and relations of the four compartments of the human heart. Physiologically the heart of Fishes answers to the venous or pulmonary division, viz. the right auricle and ventricle of the mammalian heart, and its quadripartite structure in Fishes illustrates the law of vegetative repetition, rather than that of true physiological complication.† The auricle and the ventricle are, however, alone proper to the heart itself: the sinus is a development of the termination of the venous system, as the muscular bulb is a superaddition to the commencement of the arterial trunk.

Some of the higher organised Fishes, which present the normal structure of the heart, have, like the Myxinoids, a perforated pericardium. In the Sturgeon the communication with the peritoneum is by a single elongated canal extending along the ventral surface of the œsophagus. In the Planirostra and Chimæroids the pericardio-peritoneal canal is also single. In the Plagiostomes it bifurcates, after leaving the pericardium, into two canals, which diverge and open into the peritoneum, opposite the end of the œsophagus: no ciliary movements have been noticed on the surface of these remark-

\* XXI. ib. p. 9.

† The heart of Fishes with the muscular branchial artery will be seen to be the true 'homologue' of the left auricle, ventricle, and aorta in higher Vertebrata, as we trace the complication of the heart synthetically; but it performs a function 'analogous' to that of the pulmonic auricle and ventricle in them.

able conduits. The serous layer of the pericardium is defended by an outer aponeurotic coat in Osseous Fishes and Plagiostomes, which adheres to the surrounding parts. In the Sturgeon, Wolf-fish, Loach and *Muræna*, short fibrous bands supporting vessels pass from different parts of the pericardium to the surface of the heart: in most other fishes the heart hangs freely except at the two opposite poles, viz., where the sinus communicates with the auricle, and where the *bulbus arteriosus* is continued into the branchial artery.

In the Plagiostomes the sinus itself is situated within the pericardium; but in Osseous Fishes between the layers of the posterior aponeurotic partition between it and the abdomen. The heart is situated below the hind-part of the gills, and, as these are more concentrated in the head in all Fishes above the *Dermopteri*, so the position of the heart is more advanced (*fig. 61. p, e*). In the Plagiostomes, the Sturgeons, the Perch, the Angler (*Lophius*, prep. 904.), and the Sun-fish (*Orthogoriscus*, prep. 905.), the orifice by which the great sinus communicates with the auricle is guarded by two semilunar valves; but these are far from being constant in Osseous Fishes. The auricle, when distended, is larger in proportion to the ventricle in Fishes than in higher Vertebrates. Its relative position to the ventricle varies in different species, and permanently represents as many similar variations displayed temporarily during the course of the development of the heart in higher Vertebrates; thus in the *Scorpena scrofa*, as in the *Myxinoids*, the auricle is posterior to and in the same longitudinal line with the ventricle: in the Carp, Sole, and Eel, it has advanced to the same transverse line, on the dorsal and left side of the ventricle: in most Osseous Fishes, the Ganoids, (*fig. 70, B.*), the *Sturionidæ* (*fig. 61. p*), it extends more forward, dorsad of both ventricle and *bulbus arteriosus*, and the heart, including the venous sinus, is now bent into a sigmoid form. The walls of the auricle are membranous, with thin muscular fasciculi decussating and forming an open network; but these are closer and stronger in the Sun-fish, Sturgeons, and Plagiostomes. The cavity is simple, but its inner surface is much fasciculated in the Sun-fish and Sturgeon, where the ends of the valves of the sinus are attached to the strongest muscular bands. Only in the *Lepidosiren* is there any vestige of a septum, and this is reticulate. The auricle communicates by a single orifice, commonly with the dorsal or the anterior part of the ventricle: this is guarded usually by two free semilunar valves; but in the Sturgeon, their margins and their surface next the ventricle are attached to numerous ‘*chordæ tendineæ*.’ In the *Orthogoriscus* the auricular aperture is guarded by four semilunar valves, the two smaller ones being placed at right angles with and on the auricular side of the two larger and normal valves: their margins are free.

The ventricle (*fig. 61. q*) usually presents the form of a four-sided pyramid, one side dorsad towards the auricle; one angle ventrad, and the base forwards. In the *Lepidosteus* and *Polypterus*, however, it is pyriform: in the Pike it is lozenge-shaped: in the *Lophius*, as in the *Myxinoids* and *Lampreys*, it is oval: in most *Plagiostomes* its transverse diameter is the longest, as if preparatory to a division. Its cavity is, however, simple in all fishes. The parietes of the ventricle are very muscular, and the fibres are redder than those of any other part of the muscular system; but the colour is less deep in the ground-fishes than in those that swim nearer the surface, and enjoy more active locomotion and respiration. The exterior muscular fibres decussate and interlace together irregularly and inextricably; but the deeper-seated ones form more regular layers, the innermost being transverse and circular, and separating readily by slight decomposition from the outer and more longitudinal layers. Some of the internal fasciculi send off the 'chordæ tendineæ' above mentioned in the Sturgeon; but in almost all other fishes those 'chords' are absent, and the auricular valve is free. In most osseous fishes the orifice at the base of the *bulbus arteriosus* is provided with a pair of semilunar valves (prep. 606.): the Sun-fish (prep. 905.) has four such valves there. But the *Ganoids*, *Holocephali*, and *Plagiostomes* have two or more transverse rows of semilunar valves attached to the inner surface of their long and muscular *bulbus arteriosus*. The preparation, No. 911., shows two rows of three valves in the Grey Shark (*Galeus*); the same is found in the Blue Shark (*Carcharias*), in the Dog-fish (*Scyllium*), and in the *Chimæroids*: the *Amia* has two rows of six valves: in the genera *Sphyrna*, *Mustelus*, *Acanthias*, *Alopias*, *Lamna*, *Rhinobatus*, *Torpedo*, and *Accipenser* there are three rows of valves: the preparation of the Sturgeon's Heart (No. 908.) shows five valves in the anterior row, and four valves in each of the other rows; and the free margins of the valves are connected by short 'chordæ tendineæ' to the parietes of the bulb. The genera *Hexanthus*, *Heptanchus*, *Centrophorus*, and *Tryggon* have four rows of valves. The preparation of the heart of the *Raia Batis* (No. 909.) shows five rows, the valves increasing in size to the last row, which is at the termination of the bulb. *Scymnus*, *Squatina*, and *Myliobates* have also five rows of valves. In the *Cephaloptera* the large *bulbus arteriosus*\* presents internally three longitudinal angular ridges, at the sides of which are small valves disposed in pairs, and in four or five rows: besides these there are three larger valves at the beginning, and three at the end of the bulb. The valves are still more numerous in the

\* I found its cavity more capacious than that of the contracted ventricle.

Ganoid fishes, and are arranged in longitudinal rather than in transverse rows: the *Polypterus* shows three such rows of nine or ten larger semilunar valves alternating with as many rows of smaller valves. The *Lepidosteus* has five longitudinal rows of sub-equal valves: those at the end of the bulb being always the largest and most efficient.\* In the *Lepidosiren* the place of valves is supplied in its long and twisted *bulbus arteriosus* by two longitudinal ridges (*fig. 71. c*) †; the interesting stages, which we have been tracing through the highly organised Ganoids and Plagiostomes, in the partition of the bulb into distinct arterial trunks for the systemic and pulmonic circulation, being most advanced in this amphibious fish.

The auricle in the *Lepidosiren annectens* is essentially single, but has two ear-like appendages.‡ The venous sinus communicates with it without any intervening valve; the auricle receives the vein from the air-bladder by a distinct aperture, close to the opening into the ventricle; regurgitation into the vein being prevented by a hard valvular tubercle, which also projects into the ventricle.§ The ventricle (*ib. b*) is single, like the auricle; its inner parietes are very irregular: a ‘trabecula’ projects from the lower part of the cavity, like a rudimental septum: a smaller transverse ‘trabecula’ arches over and acts as a valve to the single auriculo-ventricular opening; but there are no proper membranous semilunar valves.

The muscular parietes of the ‘*bulbus arteriosus*’ are distinct in all fishes from those of the ventricle; they may be overlapped by these, but an aponeurotic septum intervenes between the origin of the bulb and the overlapping ventricular fibres (see prep. No. 910.).

#### BRANCHIAL VESSELS AND GILLS.

The primary division of the branchial artery in the Myxinoids has been already described. Each gill-sac receives, either from the trunk or its bifurcations, its proper artery. The leading condition of the gills in other fishes may be understood by supposing each compressed

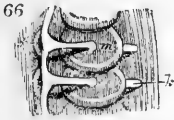
\* xxv. pl. ii.

† xxxiii. p. 343. pl. xxvi. fig. 2. c.

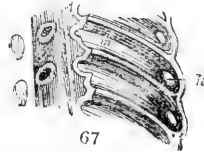
‡ *Ib.* p. 345.

§ A true second auricle consists essentially of a dilatation of this homologue of the ‘*vena pulmonalis*.’ Hyrtl (cxxxiv.) errs in stating that the fibro-cartilaginous tubercle below the auriculo-ventricular aperture was “weder von Bischoff noch Owen angegeben.” It is described in my Memoir (xxxiii.), p. 345.: “It empties its contents into the ventricle by a distinct orifice, *protected by a cartilaginous valvular tubercle* ;” and the tubercle is figured, from the auricular side, in pl. xxvi. fig. 2., where a bristle is placed above it, as in fig. 71. Hyrtl gives a figure of the same ‘cartilaginous tubercle’ as “*dicken eiförmigen harten faserknorpel*” (p. 35.), or “*fibro-cartilaginöse Stempfel*” (p. 60.), from the ventricular side, tab. i. fig. 3. c. It is true that this singular body escaped the notice of Dr. Bischoff, who, believing that the *Lepidosiren* was a reptile, overlooked many things that were, and saw some things that were not, in its organisation; as, *e. g.* two distinct auricles, and a nasal meatus communicating with the mouth.

sac of a *Myxine* (*fig. 66. m*) to be split through its plane, and each half to be glued by its outer smooth side to an intermediate septum, which would then support the opposite halves of two distinct sacs, and expose their vascular mucous surface to view. Produce these vascular surfaces into lamellæ, pectinated processes, tufts or filaments, proceed-



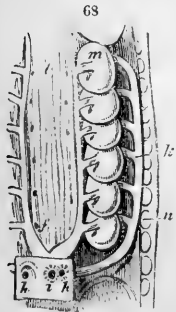
Two gill-sacs, *Bdellostoma*.



Two gill-sacs, *Lamprey*.

ing from an intermediate arch or basis of support, and you have the gill of an ordinary osseous or cartilaginous fish. Such a gill is the homologue, not of a single gill-sac, but of the contiguous halves of two distinct gill-sacs, in the *Myxines*. Already, in the *Lampreys*, the first stage of this bi-partition may be seen (*fig. 67. m*), and consequently in these *Dermopteri*, as in all higher fishes, a different artery goes to the anterior branchial surface of each sac or fissure from that which supplies the posterior branchial surface of the same fissure; whilst one branchial artery is appropriated to each supporting septum or arch between the fissures. Before describing the branchial vessels it will be necessary to describe the organs upon which they ramify.

In the *Lampreys* and *Plagiostomes* each supporting septum of the two (anterior and posterior) branchial mucous surfaces is attached to the pharyngeal and dermal integuments by its entire peripheral margin, and the streams of water flow out by as many fissures in the skin (*ib. k*) as those by which it enters from the pharynx (*ib. f*): these are called 'fixed gills,' and the species possessing them are characterised



Branchial organs, *Myxine*.

as 'pisces branchiis fixis.' In all *Ossceous*, *Plectognathic*, *Lophobranchiate*, *Ganoid*, and *Holocephalous* fishes the outer border of the supporting branchial arch is unattached to the skin, and plays freely backwards and forwards, with its gill-surfaces, in a common gill-cavity which has a single outlet, usually in the form of a vertical fissure: the species with this structure are called 'pisces branchiis liberis.' In the *Myxine* the outlets of the six lateral branchial sacs (*fig. 68. m*) on each side are produced into short tubes, which open into a longitudinal canal (*k*), directed backwards, and discharging the branchial stream by an orifice (*h*) near the middle

line of the ventral surface: between the two outlets of these lateral longitudinal canals, but nearer the left one, is a third larger opening (*i*), which communicates by a short duct with the end of the long œsophagus (*l*) and admits the water, which passes from that tube by the lateral orifices (*f*) leading into the branchial sacs. This is the first step in development beyond that simpler condition which prevails in the Lancelet, where the whole parietes of a much dilated œsophagus (*fig. 46. rr*) are organised for respiration; and besides the pharyngeal opening (*ph*), the sac communicates by a short and wide 'ductus œsophago-cutaneus' (*ib. od*), with the external surface, and also with the peritoneal cavity. The common respiratory surface of the œsophagus is ciliated in the Lancelet. The sacs developed from the œsophagus, and specially set apart for respiration in the Myxinoids, have a highly vascular, but not a ciliated mucous surface: this is disposed in radiated folds, and is further increased by secondary plicæ. The seven branchial sacs on each side of the œsophagus have short external ducts (*fig. 66. k*), which open by as many distinct orifices in the skin, in a species of *Bdellostoma* hence called *heptatrema* (prep. 1018.): the internal branchial ducts communicate by as many openings (*ib. f*) with the œsophagus. In the Lampreys there are, also, seven stigmata on each side; but another stage in the separation of the respiratory from the digestive tract is here seen, for each internal duct (*fig. 67. f*) communicates with a median canal, beneath and distinct from the œsophagus, terminating in a blind end behind, and communicating anteriorly with the fauces by an opening guarded by a double membranous valve.

In all higher fishes the inlets to the branchial interspaces are situated on each side the fauces, and are equal in number with those interspaces. The outlets are, with the exception of the Plagiostomes, single on each side: they vary much in size; are relatively largest in the Herring and Mackerel families, smallest in the Eels and Lophioid fishes; in some of the small Frog fishes (*Antennarius*), the circular branchial pore is produced into a short tube above each pectoral fin. The power of existing long out of water depends chiefly on these mechanical modifications for detaining a quantity of that element in the branchial sacs; for fishes perish when taken out of water, chiefly by the cohesion and desiccation of their fine vascular branchial processes, through which the blood is thereby prevented from passing.\* If sufficient water can be retained to keep the gill-plates floating, the oxygen which is consumed by the capillary branchial circulation is supplied to the water retained in the branchial sac directly from the air. In some of the Eel tribe the small branchial outlets are closely approximated below, as in *Sphagebranchus*; and

\* *cvr. p. 124.*

they are blended into a single orifice in *Symbranchus*, analogous to that in the *Myxine*. In some Ganoids, many Plagiostomes, and all Sturgeons, a canal leads from the fore part of each side of the branchial chamber to the top of the head; the outlets are called 'spiracles,' the canals 'spiracular.' The nasal sac communicates in the Lamprey with the single homologous canal.

The main purpose of the gills of fishes is to expose the venous blood in a state of minute subdivision to the influence of streams of water; for that purpose the branchial arteries rapidly divide and subdivide until they resolve themselves into microscopic capillaries, which are supported by a delicate membrane. Both this membrane and the tunics of the capillaries which it covers are so thin as to allow the chemical interchange and decomposition to take place between the carbonated blood and the oxygenated water. The requisite extent of the supporting membrane, or the respiratory field of capillaries, is gained by various modes of multiplying the surface within a limited space. In the *Marsipobranchii* and *Plagiostomi*, for example, by folds of the membrane on plane surfaces: in the *Lophobranchii* by filamentous processes of the membrane grouped into tufts: in the *Protopteri*, by double or single fringes of filaments: in the rest of the class by the production of the membrane upon a double row of long, compressed, slender, pointed processes, extending, like the teeth of a comb, from the convex side of each branchial arch.

Each pair of processes has its flat sides turned towards contiguous pairs, and the two processes of each pair stand edgeways towards each other, and are commonly united for a greater or less extent from their base: hence Cuvier describes each pair as a single bifurcated plate ('feuille').\*

In the Swordfish (*Xiphias*), the processes of the same pair stand quite free from each other; whence Aristotle described this fish as having double the usual number of gills.† But to compensate for this independence, and to prevent the inconvenience of mutual pressure, the processes of the same series are united together by little vascular lamellæ, so that the surface of the gill is reticulate rather than pectinate.

In a few species the processes of each pair are joined together to near their apices: the most common extent to which they are connected is about two-fifths of their whole length, as in the Salmon. In the *Orthogoriscus* the processes of each series are not opposite, but alternate. In the Sturgeon, in which the processes of the same pair

\* xxiii. i. p. 379.

† xxiii. t. viii. p. 192.

are joined together nearly to their apices, the musculo-membranous medium of union extends from pair to pair throughout the entire gill, forming a true 'septum branchiale,' and presenting a beautiful transition to the more complete septum which divides the respiratory vascular surfaces in the Plagiostomes.

In some osseous fishes certain of the branchial arches support only one series of processes; such are called 'uniserial,' or 'half' gills; but, as a general rule, they support 'biserial,' or 'whole' gills. Most of the Labroids, the genera *Cottus*, *Scorpaena*, *Sebastes*, *Apistes*, *Zeus*, *Antennarius*, *Polypterus*, *Gobiosox*, *Lepadogaster*, and the *Cyclopterus liparis* have three biserial gills and one uniserial gill; the genera *Lophius*, *Batrachus*, *Diodon*, *Tetrodon*, *Monopterus*, *Cotylis*, have three biserial gills; *Malthæa* and *Lepidosiren* have two biserial gills and one uniserial gill; the Cuchia (*Amphipnous*) has only two gills. The above enumeration refers only to the branchial organs of one side—they are symmetrical in all fishes, and the uniserial opercular gill is not counted, as not being attached to a proper branchial arch.

The processes which radiate from the convexity of the branchial arches are bony in some fishes (e. g. *Salmo*, *Alosa*), gristly in most (*Perca*, *Cottus*, *Trigla*, &c.). They break up, in the Sturgeon, into delicate branched fringes, along their outer or free margin. Small 'interbranchial' muscles extend, through the uniting septum, between the bases of the processes, for effecting slight reciprocal movements.\* The mucous membrane supported by the processes is puckered up into minute transverse folds, crossing their flat sides and producing an enormous extent of surface for the branchial capillaries.†

The concave borders of the branchial arches are usually beset by defensive processes, fringes, or tubercles, and these sometimes supporting small teeth which aid in deglutition; but the chief office of these appendages, which project inwards towards the mouth, is to prevent the passage of any solid, nutrimental, or other particles taken into the mouth from entering the interspaces of the gills, and irritating their delicate texture. In the edentulous Sturgeon and Paddlefish each arch supports a close-set series of such retroverted slender tapering filaments (*fig. 61. t*), which are longer than the opposite branchial processes (*ib. u*): they are developed even from the fifth or pharyngeal arch, which has no gill. Similar fringes of extreme delicacy defend the branchial slit in the Mullet (*prep. 1034*). Frequently such a fringe is developed only from the first branchial arch (*Mackerel and Cod, fig. 69.*), the rest supporting dentated tubercles,

\* CXII. CXIII.

† See *Prep. 1038*. (*Conger*), and its description (*xx. 1834, p. 83.*). Dr. Hyrtl counted 1000 transverse folds on a single process or tooth of the pectinate gill of the Salmon, and from 1400 to 1600 in a similar process in the Sterlet.

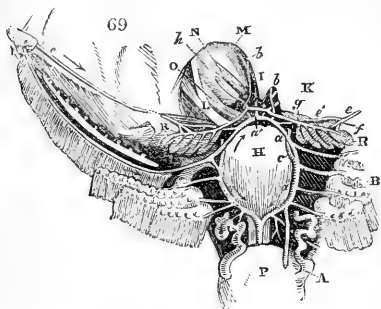


and the last or pharyngeal arch beset with teeth only. In the Remora and many other Fishes, the defensive tubercles on opposite sides of the same branchial fissure interlock, like the teeth of a cog-wheel. In the *Lepidosiren annectens*, or *Protopterus*, short valvular processes are developed from the sides of those branchial fissures only which lead to the gills, the first and second arches having no gills. In the Conger, all the branchial arches are devoid of defensive fringes or tubercles.

The immediate force of the heart's contraction is applied by a short and rapidly divided arterial trunk upon the branchial circulation. Only in a few fishes is the heart removed backwards from the close proximity of the gills, and then the branchial artery is proportionally elongated; as in the Eel tribe, especially the *Synbranchidæ*: the artery is long in the *Planirostra* (*fig. 61. s*). The primary branches are always opposite and symmetrical, but vary in number in different species. Very commonly, as in the Perch, they are three in number on each side; the first branch dividing to supply the fourth and third gills, the second going to the second, and the third to the first gill. In the Polypterus and Skate there are only two primary branches of each side: the first supplies the three posterior gills; the second, formed by a terminal bifurcation of the branchial trunk, supplies the anterior gill in the Polypterus, and in the Skate bifurcates to supply also the uniserial, opercular, or hyoid gill. The Fox-Shark (*Alopias*) and the Lepidosteus (*fig. 70.*) give examples of four pairs of primary branches from the branchial trunk. In the Shark the first pair come off close together from the dorsal part of the trunk: the arteries of the last pair quickly bifurcate, and thus each of the five branchial fissures receives its artery. We saw in the Myxinoids the exceptional instances of the bifurcation of the branchial trunk by a vertical division into two lateral forks, extended in one species to near its base: the Lepidosteus presents the still rarer example of the trunk being cleft horizontally into an upper and lower primary division; the upper or dorsal division sends off two branches on each side, the posterior dividing to supply the fourth (*fig. 70, 5*) and third (*ib. 4*) gills, the anterior going to the second gill (*ib. 3*): the lower division sends off the pair of arteries to the first pair of gills (*ib. 2*), then extends forward and bifurcates to supply the uniserial opercular gills (*fig. 1.*), which are present in this ganoid genus, as in the Sturgeon.\* In all osseous fishes the artery of each biserial pectinated gill extends along the grooved convexity of the branchial arch, between the bases of the processes, exterior to the vein: it gives off two branches opposite each pair of processes, which pass

\* See Prof. Müller's admirable Memoir, xxv.

outwards to the end of the uniting substance, and there subdivide, (in the Cod,) one twig extending along the internal margin of the branchial process to its extremity, the other retrograding along the same margin to its base: from these marginal twigs the minute transverse vessels are distributed to the fine branchial laminae upon the sides of the process. The arterialised blood is carried to an efferent



Commencement of Systemic Circulation :  
*Gadus Callarias*, Müller.

vessel, returning along the external margin of each branchial process, and by these is poured into the branchial vein (*fig. 69. B*). The four veins on each side, which are analogous to the pulmonary veins in man, unite to form the 'aortic circle' (*ib. a*) which encompasses the basi-sphenoid ( $\Pi$ ). The current of arterialised blood flows forward at the fore-part of this circle

into the hyo-opercular (*e'*) and orbito-nasal (*b*) arteries; but the main streams are directed backwards, and converge in the direction of the arrows to the aortic trunk. The carotids (*c*), the homologues of the subclavians (*d*) sent to the pectoral fins, and sometimes the coronary vessels of the heart, are sent off from the aortic circle. But no systemic heart or rudiment of a propelling receptacle is developed in any fish at the point of confluence of the branchial veins.

Small vessels are sent off from the marginal branchial venules by short trunks, which ramify beneath the branchial membrane, and become the 'arteriæ nutritiæ' of the gills: their capillaries are collected into venous trunks, which quit the gills commonly at both their extremities, those from the dorsal ends joining the jugular veins, those from the ventral ends emptying themselves into the præ-cavals, or directly into the great auricular sinus.\*

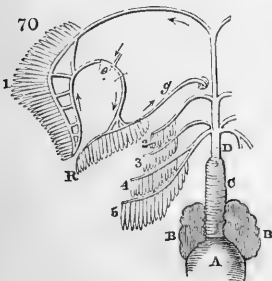
Such is the outline of the general structure of the beautiful and complex mechanism of the normal or pectinated gills of fishes.

There are many minor modifications of this form, some of which I am tempted to notice from the explanation of their 'physical cause,' which they receive from the known phenomena in the development of the gills; or from the light which the known habits of the species throw upon their 'final purpose.' But, first, a brief sketch

\* These 'venæ nutritiæ' are unusually large in the Carp; but are not, as Du Verney supposed (*civiii.*), directly continued from the true 'venæ branchiales;' and they do not, therefore, divert any of the stream of arterialised blood from the aorta to pour it directly into the venous sinus. See Müller, *xxi.* 1841, p. 28.

of branchial development, taken chiefly from the observations of Rathké\*, must be premised.

Five branchial arches and five branchial arteries, or vascular hoops, are developed on each side in the embryo of all fishes above the Dermopteri, as a general rule.† At first the trunk of the branchial arteries simply bifurcates, the divisions passing round the pharynx and reuniting on its dorsal surface, to form the aorta. Behind this primary circle, which corresponds with the fold developing the hyoid and mandibular arches, four additional arterial hoops are sent off, which traverse, without further ramifications, the convex side of the four anterior simple branchial arches, and reunite above in the aortic trunk (*fig. 79, n, n*). If a sixth arterial arch is developed, corresponding with the fifth branchial arch, as its presence in the Lepidosiren would indicate, it has not been observed, and must soon disappear in most osseous fishes. In these the gills make their appearance as leaflets budding out from the convexity of the four anterior branchial arches, each leaflet supporting a corresponding loop of the branchial artery; and, as the bifurcation and extension of the primary leaflets and the pullulation of secondary laminae and loops proceed, the vascular arch begins to separate itself lengthwise into two channels, traversed by opposite currents, and thereby establishing an arterial and a venous trunk in relation to the loops and their vascular developments on the branchial processes. In osseous fishes the primary arterial arch, corresponding with the anterior or hyoid arch, develops either a simple (uniserial) gill, or a plexiform, plumose, rudiment of a gill, or both, or neither. In the Lepidosteus the anterior vascular arch retains its primitive connection with the extremity of the branchi-



Branchiæ and pseudo-branchia :  
*Lepidosteus*, Müller.

arterial trunk, and develops on each side a small uniserial pectinated gill (*fig. 70. 1*) from the membrane clothing the inner surface of the cerato-hyoid and pre-opercular bones: the vein or efferent vessel (*e*) of this gill goes to a smaller pectinated organ (*ib. r.*), consisting likewise of one series of vascular filaments, which agrees with the 'pseudo-branchia' of other fishes in being supplied with arterial blood. In the Sturgeon, the Lepidosiren, and the Plagiostomes the representative

of the primary vascular arch has become, by partial bifurcation of

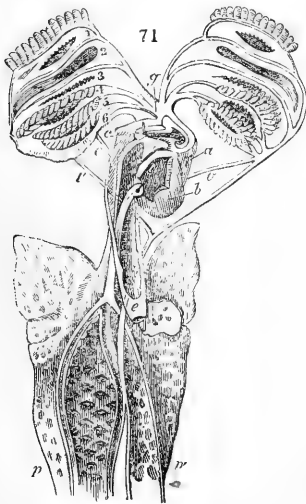
\* CIX. CX. CXI.

† The six-gilled Shark (*Hexanchus*) and the seven-gilled Shark (*Heptanchus*) are among the few exceptions.

the branchi-arterial trunk, a secondary branch, sent off by the artery of the first branchial arch: but it nevertheless develops a simple gill, of one series of filaments in the *Lepidosiren* (*fig. 71. 1*), and of one series of lamellæ in the *Plagiostomes*: and this series is attached, like the opercular gill of the *Lepidosteus* and *Sturgeon*, to the membrane supported by the hyoid arch.

In most osseous fishes we recognise the reduced homologue of the anterior primary vascular arch in that vessel (*fig. 69. e.*), which is continued from the venous or reflux division of the second primary vascular arch; not, as in the foregoing fishes, from the arterial division of that arch, or from the branchial trunk. The vessel in question carries, therefore, arterial blood: it manifests its primitive character by returning into the *circulus aorticus* (as at *e'*, *fig. 69.*), but now receives blood from it, and is called 'arteria hyo-opercularis:': the pseudo-branchia, when present (as at *r*), is developed from it.

In osseous fishes the four normal biserial pectinated gills are developed only from the four anterior branchial arches; the fifth and last arch has no gill developed from it, but is converted, as we have seen,



Circulating and respiratory Organs:  
*Lepidosiren.*

into a pair of accessory jaws. In the *Lepidosiren*, as in *Hexanchus*, the fifth arch supports a uniserial gill (*fig. 71. 6*). In the *Planirostra*, although the branchial pecten is not developed from it, yet the same kind of long slender filamentary processes project inwards from its concavity, as from that of each of the anterior four pairs of branchial arches. The five interspaces between the hyoid arch and the five branchial arches are originally exposed on the sides of the head of the embryo osseous fish; the opercular and branchiostegal appendages are later developments, and the single branchial outlet is the result of the formation of the gill-cover. Thus the numerous branchial apertures in the cartilaginous

fishes, like the substance of their skeleton, are retentions of embryonic structures. Very interesting arrests of development are also found in bony fishes. We have seen that the primary vascular hoops sweep over their respective arches without sending off any branches, the (subsequently) branchial veins being in the embryo direct continuations of the branchial arteries. This primitive condition is persistent in the fourth branchial arch of certain *Muraenoid* fishes of the

Ganges (*Monopterus*, *Symbranchus*)\*; it is persistent in the first and second branchial arches of the eel-like *Lepidosiren* (*fig.* 71, 2, 3). Such arches are, therefore, gill-less, and a certain proportion only of the blood transmitted from the heart is aerated in the gills: about one fourth, *e. g.* in *Monopterus*, goes direct to the aorta in its venous state; a larger quantity would pass into the roots of the aorta (*ib. o, o*), and mix with the general circulation in the *Lepidosiren*, were no part of the current diverted by the vessels *l, l'*, into the lung-like modification of its air-bladder.

The Hunterian specimens, Nos. 3255. and 3260. show the external branchial filaments in the embryos of a Dog-fish and Shark; three such filaments are retained on each side, for a long period, in the *Lepidosiren annectens*. Accessory respiratory organs, analogous to, if not homologous with, the opercular gills, are developed from the upper part of the pharynx in the Climbing Perch (*Anabas scandens*) and allied fishes of amphibious habits; they are complex folds of highly vascular membrane supported on singular sinuous plates developed from the epibranchials of the anterior branchial arches (*fig.* 39. 48); whence this family of fishes is called *Labyrinthibranchii*. An accessory branchial ramified vascular organ is similarly situated in the genus thence called *Heterobranchus*. From the rich vascularity of these organs they resemble miniature trees of red coral; they are hollow and muscular, serving not only for respiration, but, as Cuvier suggests, to aid in propelling the arterialised blood into the aorta. In the *Cuchia* (*Amphipnous*), a finless, snake-like fish, which lurks in holes in the marshes of Bengal, the second branchial arch supports a few long fibrils, and the third a simple lamina fringed at its edge; the first and fourth arches have not even the rudiment of a gill. The branchial function is transferred to a receptacle on each side of the head, above the branchial arches, covered by the upper part of the opercular membrane; these receptacles have a cellular and highly vascular internal surface; the cavity communicates with the mouth by an opening between the hyoid and first branchial arch, and receives its blood from the terminal bifurcation of the branchial artery, and also from the efferent vessels of the rudimental gills. Those from the supplemental lung-like vascular sacs are collected into two trunks, which unite with the posterior unbranched branchial arteries to form the aorta. Thus about one half of the volume of blood transmitted from the heart is conveyed to the aorta without being exposed to the action of the air. This amphibious fish is, as might be expected, of a sluggish and torpid nature, and remarkable for its tenacity of life. The homologues of the superior branchial sacs extend in a Gangetic Siluroid

\* Taylor, cxvii.

fish, the Singio, beyond the cranium, backwards beneath the dorsal myocommata upon the neural arches of the vertebræ to near the end of the tail, where they terminate in blind ends. The inner tunic of the sacs is a delicate vascular membrane, supplied by a continuation of the posterior branchial artery. The position of the palatal opening of the sac, in relation to the laminae of the second and third arches, is such that water can with difficulty penetrate them, and they are usually found to contain air. They are not, however, the homologues of the air-bladder or of lungs, though they are analogous to the latter in function. By this extreme modification of the opercular gill the Singio (to which the generic name *Saccobranchus* is given by Cuvier) is enabled to travel on land to a great distance from its native rivers or marshes, and, like the Cuchia, is remarkable for surviving the infliction of severe wounds.\* In most fishes a rich development of follicles on the walls of the gill-chamber supplies the branchial machinery with a lubricating mucus.

#### ARTERIES.

The first structure most worthy of notice, in connection with this system, is the vascular body already alluded to under the name of 'pseudobranchia.' *Mormyrus*, *Cobitis*, *Silurus*, *Gymnotus*, *Muraenophis*, and *Muraena* are examples of the few genera in which it has not been detected. In almost all other osseous fishes it is present, situated on each side of the head, in advance of the dorsal end of the first biserial gill, under the form either of a small exposed row of vascular filaments, like a uniserial gill (as in all Sciaenoids and many other *Acanthopteri*, the *Pleuronectidae*, and the *Lepidosteus* (fig. 70. R); or, as a vaso-ganglionic body, composed of parallel vascular lobes, and covered by the membrane of the branchial chamber (as in *Esox*, *Cyprinus*, *Gadus*, fig. 69. R). In both cases the vein or efferent vessel of the pseudobranchia becomes the ophthalmic artery (ib. *h*), and the choroid 'vaso-ganglion,' when present, is developed from it. The Sturgeon, like the *Lepidosteus* and *Lepidosiren*, has a uniserial opercular gill, the homologue of the first so-called 'half-gill' of the Plagiostomes. But, besides this, Von Baer discovered, on the anterior wall of the 'spiracular canal,' a small vascular lamellate body, which is the true pseudobranchia. It receives arterialised blood by a vessel sent off from the vein of the first biserial gill; which blood, after being subdivided amongst the innumerable pinnatifid capillaries of the pseudobranchia, is collected again into the efferent vessel of that

\* CXVII.

body, which divides into the artery for the brain (encephalic), and that for the eye (ophthalmic). The pseudobranchia is thus a kind of rete mirabile for both the cerebral and ophthalmic circulation in the Sturgeon\*: in osseous fishes it stands in that relation to the eye only, and is most generally associated with the more immediate ophthalmic 'rete mirabile,' called 'choroid gland' (*fig. 56. o*). The pseudobranchia coexists with the hyoid uniserial gill in most Plagiostomes; and in those that have the spiracula it is developed, as in the Sturgeon, on the anterior wall of each of those temporal outlets from the branchial cavity: its 'vena arteriosa' supplies the eyes and part of the brain; and it is important, also, in reference to a true and clear idea of the function and homology of the 'pseudobranchia' in fishes generally, to bear in mind that it co-exists in the Plagiostomes, Chimæroids, Sturgeons, and some osseous fishes, with the vasoganglion supplied by vessels from the anterior branchial veins, which lies between the anterior basi-branchials and the sternohyoid muscles.† Besides the small nasal and orbital arteries, and

\* See *xxi.* 1841, pp. 41—67. 75. for a most valuable and exact specification of the structure, relations, and varieties of the Pseudobranchiæ.

† This body has already been alluded to in connection with the salivary system (*p.* 230.). Mr. Simon's opinion, that it is the 'thyroid gland' of Cartilaginous Fishes is more in accordance with its nature as a vaso-ganglion, and its relative position. But since it co-exists in Cartilaginous Fishes with the actual homologue of the pseudobranchiæ of Osseous Fishes, these cannot be, as Mr. Simon contends, the thyroid glands of such fishes. That the parts which the accomplished author of the paper *cxvi.* describes as the thyroid glands in the *Exocætus*, Pike, Anableps, Carp, and some species of the Cod tribe, are the same bodies which Müller had previously described as 'pseudobranchiæ' in those fishes, will be manifest by comparing the descriptions of the two anatomists. "In the *Gadida* the gland is double; one portion lies on each side, not as in the last case [the sublingual vasoganglion of the Sturgeon is alluded to] at the anterior extremity of the first branchial arch, but near its posterior or vertebral end." (*Simon, Philos. Trans.* 1844, *p.* 300. Compare with this Müller, *xxi.* 1841, *p.* 47. *tab.* iii. *fig.* 13.)

Prof. Müller's description of the 'pseudobranchiæ' of the Carp is as follows:—  
'Die verborgenste Lage hat das Organ bei *Cyprinus Carpio* und *Carassius*. Es ist nicht bloss von dem beweglichen dicken Gaumenorgan bedeckt, sondern selbst von knochen verhüllt. Man findet es nach Wegnahme des contractilen Gaumenorgans zwischen dem hintern Ende des queren Gaumen-muskels und den obern Schlundknochen.' (*xxi.* 1841, *p.* 47.) Mr. Simon's account of the thyroid gland in the same species is as follows:—

"In the Carp especially it is at considerable depth, being hidden by the extraordinary thickness of the soft palate, and imbedded between the surface of the pterygoid muscle and the outer extremity of the branchial bone." (*Philos. Trans.* 1844, *p.* 300.)

It is obvious that all the parts described as 'thyroid glands' by Mr. Simon, in Osseous Fishes, are the pseudobranchiæ; and the author recognises that homology in regard to the free gill-like forms of pseudobranchiæ described by Broussonet and Meckel in *Acanthopterygii* and *Pleuronectidæ*. That these 'pseudobranchiæ' receive arterialised blood, and are thus essentially distinct from the hyoid or opercular uniserial fin in the Sturgeon, *Lepidosteus*, &c., had been clearly demonstrated by Prof. Müller (*l. c.* 1841). There remains, then, to consider the relations of the 'pseudobranchiæ' of Fishes with the thyroid glands of Mammals. These may be either relations of analogy or of homology. The former would be determined by

the hyo-opercular, from which the proper ophthalmic artery is derived, the carotids are usually sent off from the 'circulus aorticus.' In the *Chimæra* the carotids are transmitted directly from the anterior branchial veins; and, in the Pike, the artery of the pectoral fins (brachial) is transmitted from the common trunk of the two anterior branchial veins. In the *Myxines* an anterior, as well as a posterior, aorta is continued from the common confluence of the branchial veins. In all higher fishes the posterior aorta is the only systemic trunk so formed.

This aorta extends beneath the bodies of the vertebræ along the abdomen and through the hæmal canal to the end of the tail. In many Cyprinoid fishes it dilates beneath each abdominal vertebra into a sinus. It gives off intercostal arteries, and, with less regularity, numerous small branches to the kidneys. The first principal visceral branch is the 'cæliac,' which sometimes, as in the Burbot, is

showing that the parts in question performed the same functions in the two classes.

Mr. Simon conceives that the thyroid gland "maintains an intimate *relation to the vascular supply of the brain.*" The pseudobranchiæ, however, are not diverticula to the cerebral circulation in Osseous Fishes, but only to the ophthalmic circulation, and in most cases are subsidiary, in this respect, to the choroid vaso-ganglion. The internal carotid or encephalic artery in Osseous Fishes is a division of an artery sent off from a part of the 'circulus aorticus,' formed by the three posterior pairs of branchial veins: the artery of the pseudobranchiæ is given off from the anterior branchial vein, or from the hyo-opercular artery, or from both: its subsequent modification cannot therefore affect the currents of circulation through the gills, with whose efferent vessels it has no connection, and from which vessels the encephalic arteries are derived. In the Sturgeon and Plagiostomes, indeed, the pseudobranchiæ may, and doubtless do, act as diverticula to the cerebral circulation; but it is precisely in these fishes that Mr. Simon transfers the name and function of thyroid gland to another vaso-ganglionic body, viz. Retzius's sublingual gland. Mr. Simon was acquainted with the existence of this body, and also of the supplementary opercular gill in the Sturgeon, but he seems to have overlooked the pseudobranchiæ, which, in this fish, hold precisely that relation to the cerebral vessels which would have best supported Mr. Simon's determination of the pseudobranchiæ as the thyroid gland. I consider, however, Professor Müller's comparison of the pseudobranchiæ in the Sturgeon with the ento-carotid plexuses of the Ruminants to be a truer and more natural view of their analogies. As to the question of 'homology,' which is to be determined by consideration of the organic connections, relative position, and development of the parts in question, it is obvious that if, by a consideration of these characters, we admit the sublingual body of the higher Cartilaginous Fishes to be, of all the vascular ganglions in or near the head, that which most nearly repeats the homological conditions of the thyroid gland of higher Vertebrates, we cannot regard the vascular ganglions, which maintain a diametrically opposite position in regard to the branchial arches, as being also parts answerable to the thyroid glands.

If any thing were wanting to convince an anatomist holding that view, viz. that the pseudobranchiæ are the homologues of thyroid glands, of the fallacy of such a view, it would be the fact of their co-existing in some fishes with a vaso-ganglion having a much better title to be so considered, and which is actually described by the ingenious author of the paper in the *Philosophical Transactions* as the thyroid gland in those fishes; though its relations to the heart and great vessels in the Plagiostomes and Sturgeons seem to give it more claim to be regarded as the homologue of the thymus.



sent off from the posterior part of the 'circulus aorticus;' and in some Sharks by two trunks from the same part. The next branch is a posterior mesenteric, which varies in size according to the extent of the intestinal canal supplied by the cæliac. Between these, in some fishes, the brachial arteries are sent off from the abdominal aorta: these vessels in the large-finned Torpedos and Chimæræ have a partial investment of muscular fibres, like secondary bulbs, to accelerate the circulation through them.\*

In the Porbeagle Shark (*Lamna cornubica*) the two cæliac arteries each split into a bundle of small arterioles, which interlace with a similar resolution of the hepatic veins to form a mixed fasciculate 'plexus mirabilis' between the pericardial septum and the liver. The arterial blood is collected again into a trunk on the outer side of each plexus; and is distributed by the ramifications of those trunks in the ordinary way to the stomach and intestines.† The arterial branches to the spiral valve in the Fox Shark are remarkable for the rich bundles of twigs by which they distribute the blood to that production. In the Mediterranean Tunnies (*Thynnus* and *Auxis*) the branches of the cæliaco-mesenteric artery sent to the stomach, the pancreas and the intestines, severally split up into similar fasciculate plexuses, which are interlaced with corresponding plexuses of the veins from those viscera prior to the formation of the portal trunk. But the most common modification of the visceral vascular system is the sudden division and termination of a branch, usually of the gastric artery, in a small body chiefly composed of the cellular beginnings of the returning veins, forming the vaso-ganglion so constant in all higher Vertebrates, and called the 'spleen' (*fig.* 61. *n*). It is not present in the Lancelet; and the gland-like bodies near the cardia in the Cyclostomes, and near the pylorus in the Lepidosiren, which some have called 'spleen,' are more like the recognised remnants of the vitellicle in osseous fishes, where a true spleen is actually present. The vein of the spleen always contributes to form the 'vena portæ;' but it is important to note that it is not essential to the formation of that vessel. The absence of the spleen in fishes is concomitant with the absence of the pancreas; and the increased size and complexity of the spleen is associated in some fishes with a corresponding development of the pancreas. Thus there is an accessory spleen in the Sturgeon; and the spleen is divided into numerous distinct lobules in *Lamna*, *Selache* (see part of the organ in *fig.* 64. *s*), and some other highly organised Plagiostomes. In most osseous fishes the spleen is appended by its vessels, and a meso-splenic fold of

\* Duvernoy, xc.

† xxi. 1841, p. 99. pl. 5.

peritoneum to the hinder end or bend of the stomach, or to the beginning of the intestine: it is of variable but commonly triangular shape; of a deep red or brown-red colour, and soft and spongy: the venous cells of which it is chiefly composed are filled with granular corpuscles.

## LECTURE XI.

### PNEUMATIC AND RENAL ORGANS.

#### AIR-BLADDER.

THE organ so denominated is found, in most osseous fishes, in the form of an elongated bladder, tensely filled by air, extending along the back of the abdomen, between the kidneys and the chylopoietic viscera, and sometimes (*Gymnotus*, *Ophiocephalus*, *Coius*) beneath the caudal vertebræ to near the end of the tail. It is seldom bifurcated (as we see it in some species of *Diodon*, *Tetrodon*, *Dactylopterus*, *Pimelodus*, *Prionotus*); still more seldom divided lengthwise into two bladders (*Arius*, *Gagora*, *Polypterus*, *Lepidosiren*, fig. 71. *p, p*): it is oftener divided crosswise into two compartments, which intercommunicate by a contracted orifice (*Cyprinidæ*, fig. 58. *p q*, *Characinidæ*); or are quite separate (*Bagrus filamentosus*, *Gymnotus equilabiatus*.) In the Siluroid genus *Pangasius* the air-bladder is divided into four longitudinally succeeding portions. In the *Trigla hirundo* the swim-bladder is notched anteriorly by one indent, and posteriorly by two indents, from which notches septa project inwards: sometimes the air-bladder is divided partially, both lengthwise and crosswise (*Cobitis fossilis*, *Auchenipterus furcatus*, some species of *Pimelodus*). Sometimes the bladder sends forwards two blind processes from its forepart (*Sphyræna barracuda*, *Trigla cuculus*, *Conodon antillanus*, some species of *Micropogon* and *Otolithus*); sometimes from its hind part (*Cantharis vulgaris*, *Lethrinus atlanticus*, *Heliases insolatus*, some species of *Sillago*, *Mæna*, and *Smaris*); sometimes from both ends (*Dules maculatus*, *Pimelipterus altipennis*, *Lactarius delicatulus*). The Bearded Umbrina has three slender cæcal processes from each side of its air-bladder; the allied

“Maigre” and other species of *Sciæna*, with most of the *Corvinæ*, have very numerous lateral pneumatic cæca, which are more or less ramified.\* In some species of *Cheilonemus* and *Gadus* blind processes are continued from both the sides and ends of the air-bladder (see the anterior ones in *Gadus callarias*, fig. 69. A, p). In *Gadus Navavaga* the lateral productions expand, and line corresponding expansions or excavations of the abdominal parapophyses, thus foreshadowing the pneumatic bones of birds.

The proper walls of the air-bladder of ordinary osseous fishes consist of a shining silvery fibrous tunic, the fibres being arranged for the most part transversely or circularly, and in two layers (fig. 58, q r): they are contractile and elastic; but the walls of the anterior compartment of the air-bladder of Cyprinoids (ib. p) are much more elastic than those of the posterior one. The air-bladder is lined by a delicate mucous membrane, with a ‘plaster-epithelium;’ it is more or less covered by the peritoneum. Its cavity is commonly simple; in the Sheat-fish it is divided by a vertical longitudinal septum along three-fourths of its posterior part. † The lateral compartments are subdivided by transverse septa in many other Siluroids (e. g. genus *Bagrus*): the large air-bladder of some species of *Erythrinus* (e. g. *E. salvus*, *E. tæniatus*) is partially subdivided into smaller cells. The cellular subdivision is such in the air-bladder of the *Amia*, that Cuvier compared it to the lung of a reptile ‡; and the transition from the air- or swim-bladder to the lung is completed in the *Protopterus* or *Lepidosiren annectens*, in which the cellular subdivision and multiplication of the vascular surface are combined with a complete bilateral partition of the bladder into two elongated sacs, with a supply of venous blood from a true pulmonary artery, and with the communication of the ductus pneumaticus, as in the *Polypterus*, with the ventral surface of the œsophagus.

At the first introduction into the Animal Kingdom of a true lung, or air-breathing organ communicating with the pharynx or œsophagus, much variety of form and structure, much inconstancy even as to existence, might be expected, especially in that class in which the normal function of the new organ could be so seldom in any degree exercised, and in which, therefore, different accessory or subordinate offices predominate in such rudimental representative of the pulmonary organ. There is no swim-bladder, for example, in the orders *Dermopteri*, *Holocephali*, and *Plagiostomi*; it is present in one of the families (*Gadidæ*) of the thoracic suborder of *Anacanthini*,

\* See xxxix. i. p. 94., after Cuvier et Valenciennes, xxiii. pl. 138, 139.

† cxiv. ii. p. 33. pl. 6. fig. 4.

‡ xxiv. ii. p. 377.

and not in the other family (*Pleuronectidæ*); here we can associate its absence with the peculiar flattened form and grovelling habits of the species. In like manner we may account for the absence of the air-bladder in the Angler (*Lophius*), which habitually keeps the sea-bottom: but the mechanical explanation of the absence or rudimental condition of the swim-bladder is not so obvious in regard to the Acanthopterous genera *Percis*, *Percophis*, *Eleginus*, *Auxis*, *Trachypterus*, and *Gymnetrus*. A large and often complex air-bladder exists in most of the Siluroid fishes; but the genera *Loricaria*, *Rhinelepis*, and *Hypostoma* are exceptions in that family, having no air-bladder. What is more inexplicable is, that while some species of the same genus, *Polynemus* and *Scomber* for example, have a large swim-bladder, others want it, or have it of extremely small size. The variation in respect to the presence or absence of an air-duct (*ductus pneumaticus*) is expressed in the characters of the orders in the Classification of Fishes, pp. 48—50. The duct, which is shown by its place of communication with the beginning of the œsophagus, and by the rudimental larynx, in Polypterus and Lepidosiren, to be the homologue of the trachea of air-breathing Vertebrates, is a simple and delicate membranous tube; but it presents considerable variation in its length, diameter, and place of communication with the alimentary tract. In the Herring the ductus pneumaticus is produced from the posterior attenuated end of the cardiac division of the stomach\*, and opens into the fusiform air-bladder at the junction of the middle and posterior thirds of that organ. The long, narrow, and flexuous ductus pneumaticus is continued from the fore-part of the posterior division of the air-bladder in the Cyprinoids, and opens into the dorsal part of the œsophagus (*fig. 58. su*): the short, straight, and wide ductus pneumaticus, in the Lepidosteus, opens also into the dorsal part of the œsophagus, the orifice being served by a sphincter: in the *Erythrinus* the air-duct communicates with the side of the œsophagus; in the Polypterus, with the under or ventral part of the beginning of the œsophagus.†

The principal seat of the vascular ramifications in the air-bladder, like that in a true lung, is the mucous lining membrane; but the modes of ramification in the primitive piscine form of the air-breathing organ are as variable as any of its other properties. The arteries of the air-bladder are derived sometimes directly from the

\* cxiv. ii. pl. viii. fig. 1.

† These variations show how futile is the objection drawn from the dorsal communication of the swim-bladder in Lepidosteus to the determination of the Lepidosiren to the class of fishes, and of the homology of its lungs with the swim-bladder in that class.

abdominal aorta, sometimes from the cœliac artery, sometimes from the last branchial vein; and in the *Lepidosiren* they are continued from the aortic termination of the two non-ramified branchial arteries (*fig. 71. l'*), and, therefore, convey venous blood to the cellular, lung-like, double air-bladder. The veins of the air-bladder return, in some fishes, to the portal vein; in some, to the hepatic vein; in some, to the great cardinal vein; and, in the *Lepidosiren* (*ib. p'*), they penetrate, by a common trunk, the great post-caval vein (*ib. e*), formed by the confluence of the visceral and vertebral veins of the trunk; but instead of terminating there, the pulmonary venous trunk passes forwards, through the sinus and auricle, to the entry into the ventricle, and there terminates above the valvular cartilaginous tubercle. Thus the aerated blood from the lungs enters the ventricle directly, instead of being previously mixed with the venous blood in the auricle.

The vascular system of the lung-like air-bladders of the Protopterous and Ganoid fishes forms no 'retia mirabilia' or vaso-ganglions, but resolves itself into a generally diffused reticular capillary system, which is much richer and closer in the more subdivided and thicker cellular structure of the anterior than of the posterior parts of the bladders in the *Lepidosiren*.

In the osseous fishes the principal forms of the terminal divisions of the arteries of the air-bladder are as follows:—1st. A resolution of the smaller ramifications into fan-like tufts of capillaries over almost every part of the inner surface (*Carp*). 2d. The formation of similar, but larger and more localised, radiating tufts (*Pike*); in both without any special aggregation of the capillaries to form a 'vaso-ganglion.' 3d. The conversion of the tufts by rapid subdivision into capillaries aggregated so as to form red gland-like bodies; the capillaries reuniting into larger vessels, which again ramify richly round the border of the gland-like body; the rest of the inner surface of the air-bladder having the ordinary simple capillary system (*Perch* and *Cod*). In the *Cod*-fish, a large artery, a branch of the cœliac, and a still larger vein, which empties itself into the mesenteric, perforate together the fibrous tunic of the swim-bladder. Before they reach the inner surface, they divide into some branches, which then radiate and subdivide upon the mucous membrane: the arterioles frequently anastomose together; and the venules as frequently anastomose with each other: both are inextricably interwoven and form the basis of the so-called 'air-gland,' which is essentially a large 'bipolar rete mirabile' of Müller, or vaso-

\* XXI. 1841, p. 194.

ganglion. This organ, however, is further composed of a number of peculiarly arranged, elongated corpuscles, which depend in two rows from each vascular branch, and are bound together by a loose cellular tissue: the corpuscles are beset with fine villiform processes. The blood returns from the vaso-ganglions by small veins which rarely accompany, more commonly cross, the arteries. 4th. The two chief 'retia mirabilia,' or vaso-ganglions, in the air-bladder of the Eel and Conger, which are situated at the sides of the opening of the air-duct, are also 'bipolar,' and consist of both arterioles and venules: their efferent trunks do not ramify in the immediate margin of the vaso-ganglion from which they issue, as in the vaso-ganglions of the Cod, Burbot, Acerine, and Perch, but run for some distance before they again ramify to form the common capillary system of the lining membrane of the air-bladder. Rathké\* failed to detect the opening of the air-duct with the œsophagus in the Eel; but De la Roche had well described the oblique aperture †, and accurately cites the whole family of the Eels as fishes having both the so-called 'air-gland' and the pneumatic duct. It had been supposed that the vascular 'air-gland' was present only in those fishes which could not derive the gaseous contents of their swim-bladder from without; and unquestionably in those fishes which have the shortest and widest ducts (Sturgeon, Amia, Erythrinus, Lepidosteus, Lepidosiren, Polypterus), the supposed air-secreting vaso-ganglions are not developed. Since Professor Magnus has determined the existence of free carbonic acid gas, of oxygen and of azote in the blood, and dissolved in different proportions in the venous and the arterial blood, it may be readily conceived, as Professor Müller well remarks ‡, that the venules of the vaso-ganglions may withdraw carbonic acid gas from the arterioles, and that these may reach the inner surface of the air-bladder richer in oxygen and poorer in carbonic acid than when they penetrated the vaso-ganglions.

The air-duct may allow the gas to escape under certain circumstances; and the small size and obliquity of its orifice in many osseous fishes (Carp, Eel) seem only to adapt it to act as a safety-valve against high pressure when the fish sinks to great depths, or sudden expansion of the gas when they rise to the surface §: but

\* cix. 'Ueber die Schwimm-blase einiger Fische,' p. 98. † cxv. p. 201.

‡ xxi. 1841, p. 98. See also Dr. J. Davy, in Phil. Trans. 1838.

§ Neither the air-duct nor the elasticity of the air-bladder are equal to prevent the consequences of a too rapid removal from the enormous pressure which fishes sustain at great depths in the sea: those that are drawn up quickly by the hook are often found to have the air-bladder ruptured, and sometimes the stomach is protruded from the mouth by the pressure of the suddenly extricated and expanded gas.

in the higher organised species above-cited, with short and wide air-ducts, these may, likewise, convey air to the bladder.

The contents of the air-bladder consist, in most fresh-water fishes, of nitrogen, and a very small quantity of oxygen, with a trace of carbonic acid gas: but in the air-bladders of sea-fishes, and especially of those which frequent great depths, oxygen predominates.\*

In the genera *Auchenipterus*, *Synodon*, *Malapterurus*, and some other Siluroids, the axis vertebra sends out on each side a slender process, which expands at its end into a large round plate: this is applied to the side of the air-bladder, and can be made to press upon it, and expel the air through the duct by the action of a small muscle arising from the skull. In some species of *Gadus* muscular fibres extend from the vertebral column upon the air-bladder. The nerves of the air-bladder are derived from the vagus after it has received organic fibres from the sympathetic (*fig. 58. t*).

Viewing the general modifications and relations of the air-bladder throughout the class of fishes, we cannot but discern and admit, notwithstanding some seeming capricious varieties, that its chief and most general function is a mechanical one, serving to regulate the specific gravity of the fish, to aid it in maintaining a particular level in its element, and to rise or sink as occasion may serve. The general law of its absence in the parasitic and suctorial *Dermopteri*, and in all ground-fishes, as the *Pleuronectidæ* and Ray-tribe, supports the above conclusion. Borelli found that those fishes, whose air-bladders were burst, sank to the bottom and were unable to rise. Nor does the absence of the air-bladder in the surface-swimming Sharks militate against this view of its physical function: for though the air-bladder serves, it also enslaves. It opposes, for example, those fishes that possess it in their endeavours to turn on one side, and it demands a constant action of the balancing fins to prevent that complete upsetting of the body which it occasions from the weight of the superimposed vertebral column and muscles when life and action are extinct. The Sharks require, by the position of their mouth and their common pursuit of living prey, freedom in turning and great variety as well as great power of locomotion: if they are not aided by a swim-bladder, neither are their muscular exertions impeded by one; whilst their swimming organs acquire that degree of development and force

\* Humboldt found the gas in the air-bladder of the electric *Gymnotus* to consist of 96° of nitrogen and 4° of oxygen. Biot found 87° of oxygen in some of the deep-sea Mediterranean fishes, the rest nitrogen, with a trace of carbonic acid. No hydrogen has ever been detected in the air-bladders of fishes.

† cxxxix. cap. 23.

which suffices for all the evolutions they are called upon to perform. With regard to the accessory offices of the air-bladder in relation to the sense of hearing, the chief of these remarkable modifications by which it is brought into communication with the acoustic labyrinth have been already described in a former Lecture (p. 210.). In a few genera (*Trigla*, *Pogonias*) the air-bladder and its duct are subservient to the production of sounds.

Under all its diversities of structure and function the homology of the swim-bladder with the lungs is clearly traceable; and finally, in those orders of fishes which lead more directly to the Reptilia, as, for example, the salamandroid *Ganoidei* and *Protopteri*, those further modifications are superinduced upon the air-bladder, by which it becomes also analogous in function to the lungs of the air-breathing Amphibia.

The species of *Lepidosiren*, the anatomy of which is described in the Linnæan Transactions\* and in these Lectures, inhabits a part of the river Gambia, which in the rainy season overflows extensive tracts, that are again left dry in the dry season. The *Lepidosirens*, which do not follow the retreating waters, escape from the scorching rays of the African sun by burrowing in the mud, which is soon baked hard above them; but they maintain a communication with the air by a small aperture, and coiling themselves up in their cool chamber, clothe themselves by a layer of thick mucous secretion, and await, in a torpid state, the return of the rains and the overflowing of the mud-banks. The advent of their proper element wakes them into activity: they then emerge from the softened mud, swim briskly about, feed voraciously, and propagate.

The peculiar modifications of the gills and air-bladder of the *Lepidosiren* are precisely those which adapt them to the peculiar conditions of their existence. In the inactive state into which they are thrown by their false position as terrestrial animals, the circulation, which would have been liable to be stopped had all the branchial arteries developed gills, as in normal fishes, is carried on through the two persistent primitive vascular channels (*fig. 71. 2 and 3*). Whatever amount of respiration was requisite to maintain life during the dry months is effected in the pulmonary air-bladders; its short and wide duct or trachea, the œsophageal orifice of which is kept open by a laryngeal cartilage, introduces the air directly into the bladders: the blood transmitted through the branchial arches to the pulmonary arteries (*ib. V'*) is distributed by their ramifications over the cellular surface of the air-bladders, and is returned arterialised

\* XXXIII.



by the pulmonary veins (ib. *p*, *p'*). A mixed venous and arterial blood is thence distributed to the system, and again to the air-bladders. True arterial blood exists only in the pulmonary veins, and unmixed venous blood only in the system of the *venæ cavæ*; whence the necessity, apparently, for that peculiar arrangement by which the arterial blood is conveyed directly to the ventricle by the pulmonary vein. When the *Lepidosiren* resumes its true position as a fish, the branchial circulation is vigorously resumed, a larger proportion of arterialised blood enters the aorta, and both the nervous and muscular systems receive the additional stimulus and support requisite for the maintenance of their energetic actions.

Anatomists and physiologists are not yet unanimous as to the homologies and analogies of the respiratory organs of fishes. Indeed the essential distinction of those relations has seldom been clearly kept in view. When we read in the latest edition of the *Comparative Anatomy of Cuvier*: "the gills are the lungs of animals absolutely aquatic\*;" and, with regard to the cartilaginous or osseous supports of the gills, "they are in our opinion, to the gills of fishes, what the cartilaginous or osseous tracheal rings are to the lungs of the three superior classes †:" we are left in doubt whether it is meant that the gills and their mechanical supports merely perform the same function in fishes which the lungs and windpipe do in mammals, or whether they are not also actually the same parts differently modified in relation to the different respiratory media of the two classes. Geoffroy St. Hilaire leaves no doubt as to his meaning where he argues that the branchial arches of fishes are the modified tracheal rings of the air-breathing classes; we perceive that he is enunciating a relation of homology. The truth of his proposition will be best tested by first considering the homologies of the air-bladder of fishes. Dr. Peters, Prof. Hyrtl, and others, who have prosecuted the anatomy of the *Lepidosiren* since Dr. Bischoff advocated its reptilian nature, have confirmed my previous determination of that genus to the class of fishes: and it may be presumed that its gelatinous chorda dorsalis, its vertebral inferior transverse processes (parapophyses), the normal attachment of the scapulæ to the occiput, the branchiostegal covering of the permanent gills, the opercular bones, the absence of pancreas, the presence of a spiral intestinal valve, the relative position of the anus, the extra-oral nasal sacs, the

\* "Les branchies sont les poumons des animaux absolument aquatiques." (XIII. t. vii. p. 164.)

† "Elles sont, à notre avis, aux branchies des poissons, ce que les cerceaux cartilagineux ou osseux des voies aériennes sont aux poumons des trois classes supérieures." (Ib. p. 177.)

scaly integuments, the mucous tubes and pores on the head, the 'lateral line,' and, in short, the totality of the organisation of the *Lepidosiren*, will be deemed to fully prove its true ichthyic nature. It is extremely interesting to find the Ganoid *Polypterus*, which of all osseous fishes most closely resembles the *Lepidosiren* in its spiral intestinal valve, in the bipartition of the long air-bladder, the origin of the arteries of that part, and the place and laryngeal mode of communication of the short and wide air-duct or windpipe, also presenting the closest agreement with the *Lepidosiren* in the important character of the form of the brain. The common objection to the view of the air-bladder of fishes being the rudimental homologue of the lungs of air-breathing Vertebrates has been, that the artery of the air-bladder carries arterial blood, that of the lungs venous blood. Let us compare the air-bladders of the *Polypterus* and *Lepidosiren* in reference to this character. The arteries of both are derived from the returning dorsal portions of the branchial vascular arches before their union to form the aorta. In the *Polypterus*, according to Müller, the artery of each air-sac is formed by the union of the efferent vessels of the last gill: the blood is, therefore, arterialisied before entering the artery of the air-sac. In the *Lepidosiren*, by reason of the non-development of gills on two of the branchial arches, the blood transmitted to the air-sac is venous. But this difference relates only to the presence or absence of a particular development of the branchial vascular arches, from which the air-bladders of the two species are supplied with blood: it is a difference which modifies the function without at all changing the essential nature of the air-bladders themselves: the relative position of these vascular sacs, their form and size, their mode of communication with the œsophagus, — in short, every character by which relations of homology are determined, — are the same in both *Polypterus* and *Lepidosiren*.\* The lungs of the *Lepidosiren* being, then, unequivocally the homologues of the air-bladder of the *Polypterus*, it follows that they must be homologous with the air-bladders of other fishes, whatever be the modifications of form or function of such air-bladders. Between the completely divided air-bladder of the *Polypterus* and the undivided air-bladder of *Lepidosteus* there are numerous degrees of bifurcation in the series of fishes: it is to the undivided state of the air-bladder in the *Lepidosteus* that its more strictly dorsal position, and its communication with that aspect of the œsophagus, are due: these modifications,

\* Compare xxxiii. pl. xxvii. figs. 3 and 4. with xxv. pl. ii. figs. 5 and 6., and fig. 54. xxxiii. p. 182. with xxv. pl. ii. fig. 7.

however, do not affect its relation of homology with the divided air-bladder of the allied ganoid genus *Polypterus*, any more than with the divided air-bladders of the *Cobitis barbatula* or *Arius gogora*, in which the divisions are confined to the anterior part of the abdomen, and inclosed in osseous cups developed from vertebrae answering to the second or third cervicals.

Thus the series of transitions traceable in the organs universally acknowledged as the air-bladders of fishes prove those of the Lepidosiren to be the homologous organ; whilst the development, relative position, and connection of the lungs of the Batrachia equally prove those lungs to be the homologues of the air-bladders of the Lepidosiren. Therefore, it follows that the air-bladder of the fish is homologous with the lungs of the Batrachian, and of all other air-breathing Vertebrates; although the air-bladder of the fish does not, as a general rule, perform the functions of a lung. But the air-bladder in most fishes is analogous to the air-chambers of the shell of the polythalamous Cephalopods, and in some fishes it is analogous to the tympanum of the higher Vertebrates.\*

In tracing the development of the windpipe and larynx, from the more lung-like forms of the air-bladder in fishes, through the Perennibranchiate Batrachia upwards, we obtain incontrovertible proof that the so-called 'ductus pneumaticus' in fishes is the homologue of the trachea. It follows, therefore, that the branchial cartilaginous and osseous supports of the gills are not the homologues of the trachea and bronchiæ, any more than the gills themselves are the homologues of the lungs. We shall find the branchial arches and gills developed in the larvæ of Batrachia, and disappearing as the true trachea and lungs are formed, without being converted into them. The only parts of air-breathing Vertebrates with which the branchiæ of fishes are homologous are the persistent or deciduous branchiæ of the Batrachia. The relations of the branchial arches and gills of fishes with the trachea and lungs of higher air-breathing Vertebrates are those of analogy merely. The branchial apparatus, in relation to the entire vertebrate scheme or type of organization, is to be regarded as a temporary graft on such type, introduced to serve the purposes of the lowest embryo-like forms, and to give way to another and higher and more persistent form of respiratory organ: in this respect the branchial organization is to the vertebrate series what the placenta is to the mammalian individual.

\* In the Loach (*Cobitis*) the whole alimentary canal is analogous to a lung, inasmuch as this fish swallows air and voids carbonic acid.

## RENAL SYSTEM.

In all Vertebrates an excretory organ is very early developed in the form of a tube, extending from each side of the cloaca forwards, along the dorsal region of the abdomen, close to the spine, where it communicates with a number of short slender blind tubes placed at right angles to it; the longitudinal trunk-tube serving as the excretory duct of the shorter transverse secerning cæca. These glands are transitory in the air-breathing Vertebrates, and are called, from their discoverer, 'corpora Wolffiana;' they are persistent in fishes\*; and are called 'kidneys:' in both they are renal organs and secrete urine. A slightly opaque, slender, elongated glandular body, in the situation marked *h* in *fig.* 46., has appeared to me to represent the renal organ in the *Branchiostoma*. The structure of this organ is more obvious in the Myxinoids: it is double: each long duct, as it extends from the cloaca through the abdominal cavity, sends off, at regular but distant intervals from its outer side, a short wide tube, which communicates by a narrow opening with a blind sac. At the bottom of this sac or cæcum there is a small vaso-ganglion, free on all sides save that by which the vessels enter and quit it †: there are no uriniferous tubes in this 'placentula;' the contents of the cæcum must react through its thin parietes, and those of the capillaries with which it is in contact, upon the blood in those capillaries, and extract therefrom the azotized uric excretion. Analogous vascular bodies, formed chiefly by convoluted tufts of arterial capillaries, are present in the Wolffian bodies of Mammals, and in the persistent renal organs of all Vertebrates. They are called, after their discoverer, 'Malpighian corpuscles,' and Mr. Bowman ‡ has admirably shown how the uriniferous tubes take their rise from these vascular corpuscles, viz. by a sacciform blind beginning applied over the vascular placentule or tuft.

The combined secerning cæca and vaso-ganglia form in the Sandprides and Lampreys § a continuous narrow elongated gland, which extends in the former (*Ammocetes*) throughout the abdomen, in the latter (*Petromyzon*) along the posterior two-thirds: in both confined to the dorsal part of the cavity. The ureters (*fig.* 74. *k*) open into the short canal (*ib.* *l*), leading to the papillary production of the peritoneal outlets close to the anus. ||

\* CXXXVII. ii. p. 314.

† XXI. 1841, p. 13.

‡ CXXV.

§ In the *Petromyzon marinus* the diameter of the tubuli uriniferi is  $\frac{1}{284}$ th of an inch, that of the capillaries of the kidneys being  $\frac{1}{1800}$ th of an inch.

|| XX. iv. pl. 56. fig. 1. e.

In most osseous fishes the kidneys are long and narrow, and extend through the whole or a great part of the dorsal region of the abdomen, firmly attached to the vertebral column; they are usually broadest and thickest anteriorly, where they sometimes present a lobulated surface; they contract, approximate, and frequently blend together as they extend backwards (prep. 1177. *Cyclopterus*); sometimes penetrating the hæmal canal in the tail. In the *Gymnotus* the kidneys are distinct and thickest at their posterior ends, as they are in the Gurnard (*fig. 72. k*) and in most Sharks. The kidneys have not a well-defined capsule in osseous fishes, but their ventral surface is immediately covered by an aponeurotic membrane, against which the peritoneum, and the air-bladder when present, are applied. The renal tissue is soft and spongy, firmest at the fore-part of the gland; usually of a reddish-brown colour; sometimes soaked, as it were, with dark pigment (as in *Lepidosiren*, XXXIII. p. 349.). It is supplied by numerous small arteries from the abdominal aorta\*, which form Malpighian corpuscles; but these are fewer in number and less complex than in the true kidneys of higher Vertebrates. The primary branches of the tubuli uriniferi, given off from the long ureter, are extremely numerous; their divisions in the renal substance are comparatively few; they are in most fishes convoluted and of equal diameter, extending through the whole renal substance, which shows no distinction of cortical and medullary parts, and has no mammillæ: they are lined by a ciliated epithelium. Sometimes a single common ureter quits the coalesced hinder ends of the kidneys, as in the Pike, and terminates in a urinary bladder. More frequently the essentially duplex nature of the kidneys is manifested by the emergence of two ureters from the ventral surface of their posterior ends when these have coalesced: in some fishes these unite together after quitting the kidneys, and terminate by a common gradually widening canal in the urinary bladder. Sometimes they enter the urinary bladder separately, as in the Wolf-fish, where they both terminate on its left side, half-an-inch above the cervix: rarely are any smaller accessory ureters seen, as *e. g.* in the Stickleback, to terminate also, separately, in the bladder. This, in aquatic animals apparently needless, receptacle of a fluid excretion is, nevertheless, rarely absent in osseous fishes; the Pilchard, the Herring, and the Loach are among the few instances where it is not developed. In the Loach a very short, in the Herring a long, common ureter terminates behind the anus. In the *Gymnotus* the common ureter is so wide as to serve as a receptacle, and it is directed forwards to reach

\* Hunter, VII. t. ii. p. 112.

its termination immediately behind the advanced vent. The urinary bladder is sometimes round (*fig. 72. b*), sometimes oval or pyriform, often bifid at its fundus or two-horned; it is largest in those fishes, as the *Pleuronectidæ*, the *Lophius*, the *Orthogoriscus*, and the *Cyclopterus*, in which the air-bladder is absent. In the *Callyomymus* the bifid urinary bladder extends the whole length of the abdomen. It always lies behind the rectum, generally receives the ureter or ureters nearer its fundus than its cervix, and the latter is prolonged usually into a prominent papilla behind the vent. The long cervix vesicæ in the Salmon is surrounded by a venous plexus. In the Sturgeon the wide ureters extend along the outer borders of the kidneys, and receive the vasa deferentia or oviducts in their course towards the cloaca, where they unite into a short duct which forms the common outlet of the urinary and generative products.

The kidneys are long, narrow, but distinct from each other in all the ganoid fishes and in the Lepidosiren. In the *Lophius* the kidneys present a more compact form, and are situated wide apart, far forwards in the abdomen, in depressions on either side of the origins of the 'retractores palati.' The kidneys of the Plagiostomes are also of a more compact form than in osseous fishes, and are always distinct, and generally show a cerebriform convoluted or lobulated exterior: the primary branches of the uriniferous tubes are fewer, and their dichotomous ramifications more numerous\*: the ureteric trunk becomes superficial along the inner and fore-part of the hinder half of each kidney; after quitting which it dilates in the Grey Shark (*Galeus*) into a kind of receptacle behind each oviduct or vas deferens, and communicating with its fellow near the cloaca, terminates by a single urethral canal upon a kind of penis or clitoris (*fig. 75. k*) at the back of the anus, within a large common cloaca. In the Torpedo, the ureters terminate on the cloacal papilla by two distinct orifices.† In the Skate and Thorn-back each ureter terminates in the neck of a short bifid bladder: these open by a common urethra upon the cloacal papilla. The Lepidosiren has a small urinary bladder situated, as in all fishes, behind the rectum and in front of the oviducts: the ureters do not communicate directly with it, but terminate separately on small papillæ in the oviducal compartment of the cloaca.‡ With regard to the circulation in the kidney in those fishes, as *e. g.* the Plagiostomes the *Lophius* and the Lepidosiren, in which the organ is best defined, the vein on the outer side of the kidney which receives blood from

\* In the Ray the diameter of the terminal branches of the tubuli uriniferi are  $\frac{1}{164}$ th of an inch, that of the capillary renal arteries being  $\frac{1}{1650}$ th of an inch.

† CXXXIV.

‡ XXXIII. pl. 27.

the tail, the abdominal parietes, and the generative organs has so far the aspect of a 'portal' or inferent vessel, that a second and larger vein, whose roots take their rise in part from the renal substance, extends from the inner and anterior part of the kidney to convey its blood to the vena cava. The exterior vein is not, however, completely expended in the kidney, but is also continued forwards from the anterior end to join the veins from the anterior abdominal parietes, and sometimes those from the pectoral fins. Whether the blood takes a retrograde course in these towards the kidney, and meets the stream from the hinder commencement of the exterior vein, is undetermined. In all fishes the kidneys maintain the same relations with the cardinal veins that their transitory homologues, the 'Wolfian bodies,' do in the embryo of the higher Vertebrates.

#### SUPRA-RENAL BODIES.

Professor Müller has described two small oval lobulated bodies, situated in advance of the kidneys, close to the portal sinus and near the pericardium, in the Myxinoid Fishes, as the 'glandulæ suprarenales.'\* In the typical Osseous Fishes they have been recognised as roundish bodies of a light grey colour; commonly two, rarely three in number; situated, sometimes near the middle, oftener at the hinder extremities of the kidneys, at or near the entry of the hæmal canal: sometimes they lie free, sometimes they are imbedded in the renal tissue (Pike, Salmon, Eel); but they always possess a proper capsule, and present what seems to be a minutely granular texture, without distinction of cortical and medullary parts. In the yellowish supra-renal bodies of the Sturgeon, the granules are minute spherical cells filled by microscopic nucleated corpuscles. In the Plagiostomes, the supra-renal glands are represented by elongated narrow yellowish bodies, situated behind the kidneys, and sometimes extending behind the dilated ureters.

\* XXI. *Angiologie*, 1841, pp. 14—17. tab. ii. fig. 2. n.

## LECTURE XII.

## GENERATION AND DEVELOPMENT OF FISHES.

## MALE ORGANS.

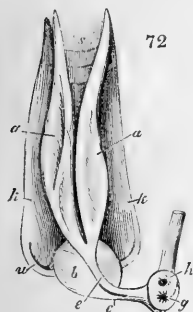
ALL fishes are diœcious or of distinct sex. The male parts of generation present a progressive gradation of complexity from the essential gland, or testis, as a single organ distinguishable only by microscopic examination of its contents from an ovarium, to a more definite and concentrated form of testis with complete bipartition, then to the development of a proper duct or 'vas deferens,' next of a vesicula seminalis and prostate, afterwards of an intromittent organ, and finally of superadded 'claspers,' or mechanical instruments for retention of the female *in coitu*. The preparation of the *Petromyzon marinus* (No. 2373.) shows the testis in the form of a series of thin transverse lobes, or folds closely attached by a duplicature of the peritoneum to the median line of the back of the abdomen, between the kidneys; the extension of the over-lapping oblique folds to the right and left of the line of attachment indicates the duplex character of the gland. Its tissue consists of small spherical cells filled with the minute corpuscular spermatozoa.\* These escape by dehiscence of the cells and rupture of the peritoneal covering into the abdominal cavity, and are expelled by reciprocal pressure of the intertwined sexes, from the peritoneal outlets at the cloaca. The Eel closely resembles the Lamprey in the general form and condition of the male organs; but the right and left sides of the plicated testis are more distinct, and the spermatid cells are more numerous and minute.

The Sand-Eel (*Ammodytes*, No. 2378.) has a single testis, compacted into an elongated triedral form, and impressed by a median longitudinal fissure: it usually inclines a little to the right side. In the Perch the single testis inclines to the left; in the Blenny and the Loach it lies in the middle line. In these osseous fishes the glandular part of the testis is inclosed in a proper fibrous capsule,

\* Sir E. Home and Mr. Bauer, misled by this close resemblance to an ovarium, inferred the identity of the testis with that body, described the kidneys as the testis, and the Lampreys as hermaphrodite fishes. Hunter had recognised the true structure. (vii. t. iv. pp. 204—206. pl. 59. fig. 1. h.) Mr. Bauer gives a good microscopic view of the cellular structure of the testis in Phil. Trans. 1828, pl. xv.



which is continued from the posterior end of the gland, with its serous covering, into a short and simple 'vas deferens,' which opens usually into or receives the urethral prolongation of the urinary bladder. In the Gurnard the testes (*fig. 72. a*) are distinct from



Renal and Male Organs:  
*Trigla lyra*, Carus.

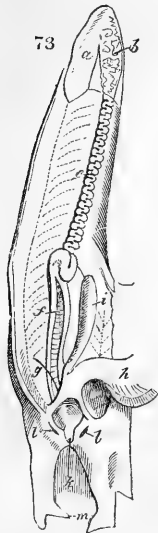
each other, but their 'vasa deferentia' almost immediately unite into a common duct, which joins the urethra (*c*) behind the rectum (*h*), and terminates at the outlet (*g*). In the Salmon and the Herring, the 'vasa deferentia' do not unite together until near their termination in the urethra. In the Cod and the Bull-head (*Cottus*) the common portion of the efferent duct is much dilated: it forms a saccular seminal reservoir in the Sole. The canal common to the ureter and vas deferens is of great length in the Sturgeon: a valve prevents the regurgitation of the urine into the spermatic duct. The urethra is usually produced into a papilla, which pro-

jects conspicuously from the back part of the cloaca in the viviparous Pœcilia, Anableps, and Blenny: it is large also in the Lump-fish. The testes are almost entirely extra-abdominal in the Flounder and some other *Pleuronectidæ*, extending backwards into a kind of concealed scrotum between the integuments and muscles on each side above the anal fin. The testes differ much in form in different Osseous Fishes, but are remarkable in all for their enormous seasonal increase: when fully developed they are commonly known as the 'milt' or 'soft roe.' In the Pipe-fishes (*Syngnathi*) they present the form of two simple elongated straight tubes (prep. 2375.). In the Lump-fishes (*Cyclopteri*) they are divided by incisions into lobes: in the Cod a vast extent of the vascular surface of the glandular substance is packed into a small compass, by being disposed in convolutions upon the edge of the 'mesorchium.' The primitive spermatic cells, which are persistent in the Cyclostomes, have coalesced into tubes (tubuli seminiferi) in osseous fishes; the tubes open at one end in the wide and sometimes saccular commencement of the vas deferens, and terminate at the other either by blind free extremities, or by reticulate anastomoses.\*

In the Plagiostomes the testes (*fig. 73. a*) are always distinct from one another, and usually of a circumscribed compact form, situated far forwards in the abdominal cavity. They have a proper

\* cxx. p. 105. pl. xv. fig. 7. in the Shad.

capsule or 'tunica albuginea,' and a peritoneal covering: the capsule sends many 'septa' into the testes; and the lobes thus formed consist



Male Organs,  
left side: *Spinax*.

chiefly of the tubuli testis, and their expanded cell-like extremities, filled with the spermatozoa: the convolutions of the 'tubuli' are plainly discernible in the portion of the testis of the great Basking Shark preserved in No. 2396. A. Numerous 'vasa efferentia' convey the 'semen' to the beginning of the 'vas deferens'\* which forms a large 'epididymis' (ib. *b*) by its manifold convolutions. These gradually decrease as the duct (*e*) approaches the cloaca, when it becomes straight, and expands into an elongated reservoir (ib. *f*), the mucous surface of which is commonly increased by numerous transverse plicæ (*Selache*.) Behind the termination of the rectum the 'vasa deferentia' suddenly diminish, approximate, communicate with the ureters, and terminate upon the rudimental cloacal penis (ib. *g*, *k*, and prep. 2396.).

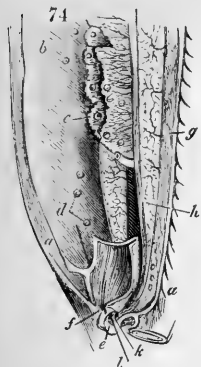
The claspers (ib. *m*) are present in the Chimæroid Fishes as well as in the Plagiostomes. They project backwards as appendages to the bases of the anal fins, and are sometimes bent inwards at their free extremities. Near this part may be discerned a fissure which is the outlet of a blind sac extending forwards from the base of the clasper beneath the muscles and skin, at the sides of the cloaca. The inner surface of the cavity is smooth, and lubricated by a fluid mucus: the attached vascular surface is richly supplied with vessels, especially with veins: in the Rays a glandular body adds its secretion to that of the surface of the cavity.

#### FEMALE ORGANS.

The gradations of structure of the female organs correspond very closely with those of the male. In the young Lamprey the ovarium is a simple longitudinal membranous plate, suspended by a fold of the peritoneum (mesoarium) along the under part of the vertebral column: it increases in breadth and thickness as the ova are developed in it, and still more so in length, being accommodated to its locality by numerous folds (*fig. 74. c*). But no superadditions are made to this primitive structure: the ova (*d*) escape by rupture of their

\* CXXXIV.

capsules into the abdomen (*b*), and are excluded by the peritoneal apertures (*ib. l*). In all other fishes in which vasa deferentia are absent



Renal and Female Organs:  
*Petromyzon*, Hunter.

in the male, oviducts are absent in the female. But it does not always happen, where vasa deferentia are developed in the male, that the homologous ducts exist in the female: the Salmon is an example in which the ova are discharged by dehiscence into the abdominal cavity, and escape by peritoneal outlets, as in the Eel and Lamprey.

With this exception, the parallelism of the male and female organs is very close. Thus the ovarium is single in those bony fishes, as the Perch, the Blenny, the Loach and the Ammodyte (prep. 2675. A), in which the testis is single: the median cleft of the ovary of the Ammodyte is deeper than that of the testis, but the continuity of the two seemingly distinct glands is obvious at the upper and lower ends. In most osseous fishes the ovaria form two elongated sacs of mucous membrane, with a thin fibrous tunic and a peritoneal covering: closed anteriorly, but produced posteriorly into a short, straight, and commonly wide oviduct, terminating behind the anus, and commonly before the urethra. In the Pipe-fishes the oviducts continue distinct to the cloaca. In most fishes the oviducts coalesce, sooner or later, into a single tube before arriving at the cloaca: the common terminal portion becomes much dilated in the Cod-fish, the Lump-fish, and some others. The 'stroma,' or cellular tissue, which is the seat of development of the ova, is interposed between the mucous and fibrous tunics of the ovarian sac: it sometimes, though rarely, is co-extensive with the mucous membrane. In the *Lophius* the two ovaria are long and large plicated tubes, flattened when empty, cylindrical when inflated, with the ovigerous stroma lining, as it were, only the ventral half of the walls of the cylinder, and terminating where the oviducal portions of each sac unite together to form the common short efferent canal. The inner surface of the 'stroma' is beset by small tubercles, arranged in interrupted linear series, each tubercle supporting four or five papilliform ovisacs. In the Pike the stroma forms a longitudinal strip, in short transverse plaits, along the median side of the long ovarian sacs. In the Wolf-fish the stroma extends over the whole of the internal surface of the ovary, into the cavity of which it projects in the form of numerous oval compressed processes. In general, its superficies is extended by being plaited

into numerous folds, which are transverse in the Cod and Salmon\*, oblique in the Mackerel, and longitudinal in some other fishes. In the osseous fishes that retain and hatch their ova the stroma does not extend to the posterior part of the ovarian sac, but this serves as a kind of uterus, and contains an abundant albuminous secretion at the season of the internal incubation. The viviparous Blenny (*Zoarces*), the Anableps, the Pœcilia, and some Siluroids are examples of ovo-viviparous osseous fishes, and at the same time manifest naturally, what occurs as a rare abnormality in higher Vertebrates, viz. ovarian gestation. In the Plaice and other Pleuronectidæ the parallelism between the male and female organs is so close, that the ovaria also escape from the abdomen, and become lodged in greater or less proportion in sub-cutaneous scrotal cavities above the basis of the anal fin.†

In the Lamprey the short and narrow lateral infundibuliform passages behind the rectum, into which the ureters open, and which terminate in the peritoneal outlets (*fig. 74. e, l*), have been compared to short oviducts. In the Sturgeon actual oviducts are continued from the ureters forward, which open by wide infundibular apertures, comparable to the 'morsus diaboli' of anthropotomy, into the general peritoneal cavity, and receive the ripe ova as they burst from the ovarium. The urine is prevented from regurgitation into the serous cavity through the same passage, by a valve which only allows the passage of the ova backwards into the common uro-genital duct. The higher grade of the sexual organisation of the female Plagiostome, as compared with the cartilaginous Ganoid fish, is manifested chiefly by modification of the oviducts; they are always two in number, and distinct from one end to the other, but are brought into close proximity, or coalesce at both ends: they are always distinct from the ureters, which terminate on the prominent urethral clitoris, between the oviducal outlets. Different parts of the oviducts are modified, moreover, for special functions, superadded to that of effecting the safe transit of the generative product. The ovaria of Plagiostomes (*fig. 75. a*) are relatively much smaller than in other fishes, of a more compact form, and confined to the fore part of the abdominal cavity: they are sometimes blended into a single body. The stroma is not spread over the walls of a cavity, but is collected into a loose cellular mass, circumscribed by a fibrous membrane, and suspended by a duplicature of peritoneum to the dorsal parietes of the abdomen, at the sides of the œsophagus. The ova are much fewer in number than in the 'roe' of osseous fishes, and are seen in different

\* In the Salmon the free surface of the stroma is exposed.

† XLIII. v. pl. 4. fig. 1.

stages of growth, being developed more consecutively. The approximated or confluent abdominal apertures of the oviduct (ib. *b*) are anterior to the ovarium, between the liver and the pericardial septum; they form together a heart-shaped opening, with entire margins, attached by two diverging ligaments (ib. *c*) to the abdominal walls. The oviducts narrow, and with thin tunics at their commencement (ib. *d d*), diverge from each other, arching over the fore part of the ovaria, and then descend along the ventral surface of the kidneys, to terminate at the lateral and posterior parts of the cloaca. A glandular body (ib. *e*) is developed in their coats, after the first fifth or sixth part of their extent, and their terminal half or third part (ib. *f*) is dilated: the sizes of the glandular and of the uterine parts of the oviduct are usually in inverse proportion: in the oviparous Plagiostomes the gland is large, the uterus small, and the reverse obtains in the viviparous species. The inner surface of the Fallopian portion of the oviduct presents longitudinal or very oblique folds of the delicate mucous membrane; but near the aperture the folds resolve themselves into minute compressed villi. The



Female Organs:  
*Spinax*, Hunter.

glandular part varies in structure as well as in size in different species. In the viviparous Dog-fish (*Spinax acanthias*) it consists of two elliptic flattened lobes, of laminated structure, the free surface presenting minute transverse striæ, beset with pores, the orifices of secerning tubes, the aggregate of which composes the layer of glandular substance. In the oviparous Homelyn (*Raia maculata*) the lobes of the large rudimental glands are reniform. Prep. 3234. shows well the inner free margins and interspaces of the close-set layers of secerning tubes. In the *Galeus* the lobes of the gland present the same essential structure, but are conical, subspiral, and hollow. The uterine part of the oviduct in the viviparous Dog-fish has the lining membrane produced into longitudinal folds, with wavy margins, each of which contains a single vessel following its sinuositics, and sending off branches to the parietes of the oviduct: the folds gradually subside at the outlet of the oviduct. In the ovoviviparous Dog-fish (*Scyllium*) the folds of the lining membrane of the corresponding part of the oviduct are oblique, and their vessels are derived from trunks in the walls of the oviduct, and are distributed in minute and tortuous ramifications on the folds (prep. 2683). The preparation (No. 2684) of the Smooth Dog-fish (*Galeus levis*; *Emissole lisse*, Cuvier) shows several uterine cotyledons developed

from the internal surface of the dilated part of the oviduct. Professor Müller has well described the corresponding foetal cotyledons which are developed from the vitellicle of the embryo.

In reviewing the various forms of the Generative Organs of Fishes, we find that they resolve themselves into four well-marked grades of complexity. First, reduced to the essential gland, the testis, or the ovarium, without excretory canal. Secondly, with a simple duct, continuous with testis or ovarium. Thirdly, a partial oviduct, as in the Sturgeon, not continuous with the ovarium, and not separated from the ureter. Fourth, a more compact form of testis and ovarium, with a long and complex duct, distinct from the ureter; the beginning of the vas deferens convoluted into an epididymis and its end dilated into a seminal reservoir, with a plicated glandular inner surface; the oviduct presenting a nidamental gland near its commencement and dilating into an interior receptacle, with a plicated surface at its terminal half. Besides the 'claspers' of the Plagiostomes, there are other accessory organs of generation; viz. the subcaudal marsupial tegumentary folds in the male of some species of *Syngnathus* (preps. 3226—3228), and the sub-abdominal marsupial pouch in the male Hippocamps (preps. Nos. 3230 and 3231).

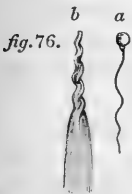
#### DEVELOPMENT OF FISHES.

This, the most intricate and difficult, but the most interesting part of the physiology of fishes, is divided, as in other animals, into seven distinct processes:—1. *Semination*, or the development of the impregnating corpuscles called seminal animalcules, or 'spermatozoa':—2. *Germination*, or the development of the germ or ovum susceptible of impregnation:—3. *Fecundation*, or the act of impregnation, which is sometimes, though rarely in the present class, accompanied by intromission:—4. *Fœtation*, or development of the embryo within the ovum or uterus:—5. *Extrication*, or escape of the embryo from the ovum:—6. *Exclusion*, or expulsion of the generative product from the parent:—7. *Growth*, or development from the period of exclusion, or of extrication from a previously excluded ovum, to maturity.

*Exclusion* of the male generative product is called 'emission;' that of the female generative product, 'oviposition;' that of the previously extricated embryo, 'birth:' but these are modifications of the same essential process. The stages of development do not succeed each other as here enumerated, in all fishes: in the Dermopteri and most osseous fishes 'exclusion' precedes 'fecundation,' 'fœtation,' and 'extrication.' In a few osseous fishes and a larger proportion of the Plagiostomes, 'fecundation,' 'fœtation,' and 'extrication' precede

'exclusion.' When the membranes or appendages of the intra-uterine embryo contract no adhesion with the parietes of the uterus, the fish is said to be 'ovo-viviparous:' when such adhesion by interlacement of vascular surfaces takes place, the species is said to be 'viviparous.' The period of fœtation passed within the body of the parent is called 'gestation:' that which takes place in natural cavities on the exterior of the body of the parent, or in nests artificially prepared, is called 'incubation;' but these are accidents to fœtation, which may go on, as it does in most osseous fishes, independently of either kind of protection.

*Semination.*—The progress of the testis to maturity, when it attains in all osseous fishes a larger proportional bulk than in any other vertebrate animals, commences by the appearance in its tissue of extremely delicate, closed cells, 'the sperm-sacs.' In these the spermatozoa are developed.\* They are discharged, as we have seen, in the lowest organised fishes, by a general rupture of the sacs into the abdomen, and are excluded by the peritoneal canals. In the growing milt of osseous fishes the sperm-sacs also yield to the pressure of their contents, but partially coalesce and form tracts or canals, frequently reticulate in their disposition, as in the Shad, and which ultimately discharge their contents into the efferent prolongation of the general capsule of the gland. The spermatozoa are, at first, mere nucleated cells; they acquire in the Loach a pyriform figure, with a minute knob at the apex, from which the filamentary



a. Spermatozoon of Loach

b. Fasciculus of Spermatozoa: *Raia Oxyrhynchus*, Wagner, magnified.

vibratile tail is continued (*fig. 76. a*). Professor Wagner estimates the length of the pyriform body at  $\frac{1}{500}$ th of a line, and that of the tail at  $\frac{1}{40}$ th of a line.† Prevost and Dumas, and Siebold have described the vibratile filamentary appendage in the spermatozoa of other osseous fishes. In the Cyclostomes the body of the spermatozoa is cylindrical; in Sharks it is long and spirally twisted; in Rays they are developed in bundles (*fig. 76. b*), which are arranged in a radiated disposition in the sperm-sac before its rupture. Dr.

Davy‡ observed many of the spermatozoa grouped together in the vas deferens of the Thornback. The abundance of these locomotive ciliated cells, and of the minuter granular matter in the fluid in which they float, give to the secretion of the testis or soft roe an opaque milk-white colour.

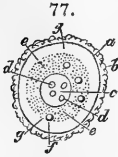
*Germination.*—The ova are developed in the 'stroma ovarii, almost simultaneously in Dermopteri and osseous fishes, more suc-

\* cxxxviii.

† cxxi. p. 68.

‡ cxxxiv.

cessively in the Plagiostomes. They are much fewer in number in the latter : from four to fourteen ova, for example, are developed at each breeding season in the *Torpedo marmorata*.\* In all fishes the ova are formed in chambers of the 'stroma,' called 'ovisacs.' In osseous fishes the ovisac† consists of a delicate membranous hollow



Ovarian Ovum :  
Osseous Fish,  
magnified.

sphere—the 'ovarian vesicle' (fig. 77. a) ‡, surrounded by a thin layer of the proper tissue or 'stroma' (b) of the ovary, which, as it protrudes into the ovarian cavity, carries before it a covering of the delicate vascular mucous membrane. This tunic is not present in Cyclostomes or Plagiostomes. The ovum consists of the primordial or germinal vesicle, 'germ-cell' (c), which, in osseous fishes, shows several nuclei or 'germ-spots' (d), but in Plagiostomes only a single nucleus. Around the germ-cell there accumulates a collection of minute yolk-granules (e) with oil-like globules (f), the whole contained in a delicate yolk-membrane (g). The increase of the ova is due chiefly to the accumulation of the yolk, and its colour to that which the oil-globules acquire as the ova approach maturity. At this period the ova in osseous fishes escape into the cavity of the ovarium ; and to their then outer covering, the yolk membrane, is added a second tunic called 'chorion.' The ovisac remains behind and coalesces with the stroma, to form, according to Barry§, a "vesicle analogous to the Graaffian vesicle of Mammals : " but the evacuated ovisacs collapse and speedily disappear in the shrunken ovarium, after the discharge of the ova, in Dermopteri and osseous fishes : they are longer recognisable in the Skate.

The periodical, but rapid and enormous increase of the hard and soft roes in osseous fishes, admits of no rigid cinctures, no unyielding bony hoops around the abdominal cavity, such as would have resulted from a conversion of the pleurapophyses, by their junction with hæmapophyses and a sternum, into 'true ribs.' We see, therefore, in the fecundity of fishes,—in this compensation for their limited intelligence and numerous foes,—the physiological condition of their free or 'floating' ribs.

*Fecundation.*—Certain changes and peculiar phenomena attend the increase of size of the soft and hard roes during these primary processes of generation. The colours of the fishes become more marked and brilliant ; the different sexes are often distinguished by peculiar tints ; as the male Stickleback by his bright red throat, for example. The claspers in the male Plagiostomes then acquire their full development and force ; the basal glands in those of the Rays enlarge. As

\* LXXXI.

† 'Ovisac' of Barry, cvii. 1st series.

‡ xx. iv. 1838, p. 131.

§ cvii. 1st series, p. 314.



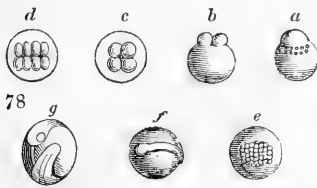
the period of 'fecundation' approaches, the female osseous fish seeks a favourable situation for depositing her spawn, usually in shoal water, where it can be most influenced by solar warmth and light. The marine Herring, Mackerel, and Pilchard approach the shore in shoals: the fluviatile Salmon quits the estuary to ascend the river, overcoming, with astonishing perseverance and force, the rapids or other mechanical difficulties that impede its migration to the shallow sources, whither the sexual instinct impels it as the fit place for oviposition. The female fish is closely pursued by the male, sometimes by two; in the Capelin (*Mallotus*), these swim on each side of her, aiding by their pressure in the expulsion of the spawn, and at the same time impregnating it by diffusing over it the fluid of the milt: thus absorbed in the sexual passion, they have been seen, on the shores of Newfoundland, to rush on land in their spasmodic course over the shallows, which they strew with the fecundated ova. In some genera violent combats take place between the males. Mr. Shaw\*, a most able observer of the development of the Salmon, states:—"On the 10th of January, 1836, I observed a female salmon of about 16lbs., and two males of at least 25lbs., engaged in depositing their spawn. The two males kept up an incessant conflict during the whole day for possession of the female, and, in the course of their struggles, frequently drove each other almost ashore, and were repeatedly on the surface displaying their dorsal fins, and lashing the water with their tails." "The female throws herself at intervals of a few minutes upon her side; and while in that position, by the rapid action of her tail, she digs a receptacle for her ova, a portion of which she deposits, and again turning upon her side she covers it up by the renewed action of the tail; thus alternately digging, depositing, and covering the ova, until the process is completed by the laying of the whole mass, an operation which generally occupies three or four days."

In the ovo-viviparous osseous fishes, the well-developed cloacal papilla, in which the sperm-duets terminate, doubtless serves to ensure intromission. The superadded claspers in the male Plagiostomes lend more effectual aid in the act of internal impregnation; for in those species that are oviparous the ova are impregnated and covered by a nidamental coat or 'shell' prior to exclusion.

*Fætation.*—The observation of the more simple mode of impregnation in osseous fishes, so analogous to that of the dioecious palms in which the fertilising pollen is wafted through the aerial ocean and strewed over the humid papillose stigmata of the female flower, naturally suggested the idea of artificial impregnation, of which

\* CXXII.

MM. Prevost\*, Rusconi†, and Vogt‡ have availed themselves, in the investigation of the nature of that mysterious act, and of the changes thence ensuing in the impregnated ovum of fishes. The first change observed when the ovum falls into the water is a separation of the outer covering, or ‘chorion,’ from the inner tunic or ‘membrana vitelli.’ It is probable, from observations on other animals, but not proved in respect to the ova of fishes, that the contents of the sperm-cell (body of the spermatozoon) enter the ovum. After the contact of the spermatozoon with the ova, the following changes take place in the germ-vesicle. It loses its unimpregnated character, becomes opaque, enlarges, and, in the ovum of the Tench, according to Rusconi, forms with surrounding granular matter an intumescence beneath the membrana vitelli. Rusconi does not, indeed, interpret this appearance as due to development and metamorphosis of the germ-vesicle and its nuclei; but Vogt has confirmed, by observation of the ova of the *Corregonus*, the important discovery by Barry of the part which the germinal vesicle and its nucleus or nuclei take in the first steps of embryonic development. “The small granules,” observes Rusconi, “previously dispersed through the yolk, now become collected at the base of the intumescence (*fig. 78, a*).



First steps in the development of a Tench: Rusconi.

Half an hour after the occurrence of this first change, two furrows intersecting each other at right angles appeared at the prominent part of the yolk (*ib. b, c*). A quarter of an hour later, two other furrows were observed at each side of the first, so that the prominent part of the yolk, which previously was divided into four lobes, now appeared to be formed of eight lobes (*ib. d*). After the lapse of another quarter of an hour, each of these eight lobes was seen to be subdivided into four smaller lobes, by the formation of six fresh furrows, intersecting each other at right angles. At the end of another half-hour, several new furrows appeared, which crossed those which already existed, and subdivided the lobes of the prominent part of the yolk still further, rendering them so small and numerous that it was now scarcely possible to count them (*ib. e*). The process continued until the surface of this portion of the yolk regained the smoothness which it had before the first furrow appeared.”

If this account, abridged by Professor Müller§ from the Memoir of the celebrated Italian physiologist, be compared with the description of the first steps in the development of the intestinal worm

\* CXXX.

† CXXXI.

‡ CXXXII.

§ LXXIV. ii. p. 1510.

("Lectures on Invertebrata," p. 77.), the correspondence will be seen to be extremely close. In the Entozoon the entire yolk is the seat of the successive subdivision produced by reiterated processes of development, liquefaction, and assimilation, of nucleated cells, until the property of the primary impregnated germ-cell has been distributed throughout the mass; when the whole mass, by subsequent metamorphosis of the cells, is converted into the embryo. In the fish a part only of the yolk is the seat of these processes, superficially indicated by fissures of that part, and the resulting embryo is connected with the remainder of the yolk; this remainder is called the nutrient yolk, or 'vitellicle;' the other part is the 'germinal yolk,' sometimes called the 'germinal membrane,' from its being thinly spread over more or less of the nutrient yolk before the embryo arises out of it. In the Tench and other Cyprinoids it overspreads the whole nutrient yolk\*: in the Blenny, Rathké† found the embryo considerably advanced before the nutrient yolk was so included. The surface of the so-covered yolk is ciliated, and, with the embryonal part, performs a slow but regular rotation within the albuminous fluid of the chorion.‡

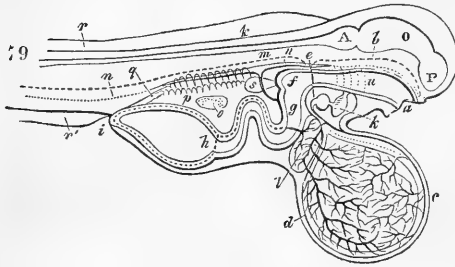
The first traces of the embryo are two parallel ridges, the 'laminæ dorsales,' which coalesce, and form the neural axis and the rudiments of the chorda dorsalis (*fig. 78. f*). The germinal membrane separates into an outer 'vertebral' and an inner 'visceral' layer: from the former are developed the brain and myelon, the vertebræ and their appendages, the muscles and nerves, and the skin; from the latter are developed the digestive, excretory, and generative viscera. The outer layer has been called the 'serous' and 'animal' layer; the inner one the 'mucous' and 'organic' layer. Between these are developed the organs of circulation and respiration. The 'laminæ dorsales' consist of the extension of the vertebral layer upwards (the embryo being supposed to be prone) to inclose the neural axis: the 'laminæ ventrales' are downward extensions of the same layer, to inclose the viscera and the nutrient yolk; consequently the so-extended 'laminæ ventrales,' when they coalesce below, form the external (serous, or more properly tegumentary) layer of the yolk-sac. After the trunk is developed, the head and the tail appear, and project freely from the supporting surface, and the embryo encircles the yolk, in the form of an apodal fish (*ib. g*). With regard to the skeleton, the aponeurotic septa of the vertebral segments of the body first appear; then the 'chorda dorsalis;' afterwards the rudiments of the neurapophyses along the sides of the neural axis; and, lastly, the hæmal arches and their appendages. At this time may be discerned the characteristic striæ of the muscular fibre. The development of the skull is described at p. 71.

\* XLIII. (1831).

† CXXVIII.

‡ CXXXII.

The inner (mucous) layer of the globular yolk-sac sends from its upper part a cæcal process forwards and another backwards, almost co-extensive at first with the trunk above. But their growth is checked by the adhesion of their blind ends to points of the serous layer on the under part of the cephalic and caudal extensions of the trunk: which points of adhesion become perforated, and establish the mouth (*fig. 79. a*) and vent (*ib. i*): the intermediate mucous tract forms,



Embryo Osseous Fish.

at first, a short and straight alimentary canal, communicating by a gradually constricted aperture with the remaining yolk-sac (*ib. d*). In the Cyprinoid fishes the vitellicle is sessile; i. e., it does not hang, as a pedunculate sac, from the exterior of the body: the young Salmon

quits the ovum with the vitellicle in the form of a vascular oblong appendage from the fore part of the abdomen. In both cases the vitellicle is included, together with the intestinal canal, within the parietes of the abdomen (*ib. c*), formed by the before-mentioned development and coalescence of the laminae ventrales. In the Tench the yolk is divided only by the constricted communication with the intestine, and is said to be 'internal;' in the Salmon, and, also, in *Zoarces* and *Cottus*, the yolk is divided by a second constriction, where it hangs from the ventral integuments; the part within the abdomen is called the 'internal yolk,' the part without is called the 'external yolk.'

The vascular channels, which are excavated in the soft embryonic tissues of both the vertebral and visceral systems, and which convey, at first, a plasma with colourless nucleated cells, unite into a longitudinal sinus in the interspace of the two systems, where the aortic trunk (*n*) and the cardinal veins (*m*) are afterwards situated. This, at first simple canal, receives or transmits vascular loops or arches upwards to the laminae dorsales, and downwards to the laminae ventrales; those of the latter being most conspicuous that spread over the vitellicle: it is here, also, that the red-colour of the circulating cells, or blood-discs, is first perceived. The vitelline vessels in osseous fishes are ramifications of a mesenteric vein, analogous to that subsequently established to form the portal system of the liver.

The heart is not developed from the longitudinal vessel in the dorsal region of the abdomen. The larger branches, which ramify on the vitellicle, unite into a trunk at its anterior part, which, being

joined by the precaval vein (*e*), becomes first a pulsating tube, and afterwards, by extension, constrictions, and intervening dilatations, an auricle, a ventricle (*k*), and a bulbus arteriosus; from which the hyoid vascular arch (*u*), succeeded by the branchial vascular arches, pass upwards to communicate with, and impart new vigour to the flow of blood in, the primitive longitudinal dorsal vessel. The 'laminae ventrales,' continued down the sides of the head, form vertical folds or arches, the interspaces of which are converted into clefts communicating with the commencement of the alimentary canal. The first of these arches is the largest, and from its blastema the mandibular and hyoidean arches, with their appendages, are developed; the five succeeding arches are the true branchial ones. The metamorphoses of the corresponding vascular arches, and the development of the gills, have been already explained, (p. 265.). The jugular (*b*) and cardinal (*m*) veins unite to form the precaval (*e*), which joins the hepatic and vitelline veins in a common trunk, or sinus, opening into the auricle.

The first three successive enlargements at the fore part of the neural axis are connected respectively with the olfactory, optic, and acoustic nerves; the first (*p*) becomes, then, divided into prosencephalon and rhinencephalon; the second (*o*) rapidly gains superior bulk in connection with the large and early-developed eyes; and the pineal and pituitary appendages appear. The cerebellum is the last part which is formed, upon the epencephalon (*A*).

In the mean while the liver (*l*) has been developed from the back part of the intestinal neck of the vitellicle; the pancreas being a later pullulation of cæca from the intestine itself. The kidneys (*p*) and generative glands (*o*) are formed out of blastema beneath the primitive vascular sinus; but their ducts are cæcal developments from the posterior part of the intestine: this latter stage of development is never attained, as regards the generative organs, in the *Dermopteri*. Rathke\* detected in the embryo Blenny, what Carus afterwards found in the human foetus, germinal vesicles in the nascent ovarium prior to birth, — two generations successively included in the parent.

The ureter (*q*) always makes its appearance very early before the embryo quits the ovum; it communicates with the extremities of the transverse parallel tubuli uriniferi formed by confluence of primitive cells in the renal blastema. The cardinal veins traverse or groove the kidneys, as they do the Wolffian bodies in the embryos of higher vertebrata; and this primitive relation of the vascular to the renal system is not changed in fishes by the substitution of true kidneys for the primordial renal organs.†

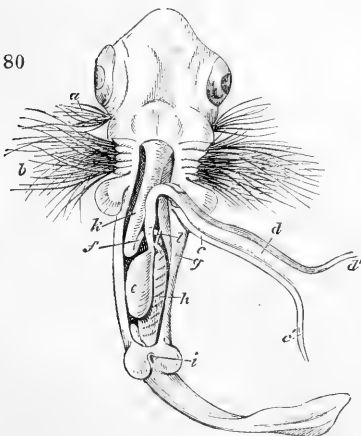
\* cxxviii.

† Von Baer appears to have first appreciated this interesting homology. "Alles

The duct of the air-bladder (*s*) is developed from the dorsal aspect of the pyloric end of the stomach; even in those fishes where the communication of the air-duct is afterwards found at the œsophagus; the posterior compartment of the air-bladder is first developed in the Cyprinoids, which accounts for the connection of the air-duct with that part. In the Herring, the primitive place of its connection with the alimentary canal is retained. The communication is obliterated in the fishes without the air-duct; and the whole posterior compartment disappears with the duct in the Loach. The scales are formed late in all osseous fishes; their integuments remain smooth and lubricous, as in the Dermopteri, some time after the disappearance of the vitellus.

The inferior position of the mouth is an embryonic character common to all fishes, and is retained, together with the unossified skeleton and the continuation of the cartilaginous vertebræ into the upper lobe of the caudal fin, in all the Plagiostomes. The singular productions of the rostrum in many of these fishes, like the elongation of the jaws in osseous species, are later phenomena of development. It is interesting to find the broad, depressed, obtuse embryonic form of head common to all the known fishes of the old red-sandstone. M. Agassiz thus accounts for the extreme rarity of the ichthyolites of this formation presenting a profile view of the head: it lies in most cases upon the upper or the under surface.

All the Plagiostomes have the external as well as the internal di-



Embryo Scyllium.

vision of the vitellicle (*fig. 80.*); the peduncle of the external one is longer, in some species considerably so, than in osseous fishes, and it is beset with villi in *Carcharias* and *Zygæna*.\* The tegumentary covering of the outer yolk (*ib. d.*), is denser and more opaque in Plagiostomes: the inner yolk (*ib. e.*) consists, of course, only of the proper vitelline tunic, which is thin and transparent: it communicates with the small intestine (*g*) i. e., with the short tract which intervenes between the pylorus and the valvular straight gut (*h*):

it receives the external yolk (*d' e'*) as this is progressively squeezed into the abdomen by the contraction and interstitial absorption of its

diess führt zu der Ueberzeugung, das der Fisch-Nieren stehen gebliebene Primordial-nieren anderer Thiere sind." (cxxxvii. 1337, p. 314.)

\* cxxiii. tf. iii.

tunics: and, as no part of the foetal abdominal appendage is cast off, nor the chord divided, there is no cicatrix — no umbilicus. The arterial vessels of the yolk are derived, not from the mesenteric vein as in osseous fishes, but from ramifications of a branch of the mesenteric artery, and the blood is returned to the mesenteric vein. The Hunterian preparations of the embryo *Carcharias* (No. 1061), *Scyllium* (No. 3250), *Spinax* (No. 3255), and *Alopias* (No. 3261), demonstrate another foetal peculiarity which later researches\* have shown to be probably common to all Plagiostomes, viz. the external fringe of filaments developed from the branchial surfaces (*b*): a tuft extends out of each aperture, and even from the spiracula (*a*) in the genera, with those accessory openings. Each filament contains a single capillary loop †: they disappear early, being removed by absorption. The last remnants may be seen in the foetal Saw-fish (*Pristis*, No. 3263), which is eight inches in length, including the saw, and has the duct of the external vitellicle attached. In the oviparous Sharks, the branchial filaments re-act on the streams of water admitted into the egg by the apertures (*fig. 81. c*). In the ovo-viviparous Sharks the size and position of the cloacal apertures of the uteri would seem adapted to allow free ingress of sea-water (No. 3255); so that, whilst the vitellicle administers to the nutriment of the embryo, the external branchiæ may perform the respiratory function. In the species of Shark, the smooth Emissole, in which Prof. Müller has shown that vascular cotyledons are developed from the vitelline (omphalo-mesenteric) capillaries, which are firmly connected to the uterine cotyledons, the vitellicle, like a true placenta, may perform both the nutrient and respiratory functions: the external branchiæ disappear some time before the exclusion of the Embryo and the absorption of the yolk. In the *Lepidosiren annectens* ‡ three small external branchial filaments project from the single opercular aperture on each side, and are long retained, if they be not permanent in that remarkable osculant form between the osseous and cartilaginous fishes.

Some of the plagiostomous fishes are oviparous, but not as in the majority of osseous fishes; a remarkable transposition in the periods of the processes of fecundation and exclusion marks the distinction. In the oviparous osseous fishes the ova are first excluded, then impregnated: in the oviparous Plagiostomes impregnation is internal, and precedes oviposition. The eggs are much fewer in number, but their impregnation is more certain than in the scattered indiscriminate act of spawning of the common fishes, where the countless numbers of the ova seem to compensate for the chances that may intervene to

\* Rudolphi, LXXV. Rathké, CIX.; Leuckart, CXXIII.; J. Davy, LXXXI.

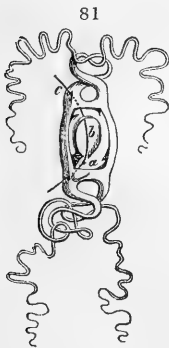
† A. Thompson, CXI.

‡ Jardine, CXXXV.; and Peters, CXXXVI.

prevent the contact of the milt. The ovarian, or abdominal aperture of the oviduct is free and distinct from the ovary itself in the Plagiostomes, the Lepidosiren, the Sturgeons, and Polypterus. If a little powdered charcoal be sprinkled on the ovarian orifices and ligaments exposed by opening the abdomen in a fresh caught female Dog-fish, the particles will be seen to move towards and enter the common oviducal aperture, indicative of a ciliated epithelium in the serous membrane, which may aid in the transport of the ova to that aperture.

There is reason to suppose that impregnation of the eggs of both Sharks and Rays takes place in the ovarium or the contiguous part of the oviduct; for they become enveloped in the dense albuminous secretion of the nidamental glands after having passed that part, which covering would prevent the subsequent influence of the spermatozoa. The form of the egg, when thus invested, is remarkable, and very different in different genera of Plagiostomes. In the Skate the ovum is an oblong, four-sided, flattened case, with the angles produced forwards and backwards, like those of a butcher's tray (prep. 3235).

✓ The embryo skate is packed in the cavity with its broad pectorals bent upon its back, and its tail coiled round the body: the vitellicle is appended by a short and contracted neck. In the spotted Dog-fish (*Scyllium*, No 3249) the ova are also quadrilateral, but longer, and the angles are extended into long filamentary tendrils, which attach themselves to floating sea-weed, and thus keep the ovum near the surface, where the influence of solar heat and light is greatest



81  
Egg and Embryo; *Scyllium*.  
One fourth nat. size.

(fig. 81). The eggs of the *Calorhynchus* themselves resemble some broad-leaved fucus, and thus, probably, deceive the fish that might otherwise devour them: they are in the form of a long depressed ellipse, with a broad plicated and fringed margin (No. 3235, A and B). The large Shark's ovum (prep. 3245), resembles that of the *Scyllium*, with the addition of a series of transverse parallel ridges crossing the anterior and posterior surfaces. An elongated pyriform shell of a plagiostomous ovum, transmitted to me from Australia, as that of the *Cestracion*, is characterised by a broad ridge or plate, which is wound edge-wise around the ovum in five spiral circumvolutions. The substance of all these egg-coverings is a light, but firm, albuminous horn-like tissue, of a more or less deep brown colour: the orifices (fig. 81. c) admit the sea-water to the pendant respiratory filaments of the inclosed embryo (a). The yolk-bag is shown at b.

The essential difference between the oviparous and ovo-viviparous



fishes is the transposition of the periods of extrication and exclusion: in the Ovipara the generative product or ovum quits the parent before the embryo extricates itself from the egg: in the Ovo-vivipara the embryo escapes from the egg before it quits the parent: the young Blennies tarry three months in utero, from September to January, after extrication from the chorion. The great difference between viviparous fishes and mammals is, that the former rupture the chorion long before they are born, even in the Sharks where there is a kind of pseudo-placental attachment: in the foetal mammal birth and exclusion are commonly coincident.

*Growth.*— There are few fields of Natural History that have been less cultivated, or would better reward the scientific labourer, than that extensive and varied one relating to the generation of fishes.

The mercantile value of the Salmon, and the necessity for basing laws that are to operate in its preservation, upon a knowledge of its natural history, have led to some very interesting observations; the following are the chief results of those recorded by Mr. John Shaw in the Transactions of the Royal Society of Edinburgh, for 1840.

The embryo fish, developed from the ova spawned on the 10th January, were conspicuous by the two dark eye-specks and the vascular vitelline sac, and presented some appearance of animation in the ovum, on February 26th, that is, forty-eight days after being deposited; and on 8th April, or ninety days after impregnation of the ova, the young were excluded. The head is large in proportion to the body, which measures  $\frac{3}{8}$ ths of an inch in length; the vitellicle is  $\frac{2}{8}$ ths of an inch in length, and resembles a light red currant; the tail is margined like that of the tadpole, with a continuous fin running from the dorsal above to the anal beneath. The vitelline sac and its contents were absorbed by the 30th May, or in about fifty days, until which time the young fish did not leave the gravel. This quiescent state in their place of concealment, from the period of exclusion to the absorption of the yolk, seems to be common to osseous fishes; but the time varies in different fishes, it is much shorter in the Tench, for example, than in the Salmon. When the young of this fish emerge, the terminal fringe-like fin begins to divide itself into the dorsal, adipose, caudal and anal fins; and the transverse bars on the side of the body make their appearance. At this period, the young Salmon measures an inch in length, and is very active, and continues in the shallows of its native stream till the following spring, when it has attained the length of from three to four inches, and is called the "May-parr:" they now descend into deeper parts of the river, and are believed by Mr. Shaw to remain there over the second winter. In April, the caudal, pectoral, and

dorsal fins assume a dusky margin; the lateral bars begin to be concealed by a silvery pigment; and the migratory dress, characteristic of the Salmon fry, or 'smolt,' is assumed. The fish now begin to congregate in shoals and to migrate seaward.

*Incubation.* — Eckstroem first published a clear account, in 1831\*, of the singular marsupial economy of the Pipe-fishes. In the *Syngnathus acus* the sexes come together in the month of April, and the ova pass from the female and are transferred into the subcaudal pouch of the male, being fecundated *in transitu*, and the valves of the pouch immediately close over them. In the month of July the young are hatched and quit the pouch, but they follow their father, and return for shelter into their nursery when danger threatens.

Aristotle signalises the *Phycis*, since recognised as a Mediterranean species of *Gobius*, as the only sea-fish that makes a nest and deposits its spawn therein. Olivi confirmed the statement, and describes the nest as being composed of sea-weeds (algi and zostera), adding that the male fish guards the female during the act of oviposition and the young fry during their development. †

Dr. Hancock has observed similar habits in certain fresh-water siluroid fishes of Demerara called 'Hassars,' which belong to the genus *Callichthys*: the Round-headed Hassar forms its nest of grass, the Flat-headed Hassar of leaves. "They are monogamous; both male and female remain by the side of the nest till the spawn is hatched, with as much solicitude as a hen guards her eggs, and they courageously attack any assailant. Hence the negroes frequently take them by putting their hands into the water close to the nest; on agitating which, the male *Hassar* springs furiously at them, and is thus captured." Through the kind interest of the Earl of Enniskillen, a trustee of the Hunterian Museum, a specimen of the nest with the spawn and parent fish, has been transmitted to the College and is now placed in the Hunterian series of Nidamental structures (No. 3787. B. b). ‡

\* See also xxxix. ii. p. 327.

† xxiii. t. xii. p. 6.

‡ This specimen was exhibited at the Lecture.

END OF THE SECOND VOLUME.

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