THE SKELETON OF INVERTEBRATA.

A great and fundamental distinction exists, however, between those lowly organisms known as *Protozoa* or *Hypozoa*—which are generally reckoned as animals—on the one hand and all the higher forms, both Vertebrate and Invertebrate, on the other. It is a distinction which renders it difficult to regard any skeletal structures of the *Hypozoa* as answering to, in the sense of being the homologues[1] of, any of the skeletal structures of higher animals. This great fundamental distinction consists in the fact that the bodies of all the higher animals are made up of distinct "tissues," which are derived from three different layers of cells, of which the embryos of all[2] of them are for a time composed, whereas the bodies of the *Hypozoa* either consist of but a single cell or else of a smaller or larger number of cells more or less loosely aggregated and not forming any distinct tissue. It follows of course that their reproduction does not take place by means of embryos formed of cellular layers.

Nevertheless the *Hypozoa* or *Protozoa* may exhibit very distinct protective structures. Thus the outermost layer of the substance of an *Amœba*, called its ectosarc, is of a firmer consistency than its interior, and it may in allied forms take on a chitinous character or become quite hard through the deposition within it of calcareous salts (as in the sometimes singularly complex shells of the *Foraminifera*) or form symmetrical cases of silica.

In the *Radiolaria*, the skeleton of the *Protozoa* attains its maximum of beauty and complexity. It consists of spicules which are generally siliceous, but may consist of a peculiar firm organic substance termed "acanthin." The spicules arrange themselves in an extraordinarily symmetrical manner, generally radiating from the central portion of the organism and being connected with one or more series of encircling spicules which may constitute a series of concentric spheres.

Among the *Infusoria* we also find examples of a hardening of the external cuticle, as in *Tintinus lagenula* and in some other forms.

When we pass to that vast group of animals—the *Metazoa*—which includes all but the *Protozoa* (and all those therefore the bodies of which are formed of tissues derived from the three primitive layers), a distinction again requires to be drawn between the Sponges (*Porifera*), which constitute its lowest group, and all higher forms. The three primitive or germinal layers of the *Metazoa* are termed respectively—(1) the epiblast, (2) the mesoblast, and (3) the hypoblast. Of these three layers the epiblast and the hypoblast are to be regarded as primary.[3] The epiblast is essentially the primitive integument, and its cells give rise to the epidermis and cuticle and to the organs of sense. The hypoblast is essentially the digestive layer, and gives rise to the epithelium lining the alimentary canal. The mesoblast seems to originate from one or both of the two preceding layers, and gives rise to the general substance of the body—including that part of the skin which is beneath the epidermis, the muscles, and the blood-vessels. It may divide into two layers, whereof the more external is distinguished as "somatic," while the more internal is called "splanchnic." Such is the general condition of the three germinal layers in the *Metazoa*. In the Sponges, however, it seems probable[4] that the germinal layers have a different nature—the epiblast and mesoblast being respectively the digestive and sensory layers.

The skeletal structures of the Sponges have the form of spicules, which may vary greatly in different genera as to their form, while they may be siliceous, calcareous, or horny. Sometimes they constitute structures of singular beauty. They appear to be formed in or on the cells of the mesoblast, and it does not seem that any skeletal structures arise in the epiblast or hypoblast of the *Porifera*. Should such, however, be hereafter found, then it must be borne in mind that their homologies with analogous skeletal structures of other organisms must depend on the final decision of the question of the exact relations which may exist between such germinal layers in Sponges and the epiblast and hypoblast of higher *Metazoa*.

In the great group of the *Cœlentera*, the skeleton may be either epiblastic or mesoblastic in nature. Thus in the *Hydrozoa*—where it mostly has the form of a horny investment, but may be (as in the Millepores) calcareous—it is epiblastic. In the *Actinozoa*—which includes the true coral animals—it is generally mesoblastic, although it is formed from the epiblast in the *Gorgoniæ*, *Isidinæ*, and *Pennatulidæ*.

In *Isis* the skeleton curiously consists of a series of segments which are alternately horny and calcareous.

In the *Echinodermata* we generally have, notably in the Sea-Urchin (*Echinus*), a wonderfully complex skeleton, which is so near the outer surface that at the first glance it seems necessarily a most external form of skeleton. Nevertheless the plates which compose it are mesoblastic in nature and are independent of the epidermis.

The two valves forming the shell of the Lamp-shells (*Branchionopoda*), and the very different two valves which constitute the shells of creatures of the Oyster class (*Lamellibranchiata*), as well as the single shells of the Snail and Whelk class (*Gasteropoda*), are all epiblastic in nature, and are calcifications of the outer part of the epidermis. The same is the origin of the apparently internal shell of the Slug, which is at first external in the embryo and subsequently becomes enclosed.

Similar is the nature of both the internal and external shells of the Squids, Cuttle-fishes, and Nautili, *i.e.*, of the class *Cephalopoda*. In the last-named class, as in some Gasteropods, there is a cartilaginous structure inside the head, which structure supports and partly protects the brain. It is unlike any skeletal part yet mentioned save in its mode of origin, which, like the skeleton of some of the *Actinozoa*, is mesoblastic.

Lastly may be mentioned the hard protecting external coat of insects and animals of the Crab and Lobster class—in short, the external skeleton of that primary division of animals which is called *Arthropoda*. This is again epiblastic, and a hardening of a cuticle on the outer surface of the epidermis—a hardening effected generally by chitinization (the deposition in it of a substance termed "chitin"), or, as in many *Crustacea* and some *Myriapoda*, by calcification.

GENERAL SKELETAL CONDITIONS.

Having thus briefly glanced at the leading skeletal structures of a number of groups of lower organisms, we may make the following generalization, which will be of use to us in helping us to understand how the skeletal parts of backboned animals stand related to the skeletal parts of animals lower in the scale :—

(1) Skeletal structures may conceivably arise in parts which are epiblastic, or mesoblastic, or hypoblastic.

(2) Skeletal structures belonging to any one of those three categories may be further divisible into two subordinate categories according as they belong to a superficial or a deep part of the layer to which they appertain.

(3) Skeletal structures may be siliceous, chitinous, calcareous, cartilaginous, or horny.

(4) In certain animals the mesoblast subdivides into two layers, one *somatic* and the other *splanchnic*. Obviously, then, there may be skeletal parts corresponding to either of these last-named layers, and conceivably to a deeper or more superficial portion of either of them.

THE SKELETON OF VERTEBRATA.

The skeleton of the *Vertebrata*—that is, of the five classes of animals named *Pisces*, *Amphibia*, *Reptilia*, *Aves*, and *Mammalia*—may in the first place be most conveniently considered as consisting of two parts—a dermal skeleton, or *exoskeleton*, and an internal framework, or *endoskeleton*. The latter, which is generally much the more considerable, is mesoblastic, and the muscles are external to it.

External Skeleton of Vertebrata.

This division of the skeleton is itself again made up of two parts. The more external of these is the epidermis and is of epiblastic origin, and dense epidermal structures may arise towards its inner or its outer surface. The more internal constituent of the exoskeleton is the dermis and dense structures formed in it, and these are from the outer portion of the mesoblast.

Epidermal hard structures formed towards either surface of the epidermis may become intimately united with subjacent dermal hard structures, and then again, as we shall see, with parts of the true endoskeleton.

[1] "Homologous parts," or "homologues," are parts of an organism which correspond in relative position, that is, in their relation to surrounding structures, whether or not they serve the same ends. They thus differ from "analogous parts," which are parts performing similar functions whether or not they agree as to their relations of position to surrounding structures. Thus, *e.g.*, the nail of a man's middle toe and the hind hoof of a horse are "homologous parts," but the hoof, as the support of the body and agent in locomotion, is analogous to the whole foot of a man.

[2] Certain Cœlenterate animals consist but of two layers.

[3] See F. Balfour's *Comparative Embryology*, vol. i. p. 193.

[4] *Op. cit.*, vol. i. p. 122, and vol. ii. p. 285.

Any hard structures formed in the walls of the alimentary canal—the lining of which is continuous at either end with the external skin—are to be reckoned as fundamentally exoskeletal. In the process of development the epiblast becomes inflected more or less into either extremity of the alimentary tube, but the intermediate portion, together of course with any hard structures developed in it, is of hypoblastic origin.

In the great majority of Vertebrate animals the two layers of the skin, the epidermis and the dermis are, as in man, soft, though locally provided with certain denser appendages, such as epidermal and dermal scales, hairs, nails, scutes, and teeth.

The soft, general exoskeleton or skin invests the body of Man pretty closely, though slightly projecting folds of it extend between the roots of the fingers and toes. In some abnormal cases these folds extend so far and bind the digits together so much that the thus malformed person is said to be "web-fingered" or "web-toed." Such a condition is found normally in many animals, as notably in Ducks and Geese, and such parts form a large portion of the "wing" of the Bat.

Other extensions of the skin of the body are noteworthy. Thus in the "Flying" Squirrels and Opossums, and the curious Rodent named *Anomalurus*, the skin of the sides, between the arms and the legs, is much expanded, serving for a parachute. There may be a skin parachute supported by long free movable ribs, such as we shall see exist in the little Lizards called "Flying Dragons." There may be a very remarkable extensive skin round the neck, as in the Frilled Lizard, and folds of skin may hang freely, as in the "dewlap" of Cattle, or may be formed here and there as in the Rhinoceros, the skin of which animal is so thick as to necessitate the existence of such folds to allow free movements to the body and limbs. Long filamentary processes may be formed along the back, as in the Iguana and various other Lizards.

In the Seals a fold of skin connects together the hind legs and the tail, and also in our common Bats, which have in addition their very elongated webbed fingers connected with the sides of the body and legs by another great fold of skin which, with those between the fingers, forms the entire bat's "wing."

The integument may be very distensible, as in those Fishes (*e.g.*, *Diodon*) which distend themselves with air and then float belly upwards.

The epidermis of many Vertebrates, and of Man, is shed in minute fragments, constantly removed by friction and ablution, and constantly replaced; only under abnormal conditions and after certain diseases does it come away in large and continuous patches. In some other Vertebrates, as notably in Snakes, the entire epidermal investment of the body, even that of the eyes, is cast off entire as one whole.

The epidermis never has its superficial layer connected with bone, but it often becomes thickened and horny, as we see in the sole of the foot, or the labourer's hand, and in those abnormal thickenings called "corns." Certain local thickenings which are not abnormal may exist in animals; such are the callosities on the inner side of the legs of the Horse, on the breast of the Camel, and on the nates of the lower Old-World Apes.

Of the appendages of the epidermis the most simple are scales, such as we find on the legs of Birds and the bodies of Serpents and Reptiles generally.

A *scale*—a true scale, such as those of Snakes and Lizards—consists of papillæ of the dermis invested by the epidermis, the whole being covered by a cornification of the external part of the epidermis. Scales may be very diverse in shape, prominence, and relative size, and may form very large plates. The so-called scales of Fishes are of deeper origin and are a form of scutes.

A *hair* differs from a scale in that, instead of being an epidermic investment of a dermal projection outwards, it originates by an epidermal projection inwards into the subjacent dermis. A small papilla of the dermis, however, soon projects upwards, in turn, into the descending epidermal process, and then cornification sets in (at first in the immediate vicinity of the dermal papilla) in the cells around the axis of the epidermal descending projection, and this hardened portion soon projects beyond the surface of the body, while the part of the epidermis about its deepest part becomes modified into its so-called "root."

A *nail* or *claw* arises as a cornification of the epidermis (but not of its deepest layer) lying upon numerous very vascular ridges (or transversely elongated papillæ) of the dermis, forming the primitive bed of the nail, and enclosed in a deep fold of the integument. One end of the structure becomes free and projecting superficially, while the opposite region grows by epidermal additions from beneath and at its attached extremity.

A *feather* is more nearly related to a scale than it is to a hair. It consists at first of an upwardly-projecting dermal papilla invested with epidermis, and it is only at a later stage that its base sinks into a sack or "feather follicle." The outermost layer of epidermis becomes converted into a horny sheath, which is thrown off when the feather is completed. The *quill* is formed by cornification of the deepest and more superficial layer of epidermis investing the base of the dermal and vascular papilla, and is open at both ends. The vascular papilla it encloses shrinks up when the feather is fully formed. The *vane* of the feather is formed from the more apical portion of the papilla, and its central part, or *shaft*, is continuous with the quill, while ridge-like thickenings of epidermis diverging from either side of this central part constitute the barbs of the vane, from each of which yet smaller processes or barbules proceed.

A *scute* is a hardening of the outermost portion of the dermis, with an investment from the deepest layer of the epidermis. Such are the so-called scales of ordinary Fishes, which may be represented by the bony plates and processes called placoid scales—so common in the groups of Sharks and Rays. In these latter structures dermal papillæ appear and calcify, forming a dense structure without corpuscles, called dentine, beneath which may be a corpusculated structure of true bone. The calcifying papillæ receive an investment of still denser calcareous tissue, called enamel, from the deepest layer of the epidermis. These placoid structures often come to project outwards on the surface of the body as long spines or as shorter tooth-like processes, or they may protect the surface of the body as flat plates. Often the dentine more or less entirely atrophies, so that the structure comes to be formed almost entirely of true bone or of that peculiar calcified tissue of which the scales of ordinary Fishes (such, *e.g.*, as the Perch and Carp) are composed.

A *tooth* is a structure closely related to a scute. It differs from the latter just as a hair differs from a scale—namely, by owing its origin to an ingrowth of the epidermis instead of merely to a primitive outgrowth of the dermis.

The so-called teeth of the Lamprey are not true teeth, but are merely horny epidermal structures essentially similar to scales.

In the origin of a true tooth a process of the epiblastic layer of the mouth—the buccal epithelium—grows into the subjacent dermis, and, assuming a cup-like form (with the concavity of the cup turned away from the epithelial surface of the mouth), a dermal papilla rises into the cup. The apex of this papilla then superficially calcifies into dentine, and becomes invested with a layer of enamel formed from the immediately adjacent surface of the epidermic cup or "enamel organ." An investment of connective tissue called the dental capsule becomes formed round the whole. The dentine then increases, a remnant of the papilla remaining as the "pulp." The young tooth gradually approaches the buccal surface, and the base of the papilla becomes formed into the root or fang of the tooth. The enamel organ does not descend so far, but only invests the crown of the tooth. The inner layer of the capsule, however, investing the fang gives rise to a third dental tissue known as the cement. A bud may or may not be given off from the developing tooth to serve as its future successor.

Thus teeth are normally both epiblastic and mesoblastic structures, but in certain Fishes they line parts of the throat (the branchial arches), the superficial membrane of which is derived from the hypoblast, and such may of course be considered as hypoblastic skeletal elements, and, thus considered, must be reckoned as constituting a separate category of teeth.

Such being the various kinds of dense structures which enter into the composition of the Vertebrate exoskeleton, each kind may be developed to a greater or less extent in different groups of Vertebrate animals.

Exemplifications of Epidermal Skeletal Parts.

Scales entirely clothe the bodies of most Lizards and Snakes and the legs of Birds. In Tortoises and Turtles they take the form of large plates, which in one species are known as tortoise-shell. The shape and size of scales are made great use of as distinctive characters for classification. See REPTILES. The scales of a Serpent are held together by their epidermic investment in such a way that it and they are cast off as one whole each time the animal effects that process known as changing its skin. In the Rattle-snakes curiously modified thickenings of epidermis surrounding the end of the tail are not cast off but continue partially adherent; as growth proceeds and successive castings of the skin take place, these ring-like thickenings become numerous, and so knock one against the other, when the end of the tail is vibrated, as to produce a singular sound—the so-called rattling of the system of rings or "rattle."

Hairs form the characteristic clothing of the class *Mammalia*, though certain Mammals, such as Whales and Porpoises in their adult condition, are naked. Man is quite exceptional in having the ventral surface of the body more hairy than its dorsum. Long hair on the head, and whiskers and beard, are variable human characters, also possessed by some Apes; and many animals—as the Lion, the Horse, the Aardvark, &c.—have long hair in one or other region of the body. Some hairs may be especially thickened and serve as feelers, as in the "vibrissæ" or "whiskers" of the Cat tribe. But the maximum of development is shown in such creatures as the Hedgehog and the Porcupine, where hairs become dense and solid spines.

Nails do not exist in the class of Fishes and rarely in that of Batrachians. They first make their appearance in the most simple form—that is, in the form of slight thickenings of the epidermis—at the ends of the digits in certain Toads and of one kind of Eft. A nail is at its maximum of development when it quite surrounds and encloses the last or end bone of the digit which bears it. Such nails exist in Horses, Oxen, &c., and are called hoofs. A nail when produced into a sharp point is called a claw,—as in the familiar case of the Cat, and also in Birds. Nails may, however, be much reduced in size and not nearly extend to the end of the digits which support them, as in the Sea Bears. They may be altogether wanting, even in Mammals, as in the Porpoise, or attain a prodigious relative size, so that the body can be suspended by them in progression, as in the Sloth.

Nail-like structures may be developed from the side of the hand, as in certain Birds (*e.g.*, *Palamedea*), which are said to be "spur-winged," and in a Mammal (*Ornithorhynchus*) a hollow horny spur grows upon each ankle.

In the Rhinoceros we meet with a horn, or two horns, which grow up from the dorsum of the muzzle like a great blunt nail, long dermal papillæ extending into it and answering to the dermal ridges beneath a true nail. In Owen's Chameleon no less than three long horns are developed—one from the nose and a symmetrical pair from the front of the head.

Other horns which do possess bony cores are developed from the head in pairs on the so-called hollow-horned Ruminants, *i.e.*, the Oxen, Antelopes, Goats, and Sheep; and only in one anomalous form, the Prongbok (*Antilocapra*), are these horny structures shed at intervals; in the rest they persist throughout life. Normally there is never more than one pair amidst existing Ruminants, with the exception of the Four-horned Antelope, which has two pairs. Such horns may be straight or curved or spirally twisted, but they are never branched, with the single exception of the Prongbok.

Sharp-edged, overlapping, horny plates (each of which is comparable with a nail) may be developed beneath the proximal part of the tail, as in the curious Rodent *Anomalurus*. Such plates may clothe the entire body, head, limbs, and tail, as in the scaly Manis or Pangolin.

The epidermis and epithelium which respectively line the outside and inside of the jaws may both be converted into horn, forming a small beak which may be composed of a number of close-set processes and may be temporary, as in the Tadpole, or permanent, as in the Siren. Larger and denser structures of a similar kind form the beak of Birds and of the Turtle and of that most exceptional Mammal, the Ornithorhynchus.

The epithelium within the mouth may be locally cornified, forming horny teeth which have, as before mentioned, rather the nature of scales—as in the suctorial mouth of the Lamprey.

In certain Beasts, as the Cow and the Sheep, the front edentulous part of the upper jaw is invested by a horny epithelial pad against which the teeth of the front of the lower jaw bite. A much more developed structure is met with in the Dugong. The front of both jaws is furnished with a dense horny plate formed like the horn of the Rhinoceros, though of course widely different in shape. But the maximum development of this kind of structure is found in the Whalebone Whales. The upper jaw in these is furnished with very numerous horny plates, termed *baleen*, which hang down from the palate along each side of the mouth. They thus form two longitudinal series, each plate of which is placed transversely to the long axis of the body, and all are very close together. The outer edge of each plate is entire, but its inner edge gives forth numerous hair-like processes. These are some of the constituent fibres of the horny plates which thus, as it were, fray out and line the sides of the buccal cavity with a network of countless fibres formed by the inner edges of the two series of plates. This network acts as a sort of sieve, allowing water to escape between the plates but retaining in the mouth the small creatures on which the whale feeds.

Cornifications of the tongue may exist. Thus in some Birds, as in Woodpeckers, the structure of its apical portion becomes so dense that it serves as a dart or spear. Its surface may be more or less cornified in Beasts. Thus it may be furnished all round with backwardly-pointing spines, as in the Lesser Anteater (*Tamandua*). There may be a large horny papilla on each side of it, as in the Manatee or Ornithorhynchus, or there may be horny plates on the tongue, as in the Java Porcupine.

Horny structures also exist which cannot be considered as either epiblastic or mesoblastic, but must be hypoblastic in origin. Such are the horny linings of the stomachs or gizzards of Birds, and the similar lining of the stomach of the Great Anteater, *Myrmecophaga jubata*.

Feathers are the universal and peculiar cutaneous appendages of Birds, and generally differ much in size in different parts of the body, long and strong feathers constituting the most conspicuous part of the wings and so-called "tails" of Birds. Feathers are implanted on the body neither in an irregular nor in a uniform manner, but are aggregated together in different modes in different groups of Birds—each definite patch of implanted feathers being called a feather tract. The arrangement of these tracts in a bird is called its "pterylosis," and serves amongst other characters to distinguish different groups of Birds one from another.

Exemplifications of Dermal Skeletal Parts.

Scutes.—True dermal ossifications are met with in some kinds of Mammals. Thus the Armadillos possess a very complete external *dermal* skeleton formed of small many-sided bony scutes, the margins of which are adjusted together, and which are differently aggregated—into transverse bands or into larger inflexible masses—in different species. In the extinct *Glyptodon*, the body was invested, from the neck to the root of the tail, with one such solid case.

In the Armadillos a horny *epidermal* skeleton is so adjusted to the bony case that the former is divisible into small scales corresponding with the several scutes. Amongst Reptiles, we find in the Tortoises and Turtles (*e.g.*, *Emys*, *Testudo*) a solid exoskeleton, the dorsal part of which is called the "carapace," while the ventral portion is named the "plastron." The former consists of a median series of scutes, to each side of which is annexed a series of lateral scutes which are more elongated transversely to the long axis of the animal's body, and these three series are intimately united with subjacent portions of the internal skeleton. The carapace is completed by a series of smaller scutes, which surround it and are therefore called "marginal" scutes. The plastron consists of eight pairs of scutes and one azygous scute. In the Box-Tortoises the ends of this plastron are movable, and (the head and limbs of the animal being drawn in within the shell) can be applied to the ends of the carapace, so that all the soft parts can be completely enclosed within the dense exoskeleton. As in the Armadillos, the bony scutes are covered by epidermal scales, some of which have been already referred to as constituting "tortoise shell." Unlike the Armadillos, however, the segments of the epidermal and dermal skeletons do not correspond. The dorsal scales are much larger and less numerous than are the scutes, but, while the scutes of the plastron are but nine in number, it has twelve horny plates or large scales.

Amongst the *Amphibia* certain Frogs (*e.g.*, *Ephippifer* and *Ceratophrys*) develop dorsal osseous scutes, and these, as in the Tortoises, are more or less united with parts of the subjacent internal skeleton.

A solid skeleton of juxtaposed osseous scutes may exist in Fishes, as in the Bony Pike *Lepidosteus*, where the scutes are enamelled and united by a peg-and-socket articulation. *Polypterus* also has an investment of bony scutes, and in the extinct fish *Pterichthys* they were developed into large plates on both the dorsal and ventral surfaces of the body. The Sharks and Rays may have their scutes thickly distributed over the surface of the body, but quite small. A skin so furnished is called "shagreen." They may also be larger and fewer, and placed far apart, with elegant patterns on their exposed surfaces; or they may take the form of strong defensive spines. In the Sturgeon the scutes are arranged in rows along the body, separated from each other by softer portions of integument.

In the ordinary bony Fishes, or *Teleostei*, the scutes (commonly but erroneously called "scales") are differently calcified from the scutes of Sharks, and may have their free projecting margin smooth, when they are described as *cycloid*, or in toothed-like processes, when they are termed *ctenoid*; or they may be intermediate between these two types of form. The Teleostean scutes are generally separate, but they may coalesce to form a connected

solid investment, as in *Ostracion* and the Seahorses (*Lophobranchii*), or develop strong projecting spines, as in *Diodon*.

Fishes have two other very important exoskeletal structures, which may be bony or cartilaginous. One set of these structures consists of filamentary processes, which may be either horny or calcareous, and which support the skin of the fins, whether those of the back, belly, and tail, or those of the limbs; such structures are termed "fin-rays." The other set consists of bony or cartilaginous hard parts, which serve to support the fin-rays, which therefore lie more deeply, or at least are less projecting, and are commonly termed "interspinous bones or cartilages," but which may be conveniently distinguished as *radials*; they are very important elements of the fins of Elasmobranchs.

Certain Siluroid fishes exhibit in the adjustment of portions of their dermal exoskeleton an altogether peculiar mode of articulation, called a shackle joint. This is in the form of a dermal scute articulated with a superposed spine. The scute has an osseous ring on its dorsal surface, and through this passes another osseous ring which forms part of the base of the superimposed spine.

In connexion with dermal scutes and spines may be mentioned those familiar yet exceptional structures, the bony horns of Ungulates. In the Oxen, Goats, and their allies horns exist on the head as bony cores, persisting throughout life, and supporting those "hollow horns" before noticed amongst the epidermal or epiblastic parts of the exoskeleton. As is the case with the scutes of Chelonians, these bony parts are intimately united with subjacent parts of the true endoskeleton. In the Giraffe there are three such bony prominences, which arise as distinct ossifications, and only later anchylose with the skull. These are the Giraffe's pair of short horns, together with the median prominence in front of them. In the Deer we find bony antlers, which are shed annually and are destitute of any horny covering. Antlers may exist in both sexes, as in the Reindeer, but generally they are present in the males only. They arise as soft highly vascular prominences, and when fully grown become hardened by calcareous deposit. In some months the investing skin dries up and is got rid of; and the horn itself falls off after the breeding season, leaving a stump whence a new antler shoots forth again in the following year. Antlers, as a rule, are branched—more so as the individual becomes older, till maturity is attained. Some Deer have enormous antlers, weighing as much as 70 ℔, and formed at the rate of 1 ℔ a day.

Teeth.—The differences in structure, number, form, and development of the dental organs are so great that they cannot here be treated of. See vol. vii. pp. 232 *sq.*; also vol. xv. pp. 349 *sq.*

INTERNAL SKELETON OF VERTEBRATA.

The most essential part of the Vertebrate internal skeleton is the spinal column, the foundation of which is laid by a temporary or permanent structure called the notochord or *chorda dorsalis*. At the anterior end of the spinal column there is almost always a solid structure known as the cranium or skull, to which mandibular, hyoidean, and branchial arches may or may not be attached. The spinal column may be divisible into cervical, thoracic, lumbar, sacral, and caudal portions, and may have processes projecting from it upwards, downwards, or laterally, with arches of varying extent, as neural arches, chevron bones, and ribs, together with a median ventral portion—the sternum. The whole of these parts taken together constitute the axial skeleton. This may exist alone if the body is limbless, but otherwise additional hard structures are found which together constitute the appendicular skeleton.

Vertebrate animals never have more than two pairs of limbs, and each pair is attached to the body by the help of certain skeleton elements termed a limb-girdle, diverging from which are the hard parts which constitute the skeleton of either "appendage" or "limb." In addition to these we find in Fishes certain azygous structures—the unpaired fins,—the osseous or cartilaginous supports of which must be reckoned as a part of the appendicular skeleton. With the occasional (or possibly constant) exception of the notochord, the whole Vertebrate internal skeleton is a mesoblastic structure. In the great majority of the *Vertebrata* the skeleton is more or less bony, but it always in part consists of cartilaginous and fibrous structures.

The number and nature of the solid parts vary with age in the same species. When, in the earlier stages of existence, the process of ossification has once begun, it goes on more or less rapidly till maturity is attained, and is continued, to a certain extent, throughout the whole of life.

The points at which bone formation begins and whence it radiates are termed "centres of ossification," and there may be one, two, or several of these in what is ultimately to become a single bone. Sometimes these "centres" have an important morphological significance, and in other instances they would seem to be determined by the size of the future structure.[1] Bones are classed as "cartilage bones" or "membrane bones" according as they are formed either through the previous formation of a cartilage which subsequently ossifies or directly from membrane without the intervention of cartilage. These two classes can generally be easily distinguished, but there are instances in which it would seem that what is really the same corresponding bone differs as to its mode of origin in different animals. Moreover, a compound bone, formed of a membrane bone and a cartilage bone intimately united, may come to lose either its cartilaginous or its membranous elements, and thus further difficulties of interpretation may arise. There are also cases (as in the carapace of Chelonians) in which exoskeletal dermal bones coalesce with subjacent bones of the endoskeleton. Such bones may become deeper in position as development advances, and there is reason to think that not a few bones ordinarily reckoned as parts of the endoskeleton are of dermal origin, and first appeared in ancestral forms as placoid scutes or dermal spines.

As the development of the skeleton proceeds, ossification tends to fuse together more and more bones which at their first appearance were separate and distinct. This is notably the case in warm-blooded animals, and is most noteworthy in the warmest-blooded class—that of Birds.

Besides the coalescence of distinct bones, another fusion of bony structures occurs. This is due to the fact that the ends, or projecting portions, of what are essentially and ultimately one bone may for a time persist as distinct bony parts, termed "epiphyses." Thus, in the case of Man, the ends of the long bones of the limbs are at first separate from the main part (or shaft) of each long bone, and do not become continuous with the latter till the human frame has nearly attained maturity.

The hard parts of the internal skeleton, being those which as a framework support the body, form points of attachment for the muscles which move the body,—such hard parts being used as either levers or fulcra, as the case may be. The great majority of the bones are thus intended to move one upon another. The contiguous surfaces of bones form "joints," which may be immovable, mixed, or movable. The bones of the skull are united by immovable joints, called "sutures." Joints are said to be mixed when the motion allowed is exceedingly slight, as when two bones are allowed to be slightly separated from each other by the intervention of a softer substance which is attached to both. We have examples of movable joints in the human neck, the two uppermost bones of which are articulated on the principle of a pivot; in the elbow, which forms a hinge; and in the shoulder, where the upper arm joins the shoulder-blade in a ball and socket joint.

If one convex articulating surface be globular, it is termed a head; if it be elongated, it is called a condyle. If either of these is borne upon a narrow portion of bone, this latter is called a neck; if a pulley-like surface is formed by such a juxtaposition of two condyles as to leave a depression between them, such an articular surface is named a trochlea.

The curious and exceptional arrangement termed a

[1] Balfour's *Comparative Embryology*, vol. ii. p. 448.

shackle joint has been already noticed under the head of "Scutes."

AXIAL SKELETON.

The whole axial skeleton—including both the cranium and the spinal skeleton—apart from the notochord, is formed from the mesoblastic tissue bordering the medullary groove of the embryo. As the essential part of the axial skeleton is the spinal column, so the essential foundation of this column itself is what is known as the "notochord." This is an elongated cylindrical rod of soft tissue running along the antero-posterior axis of the body immediately subjacent to the central portion of the nervous system. Its mode of origin from the germ-layers of the embryo has yet to be finally determined. It is said by Balfour[1] to be developed, in most if not all cases, as an axial differentiation of the hypoblast. The cells of the notochord form a tissue resembling cartilage, and it becomes surrounded by a more or less dense fibrous sheath. Such an organ is found to exist, temporarily or permanently, in certain lower creatures—Ascidians—which in most other respects widely differ from Vertebrate animals. Some few of these animals are furnished with a tail throughout the whole of life, while others are furnished with such an organ only in their larval or immature condition. It is alone in such permanent or temporary tail, and not in the body of Ascidians, that a structure of this kind is met with.

In every Vertebrate animal the notochord is the first part of the skeleton to appear, and it extends throughout the whole length of the body, as well as of the tail. In every such animal, except the Lancelet (*Amphioxus*), it becomes arrested anteriorly in the midst of that secondarily formed skeletal region which becomes the skull. In *Amphioxus*, however, in which no skull is ever formed, the notochord extends to quite the anterior end of the body. It is enclosed in a strong sheath, within which its substance is segmented so as to resemble a longitudinal series of coins[2] or counters. The only other representatives of the internal skeleton in this animal are—(1) longitudinal ligaments (strengthening the sheath of the notochord above and below); (2) fibrous septa which pass out laterally from it between the muscles of the body, to the fibres of which they give attachment; (3) a longitudinal membranous sheath of the central part of the nervous system, forming an elongated antero-posteriorly directed cylinder above the notochord; (4) two vertical septa,—one dorsal, ascending medianly from such neural sheath, and one ventral, descending medianly from the sheath of the notochord in the region of the tail; (5) two jointed cartilaginous filaments which lie one on each side of the longitudinal slit which serves the lancelet for a mouth; and (6) certain cartilaginous filaments which strengthen the sides of the branchial cavity between the intervening vertical fissures of the walls of that cavity.

In all other Vertebrate animals the axial skeleton is divisible into that of the head, or the cranial skeleton, and that of the axial skeleton behind the head, or the spinal skeleton.

Spinal Skeleton.

In all Vertebrate animals except the Lancelet, the axial skeleton is complicated by a longitudinal series of additional hard parts—cartilaginous or osseous—which serve to protect the spinal cord, or marrow, above it, or the great blood-vessels beneath it, and which hard parts support, encroach upon, or replace the notochord itself. Nevertheless, the notochord persists throughout the whole of life in certain Fishes both of the lowest and highest types of piscine organization, but it does not persist in its entirety in any adult Vertebrate which is not a Fish.

In the Lamprey the notochord persists, but a longitudinal series of small, similarly shaped cartilages strengthen the sides of the more anterior part of the membranous dorsal canal which encloses the spinal marrow. In the Chimæra these are more developed, while numerous circular calcifications appear in the notochordal sheath. In the most anterior part of the trunk the cartilaginous elements unite to form a continuous investment of the notochord. Amongst the Ganoid Fishes, the notochord persists unconstricted and cylindrical in the Sturgeon and the Lepidosiren, but cartilaginous or bony parts appear about it and form a longitudinal series of arches above and below it for the protection respectively of the spinal marrow and sub-vertebral blood-vessels. In different kinds of Sharks further complications arise, and the notochord becomes encroached upon, in different modes, by chondrification and calcification, till it becomes segmented by the intervention of a series of thus formed hard parts called "bodies" or "centra," between which relics of the notochord still remain. By this process of segmentation there come to be formed what are called vertebræ, the presence of which in the overwhelming majority of Fishes, as well as in all the higher classes of animals, has led to the whole group being called *Vertebrata*.

In the vertebræ of most Vertebrates we have a solid body or centrum, from the dorsum of which there arises on each of its two sides a neural plate, which then bends inwards to meet its fellow of the opposite side, thus forming an arch (the neural arch) for the protection of the spinal cord, or marrow, which passes through it. From the dorsal side of such neural arch a process called the neural spine very commonly ascends. From the sides of the centrum or neural arch, or of both, a single process, or two superimposed processes, may jut outwards, which are known as the transverse process or processes, to which the ribs are generally articulated when ribs are present. Inferiorly directed processes, single or double, may descend from beneath the centrum, or may be developed in the intervals between adjacent centra, and are generally related to the protection of large blood-vessels, though they may only serve for muscular attachment.

Adjacent vertebræ are commonly connected together by special modifications of the neural arches or the centra, or of both. Mostly the opposed margins of the neural arches develop special processes for attachment called articular processes or zygapophyses, and there may be additional interarticulations. There may be as few as ten or as many as four hundred vertebræ.

Vertebræ may be divisible, as in the highest animals, into five categories:—(1) cervical, or those of the neck; (2) dorsal, or those of the back; (3) lumbar, or those of the loins; (4) sacral, or those with which the pelvic limbs are connected; and (5) caudal, or those which are posterior to the sacral vertebræ, or which support the tail when such an organ is present. There may be only two categories (dorsal and caudal), as in Fishes.

In most Fishes and some exceptional Reptiles the body or centrum of each vertebra is so imperfectly ossified as to remain biconcave or amphicœlous,—that is to say, it presents a deeply concave cup-like form both in front and behind. The space thus enclosed by the adjoining cups of each pair of successive vertebræ is filled up by a soft, spheroidal remnant of the notochord, which thus serves as an intermediate connecting substance. The cups may become filled up by ossification, as in Man and Beasts, the flattened surfaces being connected by what are called intervertebral disks. Each such disk is made of fibrous lamellæ which surround a soft elastic central portion which is a last remnant of the notochord. Often the vertebræ may

[1] *Comparative Embryology*, vol. ii. p. 449.
[2] Owen's *Anatomy of Vertebrates*, vol. i. p. 31.

have the centrum very convex at one end and very concave at the other, and so give rise to a ball-and-socket joint at each junction between the successive centra. Such vertebræ may be procœlous (*i.e.*, have the cup in front and the ball behind), as in existing Crocodiles, or opisthocœlous (*i.e.*, with the cup behind and the ball in front), as in the Bony Pike Fish (*Lepidosteus*), the Land Salamander, and the cervical vertebræ of Ruminants; sometimes a vertebra may be biconvex (*i.e.*, have a ball at each end of its centrum), as in the first caudal vertebra of the Crocodile; or, very rarely, there may be two prominences, or the cups may exist side by side on one surface of a centrum, as in some cervical vertebræ of Chelonians. Instead of intervertebral disks, with spheroidal remnants of the notochord, adjacent vertebræ are often (as in Snakes) united by what are called synovial sacs, or membranous closed bags containing an albuminous fluid called "synovia" and commonly known as "joint-oil."

The various parts of a vertebra may be all united to form one single bone, as is generally the case in the higher animals, but such is by no means universally the case. In the Ichthyosaurus we find the neural arch permanently distinct from the centrum; and in the Carp the transverse processes are separate. The neural arch itself may be made up of two separate pieces on each side, as in some Elasmobranch Fishes, *e.g.*, *Raia* and *Spinax*.

Sometimes the neural arch, instead of reposing upon its own centrum only, appears, as it were, shifted so as to be connected with two adjacent centra, as is the case, *e.g.*, with the dorsal vertebræ of Tortoises.

Generally the nerves which pass outwards from the spinal marrow which lies in the neural canal pass out in the intervals between adjacent neural arches. Instead of this, however, they sometimes perforate the neural arch.

Neural spines, though generally single, may be double or altogether absent, and sometimes, as in Tortoises, they may intimately coalesce with superimposed dermal plates.

Cervical Vertebræ.—As has been already indicated, no vertebræ can be distinguished as cervical in the class of Fishes. Nevertheless the first three or four vertebræ next the head may, in some of these animals, present a marked difference from the succeeding vertebræ, being much elongated and united to each other by suture, as in *Fistularia* and *Bagrus*, and they may, as in the latter Fish, develop a continuous inferior vascular canal. The second and third vertebræ may form a hollow bladder-like case of bone, as in *Cobitis*, or send outwards or downwards special processes, as in the Carp.

In Amphibians only a single vertebra can be called cervical, but in Sauropsidans the number may be very large. Thus in the Swan it amounts to twenty-five, while in some of the Plesiosaurians it exceeded forty. Birds, being animals which have to perform with the beak functions which in most animals are performed by limbs, require to have a very movable neck; and consequently a considerable number of joints (and therefore of vertebræ) are required in the neck, which is the only part of the spinal column that is very flexible. In Serpents, which have the whole spinal column very flexible, no really satisfactory line can be drawn between cervical and dorsal vertebræ. In Lizards there are usually from seven to nine, but in the whole class of Mammals (whether the neck be very long, as in the Giraffe, or, like that of the Porpoise, extremely short) there are constantly but seven cervical vertebræ, except in the Sloths, which may have from nine to six, the Manatee, which has but six, and the Manis, which may have eight. All the cervical vertebræ may become anchylosed together into a single mass, as usually in the true Whales. Ordinarily in Mammals the transverse process is said to be perforated, *i.e.*, there are two such on each side, which are short and connected at their distal ends by a bony bridge which represents what, in the thorax, is known as a rib, as is shown by their condition in other classes of Vertebrates. Indeed in the lowest Mammals (*Echidna* and *Ornithorhynchus*) these osseous bridges have the form of distinct, more or less Y-shaped bones, as also in the Crocodile, where they are much prolonged. In many Lizards and Birds the posterior cervical vertebræ bear long ribs, and are only counted as cervical because such ribs do not reach the breast bone, while more posteriorly placed ribs do attain it. The two superimposed transverse processes, with the rib joining them attached to succeeding vertebræ, form on each side of the neck a sort of bony canal in which runs the vertebral artery. Sometimes, however, as in the Camels and Llamas, this canal is replaced by one excavated in the neural arches. In some Cetaceans the external bar (or rudimentary rib) is wanting, so that there come to be two elongated transverse processes on each side.

Successive cervical vertebræ may differ strikingly one from another. Thus in the common European Terrapin we find the fourth cervical vertebra with its centrum convex in front and concave behind. The centrum of the fifth is biconvex. That of the sixth is concave in front with a double convexity behind. The seventh is doubly convex both in front and behind. The eighth is doubly concave at each end. The ninth is doubly convex in front and singly so behind.

The first cervical vertebra is known as the atlas, and joins the skull, which in Man it supports. It may be fused in one solid mass with the skull, as in the Sturgeon, or with a certain number of vertebræ, as in the Rays. It may be united by suture, as in *Bagrus*. The vertebral part of the atlas may be unossified, as in the Wombat, or remain a distinct bone, as in the Thylacine. The neural spine may be detached from the neural arch, as in the Crocodile and Tunny. Its ventral part may send out a pointed process towards the head, as in *Amphiuma*. It may develop two concave surfaces to articulate with the skull, as in Amphibians and Mammals, or only a single cup, as in Sauropsidans generally.

The second cervical vertebra is known as the axis, and is distinguishable in all Vertebrates above the *Ichthyopsida*. Its centrum develops anteriorly a special peg-like or tooth-like prominence known as the odontoid process, round which the head and atlas vertebra turn as on a pivot. This process may (as in many Reptiles and in the *Ornithorhynchus* amongst Mammals) remain a distinct bone, and is regarded as the true centrum of the atlas, which thus generally coalesces into the axis vertebra instead of with the other portions of its own vertebra. The odontoid process may be absent in certain Mammals, as amongst Cetaceans.

Dorso-Lumbar Vertebræ.—The vertebræ which come between the cervical vertebræ and those (sacral) which support the pelvic limbs, or, when these latter are absent, the vertebræ between the cervical and the caudal vertebræ, form the vertebræ of the trunk. These are subdivisible into dorsal and lumbar when some of them (always the more anterior) bear ribs and others do not but have transverse processes only.

The number of trunk (or dorso-lumbar) vertebræ varies greatly, being very few in Frogs and Tortoises and very numerous in Serpents. In Mammals it ranges from about seventeen, in some Primates, to twenty-seven, in *Hyrax*. A definite number of trunk vertebræ is characteristic of certain groups of Mammals, though this number may be made up by different numbers of dorsal and lumbar vertebræ.

Dorsal Vertebræ.—Rib-bearing vertebræ are structures constantly found in all Vertebrate animals save certain Fishes and Amphibians. Dorsal vertebræ must be considered as including the whole number of trunk vertebræ in Serpents, since in those animals the whole series of the latter support ribs.

An ordinary Mammalian dorsal vertebra consists of a body and neural arch with articular processes or zygapophyses and with a more or less elongated neural spine, and a transverse process which juts out and bears an articular surface at its end. This process answers to the more dorsal of each pair of transverse processes on each side of a cervical vertebra. Another articular surface placed at about the junction of the neural arch and centrum answers to the more ventral of each pair of transverse processes on each side of a cervical vertebra.

The rib which on each side of the vertebra articulates with these two surfaces has generally itself such a surface at its proximal end (or head) and another on a more or less marked prominence called the tubercle of the rib. These are respectively designated the capitulum and tuberculum, and therefore the processes or articular surfaces of the vertebra to which the capitulum and tuberculum are respectively attached are called the capitular and tubercular processes or surfaces, as the case may be.

Sometimes each vertebra carries but one such articular surface (that for the capitulum of the ribs), as in the Dolphin. The two articular surfaces may co-exist at different levels on one single process, as in the dorsal vertebræ of the Crocodile, or they may be in close apposition, and, as it were, fused together, as in Serpents. They may, however, be supported by two quite distinct processes—one dorsal, the other ventral,—as in *Ichthyosaurus* and *Menobranchus*.

Man has twelve dorsal vertebræ. This is a little below the average of his class, where there may be twenty-four, as in the Two-toed Sloth. There are more than twelve in most Reptiles, while in Birds there are mostly but seven to nine, or, very rarely, eleven, while there may, as in *Ciconia alba*, be but three reckoned as dorsal on account of the great extent of ossification in the sacrum or part connected with the legs.

The most remarkable modification of dorsal vertebræ is that in Tortoises and Turtles, where neural spines expand at their