H. C. Stetson

M. C. Z.

TEXT-BOOK OF PALAEONTOLOGY

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OF

PALAEONTOLOGY

BY

KARL A. VON ZITTEL

PROFESSOR OF GEOLOGY AND PALAEONTOLOGY IN THE UNIVERSITY OF MUNICH

TRANSLATED AND EDITED BY

CHARLES R. EASTMAN, PH.D.

IN CHARGE OF VERTEBRATE PALAEONTOLOGY IN THE MUSEUM OF COMPARATIVE ZOOLOGY
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IN COLLABORATION WITH THE FOLLOWING SPECIALISTS:

FISHES, A. S. WOODWARD; AMPHIBIA, E. C. CASE; REPTILIA, J. B. HATCHER.
H. F. OSBORN, S. W. WILLISTON; AVES, F. A. LUCAS

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EDITOR'S PREFACE

THE present volume continues the translation of Professor VON ZITTEL'S *Grundzüge der Palaeontologie* through the Vertebrates as far as the class *Aves*, and corresponds in scope, though not in extent, to the third volume of the well-known *Handbuch* by the same author. The final volume, when published, will be devoted exclusively to the Mammalia.

The translation of the Vertebrates has been conducted on the same plan as the preceding volume, and, like it, has been appreciably enlarged. Although nearly all portions have received the benefit of expert revision, and some are of composite authorship, yet on the whole the original text has been more closely adhered to than in the case of the Invertebrates. The classification, also, departs from that of the *Grundzüge* in only a few minor particulars. The chapters on Fishes and Amphibians are chiefly in the nature of a literal translation; those on Reptiles and Birds are more modified, at least in certain parts.

Dr. ARTHUR SMITH WOODWARD, of the British Museum, is to be credited with the entire translation and revision of the class *Pisces*, on which group he is acknowledged to be the most eminent living authority. He has been careful, however, to subordinate his views on various taxonomic points to those of the Author. In the same way Dr. E. C. CASE, of the State Normal School at Milwaukee, Wisconsin, performed the principal labour of translating and revising the chapter on *Amphibia*, and assisted in the task of rendering the text on *Reptilia* into English. Owing to the untimely loss of the late Dr. GEORGE BAUR, of Chicago University, the text for the various orders of *Reptilia* failed to receive the benefit of his collaboration. It is also to be deplored that the arrangements made with Professor O. C. MARSH for the revision of the *Dinosauria* were cut short by the final passing in 1898 of this distinguished patron of Palaeontology.

Grateful acknowledgments are due to Professor H. F. OSBORN and Dr. O. P. HAY, of the American Museum of Natural History in New York, and to Mr. J. B. HATCHER, of the Carnegie Museum at Pittsburgh, for valuable notes and suggestions on the group of Reptiles, especially the order *Dinosauria*; and to Professor S. W. WILLISTON, of the State University of Kansas, for his revision of the Reptilian orders *Squamata* and *Pterosauria*, with notes on the *Plesiosauria* and *Chelonia*. To Mr. FREDERIC A. LUCAS, of the United States National Museum at Washington, was confided the task of arranging the text for the class *Aves* in its present shape, which involved the rewriting of the entire systematic and most of the general or introductory part. The balance of the present volume, in so far as it departs from the original text, owes its condition conjointly to the work of the Author and Editor.

In spite of the imperfections inevitable to a treatise produced in this manner, the hope is expressed that the subject-matter will be found more nearly up to date, and on the whole better adapted to the needs of English-speaking students than would have been the case had the Editor contented himself with bringing out a strictly literal translation. He would likewise speak a word of gratitude for the many favours and indulgences he has received at the hands of his friend and master, the Author.

CHARLES R. EASTMAN.

HARVARD UNIVERSITY,
July 1902.

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Phylum VIII. VERTEBRATA

Bilaterally symmetrical animals, with a cartilaginous or ossified vertebral axis, which is usually composed of a series of similar segments, the same supporting the central nervous system and dividing the trunk into a dorsal and a ventral portion. Never more than two pairs of limbs.

The vertebral column develops from a rod-like cellular tissue of gelatinous consistency (*chorda dorsalis*), of which the outer (skeletogenous) layer gradually subdivides into a number of similar segments, which are originally cartilaginous but subsequently calcified by the deposition of phosphate of lime or are replaced by bone substance. At the anterior end of the vertebral column is the cranial capsule enclosing the brain, also the visceral skeleton. The appendicular skeleton is likewise preformed in cartilage, and among the higher Vertebrata usually develops completely into bone substance. Only some of the lowest Vertebrata exhibit a persistently cartilaginous internal skeleton. The calcification of the cartilage in the sharks and skates takes place in such a way that a homogeneous limey substance is deposited between the cartilage cells, while in ossification the original cartilage cells disappear, and by resorption of the intercellular substance there arise canals with blood vessels (Haversian canals) as well as small hollow spaces (lacunae, bone corpuscles) filled with bone cells (osteoblasts). The latter are connected with the Haversian canals by very fine tubules (*primitivröhrchen*) radiating in all directions. In many fishes the lacunae (bone corpuscles) are wanting, so that the primitive tubules arise directly from the Haversian canals.

The skeleton of the extremities consists of several articulated segments which exhibit an extraordinarily varied arrangement according to the function of the limbs.

The nervous system consists of a central organ divided into brain and spinal chord, from which numerous nerves arise and extend throughout the whole of the body. The blood is first driven to the organs of respiration (gills or lungs) by means of a heart provided with one or two auricles, and after it has traversed the body in numerous veins it returns to the heart. The oesophagus, stomach, intestine, liver, kidneys, and spleen, as well as the organs of generation, lie in the ventral part of the body. The skin is often provided with hairs, spines, scales, feathers, or bony plates.

As a rule only remains of the bony skeleton, teeth, or hard ossified parts of the skin are available to the palaeontologist for investigation; but these can generally be determined with great certainty.

The following five classes of Vertebrates are distinguished:—*Pisces*, *Amphibia*, *Reptilia*, *Aves*, and *Mammalia*. Recently the numerous groups of *Tunicata* and *Leptocardii* have been placed with these as special classes and often regarded as the ancestors of the Vertebrates. As these have left no fossil remains in the rocks, the palaeontologist discovers no clue to the origin of the *Vertebrata*.

Class 1. PISCES. Fishes.

Cold-blooded animals living in water and usually breathing exclusively by gills. Limbs in the form of fins. Skin with scales or bony plates, rarely naked. Vertebral axis ending in a vertical caudal fin. Heart with a single ventricle and auricle. No amnion or allantois.

To the skin structures of fishes belong the scales, dermal bones, spines, fin rays, and teeth.

Scales.—Louis Agassiz distinguished four kinds of scales, to which in his system there correspond as many orders.

1. *Placoid scales* occur only among the Selachians. They are usually small rhombic plates, star-shaped, leaf-shaped, pointed, spade-shaped, or even conical structures which lie close together and form a rough mosaic (shagreen). The placoid scales are often of variable form on different parts of the body, and sometimes (*e.g.* among the rays) single tubules are conspicuous by their large size and sculpture, and appear as thick plates externally roughened or provided with spines. Placoid scales (Figs. 1-3) have the structure of teeth and consist of a basal plate (of thick phosphate of lime) penetrated by vertical bundles of connective tissue fibres sunk in the skin, and a freely projecting upper part composed of dentine and penetrated by coarser and finer little canals. All the canals arise from a cavity (pulpa, *p*) filled with connective tissue and tooth cells (odontoblasts, *o*), and subdivided outwards into continually finer branches. Besides phosphate of lime the dentine comprises small quantities of fluoride and carbonate of lime. The core of dentine is covered by a thin, shining, very hard structureless outer layer, which corresponds histologically and chemically with the enamel of

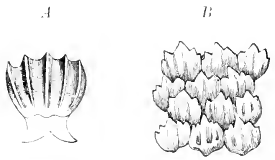


Fig. 1.

A, Scale of *Scyllium canicula*. Recent. $^{5}/_{1}$. *B*, Scales of *Carcharias* (*Prionodon*) *gangeticus*. Recent. Magnified.

Fig. 2.

Large placoid scale of *Raja antiqua*, with spine. Pliocene. Nat. size.

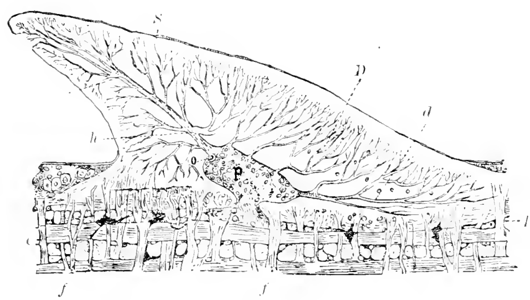


Fig. 3.

Sagittal section through a scale of *Segmnus lichia*. Recent. $^{60}/_{1}$. *B*, Basal plate. *D*, Dentine. *S*, Enamel; *c*, Cutis; *d*, Horizontal dentine canals; *f*, Bundles of connective tissue; *h*, Large principal dentine canal extending upwards; *o*, Odontoblasts; *p*, Pulp cavity (after O. Hertwig).

teeth. Placoid scales often fall out and are replaced like teeth by successional tubercles.

2. *Ganoid scales* (Figs. 4-7) attain a larger size than placoid, and usually cover the whole trunk. They are of rhombic or rounded shape, and in the latter case overlap one another like roofing tiles. Those of rhombic form are usually arranged in regular rows, and are movably articulated by a tooth-like process of the upper margin which fits into a corresponding hollow on the inner side of the adjoining scale. The exposed outer face is covered by an enamel layer (ganoine); it is usually thick and shining, sometimes dark-coloured, smooth, rugose, or ridged, and beneath it there is a basal plate consisting of bone substance and pierced by numerous canals. Among the Palaeozoic genera, indeed, the basal plate shows great complexity. The deeper layers include numerous lacunae

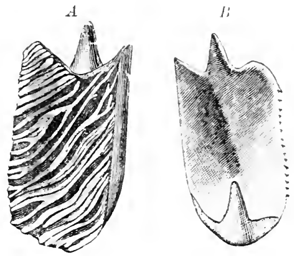


Fig. 4.
Scale of *Cosmoptychius striatus*, Ag. sp. Outer (*A*) and inner (*B*) aspects. Lower Carboniferous. $^3/_1$.

Fig. 5.
Two scales of *Polypterus bichir*, Bonap. Recent. Inner aspect. Nat. size.

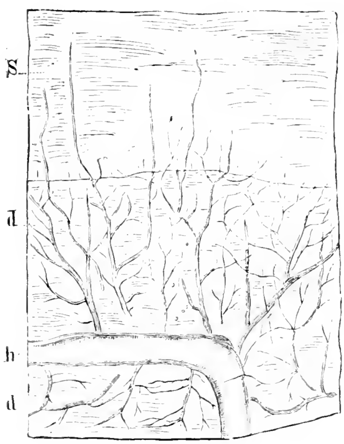


Fig. 6.
Vertical section of a scale of *Lepidosteus*. Recent. *S*, Enamel; *d*, Dentine tubules; *h*, Haversian canal. $^{300}/_1$ (after O. Hertwig).

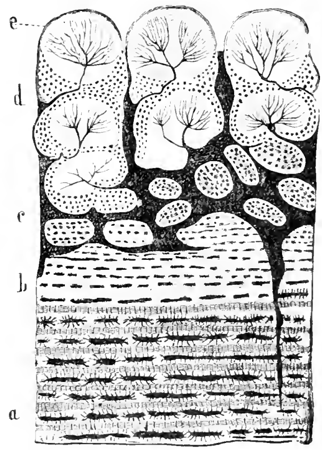


Fig. 7.
Vertical section of a scale of *Glyptolepis*, highly magnified. Devonian. *a*, *b*, Layer of vasodentine with spindle-shaped bone lacunae; *c*, Bony layer with Haversian canals; *d*, Layer with fine, branching dentine tubules (cosmine); *e*, Enamel (after Pander).

(bone corpuscles) and Haversian canals, while the upper layers as a rule are traversed only by fine dentine tubules.

3. *Cycloid and ctenoid scales* are exactly alike in general characters, being thin, elastic, and of rounded, elliptical, four-, five-, or six-sided shape. They consist of a homogeneous, transparent shining surface-layer of phosphate of lime, and of a base of connective tissue deficient in alkalies. The scales are

developed in special folds of the cutis, and generally overlap one another like roofing tiles. Cycloid scales (Fig. 8, *A-C*) generally exhibit a rounded or oval form and a simple non-serrated hinder border. In ctenoid scales (Fig. 8, *D*, *E*) there project from the hinder border small points and denticles, which are sometimes arranged in several series one behind the other, and may indeed cover a considerable part of the hinder surface and have the same structure as the superficial layer. From the so-called primitive field divergent lines radiate chiefly forwards and backwards, and sometimes also pass into reticulations; these lines being merely fissure-like interruptions in the outer layer (Fig. 9). Between the upper parallel layers of the fibrous connective tissue of the base there are often intercalated small, round, concentrically marked calcareous bodies, which are most numerous beneath the primitive field, sometimes fused with each other into a continuous layer, and here and there exhibit bone cells. Such scales are not essentially different from very thin ganoid scales.

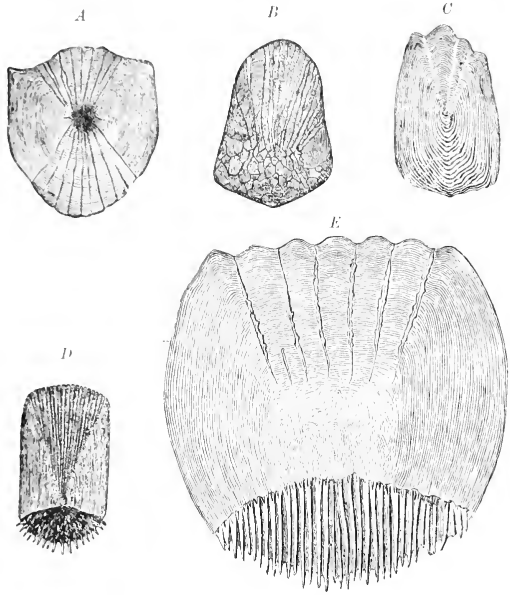


Fig. 8.
Cycloid scales of *A*, *Leuciscus*, *B*, *Mormyrus*, and *C*, *Naucrates*. Ctenoid scales of *D*, *Solea*, and *E*, *Holacanthus*. Much magnified.

The large plates, shields, spines, etc., which partly cover the body and partly the head of many fishes (*Arthrodira*, *Siluridae*, *Acipenseridae*), consist either of uniform bone substance, or, like the ganoid scales, of layers of ostaine, dentine, and enamel.

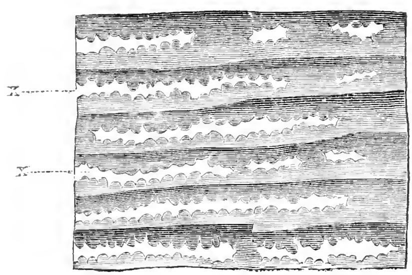


Fig. 9.
External surface of a scale of *Pleuronectes*, to show the vacuities (*x*) between the raised concentric lines. Very much magnified (after Baudelot).

Large spines (Ichthyodorulites), (Fig. 10) generally occur on the front margin of the median, and more rarely of paired fins, or on the head of cartilaginous fishes (*Selachii*). They are usually implanted loosely in the muscles by an elongated base, only exceptionally (*Chimaera*) articulated with a lower piece. Like the scales and teeth of Placoid fishes they consist either entirely of dentine or of dentine and vasodentine. Ichthyodorulites often attain a remarkable size, and occur isolated in a fossil state, while the Palaeozoic examples are sometimes characterised by a rich sculpturing.

The outer projecting parts of the fins are also to be regarded as dermal structures. They arise as folds of skin, which gradually become strengthened by numerous horny fibres (Selachii, Dipnoi). In most Ganoids and Teleosteans these fibres are replaced by bony rays, which consist of two closely apposed halves. In the Acanthopterygii (Fig. 11) each half consists of a single piece; in the Malacopterygii the rays are subdivided by transverse sutures into numerous little pieces and often branch towards the end. Spiny and articulated rays frequently occur in one and the same fin, and in this case the spines are always in front. The rays of the unpaired fins are borne as a rule on flat cartilaginous or bony supports with which they articulate (Fig. 11, *C*). These fin supports penetrate between the spinous processes of the vertebrae and are known as axonosts or (according to their position) as interneurals and interhaemals.

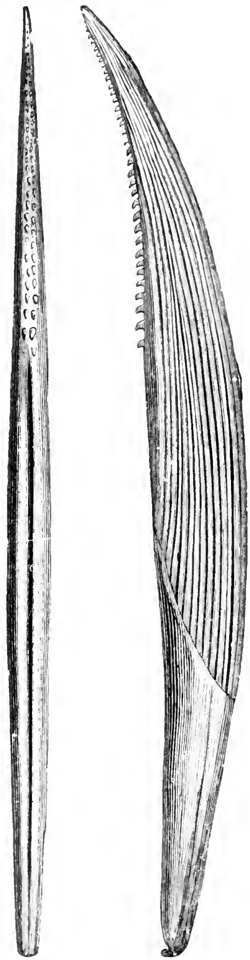


Fig. 10.

Dorsal fin spine of *Hybodus*. Upper Lias; Boll, Würtemberg.

In many Selachians (*Pristiophorus*, *Raja*) every gradation can be observed between the Placoid scales of the external skin and the teeth; and as both exhibit essentially the same histological structure, while the teeth only assume a firm connection with the head bones in the higher fishes, the teeth must indeed be regarded as dermal structures.

Among fishes all the cartilages or bones surrounding the mouth and gill cavity may bear teeth. They originate in the calcification of skin papillae, consisting of a crown which freely projects, and of a root which is surrounded with connective tissue or united with the head bones. Their form and proportions are extraordinarily variable according to their functions. All gradations exist from the minute granular denticles of the perch to the long brush-like teeth of the sheat-fish, to the robust prehensile teeth of the pike and the powerful conical or laniary teeth of *Dendrodus* or *Portheus*. Among the sharks there often occur teeth shaped like an arrow-head, flattened on one side, with or without lateral denticles. To crush the food there are sometimes obtusely conical teeth, sometimes bean-shaped, hemispherical, or pavement-like teeth, and in certain Selachii the teeth are closely pressed together into a continuous mosaic. Peculiar cutting dental plates of considerable size occur in *Diodon*, *Arthrodira*, and *Chimaera*.

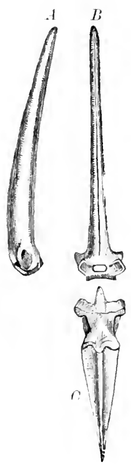


Fig. 11.

A, *B*, Rays from the dorsal fin of an Acanthopterygian. *C*, Fin support or interspinous bone.

The number of the teeth in fishes is also as varied as their shape. While the Dipnoi, Chimaeroidei, and Gymnodonts possess only four to six teeth in all, in many Sharks and Teleosteans these are numbered by hundreds.

In the young of almost all fishes the teeth are fixed to the cartilaginous or bony support by fibrous connective tissue, and in sharks and in many bony fishes this arrangement persists throughout life, so that after long maceration the teeth can easily be stripped off their base. In bony fishes and many ganoids the roots of the teeth become fused with the bone, and a socket-like elevation usually grows round the teeth. Exceptionally, teeth are also implanted in distinct sockets. The successional teeth are usually developed by the side of the functional teeth and continually push them out.

With few exceptions the crown of the tooth consists of dentine, vasodentine, and enamel, the root of vasodentine or osteodentine. The enamel forms a very thin brilliant homogeneous superficial layer, as hard as glass, and

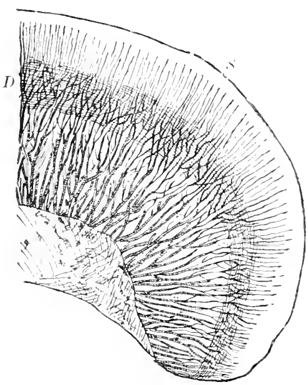


Fig. 12.

Vertical section of a tooth of *Lepidotus* (*Sphaerodus*) *gigas*, Ag. Consisting of dentine (*D*) and enamel (*S*). Upper Jurassic. Much magnified.

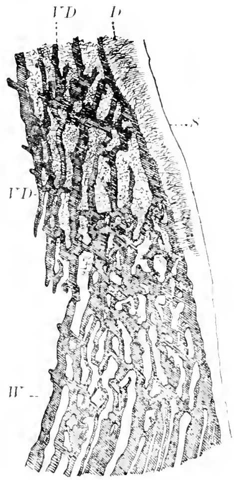


Fig. 13.

Vertical section of part of a tooth of a pike (*Esox*). Recent. *D*, Dentine. *S*, Enamel. *VD*, Vasodentine. *W*, Root of tooth. Much magnified (after Sternberg).

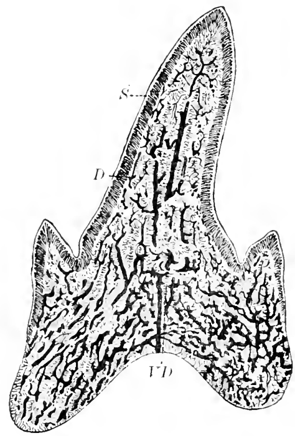


Fig. 14.

Vertical section of a tooth of *Otodus*. Eocene. *D*, Dentine. *S*, Enamel. *VD*, Vasodentine. Much magnified.

is easily recognised in polarised light by its double refraction. Very fine unbranched tubules frequently pass from the dentine into the enamel. It is composed of phosphate of lime, with a little fluoride of lime, a little carbonate of lime, phosphate of magnesia, and a very small quantity of organic matter. The dentine or tooth substance contains no fluoride of lime but much more organic matter than the enamel, is less hard, and dissolves more slowly in acids. Typical dentine (Fig. 12, *D*) is traversed by very fine outwardly branching tubules, which radiate outwards from the pulp or its branches, and contain thread-like processes of the tooth cells (odontoblasts). The dentine is also very frequently traversed by large anastomosing canals (Haversian canals), in which blood-vessels penetrate, and the walls of which are covered with odontoblasts. Fine dentine tubules then radiate in a peripheral direction from these large canals. This vascular modification of tooth substance is known as vasodentine (Figs. 13, 14, *VD*).

The root of the teeth of fishes is distinguished from the crown by the absence of an enamel layer. It consists either entirely of vasodentine, or also exhibits bone cells with radiating primitive tubules (osteodentine).

The internal skeleton of fishes shows that in the different orders of this class there persist until adult life almost all the stages of development which are only temporary among the higher Vertebrates. The whole process of the gradual segmentation, chondrification, and ossification of the vertebral column and of the rest of the skeleton is quite clear in the different groups of fishes, and the fossil forms from the Palaeozoic and Mesozoic deposits furnish the most important information in this respect.

Vertebral Column.—The first trace of the internal skeleton in all Vertebrata is confined to an elastic rod-like structure (*chorda dorsalis*) extending longitudinally on the dorsal side of the body, consisting of oil-bearing cells, and enveloped in a laminated sheath. Upon the chorda dorsalis lies the spinal chord; below it, the ventral cavity of the body.

The vertebral column persists throughout life in this primitive stage only in *Amphioxus*. The notochord, indeed, still remains unsegmented in the Cyclostomes, but the spinal chord is already protected by arch-shaped bars of cartilage developed in the sheath of the notochord (neural arches); and at the front end there is developed a cartilaginous capsule for the reception of the brain.

In all typical fishes the notochord is divided into ring-shaped segments (vertebrae), and is partly or completely cartilaginous or bony. The chondrification or ossification always arises in the outer skeletogenous layer of the notochordal sheath, and begins with the upper and lower arches.

A complete vertebra consists of a vertebral body (centrum) surrounding the notochord, two upper half-arches surrounding the neural canal (neuropophyses), and two lower half-arches (hemapophyses). The upper arches are united with a dorsal spinous process (processus spinosus, spina dorsalis, or neural spine), while the lower arches either unite in the caudal region into a ventral spinous process (spina ventralis), or remain as lower transverse processes (parapophyses).

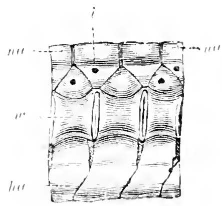


FIG. 15.

Three caudal vertebrae of *Centrophorus* in side view. *ha*, Haemal arches; *i*, Intercalary cartilages; *na*, Neural arches; *v*, Vertebral centra (after Hasse).

In many fishes provided with a cartilaginous vertebral column (Selachians and Acipenseroids), there are interposed between the upper and lower arches cartilaginous intercalary pieces (intercalaria) which sometimes exceed the arches in size (Fig. 15, *i*).

The *vertebral centra* or vertebral bodies in cartilaginous fishes usually surround a persistent remnant of the notochord, which pierces the whole of the vertebral column and partly fills the intervertebral spaces. The cartilaginous, calcified, or bony anterior and posterior faces of the vertebral bodies are deeply hollowed like double cones (amphicoelous), and thus give the centrum an hour-glass shape. In the Selachii there is usually a partial calcification, in the Ganoidei and Teleostei an ossification of the primitive cartilaginous centrum. While, however, the bony fishes generally exhibit complete ossification of the whole vertebra with all its processes, the ganoids of the Palaeozoic and Mesozoic deposits display every possible stage in the process of ossification. In completely ossified vertebrae the anterior and posterior edges of the amphicoelous centra are in close contact and also bound together by ligaments: the notochord persists only in the intervertebral spaces, and does not form a continuous thread. The arches are firmly fused with the centrum, and on the anterior margin of the upper arches there usually projects a short process (zygapophysis), which overlaps a similar posterior process of the centrum on each side, and thus strengthens the union of contiguous vertebrae (Fig. 17). In the hinder or caudal region the lower arches form a ventral spinous process (Fig. 17); in the anterior or abdominal region the lower arches project as short parapophyses, and serve as supports for the movable ribs. True transverse processes (diapophyses, processus transversi), to which the ribs are attached in the higher Vertebrata, and which arise from the upper arches, occur only exceptionally (*Polypterus*, *Pleuronectes*) besides the parapophyses. In the Cyclostomi and Chimaeras ribs are entirely absent; in the Selachii and cartilaginous ganoids they are usually feebly developed or rudimentary. The ribs of the two sides are never united with each other at the ventral border either directly or through the intervention of a sternum. The *intermuscular bones*, which arise in the membrane between the muscle plates, must not be confounded with ribs; they are delicate bony filaments, often forked at one end, which are disposed between the muscles, and rest on the vertebral centra, arches, or ribs.

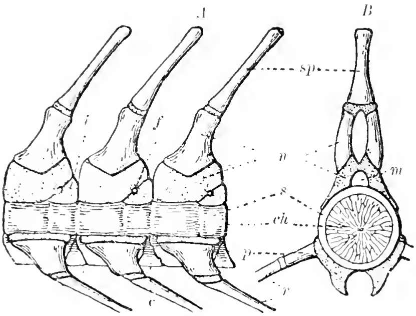


Fig. 16.

Vertebrae from the abdominal region of the Sturgeon (*Acipenser*), in side view (*A*) and in vertical transverse section (*B*). Cartilage dotted, bone white. *ch*, Notochord; *f*, Nerve foramina; *ha*, Haemal arches; *i*, Intercalary pieces; *m*, Neural canal; *n*, Neural arches; *p*, Transverse processes (parapophyses); *r*, Ribs; *s*, Sheath of notochord; *sp*, Neural spines (after R. Hertwig).

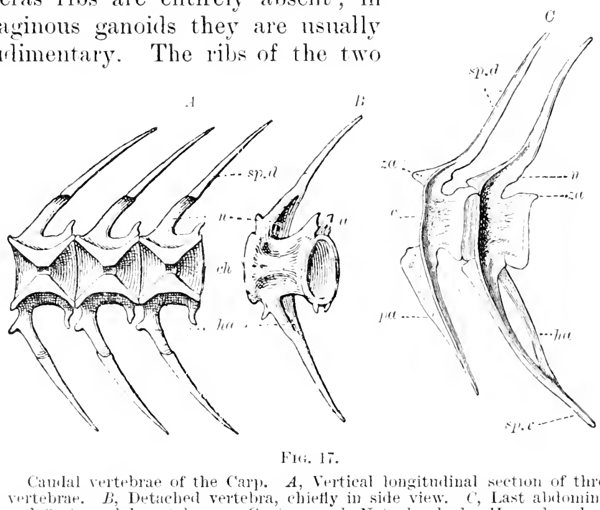


Fig. 17.

Caudal vertebrae of the Carp. *A*, Vertical longitudinal section of three vertebrae. *B*, Detached vertebra, chiefly in side view. *C*, Last abdominal and first caudal vertebra. *c*, Centrum; *ch*, Notochord; *ha*, Haemal arches; *n*, Neural arches; *sp.d*, Neural spines; *za*, Zygapophyses (after R. Hertwig).

The number of the vertebrae in fishes varies most remarkably in the different groups. In certain bony fishes (*Ostracion*) only 15 are to be counted, while in others there are 70 to 80, in the eel about 200, in many sharks from 350 to 400.

The hinder end of the vertebral column in the embryonic stage of all fishes is *diphycercal* or *heterocercal*. In the first condition the vertebral column extends in a straight line to the end of the trunk, and is symmetrically fringed above and below with the caudal fin. The Cyclostomi, Dipnoi, and many Crossopterygii (Fig. 18) remain in this embryonic stage throughout life. In the heterocercal fishes (sharks, rays, many ganoids) the end of the vertebral

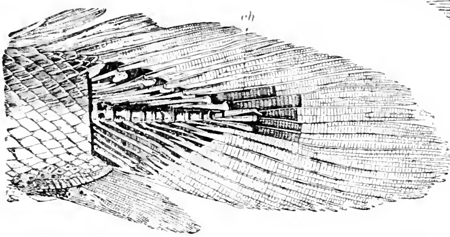


FIG. 18.

Diphycercal caudal fin of *Polypterus bichir*, Bonap. Recent. *ch*, Hinder end of vertebral column (after Kölliker).

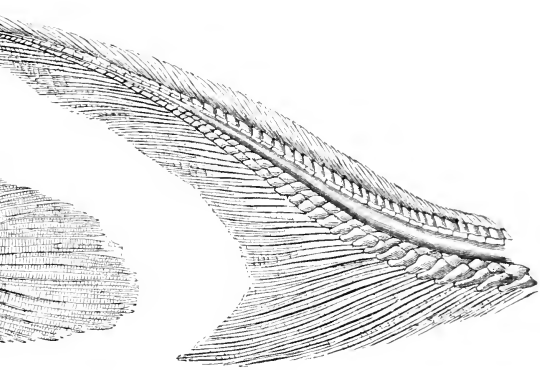


FIG. 19.

Externally and internally heterocercal caudal fin of the Sturgeon (*Acipenser*).

column is bent upwards, and completely passes into the upper lobe of the caudal fin, which is usually elongated, and exceeds the lower lobe in size (Fig. 19). Between the diphycercal and heterocercal types of tail there are many gradations. In the hetero-diphycercal tail the vertebral column is elongated in a gentle upward curve at its hinder end, and fringed above and below with

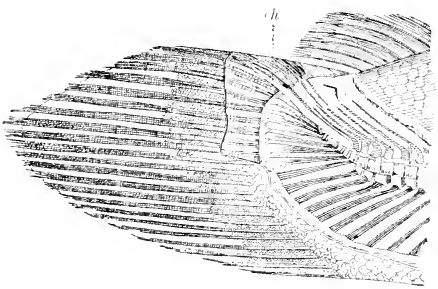


FIG. 20.

Internally heterocercal caudal fin of *Amia*, Recent. *ch*, Cartilaginous hinder end of the vertebral column, with rudiment of notochord (after Kölliker).

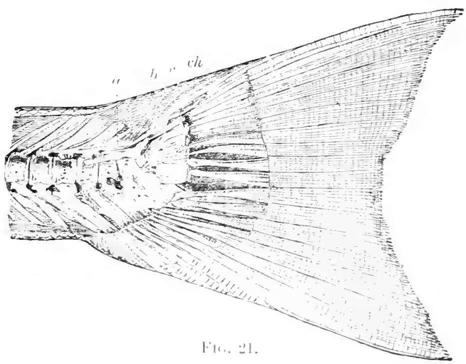


FIG. 21.

Externally homocercal (stegurous) caudal fin of the Salmon (*Salmo salar*). *a*, *b*, *c*, Upper roofing bones of the end of the notochord; *ch*, Projecting end of the notochord (after Kölliker).

fin rays; but the rays of the upper lobe are much less developed than those of the lower lobe. Sometimes also the external caudal fin consists of two similar lobes, while the vertebral column is bent upwards, and extends far into the upper lobe (Fig. 20). Such fins are externally homocercal, internally heterocercal. In the hemi-heterocercal tail the upper lobe of the externally symmetrical caudal fin is still partly or completely covered with scales.

In all cycloid and ctenoid fishes the caudal fin is externally and internally homocercal (Fig. 21). The vertebral column terminates in front of the fin with a vertebra bearing a broad, vertical, fan-shaped plate (hypural), which is formed by the fusion of several fin supports and haemapophyses. This terminal plate generally encloses a short, upwardly directed remnant of the notochord or a bony style (urostyle). There is thus an internal heterocercy as the basis of the homocercal tail.

Nearly all Palaeozoic fishes have a diphycercal or heterocercal tail; hemi-heterocercal forms begin with *Acentrophorus* in the Upper Permian, and are common in the Triassic and Jurassic. The Cretaceous, Tertiary, and Recent bony fishes, when adult, exhibit a homocercal tail; but in their immature condition there is always a diphycercal or heterocercal stage.

Skull.—The head forms the anterior end of the vertebral axis, and its skeleton exhibits a greater complexity in fishes than in the higher Vertebrates. Except

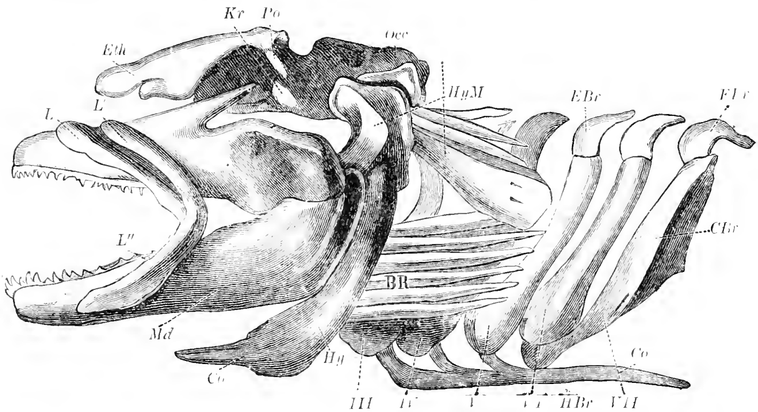


Fig. 22.

Skull and branchial apparatus of *Squatina vulgaris*, Risso. Recent. *BR*, Rays of the hyoid arch; *CBr*, Ceratobranchial; *Co*, Copula of the hyoid arch; *Co'*, Hindermost copula of the branchial arches; *EBr*, Epibranchial; *Eth*, Ethmoidal region; *Hy*, Hyoid arch; *HBr*, Hyobranchial; *HyM*, Hyomandibular; *L*, *L'*, *L''*, Anterior (premaxillary), posterior (maxillary), and inferior (premandibular) labial cartilages; *Md*, Lower jaw or mandible; *Occ*, Occipital region; *Po*, Postorbital process; *PQ*, Palatoquadrate. *III-VII*, Branchial arches (after Gegenbaur).

in *Amphioxus*, the brain is enclosed in a cartilaginous or bony capsule, the skull or cranium, which also contains the organs of hearing, sight, and smell. With the skull are connected a large number of paired cartilaginous or bony pieces, which together form the so-called visceral skeleton.

The embryonic primordial cranium of all Vertebrates is cartilaginous, and is developed like the vertebral column round the notochord, which always extends far into the base of the skull.

Among the Selachii (Fig. 22) the whole cranial skeleton is cartilaginous, and only exceptionally hardened by the deposition of phosphate of lime (Ichthyotomi). The long cranial capsule does not exhibit any sutures, and comprises in its anterior part (ethmoidal region) the olfactory nerves, in the middle (orbital region) the optic nerves and eyes, in the hinder part the organs of hearing and the hemispheres of the cerebrum and cerebellum. The visceral skeleton consists of a number of variously shaped cartilaginous arches, of which the foremost (palatoquadrate) surrounds the cleft of the mouth, and is characterised by its relatively large size. The two movable branches of the lower jaw are articulated with the palatoquadrate. Two small labial cartilages, sometimes termed maxilla and premaxilla, occur on each side in front of and below the palatoquadrate. The latter element is connected with the skull in the ethmoidal region by ligament, and in the hinder portion by the second visceral arch, of which the upper portion (hyomandibular) is in contact with the auditory region of the skull, while the lower portion forms the hyoid arch. The palatoquadrate and mandible are provided with teeth. Behind the hyoid arch there follow five (rarely seven) other visceral arches, which serve for the support of the respiratory organs, are composed of several pieces, and united ventrally by median intercalary pieces (copulae). Both the gill arches and the hyoid bear cartilaginous gill rays. In the Holocephali the palatoquadrate and hyomandibular fuse together and with the cranial capsule. The mandible thus becomes autostylic, *i.e.* articulates directly with the cranium.

In the cartilaginous ganoids (*Acipenser*, *Spatularia*), bony elements begin to take part in the formation of the head. The cranial capsule, indeed, remains for the most part cartilaginous; but externally there are a number of bony plates, which cover the cranium on the top and sides, and there is also developed below the base of the skull a long, delicate, dermal bone (parasphenoid), which extends forwards to the ethmoidal region and backwards even beyond the occiput. The palatoquadrate, hyomandibular, and mandible are also covered with bone; and the fold of skin covering the gill clefts is likewise ossified as a single gill cover (operculum). The palatoquadrate and hyomandibular form the freely movable (hyostylic) supports of the mandible.

The Dipnoi resemble the cartilaginous ganoids, except that in them the palatoquadrate and hyomandibular are fused with the cranium (autostylic).

In the scaly ganoids and bony fishes a more or less complete ossification of the cranial capsule and visceral skeleton occurs. The ossification begins first, as in the cartilaginous ganoids, with dermal bones, and then the substitution of bony substance for cartilage follows. The distinction between dermal bones and ossified cartilage (cartilage bones) can, however, only be made by determining their mode of development.

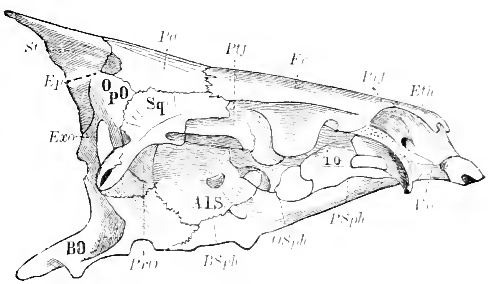


Fig. 23.

Cranium of the Carp (*Cyprinus carpio*, Linn.). *AlS*, Alisphenoid; *BO*, Basioccipital; *BSph*, Basisphenoid; *Ep*, Epiotic; *Eth*, Ethmoid; *Exo*, Exoccipital; *Fr*, Frontal; *io*, Interorbital; *Opo*, Opisthotic; *OSph*, Orbitosphenoid; *Prf*, Prefrontal; *Pro*, Proötic; *Ptf*, Postfrontal; *SO*, Supraoccipital; *Sq*, Squamosal; *Vo*, Vomer (after R. Owen).

In the cranium proper (Fig. 23) three regions are distinguishable—the occipital portion, the auditory, and the orbito-ethmoidal regions. The hindermost or occipital region consists of four cartilage bones:—(1) The lower occipital bone (occipitale basilare, basioccipital), which usually contains a persistent remnant of the notochord, and is in contact with the vertebral column with its deeply hollowed hinder end; (2, 3) a right and left lateral occipital (occipitalia lateralia, exoccipitals), which bound the greater part of the foramen magnum; and (4) an upper occipital (occipitale superius, supraoccipital), which belongs to the cranial roof, often thrust between the parietal bones, and provided with a vertical median crest.

The auditory capsules are surrounded laterally by several pairs of bones often completely covered by the facial and other membrane bones. Among them are distinguished immediately in front of the exoccipitals the opisthotic (*OpO*), the epiotic (*EpO*), adjoining the latter in its hinder upper part, and the proötic (*PrO*), which is usually pierced by the trigeminal nerve. With these bones, which form the auditory capsule proper, there is connected a bony plate on each side above and in front of the opisthotic, which originates partly from membrane, partly from cartilage, and is named the squamosal (*Sq*) or pterotic (W. K. Parker); the mandibular suspensorium (hyomandibular) articulates with its lower face.

The lateral investment of the middle orbital region of the skull, which sometimes remains cartilaginous or membranous, and is sometimes more or less completely ossified, consists externally of facial bones. Two pairs of bones can be distinguished here, posteriorly the alisphenoid placed just in front of the proötic, and anteriorly the orbitosphenoid; both pairs, but especially the orbitosphenoids, often fuse together completely in the middle line. The base of the skull is formed by a large dermal bone, the long, sword-shaped parasphenoid, which abuts behind on the basioccipital, in front on the vomer.

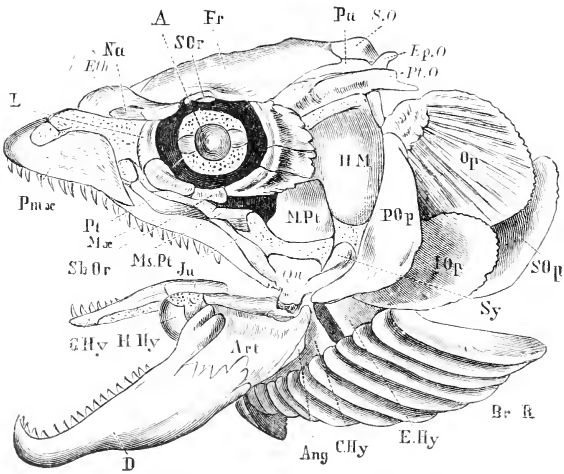


FIG. 24.

Cranial skeleton of the Salmon. The persistent cartilage of the cranium dotted; the bones developed from cartilage lettered in italics, the membrane bones in Roman type. *A*, *Eye*; Ang, Angular; *Art*, *Articular*; Br.R, Branchiostegal rays; *C.Hy*, *Ceratohyal*; D, Dentary; *E.Hy*, *Epihyal*; *Ep.O*, *Epiotic*; *Eth*, *Ethmoid*; Fr, Frontal; *G.Hy*, *Glossohyal*; *H.Hy*, *Hypohyal*; *HM*, *Hyomandibular*; IOp, Interoperculum; Ju, Jugal; L, Lachrymal; *M.Pt*, *Metapterygoid*; *Ms.Pt*, *Mesopterygoid*; Mx, Maxilla; Na, Nasal; Op, Operculum; Pa, Parietal; Pmx, Premaxilla; POp, Preoperculum; *Pt*, *Palatine*; *Pt.O*, *Pterotic* (with squamosal); *Qu*, *Quadrate*; *S.O*, *Supraoccipital*; Sb.Or, Suborbitals; SOp, Suboperculum; SOr, Supraorbital; *Sy*, *Symplectic* (after Parker).

The roof of the two hinder regions of the skull only rarely arises in cartilage; it usually consists of membrane bones, which are intimately connected with the cartilage elements. There are thus intercalated between the supraoccipital and the squamosals two parietal bones, and these are followed in front by the two frontal bones, which often fuse together into a large simple plate. By the side of the latter and in front of the squamosal there occurs the postfrontal (sphenotic, W. K. Parker), which belongs to the membrane series in the Ganoids, but is a cartilage bone in the Teleosteans. There is also occasionally a small supraorbital above the eyes.

The anterior ethmoidal region possesses as its base the vomer (*Vo*) or ploughshare bone, which also forms the anterior part of the roof of the hard palate. From the vomer on either side there slopes upwards and outwards a prefrontal bone (ethmoidale laterale, W. K. Parker), which is connected above with the frontal and with the ethmoid (*Eth*), which surrounds the nasal capsule above, in front, and partly at the side. One or more small ossifications above each nasal opening, which are sometimes fixed to the outer face of the ethmoid, are termed nasal bones or nasalia (*Na*).

To the visceral skeleton (Figs. 24, 25) belong the jaw apparatus, the facial bones, and the gill arches. The hyomandibular is in close connection with the hinder part of the palatoquadrate. Thus arises the so-called suspensorium, which, as support of the mandible, is movably connected by ligaments with the skull. The quadrate articulates below with the mandible, and is firmly fixed above with the symplectic which occurs at the lower end of the hyomandibular. From the quadrate there extends forwards the angularly bent ectopterygoid, upwards the metapterygoid, and again forwards the mesopterygoid, of which the anterior end is connected with the palatine. The latter is fixed by cartilaginous ligaments at its anterior border to the vomer and the ethmoidal region.

In front of the palatine on each side there occur two pairs of rather large bones, which are usually provided with teeth. The anterior of these, the premaxilla or intermaxilla, meets its fellow of the opposite side in a symphysis in front of the ethmoid region. The hinder bone, or maxilla, is sometimes connected with the quadrate through the intervention of a slender jugal or supramaxillary.

The lower jaw (mandibula) consists of the articular, a postero-inferior angular, which often remains cartilaginous, and the large principal piece or dentary (dentale), which usually bears teeth. On the inner side there is also a membrane bone, the splenial (or operculare), which not unfrequently bears teeth, and sometimes (as in the Crossopterygii) consists of two or more bony pieces.

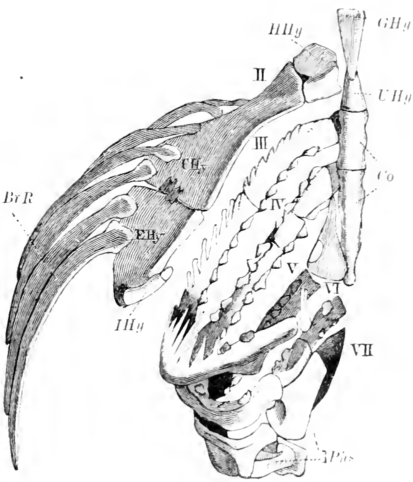


FIG. 25.

Right half of the hyoid and branchial arches of the Perch (*Perca fluviatilis*, Linn.). *BrR*, Branchiostegal rays; *Co*, Copulae of branchial arches; *EHy*, Epihyal; *GHy*, Glossohyal; *HHy*, Hypohyal; *IHy*, Interhyal; *Phs*, Upper pharyngeal bones; *UHy*, Urohyal; II, Hyoid arch; III-VI, Branchial arches (after Cuvier).

Several opercular bones arising from a fold of skin attain a remarkably great development both in the Ganoidei and Teleostei. The foremost, or preoperculum, is usually a rather long, slender, slightly arched, bony plate, which is connected above with the hyomandibular, below with the quadrate. Behind this there is an operculum, usually of relatively large size, bounded below by a suboperculum, often also by an interoperculum, which is connected with the hinder end of the mandible.

A variable number of small dermal bones or suborbitals (suborbitalia) form the arched posterior and inferior margin of the orbit. The supraorbital (*SOr*) above and the lachrymal (*L*) in front are small dermal bones, which are in close connection with the cranium, but are only rarely developed.

The gill apparatus (Fig. 25) of the Ganoidei and Teleostei does not differ essentially from that of the Selachii, except that the gill rays supported by the hyomandibular in the latter are replaced here by opercular plates, while behind the hyoid there are never more than five (rarely four) bony arches, and the branchiostegal rays of the hyoid arch become robust bony pieces or plates. The hyoid is subdivided into an upper epihyal, a middle ceratohyal, and a small hypohyal (basihyal) consisting of two pieces; the median connecting piece (copula) is extended more or less forwards into the tongue as a glossohyal, and is sometimes covered with teeth, sometimes toothless; a second segment of bone belonging to the copula, directed backwards, is named urohyal. The gill branches (branchialia) also consist each of three pieces (epi-, cerato-, and hypo-branchiale), connected in the median line with copulae, and beset throughout their entire length with delicate cartilaginous rays, sometimes also on their inner side with tooth-like prominences or spines. With the epibranchials are also connected the short upper pharyngeal bones, which often bear teeth. The last branchial arch is usually more or less modified, and forms the lower pharyngeal bones.

The limbs of fishes comprise not only the paired, but also the unpaired fins, since both function as organs of locomotion. While, however, the latter are exclusively dermal structures, the paired fins belong at least in part to the internal skeleton, and correspond with the extremities of the higher Vertebrata, the pectoral fins with the anterior, the pelvic or ventral fins with the posterior limbs.

Both the pectoral and pelvic fins are connected with originally cartilaginous arches (pectoral and pelvic girdles), which may become ossified and covered with bony plates in variable number. They are entirely absent only in *Amphioxus* and the Cyclostomi. Except in the Selachii, the pectoral girdle is usually fixed to the supraoccipital or squamosal bone. In the Selachii (Fig. 28, *A*) it forms a simple arch of cartilage, ventrally closed, situated behind the gills, its upper ends either terminating freely (sharks) or connected with the vertebral column (rays); it is bent upwards at the insertion for the fins, and pierced by nerve foramina. In many Ganoids (Chondrostei, Heterocerci, Crossopterygii) the primary cartilaginous pectoral girdle, divided into two pieces by a ventral suture, is covered on each side by three membrane bones, of which the median and largest is termed clavicula, the lower one infraclavicula, the upper one supraclavicula. The latter is sometimes divided into two pieces, of which the upper is named post-temporal. In the other Ganoids and the Teleosteans the primary pectoral girdle is entirely replaced by ossification. The girdle is here formed of two bones united by jagged suture on the postero-internal face of the very large clavicle, the hinder element homologous with the scapula, the antero-anterior element with the coracoid. In several families there is also a third, slender, arched bar (*Spangenstück* or precoracoid), extending downwards and inwards to the lower end of the clavicle.

The clavicle is always the principal bone of the pectoral girdle in the Teleostei, and its size and form vary remarkably. A supraclavicle and a post-temporal (*Pt*) rest on its upper end; while an ordinarily slender accessory dermal bone, the post-clavicle, overlaps it behind.

The pectoral fins themselves can only be homologised in part and with difficulty with the anterior extremities of the higher Vertebrata. If we accept, with Gegenbaur, the biserial fin of *Ceratodus* (Fig. 26) as the basal type most closely approaching the primitive fin (archipterygium), we observe, fixed to the mainly cartilaginous pectoral girdle, two large pieces of cartilage, followed by a long row of smaller cylindrical or square segments, from which cartilaginous rays diverge on each side. The extinct Selachian genus *Pleuracanthus* also possessed a central axis in the pectoral fin; but in all the other Selachii the cartilaginous rays are in one series. In the latter there are three large adjacent basal cartilages, the promeso-, and metapterygium, connected with the pectoral girdle, and each bears several rays consisting of pieces of cartilage (Fig. 27). The metapterygium is always the stoutest; the two others are often much reduced or may even be completely absent. The dermal part of the fin is itself always supported by numerous horny filaments in pairs.

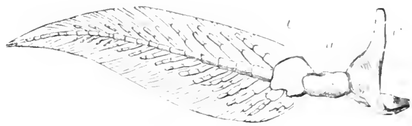


FIG. 26.

Pectoral fin of *Ceratodus forsteri*, Krefft. Recent: Queensland. *a*, Basal cartilage; *b*, Fin; *C*, Pectoral arch.

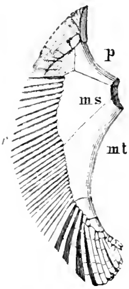


FIG. 27.

Pectoral fin of *Squatina vulgaris*, Risso. With outer dermal rays removed. *ms*, Mesopterygium; *mt*, Metapterygium; *p*, Propterygium; *r*, Radials.

In the Ganoidei, and still more in the Teleostei, the segments radiating from the basal pieces are extremely degenerate. *Polypterus* (Fig. 28, *B*) retains the three basal pieces of the Selachii, but in most of the other Ganoids the metapterygium forms almost the sole support for the fin—the meso- and propterygium are atrophied. Two or three rays, however, enter the same row as the basal pieces and are connected with the shoulder girdle.

In the same manner the base of the pectoral fin in the Teleostei (Fig. 28, *C*) consists almost invariably of four to five similar, flattened, bony pieces, with which a varying number of short little cartilages are connected. In proportion as the peripheral parts of the primary fin skeleton degenerate, ossified fin rays are developed as secondary structures on each side of the dermal fin expansion.

The so-called pelvic girdle of the hinder extremity is considerably simpler than the pectoral girdle. Among the Selachii it appears as a paired or unpaired rod pierced by nerve foramina, either lying in the longitudinal axis of the body or forming an arch, convex in front, concave behind. To this girdle are attached the two basal pieces (pro- and metapterygium) of the pelvic fin, which bear a single series of cartilaginous rays on their outer side. Among

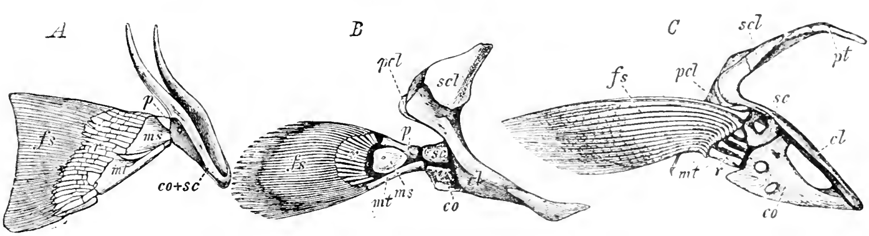


FIG. 28.

Pectoral arch and fin of *A*, *Heptanchus* (Selachii). *B*, *Polypterus* (Ganoidei). *C*, *Salmo* (Teleostei). *cl*, Clavicle; *co*, Coracoid; *fs*, Outer dermal fin rays (exoskeletal); *ms*, Mesopterygium; *mt*, Metapterygium; *p*, Propterygium; *pcl*, Postclavicle; *pt*, Post-temporal; *r*, Basal rays (endoskeletal); *sc*, Scapula; *scl*, Supraclavicle.

the Ganoids *Polypterus* alone retains two small pieces of cartilage as remnants of a pelvic girdle; in all other ganoids, as well as in the Teleostei, the pelvic girdle is completely wanting, but the metapterygium of each side attains a remarkable size, and forms the whole fin support, sometimes as a simple elongated bone, sometimes as a plate forking into two pieces. In the Ganoidei the rays belonging to the fin skeleton are occasionally bony; in the Teleostei, on the other hand, they are usually cartilaginous, much reduced, sometimes indeed completely absent. The membrane of the fin itself comprises numerous articulated bony rays. In the Dipnoi the pelvic girdle exhibits a peculiar development. It consists of an unpaired, quadrangular plate of cartilage, which is produced forwards into a long process, and supports the cartilaginous axis of the biserial fin.

While the pelvic fins of the Selachii, Ganoidei, and Dipnoi are always situated near the hinder end of the abdominal cavity, they are often displaced forwards in the Teleostei, becoming even connected with the pectoral girdle. Through this forward displacement of the pelvic fins there arise striking modifications in the general aspect of the bony fishes, which are of great importance as a means of classification.

The fossil bones of fishes can generally be recognised with certainty by their external form. Their outer surface usually exhibits a characteristic aspect, on account of numerous small rugosities, openings of canals, and striations; while tubular bones with a medullary cavity are here entirely wanting. From the histological point of view, the bones of many fishes are noteworthy for the absence or very sparse development of bone cells.

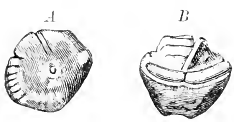


Fig. 29.

Ear bones (otoliths) of a Teleostean fish, outer (*A*), and inner (*B*), aspects. Oligocene; Lattdorf. Nat. size.

Fossil ear bones or *otoliths* (Fig. 29) are also sometimes found with the hard dermal structures and the skeleton. These do not consist of phosphate, but of carbonate of lime, and exhibit great variety in their shape, the sculpturing of their surface, and the nature of their borders.

Since the work of Aristotle, the classification of fishes has been based chiefly on the characters of the internal and external skeleton, on the nature and arrangement of the fins, and on the organs of respiration. Artedi, Bonaparte, Lacépède, Cuvier, and Valenciennes distinguished the cartilaginous fishes from those provided with a bony skeleton, and again subdivided both sections in different ways into several groups. In this classification no reference was made to fossil fishes, although sharks' teeth, for example, teeth of various bony fishes (the so-called bufonites, chelonites, toad-stones, and snakes' eyes), and also complete skeletons from different localities (*e.g.* Eisleben, Solenhofen, Oeningen, Monte Bolca, and Glarus) were already known in the eighteenth century and numbers of them had been described. The epoch-making work of L. Agassiz (1833-1844) afforded a complete survey of all the fossil fishes known at the time, and also established on scale characters a new subdivision of the fishes into four principal groups, namely, *Placoidei*, *Ganoidei*, *Cycloidei*, and *Ctenoidei*. Johannes Müller united the two latter groups under the denomination of *Teleostei* (bony fishes), defined the ganoids more precisely, and subdivided the cartilaginous fishes into four sub-classes, namely, *Leptocardii*, *Cyclostomi*, *Selachii*, and *Dipnoi*. The most important of the later changes in classification consist in the establishment of the *Leptocardii* (*Amphioxus*) and *Cyclostomi* (lampreys and hag-fishes) as independent classes equivalent to that of the fishes, and in the closer union of the ganoids and bony fishes, which are frequently grouped under the common denomination of *Teleostomi*. The class of fishes in its restricted sense thus comprises the four still-existing sub-classes of *Selachii*, *Dipnoi*, *Ganoidei*, and *Teleostei*; while to these must be added the extinct sub-classes of *Ostracodermi* (or *Ostracophori*) and *Arthrodira*, which are restricted to the Palaeozoic.

No fossil remains of *Leptocardii* are known. It must also be remarked that there is no satisfactory evidence of extinct representatives of the *Cyclostomi* or *Marsipobranchii*. Certain annelid jaws from the Palaeozoic formations, known as Conodonts, were once erroneously supposed to be teeth of this class (see vol. i. p. 255). The problematical organism from the Old Red Sandstone of Achanarras, Caithness, named *Palaeospondylus gunni*[1] by Traquair (Fig. 30), is likewise very doubtfully placed here. The largest specimens of this form do not exceed 0·05 m. in length. The skull terminates in front in a ring of calcified cirri (*d.c*, *l.c*, *v.c*), which surround a large bilaterally symmetrical orifice (*n*). Behind the skull there extends backwards a pair of elongated cartilages (*x*), usually lying in the fossil parallel with the vertebral column. There are vertebral centra in the form of broad rings; in the abdominal region these bear short and stout neural spines, but no ribs; in the caudal region the neural and haemal spines are very slender, while the former are longer than the latter and distinctly dichotomise at the distal end. There is no undoubted evidence of paired limbs.

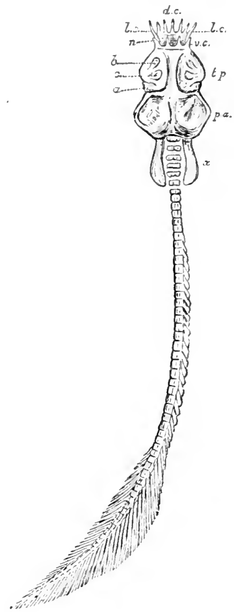


Fig. 30.

Palaeospondylus gunni, Traquair. Lower Old Red Sandstone; Caithness. *a*, Separate small lobe; *b*, Anterior depression or fenestra; *c*, Posterior depression or fenestra; *d.c*, Dorsal cirri; *l.c*, Lateral cirri; *n*, Supposed narial opening; *p.a*, Parachordal portion of skull; *t.p*, Trabeculo-palatine portion of skull; *v.c*, Ventral cirri; *x*, Problematical post-occipital plates; $^1/_3$ (after Traquair).

Sub-Class 1. SELACHII. Cuvier.

(*Elasmobranchii*, Bonap.; *Chondropterygii*, Günther; *Placoidei*, Ag.)

Endoskeleton cartilaginous; exoskeleton, when present, structurally identical with the teeth (placoid scales). Usually five (rarely six or seven) pairs of branchial arches, the clefts exposed or covered only by a flap of skin, without operculum. In the living forms—optic nerves not decussating but forming a chiasma; bulbus arteriosus of the heart with two, three or more series of valves; air-bladder absent; intestine with a spiral valve; ovaries with few large ova.

The unsegmented cartilaginous cranium of the Selachii is more or less imperfectly hardened with polygonal granules of phosphate of lime; but the vertebrae are very variously calcified, can thus be readily preserved in a fossil state, and, according to Hasse, display features of special importance for the

[1] *Dean, B.*, The Devonian "Lamprey" Palaeospondylus gunni, Traquair (Mem. N.Y. Acad. Sci. vol. II. pt. 1), 1900. Bibliography.—*Traquair, R. H.*, A still further contribution to our knowledge of Palaeospondylus (Proc. Roy. Phys. Soc. Edinb. vol. XII.), 1894.

purposes of classification. In the sharks and skates the pterygoquadrate cartilage of the upper jaw is movably suspended from the cranium, and the vertebral axis is often distinctly segmented; in the Chimaeroids (*Holocephali*) the upper jaw is fused with the cranium and the mandible articulates directly with this, while the notochord remains unsegmented, so that the vertebrae are always indicated only by the arches.

Among the sharks (*Plagiostomi*) the Notidanidae exhibit the most primitive vertebral axis (Fig. 31). Here regularly spaced thickenings of the notochordal sheath constrict the chord itself and form divisions pierced through the middle (*Diplospondyli*). The term *Cyclospondyli* is applied by Hasse to those vertebrae in which a calcified ring appears uniting the

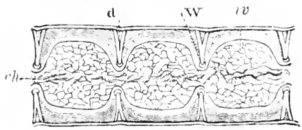


Fig. 31.

Longitudinal section of the anterior part of the vertebral column of *Heptanchus*. *ch*, Notochord; *d*, Incipient calcified double-cone (basis of centrum); *iv*, Intervertebral space filled with notochord; *w*, Constriction of notochordal sheath (after Kölliker).

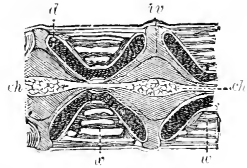


Fig. 32.

Longitudinal section of the tectospondylic vertebral column of *Squatina angelus*, Linn. *ch*, Notochord; *d*, Calcified double-cone (basis of centrum); *iv*, Intervertebral space; *w*, Vertebral centra with concentric calcified rings (after Hasse).

ordinarily calcified anterior and posterior borders of the primitive constricted centrum (Fig. 33, *A*). When additional calcified lamellae concentric with the first are developed in the intravertebral space, the *Tectospondyli* (Figs. 32, 33, *B*) are recognised; when, on the other hand, calcified plates or ridges radiate from the centre to the periphery, the vertebrae are termed asterospondylic, and the group *Asterospondyli* (Fig. 33, *C*).

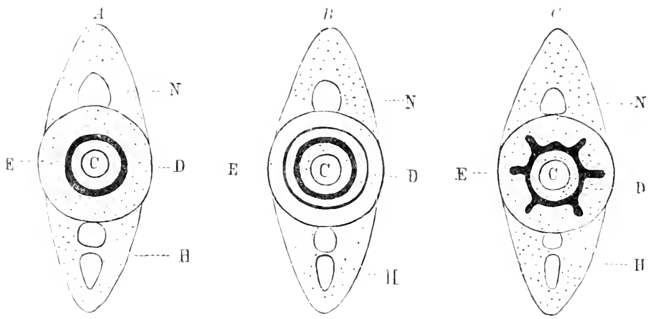


Fig. 33.

Diagrammatic vertical section through the middle of Selachian vertebrae of the *cyclospondylic* (*A*), *tectospondylic* (*B*), and *asterospondylic* (*C*) types. C, Space for notochord; D, Central calcified ring or double cone; E, Elastica externa; H, Haemal arch; N, Neural arch (after Hasse).

With the vertebrae there occur most abundantly in the fossil state teeth, fin spines, and occasionally dermal plates. Sharks' teeth are among the fossils which have been longest known, and are frequently mentioned in the older writings under the names of glossopetrae, birds' tongues, and snakes' tongues. The form of the teeth is very variable, often sharply pointed with cutting edges, single- or many-cusped, but frequently also pavement-like, with a flattened, bluntly conical crown. They consist essentially of vasodentine, dentine, and structureless enamel (ganodentine). Except perhaps in some extinct Acanthodii, they are always fixed by ligament, never fused with the supporting jaw.

Order 1. PLEUROPTERYGII. Dean.[1]

Endoskeleton well calcified. Notochord apparently not segmented. Pterygoquadrate arcade movably articulated with the cranium. Orbit surrounded with a ring of thin plates of dentine. Paired fins supported by unjointed, parallel radial cartilages, which may be partly fused at the base, but extend directly outwards to the edge of the fin membrane. Pelvic fins of male without claspers.

According to Bashford Dean and Smith Woodward, the Pleuropterygii include the most primitive known representatives of the Selachii. Their vertebral axis seems to have remained unsegmented, and in the typical genus *Cladoselache*, the tail is strongly heterocereal. Their teeth are of the form commonly known as *Cladodus* (Fig. 35) in the Carboniferous formations, and several series must have been functional at one and the same time.

Cladoselache, Dean (Fig. 34). The only well-defined genus hitherto discovered. The form is elongated and round-bodied, with a short blunt snout and

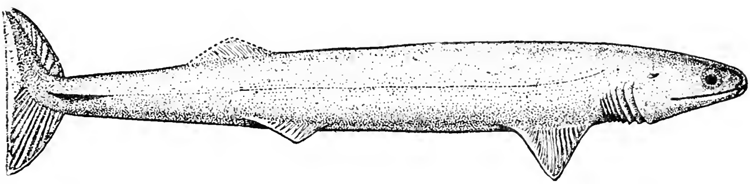


Fig. 34.
Restoration of *Cladoselache newberryi*, Dean. Cleveland Shale (Upper Devonian); Ohio. An anterior dorsal fin has been discovered since this illustration was made (after Dean).

forwardly placed eye. Circumorbital ring consisting of several series of thin, irregularly quadrangular small plates. Mouth terminal, and hyomandibular cartilage slender. Teeth largest, longest, and most acutely pointed at the symphysis of the jaw, smallest and shortest at the angle of the mouth. Each tooth with one principal cusp and a variable number of lateral cusps, fixed on the anterior border of a horizontally expanded base; the base of each tooth overlapped by its successor behind. Paired fins lappet-like, the pelvic pair with somewhat extended base line. Two low dorsal fins, without spine. Anal fin not yet observed. A short dermal expansion forming a horizontal keel on each side of the caudal pedicle just in advance of the strongly heterocercal caudal fin. Skin more or less armoured with minute lozenge-shaped denticles, which are apparently not enamelled. *C. kepleri*, *C. fyleri*, and other species sometimes two metres in length, from the Cleveland Shale of Ohio.

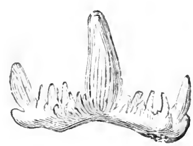


Fig. 35.
Cladodus striatus, Ag. Tooth, natural size. Carboniferous Limestone; Armagh, Ireland (after Davis).

The teeth termed *Cladodus* (Fig. 35) occur isolated in the Lower Carboniferous of England, Scotland, Ireland, Belgium, Russia, India, and North America. They are also recorded from the Upper Carboniferous both of Europe and North America, but it is difficult to distinguish them from those of the genus *Sphenacanthus* (p. 27). It is possible, however, that these teeth do

[1] *Dean, Bashford*, Contributions to the Morphology of *Cladoselache* (Journ. Morphol. vol. IX.). 1894.—A new Cladodont from the Ohio Waverly Trans. New York Acad. Sci. vol. XIII.), 1894. —The Finfold Origin of the Paired Limbs (Anat. Anz. vol. XI. No. 22), 1896.

not all belong to the Pleuropterygii. *Cladodus neilsoni*, from the Calciferous Sandstones of East Kilbride, Lanarkshire, is known by the imperfect head associated with a very remarkable pair of pectoral fins (Traquair, *Trans. Geol. Soc., Glasgow*, vol. xi. 1897, p. 41).

The genera *Dicentrodus*, Traquair; *Phoebodus*, *Lambdodus*, *Hybocladodus*, St. John and Worthen; *Dicrenodus*, Romanowsky (*Carcharopsis*, Ag.; *Pristicladodus*, M'Coy), are founded on detached teeth, mostly from the Carboniferous Limestone, of uncertain affinities. *Protodus*, Smith Woodward, founded on teeth from the Lower Devonian of Canada and Scotland, may also be mentioned as a possible Pleuropterygian.

Order 2. ACANTHODII. Agassiz.[1]

Endoskeleton well calcified, with dermal and membrane calcifications in the region of the skull and pectoral arch. Pterygoquadrate arcade movably articulated with the cranium. Orbit surrounded with a ring of thin plates of dentine. Teeth, when present, firmly fixed to the calcified sheathing plates of the pterygoquadrate and mandibular cartilages. Endoskeletal cartilages of all the fins much reduced, and the dermal expansion almost or completely destitute of rays; each of the fins except the caudal with a robust anterior spine implanted in the flesh. Pelvic fins of male without claspers. Dermal armature of trunk consisting of small, closely arranged, quadrate granules, which also extend over the greater portion of the fins; lateral line passing between two series of the granules.

Two families of this order are distinguished, the Acanthodidae with one dorsal fin, and the Diplacanthidae with two dorsal fins. These fishes were originally assigned to the Ganoidei by Agassiz, but their close relationships to the Selachii were observed by Lütken, Fritsch, and Huxley. While, however, they were arranged by Lütken and Fritsch among the Selachii, they were regarded by Huxley as intermediate between the Ganoidei and Selachii. Later researches by Traquair, Smith Woodward, and Reis seem to have justified the reference of the order to the Selachii.

The Acanthodii comprise not only a number of more or less completely known genera from the Devonian, Carboniferous, and Permian formations, but also a few genera which are still represented only by isolated fin spines (*Haplacanthus*, Ag.; *Homacanthus*, Ag.; *Gyracanthus*, Ag.; and *Machaeracanthus*, Newberry). The close resemblance between the spines of *Climatius* and the Ichthyodorulites named *Onchus* suggests that at least some of the latter, which range throughout the Upper Silurian and Lower Devonian, also belong to Acanthodians.

Family 1. Acanthodidae. Smith Woodward.

A single dorsal fin. Free spines between paired fins usually absent, sometimes represented by one rudimentary pair. Lower Devonian to Lower Permian.

[1] *Fritsch, A.*, Fauna der Gaskohle in Böhmen, vol. II. Prague, 1889.—*Huxley, T. H.*, Preliminary Essay upon the Systematic Arrangement of the Fishes of the Devonian Epoch (Mem. Geol. Surv. dec. x.), 1861.—*Kner, R.*, Sitzungsb. k. Akad. Wiss. Wien, Math.-naturw. Cl. vol. LVII. p. 290, 1868.—*Powrie, J.*, On the earliest known Vestiges of Vertebrate Life (Trans. Edinb. Geol. Soc. vol. IX.), 1869.—*Roemer, F.*, Ueber *Acanthodes gracilis* (Zeitschr. deutsch. geol. Ges. vol. IX.), 1857.—*Reis, O.*, Zur Kenntniss des Skelets der Acanthodinen (Geogn. Jahreshefte, München), 1890 and 1894.—*Traquair, R. H.*, Geol. Mag. 1888, p. 511, and 1889, p. 17.

Mesacanthus, Traquair (Fig. 36). A gracefully fusiform fish with slender spines. Circumorbital ring of four plates. Pelvic fins not much smaller than the pectorals, about midway between these and the anal; a pair of minute spines between the paired fins. Dorsal fin more or less opposed to the anal, but not in advance of it. *Mesacanthus mitchelli*, Egert. sp. (Fig. 36); *M. peachi*, Egert. sp.; and *M. pusillus*, Ag. sp., from the Lower Old Red Sandstone of Scotland. *M. affinis*, Whiteaves sp., an equally small species from the Upper Devonian of Scaumenac Bay, Province of Quebec, Canada.

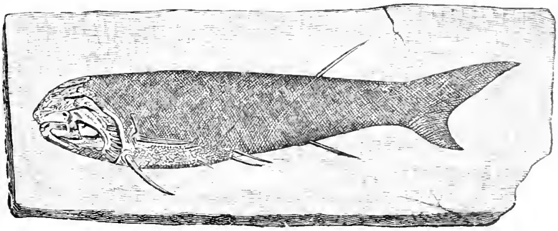


FIG. 36.
Mesacanthus mitchelli, Eg. sp. Lower Old Red Sandstone; Farnell, Forfarshire. Nat. size (after Egerton).

Acanthodes, Ag. (*Acanthoessus*, Ag.; *Holacanthodes*, Beyr.; *Traquairia*, Fritsch), (Figs. 37, 38). A more elongated fish with similarly remote dorsal fin, but the pelvic fins relatively small and advanced forwards, the pectorals larger, and intermediate spines absent. Teeth minute or absent; circumorbital ring of four more or less sculptured plates. Pectoral fin spine supported by a hollow, mesially constricted element (Fig. 37, *b*), which abuts against the side of its proximal end; a close series of short, fine dermal rays (*r*) sometimes appearing below this in the fin-membrane. Scales smooth. Ranging throughout the Carboniferous in Scotland, the Coal Measures in England and North America, and the Lower Permian in France, Germany, Bohemia, and Siberia. *A. bronni*, Ag., the typical species, about 0·3 m. in length, from the Rothliegende of Rhenish Prussia (Lebach and Saarbrücken). *A. gracilis*, Beyr. (Fig. 38), from Klein Neundorf, Silesia, probably identical with the latter. *A. wardi*, Egert., from Coal Measures, Longton, Staffordshire.

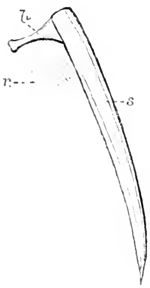


FIG. 37.
Acanthodes wardi, Eg. Skeletal parts of pectoral fin, nat. size. Coal Measures; England. *b*, Hollow basal element; *r*, Dermal rays; *s*, Dermal spine forming anterior border of fin (after Smith Woodward).

Cheiracanthus, Ag. Like *Acanthodes*, but dorsal fin arising in advance of anal, and scales sculptured. *C. murchisoni*, Ag., and other species from Lower Old Red Sandstone, Scotland.

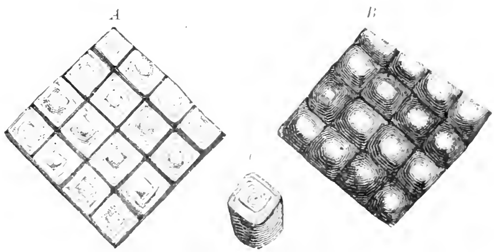


FIG. 38.
Acanthodes gracilis, Beyr. Scales from the outer (*A*, *C*) and inner (*B*) aspects, much enlarged. Lower Permian; Germany.

Acanthodopsis, Hancock and Atthey. Jaws with few large, laterally compressed, triangular teeth. *A. wardi*, H. and A., from Coal Measures of Northumberland and Midlothian.

Family 2. **Diplacanthidae.** Smith Woodward.

Two dorsal fins. Free spines between paired fins conspicuous. Upper Silurian to Upper Devonian.

Diplacanthus, Ag. (*Rhadinacanthus*, Traquair). Trunk fusiform, probably not much laterally compressed. Teeth minute or absent; orbit with ring of four circumorbital plates. Pectoral fins large, and a median pair of stout spines fixed between these to the well-developed basal supports; a single pair of free spines between the pectoral and pelvic fins. *D. striatus*, Ag., about 0·1 m. in length, and other species from the Lower Old Red Sandstone of Scotland. *D. horridus*, Smith Woodward, from Upper Devonian, Scaumenac Bay, Canada.

Ischnacanthus, Powrie (*Ictinocephalus*, Page). Much resembling *Diplacanthus*, but the inner pectoral spines wanting, and the jaws provided with a powerful dentition. A few large, smooth, conical teeth alternating with minute cusps. Scales smooth. *I. gracilis*, Egert. sp., from Lower Old Red Sandstone, Turin Hill, Forfarshire.

Climatius, Ag. (*Brachyacanthus*, Egert.), (Fig. 39). Trunk fusiform and laterally compressed. Teeth minute or absent; orbit with ring of four circumorbital plates. Fin spines remarkably broad and marked with coarse longitudinal ridges, sometimes with posterior denticles. Pectoral fins not much larger than the pelvic pair; three or four pairs of free spines, resembling the fin spines, between the paired fins. *C. reticulatus*, Ag., and *C. scutiger*, Egert. (Fig. 39), are known by nearly complete fishes from the Lower Old Red Sandstone of Forfarshire. Similar spines occur in the Passage Beds (Downtonian) of Herefordshire, and in the Lower Devonian of Campbellton, New Brunswick.

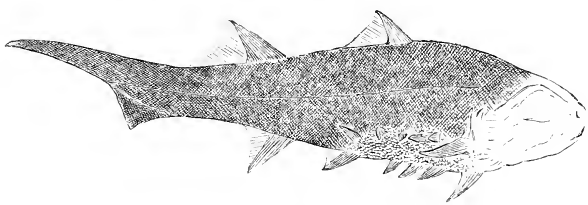


Fig. 39.
Climatius scutiger, Egerton. Lower Old Red Sandstone; Forfarshire. Nat. size (after Powrie).

Euthacanthus, Powrie. Essentially identical with *Climatius*, but with narrower straight spines. Lower Old Red Sandstone, Forfarshire.

Parexus, Ag. Much resembling *Climatius*, but the anterior dorsal spine enormously elongated and with large posterior denticles. *P. incurvus*, Ag., and *P. falcatus*, Powrie, from Lower Old Red Sandstone, Forfarshire.

Order 3. ICHTHYOTOMI. Cope.[1]

(*Proselachii*, Döderlein.)

Endoskeleton well calcified, but no membrane calcifications. Pterygoquadrate arcade movably articulated with the cranium. No circumorbital plates. Neural and haemal

[1] *Beyrich*, *E.*, Monatsb. Berlin Akad. 1848, pp. 24-33.—*Brongniart*, *C.*, Bull. Soc. Industrie Min. (Saint Etienne), ser. 3, vol. II. livr. 4, 1888.—*Cope*, *E. D.*, Proc. Amer. Phil. Soc. 1884, p. 572.—*Davis*, *J. W.*, On the fossil Fish-remains of the Coal Measures in the British Islands. I. Pleuracanthidae (Trans. Roy. Dublin Soc. ser. 2, vol. XII.), 1889.—*Döderlein*, *L.*, Zool. Anzeig. vol.

arches of vertebral axis long and slender. Pectoral fins with long, segmented axis from which smaller cartilages diverge on either side ; pelvic fins of male with appended clasper ; caudal fin diphycercal.

Family 1. **Pleuracanthidae.** Cope.

Body slender, but slightly depressed ; mouth terminal. Teeth with two principal divergent cusps. Branchial arches provided with clusters of minute denticles. Dorsal fin elongate, low, continuous along the back from a point shortly behind the head ; slender fin supports more numerous than the neural spines. Lower Carboniferous probably to Upper Triassic.

The Pleuracanthidae occur in the coal-bearing strata of the Carboniferous system and in the Lower Permian of Europe and North America. One species is also known by a nearly complete skeleton from the Hawkesbury Formation of New South Wales. For the isolated teeth of *Pleuracanthus* various generic names have been proposed, e.g. *Diplodus, Ochlodus, Aganodus, Pternodus, Triodus, Thrinacodus* ; for isolated spines, the generic names *Compsa-*

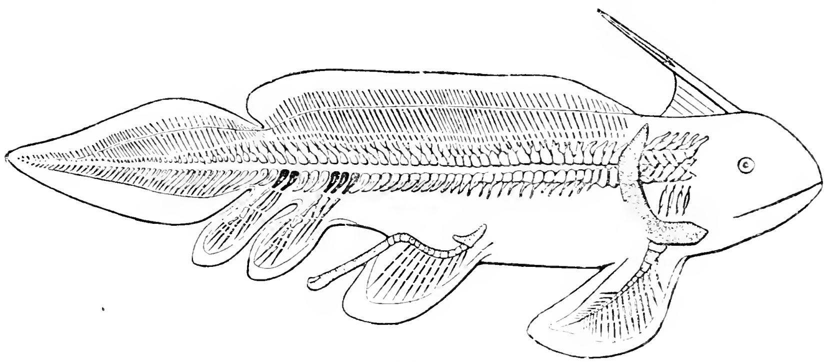


Fig. 40.

Restoration of *Pleuracanthus gaudryi*, Brongn. Coal Measures ; Commentry, Allier (after C. Brongniart).

canthus, Orthacanthus, and *Lophacanthus* : for the clustered denticles of the branchial arches, the name *Stemmatias* (*Stemmatodus*).

Pleuracanthus, Ag. (*Xenacanthus*, Beyrich ; ? *Didymodus*, Cope), (Figs. 40-43). Head broad, semicircular in front, and provided behind with a long, slender dermal spine, which is hollow, either rounded in section or antero-posteriorly compressed, and bears a double longitudinal series of recurved denticles (Fig. 42). Teeth (Fig. 43) with two large divergent cusps fixed on a stout common base, and frequently a small third cusp between these. Five branchial clefts laterally placed in advance of the stout and broad, arched pectoral girdle, of which the two halves are fused ventrally but separated dorsally. Pectoral fins large, articulated with the postero-inferior angle of the pectoral girdle, and consisting of a segmented axis fringed on either side by cartilaginous rays. Pelvic supports in the form of a pair of separate triangular cartilages ; basi-

II. 1889, p. 123.—*Fritsch, A.*, Fauna der Gaskohle, vol. II. Prague, 1888-89.—*Goldfuss, A.*, Neues Jahrb. 1847, p. 404, and Beiträge zur vorweltlichen Fauna des Steinkohlengebirges, p. 23, pl. v. Figs. 9, 10.—*Kner, R.*, Sitzungsb. k. Akad. Wiss. Wien, math.-naturw. Cl. vol. 551, 1867, p. 540, with 10 plates.—*Koken, E.*, Sitzungsb. Ges. naturf. Freunde, Berlin, 1889, p. 77.

pterygium of pelvic fins segmented, fringed on one side with a series of cartilaginous rays, and continued behind into the spine-shaped clasper in the male. Two small anal fins, directly supported by the haemal arches. Caudal fin

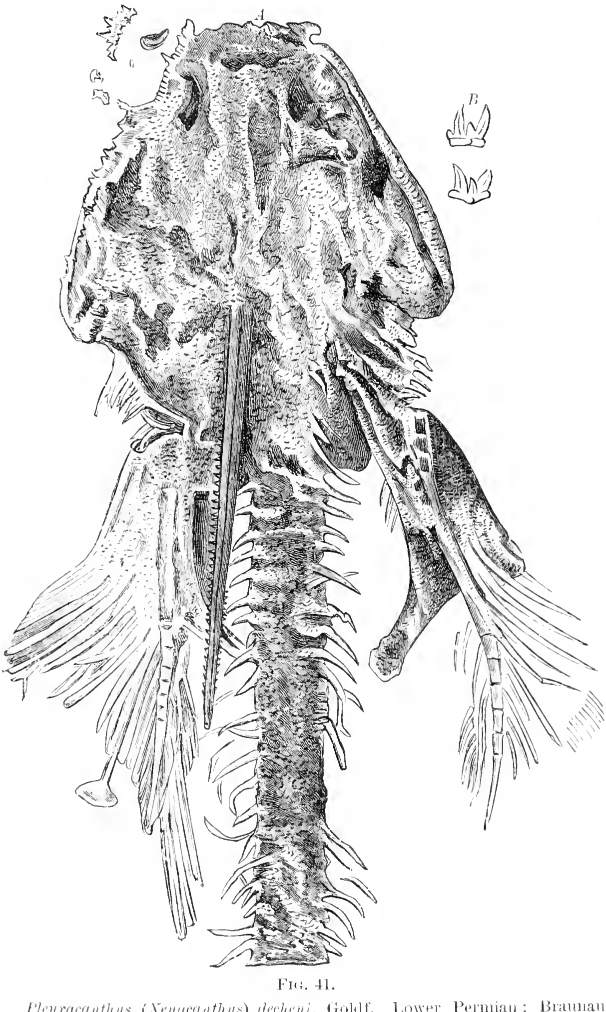


Fig. 41.

Pleuracanthus (*Xenacanthus*) *decheni*, Goldf. Lower Permian; Braunau, Bohemia. × 1/2. *A*, Anterior portion of fish. *B*, Detached teeth, magnified (after F. Roemer).

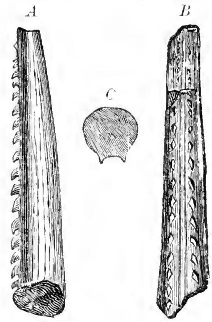


Fig. 42.

Pleuracanthus (*Orthacanthus*) *bohemicus*, Fritsch. Lower Permian (Gas-Coal); Krotschow, Bohemia. *A*, Side view. *B*, Hinder view. *C*, Transverse section. Natural size.

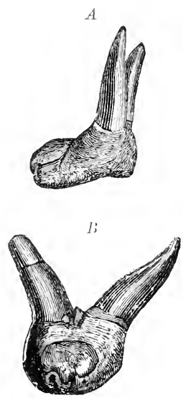


Fig. 43.[1]

Pleuracanthus (*Diplodus*) *bohemicus*, Quenst. Teeth in side view (*A*), and hinder view (*B*). Lower Permian (Gas-Coal); Nyřan, near Pilsen, Bohemia. Natural size.

separated both from the anals and from the dorsal. Skin probably destitute of shagreen.

Complete skeletons are known from the Rothliegenden of Lebach, near Saarbrucken, in Rhenish Prussia, and of Braunau and Ruppersdorf in Bohemia; from the Lower Permian Gas-Coal of Bohemia; from the Coal Measures of Commentry in France (Fig. 40); and from the Lower Hawkesbury Formation of New South Wales. Complete skulls have been found in the Coal Measures of Northumberland and in the Permian of Texas (*Didymodus*). Isolated teeth and spines are very abundant in the Carboniferous and Permian.

Anodontacanthus, Davis. Dorsal spines without denticles. Carboniferous; England and Scotland.

Order 4. PLAGIOSTOMI. Duméril. Sharks and Rays.[1]

Endoskeleton more or less calcified, but no membrane calcifications. Pterygoquadrate arcade movably articulated with the cranium. Vertebral axis segmented. Paired fins with two or three short basal cartilages; pelvic fins of male with appended claspers.

According to the condition of their vertebral column, the Plagiostomi have been divided by Hasse into the four sub-orders of *Diplospondyli*, *Cyclospondyli*, *Asterospondyli*, and *Tectospondyli*.

Sub-Order A. DIPLOSPONDYLI. Hasse.

Notochord imperfectly segmented by vertical partitions. Gill clefts six or seven in number on each side. Teeth numerous, in several series. Upper Jurassic to Recent.

Family 1. Notidanidae.

Body fusiform, with a single unarmed dorsal and anal fin, and a large heterocercal caudal fin. Teeth with two or more sharply-pointed cusps. Upper Jurassic to Recent.

Notidanus, Cuv. (*Hexanchus*, *Heptanchus*, Müller and Henle), (Figs. 44, 45). Principal teeth consisting of a series of compressed cusps fixed upon a long base; all the cusps inclined in one direction, the anterior larger than the others, with or without small denticles at its base in front. Anterior teeth of the upper jaw clustered, awl-shaped; a median symphysial series in the lower jaw. Principal teeth of the upper jaw less laterally elongated, with fewer cusps than those of the lower jaw. Range from Upper Jurassic to present day. *N. muensteri*, Ag., represented by a complete skeleton from the Lithographic Stone (Lower Kimmeridgian) of Solenhofen,

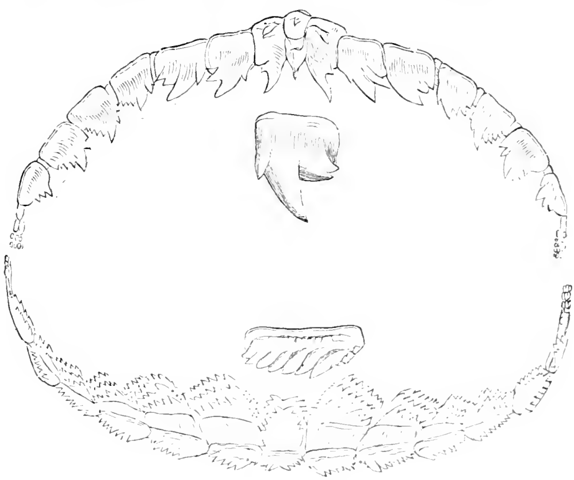


Fig. 44.
Dentition of the Recent Indian Grey Shark. *Notidanus (Heptanchus) indicus.*

[1] *Bonaparte, C. L.*, Selachorum tabula analytica (Mém. Soc. Sci. Nat. Neufchatel). 1839.—*Davis, J. W.*, On the Fossil Fishes of the Carboniferous Limestone Series of Great Britain (Trans. Roy. Dublin Soc. ser. 2, vol. I.), 1883.—*Hasse, C.*, Das natürliche System der Elasmobranchier auf

Bavaria, and *N. gracilis*, Davis, by a smaller skeleton from the Upper Cretaceous of Sahel Alma, Mount Lebanon. Detached teeth from the Oxford Clay of England and Corallian of Würtemberg; from the Chalk of England (*N. microdon*, Ag.) and the Cretaceous of New Zealand (*N. dentatus*, Sm. Woodw.); and numerous species from Tertiary formations (e.g. *N. primigenius*, Ag., Fig. 45).

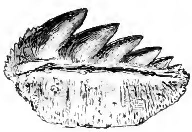


Fig. 45.
Notidanus primigenius, Ag. Lower tooth. Oligocene: Weinheim, Hesse Darmstadt. Natural size.

Chlamydoselache, Garman. Teeth with broad, backwardly extended base, and the crown consisting of three slender, curved, subconical cusps, which are separated by a pair of rudimentary denticles. Wide distribution in existing deep sea. Isolated teeth in Pliocene of Tuscany (*C. lawleyi*, Davis).

Sub-Order B. CYCLOSPONDYLI. Hasse.

Vertebral centra in form of simple constricted cylinders pierced by the notochord. Teeth numerous, triangular, and acuminate, simple or with small lateral cusps. Rare in the fossil state; Upper Cretaceous to Recent.

Family 1. **Spinacidae**. Müller and Henle. Spiny dog-fishes.

Body fusiform to trihedral, somewhat depressed. Mouth gently arched; snout obtuse. Gill clefts small, lateral; spiracles large, behind the eye. Pectoral fins not notched at their origin and not produced forwards; the two dorsal fins often armed with a spine; anal fin absent. Upper Cretaceous to Recent.

Centrophorus, Müller and Henle (Fig. 46). Dorsal fin spines present. Upper teeth erect, triangular, or narrow lanceolate, with a single cusp; lower teeth triangular and compressed, with the apex much turned aside. Upper Cretaceous, Sahel Alma, Mount Lebanon (*Spinax primaevus*, Pictet). Recent.

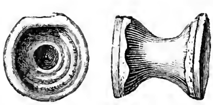


Fig. 46.
Vertebra (central double-cone) of *Centrophorus*. Upper Cretaceous: Maastricht (after Hasse).

Fig. 47.
Acanthias radicans, Probst. Tooth, × 2. Miocene (Molasse): Baltringen, Würtemberg (after Probst.)

Fig. 48.
Scymnus triangulus, Probst. Tooth, × 2. Miocene (Molasse): Baltringen (after Probst.)

Acanthias, Risso (*Centrophoroides*, Davis), (Fig. 47). As *Centrophorus*, but teeth in upper jaw as in lower jaw. Upper Cretaceous, Sahel Alma, Mount Lebanon (*Centrophoroides latidens*, Davis). Tertiary (*A. radicans*, Probst) and Recent.

Centrina, Cuv. Pliocene and Recent.

Scymnus, Cuv. (Fig. 48). No dorsal fin spines. Upper teeth small, pointed; lower teeth much larger, broad and compressed, triangular, erect or only slightly inclined laterally. Eocene to Recent.

Echinorhinus, Blainv. (*Goniodus*, Ag.) Pliocene and Recent.

Grundlage des Baues und der Entwickelung ihrer Wirbelsäule. Jena, 1879, with Appendix, 1885. —*Müller, J.*, and *Henle, J.*, Systematische Beschreibung der Plagiostomen. Berlin, 1841.—*Jaekel, O.*, Die eocänen Selachier vom Monte Bolca. Berlin, 1894.—*Noetling, F.*, Die Fauna des samländischen Tertiärs (Abhandl. geol. Specialk. Preussen, vol. VI. pt. 3), 1885.—*Probst*, Beiträge zur Kenntniss der fossilen Fische aus der Molasse von Baltringen (Württemb. naturw. Jahresh.), 1874, 1877, 1878, and 1882.

Sub-Order C. ASTEROSPONDYLI. Hasse.

Vertebral centra when completely formed amphicoelous, strengthened by secondary plates of calcified tissue which radiate outwards from the excessively constricted primitive cylinder. Five gill clefts on each side. Two dorsal fins and one anal fin present. Lower Carboniferous to Recent.

Family 1. Cestraciontidae. Agassiz.

Dorsal fins each armed with a spine. Teeth numerous, mostly obtuse, never fused into continuous plates: several series simultaneously in function. Radiating plates of the vertebral centra few and short; vertebral column not calcified in the earlier forms. Lower Carboniferous to Recent.

This family is characteristic of the later Palaeozoic and the Mesozoic formations; it is represented in existing seas solely by one genus, *Cestracion.*

Orodus, Ag. (Fig. 49), known only by obtuse elongated teeth. The dental crown raised in the middle, and its surface marked with more or less prominent wrinkles, which rise from each long margin or from a median longitudinal crest. Base of tooth very stout. *O. ramosus*, Ag. (Fig. 49), and other species from the Carboniferous Limestone of Britain, Belgium, and Russia. Also numerous species in corresponding American formations.

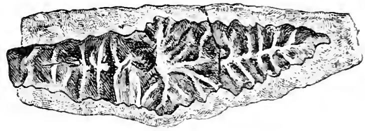


Fig. 49.
Orodus ramosus, Ag. Carboniferous Limestone; Armagh (after Davis). 1/2.

Campodus, Kon. (*Agassizodus*, St. J. and W.; *Arpagodus*, Traut.). Teeth almost identical with *Orodus*, but distinguished by buttressed condition of the outer border of the crown. Symphysial series greatly enlarged, and fused. Carboniferous. *Edestus*, Leidy; *Campyloprion*, Eastm.; and *Helicoprion*, Karp., known only by their arched or coiled symphysial dentition. Carboniferous and Permian.

Fig. 50.
Tristychius arcuatus, Ag. Dorsal fin-spine (*A*), shagreen-scale (*B*), and tooth (*C*), about natural size. Lower Carboniferous; Scotland (after Stock).

Tristychius, Ag. (*Ptychacanthus*, Ag.), (Fig. 50). Dorsal fin spines with a few sharp longitudinal ridges distally, three only—one upon the front margin and one on each side—extending far downwards. Teeth probably as in *Sphenacanthus*. *T. arcuatus*, Ag. Carboniferous.

Sphenacanthus, Ag. Teeth rather high-crowned, with a large principal cusp and smaller lateral cusps diminishing in size outwards, more or less marked by superficial wrinkles; base depressed, forming a slight expansion backwards. Notochord persistent. Dorsal fin spines marked with robust longitudinal ridges, in part nodose: posterior denticles small and numerous, in two series, one upon each lateral margin of the flattened or slightly concave posterior face. Few minute comb-shaped shagreen granules. *S. costellatus*, Traquair sp., known by nearly complete fish from Calciferous Sandstones (Lower Carboniferous) of Eskdale, Dumfries.

S. hybodoides, Egert. sp., represented by fin spines and teeth in English, Welsh, and Scottish Coal Measures.

Hybodus, Ag. (*Meristodon*, Ag.), (Fig. 51). Teeth and dorsal fin spines almost as in *Sphenacanthus*: but double series of denticles on hinder face of fin-spine median, not laterally placed. Symphysial teeth few and relatively large. Notochord persistent, but vertebral arches calcified. One or two large hook-shaped, semi-barbed dermal spines (*Sphenonchus*) immediately behind each orbit, at least in the male. Shagreen sparse, consisting of small conical, radiately grooved tubercles, which are sometimes fused into groups of three. Numerous species ranging from the Trias to the Lower Cretaceous. Teeth of *H. plicatilis*, Ag. (Fig. 51, *A*), abundant in the Muschelkalk. Nearly complete skeletons from the Lower Lias of England (*H. delabechei*, Charlesworth; *H. reticulatus*, Ag., Fig. 51, *B*) and the Upper Lias of Würtemberg (*H. hauffianus*, Eb. Fraas). Fine skulls from Wealden, Pevensey Bay, Sussex (*H. basanus*, Egert.).

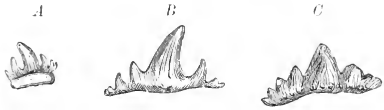


Fig. 51.

Teeth of *Hybodus*. *A*, *H. plicatilis*, Ag. Muschelkalk; Laineck, near Bayreuth. *B*, *H. reticulatus*, Ag. Lower Lias; Lyme Regis, Dorsetshire. *C*, *H. polyprion*, Ag. Lower Oolite (Dogger); Stonesfield, Oxfordshire.

Acrodus, Ag. (*Thectodus*, Plieninger), (Fig. 52). A genus only differing from *Hybodus* in the rounded, non-cuspidate character of the teeth. Common

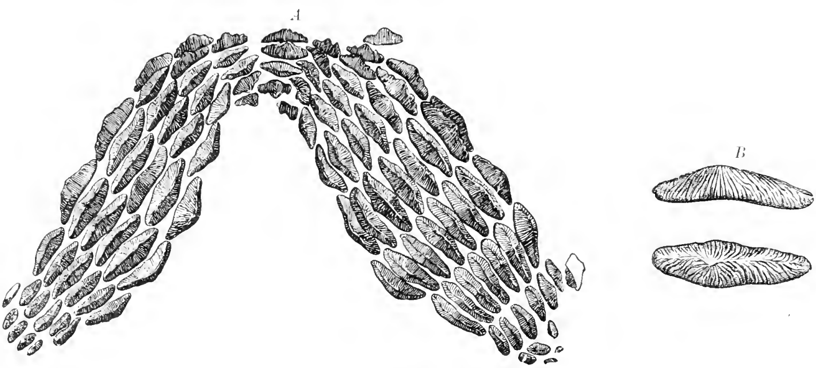


Fig. 52.

Acrodus anningiae, Ag. Dentition, $1/3$ natural size. Lower Lias; Lyme Regis. *A*, Symphysis. *B*, Detached tooth, seen from side and above, natural size.

in the Triassic and Jurassic, and ranging to the Upper Cretaceous. *A. gaillardoti*, Ag., teeth from Bunter, Muschelkalk, and Keuper of Germany and France. *A. minimus*, Ag., common in European Keuper and Rhaetic. *A. anningiae*, Ag. (Fig. 52), and *A. nobilis*, Ag., known by fine specimens from the Lower Lias, Lyme Regis. *A. levis*, Sm. Woodw., teeth from English Gault.

Palaeobates, Meyer. Teeth depressed, rounded, without lateral denticles and not keeled. European Triassic.

Asteracanthus, Ag. (*Strophodus*, Ag.; *Curtodus*, Sauvage), (Figs. 53, 54). Principal teeth elongated, irregularly quadrate, with slightly arched but flattened crown; symphysial teeth few, smaller but relatively large, much arched, without lateral denticles, and longitudinally keeled; all superficially marked by reticulating ridges. Notochord persistent. Head spines as in *Hybodus* and *Acrodus*. Dorsal fin spines marked by stellate tubercles, sometimes partly fused into longitudinal ribs; also bearing a median longitudinal double series of tubercles on their hinder face. Middle and Upper Jurassic. *A. ornatissimus*, Ag. (*Strophodus reticulatus*, Ag.), (Fig. 54), well known from Corallian, Oxfordian, and Kimmeridgian of Europe.

Palaeospinax, Egerton. Dentition comparatively specialised; the few anterior teeth high-crowned and prehensile, with a single pair of lateral denticles; posterior teeth low-crowned, with two or three pairs of lateral denticles reduced to minute beads. Vertebrae very slightly asterospondylic. Dorsal fin spines smooth and enamelled, without posterior denticles. Shagreen fine and dense; no head spines. *P. priscus*, Egert., known by nearly complete specimens from Lower Lias, Lyme Regis. Fragments of other species from Upper Lias, Würtemberg.

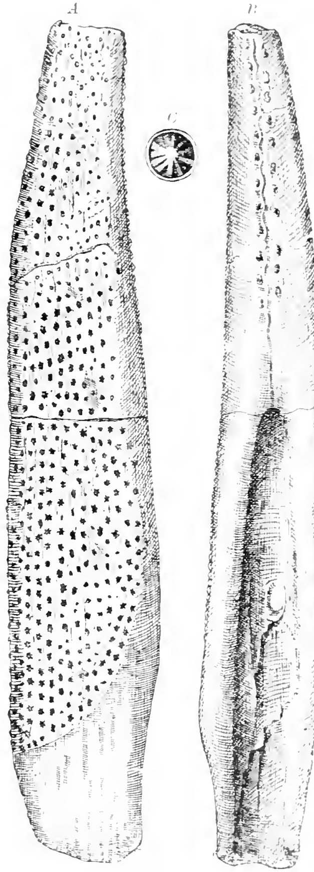


FIG. 53.

Asteracanthus ornatissimus, Ag. Dorsal fin-spine, lateral view (*A*), posterior view (*B*), and detached tubercle enlarged (*C*). Portlandian; Soleure, Switzerland.

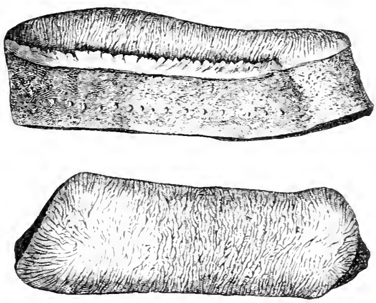


FIG. 54.

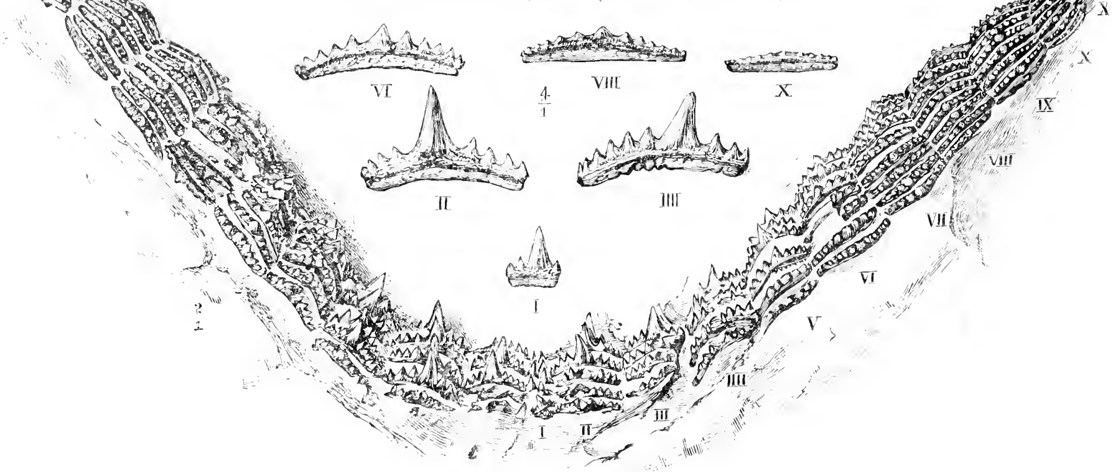
Tooth of *Asteracanthus* (*Strophodus reticulatus*, Ag.), inside view and upper view. Corallian: Tonnere, Yonne.

Synechodus, Smith Woodward (Fig. 55). Almost identical with *Palaeospinax*, but teeth with more numerous lateral denticles, and vertebrae more distinctly asterospondylic. Complete jaw of *S. dubrisiensis*, Mackie sp. (Fig. 55), and greater part of skeleton of same species known from the Lower Chalk of England. Teeth of other species from various Cretaceous formations in Europe, Cretaceo-Tertiary of New Zealand and Patagonia, and one (*S. clarki*, Eastman) from the Maryland Eocene.

Cestracion, Cuv. (*Heterodontus*, Blainv.: *Drepanephorus*, Egert.), (Figs. 56, 57). Symphysial teeth small, numerous and prehensile, with a median cusp and one pair of lateral denticles; lateral teeth in oblique series, with faintly keeled and finely rugose crown. Vertebrae asterospondylic. Dorsal fin

FIG. 55.

Synechodus dubrisiensis, Mackie sp. Dentition, twice nat. size, with six teeth enlarged four times. Lower Chalk; Sussex (after Smith Woodward).



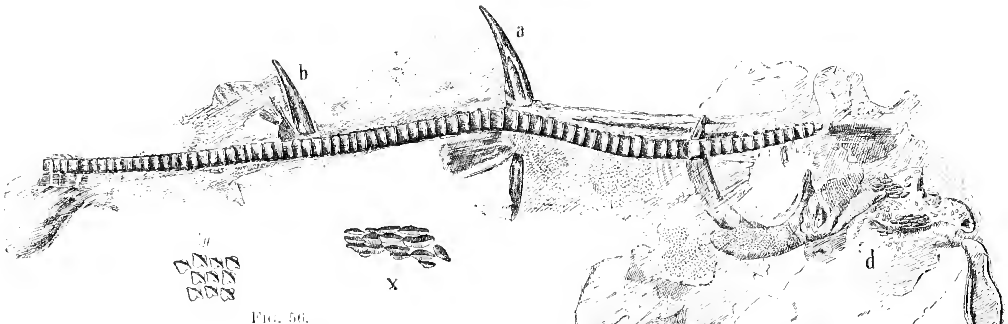


FIG. 56.

Cestracion falcifer, Wagen. Skeleton 1/3 nat. size. Upper Jurassic (Lithographic Stone); Solenhofen, Bavaria. *a*, *b*, Anterior and posterior dorsal fin-spines; *d*, Teeth; *p*, Pectoral fin; *x*, Teeth, nat. size; *y*, scales, nat. size.

spines smooth, without posterior denticles. Nearly complete skeletons from the Lithographic Stone (Upper Jurassic) of Bavaria (*C. falcifer*, Wagn., Fig. 56) and the Chalk of England (so-called *Drepanephorus canaliculatus*, Egert.). Teeth from Lower and Middle Eocene of England and Belgium. Existing in Australian and other seas.

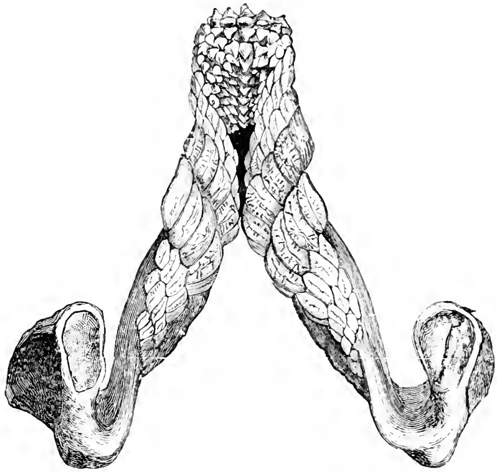


FIG. 57.
Lower jaw of Recent Port Jackson Shark, *Cestracion philippi*, Cuv. Australia.

Family 2. **Scylliidae.** Müller and Henle.

Dorsal fins without spines, the anterior situated above or behind the pelvic fins. Teeth small, numerous, and pointed, several series being generally in function. Vertebrae with eight stout radiating plates. Upper Jurassic to Recent, but fossils rare.

Palaeoscyllium, Wagn. Anterior dorsal fin opposite pelvic pair, and posterior dorsal arising in advance of anal, which is small. *P. formosum*, Wagn., and *P. minus*, Sm. Woodw., known by nearly complete fishes from Lithographic Stone, Bavaria.

Scyllium, Cuv. (*Thyellina*, Ag.), (Fig. 58). Origin of anal fin always in advance of that of posterior dorsal fin. Teeth delicate with a high middle cusp and generally one or two small lateral denticles. Nearly complete fishes from the Upper Cretaceous of Westphalia (*S. angustum*, Ag. sp.) and Mount Lebanon (*S. elongatum*, Davis sp.); also numerous detached teeth from the Chalk and Tertiaries (Fig. 58). Recent.

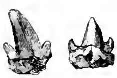


FIG. 58.
Scyllium distans, Probst. Tooth, × 2. Miocene (Molasse); Baltringen (after Probst.).

Pristiurus, Bonap. As *Scyllium*, but with a series of small flat spines on each side of the upper edge of the caudal fin. *P. hassei*, Sm. Woodw., a small species from the Lithographic Stone of Eichstädt, Bavaria. Recent.

Mesiteia, Kramberger. Snout produced. Teeth minute and tricuspid. Anterior dorsal fin above or behind pelvic pair; anal fin much extended. Tail excessively elongated, without dermal scutes or spines. Shagreen absent or very delicate, and lateral line supported by a series of calcified rings as in Chimaeroids. *M. emiliae*, Kramberger, from Upper Eocene, Monte Bolca, near Verona; *M. sahel-almae*, Pict. and Humb. sp., from Upper Cretaceous, Mount Lebanon.

Chiloscyllium, Müll. and Henle, and *Ginglymostoma*, Müll. and Henle (*Plicodus*, Winkler; *Acrodobatis*, Leidy). Tertiary and Recent.

Family 3. **Carchariidae.** Müller and Henle.

Dorsal fins without spines, the anterior situated opposite to the space between the pectoral and pelvic fins. Teeth hollow, pointed and triangular, with smooth or *serrated lateral borders. Vertebral centra with four radiating ridges which widen outwards.* Tertiary and Recent.

Hemipristis, Ag. (*Dirrhizodon*, Klunzinger), (Fig. 59). Principal teeth large, triangular and compressed, with coarsely serrated edges; anterior lower teeth slender, subulate, inwardly curved, and without denticulations or with one or two minute points at the base. *H. serra*, Ag. (Fig. 59), common in the Miocene of Europe and in the Tertiary Phosphate Beds of South Carolina and Maryland Miocene. *H. curvatus*, Dames, from Oligocene, Birket-el-Qurūn, Egypt. One existing species.

Galeocerdo, Müller and Henle (Fig. 60). Teeth oblique, serrated on both margins, with a deep notch posteriorly. Eocene to Recent. *G. latidens*, Ag., from Bracklesham Beds and Maryland Miocene. *G. aduncus*, Ag. (Fig. 60, *A*), species, apparently ranging to the Pliocene. *G. contortus*, Gibbes, and *G. triqueter*, East., from the American Miocene.

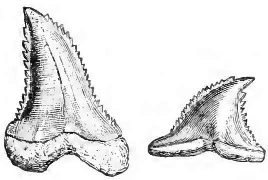


Fig. 59.

Hemipristis serra, Ag. Miocene: Neudörfl, Hungary.

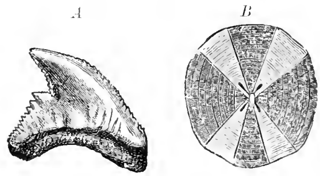


Fig. 60.

A, Tooth of *Galeocerdo aduncus*, Ag. Miocene (Molasse); Pfullendorf, Baden. *B*, Section of vertebra of *Galeocerdo*. Miocene (Molasse); Baltringen (after Hasse).

Fig. 61.

Galeus affinis, Probst. Miocene (Molasse); Baltringen (after Probst.).

Alopiopsis, Lioy, and *Pseudogaleus*, Jaekel. Nearly complete fishes from Upper Eocene, Monte Bolca, near Verona.

Galeus, Ag. (*Protogaleus*, Molin.), (Fig. 61). Teeth small and oblique, the margins only serrated at the base, and a deep notch posteriorly. Eocene to Recent.

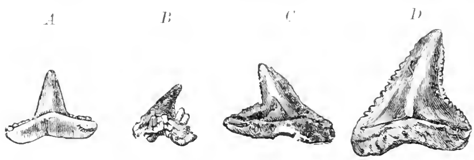


Fig. 62.

A, *Carcharias* (*Aprionodon*) *frequens*, Dames. Eocene; Birket-el-Qurun, Egypt (after Dames). *B*, *Carcharias* (*Hypoprion*) *singularis*, Probst. *C*, *Carcharias* (*Scoliodon*) *kraussi*, Probst. *D*, *Carcharias* (*Prionodon*) *similis*, Probst. Miocene (Molasse); Baltringen (after Probst.).

Carcharias, Cuv. (Fig. 62). Teeth mostly oblique and triangular, without lateral denticles, usually different in the two jaws. The lateral edges serrated to the apex (*Prionodon*, Müller and Henle) or only at the base (*Hypoprion*, M. and H.), or sharp-edged but not serrated (*Scoliodon*, *Physodon*, M. and H.), sometimes also erect and sharp-edged (*Aprionodon*, Gill). Tertiary and Recent.

Sphyrna, Raf. (*Zygaena*, Cuv.). Hammerhead sharks. Tertiary and Recent. *S. prisca*, Ag.

Mustelus, Cuv.; *Triaenodon*, *Triacis*, M. and H. Recent.

Family 4. **Lamnidae.** Müller and Henle.

Dorsal fins without spines, the anterior situated opposite to the space between the pectoral and pelvic fins. Teeth pointed and usually large, with or without lateral *denticles, and the pulp cavity completely filled with vasodentine. Vertebral centra with eight bifurcating plates which radiate outwards.* Upper Jurassic to Recent.

Orthacodus, Sm. Woodw. (*Sphenodus*, Ag., *non* Gray, *nec* Lund), (Fig. 63). Teeth very slender and erect, compressed, without lateral denticles; the root broad and depressed, simple. *O. longidens*, Ag. sp. (Fig. 63), and other species are Upper Jurassic. Apparently also a Lower Cretaceous genus.

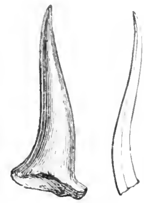


Fig. 63.
Orthacodus longidens, Ag. sp. White Jura γ; Böllert, Würtemberg.

Scapanorhynchus, Sm. Woodw. (*Rhinognathus*, Davis *non* Fairmaire; ? *Mitsukurina*, Jordan). Body slender, snout much elongated. Second dorsal fin small, opposed to a much extended anal fin; caudal fin much elongated, inferiorly notched near the extremity. Teeth as in *Odontaspis*. Complete skeletons of *S. lewisi*, Davis sp., and *S. elongatus*, Sm. Woodw., from the Upper Cretaceous of Sahel Alma, Mount Lebanon. Detached teeth (*S. rhaphiodon*, Ag. sp.) in Upper Cretaceous of Europe, probably also in North America, India, and New Zealand. Apparently living in the deep sea off Japan (*Mitsukurina owstoni*, Jordan).

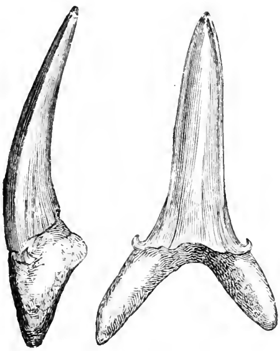


Fig. 64.
Odontaspis cuspidata, Ag. sp. Oligocene; Weinheim, near Alzey.

Odontaspis, Ag. (*Triglochis*, M. and H.; *Otodus*, Ag. in part.), (Fig. 64). Snout not much elongated. Second dorsal fin and the anal of equal size, scarcely smaller than the first dorsal. Side of tail without keel. Teeth with a slender principal cusp, with sharp lateral edges, flattened outer face, and convex inner face, also one or two pairs of small lateral denticles; root large and bifurcated. Upper Cretaceous, Tertiary and Recent. *O. bronni*, Ag. U. Cretaceous, Maastricht and Ciply. *O. elegans*, Ag. sp., and *O. cuspidata*, Ag. sp. (Fig. 64), from Lower Tertiaries.

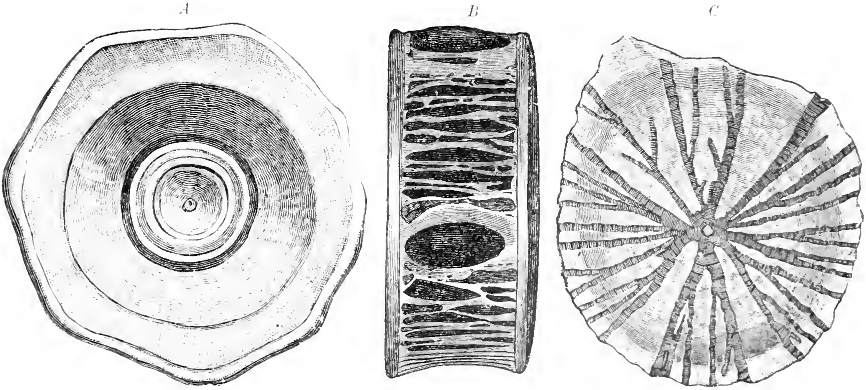


Fig. 65.
Vertebra of *Lamna*, in front (*A*) and side view (*B*), and in vertical median section (*C*). Nat. size. *A*, *B*, From Oligocene of Flonheim. *C*, From London Clay, Sheppey.

Otodus, Ag. (Figs. 65-67). Very robust teeth with stout lateral denticles, of rather doubtful relationships. Most species described under this name referable to *Lamna* and *Odontaspis*. Cretaceous and Eocene.

Lamna, Cuv. Second dorsal fin and the anal very small. Side of tail with keel. Teeth as in *Odontaspis*, but the principal cusp usually somewhat broader and the lateral denticles larger. Very abundant in the Chalk, Tertiaries, and existing seas.

Oxyrhina, Ag. (Fig. 68). Only differing from *Lamna* in the teeth lacking lateral denticles. Cretaceous to Recent. *O. mantelli*, Ag., the commonest Cretaceous species both in Europe and North America, the nearly complete dentition known from Kansas. *O. desori*, Ag., chiefly Lower Tertiary; *O. hastalis*, Ag., chiefly Upper Tertiary.

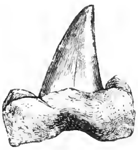


Fig. 66.
Otodus appendiculatus, Ag. Pläner; Quedlinburg.

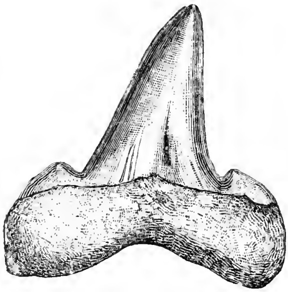


Fig. 67.
Otodus obliquus, Ag. External aspect of tooth. Eocene; Sheppey.

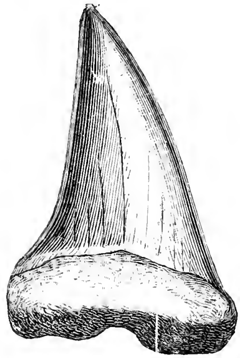


Fig. 68.
Oxyrhina plicatilis, Ag. Miocene; Neudörfl, Hungary.

Alopecias, M. and H. Tertiary and Recent.

Corax, Ag. (Fig. 69). Known only by low triangular teeth with sharp, serrated edges, and a large root. Common in the Middle and Upper Cretaceous. *C. pristodontus*, Ag., from Maastricht, North Africa (Fig. 69), and supposed Eocene of Alabama. *C. falcatus*, Ag., European and North American Cretaceous.

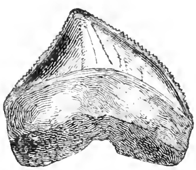


Fig. 69.
Corax pristodontus, Ag. Upper Chalk; Oasis of Dachel, Libyan Desert.

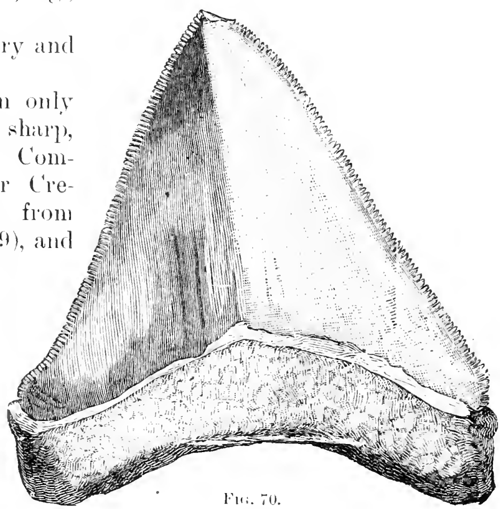


Fig. 70.
Carcharodon megalodon, Ag. Miocene; Malta.

Carcharodon, M. and H. (Fig. 70). Second dorsal fin and the anal very small. Side of tail with keel. Teeth very large and triangular, with serrated lateral edges, flattened outer face, convex inner face. One Upper

Cretaceous (*C. longidens*, Pillet) and one existing species (*C. rondeleti*, M. and H.); the others Tertiary. *C. megalodon*, Ag. (Fig. 70), and allied species are represented by very large teeth in the Tertiary and later formations of nearly all parts of the world, also on the bed of the existing oceans.

Cetorhinus, Blv. (*Selache*, Cuv.). Teeth very small and conical, without lateral denticles. Claspers of male with horn-shaped spines, which have been found in the Pliocene of England and Belgium. The existing "basking shark."

Sub-Order D. TECTOSPONDYLI. Hasse.

Vertebral centra when completely formed amphicoelous, strengthened by secondary plates of calcified tissue which are concentric with the constricted primitive cylinder. Five gill clefts on each side. Anal fin absent. Body usually depressed, with very large pectoral fins forming a "disk."

To the Tectospondyli belong the still existing rays, monk-fishes, and saw-fishes, perhaps also the Palaeozoic families of Cochliodontidae, Psammodontidae, and Petalodontidae.

Family 1. Cochliodontidae. Owen.

Palaeozoic fishes with few convex teeth, which are more or less arched, hollowed at the base, punctate on the crown, and often marked with obtuse transverse folds or grooves. A large posterior dental plate, above and below on each side, a smaller anterior dental plate, and one or more series of separate smaller anterior teeth. Head and perhaps also the pectoral fins armed with paired tuberculated spines. Carboniferous and Permian.

Our knowledge of this most remarkable Upper Palaeozoic family is still very incomplete. Of two genera (*Helodus* and *Menaspis*) the impression of the trunk is known; of all the others only teeth or fin spines and, very rarely, complete jaws occur. According to Jaekel we may place here the unsymmetrical Ichthyodorulites, with tubercles, bosses, or spines and destitute of a root, which have been described under the names of *Oracanthus*, *Pnigeacanthus*, *Cladacanthus*, *Platyacanthus*, *Gampsacanthus*, *Physonemus*, *Stichacanthus*, etc. Owen has pointed out that the dentition in the typical genera *Cochliodus* and *Streblodus* corresponds with that of a Cestraciont, but differs from the latter in the fusion of two or more transverse series of teeth into continuous plates. Smith Woodward has thus proposed to place the typical Cochliodontidae near the Cestraciontidae, removing *Menaspis* to the Chimaeroid family of Squaloraiidae.

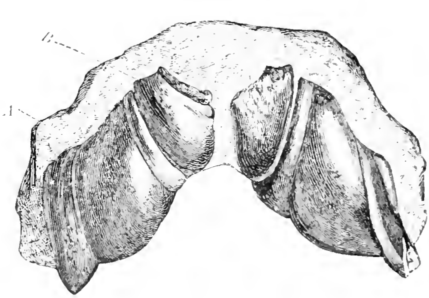


Fig. 71.

Cochliodus contortus, Ag. Dentition. $^3/_4$ nat. size. Carboniferous Limestone; Armagh. *A*, Large posterior tooth. *B*, Middle tooth; anterior teeth wanting.

Cochliodus, Ag. (Fig. 71). Two strongly arched dental plates on each ramus of the mandible; the posterior one very large, with a broad median area bounded in front and behind by an oblique transverse furrow; the anterior plate comparatively small, rhomboidal in shape. Symphysial series of *C. latus*, Leidy, from Keokuk Limestone of Mississippi Valley, the largest known species, originally described as *Helodus coxanus*, Newb. Lower Carboniferous; Ireland, England, Belgium, and North America.

Streblodus, Ag. As *Cochliodus*, but hinder tooth with two to three broad, oblique, transverse folds. *S. oblongus*, Ag., and *S. colei*, Davis, from Carboniferous Limestone, Armagh. Other species from England and North America.

Sandalodus, Newberry and Worthen (*Trigonodus*, *Vaticinodus*, N. and W.; *Orthopleurodus*, St. John and Worthen). Supposed upper teeth triangular, thick, slightly inrolled. Supposed lower teeth more strongly inrolled; the hinder one subtriangular or twisted and elongate, with one to two diagonal ridges, and anteriorly coiled in a distinct whorl; the anterior one short, truncated in front, strongly inrolled. Carboniferous; Ireland, England, Belgium, and North America.

Deltoptychius, Ag.; *Chitonodus*, St. John and Worthen; *Poecilodus*, Ag.; *Deltodus*, Ag. (*Taeniodus*, St. J. and W.); *Xystrodus*, Ag. Carboniferous Limestone; Europe and North America.

Psephodus, Ag.[1] (Fig. 72). Large rhombic or rhomboidal teeth, convex and gently arched, with crenulated border. With these large teeth are

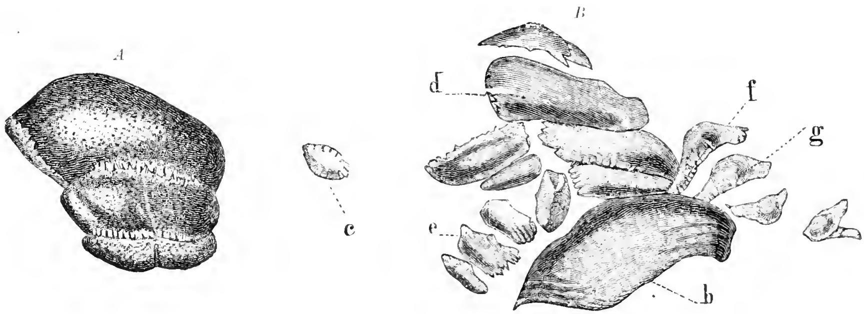


FIG. 72.

Psephodus magnus, Ag. *A*, Three teeth in connected series, nat. size, from the Carboniferous Limestone of Armagh (after Davis). *B*, Associated upper teeth from remains of head found in Calciferous Sandstones, East Kilbride, Lanarkshire. *b*, Large tooth somewhat broken; *c*, Small tooth identical with *Helodus rudis*, M'Coy; *d*, Slender teeth identical with *Helodus planus*, Ag.; *e*, Helodont teeth; *f*, *g*, Teeth identical with *Lophodus didymus* and *L. laevissimus*, Ag. sp. (after Traquair).

sometimes associated more numerous transversely elongated small teeth, of which isolated examples have been described under the names of *Helodus*, *Lophodus*, and *Aspidodus*. Carboniferous Limestone; Europe, India, and North America.

Pleuroplax, Sm. Woodw. (*Pleurodus*, Hancock and Atthey, *non* Wood, *nec* Harlan). Teeth with feeble antero-posterior ridges, and the antero- and postero-lateral borders indented between these ridges. These teeth sometimes associated with others of the *Helodus*-type. At least one dorsal fin, with an unornamented spine. *P. rankinei*, H. and A., from English Coal Measures. Other species from Upper and Lower Carboniferous of Europe and North America.

Menaspis, Ewald, emend. Jaekel[2] (*Dichelodus*, Giebel; *Chalcodus*, Zittel),

[1] *Traquair, R. H.*, Trans. Geol. Soc., Glasgow, vol. VII. 1885, p. 392.

[2] *Jaekel, O.*, Ueber *Menaspis* (Sitzungsb. naturf. Freunde, Berlin, 1891, p. 115).—*Reis, O.*, Ueber die Kopfstacheln von *Menaspis armata*, Munich, 1891.

(Fig. 73). Head and back covered with longitudinal series of tuberculated or spiny, partially keeled placoid scales and small shagreen granules. On each side of the front portion of the head a triangular spine, provided with a broad, hollow base and covered with tubercles of dentine. Further back on each side three smooth, thin, arched spines fixed by a conspicuous basal process in the skin of the head, curved inwards, and apparently consisting of calcified cartilage; the middle pair of these spines more than twice as long as the others. Dentition consisting of one pair of Cochliodont teeth in each jaw (Fig. 73). *M. armata*, Ewald, from Kupferschiefer of Germany.

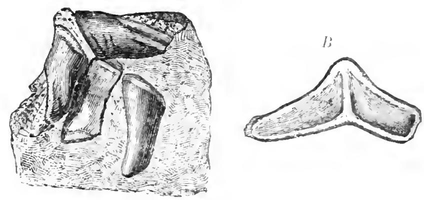


Fig. 73.
Menaspis armata, Ewald (*Chalcodus permianus*, Zittel). Dentition from above (*A*), and below (*B*), nat. size. Kupferschiefer; Glucksbrunn, Thuringia.

Family 2. **Psammodontidae.** De Koninck.

Known only by large, flat, or slightly arched teeth, with punctate or finely rugose grinding surface. The teeth are of quadrate or oblong shape, and were originally arranged in one, two, or more longitudinal series. Lower Carboniferous.

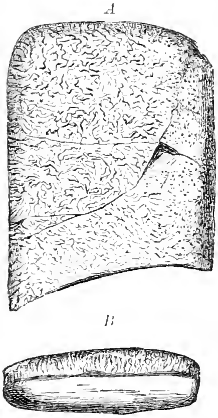


Fig. 74.
Psammodus rugosus, Ag. Imperfect tooth from above (*A*), and in transverse section (*B*), nat. size. Carboniferous Limestone; Armagh.

Psammodus, Ag. (*Homalodus*, *Astrabodus*, Davis), (Fig. 74). Teeth quadrangular, with relatively thick base, smooth or feebly striated on the attached surface, arranged in the jaw in paired longitudinal series. *P. rugosus*, Ag. (Fig. 74), from Carboniferous Limestone of Ireland, Scotland, England, Wales, and Belgium. Allied species in Russia and North America.

Archaeobatis, Newberry. Teeth scarcely distinct from *Psammodus*. An associated group of *A. gigas*, Newb., known from St. Louis Limestone, Greencastle, Indiana (*Ann. New York Acad. Sci.* vol. i. 1878, p. 190).

Copodus, Davis (*Mesogomphus*, *Rhymodus*, *Characodus*, *Pinacodus*, Davis). Comparatively small median teeth, narrower in front than behind, divided into two unequal parts by a transverse suture. *C. cornutus*, Davis, and allied species from Carboniferous Limestone of Ireland, England, and North America.

Family 3. **Petalodontidae.** Newberry and Worthen

Teeth antero-posteriorly compressed, transversely elongated, arranged in longitudinal and transverse rows and forming a pavement. Crown enamelled, more or less bent backwards, either with a sharp cutting edge or very obtuse, the anterior face convex, the posterior face concave; root separated from the crown by a constriction, usually with enamel folds immediately above it. Carboniferous and Permian.

Of this extinct family, *Janassa* is the only genus of which more than the dentition is known. This fish exhibits a ray-shaped trunk covered with smooth, rounded shagreen granules; the large pectoral fins extend forwards to the head, and the pelvic pair are separated from them by an interspace; the tail is slender, and mouth narrow. There are no fin spines.

Petalodus, Owen (*Chomatodus*, Ag. in part; *Sicarius*, Leidy; *Antliodus*, Newb.; *Lisgodus*, St. John and Worthen), (Fig. 75). Teeth much antero-posteriorly compressed and transversely elongated. Crown leaf-shaped, with cutting edge and sharp basal margin with enamel folds; root long and comparatively slender, truncated below. *P. acuminatus*, Ag. sp., and other species from the Carboniferous Limestone of England, Scotland, Ireland, Belgium, Russia, and North America. Rare in the Coal Measures of North America.

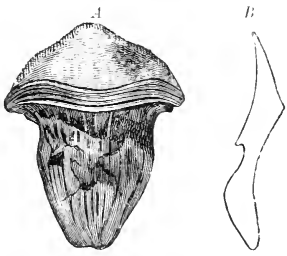


Fig. 75.

Petalodus alleghaniensis, Leidy. Tooth in front view (*A*) and transverse section (*B*), 1/2 nat. size. Coal Measures; Springfield, Illinois (after Newberry).

Petalorhynchus, Newb. and Worth. Dentition consisting of six transverse rows of three acuminate cutting teeth with undivided root. Carboniferous Limestone; Europe and North America.

Janassa, Münster (*Dictaea*, *Byzenos*, Münster; *Climaxodus*, M'Coy; *Peltodus*, Newb.; *Tanaodus*, St. John and Worthen), (Fig. 76). Dentition consisting of narrow and elongated teeth with a reflexed punctate crown, which are arranged in five to seven longitudinal, and seven transverse rows, three on either side of the symphysial series. The oral

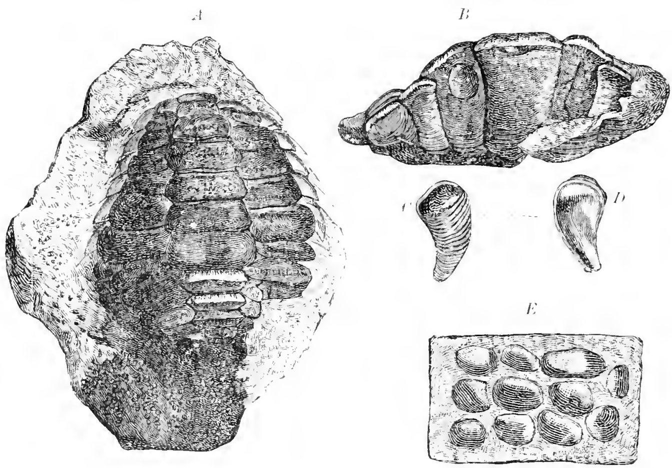


Fig. 76.

Janassa bituminosa, Schloth. sp. Kupferschiefer; Glücksbrunn, Thuringia. *A*, Upper and lower dentition. *B*, Cross-section. *C*, Tooth from in front, and *D*, from behind. *E*, Dermal tubercles, enlarged.

cutting margin is formed entirely by the anterior face of the crown, which is bent backwards sharply and overlaps the next older tooth in front, which serves as a support. The long, tapering root of each tooth is much compressed antero-posteriorly, slightly arched, transversely ridged on the convex anterior face, smooth on the concave hinder face. Skin covered with oval or quadrate, smooth, shagreen granules. *J. bituminosa*, Schloth. sp. (Fig. 76), represented by important specimens from the Kupferschiefer of Hesse and Thuringia, also from the Marl Slate of Durham. Detached teeth of other species (so-called *Climaxodus*, etc.) from Upper and Lower Carboniferous of England, Scotland, Ireland, and North America.

Fissodus, St. John and Worthen. Carboniferous Limestone; North America and Scotland.

Glossodus, M'Coy; *Mesolophodus*, Sm. Woodw. Carboniferous Limestone; Ireland.

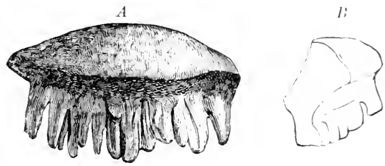


FIG. 77.

Polyrhizodus magnus, M'Coy. Tooth in front view (*A*), and transverse section (*B*), $^1/_2$ nat. size. Carboniferous Limestone; Armagh (after M'Coy).

Polyrhizodus, M'Coy (*Dactylodus*, Newb.), (Fig. 77). Teeth robust, with a tumid crown tapering to a transverse cutting edge, and the root much subdivided. *P. magnus*, M'Coy, and other species from the Carboniferous Limestone of Ireland, England, Russia, and North America.

FIG. 78.

Callopristodus pectinatus, Ag. sp. Coal Measures; Scotland.

Ctenoptychius, Ag. (*Ctenopetalus*, *Harpacodus*, *Petalodopsis*, Davis; *Serratodus*, de Koninck. Teeth small, antero-posteriorly compressed, with sharp serrated edge. Coal Measures and Carboniferous Limestone; England, Scotland, Ireland, Belgium, and North America.

Callopristodus, Traquair (Fig. 78). As *Ctenoptychius*, but root subdivided. *C. pectinatus*, Ag. sp., from the Coal Measures of England and Lower Carboniferous of Scotland, also from Coal Measures of Nova Scotia.

Peripristis, St. John (*Pristodus*, Davis). Lower Carboniferous; Great Britain and U.S.A.

Family 4. **Squatinidae.** M. and H.
Angel-fishes or Monk-fishes.

Trunk broad and depressed. Pectoral fins large, separated by a cleft from the head, so that the branchial openings are still directed laterally. Teeth pointed and conical, without lateral denticles. Two dorsal fins on the tail, without spines. Skin covered with small placoid scales. Jurassic to Recent.

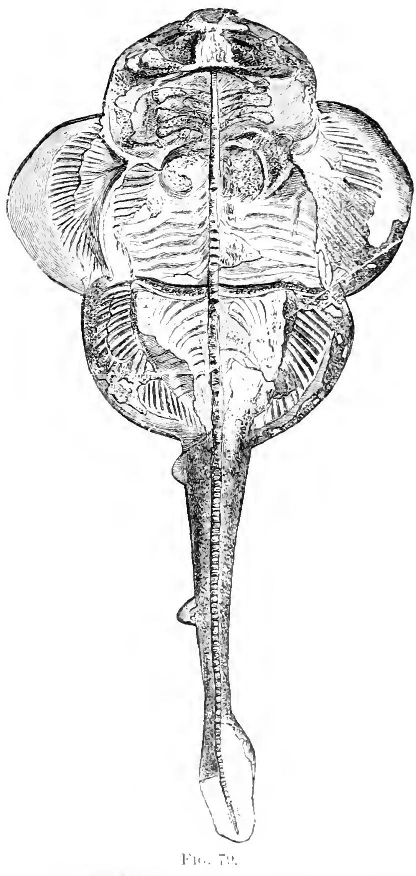


FIG. 79.

Squatina alifera, Münst. sp. (= *Squatina acanthoderma*, Fraas). Upper Jurassic; Eichstadt, Bavaria. (Original in Palaeontological Museum, Munich.)

The single genus *Squatina*, Aldrovandi (*Rhina*, Klein; *Thaumas*, Münst.; *Phorcynis*, Thioll.; *Scaldia*, Le Hon; *Trigonodus*, Winkler), (Figs. 79-81), first appears in the Upper Jurassic and survives in the existing fauna. Complete skeletons of *S. alifera*, Münst. sp.; *S. speciosa*, Meyer; and *S. acanthoderma*, Fraas, occur in the Lithographic Stone of Bavaria and Würtemberg (Nusplingen); and the genus is also represented in the corresponding formation of Cerin, Ain, France. A complete skeleton of *S. baumbergensis*, von der Marck, is known from the Upper Cretaceous of the Baumberg, Westphalia; and more

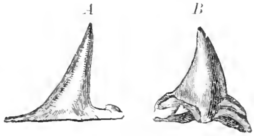


FIG. 80.

A, *Squatina alifera*, Münst. sp. Tooth, × 2. Upper Jurassic (Lithographic Stone); Solenhofen. *B*, *Squatina fraasi*, Probst. Tooth, × 2. Miocene (Molasse); Baltringen.

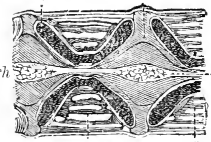


FIG. 81.

Longitudinal section of the tectospondylic vertebral column of *Squatina angelus*, Linn. *ch*, Notochord; *d*, Calcified double-cone (basis of centrum); *iv*, Intervertebral space; *w*, Vertebral centra with concentric calcified rings (after Hasse).

fragmentary remains of *S. cranei*, Sm. Woodw., occur in the English Chalk. Numerous teeth and vertebrae in the Tertiary. *S. occidentalis*, East., from the Maryland Miocene.

Family 5. **Pristiophoridae.** Günther.

Trunk fusiform. Snout much elongated and flattened, without lateral cartilages, but fringed on each border with pointed dermal teeth. Branchial clefts lateral. The two dorsal fins without spines. Upper Cretaceous to Recent.

Pristiophorus, M. and H. Miocene to Recent. An undescribed form in the Upper Cretaceous of Mount Lebanon (Smith Woodward).

Family 6. **Pristidae.** Günther. Saw-fishes.

Trunk elongated, slightly depressed. Pectoral fins rather large, united with the head, but not extended to the long, depressed, sword-like rostrum, strengthened with lateral cartilages, and armed with a row of large, dermal teeth on each lateral border. Branchial clefts on the ventral surface. Teeth of the mouth minute and obtuse. Upper Cretaceous to Recent.

Sclerorhynchus, Sm. Woodw. Teeth of rostrum comparatively small and not fixed in sockets. Rostrum thus resembles that of *Pristiophorus*, but differs from the latter and agrees with *Pristis* in the great development of a pair of lateral cartilages. *S. atavus*, Sm. Woodw., known by nearly complete skeletons from Upper Cretaceous, Mount Lebanon.

Pristis, Latham. Teeth of rostrum peg-like, firmly implanted in sockets of calcified cartilage. Middle Eocene (Bracklesham Beds) to Recent.

Propristis, Dames. Rostral teeth as in *Pristis*, but not implanted in cartilage. Upper Eocene; Birket-el-Qurūn, Egypt.

Family 7. **Rhinobatidae.** Müller and Henle.

Trunk depressed, but elongated. Pectoral fins large, connected with the head, but the cartilaginous rays not reaching the end of the somewhat elongated snout. Branchial clefts on the ventral side. Teeth small and obtuse. Tail robust, with two dorsals and a large caudal fin. Upper Jurassic to Recent.

Rhinobatus, Bloch (*Euryarthra*, Ag.; *Spathobatis*, Thioll.), (Fig. 82). Dorsal fins without spines. Skin with small shagreen granules. Complete skeletons from the Lithographic Stone of Bavaria and France, the Upper Cretaceous of Mt. Lebanon and Italy, and the Upper Eocene of Monte Bolca. Also later Tertiary and Recent.

Asterodermus, Ag. Dorsal fins with small spines. Shagreen granules rather large, stellate. *A. platypterus*, Ag., a small species from the Lithographic Stone of Bavaria.

Belemnobatis, Thiollière. Lithographic Stone; Cerin, Ain, France.

Trygonorhina, *Platyrhina*, M. and H. Eocene to Recent.

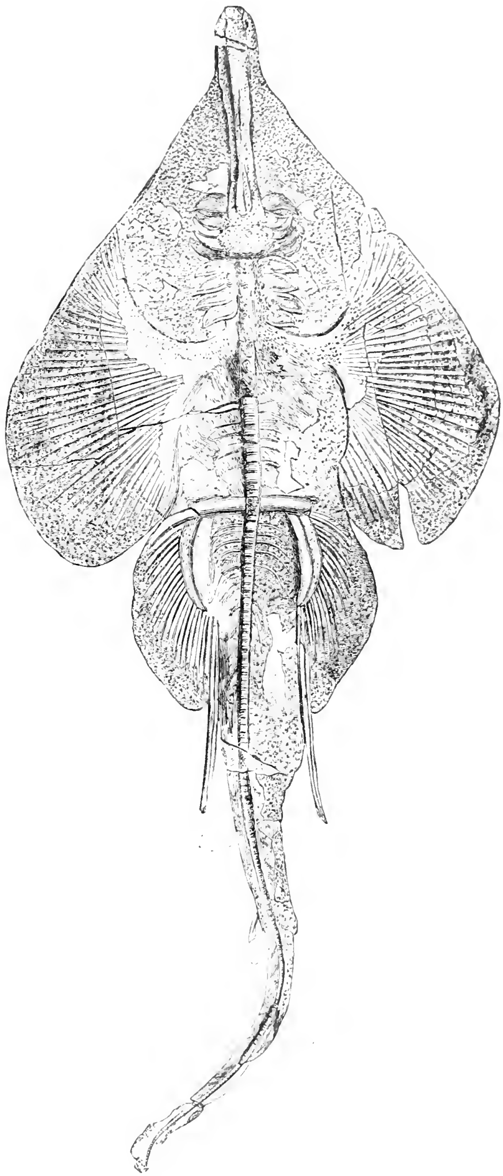


Fig. 82.

Rhinobatus mirabilis, Wagn. Upper Jurassic (Lithographic Stone); Eichstadt, Bavaria. (From a specimen 1·7 m. long in the Palaeontological Museum, Munich.)

Family 8. **Tamiobatidae**.

This family, represented by the unique *Tamiobatis vetustus*, Eastman, from the Devonian or Lower Carboniferous of Kentucky, is of uncertain systematic position, but intermediate between existing sharks and rays.

Family 9. **Rajidae**. Müller and Henle. Skates.

Trunk much depressed, forming a broad, usually rhombic disk with the pectoral fins, which extend from the snout to the pelvic fins. The latter fins with a strong, unsegmented, cartilaginous ray in front. Teeth small, with bifurcated root and rhombic crown, forming a close pavement in each jaw. Tail very slender, without spines, and the caudal fin small or absent. Skin with small, pointed shagreen granules and larger, scattered, spinous, placoid tubercles. Upper Cretaceous to Recent.

Cyclobatis, Egerton. Disk circular or oval, and tail very short, without median fins. Rays of paired fins few and well-spaced, the pectorals united in front of the head. Pelvic arch with very large pre-pubic processes. *C. oligodactylus*, Egerton, from Upper Cretaceous, Hakel and Hajoula, Mount Lebanon.

Raja, Cuv. (*Actinobatis*, Ag.), (Fig. 2). Upper Cretaceous (Mount Lebanon) to Recent. Dermal tubercles of existing *R. clavata*, Linn., in Pliocene Crags of Norfolk and Suffolk.

Family 10. **Torpedinidae.** Müller and Henle. Torpedoes.

Trunk much depressed, forming a broad and rounded disk with the pectoral fins, which do not extend forwards to the broadly rounded anterior end of the head. Tail short and fleshy, with well-developed dorsal and caudal fins. Skin naked. An electric organ between the pectoral fins and the head. Eocene to Recent.

Torpedo, Duméril (*Narcobatis*, Blv.). Sometimes supposed to be represented by skeletons in Upper Eocene of Monte Bolca, but doubtful. Recent.

Narcine, Henle. Upper Eocene of Monte Bolca, and Recent.

Family 11. **Trygonidae.** Müller and Henle. Sting-rays.

Trunk much depressed, forming a disk with the very broad pectoral fins, which meet in front of the snout, and constitute the anterior border of the head. Tail very slender, sharply separated from the disk, the dorsal fins usually replaced by several stout imbricating spines of vasodentine, which are antero-posteriorly compressed and armed with a row of recurved hooklets on each lateral border. Teeth small, rhombic or polygonal, with bifurcated root, and forming a close pavement. Skin naked, with large conical plates of vasodentine, sometimes fused into groups, usually raised into a short spine. Tertiary and Recent.

Trygon, Adanson (*Trygonobatus*, Blv.; *Alexandrinum*, Molin), (Figs. 83, 84). Tail elongated, with long, flattened dorsal spines. Dermal plates of very variable form and size. *T. gazolae*, Ag.; *T. (Alexandrinum) molini*, Zigno; *T. zignoi*, Molin. known by nearly complete skeletons from the Upper Eocene of Monte Bolca. Isolated dermal plates (Fig. 84) have been described as referable to *Raja*, *Acipenser*, *Dynatobatis*, Larrazet, and *Acanthobatis*, Larr.

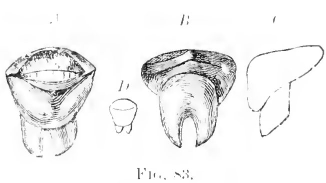


Fig. 83.

Trygon rugosus, Probst. Tooth, anterior (*A*), posterior (*B*), and lateral (*C*), aspects, enlarged, and the same nat. size (*D*). Miocene (Molasse); Baltringen (after Probst.).

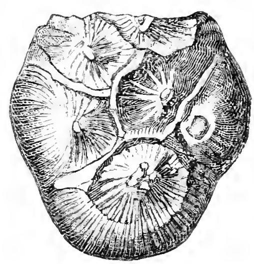


Fig. 84.

Trygon (Acanthobatis) tuberculosus, Probst. sp. Dermal tubercle, nat. size. Miocene (Molasse); Baltringen.

Taeniura, *Urolophus*, M. and H. Upper Eocene (Monte Bolca) and Recent.

Xiphotrygon, Cope (*Heliobatis*, Marsh). Resembling *Trygon*, but teeth cuspidate. *X. acutidens*, Cope, known by complete skeletons from Eocene Green River Shales of Wyoming.

Oncobatis, Leidy. Dermal tubercles. Pliocene; Idaho.

Family 12. **Myliobatidae.** Müller and Henle. Eagle-rays.

Trunk much depressed, forming a broad disk with the very large pectoral fins, which are interrupted at the sides of the head, but reappear as one or a pair of small cephalic fins at the extremity of the snout. Tail very slender, with one or several flattened spines behind the single dorsal fin. Teeth rather large, forming a close pavement in both jaws. Skin naked. Cretaceous (?), Tertiary and Recent.

Most of the surviving genera of this family are represented in the Tertiary by isolated teeth and spines, or by the complete dentition.

? *Ptychodus*, Ag. (*Aulodus*, Dixon), (Figs. 85, 86). Known only by the dentition and vertebrae, and hence of uncertain systematic position. Teeth quadrangular, with a raised crown, which is transversely or radially ribbed, and sharply separated by a constriction from the smaller, smooth root. The teeth are solid, and the ganodentine investing the crown is thick. They are arranged in about thirteen antero-posterior series (Fig. 86). In one jaw, presumably lower, the median series of teeth is the largest, and the lateral rows are disposed symmetrically, diminishing in size outwards. In the opposing jaw the median series is very small, and the first lateral row on each side large, with the outer lateral series diminishing. Common in the Chalk of Europe and North America, rarer in the Greensand.

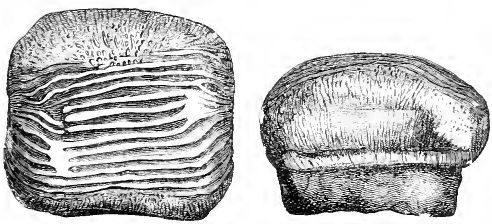


FIG. 85.
Ptychodus polygyrus, Ag. Tooth, oral and posterior views. nat. size. Greensand; Regensburg.

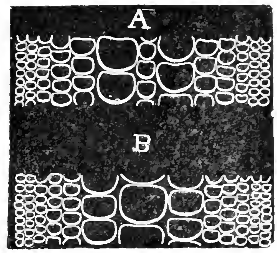


FIG. 86.
Ptychodus decurrens, Ag. Diagram of arrangement of teeth in upper (*A*), and lower (*B*) jaws, much reduced. Lower Chalk; England (after Smith Woodward).

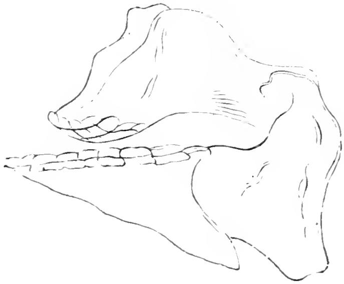


FIG. 87.
Jaws of Recent *Myliobatis*, lateral aspect.

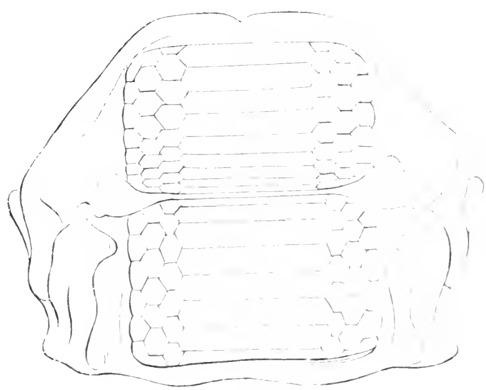


FIG. 88.
Jaws of *Myliobatis aquila*, Cuv. Anterior aspect. Recent; Mediterranean (after Agassiz).

Promyliobatis, Jaekel. A skeleton from the Upper Eocene of Monte Bolca, apparently showing pectoral fins less completely interrupted at side of head than in recent *Myliobatis*, otherwise resembling the latter. *P. gazolae*, Zigno sp.

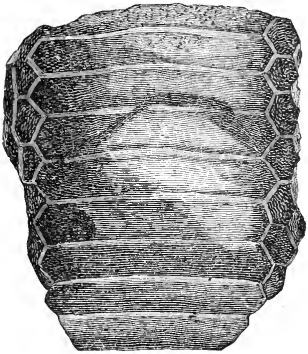


FIG. 89.

Myliobatis toliapicus, Ag. Imperfect dentition. Middle Eocene; Bracklesham, Sussex.

Myliobatis, Cuv. (*Pastinaca*, Gronow), (Figs. 87-90). The dental pavement of the jaws consists of seven antero-posterior rows of hexangular flattened teeth closely pressed together. The lower dentition is longer and less arched than that of the upper jaw. In young examples all the teeth are similar in form and size, but during growth the median series rapidly increases in width, and eventually becomes from three to six times as broad as long, while the shape of the lateral series remains unchanged. The strongly developed root of each tooth is marked with parallel grooves on its lower and lateral faces. Numerous species represented by the dentition in the Tertiaries, and caudal spines also known. *M. dixoni*, Ag.; *M. striatus*, Buckl.; *M. toliapicus*, Ag., from English Eocene. *M. pentoni*, Sm. Woodw., the largest known species, from Eocene, Mokattam Hills, Cairo. *M. magister*, Leidy, the largest American species, known by complete dentition from the South Carolina Eocene.

FIG. 90.

Myliobatis serratus, H. v. Meyer. Caudal fin-spine. Oligocene; Weinheim, near Alzey.

Rhinoptera, Müller (*Zygobates*, Ag.; *Mylorhina*, Gill). Dentition of both jaws strongly arched antero-posteriorly. Teeth flattened and hexangular, in five to nine antero-posterior rows, and mostly broader than long, but diminishing in breadth outwards. Tertiary and Recent. *R. daviesi*, Sm. Woodw., from London Clay, Sheppey.

Aetobatus, M. and H. (*Goniobatis*, Le Hon). Teeth very broad, in a single antero-posterior series. Tertiary and Recent; wide distribution.

Order 5. HOLOCEPHALI. Chimaeras.

Pterygoquadrate arcade completely and immovably fused with the cranium. Mandible provided with a very large dental plate on each side, meeting one or two pairs of dental plates in the upper jaw. Gill clefts covered by a fold of skin, so that there is only one external opening. Vertebral axis not distinctly segmented, and the notochord surrounded by numerous partially calcified rings of cartilage. Paired fins with two or three short basal cartilages; pelvic fins of male with appended claspers.

The Holocephali occupy a unique position among the Selachii, on account of (1) the incompletely segmented character of the vertebral axis, in which the number of the cartilaginous rings considerably exceeds that of the arches and processes; and (2) the fusion of the upper jaw with the skull. Their trunk resembles that of the sharks, while the dentition is distinguished by the remarkably peculiar form and structure of the few very large teeth or dental plates. Of the four surviving genera, *Chimaera* lives off the European coasts, Japan, and the Cape of Good Hope; *Callorhynchus* in the seas of the southern hemisphere; *Harriotta* in the deep Atlantic off North America; and *Rhinochimaera* in deep water off Japan. In all these genera the anterior dorsal fin is provided in front with a strong spine, which is supported by a broad plate of cartilage fixed to the vertebral column, and is united with this plate by a cartilage articulation. Besides the fin spine, the males of recent forms bear on the frontal region a spine which is rounded in front and covered with prickles, as well as smaller prickly spines in front of the pelvic fins. The long copulatory organs are also strengthened by thin calcified rods. The skin of the existing genera is naked, but in some extinct genera it is partly covered with shagreen granules and plates. A remarkable peculiarity of the Chimaeroids consists in the unusually conspicuous character of the mucous-canals, which traverse the skin of the head and form the very prominent lateral line of the trunk. These are surrounded by numerous, closely arranged, calcified rings of cartilage.

The existing representatives of the Holocephali are only an insignificant remnant of a former much more extensively developed group of Selachians, which appears first in the Devonian, and is perhaps genetically connected with the Cochliodontidae.

Family 1. **Ptyctodontidae.** Smith Woodward.[1]

Known only by dental plates, which are laterally compressed, seem to form a single pair meeting at the symphysis of each jaw, and exhibit either few tritoral areas, or sharp cutting edges. Devonian.

Ptyctodus, Pander (*Aulacosteus*, Eichwald; *Rinodus*, Newb. and Worth.). Tritoral area composed of very hard, punctate, superimposed laminae, arranged obliquely to the functional surface. *P. obliquus*, Pander, from Middle Devonian, North Russia. *P. molaris*, East.; Eifel Devonian. *P. calceolus*, Newb., and *P. ferox*, East.; Middle and Upper Devonian, Wisconsin, Illinois, and Iowa.

Rhynchodus, Newb. Dental plates with sharp cutting edges, and no well-differentiated tritors. North America, and the Eifel, Germany.

Palaeomylus, Sm. Woodw. Robust teeth, with broad symphysial surface, and one punctate tritoral area, not laminated. North America.

Family 2. **Squaloraiidae.** Smith Woodward.

Trunk depressed and elongated, and head produced into a long, slender snout. Lower dentition comprising one pair, upper dentition two pairs of thin corrugated dental plates without definite tritors. Males with a prehensile spine on the snout. Dorsal fin spine absent. Numerous conical or stellate dermal tubercles. Lower Jurassic.

Squaloraja, Riley (*Spinacorhinus*, Ag.). Tail tapering to a point. Rostral spine with expanded base, tapering to a point in front. Vertebral rings well calcified, consisting of several concentric lamellae. *S. polyspondyla*, Ag., known by nearly complete skeletons 0·45 in length, from the Lower Lias of Lyme Regis, Dorsetshire.

[1] *Eastman, C. R.*, Dentition of Devonian Ptyctodontidae (Amer. Nat. vol. XXXII.), 1898.

Family 3. **Myriacanthidae.** Smith Woodward.

Trunk elongated. Two upper pairs and one lower pair of thin dental plates, also a stout, median, incisor-like tooth at the symphysis of the mandible. Head with a few dermal plates. Males with a prehensile spine on the snout. Anterior dorsal fin above the pectorals, with a long, straight, robust spine. Jurassic.

Myriacanthus, Ag. (*Prognathodus*, Egerton; *Metopacanthus*, Zittel). Rostrum with a terminal cutaneous flap. Anterior upper dental plate smaller than the posterior plate. Dorsal fin spine long and slender, somewhat laterally compressed, with a large internal cavity; sides ornamented with small tubercles; a series of large, thorn-shaped tubercles arranged along each edge of the flattened posterior face, passing into a single median row distally, and a single series of similar denticles on the anterior border. Rostral spine elongated and pointed, with expanded base. Dermal plates tuberculated. *M. paradoxus*, Ag., and *M. granulatus*, Ag., from Lower Lias of Lyme Regis.

Chimaeropsis, Zittel (Fig. 91). Mandibular dental plates (*md*), slightly arched, with a large tritoral area; the symphysial tooth (*x*) externally

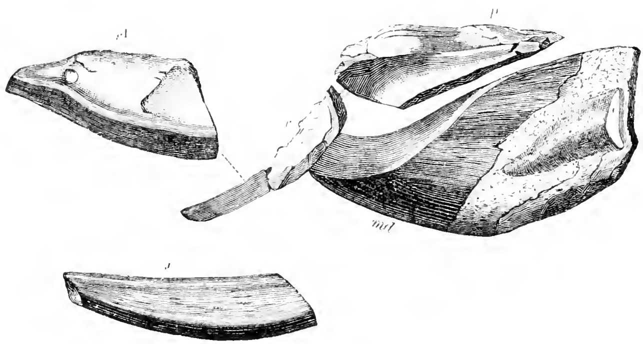


Fig. 91.

Chimaeropsis paradoxa, Zitt. Upper Jurassic (Lithographic Stone); Eichstädt, Bavaria. 1/2 nat. size. *md*, Mandibular tooth; *p*, Hinder upper tooth; *r*, Anterior upper tooth in side view; *r*[1], Same from lower side; *x*, Slender premandibular tooth.

(inferiorly) convex, internally (superiorly) flat or concave. Anterior (*r*) and posterior (*p*) upper dental plates triangular, the former not smaller than the latter, and tapering in front, the latter tapering behind. Fin spine as in *Myriacanthus*. Body covered with small, conical, radiately grooved placoid scales. Upper Jurassic (Lithographic Stone) of Bavaria.

Family 4. **Chimaeridae.** Chimaeras.[1]

Trunk elongated, shark-like. Teeth forming two pairs of robust dental plates in the upper jaw, the foremost the smaller, both pairs thickened and closely apposed in the longitudinal mesial line of the mouth; lower dentition comprising a single pair of beak-shaped plates meeting at the symphysis; the plates usually with several tritors. Pectoral fins very large, fan-like, with simple, horny rays; anterior dorsal fin above the pectorals, with a large spine articulated to a cartilaginous base; posterior dorsal

[1] *Newton, E. T.*, The Chimaeroid Fishes of the British Cretaceous Rocks (Mem. Geol. Survey, Mon. No. IV.), 1878.

fin low, much extended. Skin naked, or with shagreen granules. Jurassic to Recent.

Ischyodus, Egerton (*Leptacanthus*, Ag.; *Auluxacanthus*, Sauvage; *Chimaeracanthus*, Quenstedt), (Fig. 92). Lower dental plates rhomboidal, with a narrow symphysial facette; upper part of outer face covered with a thick layer of dentine, and oral margin sharp; four rough punctate tritors present. Posterior upper dental plates triangular, tapering in front, with four tritors; anterior upper teeth square, antero-posteriorly compressed. Dorsal fin spine laterally compressed, smooth or longitudinally striated, with a double longitudinal series of denticles on the hinder face. Males with a short, arched head spine, bearing a cluster of denticles at the end. Nearly complete skeletons of *I. avitus*, Meyer sp. (Fig. 92), and *I. quenstedti*, from the Lithographic Stone of Bavaria. Detached teeth from the Bathonian (Stonesfield Slate) to the Upper Cretaceous of England, France, Germany, and Switzerland; also from Cretaceous of Amuri Bluff, New Zealand.

Ganodus, Ag. Dentition as in *Ischyodus*, but posterior upper dental plate deeply excavated behind, with a double longitudinal series of numerous small tritors. Bathonian (Stonesfield Slate), England. *G. oweni*, Ag., and other species.

FIG. 92.

Ischyodus avitus, H. v. Meyer. Almost complete skeleton, 1/2 nat. size. Upper Jurassic (Lithographic Stone); Eichstädt (after H. v. Meyer).

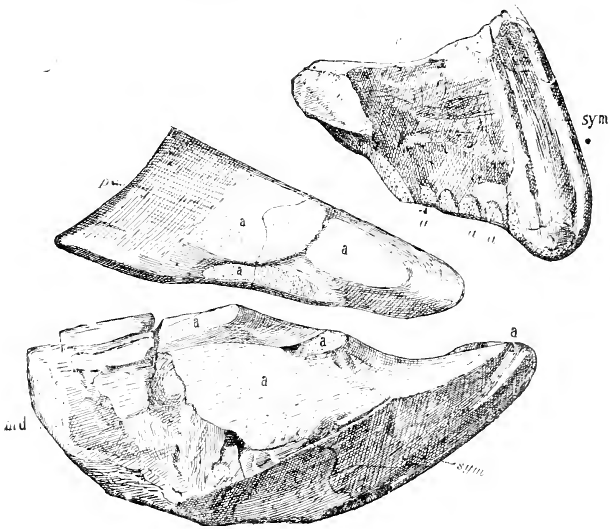


FIG. 93.

Edaphodon sedgwicki, Ag. sp. Teeth, 1/2 nat. size. Lower Chalk: Lewes. *md*, Left mandibular tooth, inner aspect; *p*, Left hinder upper tooth, oral aspect; *r*, Left anterior upper tooth, inner aspect; *a*, Tritors; *sym*, Symphysial border (after E. T. Newton).

Pachymylus, *Brachymylus*, Sm. Woodw. Upper Jurassic: England.

Edaphodon, Buckland (*Passalodon*, Buckl.; *Eumylodus, Mylognathus*, Leidy; *Dipristis*, Marsh; *Leptomylus*, Cope), (Fig. 93). Lower dental plates with a broad symphysial facette; posterior upper dental plates tapering in front, truncated behind, and with three tritors. Cretaceous, Eocene, and Oligocene of Europe and North America.

Elasmodectes, Newton (*Elasmognathus*, Newton, *non* Gill). Mandibular teeth laterally compressed and trenchant, with a series of small tritors along the oral border. *E. willetti*, Newton, from Lower Chalk, Kent.

Amylodon, Storms. Lower Miocene (Rupelian); Belgium.

Elasmodus, Egerton. Upper Cretaceous of Belgium; Eocene of England and Prussia.

Dental plates of the existing genus *Callorhynchus*, Gronow, have been identified from the Cretaceous of Amuri Bluff, New Zealand; of the existing genus *Chimaera*, Linn., from the Upper Tertiary of Europe and Java.

Ichthyodorulites.

Fossil fin spines consisting of dentine or vasodentine, and thus presumably referable to the Selachii, are frequently found isolated especially in the Palaeozoic formations, and can only be in part assigned to definite genera. These are therefore described under provisional generic names. Most of them are bilaterally symmetrical, and may be regarded as median dorsal spines; but several are distinctly rights and lefts, and belong either to the paired fins, as in Acanthodidae, or to the side of the head, as in *Menaspis* among Cochliodontidae. In the unsymmetrical spines, the base is, as a rule, abruptly truncated; in the bilaterally-symmetrical dorsal spines, on the other hand, it is usually elongated and tapers to the proximal end.

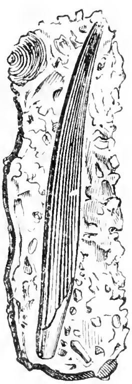


Fig. 94.

Onchus tenuistriatus, Ag. Fin-spine, nat. size. Upper Silurian; Ludlow, England.

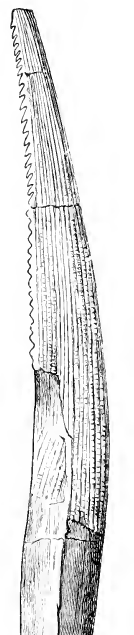


Fig. 95.

Ctenacanthus denticulatus, M'Coy. 1/2 nat. size. Carboniferous Limestone; Monaduff, Ireland (after M'Coy).

Among the Ichthyodorulites not yet referable with certainty to definite genera or families, the following may be enumerated.—

(*a*) Slender, bilaterally-symmetrical spines, with a smooth base sharply separated from the exserted portion; internal cavity open posteriorly towards the base. Probably for the most part referable to the Cestraciontidae. *Onchus*, Ag. (Fig. 94); Upper Silurian and Devonian, Europe and eastern North America. *Ctenacanthus*, Ag. (Fig. 95), possibly the fin spines of *Orodus*; Lower Carboniferous, Europe and North America. *Homacanthus*, Ag.; Devonian and Lower Carboniferous. *Acondylacanthus*, St. J. and Worth.; *Asteroptychius*, M'Coy; *Lispacanthus*, Davis; *Geisacanthus*, St. J. and Worth.; Lower Carboniferous. *Lepracanthus*, Owen; British Coal Measures. *Wodnika*, Münster; Permian (Kupferschiefer of Germany). (Fig. 96). *Nemacanthus*, Ag.; Rhaetic and Lower Jurassic.

(*b*) Slender, bilaterally-symmetrical spines, with little or no smooth inserted portion, and internal cavity only open at the proximal end. *Gnathacanthus*, Davis; Lower Carboniferous, Armagh, Ireland. *Pristacanthus*, Ag.; Bathonian, Oxfordshire and Normandy.

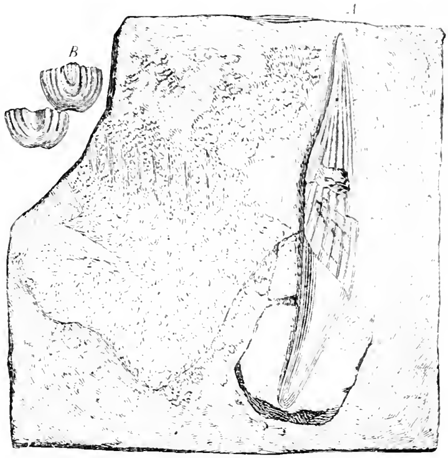


FIG. 96.
Wodnika striatula, Munst. Enlarged. Kupferschiefer; Riechelsdorf, Hesse. *A*, Fin-spine. *B*, Shagreen granules.

(*c*) Right and left paired spines, most probably connected with fins. *Machaeracanthus*, Newb. (Fig. 97); *Heteracanthus*, Newb.; *Haplacanthus*, Ag. Devonian; Europe and North America. *Gyracanthus*, Ag. Lower Devonian (Canada) to Upper Carboniferous (Europe and North America).

FIG. 97.
Machaeracanthus major, Newberry. Middle Devonian; Sandusky, Ohio. ½ nat. size (after Newberry).

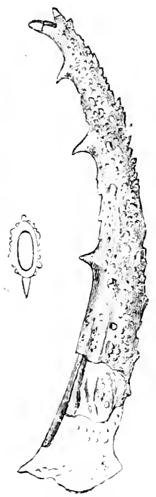


FIG. 98.
Gampsacanthus typus, St. John and Worthen. Carboniferous Limestone; St. Louis, Missouri (after St. John and Worthen).

(*d*) Paired spines, usually with a broad, truncated base, a large internal cavity and the outer face tuberculated. Probably lateral head spines, as in *Menaspis* among Cochliodontidae. *Oracanthus*, Ag. (*Platyacanthus*, M'Coy; *Pnigeacanthus*, St. J. and Worth.; *Pholeracanthus*, Davis.) Carboniferous of Europe and North America (spines already observed on either side of head in one example of *O. armigerus*, Traquair, from Calciferous Sandstones of Eskdale, Dumfries). *Physonemus*, M'Coy (*Xystracanthus*, Leidy; *Drepanacanthus*, Newb.); *Erismacanthus*, M'Coy; *Gampsacanthus*, St. J. and Worth. (Fig. 98); *Lecracanthus*, St. J. and Worth.; *Dipriacanthus*, M'Coy, etc. Lower Carboniferous.

(*e*) Spines of entirely doubtful position. *Cynopodius*, Traquair. Lower Carboniferous; Scotland. *Euctenius*, Traquair. Coal Measures; Scotland, England, and Ohio, U.S.A. *Stethacanthus*, Newb. Upper Devonian and Lower Carboniferous; Ohio, Illinois, and Iowa.

Sub-Class 2. OSTRACODERMI. Cope.

Early Palaeozoic fishes with persistent notochord, and endoskeleton not calcified. Mandible and arches for paired fins apparently absent. Exoskeleton well developed, the head and anterior portion of the trunk usually covered with plates. Mouth without hard parts.

The Ostracoderms form one of the most characteristic groups of the early Palaeozoic fish-fauna; but their true systematic position is still uncertain. Their remains were formerly compared with the armour of reptiles such as tortoises, and also with crabs and water-beetles; while more lately they have even been supposed to exhibit resemblances to Arachnids. They were first recognised as fishes by Agassiz, and referred by him to the Ganoidei. Unless appearances in the fossils are deceptive, they are distinguished from all typical fishes, and agree with the *Cyclostomi* in the lack of a lower jaw and of arches for paired limbs; but there seems to be evidence of paired nasal openings in *Pterichthys* and *Bothriolepis*.

Four orders of Ostracophores may be recognised as follows:—*Heterostraci*, *Anaspida*, *Aspidocephali*, and *Antiarcha*. In the first, the exoskeleton sometimes consists of placoid tubercles of dentine, as in sharks; in the second the tubercles on the head region are never fused. In the more typical Heterostraci, as also in the Aspidocephali and Antiarcha, this primitive armour is modified so that the head and anterior abdominal region become invested with dermal plates, which are usually as well developed as in modern sturgeons and certain bony fishes (Siluridae). The sub-class is restricted to the Upper Silurian and Devonian.

Order 1. HETEROSTRACI. Ray Lankester.[1]

Exoskeleton consisting of shagreen, plates, or scales, without bone cells; each fully formed plate comprising three superimposed layers—an inner "nacreous" layer of lamellae, a relatively thick middle zone with numerous vacuities, and an outer hard layer of vaso-dentine. Dorsal shield, when present, of few pieces, and orbits wide apart, laterally placed. No paired appendages.

Family 1. Coelolepidae. Pander.

Head and trunk relatively large and depressed, completely covered with placoid tubercles of dentine, scarcely if at all fused into groups; the small, slender caudal region sharply constricted from the head region and distinctly heterocercal. Upper Silurian and Lower Devonian.

The dermal tubercles of genera of this family have long been known from the Upper Silurian of England and the Isle of Oesel in the Baltic Sea; but until the discovery of complete specimens in the Upper Silurian of Lanark-

[1] *Alth, A. von*, Ueber *Pteraspis*, *Cyathaspis*, und *Scaphaspis* (Beitr. Palaeont. Oesterr.-Ungarns, vol. II.), 1886.—*Huxley, T. H.*, On *Cephalaspis* and *Pteraspis* (Quart. Journ. Geol. Soc. vols. XII., XIV., XVII.), 1856, 1858, 1861.—*Kner, R.*, Ueber *Cephalaspis lloydii* und *lewisii* (Haidinger's Naturw. Abhandl. vol. I.), 1847.—*Kunth, A.*, Ueber *Pteraspis* (Zeitschr. deutsch. geol. Ges. vol. XXIV.), 1872.—*Lankester, Ray*, and *Powrie, J.*, A Monograph of the Fishes of the Old Red Sandstone. I. Cephalaspidae (Mon. Palaeont. Soc.), 1868.—*Roemer, Ferd.*, Ueber *Palaeoteuthis dunensis* (Palaeontogr. vol. IV.), 1856.—*Traquair, R. H.*, Report on Fossil Fishes, etc. (Trans. Roy. Soc. Edinb. vol. XXXIX. Nos. 21, 32), 1899.

shire, they were commonly supposed to belong to sharks. The latter discovery is considered by Traquair to indicate some close relationship between the Ostracophores and the primitive Selachii.

Thelodus, Ag. (*Coelolepis*, *Pachylepis*, *Thelolepis*, Pander; *Cephalopterus*, Powrie; *Turinia*, Traq.), (Fig. 99). Dermal tubercles small, quadrangular, and nearly uniform. A small dorsal fin near base of heterocercal tail. No enlarged ridge scales. *T. parvidens*, Ag.; detached tubercles in Ludlow Bonebed and Oesel Limestone. *T. scoticus*, Traq.; complete skeletons in Upper Ludlow, Logan Water, Lanarkshire. *T. pagei*, Powrie sp.; complete skeleton, Lower Old Red Sandstone, Turin Hill, Forfarshire.

Fig. 99.

Thelodus parvidens, Ag. Dermal tubercles, nat. size (above) and enlarged. Upper Silurian (Ludlow Bone Bed); Ludlow.

Lanarkia, Traq. Dermal tubercles are small, pointed, hollow spines, not of uniform size. *L. horrida*, Traq., and other species represented by skeletons in the Upper Silurian Passage Beds of Birkenhead Burn and Seggieholm, Lanarkshire.

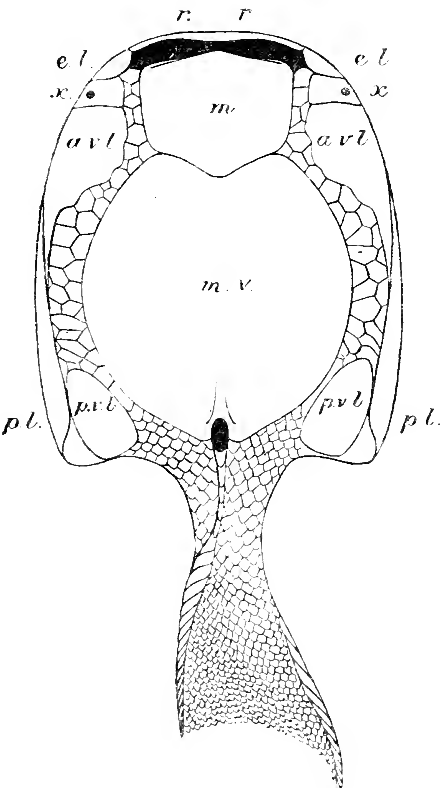


Fig. 100.

Drepanaspis gemuendenensis, Schluter. Restored outline of ventral aspect, surface ornament omitted. Lower Devonian: Gemünden, Eifel. *m.v*, Median ventral plate; *p.l*, Postero-lateral plates; *p.v.l*, Postero-ventro-lateral plates; *r*, Rostral plates; *x*, Orbits. 1/4 (after Traquair).

Family 2. **Psammosteidae.** Traquair.

Dermal armour of head region more or less completely fused into large plates. External layer of each dermal plate forming a tubercular ornament. Dermal sense organs not penetrating the tissue of the armour. Devonian.

Psammosteus, Ag. (*Placosteus*, Ag.; *Psammolepis*, Ag.). External ornament of very closely arranged, rounded, or elongated tubercles which are usually crimped round the margin. Orbit probably enclosed in the shield. Paired spines (of uncertain position) broad and triangular, with a large internal cavity and short base of insertion. Large ridge scutes on the tail, ornamented as the body shield and paired spines. *P. maeandrinus*, Ag., and *P. paradoxus*, Ag., from Upper Devonian, Russia. *P. taylori*, Traq., from Upper Old Red Sandstone, Elgin. Other species from the Lower Old Red Sandstone of west of England, and from Upper Devonian, Spitzbergen.

Drepanaspis, Schlüter (Fig. 100). Head region covered with one large median plate, two postero-lateral plates, two rostral plates, and intervening small polygonal plates. Tail as in *Psammosteus*. *D. gemuendenensis*, Schlüt., from Lower Devonian, Gemünden, Eifel.

Family 3. **Pteraspidae.** Smith Woodward.

Dermal armour of head region completely fused into large plates. External layer of each dermal plate forming an ornament of very fine, concentric, closely arranged ridges, parallel with the outer margin; middle layer with large polygonal cancellae. Dermal sense organs well developed, arranged in canals traversing the middle layer of the shield and opening by a double series of pores externally. Ventral shield simple. Tail presumably heterocercal, and scales of caudal region, when preserved, numerous and rhomboidal. Upper Silurian and Lower Devonian.

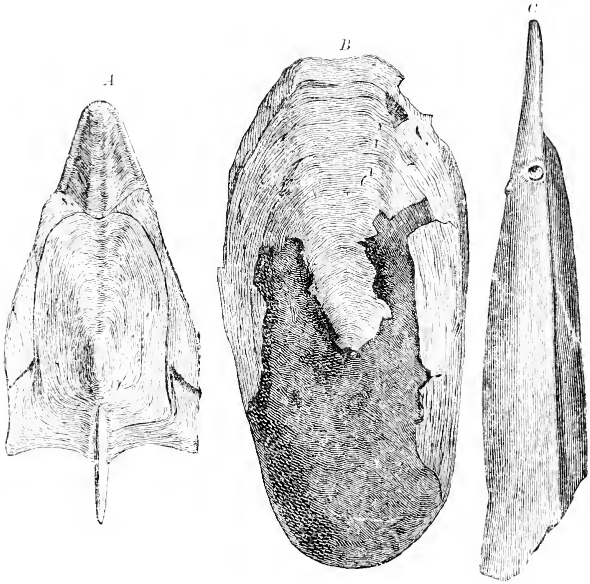


Fig. 101

A, B, Pteraspis rostrata, Ag. sp. Lower Old Red Sandstone (Cornstones); Herefordshire. *A*, Dorsal shield, 1/2 nat. size, restored. *B*, Ventral shield (*Scaphaspis lloydi*, Ag. sp.), 2/3 nat. size (after Ray Lankester). *C*, Dorsal and ventral shields of *Pteraspis*, lateral aspect, restored from a specimen found in Galicia (after Alth).

Three genera of this family are distinguished according to the complexity of the dorsal shield. The simple ventral shield, similar in each form, was originally mistaken for dorsal armour, and named *Scaphaspis* by Lankester.

Pteraspis, Kner (*Palaeoteuthis*, *Archaeoteuthis*, F. Roemer), (Figs. 101-103). Dorsal shield arrowhead-shaped, consisting of seven separately calcified plates—a large central disc; a triangular rostral plate in front; a median spine behind; a pair of orbital plates, completely enclosing the orbit on either side, and partially inserted between the rostrum and central disc; and a pair of lateral cornua, each

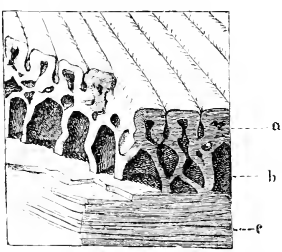


Fig. 102.

Pteraspis rostrata, Ag. sp. Piece of shield, much magnified. *a*, Upper, *b*, Middle, and *c*, Lower layer (after Ray Lankester).

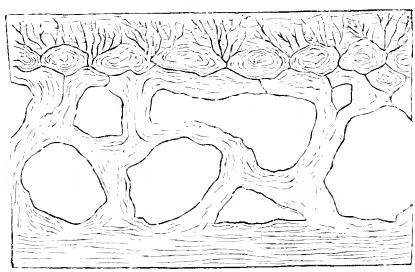


Fig. 103.

Pteraspis rostrata, Ag. sp. Vertical section of head shield parallel with a longitudinal rib, highly magnified (after Ray Lankester).

pierced by a large, apparently branchial foramen. *P. rostrata*, Ag. sp. (Fig. 101), and other species from the Lower Old Red Sandstone of England, Scotland, Rhenish Prussia, and Galicia; also from the Upper Silurian of Galicia, and probably from the Lower Devonian of Spitzbergen.

Palaeaspis, Claypole (*Holaspis*, Lank. *non* Gray). Dorsal shield apparently simple, without posterior spine; orbits merely forming notches. *P. americana*, Clay., from Upper Silurian (Onondaga Group), Pennsylvania. *P. sericea*, Lank. sp., from Lower Old Red Sandstone, Monmouthshire.

Cyathaspis, Lank. (*Diplaspis*, Matthew). Dorsal shield consisting of a large central disc; two long and slender lateral cornua, which are notched anteriorly by the orbits and pierced further back by the supposed branchial foramen, and a short and broad rostral plate. *C. banksi*, Huxley and Salter sp., from Upper Silurian (Ludlow Bone-bed and Passage Beds) of Herefordshire. *C. schmidti*, Geinitz, from Wenlock Limestone of Isle of Gotland. Other species from corresponding formations in Germany, Galicia, and New Brunswick. The so-called *Scaphaspis ludensis*, Salter sp., from Lower Ludlow, Leintwardine, probably belongs to this genus.

Order 2. ANASPIDA. Traquair.[1]

Tubercles only on the head region, not fused into plates; the calcifications probably in part with bone cells. No paired appendages.

Family 1. Birkeniidae. Traquair.

External ornament, when present, tubercular. Branchial openings a series of small perforations laterally placed. One small dorsal fin; tail heterocercal. Upper Silurian.

Birkenia, Traq. (Fig. 104). Trunk irregularly covered with deepened

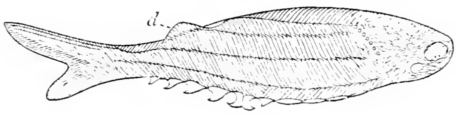


FIG. 104.

Birkenia elegans, Traq. Restored outline in side view, about nat. size. Upper Silurian; Lanarkshire (after Traquair). *d*, Dorsal fin.

scales; a series of large scutes along the ventral border. *B. elegans*, Traq. Upper Silurian; Lanarkshire.

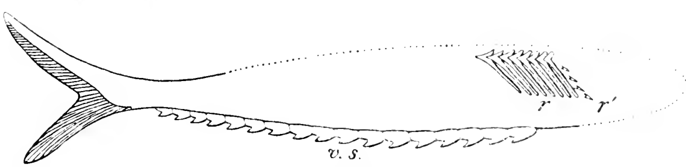


FIG. 105.

Lasanius problematicus, Traq. Restored outline, about nat. size. Upper Silurian; Lanarkshire. *r*, Postcephalic rods; *r'*, Chain of ossicles; *v.s.* Ventral scutes (after Traquair).

Lasanius, Traq. (Fig. 105). Trunk naked, except immediately behind the

[1] *Traquair, R. H.*, Report on Fossil Fishes collected by the Geological Survey of Scotland in the Silurian Rocks of the south of Scotland (Trans. Roy. Soc. Edinb. vol. XXXIX., with 5 pls.), 1899.

head, where rudiments occur; a series of large scutes along the ventral border. *L. problematicus*, Traq. Upper Silurian; Lanarkshire.

Family 2. **Euphaneropidae.** Smith Woodward.

As Birkeniidae, but no series of branchial openings. Upper Devonian.

Euphanerops, Sm. Woodw. *E. longaevus*, Woodw., the type species, is the only known Ostracophore which displays traces of the axial skeleton of the trunk. Upper Devonian; Canada.

Order 3. ASPIDOCEPHALI. Brandt.[1]

(*Osteostraci*, Ray Lankester.)

Exoskeleton consisting of calcifications, partly with bone cells; each plate in the head region comprising three superposed layers—an inner laminated layer with spindle-shaped bone cells; a relatively thick middle layer of polygonal cancellae which may be more or less solid though with a coarse reticulation of large vascular canals; also an outer hard layer of vaso-dentine. Orbits close together. No paired appendages.

Family 1. **Ateleaspidae.** Traquair.

Head shield rounded or tapering in front, abruptly truncated behind, consisting of loose plates. Body covered with quadrangular scales which are deepened on the flank. Tail heterocercal. Upper Silurian.

Ateleaspis, Traq., from the Upper Silurian Passage Beds of Seggieholm, Lanarkshire. The tubercles of the head region are fused together into small plates. The genus may be a link between the Heterostraci and Osteostraci, but the microscopical structure of the armour agrees with that of the latter.

Family 2. **Cephalaspidae.** Agassiz.

Head shield rounded or tapering in front, abruptly truncated behind; interorbital piece firmly fixed; an ornament of rounded or stellate tubercles. Dermal sense organs leaving no impressions on the exoskeleton. Body covered with quadrangular scales, which are deepened on the flank. One small dorsal fin; tail heterocercal. Upper Silurian to Upper Devonian.

Cephalaspis, Ag. (*Eucephalaspis*, *Hemicyclaspis*, *Zenaspis*, R. Lank.), (Figs.

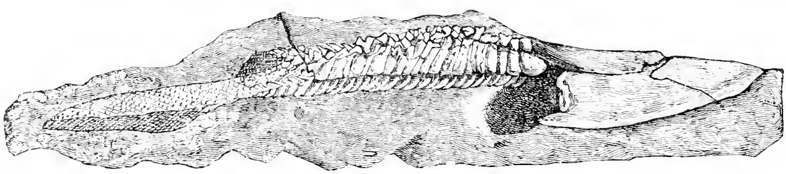


FIG. 106.

Cephalaspis lyelli, Ag. Lower Old Red Sandstone; Arbroath, Scotland. 1/2 nat. size (after Ray Lankester).

106, 107). Postero-lateral angles of shield more or less produced into pointed cornua, external to a small flexible flap on each side, which is stiffened by

[1] *Huxley, T. H.*, On Cephalaspis and Pteraspis (Quar. Journ. Geol. Soc. vols. XII., XIV., XVII.), 1856, 1858, 1861.—*Lankester, E. R.*, The Cephalaspidae (Monogr. Palaeont. Soc.), 1867-69.—*Schmidt, Friedr.*, Verhandl. k. russ. mineral. Ges. 1873 and 1886; and Bull. Acad. Imp. Sci. St. Petersb. 1894.—*Rohon, J. V.*, Die obersilurischen Fische von Oesel I. (Mem. Acad. Imp. Sci. St. Petersb., ser. 7, vol. XXXVIII.). 1892; also Bull. Acad. Imp. 1893.

bony plates, and seems to represent an operculum. Body triangular in transverse section, the flanks covered with three longitudinal series of deepened scales, the middle series deepest. Ventral scales small. Dorsal fin triangular, at the base of the heterocercal tail; membrane of dorsal and anal fins stiffened with very small calcifications which are arranged in parallel rows simulating rays. *C. lyelli*, Ag. (Fig. 106), from Lower Old Red Sandstone of Scotland and west of England. *C. magnifica*, Traq., the largest known species, with shield measuring 0·22 m. across, from Caithness Flagstones. Other species from Upper Silurian and Lower Devonian of Scotland, England, and Canada. One species (*C. laticeps*, Traq.), from Upper Devonian, Scaumenac Bay, Canada.

Eukeraspis, Lank. (*Sclerodus*, *Plectrodus*, Ag.). As above, but posterior cornua excessively elongated, and a row of twelve large "marginal cells" around the rim in front. The detached denticulated cornua were originally mistaken for jaws. *E. pustulifera*, Ag. sp., from Upper Silurian, Herefordshire.

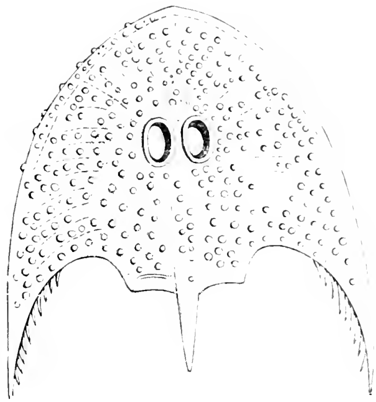


Fig. 107.

Head shield of *Cephalaspis lyelli*, Ag. Lower Old Red Sandstone; Herefordshire (after Lankester). 1/2.

Thyestes, Eichw. (*Auchenaspis*, Egerton). Head shield as in *Cephalaspis*, but three or four series of dorso-lateral scales fused into a continuous plate immediately behind it. Body depressed, ovoid in transverse section. Known species very small. *T. verrucosus*, Eichw., from Upper Silurian, Isle of Oesel. So-called *Auchenaspis* from Upper Silurian and Lower Old Red Sandstone Passage Beds of Herefordshire.

Family 3. **Tremataspidae.** Smith Woodward.

Head shield rounded or tapering in front, fused with the dorsal body-shield, which is truncated behind; interorbital piece not fixed. Upper Silurian and Lower Devonian.

Trematuspis, Schmidt. Dorsal shield rounded in front, gently arched, without cornua; ventral shield simple. External surface covered with punctate ganoine, the punctations often arranged in reticulating lines; superficial tuberculations almost or entirely absent. Two pairs of large openings laterally placed in the anterior half of the dorsal shield are interpreted by Smith Woodward as occurring in the roof of the branchial chamber, covered over during life but ensuring flexibility. Ventral aspect immediately behind the position of the mouth covered with a number of symmetrically arranged polygonal plates, between which and the great ventral plate of the trunk is a transverse series of nine small openings on each side, probably of branchial nature. Tail covered with rhombic and polygonal scales, which have been named *Dasylepis*, *Dictyolepis*, *Melittomalepis*, and *Stigmolepis* by Pander. *T. schrenki*, Pander sp., and other species in the Upper Silurian, Isle of Oesel, Baltic Sea.

Didymaspis, Lankester. *D. grindrodi*, Lank., from Lower Old Red Sandstone, Ledbury, Herefordshire.

Order 4. ANTIARCHA. Cope.[1]

Dermal armour fused into large plates on the head and abdominal region. Exoskeleton consisting of calcifications with bone corpuscles, and invested with a more or less continuous layer of ganoine. Dermal sense organs occupying open grooves on the exoskeleton. Dorsal and ventral shields consisting of several symmetrically arranged pieces, and the head articulated with the trunk. Orbits close together. A pair of paddle-like pectoral appendages, invested in dermal plates, articulated with the anterior ventro-lateral plates of the trunk. Median fins not continuous.

The bony plates of the Antiarcha consist of three layers with numerous bone cells, the middle layer traversed by large canals and lacunae, while the outer and inner layers exhibit a more compact texture.

Family 1. Asterolepidae. Traquair.

Exoskeleton robust and tuberculated. Dorsal and ventral shields of trunk firmly united by the lateral plates. Interorbital piece not fixed. A pair of paddle-like appendages, completely encased in dermal plates, movably articulated by a complex joint with the anterior ventro-lateral plates of the trunk. Tail heterocercal, and one small dorsal fin. Devonian.

Pterichthys, Ag. (*Pterichthyodes*, Bleeker), (Figs. 108, 109). From 3 to 20

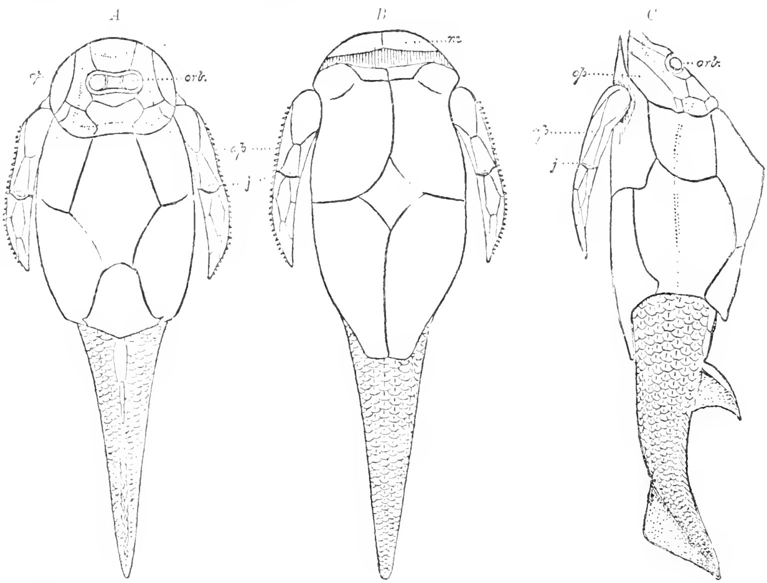


Fig. 108.

Pterichthys milleri, Ag. Restoration from above (*A*), below (*B*), and in side view (*C*). Lower Old Red Sandstone; Scotland. *cp*, Pectoral appendages; *j*, Articulation; *op*, Operculum; *orb*, Orbit (after Traquair).

cm. in length, with a small head, which is rounded in front, a broad and deep trunk flattened below, and a scaly tail. The upper surface of the head is

[1] *Pander, C. H.*, Die Placodermen des devonischen Systems. St. Petersburg, 1857.—*Traquair, R. H.*, Ann. Mag. Nat. Hist. ser. 6, vol. II. 1888; and Mon. Palaeont. Soc., 1894.

covered with four pairs of lateral plates and four unpaired median plates, which are united by straight sutures. On the lower surface the cleft for the mouth is bounded in front by a pair of transversely elongated plates, which are sometimes supposed to represent the upper jaw. Behind the cleft a pair of smaller plates occurs fixed to the front of the abdominal shield. The trunk is armoured above by two large median and two pairs of lateral plates; on its ventral surface four large ventro-laterals surround a small rhombic ventro-median element. The ventro-laterals are sharply bent upwards and outwards near their lateral border to take part in covering the flank. Both the head plates and the dorso-lateral plates of the trunk are traversed by sensory grooves, those of the head being united by two parallel commissures. The two hinder lateral plates of the head and the adjoining body plates have bevelled edges, so that the former overlap the latter. The anterior median dorsal plate of the trunk somewhat overlaps the lateral plates, and is overlapped behind by the border both of the posterior dorso-laterals and of the posterior median dorsal plate. The orbits occur at the two ends of a transverse cleft on the upper surface of the head, and are separated by a quadrangular median plate (*os dubium* or *os pineale*), which exhibits a small deep pit on its inner face. The two anterior ventro-lateral plates of the trunk are provided in front with an articular hollow on each side, in which are fixed the armoured paddle-shaped pectoral appendages. The latter do not reach the hinder end of the body shield, and exhibit one transverse articulation (*j*) at about their middle. The tail is covered with thin, rounded, or six-sided, overlapping scales. The single dorsal fin is small. The tail is heterocercal, with large fulcral scales on its upper border, and the fin membrane confined to the lower lobe. *P. milleri*, Ag., and other species represented by complete but usually ill-preserved examples in the Lower Old Red Sandstone of Scotland. Fragments in the Middle Devonian of the Eifel.

FIG. 109

Pterichthys milleri, Ag. Lower Old Red Sandstone; Gamrie, Scotland. *A*, Specimen in nodule. 1/2 nat. size. *B*, Scale enlarged (after Egerton).

Asterolepis, Eichw. (*Narcodes*, *Odontacanthus*, Ag.). As *Pterichthys*, but often larger, and the anterior median dorsal plate overlaps both the anterior dorso-laterals and the posterior dorso-lateral plates. Chiefly represented by detached plates in the Devonian of N.-W. Russia and in the Upper Old Red Sandstone of Scotland. More doubtful fragments from the Devonian of Bohemia, the Eifel, East Greenland, and Australia.

Microbrachius, Traquair. *M. dicki*, Traquair, from Lower Old Red Sandstone, Caithness and Orkney.

Bothriolepis, Eichw. (*Pamphractus*, *Placothorax*, *Homothorax*, *Glyptosteus*, Ag.). Armour nearly as in *Pterichthys*, but the pectoral appendages reaching backwards beyond the body shield, and the hinder mucous canal commissure on the head V-shaped. Tail unknown, probably not scaly. An Upper Devonian genus, known from N.-W. Russia, Scotland, England, Canada, and Pennsylvania. Remarkably fine examples of the armour of *B. canadensis*, Whiteaves, 0·20 m. in length, from Scaumenac Bay, Province of Quebec, Canada.

? *Ceraspis*, Schlüter; *Belemnacanthus*, Eastm. Middle Devonian; Eifel.

Incertae Sedis.

Macropetalichthys, Norwood and Owen. Plates of cranial shield fused together in adult; orbits completely enclosed in the shield; sensory canals forming large tubular excavations in the bone, opening at the external surface by a continuous narrow slit or a series of pores. Jaws and other parts of the skeleton unknown. Middle Devonian (Corniferous Limestone); U.S.A. Also Upper and Lower Devonian of Eifel.

Asterosteus, Newb. Known only by the flattened and elongated cranial shield, which has the constituent elements fused in the adult. Orbits placed far forwards and forming broad notches. Corniferous Limestone; Ohio.

Sub-Class 3. ARTHRODIRA. Smith Woodward.

Early Palaeozoic fishes with persistent notochord, and endoskeleton superficially calcified. Head and trunk armoured with symmetrically arranged bony plates, some of which are traversed by sensory grooves: head shield movably articulated by a pair of ginglymoid joints with the body shield. Paired fins rudimentary or absent.

The Coccostean fishes were originally grouped by M'Coy with *Asterolepis* and *Pterichthys* in the "family Placodermi," and they are included by Pander in his "Placodermen." The resemblance between their jaws and those of the existing Dipnoi was pointed out by Newberry and Traquair; and they were provisionally regarded as an order of Dipnoi by Smith Woodward. Dean elevates them to the rank of an independent class, removing them from *Pisces* on the ground that their jaw elements are merely dermal ossifications, and are not articulated with the skull.

Family 1. Coccosteidae. Smith Woodward.[1]

Head shield comprising three pairs of lateral plates, one large median occipital plate, and two symmetrical pairs of plates in front of the latter, the foremost pair surrounding one or two small median plates. Orbits lateral; nasal openings small and far forwards; dental plates movable, toothless, or provided with cusps of dentine. Trunk with a large median dorsal plate often bearing a longitudinal median keel on its under surface; also two pairs of lateral plates, the anterior with a pair of articular

[1] *Traquair, R. H.*, On the Structure of *Coccosteus decipiens*, Ag. (Ann. Mag. Nat. Hist. ser. 6, vol. V. p. 125), 1890.—*Dean, B.*, Palaeontological Notes (Mem. N. Y. Acad. Sci. vol. II. pt. 3), 1901.—*Eastman, C. R.*, Some new points in Dinichthyid Osteology (Amer. Nat. vol. XXXII. p. 747), 1898.

processes for union with the head shield. Ventral body armour comprising two or three pairs of lateral plates and two small unpaired median plates. All external plates more or less tuberculated. Dorsal fin small; anal fin unknown; tail diphycercal or heterocercal. Devonian.

Coccosteus, Ag. (*Liognathus*, Newb.), (Figs. 110, 111). Head and trunk broad, the dermal plates covered with stellate tubercles. Cranial plates united by sutures, not fused. Orbit forming a notch in the anterior part of the lateral border of the shield; a bony sclerotic ring present. Besides the "maxilla" and "premaxilla," one or two inner pairs of dentigerous bones also

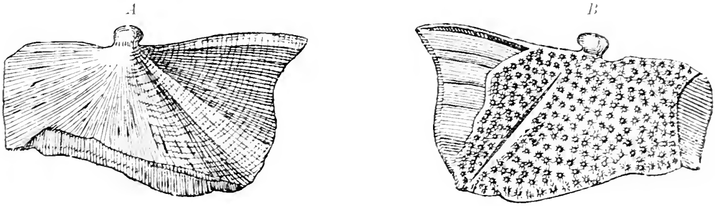


Fig. 110.

Coccosteus decipiens, Ag. Left antero-dorso-lateral plate of trunk, inner (*A*), and outer (*B*), aspects. Lower Old Red Sandstone; Scotland.

present in the upper jaw. In front of the ventral body shield occur a pair of transversely elongated slender plates, perhaps representing the pectoral arch; a small pectoral spine, but never any traces of pectoral fins observed. Ribs absent. Dorsal fin short-based. Tail destitute of scales. Nearly complete but imperfectly preserved skeletons of *C. decipiens*, Ag. (Figs. 110, 111), occur in the Lower Old Red Sandstone of Scotland. Fragments of other

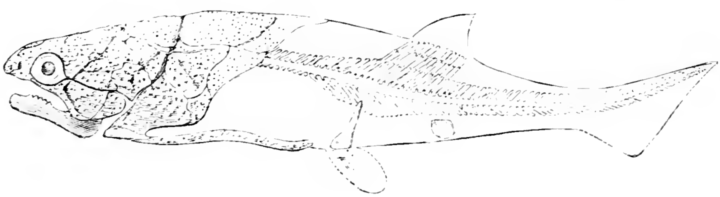


Fig. 111.

Coccosteus decipiens, Ag. Restoration, 1/2. Lower Old Red Sandstone; Scotland (after Smith Woodward).

species in the Upper Devonian of England, Ireland, Germany, Russia, and Canada. Also from Corniferous Limestone (Middle Devonian), Ohio, U.S.A.

Brachydirus, v. Koenen. Considered by von Koenen to differ from *Coccosteus* in the presence of a pair of hollow spines which perhaps represent pectoral fins. Upper Devonian; Bicken, Nassau.

Phlyctaenaspis, Traquair. Lower Devonian; Canada, west of England, and Russian Poland. *Acanthaspis*, Newb. Lower and Middle Devonian: U.S.A.

Chelyophorus, Ag. Upper Devonian: Russia.

Dinichthys, Newberry (Fig. 112). Very large, the head sometimes measuring 1 m. in length and 0·7 m. in breadth. Median occipital plate subtriangular with prominent median process behind; lateral occipital plates with very deep articular sockets for the reception of the process on the antero-dorso-lateral plates of the body shield. Orbit forming a notch as in *Coccosteus*. Premaxillae and symphysial end of mandibular bones with a pair of stout cusps or beaks, and the trenchant margin behind these sometimes toothed. Median dorsal plate very thick, often over 0·6 m. long and broad. Antero-dorso-lateral

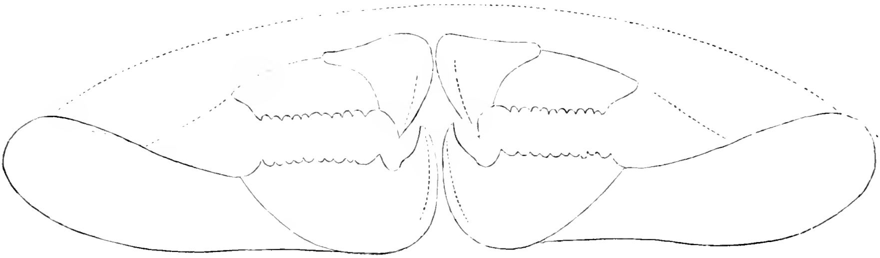


FIG. 112.

Dinichthys herzeri, Newberry. Diagrammatic front view of upper and lower jaws, 1/6. Upper Devonian (Huron Shales); Delaware, Ohio (after Newberry).

plate overlapped by the large "clavicular." Several species in the Middle and Upper Devonian of Iowa, Wisconsin, Ohio, New York, and Canada; others in the Devonian of the Eifel, Bohemia, and Russia.

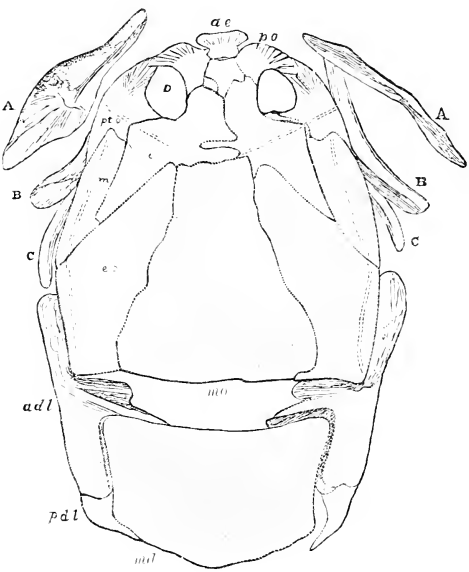


FIG. 113.

Homosteus milleri, Traq. Cranial and dorsal shield, 1/6 nat. size. Lower Old Red Sandstone; Caithness. *A*, *B*, *C*, Undetermined bones; *adl*, Anterior dorso-lateral; *ae*, Ethmoid; *c*, Central; *eo*, External occipital; *m*, Marginal; *md*, Median dorsal; *mo*, Median occipital; *o*, Orbit; *pdl*, Posterior dorso-lateral; *po*, Preorbital; *pto*, Postorbital. Pineal plate behind "ethmoid" or rostral. The double lines indicate the course of the sensory grooves (after Traquair).

Titanichthys, Newb. Cranial shield very large, thin and flattened, arrangement of plates closely similar to that of Dinichthys. Jaw elements much reduced, edentulous, probably sheathed in horn. Dorso-median without an inferior longitudinal keel, deeply emarginate in front. Antero- and postero-dorso-laterals fused, articulated to the cranial shield by a long hinge, and overlapped by the large claviculars. *T. agassizi*, N., has a horizontal expanse of 1·9 m. across head-shield and claviculars. Cleveland Shale (Upper Devonian); Ohio.

Homosteus, Asmuss. (Fig. 113). Very large fishes, broad and depressed. Orbits completely enclosed in the head shield; jaws slender and toothless. Median occipital plate antero-posteriorly elongated; median dorsal plate of the trunk broader than long. *H. milleri*, Traq., from Lower Old Red Sandstone, Caithness and Orkney. Other species in Upper Devonian of Livonia.

Heterosteus, Asmuss. Nearly resembling *Homosteus*, but larger, and anterior dorso-lateral body plates with an enormous anteriorly directed process which clasps the head shield on each side. *H. asmussi*, Ag. sp., common in Upper Devonian of Livonia, but known only by the massive detached plates.

Aspidichthys, *Glyptaspis*, *Trachosteus*, Newberry; *Anomalichthys*, v. Koenen; *Asteroplax*, Sm. Woodw. Devonian.

Mylostoma, *Diplognathus*, Newberry; *Selenosteus*, *Stenosteus*, Dean. Upper Devonian (Cleveland Shale); Ohio.

Most of the genera enumerated on this and the preceding page are regarded by Dean and others as types of distinct families.

Sub-Class 4. DIPNOI, Müller.[1] Lung-fishes.

Skeleton partially ossified, with numerous well-developed membrane bones. Pterygoquadrate arcade completely and immovably fused with the cranium; gill clefts feebly separated, opening into a cavity covered with a bony operculum. Paired fins paddle-like, with a long, segmented cartilaginous axis (archipterygium of Gegenbaur); tail diphycercal or heterocercal. In the living forms—optic nerves not decussating, but forming a chiasma, bulbus arteriosus of the heart with numerous valves, intestine with a spiral valve, and air-bladder lung-like.

The internal skeleton of the Dipnoi is chiefly cartilaginous, but the upper and lower vertebral arches, the ribs and fin-supports, all exhibit some tendency towards ossification.

The Dipnoi differ so much from all fishes, in the modification of the air-bladder into a single or double elongated sac with numerous cellular spaces, which serves as a lung and is connected by a short tube with the anterior wall of the gullet; moreover, in the peculiar characters in the structure of the heart, in the presence of internal narial openings, and in the possession of the faculty of existing for a considerable period out of water, that they have often been regarded as fish-like Amphibia or scaly Sirens. The discovery of the "Barramunda" (*Ceratodus forsteri*) in the rivers of Queensland confirmed the idea of their relationship to the Palaeozoic Crossopterygians previously suggested by Huxley. Nevertheless, they are distinguished from these and from all other Ganoids and Teleosteans by the autostylic arrangement of the jaws. They are divided into the two orders of *Ctenodipterini* and *Sirenoidei*.

Order 1. CTENODIPTERINI. Pander.

Cranial roof bones small and numerous. Rays of median fins very fine, much more numerous than their supports, which are directly apposed to the vertebral arches.

Family 1. Uronemidae. Traquair.

Upper dentition comprising a cluster of small, blunt, conical denticles on the palatine bones; lower dentition of similar denticles on the splenial. Median fins continuous and tail diphycercal. Lower Carboniferous to Lower Permian.

[1] *Günther, A.*, Description of *Ceratodus* (Phil. Trans. vol. CLXI.), 1871-72.—*Huxley, T. H.*, Proc. Zool. Soc. 1876, p. 24.—*Miall, L. C.*, Monograph of the Sirenoid and Crossopterygian Ganoids (Palaeont. Soc.), 1878.—*Pander, C. H.*, Ueber die Ctenodipterinen, etc., des devonischen Systems. St. Petersburg, 1858.—*Traquair, R. H.*, On the genera *Dipterus*, *Palaedaphus*, *Holodus*, and *Cheirodus* (Ann. Mag. Nat. Hist. ser. 4, vol. XVII.), 1878 (also *ibid.* ser. 5, vol. II.).—*Teller, F.*, Ueber *Ceratodus sturi* (Abh. k.k. geol. Reichsanst. Wien. vol. XV.), 1891.—*Zittel, K. A. von*, Ueber *Ceratodus* (Sitzungsb. k. bay. Akad. Wiss., math.-phys. Cl.), 1886.

Uronemus, Ag. (*Ganopristodus*, Traq.). Body laterally compressed, with small and very thin scales, which are faintly striated. Paired fins acutely lobate. Dorsal fin arising shortly behind the head. *U. lobatus*, Traq., from Lower Carboniferous (Calciferous Sandstones), Burdiehouse, near Edinburgh.

Conchopoma, Kner. Lower Permian; Rhenish Prussia.

Family 2. **Ctenodontidae**. Traquair.

A pair of dental plates on the palatine bones, and an opposing pair on the splenials; these plates usually retaining traces of their component denticles. Jugular plates usually present. Tail diphycercal or heterocercal.

Dipterus, Sedgw. and Murch. (*Catopterus*, *Polyphractus*, Ag.), (Figs. 114, 115). Small fishes. Bony plates of head covered with punctate ganoine, but cranium apparently quite cartilaginous. Base of cranium covered with a

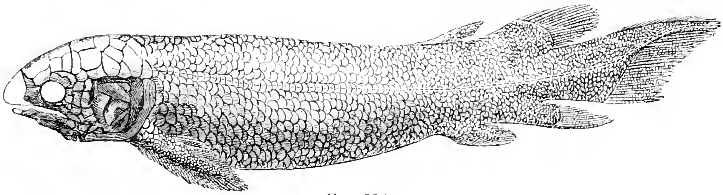
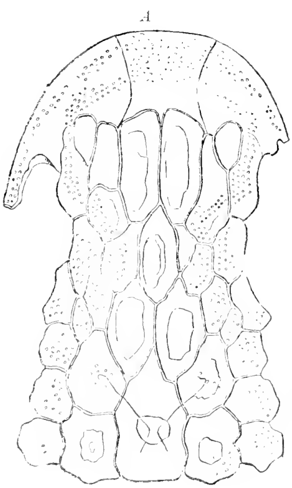


Fig. 114.

Dipterus valenciennesi, Sedgw. and Murch. Restoration, $^1/_3$ nat. size. Lower Old Red Sandstone; Banniskirk, Orkney (after Pander).

broad, rhombic parasphenoid (*PSph*), which is flanked on either side by a pterygo-palatine (*P*) extending forwards into a triangular pointed plate, which serves as base for a large triangular tooth (*d*) bearing tuberculated radiating ridges. The two palatine bones meet in the middle in a straight line. The mandible is completely ossified, with a single, large dental plate on



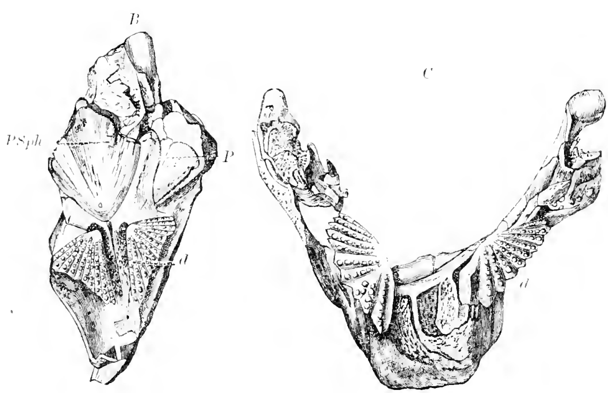


Fig. 115.

Dipterus valenciennesi, Sedgw. and M. Lower Old Red Sandstone; Banniskirk. *A*, Roof of skull. *B*, Imperfect palate (*PSph*, Parasphenoid; *P*, Pterygo-palatine, accidentally divided into two pieces behind by a broken line; *d*, Palatine tooth). *C*, Imperfect mandible with tooth (*d*), after Pander).

the splenial of each side, and its tuberculated ridges radiating fan-like from within outwards. Two pairs of jugular plates. Paired fins acutely lobate, the pelvic pair remote and opposed to the anterior of the two dorsal fins; anal fin opposite the posterior dorsal; tail heterocercal. Trunk and fins covered with thick, deeply overlapping scales, which are nearly rhombic in their exposed portion and invested with punctate ganoine. Complete, but mostly flattened and distorted examples of *Dipterus* are not uncommon in the Lower Old Red Sandstone of Northern Scotland. Dental plates very abundant in Middle and Upper Devonian of central and eastern United States.

Scaumenacia, Traq. Upper Devonian; Canada.

Phaneropleuron, Huxley (Fig. 117). Upper dental plates triangular, with straight and crenulated radiating ridges. Long dorsal fin continuous with the caudal, but small anal fin separate. Scales very thin and cycloid, marked with delicate radiating striae. *P. andersoni*, Huxl., known by well-preserved specimens from Upper Old Red Sandstone, Fifeshire.

Palaedaphus, van Beneden (*Heliodus*, Newb.), (Fig. 118). Only known by mandible and detached dental plates. In *P. insignis*, van Ben. and de Koninck, each lower dental plate, measuring 0·17 m. in length, bears four smooth, obtuse radiating ridges. Upper Devonian; Belgium and Pennsylvania.

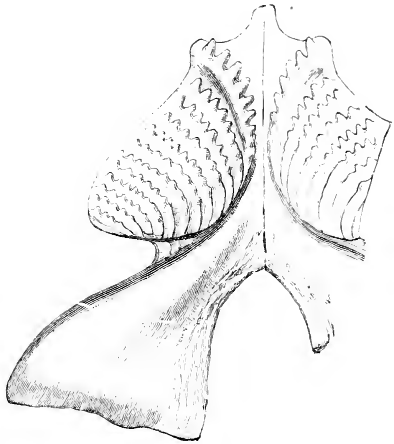


Fig. 116.

Ctenodus tuberculatus, Atthey. Pterygo-palatine with palatal teeth, 1/3 nat. size. Coal Measures; Newsham, Northumberland (after Hancock and Atthey). Oral surface of teeth really concave.

Conchodus, M'Coy; *Synthetodus*, Eastman. Devonian.

Ctenodus, Ag. (Fig. 116). Hinder border of cranial roof with one median occipital plate, with a pair of plates immediately adjoining in front. Dental

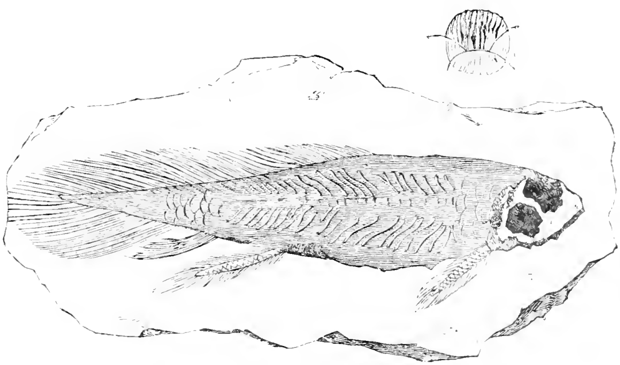


Fig. 117.

Phaneropleuron andersoni, Huxley. Upper Old Red Sandstone; Dura Den, Fifeshire. 1/3 nat. size (after Page).

plates with numerous tuberculated or crenulated radiating ridges. Dorsal and anal fins continuous with the caudal, which is diphycercal; scales very large and thin, without a ganoine layer, almost quadrate in shape, but with rounded angles; marked more or less distinctly with reticulations, as in *Ceratodus*. Dental plates common in the Carboniferous of Europe and North America; fine portions of skeleton in the English Coal Measures.

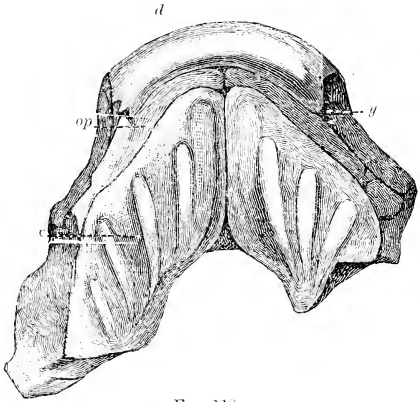


FIG. 118.
Palaedaphus insignis, van Beneden and de Koninck. Imperfect mandible, 1/4 nat. size. Devonian; Liége. *c*, Tooth; *d*, Dentary; *op*, Splenial; *g*, Lateral fossa (after Traquair).

Sagenodus, Owen (*Megapleuron*, Gaudry; *Ptyonodus*, Cope). As *Ctenodus*, but dental plates with fewer ridges, and median occipital plate with another unpaired plate immediately in front of it. Scales and dental plates common in the Carboniferous and Lower Permian of Europe and North America; fine skeletons in the Lower Permian of Bohemia and France.

Order 2. SIRENOIDEI.

Cranial roof bones large and few. Rays of median fins very fine, much more numerous than their supports, which are directly apposed to the vertebral arches.

Family 1. Lepidosirenidae.

A pair of dental plates on the palatine bones, and an opposing pair on the splenials; also a pair of small cutting teeth on the vomer. Jugular plates absent. Median fin continuous, and tail diphycercal. Body covered with thin, elastic, cycloid scales without a bony basis. Triassic to Recent.

Of the three genera referable to this family, *Lepidosiren* lives in the tropical swamps of South America, *Protopterus* in those of Africa, and *Ceratodus* in the rivers of Queensland.

Ceratodus, Ag. (Fig. 119), is covered with large, thin cycloid scales; the dorsal and anal fins are continuous with the diphycercal caudal. The pectoral and pelvic fins are fringed with membrane stiffened by fine rays. The upper vertebral arches, spinous processes, ribs, and fin supports are encased in thin bony sheaths. The flattened roof of the skull consists of two large median plates, one behind the other, and two pairs of lateral plates. On the lower side of the chondrocranium there occurs the long parasphenoid (*PSph*), with its rhombic anterior expansion flanked on either side by the pterygo-palatines (*Pt*). The latter bones meet in a median suture in front, and each bears a large triangular dental plate (*d*), with radiating ridges. . The vomerine cartilage (*Vo*) bears a pair of sharp, chisel-shaped teeth (*d'*). On the splenial of each ramus of the mandible there is also a dental plate with deep, radiating ridges. The opercula, sub-opercula, hyoid bones, and branchial arches are ossified; the quadrate remains cartilaginous.

In the living *Ceratodus* (*Epiceratodus*, Teller), the upper and lower dental plates bear six ridges radiating outwards. The corresponding plates occurring in the Trias, namely, in the bone beds of the Muschelkalk, Lettenkohle, and Rhaetic, are distinguished by their larger size and a different number of ridges. As a rule, the upper dental plates exhibit five, the lower ones only four radiating ridges. The oldest known species (*C. arenaceus*, Quenst.) was

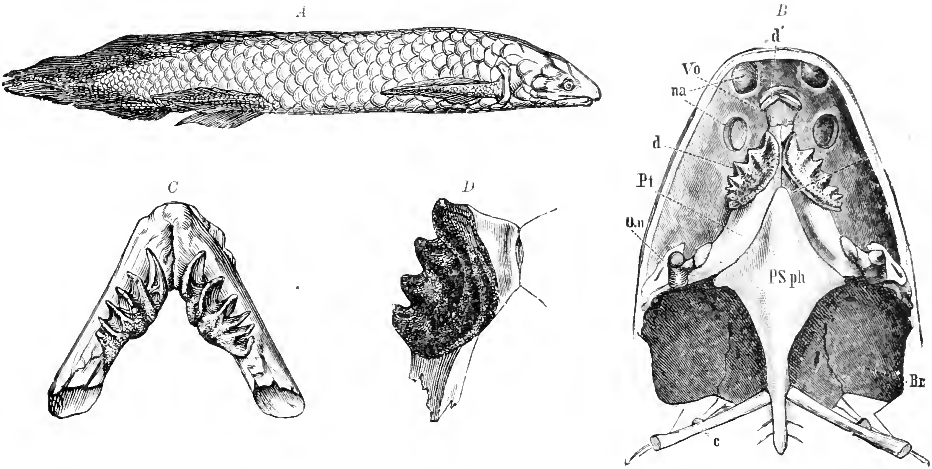


Fig. 119.

Ceratodus forsteri, Krefft. Lateral aspect of fish (*A*), base of skull (*B*), and mandible (*C*). Recent; Queensland. *Br*, Branchial cavity; *c*, Foremost rib; *d*, Teeth; *na*, Nasal openings; *PSph*, Parasphenoid; *Pt*, Pterygo-palatine; *Qu*, Quadrate; *Vo*, Vomer (after Günther). *D*, *Ceratodus kaupi*, Ag. Mandibular tooth on bony base, $^1/_3$ nat. size. Lettenkohle; Hoheneck, near Ludwigsburg.

obtained from the Bunter Sandstone of Würtemberg; the latest, which are the smallest, are discovered in Europe in the Bathonian of Stonesfield and Northampton, England, in North America in the Upper Jurassic of Colorado. Other examples occur in the Kota-Maleri beds of India, in the Karoo Formation of South Africa, and in later deposits in Patagonia. A well-preserved skull of *C. sturi* has been described by Teller from the Upper Keuper of Polzberg, near Lunz, in Lower Austria.

Sub-Class 5. GANOIDEI. Agassiz.[1] Enamel-scaled Fishes.

Trunk and tail usually covered with ganoid scales, rarely naked or with bony plates. Skull covered with dermal bones, or completely ossified; pterygo-quadrate arcade movably articulated with the cranium (hyostylic); gill clefts feebly separated, opening into a cavity covered with a bony operculum. Vertebral column cartilaginous, or with various degrees of ossification. Fin rays articulated, and fulcra usually

[1] *Cope, E. D.*, Trans. Amer. Phil. Soc. vol. XIV. 1871, p. 445; and Amer. Nat. vols. XIX., XX., XXI., XXIII. (1885-89).—*Huxley, T. H.*, Preliminary Essay upon the Systematic Arrangement of the Fishes of the Devonian Epoch (Mem. Geol. Surv. dec. X.), 1861.—*Kner, R.*, Betrachtungen über die Ganoiden als natürliche Ordnung (Sitzungsb. k. Akad. Wiss. Wien. math.-naturw. Cl. vol. LIV.), 1866.—*Lütken, Chr.*, Ueber die Begrenzung und Eintheilung der Ganoiden (Palaeontogr. vol. XXII.). 1868.—*Müller, Joh.*, Ueber den Bau und die Grenzen der Ganoiden (Abhandl. k. Akad. Wiss. Berlin. 1834, 1836.—*Traquair, R. H.*, The Ganoid Fishes of the British Carboniferous Formations. I. Palaeoniscidae (Palaeont. Soc.), 1877. No. 2. 1901.—*Vogt, C.*, Quelques Observations qui servent à la Classification des Ganoides (Ann. Sci. Nat., Zool. ser. 3, vol. IV.).

present. Paired fins well developed, tail diphycercal, heterocercal, or hemi-heterocercal. In the living forms—optic nerves not completely decussating but forming a chiasma, bulbus arteriosus of the heart with numerous valves, intestine with a spiral valve, and air-bladder connected by a tube with the gullet.

When founding the "order" of Ganoids, Agassiz paid attention exclusively to the dermal skeleton, and included under this denomination all fishes with scales which consisted of a bony lower layer and a superficial covering of enamel.

Johannes Müller first attempted to define the Ganoids from anatomical characters. After the removal of the Plectognathi, Lophobranchii, and Siluroids recognised as true bony fishes, and after the assignment of *Lepidosiren* to the Dipnoi, there still remained as true Ganoids a large number of recent and fossil fishes, which, according to Johannes Müller, formed a distinct sub-class between the Selachii and the bony fishes. While the condition of the muscular bulbus arteriosus, the incomplete decussation of the optic nerves, and the spiral valve in the intestine agree with the former, the arrangement of the head bones, the structure of the fins, and usually also the ossification of the skeleton, are suggestive of the bony fishes. After C. Vogt had recognised in the anatomical structure of *Amia* a true Ganoid, with thin elastic cycloid scales and a completely ossified skeleton, the line of demarcation between the Ganoidei and Teleostei seemed to have been absolutely destroyed. Kner, Thiollière, Owen, and more recently Cope and Smith Woodward have ventured still further, suppressing the Ganoidei as a separate group, and uniting its members with the Teleostei under the general denomination of *Teleostomi*.

The most conspicuous, even if not the distinctive feature of the Ganoids, consists in their dermal covering. No other sub-class of fishes possesses scales which consist of a thick bony inner layer and an outer enamel layer. In no other group is there a union of scales by peg-and-socket articulations, such as is characteristic of the rhombic-scaled Ganoids. There are, however, ganoid scales of rounded form, which overlap each other exactly like cycloid and ctenoid scales, and which are sometimes not perceptibly thicker than the latter; but these rounded scales (*Caturus*, *Megalurus*, *Macrorhipis*, *Amia*) exhibit beneath the enamel covering an inner layer with bone cells, though sometimes its thickness is excessively reduced. The Spatularias are characterised by the complete absence of scales, except on the upper lobe of the tail; in the Sturgeons the body is partly covered with large bony plates.

The structure of the internal skeleton of the Ganoids is of special interest, notably that of the vertebral column. In some Chondrostei (*Acipenser*) the vertebral axis, with its arches and spines, remains completely cartilaginous; but in *Spatularia*, the older Crossopterygii, almost all Heterocerci and Pycnodonts, and part of the Lepidostei, there is a partial or complete ossification of the arches, spinous processes, and supports of the median fins, this beginning at the surface and extending inwards, so that a cartilaginous core is usually surrounded by a hollow bony cylinder. These are termed "naked vertebrae" (*Nacktwirbel*), (Fig. 120), in contradistinction to the so-called "hemi-vertebrae" (*Halbwirbel*), and "ring vertebrae" (*Hohlwirbel*). In the first (Fig. 121) there develops below the notochord a horseshoe-shaped bony plate (hypocentrum, intercentrum), to which the haemal arches in the caudal region are fixed; the upwardly directed side-pieces of these hypocentra are mostly attenuated and pointed. The vertebral centrum proper is represented by a pair of lateral bony plates (pleurocentra), which are usually pointed below and frequently fused together dorsally, thus forming a second horseshoe-shaped half-ring. According to their size the hypocentra and pleurocentra more or less completely surround the soft, unsegmented notochord. Sometimes when the upper and lower lateral pieces do not taper but continue of uniform width, and meet together

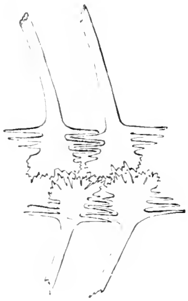


FIG. 120.
Two caudal vertebrae of *Pycnodus platessus*, Ag. (after Heckel).

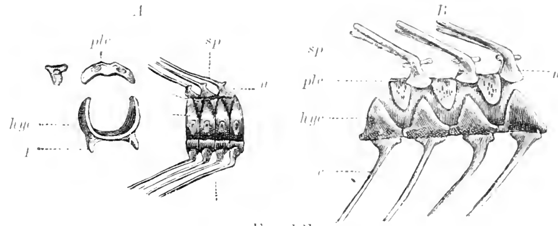


FIG. 121.
Vertebrae of *Euthynotus* (*A*), and *Caturus furcatus*, Ag. (*B*). *r*, Rib; *hyc*, Hypocentrum; *n*, Neural arch; *p*, Parapophysis; *plc*, Pleurocentrum; *sp*, Cleft neural spine.

dorsally and ventrally, they form two half-rings, which completely enclose the notochord (Fig. 121). In many genera (*Eurycormus*) the anterior abdominal region consists of half vertebrae, while the caudal region consists of ring vertebrae, which are composed of two halves (Fig. 122). By the complete fusion of the two half rings, there arise simple, sheath-like ring vertebrae (Fig. 122). In the Amiidae the vertebral centra of the abdominal region

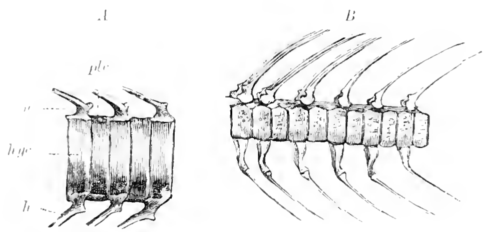


FIG. 122.
A, Caudal vertebrae of *Eurycormus speciosus*, Wagn. *B*, Vertebrae of *Amia calva*, Linn. From anterior part of caudal region. *h*, Haemal arch; *hyc*, Hypocentrum; *n*, Neural arch; *plc*, Pleurocentrum.

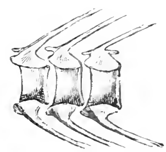


FIG. 123.
Aspidorhynchus, sp. Caudal vertebrae, each bearing a neural and haemal arch.

are completely ossified and amphicoelous, while some of those of the caudal region are still divided into two halves, which correspond with the hypo- and pleuro-centra of the Lepidostei (Fig. 122, *B*).

The complete ossification of the vertebral column, as in the bony fishes, is observed only among the latest representatives of the Ganoids, namely, the Polypteridae and the Lepidosteidae. Among the latter, moreover, the vertebral centra are only concave behind, convex in front (opisthocoelous).

The hinder end of the vertebral column is always produced into the caudal fin. The true *diphycercal* condition (see p. 8) constantly persists in some Crossopterygians (Coelacanthidae) and Chondrosteans (Belonorhynchidae). In most Crossopterygians the caudal fin is *hetero-diphycercal*, that is, the vertebral column extends straight, but the rays of the upper lobe of the fin are more delicate and shorter than those of the lower lobe. True *heterocercy* and *hemi-heterocercy* (internal heterocercy, external homocercy, see p. 10) are very common.

In many Ganoids the unpaired fins, and sometimes also the paired fins, are fringed on the anterior border with the so-called *fulcra*—scale-like spines or plates covered with enamel, which are serially arranged and partly overlap one another. All the fin rays consist of two (right and left) halves, and are transversely jointed, usually also branched distally.

Like the vertebral column, the skull also exhibits very variable degrees of ossification. In the cartilaginous Ganoids this is almost exclusively confined to a number of investing plates on the cranial roof and the basicranial axis. The pterygoid and palatine bones are still fused together; the mandible and parts of the hyoid apparatus are ossified; the opercular apparatus is feebly developed. In the Crossopterygii, Heterocerci, and Lepidostei the ossification closely resembles that of the Teleostei, while the number and arrangement of the several bones agree essentially with the corresponding features in some of the least specialised members of the latter sub-class.

In the structure of the pectoral arch, and especially of the anterior limbs, the various orders of Ganoids exhibit considerable differences, and represent intermediate links between the Dipnoi, Selachii, and Teleostei. In the Crossopterygii, Chondrostei, and Heterocerci the clavicle still consists of three separate membrane bones; while in the Lepidostei and Amioidei the lower segment (infraclavicle) is completely fused with the clavicle. The small structures behind and within the clavicle, corresponding with the scapula, coracoid, and precoracoid remain cartilaginous in the Chondrostei, probably also in the fossil Crossopterygii; in the remaining Ganoids, on the other hand, they are ossified exactly as in the Teleostei. Moreover, with reference to the position and number of the basal supports in the pectoral fins, most Ganoids agree with the bony fishes; the earlier Crossopterygii alone possessed a segmented cartilaginous axis, with biserial radialia, as in the Dipnoi.

Besides the anatomical characters in the dermal covering and the internal skeleton there are still others indicating that the Ganoids are a natural group of fishes. For example, the somewhat elongated muscular base of the principal artery (bulbus arteriosus) is provided internally, as in the Selachii, with several rows of valves, which prevent the return of the blood from the artery to the auricle of the heart. The gills, on the other hand, as in the Teleostei, always lie free under an operculum, which usually consists of several bony plates. Again, by the possession of a spiral valve in the intestine, as well as in the structure of the urinogenital system, the Ganoids approach the Selachii more closely than the Teleostei; on the other hand, they all possess an air-bladder opening into the gullet, and also produce numerous small eggs. By the complete decussation of their optic nerves, the Teleostei are distinguished from the Ganoidei, in which the branching optic nerves form a so-called chiasma.

The Ganoids exhibit their greatest development in Palaeozoic, Triassic, and Jurassic formations; and from the base of the Cretaceous system upwards they become more and more replaced by the bony fishes. The few still existing Ganoids live either exclusively, or at least partly, in fresh water, while the large majority of the fossil forms occur in purely marine deposits. As a rule, only the Tertiary Ganoids occur in freshwater formations.

The Ganoidei may be divided into five orders:—(1) Crossopterygii; (2) Chondrostei; (3) Heterocerci; (4) Lepidostei; (5) Amioidei.

Order 1. CROSSOPTERYGII. Huxley. Fringe-finned Ganoids.

Notochord persistent or vertebrae ossified. Tail diphycercal or hetero-diphycercal. Infraclavicle present. Paired fins with a scaly axis fringed on both sides by dermal rays. Branchiostegal apparatus between the rami of the mandible consisting of a pair of large jugular plates, these in many Palaeozoic genera flanked by a series of small lateral jugulars and an anterior median plate. Ganoid scales rhombic or cycloidal, completely covering the trunk and tail.

Family 1. Holoptychiidae. Traquair.

Body covered with imbricating, cycloidal ganoid scales. No ossified vertebrae.

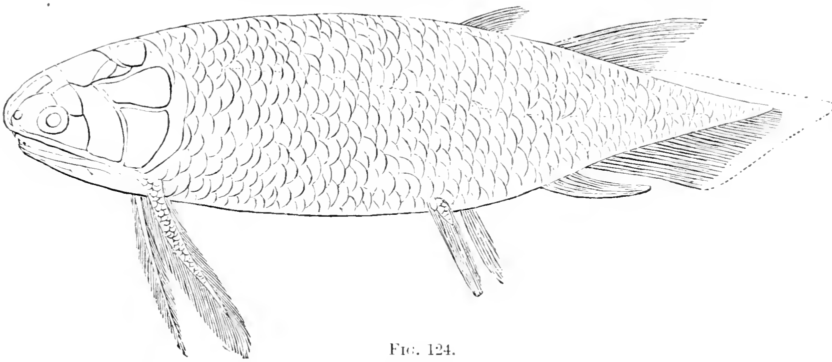


Fig. 124.

Holoptychius nobilissimus, Ag. Upper Old Red Sandstone; Scotland (restoration after Huxley).

Pectoral fins acutely lobate. Two dorsal fins and one anal fin, each borne by a single distally expanded support (axonost), followed by one or two rows of short basal pieces (baseosts), which support the very numerous,

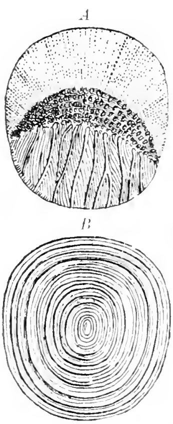


Fig. 125.

Scale of *Holoptychius* (*Glyptolepis*). Outer (*A*), and inner (*B*) aspect. Old Red Sandstone; Wik, Russia (after Pander).

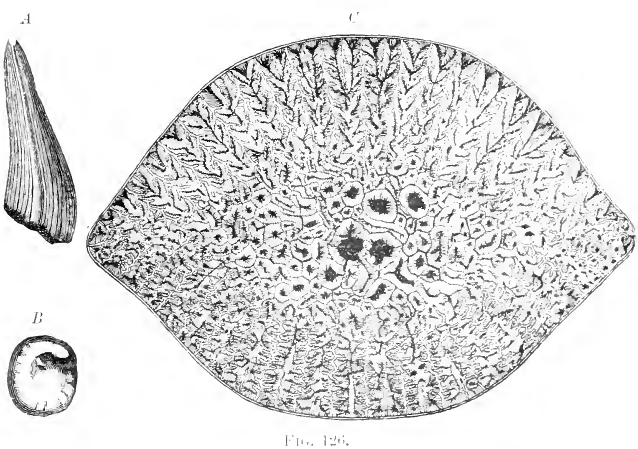


Fig. 126.

Dendrodus biporcatus, Ag. Tooth in side view (*A*), and from below (*B*), nat. size, and transverse section of the same (*C*), highly magnified (after Pander).

fine, dermal fin rays. Lateral jugular plates, clavicle, and infraclavicle present.

Head and branchial region covered with enamelled dermal bones. Teeth numerous, acutely conical, arranged on the border of the jaws: enlarged laniary teeth in a second inner series on several separate splenial bones. The teeth distinguished by a very complicated, meandering, folded structure (dendrodont). Devonian.

The only satisfactorily known genus referable to this family is *Holoptychius*, Ag. (*Glyptolepis*, *Platygnathus*, Ag.), (Figs. 124, 125), from the Old Red Sandstone of Scotland, England, and Ireland, and from the Devonian of N.-W. Russia, Bohemia, Belgium, the Eifel, the United States, Canada, and Greenland. Several species attain a large size. Detached teeth have been described as *Dendrodus*, Owen (Fig. 126); *Lamnodus*, Ag.; and *Apedodus*, Leidy.

Family 2. **Rhizodontidae**. Traquair.

Closely resembling preceding family, but both paired fins with a short, obtuse lobe. Teeth few and conical, with a well-defined pulp cavity, the wall of which is radiately folded in the lower part of the crown. Usually several tooth-bearing splenial bones on the inner side of the mandible. Devonian, Carboniferous, and Lower Permian.

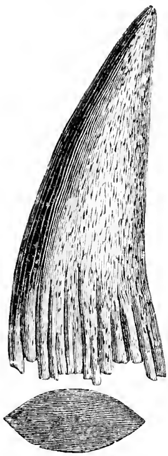


Fig. 127.

Rhizodus hibberti, Ag. Tooth, ½ nat. size. Lower Carboniferous; Edinburgh.

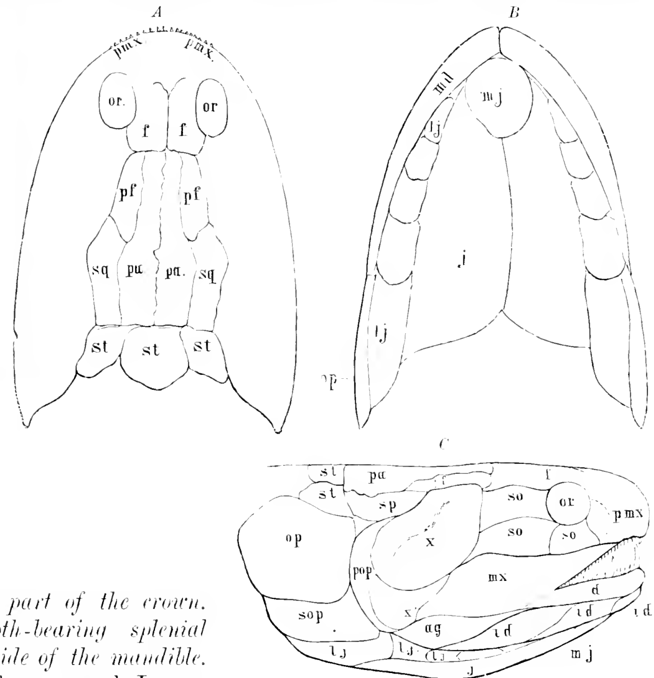


Fig. 128.

Rhizodopsis sauroides, Williamson sp. Outline restorations of head and opercular apparatus from the upper (*A*), lower (*B*), and lateral (*C*) aspects, about ½ nat. size. Upper Carboniferous; Staffordshire. *ag*, Angular; *d*, Dentary; *f*, Frontal; *id*, Infradentary; *j*, Principal gular (jugular); *lj*, Lateral gular (jugular); *mj*, Median gular (jugular); *mn*, Mandible; *mx*, Maxilla; *op*, Operculum; *or*, Orbit; *pf*, Postfrontal; *pmx*, Premaxilla; *pop*, Preoperculum; *pa*, Parietal; *so*, Suborbital; *sop*, Suboperculum; *sq*, Squamosal; *st*, Supratemporal; *x*, *x'*, Cheek-plates (after Traquair).

Rhizodus, Owen. (*Megalichthys*, Ag. p.p.), (Fig. 127). Very large, incompletely known fishes with rough, rugose cycloidal scales. Infraclavicle with a long upwardly directed process. Teeth smooth, compressed to a sharp edge in front and behind. *R. hibberti*, Ag., and *R. ornatus*, Traq., from Lower Carboniferous, Scotland and Northumberland. Allied species in Coal Measures of North America.

Strepsodus, Young (*Dendroptychius*, Young; *Archichthys*, Hanc. and Atth.). Large and medium-sized fishes with slender and somewhat curved teeth, which are not compressed to sharp edges. *S. sauroides*, Binney sp., from Coal Measures of England, Scotland, and Ireland. Other species from Lower Carboniferous of Scotland, Ireland, and Nova Scotia.

Rhizodopsis, Young (*Dittodus*, *Ganolodus*, *Characodus*, *Gastrodus*, Owen). (Fig. 128). Scales oval, with an extremely thin layer of punctate ganoine. Teeth round in section, smooth. Vertebral axis with ring vertebrae. The small type species represented by fine examples in the English Coal Measures. Fragments in the Coal Measures of Silesia, Nova Scotia, and Illinois.

Gyroptychius, M'Coy; *Tristichopterus*, Egerton; *Eusthenopteron*, Whiteaves; *Polyplocodus*, Pander; *Sauripterus*, Hall. Devonian and Old Red Sandstone: Europe and North America.

Family 3. **Osteolepidae**. Smith Woodward.

Body slender, covered with rhombic ganoid scales. Ring vertebrae at least in the caudal region. Paired fins with a short, obtuse lobe. Teeth conical, only externally folded at the base, as in Rhizodontidae. Devonian and Carboniferous.

Osteolepis, Ag. (*Tripterus*, *Triplopterus*, M'Coy), (Fig. 129). Cranial roof bones in advance of the parietals fused into a continuous shield, pierced by a

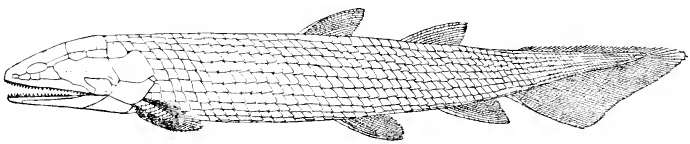


Fig. 129.
Osteolepis macrolepidotus, Ag. Lower Old Red Sandstone; Scotland (restoration after Pander).

median frontal (pineal) foramen. An anterior median jugular plate present. Teeth round in section. First dorsal fin in front of the pelvic pair. Scales smooth and punctate. *O. macrolepidotus*, Ag., and *O. microlepidotus*, Pander. Lower Old Red Sandstone: Scotland.

Thursius, Traq. As *Osteolepis*, but first dorsal opposite pelvic fins. Lower Old Red Sandstone: Scotland.

Diplopterus, Ag. Lower Old Red Sandstone; Scotland.

Megalichthys, Ag. (*Centrodus*, M'Coy; *Rhomboptychius*, Young; *Ectosteorhachis*, Cope). Cranial roof bones in advance of the parietals rarely fused into a continuous shield, without a median frontal foramen. Teeth round in section. First dorsal fin nearly opposite the pelvic pair. Scales smooth and punctate. Carboniferous of Great Britain and North America. Lower Permian of Texas. *M. hibberti*, Ag., the best known British species from the Coal Measures.

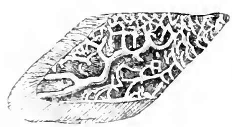


Fig. 130.
Glyptopomus kinnairdi. Huxley. Scale, enlarged. Upper Old Red Sandstone: Dura Den. Fifeshire (after Huxley).

Glyptopomus, Ag. (*Glyptolaemus*, Huxley), (Fig. 130). Bones of cranial roof not fused together: a median frontal (pineal) foramen. External bones and scales ornamented with irregular reticulating rugae or fused series of tubercles. Upper Old Red Sandstone: Scotland, possibly also Belgium and Pennsylvania.

Family 4. **Coelacanthidae.** Huxley.[1]

Body covered with thin, cycloidal ganoid scales. No ossified vertebrae. Arches, spinous processes, and supports of caudal fin superficially ossified. Air bladder ossified. Paired fins with a short, obtuse lobe. Each of the two dorsal fins and the anal fin supported by a simple, usually proximally forked plate, which in the anterior dorsal is in direct contact with the dermal rays. Caudal fin distinctly diphycercal, borne above and below by numerous simple supports, and terminating in a small projecting tufted fin. Only one opercular bone on each side and a pair of jugular plates ; but several splenial bones present. Upper Devonian to Upper Cretaceous.

Coelacanthus, Ag. (*Hoplopygus*, Ag.; *Conchiopsis*, Cope ; *Rhabdoderma*, Reis). Teeth absent on the margin of the jaws, but a few hollow, conical teeth within. Supplementary caudal fin prominent. External bones and scales ornamented with series of tubercles or fine ridges of ganoine ; fin rays not denticulated. Carboniferous and Permian of England, Scotland, Germany (Kupferschiefer), and North America. Fragments probably also in Upper Devonian of Harz Mountains.

Graphiurus, Kner ; *Heptanema*, Bellotti. Trias of Raibl and Perledo.

Diplurus, Newb. Trias ; New Jersey and Connecticut.

Undina, Münster (*Holophagus*, Egerton), (Fig. 131). Supplementary caudal fin prominent. All the fin rays robust, broad, and closely articulated

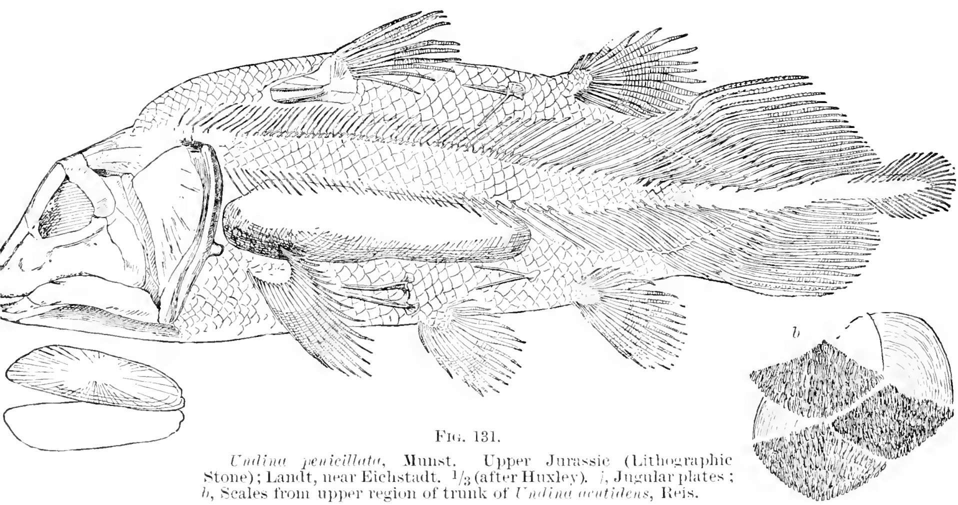


Fig. 131.

Undina penicillata, Munst. Upper Jurassic (Lithographic Stone); Landt, near Eichstadt. 1/3 (after Huxley). *j*, Jugular plates ; *b*, Scales from upper region of trunk of *Undina acutidens*, Reis.

distally ; the anterior rays of the first dorsal and caudal fins denticulated or tuberculated. External bones and scales rugose and tuberculated. Lower Lias to Lower Kimmeridgian.

Libys, Münst.; *Coccoderma*, Quenst. Lithographic Stone (Lower Kimmeridgian) ; Bavaria and Würtemberg. *C. substriolatum*, Huxl. sp., from Kimmeridge Clay, England.

[1] *Huxley, T. H.*, Illustrations of the Structure of the Crossopterygian Ganoids (Mem. Geol. Surv. dec. XII.), 1866.—*Reis, O.*, Die Coelacanthinen (Palaeontogr. vol. XXXV.), 1888 ; also Geogn. Jahresh., München, 1892.

Macropoma, Ag. Maxilla, vomer, and palatine with conical teeth. Supplementary caudal fin unknown. Fin rays robust and straight, not expanded distally, with distant articulations; a double series of small, upwardly pointing denticles on nearly all the rays of the first dorsal and caudal fins. Turonian and Senonian of Europe. *M. mantelli*, Ag., especially well preserved in the English Chalk.

Family 5. **Polypteridae.** Huxley.

Body covered with thick, rhombic ganoid scales. Vertebrae and the complete internal skeleton ossified. Tail diphycercal. Pectoral fins with short, obtuse lobe, the numerous, short, fan-like basalia attached to two diverging bones (propterygium and metapterygium) and a median mesopterygium. Dorsal fin single, remarkably extended, the spine-like rays borne by a corresponding number of supports. Only a single pair of jugular plates. Teeth sharply conical, with simple pulp cavity. Recent.

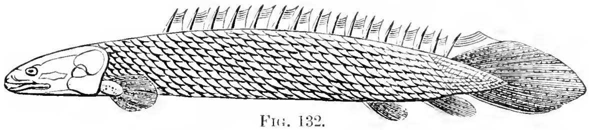


FIG. 132.
Polypterus bichir, Geoffr. Recent; Upper Nile.

To this family belong the two genera, *Polypterus* (Fig. 132) and *Calamoichthys*, living in the rivers of tropical Africa.

Order 2. **CHONDROSTEI.** Cartilaginous Ganoids.

Notochord persistent, and endoskeleton chiefly cartilaginous; head covered with bony dermal plates. Teeth small or wanting. Opercular apparatus imperfectly developed, the branchiostegal rays usually absent. Infraclavicle present. Paired fins without a scaly axis, but each pelvic fin with a row of cartilaginous basal supports. A single dorsal and anal fin, with dermal rays more numerous than their supports. Caudal fin heterocercal (rarely diphycercal), and the upper lobe usually covered with rhombic scales. Trunk almost or completely naked, or with rows of bony plates.

Family 1. **Chondrosteidae.** Smith Woodward.[1]

Parietal and frontal bones paired; a large squamosal bordering the parietals on each side. Jaws toothless, and premaxilla absent. Operculum small, suboperculum large; a few branchiostegal rays present. Trunk naked, only the upper fulcrated lobe of the tail with elongated, oat-shaped ganoid scales. Lias.

Chondrosteus, Egerton. Mouth very small and inferior; jaws toothless; maxilla arched, much expanded behind and tapering in front. About ten branchiostegal rays, but no gular plate. Dorsal fin short-based, opposed to the pelvic pair. Trunk naked. *C. acipenseroides*, Eg., about a metre in length, known by nearly complete skeletons from the Lower Lias of England.

Gyrosteus, Sm. Woodward (*ex* Ag. MS.). Usually much larger than *Chondrosteus*, and the toothless maxilla expanded in its front portion for a palatine articulation. *G. mirabilis*, Sm. Woodw. (*ex* Agassiz, MS.), represented by fragments in the Upper Lias of Whitby.

[1] *Woodward, A. S.*, On the Palaeontology of Sturgeons (Proc. Geol. Assoc. vol. XI.), 1889; also Proc. Yorks. Geol. and Polyt. Soc. vol. XIII. 1898, p. 461.

Family 2. **Acipenseridae.** Sturgeons.

Elongated fishes with a produced snout, and small toothless mouth without premaxilla. Parietal and frontal bones large, unsymmetrical, and granulated. Operculum incompletely developed, not quite covering the branchial opening; branchiostegal rays absent. Dorsal and anal fins borne by two rows of supports (axonosts and baseosts); caudal fin strongly heterocercal, the large upper lobe ridged with fulcral scales. Trunk with five longitudinal series of keeled bony plates. Tertiary and Recent.

The sturgeons of the two living genera, *Acipenser* and *Scaphirhynchus*, inhabit the seas of the northern hemisphere, and enter the rivers of Europe, Asia, and North America. Fossil remains are rare. An Eocene species (*Acipenser toliapicus*, Ag.) is represented by scutes in the London Clay of Sheppey. Scutes and pectoral fin rays are also known from Upper Eocene and later deposits in Europe, and from the Miocene of Virginia, U.S.A.

Family 3. **Polyodontidae.** Paddle-fishes.

Snout very long and spatulate. Parietal and frontal bones paired. Mouth large, with minute teeth in both jaws; no premaxilla. Branchiostegal rays absent. Scales rudimentary or absent, except on the sides of the upper caudal lobe, which is ridged with large fulcral scales. Cretaceous (?) or Eocene to Recent.

Crossopholis, Cope. Rostrum covered with small stellate bones. Scales of trunk small, thin, and separated; each being a grooved disc with posterior denticulations like a fringe. *C. magnicaudatus*, Cope; Eocene (Green River Shales), Wyoming.

Pholidurus, Sm. Woodw. Known by caudal ridge scales only, from the Upper Chalk, Kent.

Polyodon (*Spatularia*) living in the Mississippi, *Psepharus* in Chinese rivers.

Family 4. **Belonorhynchidae.** Smith Woodward.[1]

Slender fishes with a much elongated, pointed snout. Mouth very large, and jaws with numerous conical teeth of different sizes. Opercular apparatus reduced, without branchiostegal rays. Fin fulcra minute or absent; dorsal and anal fins small and remote; caudal fin diphycercal. Trunk with four longitudinal rows of small, keeled, scale-like plates. Trias and Lias.

Belonorhynchus, Bronn. (*Ichthyorhynchus*, Bellotti; *Saurorhynchus*, Reis.),

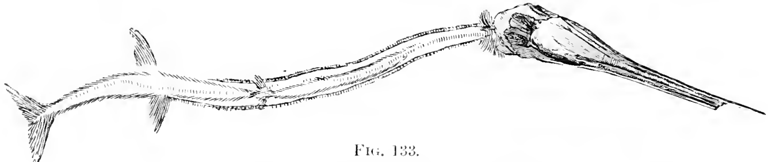


Fig. 133.
Belonorhynchus striolatus, Bronn. Keuper; Raibl, Carinthia. Nat. size.

(Fig. 133). Head and trunk excessively elongated. Jaws approximately equal in length, and mandible remarkably deep behind. Head bones exter-

[1] *Woodward, A. S.*, The Fossil Fishes of the Hawkesbury Series (Mem. Geol. Surv. N. S. Wales, Palaeont. No. 4), 1890.—*Reis, O.*, Geogn. Jahresh., IV. München, 1891.

nally ornamented with striae, rugae, or reticulations. The remote dorsal and anal fins opposed to each other; the diphycercal caudal fin truncated at its hinder margin. Of the four series of imbricating keeled dermal scutes one extends along the back, another along the ventral border, and the other two smaller series along the flanks. The ventral scutes form a ring round the region of the anus. *Belonorhynchus* occurs in the Trias of the Alps (Raibl, Perledo, Seefeld) and Australia (Hawkesbury Formation), and is represented by skulls and other fragments in the Lias of England and Germany (*Belonostomus acutus*, Ag.). The teeth, jaws, and skulls from the Muschelkalk, Keuper, and Rhaetic, described under the name of *Saurichthys*, Ag. (Fig. 134), probably belong to *Belonorhynchus*.

FIG. 134.

Saurichthys acuminatus, Ag. Tooth. nat. size. Rhaetic; Kemnath, Würtemberg.

Order 3. HETEROCERCI. Zittel.[1]

Notochord persistent, but arches, spinous processes, and fin supports more or less ossified; head covered with bony dermal plates. Opercular apparatus well developed, and branchiostegal rays numerous. Infraclavicle present. Unpaired, and usually also paired fins fringed with fulcra. Paired fins without scaly axis, but each pelvic fin with a row of imperfectly ossified basal supports. A single dorsal and anal fin, with articulated rays which are more numerous than their supports. Caudal fin heterocercal. Scales rhombic or rhomboidal, rarely cycloidal.

In their skeletal structure and the characters of their paired fins, the Heterocerci agree so closely with the Chondrostei, that they are united with the latter by Traquair under the ordinal name of Acipenseroidei. In their outward aspect they bear a superficial resemblance to the Lepidostei. The Chondrostei, Heterocerci, and Lepidostei, probably form three different specialised branches from one and the same primitive group.

Family 1. **Palaeoniscidae.** Vogt emend. Traquair.

Trunk elongate-fusiform. Head bones more or less enamelled. Teeth slender, conical or styliform. Scales ganoid, rhombic in shape, rarely cycloid on the trunk. Devonian to Upper Jurassic.

Cheirolepis, Ag. Jaws with an outer row of minute teeth and an inner row of stouter teeth. Dorsal fin remote, arising behind the origin of the anal fin. Scales very small, rhombic, or almost square. *C. cummingiae*, Ag.; Lower Old Red Sandstone, Scotland. *C. canadensis*, Whiteaves. Upper Devonian: Scaumenac Bay, Canada.

Canobius, *Gonatodus*, Traquair. Lower Carboniferous: Scotland. *G. molyneuxi*, Traq.: English Coal Measures.

Amblypterus, Ag. Mouth and teeth small. Fins with delicate fulcra. Scales smooth. Several species from Lower Permian (Rothliegendes) of Rhenish Prussia, Bohemia, and France. *A. latus*, Ag.: *A. duvernoyi*, Ag. sp.

Eurylepis, Newb. (Fig. 135). Small fishes with small fins, the fin rays not

[1] *Traquair, R. H.*, The Ganoid Fishes of the British Carboniferous Formations (Palaeont. Soc.) No. 1, 1877, No. 2, 1901.—On *Amblypterus*, *Palaeoniscus*, *Gyrolepis*, and *Pygopterus* (Quart. Journ. Geol. Soc. vol. XXXIII.), 1877.—On Eskdale Fishes (Trans. Roy. Soc. Edinb. vol. XXX.), 1881.

divided distally, and the caudal obliquely truncated. Teeth small. Scales rugose, denticulated on the hinder border; two or more rows of scales on the flank remarkably deepened. Coal Measures; Ohio, and rarely England.

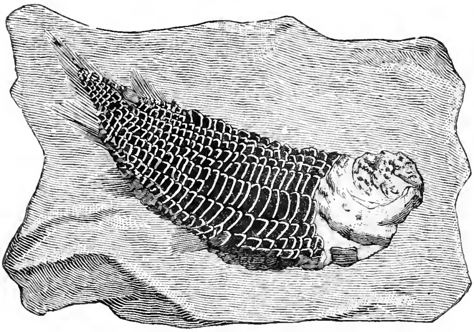


Fig. 135.
Eurylepis tuberculatus, Newb. Coal Measures; Linton, Ohio.

Nematoptychius, *Rhadinichthys*, Traquair; *Cycloptychius*, Young. Carboniferous.

Pygopterus, Ag. Kupferschiefer.

Palaeoniscus, Blv. emend. Traquair (Fig. 136). Slender fishes, small or of moderate size. Teeth sharply pointed, of different sizes. Fins small, the rays articulated and divided distally. Dorsal in front of the anal fin. Scales rhombic, marked with irregular oblique furrows.

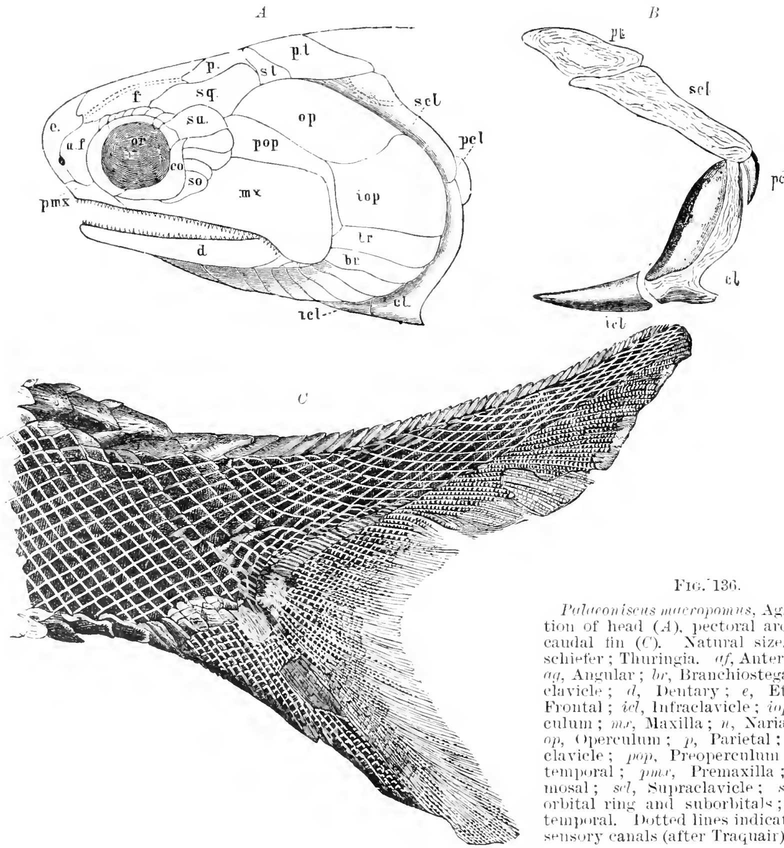


Fig. 136.
Palaeoniscus macropomus, Ag. Restoration of head (*A*), pectoral arch (*B*), and caudal fin (*C*). Natural size. Kupferschiefer; Thuringia. *af*, Anterior frontal; *ag*, Angular; *br*, Branchiostegal rays; *cl*, clavicle; *d*, Dentary; *e*, Ethmoid; *f*, Frontal; *icl*, Infraclavicle; *iop*, Suboperculum; *mx*, Maxilla; *n*, Narial opening; *op*, Operculum; *p*, Parietal; *pcl*, Postclavicle; *pop*, Preoperculum; *pt*, Posttemporal; *pmx*, Premaxilla; *q*, Squamosal; *scl*, Supraclavicle; *so*, Circumorbital ring and suborbitals; *st*, Supratemporal. Dotted lines indicate course of sensory canals (after Traquair).

P. freieslebeni, Blv. (Fig. 136), and other species very common in the Kupferschiefer of Thuringia and Riechelsdorf, Hesse; also found in the Upper Permian of England, France, and Russia.

Elonichthys, Giebel (*Rhabdolepis*, Troschel; *Cosmoptychius*, Traquair), (Figs. 137, 138). Teeth of different sizes. Fins large, with fulcra, and the rays distally divided. Dorsal in front of the anal fin. Scales rhombic, obliquely sculptured. *E. germari*, Gieb., from Coal Measures of Saxony. Other species

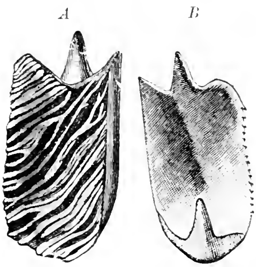


FIG. 137.
Elonichthys (*Cosmoptychius*) *striatus*, Ag. sp. Scale from outer (*A*), and inner (*B*) aspects, three times nat. size. Lower Carboniferous; Edinburgh (after Traquair).

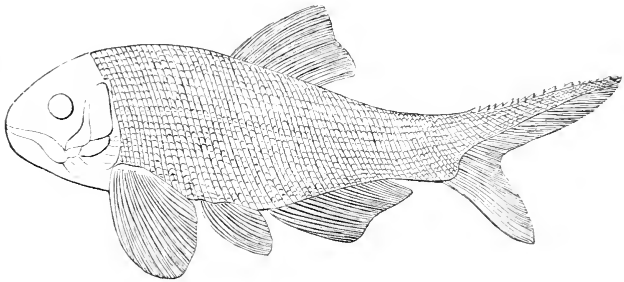


FIG. 138.
Elonichthys (*Rhabdolepis*) *macropterus*, Bronn sp. Lower Permian (Rothliegenden), Lebach, near Saarbrücken Rhenish Prussia (restoration after Agassiz).

from the Carboniferous of England, Scotland, and North America; also from the Lower Permian of Rhenish Prussia and Bohemia.

Acrolepis, Ag. Closely resembling *Elonichthys*, but scales more deeply overlapping. *A. sedgwicki*, Ag., from Upper Permian (Marl Slate of Durham and Kupferschiefer of Germany). Other species in Carboniferous of England, Scotland, and Belgium.

Gyrolepis, Ag. (Fig. 139). Anterior rays of pectoral fins not articulated. Operculum deep and narrow. Scales marked with irregular oblique and curved rugae. Common in the Muschelkalk and Rhaetic Bone-bed, but usually only isolated scales.

FIG. 139.
Gyrolepis ornatus, Gieb. Scales enlarged. Muschelkalk; Esperstadt (after Dames).

Myriolepis, Egerton. Scales very small. *M. clarkei*, Eg., from Trias (Hawkesbury Formation), New South Wales. An allied fish in the Coal Measures of Kilkenny, Ireland.

Oxygnathus, Egerton (*Thrissonotus*, *Cosmolepis*, Egerton). Fins large, with small fulcra. Pectoral fin rays only articulated distally. Dorsal in front of anal fin. Scales small, but thick, obliquely sculptured. *O. ornatus*, Eg., from Lower Lias, Lyme Regis.

Centrolepis, Egerton. Lower Lias; Lyme Regis.

Atherstonia, Sm. Woodw. Trias (Karoo Formation); Colesberg, South Africa.

Coccolepis, Ag. Scales thin, rounded, and very deeply overlapping; ornamented with tubercles. Fulcra minute or absent. Dorsal in front of anal fin. Small species in the Upper Jurassic Lithographic Stone of Bavaria (*C. bucklandi*, Ag.), the Purbeck Beds and Lower Lias of England. A larger species (*C. australis*, Sm. Woodw.) in the Hawkesbury-Wianamatta Formation of New South Wales. Only known Palaeoniscid ranging above the Lias.

Cryphiolepis, Traquair. Fins large, with fulcra. Scales large and thin, more or less rounded, very deeply overlapping, and externally striated. Lower Carboniferous; Scotland.

Family 2. **Platysomidae.** Traquair.

Trunk deeply fusiform or irregularly rhombic and laterally compressed. Head bones enamelled; hyomandibular nearly vertical and mouth small; teeth, when present, more or less blunt, chiefly on the pterygoid and splenial bones. Fins with fulcra; pelvic fins small or absent; dorsal fin single, much extended. Scales rhombic, deepened on the flank, each with an inner vertical keel projecting as a peg at the upper border. Carboniferous and Permian.

Eurynotus, Ag. (*Plectrolepis*, Ag.). Trunk deeply fusiform. Teeth short, obtusely conical to spheroidal. Pectoral fins large; dorsal fin arising opposite the pelvic pair and extending to the caudal fin; anal fin short-based. *E. crenatus*, Ag., from Lower Carboniferous, Scotland; other species from Ireland and Belgium.

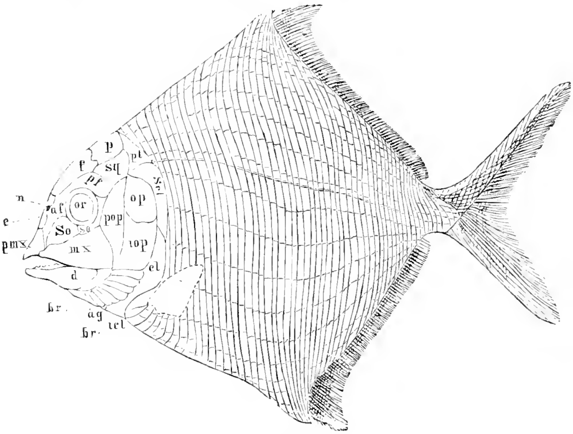


Fig. 140.

Cheirodus granulosus, Young sp. Coal Measures; North Staffordshire. Restored. Lettering as in Fig. 136 (after Traquair).

Mesolepis, Young; *Wardichthys*, Traquair. Carboniferous; Scotland and England.

Cheirodus, M'Coy (*Amphicentrum*, Young), (Fig. 140). Trunk deep, rhombic. Pectoral fins very small, pelvic fins absent. Dorsal and anal fins directly opposed, and both much extended. Teeth absent, but pterygoid and splenial with denticulated

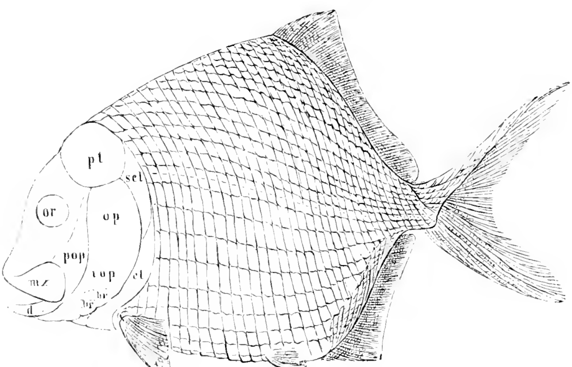


Fig. 141.

Platysomus striatus, Ag. Upper Permian (Magnesian Limestone); Durham. 1/4 nat. size (restoration after Traquair).

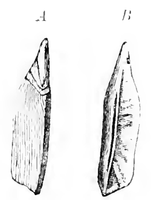


Fig. 142.

Platysomus parvulus, Ag. Scale, outer (*A*), and inner (*B*) aspects, twice nat. size. Coal Measures; England.

border. *C. granulosus*, Young sp. (Fig. 140), from English and Scottish Coal Measures. Other species in Lower Carboniferous, England and Scotland.

Cheirodopsis, Traquair. Lower Carboniferous; Scotland.

Platysomus, Ag. (Figs. 141, 142). Trunk deep, rhombic or discoidal. Teeth small, styliform. Pectoral and pelvic fins small. Scales finely striated. *P. striatus*, Ag. (Fig. 141), from Upper Permian (Marl Slate of England, Kupferschiefer of Germany). Upper and Lower Carboniferous of England and Scotland; Coal Measures of North America; Permian of Orenburg, Russia.

? *Dorypterus*, Germar. A scaleless fish, showing internal skeleton. Rare in Upper Permian (Marl Slate of Durham and Kupferschiefer of Germany).

Family 3. **Catopteridae.** Woodward.

Trunk elongate or elongate-fusiform; tail abbreviate heterocercal. Head bones well developed, ganoid; no median series of cranial roof bones; teeth slender, conical. Dorsal fin single and not much extended. Scales rhombic, ganoid. Trias.

Dictyopyge, Egerton. Teeth small. Dorsal opposite or slightly in front of the anal fin. Upper lobe of tail very short; caudal fin forked. Scales rhombic, smooth or with few oblique furrows. All species small. Upper Trias of England, Germany, Virginia, U.S.A., South Africa, and Australia. Also *D. rhenana*, Deecke, from Lower Trias (Bunter), near Basle, Switzerland.

Catopterus, Redfield (*Redfieldius*, Hay). As *Dictyopyge*, but origin of dorsal behind that of anal fin. Fulcra fine. Trias; North America.

Order 4. LEPIDOSTEI. Huxley.[1]

Notochord persistent, or vertebrae in various degrees of ossification. Opercular apparatus usually complete, with branchiostegal rays, and often a gular plate; at least one series of postorbitals on the cheek between the orbit and preoperculum. Teeth pointed or conical. No infraclavicle. Unpaired, and usually also paired fins fringed with fulcra; supports of dorsal and anal fins equal in number to the dermal rays. Caudal fin hemi-heterocercal. Scales rhombic or rhomboidal, arranged in oblique series, and frequently united above and below by peg-and-socket articulations.

To the Lepidostei are referred the "bony pikes" at present distributed throughout the freshwaters of North America, besides a large number of fossil genera from Mesozoic formations. They are remarkably closely related to the Palaeoniscidae, and in the ossification of their internal skeleton they represent a higher grade of the same type. Except a single genus from Permian deposits (*Acentrophorus*), the Lepidosteoids are confined to the Trias, Jurassic, Cretaceous, and Tertiary, both in Europe and North America. Their maximum development occurs in the Jurassic period. While the Lepidosteoids are closely related on the one hand to the Palaeoniscids, they approach so closely to the Amioids on the other, that it is impossible to separate them distinctly from the latter.

[1] *Egerton, P. M. G.*, Figures and Descriptions of British Organic Remains (Mem. Geol. Surv. dec. VI., VIII., IX., XIII.).—*Kner, R.*, Die Fische der bituminösen Schiefer von Raibl in Kärnthen (Sitzungsb. k. Akad. Wiss. Wien, math.-naturw. Cl. vol. LIII.), 1866; and Nachtrag, *ibid.* vol. LV. 1867.—Die fossilen Fische der Asphaltschiefer von Seefeld in Tyrol (*ibid.* vol. LIV.), 1866; and Nachtrag, *ibid.* vol. LVI. 1867.—*Vetter, B.*, Die Fische aus dem lithographischen Schiefer im Dresdener Museum (Mittheil. k. mineral.-geol. Mus. Dresden), 1881.

Family 1. **Stylodontidae.** Wagner.[1]

Jaws and vomer with several rows of teeth, those of the outer row styliform. Vertebral column consisting of hemi-vertebrae or ring-vertebrae. All fins fringed with fulcra. Caudal fin both internally and externally hemi-heterocercal, the upper lobe more extensively scaled than the lower lobe. Upper Permian to Upper Jurassic.

Acentrophorus, Traq. Trunk fusiform. Dorsal fin short, opposite the space between the pelvic and anal fins. No enlarged ridge scales. *A. varians*, Kirkby sp., and other species from Magnesian Limestone, Durham. *A. chicopensis*, Newb. Trias; Connecticut Valley, U.S.A.

Semionotus, Ag. (*Ischypterus*, Egert.). Trunk fusiform. Dorsal fin large and extended, its hinder part opposed to the anal fin. Dorsal series of pointed ridge scales forming a prominent crest. Fin fulcra sometimes very large. Scales and head-bones smooth or but feebly ornamented. *S. bergeri*, Ag., from Keuper of Coburg and Thuringia. *S. kapffi*, Fraas (Fig. 143), from Keuper, Haslach, near Stuttgart. Other species from the Bunter, Muschelkalk, Keuper, and Rhaetic of Europe, also from the Upper Karoo Formation of South Africa, the Hawkesbury Formation of New South Wales, and Trias of Connecticut Valley and New Jersey, U.S.A.

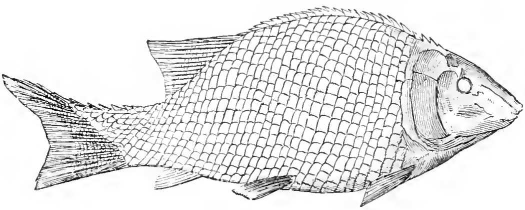


Fig. 143.
Semionotus kapffi, Fraas. Keuper (Stubensandstein); Stuttgart. $^2/_3$ nat. size (after O. Fraas).

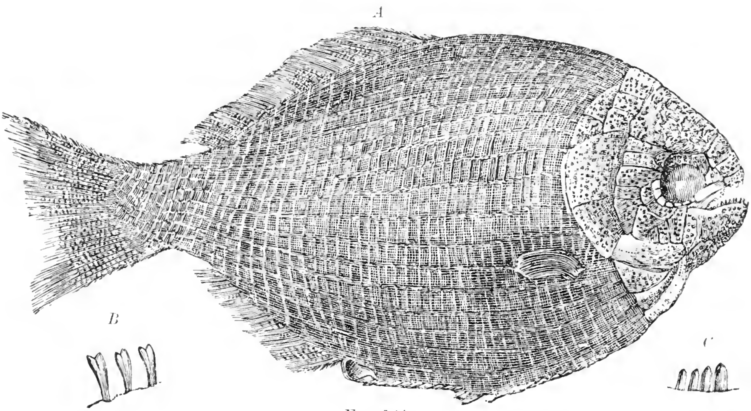


Fig. 144.
Dapedius pholidotus, Ag. Upper Lias; Boll, Würtemberg. $^1/_2$ nat. size.
B, *C*, Teeth, nat. size (after Quenstedt).

Crenilepis, Dames. Muschelkalk. *Homoeolepis*, Wagner. Upper Lias; Boll.

Dapedius, de la Beche (*Amblyurus*, Ag.; *Aechmodus*, Egerton), (Figs. 144,

[1] *Strüver, J.*, Fossile Fische aus dem Keupersandstein von Coburg (Zeitschr. deutsch. geol. Ges. vol. XVI.), 1864.—*Wagner, A.*, Die Griffelzähner (Stylodontes), (Gelehrt. Anzeig. k. bay. Akad. vol. L.), 1860.—*Deecke, W.*, Ueber Fische aus verschiedenen Horizonten der Trias (Palaeontogr. vol. XXXV.), 1888.—*Newberry, J. S.*, Fossil Fishes and Fossil Plants of the Triassic Rocks (Monogr. U.S. Geol. Surv. vol. XIV.), 1888.—*Schellwien, E.*, Ueber Semionotus Agassiz (Schriften Phys.-ökon. Gesellsch. Königsberg), 1901.

145). Trunk much laterally compressed, deeply fusiform or cycloidal. External bones ornamented with tubercles and ridges of ganoine. Eye surrounded by a complete ring of small quadrangular plates (*co*), behind which are from five to eight postorbitals (*so*, cheek-plates). The supra-temporal plates (*st*) also numerous. Operculum, suboperculum, and interoperculum large, arranged in an arch. Preoperculum narrow, almost or completely covered by the postorbitals. A median gular plate between the laminar branchiostegal rays. Fin-fulcra Λ-shaped, the two halves being fused at the apex. Pectoral and pelvic fins small; dorsal and anal fins much extended and opposed; caudal fin slightly forked. Scales on the middle of the flank deeper than broad; no prominent ridge scales; all the scales thick and enamelled, sometimes tuberculated. The earliest species in the Alpine Trias (Seefeld, St. Cassian). Common in the Lower Lias of England and the Upper Lias of Würtemberg (Boll, Holzmaden), Bavaria (Banz), Northern France (Calvados), (*D. pholidotus*, Ag.; *D. caelatus*, Quenst.). Also found in the Gondwana Beds of India.

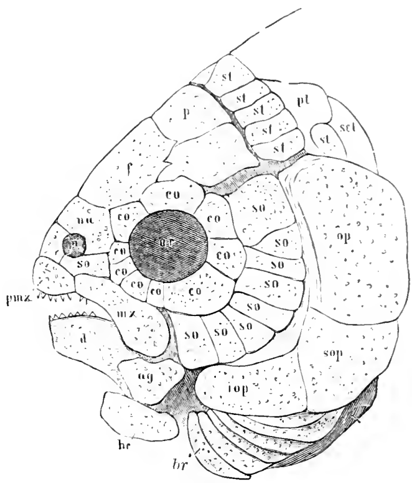


FIG. 145.

Head of *Dapedius*. *ag*, Angular; *br*, Gular plate; *br'*, Branchiostegal rays; *cl*, Clavicle; *co*, Circumorbitals; *d*, Dentary; *f*, Frontal; *iop*, Interoperculum; *mx*, Maxilla; *na*, Nasal; *op*, Operculum; *or*, Orbit; *p*, Parietal; *pmx*, Premaxilla; *pt*, Post-temporal; *scl*, Supraclavicle; *so*, Suborbitals; *sop*, Suboperculum; *sq*, Squamosal; *st*, Supratemporal (after Traquair).

Heterostrophus, Wagner. Lithographic Stone (Upper Jurassic); Bavaria.

Cleithrolepis, Egerton. Hawkesbury Formation; New South Wales. Karoo Formation; Orange River Colony.

Tetragonolepis, Bronn (*Pleurolepis*, Quenst.). Small oval or almost cycloidal fishes, laterally compressed, with small pectoral and pelvic fins. Dorsal and anal fins much extended. Scales deepened on the flank, their front border thickened and forming a vertical ridge. *T. semicinctus*, Bronn, from Upper Lias, Würtemberg and Bavaria. Other species in the Upper Lias of England, and the Kota Formation of the Deccan, India.

Family 2. **Semionotidae.** Woodward.[1]

Premaxilla, maxilla, and dentary with obtusely conical or chisel-shaped teeth; vomer, pterygo-palatine arch, and splenial with several rows of stouter hemispherical teeth. All fins fringed with fulcra. Caudal fin hemi-heterocercal. Scales thick and rhombic. Trias to Cretaceous.

Colobodus, Ag. (*Asterodon*, Münst.; *Tholodus*, Meyer; *Dactylolepis*, Kunisch). Teeth hemispherical and irregularly crowded, usually with a mammiform eleva-

[1] *Quenstedt, F. A.*, Ueber *Lepidotus* in Lias ε. Tübingen, 1847.—*Sauvage, H. E.*, Mémoire sur les *Lepidotus maximus* et *palliatus* (Mém. Soc. géol. France, ser. 3, vol. I.), 1877.—*Meyer, H. von.* Fossile Fische aus dem Muschelkalk (Palaeontogr. vol. I.), 1850.—*Dames, W.*, Die Ganoiden des deutschen Muschelkalks (Palaeont. Abhandl. vol. IV.), 1888.—*Branco, W.*, Ueber eine neue Lepidotus-Art aus dem Wealden (Jahrb. k. preuss. geol. Landesanst.), 1885.

tion in the middle of the crown. Scales marked with more or less parallel ridges, ending in denticulations at the hinder border. Common in the Muschelkalk and Lettenkohle.

The generic names *Nephrotus*, *Cenchrodus*, *Omphalodus*, *Hemilopas*, Meyer, and *Sargodon*, Plieninger (Fig. 146), are applied to rounded or chisel-shaped teeth from the Trias and Rhaetic.

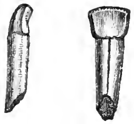


Fig. 146.
Sargodon tomicus, Plien. Rhaetic; Kemnath, Würtemberg.

Lepidotus, Ag. (*Sphaerodus*, p.p. Ag.; *Plesiodus*, Wagner; *Prolepidotus*, Michael), (Figs. 147, 148). Trunk fusiform and only moderately compressed, covered with thick, smooth, or obliquely striated scales, which are deeply imbricating and have the angles of the overlapped border more or less produced. Head and opercular bones more or less enamelled, smooth or tuberculated. Teeth hemispherical to obtusely conical. Successional teeth numerous, the incipient germ lying exactly in the opposite direction to that of the functional tooth, thus making a revolution of 180° while the root of the old tooth is absorbed and it prepares to appear

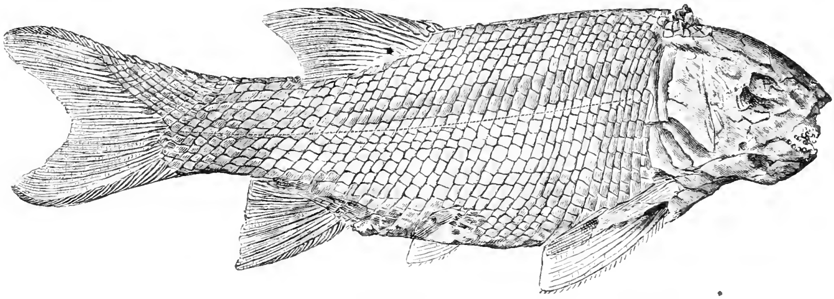


Fig. 147.
Lepidotus notopterus, Ag. Upper Jurassic (Lithographic Stone); Solenhofen. 1/5 nat. size.

(Fig. 148, *A*). Fin fulcra very large and biserial (Fig. 148, *D*), present on all the fins. Pectoral fins large; pelvic fins small; large dorsal fin opposed to the pelvic pair; caudal fin more or less forked. Ranging from the Keuper

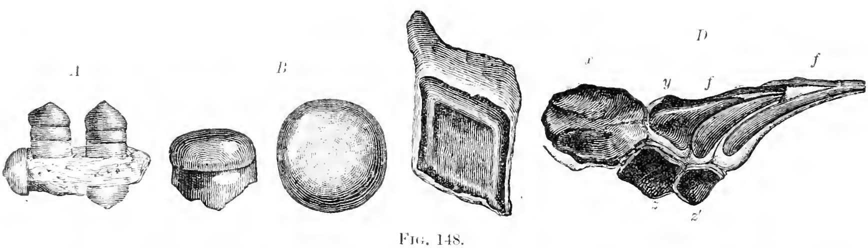


Fig. 148.
Lepidotus. *A*, Fragment of jaw with successional teeth. *B*, Tooth in side view and from above. *C*, Scale. *D*, Fulcral armature of dorsal fin. *f*, Fulcra; *x*, Unpaired dorsal scale; *y*, First basal scale of dorsal fin; *z*, *z'*, lateral scales. Nat. size.

to the Lower Cretaceous, some of the later species having the largest, stoutest teeth and well-developed ring-vertebrae. The type species, *L. elvensis*, Blv. sp., common in the Upper Lias of Würtemberg, Bavaria, France, and England. *L. maximus*, Wagn., *L. notopterus*, Ag. (Fig. 147), and other species well preserved in the Lithographic Stone (Upper Jurassic) of Germany and France. *L. mantelli*, Ag., from Wealden. Also Jurassic of India and Siberia, and Cretaceous of Brazil.

Family 3. **Eugnathidae.** Woodward.

Trunk slender, covered with rhomboid enamelled scales. Marginal teeth conical. Cranial and facial bones moderately robust, externally enamelled, and opercular apparatus complete. Snout not produced. Fin-rays robust, fulcra conspicuous. Dorsal fin short and acuminate. Vertebral column rarely more than incomplete rings. Tail externally homocercal or hemi-heterocercal. Trias to Cretaceous.

Eugnathus, Ag. (*Heterolepidotus*, Egerton). Cleft of mouth wide, with large, conical, pointed laniary teeth and numerous smaller pointed teeth between these. Head and opercular bones smooth or tuberculated. Fins powerful, the dorsal arising opposite the pelvic pair, stouter and longer than the anal fin; caudal fin forked, externally hemi-heterocercal. Scales rather thick, mostly longer than deep, and with serrated hinder border. The type species, *E. orthostomus*, Ag., a slender fish, common in the Lower Lias of Lyme Regis, Dorset. Other species in the Lias, and ranging upwards to the Lithographic Stone (*E. microlepidotus*, Ag.) and Purbeck Beds.

Caturus, Ag. (*Uraeus*, Ag.), (Fig. 149). Essentially identical with *Eugnathus*, but scales thinner, more deeply overlapping, and less narrowed near the ventral

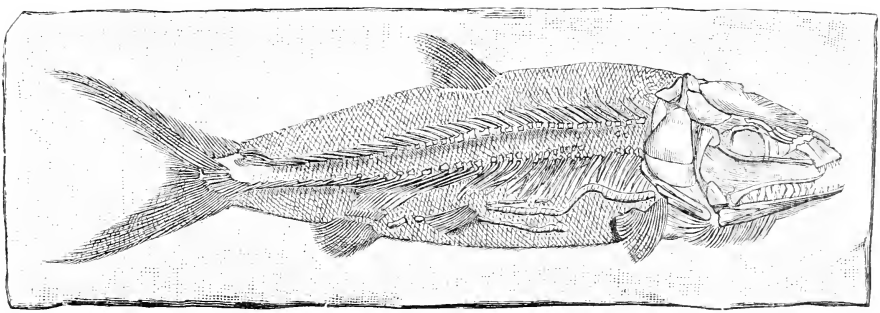


FIG. 149.

Caturus elongatus, Ag. Upper Jurassic (Lithographic Stone); Cerin, Ain, France. 1/2 nat. size.

border of the fish. Endoskeleton of trunk usually well displayed in the fossils, showing hemi-vertebrae, short ribs, and free neural spines in the abdominal region. Ranging from the Trias to the Upper Jurassic, especially fine specimens being known from the Lower Lias of England (*C. heterurus*, Ag. sp., etc.), and the Lithographic Stone of France, Bavaria, and Würtemberg (*C. furcatus*, *elongatus*, *maximus*, Ag., etc.).

Strobilodus, Wagner; *Ditaxiodus*, Owen. Large fishes resembling *Caturus*. Upper Jurassic of Europe.

Callopterus, Thiollière. Lithographic Stone of Bavaria and France.

Eurycormus, Wagner (Fig. 122). Much resembling *Caturus*, but vertebral column consisting of hemi-vertebrae, which become two similar complete rings in the caudal region. Dentition comparatively feeble. *E. speciosus*, Wagn., from Lithographic Stone, Bavaria. Other species in Oxford and Kimmeridge Clays, England.

Ptycholepis, Ag. Head and opercular bones ornamented with ridges of ganoine; teeth minute. Scales thick, much longer than deep, externally marked with longitudinal grooves. *P. bollensis*, Ag., from Upper Lias of England, France, Bavaria, and Würtemberg. Other species in Lower Lias of England. Smaller species in Trias of Raibl, Carinthia, and Connecticut.

Family 4. **Macrosemiidae.**

Marginal teeth styliform; dorsal fin elongated; scales rhombic.

Ophiopsis, Ag. Trunk much elongated and slender, with a high dorsal fin extending half its length. Anal fin small. Caudal fin hemi-heterocercal. Ranging from the Muschelkalk to the Purbeck Beds. *O. procera*, Ag., and other species common in the Lithographic Stone of Bavaria.

Macrepistius, Cope. Lower Cretaceous; Texas. *Eusemius*, Vetter. Upper Jura; Bavaria.

Notagogus, Ag. Trunk elongated, with extended dorsal fin subdivided into two parts, the anterior portion with comparatively widely spaced rays, and not deeper than the posterior portion. Stout ring-vertebrae. *N. pentlandi*, Ag., from Neocomian, Castellamare, near Naples. Other species in the Lithographic Stone of Bavaria.

Propterus, Ag. As *Notagogus*, but trunk deeper and anterior portion of dorsal fin deeper than posterior portion. Ring-vertebrae. Scales almost six-sided, deeper than long. Jura.

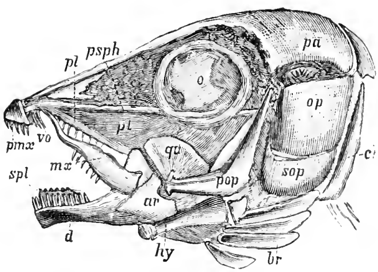


FIG. 150.

Macrosemius latiusculus, Wagn. Head, nat. size. Upper Jurassic (Lithographic Stone); Kelheim. *ar*, Articular; *br*, Branchiostegal rays; *cl*, Clavicle; *d*, Dentary; *hy*, Ceratohyal; *mx*, Maxilla; *o*, Orbit; *op*, Operculum; *pa*, Parietal; *pl*, Palatine; *pmx*, Premaxilla; *pop*, Preoperculum; *psph*, Parasphenoid; *pt*, Pterygoid; *qu*, Quadrate; *sop*, Suboperculum; *spl*, Splenial; *vo*, Vomer.

Histionotus, Egerton. The back of the elongated trunk elevated and sharply bent anteriorly, a single long dorsal fin extending backwards from the bend almost to the caudal fin, which is deeply forked. Uniserial fulcra on both paired and median fins. Scales of flank deeper than broad. *H. angularis*, Eg., from the English Purbeck Beds. Other species from the Lithographic Stone of Bavaria and France.

Macrosemius, Ag. (*Distichdepis*, Thioll.), (Fig. 150). Trunk elongated, and dorsal fin extending from the occiput to the caudal fin, which is rounded. No fin fulcra. Jaws and pterygoid with powerful conical or styliform teeth. Scales thin and rhombic. *M. rostratus*, Ag., *M. latiusculus*, Wagn. (Fig. 150), and other species in the Lithographic Stone of Bavaria and France. Small species of this or an allied genus in the Purbeck Beds of Wiltshire and the Portlandian of Meuse, France.

Petalopteryx, Pictet. Upper Cretaceous; Mount Lebanon.

Family 5. **Pholidophoridae.**

Trunk fusiform; teeth small and conical; scales rhombic and deeply overlapping; dorsal and anal fins small; vertebrae forming complete rings.

Pholidopleurus, Bronn (Fig. 151). Trunk slender. Scales smooth, one series short and very deep on the flank, those on the back and ventral region longer than deep. Dorsal and anal fins delicate, elongated, and low, directly opposed on the hinder part of the caudal region. Caudal fin externally homocercal, slightly forked. Trias; Raibl, Carinthia.

Pleuropholis, Egerton. Upper Jurassic (English Purbeck Beds, and French and Bavarian Lithographic Stone). *P. egertoni*, Wagn.

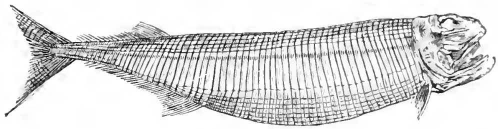


FIG. 151.
Pholidopleurus typus, Bronn. Keuper; Raibl, Carinthia. $^2/_3$ nat. size (after Kner).

Pholidophorus, Ag. (Figs. 152, 153). Body shaped like a carp. Scales thin, deeper than long on the flank, enamelled, smooth or finely striated and serrated. Small dorsal fin opposed to the pelvic pair. Caudal fin externally homocercal, deeply forked; a large, unpaired dorsal scale often at its base. Common in the Alpine Trias of Raibl (*P. bronni*, Kner) and Seefeld; in the Lias of Lyme Regis (*P. bechei*, Ag., *P. limbatus*, Ag.), Whitby, Calvados, Würtemberg, and Bavaria (*P. germanicus*, Quenst.); in the Lithographic Stone of Bavaria and France; in the Purbeck Beds of England and Lower Jura of the Black Hills, South Dakota.

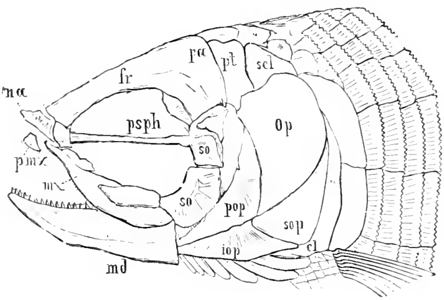


FIG. 152.
Pholidophorus striolaris, Ag. Head, nat. size. Upper Jurassic (Lithographic Stone); Eichstädt. *cl*, Clavicle; *fr*, Frontal; *iop*, Interoperculum; *md*, Mandible; *mx*, Maxilla; *na*, Nasal; *op*, Operculum; *pa*, Parietal; *pmx*, Premaxilla; *pop*, Preoperculum; *psph*, Parasphenoid; *pt*, Post-temporal; *scl*, Supraclavicle; *so*, Suborbitals; *sop*, Suboperculum.

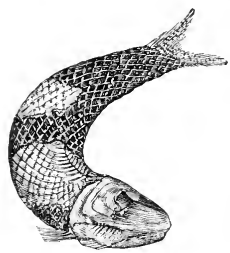


FIG. 153.
Pholidophorus pusillus, Ag. Rhaetic; Seefeld, Tyrol. Nat. size.

Isopholis, Zittel. As *Pholidophorus*, but scales of equal size and rhombic. Pectoral and anal fins large. Lithographic Stone of Bavaria and France.

Family 6. **Pycnodontidae**. Agassiz.

Trunk laterally compressed, very deep, oval. Notochord persistent. Ribs, vertebral arches, and spines well ossified. Opercular apparatus incomplete, with one or two branchiostegal rays. Premaxilla with two to four prehensile front teeth; maxilla thin, deepened behind, toothless; palatine and vomerine bones fused together, usually with five longitudinal series of round or oval grinding teeth; splenial of mandible large, with coronoid process, and three, four, five, or more rows of grinding teeth; dentary small and terminal, fitting in a groove of the splenial, and bearing two to four prehensile front teeth. Branchial arches with very numerous, closely arranged, bony filaments. Clavicle broadly ovate at the lower end. Fin fulcra absent. Pelvic fins small. Dorsal and anal fins much extended. Scales deeper than long, with a thickened, ridge-like anterior margin. Lower Lias to Upper Eocene.

Gyrodus, Ag. (Figs. 154-157). Trunk completely covered with scales.

Frontal profile steep. Vomero-palatine with five rows of rounded, bean-shaped teeth, of which the convex crown has a rugose border and mammillated apex; the middle row larger than the lateral rows. Splenial with four rows of similar teeth; dentary with three stout prehensile teeth. Caudal fin deeply forked, symmetrical. Common in the Upper Jurassic (Lithographic Stone) of Solenhofen, Eichstädt, Kelheim, Cerin (Ain); also in the Kimmeridgian of England, France, and Switzerland, in the Portlandian and Neocomian of

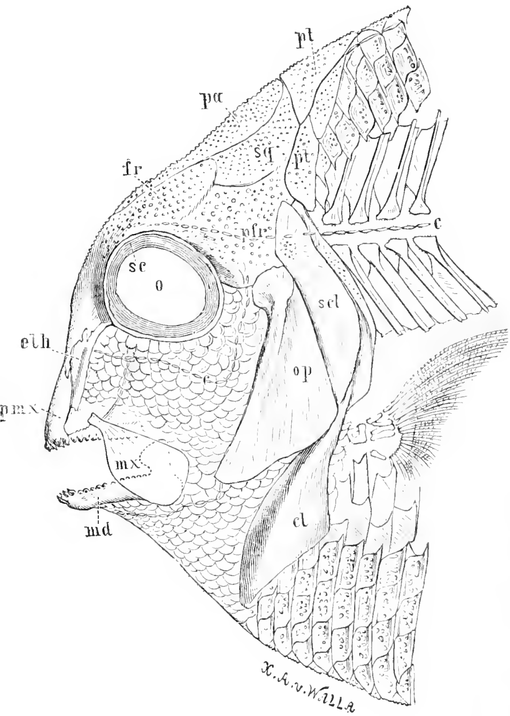


Fig. 154.

Head of *Gyrodus macrophthalmus*, Ag. Upper Jurassic (Lithographic Stone); Kelheim, Bavaria. *c*, Slime canals; *cl*, Clavicle; *eth*, Ethmoid; *fr*, Frontal; *md*, Mandible; *mx*, Maxilla; *o*, Orbit; *op*, Preoperculum; *pa*, Parietal; *pfr*, Post-frontal; *pmx*, Premaxilla; *pt*, Post-temporals; *se*, Sclerotic ring; *scl*, Operculum; *sq*, Squamosal.

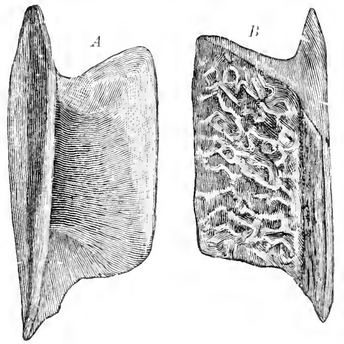


Fig. 155.

Gyrodus titanius, Wagn. Scale, inner (*A*) and outer (*B*) aspects, nat. size. Kelheim.

France and Switzerland, and the Tithonian of Sicily. Some species from the Lithographic Stone (*G. titanius*, Wagner) attain a length and depth of 1 m.

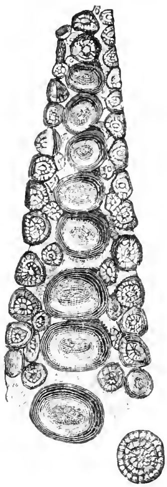


Fig. 156.

Gyrodus titanius, Wagn. Palatal plate with teeth, nat. size. Kelheim.

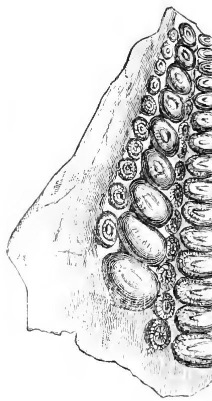


Fig. 157.

Gyrodus titanius, Wagn. Right splenial with four rows of teeth, nat. size. Upper Jura; Kelheim.

Microdon, Ag. (Figs. 158, 159). Hinder half of trunk with very thin scales, which are often wanting. Vomero-palatine slender, with five rows of quadrate, smooth, and flattened teeth; between the large teeth of the middle row the smaller teeth of the two inner lateral rows are alternately pressed inwards. Splenial with one row of large, obliquely quadrate, smooth teeth, which is flanked inside by one, outside by two rows of smaller teeth. Caudal fin slightly forked, symmetrical. Common in the Upper Jurassic (Lithographic

Stone) of Bavaria and France, and in the Purbeck Beds of England. Earliest

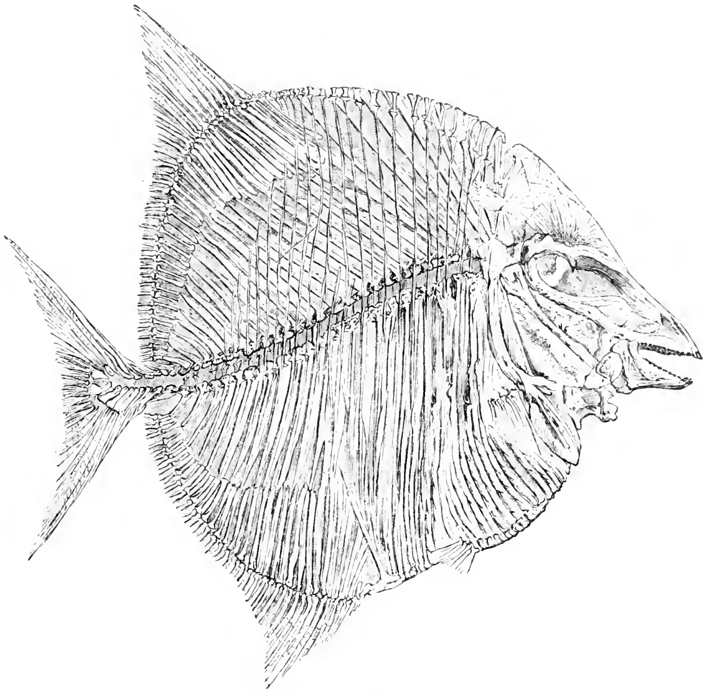


FIG. 158.
Microdon wagneri, Thiollière. Upper Jurassic; Cerin, Ain, France. $1/3$ nat. size (after Thiollière).

fragments in the Stonesfield Slate (Bathonian), Oxfordshire. Also Corallian and Kimmeridgian, Hanover and Switzerland.

Mesodon, Wagner. As *Microdon*, but teeth on vomero-palatine in five

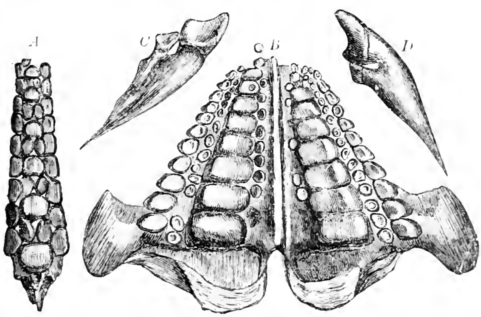


FIG. 159.
Microdon elegans, Ag. Vomeropalatine (*A*), splenials of mandible (*B*), and anterior teeth of mandible, inner view (*C*), and outer view (*D*), nat. size. Upper Jurassic; Kelheim.

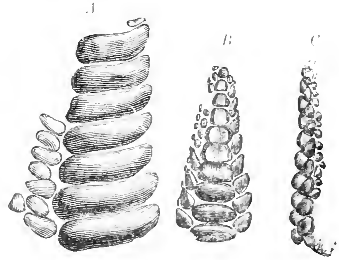


FIG. 160.
Anomoeodus muensteri, Ag. sp. Mandibular (splenial) teeth (*A*), and vomero-palatine teeth, oral aspect (*B*), and side view (*C*), nat. size. Greensand; Kelheim.

regular rows, and the large teeth on splenial flanked by three or four irregular rows of smaller teeth. Caudal fin rounded behind, not excavated. *M. liassicus*, Egert. sp., from the Lower Lias of England, is the oldest known Pycnodont, the genus ranging upwards to the Lower Cretaceous both in Europe and North America. Fine specimens in the Lithographic Stone of Bavaria and France.

Mesturus, Wagner.[1] Much resembling *Gyrodus*, but with more irregular teeth, rounded caudal fin, and scales often united above and below by jagged sutures. *M. verrucosus*, Wagn., from Lithographic Stone of Bavaria. *M. leedsi*, Sm. Woodw., represented by fine specimens displaying osteology from Oxford Clay, Peterborough.

Stemmatodus, Heckel. Small, resembling *Microdon*. Vomero-palatine teeth in five, splenial in three rows, all teeth rounded and not very unequal in size. Lower Cretaceous; Castellamare.

Coelodus, Heckel. Hinder half of trunk scaleless. Vomero-palatine teeth with one median row of large, transversely elongated, smooth, oval teeth, and two lateral rows of small teeth. One row in the splenial dentition relatively very large, its teeth transversely elongated. Caudal fin either slightly excavated or convex mesially and slightly hollowed laterally. Lower Cretaceous of Istria, Dalmatia, Southern Italy, and England; also Cenomanian and Turonian in Europe and North America.

Anomoeodus, Forir (Fig. 160). Vomero-palatine teeth in three or five longitudinal series, more or less irregular. Splenial dentition with one row relatively large, the lateral series more or less irregular, and not reaching the oral border of the bone. *A. subclavatus*, Ag. sp., from Upper Cretaceous, Maestricht. *A. muensteri*, Ag. sp., and other species from the European Greensand. Also North America.

Palaeobalistum, Blv. Upper Cretaceous; Europe, Asia, and Brazil. Upper Eocene; Monte Bolca.

Pycnodus, Ag. Trunk rather elongated, with slender caudal pedicle and forked caudal fin. Dorsal much more extended than the anal fin. Scales thin, absent on the caudal region. Teeth of the three middle rows of the vomero-palatine rounded, those of the two outer rows somewhat smaller and elliptical. *P. platessus*, Blv. sp., from Upper Eocene; Monte Bolca. Dentition in the Eocene of several European localities. *P. mokattamensis*, Priem, from Eocene, Mokattam Hills, Egypt.

Family 7. **Aspidorhynchidae.** Woodward.[2]

Very slender, elongated fishes, with enamelled rhomboid scales of different sizes. Snout beak-like, elongated, and pointed. Maxilla loose; mandible with a movable praemandibula ("presymphysial bone"). Teeth conical, pointed. Branchiostegal rays numerous. Notochord with ring-vertebrae. Caudal fin externally homocercal. Fin fulcra minute. Bathonian to Upper Cretaceous.

Aspidorhynchus, Ag. (Fig. 161). Thin, slender fishes, attaining a metre in length, with enamelled ganoid scales, which are yellow or brown in colour, more or less rugose externally, and not remarkably thick. Pectoral fin with very broad rays, which are jointed only in their distal quarter; no fulcra. Pelvic fin somewhat behind the middle point of the trunk. Anal fin opposed to the small dorsal fin. Caudal fin deeply forked, with delicate fulcra. Lower jaw much shorter than the snout, which is formed by the mesethmoid and pre-

[1] *Woodward, A. S.*, Ann. Mag. Nat. Hist. ser. 6, vol. XVII. 1896, p. 1.

[2] *Reis, O.*, Ueber *Aspidorhynchus*, *Belonostomus*, und *Lepidosteus* (Sitzungsb. k. bay. Akad. Wiss., math.-phys. Cl.), 1887.

maxillae. The oldest known species is *A. crassus*, Sm. Wood., from the Stonesfield Slate (Bathonian) of Oxfordshire. Well-preserved fishes in the Lithographic Stone of Bavaria (*A. acutirostris*, Blv. sp.) and France; also in the English Purbeck Beds (*A. fisheri*, Egerton).

Belonostomus, Ag. As above, but mandible almost as long as the snout. Kimmeridgian to Upper Cretaceous. Fine skeletons in the Lithographic

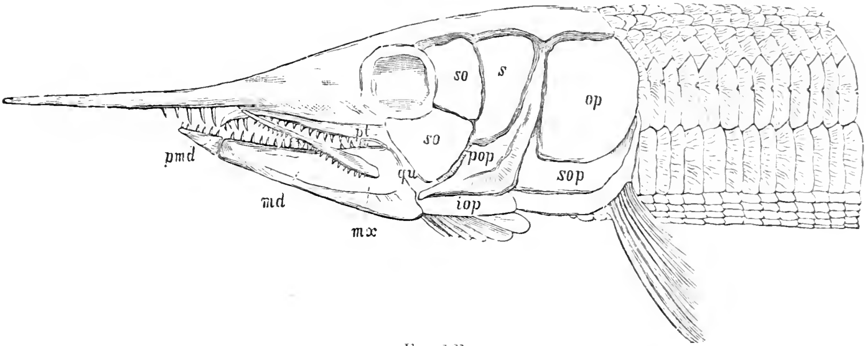


FIG. 161.

Aspidorhynchus acutirostris, Ag. Upper Jurassic; Solenhofen. *iop*, Interoperculum; *md*, Mandible; *mx*, Maxilla; *op*, Operculum; *pmd*, Predentary; *pop*, Preoperculum; *pt*, Pterygoid; *qu*, Quadrate; *s*, Hinder cheek-plate; *so*, Suborbitals; *sop*, Suboperculum.

Stone of Bavaria (*B. sphyraenoides*, Ag., etc.) and the Cretaceous of Europe, India, Brazil, and Queensland.

Family 8. **Lepidosteidae**. Bony pikes.[1]

Trunk elongated, with thick, enamelled rhombic scales. Snout much produced, the very long maxilla divided by a series of vertical sutures into several pieces, which bear large pointed laniary teeth and small clustered teeth; premaxilla short and toothed. Vomer double. Vertebral column completely ossified, bent upwards into the superior lobe of the tail; vertebrae opisthocoelous. All fins with biserial fulcra. Dorsal and anal fins very remote, near the hemi-heterocercal, rounded caudal fin. Tertiary and Recent.

Lepidosteus, the only genus of this family, survives in the rivers of the southern United States, Central America, and Cuba. Complete individuals occur also in the Eocene and Lower Miocene of Europe and North America. *L. atrox*, Leidy, from the Middle Eocene Green River Shales of Wyoming, attains a length of 1·7 m.

Order 5. AMIOIDEI. Lütken.

Notochord persistent, or vertebrae in various degrees of ossification. Opercular apparatus always complete, with lamelliform branchiostegal rays and a well-developed gular plate. Teeth pointed or conical. No infraclavicle. Fulcra present or absent. Supports of dorsal and anal fins equal in number to the dermal rays. Caudal fin hemi-heterocercal. Scales very thin, overlapping, rounded or rhombic at the hinder border.

The Amioids are distinguished from the Lepidostei by their thin, cycloid or rhombic scales, which are not articulated with each other, but merely

[1] *Eastman, C. R.*, Fossil Lepidosteids from the Green River Shales of Wyoming (Bull. Mus. Comp. Zool. vol. XXXVI. p. 67), 1900. Also Geol. Mag. [4] vol. VII. p. 54, 1900.

overlap. Notwithstanding their thinness, however, the scales exhibit the characteristic structure of true ganoid scales; the base contains bone cells, the surface is covered with enamel. In many Jurassic genera the vertebral column consists of hemi-vertebrae or complete rings, but it is also often completely ossified. Contrary to the arrangement in certain closely related bony fishes (Physostomi), the terminal vertebrae are continued some distance into the upper lobe of the tail.

Only one genus (*Amia*) still survives in the rivers of the southern United States and Central America. The order ranges upwards from the Upper Lias.

Family 1. **Pachycormidae.** Döderlein.

(*Microlepidoti* and *Cyclolepidoti*, Zittel.)

Vertebral axis with very numerous segments, with or without hemi-vertebrae. Ethmoid forming a prominent rostrum. Branchiostegal rays very numerous (thirty to forty). Neural spines in abdominal region separate from arches. Caudal fin deeply forked, powerful, only internally heterocercal. Teeth laterally compressed, lanciform, in two series, the largest of which are set in alveoli. Upper Lias to Upper Cretaceous.

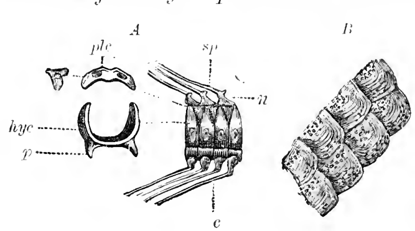


Fig. 162.

Euthynotus micropodius, Ag. sp. Upper Lias; Boll, Würtemberg. *A*, Vertebrae (*c*, Haemal arches; *hyc*, Hypocentrum; *n*, Neural arches; *p*, Parapophyses; *plc*, Pleurocentrum; *sp*, Neural spine). *B*, Scales.

Pachycormus, Ag. Large, salmon-shaped fishes, with hemi-vertebrae only in the caudal region. Operculum, sub-operculum, and suborbitals very large. Rays of all the fins with distant articulations. Pectoral fins large; pelvic fins absent; short dorsal fin arising in front of the anal; deeply forked caudal with elongated fulcra on each lobe. *P. macropterus*, Blv. sp., and other species in the Upper Lias of Germany, France, and England.

Euthynotus, Wagner (*Heterothrissops*, *Pseudothrissops*, Sauvage), (Fig. 162). Hemi-vertebrae present. Fin fulcra minute. Pelvic fins present; dorsal fin opposed to much extended anal fin. Scales rhombic, rounded at the angles. *E. speciosus*, Wagn., and other species in the Upper Lias of Germany and France.

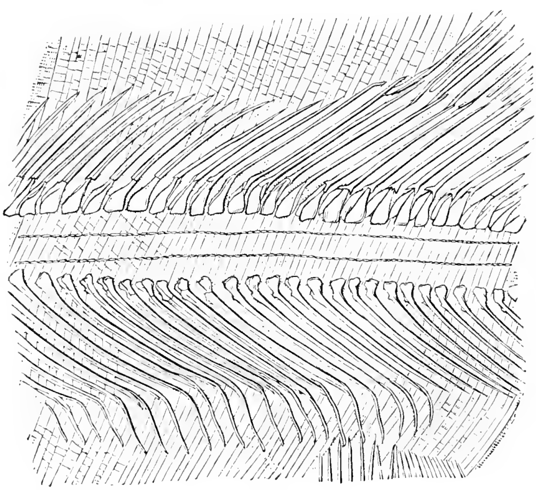


Fig. 163.

Hypsocormus insignis, Wagn. Portion of trunk. Upper Jurassic (Lithographic Stone); Eichstädt, Bavaria.

Hypsocormus, Wagner (Fig. 163). Large fishes, with very small rhombic scales, much resembling

Pachycormus, but with larger teeth, small pelvic fins, and a much extended anal fin. Large teeth rounded in section, of complex structure. *H. insignis*, Wagn., from Lithographic Stone of Bavaria. *H. leedsi*, Sm. Woodw., from Oxford Clay, Peterborough.

Protosphyraena, Leidy[1] (*Erisichthe*, *Pelecopterus*, Cope), (Fig. 164). Known only by fragments of head and fins much resembling those of *Hypsocormus*, but teeth laterally compressed, and snout more produced. *P. ferox*, Leidy, and other species, in the Upper Cretaceous of Europe and North America. The teeth were wrongly ascribed to *Saurocephalus*, Harlan, by Agassiz.

Fig. 164.
Tooth of *Protosphyraena ferox*, Leidy. Upper Chalk; Maestricht. Nat. size.

Family 2. **Amiidae.** Günther.

(*Megaluridae*, Zittel; *Halecomorphi*, Cope.)

Vertebral column well ossified, and flexed upwards behind into the upper part of the rounded caudal fin. Pleurocentra and hypocentra forming complete alternating discs in part of the caudal region, the alternate discs bearing the neural and haemal arches. Teeth powerful. Branchiostegal rays broad and few; gular plate large. Fulcra present or absent. Scales very thin and cycloid. Upper Jurassic to Recent.

Megalurus, Ag. (Figs. 165, 166). Vertebral column much produced into

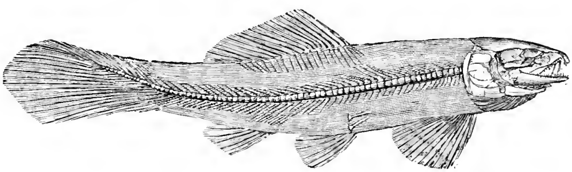


Fig. 165.
Megalurus elegantissimus, Wagn. Upper Jurassic; Solenhofen, Bavaria. 2/3 nat. size.

A B

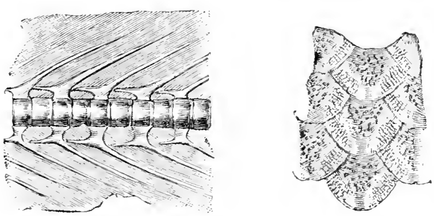


Fig. 166.
Megalurus polyspondylus, Münst. Upper Jurassic; Kelheim. *A*, Portion of vertebral column, nat. size. *B*, Scales, enlarged.

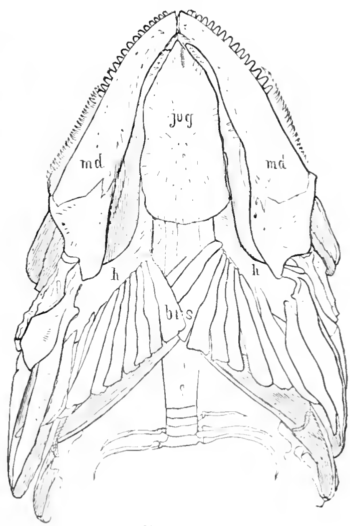


Fig. 167.
Amia calva, Linn. Head, from beneath. Recent; South Carolina. *brs*, Branchiostegal rays; *h*, Ceratohyal; *jug*, Gular plate; *md*, Mandible

the upper caudal lobe; caudal hemi-vertebrae rather elongated. Fulcra present. Dorsal fin considerably extended, arising opposite the pelvic fins,

[1] *Felix, J.*, Zeitschr. deutsch. geol. Ges. vol. XLII. 1890, p. 278.—*Woodward, A. Sm.*, Ann. Mag. Nat. Hist. ser. 6, vol. XIII. 1894, p. 510.

and reaching the hinder end of the anal fin; caudal fin convex behind, very large. Several species in the Upper Jurassic (Lithographic Stone) of Bavaria, Nusplingen, and Cerin, and in the English Purbeck Beds. *M. mawsoni*, Sm. Woodw. From Cretaceous of Bahia, Brazil.

Liodesmus, Wag. (*Lophiurus*, Vetter). Lithographic Stone; Bavaria.

Opsigonus, Kramberger; *Amiopsis*, Kner. Lower Jura; South Dakota. Lower Cretaceous; Dalmatia and Istria.

Amia, Linn. (*Cyclurus*, *Notaeus*, Ag.), (Fig. 167). Fulcra absent. Dorsal fin arising in front of the pelvic pair and extending to the caudal fin. Living in North America; fossil in the Upper Eocene and Lower Miocene freshwater formations of Europe and North America. *A.* (*Notaeus*) *longicauda*, Ag. (Montmartre), *A.* (*Cyclurus*) *valenciennesi*, Ag. (Armissan), *A. kehreri*, Andreae (Messel, near Darmstadt), *A. anglica*, Newton (Isle of Wight).

Pappichthys, Cope. Eocene; North America.

Family 3. **Oligopleuridae.** Smith Woodward.

Vertebrae well ossified, with no distinct pleurocentra and hypocentra. Mouth wide, with teeth small or of moderate size. Fulcra present. Scales very thin and cycloid. Upper Jurassic to Upper Cretaceous.

Oligopleurus, Thiollière (Fig. 168). Teeth very small, and mandible prominent. Vertebral centra not pitted. Dorsal fin short-based, opposed to

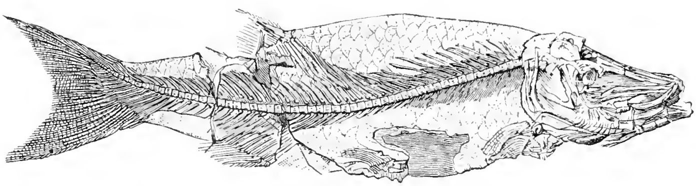


Fig. 168.
Oligopleurus esocinus, Thioll. Upper Jurassic (Lithographic Stone); Cerin, Ain, France. 1/4 nat. size (after Thiollière).

anal fin. Caudal fin slightly forked. Scales rather large. *O. esocinus*, Thioll., from Lithographic Stone, Cerin (Ain, France). Other species in English Wealden and Purbeck Beds.

Oenoscopus, Costa (*Attakeopsis*, Thioll.; *Macrorhipis*, Wagn.). Almost as above, but vertebral centra with two lateral pits, and greater portion of dorsal in advance of anal fin. *O. petraroiae*, Costa, from Lower Cretaceous, Pietraroja, Prov. Benevento, Italy. Other species in French and German Lithographic Stone.

Spathiurus, Davis. With much extended dorsal fin. Upper Cretaceous; Mount Lebanon.

Sub-Class 6. **TELEOSTEI.**[1] Bony fishes.

Skin with thin, elastic, cycloid or ctenoid scales, rarely with bony plates. Vertebral column ossified; tail internally and externally homocercal. Intermuscular bones more

[1] *Bassani, Fr.*, Descrizione dei pesci fossili di Lesina accompagnata da appunti su alcune altre ittiofaune cretacee (Denkschr. k. Akad. Wiss. Wien, math.-naturw. Cl. vol. XLV.), 1882.—*Kner, R.*, Ueber einige fossile Fische aus Kreide und Tertiärschichten von Comen und Podsuded (Sitzungsb.

or less numerous. Fin fulcra absent. In the living forms—optic nerves completely decussating, conus arteriosus of the heart with only two valves, and intestine without a spiral valve.

The distinction between the bony fishes and ganoids consists partly in the dermal skeleton and partly in anatomical characters, which cannot usually be verified by palaeontologists. The two sub-classes are most closely related to each other, and the line of demarcation between the Amioidei and the Physostomi is often almost obliterated. This applies specially to the scales, which have already become thin and elastic in the former, and are not distinguishable in any respect from those of certain Physostomi, in which a thin calcified layer with bone cells happens to be developed beneath the outer smooth layer. Among Teleostei the internal skeleton is often characterised by its very dense structure and the sparse development of bone cells. The caudal fin, unlike that of the ganoids, is usually both internally and externally homocercal. In the more specialised forms the pelvic fins are sometimes displaced far forwards, while the rays of the dorsal fins are sometimes articulated, sometimes spinous.

The Teleostei are divided into the two orders of Physostomi and Physoclysti.

Order 1. PHYSOSTOMI. Müller.

Air bladder, when present, connected by a tube with the oesophagus. Pelvic fins abdominal ; all fin rays articulated, except the foremost rays of the pectoral and dorsal fins, which are sometimes spinous. Scales, when present, usually cycloid.

Of all the bony fishes the Physostomi approach most closely the ganoids, especially the Amioidei. They probably originated from the latter in the Trias, becoming specialised in their own line, and soon considerably exceeding their ancestors in diversity of form. They already exhibit an important development in the Upper Jurassic and Lower Cretaceous, but attain their widest distribution in the Tertiary and at the present day. They live partly in the sea, partly in fresh-waters.

Family 1. **Leptolepidae.** Smith Woodward.

Trunk elegantly fusiform. Head with delicate membrane bones and well-developed cheek plates, more or less enamelled ; parietals meeting in middle line, flanked by large squamosals ; premaxilla very small ; maxilla large, entering the gape, loosely attached and with two supramaxillaries ; teeth small and conical. Opercular apparatus complete. A single dorsal fin. Scales ganoid and with bony layer. Upper Lias to Lower Cretaceous.

Leptolepis, Ag. (*Tharsis*, Giebel), (Figs. 169, 170). Usually small fishes. Dorsal fin in front of anal fin, which is not much extended. Dentary bone sharply rising into a thickened obtuse elevation near its anterior end. Teeth

k. Akad. Wiss. Wien, math.-naturw. Cl. vols. XLVIII., LVI.).—*Kner* and *Steindachner*, Neue Beiträge zur Kenntniss der fossilen Fische Oesterreichs (Denkschr. Akad. Wien, vol. XXI.), 1863. —*Kramberger, D. G.*, Die eocänen Fische der Baschker Schichten (Palaeontogr. vol. XXIV.).—Die jungtertiäre Fischfauna Croatiens, I., II. (Beitr. Palaeont. Oesterr.-Ungarns. vols. II., III.), 1882-83. —*Meyer, H. v.*, Palaeontogr. vols. II., VI.—*Sauvage, H. E.*, Bull. Soc. géol. France, ser. 3, vols. II., III., VI., XI.—*Steindachner, F.*, Beiträge zur Kenntniss der fossilen Fischfauna Oesterreichs, I.-IV. (Sitzungsb. Akad. Wien, vols. XXXVII., XXXVIII., XL., XLVII.), 1859-63.—*Wettstein, A.*, Ueber die Fischfauna des tertiären Glarnerschiefers (Abh. schweiz. palaeont. Ges. vol. XIII.), 1886.

minute. *L. bronni*, Ag., and other comparatively small species in the Upper Lias of England, France, and Germany. *L. dubius*, Blv. sp., *L. sprattiformis*, Ag. (Fig. 170), and other species in the Upper Jurassic (Lithographic Stone)

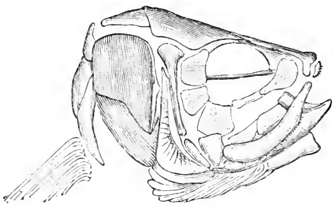


Fig. 169.
Head of *Leptolepis knorri*, Ag. Upper Jurassic; Kelheim. Reduced.

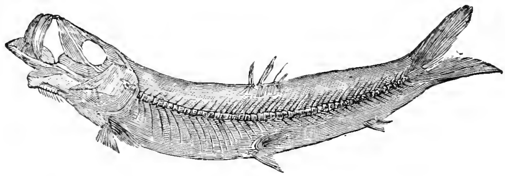


Fig. 170.
Leptolepis sprattiformis, Ag. Upper Jurassic; Eichstädt, Bavaria. Nat. size.

of Bavaria and France; also from the English Purbeck Beds, the Lower Cretaceous of the Isle of Lesina, Dalmatia, and the Wianamatta Formation of New South Wales. Fragments from King Charles Land, Spitzbergen.

Thrissops, Ag. Sometimes attaining rather large size. The short dorsal fin opposed to the much extended anal fin. Ribs very stout. Upper Jurassic and Lower Cretaceous of Europe, the type species being *T. formosus*, Ag., from the Bavarian Lithographic Stone.

Aethalion, Münster. Lithographic Stone: Bavaria.

Family 2. Elopidae.

Trunk fusiform, and caudal region relatively short. Head with well-developed cheek plates, not enamelled; jaws as in Clupeidae. Opercular apparatus complete, with numerous branchiostegal rays, and usually a gular plate. A single dorsal fin, without adipose dorsal. Scales thin and cycloid, without bony layer. Lower Cretaceous to Recent.

Elopopsis, Heckel. Gape of mouth wide, with large teeth. *E. fenzli*, Heckel, from Neocomian, Comen, Istria. *E. ziegleri*, v. d. Marck, and other species in the Upper Cretaceous of Europe.

Osmeroides, Ag. (*Rhabdolepis*, v. d. Marck *non* Troschel; *Holcolepis*, v. d. Marck). Salmon-shaped fishes with minute clustered teeth, and very deeply overlapping scales. *O. lewesiensis*, Mantell sp., from English Chalk. Other species in the Upper Cretaceous of Westphalia and Mount Lebanon.

Thrissopater, Günther. Gault; Folkestone. *Pachyrhizodus*, Dixon (*Hypsodon*, Ag.). Upper Cretaceous; Europe and North America.

Rhacolepis, Ag. Upper Cretaceous; Brazil. *Megalops*, Lacép.; *Elops*, Linn. Eocene to Recent.

Family 3. Albulidae.

Clupeoids with very small mouth, and some inner bones with grinding teeth. Branchiostegal rays few, and gular plate absent. Upper Cretaceous to Recent.

Istieus, Ag. An elongate fish, with much extended dorsal fin, small anal fin, and forked tail. Teeth very small. Closely resembling the existing deep-sea fish, *Bathythrissa*, Günther. About three species in the Upper Cretaceous of Westphalia and Syria.

Pisodus, Owen. Large hemispherical or flattened crushing teeth on the parasphenoid. Closely resembling existing *Albula*. Lower and Middle Eocene of England and Belgium.

Family 4. Ichthyodectidae. Crook.[1]

Large extinct predaceous fishes, with a row of strong conical teeth fixed in sockets on the margin of the jaws. Upper jaw formed by short and deep premaxilla, and long stout maxilla; mandible deep, truncated in front, without any presymphysial bone. Vomer and parasphenoid toothless; palato-pterygoid arch with patches of small teeth. Paired fins composed of a very broad, anterior, and numerous narrower rays, finely divided and articulated quite at the distal end. Dorsal fin short and remote; anal fin not much extended; caudal fin forked. Cretaceous.

This family is very closely related to the existing *Chirocentridae*, of which only one genus (*Chirocentrus*) is known, inhabiting the Indian Ocean.

Portheus, Cope (*Xiphactinus*, Leidy; *Hypsodon*, Ag. p.p.). (Fig. 171). Powerful fishes, sometimes of gigantic size. Teeth of variable size, oval in transverse section. Palatine movably articulated with ethmoid, with hammer-shaped thickening. Eye with ossified sclerotic; three sub-orbital plates. Operculum well developed and large. *P. molossus*, Cope (Fig. 171), and other species occur in the Chalk of Kansas, U.S.A. *P. mantelli*, Newton, and other species in the Chalk and Gault of England, France, Belgium, Bohemia, and Saxony. Fragments also in Cretaceous of Rolling Downs, Queensland.

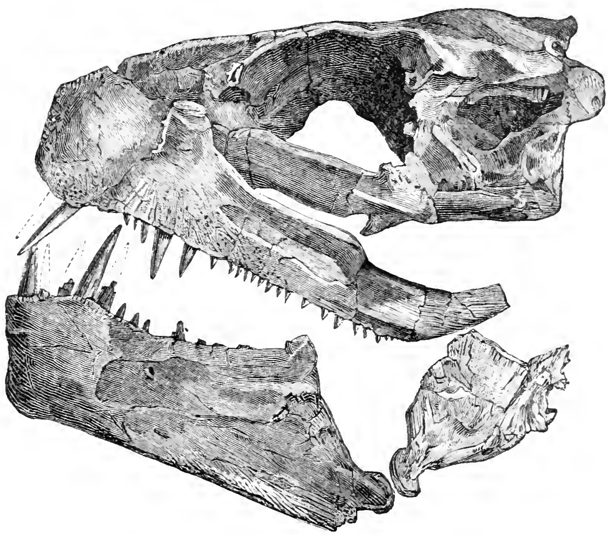


Fig. 171.
Head of *Portheus molossus*, Cope. Niobrara Cretaceous; Fox Cañon, Kansas. ¼ nat. size (after Cope).

Ichthyodectes, Cope. As *Portheus*, but smaller, and teeth of uniform size. Chalk of Kansas and England.

Gillicus, Hay. Like the preceding, but teeth small and fringe-like. Upper Cretaceous; Kansas.

Spathodactylus, Pictet. Type specimen displaying fins. Neocomian; Voirons, Switzerland.

[1] *Crook, A. R.*, Ueber einige Knochenfische aus der mittleren Kreide von Kansas (Palaeontogr. vol. XXXIX.), 1892.—*Loomis, F. B.*, Die Anatomie und die Verwandtschaft der Ganoid und Knochenfische aus der Kreide von Kansas (Palaeontogr. vol. XLVI.), 1900.—*Stewart, A.*, Teleosts of the Upper Cretaceous (Univ. Geol. Surv. Kansas, vol. VI.), 1900.

Family 5. **Saurodontidae.** Cope (*non* Zittel).

Skull laterally compressed; jaws powerful, and bearing a single row of compressed, knife-like teeth, with nutrient foramina or notches below the internal alveolar border; a presymphysial bone present and without teeth. Cretaceous.

The two genera constituting this family, *Saurocephalus*, Harlan (*non* Ag.), and *Saurodon*, Hays (*Daptinus*, Cope), differ from the *Ichthyodectidae* in the presence of a presymphysial bone and in the form and manner of succession of teeth. In the first-named genus the crowns of the teeth are short and compressed, with nutrient foramina below the alveolar border on the inner face of the jaw; and in *Saurodon* the inner margin of each dental alveolus is deeply notched. Upper Cretaceous; New Jersey and Kansas.

Family 6. **Clupeidae.** Herrings.

Trunk elegantly fusiform. Supraoccipital bone separating parietals, and otic region prominent; cheek plates reduced; premaxilla very small; maxilla large, entering the gape, with two supramaxillaries; dentition feeble. Opercular apparatus complete, but few branchiostegal rays, and no gular plate. A single dorsal fin, nearly median, without adipose dorsal. Scales thin and cycloid, without bony layer. Lower Cretaceous to Recent.

Diplomystus, Cope. Abdomen compressed to a sharp edge, and bordered with large ridge scutes; back between the occiput and dorsal fin armoured with smaller ridge scutes. *D. dentatus*, Cope, and other species finely preserved in the Eocene Green River Shales of Wyoming, U.S.A. Smaller species in the Upper Cretaceous of Mount Lebanon (*D. brevissimus*, Blv. sp.) and Brazil, and in the Oligocene of the Isle of Wight. Living in the rivers of New South Wales and Chili.

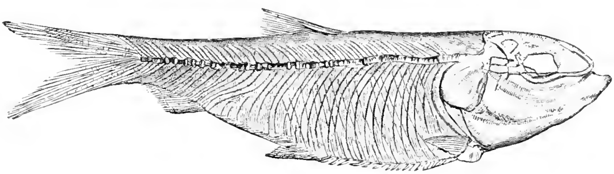


Fig. 172.
Clupea ventricosa, H. v. Meyer. Lower Miocene; Unterkirchberg, near Ulm, Würtemberg.

Scombroclupea, Kner. As *Clupea*, but finlets spaced out between the small anal and the forked caudal fin. *S. macrophthalma*, Heckel sp., from Upper Cretaceous of Mount Lebanon and Comen, Istria.

Clupea, Linn. Herrings. (Fig. 172.) Abdomen compressed to a sharp edge, and bordered with large ridge scutes; no dorsal scutes. Teeth minute on the jaws and palatines, larger on the vomer and hyoid. Dorsal fin small and

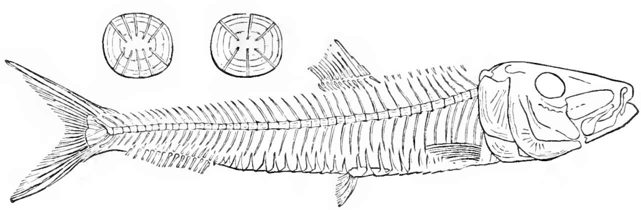


Fig. 173.
Meletta sardinites, Heckel. Lower Oligocene; Radoboj, Croatia (after Heckel).

median. Not certainly known below the Upper Eocene of Monte Bolca, near Verona. Small species in the freshwater Lower Miocene of Unterkirchberg, near Ulm, Würtemberg.

Alosa, *Engraulis*, Cuv. Tertiary and Recent.

Meletta, Val. (Fig. 173). Small slender fishes with thick cycloid scales, which are marked with three to six pairs of radiating grooves. Jaws toothless. Ventral ridge scutes large. Tertiary and Recent. Very common in the Lower Oligocene (Melettaschiefer) of the Carpathians, Croatia, Glarus, Alsace, etc.

Family 7. **Salmonidae.** Salmon.

As Clupeidae, but a small adipose fin behind the dorsal fin. Upper Tertiary and Recent.

Fossil skeletons of the existing *Mallotus villosus*, Müll., are very common in nodules in Pleistocene Clay on the coast of Greenland and in the glacial deposits of Canada.

Family 8. **Osteoglossidae.**

Head bones much thickened, and cheek plates robust. Margin of upper jaw formed both by premaxilla and maxilla. Scales large and thick, composed of mosaic-like pieces. Upper Cretaceous to Recent.

Phareodus, Leidy (*Dapedoglossus*, Cope). Laterally compressed deep-bodied fishes from the Eocene Green River Shales of Wyoming, U.S.A.

(?) *Brychaetus*, Ag. London Clay; Sheppey. *Plethodus*, Dixon. Cretaceous; England. *Anogmius*, Cope. Upper Cretaceous; Kansas.

Osteoglossum and other genera are large freshwater fishes living in the tropics.

Family 9. **Halosauridae.** Günther.

Eel-shaped fishes with pectoral and pelvic fins, a short dorsal fin, an extended anal fin usually confluent with the diminutive caudal, and both head and trunk covered with cycloid scales. Margin of upper jaw formed both by premaxilla and maxilla. Vertebral centra as delicate cylinders. Lateral line with luminous organs along the ventral border of the flank. Upper Cretaceous to Recent.

Halosaurus, Johnson, living at great depths in the ocean. *Echidnocephalus*, W. von der Marck, an almost identical genus from the Upper Cretaceous of Sendenhorst, Westphalia.

Family 10. **Dercetidae.** Smith Woodward (*Hoplopleuridae*, Pictet p.p.).

Eel-shaped fishes with pectoral and pelvic fins, a more or less extended dorsal fin, and separate anal and caudal fins. Parietal bones large and in contact mesially; premaxilla forming margin of upper jaw. Vertebral centra as delicate cylinders, with transverse processes bearing the ribs. No overlapping scales; but paired longitudinal series of bony scutes. Cretaceous.

Dercetis, Agassiz. Snout elongated and pointed; teeth minute and clustered. Dorsal fin occupying greater part of back, and pelvic fins inserted opposite to it; anal fin short, opposite hinder end of dorsal; caudal fin forked. Dermal scutes more or less angulated and ornamented with tubercles or spines;

two dorsal series, two ventral series, and a paired series supporting the lateral line. *D. scutatus*, Ag. Upper Cretaceous; Westphalia.

Leptotrachelus, W. v. d. Marck (*Triaenaspis*, Cope). As *Dercetis*, but dorsal fin not occupying more than middle third of back, and anal fin behind it. *L. triqueter*, Pict. sp., and other species from the Cretaceous of the Lebanon, Westphalia, and South Dakota, U.S.A. *L. lewesiensis*, Mant. sp., from English Chalk.

Pelargorhynchus, v. d. Marck. Upper Cretaceous; Westphalia.

Stratodus, Cope. Premaxilla short, with several rows of teeth; palatine and mandibular teeth large, numerous, in several rows, all with pulp cavity. Upper Cretaceous; Kansas.

Family 11. **Enchodontidae.** Smith Woodward (*Hoplopleuridae*, Pictet p.p.).

Rapacious fishes with more or less fusiform trunk. Parietal bones very small, separated by the supraoccipital; delicate premaxilla extended and nearly excluding the rod-like maxilla from the margin of the upper jaw, which bears very small teeth; powerful teeth fused with the palato-pterygoid and dentary bones. Vertebral centra robust, none with transverse processes. A small adipose fin probably present behind the single dorsal fin. No scales; but a median series of dorsal bony scutes, and often a paired series of similar scutes supporting the lateral line. Cretaceous.

Enchodus, Ag. (*Eurygnathus*, Davis; *Ischyrocephalus*, v. d. Marck; *Holcodon*, Kramb.), (Fig. 174). The largest and longest tooth at the anterior end of the palatine; large teeth of dentary spaced, increasing in length to the symphysis. External bones more or less tuberculated. Three or four oval median scutes between the occiput and dorsal fin; an adipose dorsal on the tail; caudal fin forked. No postclavicular plate; no scutes along course of lateral line, but a recurved hooklet on each side of the caudal pedicle. *E. lewesiensis*, Mant. sp., from the Lower Chalk, S.-E. England. Well-preserved skeletons of other species in the Upper Cretaceous of Westphalia and the Lebanon. Fragments in the Upper Cretaceous of North America, and Maastricht Beds, Holland.

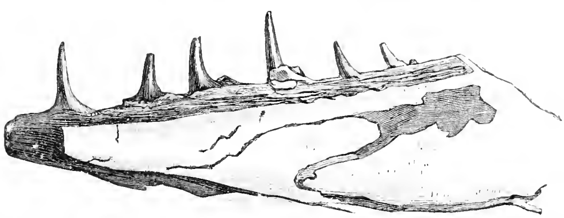


FIG. 174.
Imperfect dentary bone of *Enchodus lewesiensis*, Mant. sp. Lower Chalk; Lewes (after Agassiz).

Eurypholis, Pictet (*Saurorhamphus*, Heckel). As *Enchodus*, but a large postclavicular plate, and well-developed scutes along the course of the lateral line. *E. boissieri*, Pictet, from Upper Cretaceous of Hakel, Mount Lebanon. An imperfectly known species, erroneously restored by Heckel under the name of *Saurorhamphus freyeri*, Heck., from Lower Cretaceous, Comen, Istria.

Cimolichthys, Leidy. Largest teeth in middle of palato-pterygoid arcade semi-barbed at apex. Clustered teeth in mandible, with simply pointed larger teeth at intervals. *C. lewesiensis*, Leidy, from Lower Chalk, S.-E. England. The semi-barbed teeth common in the European Chalk, known also in North America.

Prionolepis, Egert.; *Leptecodon*, Williston. Upper Cretaceous.

Halec, Ag. (*Pomognathus*, Dixon; *Archaeogadus*, v. d. Marck). Premaxilla very slender, with minute teeth; maxilla equally slender, with a few relatively large spaced teeth at its hinder end. Palato-pterygoid teeth closely arranged, laterally compressed cones, largest in the middle of the arcade. No dermal scutes, except a pair of recurved hooklets on the caudal pedicle. *H. eupterygius*, Dixon, well preserved in Lower Chalk, S.-E. England. *Halec sternbergi*, Ag., in Turonian, Bohemia. Other species in Upper Cretaceous, Mount Lebanon, and in Lower Cretaceous, Isle of Lesina, Dalmatia.

Empo, Cope. Double series of teeth on palatine, none barbed. Premaxilla elongate, with one row of small teeth; mandibular teeth in two series, of which the outer are small and in several rows, while the inner are very large. Upper Cretaceous of Kansas and S.-E. England.

Family 12. **Scopelidae.**

Premaxilla much extended, excluding maxilla from upper margin of mouth. Skull and skeleton as in Enchodontidae. A small adipose fin behind the dorsal fin. No air bladder. Trunk naked or scaly, without bony scutes. Cretaceous to Recent.

Exclusively marine fishes, for the most part pelagic or deep-sea forms.

Sardinioides, v. d. Marck. Teeth minute; maxilla expanded behind. Dorsal fin median; paired fins small; caudal fin slightly forked. Scales large, serrated at the hinder border. *S. monasteri*, Ag. sp., from Upper Cretaceous, Sendenhorst, Westphalia. Other species from Mount Lebanon.

Sardinius, v. d. Marck. Upper Cretaceous; Westphalia. *Leptosomus*, v. d. Marck. Upper Cretaceous; Westphalia and Mount Lebanon. *Opisthopteryx*, Pictet and Humb. Lebanon.

Scopeloides, Wettstein. Upper Eocene; Canton Glarus.

Parascopelus, *Anapterus*, Sauvage. Upper Miocene; Licata, Sicily.

Rhinellus, Ag. (*Ichthyotringa*, Cope), (Fig. 175). Slender fishes with very large pectoral fins, and the premaxillae produced forwards into a long pointed

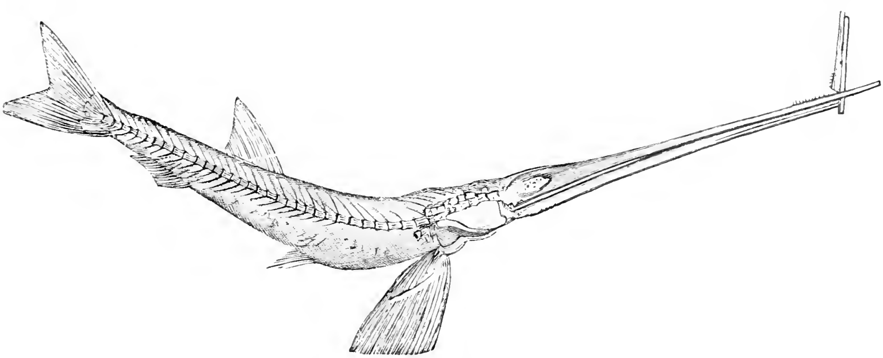


FIG. 175.
Rhinellus furcatus, Ag. Upper Cretaceous; Sendenhorst, Westphalia (after W. v. d. Marck).

rostrum. Teeth slender and pointed. Dorsal fin small, in advance of the still smaller anal fin; caudal fin forked. Scales smooth, slightly enlarged along the course of the lateral line. Upper Cretaceous; Westphalia, Mount Lebanon, and Dakota.

Family 13. **Gonorhynchidae.**

Premaxilla smaller than maxilla, but excluding latter from margin of upper jaw. No adipose dorsal fin. No air bladder. Scales deeply overlapping, fringed behind with short spines. Cretaceous to Recent.

Charitosomus, W. v. d. Marck. Upper Cretaceous; Westphalia and Lebanon.

Notogoneus, Cope (*Sphenolepis*, Ag.). Freshwater Eocene (Green River Shales); Wyoming, U.S.A. Upper Eocene; France and Germany.

Family 14. **Cheirothricidae.** Smith Woodward.

Scopeloids with enormously enlarged pelvic fins. Abdominal vertebrae with transverse processes. Cretaceous.

Cheirothrix, Pictet and Humbert (*Megapus*, Schlüter; *Megistopus*, Landois). Branchiostegal rays very large, eight or nine in number. Pectoral fins comparatively small and delicate, with only one ray considerably elongated; the enlarged pelvic fins close to the pectorals, with about seventeen rays; dorsal fin deep, arising immediately behind the head; anal fin small; caudal fin forked. *C. libanicus*, P. and H., from Upper Cretaceous, Mount Lebanon. *C. guestphalicus*, Schlüter sp., from Westphalia.

Family 15. **Esocidae.** Pikes.

Trunk elongated, with large cycloid scales. Premaxilla and maxilla entering upper border of mouth. Premaxilla, mandible, palatine, and vomer with stout, pointed teeth; maxilla toothless. Dorsal fin remote. Miocene to Recent.

Fine specimens referable to the existing genus *Esox*, Cuv., occur at Oeningen and in other Miocene freshwater formations in Europe.

Family 16. **Cyprinodontidae.** Toothed carps.

Small freshwater fishes with cycloid scales. Premaxilla excluding maxilla from upper margin of mouth; no barbels. Margin of jaws and pharyngeal bones with pointed teeth. No anterior vertebrae fused together. No adipose dorsal fin. Tertiary and Recent.

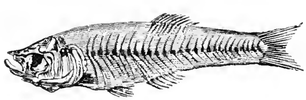


Fig. 176.
Lebias meyeri, Ag. Litorinella-clay; Frankfurt-a.-M. Nat. size.

Of the genera of this family, *Prolebias*, Sauvage, allied to *Lebias*, Cuv. (Fig. 176), is remarkably common in the Oligocene and Miocene of Europe.

Family 17. **Cyprinidae.** Carps.

Freshwater fishes with cycloid scales. Premaxilla excluding maxilla from upper margin of mouth; barbels present or absent. Mouth toothless, but lower pharyngeals falciform and bearing one to three rows of hollow prehensile teeth. Usually only three branchiostegal rays. Anterior vertebrae fused together, and air bladder connected with organ of hearing by a chain of ossicles. Upper Tertiary and Recent.

The Cyprinoids are numerous in the fresh-waters of the Old World and

North America, but do not occur in South America. Most of the known fossil species, all from freshwater formations, belong to the existing genera *Leuciscus*, Klein (Fig. 177), *Tinca*, *Gobio*, *Barbus*, Cuv., *Rhodeus*, *Aspius*, Ag. (Fig. 178), *Cyprinus*, *Cobitis* (Artedi), Linn., *Nemachilus*, Cuv., *Thynnichthys*, Bleeker, etc. The only extinct genera, such as *Amyzon*, *Diastichus*, *Oligobelus*, Cope, and others, are closely related to existing forms.

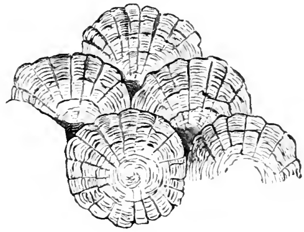


Fig. 177.
Scales of *Leuciscus oeningensis*, Ag. Upper Miocene; Oeningen, Baden. Enlarged (after Winkler).

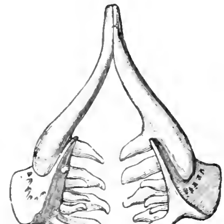


Fig. 178.
Pharyngeal bones and teeth of *Aspius rapax*, Ag. Recent (after Heckel and Kner).

Family 18. **Siluridae.** Cat-fishes.

Scaleless fishes, naked or armoured with bony plates. Premaxilla excluding maxilla from upper margin of mouth, the rudimentary maxilla usually supporting a barbel. Suboperculum absent. Infraclavicular plates present. Anterior pectoral fin ray usually a strong bony spine. Anterior vertebrae and air bladder as in Cyprinidae. Eocene to Recent.

The Siluroids form a very numerous family of freshwater fishes, ranging over all temperate and tropical regions, and a few sometimes passing into the sea round the coasts. Fossil remains are rare, and represent fishes closely resembling those still surviving. The oldest known fragment is a portion of head (*Bucklandium diluvii*, König) from the London Clay of Sheppey. Typical remains of *Arius* occur in the Middle and Upper Eocene of the Hampshire Basin and Belgium. Other genera are recorded from the Eocene of Wyoming, U.S.A. (*Rhineastes*, Cope), the Lower Pliocene of the Siwalik Hills, India, and a Tertiary Lignite near Padang, Sumatra.

Family 19. **Muraenidae.** Eels.

Body much elongated, cylindrical or ribbon-shaped. Premaxillae fused with ethmoid and vomer; upper jaw formed laterally by the toothed maxilla. Dorsal fin much extended, often meeting the anal round the tail. Pectoral arch not suspended from the cranium; pelvic fins wanting. Skin naked, or with small, rudimentary, cycloid scales. Upper Cretaceous to Recent.

Urenchelys, Sm. Woodw. With separate caudal fin. Upper Cretaceous; Sahel Alma, Lebanon, and English Chalk.

Eomyrus, Storms. Middle Eocene; Belgium.

Species of existing genera from marine Upper Eocene, Monte Bolca, and freshwater Upper Miocene, Oeningen.

Order 2. PHYSOCLYSTI. Gill.

Air bladder, when present, not connected by a tube with the oesophagus in the adult (except in certain Berycidae). Gills pectinate. Pelvic fins usually far forwards; fin rays articulated or spinous. Scales, when present, cycloid or ctenoid.

Sub-Order 1. ANACANTHINI. Müller.

All fin rays flexible and articulated. Pelvic fins jugular or thoracic. Pharyngeal bones not fused together.

Family 1. Gadidae. Cod-fishes.

Elongated fishes with broad head, and the toothed premaxilla excluding the maxilla from the upper margin of the mouth. Pelvic fins jugular. Dorsal fin extending almost the whole length of the back, sometimes subdivided into two or three parts; anal fin much extended, sometimes divided into two. Scales small and smooth. Eocene to Recent.

Fossil representatives of this family are rare. *Nemopteryx troscheli*, vom Rath, occurs in the Upper Eocene slates of Canton Glarus. Remains of *Phycis*, *Strinsia*, *Gadus*, and *Brosmius* have been described from the Miocene of Hungary, Croatia, and Sicily. Undetermined skulls are known from the London Clay of Sheppey.

Family 2. Pleuronectidae. Flat-fishes.

Disc-shaped fishes, much laterally compressed and asymmetrical, with both the eyes on one side of the head—the upper side when at rest. Dorsal and anal fins extending almost the whole length of the trunk. Pelvic fins jugular, in front of the pectorals. Air bladder absent. Scales, when present, minute and ctenoid; upper side of body coloured, lower side colourless. Upper Eocene to Recent.

The flat-fishes are very numerous in the existing fauna, living on sandy coasts, and some of them entering the mouths of rivers. They are extremely

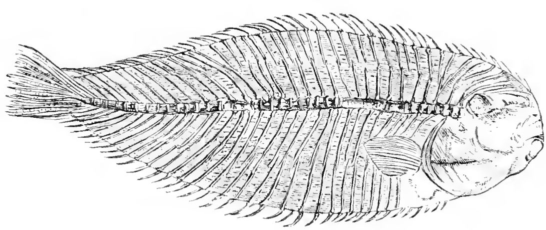


Fig. 179.

Solea kirchbergana, H. v. Meyer. Lower Miocene; Unterkirchberg, near Ulm. Nat. size.

rare among fossils. A small species of *Rhombus*, Klein, occurs in the Upper Eocene of Monte Bolca. *Solea*, Cuv., is known from the Lower Miocene of Würtemberg (Fig. 179).

Sub-Order 2. PHARYNGOGNATHI. Müller.

Fin rays articulated or partly spinous. Lower pharyngeal bones fused together.

Family 1. Scombresocidae.

Premaxilla and maxilla forming margin of upper jaw. Pectoral fins sometimes much enlarged, wing-like; pelvic fins abdominal; dorsal fin remote, opposite the anal fin; all fin rays articulated and flexible. Scales cycloid. Eocene to Recent.

Holosteus, Ag., from the Upper Eocene of Monte Bolca, and extinct species of *Belone*, Cuv., and *Scombresox*, Lacép., from the Miocene of Europe, are referred to this family.

Family 2. Pomacentridae.

Short, laterally compressed, spiny-finned fishes, with ctenoid scales. Dentition feeble. Palatines toothless. Pelvic fins thoracic, with one spine and five divided rays; dorsal fin extended, with numerous spines; anal fin with two or three spines. Eocene to Recent.

Here are placed *Odonteus*, Ag., from the Upper Eocene of Monte Bolca, and *Priscacara*, Cope, from the Eocene Green River Shales of Wyoming.

Family 3. Labridae. Wrasses.

Brilliantly coloured fishes with cycloid scales and thick fleshy lips. Teeth on margin of jaws powerful; palate toothless. United lower pharyngeals much thickened and forming a plate beset with rounded, rarely acuminate grinding teeth; upper pharyngeals usually separate, bearing similar teeth. Eocene to Recent.

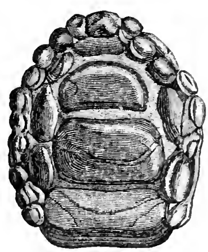


Fig. 180.

Phyllodus medius, Ag. Lower pharyngeal dentition, nat. size. London Clay; Sheppey (after Cocchi).

The wrasses chiefly inhabit tropical seas at the present day.

Phyllodus, Ag. (Fig. 180). Known only by pharyngeals bearing smooth, thin, flattened grinding teeth. Grinding surface of upper plate slightly concave, lower convex. Teeth arranged in rows, the middle row large. Several layers of successional teeth usually lie beneath those in function. Eocene and Miocene; Europe and North America.

Nummopalatus, Rouault (*Pharyngodopilus*, Cocchi), (Fig. 181). Lower pharyngeals triangular, covered with a pavement of numerous, small, round or oblong grinding teeth, of which there are always several superimposed layers. Upper pharyngeals separate, triangular, covered with grinding teeth. Eocene; Virginia. Miocene and Pliocene; Europe.

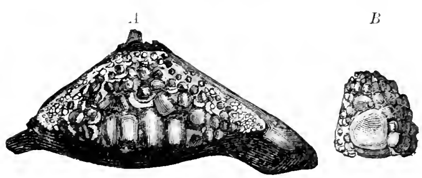


Fig. 181.

Nummopalatus multidens, Munst. sp. Miocene; Neudörfl a. d. March. *A*, Lower pharyngeal with dentition. *B*, An upper pharyngeal. Nat. size.

Taurinichthys, Cocchi. Miocene.

The existing genera *Labrus*, Artedi, and *Scarus*, Forsk., are also represented in the Upper Tertiaries.

Sub-Order 3. ACANTHOPTERI. Müller.

Some of the rays of the pelvic and median fins spinous, not articulated. Pelvic fins usually advanced far forwards. Lower pharyngeals separate.

In the existing fauna the Acanthopteri form by far the most numerous group of fishes.

Family 1. Berycidae.

Trunk short, compressed, and rather deep, with ctenoid or cycloid scales, rarely naked. Head bones ridged to form large mucous-cavities; orbits large and lateral; mouth usually oblique, the jaws and generally also the palate with small pointed teeth. Operculum more or less serrated or ridged. Pelvic fins thoracic, with an anterior spine and more than five divided rays. Upper Cretaceous to Recent.

The living Berycidae are marine fishes, most of them inhabitating considerable depths.

Hoplopteryx, Ag. (Fig. 182). Head short. Dorsal fin deep, with a few spaced spines in front; anal fin with four or five spines. Scales large and ctenoid. Common in the Upper Cretaceous. *H. lewesiensis*, Mant., from the English Chalk, and other species originally referred to the surviving genus *Beryx*.

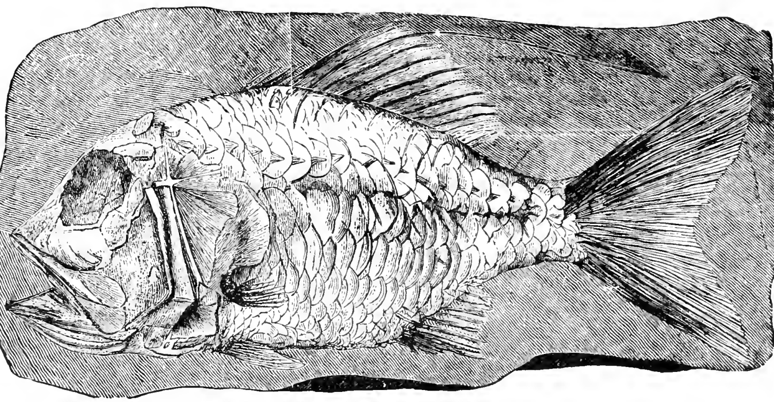


FIG. 182.
Hoplopteryx zippei, Agassiz sp. Lower Pläner; Wehlowitz, Bohemia. 1/3 nat. size (after Fritsch).

Sphenocephalus, Ag. Upper Cretaceous, Westphalia. *Pycnosterinx*, Heckel. Upper Cretaceous, Mount Lebanon.

The two surviving genera, *Holocentrum* and *Myripristis*, Cuv., are represented by extinct species in the Upper Eocene of Monte Bolca.

Family 2. Percidae. Perches.

Trunk elongated, with ctenoid scales. Premaxilla, mandible, vomer, and palatine with pointed teeth; six or seven branchiostegal rays. Pelvic fins thoracic with an *anterior spine and not more than five divided rays; one or two dorsal fins, the foremost part with long spines.* Eocene to Recent.

The perches are predaceous fishes of the tropical and temperate seas and fresh-waters. Numerous fossil representatives occur in the Tertiary formations of Europe and North America. Some belong to extinct genera, such as *Paraperea*, Sauvage, *Smerdis*, Ag. (Fig. 183), *Acanus*, Ag., *Mioplosus*, Cope, and *Erismatopterus*, Cope. Others have been referred to the existing genera *Serranus*, *Pelates*, *Dules*, *Gerres*, *Labrax*, and *Lates*, Cuv.

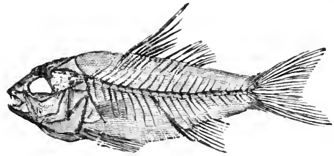


Fig. 183.
Smerdis minutus, Ag. Oligocene; Aix, Provence. Nat. size.

Family 3. **Sparidae.** Sea-breams.

Brightly coloured, rather deep-bodied fishes, with very delicately serrated ctenoid scales. Margin of jaws provided in front with conical or cutting teeth of different shapes, which are usually followed behind by several rows of round or oval grinding teeth; palatine and vomer toothless. Pelvic fins thoracic, with one spine and five divided rays; dorsal fin single, the anterior spinous part almost similar to the posterior soft part; anal fin with three spines. Cretaceous to Recent.

The sea-breams, which are easily recognised by their peculiar dentition, live at the present day in the tropical seas, feeding especially on Mollusca and Crustacea, which they crush with their teeth.

Sparnodus, Ag., occurs in the Upper Eocene of Monte Bolca. *Sargus*, Cuv., *Trigonodon*, Sismonda (Fig. 184), and *Chrysophrys*, Cuv. (*Capitodus*, Münst.), (Fig. 185), range from the Miocene to existing seas.

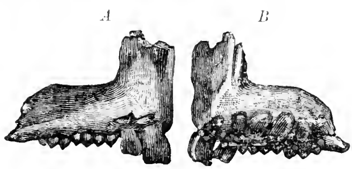


Fig. 184.
Premaxillae of *Sargus*, outer (*A*) and inner (*B*) views. Recent; Mediterranean. Nat. size.

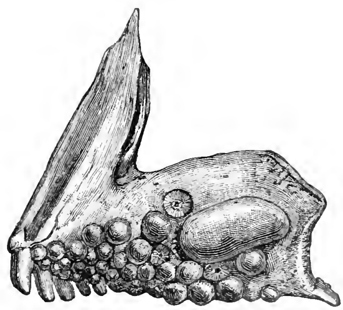


Fig. 185.
Right premaxilla of *Chrysophrys aurata*, Linn. Inner aspect. Recent; Mediterranean. Nat. size.

Stephanodus, Zittel. Cutting teeth from Upper Cretaceous, Libyan Desert.

The families **Pristipomatidae**, **Scorpaenidae**, **Teuthididae**, **Xiphiidae**, and **Chaetodontidae** are represented in the Tertiaries by fishes scarcely differing from the surviving forms.

Family 9. **Palaeorhynchidae.**

Elongated, low, and laterally compressed fishes. Snout produced into a long beak; jaws toothless or with very small denticles. Vertebrae long and slender;

spinous processes and ribs delicate. Pelvic fins thoracic, with several rays; dorsal fin extending from the occiput to the tail; anal fin extending from the anus to the cleft caudal fin. Eocene.

The two sufficiently well-known genera *Palaeorhynchus*, Blv., and *Hemirhynchus*, Ag., occur abundantly in the Middle Eocene Calcaire Grossier of

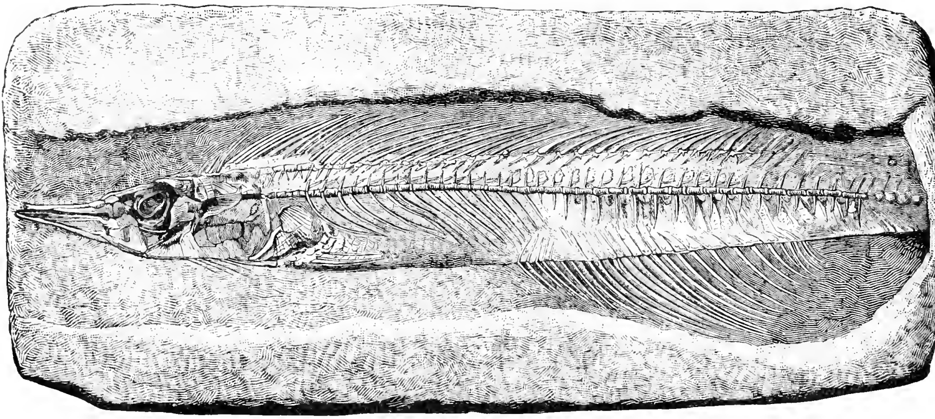


FIG. 186.
Palaeorhynchus zitteli, Kramb. sp. Upper Eocene; Rajcza, Galicia. 1/3 nat. size.

Paris, the Upper Eocene sandstone of Galicia, in the black slates of Glarus, and near Buchsweiler in Alsace. *P. glarisianus*, Blv., *H. deshayesi*, Ag., and *P. zitteli*, Kramb. sp. (Fig. 186).

Family 10. Trichiuridae.

Elongated and laterally compressed, almost ribbon-shaped predaceous fishes.

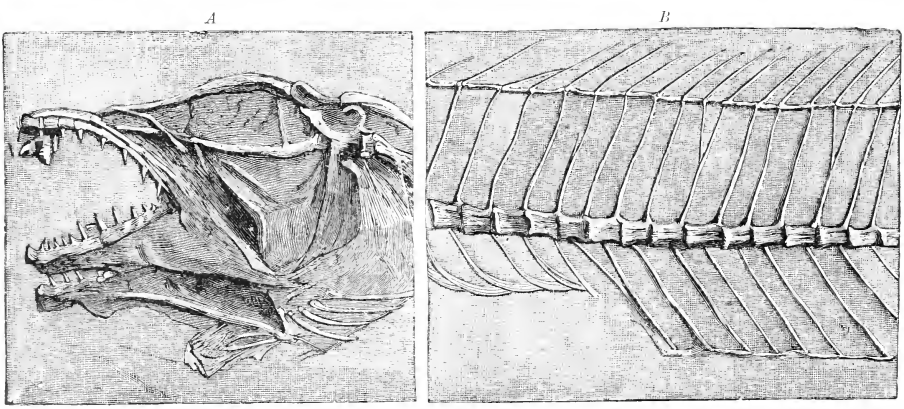


FIG. 187.
Lepidopus (*Anenchelum*) *glarisianus*, Ag. Upper Eocene; Matt, near Glarus.
A, Head. *B*, Portion of trunk. Nat. size (after Wettstein).

Gape of mouth wide, jaws and palatine bones with powerful conical teeth. Dorsal *and anal fins much extended with unarticulated spines; pelvic fins sometimes rudimentary or wanting.* Upper Eocene to Recent.

The Trichiuridae are predaceous fishes of the tropical and sub-tropical seas, living both near the coasts and also in deep water. Several well-marked fossil forms occur in the Eocene and Miocene.

Extinct species of the existing *Lepidopus*, Gouan (*Anenchelum*, Blv., *Lepidopides*, Heckel), are found in the black slates of Glarus (Fig. 187), in the Menilite shales of the Carpathians (*L. carpathicus*, Kramb.), and in the Upper Miocene of Sicily and Tuscany.

Trichiurichthys, *Hemithyrsites*, Sauvage. Upper Miocene; Licata, Sicily.

Family 11. **Acronuridae.**

Trunk deep and laterally compressed, covered with small scales. The tail in adult examples provided with one or several bony plates or spines. Jaws with a row of cutting teeth. Anal fin with three spines. Eocene to Recent.

The living genera dwell chiefly in the vicinity of coral reefs.

The existing genera *Acanthurus*, Forsk., and *Naseus*, Commerson, are recorded from the Upper Eocene of Monte Bolca; the former also from the Calcaire Grossier of Paris and the Miocene of Vienna.

Aulorhamphus, Zigno (*Calamostoma*, Steind. *non* Ag.). Eocene.

Family 12. **Carangidae.**
Horse-mackerels.

Trunk laterally compressed, deep or elongated, naked or with small scales. Teeth conical. Spinous portion of the dorsal fin shorter than the soft portion; pelvic fins thoracic, sometimes rudimentary or absent. Eocene to Recent.

Marine predaceous fishes of the tropical and temperate zones, common in Tertiary formations.

Platax, Cuv. Fossil in the Upper Eocene of Monte Bolca and in the Crag (Lower Pliocene) of Norfolk. Recent.

Zanclus, Commers. Eocene and Recent.

Fig. 188.
Semiophorus velifer, Ag. Upper Eocene; Monte Bolca. ½ nat. size (after Agassiz).

Semiophorus, Ag. (Fig. 188). Upper Eocene; Monte Bolca and Belgium.

Other genera with extinct representatives are the following:—*Amphistium*, Ag., *Vomer*, Cuv., *Caranx*, Cuv., *Carangopsis*, Ag., *Lichia*, Cuv., *Ductor*, Ag., *Trachinotus*, Lacép., *Seriola*, *Equula*, Cuv., *Acanthonemus*, Ag., etc.

Family 13. **Coryphaenidae.**

Trunk laterally compressed. Teeth small and conical or wanting. Dorsal fin extended, without spines. Eocene to Recent.

Here is placed the genus *Mene*, Lacép. (*Gasteronemus*, Ag.), with extinct species in the Upper Eocene of Monte Bolca.

Family 14. **Scombridae.** Mackerels.

Trunk elongated, naked or with small scales. Teeth conical. Pelvic fins thoracic; two dorsal fins, the hinder usually consisting of separate tufts. Eocene to Recent.

Thynnus, Cuv. The existing tunny. Mostly large cylindrical fishes, covered with small scales. Anterior dorsal fin with twelve to fourteen spines, which are not remarkably elongated; six to nine small, separate, tufted fins behind the posterior dorsal fin. Teeth small. Several species in the Upper Eocene of Monte Bolca, the Miocene of Oran, Algeria, and the Pliocene Crags of Belgium and England.

The genera *Palimphyes*, Ag.; *Isurichthys*, Woodw.; *Opisthomyzon*, Cope (allied to *Echeneis*, Art.), occur in the black slates of Glarus; *Orcynus*, Cuv., in the Upper Eocene of Monte Bolca; *Megalolepis*, Kramb., in the Lower Menilite shales of Baschka in Galicia. The existing genera *Scomber*, Art., *Auxis*, Cuv., are represented in the Miocene of Croatia, and *Cybium*, Cuv., in the Eocene, Oligocene, and Miocene.

The families **Cyttidae**, **Trachinidae**, **Lophiidae**, **Cataphracti**, **Cottidae**, **Bleniidae**, and **Gobiidae** have very few fossil representatives in the Tertiary.

The earliest members of the families **Mugilidae**, **Sphyraenidae**, and **Atherinidae** occur in the Upper Cretaceous of England, Colorado, and New Mexico (*Calamopleurus*, Dixon; *Syllaemus*, *Apsopelix*, *Pelycorapis*, Cope). *Sphyraena*, Bloch, *Rhamphognathus*, Ag., *Mesogaster*, Ag., and *Atherina*, Linn., occur in the Upper Eocene of Monte Bolca; *Mugil princeps*, Ag., in the Upper Eocene of Aix-en-Provence.

Family 25. **Aulostomidae.** Flute-mouths.

Elongated marine fishes, with elongated tube-shaped snout and remote dorsal fin. Occiput movably articulated with the vertebral column; teeth small. Spines little developed. Pelvic fins abdominal or thoracic. Scales small or absent. Eocene to Recent.

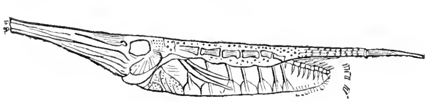


FIG. 189.

Amphisyle heinrichsi, Heckel. Upper Eocene; Krakowiza, Carpathians. Nat. size (after Heckel).

At the present day the Aulostomes chiefly inhabit tropical seas. *Fistularia*, Linn., and *Aulostoma*, Lacép., and the extinct genera *Urosphen*, Ag., and *Rhamphosus*, Ag., occur in the Upper Eocene of Monte Bolca. The small, dorsally armoured genus *Amphisyle*, Klein, which still survives, characterises the Upper Eocene Menilite shales of Galicia (Fig. 189), and the *Meletta* shales in Upper Alsace and the Vienna Basin.

Family 26. **Blochiidae.**

Elongated fishes with very long beak-shaped snout, which is formed by the equally produced and finely toothed jaws. The entire trunk covered with cordiform or rhombic bony scales, which are mostly keeled and overlap each other. Pelvic fins small, beneath the pectoral pair; dorsal fin arising at the occiput and extending

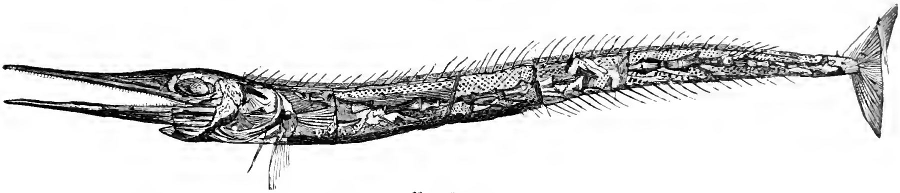


FIG. 190.
Blochius longirostris, Volta. Upper Eocene; Monte Bolca. $1/6$ nat. size (after Agassiz).

almost to the caudal fin, composed of a spaced series of long spines; anal fin also much extended and consisting of similar spines; caudal fin large. Eocene.

The only known genus is *Blochius*, Volta (Fig. 190), from the Upper Eocene of Monte Bolca.

Sub-Order 4. LOPHOBRANCHII. Cuvier.

Gills arranged in tufts on the branchial arches and protected by an operculum. Snout with tubular extension, and jaws toothless. Pelvic fins, often also the anal and caudal fins wanting. Skin armoured with thin bony plates.

Only very few fossil representatives of the two families of this remarkable group are known. The elongated **Solenostomidae**, in which all the fins are developed, have an Eocene forerunner in the genus *Solenorhynchus*, Heckel, from Monte Postale. Extinct species of *Siphonostoma*, which is still common

FIG. 191.
Siphonostoma albyi, Sauvage. Upper Miocene; Licata, Sicily (after Sauvage).

in the Mediterranean, also occur in the Upper Miocene of Licata, Sicily (Fig. 191), and of Tuscany. Several Tertiary forms of **Syngnathidae** are known; *Syngnathus*, *Pseudosyngnathus*, and an extinct genus *Calamostoma*, Ag., occur in the Eocene.

Sub-Order 5. PLECTOGNATHI. Cuvier.

Skin covered with roughened scales, bony spines or plates, rarely naked. Skeleton incompletely ossified. Maxillae and premaxillae fused together into a solid beak. Gills pectinate. Pelvic fins wanting or represented by spines; dorsal fin with articulated rays opposed to the anal fin.

Family 1. **Gymnodontidae.** Cuvier.

Trunk short and deep, naked or covered with bony spines. Jaws beak-shaped, with a cutting dental plate above and below, either undivided or in right and left halves. No dorsal spines. Eocene to Recent.

Fossil remains of this family are very rare. Large jaws of *Orthagoriscus* have been found in the Oligocene of Belgium. *Diodon* occurs in the Eocene, Oligocene, and Miocene; *Gymnodus* in the Miocene; *Heptadiodon* in the Upper Eocene of Monte Postale.

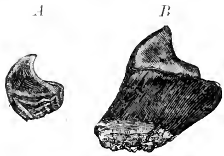


Fig. 192.

Pharyngeal teeth. *A, Ancistrodon libycus*, Zitt. Upper Chalk; Gasr Dachl, Libyan Desert. *B, Ancistrodon armatus*, Gervais sp. Eocene; Mokattam, near Cairo (after Dames).

Family 2. **Sclerodermidae.** Cuvier.

Jaws with a small number of separate teeth. Skin with scales or roughened. Dorsal spines usually present. Eocene to Recent.

The existing genera *Ostracion* and *Balistes* (*Protobalistum*, Massal.) have representatives in the Upper Eocene of Monte Bolca. The extinct genera *Acanthoderma* and *Acanthopleurus*, Ag., occur in the Upper Eocene black slates of Glarus. The teeth described as *Ancistrodon*, Roemer (Fig. 192), from the Upper Cretaceous, Eocene, and Oligocene, may belong, at least in part, to the pharyngeal dentition of Sclerodermis.

Range and Distribution of Fossil Fishes.

Notwithstanding the apparently favourable circumstances for the preservation of fishes due to their aqueous habitat, their geological history is still very imperfectly known. Complete skeletons, it is true, are rather numerous in clayey, calcareous, or marly shales, which were laid down as fine mud on the bottom of former lakes and near the shore in seas. On the other hand, in rocks of coarser grain (sandstone), in very many shore deposits, and also in deep-sea limestones, there are usually only isolated teeth, scales, dermal plates, vertebrae, scattered bones of the skeleton, and otolites, which are extremely difficult to determine. In very many marine, lacustrine, and fluviatile deposits, fish remains are almost completely wanting, so that the formations rich in fossils are usually separated from each other by a series of strata which represent long periods of time.

The oldest undoubted traces of fishes both in Europe and North America occur in rocks of Silurian age. They are found in the Ludlow Bone-bed, in the light, dolomitic, fissile limestone of the island of Oesel in the Baltic, and in sandy shales in Podolia and Galicia. They are also found in the Onondaga Group of Pennsylvania. The determinable forms are all Selachii and primitive Ostracodermi (Coelolepidae, Pteraspidae, and Cephalaspidae).

In the Devonian era fishes begin to attain a great development, and are sometimes discovered in a remarkable state of preservation, especially in the Old Red Sandstone of Great Britain, the Russian Baltic provinces, Podolia, and Galicia, and in the corresponding formations of North America. Scattered fish remains, such as plates of Ostracodermi and spines of Selachii, also occur in the uppermost stages (*F*, *G*) of the Silurian basin of Bohemia, and in the

Devonian of the Eifel, Nassau, Westphalia, and Belgium. Gigantic Arthrodires (*Dinichthys*, *Titanichthys*, *Diplognathus*) and Selachii are remarkably abundant in the Middle and Upper Devonian of Ohio, Wisconsin, and New York. The Devonian fish fauna consists of Arthrodires, Ostracoderms, many Ganoids (Crossopterygii and Heterocerci), Dipnoans (Ctenodipterini), and Selachians (Pleuropterygii, Acanthodii, Holocephali).

The fishes of the Carboniferous System are obtained partly from the marine Carboniferous Limestone, partly from the shales and sandstones of the productive Coal Measures. The enormous development of the Selachii,[1] of which, however, only teeth and fin spines are commonly preserved, sharply distinguishes the Carboniferous fish fauna from that of the Devonian period. The Cochliodontidae, Psammodontidae, and Petalodontidae are almost exclusively confined to the Carboniferous Limestone, while the Cestraciontidae are also well represented; the Acanthodians and Pleuropterygians continue, the Pleuracanthidae begin. The heterocercal Ganoids are the principal associates of the Selachii; the Crossopterygii and Ctenodipterini are still present, but in diminished numbers.

The fishes of the Permian system are closely similar to those of the productive Coal Measures. They occur in the Rothliegenden of the Saar Basin, Bohemia, Saxony, Silesia, and France; in the Magnesian Limestone of England; in the Kupferschiefer of Thuringia and Hesse; and in the probably contemporaneous strata of Texas and New Mexico. The Heterocerci are by far the most numerous. Of the Crossopterygii, *Coelacanthus* and *Megalichthys* alone survive in Europe. Among the Dipnoi, the genera *Ctenodus* and *Sagenodus* are especially widely distributed. In comparison with the Carboniferous fish fauna, that of the Permian period is noticeably destitute of Selachii. Here, however, the remarkable Pleuracanthidae attain their maximum development, and are associated with a few Cochliodontidae (*Menaspis*), Petalodontidae (*Janassa*), and Acanthodidae.

The abrupt break in development, which is observable in most sections of the animal and plant world at the close of the Palaeozoic epoch, is also conspicuous among the fishes, although the Triassic fish fauna exhibits many resemblances to that of the Permian. Among Selachii, the Pleuracanthidae, Cochliodontidae, and Petalodontidae are wanting; the Plagiostomi, on the other hand, are well represented. Teeth and fin spines of the Cestraciontidae, for example, are very numerous in the Muschelkalk and uppermost Keuper. The occurrence of heterocercal scaly Ganoids of the family Palaeoniscidae, as well as the persistence of a few Crossopterygians, is indeed reminiscent of Palaeozoic times; but the most numerous and best preserved Triassic fishes belong to the enamel-scaled Lepidostei, of which the Permian system affords only a single genus (*Acentrophorus*). Among the Dipnoi the persistent *Ceratodus*, represented principally by teeth, plays an important part. The Teleostei are already represented by some small Clupeoids (*Megalopterus*).

The fish fauna of the Lias is a direct continuation and further development of that of the Trias. No less than 152 species were described by Agassiz and Egerton, and of these 79 occur only in the Lower Lias of Lyme Regis in Dorset. The Middle Lias contains few fishes; but the Posidonia shales and bituminous limestone of the Upper Lias ε in Swabia and Franconia, as well as

[1] *Hay, O. P.*, The Chronological Distribution of the Elasmobranchs (Trans. Amer. Phil. Soc. vol. XX.), 1901.

the corresponding strata of Werther, near Halle, the Departments of Calvados, Yonne, and Côte-d'Or in France, and of Ilminster and Whitby in England, again yield a considerable number of species. The Selachians persist in undiminished numbers. *Undina gulo*, Egerton, from Lyme Regis represents the Coelacanthidae, *Chondrosteus* the cartilaginous ganoids. The majority of the Liassic fishes, however, belong to the scaly Ganoids of the order Lepidostei, though a few genera of the heterocercal Palaeoniscidae still survive. A new element in the Liassic fish fauna is formed by the thin-scaled Amioids, in which the vertebral column is still bent upwards to the upper lobe of the tail, and remains incompletely ossified. A single species from the Lower Lias of England (*Mesodon liassicus*, Eg.) indicates the first appearance of the Pycnodontidae. Among bony fishes a few small Clupeoids (*Leptolepis*) may be mentioned. *Ceratodus* and *Pholidophorus* are present in the Lower Jura of the Western United States.

In the Middle Jura shaly deposits with well-preserved fish skeletons are wanting. Our knowledge of the fish fauna of the period is thus confined to detached teeth, fin spines, bones, and scales, which occur occasionally. Almost all the genera observed in the Dogger occur in addition in the Lias or the Upper Jurassic. Of the latter the most numerous discoveries have been made in the fissile limestones of the neighbourhood of Solenhofen, Kelheim, and Eichstädt in Bavaria, Nusplingen in Würtemberg, and Cerin in the Department of Ain, France. An abundance of beautifully preserved skeletons of Selachians, Ganoids, and Teleosteans have been obtained from these localities, to which must be added the Portlandian Limestone of Soleure, Neuchâtel, Hanover, and Boulogne-sur-Mer, and the Purbeck Beds of England as formations yielding well-preserved jaw-bones, teeth, spines, scales, and vertebrae. The heterocercal Palaeoniscids have become reduced to a single genus (*Coccolepis*). Of sharks and rays, complete or partially well-preserved skeletons are known, which indicate close relationships or absolute identity with various still surviving genera. The Cestraciontidae and Lamnidae are also represented by several extinct genera, and the Holocephali are much more numerous than in the Lias. Among the Ganoids the Coelacanthidae attain their maximum development in varied forms. The large majority of the Upper Jurassic fishes consist of Lepidostei and Amioidei, with Teleostei of the family Leptolepidae.

With the beginning of the Cretaceous system there is an important change in the fish fauna, so that the previously dominant Ganoids become more and more displaced by Teleosteans. This substitution is almost complete in the middle and upper divisions of the Chalk; in the Lower Cretaceous, on the other hand, there are still a few types of Ganoids surviving from Jurassic times. The fish fauna of the Cretaceous system thus falls into two well-marked sections, to the lower of which belong the light-coloured fissile limestones of Pietraroza, the limestones of Castellamare, and Torre d'Orlando near Naples, of Comen (Istria), Crespano (Vicentin), Lesina (Dalmatia), and Grodischt in the Carpathians, and the Neocomian deposits of the Voirons, near Geneva. The normal deposits of the Middle and Upper Chalk chiefly contain teeth, vertebrae, and isolated fragments of Selachians, Chimaeroids, Pycnodonts, and Physostomes; the fissile limestones of the Lebanon, the marly sandstone of Westphalia, and the Niobrara Chalk of Kansas, on the other hand, yield a considerable number of well-preserved skeletons. Among these the Ganoids are extremely rare, while the Physostomi constitute about three-quarters of all the known species. The Physoclysti, like the Physostomi, are represented chiefly by extinct genera.

With the beginning of the Tertiary period there is a still closer approximation to the condition of affairs at present prevailing.

The oldest Eocene fish fauna of Europe, from the London Clay of southern England, is incompletely investigated. The contemporaneous deposits in the Paris Basin yield only a few fish remains, but among these are scales of the Ganoid genus *Lepidosteus*, which still exists in North America. The most important and best known deposit of Eocene fishes is the light-coloured fissile limestone of Monte Bolca, near Verona, which corresponds in age approximately with the Calcaire Grossier of the Paris Basin. No less than 94 genera and 170 species, including several sharks and rays, have been described from it. Of Ganoids only the Pycnodonts here survive; all the other fishes belong to the Teleostei, most of them indeed to genera which at present live in the Indo-Pacific and Red Sea, in the tropical Atlantic, and to a smaller degree also in the Mediterranean. The most interesting feature in this fauna is the great increase of the Acanthopteri and the decrease of the Physostomi.

A remarkable fish horizon, partly marked by deep-sea fishes, occurs at the summit of the Eocene, represented in the black slates of Matt in Canton Glarus, the contemporary Menilite Shales of Styria, Upper Bavaria (Siegsdorf), Upper Alsace, and other localities. From Glarus, the richest locality for this zone, 29 species of fishes are known, according to Wettstein, and all of these belong to the Teleostei. In a remarkable way the extinct genera here considerably exceed those which survive to the present day.

In the western states of North America, in the so-called Puerco, Wasatch, and Bridger formations of New Mexico and Wyoming, fossil fishes are also abundant; but these, since they occur in freshwater deposits, have little in common with the Eocene forms of Europe, which are met with almost exclusively in marine or estuarine deposits. It is interesting to note that the existing North American Ganoid families, Lepidosteidae and Amiidae, are represented here.

The Oligocene and Lower Miocene yield but scanty fish remains. The occurrence in Europe of *Amia* (*Notaeus*) and *Lepidosteus* is noteworthy.

The Middle Miocene Molasse of Switzerland, Swabia (Baltringen), and Upper Bavaria, the marine deposits of the Vienna basin, the valley of the Rhine, and the Aquitaine basin sometimes contain an abundance of fish remains, among which the teeth, dermal plates, and spines of sharks, rays, and chimaeras, the vertebrae, teeth, and scattered bones of Teleostei are especially common. With few exceptions these remains are referable to recent genera. The brackish-water clay of Unterkirchberg, near Ulm, the freshwater marl of Oeningen and Steinheim, the Sarmatian deposits of Radoboj and other localities in Croatia, and the *Cerithium* marl of the Vienna basin, also show that at the time of their formation the fish fauna of the fresh and brackish waters of Germany was not very different from that still surviving in southern Europe and Asia Minor.

The remarkably rich Upper Miocene fauna of Licata in Sicily exhibits a mixture of marine and freshwater fish remains, which is also partially noticeable in the neighbourhood of Girgenti, in the gypseous marls of Sinigaglia, near Gabbro in Tuscany, Lorca in Spain, and Oran in Algeria. In his monograph of 1873, Sauvage describes 52 species from Licata, and of these 44 are of marine origin. The character of this fish fauna is essentially Mediterranean, but without exception the species are extinct. So far as fishes are concerned, there is scarcely any noteworthy difference between the Pliocene fauna and that of the present day.

The distribution of fishes in time affords many facts illustrating the development of this class. In the Palaeozoic epoch there were only Selachii, Holocephali, Dipnoi, Ostracodermi, and Ganoidei; the Selachii and Ganoidei, indeed, appearing together in the Silurian. These two main divisions of the phylum of fishes must thus have become separated very early, if indeed they originated from a common stock.

Fossils beginning in the Old Red Sandstone, and ranging through all later formations, prove that the Holocephali had already diverged from the Selachii in Palaeozoic times, and the branch has been preserved with its partially embryonic characters (polyspondyly, autostyly) until the present day.

The origin of the Dipnoi is quite obscure. Their Palaeozoic representatives agree in many respects with the Crossopterygii. As, moreover, the Dipnoi also share important characters with the Holocephali, it seems probable that the Holocephali, Dipnoi, and Ganoidei arose from a common stock.

So far as the development of the internal skeleton is concerned, the Ostracodermi and Arthrodira are quite primitive. Their origin is wholly unknown. Among the Ganoids the Crossopterygii form an isolated group, well separated from the other orders both phylogenetically and systematically, having its last survivors in the modern Polypteridae, and probably more closely related to the Dipnoi and Amphibia than to the other Ganoids. The Heterocerci, Lepidostei, and Amioidei form a closely connected group of Ganoids. It has already been remarked that the first order not only precedes the Lepidostei in time, but is also probably ancestral to them. The Amioids may have diverged from the Lepidostei during the Triassic or Jurassic period.

The Teleosteans are merely a great lateral branch of the Ganoids. It is, however, improbable that they are of monophyletic origin; for although the Clupeoids are the ancestral group of most of the Physostomi, which have arisen from the Mesozoic Amioids, other families even on their first appearance seem to be so remotely allied to Clupeoids that a different origin must be sought for them. The Physoclysti are indeed only derivations of the Physostomi differentiated in various directions.

[The section Pisces has been translated and revised by Dr. Arthur Smith Woodward, of the British Museum, who has attempted to bring the subject up to date, while preserving in the main the author's methods and principles of classification.—Ed.]

Class 2. AMPHIBIA. Amphibians and Batrachians.[1]

Cold-blooded vertebrates, aquatic or terrestrial in habit, usually naked, but sometimes with a corneous or osseous dermal covering; respiration both branchial and pulmonary in early stages, and in some forms gills remain functional throughout life. Development by metamorphosis, but without amnion and allantois. Skull with two occipital condyles. Ribs never attached to sternum. Limbs adapted for ambulation or natation, never in the form of fins, and rarely absent.

[1] *Hoffmann, C. K.*, Die Amphibien. Bronn's Classen und Ordnungen des Thierreichs, vol. VI. pt. 2, 1873-78.—*Wagner, J.*, Natürliches System der Amphibien, 1828-33.

In external appearance amphibians more nearly resemble reptiles than fishes. The body is generally elongate, and terminates as a rule in a well-developed tail, although some small forms (*Anura*) are ecaudate. Among recent amphibians limbs are wanting only in the Coecilians (*Gymnophiona*). Certain extinct Stegocephalians (*Aistopoda*) appear also to have been completely apodal; but elsewhere two pairs of limbs are invariably present, the anterior usually terminating in four digits and the posterior in five.

Recent amphibians are naked with the exception only of the Coecilians, which are covered with small scales arranged in transverse rings. The fossil Stegocephalians usually have a scaly armature on the ventral surface, and sometimes on the dorsal as well.

The number of vertebrae in the spinal column is extremely variable (10-150), depending upon the length of the body and especially the tail. Cervical, dorsal, sacral, and caudal regions are distinguished.

The most primitive form of vertebrae occurs in the Palaeozoic Stegocephalians, where the notochord is enclosed by thin cylinders of bony tissue, or by separate pleurocentra and hypocentra, as in early Ganoids. Where the column is more completely ossified, three types of vertebrae are exhibited. The first, or *amphicoelous*, is biconcave; the *procoelous* has the anterior vertebral face concave and the posterior convex; and in the *opisthocoelous* type the anterior face is convex and the posterior concave.

The cervical region comprises but a single vertebra, the atlas, although this probably corresponds to both atlas and axis of higher classes. Its concave anterior face receives the bony or cartilaginous occipital condyles, and is often provided with a spatulate, forwardly directed basal process. Each of the dorsal vertebrae supports a neural arch (*neurapophysis*), which becomes earlier and more completely ossified than the centrum, and may be either suturally united or anchylosed with the latter. The two halves of the neural arch unite above to form a more or less strongly developed spinous process (*spina dorsalis*); and they bear anteriorly and posteriorly a pair of oblique articular processes (*processus obliqui, zygapophyses*), the forward pair of each vertebra overridden by the hinder pair of the next in front. The neural arch also supports, as a rule, a pair of transverse processes (*diapophyses*) for the attachment of ribs. When the latter are double-headed, as is often the case, another and shorter lateral process (*parapophysis*) is developed by the body of the vertebra.

The sacral region is also formed by a single vertebra, which supports the pelvis, the latter being attached either directly by means of exceptionally stout transverse processes, or by sacral ribs, usually of peculiar form. Haemal arches (*haemapophyses*, "chevron bones") are commonly borne by the caudal series, the foremost of which sometimes have ribs attached to the transverse processes of the neural arch. The entire series of caudals in the *Anura* is fused into a single elongate piece called the *coccyx*.

The primordial *cranium* remains partly cartilaginous throughout life, and is partly replaced by bony pieces, which are either direct ossifications of the cartilaginous capsule (exoccipitals, auditory capsules, quadrate, sphen-ethmoid), or are investing bones (parietals, frontals, nasals, vomer, parasphenoid). The basioccipital and supraoccipital usually remain small cartilaginous tracts; but save in certain *Stegocephalia* and a few other forms, the exoccipitals are completely ossified, and bear the articular condyles. The exoccipitals are of considerable size, and enter into the border of the tympanic region. The latter is roofed by several small bones corresponding to the proötic and opisthotic of fishes, or these may unite into a single element called the petrosal. The antero-lateral walls of the skull remain cartilaginous; but in the ethmoidal region an ossification takes place, forming the orbitosphenoid which is usually separate, but sometimes (*Anura*) fuses with the median elements to form a single ring-shaped bone (sphen-ethmoid).

The cranial roof is formed by the paired parietals, frontals, pre- and post-frontals, and nasals; and in Stegocephalians there are present in addition the so-called supratemporals, squamosals, postorbitals, and lachrymals. The palate is formed as in fishes by a large median parasphenoid, and usually paired vomers, and palatines. There is no movable suspensorium for the lower jaw; the cartilage representing it unites with the squamosal above, and quadrato-jugal below. Sometimes an ossified quadrate is formed at the end of the suspensorial cartilage. Attached to the quadrato-jugal in front are the maxillae, and anterior to these the premaxillae, which complete the rim of the upper jaw in front. Many of the Urodeles have the maxillae and quadrato-jugal replaced by connective tissue. Between the quadrate and parasphenoid is placed the pterygoid, usually a trifid bone which joins the parasphenoid by its shorter arm, while its anterior branch forms the outer border of the palatal vacuity. The palatines, when present, usually join the anterior ends of the pterygoids, and extend parallel with the maxillae. The mandibular ramus is composed of three or four elements, as in fishes. The visceral skeleton is formed by the paired hyoid bones, and, in gill-breathers, by three or four partially ossified branchial arches.

The *teeth* are acutely conical, and are commonly borne by the mandible, maxillae, premaxillae, vomer, and palatines. Rarely the parasphenoid and pterygoid are armed with minute teeth, and only certain *Anura* are edentulous. Teeth of the acrodont type have their bases implanted directly upon the rim or top of the jaws; those of the pleurodont type are sunk against the inner side of the jaws. As in Ganoids and bony fishes, worn teeth are not replaced by successional ones developed beneath them, but new ones are formed independently alongside the old, and gradually oust the latter as their basal parts become reabsorbed. Amphibian teeth differ from those of fishes chiefly in the absence of vasodentine; and the spacious pulp cavity which during life contains vascular or connective tissue, occurs in the fossil state either hollow or impregnated with mineral matter. Some Stegocephalians have complex or "labyrinthodont" teeth, the dentine being strongly folded, as in certain Crossopterygian fishes.

In the *pectoral arch* the scapula is ossified in at least its proximal portion, where it joins the coracoid and pre-coracoid, and forms the articular face for the humerus. A bony sternum is usually absent. Stegocephalians are peculiar in possessing between the pectoral limbs one median and two paired exoskeletal plates, commonly regarded as interclavicle and clavicles. The fore-limb is composed of the usual bones, humerus, radius, and ulna; a carpus which is either cartilaginous or consists of two rows of ossicles; and three, four, or five metacarpals which support digits with from one to four phalanges.

The *pelvic arch* is composed of a long and slender bony ilium, which is attached either directly to the transverse process of the sacral vertebra, or to the sacral ribs, and is directed obliquely downward; a flattened, sometimes discoidal bony ischium; and a cartilaginous or ossified pubis lying immediately in advance of the ischium. The ilium and ischium usually take part together in the formation of the acetabulum, which receives the femoral head. In the *Anura* the tibia and fibula are fused. The tarsus is cartilaginous or composed of several small ossicles, and the pes resembles the manus, except that it is usually pentadactyle.

Four orders of Amphibians are recognised as follows :—*Stegocephalia*, *Gymnophiona*, *Urodela*, and *Anura*.

Order 1. STEGOCEPHALIA.[1]

Salamander or lizard-like caudate amphibians, the cranial roof and whole of the cheek covered with plates; cranial roof posterior to the orbits formed by two pairs of median and two pairs of lateral elements; pineal foramen always occurring in the parietal. Teeth sharply conical, with large pulp cavity, and walls sometimes highly complicated by infolding of the dentine. Vertebrae consisting either of simple cylinders, or of separate pleurocentra and hypocentra, or of completely ossified amphicoelous centra. Three exoskeletal plates present in the thoracic region, interpreted as clavicles and interclavicle. Usually a ventral and sometimes a dorsal armouring of small overlapping scales.

The Stegocephalians range from the Carboniferous to Upper Trias, and comprise the largest known amphibians. A tail is invariably present, and in most cases, two pairs of limbs; only a few genera are apparently destitute of appendages.

Unlike recent amphibians, most *Stegocephalia* possess a well-developed dermal armour of bony scales or scutes, which almost always covers the ventral surface of the body, and sometimes extends to the under side of the limbs and back as well. Dorsal scales, however, are thinner than the abdominal, and are usually round or oval. The ventral scutes are sometimes thickened, and always arranged in regular series. The abdominal series form oblique rows meeting at a sharp angle along the median line, but those covering the thoracic, pectoral, and caudal regions, and under side of the limbs are arranged in different patterns. The scales are of true bony tissue, and vary considerably

[1] Literature:

Ammon, L. v., Die permischen Amphibien der Rheinpfalz. Munich, 1889. [Extensive bibliography.]—*Baur, G.*, The Stegocephali: a Phylogenetic Study (Anat. Anz. vol. XI. No. 22), 1896.—*Broili, F.*, and *Stickler, L.*, Ueber Eryops megacephalus Cope (Palaeontogr. vol. XLVI.), 1899.—*Burmeister, H.*, Die Labyrinthodonten aus dem bunten Sandstein von Bernburg. Berlin, 1840.—Die Labyrinthodonten aus dem Saarbrücker Steinkohlengebirge. Berlin. 1850.—*Cope, E. D.*, Synopsis of the extinct Batrachia and Reptilia of North America (Trans. Amer. Phil. Soc. vol. XIV.). 1869.—*Ibid.* N.S., vol. XVI., 1886.—Batrachia of the Permian Period of North America (Amer. Nat. vol. XVIII.), 1884.—*Credner, H.*, Die Stegocephalen aus dem Rothliegenden bei Dresden. Parts I.-X. (Zeitschr. deutsch. geol. Ges.), 1881-93.—*Fraas, E.*, Die Labyrinthodonten der schwäbischen Trias. (Palaeontogr. vol. XXXVI.), 1889.—*Fritsch, A.*, Die Fauna der Gaskohle und der Kalksteine der Permformation Böhmens. vols. I.-III., 1883-94.—*Huxley, G. H.*, Vertebrate Remains from Kilkenny (Trans. Roy. Irish Acad. vol. XXIV.). 1867.—*Jaekel, O.*, Die Organisation von Archegosaurus (Zeitschr. deutsch. geol. Ges. vol. XLVIII.), 1896.—Ueber die Körperform und Haut bedeckung von Stegocephalen (Setzber. Ges. naturf. Freunde, Berlin), 1896.—*Meyer, H. v.*, Zur Fauna der Vorwelt, pt. 2. Frankfort, 1847.—Ueber den Archegosaurus (Palaeontogr. vols. I., VI. XV.), 1851, 1857, 1866.—*Idem*, and *Plieninger, T.*, Beiträge zur Palaeontologie Württembergs. Stuttgart, 1844.—*Miall, L. C.*, Report on the Structure and Classification of the Labyrinthodonts (Rept. Brit. Assoc. 42nd and 43rd Meet.), 1874-75.

in form, the more common varieties being oval, rhomboid, oblong, fusiform, or rod-shaped (Fig. 193).

The *vertebral column* usually remains in an embryonic condition, and recalls that of Ganoid fishes. The degree of persistence of the notochord is very variable, but only the most specialised genera have it completely

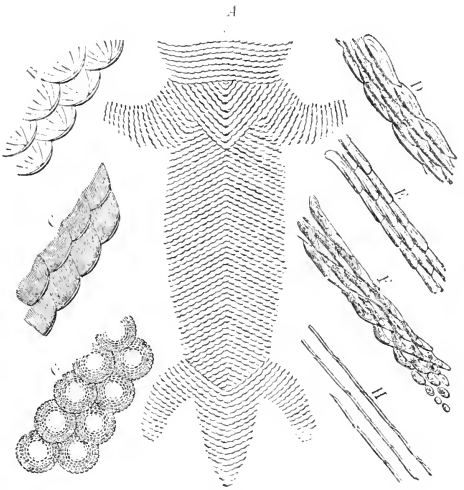


FIG. 193.

A, Ventral armour of *Branchiosaurus*. *B*, Scutes of *Branchiosaurus*; *C*, of *Hylonomus*; *D*, of *Pelosaurus*; *E*, of *Archegosaurus*; *F*, of *Sclerocephalus*; *G*, of *Discosaurus*; *H*, of *Petrobates* (after Credner).

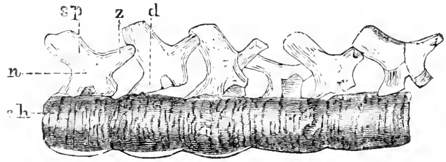


FIG. 194.

Phyllospondylous vertebrae of *Branchiosaurus amblystomus*, Credner. Enlarged (after Credner). *ch*, Notochord; *n*, Neural arch; *sp*, spinous process; *d*, transverse process; *z*, Zygapophysis.

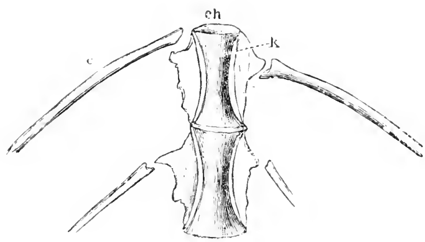


FIG. 195.

Lepospondylous vertebrae of *Hylonomus*. *ch*, Notochord replaced by mineral matter; *k*, Bony cylinder of the centrum; *c*, Rib (after Credner).

interrupted by ossification of the centra; in the *Branchiosauria* it is completely persistent.

Ossification of the vertebral column is least complete among the *Phyllospondyli* (Fig. 194), where, in the absence of pleurocentra, the neural arch itself extends downward and joins with a pair of delicate hypocentra (or intercentra) to enclose the notochord and to form transverse processes for support of the ribs. In the *Lepospondyli* (Fig. 195) the notochord is persistent and encased in constricted bony cylinders, which are hourglass-shaped in longitudinal section. In some genera, however, the continuity of the chord is all but interrupted by ossification of the middle portion of the centra.

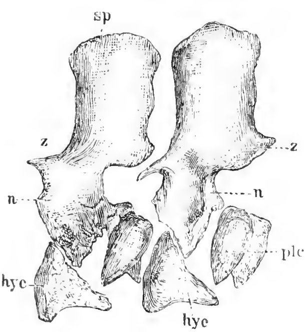


FIG. 196.

Rhachitomous dorsal vertebrae of *Archegosaurus*. *sp*, Spinous process; *z*, *z′*, Zygapophyses; *n*, Neural arch; *hyc*, Hypocentrum; *plc*, Pleurocentrum.

The *Temnospondyli* (Fig. 196) have the vertebrae composed of several distinct pieces. Ossification begins with the neural arch, whose halves remain separate at first, but later coalesce and are continued above into a stout and sometimes distally thickened spinous process. The centra may be either *rhachitomous* or *embolomerous*. Those of the rhachitomous type are formed by a horseshoe-shaped basal piece (hypocentrum or intercentrum, the tapering extremities of which are directed upward), and a pair of lateral pieces, or pleurocentra; a structure which is paralleled in certain Ganoids (*cf.* Fig. 121). The hypocentrum usually ossifies in advance of the pleurocentra, and lies directly underneath the neural arch. Occasionally a small horizontal basal piece is inserted beneath the pleurocentra and between the hypocentra. This piece, according to von Meyer, appears to be divided in the anterior caudals of *Archegosaurus* (Fig. 197).

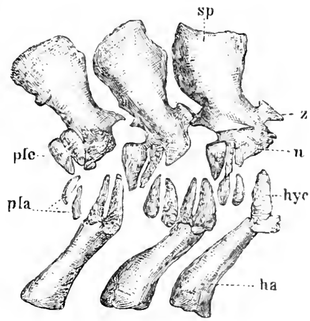


Fig. 197.

Rhachitomous caudal vertebrae of *Archegosaurus*. Lettering as in Fig. 196.

The rhachitomous type of vertebrae passes over into the embolomerous when the pleurocentra unite with the hypocentrum to form a complete bony ring, which coössifies with the neural arch above (Fig. 198). Or occasionally the crescentic intercentrum develops into a complete ring, and the pleurocentra unite with each other below and the neural arch above to form a second ring. Some genera (*Cricotus*) have rhachitomous dorsal, and embolomerous caudal vertebrae.

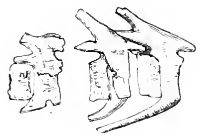


Fig. 198.

Embolomerous vertebrae of *Diplovertebron punctatum*, Fritsch. Lower Permian; Bohemia. 1/1 (after Fritsch).

The most advanced stage of vertebral ossification occurs among the Labyrinthodonts, where the centra are solid bony discs, slightly amphicoelous; sometimes they are pierced for the passage of the notochord (Fig. 199), or a channel is visible below the neural canal through which it extended (*Stereospondyli*).

There is usually but one cervical vertebra, the atlas, which is concave in front and facetted to receive the exoccipital condyles, but bears neither ribs nor anterior zygapophyses. Most or all of the presacral or dorsal series bear ribs, which may be either single or double-headed. The single sacral vertebra is provided with a pair of stout transverse processes for the attachment of sacral ribs. Haemal arches (haemapophyses, "chevron bones") are borne by the caudal series, being joined to the centrum (pleurocentrum) or intercentrum.

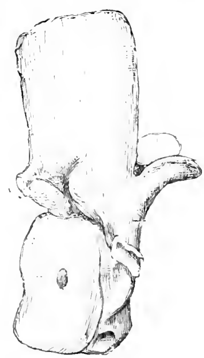


Fig. 199.

Dorsal vertebrae of *Loxomma allmani*, Huxley. 1/2.

The *cranium* (Fig. 200) exhibits the depressed, broadly triangular form characteristic of amphibians, but is invested by bony plates which form a very different pattern from the usual amphibian type, while resembling in some respects those of Ganoids and Crocodiles. The cranial plates are usually ornamented externally with radiating sculpture, pittings, or punctae, and sensory canals are often conspicuous.

The cranial roof is pierced by several apertures, the largest of which are the orbits, and around them there is often a sclerotic ring. The anterior nares are placed close to the border of the snout, and separated from each other by a considerable interval. Another and smaller opening occurs at the median suture between the parietals, corresponding in position to the so-called parietal foramen of Lizards.

The thin, flat bones constituting the cranial roof are of dermal origin, as in the case of cartilaginous Ganoids. The brain cavity is protected by the large, paired parietals, posterior to which are two pairs of supratemporals, the outermost being the larger and forming the hinder border of the auditory notch. The inner or median pair of supratemporals are commonly described as supraoccipitals (*so*), and the outer or lateral pair as "epiotics" (*ep*), although clearly of dermal origin. The plate anterior to the epiotic is usually called the squamosal (*sq*), and in front of this lie the postorbitals (*por*) and large, posterior cheek plate (*st*), which is also identified with the supratemporals. The two last-named pairs, together with the so-called epiotics, are wanting in all modern amphibians. Anterior to the parietals and between the orbits is a pair of usually elongate narrow frontals, and anterior to these a pair of large nasals with openings for the external nares at their antero-lateral angles. A pair of curved dentigerous premaxillae (*pmx*) terminate the snout in front.

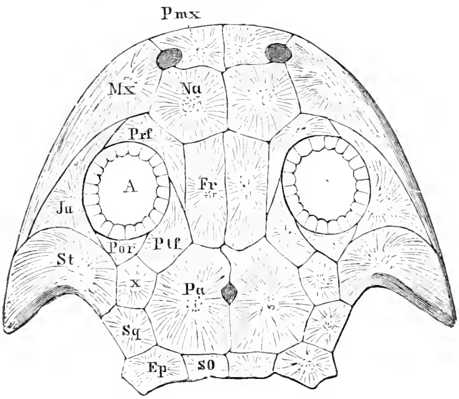


FIG. 200.

Dorsal aspect of the skull of *Melanerpeton pulcherrimum*, Fritsch. Restored. 1/1 (after Credner). *A*, Orbit; *Pmx*, Premaxilla; *Mx*, Maxilla; *Na*, Nasal; *Prf*, Prefrontal; *Fr*, Frontal; *Ptf*, Postfrontal; *Pa*, Parietal; *Por*, Postorbital; *x*, Anterior; *Sq*, Posterior squamosal; *Ep*, Epiotic; *St*, *So*, Supratemporal; *Ju*, Jugal.

The frontals rarely enter into the border of the orbits. These openings are usually bounded behind by the postorbital and postfrontal, the latter plate being invariably present; mesially by the postfrontal and prefrontal; and exteriorly by a long cheek plate called the jugal. Very often a narrow triangular bone, the lachrymal, is inserted between the prefrontal and jugal, but is usually pushed forward in advance of the orbit. The postero-inferior cranial angle is formed by the quadrato-jugal, which sometimes develops a process on the under side for articulation with the lower jaw. In some of the larger Stegocephalians the distal end of this process is separated off from the quadrato-jugal by a suture, and forms a distinct quadrate bone. Joining the quadrato-jugal in front is the maxillary, a long, narrow, gently curved bone, which completes the outer border of the cranium as far as the premaxillae.

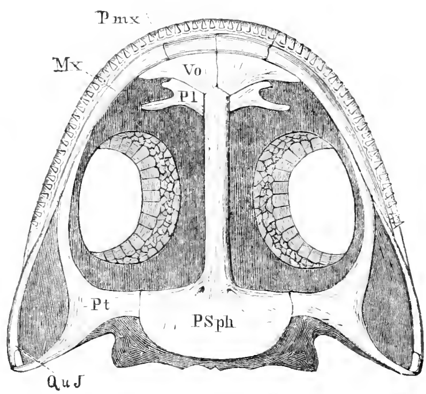


FIG. 201.

Palatal aspect of the skull of *Branchiosaurus*. Restored. 2/1 (after Credner). *Pmx*, Premaxilla; *Mx*, Maxilla; *QuJ*, Quadrato-jugal; *Pt*, Pterygoid; *PSph*, Presphenoid; *Pl*, Palatine; *Vo*, Vomer.

Most Palaeozoic Stegocephalians had the basioccipnt cartilaginous, but in the Labyrinthodonts and certain other forms the supratemporals are followed by a pair of obliquely inclined bony exoccipitals, which bear the articular condyles.

The under side of the cranium is remarkable for the large size of the palatal vacuities, and great development of the parasphenoid, which expands posteriorly into a broad, thin plate. It extends forwardly as a long, slender process, and unites with the relatively large-sized vomer, the latter element being paired in the earlier, unpaired in the later forms. The vomer usually joins the premaxillae anteriorly, and is bounded exteriorly by the maxillae, the internal nares, and front portion of the palatines. Its broad, flat surface is either edentulous or set with minute teeth, but occasionally one or two powerful tusks are present in front of the narial openings, and there is a series of smaller teeth bordering the anterior and lateral edges of the vomer.

The posterior expansion of the parasphenoid unites with a trifid bone, the pterygoid. The short inner arm of the latter in fact often envelops the parasphenoid; its long, forwardly directed process extends parallel with the palatine and maxilla, forming the outer border of the palatal vacuity; and its short posterior branch unites with the quadrato-jugal and limits the temporal vacuity. The palatines lie between the vomer and anterior extremities of the pterygoid. They are bordered externally by the maxillae, as a rule, and anteriorly by narial openings. They frequently bear a series of small teeth.

The lower jaw (Fig. 227) of all Stegocephalians extends the full length of the skull, and in consequence the gape of the mouth is very wide, as in *Anura*. The mandibular ramus is composed of three pieces, of which the dentary forms the tooth-bearing anterior portion, and the angular the lower portion; behind the dentary and above the angular is the articular, which bears a deep transverse articular facette terminated behind by an elevated process. Superimposed on these three pieces on the inner side of the jaw is a membrane bone called the splenial (or opercular). Teeth occur in regular series, decreasing in size posteriorly; and sometimes one or two greatly enlarged teeth occur at the symphysis. The union of the two rami in front was probably ligamentous in most cases.

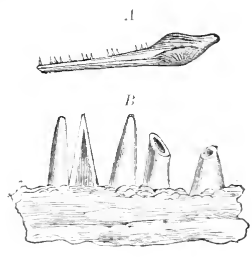


FIG. 202.
Lower jaw of *Branchiosaurus* with simple, smooth teeth. *A*, $^1/_1$. *B*, Enlarged (after Credner).

The *teeth*[1] of the smaller Palaeozoic Stegocephalians are smooth, slender, hollow, and conical (Fig. 202), and implanted either directly in the supporting bone, or attached by a cement-base. Very often the lower half or two-thirds of the crown is externally grooved or striated, in which case a radial infolding of the dentine extends for an equal height (Fig. 203). Numerous fine dentine tubules extend downward toward the periphery, and tangentially to the walls of the radial prolongations of the pulp cavity. In the more complicated teeth, secondary and even tertiary branching of dentine tubules may occur, and at the same time undulating or tortuously folded layers of cement, such as covers the exterior of the tooth, may become intercalated between the bundles of dentine

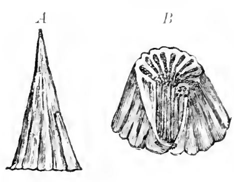


FIG. 203.
Tooth of *Archegosaurus*, enlarged. *A*, Outer surface. *B*, Lower half with a portion broken away to show the folded dentine.

[1] *Credner, H.*, Zur Histologie der Faltenzähne palaeozoischer Stegocephalen (Abhandl. sachs. Ges. Wiss. vol. XX.), 1893.

tubules. This gives rise to the highly characteristic "labyrinthodont" structure, which reaches its extreme development among the larger and geologically later Stegocephalians (Fig. 204). The internal structure becomes progressively less complicated toward the apex of the tooth, above the zone where radial infoldings of the walls leave off, the dentine is traversed simply by straight tubules radiating from the pulp cavity. The insertion of the teeth may be of the acrodont or pleurodont type, as already described, or they may be seated in shallow alveoli.

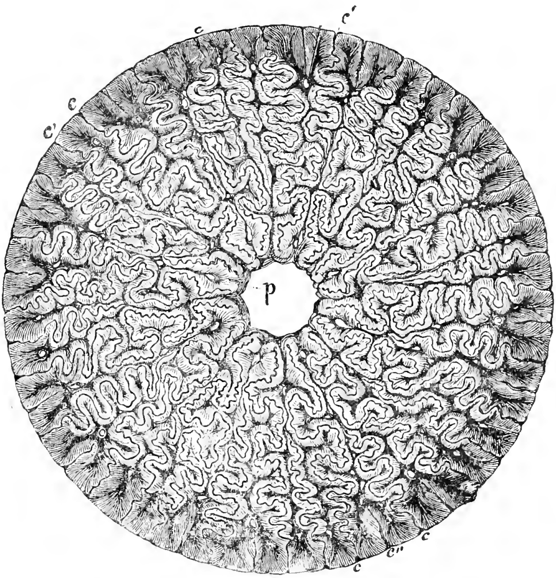


Fig. 204.
Cross-section of a tooth of *Mastodonsaurus jaegeri*. $^3/_1$ (after Owen). *P*, Pulp cavity; *c*, Dentine tubules.

Traces of branchial arches being conspicuous in the young of several Palaeozoic genera, the supposition is natural that respiration was by gills during the early stages of all Stegocephalians.

The Stegocephalian *pectoral arch* (Fig. 205) is of unique construction, differing from that of other amphibians in notable respects. The most characteristic, as well as the largest and usually best preserved bones, occupy an external position on the thorax between the pectoral limbs. These bones are three in number, and as a rule prominently sculptured. The median element identified as the interclavicle (or entosternum) varies considerably in form and size amongst different genera. Most frequently it is rhombic, but sometimes transversely oval, and may terminate behind in a long median extension.

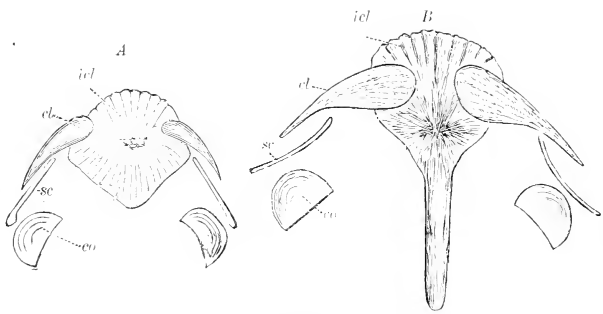


Fig. 205.
A, Pectoral arch of *Branchiosaurus*. *B*, *Melanerpeton* (after Credner). *icl*, Interclavicle; *cl*, Clavicle; *co*, Coracoid; *sc*, Scapula [=cleithrum of Gegenbaur].

Partly overlapping the forward portion of the interclavicle are the paired plates which correspond to the clavicles of other amphibians. Their posterior ends are slender and slightly curved upwards; the anterior end is expanded into a triangular or oval plate, often sculptured, but sometimes smooth as if it had been embedded in the integument. A flat, semicircular, or lunate plate, interpreted as the coracoid, is placed at a slight distance behind the clavicles, and there is also a narrow or rod-like piece with expanded distal extremities, corresponding to the scapula of other groups. [Gegenbaur, and following him G. Baur, interpret these bones differently, holding that the coracoid was in all probability cartilaginous, and identifying the bone commonly known by that name as the scapula, and the so-called scapula as the *cleithrum*. The latter, as shown by Gegenbaur, was attached to the distal end of the clavicle.]

The bones of the appendicular skeleton, so far as known, agree in form, number, and arrangement with those of living Urodeles. The humerus is rarely furnished with articular condyles, its extremities remaining as a rule cartilaginous. Ulna and radius are always separate, simple, more or less elongate, and without articular faces. The carpus is imperfectly known; in many Palaeozoic genera it appears to have been cartilaginous, in others partly ossified. The metacarpals and phalanges are slender and elongate.

The *pelvic arch* (Fig. 206) is strongly developed, but seldom so well preserved that the form and position of all the parts are clearly distinguishable. The ilium is short, stout, somewhat expanded at the extremities, and attached to the sacral ribs. Ischium and pubis sometimes unite to form a single large plate (ischio-pubis), or they may remain separate. The inner edges of the ischia form a symphysis in the median line. The pubes, which are smaller, sometimes remain cartilaginous amongst Palaeozoic forms.

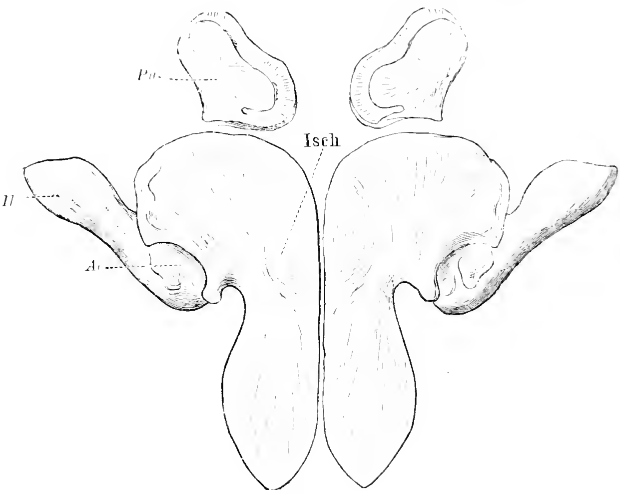


FIG. 206.
Pelvic arch of *Mastodonsaurus giganteus*, Jaeg. (after Fraas). *Il*, Ilium; *Isch*, Ischium; *Pu*, Pubis; *Ac*, Acetabulum.

The *hind-limb* is almost always more strongly developed than the fore-limb. The femur is a strong, elongate bone, without an ossified capitulum, but often with well-formed distal condyles. Tibia and fibula remain separate, and resemble the corresponding bones of the anterior limb. The tarsus is either cartilaginous or composed of two rows of small bones. The pes is provided with five digits, but is otherwise closely similar to the manus; sometimes the second digit is the longest, in other cases the third.

Habitat.—The mode of occurrence of Stegocephalians in the Coal Measures, Lower Permian, and Keuper, indicates that they were either freshwater inhabitants, or terrestrial forms. Some of the smaller genera appear to have sequestered themselves in hollow tree-stumps, since in Nova Scotia, at least, their remains are commonly found in cavities of decayed Sigillaria and

Lepidodendron trunks. The larger forms, some of which attained gigantic size, were predatory, and probably subsisted on other amphibians, fishes, and crustaceans.

Sub-Order A. PHYLLOSPONDYLI. Credner. (*Branchiosauria.*)

Notochord persistent and encased in imperfect barrel-shaped vertebrae formed by a pair of delicate hypocentra and downward prolongations of the neural arch, but without pleurocentra. Teeth simple, hollow.

Family 1. Branchiosauridae. Fritsch.

Lizard-like Stegocephalia with broad, obtusely rounded heads. Basiocciput cartilaginous, and also the carpus, tarsus, and pubis. Ribs short and straight, with simple, thickened proximal ends. Pubis not ossified. Ventral scales thin, small, pointed, and arranged in regular series. Carboniferous and Permian.

Branchiosaurus, Fritsch (*Protriton*, *Pleuroneura*, Gaudry), (Figs. 201, 202, 205, 207, 208). Body 15-20 mm. long. Head about as broad as long, truncate behind, with shallow auditory notch, and very large elliptical orbits. Sclerotic ring of about 30 small plates, and also a supplementary series of smaller plates irregularly arranged. Cranial plates radially striated or punctate. Parasphenoid greatly expanded behind, and uniting with trifid pterygoid. Vomer paired, the two pieces triangular; palatines imperfectly known. Jaws with a single series each of slender, closely spaced conical teeth. Interclavicle sub-rectangular, externally furrowed. Ilium stout, hourglass-shaped; ischium delicate, triangular.

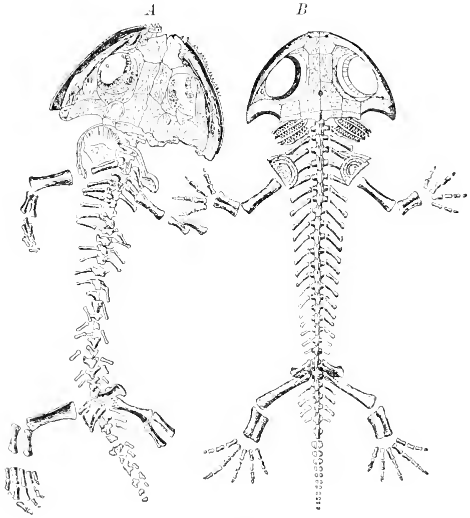


Fig. 207.

Branchiosaurus amblystomus, Credner. Rothliegendes, Niederhässlich, near Dresden. *A*, Skeleton of adult individual, $^1/_1$. *B*, Restoration of a larval form with gill arches (after Credner).

Fig. 208.

Branchiosaurus petrolei, Gaudry sp. Lower Permian; Autun. $^1/_1$ (after Gaudry).

The entire ventral surface of the body, together with a portion of the tail and limbs, was protected by deeply overlapping cycloidal scales (Fig. 193) arranged in several distinct series. Those of the thoracic region form transverse rows; those of the pectoral region oblique rows converging posteriorly toward the median line; those of the abdominal region oblique rows, converging at a lesser angle in the opposite direction; and those of the under side of the tail and legs form slightly curved transverse rows. Functional gill arches are indicated in many immature examples by the regular series of minute denticles which were originally arranged on them. Tail known to have been about as long as trunk with the head, but most of the caudals unossified.

This genus and *Archegosaurus* furnish the commonest and best known examples of Palaeozoic Amphibians. Remains of *Branchiosaurus* are abundant in the fine-grained limestone of the middle Rothliegendes, near Dresden, where the small bones are clearly outlined in white against a grayish-coloured matrix. Credner's elaborate researches on the structure and development of this form were based on comparisons of over 1000 specimens. Several species occur also in the Lower Permian of Nürschan (Nyřan) and Kunova in Bohemia, and Oberhof and Friedrichsroda in Thuringia.

Pelosaurus, Credner (Fig. 193, *d*). 18 to 20 cm. long. Skull relatively very large, with lachrymal in front of orbits, and no supplementary sclerotic plates. Lower Permian; Niederhässlich, near Dresden. *P. laticeps*, Credner.

Melanerpeton, Fritsch (Figs. 200, 205, *b*). 2·5 to 13 cm. long. Skull as in *Branchiosaurus*, but more produced posteriorly, and squamosal divided (*sq* and *x*). Interclavicle extended into a long posterior process. A distinct dermal armouring not present, but quantities of small calcareous shagreen-like particles sometimes observed instead. Branchial arches present in young examples. Lower Permian of Braunau, Bohemia; Lhotka, Moravia; and Niederhässlich, Saxony.

Dawsonia, Fritsch. Jaw-bones, vomer, palatines, and parasphenoid armed with teeth. Lower Permian; Bohemia.

Amphibamus, Cope; *Pelion*, Wyman. Coal Measures; Linton, Ohio.

Sub-Order B. **LEPOSPONDYLI.** Zittel. (*Microsauria.*)

Notochord persistent and enclosed in constricted bony cylinders, hourglass-shaped in longitudinal section. Teeth simple, conical, hollow.

Family 1. **Microsauridae.** Dawson.

Salamander or lizard-like, usually longicaudate Stegocephalia. Fore-limbs less robust than the hinder pair, carpus and tarsus ossified or cartilaginous. Ribs long and slender, curved, generally double-headed. Pubis ossified. Ventral, and in rare cases also the dorsal surface covered with small, round, oblong, oval or oat-shaped scales. Carboniferous and Permian.

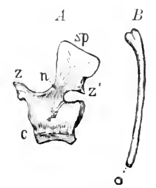


Fig. 209.

A, Vertebra, and *B*, Rib of *Hylonomus lyelli*, Dawson. Coal Measures; Joggins, Nova Scotia.

Hyloplesion, Fritsch. Cranial bones smooth, finely striated or punctate. Orbits large, with sclerotic ring. Tarsus ossified. According to Fritsch, both dorsal and ventral armatures were present, composed of overlapping oval scales with thickened posterior border. Lower Permian; Nürschan, Bohemia, and Niederhässlich, Saxony.

Hylonomus, Dawson (Fig. 209). Small and imperfectly known, perhaps identical with the preceding. Coal Measures; Nova Scotia. Other allied American genera are *Amblyodon*, Dawson;

Hylerpeton, Owen; and *Brachydectes*, Cope, all small and fragmentarily preserved.

Seeleya, Fritsch. Larval, lizard-like forms under 2·5 cm. in length, with rounded snout. Teeth smooth, simple, hollow, present on all bones of the palate, those of the premaxillae much larger than the maxillary teeth. Parasphenoid a long slender bone expanding behind into a rectangular plate. Gill arches, and both dorsal and ventral armour present. Scales elongated oval, ornamented with undulating or dichotomising lines. Very rare in Lower Permian of Nürschan, Bohemia. *S. pusilla*, Fritsch.

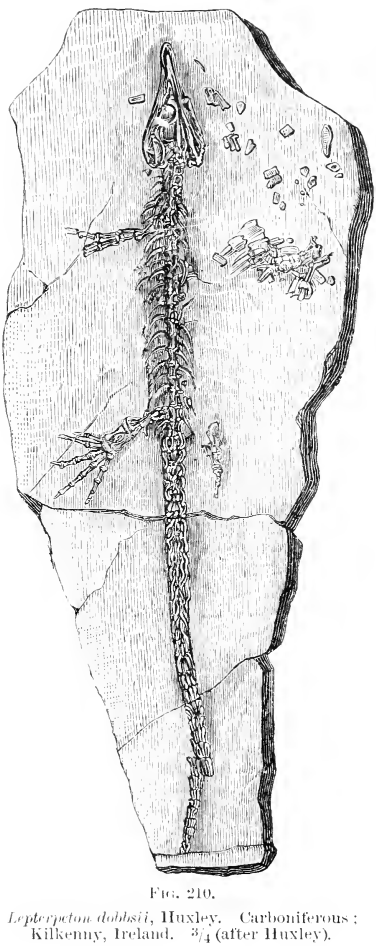


Fig. 210.
Lepterpeton dobbsii, Huxley. Carboniferous; Kilkenny, Ireland. $^3/_4$ (after Huxley).

Ricnodon, Orthocosta, Microbrachis, Limnerpeton, Fritsch. Lower Permian; Nürschan, Bohemia.

Tuditanus, Cocytinus, Colosteus, Leptophractus, Pleuroptyx, Cope. Coal Measures; Linton, Ohio.

Lepterpeton, Huxley (Fig. 210). Lizard-like, longicaudate, with narrow, elongated head and tapering snout. Orbits midway the length of the skull; carpus and tarsus cartilaginous. Hind-limb slightly stouter than the anterior. Ventral scales elongated rhombic. Coal Measures; Kilkenny, Ireland.

Keraterpeton, Huxley (*Ceraterpetum*, Huxley). Salamander-like, with much elongated tail; total length upwards of 50 cm. Skull broad, rounded anteriorly, orbits far forward, and external bones sculptured. A pair of large, backwardly directed horns firmly attached to the postero-lateral cranial angles. Very small ventral scutes, and no dorsal armour. Coal Measures; Kilkenny, Ireland, and Linton, Ohio.

Scincosaurus, Fritsch (Fig. 211). Skull smaller in proportion to the body than in *Keraterpeton*, with more numerous presacral vertebrae, and distinct ossifications in carpus and tarsus. Lower Permian; Bohemia. *S. crassus*, Fritsch.

Urocordylus, Huxley and Wright (*Oestocephalus, Ptyonius*, Cope), (Fig. 212). Body and tail elongate, total length about 50 cm. Fore-limb slightly less developed than the hind, both pentadactyle. Skull depressed, triangular, posteriorly truncate. Orbits forwardly situated. Tail nearly twice as long as the trunk with the head. Caudal vertebrae about 80 in number, with long neural and haemal spines, expanded and crenulated distally. Ventral armour composed of upwards of 100 rows of scutes converging toward the median line, in form elongated oval, fusiform or oat-shaped. Coal Measures;

Kilkenny, Ireland. Lower Permian; Nürschan, Bohemia. *U. scalaris*, Fritsch.

Acanthostoma, Credner (Fig. 213). Skull 25-35 cm. long, sharply parabolic in outline, externally pitted. Orbits relatively small, rounded, placed

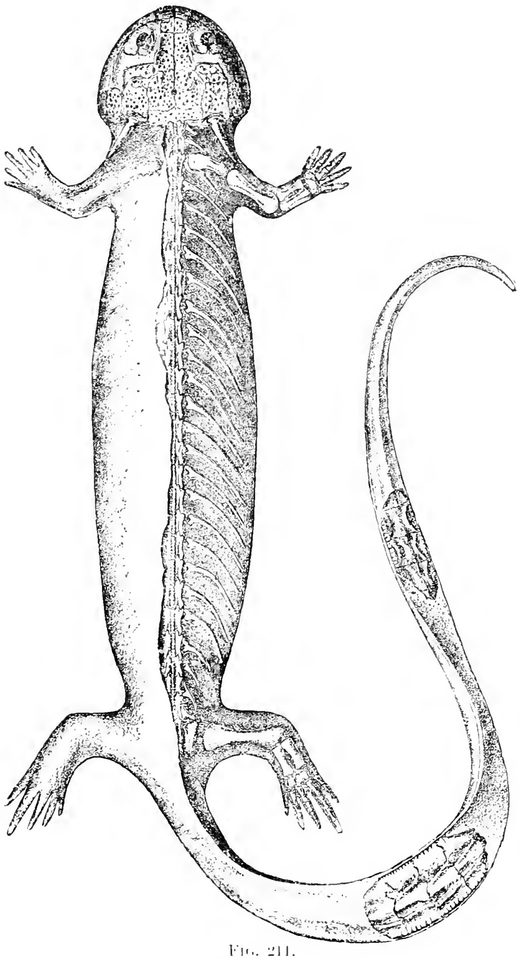


FIG. 211.

Keraterpeton crassum. Fritsch. Lower Permian; Nürschan, Bohemia. Restored. 1/1 (after Fritsch).

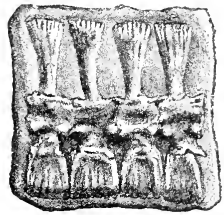


FIG. 212.

Urocordylus wandesfordii, Huxley. Coal Measures; Kilkenny, Ireland. Caudal vertebrae, 1/1 (after Huxley).

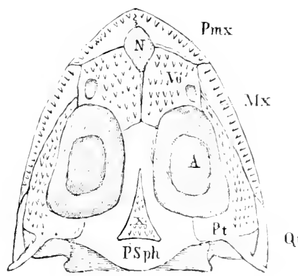


FIG. 213.

Palatal aspect of skull of *Acanthostoma vorax*, restored. 1/1 (after Credner). *A*, Orbit; *N*, Internal nares; *Pmx*, Premaxilla; *Mx*, Maxilla; *Qul*, Quadratojugal; *PSph*, Parasphenoid; *Pt*, Pterygoid.

in posterior half of the skull, and with sclerotic ring. All bones of the buccal cavity set with teeth. Lower Permian; Saxony.

Family 2. **Aistopodidae.** Miall. (*Aistopoda.*)

Body serpentiform, without either limbs or arches for their support. Vertebrae constricted amphicoelous cylinders. Teeth simple, conical, hollow. Ribs slender, with one or two processes. Carboniferous and Permian.

Dolichosoma, Huxley (? *Phlegethontia*, ? *Molgophis*, Cope), (Fig. 214). Skull relatively small, triangular, with tapering snout; external bones smooth, and median ones more or less fused. Premaxillae very small. Over 150 vertebrae, and total length upwards of 1 m. Neural spines atrophied. Ribs slender, the foremost ones angularly bent, later ones straight. Dermal armature not observed. Coal Measures; Kilkenny, Ireland. Lower Permian; Bohemia.

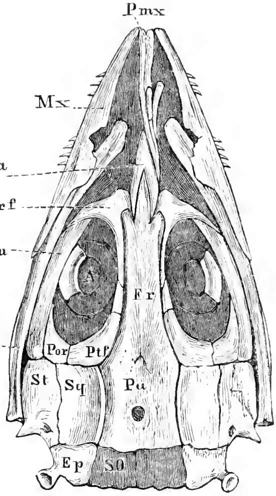


FIG. 214.
Dolichosoma longissimum, Fritsch. Lower Permian; Nürschan, Bohemia. Restored. $^3/_1$.

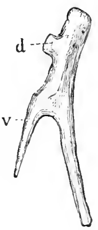


FIG. 215.
Ophiderpeton granulosum, Fritsch. Rib. $^6/_1$. Permian; Bohemia. *d*, Dorsal; *v*, Ventral process.

Ophiderpeton, Huxley (Fig. 215). Skull imperfectly known, shorter and more obtuse than in *Dolichosoma*. Ribs slender, resembling intermuscular bones of fishes, with dorsal and ventral processes. Ventral scutes small, oat-shaped; dorsal ossicles shagreen-like. *O. brownriggi*, Huxley, from the Irish Coal Measures, 40-60 cm. long. Five smaller species known from the Permian of Bohemia.

Sub-Order C. TEMNOSPONDYLI. Zittel.

Vertebrae composed of several pieces, usually of the rhachitomous type, sometimes embolomerous. Basioccipital region usually, and carpus and tarsus always ossified. Teeth with radially infolded walls. Carboniferous to Lower Trias.

Archegosaurus, v. Meyer (Figs. 196, 203, 216, 217). Total length upwards of 1·5 m. Skull in the young obtusely triangular, scarcely longer than broad, but becoming greatly elongated in the adult, with broad, anteriorly rounded snout. External bones radially sculptured, sensory canals feebly marked. Orbits situated in about the middle of the skull in the young, and in hinder portion in mature individuals; sclerotic ring of 20-23 plates. Anterior nares elongate. Postorbitals triangular, supratemporals large, lachrymals long and narrow, basioccipital region not ossified, palatal vacuities large. Parasphenoid and pterygoids toothless, vomer with one or two pairs of relatively large teeth, and maxillae, premaxillae, and palatines each with a single series of teeth. Dentine deeply and simply folded in lower half of the crown. Denticles of branchial arches observed in young individuals. In the caudal region stout chevron bones are attached to the hypocentra, and intercalated between these are two wedge-shaped pieces (Fig. 197).

The interclavicle is rhomboidal, about half as long as the skull, and radially sculptured. Clavicles triangular, with short posterior pedicle; coracoid and scapula ossified. Fore-limb less strongly developed than the hind, and with four digits. Ventral armouring of small, overlapping, transversely elongated scales, keeled, and pointed at one end (Fig. 193, *E*).

In H. von Meyer's elaborate Monograph, published in 1858, no less than 271 examples from the Lower Permian of Lebach, near Saarbrücken, are described, of which 102 are figured. The remains, lacking usually the tail, occur here in siderite nodules. *A. decheni*, v. Meyer.

Sparagmites, Fritsch; *Discosaurus*, Credner (Fig. 193, *G*). Lower Permian; Saxony and Bohemia.

Chelidosaurus, Fritsch. Like *Archegosaurus*, but with broader and shorter skull, and no lachrymals. Lower Permian: Bohemia. *C. vranyi*, Fritsch.

Actinodon, Gaudry (Fig. 218). Basiocciput ossified. Vomers each with one large tooth and numerous rugosities. Vertebrae rhachitomous. Lower Permian of Autun, France, and Rhenish Prussia.

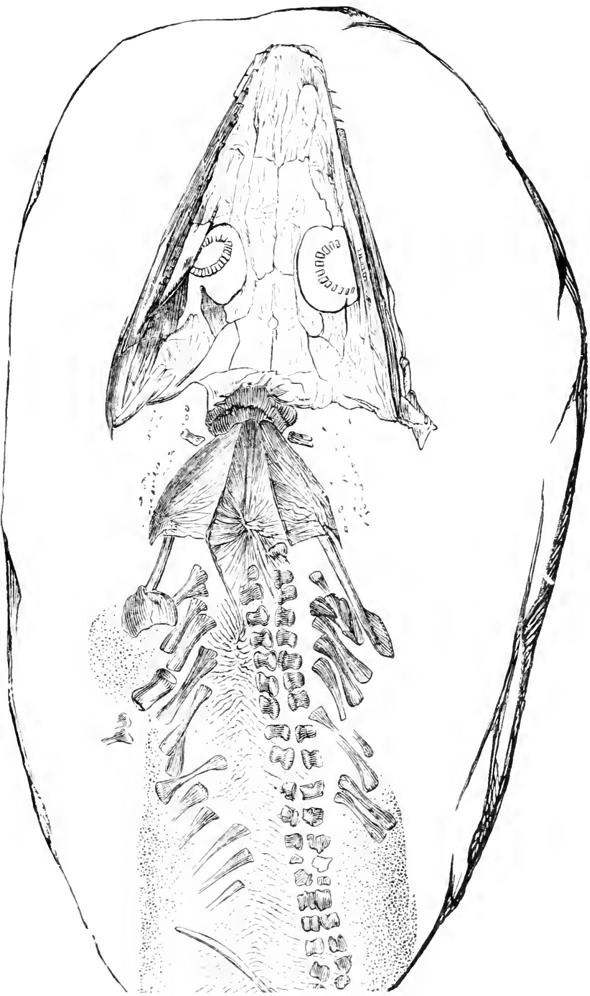


FIG. 216.

Archegosaurus decheni, v. Meyer. Lower Permian; Lebach, near Saarbrucken. Young individual with traces of gill arches. 1/1 (after H. v. Meyer).

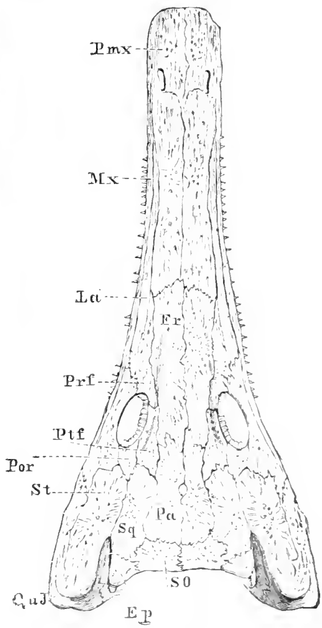


FIG. 217.

Archegosaurus decheni, v. Meyer. Skull of adult individual, 1/2. Permian; Lebach, near Saarbrucken. *Pmx*, Premaxilla; *Mx*, Maxilla; *La*, Lachrymal; *Prf*, Prefrontal; *Ptf*, Postfrontal; *Por*, Postorbital; *St*, *SO*, Supratemporals; *Sq*, Squamosal; *Pa*, Parietal; *QuJ*, Quadrato-jugal; *Ep*, "Epiotic" (=Supratemporal).

Gaudrya, *Cochleosaurus*, Fritsch. Lower Permian; Nürschan, Bohemia. *Euchirosaurus*, Gaudry. Permian; France.

Sclerocephalus, Goldfuss (*Onchiodon*, Gein.; *Weissia*, Branco). Over 1 m.

long. Skull rounded anteriorly, orbits in hinder third, anterior nares far forwards, external bones coarsely sculptured. Palatines with minute teeth, maxillae and premaxillae with a series of large, conical, vertically grooved teeth. Dentine deeply folded. Vertebrae rhachitomous. Coracoid expanded, with concave posterior border; scapula long, slender, tapering. Ventral scales oat-shaped. Lower Permian; Rhenish Prussia and Saxony.

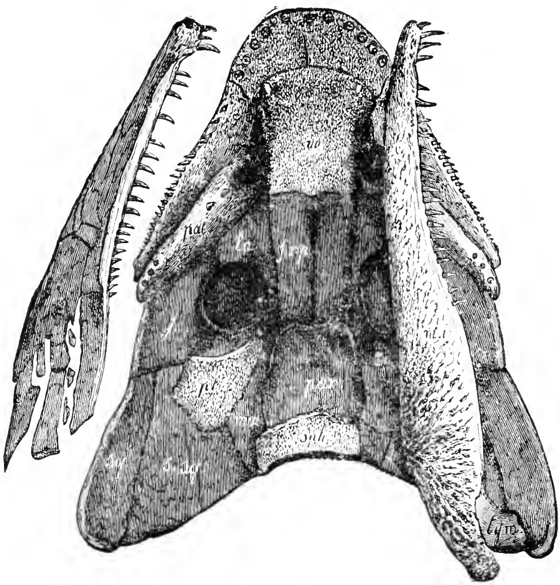


Fig. 218.
Actinodon frossardi, Gaudry. Permian; Muse, near Autun, France. Palatal aspect of skull, with lower jaws. $^2/_5$ (after Gaudry).

Melosaurus, *Chalcosaurus*, v. Meyer; *Zygosaurus*, Eichwald; *Platyops*, Trautschold. Permian; Russia.

Dendrerpeton, Owen. Coal Measures; Nova Scotia and Bohemia.

Trimerorhachis, *Zatra-*

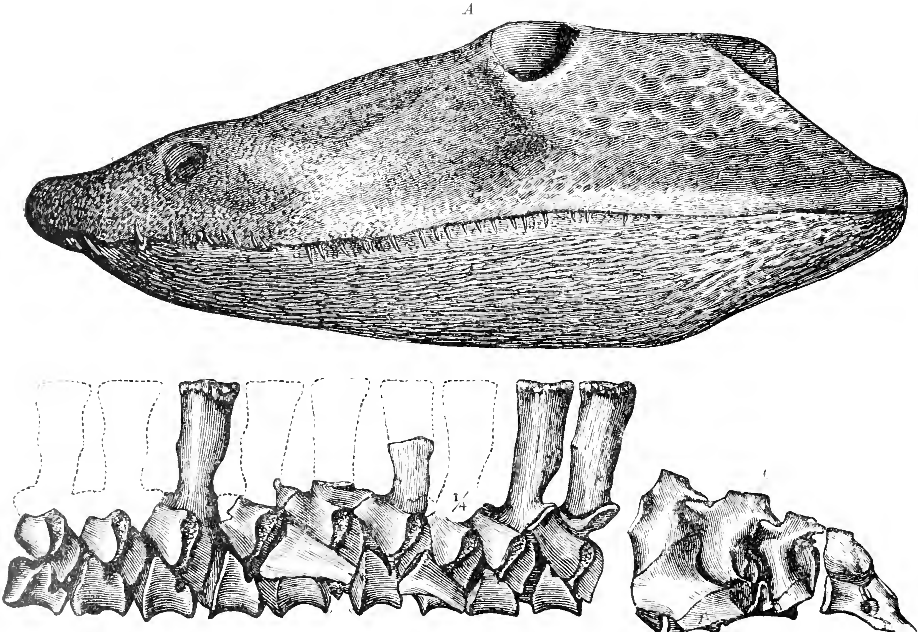


Fig. 219.
Eryops megacephalus, Cope. Permian; Texas.
A, Lateral aspect of skull. $^1/_5$. *B*, Portion of the vertebral column. *C*, Caudal vertebrae. $^1/_4$ (after Cope).

chis, *Dissorophus*, *Acheloma*, *Anisodexis*, Cope. Permian; Texas and New Mexico.

Eryops, Cope (*Rhachitomus*, *Epicordylus*, *Parioxys*, Cope), (Fig. 219). Largest of North American Stegocephalians. Skull 40-60 cm. long, and 30-46 cm. wide at occiput, elongated triangular, with somewhat tapering snout. Orbits round, relatively small, placed in hinder half of the skull. Anterior nares large, widely separated. Cranial bones rugose, sutures indistinct. Parasphenoid very thick, dagger-shaped. On the palatine two large conical teeth. Maxilla and premaxilla with teeth of various sizes. Teeth sharply conical, on the top smooth, at the base ribbed. Vertebrae rhachitomous. Caudal vertebrae few in number, the posterior ones fused into a triangular piece, tapering acutely behind. Ribs strong, those of the sacrum very broad and short. Permian; Texas and New Mexico.

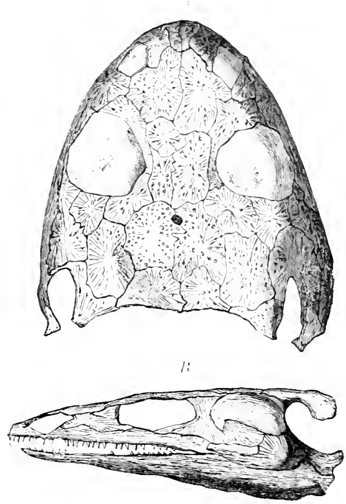


Fig. 220.

Micropholis granulata, Owen sp. Trias: Table Mountain, South Africa. *A*, Skull, from above. *B*, From the side ×1/1 (after Owen).

Cricotus, Cope. Total length, 3 m. General form elongate, with triangular skull and short, stout limbs. Snout narrow, orbits large, elongated oval, situated near the middle of the skull. External bones faintly sculptured, sensory canals conspicuous, parietal foramen large. Teeth conical, of unequal size. Presacral vertebrae composed of horseshoe-shaped pleurocentra and hypocentra, the former alone supporting the neural arch. In the caudals the pleurocentra and hypocentra form complete rings, and both elements take part in support of the neural arch, but the haemal arch is borne exclusively by hypocentra. Permian; Texas and Illinois. *C. heteroclitus*, Cope.

Diplovertebron, Fritsch (Fig. 198). Imperfectly known. Lower Permian; Bohemia. *Brachyops*, Owen; *Gondwanosaurus*, Lyddeker. Trias (Gondwana Beds); East India.

Bothriceps, Huxley. Skull triangular, with very large parietals, and coarsely sculptured plates. Anterior nares far forwards. Teeth acutely conical, vertically grooved. Trias; Australia and South Africa.

Sub-Order D. STEREOSPONDYLI. Zittel.

Vertebrae completely ossified, slightly amphicoelous, sometimes centrally perforated for passage of the notochord. Basioccipital region ossified; sensory canals forming a lyra between the orbits and anterior nares. Teeth with complicated infolding of the dentine.

Family 1. Gastrolepidotidae. Zittel.

Ventral armour consisting of elongated bony scutes. Radial prolongations of pulp cavity only moderately branched. Carboniferous and Permian.

Anthracosaurus, Huxley. Skull broadly triangular, 36 cm. long, externally pitted. Orbits very small, situated in hinder third of the skull. Teeth externally furrowed, of nearly uniform size. Vomer toothless, palatines with a large tooth, and several of smaller size. Dermal scales externally convex, sharpened at the ends. Coal Measures; Northumberland. *A. russelli*, Huxley.

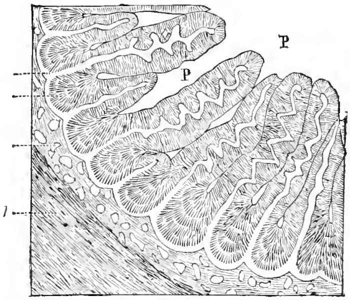


FIG. 221.
Cross-section of tooth of *Loxomma allmani*, Huxley, near the base. Enlarged. Coal Measures; Northumberland (after Embleton and Abbey).

Loxomma, Huxley (Figs. 199, 221). Like the preceding, but orbits very large, irregularly oval, and teeth of unequal size. Coal Measures; Northumberland and Bohemia.

Eosaurus, Marsh. Known only by a few detached amphicoelous vertebrae. Coal Measures; Nova Scotia.

Macromerion, Fritsch. Imperfectly known. Permian; Bohemia.

Family 2. **Labyrinthodontidae.** (*Euglypta*, Miall.)

Ventral armouring and sclerotic ring absent. Pectoral plates large, coarsely sculptured. Infoldings of the dentine completely labyrinthodont. A few excessively developed teeth present on the palatines, and sometimes on the vomer and symphysis of lower jaw. Trias.

Trematosaurus, Braun (Fig. 222). Skull elongated triangular, about 25 cm. long, with orbits near the middle. Teeth present on jaw-bones, palatines, and vomer, and inner border of posterior nares fringed with small denticles. A pair of greatly enlarged teeth present on symphysis of lower jaw, and behind these a supplementary row of small teeth. Two large vomerine tusks in advance of the posterior nares, and three or four palatine ones behind the same. Interclavicle rhomboid, with posterior pedicle. Abundant in the Buntsandstein of Bernburg. *T. brauni*, Burm.

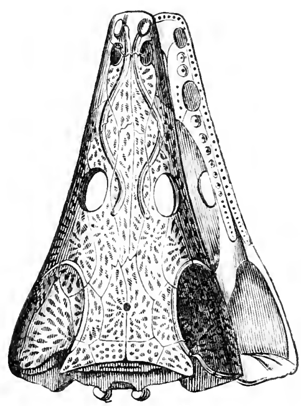


FIG. 222.
Skull of *Trematosaurus brauni*, Burmeist. Buntsandstein; Bernburg. 1/4 (after Burmeister).

Metopias, v. Meyer (*Metoposaurus*, Lydekker), (Fig. 223). Skull large, broadly triangular, with elliptical orbits in anterior half, and large narial openings Nasals shorter than frontals and parietals. Pectoral plates very large. Ribs very powerful, distally expanded. Dentition weak, teeth strongly fluted externally, especially at the base, with but slight internal foldings. Teeth apparently arranged like those of *Capitosaurus*. Keuper; Würtemberg.

Capitosaurus, Münst. (Figs. 224, 227). Skull with muzzle often broad and obtusely rounded. Orbits small, behind the middle of skull. Nasals of equal size with the frontals or larger. A small auditory notch adjacent to the so-called epiotic. One or two powerful tusks present on vomer in front of the internal nares and on palatines behind the same. Between the vomer and premaxillae is an aperture to give play to the two median tusks of the lower jaw. Keuper; Würtemberg, Franconia, Silesia.

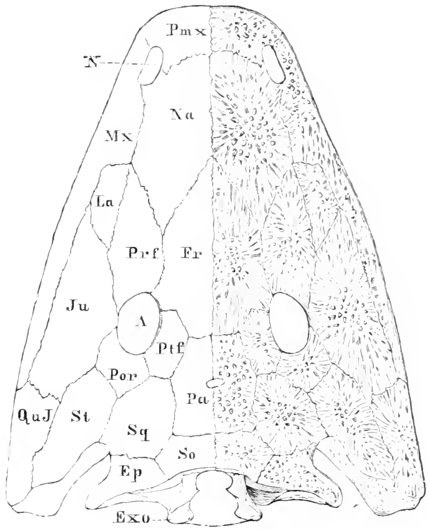


Fig. 223.
Capitosaurus nasutus, v. Meyer. Buntsandstein; Bernburg. Dorsal aspect of skull.

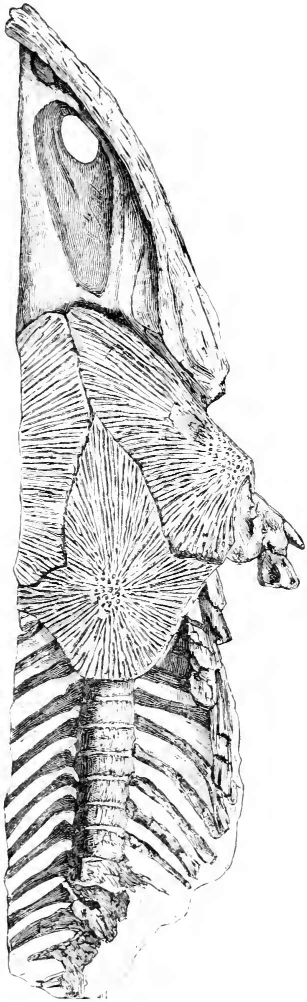


Fig. 224.
Metopias diagnosticus, v. Meyer. Ventral aspect of skeletal fragment. Keuper; Hahnweiler, near Stuttgart. 1/8 (after E. Fraas).

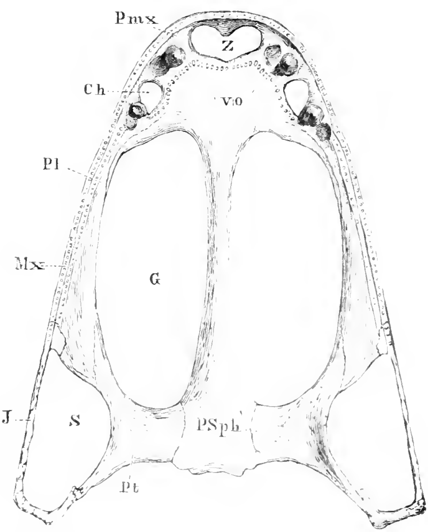


Fig. 225.
Cyclotosaurus robustus, v. Meyer. Keuper; Feurerbach, near Stuttgart. Palatal aspect of skull.

Cyclotosaurus, Fraas (Fig. 225). Similar to *Capitosaurus*, except that the auditory notch is closed behind by the union of the external supratempora with the prosquamosal. Keuper; Würtemberg.

Mastodonsaurus, Jaeger (Figs. 204, 206, 226). Largest of all Labyrinthodonts, skull 1·25 m. long, depressed, and with large orbits behind the middle. External bones sculptured, sensory canals prominent. Premaxillae pierced for the passage of the two greatly enlarged teeth at symphysis of lower jaw. Vomers with a pair of tusks in front of the posterior nares, and another near the hinder margin; palatines with a single series of large teeth. Dentine excessively complicated. Interclavicle rhomboidal, clavicles triangular, all strongly sculptured. Ischium very large, pubis small, ilium elongated, and articulating with the sacral ribs. Limbs very imperfectly known, and dermal armour not observed. The most perfect remains are from the Lettenkohle of Gaildorf and Oedendorf in Würtemberg. Fragments occur also in the Upper Trias of England and India, and possibly also in the Buntsandstein of Alsace and the Black Forest.

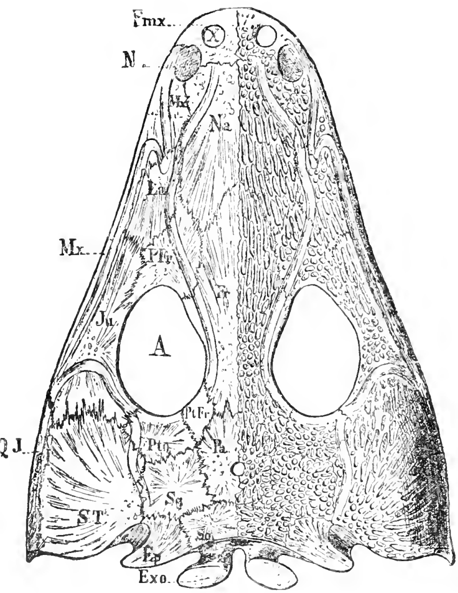


Fig. 226.

Skull of *Mastodonsaurus giganteus*, Jaeger. *A*, Orbit; *N*, External nares; *X*, Openings for the passage of the tusks of lower jaw; *Pmx*, Premaxilla; *Mx*, Maxilla; *Na*, Nasal; *La*, Lachrymal; *Pfr*, Prefrontal; *Fr*, Frontal; *Ptf*, Postfrontal; *Pa*, Parietal; *PtO*, Postorbital; *Sq*, Squamosal; *SO*, Supratemporal; *Ep*, Epiotic; *J*, Jugal; *Qj*, Quadrato-jugal; *ExO*, Exoccipital (after E. Fraas).

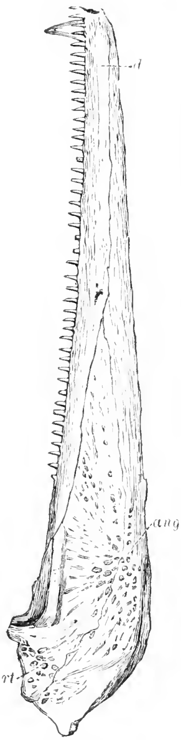


Fig. 227.

Lower jaw of *Capitosaurus nasutus*, v. Meyer. Trias Bernburg.

Fig. 228.

Footprints of *Cheirotherium barthi*, Kaup. Buntsandstein; Hessberg, near Hildberghausen. 1/6 (after Owen).

Labyrinthodon, Owen. Upper Trias; England. *Rhytidosteus*, Owen. Karoo Formation; Orange Free State. *Pachygonia*, *Gonioglyptus*, Huxley. Trias; East India.

Footprints.—Stegocephalian footmarks are not uncommon in the Coal

Measures of Nova Scotia, Pennsylvania, Kansas, and elsewhere. They occur also in the Rothliegendes of Thuringia, Saxony, and Bohemia; in the Karoo Formation of South Africa, and the Connecticut Valley Trias. More notable still are the Buntsandstein localities in Thuringia (Fig. 228) and Franconia, and those of the English and Franconian Keuper. The impressions always occur along stratification planes, and on removal of the superjacent layer the counterpart appears in relief, and is usually accompanied by a series of fossil mud-cracks. Most of these tracks are five-toed, although some occur in which the manus, which is invariably of smaller size than the pes, has but four digits.

Order 2. GYMNOPHIONA. (*Apoda*, Oppel.)

Vermiform amphibia covered with small scales, arranged in transverse rings, and without limbs. Vertebrae amphicoelous, with persistent notochord. Cranium ossified; maxillae and palatines with small, backwardly curved teeth. Ribs weakly developed. Pectoral and pelvic arches absent.

The Coecilians constitute a small group restricted to the South American and Indo-African tropics, and are unknown in the fossil state.

Order 3. URODELA.[1] (*Caudata; Batrachia gradientia.*)

Elongate amphibia with naked skin, usually with two pairs of short limbs and perennial tail, with or without external gills. Cranium without supraoccipital, post-orbitals, and supratemporals. Vertebrae usually completely ossified. No parietal foramen. Ilio-sacral connection acetabular.

Urodeles are distinguished from Stegocephalians chiefly by their naked body, solid vertebrae, extremely short ribs, and peculiarities in the conformation of the skull and pectoral arch. The vertebrae may be either amphicoelous or opisthocoelous, are rarely pierced for the notochord, and have weakly developed spinous and transverse processes.

The *skull*, which is broad, flattened, and anteriorly rounded, remains partly cartilaginous even in the adult, and both membrane and cartilage bones are among its components. The cranial roof is formed by the parietal, frontal, and prefrontal elements, adjoining which on either side are the large temporal fossae and orbits. The nasal capsule is sometimes covered by ossified nasals, and sometimes remains cartilaginous. The anterior and lateral margins of the skull are formed by the premaxillae and maxillae, but the latter are sometimes entirely wanting. In the basioccipital region only the exoccipitals are ossified, and the auditory capsule remains either cartilaginous or partially ossified, being covered by a thin, transversely elongated squamosal. Jugal and quadrato-jugal are absent, the quadrate is small, and only its articular extremity is ossified. Parasphenoid, vomers, and pterygoids are conspicuous on the under side of the skull, but the palatines are frequently atrophied.

[1] *Meyer, H. von*, Zur Fauna der Vorwelt, pt. 2. Frankfort, 1845.—Salamandrinen aus der Braunkohle, etc. (Palaeontogr. vol. VII.), 1860; also vol. II. p. 70, and vol. X. p. 292.—*Strauch, A.*, Revision der Salamandridengattungen. St. Petersburg, 1870.—*Wiedersheim, R.*, Salamandrina perspicillata, Versuch einer vergleichenden Anatomie der Salamandrinen. Wurzburg, 1875.—Das Kopfskelet der Urodelen. Leipzic, 1877.—*Dollo, L.*, Note sur le Batracien de Bernissart. (Bull. Mus. Roy. d'Hist. Nat. Belg. vol. III.), 1884. [*Hylaeobatrachus.*]

Small, acutely conical pleurodont teeth (Fig. 229) are present in both jaws, and also on the vomer and palatines.

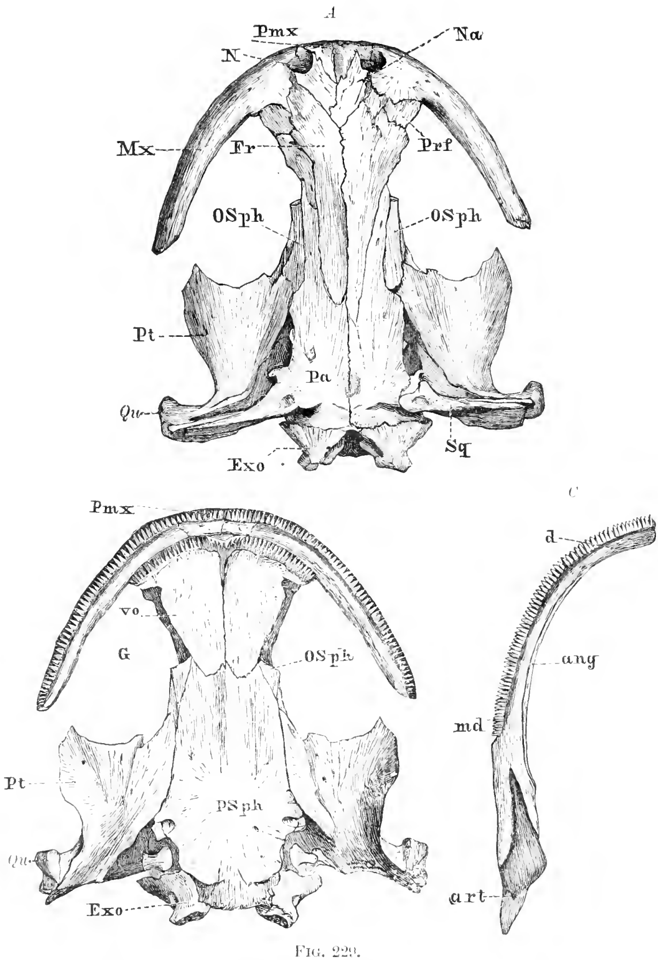


FIG. 229.

Skull of *Cryptobranchus japonicus*, v. d. Hoeven. *A*, Dorsal; and *B*, Palatal aspects. *C*, Lower jaw. *Pmx*, Premaxilla; *Mx*, Maxilla; *Na*, Nasal; *Prf*, Prefrontal; *Fr*, Frontal; *Pa*, Parietal; *OSph*, Orbitosphenoid; *ExO*, Exoccipital; *Qu*, Quadrate; *Sq*, Squamosal; *Pt*, Pterygoid; *PSph*, Parasphenoid; *Vo*, Vomer; *G*, Palatine vacuity; *N*, External nares.

The *pectoral arch* remains for the most part cartilaginous. Only the ventral portion of the scapula, together with the proximal ends of the coracoid and precoracoid unite to form a common osseous plate. In the pelvic arch only the ilium and large ischia are regularly ossified, the pubis remaining, as a rule, cartilaginous. The limbs do not differ essentially from those of Stegocephalians, and the carpus and tarsus exhibit various degrees of ossification.

Urodeles are fresh-water inhabitants, or live in damp shady places on the land, subsisting on worms, gastropods, small aquatic animals, and fish spawn. Fossil remains occur only in fresh-water deposits, and are always very rare. But one Mesozoic skeleton is known, and the few Tertiary genera are scarcely distinguishable from those now living.

Sub-Order A. ICHTHYOIDEA.

Vertebrae amphicoelous, with persistent remnants of notochord. Three pairs of perennial external gills, or in their absence a persistent branchial aperture. Eyes small, without distinct lids. Aquatic habitat.

To this group probably belong the unique *Hylaeobatrachus croyi*, Dollo, from the Wealden of Bernissart, Belgium, earliest known Urodele; and also the giant salamander from the Miocene of Oeningen, Baden (*Andrias scheuchzeri*, Tschudi, Fig. 230), originally described by Scheuchzer as *Homo diluvii testis.* The latter genus attains a length of about 1 m., and differs but slightly from the recent *Cryptobranchus*, v.d. Hoeven (*Megalobatrachus*, Tschudi), of Japan. A somewhat smaller species (*Andrias tschudii*, v. Meyer) occurs in the Miocene lignite of Rott, near Bonn.

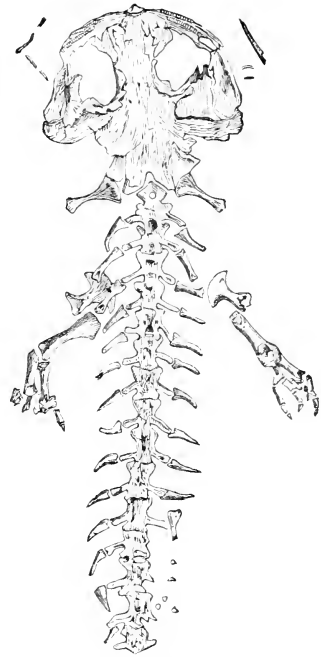


Fig. 230.
Andrias scheuchzeri, Tschudi. Miocene; Oeningen, Baden. 1/6.

Sub-Order B. SALAMANDRINA.

Vertebrae opisthocoelous, completely ossified. Without gills or gill aperture; well-developed eyelids always present. Maxillae present; both jaws toothed.

Several genera resembling recent newts and salamanders occur sparsely in the Upper Eocene (or Oligocene) of Quercy and Sansan in France; Lower Miocene of Rott and Erpel, near Bonn; and the Bohemian Tertiary. Among these may be mentioned *Polysemia*, *Heliarchon*, and *Archaeotriton*, v. Meyer; *Megalotriton*, Zittel; and possibly *Molge* (*Triton*) itself.

Order 4. ANURA. (*Ecaudata, Batrachia salientia.*[1])

Naked, tailless amphibia of compact form, and with usually procoelous vertebrae. Caudal vertebrae coalesced into a slender elongate piece, or coccyx. Pubis and ischium fused. Carpus and tarsus ossified, and the two bones forming the proximal row of the latter greatly elongated. Development by metamorphosis. No gills in the adult. Ilio-sacral attachment extremely pre-acetabular.

The vertebral column consists in the adult of from ten to twelve usually procoelous vertebrae, all of which with the exception of atlas and coccyx bear stout transverse processes. Short ribs are present in the *Discoglossidae*, but are elsewhere wanting in this order. All the post-sacral vertebrae become fused during metamorphosis into a single caudal piece, or coccyx or urostyle (Fig. 231).

The *skull* (Fig. 232) is flattened, with very large orbits. Parietals and frontals are fused into an elongated pair of median elements, in front of which lie the ring-shaped sphenethmoid (or orbitosphenoid) and nasals.

[1] *Meyer, H. von*, Zur Fauna der Vorwelt, pt. 1. Frankfort, 1845.—Also articles in Palaeontogr. vol. II. p. 70; vol. VII. p. 46; and Neues Jahrb. für 1843, pp. 395, 580; 1845, p. 798; 1846, p. 351; 1847, p. 192; 1851, p. 78; 1852, pp. 57, 465; 1853, p. 162; 1858, p. 202; and 1863, p. 187.—*Wolterstorff, W.*, Ueber fossile Frösche insbesondere Palaeobatrachus [with complete bibliography]. (Jahresb. naturw. Vereins Magdeburg für 1885, '86), 1886-87.

The basioccipital region and auditory capsules are ossified; the parasphenoid is inverted T-shaped; and the pterygoid, palatine, and jugal are well developed, the last-named joining the maxilla in front and quadrato-jugal behind. Small, bristle-like pleurodont teeth occur on the jaw-bones and vomer, or may be entirely wanting.

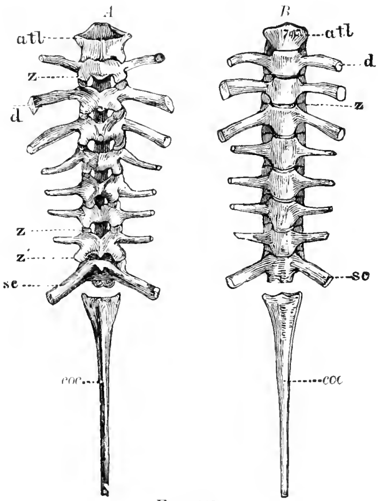


Fig. 231.

Vertebral column of *Rana esculenta*. *A*, Dorsal; and *B*, Ventral aspect. 1/1. *atl*, Atlas; *d*, Transverse process; *z*, Anterior; *z'*, Posterior zygapophyses; *se*, Sacral vertebra; *coc*, Coccyx.

The *pectoral arch* (Fig. 233) is remarkable for its large-sized scapular element, which is commonly divided and incompletely ossified, and joins with the coracoid and precoracoid. The sternum is also large and more or less cartilaginous; of its three ossified portions, the anterior is called the omosternum; the middle piece is the sternum proper; and the posterior, which terminates in a semicircular cartilaginous expansion, is the xiphisternum. Ulna and radius are fused, the two rows of small carpals are ossified, and the manus is provided with four digits.

The three elements of the *pelvic arch* are coössified at the acetabulum on either side to form a single piece, which joins its fellow in a median symphysis. Tibia and fibula are fused, the two bones forming the proximal row of the tarsus (astragalus and calcaneum) are much elongated. and the pes has five digits.

Fossil *Anura* are rare, the oldest clearly identifiable remains occurring in the Eocene of East India (*Oxyglossus pusillus*, Owen sp.) and Wyoming. A few

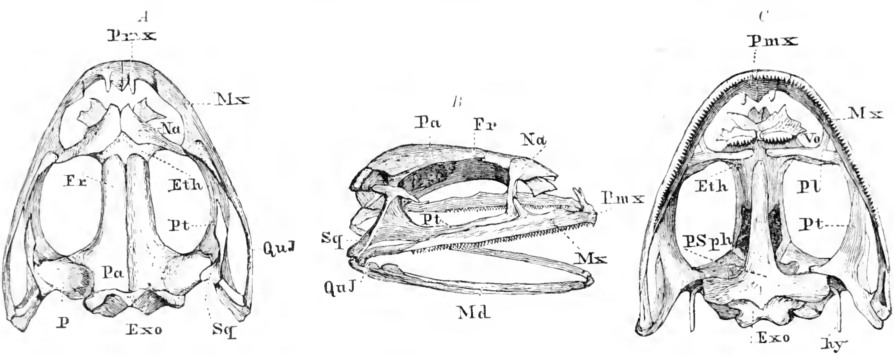


Fig. 232.

Skull of *Rana esculenta*, Linn. *A*, From above. *B*, From the side. *C*, From below. *Pmx*, Premaxilla; *Mx*, Maxilla; *Na*, Nasal; *FrPa*, Fronto-parietal; *Sq*, Squamosal (tympanic); *QuJ*, Quadrato-jugal; *hy*, Hyoid; *md*, Lower jaw; *PSph*, Parasphenoid; *Vo*, Vomer; *Pl*, Palatine; *Pt*, Pterygoid; *Eth*, Ethmoid (Orbitosphenoid); *P*, Petrosal.

genera are known from the Upper Eocene, Oligocene, and Lower Miocene of Southern France, Northern Italy, and Germany, *Rana* and *Palaeobatrachus* being the commonest forms. Phosphatised mummies both of *Rana* and *Bufo* occur in the Eocene (or Oligocene) Phosphorites of Quercy. The Miocene lignites near Bonn yield not only numerous perfect skeletons, but impressions

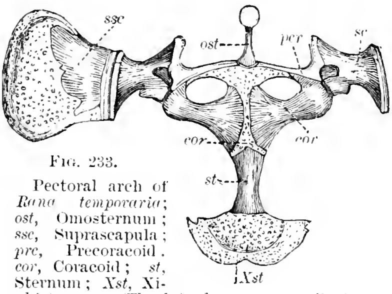


FIG. 233.
Pectoral arch of *Rana temporaria*; *ost*, Omosternum; *ssc*, Suprascapula; *prc*, Precoracoid. *cor*, Coracoid; *st*, Sternum; *Xst*, Xiphisternum. (The dotted parts are cartilaginous.)

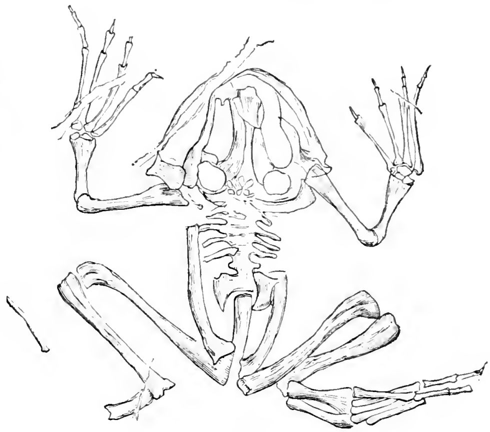


FIG. 234.
Palaeobatrachus grandipes, Giebel. Lignite; Orsberg in Siebengebirge. 2/3 (after Wolterstorff).

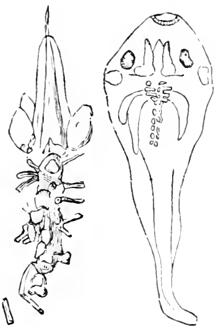


FIG. 235.
Larvae of *Palaeobatrachus fritschii*, Wolterstorff. Miocene Lignites; Kaltennordheim, Rhön. 1/1 (after Wolterstorff and Meyer).

of tadpoles belonging to the genus *Palaeobatrachus*, Tschudi, are plentiful (Figs. 234, 235).

Perfect skeletons of large toads (*Latonia seyfriedi*, v. Meyer; *Pelophilus agassizi*, Tschudi) are known from the Miocene freshwater marls of Oeningen, Baden. The equivalent deposits of Günzburg, Sansan, and Sinigaglia likewise yield remains of tailless Batrachians. Pleistocene *Anura*, like late Tertiary Urodeles, belong exclusively to recent genera.

VERTICAL RANGE OF AMPHIBIANS.

	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Eocene.	Oligocene.	Miocene.	Pliocene.	Recent.
STEGOCEPHALIA												
Lepospondyli . . .			■	■								
Temnospondyli . . .			■	■								
Stereospondyli . . .			■	■	■							
GYMNOPHIONA												■
URODELA												
Ichthyoidea . . .							■	····	·····	■	■	■
Salamandrina . . .								■	■	■	■	■
ANURA								■	■	■	■	■

[The preceding chapter on **Amphibia** has been translated and extended, without altering the classification, by Dr. E. C. Case, of the State Normal School at Milwaukee, Wisconsin. —EDITOR.]

Class 3. REPTILIA.[1]

Cold-blooded, naked, scaly or armoured vertebrates, with exclusively pulmonary respiration, and terrestrial or aquatic in habit. Skeleton completely ossified: embryo with amnion and allantois, development without metamorphosis. Skull with a single basioccipital condyle. Two pairs of limbs usually present; metapodal bones separate.

In external appearance reptiles closely resemble amphibians, but are vastly more differentiated as a class, and are mostly of greater size. Their extremities exhibit great diversity in structure and function. Among the *Pterosauria* the anterior limb is transformed into a volant organ provided with a flexible wing membrane; among Dinosaurs the appendicular skeleton attains a size and ponderosity unsurpassed by the largest land mammals; in marine reptiles the limbs are paddle-shaped; and in most Lacertilians, Theromorphs, Crocodiles, and Dinosaurs the limbs are ambulatory; while the only apodal forms occur among the *Squamata* (snakes and certain lizards).

The *integument* of reptiles is tougher than that of amphibians, and a more or less perfect exoskeleton is often developed in consequence of the ossification of the cutis and cornification of the epidermis. The former may give rise to bony scutes overlapping one another in a tectiform manner, or to larger bony plates with closely applied edges, arranged so as to form a more or less continuous shield, as in tortoises.

The *vertebral column* is always ossified, although remnants of the notochord may persist in the centra. In all cases where both pairs of limbs are present, cervical, dorsal, sacral, and caudal regions are distinguishable, and the dorsal series may be often subdivided into thoracic and lumbar vertebrae. The vertebral centra exhibit all gradations between amphiplatyan, amphicoelous, procoelous, and opisthocoelous; and the union between the centra and their neural arches may be cartilaginous, sutural, or by anchylosis. The neural spines are always ossified. Sometimes they are enormously produced, in other cases (*Chelonia*) laterally expanded and united with dermal plates. The anterior zygapophyses have facettes looking inward and upward which are overriden by the post-zygapophyses of the vertebra immediately in front; and in the *Squamata* and *Dinosauria* the vertebrae are still further conjoined by a median process given off from the anterior (*zygosphene*) or posterior (*hyposphene*) end of the neural arch, and received into a notch of the arch next behind (*zygantrum*) or in front (*hypantrum*). The cervicals generally bear short tranverse processes (*diapophyses*) attached to the sides of the centra, but in the dorsal series these processes are given off from the neural arches. The haemapophyses or "chevron bones" of the caudal series sometimes form true

[1] Literature:

Baur, G., On the phylogenetic arrangement of the Sauropsida (Journ. Morphol. vol. I. No. 1), 1887.—Bemerkungen über die Osteologie der Schläfengegend der höheren Wirbelthiere (Anat. Anz. vol. X. p. 315), 1894.—*Cope, E. D.*, Synopsis of the extinct Batrachia, Reptilia and Aves of North America (Trans. Amer. Phil. Soc. vol. XIV.), 1869.—On the homologies of the posterior cranial arches in the Reptilia (*ibid.* vol. XVII.), 1892.—*Fürbringer, M.*, Zur vergleichenden Anatomie des Brustschulterapparats und der Schultermuskeln. IV. Theil. (Zeitschr. für Naturwissensch. vol. XXXIV.), 1900.—*Hoffmann, C. K.*, Die Reptilien, in Bronn's Classen und Ordnungen des Thierreichs, vol. VI. pt. 3, 1879-89.—*Lydekker, R.*, Catalogue of the fossil Reptilia and Amphibia in the British Museum, vols. I.-IV. London, 1888-90.—*Meyer, H. von*, Zur Fauna, der Vorwelt. Pt. I.-IV. Frankfort, 1845-60.—*Owen, R.*, Report on British fossil Reptilia (Rept. Brit. Assoc. Adv. Sci. 9th Meet. p. 43), 1839. Also *ibid.* 11th Meet. p. 60, 1841.—A History of British fossil Reptiles [Reprint]. London, 1849-84.

haemal arches, or their halves may unite in a single piece. Among existing reptiles there are never more than two sacral vertebrae, but the sacrum of Dinosaurs sometimes comprises as many as ten, and that of Pterosaurs from three to six. When more than three are present, however, they are usually coössified into a single piece (*synsacrum*). Only among Ophidians, Pythonomorphs, and Ichthyosaurs is there no differentiated sacral region. Small cuneiform intercentra (*hypocentra*) may be inserted between the cervicals, caudals, and a portion or all of the dorsals.

All the vertebrae with the exception of the posterior caudals may bear ribs. Cervical ribs are as a rule short, and have the distal end expanded in hatchet-shaped fashion. When a sternum is present, the ribs with which it is connected facilitate the distinction between cervical and dorsal regions. The posterior dorsal ribs have free extremities, and lumbar vertebrae are always non-costiferous. Cervical ribs are usually double-headed, and the centra exhibit two facettes for their attachment. Dorsal ribs may be either single or double-headed, and in Chelonians are remarkable for their union with the broad costal plates of the carapace. Many of the *Reptilia* develop so-called abdominal ribs, which are ossifications of the connective tissue, and correspond to the ventral scales of Stegocephalians.

The *skull* agrees more nearly with that of birds than amphibians in its general features, and the ossification of the primordial cranium is much more complete than in the latter group. The investing membrane bones are so intimately united with true cartilage bones that a distinction is often impossible. The basiocciput articulates with the atlas by means of a single, sometimes tripartite condyle, formed either by the basioccipital alone, or by this bone in conjunction with the exoccipitals. Both the basioccipital and supraoccipital may be excluded from the borders of the *foramen magnum*. Of the bones forming the auditory capsule, the proötic (petrosal) is situated in front of the lateral parts of the occipital region; it occurs as a separate bone, and its front margin is pierced for the third branch of the trigeminus nerve. The opisthotic is often fused with the exoccipital, and the epiotic with the supraoccipital. Besides the usual auditory opening, or *fenestra ovalis*, there is commonly a *fenestra rotunda;* the position of the former is either between the exoccipitals, or between the opisthotic and proötic. At the base of the skull immediately in front of the basioccipital occurs the basisphenoid, a true cartilage bone, in place of a parasphenoid; and this is continued in front by the presphenoid.

Alisphenoids and orbitosphenoids are as a rule wanting, or are replaced by downwardly directed processes of the parietals and frontals. The last-named bones are usually of large size, and may be either paired or unpaired. Applied to the parietals on either side is a large squamosal, which takes part in the posterior cranial border and that of the supratemporal vacuity. The lower end of the squamosal usually abuts against the quadrate, which is always strongly developed, and bears a condyle for articulation with the lower jaw. Sometimes the squamosal is divided, the upper portion being identified as the prosquamosal or supratemporal. In *Sphenodon* the two components later become coalesced.

Among the *Squamata* the quadrate is movably articulated with the squamosal, being united by ligaments only (*Streptostylica*): but among other reptiles it is rigidly attached to the skull by sutures (*Monimostylica*). The quadrato-jugal, when present, lies above and anterior to the quadrate, connecting it with the jugal. The latter joins the hinder end of the maxilla, and forms with it the inferior border of the orbit. The bony arcade separating the orbits and temporal fossae is formed by either the postorbital alone, or by that bone in connection with the postfrontal and jugal. The prefrontals are usually well developed, and adjoin the frontals on either side; sometimes they exclude the latter from the superior border of the orbit, and assist the lachrymals in forming its anterior border. The nasal capsule is roofed by the prefrontals and nasals, and bounded anteriorly by the paired or unpaired premaxillae. The latter, together with the maxillae, complete the front rim of the upper jaw.

The chief modifications of the skull amongst different orders consist in the rearrangement of the bones of the postero-lateral regions into separate bars or arcades, accompanied by the formation of temporal vacuities (Fig. 236).

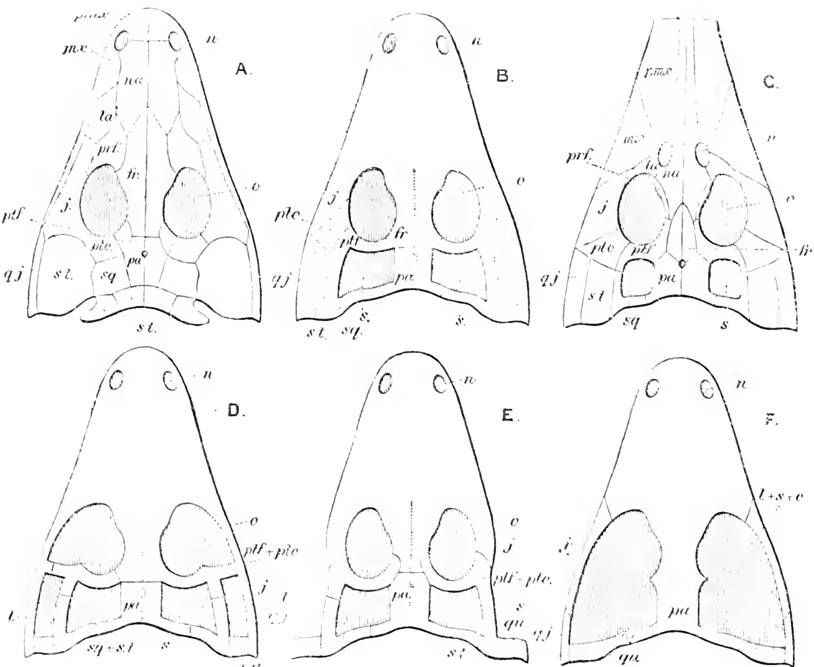


Fig. 236.

Diagram of the cranial roof in a Stegocephalian, various types of Reptiles, and a Bird, showing modifications in the postero-lateral region. *A*, *Mastodonsaurus*, $^1/_{15}$. *B*, Generalised Theromorph or Sauropterygian, passing with slight modification into the Chelonian (sutures dotted to denote inconstancy in fusion of elements). *C*, *Ichthyosaurus*, $^1/_{20}$. *D*, Generalised Rhynchocephalian, Dinosaurian, Crocodilian, or Ornithosaurian. *E*, Generalised Lacertilian. *F*, Generalised Bird. *fr*, Frontal; *j*, Jugal; *l*, Lateral temporal vacuity; *la*, Lachrymal; *mx*, Maxilla; *n*, Narial opening; *na*, Nasal; *o*, Orbit; *pa*, Parietal; *pmx*, Premaxilla; *prf*, Prefrontal; *ptf*, Postfrontal; *pto*, Postorbital; *qj*, Quadrato-jugal; *qu*, Quadrate; *s*, Supratemporal vacuity; *sq*, Squamosal. Vacuities shaded with vertical lines, cartilage bones dotted (from A. S. Woodward).

Among *Theromorpha*, *Sauropterygia*, *Chelonia*, and *Ichthyosauria*, a supratemporal vacuity is produced by the squamosal being thrust outward to form with the quadrato-jugal and jugal a broad arch along the cheek. A further stage is exhibited by the Rhynchocephalians, Dinosaurs, Crocodiles, and Pterosaurs, where the arrangement of the squamosal is the same, but the broad arch of the cheek plates is pierced by a lateral temporal vacuity, leaving a narrow bar above and another narrow bar below. Among Lacertilians this lower bar becomes lost, and finally among Snakes both bars disappear, leaving but one extensive vacuity. For those orders of reptiles distinguished by having two temporal arches, namely, the Rhynchocephalians, Crocodilians, Dinosaurs, and Pterosaurs, Cope has proposed the term **Archosauria.** This group properly includes also the *Squamata*, in which one or both arches have become obsolete.

On the under side of the skull the pterygoid forms the connection between quadrate, basisphenoid, and palatines. It varies considerably in size and shape amongst the different orders, according as the quadrate and maxillo-palatine apparatus are movably or rigidly united with the wall of the skull. In many forms a transverse bone (ectopterygoid) is developed between the pterygoid and maxilla, and a slender column-like bone called the columella or epipterygoid, extends between the parietal and pterygoid (Fig. 253). Sometimes a flat expansion of the maxillae joins with the palatines, and enters with these bones, the vomers, premaxillae, and pterygoids into the formation of a secondary bony palate. The lower jaw is composed, as in Amphibians, of a dentary, splenial, coronoid, angular, and surangular formed from membrane ossifications, and an articular formed from Meckel's cartilage. Crocodiles have the lower jaw as well as many of the cranial bones hollow and pneumatic.

Teeth are wanting only among Chelonians and isolated representatives of other groups. As a rule they occur extensively on the jaw bones, and in some cases also in the palatines, pterygoids, and vomers. The greater number are single-rooted, those with divided roots being very exceptional. The crown consists chiefly of dentine, covered with a layer of enamel; cement enters but slightly into its composition, and vasodentine is entirely wanting. The form is usually sharply conical, either erect or recurved, but there are many other varieties, such as depressed, hemispherical, or even pavement-like; some have bevelled edges, or are chisel- or spade-shaped, and a few are multicuspidate. Pleodont teeth have solid crowns, as contrasted with coelodont, which grow from persistent pulps. *Thecodont* or socketed teeth are inserted in alveoli, *acrodont* fused with the supporting bone along the outer rim or top, and *pleurodont* teeth are developed laterally along the flange-like inner rim of the jaw.

With the exception of Snakes and certain Lacertilians, two pairs of limbs are always present. In the *pectoral arch* the principal bones are the coracoid and scapula, the former usually exceeding the latter in size, and forming either alone or in connection with the scapula the glenoid cavity for the humerus. Clavicular and interclavicular elements may or may not be present, and the same is true of the precoracoid, which occurs usually as an anteriorly directed process of the coracoid. The scapulae are normally directed upward and backward, and are well separated by the clavicular arch when present. The interclavicle (or episternum), may be rhomboidal, cruciform, or T-shaped, and differs from the adjacent bones in being of membranous origin. Posterior to the interclavicle is usually a flat, rhomboidal, or aspidate sternum, to which the anterior dorsal ribs are attached by means of intermediate pieces. Very frequently the sternum is wanting; when present its antero-lateral margin is always applied against the coracoid, and when absent the coracoids unite in a median symphysis or are joined together by ligaments.

The appendicular skeleton is constituted essentially as in Amphibians. In the fore-limb the humerus of some fossil forms is pierced at its distal end by one or two foramina, as in certain mammals; but among living reptiles this character appears only in *Sphenodon*. The ulna sometimes exceeds the radius in length, and is sometimes provided proximally with an olecranon process. The carpus consists always of two rows of bones, of which the proximal contains two or three, and the distal from three to six elements; occasionally these rows are separated by one or two centralia. The bones of the manus undergo excessive modifications correlating with their function. There are commonly from two to five digits, and among Ichthyosaurs even more than five. The third and fourth digits usually possess a larger number of phalanges than the rest. The most generalised type of manus and pes is found among Chelonians.

Numerous modifications occur also in the pelvic region and posterior limb. A sacrum, consisting normally of two vertebrae, is present in all reptiles with the exception of Snakes, Ichthyosaurs, and Pythonomorphs. Among Snakes the pelvis is either entirely wanting, or represented by vestigial ischia; and rudimentary ilia are present among apodal Lizards. All other reptiles have a pelvis composed of the three usual elements, and as a rule they all take part in the formation of the acetabulum. The ilium is often much extended antero-posteriorly. The ischia are generally larger than the pubes, and both pairs converge ventrally in front, and join in median symphyses. A decided bird-like aspect is observed in the pelvis of Dinosaurs, owing to the downward and backward extension of the greatly elongated ischium, and the anterior prolongation of the dorsal part of the ilium. The hind limb closely resembles the fore in most cases. One or two trochanters may occur on the proximal portion of the femur, and there are generally two rows of tarsals. The *Sauropsida* (Reptiles and Birds) differ from mammals in having the ankle-joint between the two rows of tarsals, and never between the tibia and proximal tarsals. Various modifications of the hind limb occur, which are noted in the discussion of the different groups.

Habitat.—Their respiration being exclusively pulmonary, reptiles are adapted to a terrestrial or amphibian existence. Even the small number of marine Chelonians and Lacertilians visit the shores periodically for the purpose of depositing their eggs. Among extinct forms, Ichthyosaurs, Sauropterygians, and Pythonomorphs were truly marine, and provided with paddle-shaped extremities. The majority of fossil reptiles, however, were land forms; some appear to have been arboreal, and the Pterosaurs, as their name implies, were volant, or at least capable of gliding through the air. There is reason to suppose that Dinosaurs were viviparous, as is known to be true of Ichthyosaurs, and some of the former were of bipedal gait.

Over 3500 recent species of reptiles have been described, a number greatly exceeding the known fossil forms. The latter, however, exhibit far greater diversity in structure than living species, and hence a knowledge of their organisation is indispensable for an understanding of the class. The earliest undoubted reptilian remains (*Proterosauria*) are of Lower Permian age, and although not plentiful here, numerous forms are known from the Upper Permian of Europe, North America, and South Africa. The culmination of the class occurred during the Jura-Trias, after which Reptiles steadily declined.

Taxonomy.—The separation between Reptiles and Amphibians was first effected by Blainville in 1816, and approved by Merrem in 1820, but a satisfactory classification was impossible until after the researches of Owen, Huxley, von Meyer, Marsh, Cope, Osborn, Baur, and others had vastly increased our knowledge of fossil forms. Universal agreement does not by any means obtain regarding the limitations of the different groups, but most modern authorities are in favour of recognising nine independent orders, as follows :—*Rhynchocephalia*, *Squamata*, *Ichthyosauria*, *Sauropterygia*, *Theromorpha*, *Chelonia*, *Crocodilia*, *Dinosauria*, and *Pterosauria*. Of these the Permian Rhynchocephalians include the earliest and most primitive forms, and may be regarded in a broad sense as ancestral to all **Archosauria** (or reptiles with two temporal arches), as well as *Aves*.

Order 1. RHYNCHOCEPHALIA.[1]

Lacertiform reptiles with amphicoelous vertebrae, sometimes pierced for the notochord. Upper and lower temporal arcades well defined. Quadrate fixed, and buttressed by the pterygoids, which extend forward to the vomer; premaxillae paired. Mandibular symphysis usually ligamentous; teeth acrodont. Sternum present; sacrum composed of two, or in the Pelycosauria of three vertebrae. Limbs ambulatory, pentadactyle. Dermal armour of corneous scales.

The existing genus *Sphenodon* (*Hatteria*) of New Zealand is the sole survivor of an ancient and primitive order of reptiles which attained its maximum specialisation in the Trias, and whose earliest representatives (*Proterosauria*) resemble the Microsaurian *Stegocephalia* in noteworthy respects. This primitive Permian group also occupies the cleft between *Squamata*, *Crocodilia*, and *Dinosauria*, and is in all probability ancestral to birds through a primitive Dinosaur-avian stem.

The body in Rhynchocephalians is lizard-like, long-tailed, sometimes scaly; the vertebral centra are amphicoelous or amphiplatyan, with persistent notochord, and often with small intercentra (hypocentra). The neural arches are well ossified, and zygapophyses and diapophyses usually conspicuous. With the exception of the anterior cervicals and posterior caudals, all the vertebrae bear strong single-headed ribs. Several or numerous longitudinal series of abdominal ribs occur between the limb girdles, and correspond to the ventral armouring of Stegocephalians.

The *skull* (Fig. 237) is remarkable for the large size of the orbits and temporal vacuities. There are always two temporal arcades, the upper one

[1] Literature:

Baur, G., Palaeohatteria and the Proganosauria (Amer. Journ. Sci. [3], vol. XXXVII. p. 310), 1889.—*Boulenger, G. A.*, On British remains of Homaeosaurus, with remarks on the classification of the Rhynchocephalia (Proc. Zool. Soc. p. 167). 1891.—*Credner, H.*, Ueber Palaeohatteria und Kadaliosaurus (Zeitschr. deutsch. geol. Ges. vol. XL. p. 488), 1888.—*Dollo, L.*, Première note sur le Simaedosaurus d'Erquellinnes (Bull. Mus. Roy. d'Hist. Nat. Belg. vol. III.), 1884. — Sur l'identité des genres Champsosaurus et Simaedosaurus (Bull. Soc. Belg. Geol. vol. V. p. 151). 1891. —*Günther, A.*, Contribution of the anatomy of Hatteria (Phil. Trans. vol. CLVII.), 1867.—*Huxley, T. H.*, On Hyperodapedon, etc. (Quar. Journ. Geol. Soc. vols. XV. p. 435 ; XXV. p. 138 ; XLIII. p. 675), 1859-87.—*Lortet. L.*, Les reptiliens fossiles du bassin du Rhône (Arch. Mus. d'Hist. Nat. Lyon, vol. V.), 1892.—*Meyer, H. von*, Zur Fauna der Vorwelt (vols. III., IV.), 1857-60.—*Seeley, H. G.*, On Proterosaurus (Phil. Trans. vol. CLXXVIII. p. 187), 1887.—*Siebenrock, F.*, Zur Osteologie des Hatteria-Kopfes (Sitzber. Akad. Wiss. Wien, vol. CII. pt. 1), 1893.—*Wagner, A.*, Saurier aus dem lithographischen Schiefer (Abhandl. Bayer. Akad. Wiss. vols. VI., VII., IX.), 1852-61.

being formed by the postorbital and squamosal, and the lower arcade by the quadratojugal and jugal. The latter bone is always fixed, and buttressed by the pterygoids, which extend forwards to the vomer. The brain cavity is of small size, and roofed by the narrow parietals, between which and the pterygoids is a vertical columella (epipterygoid). A parietal foramen is generally present. The paired external nares are almost terminal in position. Vomer, palatines, and pterygoids together form an extensive bony palate. Acrodont teeth occur in regular series on the narrow premaxillae, maxillae, and mandibles, and in some cases the vomer and palatines are also dentigerous. Occasionally the teeth are inserted in shallow alveoli, and very rarely are absent altogether.

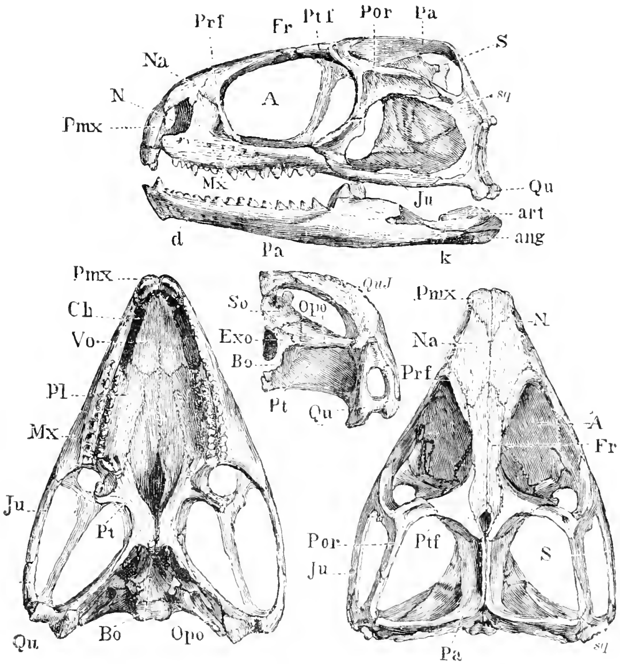


Fig. 237.

Sphenodon punctatus, Gray. Recent; New Zealand. Lateral, palatal, posterior, and superior aspects of skull. 2/3. (*A*, Orbit; *ang*, Angular; *art*, Articular; *bo*, Basioccipital; *ch*, Internal nares; *d*, Dentary; *exo*, Exoccipital; *fr*, Frontal; *ju*, Jugal; *k*, Surangular; *mx*, Maxilla; *N*, External narial opening; *na*, Nasal; *opo*, Opisthotic; *pa*, Parietal; *pl*, Palatine; *pmx*, Premaxilla; *por*, Postorbital; *prf*, Prefrontal; *pt*, Pterygoid; *ptf*, Postfrontal; *qu*, Quadrate; *quj*, Quadrato-jugal; *S*, Supratemporal vacuity; *so* Supraoccipital; *sq*, Squamosal; *vo*, Vomer.)

The *pectoral arch* is incompletely ossified. The scapula is represented by an elongated rectangular bone, and the inner border of the small elliptical coracoids remains cartilaginous. The clavicle is a slender bent rod connecting the scapula with a large rhomboidal or T-shaped interclavicle, which overlies the cartilaginous sternum. The distal end of the humerus is pierced in the fossil forms by an entepicondylar foramen, but in *Sphenodon* both entepicondylar and ectepicondylar foramina or grooves occur. In general the articular surfaces of the humerus, radius, and ulna are not completely ossified. Five distinct elements occur in the distal row of the carpus, and two centralia are often present. The extremities are pentadactylate.

The *pelvic arch* consists of a small, nearly vertical ilium, a discoidal pubis with obturator notch, and a somewhat expanded ischium, which remains separated from the pubis. Both pubis and ischium are imperfectly ossified among the earlier forms. The hinder is somewhat longer than the fore-limb, and resembles that of Lacertilians and Theromorphs.

Sub-Order 1. PROTEROSAURIA. Seeley. (*Proganosauria*, Baur.)

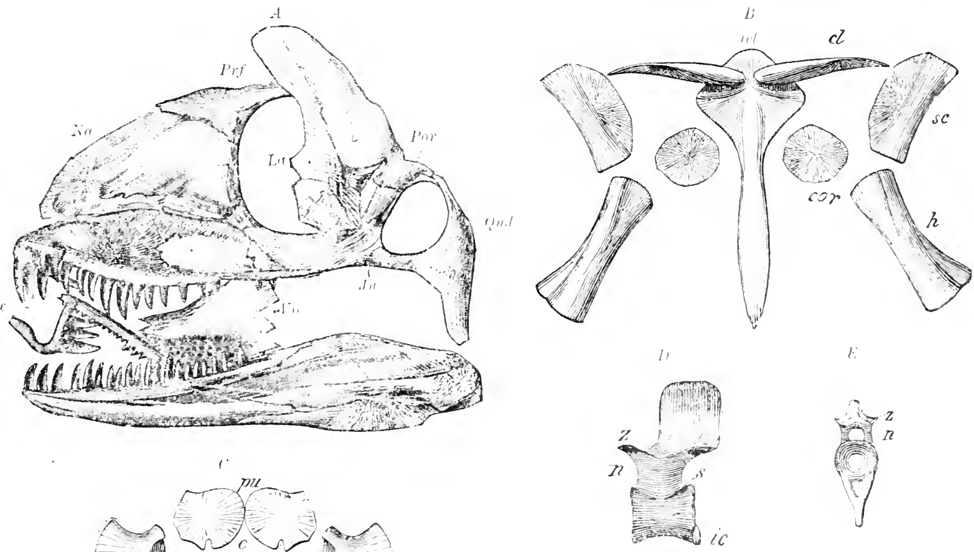
Abdominal ribs small, arranged in several longitudinal series. Pubis and ischium imperfectly fused. Fifth metatarsal not dissimilar from the rest. Marginal teeth in a single uniform series.

The sub-order is of interest as comprising some of the most primitive and most ancient reptiles known to science. They are regarded by many authors as ancestral not only to the *Sphenodon* group, but to all **Archosauria**, or reptiles with two cranial arches. There is much reason to suppose that from these forms also a Dinosaur-avian stem was evolved in the Permian, from which birds have come down to us.

Family 1. Proterosauridae.

Maxillae, premaxillae, and mandibles with a series of large conical teeth, either acrodont or implanted in shallow alveoli, and smaller teeth present on the palatines and vomer. Interclavicle elongate, with a rhombic expansion at its anterior end. Permian and Trias.

Palaeohatteria, Credner (Fig. 238). Body lizard-like, about 25 cm. long. Vertebral centra in the form of delicate constricted amphicoelous cylinders,



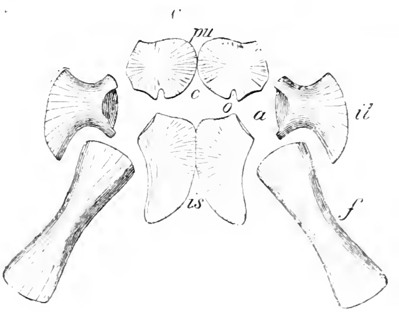


FIG. 238.

Palaeohatteria longicaudata, Credner. Lower Permian; Saxony. *A*, Skull, somewhat distorted, $^1/_1$. *B*, Pectoral arch. *C*, Pelvic arch. *D*, Dorsal vertebra; *E*, Caudal vertebra, anterior aspect. (*a*, Acetabulum; *cl*, Clavicle; *cor*, Coracoid; *f*, Femur; *h*, Humerus; *ic*, Intercentrum; *icl*, Interclavicle; *il*, Ilium; *ju*, Jugal; *la*, Lachrymal; *n*, Pedicle of neural arch; *na*, Nasal; *o*, Obturator notch; *pmx*, Premaxilla; *por*, Postorbital; *prf*, Prefrontal; *pu*, Pubis; *qu*, Squamosal and quadrate; *vo*, Vomer (displaced); *z*, Zygapophysis. Orbit overlaid by displaced facial bones of the right side). (after Credner).

with persistent notochord; small intercentra occur between all in advance of about the sixth caudal, and single-headed ribs borne by all the vertebrae as far as the seventh caudal. Abdominal ribs represented by numerous small oat-shaped scutes. Premaxillae small, with three or four recurved teeth. Inferior border of orbit formed by jugal alone. Digits clawed. Habits probably aquatic, as indicated by the comparatively unossified extremities of limb bones. Lower Permian (Rothliegendes); Niederhässlich, near Bonn.

Kadaliosaurus, Credner. A land form accompanying the preceding; limb bones completely ossified proximally and distally, with spongy interior. Extremities much longer than in *Palaeohatteria;* humerus and femur of equal length, but metacarpals shorter than metatarsals.

Proterosaurus, v. Meyer. Attaining a length of 1·5 m. Vertebral centra completely ossified, and united with their neural arches by suture. Intercentra occur only between the cervical vertebrae, which are elongate, and bear slender ribs. Skull tapering anteriorly, its structure not clearly shown. Hind limb considerably longer than the fore, and distal tarsals less than five in number. Upper Permian (Kupferschiefer) of Thuringia and Hesse, and Magnesian Limestone of Durham, England. *P. speneri*, v. Meyer; *P. lincki*, Seeley.

Aphelosaurus, Gervais; *Haptodus*, Gaudry. Lower Permian; Autun and Lodève, France. *Telerpeton*, Mantell. Supposed Trias of Elgin, Scotland.

Sub-Order 2. PELYCOSAURIA. Cope.[1]

Anterior teeth enlarged, incisor- and canine-like, the remainder conical and molariform; none of the teeth with lateral cusps, but sometimes serrated. Neural spines enormously developed in some genera. Sacrum of three vertebrae. Limbs very short and strong.

Family 1. Clepsydropidae. Cope.

Skull long and narrow, truncated posteriorly. External nares separated, terminal, opening directly into the mouth. Orbits large, round, placed behind the middle of the skull; supratemporal vacuity small. Quadrate small, nearly enclosed by surrounding bones. Anterior incisors and canines of upper jaw much larger than other teeth. Numerous small conical teeth present on palatines, pterygoids, and vomer. Proximal tarsals two in number. Permian.

Clepsydrops, Cope. Neural spines of the lumbar and sacral regions greatly elevated. Intercentra present between the dorsal and caudal vertebrae; anterior ribs double-headed, posterior single-headed. Teeth large, with sharp cutting edges. Permian; Texas, Illinois, and Kansas.

Dimetrodon, Cope. Larger than the preceding, skull upwards of 0·5 m. long, and with similar dentition. Intercentra present between the dorsals; all the ribs double-headed from the axis on. Neural spines rising from the axis until in the dorsal region they are many times longer than the diameters of the centra. Permian; Texas.

[1] Literature:
Baur, G., and *Case, E. C.*, On the morphology of the skull of the Pelycosauria and the origin of the Mammals (Anat. Anz. vol. XIII. p. 109), 1897.—The history of the Pelycosauria, with a description of the genus Dimetrodon (Trans. Amer. Phil. Soc. vol. XX. pt. 1), 1899.—*Case, E. C.*, The Vertebrates from the Permian Bonebed of Illinois (Journ. Geol. vol. VIII. p. 698), 1900.

Naosaurus, Cope (Fig. 239). Differs from the last in that the neural spines bear transverse processes. Permian; Texas and Bohemia.

Embolophorus, *Theropleura*, *Archaeobolus*, *Lysorophus*, Cope. Permian: Texas. *Stereorachis*, Gaudry; *Callibrachion*, Boule and Glengeaud. Permian; Autun, France. Known by imperfect remains apparently allied to *Dimetrodon*.

Sub-Order 3.
RHYNCHOCEPHALIA VERA.

Abdominal ribs reduced to three relatively large longitudinal series; pubis and ischium well ossified; fifth metatarsal very much shortened, and somewhat expanded. Marginal teeth in one or more uniform series.

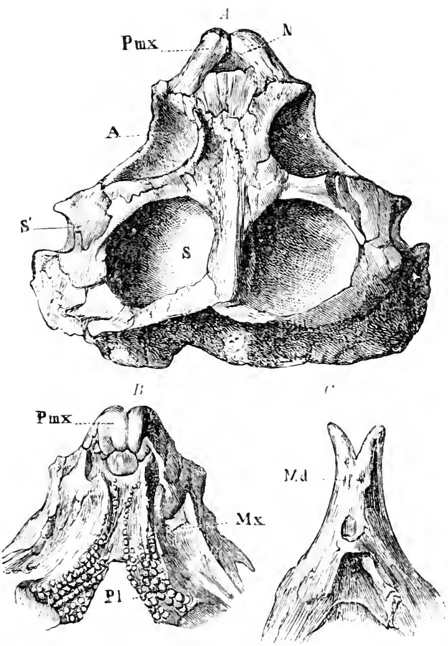


FIG. 240.

Hyperodapedon gordoni, Huxley. Upper Trias; Elgin, Scotland. *A*, Superior aspect of skull, 1/4. *B*, Palate. *C*, Mandibular symphysis from below. *a*, Orbit; *md*, Mandibular fork; *mx*, Maxilla; *n*, Nasal; *pl*, Palatine; *pmx*, Premaxilla; *s*, Supratemporal vacuity; *s'*, Lateral temporal vacuity). (after Huxley).

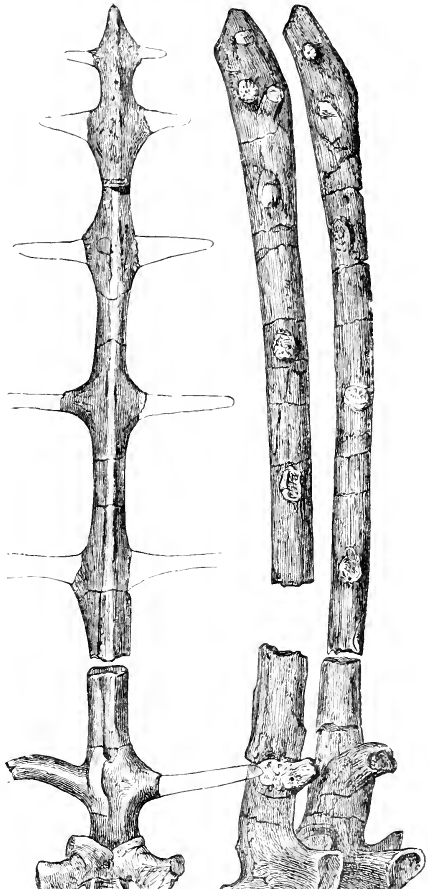


FIG. 239.

Naosaurus claviger, Cope. Permian; Texas. Dorsal vertebrae, anterior and lateral aspects, 1/4 (after Cope).

Family 1. Rhynchosauridae.

Skull short and broad, with a beak-like rostrum formed by the downwardly curved, slender, toothless premaxillae. Mandibles with a single, and maxillae and palatines with several longitudinal series of depressed conical teeth. External nares confluent. Trias.

Hyperodapedon, Huxley (Fig. 240). Body stout, upwards of 2 m. long.

Mandibular rami fused in a long symphysis, which is slightly forked at its toothless anterior end; posteriorly with a single series of obtuse teeth. Parietal foramen and intercentra apparently wanting. Cervical vertebrae opisthocoelous; limbs imperfectly known. Supposed Trias of Elgin, Scotland, and Central India.

Rhynchosaurus, Huxley. Smaller and with fewer teeth than the preceding; mandible toothless or with minute teeth, maxillae with a single row, and palatines with a double row of small teeth. Vertebrae amphicoelous; abdominal ribs well developed. Upper Trias; Shropshire and Warwickshire.

Family 2. **Mesosauridae.**[1]

Small lacertiform reptilia, with very numerous, extremely long and acicular teeth in the upper and lower jaws. Vertebral centra amphicoelous, with remnants of the notochord. Cervical vertebrae with short hatchet-shaped ribs. Dorsal ribs single-headed, very thick. Ventral ribs well developed. Tarsus with two rows of small bones. Extremities with five toes.

Mesosaurus, Gervais (*Ditrochosaurus*, Gürich). Karoo formation of South Africa.

Stereosternum, Cope, from the Permian or Lower Trias of Brazil is possibly identical with, in any case very similar to Mesosaurus.

Family 3. **Champsosauridae.**

Skull with elongated gavial-like snout. A single series of large conical teeth present on the jaw-bones and palatines, and irregular longitudinal series of minute teeth on the vomers, palatines, and pterygoids. External nares terminal and confluent. Mandibular rami suturally united at the symphysis. Only two intercentra present at anterior end of the neck. Vertebral centra completely ossified, slightly biconcave, or amphiplatyan, and suturally united with their neural arches. Cretaceous and Lower Eocene.

Champsosaurus, Cope (*Simaedosaurus*, Gervais). Large aquatic reptiles attaining a length of 2·5 m. Premaxillae elongated into a gavial-like rostrum; cervical ribs short and double-headed; abdominal ribs stout. Humerus with ectepicondylar groove instead of foramen. Known by fragmentary remains from the Laramie Cretaceous, and Lower Eocene of the United States, and by complete skeletons from the Lower Eocene of France and Belgium.

Family 4. **Sauranodontidae.**

Small long-tailed Rhynchocephalia with edentulous jaws and beak-like rostrum. Temporal fossae small, parietal foramen wanting, postorbital very large, external nares undivided. Vertebrae well ossified; second sacral rib distally divided; abdominal ribs stout. Fore-limb shorter than the hind, both pentadactylate. Dermal scales rectangular. Upper Jura.

Sauranodon, Jourdan. This, the solitary genus, is known by perfect skeletons from the Upper Jura of Cerin, France. *S. incisivus*, Jourdan, attains a length of about 0·7 m.

[1] *Geinitz, H. B.*, Sur Stereosternum tumidum, Cope (Ann. Soc. Geol. Belg. vol. XXV. *bis* p. 35), 1900.—*Woodward, A. S.*, On a new specimen of Stereosternum (Geol. Mag. [4], vol. IV. p. 145), 1897.

Family 5. **Sphenodontidae.**

Vertebrae amphicoelous, sometimes with persistent notochord; intercentra present in cervical and caudal regions. Premaxillae each with a small pointed tooth. A single series of depressed, triangular, acrodont teeth present on maxillae, mandibles, and outer edge of the palatines; vomer toothless. External nares separated; interclavicle T*-shaped; dermal scales subrectangular.* Upper Jura to Recent.

Homaeosaurus, v. Meyer (*Sapheosaurus*, v. Meyer), (Fig. 241). Attaining a length of between 20 and 40 cm., and differing from the recent *Sphenodon* in that intercentra are absent between the dorsal vertebrae, ribs without uncinate processes, and humerus not pierced by entepicondylar foramen. Mandibular rami united at the symphysis by ligaments; second sacral rib bifid distally. Upper Jura (Lithographic Stone); Bavaria, and Cerin, France. Kimmeridgian of Hanover, and Purbeckian of England. *H. maximiliani*, v. Meyer.

Ardeosaurus, *Acrosaurus*, v. Meyer; *Euposaurus*, Jourdan. Upper Jura (Lithographic Stone); Bavaria, and Cerin, France.

Pleurosaurus, v. Meyer (*Anguisaurus*, Münst.; *Saurophidium*, Jourdan). Body serpentiform, upwards of 1·5 m. long, the tail forming one-third the total length. Snout tapering in front. Presacral vertebrae with stout single-headed ribs; abdominal ribs well developed. Fore-limbs shorter than the hinder pair. Upper Jura (Lithographic Stone); Bavaria, and Cerin, France. *P. muensteri*, Wagner.

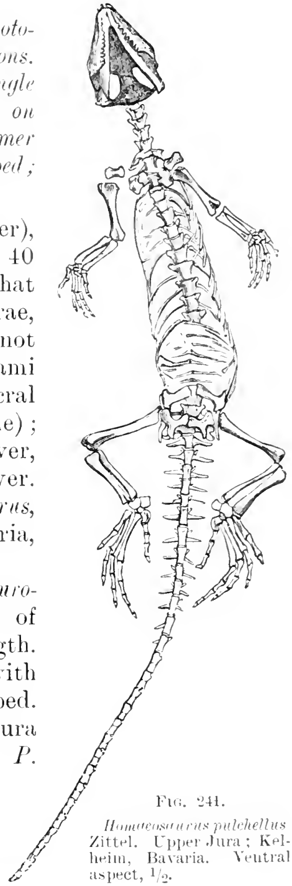


Fig. 241.
Homaeosaurus pulchellus Zittel. Upper Jura; Kelheim, Bavaria. Ventral aspect, 1/2.

Sphenodon, Gray (*Hatteria*, Gray). Inferior border of the large orbits formed by maxilla; external nares divided; a single tooth on either side of the premaxillary beak; intercentra present between all the vertebrae, humerus with both entepicondylar and ectepicondylar foramina or grooves. Recent, inhabiting certain islands off New Zealand.

VERTICAL RANGE OF THE RHYNCHOCEPHALIA.

Divisions.	Permian.	Trias.	Jura.	Cretaceous.	Eocene.	Neocene.	Recent.
I. Proterosauria	—	—					
II. Pelycosauria	—						
III. Rhynchocephalia Vera.							
1. *Rhynchosauridae*		—		?			
2. *Mesosauridae*	—	—					
3. *Champsosauridae*				—	—		
4. *Sauranodontidae*			—				
5. *Sphenodontidae*			—				—

Order 2. SQUAMATA. (Lepidosauria, Streptostylica.)[1]

Body elongate, covered with corneous, or more rarely with dermal scales or scutes. Quadrate movably attached to the skull; the lower temporal arcade always, and upper temporal arcade frequently wanting. Palatal vacuities large, pterygoids not in contact with vomer; external nares separated; teeth acrodont or pleurodont. Vertebrae well ossified, usually procoelous, rarely amphicoelous; sacral vertebrae not more than two in number. Post-cervical intercentra and abdominal ribs wanting; dorsal ribs single-headed. Limbs adapted for ambulation or natation, absent only among Ophidia and a few Lacertilia.

This order comprises Lizards, Snakes, and two extinct groups of aquatic reptiles,—*Dolichosauria* and *Pythonomorpha*,—the earliest clearly recognised members of which occur in the Cretaceous. The *Squamata* are evidently very closely allied to Rhynchocephalians, and in all probability their origin is to be traced to that group.

Sub-Order 1. DOLICHOSAURIA.

Small, aquatic, serpentiform reptiles, with well-developed lizard-like limbs and limb-girdles. Vertebrae procoelous, and articulated both by zygapophyses and zygosphene-zygantrum arrangement. Sacral vertebrae not anchylosed. Mandibles with sutural symphysis. Teeth pleurodont.

The family *Dolichosauridae* comprises a few genera from the English Chalk and the Upper Cretaceous of Istria and Dalmatia, the largest of which attain a length of between two and three metres. *Dolichosaurus*, Owen, has no less than seventeen cervical vertebrae and large hollow ribs. *Acteosaurus*, *Adriosaurus*, *Aigialosaurus*, *Carsosaurus*, *Pontosaurus*, and *Mesoleptos* are allied Istrian genera. Most of the detached vertebrae of Cretaceous age, commonly classed as Ophidian, are doubtless Dolichosaurian. Like the Pythonomorphs, these forms probably passed away without leaving any post-Cretaceous descendants.

Sub-Order 2. PYTHONOMORPHA. Cope.[2]

Large marine reptiles with elongate body and two pairs of paddle-shaped appendages. Skull lizard-like, elongate, depressed; superior temporal arcade and pineal

[1] *Cope, E. D.*, Crocodiles, Lizards, and Snakes of North America (Ann. Rept. Smithsonian Inst., 1898), 1900.

[2] Literature:

Baur, G., Morphology of the skull of the Mosasauridae (Journ. Morphol. vol. XII., No. 1), 1892. —*Cope, E. D.*, The Reptilian orders of Pythonomorpha and Streptosauria (Proc. Boston Soc. Nat. Hist. vol. XII. p. 250), 1869.—The Vertebrata of the Cretaceous Formations of the West (Rept. U.S. Geol. Surv. Territ. vol. II.), 1875.—Professor Owen on Pythonomorpha (Bull. U.S. Geol. Surv. Territ. vol. IV. p. 299), 1878.—*Cuvier, G.*, Sur le grand animal fossil de la craie de Maestricht (Ann. Mus. d'Hist. Nat. vol. XII.), 1808.—*Dollo, L.*, Note sur l'ostéologie des Mosasauridae (Bull. Mus. Roy. d'Hist. Nat. Belg. vol. I.), 1882.—*Ibid.* vol. IV., 1885.—Nouvelle Note, etc. (Bull. Soc. Belg. de Geol. Pal. et Hydrol. vols. III.-VII.), 1889-94.—*Gibbes, R. W.*, A Memoir on Mosasaurus, etc. (Smithson. Contr. Knowl. vol. II.), 1864.—*Goldfuss, A.*, Der Schädelbau des Mosasaurus (Nova Acta Acad. Caes. Leop. Car. nat. cur. vol. XXI.), 1843.—*Leidy, J.*, Cretaceous Reptiles of the United States (Smithson. Contrib. Knowl.), 1864.—Extinct Vertebrate Fauna of the Western Territories (Rept. U.S. Geol. Surv. Territ. vol. I.), 1873.—*Marsh, O. C.*, Characters of Mosasauroid Reptiles (Amer. Journ. Sci. [3], vol. I.), 1871.—*Ibid.* vol. III. (1872); and XIX. (1880).—*Merriam, J. C.*, Die Pythonomorpha der Kansas Kreide (Palaeontogr. vol. XLI.), 1894.—*Osborn, H. F.*, A complete Mosasaur Skeleton (Mem. Amer. Mus. Nat. Hist. vol. I. pt. 4). 1899.—*Owen, R.*, On the *foramen present; premaxillae and nasals fused into a simple rostrum; quadrate large, perforate, and movably attached to squamosal and prosquamosal; parietal unpaired and joined to the supraoccipitals and proötics by decurved lateral processes. Mandibular rami united at the symphysis by ligament, and with a movable articulation behind the middle of each ramus. Teeth large and conical, fixed by tumid bases in shallow alveoli of the jaw-bones and pterygoids. Sclerotic ring present. Vertebrae procoelous, cervicals with hypapophyses. Sacrum wanting; sternum probably never ossified; interclavicle (episternum) sometimes present, but no clavicular arch. Limb-bones short, but the digits are lengthened by an increased number of phalanges, the ungual ones clawless.*

The *vertebral column* comprises 115-130 or perhaps more procoelous vertebrae, and is sometimes divisible into cervical, dorsal, lumbar, and caudal regions. The distinction between dorsal and lumbar series is not very decided, however, except that the latter bear shorter ribs. The transverse processes are short and thick in the precaudal vertebrae for the attachment of single-headed ribs; in the caudals they are flattened and elongated but not costiferous, and become obsolete at about the middle of the tail. The neural arches are always, even in young individuals, thoroughly coössified with their centra; the neural spines are of moderate length, but sometimes notably elongated in the posterior region of the tail. The zygapophyses are strong in the cervical and anterior thoracic region, but become weaker and finally disappear in the tail. Y-shaped haemapophyses or chevron bones are present in all the caudals with the exception of the first five or more, to which the name "pygals" has been given; each chevron articulates only with its own centrum. The atlas is composed of a wedge-shaped intercentrum below, and two lateral pieces or neuropophyses, as in lizards, its centrum being represented by the odontoid process of the axis. A wedge-shaped intercentrum occurs between the atlantal intercentrum and the axis. The axis and five following cervicals bear each a more or less stout exogenous hypapophysial process, to the extremity of which is attached a small, free epiphysis, corresponding morphologically to an intercentrum (Fig. 242). This is wanting in the last cervical, and the process itself is rudimentary.

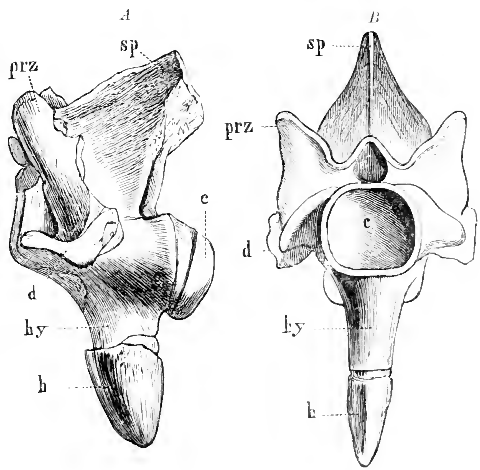


Fig. 242.

Clidastes stenops, Cope. Upper Cretaceous; Kansas. Anterior cervical vertebrae. *A*, From the side. *B*, From in front, 1/2. (*c*, Centrum; *d*, Transverse process; *h*, Hypapophysial epiphysis or intercentrum; *hy*, Hypapophysis; *prz*, Prezygapophysis; *sp*, Neural spine), (after Cope).

The *skull* (Figs. 243, 244) resembles that of *Varanus* more nearly than that of other living reptiles. The parietals, frontals, and pre-

rank and affinities of the Mosasauridae (Quar. Journ. Geol. Soc. vol. XXXIII. p. 682), 1877.—*Ibid.* vol. XXXIV. (1878), p. 748.—*Williston, S. W.*, On Mosasaurs, etc. (Kansas Univ. Quar. vol. ii. p. 83), 1893.—*Ibid.* vol. III. (1895), p. 165.—University Geol. Surv. Kansas. vol. IV. Topeka, 1898. —*Williston, S. W.*, and *Case, E. C.*, Kansas Mosasaurs (Kansas Univ. Quar. vol. I. p. 1), 1892.

maxillae are all unpaired, as are also the nasals, which are fused with the premaxillae. The supratemporal vacuity is bounded externally by the prosquamosal and postorbital, which form a narrow arcade. The squamosal is intercalated between the exocciptal (=parocciptal, Baur) and the prosquamosal, and sends a slender process inwards between the exoccipital and proötic, extending nearly as far as the brain cavity. The suture between the postorbital and postfrontal is often obliterated. Superciliary plates have not been observed, and are often functionally replaced by the horizontally expanded prefrontals. The jugal unites with a descending process of the postfrontal, and these two bones together with the prefrontal completely enclose the orbit. There is a complete parietal arch formed by a slender process of the parietal uniting with a process of the squamosal.

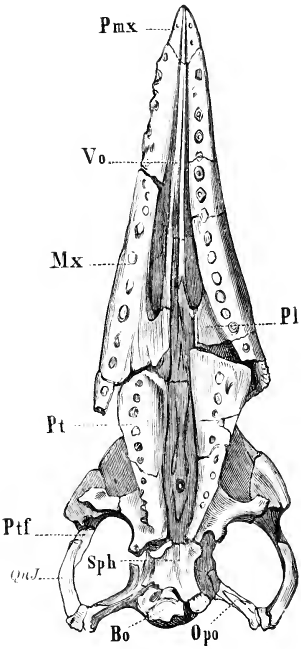


FIG. 243.

Clidastes propython, Cope. Upper Cretaceous; Kansas. Palatal aspect of skull, partly restored. (*bo*, Basioccipital; *mx*, Maxilla; *pl*, Palatine; *pmx*, Premaxilla; *pt*, Pterygoid; *ptf*, Postorbito-frontal; *opo*, Supratemporal; *quj*, Squamosal; *sph*, Basisphenoid; *vo*, Vomer.)

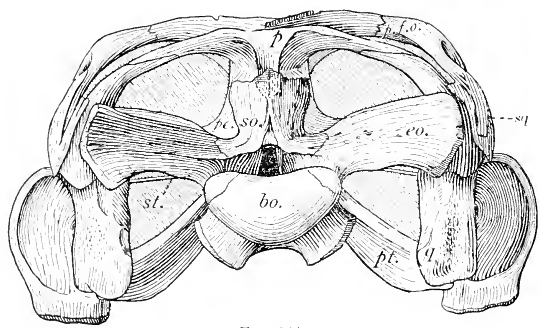


FIG. 244.

Platecarpus coryphaeus, Cope. Upper Cretaceous; Kansas. Posterior aspect of skull, $^1/_4$. (*bo*, Basioccipital; *eo*, Exoccipital; *p*, Parietal; *pe*, Proötic; *pfo*, Postorbito-frontal; *pt*, Pterygoid; *q*, Quadrate; *so*, Supraoccipital; *sq*, Squamosal; *st*, Stapes), (after Williston.)

The quadrate (Figs. 245, 246) is relatively large, and movably articulated with the squamosal and prosquamosal. Its antero-superior margin is dilated into a broad thin plate, and its posterior margin is notched or perforated for the auditory meatus. This opening is either partially or completely enclosed posteriorly by the stout suprastapedial process, which is especially characteristic of the Mosasaur quadrate. On the concave inner side of the quadrate, near the upper part of the meatal notch, is a small pit for the lodgment of the outer end of the stapes. The quadrate exhibits wide variation in form and size amongst the different genera.

The transverse bone, or ectopterygoid, is always small, and joins the pterygoid and jugal only. A slender columella, or epipterygoid, is present in all cases. The mandibular rami were united at the symphysis by ligaments. Somewhat back of the middle of each ramus, between the angular and splenial, and the dentary and surangular, there is a movable articulation permitting of a wide distension of the jaws.

A single series of large conical teeth occurs in both upper and lower jaws, those of the pterygoid being inferior to the rest in size. The crown often exhibits slight anterior and posterior carinae, and may be bevelled into several longitudinal facettes; and the enamelled surface may be either smooth or

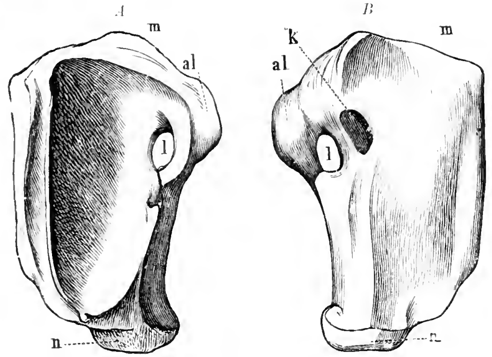


FIG. 245.

Mosasaurus camperi, v. Meyer. *A*, Outer; and *B*, Inner aspect, $^1/_4$. (*al*, Suprastapedial process; *k*, Stapedial pit; *l*, Meatus; *m*, Superior margin; *n*, Inferior margin), (after Owen.)

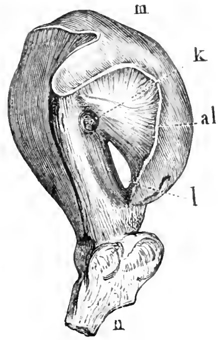


FIG. 246.

Clidastes propython, Cope. Quadrate, inner aspect, $^2/_3$. (Lettering as in Fig. 245), (after Cope).

delicately striated. All the teeth are fixed by tumid osseous bases in shallow pits of the supporting bone. Successional teeth arise alongside the functional ones, and gradually displace them by pressure against the crown on the inner side.

The *pectoral arch* (Fig. 247) exhibits a rather large and flattened coracoid, the articular border of which is thickened and divided into two facettes

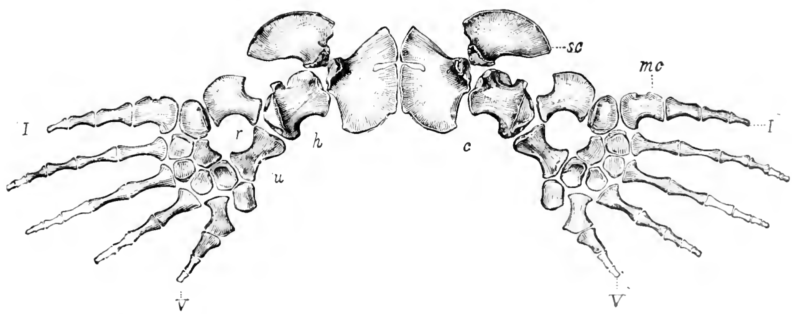


FIG. 247.

Clidastes velox, Marsh. Pectoral arch, dorsal aspect, $^1/_5$. (*c*, Coracoid; *h*, Humerus; *mc*, Metacarpus; *r*, Radius; *sc*, Scapula; *u*, Ulna; I-V, Digits), (after Marsh).

meeting at an obtuse angle, while the thin inner edge is rounded, and often incised by a deep notch or emargination. There is a small coracoid foramen situated toward the articular border. Posteriorly the coracoids meet the sternum, which was probably never ossified, but composed of calcified cartilage, quite like the sternal ribs. The coracoids are separated from each other by a broad epicoracoidal expanse of cartilage. The scapula is placed as in Rhynchocephalians; a slender interclavicle (episternum) is present, but clavicles are wanting. The humerus is short and stout, its articular ends expanded, and the distal end with two facettes for the bones of the second segment. Of the latter the radius is distally expanded. The carpals vary in number from seven (arranged in two rows) in *Clidastes* and *Mosasaurus*, to one or two rudimentary ossicles in *Tylosaurus*. There are five metacarpals, differing in shape amongst the various genera, and supporting a variable number of phalanges; these last being comparatively few in *Clidastes* and *Mosasaurus*, and as many as eleven or twelve in the paddles of *Tylosaurus*. None of the digits are clawed.

The *pelvic arch* (Fig. 248) is more weakly developed than the pectoral. The ilium is a slender rod-shaped bone, its superior end free or loosely attached to the single vertebra which functions as a sacrum. The pubes probably do not meet in a ventral symphysis, but the ischia are joined along

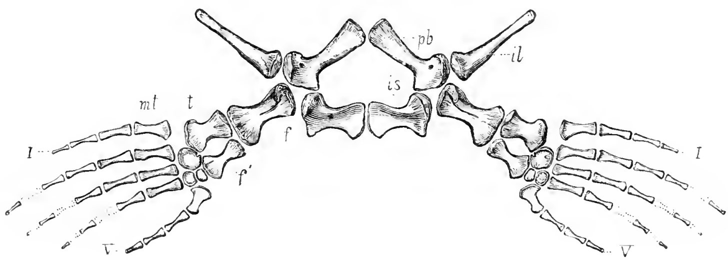


FIG. 248.

Platecarpus simus, Marsh sp. Upper Cretaceous; Kansas. Pelvic arch and paddles, $^1/_{12}$. (*f*, Femur; *f′*, Fibula; *il*, Ilium; *is*, Ischium; *mt*, Metatarsus; *pb*, Pubis; *t*, Tibia; I-V, Digits), (after Marsh).

an extensive articular surface. The bones of the hind limb resemble those of the fore, but are more slender, and somewhat smaller. There are probably never more than three tarsals, and sometimes only one. Four or five digits are developed, with a variable number of phalanges. As a rule the posterior paddles are smaller than the anterior pair.

The limbs of Pythonomorphs and Cetaceans furnish an excellent illustration of the influence of environment in producing analogous structures among widely divergent groups. As a result of their complete adaptation for an aquatic existence, Mosasaurs and whales have developed a very similar form of body. Most of the Pythonomorphs were of large size, and enjoyed a wide distribution, their remains being known from the Upper Cretaceous of Europe, North and South America, and New Zealand.

The Pythonomorphs were covered externally with scales very similar in size and structure to those of *Varanus*. These scales have been found impressed upon the bones of the skull, indicating the absence of corneous plates. There were no dermal ossifications of any kind. Small or medium-sized fishes have been observed in the fossilised stomach contents in several instances.

The earliest discovered cranium, found in the Maestricht Chalk in 1780, was mistaken for that of a Cetacean or Crocodilian until Cuvier demonstrated its remarkable similarity to the skull of *Varanus*. Owen united Mosasaurs with lizards under the designation of *Lacertilia natantia*. The name *Pythonomorpha* was proposed in 1869 by Cope, who regarded the group as intermediate between snakes and lizards. It is argued by Dollo and Williston, however, that Pythonomorphs could not have been ancestral to the modern *Squamata*, since it is impossible to suppose that forms which became so highly specialised and completely adapted to an aquatic existence, should have ever again reverted to a generalised condition, and reassumed terrestrial habits. Pythonomorphs arose undoubtedly from land animals, and may have sprung from Dolichosaurian ancestors; but they appear to have passed completely out of existence near the end of the Cretaceous, without leaving any progeny. Their extreme differentiation is attested by the loss of a sacrum, multiplication of phalanges, degeneration of the hind paddles, development of a mandibular joint, and other characters, of which no heritage remains amongst modern *Squamata*.

Family 1. **Mosasauridae.**

This family, with the characters of the sub-order, comprises three rather divergent groups, which are considered of sub-family value. Restricted to the Upper Cretaceous.

Sub-Family A. Tylosaurinae. Williston.

Hind limb functionally pentadactyle. Trunk short, tail proportionately long. Premaxillae produced into a long rostrum in advance of the teeth; quadrate with short suprastapedial process. Carpus and tarsus almost wholly unossified; phalanges numerous. Vertebrae without, or with very rudimentary zygosphenes.

Tylosaurus, Marsh (*Liodon*, Cope; *Macrosaurus*, Owen; *Rhinosaurus*, Marsh). Skull 0·7 to over 1 m. long. Superior surface of parietal smooth and produced to the posterior margin in the median line, with nearly parallel sides; foramen at its anterior margin. Postfrontal and prefrontal meeting on the superior border of the orbit; quadrate stout, with very short suprastapedial process; maxilla with about thirteen large teeth. One or two carpal and tarsal bones present, not articulating with adjacent elements. Coracoid not emarginate; limbs about equally developed; phalanges numerous; fifth digit elongate. Haemapophyses loosely articulated; no zygosphenes. Niobrara Group; Kansas, New Mexico, and Texas. *T. proriger*, *T. dyspelor*, Cope.

Hainosaurus, Dollo. Skull upwards of 1·5 m. long. Frontal broad; prefrontal and postfrontal meeting over the orbit; teeth of unequal size. Carpals reduced in number; phalanges fewer than in *Tylosaurus*, and paddles relatively larger. Haemapophyses loosely articulated; cervicals with small zygosphenes. Upper Cretaceous; Belgium.

Sub-Family B. Platecarpinae. Williston.

Hind limb functionally pentadactyle. Trunk short, tail proportionately long. Premaxillae short, very obtuse, and projecting but little in front of the teeth. Quadrate large, with a long suprastapedial process. Carpus and tarsus imperfectly ossified. Vertebrae with rudimentary (or functional?) zygosphenes. Interclavicle probably present in all forms.

Platecarpus, Cope (*Lestosaurus*, Marsh; ? *Holcodus*, Gibbes), (Figs. 248-250). Total length about 5 m., of which the skull forms one-eighth. Superior surface of parietal small, triangular, not reaching beyond the middle of the bone; large oval foramen at its anterior border. External nares much dilated anteriorly. Quadrate large, with prominent suprastapedial process extending below the middle of the bone; opening for the auditory meatus large, not entirely enclosed. Teeth slender and recurved, facetted on the outer side, striate on the inner; maxillae with about twelve, and pterygoid ten to twelve teeth. Coracoid deeply emarginate on inner border. Four carpals and three tarsals present, closely articulating. Fifth digit shorter than the fourth, and divergent. Chevron bones large, loosely articulated. Abundant and represented by numerous

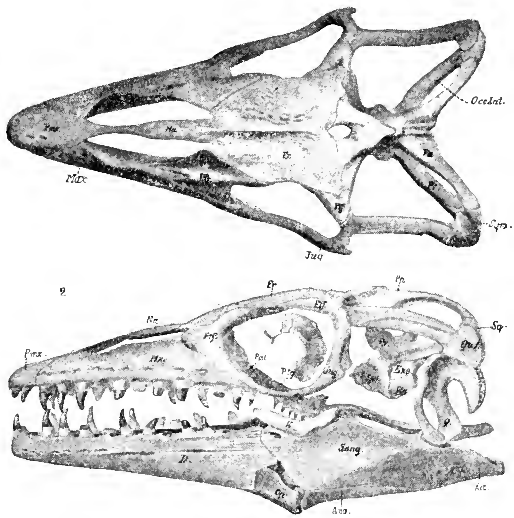


FIG. 249.

Platecarpus coryphaeus, Cope. Upper Cretaceous; Logan County, Kansas. Skull, superior and lateral aspects, $^1/_7$ (after Merriam).

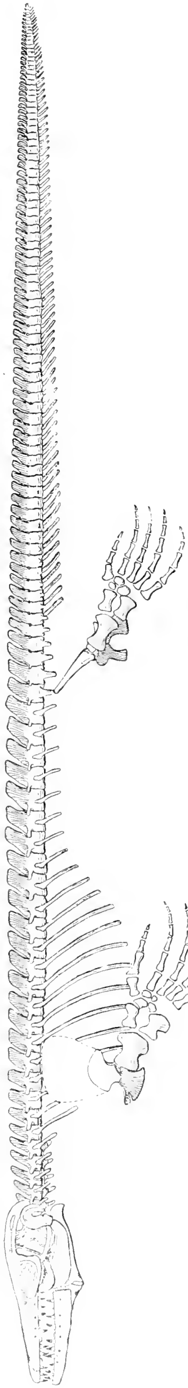


FIG. 250.

Platecarpus coryphaeus, Cope. $^1/_{30}$. Restored after Williston.

species in the Upper Cretaceous of Kansas, Colorado, Texas, North Dakota, and France.

Holosaurus, Marsh. Very similar to the preceding, except that the coracoids are not emarginate; there are no zygosphenes in the only known specimen. Kansas.

Plioplatecarpus, Dollo (*Oterognathus*, Dollo). Similar to *Platecarpus*, but with smaller chevron bones. Quadrate with large meatal opening. Mandible slender. coronoid rudimentary. Teeth long and slender, facetted, and striate. Danian of Maestricht, and Upper Senonian of Belgium.

Prognathosaurus, Dollo. Skull about 0·6 m. long. Pterygoids nearly as large as the maxillae, and with very powerful teeth. The large suprastapedial process of the quadrate coössifies with the infrastapedial process, and encloses an oval foramen. A wide canal present in lower part of the basioccipital. Mandible strong, upper edge concave, coronoid process prominent. Coracoid non-emarginate; chevrons loosely articulated. Brown Phosphate Chalk; Belgium.

Brachysaurus, Williston. Frontal large and broad; no median basioccipital canal. Suprastapedial process of quadrate coössified with the infrastapedial. No zygosphenes; chevrons fused with their centra. Possibly identical with preceding genus. Ft. Pierre Cretaceous; South Dakota.

Phosphorosaurus, Dollo. Imperfectly known. Frontal very narrow, with nearly parallel sides, and taking part in the superior border of the orbit. Parietal small; its exposed surface triangular, and with very large foramen at its front margin. Suprastapedial process much elongated and united with the infrastapedial, enclosing an elongated meatal opening. Tympanic cavity extended and shallow. Upper Cretaceous; Belgium.

Taniwhasaurus, Hector. Allied to *Platecarpus*. Cretaceous; New Zealand.

Sub-Family C. Mosasaurinae. Williston.

Hind limb tetradactyle. Trunk elongated, tail much dilated distally. Premaxillae forming a short and obtusely conical rostrum. Prefrontals more or less dilated into a horizontal plate posteriorly. Quadrate small, with moderate-sized suprastapedial process. Coronoid large, articulating with the splenial on the inner side. Humerus with strong radial process at distal end. Carpus and tarsus completely ossified; not more than six phalanges in any of the digits. Zygosphenes rudimentary or functional, chevrons fused with their centra.

Clidastes, Cope (*Edestosaurus*, Marsh), (Figs. 242, 4. 6, 7, 251). Skull 0·4 to 0·7 m. long; slender, tapering, depressed. Frontal not emarginate posteriorly in the median line. Parietal foramen entirely within the parietal plate. Teeth facetted on outer side, and smooth on the inner or on both faces. Dentary with about seventeen teeth, maxilla fifteen, pterygoid twelve to fifteen. Zygosphenes functional; chevrons long. Neural spines elevated in posterior half of the tail, suggesting presence of a caudal fin. Upper Cretaceous; Kansas, Alabama, and New Jersey.

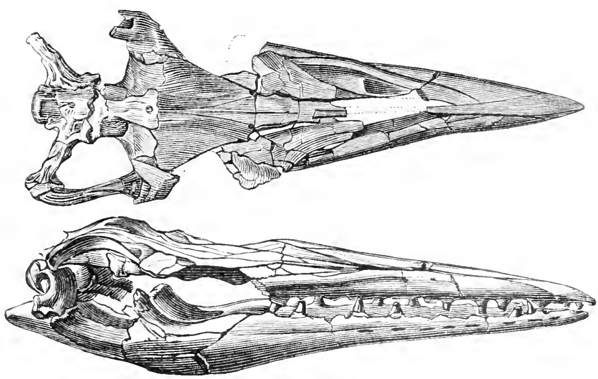


Fig. 251.

Clidastes propython, Cope. Upper Cretaceous; Uniontown, Alabama. Skull, superior and lateral aspects, $^1/_5$ (after Cope).

Mosasaurus, Conyb. (*Leiodon*, Owen; *Pterycollasaurus*, Dollo), (Figs. 243, 252). Skull attaining a length of 1·2 m., and total length of about 12 m. Distinguished from *Clidastes* chiefly by absence of a zygosphene-zygantrum arrangement. There are more than 130 vertebrae in the column, of which 46 are precaudal. The massive upper jaws are armed with about fourteen powerful teeth on either side, and the pterygoids support about eight smaller

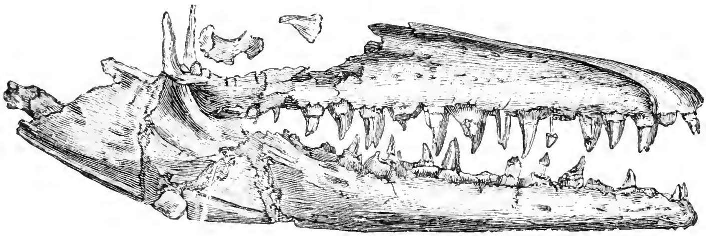


FIG. 252.
Mosasaurus camperi, v. Meyer. Upper Cretaceous; Maestricht, Holland. Skull, lateral aspect, $^1/_{12}$ (after Dollo).

teeth, all with anterior and posterior carinae. Upper Cretaceous: Holland, Belgium, France, Northern Germany, and the United States.

[The text for the preceding chapter on *Pythonomorpha* has been revised and modified in accordance with the latest researches by Dr. S. W. Williston, Professor of Geology and Palaeontology in the University of Kansas, at Lawrence.—EDITOR.]

Sub-Order 3. LACERTILIA. Saurii. Lizards.[1]

Scaly, long-tailed reptiles, with elongated and sometimes serpentiform body. Superior temporal arcade often wanting, and quadrate loosely attached to the cranium. Columella rod-like or rudimentary; alisphenoid and orbitosphenoid not ossified. Mandibular rami suturally united at symphysis; teeth acrodont or pleurodont. Sternum usually, and limb girdles always present, but one or both pairs of appendages sometimes wanting. Limbs ambulatory, and usually provided with five clawed digits.

The majority of lizards possess a dermal covering of corneous or in some cases of osseous scales, scutes, or spines, extending over the head and whole of the body. The vertebral column consists of numerous procoelous vertebrae (amphicoelous only among the *Geckonidae* and *Uropeltidae*), in which the neural arches are thoroughly coössified with their centra. There are seldom more than nine cervicals, and the atlas is composed of two dorsal pieces, either separate or united, and one ventral piece in the form of a free hypapophysis or intercentrum. Both the cervical and dorsal series have the transverse processes weakly developed, so that the ribs appear attached by a short tubercle. All of the ribs are single-headed. They are wanting on the anterior cervicals, some of the lumbar, and all of the caudal vertebrae. The sacrum is composed of two vertebrae. Stout transverse processes and chevron bones are borne by the caudals.

A sternum is present, although sometimes rudimentary, in all lizards except *Amphisbaena*; it usually occurs as a large rhombic or shield-shaped bone, sometimes pierced by two foramina. The ventral portion of the anterior

[1] Literature:
Cope, E. D., The Vertebrata of the Tertiary Formations of the West (Rept. N.S. Geol. Surv. Territ. vol. III.), 1883.—*Marsh, O. C.*, On Glyptosaurus, Tinosaurus, etc. (Amer. Journ. Sci. [3], vol. I. p. 456), 1871; and *ibid.* vol. IV. (1872), p. 298.—*Meyer, H. von*, Lacerten aus der Braunkohle des Siebengebirges (Palaeontogr. vol. VII. p. 74), 1860.—*Parker, W. K.*, On the structure and development of the skull in the Lacertilia (Phil. Trans. vol. CLXX.), 1880.

dorsal ribs which join the sternum are sometimes cartilaginous, and in other cases bony.

The *skull* (Fig. 253) is distinguished from that of Rhynchocephalians chiefly by its large free quadrate, a delicate rod-like columella, and the constant absence of a lower and occasional absence of an upper temporal arcade.

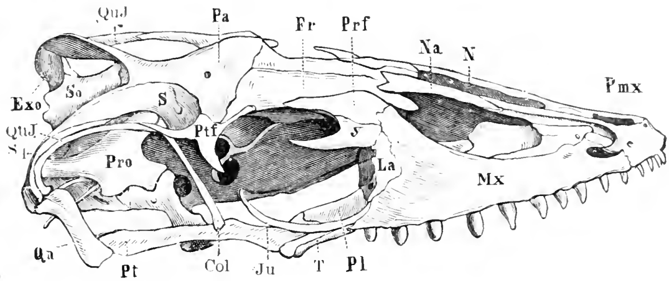


Fig. 253.

Monitor niloticus, Hassl. Recent; Egypt. Skull, lateral aspect, 1/1. (*col*, Columella or epipterygoid; *exo*, Exoccipital; *fr*, Frontal; *ju*, Jugal; *la*, Lachrymal; *mx*, Maxilla; *N*, Narial opening; *na*, Nasal; *pa*, Parietal; *pl*, Palatine; *pmx*, Premaxilla; *prf*, Prefrontal; *pro*, Proötic; *pt*, Pterygoid; *ptf*, Postfrontal; *qu*, Quadrate; *quj*, Quadrato-jugal; *S*, Supratemporal vacuity; *so*, Supraoccipital; *sq*, Squamosal; *t*, Transverse bone or ectopterygoid; *y*, Superciliary), (after Cuvier).

The vomer is unpaired, and not in contact with the pterygoids; and the latter, together with the palatines, form a flat thin palate pierced by large vacuities. A transverse bone (ectopterygoid) occurs between the maxillae and pterygoids. The external nares are separate, and commonly placed near the orbits. The opisthotic is fused with the exoccipital, forming the so-called parotic process of the posterior temporal region. The distal end of this process serves with the posterior ends of the squamosal and prosquamosal as a buttress to which the movable quadrate is attached. The squamosal itself

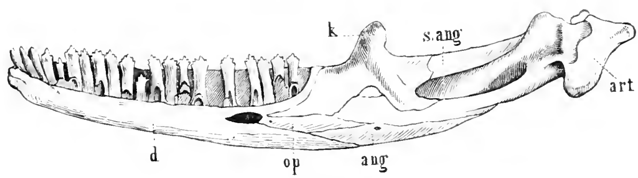


Fig. 254.

Iguana tuberculata, Laur. Recent; West Indies. Inner aspect of right ramus of mandible, showing pleurodont teeth. (*ang*, Angular; *art*, Articular; *d*, Dentary; *k*, Coronoid; *op*, Splenial; *s.ang*, Surangular), (after Cuvier).

is of small size and situated between the outer angle of the parietal and distal end of the prosquamosal. The postorbito-frontal unites with the forward end of the prosquamosal to form the lower border of the superior temporal fossa, and also unites with the jugal to form with this bone the posterior border of the orbit. In lizards the jugal is never in direct connection with the quadrate. A parietal foramen occurs, and the parietal is frequently unpaired.

The mandibular rami (Fig. 254) are suturally united at the symphysis; they exhibit the same structure as in Pythonomorphs, except that there is no movable articulation behind the middle of each ramus. Teeth are always present in upper and lower jaws, and occur rarely on the palatines, pterygoids, and vomer. They are either acutely or obtusely conical, chisel- or arrowhead-shaped, serrated or carinated on the anterior and posterior edges, or in some cases their form may be hemispherical. Their bases are completely fused with the supporting bone, and their arrangement is either acrodont or pleurodont. Successional teeth are developed on the inner side of the functional ones, and gradually displace them.

As a rule two pairs of limbs provided with five clawed digits are present, although the hinder pair may be rudimentary, and in some cases both pairs are wanting. The limb girdles persist, however, even among apodal forms, but the pelvic arch may become reduced. The coracoid is relatively large, and develops an anterior process, or precoracoid. The scapula also consists of two portions, of which the distal (suprascapula) is the larger and usually remains cartilaginous. The scapula proper is in some cases bifid at its distal extremity. The rod-shaped clavicle connects the anterior border of the scapula with the T-shaped or cruciform interclavicle, which is situated in front of the sternum. The bones of the fore-limb resemble those of Rhynchocephalians, except that the humerus never displays distal foramina. There are eight small carpals arranged in two rows, and the usual phalangeal formula is 2, 3, 4, 5, 3.

Where the hind limb is normally developed, the ilia are movably attached to the cartilaginous ends of the sacral ribs. Pubes and ischia meet in a ventral symphysis, and the anterior border of the former frequently develops a strongly curved process. The femur generally exceeds the humerus in length, and the bones of the crus remain separate. The proximal tarsals consist of a large tibiale (astragalus) and fibulare (calcaneum); there are often but two free tarsals present in the distal row (Nos. III. and IV.), the remainder being fused with the metatarsals. The phalangeal formula of the pes is usually 2, 3, 4, 5, 4.

Lizards of the present day are restricted almost exclusively to the tropical and temperate zones, and according to Hoffmann they comprise 434 genera and 1925 species. In comparison to these, the number of known fossil forms is very insignificant. The oldest remains commonly associated with lizards are the fragmentary jaws and procoelous vertebrae from the English Purbeckian, known as *Macellodus brodiei*, but these are too imperfect for accurate determination. Most of the detached vertebrae and other fragments of Cretaceous age which have been referred to Lacertilians or Ophidians are probably Dolichosaurian.

Even the known Tertiary fossils are very fragmentary, and belong for the most part to existing families. From the Lower Eocene of Wyoming representatives are known of the *Varanidae* (*Tinosaurus*), *Anguidae* (*Glyptosaurus*, *Sanira*, *Xestops*), *Iguanidae* (*Iguanavus*), and *Chamaeleonidae*. *Iguana* itself, now restricted to the western hemisphere, occurs in the European Tertiary. Fragmentary remains of a number of other recent genera are found in the Eocene (or Oligocene) Phosphorites of Quercy, and Gypsum Beds of Apt, in France, among which may be mentioned the following:—*Proiguana* (Fig. 255), *Plestiodon* (Fig. 256), *Palaeovaranus* (Fig. 257), *Agama*, *Diploglossus*, and *Lacerta*.

The Miocene also yields a number of Lacertilian fragments identifiable with recent genera, the principal localities being Auvergne, France; the lignites of Rott, near Bonn; and the freshwater strata of Steinheim, Haslach, Günzburg, Sansan, and Colorado. The most gigantic of all lizards are

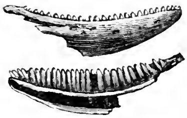


FIG. 255.

(?) *Proiguana*, sp. Phosphorite of Quercy. Inner and outer aspect of dentary, 1/1.

FIG. 256.

Plestiodon cadurcensis. Filhol. Phosphorite of Quercy. Inner aspect of dentary, 1/1.

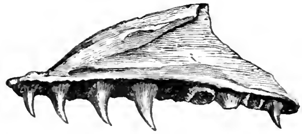


FIG. 257.

Palaeovaranus cayluxi. Filhol. Phosphorite of Quercy. Maxillary fragment, 1/1.

Megalania and *Notiosaurus*, from the Pleistocene river deposits of Queensland. The former is estimated to have been about 10 m. in length, and belongs to the Varanidae.

Sub-Order 4. OPHIDIA. Snakes.[1]

Body serpentiform, without limbs, covered with corneous scales. Vertebrae procoelous, with zygosphene-zygantrum articulation, and the anterior centra with strong simple hypapophyses. Both upper and lower temporal arcades, columella, sacrum, sternum, pectoral arch, abdominal ribs and haemapophyses are wanting. Parietal unpaired, without foramen, the sides extended downward and fused with the proötic, alisphenoid, and orbitosphenoid. Anterior portion of brain case completely ossified. Quadrate and pterygoid movably attached to skull by ligament. Maxillae and palatines usually freely movable, always displaceable. Premaxillae much reduced; mandibular symphysis ligamentous.

Snakes are chiefly conspicuous for the absence of limbs. The body is greatly elongated, and the number of vertebrae very considerable, sometimes exceeding 400. The centra are concave in front and convex behind, the connection being by free ball-and-socket joints; and their articulation is further strengthened by zygapophyses and a zygosphene-zygantrum arrangement. The neural arches are thoroughly coössified with their centra. Simple hypapophyses are developed by the anterior vertebrae as far as sometimes the thirtieth, and the transverse processes are short and tumid (Fig. 258). Ribs are almost always present in the trunk region, beginning with the third vertebra; and being freely articulated, are able to assist in propelling the body. They are long, curved, and frequently hollow; in the caudal region they are replaced by elongate transverse processes. Haemapophyses are wanting among snakes, and in their stead occur stout descending branches of the transverse processes (Fig. 259).

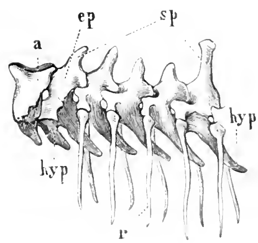


FIG. 258.

Python bivittatus, Schn. Recent: Sumatra. Anterior cervical vertebrae, 1/1. (*a*, Atlas; *ep*, Axis; *hyp*, Hypapophysis; *r*, Rib; *sp*, Neural spine), (after d'Alton.)

[1] Literature:

Cope, E. D., The Vertebrata of the Tertiary Formations of the West (Rept. U. S. Geol. Surv. Territ. vol. III.), 1883.—*Filhol, H.*, Ann. Sci. Géol. vol. VIII. (1887), p. 270.—*Fischer, G.*, De serpentibus quibusdam fossilibus dissertatio. Bonn, 1857.—*Meyer, H. von*, Coluber atavus aus dem Siebengebirge (Palaeontogr. vol. VII.), 1860.—*Rochebrune, A. F. de*, Revision des Ophidiens fossiles (Nouv. Arch. Musée d'Hist. Nat. Paris [2], vol. III.), 1880.—*Roemer, F.*, Ueber Python euboeicus (Zeitschr. deutsch. geol. Ges. vol. XXII.), 1870.

The serpent *cranium* (Fig. 260) differs from that of lizards in the constant absence of both temporal arcades; complete ossification of the anterior part of the brain case; reduction of the premaxillae; absence of a columella; strong development of the ectopterygoid, which joins the maxillary and palato-pterygoid arches; and movable connection between not only all of the last-named bones, but between the squamosal and occipital region, and between the rami of the lower jaw. The brain cavity is very long, and its lateral walls as far as the middle portion are formed by descending processes of the parietal and frontal. The exoccipital and opisthotic are fused, and the maxilla is often much reduced. All the cranial bones are dense and ivory-like, and united by smooth sutures.

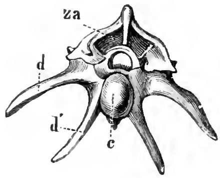


Fig. 259.

Python bivittatus, Caudal vertebra, posterior aspect. *c*, Centrum; *d*, *d'*, Transverse process and its descending branch; *za*, Zygantrum.

Acicular, recurved, acrodont teeth are usually present on the maxillae, premaxillae pterygoids, palatines, and dentary bones. Occasionally they are wanting on the palatines (*Uropeltidae*), and often also on the rudimentary premaxillae. In the venomous snakes some of the maxillary teeth are hollow and traversed by a canal or groove ending in a slit-like opening at the end of the tooth. The canal is connected with the duct of a poison gland, and through it the secretion of the latter is forced when the animal strikes. Some of the non-poisonous snakes also have grooved teeth immovably fixed to the maxillae.

Locomotion among snakes is accomplished by the lateral movements of the vertebral column, assisted by the ribs, the latter being alternately pushed forward and the dermal scutes drawn after them.

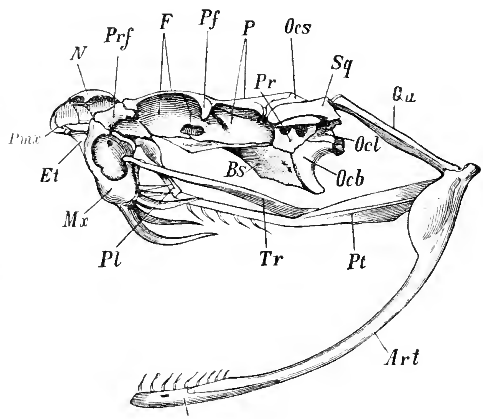


Fig. 260.

Crotalus horridus, Linn. Recent; South America. (*art*, Articular; *bs*, Basisphenoid; *d*, Dentary; *et*, Ethmoid; *f*, Frontal; *mx*, Maxilla; *n*, Nasal; *ocb*, Basioccipital; *ocl*, Exoccipital; *ocs*, Supraoccipital; *p*, Parietal; *pf*, Post-frontal; *pl*, Palatine; *pmx*, Premaxilla; *pr*, Proötic; *prf*, Prefrontal; *pt*, Pterygoid; *qu*, Quadrate; *sq*, Squamosal; *tr*, Transverse or ectopterygoid), (after Claus).

The *Ophidia* are distributed principally in the warmer regions, only the smaller forms extending into the northern temperate zone. By far the greater number are terrestrial, although some are amphibious, and a few are exclusively marine. About 400 recent genera and nearly 1800 species are known, as compared with only about 35 fossil forms, the majority of which are very imperfect. Most of the detached vertebrae of Cretaceous age originally regarded as Ophidian are doubtless Dolichosaurian, and the known Tertiary species are scarcely to be distinguished from those now living. Tolerably complete skeletons occur rarely in the freshwater Miocene of Oeningen and Euboea, as well as in the lignites near Bonn, and belong chiefly to the non-poisonous varieties.

Typically Ophidian vertebrae (*Palaeophis*) from the Lower Eocene of

Sheppey and Bracklesham, England, and Cuise la Mothe France, are ascribed to marine *Pythonidae* which may have attained a length of 6 m. A vicarious genus, *Titanophis*, occurs in the Eocene of New Jersey, and several genera (*Helagris*, Cope ; *Boavus*, *Lithophis*, and *Limnophis*, Marsh) have been described from the Eocene of Wyoming and New Mexico. Among the Upper Eocene (or Oligocene) forms of France, Switzerland, and England may be mentioned *Palaeopython* (Fig. 261) and *Scytalophis*, Rochebrune, and *Paleryx*, Owen.

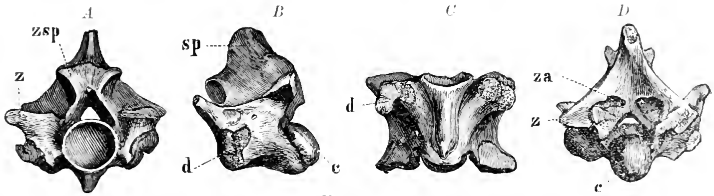


FIG. 261.

Palaeopython cadurcensis, Filhol sp. Phosphorite of Quercy, France. *A*, Anterior. *B*, Lateral. *C*, Inferior. *D*, Posterior aspect of vertebra, $^1/_1$. (*c*, Centrum ; *d*, Transverse process with costal tubercle ; *sp*, Neural spine ; *z*, Zyapophysis ; *za*, Zygantrum ; *zsp*, Zygosphene.)

One of the best preserved Miocene serpents is *Heteropython euboeicus*, Roemer, from Kumi, on the island of Euboea. Representatives of the *Colubridae* (*Elaphis*, Aldr. ; *Coluber*, Linn.), and *Erycidae* (*Scaphophis*, Roch.) have been described from the freshwater Miocene of Oeningen, Steinheim, Günzburg, Haeder, Weisenau, Ulm, Sansan, Touraine, and other localities, as well as from the lignites of Rott, near Bonn. A number of *Erycidae* and *Crotalidae* are also known from the Miocene of Colorado and Oregon. All known Pleistocene remains are identifiable with existing genera.

Order 3. ICHTHYOSAURIA. (*Ichthyopterygia.*[1])

Primitive marine reptiles with fish-like body, long head and tail, and no distinct neck. Investing bones of temporal region contracting into a single broad arcade ; quadrate fixed. Rostrum long and tapering ; orbits large, laterally placed, with sclerotic ring. External nares separate, slightly in advance of orbits. Parietal foramen and supra-temporal vacuities large. Teeth acutely conical, inserted in a continuous groove on the maxillae and elongated premaxillae and mandibles, but sometimes wanting. Vomer edentulous. Vertebrae numerous, very short, deeply amphicoelous. Ribs long, abdominal ribs present, but sternum absent. Pectoral arch consisting of coracoids, scapulae, clavicles, and a T*-shaped interclavicle. Limbs short, paddle-shaped, sometimes with more than five rows of phalanges, and a layer of cartilage around the carpals, tarsals, and phalanges. No dermal armour.*

[1] *Baur, G.*, On the morphology and origin of the Ichthyopterygia (Amer. Nat. vol. XXI. p. 837), 1887 ; also Bericht, 20th Versammlung Oberrhein. geol. Vereins (1887), p. 20 ; and Anat. Anz. vol. X. (1894), p. 456.—*Cope, E. D.*, On the cranium of Ichthyopterygia (Proc. Amer. Assoc. Adv. Sci. vol. XIX. p. 197), 1870.—*Fraas, E.*, Die Ichthyosaurier der süddeutschen Trias und Jura Ablagerungen. Tübingen, 1891.—Die Hautbedeckung von Ichthyosaurus (Württ Jahresh. p. 493), 1894.—*Hawkins, T.*, Memoirs of Ichthyosauri and Plesiosauri. London, 1834.—*Marsh, O. C.*, On Baptanodon, etc. (Amer. Journ. Sci. [3], vol. XVII. p. 86), 1879 ; also *ibid.* vol. XIX. (1880), p. 491 ; and vol. L. (1895), p. 405.—*Merriam, J. C.*, Triassic Ichthyopterygia (Bull. Californ. Univ. vol. III. p. 63), 1902.—*Owen, R.*, Monograph of the fossil Reptilia of the Liassic Formations, Part III. (Palaeontogr. Soc.), 1881.—Monograph of the fossil Reptilia of the Cretaceous Formations (*ibid.*), 1851.—*Seeley, H. G.*, On Ophthalmosaurus, etc. (Quar. Journ. Geol. Soc. vol. XXX. p. 696), 1874.—On the skull of an Ichthyosaurus (*ibid.* vol. XXXVI. p. 635), 1880.—*Theodori, C.*, Beschreibung des kolossalen Ichthyosaurus trigonodon zu Banz. Munich, 1854.

The members of this order differ conspicuously from all living reptiles, and are distinguished chiefly by their fish-like form of body, paddle-shaped limbs with numerous oval or polygonal phalanges, large head with elongated rostrum, short amphicoelous vertebrae, and naked integument. The snout resembles that of a dolphin, the teeth are crocodilian-like, the skull and pectoral girdle suggest those of lizards, the limbs are very similar to the flippers of marine mammals, and the vertebrae and caudal fin are decidedly fish-like. As regards external form, limb-structure, and adaptation to a marine existence, they depart as widely from other reptiles as whales do from land mammals, and occupy as isolated a position.

The absence of branchial arches and shape of the hyoid bones prove that respiration was pulmonary among Ichthyosaurs; and their viviparous habit is demonstrated by a number of well-preserved skeletons in the Lias of England and Würtemberg, which exhibit as many as seven embryonic individuals in the abdominal cavity. Large quantities of their coprolites occur in various localities, and contain the scales and bones of fishes, and fragments of cephalopods. Ichthyosaurian remains are found exclusively in the marine deposits of the Mesozoic, and are most abundant in the Lias. Of their origin nothing is known, although it is certain that they were derived from land animals. The earlier (Triassic) forms have less completely paddle-shaped extremities than the later. Some species attain a length of 9 m., and the smallest are only about 1 m. long.

The *skull* (Fig. 262) is conspicuous for its elongated, dolphin-like rostrum and enormous orbits, which are surrounded by a ring of fifteen to nineteen scler-

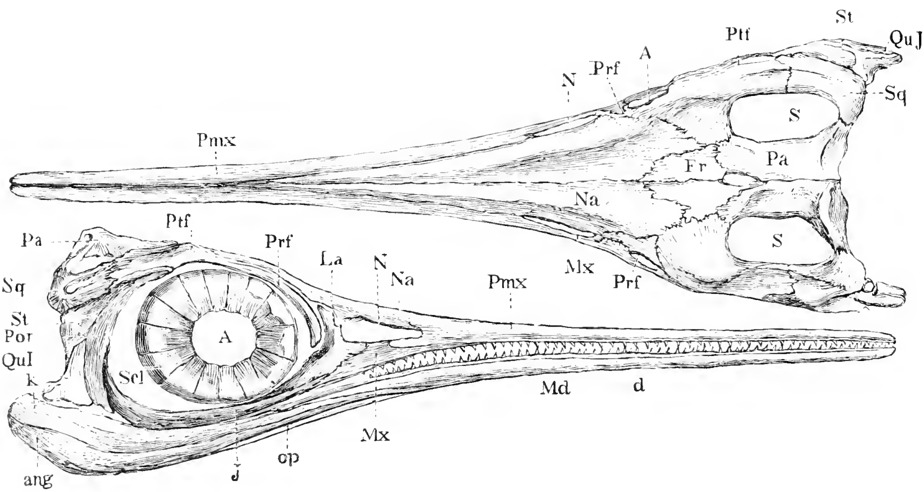


Fig. 262.

Ichthyosaurus acutirostris, Owen. Upper Lias; Curey, Calvados. Skull, superior and lateral aspects, 1/4. *A*, Orbit; *ang*, Articular; *d*, Dentary; *fr*, Frontal; *j*, Jugal; *k*, Surangular; *md*, Mandible; *mx*, Maxilla; *N*, External narial opening; *na*, Nasal; *op*, Splenial; *pa*, Parietal; *pmx*, Premaxilla; *por*, Postorbital; *ptf*, Postfrontal; *quj*, Quadrato-jugal; *S*, Supratemporal vacuity; *scl*, Sclerotic plates; *sq*, Squamosal; *st*, Supratemporal or prosquamosal (after E. Deslongchamps).

otic plates. The paired parietals and frontals are of small size, and a large parietal foramen occurs at their junction in the median line. Adjoining the parietals on either side are the large oval supratemporal vacuities (*S*), bounded externally by the squamosal and postfrontal. The external nares are triangular and placed close to the orbits; the nasals are extended in front, and the premaxillae greatly produced. The superior border of the orbit is formed by the postfrontal, and prefrontal, the latter a narrow, triangular plate. In front of the orbit, and separating it from the narial opening, is a triangular lachrymal. A long, slender, rod-like jugal bounds the orbit below, and a curved oblique postorbital encloses it behind. Joining the postorbital and jugal posteriorly is the quadrato-jugal, which forms the postero-lateral angle of the skull, and together with the quadrate furnishes the connection for the lower jaw. An irregularly triangular or rectangular plate, the supratemporal (or prosquamosal, *St*), is inserted between the quadrato-jugal and squamosal, and behind the postorbital and postfrontal. The maxilla is an elongate triangular bone, inserted between the jugal, lachrymal, and premaxilla.

The basioccipital (Fig. 263) is very strongly developed, and bears a stout articular condyle. Above it and on either side of the foramen magnum are the paired exoccipitals, capped by the supraoccipital. Adjoining the exoccipitals are the opisthotics, which remain separate from the proötics. The bones of the occipital and otic regions are rather loosely united, and the base and lateral walls of the brain case appear to have been cartilaginous; there is no ossified alisphenoid or orbitosphenoid.

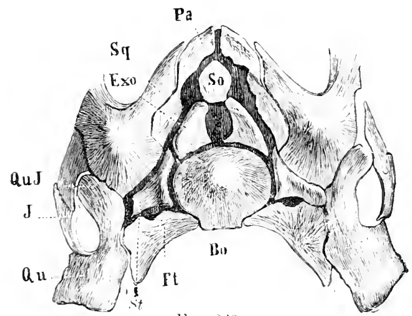


FIG. 263.

Ichthyosaurus acutirostris, Owen. Upper Lias; England. Skull, posterior aspect, $^1/_4$. (*bo*, Basioccipital condyle; *eo*, Exoccipital on either side of foramen magnum; *j*, Quadrato-jugal; *pa*, Parietal; *pt*, Pterygoid; *qu*, Quadrate; *quj*, Supratemporal, missing on the right-hand side; *so*, Supraoccipital; *sq*, Squamosal; *st*, Opisthotic), (after Owen).

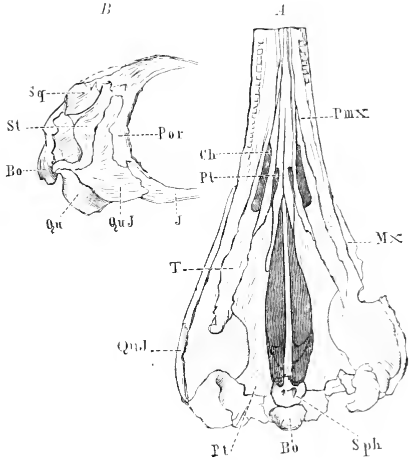


FIG. 264.

Ichthyosaurus acutirostris, Owen. Upper Lias; England. *A*, Palatal aspect of skull. *B*, Right temporal region, $^1/_5$. (*ch*, Internal nares; *pl*, Vomer; *sph*, Basisphenoid, its rostrum dividing interpterygoid vacuity; *t*, Palatine, not extending so far in either direction as shown. Lettering otherwise as in preceding figures), (after Seeley).

Abutting against the basioccipital on the lower side of the skull (Fig. 264) is a more or less discoidal basisphenoid, which develops a long, splint-like anterior process (presphenoid), extending along the middle of a large interpterygoid vacuity. The pterygoids are long and relatively large-sized bones joining the vomer and palatines in front, and the basisphenoid and quadrate behind. There is a well-developed columella or epipterygoid, but no ectopterygoid has been observed. The posterior nares occupy their primitive position on either side of the narrow vomers. A pair of stout, rib-like hyoid bones is known to have been present.

The slender rami of the lower jaw unite in an extensive symphysis, and are without a coronoid process. Each ramus consists of five or sometimes six pieces. A deep groove extends along the outer side of the dentary on its upper border, but becomes interrupted anteriorly into a series of pits for the blood-vessels.

The *teeth* (Fig. 265) are acutely conical, smooth or vertically striate, sometimes with anterior and posterior carinae, and with a tumid root usually larger than the crown. As many as 180-200 occur in single series in upper and lower jaws (Fig. 266), being confined to the maxilla, premaxilla, and dentary. They are placed in a deep groove, usually continuous, and were

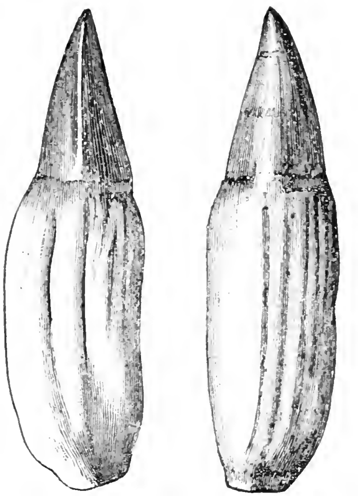


Fig. 265.

Ichthyosaurus platyodon, Conyb. Lower Lias: Lyme Regis, England. Tooth, lateral and anterior aspects, $^1/_1$ (after Lydekker).

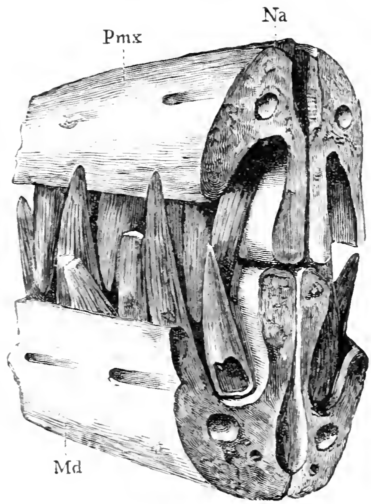


Fig. 266.

Ichthyosaurus quenstedti, Zittel. Upper Jura; Wurtemberg. Jaw-fragment, $^3/_4$. (*md*, Dentary; *na*, Nasal; *pmx*, Premaxilla), (after Quenstedt).

held in place by the tissues and edges of the groove. Some of the later Mesozoic forms are edentulous. The crown is composed of dentine, covered with a layer of enamel, and over this there may be sometimes still another layer of cement. A vertical folding of the walls similar to that occurring in Labyrinthodonts is occasionally observed. The large root is composed of an osseous cement containing bone cells and vascular canals, and is enveloped by a more or less plicated covering of dentine.

The *vertebral column* comprises but two regions—caudal and precaudal. There is no true neck, and no sacrum. There are between 120 and 150 vertebrae, of which about 100 are caudal. The centra are extremely short, and deeply biconcave, as among Selachians and Labyrinthodonts. The neural arches are strongly developed, never fused with their centra, and articulate with one another by feeble zygapophyses. Adult individuals almost invariably have the atlas and axis fused, and before and behind each of them are subvertebral hypocentra or intercentra. The remaining precaudal vertebrae are of nearly uniform character (Fig. 267), each centrum being provided with two pairs of tubercles for attachment with the double-headed ribs, and exhibiting dorsally a neural canal, with a rugose pit on either side for the pedicles of the neural arch. The anterior caudals bear only a single pair of tubercles for the support of the single-headed ribs, and these gradually disappear posteriorly

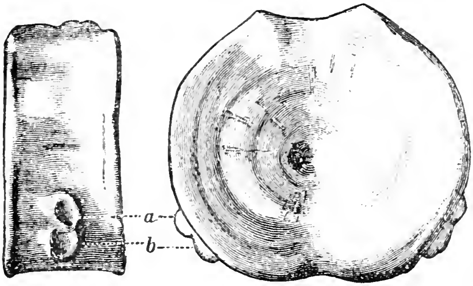


FIG. 267.

Ichthyosaurus trigonus, Owen. Kimmeridge Clay; Wooton-Basset, England. Posterior dorsal vertebra, 1/3. *a, b*, Tubercular and capitular facettes for ribs (after Lydekker).

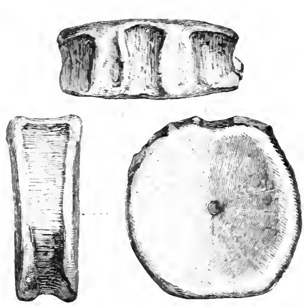


FIG. 268.

Ichthyosaurus, sp. Upper Lias; Banz, Franconia. Caudal vertebra, 1/1.

(Fig. 268). The halves of the chevron bones usually remain separate, but the neural arch of each vertebra except the atlas is undivided. A sharp downward deflection of the column occurs in the posterior part of the tail, where

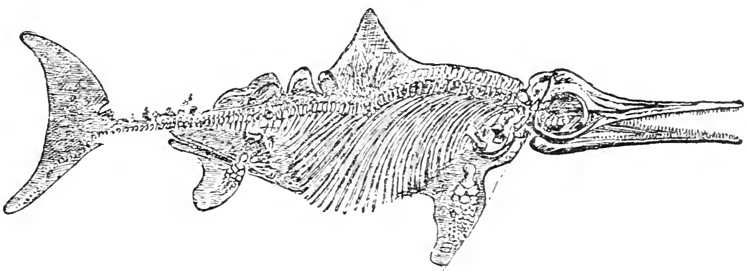


FIG. 269.

Ichthyosaurus quadricissus, Quenst. Upper Lias; Holzmaden, Wurtemberg. Skeleton showing outline of integument and dorsal and caudal fins. 1/10 (after E. Fraas).

the vertebrae enter the base of the large, triangular caudal fin. The latter is expanded in a vertical instead of horizontal plane, and must have been a very powerful swimming organ. A median dorsal fin has also been observed in a specimen from the Lias of Würtemberg (Fig. 269).

Ribs are present on all the precaudal vertebrae, and reach their greatest elongation between the tenth and thirteenth centrum, after which they gradually decrease in size toward the pelvis. From here on they continue single-headed, straight, and more like lateral processes than ribs, and become obsolete toward the caudal fin. The long slender ribs of the trunk are recurved, subcylindrical in section, and in most species longitudinally grooved. A median longitudinal and one or two paired lateral series of splint-like abdominal ribs are developed.

The *pectoral arch* (Fig. 270) is unusually powerful, and indicative of excellent swimming ability. There is no ossified sternum for the attachment of ribs, but a T-shaped interclavicle is present in the median line, in part overlapping the robust coracoids, whose inner edges meet in a long symphysis.

The anterior border of the coracoids is somewhat deeply excavated, the posterior margin entire and rounded. Its lateral margin is developed into a short, stout, and thickened process bearing two articular facettes, the foremost for receiving the proximal end of the scapula, and the hinder for the head of the humerus. The clavicles are slender curved bones, usually meeting in the middle line at the anterior margin of the interclavicle. Their union may be either by suture or fusion, or sometimes even by a joint.

Humerus, radius, and ulna are all short stout bones (Fig. 271), and relatively much reduced. The proximal end of the humerus is thickened, the distal flattened, and provided with radial and ulnar articular facettes, which are remarkable for being concave. The remaining bones of the paddle, of which the first two rows correspond to the carpus, and the third to the metacarpus, are small and polygonal, and usually arranged in a sort of mosaic. There are commonly from three to five digits, but as some of the phalangeal rows subdivide, the number of the latter is occasionally increased to eight or nine. As many as 100 phalanges are sometimes present. A deep incision is often observable on the radius and three succeeding bones of the paddle, the significance of which is not understood.

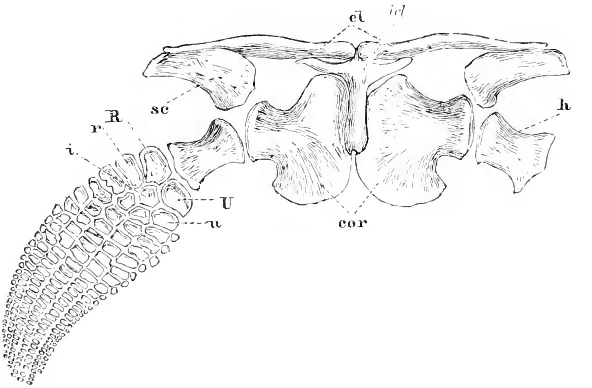


Fig. 270.

Ichthyosaurus communis, Conyb. Lower Lias; England. Pectoral arch and right fore limb, ventral aspect, 1/4. *cl*, Clavicle; *cor*, Coracoid; *h*, Humerus; *i*, Intermedium; *icl*, Interclavicle (partly covered by clavicles); *R*, Radius; *r*, Radiale; *sc*, Scapula; *U*, Ulna; *u*, Ulnare.

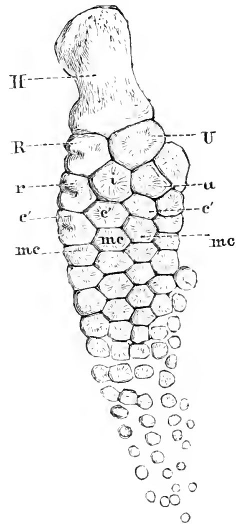


Fig. 271.

Ichthyosaurus tricissus, Quenst. Upper Lias; Boll, Würtemberg. Left fore paddle, dorsal aspect. *c'*, Distal carpals; *mc*, Equivalents of metacarpals. Other letters as in Fig. 270.

The *pelvic arch* is weakly developed, and freely suspended in the abdominal muscles. Ilium, pubis, and ischium are all long and slender bones, and apparently meet at the acetabulum. The femur is short and stout, but relatively longer than the humerus, and the rest of the hind paddle practically duplicates the structure of the anterior limb. The femur and humerus of this order are unique in that, instead of having convex condyles for the articulation of the epipodial bones, they present pre- and post-axial concavities for their reception (Fig. 271). Impressions of the leathery integument are retained by some specimens, as well as of the cartilaginous layer which surrounded the phalanges and completed the outline of the paddles. Dermal armour was not developed.

Family 1. **Ichthyosauridae.**

With the characters of the order. Trias to Cretaceous.

Mixosaurus, Baur. Most of the smaller-sized Triassic remains are placed in this genus as distinct from *Ichthyosaurus*, the teeth being in less uniform series, and the limbs less completely paddle-shaped. The radius and ulna are elongated, and separated by an interstice throughout their length. *M. cornalianus*, Bassani, the typical species, varies from 0·5 to 1 m. in length, and occurs in the Upper Trias of Besano, Lombardy. *M. atavus*, Quenstedt, is known by fragments from the Muschelkalk of Würtemberg.

Ichthyosaurus, König (Figs. 262-271). Teeth conical and in uniform series. Radius and ulna shorter than broad, proximally in contact. Humerus and femur with two concave distal facettes. Total length of largest forms upwards of 10 m.

This genus is most abundant in the Lias, *I. communis* and *I. intermedius* being familiar English species. Localities noted for the excellence of their fossil remains are Dorsetshire (Lyme Regis) and Somersetshire in the Lower Lias, and Yorkshire, Calvados, Würtemberg (Boll, Holzmaden), and Franconia (Banz, Altdorf) in the Upper Lias; and the species of the one division are for the most part distinct from those of the other. *I. communis, intermedius, latimanus, platyodon*, and *tenuirostris* are especially characteristic of the Lower Lias, and *I. acutirostris, ingens, quadricissus*, and *trigonodon* of the upper member. Remains of *Ichthyosaurus* are sparse in the Middle Jura, but a number of species occur in the Upper Jura of Solenhofen and Kelheim, Bavaria, Northern France, and England. Cretaceous forms are known from England, France, the East Indies, Australia, New Zealand, and Chili.

Ophthalmosaurus, Seeley. Edentulous or with minute teeth confined to front of the jaw. Humerus and femur with prominent trochanteric ridge and with three concave distal facettes; all remaining limb bones more or less rounded and separated. Clavicles separated. Upper Jura and Lower Cretaceous; England.

Baptanodon, Marsh (*Sauranodon*, Marsh *non* Jourdan). Similar to the preceding, but completely edentulous. Interclavicle not observed; digit arising from the intermedium consisting of two longitudinal rows of ossicles. Coracoids unite in the median line in large elliptical facettes. Upper Jura: Wyoming.

Shastasaurus, Merriam. Includes several large species from the Upper Trias of northern California. Pelvis very robust; all but first ten ribs single-headed. *Cymbospondylus*, Leidy, from Middle Trias of Nevada, is imperfectly known.

Order 4. SAUROPTERYGIA. Owen.[1]

Primitive aquatic reptiles with long neck, lizard-like body, and moderately short tail. Cranium small, with parietal foramen and large supratemporal vacuities.

[1] *Andrews, C. W.*, On Plesiosaurus, Pliosaurus, etc. (Quar. Journ. Geol. Soc. vol. XXXVII. p. 440), 1881.—Also *ibid.* vol. LIII. (1897), p. 177, and various articles in Geol. Mag. [4], vol. II. (1895), p. 241; *ibid.* vol. III. (1896), p. 145; Ann. Mag. Nat. Hist. [6], vol. XV. (1895), p. 333; *ibid.* vol. XVI. (1895), p. 429.—*Bassani, F.*, Sui fossili degli schisti bituminosi triassici di Besano (Atti Ist. Veneto Sci.), 1886.—*Beneden, P. J. van*, Deux Plesiosaures du Lias inférieure du Luxembourg (Mem. Acad. Roy. Belg. vol. XLIII. p. 1), 1880.—*Boulenger, G. A.*, On a Nothosaurian Reptile referable to Lariosaurus (Trans. Zool. Soc. vol. XIV. p. 1), 1896.—*Cope, E. D.*, On the structure of the skull in

Investing bones of temporal region forming a single broad arcade; quadrate fixed. Premaxillae not elongated; pterygoids extensive, meeting along the middle line; narial openings divided. Teeth conical, thecodont, in single series along margin of jaws. Vertebrae amphiplatyan; sacrum composed of two to four vertebrae. Cervical ribs articulating only with centra, never with their arches; dorsal ribs single-headed; abdominal ribs present between the robust limb girdles; no ossified sternum. Limbs more or less completely paddle-shaped, pentadactylate. Humerus with entepicondylar foramen, and large conical epiphyses; digits sometimes with super-numerary phalanges. Dermal armour and sclerotic ring not developed.

This reptilian order ranges from the Trias to the end of the Mesozoic era. The earlier forms are mostly small amphibious animals with slender, elongated limbs, and the later ones large-sized and completely adapted for a marine existence.

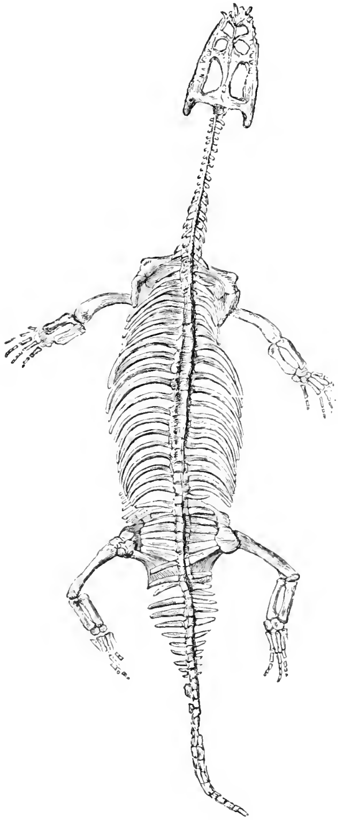


FIG. 272.

Lariosaurus balsami, Curioni. Muschelkalk; Perledo on Lake Como, Lombardy. Skeleton, dorsal aspect, 1/10.

Family 1. **Nothosauridae.**

Limbs comparatively slender and elongated, with five digits and normal number of phalanges. Coracoids not much extended along their median symphysis, and not in contact with interclavicle: scapulae well separated by a clavicular arch. Trias.

Lariosaurus, Curioni (*Macromirosaurus*, Cur.), (Fig. 272). Body lizard-like, 20-90 cm. long, tail forming about one-third the total length. There are about twenty cervicals, twenty-four to twenty-six dorsals, four sacrals, and over forty caudals. Cervical ribs small and double-headed; dorsal ribs very robust, and borne directly by the neural arches. A median longitudinal and two

the Plesiosaurian Reptilia (Proc. Amer. Phil. Soc. vol. XXXIII. p. 110), 1894.—*Dames, W.*, (Abhandl. preuss. Akad. Wiss. p. 1), 1895.—*Deecke, W.*, Ueber Lariosaurus, etc. (Zeitschr. deutsch. geol. Ges. vol. XXXVIII. p. 170), 1886.—*Hawkins, T.*, Memoirs on Ichthyosauri and Plesiosauri. London, 1834.—*Hulke, J. W.*, Anniversary Address (Quar. Journ. Geol. Soc. vol. XXIX.), 1893. Also Proc. Roy. Soc. vol. LI. (1892).—*Huxley, T. H.*, On Plesiosaurus, etc. (Quar. Journ. Geol. Soc. vol. XIV. p. 281), 1858.—*Knight, W. C.*, Some new Jurassic Vertebrates from Wyoming (Amer. Journ. Sci. [4], vol. V. p. 378), 1898. Also *ibid.* vol. X. (1900), p. 115.—*Meyer, H. von*, Zur Fauna der Vorwelt, pt. II. Frankfort, 1847.—*Owen, R.*, Monograph of the fossil Reptilia of the Liassic Formations, pt. III. (Palaeontogr. Soc.), 1865. Also Geol. Mag. vol. VII. (1870), p. 49; and Quar. Journ. Geol. Soc. vol. XXXIX. (1883), p. 133.—*Seeley, H. G.*, The nature of the shoulder girdle and clavicular arch in Sauropterygia (Proc. Roy. Soc. vols. LI. p. 119, and LIV. p. 160), 1892-93. Also various articles in Ann. Mag. Nat. Hist. [3], vol. XV. (1865), pp. 49, 232; vol. XVI. (1865), p. 352; [4], vol. VIII. (1871); Quar. Journ. Geol. Soc. vol. XXX. (1874), pp. 197, 436; vol. XXXIII. (1877), p. 541; vol. XXXVIII. (1882), p. 350; Ann. Rep. Yorks. Phil. Soc. (1895), p. 20.—*Sollas, W. F.*, On Plesiosaurus conybearei (Quar. Journ. Geol. Soc. vol. XXXVII. p. 440), 1881.—*Williston, S. W.*, A new Plesiosaur, etc. (Trans. Kansas Acad. Sci.), 1890.

paired lateral series of abdominal ribs present. Proximal tarsals consisting of two large elements, the distal five each supporting a digit; phalangeal formula, 2, 3, 4, 4, 3. Hind limb longer and stouter than the anterior, but otherwise very similar; phalangeal formula 2, 3, 4, 5, 4. Palate with suborbital and infratemporal vacuities, but no interpterygoidal. Middle Trias; Lake Como, Italy.

Pachypleura, Cornalia (*Neusticosaurus*, Seeley). Similar to the preceding but smaller (25-30 cm. long), with much shorter neck; about sixteen cervicals

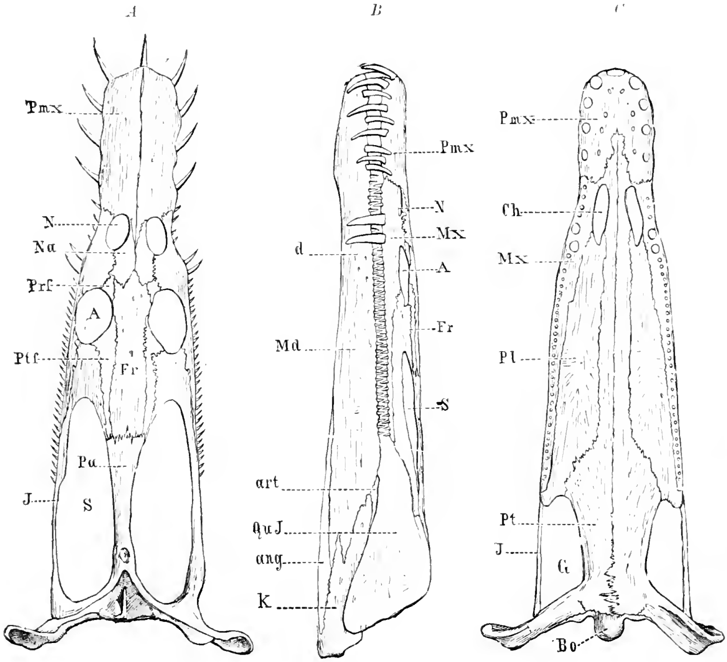


FIG. 273.

Nothosaurus mirabilis, Münst. Muschelkalk; Bayreuth, Germany. Skull, slightly restored, 1/4. *A*, Dorsal aspect (after Quenstedt). *B*, Lateral aspect. *C*, Palatal aspect (after v. Meyer). *A*, Orbit; *ang*, Angular; *art*, Surangular; *bo*, Basioccipital condyle; *ch*, Internal nares; *d*, Dentary; *fr*, Frontal; *G*, Infratemporal vacuity; *j*, Jugal; *k*, Articular; *md*, Mandible; *mx*, Maxilla; *N*, External narial opening; *na*, Nasal; *pa*, Parietal; *pl*, Palatine; *pmx*, Premaxilla; *prf*, Prefrontal; *pt*, Pterygoid, bounded in front by vomer (suture not shown); *ptf*, Postfrontal; *qu*, Quadrate; *quj*, Quadrato-jugal fused with squamosal and supratemporal; *S*, Supratemporal vacuity.

FIG. 274.

Tooth, 1/1, of species shown in Fig. 273.

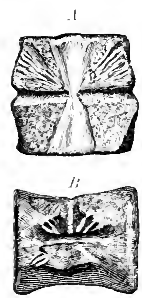


FIG. 275.

Cervical vertebra, 1/1, of species shown in Fig. 273. *A*, *B*, Dorsal and lateral aspects.

and forty caudals. Upper Trias (Raibl Beds); Besano, Lombardy, also Lettenkohle of Hoheneck, near Ludwigsburg.

Dactylosaurus, Gürich; *Anarosaurus*, Dames; *Cymatosaurus*, Dames. Muschelkalk; Silesia and Thuringia.

Nothosaurus, Münst. (Figs. 273-277). Distinguished from *Lariosaurus* by its larger size, closure of suborbital vacuity in the palate, and presence of short and stout transverse processes on neural arches of dorsal vertebrae.

The skull is elongated and somewhat contracted anteriorly, attaining a length of 35 cm. in the typical species. The supratemporal vacuities are very large, the unpaired parietal being reduced to a narrow bar, pierced posteriorly by a parietal foramen. The orbits are oval, relatively small, and placed slightly in front of the middle; not far removed from them are the external nares. The unpaired frontal is much elongated, the premaxillae only moderately so, and the prefrontals are small and triangular. The long and narrow maxillae unite posteriorly with a slender jugal,

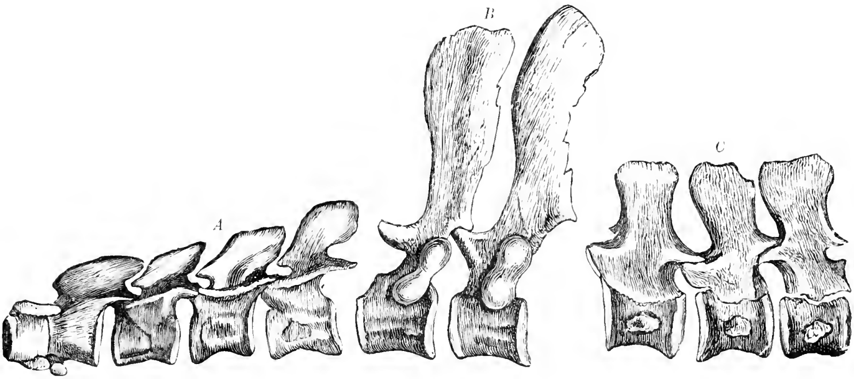


FIG. 276.

Nothosaurus mirabilis, Münst. Muschelkalk; Bayreuth, Germany. *A*, The five anterior cervicals. *B*, Two dorsals. *C*, Three caudal vertebrae, $^1/_2$ (after von Meyer).

which enters into the temporal arcade. Pterygoids and palatines are strongly developed; the internal nares are placed far forwards, on either side of the paired vomer. A single series of conical, slightly curved, and striated teeth (Fig. 272) is borne by the maxillae, premaxillae, and dentary. All of the rostral and one or two of the anterior maxillary teeth are considerably enlarged.

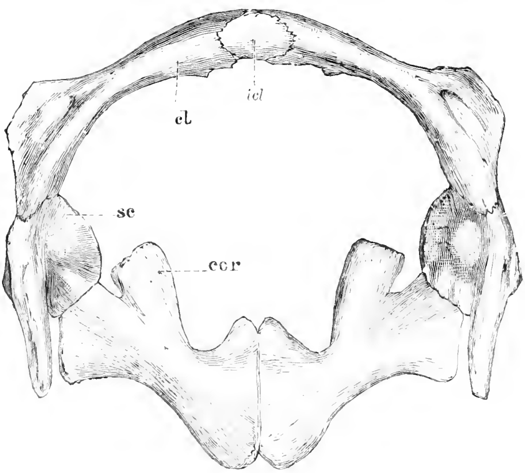


FIG. 277.

Nothosaurus mirabilis, Münst. Muschelkalk; Bayreuth, Germany. Dorsal aspect of pectoral arch, $^1/_5$. *cl*, Clavicle; *cor*, Coracoid; *icl*, Interclavicle; *sc*, Scapula.

Owing to the sutural union between the vertebral centra and their neural arches, the former are usually found detached in the fossil state, and exhibit a cruciform impression on the dorsal surface (Fig. 275). There are about twenty cervicals (Fig. 276), all of which excepting atlas and axis bear short, curved, double-headed ribs. The ribs of the trunk region are stout, single-headed, and attached to the transverse processes of the neural arches. In this region the neural spines are more strongly developed, and the zygapophyses more weakly, than elsewhere in the vertebral column. The caudal vertebrae have single-headed ribs attached to their centra, and also small chevron bones. The abdominal ribs comprise a median longitudinal series sharply bent in the middle line, and a paired lateral series.

In the pectoral arch (Fig. 277) the clavicles are well developed, and form a regular arch into which a small, oval interclavicle enters. The ends of the clavicular arch are suturally united with a pair of stout scapulae, which develop oblique dorsal processes. The coracoids are not much extended in the median line, and their antero-internal margin is notched and incomplete; apparently the space between them and the clavicular arch was filled during life by cartilage. The humerus is moderately long, curved, and very robust; it is pierced distally by an entepicondylar foramen. Radius, ulna, and metacarpals are likewise rather long and slender, the paddle-shaped form of limb being not yet fully acquired.

The bones of the pelvic arch are robust, and owing to their loose articulation, usually occur detached in the fossil state. The ilium is very short and stout, somewhat expanded distally, and provided with two articular facettes. Pubis and ischium are both of large size, narrowed and thickened at the acetabulum, and distally expanded; a small obturator foramen persists in the pelvis. The femur is longer and more slender than the humerus, nearly rectilinear, moderately thickened at the extremities, and with rounded articular faces. The remaining bones of the hind limb are imperfectly known.

Nothosaurus is an exclusively Triassic genus, and occurs most abundantly in the Muschelkalk of Southern Germany. *N. mirabilis*, Münster, is the typical and best-known species, attaining a length of fully 3 m. Smaller species are known from the Buntsandstein and Lettenkohle. The so-called *Parthanosaurus*, Skuphos, from the Raibl Beds of Vorarlberg, is doubtfully distinct.

Conchiosaurus, v. Meyer. Muschelkalk; Esperstädt, Brunswick.

Simosaurus, v. Meyer. Skull broad and depressed, with obtuse snout. Teeth short, obtusely conical or clavate, the crown strongly striated. Muschelkalk and Lettenkohle.

Pistosaurus, v. Meyer. Known only by the skull, which tapers anteriorly, and attains a length of 35 cm. Premaxillae elongate and slender, the small narial openings placed between them and the maxillae. Nasals greatly reduced and displaced posteriorly. Palate with an unpaired vacuity between the premaxillae. Muschelkalk; Franconia and Silesia. This genus is made by Baur the type of an independent family.

Family 2. **Plesiosauridae.**

Limbs paddle-shaped, bones of second segment much shortened, and the five digits elongated by supernumerary phalanges. Clavicular arch tending to diminish in size as the scapulae increase, the latter sometimes becoming fused with each other and the coracoids in the median line. Coracoids much extended along median symphysis, and uniting with either the scapular or clavicular arch anteriorly. Sclerotic plates present. Trias to Cretaceous.

Plesiosaurus, Conyb. (Figs. 278-280). Head small, neck very long, tail of moderate length. Snout not elongated, orbits elliptical and placed near the middle of the skull, supratemporal vacuities large, irregular. External nares small and close to the orbits. Postero-lateral angles prominent. Interpterygoidal and posterior palatine vacuities small. Mandibular symphysis short. Teeth acutely conical, longitudinally grooved; anterior ones somewhat enlarged. Coracoids meeting in a long symphysis, scapulae separated by a well-developed clavicular arch.

The number of cervical vertebrae varies among the different species between thirty and forty. The centra are but slightly biconcave, and united to the neural arches by suture; the marks of their attachment form with the neural canal a cruciform impression on the dorsal side of the centra. With the exception of atlas and axis, all the cervicals bear short, double-headed ribs, attached directly to the centra. There are about twenty dorsal vertebrae with well-developed transverse processes and single-headed ribs. The two sacral vertebrae are characterised by having somewhat shorter transverse processes and broader ribs than the rest. There are between thirty and forty caudals, most of which bear short, single-headed ribs articulated with their centra, and chevron bones whose right and left halves do not fuse below. The abdominal ribs are very robust, and consist of a median and three paired lateral series.

In the pectoral arch (Fig. 279) the coracoids are characterised by their large size, being considerably longer than broad, and joined in a long median symphysis. There is no sternum, and as a rule no separate interclavicle, but the clavicular arch is represented by a single, broad, bilaterally symmetrical bone to which the coracoids and scapulae are firmly united. The latter are somewhat extended ventrally underneath the clavicular arch, but do not meet in the median line.

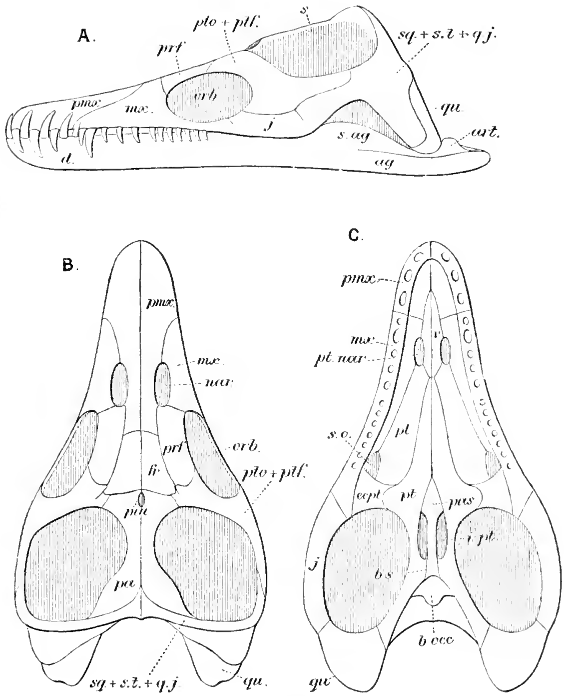


FIG. 278.

Plesiosaurus macrocephalus, Owen. Lower Lias; Lyme Regis, Dorsetshire. *A*, Lateral; *B*, Superior; *C*, Palatal aspects of skull, $^1/_6$. *ag*, Angular; *art*, Articular; *bocc*, Basioccipital; *bs*, Basisphenoid; *d*, dentary; *ecpt*, Transverse or ectopterygoid; *fr*, Frontal; *ipt*, Interpterygoid vacuity; *j*, Jugal; *mx*, Maxilla; *nar*, External narial opening; *orb*, Orbit; *pa*, Parietal; *pas*, Parasphenoid; *pin*, Pineal foramen; *pl*, Palatine; *pmx*, Premaxilla; *prf*, Prefrontal; *pt*, Pterygoid; *ptnar*, Posterior nares; *ptf*, Postfrontal; *pto*, Postorbital; *qj*, Quadrato-jugal; *qu*, Quadrate; *s*, Supratemporal vacuity; *sag*, Surangular; *so*, Suborbital vacuity; *st*, Supratemporal or prosquamosal; *sq*, Squamosal; *v*, vomer (from Woodward, after Andrews).

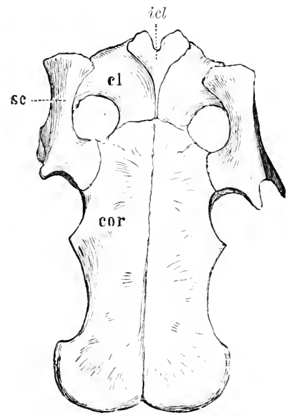


FIG. 279.

Plesiosaurus laticeps, Owen. Lower Lias; Dorsetshire. Pectoral arch, ventral aspect, $^1/_{10}$. *cl*, Clavicle; *cor*, Coracoid; *icl*, Interclavicle; *sc*, Scapula.

The humerus is robust and distally much expanded, but without epicondylar foramen or groove. This bone and the femur are noteworthy as exhibiting large, conical epiphyses, similar to those of frogs and certain Chelonians. The radius and ulna are both a little longer than broad. Four elements are usually present in the proximal, and three in the distal row of the carpus; the five constricted metacarpals are similar in form to the phalanges. The phalangeal formula is inconstant, but the third and fourth digits are always the longest, sometimes comprising as many as nine phalanges. The hind limb differs in no respect from the fore, except that it is slightly stouter. Probably both were invested with a cartilaginous membrane, as in Ichthyosaurs. The pubes are relatively large, with convex anterior and notched posterior margin, but not pierced by a foramen. They meet, as do also the much smaller ischia, in a long median symphysis. The ilium is slender, and articulated only with the ischium.

Several nearly perfect skeletons of *Plesiosaurus* are known from the Lower and Upper Lias of England and Germany, and supposed fragments are known from the Rhaetic. The typical species, *P. dolichodeirus*, Conybeare, from the Lower Lias of Lyme Regis, England, attains a total length of 3 m. Other species from the same locality are *P. hawkinsi*, *P. rostratus*, and *P. macrocephalus*, Owen; and *P. conybearei*, Sollas, the latter sometimes attaining a length of 5 m. Beautiful skeletons are preserved in the British and Berlin Museums. Several North American species have been referred to this genus.

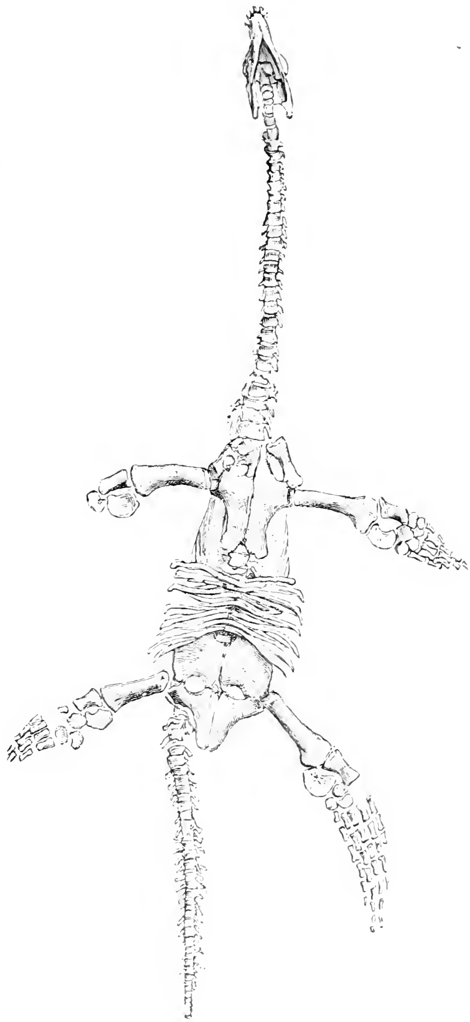


FIG. 280.

Plesiosaurus dolichodeirus, Conyb. Lower Lias: Lyme Regis; Dorsetshire. Skeleton, ventral aspect, $^1/_{13}$ (after Hawkins).

Eretmosaurus, Seeley. Coracoids truncated anteriorly, and not extending in front of the glenoid cavity for the humerus. Scapulae extending downward and inward so as to become fused with each other and also with coracoids in the median line. Clavicular arch degenerate. Lower Lias; England.

Rhomaleosaurus, Seeley. *R. cramptoni*, Carte sp. *Colymbosaurus*, *Muraenosaurus*, Seeley. Upper Jura; England.

Cryptocleidus, Seeley. Resembles *Plesiosaurus*, except that the ribs are all single-headed, and pectoral arch is like that of *Eretmosaurus*, *Elasmosaurus*, etc. Upper Jura; England.

Cimoliasaurus, *Oligosimus*, *Brimosaurus*, Leidy; *Piptomerus*, *Orophosaurus*, *Embaphias*, *Polycotylus*, *Uronautes*, Cope; *Trinacromerum*, Cragin; *Mauisaurus*, Hector. These genera from the Upper Cretaceous of North and South America and New Zealand are for the most part yet insufficiently characterised, and include very diverse forms. The first-named is also European.

Pliosaurus, Owen (*Ischyrodon*, *Thaumatosaurus*, v. Meyer; *Peloneustes*, Lydd.; *Liopleurodon*, Sauv.), (Fig. 281). Gigantic Plesiosaurs with relatively large head and short neck. Skull depressed and narrow, attaining a length of 1·3 m. Internal nares remotely situated, mandibular symphysis considerably extended. Margin of upper jaw on either side with a series of about thirty powerful carinated teeth, sometimes 25 cm. long; the crown traversed for a portion of its height by strong elevated ridges. About twenty very short cervicals with double-headed ribs. Limb girdles similar to those of *Plesiosaurus*. Lias to Upper Jura; England, Northern France, Switzerland, Bavaria, Russia, and India.

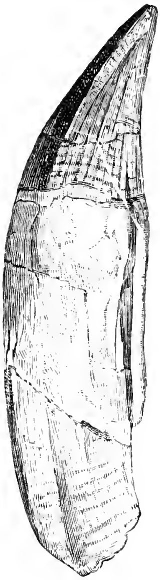


Fig. 281.
Pliosaurus grandis, Owen. Kimmeridgian; Dorsetshire. Tooth, 1/4 (after Owen).

Megalneusaurus, Knight. Largest known Plesiosaur, the humerus attaining a length of 1 m., or about one-half the length of the entire fore-limb, and articulating only with the radius and ulna. The latter bones are polygonal and closely applied against each other and the three proximal carpals. Coracoids produced in front of the glenoid cavity; vertebrae elongated. Upper Jura; Wyoming. *M. rex*, Knight.

Elasmosaurus, Cope (Fig. 282). A skeleton in Philadelphia lacking the head exceeds 13 m. in length. The seventy-two cervicals are longer than deep, and bear short, single-headed ribs. The neural arches are all fused with their centra, but the chevron bones are articulated with the caudals. Pectoral arch similar to that of *Cryptoclidus*. Limbs and greater part of the skull unknown. Upper Cretaceous; Kansas.

Dolichorhynchus, Willist. Head long, snout very slender; mandibular symphysis much elongated; teeth small, numerous; vomers very long; posterior nares small, included between vomer and palatines; no posterior palatine foramina; pterygoids contiguous only at extremities. Neck shorter than head; cervical ribs single-headed; axis with ribs; nineteen cervicals and about thirty dorsals are present; tail very short, conical. Clavicular arch complete, the clavicles articulating with the long precoracoidal process. Ischium elongate. Humerus and femur moderately expanded; three propodials. Known by a nearly complete skeleton about 3 m. in length from the Niobrara Cretaceous of Kansas.

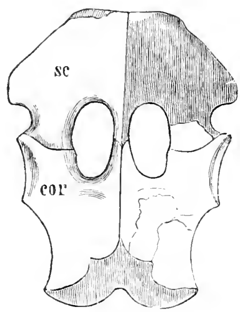


Fig. 282.
Elasmosaurus platyurus, Cope. Upper Cretaceous; Kansas. Pectoral arch, shaded parts restored; greatly reduced. *cor*, Coracoid; *sc*, Scapula (after Cope).

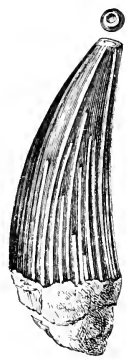


Fig. 283.
Polyptychodon interruptus, Owen. Cenomanian; Kelheim Bavaria. Tooth, 1/1.

Polyptychodon, Owen (Fig. 283). Imperfectly known, teeth resembling those of *Pliosaurus*, but with more prominent coronal ridges, some of which extend to the apex. Middle and Upper Cretaceous: England, Germany, and Russia.

Order 5. THEROMORPHA. Cope. (*Anomodontia*, Seeley, *non* Owen.)[1]

Primitive land reptiles with more or less biconcave vertebrae and limbs adapted for habitual support of the body. Investing bones of temporal region either forming a continuous shield or contracting into a single broad arcade, sometimes irregularly perforated. Quadrate fixed, often reduced in size. Pineal foramen present. Teeth thecodont, occasionally wanting. Pectoral arch with well-developed epicoracoids (precoracoids), clavicles, and T*-shaped interclavicle, besides scapulae and coracoids. All the elements in both limb girdles either fused or immovably united by suture. Humerus with entepicondylar foramen and prominent delto-pectoral crest. Extremities pentadactylate. Sacrum consisting of two to six vertebrae; anterior ribs completely or imperfectly double-headed, abdominal ribs wanting.*

Many widely dissimilar characters are exhibited by the various groups of ancient reptiles, which have received the general designation of *Theromorpha*, in allusion to their resemblance in certain skeletal peculiarities to the lowest mammals (*Monotremata*). They are also often called Anomodonts, on account of their remarkable dentition. There can be no doubt that these creatures occupy an intermediate position between the highest Labyrinthodonts, such as *Mastodonsaurus*, and monotreme mammals; and it is altogether probable that from amongst some of their number with one robust zygomatic arch and triconodont teeth, the *Mammalia* arose.

Theromorphous reptiles represent not only a transitional stage between mammals and amphibians, but they form a collective group, uniting in themselves characters that are elsewhere found distributed amongst various subdivisions of both reptiles and mammals. No other reptilian order has the three elements of the pelvic arch on each side fused into an innominate bone, as in mammals. The intimate union of the bones of the pectoral arch is paralleled among the *Salamandridae* and *Sauropterygia*; and the sacrum, formed sometimes of a number of vertebrae, resembles that of Dinosaurs and mammals. The differentiation of the marginal teeth into incisors, canines, and molars, and the occasional development of a strikingly mammalian form of limb (*Theriodesmus*) and a tripartite or even dicondylic basioccipput (*Cynognathus*), are significant characters. A distinguishing feature between this order and *Squamata* is the fixation of the quadrate; and the absence of a lateral temporal vacuity, with an arcade above and below, distinguishes it from all other *Archosauria* (Rhynchocephalians, Dinosaurs, Crocodiles, and Pterosaurs).

The term *Anomodontia*, although restricted by Owen to the group of Dicynodonts, is made synonymous by some authors with *Theromorpha*, or *Theromora*, as they are sometimes called.

[1] Literature:
Cope, E. D., The Reptilian order Cotylosauria (Proc. Amer. Phil. Soc. vol. XXXIV. p. 436), 1896. —*Ibid.* vol. XXXV. (1896), p. 122.—*Newton, E. T.*, Some new Reptiles from the Elgin Sandstone (Phil. Trans. vol. CLXXXIV. p. 436). 1893.—*Owen, R.*, On Dicynodon (Trans. Geol. Soc. vol. VII. p. 59), 1845.—On some Reptilian fossils from South Africa (Quar. Journ. Geol. Soc. vol. XVI. p. 49). 1860.—*Ibid.* vols. XXXII. (1876), p. 95; XXXVI. (1880), p. 414; XXXVII. (1881), p. 261; and XL. (1884), p. 146.—On Dicynodont Reptiles (Phil. Trans. vol. CLII. p. 442), 1862.—Catalogue of the fossil Reptilia of South Africa in the British Museum. London, 1876.—*Seeley, H. G.*, Researches on the Anomodont Reptiles and their allies (Phil. Trans. vol. CLXXIX. p. 59). 1888.—*Ibid.* vols. CLXXX. (1889), p. 215; CLXXXIII. (1892), p. 311; CLXXXIV. (1893), p. 488; CLXXXV. (1894), p. 987; and CLXXXVI. (1895), p. 59. Also Ann. Mag. Nat. Hist. [7], vol. i. (1898), p. 164, and Quar. Journ. Geol. Soc. vol. LVI. (1900).

Sub-Order I. PAREIASAURIA. Seeley. (*Cotylosauria*, Cope.)

Head completely covered by a bony roof; parietal foramen large; narial openings separate. Marginal teeth arranged in a more or less uniform series. Vertebral centra pierced for the persistent notochord.

The skeletal characters of this group proclaim a very close relationship with the higher Labyrinthodont Amphibians. In the typical genus, *Pareiasaurus*, the external bones of the skull are sculptured, but no true mucous canals have been observed.

Family 1. Pareiasauridae. Cope.

Teeth conical, or with compressed, cuspidate crown, those on the margin of the jaws arranged in close regular series. Smaller teeth usually present on palatines, pterygoids, and vomers. Pelvic bones fused in the adult. Limbs short and stout. Permian and Trias.

Pareiasaurus, Owen (Fig. 284). Known by tolerably complete skeletons over 2·5 m. long from South Africa and Northern Russia. Skull broad, depressed, and triangular in form, the external bones coarsely sculptured, but their sutures not clearly distinguishable. Orbits relatively small, laterally

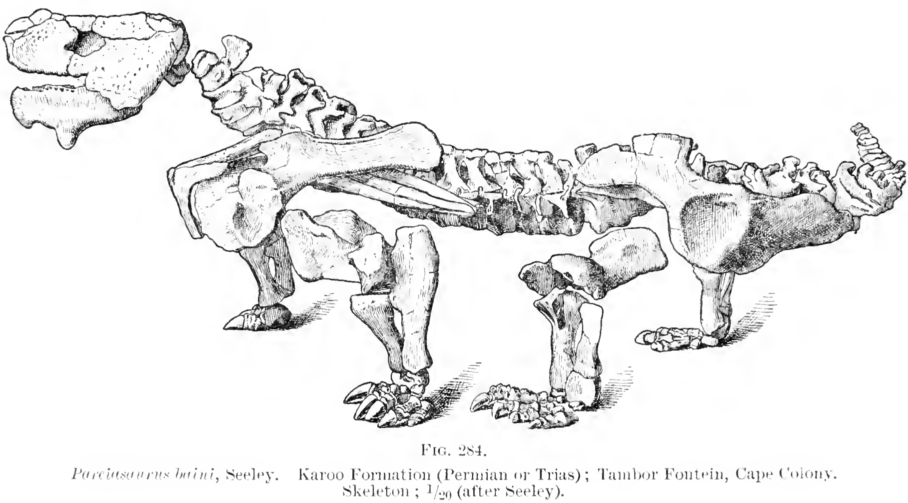


Fig. 284.

Pareiasaurus baini, Seeley. Karoo Formation (Permian or Trias); Tambor Fontein, Cape Colony. Skeleton; $^1/_{20}$ (after Seeley).

placed. Occipital condyle slightly indented. Bones of the palate fused, and bearing several series of small teeth. There are about eighteen presacral vertebrae, each with a deepened articulation for the single-headed ribs. Small intercentra occur between all the dorsal vertebrae; the four sacrals are not fused. About thirty caudal vertebrae, the anterior ones with short ribs, and nearly all with neural arches and chevron bones. Scapula very long, like that of Dinosaurs. Coracoid small and subrectangular, epicoracoid narrow and triangular; clavicles robust, meeting in the middle line and resting on the front border of the large T-shaped interclavicle. A supraclavicle also said to be present on each side. Humerus short, massive, expanded at the ends; epicondylar foramen not observed. Ulna very stout, with prominent olecranon process. Pelvic bones massive, coössified; acetabulum closed. Hind limb slightly shorter than the fore, and digits rather smaller; the five ungual phalanges clawed. *P. bombifrons*, *P. serridens*, Owen: *P. baini*, Seeley. ? *Tapinocephalus*, *Anthodon*, Owen. Karoo Formation; South Africa.

Elginia, Newton. Known only by the skull, which is about 15 cm. long, triangular, coarsely sculptured, and provided with a number of paired bosses and spinous or horn-like defences. These occur along the posterior and lateral margins, and on the parietal, frontal, and nasal elements. Teeth with slightly constricted base and serrated crowns. Supposed Trias of Elgin, Scotland.

Procolophon, Owen (Fig. 285). Skull about 5 cm. long, short and triangular, not externally sculptured. Orbits greatly enlarged, and temporal

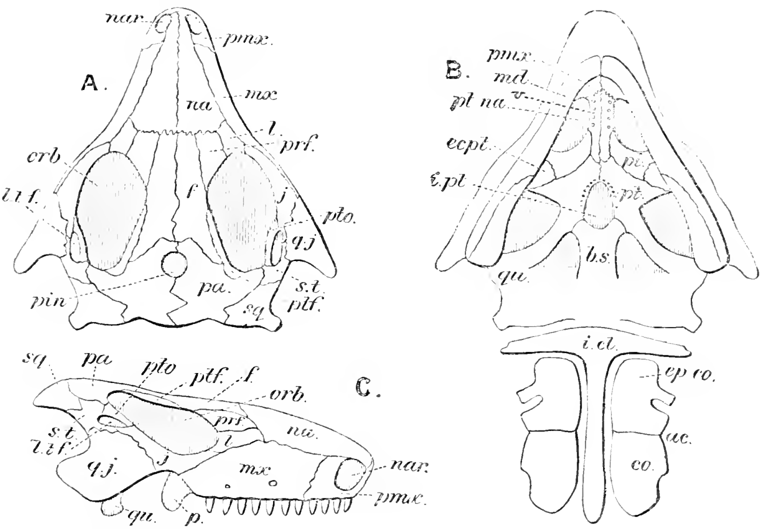


FIG. 285.

Procolophon trigoniceps, Owen. Karoo Formation (Permian or Trias); South Africa. Restoration of skull from superior (*A*), inferior (*B*), and lateral (*C*) aspects, also part of the pectoral arch, slightly reduced. *ac*, Glenoid cavity for humerus; *bs*, Basisphenoid; *co*, Coracoid; *ecpt*, Ectopterygoid; *epco*, Epicoracoid; *f*, Frontal; *icl*, Interclavicle; *ipt*, Interpterygoid vacuity; *j*, Jugal; *l*, Lachrymal; *ltf*, Lateral temporal vacuity; *md*, Mandible; *mx*, Maxilla; *na*, Nasal; *nar*, Anterior nares; *orb*, Orbit; *p*, Downward ectopterygoid process; *pa*, Parietal; *pin*, Pineal foramen; *pl*, Palatine; *pmx*, Premaxilla; *prf*, Prefrontal; *pt*, Pterygoid; *ptna*, Posterior nares; *ptf*, Postfrontal; *pto*, Postorbital; *qj*, Quadrato-jugal; *qu*, Quadrate; *st*, Supratemporal or prosquamosal; *sq*, Squamosal; *v*, Vomer (from A. S. Woodward).

arcade pierced by a slight vacuity. Teeth conical; a series of minute teeth present on vomer and pterygoids. Interclavicle T-shaped, with elongated arms; epicoracoid notched. Karoo Formation; South Africa.

Aristodesmus, Seeley. Lower Trias; Switzerland. ? *Phanerosaurus*, v. Meyer. Permian; Saxony.

Family 2. **Pariotichidae.** Cope.

Teeth in more than one series in one or both jaws, and with cylindric roots; vertebrae ossified. Permian.

Otocoelus, Cope. Skull about 12 cm. long, externally sculptured, but without bosses. Dorsal carapace consisting of a series of twelve or more transversely elongated bands of bone alternating with the ribs. Permian; Texas. *O. testudineus*, Cope.

Pariotichus (*Ectocynodon*), *Isodectes*, *Pantylus*, *Hypopnous*, Cope. Texas.

Family 3. **Diadectidae.** Cope.

Anterior teeth obtusely conical, the other marginal teeth laterally expanded, with tumid bases and inner and outer cusps of unequal height. Vomer with minute teeth. Basioccipital loosely articulated. Permian.

Empedias, Cope (*Empedocles*, Cope). Skull triangular, 50 cm. long. Sacrum of two vertebrae; pelvic bones fused. Permian; Texas.

Diadectes, *Chilonyx*, *Bolbodon*, Cope. Permian; Texas.

Sub-Order 2. **THERIODONTA.** Owen. (*Cynodontia*, Owen.)

Investing bones of temporal region contracting into a single broad arcade, sometimes irregularly perforated; supratemporal vacuity large, quadrate small. External bones not sculptured. Occipital condyle bilobate; premaxillae separate; marginal teeth differentiated into incisors, canines, and molars. External nares terminal, separate, or undivided; internal openings displaced backwards, owing to development of secondary palate.

The skull of Theriodonts is remarkably similar in form to that of carnivorous mammals, and the dentition exhibits modifications unusual among reptiles. The mandible bites within the upper jaw, and the lower canines cross in front of the upper as in mammals. Owing to the development of a secondary or false palate by plates from the maxillae and palatines, the opening of the internal nares on the roof of the mouth is displaced backward, as in crocodiles and mammals. An approach to the dicondylic condition of the mammalian skull is also frequently observed. The skeleton of the trunk and limbs is imperfectly known.

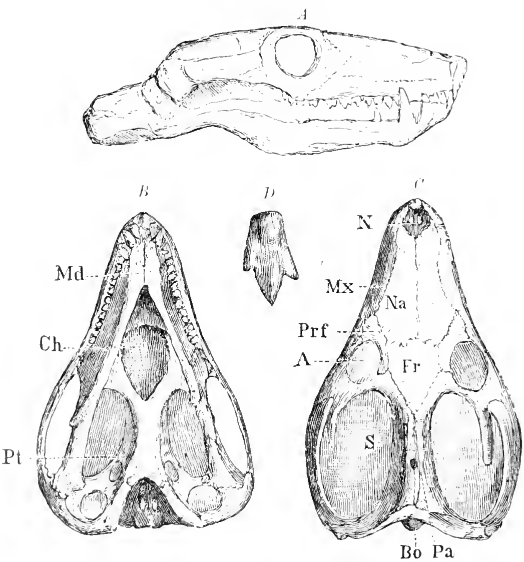


Fig. 286.

Galesaurus planiceps, Owen. Karoo Formation; Basutoland, South Africa. Skull, slightly restored, from lateral (*A*), palatal (*B*), and superior (*C*) aspects, $^1/_2$. *D*, Posterior tooth, enlarged. *a*, Orbit; *bo*, basioccipital; *ch*, Posterior nares; *fr*, Frontal; *md*, Mandible; *mx*, Maxilla; *N*, Anterior narial opening; *na*, Nasal; *pa*, Parietal; *prf*. Prefrontal; *pt*, Pterygoid (after Owen).

Family 1. **Galesauridae.** Lydekker.

Palatal teeth insignificant or wanting; external narial openings confluent or separated; limb bones slender. Trias.

Galesaurus, Owen (*Nythosaurus*, Owen), (Fig. 286). Known only by the skull, which is less than 10 cm. long, and has the nares divided by a median septum. Four incisors above and three below, with one canine and a number of tricuspidate molars in each jaw. Karoo Formation; South Africa.

Lycosaurus, Owen (Fig. 287). Like the preceding, except that the molariform teeth are all simple cones, though more or less compressed and with finely serrated edges. There are about five of them on each side above and below. Karoo Formation; South Africa.

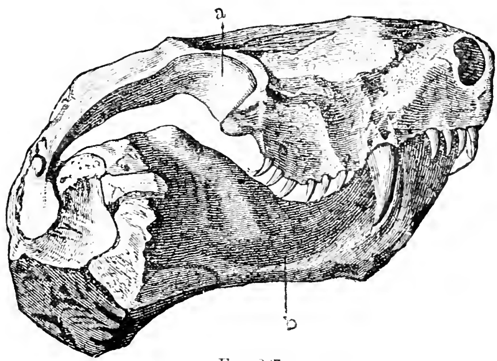


Fig. 287.
Lycosaurus curvimola, Owen. Karoo Formation: Kugaberg, Cape Colony. Skull, lateral aspect, 1/3. *a*, Orbit; *b*, Mandible (after Owen).

Aelurosaurus, Owen. Differs from *Lycosaurus* in having small, pointed teeth irregularly grouped on anterior half of the palate. Same horizon.

Cynognathus, Seeley. Skull remarkably mammalian-like, about 40 cm. long, with divided nares and two prominent convex condyles below the foramen magnum, composed chiefly of the exoccipitals. There are four serrated incisors in the upper and three in the lower jaw; and one canine and nine molars above and below on each side. Six cervicals, eighteen dorsals, five lumbars, and three or four sacrals. Accompanies the preceding. *C. crateronotus*, Seeley.

Cynochampsa, *Cynodraco*, *Cynosuchus*, *Gorgonops*, *Tigrisuchus*, Owen. Founded on more or less imperfect remains from the Karoo Formation of South Africa.

Family 2. **Deuterosauridae**. Seeley.

Canines large, with serrated anterior and posterior margins; no palatal teeth. Sacrum of two anchylosed vertebrae. Ribs double-headed. Scapula flat; ilium not produced anteriorly; acetabulum closed. Permian; Russia.

Deuterosaurus, Eichw. Skull with a median crest; incisors large and transversely compressed. Lachrymals greatly developed; quadrate large; scapula distally expanded.

Rhopalodon, Fischer. Like the preceding, but with serrated incisors, and lanceolate molars behind the canines. Supratemporal vacuity very small; sclerotic ring present.

The fragmentary remains described as *Brithopus*, *Orthopus*, and *Syodon* by Kutorga, and *Dinosaurus* by Fischer, are probably identifiable with the above genera, which they accompany. *Cliorhizodon*, Twelvetrees, is of uncertain position.

Family 3. **Tritylodontidae**. Cope.

Snout broad and obtuse. A pair of large incisors or canine-like teeth in front, apparently growing from a persistent pulp. Molariform teeth bearing two or three longitudinal series of tubercles. Posterior nares remote, and roofed over by secondary palate. Quadrate reduced. Trias.

This family is regarded by Seeley as typical of a distinct order of reptiles, *Gomphodontia*, and ancestral to mammals.

Tritylodon, Owen (Fig. 288). Known by small, decidedly mammalian-like crania. Karoo Formation; South Africa.

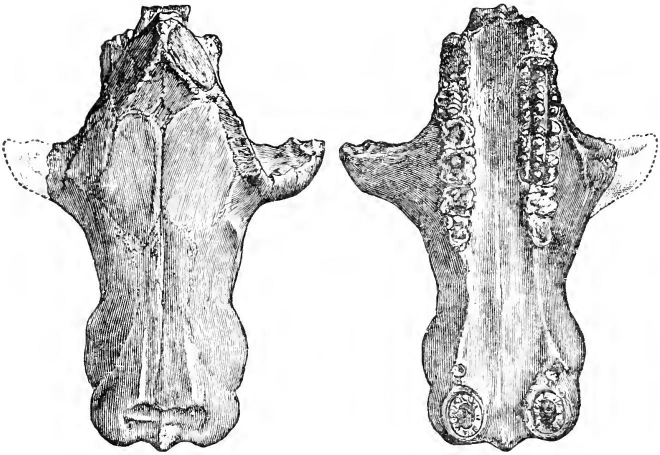


Fig. 288.
Tritylodon longaevus, Owen. Trias; Taba-chow, Basutoland, South Africa. Skull from superior and palatal aspects, 2/3 (after Owen).

Gomphognathus, *Diademodon*, *Microgomphodon*, *Trirachodon*, Seeley. The first-named has a double occipital condyle,

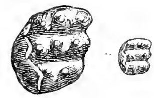


Fig. 289.
Triglyphus fraasi, Lyd. Upper Trias; Hohenheim, Würtemberg. Upper molar, 1/1 and 2/1 (after Fraas).

and its single zygomatic arch resembles that of mammals. *Theriodesmus*, Seeley, is known by a remarkably mammalian-like fore-limb and manus. Karoo Formation; South Africa.

Triglyphus, Fraas (Fig. 289). Known only by minute teeth from the Upper Triassic Bone-bed of Hohenheim, near Stuttgart.

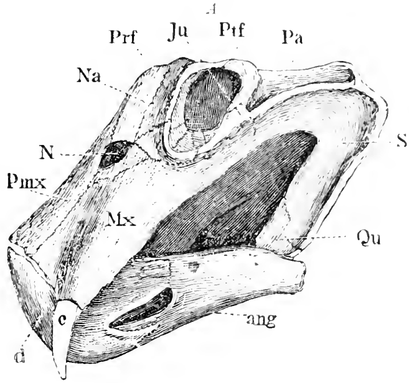
Sub-Order 3. ANOMODONTIA. Owen. (*Dicynodontia*, Owen.)

Investing bones of temporal region contracting into a single broad arcade, formed principally by the enormously developed squamosal. External bones not sculptured; supratemporal vacuity large; quadrate small; premaxillae fused; external nares separated. Jaws edentulous, or with a single pair of tusk-like teeth in the maxillae set in deep alveoli and growing from persistent pulps. Cervical ribs double-headed, dorsal single-headed. Sacrum of five or six vertebrae.

The Anomodonts or Dicynodonts are mostly large terrestrial reptiles of Triassic age, of which no complete skeletons have yet been discovered, but numerous crania, vertebrae, and other fragments are known from South Africa, East India, Ural, and Scotland.

The vertebral column consists of seven or eight cervical, twelve or thirteen dorsal, five or six sacral, and about twenty caudal vertebrae. The centra are short and slightly amphicoelous. Double-headed ribs are borne by the cervical, and single-headed ribs by the dorsal vertebrae. The cranial sutures (Fig. 290) are frequently obscure and difficult to determine. The brain cavity is very small and the surfaces for attachment of the muscles of the jaw unusually large. On either side of the upright occiput is an enormously developed squamosal, which forms the greater part of the single temporal arcade, and is fused with the small quadrate below. A foramen is enclosed by the parietals, which are small, and sometimes much reduced. The frontal and prefrontal form the superior border of the orbit, and the maxilla, lachrymal, and prefrontal the anterior. The orbits are laterally placed in about the middle of the skull, and in one genus (*Ptychognathus*) traces of a sclerotic ring have been observed. A narrow, curved bar, the postorbital, separates the orbit from the supratemporal vacuity, and the lower orbital boundary is formed by the maxilla together with a very massive jugal.

The nasals are steeply inclined toward the front, and form with the unpaired premaxilla a sometimes elongated rostrum. Small internasals are occasionally present below the anterior nares, which are placed laterally at the junction of the nasals, lachrymals, and premaxillae. The oral border of the



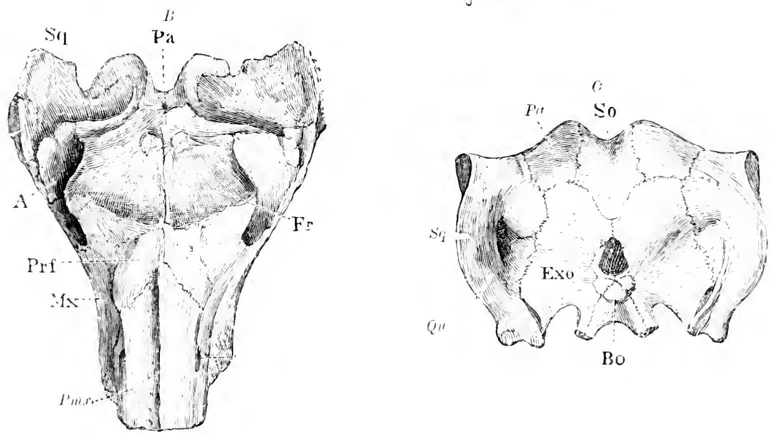


FIG. 290.

Ptychognathus declivis, Owen. Karoo Formation; Rhenosterberge, Cape Colony. Skull from lateral (*A*), superior (*B*), and posterior (*C*) aspects, $^1/_3$. *A*, Orbit; *ang*, Angular; *bo*, Basioccipital; *c*, Maxillary tusk; *d*, Dentary; *eo*, Exoccipital; *fr*, Frontal; *ju*, Jugal; *mx*, Maxilla; *N*, External narial opening; *na*, Nasal; *pa*, Parietal; *pmx*, Premaxilla; *prf*, Prefrontal; *ptf*, Postfrontal; *qu*, Quadrate; *so*, Supraoccipital; *sq*, Squamosal (after Owen).

latter forms a sharp, cutting edge, and was probably sheathed during life of the animal by a corneous layer, as in Chelonians and Aves. A pair of powerful, decurved, tusk-like teeth, one on each side, is developed by the maxillae, and the deep alveoli in which they are seated are indicated by an external folding of the plate. Even among toothless forms alveoli are present, but are occupied by osseous substance.

The basioccipital is short and takes part in the occipital condyle. In front of it on the lower side (Fig. 291) is placed a subrectangular basisphenoid which joins the very large pterygoids. The latter meet in the middle line, but leave a small interpterygoidal vacuity behind the narrow vomer. The backwardly directed internal nares are scarcely if at all covered by a secondary development of the palatine plates. The mandible is without a coronoid process, and the rami are fused at the symphysis. Their oral borders are sharp, and were probably once encased in horn.

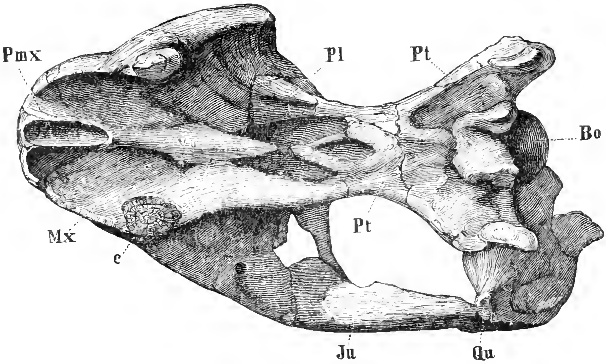


FIG. 291.

Dicynodon pardiceps, Owen. Karoo Formation; Fort Beaufort, Cape Colony. Palatal aspect of skull, 1/4. *bo*, Basioccipital; *c*, Maxillary tusk (fractured); *ju*, Jugal; *mx*, Maxilla; *pmx*, Premaxilla; *pl*, Palatine; *pt*, Pterygoid; *qu*, Quadrate (after Owen).

FIG. 292.

Dicynodon pardiceps, Owen. Anterior aspect of humerus, 1/4. *b*, Delto-pectoral ridge; *c*, Entepicondylar foramen (after Owen).

The scapula is a very long bone, similar to that of Monotreme mammals. It bears an acromial process and is attached by its proximal end to the coracoid and epicoracoid. The humerus is short and excessively stout, with an entepicondylar foramen; ulna and radius are separated. In the pelvic arch the three elements of each side are fused into an innominate bone which joins its fellow in a median

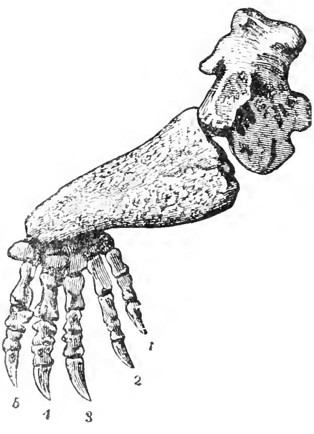


FIG. 293.

Eurycarpus oweni, Seeley. Karoo Formation; Schneebergkette, Cape Colony. Left fore-limb with impression of dermal covering, 1/3 (after Owen).

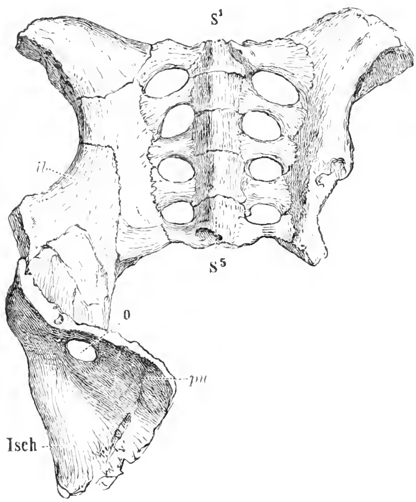


FIG. 294.

Platypodosaurus robustus, Owen. Karoo Formation; Cape Colony. Ventral aspect of sacrum and right half of pelvis. *il*, Ilium; *isch*, Ischium; *o*, Obturator foramen; *pu*, Pubis; s^1—s^5, Sacral vertebrae.

symphysis. The femur and crus are somewhat longer than the corresponding bones of the fore-limb.

Dicynodon, Owen (Figs. 291, 292). Skull attaining a length of 0·5 m. Transition from parieto-frontal to nasal region gradual; maxillae with a pair of tusk-like teeth. Abundant and represented by over a dozen species in the Karoo Formation of South Africa.

Oudenodon, Owen. Like the preceding, but toothless; possibly referable to females of *Dicynodon*.

Ptychognathus, Owen (*Lystrosaurus*, Cope), (Fig. 290). Frontal and nasal regions sloping at a sharp angle from top of the skull. Smaller than *Dicynodon*, which it accompanies.

Gordonia, Newton. Form of skull similar to *Dicynodon*, but much smaller, with more delicate bones and diminutive teeth; premaxilla nearly vertical. Supposed Trias of Elgin, Scotland.

Geikia, Newton. Resembling *Ptychognathus*, but toothless. Elgin Trias.

Eurycarpus, Seeley (Fig. 293); *Keirognathus*, Seeley; *Theriognathus*, *Titanosuchus*, *Platypodosaurus* (Fig. 294), Owen. All founded on fragmentary remains from the Karoo Formation of South Africa.

Sub-Order 4. PLACODONTIA. von Meyer.[1]

Bones of temporal region forming a single broad arcade; supratemporal vacuity large, opening superiorly; orbits and external nares laterally placed; the latter separate and remote. Palate with a paired longitudinal series of pavement teeth, and similar ones present in single series on the dentary. Anterior teeth above and below cylindro-conical; maxillae with a series of depressed, conical, or molariform teeth.

Placodonts are remarkable for their peculiarly modified dentition, which is unparalleled among reptiles. The pavement-like crushing teeth of the palate and lower jaw attain considerable size, and exhibit flat or slightly arched crowns, usually dark-coloured, and smooth or finely wrinkled. They are replaced by successional teeth developed beneath them.

The skull is similar in form to that of Dicynodonts and certain Theriodonts; and as in these groups the temporal and jugal arches unite to form a single, broad, bony arch across the postero-lateral region of the cranium. The quadrate is fused with the squamosal and jugal, and exposes a prominent transverse condyle. On the under side the palatines and pterygoids unite to form an extensive bony palate for the support of the pavement teeth. The internal nares are placed far forwards, but the external openings and orbits occupy similar positions to those in *Dicynodon*. Of the rest of the skeleton nothing is known. The detached teeth were for a long time confounded with fishes, until their reptilian nature was demonstrated by Owen. All the remains are from the marine Trias of central Europe.

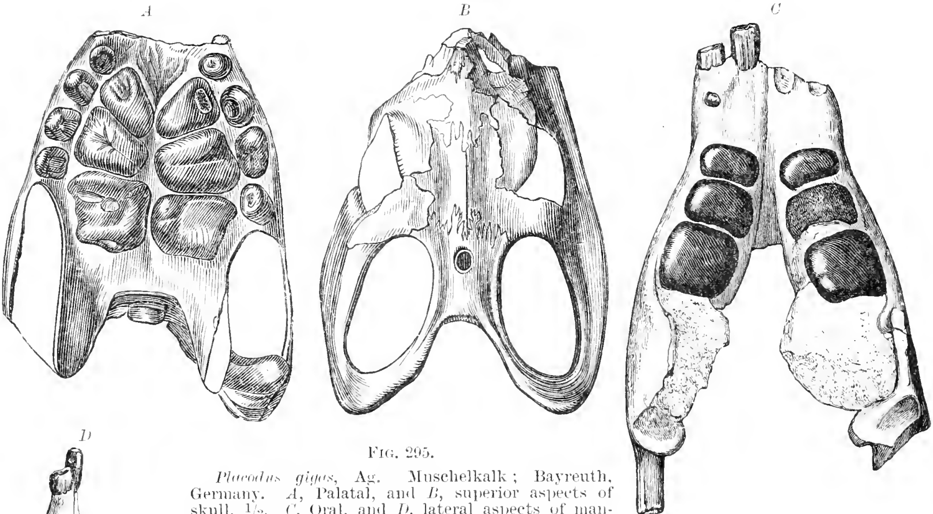
Placodus, Agassiz (Figs. 295, 296). Skull not much longer than broad, superiorly arched, the snout somewhat produced. Premaxillae and symphysis of lower jaw with cylindro-conical incisors. On either side of the palate and

[1] Literature:

Meyer, H. von, Unterkiefer von Placodus andriani (Palaeontogr. vol. X. p. 59), 1862.—*Ibid.* vol. XI. 1863.—*Münster, G. von*, Ueber einige ausgezeichnete fossile Fischzähne aus dem Muschelkalk bei Bayreuth. 1830.—Ueber Placodus rostratus (Beiträge zur Petrefaktenkunde, pt. 4), 1843.—*Owen, R.*, Description of the skull and teeth of Placodus laticeps (Phil. Trans. vol. XLIX.), 1858.

on the dentary are three large rectangular pavement teeth; maxillae with a single series of depressed, conical teeth. Detached teeth are abundant in the Muschelkalk of Southern Germany and France, rare in the Wellendolomite and Alpine Keuper.

Cyamodus, v. Meyer. Skull triangular, snout much compressed. Supratemporal vacuity elongated oval, nearly three times as large as the orbits,



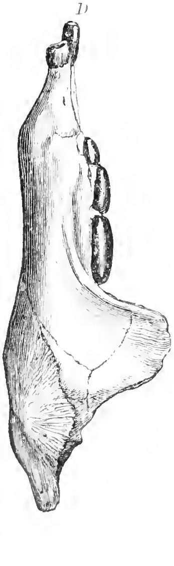


FIG. 295.

Placodus gigas, Ag. Muschelkalk; Bayreuth, Germany. *A*, Palatal, and *B*, superior aspects of skull, $^1/_3$. *C*, Oral, and *D*, lateral aspects of mandible, $^1/_3$.

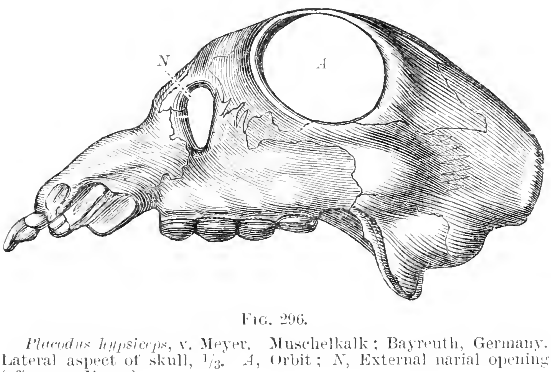


FIG. 296.

Placodus hypsiceps, v. Meyer. Muschelkalk; Bayreuth, Germany. Lateral aspect of skull, $^1/_3$. *A*, Orbit; *N*, External narial opening (after von Meyer).

which are placed in anterior third of the skull. Anterior nares small, separate, nearly terminal. On either side of the palate are placed two or three rounded or elliptical-crushing teeth, the hindmost at least twice the size of the anterior. Muschelkalk; Bavaria. *C. rostratus*, Münster sp.

Range and Distribution of the Theromorpha.

Divisions.	Permian.		Trias.	
	Europe.	N. America.	Europe.	S. Africa.
I. PAREIASAURIA.				
1. *Pareiasauridae*	———		———	———
2. *Pariotichidae*		———		
3. *Diadectidae*	(Ural ?)	———		
II. THERIODONTIA.				
1. *Galesauridae*	·····	·····	·····	———
2. *Deuterosauridae*	———			
3. *Tritylodontidae*	··		———	———
III. ANOMODONTIA		·····	———	———
IV. PLACODONTIA	·····	·····	———	

Order 6. CHELONIA. (*Testudinata.*)[1]

Reptiles of stout and wide form of body, encased in a more or less complete bony shell. Quadrate immovably united to the cranial arches. Jaws toothless, but covered with horny sheaths; premaxillae very small, palate completely closed by junction

[1] Literature:
Baur, G., Osteologische Notizen über Reptilien (Zool. Anz. vol. IX. No. 238), 1886.—*Ibid.* vol. XI. (1888), pp. 417, 592; and vol. XII. (1889), p. 40.—Notes on some little known American fossil Tortoises (Proc. Acad. Nat. Sci. Philadelphia, p. 411), 1891.—Bemerkungen über die Phylogenie der Schildkröten (Anat. Anz. vol. XII. p. 561), 1896.—*Boulenger, G. A.*, Catalogue of Chelonians in the British Museum. London, 1889.—*Case, E. C.*, On the osteology and relationships of Protostega (Journ. Morph. vol. XIV. No. 1), 1897.—*Cope, E. D.*, The Reptiles of the American Eocene (Amer. Nat. vol. XVI. p. 979), 1882.—*Ibid.* vol. XXX. p. 398, 1896.—*Dames, W.*, Die Chelonier der norddeutschen Tertiärformation (Palaeont. Abhandl. Dames und Kayser, vol. VI.), 1894.—*Dollo, L.*, Note sur les Cheloniens de Bernissart (Bull. Mus. Roy. d'Hist. Nat. Belg. vol. III. p. 63), 1884; *ibid.* vol. IV. (1886), pp. 69, 129; and *ibid.* vol. V. (1888), p. 59.—On the humerus of Euclastes (Geol. Mag. [3], vol. V. No. 6), 1888.—*Fraas, E.*, Proganochelys Quenstedtii Baur (Jahresh. Vereins Naturk. Württb.), 1899.—*Gray, J. E.*, Notes on the families and genera of Tortoises (Proc. Zool. Soc. vol. XII. p. 165), 1869.—*Hoffmann, C. K.*, Chelonia, in Bronn's Classen und Ordnungen des Thierreichs, vol. VI. 1879.—*Lydekker, R.*, Siwalik and Narbada Chelonia (Palaeont. Indica, ser. X. vol. III.), 1886.—Catalogue of the fossil Reptilia and Amphibia in the British Museum, Part III. London, 1889.—*Maack, G. A.*, Die bis jetzt bekannten fossilen Schildkröten, etc. (Palaeontogr. vol. XVIII.), 1869.—*Meyer, H. von*, Zur Fauna der Vorwelt, Parts I. and IV. Frankfort, 1845-60.—*Owen, R.*, and *Bell, R.*, Monograph of the fossil Reptilia of the London Clay. Part I. (Palaeont. Soc.), 1851.—*Owen, R.*, Monograph of the fossil Chelonian Reptilia, etc., *ibid.* 1852-53.—*Pictet, F. J.*, and *Humbert, A.*, Monographie des Cheloniens de la Molasse Suisse. Geneva, 1856.—*Portis, A.*, Ueber fossile Schildkröten aus dem Kimmeridge von Hanover (Palaeontogr. vol. XXV.), 1878.—Les Cheloniens de la Molasse Vaudoise (Mém. Soc. Paléont. Suisse, vol. IX.), 1882.—*Reinach, A. v.*, Schildkrötenreste im Mainzer Tertiärbecken, etc. (Abhandl. Senckenb. naturf. Ges. vol. XXVIII.), 1900.—*Rütimeyer, L.*, Die fossilen Schildkröten von Solothurn (Denkschr. Schweiz. naturf. Gesellsch. vol. XXII.), 1867; and *ibid.* vol. XXV. (1873).—Ueber den Bau von Schale und Schädel bei lebenden und fossilen Schildkröten (Verhandl. naturf. Gesellsch. Basel, vol. III. p. 255), 1872.—*Sacco, F.*, Cheloni Astiani del Piemonte (Mem. Acad. Torino, vol. XXXIX.), 1889.—*Wagner, J. A.*, Schildkröten und Saurier aus den lithographischen Schiefer (Abhandl. bayer. Akad. Wissensch. II. Classe, vol. VII. p. 291), 1853; and *ibid.* vol. IX. (1861), p. 68.—*Wieland, G. R.*, On Archelon ischyros, Protostega, etc. (Amer. Journ. Sci. [4], vol. II. p. 399), 1896; and *ibid.* vol. V. (1898), p. 15.—*Williston, S. W.*, A new turtle from the Kansas Cretaceous (Trans. Kans. Acad. Sci. vol. XVII. p. 195), 1901.

of the pterygoids with the basisphenoid, and frequently also with one another. Narial opening single and terminal. No sternum; ribs single-headed; two sacral vertebrae. Pubes and ischia forming symphyses. Humerus without entepicondylar foramen. Pentadactyle walking limbs or paddles.

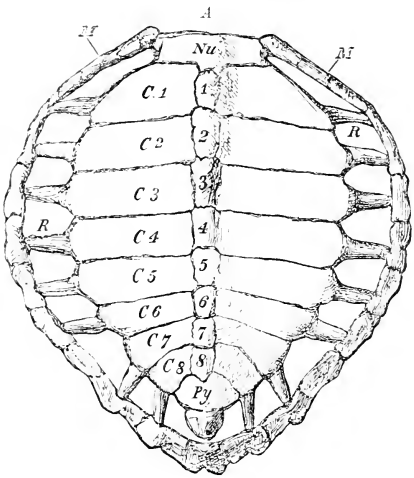
Chelonians form an extremely homogeneous and narrowly circumscribed group, their peculiar organisation separating them widely from all other reptiles, and their origin and phylogeny being very obscure. A relationship with the Triassic Dicynodonts is perhaps indicated by the skull, which is strikingly similar; and certain features of the palate and pectoral girdle are suggestive of the Sauropterygia, Rhynchocephalia, and Labyrinthodont Stegocephalians. Chelonians first make their appearance in the Upper Keuper of Southern Germany (*Proganochelys*) and exhibit all the typical characters of the order; nor do they undergo any noteworthy modifications in structure during all their subsequent history.

Shell.—The most distinctive character of the group is the investment of the body in a more or less rigid shell or box, which is composed partly of the modified neural spines of the dorsal vertebrae, and partly of dermal ossifications more or less intimately united with the former. Into this capsule the limbs, tail, and usually also the neck and head are capable of being retracted.

In most forms both the dorsal shell or *carapace*, and the ventral or *plastron*, are superficially covered with a leathery or corneous epidermal layer, which is divided by indented sutures into a few large scutes or *shields*. These epidermal shields are arranged quite independently of the subjacent osseous plates, and are wanting only in *Trionychoidea* and *Dermochelys*. They afford valuable diagnostic characters amongst recent forms, but as a rule are completely destroyed by the fossilisation process, their sutures being merely indicated by shallow sulci. On the carapace they form a median dorsal and a paired lateral series, there being usually five unpaired or *vertebral shields*, and four or five pairs of *costal shields* (Figs. 305, 306). Round the periphery there is also a series of about twenty-four *marginals* (*marginalia*), the anterior of which is called the *nuchal*, and the posterior, sometimes double, the *caudal* or "supracaudal" shield. Five or six pairs of epidermal shields are present in the plastron, but there is no median series. The anterior pair is designated as gulars, following which in the order named are the humerals, pectorals, abdominals, femorals, and anals. Occasionally the gulars are separated in front by a single or double intergular shield.

The osseous plates of the *carapace* (Fig. 297) are formed partly by lateral expansions of the spinous processes of eight dorsal vertebrae (second to ninth), and of the ribs belonging to these vertebrae; and in still greater part by dermal ossifications overlying the ribs and joining the expanded spinous processes on either side of the median line. The plates of the carapace thus differ in number and arrangement from the epidermal shields, inasmuch as they coincide with the vertebrae and ribs. The latter retain their individuality more or less distinctly on the visceral side of the costal bones, and extend across the vacuities when the carapace is incomplete.

The median series of eight bony plates in the carapace are called *neurals* or "vertebrals"; and the lateral pieces lying superjacent to the ribs, which are firmly united to one another and to the neurals by suture, are termed *pleurals* (or "costals"). Sometimes not all of the neural bones are developed, and among the recent *Pleurodira* of Australia they are wanting altogether. In front of the series of neural plates is a large hexagonal plate, the nuchal, which is broader than long, and situated above the first dorsal vertebra. This plate, which is present in all Chelonians, is a cartilage bone, developed simultaneously with the neurals, and has been supposed to represent the modified ribs of the last cervical. Continuing the series of neurals behind are two to four unpaired membrane bones termed the *pygal* plates or "postneurals," the last of which, in shape and position, forms part of the peripheral series. In addition to the posterior azygous peripheral or pygal, there are eleven (exceptionally twelve) peripheral plates on each side, except in *Staurotypus* and *Cinosternum*,



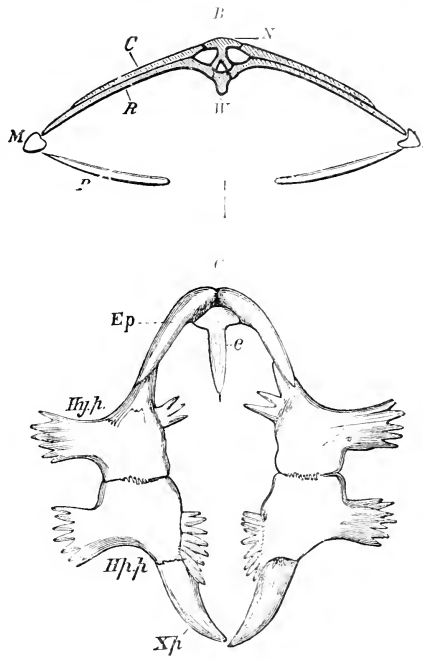


FIG. 297.

Chelone midas, Latr. Recent; Atlantic Ocean. *A*, Dorsal aspect of carapace. *B*, Section of shell. *C*, Ventral aspect of plastron. *c*1—*c*8, Costal plates; *e*, Entoplastron; *ep*, Epiplastron; *hyp*, Hyoplastron; *hpp*, Hypoplastron; *m*, Marginals; *n*, Expanded neural spine; *nu*, Nuchal; *p*, Plastron; *py*, First suprapygal; *r*, Ribs; *w*, Vertebral centrum; *xp*, Xiphiplastron; 1—8, Neural plates, followed by two suprapygals and pygal.

which have but ten. The peripherals and pygals owe their origin entirely to dermal ossification.

There are normally eight pairs of neural plates, but some fossil marine forms have nine or ten. The first neural is constantly the broadest, the last the smallest; in a few forms these plates are of unequal width, alternately widening proximally and narrowing distally. The distal extremity of the rib persists as a free point fitting into a corresponding socket of the peripheral plate. In a number of forms there are persistent fontanelles or vacuities between the neural and peripheral plates, and also in the plastron.

The *plastron* arises exclusively from dermal ossification, and is entirely independent of the pectoral arch, with which it has sometimes been homologised. It consists usually of nine bones, a median anterior entoplastron (or "interclavicular"), and on each side following this in the order named, an epiplastron, a hyoplastron, a hypoplastron, and a xiphiplastron. Some authors have regarded the epiplastra as equivalent to the clavicles, the entoplastron to the interclavicle, and the other elements as modifications of the Stegocephalian and Rhynchocephalian abdominal ribs. An entoplastron is wanting among the *Cinosternidae*, and in *Baëna* and the *Pelomedusidae* the usual number of nine bones is increased to eleven, the additional elements being the mesoplastra, situated between the hyo- and hypo-plastra. The mesoplastra may have served in the primitive condition to close the lateral vacuities. Until late in life in the *Chelydridae*, and throughout in the *Chelonidae*, the paired abdominal bones are separated by wide fontanelles (Fig. 297, *C*), whilst in all other recent Cryptodires the plastron forms in the adult a solid shell, which may be divided into two or three portions by the presence of one or two transverse ligamentous hinges, as in *Cistudo*, *Emys*, etc.

"In the adult of most genera the hyo- and hypo-plastra are united with the marginal plates by suture; in a few they are narrowly separated from the latter by ligament, or the outer border of these bones form digitate dentations, which may either articulate by gomphosis with the marginals or be entirely free. The space between the body of the plastron and the marginals is called the bridge; it is particularly short or absent in those *Testudinidae* in which the plastron is movable, and long and narrow in those forms (*Chelydridae*) in which the plastron is particularly small, the whole shield being cruciform. In such *Testudinidae* as have the plastron suturally united with the carapace, the hyo- and hypo-plastron each sends up a process, respectively termed the axillary and inguinal buttress, which anchylose either with the inner surface of the marginals or with the costals; these buttresses are least developed in the land tortoises and most of the *Testudinidae* frequenting deep water, in which genera they form very large septa, nearly reaching the vertebral region and forming two lateral chambers occupied by the lungs" (Boulenger).

Vertebral column.—The cervical region is extremely flexible, and comprises eight non-costiferous vertebrae, the first of which is biconcave, and the last biconvex. Transverse processes are absent or extremely rudimentary in this region. The ten rib-bearing dorsal vertebrae are immovably united with one another and with the carapace, following which are two amphiplatyan sacral vertebrae. The sacral ribs are, as on the last dorsal vertebra, suturally united with both centrum and neural arch; the first is the most developed, and considerably expanded distally. The caudal vertebrae range in number between sixteen and thirty-five, the more usual number being from twenty to twenty-five. The centra are in most cases procoelous, but sometimes opisthocoelous. Transverse processes or costoids are present on most of the vertebrae, and connected with the centrum and the arch. Neural spines are not developed, and chevron bones are absent or vestigial.

Skull.—The bones of the skull form a broad, often very convex roof, which is prolonged posteriorly in a strongly developed supraoccipital crest. The orbits are large and placed laterally in advance of the middle of the skull; the deeper the skull, the larger the orbits. The latter are completely encircled by four or five bones—the maxilla, prefrontal, sometimes the frontal, the postfrontal, and the jugal. The external nostril is single and terminal, bounded by the premaxillae, maxillae, and prefrontals or nasals. The parietals are of large size and distinct, being connected with the palate (except in the *Dermochelyidae*) by descending processes. An independent lachrymal bone is never present, and nasals occur only rarely among the *Pleurodira* and some *Cryptodira*. The anterior margin of the snout is formed by the small, usually distinct premaxillae.

The postfrontals are large in most Cryptodires, forming a postorbital arch; in the marine turtles the postfrontal unites in a long suture with the parietal, the whole or greater part of the temporal region being roofed over by bone. The temporal roof attains its greatest development in the *Chelonidae*, where three cranial arches are present—the postfronto-squamosal, the jugo-quadratojugal, and the parieto-squamosal. In all other Cryptodires the parietal is widely separated from the squamosal, and as a rule the squamosal is separated from the postfrontal. In a few genera there is no bony temporal arch, and the quadrato-jugal is rudimentary or absent. The jugal, when present, takes part with the maxilla in the lower border of the orbit, being excluded from it only in the genus *Platysternum*. The proötic and opisthotic

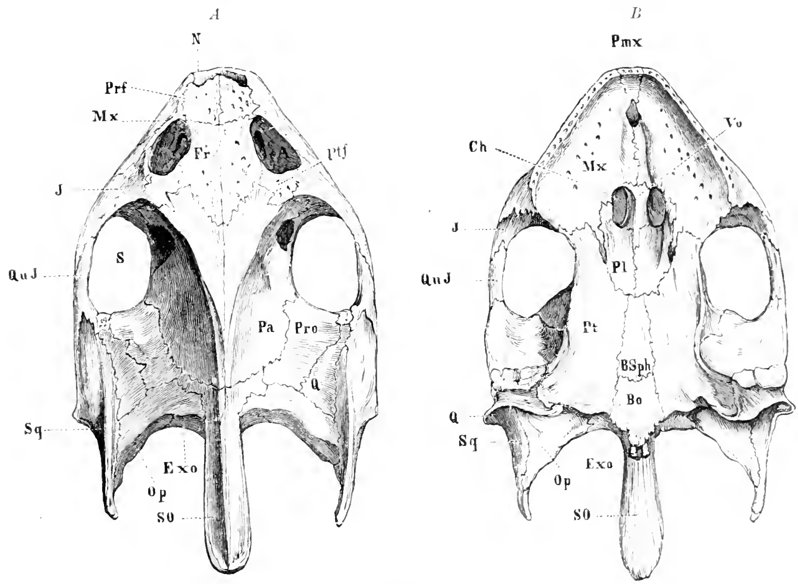


FIG. 298.

Trionyx gangeticus, Cuvier. Recent; India. Superior (*A*), and palatal (*B*) aspects of skull, reduced, *bo*, Basioccipital; *bsph*, Basisphenoid; *ch*, Internal nares; *exo*, Exoccipital; *fr*, Frontal; *j*, Jugal; *mx*, Maxilla; *N*, External nostril; *op*, Opisthotic; *pa*, Parietal; *pl*, Palatine; *pmx*, Premaxilla; *prf*, Prefrontal + nasal; *pro*, Proötic; *ptf*, Postfrontal; *q*, Quadrate; *quj*, Quadrato-jugal; *S*, Supratemporal fossa; *so*, Supraoccipital; *sq*, Squamosal; *vo*, Vomer.

are both stout plates, situated in their usual positions. The exoccipital sometimes fuses with the supraoccipital, which is produced beyond a line drawn between the posterior extremities of the squamosal. The foramen magnum is deeper than broad, and bounded by the supraoccipital and the exoccipitals, and occasionally also by the basioccipital.

The squamosal joins both the proötic and opisthotic, and is buttressed by the quadrate, which penetrates the otic region by means of a superiorly or inwardly directed process, and is suturally united with the quadrato-jugal. The quadrate sometimes joins both the basisphenoid and basioccipital, but in all Cryptodires it is separated from the basisphenoid by the pterygoids, which form a suture with the basioccipital, or very nearly reach the latter bone, and are in contact with the maxillae (except in the *Chelonidae*). In none of the Pleurodires do the pterygoids extend posteriorly beyond the quadrate.

The mandibular elements, which are six in number, are so intimately united in the adult as to appear like a single piece. A symphysial suture is present in the *Chelydridae*, however, at least in young individuals. Teeth are entirely wanting, both on the palate and jaw-bones, but the edges of the latter are covered with sharp, horny sheaths like the beak of a bird.

Limb-girdles.—The limb-girdles (Fig. 299) are remarkable for being enclosed within the external shell, but as they precede the development of the anterior and posterior dorsal ribs in the embryonic state, their apparently abnormal position is seen to be a secondary modification. Of the three branches which constitute the pectoral arch, namely, the scapula, precoracoid, and coracoid, the latter is longest in the *Chelonidae*, the former in all other Cryptodires. The coracoids are long, distally expanded bones, directed backwards and inwards, but not meeting in the median line. The scapula is slender, rod-like, and upwardly directed. Its distal extremity is attached by ligaments or cartilage to the anterior costal bone, and its proximal end is fused with the precoracoid, which corresponds to an elongated acromial process ("proscapula," Baur; "clavicle," Cuvier, Owen). The latter is directed forwards and downwards, and its expanded distal end is attached by ligaments to the entoplastron. The humerus exhibits a large spherical head, and a more or less strongly curved shaft. The radius and ulna are of about equal length, except in the *Chelonidae*, where the former is much longer and situated below the ulna. The proximal carpals are commonly four in number, and the distal five; numerous variations, however, are exhibited by the bones of the manus amongst the different families and genera. Five digits are always present, but sometimes not more than three are clawed.

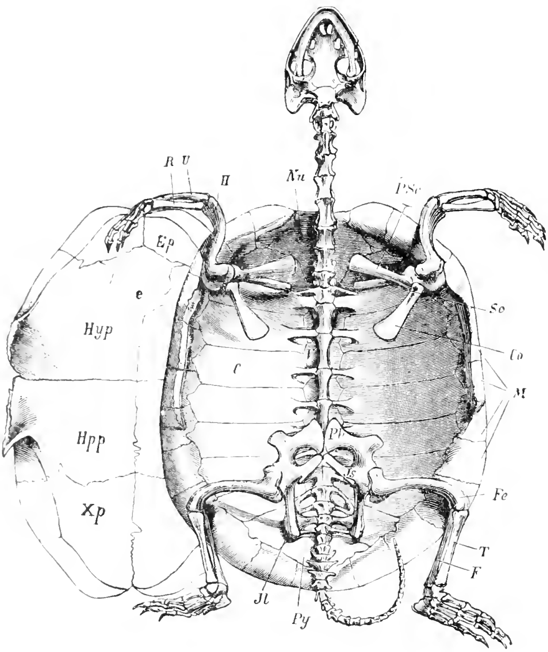


Fig. 299.

Cistudo lutaria, Marsili. [*C.* (*Emys*) *europaea*, Schneid.] Recent; Europe. Ventral aspect, the plastron removed to one side. *c*, Costal plates; *co*, Coracoid; *e*, Entoplastron; *ep*, Epiplastron; *f*, Fibula; *fe*, Femur; *h*, Humerus; *hpp*, Hypoplastron; *hyp*, Hyoplastron; *jl*, Ilium; *is*, Ischium; *m*, Marginals; *nu*, Nuchal; *pb*, Pubis; *psc*, Precoracoid; *py*, Suprapygal; *r*, Radius; *sc*, Scapula; *t*, Tibia; *u*, Ulna; *xp*, Xiphiplastron.

In the pelvic arch the long ilium is loosely attached to the sacrum and eighth costal plate in the *Cryptodira*, to the sacral ribs in the *Trionychoidea*; but in all existing *Pleurodira* the pelvis is solidly united with the carapace and plastron, and bears no trace of sacral attachment (Fig. 307). The pubis and ischium of Cryptodires form a ventral symphysis, and their symphysial branches are either widely separated from each other, or in contact and limiting two obturator foramina (*Testudinidae*). The pubis sends off a more or less developed process, directed forwards and outwards, which may be subcylindrical, rod-like, or flat and expanded distally; a lateral process is also present, but usually less developed than that of the pubis, on the ischium of all Cryptodires except in the *Chelonidae* (Boulenger). The femur is a curved cylindrical bone, and the tibia and fibula are subequal in length. An astragalus (formed of the tibiale + intermedium) which is in contact with both tibia and fibula, and a small outer calcaneum (fibulare) constitute the proximal tarsals; or among the Emyds, these may coalesce in a single piece. A centrale is distinct in the *Chelydridae* and most Pleurodires; and except in the *Chelonidae*, which have four, the distal row of tarsals contains five bones.

Habitat and Geological History.—Many of the *Chelonia* are terrestrial in habit, a greater number are aquatic, and a few are exclusively marine. About 200 recent species are regarded as well established, most of which are limited to the tropics or warm temperate zones. The earliest known fossil remains are from the Upper Keuper of Würtemberg (*Proganochelys*, *Chelytherium*), and are fortunately tolerably well preserved. None have been discovered in Lower Jurassic rocks, but from the Upper Jura of Solothurn, Northern France, Germany, England, and the United States, a number of forms are known, all of which are closely similar to existing genera. Numerous Chelonian remains occur in the Cretaceous and Tertiary, but complete skeletons in association with the skull are extremely rare. The only noteworthy marks of evolution affecting the order since early Cretaceous time are degeneration of the carapace and plastron in certain types, and elongation of the phalanges in truly marine forms.

Baur supposes ancestral Chelonians to have had a habitat similar to that of modern Crocodiles, namely in shallow water or in swamps. A branch then arose which inhabited rivers, and whose most specialised members are the three-clawed mud-turtles (*Trionychoidea*). That these forms with soft marginal plates are descended from a group having completely ossified marginals there can be little doubt. From a fluviatile habitat, according to Baur, these early Chelonians passed on to a marine, prior certainly to the Cretaceous period, since we find here such specialised genera as *Protostega*, *Protosphargis*, *Allopleuron*, etc.: and the most specialised of all is the recent *Dermochelys*. Still another branch acquired amphibian habits, like many of the *Emydidae*, and in time some of these (*Terrapene*, *Nicoria*, etc.) became truly terrestrial. The land tortoises (*Testudinidae*), a highly specialised group, are initiated in the Eocene (*Hadrianus*), and are completely adapted for a terrestrial existence.

Sub-Order A. TRIONYCHOIDEA. Bonaparte.

Dorsal vertebrae and ribs fused with the dermal plates to form an incompletely ossified carapace ornamented with coarse vermiculating sculpture; no epidermal shields. Neck bending by a sigmoid curve in a vertical plane. Skull with descending parieto-pterygoidal processes. Pterygoids broad throughout, separated from each other, the basisphenoid joining the palatines. Cervical vertebrae without transverse processes. Sacral and caudal ribs generally attached to well-developed transverse processes of the neural arches. Pelvis free from the carapace and plastron. Limbs modified into paddles, the fourth digit with at least four phalanges, and only the three *inner digits clawed. Marginal bones absent or forming an incomplete series, not connected with the ribs. Nine plastral elements; epiplastra separated from the hyoplastra by the V-shaped entoplastron.*

The group of three-clawed mud-turtles, which appears first in the Upper Cretaceous of the United States, and next in the lowest Tertiary strata of both Europe and North America, exhibits the most generalised structure of all Chelonians. The shell is incompletely ossified, and the plastral elements remain separate throughout life. Vacuities persist in the carapace, and various portions of the skeleton afford evidence of imperfect ossification. There are no free nasals, and no parieto-squamosal arch; the descending processes of the prefrontal may or may not be connected with the vomer, the epipterygoids are free, and the dentaries distinct. The stapes is entirely surrounded by the quadrate. The pterygoid is broad, without lateral expansions, separating the quadrate and basisphenoid. Only one family is recognised.

Family 1. **Trionychidae.** Gray.

Skull depressed, the small orbits directed more or less upwards and approximated towards the nares; temporal fossae completely open, and squamosal and supra-occipital with very long posterior processes. Plastron totally distinct from the carapace, with large vacuities. Humerus much curved. Eocene to Recent.

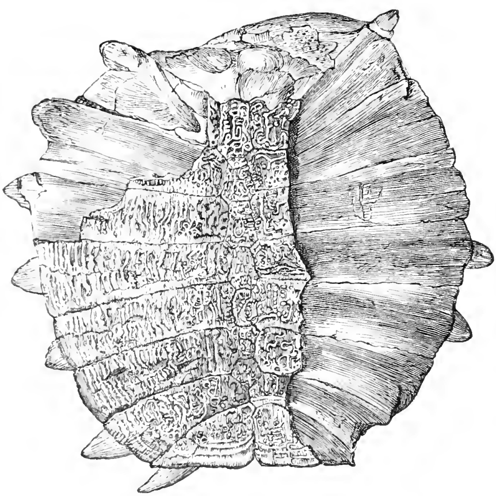


Fig. 300.
Trionyx stiriacus, Peters. Miocene lignites; Ebiswald, Styria. Imperfect carapace and cast of ribs. 1/4 (after Peters).

The existing members of this family, numbering in all about twenty-five species, are of fluviatile habit, and distributed in the tropical and temperate zones of all the continents except South America. Most of the fossil forms belong to the genus *Trionyx*, Gray (Fig. 300), which survived in Europe throughout the Eocene and Miocene, and still inhabits the rivers of Asia, Africa, and North America. *Axestus* and *Plastomenus*, Cope, from the Eocene of Wyoming and New Mexico, are closely related genera. *Chitra*, Gray, is Pliocene and Recent.

Sub-Order B. CRYPTODIRA. Duméril.

Dorsal vertebrae and ribs fused and expanded into bony plates forming a carapace. Neck bending by a sigmoid curve in a vertical plane. Cervical vertebrae without or with mere indications of transverse processes. Posterior cervicals with two articular faces. Skull with descending parieto-pterygoidal processes (except in the Dermochelyidae). No free nasals; parieto-squamosal arch present or absent; descending process of the prefrontals connected with the vomer; stapes in an open groove, entirely covered by the *quadrate behind. Pterygoids narrow in the middle, in contact only along the median line, without wing-like lateral expansions, separating the quadrate and basisphenoid. Pelvis not anchylosed with carapace or plastron. Digits with not more than three phalanges. Epiplastra in contact with hyoplastra; entoplastron oval, rhomboidal, or* T*-shaped. A complete series of marginal bones, connected with the ribs.*

This sub-order comprises the majority of existing and fossil Chelonians. As distinguished from Pleurodires, the head is retracted by curvature of the neck in a vertical plane, and the pelvis is unconnected with the plastron. The different families are conveniently grouped by Baur in four superfamilies, as recognised in the sequel.

Superfamily 1. CHELONOIDEA. Baur.

A parieto-squamosal arch; no foramen palatinum between palatines and maxillae; articular faces between the sixth and seventh cervical vertebrae plane; nuchal with a distinct process on the lower side for articulation with the neural arch of the eighth cervical vertebra, and without lateral processes. One biconvex cervical vertebra.

Family 1. **Dermochelyidae.** Gray. (*Athecae*, Cope.)

Carapace broken up into numerous mosaic-like pieces of dermal ossification, wholly unconnected with the vertebrae and ribs. Epidermal shields absent. Skull without descending parietal processes; temporal region completely roofed, the squamosal joining the parietal. Humerus flattened; limbs paddle-shaped, clawless, the digits of the manus much elongated; phalanges without condyles. Tertiary and Recent.

Eosphargis, Lyd. Carapace represented by a single median row of broad carinated scutes and a series of marginals on either side. Plastron probably devoid of tesserae. Skull broad and flat. Eocene; England.

Psephophorus, v. Meyer (*Macrochelys*, van Beneden *non* Gray). Skull shorter, thicker, and relatively larger than in *Dermochelys;* shell completely tessellated, sculptured; scutes of the larger longitudinal row of the carapace devoid of carinae. Eocene and Oligocene; Europe.

Dermochelys, Blv. (*Sphargis*, Merrem). Carapace completely, plastron incompletely bony in the adult, the former with seven, the latter with five keels; plastral elements eight. Recent; Atlantic, Pacific, and Indian Oceans. In this, the largest and sole surviving member of the family, the separation of the vertebral column from the carapace was deemed by Cope, Dollo, and others a character of sufficient importance to warrant the establishment of a group (*Athecae*) equal in value to the rest of the *Chelonia*. Baur has endeavoured to prove that the mosaic-like carapace was an acquired character, and that this and the following family are directly related to the *Chelonidae.*

Family 2. **Protostegidae.** Cope.

Carapace represented merely by a row of marginals, but the plastron very strongly developed and composed of thick ossifications. Skull with descending parietal plates. Humerus with the radial process short, blunt, and approximated to the head. Cretaceous and Tertiary.

Protostega, Cope. Descending parietal plates well developed. Carapace intermediate between Dermochelyidae and Chelonidae, with several primitive characters regarded as ancestral to both. Plastron with larger bones and a much smaller fontanelle than in *Dermochelys*. Body elongate, the posterior end truncated; limbs paddle-shaped. Post-axial border of humerus more or less deeply emarginate. Upper Cretaceous; North America.

Archelon, Wieland. Larger than the preceding, but similar in most respects. Ft. Pierre Cretaceous; South Dakota.

Protosphargis, Cap. Skull unknown. Body skeleton similar to that of *Protostega*, but bones of plastron more slender, and median fontanelle larger. Uppermost Cretaceous; Italy.

Pseudosphargis, Dames. Skull flat and wide, like that of the Dermochelyidae, but with descending parietal processes. Oligocene; Germany.

Family 3. **Chelonidae.** Gray. (Marine Turtles.)

Shell more or less incompletely ossified, covered with epidermal shields. Carapace frequently cordiform; plastral bones nine, distinct from the carapace, and with vacuities and digitate lateral extremities; nuchal without costiform process. Temporal region of skull completely roofed over; squamosal joining the parietal, and the latter articulating with the postfrontal. Limbs paddle-shaped, phalanges without condyles, terminal claws reduced to one or two. Supramarginal shields present, and sometimes an intergular. Upper Cretaceous to Recent.

Osteopygis, Cope (*Catapleura*, Cope). Carapace practically closed; marginals eleven. Upper Cretaceous.

Allopleuron, Baur. Carapace long and narrow, nuchal deeply emarginate, neurals short and wide with a long keel; marginals long and slender. Upper Cretaceous.

Lytoloma, Cope (*Euclastes*, *Puppigerus*, p.p., Cope; *Glossochelys*, Seeley; *Erquelinnesia*, *Pachyrhynchus*, Dollo). Skull resembling that of *Thalassochelys*. Carapace rounded posteriorly, vacuities of shell more obliterated than in *Thalassochelys*; epiplastrals narrow; exposed portion of entoplastron very short, xiphiplastrals uniting extensively in the median line. Upper Cretaceous and Eocene.

Argillochelys, Lyd. Skull short and wide. Shell and bones of the pectoral arch similar to those of *Thalassochelys*, except that the carapace has but four costal shields, and the xiphiplastrals unite extensively along the median line. Eocene; England.

Thalassochelys, Fitz. (Fig. 301). Carapace completely ossified in the adult, with at least five pairs of costal shields, and vacuities more or less obliterated. A series of inframarginal plastral shields present. Eocene to Recent.

Chelone, Brong. (*Mydas*, Gray; *Cimochelys*, Owen), (Figs. 297, 302). Skull comparatively long, narrow, with the orbits lateral. Shell cordiform or pointed at both ends, with four costal shields, the plastral vacuities persisting for a long period. An intergular and a series of inframarginal shields present. Upper Cretaceous to Recent.

Lembonax, Cope. Eocene; North America. *Chelyopsis*, van Beneden. Oligocene; Belgium and Northern Germany.

During the Cretaceous and Tertiary numerous marine turtles existed which are perhaps most nearly related to the *Chelonidae*, but owing to their diversity have been placed by some authors in independent families. Most of them, however, are too imperfectly known to admit of a precise account of their structure or taxonomy.

Propleura and *Peritresius*, Cope, from the Upper Cretaceous of the United States, are represented by a few species, all under 1 m. in length. *Desmato-*

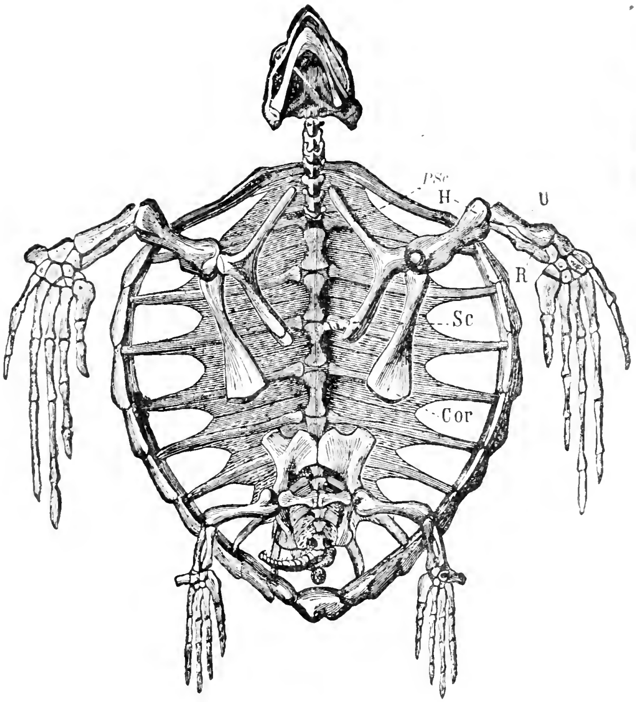


FIG. 301.

Thalassochelys caretta, Linn. sp. Recent; Mediterranean. Ventral aspect of skeleton, the plastron removed. *cor*, Coracoid; *h*, Humerus; *psc*, Precoracoid ("prescapula," Baur); *r*, Radius; *sc*, Scapula; *u*. Ulna.

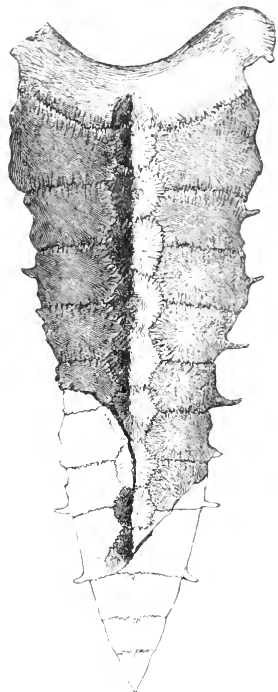


FIG. 302.

Chelone hofmanni, Gray. Upper Cretaceous; Maestricht, Holland. Portion of carapace, 1/4.

chelys, Williston, from the Fort Benton Cretaceous of Kansas and Nebraska, is a peculiar form with some aberrant characters, such as free nasals, stout transverse processes on the cervical vertebrae, and a single articular face on the posterior cervicals. *Puppigerus*, Cope, occurs in the Miocene of New Jersey.

Superfamily 2. CHELYDROIDEA. Baur.

No parieto-squamosal arch; a foramen palatinum between palatine and maxilla; articular faces between the sixth and seventh cervical vertebrae not plane; nuchal without lower process, but with more or less strong lateral process underlying the peripherals; one biconvex cervical; a complete series of inframarginals.

Family 1. Thalassemydidae. Rütimeyer. (*Acichelyidae*, Lydekker.)

Temporal fossae of skull partially roofed. Shell cordiform, more or less incompletely ossified, the fontanelle in plastron persisting for a long period or throughout *life. Nuchal without costiform process. Plastron connected with carapace by axillary and inguinal buttresses. Humerus with imperfectly developed head and nearly straight shaft. Phalanges with articular condyles, all the terminal ones clawed.* Upper Jura and Cretaceous.

This family includes a number of Mesozoic genera which combine the characters of both marine and marsh turtles, and are probably directly ancestral to the Chelonidae. They appear to have been mainly of marine habits. The very incomplete ossification of the carapace and persistent fontanelle of the plastron present the same conditions as in sea-turtles, while the form of the plastral elements and the outwardly bent extremities of the hyo- and hypo-plastrals are suggestive of marsh forms. The five functional toes with articulating phalanges were all clawed and probably webbed in life, having been adapted for both progression on land and for swimming.

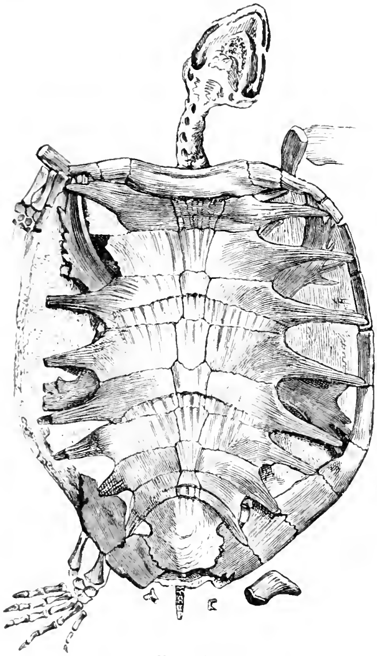


Fig. 303.
Eurysternum wagleri, v. Meyer. Upper Jura; Zandt, near Eichstädt, Bavaria. 1/3.

Thalassemys, Rüt. (*Enaliochelys*, Seeley). Carapace moderately thick, flattened, with well-ossified pleurals, the posterior neurals not forming a tectiform ridge. Vertebral shields narrow. Very large persistent vacuities in the plastron. Upper Jura; Switzerland and England.

Eurysternum, Wagler (*Achelonia*, *Acichelys*, *Aplax*, *Palaeomedusa*, v. Meyer; *Euryaspis*, Wagner), (Fig. 303). Carapace flattened, distinctly emarginate anteriorly, with the pleurals well ossified and posterior neurals not forming a tectiform ridge. Vertebral shields very wide, marginals long and narrow. Plastron with large persistent vacuities. Upper Jura (Lithographic Stone); Bavaria and Cerin, Ain.

Tropidemys, Rütimeyer; *Pelobatochelys*, Seeley. Upper Jura and Wealden; Europe.

Chitracephalus, Dollo. Cranium much elongated and depressed, with an extremely short facial region, and temporal fossae not roofed. Cervical vertebrae without transverse processes. Pleurals narrowed at their outer ends, with vacuities within the well-developed border of the peripherals. Plastral elements similar to those of *Chelone*. Digits clawed, not greatly elongated. Wealden; Belgium. *C. dumoni*, Dollo.

Family 2. **Chelydridae.** Agassiz.

Temporal region of skull incompletely roofed over; no parieto-squamosal arch. Frontals excluded from orbit: maxilla separated from the quadratojugal; squamosal in connection with postorbito-frontal. Epidermal shields absent in some cases; number of neurals complete; posterior pleurals meeting in the median line. Shell usually not *fully ossified until late in life. Plastron frequently small, cruciform, articulating with the carapace by gomphosis; an entoplastron present. Nuchal emarginate, with a long costiform process underlying the anterior marginals. Number of marginals eleven; a series of inframarginals. Limbs not modified into paddles: digits moderately elongate, webbed; claws four or five.* Upper Jura to Recent.

Tretosternum, Owen (*Peltochelys*, Dollo). Carapace with pustulate sculpture, the anterior border deeply emarginate; plastron with an intergular and five pairs of plastral shields. Epidermal shields present. Purbeck and Wealden; England and Belgium.

Platychelys, Wagner, from the Upper Jura, is sometimes referred to this family.

Toxochelys, Cope. Skull with tympanic ring open. Caudal vertebrae procoelous, with well-developed chevron bones. Upper Cretaceous: United States.

Porthochelys, Will. Skull broad, alveolar margin very deep. Carapace completely ossified, smooth, the arrangement of bones and shields nearly as in *Chelydra*. Plastron with very small fontanelles and no sternal bridge. Upper Cretaceous; United States.

Anostira, Leidy. Shell with vermiculated sculpture and without (or with very thin) epidermal shields. Plastron articulated with the carapace by suture, and bridge without distinct inguinal notch. Skull unknown. Upper Eocene; United States.

Pseudotrionyx, Dollo. Eocene; Belgium and England. *Acherontemys*, Hay. Miocene; Washington.

Chelydra, Schweig. Shell with the emargination of the nuchal not very deep; neural bones mostly hexagonal; supramarginal shields absent; posterior border of carapace serrated. Miocene to Recent. *C. murchisoni*, Bell. Upper Miocene; Switzerland.

Macroclemmys, Gray (*Macrochelys*, Gray; *Gypochelys*, Agassiz). Recent.

Family 3. **Dermatemydidae**. Gray.

Skull with open temporal fossae; frontals not excluded from orbit; maxilla unconnected with quadratojugal, and squamosal separated from postorbito-frontal. Shell covered with epidermal shields; plastral bones nine: plastral shields separated from the marginals by a series of inframarginals. Plastron united with the carapace by suture or ligaments. Nuchal bone produced into costiform processes, underlying the marginals. Number of neurals incomplete; posterior pleurals not meeting in the median line. Pubic and ischiadic symphyses widely separated. Digits moderately elongate, claws four or five. Cretaceous to Recent.

This family comprises three existing genera restricted to Central America, and a number of fossil forms, such as *Adocus*, *Agomphus* (*Amphiemys*), and *Polythorax*, Cope; *Baptemys*, Leidy; and *Trachyaspis*, von Meyer. The family is intermediate in position between the Chelydridae and recent Cinosternidae, and in some respects suggestive of Pleurodires. *Adocus*, from the American Cretaceous, was made by Cope the type of an independent family, characterised by the abortion of the heads of the ribs.

The Cinosternidae, including *Cinosternum* (*Kinosternon*), *Aromochelys*, and *Goniochelys*; and the Staurotypidae, including *Staurotypus* and *Claudius*, are without representatives in the fossil state. The same is true of the third superfamily recognised by Baur, the PLATYSTERNOIDEA, comprising the family Platysternidae with the solitary genus *Platysternum*, Gray.

Superfamily 4. TESTUDINOIDEA. Baur.

Skull without parieto-squamosal arch, and squamosal separated from postorbito-frontal, with a foramen palatinum between the palatine and maxilla. Articular faces between the sixth and seventh cervical vertebrae not plane, and two of the cervicals biconvex. Nuchal without well-developed costiform processes; series of inframarginals incomplete.

Family 1. Emydidae. Gray. (Marsh Turtles.)

Shell completely ossified in the adult, covered with epidermal shields. Carapace only moderately convex. Plastron sometimes hinged, with long sternal bridge and large sternal chambers, the marginals of bridge without median processes interlocking with the rib-ends. Plastral bones nine, mesoplastron and intergulars wanting. Lateral temporal arch usually present, quadrate open behind. Digits short and stout, the second and third with more than two phalanges; claws four or five. Tertiary and Recent.

The Emyds or Marsh Turtles are very closely related to the Land Tortoises, and are sometimes included with them in the same family. The shell, how-

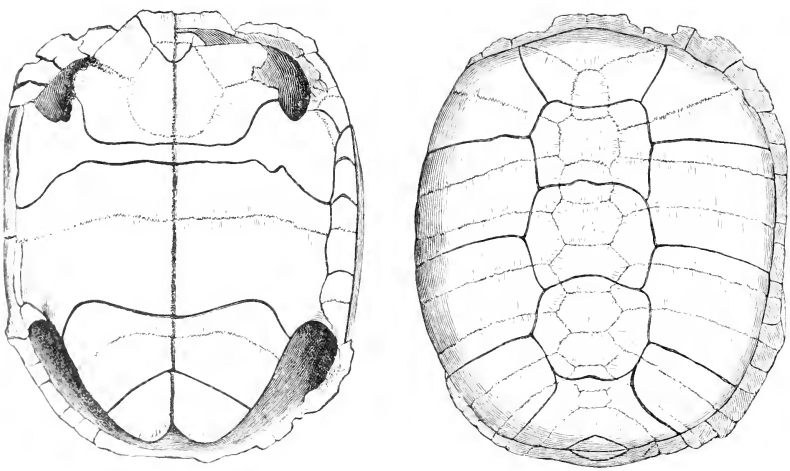


FIG. 304.

Stylemys nebrascensis, Leidy. White River Oligocene; South Dakota. Plastron and carapace. 1/3 (after Leidy).

ever, in the Emyds is less convex, the sternal chambers are larger, and their limbs are without dermal ossifications. Their distribution at the present day is world-wide with the exception of the Australian region. Fossil marsh turtles make their first appearance in the Eocene, and belong for the most part to existing genera.

Emys, Duméril (*Lutremys*, Gray). Neural bones short, hexagonal; nuchal not distinctly emarginate. Plastron united to the carapace by ligament, and more or less hinged in the adult. Eocene to Recent.

Ptychogaster, Pomel. Neural bones short; pleurals alternately long and short at their inner and outer extremities; nuchal emarginate. Hyoplastrals united to the carapace by suture, the hypoplastrals joining it by a straight ligamentous union, and movable upon a transverse hinge. Oligocene or Lower Miocene: France.

Stylemys, Leidy. Skull unknown. Shell with the general characters of *Testudo*, but with all or nearly all of the neural bones hexagonal, with short antero-lateral surfaces; the nuchal not emarginate; posterior caudals not alternating in length: caudal shield undivided. Oligocene to Pliocene; Western United States. *S. nebrascensis*, Leidy, the type species, is very abundant.

Cistudo, Fleming (Fig. 299); *Cyclemys*, Bell. Recent. *Damonia*, *Bellia*, *Nicoria*, Gray. Pliocene and Recent. *Ocadia*, Gray; *Clemmys*, Wagler. Miocene to Recent.

Family 2. **Testudinidae**. Gray. (*Chersidae*.) Land Tortoises.

Skull with open temporal fossae; quadrate closed behind. Shell completely ossified even in the young, more or less ovoid, and covered with epidermal shields. Plastron suturally united with the marginals; an entoplastron present. Sternal bridge long, sternal chambers very slightly developed; anterior and posterior extremities of hyo- and hypo-plastron little extended inwards; marginals of bridge with median processes interlocking with rib ends. Skull with open temporal fossae; quadrate closed behind. Pubic and ischiadic symphyses firmly connected with each other. Limbs with free digits, which are short and moderately elongate: terminal claws four or five. Second and third digit of pes never with more than two phalanges. Tertiary and Recent.

Cinixys, Bell (*Kinixys*, Bell: *Cinothorax*, Fitz.). Posterior portion of carapace movable in the adult, hinged between the seventh and eighth marginals and the fourth and fifth pleurals. Gulars distinct. Recent: Africa.

Pyxis, Bell. Carapace without hinge; front lobe of plastron mobile. Recent.

Homopus, Dum. and Bibr. Carapace and plastron without hinge. Palate without oral ridge. Eocene to Recent.

Hadrianus, Cope. Distinguished from *Testudo* by the narrow vertebral shields, usually hexagonal neural bones, undivided caudal shield, and more uniform length of extremities of the pleural bones. Eocene: North America.

Testudo, Linn. (*Colossochelys*, Falc. and Caut.; *Manouria*, Gray: *Xerobates*, Ag.). Neural bones short; pleurals alternately short and long at their inner and outer extremities; nuchal deeply emarginate. Plastron extensively united with the carapace by suture; buttresses short, never extending beyond the edge of the costals. Vertebral shields broad, costals very short. Miocene to Recent. Some Pliocene species attain gigantic size, the shell of *T. perpiniana*, Depéret, from the Pliocene of France, having a length of 1·2 m., and that of *T. atlas*, Falconer and Cautley, from the Pliocene of the Siwalik Hills, India, upwards of 2 m.

Sub-Order C. PLEURODIRA. Duméril.

Skull with outer border of tympanic cavity completely encircled by the quadrate: pterygoids very broad throughout, forming wing-like lateral expansions, and not *separating the quadrate and basisphenoid; nasals free or united with prefrontals; the latter without descending processes. Neck bending laterally; cervical vertebrae with strong transverse processes and single articular faces. Shell usually covered with epidermal shields; a complete series of marginal bones connected with the ribs; epiplastra in contact with hyoplastra; mesoplastrals present in some forms, and an intergular in all cases where epidermal shields occur. Pelvis anchylosed to carapace and plastron. Digits with not more than three phalanges.*

In this group, as indicated by the name, the neck bends laterally, and the pelvis is anchylosed to the carapace and plastron. A number of fossil forms are known which exhibit characters intermediate between Pleurodires and Cryptodires, and are here considered (following Baur and Lydekker) as an independent sub-order, the AMPHICHELYDIA. Existing Pleurodires are restricted to the southern hemisphere, and distributed in South America, Southern India, Africa, and Australia.

Family 1. **Proganochelyidae.**

Containing only the primitive *Proganochelys*, with the characters of that genus.

Proganochelys, Baur (*Psammochelys*, Quenst.; *? Chelytherium*, von Meyer). The following description of this, the most ancient of all Chelonians, is condensed from Fraas; known only by the carapace and plastron, in one specimen about 0·65 m. long and nearly as wide. Carapace moderately convex, with five vertebral shields greatly enlarged and the costals correspondingly reduced; a series of supramarginal epidermal scutes at the antero- and postero-lateral angles, elevated into prominences; posterior marginals large and freely projecting. Neural bones small, costals large and extending with the rib ends as far as the plastron. Sternal bridge long, mesoplastrals very large, laterally expanded, and meeting in the middle line; epi- and ento-plastron very small. Pelvis supported by two sacral vertebrae; ribs and pelvis connected with the carapace and plastron. Upper Trias (Stuben Sandstone); Würtemberg; *P. quenstedtii*, Baur (= *Psammochelys keuperiana*, Quenst.).

Family 2. **Miolaniidae.** Owen.

Shell known only by fragments. Skull with completely roofed temporal fossae, and furnished with horn-like bony protuberances; no distinct nasals; vomer dividing palatines. Caudal vertebrae opisthocoelous, with chevrons; tail long and encased in a nodose bony sheath. Pleistocene.

Miolania, Owen (*Ceratochelys*, Huxley). Cranium with three pairs of peripheral prominences in the fronto-parietal region, the head measuring in one species 0·6 m. in width to the tip of the "horns." Habits probably herbivorous and terrestrial. Related to the Testudinidae, according to Baur. Pleistocene: Queensland and Lord Howe's Island. *M. platyceps*, Owen; *M. oweni*, Sm. Woodw.

Family 3. **Chelyidae.** Gray.

A strong parieto-squamosal arch; posterior narial openings bounded by maxillae, palatines, and vomer; frontal unpaired; nasals free; premaxillae distinct. Shell *covered with epidermal shields; plastral bones nine; no inframarginal shields.* Tertiary and Recent.

The recent genus *Chelys*, Duméril, is made by Baur the exclusive representative of this family, and separate families are established for each of the following:—*Hydromedusa*, Wagler (Recent); *Chelodina*, Fitz. (Pleistocene and Recent); and *Rhinemys*, Wagler (Eocene to Recent). In *Chelodina* neural bones are absent, and the external surface is more or less vermiculated.

Family 4. **Rhinemydidae**. Baur.

A slender or broad parieto-squamosal arch present; posterior narial openings bounded by maxillae, palatines, and vomer; frontal paired; nasals free; premaxillae distinct. Tertiary and Recent.

Rhinemys, Wagler (*Phrynops*, Wagler; *Hydraspis*, Bell). Eocene; India; and Recent; South America. *Emydura*, Bonap. Pleistocene and Recent. *Platemys*, Wagler; *Elseya*, Gray. Recent.

Family 5. **Pelomedusidae**. Cope.

Quadratojugal not in connection with parietal; vomer rudimentary or absent. No parieto-squamosal arch and no free nasals; prefrontals in contact. Second cervical biconvex. Plastral bones eleven; mesoplastra present. Tertiary and Recent.

This family, as limited by Baur, includes only the recent *Pelomedusa*, Wagler, and *Sternothaerus*, Bell. Cope regards the latter as the type of an independent family, on account of the complete mesoplastrals. The **Podocnemididae** differ from the preceding genera in having the quadratojugal connected with the parietals. Under this head are included the following:—*Podocnemis*, Wagler (Fig. 305). Eocene to Recent. *Peltocephalus*, Dum. and Bibr.; *Erymnochelys*, Baur. Recent. *Dacochelys*, Lyd. Eocene; and perhaps *Taphrosphys*, Cope, from the Upper Cretaceous of New Jersey and New Zealand.

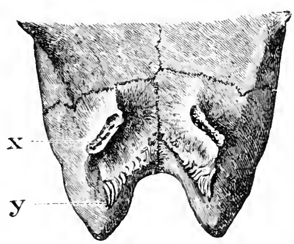


Fig. 305.

Podocnemis expansa, Wagler. Recent; Brazil. Visceral aspect of posterior end of plastron, showing places for attachment of pubes and ischia, *x*, *y* (after Rütimeyer).

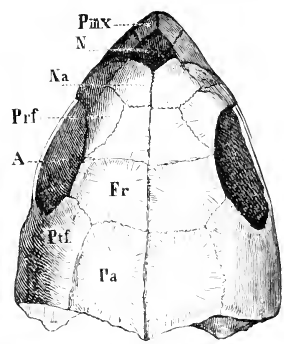


Fig. 306.

Rhinochelys cantabrigiensis, Lyd. Cambridge Greensand. Skull, $^1/_1$. *A*, Orbit; *fr*, Frontal; *N*, Nostril; *na*, Nasal; *pa*, Parietal; *pmx*, Premaxilla; *prf*, Prefrontal; *ptf*, Postfrontal (after Lydekker).

The genus *Rhinochelys*, Seeley (Fig. 306), from the Cambridge Greensand, known by well-preserved skulls and various fragments, is of uncertain family position.

Family 6. **Plesiochelyidae**.

Skull with temporal fossae roofed. Shell usually thick, without mesoplastrals, and with either a reduced or the full number of neurals and suprapygals; only the pubis uniting with the xiphiplastral; entoplastral small; inframarginal shields at least usually present. Sometimes a plastral vacuity. Phalangeals reduced. Upper Jura.

Idiochelys, v. Meyer (*Chelonemys*, Jourdan). Shell with deeply emarginate nuchal; neurals frequently short and interrupted, never exceeding seven in number, and not connected with the one suprapygal. Vertebral shields very broad. Lithographic Stone; Bavaria and Cerin, Ain. *I. fitzingeri*, v. Meyer.

Plesiochelys, Rut. (*Stylemys*, Maack, *non* Leidy), (Fig. 307). Shell attaining a length of 0·5 m., circular or cordiform, relatively thick, considerably vaulted

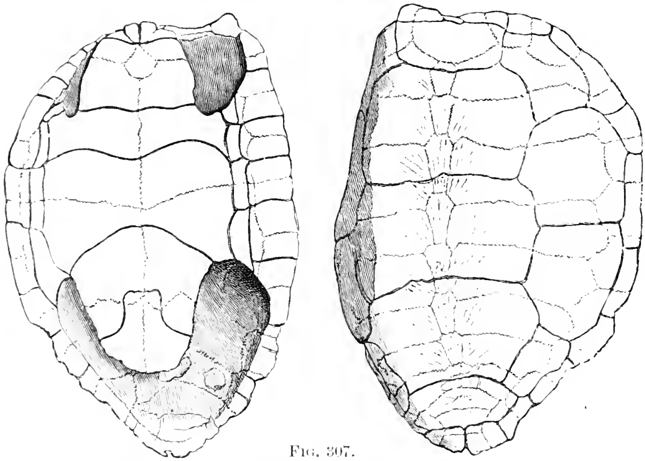


Fig. 307.
Plesiochelys solodurensis, Rütimeyer. Upper Jura (Kimmeridgian); Solothurn, Switzerland. 1/8 (after Rütimeyer).

in the adult, and with or without a persistent plastral vacuity. Nuchal more or less emarginate; neurals generally long and narrow, eight in number, and connected with the first of the three suprapygals. Plastral bridge long; sulcus between abdominal and femoral shields ascending towards the hypoplastral suture, and terminating in the middle of the inguinal notch. Upper Jura; Germany, Switzerland, and France.

Hydropelta, *Parachelys*, v. Meyer. Upper Jura; Europe. *Hylaeochelys*, Lyd. Upper Jura and Wealden; Europe.

Sub-Order D. AMPHICHELYDIA. Lydekker.

Nasals free; a squamoso-parietal arch; descending processes of prefrontals joining vomer; stapes in an open groove of the quadrate; pterygoids narrow in the middle, without wing-like lateral expansions, separating quadrate and basisphenoid; epipterygoid well developed and free; dentary bones distinct. Cervical vertebrae with well-developed transverse processes, with single articular faces, biconcave; dorsal and sacral vertebrae with well-developed ribs. Pelvis not anchylosed to the carapace and plastron. Epiplastra in contact with hyoplastra, entoplastron oval or rhomboidal; a complete series of marginals connected with the ribs.

The foregoing definition of this sub-order, as given by Baur, is based largely upon the genus *Compsemys*, Leidy, oldest North American tortoise, of which nearly all parts of the skeleton are known. The group was established by Lydekker to include a number of generalised later Mesozoic forms having a shell constructed on the plan of that in Cryptodires and Pleurodires, in which mesoplastral bones and an intergular shield are developed. The pubis may articulate, without sutural union, with the xiphiplastral. The coracoid and humerus are of a Pleurodiran type.

Family 1. **Pleurosternidae.** Lydekker.

A provisional assemblage embracing a variety of generalised fossil forms, and to be regarded as ancestral to both Cryptodires and Pleurodires.

Pleurosternum, Owen (*Megasternum*, Gray). Carapace much depressed, rounded posteriorly, without vacuities, and firmly united by a long bridge on each side with the plastron, which is also continuous. Surface of shell very

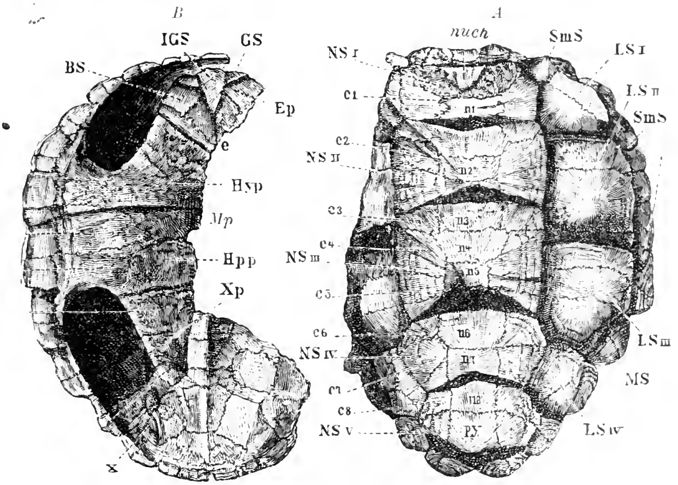


Fig. 308.

Platychelys oberndorferi, Wagner. Upper Jura; Kelheim, Bavaria. 1/4. *A*, Carapace. *B*, Plastron. *BS*, Brachial shield; *Ep*, Epiplastron; *GS*, Gular shield; *Hpp*, Hypoplastron; *Hyp*, Hyoplastron; *IGS*, Intergular; *LS* I-IV, Laterals; *Mp*, Mesoplastron; *MS*, Marginal; *NS* I-V, Neural or vertebral shields; *SmS*, Supramarginal; *Xp*, Xiphiplastron; *c*1-8, Costal plates *e*, Entoplastron; *n*1-8 Neural plates; *nuch*, Nuchal; *py*, Pygal; *x*, Pit for attachment of ilium.

finely pitted and deeply impressed with the suture-lines of the epidermal shields. Neural bones moderately elongated, hexagonal, with their antero-lateral surfaces short. Mesoplastrals well developed, meeting in the middle line; entoplastral relatively large; xiphiplastrals deeply notched. No nuchal shield; intergular shield not divided; inframarginals present. Pectoral arch resembling that of the existing *Chelys*. Upper Jura; England.

Platychelys, Wagner (*Helemys*, Rüt.), (Fig. 308). Carapace somewhat depressed, with a number of more or less distinct ridges or prominences on the neurals and costals. Neurals short and of irregular contour, the width usually much exceeding the length. Bridge short. Mesoplastrals not meeting in the middle line. Vertebral shields much wider than long; nuchal shield present; intergular undivided. No articulation between pelvis and plastron (Lydekker). Upper Jura; Bavaria, France, and England. [This genus is included by von Zittel with the *Chelydridae*.]

Baëna, Leidy. Intergular shield divided, and xiphiplastral with depressions which appear to have received the pubis and ischium. Mesoplastrals meeting at the middle line, but with the median ends much narrower than the outer ends. Upper Cretaceous and Eocene; United States.

Compsemys, Leidy. Known by nearly all parts of the skeleton, with characters as given in the definition of the sub-order. Mesoplastron complete, very much resembling that of *Pleurosternum*. Hinder lobe of plastron not notched. Upper Jura; Rocky Mountains.

[Acknowledgments are due to Drs. S. W. Williston, E. C. Case, and the late G. Baur for assistance in the revision and extension of the foregoing chapter on *Chelonia*. The published writings of Baur, Boulenger, and Lydekker have also been freely drawn upon.—EDITOR.]

Order 7. CROCODILIA. (*Hydrosauria, Loricata.*)[1]

Lizard-like reptiles, usually of large size, with long, keeled, swimming tail, and entire body covered with horny scales, underneath which along the back and abdomen are usually rows of dermal plates. Investing bones of temporal region contracting into an upper and a lower arcade; quadrate immovably attached to the skull; secondary bony palate developed; parietal foramen wanting; teeth deeply socketed, confined to margin of jaws. Vertebrae amphiplatyan or procoelous, and among the earlier forms amphicoelous. Cervicals with short, double-headed ribs attached to centra; dorsal ribs long, double-headed, attached to transverse processes. Sternum ossified; abdominal ribs present. Sacrum composed of two vertebrae. Two pairs of limbs adapted for swimming and for habitual support of the body.

Crocodiles possess the highest internal organisation known amongst reptiles. Their general form resembles that of lizards and Rhynchocephalians, but their skeletal structure is radically different; while, on the other hand, there is a fundamental resemblance between their respiratory organs and those of birds. True Crocodilians are apparently initiated in the Lias, and their subsequent evolution is clearly traceable, but their predecessors in the Trias (*Parasuchia*) are with difficulty distinguished from Rhynchocephalians and Dinosaurs.

Sub-Order 1. PARASUCHIA. Huxley.[2]

Premaxillae greatly elongated. External nares separate and placed far backward, in proximity to the small, upwardly directed orbits; internal nares occupying their

[1] Literature:

Brühl, C. B., Das Skelet der Krokodilien. Vienna, 1862.—*Dollo, L.*, Première note sur les Crocodiliens de Bernissart (Bull. Mus. Roy. d'Hist. Nat. Belg. vol. II. p. 309), 1883.—*Gray, J. E.*, Synopsis of the species of recent Crocodilians (Trans. Zool. Soc. vol. VI.), 1862.—*Huxley, T. H.*, Notes on the specific and generic characters of recent Crocodilia (Proc. Linn. Soc. vol. IV. pt. 1), 1860.—*Koken, E.*, Die Dinosaurier. Crocodilien und Sauropterygier des norddeutschen Wealden (Palaeont. Abhandl. Dames und Kayser, vol. III.), 1887.—Die Reptilien der norddeutschen unteren Kreide (Zeitschr. deutsch. geol. Ges. vol. XXXV. p. 792), 1883.—*Owen, R.*, Monograph of the fossil Reptilia of the London Clay (Palaeontogr. Soc.), 1849-58.—Monograph of the fossil Reptilia of the Wealden and Purbeck Formations (*ibid.*), 1853-64.—On the association of dwarf Crocodiles with the diminutive Mammals of the Purbeck Shales (Quar. Journ. Geol. Soc. vol. XXXV. p. 148), 1879.—*Parker, W. K.*, On the structure and development of the skull in the Crocodilia (Trans. Zool. Soc. vol. XI.), 1883.—*Woodward, A. S.*, On the literature and nomenclature of British fossil Crocodilia (Geol. Mag. [3], vol. II. p. 496), 1885.—The history of fossil Crocodiles (Proc. Geol. Assoc. vol. IX.), 1886.

[2] Literature:

Cope, E. D., On the Reptilia of the Triassic Formations of the Atlantic Region of the United States (Proc. Amer. Phil. Soc. vol. XI. p. 444), 1871.—*Ibid.* vol. XVIII. (1878), p. 213.—*Huxley, T. H.*, On Stagonolepis robertsoni, and on the evolution of the Crocodilia (Quar. Journ. Geol. Soc. vol. XXXI. p. 423), 1875.—*Marsh, O. C.*, On Belodon, etc. (Amer. Journ. Sci. [3], vol. L. p. 487), 1895.—*Meyer, H. von*, Ueber Belodon, etc. (Palaeontogr. vol. X. p. 227), 1863.

primitive position on either side of the vomers. Palatals and pterygoids not meeting in the middle line. Supratemporal vacuities very small; lateral vacuities large, completely enclosed. Parietals and frontals paired; postorbitals distinct. Teeth with anterior and posterior carinae. Vertebrae amphiplatyan. Coracoid short and rounded; clavicles present. Pubis, ischium, and ilium all entering the imperforate acetabulum.

The *Parasuchia* of the Trias are commonly regarded as ancestors of the longirostrate Crocodilians, which they resemble in numerous features, such as

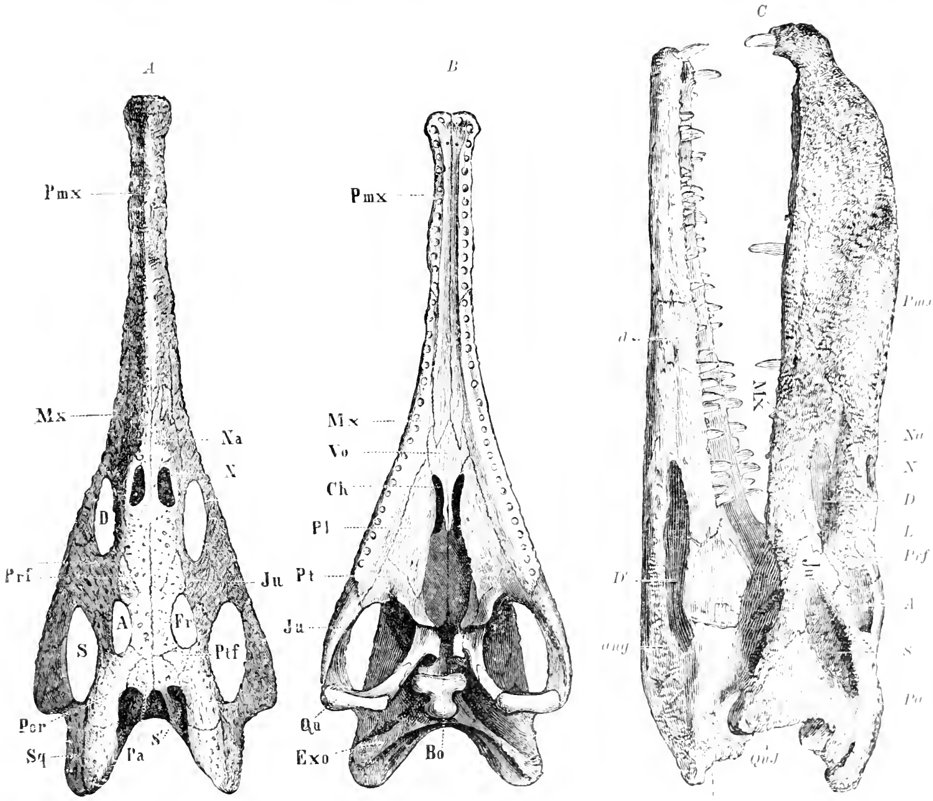


FIG. 309.

Belodon kapffi, v. Meyer. Upper Keuper; Stuttgart, Wurtemberg. Skull from superior (*A*), palatal (*B*), and lateral (*C*), aspects, $\frac{1}{7}$. *A*, Orbit; *ang*, Angular; *art*, Articular; *bo*, Basioccipital; *ch*, Internal nares; *d*, Dentary; *D*, Antorbital vacuity; *D'*, Mandibular vacuity; *exo*, Exoccipital; *fr*, Frontal; *ju*, Jugal; *l*, Lachrymal; *mx*, Maxilla; *N*, External narial openings; *na*, Nasal; *pa*, Parietal; *pl*, Palatine; *pmx*, Premaxilla; *por*, Postorbital; *prf*, Prefrontal; *pt*, Pterygoid; *ptf*, Postfrontal; *qu*, Quadrate; *quj*, Quadrato-jugal; *S*, Lateral temporal vacuity; *S'*, Supratemporal vacuity; *sq*, Squamosal; *vo*, Vomer.

their considerable size, armouring of the trunk region, elongated rostrum, coarsely sculptured cranial plates, separation of the lateral temporal vacuities from the orbits, socketed teeth, structure of the lower jaw (which is pierced in its hinder half by a vacuity), and prevalence of double-headed ribs. But in addition to these characters they possess others which render their association with Dinosaurs or Rhynchocephalians equally justifiable. Among features they share in common with Dinosaurs may be mentioned the divided, remotely situated external nares, large antorbital vacuities, form of the pterygoids and basisphenoid, and the upwardly directed transverse processes of the anterior dorsal vertebrae. With the Rhynchocephalians they agree in having an independent postorbital, paired parietals and frontals, an extensive bony palate, internal nares occupying their primitive position on either side of the vomers, well-developed abdominal ribs, and a similar clavicle and coracoid. The remaining bones of the pectoral arch, as well as those of the pelvic girdle and appendicular skeleton, are intermediate in form between the corresponding parts of modern Crocodiles and Rhynchocephalians.

The *Parasuchia* are accordingly to be regarded as a collective type of reptiles, from which the crocodilian stem early diverged and entered upon an independent course of evolution. Parasuchian remains are more or less fragmentary, and limited to the Trias of Europe, Asia, and North America.

Belodon, v. Meyer (*Phytosaurus*, Jaeger), (Figs. 309, 310). This is the only accurately known genus, and is represented by excellently preserved skulls, with portions of the skeleton and dermal armour, in the Upper Keuper of Stuttgart. It is about as large as modern crocodiles, the skull attaining a length of 0·7 m. External cranial bones pitted and rugose; lateral eustachian passages occupying open grooves on the basisphenoid; secondary palate not developed. Dorsal armour consisting of two longitudinal rows of large, overlapping keeled scutes with coarse ornamentation; sides and abdomen covered with smaller, more irregular scutes. Detached teeth not uncommon in the Keuper of Würtemberg and Franconia. Fragmentary remains also known from the Trias of North Carolina, Pennsylvania, Connecticut, New Mexico, Arizona, and Utah.

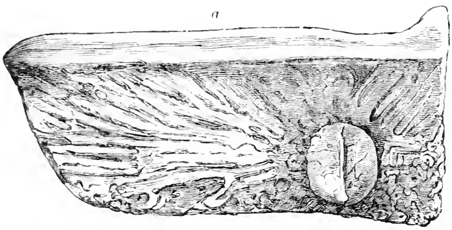


Fig. 310.

Belodon kapffi, v. Meyer. Upper Keuper; Würtemberg. Dorsal scute, $^1/_3$ (after H. v. Meyer).

Stagonolepis, Agassiz. Similar to *Belodon*, but teeth with tumid base. Ventral armour consisting of from five to eight rows of rectangular scutes. Elgin Trias.

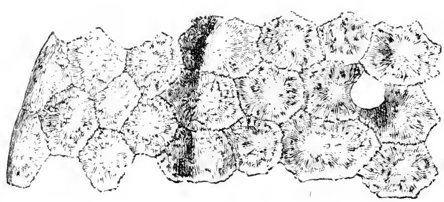


Fig. 311.

Psephoderma alpina, v. Meyer. Upper Trias; Ruhpolding, Bavaria. Ventral armour, $^1/_4$ (after H. v. Meyer).

Parasuchus, Huxley; *Episcoposaurus*, Cope. These are imperfectly known genera, the former from the Gondwana Formation of Maleri, India, and the latter from the New Mexican Trias.

? *Psephoderma*, v. Meyer (Fig. 311). Known by fragments of dermal armour from the Alpine Upper Trias, and formerly referred to Chelonians (*Dermochelydidae*).

Sub-Order 2. PSEUDOSUCHIA. Zittel.[1]

Premaxillae reduced; nasals very large. External nares paired, placed far forwards; internal nares separate, in about the middle of the palate. Orbits large, laterally directed. Parietals and frontals paired; postorbital distinct. Teeth conical, deeply socketed, confined to anterior half of the jaws. Vertebrae amphiplatyan; cervical ribs hatchet-shaped, double-headed. Fore-limb slightly shorter than the posterior; fifth digit of pes reduced, comprising but a single phalanx. Dorsal armour consisting of a paired series of oblong scutes.

Aetosaurus, Fraas (Fig. 312). Body lizard-like, longicaudate, with dorsal and ventral armouring of radially ornamented scutes; ventral scutes smaller than the dorsal, and almost square. Skull triangular, acuminate in front.

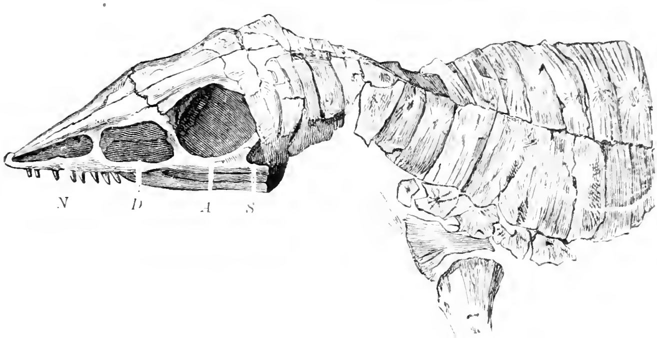


Fig. 312.

Aetosaurus ferratus, Fraas. Upper Keuper; Heslach, near Stuttgart. Head and anterior portion of trunk, ½. *A*, Orbit; *D*, Antorbital vacuity; *N*, Narial opening; *S*, lateral temporal vacuity (after O. Fraas).

Antorbital vacuities large, separated from the large external nares by a narrow ascending process of the maxilla. Posterior border of the orbits formed by the postfrontal and postorbital, the inferior border by the jugal. Parietals and frontals similar in form and size. Temporal region imperfectly known. Mandibular rami pierced by a large foramen between the articular and angular. Interclavicle blade-like. Twenty-four complete but slightly crushed individuals are preserved in the Stuttgart Museum, all on a single slab of Stuben Sandstone (Upper Keuper), from Heslach, near Stuttgart. The largest of these has a total length of 86 cm.

Dyoplax, Fraas. Upper Keuper; Stuttgart. *Typothorax*, Cope. Trias; New Mexico.

Ornithosuchus, Newton. Skull pointed in front, very similar to *Aetosaurus*. Orbits large, supratemporal vacuities small, the lateral ones triangular. Teeth slightly recurved, with finely serrated anterior and posterior cutting edges. Vertebral centra elongated, with very stout neural spines. Ilium elongated, ischium slender, pubis long and rod-like. Elgin Trias. *O. woodwardi*, Newton.

Erpetosaurus, Newton. Skull narrow and rounded in front. Orbits subelliptical, directed upwards and forwards. Supratemporal vacuities round, the

[1] Literature:

Fraas, O., Ueber Dyoplax arenaceus (Wurtt. Jahresh. vol. XXIII.), 1867. — Aetosaurus ferratus (*ibid.* vol. XXXIII.), 1877. — *Newton, E. T.*, Reptiles from the Elgin Sandstone (Phil. Trans. vol. CLXXXV.), 1894.

lateral ones triangular, and antorbital opening long and narrow. External nares small; interclavicle blade-like; dorsal scutes coarsely sculptured. Elgin Trias; Scotland.

Sub-Order 3. MESOSUCHIA. Huxley.[1]

Snout greatly elongated in the earlier forms, short and broad in some of the later. External nares unpaired and terminal; internal nares confluent, opening at posterior margin of the secondary palate formed by plates of the maxillae and palatines, there being no outgrowths from the pterygoids. Eustachian passages open grooves on the basisphenoid. Parietal and frontal unpaired. Vertebrae amphicoelous, or more rarely amphiplatyan. Clavicular elements wanting. Coracoid elongated, with slight perforation. Pubis excluded from acetabulum, and borne on an anterior process of the ischium. Anterior extremities pentadactylate; fifth digit of pes rudimentary.

The *Mesosuchia*, which comprise all the Jurassic and a few Lower Cretaceous crocodiles, were separated by Huxley from the later *Eusuchia* chiefly on account of differences in the palate, eustachian passages, and vertebral centra. In the present group the pterygoids do not develop secondary plates to prolong the canal of the nares, which opens at the hinder margin of the palatines; the eustachian canals are not closed; and the vertebrae in all but the latest forms are amphicoelous. Like the typical Cretaceous and modern families, the *Mesosuchia* comprise both long-snouted and broad-snouted crocodiles, the latter, however, not appearing until the Purbeckian. All except the latest forms are adapted for an exclusively aquatic life, and are known from Europe, Madagascar, Patagonia, and perhaps North America.

Section 1. Longirostres. Lydekker.

Snout greatly produced. Nasals, as a rule, not reaching the premaxillae and external nostril. Mandibular rami united in a long symphysis formed by the dentary and splenial. Vertebrae amphicoelous.

Family 1. Teleosauridae. Zittel.

Teeth conical, slender, closely set. Orbits entirely enclosed, superiorly or more rarely laterally directed, and notably smaller than the subrectangular supratemporal vacuities. Prefrontals small, lachrymals well developed. Antorbital vacuities small, laterally placed. Anterior limb only about half as long as the hinder pair. Dorsal armour consisting of a paired series of broad, overlapping plates; ventral plates suturally united, forming several more or less irregular series, or a mosaic of small polygonal scutes. Jura.

[1] Literature:

d'Alton, M., and *Burmeister, H.*, Der fossile Gaviale von Boll. Halle, 1854.—*Bronn, H. G.*, and *Kaup, J. J.*, Ueber die gavialartigen Reptilien der Liasformation. Stuttgart, 1841.—*Dollo, L.*, Première note sur les Crocodiliens de Bernissart (Bull. Mus. Roy. d'Hist. Nat. Belg. vol. II. p. 309), 1883. *Deslongchamps, E. E.*, Notes paléontologiques. Caen and Paris, 1863-69.—Le Jura Normand. Caen and Paris, 1877-78.—*Deslongchamps, J. A. E.*, Mémoir sur les Teléosauriens de l'époque jurassique (Mém. Soc. Linn. Norm. vol. XIII.), 1863.—*Fraas, E.*, Die Meerkrokodile (Württ. naturw. Jahresh., vol. LVII. p. 409), 1901.—Palaeontogr. vol. XLIX. pp. 1-72, 1902.—*Hulke, J. W.*, Skeletal Anatomy of the Mesosuchia (Proc. Zool. Soc. London, pt. 4), 1888.—*Koken, E.*, Thoracosaurus macrorhynchus Bl., aus der Tuffkreide von Maestricht (Zeitschr. deutsch. geol. Ges. vol. XL. p. 754), 1888.—*Lortet, L.*, Les Reptiles fossiles du Bassin du Rhone (Arch. Mus. d'Hist. Nat. Lyon, vol. V.), 1892.—*Sauvage, E.*, Mémoir sur les Dinosaurs et les Crocodiliens des Terrains jurassiques de Boulogne-sur-Mer (Mém. Soc. Géol. France [2], vol. X.), 1874.—*Winckler, T. C.*, Étude sur le genre Mystriosaurus (Arch. Mus. Tylere, vol. IV. pt. 1), 1876.

The members of this family closely resemble modern gavials in size and general appearance, except that they have smaller heads and more weakly developed fore-limbs. The principal differences are to be found in the characters of the palate, eustachian passages, vertebral centra, ventral armour, and absence of hypapophyses in the cervical region.

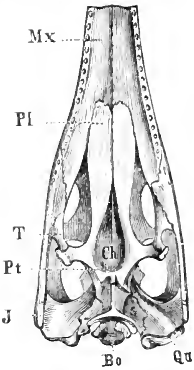


Fig. 313.

Pelagosaurus temporalis, Blv. sp. Upper Lias; Curcy, Calvados. Posterior half of skull, showing typical mesosuchian palate, 1/2. *bo*, Basioccipital; *ch*, Internal nares; *j*, Jugal; *mx*, Maxilla; *pl*, Palatine; *pt*, Pterygoid; *qu*, Quadrate.

Mystriosaurus, Kaup. Skull attaining a length of 1 m., and total length upwards of 6 m. Snout gradually tapering; orbits superiorly directed. Teeth implanted nearly vertically, with anterior and posterior carinae. Known by complete skeletons from the Upper Lias of Würtemberg, Franconia, and England. *M. bollensis*, Cuvier; *M. chapmani*, König.

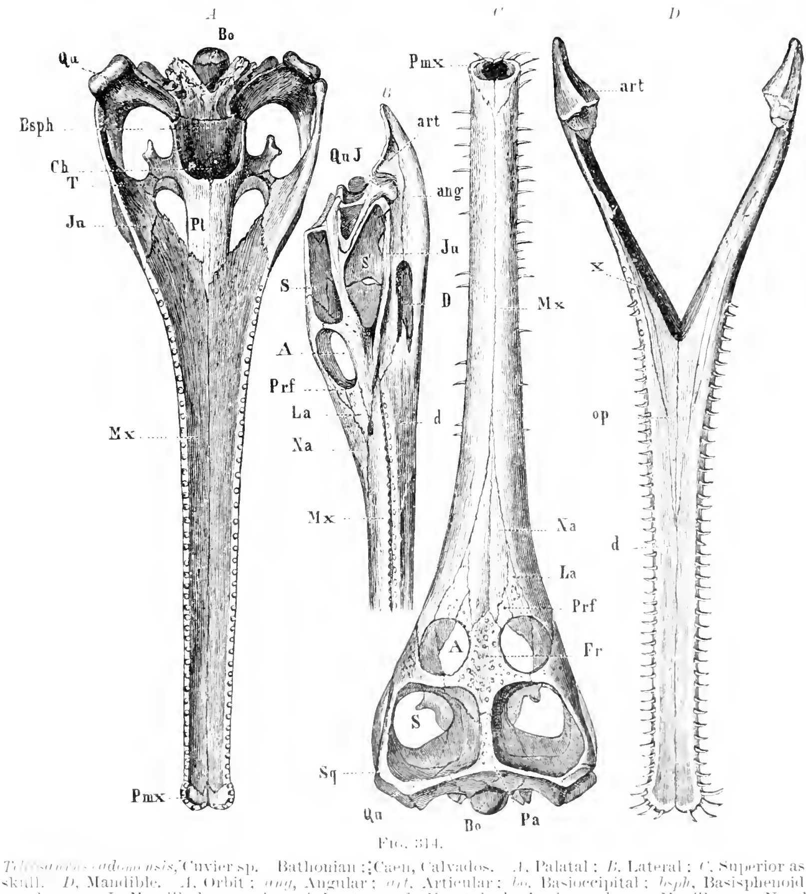


Fig. 314.

Teleosaurus cadomensis, Cuvier sp. Bathonian; Caen, Calvados. *A*, Palatal; *B*, Lateral; *C*, Superior aspects of skull. *D*, Mandible. *A*, Orbit; *ang*, Angular; *art*, Articular; *bo*, Basioccipital; *bsph*, Basisphenoid; *ch*, Internal nares; *D*, Mandibular vacuity; *d*, Dentary; *fr*, Frontal; *la*, Lachrymal; *mx*, Maxilla; *na*, Nasal; *op*, Splenial; *pa*, Parietal; *pl*, Palatine; *pmx*, Premaxilla; *prf*, Prefrontal; *qu*, Quadrate; *quj*, Quadrato-jugal; *S*, Supratemporal vacuity; *S'*, Lateral temporal vacuity; *sq*, Squamosal; *t*, Transverse (ectopterygoid); *x*, Surangular (after E. Deslongchamps).

Pelagosaurus, Bronn (Fig. 313). Like the preceding, but much smaller, the snout tapering more gradually, and orbits laterally directed. Antorbital vacuity much reduced or absent; suborbital vacuity in the palate large; posterior narial opening of pyriform outline. *P. typus*, Bronn, about 1 m. in length; some species 2 m. Upper Lias of Southern Germany and France.

Steneosaurus, Geoff. (*Sericodon*, v. Meyer). Differs from *Mystriosaurus* in having the posterior narial opening rounded, palatines more expanded, and frontal small. Upper Lias to Kimmeridgian.

Teleosaurus, Geoff. (Figs. 314, 315). Skull much elongated and narrow; snout flattened, thin, with rectilinear edges; teeth curved outwards; orbits

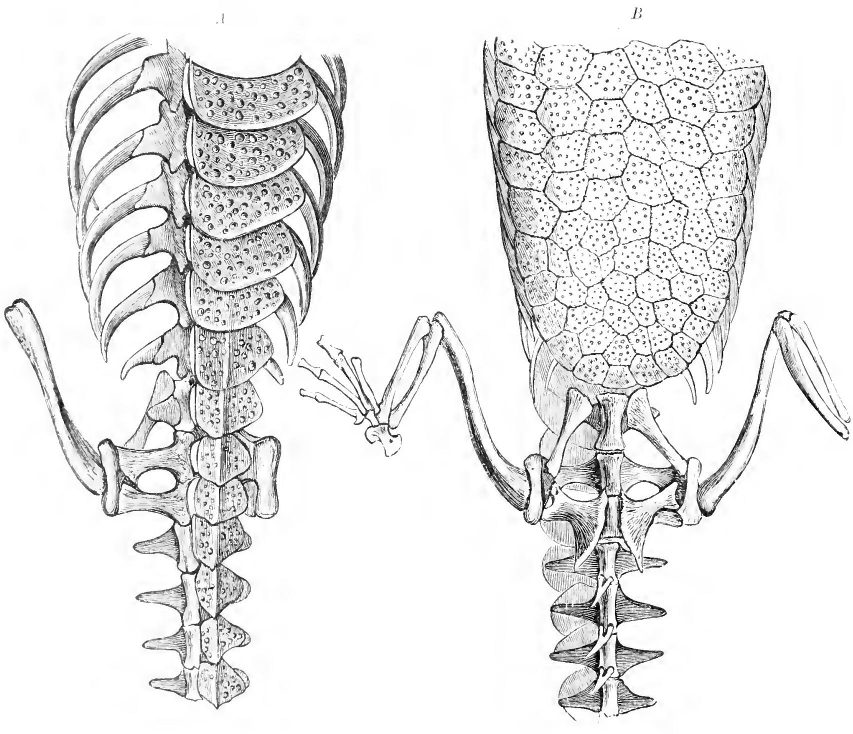


FIG. 315.

Teleosaurus cadomensis, Cuvier sp. Bathonian; Normandy.
Portion of dorsal (*A*), and ventral (*B*) armour (restored after E. Deslongchamps).

circular, superiorly directed. Dorsal scutes longitudinally keeled in sacral and caudal regions; ventral armour extending between the limb girdles. Lower, Middle, and Upper Jura. *T. cadomensis*, Geoff.

Aeolodon, v. Meyer; *Crocodileimus*, Jourdan; *Teleidosaurus*, Deslong. Upper Jura.

Family 2. Metriorhynchidae. Zittel. (*Thalattosuchia*, Fraas.)

Orbits entirely enclosed, elongated, laterally placed, with sclerotic ring. Prefrontals large; nasals broad, widening the snout region posteriorly; lachrymals *reduced. Supratemporal vacuities very large. Dermal armour completely absolete;* limbs paddle-shaped. Middle and Upper Jura.

Metriorhynchus, v. Meyer. Skull elongated and tapering, feebly sculptured. Prefrontals unusually large and forming an overhanging ledge above the orbits. External nostril large, upwardly directed; teeth slender, carinated, and slightly curved, twenty to twenty-seven present on either side of the jaws above and below; three or four anterior teeth enlarged. Fore-limbs much smaller than the hinder pair. Middle Jura. France and England.

Geosaurus, Cuvier (*Cricosaurus*, Wagner; *Rhacheosaurus*, von Meyer). Lithographic Stone; Bavaria. *Suchodus*, Lydekker. Oxfordian; England. *Plesiosuchus*, Owen. Kimmeridgian; Dorsetshire.

Dakosaurus, Quenst. Skull comparatively short and broad; nasals reaching the premaxillae; snout compressed and rounded in front. Teeth large, slightly curved, oval in section, smooth, with anterior and posterior carinae; about twenty on each side of the jaw above and below. External cranial bones smooth or feebly sculptured; mandibular rami without lateral vacuity. Middle and Upper Jura; Swabia and Bavaria. Kimmeridgian; England. A complete skeleton of *D. maximus*, Quenst., 4 m. long, preserved in the Stuttgart Museum.

Family 3. **Pholidosauridae.**

Snout long and narrow, passing abruptly into the facial region. Orbits oval, laterally placed, almost as large as the supratemporal vacuities, and confluent with the lateral temporal fossae. Nasals long and narrow, reaching the posterior tip of the elongated premaxillae. Prefrontals of moderate size. Internal narial opening bordered laterally by the pterygoids. Dorsal and ventral armour present.

The members of this family are known only from fresh-water deposits of the Purbeckian, Wealden, and Lower Cretaceous.

Pholidosaurus, v. Meyer (*Macrorhynchus*, Dunker). Teeth round or oval in section, longitudinally striated, in uniform series of about thirty on each side in either jaw. Wealden of England and Neocomian (Hils Sandstone) of Hanover.

Petrosuchus, Owen. Like the preceding, but internal narial opening enclosed by the palatines. Purbeckian: Dorsetshire.

Hylaeochampsa, Owen. Imperfectly known. Wealden; England.

Section 2. Brevirostres. Lydekker.

Snout short, broad, and rounded. Nasals usually reaching the premaxillae and external nostril. Dentary alone forming the short symphysis of lower jaw; teeth irregular in size and shape. Vertebrae amphicoelous.

Family 1. **Atoposauridae.**

Small, lizard-like crocodiles with broad, triangular skulls. Orbits much larger than supratemporal vacuities. Dorsal armour consisting of a paired longitudinal series of oblong plates. No ventral armour observed. Upper Jura.

Alligatorium, Jourdan. Total length about 40 cm. External cranial bones coarsely sculptured: hind-limbs longer and more robust than the anterior pair. Lithographic Stone; Cerin, France. and Bavaria.

Alligatorellus, Jourdan (Fig. 316). Total length 22 cm. Cranial bones faintly sculptured. Nasals elongated, and apparently dividing the external

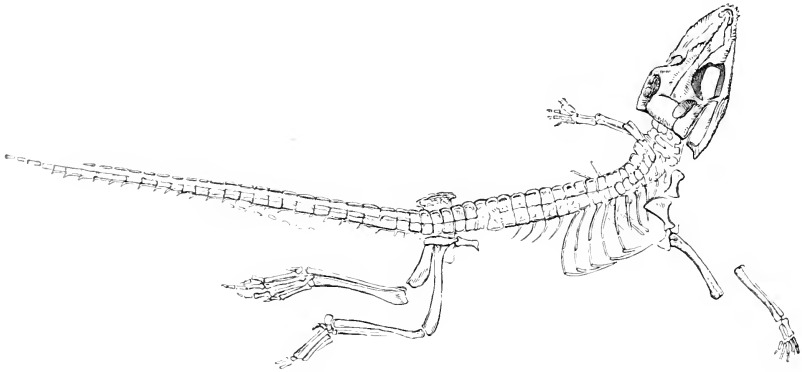


Fig. 316.
Alligatorellus beaumonti, Jourdan. Upper Jura; Cerin, Ain, France. 1/2.

nares. Tail very long; at least thirty caudals. Lithographic Stone; Cerin, France.

Atoposaurus, v. Meyer. Tail very long, comprising over fifty caudals. Dorsal armour not observed. Otherwise like the preceding. Lithographic Stone; Cerin, France, and Bavaria.

Family 2. Goniopholidae. (*Metamosuchia*, Hulke.)

Small to large-sized crocodiles. Orbits usually smaller than supratemporal vacuities. Internal narial opening remote, at hinder margin of palatines, and bounded in part by the pterygoids. Dorsal armour comprising two or more longitudinal series of overlapping and sometimes articulating scutes. Ventral scutes suturally united. Purbeckian and Wealden.

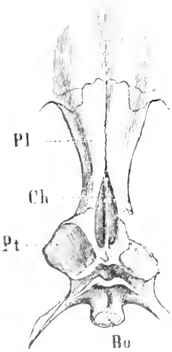


Fig. 317.
Goniopholis simus, Owen. Purbeckian; Swanage, Dorsetshire. Posterior portion of palate. *bo*, Basioccipital; Ch, Posterior nares; *pl*, Palatine; Pt, Pterygoid (after Hulke).

Goniopholis, Owen (*Diplosaurus*, Marsh; *Amphicotylus*, *Hyposaurus*, Cope), (Fig. 317). Snout moderately long, nasals not quite reaching external nostril; supratemporal vacuities larger than the orbits. Twenty-three stout teeth on each side of either jaw, carinated and vertically grooved. Ventral armour consisting of seven to ten longitudinal series of polygonal plates united by jagged sutures. Skull in some species attaining a length of 70 cm. *G. simus*, Owen, known by complete skeletons about 2 m. long, has limbs of equal size. Purbeckian and Wealden; England, Belgium, and Northern Germany. Upper Jura; Colorado.

Bernissartia, Dollo. Attaining a length of 1 m. Supratemporal vacuities smaller than the orbits, nasals not reaching the external nostril. Twenty irregular teeth on each side of either jaw; fore-limbs much shorter than the hinder pair. Dorsal armour with more than two longitudinal series of overlapping scutes; ventral scutes also overlapping. Wealden: Belgium. *B. fagesi*, Dollo.

Machimosaurus, v. Meyer (Fig. 318). Imperfectly known. Teeth obtusely conical, strongly striated. Upper Jura.

Nannosuchus, Owen. Dwarf crocodiles similar to *Goniopholis*, but with slender, curved, smooth, and more uniform teeth. Skull about 10 cm. long. Purbeckian; Dorsetshire.

Theriosuchus, Owen. Total length less than 0·5 m. General form approaching that of modern crocodiles. Supratemporal vacuities smaller than the orbits; teeth tumid and very irregular; mandibular symphysis short. Dorsal scutes overlapping and also united at their outer angles by peg-and-socket articulations; ventral scutes polygonal, united by sutures only. Purbeckian; Dorsetshire. *T. pusillus*, Owen.

FIG. 318.

Machimosaurus hugi, v. Meyer. Kimmeridgian; Lindnerberg, near Hanover. 1/1.

Sub-Order 4. EUSUCHIA. Huxley.[1]

Snout produced in some forms, but more commonly broad and short. External nostril unpaired and terminal; internal nasal passage prolonged and floored by the greatly developed secondary palate, formed by plates from the maxillae, palatines, and pterygoids. Eustachian canals completely enclosed; vertebrae mostly procoelous. Other characters as in Mesosuchia.

This group comprises the later Cretaceous, Tertiary, and modern crocodiles, among which are some long-snouted forms, but the greater number are of the broad-snouted type. As already indicated, they differ from the Jurassic *Mesosuchia* chiefly in the characters of the palate, eustachian canals, and vertebral centra, but as to their genetic relations Palaeontology affords no precise information.

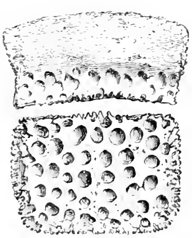


FIG. 319.

Divided ventral scute of *Diplocynodon*, sp. Oligocene; Europe.

A dorsal armour of bony scutes overlaid by the corneous epidermis is always present among *Eusuchia*, and frequently also a ventral armour. The dorsal scutes are externally pitted, more rarely radially sculptured, and are often longitudinally keeled. The ventral scutes are flattened, keelless, less prominently sculptured, and sometimes divided (Fig. 319).

The vertebral column comprises about twenty-five presacral vertebrae, two sacrals, and at least thirty-five caudals. Recent crocodiles have all the presacral vertebrae except the atlas and axis procoelous, and the sacrals and anterior caudals amphiplatyan. There are about nine cervicals. The atlas (Fig. 320) is quadripartite, and its unpaired ventral piece (*x*) has been variously interpreted as the centrum, intercentrum, or hypapophysis. The paired lateral elements are roofed by a median dorsal piece which abuts against the

[1] Literature:

Ludwig, R., Fossile Krokodilien aus der Tertiarformation des Mainzer Beckens (Palaeontogr. Supplem. vol. III.), 1877.—*Lydekker, R.*, Siwalik Crocodilia, etc. (Pal. Indica, ser. X. vol. III. p. 209), 1886.—*Vaillant, L.*, Études zoologiques sur les Crocodiliens fossiles du tertiares (Ann. Soc. Géol. vol. III.), 1872.—*Woodward, A. S.*, On the literature and nomenclature of British fossil Crocodiles (Geol. Mag. [3], vol. II. p. 496), 1885.—The history of fossil Crocodiles (Proc. Geol. Assoc. vol. IX.), 1886.

basiocciput and represents a rudimentary proatlas. The basal piece supports a pair of styliform, single-headed ribs, directed downward and backward. Properly speaking the atlantal centrum is represented by the odontoid process of the axis. The seven succeeding cervicals bear strong neural spines, transverse processes, zygapophyses, parapophyses, and frequently also ventral keels or true hypapophyses. The ribs borne by these vertebrae are all short, hatchet-shaped, and double-headed. In the first two dorsal vertebrae the parapophyses and transverse processes are separated by a narrow interspace, and the latter become more elongated, passing posteriorly (caudal). The parapophyses gradually ascend, passing on to the neural arch in the third dorsal vertebra, and thereafter both articular facettes for the double-headed ribs are borne by the transverse processes. These facettes continue to approximate, and finally become merged with each other in the posterior dorsal vertebrae, so that the last rib is single-headed. The lumbars, of which there are from four to six, have well-developed transverse processes, but are non-costiferous. The short and stout sacral ribs are as a rule distally expanded, and suturally united to their centra and neural arches. The vertebrae of the anterior half of the tail bear moderately developed transverse processes, attached like the sacral ribs to the neuro-central sutures. All except the anterior and a few of the posterior caudals bear chevron bones.

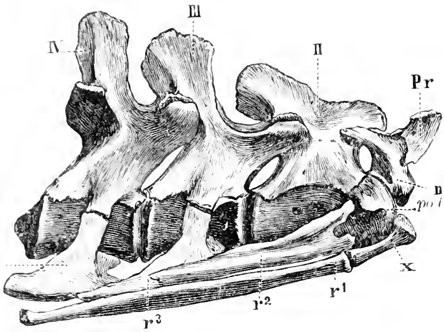


Fig. 320.

Crocodilus vulgaris, Cuv. Recent; Egypt. Anterior cervical vertebrae, I-IV. *n*, Lateral piece of atlas; *pod*, Odontoid process (=centrum of atlas); *pr*, Proatlas; r^1-r^4, Cervical ribs; *x*, Basal piece of atlas (=intercentrum).

The first and second pairs of dorsal ribs are attached to the sternum, which is a large, rhomboidal, cartilaginous plate lying immediately below and behind the interclavicle (episternum). The succeeding five to seven pairs are connected by means of sternal ribs with the so-called abdominal sternum. The sternal ribs are followed by seven pairs of abdominal ribs, of which the posterior is the most strongly developed, and unites with the pubic cartilage. Cartilaginous uncinate processes are borne by the dorsal ribs.

The external cranial bones are almost always coarsely sculptured. The oval or rounded orbits, which in the preceding sub-orders are invariably enclosed by bone, are here confluent with the lateral temporal vacuities. The size of the latter is usually in inverse proportion to that of the supratemporal vacuities, and the latter as a rule are smaller than the orbits. The parietal and frontal are unpaired in the adult condition, and there is never a parietal foramen. The squamosal is a triangular bone forming the postero-external border of the supratemporal vacuity. Postfrontals, prefrontals, and lachrymals are all variable in size. The nasals are long, triangular bones, usually reaching the premaxillae, and sometimes even the external nostril in front, and applied against the acute median process of the frontal posteriorly. The nostril opening is undivided, terminal, and enclosed by the short, paired premaxillae. The quadrate is broad and immovably united with the surrounding elements.

The under side of the skull is characterised by a great development of the secondary palate, formed by horizontal expansions of the premaxillae, maxillae, palatines, and pterygoids, and pierced by a moderate or large-sized infraorbital vacuity. This extensive roofing of the buccal cavity conceals the vomers and causes the internal opening of the nasal passage to be displaced far backwards, at the posterior border of the pterygoids, whereas in the *Mesosuchia* the opening is never further remote than the hinder margin of the palatine plates (cf. Fig. 313 with Fig. 321). A transverse bone (ectopterygoid) is present, connecting the pterygoids with the maxillae and jugal (Fig. 321, *T*). Modern gavials exhibit in the adult a pair of bulbous outgrowths (*bu*) of the palatines which communicate with the nasal passage and function as air-reservoirs.

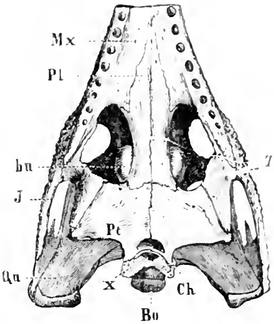


FIG. 321.

Gavialis gangeticus, Geoffr. Recent; India. Oral aspect of posterior half of skull, showing eusuchian secondary palate. *bo*, Basioccipital; *bu*, Ossified air-chambers; *ch*, Posterior nares; *j*, Jugal; *mx*, Maxilla; *pl*, Palatine; *pt*, Pterygoid; *qu*, Quadrate; *t*, Ectopterygoid; *x*, Opening of eustachian canals.

The mandibular ramus is composed of the usual six pieces, one of which, the articular, is pneumatic. A large foramen communicating with the inner cavity of the jaw is almost invariably present between the angular, surangular, and dentary. The symphysis is formed by the latter element alone in the broad-nosed forms, by the dentary and splenial together among the longirostrate species.

Numerous conical teeth of oval or circular cross-section, smooth or striated, and frequently carinated, are implanted in deep alveoli along the margin of the jaws. They are often irregular in form and size, but their number remains constant for particular species, and in many cases also for the genus.

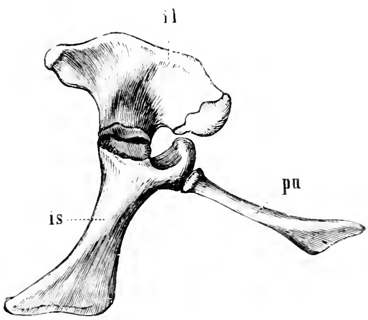


FIG. 322.

Pelvis of Crocodile.
il, Ilium; *is*, Ischium; *pu*, Pubis.

In the pectoral arch clavicles are wanting. The scapula is elongated and expanded at either end, as is also the coracoid. The latter is thickened in its proximal portion, and pierced by a round foramen. The humerus is stout, slightly curved, and exhibits near the head a conspicuous process as well as a deltoid crest. Its distal end is furnished with two facettes for the bones of the second segment, of which the ulna is generally somewhat the longer (Fig. 323). The proximal row of the carpus contains two elongated elements (radiale and ulnare, both constricted in the middle), and a small pisiforme to which the fifth metacarpal is attached by ligaments. The two radial digits are slightly stouter than the three ulnar.

FIG. 323.

Right fore-limb of Crocodile. *R*, Radius; *U*, Ulna; *c5-3*, Distal carpals; *p*, Pisiforme; *r*, Radiale; *u*, Ulnare; *I—V*, Digits.

Of the three elements of the pelvic arch (Fig. 322), the pubis is excluded from the acetabulum, and borne on a prominent anterior process of the ischium. The pubis is more or less spatula-shaped; the ischium resembles the scapula; and the ilium is a strong bone with curved upper margin, and extended antero-posteriorly. Its enlarged anterior portion is attached to the sacral ribs. The femur is longer and more slender than the humerus, and without an inner trochanter; tibia and fibula are of about equal proportions. There are two rather large proximal tarsals, a calcaneum (fibulare) and astragalo-scaphoid, the latter representing the coössified tibiale, centrale, and intermedium. Two bones are likewise present in the distal row, of which the cuboid is the larger, and supports the third, fourth, and the rudimentary fifth metatarsal. The three inner digits of both pes and manus are provided with claws.

A longirostrate section of *Eusuchia* is constituted by the gavials, which correspond to the mesosuchian Teleosaurs, and may possibly have been descended from them. Modern crocodiles and alligators form the brevirostrate section, but between these types are some annectant fossil forms, such as *Tomistoma*, etc.

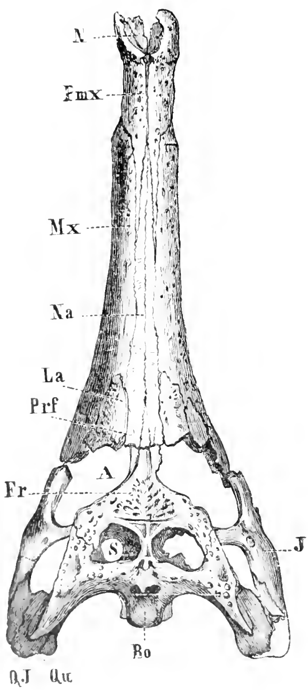


Fig. 324.

Tomistoma eggenburgensis, Toula and Kail. Miocene; Eggenburg, near Horn, Austria. Dorsal aspect of skull, $^1/_{10}$. Lettering as in Fig. 325.

Family 1.

Tomistomidae. (*Rhynchosuchidae*, Huxley.)

Snout much produced, passing gradually into the facial region. Nasals long and narrow, their anterior ends intercalated between slender processes of the premaxillae, but not reaching the external nostril. Prefrontals small, lachrymals large. Orbits irregularly oval, nearly as large as, or larger than the supratemporal vacuities, and confluent with the lateral temporal fossae. Ventral armour absent. Upper Cretaceous to Recent.

Thoracosaurus, Leidy (*Sphenosaurus*, Ag.). Premaxillae spatulate in form, lachrymals unusually large. Supratemporal vacuity transversely oblong, slightly larger than the orbits; small antorbital vacuity present. About twenty-four curved teeth on either side in each jaw. Upper Cretaceous; New Jersey, Holland, and France.

Holops, Cope. Like the preceding, but without antorbital vacuity, and orbits of equal size with supratemporal vacuities. Upper Cretaceous; New Jersey.

Tomistoma, Müller (*Rhynchosuchus*, Huxley, *Gavialosuchus*, Toula and Kail), (Fig. 324). Orbits almost twice the size of supratemporal vacuities. Parietals small, lachrymals moderately developed. About twenty teeth on either side in each jaw. Miocene; Hungary, Malta, and Sardinia, and Recent in Borneo.

Family 2. Gavialidae.

Snout produced into a long, narrow rostrum, and passing abruptly into the facial region. Nasals separated from premaxillae by a wide interval. Mandibular symphysis extended. Teeth numerous, approximately uniform, slightly curved, acuminate, and finely striated. Tertiary and Recent.

Gavialis, Oppel (*Leptorhynchus*, Clift; *Rhamphostoma*, Wagler), (Fig. 321). Recent in India and Burmah. Fossil in Pliocene of Siwalik Hills, India, where it accompanies the gigantic and closely allied *Rhamphosuchus crassidens*. Falconer and Cautley (total length 15 m.), and possibly also present in the Eocene of Sussex.

Leptorhamphus, *Oxydontosaurus*, Ameghino. Tertiary; Argentina.

Family 3. Alligatoridae.

Snout broad and short. Orbits larger than supratemporal vacuities, and conterminous with the lateral temporal fossae. Mandibular symphysis short. Teeth irregular; the anterior tooth of lower jaw always, and as a rule also the fourth tooth, fitting into pits of the upper jaw. Suture between maxillae and premaxillae on the palate either transverse or convex toward the front. Dorsal armour consisting of more than two rows of scutes, either articulated together or lying free in the integument; cervical scutes separated from the dorsal. Ventral armour, when present, comprising numerous series of articulated scutes, each of which consists of two pieces united by suture. Upper Cretaceous to Recent.

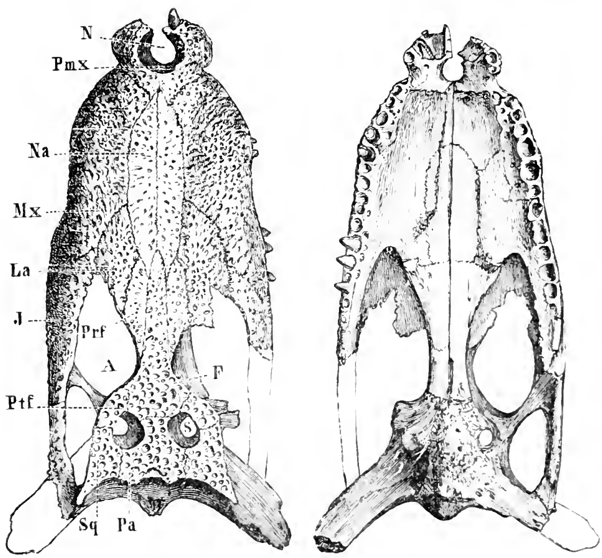


Fig. 325.

Diplocynodon gervaisi, Aymard. Oligocene; Ronzon, near Le Puy, France. Superior and palatal aspects of skull, $^1/_2$. *A*, Orbit; *f*, Frontal; *j*, Jugal; *la*, Lachrymal; *mx*, Maxilla; *N*, External nostril; *na*, Nasal; *pa*, Parietal; *pmx*, Premaxilla; *prf*, Prefrontal; *ptf*, Postfrontal; *S*, Supratemporal vacuity; *sq*, Squamosal.

In alligators the lower teeth bite entirely within the upper, and the first and fourth lower teeth are received into pits of the upper jaw; but in crocodiles the upper and lower teeth mutually interlock, while the first lower tooth bites into a perforation or pit in the cranium, and the fourth into a lateral notch. Modern alligators inhabit the warmer regions of North America and China, and fossil remains occur in the fresh-water. Cretaceous and Tertiary of both Europe and America.

Diplocynodon, Pomel (Figs. 319, 325). Third and fourth teeth of lower jaw equally enlarged, and either both received into pits of the upper jaw, or the fourth passing into a marginal notch between the maxillae and premaxillae. Dermal armour strongly developed. Abundant in Upper Eocene. Oligocene and Miocene of England, France, and Germany.

Bottosaurus, Agassiz. Imperfectly known, but with alligator-like dentition. Upper Cretaceous; New Jersey, Colorado, and Montana.

Alligator, Cuvier. Recent; North America and China. *Caiman*, Spix; *Jacare*, Gray. Central and South America.

Family 4. Crocodilidae.

Skull anteriorly compressed. Orbits larger than supratemporal vacuities, confluent with the lateral temporal fossae. Teeth irregular, eighteen or nineteen in the upper, and fifteen in lower jaw on each side, the two series mutually interlocking. Anterior tooth in lower jaw received into a pit, and fourth tooth fitting into a marginal notch (or pit). Suture between maxillae and premaxillae on the palate transverse or concave in front. Dorsal armour comprising more than two rows of scutes lying free in the integument; ventral armour wanting.

Crocodilian remains occur extensively in the fresh-water Upper Cretaceous and Tertiaries of Europe and North America, and in the Pliocene of India. Recent species are distributed in tropical Africa, East India, New Guinea, South America, and Cuba. The typical genus *Crocodilus*, Laurill. (Figs. 320, 322, 323), is divided into a number of sub-genera, and is met with in the fossil state as early as the Upper Cretaceous of Europe.

Range and Distribution of the Crocodilia.

The earliest remains referred to this order occur in the Trias of Germany, Scotland, North America, and India. They are all extremely generalised forms, belonging to the sub-orders *Parasuchia* and *Pseudosuchia*, and possess a number of characters in common with Dinosaurs, Rhynchocephalians, and Lacertilians. Many of the *Parasuchia*, in fact, are referable to Dinosaurs with as much propriety as to Crocodilians.

True crocodiles, represented by the *Mesosuchia*, appear rather suddenly in the Lias of England, France, and Germany, and persist essentially unmodified throughout the Jura. In none of them is the secondary palate developed back of the posterior margin of the palatines, there being no outgrowths from the pterygoids, and the vertebrae are amphicoelous, or at the most amphiplatyan. Their universal occurrence in marine deposits, the nature of their fossilised stomach contents and coprolites, and their general organisation, prove them to have been adapted for an exclusively aquatic existence. The earliest forms are all of the longirostrate variety, and it is not until the Upper Jura that short- and broad-headed genera with small supratemporal vacuities are initiated. Owen has suggested that the appearance of the latter is correlated with the incoming of warm-blooded prey, and points to the association of dwarf crocodiles in the Purbeck with small mammalian remains.

Toward the close of the Jura changes in external conditions seem to have created a new environment, for in the Purbeckian and Wealden remains of crocodiles are accompanied for the first time by fresh-water and terrestrial forms, and the indications suggest a fluviatile habitat. In the Wealden are found a few detached crocodilian vertebrae of the procoelous type, but it is not until the Upper Cretaceous that typical *Eusuchia* with extended secondary palate and closed eustachian passages become dominant. The *Eusuchia*, like their Jurassic forerunners, comprise both long-snouted and broad-snouted genera, but whether the gavials were derived independently from the modern crocodiles and alligators, or all are traceable to a common Mesosuchian ancestor, is still uncertain. During the Tertiary, alligators and crocodiles prevailed both in Europe and North America, only becoming extinct in Europe during the Pliocene. The alligators, which appear to have surpassed crocodiles in the Old World, and to have been inferior to them in number in the New, are now restricted to the warmer regions of North America. Remains of both gavials and crocodiles occur in the Tertiary of India, among which are comprised the most gigantic members of the order (*Rhamphosuchus*).

Order 8. DINOSAURIA. Owen.[1]

(*Pachypodes*, Owen ; *Ornithoscelida*, Huxley.)

Long-necked and long-tailed reptiles, usually of considerable and sometimes of gigantic size, with limbs adapted for habitual support of the body. Investing bones of the temporal region of the skull contracting into an upper and a lower temporal arcade, and the large quadrate firmly fixed. No pineal foramen. Teeth thecodont, confined to margin of the jaw-bones. Vertebrae opisthocoelous or amphiplatyan, rarely amphicoelous, sometimes hollow or with deep lateral cavities ; sacrum comprising from two to ten anchylosed vertebrae. Ribs double-headed. Sternum incompletely ossified, clavicles and precoracoid absent. Scapula very large, sometimes coössified with the perforate and anteriorly rounded coracoid. All three pelvic elements entering the acetabulum. Ilium large, antero-posteriorly extended. Ischia usually slender and elongated, frequently united in a median symphysis. Pubis directed downwards and forwards, sometimes developing a postpubic process extending backwards parallel with the ischium. Fore-limbs shorter than the hinder pair : progression very commonly bipedal.

The order *Dinosauria* comprises Mesozoic reptiles which are extremely varied in organisation, and exhibit a number of rhynchocephalian, crocodilian, lacertilian, and even ornithic characters, the latter due chiefly to homoplastic or parallel development. Among the latter, as first noticed by Gegenbaur,

[1] Literature :

Baur, G., Der Tarsus der Vögel und Dinosaurier (Morph. Jahrb. vol. VIII. p. 417), 1883.—Bemerkungen über das Becken der Vögel und Dinosaurier (*ibid.* vol. X. p. 613), 1885. Remarks on the Reptiles generally called Dinosauria (Amer. Nat. vol. XXV. p. 434), 1891.—*Cope, E. D.*, Palaeontological Bulletins Nos. 22-28, in Proc. Amer. Phil. Soc. 1876-77.—*Dollo, L.*, Notes sur les Dinosauriens de Bernissart (Bull. Mus. d'Hist. Nat. Belg. vols. I.-III.), 1882-84.—*Hulke, J. W.*, Presidential Addresses (Quar. Journ. Geol. Soc. vols. XXXIX., XL.), 1883-84.—*Huxley, T. H.*, On the Animals which are most nearly intermediate between birds and Dinosaurs (Proc. Roy. Soc. p. 278), 1868. Also Ann. Mag. Nat. Hist. [4], vol. I. (1868), p. 220.—Further evidence on the affinity between the Dinosaurian Reptiles and Birds (Quar. Journ. Geol. Soc. vol. XXVII. p. 12), 1870.—On the classification of the Dinosauria (*ibid.* p. 32).—*Marsh, O. C.*, Numerous contributions in Amer. Journ. Sci. [3], vols. XVI.-L. 1878-96.—The Dinosaurs of North America (16th Ann. Rep. U.S. Geol. Surv.), 1896.—*Mehnert, E.*, Untersuchungen uber die Entwickelung des os pubis der Vögel (Morph. Jahrb. vol. XIII. p. 239), 1888.—*Osborn, H. F.*, Dinosaur Contributions Nos. 1-3 in Bull. Amer. Mus. Nat. Hist. vols. X.-XII., and Memoirs, vol. I. pt. 5, 1898-99. Reconsideration of the evidence for a common Dinosaur-avian stem in the Permian (Amer. Nat. vol. XXXIV. p. 777), 1900.—*Owen, R.*, A history of British fossil Reptiles [Reprint from the publications of the Palaeontographical and other Societies], London, 1849-84.—*Seeley, H. G.*, On the classification of the Dinosauria (Proc. Roy. Soc. vol. XLIII.), 1887.

the close junction of the astragalus with the tibia, or tendency to form a tibio-tarsus, is an avian resemblance common to the majority of Dinosaurs.

While, on the one hand, the cleft between Dinosaurs, crocodiles, and lacertilians is bridged by the Rhynchocephalian Proterosaurs (*Proganosauria*, Baur), on the other it may be regarded as altogether probable that birds have come down to us from a primitive (perhaps bipedal ?) Dinosaur-avian stem which sprang off from a *Palaeohatteria*-like ancestor in the Permian.[1] The earliest known Dinosaurs (*Theropoda*) of Triassic age are shown by their limb structure and footprints to have been mainly bipedal in gait, and by their dentition to have been of carnivorous habits; of the herbivorous Dinosaurs (*Sauropoda* and *Predentata*) which range throughout the Jura and Cretaceous, some must have been bipedal and others quadrupedal. The culmination of Dinosaurs occurred during the Upper Jura and Cretaceous, in the interval between the decline of Theromorph reptiles and the dominance of the *Mammalia*. During their period of ascendency numerous hypertrophic forms were evolved, which attained proportions far exceeding those of all other known terrestrial creatures. Over-specialisation having run its course, a rapid decline and extinction followed.

A bony *exoskeleton* is developed to some extent among certain of the *Theropoda* and *Predentata*, but in the majority of Dinosaurs the skin was either naked or protected by horny scales. The dermal armour, when present, consists either of isolated bony plates or spines, or of interlocking scutes which form a continuous shield encasing portions of the trunk and tail.

The *vertebrae* are usually either amphiplatyan or opisthocoelous, more rarely amphicoelous. There are nine to fifteen cervicals, ten to eighteen dorsals, usually from two to six, but sometimes as many as ten, fused sacrals, and thirty to fifty caudal vertebrae. The union between the centra and their neural arches is commonly by suture. In the anterior cervicals the neural spines are generally short or rudimentary, and gradually increase in size toward the thoracic region. The atlas and axis, so far as known, exhibit a construction similar to that in crocodiles. All the succeeding cervicals bear double-headed ribs, of which the capitulum is attached to the parapophysis of the centrum, and the tuberculum to the transverse process of the neural arch. In the dorsal region the parapophyses mount upward from the centra on to the sides of the neural arches. Single-headed ribs do not occur.

Among the *Theropoda* and *Sauropoda* the posterior dorsal vertebrae articulate with one another not only by zygapophyses, but by a hyposphene-hypantrum arrangement. The *hyposphene* facette is a vertical or wedge-shaped projection occurring on the posterior end of the neural arch below and continuous with the post-zygapophysis. It is received into a corresponding groove, or *hypantrum*, on the anterior face of the next vertebra behind. This arrangement is similar in function to the zygosphen-zygantrum articulation among Ophidians, except that the relative positions of pegs and sockets are interchanged. The sacral vertebrae, which vary from two to ten in number, are fused together; and the chevron bones of the caudals are articulated intervertebrally.

The *skull* of most Dinosaurs is extremely small in proportion to the rest of the body, more so in *Brontosaurus*, in fact, than in any other reptile, and

[1] *Osborn, H. F.*, Reconsideration of the evidence for a common Dinosaur-avian stem in the Permian (Amer. Nat. vol. XXXIV. p. 777), 1900.

the brain cavity is exceedingly diminutive. The latter, in proportion to the size of the head, is smaller in *Triceratops* than in any known land vertebrate. Among the *Theropoda* and *Predentata* the long axis of the skull is approximately at right angles to the neck, but in the quadrupedal *Sauropoda* it continues the line of the vertebral column. The large orbits are laterally directed, and between them and the paired narial openings is frequently an antorbital vacuity, as in crocodiles, pterosaurs, and birds. The temporal vacuities are completely enclosed, and vary considerably in form and size. The large quadrate is prominently exposed, and suturally united with the squamosal and quadrato-jugal. The paired premaxillae are rather extensively developed, and either provided with teeth, or edentulous and beak-like.

The inferior aspect of the skull is similar in a general way to that of Rhynchocephalians, except that there are no teeth on the palate. The mandibular rami are united in a cartilaginous symphysis, and in the *Predentata* a crescentic, edentulous, predentary bone is developed in front of the mandible, the sharp margin of which appears to have been sheathed in a horny beak. Teeth are confined to the margin of the jaws, and are either deeply socketed or implanted in an alveolar groove open on the inner side of the jaws.

In the *pectoral arch* clavicles appear to be wanting, and the sternum is imperfectly ossified. The scapula is very strongly developed, and usually much elongated. The coracoid is flattened, with more or less rounded anterior margin, and pierced by a foramen near its articular border. Sometimes the scapula-coracoid elements are fused at their proximal ends, as in birds.

The bones of the appendicular skeleton are sometimes very massive, in other cases delicate and hollow; and the disparity between fore- and hind-quarters is often very considerable, indicating that the presacral region was ordinarily lifted from the ground. The humerus in most cases is inferior in length to the scapula; the radius and ulna are strongly developed, and always separate. The carpus is often incompletely ossified, and the number of metacarpals is sometimes reduced to three. The digits are short, and the ungual phalanges either hoofed or claw-shaped.

Many remarkably avian-like characters are to be observed in the *pelvic arch* and bones of the hind limb, especially among the *Predentata*. The ilium is depressed and more or less extended antero-posteriorly; moderately so in the triradiate type of pelvis (*Theropoda*), very much so in the quadriradiate type (*Predentata*). The long ischia extend backwards and downwards, and usually join in a median ventral symphysis. The pre-acetabular process of the ilium (*spina iliaca*) which serves for the attachment of the pubis, extends further downward than the post-acetabular or ischial process, as in birds. The acetabulum itself is partly open, and the sacrum is partly ornithic, partly reptilian.

In the *Theropoda* the pubes are long and slender, and fused in an extended ventral symphysis. Among the *Sauropoda* they are shorter, stouter, and broader than the ischia, directed simply downwards and forwards, and united distally in a median cartilaginous symphysis. In the *Predentata* (Fig. 326) the pubis is long and broad, but does not join its fellow in the median line in front. At its base, underneath the acetabulum, it gives off a long and slender process known as the *post-pubis*, which is directed downward and backward parallel with the almost equally slender but somewhat longer ischium. Although this post-pubic process is suggestive at first sight of the pubis of birds, it has been demonstrated by the embryological researches of Bunge[1] and Mehnert[2] that no homology between these structures exists. The avian pelvis is in its earliest stages of development triradiate, like that of the primitive Theropodous Dinosaurs, and the pubis is directed forwards as in reptiles. Later the pubis becomes secondarily shifted backwards, parallel with the ischium, and the *processus iliopectineus* must be regarded as a secondary structure peculiar to birds, with which the pubis of Dinosaurs has, of course, no homology. The post-pubis of the *Predentata* is accordingly to be interpreted as a special or adaptive modification, probably correlated with the function of the tail in balancing the body in locomotion, or while resting on its hind quarters.

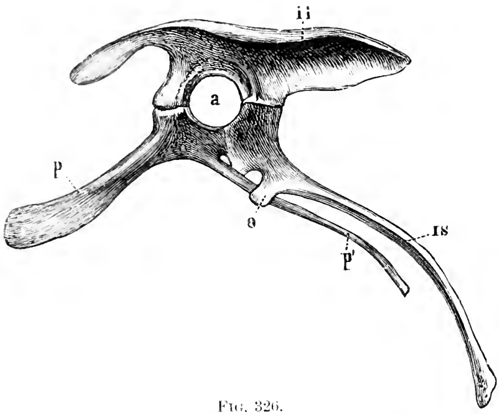


FIG. 326.

Pelvis of *Iguanodon*, 1/20. *a*, Acetabulum; *il*, Ilium; *is*, Ischium; *o*, Obturator process; *p*, Pubis; *p'*, Postpubic process.

The *femur* usually exceeds the humerus in length, and is placed vertical to the body, with its head extending inward into the acetabulum, as in birds. Dollo has shown that the femur of *Iguanodon*, with its large fourth trochanter (a process which is distinct from the "third trochanter" of mammals), is constructed more upon the avian than reptilian type, and indicates a powerful caudo-femoral musculature. Still other ornithic characters are exhibited by the tibia, which possesses a large procnemial crest, and is often completely embraced by the astragalus at its distal end. In the Stegosaurs these elements are fused, but in most of the carnivorous *Theropoda* the astragalus bears an ascending process, which is opposed to the anterior face of the lower end of the tibia, exactly as in Pterosaurs and young Ratite birds. The fibula is complete, the proximal tarsals are two in number (astragalus and calcaneum), and the distal two or three, tarsalia I-III, being usually fused into a single piece. The hind foot is either tridactyl or pentadactyl, but all five metatarsals are commonly indicated, even when the number of functional digits is reduced.

Dinosaur remains were first discovered in the English Upper Jura and Wealden during the early decades of the last century, and were described by Buckland and Mantell in 1825. Owen, in 1841, erected for them the order *Dinosauria*, and much additional light was shed on their structure and relations by Huxley, Marsh, and Cope prior to 1875. Avian resemblances were first pointed out by Gegenbaur in 1864, who observed that the tibio-tarsus of *Compsognathus* is decidedly bird-like. In this form also was detected the only

[1] *Bunge, A.*, Zur Entwicklungsgeschichte des Beckengürtels der Amphibien, Reptilien und Vögel. Dorpat, 1880.

[2] *Mehnert, E.*, Ueber die Entwicklung des os pelvis der Vögel (Morphol. Jahrb. vol. XIII. p. 259), 1888.

known evidence of viviparous habits among Dinosaurs.[1] During the last quarter of the nineteenth century an abundance of well-preserved remains was brought to light both in the Old World and in the New, which lent a fresh impetus to their study. The division of the group into three sub-orders—*Theropoda*, *Sauropoda*, and *Predentata*—was first proposed by O. C. Marsh.

Sub-Order 1. THEROPODA. Marsh.[2]

Carnivorous Dinosaurs with small cranium, the long axis of which is approximately at right angles to that of the neck. Margin of the jaws provided with laterally compressed thecodont cutting teeth. Brain-case incompletely ossified; antorbital vacuity large. Mandibular ramus without coronoid process, and usually pierced by a lateral foramen in its hinder half. Vertebral centra hollowed, the cervicals flattened in front, and concave behind; post-cervicals amphiplatyan or slightly amphicoelous. Sternum unossified; acetabulum perforate. Pubes slender, projecting simply downwards, and united distally, like the ischia, in a symphysis which is often much extended. Post-pubic process not developed. Limb bones hollow, fore-limbs considerably shorter than the hinder pair; digits three to five in number, provided with prehensile claws; hind feet digitigrade. Femur with inner trochanter; astragalus with ascending anterior process.

The *Theropoda* were carnivorous land Dinosaurs provided with clawed digits, and varying excessively in size. *Compsognathus*, the smallest known Dinosaur, was no larger than a cat, and *Megalosaurus* attained the size of an elephant. In outward appearance these animals must have been very grotesque, owing to their habit of stalking about on their hind limbs, or possibly even leaping in kangaroo-fashion (*Hallopus*), with the forward part of the body lifted from the ground, and balanced by the powerfully developed tail. The latter may have served in some cases also for a swimming organ, as well as a support for the animal when resting on its hind quarters and pelvic symphyses. The skeleton of many *Theropoda* was of very delicate construction, the vertebrae being often, and the limb bones always, hollow.

The skull is known in comparatively few genera. It is similar in the main to that of the *Sauropoda*, but the brain-case is incompletely ossified, and the sutures are often indistinct. The elongation of the cervical vertebrae is an ornithic character, as pointed out by Cope. All the vertebrae of the neck, except the atlas, are concave behind, but usually flattened on the anterior face of the centra; they are longer than the dorsals, and their neural spines are only moderately developed, indicating a less powerful musculature than among the *Sauropoda*. The cervical ribs are long and nearly straight, one of their articular heads being attached to the centrum, and the other to the neural arch. Each sacral rib is attached to two vertebrae; the caudals are without ribs, but chevron bones are strongly developed. *Megalosaurus* and *Compsognathus* are remarkable for the possession of abdominal ribs.

[1] *Marsh, O. C.*, Amer. Journ. Sci. [3], vol. XXI. (1881). p. 340.

[2] Literature:

Deslongchamps, E. E., Mémoir sur le Poikilopleuron Bucklandii (Mém. Soc. Linn. Norm. vol. VI. p. 36), 1838.—*Newton, E. T.*, On Ornithosuchus, etc. (Phil. Trans. vol. CLXXXV. B, p. 586), 1894.—*Osborn, H. F.*, Fore and hind limbs of Carnivorous Dinosaurs from the Jurassic of Wyoming Bull. Amer. Mus. Nat. Hist. vol. XII. p. 161), 1898.—*Phillips, J.*, Geology of Oxford and the Valley of the Thames. Oxford, 1871.—*Plieninger, T.*, Ueber Zanclodon, etc. (Württ. naturw. Jahresh. vol. VIII. p. 389), 1857.—*Wagner, A.*, Ueber Compsognathus longipes, etc. (Abh. Bayer. Akad. Wiss. II. Classe, vol. IX. p. 94), 1861.

In the pectoral arch the scapula is longer and stouter than the humerus, the coracoid is more or less crescentic or semicircular, and there is no ossified sternum. The fore-limbs are small, the carpus is, as a rule, incompletely ossified, and the clawed digits are of only moderate size. In the pelvic arch the ilium is low and antero-posteriorly extended, the post-acetabular portion lower and more elongated than the pre-acetabular, and the acetabulum itself is perforate. Both the pubes and ischia meet in ventral symphyses, which are often much extended, and apparently served as a support for the body when in a crouching or sitting position. The structure of the massive hind limbs indicates that progression was mainly bipedal and digitigrade. The proximal tarsals tend to form a tibio-tarsus, and in most genera the astragalus bears an ascending process, which is immovably applied against the anterior face of the tibia, as in young ostriches. *Theropoda* first appear in the Trias, and become extinct in the Cretaceous.

Family 1. **Megalosauridae.** Huxley.

Vertebrae solid and amphiplatyan, except the cervicals, which are opisthocoelous. Pubes long, projecting simply downwards and forwards, and united in an extended ventral symphysis. Extremities pentadactyl, but the inner and outer digits frequently rudimentary. Trias to Upper Cretaceous.

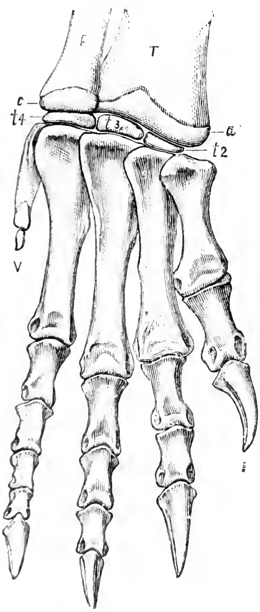


Fig. 327.

Anchisaurus major, Marsh. Trias; Manchester, Conn. 1/4. Dorsal aspect of right hind foot. *a*, Astragalus; *c*, Calcaneum; *f*, Fibula; *t*, Tibia; t_2-t_4, Distal tarsals; I–V, Digits (after Marsh).

Zanclodon, Plien. (*Plateosaurus*, *Teratosaurus*, *Smilodon*, v. Meyer; *Gresslyosaurus*, Rütim.). Teeth with serrated anterior and posterior cutting edges. Vertebral column comprising at least sixty vertebrae, three of which are sacral. Limb bones stout. Keuper; Würtemberg. *Z. laevis*, Plieninger.

Dimodosaurus, Pidancet and Chof. Keuper; Poligny, France. *Cladyodon*, Owen; *Thecodontosaurus*, *Palaeosaurus*, Riley and Stutch. Trias; Bristol, England. *Rachitrema*, Sauvage. Rhaetic; Autun, France. *Epicampodon*, Huxley. Trias; East India. *Euscelosaurus*, Huxley. Trias; South Africa. These are imperfectly known genera allied to *Zanclodon*.

Anchisaurus, Marsh (Fig. 327). Skull remarkably bird-like, with very large orbits and antorbital vacuity; narial opening relatively small; supratemporal vacuity subrectangular. Quadrate inclined steeply forwards. Teeth numerous, nearly uniform, and closely set. Fore-limb about two-thirds as large as the hinder pair, with only three clawed digits, the fourth and fifth rudimentary. In the pes the fifth digit is reduced, and the first much shorter than the rest. Total length slightly exceeding 1 m. Trias; Connecticut.

Ammosaurus, Marsh; *Bathygnathus*, Leidy; *Arctosaurus*, Adams; (*Clepsysaurus*, Lea. Represented by fragmentary remains from the Trias of North America.

Ceratosaurus, Marsh (Figs. 328, 329). Skeleton 4-5 m. long, skull relatively very large and delicate. Nasal bones long, fused, and supporting a large median horn-core; prefrontals laterally swollen and partly overhanging

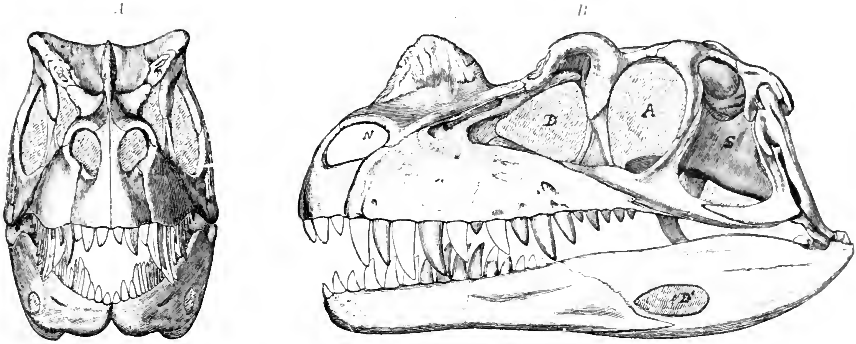


Fig. 328.

Ceratosaurus nasicornis, Marsh. Upper Jura; Colorado. Skull from anterior (*A*), and lateral (*B*), aspects, 1/9. *A*, Orbit; *D*, Antorbital vacuity; *D′*, Mandibular vacuity; *N*, External nostril; *S*, Supratemporal vacuity; (after Marsh).

the orbits, which are inferior in size to the lateral temporal vacuities. Cervical vertebrae strongly opisthocoelous, flattened in front. Tail long, compressed and deepened in its anterior portion, as indicated by the long neural spines and chevron bones. Pelvic elements fused at the acetabulum; pubic and ischial symphyses expanded. Fore-limbs very small, and manus with four digits (I-IV) each bearing a claw. Femur much curved; astragalus not fused with the tibia, but bearing a large ascending process. Digits Nos. I and V wanting in the hind foot; metatarsals fused together (pathologically?) and with the distal tarsals. Dermal ossifications observed in the neck region. Upper Jura; Colorado. *C. nasicornis*, Marsh.

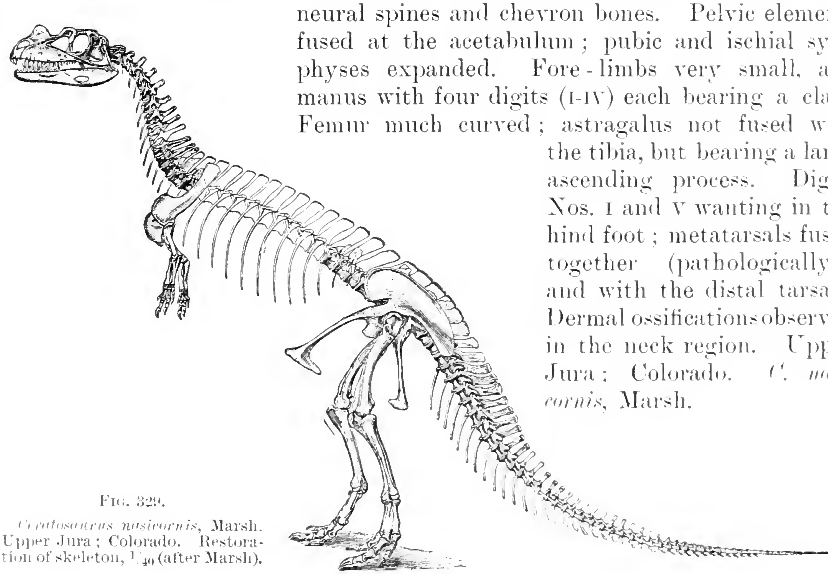


Fig. 329.

Ceratosaurus nasicornis, Marsh. Upper Jura; Colorado. Restoration of skeleton, 1/40 (after Marsh).

Allosaurus, Marsh (Fig. 330). Skull unknown. Vertebrae and appendicular skeleton resembling *Ceratosaurus*, except that the pelvic elements and metatarsals are not fused. Upper Jura; Colorado.

Labrosaurus, Marsh. Upper Jura; Colorado. *Streptospondylus*, v. Meyer, Upper Jura; Northern France and England.

Megalosaurus, Buckland (*Poikilopleuron*, Deslong.), (Fig. 331). Teeth with serrated anterior and posterior cutting edges. Cervical vertebrae slightly opisthocoelous. Femur 1 m. and scapula 0·8 m. long. Hallux directed inward as in *Apteryx*, and with a complete functional phalanx and claw. Abdominal ribs present. Lias to Wealden; Europe and North America.

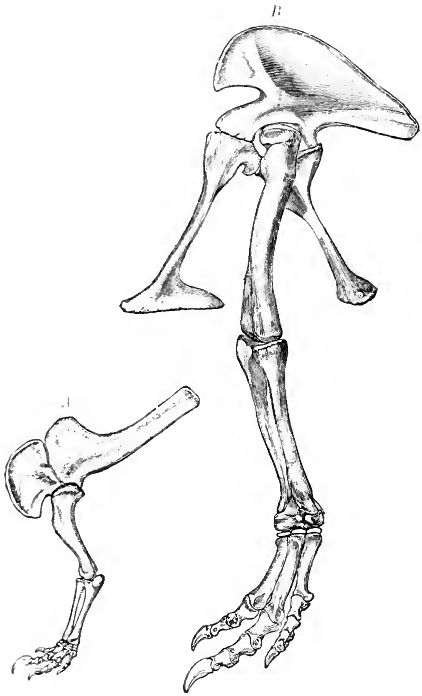


FIG. 330.
Allosaurus agilis, Marsh. Upper Jura; Colorado. Restoration of anterior (*A*), and posterior (*B*), limbs, 1/20 (after Marsh).

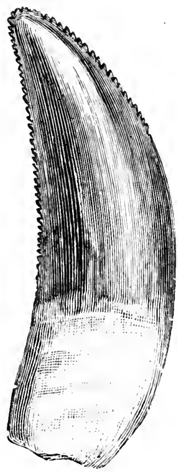


FIG. 331.
Megalosaurus bucklandi, v. Meyer. Bathonian; Stonesfield, England. Tooth, 1/1.

Laelaps, Cope (*Dryptosaurus*, Marsh). Skull and femur each about 0·6 m. long; prefrontal forming a superciliary crest; orbit scarcely separated from antorbital vacuity. Teeth and other characters similar to *Megalosaurus*. Upper Cretaceous; Montana.

Hypsirophus, Cope; *Ornithomimus*, Marsh; *Aublysodon*, *Coelosaurus*, Leidy. Known by fragmentary remains from the Upper Cretaceous of North America.

Family 2. **Compsognathidae.** Huxley.

Vertebrae and limb bones hollow. Cervical vertebrae slightly opisthocoelous, post-cervicals amphiplatyan. Neck long and flexible; cervical ribs styliform. Pubes stout, ischia shorter and more slender. Femur shorter than tibia. Metatarsals long; manus and pes with three functional digits, the inner and outer ones rudimentary. Upper Jura.

Compsognathus, Wagner (Figs. 332, 333). Represented by a unique skeleton of a fully grown individual from the Lithographic Stone of Kelheim, Bavaria, and preserved in the Munich Museum. It is the smallest known Dinosaur, and interesting in that it contains an embryo within the abdomen, first detected by Marsh. Skull bird-like, about 75 mm. long, its long axis set at right angles to the relatively long neck. The twenty-two presacral vertebrae have a combined length of 20 cm., and the caudals, of which only fifteen are preserved, measure about the same. Fore-limbs only half as long as the hinder pair. Proximal tarsals tend to form with the tibia a bird-like tibio-tarsus; astragalus with long ascending process closely applied against anterior face of tibia; distal tarsals represented by three small flattened bones. *C. longipes*, Wagner.

Hallopus, Marsh. A small form apparently related to the preceding. Fore-limb relatively short and with four digits. Astragalus without

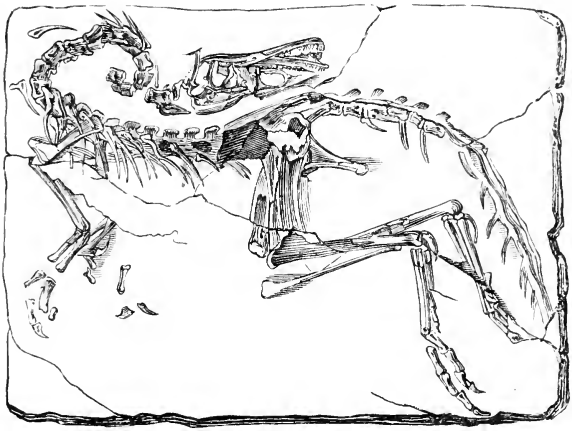


Fig. 332.
Compsognathus longipes, Wagner. Lithographic Stone; Kelheim, Bavaria. Skeleton, 1/4 (after A. Wagner).

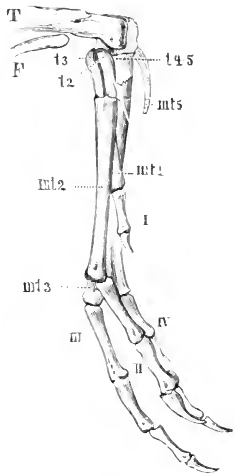


Fig. 333.
Compsognathus longipes, Wagner. Left hind foot, 1/1. *F*, Fibula; *mt*, Metatarsals; *T*. Tibia; *t2-t5*, Distal tarsals (after Baur).

ascending process; calcaneum produced into a "heel," suggestive of the power of leaping. Upper Jura; Colorado.

Family 3. **Coeluridae**. Marsh.

Skull unknown; vertebrae and all other bones of the skeleton hollow. Cervical ribs fused with their centra. Neural canal greatly enlarged. Metatarsals very long and slender. Upper Jura and Wealden.

Coelurus, Marsh (*Aristosuchus*, Seeley). Known only by portions of the vertebral column, pelvis, and limb bones. Centra, neural arches, and all processes of the vertebrae have hollow interiors, and the neural arches are suturally united with their centra. In the cervical and trunk regions the neural canal is greatly dilated. Upper Jura; Wyoming and Maryland. Wealden; England.

Thecospondylus, Seeley; *Calamospondylus*, Lydekker. Wealden; England. *Tichosteus*, Cope. Upper Jura; Colorado. All these names apply to detached vertebrae. According to Cope, the peculiar vertebrae described by von Meyer from the Muschelkalk of Bayreuth under the name of *Tanystropheus*, and occurring also in the Trias of New Mexico, belong to this family.

Sub-Order 2. SAUROPODA. Marsh. (*Cetiosauria.*)[1]

More or less massive, herbivorous, quadrupedal Dinosaurs. Skull relatively small, antorbital vacuity large. Brain-case completely ossified; no predentary bone. Teeth

[1] Literature:

Hatcher, J. B., Diplodocus, Marsh (Mem. Carnegie Museum, vol. I.), 1901.—*Marsh, O. C.*, The Dinosaurs of North America (16th Ann. Rep. U.S. Geol. Surv.), 1896.—*Osborn, H. F.*, Additional characters of the great herbivorous Dinosaur, Camarasaurus (Bull. Amer. Mus. Nat. Hist. vol. X. p. 219), 1898.—A Skeleton of Diplodocus (Mem. Amer. Mus. Nat. Hist. vol. I. pt. V.), 1899.—*Phillips, J.*, Geology of Oxford and the Valley of the Thames. Oxford, 1871.

spatulate, with anterior and posterior cutting edges. Cervical and anterior dorsal vertebrae opisthocoelous and much hollowed on each side; the rest amphiplatyan. Neural canal much expanded in the sacrum. Pubes moderately long, projecting simply downwards, and united distally by cartilage; no post-pubic process. Limb bones solid, femur without prominent inner trochanter. Fore-limbs only slightly shorter than the hinder pair. All four feet semiplantigrade, with five more or less reduced digits; distal row of carpals and tarsals apparently unossified. Dermal armour absent.

The *Sauropoda* display closer relationships with Crocodilians than do the other orders of Dinosaurs, and share a number of features in common with the *Parasuchia*. In this order are included some of the most prodigious land animals known. Their dentition and nature of the articulations prove clearly that they were herbivorous, and the parity of their limbs demonstrates the gait to have been in most cases quadrupedal. Dollo has suggested, however, that the latter habit was possibly secondary, and that all these animals were at one stage bipedal like the Iguanodonts, which have a similar form of pelvis.

The skull is incompletely known except in the genera *Diplodocus*, *Morosaurus*, and *Brontosaurus*. Teeth of long cylindrical or spatulate aspect, and with anterior and posterior cutting edges, are present in the paired premaxillae and in at least the anterior portion of the maxillae. The orbits are large and laterally directed, the antorbital vacuities are also extensive, and the external nares elongated. The position of the latter is between the premaxillae, maxillae, and nasals. A predentary bone is not developed.

The cervical and anterior dorsal vertebrae are opisthocoelous, and much hollowed along the sides. The double-headed cervical ribs are fused in part at least with their respective centra and neural arches, and the neural spines are reduced or paired, as in *Diplodocus*. In the posterior dorsal vertebrae there is a hyposphene-hypantrum arrangement, as well as pre- and post-zygapophyses. The centra of the dorsal vertebrae (Fig. 334), and sometimes also of the other regions, contain large interior cavities, which were probably pneumatic during life. These chambers, of which there are one or more on each side, are separated by a median longitudinal septum, not always continuous, and open outwardly by a foramen or elongated aperture near the base of the neural arch. In the presacral and anterior caudal vertebrae, the neural arches and spines are likewise hollowed. Each sacral vertebra supports its own rib. In *Diplodocus* the arches formed by the diapophysial laminae of the sacrum have their origin in the union of two laminae springing from distinct vertebrae, while each pair of sacral ribs originates from a single centrum. The neural canal in the sacrum is expanded to twice or three times the diameter of the brain cavity. The posterior caudals have solid centra, slightly concave behind, and flat or more rarely concave in front. Chevron bones are well developed.

In the pectoral arch the scapula is elongated, and much more expanded distally than at its proximal end. The coracoid is small, more or less rounded anteriorly, and suggestive of the corresponding element in Rhynchocephalians. The humerus has a distinct head, and is somewhat crocodilian-like. The pelvic bones are never coössified, and the acetabulum is open. The ilium exhibits only a slight pre-acetabular extension, and the slender ischium is without an obturator process. The pubes are stout, directed downwards and forwards, and meet in a cartilaginous symphysis. The femur is considerably longer than the crus, and its large head is directed inward from the shaft to enter the acetabulum. The astragalus is without an ascending process. All the phalanges are short, and the ungual ones are compressed, and were sheathed with horn, or hoof-like.

Remains of *Sauropoda* occur principally in the Middle and Upper Jura of England and Northern France, and in the equivalent formations of the western United States, especially Wyoming and Colorado. They are also known from the Wealden and Lower Cretaceous of England, and from the Upper Mesozoic of Madagascar, India, and Patagonia.

Family 1. **Camarasauridae.** Cope. (*Atlantosauridae.*)

Teeth more or less compressed, and with anterior and posterior cutting edges. Chevron bones articulated with the solid caudal vertebrae. Jura and Wealden.

Cetiosaurus, Owen (*Cardiodon*, Owen). A skeleton lacking the skull and cervical vertebrae (*C. oxoniensis*, Phillips, from the Bathonian of Oxford,

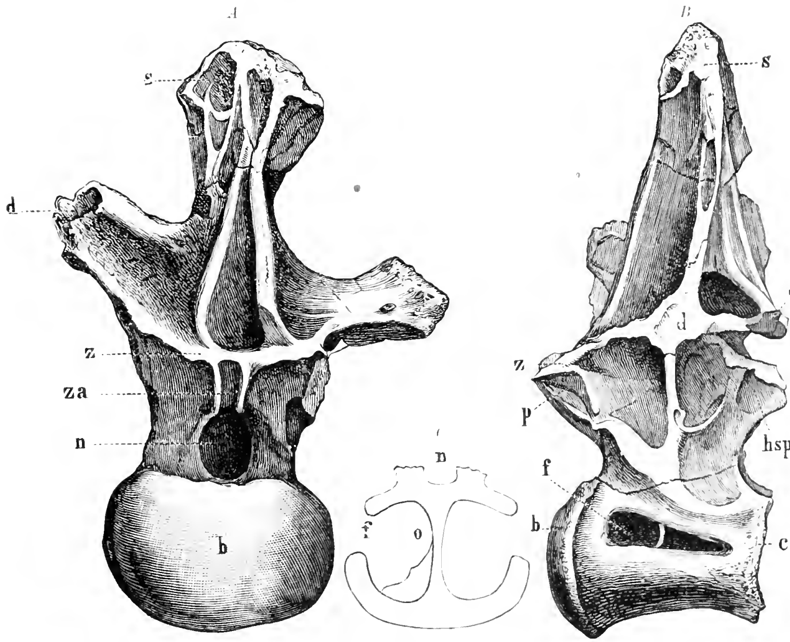


FIG. 334.

Ornithopsis hulkei, Seeley. Wealden; Isle of Wight. *A*, Anterior aspect. *B*, Lateral aspect. *C*, Cross-section of dorsal vertebra, 1/8. *b*, Anterior face of centrum; *c*, Posterior cup; *d*, Transverse process; *f*, Lateral air-cavity; *hsp*, Hyposphene; *n*, Neural canal; *o*, Median septum; *p*, Capitular facette for rib; *s*, Neural spine; *z*, *z'*, Pre- and post-zygapophyses; *za*, Hypantrum (after Hulke).

England), indicates a total length of at least 12 m., and a height of about 3 m. Humerus and femur are of about equal length, the latter 1·7 m. long. Ischia smaller than the pubes, and distally contracted. Middle Jura; England.

Camarasaurus, Cope (*Atlantosaurus*), Marsh. Fore-limbs longer than the

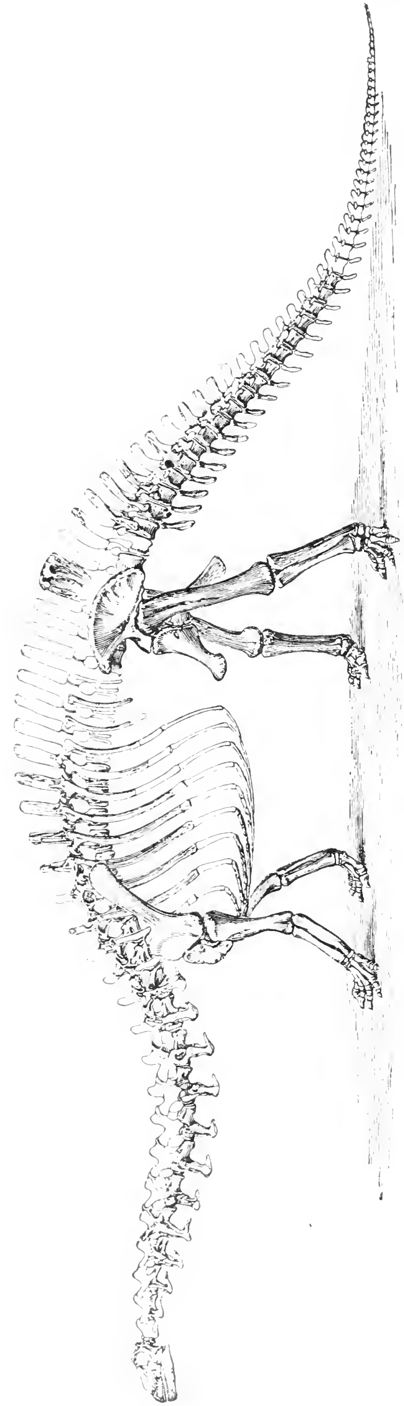


Fig. 335.
Brontosaurus excelsus, Marsh. Upper Jura; Wyoming. Restoration of skeleton, $^1/_{90}$ (after Marsh).

hinder pair, humerus of equal length with the femur, thorax proportionally large. Scapula

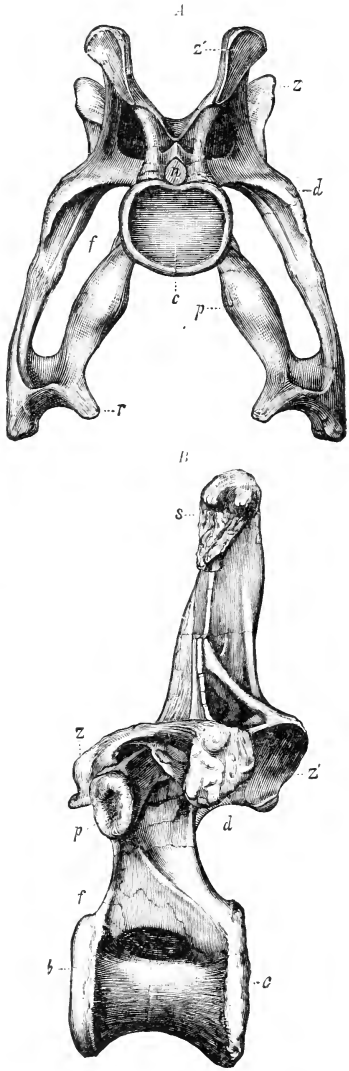


Fig. 336.
Brontosaurus excelsus, Marsh. Upper Jura Wyoming. *A*, Posterior aspect of sixth cervical vertebra. *B*, Lateral aspect of dorsal vertebra. $^1/_{12}$. Lettering as in Fig. 334 (after Marsh).

expanded at proximal end, coracoid elongate and straight at articular border. Centra of dorsal vertebrae elongate and but slightly hollowed laterally. Sacrum composed of four anchylosed vertebrae having slight cavities in the centra. Ischia distally expanded and meeting in a ventral symphysis. Anterior caudal vertebrae relatively small, having short, blunt transverse processes and no lateral cavities. Upper Jura; Colorado.

Brontosaurus, Marsh (? *Amphicoeleas*, Cope), (Figs. 335, 336). Total length upwards of 18 m. Skull remarkably small, and brain cavity exceedingly diminutive. Neck long and flexible, trunk short, and tail elongated. About thirteen cervical vertebrae, with very small neural canal, and no neural spines. Cervical ribs hatchet-shaped, the anterior ones fused with their centra, the hinder ones articulated. All the centra deeply hollowed, the inner cavities of the dorsals divided by a narrow median septum. The five sacral vertebrae are fused, as are also the neural spines of the three median sacrals. A pair of supposed sternal bones between the perforated coracoids. Ischia less robust than the pubes, somewhat expanded distally, and meeting in a ventral symphysis. Upper Jura; Wyoming and Colorado.

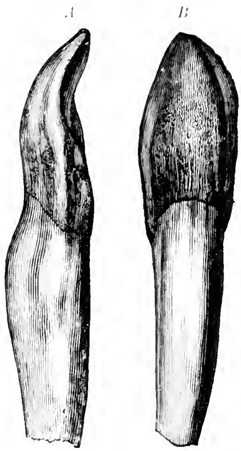


Fig. 337.

Morosaurus grandis, Marsh. Upper Jura; Wyoming. *A*, *B*, Lateral and anterior aspects of tooth, 1/2.

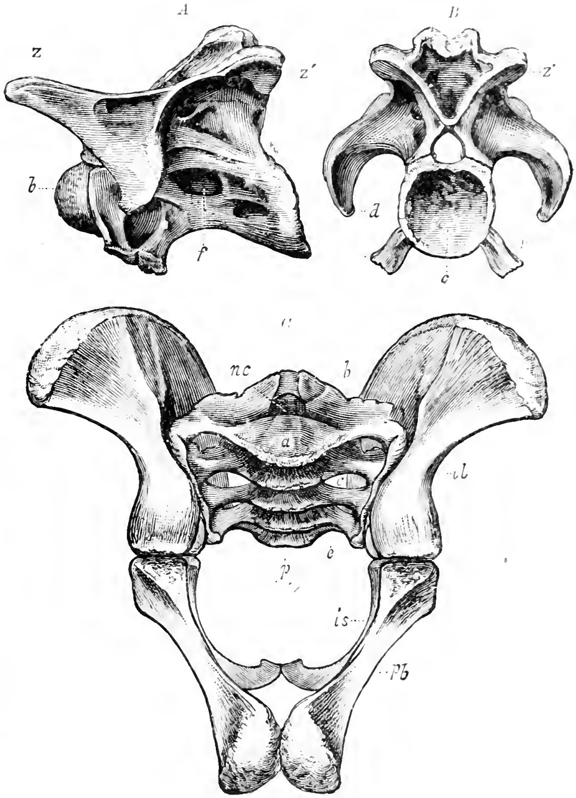


Fig. 338.

Morosaurus grandis, Marsh. Upper Jura; Wyoming. *A*, *B*, Lateral and posterior aspects of fourth cervical vertebra, 1/8. Lettering as in Fig. 334. *C*, Pelvis viewed from in front, 1/16. *a-p*, The four sacral vertebrae; *b*, *c*, *e*, Transverse processes; *il*, Ilium; *is*, Ischium; *nc*, Neural canal; *pb*, Pubis (after Marsh).

Morosaurus, Marsh (Figs. 337, 338). Cervical ribs not fused with their supporting processes. Neck extremely long and flexible, back short, with but ten dorsal vertebrae. Chevron bones articulated by two facettes, with their centra. Four sacral vertebrae. Shaft of pubes rotated distally through a quadrant of arc, so that the pubic symphysis is formed by the lateral faces instead of extremities of the bones. Upper Jura: Wyoming and Colorado.

Apatosaurus, Marsh. Upper Jura; Colorado. *Pleurocoelus*, Marsh. Lower Cretaceous; Maryland.

Ornithopsis, Seeley (*Pelorosaurus*, Mantell; *Eucamerotus*, Hulke; *Chondrosteosaurus*, *Bothriospondylus*, Owen), (Fig. 334). Cervical vertebrae elongated, dorsals with expanded neural canal. Fragmentary remains of large size frequent in the Upper Jura and Wealden of England. *O. hulkei*, Seeley.

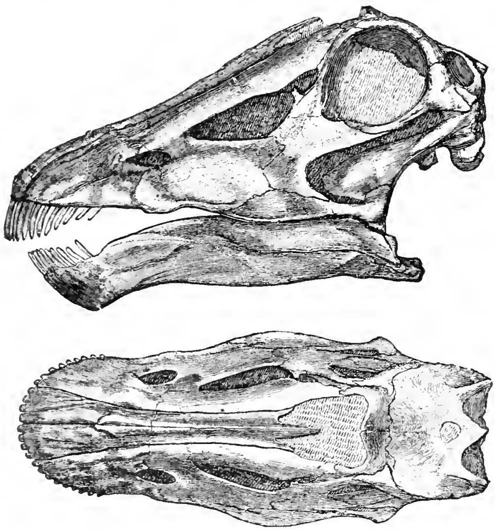


Fig. 339.
Diplodocus longus, Marsh. Upper Jura; Cañon City, Colorado. Skull, 1/8 (after Marsh).

Titanosaurus, *Argyrosaurus*, Lydekker. Supposed Cretaceous of Patagonia.

Family 2. Diplodocidae. Marsh.

Teeth slender and cylindrical, confined to front margin of the jaws. External narial opening small, unpaired, placed at apex of the skull. Caudal vertebrae elongated, ventrally excavated; chevron bones double posteriorly, each having both anterior and posterior branches. Upper Jura.

Diplodocus, Marsh (Fig. 339). Total

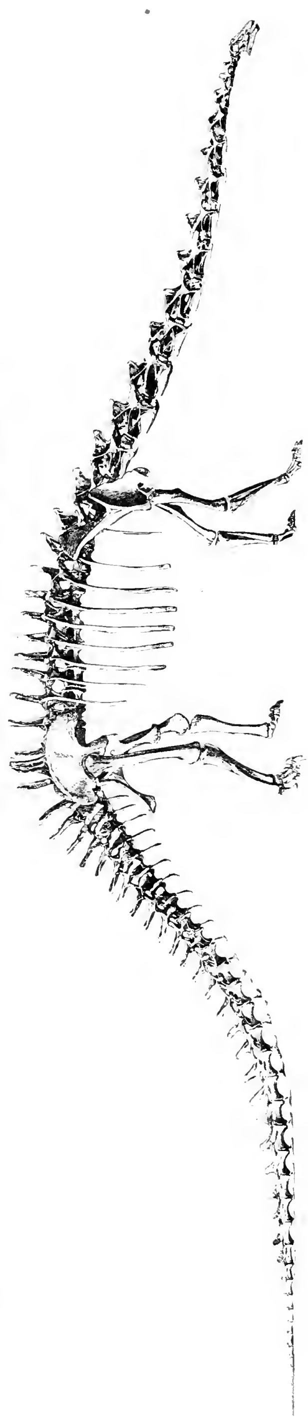


Fig. 339A.
Diplodocus carnegii, Hatcher. Upper Jura; Wyoming. 1/100 (after Hatcher).

length upward of 20 m.; skull only 0·6 m. long, elevated and laterally compressed. In front of the triangular antorbital vacuity is a small maxillary vacuity; supratemporal fossa very small; quadrate much inclined forwards. Neck extremely long and flexible, and back extremely short. At least fifteen cervicals, eleven dorsals, four sacrals, and thirty-seven or more caudals present. Sternal bones as in *Brontosaurus*. Upper Jura; Wyoming and Colorado.

Sub-Order 3. **PREDENTATA.** Marsh. (*Orthopoda*, Cope.)[1]

Large herbivorous Dinosaurs with completely ossified brain case, little or no antorbital vacuity in the skull, and toothless predentary bone in front of the mandible. Premaxillae edentulous at least in front (rarely with small lateral teeth); maxillae and dentary with stout grinding teeth, arranged in one or more functional series. Teeth usually compressed or spatulate, with serrated anterior and posterior cutting edges, but becoming worn down to flattened stumps with age. External nares large, placed at extremity of the skull. Vertebral centra solid, opisthocoelous, amphiplatyan, or sometimes even amphicoelous. Cervical ribs loosely articulated with their centra. Pubes slender and distally free. Post-pubis slender, of variable length, and directed downwards and backwards parallel with the ischium; the latter with obturator process. Limb bones solid or hollow; anterior extremities shorter than the hinder pair. Astragalus without ascending process; hind feet digitigrade or plantigrade. Dermal armour sometimes strongly developed (Stegosauria), in other cases absent (Iguanodontia).

This sub-order comprises more or less massive herbivorous Dinosaurs, some of which must have been bipedal in gait, and others quadrupedal. They are distinguished from the preceding groups chiefly by characters of the pelvis, presence of a predentary bone, and edentulous premaxillae. The unarmoured *Predentata* are represented by the bipedal *Ornithopodidae* (= *Iguanodontia*), and the armoured division by the quadrupedal *Stegosauridae* and *Ceratopsidae*.

Family 1. **Iguanodontidae.**[2]

Long axis of skull set at right angles to the neck. Antorbital vacuity small, mandibular coronoid process strongly developed. Teeth, when unworn, of petaloid aspect, socketed in a single functional row. Cervical and anterior dorsal vertebrae opisthocoelous. Pelvis of the quadriradiate type; post-pubic process long and slender; fore-limbs only about half as long as the hinder pair; pes tridactyl, clawed or hoofed; gait bipedal and digitigrade. Dermal armour absent. Upper Jura and Cretaceous.

The pelvis, as has already been pointed out (cf. Fig. 326), is more bird-like than that of any other reptilian group. The ilium generally has its pre-

[1] Literature:
Marsh, O. C., The Dinosaurs of North America (16th Ann. Rep. U.S. Geol. Surv.), 1896.

[2] Literature:
Cope, E. D., On the characters of the skull in the Hadrosauridae (Proc. Acad. Nat. Sci. Philad. p. 98), 1883.—*Dollo, L.*, Notes sur les Dinosauriens de Bernissart (Bull. Mus. d'Hist. Nat. Belg. vols. I., II.), 1882-84.—*Hulke, J. W.*, On Hypsilophodon Foxii (Quar. Journ. Geol. Soc. vol. XXIX. p. 522), 1873.—Also *ibid.* vol. XXX. (1874), p. 18, and Phil. Trans. vol. CLXXIII. (1882), p. 1035.—*Huxley, T. H.*, On Hypsilophodon (Quar. Journ. Geol. Soc. vol. XXVI. p. 3), 1870.—*Leidy, J.*, Cretaceous Reptiles of the United States (Smithson. Misc. Contrib.), 1864.—*Mantell, G. A.*, Observations on Iguanodon, Hylaeosaurus, etc. (Phil. Trans.), 1825, 1841, 1848, 1849.—*Marsh, O. C.*, On Hypsilophodon, etc. (Amer. Journ. Sic. [3], vol. L.), 1895.—*Nopcsa, Jr., F. B.*, Dinosaurienreste aus Siebenbürgen (Denkschr. Akad. Wissensch. Wien, vol. LXVIII.), 1899.

acetabular portion much extended, and the ischium has an obturator process. Supposed sternal ossifications sometimes occur.

Camptosaurus, Marsh (*Camptonotus*, Marsh). Attaining a total length of about 10 m. Cervical ribs short; dorsal vertebrae amphiplatyan; sacrals not anchylosed. Pubis robust, post-pubis of equal length with the long and slender ischium. Pendent inner fourth trochanter of femur very marked. Proximal tarsals separated. Upper Jura; Wyoming and Colorado. Kimmeridgian and Wealden; England.

Laosaurus, *Dryosaurus*, *Nanosaurus*, Marsh. Upper Jura; Wyoming and Colorado.

Hypsilophodon, Huxley. Premaxillae each with five small deeply-socketed lateral teeth, edentulous and beak-like in front; nasals elongated. Vertebrae amphiplatyan. Sternum partly ossified. Post-pubis of equal length with the

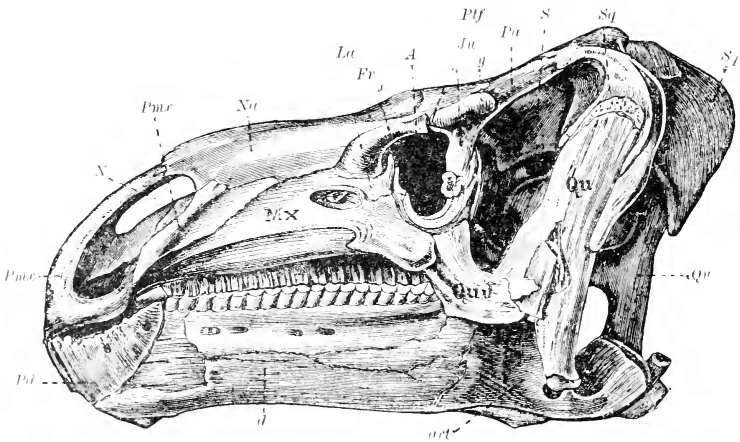


FIG. 340.

Iguanodon bernissartensis, Boul. Wealden; Bernissart, Belgium. Skull, 1/8. *A*, Orbit; *art*, Articular; *d*, Dentary; *fr*, Frontal; *ju*, Jugal; *la*, Lachrymal; *mx*, Maxilla; *N*, External nostril; *na*, Nasal; *pa*, Parietal; *pd*, Predentary; *pmx*, Premaxilla; *ptf*, Postfrontal; *qu*, Quadrate; *quj*, Quadrato-jugal; *S*, Supratemporal vacuity; *sq*, Squamosal; *x*, *y*, Supraorbitals (after Dollo).

ischium; proximal tarsals separated; manus and pes each with four clawed digits. Known by several complete skeletons 1·5 m. long from the Wealden of the Isle of Wight.

Iguanodon, Mantell (Figs. 340-342). Skull laterally compressed, with large, nearly terminal nostrils, and small antorbital vacuity. Orbits deeper than wide, smaller than the irregularly triangular or elongated lateral temporal vacuity. Supratemporal vacuities of moderate size, separated by the narrow parietals, which meet in a sharp median crest. Two small supraorbital bones above the eye, but no sclerotic ring. Frontals flattened and apparently fused; nasals elongated. Mandibular suspensorium nearly vertical; articular portion of the quadrate at the base of an unusually deep pedicle. Jugal crescentic, bounding the orbit inferiorly; quadrato-jugal rather large; lachrymal small. Premaxillae toothless, but with sharpened margin. Maxillae and dentary with numerous closely-set grinding teeth arranged in a single row; the teeth when unworn are spatulate, loosely socketed, and with serrated margins; successional teeth well formed below those of the functional row. Mandibular ramus composed of six pieces, and with slender coronoid process. There are ten cervical, eighteen dorso-lumbar, four to six sacral, and forty to fifty caudal vertebrae. All the presacral vertebrae except the atlas and a few lumbars bear ribs, as do also the thirteen anterior caudals. Ossified tendons frequently observed along the neural spines of the back and tail. Scapula very long and slender: coracoid small and rounded, notched or perforate at its articular border: supposed pair of sternal bones

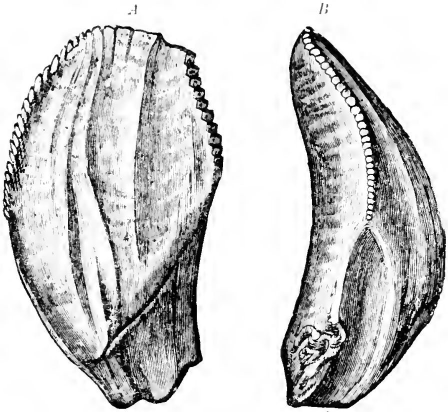


FIG. 341.

Iguanodon mantelli, Owen. Wealden; Isle of Wight. Inner (*A*), and posterior (*B*) aspects of mandibular tooth (after Mantell).

triangular. Manus pentadactyl, the pollex reduced to a single spur-like phalanx; the others having a formula of 3, 3, 3, 4. Ilium greatly extended on either side of the acetabulum. Post-pubis process slender and rod-like, shorter than the ischium. Femur scarcely longer than the crus,

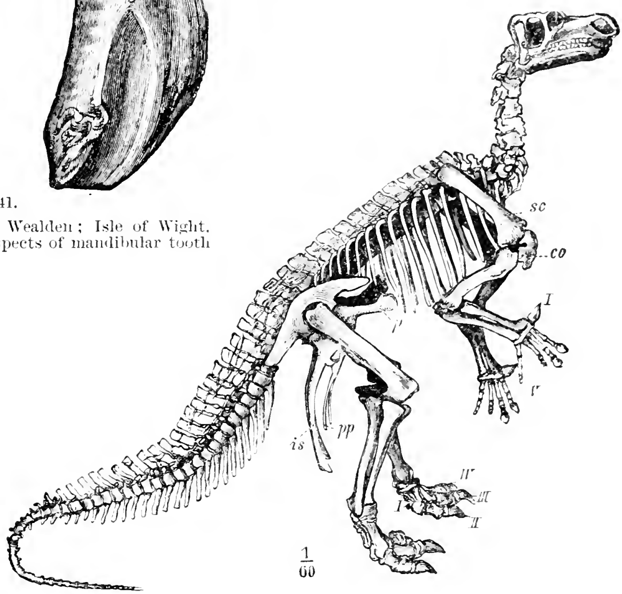


FIG. 342.

Iguanodon bernissartensis, Boul. Wealden; Bernissart, Belgium. Complete skeleton, $^1/_{60}$. *co*, Coracoid; *is*, Ischium; *p*, Pubis; *pp*, Postpubic process; *sc*, Scapula; *I—V*, Digits (after Dollo).

and with prominent pendent inner trochanter. This, according to Dollo, is distinct from the third trochanter of mammals, and indicates a powerful caudo-femoral musculature, as in birds. Metatarsal No. I rudimentary, No. V wanting; the three ungual phalanges broad and claw-shaped; formula of pes, 0, 3, 4, 5, 0.

Iguanodon is known by numerous complete skeletons from the Wealden of Bernissart, near Mons, Belgium, as many as twenty-three being exhibited in the Brussels Museum. Fragmentary remains occur also in the English Wealden. Lower Greensand, Purbeckian, and perhaps also in the Kimmeridge Clay. The typical species, *I. mantelli*, Owen, from the Wealden of England, attains a total length of 6 m., and *I. bernissartensis*, Boulenger (= *I. seeleyi*, Hulke), is between 8 and 10 m. long. As proved by its three-toed footmarks, the animal walked on its hind feet in a kangaroo-like attitude, thus leaving the hands free for prehension.

Trachodon, Leidy (*Hadrosaurus*, *Thespesius*, Leidy; *Diclonius*, Cope), (Figs. 343-345). Skull elongated, depressed, with broad, beak-like snout, very large

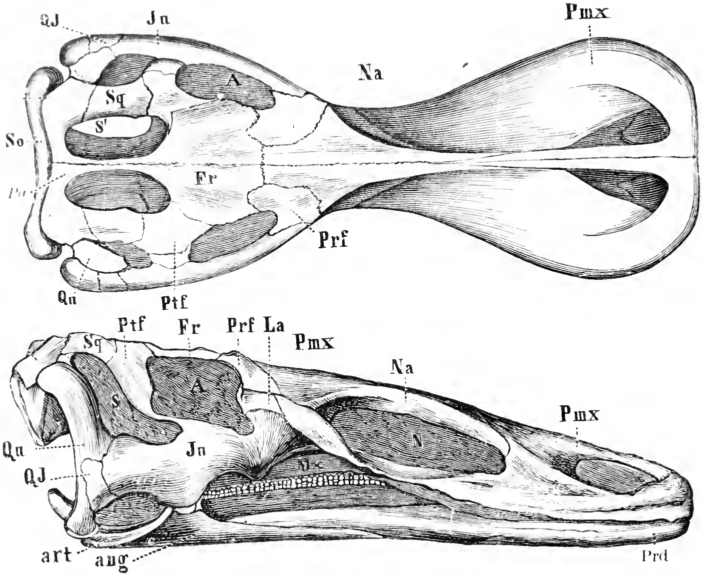


Fig. 343.

Trachodon mirabilis, Leidy. Uppermost Cretaceous (Laramie Formation); Dakota. Superior and lateral aspects of skull, $^1/_{12}$. *A*, Orbit; *ang*, Angular; *art*, Articular; *fr*, Frontal; *ju*, Jugal; *la*, Lachrymal; *mx*, Maxilla; *N*, Antorbital vacuity; *na*, Nasal; *pa*, Parietal; *pmx*, Premaxilla; *prd*, Predentary; *prf*, Prefrontal; *ptf*, Postfrontal; *qu*, Quadrate; *quj*, Quadrato-jugal; *S*, Lateral temporal vacuity; *S'*, Supratemporal vacuity *so*, Supraoccipital; *sq*, Squamosal (after Cope).

nostrils, subrectangular orbits, and long and narrow temporal vacuities. Parietal

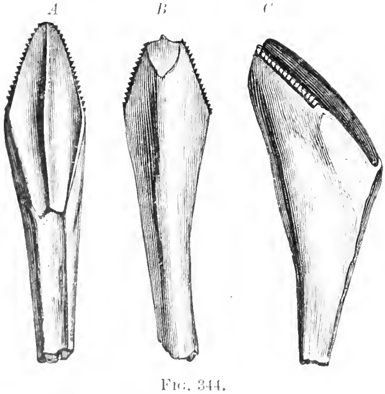


Fig. 344.

Trachodon foulki, Leidy. Upper Cretaceous; New Jersey. Inner (*A*), outer (*B*), and (*C*), lateral aspects of mandibular tooth, somewhat worn, $^1/_1$ (after Leidy).

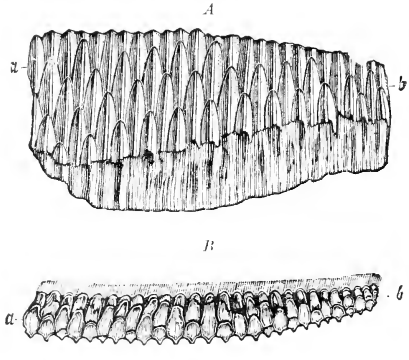


Fig. 345.

Trachodon breviceps, Marsh sp. Upper Cretaceous; Montana. *A*, Inner, and *B*, Superior aspect of functional and successional teeth of dentary, $^1/_4$ (after Marsh).

very small; premaxillae edentulous. Teeth closely arranged in an alveolar groove opening inwardly, the successional teeth forming several tectiform series. Dorsal vertebrae opisthocoelous; caudals amphiplatyan. Other characters as in *Iguanodon*. Upper Cretaceous; New Jersey, Dakota, and Montana.

Claosaurus, Marsh. Skull very similar to the preceding, and the genus possibly not distinct from *Trachodon*. Nostrils large, and no supra-orbital bones observed. There are thirty presacral vertebrae, nine fused sacrals, and about sixty caudals. All the presacrals are opisthocoelous and costiferous; anterior caudals also opisthocoelous, and with very long chevron bones. Fore-limbs unusually short and small in proportion to the hinder pair. In the manus digit I is rudimentary, and No. V is wanting; functional digits hoofed, each with three phalanges. Functional digits of hind foot very massive, with broad hoofs; their formula 0, 3, 4, 5, 0. *C. annectans*, Marsh, attains a length of 9 m. A complete mounted skeleton in Yale Museum. Upper Cretaceous; Colorado, Wyoming, and Montana.

Limnosaurus, Nopsca. Cretaceous; Austria.

Family 2. **Stegosauridae**. Marsh. (*Scelidosauridae*, Huxley.)[1]

Skull small, without antorbital vacuity; nostrils large and placed far forwards; premaxillae edentulous. Vertebrae amphicoelous or amphiplatyan, and solid throughout, like the limb bones. Post-pubic process robust; fore-limbs much smaller than the hinder pair. Feet plantigrade, tri- or penta-dactyle, with short, hoof-like, ungual phalanges. Exoskeleton strongly developed, consisting of a series of large dermal plates and spines. Lias to Upper Cretaceous.

This family comprises moderate or large-sized *Predentata*, with well-developed exoskeleton, solid limb bones, and solid amphicoelous or amphiplatyan vertebrae. The dermal armour usually consists of large bony plates or spines, but in a few genera the back is encased in a continuous shield of fused plates (*Polacanthus*). The neural canal of the sacrum is sometimes enormously expanded. In the pelvis the post-pubic process is greatly extended, as in the *Ornithopodidae*, and there is likewise a marked disparity between the fore- and hind-limbs. The gait was probably in most cases quadrupedal, although a study of femoral characteristics has led Dollo to suggest that they may have been at least at one stage bipedal.

Stegosaurus, Marsh (Figs. 346-348). Skull narrow and depressed, relatively very small, and brain cavity in proportion to size of the body more diminutive than in any other land vertebrate. Orbits small; laterally directed; supra-temporal vacuities small and rounded: nasals nearly half as long as the skull. Mandibular ramus deep, pierced by a lateral foramen. Teeth very numerous, bluntly pointed, more or less spatulate in form, loosely socketed in a single functional series. Vertebrae slightly amphicoelous or with flat ends, the cervicals with short ribs and dorsals with much elevated neural arches, on which the stout dorsal ribs are borne. Sacrum of four fused vertebrae, sometimes with one or more lumbars added on in front: their neural canal enlarged

[1] Literature:
Bunzel, E., Reptilien der Gosauformation (Abhandl. Geol. Reichs. Anstalt. vol. V. pt. 1), 1871. —*Davies, W.*, On the exhumation of Omosaurus (Geol. Mag. [2], vol. III. p. 193), 1876.—*Hulke, J. W.*, On Polacanthus (Phil. Trans. vol. CLXXVIII. B. p. 169), 1887.—*Marsh, O. C.*, On Scelidosaurus, etc. (Amer. Journ. Sci. [3], vol. L.). 1895.—*Seeley, H. G.*, The Reptile Fauna of the Gosau Formation (Quar. Journ. Geol. Soc. vol. XXVI. p. 620). 1881.—On Polacanthus, etc. (*ibid.* vol. XLVIII. p. 81), 1892.

to ten times the capacity of brain cavity (Fig. 347). Anterior caudal vertebrae

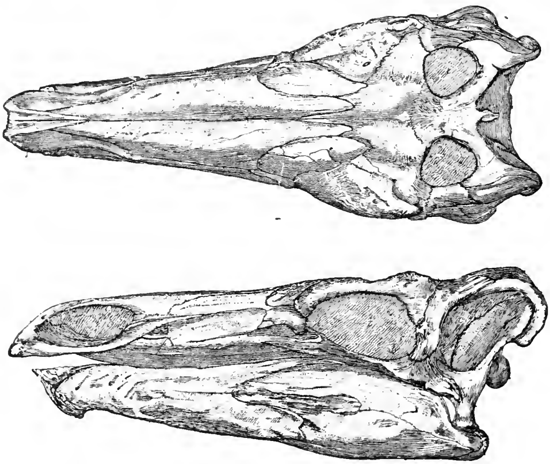


FIG. 346.

Stegosaurus stenops, Marsh. Upper Jura; Colorado. Superior and lateral aspects of skull, $^1/_6$ (after Marsh).

the largest in the column, and with strong chevron bones. Fore-limb short and stout, ulna with large olecranon process. Manus short, apparently pentadactyle. Femur large and straight, without inner trochanter; tibia and fibula much shorter. Astragalus and calcaneum fused with opposing bones of the crus; pes tridactyle, digit No. I rudimentary, and No. V wanting. Dermal armour consisting of two rows of flattened bony plates extending from the back of the head well down the tail, the largest plates situated immediately over the pelvis. Four spines on the tail, and throat protected by a shield of irregular ossicles. Known by complete skeletons from the Upper Jura of Wyoming and Colorado. *S. ungulatus*, Marsh, over 9 m. long.

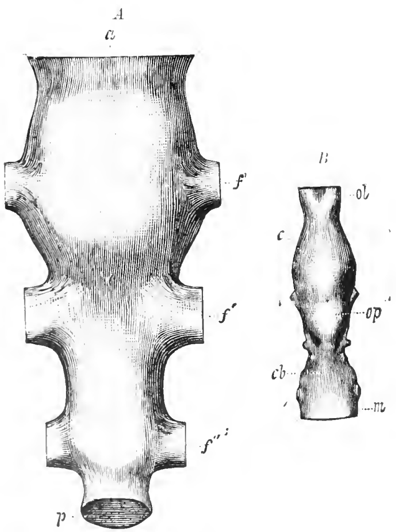


FIG. 347.

Stegosaurus ungulatus, Marsh. Upper Jura; Colorado. *A*, Gutta-percha cast of neural canal in sacrum, dorsal aspect, $^1/_4$. *B*, Same of brain cavity, $^1/_4$. *a*, Anterior end; *c*, Cerebral hemispheres; *cb*, Cerebellum; *f*, Vacuities between transverse processes of sacrum; *m*, Medulla oblongata; *ol*, Olfactory lobe; *op*, Optic lobe; *p*, Posterior end.

Diracodon, Marsh. Is probably founded on the young of this species.

Scelidosaurus, Owen. Skull only about 0·25 m. long. Teeth with triangular or spatulate crowns, coarsely serrated on the margins. All the centra amphicoelous, some with an internal cavity, and the neural canal not expanded. There are six or seven cervicals, sixteen dorsals, one lumbar, four sacrals, and about forty caudals. Femur, tibia, and fibula hollow, the crus somewhat shorter than the femur and not fused with proximal tarsals. Hind foot functionally tridactyle, the hallux reduced, and digit No. v wanting; phalangeal formula 2, 3, 4, 5, 0. Dermal armour of longitudinal series of small tubercles and triangular or conical scutes covering the back and tail. *S. harrisoni*, Owen, attains a length of 4 m. Lower Lias; England.

Echinodon, Owen. Purbeckian; England. *Hylaeosaurus*, Mantell; *Vectisaurus*, Hulke; *Stenopelix*, v. Meyer. Wealden. All imperfectly known.

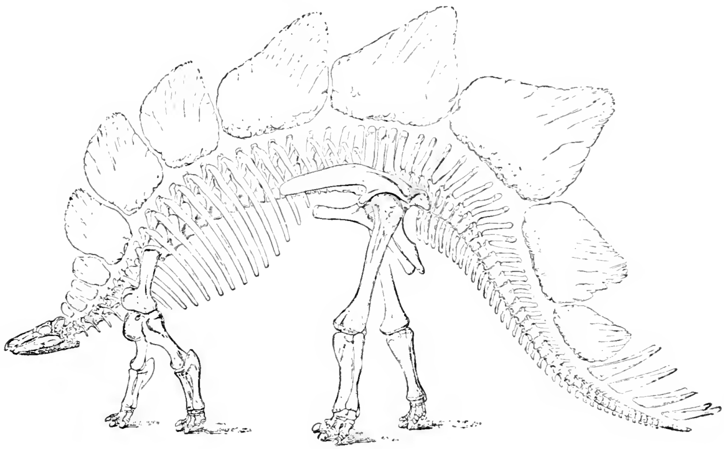


FIG. 348.
Stegosaurus ungulatus, Marsh. Upper Jura; Colorado. Restoration of skeleton, 1/60 (after Marsh).

Polacanthus, Owen. Lumbar-sacral region completely encased in a continuous shield of fused plates, which press the ilium downwards. Wealden; Isle of Wight.

Priconodon, Marsh. Founded on detached teeth from the supposed Upper Jura of Maryland.

From the Upper Cretaceous of Austria and North America a number of fragmentary remains of armoured *Ornithopoda* have been described under the names of *Struthiosaurus* and *Danubiosaurus*, Bunzel; and *Crataeomus*, *Oligosaurus*, and *Hoplosaurus*, Seeley, etc. Like the members of the following family, they are supposed to represent a highly specialised group of Stegosaurs.

Family 3. **Ceratopsidae.** Marsh.

Skull of enormous size, wedge-shaped in form, very narrow in the facial portion, with two very large pointed horns on the frontals, a median nasal horn anteriorly, and a row of sharp projections around the margin of the posterior hood, which is formed by the parietals and squamosals. An upper toothless beak is formed by the premaxillae together with a median "rostral" bone corresponding to the predentary of lower jaw. Teeth with a divided root fixed in sockets. Vertebrae amphiplatyan; dorsal centra extremely short. Limbs nearly equal; five hoofed digits in the fore-, three in the hind-foot. Dermal armour imperfectly known.

Most of the forms here included attain gigantic proportions, and are known only from the Uppermost Cretaceous (Laramie Formation) of Montana, Wyoming, Colorado, and Dakota. They are chiefly remarkable for the armature of the huge skull, the strong, pointed horn-cores of which resemble those of the *Bovidae.* Their rugose outer surface exhibits distinct vascular impressions, and was doubtless once sheathed with horny tissue. Internally they are hollow at the base, but become solid higher up.

Triceratops, Marsh (*Polyonax*, *Agathaumas*, Cope), (Figs. 349, 350). Skull over 1·5 m. long, exceeding in size that of any known land animal. Facial region compressed and pointed, hinder half greatly expanded and hood-like. There is a sharp cutting beak in front, a strong nasal horn-core, a pair of large pointed horns over the orbits, and a row of sharp projections around the margin of the posterior hood. External nares very large, placed between the nasals and rostral bone. Brain cavity smaller in proportion to the skull than in any other known reptile. Besides the dentary, which develops a large coronoid process, an articular, angular, surangular, and splenial are distinguishable in the lower jaw. Atlas and axis are fused with the next cervical to support the head; the two lumbars and first four caudals fused with the sacrum, which has double transverse processes, and the neural canal is not especially enlarged. Tail of moderate length, chevron bones placed intervertebrally. The small per-

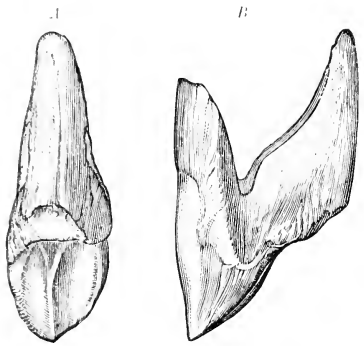


FIG. 349.

Triceratops serratus, Marsh. Upper Cretaceous; Montana. Outer (*A*), and lateral (*B*) aspect of worn maxillary tooth, $^1/_1$ (after Marsh).

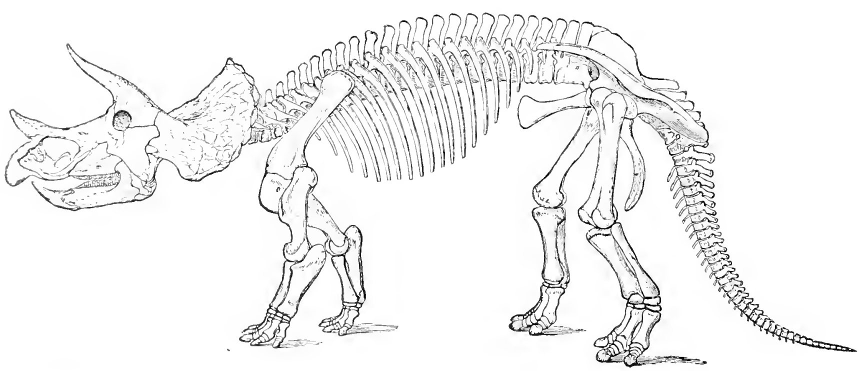


FIG. 350.

Triceratops prorsus, Marsh. Upper Cretaceous: Montana. Restoration of skeleton, $^1/_{70}$ (after Marsh).

forated coracoid sometimes fused with the scapula in old individuals. Radius and ulna short and stout, the latter with large olecranon process; manus with five hoofed digits. Ilium much elongated; pubis massive, but with slender post-pubic process. Ischium smaller and more elongated than the pubis. Femur not much longer than the humerus, tibia and fibula short, the latter very slender. Astragalus usually fused with distal end of tibia; pes with three hoofed digits. Dermal armour not observed. Laramie Formation; Montana, Wyoming, and Colorado.

Ceratops (*Monoclonius*, Cope), *Sterrholophus* (Fig. 351), *Torosaurus*, Marsh.

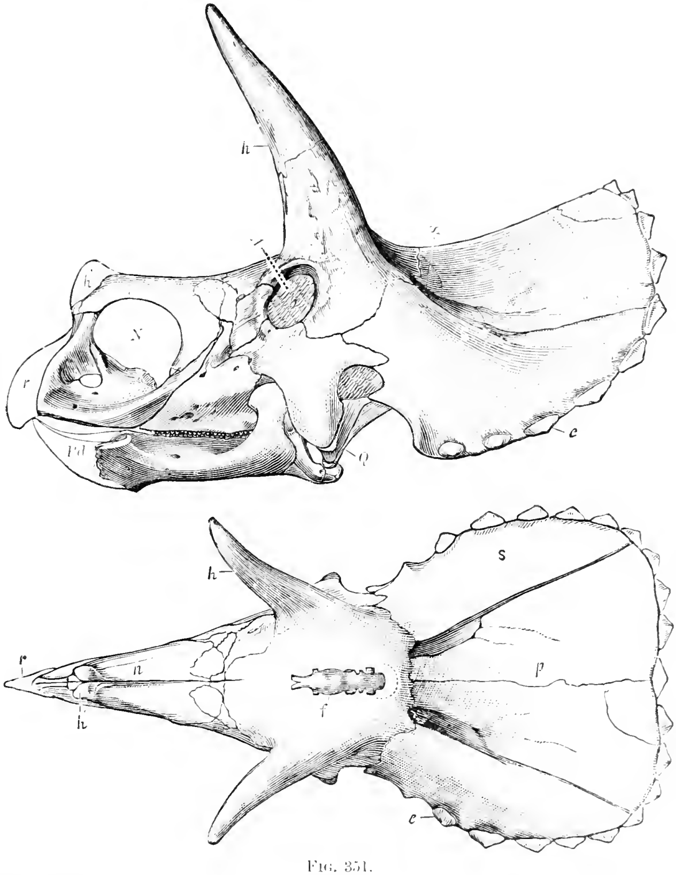


Fig. 351.

Sterrholophus flabellatus, Marsh. Uppermost Cretaceous; Montana. Lateral and superior aspects of skull, 1/20. *A*, Orbit; *e*, Marginal bosses ("epioccipital plates"); *f*, Brain; *h*, Horn-core; *h'*, Nasal horn-core; *N*, External narial opening; *n*, Nasal; *p*, Parietal; *pd*, Predentary (restored in outline); *q*, Quadrate; *r*, Rostral bone (restored in outline); *S*, Supratemporal vacuity; *s*, Squamosal (after Marsh).

These are less perfectly known, but apparently allied genera accompanying the preceding in the Laramie Formation.

Range and Distribution of the Dinosauria.

The remarkable and by no means homogeneous group of *Dinosauria* arose during the Trias, attained its maximum development in the Upper Jura and Cretaceous, and passed entirely away at the close of the latter period. The abundance of Dinosaurs during the Trias is indicated by countless footprints in the sandstones of that age in Massachusetts, Connecticut, Pennsylvania, Virginia, and North Carolina, where hordes of these creatures roamed along the beaches in quest of prey. Upwards of 100 different varieties of footprints have been discovered in the Connecticut Valley, varying between 2·5 cm. and 60 cm. in length. Most of these imprints are three-toed, although four- and five-toed tracks also occur, and their paths are often traceable for a number of meters. Since many of these indicated creatures of bipedal gait, early writers (notably Hitchcock in 1837 and 1858) very naturally attributed them to birds, and designated them by various names. The paucity of skeletal remains in the strata where footprints are so conspicuous a feature is remarkable.

The earliest known Dinosaurs belong to the carnivorous group of *Theropoda*, and are extremely generalised. Their obvious relations to the *Rhynchocephalia*, *Crocodilia*, and *Theromorpha* have already been discussed, and attention directed to avian resemblances pervading both this and the herbivorous sub-orders. It need only be repeated in this connection that, in spite of the remarkable similarity between birds and Dinosaurs, there is no evidence to prove that the former have come down to us through any known type of the latter. And yet it would appear rather more probable that the avian phylum should have originated from primitive Dinosaurs—that is to say, from a Dinosaur-avian stem, than that the two groups arose independently from some common stock.

TABLE SHOWING VERTICAL RANGE OF THE DINOSAURIA.

Families.	Trias.	Lias.	Middle Jura.	Upper Jura.	Lower Cretaceous.	Upper Cretaceous.
THEROPODA						
1. *Megalosauridae*	—	—	—	—	—	—
2. *Compsognathidae*				—		
3. *Coeluridae*	?			—		
SAUROPODA						
1. *Camarasauridae*			—	—	—	
2. *Diplodocidae*				—		
PREDENTATA						
1. *Iguanodontidae*				—	—	—
2. *Stegosauridae*		—		—	—	—
3. *Ceratopsidae*						—

[The text for the introductory portion of the preceding chapter on Dinosaurs has been revised to a slight extent by Professor H. F. Osborn; that for the systematic part has been revised by Mr. J. B. Hatcher, of the Carnegie Museum at Pittsburgh.—EDITOR.]

Order 9. PTEROSAURIA. Kaup. (*Ornithosauria*, Fitzinger.)[1]

Reptiles of more or less bird-like aspect, with hollow bones, well-formed articulations, and fore-limbs adapted for flight. Skull with acuminate snout, and long

[1] Literature:

Burmeister, H., Kritische Beleuchtung der Pterodactylus-Arten (Sitzungsber. naturf. Gesellsch. Halle, vol. III.), 1855.—*Fraas, O.*, Ueber Pterodactylus suevicus (Palaeontogr. vol. XXV. p. 163). 1878.—*Goldfuss, A.*, Reptilien aus dem lithographischen Schiefer (Nova Acta Acad. Leop. vol. XV.

axis extending nearly at right angles with the neck. Investing bones of temporal region contracting into an upper and a lower arcade; sutures becoming obliterated in the adult. Quadrate large, firmly fixed; orbit very large, and usually with sclerotic ring; antorbital vacuity large, sometimes confluent with external nares. Teeth, when present, slender, conical, thecodont, and confined to margin of the jaws. Mandibular rami fused at the symphysis. Presacral vertebrae procoelous, caudals amphicoelous; sacrals four to seven in number, usually fused. Cervical and anterior dorsal ribs double-headed. Sternum large, clavicular elements wanting, scapula and coracoid long and slender. Fifth digit of manus enormously elongated and reflexed to support the wing membrane. Pubis excluded from the closed acetabulum. Both rows of tarsals ossified, the astragalus sometimes fused with the tibia. Two to four digits of the pes bear claws, the fifth digit sometimes vestigial. Abdominal ribs present; no dermal armour.

The *Pterosauria* or *Ornithosauria*, as they are also called, constitute an extraordinary group of extinct reptiles, ranging from the Lias to the Upper Cretaceous. They are remarkably bird-like in general appearance, and their whole organisation is modified for the accomplishment of flight through the air. In the larger number, however, the power of flight was more limited than in birds, and may have been in many forms feebler than in bats. The skeleton was more or less pneumatic, like that of birds, and the general avian appearance was accentuated by the articulation of the head at right angles to the cervical axis. Some of these bizarre creatures were no larger than sparrows, but others, with whose extinction the history of the race terminates, were of gigantic size, the spread of their cutaneous expansion being nearly 6 m. from tip to tip.

The vertebral column comprises seven true cervicals, twelve to sixteen dorsals, four to seven sacrals, and ten to forty caudals. The presacral vertebrae are procoelous, and the caudal amphicoelous. The neural arches are usually fused with their centra, and the sides of the latter are more or less extensively hollowed. Cervical ribs, when present, are very much shorter than the dorsal ribs. The latter are double-headed anteriorly, but become single-headed and more slender toward the sacral region. Transverse processes are very strongly developed in the anterior sacral vertebrae. There is a triple series of small V-shaped abdominal ribs along the ventral wall of the body cavity.

The *skull* (Fig. 352) is remarkably bird-like in form, and its constituent elements usually become anchylosed at an early age. The orbits are very large, laterally placed, and surrounded by a sclerotic ring of small plates. An

p. 63), 1831.—*Huxley, T. H.*, On Rhamphorhynchus Bucklandi (Quar. Journ. Geol. Soc. vol. XV. p. 658), 1860.—*Marsh, O. C.*, Various articles in Amer. Journ. Sci. [3], 1871-84 (vols. I. p. 472; III. p. 241; XI. p. 507; XII. p. 479; XVI. p. 233; XXI. p. 342; XXIII. p. 251; XXVII. p. 423, etc.).—*Meyer, H. von*, Reptilien aus dem lithographischen Schiefer (Fauna der Vorwelt, pt. IV.), 1860.—*Newton, E. T.*, On the skull, brain, and auditory organ of Scaphognathus purdoni (Phil. Trans. vol. CLXXIX. B, p. 503), 1888.—Notes on Pterodactyles (Proc. Geol. Assoc. vol. X.), 1888.—*Owen, R.*, Reptilia of the Liassic Formations (Palaeontogr. Soc. pt. II.), 1863.—*Plieninger, F.*, Campylognathus Zitteli (Palaeontogr. vol. XLI.), 1894.—Beiträge zur Kenntniss der Flugsaurier (*ibid.* vol. XLVIII.), 1901.—*Quenstedt, F. A.*, Ueber Pterodactylus suevicus. Tübingen, 1855.—*Seeley, H. G.*, The Ornithosauria. Cambridge, 1870.—On the organisation of the Ornithosauria (Journ. Linn. Soc. vol. XIII.), 1884.—The Ornithosaurian pelvis (Ann. Mag. Nat. Hist. [6], vol. VII. p. 237), 1891.—On the shoulder-girdle in Cretaceous Ornithosauria (*ibid.* p. 438).—Dragons of the Air, London, 1901.—*Wagner, A.*, Contributions on Upper Jurassic Pterosaurs in Abhandl. Bayer. Akad. Wissensch. math.-phys. Classe, vols. II. p. 163; VI. pp. 129, 690; VIII. p. 439 (1837-58).—*Williston, S. W.*, On the skull of Ornithostoma (Kansas Univ. Quar. vol. IV. p. 195), 1896.—Restoration of Ornithostoma (Pteranodon), (*ibid.* vol. VI. p. 35), 1897.—*Zittel, K. A.*, Ueber Flugsaurier aus dem lithographischen Schiefer (Palaeontogr. vol. XXIX. p. 49), 1882.

antorbital vacuity is present as in birds and Dinosaurs, and is either confluent with the external nostril on each side, or separated from it by a narrow bar. The supratemporal vacuity is small, entirely enclosed, and placed far backwards. The lateral temporal vacuity appears as a narrow slit behind the orbit, extending downward and forward, and bounded posteriorly by the quadrate. The cranial roof is formed by the unpaired frontal and the smaller parietals, which are without a foramen. At the base of the skull is placed the single occipital condyle, by means of which the head is carried approximately at right angles to the long axis of the neck.

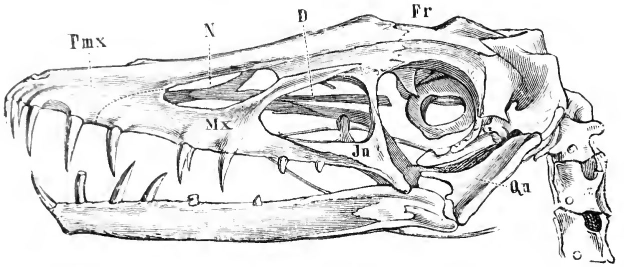


Fig. 352.

Scaphognathus crassirostris, Goldf. sp. Upper Jura; Eichstädt, Bavaria. *D*, Antorbital vacuity; *fr*, Frontal; *ju*, Jugal; *mx*, Maxilla; *N*, Narial opening; *pmx*, Premaxilla; *qu*, Quadrate.

Natural casts of the brain cavity prove it to have been remarkably bird-like, though smaller in proportion to the size of the skull. It was entirely roofed by the frontal plate, which sometimes extended as far forwards as the anterior border of the orbits, and formed not only their upper, but also a part of their posterior border. The orbit is separated from the lateral temporal vacuity by a trifid post-frontal plate, one branch of which joins the squamosal, and forms at the same time the outer bar of the supratemporal vacuity. The orbit is bounded anteriorly by slender processes of the jugal and prefrontal, which meet each other half-way, both of these plates being small and triangular. The quadrate is a relatively long and narrow bar, united with the squamosal above, and with a buttress of the pterygoid below. In the facial region, which closely resembles that of birds, sutures are always difficult to determine. The snout is pointed in front, or in some cases slightly rounded, and is formed by the enlarged premaxillae, which constitute the greater part of the upper jaw. Teeth, when present, occur in single series at more or less irregular intervals along the margin of the jaws. They are invariably simple and conical, and implanted in distinct sockets. In some genera the sharp margins of the jaws are completely edentulous, and may have been sheathed with a horny layer, as in birds.

The mandibular rami are straight and elongate, and fused together at the symphysis. They are composed of the usual six elements, but the sutures between the latter are seldom determinable. A coronoid process is lacking, and the suspensorium is sometimes inclined forwards at a considerable angle, so that the articulation with the quadrate is placed underneath the orbits.

The *pectoral arch* comprises merely a pair of long, narrow scapulae, and equally long but somewhat stouter and imperforate coracoids, which articulate with the large sternum by a synovial joint. There is no clavicular arch, nor any indication of precoracoid elements. The humerus is of moderate length, much expanded proximally, and exhibits a deltoid crest. The axis of the distal articular facette is approximately at right angles to that of the head of the same bone. Radius and ulna sometimes doubly exceed the length of the humerus, and are about equally developed. The number of carpal elements in both rows varies considerably. The first digit of the manus is either wanting or represented by a backwardly directed styliform bone. The second, third, and fourth metacarpals are closely apposed and nearly uniform in size, but the fifth is very much stouter than the rest, and bears a series of four enormously elongated phalanges, turned backward to support the wing-membrane. Sometimes metacarpals, Nos. II to IV are incomplete, and either filiform or tapering to a point proximally, being fixed only to the side of the greatly

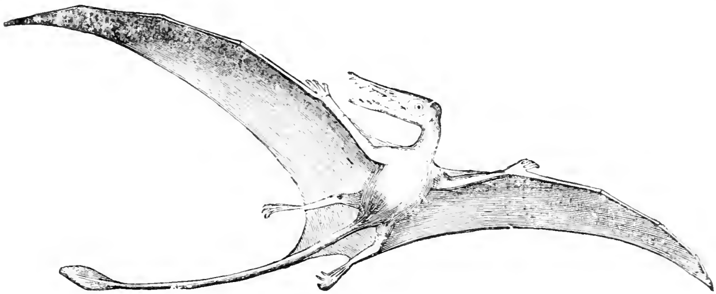


FIG. 353.

Rhamphorhynchus phyllurus, Marsh. Upper Jura (Lithographic Stone); Bavaria. Restoration, showing extent of cutaneous expansions, 1/7 (from A. S. Woodward, after Marsh).

developed metacarpal of the wing-digit. The three inner digits are clawed and exhibit the phalangeal formula 2, 3, 4. They are entirely free from the membranous expansion of the fifth digit (Fig. 353). Attached to the radial side of the carpus is sometimes observed a slender splint-like bone, which is directed backward nearly parallel with the radius and ulna. This is the so-called

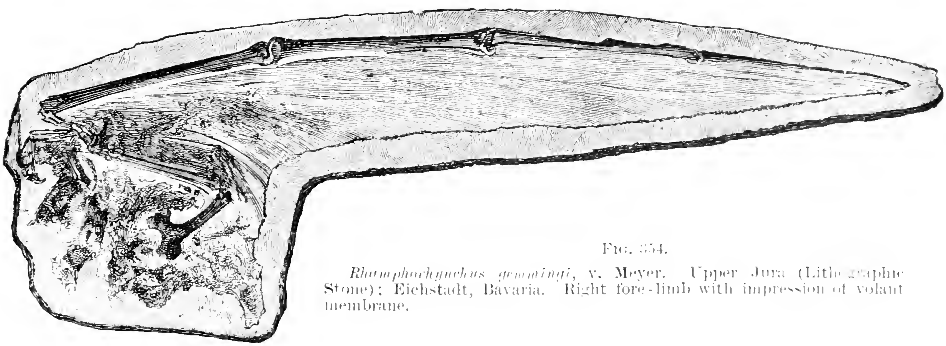


FIG. 354.

Rhamphorhynchus gemmingi, v. Meyer. Upper Jura (Lithographic Stone); Eichstadt, Bavaria. Right fore-limb with impression of volant membrane.

"pteroid bone" (*Spannknochen*, von Meyer), which some writers have regarded as an ossified tendon, or as a support for the wing membrane; but it is more properly interpreted as a rudimentary, abnormally reflexed first metacarpal. The cutaneous expansion, or patagium (Fig. 354), is quite narrow and tapering, in this respect resembling the wing of a swallow or sea-gull. It was attached at its base along the sides of the body wall, and extended beyond the hind limbs to the base of the tail. In at least one genus (*Rhamphorhynchus*) it also developed a leaf-like expansion at the extremity of the tail (Fig. 353). The impressions of the membrane exhibit a number of longitudinal wrinkles or folds, and also numerous fine parallel striae, but are otherwise smooth.

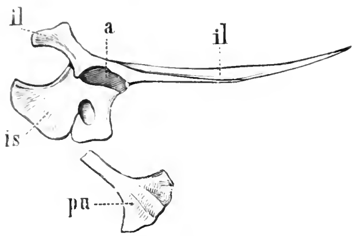


FIG. 355.

Pterodactylus antiquus, Sömm. sp. Upper Jura; Bavaria. Right lateral aspect of pelvis. *a*, Acetabulum, below which is obturator foramen; *il*, Ilium; *is*, Ischium; *pu*, Pubis.

In the *pelvic arch* (Figs. 355, 356) the ilium is low and extended antero-posteriorly on either side of the imperforate acetabulum as in Dinosaurs, the pre-acetabular portion being much longer than the post-acetabular. Its anterior extremity is sometimes expanded (*Rhamphorhynchus*), in other cases slender and tapering (*Pterodactylus*). The ischium usually fuses with the ilium, and excludes the pubis from the acetabulum; it is a much-expanded bone, pierced in most cases by a small perforation. The pubis appears to have been very loosely attached to the antero-inferior portion of the ischium, and almost invariably occurs displaced. Some authors regard this bone as a pre-pubis, and interpret the posterior ventral element as a fused ischio-pubis. In *Pterodactylus* the bone here called the pubis is much expanded distally, and was probably united with its fellow in a cartilaginous symphysis. But in *Rhamphorhynchus*, *Pteranodon*, and *Nyctodactylus*, it is narrow and band-like, extending forwards for a certain distance, and then bent inwards approximately at right angles so as to meet its fellow of the opposite side, with which it becomes fused in a ventral symphysis.

The femur is rather longer and more slender than the humerus in some forms, but in others is very much shorter, as in birds; and as in birds also, it is exceeded in length by the tibia, which is stout and straight. The fibula is reduced to a mere splint, often fused with the tibia, and its pointed distal end extending scarcely half-way down the shaft of the tibia, or it may be absent altogether. There are two proximal tarsals (astragalus and calcaneum), which in the *Rhamphorhynchidae* and *Ornithocheiridae* are always fused with the tibia. At least two distal tarsals are always present.

The hind foot is characteristically reptilian in structure. The four inner metatarsals are about equally developed, and bear clawed phalanges, having the formula 2, 3, 4, 5, or sometimes, when the first two digits are clawless, the formula is 1, 2, 4, 5. The fifth digit is almost always shorter than the rest, its metatarsal reduced to a mere stump, sometimes without phalanges, and sometimes with

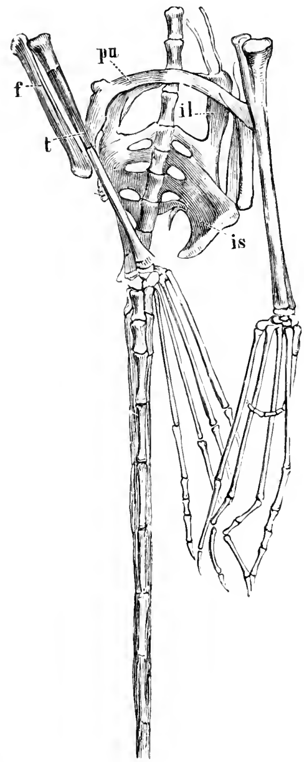


FIG. 356.

Rhamphorhynchus gemmingi, v. Meyer. Upper Jura; Eichstädt, Bavaria. $^1/_1$. *f*, Femur; *il*, Ilium; *is*, Ischium; *pu*, Pubis; *t*, Tibia.

as many as three. In *Rhamphorhynchus* and *Dimorphodon* it was divaricated, and doubtless assisted in the support of the patagium. The claws are usually sharp and delicate, and during life were doubtless sheathed with horn.

Sub-Order 1. **PTERODERMATA.** Seeley.

Tail elongated; wing metacarpal less than half the length of the bones of the antebrachium; fifth digit of pes with one to three phalanges. Jaws dentigerous; external nares completely separated from antorbital vacuity.

This group comprises the earlier and more generalised Pterosaurs, none of which survived the Jurassic so far as known. Teeth are always present, increasing in size posteriorly, but sometimes do not extend to the anterior extremity of the jaws. The scapulae and coracoids are often fused proximally, and the proximal tarsals are fused with the tibia.

Family 1. **Rhamphorhynchidae.**

With the characters of the sub-order. Jurassic.

Dimorphodon, Owen (Fig. 357). Skull relatively very large, deepened in form, and extremely light; brain case unusually small. External narial

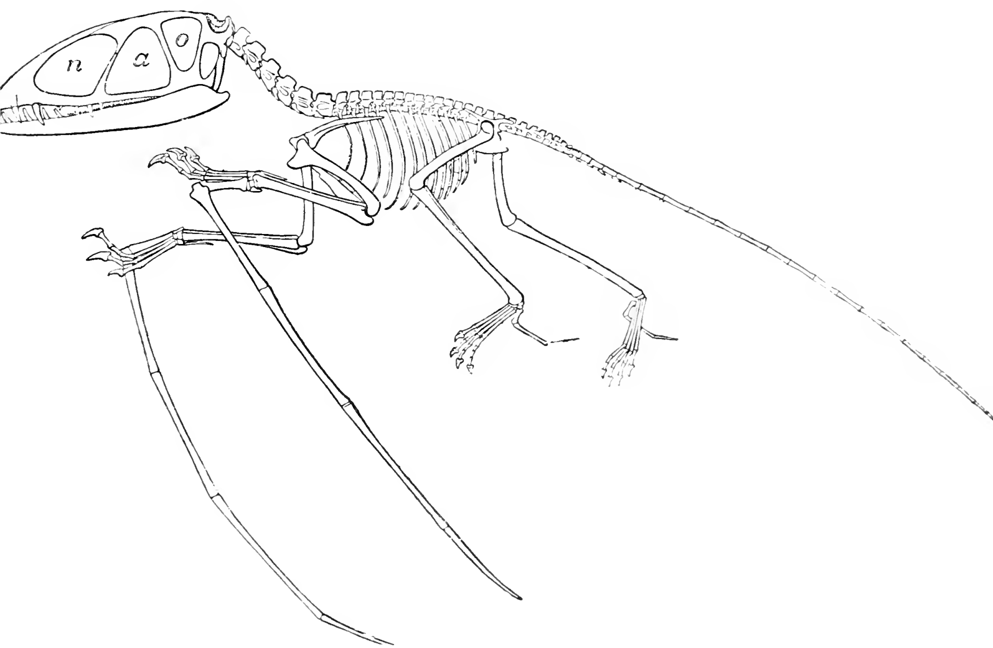


Fig. 357.

Dimorphodon macronyx, Owen. Lower Lias; Dorsetshire. Restoration of skeleton, 1/7. *a*, Antorbital vacuity; *n*, External narial opening; *o*, Orbit (from A. S. Woodward, after Owen).

openings and antorbital vacuities very large. Jaws toothed to the extremity, the anterior teeth very large and irregularly spaced; mandibular suspensorium vertical. Probably four sacrals, and at least thirty caudals present, some of the latter with chevron bones. Scapula and coracoid fused. First digit of manus represented by a styliform ("pteroid") bone, and first wing phalanx shorter than the antebrachium. Ischium large, distally expanded. The first four clawed digits of the pes are normal, and the fifth divaricated; the latter with an attenuated metatarsal and two phalanges. The skull of *D. macronyx*,

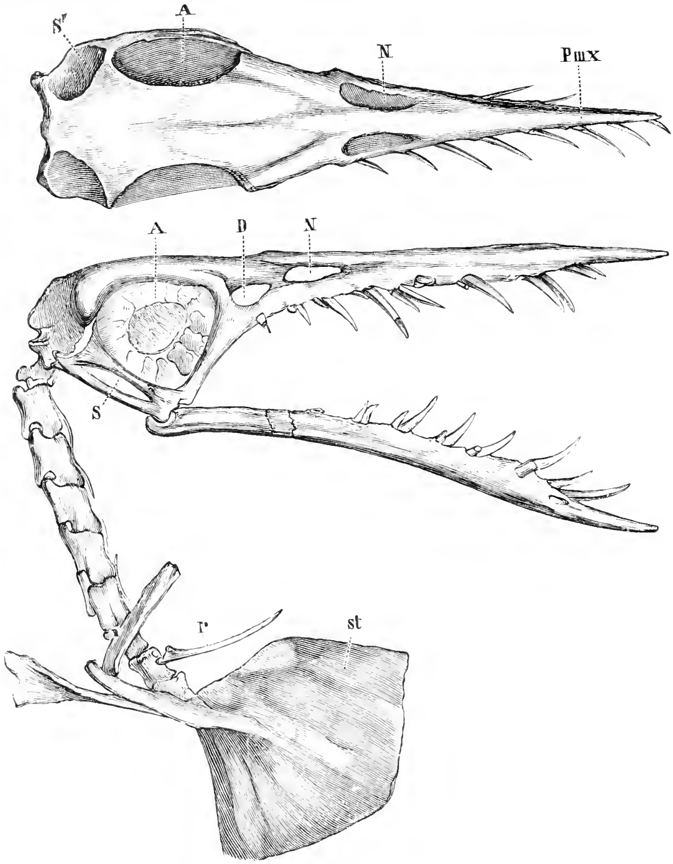


FIG. 358.

Rhamphorhynchus gemmingi, v. Meyer. Lithographic Stone; Eichstädt, Bavaria. *A*, Orbit; *D*, Antorbital vacuity; *N*, External narial opening; *pmx*, Premaxilla; *r*, Rib; *S*, Lateral temporal vacuity; *S'*, Supratemporal vacuity; *st*, Sternum.

Owen, the only described species, attains a length of 20 cm. Lower Lias; Dorsetshire.

Dorygnathus, Oppel. Upper Lias; Würtemberg and Franconia. *Rhamphocephalus*, Seeley. Bathonian; Stonesfield, England. Imperfectly known genera.

Campylognathus, Plien. Known by a complete skeleton from the Upper Lias of Holzmaden, Würtemberg. Skull less deep than in *Dimorphodon*, toothed to the extremity of the jaws; the anterior tooth above and the first two below large and recurved. Mandibular rami toothed nearly to the extremity, which is deflected downward. Narial opening larger than the antorbital vacuity. Proximal phalanx of wing digit more than double the length of antebrachium. Type, *C. zitteli*, Plieninger. Palate and brain cast known in *C. purdoni*, Newton, from the Upper Lias of Yorkshire.

Scaphognathus, Wagner. Like the preceding, but mandibular rami toothed quite to the extremity, and not deflected. External nares smaller than the antorbital vacuity. *S. crassirostris*, Goldfuss, the type species, occurs in the Lithographic Stone of Bavaria.

Rhamphorhynchus, v. Meyer (Figs. 354, 356, 358). Skull sometimes attaining a length of 20 cm. Snout produced and acuminate; teeth large, irregular, inclined forwards, and not extending to anterior end of the jaws. Orbits very large, with sclerotic ring; narial opening and antorbital vacuity very small. Four sacrals and upwards of forty caudals present. Sternal keel extending downward as a slender process, scapula and coracoid usually fused. Pubis in the form of a slender bar, bent inwards nearly at right angles to meet its fellow, with which it fuses in a median symphysis. Limbs similar to those of *Dimorphodon*, except that the fifth toe comprises three phalanges. Upper Jura (Lithographic Stone); Bavaria and Würtemberg.

Sub-Order 2. ORNITHOCHEIROIDEA. Seeley.

Tail short: wing metacarpal at least as long as the bones of the antebrachium: fifth digit of pes vestigial, without phalanges. Teeth sometimes absent. No cervical ribs.

The members of this sub-order vary greatly in size, some being no larger than a sparrow, and the largest having a wing expanse of nearly 6 m. Initiated in the Upper Jura, the group culminated in the Upper Cretaceous, and became extinct before the close of that period. This sub-order probably includes all known forms of Cretaceous Pterosaurs.

Family 1. Pterodactylidae.

Skull with very small lateral temporal vacuities, and large external nares incompletely separated from the antorbital vacuity. Coracoid and scapula separated, the distal end of the latter spatulate, and not articulating with vertebral column. Anterior dorsal vertebrae without supraneural plate. Elements of carpus and tarsus distinct. Teeth, when present, extending to extremity of jaws. Upper Jura and Cretaceous.

Pterodactylus, Cuvier (*Ornithocephalus*, p.p. Sömm.; *Diopecephalus*, *Cycnorhamphus*, Seeley; *Ptenodracon*, Lyd.), (Figs. 355, 359, 360). Teeth invariably present. Represented by numerous species varying in size between that of a sparrow and that of an eagle. The most perfectly preserved skeletons occur in the Lithographic Stone of Bavaria, Würtemberg, and Cerin, France. Certain detached fragments from the Kimmeridge Clay of England are perhaps referable to this genus.

Nyctodactylus, Marsh (Fig. 361). Known by a nearly complete skeleton from the Niobrara Cretaceous of Kansas. Head slender, jaws edentulous. Lateral pieces of atlas not fused with axis; cervicals seven, dorsals twelve, sacrals six, caudals ten to fourteen. Anterior ribs stout, double-headed; posterior very slender and single-headed; three pairs of flat V-shaped abdominal ribs connecting the xiphisternal process with the anterior processes of the coössified pubes. Ischiadic foramen very large. Proximal row of tarsals united to tibia by persistent suture; three carpals present. Wing expanse in typical species about 2 m.

Dermodactylus, Marsh. Imperfectly known, perhaps belonging among the Pterodermata. Upper Jura (Como Beds); Wyoming.

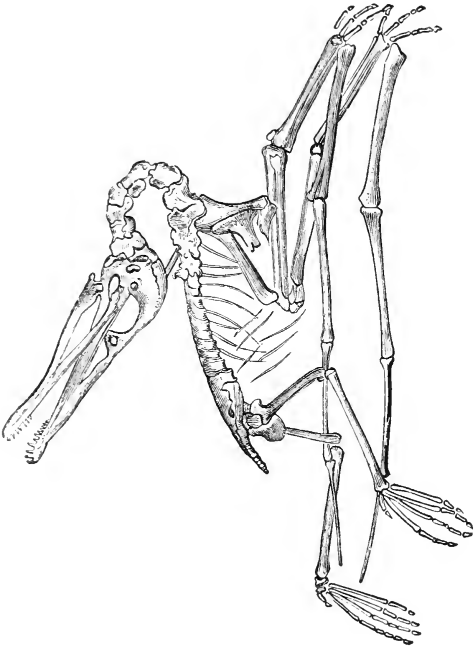


FIG. 359.
Pterodactylus elegans, Wagner. Lithographic Stone; Eichstädt, Bavaria. $^1/_1$.

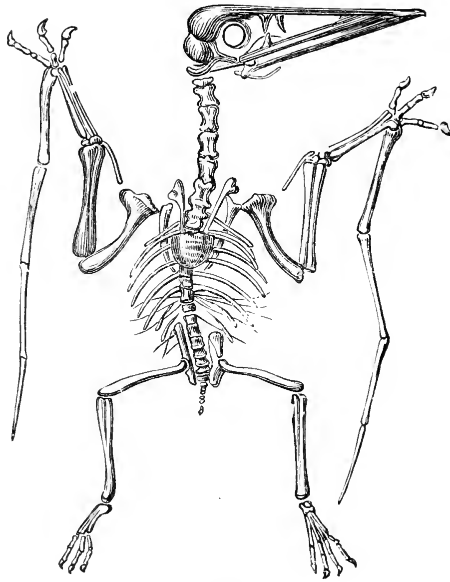


FIG. 360.
Pterodactylus spectabilis, v. Meyer. Lithographic Stone; Eichstädt, Bavaria. $^3/_4$ (after H. v. Meyer).

Family 2. **Ornithocheiridae.** Seeley.

External nares confluent with antorbital vacuity. Teeth, when present, restricted to posterior portion of the jaws. Pectoral arch strong, coracoids and scapulae firmly fused; the former articulating with the sternum, and the latter by a large oblique facette with a supraneural plate above the coössified anterior dorsal vertebrae. Proximal tarsals fused with the tibia; no fibula. Cretaceous.

This family includes the largest known Pterosaurs, their wing expanse varying between 1·5 and 5·8 m. In these highly specialised forms the anterior extremities attained their greatest power, while the posterior pair were weakened, and probably of slight use as locomotive organs.

Pteranodon, Marsh (? *Ornithostoma*, Seeley). Skull considerably elongated, with slender, pointed, edentulous jaws, and a long thin supraoccipital crest. Sclerotic ring present. Sternum keelless, but with a stout anterior median projection. Sacral vertebrae seven in number. Anterior ribs stout, coössified with their centra. Carpus composed of three bones in two rows. Pubes band-like, coössified in the middle. Hind limbs relatively small; femur short and curved, with a small trochanter; tarsus consisting of two free bones in a single row. Fifth digit represented by a small claw-like metatarsal; median phalanges of second, third, and fourth digits very short; first and second digits without claws. Niobrara Cretaceous; Kansas.

Ornithostoma, Seeley, from the Cambridge Greensand, presents no generic differences from *Pteranodon* so far as known, and may prove to be identical.

Ornithocheirus, Seeley. Similar in all essential respects to *Pteranodon*, except for the presence of well-developed teeth in both jaws. Pelvis and hind limbs imperfectly known. Cambridge Greensand; England.

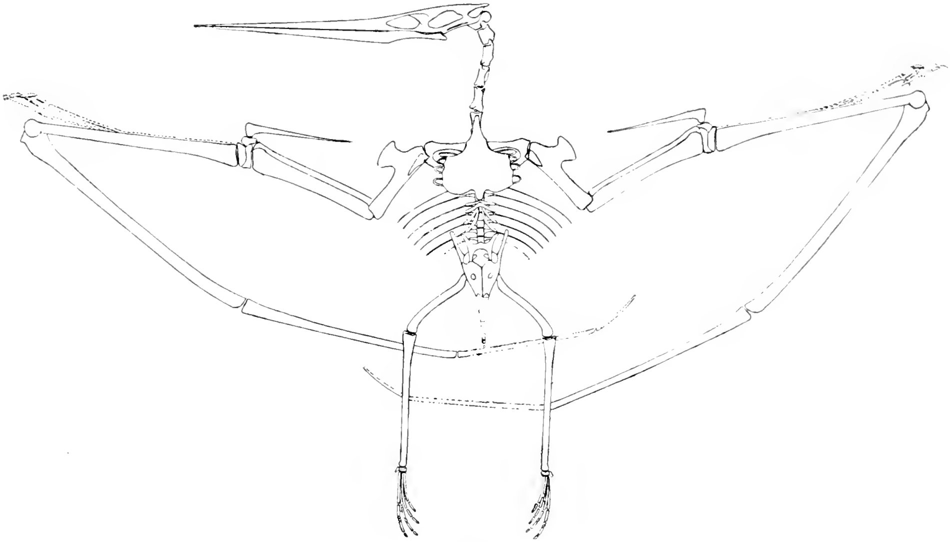


FIG. 361.
Nyctodactylus gracilis, Marsh. Niobrara Cretaceous; Kansas. 1/9 (after Williston).

Ornithodesmus, *Doratorhynchus*, Seeley; *Palaeornis*, Mantell. Founded on fragmentary remains from the Wealden and Purbeck of England.

Range and Phylogeny of the Pterosauria.

The earliest undoubted remains of Pterosaurs occur in the Lower Lias of England, from which horizon the history of the group is traceable to near the close of the Mesozoic era. Regarding its origin and evolution very little can be affirmed. *Dimorphodon*, the oldest known genus, appears suddenly and fully differentiated in the same manner as do the earliest Chelonians; nor are there any essential modifications to be observed among its successors throughout the Jura and Cretaceous, except that some of the latest survivors were toothless and of gigantic size. The group attained its maximum development during the Upper Cretaceous, and passed away with the Dinosaurs, Pythonomorphs, and Plesiosaurs towards the close of this period.

Although Pterosaurs exhibit a number of avian resemblances, they can in no sense be regarded as the ancestors of birds, and are in fact even more widely separated from them than from other orders of reptiles. They are known to us simply as a race of peculiarly modified *Archosauria*, or reptiles with two temporal arches, whose origin is as yet mysterious, and whose hypertropic specialisation precipitated their decline, and finally swept them from off the face of the earth.

[The text for the preceding chapter on *Pterosauria* has been revised by Dr. S. W. Williston, of the University of Kansas, who has also put the chapters on Pythonomorphs and Plesiosaurs in their present shape.—EDITOR.]

Class 4. AVES. Birds.[1]

Feathered, warm-blooded, oviparous vertebrates with chambers of the heart completely separated. There is a single occipital condyle, the quadrate is free, and the fore-limbs are modified into wings. Proximal tarsals fused with tibia to form a tibio-tarsus: metapodal bones fused with one another, and with the distal tarsals to form a tarso-metatarsus. Fifth digit of the pes always absent.

Of all classes of vertebrates, birds constitute the most homogeneous and narrowly circumscribed group, and exhibit everywhere the most remarkable uniformity. Descended without question from reptiles, their affinities with that class are so intimate that Huxley included them both under the common designation of *Sauropsida*. This proposed merging of the two classes, however, is hardly compatible with such trenchant distinguishing characters as the epidermal covering of feathers, heterocoelous vertebrae, and warm-blooded (homothermic) condition.

The *exoskeleton* of birds consists of feathers, the horny covering of the beak, claws, and spurs, and certain corneous plates often found on the tarsus and feet. Save in penguins the feathers do not cover the body uniformly, but are arranged in certain definite tracts (pterylae), between which are bare spaces (apteria). These apteria are best seen on the abdomen and on the sides of the neck in many birds. Although struthious birds are also commonly said to be uniformly covered with feathers, Pycraft has shown the presence of small apteria in most species. Under exceptionally favourable conditions, as in the Lithographic Stone of Bavaria, and the Green River Eocene of Wyoming, imprints of feathers may be preserved in the rocks.

The *skeleton* of birds is remarkable for its combination of compactness and lightness, and for its pneumaticity, or permeation by air cavities. The walls of the bones are very thin, but of dense texture, owing to their richness in calcium phosphate. In young birds the cavities of the long bones are filled with marrow, and this may persist in some bones throughout life, as in a number of water birds; on the other hand, the marrow may disappear and the interstices become filled with air, as in the long bones of birds which sail or soar, and many others; finally, the long bones may be completely filled with spongy bone or cancellar tissue, as is the case with penguins. The skull, humerus, and femur may be said to be pneumatic in the majority of birds.

The *vertebral column* of birds is divisible into cervical, dorsal, sacral, and

[1] Literature:

Beddard, F. E., The structure and classification of Birds. London, 1898.—*Fürbringer, M.*, Untersuchungen zur Morphologie und Systematik der Vögel. Amsterdam, 1888.—*Huxley, T. H.*, On the classification of Birds (Proc. Zool. Soc. London, p. 415), 1867.—*Lydekker, R.*, Catalogue of fossil Birds in the British Museum. London, 1891.—*Marsh, O. C.*, Odontornithes: a monograph of the extinct toothed Birds of North America. Washington, 1880.—*Meyer, A. B.*, Abbilddungen von Vogel-Skeleten. Dresden, 1879-90.—*Menzbier, M. von*, Vergleichende Osteologie der Pinguine in Anwendung zur Haupteintheilung der Vögel (Bull. Soc. Imp. Moscow), 1887.—*Milne-Edwards, A.*, Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France. Paris, 1867-72.—*Newton, A.*, Dictionary of Birds. London, 1893-96.—*Pycraft, W. P.*, Contributions to the osteology of Birds (Proc. Zool. Soc. London), 1898 *et seq.* [An important series of papers not yet (1901) completed.]—*Selenka, E.*, and *Gadow, H.*, Aves, in Bronn's Classen und Ordnungen des Thierreichs, 1869-91.—*Seeley, H. G.*, On the British fossil Cretaceous Birds (Quar. Journ. Geol. Soc. vol. XXXII.), 1876.

caudal regions, but, as will presently be explained, the sacrum or synsacrum of birds is a complex mass of vertebrae not comparable as a whole with the sacrum of other vertebrates. The vertebrae are remarkable for their peculiar saddle-shaped articulations, which allow great freedom of movement. In the

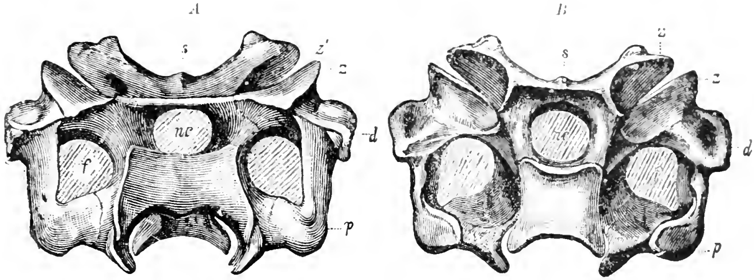


Fig. 362.

Hesperornis regalis, Marsh. Upper Cretaceous; Kansas. Anterior (*A*), and posterior (*B*) aspect of thirteenth cervical vertebra, 1/1. *d*, Transverse process; *f*, Costal canal for vertebral artery; *nc*, Neural canal; *p*, Parapophysis; *s*, Rudimentary neural spine; *z*, *z'*, Anterior and posterior zygapophyses (after Marsh).

Mesozoic *Archaeopteryx* and *Ichthyornis* the centra are slightly amphicoelous, as is also the case in modern embryonic birds and in some of the caudal vertebrae of adults. Opisthocoelous vertebrae occur among the dorsals of penguins and in a few other birds, such as cormorants and gulls, but the atlas is the only procoelous vertebra in the backbone of birds.

The cervical region consists of from thirteen to twenty-five vertebrae, the commonest number being fourteen or fifteen. The centra are mostly elongate and freely movable upon one another, save that in hornbills the atlas and axis may unite, and in a few other birds, the tinamous for example, the last cervical may fuse with the dorsals. The dorsal vertebrae number from six to ten, the first of the series being always the first vertebra connected with the sternum by a dorsal and sternal rib. The dorsal series includes also those rib-bearing vertebrae which are united with the sacrum, and the number of free dorsals is much less, being as few as three in *Petroica*, only seven in the long-bodied grebe, and eight in the crested auklet. The centra of these vertebrae are comparatively short.

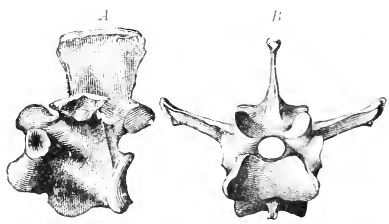
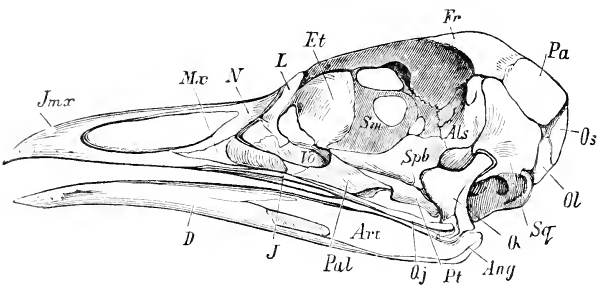


Fig. 363.

Hesperornis regalis, Marsh. Upper Cretaceous; Kansas. Lateral (*A*), and anterior (*B*), aspects of dorsal vertebra, 1/2 (after Marsh).

In water birds (*e.g.* penguins and some auks) all the presacral vertebrae may be free though their motion is restricted, but usually from two to four of the dorsals are fused to stiffen the trunk for flight, one free vertebra being left between these and the synsacrum. The latter is a very complex bone, usually composed in the adult of dorsal, lumbar, sacral, and caudal vertebrae united in one solid mass, as many as twenty vertebrae taking part in its formation. The true sacrals are those two lying behind the cavity containing the kidneys, having transverse processes and sacral ribs, reaching from their centra to the ilia. The rib-like nature of these may be seen in embryos, particularly of the ostrich, which as well as the apteryx has three sacrals. The greater number of vertebrae in the synsacrum are united with the ilia by diapophyses, or transverse processes given off from the neural arch. The anchylosed vertebrae behind the true sacrals are the urosacrals, and belong to the caudal series; their number may vary slightly within specific limits. The free caudals in existing birds usually number about six, besides the terminal ploughshare-bone or pygostyle, which is composed of from four to six fused vertebrae. In the Jurassic



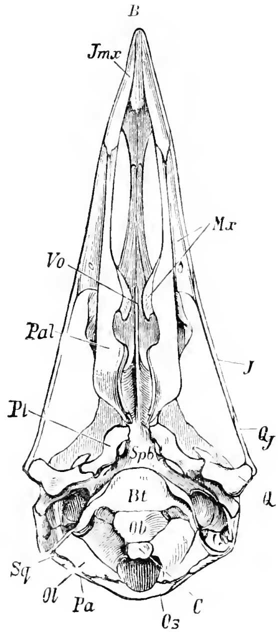


Fig. 364.

Otis tarda, Linn. Recent; Europe. Lateral (*A*), and palatal (*B*), aspects of skull, 1/1. *als*, Alisphenoid; *ang*, Angular; *art*, Articular; *bo*, Basioccipital; *bt*, Basitemporal; *c*, Occipital condyle, underneath foramen magnum; *d*, Dentary; *et*, Median ethmoid; *fr*, Frontal; *j*, Jugal; *jmx*, Premaxilla; *l*, Lachrymal; *mx*, Maxilla; *N*, External nares; *ol*, Exoccipital; *os*, Supraoccipital; *pa*, Parietal; *pal*, Palatine; *pt*, Pterygoid; *q*, Quadrate; *sm*, Interorbital septum; *spb*, Basisphenoid; *sq*, Squamosal; *vo*, Vomer (after Claus).

Archaeopteryx there were at least twenty free and long caudals with a pair of rectrices to each vertebra.

All the presacral vertebrae with the exception of the atlas are usually costiferous, and ribs may be present also on the anterior two or three sacrals; those of the cervical region fuse with the vertebrae, except the last two or three. The true character of the cervical processes thus formed may be seen in embryos and to particular advantage in the young ostrich, where they remain for some time free, as they did permanently in *Archaeopteryx*. With few exceptions the last cervical rib and all the thoracic ribs save the last one or two bear uncinate processes, or thin flat blades of bone directed obliquely upward and backward to overlap the succeeding rib. These processes usually unite with the ribs, but in some cases (Moas and many water birds) remain free. The screamers, *Chauna*, *Palamedea*, are exceptional in that the ribs are devoid of uncinate processes, while they are vestigial in the Secretary Bird. Appended to the thoracic ribs are sternal or abdominal ribs, from two to five pairs of which are attached to the sternum.

A *sternum* is always present, except possibly in *Archaeopteryx*, and this is externally convex and generally broad. It may cover only the anterior portion of the thorax, or may be so prolonged, as in water birds, that its posterior end underlies the pelvis, or extends nearly to the pubes, as in humming-birds. In birds of flight or those which use their wings in swimming, as the penguins and auks, the sternum is keeled beneath; but in flightless birds (Ratites) it may be quite smooth. The anterior end may or may not bear a manubrial process, the posterior portion may be pointed, rounded, emarginate, or have two or four notches, sometimes very deep. The coracoids are attached to the front portion of the sternum, and immediately behind these are two processes, one on either side, known as the costal processes, to which some of the abdominal or sternal ribs are articulated.

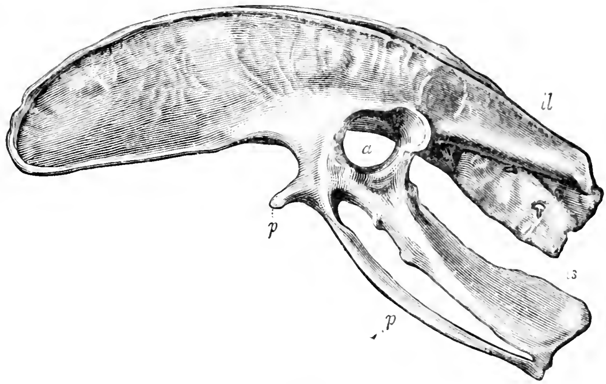


FIG. 365.

Apteryx australis, Owen. Recent; New Zealand. Left lateral aspect of pelvis, $^3/_4$. *a*, Acetabulum; *il*, Ilium; *is*, Ischium; *p*, Ilio-pectineal process; *p'*, Pubis (after Marsh).

The *skull* (Fig. 364) is characterised by the early fusion of its constituent bones, especially those forming the brain case where the sutures are completely obliterated in the adult. In the tinamous, however, the suture between the parietals and frontals seems to remain permanently open. The brain cavity is relatively less diminutive than in reptiles, exceeding even that of Pterosaurs by a considerable margin. The cranial osteology is very similar to that of the *Archosauria*, the chief difference consisting in the constant absence of an upper, and constant presence of a lower temporal arcade. The large orbits look forward in the owls, but are laterally directed in the majority of birds, and except in parrots are incompletely enclosed on the inferior margin. A sclerotic ring of numerous bony pieces is very generally developed around the eye. An antorbital vacuity is present, as in Dinosaurs, Pterosaurs, and Crocodilians, close in front of which, near the base of the beak, are placed the paired external narial openings.

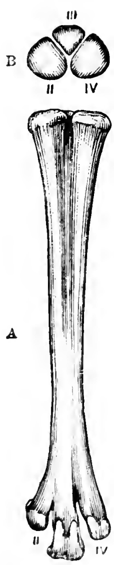


FIG. 366.

Meleagris gallipavo, Linn. Anterior (*A*), and proximal (*B*), aspect of tarsometatarsus of young individual.

The single occipital condyle, formed mainly by the basioccipital, is shifted downwards and forwards so that the long axis of the head is approximately at right angles to that of the neck. The paired parietals are exceeded in size by the large frontals, which form the greater part of the cranial roof and superior border of the orbits. Independent postorbitals and postfrontals are not developed, and there is, of course, no supratemporal vacuity. The inferior temporal arcade, formed by the slender jugal and quadrato-jugal, connects the equally slender maxilla with the quadrate.

The squamosal and periotic elements (proötic, epiotic, and opisthotic) fuse to form a single bone which is united with the occipital and parietals, and to which the large quadrate is movably attached. An independent lachrymal is often present at the anterior margin of the orbit, and there is an ossified or membranous interorbital septum of considerable size. In the anterior prolongation of the latter is a vertically placed unpaired ethmoid, which is continued in front as a bony or cartilaginous nasal septum. The lateral ethmoids are placed between the orbits and external nares, and are pierced for the passage of the olfactory nerves. The greater part of the beak is formed by the fused premaxillae, with the sides of which the maxillae are fused; its margins are sheathed with a horny layer, and it is often movably connected with the skull. When the mouth is opened, the end of the beak is raised by pressure transmitted to it from the quadrate by means of the pterygoid and palatine bones, and more especially by the rod-like quadrato-jugal.

Broadly speaking, the bones of the palatal portion of the skull are arranged on two plans. In the one the vomer is broad and unites in front with the maxillo-palatines, while behind it receives the posterior extremities of the palatines and the anterior ends of the pterygoids, which are thus excluded from contact with the sphenoidal rostrum. This is the *dromaeognathous* type of palate found in struthious birds, the apteryges and tinamous. In birds with this arrangement the head of the quadrate usually has but a single articular face, or is but faintly divided into two portions; and rather long basipterygoid processes from the sides of the sphenoid give this bone somewhat of a cruciform shape.

In the second type of palate, which may be called the *euornithic*, the vomer embraces posteriorly the sphenoidal rostrum between the palatines, and these latter articulate with the pterygoids and with the sphenoid. This arrangement predominates in the vast majority of birds, and they also have the head of the quadrate double, or with two articular facettes. Basipterygoid processes are present in some euornithic skulls, but these most frequently assume the form of low facettes on the sphenoidal rostrum, with which the pterygoids are movably articulated. The euornithic type of skull is subject to various modifications in the development of the vomer and those inwardly directed processes of the maxillae termed the maxillo-palatines. When the vomer is pointed in front and entirely free from the maxillo-palatines, and these are free from each other, the skull is termed schizognathous; when the maxillo-palatines are expanded and fused with each other, the vomer being small or absent, the skull is desmognathous; when the vomer is expanded in front and free from the maxillo-palatines, and these are slender at their point of origin and disjoined, the skull is said to be aegithognathous.

Two terms applied to conditions of the bones bounding the narial openings and much used in classification, *holorhinal* and *schizorhinal*, may be explained here. In the holorhinal type the openings are more or less oval, the posterior border curved and lying in advance of the posterior ends of the premaxillaries. In the schizorhinal type the openings are more or less elongate with the posterior border angular or slit-like and lying back of the posterior ends of the premaxillaries.

In all modern birds the mandibular rami become fused at an early stage into a long symphysis, and only among certain Mesozoic forms (*Ichthyornis*) are they united by suture or by ligaments as in reptiles. The six elements of which the mandible is composed fuse into a single piece as in modern birds, and there is frequently a lateral vacuity between the dentary and splenial, as in crocodiles. Although the earliest known birds have conical thecodont teeth, and dental papillae or a dental ridge sometimes occur in the jaws of some modern embryos (parrot, ostrich), true teeth are invariably wanting among existing species.

The *pectoral arch* is firmly attached to the thorax, in conformity with the mechanical requirements of flight. The long blade-like scapula has no ridge, extends along the dorsal side of the thoracic ribs, and takes part with the coracoid in the glenoid cavity for the head of the humerus. Penguins are exceptional in having the scapula broadly expanded posteriorly. The coracoids are stout and pillar-like, their function being to receive the downward pull of the wing muscles during flight. The clavicles, which are usually united in a forked bone (*furcula*), sometimes act as supports; and by their union with the coracoids at the shoulder-joint, and with the sternal keel below in the centre, tend to resist the thrust of the wing muscles in flight. In some birds of powerful flight (pigeons, humming-birds), however, the clavicles are so weak as to be of no service from a mechanical standpoint. Among Ratites and also a few Carinates (toucans, parrots) the clavicles are rudimentary or wanting, and never unite to form a furcula. The furcula of Carinates may anchylose either with the keel of the sternum (*Steganopodes*) or with the coracoids (*Opisthocomus*), and in the frigate birds with both at once.

The humerus of Carinates is expanded at both ends, and provided at its proximal extremity with a strong pre-axial delto-pectoral ridge for the attachment of the pectoral muscles. Its articular head is vertically elongated, and there is often a pneumatic foramen adjoining it on the inner side. At its distal extremity is a prominent oblique condyle on the inner side of the palmar aspect for articulation with the radius, but there are never any condylar foramina. The humerus of flightless birds is degenerate, and sometimes absent altogether, as in many Moas. In the fore-wing, which is generally longer than the humerus, the ulna is more strongly developed than the radius, and often exhibits a row of tubercles along its lower edge for the attachment of the secondaries. The carpus of adult modern birds contains only two bones (radiale and ulnare); a distal row, however, is indicated in embryos by two separate cartilaginous elements, which later become fused with the metacarpals. The latter are never more than three in number, are unequally developed, and in existing Carinates are more or less completely fused. Metacarpal No. I is much reduced, and bears one or more, rarely two, short phalanges for the support of the so-called bastard wing (*alula*); the second metacarpal usually bears two phalanges and the third, one. The first and second digits are sometimes clawed (*Struthio*, *Rhea*, *Chauna*), and in *Archaeopteryx* all three terminate in claws.

The three elements of the *pelvis* are anchylosed (except in *Archaeopteryx*), and usually unite with the synsacrum. In water-birds this union takes place somewhat slowly, and in penguins and the great auk not at all. The ilium is elongate, and may, as in birds of prey, extend much further in front of the acetabulum than behind it. Ischium and pubis are both directed backwards. The pubes often remain free from the ilia, and never unite with one another to form a symphysis except in the ostrich. Since the retroversion of the pubis is proved by embryological researches to be a secondary modification, no homology can exist between this and the post-pubis of Ornithopodous Dinosaurs, and the *processus iliopectinealis* (Fig. 365) must be regarded as a structure peculiar to birds alone.

The femur in birds is short and stout, with the neck and head extending inwards into the acetabulum at right angles to the shaft. The latter is directed forwards and slightly downwards during life, and is concealed beneath the flesh and feathers of the abdomen in such a way that the knee-joint is not visible externally. Its distal condyles are large and antero-posteriorly elongated, and a patella is present in most cases. The tibia is a stout bone considerably longer than the femur. Its expanded proximal end exhibits a procnemial crest, which may extend above the knee-joint, and the distal extremity has a trochlea-like surface, transversely elongated, and slightly hollowed in the middle. In young Ratites, and in the embryos of Carinate birds, the presence of a suture near the distal end of this bone indicates that an astragalus and calcaneum are fused with it, thus forming a tibio-tarsus. In the Moas the united astragalus and calcaneum remain for some time quite free from the tibia.

The fibula in birds is a degenerate bone, and best developed in the Moas, where, although short, it is stout and free. In most birds it is more or less fused with the tibia, and is longest in the penguins, the fish-hawk, and some owls, where it reaches almost to the ankle-joint.

The distal row of tarsals fuses with the coössified metatarsals to form a tarso-metatarsus (Fig. 366). This bone is peculiarly characteristic of birds, and its variations, together with those of the tibia, cause the differences in the length of the leg among different forms, which are sometimes enormous. The fifth metatarsal is never developed, and the first, when present, is always rudimentary, being attached to the inner side of the tarso-metatarsus by ligament, or more rarely by suture. Metatarsals Nos. II to IV are imperfectly united in *Archaeopteryx*, and completely separated in the embryos of modern birds; but in the adult condition they are always fused into a single bone, although the three components are plainly distinguishable in penguins. This metapodal element terminates distally in three pulley-like surfaces for the articulation of the phalangeals. Generally the median condyle is thrust forward in advance of the other two, and the modifications of this region afford important taxonomic characters. There is remarkable constancy in the number of phalanges present in the toes of birds, the formula being 2, 3, 4, 5 in almost all cases where the full complement of digits is present. The hallux, however, is frequently wanting, and in the ostrich only digits Nos. III and IV are developed. An apparent exception to the usual formula occurs among some swifts and goatsuckers, where owing to fusion of some of the phalanges the formula is 2, 3, 3, 3.

Fossil egg-shells or casts of the same have been obtained from the Cretaceous and various Tertiary horizons, but are naturally much less commen than bones of the skeleton. They belong for the most part to cursorial or wading birds. The largest known eggs are those of *Aepyornis*, from the superficial deposits of Madagascar, which have a capacity of about eight liters. Foetal bones are occasionally found in Moa eggs from New Zealand. Certain three-toed footprints occurring in the Trias of the Connecticut Valley were formerly ascribed to an avian origin, but are doubtless referable for the most part to bipedal Dinosaurs. The presumable kinship between birds and Dinosaurs has already been discussed under the head of the latter group

In comparison to the large number of recent species, of which over 12,000 have been described, the 400 or 500 known fossil forms yield but an insignificant record of the ancient avian faunas. Yet as far as the record shows, Tertiary ornithic faunas were essentially like the modern, and it is only as we direct attention to the Mesozoic that signal differences are to be observed. In *Archaeopteryx*, the oldest known bird, the tail had not become atrophied, nor the teeth lost in the adult; the pelvis was not fully developed, and the vertebrae had not yet acquired the saddle-shaped articulations characteristic of post-Jurassic forms.

The Classification of Birds.—Classification, as here employed, is an attempt to place together related species and to arrange the groups thus formed so as to indicate the extent to which each has been modified, or has departed from what is conceived to be the most generalised or lowest type. Further than this a linear or tabular arrangement cannot go, and it is obviously impossible to express in such a manner the interrelationships of the various groups; moreover, such a series cannot be so arranged that we may pass by regular gradations from the lower to the higher forms.

The difficulties attending the classification of birds are at once their great general similarity of structure and their numerous adaptive modifications, sometimes slight, sometimes so great as to obscure characters of real value. There are, besides, a certain number of aberrant forms whose exact position is a matter of uncertainty, and others in which there are departures more or less pronounced from the general structure of the group in which they should obviously be placed. For it must be constantly borne in mind that in palaeornithology we are not dealing with the entire class of birds, but only with a certain portion of it, since the number of known fossil birds is very small, and it is consequently impossible to trace the lines of descent of existing species; we do not even have broken lines to guide us, but merely isolated dots to indicate their probable existence. For the proportion of fossil to existing birds is small indeed, about 500 extinct to 12,000 living species, and most of these are from the Miocene or later horizons; they are easily referable to existing families and often to existing genera, so that they throw little light on the phylogeny of modern birds.

The reasons for the remarkable dearth of fossil avian remains are obscure, and those usually adduced, such as the imperfection of the geological record, do not seem altogether satisfactory, the more so since in some favoured localities, such as Allier in Southern France, and Fossil Lake, Oregon, bones of birds have been found in considerable numbers. The palaeontologist is further hampered by having to restrict himself to characters offered by the skeleton alone, and while these are of primary importance, much valuable evidence may be gathered from the muscles, viscera, and plumation. And birds must be classified by the resultant of all their characters, not by any one set, for the exceptions to any general rule are nowhere more numerous among vertebrates than in this particular class. Finally, there is the personal equation, or the individual opinion of the classifier, as to the relative values of the characters on which we must rely for uniting or separating species. For these reasons no two systems will be found to agree in all their details, certain birds or groups of birds being particularly liable to shifting about at the hands of the taxonomist.

The divisions here employed are practically those of Stejneger,[1] although

[1] Standard Natural History, vol. III.—Birds. Boston, 1885 (afterwards changed to the Riverside Natural History).

the *Hesperornithes*, *Ichthyornithes*, and *Impennes* have been reduced to a lower grade than that assigned them in his system, as has been done by Fürbringer and others. These divisions, which correspond in a great measure to the sub-orders of Fürbringer, are larger than those usually considered as orders, and often comprise some very diverse forms. An alternative is to treat each group separately, which gives from twenty to forty divisions, variously designated as families, sub-orders, or orders.

Fig. 367.

Archaeopteryx lithographica, v. Meyer. Lithographic Stone; Eichstadt, Bavaria. 2/7. *c*, Carpal; *cl*, Furcula; *co*, Coracoid; *h*, Humerus; *r*, Radius; *sc*, Scapula; *u*, Ulna. Original in Berlin Museum (from Steinmann and Doderlein).

Sub-Class 1. SAURURAE.[1]

Tail feathers arranged in pairs on either side of the elongate caudal vertebrae. Sternum rudimentary; dorsal ribs without uncinate processes; cervical ribs free; vertebrae amphicoelous. Pelvic elements separate, as are also the metacarpals; digits clawed.

Order 1. ARCHAEORNITHES.

Skull typically bird-like, provided with a series of conical, socketed teeth along the margin of the upper and lower jaws. Vertebrae amphicoelous, and the lizard-like tail longer than the presacral portion of the column. Remiges and rectrices, with their coverts, well developed. Upper Jura.

Archaeopteryx, von Meyer (*Gryphosaurus*, Wagner), (Fig. 367). This unique and in many respects remarkable genus is known by two nearly complete skeletons from the Lithographic Stone of Bavaria, one of which is preserved in the

[1] *Dames, W.*, Ueber Archaeopteryx (Palaeont. Abhandl. Dames und Kayser, vol. II. p. 119), 1884. Ueber Brustbein, Schulter- und Beckengürtel der Archaeopteryx (Sitzungsber. preuss. Akad. Wissensch. vol. XXXVIII. p. 818), 1897. *Owen, R.*, On the Archaeopteryx of von Meyer (Phil. Trans. vol. CLIII. p. 33), 1863. *Pycraft, W. P.*, The Wing of Archaeopteryx (Nat. Sci. vol. VIII. p. 261), 1896. *Seeley, H. G.*, Professor C. Vogt on Archaeopteryx (Geol. Mag. [2], vol. VIII. p. 454), 1881. *Vogt, C.*, Sur l'Archaeopteryx macrura (Revue Scient. [2], vol. XXIII. p. 241), 1879.

British and the other in the Berlin Museum. They are considered as representing two species, *A. macrura* and *A. siemensi*, and fortunately supplement each other in such wise that the osteology is known with tolerable accuracy. Contrary to the usual condition among birds, none of the bones appear to have been pneumatic.

The skull is shaped like that of a typical bird, its constituent elements being fused together, and the quadrate apparently free. A sclerotic ring is present, and there is a series of thirteen conical teeth on each side in the upper jaw, fixed probably in distinct sockets. The vertebral column comprises about fifty vertebrae, of which ten or eleven are cervical, eleven or twelve dorsal, two lumbar, six or seven sacral, and about twenty caudal. The cervical and dorsal vertebrae seem to have been amphicoelous, or amphiplatyan, as in reptiles, and bear weakly developed transverse processes and neural spines. The ribs are very slender, free in the neck region, and without ossified uncinate processes in the thoracic region. Twelve or thirteen pairs of abdominal ribs are present in the ventral wall of the body cavity. In the pectoral arch the long and slender scapula is essentially bird-like, and exhibits a well-developed acromion. The sternum is unfortunately not well preserved, but the coracoids and U-shaped furcula resemble those of modern Carinate birds. The wing is relatively small, and its bones slender. Radius and ulna are straight, and but little shorter than the humerus. The carpus is imperfectly known, and the three metacarpals appear to have been free. Metacarpal No. I is quite short, and No. II longer and stouter than the first or third. The lizard-like manus terminates in three clawed digits having the phalangeal formula 2, 3, 4.

The three pelvic elements appear to have been distinct, and united with each other by persistent sutures. The acetabulum is perforate. The hind limb is essentially avian, and conspicuous only for the weak development of the cnemial crest of the tibia. There are four clawed digits in the pes (Nos. I to IV), with the phalangeal formula 2, 3, 4, 5. In the wing are observed seven primary and ten secondary remiges with their coverts. The rectrices of the tail are arranged in pairs, directed obliquely backward, one pair to each vertebra. Contour feathers are also indicated on the neck and along the tibia.

Archaeopteryx appears to have been intermediate in size between an ordinary pigeon and crow, and to have enjoyed a moderate power of flight. The clawed digits of the manus were doubtless effective in climbing trees and rocks. In this connection the quadrupedal habits of young modern birds, especially the hoactzin (*Opisthocomus*), cormorant, and certain water-fowls, are of significance as indicating a possible survival, "handed down from the very dawn of avian development" (Pycraft).

Sub-Class 2. ORNITHURAE.

Tail feathers arranged like a fan around the terminal portion of the shortened caudal vertebrae, a number of which are usually united to form a pygostyle. Sternum well developed: dorsal ribs (save in Palamedea and Chauna) with uncinate processes; cervical ribs united with their vertebrae. Pelvic elements proximally united; metacarpals united.

Super-Order 1. ODONTOLCAE.[1]

Birds with teeth implanted in a continuous groove; mandibular rami united at the symphysis by ligament only, and with their component bones free from one another. Clavicles free from one another. Basipterygoid processes wanting; palatal structure imperfectly known, but the head of the quadrate is single and the vomer is probably paired. Bones of pelvis free posteriorly; vertebral articulations saddle-shaped.

The order *Hesperornithes* contains members of the genus *Hesperornis* (Figs. 362, 363, 368) and their allies from the Upper Cretaceous of Kansas. So far

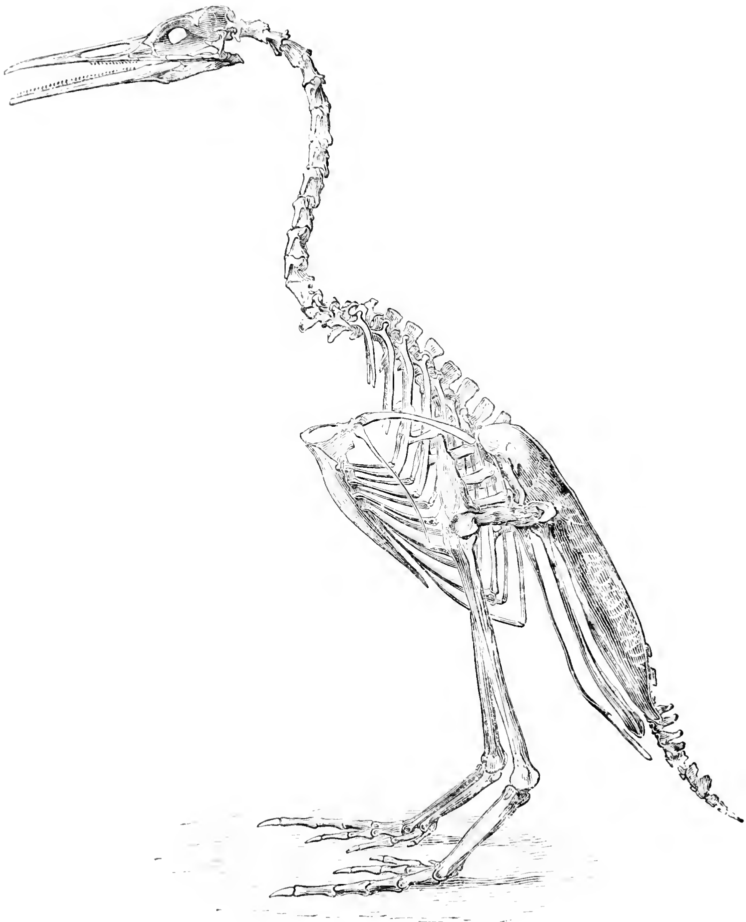


Fig. 368.

Hesperornis regalis, Marsh. Upper Cretaceous; Kansas. Restoration of skeleton, 1/8 (after Marsh).

as is known the teeth in the upper mandible were confined to the maxilla, for

[1] *Marsh, O. C.*, Odontornithes: A Monograph on the Extinct Toothed Birds of North America. Washington, 1880. *Williston, S. W.*, Plumage of Hesperornis (Kan. Univ. Quart. vol. V. p. 53), 1896.

in *Hesperornis* the extremely long premaxillae are toothless. In the mandible the teeth extend to the tip. *Hesperornis* was a flightless and highly specialised diving bird of great size, having the wing represented by the humerus only. The coracoid is short and wide, but the clavicle articulates with the inner side of the head as is customary among birds.[1] The pelvis is greatly compressed, the femora short and massive, the patella enormous and functioning as a cnemial process, the tibiae hollow. The outer digit of the four-toed foot is much the largest, being nearly twice the length of the third digit; the toes appear to have been lobed, and the tarsi were directed outwards from the sides of the body and not downwards as in modern birds.

Enaliornis, from the Cambridge Greensand, has been considered as a related form, and another genus, *Baptornis*, also occurs in the Kansas Cretaceous.

Super-Order 2. ODONTORMAE.[2]

Birds with teeth in separate sockets and with slightly amphicoelous vertebrae. Palatal structure unknown, but the quadrate has but a single head.

The order *Ichthyornithes* is best known by *Ichthyornis victor*, Marsh (Figs. 369-371), a bird about the size of a pigeon, from the Cretaceous of Kansas. The deeply keeled sternum and the humerus indicate a bird of powerful flight, but as in *Hesperornis* and most *Dromaeognathae*, the component bones of the pelvis are posteriorly free. As in *Hesperornis*, the teeth of the separated halves of the lower mandible extend the full length of the dentary, while in the upper jaw they were confined to the maxilla.

FIG. 369.

Ichthyornis victor, Marsh. Upper Cretaceous; Kansas. Restoration of skeleton. 1/2 (after Marsh).

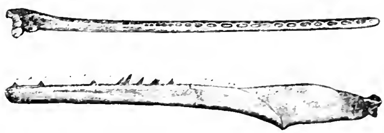


FIG. 370.

Ichthyornis dispar, Marsh. Upper Cretaceous; Kansas. Mandible, 3/4 (after Marsh).

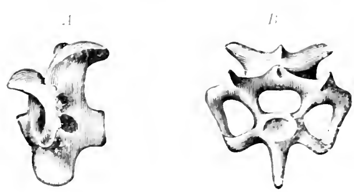


FIG. 371.

Ichthyornis dispar, Marsh. Lateral (A), and anterior (B), aspect of cervical vertebra, 2/1 (after Marsh).

[1] This is quite different from what is shown in Professor Marsh's figure, but a specimen in the United States National Museum shows that in his specimens the clavicles were slightly imperfect.

[2] *Marsh, O. C.*, Odontornithes, etc. Washington, 1880.

Super-Order 3. DROMAEOGNATHAE.[1]

The skull is of the Dromaeognathous type, and the head of the quadrate is single, save in the *Apteryges*, in which the articular head is broad, and almost, or quite, double. While the single-headed quadrate is also found in the toothed birds *Ichthyornis* and *Hesperornis*, in these the halves of the lower mandible are free from one another, a point wherein they differ from other birds. The ischia are never united with the ilia save at the extreme distal portion, and are usually slender and free, while the aspect of the entire pelvis is quite different from that of the *Euornithes*. The upper end of the tarsus is never perforated for the passage of tendons, and the terminal caudals do not fuse to form a pygostyle.

The *Dromaeognathae* comprise a small number of birds differing from one another in important particulars, but all evidently related to, or directly descended from, old and primitive forms; they may be considered as the scattered survivors of the ancient avi-fauna of the globe, and some are confined to a remarkably small area. It is scarcely too much to say that greater differences of structure are to be found among the few members of this division than among all other existing birds, and these differences are such that they are frequently placed in different orders. The flightless struthious birds have a sternum devoid of a keel, and very variable in shape posteriorly, while the shoulder girdle exhibits various degrees of degeneration from the absence of clavicles to the lack of the entire wing. The pelvic region is also very variable as to the ischia and pubes.

Order 1 STRUTHIONES.

This order comprises the true ostriches (*Struthio*), the rheas (*Rhea*), the cassowaries, and emeus (*Casuarius* and *Dromaius*), these forming three groups in the order given, which are sometimes raised to ordinal rank, but more often considered as families, super-families, or sub-orders. The extinct Moas forming the family *Dinornithidae* form a distinct division, and the *Aepyornithes* of Madagascar still another, although owing to lack of knowledge of their palatal structure these last cannot be accurately placed.

These are all large flightless birds, having, so far as known, a typically Dromaeognathous skull with the long basipterygoid processes arising from the body of the parasphenoid, giving it something of a cruciform shape; the nostrils are holorhinal. The sternum is not keeled; the scapula and coracoid are short and fused with one another, and the wings small. All these, however, are negative characters correlated with loss of the power of flight.

Family 1. Struthionidae.

In the *Struthionidae*, or ostriches, the pubes are united in a ventral symphysis, the toes reduced to two, the third and fourth digits only being present,

[1] *Pycraft, W. P.*, Morphology and Phylogeny of the Palaeognathae (*Ratitae* and *Crypturi*) and Neognathae (*Carinatae*), (Trans. Zool. Soc., London, vol. XV. p. 149), 1900. This important paper contains a very full bibliography of works relating to the group here called *Dromaeognathae*. Mr. Pycraft shows very clearly that the groups *Ratitae* and *Carinatae* are artificial, and that the Tinamous belong with the Ostriches.

and the weight of the body carried mainly by the third, a high degree of specialisation due to modification for running. Fossil remains of these birds occur in the Lower Pliocene of the Siwalik Hills and the Island of Samos, while fossil eggs, slightly larger than those of the living ostrich, have been described under the name of *Struthiolithus*, from superficial deposits of Southern Russia and Northern China. This would seem to indicate that the range of the group has been restricted through the agency of man.

Family 2. Rheidae.

The rheas have the ischia turned inward, so that they meet and are united beneath the ilia, while a number of the anterior caudal vertebrae are crowded out and aborted; they have three digits in the foot. The species of this family are confined to southern South America, where remains referable to existing species occur in Pleistocene deposits.

Diatryma, Cope, from the Eocene of New Mexico, was assigned to this group by Cope, but it is very doubtful if this is correct; the affinities of *Diatryma* appear to be rather with the South American *Phororhacidae*.

Family 3. Dromaiidae.

The emeus from Australia, and the cassowaries from Northern Australia, and a number of the islands to the northward, have no striking peculiarities of the pelvic region, and are three-toed. The bones of the wing are very greatly reduced in size. Allied to the emeus is *Genyornis* from the Pleistocene of Australia, a bird of massive build with a skull 0·3 m. in length. *Hypselornis* occurs in the Pliocene of India.

Family 4. Aepyornithidae.[1]

The *Aepyornithidae*, although known only by fossil remains, including entire egg-shells, from Northern Madagascar, have become extinct at a comparatively recent epoch. They were birds of great size and massive build, having a relatively small skull and an unusually short and broad sternum, with well-developed facettes for the coracoids. Foot normally with four digits, but the hallux is sometimes wanting. The nearest relatives of these birds are considered to be the cassowaries and emeus. The typical species is the unfortunately named *Aepyornis maximus*, a species considerably exceeded in size by *A. titan*, which has a tibia 80 cm. in length.

Family 5. Dinornithidae.

The *Dinornithidae*[2] comprise about twenty or twenty-five species of birds popularly known as Moas.

[1] *Andrews, C. W.*, Skeleton of Aepyornis (Ibis, p. 376), 1896. Also, Geol. Mag. [4], vol. IV. (1897), p. 241.—*Bianconi, G. G.*, Recherches sur l'Epyornis maximus (Ann. Sci. Nat. Zool. [5], vol. III. p. 58), 1865.—*Capellini, G.*, Sul primo uovo di Aepyornis maximus arrivato in Italia (Mem. Acad. Sci. Ist. Bologna [4], vol. X.), 1889.—*Milne-Edwards, A.*, and *Grandidier, A.*, Ann. Sci. Nat. Zool. [5], vol. XII. p. 167), 1870.

[2] For papers relating to *Dinornithidae*, see *Hamilton, A.*, Bibliography of Dinornithidae (Trans. New Zeal. Inst. XXVI. (1893), p. 229). Also, *Hutton, F. W.*, New Zeal. Journ. Sci., Nov. 1891, p. 6.—*Parker, T. J.*, On the Cranial Osteology, etc. of Dinornithidae (Trans. Zool. Soc., London, vol. XIII. p. 373), 1895.—*Andrews, C. W.*, Skeleton of Megalapteryx (Novit. Zoologicae, vol. II. p. 188), 1897.

The wings and pectoral arch extremely rudimentary or absent. Beak short and slightly deflected. Hind limbs in most species exceptionally massive. Femur usually without pneumatic foramina. Tibio-tarsus with bony bridge over the groove for extensor tendons. Hallux sometimes present in addition to the three usual digits.

The "Moas" are birds of large or gigantic size, and of exceptionally massive build, which existed in New Zealand in great abundance and variety during the late Tertiary, and became extinct only in comparatively modern times. Their charred bones and egg-shells occur in the refuse heaps of the Maoris, and large numbers of bones or occasionally complete skeletons have been found, especially in swamps. A few specimens have been found in caves with some of the ligaments and portions of the integument preserved. No remains are known older than the Pliocene. The plumage, so far as known, resembles that of emeus and cassowaries.

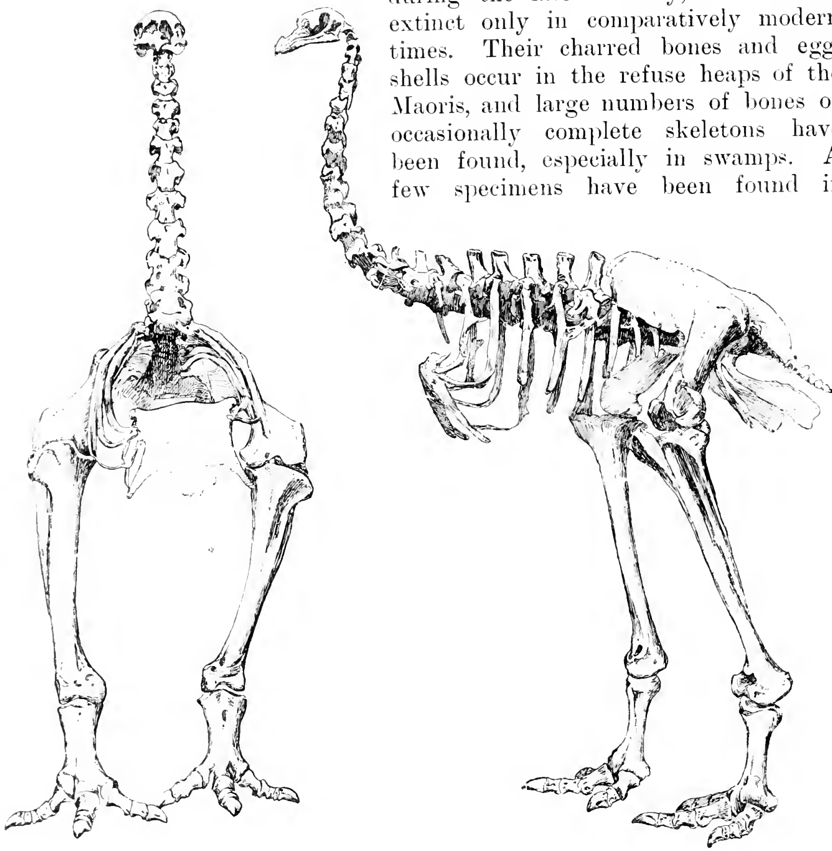


FIG. 372.
Palapteryx elephantopus, Owen sp. Pleistocene; New Zealand. $^{1}/_{18}$ (after Owen).

Dinornis, Owen. Beak relatively wide and pointed, temporal fossae large. About twenty vertebrae present in cervical and sacral regions respectively. Sternum about as long as broad, very convex, with small coracoidal facettes, three costal facettes on each side, widely divergent lateral processes, and a xiphi-sternal notch. Scapulo-coracoid element without glenoid cavity for the humerus. Pelvis narrow, with elevated ilium. Femur comparatively long, its medullary cavity with very thick walls. Tibio-tarsus and tarso-metatarsus also long and slender; hallux rudimentary or absent. *D. maximus*, Owen, attained a height of over 3·5 m. when standing.

Palapteryx, Owen (*Euryapteryx*, Haast), (Fig. 372). Smaller but much stouter than the preceding. Beak short and rounded; sternum flat, broader than long, without coracoidal facettes; pelvis low and broad. Hind limbs extremely massive, crus relatively short; hallux present. Total height less than 2 m.

Anomalopteryx, Reich. Small birds of comparatively slender build. Skull narrow and elevated, with sharply-pointed beak. Sternum much longer than broad, moderately flattened, with faint or no coracoidal facettes, three costal facettes on each side, and a pair of long and slender lateral processes. Tarso-metatarsus shorter than the femur, and scarcely half as long as the tibio-tarsus; hallux present.

Megalapteryx, *Mesopteryx*, Haast. These genera accompany the preceding, but are less satisfactorily known.

Order 2. APTERYGES.[1]

This order contains the small, flightless birds of the genus *Apteryx*, found only in New Zealand. They are readily distinguished by their long, rather slender beaks, and by the nostrils opening at the end of the beak, a point wherein they differ from all other birds. The sternum is broad, the wings minute, the foot four-toed, the first digit being small, and above the level of the others. Remains of several species of *Apteryx*, mainly ascribable to living species, occur in superficial deposits of New Zealand.

Order 3. CRYPTURI.

The tinamous, constituting the order *Crypturi*, are *Dromaeognathae*, having a long, narrow keeled sternum, with a long, slender lateral process on either side. In the shortening of the vomer, and moving forward of the palatine region, they show an approach towards the *Euornithes*. The tinamous resemble little ostriches in their appearance, but have a limited power of flight; and because of this, their small size, and keeled sternum, they have been kept near the gallinaceous birds. It may well be that they retain the primitive characters of the group from which some of the Gallinae have been derived, but it is of interest to note that while in some details of their musculature they resemble the fowls, in other and more striking points they resemble the ostriches. The group is eminently characteristic of South America, although it extends northwards into Mexico. So far very few fossil remains of the tinamous have been found, and these from comparatively recent deposits.

Super-Order 4. EUORNITHES.

The super-order *Euornithes* comprises the vast majority of existing birds, and is the equivalent of the *Carinatae*, less *Ichthyornis*, and the tinamous. Its members are characterised by having the Euornithic type of skull (see p. 260),

[1] *Parker, T. J.*, Anatomy and Development of Apteryx (Phil. Trans. Roy. Soc.), London, 1891.

and the ilium and ischium are always fused posteriorly. The hypotarsus has one or more tendinal canals, and the sternum is generally keeled, although this is a character of little value, since any group may have its flightless forms. Thus we have the owl parrot (*Stringops habroptilus*), Harris's cormorant (*Halieus harrisi*), the weka rail (*Ocydromus australis*), and the dodo (*Didus ineptus*), each representing a different order.

Limits of space preclude more than a brief survey of the various subdivisions of the *Euornithes*, and the student will no doubt be struck by the slight and often unsatisfactory nature of the osteological characters used to define them. It is hoped that failure in this respect may be pardoned, since Huxley, Fürbringer, and Beddard were all forced to rely largely on the muscles and pterylosis to define their divisions of birds.

Order 1. IMPENNES. Penguins.[1]

The penguins deserve particular notice on account of their high specialisation as swimming birds, while at the same time they present some primitive characters. The wings are shortened, flattened, and modified into paddles, but as they are moved by the muscles employed by other birds in flight, the sternum retains its keel. The skull is schizognathous, and the component bones remain free from one another for an unusual length of time; the pterygoids are very large. The scapula is unique among birds in being expanded posteriorly. The dorsal vertebrae are markedly opisthocoelous. The tarsus is short and wide, and its three component tarsals plainly indicated by their imperfect fusion.

On account of these characters and peculiarities found in the pterylosis and muscles, Gill, Stejneger, and Menzbier have considered the penguins as forming a group equal in value to the rest of the *Euornithes*; but this seems too exalted a rank, and does not take purely adaptive features sufficiently into account. The group is characteristic of the southern parts of the southern hemisphere, but extends to the equator off the west coast of South America. Its geological history is imperfectly known, but the penguins must have attained their specialisation at an early date, as one genus (*Palaeospheniscus*) has been obtained from the Eocene of Patagonia, and a giant form (*Palæeudyptes*) is known from the Eocene of New Zealand.

Order 2. CECOMORPHAE.

The *Cecomorphae* include the auks, gulls, divers, and petrels, these last diverging from the other members of the order and often placed in an order by themselves, the *Tubinares*. The divers (*Colymbidae*) and petrels are considered, among existing birds, to be those nearest the penguins, the *Tubinares* again having some points of resemblance to the storks (*Grallae*). The *Cecomorphae* are swimming birds, having a schizognathous palate and the angle of the mandible truncate.

An albatross, *Diomedea anglica*, occurs in the Red Crag, Pliocene, of England, and remains of gulls are numerous in the Miocene of the south of

[1] *Watson, M.*, Report on the Penguins collected by the *Challenger* (Challenger Reports, vol. VII. Part XVIII.). 1883.

France; and it is of interest to note that the earliest known auk, *Mancalla californiensis*, from the Upper Miocene of California, was a highly specialised and flightless form.

Order 3. GRALLAE.

The *Grallae* are a group of wading birds having a schizognathous skull without basipterygoid processes and schizorhinal nostrils. The order embraces the cranes, snipe, bustards, and rails, and includes an unusual number of aberrant forms, such as the South American trumpeter, *Psophia;* the Seriema, *Cariama;* and the New Caledonian *Rhinochoetus*, birds which retain some of the characters of their ancestral forms, and hence being more generalised than their modern relatives, are hard to fit into any scheme of classification.

The plovers closely approach the gulls among the *Cecomorphae*,[1] while through *Cariama* the *Grallae* point towards the birds of prey, and there is a strong and probably more than superficial likeness between this and the equally aberrant accipitrine secretary bird.

The gigantic birds of the genus *Phororhacos*, and their allies from the Miocene of Patagonia, are gralline birds related to *Cariama*, although some structural details seem to point towards the herons. They are distinguished by a large skull having a high, compressed, and sharply hooked beak, and by a small sternum and shoulder girdle; the pubis, save the anterior end, is lacking. The skull of the largest species, *Phororhacos longissimus*, was 0·6 m. long, and the cervical vertebrae 13 cm. across, far exceeding in their dimensions those of any other bird. Their structure suggests that they were cursorial birds of prey in their habits. These highly specialised forms are from the Santa Cruz beds of the Miocene of Patagonia. It is probable that *Diatryma* from New Mexico is related to these birds. A crane, *Palaeogrus*, occurs in the Eocene of Italy; and another, *Aletornis*, in the Eocene of Wyoming. A rail, *Gypsornis*, is found in the Eocene of Montmatre.

Order 4. CHENOMORPHAE.

The *Chenomorphae*, or ducks, after excluding one or two debatable species, form a sharply defined group of water-birds, whose skull is typically desmognathous, either by the direct fusion of the maxillo-palatines or their indirect union through the ossified narial septum. Low basipterygoid facettes are present, well forward on the sphenoid, and on these the pterygoids slide, allowing a slight motion of the beak. The posterior end of the mandible is produced and recurved.

The "outliers" of the *Chenomorphae* are three species of South American birds representing the genera *Palamedea* (or *Anhima*) and *Chauna*, which form either a separate order, sub-order, or superfamily, the *Palamedeae*. These birds have neither webbed feet nor duck-like bills, and bear a slight superficial resemblance to the fowls, although anatomical characters place them near the ducks.

The flamingoes form another debatable group, assigned by some to the

[1] That Beddard includes both gulls and plovers in his *Limicolae* may serve as an illustration of the slight variations among birds, and the extent to which individual opinion enters into the classifying of birds.

Chenomorphae, by others to the *Herodiones*, their affinities to both leading Huxley to place them in a separate group termed *Amphimorphae*. It may be that we have in the flamingoes the survivors of a group from which both the storks and ducks were derived, since the group is an old one and its range formerly much more extensive than at present. The earliest known member is *Scaniornis*, from the Cretaceous of Sweden, while the allied genus *Agnopterus* comes from the Eocene of the Paris Basin, and *Elornis* from the Eocene and Miocene. Several species of *Palaeolodus*, a shorter-legged bird than the flamingo, also occur in the Miocene of France, and a true *Phoenicopterus* in the Pliocene of Oregon and Miocene of France.

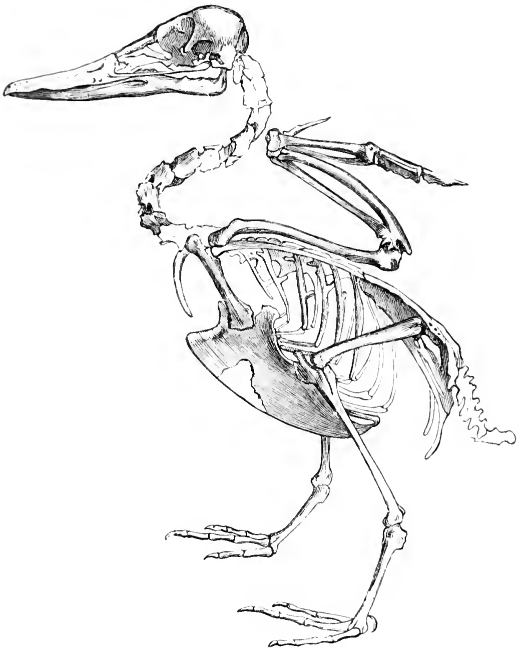


Fig. 373.

Anas blanchardi, Milne-Edw. Miocene; St. Gerand-le-Puy, France. Restoration of skeleton, 3/8 (after Milne-Edwards).

Gastornis, from the Eocene of Europe, is a large bird, placed at first with the ostriches, but more generally regarded as an aberrant member of the *Chenomorphae*. It is remarkable from the fact that the bones of the skull seem to have remained free from one another throughout life.

Ducks are not uncommon in the Miocene of France and Pliocene of Oregon, and a large, flightless species, *Cnemiornis calcitrans*, occurs in the Pleistocene of New Zealand. This bird well exemplifies some of the difficulties in the way of determining the exact affinities from isolated bones, since from the tibia Owen considered it to belong with the Moas, while from the sternum Parker believed it to be a rail; the discovery of the skull showed it to be unequivocally a goose. Numerous species of *Anas* (Fig. 373), as well as isolated representatives of *Anser*, *Cygnus*, *Fuligula*, *Spatula*, *Mergus*, and the like are known from the late Tertiary of various European localities.

Order 5. HERODII.

The *Herodii*, containing the herons, storks, and ibises, may be defined as wading birds with unusually long legs, having desmognathous skulls without basipterygoid processes, and (save for few exceptions) with the angle of the mandible truncate, the exceptions occurring in the spoonbills, *Platalea*.

The herons appear first in the Lower Eocene, *Proherodius* occurring in England, and *Gypsornis* and *Propelargus* from the Upper Eocene of France. An ibis, *Ibidopsis*, is found in the Upper Eocene of England, and *Ibidopodia* in the Lower Miocene of France, while from the same formation and locality comes *Leptoptilus*, now confined to warmer regions of Asia and Africa. From the Middle Miocene comes a true heron, *Ardea*, and above that the species represented are of existing genera. The flamingoes are discussed under the *Chenomorphae*.

Order 6. STEGANOPODES.

The *Steganopodes* include the pelicans, cormorants, gannets, frigate birds, and tropic birds, and form a fairly homogeneous group of birds with a desmognathous skull, a sternum with a feeble keel, on the forwardly produced anterior portion of which the lower ends of the clavicles rest and are frequently joined by anchylosis. A distinctive external feature is the union of all four toes by a web.

The desmognathism of this group, as indicated by the species that have been most carefully studied, is of a different nature from that of the *Accipitres*, being a secondary character acquired after the bird has been hatched, and due to the extension of ossification into the palatal region, which finally unites the various portions. In the cormorants, *Phalacrocoracidae*, and probably in the gannets, *Sulidae*, this is concomitant with the closing of the external nostrils, for the cormorants when hatched are schizognathous and holorhinal, and this condition lasts up to about the time they take to the water. The changes that occur are directly connected with the bird's habits, for the cormorants pursue their prey beneath the surface, while the gannets plunge down upon it from above. This absence of nostrils is associated with absence of the supraorbital glands, and this in turn with the lack of the depressions to contain them, which are such obvious characters in the skulls of aquatic birds with open nostrils, such as ducks, gulls, petrels, and penguins.

The *Steganopodes* seem to have differentiated early, for a cormorant, *Graculavus*, occurs in the Cretaceous of the United States. *Cyphornis magnus* is known from the Eocene of Vancouver, and *Prophaëthon shrubsolei* and *Odontopteryx toliapicus* from the London Clay, Lower Eocene. It is possible that this last may not belong to the order, although believed to be related to the gannets; it is distinguished by having the mandible armed with tooth-like projections. The genus *Phalacrocorax* ranges from the Eocene of Montmatre to the present, and other members of the order are found in the Miocene of Europe and Pliocene of the United States.

Order 7. OPISTHOCOMI.

The order *Opisthocomi* contains but a single species, the extraordinary hoactzin (*Opisthocomus cristatus*) of South America. The skull is schizognathous, without basipterygoid facettes. The sternum is widest posteriorly, and the keel is cut away in front, a peculiarity connected with the presence of a large crop; the furculum is anchylosed to the coracoids above and to the sternum below. In the nestling the thumb is large, clawed, and used in climbing, but in the adult it is clawless, and even smaller than in the majority of birds, being a remarkable instance of rapid retrogression. The hoactzin seems to have affinities with fowls, on the one hand, and the plantain-eaters, *Musophagi*, on the other, and is considered as a survival of a primitive type, a supposition that gathers strength from the presence of an allied form, *Filholornis*, in the Upper Eocene of Southern France.

Order 8. GALLINAE.

The *Gallinae* are birds having a typically schizognathous skull, the maxillo-palatines being (with rare exceptions) widely separated, the vomer sometimes absent, small and pointed when present; there are basipterygoid facettes on the sphenoid. The sternum is four-notched, very deeply cleft in the true fowls, and much less so in the curassows and Australian *Megapodes*, the other two groups included in the order. The probable affinities of the fowls with the tinamous have already been noticed; through the sand-grouse, *Pterocletes*, they are connected with the pigeons, *Columbae*, both of which are placed in orders by themselves, although the former is not here noted. Another order, *Hemipodii*, is usually made for the reception of the small birds of the genera *Coturnix* and *Pedionomus*, familiarly known as button quails or bush quails, and ranging from Spain to Australia.

A small, generalised form, *Gallinuloides*, nearly related to the existing *Ortalis*, but considered as representing a distinct family, has been described from the Green River Eocene of Wyoming, and true *Gallinae* of the genera *Palaeortyx*, *Taoperdix*, and *Tetrao* occur in the Upper Eocene of France. The genus *Phasianus*, not found native in Europe as an existing genus, occurs in the Miocene of France. *Coturnix* dates back to the Eocene, and *Columba* to the Lower Miocene of Europe.

Order 9. COLUMBAE.

The *Columbae*, or pigeons, have a schizognathous skull and schizorhinal nostrils, a point wherein they differ from fowls. The furculum is U-shaped and devoid of a hypocleidium, the sternum four-notched and normally with a deep keel, the pigeons as a rule being birds of powerful flight. The angle of the mandible is usually truncate, and the deltoid crest of the humerus produced into a point.

Remains of existing genera occur from the Miocene upwards in various parts of the world.

Order 10. ACCIPITRES.

The *Accipitres*, as here considered, contain the diurnal birds of prey, the owls, the American vultures, and the secretary bird, four very distinct groups. They have an imperfectly desmognathous skull, the spongy maxillo-palatines being only partly united with one another, and in some species even free. Basipterygoid facettes are absent in the diurnal birds of prey, but present in the other members of the order. The owls, or *Striges*, are thought to be related to the *Caprimulgi*, and are characterised by having the orbits facing forwards, and by the reversion of the outer toe, this last feature being possessed also by the somewhat exceptional and widely distributed osprey, *Pandion*.

The earliest known members of the order are *Lithornis* from the London Clay, Eocene, *Palaeocircus* from the Eocene of the Paris Basin, and *Bubo* from the Eocene of Wyoming. *Teracus*, *Palaeohierax*, and representatives of modern genera are found in the Miocene of France. *Gypogeranus* occurs in the Miocene of Africa, and *Palaeoborus*, a form allied to *Polyborus*, comes from the Pliocene of Mexico. *Harpagornis*, a bird much larger than any existing eagle, has been found in the Pleistocene of New Zealand.

Order 11. PSITTACI.

The *Psittaci*, parrots, have a desmognathous skull devoid of basipterygoid facettes, with the beak so hinged to the cranium as to permit considerable movement. The quadrate has a peculiar, long neck, and there are processes from the lachrymal, post-frontal, and squamosal, which in a number of species unite to form a suborbital bar, a feature not found in any other birds. The tarsus is short, the outer toe reversed.

Fossil parrots are rare, but the African genus *Psittacus* is found in the Lower Miocene of France.

Order 12. PICARIAE.

The *Picariae* comprise such a variety of forms that it has been termed the "avian waste-basket," while the limits of the group and its subdivisions are variously defined by different authors. The well-marked groups embraced under the term *Picariae*, and often, or usually, given the rank of orders, are as follows:—*Pici*, *Alcedines*, *Colii*, *Trogones*, *Coraciae*, *Bucerotes*, *Macrochires*, *Caprimulgi*, *Cuculi*, *Musophagi*.

That this is not a natural assemblage may be considered as evident from the fact that no diagnosis based on osteological characters alone can be framed to include all members, though a better agreement is to be found in the pterylosis and muscles. It may be regarded as a convenient grouping of heterogeneous forms, including many that have become specialised in some ways, while at the same time retaining other characters inherited from their ancestors, and distinguished by what they lack rather than what they possess.

The sternum is variable, but the manubrium is lacking, or small, and the posterior margin most often four-notched. The hypotarsus never contains the number of tendinal perforations found in the *Passeres*, and there are often peculiarities in the arrangement of the toes; thus some swifts and goatsuckers have the number of phalanges 2, 3, 3, 3; the woodpeckers, cuckoos, and toucans have the fourth toe reversed; in the colies the first toe may be turned forwards; and in the trogons the first and second toes are directed backwards. The *Pici*, characterised by a degenerate palatal structure, and the decurved end of the scapula, are united by Fürbringer to form his *Pico-Passeres*.

Through the plaintain-eaters, *Musophagi*, the *Picariae* seem to point to a distant connection with *Opisthocomus* and the fowls, while the *Caprimulgi* are considered as related to the owls, and through the generalised Asiatic tree-swifts, *Macropteryx*, from which we pass to the true swifts, *Micropodidae*, and thence to the humming-birds.

Uintornis, related to the woodpeckers, and *Cryptornis*, a relative of the hornbills, occur respectively in the Eocene of Wyoming and France. *Cypselus*, *Limnatornis*, a hoopoe, *Trogon*, and *Necrornis*, one of the *Musophagidae*, are from the Miocene of France, the last two hinting at a former more northerly extension of the African avifauna.

Order 13. PASSERES.

The order *Passeres* embraces about one-half, or, in round numbers, 6000 species of existing birds, mostly of small size, the raven being the giant of the order, widely distributed over the globe. The skull is aegithognathous;[1] the sternum bears a Y-shaped manubrium, and is deeply two-notched behind (*Conopophaga* and a few others are four-notched). The hypocleidium (interclavicle) is well developed save in *Menura* and *Atrichia*, and almost rests upon the anterior part of the sternal keel.

With the single exception of *Cholornis*, in which the fourth toe is a mere vestige, there are three toes in front and one behind; the hypotarsus is more highly specialised than in any other group, having four large tendinal perforations, and sometimes two smaller ones in addition; the typical number of presacral vertebrae is nineteen, fourteen of which are cervical, the Australian genus *Petroica* being exceptional in having thirteen. The skeletal variations in all this great group of birds are small, so small indeed that it is almost impossible to use them in making subdivisions, external differences, such as slight variations in the proportions of the toes and form of the beak being used for this purpose.

It is instructive to note that Huxley and Fürbringer, who used skeletal characters, made two families of the *Passeres*, while Sharpe, using external characters, makes forty-nine. The Australian lyre birds (*Menuridae*), however, form a distinct group, and so do the Asiatic broadbills (*Eurylaimidae*), as well as the American tyrant flycatchers (*Tyrannidae*), and their relatives; also the ant thrushes (*Formicariidae*), and their relatives. The order dates from the Eocene, *Palaeospiza*[2] coming from the Florissant Shales of Wyoming, and *Palaegithalus* and a starling (*Laurillardia*) from the Eocene of the Paris Basin. Above that horizon more occur, but the small size of most Passeres is a good reason for the lack of discovery, or lack of preservation, of many species.

In conclusion, it may be well to repeat that our knowledge of the phylogeny of the various groups of birds is very imperfect, and that most of the fossil forms are not only representatives of well-known families, but often belong to the same genera as species now living in the same geographic area in which the fossils occur. This is in marked contrast with what we find in the Mammalia, for not a family of these found in the Eocene, and few from the Miocene, are represented by living species.

From the fact that the majority of birds possess the power of flight they throw little light on the problems of former land connections and lines of distribution, although they may to some extent indicate climatic differences between the past and the present. There is a great gap between the birds of the Eocene and the toothed birds of the Cretaceous, and a greater one between these and the Jurassic *Archaeopteryx*, while the point at which birds diverged from reptiles, and put on their dress of feathers, is wholly unknown.

[The preceding chapter on *Aves* has been revised, and in large part rewritten by Mr. Frederic A. Lucas, of the United States National Museum at Washington, D.C.—EDITOR.]

[1] *Parker, W. K.*, On the Skull of Aegithognathous Birds (Trans. Zool. Soc. London, Part I. vol. IX. pp. 289-352; Part II. vol. X. pp. 251-314). 1873, 1878.

[2] This specimen seems to have been lost, but one is inclined to doubt from the figure that this bird is truly a passerine.

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[Names of genera regarded as synonyms are printed in *italics*, all others in Roman type.]

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