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OUTLINES OF

VERTEBRATE PALÆONTOLOGY

FOR STUDENTS OF ZOOLOGY

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VERTEBRATE PALÆONTOLOGY

FOR STUDENTS OF ZOOLOGY

BY

ARTHUR SMITH WOODWARD,

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PREFACE.

THE brief sketch of our present knowledge of extinct vertebrated animals attempted in this volume, is intended for students of Vertebrate Morphology and Zoology who are desirous of examining in detail the palæontological aspect of their subject. The advanced student has long appreciated the necessity for a more extended acquaintance with the facts of Embryology on completing his elementary course: he now begins to perceive that to understand the varied problems aright, he must also enter somewhat minutely into the past history of life on the globe as revealed by Palæontology. The latter task in most cases proves more difficult than the former, since the trained powers of observation needed for interpreting the remains of organisms embedded in rock are somewhat different from those acquired in the study of fresh tissues and organs. Moreover, much of the essential literature of the subject is contained in unfamiliar works and serials dealing chiefly with rocks and minerals. An elementary handbook, presenting only the broad outlines of this branch of biological enquiry, will thus perhaps be found useful as an introduction to more elaborate treatises and original memoirs, which are difficult to understand without some preliminary idea of general principles.

It is hoped that the plan adopted in the following pages will facilitate the comprehension of these general principles. The more important facts and generalizations are printed in large type; while the more technical and descriptive matter, which ought to be studied with specimens in a museum, is intercalated in paragraphs of small type. Each of these technical paragraphs deals with a typical genus which is comparatively well-known; and the description is not a generic diagnosis, but merely a statement of the principal facts already ascertained concerning the fossils on which our knowledge of the animal in question is based. Still further by way of encouraging, instead of supplanting personal observation, a large proportion of the illustrations are explanatory diagrams rather than drawings of actual fossils. The classification adopted is mainly that of the British Museum Catalogues of Fossil Vertebrata, with such slight modifications as the recent progress of research seems to necessitate; and the various sections are purposely treated at unequal length, those concerning which Palæontology affords little or no information being very briefly dismissed.

During the preparation of the work I have received much kind assistance from several friends and colleagues, to whom my best thanks are due. For the loan of numerous illustrations I am especially indebted to Dr Henry Woodward, Professor Gaudry, Professor Marsh, Professor Hermann Credner, Mr Lydekker, and the proprietors of *Natural Science.* My colleague Mr Anthony Gepp has also prepared some useful photographs. Most of the new illustrations have been drawn by Mr James Green; but for the originals of figs. 44, 65, and 74 I am indebted to Miss G. M. Woodward. Mr Boulenger has kindly read the chapters on Batrachia and Reptilia, Professor Marsh the section on Dinosauria, and Mr C. W. Andrews the chapter on Aves. Mr Lydekker has helped me not only personally but also by his numerous published writings, among which may be particularly mentioned his valuable and suggestive volume, "A Geographical History of Mammals." Dr Forsyth Major has also most kindly given me the benefit of his wide experience in the study of the Mammalia, by reading and annotating the whole of the proofs relating to this class. Finally, I am indebted to Mr Shipley for numerous valuable suggestions and continual help during the passing of the proofs for press.

Such generous co-operation has removed many errors which would otherwise have escaped unnoticed; and it is only necessary to add that for whatever imperfections remain I alone am responsible.

A. SMITH WOODWARD.

LONDON,
April 12, 1898.

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INTRODUCTION.

THE past history of the vertebrated animals as revealed by fossils is not merely a subject of absorbing interest in itself: it is also of prime importance in Biology from the possibilities it affords for elucidating some of the most fundamental principles in the evolution of life. Since these organisms represent the highest phase of development to which the animal kingdom has attained, they appear latest and become dominant latest in the geological series. The evolution of all except perhaps the larger groups, is thus contemporaneous with the deposition of the series of rocks which yield the most numerous and satisfactory fossils. Moreover, the skeleton of the Vertebrata is more intimately related to the soft parts than that of any of the lower forms of life; hence the greater value of such remains as can be fossilized in determining the precise nature of the original animals to which they belonged.

Order of Succession. The order in which the various divisions of the Vertebrata appear in geological time, according to present knowledge, depends entirely upon their degree of specialization, the simplest first, the more complex afterwards. The earliest organisms which seem to have possessed a notochord, occur in the Upper Silurian; and none of these ancient types hitherto discovered exhibit either a lower jaw or true paired limbs. Typical fishes appear first in the passage beds between the Upper Silurian and Lower Devonian, and become abundant in the latter formation. Batrachia begin to occur in the Lower Carboniferous, and are dominant in the Permian. Undoubted reptiles are found in the Lower Permian, but do not become dominant until the Triassic and Jurassic. Fragments either of mammals or of reptiles which approach the latter extremely closely, are met with in the Triassic, and there are undoubted small mammals in the Jurassic; but these are insignificant before the Tertiary period. Birds occur first in the Upper Jurassic, but both on this horizon and in the Cretaceous they retain conspicuous characters of their ancestry which have subsequently disappeared; they seem to have become dominant contemporaneously with the mammals at the beginning of the Tertiary period.

Range in Time. Gradual evolution—whether in the form of progression, retrogression, or differentiation—is usually observable even in the minor divisions when their range can be traced through the geological formations; and characters change more or less slowly in proportion to their magnitude. In all satisfactorily known instances, an order exhibits a longer geological range than any of its contained families; its family-types persist for a longer time than any of the genera grouped under them; while the genera themselves remain for a more extended period than the species. A highly specialized member of any division is also more liable to early extinction than its more generalized congeners, probably from its less adaptability to changes in the environment. An illustrative case may be cited. The order Ungulata (hoofed-mammals) is known to range from the very earliest Eocene strata to the present day; the family Equidæ (horses), as commonly understood, arises in the Upper Miocene; the typical species of the surviving genus *Equus* appear first in the Lower Pliocene. One genus of this family (*Hipparion*), with highly complex teeth, was restricted in its range to the Upper Miocene and Lower Pliocene periods, while another (*Hippidium*), with much specialized nasal region, had only a brief existence in South America; whereas *Equus* itself with more normal teeth and rostrum has survived from the Lower Pliocene to the present day. In like manner, the highly specialized rhinoceros, *Elasmotherium* (Pleistocene of Russia), had a very limited range in time and space compared with its more ordinary allies.

Persistent Types. There are a few noteworthy exceptions to the common rule last mentioned, which still await explanation. These are generally referred to as "persistent types." There is one remarkable, highly specialized family of Crossopterygian fishes, the Cœlacanthidæ, ranging from the base of the Carboniferous to the top of the Crétaceous with scarcely any modifications which can be regarded even as denoting change in the genera representing it (see p. 78). The case of the Tapirs ranging practically unaltered from the early Miocene to the present day, is also a striking illustration (see p. 321).

Imperfection of the Geological Record. The difficulties in ascertaining and interpreting the facts of Palæontology are, of course, greatly enhanced by the imperfection of the geological record on which we depend. Every item of knowledge acquired may indeed be literally described as owing to a chapter of accidents. Firstly, the organism must find its way into water where sediment is being deposited and there escape all the dangers of being eaten; or it must be accidentally entombed in blown sand or a volcanic accumulation on land. Secondly, this sediment, if it eventually happens to enter into the composition of a land area, must escape the all-prevalent denudation (or destruction and removal by atmospheric and aqueous agencies) continually in progress. Thirdly, the skeleton of the buried organism must resist the solvent action of any waters which may percolate through the rock. Lastly, man must accidentally excavate at the precise spot where entombment took place, and someone must be at hand capable of appreciating the fossil and preserving it for study when discovered. Having due regard to the doctrine of chances, the palæontologist will thus not be surprised to learn, for example, that the Lower Devonian chordate animal *Palæospondylus*, the unique representative of its group at present known, has hitherto been found only in one stratum of flagstone a few inches thick in one quarry in Caithness (see p. 3); that *Archæopteryx*, perhaps the most precious of Jurassic vertebrates, is known only by two specimens and a feather from the lithographic stone quarries of Bavaria which have been worked from time immemorial (see p. 232); and that the sole known evidence of a Pleistocene monkey in Britain is a detached molar tooth from one of the brick-fields near Grays, Essex. Furthermore, it must be remembered that in every region the series of strata contains only a very discontinuous record of its successive faunas and floras. When a region is a land area, as a rule, no deposit capable of preservation for long periods can accumulate, and the characters of its life can only be inferred from fossils which have been entombed in sediments apparently of the period in question elsewhere. When the region happens to be covered with comparatively deep water, the sediments will contain scarcely any but aquatic organisms, rarely yielding a trace of the life on the nearest land.

Definite Direction of Evolution. Under such circumstances it can be readily understood, that the time has not yet arrived for deducing general laws from the data of Palæontology. In fact, our knowledge of the evolution even of the Vertebrata is most casual and fragmentary in character. Nevertheless, sufficient is known to indicate that changes in the vertebrate skeleton have taken place in a certain definite and irreversible order; and the relative age of two skeletons of the same type of animal of widely different periods can readily be determined at a glance by an expert. For example, among the early Palæozoic fishes there are many heavily armoured forms with very little ossification in the endoskeleton and only incipient vertebral centra. The endoskeleton does not begin to ossify to any noteworthy extent until the exoskeleton atrophies; eventually at a later period the bony endoskeleton is the all-important part of the framework. Now, it so happens that in certain Mesozoic Pycnodont fishes (*Mesturus*) and the Tertiary coffer-fishes (Ostraciontidæ), the rigid dermal armour is again acquired; but it is apparently contrary to law for the endoskeleton to revert to its primitive state as observed in the Palæozoic fishes just mentioned—the parts of the axial skeleton simply become rigidly fixed and are nearly as well ossified as in the unarmoured contemporaries and relatives. When the vertebral centra have once become fully formed, indeed, they never degenerate to allow the unconstricted notochord to persist again. To take another example, the lobate fins with endoskeletal supports in the earliest fishes always appear to tend towards atrophy, while the dermal rays surrounding them become stouter; and when the endoskeletal base of the fin has been reduced to one small row of elements, these never multiply again—even the lobe of the great pectoral fin of the modern angler-fish (*Lophius*) is formed solely by the elongation of two of these little elements. The same phenomenon is observed among mammals; the number of digits may be reduced even to one, but when any reduction has taken place the original pentadactylism is never restored. Finally, in the case of all vertebrates, the teeth tend to degenerate; first the supply of successional teeth is stopped, then the one "permanent" set disappears—and when either of these phases of degeneration is accomplished, the original state is never recovered.

Specialization. It is thus evident that among animals there are certain definite and irreversible lines of progression, and other equally definite and irreversible lines of degeneration. At the same time the Palæontology of the Vertebrata shows most clearly that, on the whole, the evolution of these organisms has proceeded from the general to the special, while in every successive period of the earth's history some group has risen to a higher position in the zoological scale than any previously attained. This phenomenon has already been mentioned in recounting the order of succession of the various classes (p. xvii).

Expression Points. All known facts appear to suggest that the processes of evolution have not operated in a gradual and uniform manner, but that there has been a certain amount of rhythm in the course. A dominant old race at the beginning of its greatest vigour seems to give origin to a new type showing some fundamental change; this advanced form then seems to be driven from all the areas where the dominant ancestral race reigns supreme and evolution in the latter becomes comparatively insignificant. Meanwhile the banished type has acquired great developmental energy, and finally it spreads over every habitable region, replacing the effete race which originally produced it. Another "expression point" (to use Cope's apt term) is thus reached, and the phenomenon is repeated. The actinopterygian fishes furnish an interesting illustration. The earliest known member of this order (*Cheirolepis*) appears as an insignificant item in the Lower Devonian fauna, where crossopterygian and dipnoan fishes are dominant. When the latter begin to decline in the Lower Carboniferous, the sub-order to which *Cheirolepis* belongs (Chondrostei) suddenly appears in overwhelming variety. By the period of the Upper Permian another fundamental advance has taken place—the Protospondyli have arisen; but only a solitary genus is observed among the hosts of the dominant race. In the Trias the new type becomes supreme, and at the same time the next higher sub-order, that of the Isospondyli, begins to appear. This lingers on in the midst of the dominant Protospondyli during the Jurassic period, and then in the Cretaceous this and still higher sub-orders suddenly replace the earlier types and inaugurate a race which has subsequently changed only to an insignificant extent. The Mammalia afford another illustration of the same phenomenon. The reptilian class shows the closest approximation to that of the Mammalia at the dawn of the Mesozoic epoch, when it is just beginning to replace the older Batrachia. In rocks of this age on all four continents—Europe, Asia, Africa, and America—there are numerous remains of the mammal-like Anomodontia (as they are termed, p. 144). Afterwards, not a trace of these "missing links" is known; and, with the exception of the insignificant small jaws of possible Prototheria and Metatheria in the Jurassic and Cretaceous of England and North America, mammals do not appear either in Europe, Africa, or North and South America until the base of the Eocene, when they suddenly become dominant and are already differentiated.

Parallelism in Evolution. As nothing is yet known of the supposed refuges to which the incipient new races have betaken themselves to differentiate and acquire vital energy, we can merely assume them as a tentative hypothesis. But even when the facts are abundantly manifest, it is often difficult to settle the most elementary questions by direct reference to them. The problem of parallelism in evolution is one of these. It is necessary to determine whether the same animal can be evolved simultaneously in more than one region from distinct series of ancestors. Are the pumas and jaguars of America, for example, wandering cousins of the lions and leopards of the Old World, or have they been evolved on the other side of the globe through a distinct set of carnivorous ancestors? The case of the horses is often cited as suggesting that such a parallelism in evolution may have occurred; because the series of ancestral horses traced through the Tertiary strata of Europe is closely similar to, but not quite identical with the ancestral series found in the same order in the corresponding rocks of North America. Here the facts are tolerably well-known, but they admit of more than one interpretation. An easy land-connection between Europe and North America, throughout the Tertiary period, if allowed by geological considerations, might account for the phenomena observed even if all the horse-like animals were evolved from one stock in one and the same area.

Theory of Recapitulation. There is also the well-known and widely-accepted principle that the stages in the development of an individual organism at the present day repeat in a general manner the successive phases through which the ancestors of that organism have passed in former periods of the earth's history. There is no doubt, for example, that in the course of its individual development the homocercal tail of a modern bony fish passes through the same stages as those successively exhibited by the majority of the adult fishes at the different geological epochs. It is also evident that the family of deer (Cervidæ) has gradually acquired complex antlers in precisely the same manner as every modern stag acquires them during the course of its individual life. Again, the "cloven foot" of the existing ruminant appears in the embryo with separated metapodial bones, like those of the adult ancestral ruminants. It is also tolerably certain (though fossils have not yet provided absolute demonstration) that the rudimentary teeth and hind limbs of the existing whalebone whales (Mystacoceti) are inherited from functionally toothed quadrupedal ancestors. Embryology, however, cannot afford much precise information concerning these processes of evolution, because an embryo usually exists under physiological conditions totally distinct from those influencing an adult. The embryo exhibits features derived from its ancestors (*palingenetic* characters) inextricably mingled with features due to the peculiar circumstances under which it develops (*cœnogenetic* characters). In most cases it has hitherto been impossible to distinguish these two sets of characters satisfactorily; and a final appeal must thus be made to Palæontology, notwithstanding its imperfections, to determine the laws by which evolution proceeds.

Origin of the Vertebrata. Perhaps the most disappointing element in palæontological results thus far, is the lack of all information concerning the origin of the great sub-kingdoms or phyla of animals. Even in what might appear to be the most promising case, namely, that of the Vertebrata, there are no known facts distinctly favouring any of the rival theories concerning their origin based on embryology. Possibly all the earliest types were destitute of hard parts and thus incapable of fossilization. In any case, the oldest Ostracoderms (p. 3) from the Upper Silurian and Lower Devonian, sometimes claimed as the immediate allies of the Crustacean or Arachnid Merostomata of the same period, are fundamentally different from the latter in every character which admits of detailed comparison; they are to be regarded merely as an interesting example of mimetic resemblance between organisms of two different grades adapted to live in the same way and under precisely similar conditions.

ERRATUM.

Page 36, lines 5—7. Dr Traquair points out to the author that the appendages of the gill-arches of the Acanthodians are fixed upon their anterior or concave border, and thus cannot be interpreted as in the text.

CLASS AGNATHA.

Sub-Classes.	*Orders.*
1. **Cyclostomi.**	1. *Hyperoartia.*
	2. *Hyperotreti.*
	3. Cycliæ.
2. **Ostracodermi.**	1. Heterostraci. Anaspida
	2. Osteostraci.
	3. Antiarchi.

It is generally admitted that the existing Cyclostomes or Marsipobranchs are the degenerate representatives of a Class which must have attained a much more extensive development at some remote period; but the only known fossils as yet capable of being referred to such a Class have been obtained from the Upper Silurian and the Devonian rocks. Even these are quite of a problematical character; but as none of them have hitherto exhibited certain traces either of a lower jaw or paired limbs, they may be conveniently ascribed to this lowly group for the present. One of them seems to be clearly monorhinal, though with a calcified endoskeleton; all the others possess a strong dermal armour, without any calcification of the endoskeletal parts. It is probable that no member of the Class with hard structures capable of fossilization has existed since Palæozoic times.

Sub-Class 1. **Cyclostomi.**

The minute denticles known as **Conodonts,** met with in Palæozoic rocks from the Lower Silurian to the Carboniferous Limestone inclusive, are frequently compared with the teeth of the modern lampreys and hag-fishes. Their histological structure, however; is so different from that of any teeth known, that their affinities are quite indeterminable. They are apparently formed of structureless concentric lamellæ, without any trace of vascular canals or capillaries; and the substance of the fossils is chiefly carbonate of lime. Some conodonts consist only of a single cusp, others of a series of cusps upon one base; and minute plates, ornamented on one side with tubercles, are sometimes found in association with them. They may even be the teeth of unknown Nudibranchs or Annelids, or the hooks of Cephalopods, and can thus be dismissed as fragments too inconclusive for consideration here.

Fig. 1.

Palæospondylus gunni; ventral aspect of head, lateral aspect of vertebral column, restored by R. H. Traquair, nearly twice nat. size.—L. Old Red Sandstone; Caithness. *a*, separate small lobe; *b*, anterior depression or fenestra; *c*, posterior depression or fenestra; *d.c.*, dorsal cirri; *l.c.*, long 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.

ORDER 3. CYCLIÆ.

Much more satisfactory are some small skeletons from the Lower Old Red Sandstone of Scotland, which make known an extinct order differing from the two existing orders in the remarkable degree of calcification of the skeleton. All the cartilages seem to have been calcified, and vertebral centra are represented by a series of broad rings in the notochordal sheath. The family of **Palæospondylidæ** (with naked, eel-shaped body, and supposed unpaired narial opening encircled by barbels) is represented by a single genus.

Palæospondylus (fig. 1). The general aspect of the skull, so far as recognizable, closely agrees with that of a recent lamprey, and there is no evidence of jaws or separate ossifications. When viewed from below (fig. 1) the basicranial cartilage is shown to be continuous, without fontanelles; and the skull terminates in front in a ring of calcified cirri (*d.c.*, *l.c.*, *v.c.*) surrounding a large bilaterally-symmetrical orifice (*n*), which seems best interpreted as that of an unpaired nasal organ. Behind the skull there extends backwards a pair of undetermined elongated cartilages (*x*), usually lying in the fossil parallel with the vertebral column. The vertebral rings are spaced in this (presumably the branchial) region, but throughout the rest of the axis they are closely apposed. There are short and stout neural spines in the abdominal region, but no ribs; the neural and hæmal spines in the caudal region are very slender, while the former are longer than the latter and distinctly bifurcate at the distal end. One known specimen has been supposed to exhibit faint indications of a series of fin-supports on either side of the vertebral column in the anterior abdominal region; but the precise nature of these appearances cannot yet be determined. A single species, *P. gunni*, is found in the Caithness Flagstones at Achanarras, near Thurso. The largest specimens are about 0·05 m. in length.

Sub-Class 2. **Ostracodermi** (or **Ostracophori**).

In their fossilized state none of these organisms exhibit the slightest trace of ordinary jaws, or a segmented axial skeleton in the trunk, or arches for the support of paired limbs. Median fins, however, are present. The head and trunk are invested with a dermal armour remarkable for the extent to which vascular spaces are developed in its middle layer. There is always a shield covering the dorsal aspect of the head, usually followed by a similar shield over the abdominal region; and opposed to the latter is a ventral armature which meets the dorsal plate at each side in an open suture. The dorsal armour is often fused into a continuous cephalothoracic shield; and the tail seems to have always remained flexible, either with or without a strong squamation.

The mouth must have been situated on the ventral aspect, with the nasal sac (or sacs) immediately in front; and in most cases it is evident that the gill-pouches opened outwardly into a covered space communicating with the exterior by a single hinder orifice. The position of the eyes is also always distinct, but the arrangement of the other soft parts can only be provisionally determined by inference. The impressions on the visceral aspect of the dorsal shield of *Cyathaspis* (fig. 2), however, are very suggestive in this connection. A small deep pit (*pin.*) between the eyes occupies the precise position that would have been held by the pineal body of a vertebrate brain, had such been present. Further back there is a pair of >-shaped impressions, such as might result from contact with ridges upon the auditory capsules, due to a great development of the semicircular canals, as in sharks. On either side, extending nearly as far forwards as the position of the orbits,

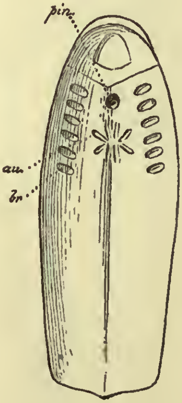

Fig. 2.

Cyathaspis sturi; natural mould from visceral face of dorsal shield, nat. size.—U. Silurian; Galicia. *au.*, supposed impressions of auditory organs; *br.*, impressions of branchial sacs; *pin.*, pit for pineal body. The eyes would be situated laterally near the extremities of the bent transverse line.

there occurs a regular series of small indentations, to the number of five or six, which suggest the original presence of well-separated gill-pouches; and these would have opened into an external chamber under the shield, with an outlet near the postero-lateral angle of the armour.

The simplest Ostracoderms (HETEROSTRACI) occur in the Upper Silurian and Lower Devonian, and exhibit no bone-cells in any part of their dermal armour; the second order (OSTEOSTRACI) is confined as a rule to the same horizons, though also rarely met with in the Upper Devonian; the third order (ANTIARCHI), with a complex of dermal plates and a remarkable pair of appendages, is essentially Devonian, and as abundant in the uppermost, as in the lowest strata. Nearly all the genera mimic in a curious manner the contemporaneous Eurypterids.

ORDER 1. HETEROSTRACI.

The structure of the hard shield in the Pteraspidians, or Heterostraci, is unique among the Chordata. Each plate consists of three superposed layers—an inner "nacreous" layer of lamellæ, a relatively thick middle zone of polygonal cancellæ, and an outer hard layer of vaso-dentine. Dermal sense-organs are well-developed and arranged in canals, which traverse the middle layer and open externally by a double series of pores. The dorsal shield comprises few pieces, firmly united in the adult; and the orbits are wide apart, being laterally placed. The ventral shield is in a single piece (named *Scaphaspis*). Paired appendages appear to be absent.

The only known family of Heterostraci is that of the **Pteraspidæ**, in which the external layer of each dermal plate forms an ornament of very fine, concentric, closely arranged ridges, parallel with the outer margin. The rostral region is relatively small. The scales of the caudal region, when present, are numerous and rhomboidal. Three genera are distinguished according to the complexity of the dorsal shield.

Cyathaspis (figs. 2, 3). Known only by the dorsal and ventral shields, which have sometimes been found in natural association. The dorsal shield (fig. 3) is oval, consisting of four separately calcified portions—a large central *disc* (*d*), with a short azygous *rostral plate* (*r*) anteriorly, and a pair of large *cornua* (*c*) on the sides. A rudiment of a median dorsal spine (*s*) also appears behind. The orbits are not completely enclosed in the shield, and notches for them are rarely seen. The markings on the visceral aspect of the shield are described above (p. 4, fig. 2). These fossils are always small, never more than about 0·05 m. in length, and form perhaps the earliest satisfactory evidence of chordate animals hitherto discovered. One species is recorded from the Wenlock Limestone of the Island of Gothland. The typical species, *Cyathaspis banksi*, occurs in the Ludlow Bone-bed and the Downton Sandstone of Herefordshire; while the ventral shield named *Pteraspis ludensis*, from the Lower Ludlow of Leintwardine, also probably belongs to this genus. Other species are met with in the Lower Old Red Sandstone of Herefordshire, and in the Upper Silurian of Galicia and New Brunswick. *Cyathaspis integer*, from a supposed Upper Silurian boulder found near Berlin, was the first species to exhibit the dorsal and ventral shields in association.

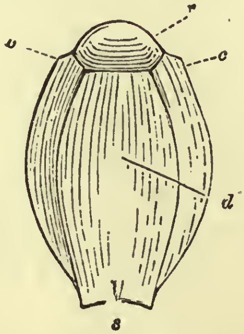

Fig. 3.

Cyathaspis banksi; diagram of dorsal shield, external aspect, slightly reduced. —U. Silurian; Herefordshire. *c*, cornua; *d*, median disc; *o*, position of orbit; *r*, rostral plate; *s*, posterior dorsal spine. (After Lankester.)

Palæaspis (Holaspis). A simple dorsal shield resembling that of *Pteraspis* in form, but only notched by the orbits, and without posterior spine. One species, *Palæaspis* (*Holaspis*) *sericea*, from the Lower Old Red Sandstone of Monmouthshire, beautifully displays the arrangement of the sensory canals. Another species, *P. americana*, occurs in the Upper Silurian (Onondaga Group) of Perry Co., Pennsylvania, and is known by associated dorsal and ventral shields.

Pteraspis (figs. 4—6). The only genus in which traces of the scaly caudal region have been observed. The dorsal shield (fig. 4) is arrow-head-shaped, and consists of seven separately calcified portions. There is a large central *disc* (*d*), with a triangular *rostral plate* (*r*) anteriorly

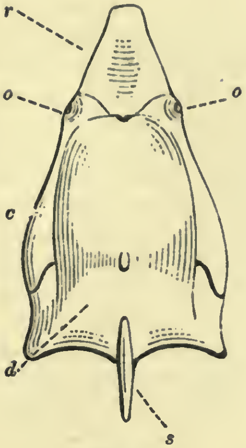

FIG. 4.

Pteraspis rostrata; diagram of dorsal shield, external aspect, about one-third nat. size.—L. Old Red Sandstone; Herefordshire district. *c*, cornua, with branchial cleft across hinder portion; *d*, median disc; *o*, orbit, surrounded by small orbital plate; *r*, rostral plate; *s*, posterior dorsal spine fixed in cleft of median disc. (After Lankester.)

FIG. 5.

Pteraspis crouchi; imperfect dorsal shield (median disc), with most of the external layer destroyed, exhibiting the sensory canals infiltrated by dark mineral matter, nat. size.—L. Old Red Sandstone; Herefordshire.

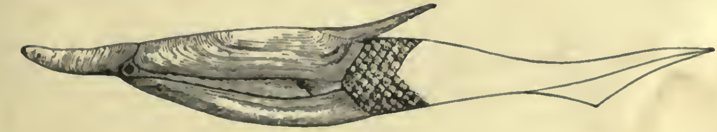

FIG. 6.

Pteraspis rostrata; restoration, lateral aspect, about one-third nat. size.—L. Old Red Sandstone; Herefordshire district. (From *Brit. Mus. Catal.*)

and a large median *dorsal spine* (*s*) posteriorly; a pair of *orbital plates* occurs, one completely surrounding the orbit (*o*) on either side and partially inserted between the rostrum and central disc; and there is a pair of postero-lateral *cornua* (*c*), each pierced with a large (probably branchial) cleft or foramen. The typical species is *Pteraspis rostrata*, from the Lower Old Red Sandstone of Herefordshire, Monmouthshire, and Glamorganshire, and its shield sometimes measures about 0·14 m. in length. A single fragment in the British Museum shows parts of the dorsal and ventral shields in natural association, with a few small rhomboidal scales of the caudal region, which slightly overlap each other and are ornamented with few, delicate, imbricating ridges, parallel to the overlapped anterior margins. One specimen of a second species, *P. crouchi*, from the same formation, is important as showing the sensory canals infiltrated with manganese (fig. 5). The genus is also common in the Lower Devonian of Galicia, and species are recorded from Forfarshire and the Eifel.

ORDER 2. OSTEOSTRACI.

The dermal shield in this order also comprises three layers, but the middle vascular zone does not consist of cancellæ or spaces, being traversed instead by an abundant network of blood-vessels which subdivide the hard tissue into large polygonal areas in which no such vessels are conspicuous. The calcification both of this and the dense inner layer exhibits many bone-cells; the outer layer, which develops a tubercular ornament, consists of vascular dentine. There are no traces of dermal sense-organs either upon or within the shield. The dorsal shield consists of one principal piece, in which the orbits are placed close together mesially; but the vacuity between these, as also another median space immediately behind them, is closed by a separately-calcified small plate. There is also often a supplementary plate behind, which seems to consist of fused body-scales. A ventral plate opposes at least the latter. There are no paired appendages, except those apparently connected with respiration.

The **Cephalaspidæ** are the best-known family of Osteostraci, having the trunk completely covered with overlapping scales, which are much deepened on the flank. The dorsal shield is rounded or tapering in front, abruptly truncated behind, and the interorbital piece is firmly fixed. The median fins are small.

Cephalaspis (figs. 7—10). In this genus the body is elevated, triangular in transverse section, and none of the scales are fused into a plate behind the head-shield. An outline of the shield viewed from above is given in fig. 7. The postero-lateral angles are produced into short cornua (*p.c.*), and there is a more or less conspicuous median spine (*p.s.*). Each orbit has a surrounding rim (*o.r.*) extended in front into a small antorbital prominence (*a.p.*); and between the eyes is an elongated interorbital prominence (*i.p.*) evidently hollow, not improbably for the reception of a pineal body. Immediately in advance of this, on the visceral aspect of the shield, is a short, narrow, median longitudinal septum, between which and the antorbital prominences a pair of small antorbital fossæ (*a.f.*) are exposed when the substance of the shield is removed. Behind a transverse ridge or groove (*i.g.*) joining the posterior borders of the orbits, a large 'postorbital valley' (*p.o.v.*) is also conspicuous, and this is always filled by a plate different in texture from the rest of the shield. Inexplicable concavities immediately beneath the cranial roof near the rostrum are named "marginal cells" (*m.c.*); and when the fossil is so preserved as to show the contour of some of the originally soft parts, the cast of a pair of great rounded lobes, meeting in the

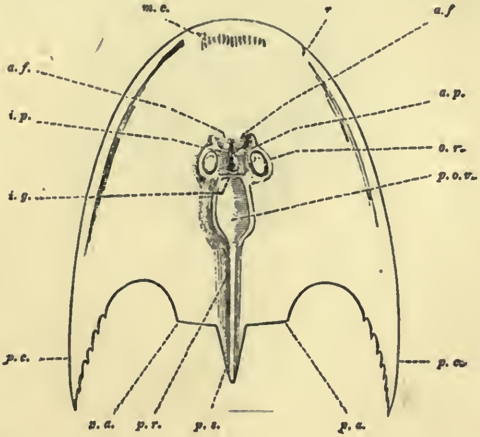

Fig. 7.

Cephalaspis lyelli; diagram of dorsal shield, about one-half nat. size.—L. Old Red Sandstone; Forfarshire, and Herefordshire district. *a.f.*, antorbital fossæ; *a.p.*, antorbital prominences; *i.g.*, interorbital ridge or groove; *i.p.*, interorbital prominence; *m.c.*, marginal cells; *o.r.*, orbital rim; *p.a.*, posterior angle; *p.c.*, posterior cornu; *p.o.v.*, postorbital depression, occupied by separate small plate; *p.r.*, posterior ridge; *p.s.*, posterior spine; *r*, rim. (After Lankester.)

middle line, is conspicuous in advance of the orbital region. As shown from beneath (fig. 8), the margin of the shield is reflexed inwards to form a flattened and ornamented inferior rim, wider behind than in front; and, as proved by transverse sections (fig. 9), the inner border of this rim is continued upwards into a delicate smooth lamina of calcified tissue (*i*), which lies beneath the outer or superior lamina (*s*) of the shield proper. At each postero-lateral angle of the shield, the middle

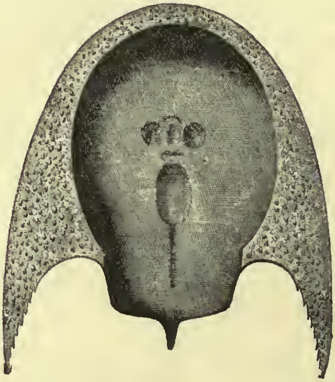

Fig. 8.

Cephalaspis; diagram of lower aspect of dorsal shield, showing inferior rim. (After Lankester.)

Fig. 9.

Cephalaspis; transverse section of dorsal shield. *i*, inferior lamina; *m*, margin; *s*, superior lamina. (After Lankester.)

vascular layer of its substance is continued backwards as a flexible flap, which is sometimes nearly half as long as the shield (fig. 10). This is probably related to the outlet for the water from the branchial chamber. Nothing is known of the endoskeleton. There is one small remote dorsal fin, and the tail is heterocercal; but no well-defined fin-rays can be observed, the supporting structures of the fin-membrane being small, oblong, calcified plates, closely fitted together, and placed end to end in vertical parallel series. The earliest known fragment of *Cephalaspis* was obtained from the Ludlow Tilestones, while fine examples of *C. murchisoni* (fig. 10) occur in the Passage Beds immediately below the Old Red Sandstone at

Ledbury, Herefordshire. The typical species *C. lyelli*, with well-developed cornua, is characteristic of the Lower Old Red Sandstone of Forfarshire. Other species are known from corresponding horizons in Caithness, Ayrshire, and New Brunswick; while one specimen is recorded from the Upper Devonian of Scaumenac Bay, P. Q., Canada. The largest known head-shield (*Cephalaspis magnifica*, from the Caithness flagstones) measures 0·22 m. in length.

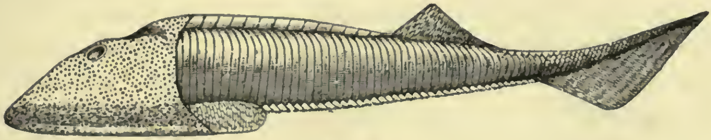

Fig. 10.

Cephalaspis murchisoni; restoration, lateral aspect, about one-half nat. size.—U. Silurian and L. Old Red Sandstone Passage Beds; Herefordshire. (From *Brit. Mus. Catal.*)

Auchenaspis (or *Thyestes*) comprises only small species, differing from *Cephalaspis* in their depressed form and in the fusion of some of the anterior body-scales with the head-shield. *A. salteri* occurs in the Ludlow Tile-stones, *A. egertoni* (fig. 11) in the Lower Old Red Sandstone Passage Beds of Ledbury, and *A. verrucosa* in the Upper Silurian of the Isle of Oesel, Baltic Sea. *Eukeraspis* is a name given to small shields from the Upper Ludlow and Downton Sandstone of Herefordshire, characterized by much-produced slender cornua.

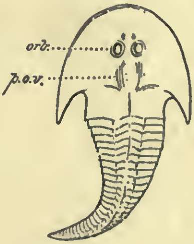

Fig. 11.

Auchenaspis egertoni; head and trunk, upper aspect, nat. size.—L. Old Red Sandstone Passage Beds; Herefordshire. *orb.*, orbits; *p.o.v.*, postorbital depression.

The **Tremataspidæ**, of which only the shield is certainly known, differ from the Cephalaspidæ in the circumstance, that their interorbital piece is loose and often lost in the fossils. *Tremataspis schrenki* and other species occur in the Upper Silurian of Oesel.

ORDER 3. ANTIARCHI.

The dermal skeleton of the Antiarchi is much more complex than that of the two preceding orders. The bone is dense, though with vascular cancellæ in the middle layer of the more thickened plates; the sensory canals traverse the armour along well-defined superficial grooves. The external ornament always consists of tubercles and coarse rugæ. A pair of armoured appendages, usually moveable, is fixed to the antero-lateral angle of the body-shield, which is always moveably articulated with the head-shield. A description of the best-known genera, *Pterichthys* and *Bothriolepis,* will serve to enumerate the principal features of the group.

Pterichthys (fig. 12). The whole of the armour is composed of overlapping plates, which exhibit a bilaterally-symmetrical arrangement. The cranial shield is small compared with the armour of the trunk, and is confined to the dorsal and lateral aspects. The eyes (*orb.*) are placed close together near the middle, and the quadrangular plate between them is loose. This plate is marked by a deep pit on its visceral aspect, perhaps for the reception of a pineal body, and is supplemented by another narrow element in front. A thin oval ossification in the position of each eye, appears to represent a partially hardened sclerotic. On either side of the head-shield there is a loose plate (*op.*), which seems to have formed an operculum, for its posterior margin was evidently free, while its anterior strongly convex margin is notched in such a manner as to suggest the ordinary articulation of a fish-operculum. Below the head-shield in front of the position which must have been occupied by the mouth, there is also a pair of loosely attached plates (*m.*), which meet in the middle line and are much broader than long. Each is notched at its postero-external angle, as if for the openings of a paired nasal organ. Though the head is moveably articulated with the trunk, there are no ginglymoid processes or surfaces. The body-armour surrounds the trunk completely and extends backwards for a very considerable distance, but does not include the anus. Its ventral surface is flattened, while the dorsal shield is much arched. Near their front extremity the ventrolateral plates are strengthened by a robust transverse ridge on the visceral aspect, and close to this the pectoral appendages are fixed by a most complex, ginglymoid articulation. Each appendage (*ap.*) is completely encased in closely-fitting plates and jointed once at about its middle (*j*); while a large orifice in the supporting articular facette bears witness to the passage of well-developed blood-vessels and nerves into its interior. Near the hinder end of the posterior ventro-lateral plates there is a distinct constriction with another inner transverse thickening, which seems to mark the termination of the abdominal cavity. The tail is comparatively small, covered with imbricating rounded or hexagonal scales, with a series of large azygous ridge-scales on the dorsal aspect.

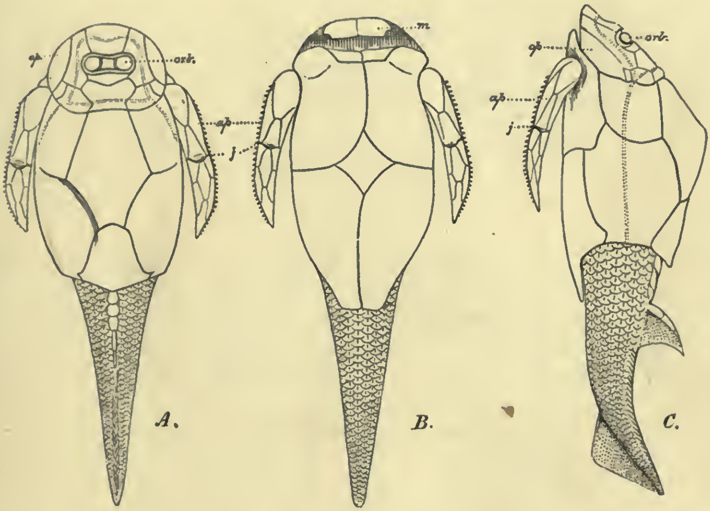

Fig. 12.

Pterichthys milleri (*testudinarius*); restoration by R. H. Traquair, from the dorsal (*A*), ventral (*B*), and lateral (*C*) aspects, about one-half nat. size.—L. Old Red Sandstone; Scotland. *ap.*, pair of lateral appendages; *j*, joint in appendage; *m.*, supposed upper jaw, with notches for narial openings; *op.*, operculum; *orb.*; orbits; double dotted lines indicating grooves for sensory canal. (For names of dorsal and lateral plates, see lettering of figs. 13 and 15.)

The ridge-scales are soon interrupted by a small triangular dorsal fin, which is membranous and only stiffened on its front margin by one, two, or perhaps three bent scales; behind the fin they are very deeply imbricating to the end of the tail, which is somewhat upturned, and is bordered below by a large membranous caudal fin of uncertain shape. The finest specimens of *Pterichthys* are obtained from the Lower Old Red Sandstone of Scotland, but the genus also occurs in the Eifel, Germany. The largest known example is about 0·16 m. in length.

Bothriolepis (figs. 13—15). An Upper Devonian genus differing from *Pterichthys* in its larger appendages and in minor points relating to the proportions of the plates and the arrangement of the sensory canals. The tail also appears to have been scaleless, no undoubted traces of this part of the body having hitherto been discovered. The great interest of the genus, however, consists in the arrangement of its mouth-parts, discovered in the fine examples of *B. canadensis* from Scaumenac Bay, Canada. Beneath the head-shield at its front extremity (fig. 14) there is observed a pair of transversely elongated plates much resembling those of *Pterichthys*, but not so extensively in contact at the median symphysis. These are in contact with the edge of the dorsal shield in front, but their posterior border is free and convexly arched. A notch at each outer margin, as before, may indicate the opening of a nasal sac. The greater part of the outer face of each plate is feebly rugose and marked by a

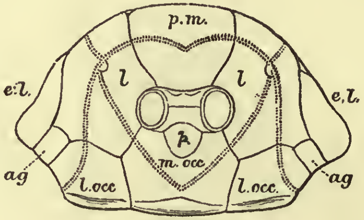

Fig. 13.

Bothriolepis canadensis; diagram of head-shield, upper aspect, about one-half nat. size.—U. Devonian; Scaumenac Bay, Canada. *ag.*, angular; *e.l.*, extra-lateral (operculum); *l*, lateral; *l.occ.*, lateral occipital; *m.occ.*, median occipital; *p*, postmedian; *p.m.*, premedian; double dotted lines indicating grooves for sensory canal. (After Traquair.)

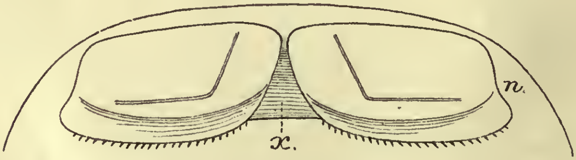

Fig. 14.

Bothriolepis canadensis; inferior aspect of head, showing supposed upper jaw-plates, nat. size.—U. Devonian; Scaumenac Bay, Canada. *n*, lateral notch, possibly for narial opening; *x*, smooth delicate lamina of bone; bent double line indicating groove for sensory canal. (From specimens in British Museum, nos. P. 6761—62.)

sharply bent sensory canal; but there is a conspicuous smooth band immediately adjoining the posterior border, and this is further remarkable for exhibiting an irregular series of minute sharp denticles different in aspect from the bosses and points of the ordinary surface-ornament. It appears, indeed, as if this pair of plates formed the anterior margin of the mouth, covered with an overlapping lip of soft tissue and provided with a minute denticulation. It may be added that a very thin lamina of smooth bone of uncertain size and form occurs on the visceral aspect of this pair of jaw-plates, and its straight hinder margin is indicated in the accompanying fig. 14. The typical species of *Bothriolepis* is *B. ornata*, known only by fragments from the Upper Devonian of N.W. Russia. Fragments of other large species occur in Scotland, while two comparatively dwarfed forms are met with at Dura Den, Fifeshire (*B. hydrophila*, fig. 15), and at Farlow, Shropshire (*B. macrocephala*). The finest known specimens, about 0·2 m. in length, are those of *B. canadensis* (figs. 13, 14), to which special reference has been made.

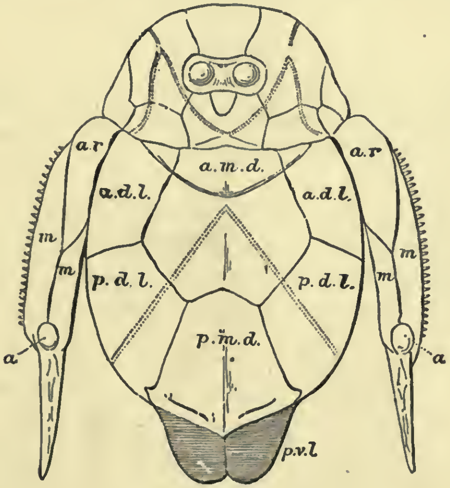

FIG. 15.

Bothriolepis hydrophila; restoration by R. H. Traquair, dorsal aspect, nat. size.—U. Old Red Sandstone; Dura Den, Fifeshire. *a*, anconeal plate; *a.m.d.*, anterior median dorsal; *a.d.l.*, anterior dorso-lateral; *ar.*, articular; *m*, marginal; *p.d.l.*, posterior dorso-lateral; *p.m.d.*, posterior median dorsal; *p.v.l.*, posterior ventro-lateral; double dotted line indicating grooves for sensory canal.

Asterolepis is a genus closely resembling *Pterichthys* and *Bothriolepis*, known only by fragments from the Upper Old Red Sandstone of Scotland and Livonia.

A remarkable fossil from the Lower Devonian of Spitzbergen, named *Acanthaspis decipiens*, has a dermal armour resembling that of the Antiarchi in minute structure, and a ventral plastron quite similar to that of the latter. The lateral appendages, however, instead of being complex and moveable, are simple and fixed. As shown in the accompanying diagram (fig. 16), the hollow plate forming this appendage on each side is firmly fixed to a lateral prominence of the body armour. It is, in fact, merely a fixed spine. The paired appendages of the Antiarchi are therefore very probably not homologous with those of the Class Pisces.

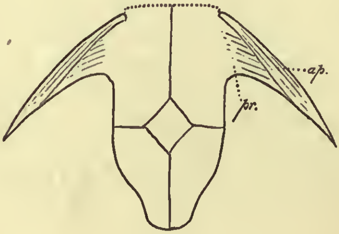

Fig. 16.

Acanthaspis decipiens; diagram of body-shield, ventral aspect, less than half nat. size.—L. Devonian; Spitzbergen. *ap.*, lateral appendage in form of spine; *pr.*, process supporting appendage.

CLASS PISCES.

Sub-Classes.	*Orders.*	*Sub-Orders.*
1. **Elasmobranchii.**	1. Pleuropterygii.	
	2. Ichthyotomi.	
	3. Acanthodii.	
	4. Selachii	1. Asterospondyli.
		2. Tectospondyli.
2. **Holocephali.**	1. Chimæroidei.	
3. **Dipnoi.**	1. Sirenoidei.	
	2. Arthrodira.	
4. **Teleostomi.**	1. Crossopterygii	1. Haplistia.
		2. Rhipidistia.
		3. Actinistia.
		4. *Cladistia.*
	2. Actinopterygii	1. Chondrostei
		2. Protospondyli.
		3. Aetheospondyli.
		4. Isospondyli.
		&c. &c.

Among the fishes existing at the present day there may be observed two distinct plans of cranial structure, between which no definitely intermediate conditions can be recognized. In *Chimæra*, *Protopterus*, *Ceratodus*, and their allies, the upper segment of the mandibular arch is directly fused with the chondrocranium, while the corresponding segment of the hyoid arch is atrophied or absent; in the Elasmobranchs and the so-called "Ganoidei" and "Teleostei," the same elements are loosely articulated with the chondrocranium, the upper segment of the hyoid arch forming a moveable suspensorium. The first condition is now commonly known as the *autostylic*, and the second as the *hyostylic*; the former attaining its highest phase of development as fishes pass into batrachians, and the latter as the Palæozoic forerunners of the typical modern fishes reach the high degree of specialization observable in certain groups of the existing fauna.

Again, by the nature of the exoskeleton two groups both of the autostylic, and of the hyostylic fishes, can also be distinguished. Some families exhibit mere "placoid" dermal calcifications, traversed by delicate branching nutritive canals, these isolated plates never uniting even in the region of the branchial apparatus to form any covering of the clefts; other families are well encased in dermal and membrane bones, which have a definite symmetrical arrangement, and consist, at least in their basal layer, of tissue with distinct bone-cells, which are often disposed in haversian systems. Among autostylic fishes, the Chimæroids are thus readily separated from the Dipnoans; while among hyostylic fishes, the Elasmobranchs are sharply defined from the Teleostomes (to use Owen's term for "Ganoidei" + "Teleostei").

The Class Pisces may thus be divided into the four sub-classes of Elasmobranchii, Holocephali, Dipnoi, and Teleostomi; and this is the only arrangement hitherto proposed which is in full accord with the known facts of Palæontology. If the common ancestors of all the four sub-classes could be found, they would of course fall under the Elasmobranchii as here defined; and it may be that some of the early Palæozoic sharks already known bear an ancestral relation to more than the sub-class to which they technically belong. Moreover, there still remains some doubt as to how far certain Devonian Crossopterygii (Holoptychiidæ) constitute a link between the primitive Teleostomi and Dipnoi; while there are a few Holocephali of Jurassic age which make at least a slight approach to the Elasmobranchii in the nature of their dentition. Speaking generally, however, it may be said that since the beginning of Devonian times the four sub-classes in question have followed distinct courses of development. The very earliest known assemblage of undoubted fishes, presents well-characterized examples of each of the four types (assuming that Chimæroids can be determined from the evidence of detached teeth); and, if the evolution of the paired fins is correctly represented by the hypothesis that at present seems most plausible, the

Elasmobranchii and the Dipnoi certainly attained their maximum of specialization before the end of the Palæozoic Epoch.

The doctrine of the evolution of fins, resulting from the combined researches of embryologists and palæontologists, may, indeed, now almost rank as a demonstrated principle. Briefly summarized, it resolves itself into the following four propositions:—

(1) Fishes originally possessed (*a*) a continuous median dermal fold, and (*b*) a pair of continuous lateral folds, each supported by a regular series of parallel endoskeletal rods diverging from the axial skeleton.

(2) These continuous folds (the median in most cases and the lateral fold always) soon became subdivided, with a concomitant reduction in the size and number of their supports.

(3) Gradual and constant specialization has been marked by the shortening-up of the endoskeletal supports of the resulting fins, and by the concomitant strengthening of the dermal rays.

(4) In the course of this evolution the endoskeletal fin-supports have eventually lost all direct connection and correlation with the axial skeleton, those of the dorsal and anal median fins becoming correlated instead with the dermal rays, each supporting one of these rays.

It is necessary to illustrate this doctrine by the few known facts of Palæontology bearing upon the subject; for it will appear later that the only criterion at present available for determining the ordinal position of any fish in its sub-class, is afforded by the degree of specialization of its paired fins. Just as the various modifications of the pentadactyl limb in the Ungulate Mammals—the vertebrates which eventually become most completely adapted for progression on land—afford the principal means of determining the natural subdivision of the order; so among the greater groups of fishes—the vertebrates that become specially adapted for progression in water—the successive modifications of the primitive fin-folds form the most obvious clue to the phases through which the various types have passed in the course of their specialization.

To begin, then, with the median fins, reference may be made first to the earliest clearly decipherable example of an Elasmobranch median fin shown in the accompanying illustration (fig. 17). It belongs to the genus *Pleuracanthus*, of Carboniferous and Permian age. To refer to the dorsal, it will be observed that the fin-fold itself is stiffened by numerous filiform dermal rays, and is supported by a series of parallel vertical rods of cartilage, each segmented into three pieces. The outer short piece is within the fin-membrane; the other pieces are within the body between the muscles, and the outer (distal) element is termed a *baseost*, the inner (proximal) element an *axonost*. In the caudal region these supports are equal in number to the neural spines and directly apposed to the latter; while in the abdominal region they are exactly twice as numerous, and instances are supposed to occur in which each neural spine is bifurcated to meet the extremities of the two fin-supports corresponding with it. The same direct

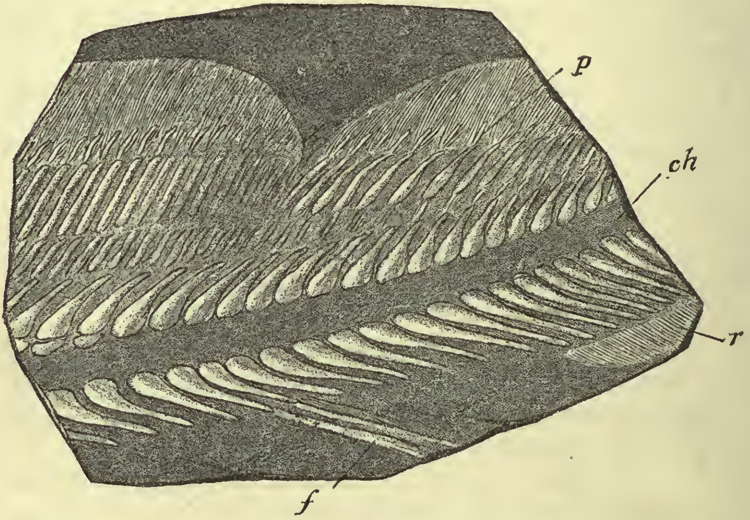

FIG. 17.

Pleuracanthus (*Xenacanthus*) *decheni*; portion of caudal region, about nat. size. —L. Permian; Bohemia. *ch.*, position of the notochord, bounded by neural and hæmal arches; *f*, anal fin; *p*, *r*, dorsal and ventral portions of caudal fin. (After A. Fritsch.)

relation between the endoskeleton of the dorsal fin and the neural arches is shown in the primitive genus *Coccosteus* (p. 67, fig. 52); and it is likely that this relation would also be observed in *Cladoselache* (p. 30) if the axial skeleton of that fish were known. On the other hand in *Pleuracanthus*, the fin-supports bear no numerical relation to the filiform dermal rays (*actinotrichia*) stiffening the fin-membrane; except that occasionally the latter are grouped in bundles round the extremities of the supports.

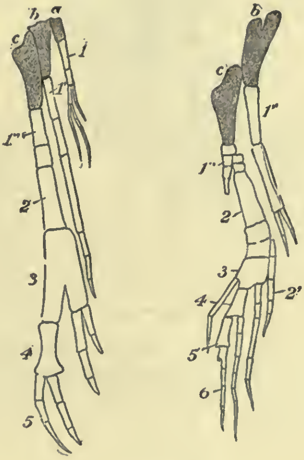

FIG. 18.

Pleuracanthus (*Xenacanthus*) *decheni;* skeleton of anal fins, about nat. size.—L. Permian; Bohemia. *a*, *b*, *c*, hæmal arches of vertebral axis; the successive segments numbered. Right border preaxial, left border postaxial. (After A. Fritsch.)

The severance of two small anal fins from the dorso-caudal membrane in *Pleuracanthus* adds further interesting information in reference to the process by which this membrane becomes subdivided. The endoskeleton of these fins is carefully drawn in fig. 18. The supports of the anterior anal are connected only with two hæmal arches (*b*, *c*), and the preaxial one (1′) is comparatively simple, differing from an ordinary support merely in the duplication and transverse articulation of the distal element. The postaxial support (1″) is remarkably complex and must evidently be regarded as a cluster of primitive supports, brought together by growth-pressure from before and behind, and exhibiting irregular transverse articulations as the result. The same kind of crowding of the endoskeletal supports is observed in the posterior dorsal fin of the Crossopterygian *Holoptychius* (fig. 19), where the basal portions (axonosts) of no

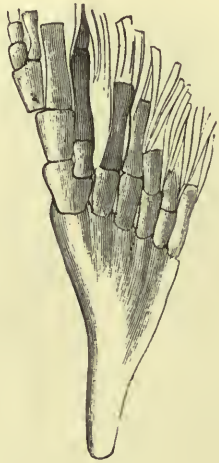

FIG. 19.

Holoptychius (*Glyptolepis*) *leptopterus;* basal cartilages of posterior dorsal fin, with some fin-rays overlapping distally, nat. size.—L. Old Red Sandstone; N. Scotland. (From *Brit. Mus. Catal.*)

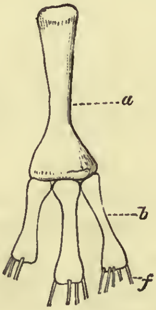

FIG. 20.

Scaumenacia curta; basal cartilages of anal fin, nat. size.—U. Devonian; Scaumenac Bay, Canada. *a*, axonost; *b*, baseosts; *f*, bases of fin-rays.

less than seven supports are fused into one mass, and remnants of a still greater number are clustered together distally. The process is again observed to some extent in the anal fin of the Dipnoan *Scaumenacia* (fig. 20). In the Cœlacanthidæ (fig. 60, p. 80) the distal cartilages (baseosts) of the hinder dorsal fin are too little calcified to be preserved, while those of the anterior dorsal fin have entirely disappeared and the dermal rays are in direct contact with the compound triangular base (axonost). The Cœlacanths are certainly a more specialized group than the Holoptychiidæ and are all of later date; hence, since the type of dorsal fin they exhibit has never been found among the Crossopterygian contemporaries of the Holoptychiidæ, it is evident that crowding and fusion of the supports take place first, shortening next. Parenthetically, it may be added that when subdivision of the dorsal fin occurs in this manner, it invariably results in two small fins, never more or less.

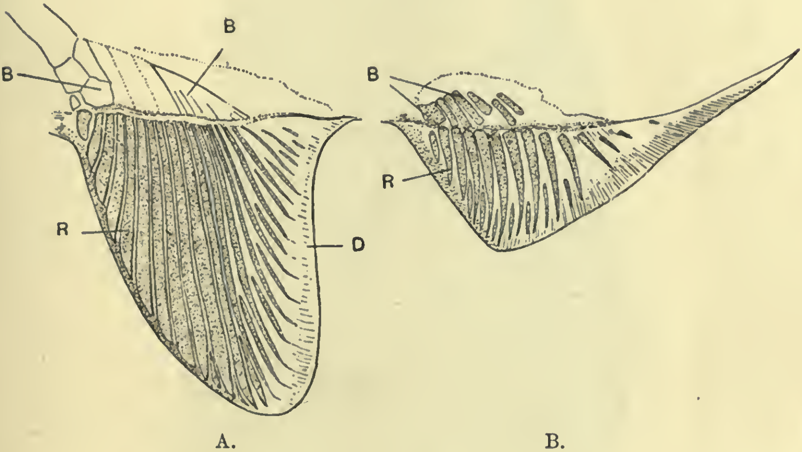

Fig. 21.

Cladoselache; pectoral (A) and pelvic (B) fins, one-half nat. size.—U. Devonian; Ohio. B, basal cartilages within body-wall; D, dermal fin-membrane; R, endoskeletal cartilaginous rays. Left border preaxial, right border postaxial. (After Dean.)

Turning to the paired fins, the few known facts of Palæontology suggest that they have originated in precisely the same manner, first by the crowding and concrescence, secondly by the shortening of endoskeletal supports which were originally parallel bars. It may even be that the unknown factor causing the dorsal fold to persist at two points operated likewise in preserving the lateral fold only at two points. The oldest known paired fins clearly observable, are those of the Devonian Elasmobranch *Cladoselache*; and here the cartilages are parallel bars, each only segmented once at the line of the body-wall, the inner segments exhibiting no fusion in the pelvic fin (fig. 21 B),

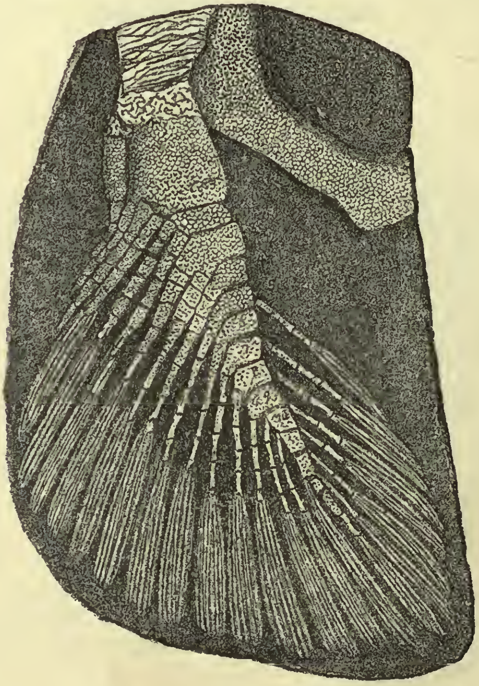

FIG. 22.

Pleuracanthus (*Xenacanthus*) *decheni;* pectoral fin, showing basal cartilages and clustered dermal rays (actinotrichia), nat. size.—L. Permian; Bohemia. Left border preaxial, right border postaxial. (After A. Fritsch.)

very slight fusion in the pectoral (fig. 21 A). It is very important to notice, however, that in both these fins, there are between the distal ends of the unaltered parallel bars the remnants of similar bars which have evidently been reduced and displaced by growth-pressure, just as the middle digit sometimes becomes reduced and displaced from connection with the carpus in *Ichthyosaurus*, some marine mammals, and birds. The next important paired fin of which we know the supports, is the pectoral of *Pleuracanthus* (fig. 22), of Carboniferous and Permian age. Here the arrangement is the

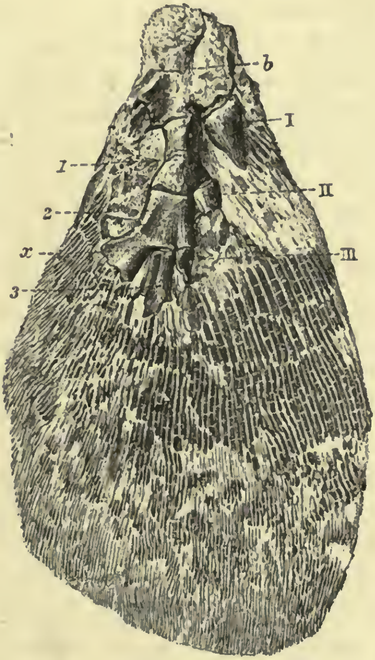

Fig. 23.

Eusthenopteron foordi; pectoral fin, nat. size.—U. Devonian; Scaumenac Bay, Canada. *b*, basal cartilage; I, II, III, three separate branches; *x*, base apparently of a fourth branch; 1, 2, 3, three successive segments; the greater part of the fin formed by the articulated and subdivided dermal rays. Right border preaxial, left border postaxial. (From specimen in British Museum, no. P. 6796.)

"archipterygium" of Gegenbaur, such as survives in the modern *Ceratodus.* The later sharks, as is well-known, have much more shortened pectoral supports. Again, it may be inferred from the elongate form of the lobe in the paired fins of the Crossopterygian *Holoptychius,* that these appendages were on the plan of the Gegenbaurian "archipterygium"; while it is known that the shortened lobate fins of the Rhizodontidæ, which became dominant after the Holoptychiidæ had passed away, were supported by a partially atrophied "archipterygium" (fig. 23); and the short lobate fin of the modern *Polypterus* is almost or quite tribasal, as in a typical existing shark.

The endoskeletal fin-supports are never correlated with the filiform dermal rays (actinotrichia) in the Elasmobranchs, and very rarely among the Crossopterygians (e.g., tail of Cœlacanthidæ, dorsal fin of *Polypterus,* in which each dermal ray may represent a fused cluster of actinotrichia). The same is true of the paired fins of the higher and later fishes, which begin with types on the level of the Chondrosteans, or sturgeons and their allies. In the latter fishes, however, the median fins are never subdivided by concrescence of the supports; the membrane seems to degenerate first, the supports afterwards. It is in these that the correlation of the supports with the dermal rays (probably now fused clusters of actinotrichia) is gradually and normally developed. All the known Palæozoic fishes with paired fins as abbreviate as those of the sturgeons (except one Permian genus), exhibit the median fin-supports in two series and much fewer than the dermal rays. A very small number of these survive in the Mesozoic and have allies at the present day; but all other post-Palæozoic "Actinopterygian" fishes and the Permian *Acentrophorus* exhibit only a single well-developed series of median fin-supports, which equal in number the dermal rays apposed to them, and the second series is never represented by more than insignificant remnants.

According to the condition of the paired fins the orders of the four great sub-classes of fishes may thus be arranged in parallel columns as follows:—

Scheme of **Sub-classes** *and* ORDERS *of the Class Pisces.*

Stages in Evolution of Paired Fins	Hyostylic Fishes		Autostylic Fishes	
	ELASMOBRANCHII	TELEOSTOMI	HOLOCEPHALI	DIPNOI
1. Supports as parallel rods	PLEUROPTERYGII (early Palæozoic)	[Unknown]	[Unknown]	[Unknown]
2. Archipterygium of Gegenbaur (elongate or abbreviate)	ICHTHYOTOMI (late Palæozoic)	CROSSOPTERYGII (Palæozoic and Mesozoic)	[Unknown]	SIRENOIDEI (Palæozoic to Recent)
3. Pectorals di- or tri-basal; pelvics abbreviate	SELACHII (late Palæozoic to Recent)	CROSSOPTERYGII (Recent)	CHIMÆROIDEI (early Mesozoic to Recent)	[Unknown]
4. Basal cartilages small or rudimentary	ACANTHODII (Palæozoic)	ACTINOPTERYGII (Palæozoic to Recent)	[Unknown]	ARTHRODIRA (early Palæozoic)

Sub-Class 1. **Elasmobranchii.**

Fin-spines and dermal tubercles consisting of vaso-dentine occur among almost the earliest known fish-remains, being met with in the Upper Ludlow Bone-bed and in the corresponding Upper Silurian rocks of the Island of Oesel in the Baltic Sea. Presumably, therefore, the sub-class of Elasmobranchs dates at least from Upper Silurian times, although no satisfactory skeletons have been discovered in older formations than the Lower Devonian.

The earliest fin-spines, of which good examples are known both from the Upper Ludlow Formation and from the Passage Beds between this and the Old Red Sandstone, much resemble the dorsal spines of the modern *Cestracion* and are provisionally named *Onchus*. They are all bilaterally symmetrical, of small size, not exceeding two or three inches in length, and having a long base of insertion sharply marked off by an oblique line from the exserted portion, which is ornamented with smooth or faintly crenulated longitudinal ridges. The internal cavity of the spine is open posteriorly towards the base, and there are no denticles on the hinder edges. The tissue is characteristic vaso-dentine, and a microscopical examination readily distinguishes the fossil from fragments of ribbed Crustacean spines often met with in the same strata.

The associated dermal tubercles are commonly named Cœlolepidæ ("hollow scales") and have been described as *Cœlolepis* and *Thelodus* or *Thelolepis*. Each is formed round a single papilla, is hollow within, and coated with structureless enamel (*ganoine*) on the surface which was originally exposed; this external layer, moreover, is separated by a constriction from the base. The tubercle is in fact the simplest type of a shagreen-granule, and it occurs in great numbers both in the Ludlow Bone-bed and in the Oesel Limestone.

A few minute Elasmobranch teeth also occur in Oesel (*Monopleurodus*, *Rhabdiodus*), but they are very simple. They all appear to exhibit a broad base, and the crown consists of one or more conical cusps.

In the Devonian strata remains of Elasmobranch dermal armour are more numerous, and fine specimens of members of the singular Order of Acanthodii are abundant. The latter admit of systematic description and are noticed below (p. 35); but the former only suffice to indicate that among the earliest Elasmobranchs there was one great group characterized by a remarkable development of the dermal armour into overlapping plates—a group which survived throughout the Carboniferous period and may even have ranged into the Permian.

The commonest of the Devonian fossils belonging to these unknown armoured sharks are named *Psammosteus*, and the plates are evidently formed by the fusion and thickening at the base of clusters of simple tubercles like those scattered through the Upper Silurian rocks. Some of the plates are extensive and ornamented only on one side, with broad smooth edges which were overlapped either by skin or by adjoining plates. Others are triangular or acuminate, sometimes solid, sometimes partly hollow, and ornamented on both sides; but in these the ornament usually extends further down one side than the other, and they may thus be compared with the paired spines of such Acanthodians as *Climatius* and *Parexus*.

The various portions of dermal armour known as *Oracanthus*, from the Lower Carboniferous, also probably belong to a fish closely resembling *Psammosteus*; and an Elasmobranch only a little less armoured, ranging throughout the Carboniferous, is *Gyracanthus*, represented by powerful paired fin-spines and by more or less conical and triangular paired spines which are almost destitute of ornament.

ORDER 1. PLEUROPTERYGII.

Judged by the condition of the paired fins, the most primitive type of Elasmobranch hitherto discovered is the Upper Devonian (or Lower Carboniferous) genus *Cladoselache*. It is the only known representative of the order PLEUROPTERYGII, which exhibit the nearest approach to the hypothetical lateral fin-fold yet met with. The small basal cartilages of the paired fins seem to be embedded in the body wall, and the unjointed radial cartilages extend directly outwards to the edge of the membrane. There are no claspers in the pelvic fins, and both these and the pectoral fins were probably mere balancers, directed somewhat downwards. The notochord must have been unconstricted, without calcifications in the sheath; and the endoskeletal cartilages are permeated with minute granular calcifications. The teeth are conical cusps upon broad bases, several series functional at the same time. A ring of dermal plates surrounds the eye; but there are no membrane-bones.

Detached teeth resembling those of *Cladoselache* have long been known from Carboniferous formations under the name of *Cladodus*; but there is reason to believe that several primitive genera—perhaps even more than one family or order—were characterized by teeth of this form, and it is therefore useless to discuss the distribution of such fragmentary fossils. It suffices to enumerate the known characters of

Cladoselache (figs. 21, 24, 25). The fish is elongated and round-bodied, with a short blunt snout and forwardly placed eye. The precise characters of the cranium are unknown; but the olfactory capsules are large, placed close together, and terminal. The mouth is also terminal, the upper and lower jaws being similar in shape and size, and supported by a slender elongated hyomandibular. The teeth are largest, longest, and most acutely pointed at the symphysis of the jaw, smallest and shortest at the angle of the mouth. The transverse series are closely apposed, and not separated as in the modern *Chlamydoselache*; they are indeed tightly wedged together, and the cusps are frequently much abraded by wear. Every tooth has a principal cusp with variable smaller lateral cusps, and the broad base of each is overlapped by its successor behind. The number of gill-arches is uncertain, but five are known, and the presence of one or two others is suggested by some specimens. The neural and hæmal arches of the axial skeleton have been observed only in the caudal region, where they are short tapering rods of cartilage, bifurcated at the base and distinctly corresponding in number with the calcified remains of the muscle-plates. Intercalary cartilages are wanting. The paired fins have already been described (p. 24, fig. 21). Two low dorsal fins have been observed (the posterior only shown in fig. 24), both destitute of an anterior spine, but strengthened by simple cartilaginous rays extending to the edge of the fin-membrane. No anal fin has been distinguished. The caudal fin (fig. 25) is strongly heterocercal and very remarkable. The neural arches (N)

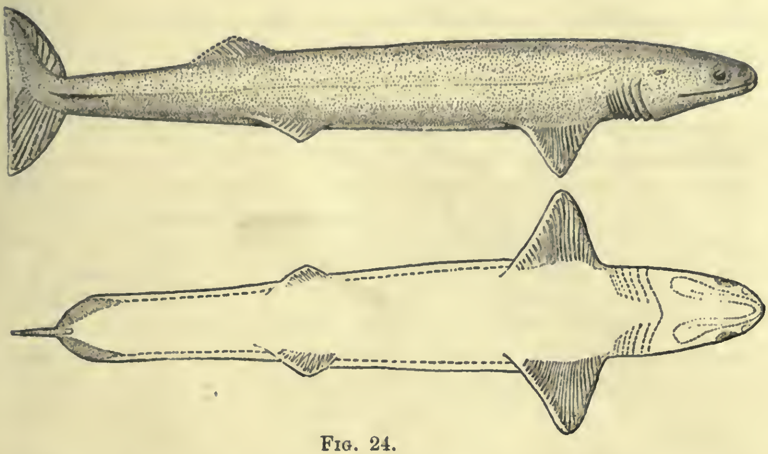

FIG. 24.

Cladoselache fyleri; restoration by B. Dean, from lateral and ventral aspects, one-seventh nat. size.—U. Devonian; Ohio. Since this restoration was made, a low anterior dorsal fin has been discovered.

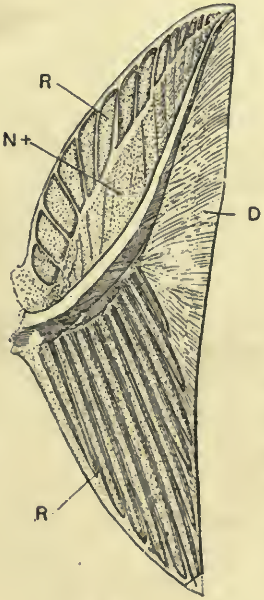

FIG. 25.

Cladoselache; caudal fin, about one-half nat. size.—U. Devonian; Ohio. D, fin-membrane; N, neural arches of upturned lobe; R, endoskeletal cartilaginous rays. (After Dean.)

seem to persist even to the end of the upturned axis, directly supporting the thick radial cartilages (R) of the superior lobe of the caudal fin. The dermal membrane (D) of the inferior lobe of the caudal fin is supported by simple cartilaginous rays (R) only in its lower portion where they extend quite to the margin. The eye is surrounded by a double series of small dermal plates; but the remainder of the fish is covered only with minute lozenge-shaped denticles, which are apparently not enamelled. The latter are slightly enlarged at the angles of the mouth, where they approximate in size and shape to the smallest of the teeth. The lateral line extends along the trunk between two series of the shagreen-granules, and was thus presumably an open canal. A short dermal expansion forms a horizontal keel on each side of the caudal lobe just in advance of its upturned end. *Cladoselache kepleri*, *C. fyleri* (fig. 24) and other species occur in the Cleveland Shale (Upper Devonian or Lower Carboniferous) of Ohio. The largest known examples measure nearly two metres in length.

ORDER 2. ICHTHYOTOMI.

Another well-known primitive type of Elasmobranch ranging from the Lower Carboniferous to the Lower Permian and perhaps surviving even later, is that exemplified by *Pleuracanthus*. It is a form of fish which might with very little modification become either a Selachian, Dipnoan, or Crossopterygian. As in the Pleuropterygii, the endoskeletal cartilages are permeated with minute granular calcifications; and some of the best-preserved crania (*Didymodus* from the Permian of Texas) exhibit a curious, symmetrical fissuring (hence the ordinal name ICHTHYOTOMI), though there are no membrane-bones. The notochord is rarely or never constricted, but slight calcifications occur in its sheath. The neural and hæmal arches are long and slender, rarely with traces of intercalary cartilages. The paired fins exhibit a long segmented axis of cartilage, fringed on one or both sides with other cartilages; and the pelvic fins in the male are produced into a pair of claspers. The right and left halves of the pectoral arch are separate; and there is no pelvic arch, each pelvic fin being supported merely by its own enlarged basipterygium. The median fins are extensive, supported by slender endoskeletal cartilages which are directly connected and correlated in number with the arches of the axial skeleton; and they are often strengthened by delicate dermal filaments (actinotrichia) which cluster round the distal part of the supports. The dermal skeleton is insignificant, never more than one median spine and small scattered tubercles. The teeth consist of sharp cusps fixed on broad bases, which overlap each other more or less and are often united by well-marked facettes.

In the typical family of **Pleuracanthidæ**, the pectoral fin exhibits a fringe of cartilages on both sides of its segmented axis. The much-extended dorsal fin is separated from the fringe-like caudal fin. The skull is amphistylic and the mouth nearly terminal. The typical and best-known genus is

Pleuracanthus (figs. 17, 18, 22, 26). The fish is elongated and round-bodied, with a straight and tapering (diphycercal) tail. Fixed upon the occipital region of the cranium is a long and slender, bilaterally-symmetrical, dermal spine, which is turned backwards when not erect, and does not appear to have supported a fin. The spine is hollow and is armed with a double longitudinal series of denticles or barbs. The foremost few neural arches are bent forwards, but from the origin of the dorsal fin backwards their direction is normal; the right and left halves of each arch remain separate. Ribs are rudimentary or absent; but in the caudal region the hæmal arches are as large as the corresponding neurals. The branchial arches are believed to be seven in number, though there may be only five. The teeth are tricuspid, but the middle denticle is comparatively minute and the name *Diplodus*, commonly applied to the isolated fossil teeth, is thus appropriate. Very delicate dermal filaments (actinotrichia) are clustered round the supporting cartilages in all the fins. In the paired fins all the fringing cartilages are segmented; in the pectoral fin those of the anterior (preaxial) border are much more numerous and better developed than those of the hinder (postaxial) border. The dorsal fin is borne by a close series of slender cartilaginous supports, which are exactly twice as numerous as the neural arches to which they are apposed; each support is segmented into three pieces, of which the proximal element is short, the middle one very long, and the outermost again short, while the latter projects into the fin-membrane. The dorsal portion of the caudal fin is similarly supported, but its cartilages are equal in number to the neural arches. The ventral portion of the caudal fin has no supports beyond the hæmal spines. The anal fin is curiously subdivided into two portions, of which the supports are crowded, partially fused together, and thus in part branching; these exhibit more numerous segments than those of the other median fins. Complete skeletons of *Pleuracanthus* have been found only in the Coal Measures

Sub-Class 1. **Elasmobranchii.**—ORDER 2. ICHTHYOTOMI.

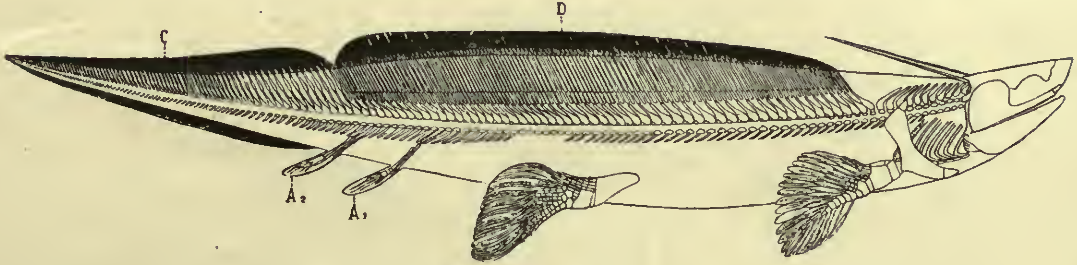

FIG. 26.

Pleuracanthus (*Xenacanthus*) *decheni;* restoration by A. Fritsch, about one-quarter nat. size.—L. Permian; Bohemia. A_1, A_2, two anal fins; C, dorsal portion of caudal fin; D, dorsal fin.

of Commentry, France, in the Lower Permian Coal Measures of Germany and Bohemia, and in the Lower Hawkesbury Formation of New South Wales; but detached spines and teeth indistinguishable from those of this genus occur also in the Coal Measures of North America and in the lowermost Carboniferous strata of Scotland, while a few teeth have been found even in the Upper Trias (Keuper) of Somersetshire.

ORDER 3. ACANTHODII.

One large and characteristic group of Palæozoic Elasmobranchs is remarkable on account of the presence of membrane-calcifications in the region of the skull and pectoral arch. So far as hitherto examined, however, all these calcifications consist merely of vasodentine or of structureless lamellæ without bone-cells; and the degree of their development is very variable. The group may be conveniently regarded as an order, which commonly bears the name of ACANTHODII, so-called from the first-described genus, *Acanthodes* (fig. 27).

FIG. 27.

Acanthodes wardi; lateral aspect, one-third nat. size.—U. Carboniferous; Staffordshire. The orbit is represented somewhat too small, and the frills of the gill-clefts are hypothetical. (From *Brit. Mus. Catal.*)

The endoskeletal cartilage in the Acanthodians is more or less permeated with granular calcifications, though the supports of the fins are apparently never preserved. The notochord must have been always persistent, while the neural and hæmal arches are long and slender, only thickened at the base of the lower lobe of the tail. The membrane-calcifications sheathing the pterygo-palatine and meckelian cartilages are best developed when the teeth are large; the latter being firmly fixed to these plates. There is a distinct ceratohyal fringed with filaments.

The cranial roof is usually covered with small dermal plates, while the orbit is surrounded by a ring of four circumorbitals. There are no remains of a gill-cover, which must thus have been only membranous if present; but each gill-arch bears on its hinder or convex border a close series of lanceolate dermal appendages, which may be either gill-rakers or the supports of frills like those of the modern *Chlamydoselache*. Each of the fins, except the caudal, is provided with an anterior spine, which resembles that met with in the dorsal fins of many well-known Selachians, and is to be similarly regarded as an enormous dermal ray. A paired series of similar spines is also present in some of the earliest genera between the pectoral and pelvic fins, and it has been suggested that these are remnants of the once-continuous lateral fin-folds (fig. 28). Some hard parts are always preserved at the base of the pectoral fins, and these seem to be merely dermal structures; but their homologies have not hitherto been satisfactorily determined. In *Acanthodes* (fig. 29) the pectoral spine (*s*) is supported by a hollow, mesially constricted element (*b*) which abuts against the side of its proximal end; and at a short distance below this there occurs a close series of short, fine dermal rays (*r*), sometimes appearing as the fringe of a short, obtuse lobe, which may mark the limit of the endoskeletal part of the appendage. In *Diplacanthus* (fig. 30) there are two spines (*s*, *m*) in each

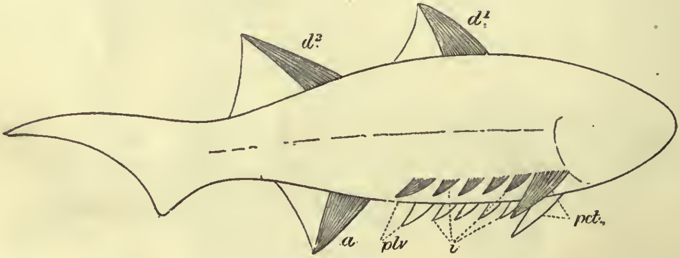

FIG. 28.

Climatius scutiger; outline of fish, with spines shaded, slightly enlarged.—L. Old Red Sandstone; Forfarshire. *a*, anal fin-spine; d^1, d^2, dorsal fin-spines; *i*, free paired ventral spines; *pct.*, pectoral fin-spines; *plv.*, pelvic fin-spines.

pectoral fin, either directly apposed at their base or united by a small, interposed third element (x). The supporting arch is complete. The greater portion of it consists of a pair of vertically elongated basal elements (b), each having a straight rod-like axis, filled with calcite in the fossils, and thus originally either hollow or occupied by uncalcified tissue; behind this axis there is a thin laminar expansion of bone, diminishing upwards, and apparently extending downwards and inwards to form an inferior limb. The pair of large elements does not meet in the median line below, but is separated by a much smaller pair of laminæ (*cl.*), united in a finely dentated mesial

FIG. 29.

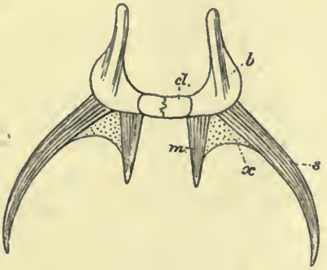

FIG. 30.

FIG. 31.

FIG. 29.

Acanthodes wardi; skeletal parts of pectoral fin, about nat. size.—U. Carboniferous; Staffordshire. b, hollow basal element; r, dermal rays (actinotrichia); s, dermal spine forming anterior border of fin. (From *Brit. Mus. Catal.*)

FIG. 30.

Diplacanthus striatus; pectoral arch and fins, nat. size.—L. Old Red Sandstone; N. Scotland. b, hollow basal element, sometimes termed clavicle or claviculoid, but probably homologous with (b) in *Acanthodes* (fig. 29) and *Parexus* (fig. 31); *cl.*, dermal plates, apparently clavicular; x, hollow skeletal base which may be homologous with the basal element (b) in *Acanthodes* (fig. 29), but more probably results from the union of the anterior (s) and posterior (m) fin-spines. (From *Brit. Mus. Catal.*)

FIG. 31.

Parexus falcatus; skeletal parts of pectoral fin, nat. size.—L. Old Red Sandstone; Forfarshire. b, hollow basal element; *cl.*, dermal plate, apparently clavicular; s, dermal spine forming anterior border of fin. (From *Brit. Mus. Catal.*)

suture. In *Parexus* (fig. 31) the broad, curved pectoral spine (*s*) is supported by a hollow triangular element (*b*), with its base directly apposed to the obliquely truncated end of the spine and its apex produced into a short slender rod. Between the two spines there is a pair of large and thin, triangular or sickle-shaped elements (*cl.*) meeting in the middle line; and the surrounding squamation is arranged in direct relation to these plates in such a manner that they are proved to be quite superficial. The pelvic fins are always present, often as large as the pectorals in the less specialized forms, smallest in the latest forms. The squamation is very fine, closely covering the whole of the trunk, and not enlarged even on the ridge of the upper caudal lobe. The scales are rectangular or slightly rhomboidal, with enamelled and frequently ornamented external surface; and there is a single "lateral line" on the flank, not piercing the scales but passing between two series. The fin-membranes are also at least in part stiffened with quadrate dermal granules of the same nature as those covering the trunk, and these are often arranged in regular lines simulating rays.

Two families of Acanthodian fishes are known, one characterized by the presence of two dorsal fins, the other by a single dorsal fin. The former, or Diplacanthidæ, are exclusively Upper Silurian and Lower Devonian, while the latter, or Acanthodidæ, range from the Lower Devonian to the Lower Permian inclusive. All the known forms are of relatively small size, the majority being less than 0·3 m. in length.

The **Diplacanthidæ** are remarkable for the great development of the dermal spines, there being sometimes not less than four or five pairs between the pectoral and pelvic fins. In *Climatius* (fig. 28) the fin-spines are remarkably broad and marked with coarse longitudinal ridges, sometimes with posterior denticles; the first dorsal spine is not excessively elongated. *Parexus* is nearly similar, but the first dorsal spine is relatively much elongated and the fin-membrane does not extend so far as its apex. These genera and *Diplacanthus* do not exhibit any teeth; but *Ischnacanthus* has a formidable dental armature. In this fish there are widely-spaced, large conical teeth, interspersed in a close series of minute cusps, all apparently fused with the membrane-calcifications in both jaws. The finest specimens of all these genera have been obtained from the Lower Old Red Sandstone.

The **Acanthodidæ** are almost destitute of the free spines between the paired fins, rarely showing even rudiments. Moreover, in course of geological time the pelvic fins degenerate exactly in proportion as the pectoral fins enlarge. In the Lower Devonian representatives of *Acanthodes* (*Mesacanthus*), for example, the pelvic fins are not much inferior in size to the pectorals, and are placed nearly midway between the latter and the anal. In the Lower Permian *A. bronni* the pelvic fins become insignificant and the pectoral fins enormous, while the two pairs are even more closely approximated than in the earlier forms. The Upper Carboniferous *A. wardi* (fig. 27) presents an intermediate condition.

Order 4. Selachii.

Palæontology teaches that the skeleton of the modern sharks and skates is extremely specialized compared with that of the early Elasmobranchs. Presumably, therefore, little reliance can be placed on the anatomy of the soft parts in seeking a clue to the primitive organization of the sub-class. All these fishes are destitute of membrane-calcifications, even when the teeth seem most in need of support. They are characterized by the presence of a well-developed pelvis. Their pectoral fins are di- or tri-basal, without a long segmented axis; that is, the basal cartilages in direct contact with the pectoral arch are normally three, sometimes two in number, while the hinder (postaxial) border of the metapterygium rarely exhibits even rudiments of fringing cartilages. In all but the least specialized genera, the vertebral centra are well-formed and strengthened by a secondary peripheral calcification; and secondarily-developed intercalary cartilages occur more or less irregularly between the neural arches. The sharks and skates thus represent a distinct order of Elasmobranchs, for which the term Selachii may be conveniently reserved.

Numerous Palæozoic teeth and fin-spines have been ascribed to this order, but only on account of their close resemblance to the corresponding hard parts of certain of its existing members. Even the nearly complete example of the Carboniferous *Sphenacanthus* in the British Museum, proves little more than that the spines were placed in front of the two dorsal fins; the supporting cartilages of the fins cannot be satisfactorily observed. There is, however, little doubt that many of the Carboniferous and Permian Elasmobranchs were closely related to the surviving Port Jackson Shark (*Cestracion*).

Entire skeletons of undoubted Selachii are known first from the Lower Lias (*Palæospinax*), and it is interesting to observe how varied is the degree of development of the vertebral centra even in genera most closely resembling each other in all remaining features. For example, the genus *Hybodus* (fig. 34, p. 45) has a persistent notochord, without calcifications in the notochordal sheath, and is known to range at least from the Lower Lias to the Wealden. The Lower Liassic *Palæospinax* scarcely differs from it except in the smoothness of the dorsal fin-spines and shagreen; but its vertebral centra are always conspicuous as constricted cylinders (the "cyclospondylic" type). The Cretaceous *Synechodus*, again, is almost identical with *Palæospinax*; but its vertebral rings are strengthened by peripheral calcifications which are chiefly disposed in longitudinal ridges or radiating plates (the "asterospondylic" type). Among Selachii, therefore, the *degree* of development of the vertebral centra is shown to be of only secondary importance. The *manner* of the specialization seems to be of more fundamental significance; for it is commonly admitted that the sharks (**Selachoidei**) and the rays (**Batoidei**) form two approximately natural groups—the one tending towards agility in swimming, the other towards expertness in feeding on the bottom—and the fully-formed vertebral centra are strengthened in a different way in these two groups. At the same time it must be remarked that the classification is merely provisional; for there is obviously much uncertainty as to the systematic position of those forms with persistent notochord and simple vertebral rings, and many of the extinct types are too imperfectly known as yet to admit of satisfactory discussion.

Sub-Order 1. *Asterospondyli.*

These are the "sharks" and "dog-fishes" of the existing fauna. Specialization results in no marked depression of the body, and the pectoral fins never grow forward towards the head; the spiracles tend to diminish and are often absent. The anal fin is always present. The vertebral centra, when fully developed, are strengthened by longitudinal ridges or radiating laminæ, which, when viewed in transverse section, are shown to predominate over the concentrically-disposed laminæ.

All the families of this sub-order are characterized by the presence of two dorsal fins, except the **Notidanidæ**, which possess only a single dorsal fin and in general occupy a unique position. One living species of *Notidanus* (*Heptanchus*) sometimes exhibits feebly asterospondylic vertebræ in the caudal region, and the teeth of the earliest known species (fig. 32 B) are almost identical with those of certain forms of *Hybodus* (fig. 32 A). There is thus some reason for placing the Notidanidæ with the primitive Asterospondyli, and it is unfortunate that so little is known of their extinct representatives. A typical skeleton of *Notidanus* itself has been discovered in the Upper Jurassic (Lithographic Stone) of Bavaria, and numerous detached teeth have been obtained both from this and subsequent formations. These teeth are of peculiar interest as showing how they were at first firmly fixed and then gradually assumed their modern characters. The Jurassic

Fig. 32.

Outlines of teeth of (A) *Hybodus polyprion* from L. Jurassic, (B) *Notidanus daviesi* from U. Jurassic, (C) *Notidanus microdon* from U. Cretaceous, and (D) *Notidanus gigas* from Pliocene; nat. size.

form of tooth (fig. 32 B) has few cusps, often worn at the apex, and the root or base is depressed. The typical Upper Cretaceous tooth (fig. 32 C) is more elongated and has the root or base slightly deepened and compressed. The most specialized tooth of all, from the Pliocene (fig. 32 D), is still more elongated, with from nine to eleven cusps, and with a remarkably compressed deep base. The existing genus *Chlamydoselache,* which is very closely related to *Notidanus,* is known among fossils merely by detached teeth from the Pliocene of Italy.

The remarkable resemblance between the teeth of *Chlamydoselache* and those from the Palæozoic rocks named *Diplodus* and *Cladodus,* originally believed to imply some close relationship between the existing and remotely extinct genera, is now proved to be of no significance for classificatory purposes. It thus still remains uncertain whether the resemblance between the dentition of the Palæozoic family of **Cochliodontidæ** and that of the modern *Cestracion,* implies any very intimate alliance between this ancient family and the Cestraciontidæ. The genus *Helodus* is the only undoubted Cochliodont hitherto discovered showing remains of the body; and it exhibits at least one spinous dorsal fin, while the pectorals are neither much enlarged nor "archipterygial." An anal fin is also present. Nevertheless the dentition of the Cochliodontidæ on the middle of each ramus corresponds exactly with that of *Cestracion,* except that the separate teeth are more or less completely fused together. *Cestracion,* as is well known, exhibits two principal series of grinding teeth on the middle of each half of the jaw (fig. 33, 1), in which there are five or six successional teeth behind (or within) the foremost row. In the Cochliodont *Psephodus* (fig. 33, 2) the equivalent of the hinder of these two series forms a great simple plate; and this is shown by abnormal specimens to consist of three teeth in succession. In *Pleuroplax* or *Pleurodus* (fig. 33, 5), *Deltodus* (6), and *Cochliodus* (3), each of the two series is fused into a continuous plate, which always distinctly exhibits traces of its components in the first two genera. In *Pœcilodus* (fig. 33, 7) and *Deltoptychius* (4), not only do the two plates occur, but they are once more fused together at their adjacent border

Sub-Class 1. **Elasmobranchii.**—ORDER 4. SELACHII.

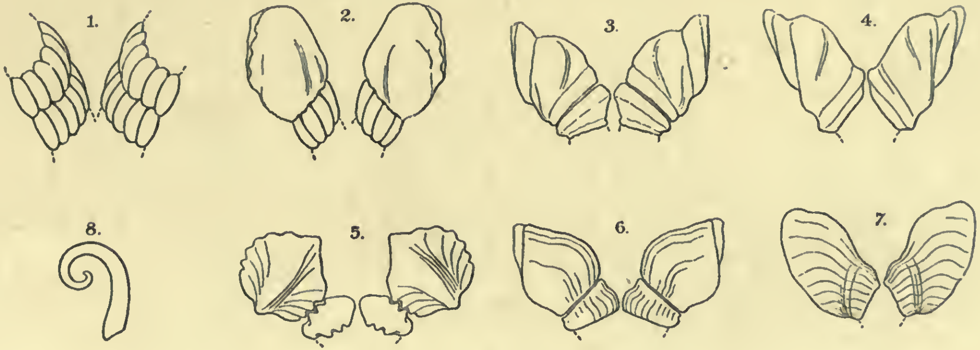

FIG. 33.

Middle teeth of *Cestracion* (1) compared with the homologous dental plates of the Carboniferous Cochliodontidæ; figures reduced in size. 2, *Psephodus magnus*; 3, *Cochliodus contortus*; 4, *Deltoptychius acutus*; 5, *Pleuroplax rankini*; 6, *Deltodus sublævis*; 7, *Pœcilodus jonesi*; 8, transverse section of principal dental plate of *Cochliodus*, showing in-rolled outer border. (From specimens in British Museum.)

into one continuous piece. The coalescence of the teeth is so complete in all cases, that their mode of growth is much changed; the once-separate outer tooth can no longer fall away from the mouth as growth of tooth-substance takes place within, and the external border thus coils inwards like a scroll, as shown in transverse section (fig. 33, 8). The compound crushing plates of the Cochliodonts hence result not only from the fusion of adjacent teeth, but also from the coalescence of several successional teeth. The typical Cochliodonts are exclusively Carboniferous, and it is noteworthy that the least specialized form of dentition (*Pleuroplax*) has the most extensive range, being found both in the lowermost and in the uppermost strata of that period.

The **Cestraciontidæ**, though now on the verge of extinction, were the most characteristic and abundant sharks of the Mesozoic Era, and it is extremely probable that *Orodus, Sphenacanthus, Tristychius* (Carboniferous), and *Wodnika* (Permian) may also be placed here. In all the satisfactorily-known genera each of the dorsal fins is armed with a spine, the first opposite to the space between the pectoral and pelvic fins. The teeth are mostly obtuse, never fused into continuous plates; and several series are simultaneously in function. So far as is known, the upper element of the hyoid arch in this family does not adequately perform the normal office of a hyomandibular; but it is noteworthy that the secondary direct articulation of the pterygo-quadrate arcade with the cranium is not always preorbital as it is in the existing *Cestracion.* In the Cretaceous genus *Synechodus*, the facette is post-orbital, exactly as in the Notidanidæ. The nearly complete skeleton of a shark hitherto not satisfactorily distinguished from *Cestracion* has been found in the Lithographic Stone (Upper Jurassic) of Bavaria (*C. falcifer*), and characteristic teeth occur in nearly all subsequent formations. The best-known extinct genera are *Hybodus, Palæospinax,* and *Asteracanthus.*

Hybodus (figs. 34, 35). The teeth are like those of *Synechodus* (fig. 36), conical or cuspidate with more or less striated crown, and there is one principal coronal elevation with one or more lateral prominences on either side diminishing outwards; the root or base is depressed. The

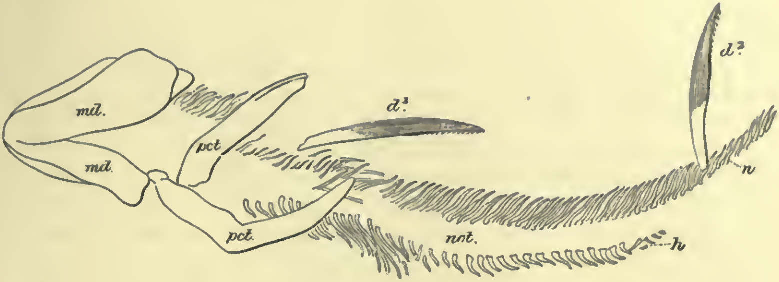

FIG. 34.

Hybodus hauffianus; imperfect skeleton, about one-tenth nat. size.—U. Lias; Würtemberg. d^1, d^2, dorsal fin-spines; *h*, hæmal arches; *md.*, mandible; *n*, neural arches; *not.*, notochord; *pct.*, pectoral arch. (After E. Fraas.)

FIG. 35.

Hybodus delabechei; outline of fossilized and distorted head, about one-quarter nat. size.—L. Lias; Lyme Regis. *m*, cleft of mouth; *orb.*, orbit; *s*, cephalic spines fixed to triradiate bases which would be imbedded in the skin. (British Museum, no. 39880.)

symphysial teeth are few and relatively large. The hyomandibular is slender, but there is no facette on the pterygo-quadrate for direct articulation with the cranium. Five pairs of branchial arches have been counted, the hindermost very delicate. The notochord must have been persistent, but the arches are calcified (fig. 34, *n*, *h*), and there are no traces of intercalary cartilages (both Liassic and Wealden specimens observed). The dorsal fin-spines (fig. 34, d^1, d^2) are longitudinally ridged and grooved, and bear two longitudinal series of denticles on the hinder face, these being arranged close together mesially. The caudal, anal, and paired fins are unknown. The shagreen is sparse and variable in development, consisting of small conical, radiately-grooved tubercles, sometimes fused into groups of three. Two large hook-shaped, semi-barbed dermal spines occur immediately above and behind each orbit in some individuals, probably males (fig. 35). Typical remains of *Hybodus* range from the Muschelkalk (Middle Trias) to the Wealden inclusive, and some species may be even of later date. The best-known species are *H. delabechei* (Lower Lias), *H. medius* (Lower Lias), *H. hauffianus* (Upper Lias), and *H. basanus* (Wealden). A closely allied genus with blunter teeth is named *Acrodus* and seems to have a still wider range, the latest teeth of this form occurring in the Gault.

Palæospinax. A small fish with dentition closely resembling that of *Hybodus*, but the symphysial teeth comparatively high-crowned and prehensile. The vertebræ are simple constricted cylinders ("cyclospondylic"), sometimes feebly asterospondylic. The dorsal fin-spines are smooth and enamelled, without posterior denticles. The shagreen is fine and dense, but there are no enlarged head-spines; large hooks occur on the claspers of the male. The typical species, *P. priscus*, occurs in the Lower Lias, represented by nearly complete specimens; and there is evidence of other species both in the Rhætic of England and the Upper Lias of Würtemberg. *Synechodus*, from the Cretaceous, is a closely allied genus with well-defined asterospondylic vertebræ, but with a nearly similar dentition (fig. 36).

Asteracanthus (fig. 37). Teeth (originally named *Strophodus*) massive and not cuspidate but rounded or keeled, and all superficially ornamented by reticulate markings; those of the symphysis few, relatively large, much arched, and without lateral denticles. The dorsal fin-spines resemble those of *Hybodus*, except that the superficial ridges are subdivided into tubercles; the large hook-shaped head-spines are also very similar in these two genera. The notochord must have been persistent. This is a Jurassic and Wealden genus, the typical and best-known species, *A. ornatissimus*, being especially characteristic of the Upper Jurassic.

The palæontology of the **Scylliidæ** presents very few features of interest. One genus (*Palæoscyllium*) closely related to the existing *Scyllium*, is known from the Lithographic Stone (Upper

Sub-Class 1. **Elasmobranchii.**—Order 4. Selachii.

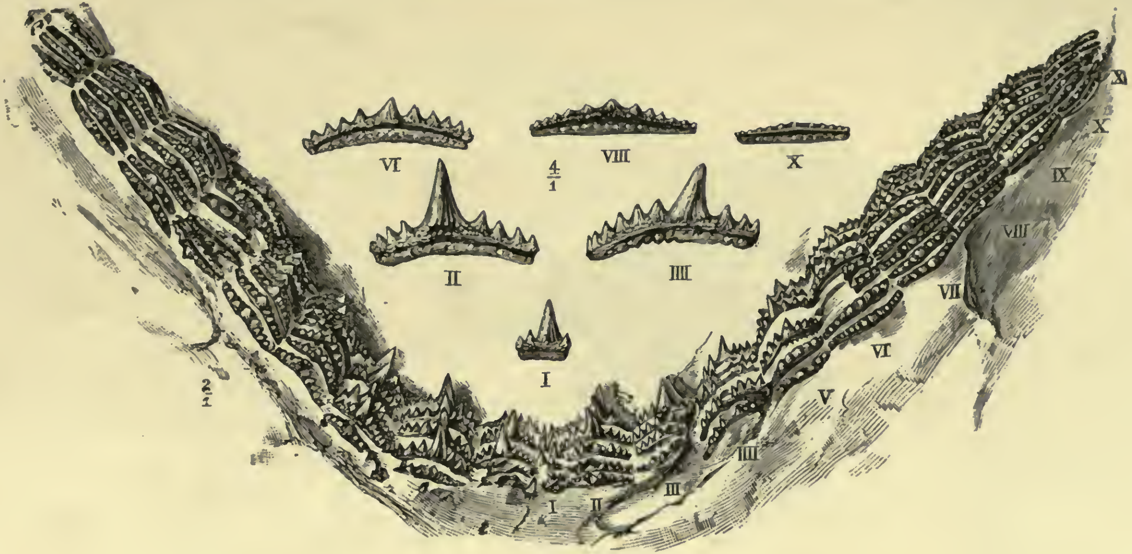

Fig. 36.

Synechodus dubrisiensis; dentition, twice nat. size, with six teeth enlarged four times.—U. Cretaceous; Sussex. (From *Brit. Mus. Catal.*)

Jurassic) of Bavaria; and another dog-fish, identified with *Pristiurus,* also occurs in the same horizon. *Scyllium* and *Ginglymostoma* range from the Upper Cretaceous; and there is an extinct genus in the Cretaceous and early Tertiary, *Mesiteia,* in which the mucus-canal of the lateral line is supported by calcified incomplete rings resembling the corresponding supports in Chimæroids.

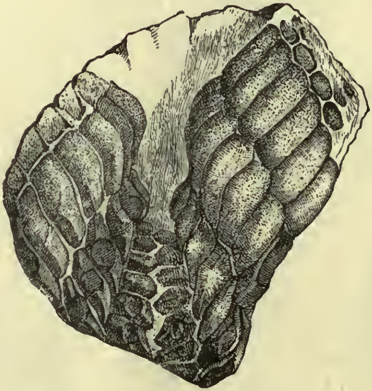

FIG. 37.

Asteracanthus (*Strophodus medius*); imperfect dentition, one-third nat. size.—L. Jurassic; Caen, Normandy. (British Museum, no. 41378.)

While the Cestracionts are typically Mesozoic, the **Lamnidæ** and **Carchariidæ** are essentially Cainozoic (Tertiary) and Recent. The teeth (fig. 38) are all cuspidate, and the crown is fixed upon a more or less bifurcated base which is much compressed antero-posteriorly and thus differs from the stout depressed base in the teeth of the earlier sharks; the teeth are, indeed, adapted merely for seizing and lacerating prey. Nothing is known of the Lamnidæ earlier than the Upper Cretaceous; but a Jurassic form of tooth (*Orthacodus*) hitherto only found detached, is often placed here, and this is remarkable as exhibiting an *Odontaspis*-like dental crown fixed on a horizontally-expanded base. The teeth and vertebræ occurring in the Cretaceous are indistinguishable from those of *Odontaspis, Lamna,* and *Oxyrhina*; but entire fishes found in the Upper

Cretaceous of Mount Lebanon show that at least some of these teeth belong to extinct genera. *Scapanorhynchus*, from the Lebanon, has teeth like *Odontaspis*, but differs from this genus in having a much-elongated rostrum and exhibiting a remarkably extended anal fin. No undoubted Carchariidæ occur below the Eocene, where extinct genera are recognized. Their teeth can be distinguished from those of the Lamnidæ by the presence of an internal cavity in the former.

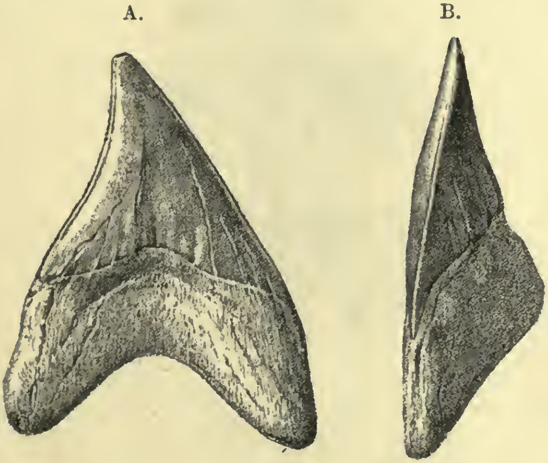

FIG. 38.

Oxyrhina crassa; tooth, external (A) and lateral (B) aspects, nat. size.—Pliocene (Red Crag); Suffolk.

Sub-Order 2. *Tectospondyli.*

The typical members of this sub-order are the existing skates, rays, and devil-fishes. Specialization results in a remarkable depression of the body and the enlargement of the pectoral fins, which often meet in advance of the head; the spiracles are always large. The anal fin is invariably wanting. The vertebral centra, when fully developed, are strengthened by concentric calcified laminæ which (with rare and partial exceptions) predominate over the radiating laminæ. As among the Asterospondyli, it is difficult to recognize the least-specialized forms in which the notochord is persistent or the vertebræ are only cyclospondylic. Here, however, may probably be placed the **Spinacidæ**, which are of little palæontological interest and are not known to date back further than the Upper Cretaceous. It is quite possible also that the Palæozoic **Petalodontidæ** and **Psammodontidæ**, as yet known only by the imperfect dentition, may prove to be early types of the same sub-order. The Lower Carboniferous teeth named *Psammodus* most nearly resemble in general aspect the grinding teeth of the existing Myliobatidæ.

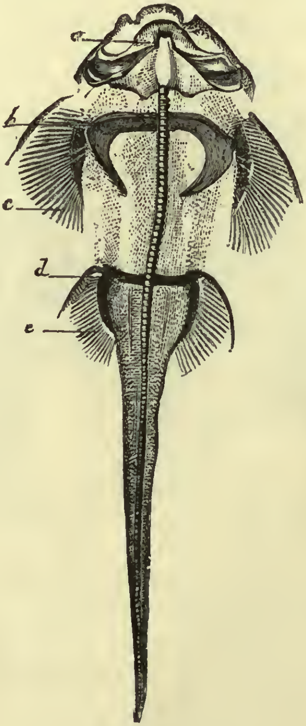

Fig. 39.

Squatina speciosa; two-thirds nat. size.—U. Jurassic (Lithographic Stone); Bavaria. *a*, mandible; *b*, pectoral arch; *c*, pectoral fin; *d*, pelvic arch; *e*, pelvic fin. (British Museum, no. 37013.)

The **Squatinidæ** (or **Rhinidæ**) are represented by the typical genus *Squatina* in the Lithographic Stone (Upper Jurassic)

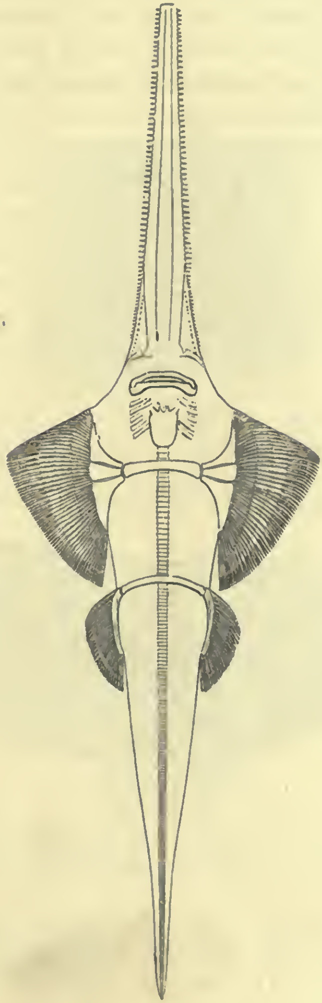

FIG. 40.

Sclerorhynchus atavus; restoration, one-seventh nat. size.—U. Cretaceous; Mt. Lebanon.

of Bavaria, where complete skeletons occur (fig. 39); the only noteworthy difference between the Jurassic and Recent species hitherto observed being, that the vertebral centra of the former exhibit fewer peripheral calcified rings than the latter. The **Pristiophoridæ** certainly range from the Upper Cretaceous onwards, an undescribed specimen from the Chalk of Mount Lebanon being preserved in the Museum of the Syrian Protestant College, Beyrout. The **Pristidæ** are of more interest, there being some evidence that their characteristically-toothed rostrum has only been acquired during Tertiary times. The earliest genus ascribed to this family is *Sclerorhynchus* (fig. 40) from the Upper Chalk of Mount Lebanon; and in this fish the rostral teeth are comparatively small, while the bases of some are not even in contact with the supporting cartilages. The Eocene *Propristis*, known only by fragments of rostrum, is described as having the rostral teeth free, not embedded in cartilage. The typical *Pristis*-rostrum also dates from the Eocene. The earliest **Rhinobatidæ** are Upper Jurassic, and the beautifully preserved skeletons from the Lithographic Stone scarcely differ from that of the existing *Rhinobatus*. Before the close of the Cretaceous period the Rhinobatidæ, Rajidæ, and Trygonidæ do not appear to have been so clearly differen-

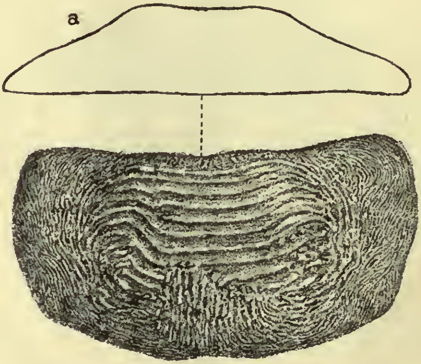

Fig. 41.

Ptychodus polygyrus; tooth, coronal aspect and transverse section of crown, about nat. size.—U. Cretaceous (English Chalk).

tiated as they have subsequently become. There is also some doubt as to the systematic position of the typically Cretaceous teeth named *Ptychodus* (fig. 41), which are known to have been arranged in the jaws in the manner indicated in the accompanying diagram (fig. 42). Probably, however, they belong to a Mesozoic forerunner of the **Myliobatidæ**, which were represented in the early Eocene by fishes having the dentition indistinguishable from that of the still-surviving genera, *Myliobatis, Aetobatis,* and *Rhinoptera.* The **Trygonidæ** seem to be represented in the Cretaceous by *Cyclobatis,* which is

Fig. 42.

Ptychodus decurrens; diagram of arrangement of teeth, much reduced.—U. Cretaceous (English Chalk). A, upper jaw; B, lower jaw. (From *Brit. Mus. Catal.*)

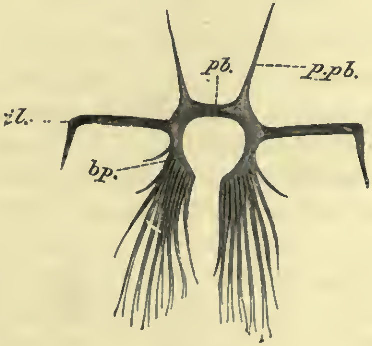

Fig. 43.

Cyclobatis oligodactylus; pelvic arch and fins, nat. size.—U. Cretaceous; Mt. Lebanon. *bp.*, basipterygium; *il.*, iliac process; *p.pb.*, prepubic process; *pb.*, pubis.

remarkable for the large size of the iliac and prepubic processes of its pelvic cartilage (fig. 43). The **Torpedinidæ**, so far as known, are typically Tertiary, but skeletons apparently referable to *Platyrhina* and *Narcine* occur in so early a formation as the Eocene of Monte Bolca, near Verona.

Sub-Class 2. **Holocephali.**

Dental plates essentially similar to those of the existing Chimæroid fishes are met with in rocks as early as the Middle Devonian; but there is still no evidence of any member of the Holocephali which cannot be included in the surviving order of Chimæroidei. Some of the early forms were certainly armed with dermal plates; but Palæontology as yet lends no support to the theory that the Chimæridæ are degenerate descendants of fishes once possessed of membrane bones. The earliest known complete skeletons are unfortunately only Liassic.

ORDER 1. CHIMÆROIDEI.

In all known Chimæroids, whether recent or extinct, the notochord is persistent and at most only partially constricted, the calcifications in the sheath, when present, consisting of slender rings more numerous than the neural and hæmal arches. The pectoral fins are abbreviate, without segmented axis; and the pelvic fins in the male are produced into a pair of claspers. In the extinct forms there is no trace of any dermal plate developed in the opercular flap. The only clear evidence of evolution hitherto observed concerns the development of the peculiar dental plates. In each of the four known families the dentition consists of a few large plates of vascular dentine of which certain areas ("tritors") are specially hardened by the deposition of salts within and around groups of medullary canals, which rise at right-angles to the functional surface. In most cases there is a single pair of such plates in the lower jaw, meeting at the symphysis, while two pairs (the so-called vomerine and palatine plates) are arranged to oppose these above. A permanent pulp remains under each plate, and growth thus takes place continually within as the oral surface is triturated by wear. In the surviving family of Chimæridæ these dental plates are much thickened, while the hinder upper pair ("palatines") are both closely apposed in the median line and considerably extended backwards. The Jurassic families of Squaloraiidæ and Myriacanthidæ, however, exhibit a more primitive arrangement. Their dental plates are thin, presenting considerable superficial resemblance to those of certain Cochliodont Elasmobranchs (see p. 42). The hinder upper plates are not closely apposed in the median line and the tritoral areas have not any very definite limits or disposition. The Cochliodont plates being proved to result from the fusion of normal crushing teeth, it is thus easy to conceive how the Chimæroid plates may have been developed in a similar manner, the evolution having only proceeded further so that growth is not restricted to the inner border, as in Cochliodonts, but extends to the whole of the attached surface.

The dental plates named *Ptyctodus*, from the Devonian of Russia and North America, are, as already remarked, essentially similar to those of modern Chimæroids, but there are no representatives of the vomerine pair. The tritors, two in number in the typical species, are well differentiated, consisting of hard, punctate, superimposed laminæ, arranged obliquely to the functional surface. The contemporaneous teeth known as *Rhynchodus* and *Palæomylus*, however, exhibit more indefinite tritoral areas. The symphysial facette is always distinct.

Spines which may be compared with those of Chimæroids are also known from Devonian and Carboniferous formations, and *Harpacanthus* may perhaps be cited as an example of a head-spine. No Chimæroid skeletons, however, have hitherto been satisfactorily determined from Palæozoic rocks.

The family of **Squaloraiidæ**, known only by the genus *Squaloraja* from the English Lias, has already been mentioned as exhibiting a comparatively non-specialized dentition. The whole of the skeleton, except that of the median fins, is now tolerably well known.

Squaloraja (fig. 44). The body is depressed but elongated, and the head is produced into a flat rostrum without lateral teeth. The tail gradually tapers to a point, and the median fins are not preserved in

Sub-Class 2. **Holocephali.**—ORDER 1. CHIMÆROIDEI.

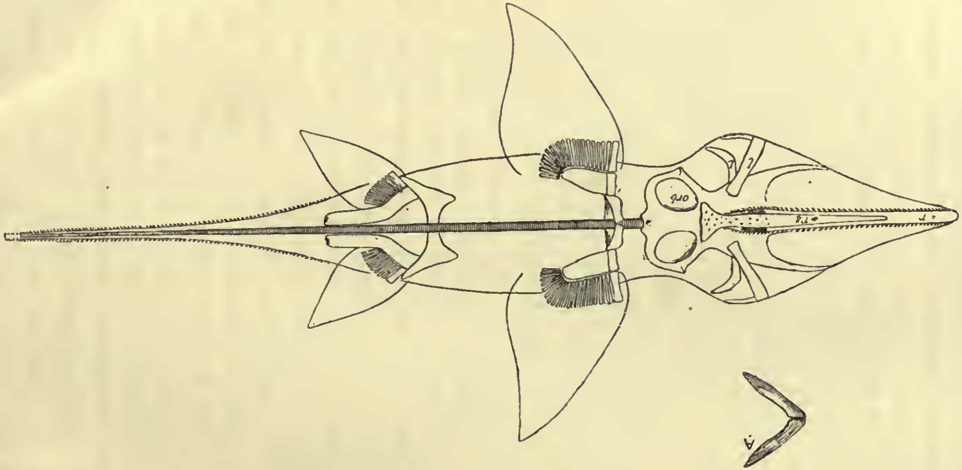

FIG. 44.

Squaloraja polyspondyla; restoration of male, dorsal aspect, one-third nat. size. A, Mandibular dental plates.—L. Jurassic (L. Lias); Dorsetshire. *l*, supposed labial cartilages; *orb.*, orbit; *r*, rostral cartilage; *r.s*, rostral spine. Outlines of fins restored from recent *Harriotta*.

any known specimen. Males exhibit a long, slender, prehensile spine (*r.s*), with a broad base, upon the snout; and there is a cluster of large recurved denticles on the lower aspect of this spine near its insertion. Conical, radiately-sculptured dermal tubercles are also sparsely arranged both on the head and trunk; but none are fused into plates. The cranium exhibits a narrow median rostral cartilage, and a pair of shorter, more slender cartilages extending forwards from the antero-external angles of the olfactory region. Laterally there are also two pairs of very large labial cartilages (*l*), tapering and sharply bent backwards at their outer extremities. The dentition (A) consists of thin, transversely curved plates, without differentiated tritoral areas, but marked with a series of hard, parallel, longitudinal corrugations. The vomerine plates are, as usual, comparatively small; the palatines are closely apposed in the median line anteriorly, but divergent posteriorly. The vertebral rings are especially robust, consisting of several well-calcified concentric lamellæ. Each pectoral fin exhibits only two basal cartilages with a single series of radials. The pelvic fins of the male are produced into claspers armed with a cluster of hooklets. The "lateral line" and the sensory canals of the head are supported by calcified ringlets. *Squaloraja* is known only from the Lower Lias of Lyme Regis, Dorsetshire, the type species being *S. polyspondyla*.

The family of **Myriacanthidæ**, represented by *Myriacanthus*, from the English Lias, and *Chimæropsis*, from the Bavarian Lithographic Stone (Upper Jurassic), is specially remarkable on account of the presence in the front of the lower jaw of a median, bilaterally-symmetrical tooth, shaped like an incisor. The normal dental plates, though appearing robust, are as thin as those of *Squaloraja*, and the punctate tritors have not any very definite limits. The rostral spine of the male resembles that of *Squaloraja*, but the form of the trunk seems to have been less depressed; and one species of *Myriacanthus* is known to exhibit in the male a prolonged snout closely similar to that of the modern *Callorhynchus*.

Myriacanthus (fig. 45). The body is laterally compressed, and the rostral cartilage is produced, bearing a terminal cutaneous flap. A few symmetrically-arranged, tuberculated dermal plates occur on the head; and males exhibit a long, pointed rostral spine with a broad base, bearing a cluster of large recurved denticles on its lower aspect. The symphysial surface of the pair of mandibular dental plates is narrow, and the oral surface is covered by an extended punctate tritoral area, almost or quite continuous. The mode of attachment of the median presymphysial tooth is unknown. Each palatine is thin and plate-like, triangular or irregularly quadrate in form, the outer margin being nearly straight, sharply deflected and thickened, the inner and posterior margins tapering gradually to a thin edge; the punctate tritoral area is continuous on its oral surface. The vomerine dental plate is smaller than the palatine, of triangular form, broad posteriorly, and provided either with a long anteriorly-directed process or with a distinct small tooth in front; its punctate tritoral area is subdivided into rounded patches. There is a large spine in front of the dorsal fin, this being long and slender, somewhat laterally compressed, and with a large internal cavity; its sides are more or less ornamented with small tubercles, while a series of large, thorn-shaped, spinous tubercles is arranged along each edge of its posterior face, passing into a single median row distally, and there is also a single series of similar denticles on at least part of the anterior border. Nothing is known of the trunk. *Myriacanthus* is represented only by two species, *M. paradoxus* and *M. granulatus*, in the Lower Lias of Lyme Regis, Dorsetshire; but several names have been given to detached fragments of the fish.

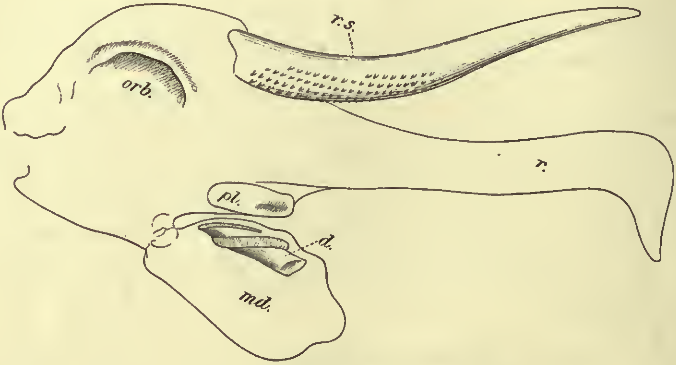

FIG. 45.

Myriacanthus granulatus; outline of fossilized imperfect head, lateral aspect, showing rostral prominence, about one-third nat. size.—L. Jurassic (L. Lias); Dorsetshire. *d*, left mandibular dental plate, oral aspect; *md.*, mandibular cartilage; *orb.*, orbit; *pl.*, so-called palatine dental plate; *r*, production of rostral region; *r.s*, rostral spine of male. (British Museum, no. 43050.)

The family of **Chimæridæ**, which still survives, appears first in the Lower Oolites, but attained its maximum development in the Cretaceous and Eocene periods. In regard to the dentition it exhibits an advance upon the preceding families, as already explained; but in the calcification of the endoskeleton and dermal armour it is comparatively degenerate. The species of the extinct genera attain a much larger size than those of the existing *Chimæra*, *Callorhynchus*, and *Harriotta;* and some idea of the variety in the arrangement of the tritors on their dental plates may be formed by an inspection of the accompanying diagrams (figs. 46, 47). The different types of tritoral arrangement are, indeed, commonly regarded as sufficiently constant to be utilized in defining the genera. Detached dental plates and fin-spines of *Ganodus* and *Ischyodus* occur in the Lower Oolites, but the earliest known complete skeletons are those of *Ischyodus* from the Lithographic Stone or Upper Jurassic (Kimmeridgian) of Bavaria. *Edaphodon* is typically Cretaceous and Eocene, but ranges into the Miocene.

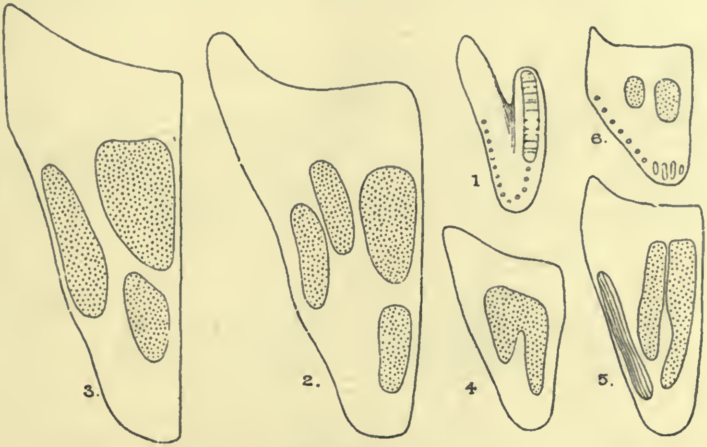

FIG. 46.

Diagram of the oral aspect of the left palatine tooth in the principal genera of Chimæridæ, showing the arrangement of tritors.—1, *Ganodus;* 2, *Ischyodus;* 3, *Edaphodon;* 4, *Callorhynchus;* 5, *Elasmodus;* 6, *Chimæra.* (From *Brit. Mus. Catal.*)

Ischyodus (figs. 46, 47, 2). The form and proportions of the fish are much like those of the existing *Chimæra.* There are no dermal plates, but the canal of the "lateral line" system is strengthened by calcified rings. The head-spine of the male is short, arched, and provided with a terminal cluster of denticles. The spine of the anterior dorsal fin, placed directly over the pectoral arch, is laterally compressed, smooth or longitudinally striated, and with a double series of posterior denticles. The dental plates are all very massive, but the symphysial union of those of the mandible is narrow. The number and disposition of the tritors on the palatine and mandibular plates are almost always as represented in fig. 46, no. 2, and fig. 47, nos. 1, 2. *Ischyodus* ranges from the Lower Oolite to the Lower Chalk; and each mandibular tooth in the type species, *I. townsendi* (from the English Portlandian), sometimes measures as much as 0·014 m. from its symphysial border to the extremity of its post-oral margin.

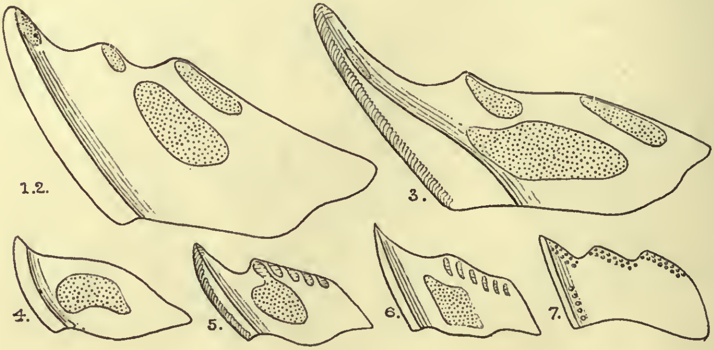

Fig. 47.

Diagram of the inner aspect of the right mandibular tooth in the principal genera of Chimæridæ, showing the arrangement of the tritors and the extent of the symphysis.—1, 2, *Ganodus* and *Ischyodus;* 3, *Edaphodon;* 4, *Callorhynchus;* 5, *Elasmodus;* 6, *Chimæra;* 7, *Elasmodectes.* (From *Brit. Mus. Catal.*)

Sub-Class 3. **Dipnoi.**

The Dipnoan fishes formed a most conspicuous feature in the Palæozoic vertebrate fauna, and did not become entirely insignificant until the period of the Muschelkalk (Trias), after which they seem to have almost, if not quite deserted the sea. Our present knowledge of the facts also suggests, that the Devonian period witnessed the maximum of their development and specialization; one order which seems to be referable to this sub-class comprising great armoured fishes which are no longer met with above the lowermost Carboniferous. The Dipnoi have always been destitute of calcifications in the sheath of the persistent notochord; the membrane-bones of the cranial roof cannot be paralleled by the normal arrangement observed among Teleostomi; the dentition has always been confined to the inner bones of the mouth; and the fin-rays have never advanced in development beyond the delicate filaments (actinotrichia) which cluster round the supports. Moreover, the supports of the median fins have always remained equal in number to the apposed neural and hæmal arches of the trunk, except where these fins have undergone subdivision.

ORDER 1. SIRENOIDEI.

The typical Dipnoi of the Sirenoid order, represented at the present day by *Lepidosiren*, *Protopterus*, and *Ceratodus* (*Epiceratodus*), have numerous Palæozoic representatives which only appear to differ from the modern types in three essential particulars. In these old fishes the cranial roof-bones are small and numerous (fig. 48); the median fins are often subdivided; and the dental plates nearly always exhibit more or less clearly the points of the originally-separate denticles of which they are

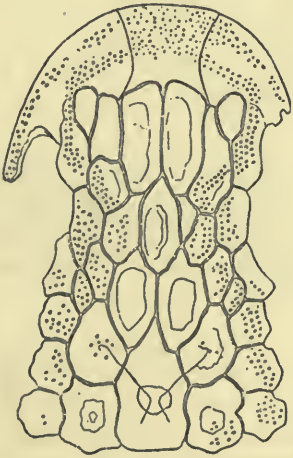

FIG. 48.

Dipterus valenciennesi; roof of skull, imperfect at the sides, and snout pointing upwards, about nat. size.—L. Old Red Sandstone; N. Scotland. (After Pander.)

composed. One family, indeed, the **Uronemidæ**, is characterized by a patch of separate denticles on the bones which ordinarily bear the grinding plates; but it is as yet represented only by one genus (*Uronemus*) from the Calciferous Sandstones and Carboniferous Limestone of Scotland, and perhaps by one other (*Conchopoma*) from the Lower Permian of Germany.

Uronemus. The cranial roof-bones are arranged as in *Dipterus* (fig. 48). The anterior part of the palato-pterygoid bone on each side is broad and flat and covered merely by small rounded tubercles, while along its outer margin there is one row of laterally compressed, basally confluent, short conical teeth. The median fin is continuous, not subdivided even in the anal region. The trunk is covered with very thin cycloidal scales of moderate size. *U. lobatus*, the typical species, attains a length of about 0·2 m.

The Permian genus *Conchopoma*, which also seems to be Dipnoan, resembles *Uronemus* in the non-fusion of the dental tubercles and in the continuity of the median fin; but its scales are smaller. The type species is *C. gadiforme* from the Lower Permian of Rhenish Prussia.

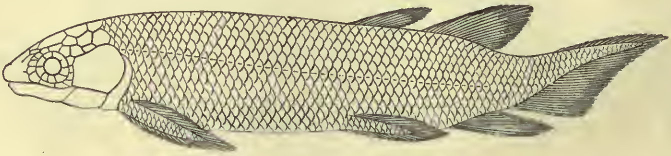

Fig. 49.

Dipterus valenciennesi; restoration by R. H. Traquair, one-fifth nat. size.—L. Old Red Sandstone; N. Scotland.

The most characteristic Palæozoic family of Dipnoi, however, is that of the **Ctenodontidæ**, in which the cranial roof-bones are small and numerous, the dental plates complete, the median fins more or less subdivided, and the scales cycloidal. The earliest genus is *Dipterus* and the latest *Sagenodus*, while *Phaneropleuron*, *Scaumenacia*, and *Ctenodus* are also tolerably well known. The endoskeletal supports of a dismembered median fin have hitherto been observed only in the anal fin of *Scaumenacia*. Here they are distinctly crowded, while at least three basal elements are fused together (fig. 20, p. 22).

Dipterus (figs. 48, 49). The head is much depressed and the snout obtuse. The dental plates, above and below, are triangular in shape, marked with outwardly radiating ridges which are tuberculated or strongly crenulated. A pair of gular plates are present. There are two separate dorsal fins, opposed to the pelvic and anal fins; and the tail is more or less distinctly heterocercal. The scales are invested with dense, punctate enamel in their exposed portion. The genus is exclusively early Devonian, the type species being *D. valenciennesi*, about 0·4 m. in length, from the Old Red Sandstone of N. Scotland.

The acutely lobate paired fins have been observed in the Devonian genera *Dipterus*, *Phaneropleuron*, and *Scaumenacia*, but the endoskeletal supports seem to have been always too slightly calcified for preservation. These genera also exhibit well-developed gular plates, but none have hitherto been recognized in the Carboniferous and Permian *Ctenodus* and *Sagenodus*. It is also curious that no known example of a Palæozoic Dipnoan exhibits certain evidence of anterior teeth corresponding with the so-called vomerine pair in *Ceratodus* (*Epiceratodus*).

The dental plates named *Ceratodus*, identical with those of the existing Barramunda of the Queensland rivers, have a very wide distribution; but they seem to be confined to rocks of Triassic, Rhætic, and Jurassic age, and are extremely rare in the latter. The fossils on which the genus was founded were obtained from the Rhætic Bone-bed of Aust Cliff, near Bristol (*Ceratodus latissimus*); and similar dental plates occur on the same horizon in Leicestershire and Würtemberg. A division of the Muschelkalk (Middle Trias) in Germany yields a great number of plates only specifically distinct, and the Lower Oolites (Jurassic) of England have furnished three diminutive specimens. The Kota-Maleri Group (Triassic) of India is also prolific in these fossils; while one small species occurs in the Karoo Formation (Upper Triassic or Rhætic) of Cape Colony, and another in the Upper Jurassic of Colorado. Dental plates of the ordinary form, as might be expected, are sometimes found in the alluvial deposits of Queensland. Only two fossils hitherto discovered, however, are of value as displaying the characters of the fish to which these dental plates originally belonged. One is an imperfect head of *Ceratodus sturi* from the Upper Keuper of Pölzberg, near Lunz, Austria; the other the caudal region of an undetermined species from the Upper Muschelkalk (Lettenkohle) of Bavaria. The Austrian specimen proves that the head of the original early Mesozoic *Ceratodus* exhibits the same arrangement of bones as that of the living fish from Queensland, only differing in its higher degree of ossification; for in *C. sturi* the cheek-plates which remain cartilaginous in *C. forsteri* are all bony, and the visceral arches are much more completely ossified. The tail from Würtemberg proves also that the dermal rays in the caudal fin are stouter than those of the existing fish.

Compared with its ancestors, the modern *Ceratodus* (*Epiceratodus*) is thus slightly degenerate in the ossification of the skeleton. The same remark applies to the existing sturgeons and batrachians.

ORDER 2. ARTHRODIRA.

The systematic position of this extinct order is indeed doubtful; but in the present state of knowledge the remarkable fishes contained in it are most satisfactorily interpreted on the supposition, that at the period of their dominance in Palæozoic times the Dipnoi attained extreme specialization and developed a tribe of armoured forms. The Devonian *Coccosteus* and its allies, which constitute the order, are fishes with both head and trunk armoured; and in the more specialized genera the shield of the abdominal region articulates with the head-shield in ginglymoid facettes which admit of free motion. The name ARTHRODIRA (joint-neck) has reference to this remarkable character. There is no trace of a hyomandibular bone in the most exquisitely preserved specimens; and all appearances in certain well-preserved American skulls of *Dinichthys* are in favour of the supposition that they are truly autostylic. The upper dentition is confined to the elements of the pterygo-palatine arch and the vomers: and only one ossification has been observed in each ramus of the mandible. The jaws of *Dinichthys* are most nearly paralleled by those of the existing *Lepidosiren* and *Protopterus*; and the loose triturating plates of *Mylostoma* only differ in unessential particulars from those of *Ceratodus*. The notochord is persistent, and in *Coccosteus* the supports of the median fin are equal in number to the apposed arches of the endoskeleton. The paired fins are rudimentary.

In the **Coccosteidæ** the head-shield consists of few plates, and is sometimes notched for the orbits, sometimes encircles them. The narial openings are seen near the front border of the shield. The maxilla and premaxilla are well-developed but toothless. The dentition, when present, consists of conical teeth fused with the oral margin of the mandible and with two inner pairs of bones in the upper jaw (presumably palatine and vomerine). The abdominal region is armoured both dorsally and ventrally, the large dorsal plate having a deep inner longitudinal keel, evidently for connection with the neural arches of the endoskeletal axis.

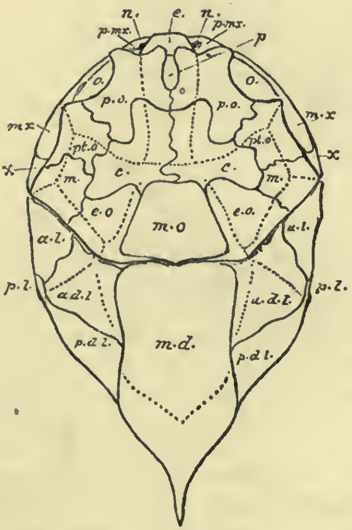

Fig. 50.

Coccosteus decipiens; restoration of cranial and dorsal shield by R. H. Traquair, about one-third nat. size.—L. Old Red Sandstone; N. Scotland. *a.d.l.*, anterior dorso-lateral; *a.l.*, anterior lateral; *c*, central; *e*, ethmoid; *e.o.*, external occipital; *m*, marginal; *m.d.*, median dorsal; *m.o.*, median occipital; *mx.*, maxillo-suborbital; *n*, narial opening; *o*, orbit; *p*, pineal; *p.d.l.*, posterior dorso-lateral; *p.l.*, posterior lateral; *p.mx.*, premaxilla; *p.o.*, preorbital; *pt.o.*, postorbital; *x*, operculum (?). The dotted lines indicate the course of the mucus-canals.

Coccosteus (figs. 50—52). The cranial shield in this genus is irregularly six-sided in shape, and the notches for the orbit (fig. 50, *o.*) are far forwards. The arrangement of the plates as seen from above is indicated in fig. 50, and the median element (*p.*), pitted on its visceral aspect apparently for the reception of the pineal body, is noteworthy. A large bone on the cheek (*mx.*) sends forwards a narrow process beneath the eye, and may be either maxilla or suborbital or both. In front it meets a small toothless plate, which is perhaps a premaxilla (*p.mx.*) and seems to bound the narial opening (*n.*) below. Behind, there is a triangular element (*x.*), which occupies the position of an operculum. Within the orbit traces of a delicate ossified sclerotic ring, apparently continuous, are sometimes observable. The chondrocranium is entirely unknown, but in an allied genus, *Chelyophorus*, the parachordal cartilages are ossified, and there seem to be distinct exoccipitals. Two pairs of bones on the palate bear conical teeth. The single bone in each ramus of the mandible has similar teeth in its middle portion, and is denticulated on the anterior margin where it meets its fellow of the opposite side. The line of separation between the cranial and abdominal armour forms a prominent cleft; and the ginglymoid articulation on each side takes place between a process on the anterior dorso-lateral plate (*a.d.l.*) and a cavity beneath the external occipital (*e.o.*). Immediately in advance

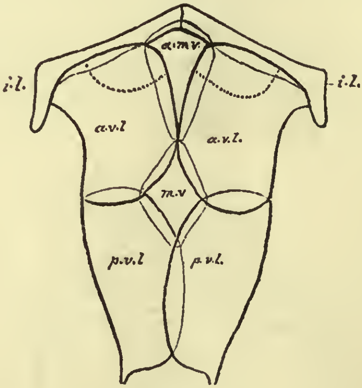

Fig. 51.

Coccosteus decipiens; restoration of ventral shield by R. H. Traquair, about one-third nat. size.—L. Old Red Sandstone; N. Scotland. *a.m.v.*, anterior median ventral; *a.v.l.*, anterior ventro-lateral; *i.l.*, inter-lateral (? clavicle); *m.v.*, median ventral; *p.v.l.*, posterior ventro-lateral. The thick lines represent the exposed borders of the plates; the thin lines indicate the extent and direction of overlap. The dotted line marks the course of a mucus-canal.

of the ventro-lateral plates of the trunk there is observed a pair of clavicle-shaped elements (fig. 51, *i.l.*), but no conclusive evidence of pectoral fins has been noted. There are, however, traces of pelvic fins (fig. 52), each supported by a stout basal cartilage. The hinder abdominal and caudal regions are destitute of armour, the only dermal calcification occurring in a narrow band along the lateral line. The notochord must have been persistent, but the stout arches are all superficially calcified, of the form and proportions shown in fig. 52. The dorsal fin-supports are equally calcified, but the fin itself appears to have been membranous. A problematical small plate, showing prominent concentric lines of growth, is also conspicuous in the abdominal region immediately behind the much-elongated hæmal arches, and may have been an internal element of support in the vertical septum between the right and left halves of some paired organ. The genus *Coccosteus* occurs in the Devonian both of Europe and America, and all the species are of comparatively small size, none probably exceeding half a metre in length. The typical and best-known species (*C. decipiens*) is met with in a fine state of preservation in the Old Red Sandstone of Banff, Nairn, Cromarty, Ross, Caithness, and the Orkney Isles.

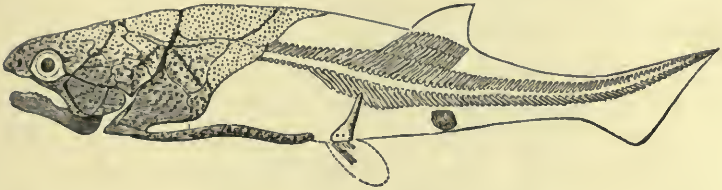

FIG. 52.

Coccosteus decipiens; restoration, lateral aspect, about one-quarter nat. size.—L. Old Red Sandstone; N. Scotland. The heterocercal caudal fin is hypothetical; the terminal fin may have been diphycercal. (From *Brit. Mus. Catal.*)

Homosteus (fig. 53). Often erroneously quoted (after Hugh Miller) as *Asterolepis.* The head-shield in this genus encircles the orbits, and the jaws appear to be toothless. The body-shield is comparatively short, and clasps the head-shield on either side by a long, forwardly-directed process outside the articular facette. The orbits (*o*) are remarkably far forwards, the pineal plate being between their front half; and the so-called occipital plates (*e.o.*, *m.o.*) are excessively elongated antero-posteriorly. The visceral face of the "median occipital" exhibits certain markings which may denote attachment of the septa occurring between the muscle-plates; and in that case the brain would be entirely in advance of this plate; the shield would, indeed, represent much more than a cranial roof. *Homosteus milleri*, from the Old Red Sandstone of Caithness and Orkney, has a shield measuring 0·3 m. across; at least one species from Dorpat, Livonia, is still larger.

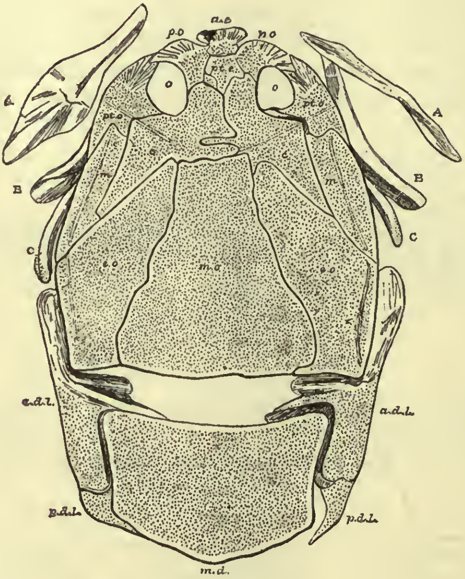

Fig. 53.

Homosteus milleri; cranial and dorsal shield, one-sixth nat. size.—L. Old Red Sandstone; Caithness. A, B, C, undetermined bones; *a.d.l.*, anterior dorso-lateral; *a.e.*, ethmoid; *c*, central; *e.o.*, external occipital; *m*, marginal; *m.d.*, median dorsal; *m.o.*, median occipital; *o*, orbit; *p.d.l.*, posterior dorso-lateral; *p.o.*, preorbital; *pt.e.*, pineal; *pt.o.*, postorbital. The double lines indicate the course of the mucus-canals. (After Traquair.)

Dinichthys. A genus comprising fishes of gigantic size, the head-shield sometimes measuring a metre across. The elements of the head-shield are almost or completely fused together in the adult, and the pineal plate exhibits a minute perforation above the pineal body. The orbits form notches in the shield, and the eyes are provided with a ring of a few sclerotic plates. The toothless maxillo-suborbital is distinct. The mandibular rami are suturally united at the symphysis, each beak-shaped in front and bearing a short, single series of acute teeth anchylosed with its border. The anterior upper teeth are also beak-shaped. The armour of the trunk closely resembles that of *Coccosteus* and *Homosteus.* The axial skeleton and pelvic fins also seem to have been similar to those of *Coccosteus.* The typical species (*Dinichthys hertzeri*) and several others occur in the uppermost Devonian of Ohio. Some from the State of New York are perhaps Lower Carboniferous. Characteristic fragments are also known from the Devonian of Belgium.

Sub-Class 4. **Teleostomi.**

The hyostylic fishes commonly named Ganoidei and Teleostei form a continuous series, and are grouped (by Owen) in a sub-class TELEOSTOMI distinguished from the preceding sub-classes by the regular development of dentigerous membrane bones on the margin of the jaw above and below. The skeleton is always more or less ossified, with well-developed membrane bones. The gill-clefts are feebly separated, opening into an external cavity covered by a bony operculum. The exoskeleton, when present, consists either of true bone, or of delicate, superposed, calcified lamellæ.

Among the earliest (Lower Devonian) Teleostomi there are representatives of both the great orders, Crossopterygii and Actinopterygii; but the former considerably predominate, and the latter only become significant in the Carboniferous. Most of the Crossopterygians became extinct before the close of the Mesozoic Era.

ORDER 1. CROSSOPTERYGII.

No Teleostomatous fish is known with a more primitive type of paired fin than the lobate form termed "archipterygium" by Gegenbaur. The lowest Order hitherto recognized is therefore that of the CROSSOPTERYGII (fringe-finned ganoids). This, however, may admit of further subdivision; for whereas all the Palæozoic and Mesozoic fishes comprised in it have unibasal paired fins (like those of *Ceratodus*), the recent *Polypterus* and *Calamoichthys* exhibit a tribasal pectoral fin (like that of typical modern Elasmobranchs). The latter type is unknown among extinct Crossopterygians, even those which have the lobate paired fin abbreviated (fig. 23, p. 25) exhibiting a single basal segment of cartilage supporting a shortened, crowded, and partially-fused "archipterygium."

The earliest Crossopterygians, especially those with acutely-lobate paired fins, exhibit a remarkable resemblance to the Dipnoi. It is also noteworthy that their larger teeth are sometimes characterized by a complexity of minute structure (fig. 54), due to infoldings of the enamelled dentine wall, only equalled and exceeded by those of the great Labyrinthodont Batrachia (fig. 90, p. 138). The hyostylic character of the skull, however, is definitely proved in several genera (e.g., *Holoptychius*, *Rhizodopsis*, and the Cœlacanthidæ); while the arrangement of the cranial roof-bones conforms to the normal Teleostomatous type, and makes no approach to the anomalous condition observable among Dipnoi. During the evolution of the Order, (i.) the paired fins become abbreviated, (ii.) the supports of the median fins tend towards reduction to a single series, (iii.) these supports sometimes become correlated in part with the dermal fin-rays, and (iv.) there is sometimes degeneration in the external armour of the head and opercular region, some plates being fused together, others being lost. The reduction in the complexity of the mandibular ramus is especially noteworthy.

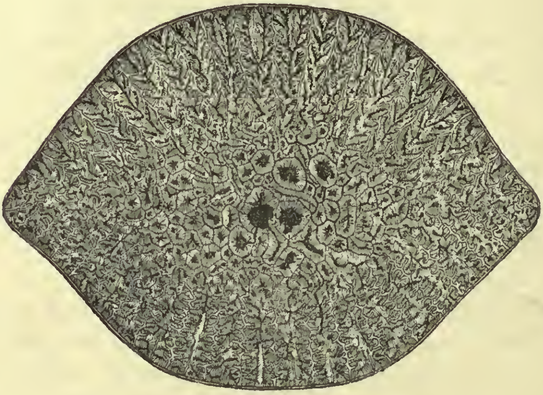

Fig. 54.

Transverse section of Holoptychian (Dendrodont) Tooth, much magnified.—Devonian; N. W. Russia. (After Pander.)

Sub-Order 1. *Haplistia.*

The sub-orders of Crossopterygians are most conveniently based on the condition of the median fins, and the first is as yet only very doubtfully determined. It is defined as comprising those families in which the supports of the median fins are in two simple regular series (i.e., baseosts above axonosts), much fewer in number than the dermal rays. The only genus which can be even provisionally placed here is the remarkable Lower Carboniferous fish named

Tarrasius. A small, elongated, laterally compressed fish, not known to attain a greater length than 0·06 m. The membrane-bones of the head and opercular fold are well developed, and their exposed faces coated with ganoine. The notochord must have been persistent. The pectoral fins are obtusely lobate, but the pelvic fins are unknown. There is one continuous median fin extending from the back to the anal region, supported apparently by a double regular series of cartilages, more numerous than the apposed arches of the axial skeleton. The abdominal region is naked, while the caudal region is enveloped in very small, thick, quadrangular, ganoid scales, which scarcely overlap but are closely arranged. The single known species, *T. problematicus*, occurs in the Calciferous Sandstones (Lower Carboniferous) of Glencartholm, Eskdale, Dumfriesshire.

Sub-Order 2. *Rhipidistia.*

In this sub-order the median fins are always more or less subdivided by the process of concentration of supports, already described in the anal fin of the Dipnoan genus *Scaumenacia* (fig. 20, p. 22). In each of the dorsal and anal fins the proximal supports (axonosts) are fused into a single piece, while the development of the distal supports (baseosts) is variable, though these are always much fewer than the comparatively delicate dermal rays which overlap them (fig. 19, p. 22). The notochord must have been more or less persistent, though some genera exhibit completed ring-vertebræ. Each ramus of the mandible comprises a series of stout, dentigerous elements between the normal splenial and dentary; and the dentary is also bordered below by three or four distinct "infradentary" plates (fig. 56 A, p. 73).

Three families of Rhipidistia are distinguishable, and of these it is noteworthy that the Holoptychiidæ, with acutely lobate pectoral fins, are the oldest. These, at least, are not known to range above the Upper Devonian, whereas the Rhizodontidæ and Osteolepidæ, though appearing equally early so far as known, seem to have attained their maximum specialization in the Carboniferous, and one genus of the latter survives even in the Lower Permian.

The **Holoptychiidæ**, or **Dendrodontidæ**, as they are sometimes termed in allusion to the complicated structure of the teeth (fig. 54, p. 70), are represented only by the typical genus *Holoptychius* and the essentially identical *Glyptolepis*.

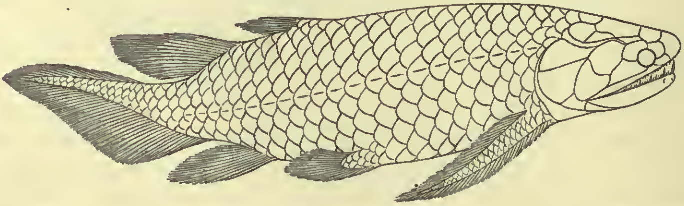

Fig. 55.

Holoptychius flemingi; outline restoration by R. H. Traquair, one-eighth nat. size, the ornamentation omitted—U. Old Red Sandstone; Dura Den, Fifeshire.

Holoptychius (figs. 19, 55). A round-bodied fish, covered with thick, deeply overlapping, cycloidal scales, which are ornamented in their exposed portion with irregular wrinkles and ridges of ganoine. The head is completely invested with dermal and membrane-bones, which are ornamented with tubercles and rugæ of ganoine. The parietals are large and separate; the frontals are also separate, not fused into a continuous plate with the adjoining elements, and there is no parietal or frontal foramen. The dentary bone of the mandible is thin and deep, bearing a series of small teeth, and with well-developed infradentaries which turn inwards below; the splenial is subdivided into a series of large, broad, shuttle-shaped bones, each supporting a large tooth. The operculum and suboperculum are present, but the preoperculum and interoperculum seem to be wanting. The gular plates entirely cover the space between the mandibular rami, comprising one large pair flanked on either side by a small lateral series. No ossifications have been observed in the notochordal sheath. The pectoral fins are long and acutely lobate, but the pelvic fins are much shorter with an obtuse lobe; the supporting cartilages are unknown. There are

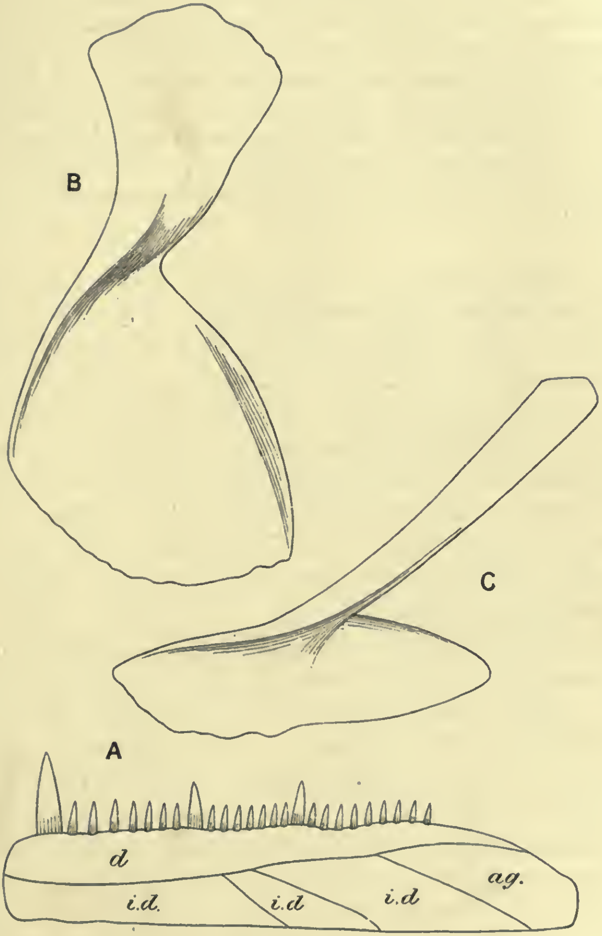

Fig. 56.

Rhizodus hibberti; left mandibular ramus from the outer aspect (A), right clavicle from inner aspect (B), and right infraclavicle from inner aspect (C), all about one-quarter nat. size.—L. Carboniferous; Midlothian. *ag.*, angular; *d*, dentary; *i.d.*, infradentaries. (From *Brit. Mus. Catal.*)

two dorsal fins, both remote and the foremost nearly opposite the pelvic pair; and their supporting elements are arranged in the sub-genus *Glyptolepis* as shown in fig. 19, p. 22. The anal fin is separate, though small; while the caudal fin is heterocercal, the upper lobe small, the lower lobe triangular and obliquely truncated. The typical species, *H. nobilissimus*, and another well-known form, *H. flemingi* (fig. 55), occur in the Upper Old Red Sandstone of South Scotland, perhaps also in the Upper Devonian of Belgium and N.W. Russia. Other fragmentary remains are found in the Upper Devonian of North America. *Holoptychius* (*Glyptolepis*) *leptopterus* is abundant in the somewhat earlier Old Red Sandstone of the north of Scotland.

The **Rhizodontidæ** exhibit the teeth with a larger central cavity and a less complicated infolding of its walls than is observable in the previous family. In this respect they are thus less specialized than the Holoptychiidæ (Dendrodontidæ); but they often show robust ossifications in the notochordal sheath, and the paired fins are always obtusely lobate, more or less abbreviated. *Tristichopterus*, *Eusthenopteron*, and *Gyroptychius* are well-known Devonian genera, while *Rhizodopsis* is equally well preserved in the Carboniferous. *Rhizodus* and *Strepsodus* are very large fishes known only by fragmentary specimens from the Carboniferous.

Rhizodus is confined to the Lower Carboniferous, and the mandibular ramus of *R. hibberti* (fig. 56 A) from the Edinburgh district usually measures about 0·3 m. in length. The largest teeth are about 0·12 m. in height, and compressed to a pair of sharp edges: they probably represent a jaw 0·6 m. in length. The most remarkable feature of the genus is the extremely firm union of the infraclavicle with the clavicle, the former element (fig. 56 C) bearing a long upwardly-directed process apposed to the hollow on the inner face of the latter (fig. 56 B), which is slightly twisted at its middle. *Strepsodus* appears to be almost identical, except that its teeth are round in section; the species range throughout the Carboniferous, but the largest and finest forms occur in the Coal Measures proper.

Rhizodopsis (fig. 57). In this, as in the other Rhizodonts, the cranial cartilage is in some degree ossified. It is entirely covered with thick membrane-bones or dermal plates, exhibiting a bilaterally-symmetrical arrangement except towards the end of the rostrum; and there is, similarly, a considerable development of membrane-bones on the roof of the mouth. The shield of the cranial roof is divided by a much-pronounced transverse suture into a small frontal, and relatively large parietal portion, the former excavated on each side at the upper border of the orbit. The parietal portion of the shield consists chiefly of a long, narrow pair of parietal bones (*pa.*) extending its whole length, flanked by a pair of squamosal elements (*sq.*) in the hinder half, and by a pair of postfrontal plates (*p. f.*) in advance of these. The posterior half of the frontal shield is formed by the frontals (*f.*), which meet in the middle line without a median (pineal) foramen. The orbits (*or.*) are remarkably far forwards. The plates over the ethmoid region are irregular, apparently more or less

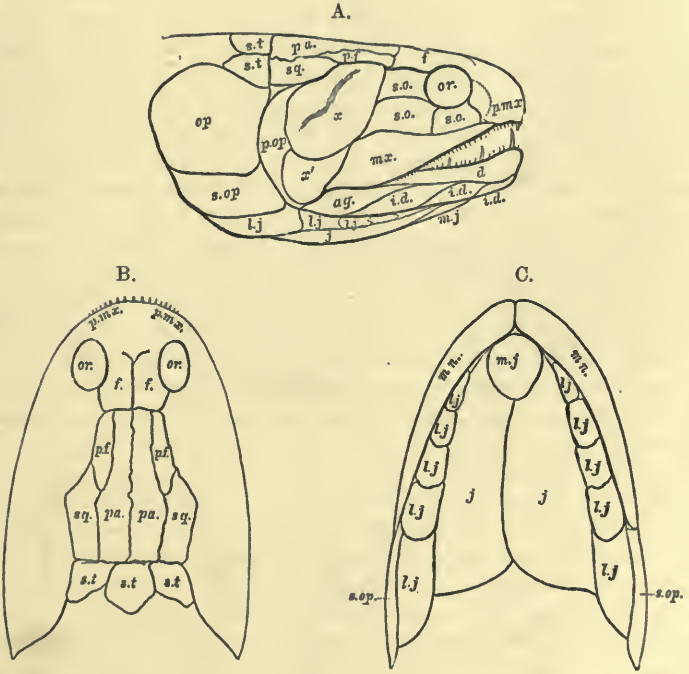

Fig. 57.

Rhizodopsis sauroides; outline restorations of head and opercular apparatus from the lateral (A), superior (B), and inferior (C) aspects, about one-half nat. size.—U. Carboniferous; Staffordshire. *ag.*, angular; *d.* dentary; *f.*, frontal; *i.d.*, infradentary; *j.*, principal gular (jugular); *l.j.*, lateral gular (jugular); *m.j.*, median gular (jugular); *mn.*, mandible; *mx.*, maxilla; *op.*, operculum; *or.*, orbit; *p.f.*, postfrontal; *p.mx.*, premaxilla; *p.op.*, preoperculum; *pa.*, parietal; *s.o.*, suborbital; *s.op.*, suboperculum; *s.t.*, supratemporal; *sq.*, squamosal; *x*, *x'*, cheek-plates. (After Traquair.)

fused together and with the premaxillæ (*p.mx.*). The cheek is entirely covered with loose plates, of which the suborbitals (*s. o.*) are conspicuous; the dentigerous maxilla (*mx.*) bounds these below, and exhibits a small, apparently jugal plate (*x'.*) behind its posterior expansion. The latter element extends far backwards, and immediately above it is a very large cheek-plate (*x.*) covering the whole of the space between the posterior suborbitals, the cranial roof, and the preoperculum. At the base of the skull there is a well-ossified parasphenoid, meeting in front a pair of vomers, each of which bears a powerful tooth; and there are some traces of an inward palatal extension both of the maxillæ and premaxillæ. The mandible exhibits the usual complexity and seems to possess a distinctly ossified articular element. The dentary bone (*d*) is relatively deep and thick at the symphysis, tapering backwards, and bears a series of small teeth, with a single large cutting tooth (laniary) in front. Its lower border is bounded by a series of four plate-like, lenticular bones, of which the hindermost seems to correspond to the angular (*ag.*), while the others are conveniently termed infradentaries (*i. d.*). A thin splenial lamina forms the inner wall of the ramus, while between this and the dentary is arranged a series of about three very stout lenticular bones, each of which bears a large tooth. A deep and narrow preoperculum (*p. op.*) is conspicuous, while the operculum (*op.*) and suboperculum (*s. op.*) are well developed, without any trace of an interoperculum. Below the suboperculum a long narrow plate forms the hinder element of the series of lateral gulars (*l. j.*) on each side; and a pair of very large principal gular plates (*j.*), with a small anterior azygous element (*m. j.*), occupies the whole of the space between these series. The teeth are round in section. The cranial roof is bordered behind by three small supratemporal plates (*s. t.*), one median and a pair lateral; but there appear to be no large scales on the posterior margin of the pectoral arch. There are well-ossified ring-vertebræ. The infraclavicle is destitute of an ascending articular process; the two dorsal fins are remote and directly opposed to the pelvic and anal fins; the tail is heterocercal, the caudal fin rhombic in form. The scales are thin, ovoid, and deeply imbricating, each marked with a median boss on its inner face. The typical species *R. sauroides*, attaining a length of not more than 0·5 m., is widely distributed in the Coal Measures.

Eusthenopteron (figs. 23, 58). A fish closely resembling *Rhizodopsis*, but with laterally compressed teeth and nearly diphycercal caudal fin, which is truncated or wavy at the hinder border. A pineal foramen occurs between the frontal bones. The eye is provided with a ring of sclerotic plates. The examples of the typical and only known species, *E. foordi*, from the Upper Devonian of Canada, are important as displaying the calcified supporting cartilages of some of the fins. The pectoral fin (figs. 23, 58) has only one stout basal cartilage, and is simply Gegenbaur's "archipterygium" partly atrophied, with some elements fused together. The bases of the second dorsal and anal fins are shown to be almost identical, each having three baseosts supported by the broad end of a single axonost, which is directly apposed to a single arch of the axial skeleton. There are calcified ring-vertebræ in the abdominal region.

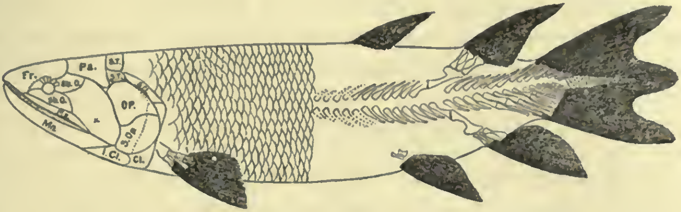

Fig. 58.

Eusthenopteron foordi; restoration by J. F. Whiteaves, one-quarter nat. size, scales omitted in caudal region to expose axial skeleton and bases of median fins.—U. Devonian; Scaumenac Bay, Canada. *cl.*, clavicle; *fr.*, frontal; *i.cl.*, infraclavicle; *mn.*, mandible; *mx.*, maxilla; *op.*, operculum; *pa.*, parietal; *s.cl.*, supraclavicle; *s.op.*, suboperculum; *s.t.*, supratemporal; *sb.o.*, suborbital; *x*, cheek-plate.

Through *Rhizodopsis* and *Gyroptychius* the Rhizodontidæ pass almost imperceptibly into the **Osteolepidæ**, which have rhombic scales and usually exhibit the fusion of the bones in the frontal portion of the skull and in the mandible. The external bones and scales are covered with a more or less continuous layer of ganoine, often punctate; and in the four

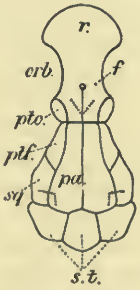

Fig. 59.

Osteolepis microlepidotus; outline of cranial roof, somewhat enlarged.—L. Old Red Sandstone; Caithness. *f.*, frontal; *orb.*, orbit; *pa.*, parietal; *pt.f.*, postfrontal; *pt.o.*, postorbital; *r.*, fused plates of rostrum; *s.t.*, supratemporals; *sq.*, squamosal. Dotted lines mark mucus-canals.

typical genera this ganoine extends over some of the anterior rays of each of the fins. *Osteolepis*, *Thursius*, and *Diplopterus* exhibit a pineal foramen in the frontal region (fig. 59), and are characteristic of the Lower Old Red Sandstone of Scotland. *Megalichthys* has no pineal foramen, and ranges throughout the Carboniferous and Lower Permian both in Europe and America.

Sub-Order 3. *Actinistia.*

Some of the Palæozoic Crossopterygians became extremely specialized chiefly by degeneration, forming the sub-order ACTINISTIA with the single family of **Cœlacanthidæ.** These have perhaps the most remarkable range of all known extinct fishes, occurring almost unchanged throughout the whole series of formations from the Lower Carboniferous to the Upper Chalk. The group is specialized in the large symmetrical caudal fin, which exhibits a series of supports directly apposed to the neural and hæmal arches, equalling in number both these and the overlapping dermal rays. It is also specialized in (i.) the fusion of the bones of the pterygo-quadrate arcade, (ii.) the reduction of the infradentaries to one, (iii.) the reduction of the opercular apparatus to the operculum on each side and a pair of gular plates, (iv.) the loss of the baseosts in the anterior dorsal fin, and (v.) the ossification of the air-bladder. An undetermined genus is represented by one fragmentary fossil from the Upper Devonian of Germany; *Cœlacanthus* ranges throughout the Carboniferous and Permian; *Undina* (fig. 60) is the best-known Jurassic genus; while *Macropoma* is Upper Cretaceous.

Macropoma. As fine specimens of this fish occur almost uncrushed in the English Chalk, it serves best to illustrate the osteological characters of the family to which it belongs. The chondrocranium is extensively ossified, but there is no interorbital septum. The membrane-bones of the roof form a continuous shield, the short parietal region being nearly parallel with the base of the skull, the longer frontal region meeting this in an angle and sloping downwards. The hinder region comprises a pair of large bones meeting in the middle line, evidently to be regarded as parietals, flanked postero-externally by a pair of triangular bones, which appear to represent the squamosal fused with the supratemporal. The frontals are long and narrow, separated by a suture at the median line and flanked on each outer margin by a single series of small square membrane-bones, which have been named parafrontals. The hyomandibular and pterygo-quadrate arcade are fused into a continuous triangular, lamelliform bone on each side, articulating with the hinder portion of the cranium above, and provided postero-inferiorly with a ginglymoid condyle for the articulation of the mandible below. In front of the pterygo-quadrates there is a small pair of thin palatine bones with more or less formidable teeth. A long slender parasphenoid bone occupies the greater part of the base of the skull ending in a spatulate expansion anteriorly, where it meets a large unpaired robust element, with a cluster of strong teeth, evidently to be regarded as the coalesced vomers. The actual termination of the snout is unknown. The eye is surrounded by a ring of small, delicate sclerotic plates. The cheek behind the eye is covered by two large plates, and immediately below these is another membrane-bone, named the post-maxillary. A single narrow suborbital plate extends from the postorbitals to the edge of the anterior portion of the cranial roof. There is a long and narrow dentigerous maxilla, but the premaxilla is not certainly known. The greater portion of each mandibular ramus is formed by a long, narrow articulo-angular element, extended a little behind its articulation with the quadrate. The small, toothless dentary meets this bone in front, reaching to the symphysis, and bounded below by a thin infradentary. A long and deep laminar splenial bone, tapering in front, but with a straight dentigerous border in the greater part of its length, is apposed to the dentary and articulo-angular on their inner face; and this forms the inner wall of a vacuity existing between the upper portion of the two outer elements. The branchial arches are in four or five pairs, like those of *Polypterus* and modern bony fishes; and the copula is a single large bone, with spatulate hinder extremity. There are no traces of ossifications in the sheath of the notochord, but the arches are superficially ossified. The two halves of each neural arch are firmly united with their appended spine; the hæmal arches are delicate and rudimentary in the abdominal region, but correspond in development with the opposed neural arches in the caudal region. The long, gently curved clavicle exhibits a robust postclavicular process, and its lower spatulate extremity is overlapped by a slender infraclavicle which meets its fellow of the opposite side below. The pelvic fins are supported by a pair of elongated, slender basipterygia with an inwardly-directed process at the distal end, by which they are loosely apposed in the median line. The cartilages in the lobe of each of the paired fins are unknown. Of the two dorsal fins, the anterior is destitute of baseosts, the stout dermal rays articulating with the upper border of the single laminar axonost. This fin therefore exhibits no lobation. The posterior dorsal fin and the opposed anal resemble the paired fins in being distinctly lobate, but none of the baseosts are preserved; the axonost in each of these fins is a forked bone. The caudal fin is symmetrical and supported by a single series of long, slender bones above and below, equalling in number and directly apposed to the blunt distal extremities of the neural and hæmal spines of the axial skeleton. A single stout dermal ray is connected with each of these elements by a simple overlapping articulation ; and a vacant space is left in the fossils apparently for the production of the extremity of the axial skeleton beyond this fin. None of the fin-rays are bifurcated, but all are more or less articulated distally, and there is a double series of small, upwardly-pointing denticles on almost all the rays of the first dorsal and caudal fins. The deeply-overlapping scales are ornamented with elongated denticles of ganoine. The ossified air-bladder is conspicuous in all fossils, its walls being formed of three paired longitudinal series of large imbricating, bony laminæ, each composed of a number of superposed lamellæ. The type species of *Macropoma* is *M. mantelli* from the Chalk of S.E. England, attaining a length of about half a metre. The genus also occurs in the Lower Chalk of Bohemia.

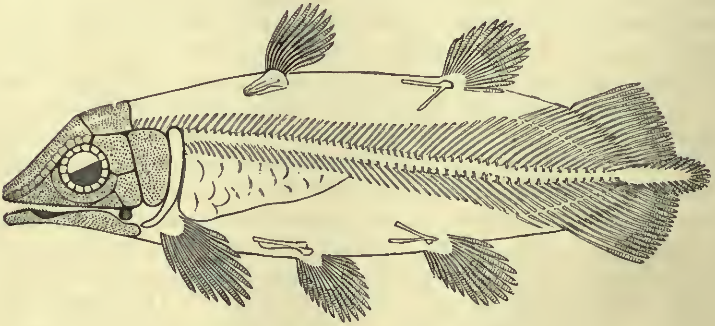

Fig. 60.

Undina gulo ; restoration, omitting scales and supraclavicle, about one-seventh nat. size.—L. Jurassic (L. Lias); Dorsetshire. The extent of the ossified air-bladder is indicated beneath the notochordal axis in the abdominal region. (From *Brit. Mus. Catal.*)

The fins of the Cœlacanthidæ are best understood from an examination of the beautifully-preserved examples of the Jurassic genus *Undina* (fig. 60). They are as already described in *Macropoma*, with the addition of a minute supplementary caudal fin, which has been observed in nearly all members of the family. The endoskeletal supports of this fin, however, are unknown.

ORDER 2. ACTINOPTERYGII. - Heterocerci

The genus *Cheirolepis*, which represents the earliest group of Teleostomatous fishes with abbreviate or non-lobate paired fins, is contemporaneous with the oldest Crossopterygians hitherto discovered. Like its numerous allies of a later period, it differs from the Crossopterygians not only in its abbreviate paired fins, but also in its completely heterocercal tail and in the development of a paired series of transversely-elongated rays to replace the pair of gular plates in the branchiostegal membrane between the mandibular rami. Nevertheless, the sub-order it represents agrees with the Crossopterygii in the feebleness of ossification in the notochordal sheath, in the presence of infraclavicular plates, and in the fact that the supports of the dorsal and anal fins are less numerous than the dermal rays apposed to them.

So far as known, this was the only type of Actinopterygian existing until the Permian period, when another sub-order arose through four simultaneous modifications in the skeleton:—(i.) the atrophy of the upper caudal lobe, (ii.) the loss of the baseosts in the pelvic fins, (iii.) the correlation in number of the dermal rays in the dorsal and anal fins with their endoskeletal supports, and (iv.) the loss of the infraclavicles. In this dominant group of the Mesozoic period, many of the same minor modifications as those of the Palæozoic sub-order may be observed.

Early in the Jurassic period a still more specialized type began to appear, when (i.) the mandibular ramus almost or completely lost all elements but two, (ii.) the baseosts of the pectoral fins were reduced to four or five, (iii.) the vertebral centra were always complete, and (iv.) the superficial ganoine gradually disappeared. All members of the latter group, except a few of the earliest, fall under the common denomination of "Teleostei," but the fossils afford little or no information as to the characters of the intestine and none as to the nature of the optic nerves and heart of the extinct forms.

Sub-Order 1. *Chondrostei.*

Palæontology seems to demonstrate that the modern sturgeons and paddle-fishes are the highly specialized (in some respects degenerate) representatives of the most primitive group of Actinopterygians to which reference has been made above. The skeletal characters they exhibit, of sub-ordinal value, are (i.) the presence of well-developed baseosts in the pelvic fins, (ii.) the non-correlation of the dermal rays of the dorsal and anal fins with their supporting cartilages which form a regular series, and (iii.) the presence of infraclavicular plates. The heterocercal tail is also of prime significance; but the degeneration of the teeth and scales and most of the minor modifications in the head appear to be characters of secondary importance. These modern fishes represent only four genera and two families, whereas at least five extinct families can be recognized, the earliest with very numerous and very varied members.

The earliest Chondrostei exhibit the most nearly complete and normal development of the external head-bones and opercular bones, while they also are characterized by the most regular squamation. They are commonly grouped together in the family of **Palæoniscidæ**, but exhibit much more variety than is usual in families among modern fishes. They range from the Lower Devonian to the uppermost Jurassic (Purbeck Beds) inclusive, but are most abundant in the late Palæozoic rocks, rare in Mesozoic formations. No single genus is sufficiently well known to exhibit all its osteological characters, and the description of the skeleton of the Palæoniscidæ must therefore be of a general nature.

The Palæoniscid chondrocranium is unsatisfactorily known, but the membrane-bones are always conspicuous in well-preserved specimens. The cranial roof is provided with a continuous shield, of which a small pair of parietals (fig. 61, *p.*) and the flanking squamosal plates (*q.*) form the hinder portion, while a large pair of elongated frontals (*f.*), with or without a separate pair of lateral plates, constitutes the middle portion; a large rostral plate (*e.*) completing the shield anteriorly, is flanked on each side by a so-called anterior frontal element (*a. f.*), and with the latter surrounds the pair of narial openings (*n.*). The parasphenoid is well developed. The maxilla (*mx.*) is a narrow, elongated element, always much expanded behind; the premaxilla (*pmx.*) is comparatively small. A narrow ring of about four circumorbital bones surrounds the eye, and these are bounded behind by other cheek-plates of the suborbital series (*s. o.*). The preoperculum (*p. op.*) also extends forwards upon the cheek. In the mandible the articular portion of the meckelian cartilage is ossified, and the rest is ensheathed outside by a large dentary (*d.*) and a small angular (*ag.*), while its inner face is equally covered by an extensive laminar splenial. No symplectic bone has hitherto been observed, though the hyomandibular is sometimes shown. The pterygo-quadrate seems to be ossified at least at the quadrate articulation; and there is evidently a large, elongated membrane-bone ensheathing its inner or oral aspect. There is no interoperculum, but the operculum, suboperculum, and branchiostegal rays are

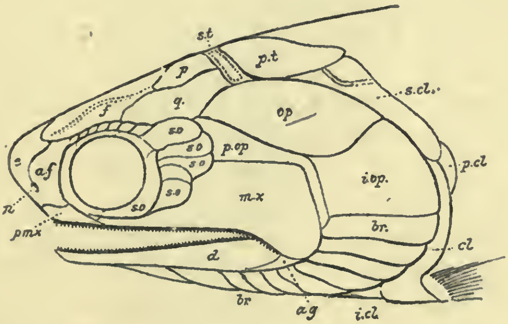

FIG. 61.

Palæoniscus macropomus; head and pectoral arch, restored in outline by R. H. Traquair, about nat. size.—U. Permian; Thuringia. *a.f.*, anterior frontal; *ag.*, angular; *br.*, branchiostegal rays; *cl.*, clavicle; *d*, dentary; *e*, ethmoid; *f*, frontal; *i.cl.*, infraclavicle; *i.op.*, suboperculum; *mx.*, maxilla; *n*, narial opening; *op.*, operculum; *p*, parietal; *p.cl.*, postclavicle; *p.op.*, preoperculum; *p.t.*, post-temporal; *pmx.*, premaxilla; *q.*, squamosal; *s.cl.*, supraclavicle; *s.o.*, circumorbital ring and suborbitals; *s.t.*, supratemporal. Dotted lines indicate course of mucus-canals.

seen in arched series, while a small median gular plate covers the space where the two sides meet in the front angle of the mandible. There is as yet no definite evidence of ossifications in the sheath of the notochord, and ribs are always wanting. In the Jurassic genus *Coccolepis*, the neural spines are not fused with the supporting arches in the abdominal region, but both these and the hæmal spines are firmly fixed to their arches in the tail. At the base of the caudal fin the hæmals are much enlarged for the direct support of the dermal rays, while the neurals become gradually aborted, and there is a series of distinct supporting ossicles beneath the fulcra of the upper caudal lobe. The pectoral arch comprises clavicle, infraclavicle, supraclavicle, and one postclavicle, while a very large post-temporal plate connects it with the skull. In *Coccolepis* the considerably extended pelvic fins have their rays directly supported by a series of elongated baseosts; but the axonost has not hitherto been observed in any genus. There is a single dorsal and anal fin, with the rays less numerous than their endoskeletal supports; and in some of the earlier types (e.g., *Elonichthys* and *Pygopterus*) these supports are distinctly shown in the dorsal fin to be arranged in two series—the proximal of slender axonosts, the distal of stout baseosts—while in *Coccolepis* the baseost series seems to have completely disappeared. The scales are typically rhombic and united on the flanks by a peg-and-socket articulation; but in some genera (e.g., *Cryphiolepis* and *Coccolepis*) they are essentially cycloidal, deeply overlapping and without articulation. The ridge-scales on the upper caudal lobe are much enlarged.

Cheirolepis (fig. 62). A genus remarkable for the very small size of the scales, which are strengthened on the inner face by a vertical ridge, but scarcely overlap. The branchiostegal rays of the foremost pair are much larger than the regular series behind. All the fins are fringed with conspicuous fulcra, intercalated between the tips of the foremost gradually lengthening rays; and the ridge-scales of the upper caudal lobe are divided into two halves at the apex. The pelvic fins have a much-extended base, and the dorsal fin is even more remote than the anal. The typical species, *C. trailli* (with many synonyms), occurs in the Old Red Sandstone of N. Scotland, and another well-preserved form, *C. canadensis*, has been found in the Upper Devonian of the Province of Quebec, Canada.

Sub-Class 4. **Teleostomi.**—Order 2. Actinopterygii.

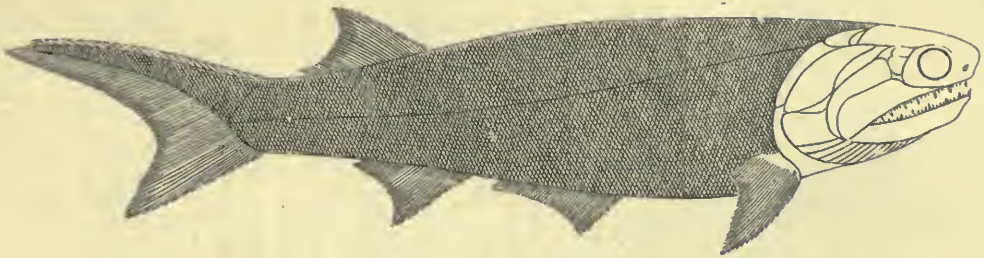

Fig. 62.

Cheirolepis trailli; restoration by R. H. Traquair (except margins of fins), one-quarter nat. size.—L. Old Red Sandstone; N. Scotland.

Palæoniscus (figs. 61, 63). An exclusively Permian genus with small fins, regular rhombic scales for the most part united by peg-and-socket, and with minute teeth. The dorsal fin is in advance of the anal. The best specimens are obtained from the Marl Slate of Northumberland and Durham, and from the Kupferschiefer of Thuringia.

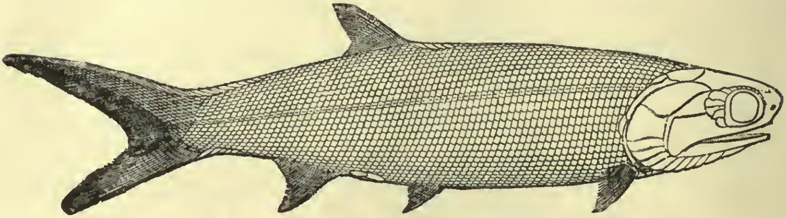

Fig. 63.

Palæoniscus macropomus; restoration by R. H. Traquair, nearly one-half nat. size.—U. Permian; Thuringia.

Holurus. Differs from all other Palæoniscids in having the caudal fin obliquely truncated, not forked, while all the fin-rays are simple, not branched, and the fulcra are minute or absent. The scales are sculptured, and there is an enlarged ridge-series between the occiput and the dorsal fin. The typical species, *H. parki*, is a small fish about one decimetre in length, from the Lower Carboniferous (Calciferous Sandstones) of Dumfriesshire.

Phanerosteon. Another small Palæoniscid from the same formation and locality as the last, remarkable as being almost or completely destitute of scales on the trunk, while the upper caudal lobe is invested with diamond-shaped ganoid scales.

Coccolepis. The latest genus of Palæoniscidæ, ranging throughout the Jurassic period, and remarkable for the deeply overlapping, almost cycloidal scales, which cover the whole of the trunk except the upper caudal lobe and are ornamented with tubercles of ganoine. The upper caudal lobe, as usual, is invested with rhombic scales. Owing to the delicacy of the squamation, the well-calcified endoskeleton of the trunk is usually conspicuous, as already described, and *Coccolepis* is the only Palæoniscid genus in which the baseosts of the much-extended pelvic fins have hitherto been observed. There are large cutting (laniary) teeth at intervals in both jaws. The dorsal and anal fins are triangular, the former in advance of the latter; the upper caudal lobe is extremely elongated, the fin deeply cleft and somewhat asymmetrical. The typical species, *C. bucklandi*, is a small fish about 0·075 m. in length, from the Lithographic Stone (Lower Kimmeridgian) of Bavaria. Other small species occur in the Lower Purbeck Beds of Wiltshire (*C. andrewsi*) and in the Lower Lias of

Lyme Regis (*C. liassica*); while a comparatively large species (*C. australis*) has been described from the Jurassic of New South Wales.

During the Carboniferous and Permian periods a family of deep-bodied fishes (**Platysomidæ**) identical in all essential points of structure with the Palæoniscidæ, also flourished in large numbers. The typical genus is *Platysomus* (fig. 64), ranging from the Lower Carboniferous to the Upper Permian in Europe, also known in the Carboniferous of North America. *Cheirodus*, *Mesolepis*, and *Eurynotus* are other British Carboniferous genera.

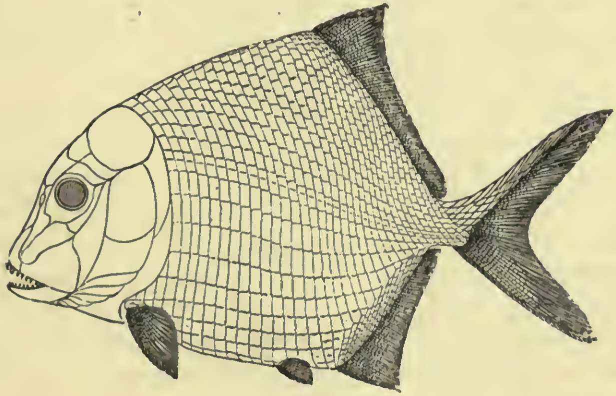

Fig. 64.

Platysomus gibbosus; restoration by R. H. Traquair, about one-quarter nat. size.—U. Permian; Germany and N. England.

Though not becoming extinct until the period of the Purbeck Beds, the Palæoniscidæ are comparatively rare in strata above the Permian. Only eight or nine genera are known with certainty, and individuals are very few above the Triassic. Simultaneously with this decline, the short-lived family of **Catopteridæ** appears in the Triassic and has a very wide geographical distribution. The two closely related genera of this family, *Catopterus* and *Dictyopyge*, are not very satisfactorily known, the specimens being usually in a bad state of preservation; but the upper caudal lobe is clearly half-atrophied, while the fins have much the aspect of those of the

Palæoniscids, and in *Dictyopyge* at least the supports of the anal fin are recorded as fewer than the apposed dermal rays. The head-bones are well developed and ganoid; the eye is far forwards, the snout prominent, and the gape of the mouth wide. A series of branchiostegal rays is present. The scales are all rhombic and ganoid. *Catopterus*, which exhibits the origin of the dorsal behind that of the anal fin, occurs in the Triassic black shales of Connecticut, Massachusetts, and New Jersey, U.S.A. The typical species of *Dictyopyge*, which has the dorsal fin further forwards, is only found in the corresponding rocks of the Richmond Coalfield, Virginia (*D. macrura*); but other forms are met with in the Keuper of Tyrone (Ireland), Warwickshire, and Coburg, in the Bunter of Switzerland, and in the supposed Triassic of New South Wales.

In strata of Triassic and Liassic age there are remains of another interesting family of fishes, which resemble the Palæoniscids in the non-correlation of the endoskeletal supports with the exoskeletal rays in the dorsal and anal fins, but exhibit an abbreviate-diphycercal tail. These are the **Belonorhynchidæ**, characterized by a remarkably elongated and slender trunk, remote and short-based dorsal and anal fins, and a discontinuous squamation, the flanks exhibiting isolated longitudinal series of scutes. The only definable genus hitherto discovered is

Belonorhynchus (fig. 65). The snout is much elongated, and the upper and lower jaws are approximately equal in length. The cranium is completely enveloped in membrane-bones, which are more or less fused together in the adult and firmly connected at the side in advance of the orbit with the similarly fused cheek-plates. The constitution of the cranial shield is not satisfactorily known, but it extends backwards beyond the skull to the hinder border of the operculum; the parasphenoid at the base of the skull is similarly produced backwards. The orbit is large, and there is a hardened, perhaps ossified sclerotic ring. The nasal opening is single on each side, and obliquely elongated. One long posterior suborbital bone is distinct, deepest behind, and produced as a narrow bar beneath the orbit; but nothing further is definitely known concerning the facial bones. The mandible is very deep behind; the angular and articular bones are fused together, and the expanded outer surface of the former is marked by radiating branches from the sensory canal which traverses its length. The dentition on the margin of both

Sub-Class 4. **Teleostomi.**—ORDER 2. ACTINOPTERYGII.

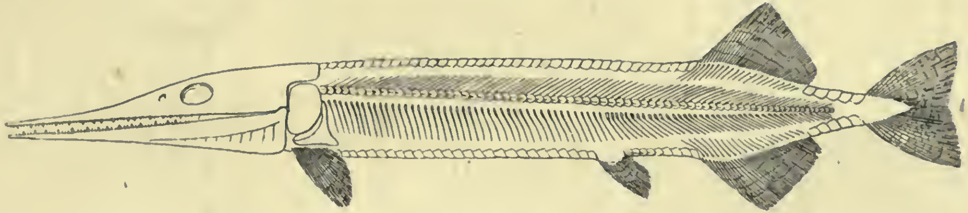

FIG. 65.

Belonorhynchus gigas; restoration, about one-quarter nat. size.—Hawkesbury Formation (Triassic?); Gosford, New South Wales. The row of dermal scutes on the flank obscures the bases of the neural arches of the vertebral axis.

jaws consists of a series of large, enamel-tipped, conical teeth, well spaced, with minute intermediate teeth; and some of the inner bones of the mouth are also provided with minute teeth. A small operculum is attached by an articulation near the upper end of its anterior border to the hyomandibular; but there is no evidence of any other ossification either in the opercular or branchiostegal membrane. The notochord is shown to have been persistent, and there are no undoubted ossifications in the notochordal sheath. The neural and hæmal arches, however, are much expanded, the former united by zygapophyses and bearing short delicate spines, the latter in the caudal region symmetrical with the neurals. Long slender ribs have also been observed in some specimens. The paired fins are small, apparently exhibiting a very feeble lobation, and consisting of delicate rays. The clavicle is also small and sickle-shaped, with a triangular plate affixed to its postero-inferior border; the pelvic fin-supports are unknown. The dorsal and anal fins exhibit a single series of robust supports much less numerous than the dermal rays; the base of the caudal fin is unknown. There are no fin-fulcra. A median longitudinal series of scutes extends along the dorsal and the ventral border; while another series supports the canal of the lateral line on each side. The typical species, *B. striolatus*, is a small fish from the Upper Keuper of Raibl, Carinthia; but species from the Keuper of Lombardy and the supposed Triassic of New South Wales probably attained a length of half a metre. Detached skulls from the Lower Lias of Lyme Regis and the Upper Lias of Würtemberg (*B. acutus*) afford most information concerning cranial osteology.

The Triassic and Rhætic teeth and fragments of jaws named *Saurichthys* belong either to *Belonorhynchus* or to a closely related fish.

It may perhaps be doubted whether the Belonorhynchidæ are correctly associated with the Palæoniscids and Acipenseroids, but the relationships of the Liassic family of **Chondrosteidæ** seem to be quite indisputable. These fishes agree with modern Acipenseroids in most essential characters; but they differ (i.) in the arrangement of the elements of the cranial shield and (ii.) in the presence of a suboperculum and a well-developed series of branchiostegal rays. In the two latter particulars they approach the Palæoniscids, and it is significant that they do not appear until this family has become of subordinate importance. So far as known, they are exclusively confined to the English Lias, and thus far only one genus has been discovered sufficiently well preserved for detailed description.

Chondrosteus (figs. 66—68). The trunk is elongate-fusiform and the tail heterocercal. Scales are entirely absent, except on the upper caudal lobe, where they are thick and rhombic, invested with ganoine. The snout must have been prominent, the eye is far forwards, and the toothless mouth is small and inferior. Nothing is known of the ossifications in the chondrocranium, but many specimens exhibit the chief membrane-bones. Those of the cranial roof form a continuous shield, without a median longitudinal series of unpaired elements (fig. 66), and comprise the ordinary pairs of parietals (*p.*), frontals (*f.*), postfrontals (*p.f.*), and squamosals (*sq.*); while immediately behind there is a regular row of supratemporal plates (*s.t.*). The rostral plates (if any) are unknown; and there appears to be only one suborbital cheek-plate (fig. 67, *s. o.*) immediately behind and below the eye. The hyomandibular (*h.m.*) is shaped as in modern sturgeons, but apparently ossified as far as its lower extremity; and a symplectic must have been present, although it is doubtful whether this was ossified in any part. The pterygo-quadrate arcade exhibits only two ossifications on each side, one being a large expanded element of pterygoid nature, and the other a small v-shaped bone articulated with the maxilla, which may be either palatine or ectopterygoid. There is a long curved maxilla (*mx.*), meeting its fellow of the opposite

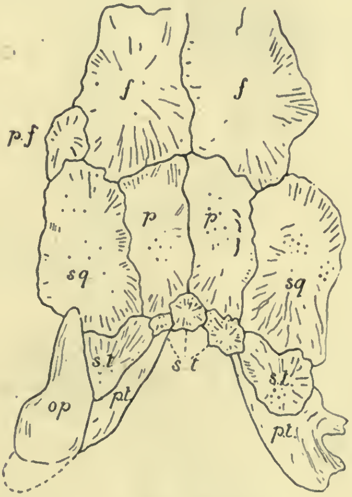

FIG. 66.

Chondrosteus acipenseroides; portion of cranial roof and adjoining plates, reduced in size.—L. Jurassic (L. Lias); Dorsetshire and Leicestershire. *f*, frontal; *op.*, operculum; *p*, parietal; *p.f.*, postfrontal; *p.t.*, post-temporal; *s.t.*, supratemporal; *sq.*, squamosal. (After Traquair.)

side in the median line in front without the intervention of a premaxilla; and another small membrane-bone abutting on its postero-superior margin, may be regarded as jugal (*j.*). The mandible exhibits three bones in each ramus, the dentary (*d*) being much the largest, the articular and angular (*ag.*) insignificant. No indications even of minute teeth have been observed. The operculum (*op.*) is relatively small, the suboperculum (*s.op.*) very large; the branchiostegal rays (*br.*) are about ten in number, but there is no median gular plate. The notochord is shown (fig. 68) to have been persistent, with no calcifications in its sheath, and the arches are only imperfectly calcified. There are no ribs. The pectoral arch is almost identical with that of *Acipenser*, but the infraclavicle is relatively smaller. The basal cartilages of the fins also resemble those of modern Acipenseroids; but there are no fulcral scales except on the upper caudal lobe, where they form a single conspicuous series. The dorsal fin is opposed to the pelvic pair, which are very remote. *C. acipenseroides*, the typical species, occurs in the Lower Lias of Dorsetshire and Leicestershire, and attains a length usually not exceeding one metre. A fish about twice as large, associated with this, is named *C. pachyurus;* but the genus is not known from any other horizon.

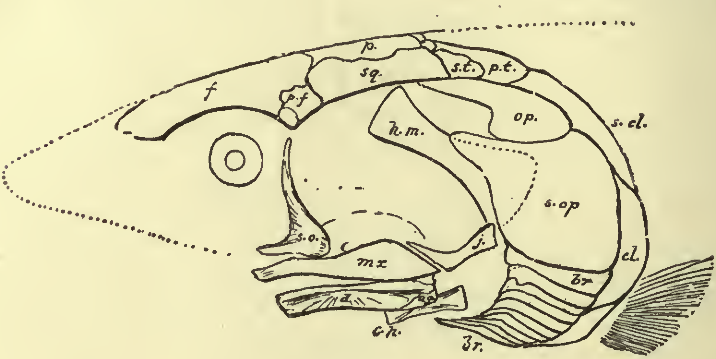

FIG. 67.

Chondrosteus acipenseroides; restoration of head and pectoral arch, lateral aspect, by R. H. Traquair, about one-quarter nat. size.—L. Jurassic (L. Lias); Dorsetshire and Leicestershire. *ag.*, angular; *br.*, branchiostegal rays; *c.h.*, ceratohyal; *cl.*, clavicle; *d*, dentary; *f*, frontal; *h.m.*, hyomandibular; *j*, jugal; *mx.*, maxilla; *op.*, operculum; *p*, parietal; *p.f.*, postfrontal; *p.t.*, post-temporal; *s.cl.*, supraclavicle; *s.o.*, suborbital; *s.op.*, suboperculum; *s.t.*, supratemporal; *sq.*, squamosal.

Gyrosteus mirabilis, from the Upper Lias of Whitby, must have closely resembled *Chondrosteus,* but is known only by

Sub-Class 4. **Teleostomi.**—ORDER 2. ACTINOPTERYGII.

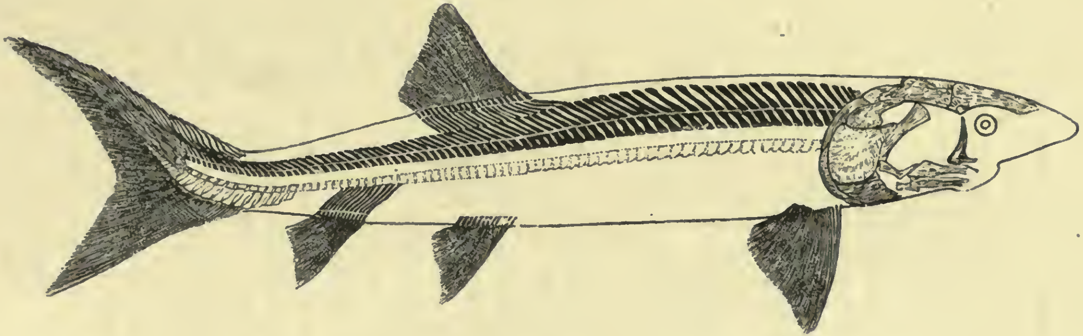

FIG. 68.

Chondrosteus acipenseroides; restoration, about one-eighth nat. size.—L. Jurassic (L. Lias); Dorsetshire and Leicestershire.

fragmentary specimens, of which the largest seem to indicate a fish about six or seven metres in length.

There is no evidence of fishes of the family **Acipenseridæ** below the Eocene Tertiary, where scutes and other fragments indistinguishable from the corresponding parts of the recent *Acipenser* occur. The earliest fossils of this character are from the London Clay of Sheppey, Kent, and bear the provisional name of *Acipenser toliapicus.* The Polyodontidæ are also represented in the Eocene by the genus *Crossopholis*, which is found well-preserved in the Green River Shales of Wyoming, U.S.A. This fish is closely similar to the recent *Polyodon*, but is remarkable for the squamation on the trunk. The scales are small and thin, arranged in oblique series but not in contact; they are merely little grooved discs, each with several posterior denticulations. The ridge-scales on the upper caudal lobe are numerous.

Sub-Order 2. *Protospondyli.*

Among fossils, no links are known between the most highly specialized Chondrostei and the representatives of the next sub-order. The nearest approximation to the higher grade appears to be made by the Catopteridæ (see p. 87). Even these fishes, however, are later in time (so far as known) than the earliest Protospondyli, which are represented by *Acentrophorus* in the Upper Permian. In the present state of knowledge, therefore, the demarcation of the Chondrostei from the Protospondyli is absolute. The latter are always characterized by (i.) a hemi-heterocercal tail, (ii.) the supports of the dorsal and anal fins in single series, equal in number to the apposed dermal rays, (iii.) the presence of more than five baseosts in the pectoral fins, (iv.) the want of baseosts in the pelvic fins, and (v.) the want of infraclavicular plates. The degree of development of the vertebral centra is variable, but even when they are completed (e.g., in *Amia*) the pleurocentra and hypocentra alternate and remain separate at least in part of the caudal region. Most usually the pleurocentra and hypocentra are alternating wedges (the *rhachitomous* type of ossification in the notochordal sheath), well seen in *Heterolepidotus, Caturus,* and the abdominal region of *Eurycormus* (fig. 77 A, B, p. 108). Frequently the hypocentral wedge fuses with the adjacent pleurocentral wedge to form a complete ring (seen in some Wealden species of *Lepidotus*). Sometimes in the caudal region (e.g., *Eurycormus*, fig. 77 C) the pleurocentra and hypocentra are completed alternating rings (the *embolomerous* type of ossification in the notochordal sheath). In the higher forms, each composite ring becomes thickened and constricts the notochord, resulting in a typical vertebral centrum; while the alternating pleurocentral and hypocentral rings of the caudal region become discs like those of *Amia*. The mandible is always tolerably complex, exhibiting splenial and coronoid (surangular) elements.

The Protospondyli are the dominant fishes of the Jurassic Period, and, like the Chondrostei of the Carboniferous and Permian, they appear to become specialized in two directions. One series, beginning with *Acentrophorus* and *Semionotus*, seems to terminate in deep-bodied fishes with grinding teeth (Pycnodontidæ); the other, beginning with *Eugnathus*, tends towards agile predaceous fishes with large conical teeth (Pachycormidæ). Both types are already well represented in Triassic, Rhætic, and Liassic formations.

The Permian genus *Acentrophorus*, already mentioned, is the earliest representative of the great family of **Semionotidæ.** These are fishes with a small mouth and forwardly-directed suspensorium, the teeth when specialized becoming tritoral. There are well-developed cheek-plates, and the opercular apparatus is complete. There are long ribs and the arches of the vertebral axis are nearly always well ossified; but the vertebral centra are never more than rings. All the fins exhibit large fulcra and robust, more or less widely-spaced rays; while the dorsal and anal fins are much extended only in the deep-bodied genera. The scales are at least in part rhombic and united by a peg-and-socket articulation; but they are sometimes thin, while in one case they are cycloidal and imbricating on the caudal region.

Semionotus. A fusiform fish with ossified ribs, entirely covered with rhombic scales, which are not much deepened on the flank; the dorsal ridge-scales form a prominent crest, and the narrow overlapped margin of the other scales is not produced at the angles. The marginal teeth are slender, conical, and somewhat spaced, the inner teeth are stouter. The paired fins are small, the dorsal fin large, and this arises at or behind the middle of the back to be in part opposed to the relatively small anal; the caudal fin is symmetrical and slightly forked. The typical species is *S. bergeri* from the Upper Trias (Keuper) of Coburg and Thuringia, and attains a length of about 0·18 m. Smaller forms also occur in the same sandstones in Würtemberg and Warwickshire; and one is known from the Lower Trias (Bunter) of Alsace. Large species are well known in addition from the Upper Karoo Formation (Stormberg Beds) of the Orange Free State, South Africa, and from the black Triassic flagstones of Massachusetts, Connecticut, and New Jersey, U.S.A. The American species are commonly described under the generic name of *Ischypterus*.

Acentrophorus. Seems to differ from *Semionotus* only in the absence of a prominent series of median dorsal scales. The typical species (*A. varians*), nearly a centimetre in length, occurs in the Upper Permian (Magnesian Limestone) of Fulwell Hill, near Sunderland. Other small forms are met with in the Marl Slate of Durham and Northumberland and in the Kupferschiefer of Saxony; while more doubtful specimens are recorded from the Triassic of Massachusetts and the Lower Permian of Bohemia.

Aphnelepis. A genus scarcely differing from *Semionotus* except in its very thin scales, which are much the thinnest on the caudal region, and do not form a conspicuous dorsal ridge. Known only from the Lower Jurassic of New South Wales (*A. australis* from Talbralgar).

Lepidotus (fig. 69). One of the best-known genera of Semionotidæ, with numerous species and having a very wide range both in space and time. The trunk is fusiform, only moderately compressed, and entirely covered with thick rhombic scales, of which the wide overlapped margin is produced into a forwardly-directed point at each angle. The chondrocranium is well ossified, and the basicranial axis is straight. The lower aspect of the basioccipital is marked by a broad longitudinal groove, with a flattened rim on each margin, probably indicating the backward extension of the basicranial canal (for the *recti* muscles of the eye) as far as the occiput. The exoccipital forms a considerable part of the lateral wall of the brain-case, and the pro-otic is still larger. The ethmoids surround a pair of long closed canals for the passage of the olfactory nerves. The membrane-bones of the cranial roof form a continuous shield, and are disposed as in *Amia*. The cheek is also completely covered, there being one circumorbital ring of plates, a semicircle of postorbitals, and a short deep series of preorbital plates. The maxilla is very delicate, deepest behind, tapering forwards, and terminating in front in an inwardly-directed process; its margin bears a series of styliform teeth. The premaxilla is a smaller, stouter bone, also with a single series of styliform teeth, and bearing at its inner extremity a very large ascending process which fits into a groove on the inferior aspect of the frontal bones. The large parasphenoid bears no teeth, but the two vomers are fused together into a stout bone which is provided with crushing teeth. The dentigerous bones of the palato-pterygoid arcade are closely connected with the vomer in front and similarly thickened. The hyomandibular is not pierced by any foramen, and the quadrate is remarkably delicate. The metapterygoid is also comparatively delicate, but shows a broad facette on an upwardly directed process, which may have articulated with some lateral element of the cranium. The hinder portion of the meckelian cartilage is ossified, and to its outer face there is apposed a large angular plate, and the coronoid elevation is completed above by a small coronoid (surangular) bone. The dentary bone, very deep in the coronoid region, becomes much narrower in its tooth-bearing portion; and a roughened surface on its inner face articulates with the robust splenial bone, which also enters the symphysis. Whereas the dentary bears only one series of teeth, the splenial has several irregular series of a more tritoral character. All the teeth are hollow, and when viewed in section, the calcigerous tubes in the dentine are shown to radiate from the central cavity. Successional teeth are numerous, and each germ turns through an angle of 180° as it gradually comes into use. The opercular apparatus is complete and there is a good series of branchiostegal rays; but no gular plate occurs. The branchial arches are delicate, and there are calcified supports for the gill-filaments, while small pointed gill-rakers are arranged in a sparse series. The notochord is proved to have been persistent, and in the earlier and smaller species no ossifications have been observed in its sheath; but in the large Wealden, and perhaps also in the large Oxfordian species, there are distinct indications of ring-vertebræ at least in the abdominal region. The ribs are ossified, and borne on short processes of the hypocentra when these ossifications occur. The right and left halves of the neural arches in the abdominal region are

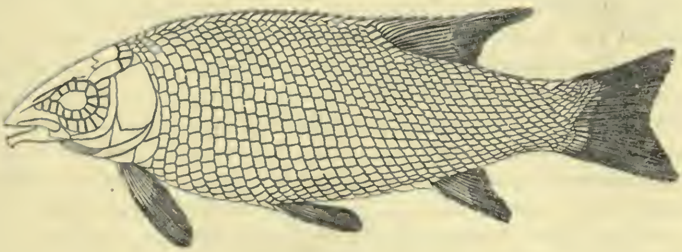

FIG. 69.

Lepidotus minor; restoration, about one-fifth nat. size.—U. Jurassic (Purbeck Beds); Dorsetshire. (From *Brit. Mus. Catal.*)

separate and not anchylosed with the neural spine. The pectoral arch comprises two pairs of membrane-bones, clavicles and supraclavicles, and the latter are very firmly articulated with the post-temporals, which are shaped as in *Amia*. The basal bones of the pectoral fin are large and much elongated, more than five in number; the pelvic fin-supports are unknown. The fulcra on all the fins are biserial. The chain of supratemporal plates is variable, but usually consists of more than one pair. There is a series of postclavicular scales, two of these being much enlarged; and there are also three enlarged scales round the anus, which seems to have been mesially placed just in front of the anal fin. Nearly all the other scales are in regular series, and those of the flank are united by a feeble peg-and-socket articulation; a single row of scales, however, at the base of the dorsal, anal, and caudal fins does not conform to the regular flank series, but is directly related to the fin-rays and fulcra. The course of the sensory canals on the trunk can be traced by perforations and notches in the scales; there is one principal "lateral line" as usual, and a second proceeds above on each side from the outer supratemporal plate to the origin of the dorsal fin. The earliest satisfactorily-known species of *Lepidotus* is *L. gallineki* from the Rhætic of Upper Silesia; and the typical species, *L. elvensis*, occurs in the Upper Lias of Bavaria, Würtemberg, N. France, and Northamptonshire. Two well-known species are obtained from the English Oxford Clay, and fine examples of other species are met with in the Lower Kimmeridgian (Lithographic Stone) of Bavaria. *L. minor* (fig. 69) is well preserved in the Purbeck Beds of Swanage, Dorsetshire, while *L. mantelli* is a well-known large species from the English Wealden. Beyond Europe, characteristic remains of *Lepidotus* have been found in the Jurassic of India and the Cretaceous of Brazil.

Dapedius (fig. 70). A genus most conspicuously differing from *Lepidotus* in the comparatively deepened form of the trunk, the presence of a gular plate, the elongation of the dorsal and anal fins, the uniserial arrangement of the small fin-fulcra, and the form of the overlapped portion of the scales, which is not produced at the angles. The chondrocranium is well ossified, and the basicranial axis is sharply bent upwards in front of the otic region. The basioccipital appears as in *Lepidotus* with some evidence of an extended basicranial canal; and there is reason to believe that the olfactory nerve extended across the orbital cavity as in *Lepidosteus*. The membrane-bones of the cranial roof form a continuous shield, and in adult individuals the paired parietals, frontals, and squamosals are usually fused into a continuous plate. Immediately in advance a pair of short and broad nasals meet in the middle line; and there is a small median plate enveloping the ethmoid in front. The premaxillæ are separate, small and short, apparently without any ascending process; the maxilla is bounded above in its hinder two-thirds by a small, narrow supramaxilla. The parasphenoid appears to have been toothless; but the vomer, which is probably single, is furnished with a dense cluster of comparatively large teeth. The mandible is constituted as in *Lepidotus*, but is remarkably short and deep. There are no traces of ossifications in the sheath of the notochord, but the vertebral arches are well calcified. The neural spines are separate from their respective arches except in the hinder half of the caudal region; and the ribs do not extend to the ventral border of the fish. There are no intermuscular bones. *Dapedius* is confined to the Lias, in which it is represented by many

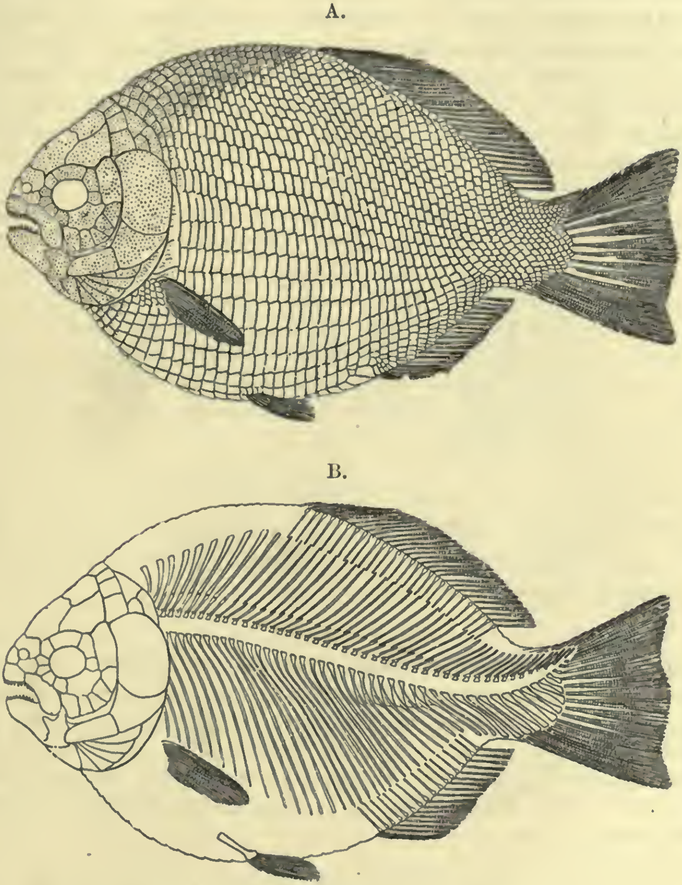

Fig. 70.

Dapedius politus; restoration, external aspect (A), and with scales removed (B), one-quarter nat. size.—L. Jurassic (L. Lias); Dorsetshire. (From *Brit. Mus. Catal.*)

species. In some forms the marginal teeth are simply pointed, in others they exhibit slightly bilobate crowns. The typical species, *D. politus* (fig. 70), from the Lower Lias of Lyme Regis, has smooth scales and attains a length of about 0·4 m. The largest known species, *D. granulatus*, from the same formation and locality, has tuberculated or pustulate scales, and is sometimes 0·6 m. in length.

Aetheolepis (fig. 71). A deep-bodied fish much resembling *Dapedius* and having nearly similar rhombic scales in the abdominal region, while these gradually pass into thin, deeply-overlapping, cycloidal scales in the caudal region (fig. 71). All the scales are ornamented with tubercles of ganoine. The only known species is *A. mirabilis* from the Jurassic of Talbralgar, New South Wales.

FIG. 71.

Aetheolepis mirabilis; series of scales of one individual, nat. size, showing gradual passage from anterior articulated rhombic scales to posterior overlapping cycloidal scales.—Jurassic; New South Wales.

Cleithrolepis. Another deep-bodied fish of irregular form, with conspicuous ridge-scales and all the flank-scales very deep, exhibiting a thick inner rib and large peg-and-socket articulation. The dorsal and anal fins are opposite and not much extended. It occurs in the supposed Triassic of New South Wales (*C. granulatus* from the Hawkesbury Beds) and South Africa (*C. extoni* from the Stormberg Beds of Orange Free State).

The family of **Macrosemiidæ** is closely related to that of the Semionotidæ, but comprises small-mouthed fishes with elongated trunk and extended dorsal fin. They range throughout the Mesozoic Period. The least specialized genus, *Ophiopsis,* seems to connect it with the family of Eugnathidæ described below (p. 106). The dorsal fin is usually single, though sometimes (e.g., *Notagogus* and *Propterus*) subdivided into two parts, and the development of fulcra is variable. The most characteristic genus is

Macrosemius. In this fish, as in other members of the family, the basicranial axis is straight, and there is no ossified interorbital septum. The cheek plates are very delicate; the cleft of the mouth is horizontal, and the rostrum does not project beyond the mandible. The sclerotic of the eye is ossified. The teeth are styliform or conical, largest on the premaxilla, vomer, and dentary. The opercular apparatus is complete, but a gular plate has only hitherto been observed in the allied genus *Ophiopsis*. The notochord is shown to have been persistent, without ring-vertebræ; the ribs are short and slender. The fins consist of very robust bifurcating rays, without fulcra except in the caudal. The pectoral fins are much larger than the pelvic pair; the dorsal fin arises immediately behind the occiput and extends continuously to the caudal pedicle; the anal fin is small, and the caudal rounded. The rays of the dorsal fin are sometimes denticulated on their posterior border. The scales are thin, with peg-and-socket articulation, and are apparently wanting towards the dorsal margin; those of the middle of the flank are largest, and some of the transverse series bifurcate above. About four very large ridge-scales occur on the lower margin of the pedicle at the base of the caudal fin. The typical species is *M. rostratus*, attaining a length of about 0·3 m., from the Lithographic Stone (Lower Kimmeridgian) of Bavaria. Other large species occur on the same horizon in the Dept. Ain, France; while diminutive species are known both from the Upper Portlandian of the Dept. Meuse, France, and from the Purbeckian of the Vale of Wardour, Wiltshire.

The systematic position of the remarkable family of **Pycnodontidæ** is uncertain, but it seems to be a specialized and partly degenerate offshoot of the *Lepidotus*-like genera. These fishes range from the Lower Lias to the Lower Eocene inclusive, and are a remarkable instance of the persistence of a specialized type—a parallel to the case of the Cœlacanthidæ already described (p. 78). They are deep-bodied fishes (fig. 74) with robust cranial bones, a small mouth and tritoral dentition (fig. 72 *a*—*c*), the opercular apparatus much reduced, and the notochord always persistent without ossifications in its sheath (fig. 72 *d*, *e*). The fin-rays are stout, articulated and divided distally; fulcra are absent. Both pectoral and pelvic fins are present, while the dorsal and anal fins are more or less extended. The scales, when present, are rhombic, united by a peg-and-socket articulation and strengthened within by a vertical rib near the anterior border (fig. 72 *f*); they are often absent on the caudal region (fig. 74), and rarely altogether wanting. The best-known genus is

Mesturus (fig. 73). This fish is entirely covered with rhombic scales, which differ from those of all other known ganoids in being united with each other above and below by jagged sutures. The paired fins are very small, and the caudal fin is not forked. The chondrocranium is well ossified and the basicranial axis is directed downwards and forwards, making a considerable angle with the axis of the trunk. There is no ossified interorbital septum. The parasphenoid is short, not extending to the occiput, while a cartilage bone which seems to be basisphenoid is exposed for a considerable area at the base of the skull. The vomers coalesce. The membrane-bones or dermal plates of the cranial roof form a continuous shield (fig. 73), but their arrangement is not quite constant. The posterior median element (*s. occ.*) is bilaterally symmetrical and unpaired; the frontals (*f.*) are the largest plates; a squamosal (*sq.*) covers the otic region on each side. The "parietal" region is occupied by two or three irregular plates (*pa.*), though there is only one parietal plate

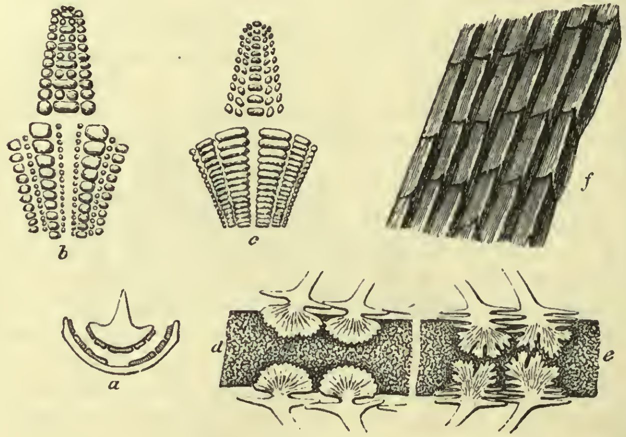

FIG. 72.

Illustrations of characters of Pycnodont Fishes. *a*, transverse section of jaws, showing the two halves of the mandibular dentition opposing the vomerine teeth; *b*, vomerine and mandibular teeth of *Microdon; c*, vomerine and mandibular teeth of *Cœlodus; d*, portion of vertebral column of *Cœlodus*, showing persistent notochord (shaded), and the expanded bases of the arches; *e*, the same of *Pycnodus; f*, inner view of scales, showing mode of interlocking by pegs and sockets, which are continued as longitudinal ribs. (After J. J. Heckel.)

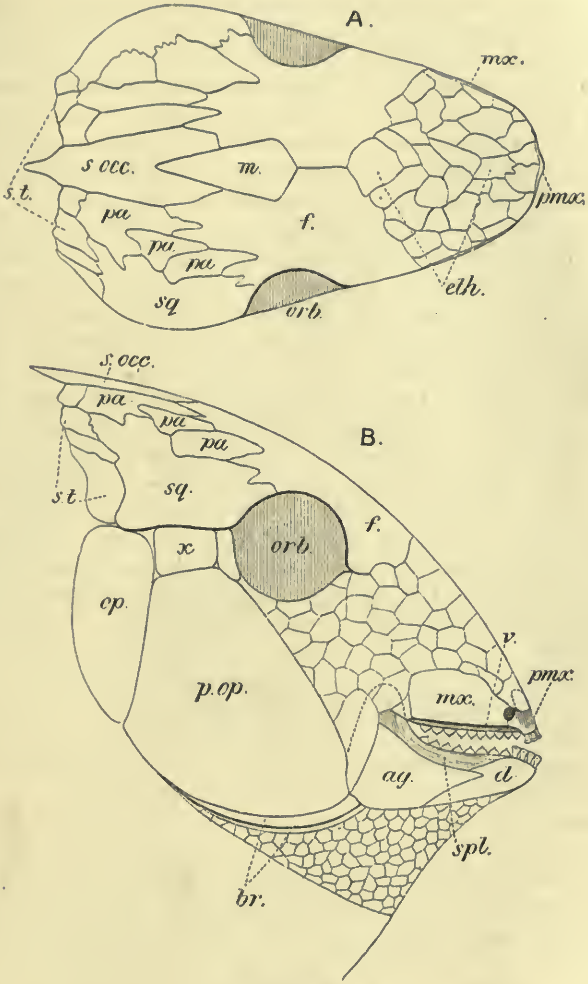

Fig. 73.

Mesturus leedsi; restoration of head and opercular apparatus, upper aspect in perspective (A) and lateral aspect (B), somewhat less than one-half the nat. size.—U. Jurassic (Oxford Clay); Peterborough. *ag.*, angular; *br.*, branchiostegal rays; *d*, dentary; *eth.*, ethmoidal dermal plates; *f*, frontal; *m*, median dermal plate; *mx.*, maxilla; *op.*, operculum; *orb.*, orbit; *p.op.*, preoperculum; *pa.*, parietal dermal plates; *pmx.*, premaxilla; *s.occ.*, supra-occipital dermal plate; *s.t.*, supratemporals; *spl.*, splenial bearing tritoral teeth; *sq.*, squamosal; *v*, vomer bearing tritoral teeth; *x*, dermal plate above preoperculum. (From specimens in Leeds Collection, British Museum.)

in other genera. The plates covering the ethmoidal region (*eth.*) are very irregular and extend backwards more or less between the frontals; the series is, indeed, continued backwards by another median plate which meets, or is even fused with the supraoccipital. The cranial shield as a whole is thus very suggestive of that of *Acipenser*. The cheek-plates (fig. 73 B) are small, thin, and apparently without any very definite arrangement. One plate, larger than the remainder, may be the maxilla (*mx.*), but it is delicate and toothless. The premaxillæ are deep and narrow, resting upon the anterior extremity of the vomer, and covered with the ethmoidal dermal plates. The hyomandibular is broadest above, tapering below; the pterygo-palatine arcade is delicate and toothless and is directly fused for a considerable distance with the edge of the basicranial axis. The thickened articular end of the quadrate is turned forwards so that the facette for the mandible is in a vertical plane. Each mandibular ramus consists of the usual five elements, the splenial preponderating and entering the symphysis. Grinding teeth are arranged on the vomer in more or less bilaterally symmetrical longitudinal series; similar teeth also occupy the enlarged splenial; but those of the premaxilla and dentary are prehensile. No successional teeth have been observed. The operculum is small, deep, and narrow; the preoperculum is very large, triangular, and much expanded below. Suboperculum and interoperculum are wanting, and there are only two branchiostegal rays. The space between the rami of the mandible is covered with small polygonal plates. The neural and hæmal arches are well ossified, but are not expanded to encircle the notochord. The clavicle is small, slightly expanded below; the pelvic fin-supports are unknown. The external bones and scales are ornamented with tubercles of ganoine, and the ridge-scales are inconspicuous. Two species are known, *Mesturus verrucosus* from the Lithographic Stone of Bavaria, and *M. leedsi* from the Oxford Clay of Peterborough.

Gyrodus. As *Mesturus*, but the caudal fin forked, and the scales not suturally united. The longitudinal series of teeth on the vomer and splenial are a little more regular than in the last genus. As additional characters may be noted, (i.) the course of the "lateral line" from the outer supratemporal to the middle of the caudal pedicle, with a second canal along the top of the flank to the origin of the dorsal fin, and (ii.) a problematical arched bone at the hinder end of the body-cavity. This has much the appearance of a median internal bone; while in some other genera it has been interpreted as a great paired dermal plate. It is certainly not an enlarged support of the anal fin, and it has no connection with the pelvic fins. Eight basal bones have been noticed in the pectoral fin. *Gyrodus* is typically an Upper Jurassic genus, the best specimens having been obtained from the Lithographic Stone of Bavaria (*G. macrophthalmus*, *G. hexagonus*, &c.).

The earliest known Pycnodont is *Mesodon liassicus* from the Lower Lias of Leicestershire and Gloucestershire, and this is in all respects a typical member of the family. The same genus ranges throughout the Jurassic period, and fine specimens occur in the Lithographic Stone of Bavaria (fig. 74). As the genera

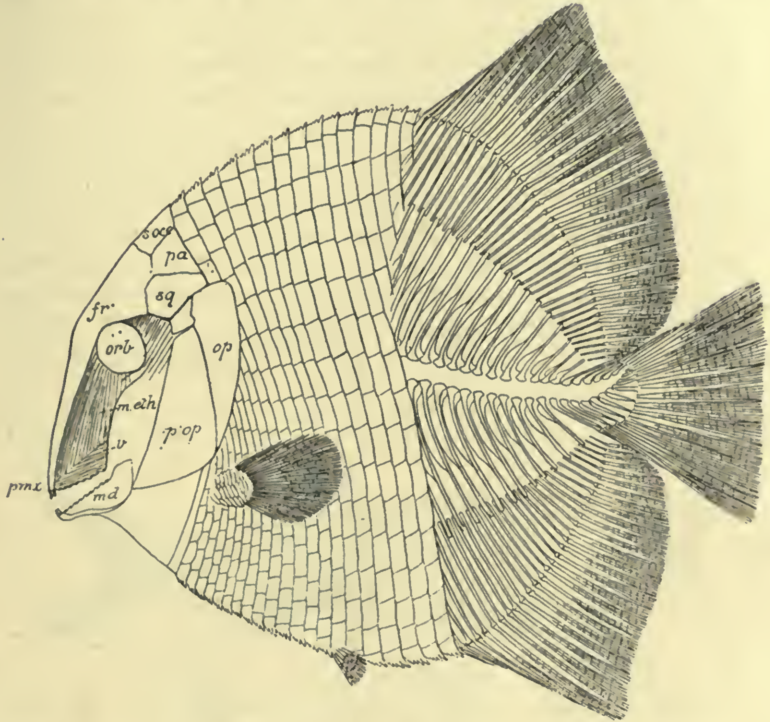

FIG. 74.

Mesodon macropterus; restoration, with cheek-plates removed, about two-thirds nat. size.—U. Jurassic (Lithographic Stone); Bavaria. *fr.*, frontal; *m.eth.*, mesethmoid; *md.*, mandible, showing narrow dentary in front; *op.*, operculum; *orb.*, orbit; *p.op.*, preoperculum; *pa.*, parietal; *pmx.*, premaxilla; *s.occ.*, supraoccipital; *sq.*, squamosal; *v*, vomer. The caudal region is destitute of scales.

are traced upwards in the rocks they become specialized chiefly (i.) in the strengthening of the backbone by the interlocking of its arches, and (ii.) in the reduction of the tritoral teeth on the vomer and splenial to a fixed arrangement in regular longitudinal series. In two rare genera from the Upper Cretaceous of Mount Lebanon, *Coccodus* and *Xenopholis*, dermal spines are also developed on the clavicle and cranial roof. The more widely distributed Cretaceous genus *Anomoeodus* sometimes seems to exhibit degeneracy in its tritoral dentition.

The **Eugnathidæ** are the forerunners of the modern *Amia*, and though the extreme types are widely different, it is very difficult to separate them from the Amiidæ in a brief definition. They are fusiform or elongate fishes with wide gape and pointed teeth. The mandibular suspensorium is nearly vertical or inclined backwards, and the snout is not produced, the premaxillæ being separate and in contact mesially. The notochord is usually persistent, the vertebræ being very rarely more than incomplete rings. The cranial and facial bones are moderately robust, externally enamelled, and the opercular apparatus is complete. The fin-rays are robust, articulated and divided distally; fulcra are conspicuous. The dorsal fin is short and acuminate. The scales are rhombic, sometimes with rounded postero-inferior angle.

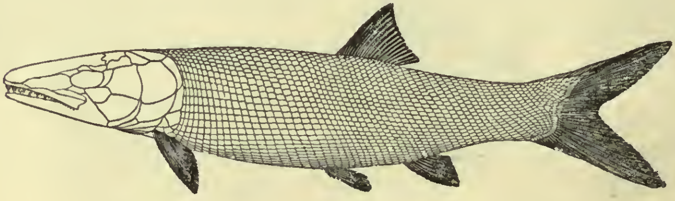

Fig. 75.

Eugnathus orthostomus; restoration, about one-seventh nat. size.—L. Jurassic (L. Lias); Dorsetshire. (From *Brit. Mus. Catal.*)

Eugnathus (fig. 75). An elongate-fusiform fish, covered with rhombic scales. The chondrocranium is well ossified, with a straight basicranial axis, but it has not been sufficiently exposed for precise description. Its base is sheathed by a large parasphenoid, which appears to terminate in advance of the occiput; and there is a pair of small vomers in front. The membrane-bones of the cranial roof form a continuous shield, which is nearly flat; the parietals and squamosals are small, the frontals very large, while both postfrontals and prefrontals are invested with superficial membrane-elements. The cheek is completely covered with thin plates, comprising one circumorbital ring, two very large suborbitals (or postorbitals), and at least one preorbital. The maxilla has a stout, inwardly directed process at its anterior extremity, and exhibits a long narrow supramaxilla above its hinder half; the premaxilla is extended along the margin of the jaw, and has a narrow upwardly-directed process near the middle of its superior border. The lower end of the hyomandibular meets both the quadrate and symplectic. The mandibular ramus exhibits the usual elements, and the splenial enters the symphysis. The teeth on the dentary are relatively large in a single spaced series, those of the premaxilla and maxilla smaller and more closely arranged; those clustered on the vomer are also powerful, but most of the inner teeth are minute or even granular. A large gular plate covers the whole of the space between the mandibular rami in front of the branchiostegal rays. The vertebral elements are never more than separate hypocentra and pleurocentra, and in the abdominal region the delicate ribs are articulated with short processes on the former. The large neural spines are free in the abdominal region. There is a single pair of transversely-extended supratemporal plates, and immediately behind these the large triangular post-temporals are observed. The fulcra on all the fins are biserial. Each scale is strengthened on its inner face with a vertical median rib; and the principal flank-scales are united by a peg-and-socket articulation. The typical species is *Eugnathus orthostomus* (fig. 75) from the Lower Lias of Lyme Regis, Dorsetshire, and the genus ranges upwards as far as the Lithographic Stone (Lower Kimmeridgian) of Bavaria, in which several forms occur.

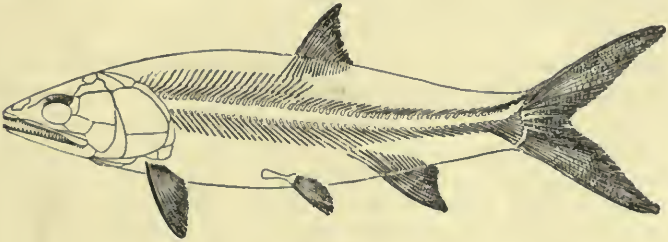

FIG. 76.

Caturus furcatus; restoration, scales omitted, about one-eleventh nat. size.—U. Jurassic (Lithographic Stone); Bavaria. (From *Brit. Mus. Catal.*)

Caturus (fig. 76). A fish apparently only differing from *Eugnathus* in two particulars, viz. (i.) the delicate character of the deeply overlapping scales, most or all of which have lost the inner rib with peg-and-socket articulation, and (ii.) the reduction of the teeth on the anterior half of the splenial to a single series. Some of the chondrocranial elements are known. In advance of the basipterygoid process of the parasphenoid there is a very large alisphenoidal ossification, much exceeding in size either of the otics behind. The pro-otic is equally well ossified, and the opisthotic is still more robust; but no undoubted traces of pterotic and opisthotic ossifications have hitherto been observed. The nasals resemble those of

Amia; and some of the small tooth-like gill-rakers are arranged on the edge of little triangular flakes of bone exactly like those of the recent genus. A few of the diamond-shaped thick scales persist on the atrophied upper caudal lobe. The typical species of *Caturus* (*C. furcatus*) occurs in the Lithographic Stone (Lower Kimmeridgian) of Bavaria, and several others are found in the Upper Jurassic ; but the genus appears to have an even wider range than *Eugnathus*, the earliest species being found in the Rhætic or Upper Triassic of Seefeld in the Tyrol, while fragments apparently to be placed here occur in the English Purbeck Beds, perhaps even in the Wealden.

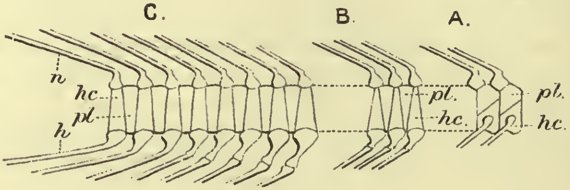

FIG. 77.

Eurycormus speciosus ; foremost abdominal vertebræ (A), posterior abdominal vertebræ (B), and caudal vertebræ (C), somewhat reduced.—U. Jurassic (Lithographic Stone) ; Bavaria. *h*, hæmal arches ; *hc.*, hypocentra ; *n*, neural arches ; *pl.*, pleurocentra.

Eurycormus (fig. 77). Intermediate between *Caturus* and *Amia.* The notochord is persistent, but the ossifications in the notochordal sheath are robust, and the pleurocentra and hypocentra form alternating completed rings in the caudal region (fig. 77 C). Fulcra are comparatively small on the median fins, unknown on the paired fins. The anal fin is considerably extended, and the caudal fin deeply forked. The typical species is *E. speciosus* from the Bavarian Lithographic Stone, while more fragmentary though characteristic specimens are known from the Oxford and Kimmeridge Clays of England.

While the Eugnathidæ thus closely approach the Amiidæ in the Jurassic period, there is fragmentary evidence of other interesting modifications in the Cretaceous. *Neorhombolepis* (English Chalk and Wealden) and *Otomitla* (Neocomian of Mexico) have completely ossified vertebræ but retain the rhombic squamation of *Eugnathus,* while the Mexican fish also appears to exhibit a subdivision of the gular plate. *Lophiostomus* (English Chalk and Cambridge Greensand) has similar scales, and a pair of prominences on the hinder half of the roof of the skull.

The **Amiidæ** proper, without fin-fulcra, are first undoubtedly represented by *Megalurus* in the Lower Kimmeridgian of Bavaria and the Dept. Ain, France, and in the Purbeck Beds of Dorsetshire. So far as known, this fish only differs from *Amia* in the comparative shortness of the dorsal fin, and *Amiopsis* from the Cretaceous of Istria cannot yet be distinguished from it. Species of the existing genus *Amia*—or of a fish exhibiting only minor differences in the dentition—occur in the Lower Tertiaries both of Europe and North America. Characteristic vertebræ are found in the Upper Eocene (Oligocene) of Hampshire and the Isle of Wight, and nearly complete fishes are known from the Upper Eocene of Montmartre, Paris, the Lower Miocene of Kutschlin, Bohemia, and the Lower Miocene lignite of central France. The genus seems to have disappeared from Europe before the deposition of the Upper Miocene strata.

The **Pachycormidæ** are a family of Amioid fishes as completely adapted for a predaceous life in the open sea as the modern sword-fishes. The ethmoidal region is more or less produced in front of the mouth, and the premaxillæ are fixed to it without meeting in the middle line anteriorly. The cheek is covered with plates, and the opercular apparatus is complete, with numerous branchiostegal rays and a large gular plate. The notochord must have been persistent, and the ossifications in its sheath are feeble or absent; the vertebral arches are very slender and numerous, often only superficially calcified. Fin-fulcra are rudimentary or absent; the pectoral fins are long and narrow with closely apposed rays; and the caudal fin is always deeply forked. The scales are thin, small, and deeply overlapping, or sometimes wanting. The least-specialized genera and *Pachycormus* are confined to the Lias. *Hypsocormus,* with a more prominent snout, is Upper Jurassic. *Protosphyræna,* with a still longer snout, is Cretaceous.

Pachycormus. This is an irregularly fusiform fish, with very narrow caudal pedicle, very deeply forked tail, sickle-shaped pectoral fins, no pelvic fins, short dorsal and anal fins (the former in advance of the latter), and small scales entirely covering the trunk. The bones of the cranial roof seem to be fused into a continuous shield, covered with a very fine granular ornament; and the median occipital portion is sharply raised into a rounded ridge to meet the deepened trunk. The cheek is covered by two large suborbitals (postorbitals) behind, apparently one preorbital, and a discontinuous series of relatively small circumorbitals. The sclerotic is ossified. The premaxilla on each side seems to be fused with the ethmoid; the maxilla is long and slender, with a small supramaxilla almost covering its posterior end. The dentary bone of the mandible is excessively large, the angular very small; and there is a thin splenial entering the symphysis. The marginal teeth above and below occur in a regular series, and none are much enlarged. The preoperculum is a wide triangular plate; the operculum is narrowed above and the suboperculum is relatively very large; the interoperculum is small. The number of branchiostegal rays varies from 40 to 50. No ossifications have been observed in the sheath of the notochord, but the vertebral arches are at least superficially ossified. The bases of the arches are narrow and deep; the neural spines are free in the abdominal region, but both neural and hæmal spines are fused with their respective arches in the caudal region; the ribs are especially delicate and are far from reaching the ventral border. A single hæmal spine at the base of the caudal fin is enlarged into a broad triangular expansion for the support of this unusually powerful appendage. So far as known, *Pachycormus* is confined to the Upper Lias, on which horizon it occurs in England, Würtemberg, Bavaria, and France. The typical species is *P. macropterus*, which attains the length of not less than one metre.

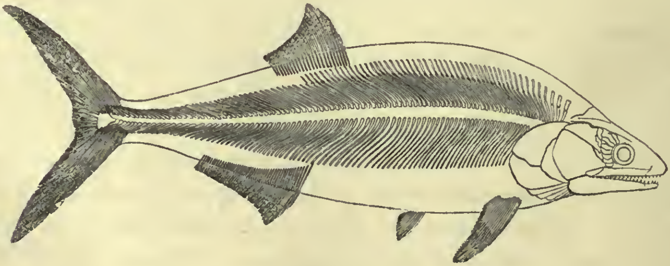

FIG. 78.

Hypsocormus insignis; restoration, scales omitted, about one-eighth nat. size.— U. Jurassic (Lithographic Stone); Bavaria. (From *Brit. Mus. Catal.*)

Hypsocormus (fig. 78). A larger fish than *Pachycormus*, often with longer rostrum, free triangular premaxilla, stouter splenial entering the mandibular symphysis, larger teeth, small pelvic fins, and much-extended anal fin. The parasphenoid bears a patch of minute granular teeth; the vomers are fused together and with the ethmoidal rostrum, bearing among other teeth one very large pair of tusks. The pterygo-palatine arcade exhibits moderately large teeth on the edge, becoming granular on the inner face. The splenial in its hinder portion is a thin deep plate covered with granular teeth; but its symphysial portion bears large teeth to oppose the vomerine pair. The large teeth on the dentary are in a single spaced series, those at the symphysis pointing a little forwards. All the teeth are round or oval in transverse section, and a slight vertical striation is due to their complex structure. They consist of a bundle of minute tubes of vascular dentine, seen as well-defined areas in a transverse section under a low power of the microscope. The typical species is *Hypsocormus insignis* (fig. 78), well preserved in the Lithographic Stone (Lower Kimmeridgian) of Bavaria, and it is associated with a still larger species, *H. macrodus.* Closely related to the latter are *H. leedsi* and *H. tenuirostris* from the Oxford Clay of Peterborough, known only by fragmentary specimens which are of importance as exhibiting many features in the osteology of the genus.

Protosphyræna. A still larger fish than *Hypsocormus*, nearly always with a longer rostrum, but as yet known only by the head, pectoral fins, and other fragments. Distinguished from *Hypsocormus*, so far as known, merely by the lateral compression of the teeth, which have opposite sharp edges, and by these teeth being fixed in complete sockets. A characteristically Upper Cretaceous genus, the type species being *Protosphyræna ferox* from the English Chalk. Fragments of several species occur in the Cambridge Greensand. Nearly complete skulls and fine pectoral fins have been found in the Chalk of Kansas, U.S.A.

Sub-Order 3. *Aetheospondyli.*

Here are provisionally placed some highly-specialized ganoids of uncertain relationships. So far as their skeleton is concerned, they differ from the Protospondyli merely in the nature of the vertebræ, which are not known to exhibit even in their most immature stages any indication of separate pleurocentra and hypocentra. In one family (Aspidorhynchidæ) the centra are ring-shaped or complete and biconcave; in the other family (Lepidosteidæ) the centra are unique among fishes in being opisthocœlous.

The **Aspidorhynchidæ** range from the Lower Oolites to the Upper Chalk inclusive. They are elongated fishes with produced rostrum, rhombic scales much deepened on the flank, all the fins small, and the dorsal and anal fins remote. The fin-rays are stout, and fulcra are minute or absent. The mandible is remarkable as exhibiting a bilaterally-symmetrical median piece (predentary bone) in front of the usual elements.

Aspidorhynchus (fig. 79). In this genus the rostrum is much produced in advance of the mouth, and the predentary bone is comparatively short. The teeth are all pointed, fixed upon the pterygo-palatine arcade, premaxilla, maxilla, dentary, splenial, and predentary bone, the latter element showing a median series of large spaced teeth. The vomer and premaxilla are fused with the base of the rostrum, but the simple and slender maxilla is very loosely attached. The cheek is completely covered with plates, and the preoperculum is very wide at its angulation. The operculum, suboperculum, and interoperculum are well developed, and there are branchiostegal rays; but no gular plate has been observed. The vertebral centra are in the form of calcified rings, narrow and separated in the young, longer and in contact in the adult. The dorsal and anal fins are short-based and directly opposed; the caudal fin is forked. Three longitudinal series of flank-scales are deepened, but those of the lateral line are not deeper than those below. The typical species is *Aspidorhynchus acutirostris* from the Lower Kimmeridgian (Lithographic Stone) of Bavaria, attaining a length of about one metre. The earliest species, *A. crassus*, from the Bathonian (Stonesfield Slate) of Oxfordshire, is very small; so also is the latest known species, *A. fisheri*, from the Purbeck Beds of Dorsetshire.

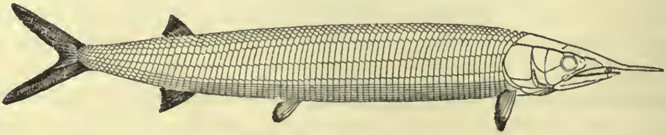

FIG. 79.

Aspidorhynchus acutirostris; restoration, about one-eleventh nat. size.—U. Jurassic (Lithographic Stone); Bavaria. (From *Brit. Mus. Catal.*)

Belonostomus. In this genus the rostrum is scarcely if at all produced in advance of the mouth, and the predentary bone is comparatively elongated. Most of the teeth are sharply pointed, but those of the very robust splenial bone, which sometimes excludes the dentary from the oral border, form a tubercular pavement. The vertebral centra are more completely ossified than in *Aspidorhynchus*, and the scales of the lateral line on the flank are excessively deepened. The genus is not certainly known below the Lower Kimmeridgian of Bavaria, where the typical species, *B. sphyrænoides*, occurs; but it ranges as far as the uppermost Cretaceous, in which the species exhibit completely ossified vertebral centra. The latter species have a very wide distribution, being found in Europe, India, Mexico, Brazil, and Queensland.

The **Lepidosteidæ** are an exclusively Tertiary family, but though now confined to the freshwaters of North America they seem to have been equally abundant in Europe during the Eocene and Lower Miocene. The earliest known remains, indeed, were obtained from the Lower Eocene of Reims, France. All the European fossils are merely fragments, such as portions of jaws, vertebral centra, and scales, which differ in no essential respects from the corresponding parts of the recent *Lepidosteus*. The latest are found in the Lower Miocene of Messel, near Darmstadt. In North America, similar fossils occur from the Eocene upwards, and one small species is known by nearly complete fishes from the Green River Shales of Wyoming. Nearly all of these differ slightly from the recent *Lepidosteus* in the dentition, and they are hence commonly described under the generic name of *Clastes*.

Sub-Order 4. *Isospondyli.*

In almost the earliest Mesozoic strata, i.e., in the Upper Triassic, fishes of a remarkably modern aspect begin to appear, only differing from such groups as the herring-tribe in the feeble ossification of the vertebral centra, the presence of minute fin-fulcra, and the possession of ganoid scales. They may be regarded as the forerunners of the ISOSPONDYLI, which exhibit an advance on all the preceding types in the simplification of the mandible. The fishes of this sub-order are characterized as follows:—The vertebral centra are more or less calcified, usually complete, and are not known to exhibit even in their most immature stages any indication of separate pleurocentra and hypocentra; none are fused together. The tail is hemi-heterocercal or homocercal. Each ramus of the mandible consists only of two pieces (dentary and angular), rarely with rudiments of a splenial. Infraclavicular plates are absent, and there are not more than four or five basal bones in the pectoral fins. There are no baseosts in the pelvic fins, which are always abdominal. The living members of the sub-order belong to the "physostomous Teleostei."

All the Jurassic fishes which *seem* to belong to this sub-order have a very small premaxilla and the parietal bones in contact; but in the Chalk there appear certain families in which the premaxilla becomes much extended and partly excludes the maxilla from the oral border, while the parietal bones are separated by the supraoccipital, and the well-ossified otics bulge outwards on either side.

The **Pholidophoridæ** are provisionally placed here on account of their remarkable resemblance to the Leptolepidæ. It is not yet quite clear that the mandible was destitute of splenial and coronoid elements, while the baseosts of the pectoral fin have not hitherto been observed. The external bones, scales, and most of the fin-rays are coated with ganoine, and minute fin-fulcra are observable. The maxilla is loose and bounded above by two supramaxillaries; the gape of the mouth is wide, and the teeth are minute. The vertebral centra are never more than rings, and there are no intermuscular bones. The dorsal fin is short and single. The scales are ordinarily rhombic, united by a peg-and-socket articulation on the abdominal flank, but sometimes very deeply overlapping and with a more or less rounded hinder margin.

Pholidophorus. Small, gracefully fusiform fishes, covered with rhombic scales which are usually thin and deeply overlapping, not much deepened on the flank, and partly united by a peg-and-socket articulation. The maxilla is arched so that its oral border is convex, and the cheek-plates are very delicate. The sensory canal exhibits radiating branches on the posterior suborbitals. The opercular apparatus is complete, and there are broad branchiostegal rays; but no gular plate has been observed. The fins are small, all fringed with minute fulcra; the dorsal is short-based, in the middle of the back; the caudal is deeply forked. The scales are sometimes smooth, sometimes serrated, and usually elaborately pectinated in the latest species. The genus ranges from the Upper Trias or Rhætic to the Purbeck Beds inclusive, the typical species, *Pholidophorus bechei*, with smooth scales, occurring in the Lower Lias of Lyme Regis. The English Purbeckian species (*P. ornatus* and *P. granulatus*) and their equivalents in the Lithographic Stone of Bavaria (*P. micronyx* and *P. macrocephalus*), are the most highly ornamented and attain larger dimensions than the earlier forms.

Thoracopterus. Much like *Pholidophorus*, but with immensely developed pectoral fins. *T. niederristi* is the only known species, about 0·15 m. in length, from the Upper Trias of Raibl, Carinthia.

Pleuropholis. Small fishes entirely covered with rhombic ganoid scales, of which one longitudinal series on the flank is excessively deepened. The lateral line is remarkable inasmuch as it does not traverse this deepened series, but turns down the second or third scale and extends along the series of normal scales immediately below. The fins are small, all fringed with minute fulcra; the dorsal and anal fins are slightly extended and directly opposed; the caudal is deeply forked. *Pleuropholis* is essentially Upper Jurassic, having been found only in the Lithographic Stone of Bavaria and Ain, France, in the Portlandian of France, and in the English Purbeck Beds. *P. lævissima* is the best-known species from Bavaria, and *P. attenuata* is the typical species from the Purbeck of Sutton Mandeville. *P. crassicauda* and *P. longicauda* occur in the Purbeckian of Swanage, while *P. serrata* belongs to a similar horizon at Hartwell, near Aylesbury.

The **Leptolepidæ** exhibit an advance upon the Pholidophoridæ only in four particulars. The vertebral centra are always well ossified in the adult, a few intermuscular bones are developed, fin-fulcra are wanting, and the scales are never united by a peg-and-socket articulation though apparently always coated with a thin film of ganoine. These fishes range from the Upper Lias at least to the Lower Cretaceous, and become modified only by the strengthening of the vertebral centra and the multiplication of the intermuscular bones.

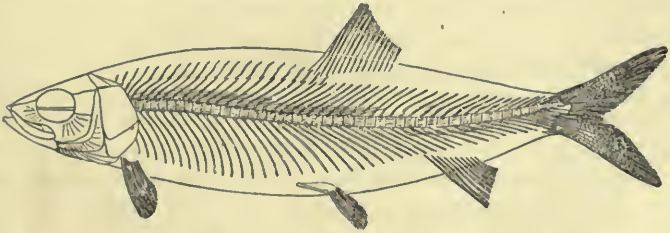

FIG. 80.

Leptolepis dubius; restoration, scales omitted, about one-third nat. size.—U. Jurassic (Lithographic Stone); Bavaria. (From *Brit. Mus. Catal.*)

Leptolepis (fig. 80). The head is shaped like that of *Pholidophorus*, and the gular plate is similarly wanting. The radiating branches of the suborbital sensory canal have been observed on the large preorbital cheek-plate. The mandible is definitely proved to consist of only two ossified elements, a dentary and an articulo-angular, and the former suddenly rises into a thickened ascending process at a short distance from the symphysis (suggestive of the same bone in the carps). The vertebral centra are constricted cylinders in close series, but are always pierced by the continuous notochord; they are simple in the Liassic species, but strengthened by secondary peripheral calcifications in the later species. The ribs are delicate and do not reach the ventral border of the fish; the neural arches in the abdominal region are not firmly fixed either with the centra or with their appended spines; but both neural and hæmal arches and spines are fused with the centra in the caudal region. The hæmal arches at the base of the tail are thickened, but not much expanded and never fused together. The short dorsal fin is opposed to the pelvic pair or immediately behind; the caudal fin is forked. The typical and earliest undoubted species of *Leptolepis* is *L. bronni* from the Upper Lias of Würtemberg, and nearly similar or identical fishes occur on a corresponding horizon in N. France and Somersetshire, Gloucestershire, and Yorkshire. *L. macrophthalmus*, from the Oxford Clay of Christian Malford, Wiltshire, is a well-known species about 0·3 m. in length. Several species occur in the Lithographic Stone (Lower Kimmeridgian) of Bavaria, and one diminutive form, *L. brodiei*, is known from the Purbeck Beds of the Vale of Wardour, Wiltshire. The genus is also represented in the Upper Hawkesbury-Wianamatta Beds (Lower Jurassic) of Talbralgar, New South Wales.

Thrissops. Differing from *Leptolepis* in its more upturned mouth, want of thickening in the elevated part of the dentary, larger and stouter neural spines and ribs in the abdominal region, more extended anal fin, and the dorsal opposed to the latter. This is an Upper Jurassic and Lower Cretaceous genus, the typical species being *T. formosus*, 0·5 m. in length, from the Lithographic Stone of Bavaria. Other species occur on the same horizon in Bavaria, Würtemberg, and Ain, France, and fragmentary remains of a very large species are also met with in the Kimmeridge Clay of Dorsetshire. *T. portlandicus* is found in the Portland Stone of the Isle of Portland, and other species are represented in the Purbeck Beds of Dorsetshire. *T. microdon* occurs in the Lower Cretaceous of Comen, Istria, and the Isle of Lesina, Dalmatia, where other species have also been determined.

The **Oligopleuridæ** are exclusively Upper Jurassic and Cretaceous fishes of moderate size. In outward aspect the head much resembles that of the Pholidophoridæ and Leptolepidæ, the arched maxilla being bounded above by the two supramaxillaries; while the dentary bone of *Oligopleurus* itself is known to be almost identical with that of *Leptolepis*. The vertebral centra are always completely ossified; the ribs are small; and there are never intermuscular bones. The hæmal arches at the base of the tail are only thickened, never much expanded and none fused together. The fins are fringed with fulcra. The scales are cycloidal and deeply overlapping.

Oligopleurus. The mandible in this genus is truncated in front and a little prominent; the teeth are minute. The branchial arches bear a close series of large bony gill-rakers. The vertebral centra are well ossified, and short ribs fit into pits. The first vertebral centrum, articulating with the basioccipital, is composed of two thin discs fused together, but the others are all simple, each bearing its own arch. The dorsal and anal fins are short-based, remote, and directly opposed; the caudal fin is forked. The typical species, *O. esocinus*, occurs in the Lower Kimmeridgian (Lithographic Stone) of Cirin, Ain, France; while there is evidence of other species in the Wealden of the Isle of Wight (*O. vectensis*), and in the Purbeck Beds of Dorsetshire.

Spathiurus. With greatly extended dorsal fin, and slightly forked caudal. *S. dorsalis* from the Upper Cretaceous of Hakel, Mount Lebanon.

The foregoing three families of Isospondyli are exclusively Mesozoic. None of those which still survive date back further than the Cretaceous, while of such the **Elopidæ** and their allies are perhaps the most important. *Elops* and *Albula*, as is well-known, are remarkable among "physostomous Teleostei" as exhibiting a rudiment of a spiral valve in the intestine, and traces of a series of valves in the conus arteriosus of the heart, while the former has a well-developed gular plate between the mandibular rami. It is therefore interesting to note that they are widely represented in the Cretaceous and Lower Tertiary periods by numerous closely-related genera. *Osmeroides lewesiensis*, from the English Chalk, is a typical Elopine with gular plate. *Elopopsis* from the Cretaceous of Istria, Bohemia, and England, has comparatively large teeth. *Albula* itself, or at least a fish with identical skull, occurs in the London Clay (Lower Eocene) of the Isle of Sheppey. *Chanos* is recorded from the Lower Miocene of Chiavon, N. Italy.

The **Osteoglossidæ**, now not extending further north than Central America in the New World, are represented in the Green River Shales (Eocene) of Wyoming by species of the extinct genus *Dapedoglossus.*

Among Isospondyli with small premaxillæ but with parietals separated by the supraoccipital, the **Clupeidæ** have of course many extinct representatives. *Clupea* itself is not certainly known below the Upper Eocene (Monte Bolca, near Verona); but a genus apparently differing from it only in the presence of a median series of dorsal scutes between the occiput and the dorsal fin, is *Diplomystus*, occurring in the Upper Cretaceous of Mount Lebanon and Brazil, the Green River Shales (Eocene) of Wyoming, the Upper Eocene (or Oligocene) of the Isle of Wight, and apparently still surviving in the freshwaters of Chili and New South Wales. *Scombroclupea*, from the Upper Cretaceous of Mount Lebanon and Comen, in Istria, differs from *Clupea* in possessing a series of detached finlets behind the anal fin.

An extinct family, closely related to the Chirocentridæ is that of the **Saurodontidæ** or **Ichthyodectidæ**, characteristic of the Cretaceous period, with some gigantic representatives in the Chalk both of Europe and America. These are predaceous fishes with teeth fixed in sockets on the border of the premaxilla, maxilla, and dentary, while the inner bones of the mouth are toothless. The supraoccipital, which completely separates the parietals, has a large median longitudinal crest. A small symplectic is present. The vertebral centra in the abdominal region do not exhibit any conspicuous processes for the support of the ribs. The opercular apparatus is complete and there are branchiostegal rays, but there appears to be no gular plate. A precoracoid arch has been observed in the shoulder-girdle. The fin-rays are remarkably stout, only divided and articulated quite at their distal end, sometimes perhaps never divided. The pelvic fins are abdominal; the caudal fin is forked. *Portheus* and *Ichthyodectes* are the best-known genera, the former with compressed teeth in a very irregular series, the latter with less compressed teeth in a nearly regular series. Both occur in the Cretaceous of Europe and America, and some species of *Portheus*, e.g. *P. molossus*, attain a very large size, perhaps not less than two metres in length. This genus is also represented in the Cretaceous of Queensland.

Another imperfectly known Cretaceous family commonly supposed to be related to the Salmonidæ, appears to be represented by *Pachyrhizodus*, from the Chalk both of Europe and America. The large conical teeth are anchylosed with the margin of the jaw, not in sockets, but with an outer flange of bone.

There are numerous Cretaceous fishes in which the parietal bones meet partially or completely in the middle line, while the premaxilla is extended so as to exclude a considerable part of the maxilla from the margin of the upper jaw. These appear to be more or less closely related to the existing family of **Scopelidæ**, and some have very delicate skeletons, which may denote a comparatively deep-sea habitat. Some are probably true Scopelidæ, such as the fish from the Chalk of Westphalia commonly named *Sardinioides monasteri;* but others doubtless represent one or more extinct families, and among these *Eurypholis, Enchodus,* and *Dercetis* are particularly noteworthy.

Sub-Order 5. *Apodes.*

Typical eels occur in the Upper Cretaceous of Mount Lebanon, but their generic determination is uncertain, and the specimens are too much crushed to obtain any satisfactory information as to their cranial osteology. *Anguilla* itself is represented in the Upper Miocene of Oeningen, Switzerland.

Sub-Order 6. *Plectospondyli.*

The physostomous fishes in which there is still a precoracoid arch and a symplectic bone, but in which some of the anterior vertebræ are fused together and there is a chain of ossicula auditus, are chiefly represented in the existing fauna by the **Characinidæ** and **Cyprinidæ.** Their palæontological history, so far as known, is of little interest, the conditions of fossilization not favouring the preservation of those minute features in their osteology which are of prime importance. *Omiodon cabassii*, from the Middle Eocene of the Province of Udine, Italy, is claimed to be a Characinoid. Remains of Cyprinoids are not uncommon in freshwater formations above the Eocene, both in Europe and North America.

Sub-Order 7. *Nematognathi.*

The Siluroid fishes (characterized by a precoracoid arch and infraclavicles but no symplectic bone, the anterior vertebræ fused together and modified, and ossicula auditus present) are first represented in the Eocene both of Europe and America. The oldest known example is an imperfect skull with pectoral arch from the London Clay (Lower Eocene) of Sheppey, named *Bucklandium diluvii* and closely similar to the modern *Auchenoglanis.* A skull from the Barton Clay (Upper Eocene) of Hampshire cannot be distinguished from that of *Arius*, and has been named *A. egertoni.*

Sub-Order 8. *Haplomi.*

The pikes (**Esocidæ**) and toothed carps (**Cyprinodontidæ**) are only known as yet among fossils by fishes almost or quite indistinguishable from existing genera. None are certainly known below the Lower Miocene (Oligocene). *Esox* occurs in the Upper Miocene lacustrine deposit of Oeningen, Switzerland; and here is also found a small fish which seems to be generically identical with the living *Poecilia* of tropical America.

Sub-Order 9. *Anacanthini.*

Palæontology as yet reveals nothing concerning the origin and evolution of the cod-fishes and flat-fishes. *Nemopteryx* from the Upper Eocene (Lower Oligocene) of Canton Glarus, Switzerland, is commonly referred to the Gadidæ; and some detached skulls from the London Clay of Sheppey are believed to represent fishes of this family. Typical fully-developed flat-fishes of diminutive size, named *Solea kirchbergana,* occur in the Miocene of Ulm, Würtemberg.

Sub-Order 10. *Percesoces.*

The **Scombresocidæ**, **Atherinidæ**, **Mugilidæ**, and **Sphyrænidæ**, may perhaps be represented in the Cretaceous, and are certainly well-developed in the Upper Eocene. Of the first family, *Scombresox* and *Belone* are recorded from the Miocene of Licata, Sicily. *Calamopleurus,* from the English Chalk and Gault, may belong to the Atherinidæ. Most of the fragmentary fossils referred to the Sphyrænidæ truly belong to Scomberoids

1 2 5 7 8 13 17 20

and extinct families; but *Sphyræna* itself, or a fish remarkably like it, occurs as nearly complete skeletons in the Upper Eocene of Monte Bolca, near Verona.

Sub-Order 11. *Percomorphi.*

The Berycoid fishes date from the Upper Cretaceous both of Europe and America, but it is very doubtful whether any existing genus occurs in the Chalk. The name *Beryx*, as commonly applied to fossils, is very indefinite. *Hoplopteryx* is a well-known extinct Cretaceous genus, differing from the existing *Beryx* by the relatively great extent of its spinous dorsal fin, which comprises six strong spines. *H. lewesiensis* is a common species of the English Chalk, and the eight soft rays besides the spine can be counted in the pelvic fin.

The other Percomorphs are almost or exclusively Tertiary, but many of the existing families are already differentiated in the Eocene. The **Scombridæ** are especially abundant, and even so highly specialized a genus as the modern Remora (*Echeneis*), with its remarkable sucker, has a representative in the Upper Eocene (Lower Oligocene) of Canton Glarus with a scarcely less developed sucker. The **Trichiuridæ** are also represented in this formation by a fish indistinguishable from *Lepidopus*.

Sub-Order 12. *Lophobranchii.*

Typical pipe-fishes occur in the Upper Eocene of Monte Bolca and Monte Postale; while a sea-horse (*Calamostoma*) only differing from the existing *Hippocampus* in the possession of a caudal fin, is also found in the quarries of Monte Bolca.

Sub-Order 13. *Hemibranchii.*

Fistularia and *Amphisyle*, or fishes almost identical with these, date from the Upper Eocene of Monte Bolca and Galicia, and there is other evidence of Hemibranchs in the same formation. Unfortunately, all the specimens are much crushed.

Sub-Order 14. *Plectognathi.*

Both the Gymnodonts and Scleroderms seem to have been already differentiated in early Eocene times, and they have subsequently exhibited very little change. Jaws indistinguishable from those of *Orthagoriscus* have been found in the Upper Eocene (Oligocene) of Belgium. Fishes closely resembling *Diodon, Ostracion,* and *Balistes* occur in the Upper Eocene of Monte Bolca.

CLASS BATRACHIA (AMPHIBIA).

Orders.	*Sub-Orders.*
1. Stegocephalia.	1. Branchiosauria.
	2. Aistopoda.
	3. Microsauria.
	4. Labyrinthodontia.
2. *Gymnophiona.*	
3. Caudata.	
4. Ecaudata.	

ORDER 1. STEGOCEPHALIA.

The earliest vertebrates shown by the arrangement of the nares to have breathed by means of lungs at least in the adult state, exhibit many resemblances to the Palæozoic Crossopterygian fishes in the dentition and the outward aspect of the skull. They agree with these fishes much more closely than with the contemporaneous Dipnoans. The conical teeth in many genera exhibit a complex infolding of their wall, such as is paralleled among fishes only in certain Palæozoic genera of Crossopterygians (e.g., *Holoptychius*, fig. 54, p. 70); enlarged vomerine teeth like those often met with in these fishes, also occur. The ring of small sclerotic plates is only paralleled among fishes, so far as known, in the Crossopterygian families of Rhizodontidæ and Cœlacanthidæ. The occurrence of an infradentary plate in the complex mandible (fig. 86 C, p. 134), if confirmed, would also be suggestive of the same element or series of elements in these early fishes. There is always a pineal foramen, and it is noteworthy that among Palæozoic fishes this feature is only distinctly exhibited by certain Crossopterygians such as *Diplopterus* and *Osteolepis* (fig. 59,

p. 77). Moreover, the bones of the cranial roof never resemble those of the known Dipnoi, but are always normal as in the Crossopterygians; while they form a continuous shield with the robust cheek-plates and the transverse chain of supratemporal elements. The accompanying diagram of the cranial roof-bones of *Pelosaurus* (fig. 81 B) shows the ordinary arrangement of these elements, which is subject only to minor variations and may be instructively compared with the skull of *Rhizodopsis* (fig. 57, p. 75), which is diagrammatically represented with the cheeks crushed outwards and the bones relettered in fig. 81 A. The parietals (*pa.*), frontals (*f*), squamosals (*sq.*), and postfrontals (*ptf.*), occupy their usual position; and there are also prefrontals (*prf.*) and nasals (*n*). The pineal foramen always occurs in the parietal, and not in the frontal region. The cheek-plates are much reduced in number, there being occasionally one in front of the eye ("lachrymal," *l*), always one below the eye ("jugal," *ju.*), and another behind ("postorbital," *pto.*); while the largest and hindermost plate of the cheek, commonly named supratemporal (*s.t.*), seems to

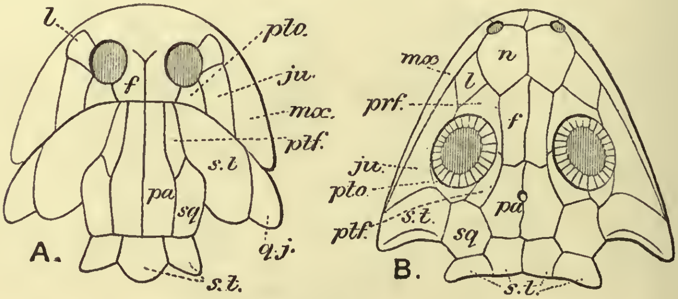

FIG. 81.

Diagrammatic outline of Cranial Roof and outwardly crushed Cheek-plates of *Rhizodopsis* (A) compared with the corresponding bones of a Stegocephalian, *Pelosaurus* (B). *f.*, frontal; *ju.*, posterior suborbital (A) or jugal (B); *l*, anterior suborbital (A) or lachrymal (B); *mx.*, maxilla; *n*, nasa; *pa.*, parietal; *prf.*, prefrontal; *ptf.*, postfrontal; *pto.*, upper posterior suborbital (A) or postorbital (B); *q.j.*, cheek-plate resembling quadrato-jugal of Stegocephalia; *s.t.*, supratemporals and cheek-plate (prosquamosal); *sq.*, squamosal. (Fig. B after Credner.)

correspond exactly with the posterior cheek-plate in *Rhizodopsis, Holoptychius*, and their allies. This and the quadratojugal are closely apposed to the quadrate, without any intervening foramen or vacuity. The true supratemporals are apparently represented in the two pairs of superficial bones (*s. t.*) which complete the covering of the cranium behind and are commonly described as supraoccipitals and epiotics. On either side of this transverse row of plates there is a notch in the hinder border of the cranial roof, of variable extent, evidently for the opening of the auditory meatus. The chondrocranium itself usually exhibits very imperfect ossification, and this is first observable in the basioccipital region, where the skull is articulated with the vertebral axis. The chief features of the palate are the large size of the palatine vacuities and the enormous development of a parasphenoid membrane-bone.

The whole of the cheek being covered with plates, these early lung-breathers are commonly grouped together under the name of STEGOCEPHALIA (roofed-head); and three chief reasons may be mentioned for regarding them as representatives of the Class Batrachia. Traces of gill-arches are conspicuous in immature skeletons of some genera. The ribs, so far as known, do not encircle the thorax or show any indications of connection with sternal elements. The mucus-canal system must have been especially well developed, as indicated by deep impressions frequently observed on the head.

The Stegocephalia first appear in the Lower Carboniferous of Western Europe, but these early representatives of the order are still very imperfectly known. The want of all information as to their limbs is particularly unfortunate, since every known limb of Upper Carboniferous and later date conforms to the normal pentadactyle type, with no approximation to the paired appendages of fishes. All (or nearly all) the genera, however, agree in possessing one median and two paired exoskeletal plates in the thoracic region between the pectoral limbs; these being commonly interpreted as interclavicle and clavicles. There are also very few exceptions to the rule, that a ventral armour of small overlapping scales or scutes is present behind these plates; and some small forms are even armoured dorsally. The degree of persistence of the notochord is very variable, the peripheral elements being sometimes merely separate pleurocentra and hypocentra, sometimes rings or cylinders; while completed biconcave centra are rare, except in the large crocodile-shaped species of the Trias. The latter were originally named Labyrinthodonts by Owen in allusion to the complex structure of their teeth (fig. 90, p. 138), and are the latest members of the Stegocephalian order hitherto identified with certainty. They make an extremely close approximation to the more generalized types of Anomodont reptiles.

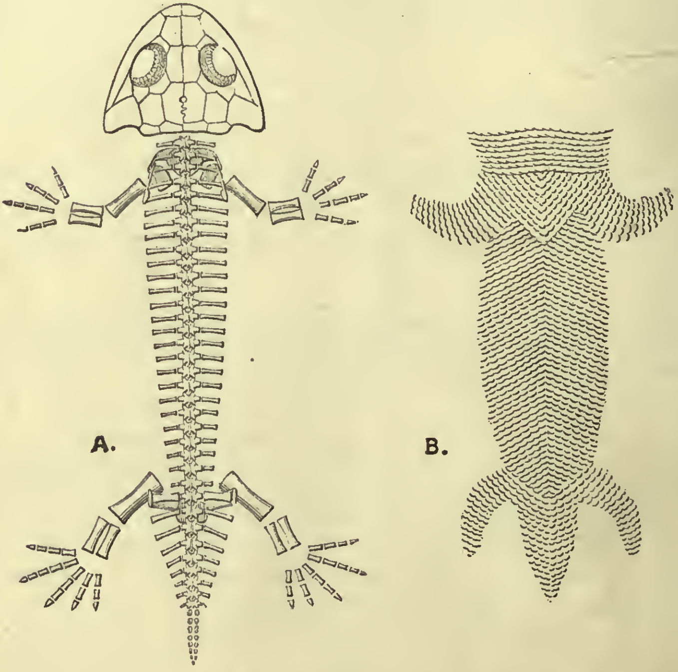

Fig. 82.

Branchiosaurus amblystomus; restoration of skeleton (A) and ventral armour (B) by H. Credner, about nat. size.—L. Permian; Saxony. The tail is known to have been much longer than the extent of the ossified caudal vertebræ.

Sub-Order 1. *Branchiosauria.*

One group of Stegocephalia from the Upper Carboniferous and Permian comprises very small salamander-shaped animals, with a long but broad tail. These are named BRANCHIOSAURIA from the presence of functional gill-arches in immature individuals, as indicated by the regular series of minute denticles which were originally arranged upon them. The teeth are simple hollow cones, not with folded walls; and those of the palate are relatively small or may be entirely wanting. The occipital region of the chondrocranium is not ossified. The notochord seems to have been completely persistent, thickening slightly in the middle of the barrel-shaped vertebræ, which are described as of the unique construction represented in fig. 83 1, 2. A pair of delicate hypocentra or intercentra (*hc.*) encircles the lower half of the notochord (*c.*) and forms part of the transverse process on each side for the support of the rib; while the neural arch itself, in the absence of pleurocentra, extends downwards to cover the superior lateral portion of the notochord, and also enters into the formation of the transverse processes (*pl.*). The ribs are single-headed, very short and stout. The sternum and pubic cartilages are not ossified; and no trace of ossifications has been observed in the carpus or tarsus.

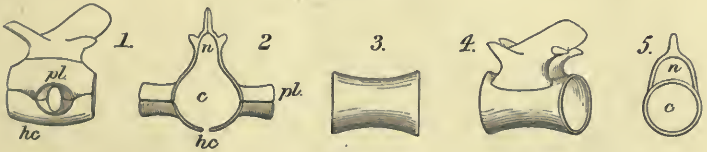

FIG. 83.

Diagrams of Branchiosaurian (1, 2) and Microsaurian (3, 4, 5) Vertebræ, much enlarged. 1. Vertebra of *Branchiosaurus*, lateral aspect. 2. The same, end view. 3. Vertebra of *Hyloplesion*, inferior aspect. 4. The same, lateral aspect. 5. The same, end view. *c*, notochordal canal; *hc.*, hypocentrum; *n*, neural canal; *pl.*, transverse process. (After Credner.)

Branchiosaurus (figs. 82, 83 1, 2, 84 A, 85 A). This is perhaps the best-known genus of Stegocephalia, being represented by innumerable specimens in all stages of growth from the Lower Permian of Saxony, Bohemia, and

France. The head is short and broad with relatively large orbits, and all the elements are clearly distinguishable. No teeth have been noticed on the palate, except perhaps on the vomers. The normal ring of sclerotic plates is supplemented above by an extensive covering of smaller and more irregular plates evidently developed in the same tissue. The presacral vertebræ are about 26, the ossified caudals about 15 in number.

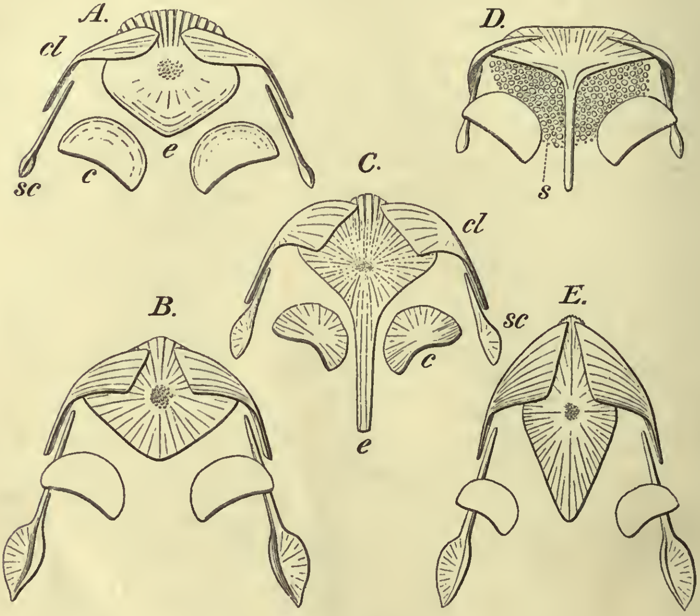

Fig. 84.

Diagrams of Pectoral Arch of Stegocephalia, ventral aspect. A. *Branchiosaurus*, three times nat. size. B. *Pelosaurus*, twice nat. size. C. *Discosaurus*, twice nat. size. D. *Hyloplesion*, twice nat. size. E. *Archegosaurus*, about one-quarter nat. size. *c*, coracoid (scapula of Gegenbaur); *cl.*, clavicle; *e*, interclavicle; *s*, calcified tesseræ in cartilage; *sc.*, scapula (cleithrum of Gegenbaur). (After Credner.)

Impressions of the soft tissues on the Lower Permian coal-shale of Nürschan (Nyřan), Bohemia, show that the tail was about as long as the trunk with the head, most of the caudal vertebræ remaining unossified and thus not observable in the fossils. The ribs are longest in the thoracic region and gradually become insignificant immediately in front of the much-enlarged single pair of sacral ribs, which, like all the others, are merely articulated (not fused) with the vertebral transverse processes.

Behind the sacrum the ribs are again large, but soon diminish as they are traced backwards, and are wanting on the hinder caudal vertebræ. The interclavicle is more or less pentagonal, without a median extension behind; the relatively small and club-shaped clavicles do not meet in the middle line (fig. 84 A). The scapula and coracoid are partially ossified, and so are all the pectoral limb-bones except the carpus. There is no clear evidence of more than four digits in the manus, and the number of phalanges is apparently 2, 2, 3, 2. The ilium is very stout and hour-glass shaped; the ischium is a delicately ossified plate; and the pubis has never been seen (fig. 85 A). There are distinctly five digits in the pes, and the phalangeal formula is 2, 2, 3, 4, 3. The ventral shield consists of deeply overlapping, cycloidal scutes, each with a thickened hinder free border, and the arrangement of this armour in the adult is shown in fig. 82 B. The shield gradually becomes more conspicuous and extends as the immature animal approaches maturity; the skull assumes a more pointed form; the pelvic arch recedes, being originally well in advance of the vertebra which develops into the sacrum; while the limbs gradually ossify and naturally become more robust. The typical species, *B. salamandroides*, from the Lower Permian of Bohemia, attains a length of about 0·065 m. *B. amblystomus*, from Saxony, is larger, sometimes measuring as much as 0·120 m. in length. The French specimens from the Lower Permian of Autun, are commonly described under the generic name of *Protriton.*

Pelosaurus (figs. 81 B, 84 B, 85 B) is much like *Branchiosaurus*, but does not appear to exhibit the supplementary sclerotic plates. *Melanerpeton* is also an allied genus. These are restricted to the Lower Permian of Saxony, Moravia and Bohemia.

Sub-Order 2. *Aistopoda.*

A group of serpentiform Stegocephalia, apparently destitute of limbs, occurs in the Upper Carboniferous both of western Europe and Ohio, and in the Lower Permian of Bohemia, but is as yet very imperfectly known. There is supposed to be a tendency to fusion of the median elements of the cranial roof. The vertebral centra are in the form of constricted cylinders, and the neural spines have atrophied. The teeth are simple cones. The comparatively slender ribs exhibit curious processes, which seem to be due to the fusion of intermuscular bones with them. Neither limb-bones nor traces of arches for the support of the appendicular skeleton have hitherto been observed. *Dolichosoma* has at least 150 vertebræ and sometimes approaches a metre in length; it is not known to exhibit a dermal armature. *Ophiderpeton* has the ordinary ventral shield of oat-shaped scutes, and seems to have been armoured with small dermal tubercles on the back.

Sub-Order 3. *Microsauria.*

The most numerous Stegocephalia of Upper Carboniferous and Lower Permian age present the outward form of lizards or salamanders, and have been provisionally grouped together under the name of MICROSAURIA. In these animals, so far as known, the basioccipital region of the cranium is always ossified. The hollow, conical teeth exhibit simple or only slightly folded walls. The vertebræ (fig. 83 3, 4, 5) are constricted cylinders, while the ribs are slender and longer than is usual in the Stegocephalian order. The pubis is always ossified (fig. 85 C, D). The degree of ossification of the carpus and tarsus varies, and these regions are often entirely cartilaginous. Very rare and perhaps doubtful instances are recorded in which immature individuals exhibit traces of branchial arches (e.g.,

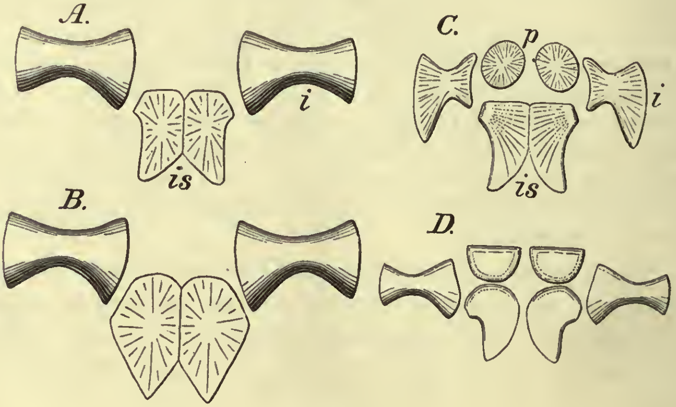

FIG. 85.

Diagrams of Pelvic Arch of Stegocephalia, enlarged. A. *Branchiosaurus.* B. *Pelosaurus.* C. *Discosaurus.* D. *Petrobates.* *i*, ilium; *is.*, ischium; *p*, pubis. (After Credner.)

Hyloplesion and *Microbrachis* from the Lower Permian of Bohemia).

The first fragmentary remains of the Microsauria were discovered in the interior of decayed tree-stumps in the Coal Measures of South Joggins, Nova Scotia; but the only satisfactorily-preserved skeletons hitherto obtained, are from the Lower Permian of Saxony and Bohemia.

Hyloplesion (figs. 83 3, 4, 5, 84 D). A small animal, rarely if ever exceeding a decimetre in length, and with very slightly ossified skeleton. The orbits are situated in the anterior half of the skull, and there is a ring of sclerotic plates. The outer cranial bones are smooth or delicately punctate; and some bones of the palate exhibit a cluster of very minute teeth. The presacral vertebræ (fig. 83 3, 4, 5) are all longer than deep and about 20 in number, while the caudal vertebræ seem to have been nearly if not quite as numerous. All except the hinder caudal vertebræ bear ribs, and these exhibit a distinct capitulum and tuberculum throughout the thoracic region. Two or three pairs of cervical ribs and about three pairs of lumbar ribs are comparatively short and single-headed, as are also those of the anterior caudal region; the single pair of sacral ribs is much thickened as usual. The interclavicle (fig. 84 D) is T-shaped, with a somewhat expanded head; the clavicle is slender and much arched. Both scapula and coracoid are ossified. A mosaic of calcified granules (*s.*) in the region of the clavicular elements may indicate a beginning of ossification in the sternal cartilage. The humerus is expanded a little at each end, and the direction of compression at one extremity is almost at right-angles to that at the other; there is no epicondylar foramen. The radius and ulna are about half as long as the humerus; there are traces of ossification in the carpus; the number of digits is uncertain. The ilium is unusually short and expanded proximally; the ischium and pubis are relatively small and delicate. The hind limb is about as large as the fore limb, but the femur is much more robust than the humerus; a few tarsal elements are ossified, and the number of digits is unknown. The ventral armour consists of overlapping oval scutes with thickened hinder margin, and there seems to have been a dorsal armature. *Hyloplesion longicostatum*, from the Lower Permian of Bohemia, and *H. geinitzi*, from the same horizon in Saxony, are the best-known species.

The imperfectly known *Hylonomus* from the Coal Measures of Nova Scotia, perhaps also of Lancashire, is closely similar to *Hyloplesion* and may be generically identical with it. The allied genus *Petrobates* (fig. 85 D), from the Lower Permian of Saxony, is remarkable for the nature of its ventral shield, which cannot be distinguished from the system of "abdominal ribs" so conspicuous in many reptiles.

Keraterpeton. A genus with comparatively large species, sometimes as much as half a metre in length. The tail is much elongated, three times as long as the trunk in the type species. The large orbits are far forwards, and the cranium itself extends backwards considerably beyond the cheeks. Its most singular feature consists in the large pair of pointed horns, of undetermined nature, firmly fixed to the postero-lateral angles of the cranium and directed backwards. The external bones are sculptured. There are about 20 presacral vertebræ, and the thoracic ribs are distinctly double-headed. The neural and hæmal arches in the caudal vertebræ are firmly fused with the centra, while their spines are expanded and curiously pectinated at the truncate end. The limbs are nearly equal in size, with unossified carpus and tarsus. The phalangeal formula of the hind foot, which has five digits, is clearly proved to be 2, 3, 4, 4, 3. The scutes of the ventral shield are very small, and there appears to have been no dorsal armour. The typical species, *K. galvani*, occurs in the Coal Measures of Kilkenny, Ireland, and Staffordshire, England, and probably does not exceed 0·3 m. in length. There is evidence of allied species in the Coal Measures of Linton, Ohio, U.S.A.; and other forms, probably generically distinct, with moveable horns ("epiotic cornua") and ossified carpal and tarsal elements, are known from the Lower Permian of Bohemia.

Sub-Order 4. *Labyrinthodontia.*

It is remarkable that the large Stegocephalia with complex teeth occur among the earliest as also among the latest known representatives of the Order. There is little or no evidence of evolution among them, except that the largest in size and those most completely "labyrinthodont" are the latest in the series.

The earliest of the Labyrinthodonts proper, however, from the Lower Carboniferous of Scotland, are very imperfectly known. It is particularly unfortunate that no satisfactory remains of the limbs have hitherto been discovered. One fragment of skull belongs to the genus *Loxomma,* better known by skulls from the Coal Measures (Upper Carboniferous) of England. Another unique fossil (named *Pholidogaster pisciformis*) represents a species more than a metre in length, with the characteristic pectoral plates, ventral armour of oat-shaped scutes, and an apparently rhachitomous vertebral axis.

The large and typical Labyrinthodonts of the Coal Measures are also known only by fragmentary specimens, chiefly skulls or portions thereof. In these the basioccipital region always appears to be ossified, and the vertebral axis varies from the rhachitomous condition (see p. 94) to a chain of complete, biconcave discs. The skull of *Loxomma* exhibits a great antorbital vacuity not separated from the orbit itself; and the grooves for the mucus-canals are especially prominent. Its teeth are laterally compressed. The skull of *Anthracosaurus*, which sometimes attains a length of nearly half a metre, is broader than that of *Loxomma*, with normal orbit, and round teeth. The vertebral centra in this genus are biconcave discs, very slightly pierced by the notochord; the thoracic ribs are double-headed.

The Lower Permian Labyrinthodonts are known by many tolerably well-preserved skeletons, the best being those of

Archegosaurus (figs. 84 E, 86, 87). The skull in this genus is much longer than broad, and the facial region elongates with age. The orbits are situated in its hinder portion, and there is a ring of sclerotic plates. The external bones are sculptured, but the course of the mucus-canals is very feebly marked. The basioccipital region is not ossified, and the palatine vacuities are very large. The parasphenoid and pterygoids are toothless, and the vomers bear only one or two pairs of relatively large teeth; but there is a single series of teeth on the maxillæ and premaxillæ, and another along each of the palatines. The latter element lies extended parallel to the maxilla on each side, and enters the hinder margin of the posterior nares, which are otherwise bounded completely by the vomers. The mandible (fig. 86 C) exhibits on its outer face a lower marginal element (*i.d.*), which may be either the exposed border of the splenial or a distinct infradentary bone. Branchial arches with denticles have been observed in immature individuals. The notochord is shown to have been persistent, encircled throughout its length by paired pleurocentra and median bilaterally-symmetrical hypocentra. In the presacral region, which comprises about 25 vertebræ, the pleurocentra are normal; but in the anterior part of the caudal region there is a supplementary pair of smaller cartilages below the ordinary pleurocentra of each vertebra. The sacrum seems to include the elements of only one vertebra. There are well-developed neural arches united by zygapophyses; and in the caudal region there are chevron bones fused with the hypocentra. Ribs are present throughout the trunk and in the front portion of the tail. All are expanded at the extremities, and the foremost are articulated by a double head, the upper facette with the short transverse process of the neural

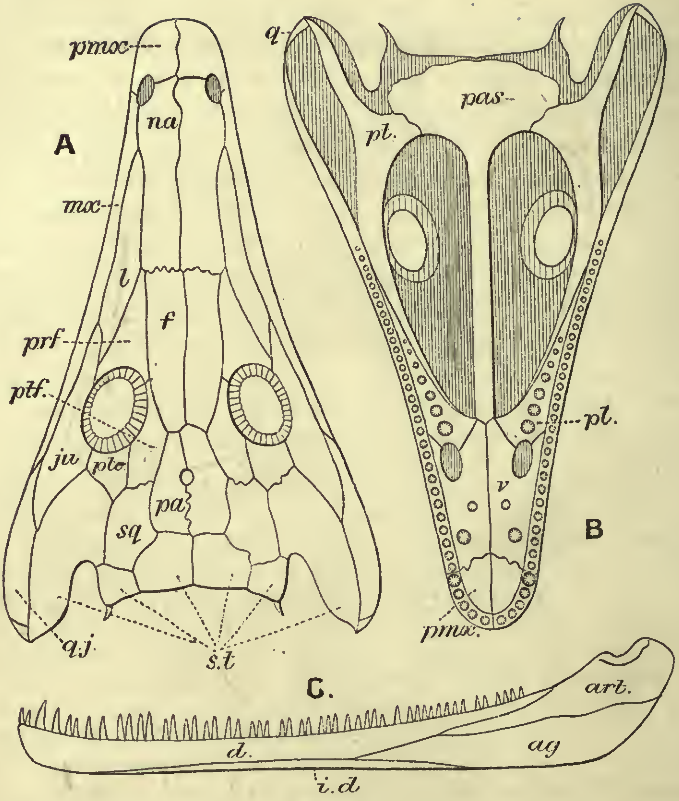

Fig. 86.

Archegosaurus decheni; restoration of skull from the superior (A) and palatal (B) aspects, and left mandibular ramus from the outer aspect (C), about one-third nat. size, sculpturing omitted.—L. Permian; Rhenish Prussia, Saxony, and Bohemia. *ag.*, angular; *art.*, surangular covering articular; *d*, dentary; *f*, frontal; *i.d.*, (?) infradentary or exposed lower margin of splenial; *ju.*, jugal; *l*, lachrymal; *mx.*, maxilla; *na.*, nasal; *pa.*, parietal; *pas.*, parasphenoid; *pl.*, palatine; *pmx.*, premaxilla; *prf.*, prefrontal; *pt.*, pterygoid; *ptf.*, postfrontal; *pto.*, postorbital; *q*, quadrate; *q.j.*, quadratojugal; *s.t.*, supratemporals (and prosquamosal); *sq.*, squamosal; *v*, vomer. (Figs. A, B after Credner, C after Jaekel.)

arch, the lower facette with the hypocentrum. The hinder ribs exhibit a single articular facette, connected with the neural arch. The interclavicle is rhomboidal (fig. 84 E), and the clavicles are triangular in form; all exhibit a radiating sculpture. Both coracoid and scapula are ossified. The limbs are stout, with four digits in the anterior, and five digits in the posterior pair. There are also ossifications in the carpus and tarsus. The fore limb is only about half as large as the hind limb, and not so well known as the latter. Seven carpal bones have been observed in one specimen. The best-preserved tarsus hitherto discovered is shown of one-half the natural size in fig. 87, and a plausible interpretation of it is indicated by the lettering. The number of phalanges in the digits of the hind foot is determined to be 2, 2, 3, 4, 3. There is a ventral armour of overlapping, transversely-elongated scutes; and small irregular dermal calcifications are scattered over the trunk and limbs. The typical species, *Archegosaurus decheni*, attains a length of not less than 1·5 m., and is found chiefly in the Lower Permian of Rhenish Prussia; more fragmentary specimens are recorded from corresponding formations in Saxony and Bohemia.

FIG. 87.

Archegosaurus decheni; portion of hind limb, one-half nat. size.—L. Permian; Rhenish Prussia. F, fibula; T, tibia; *a*, *b*, doubtful ossifications; *c*, centralia; *f*, fibulare; *i*, intermedium; *t*, tibiale; *x*, doubtful centrale; 1—4, tarsalia; I—IV, metatarsalia, one wanting. (After Baur.)

Actinodon is closely similar to *Archegosaurus*, but has a shorter and broader skull with an ossified basioccipital region.

It occurs in the Lower Permian of Rhenish Prussia, but the finest specimens have been obtained from Autun, France. *Euchirosaurus*, from Autun, is more imperfectly known, exhibiting truly rhachitomous vertebræ with the neural spines expanded at the upper end (fig. 88). *Dissorophus*, from the Permian of Texas, has the neural spines still more expanded at the upper end, these supporting a carapace of transversely-elongated bony dermal scutes. *Eryops*, from the Permian of Texas, also seems to be related, but bears minute denticles on the inner side of the mandibular ramus.

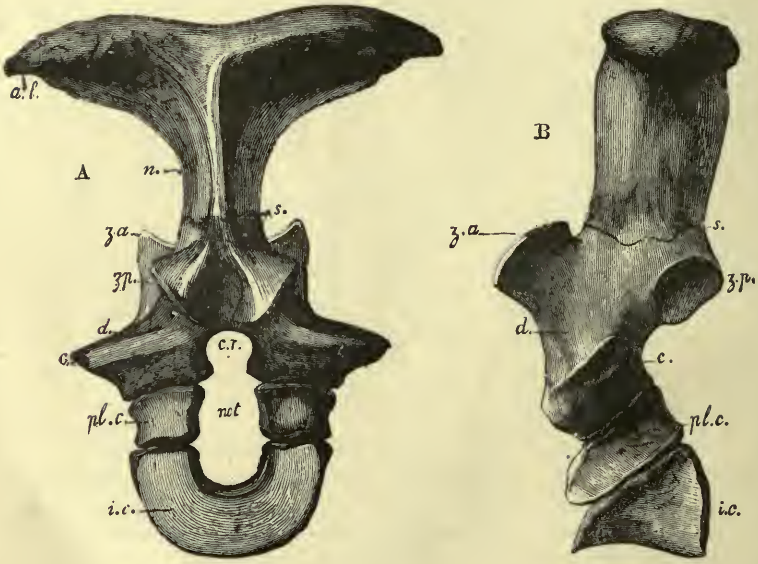

Fig. 88.

Euchirosaurus rochei; posterior (A) and lateral (B) aspects of rhachitomous vertebra, about nat. size.—L. Permian; France. *al.*, lateral expansion of neural arch; *c*, facette for rib; *c.r.*, neural canal; *d*, transverse process of neural arch; *i.c.*, hypocentrum; *n*, neural spine; *not.*, space originally occupied by notochord; *pl.c.*, pleurocentra; *s*, suture between neural arch and spine; *z.a.*, *z.p.*, anterior and posterior zygapophyses. (After Gaudry.)

Cricotus. This imperfectly-known genus is chiefly interesting on account of the condition of the vertebral column. In the presacral region the pleurocentra and hypocentra are horse-shoe-shaped, the former alone bearing the neural arches, which have each a pair of transverse processes.

In the caudal region both the pleurocentra and hypocentra are complete rings, and the neural arch is jointly supported by one of each of these elements; while the hæmal arches (chevron bones) are borne exclusively by the hypocentra.

Mastodonsaurus (figs. 89, 90, 91 A). This is the largest known Labyrinthodont, the skull of *M. giganteus* attaining a length of 1·25 m. At least one specimen has been discovered with the greater portion of the trunk in natural association with the skull. The skull (fig. 91 A) is depressed, a little longer than broad, with the orbits behind its middle. The external bones are sculptured and bear conspicuous marks of the mucus-canal system. The basioccipital region (fig. 89) is ossified and exhibits a pair of large condyles (*c.*) for articulation with the vertebral column. The exoccipitals (*ex. occ.*) are also ossified, but do not enter into the formation of the articular condyles; while the supraoccipital must have been cartilaginous, as it is represented in the fossils by a vacant space (*s. occ.*). The palatine vacuities are very large, while the toothless pterygoids and parasphenoid exhibit their usual development. The palatine lies extended parallel to the maxilla on each side and bears a single longitudinal series of teeth as large as those on the margin of the jaw. The paired vomers, partly separated by the parasphenoid, exhibit two pairs of relatively-large tusks, one near the hinder end, the other in front of the posterior nares. The premaxillæ are pierced to accommodate a pair of much-enlarged teeth at the symphysis of the mandible. The mandibular rami are connected by suture at the symphysis, and there is a coronoid process on each side, as also a short post-articular extension; but the limits of the component elements are still very uncertain. The infoldings of the wall of the teeth are extraordinarily complex (fig. 90). The vertebræ are short, biconcave, and pierced by a remnant of the notochord, while all except the atlas (perhaps also except the hinder caudals) bear a pair of ribs and a loosely-

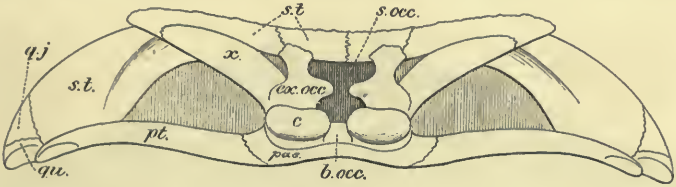

FIG. 89.

Mastodonsaurus giganteus; hinder view of occiput, about one-sixth nat. size.—U. Triassic; Würtemberg. *b.occ.* basioccipital; *c*, occipital condyle; *ex.occ.*, exoccipital; *pas.*, parasphenoid; *pt.*, pterygoid; *q.j.*, quadratojugal; *qu.*, quadrate; *s.occ.*, space occupied by cartilaginous supraoccipital; *s.t.*, supratemporals and (the large lateral plate) prosquamosal; *x*, process of exoccipital. (After E. Fraas.)

articulated neural arch. The atlas exhibits a double concave facette for articulation with the occipital condyles of the skull, and its small neural arch is firmly fused with the centrum. The well-developed neural arches of the other vertebræ are provided with a pair of zygapophyses in front and behind, and a large pair of transverse processes for the support of the upper articulation of the ribs. The latter are all double-headed, though the two facettes are sometimes imperfectly separated. Of the shoulder-girdle, only the clavicular plates are known with certainty. These are externally sculptured ; the interclavicle is rhomboidal in form, and slightly overlapped by the clavicles, which do not meet in the middle line. There is good reason to believe that the pelvis consists of three separate elements ; and the ilium is elongated, articulating with a single pair of sacral ribs.

FIG. 90.

Transverse section of sector of Labyrinthodont Tooth (*Mastodonsaurus gigantues*), highly magnified.—U. Triassic; Würtemberg. *a*, pulp cavity; *b*, *b′*, longer and shorter folds of wall of tooth. (After Owen.)

The limbs are scarcely known, and no traces of a ventral shield or other dermal armour have hitherto been observed. The finest known examples of *Mastodonsaurus* were obtained from the Upper Trias of Würtemberg, and are now in the Museums of Stuttgart and Tübingen. Fragments are also recorded from the Trias of England and India.

Metopias, Capitosaurus, and *Trematosaurus* are allied genera from the Trias of Germany. The contemporaneous *Cyclotosaurus* is peculiar in having the auditory notch closed behind by the union of the external supratemporal with the prosquamosal.

Labyrinthodonts are also known from the Karoo Formation (Permian and Trias) of South Africa, and from the probably equivalent Lower Hawkesbury Formation of New South Wales. An imperfect skull (*Rhytidosteus capensis*) from Beersheba, Orange Free State, exhibits an unusual extension of the bones of the palate, which are tuberculated.

The so-called Chirotherian footprints from the Trias of England and Germany were probably made by some of these Labyrinthodonts. Both extremities are shown to have been pentadactyl, and the manus is much smaller than the pes.

ORDER 2. GYMNOPHIONA.

The Cæcilians are entirely unknown among fossils.

ORDER 3. CAUDATA (OR URODELA).

The known extinct representatives of the newts and salamanders do not afford any information as to their origin and development. Only one skeleton of Mesozoic age has hitherto been discovered, namely, *Hylæobatrachus croyi* from the Wealden of Bernissart, Belgium. This specimen is tolerably well-preserved, about 0·1 m. in length, and seems to indicate a perennibranchiate animal. There are traces of a maxillary arch, and of three pairs of ossified branchial arches. The fore limbs are shorter than the hind limbs, the digits of the former being four, of the latter five in number. The ribs are extremely short, and there are at least fifteen caudal vertebræ.

Throughout the Tertiary formations, remains of Caudata are very rare, and most of them can scarcely be distinguished from existing genera. *Megalotriton*, known only by detached vertebræ and limb-bones from the Upper Eocene or Lower Oligocene of France, seems to be an extinct newt. *Molge* (*Triton*) itself is supposed to be represented by skeletons in the Lower Miocene lignite of Rott, near Bonn. Giant salamanders apparently of the genus *Cryptobranchus*, at least as large as those now surviving in Japan, are known by well-preserved skeletons from the Upper Miocene of Oeningen, Switzerland. One of these, now in the Teyler Museum, Haarlem, is the famous *Homo diluvii testis* of Scheuchzer.

ORDER 4. ECAUDATA (OR ANURA).

Palæontology affords as little information concerning the evolution of the frogs and toads, or tail-less Batrachians, as concerning that of the newts and salamanders. Phosphatized mummies both of frogs and toads, apparently indistinguishable from the modern genera *Rana* and *Bufo*, occur with their bones in the Upper Eocene (or Lower Oligocene) Phosphorites of S.-W. France. Even if these happen to have been accidentally introduced into the deposit from the surface, there are many undoubted typical skeletons of Ecaudata in European deposits of very little later date. One extinct family, that of the **Palæobatrachidæ**, occurs in the Lower Miocene lignite of Rott, near Bonn, Germany, and in apparently contemporaneous deposits both in Bohemia and France. These are toads related to the **Pelobatidæ**, of very ordinary size, with teeth in the upper jaw, procœlous vertebræ, no separate dorsal ribs, the sacral transverse processes much expanded distally, and the urostyle articulating with the sacrum by two condyles. The typical genus is *Palæobatrachus*, represented in the lignites both by complete adult skeletons and by impressions of the tadpoles. Complete skeletons of *Discoglossus* have also been found in the same formation (*D. troscheli*).

CLASS REPTILIA.

Orders.	Sub-Orders.
3 1. Anomodontia.	1. Pariasauria.
	2. Theriodontia.
	3. Dicynodontia.
4 2. Sauropterygia.	
2 3. Chelonia.	1. Cryptodira. 2
	2. Pleurodira. 1
	3. Trionychia. 3
5 4. Ichthyopterygia.	
7 5. Rhynchocephalia.	1. Proterosauria.
	2. Rhynchocephalia Vera.
6 6. Squamata.	1. Dolichosauria.
	2. Pythonomorpha.
	3. Lacertilia.
	4. Ophidia.
9 7. Dinosauria.	1. Theropoda.
	2. Sauropoda.
	3. Ornithopoda.
8 8. Crocodilia.	1. Parasuchia. Pseu
	2. Mesosuchia.
	3. Eusuchia.
9. Ornithosauria.	

On the evidence of skeletons alone it is impossible in many cases to determine whether the early lung-breathers were Amniota or Anamniota. It is therefore difficult to state precisely to what period must be assigned the dawn of the class of reptiles, which exhibit an advance upon the Batrachia or Amphibia not only in being provided with the fœtal envelope known as the amnion, but also in breathing by lungs throughout life and never possessing branchiæ at any stage. In the existing fauna, however, the degeneration of the parasphenoid bone and its functional replacement in the basicranial axis by the pterygoids (compare fig. 86 B, p. 134, with fig. 94 B, p. 149) mark this higher grade. If this feature in the palate has always been distinctive, *Palæohatteria*, from the Lower Permian of Saxony, is the earliest member of the Class Reptilia hitherto discovered; and it is certain that during the Upper Permian age there were numerous reptiles both in Europe and America, probably also in South Africa.

As the various groups become differentiated and specialized, the most conspicuous of the fundamental modifications in the skeleton occur in the postero-lateral regions of the skull, where the bones surrounding the temporal and masseter muscles and those supporting the lower jaw are variously rearranged in separate bars and partly disappear. The form of the otic region changes, while the squamosal plate, which directly covers this mass in fishes (and presumably in Stegocephalia), is thrust from all connection with it except at the hinder angle, and its larger portion is a free bar over the muscles, connected with the other plates of the cheek. In one great group of reptiles, comprising the Anomodontia, Sauropterygia, Chelonia, and Ichthyopterygia (fig. 91 B, C), this outward thrust of the squamosal first begins, and is the sole modification of the primitive type; though the cheek-plates in the broad arch thus formed may be variously fused together, sometimes even irregularly perforated—showing at first, indeed, the usual inconstancy of a new and not completely established feature. From the earliest members of this prime division of reptiles, Palæontology seems to demonstrate that the Mammalia (with one robust zygomatic arch) arose; some of the skeletons belonging to this division might, indeed, be claimed as actually mammalian, if it were not for the complexity of the mandible and the presence of a free quadrate bone. In a second group, comprising the Rhynchocephalia, Dinosauria, Crocodilia, and Ornithosauria (fig. 91 D), there is the same arrangement of the squamosal, while the broad arch of cheek-plates is pierced by a more or less extensive vacuity ("lateral temporal vacuity"), which leaves a narrow bar above and another narrow bar below. By the constant loss of the lower, and the frequent loss of the upper bar, this group

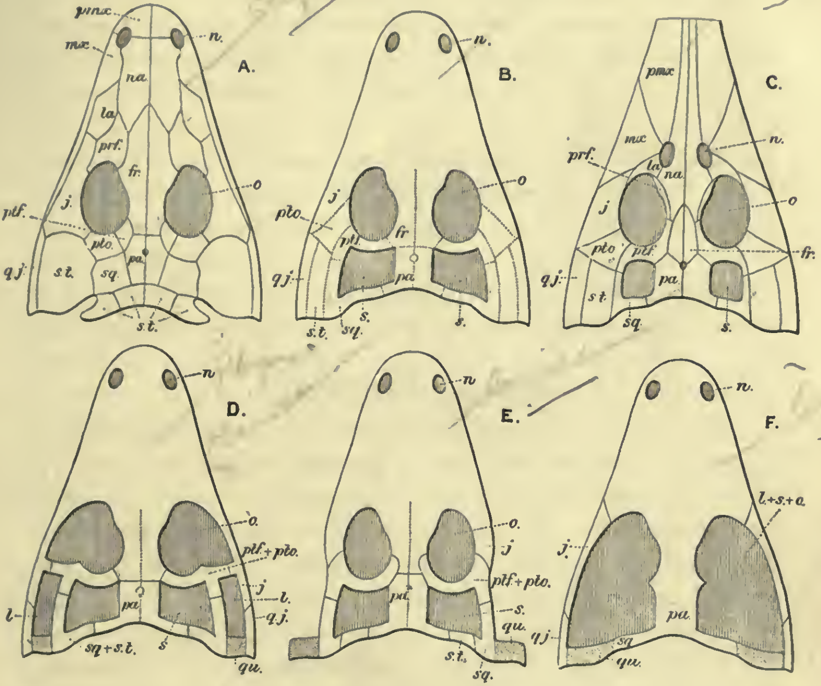

FIG. 91.

DIAGRAM OF THE CRANIAL ROOF IN A STEGOCEPHALIAN, VARIOUS TYPES OF REPTILES, AND A BIRD, SHOWING MODIFICATIONS IN THE POSTERO-LATERAL REGION.

A. Stegocephalian (*Mastodonsaurus giganteus*, about one-fifteenth nat. size, after E. Fraas). B. Generalized Anomodont or Sauropterygian, passing with slight modification into the Chelonian (sutures dotted to denote inconstancy in fusion of elements). C. *Ichthyosaurus*. D. Generalized Rhynchocephalian, Dinosaurian, Crocodilian, or Ornithosaurian. E. Generalized Lacertilian, often losing even the arcade here indicated. F. Generalized 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; *q.j.*, quadrato-jugal; *qu.*, quadrate; *s*, supratemporal vacuity; *s.t.*, supratemporals and prosquamosal; *sq.*, squamosal. Vacuities shaded with vertical lines, cartilage bones dotted.

passes into the Squamata (Lacertilia + Ophidia) in comparatively late geological times (fig. 91 E); while some of its early divisions are generally believed to be related in an undetermined way to the ancestry of the class Aves, which never possesses the upper, though always the lower bar in question (fig. 91 F).

It is noteworthy that nearly all reptiles with well-formed limbs—whether adapted for habitual support of the body on land, for flight, or for constant swimming—flourished only before mammals and birds became dominant; the vast majority of the survivors during the Tertiary period and in the existing world being comparatively degenerate types.

ORDER 1. ANOMODONTIA.

The dominant group among the earliest reptiles in each quarter of the globe where they have as yet been discovered, is directly intermediate in skeletal characters between the highest Labyrinthodonts (*Mastodonsaurus* and its allies) and the lowest Mammals (Monotremata). Its members first received the general name of ANOMODONTIA in allusion to the varied modifications of the dentition, so unusual among reptiles. They were afterwards named THEROMORPHA or THEROMORA, in an equally general manner, in allusion to the many obvious resemblances in their skeleton to that of the monotreme mammals. Like most palæontological terms, both of these were suggested prematurely before definition became possible, and it seems preferable to retain the first until the osteology of these reptiles is known with sufficient completeness to arrange them in natural order.

The Anomodonts, as now understood, are all land-reptiles with limbs adapted for habitual support of the body. Some are of very massive build, while others must have been as agile as a modern feline or canine Carnivore. The investing bones of the temporal region of the skull either form a continuous shield or contract into a single broad temporal arcade, which is sometimes slightly pierced; and the firmly-fixed quadrate is often much reduced in size. There is always a pineal foramen. The teeth are placed in sockets, though sometimes also fused with the supporting bone. The posterior (internal) nares occupy their primitive forward position on either side of the vomers; and the development of a secondary palate never advances further than that in certain Chelonia. The most characteristic feature in the pectoral arch consists in the presence of ossified epicoracoids (sometimes termed precoracoids) as large as those in existing Monotremes; while clavicles and a T-shaped interclavicle are also well-developed. There is an entepicondylar foramen in the humerus, and the delto-pectoral crest is very prominent. The vertebral centra are more or less biconcave, and the anterior ribs are completely or imperfectly double-headed. The number of sacral vertebræ is variable, and intercentra (hypocentra) are usually rudimentary or absent. No abdominal ribs and very rare traces of dermal armour have been observed.

All known Anomodonts seem to be of Permian and Triassic age.

Sub-Order 1. *Pariasauria.*

The nearest approach to the Labyrinthodonts is exhibited by the PARIASAURIA, which have the head completely covered by a bony roof. The constitution of this roof in the typical genus *Pariasaurus*, however, is as yet uncertain; and no undoubted impressions of mucus-canals have hitherto been observed, although the external bones in this animal are sculptured like those in many Labyrinthodonts. The teeth are conical or with a compressed, cuspidate crown; while those on the margin of the jaw are arranged in a more or less uniform series.

Pariasaurus (figs. 92, 93). This is an animal of massive build, with short tail, and especially stout limbs. It is known from one almost complete skeleton (fig. 92) nearly three metres in length, and from other more incomplete specimens. The head is triangular in form, short, broad, and depressed. The cranial roof is coarsely sculptured, but not ornamented with bosses; and the sutures between its component elements have not been clearly observed. There is a double narial opening in front; the small orbits are laterally-placed; and there is a conspicuous pineal foramen. The temporal fossa is open behind on each side; and the very large single occipital condyle exhibits a slight indent. The sutures between the elements of the palate cannot be traced in the known specimens; but the general aspect of this region is indicated in the accompanying diagram (fig. 93). The basioccipital (*b. occ.*) is short, the basisphenoid (*b. s.*) longer; and the latter bears the usual stout lateral processes for articulation with the pterygoids. Immediately in front of this articulation there is the usual interpterygoid vacuity (*i. pt.*). Each pterygoid sends outwards and backwards a robust branch (*p. pt.*) to the quadrate (*qu.*), but loses its identity in the other bones of the palate in front. These are remarkable for the numerous series of small teeth which they bear, arranged as indicated by the minute circles in the diagram. The two foremost longitudinal series of teeth (*v*) are doubtless fixed on the vomers, which separate the large posterior nares (*pt. na.*). The maxillæ and premaxillæ do not appear to possess a palatal extension; they are provided with a single uniform series of much larger teeth than those of the palate, each with a slightly expanded and compressed, serrated crown. These teeth are directed a little inwards, while those of the comparatively small mandible are inclined slightly outwards to meet them; but no traces of wearing have been observed. The mandible is not produced behind the articular facette, and the sutures between the various elements cannot be traced; but the two rami apparently meet in open suture at the symphysis. A curious feature consists in the presence of a slight boss below the symphysis, and a larger pair of bosses behind, one on the inferior aspect of each ramus. The vertebral centra are biconcave, and there are relatively small wedge-shaped intercentra (hypocentra) between all those of the dorsal region. The number of presacral vertebræ is about 18 in *P. baini*, and each (except perhaps the atlas) shows a deepened but undivided articulation for the single-headed rib. The sacrum comprises four vertebræ, which are not fused together.

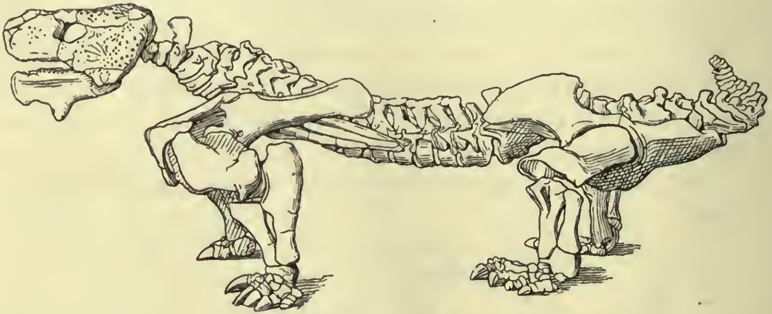

FIG. 92.

Pariasaurus baini; side view of skeleton, about one-thirtieth nat. size.—Karoo Formation (Permian or Triassic); Cape Colony, South Africa. (After Seeley.)

There are about 30 caudal vertebræ, which rapidly become very small, but nearly all bear neural arches and chevron bones; after the sixth vertebra they become laterally compressed and the transverse process disappears as a tubercle. In the pectoral arch the clavicles rest on the front border of the large T-shaped interclavicle, meeting in the middle line and arched to meet the median process of the scapula. There also appears to be a supraclavicle on each side. The epicoracoid seems to be entirely in front of the glenoid cavity for the humerus, and there is a foramen between the former element and the coracoid-proper. The humerus is constricted in the middle and much expanded at each end; the epicondylar foramen has not been observed. The very stout ulna has a conspicuous olecranon process. The carpus and manus are very imperfectly

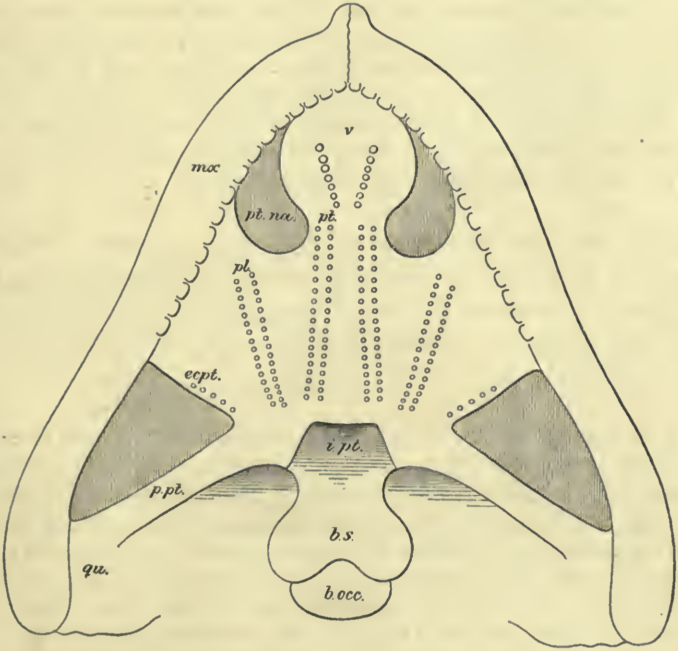

FIG. 93.

Pariasaurus baini; diagram of palate, one-seventh nat. size.—Karoo Formation (Permian or Triassic); Cape Colony. *b.occ.*, basioccipital; *b.s.*, basisphenoid; *ecpt.*, ectopterygoid region; *i.pt.*, interpterygoid vacuity, opening backwards; *mx.*, maxilla; *p.pt.*, hinder lateral process of pterygoid extending to quadrate; *pl.*, palatine region; *pt.*, anterior median part of pterygoid region; *pt.na.*, posterior nares; *qu.*, quadrate; *v*, vomerine region. The small circles indicate the bases of conical teeth.

known. The pelvic bones are fused together in the adult, and the acetabulum is closed. There is no vacuity between the pubis and ischium, but the usual small foramen pierces the pubic region. An epigastroid ossification seems to occur between the pubes. The hind limb is slightly shorter than the fore limb, and its digits are rather smaller. The femur is imperfectly known, but exhibits a curious small intercondylar foramen at its distal end. The tibia and fibula appear to articulate with one large proximal tarsal bone, and there seem to have been five digits in the hind foot. All ungual phalanges hitherto discovered are pointed claws. Small dermal scutes seem to have been arranged in sparse series on the back. All the known species of *Pariasaurus* were obtained from the Karoo Formation (Permian or Trias) of South Africa, the typical species being *P. serridens*, known only by the head. *P. bombidens* and *P. baini* (fig. 92) are represented by comparatively complete skeletons.

Elginia, from the supposed Triassic sandstones of Elgin, seems to be related to *Pariasaurus,* but is known only by the skull, which is about 0·15 m. in length. It is chiefly remarkable for the pairs of bosses and horn-shaped defences affixed to the cranial roof.

Procolophon (fig. 94). This is a small animal, apparently not attaining a greater length than 0·3 m., but very similar to *Pariasaurus* in general proportions. The skull (fig. 94) is short and triangular in shape, exhibiting the sutures between most of the bones and not externally sculptured. It is remarkable for the relatively enormous size of the orbits (*orb.*) and pineal foramen (*pin.*); also for the slight perforation of the temporal arcade by an oblong foramen which evidently represents the beginning of a lateral temporal vacuity (*l.t.f.*) The narial opening (*nar.*) is terminal and paired. The parietal bones (*pa.*) are relatively large, and the identification of the element (*sq.*) at the postero-lateral angle of the cranium is a little uncertain. Outside the latter there is a deep notch or excavation, evidently for the passage of the external auditory meatus; which, however, does not affect the quadrate. On the palate the pterygoids (*pt.*) distinctly extend forwards to reach the vomers (*v*), but they do not meet in the middle line so far back as in *Pariasaurus.* The palatines (*pl.*) bound the posterior nares behind. The teeth are simple cones, those on the margin of the jaws sometimes broader than long, and arranged in a close, regular series of moderate size; comparatively minute teeth occur in a single longitudinal series on each pterygoid (*pt.*), and in at least one longitudinal series on each vomer (*v*). The mandible bites within the upper jaw. The T-shaped interclavicle (*i.cl.*) has a very long median arm, extending beyond the ossified coracoid region, which comprises two elements on each side as usual (*co.*, *ep. co.*). *Procolophon* has hitherto been found only in the Karoo Formation of South Africa, the type species being *P. trigoniceps* (fig. 94). All the known specimens are fragmentary.

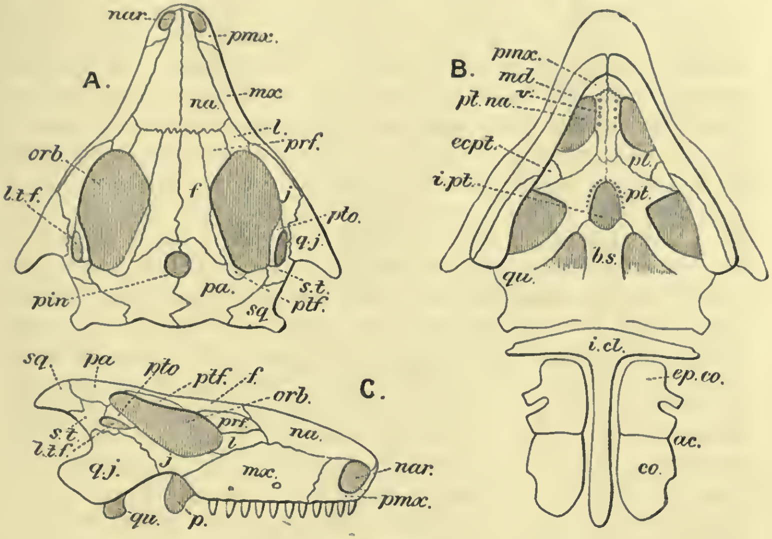

Fig. 94.

Procolophon trigoniceps; restoration of skull from the superior (A), inferior (B), and lateral (C) aspects, also part of the pectoral arch, slightly reduced.—Karoo Formation (Permian or Triassic); South Africa. *ac.*, glenoid cavity for humerus; *bs.*, basisphenoid; *co.*, coracoid; *ecpt.*, ectopterygoid; *ep.co.*, epicoracoid; *f*, frontal; *i.cl.*, interclavicle; *i.pt.*, interpterygoid vacuity; *j*, jugal; *l*, lachrymal; *l. t. f*, 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 (with palatal extension in fig. B); *prf.*, prefrontal; *pt.*, pterygoid; *pt. na.*, posterior nares; *ptf.*, postfrontal; *pto.*, postorbital; *q. j.*, quadrato-jugal; *qu.*, quadrate; *s. t.*, supratemporal (prosquamosal); *sq.*, squamosal; *v*, vomer. (From specimens in British Museum.)

Aristodesmus ruetimeyeri (originally ascribed in error to *Labyrinthodon*) seems to be related to *Procolophon.* It is known only by the impression of a small skeleton from the Bunter Sandstone (Lower Triassic) of the neighbourhood of Basle, Switzerland.

Otocœlus. A small animal remarkable for the possession of a bony dorsal shield. The head is triangular in form, short, broad, and depressed. The cranial roof is coarsely sculptured, but not ornamented with bosses;

and the sutures between its component elements have not been clearly distinguished. There is a double narial opening in front; the orbits are of moderate size, directed both laterally and superiorly; while the notch or excavation of the postero-lateral border for the external auditory meatus is unusually large and deep, affecting even the quadrate bone. The occipital condyle has not been seen. The mandible is not produced behind its articular facette. Of the dentition, only the marginal series have been observed; these teeth being simple smooth cones, not folded at the base, in a single row in each jaw. Two of the anterior dorsal vertebræ are proved to be amphicœlous, and large intervertebral wedge-bones occur with them. The ribs are much expanded, but do not touch each other. Upon them rests the carapace, consisting of a series of bilaterally symmetrical, transversely elongated bands of bone; but the shield thus formed does not appear to extend quite so far forwards as the occiput. The bands of the carapace, which are at least twelve in number, alternate with the supporting ribs, resting on their adjacent edges and separated by narrow interspaces. In the anterior part the superior costal surfaces rise between these bands to the plane of the latter, forming a closer surface than posteriorly. The pectoral arch comprises a pair of bent clavicles, expanded at each end, overlapping a short and broad interclavicle. The coracoid is small, not notched, and may be co-ossified with the scapula. The humerus exhibits a much expanded head and slender shaft. The femur is longer than the tibia. *Otocœlus* occurs in the Permian of Texas, where it seems to be represented by two species. The type form, *O. testudineus*, is known by an imperfect skull associated with remains of the pectoral arch and fore limb, also almost certainly with two dorsal vertebræ, numerous ribs, and part of both hind limbs. The type specimen of *O. mimeticus* exhibits the nearly complete skull and mandible in undoubted association with the carapace and some limb-bones. The skull in each species measures about 0·12 m. in length.

Pariotichus and other genera, known by fine skulls and other remains, also apparently represent the Pariasauria in the Permian of Texas, U. S. A.

Sub-Order 2. *Theriodontia.*

Another group of Anomodonts is remarkable for the resemblance in form of the skull to that of the carnivorous mammals, and in the differentiation of the marginal teeth (so far as shape is concerned) into incisors, canines, and molars. The sub-order they represent is thus named THERIODONTIA. The external bones are never sculptured. There is a large supratemporal vacuity, the bones contracting into a single broad temporal arcade; and the quadrate bone exhibits a tendency to extreme reduction in size. The occipital condyle is distinctly bilobate. The premaxillæ are separate. The meeting of palatal plates from the maxillæ in the middle line, sometimes followed behind by similarly united plates from the palatines (fig. 95, *s.p.*), causes the actual opening of the posterior nares on the roof of the mouth to be displaced backwards, as in certain chelonians and in mammals. Teeth on the palate are insignificant and rare. The mandible bites within the upper jaw and usually exhibits a persistent suture at the symphysis of its two rami, but never any vacuity in the latter. The skeleton of the trunk is imperfectly known; but the humerus has an expanded distal end, sometimes with an ectepicondylar as well as an entepicondylar foramen; the scapula has a large "spine," quite mammalian in aspect; and there is a small vacuity between the pubis and ischium in the pelvis.

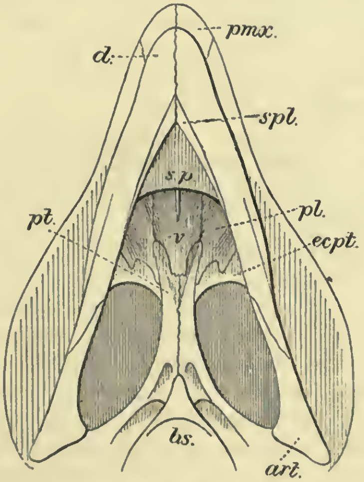

Fig. 95.

Galesaurus planiceps; palatal aspect of skull, with mandible, two-thirds nat. size.—Karoo Formation (Permian or Triassic); South Africa. *art.*, articular; *b.s.*, basisphenoid; *d*, dentary; *ecpt.*, ectopterygoid; *pl.*, palatine; *pmx.*, premaxilla; *pt.*, pterygoid; *s.p.*, secondary palate obscuring the primitive opening of the posterior nares; *spl.*, splenial; *v*, single vomer with median vertical plate in front descending to meet the secondary palate. (From specimen in British Museum, no. R. 511.)

Galesaurus (fig. 95). A small animal known only by the skull, which is depressed behind, compressed in front, and has the anterior nares subdivided by a median partition. There are 4 pairs of incisor teeth above, 3 pairs below, one pair of large canines in each jaw, and an undetermined number of molars, which are laterally compressed and in part tricuspidate. The upper canine is borne by the maxilla, and its pulp-cavity is shown to be closed. The palate, so far as known, is represented in the accompanying diagram (fig. 95). The vomer (*v*) extends backwards to the pterygoids, bounded laterally in its hinder portion by the palatines (*pl.*); the relatively large pterygoids (*pt.*) meet in the middle line, sending backwards and outwards a process to the quadrate, while forwards they seem to join the ectopterygoid or transverse bone (*ecpt.*) in forming the short descending process which abuts against the inner face of the mandible on each side. It is not certain whether the palatines contribute to the false palate (*s.p.*) formed by the plates from the maxilla. The skull of the typical species, *Galesaurus planiceps*, measures 0·09 m. in length, and is known from the Karoo Formation both of Cape Colony and of the Orange Free State.

Lycosaurus. Also known with certainty only by the skull, which is compressed rather than depressed, and differs from *Galesaurus* in its molariform teeth being all simple cones, though more or less compressed and finely serrated. These teeth are well-spaced and only about five in number on each side above and below. The two known species are from the Karoo Formation of Cape Colony.

Aelurosaurus. Like *Lycosaurus*, but with small pointed teeth irregularly grouped on the anterior half of the palate. *Aelurosaurus felinus* is known only by a small skull wanting the occipital region, from the Karoo Formation of Cape Colony.

Cynognathus (fig. 96). The only Theriodont hitherto described in which the vertebral column and limb-arches are definitely associated with the skull. The typical species attains a large size, the skull measuring nearly 0·4 m., and the vertebral column to the first sacral vertebra about 0·95 m. in length. The skull (fig. 96) is laterally compressed and the anterior nares are divided by a median partition; the parietal crest (*pa.*) is much elevated; the sutures bounding the postfrontal (*ptf.*), prefrontal (*prf.*), lachrymal (*la.*), and nasal (*na.*) bones are not clearly observable. A small vacuity (*l.t.f.*) occurs in the temporal arcade, but this is absent in a closely allied species; and there is a little prominence on the lower margin of this arch suggesting the downward process it bears in certain Edentate mammals. The suture between the squamosal (*sq.*) and supratemporal (*s.t.*) seems to be obliterated, as also that between the jugal (*j*) and postorbital (*pt.o.*). A pair of indents on the snout at the meeting of the nasal and maxillary bones may have lodged glands, and roughened bone between suggests a possible callosity or horn. The pineal foramen is obscured by crushing in the only known specimen, and the sutures between the bones of the brain-case are not distinctly seen. The two rami of the mandible are anchylosed at the symphysis, and the coronoid process is remarkably high. There are four pairs of serrated incisors in the upper jaw, probably only three pairs in the lower jaw; the upper canine, likewise partly serrated, is fixed in the maxilla. There are nine molars above and below on each side, the first five smaller and simpler than the posterior four; they are laterally-compressed cones with a serrated edge more or less notched into a separate denticle at the base.

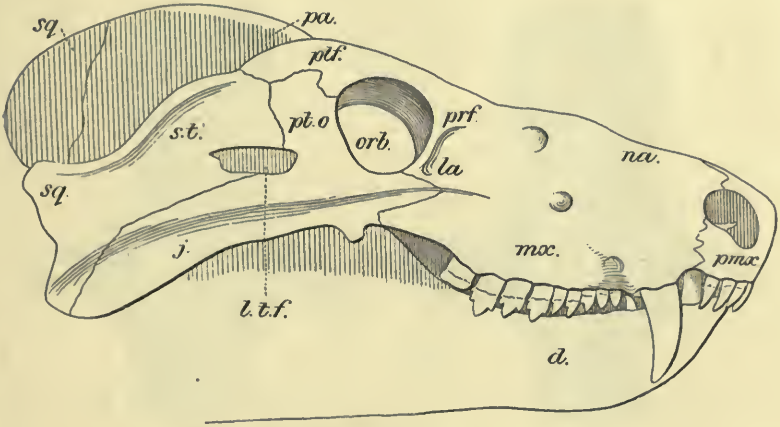

FIG. 96.

Cynognathus crateronotus; right lateral aspect of skull, with imperfect mandible, one-quarter nat. size.—Karoo Formation (Permian or Triassic); South Africa. The present writer has only been able to distinguish the sutures here indicated, but the various regions are lettered in accordance with their probable constitution; the molariform teeth may perhaps project further from their sockets than during life, and the crown of the hindermost tooth is broken. *d*, dentary; *j*, jugal; *l.t.f.*, incipient lateral temporal vacuity; *la.*, lachrymal; *mx.*, maxilla; *na.*, nasal; *orb.*, orbit; *pa.*, parietal; *pmx.*, premaxilla; *prf.*, prefrontal; *pt.o.*, postorbital; *ptf.*, postfrontal; *s.t.*, supratemporal (prosquamosal); *sq.*, squamosal. (Slightly restored from photograph of type specimen in British Museum.)

It is not known whether any of these teeth have divided roots. There are 29 presacral vertebræ, 6 being counted as cervical, 18 as dorsal, and 5 as lumbar. The centra are amphicœlous, and there are small wedge-bones between the cervicals, though apparently none behind. The ribs are double-headed or expanded to exhibit a double articulation, with the neural arch and wedge-bone in the cervical region, with the neural arch and the suture between two adjoining centra in the dorso-lumbar region.

In the hinder dorsal and lumbar region the ribs are curiously expanded and imbricating. Three or four vertebræ are comprised in the sacrum, and the tail must have been small, apparently without free caudal ribs. The scapula exhibits its great spine. The ilium is a little expanded, projecting further backwards than forwards, and all three elements of the pelvis enter the acetabulum. The vacuity between the pubis and ischium is distinct. The typical species *Cynognathus crateronotus*, and allied species, occur in the Karoo Formation of Cape Colony.

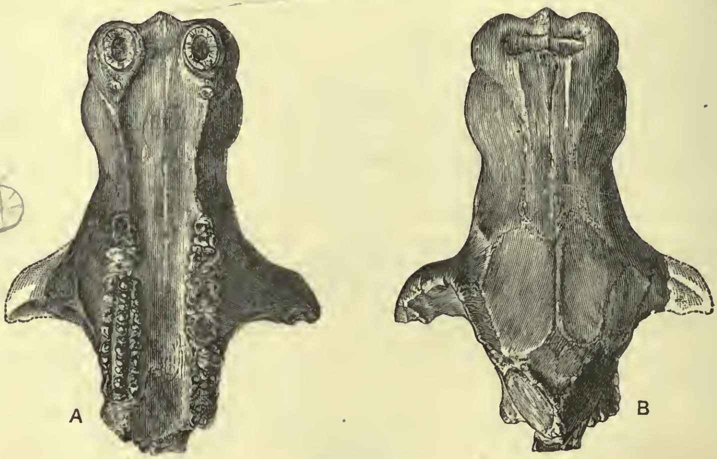

FIG. 97.

Tritylodon longævus; skull wanting hinder occipital end, from the palatal (A) and upper (B) aspects, two-thirds nat. size.—Karoo Formation (Permian or Triassic); Basutoland, South Africa. (After Owen.)

Tritylodon (fig. 97). Some Theriodonts exhibit the molariform teeth not laterally compressed but transversely expanded and adapted for grinding. An extreme example probably of this type is the imperfect skull from the Karoo Formation of Basutoland, described under the name of *Tritylodon longævus* and commonly ascribed to a mammal. The pair of incisor or canine-like teeth in front seem to have grown from a persistent pulp. The molariform teeth preserved bear three longitudinal series of tubercles, and their roots are either divided or impressed with a very deep vertical groove on the outer face.

An extraordinarily mammalian fore limb and manus from the Karoo Formation of Cape Colony, described under the name of *Theriodesmus phylarchus*, probably belongs to a Theriodont, and two interpretations of the characters of the manus are given in the accompanying figs. 98 A, B. The ulna exhibits a well-defined olecranon process.

Numerous remains which seem to be referable to Theriodonts are known from the Permian of Texas and Illinois, U.S.A.;

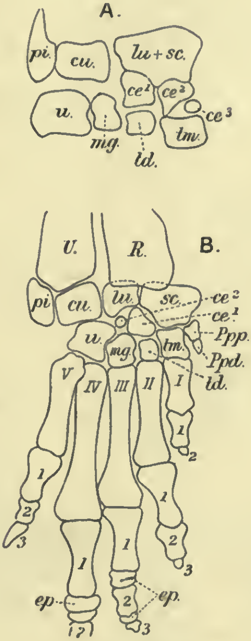

FIG. 98.

Theriodesmus phylarchus; restoration of carpus (A) by Seeley, of the whole manus (B) by Bardeleben, slightly reduced.—Karoo Formation (Permian or Triassic); Fraserberg, Cape Colony. R, radius; U, ulna; *ce.*, centralia; *cu.*, cuneiform; *ep.*, epiphyses; *lu.*, lunar; *mg.*, magnum; *pi.*, pisiform; *Ppd.*, distal segment of pre-pollex; *Ppp.*, proximal segment of pre-pollex; *sc.*, scaphoid; *td.*, trapezoid; *tm.*, trapezium; *u*, unciform; I—V, metacarpals; 1—3, phalanges.

and the fragmentary skulls named *Deuterosaurus* and *Rhopalodon* from the Permian of Russia also represent animals of much the same type. Some of these forms do not appear to have possessed the false palate below the true posterior nares, while *Rhopalodon* distinctly exhibits a ring of sclerotic plates.

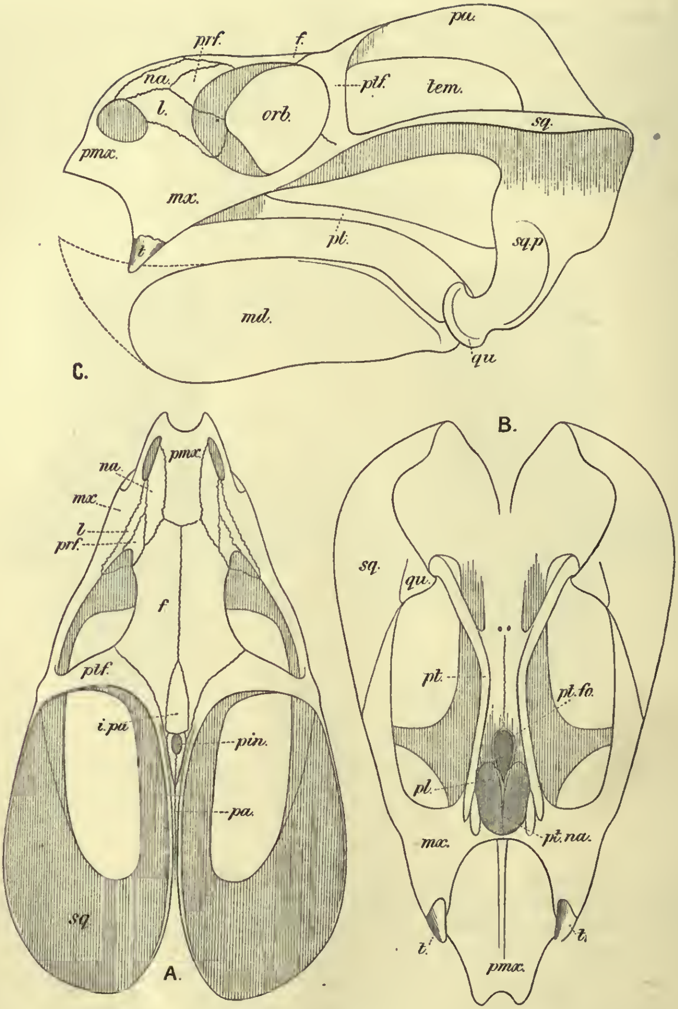

Fig. 99.

Gordonia traquairi; restoration of skull from the superior (A), inferior (B), and lateral (C) aspects, somewhat less than one-half nat. size.—Triassic (?); Elgin. *f*, frontal; *i.pa.*, so-called interparietal; *l*, lachrymal; *md.*, mandible, the lateral vacuity not shown, and the symphysial region added in outline to the front border of the fossil; *mx.*, maxilla; *na.*, nasal; *orb.*, orbit; *pa.*, parietal crest, of undetermined constitution, but the pair of small bones encircling the pineal foramen probably to be regarded as parietals; *pin.*, pineal foramen; *pl.*, vomero-palatine region; *pmx.*, premaxillary region; *prf.*, prefrontal; *pt.*, pterygoid; *pt.fo.*, interpterygoid vacuity; *pt.na.*, hollow into which the backwardly-directed posterior nares open; *ptf.*, postfrontal and postorbital bar; *qu.*, quadrate; *sq.*, squamosal; *sq.p.*, downward process of squamosal tipped by quadrate; *t*, maxillary tooth; *tem.*, supratemporal vacuity. (After E. T. Newton.)

Sub-Order 3. *Dicynodontia.*

The most specialized group of Anomodonts exhibits either toothless jaws or the dentition reduced to a single pair of tusk-like teeth in the maxillæ growing from persistent pulps. They are named DICYNODONTIA in allusion to the latter feature (fig. 99). The external bones are never sculptured. There is a large supratemporal vacuity (*tem.*), and the squamosal bone (*sq.*) is enormously developed, not only forming the greater part of the single broad temporal arcade but also produced into a deep stout pedicle (*sq. p.*) over the comparatively small quadrate (*qu.*), which is exposed only quite at the end for the articulation of the mandible. The basioccipital (fig. 100, *b. occ.*) enters the occipital condyle and imparts to it the trefoil aspect well-known in Chelonia. The occiput (fig. 100) is an upright flattened plate, usually with only one pair of small vacuities (? auditory openings, *au.*) at the outer margin of the exoccipitals (*exocc.*); the antorbital region is shortened and more or less bent downwards; the premaxillæ (fig. 99, *pmx.*) are fused together. The

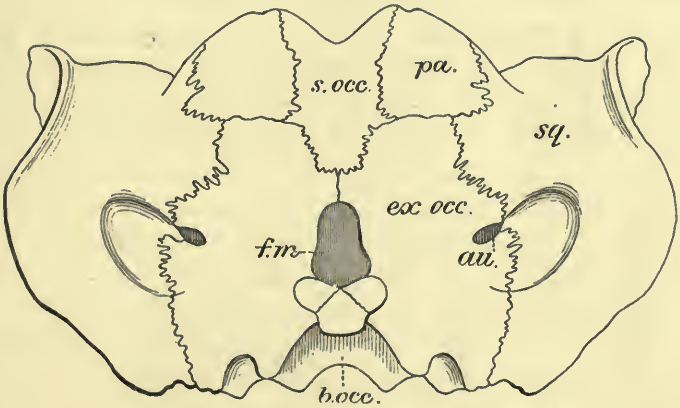

FIG. 100.

Ptychognathus declivis; **occipital view of skull, nearly half nat. size.—Karoo Formation (Permian or Triassic); Cape Colony. *au.*, supposed auditory opening; *b.occ.*, basioccipital; *exocc.*, exoccipital; *f.m.*, foramen magnum; *pa.*, parietal; *s.occ.*, supraoccipital; *sq.*, squamosal. (Restored from specimen in British Museum, no. 36221.)**

posterior nares (*pt. na.*) are scarcely if at all covered by the secondary development of palatine plates, and the very large pterygoids (*pt.*) meet in the middle line in advance of the basisphenoid, though leaving a small median vacuity (*pt.fo.*). The mandible exhibits no coronoid process, but is pierced by a large lateral vacuity. As to other features in the cranial osteology there is still difference of opinion, owing to the difficulty of distinguishing sutures and cracks. The accompanying diagrams, however, give one plausible interpretation of the arrangement of the bones in *Gordonia* (fig. 99). No complete skeleton of a Dicynodont has hitherto been discovered, but many portions of the trunk have been placed here with much probability of correctness, and they agree closely with the corresponding bones of the Theriodonts. Characteristic pectoral and pelvic arches are shown in figs. 101 A, B.

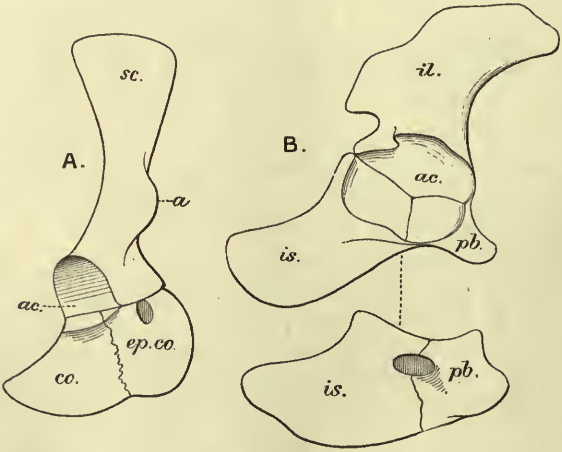

FIG. 101.

Right Pectoral Arch, outer aspect (A), and right Pelvic Arch, outer and inferior aspects (B), of a Dicynodont Reptile, much reduced.—Karoo Formation (Permian or Triassic); Cape Colony. *a.*, acromial process; *ac.*, glenoid cavity for humerus, and acetabulum for femur; *co.*, coracoid; *ep.co.*, epicoracoid; *il.*, ilium; *is.*, ischium; *pb.*, pubis; *sc.*, scapula. (Restored from specimens in British Museum.)

The skull of the typical *Dicynodon*, from the Karoo Formation of Cape Colony, sometimes attains a length of 0·5 m. (*D.*

tigriceps). *Ptychognathus* (*Lystrosaurus*), from the same formation, and also from corresponding deposits in India, is smaller. Toothless forms of skull from the Karoo Formation are named *Oudenodon*, but may possibly be referable to the females of *Dicynodon*. Closely related genera are represented by small species in the supposed Trias of Elgin, Scotland, one of these (*Gordonia*, fig. 99) much resembling *Dicynodon* in the form of the skull, the other (*Geikia*) similarly suggestive of *Ptychognathus*, but the first with only diminutive tusks, the second absolutely toothless.

ORDER 2. SAUROPTERYGIA.

Another primitive group of reptiles in which the investing bones of the temporal region of the skull contract into a single broad zygomatic arch, is represented by small amphibious animals in the Trias and by larger truly aquatic animals throughout the remainder of the Mesozoic period. Notwithstanding their ultimate complete adaptation to life in the open sea, these reptiles always retain their two pairs of limbs and their lizard-like form; they are thus named SAUROPTERYGIA in contradistinction to the Ichthyopterygia, which have an extremely shortened neck and are quite fish-like in shape.

The skull in the Sauropterygia exhibits a pair of large supratemporal vacuities and also a pineal foramen. The conical teeth, forming a single series on the margin of the jaws, are placed in distinct sockets; and there are no teeth on the palate, except rarely in some of the Triassic genera. The posterior nares always occupy their primitive position on either side of the vomers, and are never covered by secondarily-developed palatine plates; the relatively large pterygoids meet in the middle line, leaving no interpterygoid vacuity in the earliest genera, and only a small vacuity in the later genera. No sclerotic plates have been observed. The number of cervical vertebræ is always considerable, but is largest in certain genera from the Upper Jurassic and Cretaceous; while the tail in the typically marine forms is invariably short. The ribs in the cervical region are remarkable as articulating only with the vertebral centrum, never even in part with its arch; although nearly all these are distinctly double-headed in the earliest

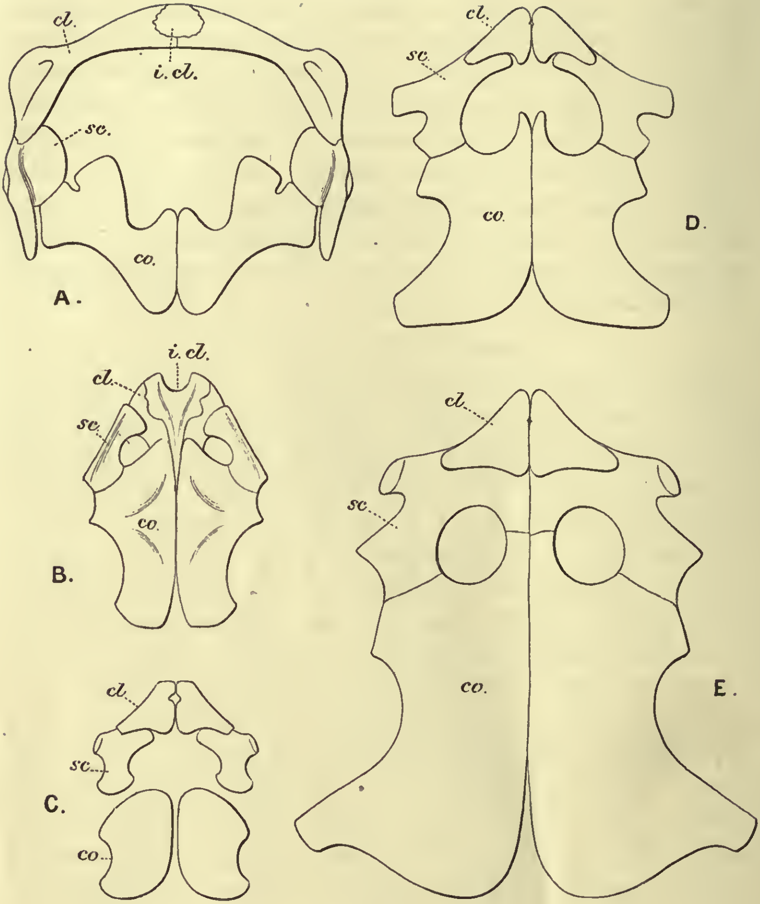

Fig. 102.

Diagram of Pectoral Arch of Sauropterygia, showing gradual atrophy of Clavicular Elements.

A. *Nothosaurus mirabilis;* dorsal aspect, about one-seventh nat. size.—M. Triassic (Muschelkalk); Würtemberg. (After H. von Meyer.)

B. *Plesiosaurus;* ventral aspect (the dorsal aspect not yet seen), about one-tenth nat. size.—L. Jurassic (L. Lias); Lyme Regis. (British Museum, no. R. 1315.)

C, D, E. *Cryptoclidus oxoniensis;* dorsal aspect of three successive stages of growth, about one-eleventh nat. size.—U. Jurassic (Oxford Clay); Peterborough. (Leeds Collection, after C. W. Andrews.)

cl., clavicle; *co.*, coracoid; *i.cl.*, interclavicle; *sc.*, scapula.

genera, only single-headed in the majority of the later forms. About two vertebræ form a passage to the trunk-region, where all the ribs are single-headed and articulate with the transverse processes of the neural arch. The feeble sacrum, apparently without fusion of centra, comprises from two to four vertebræ. The caudal vertebræ exhibit both single-headed ribs articulated with the centra, and also small chevron bones. The limb-girdles become more robust and the limbs themselves more paddle-like as the various successive genera are evolved. At first (fig. 102 A) the median symphysis of the coracoids is not much extended, and the scapulæ are normal, well-separated by a clavicular arch. In later forms (figs. 102 B—E) the scapulæ tend to meet in the middle line in front, while the clavicular arch degenerates; and the latter eventually becomes a mere vestige, as the scapulæ not only fuse together by a ventral extension but also meet the much-lengthened coracoids again in a median bar (fig. 102 E). An obturator foramen always persists in the pelvis, but the ilium becomes displaced backwards, articulating only with the ischium (fig. 106 G). The limbs are elongated and comparatively slender in the Triassic genera, with five digits, the normal number of phalanges, and often modified ungual phalanges; there is also an entepicondylar foramen in the humerus. In later genera they are true paddles, with shortened radius and ulna, tibia and fibula, and still only five digits, but the latter elongated by the addition of supernumerary phalanges and destitute of modified claws. The humerus and femur are noteworthy as exhibiting large conical epiphyses (fig. 106 J), much like those of frogs and certain Chelonia. Between the pectoral and pelvic arches the abdominal wall is strengthened by a system of ventral ribs, especially well-developed in the post-Triassic genera. The skin appears to have been destitute of armour, and one Liassic fossil suggests that there was a small, vertically extended caudal fin.

One small nodule is known from the Upper Lias of Whitby, having the outward appearance of a group of embryonic Plesiosaurs. It thus seems likely that some of these aquatic reptiles will prove to have been viviparous; although no conclusive evidence on the subject has yet been obtained.

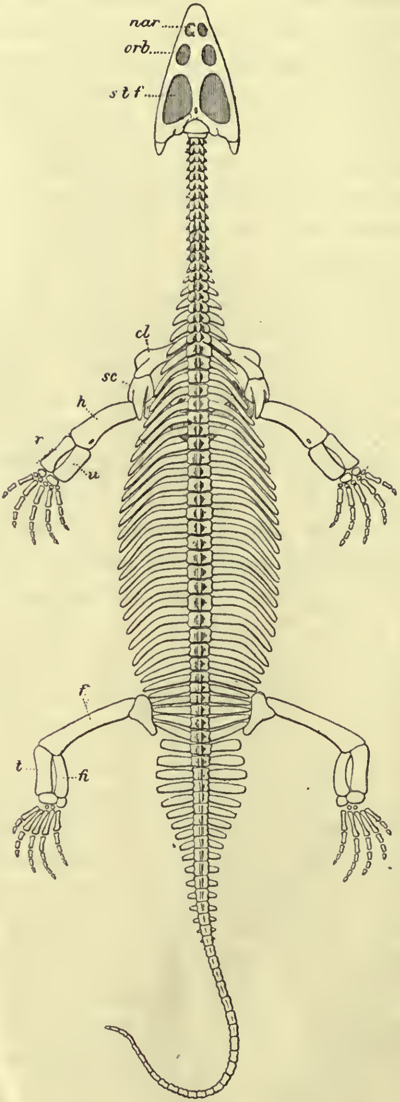

FIG. 103.

Lariosaurus balsami; dorsal aspect of skeleton, restored, about one-eighth nat. size.—M. Triassic (Muschelkalk); Lombardy. *cl.*, clavicle; *f*, femur; *fi.*, fibula; *h*, humerus; *nar.*, external nares; *orb.*, orbit; *r*, radius; *s.t.f.*, supratemporal vacuity; *sc.*, scapula; *t*, tibia; *u*, ulna.

Lariosaurus (figs. 103, 104). This genus comprises small animals rarely attaining a metre in length, all of Triassic age and much more lizard-like in shape than those of the genera of Liassic and later date. The head is of moderate size, with numerous prehensile teeth and very large supratemporal vacuities. One small specimen shows the posterior or internal nares exposed on the palate (fig. 104) in their primitive position on either side of the vomers, bounded behind by the palatines; there are also suborbital and infratemporal vacuities in the palate; and the pterygoids seem to meet throughout their length in the median line, reaching the vomers in front, and each bearing a longitudinal series of small teeth at the margin bounding the infratemporal vacuity. There are

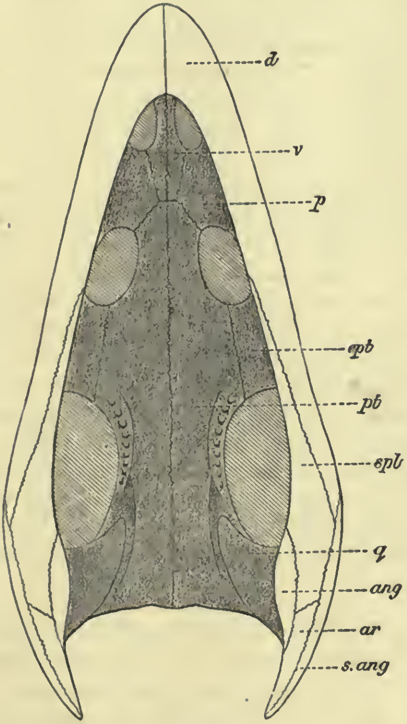

Fig. 104.

Lariosaurus balsami; restoration of palate, with outline of mandible, about nat. size.—M. Triassic (Muschelkalk); Lombardy. *ang.*, angular; *ar.*, articular; *d*, dentary; *ept.*, ectopterygoid; *p*, palatine; *pt.*, pterygoid; *q*, quadrate; *s.ang.*, surangular; *spl.*, splenial; *v*, vomer. The three pairs of vacuities are respectively the posterior nares, the suborbital vacuities, and the infratemporal vacuities. (After Boulenger.)

about 20 cervical vertebræ, slightly more in the trunk region, perhaps four in the sacrum, and not less than 40 in the tail. All the centra are biconcave. The cervical ribs are small and distinctly double-headed, while those of the trunk are extremely robust and borne directly by the neural arches, which are almost or completely destitute of transverse processes. About ten anterior caudal vertebræ also bear relatively large straight ribs. In the pectoral arch the symphysis of the coracoids is short and the scapulæ are widely separated, the interval between the latter being bridged over by a pair of slender clavicles with a minute triangular interclavicle at their point of meeting. The humerus is a little arched and expanded distally, with an entepicondylar foramen, while the radius and ulna are comparatively elongated slender bones. There are only two elements, of unequal size, in the proximal row of the carpus, while five small bones form the distal row, one supporting each digit. The digits increase in length to the third, which equals the fourth, while the fifth is intermediate in length between the first and second. The phalangeal formula is 2, 3, 4, 4, 3; and none of the phalanges exhibit condyles, although the distal one is modified by flattening. The pelvis is imperfectly known. The hind limb is larger and stouter than the fore limb, but otherwise very similar; the digits increase gradually in length from the first to the fourth, while the fifth is shorter again, and the phalangeal formula is 2, 3, 4, 5, 4. Abdominal ribs seem to occupy the whole of the ventral wall of the body between the pectoral and pelvic arches, there being one median longitudinal series sharply bent in the middle line, and at least two paired lateral series. The typical species, *Lariosaurus balsami*, is known by nearly complete skeletons from the black Triassic shales of Perledo, on the shore of the Lake of Como.

Other genera allied to *Lariosaurus* are known from the German Muschelkalk, while *Mesosaurus*, from the Karoo Formation of South Africa, and *Stereosternum*, probably from an equivalent horizon in Brazil, seem to represent an allied group. In the two last-mentioned genera the scapula and coracoid are described as fused together, while the pubis is pierced by a foramen. The vertebræ and ribs are remarkably thickened by hyperostosis.

Nothosaurus (figs. 102 A, 105). Larger Triassic Sauropterygians known only by fragmentary specimens, apparently distinguished from the foregoing by the closure of the suborbital vacuity in the palate (fig. 105) and by the presence of short, stout transverse processes on the arches of the dorsal vertebræ. In the pectoral arch (fig. 102 A) the coracoid exhibits a notched and incomplete antero-internal margin, which was evidently completed in an undetermined manner by cartilage. The typical species, *Nothosaurus mirabilis*, occurs in the Muschelkalk of Bavaria, and has a skull attaining a length of 0·35 m. Nearly all known remains of the genus were obtained from the Muschelkalk-series of Germany and France.

Plesiosaurus (figs. 102 B, 106 A—D, F, H, I). Known by several nearly complete skeletons from the Lower and Upper Lias of Europe. The head is small, the neck very long, the tail also of moderate length. The symphysis of the mandible is short and the anterior teeth are somewhat enlarged. The interpterygoid and suborbital vacuities are small but distinct on the palate. There is a "columella" (epipterygoid) rising to the prefrontal. The number of cervical vertebræ varies between 30 and 40, and the neck is stiffened by the overlapping of the hatchet-shaped cervical ribs, which are all double-headed. The trunk in front of the sacrum comprises about 20 vertebræ, and the sacrals seem to be two in number; these all bear single-headed ribs. The number of caudal vertebræ is uncertain, but there must sometimes have been not less than 40; most of them bear short caudal ribs and chevron bones of which the right and left halves are not fused together below in the median line. In the pectoral arch the coracoids are antero-posteriorly elongated, with the long symphysis produced a little forwards in front of the glenoid cavity for the humerus; and the scapulæ do not meet in the middle line below, but are distinctly extended ventrally beneath the outer borders of the large bilaterally-symmetrical triangular plate which represents the clavicular arch (fig. 102 B). The humerus is much expanded distally, but without trace of an epicondylar foramen or groove; the radius and ulna are both a little longer than broad. There are four elements in the proximal, and three in the distal row of the carpus, while the fifth metacarpal is in direct contact with one of the former. The phalangeal formula is variable, but seems to be 4, 6, 9, 8, 7,

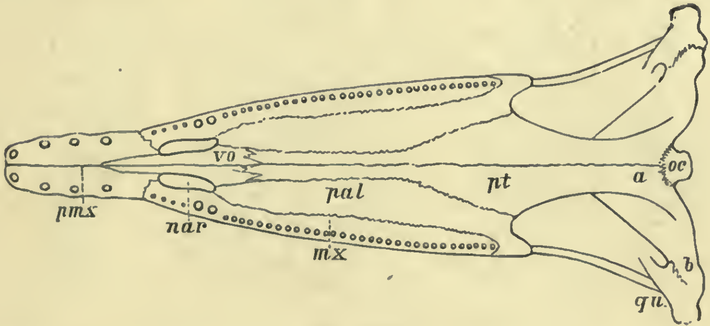

FIG. 105.

Nothosaurus mirabilis; restoration of palatine aspect of skull, one-quarter nat. size.—M. Triassic (Muschelkalk); Bavaria. *a*, hinder extension of pterygoid; *b*, suture of same with quadrate; *mx.*, maxilla; *nar.*, posterior nares; *oc.*, occipital condyle; *pal.*, palatine (possibly with ectopterygoid at hinder end); *pmx.*, premaxilla; *pt.*, pterygoid; *qu.*, quadrate; *vo.*, vomer. (After Lydekker.)

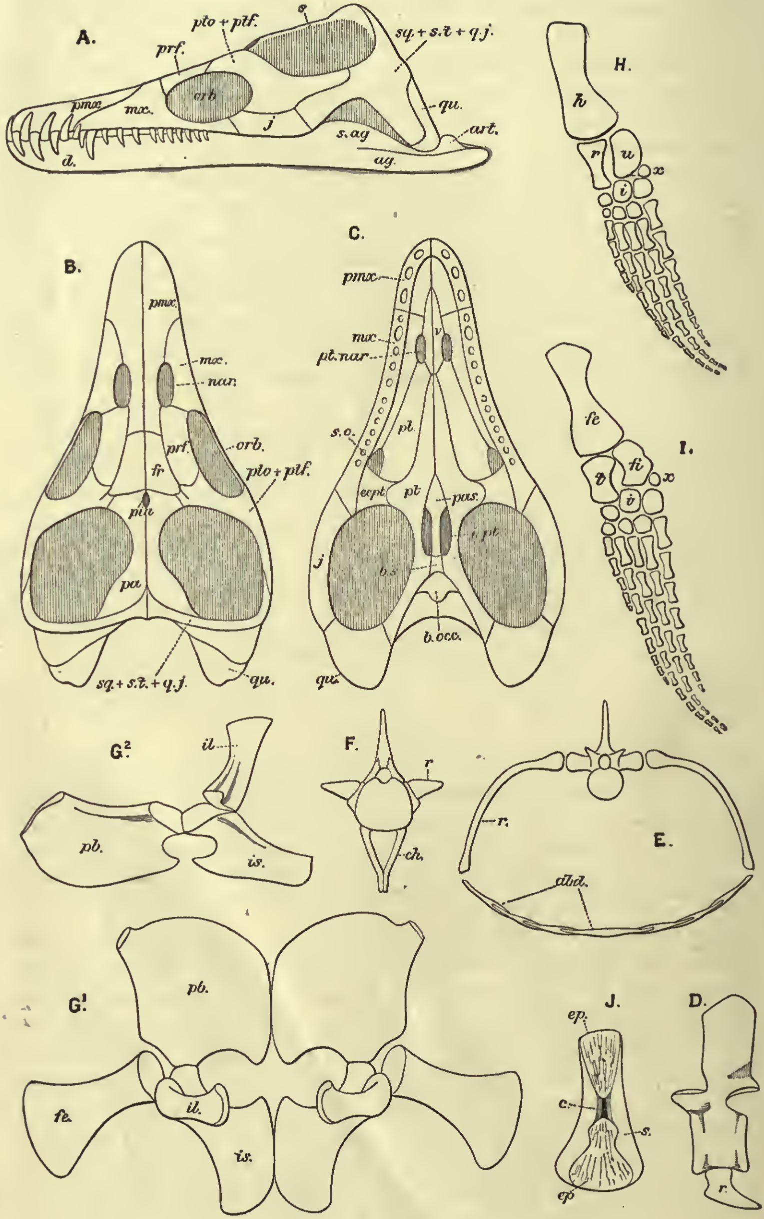
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Fig. 106.

FIG. 106.

DIAGRAM ILLUSTRATING THE PRINCIPAL CHARACTERS OF THE PLESIOSAURIAN REPTILES.

A, B, C. *Plesiosaurus macrocephalus;* skull from the lateral, superior, and palatal aspects, one-sixth nat. size.—L. Jurassic (L. Lias); Lyme Regis, Dorsetshire. *ag.*, angular; *art.*, articular; *b.occ.*, basioccipital; *b.s.*, basisphenoid; *d*, dentary; *ecpt.*, ectopterygoid; *fr.*, frontal; *i.pt.*, 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; *pt.nar.*, posterior nares; *ptf.*, postfrontal; *pto.*, postorbital; *q.j.*, quadrato-jugal; *qu.*, quadrate; *s*, supratemporal vacuity; *s.ag.*, surangular; *s.o.*, suborbital vacuity; *s.t.*, supratemporal (prosquamosal); *sq.*, squamosal; *v*, vomer. (Slightly modified after C. W. Andrews.)

D. *Plesiosaurus dolichodirus;* cervical vertebra, left lateral aspect, one-quarter nat. size.—L. Lias; Lyme Regis. *r*, rib.

E. *Cryptoclidus oxoniensis;* transverse section of abdominal region, about one-tenth nat. size.—U. Jurassic (Oxford Clay); Peterborough. *abd.*, abdominal ribs; *r*, rib. (From immature specimen shown in the photograph, fig. 107.)

F. *Plesiosaurus dolichodirus;* caudal vertebra, anterior end-view, one-quarter nat. size.—L. Lias; Lyme Regis. *ch.*, chevron bone; *r*, rib.

G[1], G[2]. *Muræenosaurus leedsi;* pelvis from the superior and left lateral aspects, one-fourteenth nat. size.—Oxford Clay; Peterborough. *fe.*, femur; *il.*, ilium; *is.*, ischium; *pb.*, pubis. (After C. W. Andrews.)

H, I. *Plesiosaurus dolichodirus;* pectoral (H) and pelvic (I) paddles of same individual, one-twelfth nat. size.—L. Lias; Lyme Regis. *fe.*, femur; *fi.*, fibula; *h*, humerus; *i*, intermedium; *r*, radius; *t*, tibia; *u*, ulna; *x*, pisiform bone. (British Museum, no. R. 1756.)

J. Plesiosaurian propodial bone (humerus or femur), in median longitudinal section, one-fourteenth nat. size.—U. Jurassic (Kimmeridge Clay); Ely. *c*, central cavity; *ep.*, epiphyses; *s*, shaft. (British Museum, no. R. 1381.)

ORDER 2. SAUROPTERYGIA.

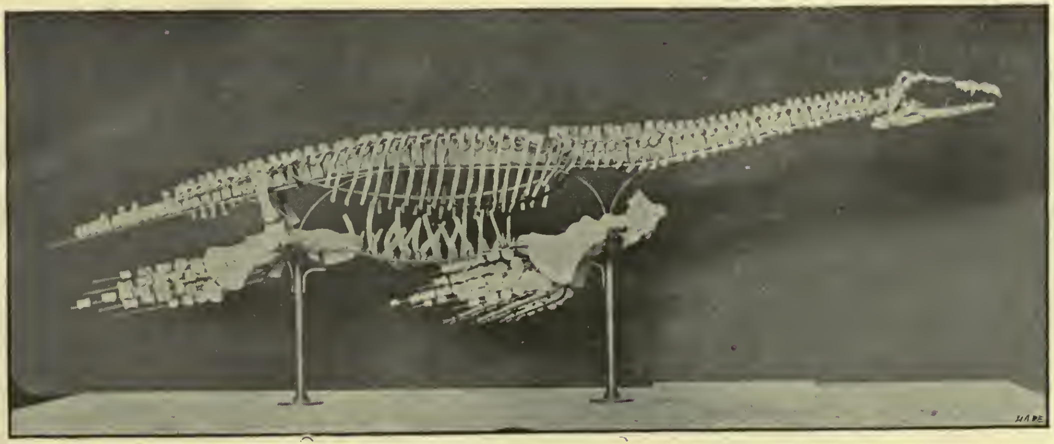

FIG. 107.

Cryptoclidus oxoniensis; photograph of immature skeleton in the Leeds Collection, British Museum, one-sixteenth nat. size.—U. Jurassic (Oxford Clay); Peterborough. (After C. W. Andrews.)

in the type-species, *P. dolichodirus;* all the phalanges are elongated, and the third and fourth are the longest digits. In the pelvic girdle the pubes are relatively large, not pierced by any foramen; the slender ilium seems to articulate only with the ischium. The pelvic is almost identical with the pectoral limb, though its phalangeal formula in *P. dolichodirus* is apparently increased to 4, 7, 10, 9, 7. The abdominal ribs between the pectoral and pelvic arches are especially robust, in three paired and one median series, those of the latter not angularly bent or keeled. The typical species is *Plesiosaurus dolichodirus*, attaining a length of about three metres, from the Lower Lias of Lyme Regis; *P. macrocephalus* and *P. conybeari* are larger species, known by tolerably complete skeletons from the same locality, the latter sometimes more than five metres in length. A fine large skeleton from the Upper Lias of Würtemberg, now in the Berlin Museum, is named *P. guilelmi imperatoris.*

Cryptoclidus (figs. 102 C—E, 106 E, 107). A genus much resembling *Plesiosaurus* in the general proportions of the animal, but differing in having all the ribs single-headed, and in the reduction of the clavicular arch concomitantly with the downward and inward extension of the scapulæ which meet in the middle line. The head is small and the mandibular symphysis short. In the typical species about 32 cervical vertebræ can be counted, and the cervical ribs are scarcely expanded distally. The trunk comprises nearly 30 vertebræ, of which three or four may be regarded as sacral. The clavicular arch (figs. 102 C—E, *cl.*) is reduced to a pair of triangular clavicles which meet in the middle line; and in the adult the scapulæ grow together below in the median line, where they also become fused with the forward process of the coracoids (fig. 102 E). The vestigial clavicles in the adult are thus entirely on the visceral aspect of the inferior processes of the scapulæ; immature specimens are known, on the other hand, in which (fig. 102 C, fig. 107) the clavicular arch occupies its more normal position as in *Plesiosaurus* (fig. 102 B). The pubis is relatively large, not pierced by a foramen; the slender ilium articulates only with the ischium. Both humerus and femur are much expanded distally, each articulating with three bones, which seem to be radius, ulna (tibia, fibula) and an ulnar (fibular) sesamoid. The abdominal ribs are proved to occur in three paired and one median series. Fine skeletons, in all stages of growth, have been obtained from the Oxford Clay of Peterborough.

Pliosaurus. Imperfectly-known gigantic Plesiosaurs of Upper Jurassic age, with relatively large head and short neck. The symphysis of the mandible is considerably elongated. The cervical vertebræ are very short, the cervical ribs double-headed, and all the vertebral arches loosely articulated with the centra. *Pliosaurus grandis* occurs in the Kimmeridge Clay, and *P. ferox* in the Oxford Clay.

Cimoliosaurus and other genera represent *Cryptoclidus* in the Cretaceous of Europe, N. and S. America, and New

Zealand. *Polyptychodon* is a European Cretaceous representative of *Pliosaurus* known only by teeth and fragments.

ORDER 3. CHELONIA.

Palæontology as yet affords no information concerning the origin of the tortoises, turtles, and their allies, and very little as to the evolution of the order they represent. The skull in the Triassic Dicynodonts, as already remarked, is curiously Chelonian in aspect. The armoured Permian Pariasaurian, *Otocœlus* (p. 149) is also suggestive of a possible ancestral Chelonian type. The scapula in Plesiosaurians exhibits a great ventral production much resembling the same feature in Chelonians; and it is conceivable that the very highly developed system of abdominal ribs in the order just mentioned might admit of modification into a Chelonian plastron. Other characters, such as the conical epiphyses of certain limb-bones, also seem to imply community of origin of the Chelonia with the Sauropterygia and Batrachia. The earliest known remains of a Chelonian shell, however, from the Upper Trias of Germany, are as typical of the order as the corresponding parts of a modern tortoise. It is only to be regretted that no satisfactory evidence of the head, neck, and limbs has hitherto been discovered below the Upper Jurassic.

The earliest known Chelonian remains, from the Upper Keuper of Würtemberg, comprise a natural sandstone mould of the interior of a shell (*Proganochelys quenstedti* or *Psammochelys keuperina*) in the Tübingen Museum, and various fragments of a carapace (*Chelytherium obscurum*) in the British Museum. The first shows that the costal plates are present to the normal Chelonian number of eight pairs, while the only vacuities in the shell are a series of small openings along the junction between the carapace and plastron on each side. The remains of *Chelytherium* indicate that each dorsal rib was single-headed, articulating at the line of contact between two vertebral centra in the ordinary manner; and deep sulci on the outer aspect of the bones of the carapace evidently denote the boundaries of epidermal shields present during the life of the animal.

In Lower Jurassic rocks no Chelonian remains are known, except possibly some epidermal shields from the Stonesfield Slate in the neighbourhood of Oxford. In the Upper Jurassic all the genera hitherto discovered are so closely similar to those now existing, that as yet they scarcely unite the three sub-orders which are completely differentiated in the modern fauna. The only known skulls are entirely toothless and nearly all exhibit a roof over the temporal muscles like that of the existing *Chelone.* The digits comprise the small number of phalanges so generally characteristic of the Chelonian order. The carapace and plastron are fully formed, and always bear marks of the presence of epidermal shields. In fact, so far as present evidence permits of judgment, it seems that since early Cretaceous times, degeneration of the carapace and plastron in certain types and elongation of the phalanges in the truly marine forms, are the only conspicuous marks of evolution in the order. The enlargement of the vacuities in turtles like *Chelone,* and the degeneration of the entire armour of the leathery turtles (*Sphargis* and its allies) have happened in the interval. The sub-order of Trionychia, destitute of epidermal shields, seems also to have arisen. The development of the neural bones has become more irregular in some groups, and the occurrence of mesoplastral elements seems to be now less common than it was in Mesozoic times.

It will suffice to enumerate the characters of three of the best-known Jurassic genera, the first two perhaps Cryptodiran, while the third may be a primitive Pleurodiran.

Eurysternum. A genus known by individuals in many stages of growth from the Lithographic Stone (Upper Jurassic) of Bavaria and France. The temporal fossæ in the skull are extensively roofed. Large vacuities persist throughout life in the plastron and between the extremities of the costal bones. There are distinct marks of epidermal shields both on the carapace and plastron. The tail is short. The limbs are completely known and distinctly those of a land-animal, the digits five in number on each foot, with short phalanges and terminal claws. The pelvis is not fused either with the carapace or with the plastron. The typical species is *E. wagleri*, of quite small size.

Chitracephalus. A genus known only by one nearly complete skeleton (*C. dumoni*) from the Wealden of Bernissart, Belgium. The cranium is much elongated and depressed, with an extremely short facial region, and the temporal fossæ not roofed. The cervical vertebræ do not exhibit transverse processes. There are marks of epidermal shields both on the carapace and plastron. The costal bones are narrowed at the outer end, so that there is a series of vacuities within the well-developed border of marginal bones. The elements of the plastron also resemble those of the modern *Chelone.* The digits bear large claws and are not much elongated; the phalangeal formula of the manus is proved to be 2, 3, 3, 3, 3.

Pleurosternum (figs. 108, 109). This genus is known chiefly by the shell, of which many fine examples have been found in the Purbeck Beds of Swanage, Dorsetshire. Parts of the pectoral and pelvic arches are the only other parts identified with certainty. The surface of the shell is very finely pitted and deeply impressed with the suture-lines of the epidermal shields. The carapace is much depressed, without vacuities, and firmly united by a long bridge on each side with the plastron (fig. 108), which is also continuous. There is a well-developed pair of mesoplastral bones meeting in the middle line. A median intergular epidermal shield is distinctly indicated. The pectoral arch closely resembles that of the existing Pleurodiran *Chelys*, and the coracoid is much expanded distally. The pubis articulates, without sutural union, with the plastron (fig. 109). The

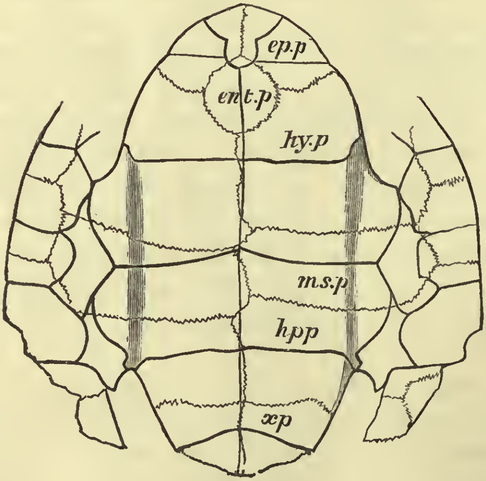

Fig. 108.

Pleurosternum portlandicum; imperfect plastron, inferior aspect, showing the sutures (delicate wavy lines) and impressions of the borders of the epidermal scutes or shields (bold dark lines), about one-quarter nat. size.—U. Jurassic (Portland Beds); Dorsetshire. *ep.p.*, epiplastron; *ent.p.*, entoplastron; *hp.p.*, hypoplastron; *hy.p.*, hyoplastron; *ms.p.*, mesoplastron; *xp.*, xiphiplastron. (After Lydekker.)

typical species is *P. bullocki*, having a shell sometimes about 0·5 m. in length. *P. portlandicum*, from the Portland Beds of the Isle of Portland (fig. 108), is smaller.

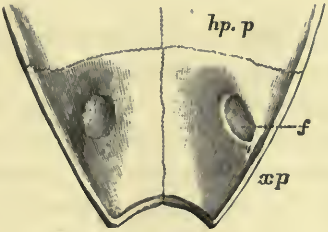

FIG. 109.

Pleurosternum bullocki; visceral aspect of posterior end of plastron, about one-quarter nat. size.—U. Jurassic (Purbeck Beds); Dorsetshire. *f*, facette for pubis; *hp.p.*, hypoplastron; *xp.*, xiphiplastron. (After Lydekker.)

Sub-Order 1. *Cryptodira.*

The majority of existing Chelonia belong to that section in which the head is retracted by curvature of the neck in a vertical plane, while the pelvis is unconnected with the plastron. Most known extinct types may also be placed in the same group.

Typical marine turtles first occur in the Upper Cretaceous of western Europe, one large form (*Chelone hofmanni*) being met with in the yellow chalk of Maastricht, Holland, other fragments and a diminutive shell (*Chelone benstedi*) being known also from the English Chalk. The first evidence of turtles with an extremely degenerate shell has also been discovered in the Upper Cretaceous of Italy, and of Kansas and Dakota, U.S.A. The Italian fossil, *Protosphargis veronensis*, is a shell measuring nearly three metres in length. Its costal bones are slightly more developed than in the surviving "leathery turtle" (*Sphargis* or *Dermochelys*), but nothing is known of any outer dermal armour. Its marginal bones are very slender. The plastron lacks the entoplastron (interclavicle). The best-preserved American fossil, *Protostega gigas*, comprises part of the skull, some crushed vertebræ, and fragmentary remains both of the shell and pectoral limbs. It is as large as *Protosphargis* and very similar in all respects, but with the plastron a little more developed. A fine carapace, with some associated limb-bones, from South Dakota, is named *Archelon ischyros.*

Gigantic marine turtles with extremely degenerate shell are still better known from the Eocene of western Europe. They agree with the modern "leathery turtle" in exhibiting a dermal bony shield external to the ordinary carapace; but the two best known forms seem to have a relatively larger head. *Eosphargis gigas*, from the Lower Eocene (London Clay) of the Isle of Sheppey, possesses a median dorsal row of large keeled plates broader than long, and apparently a series of large marginals. *Psephophorus*, of which the most satisfactory specimens hitherto obtained are from the Upper Eocene (Oligocene) of Belgium, must have been covered both dorsally and ventrally with a continuous mosaic of small polygonal bony plates. The same genus seems to be represented by fragments of armour in the Middle Eocene of the Hampshire Basin, the Upper Eocene of Alabama, U.S.A., the Miocene of France and the Vienna Basin, perhaps also by a humerus in the Pliocene of Antwerp.

Several extinct genera (e.g., *Lytoloma*, *Argillochelys*, etc.) of marine or estuarine turtles, comprising chiefly small species, occur in the Eocene both of Europe and America. The mandibular symphysis is remarkably long, and the vacuities in the shell are comparatively small.

True marsh- and land-tortoises also date from the Eocene, the shells of typical Emydians occurring in the London Clay of Sheppey, and in the Upper Eocene of the Hampshire Basin, while an apparently true *Testudo* is met with in corresponding strata in Wyoming and New Mexico, U.S.A.

The freshwater *Chelydra*, confined in the existing fauna to parts of North and South America, is represented by a characteristic species in the Upper Miocene of Oeningen, Switzerland, and by another in the Lower Miocene lignite of Rott, near Bonn, Germany. This is a case of distribution parallel with that of the ganoid fishes *Lepidosteus* and *Amia* already mentioned.

Sub-Order 2. *Pleurodira.*

Although the living Chelonians of the sub-order Pleurodira are almost exclusively confined to the southern hemisphere, there is no doubt that many fragmentary fossils discovered in the Upper Mesozoic and Lower Tertiary strata, both of Europe and North America represent either typical members or ancestral forms of this group. The cervical vertebræ always exhibit transverse processes, and the only means of retraction of the head is by bending the neck on one side to rest within the margin of the shell. The pelvis is articulated or firmly anchylosed both with the carapace and plastron. The extinct European and American genera, however, add nothing of importance to our knowledge of the morphology of these Chelonians, and are of little phylogenetic interest. The remarkable genus *Miolania* from Pleistocene deposits in Queensland, and from Lord Howe's Island (nearly 400 miles distant from the Australian coast), need alone be mentioned. The typical species, *M. oweni*, from Queensland, must have attained a very large size, the head measuring 0·58 m. in width to the tip of the "horns." Both the head and tail (fig. 110) are armoured with large bony bosses symmetrically arranged, imparting to the skull a horned appearance, and causing the tail to be enveloped in a continuous bony sheath. Its carapace and plastron are almost unknown.

FIG. 110.

Miolania oweni; right lateral aspect of the extremity of the caudal sheath (A) and anterior aspect of the cranium (B), about one-tenth nat. size—Pleistocene; Queensland. (After Owen.)

Sub-Order 3. *Trionychia.*

The three-clawed mud-turtles appear suddenly with all their typical characters in the lowest Tertiary strata both of Europe and North America. Numerous fine specimens of *Trionyx* itself are known from the Upper Eocene of Hordwell, Hampshire, and the genus seems to have survived in Europe throughout the Miocene period.

ORDER 4. ICHTHYOPTERYGIA.

As already remarked (p. 142) there is still a fourth well-defined group of primitive reptiles, in which the investing bones of the temporal region of the skull contract into a single broad arcade. These are the Ichthyopterygia (fish-limbed reptiles), which range throughout the Mesozoic period with very little structural modification, and arise in the Trias as abruptly as they disappear in the Chalk. In outward form they must have closely resembled the Cetacean mammals of the present day, having a large head, long rostrum, and no real neck; but their hind limbs never disappeared (although these were sometimes extremely reduced), and the caudal fin was expanded in a vertical, not in a horizontal plane. Like the Cetaceans, moreover, there is some reason to believe that the Ichthyopterygia were originally derived from land-animals; for the radius and ulna in the known Triassic types are invariably more elongated and less pressed together than in the later forms, the limb being thus less completely paddle-shaped than in the latter. It is also interesting to note that in the jaws from the Trias the teeth are in a less uniform series than in those from the Jurassic and Cretaceous; while a few of the Upper Jurassic and Cretaceous forms are almost or completely toothless. Some of the later paddles, too, are broader and rendered more flexible than those of earlier date by the persistence of a considerable layer of cartilage round their carpals, tarsals, and phalanges.

What the land-dwelling ancestors of the Ichthyopterygia may have been, it is still impossible to determine. It is, however, worthy of remark that these reptiles exhibit a vertical folding of the walls of the conical teeth (fig. 111 F) paralleled only by that observed in many Labyrinthodonts; while their short, biconcave vertebral centra are best compared with those of such Labyrinthodonts as *Mastodonsaurus*.

The rostrum of the Ichthyopterygian skull (fig. 111 A—D) is formed by the enormously enlarged premaxillæ (*pmx.*) and the equally extensive mandibular symphysis. The external nares (*nar.*) thus remain close to the orbit, while the only noteworthy disproportion in the other cranial bones is observed in the diminishing frontals (*fr.*) and in the extending nasals (*na.*). There is a very large pineal foramen (*pin.*) at the junction of the parietals and frontals. The supratemporal vacuities are also large; and the sutures between all the component elements of the temporal arcade remain distinct. There is a conspicuous foramen between the quadrate (*qu.*) and the overlapping quadrato-jugal plate (*q.j.*). The otic bones are well-ossified, and the pro-ōtic and opisthotic (*op.o.*) remain separate. All the external bones are unornamented. The large eye is protected by a ring of well-developed sclerotic plates (*scl.*). The conical teeth forming a single series on the margin of the jaws are placed in a groove only exceptionally sub-divided into sockets; and there are no teeth on the palate. The posterior nares (*pt.nar.*) always occupy their primitive position on either side of the vomers (*v*), and are never covered by secondarily-developed palatine plates; the relatively large pterygoids (*pt.*) meet the vomers in front, abut against the quadrates (*qu.*) and the basipterygoid processes of the basisphenoid (*b.s.*) behind, and are separated for the greater part of their length by a large interpterygoid vacuity (*i.pt.*), along the middle of which the well-developed parasphenoid splint (*pas.*) is conspicuous. The transverse bone (ectopterygoid) has not been observed, though there are indications of its having been articulated with part of the hinder border of the maxilla (at *x*). There is a well-developed "columella" (epipterygoid) rising to the prefrontal. All the precaudal vertebræ (fig. 111 H) are essentially similar in character, each centrum bearing two pairs of tubercles for the support of the double-headed ribs. The atlas and axis are alone peculiar. They (fig. 111 G) are almost invariably fused together

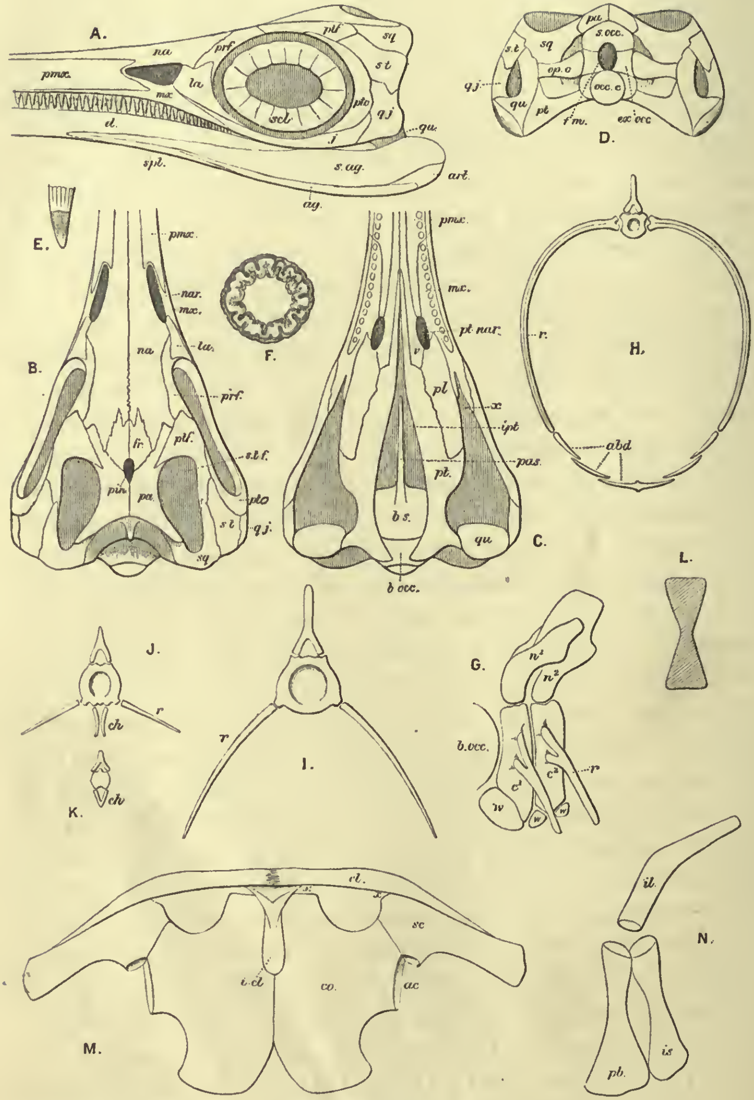
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FIG. 111.

Fig. 111.

Diagram illustrating the Principal Characters of *Ichthyosaurus.*

A, B, C, D. *Ichthyosaurus longifrons;* skull from the lateral, superior, palatal, and posterior aspects, wanting the anterior part of the rostrum, one-fifth nat. size.—L. Jurassic (U. Lias); Normandy. *ag.*, angular; *art.*, articular; *b.occ.*, basioccipital; *b.s.*, basisphenoid; *d*, dentary; *ex.occ.*, exoccipital; *f.m.*, foramen magnum; *fr.*, frontal; *i.pt.*, interpterygoid vacuity; *j*, jugal; *la.*, lachrymal; *mx.*, maxilla; *na.*, nasal; *nar.*, external narial opening; *occ.c.*, occipital condyle; *op.o.*, opisthotic; *pa.*, parietal; *pas.*, parasphenoid; *pin.*, pineal foramen; *pl.*, palatine; *pmx.*, premaxilla; *prf.*, prefrontal; *pt.*, pterygoid; *pt.nar.*, posterior nares; *ptf.*, postfrontal; *pto.*, postorbital; *q.j.*, quadrato-jugal; *qu.*, quadrate; *s.ag.*, surangular; *s.occ.*, supraoccipital; *s.t.*, supratemporal (prosquamosal); *s.t.f.*, supratemporal vacuity; *scl.*, sclerotic plates; *spl.*, splenial; *sq.*, squamosal; *x*, space for ectopterygoid (?); *v*, vomer. (Restored from specimen in British Museum, no. 33157.)

E. *Ichthyosaurus communis*; upper tooth, showing extent of enamelled crown and fluted base, one-sixth nat. size.—L. Jurassic (L. Lias); Dorset.

F. Ditto; transverse section of base of tooth.—Ibid. (After Owen.)

G. *Ichthyosaurus longifrons;* atlas and axis, left lateral aspect, about one-third nat. size.—U. Lias; Normandy. *b.occ.*, basioccipital condyle of skull; c^1, centrum of atlas; c^2, centrum of axis; n^1, paired neural arch of atlas; n^2, single neural arch of axis; *r*, ribs; *w*, subvertebral wedge-bones (intercentra or hypocentra). (After Owen.)

H. Ichthyosaurian dorsal vertebra and ribs, anterior aspect, much reduced.—L. Lias; Dorset. *abd.*, abdominal ribs; *r*, rib. (After Owen.)

I, J, K. Ichthyosaurian vertebra from base of tail and two caudals, anterior aspect, much reduced.—Ibid. *ch.*, chevron bone; *r*, rib. (After Owen.)

L. Vertical transverse section of Ichthyosaurian caudal vertebra, much reduced.—Ibid.

M. *Ichthyosaurus communis;* pectoral arch, ventral aspect, much reduced.—Ibid. *ac.*, glenoid cavity for humerus; *cl.*, clavicle; *co.*, coracoid; *i.cl.*, interclavicle (anterior transversely-extended portion covered by the clavicles); *sc.*, scapula; *x*, edges originally bordered by cartilage. (Restored from specimens in British Museum.)

N. *Ichthyosaurus communis;* left pelvic arch, outer aspect, one-third nat. size. —Ibid. *il.*, ilium; *is.*, ischium; *pb.*, pubis. (From specimen in British Museum, no. 41849.)

in the adult, and they bear three subvertebral wedge-bones (hypocentra or intercentra, *w*), the largest between the occipital condyle (*b.occ.*) and the atlas (c^1), the next between the atlas and axis (c^2), the smallest between this and the third centrum. The two halves of the neural arch of the atlas (n^1) are separate; each of the other neural arches of the vertebral column is in a single piece, articulating with its neighbours by feeble zygapophyses, and never fused with the centrum. There is no sacrum, and the pelvic arch (fig. 111 N) is freely suspended in the abdominal muscles. The anterior caudal vertebral centra (fig. 111 J) bear a single pair of tubercles for the support of single-headed ribs (*r*), which gradually disappear behind when the vertebræ enter the caudal fin. The two halves of the chevron bones (*ch.*) remain separate. The pectoral arch (fig. 111 M) comprises a pair of robust coracoids (*co.*) meeting in a long median symphysis, a pair of scapulæ (*sc.*) without any marked prescapular process, also slender clavicles (*cl.*) and a T-shaped interclavicle (*i.cl.*). The humerus, radius, and ulna in the typical genera are short and stout, and insignificant in size compared with the remainder of the paddle, which comprises a variable number of irregular digits, each with very numerous phalanges usually pressed together into an almost inflexible mosaic. Each half of the freely suspended pelvis consists of the usual three elements, which are all long and slender and apparently meet in the acetabulum. The hind limb is of the same character as the fore limb. Abdominal ribs (fig. 111 H; *abd.*) are well-developed throughout the ventral body-wall between the pectoral and pelvic arches; but there is no dermal armour. A median dorsal and a triangular caudal fin are known to occur in one species of *Ichthyosaurus* as mentioned below.

Some of the Ichthyopterygia at least must have been viviparous, examples of *Ichthyosaurus* from the Upper Lias of Würtemberg occasionally exhibiting as many as seven embryonic skeletons within the abdominal region.

Mixosaurus. To this genus are referred most of the known fragmentary remains of Ichthyopterygia from the Triassic formations, and nearly all of these are comparatively small. The teeth are fewer than in *Ichthyosaurus*, more variable in size and in the degree of folding of their wall, and are sometimes enclosed in completed sockets. The vertebral centra resemble those of *Ichthyosaurus*, but their neural arches are relatively stouter and articulated to each other by distinctly paired zygapophysial facettes. The anterior paddle is known to be typically Ichthyopterygian in most respects, but the radius and ulna are longer than broad, not closely apposed but separated by a vacuity throughout their length. The typical species is *Mixosaurus cornalianus*, known by imperfect skeletons varying from half a metre to a metre in length, from the Trias of Besano, Lombardy. Detached vertebral centra and neural arches, fragments of jaws, and a humerus from the Muschelkalk of Würtemberg are ascribed to *M. atavus*. Vertebræ, ribs, and portions of jaws of *M. nordenskjöldi* have been obtained from the Trias of Spitzbergen. The so-called *Shastasaurus pacificus*, founded on vertebræ and a coracoid from the Upper Trias of Shasta County, California, may also belong to the same genus.

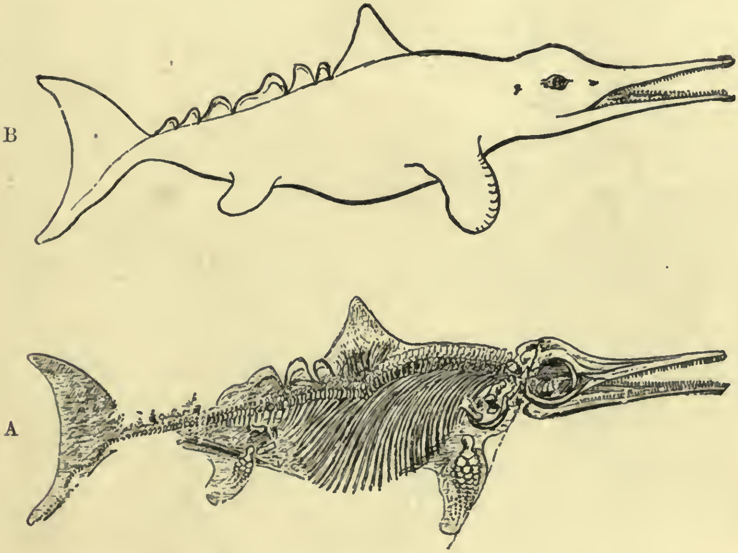

Fig. 112.

Ichthyosaurus quadriscissus; fossilized skeleton (A) and outline restoration (B), showing outline of integument with dorsal and caudal fins, one-tenth nat. size.—L. Jurassic (U. Lias); Würtemberg. (After E. Fraas.)

Ichthyosaurus (figs. 111, 112, 113 A). In the jaws of *Ichthyosaurus* the teeth are conical and uniform in character, with a very large implanted base, which in some species is much thickened by an enveloping layer of cement. The neural arches of the vertebræ are much laterally compressed, and there is usually only one median zygapophysial facette. The humerus and femur exhibit only two distal facettes, in the first case for radius and ulna, in the second for tibia and fibula. The carpal, tarsal, metacarpal, and metatarsal bones are for the most part completely ossified in the adult and closely pressed together like an irregular mosaic. The radiale (tibiale), intermedium, and ulnare (fibulare) are always recognizable, but it seems impossible to determine the precise homologies of any of the more distal components of the limb, or to decide upon the primitive number of digits. The best-preserved skeletons hitherto discovered are from the European Lias, and they sometimes display traces of the unarmoured integument. One example of *I. quadriscissus* from the Upper Lias of Würtemberg (fig. 112) exhibits remains of a triangular dorsal fin and also a large, vertically extended caudal fin,

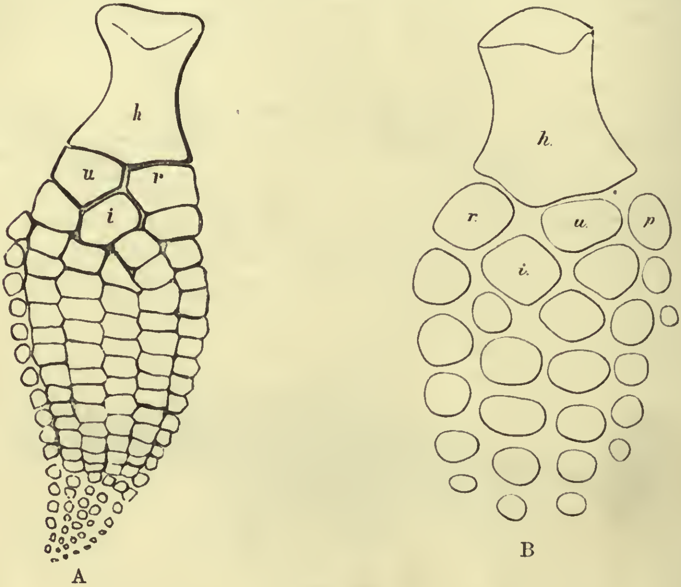

Fig. 113.

Pectoral paddles of Ichthyopterygia.

A. *Ichthyosaurus conybeari;* ventral aspect of left pectoral limb, about one-half nat. size.—L. Jurassic (L. Lias); Lyme Regis. (After Lydekker.)

B. *Ophthalmosaurus icenicus;* ventral aspect of right pectoral limb, about one-seventh nat. size.—U. Jurassic (Oxford Clay); Peterborough. (From specimen in Leeds collection, British Museum, no. 85.)

h, humerus; *i*, intermedium; *p*, pisiform; *r*, radius; *u*, ulna.

into the lower lobe of which the hindermost caudal vertebræ extend. A similar caudal fin has been found in the Lithographic Stone (U. Jurassic) of Bavaria. It is also noteworthy that the hinder end of the vertebral column is sharply bent downwards in several skeletons from the English Lias. The largest known species occur in the Lias, the skull of *I. trigonodon*, from the Upper Lias of Banz, Bavaria, attaining a length of about two metres, while the total length of this animal cannot have been less than ten metres. *I. platyodon*, from the Lower Lias of Lyme Regis, Dorsetshire, must have been nearly as large. *I. intermedius* and *I. communis*, of moderate size, are the commonest species in the English Lower Lias. Various fragments, more or less unsatisfactory, seem to indicate that *Ichthyosaurus* ranges from the Rhætic to the Lower Chalk inclusive; while those of Cretaceous age occur not only in Europe but also in the East Indies, Australia, New Zealand, and South America. Two vertebral centra are also recorded from the neighbourhood of Mombasa, East Africa.

Ophthalmosaurus (fig. 113 B). This is an Upper Jurassic and Lower Cretaceous genus in which the teeth are either absent in the adult or are minute and confined to the front of the jaw. The pubis and ischium are fused together, leaving a small obturator foramen. The humerus and femur exhibit three distal facettes for the bones of the second segment of the limb, these being apparently the ordinary two elements with the addition of a sesamoid bone on the ulnar (fibular) side (fig. 113). All the elements of the carpus, tarsus, metacarpus, metatarsus, and phalanges are more or less rounded or oval in shape, the ossifications not fitting together, but having been originally surrounded each by a layer of persistent cartilage. The typical species is *O. icenicus* from the Oxford Clay of Peterborough, and there is doubtful evidence of the genus on so high an horizon as the English Upper Greensand. *Baptanodon*, from the Jurassic of Wyoming, U. S. A., is remarkably similar to the European fossil, and perhaps generically identical.

ORDER 5. RHYNCHOCEPHALIA.

The small lizard-like *Sphenodon* or *Hatteria* now existing in certain islands off New Zealand, is the sole survivor of an order which is already clearly recognizable in the Permian, and seems to have attained its maximum specialization so long ago as the Triassic period. The order is named RHYNCHOCEPHALIA in allusion to the beak-shaped rostrum of several of the typical genera. So far as can be determined, its earliest members, like the latest, are characterized (i.) by a well-defined upper and lower temporal arcade, (ii.) by a large fixed quadrate buttressed by the pterygoids which extend forwards to the vomers, and (iii.) by teeth fused with the supporting bone. The ribs are single-headed, except sometimes in the cervical region, and the phalangeal formula of the digits usually resembles that of the lizards, namely 2, 3, 4, 5, 3 [4]. The only definite evidences of evolution consist (i.) in the reduction of the numerous small abdominal ribs to three comparatively large longitudinal series, (ii.) in the superior ossification of the pubis and ischium, and (iii.) in the modification of the fifth metatarsal bone. It is noteworthy that this evolution happened before the period of the Upper Trias.

Sub-Order 1. *Proterosauria.*

The Permian Rhynchocephalia seem to connect the later and more typical members of the order with the Microsaurian Stegocephalia (p. 130) in several respects. The Lower Permian *Palæohatteria,* for example, has the pectoral and pelvic arches strikingly similar to those of the Microsauria, while its abdominal ribs are merely the ventral armour of the latter slightly modified. Its skull, however, is typically Rhynchocephalian, and the genus must doubtless be placed with the somewhat later Permian reptile, *Proterosaurus,* in the primitive sub-order, PROTEROSAURIA. As already indicated, this is characterized by the numerous longitudinal series of abdominal ribs, the imperfectly-ossified aspect of the pubis and ischium, and the non-modified character of the fifth metatarsal bone.

Palæohatteria (fig. 114). A long-tailed, lizard-like reptile, of small size. The skull exhibits a very short rostral region, enormous orbits, narrow frontals, and slender temporal arcades. There is a pineal foramen, and the external nares form a pair of small openings at the end of the snout. All the external bones are smooth, and there is a ring of sclerotic plates surrounding the eye. The premaxillæ are very small, the maxillæ large; and large conical teeth in a single series are fused with the margin of the jaw. Smaller teeth occur on the vomers and palatines. The vertebral centra are delicate constricted cylinders, and small wedge-shaped intercentra (hypocentra) occur between all those in advance of about the sixth caudal. The neural arches are united with the centra only by suture; zygapophyses are conspicuous, but there are no transverse processes. Ribs with an expanded articular end are borne by all the vertebræ as far as the seventh caudal. The approximate number of

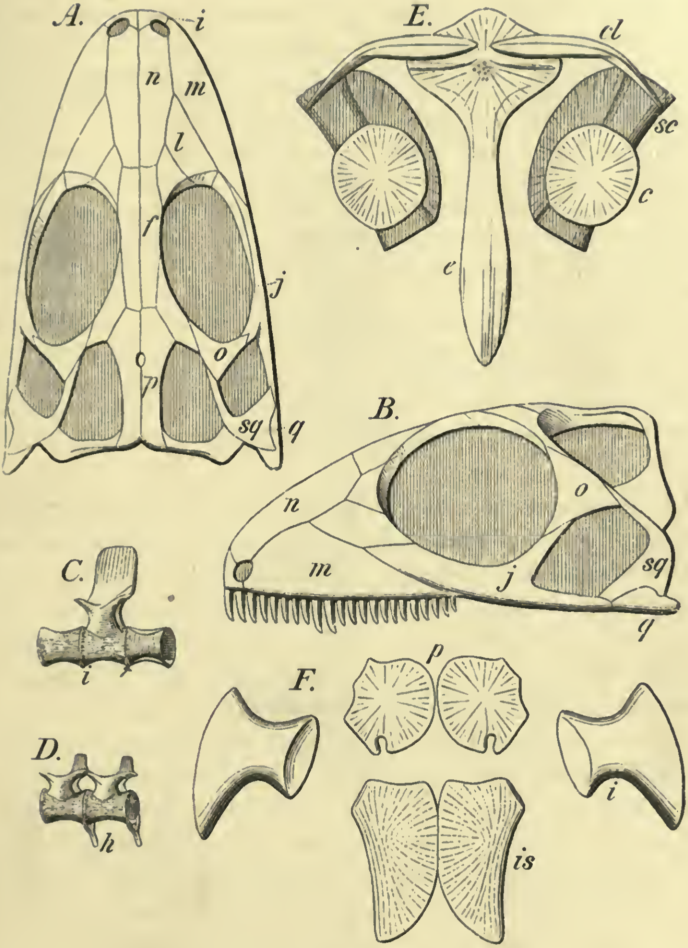

Fig. 114.

Palæohatteria longicaudata; diagram illustrating the principal characters of the skeleton, about nat. size.—L. Permian; Saxony. (After Credner.)

A, B. Skull from the superior and lateral aspects. *f*, frontal; *i*, premaxilla; *j*, jugal; *l*, lachrymal; *m*, maxilla; *n*, nasal; *o*, postorbital; *p*, parietal; *q*, quadrate; *sq.*, squamosal.

C. Three dorsal vertebræ, lateral aspect, the middle one bearing the neural arch. *i*, rudimentary intercentrum (hypocentrum).

D. Two caudal vertebræ. *h*, chevron bone.

E. Pectoral arch, ventral aspect. *c*, coracoid; *cl.*, clavicle; *e*, interclavicle; *sc.*, scapula.

F. Pelvic arch. *i*, ilium; *is.*, ischium; *p*, pubis.

vertebræ is 6 in the neck, 20 in the trunk, 3 or 4 in the sacrum (not fused together), and 50 in the tail. The largest element in the pectoral arch is the interclavicle, which exhibits a rhombic expansion at its anterior end; the clavicles are small and bent; the coracoids, without foramen, have an imperfectly ossified aspect. There is an entepicondylar foramen at the expanded distal end of the humerus. In the pelvic arch, the pubis and ischium are thin and laminar, the former with an obturator notch; the ilium is more robust and considerably expanded at its upper end. A calcaneum (fibulare), an astragalus (tibiale), and five separate distal elements are observed in the tarsus. All the digits, both of the fore and hind feet, must have borne a claw. The hinder is a little longer than the fore limb. The representatives of the abdominal ribs are small and relatively numerous oat-shaped scutes, apparently without any keeled or sharply bent median element. The typical and only known species, *Palæohatteria longicaudata*, occurs in the Lower Permian (Middle Rothliegendes) near Dresden, and attains a length of about 0·45 m.

Proterosaurus is a larger reptile from the Upper Permian (Kupferschiefer) of Thuringia, with completely ossified vertebral centra and with limb-bones comparatively well-ossified at the extremities. Wedge-shaped intercentra (hypocentra) occur only between the vertebræ of the neck. The skull and limb-girdles are too imperfectly known for description. The bones in the distal row of the tarsus appear to be less than five in number.

The so-called PELYCOSAURIA, as yet only known by fragmentary specimens, seem to be early Rhynchocephalians allied to the genera just mentioned. They are known chiefly from the Permian of Texas, U.S.A., but have also been found in the Lower Permian of Bohemia and perhaps of France. They are described under the generic names of *Clepsydrops*, *Dimetrodon*, *Naosaurus*, etc., and are remarkable for the enormous development of the neural spines of the dorsal vertebræ, which sometimes bear branches (fig. 115). The quadrate bone, so far as known, is rather small and completely enclosed in the surrounding elements.

Sub-Order 2. *Rhynchocephalia Vera.*

The typical Rhynchocephalia seem to have attained their maximum specialization and widest geographical distribution in the latter part of the Triassic period. Some European Jurassic genera differ very little from the existing *Sphenodon* of New Zealand. One genus (*Champsosaurus*) comprising comparatively large animals from the uppermost Cretaceous of North America, and the lowest Eocene both of North America and western Europe, was adapted to an aquatic existence and had a crocodile-like snout. Unlike *Sphenodon,* none of these extinct forms have a humerus exhibiting both entepicondylar and ectepicondylar foramina or grooves.

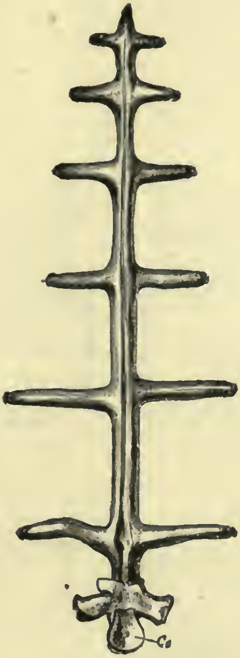

Fig. 115.

Naosaurus claviger; restoration of dorsal vertebra, anterior aspect, one-sixth nat. size.—Permian; Texas. *ce.*, centrum. (After Lydekker.)

Hyperodapedon (fig. 116). A very stout reptile of large size. The massive skull is short and broad, and triangular in form, with a very short rostrum formed by the downwardly-curved, slender toothless premaxillæ. The sutures between the various bones have not yet been determined, but those indicated in the accompanying fig. 116 seem to be distinguishable. No pineal foramen can be observed in the only known specimen, and there is no bony bar or septum between the external nares.

The orbits are large, and the temporal arcades remarkably stout. The mandibular rami are apparently fused in the long symphysis, which is slightly forked at its toothless anterior end. The teeth are depressed cones, apparently in single series in the mandible, but in several longitudinal series on the maxilla and palatine. The vertebral centra are well-ossified, and there are about 24 in front of the sacrum, which comprises two vertebræ; those of the cervical region seem to be opisthocœlous, and no intercentra (hypocentra) have been observed. The anterior cervical ribs are longer and stouter than those of *Sphenodon*, those beyond much resemble the ribs of the existing genus; it is uncertain, however, whether there were uncinate processes. The limbs are very imperfectly known, but the fore foot is proved to have been remarkably short and

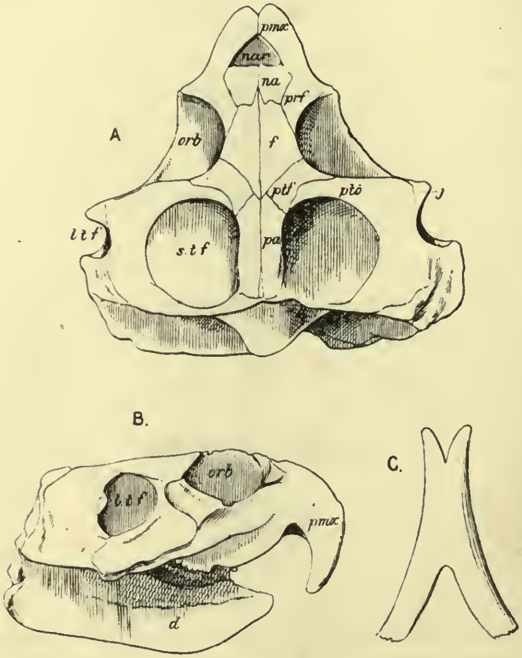

Fig. 116.

Hyperodapedon gordoni; skull from the superior aspect (A), right lateral aspect (B), and inferior aspect of mandibular symphysis (C), one-quarter nat. size.—Triassic (?); Elgin. *d*, dentary; *f*, frontal; *j*, jugal; *l.t.f.*, lateral temporal vacuity; *na.*, nasal; *nar.*, external narial opening; *orb.*, orbit; *pa.*, parietal; *pmx.*, premaxilla; *prf.*, prefrontal; *ptf.*, postfrontal; *pto.*, postorbital; *s.t.f.*, superior temporal vacuity. (British Museum, no. R. 699.)

thick. The typical species is *Hyperodapedon gordoni*, perhaps about two metres in length, known best by an imperfect skeleton from the supposed Trias of Elgin. A larger species, *H. huxleyi*, is represented by fragments in the Maleri Beds (supposed Trias) of Central India.

Rhynchosaurus much resembles *Hyperodapedon*, but is comparatively small, with fewer teeth, distinctly amphicœlous vertebræ, and a longer manus. Beautiful skeletons are found in the Upper Trias of Grinsill, Shropshire.

Homœosaurus is the Jurassic representative of *Sphenodon*, from which it differs essentially, (i.) in lacking intercentra or wedge-bones between the vertebral centra of the dorsal region, (ii.) in the absence of uncinate processes to the ribs, and (iii.) in the humerus lacking its entepicondylar foramen. Like the surviving genus, it has separated external nares, toothed premaxillæ, the vertebral centra deeply biconcave, and the rami of the mandible united at the symphysis only by ligament. The typical species is *H. maximiliani*, known by nearly complete skeletons about 0·2 m. in length, from the Lithographic Stone (Lower Kimmeridgian) of Bavaria.

Champsosaurus. A large animal, representing a family of aquatic Rhynchocephalia without dermal armour. The premaxillæ are much elongated into a gavial-like rostrum, and each bears a single series of large conical teeth. The external nares are terminal and apparently undivided. The hinder region of the skull, though imperfectly known, is proved to have been Rhynchocephalian in plan, and the palate exhibits the usual arrangement of its elements. The maxillæ bear a single series of large teeth; the vomers, palatines, and pterygoids exhibit irregular longitudinal series of comparatively small teeth. In the mandible, the splenials enter the long symphysis, and there is no coronoid elevation. The vertebral centra are slightly biconcave or have flat ends, and two form the sacrum; only two intercentra (hypocentra) or wedge-bones are observed at the anterior end of the neck. The short cervical ribs are double-headed. In the pectoral arch the interclavicle and clavicles are conspicuous; in the pelvic arch all three elements are considerably expanded and enter the acetabulum. The humerus exhibits an ectepicondylar groove at its distal end, but no foramen. The hind limb is a little longer than the fore limb, and the digits in both must have been free or only connected by a web. No angularly-bent median element has hitherto been observed among the remains of abdominal ribs. *Champsosaurus* is known not only by fragments from the Upper Cretaceous of the United States, but by more nearly complete skeletons from the Lower Eocene of Reims, France, and Erquelinnes, Belgium. + Alberta

ORDER 6. SQUAMATA.

The lizards and snakes are of comparatively recent origin, none being known with certainty to date back beyond the Cretaceous period. The hinder region of the skull is degenerate, the lower temporal arcade always, and the upper temporal arcade frequently wanting, so that the quadrate is loosely fixed to the cranium; the palate also, though primitive in the arrangement of the internal nares, exhibits remarkably large vacuities, and the palatines exclude the pterygoids from articulation with the vomers. The vertebral centra are well-ossified, usually procœlous; and intercentra (hypocentra) or intervertebral wedge-bones are rarely observed.

The earliest known fossils commonly ascribed to the Squamata are fragmentary jaws and procœlous vertebræ from the English Purbeck Beds (*Macellodus brodiei*), which much resemble those of pleurodont lizards but are too imperfect for discussion. The first satisfactory skeletons, of Cretaceous age, are all referable to aquatic members of the order and seem to represent two extinct sub-orders.

Sub-Order 1. *Dolichosauria.*

One of the Cretaceous sub-orders comprises small aquatic animals remarkably snake-like in shape, but with the limbs and their supporting arches completely formed. In allusion to their elongate proportions they are termed DOLICHOSAURIA. The vertebræ are procœlous and resemble those of snakes in being articulated both by zygapophyses and by a zygosphene-zygantrum arrangement. The typical genus and species, *Dolichosaurus longicollis*, from the English Chalk, must have been an animal about 0·7 m. in length, but only one satisfactory specimen is known. Its head is relatively small and the dentition is pleurodont, the teeth being simple obtuse cones. It has about 60 presacral vertebræ, of which no less than 17 are in advance of the scapular arch and may thus be termed cervicals. The ribs are hollow. There are the usual two sacral vertebræ, but these are not anchylosed. The limbs are imperfectly known. The apparently allied genera *Pontosaurus* and *Aigialosaurus*, from the Upper Cretaceous of the Island of Lesina, Dalmatia, exhibit a comparatively short neck with from 7 to 9 cervical vertebræ; and one specimen of *Pontosaurus* shows the complete hind limb which is described as essentially Lacertilian, with the phalangeal formula 2, 3, 4, 5, 4. The largest of the Upper Cretaceous specimens from Istria and Dalmatia indicate species between two and three metres in length.

Sub-Order 2. *Pythonomorpha.*

The members of the second group of Cretaceous Squamata are still more completely adapted for an aquatic existence than the Dolichosauria. Most of them attain a large size, and they seem to have usurped the place in the economy of nature left by the declining orders of Sauropterygia and Ichthyopterygia in Cretaceous seas. They must have had a very wide distribution, remains being met with in Europe, North and South America, and New Zealand. Their precise systematic position is uncertain, but they seem to represent an early stage in the evolution of the Squamata before the modern Lacertilia and Ophidia had become differentiated.

The skull in these aquatic reptiles is remarkably similar in general aspect to that of certain lizards such as the Varanidæ, but the pterygoid bones bear teeth like those on the margin of the jaw. All the teeth are large and conical, fixed by tumid bases to the oral border of the supporting bone. The premaxillæ and nasals are fused together into a simple rostrum; the superior temporal arcade remains; and a pineal foramen is always present. The vertebral centra are all procœlous, and there is no sacrum; traces of a zygosphene-zygantrum articulation are observed in some genera. Each chevron bone in the tail articulates only with its own centrum. The pectoral arch seems to be nearly always destitute of clavicles, though rudiments may occur and an interclavicle has occasionally been detected; the sternum appears to have been rarely calcified and perhaps never truly ossified. Both pairs of limbs are present and modified into paddles, the digits being destitute of claws and slightly lengthened by an increase in the number of

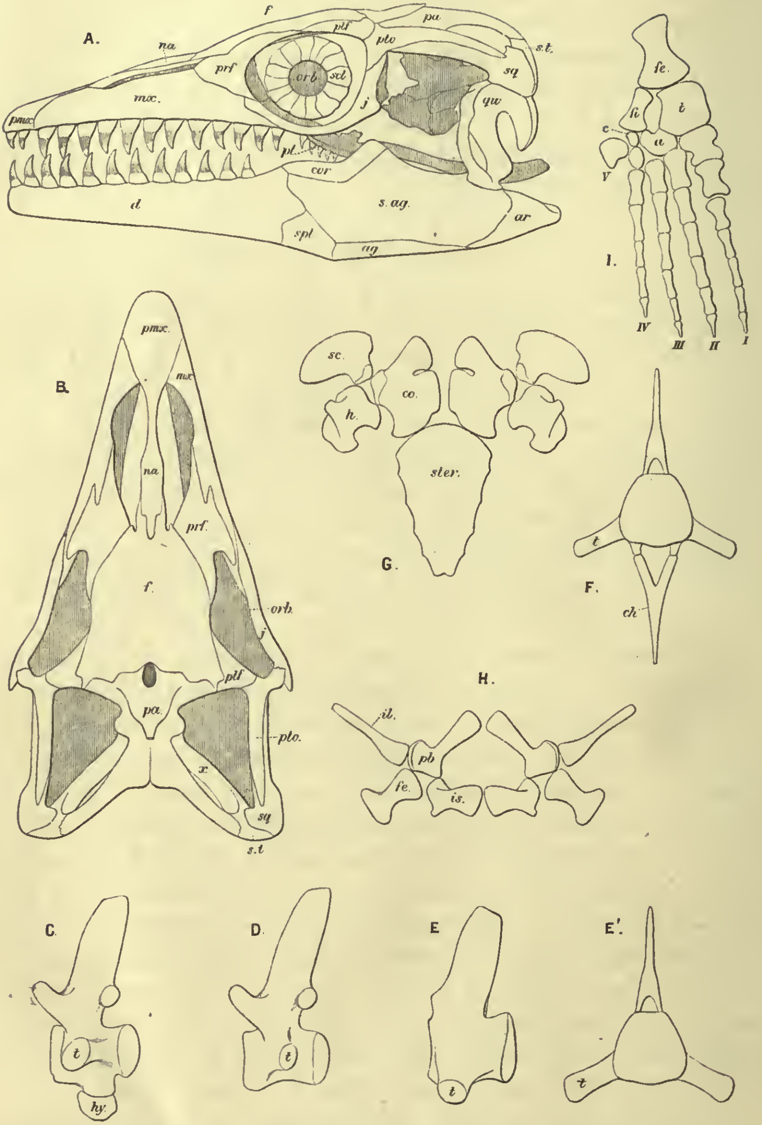
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FIG. 117.

Fig. 117.

Diagram illustrating the Principal Characters of the Pythonomorpha.

A, B. *Platecarpus coryphaeus;* skull from the lateral and superior aspects, about one-seventh nat. size.—U. Cretaceous; Kansas. *ag.*, angular; *ar.*, articular; *cor.*, coronoid; *d*, dentary; *f*, frontal; *j*, jugal; *mx.*, maxilla; *na.*, nasal; *orb.*, orbit; *pa.*, parietal; *pmx.*, premaxilla; *prf.*, prefrontal; *pt.*, pterygoid; *ptf.*, postfrontal; *pto.*, postorbital; *qu.*, quadrate; *s.ag.*, surangular; *s.t.*, supratemporal (prosquamosal); *scl.*, sclerotic; *spl.*, splenial; *sq.*, squamosal; *x*, exoccipital, etc. (Slightly restored after Merriam.)

C. *Mosasaurus camperi;* cervical vertebra, left lateral aspect, one-seventh nat. size.—U. Cretaceous; Maastricht, Holland. *hy.*, hypapophysis; *t*, transverse process.

D. Ditto; anterior dorsal vertebra, left lateral aspect, one-seventh nat. size.—Ibid. *t*, transverse process.

E, E′. Ditto; posterior dorsal vertebra, left lateral and hinder aspects, one-seventh nat. size.—Ibid. *t*, transverse process.

F. Ditto; anterior caudal vertebra, hinder aspect, one-seventh nat. size.—Ibid. *ch.*, chevron bone; *t*, transverse process.

G. *Edestosaurus dispar;* pectoral arch, ventral aspect, one-fifth nat. size.—U. Cretaceous; Kansas. *co.*, coracoid; *h*, humerus; *sc.*, scapula; *ster.*, calcified sternum. (After Marsh.)

H. *Lestosaurus simus;* pelvic arch, one-thirteenth nat. size.—U. Cretaceous; Kansas. *fe.*, femur; *il.*, ilium; *is.*, ischium; *pb.*, pubis. (After Marsh.)

I. *Mosasaurus lemonnieri;* pelvic limb, one-sixteenth nat. size.—U. Cretaceous; Belgium. *a*, astragalo-central; *c*, calcaneum; *fe.*, femur; *fi.*, fibula; *t*, tibia. I—V, the five digits, the fifth represented only by its metatarsal. (After Dollo.)

phalanges. There are sclerotic plates round the eye, but the dermal armour is apparently never more than a covering of small scaly granules.

Mosasaurus (fig. 117 c—f, i). The typical genus was first discovered in the Upper Cretaceous of Maastricht, in the valley of the Meuse, and hence named *Mosasaurus*. The massive jaws are provided with teeth as far as their anterior extremity, and sclerotic plates are present. The vertebræ are more than 130 in number, 7 being cervical, 39 dorsal, 12 lumbar, and the remainder caudal. The centrum of the atlas is fused with that of the axis to form its odontoid process, and both these vertebræ bear neural arches. The other vertebræ are all similar in type, the neural arch always fused with the centrum and bearing zygapophysial facettes but no zygosphene or zygantrum; the zygapophyses, however, are more or less rudimentary in the hinder dorsal and caudal regions. The axis, other cervical vertebræ, and the dorsal vertebræ bear ribs, which become longest on the 18th dorsal; the centra of the lumbars and caudals exhibit only transverse processes. Between the atlas and the basi-occipital there is a small proatlas in the form of a free hypapophysis; the atlas itself and also the other six cervicals have a separate hypapophysis. The chevron bones in the tail are fused with their respective centra, at least in its middle and hinder portions. The fore limbs have not been satisfactorily observed, but the hind limbs are known by specimens completely preserved in a hard matrix, and the arrangement of their bones is thus definitely ascertained (fig. 117 i). The femur is a little longer than the tibia, while the tarsus and foot are about four times as long as the latter; none of the bones exhibit condyles, but are merely apposed by flat articular facettes. The tarsus comprises only three bones, which are displaced towards the fibular side, so that the first metatarsal articulates directly with the tibia. Digits i—iv, are complete, and exhibit phalanges to the number of 6, 5, 5, 4; digit v is represented merely by its displaced and stunted metatarsal. The pelvic bones are comparatively small and slender, all meeting in the acetabulum, and the pubis is pierced by a small foramen. The typical species, *Mosasaurus camperi*, from the Upper Cretaceous (Danian) of Maastricht, probably sometimes attained a total length of 15 metres. *M. lemonnieri*, from the Upper Cretaceous (Upper Senonian) of Mons, Belgium, is known by more nearly complete skeletons only 5 metres in length.

Platecarpus (fig. 117 a, b) closely resembles *Mosasaurus*, and is represented by nearly complete skeletons from the Cretaceous of Kansas, U.S.A. The skull (figs. 117 a, b) is not much depressed, and teeth extend to the extremity of the jaws. There are 7 cervical vertebræ, 23 dorsals, and over 80 caudals; the zygapophyses are well-developed, but the zygosphene-zygantrum articulation is almost or completely wanting. The centrum of the atlas is fused with that of the axis to form its odontoid process; there are also a basal piece, a large hypapophysis, and two lateral pieces. The axis bears a high neural spine. The other cervicals bear separate hypapophyses. The chevron bones are loosely articulated with the caudal centra.

The genus *Edestosaurus* (*Clidastes*), typically represented in the Upper Cretaceous of North America, comprises excessively elongated animals, with vertebræ very commonly united by a zygosphene-zygantrum articulation. One skeleton ascribed to it exhibits much lengthened neural spines on some of the vertebræ in the hinder half of the tail, suggesting the original presence of a laterally compressed caudal fin.

Sub-Order 3. *Lacertilia.*

Palæontology as yet affords no information concerning the evolution even of the more specialized groups of lizards. All the known fossils are very fragmentary. It is interesting to note that during the early Tertiary period certain forms (e.g., *Iguana*) now confined to the New World, were represented in Europe—a distribution paralleled by that of the fishes, *Amia* and *Lepidosteus*, already mentioned (pp. 109, 113). It may be also added that the most gigantic lizard hitherto discovered, is an extinct Varanoid, *Megalania prisca*, known by numerous vertebræ and a fragment of skull from the Pleistocene river-deposits of Queensland. This is estimated to have been nearly ten metres in length.

Sub-Order 4. *Ophidia.*

Except one fine specimen from the supposed Cretaceous of Patagonia, the snakes are likewise known only by a few imperfect Tertiary fossils, which scarcely admit of satisfactory discussion. The detached vertebræ of Cretaceous age sometimes referred to this sub-order, are probably Dolichosaurian. Typically ophidian vertebræ from the Lower Eocene of Sheppey and the Middle Eocene of Bracklesham, are named *Palæophis* and ascribed to sea-snakes which may have attained a length of six metres.

ORDER 7. DINOSAURIA.

During the Triassic period a race of land-reptiles arose, at first so generalized that it is difficult to separate them from the Rhynchocephalia and Crocodilia, but afterwards constituting at least one distinct order. These are the so-called DINOSAURIA (also named PACHYPODA and ORNITHOSCELIDA), which became dominant during the Jurassic and Cretaceous periods, in the interval between the decline of the Anomodonts and the dominance of the Mammalia. Their remains have been discovered in Europe, Syria, India, South Africa, Madagascar, North Australia, South America, and North America.

All the Dinosaurs possess limbs adapted for habitual support of the body on land, and some exhibit hind quarters so disproportionately massive that there is not much doubt these walked ordinarily on their hind limbs. The form and great size of the tail, however, suggest that they were amphibious in habit, the caudal appendage being admirably adapted for swimming. Some are very massive, others with delicate and hollow bones; the teeth of some show that they were carnivorous, while those of others prove with equal certainty that they were herbivorous.

In the skull the investing bones of the temporal region contract into an upper and a lower temporal arcade, and the large quadrate is firmly fixed. A pineal foramen has not been clearly observed. There are no teeth on the palate. The cervical and thoracic ribs are distinctly double-headed, and the neural arches bearing the latter are much raised for the enlargement of the thoracic cavity. The sacral vertebræ, two or more in number, are fused together. The chevron bones of the tail are articulated intervertebrally. The pectoral arch is imperfectly known, but clavicles seem to be absent, while a pair of problematical ossifications sometimes found, appear to be referable to the sternum. All three elements of the pelvis enter the acetabulum, and the ilium is extended antero-posteriorly. The tibia exhibits a large cnemial crest, the fibula is complete, and the proximal tarsals are only two in number, an astragalus and a calcaneum. The astragalus sometimes bears an ascending process apposed to the anterior face of the lower end of the tibia, exactly as in young Ratite birds.

Sub-Order 1. *Theropoda.*

All the earliest known Dinosaurs, of Triassic age, are carnivorous, with cutting teeth implanted in distinct sockets. Their bones are of comparatively delicate construction, the vertebræ and limb-bones being hollow. The fore limbs are small, locomotion having doubtless been mainly bipedal, and the hind feet are digitigrade. The digits are provided with prehensile claws. The brain-case is incompletely ossified, and there is a large antorbital vacuity in the skull. There is no predentary bone. The sternum is unossified. The pelvic acetabulum is

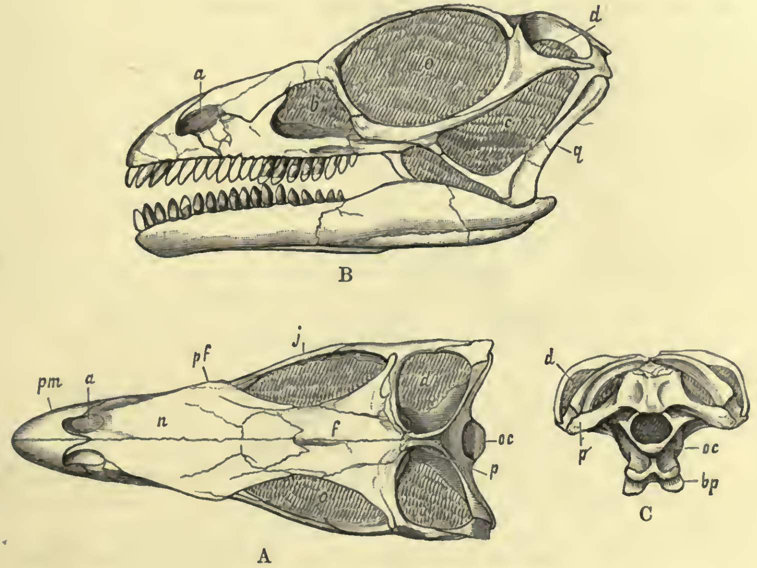

FIG. 118.

Anchisaurus colurus; skull from the superior (A), lateral (B), and occipital (C) aspects, one-half nat. size.—Triassic; Connecticut. *a*, external narial opening; *b*, antorbital vacuity; *bp.*, basipterygoid process of basisphenoid; *c*, lateral temporal vacuity; *d*, supratemporal vacuity; *f*, frontal; *j*, jugal; *n*, nasal; *o*, orbit; *oc.*, occipital condyle; *p*, parietal; *p′*, paroccipital process; *pf.*, prefrontal; *pm.*, premaxilla; *q*, quadrate. (After Marsh.)

perforate. The pubes project simply downwards and are united in a symphysis distally; the ischia similarly meet, and the symphysis in both cases is often much extended evidently to serve as a kind of "foot" when the animal rested on its hind quarters. Certain impressions among footprints in the Triassic sandstones of Connecticut suggest this idea.

Similar Dinosaurs range throughout the Mesozoic period both in Europe and North America, and they are provisionally grouped together under the name of THEROPODA.

FIG. 119.

Anchisaurus colurus; restoration of skeleton by O. C. Marsh, one-twenty-fourth nat. size.—Triassic; Connecticut.

Anchisaurus (figs. 118, 119). Small Triassic Dinosaurs known by nearly complete skeletons. The skull (fig. 118) is remarkably bird-like and the orbit is very large; the quadrate is much inclined forwards. The teeth are numerous, closely arranged, and nearly uniform. The cervical vertebræ are long and slender; the dorsals are also elongated but more robust; the sacrals seem to be three in number. The fore limb is approximately two-thirds as large as the hind limb. The coracoid is remarkably small, without perforation; and the elongated scapula is about as long as the humerus. The radius and ulna are nearly equal in size. There are five digits in the manus, but only the first three bear claws, the fourth and fifth being rudimentary. The ilium is small, with a slender forwardly-directed process; the ischium and pubis are long and slender, and the last-named bone is not perforated. The femur is much curved and longer than the tibia. The astragalus and calcaneum are small, neither with any process; and only two bones have been observed in the distal row of the tarsus. There are four functional digits in the hind foot, and the fifth is represented by its metatarsal. The phalangeal formula is 2, 3, 4, 5, 0. The first digit, however, is so much shorter than the second, third, and fourth, that this foot would probably make a three-toed track like the supposed bird-tracks of the Connecticut Triassic sandstone, in which the only known remains of *Anchisaurus* have been found.

Other Triassic Theropoda, known by more fragmentary specimens, are described under the names of *Zanclodon* or *Teratosaurus* (Würtemberg), *Dimodosaurus* (France), *Thecodontosaurus* (Bristol, England), *Ornithosuchus* (Elgin, Scotland), *Euskelesaurus* (South Africa), and *Massospondylus* (South Africa and India). Numerous fragments of later date, both Jurassic and Cretaceous, found in Europe, are named *Megalosaurus*. One nearly complete small skeleton from the Lithographic Stone (Lower Kimmeridgian) of Bavaria, known as *Compsognathus longipes*, seems to exhibit an embryo within the abdomen. The best known skeleton of a Jurassic genus is that of *Ceratosaurus* from North America.

Ceratosaurus (fig. 120). The skull in this genus is relatively large and very delicate in construction. The nasal bones are firmly fused together and support a large median horn-core; the premaxillaries are separate and toothed; the prefrontal bone partly overhangs the orbit on each side. The usual vacuity occurs in the hinder half of the mandible. All the cervical vertebræ, except the atlas, are strongly opisthocœlous, but always flattened, not ball-shaped, on the anterior face of the centrum. The other vertebral centra are slightly amphicœlous, and five are co-ossified in the sacrum. Each sacral rib is supported by two vertebræ. The tail is long, compressed and deepened in its anterior portion, as indicated by the considerable length of the chevron bones. The fore limbs are very small, and the humerus is short, with a strong radial crest. The carpal bones are only imperfectly ossified, and there are four digits (I to IV) in the manus, each bearing a claw; nos. II and III are much larger than nos. I and IV. The elements of the pelvis differ from those of all other known Dinosaurs, except the Cretaceous *Ornithomimus*, in being fused together. The symphysis both of the pubes and the comparatively slender ischia is much expanded, forming a kind of "foot." The femur is much curved and somewhat longer than the tibia; the astragalus is not fused with the latter, but exhibits a large ascending process. The hind foot comprises only three digits, probably II—IV., and the metatarsals are unique among Dinosaurs in being fused together and with the distal row of tarsals; possibly, however, this character, known only in one specimen, is pathological. The typical and only known species is *Ceratosaurus nasicornis* from the Upper Jurassic of Colorado.

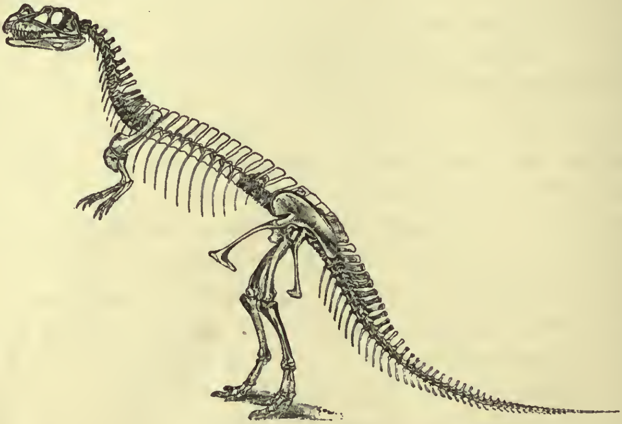

Fig. 120.

Ceratosaurus nasicornis; restoration of skeleton by O. C. Marsh, one-sixtieth nat. size.—Jurassic; Colorado.

It may be added that one imperfect small reptilian skeleton from the Jurassic of Colorado is believed to represent a Theropodous Dinosaur with the power of leaping. It is named *Hallopus victor.* The fore limb is relatively small with four digits. In the hind limb the femur is shorter than the tibia, and there are only three functional digits with much-elongated metatarsals. The astragalus is destitute of an ascending process, and the calcaneum is much produced into a "heel."

Sub-Order 2. *Sauropoda.*

These are more or less massive herbivorous Dinosaurs, with fore and hind limbs nearly equal in size and therefore presumably quadrupedal in gait. The feet are plantigrade, each with five hoofed digits, while the distal series of carpal and tarsal bones are apparently unossified. The brain-case is completely ossified, and there is a large antorbital vacuity in the skull. There is no predentary bone. The anterior vertebræ are opisthocœlous and much hollowed on each side, with very light neural arch; the cervical ribs, at least in part, are fused with their respective vertebræ. The neural canal is much expanded in the sacrum, and each sacral vertebra supports its own rib. The pubes project simply downwards and are united distally by cartilage. The limb-bones are solid.

Some of the Jurassic Sauropoda are the largest known land-animals, the femur of *Atlantosaurus immanis* from the Upper Jurassic of Colorado, measuring nearly two metres in length. *Cetiosaurus oxoniensis,* from the Lower Jurassic of England, is smaller. So also is *Ornithopsis hulkei* from the Wealden of the Isle of Wight. All these are known only by fragmentary remains, and very similar bones occur in the Jurassic and Cretaceous of Madagascar, of India, and in the supposed Cretaceous of the Territory of Neuquen, north of Patagonia. One of the best-preserved skeletons is that of

FIG. 121.

Brontosaurus excelsus; restoration of skeleton by O. C. Marsh, one-one-hundred-and-eightieth nat. size.—Jurassic; Wyoming.

Brontosaurus (figs. 121, 122). The head in this reptile is remarkably small, probably smaller in proportion to the body than in any other known reptile. The neck is long and flexible, the body short, the tail much elongated. There are about thirteen cervical vertebræ, with very small neural canal and no neural spines. The hatchet-shaped ribs are fused with the anterior cervicals, but free on those behind; all the centra exhibit a deep excavation of the sides. The centra of the dorsal vertebræ are short, and their lateral excavations are so deep that they are separated only by a thin median partition. They are opisthocœlous, but a few "lumbars" in advance of the sacrum have flat or slightly excavated ends. The latter vertebræ also bear free ribs of moderate size. The sacrum comprises five vertebræ, and the last "lumbar" is sometimes fused with it. The whole of the sacrum is hollow, the cavity in the fused centra being partially divided by a median longitudinal partition. The elevated neural spines of the sacral vertebræ are fused into a large vertical plate with thickened summit. The caudal vertebræ are solid, the three anterior caudals alone excavated at the side. The scapula (fig. 122, *s*) is expanded at its base, but slender distally; the coracoid (*c*) exhibits a small perforation. A single pair of smaller bones (*os.*) are interpreted as ossifications in the sternal cartilage. In the pelvic arch the pubis is more robust than

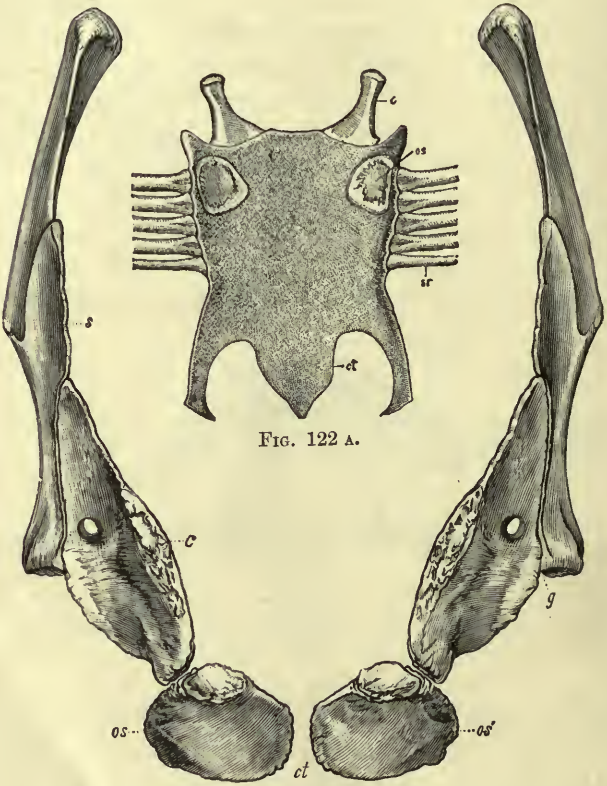

Fig. 122 a.

Fig. 122.

Brontosaurus excelsus; pectoral arch, anterior aspect, one-sixteenth nat. size, with sternum of young ostrich (*Struthio camelus*) for comparison (fig. 122 a). —Jurassic; Wyoming. *c*, coracoid; *ct.*, sternal cartilage; *g*, glenoid cavity for humerus; *os.*, sternal bone; *s*, scapula; *sr.*, sternal ribs. (After Marsh.)

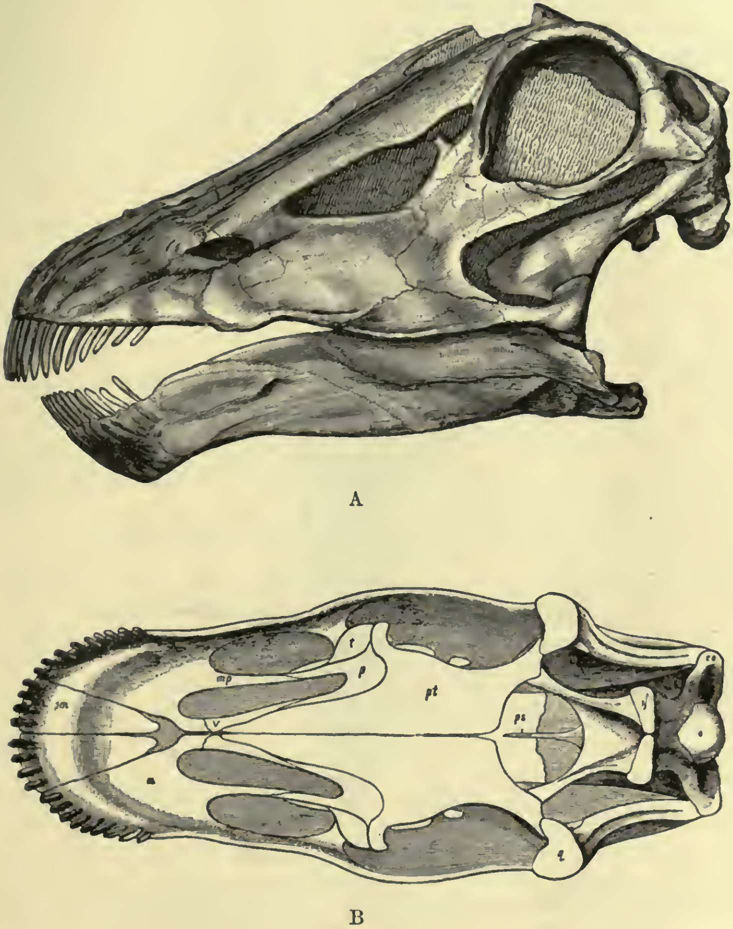

Fig. 123.

Diplodocus longus; skull from the left lateral (A) and palatal (B) aspects, one-sixth nat. size.—Jurassic; Colorado. *b*, basioccipital; *eo.*, exoccipital; *m*, maxilla; *mp.*, extension of maxilla; *o*, occipital condyle; *p*, palatine; *pm.*, premaxilla; *ps.*, parasphenoid; *pt.*, pterygoid; *q*, quadrate; *t*, ectopterygoid; *v*, vomer. In the upper figure (A) the external narial opening is seen at the vertex of the skull, while the antorbital and small maxillary vacuities are shown on the face. In the lower figure (B), the posterior (internal) nares are the pair of vacuities adjoining the vomers. (After Marsh.)

the ischium, expanded at its proximal end for union with the latter, and showing the usual perforation. No dermal armour has been observed. The length of the typical skeleton of *Brontosaurus excelsus* from the Upper Jurassic of Wyoming, is not less than 17 metres.

Diplodocus (figs. 123, 124). This genus has an elevated, laterally compressed skull, with a relatively long and downwardly curved facial region, and the feeble slender teeth confined to the anterior end of the jaws (fig. 123 A). The external narial opening is very large, single, and placed at the apex of the skull, while the nasal bones are excessively shortened as in the Cetacean mammals. In advance of the usual antorbital vacuity, there is another comparatively small vacuity in the maxilla. In the type specimen there is also an irregular vacuity (perhaps accidental) in the parietal region. The orbit is large and laterally placed; the supratemporal vacuities are very small; and the mandibular suspensorium is much inclined forwards. The palate (fig. 123 B) is remarkable

Fig. 124.

Diplodocus longus; transverse section of maxilla showing functional tooth (fourth) in position and five successional teeth (2—6) in dental cavity, one-half nat. size.—Jurassic; Colorado. *a*, outer wall; *b*, inner wall; *c*, cavity; *f*, foramen. (After Marsh.)

for the extension of the maxillæ (m) and premaxillæ ($pm.$), the length of the basipterygoid processes, the great extent of the pterygoids ($pt.$), and the very small development of the vomers (v). The successional teeth are beautifully shown in a cavity of the bone both in the upper and lower jaws (fig. 124). The chevron bones of the tail are unique in being double, each having both anterior and posterior branches (hence the generic name). The sternal bones have been discovered as in *Brontosaurus* (fig. 122, p. 202). The genus is known only from the Jurassic of North America, and the typical species, *Diplodocus longus*, must have attained a length of about twelve metres. The position of the external nares suggests aquatic habits.

Sub-Order 3. *Ornithopoda* (or *Predentata*).

These are also herbivorous Dinosaurs of very varied proportions, ranging throughout Jurassic and Cretaceous strata. Some must have been bipedal in gait, others quadrupedal; but all agree in the characters of the pelvis and the presence of a predentary bone in front of the mandible. The brain-case is completely ossified, and there is little or no antorbital vacuity in the skull. The cervical ribs loosely articulate with their respective vertebræ. The pubis is slender and directed downwards and forwards, but does not meet its fellow in the median line in front; at its base there arises a slender post-pubis which is directed backwards and downwards parallel with the equally slender ischium. The astragalus does not exhibit an ascending process.

The typical unarmoured Ornithopoda must have been bipedal in gait and digitigrade. They are represented by the three-toed *Iguanodon* and the four-toed *Hypsilophodon* in the European Wealden; by *Camptosaurus* and *Laosaurus* in the Jurassic, *Hadrosaurus* and *Claosaurus* in the Cretaceous of North America.

Iguanodon (figs. 125—127). This is one of the first-discovered Dinosaurs, thus named from the resemblance of its teeth to those of the modern lizard, *Iguana.* Complete skeletons are known from the Wealden of Bernissart, near Mons, Belgium. The only skulls hitherto found are very much fractured, though exhibiting the limits of most of the elements. The head (fig. 126) is laterally compressed, the nostrils are relatively large, nearly terminal, and there is a very small antorbital vacuity. The frontals are flattened and apparently fused together, the parietals meet in a sharp median crest, and the quadrate forms a remarkably deep pedicle. There are small supraorbital bones above the eye, but no sclerotic plates have been observed. Each ramus of the mandible comprises at least six elements and exhibits a slender coronoid process behind; the predentary bone is crescentic, with a regularly jagged margin which seems to have been ensheathed in a horny beak. The premaxilla is also toothless, but the maxilla and dentary bear closely arranged stout grinding teeth. All the teeth, when unworn, are of the form shown in the accompanying fig. 127; when worn they are reduced to a flattened stump. They are fixed in separate incomplete sockets in very close order, the successional teeth well-formed below those of the functional row; the crowns of the upper teeth are a little inclined inwards to meet those of the lower jaw which are similarly inclined outwards. The vertebral column comprises more than 80 vertebræ, 10 being cervical, 18 dorso-lumbar, from 4 to 6 sacral, and the remainder caudal. The vertebral centra are solid; and those of the cervical and apparently anterior dorsal regions are opisthocœlous, while those beyond are only slightly amphicœlous. All the cervical vertebræ except the atlas bear ribs, and there are only one or two lumbar vertebræ destitute of them; separate short ribs also appear at least on the anterior 13 caudal vertebræ. The proximal ends of the chevron bones are united by a delicate bridge, and are placed intervertebrally between the 3rd and about the 36th caudal vertebræ. In the pectoral arch, the

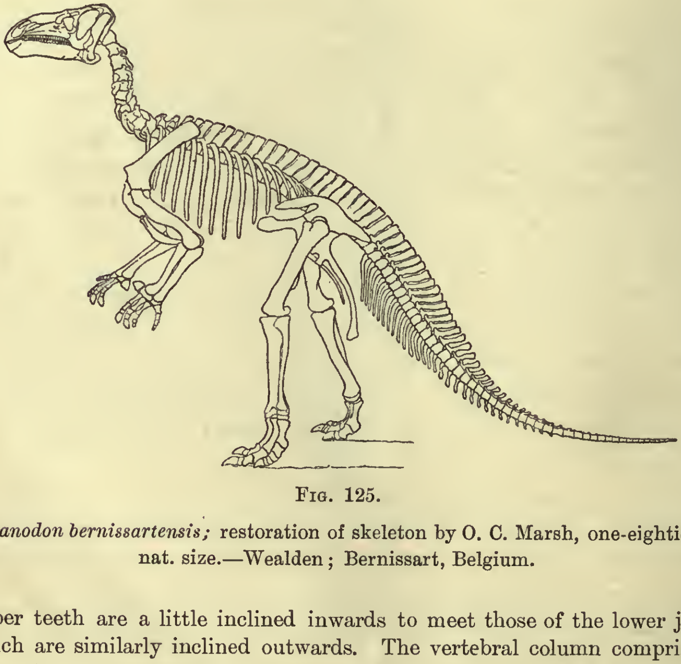

Fig. 125.

Iguanodon bernissartensis; restoration of skeleton by O. C. Marsh, one-eightieth nat. size.—Wealden; Bernissart, Belgium.

scapula is remarkably long and slender, while the coracoid is small and rounded, notched or pierced by a foramen at its articular border. A pair of almost triangular bones seem to represent postero-lateral ossifications in the sternum, though this determination is uncertain. The humerus is a little curved, with a prominent radial crest; both the radius and ulna are robust; and the carpus is ossified, though its elements have not yet been definitely determined. There are five digits in the manus, the first reduced to a mere "spur" consisting of one pointed phalange, the others having the phalangeal formula 3, 3, 3, 4. The second, third, and fourth digits exhibit long metacarpals, and the two first are tipped with hoof-shaped unguals; the fifth digit is borne by a much smaller metacarpal and is comparatively feeble. In the pelvic arch the antero-posterior

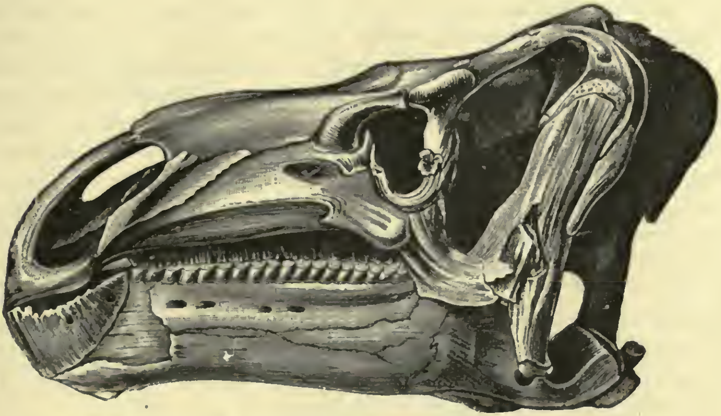

Fig. 126.

Iguanodon bernissartensis; skull from the left lateral aspect, showing predentary bone of mandible, one-eighth nat. size.—Wealden; Bernissart, Belgium. (After Dollo.)

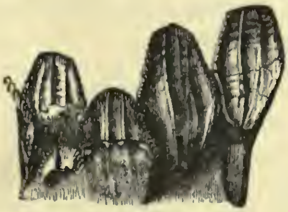

Fig. 127.

Iguanodon mantelli; four unworn lower teeth in fragment of jaw, inner aspect, one-half nat. size.—Wealden; Sussex. (After Owen.)

extension of the depressed ilium is very marked. The pubis is spatulate in form and its post-pubic process is extremely slender, not so long as the much produced ischium. The femur is characterized by a prominent pendent trochanter on the postero-inner face of the shaft. The tibia and fibula are approximately as long as the femur. The astragalus and calcaneum, as usual, form the proximal row of the tarsus, and two elements have been observed in the distal row. Digit no. I is represented only by a rudiment of its metatarsal, and no. V is wanting, so that the hind foot is tridactyl. It is digitigrade with broad, claw-shaped, ungual phalanges, and the phalangeal formula is 0, 3, 4, 5, 0. The fore limbs are not much more than half as long as the hind limbs, and the animal is proved by footprints to have walked in a kangaroo-like attitude. The back is strengthened by ossified tendons extending across the neural spines. No dermal armour has been observed. The typical species is *Iguanodon mantelli* from the Lower Greensand of Maidstone, Kent, and the Wealden of Bernissart, Belgium, measuring 5 or 6 metres in length. A larger species, 8 to 10 metres in length, from the Wealden of Bernissart and S. E. England, is named *I. bernissartensis* or *I. seelyi*. Fragmentary remains also occur in the Purbeck Beds, and an imperfect skeleton of a nearly similar Dinosaur, of small size, has been found in the Kimmeridge Clay of Oxford.

Claosaurus (fig. 128). One of the latest genera of Dinosaurs, in many respects much specialized. The skull is much like that of *Iguanodon* with edentulous premaxillæ, but with enormous narial openings, and destitute of supraorbital bones. There are 30 presacral vertebræ, 9 sacrals fused together, and about 60 caudals. All the presacral vertebræ are opisthocœlous, and even the hindermost bear free ribs. The anterior caudal vertebræ are also opisthocœlous, and the first and second do not bear chevron bones; behind these the chevrons are very long. The back is strengthened by ossified tendons extending across the neural spines. The limb-bones are solid, and the fore limbs are unusually small compared with the hind limbs. The scapula is large and much curved, the coracoid very small and perforated by a large foramen. Bones resembling the supposed paired sternals of *Iguanodon* have also been found. The humerus is comparatively short, with a prominent radial crest; the stout ulna is slightly longer than this and exhibits a conspicuous olecranon process. The carpal bones are imperfectly ossified, and the manus is elongated; there are only three functional digits (II—IV) with elongated metacarpals and three phalanges in each, but digit I appears as a rudiment with two phalanges. The functional digits are hoofed. In the pelvis, the upper border of the ilium is considerably overturned, the pubis is remarkably large and expanded, with a much-reduced post-pubis, and the shaft of the ischium is greatly elongated. The femur is long and straight, with the large trochanter at its middle. The tibia and fibula are shorter than the femur, while the astragalus and calcaneum remain free though closely apposed to their lower end. The first and fifth digits are entirely wanting in the hind foot, but the three others are very massive with broad hoofs, and the phalangeal formula is 3, 4, 5. The typical species is *Claosaurus annectens*, known by two tolerably complete skeletons from the Laramie Beds (uppermost Cretaceous) of Wyoming, U.S.A. It is about nine metres in length.

FIG. 128.

Claosaurus annectens; restoration of skeleton by O. C. Marsh, one-eightieth nat. size.—Cretaceous; Wyoming.

The armoured Ornithopoda—or STEGOSAURIA, as they are often termed—range from the Lower Lias to the Cretaceous inclusive in England, and are both Jurassic and Cretaceous in North America. *Scelidosaurus*, from the Lower Lias of Dorsetshire, is only moderately armoured; *Stegosaurus*, from the Jurassic of the United States, and *Omosaurus*, from the Upper Jurassic (Oxford and Kimmeridge Clays) of England, are provided with great spines and dermal plates; while *Polacanthus*, from the English Wealden, has the lumbar-sacral region completely encased in a continuous shield of fused plates, which press the ilium downwards. The latter is particularly remarkable because the tips of the hindermost ribs in the only known specimen seem to penetrate between the anterior extension of the ilium and its superincumbent armour.

Scelidosaurus (fig. 129). This early genus is known by one nearly complete skeleton, besides many fragments. The head is remarkably small. The end of the snout is unfortunately unknown, but the greater part of the skull has been discovered, and the teeth are those of a herbivorous animal, the crowns being more or less spatulate and serrated on the edge. All the vertebræ are amphicœlous, and some of the centra are proved to have an internal cavity. There are 6 or 7 cervical vertebræ, 16 dorsals, 1 lumbar, 4 sacrals, and probably about 40 caudals. The scapula is long and narrow, the small coracoid disc-shaped and exhibiting a perforation; but the pectoral limb is imperfectly known. The ilium is much extended, as usual. The femur, tibia and fibula are hollow, and the latter are somewhat shorter than the first. The astragalus and calcaneum are not fused with the tibia and fibula, and the imperfectly determined small distal elements of the tarsus are ossified. The fifth metatarsal is merely a small rudiment, but the others are well-developed and the phalangeal formula is 2, 3, 4, 5, 0. Digit no. I, however, is comparatively small and slender, so that the hind foot is functionally tridactyle. The armour seems to have consisted of symmetrically disposed longitudinal series of small tubercles and triangular or conical scutes. The typical species is *Scelidosaurus harrisoni*, from the Lower Lias of Lyme Regis, and seems to have attained a length of about four metres.

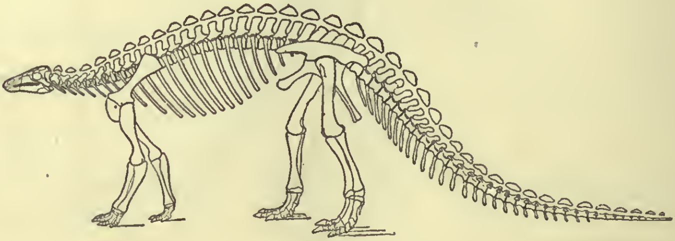

Fig. 129.

Scelidosaurus harrisoni; restoration of skeleton by O. C. Marsh, one-thirty-sixth nat. size.—L. Jurassic (L. Lias); Dorsetshire.

Stegosaurus (figs. 130, 131). All the bones of this heavily armoured Dinosaur are solid. The head is remarkably small, and the brain seems to have been smaller in proportion to the size of the animal than in any known land vertebrate. The teeth are very numerous, bluntly pointed, and cylindrical or spatulate in form, arranged loosely in sockets in one functional series on the maxilla and dentary; their successors are lodged in a large cavity in the bone. The vertebræ are slightly amphicœlous or with flat ends, and most of the summits of the neural spines are expanded for the support of the dermal armour. All the cervical vertebræ bear short ribs; the dorsals exhibit especially elevated neural arches on which the stout ribs are borne. The sacrum comprises four co-ossified vertebræ, sometimes with one or more lumbars added in front; the anterior caudal vertebræ are the largest in the whole series, and the limbs of the chevron bones are not united by a bridge. The fore limb is very powerful, though small, its most striking feature being the large olecranon process of the ulna. There are only three bones in the proximal carpal series, while the distal carpals seem to have been unossified; and there is imperfect evidence of five digits. The pelvis is extremely massive for the support both of armour and the large hind limbs. The ilium extends far in advance of the acetabulum, and its superior crest curves inwards to the neural arches of the sacrum with which it is fused. The femur is large and straight, without any inner trochanter, while the tibia and fibula are comparatively short. The astragalus is firmly fused with the tibia, and the calcaneum less securely so with the fibula, while three well-ossified distal tarsals are distinct. The hind foot is imperfectly known, but there seem to be only three functional digits, no. I being rudimentary and no. V entirely wanting. The arrangement of the dermal armour is a little uncertain; but there seems to have been a median crest of very large triangular bony plates along the back, and there are indications of a shield of small rounded ossicles below the mandible and on the throat. *Stegosaurus* is known only from the Upper Jurassic

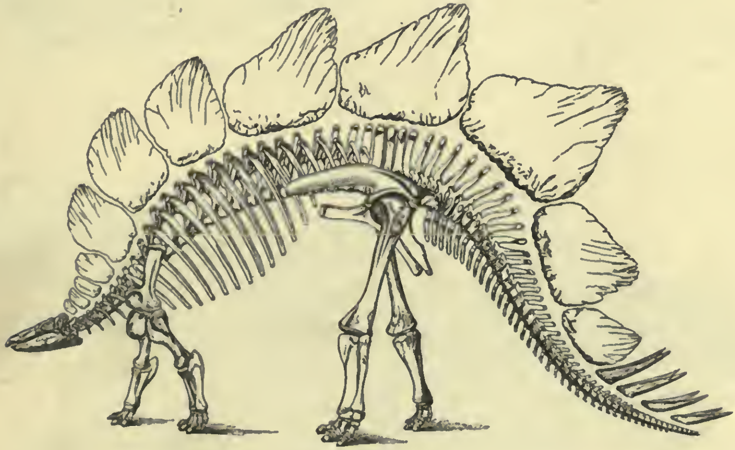

FIG. 130.

Stegosaurus ungulatus; restoration of skeleton by O. C. Marsh, one-sixtieth nat. size.—Jurassic; Wyoming.

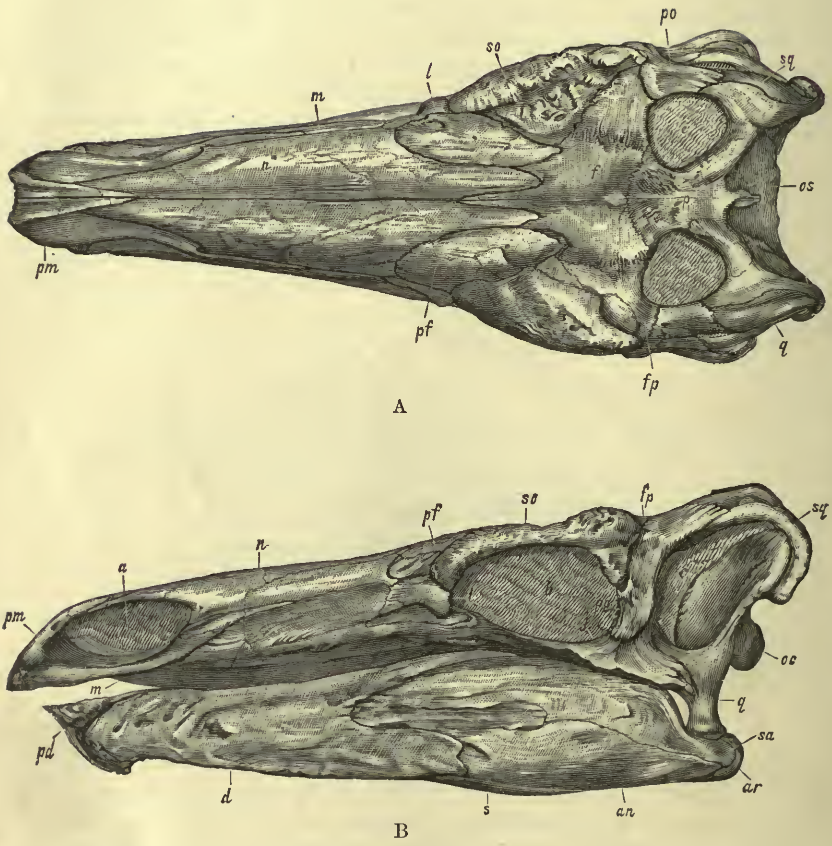

Fig. 131.

Stegosaurus stenops; skull from the superior (A) and left lateral (B) aspects, one-quarter nat. size.—U. Jurassic; Colorado. *a*, external narial opening; *an.*, angular; *ar.*, articular; *b*, orbit; *c*, lateral temporal vacuity; *d*, dentary; *e*, supratemporal vacuity; *f*, frontal; *fp.*, postfrontal; *j*, jugal; *l*, lachrymal; *m*, maxilla; *n*, nasal; *oc.*, occipital condyle; *os.*, supraoccipital; *p*, parietal; *pd.*, predentary; *pf.*, prefrontal; *pm.*, premaxilla; *po.*, postorbital; *q*, quadrate; *s*, splenial; *sa.*, surangular; *so.*, supraorbital; *sq.*, squamosal. (After Marsh.)

of Colorado and Wyoming, where nearly complete skeletons have been found. The typical species, *S. ungulatus*, probably attained a length of about nine metres.

Towards the close of the Mesozoic period, when the Dinosaurs gradually become extinct, a remarkable group of gigantic horned animals appears, supposed to be a highly specialized branch of the tribe to which the armoured Stegosauria belong. Unsatisfactory fragments of these reptiles from the Upper Cretaceous, both of Austria and North America, have received many names (e.g., *Struthiosaurus*, *Agathaumas*, *Polyonax*, and *Monoclonius*); but the only important specimens hitherto discovered are those from the Laramie Formation of Wyoming, U.S.A., termed *Ceratops*, *Triceratops*, and *Sterrholophus*, the first two thus named in allusion to the great horns of which one pair is placed above the eyes.

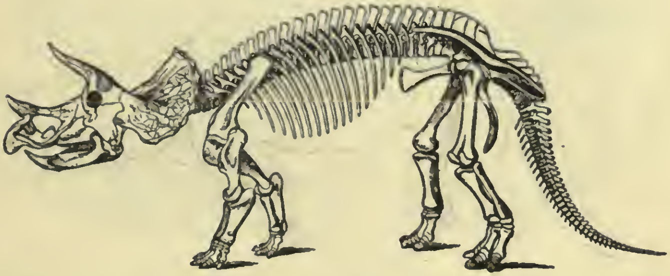

FIG. 132.

Triceratops prorsus; restoration of skeleton by O. C. Marsh, one-eightieth nat. size.—Cretaceous; Wyoming.

Triceratops (figs. 132, 133). The greater part of the skeleton of this genus is known, and indicates an animal of robust proportions which would be quadrupedal in gait. All the bones are solid. The skull of the largest individuals exceeds in size that of any land-animal hitherto discovered, and is only surpassed by that of some of the modern Cetaceans. It is chiefly remarkable for its armature (fig. 133). There is a sharp cutting beak in front, a strong horn on the nose, a pair of very large pointed horns on the top of the head, and a row of sharp projections round the margin of the posterior crest—all these doubtless encased in a layer of horny tissue. The skull itself is wedge-shaped in form, and very narrow in the facial portion. The upper toothless beak is formed by the premaxillæ, with the addition of a median "rostral" bone in front, and these fuse together in old individuals. The nasal bones are large and massive and much thickened anteriorly to support the nasal horn-core. The frontals are small, and the enormous horn-cores above the eyes, which are hollowed at the base, are supported by the enlarged postfrontals, partly also by the supraorbitals and postorbitals. The postfrontals meet in the middle line, and at the median point of their union with the parietals in young individuals there seems to be a perforation which may perhaps be interpreted as a "pineal foramen." The great posterior crest of the skull is formed chiefly by the parietals, and the narrow supratemporal vacuity on each side is bounded outwardly by a separate squamosal. The brain-cavity is especially diminutive, smaller in proportion to the skull than in any other known reptile. A toothless predentary bone is observed in front of the mandible, and the dentary rises behind into a large coronoid process. Articular, angular, surangular, and splenial elements are distinguishable. The teeth are arranged in a single functional series on the maxilla and dentary, and are not displaced vertically by their successors, but from the side. They are broader than long and implanted by a forked root, the inner and outer branches of which are described as fixed in more or less distinct sockets; the dental crown is adapted for a herbivorous diet. The atlas

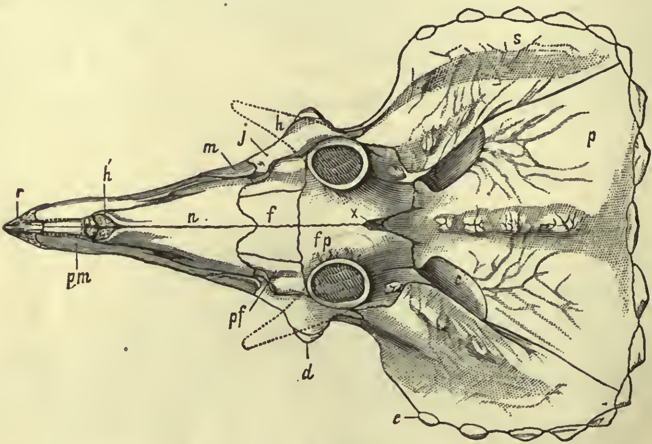

FIG. 133.

Triceratops serratus; diagram of skull from the superior aspect, one-twentieth nat. size.—Cretaceous; Wyoming. *c*, supratemporal vacuity; *d*, epijugal plate; *e*, epi-occipital plates; *f*, frontal; *fp.*, postfrontal; *h*, horn-core; *h′*, nasal horn-core; *j*, jugal; *m*, maxilla; *n*, nasal; *p*, parietal; *pf.*, prefrontal; *pm.*, premaxilla; *r*, rostral bone; *s*, squamosal; *x*, perhaps a pineal foramen. (After Marsh.)

and axis are fused with one or more of the succeeding cervical vertebræ to support the massive head, and the articular ends of the free centra are flattened. The dorsal vertebræ have remarkably short centra. The true lumbars, two in number, are fused with the sacrum, which comprises four vertebræ, firmly united both by the centra and neural spines, and bearing double transverse processes. The neural canal in the sacrum is not specially enlarged. The first four caudal vertebræ are also fused with the sacrum, and the transverse processes of three of these abut against the ilium. The tail is of moderate length, with small chevron bones placed intervertebrally. In the pectoral arch the coracoid, perforated as usual, is rather small, and is sometimes fused with the scapula in old individuals. The humerus resembles that of *Stegosaurus*, but is nearly as long as the femur. The radius and ulna are comparatively short and stout, and the latter exhibits a very large olecranon process. There are five hoofed digits in the manus. In the pelvic arch the ilium is much elongated, and its anterior extension forms a horizontally expanded plate; the pubis is massive, but exhibits only a very slight trace of a post-pubis; the ischium is smaller than the pubis, more elongated, and not in close contact with its fellow of the opposite side.

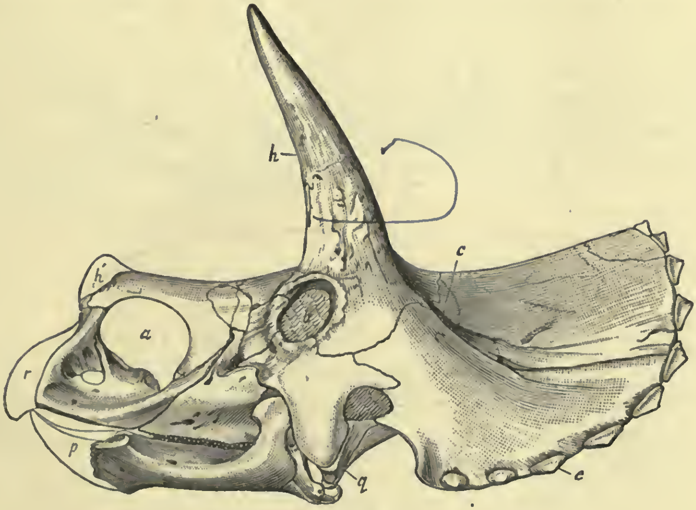

FIG. 134.

Sterrholophus flabellatus; skull from the left lateral aspect, one-twentieth nat. size.—Cretaceous; Wyoming. *a*, external narial opening; *b*, orbit; *c*, supratemporal vacuity; *e*, epi-occipital plates; *h*, horn-core; *h'*, nasal horn-core; *p*, predentary (restored in outline); *q*, quadrate; *r*, rostral bone (restored in outline). (After Marsh.)

The femur is short compared with the size of the animal, the tibia still shorter, and the fibula extremely slender. The astragalus is fused with the distal end of the tibia. There seem to have been three hoofed digits in the hind foot. The dermal armour comprises numerous bony tubercles and bosses, of which the arrangement is not definitely known. *Triceratops prorsus*, restored in the accompanying fig. 132, attained a length of at least eight metres. The known remains include one nearly complete skeleton from the uppermost Cretaceous (Laramie Formation) of Wyoming, U.S.A.

In *Sterrholophus*, of which the skull is shown of one-twentieth the natural size in fig. 134, the whole of the posterior face of the parietal crest must have been covered with the ligaments and muscles supporting the head; whereas in *Ceratops* and *Triceratops* a wide margin of this face was clearly exposed and protected by a thick horny covering.

ORDER 8. CROCODILIA.

It is as yet impossible to distinguish the Triassic ancestors of the Crocodilia from those of the Rhynchocephalia and Dinosauria. True crocodiles, however, are known to range from the earliest Jurassic rocks upwards. In all these forms, the teeth are confined to the margin of the jaws, there is a great development of the secondary palate, and there is a tendency to the enclosure of the eustachian passages by bone. As in modern crocodiles, also, the pubis is always excluded from the acetabulum and carried on an anterior process of the ischium. Some marked changes, however, have taken place in the course of their evolution. In all the known Jurassic crocodiles the hinder margin of the secondary palate is formed by the palatines, there being no outgrowths from the pterygoids; while the lateral eustachian passages occupy merely open grooves on the basisphenoid bone. All except very few of the latest forms possess amphicœlous vertebræ; and it is only in the Upper Jurassic that short- and broad-headed genera, with small supratemporal vacuities, begin to appear. In the Cretaceous period all the known crocodiles, except two remarkable genera from northern Patagonia, exhibit the extended secondary palate, closed eustachian passages, and procœlous vertebræ familiar in the genera of the present day.

Sub-Order 1. *Parasuchia.*

The Triassic reptiles commonly claimed as ancestral crocodiles, are capable, in the present state of knowledge, of being assigned with equal appropriateness to the Dinosauria. They are met with in Europe, Asia, and North America, but are only known by comparatively fragmentary specimens. *Belodon* (*Phytosaurus*), from the Upper Keuper of Stuttgart, is already represented by fine skulls and other portions of the skeleton; and the same genus appears to occur in corresponding strata in North America. *Stagonolepis* is found in the Triassic sandstones of Elgin, Scotland, but it is in an unsatisfactory state

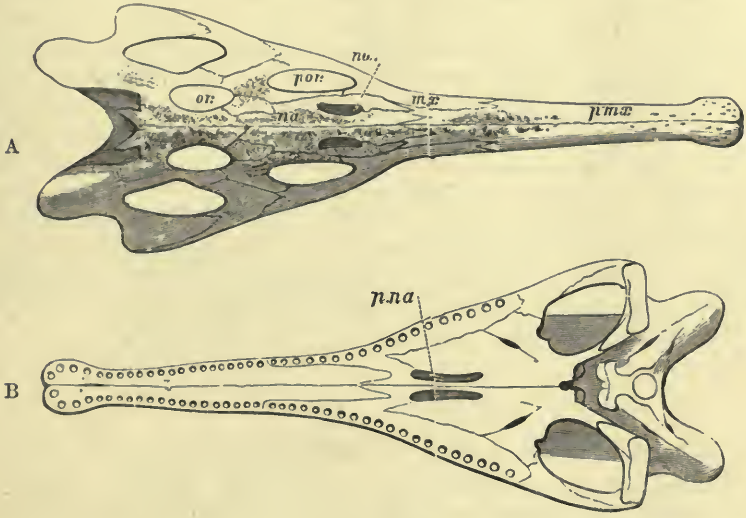

FIG. 135.

Belodon kapffi; skull from the superior (A) and palatal (B) aspects, one-seventh nat. size.—U. Triassic; Würtemberg. *mx.*, maxilla; *na.*, nasal; *nar.*, external narial openings; *or.*, orbit; *p.na.*, posterior nares; *pmx.*, premaxilla; *por.*, antorbital vacuity. External to the orbit the large lateral temporal vacuity is conspicuous; the supratemporal vacuity is very small, indicated only by the pair of notches in the figure above the occiput. (After H. von Meyer.)

of preservation. *Parasuchus* is the name of fragments from the Gondwana Formation of Maleri, Central Provinces, India.

Belodon (fig. 135). The skull of *Belodon* is marked by a pitted and rugose ornament, and the snout is much produced, not by the elongation of the whole facial region, but by the enormous development of the premaxillæ. There is no pineal foramen, and the orbits are directed upwards; the supratemporal vacuities are extremely small, and the lateral temporal vacuities are large. An extensive antorbital vacuity is conspicuous, and the external nares are paired. Neither of the eustachian passages is enclosed by bone; while the palatines and pterygoids do not develop secondary plates to displace the actual primitive opening of the posterior nares. There is a vacuity in the hinder half of the mandibular ramus. The vertebræ are amphicœlous, and only two are comprised in the sacrum. The coracoid is short and rounded, with a very large fontanelle; and clavicular elements seem to have been present. The pubis enters the acetabulum, which seems to have been completely closed. The dorsal armour comprises a symmetrical pair of large, overlapping, keeled scutes, ornamented like those of modern crocodiles; and there was probably a ventral armour of smaller, more irregular scutes. The typical species is *Belodon kapffi*, with a skull attaining a length of at least 0·7 m.

Sub-Order 2. *Mesosuchia.*

These are the Jurassic crocodiles, all except the latest adapted for an exclusively aquatic life. As already remarked, they are distinguished from the typical Cretaceous and modern families by the characters of the palate, eustachian passages, and vertebral centra; but they never exhibit more than two sacral vertebræ. Their remains are known only from Europe, Madagascar, South America, and perhaps North America.

It has been suggested that the appearance of the broad-nosed genera in the Purbeck and Wealden is correlated with the in-coming of warm-blooded prey, whether mammalian or avian. It is, at any rate, curious, that dwarf crocodiles of this kind (*Theriosuchus*, *Nannosuchus*) are associated with the remains of diminutive mammals in a stratum of the Purbeck Beds near Swanage.

Pelagosaurus (fig. 136). This genus is known by nearly complete skeletons from the Upper Lias of Würtemberg, Normandy, Yorkshire, and Somersetshire. The skull is much elongated and narrow, with numerous slender teeth placed nearly upright in the jaw. The two parietal bones and the two frontal bones are fused together, and the nasals do not extend forwards beyond the basal half of the snout. The supratemporal vacuities are very large, the orbits are also very large and directed laterally, while the antorbital vacuity is a mere remnant or absent. On the palate the suborbital vacuities are large, and the posterior narial opening is pear-shaped, extending forwards a little between the secondary plates of the palatines. The vertebræ resemble those of a modern crocodile, except that the centra are amphicœlous, and that the centrum of the atlas is not fused with that of the axis. The dorsal armour comprises a symmetrical paired series of broad, overlapping scutes; the ventral shield consists of a mosaic of small irregular polygonal scutes, united by jagged sutures. These and the external bones of the head, including the postorbital bar, are marked by a pitted ornamentation. The type species is *P. typus*, about one metre in length; other forms are at least twice as large as this.

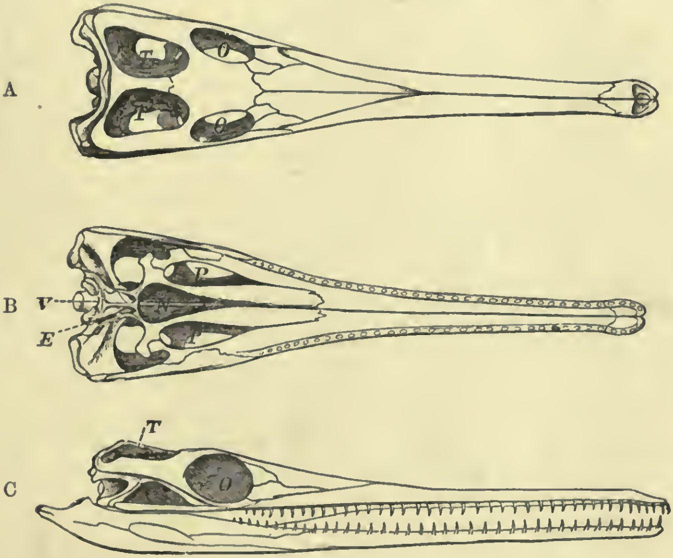

FIG. 136.

Pelagosaurus typus; skull from the superior (A), palatal (B), and right lateral (C) aspects, one-half nat. size.—L. Jurassic (U. Lias); Normandy. E, aperture of eustachian canal; N, posterior nares; O, orbit; P, suborbital vacuity; T, supratemporal vacuity; V, venous foramen. (After Owen.)

Teleosaurus and *Steneosaurus* are armoured marine crocodiles closely related to *Pelagosaurus*, the former confined to the Lower Oolites, the latter ranging from the Upper Lias upwards to the Kimmeridge Clay. They are noteworthy for the very small size of the fore limbs compared with the hinder pair—a disproportion still more marked in the next genus.

Metriorhynchus. An Upper Jurassic genus, known by nearly complete skeletons from the Oxford Clay of Peterborough, and by various remains from other parts of England, France, and Germany The skull has an elongated tapering form, and is feebly sculptured. The premaxillæ are scarcely expanded, and the nasals do not reach them; the external narial opening and the supratemporal vacuities are very large; and the orbits are directed chiefly laterally, while the prefrontal bones are unusually large and form an overhanging ledge. The teeth are slender and carinated, at least 20 in number in each half of the jaw above and below. Sclerotic plates occur in the eye. No trace of dermal armour has been met with.

Dakosaurus, also an Upper Jurassic genus, has the skull comparatively short and broad, with the nasals reaching the premaxillæ and the external narial opening. The teeth are relatively larger and fewer than those of the genera mentioned above, not exceeding 20 in number on each side of either jaw; they are oval in section, smooth, and with two opposite keels. There is no vacuity in the side of the mandibular ramus. The remainder of the skeleton is very imperfectly known. The external head-bones are smooth or only feebly sculptured, and no dermal scutes have been observed. The typical species, *D. maximus*, was founded on fragments from the Corallian and Lower Kimmeridgian of Würtemberg and Bavaria. Fine skulls are known from the English Kimmeridge Clay.

Theriosuchus. This is a dwarf crocodile, only about 0·45 m. in length, and the earliest type closely approaching the modern crocodiles and alligators in outward form. The facial portion of the skull, in advance of the orbits, constitutes only about one-third of its entire length, thus retaining in the adult condition somewhat analogous proportions to those observed temporarily in the young of living Crocodilia; and the nasal bones overhang the aperture of the external nostril, which seems to have been terminal. The supratemporal vacuities are smaller than the orbits; and the opening of the posterior nares on the palate is definitely proved not to have been displaced backwards by secondary outgrowths from the pterygoid bones. The teeth are tumid, and more varied both in size and shape than those in any other known member of the order. The mandibular symphysis is short. The body is protected, both dorsally and ventrally, by pitted scutes, the upper shield consisting of only two longitudinal rows, and the lower of more irregular rows. The dorsal scutes are rectangular, not only overlapping but also united at their outer angles by a "peg-and-socket" articulation such as occurs among the scales of many ganoid fishes; the ventral scutes are polygonal and unite exclusively by suture, not by overlapping. The proportions of the limbs resemble those of modern crocodiles. The only known species is *Theriosuchus pusillus*, from the Purbeck Beds of Dorsetshire.

Goniopholis is a larger Purbeckian and Wealden crocodile, much resembling *Theriosuchus*, but with somewhat larger supratemporal vacuities, more normal stout teeth, and the nasal bones not quite reaching the external narial opening. The typical species, *G. crassidens*, is known by fragmentary specimens from the English Purbeck and Wealden. Another form, *G. simus*, is represented not only by a skull from the Purbeck of Swanage, but also by two nearly complete skeletons from the Wealden of Bernissart, Belgium. In these skeletons, which are about two metres in length, the fore limbs are as large as the hind limbs.

Bernissartia, of Wealden age, still more closely resembles the modern crocodiles, though retaining the essential characters of the Mesosuchia. The supratemporal vacuities are smaller than the orbits, and the nasal bones do not reach the external narial opening. The dorsal armour, like that of the Tertiary and Recent Crocodilia, comprises more than two longitudinal series of scutes, which are overlapping but do not unite by a peg-and-socket articulation. The ventral scutes similarly overlap each other. The fore limbs are much shorter than the hinder pair. The typical species is *B. fagesi*, from Bernissart, Belgium, represented by a nearly complete skeleton about a metre in length.

Notosuchus (fig. 137). A small unarmoured crocodile known by the greater part of the skeleton from supposed Cretaceous rocks in the Territory of Neuquen, north of Patagonia, South America. The skull (fig. 137) is short and broad, with a much abbreviated rostrum, and the outer bones are externally rugose. The supratemporal vacuities are smaller than the orbits, which are relatively very large, directed both superiorly and laterally, and separated from the lateral temporal vacuity only by a slender internal postorbital bar. A small antorbital vacuity occurs between the lachrymal and maxillary bones; and the nasals reach the single large narial opening, which is directed forwards. The palate is proved to be typically Mesosuchian, without any secondary plates from the pterygoid bones to prolong the canal of the nares. The mandible is slender, biting within the upper jaw, and its articular end is not curved upwards; there is a large vacuity in the side of each ramus, and the splenials enter the short pointed symphysis. The teeth are few in number and laterally compressed, and no successors have been observed; those of the upper jaw are extraordinarily differentiated, the premaxilla bearing three small incisors and one very large canine, while the maxilla has seven teeth of nearly uniform size; there are about ten lower teeth, gradually increasing in size backwards without an enlarged canine. The

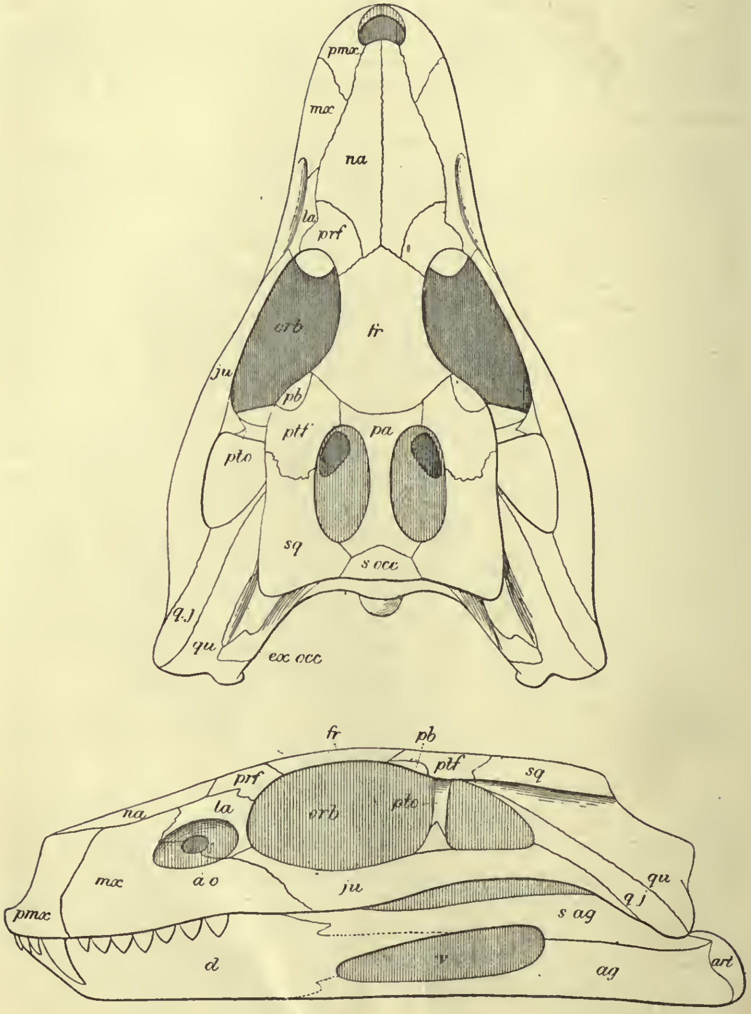

Fig. 137.

Notosuchus terrestris; restoration of skull from the superior (A) and right lateral (B) aspects, one-half nat. size.—Cretaceous; Neuquen, Argentina. *a.o.*, antorbital vacuity; *ag.*, angular; *art.*, articular; *d*, dentary; *ex.occ.*, exoccipital; *fr.*, frontal; *ju.*, jugal; *la.*, lachrymal; *mx.*, maxilla; *na.*, nasal; *orb.*, orbit; *pa.*, parietal; *pb.*, palpebral; *pmx.*, premaxilla; *prf.*, prefrontal; *ptf.*, postfrontal; *pto.*, postorbital; *q.j.*, quadrato-jugal; *qu.*, quadrate; *s.ag.*, surangular; *s.occ.*, supraoccipital; *sq.*, squamosal; *v*, vacuity.

vertebræ are slightly amphicœlous. The limbs are typically crocodilian in every respect, and the fore limb is not much smaller than the hind limb. The typical species is *Notosuchus terrestris*, with the skull about 0·18 m. in length. A closely related genus, *Cynodontosuchus*, from the same formation and locality, also exhibits the highly specialized dentition, but has large canines in the lower jaw, crossing and working upon those of the upper jaw.

Sub-Order 3. *Eusuchia.*

Like the Mesosuchia, the Eusuchia comprise both long-snouted and broad-snouted crocodiles, besides intermediate forms (*Tomistoma*). The majority, however, are of the broad-snouted type represented by the Crocodiles and Alligators of the present day. They all agree (i.) in the flooring of the secondary nasal passage by plates from the pterygoid bones, (ii.) in the enclosure of the eustachian canals by bone, and (iii.) in the procœlous character of the vertebral centra. They form so homogeneous a group that it is difficult to believe that they arose from more than one common Mesosuchian ancestor; but Palæontology as yet does not afford any evidence on the subject. It remains uncertain whether Teleosaurs passed into Gavials, while *Goniopholis*-like Mesosuchians became Crocodiles and Alligators, or whether the modern Eusuchia, as such, have diverged from one central primitive type. The earliest known procœlian vertebræ which seem to be crocodilian occur in the English Purbeck and Wealden strata (*Heterosuchus*), but they are too unsatisfactory for discussion; the same remark applies to other detached vertebræ found in the Cambridge Greensand. *Thoracosaurus*, from the Cretaceous of New Jersey, U.S.A., Holland, and France, is a Gavial-like Eusuchian with a remnant of the antorbital vacuity found in some Teleosaurs; but this persistent character may not be of much significance.

The only interest of the extinct Eusuchian Crocodilia consists in their geographical distribution, and in the intermediate (generalized) character of those dating back to the Lower Tertiary. Skulls indistinguishable from that of *Tomistoma* (now living in the Malay Archipelago) occur in the Miocene of Austria and Malta. Remains of more typical Gavials are met with in the Pliocene of the Siwalik Hills, India, and in the

Middle Eocene of Bracklesham, Sussex (*Gavialis dixoni*). Crocodiles and Alligators are found extensively both in Europe and North America, and they appear not to have become completely extinct in Europe before the Pliocene period. *Diplocynodon* is an interesting extinct generalized Alligator, characterized by the third lower tooth as large as the fourth, and a strong ventral armour. *D. hantoniensis* is well known in the Upper Eocene sands of Hordwell, Hampshire; other species occur in the London Clay; and others are found in the Lower Tertiaries of France and Germany as late as the Miocene. It is also worthy of note that the Alligator-like character of the lower teeth biting entirely within the upper teeth, is observable in a gigantic Gavial, *Rhamphosuchus crassidens*, known only by fragments from the Pliocene of the Siwalik Hills, India. This is probably the largest known crocodilian, and cannot have attained a length of less than fifteen metres.

ORDER 9. ORNITHOSAURIA.

Reptiles with hollow bones, well-formed articulations, and fore limbs adapted for flight, occur throughout all Mesozoic formations from the Lower Lias upwards. They are completely evolved at their earliest known appearance (*Dimorphodon*); and they exhibit little essential change as they are traced through the successive deposits in which they occur. It can only be said that some of these reptiles become toothless and attain enormous dimensions in the Cretaceous; the wings eventually becoming so large, that the scapula articulates directly and firmly with the neural arches of some dorsal vertebræ fused together for support.

These flying reptiles are grouped in an order variously termed ORNITHOSAURIA or PTEROSAURIA. The skull is large, remarkably bird-like in shape, and its constituent bones are fused together in the adult. The single occipital condyle is fixed on the base of the skull, so that the long axis of the head is approximately at right angles to that of the neck; the enlarged premaxillæ form the greater part of the upper jaw; and the two rami of the mandible are fused together at the symphysis. The investing bones of the temporal region, however, do not disappear to the extent observed in birds, there being always an upper as well as a lower temporal arcade; and the large quadrate bone is firmly fixed, both at its upper end and against a buttress of the pterygoid. There is no pineal foramen. The orbit is very large, and the eye is usually surrounded by a ring of sclerotic plates; the external narial opening on each side is separated from the orbit by an antorbital vacuity, with which it may be confluent. The posterior nares (known only in *Scaphognathus purdoni* and *Rhamphorhynchus*) are not covered with a secondarily-developed palate, but the narrow vomer separating them is raised far above the plane of the roof of the mouth formed by the premaxillæ and maxillæ. The basipterygoid processes of the basisphenoid are excessively elongated, to reach the very slender pterygoids, which are separated by a large interpterygoid vacuity throughout the greater part of their length, but meet in front where they articulate with the vomer. The brain (best known from the natural cast in *Scaphognathus purdoni*) is remarkably bird-like, but is very small in proportion to the size of the skull. The large optic lobes are visible from above, but seem to have been separated by a forward extension of the cerebellum; and there is distinct evidence of the flocculus on each side of the medulla oblongata. The teeth, when present, are always restricted to the margin of the jaws; they are simply conical in form, fixed in a series of complete sockets, and usually more or less irregular in arrangement. The presacral vertebræ are procœlous, and the cervicals are longer than the dorsals; the sacrum comprises from three to six vertebræ, usually fused together; and the caudal vertebræ are amphicœlous. The cervical and anterior dorsal ribs are double-headed. The clavicular arch is wanting, but there is a large keeled sternum, with which the slender coracoids articulate by a synovial joint; the scapula is long and slender. The humerus is short and much expanded proximally; the radius and ulna are longer and about equal in stoutness. The carpus varies considerably in the number of its elements; some Jurassic genera exhibit two proximal and four distal bones, while certain Cretaceous forms seem to possess only one large proximal, one large distal, and one smaller lateral element. The first digit of the manus is rudimentary or absent; nos. II to IV are short, and bear large claws; while no. V is enormously elongated, and bent backwards to support the wing-membrane. In the pelvis, the ilium is extended both forwards and backwards, and fused with the much-expanded ischium, which is pierced by a small perforation; the acetabulum is closed, and the pubis is excluded from it. The relationships of the latter element are not quite clear, and it has been regarded as a prepubis, the other large inferior element being then interpreted as fused ischium and pubis. The femur is slender and shorter than the tibia; the fibula is incomplete, a mere pointed style, often fused with the tibia; the astragalus and calcaneum are distinguishable, the former sometimes fused with the tibia: and of the five digits in the pes four bear claws. No dermal armour has been observed, but there are abdominal ribs in the ventral wall of the body-cavity. The smooth wing-membrane has been observed in impression on the Bavarian Lithographic Stone, and one specimen (fig. 139) proves that it extended beyond the hind legs to the basal portion of the tail; the long tail of the same specimen exhibits a rhomboidal flap of membrane at the distal extremity.

Dimorphodon (fig. 138). The oldest known genus, *Dimorphodon*, is represented by nearly complete skeletons. The skull is of relatively enormous size, deepened in form, and of extreme lightness; the brain-case is unusually small. The large narial opening on each side is separated from the orbit by an equally large or larger antorbital vacuity. The long axis of the quadrate bone is vertical. The jaws are toothed to the extremity; there being large, irregularly spaced teeth in front, very small and more closely arranged teeth behind. The number of the presacral vertebræ is unknown, but one of them seems to be lumbar (destitute of ribs), and there are probably four in the sacrum; the caudal vertebræ are at least 30 in number, much elongated, and some with chevron bones. The tail is stiffened by ossified tendons. The ribs increase in length to the fifth or sixth, and seem to exhibit traces of epipleural cartilages. The pectoral arch is imperfectly known, but the scapula and coracoid are clearly fused together. In the manus the first digit is represented merely by a styliform bone; nos. II to IV are clawed and exhibit the phalangeal formula 2, 3, 4; no. V, or the wing-digit, has a

ORDER 9. ORNITHOSAURIA.

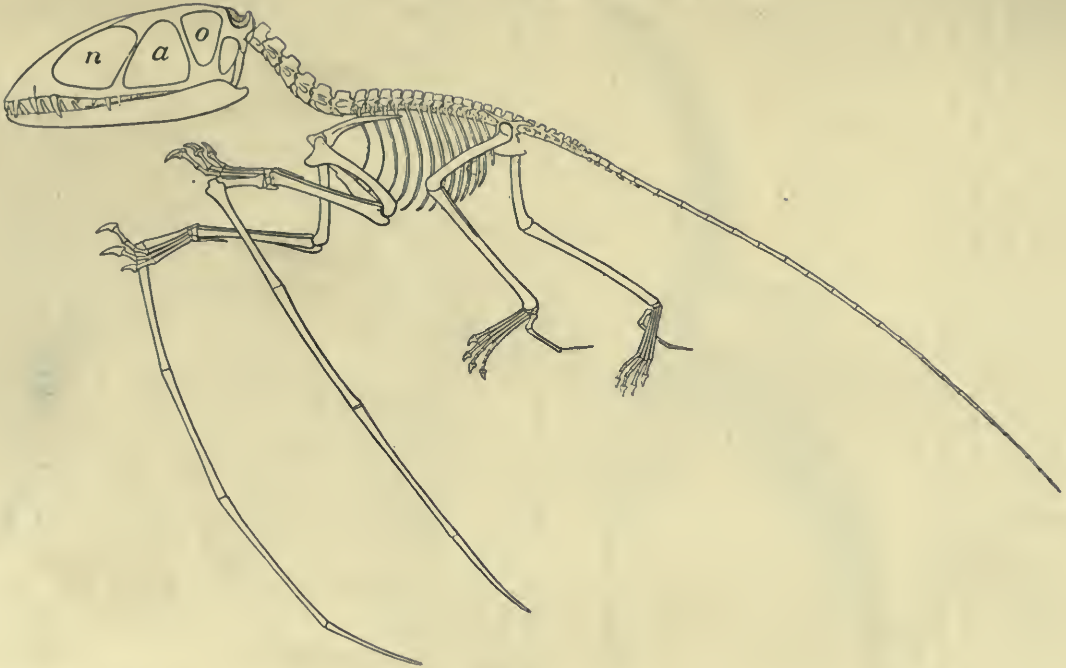

FIG. 138.

Dimorphodon macronyx; restoration of skeleton, one-seventh nat. size.—L. Jurassic (L. Lias); Dorsetshire. *a*, antorbital vacuity; *n*, external narial opening; *o*, orbit. (After Owen, modified by Ridewood.)

very stout metacarpal and four much-elongated phalanges, the last slender and tapering to a point. The pubis is small and club-shaped and attached to the ischium only by its slender end. The phalangeal formula of the hind foot is 2, 3, 4, 5, 2, each of the first four digits normal and bearing a large claw, the fifth digit opposable, with very short metatarsal, one long proximal phalange and an attenuated distal phalange. The only known species is *Dimorphodon macronyx*, with skull attaining a length of about 0·2 m., from the Lower Lias of Lyme Regis, Dorsetshire.

Fig. 139.

Rhamphorhynchus phyllurus; restoration by O. C. Marsh, showing the extent of the volant membranes, one-seventh nat. size.—U. Jurassic (Lithographic Stone); Bavaria.

Rhamphorhynchus (fig. 139). Another long-tailed Pterodactyl, with much-elongated head, very large eye, very small antorbital and narial vacuities. The long axis of the quadrate is inclined downwards and forwards. The jaws bear large, irregular teeth, pointing forwards, but not extending quite to the anterior end of the jaws, which seem to have terminated in a short beak. The sacrum comprises 4 vertebræ, and the tail, strengthened by ossified ligaments, sometimes exhibits nearly 40 vertebræ. The keel of the sternum extends forwards as a slender process, and the scapula is usually fused with the coracoid. The pubis is a slender bar, bent approximately at right angles, not expanded where it meets its fellow of the opposite side, but fused with its fellow at this symphysis. The limbs much resemble those of *Dimorphodon*, except that the fifth digit of the hind foot is smaller than the others and comprises three phalanges. One specimen, named *Rhamphorhynchus phyllurus*, exhibits impressions of the wing-membrane to the extent shown in the accompanying restoration (fig. 139). The typical species is *Rhamphorhynchus longicaudatus*, from the Lithographic Stone (Lower Kimmeridgian) of Bavaria. All the satisfactorily known species have been obtained from this formation in Bavaria and Würtemberg, and the largest (*R. grandis*) has a skull about 0·2 m. in length.

Pterodactylus and allied genera are small, short-tailed Pterodactyls from the Lithographic Stone of Bavaria and Würtemberg. In *Pterodactylus* itself the pubis much resembles that of *Dimorphodon*, and the fifth digit of the pes is a mere rudiment.

Pteranodon (fig. 140). This genus comprises large and even gigantic species of Cretaceous age. The skull is much elongated and laterally compressed, and an enormous occipital crest is produced upwards and backwards (fig. 140, *c*). The long axis of the quadrate (*q*) is inclined downwards and forwards, and the orbit (*b*) is smaller than the confluent antorbital and narial vacuities (*a*); there is a small supratemporal vacuity, not shown in the accompanying figure. Sclerotic plates have been observed. The jaws are entirely toothless, and the symphysis of the mandible is unusually elongated; the texture of the bone suggests that there was no horny beak. The occipital condyle is very small, hemispherical, and not directed downwards so much as in the Jurassic genera. The cervical vertebræ are elongated, and the tail is short. The scapula and coracoid are fused together, and the support for the wing is further strengthened by the articulation of the upper end of the scapula with the neural spines of some fused anterior dorsal vertebræ. The radius and ulna are separate and complete. The carpus comprises three bones, one proximal, one distal, and one lateral; and of these the proximal is the largest, exhibiting distinct facettes for articulation with the radius and ulna. In the manus the first digit is represented merely by a styliform bone; nos. II to IV are clawed, and exhibit the phalangeal formula 2, 3, 4, but their metacarpals are incomplete, tapering to a point proximally, and fixed only to the side of the enormously developed metacarpal of the fifth or wing-digit. The latter has four much-elongated phalanges. The hind

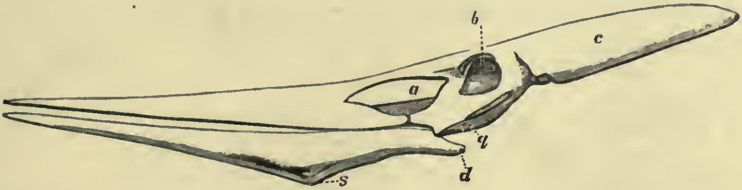

Fig. 140.

Pteranodon longiceps; skull from the left lateral aspect, one-twelfth nat. size.—Cretaceous; Kansas. *a*, antorbital vacuity, including external narial opening; *b*, orbit; *c*, supraoccipital crest; *d*, angle of mandible; *q*, quadrate; *s*, symphysis of mandible; the lateral temporal vacuity indicated, but the supratemporal vacuity omitted in the figure. (After Marsh.)

limb is large, though very feeble. The pubic bones are fused at their symphysis. The femur is much shorter than the tibia, considerably curved, with a slender neck set at only a slight angle with the shaft, a nearly spherical head, and a small trochanter. The tibia has no conspicuous cnemial crest. There are two or three elements in the tarsus, and the fifth digit is rudimentary or absent. The typical species is *Pteranodon longiceps* (fig. 140), with skull 0·76 m. in length; *P. ingens* is still larger. These and other forms are represented by large portions of skeletons from the Chalk of Kansas.

Isolated bones, mostly in a very imperfect state, represent *Pteranodon* and its allies in the Cambridge Greensand and other European Cretaceous formations. Some specimens show the characteristic articulation of the scapula with the spines of the fused anterior dorsal vertebræ. Some exhibit formidable teeth (*Ornithochirus*), others appear to have been toothless (*Ornithostoma*).

CLASS AVES.

Sub-Classes.	*Orders.*	*Sub-Orders.*
1. **Archæornithes.**	1. Saururæ.	
2. **Neornithes.**	1. Ratitæ	1. Odontolcæ.
		2. Æpyornithes.
		3. Apteryges.
		4. Immanes.
		5. Megistanes.
		6. Rheæ.
		7. Struthiones.
	2. Carinatæ	1. Odontormæ.
		2. Impennes.
		3. Pygopodes.
		4. Tubinares.
		&c. &c.

The earliest known birds exhibit a distinct approach to the Reptilia in several characters, but do not afford any indication as to the particular group from which they evolved. The general opinion is, that they are more closely related to certain Dinosauria than to any other forms hitherto discovered. The facts at present known merely show, that birds had already become differentiated and acquired the characteristic covering of feathers before the tail atrophied and the pelvis fully developed; that the vertebræ next began to acquire their saddle-shaped articulations; and that after this the teeth were habitually lost, at least in the adult. There is also reason to believe that the Ratite and Carinate birds were already differentiated before the vertebræ and beak had assumed the characters now universal in the Class. This evolution, however, was almost, if not quite completed during the latter part of the Cretaceous period; and the known Mesozoic birds are still so few, that the stages in the process are as yet only very imperfectly traceable.

Sub-Class 1. **Archæornithes.**

ORDER 1. SAURURÆ.

The primitive "lizard-tailed" birds are only definitely known by two fine examples of one genus (*Archæopteryx*) from the Upper Jurassic of Bavaria. They are preserved in slabs of Lithographic Stone, which is capable of retaining the most delicate impressions and thus displays even the feathers.

FIG. 141.

Archæopteryx macrura; skull and mandible, right lateral aspect, nat. size.—U. Jurassic (Lithographic Stone); Bavaria. (After Dames.)

Archæopteryx (figs. 141, 142). The skull is shaped like that of a typical bird, the brain-case being relatively large, its constituent elements fused together, and the quadrate apparently free. Sclerotic plates are observable. There is a regular series of conical teeth, these probably fixed in distinct sockets. The vertebral column comprises about 50 vertebræ, of which 10 or 11 belong to the neck, 11 or 12 to the dorsal region, 2 to the lumbar region, 6 or 7 to the sacrum, and about 20 to the tail. The vertebral centra seem to have been either amphicœlous or with flat ends. The ribs are very slender, free in the cervical region, and not bearing ossified uncinate processes in the thoracic region. The sternum is not satisfactorily known, but the U-shaped furcula resembles that of modern Carinate birds. The wing is relatively small, and exhibits three digits (nos. I to III), each terminating in a claw; the phalangeal formula is 2, 3, 4. It is not quite certain whether the metacarpals were fused together, and the carpus is still too imperfectly known for discussion. In the pelvis, the ilium is considerably extended forwards and backwards, while the acetabulum is perforate; the sutures between the elements were probably persistent. The hind limb is essentially avian, only remarkable for the unusually small development of the cnemial crest on the tibia. The metatarsals are fused together, and there are four clawed digits (nos. I to IV) with the phalangeal formula 2, 3, 4, 5. Slender abdominal ribs are observable in the ventral wall of the body-cavity. The impressions of feathers seem to prove that there are seven primary and ten secondary remiges in the wing, while these are distinctly overlain with coverts; the quill-feathers of the tail are arranged in pairs, one apparently for each vertebra. Contour feathers are also recognisable on the neck, perhaps also round the tibia. All the known remains of this bird have been obtained from the Lithographic Stone (Lower Kimmeridgian) of Bavaria. The name *Archæopteryx lithographica* was originally given to a detached feather. A nearly complete skeleton, wanting the head, now in the British Museum, is described as *Archæopteryx macrura;* and a still more nearly complete skeleton, with the head, now in the Berlin Museum, is named *Archæopteryx siemensi*, apparently showing several differences in the proportions of the bones. These specimens are about as large as an ordinary rook.

FIG. 142.

Archæopteryx macrura; restoration by W. P. Pycraft, about one-quarter nat. size.—U. Jurassic (Lithographic Stone); Bavaria. The tail appears pointed because foreshortened in the drawing.

Sub-Class 2. **Neornithes.**

ORDER 1. RATITÆ.

A study of the structure of the wing in the existing Ratite (raft-breasted) birds, suggests that they are all descended from families which once had the power of flight; and there are many reasons for believing that their ancestors were already differentiated into several well-marked groups before the gradual loss of functional wings commenced. These ancestors, however, must have represented a lower grade in avian evolution than the vast majority of existing Carinatæ, as indicated by such characters as those of the palate and quadrate bone. Except in the highly modified Ostrich (*Struthio*), the vomer is always broad behind, where interposed between the pterygoids, palatines, and basisphenoidal rostrum. The basipterygoid processes are large and functional. The proximal articular end of the quadrate is undivided. The characters of the pectoral arch seem to be the result of the degeneration of the wings. The long axes of the fused scapula and coracoid are thus placed approximately in the same line; the furcula is incomplete or wanting; and the sternum is invariably destitute of all traces of a keel.

Sub-Order 1. *Odontolcæ.*

All the known Tertiary Ratites are running birds, not adapted for swimming; but one Upper Cretaceous family seems to represent a less-specialized group of this order which must have been of aquatic habits. These are primitive birds in which (so far as the skeleton is concerned) Ratite characters appear to predominate, though many close resemblances are observed to certain modern Carinates, such as *Colymbus*. They may, indeed, be regarded as an early specialized offshoot from the common ancestral type of the two great surviving orders. They are conveniently grouped together in a division named ODONTOLCÆ, in allusion to their possession of teeth in grooves. Their vertebræ resemble those of modern birds, but the vomer is perhaps more primitive than usual in that it is subdivided into right and left halves in the only satisfactorily known genus.

Hesperornis (fig. 143). This bird is known by nearly complete skeletons. The snout is much elongated, and the premaxillæ are forked considerably in their hinder portion. The cranial bones are fused together, and exhibit deep supraorbital pits. Casts of the brain-cavity prove it to have been small, and the cerebral hemispheres must have been very little developed. The relations of the vomer are not quite clear, but it is

FIG. 143.

Hesperornis regalis; skeleton, one-eighth nat. size.—U. Cretaceous; Kansas. (After Marsh.)

certainly a paired element. The proximal articulation of the single-headed quadrate exhibits a slight division into two facettes of unequal size. There are teeth in both jaws, all arranged in continuous grooves; those of the mandible extending to the anterior end, but those of the upper jaw confined to the maxillæ. The sutures between the beak and frontal region are persistent, as also are those between the several elements of the mandible and at the mandibular symphysis. The mandibular ramus extends into a considerable process behind its articular facette. There are 23 presacral vertebræ, with centra united by saddle-shaped articulations like those of modern birds. Seventeen of these vertebræ are cervicals, and the last three bear ribs; all the thoracic ribs exhibit large uncinate processes, and the first four pairs are connected with the sternum, while the two hindermost pairs are free, long and slender. Fourteen vertebræ are fused together in the much-extended sacrum, and there are twelve caudals, of which the first eight or nine are quite free. The sternum is relatively broad, though elongated and flattened, and destitute of a keel. The coracoid is short and very broad, its long axis continuing that of the free elongated scapula in a gentle curve. The very slender clavicles appear to meet in the middle line without fusion. Of the wing, only the much reduced humerus is known, but this bears articular facettes for the radius and ulna which must have been present. The hind limbs are adapted for swimming, much like those of the modern Colymbidæ. The elements of the pelvis are fused together, but the ischium and pubis are very slender and quite free at their distal end; the pectineal process is conspicuous; and the acetabulum exhibits a much smaller perforation than is usual in birds. The ilium is anchylosed with the sacrum only in the acetabular region. The femur is remarkably short and stout, and flattened antero-posteriorly. It is not pneumatic, but exhibits a medullary cavity. The tibio-tarsus is the largest bone in the skeleton, very long and powerful. It is also hollowed by a medullary cavity. The patella is very large, and separate from the tibio-tarsus. There are the usual four digits in the foot, the metatarsals of the second, third and fourth being firmly fused together in the tarso-metatarsus. The fourth, or outer toe, is much the largest. One specimen shows traces of feathers, which are believed to have been plumulaceous over the whole body, extending even over the tarsus. The genus *Hesperornis* is known only from the Chalk of Kansas, and the typical species, *H. regalis*, seems to have attained a height of about a metre when standing.

Fragmentary bones which seem to represent a bird (*Enaliornis*) closely allied to *Hesperornis*, occur in the Cambridge Greensand, but the pectoral arch and wing still remain unknown.

Sub-Order 2. *Æpyornithes.*

The palæontology of the ordinary Ratite birds is chiefly of interest as demonstrating the much wider geographical range of the order in late Tertiary times than at present. It also reveals certain extinct genera, which can scarcely be claimed as more primitive than their modern representatives but add considerably to the known modifications of which the Ratitæ are capable. Among the most important of these may be mentioned the ÆPYORNITHES, of which the bones and egg-shells occur abundantly in the superficial deposits of Madagascar. These birds are as yet only imperfectly known, but seem to be most closely related to *Apteryx* and the extinct Dinornithidæ of New Zealand.

Æpyornis. In this, the typical genus, the skull is relatively small, as usual in the Ratitæ, and the single-headed quadrate has been observed. The large basipterygoid processes are especially conspicuous, and there is an open eustachian groove (as in *Dinornis*). A number of large pits on the top of the skull seem to indicate an enlarged frontal crest of feathers. The sternum is remarkably short and wide, much like that of *Apteryx*. The grooves for the reception of the coracoids are well developed. The coracoid and scapula are fused together, and resemble those of *Casuarius* more than those of any other known genus. There is a distinct glenoid cavity for the humerus, which is short and much reduced. The remainder of the wing is not definitely known; but it is very probable that a terminal bone represents the radius, ulna, and manus fused together. The leg-bones are very massive. The femur exhibits pneumatic foramina, and the tibio-tarsus is destitute of a bony bridge over the groove for the extensor tendons. There is no intercondylar tuberosity in the tarso-metatarsus. There are four digits in the pes, except possibly in rare instances, where the hallux may be absent. *Æpyornis maximus*, the type species, is of gigantic dimensions; but *Æ. titan* is still larger, the length of the femur being 0·415 m., that of the tibio-tarsus no less than 0·8 m.

Mullerornis comprises smaller birds of slighter build, with the frontal bones raised into a small prominence. Their skull is Casuarine in several features.

Sub-Order 3. *Apteryges.*

The *Apteryx* of New Zealand is not known to have any extinct allies, except closely similar birds represented by scattered bones in the superficial deposits of the same country.

Sub-Order 4. *Immanes.*

The extinct "Moas" (**Dinornithidæ**) survived in New Zealand until comparatively modern times and were regularly hunted by the Maories. They are, however, known only from accidentally dried "mummies" occasionally found in fissures or caves, and from bones and egg-shells met with abundantly both in superficial deposits (especially swamps) and in the refuse heaps at the cooking places of the old natives. No remains hitherto discovered seem to date back beyond the Pleistocene period, except perhaps a few very fragmentary bones from beneath a lava-stream near Timaru, which may be Pliocene. The birds represented belong to a very large number of forms; but so many isolated and theoretically-grouped bones have received desultory names, that their taxonomy is in almost complete confusion. Several genera are certainly represented, but it is still impossible to assign definite limits either to the genera or species. The Moas seem to have lived under the conditions most favourable for endless variation; for they were a herbivorous race apparently well supplied with food and without the check due to the presence of carnivorous animals preying upon them. In all the genera the wings are extremely rudimentary or entirely wanting; the femur is usually destitute of pneumatic foramina; the tibio-tarsus exhibits a bony bridge over the groove for the extensor tendons; while digits II to IV are always present, and no. I (the hallux) sometimes occurs. The beak is short and slightly deflected. The only known feathers bear a large aftershaft, thus differing from those of the New Zealand *Apteryx*, and resembling the feathers of the Emeus and Cassowaries.

Dinornis (fig. 144 B). This is the typical genus of the Dinornithidæ and comprises the largest known species. In the skull the occipital plane is inclined forwards, and the occipital crest is usually indistinct; the temporal fossæ are large. The beak is relatively wide, though pointed. The quadrate is antero-posteriorly extended, and with a very large pneumatic foramen. The vertebræ are nearly 60 in number, one-third of which are cervical, and another third included in the sacrum. The sternum is about as long as broad and very convex, with small coracoidal facettes, three costal facettes on each side, the lateral processes widely divergent, and a xiphisternal notch. The scapular arch is reduced to a long and slender scapulo-coracoid bone on each side, destitute of a glenoid cavity for the humerus. The pelvis is narrow, with elevated ilium, and a slight pectineal process on the pubis. The femur is comparatively long and slender, with a short neck; it exhibits a medullary cavity with very thick walls. The tibio-tarsus and tarso-metatarsus are also long and slender, the length of the latter at least equalling that of the femur and exceeding half that of the tibio-tarsus. The hallux is either rudimentary or absent. The typical species is *Dinornis novæ-zealandiæ* or

FIG. 144.

A. *Pachyornis elephantopus;* skeleton, restored from more than one individual, with too few cervical vertebræ, about one-eighteenth nat. size.—Pleistocene; New Zealand. (After Owen.)

B. *Dinornis giganteus;* right hind limb, anterior aspect, about one-twentieth nat. size.—Pleistocene; New Zealand. (After Owen.)

D. giganteus, as yet only imperfectly known; *D. maximus* is larger and better known, the tibio-tarsus being nearly a metre in length, and the total height of the bird over 3·5 metres.

Pachyornis (fig. 144 A). A genus comprising smaller but much stouter species. In the skull the occipital plane is vertical or slightly inclined backwards, and the occipital crest is prominent; the temporal fossæ are large. The beak is relatively wide, though pointed. The sternum is short, broad, and flattened, with no coracoidal facettes, only two costal facettes on each side, the lateral processes broad and very widely divergent, and a relatively small xiphisternal notch. The pelvis is remarkably low and broad, and the pectineal process is wanting. The hind limbs are extremely massive, and the tibio-tarsus relatively short. No evidence of a hallux has been observed. The typical species is *Pachyornis elephantopus.*

Anomalopteryx. Small birds of comparatively slender build. The skull is narrow and elevated, with a sharply pointed beak; the pneumatic foramen in the quadrate is small. The sternum is much longer than broad, moderately flattened, with little or no coracoidal facettes, three costal facettes on each side, and a pair of long, slender, lateral processes. The pelvis much resembles that of *Pachyornis*, but the hind-limbs are not very massive. The tarso-metatarsus is shorter than the femur, and scarcely half as long as the tibio-tarsus. A hallux is present. The typical species is *Anomalopteryx didiformis. A. parva* is the smallest known member of the Dinornithidæ, the species being founded on a nearly complete skeleton scarcely a metre in height.

Other genera commonly recognized among the Dinornithidæ of New Zealand, are named *Emeus, Megalapteryx,* and *Mesopteryx.* There is no certain evidence of the occurrence of the family in Australia or elsewhere.

Sub-Order 5. *Megistanes.*

Palæontology adds nothing to our knowledge of the distribution of the Emeus and Cassowaries. An extinct emeu (*Dromornis*) is known by fragmentary remains from the superficial deposits of eastern Australia.

Sub-Order 6. *Rheæ.*

Remains of the Rheas are likewise known only from the superficial deposits of South America, where these birds still exist.

Sub-Order 7. *Struthiones.*

The only Ratite birds whose range at the present day extends to the northern hemisphere are the Ostriches or STRUTHIONES. They are represented by a single genus, *Struthio*, in Africa and Arabia; but a two-toed bird not yet generically distinguished from this occurs in the Lower Pliocene of the Siwalik Hills, India, and in that of the Island of Samos, in the Turkish archipelago.

RATITÆ INCERTÆ SEDIS.

There is some reason to believe that other Ratites, of an extinct primitive type, ranged into the northern hemisphere both in Europe and in America during the early Tertiary period. *Gastornis*, at least, from the Lower Eocene of western Europe, is generally regarded as a bird of this kind, with the pectoral arch less modified than that of the later genera. *Dasornis* may have been another Ratite, but is only known by one imperfect cranium from the London Clay of Sheppey; while *Diatryma*, represented by a tarso-metatarsus from the Eocene of New Mexico, may represent the order in North America.

Gastornis. The best-known species of this genus (*G. edwardsi*) is represented by fragments of the head, cervical and caudal vertebræ, portions of ribs, the furcula, coracoid, humerus, radius, metacarpus, ischium, pubis, femur, tibia, tarso-metatarsus, and phalanges. The skull is relatively large, and the sutures between its elements are unusually persistent. The premaxillæ bear a pair of rounded bosses of bone, each of which may possibly have supported a tooth, though this remains uncertain. The mandible exhibits a conspicuous post-articular process. The caudal vertebræ are small and cannot have borne more than a very small pygostyle. The clavicles are fused into a furcula, and the coracoids are much more slender than usual in the Ratitæ. The sternum is known only by fragments of the lateral margin. The humerus is large and with well-formed distal condyles; the elements of the metacarpus do not appear to have been fused together. The pelvis seems to have had a relatively short postacetabular portion; and the distal end of the ischium is expanded upwards towards the hinder portion of the ilium. The great trochanter of the femur does not rise above the level of its head. The tibio-tarsus exhibits a bony bridge over the groove for the extensor tendons. The tarso-metatarsus is long and slender, with the fourth trochlea slightly longer than the second, and a large perforation in the groove between the third and fourth trochlea. The typical species is *Gastornis parisiensis*, founded on a tibio-tarsus about 0·5 m. in length from the Lower Eocene (Argile Plastique) of Meudon, near Paris; a femur and other fragments from the Paris basin are ascribed to it. Similar portions of the hind limb from the Woolwich and Reading Beds, near Croydon, Surrey, are named *G. klaasseni*. The *G. edwardsi*, already referred to, occurs in corresponding beds near Rheims, France, and at Mesvin, near Mons, Belgium.

ORDER 2. CARINATÆ.

The earliest distinctly carinate birds of which there is as yet any precise information are the toothed genera, *Ichthyornis* and *Apatornis*, from the Upper Cretaceous of North America. They constitute the extinct

Sub-Order 1. *Odontormæ.*

The teeth are fixed in distinct sockets, hence the name ODONTORMÆ. The mandibular rami are not anchylosed at the symphysis; and the vertebræ are all amphicœlous (biconcave).

Ichthyornis (fig. 145). This is a small bird, known by imperfect skeletons. The bones are delicate and more or less pneumatic. The cranial bones are fused together, and the brain is relatively small. The snout is elongated, and the premaxillæ seem to have been toothless; but teeth occur in distinct sockets in the maxilla and throughout the whole length of the dentary bone. These teeth are laterally compressed, and have vertical successors. Though the symphysial suture remains open, the elements of the mandibular ramus are almost completely fused together. The quadrate bone is remarkable in exhibiting only a single facette for articulation with the skull. The number of cervical vertebræ is uncertain, but the third is interesting as showing a passage between the biconcave and saddle-shaped form. There are six or seven dorsals, ten vertebræ comprised in the sacrum, five free caudals, and a small, though typical pygostyle. The clavicles are unknown, but the remainder of the pectoral arch is proved to be like that of a normal bird of flight, and the wing is well-formed, the humerus bearing an enormous pectoral crest. The pelvis is relatively small, and all its elements are fused together. There is a moderately large acetabular perforation, while both ischium and pubis are free at their distal end. The femur is long and slender, the tibio-tarsus still longer, without a bridge over the groove for the extensor tendons; the completely formed tarso-metatarsus is short, and the fibula much reduced. *Ichthyornis* has hitherto been found only in the Cretaceous of Kansas, and perhaps of Texas, U.S.A., the typical species being *I. dispar*, and a better-known form, *I. victor* (fig. 145). None would be more than 0·3 m. in height when standing erect.

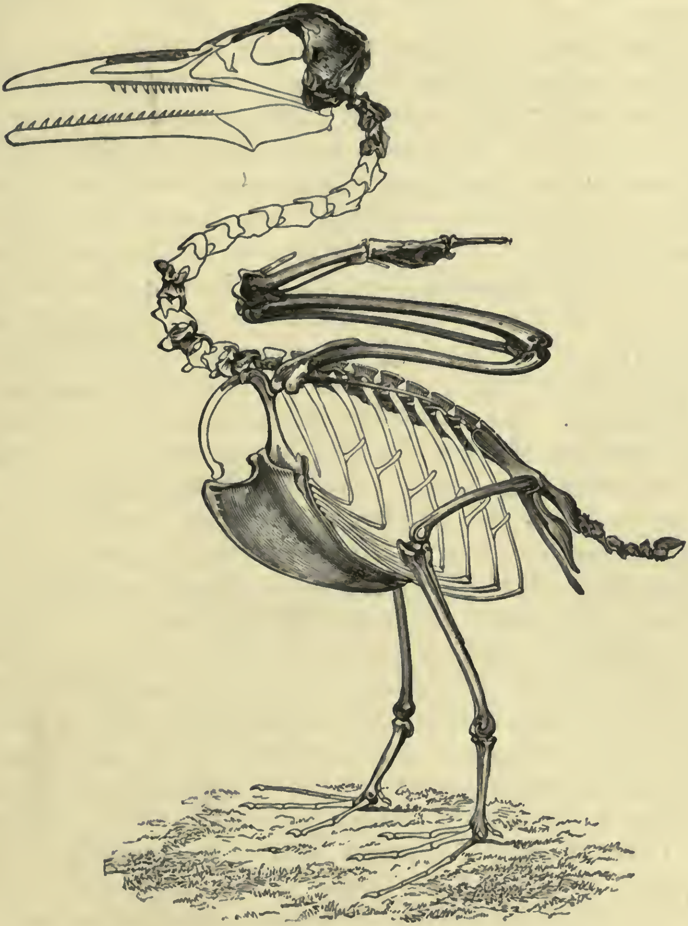

Fig. 145.

Ichthyornis victor; restored skeleton, one-half nat. size.—U. Cretaceous; Kansas. (After Marsh.)

Modern Carinate Birds.

The extinct representatives of the modern carinate birds are too imperfectly known to be noticed here in detail. Many early Tertiary forms are certainly annectent types, and the past distribution of several sub-orders differs much from that of the present day. It will suffice, however, to mention a few salient points.

The Impennes (Penguins) are known by fossils only in the southern regions they still inhabit, and these afford no information concerning their ancestry. The Albatrosses (*Diomedea*) were more widely distributed in the Pliocene period than at present, the tarso-metatarsus of an extinct species having been found in the Red Crag of Suffolk. The extinct Rails of New Zealand (*Aptornis*), the Chatham Islands (*Diaphorapteryx*), and Mauritius (*Aphanapteryx*), are of much interest on account of their close affinities to each other and to the living *Ocydromus* of New Zealand. Gigantic extinct raptorial birds which may be related to the Cariamas (*Phororhachos*) occur in Tertiary strata in Patagonia. The remarkable Gallinaceous bird, the Hoatzin (*Opisthocomus*) of South America, is represented by a closely similar genus (*Filholornis*) in the Upper Eocene (Phosphorites) of southern France. The Dodo (*Didus*) and Solitaire (*Pezophaps*) are large extinct ground-pigeons, whose remains occur in the surface deposits of Mauritius and Rodriguez respectively. A generalized Flamingo (*Palælodus*) is very common in the Miocene of Allier, France. A fish-eating bird apparently related to the Gannet (*Sula*) is represented by an imperfect skull from the London Clay (Lower Eocene) of Sheppey, Kent. This is named *Odontopteryx toliapica,* and is remarkable for the denticulation of the jaw, pointed bony processes (not teeth) rising into what were no doubt similar processes of the horny beak. A second skull from Sheppey (*Argillornis longipennis*) seems to belong to the same group, but is too imperfect to show the precise character of the jaws. A Secretary Vulture with somewhat stouter limbs than the South African form, occurs in the Miocene of Allier (*Serpentarius robustus*); and there seems to be an ancestral Trogon (*Archæotrogon*) in the Upper Eocene of southern France. A parrot (*Psittacus veneauxi*) rather smaller than the Grey Parrot, is also recorded from Allier.

CLASS MAMMALIA.

Sub-Classes.	*Orders.*	*Sub-Orders.*
1. **Prototheria.**	1. Multituberculata.	
	2. Monotremata.	
2. **Metatheria.**	Marsupialia.	1. Polyprotodontia.
		2. Diprotodontia.
3. **Eutheria.**	1. Cetacea.	1. Archæoceti.
		2. Odontoceti.
		3. Mystacoceti.
	2. Sirenia.	
	3. Edentata.	
	4. Ungulata.	1. Condylarthra.
		2. Hyracoidea.
		3. Amblypoda.
		4. Proboscidea.
		5. Ancylopoda.
		6. Typotheria.
		7. Toxodontia.
		8. Litopterna.
		9. Perissodactyla.
		10. Artiodactyla.
	5. Rodentia.	1. Tillodontia.
		2. Duplicidentata.
		3. Simplicidentata.
	6. Carnivora.	1. Creodonta.
		2. Carnivora Vera.
		3. Pinnipedia.
	7. Insectivora.	1. Insectivora Vera.
		2. Dermoptera.
	8. Chiroptera.	1. Megachiroptera.
		2. Microchiroptera.
	9. Primates.	1. Lemuroidea.
		2. Anthropoidea.

It is as yet impossible to determine at what particular stage in the evolution of the vertebrate skeleton the lung-breathers first acquired the characteristic mammalian circulatory system, the milk-producing glands, and a dermal covering of hair. It is, however, clear that as soon as warm-blooded quadrupeds were evolved the skeleton began to assume characters and potentialities such as it had not exhibited before, and an entirely new series of modifications became possible. In the first place there was a simplification in the structure of the skull. The postfrontal and prefrontal bones quickly disappeared, probably by fusion with the frontals. The elements of the single temporal arcade invariably became reduced by fusion to two, a jugal in front, a squamosal behind; and Palæontology seems to demonstrate (through the Anomodontia) that the quadrate element, so characteristic of the lower vertebrates, is included in the articular end of the hinder bone. The mandible is also simplified, so that there is only one membrane-bone in each ramus ensheathing the meckelian cartilage, which is ossified and firmly united with its sheath at the articular end. The well-formed limb-bones, adapted for support of the trunk, exhibit a constant development of terminal epiphyses, already noted in a less perfected degree in the Batrachia and in the Sauropterygian and Chelonian reptiles; while this mode of ossification has also extended to the centra of the vertebræ. In the pectoral arch the coracoidal element soon disappears as an insignificant process of the scapula. In the pelvic arch the three bones of each side are always fused into an "innominate bone" pierced by an obturator foramen. Except in the Cetacea and rarely in certain Sirenia, the number of phalanges in the digits is never multiplied beyond 2, 3, 3, 3, 3, however long those digits may become; and the ankle-joint occurs invariably between the distal end of the crus and the tarsus, never between the two rows of tarsal bones.

This phase in the development of the vertebrate skeleton was already very closely approached, if indeed not absolutely attained, at the dawn of the Mesozoic period. It is exhibited almost in its entirety by certain of the Anomodont reptiles (especially the Theriodontia) in the Permian and Triassic ages;

and if these are not the direct ancestors of the warm-blooded quadrupeds termed mammals, they must at least be extremely close allies of those ancestral forms. Unfortunately, however, no fossils of this character have hitherto been found in Mesozoic strata of later date than the Trias in any part of the world. It is thus still impossible to trace the evolution upwards to the base of the Cainozoic or Tertiary strata, in which typical and well-preserved mammalian skeletons occur in abundance. The only mammalian fossils hitherto discovered in the Jurassic and Cretaceous rocks are merely fragments of a most unsatisfactory nature. They represent tribes of dwarfed animals not larger than rats, some probably related to the existing monotremes, others to the marsupials, none clearly belonging to the highest mammalian type (that of the Eutheria) or linking this with the grades below.

It seems, however, certain that most of the Mesozoic Mammalia, if not all, were of the primitive types which at the present day are either oviparous (Prototherian or Ornithodelphian) or non-placental (Metatherian or Didelphian); for nearly all the earliest Tertiary skeletons exhibit some features now peculiar to the latter, and these fossils undoubtedly represent the generalized forerunners of the typical placental mammals (Eutheria) which are dominant throughout the Tertiary period. The gradual evolution of the principal Eutherian orders and their smaller divisions can be traced by comparing the skeletons from the successive Tertiary formations; and it will be noticed that the chief modifications occur in the limbs and teeth, the parts by which they are brought into most intimate relationship with their environment. They seem to have inherited a generalized, plantigrade, five-fingered hand and foot from their cold-blooded ancestors, and these extremities soon undergo strange modifications never observed in any type below the mammalian. They are also assumed to have inherited simple conical or triconodont teeth (though there is as yet no demonstration of this), and these teeth immediately become complicated in various ways, apparently in accordance with certain well-defined laws of folding and cusp-development.

Sub-Class 1. **Prototheria.**

There are two chief difficulties in recognizing the remains of the extinct Prototherian mammals. Firstly, all the suspected known specimens are extremely fragmentary. Secondly, the extinct forms already indicated by these fossils seem to be highly specialized in one direction, while the few surviving representatives of the sub-class are still more highly specialized in another direction. Two little toothless burrowing animals like the *Ornithorhynchus* and *Echidna*, can only afford a very inadequate conception of the great group to which they belong; while the isolated jaws, teeth, and limb-bones hitherto found fossil are still less satisfactory for the purpose. However, there is a remarkable resemblance between the early-shed teeth of the immature *Ornithorhynchus* and the "multituberculate" (or "polybunous") molars in certain jaws found in Mesozoic and Lower Eocene strata. There is thus some justification for placing these fossils in a special group or order, variously named MULTITUBERCULATA or ALLOTHERIA, which may be assigned at least provisionally to the Prototherian sub-class.

ORDER 1. MULTITUBERCULATA.

Even now it is impossible to determine how many of the earliest remains of this character met with in Rhætic and Triassic rocks belong to the Anomodont reptiles. There is not much doubt that *Tritylodon*, from the Karoo Formation of South Africa, is referable to the latter category (p. 154); and yet its tuberculated grinding teeth exhibit deeply cleft roots. There is also some reason to suspect that other double-rooted multituberculate teeth from the Rhætic of Europe, commonly claimed as mammalian, may be similarly interpreted. The latter, however, have hitherto only been found isolated and thus do not admit of satisfactory discussion. The known specimens are quite minute, and the crown presents a median depression with a tuberculated or simply crenulated rim, like the two hinder molars of *Ptilodus* (fig. 148 *c*). They are named *Microlestes*, and two forms are recognized, *M. antiquus*, from Würtemberg, and *M. moorei*, from Holwell, near Frome, Somersetshire. A detached incisor or canine of corresponding size has also been found in the latter locality.

The small multituberculate grinding teeth from the Stonesfield Slate (Bathonian) of Oxfordshire, named *Stereognathus ooliticus*, are perhaps placed among Mammalia with a little more certainty; but only one fragment of jaw is known containing three teeth. The dental crowns are provided with crescent-shaped tubercles arranged in three longitudinal series.

There is still less doubt about the mammalian nature of some upper and lower jaws of Upper Jurassic age, discovered both in Britain and North America, and characterized by multituberculate molars. These form the family **Plagiaulacidæ**, and the best-known specimens are described under the generic names of *Plagiaulax*, *Bolodon*, *Allodon* (fig. 147 G), and *Ctenacodon*. Except two detached teeth from the Wealden, all the known British specimens have been obtained from the Middle Purbeck of Swanage, Dorsetshire, nearly all from a bed of marl only a few inches in thickness.

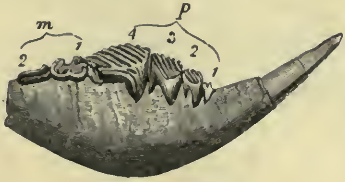

FIG. 146.

Plagiaulax minor; right mandibular ramus wanting hinder end, outer aspect, four times nat. size.—U. Jurassic (M. Purbeck Beds); Swanage, Dorsetshire. *m*, molars; *p*, premolars; the large tooth in front an incisor. (After Falconer.)

Plagiaulax (fig. 146). A genus known only by mandibular rami which meet in a loose suture at the symphysis. The mandible is short, with a high coronoid process and a low articular condyle not above the level of the dentition. The condyle is convex and much deeper than broad. The postero-inferior angle of the jaw is inflected. There is a single pair of enlarged closely apposed incisors at the symphysis, apparently not persistently growing, and without any specially thickened band of enamel on the anterior face. Then follows a diastema without any trace of a canine. Next are three or four closely arranged cutting teeth, gradually increasing in size to the fourth, which is very large, and all marked with oblique

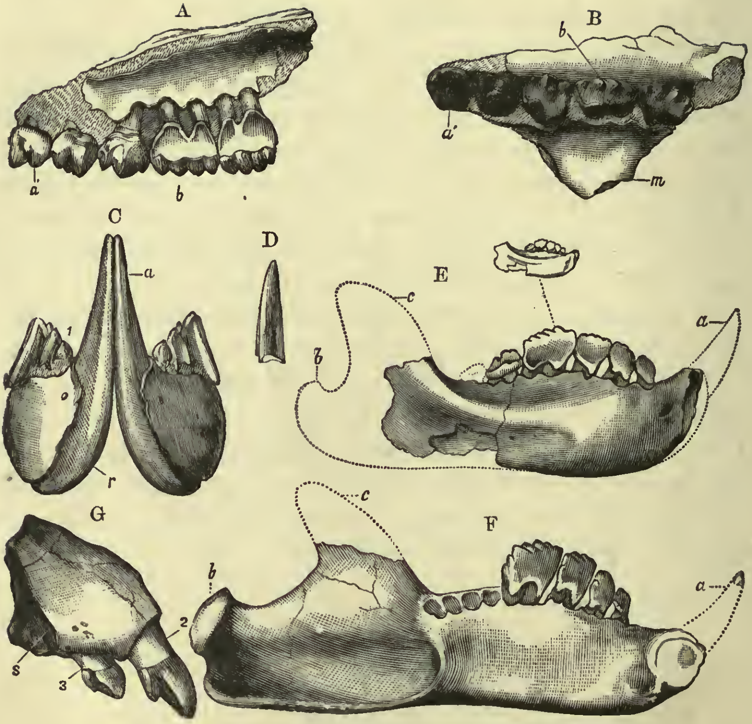

Fig. 147.

Jaws and Teeth of American Upper Jurassic Multituberculata. (After Marsh.)

A, B. *Ctenacodon potens;* right upper jaw, from the inner (A) and oral (B) aspects, four times nat. size. *a′*, first premolar; *b*, fourth premolar; *m*, base of zygomatic arch.

C. *Ctenacodon potens;* mandibular symphysis, anterior aspect, three times nat. size. *a*, incisor; *r*, root of incisor; 1, first premolar.

D. *Ctenacodon serratus* (?); incisor, anterior aspect, four times nat. size.

E. *Ctenacodon serratus;* right mandibular ramus, outer aspect, the small outline nat. size, the drawing four times nat. size. *a*, incisor; *b*, condyle; *c*, coronoid process.

F. *Ctenacodon serratus;* left mandibular ramus, inner aspect, three times nat. size. *a*, incisor; *b*, condyle; *c*, coronoid process.

G. *Allodon fortis;* right premaxilla, outer aspect, three times nat. size. *s*, suture for maxilla; 2, 3, second and third incisors.

ridges on the outer face (hence the name *Plagiaulacodon*, abbreviated to *Plagiaulax*). Nothing is known of the mode of succession, but these teeth are termed premolars. Finally, there are two relatively small molars, of which the crown is hollowed in the middle and bears tubercles round the edge. The typical species is *P. becklesi*, from the Middle Purbeck beds of Durdlestone Bay, Swanage, with mandible attaining a length of not more than 0·03 m.

Bolodon. An upper jaw from the same stratum and locality as *Plagiaulax*, and quite possibly referable to this genus. The premaxilla is short and bears at least two incisors, both a little notched and the first about twice as large as the second. There is a short diastema at the anterior end of the maxilla. Then follow three premolariform teeth, each apparently tritubercular; and finally there seem to have been four molars, all bearing a double antero-posterior series of tubercles.

Ctenacodon (fig. 147). Mandible as in *Plagiaulax*, but the four premolars smooth on the outer face, only notched at the cutting edge. An imperfect maxilla ascribed to this genus on evidence not stated (fig. 147 A, B) exhibits teeth much like those of *Bolodon*. The known species are as small as those of *Plagiaulax*, and occur in the Upper Jurassic of Wyoming, U.S.A.

Fig. 148.

Ptilodus mediævus; imperfect left mandibular ramus, from the outer (*a*) and inner (*b*) aspects, nat. size, and from the oral aspect (*c*) $\frac{2}{3}$ nat. size.—L. Eocene (U. Puerco); New Mexico. (After Cope.)

Detached teeth and fragments of jaws apparently identical with those of the Plagiaulacidæ have also been found in the uppermost Cretaceous (Laramie Formation) of Wyoming. Only the third and fourth premolars have been observed in the lower jaw, while the third is relatively small with a single root. It is also noteworthy that the large fourth premolar is often very low, its summit being elevated but little above the true molars behind it.

The family does not appear to have become extinct either in Europe or North America until early Tertiary times, for at least one genus (*Neoplagiaulax*) occurs in the Lower Eocene of Rheims, France, and another (*Ptilodus*, fig. 148) in the Puerco Eocene of New Mexico. The mandible in these genera is of much interest because it exhibits the most extreme specialization of the teeth in the family. In the French genus only the fourth premolar remains, much enlarged, while in the American genus (fig. 148) the same is observable, with only an insignificant remnant of the third premolar. The two typical multitubercular molars are present in each.

Another family (**Polymastodontidæ**) is represented by many detached teeth in the Laramie Formation and by more satisfactory remains in the Puerco Eocene of the United States. These are somewhat larger animals, with teeth arranged on the rodent pattern, and the premolars are tubercular like the molars.

Polymastodon (fig. 149). The typical species of this genus, *P. taoensis*, is known by a fragmentary skeleton equal in size to that of a large kangaroo. There is a single pair of large incisors in both jaws, with a diastema behind, and then follow three flattened grinding teeth, the foremost relatively small and counted as a premolar. A minute pair of lateral incisors is also present in the upper jaw. The crowns of the lower molars bear two longitudinal series of stout tubercles, while those of the two upper molars opposed to them are furnished with three similar longitudinal series. The angle of the mandible is inflected, and the dental foramen is at the anterior apex of a large fossa, as in most marsupials. The form of the astragalus is believed to show that the inner digits of the pes were much reduced in size, and that the outer digits were large, constituting the principal agent in progression. The tail must have been long. Puerco Eocene, New Mexico.

It may be added that the bone-beds of the Laramie Formation, which have yielded so many teeth of the Multituberculata, have also furnished limb-bones, of which some present interesting features. The pelvic bones are not fused into an os innominatum, but remain suturally united. One scapula has an articular facette for a distinct coracoid; and a **T**-shaped interclavicle is known. The two latter bones have been theoretically associated with a calcaneum and astragalus, and the whole series named *Camptomus amplus*.

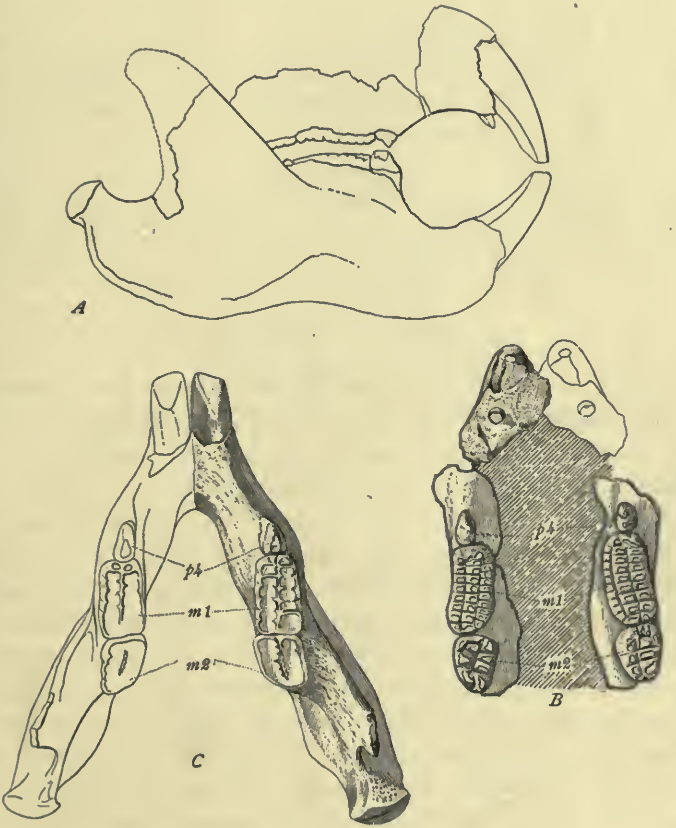

Fig. 149.

Jaws of *Polymastodon*, about one-half nat. size.—L. Eocene (Puerco); New Mexico. (After Osborn and Earle.)

A. *Polymastodon attenuatus;* outline side-view of upper and lower jaws.

B. *Polymastodon attenuatus;* upper dentition, oral aspect. *m* 1, *m* 2, first and second molars; *p* 4, fourth premolar.

C. *Polymastodon taoensis;* mandible, oral aspect. Same lettering.

ORDER 2. MONOTREMATA.

The only remains of extinct monotremes hitherto discovered are a few isolated limb-bones, one atlas vertebra, and one imperfect skull from the superficial deposits of Queensland and New South Wales. A gigantic humerus from the Pliocene of Gulgong, New South Wales, is named *Ornithorhynchus maximus.* A very small tibia and mandible, from the Pleistocene of Queensland, are described as *O. agilis.* The imperfect skull and atlas vertebra, from the Pliocene of Gulgong, are relatively very large and referred to *Echidna,* under the name of *Echidna* (*Proechidna*) *robusta.* *Echidna* (*Proechidna*) *oweni* is a species based on limb-bones of another very large form from the Pleistocene of the Wellington Caves, New South Wales.

Sub-Class 2. **Metatheria.**

There are many difficulties in interpreting the characters of the Metatherian mammals; and as Palæontology furnishes only skeletons for examination, it cannot contribute much towards the solution of the problems, which are chiefly connected with the organs of reproduction. Modern research, however, suggests that the marsupials, which are the sole surviving representatives of the Metatheria, are descended from mammals which possessed at least a rudimentary discoid allantoic placenta. If so, they have become non-placental by degeneration. It is therefore noteworthy that the earliest known complete mammalian skeletons from the Lower Eocene formations, which pass upwards by insensible gradations into undoubted Eutheria, are scarcely distinguishable from the skeletons of the more generalized existing marsupials (*e.g.*, *Thylacinus*). These ancestral types may thus have been essentially placental, and retained that character in their main line of development, while losing it in the less vigorous line which now survives only in the Australian region and tropical America. There are indeed marks of degeneration in the marsupial skeleton itself; for the lower vertebrates demonstrate clearly that the loss of successional teeth is to be interpreted as such, and no existing marsupial is known to have more than one of the teeth replaced (apparently the fourth or hindermost milk-molar), while sometimes there is no replacement whatever. Among the early Tertiary types just mentioned, this kind of degeneration is distinctly observable; for in some genera (see p. 381) all the teeth—the so-called milk-teeth—in front of the true molars are once shed and replaced by a second set, while in the so-called Sparassodonta from the Lower Tertiaries of Patagonia (p. 386), the dental series closely resembles that of the Australian Dasyuridæ in form, and not more than two or three teeth are replaced. These early Tertiary mammals, however, cannot have been the direct ancestors of the Order Marsupialia—they can only have been persistent survivors of that ancestry; for one known mandible of *Triconodon* from the Upper Jurassic (Purbeck Beds) of Dorsetshire exhibits the characteristic replacement of the last milk-molar alone, and, unless appearances are deceptive, the loss of successional teeth in the Metatherian mammals must thus have taken place at a remote time in the Mesozoic period.

ORDER 1. MARSUPIALIA.

From the foregoing considerations it is evident that the Marsupialia, as now known, are a highly specialized and modified order of their sub-class; and it is unfortunate that Palæontology teaches nothing concerning their immediate ancestors. The extinct representatives of the American types hitherto discovered are scarcely different from those still surviving; while nothing is known of the forerunners of the Australian types dating back further than quite the latest geological period in the region they still inhabit. It is thus not surprising that the division of this order into the two sub-orders of POLYPROTODONTIA and DIPROTODONTIA, as usually adopted, is not yet invalidated by the discovery of extinct forms.

Sub-Order 1. *Polyprotodontia.*

So far as can be judged from detached jaws, the majority of the Mesozoic mammalian remains hitherto found both in Britain and North America seem to be referable to this sub-order of marsupials; though some may perhaps belong to the Eutherian order of Insectivora, while the few "Diprotodonts," as already mentioned (p. 248), are more likely to have been related to the monotremes. Such remains are known only from two horizons in Britain, namely, from the Stonesfield Slate (Lower Jurassic) of Oxfordshire and the Middle Purbeck Beds (Upper Jurassic) of Dorsetshire; also only from two horizons in North America, namely, from the Upper Jurassic of Wyoming and the Laramie Formation (Upper Cretaceous) of Wyoming and Dakota. Two forms of mandible commonly placed here, *Dromatherium* and *Microconodon*, are indeed as old as the Trias; but these differ so much from those of later date that their systematic position is very uncertain, and they may belong to Anomodont reptiles (p. 144).

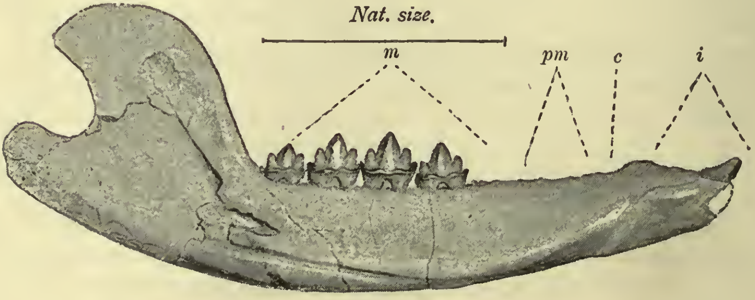

FIG. 150.

Phascolotherium bucklandi; left mandibular ramus, inner aspect, three times nat. size.—L. Jurassic (Stonesfield Slate); Oxford. *c*, position of canine; *i*, extent of incisor series; *m*, extent of molar series; *pm.*, extent of the two premolars. (After Goodrich.)

The Jurassic and Cretaceous jaws are placed among the polyprotodont marsupials because they exhibit so much resemblance to those of the existing *Myrmecobius* of Australia, while many of them are proved to have been characterized by the inflected angle. *Phascolotherium* and *Amphitherium* are the best-known examples from the Stonesfield Slate, in which a detached mammalian femur and a humerus have also been identified; *Triconodon* and *Spalacotherium* may be mentioned from the Purbeck Beds, in which a few additional limb-bones have been discovered; *Cimolestes* and other names have been given to detached teeth from the Laramie Formation.

Phascolotherium (fig. 150). Known only by three imperfect mandibular rami of *P. bucklandi* from the Stonesfield Slate, each exposed from the inner side. Mandibular dental formula:—i. 4, c. 1, pm. 2, m. 5. The incisors are slender and styliform, and the canine is nearly similar, though larger. Behind the canine is a short diastema, and then follow seven nearly similar teeth in continuous series, each with two roots. All these teeth exhibit a conspicuous basal ridge or cingulum, and the crown comprises one large central cone with a smaller cusp in front and behind. The coronoid process is enormous, and the articular condyle, on about the same level as the dentition, is borne by a slender pedicle. The lower border of the jaw towards the angle seems to have been much inflected. The type mandible measures only 0·035 m. in length.

Amphitherium. Four imperfect mandibular rami from the Stonesfield Slate are referred to this genus, three to the typical species *A. prevosti*, the fourth to a distinct species *A. oweni.* The largest measures only 0·025 m. in length. Though a little uncertain, the mandibular dental formula seems to have been thus:—i. 4, c. 1, pm. 5, m. 6. The incisors are small and styliform, and the canine appears to have had a double root. The molars are remarkably complex, of a tritubercular-sectorial type. The coronoid process is large, and the articular condyle is supported on a pedicle well above the level of the dentition. The angle of the mandible is slightly inflected. The mylohyoid groove is conspicuous.

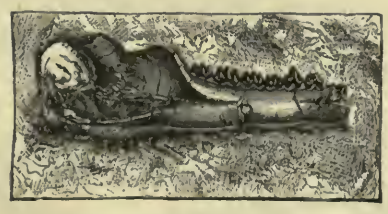

FIG. 151.

Triconodon mordax; right mandibular ramus, outer aspect, nat. size.—U. Jurassic (M. Purbeck Beds); Swanage, Dorsetshire. (After E. Willett.)

Triconodon (fig. 151). The best known of the Mesozoic Polyprotodonts, both the upper and lower dentition having been discovered. It is remarkable for the reduction in number of the molar teeth, and the simple character of the premolars as compared with the molars. The upper incisors are unknown, but there is a large upper canine with bifid root, and this is directly followed by four premolars and three or four true molars. The mandibular dental formula is as follows:—i. 3, c. 1, pm. 4,

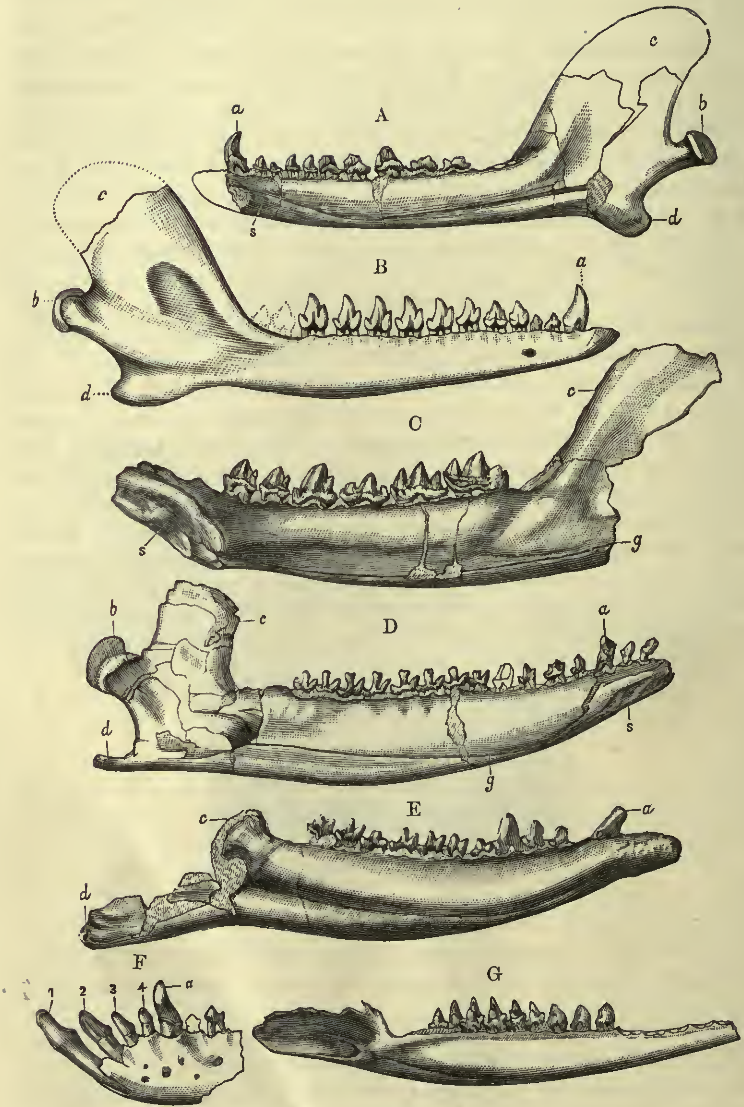

Fig. 152.

Fig. 152.

Lower Jaws of American Upper Jurassic Polyprotodont Mammals. (After Marsh.)

a, canine; *b*, condyle; *c*, coronoid process; *d*, angle; *g*, mylohyoid groove; *s*, symphysial surface.

A. *Docodon striatus;* right mandibular ramus, inner aspect, twice nat. size.

B. *Dicrocynodon victor;* right mandibular ramus, outer aspect, twice nat. size.

C. *Priacodon ferox;* right mandibular ramus, inner aspect, three times nat. size.

D. *Dryolestes priscus;* left mandibular ramus, inner aspect, three times nat. size.

E. *Dryolestes vorax;* left mandibular ramus, inner aspect, three times nat. size.

F. *Asthenodon segnis;* symphysial end of left mandibular ramus, outer aspect, showing incisors (1—4), three times nat. size.

G. *Laodon venustus;* left mandibular ramus, inner aspect, four times nat. size.

m. 3 or 4. The lower incisors are small and uniform, the crown pointed, a little recurved, and with a small posterior heel. The lower canine may have had a bifid root, but this is uncertain. The premolars and molars in both jaws exhibit a bifid root and a conspicuous cingulum, while the crown bears three cusps in one antero-posterior series, the three nearly equal in the true molars, the lateral ones much reduced in the premolars. One mandibular ramus, originally named *Triacanthodon*, shows the fourth deciduous tooth shaped like the true molars, with the fourth premolar beneath it ready to take its place. The coronoid process is large, and the articular condyle is not above the level of the dentition; the symphysis rises rather abruptly from the lower border, and there is a slight inflection of this border near the angle of the mandible. This is the commonest mammalian fossil in the Middle Purbeck Beds of Dorsetshire, and the mandible of the typical species, *Triconodon mordax*, measures 0·035 m. in length. The mandible named *T. major* would probably be as much as 0·06 m. in length. Very similar jaws occur in the Upper Jurassic of Wyoming (*Priacodon ferox*, fig. 152 c).

Spalacotherium. Definitely known only by slender mandibular rami from the Middle Purbeck Beds of Dorsetshire. Dental formula:—i. 3, c. 1, pm. 4, m. 6. The molars are tritubercular, there being one relatively large outer cusp, a pair of smaller inner cusps, and an inner cingulum. The coronoid process is very large, and the articular condyle of the mandible is placed well above the level of the dentition. The mylohyoid groove is conspicuous. The typical species is *S. tricuspidens*, with mandible about 0·03 m. in length. *Menacodon* is a related genus from the Upper Jurassic of Wyoming.

Before the close of the Cretaceous period, the typical American family of polyprotodont marsupials known as opossums or **Didelphyidæ**, appear to have established themselves at least in the northern half of the continent, for detached teeth almost indistinguishable from those of the existing *Didelphys* occur in the Laramie Formation of Wyoming (*Didelphops*). It is still more interesting to note, however, that the same animals also existed in Europe in considerable numbers during the early part of the Tertiary period, and did not become extinct here until the Miocene. The European jaws bear the generic name of *Peratherium* (or *Oxygomphius*), but they merely differ from those of *Didelphys* in the relative proportions of certain teeth, and are thus scarcely distinct. They occur in the Lower Eocene of Essex and in the Upper Eocene of Hampshire; in the Upper Eocene of Débruge and Quercy, in France; also in the Lower Miocene of the Auvergne, Rhenish Prussia, and Würtemberg. The well-known imperfect marsupial skeleton described by Cuvier from the Paris Gypsum (Upper Eocene) probably belongs to the same genus.

The **Dasyuridæ**, or typical carnivorous marsupials of the Australian region, are scarcely known among fossils, though a few remains are found in the superficial deposits of the country they now inhabit. These remains show that the "Tasmanian Devil" (*Thylacinus*), at present quite restricted to Tasmania, was represented by a still larger species on the Australian mainland in the Pleistocene period. Certain jaws discovered in the Santa Cruz Formation (supposed Miocene) of Patagonia, South America, are also curiously similar in aspect to those of the thylacine (see *Prothylacinus patagonicus*, p. 388, fig. 218).

Nothing is known of the ancestry of the **Peramelidæ**, or bandicoots, of Australia. Remains of existing genera are found in the Wellington Caves, New South Wales.

Myrmecobius is unknown among fossils.

Sub-Order 2. *Diprotodontia.*

The DIPROTODONTIA, or marsupials with a pair of enlarged lower incisors and atrophied canines, are all confined to the Australian region, except one or more aberrant families of dwarfed animals which have recently been discovered in South America. This assuming, of course, that the extinct Multituberculata (p. 248) are Prototherian rather than Metatherian mammals.

The aberrant South American groups, which seem to be comparatively primitive, are the **Epanorthidæ**, **Abderitidæ**, and their allies, chiefly represented by jaws in the Santa Cruz Formation (supposed Miocene) of Patagonia, but surviving in a genus of rat-shaped animals (*Cœnolestes*) known to occur in Ecuador and Colombia. *Epanorthus, Acdestis, Garzonia,* and *Abderites* are among the principal extinct genera.

Epanorthus. Known only by minute jaws and other fragments of the skull. Dental formula :—$\frac{\text{i. 3, c. 1, pm. 3, m. 4}}{\text{i. 1, c. 1, pm. 4, m. 4}}$. The upper incisors are relatively small and uniform; the canine is larger and strongly arched, separated by a diastema both from the incisors and the premolars; the foremost premolar is also isolated, with a simple conical crown; the remaining six teeth are in close series, the two premolars being conical and laterally compressed, the molars rapidly diminishing in size behind and losing the postero-internal quarter of the quadritubercular crown. Behind the two enlarged incisors of the lower jaw, exactly as in *Acdestis* (fig. 153), there are four nearly similar minute blunt teeth, each with a single root, which have been interpreted as a canine followed by three premolars. [These are suggestive of the teeth named *Stagodon* from the Laramie Formation of Wyoming, U.S.A.] The fourth premolar comes next with two roots and a laterally compressed conical crown. The true molars are more or less distinctly quadritubercular and quadrangular, and the first molar is much larger than the others, which decrease in size backwards. The palate exhibits two pairs of large vacuities, as in *Cœnolestes*. *Epanorthus aratœ* and other species occur in the Santa Cruz Formation of Patagonia.

Fig. 153.

Acdestis oweni; right mandibular ramus, wanting hinder end, outer aspect, about twice nat. size.—Santa Cruz Formation; Patagonia. (After Ameghino.)

Garzonia much resembles *Epanorthus*, but there is no conspicuous diastema between the teeth, and the lower premolars 3 and 4, sometimes also premolar 2, have a double root.

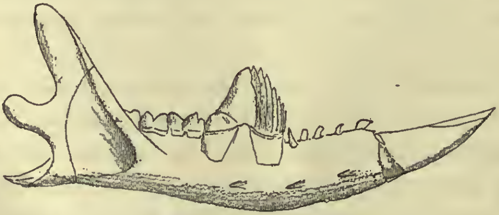

Fig. 154.

Abderites meridionalis; right mandibular ramus, outer aspect, about twice nat. size.—Santa Cruz Formation; Patagonia. (After Ameghino.)

Abderites (fig. 154). These small animals are remarkable for the development of a great cutting tooth in the middle of each ramus of the jaw above and below. The anterior end of the cranium is unknown, but the parts discovered suggest the original presence of a short proboscis.

The orbit is enormous, and there is a large antorbital foramen. The great upper sectorial tooth is evidently the last premolar, and is fixed by two roots, while its extremely compressed crown is marked by a few fine vertical flutings or grooves. The four molars immediately behind this tooth have quadricuspidate crowns, less elevated, and often with a small accessory cusp at the antero-external angle. The lower dentition (fig. 154) is especially remarkable because the sectorial tooth, shaped like that of the upper jaw opposing it, seems to be the first molar. In front there is the pair of relatively enormous incisors; then follow five very small simple teeth with a single root, which have been interpreted as one canine and four premolars; next comes the sectorial; and finally there are three cuspidate molars, the two first like those of the upper jaw, the last smaller and more elliptical in shape.

The diminutive South American Diprotodonts, so far as known, exhibit free and unmodified digits in each foot. All the Australian forms, on the other hand, are "syndactylous," having two or more digits, at least in the hind feet, enclosed in a common integument; and this strange specialization culminates in the leaping hind foot of the kangaroos.

Among these Australian groups, the existing family of **Phalangeridæ**, or phalangers, are probably the most closely related to the South American Epanorthidæ; but practically nothing is known of their ancestry, and the only extinct genus of special interest generally believed to be allied to them, is *Thylacoleo.* This is the "pouched lion" of Owen, represented by remains of the skull, and probably by certain limb-bones, in the superficial deposits of Queensland, Victoria, and New South Wales. The animal is believed to have been carnivorous by those who base their conclusions on the reduced tubercular character of the true molars and the low position of the condyle of the mandible; it is considered to have been a herbivore or a mixed feeder by those who emphasize the fact that no known existing carnivore has canines too small for grasping.

Thylacoleo (fig. 155). The skull is short and broad, with relatively large temporal fossæ, and a robust zygomatic arch, but the orbit not completely enclosed behind. There is one pair of large palatine vacuities. The dental formula is $\frac{\text{i. 3, c. 1, pm. 3, m. 1}}{\text{i. 1, c. 0, pm. 3, m. 2}}$. The anterior pair of upper incisors is much enlarged, while the two following incisors, the canine, and first two premolars are merely small obtuse cones, crowded together, and each with a single root. Then follows an enormous sectorial premolar with two roots, but no heel. Finally, a very small ovoid tubercular molar, with two roots, is closely pressed to the postero-internal angle of the sectorial. The mandible has a relatively large coronoid process, and a conspicuous inflection of the lower margin near the angle. The articular condyle is transversely extended, and placed on the same level as the dentition or even below it. There is a single pair of enlarged incisors at the symphysis, pointed and laterally compressed. Next are two diminutive premolars, immediately followed by the great sectorial premolar, which has two roots, the hinder the largest. The small first molar has two roots, while the second molar is a mere tubercular rudiment with one root, sometimes even absent. Limb-bones from the Wellington Caves, New South Wales, referred with much probability of correctness to *Thylacoleo*, denote a very nimble animal, and the innominate bone exhibits a striking resemblance to that of *Thylacinus*. The typical species is *Thylacoleo carnifex*, with skull about 0·26 m. in length, and probably all the known remains are Pleistocene or of later date.

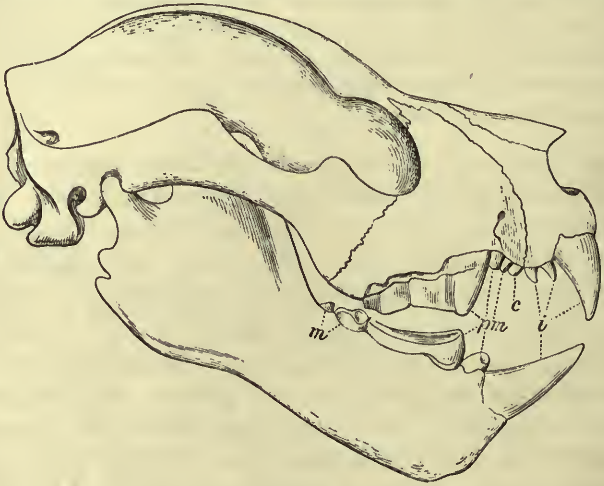

Fig. 155.

Thylacoleo carnifex; right lateral aspect of skull and mandible, about one-third nat. size.—Pleistocene; Queensland. *c*, canine; *i*, incisors; *m*, molars; *pm.*, premolars.

A family of gigantic extinct herbivorous Diprotodonts, not yet completely known, but apparently related both to the phalangers and the kangaroos, is that of the **Diprotodontidæ**, with the type genus *Diprotodon*. *Nototherium* is a smaller animal, either of this or a closely allied family.

Diprotodon (fig. 156). Represented by a single species, *Diprotodon australis*, as large as a rhinoceros, being indeed the largest known marsupial. The skull measures nearly a metre in length, and the greater part of the skeleton of the trunk and limbs is known. The dental formula is $\frac{\text{i. 3, c. 0, pm. 1, m. 4}}{\text{i. 1, c. 0, pm. 1, m. 4}}$, thus similar to that of the kangaroos, but no successional teeth have been observed. The foremost pair of upper incisors is chisel-shaped, much larger than the other two pairs, and growing from persistent pulps. The lower incisors resemble and oppose the front upper pair, also growing from persistent pulps. The premolar in both jaws is insignificant and early shed. All the molars are rooted, and each crown consists of two transverse ridges, without any small longitudinal ridge to connect them. There is a large downwardly directed process from the zygomatic arch. The limbs are of nearly equal length and adapted for walking. The humerus is remarkable as wanting an entepicondylar foramen; the radius and ulna move freely upon each other, and the latter bone has scarcely any olecranon process. The hind foot is proved to have had five very small and short toes, each with a little hoof; the fore foot appears to have been similar. *Diprotodon* occurs only in the supposed Pleistocene cave-deposits, fluviatile and lacustrine formations of New South Wales, South Australia, and Queensland.

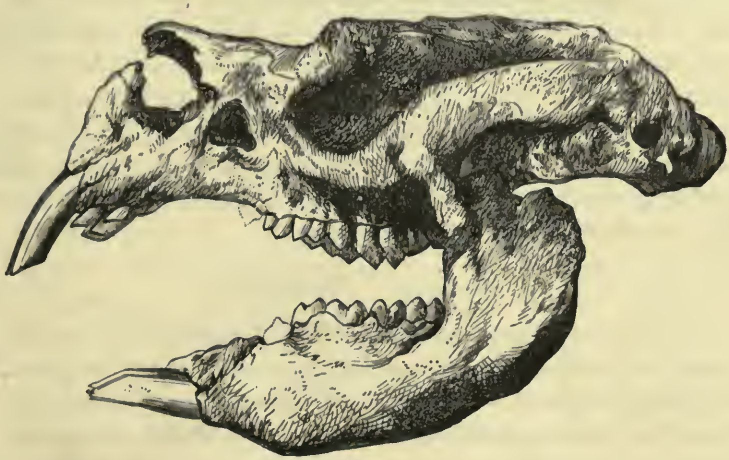

Fig. 156.

Diprotodon australis; skull and mandible, left lateral aspect, one-tenth nat. size.—Pleistocene; Queensland. (After Owen.)

Nototherium, found with *Diprotodon*, is a smaller animal than the latter, with shorter and broader skull, but a similar dental formula. The snout is somewhat constricted in front of the orbit, and the nasal bones a little expanded forwards. The enlarged anterior pair of upper incisors have a closed root, and the lower incisors are less persistently growing than those of *Diprotodon*. The humerus apparently belonging to this genus has an entepicondylar foramen, and the ulna exhibits a well-developed olecranon process. The feet are unknown. The typical species, *Nototherium mitchelli*, occurs in Queensland, and there is evidence of one or more additional species in the same region. Another form, *N. victoriæ*, is found in South Australia.

The extinct wombats or **Phascolomyidæ**, found in the superficial deposits of Australia, are closely similar to those still existing. All except one relatively large animal (*Phascolonus*) seem to belong to the recent genus *Phascolomys*.

The extinct kangaroos or **Macropodidæ**, also known only from the superficial deposits of Australia, differ in few particulars from the surviving types. The larger and more massive forms, however, seem to have had the fore and hind limbs less disproportionate in size than in the modern kangaroo. *Procoptodon* exhibits the two rami of the mandible fused together at the symphysis in the adult. The skull of *Palorchestes azael* must have measured nearly 0·4 m. in length.

Sub-Class 3. **Eutheria.**

Of the truly placental (or Eutherian) mammals there still remain two well-defined groups or orders concerning the origin and relationships of which Palæontology affords no information. These are the marine mammalia grouped under the ordinal names of Cetacea and Sirenia. There is also a third division whose origin has only lately become a little less obscure, namely that of the Edentata, from which an order termed Effodientia is now sometimes separated by zoologists. With these exceptions, however, the main lines in the evolution of the Eutheria can now be traced in a general way; and, as already remarked (p. 247), the chief modifications are to be noticed in the limbs and teeth.

Perhaps the most interesting feature is the regular and orderly manner in which the crowns of the teeth become complicated by the development of tubercles and ridges in the various groups. It has long been admitted that within any given restricted series these coronal prominences or cusps are definite individual entities identifiable and traceable in the teeth of all the different members of that series. The latest results of Palæontology suggest that this tracing of the homologous cusps may even be extended from the teeth of one great division to those of another; that, indeed, there are certain fundamental cusps common to the complicated molars of all the Eutheria. Some palæontologists have not hesitated even to identify the primitive ancestral "reptilian cone" throughout the Eutherian orders, and to propose a definite nomenclature for this and the secondary cusps by which it is accompanied. They have propounded the **Tritubercular Theory** of cusp-development, which reduces most of the known facts at least provisionally to order.

This theory or doctrine (elaborated especially by the American palæontologists, Cope, Osborn, and Scott) will be readily understood from the accompanying diagram (fig. 157), which represents ten successive plans of cusp-arrangement, those of the upper jaw being indicated by round black dots, those of the opposing lower jaw by circles. Fig. *A* represents four upper teeth and three lower teeth as simple cones, the normal reptilian condition; in *B* three teeth of both jaws have each become complicated by the addition of a pair of small lateral cusps, an arrangement observed in *Dromatherium* and other Triassic jaws. Fig. *C* shows the cusps well-separated to form a true triconodont tooth (as in the Lower Jurassic *Phascolotherium* (fig. 150) and *Amphilestes*); while *D* exhibits the lower lateral cusps thrust inwards and the corresponding upper cusps outwards, to form the tritubercular tooth (as in *Spalacotherium*). A talon is next added to the tritubercular lower molar (*E*), as in the Lower Jurassic *Amphitherium;* and this gradually increases in relative proportions (*F*, *G*), eventually bearing small new tubercles or cusps. The talon crushes into the valley of the upper tooth, so that each pair of opposed molars act mechanically as two shears and one crusher—an arrangement prevailing among most lemurs, insectivores, and carnivores. The upper molars now begin to develop a small talon and intermediate tubercles (*H*); and eventually (*I*, *J*) all the cusps become comparatively small and rounded tubercles on a crown, which soon loses its

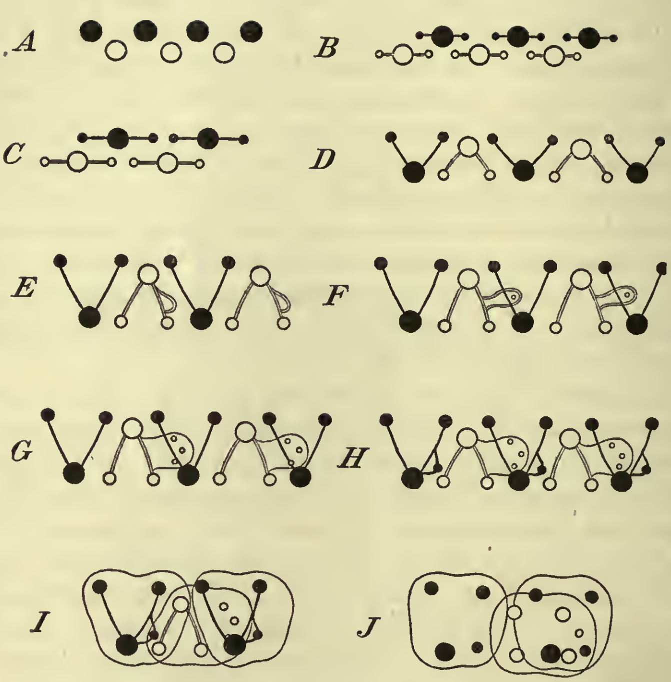

Fig. 157.

Diagram to illustrate the Tritubercular Theory of Cusp-development in the Teeth of the Mammalia. (After Osborn.)

The cusps of the upper teeth are represented by round black dots, those of the opposing lower teeth by small circles.

A. Reptilian stage, the diagram indicating four simple conical upper teeth, with their similar lower teeth alternating but somewhat inside.

B, C. Triconodont stages, three teeth and two teeth respectively.

D. First triangular or tritubercular stage, three upper and two lower teeth.

E, F, G. Stages with upper molars still simply triangular, the lower molars gradually developing a heel.

H, I. Stages in which both upper and lower molars develop a heel.

J. Stage exhibiting upper molars with four cusps, lower molar with five cusps.

triangular form and becomes more or less quadrangular. Here is the fundamental type from which the molar teeth of most herbivorous mammals may readily have been derived. The homologue of the primitive reptilian cone, according to this doctrine, is thus easily identifiable even in the most modified molars, and it has received the distinctive name of *protocone* in the upper, *protoconid* in the lower jaw. The other cones are all regarded as constant and likewise named. Examples of this nomenclature are given in the legends to figs. 183, 185, 187, 189, and 191.

Some palæontologists are inclined to believe that the advocates of this Tritubercular Theory apply it in a purely fanciful manner to the naming of the cusps in the more complicated molars, and that there is no adequate proof of the homologies they perceive. They also point to the primitive molars of the Multituberculata as a serious obstacle to its acceptance. While embryologists have adduced some striking evidence in its favour (*e.g.* identifying the three supposed primitive cones in the germs of such highly modified molars as those of *Equus* and *Bos*), they also have done much to render its basis insecure,—that is, if ontogeny can be relied upon as generally parallel to phylogeny. They have clearly shown that the order of calcification of the various cusps in the molars of many recent genera is quite different from the order of phylogenetic development of these cusps assumed by the Tritubercular Theory. Hence this at-first-sight brilliant generalization can only be accepted at present as a convenient working hypothesis which remains on its trial.

As to the rival theories concerning tooth-succession in the Eutheria, propounded and discussed by embryologists, Palæontology has not hitherto furnished any evidence of importance for consideration.

ORDER 1. CETACEA.

As already remarked, the order of whales, dolphins, and porpoises can be traced back to an early part of the Tertiary period without obtaining any real clue to its origin. The earliest forms exhibit a more normal rostrum, less unlike that of ordinary land mammals; they also differ in having a more differentiated dentition and a comparatively longer neck; but, so far as the known parts of the skeleton are concerned, they are as essentially Cetacea as their modern representatives. The results of evolution within the order are observable (i.) in the shortening and deepening of the brain-case, (ii.) in the raising of the external narial opening to the top of the base of the rostrum, (iii.) in the simplification of the teeth, their multiplication in some groups, their loss in others, and (iv.) eventually in the fusion of the vertebræ of the shortened neck.

Sub-Order 1. *Archæoceti.*

The earliest known Cetacean skulls, occurring more or less fragmentarily in the Eocene Formations of Europe, North Africa, and North America, perhaps also in New Zealand, exhibit less than 44 teeth (the normal number in Eutherian mammals); and a few of the hindermost of these teeth are implanted by two distinct roots. The temporal fossæ are large, the brain-case being elongated and surmounted by a strong sagittal crest. The nasal bones are well-developed and elongated, while the external narial opening is situated on the top of the rostrum at about its middle. Only one generic type has hitherto been recognized with certainty, namely, that commonly known as *Zeuglodon.*

Fig. 158.

Zeuglodon cetoides; upper molar, showing the low serrated crown and the two long roots, about one-fifth nat. size.—Eocene; Alabama.

Zeuglodon (fig. 158). When originally discovered in 1834, fragments of the jaws and teeth of this animal were erroneously ascribed to a reptile under the name of *Basilosaurus.* The skull, mandible, and dentition are now almost completely known; vertebræ from most regions of the trunk have also been discovered; while the scapula, humerus, and dermal plates, found with undoubted Zeuglodont remains, are probably correctly identified. The skull is elongated and much depressed, and notwithstanding the extent of the brain-case, its cavity is very small. The frontal bones are very short and broad. The nasal bones are separate, antero-posteriorly elongated elements roofing the nasal chamber, which opens externally in a single orifice on the top of the rostrum at about its middle. The premaxillæ form an unusually considerable length of the end of the snout. The symphysis of the mandible is very long. The teeth are considerably spaced, fixed in distinct sockets, and with more or less enamelled crowns. In the typical species there are three simple conical teeth in the premaxilla, and a larger tooth of the same form occurs near the anterior end of the maxilla; then follow five larger teeth, also conical, but with more compressed and longitudinally extended crowns notched or serrated on the front and hind borders, and each implanted by two distinct roots (fig. 158). Nine corresponding teeth occur on each side of the lower jaw. The dental formula is thus commonly expressed:—$\frac{\text{i. 3, c. 1, pm. + m. 5}}{\text{i. 3, c. 1, pm. + m. 5}}$. Successional teeth have not been observed with certainty. The cervical vertebræ are not shorter than the anterior dorsals, and none are fused together. The lumbar vertebræ are considerably elongated, while the caudals are short. The somewhat expanded scapula exhibits a large spine and a comparatively small coracoid process. The humerus tapers at its distal end, where slightly convex facettes for the radius and ulna can be distinguished. The supposed dermal armour, known only by fragments, consists of irregular, smooth, bony tesseræ, more or less fused together. It seems to resemble the rudimentary dermal armour of the existing *Phocæna*. The skull of the typical species, *Zeuglodon cetoides*, from the Eocene of Arkansas and Alabama, U.S.A., attains a length of nearly a metre. More fragmentary specimens, to which other specific names have been given, are known from Louisiana and Mississippi, U.S.A.; from the Barton Clay of Hampshire; from the Eocene of France, Germany, the Caucasus, and Egypt; from Malta; and also from supposed Eocene strata in South Australia and New Zealand.

Sub-Order 2. *Odontoceti.*

The typical skull of the toothed whales, or ODONTOCETI, had already been developed, and the teeth had begun to multiply, before the differentiated character of the dentition just described in the Archæoceti, disappeared. *Prosqualodon*, from the Marine Patagonian Formation (supposed Miocene) of Chubut, Argentine Republic, and *Squalodon*, from the Miocene and Pliocene of Europe (probably also North America and Australia), bear witness to this fact.

Prosqualodon. Known only by an imperfect skull and mandible, which is identical in most respects with that of a modern Odontocete but shows the small triangular nasal bones carried on a projecting ridge of the frontals in such a manner that they slightly roof the nasal chamber. The mandibular symphysis is comparatively short. So far as preserved, the teeth resemble those of *Squalodon*, but only five or six of the hinder ones are implanted by a double root. The species is named *P. australis.*

Squalodon. The skull and dentition of this genus are completely known by fine specimens discovered in the Miocene of France and Bavaria. The skull precisely resembles that of the existing Odontoceti, with the external narial opening at the base of the rostrum, and the nasal bones quite rudimentary, not roofing the nasal chamber. The teeth are more or less enamelled, very similar in form to those of *Zeuglodon* but more numerous and in closer series. In the best-known species, *S. bariensis*, there are three simple conical incisors in the premaxilla, while a similar tooth at the anterior end of the maxilla may be regarded as a canine. Then follow four more compressed, but also single-rooted teeth, which may be termed premolars. Finally, there are seven two-rooted molars. The teeth of the mandible are similar, and alternate with those of the upper jaw; the total number of teeth being thus no less than 60. The symphysis of the mandible is very long, extending backwards beyond the "premolars." Teeth and other fragments are known from the marine Miocene and Pliocene strata throughout Europe, and have been identified also in North America and Australia.

Most of the remains of the typical Odontoceti found in the Miocene and Pliocene formations of Europe and North America are too fragmentary for satisfactory discussion; but some fine skulls from the Marine Patagonian Formation (supposed Miocene) of the Argentine Republic, South America, exhibit all the principal cranial and dental characters of these early Cetacean types. One of these (*Argyrocetus*) is interesting as being bilaterally symmetrical and having functional nasal bones; hence such a form as might have easily evolved into the skull of a whalebone whale. Another (referred to *Physodon*) is the skull of a small sperm whale, differing from the modern forms of this type in still retaining teeth in the upper jaw, and having all the teeth capped with enamel.

Argyrocetus. This genus is founded on a unique bilaterally-symmetrical skull and mandible about a metre in length, from the Patagonian Formation of Chubut, and specifically named *A. patagonicus.* The occipital condyles, instead of exhibiting the adpressed form of those in the existing Platanistidæ and Delphinidæ, are as prominent as in any ordinary terrestrial mammal. The nasal bones are large square elements articulated by a broad base with the frontals, projecting over the nasal chamber, and abruptly truncated in front. The rostrum is extremely slender. The symphysis of the mandible is somewhat more than half the length of the jaw, and it terminates in front in an upwardly-directed, toothless, spatulate end, quite unlike that of any existing Odontocete. The teeth are unknown, but they seem to have been numerous and slender, and there are about 25 sockets in each ramus of the mandible. A few cervical vertebræ found with the skull are not fused together, and are moderately long, like those of the modern Platanistidæ, which are generally regarded as the most primitive of existing Cetaceans.

Physodon. This name was originally given to some enamel-capped teeth, evidently of early sperm-whales, from the Miocene and Pliocene of Europe. The skull from the Patagonian Formation of Chubut, with similar teeth, can thus only be placed provisionally under the same generic denomination. Teeth of such a form may have belonged to several genera. In any case, the South American Miocene skull described under the name of *Physodon patagonicus*, measures only about a metre and a half in length, and shows very clearly its relationship to the modern sperm-whales (Physeteridæ) by having the large deep cavity in the fronto-parietal region for the reception of the accumulated spermaceti. The nasal bones are unknown. The premaxillæ extend some distance in advance of the maxillæ, forming about a third of the rostrum, and bearing three pairs of the upper teeth. All the teeth are simple cones with an enamel cap, and they seem to have been 22 in number on each side of the upper jaw, 24 in each ramus of the mandible.

Before the end of the Pliocene period all the most specialized types of Odontoceti seem to have been evolved. The strange compact rostra of the Ziphioid genera, such as *Mesoplodon*, are even common fossils in the Pliocene of England and Belgium. Fragments of the tusk and rostrum of a narwhal (*Monodon*) are also known from the Cromer Forest Bed (base of Pleistocene).

Sub-Order 3. *Mystacoceti.*

The whalebone whales, or MYSTACOCETI, must have been derived from toothed ancestors, as is indicated by the presence of calcified rudiments of teeth in the fœtus of more than one existing genus. Apart, however, from the development of baleen and the remarkable form and proportions of the mouth, they are much less specialized than any of the surviving Odontoceti. They must therefore have diverged from the latter before these lost their olfactory organ and many other primitive characters; and the extinct Patagonian *Argyrocetus*, as already mentioned (p. 272), may well have been one of the ancestral types.

Unfortunately, Palæontology has not hitherto furnished any of the links in this process of evolution. It is merely known that small, but typical whalebone whales existed so long ago as the Miocene period both in Europe and North America; the neck in these being only a little longer than in those of the present fauna, the parieto-frontal region of the cranium also somewhat more elongated, and the nasal bones better developed. *Cetotherium* and *Plesiocetus* are typical old genera, and a skull apparently of the former is known from the Marine Patagonian Formation of Chubut, Argentine Republic. Fragments of typical modern Balænidæ are not known below the Pliocene.

ORDER 2. SIRENIA.

Like the Cetacea, the allies of the existing manatees and dugongs are also known to date back to the early part of the Tertiary period, without as yet affording any clue to the origin and relationships of the order they represent. The early extinct forms already discovered merely differ in exhibiting (i.) a less modified dentition and nasal region, (ii.) distinct disc-shaped epiphyses at the ends of the vertebral centra, and (iii.) well-developed rudiments of the hind limbs.

The oldest fossil placed here is a natural cast of a brain-cavity (named *Eotherium aegyptiacum*) from the Middle Eocene Nummulitic Limestone of the Mokattam Hills, near Cairo, where typical Sirenian teeth also occur. Another still more interesting specimen, of great but uncertain antiquity, is an imperfect skull (*Prorastomus sirenoides*) from Jamaica, displaying a very generalized dentition. *Halitherium* and *Miosiren* are known by nearly complete skeletons from the Lower Miocene of Germany and Belgium respectively. Several other more fragmentary specimens of Sirenia have also been discovered in the Miocene and Pliocene both of Europe and America; while the toothless Steller's sea-cow (*Rhytina stelleri*), exterminated only in the last century, is represented by nearly complete skeletons from superficial deposits near its old haunts on the Asiatic coast of Behring Straits.

Prorastomus. This genus is as yet known with certainty only by a unique skull 0·27 m. in length from an early Tertiary limestone in Jamaica (*Prorastomus sirenoides* of Owen). The skull is comparatively elongated, and the premaxillary region does not curve downwards over the symphysial end of the mandible, but is more normally disposed, while the cleft of the mouth is straight. The premaxillæ, however, are excessively robust, and the external narial opening is in a horizontal plane, though relatively shorter than usual in Sirenians. The teeth are rooted and enamelled, and the series is complete, the dental formula being apparently as follows:— $\frac{\text{i. }3,\text{ c. }1,\text{ pm. }5,\text{ m. }3}{\text{i. }3,\text{ c. }1,\text{ pm. }5,\text{ m. }3}$. The canine is larger than the incisors, and there is a short diastema behind this tooth above and below. Of the eight molariform teeth in continuous series, the foremost five are termed premolars on account of their comparatively small size and simple structure; they are tubercular, all with single or only partially divided roots. The three true molars seem to have been bilophodont, with two outer and two inner roots, at least in the upper jaw. Remains of the skull and molar teeth, wanting the rostral end, from the Upper Eocene of northern Italy, have also been provisionally assigned to *Prorastomus* (*P. veronense*); and one tooth ("fourth upper milk-molar") ascribed to this species exhibits a crown much like that observed in the brachyodont selenodont molars of certain artiodactyl ungulates (e.g. *Merycopotamus*).

Halitherium (fig. 159). An early Middle Tertiary genus known by the nearly complete skeleton, which attains a length of about three metres. The skull is typically Sirenian in form, with the downwardly turned premaxillary region, but the nasal bones are well-developed and meet in a suture in the longitudinal median line. The teeth are all rooted, and their crowns are enamelled. There is one pair of tusk-like, though not persistently growing, upper incisors; but the other front teeth seem to have been rudimentary and are not satisfactorily known. The molariform teeth are in continuous series, and seven in number in each jaw. Of these the first three in the adult are comparatively small and simple, evidently premolars, each with a single root; the fourth tooth, or pm. 4, is also relatively small, but with a double root at least in the lower jaw; and there is good reason to believe that some were preceded by milk-molars, though the latter have not yet been found actually in position. The three molars are irregularly tuberculated and ridged, those of the upper jaw with three roots, those of the lower jaw with two roots. The vertebral centra of immature individuals exhibit distinct epiphyses. There are seven cervical vertebræ, all free, except an occasional fusion of the second and third; nineteen dorsal vertebræ bear the usual robust ribs; next follow three lumbar vertebræ, of which the third has especially stout

ORDER 2. SIRENIA.

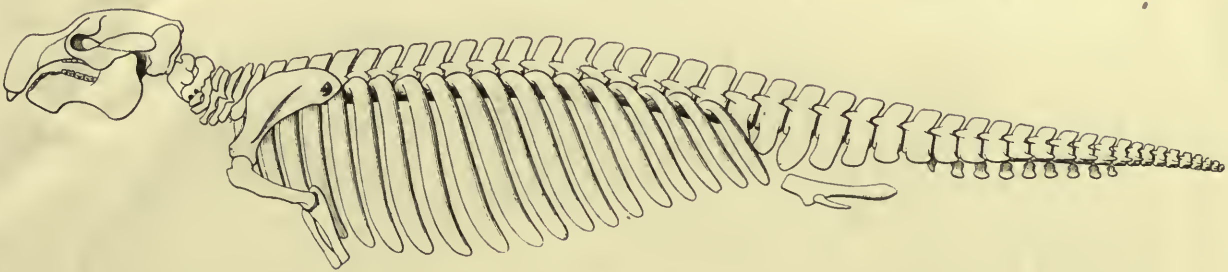

FIG. 159.

Halitherium schinzi; restoration of skeleton, except manus, about one-fifteenth nat. size.—L. Miocene; Hesse Darmstadt.

and downwardly curved transverse processes, doubtless originally connected by ligament with the rudimentary pelvis; the caudals are at least twenty-five in number. The sternum even in the adult comprises a series of three separate pieces. The radius and ulna are partially fused together. Two well-developed metacarpals and two phalanges are known, indicating the presence of a manus. The rudimentary pelvis consists of a triradiate bone on each side, displaying a small, shallow acetabular pit; and the femur is a small styliform bone, a little bent at its stout proximal end. The typical species, *Halitherium schinzi* (fig. 159), occurs in the Lower Miocene marine deposits in the basin of Mayence, Germany. Other remains of the same or almost indistinguishable genera have been described from Würtemberg, Austria, Switzerland, France, Belgium, southern Russia, Italy, Malta, Egypt, and the Pliocene Red Crag of Suffolk.

Rhytina is the largest known Sirenian, sometimes attaining a length of as much as seven or eight metres. It is toothless, displaying only the sockets of a pair of rudimentary incisors in the downwardly curved premaxillæ. The head is relatively very small. There are seven cervical vertebræ, nineteen dorsals with ribs, and between thirty and forty vertebræ forming a long tail. The nineteenth rib is a diminutive rudiment. The bones of the hand and rudimentary hind limb are unknown. The only known species, *Rhytina stelleri*, inhabited the coasts of Behring and Copper Islands, off the coast of Kamtschatka, until late in the last century, and a memoir on the animal was published by Steller in 1751. Fossil skeletons are found in the old raised beaches and peat bogs of this region.

ORDER 3. EDENTATA.

The general tendency of palæontological discovery at present is to suggest that the Edentata are not so primitive and isolated a group among the placental mammals as they were commonly supposed to be. It seems that they are rather to be regarded as degenerate types, probably derived from some of the common ancestors of the ungulates and rodents. At least, there are certain imperfectly known genera in the Eocene formations of North America, variously termed TÆNIODONTA, GANODONTA, or STYLINODONTIA, which seem to be best interpreted as ancestral Edentates, and these exhibit a decided approach to more normal placental mammals.

The early North American group just mentioned is characterized by the presence of incisors in both jaws, by a typical molar and premolar dentition, and by a trituberculate molar crown, which disappears early in life through wear and leaves the dentine exposed. In the earliest known forms the teeth are rooted and more or less completely enamelled; in the later forms the incisors gradually diminish, and all the teeth become hypsodont, rootless, and of persistent growth, while the enamel is limited to narrow vertical bands. In one tribe the facial part of the skull is short, and the only known fore limb is remarkably similar to that of the extinct ground-sloths, *Megatherium* and its allies. In another tribe the skull is more elongated, and the few known parts of the skeleton exhibit much resemblance to the corresponding bones of the modern armadillos. To the first tribe are referred *Hemiganus* and *Psittacotherium* from the Puerco Eocene, *Ectoganus* and *Calamodon* from the Wasatch Eocene, and *Stylinodon* from the Bridger Eocene. The Puerco Eocene genus *Conoryctes* represents the second tribe or family. Some teeth and a portion of mandible from the Upper Eocene of Switzerland have also been referred to *Calamodon* with much probability of correctness.

The earliest Tertiary Edentata hitherto discovered in South America, namely, those from the *Pyrotherium* Formation of Patagonia, seem to be a little more specialized than the North American forms just mentioned; but one armadillo (*Peltephilus*) at least has a series of front teeth, and several genera exhibit traces of enamel on the teeth. The armoured type is already clearly differentiated from the sloth and anteater type, but a certain amount of evolution can be observed as the various genera are traced through the successive Tertiary formations of the Argentine Republic.

The modern sloths, **Bradypodidæ**, and anteaters, **Myrmecophagidæ**, are practically unknown among fossils; but an important extinct family, that of the ground-sloths or **Megatheriidæ**, is of special interest as combining in the skeleton the characters of the two existing families just mentioned. These animals exhibit the head and teeth of a sloth, associated with the vertebræ, limbs, and tail of the anteater. Some of them, like the typical genus *Megatherium*, attain a gigantic size, at least as large as an elephant; and their remains occur not merely in South America, but also in the northern half of the continent as far as Kentucky. Some of the earliest genera exhibit a curious oblique suture across each ramus of the mandible; and they must have walked less habitually on the outer side of their feet than the later forms. It is also to be noted that the latest species are the most bulky. *Hapalops, Hyperleptus*, and other genera are known by fragmentary skeletons from the Santa Cruz Formation (supposed Miocene) of Patagonia; *Megatherium, Mylodon, Scelidotherium*, and *Megalonyx* are genera of comparatively recent date.

FIG. 160.

Megatherium americanum; mandible, oral aspect, about one-eighth nat. size.—Pampa Formation (Pleistocene); Buenos Aires, Argentina. *d*, hinder end of symphysis, between the molar teeth.

Megatherium (fig. 160). This is the largest known Edentate, the typical species, *Megatherium americanum*, measuring between five and six metres in length, the tail alone being about one and a half metres long. The head is comparatively small, with the mandible very deep in the middle of each ramus and its symphysis produced into a narrow toothless spout. The zygomatic arch is complete, with a descending process from the jugal bone. The teeth form a close grinding series, five in the upper, and four in the lower jaw. They are quadrate in shape and extraordinarily deep, each growing from a persistent pulp and exhibiting two transverse ridges on the crown, which are due to the development of two relatively hard laminæ of dentine. The vertebræ are proved to be seven in number in the cervical region, and these are followed by sixteen dorsals, three lumbars, five sacrals, and nearly twenty caudal vertebræ. The neural spines are all inclined backwards, and accessory zygapophyses are well-developed in the lumbar region. The caudal region is very massive, most of the vertebræ bearing large transverse processes, and at least 10 or 12 having chevron bones below. The foremost chevron consists of two separate halves, the others are

Y-shaped as usual. The acromion process of the scapula unites with the coracoid process, completing a foramen as in the modern sloths. The clavicle is relatively large and sigmoidally bent. The fore limb is longer than the hind limb, and is shown to have been remarkably mobile. There is no entepicondylar foramen in the humerus. In the hand, the first digit or pollex is represented merely by a rudimentary metacarpal; nos. II to IV are complete and well-developed, with enormous claws, which bear a reflected bony sheath at the base; no. V, or the outermost digit, exhibits only two small phalanges without a claw. The pelvis is very wide, and the short and stout hind limbs with the tail form a tripod on which the whole weight of the body would easily rest. The femur is extremely broad and flattened antero-posteriorly; the short tibia and fibula are fused together at each end. The tarsus is peculiar, and the calcaneum projects backwards almost as far as the toes extend forwards. The first or inner digit is entirely wanting, and the second digit is quite rudimentary; the third or middle digit is very large, and bears a great claw with its characteristic basal sheath; while the two outer digits are furnished only with relatively small phalanges and no claw. No dermal armour has been observed. The genus *Megatherium* occurs typically in the Pampa Formation (Pleistocene) of the Argentine Republic, but has also been found in superficial deposits in Chili and Brazil. No undoubted remains have hitherto been met with in North America, though similar teeth occur in the phosphates of South Carolina.

Megatherium seems to have been entirely destitute of dermal armour, and the only one of its allies in which bony plates have hitherto been found is *Mylodon*, while these are very small and not fused together. The species of *Mylodon* do not attain quite so large a size as the typical *Megatherium*. The skull in this genus is comparatively short, with the teeth more or less ovate in section, like those of the modern sloths, and the series extending almost to the anterior end of the jaws. The three inner digits of the fore foot bear claws, while the two outer digits are reduced and without claws. As in *Megatherium* the hind foot wants digit no. I, but both no. II and no. III bear claws. The typical species is *Mylodon harlani*, about as large as a rhinoceros, from the Pleistocene of Kentucky and other southern parts of North America; but the genus is still better represented in the Pliocene and Pleistocene of South America. In the South American *Scelidotherium* (fig. 161) the skull is comparatively elongated, its shape more like that of the anteater than any of the others.

ORDER 3. EDENTATA.

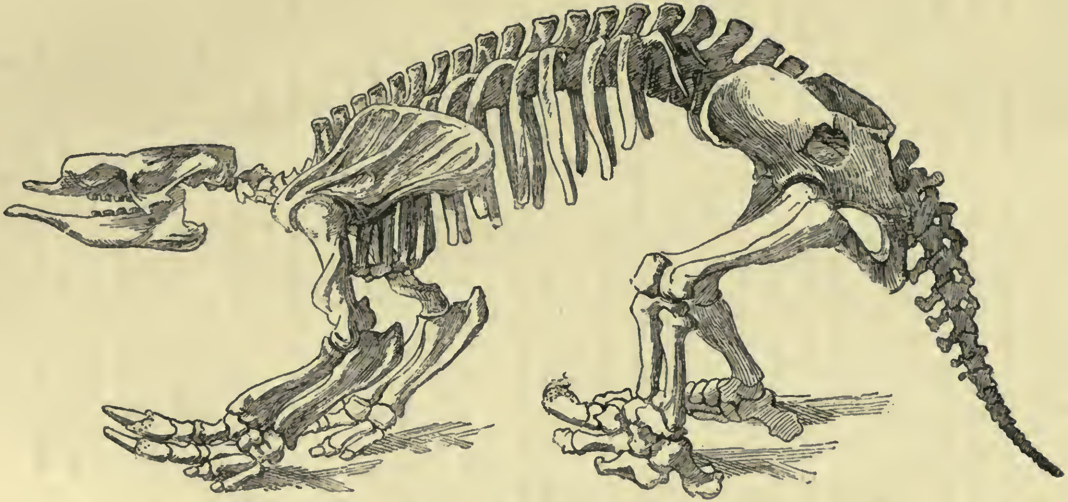

FIG. 161.

Scelidotherium leptocephalum; restored skeleton about one-sixteenth nat. size.—Pampa Formation (Pleistocene); Buenos Aires, Argentina. (After Lydekker.)

The earliest armadillos already mentioned as occurring in the *Pyrotherium* Formation of Patagonia are apparently intermediate in many respects between the **Glyptodontidæ** and Dasypoda of more modern date. So far as can be determined from fragmentary specimens the bony dermal scutes were not externally sculptured, and they seem to have been arranged in well-defined transverse rows, which were to a great extent movable and might easily have undergone modification either into the rigid carapace of the Glyptodonts or the familiar ringed shield of the surviving armadillos. *Peltephilus* is the strangest of these early forms, known only by imperfect skeletons both from the *Pyrotherium* and Santa Cruz Formations. *Propalæohoplophorus* is another less imperfectly known genus from the latter formation. The genera comprising the gigantic species of Pliocene and Pleistocene age are numerous, but *Glyptodon* and *Dœdicurus* may be cited as illustrating their principal features.

Peltephilus. The skull in this genus is comparatively short and broad, depressed in the rostral region, and with a strong sagittal crest behind. The zygomatic arch is complete, though slender, and the part of the squamosal bearing the articular facette for the mandible is segmented off by a persistent suture as a small distinct element (apparently identifiable with the quadrate of reptiles and birds). The orbit is large and not completely separated from the temporal fossa. The lachrymals are much extended on the face, but the lachrymal canal opens within the orbit. The nasals are short, and the premaxilla is fused with the maxilla on each side. The posterior nares are far back, and the pterygoids seem to have entered the secondary palate. The mandibular rami are fused together at the rounded symphysis. The teeth are all simple, have a chevron-shaped section, overlap one another and wear obliquely. There are seven pairs above and below, and they form a continuous series from the front backwards. The axis and two or three following vertebræ are fused together. The scapula exhibits a well-defined coracoid process, marked off by a persistent suture. The humerus exhibits an entepicondylar foramen, and is shaped remarkably like the corresponding bone of the existing Monotremes. The olecranon process of the ulna is longer and more robust than usual in the armadillos. The epiphyses of the long bones remain separate apparently until old age. The head bears two pairs of horn-shaped scutes. The armour of the trunk and tail consists of transverse series of bony plates loosely apposed, sometimes slightly overlapping. The typical and best-known species is *Peltephilus strepens*, with skull about 0·12m. in length, from the Santa Cruz Formation of Patagonia.

Propalæohoplophorus. This is a primitive Glyptodont known by the almost complete skeleton of the typical species, *P. australis*, also from the Santa Cruz Formation. It is a small animal, with carapace about 0·6 m. in length. The skull differs from that of all other Glyptodonts, while agreeing with the existing armadillos, in the exclusion of the maxillæ from the border of the terminal nostril. There are eight teeth on each side above and below, and the first four are so much simpler than the others that it has been suggested they may be true premolars. The vertebral column is much arched, and the dorsal vertebræ are not fused together. The limbs are long and slender. The humerus exhibits an entepicondylar foramen; the manus is unknown. The femur agrees with *Dasypus* and differs from the Glyptodonts in the position of the third trochanter, which arises at about the middle of the shaft; the tibia and fibula are not fused together, and the hind foot comprises five digits, of which the first and fifth are the smallest. A head-shield of bony polygonal plates is present. The plates of the carapace are thin, with feeble sculpturing, and arranged in distinct transverse rows; at the end of the tail-sheath the successive rows are firmly fused together. It is noteworthy that in the anterior third of the carapace three rows of scutes at and near the inferior border overlap like those of the movable bands of the carapace of the true armadillos.

Glyptodon (figs. 162, 163). This is the typical genus of the family Glyptodontidæ, comprising large species, distributed throughout the latest Tertiary formations of South America, and also found in contemporaneous deposits in Texas and Mexico. The skull is very short and truncated in front, with small flattened nasals, and the maxillæ entering the border of the terminal nostril. The nasal cavity is divided by a bony longitudinal septum. The zygomatic arch is complete, with a long descending process from the jugal bone; and the orbit is not separated from the temporal fossa. The brain is relatively very small, and the cerebral hemispheres must have been quite smooth. The pterygoids enter the secondary palate. The mandibular rami are fused together at the deep, spout-shaped, toothless symphysis. There is a close series of eight teeth on each side above and below, all more or less divided into three lobes by two deep grooves on the outer and inner face; and the arrangement of the various hard and soft areas of dentine and cement gives the worn crown a sculptured appearance, hence the generic name. The atlas vertebra is free, but the axis is fused with the four or five succeeding cervicals. The dorsals are anchylosed into a long tube, and the lumbar vertebræ are fused with the sacrum. The caudal vertebræ are free. The limbs are stout, and the digits of both feet extremely short, with almost hoof-shaped claws. The scapula is short and broad; there is no entepicondylar foramen in the

ORDER 3. EDENTATA.

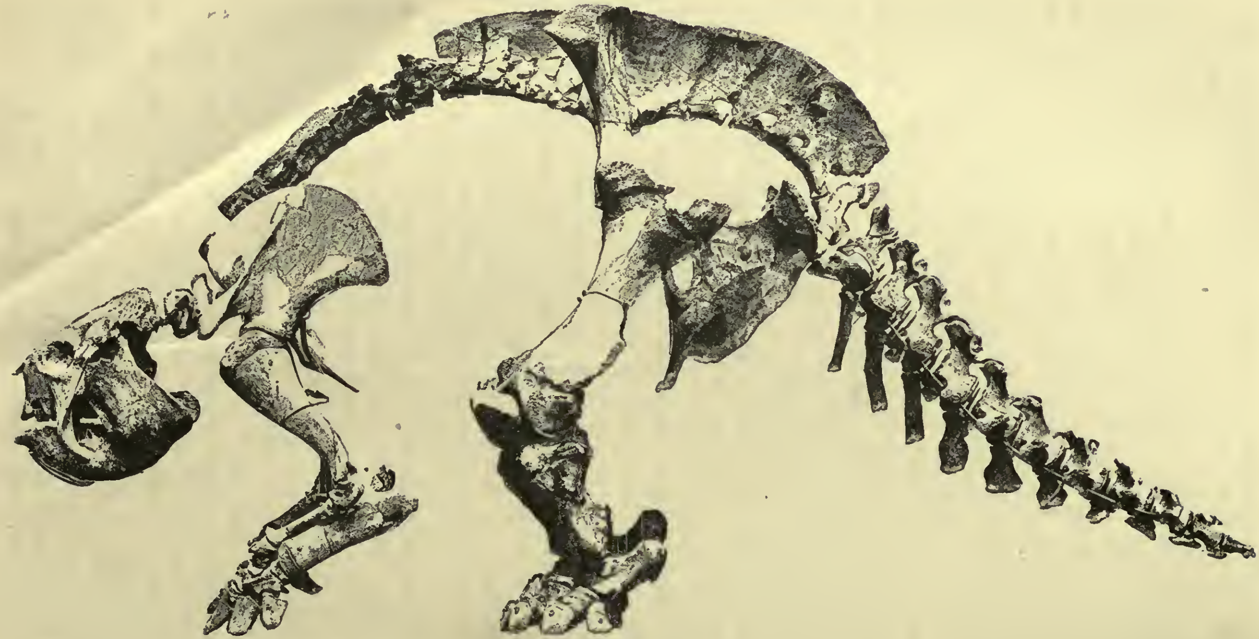

Fig. 162.

Glyptodon clavipes; immature skeleton without carapace, about one-tenth nat. size.—Pampa Formation (Pleistocene); Buenos Aires, Argentina. (After Lydekker, from specimen in La Plata Museum.)

ORDER 3. EDENTATA.

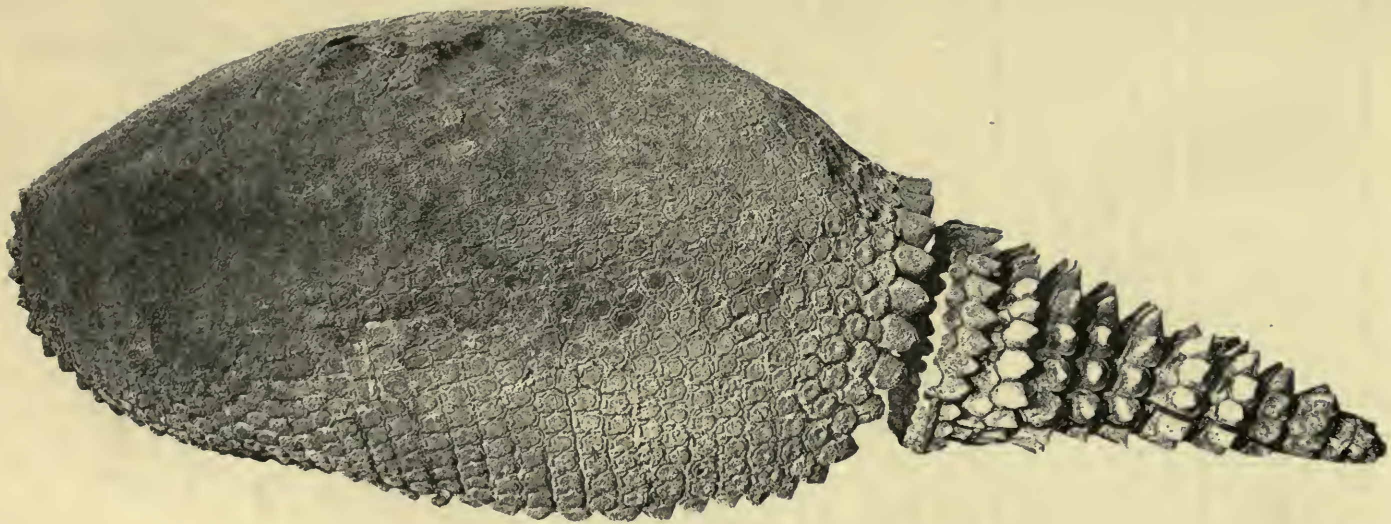

FIG. 163.

Glyptodon clavipes; carapace and tail-sheath, about one-eighteenth nat. size.—Pampa Formation (Pleistocene); Buenos Aires, Argentina. (After Lydekker, from specimen in La Plata Museum.)

humerus; the manus has only four digits. The femur exhibits the third trochanter just above the outer distal condyle; the tibia and fibula are remarkably short, and anchylosed together at their extremities; the pes has five complete digits, and the calcaneum is relatively large. There is a head-shield of thin polygonal plates, and the carapace (fig. 163) is robust, quite rigid, and usually ornately sculptured. One specimen in the Museum of La Plata exhibits horny epidermal plates covering the bone, and the arrangement of these corresponds exactly with that of the tesseræ they cover. They are not pierced by the foramina which so frequently pass through the bones, thus indicating that the latter are vascular canals and not for the insertion of hairs. The tail is relatively short and tapering, and its bony sheath comprises a series of elliptical rings gradually diminishing in size and eccentricity towards the extremity (the tail-sheath represented in the original restorations of *Glyptodon* thus belongs to another genus). The typical species is *Glyptodon clavipes* from the Pampa Formation (Pleistocene) of Buenos Aires, attaining a total length of not less than four or five metres.

Dædicurus. This genus comprises the largest and most specialized Glyptodonts. The skull is much like that of *Glyptodon*, but the orbit is separated from the temporal fossa by a bar of bone, and the descending zygomatic process is relatively shorter. The humerus has an entepicondylar foramen, and the manus seems to have consisted only of three digits, each with a broad claw. The pes comprises four digits, the three innermost with very broad claws, the outermost small and without a claw. The head-shield is unknown. The carapace is smooth, and the scutes are pierced by numerous and large vascular foramina. The tail is relatively long, and the proximal part of its sheath consists of about six rings of scutes like those of the carapace, while its distal part is a much-depressed tube, somewhat expanded at the extremity where it seems to have been ornamented with great bosses. The typical species is *Dœdicurus clavicaudatus*, from the Pampa Formation (Pleistocene) of Buenos Aires. Smaller forms occur in the slightly earlier deposits near Parana and in Monte Hermoso, near Bahia Blanca.

A fragment of ornamented tessellated dermal armour, of comparatively small size, from the Upper Eocene Phosphorites of southern France, has been compared with the carapace of the armadillos, and named *Necrodasypus galliæ.* The determination, however, is extremely doubtful.

Concerning the ancestry and true relationships of the problematical Edentata of the Old World, Palæontology as yet furnishes no information. One humerus (named *Necromanis quercyi*) from the French Phosphorites just mentioned is very similar to that of the existing pangolins (*Manis*) of Africa and Asia, and other more uncertain limb-bones perhaps of the same type occur in the same formation. The fronto-nasal region of a small narrow skull (*Leptomanis edwardsi*) has also been found here, and may be referred with even more probability to an extinct pangolin. Another humerus (named *Palæorycteropus quercyi*) from the same Phosphorites, much resembles the corresponding bone of the living aard-vark (*Orycteropus*) of Africa; and the last-mentioned animal itself is known to have had a much wider distribution in Pliocene times than at present, a typical skull being known from the Island of Samos in the Turkish archipelago, and a detached tooth from Maragha in Persia.

ORDER 4. UNGULATA.

In the earliest Eocene strata of North America, from which numerous nearly complete skeletons have been obtained, it is almost impossible to distinguish the forerunners of the herbivorous mammals with hoofs (Ungulata) from those of the carnivorous mammals with claws (Unguiculata = Carnivora, etc.). Both are small plantigrade five-toed animals, with terminal phalanges which are usually not quite in the form either of claws or of hoofs, and with a mobile fore limb; while both have more or less tubercular molars and premolars, the tubercles in the one case being only less pointed or cutting than in the other. The typical Ungulata, however, soon become differentiated, and before the close of the Eocene period, both in North America and Europe, they have already begun to diverge into the principal sub-ordinal groups.

As this course of evolution is traced upwards through the Tertiary formations, the changes in the skeleton are all much of the same type. In general terms, they relate to the modification of small marsh-dwelling or forest-dwelling animals, which were adapted to live on succulent vegetation, into hard-hoofed quadrupeds more fitted for life on grassy plains and with powerful grinding teeth capable of masticating comparatively coarse and dry herbage. The theory is indeed often advanced, that the whole of this development of the Ungulata was correlated with the incoming of grasses as a dominant feature in the earth's flora. Foremost in the advance the brain has become relatively larger and of a higher type. The brain-case usually exhibits a gradual thickening, often bearing horns and bony prominences, rarely (as in the case of the elephants) expanded for the increase of muscular attachments. Sometimes (as in the ruminants) the face becomes sharply bent downwards upon the basicranial axis. The dentition, besides being variously complicated and reduced in extent, exhibits one very constant change; the molars and premolars in all the earliest forms have very short (*brachyodont*) crowns fixed on well-developed roots, whereas the same teeth in the later forms have crowns of gradually increasing height (*hypsodont* or *hypselodont*), and eventually these teeth are persistently growing in the young and only become rooted in old age, when they have been considerably reduced by wear (see p. 320, fig. 182 E). The neck also undergoes much modification. Usually its flexibility is increased by the slight development of a ball-and-socket joint between the vertebræ and a curving of the zygapophysial facettes. In the elephants it becomes excessively shortened. Except in such persistent types as the elephants and tapirs, the limbs become more and more digitigrade; the clavicle always degenerates to a ligament, and by the atrophy of the ulna the fore limb loses all power of twisting. At first the five digits are present, while the elements of the two rows of the carpus (to a certain extent also those of the tarsus) are more or less directly opposed, each proximal bone with its own distal bone. Soon this arrangement is strengthened by the interlocking of the two series. Then all the digits become reduced or lost, except a final one or a fused pair. Meanwhile the radius and tibia increase in size at the expense of the ulna and fibula, which become degenerate remnants and usually lose their articulation with the carpus and tarsus; and the ginglymoid ankle-joint, between the double-grooved end of the tibia and double-ridged astragalus, assumes its maximum perfection.

Sub-Order 1. *Condylarthra.*

These are the small generalized early Ungulata already mentioned as most closely approaching the ancestors of the Carnivora. The brain is relatively diminutive, with smooth hemispheres and the mesencephalon more or less exposed. The teeth are brachyodont and bunodont (*i.e.* have a low crown bearing tubercles), usually 44 in total number, and the

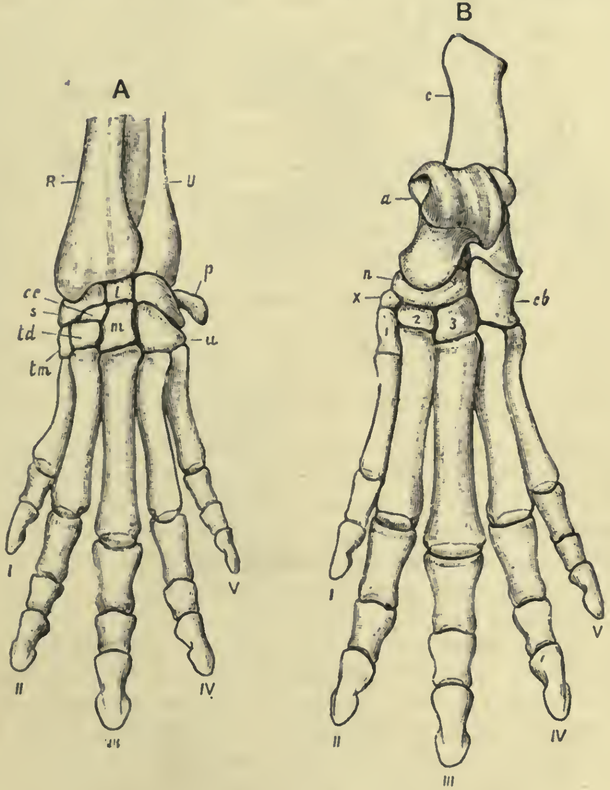

FIG. 164.

Hyracops (? *Meniscotherium*) *socialis*; left fore (A) and hind (B) feet, nat. size.—L. Eocene; New Mexico. *a*, astragalus; *c*, calcaneum; *cb.*, cuboid; *ce.*, centrale; *l*, lunar; *m*, magnum; *n*, navicular; *p*, pisiform; *R*, radius; *s*, scaphoid; *td.*, trapezoid; *tm.*, trapezium; *U*, ulna; *u*, unciform; *x*, epicuneiform; 1—3, internal, middle, and external cuneiforms; I—V, numbers of digits. (After Marsh.)

premolars are simpler than the molars. All the vertebral centra exhibit flattened articular ends, and none of the zygapophysial facettes are curved. The humerus differs from that of all other Ungulata (except the Typotheria) and resembles that of some rodents in being pierced by an entepicondylar foramen; the femur bears a third trochanter. The manus and pes are complete (fig. 164), with five hoofed digits, of which the third is the largest. They are plantigrade or slightly approaching the digitigrade position. The two series of carpal bones do not alternate, but are directly opposed; and an os centrale is sometimes distinct. In the tarsus the astragalus and calcaneum articulate respectively with the navicular and cuboid. The astragalus is shaped almost as in the Carnivora, but its upper surface, for articulation with the distal end of the tibia and fibula, is only slightly sinuous, not tongued or grooved. The calcaneum is scarcely if at all in contact with the fibula. *Hyracops* and *Phenacodus* may be mentioned as typical genera.

Phenacodus (fig. 165). The head is remarkably small. The skull is elongated, with the interorbital space wide and flat, the nasal bones abbreviated, and the premaxilla somewhat produced. The brain-cavity is relatively very small and its case is surmounted by a short but elevated sagittal crest. There is no postorbital process either on the frontal or jugal, and the zygomatic arch is not expanded behind. The mandibular rami are not fused together at the symphysis. The canine teeth are not much enlarged, and the anterior premolars are a little spaced. The foremost premolar in each jaw is simple, with only one root. Pm. 3 and 4 in the upper jaw have an inner lobe and two outer cusps; while each of the upper molars bears six tubercular cusps, two being internal, two intermediate, and two external. Each of the lower true molars bears two pairs of tubercular cusps, with an intermediate odd cusp behind. The axis exhibits a peg-shaped odontoid process and bears a large neural spine. The thoracic or dorsal vertebræ are 14 or 15 in number, the lumbars 6 or 7, and the caudals very numerous. There is no clavicle. The scapula exhibits a short coracoid process. The ilium is not much expanded, but the hind limb is relatively very large. Both feet are pentadactyl, with the axis passing through digit no. III, as in the Perissodactyla; and the metacarpal and metatarsal (or *metapodial*) bones are keeled distally. The animal may, indeed, have been as completely digitigrade as the tapir. Two species, *Phenacodus primævus* (fig. 165) and *P. wortmani*, are known by nearly complete skeletons from the Lower Eocene (Wasatch Formation) of Wyoming, the first about as large as a tapir, the second smaller. Remains of closely allied genera occur in the basal Eocene or Puerco

ORDER 4. UNGULATA. *Sub-Order* 1. *Condylarthra.*

FIG. 165.

Phenacodus primævus; skeleton as found in slab of rock, about one-seventh nat. size.—L. Eocene (Wasatch Formation); Big Horn Basin, Wyoming. (After Cope.)

Formation of New Mexico. Teeth very similar to those of *Phenacodus* are also known from the Upper Eocene of Switzerland.

Sub-Order 2. *Hyracoidea.*

The small surviving hyraces (*Hyrax* or *Procavia*, and *Dendrohyrax*) of Africa and Syria are generally believed to be the little-modified descendants of the Condylarthra; but no extinct genera of the sub-order HYRACOIDEA, to which they belong, have hitherto been identified with certainty. A typical skull from the Lower Pliocene of the Island of Samos has been recorded under the name of *Hyrax kruppi.* It is also curious that a fossil skull exhibiting a close resemblance to that of *Hyrax* has been obtained from the *Pyrotherium* Formation (probably early Tertiary) of Patagonia. This is named *Archæohyrax patagonicus.* The outer digits in the existing animals are reduced or wanting. The carpal bones of the two series are scarcely if at all alternating, and there is a distinct centrale below the scaphoid.

Sub-Order 3. *Amblypoda.*

Before the close of the Eocene period the Ungulata with a diminutive smooth brain attained their maximum development and became extinct. Many of these animals attained a remarkable size, some nearly as large as an elephant, and their limbs became very robust to support the ponderous trunk. They are generally grouped together in a sub-order named AMBLYPODA (blunt feet) or AMBLYDACTYLA (blunt toes), in allusion to their short and stumpy five-toed feet. The teeth are brachyodont, with the tubercles more or less fused into transverse ridges (thus technically described as *lophodont*); and they are never more than the normal 44 in number. All the vertebral centra exhibit flattened articular ends, and none of the zygapophysial facettes are curved. The humerus has lost the entepicondylar foramen, while the femur loses its third trochanter in the most specialized genera. The ulna and fibula are well developed. The feet are complete, small, and very stout, becoming slightly digitigrade. The two series of carpal bones scarcely alternate; but in the tarsus the broad, depressed and flattened astragalus extends from the navicular considerably over the cuboid, while the fibula distinctly articulates both with the astragalus and calcaneum. The two best-known genera are *Coryphodon* and *Dinoceras,* from the Lower and Middle Eocene respectively.

Coryphodon (figs. 166—168). The skull is elongated, with a much-produced facial region, which is somewhat expanded towards the end of the snout below the wide narial opening. The basicranial axis is straight. There are no excrescences on the top of the skull, though rudiments of these are sometimes feebly distinguishable. The zygomatic arch is massive and expanded, while the jugal unites with the maxilla in front of the orbit. The maxilla is also massive and usually deeply indented on the side behind the canine. The nasal bones taper in front. The cerebellum is proved to have been nearly or quite as large as the cerebral hemispheres, and much expanded transversely. The dental formula is $\frac{\text{i. 3, c. 1, pm. 4, m. 3}}{\text{i. 3, c. 1, pm. 4, m. 3}}$. The canines are comparatively large, especially those of the upper jaw, and there is a short diastema between the canine and the premolars in both jaws. The lophodont character of the premolars and molars is well shown in the drawing of the upper and lower dental series, figs. 166 A, B. The neck is of considerable length and flexible, and the odontoid process of the axis vertebra is a short peg. The length of the slender tail is uncertain. No clavicle has been observed. The distal end of the radius is larger than that of the ulna. The femur bears a distinct third trochanter. When in a position of rest the femur and tibia are slightly inclined to each other, and the fibula is clearly proved to

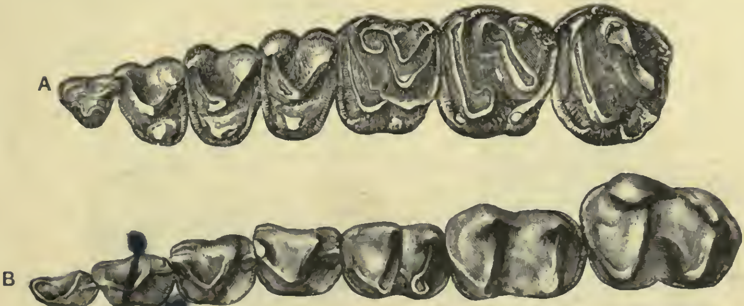

Fig. 166.

Coryphodon h[illegible]; molar-premolar series of upper (A) and lower (B) jaws, left si[illegible], o[illegible]half nat. size.—L. Eocene (Wasatch Formation); Wyoming. (After Marsh.)

articulate distally both with the astragalus and the calcaneum. The typically Amblypodous feet are well seen in figs. 167 B, C. The first-discovered evidence of *Coryphodon* was a fragment of mandible from the Lower Eocene of the London Basin, named *Coryphodon eocænus*. Other portions of jaws and limb-bones have subsequently been met with on the same horizon both in England and France. The only important specimens hitherto found, however, are American. Nearly complete skeletons, besides many fragments, have been discovered near the base of the Eocene (Wasatch stage) in Wyoming, Utah, and New Mexico, and one of the best-known forms is *Coryphodon hamatus* (fig. 168), an animal attaining a length of about two metres.

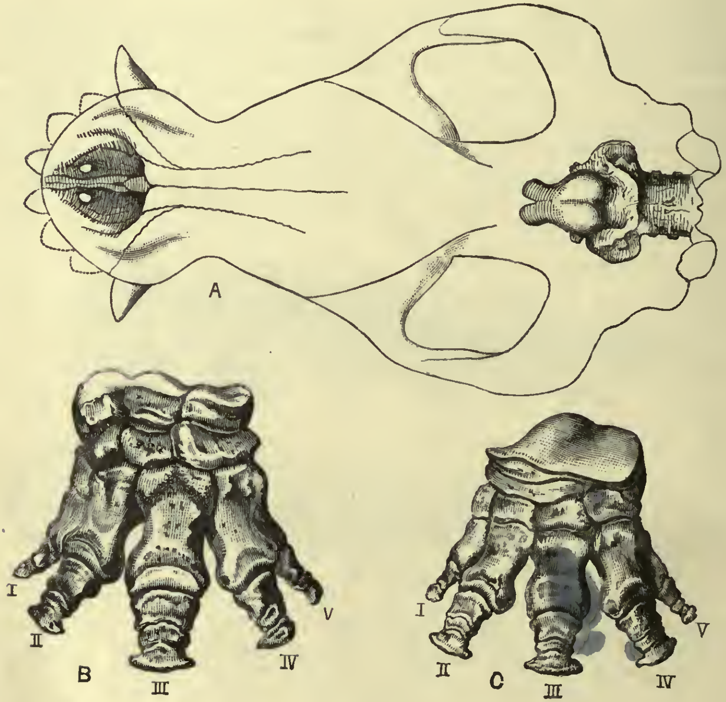

Fig. 167.

Coryphodon hamatus; outline of upper aspect of cranium, showing also size and form of brain-cavity (A), drawing of left manus (B), and drawing of left pes (C), the first being one-fifth, the others one-third nat. size.—L. Eocene (Wasatch Formation); Wyoming. (After Marsh.)

ORDER 4. UNGULATA. *Sub-Order* 3. *Amblypoda.*

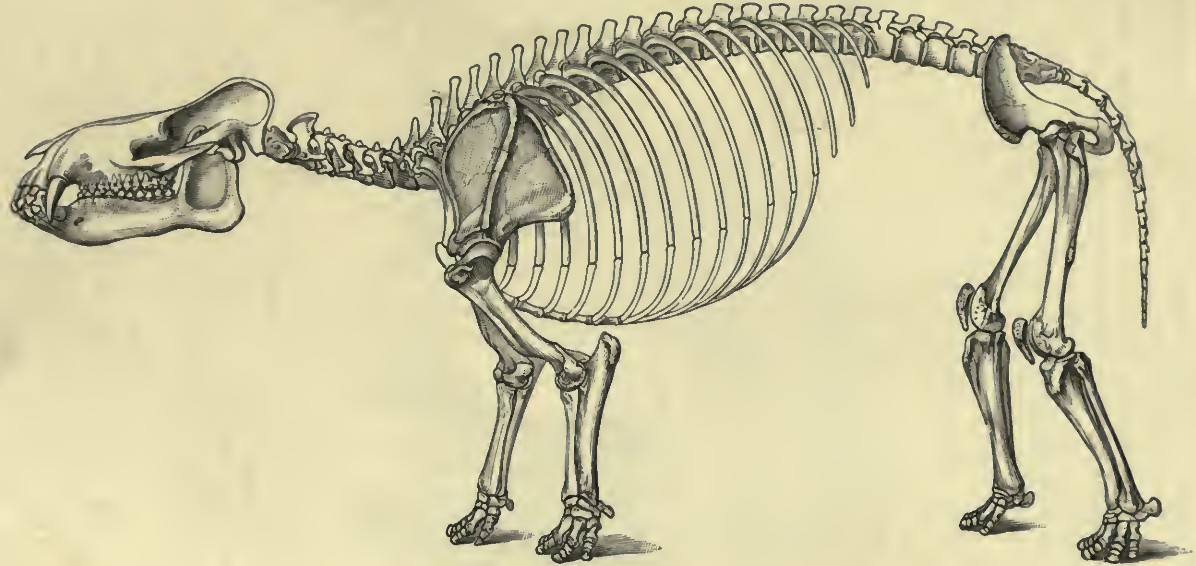

FIG. 168.

Coryphodon hamatus; restoration of skeleton by O. C. Marsh, about one-twelfth nat. size.—L. Eocene (Wasatch Formation); Wyoming.

Dinoceras (figs. 169, 170). The skull in this genus is long and narrow, with an elevated, more or less quadrangular occiput, and a much-produced facial region. The basicranial axis is straight. The top of the skull supports three transverse pairs of smooth bony prominences, which form its most conspicuous feature and are alluded to in the generic name. These prominences are not separate ossifications, but merely elevations upon the nasal, maxillary, and parietal bones respectively, and the smoothness of their surface shows that they cannot have been encased in ordinary horn. They increase in size backwards, the parietal prominences being relatively very large, and raised on a conspicuous crest which extends from near the orbits entirely round the lateral and posterior margins of the cranium. The cranial roof is thus much thickened, but air-cavities are few and rare. The orbit is large and confluent with the temporal fossa, while there is not even a postorbital prominence of the frontal region. The sutures between the various elements can usually be observed in

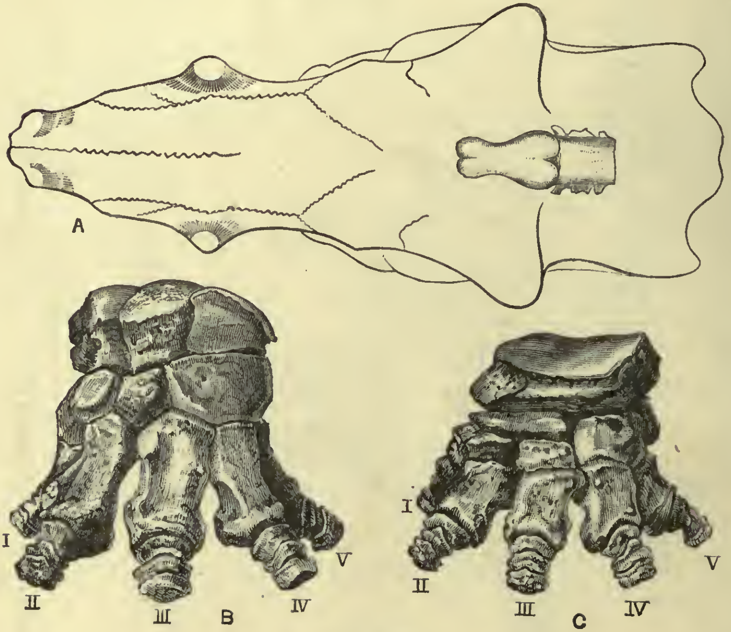

Fig. 169.

Dinoceras mirabile; outline of upper aspect of cranium showing also size and form of brain-cavity (A), drawing of left manus (B), and drawing of left pes (C), the first being one-eighth, the others one-fifth nat. size.—M. Eocene (Bridger Formation); Wyoming. (After Marsh.)

young individuals, but most of them are closed in the adult. It is clear that the parietals are relatively large, while the frontals are short. The nasals are excessively elongated, being about half as long as the entire skull; and at their anterior end there is a pair of minute prenasal ossifications, apparently homologous with the ossicle sometimes found at the extremity of the snout in the existing pigs. The jugal bone of the zygomatic arch extends well forwards to the front of the orbit, where it meets an extensive lachrymal element. The maxilla forms a large portion of the lateral surface of the skull, and bears all the upper teeth; it is perforated by a large antorbital foramen, which is obscured in direct side view (fig. 170) by a ridge extending upwards in front of the orbit. The premaxillæ are slender and toothless, but do not extend further forwards than the overhanging nasals. The mandible is comparatively slender, except at the symphysial end, where the two rami are fused in a massive symphysis, deeply excavated above, and where a pair of decurved processes protect the upper canine tusks. The condyles for articulation with the upper jaw are remarkable (unique among Ungulata) in being directed backwards, not upwards, and in being raised very little above the level of the grinding surface of the lower molars. The coronoid region is much elevated, and the angle of the mandible is sometimes distinctly

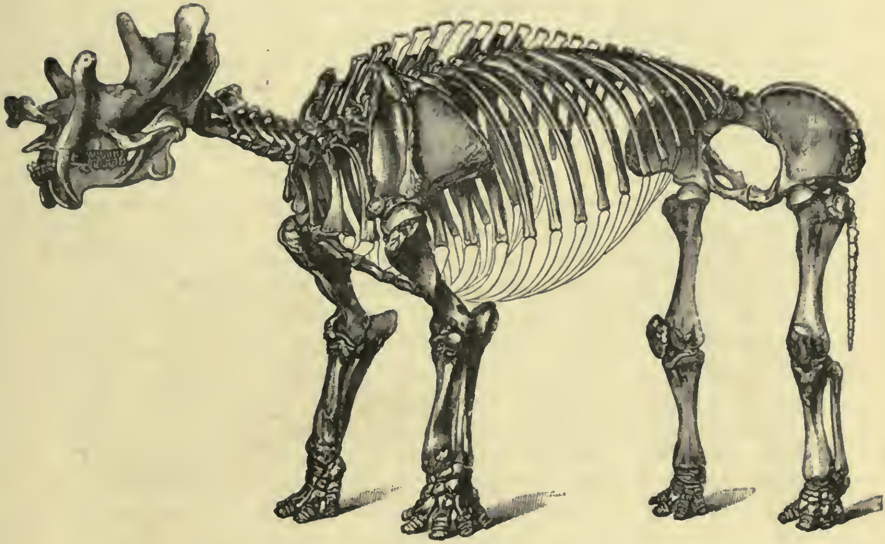

FIG. 170.

Tinoceras ingens; restoration of skeleton by O. C. Marsh, one-thirtieth nat. size.—M. Eocene (Bridger Formation); Wyoming.

inflected. The dental formula is $\frac{\text{i. 0, c. 1, pm. 3, m. 3}}{\text{i. 3, c. 1, pm. 3 or 4, m. 3}}$. No traces of incisors have been observed in the premaxillæ, even of the most immature specimens, though a series of shallow depressions are sometimes seen on the oral margin of these bones. The lower incisors, however, are always well-developed, each with a single closed root in its own separate socket, and with the crown completely invested in enamel. The upper canines are enormously developed, but relatively larger in some individuals (presumably males) than in others (presumably females). The crown forms a trenchant tusk, enamelled but not serrated; while the root is deeply implanted in the maxilla, closed in the adult, and sometimes extending even into the base of the maxillary horn-core. The lower canine is small, resembling the incisors with which it is in continuous series; while there is always a diastema between this tooth and the hinder teeth in both jaws. All the premolars and molars of the upper jaw are implanted by three roots, while those of the lower jaw exhibit only two roots. The crown is always remarkably low (brachyodont), while the transverse ridges become almost obliterated by wear. The milk-dentition is scarcely known, though there are indications that all the incisors, canines, and premolars had deciduous predecessors. The cervical vertebræ are as usual seven in number, and much resemble those of the elephants, though altogether about one-third longer and thus rendering a proboscis unnecessary. The trunk vertebræ are about twenty-three in number, with the centra relatively longer than those of the cervicals, and with thin epiphyses which are often imperfectly ossified. About nineteen bear free ribs, while at least four are lumbar. The series of sternal bones is not completely known. The sacrum comprises four vertebræ, and the tail seems to have been very slender. All the limb-bones are nearly or quite solid. There is no clavicle. The fore limb is shorter than the hind limb and considerably bent at the elbow joint, so that the muscular attachments on the robust humerus are very prominent. The radius and ulna are almost equal in stoutness, and the latter rises into a large olecranon process. The fore foot is shown in fig. 169 B. The central bone of the carpus may be separate in very young animals, but it is not observable in the adult. The hind limb when at rest forms an almost vertical column. The pelvic bones are fused together, first into two independent ossa innominata, then into a single mass, but always articulating in an open suture with the sacrum. The ilium is much expanded and rounded in outline. The femur exhibits no trace of a third trochanter, and is much longer than the tibia, which bears a very prominent tuberosity for the attachment of the patellar ligament. The fibula is comparatively slender, but thickest at its lower end. The hind foot, which is smaller than the fore foot, is shown in fig. 169 C. The typical species, *Dinoceras mirabile* (fig. 169), is almost completely known from more or less fragmentary skeletons discovered in the Bridger Eocene of Wyoming, and seems to have attained a length of about three metres; while other species are recognized in the same formation. *Tinoceras* (fig. 170), also from the Bridger Eocene of Wyoming, differs very little from *Dinoceras*; while *Uintatherium*, based on specimens too imperfect for precise determination, from the same formation and locality, is not improbably identical with the latter.

Sub-Order 4. *Proboscidea.*

The existing elephants represent a sub-order of hoofed quadrupeds which have retained nearly all the essentially primitive characters of the order, except those directly connected with the well-known unique mode of feeding which they have acquired. Apart from the possession of (i.) a trunk or proboscis, (ii.) tusks instead of incisors, and (iii.) a grinding dentition of abnormal type, they are indeed the least specialized among surviving Ungulata. Although the brain is of considerable size and the cerebral hemispheres exhibit numerous convolutions, these hemispheres do not cover the cerebellum, which is entirely posterior to them. In the circulatory system, there are two anterior venæ cavæ still persisting. In the skeleton, the limb-bones are adapted solely for the support of the massive body, with a separate and complete radius and ulna, a separate and complete tibia and fibula, and five hoofed digits on each foot. In the carpus, the bones of the two rows are still directly opposed to each other, and not alternating; while in the tarsus, the astragalus is flattened, not tongued or grooved on its articular face for the tibia.

So far as can be inferred from the disposition of the nasal bones, the cranial roof, and the shortened neck, the Proboscidea were already differentiated from the other hoofed quadrupeds by the possession of a prehensile trunk so long ago as the early part of the Miocene period. No more ancient forms have hitherto been identified, and no known group of Eocene Ungulata can yet be claimed with much plausibility as directly ancestral to them. *Pyrotherium*, from deposits which seem to date back to an early Tertiary period in Patagonia, is sometimes claimed to be a primitive Proboscidean; but its affinities still remain to be demonstrated. From the Middle Miocene onwards, however, many fine examples of the skull and dentition of elephants are known. *Dinotherium*, *Mastodon*, and *Elephas* follow each other in succession, and show how the incisors immediately became the characteristic elephantine tusks as soon as the proboscis had been acquired, while the ordinary lophodont molars were more gradually transformed, by complicated folding and deepening, into the large powerful grinders of the Pleistocene and Recent elephants. *Dinotherium* seems to have completely lost its upper incisors (though this is not quite certain), while those of the lower jaw form a unique downwardly curved pair of tusks; so that this genus cannot be regarded as an actual link between *Elephas* and its primitive ancestors. But some of the Miocene species of *Mastodon* exhibit an upper and lower pair of persistently growing functional incisors, very suggestive of the front teeth of an ordinary rodent; and at least the upper pair usually retain a longitudinal band of enamel, which is slightly disposed in a spiral direction, though evidently reminiscent of the time when it was a regular straight band to ensure a chisel-like edge as it worked against its fellow in cutting food. Most of the Pliocene species of *Mastodon* advance a grade further and are entirely destitute of the lower incisors, while the upper pair are tusk-like, usually with no traces of the enamel-band; and *Elephas*, as is well known, retains only

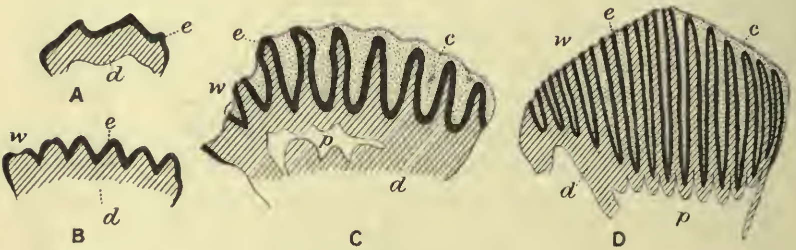

FIG. 171.

Diagrammatic vertical longitudinal Sections of Molars of Proboscidea. A. *Dinotherium*. B. *Mastodon*. C. *Elephas* (*Loxodon*). D. *Elephas* (*Euelephas*). *c*. cement; *d*, dentine; *e*, enamel; *p*, pulp-cavity; *w*, worn front portion of tooth.

the upper incisors, which are persistently growing and only enamelled at the extreme apex, which soon wears away. As to the grinding teeth (fig. 171), those of *Dinotherium* are comparatively small, with never more than two or three transverse ridges, which are about as deep as thick, invested with enamel, and separated by a deep valley (A); the molars of *Mastodon* have slightly more numerous and somewhat deeper ridges, but these are also separated by deep valleys (B); while the grinding teeth of *Elephas* exhibit still more numerous and deepened ridges (now to be described as "plates"), separated by cleft-like valleys, which are filled to overflowing by soft bony cement (C, D). As the complication of the grinding teeth and their relative increase in size take place, the successional teeth are gradually lost, and the entire series of grinding teeth cannot be accommodated in the mouth at one time. Thus arises the remarkable mode of development observed in the existing elephant, where rarely more than two—never more than parts of three—grinders are functional in each half of either jaw at one and the same time, and a series of six or seven molars succeed each other from behind forwards during the life of the animal, the new ones emerging from a socket at the back of the jaw while the worn teeth are crushed out of the mouth in front. A somewhat similar mode of succession is to be noted in the kangaroo and the manatee.

While this process of evolution in the teeth has occurred, there is also some reason to believe that the proboscis has increased in size; for the skull in some of the earlier mastodons is much less thickened by the growth of cellular bony tissue than that of the later mastodons and elephants, and there would thus be less surface available for the necessary muscular attachments in the earlier than in the later forms.

Dinotherium (figs. 171 A, 172, 173). Only one imperfect example of the skull of *Dinotherium* is known, but many fine specimens of the mandible and the dentition have been discovered. The cranium (fig. 172) is long and low compared with that of the elephant, and it seems to taper in front without space for upper incisors, though this appearance may be accidental and due to fracture. The slender mandibular rami are fused together at the symphysis, where they are bent downwards and bear a pair of recurved incisors or tusks, which seem to have grown from persistent pulps, but do not exhibit the characteristic elephantine "engine-turned" structure when examined in transverse section. The dental formula of the adult is $\frac{\text{i. } 0?, \text{ c. } 0, \text{ pm. } 2, \text{ m. } 3}{\text{i. } 1, \text{ c. } 0, \text{ pm. } 2, \text{ m. } 3}$, and all these teeth are simultaneously in use. Each of the premolars has two transverse ridges, which are connected in the upper jaw (fig. 173) by a longitudinal ridge on their outer side; the true molars, both above and below, bear respectively three, two, and two ridges. There are three milk-molars in both jaws in young individuals, which have respectively two, two, and three ridges; but the foremost tooth is small and not replaced when shed. Only two imperfect skeletons definitely associated with the characteristic jaws are known, namely, from the Miocene of Abtsdorf and Franzensbad in Bohemia; but several isolated bones have been assigned to *Dinotherium* with much probability of correctness. All comparisons of the vertebræ and limb-bones hitherto made, tend to demonstrate its truly Proboscidean nature. The typical species is *Dinotherium*

Fig. 172.

Dinotherium giganteum; imperfect skull and mandible, one-fifteenth nat. size.—L. Pliocene; Eppelsheim, Hesse Darmstadt. (After Kaup.)

giganteum, with a skull about a metre in length, from the Lower Pliocene of Hesse Darmstadt. Remains of this and other smaller species occur widely distributed in the Middle and Upper Miocene deposits of central Europe. Similar teeth are met with in the Siwalik Formation (Lower Pliocene) of India; while limb-bones from the Pliocene of the Island of Samos and from Pikermi, near Athens, have also been ascribed to the same genus. No evidence of *Dinotherium* has hitherto been discovered in America.

Mastodon (figs. 171 B, 174, 175). The Proboscideans commonly grouped under the generic name of *Mastodon* differ from *Dinotherium* in their somewhat larger and more complicated molars, which are never all simultaneously in use. Whereas the number of ridges in the six teeth (three milk-molars, three true molars) of *Dinotherium* is expressed by the figures 2, 2, 3, 3, 2, 2; in the corresponding teeth of *Mastodon* the numbers are either 1 (or 2), 2, 3, 3, 3, 4 or 2, 3, 4, 4, 4, 5, with very little variation. There is also nearly always a tendency in *Mastodon* for each ridge to divide into right and left halves; while very frequently these ridges are further subdivided into nipple-like bosses (hence the generic name), which are sometimes displaced and partly fill the valleys. The enamel on the teeth is very thick, and cement is either absent or very little developed. There are always three milk-molars in both jaws, and of these the two hindermost are usually replaced by premolars, though in some of the later species (e.g., *Mastodon americanus* or *M. ohioticus*) they persist throughout life. Some of the earlier species bear tusks in both jaws, and exhibit a much-produced mandibular symphysis (*Tetrabelodon*) others have only upper tusks, but these retaining some enamel (*Dibelodon*); while others possess only upper tusks without enamel (*Mastodon* proper). Again, in some species, as already indicated, the three "intermediate molars" (namely, m-m. 4, m. 1, m. 2) each bear three ridges, while in

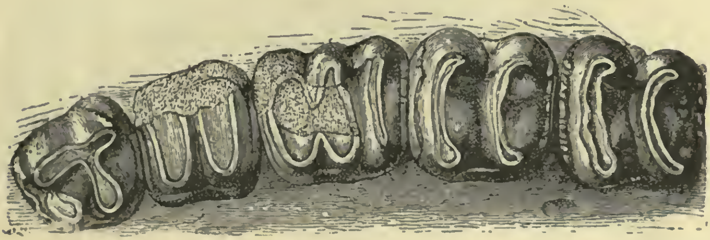

FIG. 173.

Dinotherium giganteum; left upper dentition, one-quarter nat. size.—M. Miocene; Gers, France. The two teeth to the left of the figure are the third and fourth premolars, while the other teeth are the three true molars. (After Gaudry.)

other species the same teeth have four ridges; the various forms have thus been subdivided into *Trilophodon* and *Tetralophodon* respectively. No subdivision of the genus *Mastodon*, however, is satisfactory and cogent, and it seems best to employ the term in a wide sense. The earliest species hitherto discovered are Trilophodonts from the Middle Miocene of Europe (*M. turicensis* and *M. angustidens*), and the latter is known by a nearly complete skeleton from the Department of Gers in France (fig. 175). Both Trilophodonts and Tetralophodonts are found in the Upper Miocene of Europe and North America, while a few Trilophodont molars have been met with in a formation believed to be of still more ancient date in Montana, U.S.A. *Mastodon longirostris* (fig. 174) is a well-known Tetralophodont from the Lower Pliocene of Eppelsheim (Hesse Darmstadt) and other European localities, showing much-mammillated ridges on the teeth; and closely similar forms are known by fragmentary remains from the Lower Pliocene of Pikermi, near Athens, the Island of Samos, and Maragha in Persia. *Mastodon arvernensis* is another Tetralophodont from the Upper Pliocene of the Auvergne, France, and the Val d'Arno, Tuscany. Pliocene species of *Mastodon* are also abundant in the Siwalik formation of India, and teeth have been discovered in China and Algeria. Several well-preserved teeth are known from the Pliocene Crag deposits of Norfolk and Suffolk. Before the close of the Pliocene period the genus seems to have become extinct in Europe, but some species survived in the Pleistocene both in North and South America. The best-known American Pleistocene species is a Trilophodont (*M. americanus* or *M. ohioticus*), of which entire skeletons are often discovered mired in the salt-marshes of the United States, sometimes in association with flint implements. Young individuals exhibit rudimentary lower tusks, but these are lost in the adult. The South American species are also Trilophodonts and range as far south as

Fig. 174.

Mastodon longirostris; left upper milk-molars, two-thirds nat. size.—L. Pliocene; Eppelsheim, Hesse Darmstadt. (From Gaudry's *Enchaînements*, after Kaup.)

the Argentine province of Buenos Aires. Many of the forms seem to have rivalled the largest elephants in size.

Elephas (figs. 171 C, D, 176). Some of the more highly specialized types of *Mastodon* pass almost insensibly into the more generalized forms of true elephants, and it is difficult to find a constant difference between the two genera. The ridges of the molars, however, are always more numerous in *Elephas*, and they are usually deep plates, while the intervening clefts or valleys are filled with cement. The lowest grade, known only from the Pliocene of India, Burmah, Java, the Philippine Islands, China, and Japan, is named *Stegodon*, the ridges on its teeth being roof-shaped in section and the valleys being only partly filled with cement. The number of the ridges on the "intermediate molars" of this form varies from 6 to 8. The next grade, named *Loxodon* in allusion to the lozenge-shaped areas often observed when the ridges are worn, has the "intermediate molars" with from 7 to 9 ridges, deeper and more compressed. The most advanced grade, *Euelephas*, may exhibit the "intermediate molars" with as many as 12, 15, and 16 ridges respectively, these being now indeed closely adpressed deep plates. The sub-genus *Stegodon*, as already remarked, is exclusively Asiatic, and the finest known specimens are from the Siwalik Formation of India. A skull of *Elephas* (*Stegodon*) *ganesa* in the British Museum exhibits a pair of tusks nearly 3 metres in length. The sub-genus *Loxodon* survives in the existing African elephant (*Elephas africanus*), and has extinct representatives widely distributed in the Pleistocene and later Pliocene deposits of Europe, as also in the Lower Pliocene of India. The extinct Indian species, *E. planifrons*, is unique so far as known in exhibiting two premolars to replace the milk-molars in both jaws. The European Upper Pliocene species, *E. meridionalis*, is

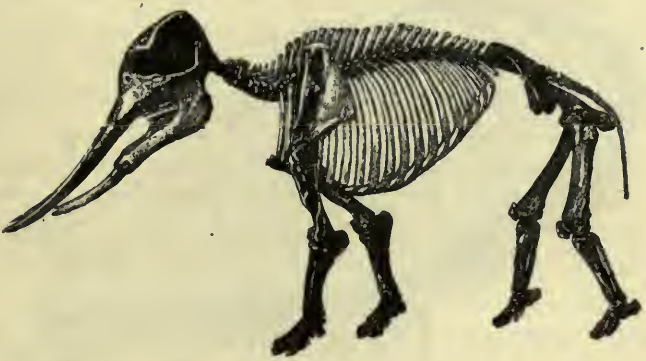

FIG. 175.

Mastodon angustidens; restoration of skeleton by A. Gaudry, one-fiftieth nat. size.—M. Miocene; Gers, France.

recorded from Italy, Hungary, Roumania, southern Russia, France, the Norwich Crag, the Cromer Forest Bed, and from a fissure in Dorsetshire: one nearly complete skeleton from Durfort (Gard), in the Paris Museum, seems to prove this to be the largest known true elephant with a height of about four metres. *E. antiquus*, closely related to the existing African elephant, is the common Pleistocene Loxodont of Europe, with dwarf varieties (*E. mnaidriensis* and *E. melitensis*) in Malta and Sicily, where remains of adult animals ranging from one to two metres in height are common in certain fissures and caves. *Euelephas* is represented at the present day by the Indian elephant (*E. indicus*), and the earliest traces of the sub-genus are met with in the Siwalik Formation. The best-known and most widely distributed extinct species, however, is the mammoth (*E. primigenius*), which is first found in the Cromer Forest Bed, and is discovered in Pleistocene deposits over the greater part of the temperate regions of the northern hemisphere, ranging even within the Arctic circle. In the Old World it is found as far south as Armenia (the so-called *E. armeniacus*), while in the New World it reaches even Mexico (the so-called *E. columbi*); and it is to be noted that the southern varieties have more coarsely ridged molars than the more northern and typical forms. Mummified carcases of this elephant have been found in the frozen earth of the Siberian tundras, proving that at least the northern race of the species was covered with reddish wool and long black hair; and it is clear that the animal fed upon the coniferous trees, from fragments of the wood discovered in the crevices of the teeth. It must

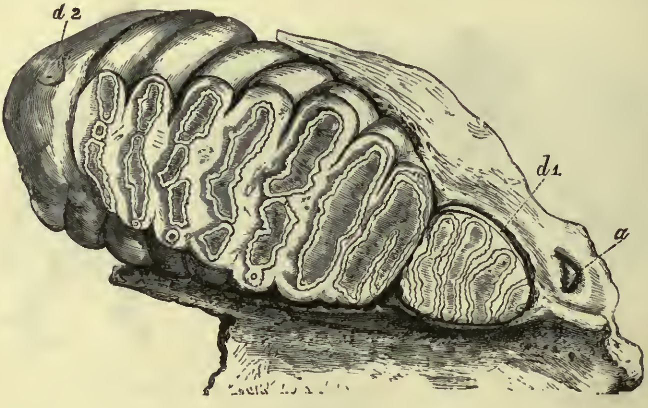

FIG. 176.

Elephas primigenius; right upper milk-molars 2 (*d.* 1) and 3 (*d.* 2), nat. size.—Pleistocene; Creswell Caves, Derbyshire. *a*, the anterior root of milk-molar 2 seen through a vacuity in the bone. (After Owen and Metcalfe.)

have lived in great numbers in the Arctic Regions, its tusks having been collected from time immemorial on account of the commercial value of the ivory. The extinct species does not appear to have exceeded the modern Indian elephant in size; and that it was contemporary with man in western Europe is proved not only by the association of its remains with flint implements, but also by a rough sketch of its outward hairy form on a fragment of tusk discovered with other traces of man's handiwork in a cavern in Dordogne, France.

Sub-Order 5. Ancylopoda.

Another primitive sub-order of Ungulata which had an extraordinarily wide geographical range in the Miocene and Pliocene periods, but then became extinct, is characterized by the structure of the feet, which exhibit considerable resemblance to those of the extinct ground-sloths of America and the existing pangolins (*Manis*) of the Old World. When the limbs alone were known, they were indeed referred to the Edentata. The weight of the body in walking seems to have been mainly supported by the outer side of the twisted foot, while the phalanges of each digit curve upwards on highly-developed ginglymoid facettes (see fig. 177) and are terminated each by a cleft, pointed, claw-shaped bone—hence the sub-ordinal name ANCYLOPODA or ANCYLODACTYLA. The dentition resembles that of some of the Perissodactyla, when worn even suggesting that of the rhinoceroses, and the anterior teeth are sometimes similarly lost by specialization; but the dental crowns are always distinctly buno-lophodont before use. The most generalized forms (*Homalodontotherium* and its allies) occur in the *Pyrotherium* and Santa Cruz Formations (early Tertiary) of Patagonia; the more specialized genera (*Macrotherium*, *Chalicotherium*, and their allies) seem to have ranged throughout the greater part of Europe, Asia, and North America.

Homalodontotherium (fig. 177). The skull is short and massive, with the narial opening very large and the premaxillary region extending far in advance of the nasals. The orbit communicates with the temporal fossa, but there is a considerable postorbital process of the frontal region. The dentition is complete, the formula being $\frac{\text{i. 3, c. 1, pm. 4, m. 3}}{\text{i. 3, c. 1, pm. 4, m. 3}}$, and the teeth form a regular close series, there being neither a diastema nor any enlargement of a canine or incisor. The incisors and canines are small, flattened, triangular teeth, with a conspicuous cingulum on the inner side. The premolars and molars may be described as intermediate in height between the brachyodont and hypsodont types. The upper and lower premolars are simpler than the molars, which when worn are quite rhinocerotic in type. The last lower molar is distinctly only bilobate.

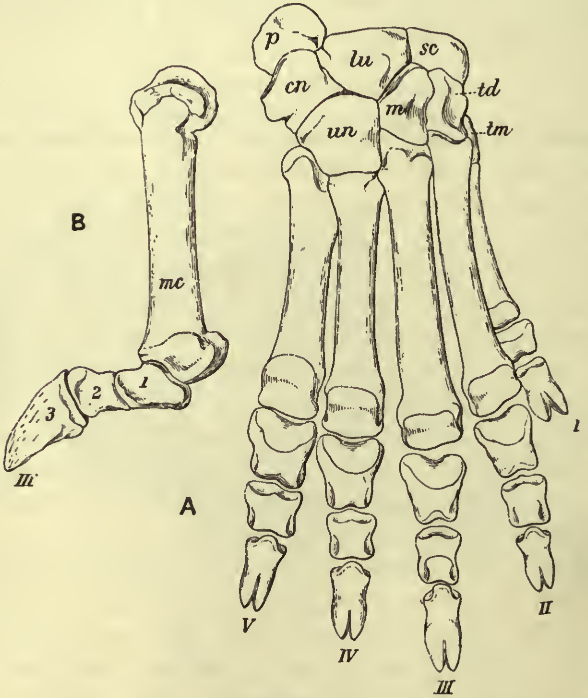

Fig. 177.

Homalodontotherium segoviæ; right manus, upper aspect (A) and third digit of the same in side view (B), two-ninths nat. size.—Santa Cruz Formation (Lower Tertiary); Patagonia. *cn.*, cuneiform; *lu.*, lunar; *m.* magnum; *mc.*, metacarpal; *p*, pisiform; *sc.*, scaphoid; *td.*, trapezoid; *tm.*, trapezium; *un.*, unciform. I—V, numbers of digits; 1—3, numbers of phalanges. (After Ameghino.)

The centra of the vertebræ exhibit flattened or slightly concave ends. The transverse process of the axis is perforated by the vertebrarterial canal; the odontoid process is peg-shaped. The humerus is short and stout, with an enormous deltoid crest, which suggests the power of burrowing or digging. The radius and ulna are complete and separate, and there is a deep fossa in the humerus for the olecranon. The two rows of carpal bones alternate, and the manus is complete (fig. 177). The metacarpal bones are comparatively long and slender, while the phalanges are short and small. The first digit is much the smallest. The femur is short, broad, and flattened, much like that of the ground-sloths, though there is a well-developed third trochanter; the form and proportions of the tibia and fibula also suggest a comparison with the same animals. The astragalus is a square and flattened bone, with a slightly convex articular surface for the tibia; it articulates directly with the navicular and does not touch the cuboid. The pes is complete, with five digits, and the metatarsals are much shorter than the metacarpals; the intermediate phalanges are also very short and stout. Many specimens of *Homalodontotherium* have been obtained from the Santa Cruz Formation of Patagonia, and nearly all the bones of the trunk and limbs have been found at different times in direct association with the skull and teeth. The typical species is *H. cunninghami*, with a skull about 0·5 m. in length. *H. segoviæ* is another well-known form of almost equally large size.

Macrotherium. This genus is known by the greater part of the skeleton found associated with the skull in the Middle Miocene of Sansan, Gers, France; by another portion of skeleton in undoubted association with the skull in the same formation at La Grive St Alban, Isère; and by many other fragments from contemporaneous strata both in France and Germany. The skull has a relatively very short facial region, and the orbital cavity is not separated from the temporal fossa. The upper incisors and canines are unknown, but so far as it can be expressed the dental formula is $\frac{\text{i. ?, c. ?, pm. 3, m. 3}}{\text{i. 3, c. 1, pm. 3, m. 3}}$. The fore limbs are considerably longer than the hind limbs. The radius and ulna are separate and slender, while the olecranon process of the ulna is small. The femur is destitute of a third trochanter. The bones of the two carpal rows alternate, and the manus comprises only three digits (nos. II, III, IV), of which the outermost is the largest. The hind foot is also similarly tridactyl, with the largest digit outside, but the metatarsals are only half as large as the metacarpals. The typical and best known species, *M. magnum*, must have been an animal nearly three metres in length.

Teeth almost identical with those of the Sansan *Macrotherium* are known from the Lower Pliocene of Eppelsheim, Hesse Darmstadt, and of Baltavar, Hungary; from China; from Canada; and from the Loup Fork Beds (Upper Miocene) of Nebraska, U.S.A.—all described under the name of *Chalicotherium*. An imperfect skull with similar molars (but wanting the snout), from the Lower Pliocene of Pikermi, Greece, and portions of another similar skull (clearly indicating the absence of upper and lower incisors and upper canines), from the

Siwalik Formation of India, have also been referred to the same genus. Various limb-bones sufficiently resembling those of *Macrotherium* have likewise been described from Pikermi and the Island of Samos, under the generic name of *Ancylotherium.* These indicate somewhat more robust limbs, of more nearly equal size than those of the Sansan fossil. There are, however, only three digits in each foot.

Sub-Order 6. *Typotheria.*

The Tertiary Formations of South America, especially those of the Argentine Republic, yield skeletons of many strange extinct ungulates which are quite unlike those hitherto found in any other country. These seem to represent at least three distinct sub-orders of which the true relationships are still entirely obscure, but which must be little-modified descendants of very primitive eutherian mammals.

The members of the first of these South American groups differ from all other known ungulates in the possession of well-developed clavicles. The teeth are deepened and more or less rodent-like; but the dental series is nearly complete as a rule, only the canines being constantly reduced or absent. The humerus is pierced by an entepicondylar foramen (as in Condylarthra and some Rodentia), and the femur has a third trochanter. The radius and ulna (tibia and fibula) are complete and usually separate, and the digits are four or five in number. The sub-order thus briefly characterized is named Typotheria from *Typotherium,* the genus first described. Its earliest representatives occur in the *Pyrotherium* and Santa Cruz Formations of Patagonia, while the latest and largest forms are met with in the Pampa Formation (probably Pleistocene) of Buenos Aires. Most of the earlier genera (e.g., *Protypotherium, Icochilus*) possess a complete dentition, with the teeth in a regular and nearly continuous series, and the incisors, both above and below, are rooted; the latest genus from the pampas (*Typotherium*) has completely lost the canines, while there is a considerable diastema, with only one pair of persistently-growing incisors in the upper jaw, two pairs in the mandible. In the course of evolution it may also be noted that the carpus loses its os centrale, while the hind foot is deprived of one digit. In the early forms with five digits on each foot, the inner digit (no. I) so far as known is opposable to the others.

Pachyrucus. A small animal known by nearly complete skeletons from the Santa Cruz and Lower Pampa Formations of the Argentine Republic. The shape of the skull is much like that of a rabbit, but the inflated auditory bullæ are exposed on the roof of the occipital region. The zygomatic arch is large, but the orbital cavity is not separated from the temporal fossa. The condyles of the mandible are rounded or a little elongated antero-posteriorly, and the rami are fused together at the symphysis. The dental formula is $\frac{\text{i. 1, c. 0, pm. 3, m. 3}}{\text{i. 2, c. 0, pm. 3, m. 3}}$, and all the teeth are hypsodont, without roots, and must thus have been persistently-growing. The upper incisors are much extended along the margin of the jaw, the width of each equalling that of the two opposed lower incisors. The molars and premolars are much laterally compressed, and those of the upper jaw do not exhibit a fold on the inner face. The vertebral column is remarkably rodent-like, and the lumbar vertebræ bear broad descending transverse processes. The radius and ulna are free, but the tibia and fibula are fused both proximally and distally. The pelvis is notably elongated.

Typotherium (fig. 178). The skull in this genus is shaped much like that of *Pachyrucus*, and the orbital cavity is similarly not separated from the temporal fossa; but the auditory bullæ are scarcely inflated and are confined to the lower part of the occipital region. The dentition is slightly more reduced, the formula being $\frac{\text{i. 1, c. 0, pm. 2, m. 3}}{\text{i. 2, c. 0, pm. 1, m. 3}}$; and the enamel on the inner face of the upper molars exhibits two vertical folds. The cervical vertebræ are short, and the lumbars bear nearly horizontal transverse processes. The sacrum is very long, comprising seven vertebræ, and the pelvic elements are also much elongated. The tail is short and small. The femur bears a large third trochanter; while the tibia and fibula, like the radius and ulna, are entirely free. The fore foot is five-toed with slightly cleft ungual phalanges; the hind foot is four-toed, with hoof-like ungual phalanges. The typical species, *Typotherium cristatum*, from the Pampa Formation of Buenos Aires, is one of the best-known and largest forms, with a skull about 0·3 m. in length.

Sub-Order 7. *Toxodontia.*

Though much resembling the Typotheria, the TOXODONTIA (thus named from the typical genus *Toxodon*) are more normal ungulates (i.) in being destitute of clavicles, and (ii.) in wanting an entepicondylar foramen in the humerus. The teeth are deepened and more or less curved, often persistently growing throughout life. The dental series is nearly complete, only the canines being constantly reduced or absent. The neck is short. The bones of the two rows of the carpus alternate; and there are only three digits on each foot.

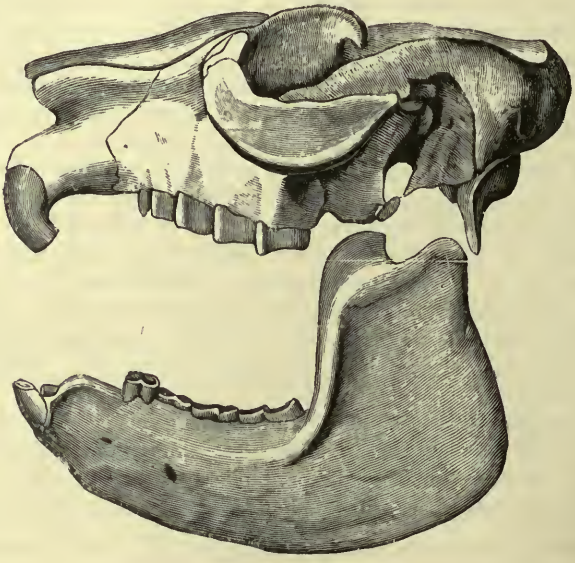

Fig. 178.

Typotherium cristatum ; skull and mandible, one-quarter nat. size.—Pleistocene (Pampa Formation); Buenos Aires, Argentina. (After Gervais.)

Toxodon (fig. 179). The skeleton in the typical genus *Toxodon* is almost completely known by associated sets of bones in the La Plata Museum. The skull is very massive, with a comparatively small facial region and the premaxillæ projecting far in front of the nasals. The orbital cavity is not separated from the temporal fossa. The auditory bullæ are small, and the meatus is directed upwards. The two rami of the mandible are fused at the symphysis, which is deeply channelled. The dental formula of the adult is $\frac{\text{i. 2, c. 0, pm. 3 or 4, m. 3}}{\text{i. 3, c. 1, pm. 2 to 4, m. 3}}$, and all these teeth grow from persistent pulps. The molars and premolars are much curved, and the latter are simpler than the former in both jaws. The upper molars are triangular in section, while the lower molars are

ORDER 4. UNGULATA. *Sub-Order* 7. *Toxodontia.*

FIG. 179.

Toxodon platensis; partially restored skeleton, one-eighteenth nat. size.—Pleistocene (Pampa Formation); Buenos Aires, Argentina. (After Lydekker, from specimen in La Plata Museum.)

compressed, with three internal folds. The upper incisors are scalpriform or chisel-shaped, but the two inner pairs of the lower jaw are directed straight forwards. The premolars are preceded by milk-molars with well-formed roots, while the incisors and canine also seem to have had deciduous predecessors. The trunk is of very robust proportions, and the back curves downwards in front to the lowly-placed neck and head. The cervical vertebræ are short, with flattened ends. The dorso-lumbar region comprises 20 vertebræ, of which the anterior dorsals bear large neural spines. The caudal vertebræ are much flattened dorso-ventrally. The fore limbs are shorter than the hind limbs. The scapula bears a very large spine; the humerus is not perforated above its lower end; the ulna has a large olecranon process, while the radius crosses this bone (as in the Proboscidea) articulating only with the outer half of the distal surface of the humerus; the carpus exhibits the characteristic alternation of the bones in its two series, while the three digits (II, III, IV) are short and stout. The ilium is a much expanded bone; the femur is destitute of a third trochanter; the tibia and fibula are anchylosed at their extremities, while the latter bone articulates considerably with the calcaneum; the three digits, like those of the fore foot, are short and stout. No dermal armour has been observed. The typical species *T. platensis* (fig. 179) has a skull about 0·7 m. in length, and is found in the Pampa Formation (Pleistocene) of Buenos Aires.

Nesodon. An early genus of Toxodonts, comprising species of small or moderate size, with the limbs (and probably also the neck) more slender than in the typical genus. The nasal bones extend considerably forwards, so that the narial opening is directed anteriorly. A cast of the brain-cavity shows that the cerebral hemispheres were large, much convoluted, and distinctly overlapping the cerebellum. The teeth are arranged in an almost continuous series, and in the adult all are distinctly rooted except upper i. 2 and lower i. 3. The formula of the milk dentition is $\frac{\text{i. 3, c. 1, m.-m. 4}}{\text{i. 3, c. 1, m.-m. 4}}$, while that of the permanent dentition is $\frac{\text{i. 3, c. 1, pm. 4, m. 3}}{\text{i. 3, c. 1, pm. 4, m. 3}}$; and the change from one dentition to the other is so gradual that it is difficult to identify the various teeth in skulls of different degrees of maturity. The trunk is imperfectly known; but the femur is proved to have been provided with a small third trochanter, while the slender tridactyl feet must have been digitigrade. All the known species were obtained from the Santa Cruz Formation of Patagonia, and the typical form, *N. imbricatus*, has a skull about half a metre in length.

Sub-Order 8. *Litopterna.*

The third group of primitive extinct ungulates peculiar to South America, comprises digitigrade animals in general proportions resembling the existing llamas and horses. These are named LITOPTERNA (smooth heel-bone) in allusion to the facette on the calcaneum for the articulation of the fibula. The brain-cavity is small. The dentition is complete or nearly so, with the canines either small or wanting; the premolars and molars usually have low crowns (brachyodont), though some approach the hypsodont form, and are all distinctly rooted. The ends of the cervical vertebræ are flattened. Clavicles are absent, and there is no entepicondylar foramen in the humerus. The femur bears a third trochanter. The bones of the two rows in the carpus and tarsus exhibit their primitive relationships, not interlocking or alternating. The digits vary in number from five to one in the different genera, the most usual number being three; but in every case the third digit is the largest, as in the Perissodactyla. The proximal end of the astragalus forms a distinct trochlear surface, while its distal end is more or less convex. The calcaneum articulates extensively with the fibula, thus differing from that of the other odd-toed ungulates (Perissodactyla) and resembling the ordinary even-toed forms (Artiodactyla).

These animals may indeed be said to mimic the Perissodactyla in their development; their distinctly lower grade in the ungulate order being indicated by the primitive characters of the brain, the teeth, the cervical vertebræ, and the carpus and tarsus. It is also interesting to note that they attained their maximum specialization at an earlier period than the Perissodactyla; for typical fragments of them have been obtained from the *Pyrotherium* Formation of Patagonia, while important portions of the skeleton of the genera with most reduced dentition and atrophied lateral digits are known from the Santa Cruz Formation (e.g., *Proterotherium* and *Thoatherium*). A comparatively generalized large animal, *Macrauchenia*, with long neck and three complete digits, is the latest representative of the group in the Pampa Formation (Pleistocene) of Buenos Aires, and in corresponding deposits in Bolivia.

Proterotherium (fig. 180 c). The rostral part of the skull is short and tapering, and the nasal bones are elongated. The orbit is completely

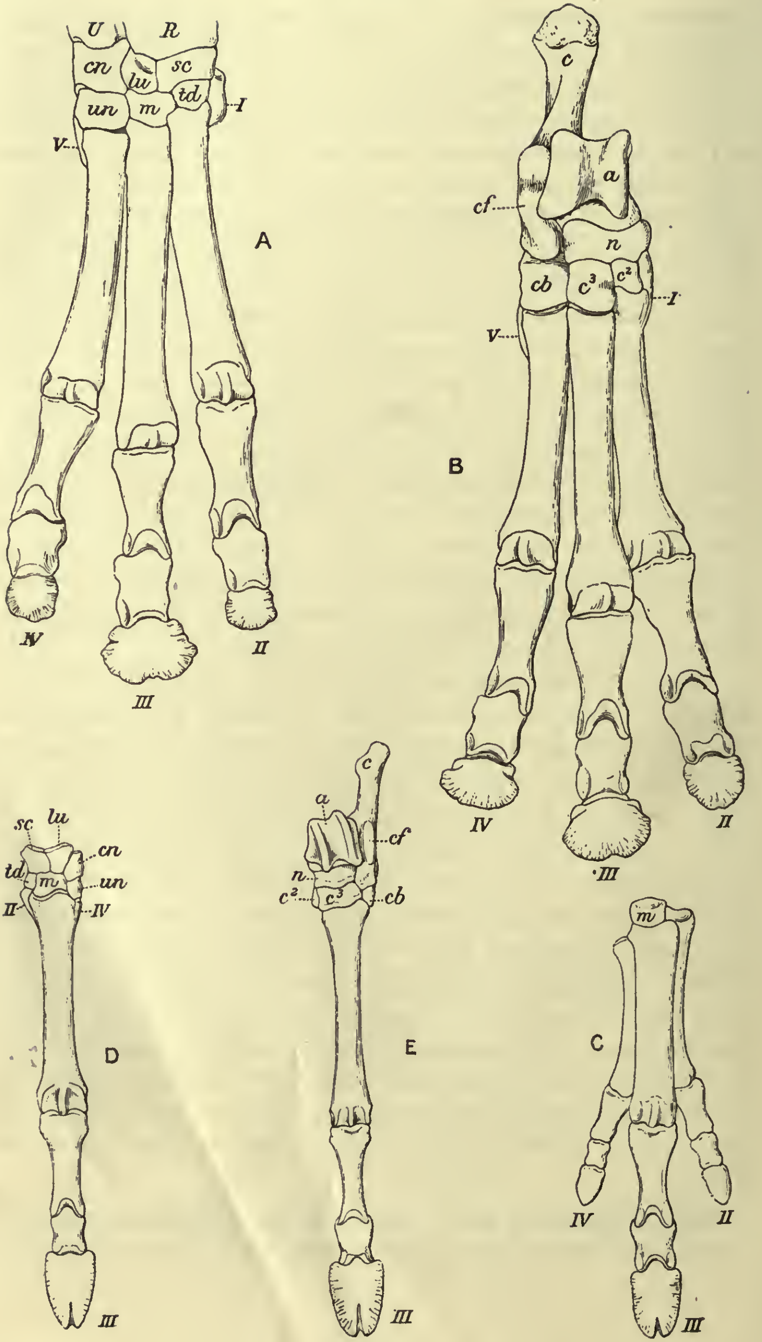
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Fig. 180.

FIG. 180.

Feet of Ungulata Litopterna from the Santa Cruz Formation (Lower Tertiary) of Patagonia. (After Ameghino.)

A, B. *Theosodon lydekkeri;* right fore and hind feet, one-third nat. size.

C. *Proterotherium intermixtum ;* right fore foot, one-third nat. size.

D, E. *Thoatherium crepidatum ;* left fore and hind feet, one-third nat. size.

a, astragalus; *c*, calcaneum; c^2, c^3, middle and external cuneiform; *cb.*, cuboid ; *cf.*, facette for fibula on calcaneum; *cn.*, cuneiform ; *lu.*, lunar ; *m*, magnum; *n*, navicular; *sc.*, scaphoid; *td.*, trapezoid; *un.*, unciform. R, radius; U, ulna; I—V, numbers of digits.

surrounded by bone, and thus separated from the temporal fossa. The dental formula of the adult is $\frac{\text{i. 1, c. 0, pm. 4, m. 3}}{\text{i. 2, c. 1, pm. 4, m. 3}}$. The upper incisors are a little enlarged, and the outer lower incisors are larger than the inner pair. The lower canine is insignificant. The grinding teeth exhibit a general resemblance to those of *Palæotherium* (p. 326), and pm. 3, 4, are almost as complex as the true molars. The hindermost lower molar exhibits a third lobe. The neck is comparatively short, and the vertebrarterial canal is normal, not penetrating the arches of the cervical vertebræ as in *Macrauchenia*. The third trochanter of the femur is well developed. Each foot (fig. 180 C) is tridactyl, with the lateral digits much reduced though complete. The genus occurs only in the Santa Cruz Formation of Patagonia, and all the species are of small size, the skull in *Proterotherium cavum* attaining a length of about 0·16 m.

Thoatherium (figs. 180 D, E). Another small animal with nearly complete dentition. The two pairs of lower incisors are about equal in size, and the hindermost lower molar is destitute of a third lobe. Both feet are monodactyl like those of the existing horses. The lateral metapodial bones are even more reduced than in these more modern ungulates, but in the hind foot the astragalus articulates only with the navicular, not extending over the cuboid (fig. 180 E). *Thoatherium crepidatum* and other species occur in the Santa Cruz Formation of Patagonia.

Macrauchenia. The skeleton of this genus is almost completely known. The skull is long and narrow, with the premaxillo-maxillary region much extended and the nasal bones rudimentary, so that the narial opening is situated far back and directed upwards. The disposition of the parts may indicate the original presence of a small proboscis. Behind the narial opening there are deep pits in the frontal region, probably for muscular attachments. The orbit is completely surrounded by bone, and thus separated from the temporal fossa. The dentition is complete, namely, $\frac{\text{i. 3, c. 1, pm. 4, m. 3}}{\text{i. 3, c. 1, pm. 4, m. 3}}$, in a regular close series, and the teeth are somewhat deepened (hypsodont). The ordinary successional teeth are known. The cervical vertebræ are large and much elongated, and the canal for the vertebral artery does not perforate their transverse processes, but passes obliquely through the pedicle of the neural arch (as in the camels, llamas, and *Myrmecophaga*). The dorso-lumbar vertebræ are about 24 in number. In the fore limb the radius and ulna are fused together, and the olecranon process of the latter is small. In the hind limb the femur bears a small third trochanter, while the fibula is an excessively slender bone partially fused with the tibia. Both feet (like those of *Theosodon* shown in figs. 180 A, B) are tridactyl, with the median digit not much larger than the lateral digits. The typical and best known species is *Macrauchenia patachonica*, about as large as a camel, with the skull half a metre in length. This occurs in the Pampa Formation (Pleistocene) of the province of Buenos Aires, Argentina. *M. boliviensis* is a small allied species known by parts of the skeleton from the highlands of Bolivia.

Sub-Order 9. *Perissodactyla.*

The existing odd-toed hoofed animals, or PERISSODACTYLA, are represented by the three distinct families of tapirs (Tapiridæ), rhinoceroses (Rhinocerotidæ), and horses (Equidæ), which are proved by the known fossils to have become gradually differentiated during the Tertiary period. So large a number of their extinct predecessors have indeed been discovered, that it is already impossible to make a satisfactory classification of the sub-order as a whole. They are all digitigrade quadrupeds, with the axis of both feet passing through the digit no. III (hence *mesaxonic*); and the bones of the two series in the carpus alternate or interlock, while the astragalus (fig. 181 A) in the tarsus is always flattened below, articulating not only with the navicular but also partly with the cuboid. There is no clavicle. The femur always bears a third trochanter. In other features of the skeleton there are many variations; but the general tendency of evolution is quite clearly that already described as characteristic of the Ungulata in general (p. 287), and it is well illustrated in the case of the horses in the

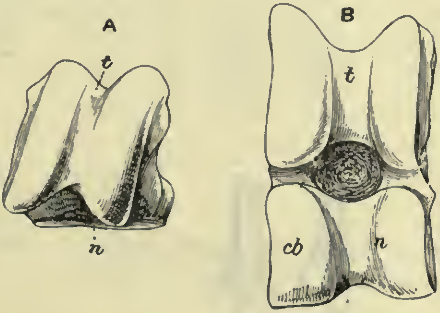

FIG. 181.

Astragalus of a Perissodactyl Ungulate (A) and an Artiodactyl Ungulate (B), anterior aspect. *cb.*, facette for cuboid; *n*, facette for navicular; *t*, facette for tibia.

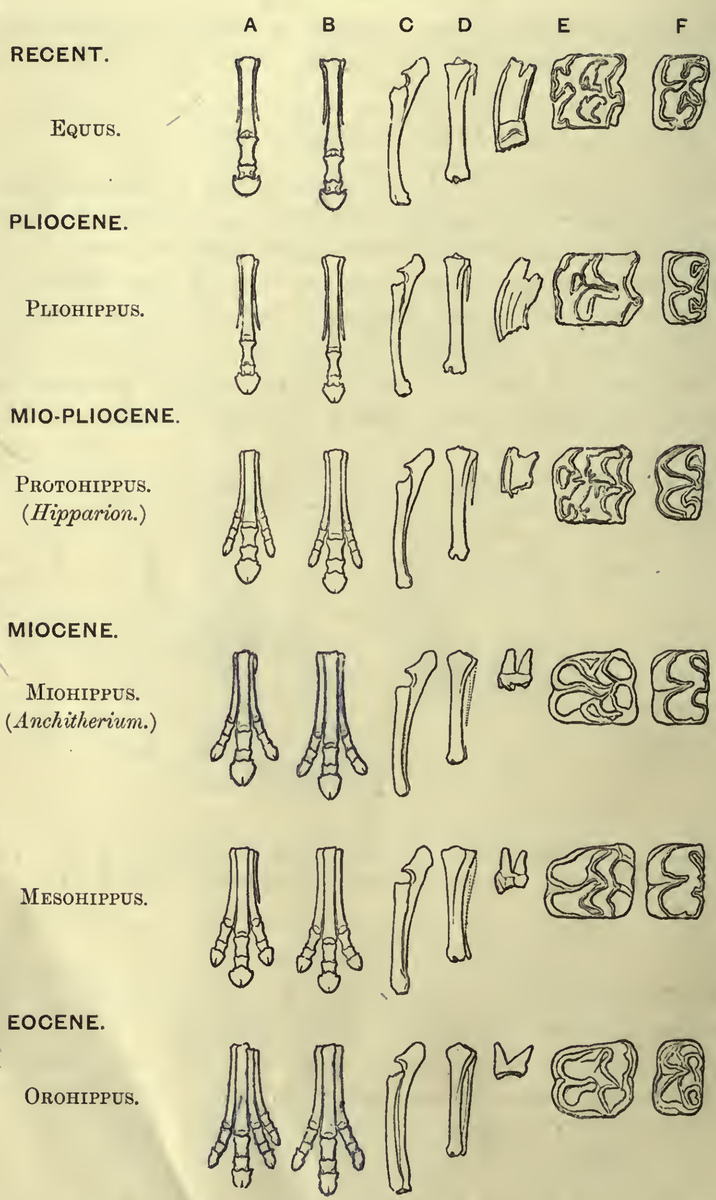

Fig. 182.

Diagram illustrating the Evolution of the Limbs and Molars in the Equine Ungulata. A, fore foot; B, hind foot; C, fore arm; D, shin; E, worn upper molar, side- and crown-views; F, worn lower molar, crown-view. (After Marsh.)

accompanying diagram (fig. 182). Here will be observed the gradual loss of the lateral digits, the atrophy of the ulna and fibula, and the deepening of the molar teeth; to which changes must be added the increased flexibility of the neck, the reduction in number of the teeth, and the advancing complexity of the premolars.

The existing tapirs or **Tapiridæ** seem to approximate most closely to the earliest Eocene Perissodactyla, and afford the best idea of the animals of this sub-order before they became differentiated. They are adapted to live in marshes, ordinarily frequenting these or dense forest in proximity to water. Their teeth are short-crowned (brachyodont), each grinder with two transverse ridges; and the hinder premolars are as complex as the molars. The dental series is either complete or only wants one premolar. There are four digits in the manus and three in the pes. The family thus characterized dates back to the Lower Miocene (White River Formation) in the United States of America, and apparently to the same remote period in Europe. In the tapirs of this early date the premolars are slightly simpler than those of the surviving genus *Tapirus*; while *Tapiravus*, ranging through the Miocene and Pliocene of North America, is still somewhat primitive in the same feature. The typical *Tapirus* itself, however, is represented in Europe by several fine specimens from the Lower Pliocene of Eppelsheim, Hesse Darmstadt (*T. priscus*), and from corresponding formations in Hungary and south-eastern Austria; also by remains from the Pliocene of France and Italy, and by detached teeth from the Red Crag of Suffolk. It is also to be noted that other teeth indistinguishable from those of *Tapirus* occur in an Upper Tertiary (probably Pliocene) formation in China. It is thus evident that during Miocene and Pliocene times these animals ranged over most of the warm and temperate lands of the northern hemisphere. Hence is explained the remarkable distribution of the existing tapirs, which are confined to two widely separated areas, namely, (i.) certain portions of the Indo-Malayan region, and (ii.) the tropical parts of America. Like the surviving Dipnoan fishes (p. 61), they are an illustration of a once-dominant race nearly exterminated but still struggling for existence where competition happens to be least severe in their particular case.

Some of the earliest Eocene perissodactyls are so remarkably similar to the tapirs, that they may be claimed with much probability as the direct ancestors of the latter. *Systemodon*, for example, known by the skull and dentition, perhaps also by part of the hind limb, from the Wasatch Formation (Lower Eocene) of Wyoming and New Mexico, seems to be one of these. It is a small animal with all the premolars simpler than the molars; and its hind foot probably bore a rudiment of digit V in addition to the usual nos. II, III, IV. Otherwise it is essentially a tapir. Contemporaneous allied forms in the same stage of evolution, so far as teeth and feet are concerned, incline less towards the tapirs but more distinctly in the direction either of the rhinoceroses or of the horses. Hence the perissodactyls at the base of the sub-ordinal series may be classified provisionally in one or more families comprising only generalized types; or they may be distributed for the most part in the surviving families of Tapiridæ, Rhinocerotidæ, and Equidæ, according as they seem to be ancestral to the one or to the other. The first-mentioned arrangement seems preferable at present, since it is not based on any hypotheses as to the genetic succession of certain forms; but it must be understood that on neither plan can the families be precisely diagnosed.

The most generalized of the early perissodactyls are thus grouped in the family of **Lophiodontidæ**, so named from the typical genus *Lophiodon*, which is known by the skull, dentition, and a few other bones from the Lower and Middle Eocene of Europe. The dentition forms a complete series, there being 44 teeth in all, and the grinding teeth are brachyodont. The tubercles on the molars of each jaw tend to fuse into two transverse ridges (i.e., become *bilophodont*), but the premolars are smaller and simpler. So far as known, the digits number four in the manus and three in the pes, precisely as in the Tapiridæ. In some genera the two ridges on the molars are more or less separate throughout; among these are included *Systemodon*, already mentioned as probably an ancestral tapir, and a more slender animal, *Hyracotherium* (with the formation of the transverse ridges on the molars more or less incomplete), which is generally claimed as an ancestral horse. In other genera the two ridges on the upper molars are connected by a longitudinal crest which forms an outer wall; and here among other types discovered in the Eocene of America may be placed *Hyrachyus*, which is regarded very plausibly as an ancestral rhinoceros. One of the best-known skeletons is that commonly described under the name of

Hyracotherium (figs. 183, 184). The skull in this genus is much elongated, with slender snout, and the long nasal bones projecting forwards above the narial opening. The sagittal crest of the cranial region is prominent, and there is a large postorbital process of the frontal; but the orbit is not completely separated by bone from the temporal fossa. A small infraorbital foramen is distinct. The slender mandible is much elevated in the coronoid region, and the rami are fused at the symphysis in the adult. The dentition is complete, comprising the usual 44 teeth; but there are three short diastemata in the upper jaw (behind i. 3, c, and pm. 1), and two in the lower jaw (behind c and pm. 1). The incisors are relatively small, in regular series, and the canines are scarcely enlarged. The characters of the premolar-molar series are well shown in fig. 183. The odontoid process of the axis vertebra is known to be a simple peg; and the centra of the cervical vertebræ are slightly opisthocœlous. The

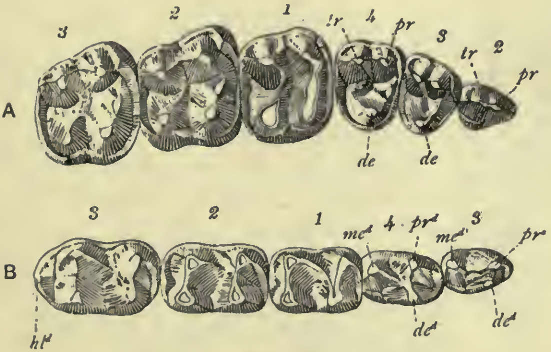

FIG. 183.

Hyracotherium tapirinum; right upper (A) and lower (B) molars and premolars, four-thirds nat. size.—L. Eocene (Wasatch Formation); Wyoming. *de.*, deuterocone; *de*^{d}., deuteroconid; *hl*^{d}., hypoconulid; *me*^{d}., metaconid; *pr.*, protocone; *pr*^{d}., protoconid; *tr.*, tritocone. (After Wortman.)

ORDER 4. UNGULATA. *Sub-Order* 9. *Perissodactyla.*

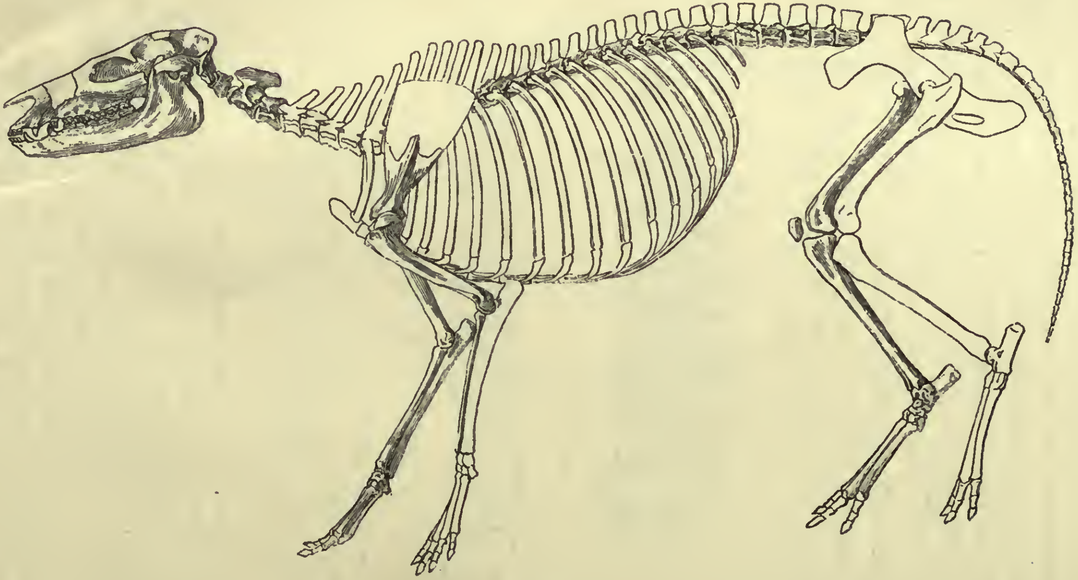

FIG. 184.

Hyracotherium (*Protorohippus*) *venticolum;* restoration of skeleton by E. D. Cope, one-third nat. size.—L. Eocene (Wind River Formation); Wyoming.

tail is proved to have been of moderate length. The scapula exhibits a larger incurved coracoid process than usual in the Perissodactyla. The limbs are slender. The ulna and radius are separate, and the manus exhibits four complete digits, without any rudiment of no. I. The tibia is relatively stout, and the separate fibula is very slender, though complete. There are only three complete digits in the pes, which is longer than the manus, but a rudiment of metatarsal no. V is sometimes present. The metapodial bones are keeled distally. *Hyracotherium* was first known by an imperfect skull and dentition, and then by the greater part of the skeleton, from the London Clay (Lower Eocene) of the London Basin (*H. leporinum*). Remains of the same and allied genera (e.g., *Pachynolophus*) are also known from the Lower and Upper Eocene of France and Switzerland. The most satisfactory skeletons hitherto obtained, however, are those from the Lower Eocene (Wasatch and Wind River Formations) of North America (fig. 184). Several species are distinguished by the dentition, none much exceeding a fox in size. *Orohippus* (fig. 182) is a well-known closely allied genus from the Middle Eocene (Bridger Formation) of Wyoming.

The next group of perissodactyls, considered both in relation to its geological age and its degree of specialization, is that of the **Palæotheriidæ**, thus named from the typical genus *Palœotherium*, which is found only in the Upper Eocene of Europe, but is succeeded by other forms occurring both in Europe and America. The dentition is complete, or wants only pm. 1, and the grinding teeth are brachyodont, without any trace of cement in the hollows of the crown. Each upper molar bears two oblique ridges united at the outer end by a **W**-shaped external ridge or wall; while each lower molar comprises two crescentic ridges. The hinder premolars in both jaws are almost or quite as complex as the molars. The canines are always well developed, though never excessively enlarged; the incisors are simple cutting blades, but in the latest genus, *Anchitherium*, they begin to exhibit traces of the pit which becomes the "mark" in the horses. There are three complete digits on each foot.

Palæotherium (figs. 185, 186). The skull in this genus considerably resembles that of an existing tapir, with large freely projecting nasal bones, pointed in front, which may perhaps indicate the original presence of a short proboscis at least in some species. The small orbital cavity is not separated by bone from the temporal fossa, while the parietal region rises into a sharp crest. In the dental series there is a considerable diastema between the first premolar and the canine, also a slight diastema between the latter tooth and the outermost incisor. All the premolars except the foremost are as complex as the molars (fig. 185); and the hindermost lower molar exhibits a third or supplementary crescent posteriorly. The canines are conical and somewhat larger than the incisors, which are nearly uniform and with a cutting edge. There are the usual 7 cervical vertebræ, a little longer than indicated in the original restoration (fig. 186); next follow 16 dorsal and 7 lumbar vertebræ; and the number of sacrals and caudals is uncertain. The blade of the scapula is considerably expanded; the deltoid crest of the humerus is not much developed; the radius and ulna are separate and about equally developed; and in the manus the median digit (III) is only slightly larger than nos. II and IV, while there is usually a small rudiment of metacarpal no. V. In the pelvis the ilium is not much expanded. The third trochanter of the femur is connected with a prominent ridge; the tibia is much stouter than the fibula, and these two bones are sometimes fused together distally; the pes resembles the manus. *Palæotherium* was thus named by Cuvier at a time when extinct genera of mammals were only just being recognized, and when none were supposed to date back beyond the Eocene. It is known not only by fragmentary remains from the Upper Eocene of several localities in France, Switzerland, Bavaria, Würtemberg, and the Hampshire Basin, but also by one nearly complete skeleton embedded in a slab of gypsum from Vitry-sur-Seine near Paris. The original specimens studied by Cuvier were obtained from the gypsum quarries of Montmartre near Paris. The largest species is *Palæotherium magnum*, about as large

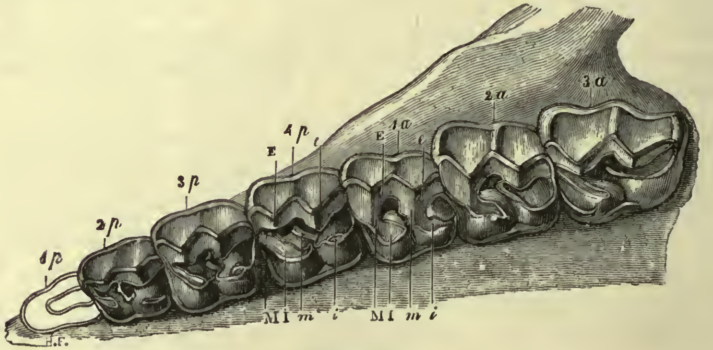

FIG. 185.

Palæotherium crassum; left maxilla with dentition, three-quarters nat. size.—U. Eocene (Gypsum); Montmartre, Paris. 1*a*—3*a*, three molars; 1*p*—4*p*, four premolars; E, *e*, paracone and metacone; I, *i*, protocone and hypocone; M, *m*, protoconule and metaconule. (After Gaudry.)

as a rhinoceros, with the skull 0·5 m. in length. *P. crassum*, *P. medium*, and others are smaller forms.

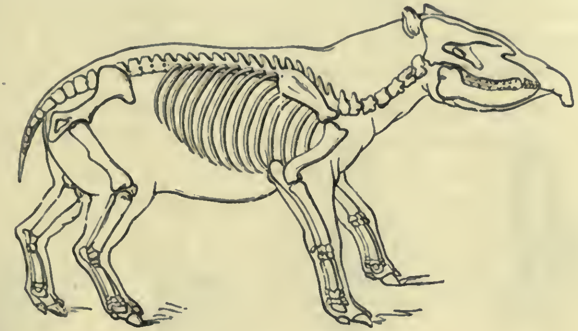

FIG. 186.

Palæotherium magnum; restoration of skeleton by Cuvier, about one-thirtieth nat. size.—U. Eocene (Gypsum); Montmartre, Paris.

Anchitherium (fig. 182). The skull and dentition in this genus are remarkably similar to those of *Palæotherium*, but the incisors begin to exhibit an apical pit or depression. There is still no trace of cement in the hollows of the dental crowns. The features in which the skeleton differs from that of *Palæotherium* tend towards the corresponding characters of the modern horses. The ulna and fibula are complete, though extremely slender, and they are more or less anchylosed with the radius and tibia respectively. The three digits (fig. 182) are no longer of equal size, nos. II and IV, though complete, being shorter and scarcely more than half as stout as the median no. III. The typical and only satisfactorily known species is *Anchitherium aurelianense*, with the skull about 0·25 m. in length, from the Middle Miocene of France, Würtemberg, Bavaria, and Austria.

FIG. 187.

Mesohippus bairdi; left upper molar-premolar series, nat. size.—L. Miocene (White River Formation); Dakota. *p*, protocone; *pp*, metaconule. (After Osborn.)

Mesohippus (figs. 187, 188). Almost identical with *Anchitherium*, but the incisors only slightly or not at all pitted. A rudiment of metacarpal V occurs in the manus. The typical species, *Mesohippus bairdi*, with a skull about 0·18 m. in length, is known by nearly complete skeletons from the Lower Miocene (White River Formation) of Dakota. There is a slight trace of a fibular facette on the calcaneum (fig. 188, *cf.*).

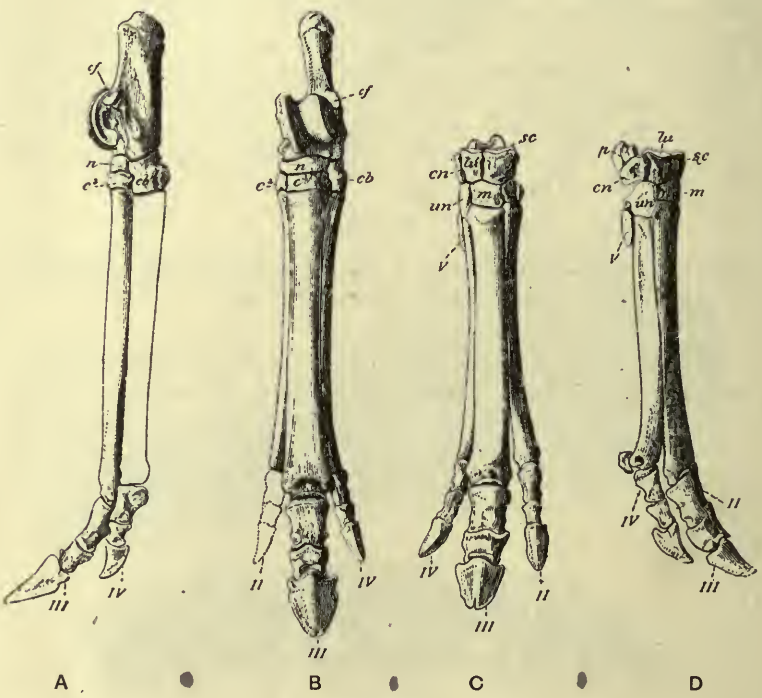

Fig. 188.

Mesohippus intermedius; left hind foot, lateral (A) and anterior (B) aspects, and right fore foot, anterior (C) and lateral (D) aspects, nearly one-third nat. size.—L. Miocene (White River Formation); Dakota. c^2, c^3, middle and external cuneiform; *cb.*, cuboid; *cf.*, facette on calcaneum for fibula; *cn.*, cuneiform; *lu.*, lunar; *m*, magnum; *n*, navicular; *p*, pisiform; *sc.*, scaphoid; *un.*, unciform. II—V, number of digits. (After Osborn and Wortman.)

The Palæotheriidæ pass almost insensibly both into the rhinoceroses and the horses, and thus presumably left descendants which are included in one or other of these comparatively recent families. Before the close of the Eocene period in North America, however, one peculiar group of primitive perissodactyls arose, comprising large animals which in the Miocene period rivalled the modern elephants in size and then suddenly became extinct. This is the family of **Titanotheriidæ** or **Brontotheriidæ**, which seems to have been a comparatively local race confined to a limited region of North America; for the only European fossils hitherto claimed to belong to similar animals are merely fragments of jaws and teeth too inconclusive for satisfactory discussion. The grinding teeth are very low-crowned (brachyodont), and there is nearly always a short diastema between the canine and the premolars. In the upper molars (fig. 189) the two external cusps are merged into a **W**-shaped outer wall, while the inner cusps are separate pointed tubercles; in the lower molars the crown consists of crescentic ridges, two in m. 1, 2, three in the hindermost m. 3. In the Eocene genera (e.g., *Palæosyops*) all the premolars are simpler than the molars, while in the Miocene forms (e.g., *Titanotherium*) one or more of the premolars approximate to the molars in complexity. The canines and incisors are at first well developed, while later they become much reduced, variable and rudimentary. The nasal bones always project freely over the large narial opening, and in the specialized Miocene genera they enter the base of a pair of bony prominences which arise from the maxillæ. The ilium is expanded like that of the elephants, and the third trochanter

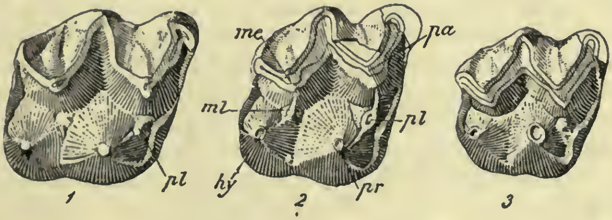

Fig. 189.

Second Right Upper Molar of *Titanotheriidæ*, two-thirds nat. size.—M. Eocene (Bridger Formation); Wyoming. 1. *Palæosyops paludosus.* 2. *Limnohyops laticeps.* 3. *Palæosyops minor.* *hy.*, hypocone; *me.*, metacone; *ml.*, metaconule; *pa.*, paracone; *pl.*, protoconule; *pr.*, protocone. (After Earle.)

of the femur is much reduced. There are four digits in the manus, nos. III and IV being more nearly equal in size than in the tapirs; the calcaneum is notably elongated, and there are only three digits in the pes.

When alive these animals must have had a very flexible nose, but they do not appear to have possessed any true proboscis like that of the tapir. The later and larger forms probably attained great longevity; for the epiphyses of their vertebræ remain long separated in the adult as in the existing elephants.

Titanotherium (fig. 190). This genus is known by nearly complete skeletons from the White River Formation (Lower Miocene) of Dakota. The skull is long and depressed, much like that of a rhinoceros, and the orbital cavity is directly continuous with the temporal fossa, not even limited by any postorbital process of the frontal region. The zygomatic arch is massive, and there is a large infraorbital foramen. A pair of bony prominences or horn-cores arise from the maxillæ in front of the orbits; while the well-developed nasals, which are firmly co-ossified, form the inner margin of their base. These prominences contain large air-cavities, and they vary considerably according to age, species, and probably sex. The premaxillæ are very small, and do not usually extend forwards so far as the end of the nasals. The brain-cavity is very small, and a cast of it shows that the much-convoluted and well-developed cerebral hemispheres did not extend at all over the cerebellum. The premolars are as complex as the molars, and small canines are always present; but the incisors vary from three pairs to none, and several generic names have been proposed to indicate their different states of development. The epiphyses of the vertebræ are loosely united in most specimens, as in the elephants. The neck is stout, of moderate length, while the cervical and most of the dorsal vertebræ are distinctly opisthocœlous. The atlas is much expanded transversely, and the odontoid process of the axis is conical; there are 17 dorsal and 3 lumbar vertebræ, the latter smaller than the former; and the tail is very slender. The dorso-lumbar region is thus shorter by 3 or 4 vertebræ than is usual in perissodactyls. The limbs are intermediate in proportions between those of the elephant and the rhinoceros. The scapula is large, with a prominent spine and small coracoid process. The humerus is stout, with very prominent radial crest; the radius and ulna are separate, the latter with a much-compressed olecranon process; the four digits of the manus (nos. II to V) are remarkably uniform in size. In the pelvis the ilium is greatly expanded. The femur has almost lost its third trochanter; the tibia and fibula are relatively short, complete and separate, but the latter bone is very slender; the calcaneum is much elongated, and the cuboid facette on the astragalus is relatively large; the

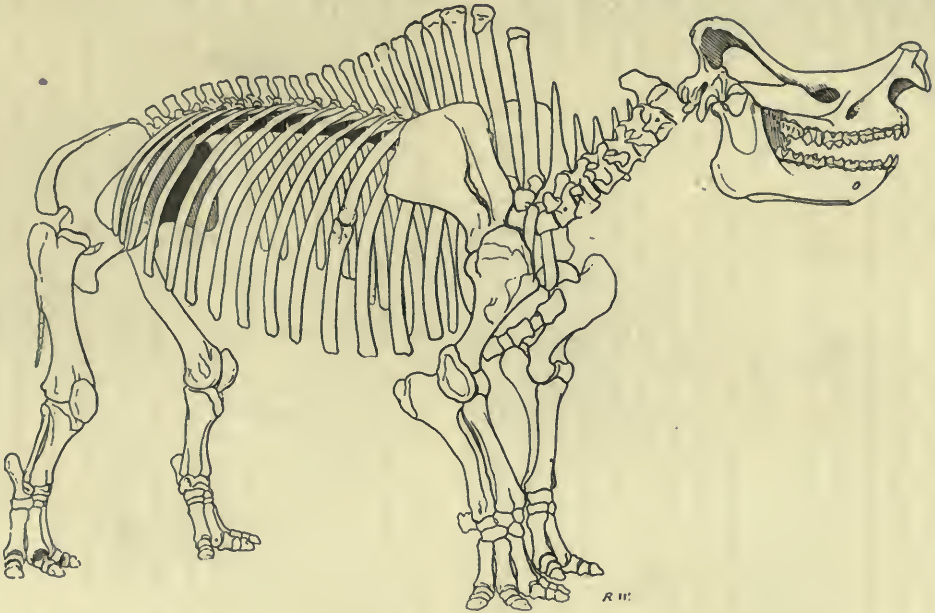

FIG. 190.

Titanotherium (Brontops) robustum; view of mounted skeleton in American Museum of Natural History, about one-thirtieth nat. size.—L. Miocene (White River Formation); Dakota. (After Osborn and Wortman.)

three digits of the pes are nearly uniform in size, and there are no rudiments of digits nos. I and V. One of the best known species is *Titanotherium* (*Brontops*) *robustum* (fig. 190), between four and five metres in length and about two-and-a-half metres high. Its dental formula is $\frac{\text{i. 2, c. 1, pm. 4, m. 3}}{\text{i. 1, c. 1, pm. 4, m. 3}}$. The generic name *Brontotherium* has been given to those forms with two incisors above and below, with the upper canine close to the first premolar, and with this premolar lost in the mandible. Various remains occur in the Lower Miocene, not only of Dakota, but also of Nebraska, Wyoming, Colorado, and the region of the Cypress Hills, District of Assiniboia, Canada.

Palæosyops, from the Lower and Middle (Wind River and Bridger) Eocene of the United States, does not bear any horn-like prominences on the skull, and its premolars are all simpler than the molars (fig. 189). The facial region is somewhat more elongated than in *Titanotherium*; the frontal bears a large postorbital process; and the parietal region rises into a sagittal crest. The cerebral hemispheres of the brain are also proved to have been less convoluted than in *Titanotherium*. The skeleton is almost completely known, and much resembles that of the latter genus, though it is of more slender proportions. The typical species *Palæosyops paludosus*, from the Bridger Eocene of Wyoming, is an animal about two metres in length and one metre in height.

The rhinoceroses, or family **Rhinocerotidæ**, begin to be recognizable towards the close of the Eocene, both in Europe and North America; and the Miocene genera in both countries differ very little in their skeleton from the surviving rhinoceroses of the Old World at the present day. At first they are entirely hornless, and some of them retain a rudimentary fourth digit (no. V) on the manus. The incisors and canines are also a more persistent feature in the earlier than in the later forms, and the premolars are sometimes simpler than the molars. In North America a normal horn does not appear to have ever been acquired, and the race disappeared before the close of the Pliocene without attaining a much higher degree of specialization than that exhibited by the Miocene *Aceratherium* of Europe. In the Old World, however, the gradual development of the horn can be clearly traced; the ancestry of the surviving rhinoceroses of Asia and Africa is revealed to a considerable extent by fossils both from Europe and Asia; and one northern rhinoceros (*Elasmotherium*), discovered in the Pleistocene deposits of Siberia and some parts of European

Russia, is specialized not only in the development of a great horn, but in the deepened (hypsodont) prismatic form of its grinding teeth.

The crowns of the molars and premolars in all the rhinoceroses are somewhat deeper than those of the other perissodactyls already noticed; but, except in the aberrant *Elasmotherium* just mentioned, the hollows between the ridges are not filled with cement. The hindermost upper molar is reduced to a triangular form by the partial atrophy of its posterior ridge; while the hindermost lower molar consists of never more than two crescents, like those in front of it. The upper molars (fig. 191), except in some of the earliest forms, are more or less complicated by the growth forwards of a prominence or "crochet" (*a.cr.*) from the posterior ridge, and by another similar prominence ("crista" or "combing plate," cr^s) growing from the outer wall into the median valley; and these two points sometimes meet. A third prominence or "anticrochet" (*cr.*) also sometimes projects backwards from the anterior ridge to meet the others. There is always a diastema in front of the premolars; while the canines and incisors are very variable in development, sometimes even absent. The orbital cavity is never separated by bone from the temporal fossa. There are always three functional digits on each foot.

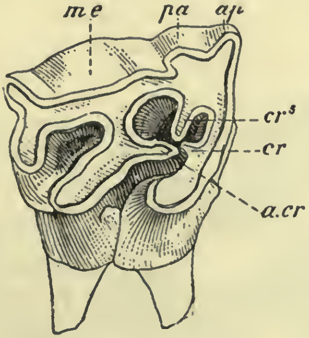

FIG. 191.

Second Right Upper Molar of *Rhinoceros*, much reduced. *a.cr.*, crochet; *ap.*, parastyle; *cr.*, anticrochet; cr^s., crista; *me.*, metacone; *pa.*, paracone. (From Osborn, after De Blainville.)

Hyracodon. The parietal region of the skull in this, as in the other primitive rhinoceroses, is raised into a sharp sagittal crest; the freely projecting nasal bones are slender and smooth. The complete series of 44 teeth is present, and the premolars resemble the molars, while the canines are uniform with the incisors; but there is a short diastema in both jaws between the premolars and the canine. The molars do not exhibit the "crochet" and "crista." The skeleton denotes a slightly-built animal, with longer limbs and a longer neck than are characteristic of the true rhinoceroses. Both feet are definitely proved to have been tridactyl. The genus occurs in the Lower Miocene (White River Formation) of Nebraska and Colorado, and the typical species, *Hyracodon nebrascensis*, has a skull about 0·25 m. in length. Some molar teeth from an early Tertiary Formation in Siebenbürgen, Hungary, have also been referred to this genus.

Fig. 192.

Aceratherium (*Aphelops*) *megalodus;* skull and mandible, one-sixth nat. size.—U. Miocene (Loup Fork Formation); Colorado. (After Cope.)

Aceratherium (fig. 192). The earliest remains apparently of rhinoceroses found in Europe (detached teeth and limb-bones from the Upper Eocene or perhaps Lower Miocene Phosphorites of Quercy, France) are too fragmentary for discussion; but the Miocene and Pliocene remains are more satisfactory, and a hornless rhinoceros, *Aceratherium*, with a rudimentary fourth toe (no. v) on the fore foot can be clearly recognized. The sagittal crest of the skull is not acute, but always more or less flattened, and the nasal bones are small, freely projecting. The premaxillary region is slender and elongated. The dental formula of the more typical species is

$\frac{\text{i. 1, c. 0, pm. 4, m. 3}}{\text{i. 1, c. 1, pm. 3, m. 3}}$. The upper incisors are large chisel-shaped teeth elongated antero-posteriorly; while the lower incisors are pointed and diminutive between the pair of large procumbent canines which meet the upper incisors. The upper molars are scarcely complicated with crests and crochets. Digit no. v on the manus is represented not only by its metacarpal but also by two phalanges; but it is comparatively small and must have been almost functionless. The finest remains of *Aceratherium* hitherto discovered are those from the Middle Miocene of Sansan and other French localities, and from the Lower Pliocene of Eppelsheim, Hesse Darmstadt. There are also traces of the genus in the Lower Pliocene of Pikermi (Greece), the island of Samos, Maragha (Persia), the Siwalik Hills (India), and in China; and detached teeth have been identified in the Red Crag of Suffolk. The typical species is *Aceratherium incisivum*, with a skull about half a metre in length, best known from Eppelsheim. Nearly complete skeletons of very similar rhinoceroses are known both from the Lower Miocene (White River Formation) and the Upper Miocene (Loup Fork Series) of North America; and some of these (e.g. *Aphelops*) are clearly destitute of a fourth digit in the manus.

Diceratherium. One small American rhinoceros closely resembling *Aceratherium*, exhibits a slight eminence on each nasal bone, as if the animal had been provided with a pair of callosities (scarcely true rhinocerotine horns) placed side by side. The nearly complete skeleton of *Diceratherium armatum*, with four digits in the manus, is known from the Middle Miocene (John Day Formation) of Oregon. In the Lower Miocene of France and Germany there seem to be traces of a nearly similar animal (the *Rhinoceros minutus* of Cuvier).

Rhinoceros (fig. 193). Typical rhinoceroses with a well-developed horn date back in Europe as far as the Middle Miocene of France (*Rhinoceros sansaniensis*); and fine skulls of a similar form have been found in the Lower Pliocene of Eppelsheim, Hesse Darmstadt (*Rhinoceros schleiermacheri*). The horns, of course, are never preserved under the ordinary circumstances of fossilization; but the bone is always roughened where they are attached, and so their original presence or absence can be determined. It appears from this criterion that the Miocene species just mentioned possessed two horns, one behind the other; and as they are likewise characterized by the presence of one pair of incisors above and below and well-developed procumbent lower canines, they may be placed in the same group (sub-genus *Ceratorhinus*) as the existing *R. sumatrensis* of Sumatra, Borneo, and certain parts of the adjoining Asiatic continent. One-horned rhinoceroses are unknown among fossils, except in the Indian region of which they are now characteristic (*R. unicornis* and *R. sondaicus*). *R. sivalensis* and *R. palæindicus* from the Lower Pliocene of the Siwalik Hills, seem to be their ancestors. The two-horned rhinoceroses in which the front teeth are quite rudimentary or wanting (sub-genus

Atelodus) had a very wide distribution in the Pliocene and Pleistocene periods, though they are now exclusively confined to Africa (*R. bicornis* and *R. simus*). They seem to appear first in the Lower Pliocene of Pikermi, Greece (*R. pachygnathus*), and become common over the greater part of southern Europe in the Upper Pliocene (*R. etruscus*)—the latter ranging as far north as the Forest Bed of Cromer, Norfolk. The Upper Pliocene species bore horns so large that the septum between the nares began to ossify for their support; and the same ossification is to be noticed in the slender-nosed *R. leptorhinus* or *hemitœchus* (fig. 193) from the early Pleistocene of the Thames Valley and parts of the adjoining continent. The ossification of the nasal septum, however, attained its maximum development in the great Woolly or Tichorhine Rhinoceros (*R. antiquitatis*), which is found in the English caves and river-deposits, in the old river-deposits at the bottom of the present North Sea, and ranged throughout northern Europe and Asia, wandering even within the Arctic Circle. Mummified remains discovered in the frozen earth of northern Siberia prove this animal to have been thickly clothed with hair and wool; and its huge horns are preserved in the same deposits.

Fig. 193.

Rhinoceros leptorhinus ; skull and mandible, one-eighth nat. size.—Pleistocene; Ilford, Essex. (After W. Davies.)

Elasmotherium. This is an aberrant rhinoceros, which ranged over Siberia and part of south European Russia in the Pleistocene period. The nasal bones are slender, but the nasal septum is ossified, and there is an enormous bony prominence on the frontal region above the eye, which must have borne a relatively large horn. The nasal region may perhaps have also carried a minute horn. The front teeth are completely absent, and the two anterior premolars have also disappeared. The remaining teeth (pm. 3, 4, m. 1—3) are deepened (hypsodont) and prismatic in shape, like those of a horse; the valleys between the ridges are completely filled with cement; and the ridges themselves are elaborately crimped. The known limb-bones are quite rhinocerotic in type. The only known species, *E. sibiricum*, has a skull at least a metre in length.

The true horses, or **Equidæ** in the most restricted sense of the term, appear first in the Upper Miocene of North America and in the Lower Pliocene of Europe. They are all agile animals with one large functional digit on each foot, and a pair of lateral digits, which are sometimes complete though small, sometimes mere splint-like rudiments. The incisors are chisel-shaped, with the apex folded into a longitudinal pit; the canines are diminutive; and the grinding teeth are deepened (hypsodont), the valleys always filled with the cement, and the two ridges (homologous with those of Palæotheriidæ, etc.) connected by a cross-crest. The premolars 2—4 resemble the molars, and the foremost premolar is rudimentary or absent. The orbit is completely surrounded by bone.

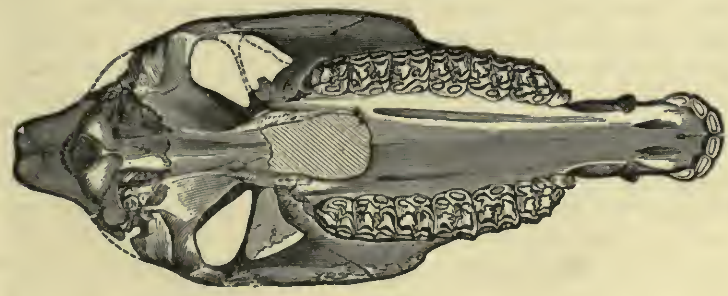

FIG. 194.

Protohippus sejunctus; palatal aspect of skull, one-third nat. size.—U. Miocene (Loup Fork Formation); Colorado. (After Cope.)

Protohippus (figs. 182, 194). In the early American genus, *Protohippus* or *Merychippus*, from the Upper Miocene (Loup Fork Series) of Nebraska and Colorado, the grinding teeth of the adult resemble those of a generalized *Equus*, only they are somewhat less hypsodont; but the milk-molars are curiously similar to those of *Anchitherium*. The small lateral digits are complete, but the ulna and fibula are already imperfect.

Hipparion or **Hippotherium** (fig. 182). This genus occurs in the Lower Pliocene of Europe, the Pliocene of North Africa, Persia, India, and China, and in the Upper Miocene (Loup Fork Series) of North America. It resembles *Protohippus* in the structure of the feet, but the teeth are a little more complicated and hypsodont. The dental formula is $\frac{\text{i. 3, c. 1, pm. 4, m. 3}}{\text{i. 3, c. 1, pm. 3, m. 3}}$, but the anterior upper premolar has no predecessor and is shed before the animal is adult. The diastemata in the dental series are as in the modern *Equus*, but the skull differs from that of existing horses in the presence of a large deep fossa in the maxillary region on each side. The best known species are *Hipparion gracile* and closely similar forms from the Lower Pliocene of Eppelsheim, Hesse Darmstadt, of Pikermi, Greece, and of many other European localities. They are smaller than the ordinary *Equus caballus*, scarcely one-and-a-half metres high at the shoulder.

Hippidium. A South American horse with comparatively simple molar teeth, and a very long slit in each side of the facial region of the skull beneath the elongated and attenuated nasal bones. From superficial deposits in Brazil and Bolivia, and from the Pampa Formation of Argentina.

Equus (fig. 182). The true monodactyl horse, with mere splint bones to represent lateral digits, appears first, so far as known, in the Lower Pliocene of the Siwalik Hills, India (*Equus sivalensis*). In the Upper Pliocene of Europe and northern Africa, one species (*E. stenonis*) is very widely distributed; and this occurs in the Cromer Forest Bed of Norfolk. These early species exhibit the depression on each side of the facial region, which is so characteristic of *Hipparion*, but absent in their successors. In the Pleistocene there is evidence of horses throughout Europe, northern Africa, Asia, and North and South America; and a large proportion of the remains can scarcely be distinguished from the corresponding parts of the existing *E. caballus*. It is strange that the horse should once have ranged over the whole of the New World, and actually have been proved a contemporary of primitive man in North America, and yet have become quite extinct on that continent before its colonization from Europe.

Sub-Order 10. *Artiodactyla.*

The existing even-toed hoofed animals, or ARTIODACTYLA, are subdivided into four very distinct groups, namely, the Suina (pigs, peccaries, and hippopotamus), Tylopoda (camels and llamas), Tragulina (chevrotains), and Pecora (deer, sheep, and cattle). As in the case of the Perissodactyla, however, so large a number of the extinct predecessors of the artiodactyls have now been discovered, that it is impossible any longer to define these four groups when treating of the sub-order as a whole. The arrangement to be provisionally adopted must correspond in a more or less vague way with the lines of descent which it seems possible to recognize as the successive extinct genera are compared one with another. All the members of the sub-order agree in being digitigrade quadrupeds, with the axis of both feet passing between digits nos. III and IV, which are almost equally developed (hence *paraxonic*); and the bones of the two series in the carpus alternate or interlock, while the astragalus in the tarsus is always convex below, articulating about half with the navicular, half with the cuboid (fig. 181 B, p. 319). The number of the dorso-lumbar vertebræ, so far as known, is curiously constant, namely, nineteen. There is no clavicle. The femur is destitute of a third trochanter; and the fibula always articulates with the calcaneum, even when it is reduced to a mere rudiment. The premolar teeth always remain simpler than the molars. In other features of the skeleton many changes are to be observed as the artiodactyls are traced upwards from the Lower Eocene to the present day, both in Europe and North America. So far as known, the earliest forms possess four or five complete digits on each foot (fig. 195 A); and even when these digits are reduced to one pair, they at first remain separate throughout the life of the animal (fig. 195 B). The two metapodials are fused together into a *cannon bone* (fig. 195 C, D) for the first time in the Upper Eocene (*Prodremotherium*), but such a consolidation of the foot is not common until the Lower Pliocene. When this stage is reached the ulna is much reduced and often fuses with the radius; while the fibula is eventually represented solely by its lower end, which continues to articulate with the calcaneum. Again, in the earliest artiodactyls the odontoid process of the axis vertebra is a simple peg, while in the later more specialized forms it becomes spatulate or semi-cylindrical in shape. In the skull, the facial region often bends downwards upon the cranial region, and the latter becomes thickened to bear horns or antlers. The grinding teeth are at first low-crowned (brachyodont, fig. 195 E), bearing separate bosses or tubercles (*bunodont,* e.g., fig. 196); somewhat later these tubercles multiply more or less irregularly (as in the pigs), or they retain their original arrangement but tend to become crescent-shaped (*buno-selenodont,* e.g., fig. 199). Subsequently, as the ruminants or Pecora are gradually evolved, the crescent-shaped tubercles are emphasized and deepened (i.e., become truly *selenodont*); while eventually the antelopes and cattle exhibit teeth (fig. 195 F) with selenodont crowns almost or quite as deep (hypsodont) as those of the horses among Perissodactyla. It is very probable that the early

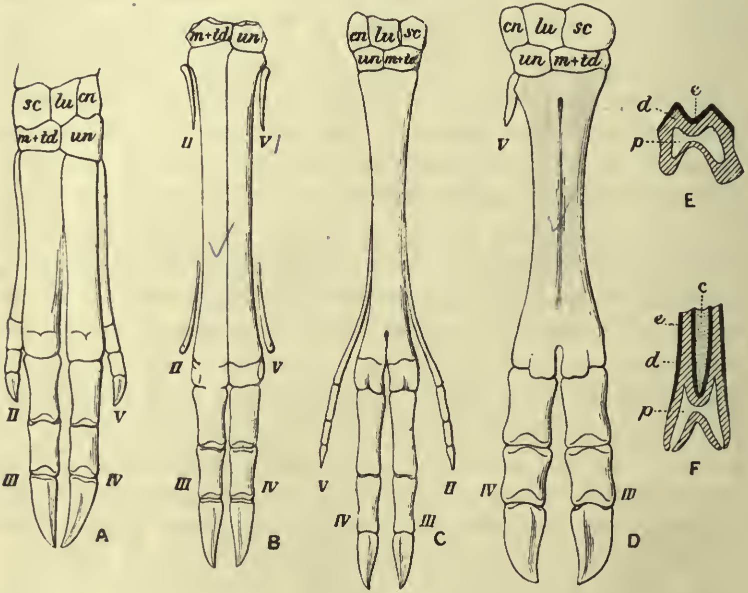

Fig. 195.

Fore Feet and Sections of Teeth of Artiodactyla.

A. Left fore foot of *Hyæmoschus,* two-thirds nat. size. B. Left fore foot of *Gelocus,* one-half nat. size. C. Right fore foot of *Capreolus,* one-third nat. size. D. Right fore foot of *Bos,* about one-quarter nat. size. E. Transverse section of molar of *Gelocus,* nat. size. F. Transverse section of molar of *Bos,* about one-third nat. size.

c, cement; *cn.,* cuneiform; *d,* dentine; *e,* enamel; *lu.,* lunar; *m,* magnum; *p,* pulp-cavity; *sc.,* scaphoid; *td.,* trapezoid; *un.,* unciform; II—V, numbers of digits.

bunodonts, like their existing representatives, had a simple stomach and did not chew the cud; and it seems likely that the powers of rumination were only acquired by the more specialized artiodactyls in the latter half of the Tertiary period.

The existing pigs and peccaries, or **Suidæ**, are the least-altered descendants of the primitive Artiodactyla. They are all bunodont animals, with the canine teeth more or less well-developed. Their carpal and tarsal bones, their metacarpals and metatarsals are never completely fused together, and rarely indeed exhibit any tendency to fusion; while the ulna and fibula are always complete and separate from the radius and tibia. Fragmentary remains of genera of this type can already be recognized among the fossils of the Lower Eocene both in Europe and North America; and the fully-differentiated characteristic artiodactyl astragalus is known from deposits of this remote period in France (Rheims), Wyoming, and New Mexico. The earliest forms are noteworthy on account of the upper molars being more or less quadrate in shape and considerably wider than the lower molars—a condition persistent among the ruminants throughout the course of their evolution, but not observed among the later and true pigs, in which the upper and lower molars are almost equally narrow. As the series of Suidæ and their allies are traced upwards, the molars sometimes exhibit phases of development curiously parallel with those to be noticed among the Proboscidea. *Listriodon*, from the Middle Miocene of Europe, exhibits lophodont teeth remarkably similar to those of *Dinotherium*; the molars of many pigs are miniatures of the corresponding teeth of *Mastodon*; while the hindermost true molar of the existing wart-hog (*Phacochœrus*) of Africa is in structure not unlike the molar of *Elephas*. It is also to be observed that, except in such persistent old types as the peccaries, the canines become transformed into tusks of persistent growth.

Homacodon (fig. 196). Small animals not larger than rabbits. The brain-case is moderately large, with a sharp sagittal crest; the orbital cavity is not separated by bone from the temporal fossa. The dentition seems to have been complete, i.e., comprising the usual 44 teeth. The canines are large, and the three anterior premolars are laterally compressed to a sharp edge; while the fourth premolar above (fig. 196 A) has a supplementary inner cone. Each upper molar (fig. 196 A) has a conspicuous bounding basal ridge or *cingulum* and bears six conical cusps in two transverse series; but in the second molar the posterior inner cusp is relatively small, while in the third molar it is quite rudimentary. Each of the lower molars (fig. 196 B) bears four conical cusps regularly arranged in two transverse pairs, and the hindermost or third molar is produced backwards into a small third lobe or talon. The cervical vertebræ are short, and exhibit oblique ends, thus indicating a curved neck; the hinder trunk-vertebræ are keeled below. There seem to have been five digits in each foot, but only four can have been functional. The typical species is *Homacodon vagans*, known by the greater part of the skeleton from the Middle Eocene (Bridger Formation) of Wyoming. Teeth and astragali from the Lower Eocene of Wyoming and New Mexico have been provisionally ascribed to the same genus. *Cebochœrus* is an allied genus, from the Upper Eocene of France and Switzerland, and from the Middle Miocene of Steinheim, Würtemberg, known only by portions of the skull and the dentition.

Fig. 196.

Homacodon vagans; right upper premolars 2—4, molars 1—3 (A) and lower premolars 3, 4, molars 1—3 (B), twice nat. size.—M. Eocene (Bridger Formation); Wyoming. (After Marsh.)

Chœropotamus. A larger animal, the mandible of the typical species, *C. parisiensis*, measuring about 0·2 m. in length. The dental series is complete, except for the loss of pm. 1 in the lower jaw. Each upper molar is quadrate in form, with a conspicuous basal cingulum, and the conical cusps acutely pointed; the median cusps are small and irregular compared with the outer and inner pairs. The hindermost upper premolar has one inner cusp, while pm. 3 bears a small inner ridge representing the latter. The lower molars exhibit small intermediate cusps, irregular like those of the opposing teeth; while lower m. 3 is produced backwards into a large third lobe or talon. The canines are well-developed. *C. parisiensis* is known only by the jaws and dentition from the Upper Eocene of the Isle of Wight and France.

Hyotherium. The skull in this genus exhibits a sharp sagittal crest, and the facial region is not bent downwards upon the cranial region. The orbital cavity is nearly separated from the temporal fossa by the close approximation of a postorbital process of the cranium to a similar process from the jugal bone. The dental series is complete, with little or no diastema; and the canines are premolar-like in shape, while that of the upper jaw is remarkable as exhibiting a cleft root (cf. *Triconodon* among Mesozoic Mammalia, p. 257). The upper teeth exhibit a prominent cingulum, and the angular cusps on the molars tend slightly towards the formation of transverse ridges. The hindermost lower molar is produced backwards into a large third lobe bearing one conical cusp. The metapodials presumably referable to this genus, bear a distal keel to work in a corresponding groove of the apposed phalangeal. The typical species, *Hyotherium sœmmeringi*, occurs in the Middle Miocene of Bavaria, Würtemberg, Austria, Switzerland, and France; it must have been about as large as the common wild boar. Other species of the same age are also recorded from the European area, and *H. perimense* is known by fragments of the dentition from the Siwalik Formation (Lower Pliocene) of Perim Island, in the Gulf of Cambay, Indian Ocean.

Listriodon. In another Miocene genus, *Listriodon*, the cusps of the upper and lower molars fuse into complete transverse ridges, and these teeth hence assume the lophodont form so characteristic of the tapirs among Perissodactyla. The skull is shaped like that of a pig; and the canines, at least in the male, are relatively large, that of the upper jaw being short, thick, and curved upwards, while that of the lower jaw is longer and sharply bent, with its hinder face working upon the opposing tooth. The dental series wants only the first premolar in each jaw. The incisors have short cutting crowns. The premolars are much simpler than the molars; and all the latter bear two transverse ridges, the hindermost lower molar alone being further complicated by the addition of a small posterior prominence or talon. The typical species is *Listriodon splendens*, with the skull about 0·36 m. in length, known by various parts of the skeleton from the Middle Miocene of Europe, notably from Sansan and other localities in France, from Switzerland, Germany, Austria, and Hungary. Teeth from the Lower Pliocene (Siwalik Formation) of the Punjab, India, have also been referred to this genus (*L. pentapotamiæ*).

Elotherium or **Entelodon** (fig. 197). The large pig-like animals which became dominant in the Miocene are the most highly specialized of the bunodont artiodactyls, so far as the feet are concerned. The best-known genus is *Elotherium* or *Entelodon*, which occurs in the Miocene both of Europe and North America. The basicranial axis of the skull is not bent, but the facial region is remarkably elongated, while the short cranial region rises into a sharp sagittal crest. The orbit is completely separated

ORDER 4. UNGULATA. *Sub-Order* 10. *Artiodactyla.*

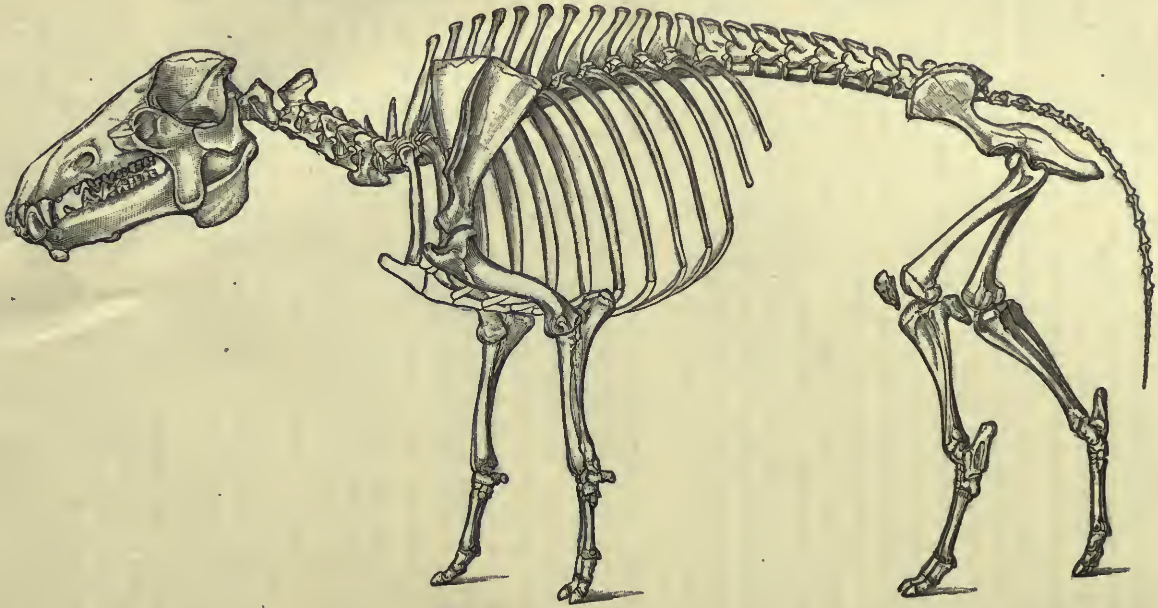

FIG. 197.

Elotherium crassum; restoration of skeleton by O. C. Marsh, one-twelfth nat. size.—L. Miocene (White River Formation); Colorado and Dakota.

from the temporal fossa by a slender bar of bone; and the jugal element of the robust, outwardly curved zygomatic arch sometimes (if not always) bears a large, downwardly-directed process. The mandible is a little produced downwards at the angle, and it also bears two other bosses on the inferior border, one below the hinder premolars, the other below the canine. The dental series is complete, consisting of the usual 44 teeth. The canines are very stout, and the incisors are pointed. All the premolars are simple compressed cones, except the fourth of the upper jaw, which is square and bears two stout conical cusps. The angular cusps of the true molars form two irregular and imperfect transverse ridges on each tooth; and the hindermost lower molar is destitute of a posterior talon or supplementary lobe. All the teeth except the canines exhibit more or less distinctly a basal cingulum. The limbs are comparatively long and slender, and remarkable on account of the reduction of both feet to two functional toes. Digits nos. III and IV are fully and normally developed, while nos. II and V are represented merely by the upper end of their respective metapodials, while no. I is entirely absent. The typical European species, *Elotherium magnum*, is known both by the skull and feet from the Upper Eocene (Quercy Phosphorites) and Lower Miocene (Ronzon, France). An allied form, *Elotherium crassum* (fig. 197), is represented by the greater portion of the skeleton from the Lower Miocene (White River Formation) of Colorado and South Dakota; and this animal must have measured not less than two metres in length by more than a metre in height. Other species are known from corresponding strata in Nebraska and in the Cypress Hills, District of Assiniboia, Canada. There is also an allied genus, with orbits not completely surrounded by bone (*Achænodon*), in the Middle Eocene (Bridger Series) of Wyoming. A fragment of a large mandible from the Lower Pliocene (Siwalik Formation) of the Punjab, India, also seems to represent a nearly related genus (*Tetraconodon*).

Hippohyus. A pig from the Lower Pliocene of the Siwalik Hills, India, in which the cusps of the grinding teeth are unusually deepened and transformed into irregularly radiating, crimped laminæ. The skull of *H. sivalensis* is completely known, and proved to be essentially similar to that of *Sus*.

Sus. The true pigs of the genus *Sus* have always been confined to the three continents of the Old World. The oldest known species is a small form from the Middle Miocene of France and N. Italy (*Sus chœroides*), with comparatively simple molars much resembling those of the *Sus andamanensis* now living in the Andaman Islands. *S. palæochœrus* is another small species from the Lower Pliocene of Eppelsheim, Hesse Darmstadt. There is evidence of larger forms in the Lower Pliocene of France, Greece, the Island of Samos, and the Red Crag of Suffolk (*S. erymanthius* and others); and the existing wild-boar (*Sus scrofa*) appears first in the Upper Pliocene of Europe. The latter animal is represented by its typical dentition in the Cromer Forest Bed, and survived in Britain so late as the seventeenth century. The largest known pigs are those whose remains occur in the Lower Pliocene (Siwalik Formation) of India (*S. titan* and *S. giganteus*); and those with the most complicated molars are also found in this formation (*S. falconeri*) and in the Pliocene of Algeria (*S. phacochœroides*). The hinder molar in the last-mentioned forms makes some approach to that of the existing African wart-hog (*Phacochœrus*), whose ancestry still remains unknown.

Dicotyles. The peccaries now living in the warmer parts of the American continent are, so far as their dentition is concerned, survivors of very primitive suillines. Their skeleton is specialized only in the feet, the metapodials III and IV being fused together at their upper end, while digit no. V has disappeared from the hind foot. The stomach, however, is also highly specialized, almost approaching that of the ruminants in complexity. Nothing is known of the ancestry of these animals, the only fossil remains hitherto discovered being of Pleistocene age and from the region they still inhabit.

The **Hippopotamidæ**, now confined to Africa, are remarkably primitive in most parts of their skeleton, but highly specialized in the front half of the jaws. The grinding teeth have somewhat deepened crowns, and their cusps exhibit a trefoil-shaped section when worn; the canines and incisors grow from persistent roots. Four stout functional digits are retained on each foot. The ancestry of the hippopotamus is still quite unknown, and the earliest fossils hitherto discovered are only slightly more generalized in the character of their incisors. The genus, so far as known, appears first in the Lower Pliocene (Siwalik Formation) of India and Burmah, where it is represented by species (*H. sivalensis* and *H. iravaticus*) with six incisors of uniform size (fig. 198). These forms may be referred to a sub-genus *Hexaprotodon*, which also occurs in the Pliocene of Algeria. In the Pleistocene of India there is a species (*H. palæindicus*) intermediate between the earlier hexaprotodont and the existing African tetraprotodont, *H. amphibius*; while during the later Pliocene and Pleistocene periods the last-mentioned species, or a very closely related form, wandered over the greater part of southern and middle Europe. In Britain the hippopotamus occurs first in the Cromer Forest Bed, and is found in Pleistocene formations as far north as Yorkshire. Remains of a particularly large herd of individuals of all ages, from the youngest calf to the very mature adult, were discovered in 1884 in the Pleistocene gravels of Barrington, near Cambridge. Two extinct dwarf species (*H. pentlandi* and *H. minutus*) are found in association with the dwarf elephants in the caverns and rock-fissures of Sicily and Malta (see p. 306). It is also noteworthy that other dwarf species, of very variable characters, have left abundant remains in the superficial deposits of Madagascar, where the hippopotamus is now quite extinct. No trace of this animal, or any allied form, has been discovered in America.

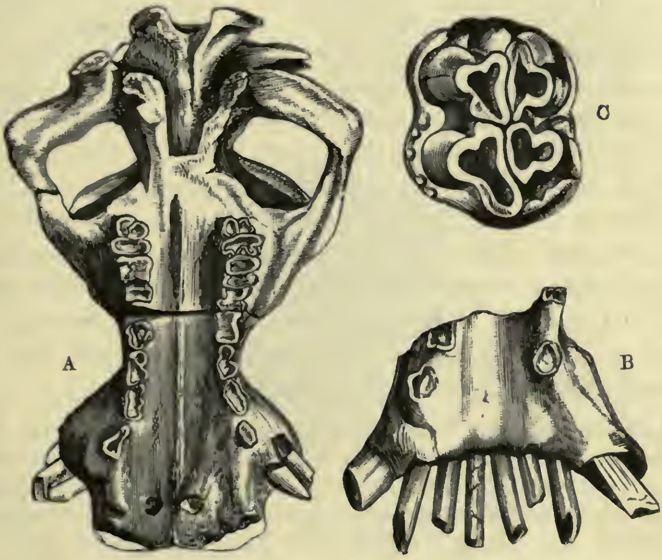

FIG. 198.

Hippopotamus (*Hexaprotodon*) *sivalensis*; palatal view of skull (A), front of mandible (B), and crown of molar (C), the first two figures one-eighth nat. size, the third one-half nat. size.—L. Pliocene (Siwalik Formation); India. (After Falconer.)

Before the close of the Eocene period many of the bunodont artiodactyls had already begun to exhibit a tendency towards a selenodont dentition, while others had actually reached this stage; and it seems very probable that some of the early Miocene genera were indeed true ruminants. The intermediate types had a very wide geographical range, and assumed considerable importance in the mammalian fauna of the Upper Eocene and the Lower Miocene.

Among these intermediate races the family of **Anthracotheriidæ** seems to have been the most widely distributed, being represented abundantly throughout the greater part of Europe, and less commonly both in India and North America. These are stoutly-built animals, some probably much resembling the pigs in outward aspect, others more nearly similar to the hippopotamus. The dentition is complete, except that pm. 1 is occasionally lost; while the cusps on the molars begin to be distinctly crescent-shaped. When the upper molars are complicated by a small supplementary fifth cusp, this is placed between the anterior, not the posterior normal pair; and the hindermost lower molar always bears a large posterior talon or third lobe. The odontoid process of the atlas vertebra is still peg-shaped or slightly approaching the spout-shaped type; and all the bones of both feet, which are either four-toed or five-toed, remain separate. The best-known genera are *Anthracotherium, Hyopotamus,* and *Merycopotamus.*

Anthracotherium. This animal receives its name (coal-beast) from the circumstance that its remains were first discovered in the lignite or brown-coal of Cadibona, Savoy. The skeleton is now almost completely known from several discoveries of bones in association with the characteristic jaws in the Upper Eocene and Lower Miocene of Europe. The skull is depressed, with an elongated facial region, and the parietal bones meet in a prominent sagittal crest. The basicranial axis is straight. The orbital cavity is not completely separated by bone from the temporal fossa, while the zygomatic arch is slender. The dentition forms a nearly continuous series; the upper molars are complicated by a small anterior median fifth cusp; the canines are relatively large, with conical crown, and closed root; the incisors are nearly uniform in size, also conical and slightly spatulate. The angle of the mandible is not produced downwards. The scapula is elongate-triangular in shape, with a robust coracoid process. The radius and ulna are separate and nearly equal in stoutness; the tibia and fibula also remain separate, but the latter element is very slender. The femur is longer than the humerus. The lateral digits (nos. II and V) are complete, though smaller than the middle digits (nos. III and IV) on each foot; those of the pes are relatively the smallest. The metapodial bones are not keeled distally. The typical species, *Anthracotherium magnum,* has a skull about half a metre in length, and must thus have been about as large as a rhinoceros. Its remains occur in the Upper Eocene and Lower Miocene of northern Italy, Switzerland, Bavaria, Hesse Darmstadt, and France (Phosphorites of Quercy). Other species, some comparatively small, are found in strata of the same age in central and southern Europe as far east as Dalmatia. Detached teeth, apparently of this genus, also occur in the Lower Pliocene (Siwalik Formation) of India; and portions of jaws with dentition are known from the Lower Miocene (White River Formation) of Dakota.

Hyopotamus or **Ancodus** (figs. 199, 200). Closely resembling *Anthracotherium* in all parts of the skeleton, but less robust. The facial portion of the skull is very slender, while a considerable diastema separates pm. 1 (when present) from the canine, usually also from pm. 2. The crescent-shaped cusps of the molars are somewhat deepened. The best-known species, *H. velaunus*, from the Lower Miocene of Ronzon, France, and from the Hempstead Beds of the Isle of Wight, has a skull about 0·35 m. in length. Teeth of a larger form, *H. bovinus* (fig. 199), are also common in the Hempstead Beds, and have been found near Barcelona in Spain; and the largest known tooth, apparently of this genus, was discovered in the Lower Pliocene (Siwalik Formation) of India (*H. giganteus*). Other portions of skull and dentition, perhaps also certain limb-bones, are known from the Siwalik Formation of India. Nearly complete skeletons have been found in the Lower Miocene (White River Formation) of Dakota; and there are at least two species, one destitute of upper pm. 1 (*H. americanus*), the other (fig. 200) with upper pm. 1 and pm. 2 in contact (*H. brachyrhynchus*). The last-mentioned species is proved to have possessed a pentadactyl manus, with the digit no. I not only complete but well developed.

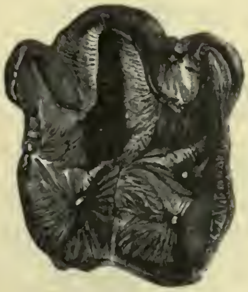

FIG. 199.

Hyopotamus bovinus; right upper molar 3, nat. size.—L. Miocene (Hempstead Beds); Isle of Wight. (After Lydekker.)

Merycopotamus. Known by the skull, mandible, and dentition; also probably by many detached bone-fragments which have been referred to it. The genus is much like *Hyopotamus*, but the upper molars exhibit only

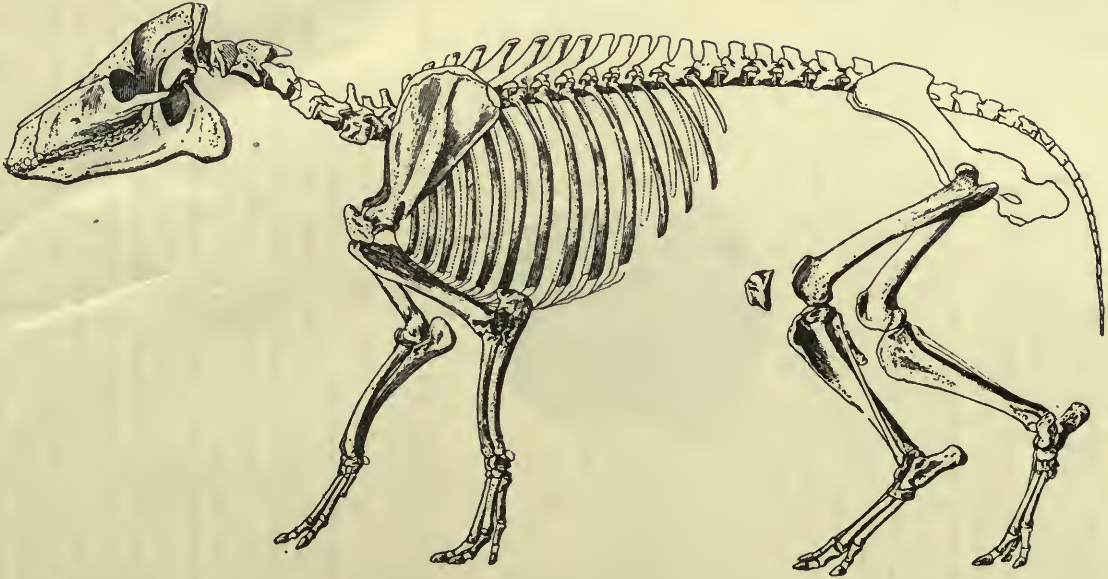

FIG. 200.

Hyopotamus brachyrhynchus; restoration of skeleton by W. B. Scott, one-tenth nat. size.—L. Miocene (White River Formation); Dakota.

the four crescentic cusps, no intermediate tubercle. The angle of the mandible is considerably produced downwards and backwards. The genus is restricted to the Lower Pliocene (Siwalik Formation) of India, and the typical species, *M. dissimilis*, has a skull about 0·4 m. in length. There is also a dwarf species, *M. nanus*.

Some of the later Eocene buno-selenodonts of the western European area are remarkable for the possession of three well-developed digits on each foot. These digits are a little spreading, and are supposed by some to have been originally connected with a web. The animals thus characterized are grouped together in the family **Anoplotheriidæ,** which had a remarkably restricted range both in space and time, and does not appear to have left any descendants. The typical genus is *Anoplotherium*, while *Diplobune* and *Dacrytherium* are associated and closely allied forms.

Fig. 201.

Anoplotherium cayluxense; right upper molars 1—3, premolars 3, 4, nat. size.—U. Eocene (Phosphorites); Quercy, France. (After Lydekker.)

Anoplotherium (fig. 201). This genus was first described by Cuvier, and thus named in allusion to its lack of all defensive weapons, whether tusks, horns, or claws. The skull is elongated, with a short and small cranial region, and the basicranial axis straight. The orbit is relatively small, and not completely separated by bone from the temporal fossa. The dentition is complete, with the usual 44 teeth, all in regular close series, approximately equal in height, not even the canines differing from the others in development. The upper molars (fig. 201) exhibit a supplementary fifth cusp between the ordinary two anterior cusps. The hindermost lower molar is produced into a third lobe posteriorly. The dorsolumbar vertebræ are proved to be 19 in number, as usual in artiodactyls; but the tail is exceptional in being very much elongated and provided with chevron bones. The animal may have inhabited swamps and marshes and employed the tail in swimming. The radius and ulna are complete, separate, and about equally stout; the fibula is also complete and separate, but relatively slender. In each foot the two principal digits (nos. III and

IV) seem to have formed a nearly symmetrical pair, while no. II, which is shorter, is considerably turned inwards. In the manus there are also rudiments of metacarpals nos. I and V, while in the pes a trace of metatarsal no. I remains. The finest specimens of the typical species, *Anoplotherium commune*, have been obtained from the gypsum (Upper Eocene) of Montmartre, Paris. The skull measures about 0·3 m. in length. Teeth and other fragmentary remains of this and allied species are also known from the French Phosphorites and other Upper Eocene formations in France, Germany, and the Isle of Wight.

The small slender artiodactyls of the Upper Eocene and Lower Miocene, which may be most probably regarded as the direct ancestors of the true ruminants of later date, are variously classified. So many genera are still imperfectly known, and so many gradational forms occur, that it is very difficult at present to suggest even a provisional arrangement. Three families, however, seem to be distinguishable, and all may be described as having selenodont molars.

Of these families, that of the **Cænotheriidæ** is perhaps the most generalized. It comprises small animals with a complete selenodont dentition in uniform series, and with four moderately stout digits on each foot. They seem to be confined to the Upper Eocene and Lower Miocene of Europe, and the typical genus is

Cænotherium (figs. 202A—C). This is known by nearly complete skeletons, rarely if ever more than 0·3 m. in length. The skull (fig. 202) exhibits an elongated facial region, usually with an irregular antorbital vacuity, and the basicranial axis is slightly bent. There is a prominent sagittal crest, and the tympanic bullæ are large and inflated. The orbital cavity is almost or completely separated from the temporal fossa by a slender bar of bone. The teeth are of almost uniform height, and the dental series is only interrupted sometimes by variable short diastemata between the premolars. The upper molars exhibit a supplementary fifth cusp between the ordinary two posterior cusps; while the hindermost lower molar is produced behind into a small third lobe. The coronoid process of the mandible is excessively elongated. The ulna and radius are complete and separate, and digits nos. II, V are much shorter than nos. III, IV. The hind limb and foot are considerably larger than the fore limb and foot, and here the lateral metapodials are not much shorter than the median pair. The fibula is very slender and fused with the tibia at the lower end. *Cænotherium commune* is the typical species from the Lower Miocene of Puy-de-Dôme, France, the Mayence Basin, and Würtemberg.

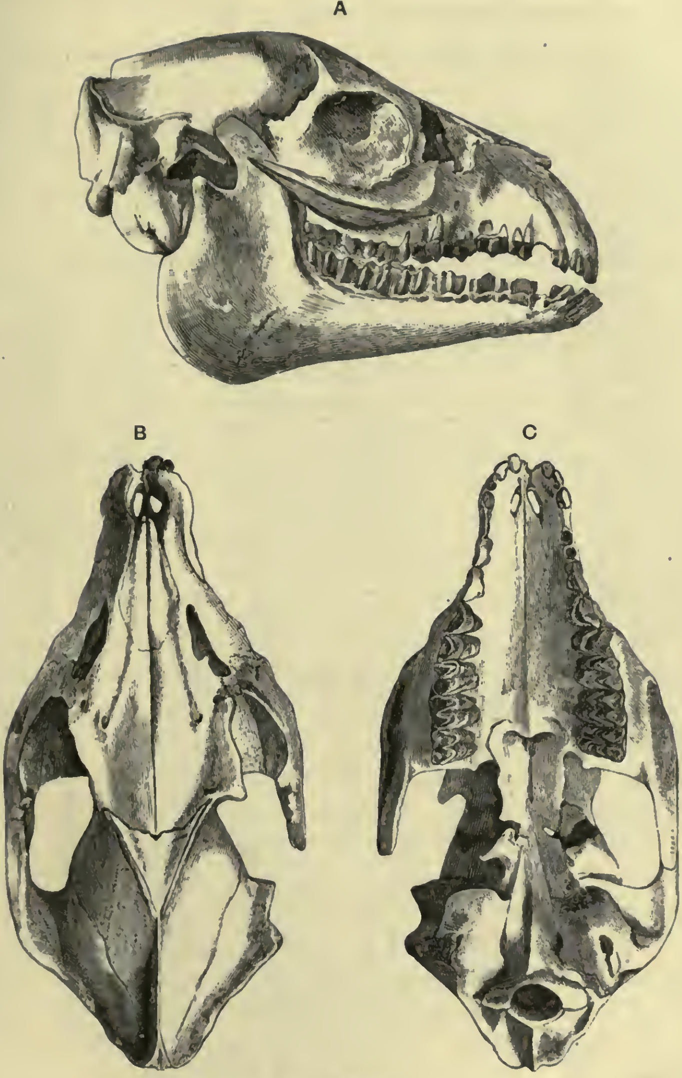

Fig. 202.

Cænotherium filholi; skull from the lateral (A), superior (B), and palatal (C) aspects, nat. size.—U. Eocene (Phosphorites); Quercy, France. (After Lydekker.)

There are other well-known forms from the same localities, and also from the Upper Eocene Phosphorites of Quercy, France.

The **Xiphodontidæ** are another family of these primitive forerunners of the ruminants from the Upper Eocene, also apparently confined to the western European area. Some of them are the largest and most slender of the artiodactyls of their age, and the only feet hitherto discovered are two-toed, with mere rudiments of the lateral digits.

Xiphodon. The dentition is complete, forming a regular series, without any conspicuous diastema or any enlargement of the canine. The upper molars exhibit a supplementary fifth cusp between the ordinary two anterior cusps; the hindermost lower molar is produced into a small third lobe posteriorly. Pm. 1 to 3 are much extended antero-posteriorly. The limb-bones are long and slender, and the lateral digits (nos. II. and V.) of both feet are represented solely by the upper end of the metapodials. The typical species is *Xiphodon gracilis* from the Upper Eocene (gypsum) of Montmartre, Paris, the contemporaneous lignites of Débruge, and the Phosphorites of Quercy; also from equivalent deposits in Switzerland. This animal seems to have attained a length of less than a metre, and it is associated with both larger and smaller species. *Dichodon* (fig. 203) and *Amphimeryx* are contemporaneous closely related genera.

The third of the primitive families already mentioned as requiring notice, is that of the **Oreodontidæ**, apparently confined to North America, but ranging from the Upper Eocene to the Upper Miocene. These are animals not larger than sheep, with a very long tail, and with four functional toes on each foot. The dentition is usually complete, though the incisors are sometimes rudimentary or even wanting in the upper jaw; and all the genera exhibit one very peculiar feature, namely, the degradation of the lower canine to the rank of an incisor, while the foremost premolar is enlarged to usurp its function in opposing the moderately large upper canine. Most of the genera are known by the nearly complete skeleton, and two of them, *Oreodon* and *Agriochœrus*, are especially noteworthy.

Oreodon. In the skull the facial and cranial regions are about equal in length, and there is a deep antorbital pit (not a vacuity). The sagittal crest is acute and prominent, while the occiput is a little overhanging. The orbit is separated from the temporal fossa by a slender bar of bone, and the zygomatic arch is not very robust. The tympanic bullæ are a

ORDER 4. UNGULATA. *Sub-Order* 10. *Artiodactyla.*

FIG. 203.

Dichodon cuspidatus; left mandibular ramus, premaxilla, and upper and lower dentition, nat. size.—U. Eocene; Hordwell, Hampshire. There are three incisors (1—3, *i*), one canine (*c*), four premolars (1—4, *p*), and three molars (1—3, *m*) above and below. Upper premolars 1—3 are shown from the grinding surface, and lower molars 1—3 are shown from the same aspect below the jaw. (After Owen.)

little inflated, but small. The dentition is complete, without any diastema. The upper molars exhibit only the four ordinary crescentic cusps, without any intermediate tubercle. The upper canine is somewhat enlarged, pointed, and triangular in section, worn on its hinder face. The upper incisors are relatively small, and nearly uniform. The hindermost lower molar is produced into a third lobe posteriorly. The foremost premolar is quite canine-like in shape, though smaller than the upper canine against which its anterior face works. The lower canine resembles the adjoining incisors, which are about as small and regular as those of the upper jaw. The cervical vertebræ are slightly opisthocœlous; there are 13 true dorsal vertebræ with ribs; and the caudals of the long tail are known to have been more than 17 in number. The scapula is elongate-triangular in shape; the humerus is comparatively stout; the radius and ulna are complete and separate; while the manus, in addition to the four functional toes, bears a much-reduced though complete digit no. I. In the hind limb the tibia is shorter than the femur, and the fibula is comparatively slender though separate. Among the tarsal bones, only the ecto- and meso-cuneiforms are fused together; and there is no trace of digit no. I. in the pes. The typical species is *Oreodon culbertsoni* from the Lower Miocene (White River Formation) of Dakota and Wyoming, with the skull about 0·2 m. in length. Other forms are also recorded from the same horizon in Dakota, Nebraska, Colorado, and Wyoming.

Agriochœrus (fig. 204). Also known by the complete skeleton. The skull differs from that of *Oreodon* in the absence of an antorbital pit and the incompleteness of the postorbital bar. The incisors have disappeared from the upper jaw, leaving the small premaxillæ toothless; there is a wide diastema in the upper jaw between the canine and premolars, and a somewhat shorter diastema in the lower jaw between the caniniform pm. 1 and pm. 2; while the hindermost premolar in both jaws is as complex as the molars. The skeleton is generally similar to that of *Oreodon*, but the ungual phalanges on both feet are relatively large and claw-shaped rather than hoof-shaped. The typical and best-known species is *Agriochœrus latifrons* (fig. 204), an animal somewhat more than a metre in length, not including the tail. It occurs in the Lower Miocene (White River Formation) of Dakota, and other forms are met with in the overlying John Day Series.

Among the artiodactyls contemporary with the Oreodontidæ in the North American area, it is interesting to be able to recognize distinctly the direct ancestors of the existing **Camelidæ,** or camels and llamas. These animals, as is well known, are unique among the ruminants in several respects and are placed by zoologists in a distinct group, named TYLO-

ORDER 4. UNGULATA. *Sub-Order* 10. *Artiodactyla.*

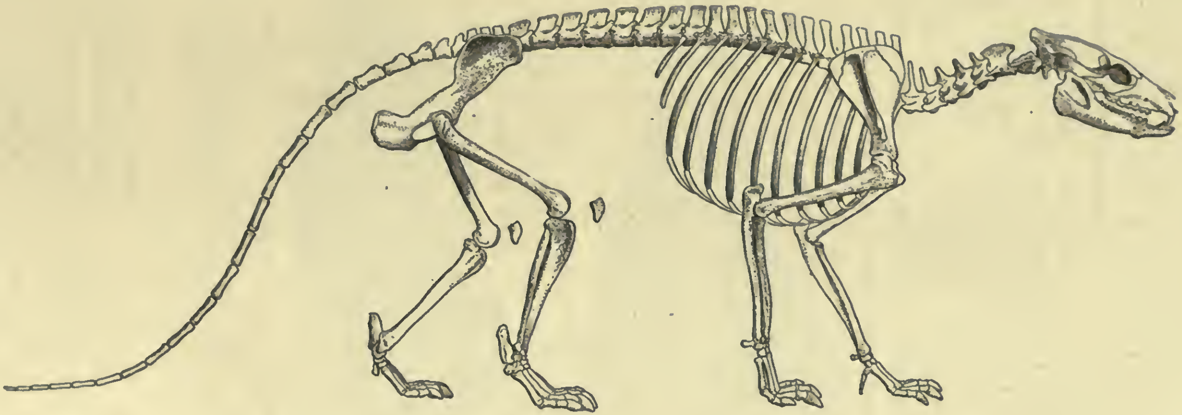

FIG. 204.

Agriochœrus latifrons; restoration of skeleton by J. L. Wortman, about one-eighth nat. size.—L. Miocene (White River Formation); Dakota.

PODA in allusion to their cushion-like feet. The skull does not bear horns, and the upper incisors do not entirely disappear, although the premolars are reduced in number and more or less dispersed. The tympanic bullæ are filled with spongy bone. The neck is somewhat elongated and resembles that of the extinct *Macrauchenia* (p. 318), in the circumstance that the canal for the vertebral artery penetrates and traverses the pedicles of the neural arches. Although the digits are reduced to two on each foot and the metapodials are fused together throughout the greater part of their length, the trapezoid and magnum in the carpus and the navicular and cuboid in the tarsus remain distinct. It is also noteworthy that the two elements of the metapodium or cannon-bone are slightly divergent at the lower or distal extremity; and the articular ends are not keeled like those of ordinary ruminants, but bluntly rounded and smooth.

It was for long a strange and inexplicable fact, that the mammals exhibiting these unique characters in the skeleton, and other equally remarkable features in the soft parts, should occur only in two widely-separated regions of the globe—the camels in Asia and perhaps northern Africa, the llamas and vicunas in South America. The explanation is now afforded by the skeletons discovered in the Miocene and Pliocene strata of North America. It appears that the family was gradually evolved from primitive artiodactyls in this area; that by early Pliocene times the fully differentiated camel had reached India, probably by some land-bridge in the north; and that when the Isthmus of Panama was upheaved at the beginning of the Pliocene period, the representatives of the llamas and vicunas wandered south, where they have since flourished exceedingly. All the members of the family became extinct in North America at the close of the Pliocene period.

Poebrotherium. An animal of slender proportions, in form and size resembling a small gazelle. The facial region of the skull is much elongated and laterally compressed; and the basicranial axis is slightly bent. The orbit is relatively large and not completely separated by a bony bar from the temporal fossa; the tympanic bullæ are relatively large. The dentition is complete, and the dental series is regular and almost continuous, with the incisors slightly spaced and only a short diastema in front of and behind pm. 1. The milk-dentition is known, and remains in place until all the true molars have appeared. The dental crowns are low, and each upper molar exhibits four crescentic cusps, while the hindermost lower molar has a third posterior lobe or talon; the anterior premolars in each jaw are antero-posteriorly extended. The canines are small. The radius and ulna are fused together, and the upper and lower ends of the imperfect fibula are fused with the tibia; but the metapodials (III, IV) are separate on each foot, and there are remnants of the upper ends of metapodials nos. II and V at least in the hind foot. The typical species, known by the greater part of the skeleton, is *Poebrotherium wilsoni*, from the Lower Miocene (White River Formation) of Nebraska, Dakota, Wyoming, and Colorado. Its skull measures about 0·15 m. in length.

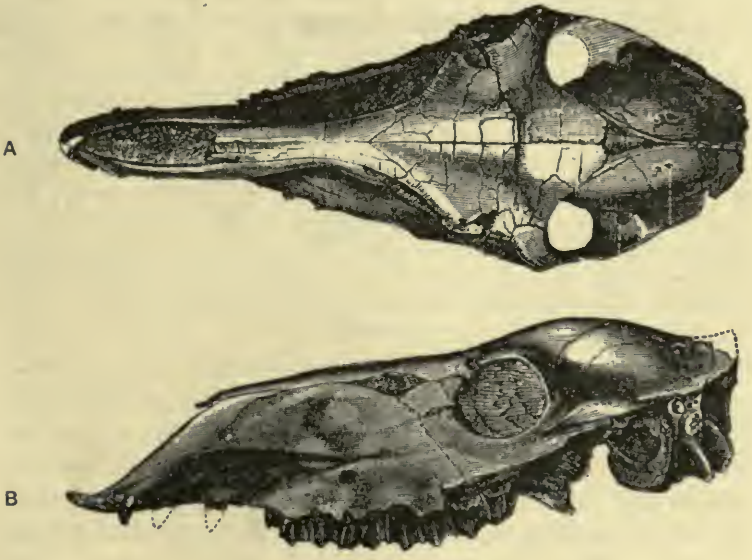

FIG. 205.

Procamelus occidentalis; skull from the superior (A) and lateral (B) aspects, one-third nat. size.—U. Miocene (Loup Fork Formation); New Mexico. (After Cope.)

Procamelus (fig. 205). More robust animals, ranging in size from that of a sheep to that of a camel. There is a small irregular vacuity on each side of the slender facial region of the skull, and the orbit is completely surrounded by bone. The upper incisors are reduced to a single, widely-separated pair, conical in shape, but the remainder of the dentition is complete. The incisor, the canine, and the first premolar, all similar in shape, are somewhat spaced in the upper jaw. The ulna and radius, as also the tibia and fibula, are fused together; the metapodials are likewise united into a cannon-bone on each foot, and there are no longer traces of the lateral digits. *Procamelus occidentalis* (fig. 205) and other species occur in the Upper Miocene (Loup Fork Series) of New Mexico, Dakota, Nebraska, and Colorado; probably also in Virginia and Florida.

Camelus. The typical camels differ from *Procamelus* in the further reduction of the dentition by the loss of one premolar in the upper, and two premolars in the lower jaw. One or two species (*Camelus sivalensis*, *C. antiquus*) are represented by numerous remains in the Lower Pliocene of the Siwalik Hills, India; and these are interesting as exhibiting a vertical ridge at the antero-external angle of the lower molars, which is no longer observed in the camels but characteristic of the South American *Auchenia*. Fragmentary traces of other species have been recorded from the Pleistocene of southern Russia, of Roumania, and of Algeria.

Auchenia. The llamas, alpacas, vicunas, and guanacos of South America are smaller and more slender animals than the existing camels, with the two toes more distinctly separated. Their premolars are still further reduced to two in each jaw. Remains of similar forms have never been found in the later Tertiary deposits of the country they now inhabit of earlier date than the latest Pliocene or the earliest Pleistocene. Two very similar genera, with only one premolar in each jaw, are known by fragmentary remains from the Upper Pliocene of Oregon, California, and Mexico (*Holomeniscus*, *Eschatius*); and these are the latest representatives of the Camelidæ hitherto discovered in the land of their origin.

The characters and mode of life of the earliest and most primitive ruminants are probably revealed in the small existing **Tragulidæ,** or chevrotains, of the Indo-Malayan region and western Africa. Palæontology shows that these little animals, unique and isolated among the Ungulata of the present day, are the scarcely-altered survivors of a great tribe which flourished abundantly in Europe, and less so in North America, before the typical and fully differentiated ruminants had made their appearance. The upper incisors have disappeared and the foremost premolar is sometimes wanting; but otherwise the dentition is complete, and the grinding teeth are in uninterrupted series. The upper molars bear the usual four crescentic cusps, quite brachyodont; and the hindermost lower molar is produced into a third posterior lobe. The basicranial axis is straight. The tympanic bullæ of the skull in the surviving genera are filled with spongy bone. There are never any frontal appendages. The odontoid process of the axis vertebra retains its primitive conical shape. The ulna and fibula are complete, but some of the carpal and tarsal bones are fused together; the metapodials nos. III and IV are usually imperfectly united to form a cannon-bone; while the lateral digits, nos. II and V, even though complete are excessively attenuated. The stomach in the two existing genera is less complex than in the true ruminants, the maniplies being rudimentary. *Prodremotherium*, known by the greater part of the skeleton from the Upper Eocene Phosphorites of Quercy, France, is almost identical with the existing *Tragulus* of the Indo-Malayan region, and exhibits the enlarged upper canines; but the lateral metapodial bones are reduced to imperfect splints. *Tragulus* itself seems to have reached its present habitat by the early Pliocene period, so far as can be determined from detached teeth found in the Siwalik Formation of India. *Gelocus* (fig. 195 B, E) from the Upper Eocene and Lower Miocene of France is another extinct ally, in which the lateral metapodial bones are represented only by their upper and lower extremities. Species of the existing *Hyaemoschus* or *Dorcatherium* (fig. 195 A) of western Africa, seem to have been widely distributed through southern and central Europe during the Miocene, and there is evidence of others in the Lower Pliocene (Siwalik Formation) of India. Allied genera, such as *Leptomeryx*, also seem to be represented in the Lower Miocene (White River Formation) of Dakota and Nebraska in North America. Since the Miocene period the Tragulidæ have been extinct in Europe and North America, and seem to have been restricted to their present geographical range.

While, however, the Tragulidæ are an essentially Old World type, some of their immediate allies in North America during the early part of the Miocene period attained a remarkable degree of specialization in the skull, and exhibited an armature unique among the Artiodactyla. These constitute the family of **Protoceratidæ,** which, like most highly specialized groups, had only a very restricted range in time and space. The skull, at least in the males, bears two or more pairs of horns or callosities, very suggestive of those of the

Dinocerata (p. 296). The typical and only satisfactorily known genus is

Protoceras (fig. 206). The skull is long and narrow, with the facial region much produced and somewhat bent downwards from the cranial region. The brain-case is large, and an impression of its cavity shows the cerebral hemispheres of the brain to have been much convoluted. The orbits are large and completely surrounded by bone. The premaxillæ are small and edentulous, and the narial opening is very large; the nasal bones are short, and so disposed that it seems probable that the animal had a long flexible nose, if not a true proboscis. The maxillæ are the largest bones in the skull; those of the male bearing the large canine tusks at the anterior end, and raised above into a pair of rounded bosses, which may have been horn-cores or tipped with callosities. The frontals in the male (fig. 206) bear another diminutive pair of bony bosses; while the comparatively small parietals are surmounted by a third pair of prominences which are much elevated. In the female skull, only the parietal prominences occur, and these are quite small. The tympanic bone is scarcely inflated. The mandible is long and slender. Apart from the loss of the upper incisors, the dentition is complete; and it is similar to that of the Tragulidæ. In the fore limb, the radius and ulna are complete, but they tend to fuse together distally; metacarpals III and IV

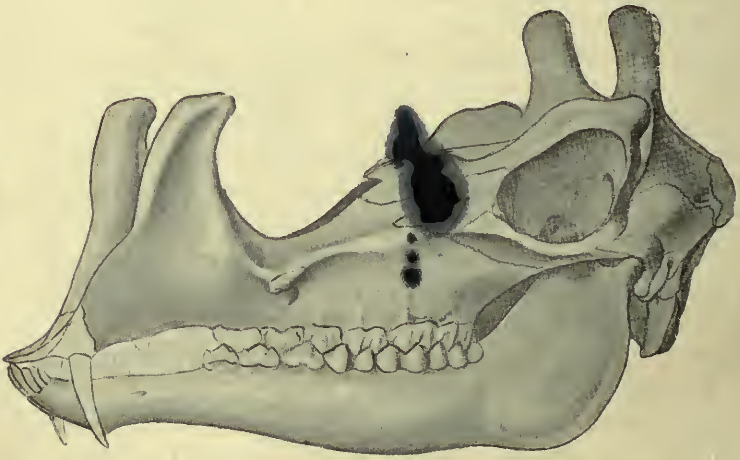

Fig. 206.

Protoceras celer; skull and mandible of male, left lateral aspect, one-half nat. size.—L. Miocene (White River Formation); Dakota. (After Marsh.)

are not united, and the slender lateral digits, nos. II and V, are completely developed. In the hind limb the fibula is reduced so much that only its distal end (the so-called *malleolar* bone) remains, as in the existing deer; the hind foot is considerably larger than the fore foot, and the lateral metatarsals, nos. II and V, are reduced to mere splints at the upper end; metatarsals nos. III and IV remain separate. The elements of the carpus and tarsus exhibit less fusion than in the Tragulidæ and true ruminants; and the keel at the distal end of the metacarpals and metatarsals is incomplete, not reaching to the anterior face of the bone. The typical species is *Protoceras celer*, known by the nearly complete skeleton from the Lower Miocene (White River Formation) of Dakota. The skull measures 0·2 m. in length, and the animal must have been about as large as a sheep.

In the Lower Miocene of Europe and the Middle or Upper Miocene of North America, undoubted **Cervidæ** or deer also appear for the first time. They agree with the Tragulidæ and Protoceratidæ in many respects, but exhibit a distinct advance upon these, not only in the prevailing and characteristic armature of the head, but also in some other features. The facial region of the skull is now slightly bent downwards upon the cranial region, and the tympanic bullæ are hollow. The odontoid process of the axis vertebra is no longer a mere peg, but has become flattened into a half-cylinder. As in *Protoceras*, the fibula is always so far reduced that only its distal end remains in the small malleolar bone. Some of the carpal and tarsal bones are fused together; and the cannon-bone is invariably complete on each foot, usually fringed by remains of the lateral digits nos. II and V (fig. 195 C).

As the various members of the family are traced from the Lower Miocene upwards, they are observed to become gradually specialized in two important respects, namely, in the horns and the teeth. Most of the earlier stages have, indeed, a few surviving representatives; but, taking the family as a whole, the advance is very evident.

The earliest known genera are hornless, but by the period of the Middle Miocene the males of some forms had acquired a small pair of bifurcated deciduous horns (or *antlers*) fixed on long bony pedicles of the frontal bones (fig. 207). It is clear that these appendages were shed at times like the antlers of modern deer, because they are marked by the characteristic *burr* or roughness round the base due to the peculiar method of growth of such defences. For the first time in the Upper Miocene and Lower Pliocene certain antlers acquired three or four prongs (or *tynes*) projecting from the main stem (or *beam*); while in the Upper Pliocene, as these appendages began to increase in relative dimensions and the bony pedicles supporting them

FIG. 207.

Antlers of Cervidæ. *b*, beam; *br.*, burr; *p*, permanent bony pedicle; *t*, tynes.

A. *Dicroceros elegans.*—M. Miocene; Sansan, Gers, France. One-quarter nat. size.

B. *Cervus* (? *Capreolus*) *pentelici.*—L. Pliocene; Pikermi, Greece. One-quarter nat. size. (After Dames.)

C. *Cervus perrieri.*—U. Pliocene; Mont Perrier, Puy-de-Dôme, France. One-eighth nat. size. (After Dawkins.)

became comparatively insignificant, a complexity was reached equalling that observed in the antlers of the majority of the Pleistocene and existing forms. It is thus interesting to note that the gradual acquisition of complex antlers by the race since Miocene times, is parallel with the gradual development of these weapons in an individual modern deer. The animal is born hornless; at the end of the first year it acquires a simple antler (or *pricket*); this is shed, and at the end of the second year a bifurcated antler is acquired; next year the antlers have two or three tynes; and so on, until the maximum complexity of the species has been reached. In all existing genera and species except the reindeer (*Rangifer tarandus*) the antlers are confined to the male sex.

With reference to the teeth, it is to be noted that the earliest genera of Cervidæ are remarkably brachyodont, and their true molars exhibit no complication of the crown beyond the four crescentic cusps. On the other hand, in the majority of the later and more specialized genera the dentition is almost or quite hypsodont, and an insignificant tubercle observed in the molars of the earlier forms on the inner side in the upper jaw, on the outer side in the lower jaw, often becomes afterwards deepened into a slender column.

The primitive hornless deer of the Lower Miocene are known only from western Europe, and their equally unarmed surviving relatives, the musk-deer (*Moschus*) and the Chinese water-deer (*Hydropotes*), are now confined to Asia. *Amphitragulus* is known by nearly all parts of the skeleton (hitherto only found isolated and hypothetically placed together) from the Lower Miocene of France and Germany. Its hornless skull is destitute of an antorbital fossa and vacuity, while its dentition is of the characteristic primitive type already mentioned, but with the upper canine elongated. The largest species would probably not exceed a modern roe-deer in size. *Dicroceros*, known not only by detached bones and teeth, but also by at least one complete skeleton (from Steinheim, Würtemberg), is the earliest deer in which antlers have hitherto been observed. These appendages (fig. 207 A) are small, fixed on long bony pedicles, and they simply bifurcate from the base, though there is sometimes also a further bifurcation of the apex. The burr is usually present, but in some small specimens it is not seen, and these are claimed as referable to very young individuals. *Dicroceros* occurs in the Middle Miocene of France, Switzerland, Germany, and Austria; *D. furcatus* from Steinheim, Würtemberg, being the best-known form. An American genus with equally simple and small, though very variable antlers, is *Cosoryx*, known by the nearly complete skeleton from the Upper Miocene (Loup Fork Formation) of Nebraska, Kansas, Colorado, and New Mexico. Some slightly more complicated antlers, relatively longer and with two, three, or four tynes, from the Lower Pliocene of France and Greece, are provisionally placed with the existing roe-deer in the genus *Capreolus* (fig. 207 B). The true roe-deer itself (*Capreolus caprea*) seems to have wandered over the greater part of Europe in Pleistocene times; and in Britain its remains are found in superficial deposits of various ages from the Cromer Forest Bed upwards. The true *Cervus* seems to occur first in the Upper Pliocene of Europe (fig. 207 C), and there is reason to believe that it acquired the largest and most complicated antlers towards the close of this period. *Cervus sedgwicki*, from the Upper Pliocene of the valley of the Arno in northern Italy and from the Cromer Forest Bed, may be specially cited as a remarkable example of specialization in the antlers. Other striking developments, such as *C. verticornis* and *C. savini*, are also represented by fragments in the Cromer Forest Bed. The common stag or red deer (*C. elaphus*) also seems to have attained a larger size during the Pleistocene period than at the present day in western Europe, some fragments of antlers found in the caves of Britain and the adjoining continent (the so-called *Strongyloceros spelæus*) rivalling those of the existing North American Wapiti in size. The stag is clearly indigenous to the British Isles, but the common fallow deer (*C. dama*) of the English parks seems to have been introduced by the Romans; although *C. browni* and *C. falconeri*, from the Cromer Forest Bed and the Pliocene Crags, seem to have been closely allied species.

Perhaps the most remarkable of all the recently extinct

Cervidæ is the so-called Irish deer (*Cervus giganteus* or *Megaceros hibernicus*), of which many complete skeletons have been reconstructed from the well-preserved remains found in the marl at the base of the Irish peat-bogs (fig. 208). The female is quite hornless, but the male bears a pair of truly colossal antlers, considerably expanded, and sometimes measuring more than three metres across from tip to tip. These antlers are very variable in shape and occur in Pleistocene deposits throughout the greater part of Europe; some may belong to distinct

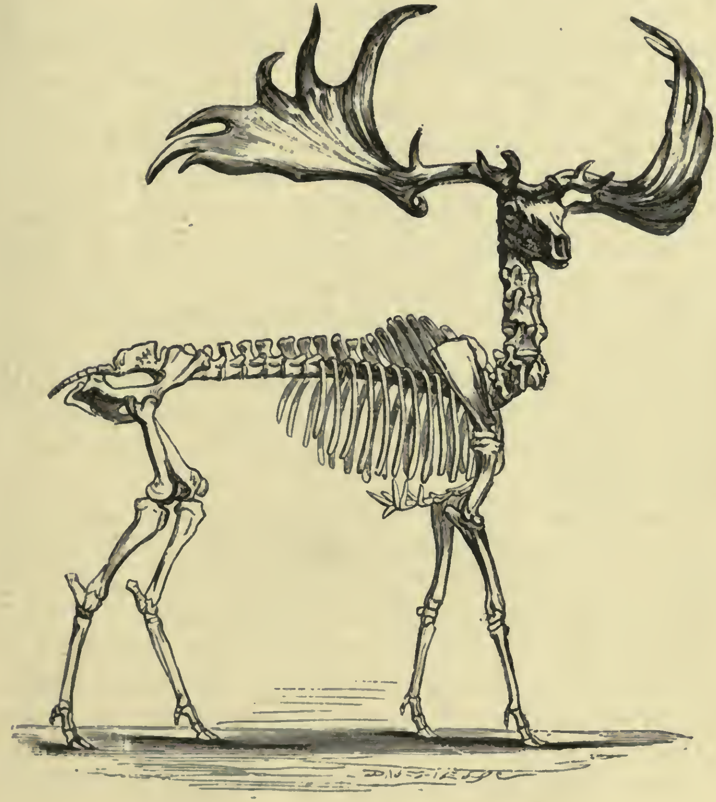

Fig. 208.

Cervus (Megaceros) giganteus; skeleton of male, about one-thirtieth nat. size.—Pleistocene or Prehistoric; Irish Peat Bogs. (After Owen.)

but closely allied species. The typical *C. giganteus* is represented by fragments in many Pleistocene river-deposits and cavern deposits in England; there are also remains of it in the Isle of Man; and the animal seems to have survived until comparatively recent prehistoric times in Ireland.

The Irish deer is sometimes described as an elk, but this is an erroneous determination; for its antlers exhibit a brow tyne, and the conformation of the nasal bones shows that the extremity of the snout was not at all elk-like. The true elk (*Alces machlis*), however, was a contemporary of the Irish deer, and during the Pleistocene period it had a much wider geographical range than at present. In Britain remains of this animal, the largest of the surviving Cervidæ, are known from many localities both north and south and in Ireland; and there are indications of a still larger extinct species, *Alces latifrons*, in the Cromer Forest Bed. In the North American Pleistocene there is an animal apparently intermediate between *Alces* and *Cervus*, named *Cervalces americanus*, and known by a nearly complete skeleton in the Princeton University Museum from New Jersey.

The reindeer (*Rangifer tarandus*), like the elk, exhibited a much wider distribution in the Pleistocene period than at the present day. It wandered southwards in Europe as far as the Pyrenees and Alps, where it was contemporary with the early Palæolithic hunter; and its remains occur in Pleistocene and later deposits throughout Great Britain and Ireland, while a few solitary survivors of the species are recorded as existing in Caithness so late as the 12th century. The fossil antlers are as variable in size and shape as the antlers of the surviving race in the north, the giant and dwarf forms being often curiously mingled in the same formation and district.

The giraffe is unique among existing artiodactyls, and is the sole surviving representative of the family **Giraffidæ**. In early Pliocene times, however, an animal with teeth, neck, and limbs remarkably like it, lived in southern Europe and Asia, associated with several closely allied genera which seem to have connected it with the primitive Bovidæ. The family as a whole is thus not clearly definable; but the cranial roof is thickened and penetrated by air-cavities, while when frontal appendages are present, these (or at least one pair of them) are small bony prominences, separately ossified, which are not shed but eventually become fused with the skull and are always covered with skin. The upper canines are absent and the molars are brachyodont. The lateral digits of the limbs are entirely wanting or represented only by the upper end of the metapodials.

In the existing giraffe (*Giraffa* or *Camelopardalis*) the pair of bony prominences is placed over the suture between the frontal and parietal bones, and is covered with hairy skin; the armature is present in both sexes and even in the newly-born young. It is not yet certain, however, whether the early Pliocene animal with equally long neck and limbs and similar teeth, was characterized by horns of the same disposition, and may therefore be placed in the same genus; for the only known remains from China, from the Siwalik Formation of India (*Giraffa sivalensis*, *G. affinis*), and from the well-known mammaliferous deposit of Pikermi in Greece (*G. attica*), are very fragmentary and do not include the top of the skull. The best-known extinct giraffe, of the same early Pliocene period, undoubtedly belongs to a distinct genus, named *Samotherium* from the discovery of the finest specimens in the Isle of Samos in the Turkish archipelago. In this animal the neck and limbs are somewhat shorter than in the surviving *Giraffa*, and the horns are confined to the male sex. The horns, moreover, are fixed entirely on the frontal region directly above the orbits (fig. 209); and the same arrangement is observed in a fine skull of *Palæotragus* from the Pikermi deposit, which was originally supposed to belong to an antelope but is now regarded as more probably giraffine. An imperfect skull from the Lower Pliocene of Maragha, Persia, also seems to be referable to *Samotherium*.

Samotherium is about as large as an ordinary giraffe, but the extinct genera exhibiting shorter neck and limbs and a more bovine aspect, comprise much larger species of remarkably stout proportions. *Helladotherium*, from Pikermi, is known by a hornless skull about 0·75 m. in length, and by the greater part of the skeleton, which seems to show that the fore and hind limbs were nearly equal in length. *Sivatherium*, from the Siwalik Formation of India, is a still larger and more stoutly built animal, with a comparatively short and broad skull, which bears two pairs of bony prominences (fig. 210). The hinder appendages are much the larger, and are placed just above the occiput probably on the parietal bones. They are somewhat expanded and flattened (*palmated*), with a few short tynes, and marked with grooves which indicate an originally vascular covering. They have not yet been found actually fixed upon the skull, so that it is uncertain whether or not they are transposed in the generally-accepted restoration (fig. 210). The small anterior bosses are fixed on the frontals, from which they are clearly separated by suture in the type specimen. The greater part of the skeleton has been identified with much probability of correctness; and a hornless skull from the Siwalik Formation has been supposed to belong

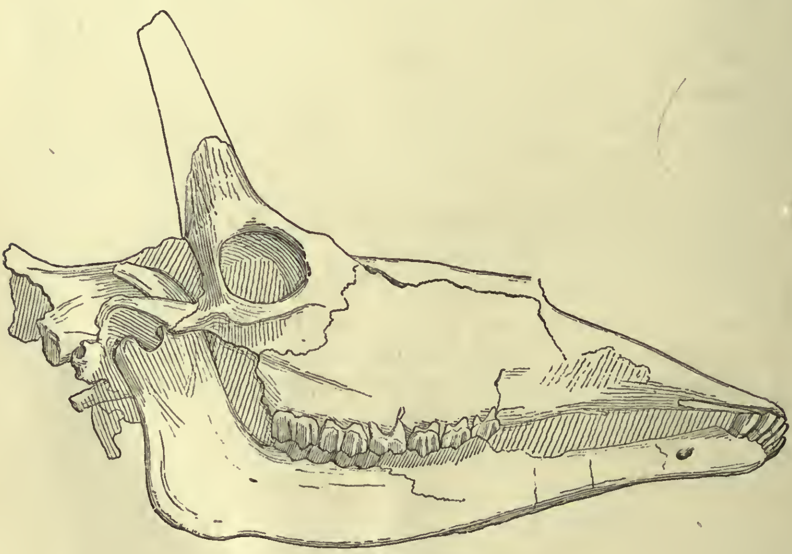

FIG. 209.

Samotherium boissieri; imperfect skull and mandible, right lateral aspect, about one-sixth nat. size.—L. Pliocene; Isle of Samos. (After Forsyth Major.)

to the female of the same genus. *Bramatherium* and *Vishnutherium* are more imperfectly known contemporaneous genera from the Indian region.

The existing prong-buck (*Antilocapra*) of the North American prairies is well known to be partly intermediate between the Cervidæ and the Bovidæ in the nature of its horns; and the hinder appendages of *Sivatherium*, as also the horns of several other early ruminants, may well have been similar to these structures. The horns have a permanent bony core, as in the Bovidæ; but the epidermal sheath does not merely wear away, it is periodically shed like the antlers of the Cervidæ. The gap between the solid-horned (cervicorn) and hollow-horned (cavicorn) ruminants, is thus partly filled even in the existing world.

Fig. 210.

Sivatherium giganteum; partially restored skull, anterior aspect, one-thirteenth nat. size.—L. Pliocene (Siwalik Formation); India. (After Lydekker.)

In the true **Bovidæ**, or antelopes, sheep, and oxen, the frontal appendages when present are always a pair of persistent bony processes (*horn-cores*), covered with true horn, which grows continuously at the base and is worn away at the apex. These are the most specialized of all the artiodactyls, and attain their maximum development at the present day; the existing forms being so numerous and so extraordinarily varied that it is difficult to classify them. They range over the greater part of Africa, Asia, and Europe, and also over the Arctic and northern temperate regions of America; but it is interesting to note that they do not appear to have reached the New World until the close of the Pliocene period.

The earliest known Bovidæ are small gazelle-like animals represented by fragments from the Middle or Upper Miocene of France (*Protragoceras chantrei*), and from the Lower Pliocene of France, England (*Gazella anglica*, Coralline Crag), Austria, Italy, Greece, the Isle of Samos, Maragha in Persia, and the Siwalik Hills in India. In the Lower Pliocene both of Europe and Asia there are also remains of comparatively large antelopes, some (as *Palæoreas*, fig. 211, from Pikermi and Tuscany) with spirally-twisted horns. In the Pleistocene period the Saiga Antelope (*Saiga tatarica*), now living on the Siberian

FIG. 211.

Palæoreas lindermayeri; skull, left lateral aspect, two-fifths nat. size.—L. Pliocene; Pikermi, Greece. (After Gaudry.)

steppes and east of the Volga, wandered as far as the extreme west of Europe, where it was hunted by the Palæolithic men in France; and one portion of skull has been discovered in the Thames valley-gravels near Twickenham.

Nothing of importance is known concerning the ancestry of the sheep and goats; but the closely-allied musk ox (*Ovibos moschatus*), now confined to the Arctic regions, is interesting as being represented by various characteristic remains in the Pleistocene deposits of Europe as far south as the Pyrenees and Alps, while allied species occur in Pleistocene formations equally far south in North America. Portions of the skull of the musk ox have been found in the Thames valley, at Freshford near Bath, and also probably in the Cromer Forest Bed.

The true oxen, so far as known, appear first in the Lower Pliocene of India (Siwalik Formation), and they reach both Europe and North America in the Upper Pliocene. In some of the early species the females seem to have been hornless (*Leptobos falconeri* from India, *L. etruscus* and *L. elatus* from Tuscany, France, and Spain). Other Siwalik species, however, are very closely related to the common domesticated *Bos taurus. Bos primigenius*, from the Pleistocene of Europe, and probably the Urus of Cæsar, seems to have been merely a gigantic race of the existing form just mentioned. The genus *Bison* is also first represented in the Lower Pliocene (Siwalik Formation) of India; and remains of the extinct forerunners of the North American "buffalo" occur in the Upper Pliocene of the United States. The *Bison bonasus*, now preserved in Lithuania and the Caucasus, ranged during the Pleistocene period throughout the greater part of Europe; and numerous remains of this animal have been found in England, both in the Cromer Forest Bed and in later Pleistocene deposits.

ORDER 5. RODENTIA.

The Rodentia, or gnawing mammals, are a well-defined order of small animals, destitute of canine teeth and one or more of the premolars, but with one of the pairs of chisel-shaped (scalpriform) incisors above and below greatly-enlarged, and growing from persistent pulps throughout life. To admit of the gnawing action of the mandible, its articulation with the skull is antero-posteriorly elongated. The masseter muscle is extended forwards at its upper end, often through an enlarged infraorbital foramen at the anterior extremity of the zygomatic arch, sometimes over the outer face of this arch; while its insertion upon the mandible usually extends forwards in a similar manner well below the tooth-bearing border. The jugal bone occupies the middle part of the zygomatic arch, and the orbit is never separated by bone from the large temporal fossa. The brain is of a very primitive type, the cerebral hemispheres being smooth and not extending backwards far enough to cover any part of the cerebellum.

The last-mentioned character, among others, suggests the great antiquity of the rodent order; and Palæontology indeed confirms this suggestion, for the skulls of typical, fully-differentiated rodents are known as low down in the Tertiary series as the Middle Eocene, at least in North America. No essential change seems to have occurred among the representatives of the order since the latter part of the Eocene period, either in the Old or New World. It may perhaps be stated that among the dominant types at the present day the reduction of the premolars and the complication of the molars are more common features than they were in earlier periods; otherwise it is difficult to recognize evidences of evolution in any direction.

Sub-Order 1. *Tillodontia.*

The only known group of early Tertiary mammals which can be claimed with much probability as connected with the direct ancestors of the Rodentia, is that of the TILLODONTIA. This is represented by *Tillotherium* in the Middle Eocene of Wyoming, and perhaps also by other genera in the Lower Eocene both of America and Europe. Here the rodent-like skull, with the form of the cerebral cavity denoting a primitive type of brain, still retains traces of the canine teeth, with most of the premolars; and the incisors are just beginning to assume their powerful gnawing functions.

Esthonyx (fig. 212). Known only by the jaws and other fragments. The dental formula is:—$\frac{\text{i. 2, c. 1, pm. 3, m. 3}}{\text{i. 3, c. 1, pm. 3, m. 3}}$. The canines are well developed in both jaws. Of the upper incisors, the middle pair seems to be entirely absent; the second pair is much enlarged, growing from a persistent pulp for a considerable period but not throughout life, and only destitute of enamel in a narrow longitudinal band on the posterior or oral face; the third incisors are somewhat smaller than the enlarged pair. Of the opposing teeth in the mandible it is also the second pair which exhibits great enlargement, and this agrees with the large upper pair in all respects; the inner lower incisors are very small, and the outer pair (no. 3) may be described as rudimentary. The species of this genus occur in the Lower Eocene (Wasatch Formation) of New Mexico, and in the Middle Eocene (Bridger Series) of Wyoming. They are all of small size, the mandible of an average type (*Esthonyx burmeisteri*) measuring about 0·1 m. in length. One imperfect skull with molars from the London Clay of Herne Bay, Kent, named *Platychœrops richardsoni*, is sometimes compared with *Esthonyx* and believed to indicate the presence of this or an allied genus in the Lower Eocene of Europe.

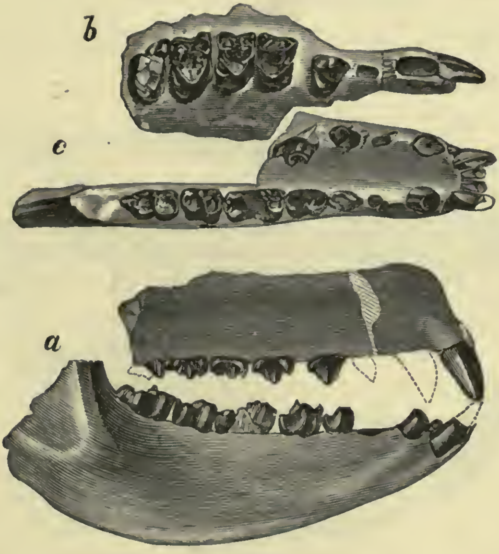

Fig. 212.

Esthonyx burmeisteri; portion of right upper and lower jaws, lateral aspect (*a*), right upper dentition, oral aspect (*b*), and imperfect mandible, oral aspect (*c*), two-thirds nat. size.—L. Eocene (Wasatch Formation); Wyoming. (After Cope.)

Tillotherium (fig. 213). The cranial region of the skull is elongated, with a sagittal crest, and the brain-cavity is relatively small; the facial region is short and slender. The zygomatic arch curves considerably outwards, and the hinder limits of the orbit are not marked by any postorbital process either from this arch or from the frontal. The auditory bullæ are relatively small. The powerful premaxillæ extend backwards upon the superior surface of the skull, between the maxillæ and slender nasals, almost as far as the frontals. The mandibular rami are fused at the symphysis and the convex articular facette is raised high above the level of the teeth, not quite so much elevated as the coronoid process. The jaw cannot have been capable of the antero-posterior movement characteristic of the rodents. The dental formula is:—$\frac{\text{i. 2, c. 1, pm. 3, m. 3}}{\text{i. 2, c. 1, pm. 2, m. 3}}$. The molars and premolars are brachyodont, and well covered with enamel; those of the upper jaw are distinctly tritubercular in pattern, while those of the lower jaw approach the same condition, but are rather of a cutting type (tuberculo-sectorial). The canine in both jaws is insignificant, interrupting the short diastema between the premolars and the incisors. One pair of incisors, evidently no. 2 of the typical mammalian series, is much enlarged in each jaw, growing from persistent pulps and enamelled only on the anterior face. The second pair of upper incisors (no. 3) is quite rudimentary, and flanks the enlarged pair, is not placed internal to them. The distal end of the humerus is expanded, with an entepicondylar

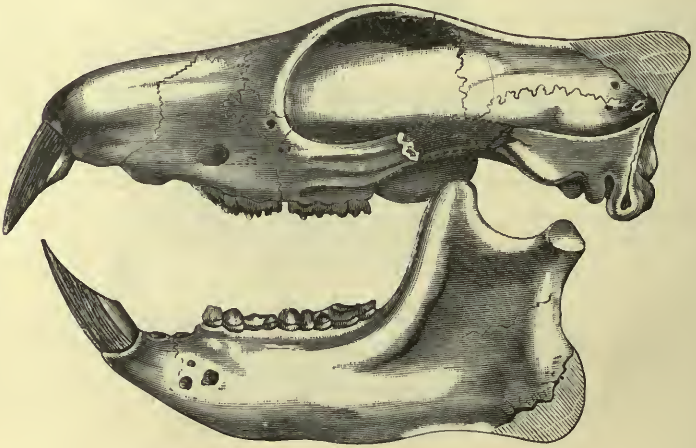

Fig. 213.

Tillotherium fodiens; skull and mandible, left lateral aspect, one-quarter nat. size. —M. Eocene (Bridger Formation); Wyoming. (After Marsh.)

foramen; the radius and ulna are separate and stout at their lower end; the manus is plantigrade and comprises five complete digits with sharp, laterally-compressed claws. The femur bears a third trochanter; the fibula is comparatively slender and somewhat arched; the astragalus is depressed, only slightly grooved above; the pes resembles the manus. The typical species *Tillotherium fodiens* (fig. 213), from the Middle Eocene (Bridger Formation) of Wyoming, is known by the greater part of the skeleton. The skull measures 0·32 m. in length, and the animal must have been a little more than half as large as a tapir.

Sub-Order 2. *Duplicidentata.*

A few of the surviving rodents still retain more than one pair of incisors in the upper jaw; and these teeth are not completely chisel-shaped (or scalpriform), their enamel not being restricted to a band on the front face but also extending considerably round the sides. In the newly-born young of these animals there are three pairs of upper incisors; but the outer pair soon disappears, while the second pair remains relatively small and is placed directly behind the middle functional pair. The ordinary single enlarged pair of incisors in the lower jaw opposes these teeth. The insertion of the masseter muscle on the mandible has not extended further forwards than the position of the hindermost molar. A primitive feature is also retained in the hind limb, the fibula still articulating with the calcaneum.

The rodents thus characterized are not only in a minority in the existing fauna, but have always been few in number compared with those retaining only one pair of upper incisors (the Simplicidentata). No extinct families are known, all the fossil genera and species being closely related to the existing hares and rabbits (**Leporidæ**) or to the tailless hares (**Lagomyidæ**). *Palæolagus* represents the first family in the Lower Miocene (White River Formation) of North America, and seems to have survived until the Pliocene. True hares and rabbits (*Lepus*) also occur in the Pliocene of Europe, Asia, and North America, and they reached South America at the dawn of the Pleistocene period. The tailless hares are known only from the Miocene and Pliocene of Europe, and seem to have reached North America at the close of the Pliocene period. The surviving genus *Lagomys* first occurs in the Upper Miocene of Oeningen, Baden.

Sub-Order 3. *Simplicidentata.*

As already mentioned, most of the known rodents, both recent and extinct, retain only one pair of incisors in the upper jaw, exactly as in the mandible; and these teeth in the recent forms are completely chisel-shaped (scalpriform), their enamel being nearly always confined to a band on the anterior face. All the surviving SIMPLICIDENTATA (as these rodents are termed) also seem to have lost the primitive articulation of the fibula with the calcaneum in the hind limb.

It is difficult to determine which are the least specialized members of this great sub-order, but the squirrels and their allies, or SCIUROMORPHA, occupy this position in some respects. Their skull exhibits a slender zygomatic arch, in which the jugal bone is not supported by any process from the maxilla, exactly as in the primitive Ungulata. Their masseter muscle is also so arranged that it does not necessitate any enlargement of the infraorbital foramen. On the other hand, the insertion of the masseter muscle on the mandible extends far forwards on the side of the jaw below the teeth. So far as the skull and dentition are concerned, the existing squirrel itself (*Sciurus*) seems to date back to the Upper Eocene in France and Switzerland, and to the Lower Miocene (White River Formation) in North America. The marmots, so far as known, are quite modern, but during the Pleistocene period they had a much wider range in Europe than at the present day. The common souslik (*Spermophilus*) is represented in the Pleistocene of England. The earliest known beaver is a small animal (*Steneofiber* or *Chalicomys*) represented both by the skull and limb-bones in the Miocene of Europe, and apparently with very close allies in the Lower Miocene (White River Formation) of North America. *Castor* itself first appears in the Upper Pliocene of Italy, France, and England; and it had a much wider range in Europe during the Pleistocene period than at the present day. The animal does not appear to have been exterminated in Britain until about the twelfth century, and there are still allusions to it in some names of places (e.g., Beverley, Nant-yr-afancwm). Numerous skeletons are found in the valley of the Lea, Essex, and in the fens of the eastern counties. A very large extinct beaver, *Trogontherium*, also ranged throughout Europe in the early Pleistocene; the finest known skull of this animal, about 0·16 m. in length, was obtained from the Forest Bed of Cromer, Norfolk.

Some of the Eocene and Miocene rodents, as also the surviving African family of **Anomaluridæ**, are intermediate between the Sciuromorpha and the porcupine-like group, or HYSTRICOMORPHA. In the latter, as a rule, the zygomatic arch is massive and the infraorbital foramen is much enlarged, while the angular part of the mandible does not arise from the inferior surface of the socket of the lower incisor, but from its outer face. The intermediate forms just mentioned exhibit the Sciuromorph mandible and zygomatic arch, with the much-enlarged infraorbital foramen. *Theridomys*, *Sciuroides* and *Pseudosciurus*, from the Upper Eocene of France, England, Germany, and Switzerland, may be mentioned as European examples; while *Ischyromys*, from the Lower Miocene (White River Formation) of Colorado, is perhaps the best-known American genus. The true Hystricomorpha have always flourished most in South America, where they still exhibit an extraordinary development and comprise the largest known members of the Rodentia. The extinct *Megamys*, from the lower beds of the Pampa Formation of the Argentine Republic, is estimated to have been nearly as large as an ox; while the surviving capybara (*Hydrochœrus capybara*) attains a length of over a metre. An equally gigantic rodent, *Castoroides ohioticus*, which seems to be Hystricomorph in most respects, is known by the complete skeleton from Indiana and by numerous fragmentary remains from other parts of North America. Its upper incisors are not completely scalpriform, but nearly surrounded with enamel. The true porcupines (*Hystrix*) are now confined to the Old World, but skeletal fragments from the Miocene and Pliocene of North America have been provisionally ascribed to the same genus.

The rats, mice, and their allies, or MYOMORPHA, seem to be the most specialized rodents and are most universal in the existing fauna. As in the higher Ungulata, the jugal bone of the zygomatic arch in the skull is supported by the maxilla. Otherwise the cranial characters are much like those of the Sciuromorpha. Typical skulls are known from the Upper Eocene of Europe (*Cricetodon*) and from the Lower Miocene (White River Formation) of North America (*Eumys*). Various remains from superficial deposits also indicate that several of the existing genera and species had a much wider range in Europe during the Pleistocene period than at the present day. Of the **Muridæ**, the lemmings (*Myodes lemmus* and *Cuniculus torquatus*), for example, wandered into the British area. A comparatively large animal (skull 0·07 m. in length), generally supposed to have been a dormouse, also lived in Malta (*Leithia melitensis*).

ORDER 6. CARNIVORA.

As already mentioned (p. 287), it is difficult among the earliest Eocene mammals to distinguish the forerunners of the Ungulata from those of the Unguiculata (or claw-bearing groups). Before the close of the Eocene period, however, not only the former but also the latter had become well differentiated; and the Carnivora and Insectivora, at least in Europe, had already diverged into their main lines of development, which have since become more distinctly separated.

Sub-Order 1. *Creodonta* (*or Carnivora Primigenia*).

The primitive Carnivora are usually grouped in a sub-order named **Creodonta** (flesh-teeth), but their characters are almost identical with those of the Condylarthra. The only differences seem to be that (i.) the skull has more nearly the aspect of that of a carnivore, (ii.) the teeth are usually more trenchant, and (iii.) the ungual phalanges are always claw-shaped. The head is large compared with the trunk and limbs; while the lumbar region of the vertebral column is made rigid by the complication of the zygapophyses. The third trochanter of the femur is comparatively small, and the bones both of the carpus and tarsus are perhaps more distinctly interlocking than those of the Condylarthra. The expanded upper portion (head) of the astragalus, with its gently sinuous surface for the articulation of the tibia and fibula, is fixed obliquely upon the small lower portion (neck), which articulates not only with the navicular but also with the cuboid. The scaphoid and lunar of the carpus only rarely fuse together.

The known Creodonta range from the base of the Eocene to the Lower Miocene both in Europe and North America, and are especially abundant in the rocks of the latter area. There is also some evidence of the same group in the Lower Tertiaries of Patagonia. The more specialized forms exhibit a dentition remarkably similar to that of the existing carnivorous marsupials of Australia; but the series of successional teeth is proved in some cases (*Hyænodon, Pterodon, Thereutherium,* and *Triisodon*) to have been nearly or quite complete, as in ordinary placentals. The known generic types are also so varied that the different groups of true Carnivora are assumed to have already begun to diverge before the creodont grade had been passed.

Arctocyon. The typically omnivorous bear-like forms are represented, among other genera, by *Arctocyon*, which is known by a large part of the skeleton. The small elongated cranial region of the skull is surmounted by a great sagittal crest, and the zygomatic arch is both very massive and strongly bent outwards; the facial region is small and slender. The cranial cavity exhibits an unusually large development of the olfactory lobes, and the impression of the cerebral hemispheres shows them to have been nearly smooth. The mandible bears a much-elevated coronoid process. The dental series is complete or nearly so, namely, with three incisors, one canine, three or four premolars, and three molars in each jaw. All the molars and premolars exhibit a prominent cingulum at the base of the crown, which sometimes bears small tubercles; the canines are well developed, acutely pointed, and with a sharp cutting edge along the hinder concave border. Upper molars 1 and 2 are nearly square in shape, while no. 3 is smaller and more rounded; and the grinding surface is tuberculated like that of the bears. Upper premolar 4 is tritubercular, while premolars 1 to 3 are relatively small and simply conical. The lower molars much resemble those of the upper jaw but are antero-posteriorly elongated; the lower premolars are simply conical and laterally compressed. The tail is proved to have been rather long. The scapula exhibits a large acromial process, and the humerus is pierced by an entepicondylar foramen; the radius is somewhat more slender than the ulna, which bears a very large olecranon process; the manus is proved to have been pentadactyl, with slightly cleft ungual phalanges. The fibula is nearly as robust as the tibia, and the upper articular face of the astragalus is scarcely sinuous. The typical and best known species is *Arctocyon primævus*, from the basal Eocene deposits in the neighbourhood of Rheims, France, with the skull about 0·21 m. in length. Part of a nearly similar dentition from the Lower Eocene (Wasatch Formation) of Wyoming, U.S.A., bears the generic name of *Anacodon*.

Mesonyx. This genus is known by at least one complete skeleton, and by numerous other good specimens. The skull is shaped much like that of the existing thylacine of Tasmania, but the brain-case is relatively smaller and the sagittal crest more prominent. The dental formula seems to be $\frac{\text{i. 3, c. 1, pm. 4, m. 2}}{\text{i. 2, c. 1, pm. 4, m. 3}}$; but as the successional teeth are unknown, it is not quite certain whether the lost tooth in the upper jaw is pm. 1 or m. 3. The three hindermost upper teeth are tritubercular, approximately similar in size and shape; the three teeth between these and the canine are laterally-compressed cones, with a more or less distinct basal denticle in front and behind. The canines in both jaws are stout and somewhat enlarged. The lower pm. 1 is minute, but the others closely resemble the opposing teeth of the upper jaw, and are followed by three nearly similar but stouter molars. The axis vertebra bears a very large neural spine. There are 14 thoracic or dorsal vertebræ, of which those anteriorly are comparatively small and slightly opisthocœlous, with much-elevated neural spines. These are followed by 6 lumbar vertebræ, which, like the posterior thoracics, bear metapophyses and are very firmly united. The tail is remarkably elongated. The fore limbs are somewhat shorter than the hinder pair, and the scapula is shaped much like that of a *Hyæna*. The humerus is slender and destitute of an entepicondylar foramen; the carpus includes a well-developed centrale, and all the bones remain separate; the manus is tetradactyl, with comparatively broad ungual phalanges which are deeply cleft, and digit no. I is represented only by the proximal end of its metacarpal. The pelvis most resembles that of a bear. The femur bears the third trochanter as usual; the fibula is complete, though relatively slender; the astragalus is slightly grooved on its upper articular face, while its lower articulation extends well upon the cuboid; and the pes is tetradactyl, only differing from the manus in the comparative slenderness of the metatarsals, which are nearly equal in length. *Mesonyx obtusidens*, with the skull 0·25 m. in length, would be about as large as a small brown bear, and is known by a complete skeleton from the Middle Eocene (Bridger Formation) of Wyoming. Other species are represented in the Bridger and Uinta Formations of Wyoming and New Mexico; and there is also some evidence of the same genus in the Lower Miocene (White River Formation) of Dakota. *Pachyæna* is a more imperfectly known allied genus from the Lower Eocene (Wasatch Formation) of Wyoming.

Fig. 214.

Stypolophus whitiæ; skull and mandible, left lateral aspect (*a*), palatal aspect of skull (*b*), anterior portion of right mandibular ramus, inner aspect (*c*), and left tarsus, anterior aspect (*d*), two-thirds nat. size.—L. Eocene (Wasatch Formation); Wyoming. (After Cope.)

Stypolophus (fig. 214). A genus comprising small slender animals with a long narrow cranium and complete dentition (44 teeth), all the teeth sharply pointed or with acute cusps. The upper m. 1, m. 2, and upper pm. 4 are tritubercular (fig. 214 *b*), while m. 3 has lost its postero-outer cusp. Each of the lower true molars develops a high *blade* in front, a low crushing heel or *talon* behind, and a distinct small inner cusp (fig. 214 *c*). The dentition thus exhibits much resemblance to that of the Viverridæ among true Carnivora (p. 396). The neck is rather long. The astragalus (fig. 214 *d*) exhibits an unusually convex distal articulation for the cuboid. *Stypolophus whitiæ* (fig. 214), from the Lower Eocene (Wasatch Formation) of Wyoming, has a skull about 0·15 m. in length; and other species are known both from the same horizon and from the overlying Bridger Formation in North America. *Proviverra* or *Cynohyænodon*, from the Upper Eocene of Switzerland and France, is characterized by a skull and dentition almost or quite generically identical with that of *Stypolophus.*

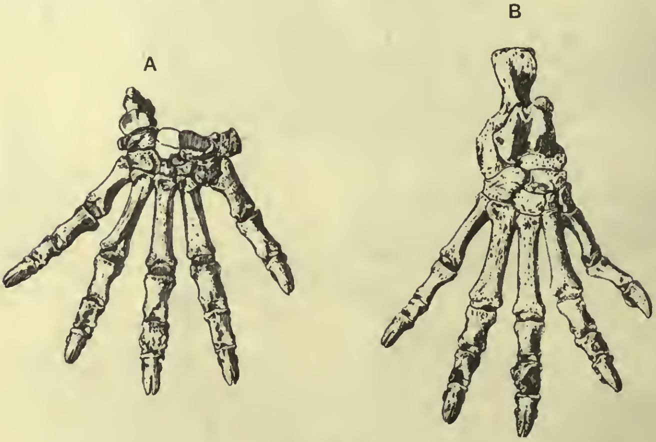

Fig. 215.

Patriofelis ferox; right manus (A) and pes (B), one-quarter nat. size.—M. Eocene (Bridger Formation); Wyoming. (After Wortman.)

Patriofelis (figs. 215 A, B). Another North-American Creodont known by the complete skeleton, and sometimes claimed to have been an amphibious animal resembling in many respects the unknown ancestors of the Carnivora Pinnipedia (sea-lions and seals). The facial region of the skull is very short and truncated in front, while the cranial region is much elongated, constricted immediately behind the postorbital processes, which are well in front of the anterior termination of the brain-cavity. The course of the external carotid artery along the alisphenoid is enclosed by bone (forming the so-called *alisphenoid canal*). The sagittal crest is unusually high and prominent, extending considerably in advance of the brain-cavity. The zygomatic arches are remarkably stout and widely expanded. The short stout jaws must thus have been very powerful, and the stout conical cusps of the teeth are often much worn. The dentition is incompletely known, but its formula seems to have been $\frac{\text{i. 3, c. 1, pm. 3, m. 1}}{\text{i. 2, c. 1, pm. 3, m. 2}}$. The atlas vertebra much resembles that of the Felidæ, while the axis bears the usual large neural spine. There seem to have been 13 thoracic or dorsal vertebræ, and there are clearly 6 lumbars. The anterior dorsals are relatively small and opisthocœlous; while the neural arches of the lumbar vertebræ bear not only zygapophyses but also anapophyses and metapophyses. The sacrum comprises three vertebræ, of which two unite with the ilium. The long tail consists of 28 vertebræ, many bearing chevron bones. The fore limb more nearly resembles that of the seals than that of the terrestrial Carnivora, and the scapula, humerus, and ulna are nearly equal in length. The humerus bears an enormous deltoid crest, and there is a large entepicondylar foramen. The pentadactyl manus (fig. 215 A) is spreading, and the cleft ungual phalanges bear a large subungual process pierced transversely by a foramen (suggestive of the correspondingly developed process in the sea-lions). In the pelvis the ilium is a strong trihedral bar of bone, and the acetabulum is shallow, with a broad cotyloid notch. The femur is longer and stouter than the tibia, with a small third trochanter. The cnemial crest of the tibia is distinct; and the fibula is comparatively stout and separate. The pes (fig. 215 B) is about as large as the manus, and closely similar to the latter in all respects. The large head of the astragalus is fixed much more obliquely upon the neck of the bone than in any terrestrial Carnivora. The largest and best-known species is *Patriofelis ferox*, with the skull about as large as that of a lion, from the Middle Eocene (Bridger Formation) of Wyoming. It seems to have been an animal of aquatic habits, and may perhaps have fed upon the freshwater tortoises which were very abundant in the Bridger Lake. Numerous coprolites containing fragments of chelonian bone occur in the same strata as its remains.

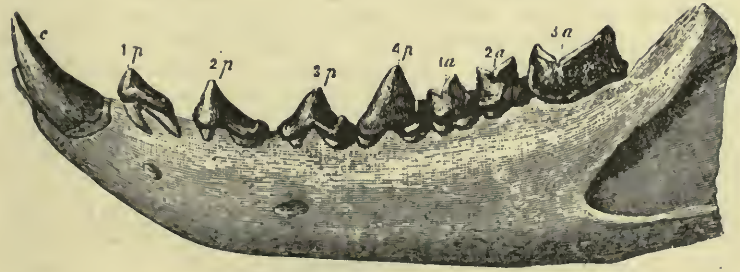

FIG. 216.

Hyænodon leptorhynchus; left mandibular ramus wanting hinder end, outer aspect, nine-tenths nat. size.—U. Eocene (Phosphorites); Mouillac, France. 1*a*–3*a*, molars; *c*, canine; 1*p*–4*p*, premolars. (After Gaudry.)

Hyænodon (figs. 216, 217). The skeleton of this highly-specialized genus is almost completely known, the restoration given in the accompanying fig. 217 being based almost entirely on the associated remains of one individual. The skull is much elongated, with the usual diminutive brain-cavity and great sagittal crest. The two rami of the mandible are firmly fused together at the symphysis, and the angle of the mandible is not inflected as in marsupials. The dental formula is $\frac{\text{i. 3, c. 1, pm. 4, m. 2}}{\text{i. 3, c. 1, pm. 4, m. 3}}$; and milk-predecessors have been observed in the mandible in connection with the incisors, canines, and all the premolars except pm. 1. The hindermost lower milk-molar resembles in shape the relatively small tricuspidate lower m. 1, which is extruded and partially worn before the milk-dentition is replaced. The two upper molars and the lower molars 2, 3, are sharp bilobate cutting teeth, the former with scarcely any trace of an inner tubercle. The canines are much enlarged in both jaws, while the incisors are small and in regular even series. The general proportions of the trunk and limbs are well shown in fig. 217. The humerus has an entepicondylar foramen. The scaphoid, lunar, and central bones of the carpus remain separate in the known American species, but seem to have been fused into a scapholunar element in the European forms. Both feet are pentadactyl, with powerful claws; and the animal was probably semiplantigrade. *Hyænodon* ranges through the Upper Eocene and Lower Miocene both in Europe and North America. The typical species, *H. leptorhynchus* (fig. 216), and others occur in France in the Phosphorites of Quercy, the Lignites of Débruge, the Paris Gypsum, and in the Lower Miocene of the Puy-de-Dôme. Portions of jaws and teeth are also known from the Upper Eocene of Switzerland and of the Hampshire Basin. *H. cruentus* (fig. 217) and other well-known species are represented by fine specimens from the Lower Miocene (White River Formation) of Nebraska, Montana, and Dakota; while there is also some evidence of the genus in the underlying Uinta Formation in North America. Detached teeth from the Siwalik Formation of the Punjab, India, have also been provisionally assigned to *Hyænodon*, but their determination is uncertain. *Pterodon* is a closely allied genus from the Upper Eocene of France, Switzerland, and the Hampshire Basin, with a third upper molar, and a well-developed inner tubercle on upper molars 1 and 2.

The representatives of the Creodonts in the Lower Tertiary formations of Patagonia are very remarkable as exhibiting still more resemblance to the carnivorous marsupials of Australia and Tasmania than the animals just described from the northern hemisphere. They have thus been referred to a distinct group termed SPARASSODONTA. Milk-teeth have only been observed preceding one or two of the premolars and the canine; while there is a distinct inflection of the angle of the mandible, as in marsupials. The palate, however, does not exhibit any

ORDER 6. CARNIVORA. *Sub-Order* 1. *Creodonta.*

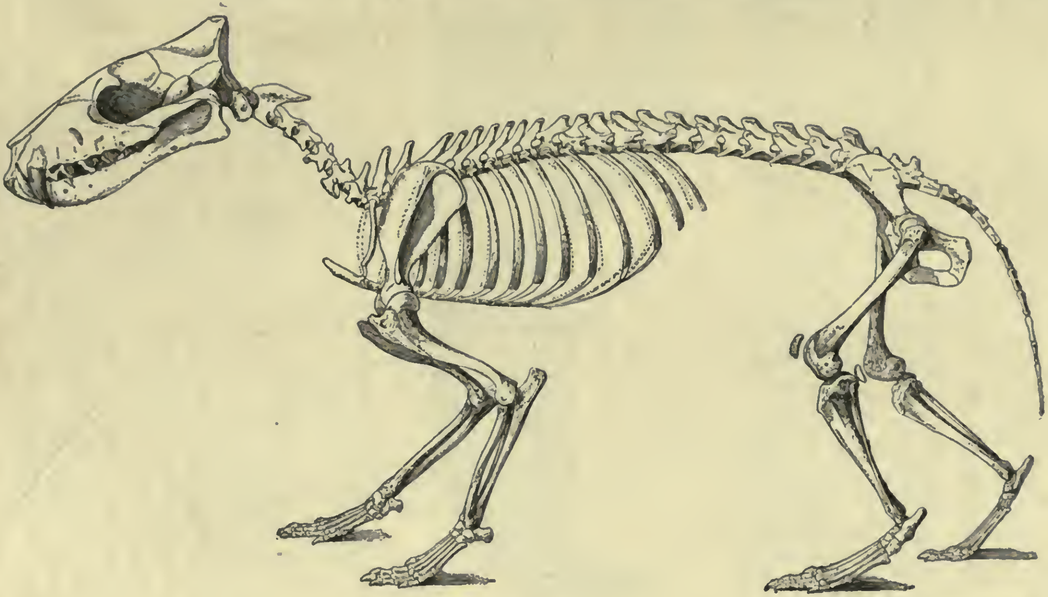

FIG. 217.

Hyænodon cruentus; restoration of skeleton by W. B. Scott, one-seventh nat. size. —L. Miocene (White River Formation); Dakota.

vacuities, while the skull and most parts of the skeleton closely resemble the corresponding bones in the typical Creodonta. The incisors are always small, but there are sometimes four pairs of these teeth; the canines are well developed; and the seven following teeth are more or less suggestive of the dentition of the Tasmanian *Thylacinus.*

Prothylacinus (fig. 218). In this genus there are four pairs of incisors above and three pairs below; and there are seven teeth in each jaw behind the enlarged canine. In the upper jaw the three foremost teeth of the series are clearly to be regarded as premolars; while the four teeth behind are triangular in form and tritubercular, and there may be a difference of opinion as to whether the first of these is to be termed pm. 4 or m. 1. The dental series, indeed, bears much general resemblance to that of the upper jaw of *Stypolophus* (fig. 214 *b*, p. 383), which is usually interpreted as comprising pm. 4, m. 3. Of the seven teeth in the mandible (fig. 218) the foremost three are simple conical premolars, each with a cleft root; the fourth is a comparatively small tooth much resembling the last lower milk-molar of *Hyænodon*; the remaining three teeth are obviously true molars. The two rami of the mandible are fused together at the symphysis. The humerus exhibits an entepicondylar foramen. The manus comprises four complete digits, with pointed ungual phalanges, but digit no. I is represented only by its metacarpal. The genus *Prothylacinus* occurs in the Santa Cruz Formation of Patagonia, and the length of the mandible in the type species, *P. patagonicus* (fig. 218), is about 0·15 m.

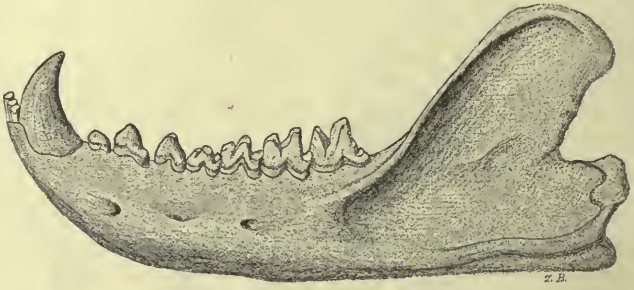

Fig. 218.

Prothylacinus patagonicus; left mandibular ramus, outer aspect, one-half nat. size.—Santa Cruz Formation; Patagonia. (After Ameghino.)

Borhyæna has only three pairs of incisors above and below, and the jaws are more robust than those of *Prothylacinus*, though the dental series behind the canine is very similar in the two genera. The canine and the third tooth behind the canine are proved to have had milk-predecessors. The humerus is destitute of an entepicondylar foramen. From the Santa Cruz Formation of Patagonia.

Sub-Order 2. *Carnivora Vera.*

In all the true terrestrial Carnivora the brain is of large or moderate size, and the cerebral hemispheres exhibit well-developed convolutions. The small incisors are almost always in three pairs above and below, rarely reduced to two pairs. One side-tooth in each jaw—namely, pm. 4 above and the opposing m. 1 below—is always specially modified for cutting, or for cutting and bruising. This is known as the *sectorial* or *carnassial* tooth, and the premolars in front of it are always more or less sharply pointed and compressed, while the molars behind it are tuberculated for crushing. The clavicle is incomplete or absent; but the limbs are always mobile, with complete and separate radius and ulna (tibia and fibula), and the clawed digits are never less than four in number. The scaphoid and lunar bones of the carpus are fused into a scapholunar element.

The existing wolves, dogs, jackals, and foxes, or **Canidæ**, are among the least altered representatives of the primitive true terrestrial Carnivora in the present fauna of the globe. Occasionally, indeed, they still retain certain features which have been plausibly interpreted as remnants of structures originally characteristic of their Metatherian ancestry; such, for example, as small epipubes like the marsupial bones (in females of *Canis bengalensis* and *C. mesomelas*), and a slight inflection of the angle of the mandible (*Otocyon*). They have always been characterized by an elongated skull and complete dentition, only with the occasional loss of the hindermost lower molar. The blade of the upper sectorial tooth consists only of two lobes, with a small inner tubercle. The auditory bullæ are inflated, but never divided by an internal septum. The limbs are always slender, and the claws are not retractile. These animals first appear, in fact, in the Upper Eocene of Europe; are abundantly represented in the Miocene both of Europe and North America; are known to have reached India by the early part of the Pliocene period; and seem to have migrated along the Isthmus of Panama to South America as soon as it emerged at the dawn of Pliocene times. More recently they have even extended their range to Australia, probably through the agency of man. Yet notwithstanding this remarkable distribution over all the continents, they have not undergone any important change in the skeleton since their earliest occurrence in the European area. Until the close of the Miocene period most, if not all, of the canine genera had the distal end of the humerus somewhat expanded, with a bridge of bone completing an entepicondylar foramen. The Pliocene and later Canidæ have lost this foramen and the accompanying expansion, while the anconeal fossa above the trochlea is extensively pierced. There is also some reason to believe that digit no. I was functional in both feet in the earlier forms; while now it is comparatively small or (in the hind foot) even rudimentary.

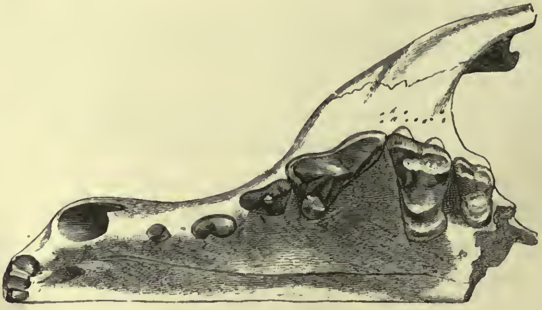

Fig. 219.

Cynodictis longirostris; left half of palate, with molars and premolars, and sockets for the canine and incisors, nat. size.—U. Eocene (Phosphorites); Quercy, France. (After Lydekker.)

Among the remains of true Carnivora in the European Upper Eocene, by far the larger proportion are referable to the Canidæ; and most of the known specimens belong to the genus *Cynodictis,* which may not only be an ancestor of *Canis,* but would serve almost as well for a forerunner of the Mustelidæ and Viverridæ. The dentition of this genus (fig. 219) closely resembles that of *Canis,* with four premolars in each jaw, and usually only two molars above, three molars below; but the lower sectorial molar is generally less extended than in the Recent genus just mentioned, its shape being more suggestive of that of the corresponding tooth in the Viverridæ. The limb-bones and vertebræ found in the same deposits as the skulls and jaws, but not yet in actual association with the latter, are quite of the canine type, except that the humerus is distally expanded as already described. The most important and numerous specimens of *Cynodictis* hitherto discovered are those from the Phosphorites of Quercy, France; but other fragments are also known from the Gypsum of Montmartre, near Paris, from the Lignite of Débruge, near Apt (Vaucluse), and from contemporaneous formations in Würtemberg and Switzerland.

The only nearly complete fossil skeletons of Canidæ yet known, are those of the famous "Fossil Fox" (*Galecynus oeningensis*) from the Upper Miocene of Oeningen, Baden, and the so-called *Galecynus geismarianus* from the equivalent John Day Formation in Oregon, U.S.A. In the first, the pollex (digit no. I) of the manus is rather larger than usual in *Canis*, and the dentition slightly differs from that of this genus. In the American skeleton, the humerus distinctly has the entepicondylar foramen as in *Cynodictis*. The extinct species of *Canis*-proper are thus represented only by fragments, and they are distinguished solely by parts of the skull and dentition. Such fossils have been determined from the Lower Pliocene (Siwalik Formation) of India, the Upper Pliocene of France and Tuscany, and the Pliocene of North America. The earliest satisfactory evidence of the occurrence of *Canis* in Britain occurs at the base of the Pleistocene in the Cromer Forest Bed, from which characteristic remains both of the wolf (*C. lupus*) and the fox (*C. vulpes*) have been obtained. Remains of the same animals are met with in the British cavern deposits, and the wolf survived both in Scotland and Ireland until the early part of the eighteenth century. It is interesting to add that one mandibular ramus from a cavern in Glamorganshire, South Wales, seems to represent an extinct ally of the Cape Hunting Dog (*Lycaon pictus*), which now inhabits south and east Africa; the fossil form is named *Lycaon anglicus*.

Some of the true Carnivora in the Upper Eocene of Europe, characterized by a dental series as nearly complete as that of the typical Canidæ, begin to exhibit a shortening of the face and jaws, with a concomitant reduction in size of the anterior premolars. The flattened tuberculated molars remain relatively large and powerful; and the skeleton, so far as can be determined from fragments, begins to increase in stoutness, eventually in the Miocene period becoming much like that of the bears. There is, indeed, not much doubt that some of the animals of this group are the direct ancestors of the bears; and the few forms already known so completely fill the gap between the Canidæ and the Ursidæ that it is no longer possible to define these two families. The genera *Cephalogale*, *Simocyon*, *Amphicyon*, *Hemicyon*, and *Hyænarctos*, may be particularly mentioned in illustration of this annectant series.

Cephalogale. Dental series as nearly complete as usual in *Canis* and *Cynodictis*, but all the premolars and molars with a strong basal cingulum, and pm. 1 to 3 relatively small in each jaw. The snout and jaws correspondingly shortened. From the Upper Eocene of France (Phosphorites of Quercy) and Switzerland, and from the Lower Miocene of France and Germany. The largest known species are scarcely so large as a wolf.

Simocyon. A small, highly specialized animal, in which the three reduced anterior premolars may entirely disappear, while only two molars remain in the lower jaw as in the upper jaw. The sagittal crest of the shortened skull is inconspicuous. *Simocyon diaphorus* is known by a mandibular ramus from the Lower Pliocene of Eppelsheim, Hesse Darmstadt; while *S. primigenius* is represented by a fine skull and mandible 0·16 m. in length, as also by other remains, from the Lower Pliocene of Pikermi, near Athens.

Amphicyon (fig. 220). The dental series is complete, but the canines are relatively very large, while pm. 1 to 3 and m. 3 in both jaws are diminutive, the latter sometimes even absent. The canines are compressed to a sharp edge posteriorly. Upper molars 1, 2 are still broader than long, but usually larger than the sectorial pm. 4, which has a sharp, two-lobed blade, with a diminutive inner tubercle. The limb-bones found in the same deposits as the jaws, and referred to *Amphicyon* with much probability of correctness, seem to indicate comparatively long legs, with short five-toed feet, evidently plantigrade. The humerus is slightly expanded at the distal end, with a large entepicondylar foramen; the ulna exhibits only a short olecranon process, as in the bears. The femur is slender, with a distinct third tròchanter. *Amphicyon* occurs in the Lower and Middle Miocene of France, Germany, and Austria; and some

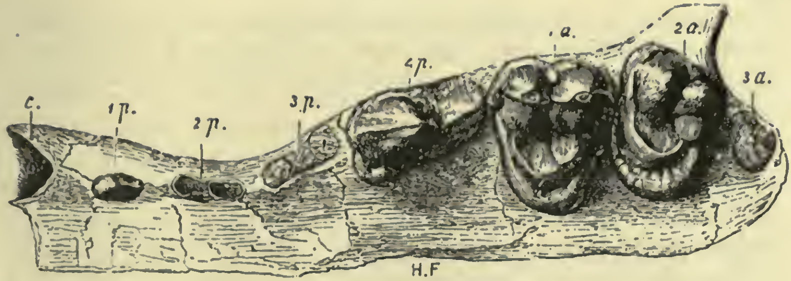

FIG. 220.

Amphicyon major; left upper dentition, three-fifths nat. size.—M. Miocene; Sansan, France. 1*a*–3*a*, molars; *c*, canine; 1*p*–4*p*, premolars. (After Gaudry.)

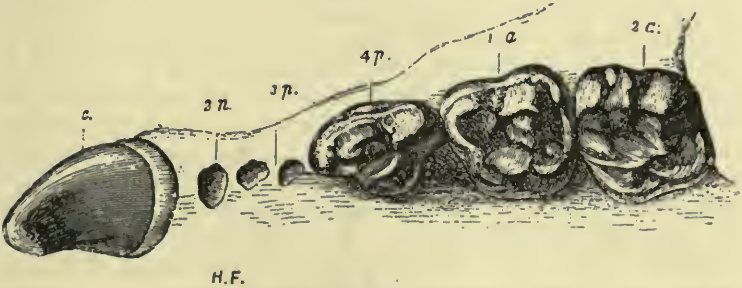

FIG. 221.

Hyænarctos sivalensis; left upper dentition, three-fifths nat. size.—L. Pliocene (Siwalik Formation); India. 1*a*, 2*a*, molars; *c*, canine; 2*p*–4*p*, premolars. (From Gaudry's *Enchaînements*, after Falconer.)

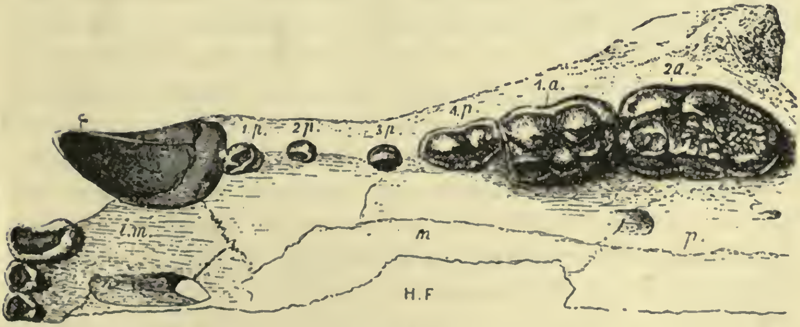

FIG. 222.

Ursus arvernensis; left upper dentition, three-quarters nat. size.—U. Pliocene; Perrier, France. 1*a*, 2*a*, molars; *c*, canine; *i.m.*, premaxilla with incisors; *m*, maxilla; *p*, palatine; 1*p*–4*p*, premolars. (After Gaudry.)

teeth from the Lower Pliocene (Siwalik Formation) of India have been provisionally ascribed to it. The largest known species is *A. giganteus*, about as large as the European brown bear, and widely distributed in the Middle Miocene deposits.

Hemicyon. The dentition lacks only upper m. 3. The other two upper molars are almost square in shape, while the sectorial pm. 4 is low-crowned and triangular in shape, the inner tubercle being relatively large and median. The typical and only known species, *H. sansaniensis*, is represented by jaws and other fragments from the Middle Miocene of Sansan, Gers, France. The animal must have been about as large as a wolf.

Hyænarctos (fig. 221). The dentition is nearly complete, but one of the diminutive premolars is sometimes wanting, while upper m. 3 seems to be always lost. The canines are remarkably stout and rounded, not compressed to an edge behind. The upper sectorial pm. 4 is low-crowned, triangular in shape, and almost as broad as long owing to the relatively great development of the inner median tubercle. Upper m. 1, 2 are nearly square in shape. The lower sectorial m. 1 and m. 2 are antero-posteriorly elongated, while m. 3 is relatively small and rounded. An ulna probably referable to this genus, exhibits a long olecranon process, thus differing from the corresponding bone of the bears and resembling that of the dogs. The typical and best-known species is *Hyænarctos sivalensis* from the Lower Pliocene (Siwalik Formation) of India, with the skull nearly half a metre in length. Large teeth have also been obtained from the supposed Pliocene of China, the Lower Pliocene of Pikermi, Greece, and the Red Crag of Suffolk. Smaller species are also represented by fragments in the Middle and Upper Miocene of France, Spain, Germany, Austria, and northern Italy.

The true bears, or **Ursidæ**, are unknown below the Lower Pliocene (Siwalik Formation) of India, and do not appear in Europe until the Upper Pliocene, while there is no record of them in North America before the Pleistocene. Their molar teeth are always relatively large, while pm. 1 to 3 are diminutive, one or more being often absent in the adult. The genus *Ursus* itself has the sectorial tooth above and below antero-posteriorly elongated, each with only two roots; while the molars (two above and three below) are also longer than broad. Characteristic portions of this dentition have been obtained from the Lower Pliocene of the Siwalik Hills (*U. theobaldi*) and from the Pleistocene of the Narbada Valley (*U. namadicus*) in India; and there is also similar evidence of small species in the Upper Pliocene of France (*U. arvernensis*, fig. 222) and Tuscany

(*U. etruscus*), while small detached teeth occur in the Red Crag of Suffolk. The most important and best known extinct species in Europe, however, is the great cave bear (*Ursus spelæus*), which first appears in the Cromer Forest Bed and seems to have ranged over the whole of Europe, though possibly not extending to Ireland, during the Pleistocene period. Complete skeletons of old individuals are common in some of the caverns of Franconia and Moravia, where the bones are mingled with a black dust apparently resulting from the decomposition of the carcases. The animals seem to have retreated to the caverns to die. Numerous remains are also discovered in the lower layers of the British cavern deposits, and the species was undoubtedly contemporaneous with "River-Drift Man" in this country, if not also with his successor "Cave Man." In this large animal the crown of the molars exhibits very complex small foldings and crimpings, while pm. 1 to 3 are entirely lost in the adult, and the lower pm. 4 is complicated by a small antero-internal tubercle. The common brown bear (*U. arctos*) also had a much wider range in Europe in Pleistocene and Prehistoric times than at present, characteristic skulls and jaws having been found in superficial deposits in England, Wales, Scotland, and Ireland; and the animal does not seem to have been exterminated in Britain until shortly before the Norman Conquest. It is also noteworthy that a mandibular ramus much like that of the *U. arctos* is known from a cavern in Malta—this group of islands being a remnant of the old land-barrier between Europe and Africa which seems to have existed towards the end of the Pliocene period.

Ursus spelæus does not appear to have reached North America, and the remains of the same genus found in the Pleistocene of that country present no special features of interest. In the Pampa Formation (Pleistocene) of South America, however, there occur skeletons of a remarkable extinct bear-like animal of large size, which differs from *Ursus* in the relatively larger dimensions of the upper sectorial tooth, the less elongated shape of the molars, and in the extreme shortness of the snout which causes the diminutive pm. 1 to 3 to be crowded. The best known species, *Arctotherium bonaeriense*, from the province of Buenos Aires, is larger than the extinct European cave bear; and its humerus is remarkable as exhibiting an entepicondylar foramen. A nearly similar skull, named *A. simum*, is also known from a cavern in Shasta County, California.

Nothing is known of the ancestors of the raccoons and their allies, or **Procyonidæ**, of America. The same remark applies to the northern Indian representative of the family, *Aelurus*. Detached teeth, however, identical with those of the latter animal occur in the Red Crag (Lower Pliocene) of Suffolk (*A. anglicus*); its former geographical range must thus have been very extensive in the Old World.

The weasels, badgers, and otters, or **Mustelidæ**, date back to the Upper Eocene in Europe, and since the early part of the Pliocene period they have been abundant and widely distributed in the northern hemisphere. Immediately before the Pleistocene many typical forms also reached South America. *Stenoplesictis* and *Palæoprionodon* are generalized weasels from the Upper Eocene Phosphorites of Quercy, France; and *Mustela* itself seems to date back to the Middle Miocene in Europe, to the Upper Miocene (Loup Fork Formation) in North America, and to the Lower Pliocene in India. The otter (*Lutra*) is an equally ancient form in Europe and North America, and appears also in the Lower Pliocene of India. *Potamotherium*, from the Lower Miocene of France and Germany, connects the otters with the Viverridæ so far as the characters of its brain and teeth are concerned. The true badgers (*Meles*) seem to be represented by fragments in the Lower Pliocene of Maragha, Persia, but are not known before the Pleistocene in Europe, when the glutton (*Gulo*) also appears and exhibits a much wider range in Europe than at the present day. Characteristic remains of the glutton have been found in several of the English and Welsh cavern deposits, and one fragment of mandible is recorded from the Cromer Forest Bed; but the animal seems to have become extinct in Britain in prehistoric times.

The civets, ichneumons, and their allies, or **Viverridæ**, seem to have been always small animals confined to the Old World. They are very generalized Carnivora, and the genus

Viverra itself seems to have persisted without change since the latter part of the Eocene period. Characteristic remains of this animal occur in the Upper Eocene of Hordwell, Hampshire (*V. hastingsiæ*) and in the contemporaneous Phosphorites of Quercy, France; other remains are also found in the Lower Pliocene (Siwalik Formation) of India.

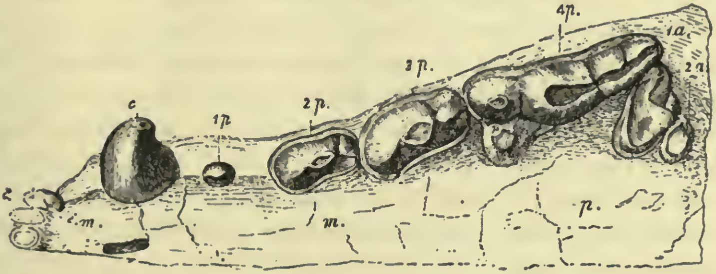

FIG. 223.

Ictitherium hipparionum; left upper dentition, slightly reduced.—L. Pliocene; Pikermi, Greece. 1*a*, 2*a*, molars; *c*, canine; *i*, incisors; *i. m*, premaxilla; *m*, maxilla; *p*, palatine; 1*p*—4*p*, premolars. (After Gaudry.)

One of the Viverroids, *Ictitherium* (fig. 223), from the Lower Pliocene of France, Hungary, Greece, the Island of Samos, and Maragha, Persia, forms a transition between the family to which it technically belongs and that of the **Hyænidæ**. Though its dental formula is that of a Viverroid, namely, $\frac{\text{i. 3, c. 1, pm. 4, m. 2}}{\text{i. 3, c. 1, pm. 4, m. 1}}$ its upper sectorial tooth is enlarged by the addition of a third lobe as in the Hyænidæ. Its skeleton is also comparatively stout, and certain coprolites found in the same deposit as its remains in France (Mt. Léberon) indicate a carnivore which ate bones like the existing hyænas. So far as the dentition is concerned, every link is known between *Ictitherium* and the true *Hyæna*, in which there is usually only one diminutive upper molar, no second lower molar, and the first lower premolar is usually wanting. These annectant forms are found in the Pliocene both of Europe and Asia, and the genus *Hyæna* itself was common in Europe until late in the Pleistocene period. The so-called *Hyæna spelæa*, which is generally believed to have been identical with the surviving spotted hyæna (*H. crocuta*) of Africa, first appears in the Cromer Forest Bed of Norfolk and is represented by numerous remains in the cavern and other Pleistocene deposits of England and Wales, ranging as far north as the vale of Pickering in Yorkshire (Kirkdale cavern). Like its contemporary, the extinct cave bear, it does not appear to have reached Ireland.

The most specialized existing family of Carnivora, the true cats or **Felidæ**, are also closely linked with the Viverroids both by the living *Cryptoprocta* of Madagascar, and by extinct forms from the Miocene of Europe. According to present knowledge, indeed, they seem to have gradually evolved in the Old World, first migrating to North America at the close of the Pliocene period, and thence eventually reaching South America. Their upper canine teeth are not excessively enlarged; their premolars are ultimately reduced to two in the lower jaw, to three in the upper jaw; and their molars are reduced to one above, two below. The upper sectorial tooth has usually three lobes, while the lower sectorial is simply a blade without an internal tubercle. *Proælurus* from the Lower Miocene of St Gérand-le-Puy, France, and *Pseudælurus* from the Middle Miocene of Sansan, France, may be mentioned among the ancestral forms. *Felis* itself first appears in the Middle or Upper Miocene of Europe, and is known by many characteristic remains from the Lower Pliocene of Pikermi in Greece, Maragha in Persia, and the Siwalik Hills in India. The largest known form, the so-called cave lion (*Felis spelæa*), was common in Europe during the Pleistocene period and inhabited Britain as far north as the vale of Pickering, Yorkshire (Kirkdale cavern). It was probably only a variety of the existing *Felis leo* of Africa and Asia. Species as large as the lion are also known from the Pleistocene of North America.

Throughout the Tertiary formations from the Upper Eocene onwards both in Europe and North America—but especially on the latter continent—there are also remains of a remarkable family of cats with a dentition still more specialized than that of the Felidæ, though retaining other skeletal features of a more primitive type. These are the **Nimravidæ** or **Machærodontidæ**, which survived until the Pleistocene both in Europe and in America and then became extinct. Some of them retain the third trochanter on the femur, and also exhibit traces of the primitive separation of the scaphoid and lunar bones of the carpus. Nevertheless, their dentition is extremely specialized, the upper canines being much enlarged and protected by the peculiar conformation of the anterior end of the lower jaw, which eventually develops a flange (fig. 224). While the upper canines increase in size, those of the mandible are reduced until they are scarcely larger than the incisors. This tribe of cats must have been differentiated quite at the dawn of the Eocene; for the earliest known form of mandible (*Eusmilus*) referable to it exhibits the maximum reduction of the teeth, and yet it dates back to the end of the Eocene period. *Hoplophoneus* and *Nimravus* may be mentioned as well-known American Miocene types; while *Machærodus* is a Miocene, Pliocene, and Pleistocene genus, apparently originating in Europe, and eventually ranging over Europe, Asia, and North and South America.

Eusmilus. A genus known only by the mandible, and perhaps by some upper teeth. The mandible is slender, with a truncated symphysis which descends into a flange for the protection of the upper canine. There are only two pairs of lower incisors, and the small lower canine immediately adjoins them, being separated by a wide diastema from the cutting teeth, which are reduced to one premolar (pm. 4) and a sectorial molar (m. 1). The last-mentioned tooth is a two-lobed blade without any trace of an internal tubercle. The typical species is *Eusmilus bidentatus*, from the Upper Eocene Phosphorites of Quercy, France, with the mandible 0·12 m. in length. A slightly larger species (*E. dakotensis*) is indicated by a mandibular ramus from the Lower Miocene (White River Formation) of South Dakota, U. S. A.

Hoplophoneus. This is the best-known Miocene genus of Nimravidæ, nearly the whole of the skeleton having been discovered. The dental formula is $\frac{\text{i. 3, c. 1, pm. 2—3, m. 1}}{\text{i. 3, c. 1, pm. 2, m. 1}}$, and the much-enlarged upper canine is laterally compressed, with finely serrated edges. The upper sectorial tooth is trilobate, but without any internal tubercle; while the lower sectorial molar has a two-lobed blade, with a low heel behind but no internal tubercle. The skull is very short and rounded, and there is a marked postorbital constriction of the brain-case. The neck is comparatively long, and the tail excessively elongated. The limbs are rather stout, and the digits must have borne completely retractile claws; but the feet are comparatively short and weak, as in the Creodonta. The humerus exhibits an entepicondylar foramen; the femur bears a distinct third trochanter. The scaphoid and lunar bones of the carpus are united, but their original line of demarcation can still be distinguished. The most completely known species is *Hoplophoneus primævus*, an animal somewhat less than a metre in length (exclusive of the tail), from the Lower Miocene (White River Formation) of Nebraska, Colorado, and Dakota.

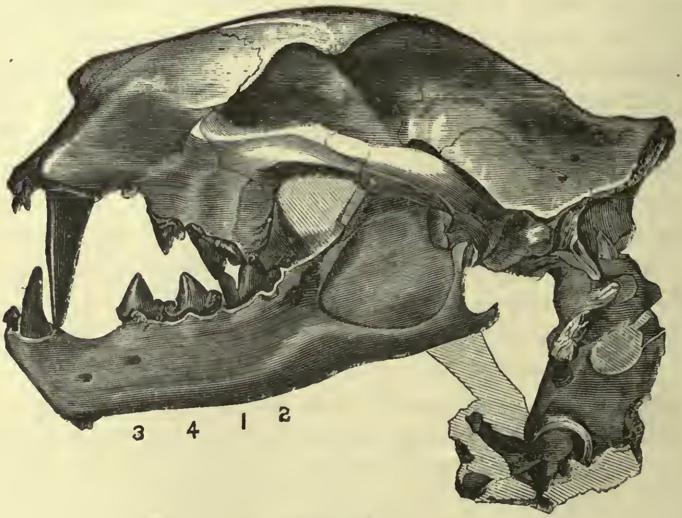

Fig. 224.

Nimravus gomphodus ; skull, mandible, and neck, left lateral aspect, two-fifths nat. size.—Middle Miocene (John Day Formation); Oregon. 3, 4, third and fourth premolars; 1, 2, first and second molars. (After Cope.)

Nimravus (fig. 224). A genus with a less specialized dentition than that of *Hoplophoneus*, the upper canine being less disproportionately large and the hinder teeth less reduced in number. There are three upper premolars, and one transversely-elongated molar; while in the mandible there are two premolars in front of the sectorial molar, with a diminutive tubercular m. 2 behind it. The femur has lost its third trochanter. The typical species is *Nimravus gomphodus* (fig. 224) from the Middle Miocene (John Day Formation) of Oregon.

Machærodus (fig. 225). This genus, in its wide sense, includes the largest and latest species of the Nimravidæ, commonly known as "sabre-toothed tigers," with enormous laterally compressed upper canines, the premolars reduced to two in the upper jaw, one or two in the lower jaw, and the molars represented only by one in each jaw. The upper sectorial tooth is much elongated, and has almost lost its inner tubercle, so that it becomes the most powerful cutting tooth known. The lower canine is reduced, as usual, but stouter than the incisors, and with a sharp, finely serrated hinder border. Complete skeletons from the Pampa Formation (Pleistocene) of Argentina, South America, prove the animal to have possessed long, powerful limbs, with shorter feet than those of *Felis*, but with completely retractile claws. There are five digits on the fore foot, but apparently only four on the hind foot of the South American species (*M. neogæus*); and the humerus of the same animal is destitute of an entepicondylar foramen. More fragmentary but characteristic remains represent *Machærodus* in the Miocene of France and Germany; in the Pliocene of France, Italy, Greece, Hungary, the Isle of Samos, Persia, and India; and in the Pleistocene of France, Germany, Italy, England, North America, Ecuador, and Brazil. In England it first appears in the Cromer Forest Bed of Norfolk, while detached teeth prove its contemporaneity with Cave Man in Kent's Cavern, near Torquay, and in the Creswell Caves near Worksop on the borders of Derbyshire.

FIG. 225.

Machærodus (*Smilodon*) *neogæus*; skull and mandible, right lateral aspect, one-seventh nat. size.—Pleistocene; Buenos Aires, Argentine Republic.

Sub-Order 3. *Pinnipedia.*

As already mentioned (p. 384), the remarkable Creodont *Patriofelis* exhibits some features in its skeleton which have been regarded as suggestive of the seals; and it is quite possible that the early Tertiary ancestors of the Pinnipedia were lake-dwelling animals which eventually wandered into the sea. At present, however, Palæontology furnishes no definite clue to their origin; and they are only known to have been already well differentiated in the Pliocene period. A characteristic mandible of a seal from the Upper Pliocene of Montpellier, France, is named *Pristiphoca occitana.* Other fragmentary remains are known from Upper and Lower Pliocene strata in different parts of Europe and North America, notably in the Crag of Antwerp (*Palæophoca, Callophoca, Platyphoca,* and others). A few fragments have been recorded from the Cromer Forest Bed of Norfolk. The walruses also date back to the Pliocene in Europe, an imperfect skull (named *Alachtherium cretsi*) having been obtained from the Crag of Antwerp, and several characteristic tusks being known both from this formation and from the equivalent Red Crag of Suffolk (*Trichechus huxleyi*). A skull of the existing *Trichechus rosmarus* has been obtained from the fen-land near Ely, a mandible from the Dogger Bank in the North Sea; and more doubtful remains are known from the Thames alluvium in London.

ORDER 7. INSECTIVORA.

The existing small mammals which are adapted to feed upon insects and worms, and are grouped in the order INSECTIVORA, are probably the little-altered survivors of some of the most primitive placentals. They agree with the Creodonta in their low type of brain and nearly always in the separation of the lunar and scaphoid bones of the carpus; but their canine teeth are comparatively feeble, and when any of the incisors are enlarged these are always the inner pair. Though nearly all the fossils are fragmentary, most of the existing families can be traced back to the Upper Eocene; but some of the portions of dentition of the extinct genera are very doubtfully determined, and may even be referable to unknown primitive Primates. *Neurogymnurus,* known by the complete skull, mandible, and dentition from the Upper Eocene Phosphorites of France, seems to have been a hedgehog of the family **Erinaceidæ**; while a typical skull of *Erinaceus* itself is known from the Upper Miocene of Oeningen, Baden. The shrews, **Soricidæ**, and moles, **Talpidæ**, are also represented by typical jaws and limb-bones in the Upper Eocene Phosphorites of France; but it is interesting to note that the humerus of *Protalpa* of this remote age is not quite so highly specialized for burrowing as that of the existing *Talpa*. The desman (*Myogale moschata*), now confined to S. E. Russia, ranged far to the west in the Pleistocene period, and characteristic remains of it occur in the Cromer Forest Bed of Norfolk. The **Chrysochloridæ**, or golden moles of South Africa, have tritubercular upper molars; and the extinct **Leptictidæ**, from the Eocene and Miocene of North America, are sometimes claimed as their immediate allies.

ORDER 8. CHIROPTERA.

Nothing is known of the ancestry of the bats. A completely developed wing, with distinct impressions of the membrane and traces of hair, has been found in the Upper Eocene of Aix-en-Provence, France. Numerous typical skulls and jaws, scarcely separable from existing genera, have also been obtained from the contemporaneous Phosphorites of the same country.

ORDER 9. PRIMATES.

The discovery of numerous fossil forms renders the precise definition of the order PRIMATES or QUADRUMANA no longer possible, several of the extinct insectivores and lemurs apparently constituting a distinct link between this group and the Insectivora. The latest studies of the skull and dentition of the various extinct genera of Primates, have also to a great extent filled the gap between the two sub-orders, Lemuroidea and Anthropoidea, into which they are usually divided.

Sub-Order 1. *Lemuroidea.*

The lemurs are clearly of a lower grade than the apes (or Anthropoidea), and some of the extinct genera commonly referred to the sub-order they represent, are doubtless to be regarded as the direct ancestors of the higher group. The skull in most forms has a more produced facial region than is observed among the apes; the lachrymal foramen nearly always opens on the cheek, not within the orbital rim; and the orbit is only divided from the temporal fossa by a post-orbital bar, not completely separated from it by a thin lamina of bone, as is the case in the apes and man. The earliest genera, so far as known, exhibit the most generalized dentition; and these animals in the Eocene period lived not only in Europe but also in North America, while at the present day they are exclusively confined to Madagascar, parts of Africa, and the southern Asiatic region. They seem to have become extinct both in Europe and in North America at the dawn of the Miocene period, when apes began to appear at least in the Old World.

Anaptomorphus. A very small animal, with short and broad rounded skull and enormous orbits, of lemuroid type. The dental formula is $\frac{\text{i. ?, c. 1, pm. 2, m. 3}}{\text{i. 2, c. 1, pm. 2—3, m. 3}}$. The canine is relatively very small, and when a third premolar is present in the lower jaw in front of the usual pm. 3, 4, this is still more diminutive. The premolars are simpler than the molars, and the lower incisors are almost or quite erect. The upper molars are triangular in shape, tritubercular, and diminish in size backwards; the lower molars are quadritubercular. The mandibular rami are not fused together at the symphysis. *Anaptomorphus homunculus*, with the skull about 0·03 m. in length, occurs in the Lower Eocene (Wasatch Formation) of Wyoming. *Necrolemur*, known by equally satisfactory remains from the Upper Eocene Phosphorites of Quercy, France, seems to be an allied genus; and the jaws named *Microchœrus erinaceus*, from the Upper Eocene of Hordwell, Hampshire, probably belong to a similar animal.

Adapis (fig. 226). The best-known Eocene lemuroid, with a complete dentition (the usual 44 teeth) in close and regular series. The cranium is elongated, with a remarkably elevated sagittal crest upon the brain-case. It exhibits all the characteristic features of a lemuroid, and the rami of the mandible are fused together at its symphysis. The incisors are small and spatulate or chisel-shaped, those of the mandible directed a little forwards. The canines are larger than the incisors. The premolars, above and below, gradually increase in size backwards, pm. 1 being diminutive or even rarely wanting; the first three are simply conical, with a basal cingulum at least on the inner side, while upper pm. 4 is tritubercular and lower pm. 4 quadritubercular. The upper molars are quadrate in shape and increase in size backwards; each bears four tubercles, the two outer ones pyramidal in form, the antero-inner tubercle V-shaped, and the postero-inner tubercle quite a diminutive cone. The lower molars are antero-posteriorly elongated like the fourth premolar, each with four tubercles, partially united into two pairs by a low, oblique, transverse ridge. The last lower molar sometimes bears a posterior heel. The limb-bones referred to *Adapis* with much probability of correctness, are typically lemuroid in every respect. The metacarpals and metatarsals are remarkably short, while the phalanges are comparatively slender. The typical species, *Adapis parisiensis*, is known by complete skulls and other remains from the Upper Eocene Gypsum of Montmartre, Paris, and from the contemporaneous Phosphorites of Quercy. Equally complete remains of a larger form, *A. magna*, with the skull 0·1 m. in length, are also known from the Phosphorites of Quercy; and more fragmentary specimens of both species have been identified from the Upper Eocene of Egerkingen, Switzerland. Teeth of *A. magna* also occur in the Upper Eocene of Hordwell, Hampshire. *Tomitherium*, represented by the mandible and various limb-bones in the Lower Eocene (Wasatch Formation) of New Mexico, U. S. A., is believed to have been closely related to *Adapis*.

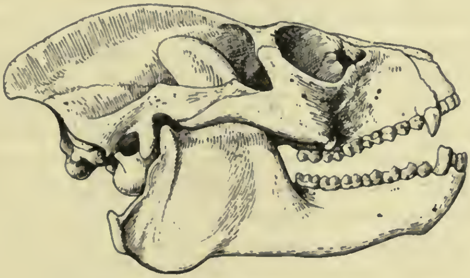

Fig. 226.

Adapis parisiensis; skull and mandible, right lateral aspect, two-thirds nat. size.—U. Eocene (Phosphorites); Quercy, France.

Megaladapis. This is the largest lemur hitherto discovered, and is known only by a skull and mandible from the surface deposits of Madagascar, where the animal seems to have survived until the latter half of the seventeenth century. The skull is unusually elongated; the orbits are relatively small; there is a prominent but thickened sagittal crest upon the brain-case; and the zygomatic arch is comparatively robust. There is no thin plate of bone separating the orbit from the temporal fossa, and the lachrymal foramen opens on the cheek outside the orbital rim. The incisor and canine teeth are unknown, but the molars and hinder premolars have been observed in both jaws. The upper molars are tritubercular, each bearing two cusps externally and one cusp internally; while the comparatively small upper premolars 3, 4, exhibit one outer, and one inner cusp. The lower molars are antero-posteriorly elongated, and the hindermost is extended into a prominent posterior talon; these and premolar 4 much resemble the corresponding lower teeth of *Adapis*. The typical skull of *Megaladapis madagascariensis* measures about 0·25 m. in length.

Nesopithecus. A remarkable large extinct lemur from Madagascar known only by parts of the skull and dentition. The facial profile of the skull is remarkably steep and the orbits are directed forwards. The orbital cavity must clearly have opened into the temporal fossa behind, and the lachrymal foramen is situated just upon its anterior rim. The dental formula is $\frac{\text{i. 2, c. 1, pm. 3, m. 3}}{\text{i. 1, c. 1, pm. 3, m. 3}}$. The upper incisors are implanted obliquely and those of the middle pair are much enlarged, while the outer pair are comparatively small. The upper canine is stout, with a well-developed basal cingulum. The upper premolars exhibit an internal cingulum, and pm. 2, 3 are antero-posteriorly elongated, while pm. 4 is longest in a transverse direction. The upper molars are quadrate in shape, diminishing in size backwards; and each bears four tubercles, the outer and inner pairs being opposite and connected by transverse ridges. The rami of the mandible are fused at the symphysis and the small front teeth, which seem to be of uniform size, project forwards, having a very oblique insertion. These probably represent one pair of incisors and a flanking pair of canines. The first of the three lower premolars, namely pm. 2, is enlarged and shaped to undertake the function of a canine—a feature common among existing lemurs. The three lower true molars are quadrate in shape, like those of the upper jaw, and diminish in size backwards. The hindermost lower molar is destitute of a posterior talon. The typical and only known species is *Nesopithecus roberti*, founded upon the facial and palatal part of a cranium from a swamp at Sirabé, Central Madagascar. The length of the upper dental series, from the canine to the hindermost molar inclusive, is 0·05 m.

Sub-Order 2. *Anthropoidea.*

The true apes, with the orbital cavity completely separated by a bony partition from the temporal fossa, appear first, so far as known, in the Middle Miocene of Europe; but all the remains hitherto discovered seem to represent forms closely related to the genera still surviving in the warmer regions of the Old World.

Most of the European fossils appear to be referable to the family of **Cercopithecidæ**, which includes all the living Old World apes except the gibbons, orangs, chimpanzees, and gorillas (Simiidæ). The oldest fragments are jaws and teeth of a comparatively large animal (*Oreopithecus bambolii*) from the Middle Miocene of Tuscany; and these are interesting as exhibiting resemblances both to the Cercopithecidæ and to the Simiidæ, as if they represented an annectant ancestral type. The best known form is *Mesopithecus pentelici*, of which numerous skulls and nearly all parts of the skeleton have been found in the Lower Pliocene of Pikermi, near Athens. The skull and dentition of this animal most closely resemble the corresponding parts of the Indian *Semnopithecus*, while the comparative shortness and stoutness of the limbs are rather suggestive of *Macacus*. An allied genus, *Dolichopithecus*, is represented by a comparatively large and elongated form of skull from the Lower Pliocene of Perpignan, France. *Macacus* itself, which still survives on the rock of Gibraltar (the Barbary Ape), also seems to have had a considerable range in Europe during the late Pliocene and early Pleistocene periods; a mandible and other remains having been identified from the Pliocene of the Val d'Arno, Tuscany, other fragments from the Pliocene of Montpellier, France, others from Pleistocene cavern deposits in southern France and Würtemberg, and a detached molar (named *Macacus pliocenus*) from the Pleistocene brick-earth of Grays, Essex.

The higher apes or **Simiidæ** are known in Europe only from the Middle Miocene to the Lower Pliocene. A mandible from the Middle Miocene of Sansan, Gers, France, named *Pliopithecus antiquus*, can scarcely be distinguished from that of the existing gibbons (*Hylobates*) of the southern Indian region; while two mandibles and the shaft of a humerus from an apparently contemporaneous deposit at St Gaudens, Haute Garonne (*Dryopithecus fontani*), seem to represent an extinct generalized ape, as large as a chimpanzee and closely related both to this animal and to the gorilla. A characteristic femur from the Lower Pliocene of Eppelsheim, Hesse Darmstadt (*Paidopithex rhenanus*), seems to be the latest evidence of a Simian hitherto discovered in Europe.

Fragmentary remains of apes are also known from the Pliocene and Pleistocene of India; the most interesting being typical portions of the dentition of baboons (*Cynocephalus*), which are now restricted in their range to Africa and Arabia.

In South America, the Santa Cruz Formation (supposed Miocene) of Patagonia yields fragmentary remains of *Homunculus* and other genera, which are closely related to the apes still inhabiting the warmer parts of the American continent.

Of the immediate ancestors of man, family **Hominidæ**, scarcely anything is known from the discovery of fossil bones.

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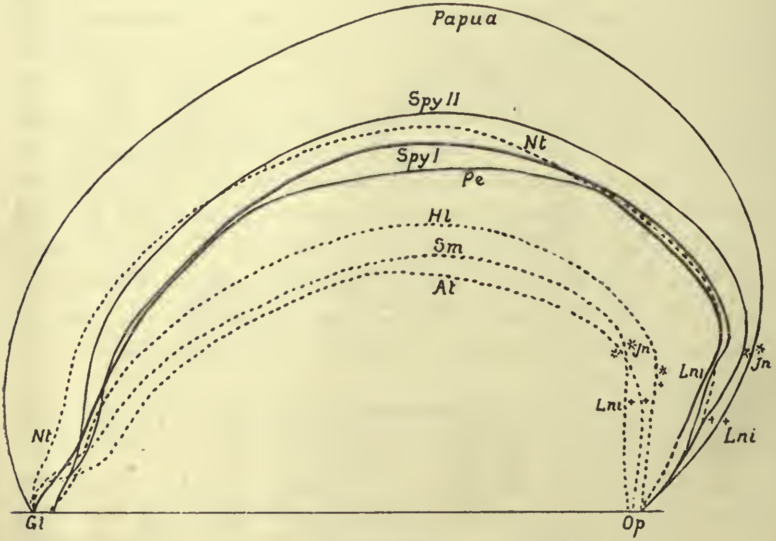

Fig. 227.

Profile Outline of the Skull of *Pithecanthropus* (*Pe.*), compared with those of a Papuan, the men of Spy, the Neanderthal man (*Nt.*), *Hylobates leuciscus* (*Hl.*), *Semnopithecus maurus* (*Sm.*), and *Anthropopithecus troglodytes* (*At.*).

Gl., glabella; *Jn.*, linea nuchæ superior; *Lni.*, linea nuchæ inferior. (After Marsh.)

Most of the evidence for the existence of the human race in the prehistoric past consists in traces of intelligent handiwork revealed by stone and other implements. A few discoveries in the Old World, however, are worthy of consideration.

The oldest known traces of a man-like skeleton seem to be an imperfect roof of a skull, two molar teeth, and a diseased femur, from a bed of volcanic ash containing the remains of Pliocene mammals, near Trinil, in central Java. These are believed to belong to one animal, which has received the name of *Pithecanthropus erectus.* The capacity of the brain-case (fig. 227, *Pe.*) is estimated to have been about two-thirds the average of that of man; the forehead is very low; and the supraorbital ridges are prominent. The inclination of the nuchal surface of the occiput is considerably greater than in the Simiidæ. The femur measures 0·455 m. in length, and denotes an upright gait.

The oldest human skeletons of which the geological age is determined with certainty, are two from the cavern of Spy, near Namur, in Belgium. These were found in association with remains of the mammoth and other Pleistocene mammals beneath a layer of stalagmite, which had never been disturbed, and which was also covered with earth containing bones of the same extinct quadrupeds. The skeletons, therefore, could not be the result of a comparatively recent burial, but were proved to have been contemporaneous with the associated animals and Palæolithic flint implements. They are essentially human in every respect, but seem to represent a race inferior in skeletal characters to any now existing. They are small, but powerfully built. The forehead is low; the supraorbital ridges are very prominent; and the chin is remarkably retreating. The radius and ulna are unusually divergent in the middle. The femur is somewhat bent, and the tibia is comparatively short; so that the leg cannot have been quite upright in walking. This type is now generally known as the *Neanderthal race*;

Fig. 228.

Human Calvarium from a Cavern in the Neanderthal, near Düsseldorf, Germany, one-quarter nat. size.

the roof of a similar skull (fig. 228) having been found associated with other fragmentary remains so long ago as 1857, in a cavern in the Neanderthal between Düsseldorf and Elberfeld, Germany.

So far as can be determined from implements, man appears to have passed through three successive grades of civilization in western Europe before Britain became separated from the mainland. The earliest stones regarded with much plausibility as bearing traces of human handiwork, occur in certain high-level or plateau gravels in the south of England, which seem to date back to the Pliocene period before the existing valleys were excavated. These are flints merely chipped round the edge to render them more serviceable as implements. They are described as *eoliths* made by *Plateau Man.* The next implements, now universally recognized as such, are met with in the older gravels deposited in the existing valleys, and sometimes in the lowest layers in the floor-deposits of caverns (as in Kent's Cavern, Torquay). These are completely chipped and fashioned into the form of hatchets and scrapers, to be held by the thickest end. They are the earliest known *palæoliths* and the handiwork of *River Drift Man.* More delicate and highly finished flint and chert implements, sometimes associated with harpoons, pins, and needles of bone, occur in many caverns which were evidently inhabited by man when the mammoth, reindeer, lion and other large quadrupeds still survived in Britain. These are ascribed to the highest and latest type of Palæolithic hunter, commonly known as the *Cave Man.* It was this type of man that lived during the so-called "Reindeer Period" in the south of France and Switzerland and left the familiar rude sketches of animals and hunting scenes on fragments of bone and teeth, which have often been described. It is also to this race of man that the Neanderthal and Spy skeletons must be referred.

TABLE OF GEOLOGICAL PERIODS AND FORMATI

Periods.		Some European Formations.	
Tertiary or Cainozoic.	Recent.		
	Prehistoric.		
	Pleistocene.		
	Pliocene.	Upper.	Val d'Arno, etc. (see p. 426
		Lower.	Marine Crags. Pikermi, etc. (p. 424).
	Miocene.	Upper.	Oeningen.
		Middle.	Sansan, etc. (p. 423).
		Lower.	Ronzon, etc. (p. 422).
	[Oligocene.]		
	Eocene.	Upper.	Hordwell, etc. (p. 421).
		Middle.	Bracklesham, etc. (p. 420).
		Lower.	London Clay, etc. (p. 420).
		Basal.	Rheims (Cernaysian).
Secondary or Mesozoic.	Cretaceous.	Upper.	Danian (Maastricht). Senonian (U. Chalk). Turonian (L. Chalk, etc.). Cenomanian (U. Greensand) Albian (Gault).
		Lower.	Neocomian (L. Greensand).
	Jurassic.	Upper.	Wealden. Purbeckian. Portlandian. Kimmeridgian. Lithographic Stone of Bava etc.
		Middle.	Corallian. Oxfordian.
		Lower.	Bathonian or Lower Oolites Lias.
	Triassic.	Upper.	Rhætic and Keuper. Muschelkalk.
		Lower.	Bunter.
Primary or Palæozoic.	Permian.	Upper.	Magnesian Limestone. Marl Slate (Kupferschiefer)
		Lower.	Rothliegendes.
	Carboniferous.	Upper.	Coal Measures. Millstone Grit.
		Lower.	Carboniferous Limestone Lower Scottish Measures. Calciferous Sandstones.
	Devonian and Old Red Sandstone.	Upper.	Sandstones with *Holoptycl* and *Bothriolepis*.
		Lower.	Strata with *Osteolepis* *Pterichthys*. Passage Beds.
	Silurian.	Upper.	Ludlow Wenlock. Llandovery.
		Lower.	
	Ordovician.		
	Cambrian.		

NS IN DESCENDING ORDER.

	Some North American Formations.	Other Formations.
	Blanco. Palo Duro.	Siwalik Formation of India.
	Loup Fork. John Day. White River.	Probably Santa Cruz Formation of Patagonia.
	Uinta. Bridger. Wind River. Wasatch. Puerco.	
	Laramie. Fox Hills. Niobrara. Dakota.	Chalk of Mt Lebanon.
a,		
	Texas, etc.	Hawkesbury-Wianamatta Series of Australia, and Karoo Formation of South Africa.
	Coal Measures.	
d al	Sub-Carboniferous.	
us	Chemung. Hamilton.	
d	Corniferous. Oriskany.	
	Onondaga. Niagara.	

THE SUCCESSION OF THE VERTEBRATE FAUNAS.

The general results of this brief sketch of the Palæontology of the Vertebrata, may now be summarized from the geological point of view. Two considerations only need be borne in mind. Firstly, owing to the imperfection of the geological record and the incomplete exploration of most formations, any statement now formulated may eventually prove to be quite a partial account of the facts, and every conclusion must be more or less provisional and tentative. Secondly, there are no means of determining the contemporaneity or otherwise of rocks containing similar fossils in different widely-separated regions of the globe; and therefore in recording the geographical range of the various faunas it is not possible to discover their limits at any given epoch, but merely to ascertain the maximum extent of their spreading and migrations during the period of their existence. The palæontologist at present can only deal with the succession of faunas as revealed in some such small area as western Europe, for example, where the series of geological formations is tolerably complete and in recognizable order. The known facts of geology are still too few to restore the life-provinces of the globe at the various stages of its past history.

Upper Silurian.

The earliest vertebrate fauna hitherto discovered is contained in shallow-water deposits towards the summit of the Silurian system. It is distributed over the greater part of the northern hemisphere, having been already found in England, Scotland, Galicia, the Baltic region, Pennsylvania, New

Brunswick, and Newfoundland. Traces of it in the southern hemisphere are also recorded from Queensland. It includes unknown fishes which resembled the modern sharks in the structure and general characters of their dermal armour; for numerous typical shagreen granules (*Cœlolepis*) and elongated spines—some clearly fin-spines (*Onchus*)—are met with in several localities. The fauna, however, chiefly consists of the remarkable group of Ostracoderms, which seem to have been below the rank of true fishes and finally became extinct at the close of the Devonian period, at least in the European and North American areas. The least specialized genus of Pteraspidæ, *Cyathaspis*, from the Wenlock Limestone of the Island of Gothland and from higher Silurian horizons both in Europe and North America, is the oldest. The Tremataspidæ occur in the Island of Oesel in the Baltic Sea; while the Cephalaspidæ are just beginning to appear (*Cephalaspis*, *Auchenaspis*) both there and on the Herefordshire and Shropshire border of Wales.

DEVONIAN AND OLD RED SANDSTONE.

There are at least three, if not four distinct and apparently successive fish-faunas in the strata grouped by geologists as Devonian. The earliest differs very little from that of the Upper Silurian, except that the Cephalaspidian Ostracoderms become relatively more numerous, while the Elasmobranch fishes (chiefly Acanthodians) are of more importance and develop into very varied forms. It also contains one new element (*Phlyctænaspis*), a forerunner of the highly specialized armoured fishes termed Arthrodira, which are so characteristic of the later Devonian formations. The highest genus of the Pteraspidæ, *Pteraspis* itself, is now abundant; and when it disappears the family becomes extinct. This fauna is characteristic of the Passage Beds and the Lower Devonian Cornstones of Herefordshire and the adjoining counties, where *Pteraspis*, *Cephalaspis*, and *Phlyctænaspis* are the commonest genera. It is represented again in the Lower Old Red Sandstone of the south of Scotland, especially in Forfarshire and Ayrshire; and the same fauna in the quarries of Turin Hill, Forfar, is remarkable for the abundance of beautifully preserved Acanthodian Elasmobranchs. It is also imperfectly known in Galicia and in Spitzbergen; while it occurs in an admirable state of preservation in the Lower Devonian shales of Campbellton, New Brunswick, where *Phlyctænaspis* is commoner than in Europe and *Pteraspis* seems to be wanting.

The next Devonian fish-fauna is best known in the north of Scotland, where it is found in the Old Red Sandstone series deposited in "Lake Orcadie." It is specially characterized by the abundance of the anomalous armoured Arthrodira (*Coccosteus, Homosteus*) and of Crossopterygian fishes belonging to the sub-order Rhipidistia (*Glyptolepis, Osteolepis, Thursius, Diplopterus*); while the Dipnoi make their first appearance (*Dipterus*), and one genus (*Cheirolepis*) represents the dawn of the Actinopterygian fishes. Except an extremely rare *Cephalaspis* (of which only one specimen has hitherto been discovered in northern Scotland), the two lower orders of Ostracoderms are now wanting; but the highly specialized order of Antiarchi appears, abundantly represented by the genus *Pterichthys*. A few small specialized Acanthodians also remain (*Mesacanthus, Cheiracanthus, Diplacanthus*). A corresponding fauna is indicated in North America in the Corniferous Limestone extending across New York and in several other of the United States, where undoubted Chimæroid teeth are met with for the first time.

The Upper Devonian fish-fauna is characterized especially by the Ostracoderm *Bothriolepis*, by armour-plated sharks like *Psammosteus*, and by the Crossopterygian genus *Holoptychius*; but there are several local variations, and all three genera do not always occur together. Dipnoan fishes are still abundant (*Phaneropleuron, Scaumenacia*), but the Arthrodira are rarely met with. This fauna occurs in the red and yellow sandstones of the Old Red Sandstone series both to the north and to the south of the Grampians; in the west of England; in Belgium, Germany, north-western Russia, and Spitzbergen; in the province of Quebec, Canada, and in the Chemung (Catskill) Formation of the United States. Fragments are also recorded from Queensland.

In the yellow Old Red Sandstone of the Baltic province of Russia, the Upper Devonian fish-fauna comprises comparatively large Arthrodira of the genera *Homosteus* and *Heterosteus,* which seem to have been toothless; but these great armoured fishes attain their maximum size and power just before they become extinct, in a series of black shales (Waverly Group and Cleveland Shales) forming passage beds between the Devonian and Carboniferous systems in the United States, especially in Ohio. *Dinichthys* is the commonest genus. Here also occur the remarkable primitive sharks of the order Pleuropterygii (*Cladoselache*), of which numerous well-preserved skeletons are now known.

CARBONIFEROUS AND LOWER PERMIAN.

A new departure is now made in the history of the Vertebrata. Certain impressions on slabs of sandstone from the Upper Devonian of Pennsylvania, have been plausibly interpreted as the foot-prints of land-animals; and quite at the base of the Carboniferous system, at least in Britain, the skeletons of such quadrupeds actually begin to occur. Throughout the Carboniferous and Lower Permian formations of Europe, the Stegocephalia, as these primitive land-dwellers are termed, are represented by many genera and numerous individuals; and since traces of a well-developed branchial apparatus have been observed in several immature specimens, the order to which the Stegocephalia belong, is usually assigned to the lowest class of lung-breathers, namely, that of the Batrachia. Some of these animals are crocodile-shaped, others lizard-shaped, others limbless like snakes; and it is remarkable that closely similar, if not identical genera also occur in the Upper Carboniferous of North America. The order is still met with throughout the Trias of Europe, and it is also sparsely represented in strata which may be either Permian or Triassic in Spitzbergen, North America, South America, India, and New South Wales.

The Carboniferous and Lower Permian fish-fauna, preserved in the same strata as these forerunners of the land-animals, is of a very uniform character, and distributed over a large part of Europe and North America, while there are slight traces of it also in Central Asia. The limestones deposited in the deeper waters yield remains of Elasmobranch fishes with a powerful crushing dentition (*Psammodus* and the Cochliodontidæ). Other sharks are also abundant, especially the Ichthyotomi (*Pleuracanthus*); and a few highly specialized Acanthodians still remain, though these become extinct with the genus *Acanthodes* in the Permian. The Arthrodira have now disappeared, but the Dipnoi are as numerous as before (*Ctenodus*). Of the Crossopterygian fishes the Holoptychiidæ are wanting, but the Rhizodontidæ and Osteolepidæ are abundant, and the remarkable Cœlacanthidæ first appear (*Cœlacanthus*). The Palæoniscidæ and Platysómidæ, however, are the dominant fishes of the period and mark the dawn of the supremacy of the order Actinopterygii.

Upper Permian, Triassic, and Rhætic.

One fish in the Upper Permian of Europe (*Acentrophorus*) indicates the beginning of the Actinopterygian sub-order of Protospondyli, which becomes dominant in the Jurassic and continues to be of importance until the upper part of the Cretaceous. The Triassic and Rhætic Teleostomi are perhaps about equally divided between the Chondrostei and the Protospondyli, apparently mingled with a few forerunners of the still higher order of Isospondyli; and this mingling is observed not only in Europe and North America, but also in New South Wales. The most noteworthy feature of the fauna, however, is the last important appearance of the Dipnoi (*Ceratodus*) among marine fishes. Ceratodont teeth occur abundantly in Triassic or Rhætic strata in England and Germany and in India, less abundantly in South Africa and New South Wales; but the only known specimens from later marine strata are two diminutive teeth from the Lower Jurassic of England and a few from corresponding strata in Colorado, U.S.A.

While the Upper Permian and Triassic fish-faunas were flourishing, undoubted reptiles began to multiply on the land,

and some of them even passed into aquatic types (*Mesosaurus, Nothosaurus, Mixosaurus*). They are known both in Europe and North America, in India, in South Africa, and in South America; so that their geographical range may almost be regarded as cosmopolitan. Most of the earlier and more generalized forms are closely similar to the Stegocephalia, some apparently derived from the typical labyrinthodonts (Pariasauria), others more probably connected with the microsaurians (Proterosauria). The later types belong to a higher grade and are more varied. In the Triassic strata of Europe there are remains of many typical Anomodontia, at least one type of ancestral Chelonia (*Proganochelys*), and ancestral Dinosauria, which might likewise in part be the forerunners of the Crocodilia. There are, in addition, some typical highly-specialized Rhynchocephalia (*Rhynchosaurus, Hyperodapedon*). Several of these forms are also represented in the Trias of North America and India; and Anomodontia greatly preponderate in the reptilian fauna of the corresponding formations of South Africa. Some small limb-bones (*Agriosaurus*) from rocks of unknown age on the N.E. coast of Australia are supposed to belong to a Triassic type of dinosaur; but these are the only indication hitherto discovered of Mesozoic land-reptiles in the Australian region.

JURASSIC.

During the Jurassic and Cretaceous periods there were many changes in the distribution of sea and land in the northern hemisphere, and most of the existing continental areas seem to have been subdivided into islands of variable extent. Considerable portions of the existing land in the southern hemisphere were also submerged at times, and the deposits formed in the seas are very extensive. None of the known marine formations of the Jurassic period, however, represent more than shallow seas, and in these the Actinopterygian fishes of the sub-order Protospondyli seem to have been the dominant race of vertebrate life. In the same fauna there are numerous Cestraciont sharks and some primitive skates; there are also true Chimæroids, some of the latter belonging to extinct families (*Squaloraja, Myriacanthus*), others referable to the existing Chimæridæ (*Ischyodus*). The Crossopterygians are represented by numerous Cœlacanthidæ (*Undina*), and the Isospondyli are just beginning to assume some importance (*Pholidophorus, Leptolepis*). Marine reptiles are also extremely abundant everywhere and belong to the three orders, Sauropterygia, Ichthyopterygia, and Crocodilia.

On land this was the age of reptiles, at least in the northern hemisphere. Both in Europe and North America the Stegocephalia and Anomodontia disappear at least with the Triassic; but the Dinosauria assume an astonishing development everywhere in the Jurassic, and some of them attain larger dimensions than any land-animal of later date. Towards the close of the period some of the crocodiles also acquire a fluviatile and terrestrial habit (*Goniopholis, Bernissartia*). Flying reptiles (Ornithosauria) are well represented throughout all Jurassic formations; and birds are first known to appear in the Upper Jurassic with the rare genus *Archæopteryx*.

No undoubted trace of the Jurassic land-fauna has hitherto been discovered in the southern hemisphere, for *Steneosaurus*, found in Madagascar, is rather to be regarded as a marine type; but it is extremely probable that on some continent in that part of the globe the Anomodontia were gradually being transformed into Mammalia. At least, in the Jurassic formations both of Europe and North America there are occasional remains of small mammals as large as rats; and the most plausible explanation of these is, that they were accidental escapes from some other region with a more advanced fauna, just as are the rats and mice of the present day in the comparatively antique realm of Australia.

CRETACEOUS.

The fish-fauna in the Lower Cretaceous deposits is closely similar to that of the Jurassic; but that of the Chalk and other Upper Cretaceous formations, is quite modern in aspect, with only a slight admixture of the Crossopterygian Cœlacanthidæ (*Macropoma*) and the Actinopterygian Protospondyli (*Neorhombolepis, Protosphyræna*, and Pycnodontidæ). Essentially modern types of sharks and skates appear; while among bony fishes, the only important groups without some representative seem to be the Anacanthini, Lophobranchii, Hemibranchii, and Plectognathi—all highly specialized. There are also the first known traces of a deep-sea fish-fauna; many of the Scopeloids having quite an abyssal aspect, while typical members of the surviving Bathythrissidæ (*Istieus*) and Halosauridæ (*Echidnocephalus*) can be easily recognized.

The marine reptiles of the orders Sauropterygia and Ichthyopterygia are rare in Cretaceous formations, and are almost replaced by aquatic lizards of the sub-orders Pythonomorpha and Dolichosauria. The first of these have a very wide distribution, being met with not only in the Chalk of Europe and North America, but also in corresponding deposits in South America and New Zealand. The land-reptiles are essentially similar to those of the Jurassic, except that they become more specialized and almost fantastic just before they disappear. But now there seems to have been at least some temporary connection again between the northern lands on which the typical Jurassic reptile-fauna developed, and the southern lands on which the Triassic Anomodonts had been left to pass into the Mammalia. In fact, gigantic Dinosauria have spread to undoubted Cretaceous strata in India, Madagascar, and South America, while in the latter country Ornithosauria and terrestrial types of Crocodilia also appear; and, on the other hand, another group of diminutive mammals of the Jurassic type occurs in the Upper Cretaceous (Laramie Formation) of North America, while very soon at the base of the Tertiary true placental mammals begin to appear both in North America and Europe. Very few birds are known, but most of them are typical members of their class, though still retaining teeth.

TERTIARY.

At the close of the Cretaceous period all the flying reptiles and dinosaurs, and most of the marine reptiles seem to have become extinct; and the Tertiary formations, so far as known, yield only forms of vertebrata essentially similar to those of the present day. Among fishes, the Protospondylic family of Pycnodontidæ is the sole typically Mesozoic group still surviving; and this is no longer met with after the Upper Eocene. All the existing sub-orders, and many of the existing families or even genera, seem to occur in the Eocene; and the chief interest of the Tertiary fish-fauna consists in its varying distribution at different times both in the seas and freshwaters. Except the ordinary turtles and a solitary rhynchocephalian (*Champsosaurus*), no vertebrates higher than fishes have been found in the marine deposits at the base of the Tertiary series; but both Cetacea and Sirenia begin to usurp the functions of the marine Mesozoic reptiles before the close of the Eocene period.

The terrestrial vertebrata are of much more importance; for the Mammalia suddenly appear as the dominant type on all the continents, and the evolution of many of their minor groups can be traced through the Tertiary formations. During the whole of this period, however, Australia and New Zealand seem to have been separated by sea from the other existing land-areas of the globe; while South America must have been quite an isolated region from the close of the Cretaceous to the dawn of the Pliocene.

Basal Eocene.

The earliest known mammalian fauna of a typical Tertiary type occurs in a deposit (Cernaysian Formation) quite at the base of the Eocene near Rheims in France, and in a still more extensive lake-deposit (Puerco Formation), doubtless of corresponding geological age, in New Mexico and Colorado, U.S.A. In this fauna there are still typical, though highly specialized members of the Jurassic group of Multituberculata (*Neoplagiaulax, Ptilodus, Polymastodon*); but the large majority of the genera belong to the Creodonta and Condylarthra, or ancestors of the Carnivora, Insectivora, and Ungulata. In the Puerco there also seem to be traces of the ancestors of the New World Edentata (the so-called Ganodonta).

Eocene.

The succession of three gradually differentiating mammal-faunas in strata of the Eocene series, is determined by stratigraphical geology both in Europe and North America. In north-western Europe many of the strata containing them are intercalated in a marine series which can be traced over a considerable area. In North America, they are contained in three successive lake-deposits, which happen to overlap in parts of Utah and Colorado, where their order of formation is clear.

The Lower Eocene fauna of Europe is represented in the Thanet Sands, London Clay, and Woolwich and Reading Beds in the south of England, also in corresponding formations in the Paris Basin. In North America it occurs in the lacustrine Wasatch Formation of New Mexico, Utah, Colorado, and Wyoming. The marsupials are still represented by opossums (*Didelphys*) on both continents. Compared with those of the basal Eocene, the Creodonta and Condylarthra are now more specialized and include many larger animals. Of the second sub-order just mentioned, *Phenacodus* is the most important and best-known genus. The true Perissodactyla are now represented among the ungulates, by ancestral types of horses (*Hyracotherium*), rhinoceroses (*Heptodon*), and tapirs (*Systemodon*). A few Artiodactyla also begin to appear; but the most characteristic ungulates of the period are the Amblypoda, represented especially by *Coryphodon*. Undoubted lemuroids and rodents likewise appear for the first time.

The Middle Eocene fauna is very imperfectly known in Europe, being found only in the marine Bracklesham Beds of Sussex and in various freshwater deposits in France and Alsace. In North America it comprises a large series of mammalian genera discovered in the lacustrine Bridger Formation of Wyoming and Colorado. All the groups of mammals are more specialized than previously, and among the ungulates the sub-orders of Perissodactyla and Amblypoda attain a remarkable development in North America. On that continent the large Titanotheriidæ begin to appear (*Palæosyops*), while *Coryphodon* has become extinct and been replaced by the still more remarkable Dinocerata (*Dinoceras*, *Uintatherium*, *Tinoceras*). The Chiroptera, or bats, make their first appearance. There are as yet no true Carnivora, and *Didelphys* still survives both in Europe and in North America. Marine snakes (*Palæophis*), a gavial (*Gavialis dixoni*), and various chelonians occur in association with fish-remains in the Bracklesham Beds.

The Upper Eocene fauna occurs in Europe in the marine Barton Clay and the overlying freshwater beds of Hordwell, Hampshire; in the freshwater limestone of Bembridge, Isle of Wight; in the gypsum of Montmartre, near Paris; and in the lignites of Débruge, near Apt, Vaucluse. In North America it characterises the lacustrine Uinta Formation of Colorado and Utah. The Creodonta are now of less importance than before, and true Carnivora are met with for the first time, at least in Europe (*Cynodictis*). The Condylarthra are few, and the Amblypoda have completely disappeared in the North American region to which they were restricted. The Perissodactyla are still numerous, and the most important new form is *Palæotherium* in Europe; but the Artiodactyla attain the most remarkable development both in Europe and North America. On the former continent there are the pig-like *Chœropotamus*, and the primitive forerunners of the ruminants, *Hyopotamus* (*Ancodus*) and *Xiphodon*; while a remarkable short-lived family exhibiting three-toed spreading feet, is represented by *Anoplotherium* and *Diplobune*. In America there are the Oreodonts (*Protoreodon*) and primitive camels (*Leptotragulus*), which must have been still more nearly ruminants. The Rodentia are now very numerous and varied; on the other hand lemurs appear for the last time on both continents. The opossums (*Didelphys*) are still abundant. Marine mammals occur for the first time, the primitive whale, *Zeuglodon*, being found in Europe, northern Africa, and North America; while a single Cetacean vertebra of a more modern type has been discovered in the Upper Eocene of Hampshire. There is also some fragmentary evidence of Sirenia in northern Italy.

It must be added that the European Upper Eocene mammalian fauna is best represented in certain phosphate-bearing earths or *phosphorites* filling an extensive series of fissures in the district of Quercy, between Villefranche and Montauban in the south of France. These fissures, however, were evidently open and being filled with earth and bones long after the close of the Eocene period, so that two or more successive faunas are mixed together and it is not possible to determine with certainty the age of any particular fossil found in this anomalous deposit. A similar mixture of Eocene and Miocene mammalian fossils, though of a more fragmentary character, also occurs in several fissure-accumulations of iron-ore (the so-called *bohnerz*) in Switzerland (as at Egerkingen), in Würtemberg (as at Frohnstetten), and in Bavaria (as at Pappenheim).

Miocene.

Between the Eocene and Miocene strata of Europe, stratigraphical geologists who base their conclusions on the marine deposits, recognise an intermediate formation termed Oligocene. So far as the vertebrate faunas are concerned, however, it does not seem possible to admit this division, and the so-called Lower Oligocene falls more naturally into the Upper Eocene, while the Upper Oligocene may be included in the Lower Miocene.

Adopting this arrangement, the Lower Miocene vertebrate fauna of Europe occurs in the Hempstead Beds which directly overlie the Upper Eocene in the Isle of Wight; in the lacustrine marl of Ronzon near Puy-en-Velay, and of other districts in southern France; in other freshwater deposits near St Gérand-le-Puy, Allier; in the lignites of Rott near Bonn, of La Rochette near Lausanne, and of Cadibona in Liguria; in the marine Rupelian formation of Belgium; in marine, brackish-water, and freshwater deposits in the neighbourhood of Mayence; and in other freshwater formations near Ulm, Würtemberg. A corresponding mammalian fauna in North America occurs in the White River Formation, which was deposited in an extensive series of lakes spread over Nebraska, Dakota, Colorado, Wyoming, and part of southern Canada. The Creodonta are now found for the last time both in Europe and North America, and seem to be represented only by one highly specialized genus, *Hyænodon.* The true Carnivora are abundant and varied, including even a cat (*Eusmilus*) on both continents; but the viverroids are confined to Europe. Among ungulates the Perissodactyla include hornless rhinoceroses on both continents; while there is a considerable advance in the line of the horses in North America, and *Titanotherium* represents the highest and last development of the peculiarly American family of Titanotheriidæ. Some of the primitive Artiodactyla attain a large size and become of importance, such as *Anthracotherium*, *Hyopotamus*, and *Elotherium*, both in Europe and America. The early ruminants are also represented in Europe by such genera as *Cænotherium* and *Amphitragulus*; while they occur in still greater variety in North America as Oreodonts (*Oreodon* and *Agriochœrus*), primitive camels (*Poebrotherium*), and strangely horned quadrupeds (*Protoceras*). The opossum (*Didelphys*) appears for the last time in Europe; so also do the freshwater ganoid fishes, *Amia* and *Lepidosteus.* Among marine mammals, *Halitherium* and *Miosiren*, from the neighbourhood of Mayence and Antwerp respectively, are the earliest well-known examples of the Sirenia.

The Middle Miocene fauna is well known from numerous localities in Europe, and of these some of the more classical may be enumerated as follows:—Sansan, Simorre, and Villefranche d'Astarac in Gers, France; Léognan and Romans, Gironde; St Gaudens, Haute Garonne; La Grive-St-Alban, Isère; Montpellier, Hérault; Käpfnach, Chauxdefonds, and Elgg, in Switzerland; Georgensgmünd, in Bavaria; Steinheim, in Würtemberg; and Monte Bamboli, in Tuscany. In North America the John Day Formation of Oregon and Montana is supposed to furnish a nearly equivalent, though distinctly more ancient assemblage of mammals. The most remarkable feature of this fauna in Europe is the sudden appearance of the Proboscidea (*Dinotherium* and *Mastodon*) and the true apes (*Oreopithecus, Dryopithecus*). It is also interesting as comprising the earliest known deer with antlers (*Dicroceros*), and the earliest rhinoceroses with a horn. The Carnivora are noteworthy as including a series of genera intermediate between the dogs and bears (*Amphicyon, Hyænarctos*). In North America there are not as yet any traces of the Proboscidea, or of deer with antlers; while the chief Carnivora of the John Day Formation are the sabre-toothed cats (*Nimravus*).

There is no clearly distinguishable Upper Miocene mammalian fauna in Europe, though the lacustrine deposits of Oeningen, Baden, may perhaps represent this stage. Here occurs the gigantic fossil salamander, *Cryptobranchus diluvii testis.* In North America, however, the mammals from the Loup Fork Formation are usually described as Upper Miocene; and the assemblage or fauna certainly exhibits a mingling of the types which are partly Middle Miocene, partly Lower Pliocene in Europe. The Loup Fork series is chiefly of lacustrine origin and very widely distributed between South Dakota and Mexico. *Mastodon* now appears for the first time in the New World, but it is not accompanied by *Dinotherium.* The rhinoceroses, which are still hornless, are now nearly extinct. Besides other genera of primitive horses, *Hipparion* is found. Deer with small antlers are also met with (*Cosoryx*); while *Procamelus* makes a very close approach to the camels, which appear in India in the Pliocene.

Pliocene.

The Lower Pliocene vertebrate fauna of the Old World is well known not only from several widely-distributed localities in Europe, but also from parts of Asia and Algeria. Among marine mammals the Sirenian *Halitherium* and the primitive Cetacean *Squalodon*, still survive; but the large majority of the remains found in the marine Antwerp Crag of Belgium, the Red and Coralline Crags of eastern England, and the equivalent sub-Apennine strata of Italy, represent genera of Cetacea and Carnivora Pinnipedia closely similar to, or even identical with, those now living. The land-mammals are very numerous, and are best known from the freshwater deposits of Mt Léberon and Cucuron (Vaucluse) and Montpellier (Hérault) in France; from Concud in Spain; from the estuarine yellow sands of Eppelsheim, Hesse Darmstadt; from the Vienna basin and Baltavár in Hungary; and from a torrent-deposit at the foot of Pentelicon in the ravine of Pikermi, near Athens. Abundant remains are also found in a volcanic tuff on the Island of Samos in the Turkish archipelago; in a similar deposit at Maragha in Persia; and in the well-known Siwalik Formation of India. There are, moreover, traces of the same fauna in China, Japan, the Philippines, Borneo, and Java. In the European area true apes are represented by a single thigh-bone from Eppelsheim, and by numerous skeletons of *Mesopithecus* from Pikermi. Among Carnivora, *Felis* and *Hyæna* appear for the first time, associated with *Ictitherium* which seems to be an ancestor of the latter; primitive types of bears (*Amphicyon, Hyænarctos*) are also common, but *Ursus* itself is not yet found. *Dinotherium* is now met with for the last time, and *Mastodon* flourishes; but there is as yet no true *Elephas*. Antelopes abound, except in the comparatively northern region of Hesse Darmstadt, and there are several ancestral types of giraffe (*Palæotragus, Helladotherium*). Typical pigs (*Sus*) are first found; and the very abundant *Hipparion* makes a close approach to the modern horses.

Tracing this fauna eastwards, there are four important additional forms to be noted in Samos, namely, another extinct giraffe (*Samotherium*), a *Hyrax*, an undoubted *Orycteropus*, and also, among birds, an ostrich. The assemblage of forms at Maragha resembles both that of Samos and that of the fresh-water sandstone of the Siwalik Hills and other parts of India. The Siwalik Formation, however, evidently contains more than one mammalian fauna; for mingled with the typically Lower Pliocene genera, there are others (such as *Anthracotherium, Listriodon*, and *Hyotherium*) of more ancient aspect, while some (such as *Equus, Elephas, Hippopotamus*, and *Leptobos*) are distinctly later, at least in Europe. The most remarkable of the typically Siwalik mammals are the horned Giraffidæ, *Sivatherium* and *Bramatherium*.

The North American fauna which seems to represent the Lower Pliocene is as yet very imperfectly known. One of the lacustrine deposits containing it, however, clearly rests unconformably upon the Loup Fork Formation at least in one part of Texas. The hornless rhinoceroses now appear for the last time, species of *Mastodon* and true *Equus* occur, and there are also llamas and peccaries.

The latest (Upper) Pliocene mammalian fauna of Europe is nearly similar to that of the Pleistŏcene, most of the genera being identical and the species only slightly different. It is best known from freshwater and estuarine deposits in the Val d' Arno, Tuscany; from a torrent-deposit at Olivola in the Carrara mountains; from Perrier, Ardé, Peyrolles and other localities in the Puy-de-Dôme, France; from Roussillon and Montpellier (Hérault), where the Lower and Upper Pliocene faunas are not quite clearly distinguished; and from the Norwich Crag of Norfolk. There are still traces of the apes in southern France and Italy. Among the Carnivora, *Hyænarctos* is just becoming extinct, and is being replaced by small bears of the genus *Ursus;* while the species of *Machærodus* are now very large. The true beavers (*Castor*) and other characteristic modern genera of Rodentia appear for the first time, and there is a large beaver-like animal, *Trogontherium. Mastodon* occurs for the last time, and *Elephas* now appears with the gigantic *E. meridionalis.* There are also true oxen (*Bos, Leptobos*) and deer of existing genera (*Cervus, Cervulus*); while a typical hippopotamus, as large as the recent *H. amphibius,* is not uncommon. The tapirs have already disappeared, but rhinoceroses survive (*R. etruscus*); and for the first time there is a completely evolved one-toed horse (*E. stenonis*).

The Cromer Forest Bed.

At the close of the Pliocene period Britain was still connected with the adjoining continent, and an interesting remnant of the mammalian fauna of this part of Europe at the time is preserved in an old land surface and associated deposits now exposed in the cliffs of Norfolk, especially in the neighbourhood of Cromer. This is the so-called Forest Bed Series. The mammals found here are chiefly those of the typical Pleistocene fauna; but a few still survive from the Upper Pliocene, such as a gazelle, some deer with very large antlers allied to the *Cervus dicranius* of the Val d' Arno, *Rhinoceros etruscus, Elephas meridionalis,* and *Trogontherium.* The Forest Bed fauna is thus intermediate in character between the Pliocene and the Pleistocene; and a similar mingling of forms has been observed in certain local deposits both in France and Italy.

Pleistocene.

The Pleistocene mammalian fauna of Europe is very remarkable. It does not include many forms which have subsequently become extinct; but throughout the central and north-central parts of the continent there is a curious mingling of northern, eastern, and southern types which it seems difficult to explain. The remains of this fauna are met with in the surface deposits and caverns of Britain, so far north as Yorkshire, quite as abundantly as on the continent; so that the bed of the North Sea and the Straits of Dover must still have been an open valley, and our island remained part of the mainland. The northern animals include the reindeer and musk-ox, which wandered as far south as the Pyrenees; the typically eastern animals comprise the saiga antelope, the jerboa, the tailless hare, and *Myogale moschata;* while among the numerous southern types may be mentioned the lion, leopard, hyæna, and hippopotamus. The principal forms which have since become extinct are *Machærodus latidens, Ursus spelæus, Cervus giganteus, Trogontherium cuvieri, Elephas primigenius, E. antiquus, Rhinoceros antiquitatis,* and the great remarkable Russian rhinoceros, *Elasmotherium sibiricum.* Of these latter, the so-called Irish deer (*Cervus giganteus*) is the only one which seems to have survived until the dawn of historic times.

The Pleistocene deposits of North America yield much fewer mammals than those of Europe; but there is a similar mingling of northern and southern types in the central region. It is also interesting to note that one of the commonest skeletons represents the latest known species of *Mastodon* (*M. americanus*). The mammoth, musk-ox, reindeer, elk, and bison are present; bears have now arrived, and the lion may also perhaps be represented; but *Equus* has already become extinct, and there are no traces of the woolly rhinoceros (*R. antiquitatis*), the cave bear, or the hyæna. In the surface deposits of the southern United States, some of the typically South American edentates occur (*Megatherium, Mylodon, Glyptodon*), these having apparently wandered northwards on the emergence of the isthmus of Panama in the early part of the Pliocene period.

North American v. Old World Mammals.

Having thus traced the series of mammalian faunas through the Tertiary formations both of the Old World and of North America, it is interesting to speculate as to where the various elements arose. At the base of the Eocene it is evident that the faunas of the east and the west were essentially identical. As they are traced upwards they gradually diverge.

The first noteworthy difference is the great development of the Condylarthra in America, and the rise in the Eocene of the large specialized Amblypoda, of which only a single genus (*Coryphodon*) has been found in the corresponding fauna of Europe. On the other hand, the still larger ungulates of the sub-order Proboscidea seem to have originated in the Old World and did not reach America until the late Pliocene.

The Perissodactyla—the tapirs, rhinoceroses, and horses—appear to have advanced on a parallel course on the two continents; though in America both the rhinoceroses and horses became extinct at the close of the Pliocene, the former without acquiring the characteristic horn.

Among Artiodactyla, both the Cervidæ and Suidæ seem to have been approximately parallel in their development on both continents, only differing in some minor branches which soon became extinct. The Camelidæ, however, are clearly American throughout, only wandering into the Old World by Asia in the Pliocene. It is almost equally probable that the Bovidæ originated in the Old World.

Among Carnivora, the Creodonta are both American and European; but on the former continent they only pass upwards into the Canidæ, Mustelidæ, and the aberrant cats of the family Nimravidæ, while in Europe they are succeeded not merely by these families, but also by the Viverridæ, Hyænidæ, Felidæ, and Ursidæ. The viverroids and hyænas never reached America, but the true cats and bears arrived in that continent at the close of the Pliocene.

Of the Primates, the primitive lemuroids appeared in the Eocene similarly on both continents; but in North America they soon became extinct, while in the Old World they were followed by the true apes and still have some specialized survivors.

South American Tertiary Faunas.

As already mentioned, South America seems to have been completely separated from North America from the dawn of the Eocene to the close of the Miocene period. Its characteristic mammalian fauna thus appears to have been developed quite independently of that of the northern hemisphere. It may well have received its mammals originally from the same unknown region which furnished the Puerco and Lower Eocene faunas of North America. Here there are undoubted lemuroids and probably ancestral edentates, which soon become extinct, but may well have flourished vigorously on the southern continent, eventually furnishing it with monkeys, sloths, and armadillos. There are also traces of generalized animals, which might have evolved into the characteristic carnivores, rodents, and ungulates which appeared in the later Tertiaries of South America. No equally remote fauna, however, has hitherto been found on the South American continent itself; and the earliest known deposits containing mammalian remains in that area (the *Pyrotherium* Formation and the Santa Cruz Formation of Patagonia) are intimately associated with a marine deposit (the Patagonian Formation), which would be termed Miocene or even Lower Pliocene if it occurred in Europe. The *Pyrotherium* and Santa Cruz mammalia, indeed, have an essentially South American aspect. They include monkeys and hystricomorphous rodents much like those now living in the same region, and several strange sub-orders of Ungulata which flourished there in the later Tertiaries and only became extinct after the dawn of the Pleistocene. They also comprise innumerable well-marked armadillos and sloths, few of them exhibiting more primitive characters than those presented by the same animals of later date. Finally, there is an abundance of small marsupials closely related to the South American opossums and Cænolestidæ of the present day. The only very noteworthy types not found in the later Tertiaries of the country are the large *Pyrotherium,* which seems to have been more or less closely related to the Amblypoda of North America, and the group of carnivorous Sparassodonta, which only appear to differ from the ordinary creodonts in exhibiting a more incomplete change of teeth. The jaguars (*Felis*), wolves (*Canis*), tapirs (*Tapirus*), deer (*Cariacus*), and llamas (*Auchenia*), now characterizing South America, also the mastodons and horses which lived there in the Pleistocene, are, of course, recent immigrants from the north. They passed over the isthmus of Panama as soon as it emerged in the beginning of the Pliocene period, just as the sloths and glyptodonts then wandered northwards. As in other regions, so in South America, the mammals were largest and most numerous during the period immediately preceding the present.

The Australian Tertiary Fauna.

So far as can be judged at present, Australia has been separated from all other existing continental areas since the remote epoch when Prototheria and Metatheria were the dominant mammals. All the existing mammals of that island-continent belong to these two sub-classes, except a few small rodents and bats, which may have crossed the sea by accident, and a species of dog (*Canis dingo*), which may have been brought by the earliest human immigrants. Unfortunately, however, no late Secondary or early Tertiary deposits have hitherto been found in Australia yielding remains of a terrestrial fauna; and nothing is known of the forerunners of the existing types except from quite recent superficial deposits, in which there is evidence of comparatively large monotremes and marsupials closely related to those still surviving. Some of the extinct genera, as might be expected, are partly intermediate between certain existing forms; but the only noteworthy feature of the old fauna, apart from the large size of many of its members, is the presence of ancestral kangaroos in which the disproportion in the development of the fore and hind limbs has not yet become very marked. Except in the specialization of the dentition, the loss of nearly all the successional teeth, and the modification of the limbs, the skeleton of these Australian marsupials does not appear to differ in any essential respects from that of the Creodonta and Condylarthra met with in the northern hemisphere at the dawn of the Eocene period. It is quite likely, therefore, that they are the direct descendants of some unknown families of the latter groups in the southern hemisphere, which did not happen to pass into a higher grade while their limbs and teeth were changing, like the allied types of the northern hemisphere. Very large lizards (*Megalania*) and tortoises (*Miolania*) are associated with the gigantic extinct marsupials in the surface deposits of Queensland and New South Wales; and there are also remains of the emeu (*Dromæus*), one of the two struthious birds which are still characteristic of the Australian region.

The Tertiary Fauna of New Zealand.

New Zealand is still more isolated than Australia. So far as known, it was never inhabited by any land-mammals until they were introduced by man; but, as in the case of Australia, there is apparently no series of Tertiary deposits in this country revealing its successive terrestrial faunas. Quite recently it was the home of the struthious birds of the family Dinornithidæ—the moas of the Maori natives; and these birds attained a development such as has never been equalled by struthious birds elsewhere. They were also associated with large rails, which are now extinct. The diminutive apteryx and weka-rail are the sole survivors at the present day. Among lizards the existing tuatera (*Sphenodon* or *Hatteria*) is noteworthy as being the sole survivor of the order Rhynchocephalia, which had numerous representatives and was very widely distributed on the globe during the early part of the Secondary era.

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