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Article VIII.— ON THE STRUCTURE AND AFFINITIES OF THE MULTITUBERCULATA.

By Robert Broom.

Plates XI and XII.

Since the first discovery of *Plagiaulax* in 1857, there has been an almost continuous controversy as to both the habits and the affinities of the form, and with nearly every discovery of new allied forms the controversy has been continued by new workers. And it is not at all a matter to be regretted, as the more the discussion the sooner are we likely to arrive at the truth.

The very fragmentary remains which had been named *Microlestes antiquus* from the Rhœtic of Germany, and *Stereognathus oölithicus* from the Stonesfield Oolitic of England, had previously been found and though Owen discussed at considerable length their affinities, too little was known to lead to very satisfactory conclusions.

In 1857 Falconer published his first description of *Plagiaulax becklesii* and *P. minor*, giving a most detailed account of the structure of the teeth and jaws, and illustrating his paper by beautiful figures.

"That the genus was a mammal," he says, "admits of no question; that it was a marsupial is inferred for the following reasons, which are given in the order of the directness of the indications:—

"1. The compressed hatchet-shaped last premolar with the serrulated edge and parallel grooving. These characters are confined, among all known mammals, to the marsupial genus *Hypsiprymnus;* the correspondence in grooving is so exact that the number of furrows is the same in the fossils and in the recent species, with which they were compared, namely, seven; the difference, that they are diagonal in the former and vertical in the latter, being trivial and not typical.

"2. The agreement in form, relative size, and direction of the solitary incisor in the fossil rami, with that of the recent *Hypsiprymni.*

"3. The indication of the raised and inflected fold of the posterior inner and lower margin of the ramus.

"4. The form and character of the symphysical suture.

"5. The absence of any character in the jaw or teeth inconsistent with the marsupial indications."

From all the facts he places *Plagiaulax* in a "position between *Hypsiprymnus* and the Phalangers."

As regards the habits, he concludes that "as the Kangaroo rats are

strictly herbivorous, gnawing scratched-up roots, it may be inferred of *Plagiaulax* that the species was herbivorous or frugivorous. I can see nothing," he adds, "in the character of their teeth to indicate that they were either insectivorous or omnivorous."

Owen in his 'Palæontology,' published in 1860, discussed at some length the affinities and habits of *Plagiaulax* and *Stereognathus*. He came to the conclusion that *Plagiaulax* was a "carnivorous Marsupial. It probably found its prey in the contemporary small insectivorous Mammals and Lizards, supposing no herbivorous form, like *Stereognathus*, to have co-existed during the upper oolitic period." This conclusion he based on the mode of implantation of the large incisor, the carnassial character of the large teeth, the reduction of the molariform teeth, the proportions of the jaw and the "broad and high coronoid process, for the adequate grasp of a large temporal muscle," and the condyle placed below the level of the grinding teeth.

In 1862 Falconer replied at length to Owen's criticisms. He shows that *Cheiromys* has a low condyle and slightly changes from his previous position by admitting that "while regarding *Plagiaulax* to have been a phytophagous type in its affinities, we should not be justified in affirming that it may not have been a mixed feeder; it may have fed on buds or fruits, like the Phalangers; or on roots, like *Hypsiprymnus;* or on a mixed regimen of fruits and insects like the Aye-Aye."

In 1871 Owen published his 'Monograph on the Fossil Mammalia of the Mesozoic Formations,' one of the most charming of the many works of the great English master of palæontology. He figures and describes all the then known specimens of *Plagiaulax* and the upper jaw which he describes as *Bolodon crassidens*. The type of *Bolodon crassidens* is a very imperfect specimen and it is not at all remarkable that he did not suspect it to be the upper jaw of *Plagiaulax*. His remark that "had there occurred any Purbeck mandibular specimen allied to the Oolitic *Stereognathus*, it might have suggested a relationship to the maxillary evidences of *Bolodon crassidens*," shows how singularly near to the truth he could come on the slenderest of evidence. Much of the concluding portion of his work is taken up with the reaffirmation of the carnivorous habits of *Plagiaulax* and with replying to those who maintained that it was closely allied to the rat-Kangaroos and was a herbivore. Falconer, Boyd Dawkins, Flower, Krefft, were unanimously against him. None of his contemporaries agreed with him, and even at the present time, I believe, I am the only palæontologist who is convinced that Owen was right. Owen concludes that "the affinity of *Plagiaulax* to *Hypsiprymnus*, and the concomitant assumption of the saltatorial and herbivorous character of the small extinct Mesozoic Marsu-

pial, are not demonstrated in any degree; the demonstration of the carnivority of *Plagiaulax* appears to be much more ample."

In 1879 Marsh described *Ctenacodon serratus*, a form allied to *Plagiaulax* from the Upper Jurassic of North America; and in 1880 he was able to give further details from new material. He proposed the name *Allotheria* for the order represented by *Plagiaulax* and *Ctenacodon*. While Marsh admits that the group may represent a suborder of the Marsupialia, he rather inclines to the view that "it cannot be satisfactorily placed in any of the present orders." In 1887 he described a number of other specimens of *Ctenacodon* and a number of upper jaws which he called *Allodon*. He admits the possibility of the European *Bolodon* being founded on the upper jaws of *Plagiaulax*. He believes the dental formula of *Allodon* to be i3, c0, p5, m2. He considers that the facts now seem to prove that the Allotheria are Marsupials, and that "among the various existing Marsupials, the Rat-Kangaroos, (Hypsiprymnidae) appear to be nearest to the oldest known forms represented in the order Allotheria." In a short note published in 1891 Marsh states his belief in the strong probability of *Bolodon* being founded on the upper jaw of *Plagiaulax*. Between 1889 and 1892 he published three papers giving figures of a large number of remains of Cretaceous Multituberculates, but in most cases the remains are isolated teeth and bones and it is difficult to be at all sure of the association. Still the remains are extremely important.

In 1884 Cope published an important paper on 'The Tertiary Marsupialia' in which he discussed the structure of *Polymastodon*, *Ptilodus*, and *Neoplagiaulax*, and their relations to *Tritylodon*, *Plagiaulax*, *Ctenacodon*, and *Thylacoleo*. He regards all these types as belonging to a suborder of the Marsupialia, to which he gives the name Multituberculata. He discusses briefly the habits of *Ptilodus* and *Thylacoleo*, and while he says that "it is difficult to imagine what kind of vegetable food could have been appropriated by such a dentition as that of *Ptilodus* and *Thylacoleo*" he admits the possibility of the large teeth having been for cutting "off pieces of fruit and other soft parts as suggested by Professor Flower," but considers it as "clearly inadmissible" that they could have been herbivorous in the manner of existing kangaroos. He makes the suggestion that the diet of *Ptilodus* "may have consisted of small eggs which were picked up by the incisors and cut by the fourth premolars," while *Thylacoleo*, he thinks, may have fed on "larger eggs, as those of the crocodiles, or even the weaker living animals."

Owen in 1884 described the anterior part of a skull from the Lower Jurassic beds of Basatoland, S. Africa, under the name *Tritylodon longaevus*. This type and only known specimen consists of a somewhat rodent like

snout with, on each side, a large rounded incisor followed by a smaller one, and then after a long diastema as in rodents certainly six, probably seven, multituberculate teeth with tubercles arranged in 3 rows not unlike the teeth of *Stereognathus*. Owen regarded the specimen as a mammal allied to the earlier known English type. For many years no one ever questioned the fact of *Tritylodon* being a mammal, but in 1894 Seeley advanced the view that it was Cynodont reptile. In 1905 I endeavoured to show that the arguments advanced by Seeley were invalid, and that *Tritylodon* was a true mammal whose "affinities seem to be more with the Monotremes than with the higher forms."

With regard to the name to be used for the group we have the choice of the two terms Allotheria and Multituberculata. Were the matter to be decided by priority there is no question that Allotheria must be used; but rules of nomenclature do not seem to demand such strict adherence to priority as in the case of genera and species, and there is the serious objection to Allotheria from the termination "theria." The mammals are subdivided by Gill and Huxley into subclasses for which the termination "theria" has been used, and as I hope to show that the Multituberculates are a subdivision of the *Prototheria*, it would seem improper to use the term Allotheria as an Order of the Prototheria. The name Multituberculata is moreover well established and very appropriate.

In 1888 Osborn published his monograph on 'The Structure and Classification of the Mesozoic Mammalia' in which he reviews all that has previously been known of the Multituberculata and gives much new information on the type specimens, most of which he had personally examined. He describes a very fine, nearly perfect upper jaw of *Bolodon*, of which he gives the dental formula as i2, c0, p3, m4. He regards the Bolodontidæ as forming a separate family of the Multituberculata. While placing the Multituberculata with the Marsupials, he admits the possibility of their being related to the Monotremes, and even goes so far as to say "whether they are to be considered as a branch of the monotreme or of the marsupial stock is an unsettled question."

Between 1891 and 1893 Osborn published three other papers dealing with the Multituberculates in which he deals chiefly with the Cretaceous genus *Meniscoessus*.

Till 1888 every writer, so far as I am aware, agreed that *Plagiaulax* and its allies were Marsupials, though Osborn expressed doubts as to their being Diprotodonts, and all except Owen agreed that *Plagiaulax* was not a carnivore. In this year Poulton discovered that *Ornithorhynchus* has in the young condition teeth which have irregular crowns slightly suggesting the molars of *Microlestes* and *Plagiaulax*, and Cope in commenting on the discovery

said, "it renders it extremely probable that the *Multituberculata* are *Monotremata*, and not *Marsupialia*." Thereafter he divided the Prototheria into three suborders, Protodonta, Multituberculata, and Monotremata.

Since 1888 the authorities have been divided, some holding that the Multituberculata are Prototherians, others that they are Marsupials, neither side being able to supply very much evidence in defence of their position.

In 1909 the first good skull of a Multituberculate was described by Gidley, who concluded from the many resemblances to the appearances presented by the typical Diprotodonts that *Ptilodus* and the other allied forms are Diprotodont Marsupials. This conclusion was accepted by most, including Osborn, and Scott.

Gregory in his 'Orders of Mammals,' published in 1910, while agreeing that the "Multituberculates" are Marsupials, is not convinced that they are true Diprotodonts for the following reasons:—"(1) because so far as indicated by Marsh's *Allodon fortis*, the enlarged incisor in Multituberculates is i^2, whereas in Diprotodonts it seems to be i^1; (2) because the Multituberculates differ greatly from the true Diprotodonts in the character of the cheek teeth; because homoplastic resemblances, especially among related groups, is so frequently shown in the dentition." In the table that he gives on p. 229, however, he derives the Multituberculates quite independently of all the other mammals from a Triassic Prototherian ancestor.

In 1910 I published a paper 'On *Tritylodon* and the relationships of the Multituberculata,' in which I argued that there were strong reasons for doubting their being Diprotodont Marsupials and no conclusive evidence of their being Marsupials at all had been advanced by Gidley. It was pointed out that the Diprotodont Marsupials as we know them today have sprung from a Polyprotodont ancestor, and that there is good reason for believing that the Polyprotodonts

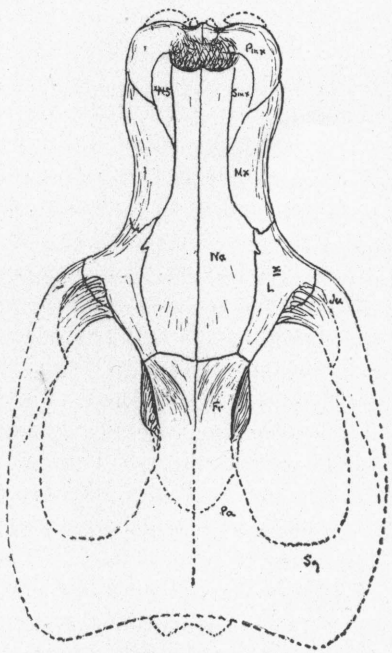

Fig. 1. Skull of *Tritylodon longævus* Owen. $\times \frac{2}{3}$. The front portion is very slightly restored from the only known specimen. The back portion is entirely hypothetical.

are not older than Cretaceous times, and that hence the Multituberculates, which can be traced back to Triassic times, cannot be at all nearly related. The conclusion to which I came was that "in the present state of our knowledge it seems wisest to leave the Multituberculata as a distinct independent group with no very near affinities with the living Monotremes, Marsupials or Eutherians." I regarded *Tritylodon* as in habit a root-eating animal.

As regards the structure of *Tritylodon* the following are some of the more important characters seen in the only known specimen:—The dental formula is probably i3, c0, p4, m3; the molariform teeth have three rows of cusps and the lower teeth have worked against them with an anteroposterior movement; the lacrymal is very large; the frontal region of the skull very narrow; there is a large septomaxillary, and evidence of at least a rudimentary internasal process of the premaxillary; the nasal is very long and very wide behind.

I have given a restoration of the skull showing what appear to me to be the probable proportions of the posterior part.

Plagiaulax *Falconer* and **Ctenacodon** *Marsh.*

Most of the known specimens have been very fully figured, and until further specimens are obtained little more can be made out with certainty. It may, however, be worth discussing the possibility of *Bolodon* being founded on the upper jaw of *Plagiaulax.* This possibility was suggested by Marsh and by Smith Woodward but by most *Bolodon* is regarded as belonging to a different family. Still it seems remarkable that a number of mandibles of *Plagiaulax* are obtained in a certain locality with no trace of any maxillary remains, and in the same locality a number of maxillaries of *Bolodon* with no trace of any mandibles.

In the case of the American Upper Jurassic genus *Ctenacodon,* a near ally of *Plagiaulax,* we have an upper jaw which Marsh quite confidently refers to the same genus, and a second type of maxilla which has been named *Allodon,* which, though different, is clearly allied, and I think it belongs to the same family, but if we assume that *Allodon* is a Plagiaulacid, *Bolodon* must also be.

The third well known upper jaw of manifestly the same type as *Bolodon* is Cope's *Chirox.* It has three premolariform teeth and three more complicated molars, and I think there can be very little doubt that the 6 teeth of *Chirox* are homologous with the posterior 6 teeth of *Bolodon.* Gidley's discovery of the complete skull of *Ptilodus* shows that *Chirox* is founded on the upper jaw of *Ptilodus,* and renders it extremely probable that *Bolodon*

is founded on the upper jaw of *Plagiaulax*. If we assume this we must regard the Plagiaulacids as having at least 3 molars in the upper jaw or we have to consider that *Bolodon* has 5 premolars as has been done by Marsh. Now we know of no recent mammals, if we except a few extremely modified types such as *Orycteropus* and *Tatu*, that have more than 4 premolars, and as even the Cynodont reptile *Diademodon* has 4 premolars it seems so extremely probable that primitive types such as *Tritylodon* and *Bolodon* which have 7 molariform teeth have 4 premolars and 3 molars that one would require very positive evidence to the contrary to believe otherwise. So far as I am aware the only reason why such a view is not universally held is that in the lower jaw there are only two molariform teeth, and the grooved tooth in front of the two manifest molars in *Plagiaulax* and allied genera looks like the grooved tooth in some Diprotodont marsupials which is manifestly a premolar. When it was believed that *Plagiaulax* was allied to *Hypsiprymnus* as was held by Falconer and so many others it was natural to assume that the large grooved teeth in the two genera were homologous, but even if it could be proven that the Multituberculates were Marsupials there would be quite as good reason for comparing the *Plagiaulax* tooth with the grooved tooth in *Abderites* where it is certainly the 1st molar. But as in my opinion the grooved teeth of *Hypsiprymnus*, *Abderites*, and *Plagiaulax* have all been quite independently evolved the nature of the teeth in these other genera need not concern us in our study of the *Plagiaulax* problem. There seems to me to be only two possible interpretations of the dental formula of *Plagiaulax* (Bolodon) — either that the formula is $\frac{p4}{p2}, \frac{m3}{m3}$ or $\frac{p3\ m4}{p1\ m4}$ and of these the former seems much the more probable. If we assume this to be the correct formula for *Plagiaulax* the complete dental formula for the more primitive *Plioprion* would probably be $\frac{i3}{i1}, \frac{c0}{c0}, \frac{p4}{p3}, \frac{m3}{m3}$ and this is probably also the formula for *Ctenacodon*, though not improbably it may have an upper canine.

Ptilodus *Cope.*

By far the best known of the Multituberculata is the genus *Ptilodus* Cope, and most of our knowledge we owe to Gidley, who has described a beautiful skull and a number of the other parts of the skeleton which are preserved in the United States National Museum, Washington. Gidley's description leaves little to be desired, and though on one or two points I differ from him, both in regard to the interpretation of structures and as to the affinities of the group, I feel I must express my views with considerable hesitation. Still, as I incline to differ from him in one or two points, I

think it well to state those points so that future workers may have their attention called to them.

The skull has been very satisfactorily illustrated, and shows comparatively little that is not seen in the figure. There is one little point to which attention might be called. The back of the lower jaw, which is shown in the side view of the skull, has the coronoid region supported by plaster, and if the figure be copied as it stands, and as has been done by Scott in his recent book, a misleading idea is given of the shape of the coronoid process. Gidley's figure "b" shows correctly the shape of the coronoid process, as does also his text figure (fig. 8).

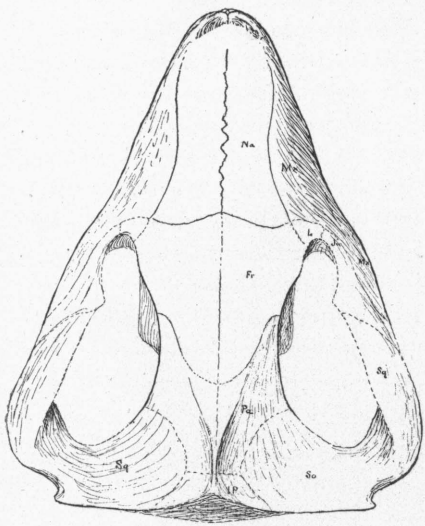

Fig. 2.

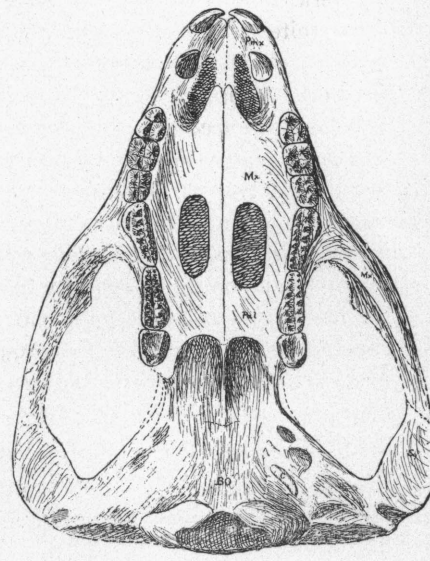

Fig. 3.

Fig. 2. Skull of *Ptilodus gracilis* Gidley. Slightly restored. Slightly less than $\frac{2}{1}$.
Fig. 3. Skull of *Ptilodus gracilis* Gidley. Palatal view slightly restored. Nearly $\frac{2}{1}$.

Gidley has correctly described the large nasal and even in the figure he gives the sutures are roughly indicated. The frontal is moderately large and in the restoration of the skull which I give, it will be seen to be partly overlapped behind by the forward extention of the lateral parts of the parietals.

The sutures between the squamosals, parietals, and interparietals cannot be made out, but are probably as I indicate.

The zygomatic arch is formed by a large anterior process of the squamosal and a well developed posterior process from the maxilla, with possibly a

relatively small jugal between. The exact limits of these elements in the arch cannot be seen with certainty as both arches are crushed and imperfect. There can, however, be no doubt that the maxillary and squamosal portions of the arch are both large, and I do not think that the jugal enters the glenoid facet.

The under side of the skull shows one or two points of interest. In front of the palatine portion of the maxilla there is evidently a very large anterior palatine foramen, and the front part of the maxilla is curiously excavated as if it retained a large nasal floor cartilage. The region of the skull between the posterior nares and the basioccipital is unfortunately slightly crushed, and it is extremely difficult to be at all certain of the structure. Pretty manifestly the vomer extends backwards some distance behind the edge of the secondary palate. The pterygoids, or transpalatines, are probably lost. In the figure I give I have indicated what looks like two large foramina in the alisphenoid region. Between the front of the alisphenoid region and the occipital condyle is what I believe to be the cast of the cochlea. I think there can be little doubt that this determination is correct, and also that the cochlea is of the typical monotrematous uncoiled form. The occipital condyle is not unlike the condyle of the marsupials or the monotremes. One very important point is that there appears to be only one foramen for the XIIth nerve. With regard to the tympanic region little can be said with certainty owing to the crushed and imperfect condition of the specimen, but there appears to me to have been no alisphenoid bulla, the structure of this region probably being not unlike that in *Ornithorhynchus*. In my opinion it cannot have been like that of any marsupial.

I have little to add to Gidley's description of the postcranial skeleton except in regard to what he believes to be the pelvis. The bones look so like ilia and ischia that I feel sure nine out of every ten who examine the specimen will agree with Gidley and it is therefore with considerable hesitation that I venture to give it as my opinion, that more probably they are the scapulae and coracoids.

In the specimen as preserved there are two girdles lying almost side by side and the right femur lies by the side of one, the whole being strikingly like the two sides of the pelvis with the femur almost in articulation with its corresponding acetabulum. A careful examination of the two girdles shows, I think, quite conclusively that the one is the right and the other the left side of either the pelvis or shoulder girdle. For convenience in discussing the structures I shall refer to the one figured by Gidley as girdle A and the other one which he has not figured as girdle B.

I have given three figures of girdle A and two of girdle B, drawing them natural size and as carefully as possible with camera lucida. Girdle

A shows an upper long moderately straight bone which has at its lower end an articular cavity. Continuing downwards the upper bone is joined to a

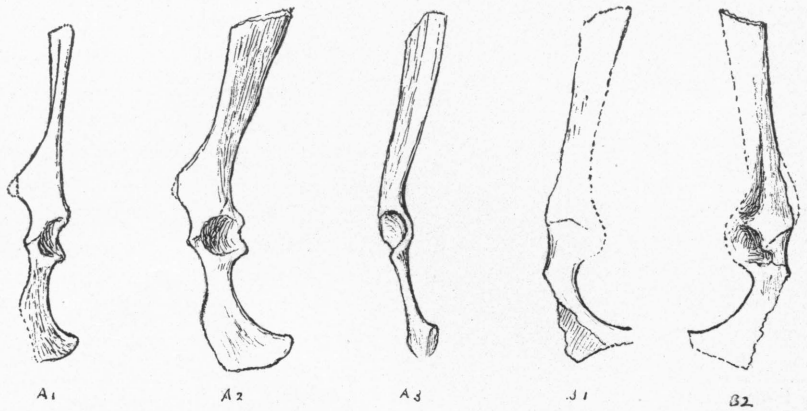

Fig. 4. A1, A2, A3, views of Girdle A. B1, B2, Views of Girdle B. All nat. size.

much shorter and much curved lower element. In front of the upper bone there is a somewhat folded anterior process.

If we look upon the girdle as is done by Gidley as the pelvis girdle A must manifestly be of the left side, and the pubis we must regard as lost. What would correspond to the pubic border of the bone is slightly imperfect in the specimen and this girdle alone would hardly be sufficient to settle the question whether a pubis had been attached and broken off. We may regard it as quite certain that the very curved border of the lower element gave no attachment to any other bone.

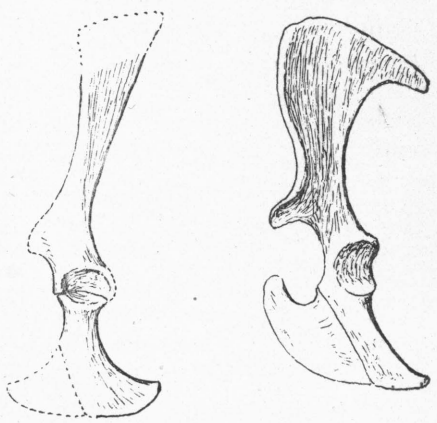

Fig. 5. Supposed shoulder of girdle of *Ptilodus gracilis* Gidley for comparison with the shoulder girdle of *Ornithorhynchus anatinus* Shaw.

Girdle B is slightly less perfectly preserved and the lower element has been slightly crushed and displaced. When an accurate drawing of the lower element of this girdle is laid on a drawing of the lower element of girdle A it is quite manifest that whatever the element is in the one it is the same in the other. If we assume that it is the ischium of girdle A then girdle A must be the left pelvis

and girdle B the right. If now we look at the drawings of girdle B assuming that the long element is the ilium and the short the ischium we require to fit the pubis on the side away from the curve of the supposed ischium, but while the specimen is a little imperfect and crushed it shows this, I think, at least clearly that no pubis or other element has been attached near the articular cavity on the side away from the ischial curve. The surface here of the bones is smooth and rounded. It does look as if there might be a small element intercalated between the upper and lower bones by the side of the articular cavity but this cannot possibly be the pubis and appears to be merely a fractured portion of the upper element. In neither girdle in the specimen as preserved was any portion of what might be regarded as a pubis present though the rest of the girdle is well preserved.

The conclusion to which I come is that the girdles are the right and left shoulder arches. The long element I believe to be the scapula and the curved lower one the coracoid. I give a figure slightly restored of the girdle as I interpret it. The anterior flattened process is, I believe, the acromion. The glenoid cavity is large and rounded and the scapular articular surface has been extended backwards a short distance. Though this backward development of the articular surface is lost from specimen A Gidley has indicated it in dotted line and in specimen B it can be still fairly well seen.

If the whole girdle be compared with the shoulder-girdle of *Ornithorhynchus* it will be seen that the structure of the two agrees fairly closely. The scapula of *Ornithorhynchus* is very curiously twisted to suit the peculiar digging and swimming habits of the animal. In *Echidna* there is much less twisting of the scapula and in the Anomodonts such as *Dicynodon* the scapula is a straight flattened bone not at all unlike the scapula of *Ptilodus*.

The element which I regard as coracoid is not at all unlike the coracoid of *Ornithorhynchus* and very likely there was a distinct precoracoid bone as in the monotremes.

Many years ago Marsh figured some bones which he regarded as probably belonging to one of the Multituberculates and named by him *Camptomus amplus*. These include the lower end of a scapula with an articular facet for a distinct coracoid and a very much more remarkable bone which he refers to the same species and which is manifestly correctly identified as an interclavicle. As a large number of the Cretaceous remains which he describes from the same beds are those of Multituberculates it seems probable that the association of at least this interclavicle with a Multituberculate is correct. Any animal which had an interclavicle like the one figured must have had a large coracoid articulating with the sternum and even if we did not know that an interclavicle of this type had been found we could have predicted that any mammal which had a large coracoid articulating with the sternum was likely to have an interclavicle.

The association of the femur with what I regard as the shoulder girdles is, I believe, purely accidental. The few bones of the skeleton of *Ptilodus* were found separate and mixed up in the matrix and there is no trace of the sacrum.

Polymastodon *Cope.*

Polymastodon, though described by Cope as early as 1878, from a fragmentary skull and lower jaws, and though known later by many other fragmentary specimens, has until now never been very satisfactorily known. The teeth are usually well preserved, and have been very fully described. There are two incisors in the upper jaw, a large pointed one which is proba-

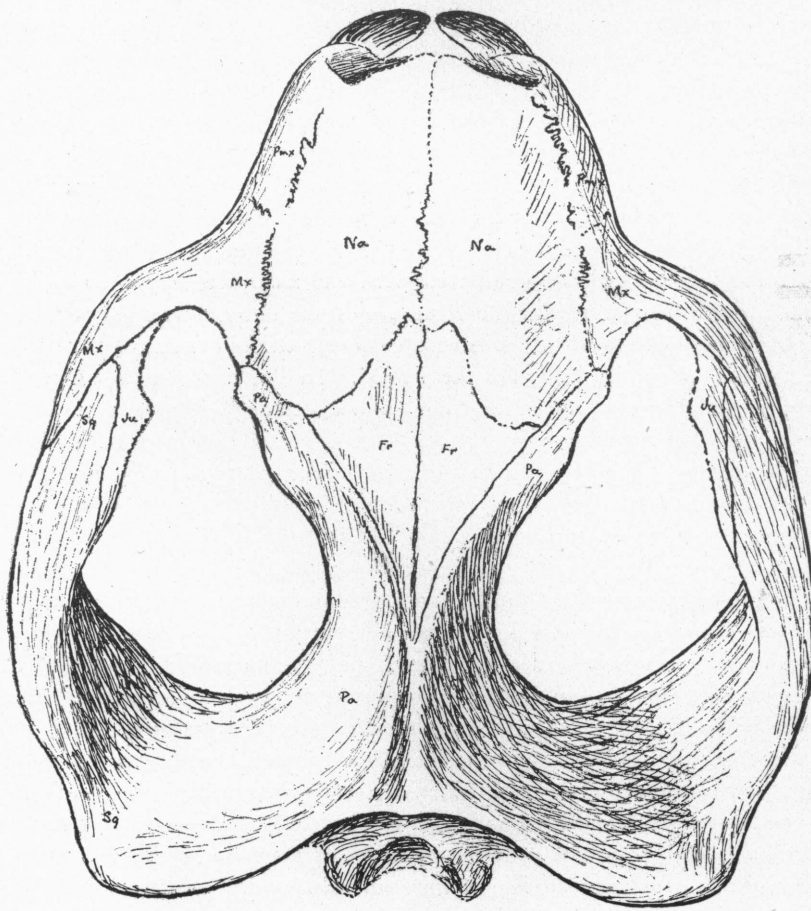

Fig. 6. Skull of *Polymastodon taoensis* Cope. $\frac{2}{3}$ nat. size.

bly i2, and a small pointed tooth behind it which is probably i3. There is no canine and the post-canine teeth are represented by two large multituberculate molars and a small tooth with a flattened edge and two roots, which is situated in front of the larger tooth. In the lower jaw there is a single incisor and three molars, of which the first is a small, flattened tooth like the small tooth above, and the two posterior molars resemble somewhat the upper teeth, but differ in having two rows of cusps instead of three. A number of skeletal remains have been figured and described by Cope, but there is some doubt as to whether these belong to *Polymastodon*, one bone at least being almost certainly not of *Polymastodon*.

The recent expedition of the American Museum to the Puerco beds of New Mexico was fortunate in finding a number of fresh specimens of *Polymastodon*, the most important of which is nearly a complete skull found by Mr. W. J. Sinclair about two miles east of Ojo Alamo. The specimen though found broken up in small fragments, has been fitted together by Mr. W. Granger and forms a skull complete except for the basioccipital, basisphenoid and some other portions of the base. The upper surface, though imperfect in a few minor details, shows almost all the sutures clearly in the greater portion, and thus reveals for the first time the structure of the skull in a Multituberculate.

Professor Osborn and Dr. Matthew have done me the great honor of asking me to describe this new skull.

The skull is unusually short and broad, the orbits are very small and not separated from the temporal fossa, which is extremely large. The zygomatic arch is unusually stout. The squamosal passes well back and the glenoid cavity is probably in a line with the front of the basioccipital, the articular region thus being much further back than in typical mammals.

The nasals are very broad both in front and behind, but somewhat broader behind. They articulate with the frontal and the parietal posteriorly, and laterally with the maxilla and premaxilla. The premaxilla is well developed and not unlike that of a rodent, it having a long suture with the maxilla posteriorly and a long suture with the nasal above. There appears to be a distinct palatine process to the premaxilla, though this region is unfortunately imperfect and the extent of the palatine process cannot be made out, nor the size of the anterior palatine foramen.

I fail to find any septo-maxillary, though a loose one may readily have been present and lost.

The maxilla is unusually large, forming not only the greater part of the palate but much of the side of the face and about two-fifths of the zygomatic arch. Above, it extends up to the nasal and also meets the parietal, completely shutting out the frontal from the orbital margin. It probably forms

most of the front of the orbit, and certainly forms its middle portion. The zygomatic portion has a long articulation with the squamosal, completely shutting out the jugal from the lower border of the arch. The palatal portion is moderately entire, there being only a small oval vacuity.

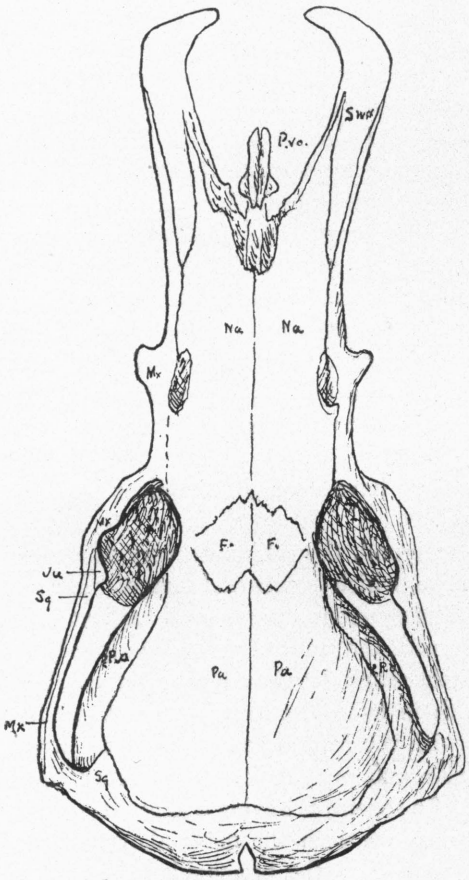

Fig. 7. Skull of young *Ornithorhynchus anatinus* Shaw. $\frac{3}{2}$ nat. size. Modified from v. Bemmelen.

The jugal is unusually small and rests on the upper border of the zygomatic portion of the maxilla and squamosal. Though imperfect, it must be practically as I have restored it. The slender back portion is perfectly preserved, and is seen to be merely a narrow splint of bone. The front portion probably had a postorbital process and certainly did not reach far round the anterior orbital margin, as shown by another specimen.

The frontal bone is quite unlike that known in any other mammal, being completely shut off from the orbit by the parietal and the nasal, and in being unusually small. The two together form a diamond shaped area on the top of the skull, the front two sides being bounded by the nasals and the posterior two by the parietals.

I can find no trace of a distinct lacrymal bone. If one occurs, it must be very small and situated low down within the orbit.

The parietal is a large bone which forms the whole of the inner margin of the temporal fossa. In *Polymastodon* the brain is exceedingly small and the parietal region is narrow and the bone so exceedingly thick that no indication of the size of the brain cavity is given by the upper view. The wide interorbital region is probably entirely occupied inside by the nasal

cavity and air sinuses. The back part of the parietal is indistinguishably fused with the squamosal and interparietal, the whole bone being very massive. Anteriorly, the parietal sweeps forward to the orbital region, articulating with the frontal, nasal and maxillary.

The squamosal is extremely large and besides forming a large part of the cranium proper, it has a powerful anterior zygomatic portion which meets the maxilla in front and on whose upper anterior portion rests the small jugal.

The occiput is very large and broad, but in only one place can any trace of a suture be seen. This is a transverse suture dividing what is probably the lateral portion of a large interparietal above from what may be opisthotic below it.

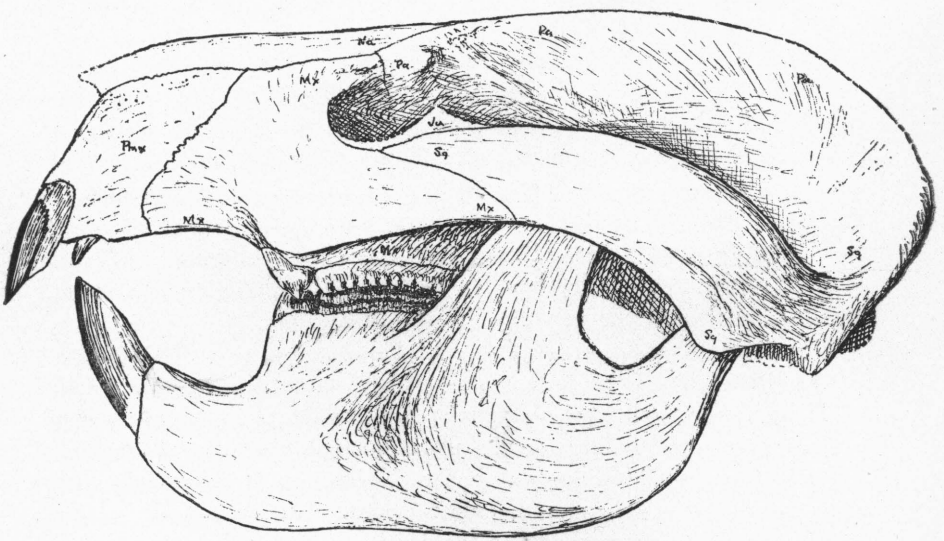

Fig. 8. Skull of *Polymastodon taoensis* Cope. $\frac{2}{3}$ nat. size.

The mandible of *Polymastodon* has previously been pretty well known though to one or two points may attention specially be called. By the large majority of writers the "inflected angle" of the Multituberculates has been brought forward as a Marsupial character. As I pointed out in a previous paper when I had only figures to go by I could not persuade myself there was anything but a very remote resemblance in this character between Marsupials and Multituberculates. In all Marsupials there is a well marked angle to the jaw which passes backwards, downwards and inwards and ends in a sharp process. In some it passes backwards behind the plane of the articulation: in some it is only slightly inflected. In neither

Plagiaulax, Ptilodus, nor *Polymastodon* is there any proper angle at all. There is an inflected border or ridge lying along part of the posterior half of the inside of the jaw, but one has only to compare a jaw of *Ptilodus* or *Polymastodon* with that of any Marsupial to see how very unlike they are. There is no doubt that the borders are homologous but owing to the ex-

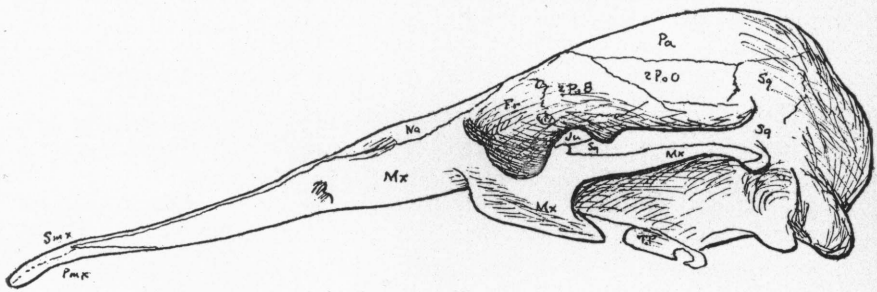

Fig. 9. Skull of young *Ornithorhynchus anatinus* Shaw. $\frac{3}{4}$ nat. size. Modified after v. Bemmelen.

tremely backward position of the articulation in the Multituberculates the internal pterygoid muscle has to be inserted further forward on the jaw. The condition of affairs in the Multituberculates is really essentially more like that in *Ornithorhynchus.*

The two jaws were rather loosely attached at the symphysis.

Affinities of the Multituberculata.

Though three well marked types of Multituberculates are known only two are represented by fairly good skulls and the third by a snout.

Tritylodon the oldest known type represented by more than isolated teeth is unquestionably also the most primitive in structure. It differs from Marsupials very markedly in the dentition — the enlarged i2, and the seven multitubercular molariform teeth, in having a well developed septomaxillary, and from most in the large size of the lacrymal. It resembles Monotremes in having a large septomaxillary, and differs from them in possessing a large lacrymal, but little can be done in the way of comparison as only the preorbital part of skull of *Tritylodon* is preserved, and the preorbital part of the skull of both known Monotremes is extremely specialised. It is almost as difficult to institute a comparison with the Cynodonts, the evidence so far as it goes seems to show that *Tritylodon* is not very nearly related to the Cynodonts, and I am of opinion that when a good skull is obtained it will prove *Tritylodon* to be a mammal more similar to living monotremes and marsupials than to the typical Cynodonts.

Plagiaulax and *Ptilodus* are doubtless members of a common family, and though *Ptilodus* occurs so very much later in time it differs from the older form surprisingly little. The large majority of palaeontologists from Falconer and Owen to Gidley have regarded the Plagiaulacidae as a family of the Diprotodont Marsupials. Practically the only arguments advanced by the early writers in favour of this view were the resemblance of the large cutting tooth in the lower jaw to the last premolar in *Hypsiprymnus* and other Rat Kangaroos, and the fact that the Plagiaulax mandible has a somewhat inflected angle. Gidley advanced the additional argument from the skull he discovered of the marsupial-like perforations of the palate. As I pointed out in my previous paper none of these arguments is of very much weight. Perforations of the palate are found in *Macroscelides* and *Erinaceus* among the Eutheria. The large grooved tooth of the Plagiaulacids is much more likely to be the 1st molar than the last premolar, and to be thus not homologous, but the result of convergence. And the inflected angle of the Plagiaulacid jaw is so very unlike the angle of the jaw of marsupials that one hesitates to call it even convergence. The Plagiaulacids might almost be said to have no proper angle to the jaw at all but only an inflected border which is not produced backwards to form an angle.

The zygomatic arch of *Ptilodus* is unfortunately too much fractured to render the structure quite certain. There can however I think, be no doubt that the maxilla and the squamosal form the greater part. In the restoration I give I have represented the jugal as separating the maxilla from the squamosal, but it is quite possible that this middle portion is either maxilla or squamosal and that the jugal is only on the upper side of the arch as in *Polymastodon*.

The most important characters in *Ptilodus* as pointing to the affinities are the uncoiled cochlea and the presence of a large coracoid.

Polymastodon, though later in time than *Plagiaulax* and considerably specialized, throws much additional light on the affinities of the group. The skull is quite unlike that of any other known mammal. Possibly some of the peculiarities are due to specialization. For example we find in some rodents a very marked reduction of the jugal with an increase in size of the zygomatic portion of the maxilla. In *Fiber* the maxilla nearly reaches the squamosal and in *Castor* and others the lacrymal is small and mainly situated within the orbit. We even find in *Castor* the frontal partly enclosed behind by the parietals. So that we have altogether in rodents quite a number of resemblances to characters found in *Polymastodon*. Most likely they are all due to convergence, though the suggestion has been made by Ameghino that the Rodents have sprung from the Multituberculates, and one would like to hesitate before denying the possibility.

In the following table I have given the principal Multituberculate characters, and the occurrence of similar characters in the Cynodontia, the Monotremata, the Marsupialia and Eutheria.

Multituberculate characters seen in other groups.

Multituberculata	Cynodontia	Monotremata	Marsupialia	Eutheria
1. Septo maxillaries (*Tritylodon*)	×	×	–	rarely (*Dasypus, Tatu*)
2. Large nasals	×	×	×	rarely (*Hystrix*)
3. Lacrymal large (*Tritylodon*)	×	–	×	most
L. small or lost (*Polymastodon*)	–	×	–	many rodents
4. Frontals small	×	×	–	–
5. Parietals overlapping frontals at side	–	×	–	–
6. Jugal small on upper side of arch (*Polymastodon*)	–	×	–	–
7. Maxilla meeting squamosal	–	×	–	some Insectivores
8. Perforated palate	–	–	×	some Insectivores
9. Palatine process of premaxilla	× (*Lycognathus*)	× (young)	×	×
10. Large vomer	×	×	×	most
11. Uncoiled cochlea	×	×	–	–
12. 3 incisors	rarely (*Lycognathus*)	–	Diprotodonts	most
13. 2nd incisor largest	–	–	–	rarely
14. Posterior molars multituberculate	–	×	–	rarely (convergence)
15. Single foramen for XIIth nerve	×	–	–	×
16. Mandible with small inflected border	–	some suggestion of inflection in *Ornithorhynchus*	marked inflected angle of diff. type	inflected angle in many rodents
17. Well developed coracoid	×	×	× (foetus)	–
18. Interclavicle (*Camptomus*)	×	×	–	–

When the known characters of Multituberculates are looked for in other groups it at once becomes manifest that the nearest affinity is with the Monotremes, and in a number of characters the agreement is so striking as to suggest that the affinity is pretty close. There is however one difficulty that arises in that *Polymastodon* comes much nearer to the Monotremes than does the very much more primitive *Tritylodon.* We might assume that the Monotremes and Multituberculates branched off independently from the Cynodont reptiles, and that all the resemblances are due to convergence; but against this is the extreme improbability of the articular and quadrate becoming converted into auditory ossicles of a similar type independently in two lines. But if we agree that the Multituberculates and Monotremes

had a common ancestor as late as Rhœtic times, when did the separation take place?

The structure of the zygomatic arch in *Polymastodon* is very remarkable. It is not primitive, for nothing exactly like it occurs in any of the Therapsida, and all known Cynodonts have well developed jugals. From what we see in rodents we may infer that the zygomatic process of the maxilla has become greatly developed in connection with the great specialisation of the posterior molars, and rodent-like movements of the jaws. But how is the similar structure of the arch in Monotremes to be explained? Presumably by their being descended from an ancestor which had a similar type of molars, and a rodent-like movement of the jaws. If this be so either the Monotremes have been descended from a primitive type perhaps allied to *Tritylodon* and by convergence acquired structures such as are seen in *Polymastodon*, or they may have sprung from a later type of Multituberculate.

Marsh has shown that in Cretaceous times there were many Multituberculates with teeth not unlike those of *Polymastodon* and not improbably in Middle Jurassic times there may have been Multituberculates which while retaining the large septomaxillaries of *Tritylodon* had by the adoption of some change of diet taken on a greater development of the posterior molars, and acquired a jugal arch like that of *Polymastodon*, with increase in size of the parietals and reduction of the lacrymals. From such an ancestor the living Monotremes may have sprung. I do not place any great weight on the pattern of the rudimentary molars of *Ornithorhynchus*, but it is certainly remarkable that in *Polymastodon* there are only two large molariform teeth, and even in the Plagiaulacids only the last two in the lower jaw are multituberculate, and that in *Ornithorhynchus* there are also only two large molars retained.

The conclusions which seem to me most probable are (1) that in Upper Triassic times the ancestral mammal arose from a generalised Cynodont; (2) that very early there branched off from the main line which gave rise to the Protodontia, the Trituberculata, the Triconodontia, and ultimately the Marsupials and Eutherians, a side branch of small herbivorous forms which losing their canines and taking on a peculiar specialisation of the incisors and molars started the line of the Multituberculates; (3) that the early Multituberculates were mainly herbivorous, the larger forms being root-eaters, and the smaller probably like mice practically omnivorous; (4) that later on some small types become mainly insectivorous and the lower premolars and 1st molar became specialised as cutting-teeth e. g. *Plioprion*; (5) that a further development along the same line resulted in the development of small carnivores such as *Plagiaulax* which probably

fed on lizards[1]; and (6) from a Middle Jurassic herbivorous Multituberculate there probably arose the line which after considerable specialisation and degeneration resulted in the Monotremes.

NOTE.— At the time of Dr. Broom's departure for Europe, when this article was in galley proof, I was engaged in the preparation of a specimen of a Plagiaulacid obtained from the Puerco formation of New Mexico last summer. The specimen consisted of the posterior portion of the skeleton and included two elements which appeared to be the two halves of the pelvis although at the time Dr. Broom last saw them they were not sufficiently removed from the matrix to be certain of their identification. Enough was exposed though to assure him that the bones were the same elements as those of the National Museum specimen, which he had figured as scapula and coracoid, whether they pertain to the shoulder or to the pelvic girdle. Further preparation has shown that these bones, without question, belong to the pelvis but to such an unusual pelvis that a misinterpretation based upon less complete and more poorly preserved material might readily be made. This note is inserted at Dr. Broom's request. A description of this new American Museum specimen will be published later.— WALTER GRANGER.

[1] When three years ago I suggested that *Plagiaulax* was a carnivorous modification of the Multituberculata specialised for killing and eating lizards I was not aware that Owen had made exactly the same suggestion though I knew that Owen regarded *Plagiaulax* as a carnivore.

POLYMASTODON TAOENSIS *Cope*.
⅔ nat. size. Am. Mus. Nos. 748 and 16321.

Polymastodon taoensis *Cope.*
$\frac{2}{3}$ nat. size. Am. Mus. No. 16321.