

MESOZOIC MAMMALIA. I. AMERICAN TRICONODONTS: PART 2.

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SYSTEMATIC DESCRIPTIONS.

*Lower Jaws.*⁶

Genus *Phascolodon* Nov.

*Phascolodon gidleyi*⁷ sp. nov.

(See Fig. 8.)

Holotype Number 2703 United States National Museum. Morrison Formation, Quarry 9, Como Bluff, Wyoming.

The only known specimen is a portion of a left mandibular ramus. One fragment, with two teeth, one badly broken, is still in the matrix, with the outer aspect exposed. Another piece, which, from the fractured surface as well as from the manuscript notations of Professor Marsh, originally formed a posterior continuation of the former, is free of the matrix and contains two perfect molars.

Dentition: The teeth preserved are all molars and include the four last ones in the original series. The most anterior of these four is rather the largest, hence, since M_1 is never the largest molar in related forms, we may conclude that it was preceded by other molars not preserved. Judging by *Phascolotherium* and *Amphilestes*, it seems probable that the present genus had five or six molars.

The first tooth preserved, which is probably the second or third molar, is broken, but was similar to, although probably somewhat larger than, the one which follows.

The second tooth preserved, the antepenultimate molar, consists of three cusps as in other triconodonts. Cusp *b* is the largest and is rather blunt, somewhat compressed, with a gibbous outer surface. The inner surface is slightly convex in horizontal section and nearly straight in vertical section. The

⁶ Continued from Part I.

⁷ *Phascolodon* in recognition of the general resemblance to *Phascolotherium*. The specific name is for J. W. Gidley to whom the writer owes the privilege of describing this and numerous other specimens in the National Museum.

accessory cusps are lower relative to the main one than in any previously known Morrison or Purbeck triconodont, closely resembling *Phascalotherium* of the Stonesfield in this respect. *A* is a little higher than *c*, and they are not exactly in a straight line through *b*, but very slightly internal to the latter. The same is noted by Osborn for *Phascalotherium*. In the present

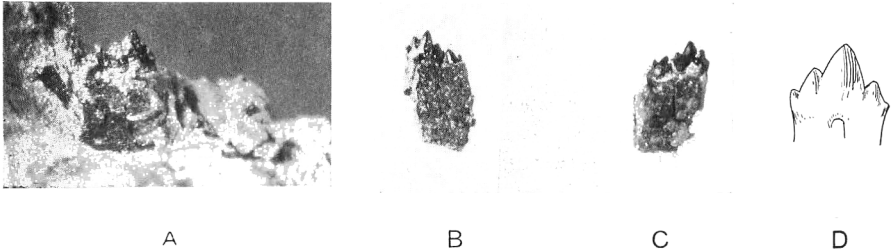


Fig. 8.—*Phascalodon gidleyi*, gen. et sp. nov. Holotype, Cat. No. 2703 U. S. N. M. A, anterior fragment, outer aspect. B, posterior fragment, outer aspect. C, posterior fragment, inner aspect. D, sketch of penultimate molar, outer aspect. A, B and C enlarged 4 diameters. D enlarged 11 diameters. Photographs from the United States National Museum.

form, at least, the accessory cusps are by no means on the internal slopes of *b* nor do they seem to represent an early stage of a transition to this position. The molar is typically triconodont although *a* and *c* point a little more internally than does *b*.

The penultimate molar resembles the foregoing save that it is smaller and a little higher relative to its length and that the disparity in height between *a* and *c* is a little greater. There is a rounded internal cingulum curving upward slightly on *b* and forming anterior and posterior cingulum cusps.

The last molar is very much smaller but of similar plan. The cingulum is sharp and nodulated in the middle. Anteriorly and posteriorly it becomes less sharp and rises onto *a* and *c* without forming separate cingulum cusps.

Mandibular Characters: Little can be inferred as to the mandible. The anterior end of the masseteric fossa apparently was not sharply defined but extended forward to beneath the last molars as a shallow median depression. The part of the internal groove here seen is pronounced and was parallel to and not far from the lower border. The lower and alveolar borders are nearly parallel in the part of the mandible preserved.

Measurements:

Length of antepenultimate molar	1.6 mm.
Length of penultimate molar	1.2 mm.
Length of last molar	0.7 mm.
Depth of ramus below penultimate molar	2.4 mm.

Genus *Aploconodon* Nov.*Aploconodon comoënsis*⁸ sp. nov.

(See Fig. 10.)

Holotype Number 2791 United States National Museum. Morrison Formation, Quarry 9, Como Bluff, Wyoming.

The only known specimen consists of part of a right mandibular ramus free of the matrix and including the crowns of the last two molars.

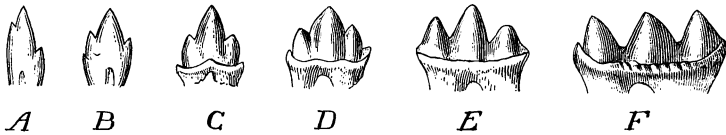


Fig. 9.—Series of lower molars seen from the inside, for comparison with *Phascalodon* and *Aploconodon*. A, *Dromatherium* and B, *Microconodon* from the Triassic of North Carolina. Redrawn after Osborn. C, *Amphilestes* and D, *Phascalotherium* from the middle Jurassic of England. Redrawn after Goodrich. E, *Priacodon*, from the Morrison of Wyoming. F, *Triconodon*, from the upper Jurassic of England. Redrawn after Owen.

Dentition: No inferences as to the dental formula are warranted by the material.

The penultimate molar consists of three cusps in a longitudinal series. The central cusp is higher and more acute than in the corresponding tooth of *Phascalodon*. The accessory cusps are very small, more so than in any other known triconodont. The internal cingulum is sharp and moderately broad anteriorly, rising here somewhat. It is obsolete in the middle and very faint posteriorly and it forms no cingulum cusps.

The last molar more closely resembles that of *Phascalodon*.

⁸ *Aploconodon* from 'ἀπλοῦς+κῶνος+δδων, "simple cone tooth" in allusion to the extreme simplicity of the penultimate molar. The specific name is derived from the locality where this and almost all the other Morrison mammals were found.

The accessory cusps are higher in proportion to the midcone than in the preceding tooth. The internal cingulum is confined to the internal surface of *a*, where it is sharp and forms a tiny internal cusp.

Mandibular Characters: The masseteric fossa was similar to that of *Phascodon*. A very peculiar feature and one that



Fig. 10.—*Aploconodon comoënsis*, gen. et sp. nov. Holotype, Cat. No. 2791 U. S. N. M. A, internal aspect, enlarged 4 diameters. B, sketch of penultimate molar, outer aspect, enlarged 10 diameters. Photograph from the United States National Museum.

is almost unique is that the internal groove begins at the lower border beneath and somewhat anterior to the dental foramen and hence runs forward, rising and passing away from the border as it goes:

Measurements:

Length of penultimate molar	1.1 mm.
Length of last molar	0.7 mm.
Depth of ramus below penultimate molar	2.0 mm.

Upper Jaws.

Owen⁹ has figured and described no fewer than four specimens of triconodont upper jaws, but neither figures nor descriptions are entirely satisfactory in elucidating the finer details of these important specimens. Osborn (1888, pp. 196-197. Plate 8, fig. 4) gives a composite restoration of the upper dentition, based on Owen's specimens and one other. Marsh neither described nor figured the American forms, but Gidley (1906) has given excellent figures of two upper molars in the Marsh collection. The most recent and at the same time the most complete description of a triconodont maxilla is, however, that of A. Smith Woodward (1912). He describes a considerable portion of the right maxilla with the last premolar and

⁹ 1871, pp. 62-63, 67-69. Plate III, fig. 17, 18. Plate IV, fig. 1, 5.

three molars, giving figures of the inner aspect of the whole specimen and the outer aspect of the crowns of the teeth.

Contrary to the usual belief, upper jaws are hardly less rare in the Marsh collection than are lower ones. In the following pages are described some seven specimens each including several teeth of the cheek dentition, and isolated teeth and fragments are not rare—a very good representation for this ancient fauna.

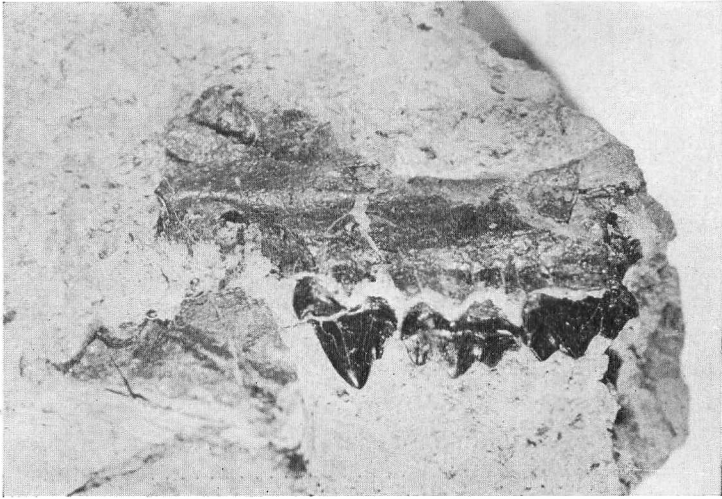


Fig. 11.—*Triconodon ?bisulcus* Marsh. Cat. No. 10344 Y. P. M. From the outside, magnified 6 diameters.

Triconodon ? bisulcus Marsh.

(See Figs. 11 and 12.)

Catalogue Number 10344 Yale Peabody Museum. Morrison Formation, Quarry 9, Como Bluff, Wyoming.

This specimen consists of part of an upper left maxilla in the matrix. Crowns of the last premolar and first two molars as well as alveoli for two more premolars are preserved.

Dentition: The last premolar is a large tooth higher than either of the preserved molars. It is similar to a typical triconodont lower premolar. The main compressed trenchant cone is rather broad fore-and-aft. The external cingulum is rounded, rising in the center, where it becomes almost obsolete.

and also at the ends, where it forms small anterior and posterior cingulum cusps.

The first molar has a rather sharp external cingulum, forming an undulating, slightly nodulated ledge. External to *a* it is very sharp and prominent, becoming fainter beneath the anterior slope of *b* and then stronger again posterior to this and forming a broad shelf postero-external to *c*. The outer surface of the crown is nearly flat across *a* and *b* with very light



Fig. 12.—*Triconodon ?bisulcus* Marsh. Cat. No. 2699 U. S. N. M. A, outer aspect. B, inner aspect. Both magnified 4 diameters. Photographs from the United States National Museum.

ridges running from the tips of each of these cusps. The outer wall of *c* is quite concave horizontally, the tip being thus thrown a little internally and out of line with the other two cusps. *B* is the highest and *c* is slightly inferior in height to *a*.

This description also applies to the second molar save that here the external cingulum is rather less pronounced, rising higher on *a* but not so sharp here, and becoming quite obsolete beneath *b*. The relief of the outer wall, slight in the first molar, is even less in the second and the cusps are almost exactly in line.

Skull: The lower border of the orbit is nearest the alveolar border above the posterior end of M^1 . The anterior border of the orbit was apparently about above the middle of the last premolar. Above the posterior end of this premolar there is a small notch in the orbital border apparently indicating the presence of the lacrymal foramen just internal to it. The lacrymo-maxillary suture is not seen in front of or below this point. The region in front of and above it is so crushed and cracked that inferences as to possible sutures here are not warranted.

The maxillo-jugal suture is nearly straight, running

obliquely backward and downward from a point on the inferior margin of the orbit directly over the anterior end of M^2 at an angle of something less than 45° to the alveolar border. Its direction and position are such as practically to preclude the possibility of there being more than one more molar (that is, three in all). The maxilla bounds most of the lower and anterior borders of the orbit.

The presence of three and no more upper molars in an English triconodont upper jaw is firmly established by Woodward in the paper mentioned above, thus adding one more bit of evidence, and a very conclusive one, to that tending to show that *Triconodon* never possessed more than this number of molars.

In the English specimen, unless the maxillo-jugal suture is obliterated, the maxilla sends back a decided zygomatic process not seen with certainty in any American triconodont. This divides the jugal from the lacrymal still further and thus seems more progressive than the conditions seen in the Morrison species.

The lower border of the orbit is formed by a low and rounded ridge which continues forward in a straight line parallel to the alveolar border. Just beneath this ridge and above the middle of the penultimate premolar is a small foramen which is the opening of a canal running up and back from this point. About 1.8 mm. anterior to this foramen is another some three times as large, the two together being exits for the maxillary nerve which branches within the pre-orbital canal. The latter is rather long.

Very little of the palate could be safely exposed. There is seen a shallow but pronounced furrow running from about the middle of the palatine process of the left premaxilla (where this specimen is broken off) backward and inward until at about 1 mm. from the midline it debouches at an evenly rounded margin which seems to be a suture or a fenestra rather than a break.

Number 2699 United States National Museum.

This specimen agrees sufficiently closely with the above to be referred provisionally to the same species. It consists of part of a maxilla with the last two premolars and first two molars.

The penultimate premolar is rather long and low, not over half as high as the last premolar. There is no external cingulum and the internal one is faint. The crown is compressed and trenchant.

The last premolar is higher and more pointed. There is a marked but rounded internal cingulum, becoming faint in the center.

Both of the first two molars have internal cingula which are well marked opposite *a* and *c*, and on the second molar true internal cingulum cusps are seen.

Priacodon ? ferox Marsh

(See Figs. 13 and 14.)

Catalogue Number 13626 Yale Peabody Museum. Morrison Formation, Quarry 9, Como Bluff, Wyoming.

This specimen, the most important of those here described, consists of a right maxilla, nearly complete, with the jugal, including the crowns of the first three molars, and alveoli for a fourth molar, for three premolars, and for a canine.

Dentition: This is the only skull in the collections in which the complete post-incisor dental formula can be determined. It is $I^2 C^1 P^3 M^4$.

The canine was quite large and pointed well forward. It was probably preceded by a large diastema and followed by a smaller one. The root is compressed. Whether it was double, as stated by Osborn for *Triconodon*, or not, cannot be ascertained, although it is probable that it was at least grooved longitudinally.

The first molar exhibits a sharp external cingulum, less prominent on the midcusp, but even here quite distinct and sharp and at about the same level. It forms no true cusps, but anteriorly it rises to form a broad, almost basin-like shelf. Posteriorly it rises very little and does not form a broad shelf. Below the tip of *b* and below the second notch in the crest are very low and broad ridges running toward but not reaching the cingulum. *A* and *c* are of nearly equal height and are very shallowly concave externally in horizontal section. The second of the two notches is much the deeper.

The second molar is closely similar save that it is larger, the cingulum is slightly nodulated, and the posterior slope of *c* is distinctly concave instead of being slightly convex.

The third molar is also similar but is more massive and shows more wear. The cingulum is quite sharp, and is not nodulated. The inner aspect has been exposed, and reveals the fact that there is a strong cingulum traversing the entire base of the crown and forming low cusps internal to *a* and *c*.



Fig. 13.—*Priacodon ?ferox* Marsh. Cat. No. 13626 Y. P. M. To show the jugal and palate, each of which is crushed a little out of its normal position. The crowns of the molars are seen somewhat obliquely. The posterior end of the palate has been reinforced with an inked line. Magnified $6\frac{1}{2}$ diameters.

The alveoli show that the fourth molar was smaller than the two preceding ones and probably about the size of M^1 .

Skull: The maxillo-jugal suture is much as in *Triconodon* ? *bisulcus*, but farther back, running in a nearly straight line from a point on the orbital border above the anterior end of M^3 obliquely backward and downward to a point just behind and above M^4 .



Fig. 14.—*Priacodon ferox* Marsh. Cat. No. 13626 Y. P. M. To show the dentition in normal external view. The jugal, which ordinarily continues the curve of the maxilla, is crushed out of position and hence seen obliquely. The dark spot in the upper right hand corner is a shadow. Magnified $6\frac{1}{2}$ diameters.

The jugal is almost entire. It has very nearly the shape of a broad isosceles triangle, the somewhat convex base facing upward, and of the two equal sides one, slightly concave, facing backward and downward, and the other, nearly straight, facing downward and forward. The surface of the jugal is only slightly convex and it continued backward the contour of the maxilla without any marked change in curvature. The origin for the masseter muscle is very plainly marked.

The maxilla is a large element. Although the cracked

nature of the bone makes it unwise to make a definite statement there appears to be no sutures on the part preserved save the maxillo-jugal one. The maxilla seems to have extended well in front of the canine (cf. *Didelphis*), and the premaxillary must have been a small element. The maxilla extended widely onto the upper part of the face. The *pars facialis* of

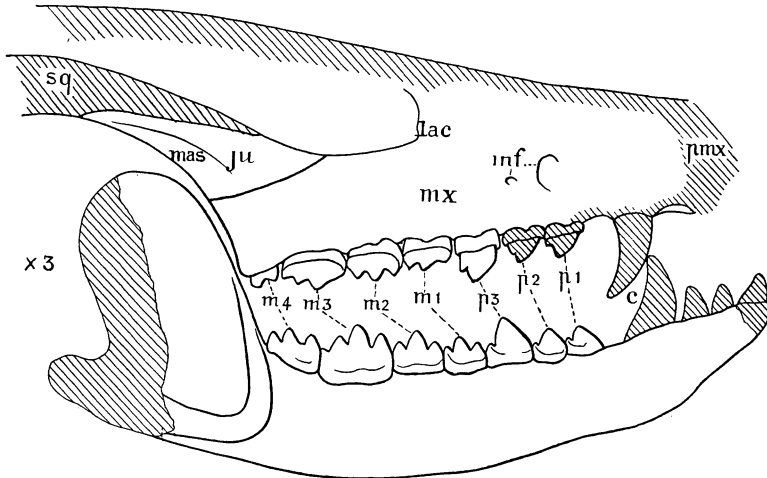


Fig. 15.—Skull and jaws of *Priacodon*, seen from the right side. The cross-lined portions are restored. In restoring the lower jaw and the anterior part of the dentition of the upper, Owen's and Osborn's figures of *Triconodon* have been used. The restoration is composite, although largely based on specimens of *Priacodon ferox*. Inf. = Infra-orbital foramina; ju. = Jugal; lac. = lacrymal notch; the foramen is just internal to this point; mas. = origin for the masseter muscle; mx. = maxilla; pmx. = premaxilla; sq. = squamosal.

the lacrymal seems to be lacking, nor is it observed in any specimen although several show the region where it would lie and although the maxillo-jugal and maxillo-palatine sutures are open.

Much of the bony covering of the region of the infraorbital foramina is gone. A cast of the preorbital canal for the maxillary nerve is seen and it shows clearly that here also the nerve branched and issued by two exits, but here the disparity in size between the small posterior and large anterior foramina is even greater.

As shown in the measurements given below, the minimum

distance from the lower border of the orbit to the alveolar border is much greater than in the species first described, without a corresponding difference in the size of the dentition.

The palate is fairly well exposed. There is a shallow groove having the appearance of a vascular impression running back and in from just inside the posterior end of P^1 , becoming

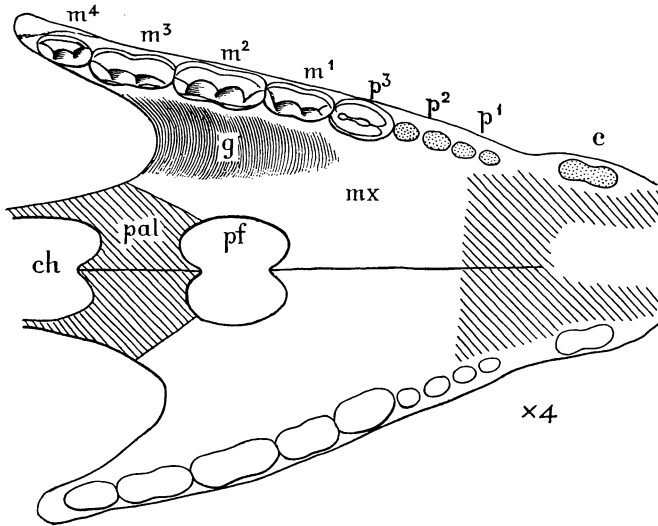


Fig. 16.—Palate of *Priacodon*, seen from below. The cross-lined portions are restored. Ch. = internal nares; g. = broad groove internal to raised alveolar border (not seen in all species of *Priacodon*); mx. = palatal process of maxilla; pal. = palatal process of palatine; pf. = palatal vacuity.

shallower and finally disappearing internal to the anterior end of M^1 . A short faint groove near and parallel to the midline joins it here and also disappears.

Internal to the midcusp of M^1 is the anterior border of a large evenly oval opening. As the posterior edge is not preserved there might be some question as to its being original and not due to post-mortem causes. The former is, however, quite surely the case: the contour is very even, a small point of bone juts backward into it anteriorly as in the palates of some marsupials in which there is a large central fenestration, and the bone, although thick elsewhere, becomes thin next to the opening and curves dorsally slightly all around it.

The edge of the specimen running from about the middle of the posterior edge of the vacuity backwards and somewhat toward the alveolar border is evidently the maxillo-palatine suture, the palatine being lost.

An unusual feature of this skull (as of all those belonging to the triconodonts) is that the secondary palate does not extend as far back as in most modern mammals. There is a deep excavation forward between the palatines and the alveolar process of the maxilla to a point opposite the middle of M³. The last molar is thus inserted in a backward projection of the maxilla just large enough to contain its fangs and quite free save for the articulation above with the jugal. Internal to the molar series is a broad groove above which the alveolar border rises abruptly. (For all these features see Fig. 16 which is constructed mainly from this specimen.)

*Priacodon lulli*¹⁰ sp. nov.

(See Figs. 17 and 18.)

Holotype Catalogue Number 13625 Yale Peabody Museum. Morrison, Quarry 9, Como Bluff, Wyoming.

This specimen consists of part of a right maxilla free of the matrix. Crowns of the last premolar and of all four of the molars are preserved, although partly broken. This is the only American specimen in which the last upper molar is preserved.

Dentition: The last premolar is of about the same size as in *Triconodon* ? *bisulcus*. The internal cingulum is very faint, rising a little at the ends but forming no cusps. The external cingulum is also faint. It is almost obsolete anteriorly and does not rise there. It rises slightly in the middle and decidedly posteriorly, where it forms a small cusp. The external slope of the crown above the cingulum is nearly straight.

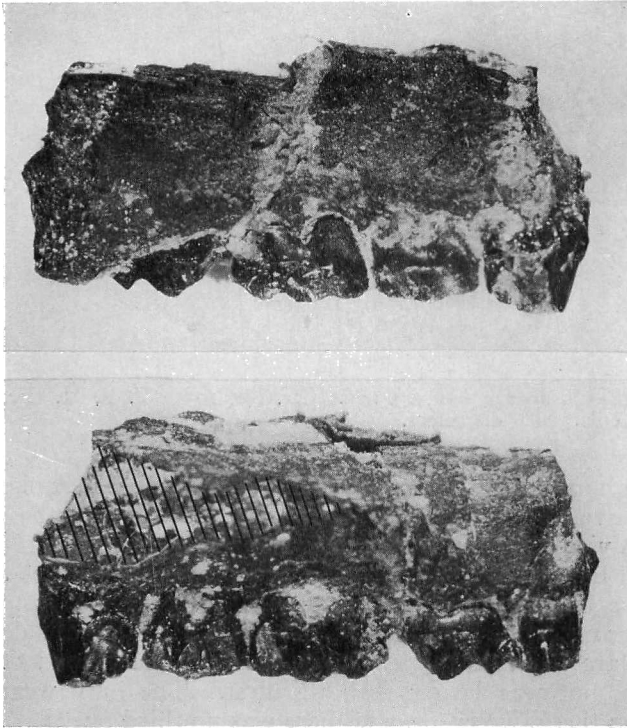
The external cingulum of the first molar is very faint, rounded, continuous, straight in the center, rising a little posteriorly, where it is nearly obsolete, and rising decidedly anteriorly where it forms an antero-external shelf. The outer wall is quite flat although with the slight relief characteristic of triconodont upper molars. The tooth is gibbous below the

¹⁰ The specific name is an inadequate expression of the deep respect and gratitude which the writer feels for his teacher, Professor Richard Swann Lull.

cingulum. The internal cingulum is very faint, low, and rounded, almost absent.

The second molar resembles the first save that the cingula are a little stronger, although the internal cingulum is still very

A



B

Fig. 17.—*Priacodon lulli*, sp. nov. Holotype, Cat. No. 13625 Y. P. M. A, from the outside. B, from the inside. The cross-hatched area is the broken section of the palate. Enlarged 6 diameters.

weak. The gibbosity below the external cingulum is pronounced.

The outer wall of the third molar shows less relief than any others yet observed on any American triconodont. It is evenly and slightly convex vertically, but almost straight horizontally. The external cingulum is about as well developed as on M^2 but sharper. The internal cingulum is weaker than on M^2

but continuous, rising at both ends. The third groove is deeply incised on the posterior slope of *c* and has produced an apparent fourth cusp posterior to this as an "erosion remnant."

The last molar, a tooth not preserved in any other known American triconodont, is unfortunately not entire. It is rather less than half the length of the preceding tooth,



Fig. 18.—*Priacodon lulli*, sp. nov. Cat. No. 10359 Y. P. M. From the outside, enlarged 6 diameters.

although about as wide. The outer slope is flanked by a downward projection of the maxilla, so that the tooth is not visible from the outside. The internal cingulum is as well developed as that of M^2 and sharper. It rises at the ends, a little higher anteriorly, but forms no cusps. The anterior cusp was columnar as seen from the internal side. Its slopes are nearly straight and vertical. The second cusp is broken, but was larger than the first. The only wear was between these two cusps, and there was no third one.¹¹

Skull: The palatal and facial characters are the same as those of the referred specimen next to be described, but were less well displayed. The type was somewhat the older animal, the teeth being more worn.

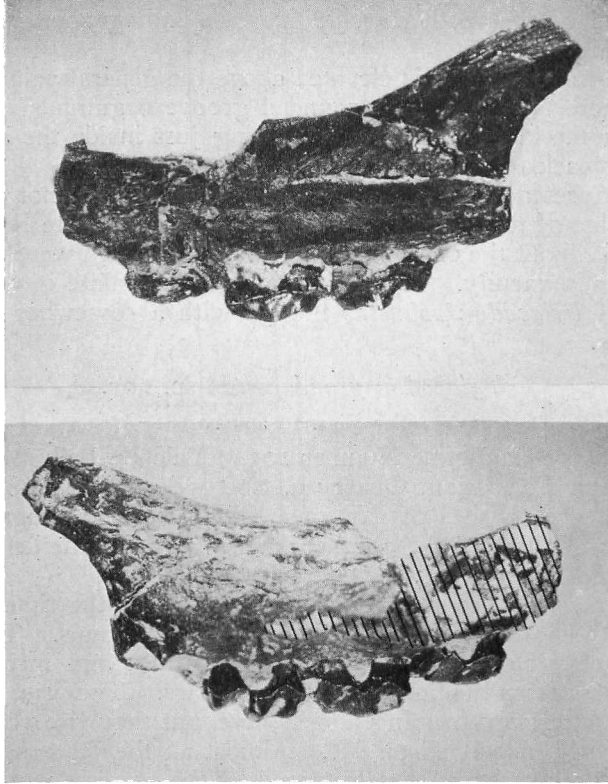
Catalogue Number 10359 Yale Peabody Museum.

This specimen, referable to the same species as the one just described, consists of part of a right maxilla with the broken crowns of the first two molars and alveoli for three premolars.

¹¹ The last (third) upper molar of *Triconodon ferox* (Woodward, loc. cit.) closely resembles the last (fourth) upper molar of *Priacodon lulli*. This matter is mentioned further below.

Dentition: The two broken crowns preserved are of the same size and character as those of the type. The cingula are perhaps a trifle stronger. The same gibbous aspect of both inner and outer slopes is seen.

A



B

Fig. 19.—*Priacodon grandaevus*, sp. nov. Holotype, Cat. No. 10349 Y. P. M. A, from the outside. B, from the inside. The cross-hatched area is the broken section of the palate. Enlarged 6 diameters.

Skull: The maxillo-jugal suture is not preserved. It must have been at least as far back as in *P. ? robustus* where it begins over the anterior end of M^3 .

The anterior border of the orbit was over the last premolar. The area above the maxilla is, as usual, too cracked to admit of the determination of sutures. There is an infraorbital foramen above the second from the last premolar, whether the

main or a subsidiary one does not appear. It has the usual position of the main one, and if so there is only one in this form.

The palate is exposed and is preserved from the alveolar border nearly to the midline. As in all other triconodont skulls the maxillary portion of the palate does not extend to the end of the tooth row, in this case ending about opposite the middle of M^2 .

The molar border is elevated above the general palate level, and there is also a large rounded groove beginning near the end of the last premolar and running just inside the alveolar border back to the end of the palate.

The presence or absence of palatal vacuities is not proven. The edge of the part of the palate preserved opposite P^3 is thin and has about the contour that would be expected were this the edge of a vacuity. If this is the case, the palate is very like that of *Priacodon robustus* though with a somewhat smaller vacuity.

*Priacodon grandaevus*¹² sp. nov.

(See Figs. 19 and 20.)

Holotype Catalogue Number 10349 Yale Peabody Museum. Morrison Formation, Quarry 9, Como Bluff, Wyoming.

The type consists of part of a left maxilla and jugal, with crowns of the first three molars and alveoli for the last molar and the last premolar.

Dentition: This individual was very old at the time of his death. The teeth are worn down to mere stumps. The cingula are prominent, continuous, undulating, and increase in sharpness from the first to the third molars. They rise considerably anteriorly forming a shelf here, but they rise very little posteriorly, not at all on M^3 . Almost all the features of the inner surfaces have been destroyed by the extreme wear.

Skull: The maxillo-jugal suture began at least as far forward as above the posterior part of M^1 and ran back at a low angle almost straight to a point above and behind the last molar. This is quite different from the conditions in the other species, and is open to some question. Although the suture seems to be perfectly definite and recognizable in the type it is not seen in the referred specimen No. 2698 U. S. N. M. There

¹² The specific name is the Latin "venerable" in allusion to the considerable geological age as well as to the great individual age of the type at time of death.

is reason to believe, however, that this suture is obliterated in the latter specimen, since, if present, it would have to be much farther back than in any other American specimen.

The excavation of the posterior edge of the palate extended at least as far forward as the anterior part of M^3 . The alveolar border is only slightly elevated above the palate.

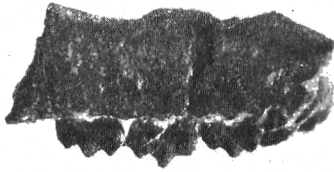


Fig. 20.—*Priacodon grandaevus*, sp. nov. Cat. No. 2698 U. S. N. M. From the outside, enlarged 4 diameters. Photographs from the United States National Museum.

There is no groove internal to this border but there are shallow pits just anterior to the junction of M^1 and M^2 and also of M^2 and M^3 .

Catalogue Number 2698 United States National Museum.

This specimen agrees fairly well in comparable features with the holotype and may be referred to this species. It is a younger individual and adds knowledge of some important characters. On M^3 the internal cingulum forms cusps opposite *a* and *c*; on *b* it is present but lower. The relief of the

MEASUREMENTS OF UPPER JAWS.

	Last Premolar	M^1	M^2	M^3	Minimum distance from orbit to M^1 alveolar border.	
<i>Triconodon ?bisulcus</i> :						
10344 Y. P. M.	2.2	2.7	2.7	2.8
2699 U. S. N. M. ..	2.1	2.6	2.8	2.9
<i>Priacodon ?ferox</i> :						
13626 Y. P. M.	ca.2+	2.0	2.6	2.7	..	3.9
<i>Priacodon lulli</i> :						
13625 Y. P. M.	2.2	2.3	3.0	ca.2.5	1.2	4.1
10359 Y. P. M.	ca.2.5	3.1	4.0
<i>Priacodon grandaevus</i> :						
10349 Y. P. M.	ca.2.1	2.3	2.4	..	3.2
2698 U. S. N. M. ..	ca.1.8	2.0	2.4	2.4	..	3.2

Measurements of teeth are maximum lengths, in millimeters.

external surface above the cingulum is greater on these molars than on any others known pertaining to American triconodonts. The outer slope of *b* is distinctly convex, there is a low ridge below the first notch, *a* is tipped well inward, and *c* is intermediate between *a* and *b* in this respect.

COMPARISON OF THE SPECIES OF UPPER JAWS.

1. <i>Triconodon ?bisulcus</i>	Probably 3 molars.	} Varying molar lengths, see measurements above.	} ? Broad groove internal to raised molar border. " Molar border little raised, no groove.
2. <i>Priacodon ?ferox</i>	4 molars		
3. <i>Priacodon lulli</i>	4 molars		
4. <i>Priacodon grandaevus</i>	4 molars		
1, cont.	External cingulum sharp, obsolete on <i>b</i> . Int. cing. forms cusps.	Max-Ju suture begins above anterior end of M ² .	
2, cont.	External cingulum sharp, continuous. Int. cing. sharp, forms cusps.	Max-Ju suture begins above anterior end of M ² .	
3, cont.	Cingula continuous but faint. No internal cusps. Bases of teeth gibbous.	Max-Ju suture either far back or obliterated on known specimens.	
4, cont.	Cingula sharp, continuous, cusps internal to <i>a</i> and <i>c</i> .	Somewhat uncertain. Perhaps began as far forward as above M ¹ , and was at a lower angle than in other species.	
1, cont.	Minimum distance from orbit to alveolar border 2.8 mm.	Anterior border of orbit over last premolar.	
2, cont.	" " " " 4.0 mm.	Over M ¹ .	
3, cont.	" " " " 4.0 mm.	Over last premolar.	
4, cont.	" " " " 3.2 mm.	?	

Occlusional Relationships of Triconodont Molars.

Osborn (1888) has noted that the wear on the upper teeth of *Triconodon* is not in the hollow between the cusps, but is rather on the postero-internal slopes of the cusps themselves. At first this authority believed that lower cusp *b* occluded between cusps *a* and *b* of the corresponding upper molar (see Fig. 21 A), and he so figured them in his composite restoration. On the other hand, in his numerous subsequent papers Osborn, in dealing with cusp evolution, has always figured lower cusp *b* as occluding between the corresponding and the preceding upper molars.

Apparent anomalies necessitated considerable attention to this fundamental detail in the course of the present study, with

the result that the latter opinion, which is the only one now current, is found to be undoubtedly correct. (See Fig. 21 B.)

Wear on the lower molars is confined chiefly to the tips of the cusps, while that on the uppers affects chiefly the grooves and postero-internal slopes of the cusps. The teeth did not shear past one another vertically as typically in modern carni-

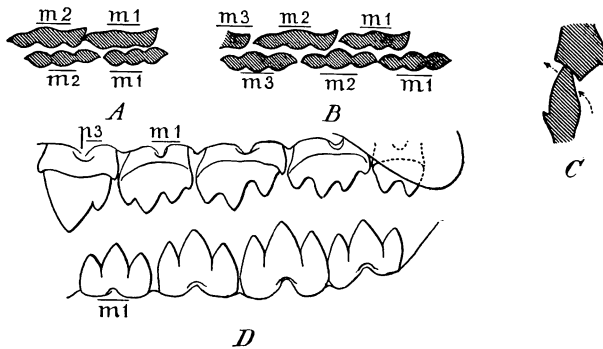


Fig. 21.—Occlusion in triconodonts. A. On the hypothesis that cusp *b* below occludes between *a* and *b* above. B. The correct relationships, with *b* below fitting between the teeth above. C. Section through the center of a lower cusp in occlusion, showing how the tip scrapes upward and inward while shearing against the upper molar. D. Somewhat schematic view of left molar series from the outside, showing the relationships of the cusps of the lower molars to the notches in the crests of the upper molars.

vores. Instead, the tips of the lower cusps passed obliquely upward, inward, and a little backward on the internal slopes of the upper molars (Fig. 21 C). When the jaw was fully closed the lower molars were thus nearer the central line of the head than when the lower jaw was open. This was facilitated by the loose symphyseal union and no doubt also by a certain amount of lateral play in the glenoid articulation. It is quite probable also that the two halves of the lower jaw could be closed separately, as they can still be in certain modern mammals.

As the lower cusps raked down the internal slopes of the upper molars they wore deep grooves in the latter. The grooves indicate by their relative depths, if irregularities of placing and the arc through which the lower jaw swings are carefully considered, the relative heights of the cusps which made them. They also indicate the distances between these

cusps. In this way it is possible to judge with reasonable accuracy the nature of the lower molar series which must have occluded with a given upper series. Figure 21 D illustrates this relationship, although in a way much clearer than is generally seen in the actual specimens, where absolute regularity in the placing of the molars is never quite obtained.

It was in this way that the identifications given above were made. The detailed grounds cannot well be given in an article devoted to facts rather than methods, but it was found that certain of the upper jaws could have occluded with *Triconodon bisulcus*, certain others with *Priacodon ferox*. They were hence assigned to those species provisionally. Certain other upper jaws could not occlude with any known lowers, and therefore two new specific names are proposed for them. This procedure is quite liable to error, obviously; at the same time it greatly increases the probability of the names used being valid, and it serves to provide names for the various well defined types which may well be used until their validity can be tested definitively by the discovery of associated material. It also obviates the necessity of describing material without at least a provisional taxonomic reference—a procedure that has often ended unfortunately in the past.

In passing it should be said that the bicuspid nature of the last molar in triconodont upper jaws not only indicates that occlusion must have been as shown above, but is itself explained by the latter fact. The fact that only the two anterior cusps of this molar were functional no doubt led to the loss of the last one, or at least permitted this reduction.

GENERA OF AMERICAN TRICONODONTS.

The term *true triconodonts* is used by the present writer to include only Mesozoic mammals the molars of which are essentially composed of three cusps arranged in a straight fore-and-aft line. *Spalacotherium* and its American ally *Tinodon* are thus excluded, and their affinities will be discussed in the next paper.

Owen proposed two genera of Purbeck triconodonts, *Triconodon* and *Triacanthodon*. Marsh noted the existence of an American species of the first genus, and also of a third triconodont genus, *Priacodon*. The latter has, following Osborn, been usually considered in the literature as a probable synonym of *Triconodon*. Their simple teeth are very similar, and if found isolated would certainly not justify generic sepa-

ration. The excellent mandibular material in the Marsh collection shows plainly, however, that the two genera are quite distinct. The chief known differences may be tabulated as follows:

<i>Priacodon</i>	<i>Triconodon</i>
P ₃ , M ₄ .	P ₄ , M ₃ .
Diastema following C.	No diastema.
Anterior and posterior cusps slightly lower relative to central one.	Anterior and posterior cusps equal or subequal to central one.
Molar cingulum very sharp, strong across the central cusp.	Molar cingulum rather less sharp and generally weaker on the mid-cone.
No pterygoid fossa, and masseter fossa rather less strongly developed than in <i>Triconodon</i> .	Usually a shallow pterygoid fossa and a strongly developed masseter fossa.

Material is insufficient to indicate whether certain other characters of *Priacodon* are generic or specific. It may also be expected that the parts still unknown in *Priacodon* will furnish other generic distinctions.

On the other hand, in the absence of figures and a detailed description of *Triconodon bisulcus*, it has sometimes been tacitly assumed that Marsh was incorrect in assigning this species to the English genus. The statement is sometimes seen that *Priacodon* [alone] represents the true triconodonts in America. The question hinges somewhat on Osborn's belief that the dental formula of *Triconodon* is P₄, M₄. If this be correct, *Triconodon bisulcus* belongs to a separate genus, while *Priacodon* is in any event distinct, since it possesses only three premolars. It may be remembered that of the numerous English triconodont jaws only *two* are known in which there are four molars. The first of these is the type of *Triacanthodon serrula* Owen, the second is the mandible later described by Willett as belonging to *Triconodon mordax* Owen. Examination of a good cast (No. 10337 Y. P. M.) shows that even outside the very great difference in size and the greater number of teeth, Willett's specimen shows other differences from *T. mordax* of at least specific value. It seems quite probable that the specimen represents a new species of *Triacanthodon*, as suggested by Osborn in case the latter genus proved valid. It is much to be desired that the specimen be redescribed and named by someone who has access to the

original, which is now in the Museum of Practical Geology, Jermyn Street, London.

On the whole, the writer is inclined to believe that the English genus *Triconodon* probably never had more than three molars, or at least that the evidence to the contrary is not very strong. The proof of the existence of an American form with four premolars and three molars lends further probability to the existence of a similar type in the closely related Purbeck fauna. Furthermore the lower jaw which occluded with the maxillary series figured by A. Smith Woodward could never have had more than three molars.

If we assume, at least provisionally, that *Triconodon* had three molars, then there is little to justify placing *T. bisulcus* in any other genus, and Marsh's reference stands at least until the English specimens have been thoroughly restudied.

Regardless of any question of nomenclature or as to the characters of the English species of *Triconodon*, the fact remains that in this more advanced group with accessory cusps nearly equal to the main cusp there are known forms with four premolars and four molars (Willett's specimen and *Triacanthodon serrula*). From this stage, known American forms show reduction in two ways: the premolar series may be reduced, with the formation of a diastema back of the canine (*Priacodon*), or the molar series may be reduced and the relative size of the remaining molars increased (at least *Triconodon bisulcus*, and probably also the English species of this genus).

A second group of genera, distinguished from the foregoing chiefly by the lesser size and importance of the accessory cusps, is here noted in the Morrison fauna for the first time and the two genera represented are named *Phascolodon* and *Aploconodon*. They may be distinguished as follows:

<i>Phascolodon</i>	<i>Aploconodon</i>
Accessory cusps about half the height of main cusp.	Accessory cusps less than half the height of main cusp.
Small anterior and posterior cingulum cusps.	No anterior and posterior cingulum cusps.
Main cusp rather blunt, gibbous externally.	Main cusp more acute and slender.

These characters seem amply to justify the generic separation of the two forms. The general structure of the molars is, however, closely similar and tends to mark these genera

as belonging to a group distinct from *Triconodon* and *Priacodon*. At the same time the molar pattern resembles that of the Stonesfield genera *Amphilestes* and *Phascolotherium* quite closely, while the presence, at least in *Phascolodon*, of more than four molars points in the same direction. The Morrison genera are quite distinct from the Stonesfield ones, however, as is clearly seen in the reduced last molar, the different character of the cingula, and other features of the former forms.

A detailed comparison is reserved for more extended discussion, but the following tentative grouping may here be given as that which seems to be most probable and convenient:

Family TRICONODONTIDAE.

Subfamily Amphilestinae

<i>Amphilestes</i>	Stonesfield
<i>Phascolotherium</i>	Stonesfield
<i>Phascolodon</i>	Morrison
<i>Aploconodon</i>	Morrison

Subfamily Triconodontinae

<i>Triconodon</i>	Morrison and Purbeck
<i>Triacanthodon</i>	Purbeck
<i>Priacodon</i>	Morrison

RÉSUMÉ

The known remains of American triconodonts thus belong to four distinct genera. These genera, especially *Priacodon*, may have included numerous species, of which only those represented by comparatively well defined material have been described. There are four well characterized species of upper jaws, of which two are referred to lower jaw species, two are described as new. The named Morrison triconodont fauna may be tabulated as follows:

Species	Lower jaws	Upper jaws
<i>Triconodon bisulcus</i> Marsh	X	X
<i>Priacodon ferox</i> Marsh	X	X
<i>P. robustus</i> (Marsh)	X	
<i>P. lulli</i> sp. nov.		X
<i>P. grandaevus</i> sp. nov.		X
<i>Phascolodon gidleyi</i> gen. et sp. nov.	X	
<i>Aploconodon comoënsis</i> gen. et sp. nov.	X	

The total range of adaptation is not great and all these species may best be referred to a single family, the Triconodontidae, the only one included in the order Triconodonta.

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