A NEW SPECIES OF THE AMBLYPOD *TITANOIDES* FROM WESTERN COLORADO.*

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INTRODUCTION.

The specimen which is the subject of the present paper forms part of a small but very interesting collection of fossils recently presented to Field Museum by Mr. Edwin B. Faber of Grand Junction, Colorado. It was collected by him in the lower levels of the Ruby[1] formation in the Grand River region. It is the first vertebrate fossil to be reported from the formation in this area and is the most complete specimen of *Titanoides* hitherto found. The specimen also represents a new species of the genus and exhibits a very interesting pathologic condition.

Grateful acknowledgments are made to Mr. Faber, in whose honor the specific name is given, for the donation of his valuable find; and to Mr. E. S. Riggs, who very kindly entrusted the specimen to the writer for description and who has given valuable advice and criticism. The drawings are by Mr. Carl F. Gronemann, staff artist, Field Museum.

Order Amblypoda Cope

Family Pantolambdidae Cope

Genus *Titanoides* Gidley

Emended diagnosis.[2] Dentition $\frac{\quad}{3,\ 1,\ 4,\ 3}$, teeth brachyodont and in series, no diastemata. Lower incisors with a median cusp and two accessory lateral cusps. Lower canine subtriangular in cross section. Lower cheek teeth comparatively high crowned. Lower premolars increasing in size posteriorly with trigonids becoming more and more V-shaped; paraconid

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[1] The name Ruby was applied by early writers to a formation extensively exposed around Mount Owen and Ruby Peak in the Ruby Range. Eldridge (1894) stated that it disappeared westward beneath the Wasatch but later investigations have shown without much question that the two formations are continuous (see Lee, 1912, p. 51). The discovery of *Titanoides* in the formation, however, suggests the presence of a Paleocene horizon. The term Ruby is, therefore, adopted for the series in this paper instead of Wasatch which is definitely associated with a lower Eocene formation.

[2] Based upon the original diagnosis given by Gidley (1917, p. 431) with additional characters provided by the new specimen and by *T. gidleyi* Jepson (1930, p. 506).

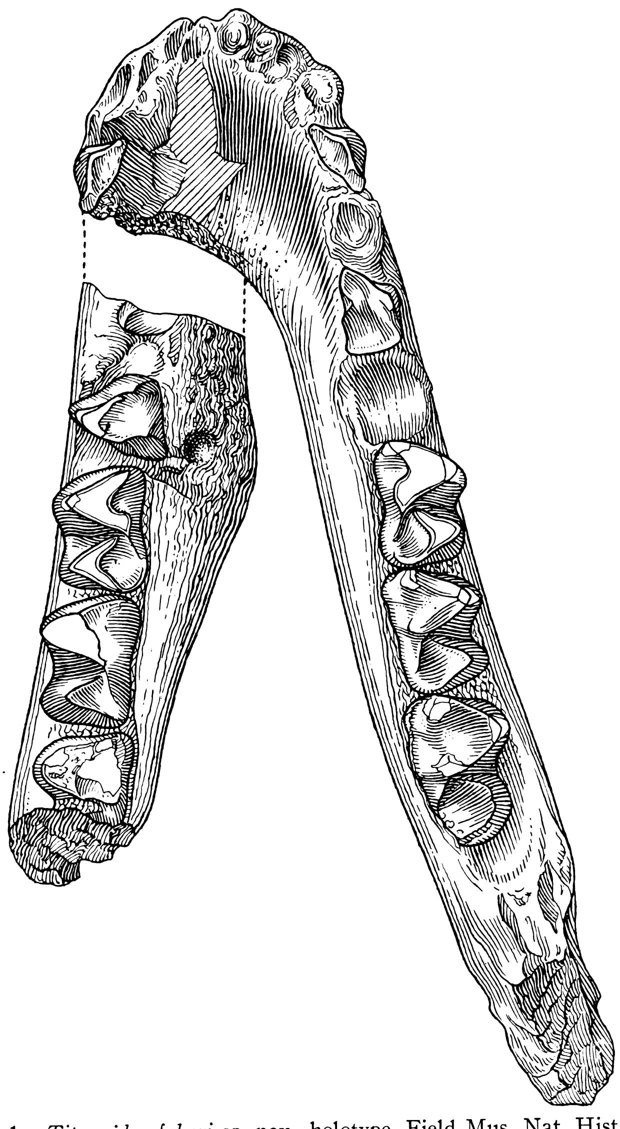


Fig. 1. *Titanoides faberi* sp. nov., holotype, Field Mus. Nat. Hist. No. P. 14637. Mandibular rami, crown view. Note the pathologic condition of the left ramus. x $\frac{2}{3}$.

and metaconid small on P_1, becoming larger and higher on the succeeding teeth of the series; talonids incipient but increasing slightly in size posteriorly. Lower molars with trigonids and talonids V-shaped; talonids lower and smaller than the trigonids; paraconids of the molars high and distinct from the metaconids; cristae obliquae (i.e., crests running from the tips of the hypoconids to the metalophids) pronounced; last molar largest, the series decreasing in size anteriorly. Mandibular symphysis wide, not sutured, sloping, very slightly recurved ventrally; mandibular ramus comparatively low, decreasing in depth from P_2, to M_3; mental foramina large, situated under P_1 and P_4.

Type species: *Titanoides primaevus* Gidley, 1917, pp. 431-435, pl. 36.

Titanoides may be distinguished from the closely related *Pantolambda* by the following characters, none of which are very striking. On the lower molars of *Titanoides* the paraconid is slightly larger and more divergent from the metaconid than in *Pantolambda*; the talonid is slightly smaller, and (judging from Osborn's figure of *P. cavirictus,* 1898, fig. 2) the crista obliqua is somewhat stronger, particularly on M_3. The mandibular symphysis is more sloping and very slightly recurved in *Titanoides* and the ramus is shallower than in *Pantolambda*.

Titanoides faberi, sp. nov.

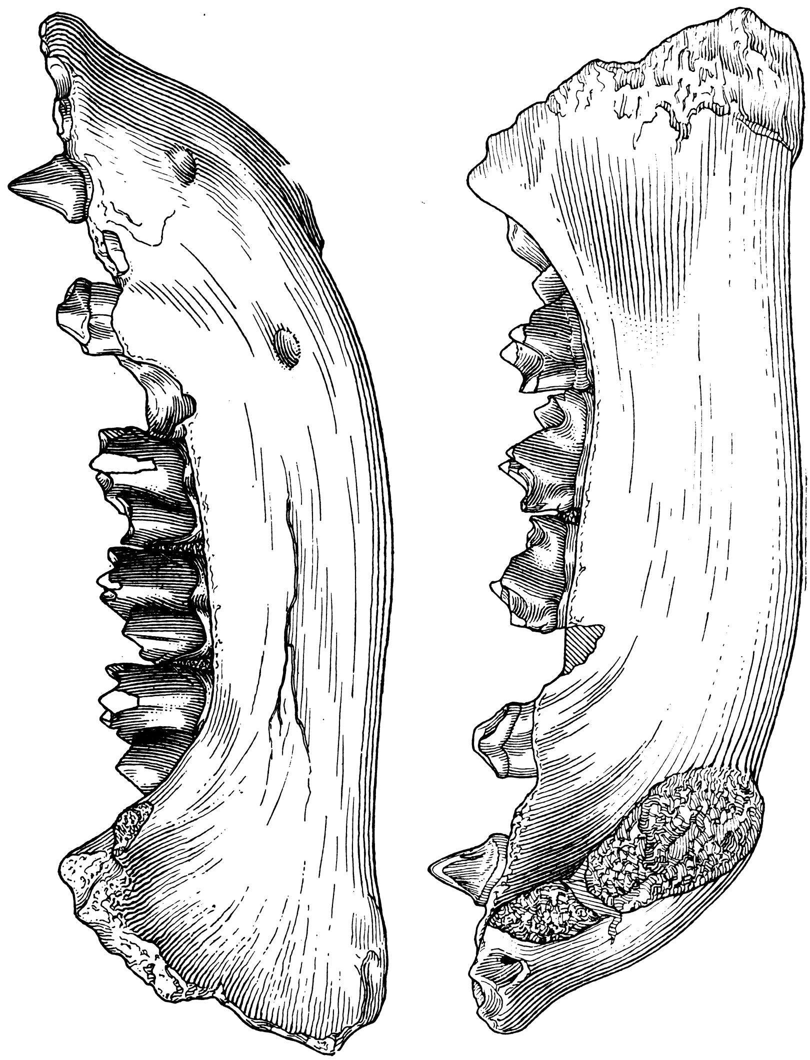
Holotype: Field Museum No. P. 14637, right mandibular ramus of a young individual with symphysis, complete molar series and dm_3; portion of left ramus with Pm_4-M_2; detached teeth. Coll. E. B. Faber, 1929, Figs. 1, 2 and 3.

Horizon: Undetermined but probably upper Paleocene. Found in a blue shale just above a layer of massive sandstone in the lower levels of the Ruby formation some twenty-five to fifty feet above the contact with the Mesaverde formation (E. B. F.[3]).

Locality: Mesa Co., Colorado. Lower part of the Plateau Creek valley (E. B. F.[3]).

Diagnostic characters: Size nearly as in *T. primaevus*. Posterior cingulum on P_4 very weak and low. Metaconids of molars very wide antero-posteriorly, sloping down into the basins of the talonids, no external basal cingulum on molars;

[3] Mr. E. B. Faber, letter to the writer, Nov. 23, 1931.



Figs. 2 and 3. *Titanoides faberi* sp. nov., holotype, Field Mus. Nat. Hist. No. P. 14637. Right mandibular ramus, external and internal lateral views. x $\frac{2}{3}$.

talonid of M_3 smaller and much narrower than the trigonid,[4] incipient metastylid on M_3.

Referred specimen: Field Museum No. P. 14898, an incomplete, isolated upper molar of an old individual, from the same horizon as the holotype but collected three miles distant from it (E. B. F.[5]). Fig. 4.

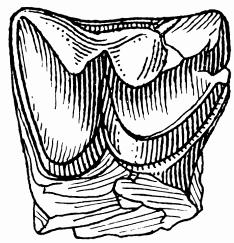


Fig. 4. *Titanoides faberi* sp. nov. (?), referred specimen, Field Mus. Nat. Hist. No. P. 14898. Upper molar, crown view. x $\frac{1}{1}$.

Description of the holotype, P. 14637: The crowns of the incisors are unfortunately missing and the roots only of the first and second are in place. These are small and oval, with the greater diameter in the antero-posterior direction. The root of the first is slightly larger than that of the second, while the third was larger than either, judging from the portion of the alveolus preserved. Although no trace of replacing teeth have been detected beneath them the writer is not certain whether the roots preserved represent the permanent or the deciduous series. Jepson (1930, pp. 506-507, pl. VI, figs. 6-7) describes and figures the incisor crown of *T. gidleyi* as having a median cusp and two small, lateral accessory cusps.

The root of the right deciduous canine is still in place, and is subcircular in section. On the left side this tooth has dropped out, exposing the tip of the permanent canine, which has a triangular outline near the base.

The first premolar of the right side is broken, the left is preserved among the detached teeth. This tooth is very slightly worn, single rooted and triangular in outline with the long axis slightly oblique to the axis of the ramus. It is practically single cusped as the paraconid is merely a slight cusp-

[4] The talonid of M_3 in *T. gidleyi* is unknown.

[5] Mr. E. B. Faber, letter to the writer, June 3, 1932.

ule on the anterior slope of the protoconid, and the metaconid consists of a small vertical ridge on the posterior half of the lingual slope. The talonid is very small, and a slight internal cingulum is present. Dm_3 is still in place on the right side but is so much worn that little of the structure can be determined. The talonid appears to have been rather prominent. A small portion only remains of the left P_3 which is not yet fully erupted. The left fourth premolar is also erupting, the right is missing. The trigonid of this tooth is well developed with a large protoconid and a prominent metaconid, the paraconid, however, is not as large as on P_4 of *T. gidleyi.* The small talonid sends a crest outward and upward which joins the metalophid midway between the protoconid and the metaconid, very much as in *Pantolambda* and *Coryphodon.* The posterior cingulum is small and low and joins the talonid only at the postero-internal corner of the tooth. On P_4 of *T. gidleyi* and P_3 of *T. primaevus* this element forms a posterior ledge.

The important features of the molars have already been given in the specific diagnosis. M_3 is the most characteristic of the series, as its small, narrow talonid and incipient metastylid sharply distinguish it from those species of both *Titanoides* and *Pantolambda* in which this tooth is fully known. The labial side of each molar is considerably higher than the lingual, and the cutting edges, when unworn, are somewhat serrate, as in *Coryphodon.*

The specimen at hand permits some observations to be made upon the order of eruption of the cheek teeth. The first tooth of the permanent series to come into place was M_1, which was followed by M_2. P_1, judging from its state of wear, was the next to appear, after which came M_3 and (presumably) P_2. The canine and P_3 and P_4 of the left side are visible in their alveoli but are not yet fully erupted. In the right ramus, P_4 is missing, and the milk canine and dm_3 are still in place. To judge from the left ramus it would appear that the third and fourth premolars came into place before the canine, but it is possible that the order of eruption in this area may have been disturbed by a pathologic condition which seriously affected the anterior portion of the left ramus. The succession in *Coryphodon* is rather different from that in *Titanoides.* In the former the first of the cheek teeth to erupt is P_1: the premolars and the first and second molars are all functioning before the third molars come into use: I_2 replaces di_2 at about the same time that M_3 erupts. The writer is greatly indebted to Mr. Walter Granger and Dr. George Gaylord Simpson for their kindness in furnishing the above unpublished data from specimens of *Coryphodon* in the American Museum.

The mandibular ramus is gently concave dorsally and gently convex ventrally with the deepest point under P_2, and the shallowest under the anterior border of M_3. The lingual alveolar border is higher than the labial, due to the greater height of the external faces of the molars. There are two large mental foramina, the anterior under P_1 and the posterior under the forward border of P_4. The symphysis is fairly long and sloping, extends posteriorly to P_1, and is very slightly recurved on the ventral surface. No trace of a suture can be detected. The symphysis of *T. faberi* apparently differs somewhat from that of the genotypic species, but the latter (judging from Gidley's description and from drawings kindly furnished by him) is so imperfect that precise comparisons are not practical.

As stated above, the anterior portion of the left ramus was seriously affected during the life of the animal, being greatly enlarged by a lesion which extended from the region of the first molar forward. That portion of the ramus from the third premolar to the canine has been lost, but the lesion apparently reached the symphysis. The lingual side of the ramus is considerably swollen, the periosteum has been destroyed, and there are several necrotic passages from the interior of the jaw. The swollen surface is extremely rugose, irregular, and covered with osteophytes of varying sizes. The external side of the ramus is not affected, at least in the portions preserved. The tumor mass on the inner side agrees very well with the early stages of actinomycosis[6] or "lump jaw," as shown by cases examined in modern animals. Present-day cattle are particularly susceptible to the disease. So far as the writer is aware there have been but two other cases of actinomycosis reported among fossil mammals, both of them by Dr. Moodie (1923, pp. 249-251). The earlier case, a very doubtful one, occurs in the type of *Merychippus cam-*

[6] This disease is due to the action of the ray fungus, *Actinomyces,* which is found in nature on grasses, spears of oats, etc. The fungi obtain entry into the jaws when plants that carry them penetrate the gums, or the alveoli of decayed teeth, of feeding animals (Salmon and Smith, 1912, pp. 447-449, 452). The writer is indebted to Dr. Edward H. Hatton, Professor of Pathology, Northwestern University Dental School, for examining the specimen and confirming the tentative diagnosis.

pestris Gidley from the upper Miocene, and the second in a specimen of *Aphelops* sp., from the Snake Creek Pliocene. If correctly diagnosed, therefore, the pathologic condition of *Titanoides faberi* is of great interest as furnishing the earliest record of this disease and carrying back the history of actinomycosis almost to the beginning of the age of mammals.

Description of referred specimen, P. 14898: The tooth, probably M^2, is incomplete and considerably abraded. It is very similar to a corresponding molar of *Pantolambda*, the paracone and metacone being approximately equal in size. A difference from the Torrejon genus may be noticed, however, in the straighter external face of the tooth at hand, which is due to the smaller size of the parastyle and metastyle. The specimen, if correctly referred to *Titanoides* is of importance, as it indicates that there was no appreciable tendency toward the *Coryphodon* pattern in the upper molars of this genus.

MEASUREMENTS.

P 14637.	Length, I_1*-M_3	169. mm.
	P_1, ant.-post. diameter	17.5 mm.
	P_1, transverse diameter	10. mm.
	dm_3, ant.-post. diameter	15. mm.
	dm_3, transverse diameter	10.5 mm.
	P_4, ant.-post. diameter	18. mm.
	P_4, transverse diameter	17. mm.
	Molar series, length	80. mm.
	M_1, ant.-post. diameter	23.5 mm.
	M_1, transverse diameter†	18. mm.
	M_2, ant.-post. diameter	24. mm.
	M_2, transverse diameter	19.5 mm.
	M_3, ant.-post. diameter	30.5 mm.
	M_3, transverse diameter	19.5 mm.
	Breadth of symphysis at canine‡	49. mm.
	Depth of ramus at dm_3, external	51. mm.
	Depth of ramus at dm_3, internal	50. mm.
	Depth of ramus at M_1, external	43. mm.
	Depth of ramus at M_1, internal	50.5 mm.
	Depth of ramus at anterior border of M_3, external‡	37. mm.
	Depth of ramus at anterior border of M_3, internal	43.5 mm.
P 14898.	M^2 (?) ant.-post. diameter	26.5 mm.

Relationships of Titanoides: In Gidley's original description this genus was considered a possible relative of the titanotheres, a determination that appears to have been accepted by Abel (1922, pp. 271, 297).[6a] Schlosser (1923, p. 598)

* Measured from alveolar border. † Transverse diameters taken across trigonids. ‡Measurement a little uncertain as specimen slightly crushed at this point.

[6a] Abel later considered *Titanoides* as a primitive pantolambdid (1928, Weber's "Die Säugetiere," vol. 2, pp. 694-695).

refers *Titanoides* to the Pantolambdidae, with reservations, and Hay, in his "Second Bibliography and Catalogue," follows the same course. Matthew (1928, p. 969) does not definitely state his views but appears to imply a rather close affinity with *Pantolambda* and a more remote one with *Coryphodon*. Simpson (1929b, p. 9) places the genus in the Pantolambdidae, Jepson (1930, pp. 506-508) refers it to the Coryphodontidae and while recognizing certain differences between the teeth of the two genera states that "*Titanoides* seems to be in a pre-*Coryphodon* stage of amblypod evolution, and may be in the direct ancestral line of *Coryphodon*." As far as the writer is aware, these are the only views that have been offered on the taxonomic position of this genus.

Gidley's conception of a titanothere relationship has not been sustained, in fact, he later abandoned the idea in favor of amblypod affinities. The assignment of *Titanoides* to the Pantolambdidae by the several writers listed above is confirmed by the new material. The lower molars of this form and of *Pantolambda* are in fundamental agreement in possessing (1) the double V-pattern of the trigonid and talonid with (2) the rather sharp angulation of the cusps of the trigonid, and (3) a prominent paraconid. The upper molar described above, if correctly referred to *T. faberi*, furnishes very definite evidence that the genus is a member of this family. *T. primaevus* and *T. gidleyi* present a trifling divergence from *Pantolambda* in the possession (1) of external cingula on the lower molars and (2) of a prominent posterior cingulum which forms a ledge on the last two premolars. *T. faberi*, with its small posterior cingulum on P_4 and lack of external cingula, is an intermediary between the two other species of the genus and *Pantolambda* in these relatively unimportant characters. Other differences between the two genera have been listed earlier in the paper. These are of a comparatively minor nature and in no way affect the reference of *Titanoides* to the Pantolambdidae. Such differences as exist between the lower molars of the two forms are, however, of some interest. The slightly larger paraconid, smaller talonid, and more pronounced crista obliqua of *Titanoides* all seem to indicate that this genus has retained, comparatively unmodified, structures which have undergone a slight modification in *Pantolambda*. The modifications in the latter (i.e., slightly smaller paraconid, slightly larger talonid, and slightly more reduced crista obliqua) are advances, even if small, towards the *Coryphodon* type of lower molar. It seems evident, if the latter genus is used as a criterion, that *Pantolambda,* although an earlier form, is a trifle more specialized in molar pattern than the later and larger *Titanoides.*[7]

In its more sloping mandibular symphysis, triangular canines and larger size, *Titanoides* presents a closer approach to *Coryphodon* than does *Pantolambda.* These resemblances are, however, more than offset by the conservative dentition which definitely allies this genus with the Torrejon form and removes it from the ancestry of *Coryphodon.* The latter makes its first appearance in the uppermost Paleocene Clark Fork (Simpson, 1929B, p. 9; Jepson, 1930, p. 493). *Titanoides* is a post-Torrejon—and hence Upper Paleocene—genus. It would appear definitely impossible for the dentition of *Coryphodon* to be derived from that of *Titanoides* in the short space of time intervening.

Bearing of Titanoides faberi on the stratigraphy of the Grand River region: The two previously described specimens of this genus are of upper Paleocene age as at present understood. *T. primaevus* was collected near Buford, North Dakota, in the type locality of the Fort Union. Thom (see Jepson, 1930, p. 497) considers that the specimen came from the lower levels of the Sentinel Butte shale which, if correct, would indicate, according to the tentative correlations given by Simpson (1929a), that it was of approximately the same age as the Bear Creek and Tiffany faunas. The specimens of *T. gidleyi* were collected in northeastern Park County, Wyoming, from a horizon above the Torrejon sandstone (Jepson, 1930, p. 497). The presence of *T. faberi* in the basal levels of the Ruby formation in western Colorado is therefore very suggestive of an upper Paleocene horizon in this area.

Several workers, particularly Gale (1910, pp. 79-80), have suspected the presence of Paleocene beds in the region but have not had sufficient paleontological evidence to decide the question. Mr. Faber's discovery is important in this connection but does not in itself prove the existence of a formation belonging to this period. Correlation on the basis of a single form, however distinctive, would be uncertain, especially in view of recent investigations which have shown that a

[7] It should be noted that this argument has been developed solely from a comparison of the published figures with *T. faberi.* A larger series of specimens may well provide intergrades in lower molar pattern between the two Paleocene forms.

considerable number of genera bridged the Paleocene-Eocene boundary. *T. faberi* is not especially close to either of the previously described species and could quite possibly be a lower Eocene representative of the genus. It is hoped that further field work, now in prospect, will contribute to the solution of the problem.

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