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A Lance Didelphid Molar

With Comments on the Problems of the Lance Therians

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An unworn, unrooted lower molar tooth of a Lance didelphid has been found in the University of Chicago collection (now in Chicago Natural History Museum). It was uncatalogued and apparently had been forgotten since 1895, when it was found in the Lance formation, together with several other mammal and reptile tooth fragments. A notation on the capsule containing them reads: "Laramie Cret. Wyo. 1895." It gives no indication of the exact locality or the identity of the collector. The specimens were probably collected by S. W. Williston's 1895 field party, for E. S. Riggs, a student member of the party, informed me that some ant-hill fossil collecting was done by this group. It is also possible that the teeth are relicts from the Bauer collection, most of which has been lost.

The exact affinities of most of the hundreds of isolated, individual Late Cretaceous didelphid lower molars are uncertain. In handling these fragments Simpson (1929b) did not assign to them a formal nomenclature, as Marsh did. He thought it better to await discovery of more complete materials, and he simply grouped the teeth into various categories according to their structure. The specimen here described (CNHM-UM 633) may be helpful in future consideration of the teeth of some of these categories because its crown surface is unworn and perfectly preserved. Didelphid affinities are suggested by the size and generalized form of the tooth and by the location of the talonid cusps; the hypoconulid is nearly twinned with the entoconid (Simpson, 1951), but Mr. Bryan Patterson has called my attention to the fact that most shrews have a similar twinning of these two cusps. Therefore, Simpson's method of distinguishing between primitive insectivores and marsupials on the basis of characteristics of their isolated cheek teeth is not reliable. Other features besides

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the twinning of the hypoconulid and entoconid serve to distinguish the teeth of the Recent shrews and marsupials, but this does not mean that an ancestral shrew (or other primitive insectivore) could be easily distinguished from a primitive marsupial if these other specialized features were lacking.

Although CNHM-UM 633 does not compare exactly with any of Simpson's nine categories, or with the molars of *Thlaeodon padanicus* (Cope, 1892; Simpson, 1929b) or *Eodelphis cutleri* (Matthew, 1916; Woodward, 1916; and Simpson, 1928, 1929b), it does bear a much closer resemblance to some of these than to others. In size and crown proportions it compares about equally well with *Thlaeodon* and with Simpson's "type 3" (*Delphodon*) and "type 4" teeth, although it is less elongate and more nearly square in crown view than the last two. Unfortunately, the one complete lower molar of *Thlaeodon* is so badly worn or eroded that closer comparison is impossible. For these reasons no certain subfamily assignment can be given at present.

Class **MAMMALIA**

Subclass **Theria**

Order **Marsupialia**

Family **Didelphidae**

Subfamily incertae sedis

Description.—The specimen (fig. 212) is a right lower molar of irregular quadrangular outline in crown view, longer on the lingual side. The trigonid is only very slightly narrower at its base than the talonid; its principal cusps form a nearly right-angled triangle, the right angle at the metaconid. An extremely small antero-lingual cuspule lies low against the anterior edge of the paraconid, and a larger one forms the terminus of the short, inwardly rising antero-external cingular ridge near the middle of the anterior face of the tooth. The protoconid is connected to the paraconid by a straight, sharp ridge that lies at about a 60° angle to the long axis of the tooth. A similarly straight and sharp ridge connects the protoconid with the metaconid at very nearly a right angle to the long axis of the tooth. Both ridges are deeply notched so that they present broadly opened V's in anterior or posterior views. All three trigonid cusps are approximately the same height and show a slight reduction in size from protoconid to paraconid to metaconid. The trigonid is only slightly higher than the talonid. The latter is broad and presents a rather deep rounded central pit. The talonid cusps are unequal in size, the hypoconid being by far the largest. A stout, postero-medially directed ridge connects the hypoconid and the hypoconulid. Immediately antero-medial to the hypoconulid lies the somewhat larger entoconid. The apices of the three lingual cusps—paraconid, metaconid, and entoconid—lie in a straight line nearly parallel to the long axis of the tooth. A cingulum is developed only along the anterolateral face.

MEASUREMENTS

	mm.
Greatest length, along axis of tooth	5.1
Greatest width, perpendicular to long axis, trigonid	3.9
Greatest width, perpendicular to long axis, talonid	4.0
Protoconid to paraconid	2.2
Protoconid to metaconid	2.0
Paraconid to metaconid	1.4
Hypoconid to protoconid	2.2
Hypoconid to paraconid	3.9
Hypoconid to metaconid	3.1
Hypoconid to hypoconulid	2.3
Hypoconid to entoconid	2.5

THE PROBLEM OF THE ISOLATED LANCE THERIAN MOLARS

Most of the therian mammals of the Lance formation are known only from isolated tooth fragments or teeth. In only one form, *Thlaeodon padanicus*, are positively associated upper and lower teeth known. A few fragments of rami and maxillaries have been found. Since most of the Lance therians are marsupials of the family Didelphidae, and since the few recognized placentals present in the fauna have recently received attention, the chief problem of the Lance therian molars is one of didelphid relationships. A restudy of the entire aggregate of Lance therians is now feasible and much needed.

There is now available a considerably greater number of specimens than Simpson had for his 1929 study of the group. Amherst, the University of California, and the University of Wyoming have each acquired additional Lance materials. Chicago Natural History Museum has a few unstudied specimens, and no doubt other small collections could be located in various other institutions. Simpson (1951) has sorted out several lower molars that were formerly classed as marsupial. These he has assigned to the Insectivora and has discussed in detail the possible Cretaceous insectivore relationships that are based primarily on dental morphology. As far as I am aware, no statistical study of all of the available Lance therians has ever been

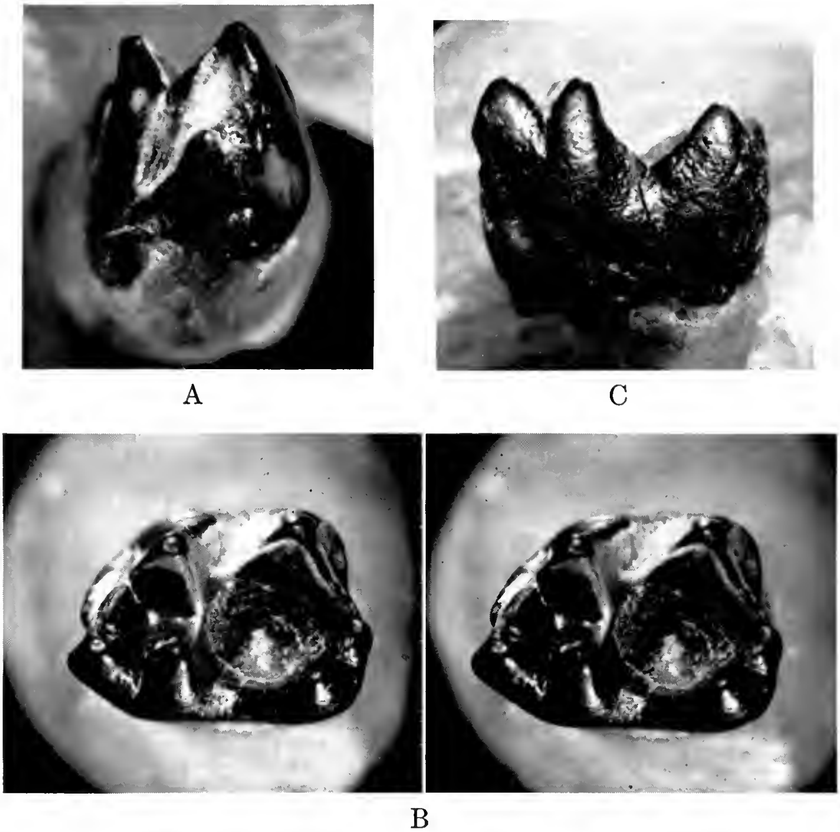

FIG. 212. Didelphid lower molar, CNHM-UM 633 (approx. × 6.5), from Lance formation. A, Anterior view. B, Crown view, in stereoscopic pair. C, Internal view.

made, and I feel certain that an attempt to relate upper and lower teeth on the basis of form, size, and frequency of occurrence would yield some positive results. It is important that an attempt be made to formalize a method of handling those faunas which are known from little besides tooth fragments, and which are so important to our understanding of early mammalian history; namely, the Rhaetic, Trinity, and Lance faunas. Two factors make the Lance fauna the logical one to start with. Neither of the others contains a form that is closely comparable with a Recent form. The most abundant Lance therians, on the other hand, are generalized didelphids—forms not too far removed from the Recent *Didelphis*. In addition, a check on such a method is soon to be available in the results of

Clemens' work at the University of California. His current studies of the Lance fauna are based on more numerous and far more complete materials than have been available heretofore.

In further studies of the isolated Lance didelphid molariform teeth, one possibility must be considered: many of these teeth may not be permanent molars at all; they may be examples of the one deciduous cheek tooth, the last deciduous premolar.[1] The size of a few of the lower "molars" suggests this possibility; also, the recognized deciduous premolars appear in only scanty numbers in the collections, while theoretically they should be expected to represent 20 per cent of the total number of molariform teeth, provided that they preserve equally well. Actually, any appreciable juvenile mortality would increase the relative number of deciduous premolars, so that one might expect them to be even more abundant than one in five. On the other hand, the nest environment of the juvenile animals may have been such that preservation of the deciduous premolars would be unlikely. Simpson (1929b) thought that his "type 8" lower molars (including the *Synconodon* lower teeth) might be milk molars. The "type 8" teeth, while truly molariform, are not completely molarized. This is evidenced by the relatively greatly elongated triangles formed by the position of the trigonid cusps and by the poorly developed paraconids as compared with those of the other molariform teeth. Simpson is doubtless correct in considering them to be milk molars. However, other fully molariform deciduous lower premolars may very well be present also, classified as molars among the remaining categories.

It would require only a slight advance in specialization beyond that of the "type 8" lower teeth to render them indistinguishable from the permanent molars. Certainly, it is not unreasonable to speculate on the likelihood that one or more members of the Lance marsupialian fauna could have been thus specialized. Such a hypothetical Lance didelphid would have deciduous lower premolars as molarized as those of *D. marsupialis,* in which the anterior molariform teeth ($dp_{\overline{3}}$, $M_{\overline{1}-\overline{3}}$) are all nearly indistinguishable from one another except by size. To gain further insight into the affinities of the Lance specimens they must be compared with the Recent *Didelphis,* or another Recent didelphid. A statistical study of all of the molariform cheek teeth of one or more of the Recent genera taken from a limited geographic range would demonstrate the form and

[1] Here designated $dp\frac{3}{3}$, with the knowledge that $dp\frac{4}{4}$ may eventually prove to be the more appropriate expression of the true homologies of these teeth.

size variation of these teeth, both from tooth to tooth within the same dentition, and from individual to individual—information that, when applied to the Lance ancestors, would be of the greatest help in clarifying their affinities. My crude statistics (pp. 534–535) indicate some of the potentialities that could derive from a thorough statistical study. Table I gives some indication of the dental variation in *Didelphis marsupialis* though from a statistical standpoint it is based on an inadequate sampling.[1]

Table I, which represents dental variation in but one species, provides the simplest basis for comparison with the Lance teeth. This comparison is, I think, reasonable, since the isolated Lance molars represent a relatively small number of genera and species. The sample was so chosen as to comprise a series of individuals of every age stage possessing developed molariform cheek teeth. An attempt was also made to have the series include a good representation of both sexes for each age, but unfortunately this representation is unequal. Figure 213 is included to explain the method of tooth measurement used and to clarify the two different measures of length and width of the $M^{\underline{4}}$'s (Table 1). The first set is the more logical when the orientation within the mouth is known, but for comparison with the Lance teeth a measure based solely upon characteristics of the teeth themselves is necessary, since they cannot be oriented exactly.

In the table one point should be noted, namely, the extreme difference in width between upper deciduous premolars and $M^{\underline{3}}$'s, the largest of the molars. In specimens CNHM 54649 and CNHM 5700 (the only two individuals in the sample with functional $dp^{\underline{3}}$'s and $M^{\underline{3}}$'s) there is but a 33 per cent and 40 per cent increase in width, respectively, from $M^{\underline{1}}$ to $M^{\underline{3}}$. In contrast to this, the penultimate molars measure 100 per cent wider than the deciduous teeth. The means of this sample indicate that these two individuals are not extreme in this regard. Now, with *Didelphis* showing a size variation of its molariform cheek teeth of this order of magnitude, unless it can be demonstrated that there were no Lance didelphids with equally advanced premolars, I feel that we must be prepared to accept as a possibility a Lance form with a similar size range in its molariform teeth. From the standpoint of size criteria alone, the one Recent

[1] There was not available an adequate sample of *Didelphis* drawn from a restricted geographic area. Specimens CHNM 18430, 41088, 55733, and the Davis specimen are from Illinois; 29747, 30271 and 56465 are from Indiana. The remainder are from more distant areas: 14936, from Florida; 19089, from Ohio; 54649, from Michigan; 5700, from West Virginia; 6869, from Oklahoma; and 55663, from Texas.

form examined shows magnitude differences approaching those shown by the Lance teeth.[1]

Thus far, the concern has been with size variation almost exclusively, but a comparison of structural categories within the cheek teeth of *Didelphis* with those within the Lance specimens might also

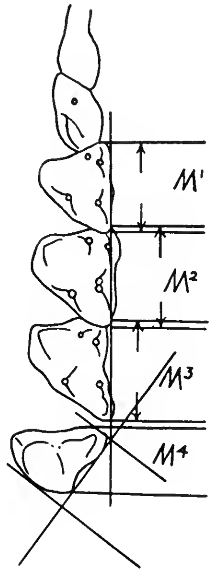

FIG. 213. Scheme to illustrate the method used in measuring Recent didelphid teeth.

be informative (see Tables II and III). Table II is compiled from Simpson's listing of the structural categories of the Lance lower molars. Table III is my attempt to classify the molariform cheek teeth of one individual of *D. marsupialis* into a comparable set of categories. Including the deciduous teeth, at least three such categories can be distinguished, or at least if found isolated as the Lance teeth are, they could be so classified (see footnote, Table III).

Since three forms of lower "molar" teeth are found in one individual of a Recent didelphid species, Simpson's list of eight structural categories of didelphid lower molars ("type 9" being referred to the Insectivora) suggests that only a few species (perhaps four or five) from two or three genera made up the Lance didelphid fauna.

[1] A spot check of other Recent didelphids shows that *Didelphis* is not alone in this respect. The spread seems to be as broad for *Philander opossum, Lutreolina crassicaudata, Chironectes minimus* and *Caluromys* sp.

To summarize briefly: The comparisons presented indicate that the relationships and affinities of the Lance molar teeth should be re-examined. A thorough statistical study of the dentitions of several Recent didelphids should first be made, and this would then serve as a sound basis for comparison. The need for such a statistical approach can hardly be overemphasized; understanding of the Lance teeth hinges on it, and possibly a basic methodology for handling similar "tooth fragment" faunas could well stem from such an approach.

My sincere thanks to Mr. Patterson and Dr. Rainer Zangerl for reading the manuscript and offering criticisms.

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TABLE I.—Measurements of Molariform Teeth in *Didelphis marsupialis*

	CNHM 14936 juv. sex?		CNHM 18430 juv. ♂		CNHM 29747 juv. sex?		CNHM 19089 juv. ♂		CNHM 54649 juv. ♂		CNHM 5700 juv. ♂		CNHM 6869 juv. ♀	
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
Length														
dp^3	5.2	5.1	5.4	5.3	4.8	4.8	4.7	4.7	5.4	5.4	5.1	S	S	S
M^1	X	X	5.9	5.9	5.4	5.4	5.7	5.7	5.9	5.9	5.8	5.8	5.7	5.7
M^2	T	T	X	X	5.9	5.9	6.5	6.5	5.9	5.9	6.4	6.4	6.4	6.5
M^3	T	T	T	T	X	X	X	X	5.9	5.9	6.5	6.5	6.8	6.8
M^4	T	T	T	T	T	T	T	T	X	X	X	X	X	X
Length														
dp_3	5.0	5.0	4.9	4.9	4.5	4.3	4.4	4.5	4.9	4.9	S	S	S	S
M_1	X	5.8	5.9	5.9	5.6	5.7	5.6	5.6	5.7	5.7	5.6	5.6	5.8	5.7
M_2	X	X	6.3	6.4	6.2	6.1	6.2	6.2	6.2	6.2	6.4	6.4	6.3	6.4
M_3	T	T	X	X	6.9	6.9	6.9	6.9	6.5	6.5	7.2	7.2	7.3	7.3
M_4	T	T	T	T	X	X	X	X	X	X	X	X	7.2	7.1
Width														
dp^3	3.2	3.2	3.2	3.2	3.0	3.0	3.0	3.0	3.0	3.0	3.3	S	S	S
M^1	X	X	5.0	4.8	4.5	4.4	4.4	4.4	4.5	4.5	4.7	4.7	4.6	4.6
M^2	T	T	X	X	5.6	5.6	5.4	5.4	5.4	5.4	5.7	5.6	5.4	5.5
M^3	T	T	T	T	X	X	X	X	6.0	6.0	6.6	6.6	6.8	6.8
M^4	T	T	T	T	T	T	T	T	X	X	X	X	X	X
Width (trigonid)														
dp_3	2.2	2.2	2.3	2.3	2.2	2.2	2.2	2.2	2.3	2.4	S	S	S	S
M_1	2.5	2.5	2.9	2.9	2.9	2.9	2.8	2.8	2.9	2.9	3.0	3.1	3.0	3.0
M_2	X	X	3.5	3.5	3.3	3.2	3.2	3.2	3.3	3.3	3.5	3.5	3.3	3.3
M_3	T	T	X	X	3.4	3.4	3.4	3.4	3.3	3.3	3.7	3.7	3.5	3.6
M_4	T	T	T	T	X	X	X	X	X	X	X	X	3.5	3.6
Width (talonid)														
dp_3	2.8	2.8	2.9	2.9	2.6	2.5	2.5	2.5	2.7	2.7	S	S	S	S
M_1	X	X	3.5	3.5	3.2	3.2	3.2	3.3	3.5	3.5	b3.4	3.5	3.2	3.2
M_2	X	X	3.8	3.8	3.7	3.6	3.7	3.7	3.7	3.7	3.8	3.8	3.5	3.5
M_3	T	T	X	X	3.8	X	3.9	3.8	3.3	3.3	4.0	4.0	3.8	3.8
M_4	T	T	T	T	X	X	X	X	X	X	X	X	3.1	3.1

S = shed through normal replacement.
M = missing from alveolus.
X = formed but not erupted far enough to measure.
T = tooth not developed.
b = broken.
* = measured according to axis of cheek tooth series (fig. 213).
** = measured according to long axis of tooth itself (fig. 213).

TABLE I.—Measurements of Molariform Teeth in *Didelphis marsupialis* (*continued*)

	CNHM 30271 juv. ♂		CNHM 55663 young ad. ?♂		CNHM 41088 young ad. ?♀		CNHM 56465 young ad. ♀		CNHM[1] young ad. ♂		CNHM 55733 ad. ♂		Mean
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	
Length													
dp^3	S	S	S	S	S	S	S	S	S	S	S	S	5.1
M^1	5.8	5.8	5.4	5.5	5.2	5.2	5.2	5.2	5.8	5.8	5.7	5.7	5.6
M^2	6.6	6.6	6.0	5.9	6.2	6.2	6.1	6.1	6.3	6.4	6.4	M	6.2
M^3	6.9	b6.8	b6.5	6.4	6.8	6.8	6.5	6.5	6.2	6.2	7.0	7.0	6.6
M^4	X	X	*4.8	4.9	3.4	3.4	M	4.0	4.3	4.3	4.4	M	4.1
			**(5.7)	(5.7)	(5.2)	(5.2)		(5.2)	(5.1)	(5.1)	(6.1)		(5.4)
Length													
dp_3	S	S	S	S	S	S	S	S	S	S	S	S	4.7
M_1	5.8	5.8	5.5	5.5	5.1	5.1	5.2	5.2	5.5	5.4	5.7	5.7	5.6
M_2	6.5	6.5	6.1	6.1	5.8	5.8	6.1	6.1	6.4	6.4	6.4	6.3	6.2
M_3	7.0	6.9	b6.4	6.6	6.7	6.7	6.6	6.6	6.4	6.5	7.2	7.2	6.8
M_4	7.2	M	6.7	6.6	6.7	6.7	6.8	6.8	6.3	6.3	6.8	6.8	6.8
Width													
dp^3	S	S	S	S	S	S	S	S	S	S	S	S	3.1
M^1	5.0	5.0	4.7	4.6	4.7	4.7	4.5	4.5	4.6	4.6	4.6	4.6	4.6
M^2	6.1	b6.0	b5.2	5.5	5.4	5.4	5.3	5.3	5.6	5.7	5.8	M	5.5
M^3	6.7	7.1	b6.0	6.1	6.4	6.4	6.0	6.0	5.9	6.1	6.6	6.6	6.4
M^4	X	X	*7.1	7.2	5.7	5.8	M	6.3	6.2	6.2	7.0	M	6.4
			**(6.5)	(5.9)	(3.8)	(4.0)		(5.1)	(4.8)	(4.9)	(5.6)		(5.1)
Width (trigonid)													
dp_3	S	S	S	S	S	S	S	S	S	S	S	S	2.3
M_1	3.0	3.0	2.8	2.7	2.8	2.9	2.8	2.8	3.0	3.1	3.0	2.9	3.0
M_2	3.3	3.4	3.2	3.3	3.2	3.2	3.3	b	3.4	3.4	3.3	3.3	3.3
M_3	3.7	b3.7	b	3.4	3.6	3.6	3.4	3.4	3.4	3.4	3.6	3.6	3.5
M_4	3.4	M	3.3	3.3	3.2	3.2	3.0	3.0	3.1	3.1	3.5	3.5	3.3
Width (talonid)													
dp_3	S	S	S	S	S	S	S	S	S	S	S	S	2.7
M_1	3.3	3.4	3.2	3.2	3.2	3.3	3.2	3.3	3.4	3.4	3.3	3.3	3.3
M_2	3.7	3.7	3.6	3.6	3.4	3.4	3.6	3.4	3.7	3.7	3.7	3.7	3.6
M_3	3.8	3.8	3.5	3.6	3.6	3.6	3.5	3.4	3.6	3.6	3.9	3.8	3.7
M_4	3.1	M	3.1	3.0	2.8	2.7	2.8	2.9	2.5	2.5	3.5	3.3	3.0

[1] Property of D. Dwight Davis, Department of Zoology.

TABLE II.—Didelphid Lower Molars from Lance Formation (as listed by Simpson)

Structural Type	Size	Relative Heights: Trd–Tald (degree)	Relative Heights: Indiv. Cusps Trigonid	Relative Heights: Indiv. Cusps Talonid	Relative Size: Trigonid	Relative Size: Talonid	Cingulum	Other
Type 1..... (*Cimolestes*)	Small	Trd > Tald (markedly)	prd > med > pad (pad reduced)	...	...	...	Anterior cingulum present*	...
Type 2..... (*Diaphorodon*)	Rel. large	Trd > Tald (somewhat)	prd = pad; med reduced	...	...	...	Anterior cingulum broad, almost basined	Trigonid compressed antero-posteriorly
Type 3..... (*Delphodon*)	Varied large to small	Trd > Tald (little)	pad = med; prd = or > pad and med	Three dist. cusps; hld and end approximated	Talonid large, with basin		Anterior cingulum not basined or pronounced	Probably represents several spp. or even genera
Type 4.....	Large	Trd > Tald (little)	pad > prd = med	Three cusps; hld and end imperfectly separated	...	...	...	May be = *Diaphorodon* (chief diff. height of prd)
Type 5.....	Very small	Trd > Tald	prd > pad = med (prd decidedly largest cusp)	...	Trigonid and talonid strongly marked off from one another		...	...
Type 6.....	Small*	Trd = Tald (nearly)	prd > med > pad	...	...	...	Anterior cingulum absent	...
Type 7.....	Very small*	Trd > Tald (somewhat)	prd > med > pad (pad much reduced)	Unusually distinct from each other and sharp	...	...	Anterior cingulum present*	...
Type 8..... (incl. *Syncon-odon* lower)	Small*	Trd > Tald (little)	prd > med > pad	...	Trigonid long and laterally compressed		Anterior cingulum absent*	Trigonid similar in lateral compression to *Didelphis**
Type 9.....	Very small*	Trd > Tald	prd = med; pad almost vestigial	Two distinct talonid cusps	...	...	...	Now placed in the Insectivora

* Either obvious from Simpson's figures, though not stated, or observed by me.

TABLE III.—Structural Categories of Molariform Cheek Teeth of *Didelphis marsupialis*

Upper Cheek Teeth

Type 1 dp^3......Molariform, but extremely compressed laterally, three-rooted, and with little stylar development anteriorly.

Type 2* M^{1-3}....Alike in that all have a good external stylar development.

Type 3 M^4......Lacks distinctly triangular outline of the other molars because of reduction of posterior portion of external stylar shelf.

Lower Cheek Teeth

Type 1 dp_3......Fully molariform, even as to cusp positioning, but with paraconid much the smallest of the trigonid cusps.

Type 2* M_{1-3}....Talonid as broad as trigonid or broader; trigonid cusps about equal; trigonid higher than talonid (increasingly so from M_1 to M_3).

Type 3 M_4......Talonid narrower than trigonid; trigonid cusps distinctly unequal.

* In these instances the structural categories are conservatively chosen. Many of the minor differences in cusp height and crown proportions could easily be singled out as the basis for additional categories.