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A REVISION OF THE FOSSIL SELENODONT ARTIODACTYLS FROM THE MIDDLE MIOCENE THOMAS FARM, GILCHRIST COUNTY, FLORIDA

By

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INTRODUCTION

Since its discovery in 1931 the fossil locality at Thomas Farm in Gilchrist County, Florida, has proven to be the most prolific Miocene deposit east of the Mississippi River. The vertebrate fauna is impressive, both in numbers of individuals and in variety of forms present, and has greatly increased our knowledge of the Florida Miocene and its correlation with western faunas of comparable age. By far the most numerous animals are the horses, which may be used in such correlations more successfully than any other group. However, it is in the Artiodactyla that the most highly specialized forms are to be found, some of which show no close relationship to known genera of the western plains.

The strange combination of characters found in *Floridatragulus* dolichanthereus, for example, has led authors in the past to place this animal in three distinct families, the Hypertragulidae, the Protoceratidae, and the Camelidae. White (1940) described the first jaw of this species as a new genus of Hypertragulidae without discussing its relationship or similarities with other known hypertragulids. Additional specimens (referred to this species in the present paper) were subsequently named as a second species of *Floridatragulus* (White, 1947), a second genus of Hypertragulidae, *Hypermekops olseni* (White, 1942), and, in the case of a partial palate, as a species of *Syndyoceras*, a protoceratid (White, 1941). Following White's determinations, Romer (1947) retained these generic names in his discussion of the mammalian fauna of Thomas Farm. It was not until 1957, when Professor Bryan Patterson prepared a manuscript catalogue of the Thomas Farm vertebrates in

the collections of the Museum of Comparative Zoology, that a major reorganization of the taxa became available. In this reference, Patterson considered all of the above specimens as a single camelid species. Although never published, this list has become incorporated, partially or completely, into almost every major taxonomic reference concerning late Tertiary Floridian mammals, most notably Ray, 1957, and Puri and Vernon, 1964.

A similarly confused story is associated with the history of *Nothokemas floridanus*, which was originally made the nominate genus of a new hypertraguloid family, the Nothokemadidae (White, 1947). This, also, was referred to the Camelidae by Patterson.

No new material has been added to the MCZ collection since 1957, but it became clear that a restudy of these artiodactyls in the light of Patterson's list was necessary. This is the purpose of the present work, which, in addition, presents a more detailed description of the species involved than has hitherto been available. A concurrent study of the postcranial remains has contributed to our knowledge of these forms.

The present study confirms Patterson's findings except for the change in rank of *Synthetoceras australis* and the interesting addition of an oreodont to the fauna.

A discussion of the perplexing geological problems involving the bone-bearing sediments of the Thomas Farm is beyond the purpose and scope of this report, but a detailed review is available in Puri and Vernon (1964). Older accounts of the quarry itself may be found in Simpson (1932), and White (1942).

I am indebted to Professor Bryan Patterson for suggesting the problem and for his helpful discussions and suggestions throughout the course of the research. I also wish to thank Dr. Malcolm Mc-Kenna for permitting the examination and loan of specimens in the American Museum and Frick collections, Mr. Morris F. Skinner for his help in the identification of the oreodont remains, and Mr. Beryl E. Taylor for his examination of some indeterminate camel molars.

Abbreviations used in this paper are as follows: American Museum of Natural History (AMNH), Carnegie Museum (CM), Florida State Geological Survey (FSGS), Museum of Comparative Zoology (MCZ), and Yale Peabody Museum (YPM).

DESCRIPTION OF SPECIES CAMELIDAE

FLORIDATRAGULINAE new subfamily¹ FLORIDATRAGULUS DOLICHANTHEREUS White

Floridatragulus dolichanthereus White, 1940, p. 35, pl. VII. Syndyoceras australis White, 1941 (in part), p. 97, pl. XV, figs. 1a, 1b. Hypermekops olseni White, 1942, pp. 11-12, pl. 8. Floridatragulus barbouri White, 1947, pp. 505-507, fig. 4.

Hypodigm: MCZ 3635, type, incomplete mandible with M_1 to M_3 and alveoli for P_1 to P_3 , anterior crescent of right M_1 and hypoconulid of right M_3 missing, both ascending rami and the symphysis anterior to the C-P₁ diastema missing; MCZ 4086 (type of *F. barbouri*), right mandible with partial symphysis and complete ascending ramus, left canine, right P_2 to M_3 and the alveoli for P_1 ; MCZ 3711 (type of *Hypermekops olseni*), incomplete skull with right I¹ and I², P⁴ to M³, left I², P⁴ to M³, and the alveoli for the remainder of the dentition; MCZ 3642 (paratype of *Syndyoceras australis*), left palate with P³ to M³; MCZ 4291, right mandible with P₃ to M₃ and alveoli for P₁ and P₂; MCZ 7780, 30 astragali; MCZ 7781, 11 calcanea; MCZ 7782, 15 cuboids; MCZ 7785, 10 second phalanges; MCZ 7786, 6 ungual phalanges; MCZ 7787, 4 metapodials.

Horizon and locality: Middle Miocene, Hawthorne Formation, Thomas Farm, 8 miles north of the town of Bell, Gilchrist County, Florida.

Redescription: The referred skull (MCZ 3711) is a reconstruction of a badly broken and incomplete specimen designated as the type of the supposed hypertragulid, *Hypermekops olseni*, by White (1942, pl. 8). Its most striking character is the narrow and very long snout, the region from P² to the anterior tip of the premaxillary being more than twice the length of the continuous premolar-molar series. The anterior teeth from I¹ nearly to P² form straight rows on each side of the snout, parallel to each other. Just anterior to P² the palate begins to widen, becoming, at the level of M³, more than twice the snout width. The skull is very low throughout, with the nasal bones nearly parallel to the palate below. Above, the frontals are expanded and send down broad, flat, postorbital processes which do not reach the zygomatic arch, the orbit being open behind. The cranium is largely missing, but

¹ See page 9 for diagnosis.

parts of the occipital and temporal regions are preserved. The supraoccipital forms a very high lambdoidal crest, considerably higher than in Paratylopus primaevus and more vertical in orientation. Although the parietals are missing, there are indications that the sagittal crest was also quite prominent. The occipital condyles are relatively narrower than in Paratylopus primaevus; these are confluent in MCZ 7764 but separated by a median groove in MCZ 3711. The auditory region is poorly known, only the posterolateral portion of the right bulla being present. It is clear that this fragment was erroneously oriented on the reconstructed skull and was almost certainly closer to the condyles, with the tympanohyal recess and groove directed posterolaterally rather than laterally, as restored. The bullae were also probably somewhat larger than figured and filled with spongy bone. The molar series is situated well forward, with the posterior edge of M³ some distance in front of the orbit; the internal nares open behind this tooth.

The lower jaw of *F*. dolichanthereus shows many specializations similar to those of the skull, especially in the great elongation and in the reduction of the premolars. The mandible is narrow anterior to P_1 and expands to approximately five and a half times that width at the angle of the jaw. The symphysis is long, ending some distance behind P_1 , with the jaws solidly fused along its length. The angle of the jaw is strongly hooked in typical camelid fashion, and the coronoid process is long and narrow. The jaw is very deep posterior to P_2 , as in *Myotylopus bathygnathus*.

The dental formula is I_3^3 , C_1^1 , P_4^4 , M_3^3 . In MCZ 3711 I¹ is a large, caniniform tooth worn posteriorly along its entire height and along a broader area lingually. It is situated on the side of the snout near the posterior margin of the elongated incisive foramen.

A long diastema separates I^1 and I^2 ; this is the longest spacing within the dental row. I^2 is also caniniform, smaller than I^1 and somewhat compressed laterally. Its anterior and posterior margins are raised to form a blade-like ridge. It is strongly recurved, and except for a small area at the very tip, is unworn.

 I^3 is separated from I^2 by a diastema equal to somewhat less than half that separating the first two incisors. This tooth is missing on both sides but the alveoli indicate a tooth similar to, but smaller than I^2 . The alveolus for the canine follows after a very short diastema equal to little more than its own diameter, and suggests a tooth no larger (and probably smaller) than I^3 . After another equally short diastema comes the alveolus for P¹. This was a single-rooted tooth and could not have been more than a mere vestige judging from the size of the socket.

A very long diastema nearly equal to that separating I^1 and I^2 separates P^1 and P^2 . The second premolar (Fig. 1) is a long, narrow, two-rooted tooth similar to that in *Poebrotherium wilsoni* and in its relation to the molars it is essentially unreduced from the condition in that species. Its three cusps are in a straight line and are connected to each other by a sharp, high ridge. A weak basal cingulum is present along the anterior and posterior of the lingual surface and a well developed parastyle runs the height of the tooth.

 P^3 is preserved on the referred palate, MCZ 3642, and is only slightly reduced, three cusped, and three rooted. It is shorter and wider than P^2 with the internal basal cingulum similarly developed, but less so than in *Poebrotherium*. Externally, the tooth is simple with the parastyle nearly indistinguishable and the mesostyle represented only by a low convex ridge.

The fourth premolar is a small triangular tooth with a shorter inner crescent that remains separate from the outer crescent until the tooth is considerably worn. The difference in length between the inner and outer crescents is about as in *Paratylopus primaevus* and, as in that species, the inner crescent is skewed anteriorly. The outer face is relatively simple with low antero- and posteroexternal styles and a low median convex ridge. Short weak cingula are present on the anterior and posterior sides of the inner crescent. This tooth is somewhat more reduced than in *Oxydactylus longipes* or *Paratylopus primaevus*, which are more nearly like *Poebrotherium* in this respect.

The molars increase in both length and width from M¹ to M³, as in *Paratylopus primaevus*, and are as brachyodont as in that species. M¹ is wider than it is long resembling the nearly square first molar of *P. primaevus* and *M. bathygnathus*, more so than the elongated M¹ of *O. longipes*. This tooth is only moderately worn in MCZ 3642 and has a strong parastyle, as in "*Paratylopus*" cameloides.² The mesostyle is directed perpendicular to the outer face of the tooth and is as strong as in *O. longipes*. The metastyle is absent. The median ridges on the outer face of the tooth are very prominent, especially on the anterior crescent, and widen somewhat near the base of the crown. This last feature is similar to the condition found in *P. primaevus* and quite unlike that in

² I am not convinced that *cameloides* belongs in this genus.

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Poebrotherium or Oxydactylus. A prominent internal pillar rises from the bases of the protocone and hypocone, particularly the latter. A similar pillar is found in *M. bathygnathus* and "*P.*" cameloides and incipiently on M^3 of *P. primaevus*. The protocone remains separated from the mesostylar region until worn nearly to the base of the crown, whereas the hypocone fuses to this area somewhat earlier. A very weak basal cingulum marks the posterior edge of the hypocone.



Figure 1. *Floridatragulus dolichanthereus. a*, Diagram of upper dentition, X 4/5. *b*, *c*, Composite crown view of left cheek teeth; *b*, upper P² to M³, *c*, lower P₂ to M₃, X1.

 M^2 is as long as it is wide in MCZ 3642, but slightly wider than long in MCZ 3711. It is similar to M^1 with the para- and mesostyle more prominent. The median ridge of the anterior crescent is considerably stronger than that of the posterior one. M^3 is similar to M^2 , but with a somewhat weaker and less compressed mesostyle. The lower incisors are unknown. A large, strongly recurved canine is present in MCZ 4086 and is heavily worn posteriorly to a point below the crown. The tooth is slightly compressed laterally and emerges from its socket at a lateral inclination of about 20 degrees from the vertical.

 P_1 is separated from the canine by a long diastema somewhat exceeding the combined length of M_1 and M_2 in the type, but variable in referred specimens. P_1 is not preserved, but the alveoli indicate a small, one-rooted tooth probably similar to P^1 and roughly equivalent to it in size.

After another long diastema the second premolar follows (Fig. 1c) and is a simple, two-rooted, three-cusped, trenchant, and laterally compressed tooth. The cusps are essentially in a straight line, the anterior cusp being very slightly inflected medially as in *Poe-brotherium eximium*, but the tooth is generally much more robust than in that species. This tooth did not occlude with the upper dentition, as shown by its completely unworn condition.

The diastema between P_2 and P_3 is quite variable; that of MCZ 4086 is 52 per cent smaller than that of the type. P_3 is similar to P_2 but more robust. The anterior cusp is more inflected producing a well defined parastylid which does not continue to the base of the crown. Only a suggestion of a posterior intermediate crest is present internal to the median cusp. The outer surface is simple and gently convex.

 P_4 follows immediately behind P_3 and is shorter and broader than the latter. This tooth strongly contrasts with its homologue in *O. longipes*, being somewhat more reduced and morphologically simplified. The anterior cusp is more inflected than in P_3 , but does not form the prominent right angle of *Poebrotherium wilsoni*, nor the sharply bent and somewhat expanded anterior column of *Oxydactylus*. The lake enclosed between the posterior and posterior intermediate crests is relatively small and shallow. Laterally the surface is simple, lacking prominent ridges and troughs.

The molars become larger from front to back, are simple and generally similar to each other. The lingual faces of the inner crescents are gently convex and for the most part lack distinct stylids and median ridges. A parastylid is only suggested on the type, but is absent on MCZ 4291, and present, although weak, on MCZ 4086. A distinct median pillar rises from the bases of the external crescents of each molar.

The metaconid remains isolated from the other crescents until worn to the base, whereas the anterior crest of the hypoconid fuses

early to the entoconid and protoconid. The hypoconulid is divided, forming two grinding surfaces; the space between these is continuous with the space between the posterior pair of crescents in young individuals. The two grinding surfaces quickly fuse at their anterior extremity and the fusion proceeds posteriorly with wear.

Discussion: From the material available, it appears that only one species of Floridatragulus is represented in the Thomas Farm fauna. As mentioned above, the P1-P2 and P2-P3 diastemata are quite variable, but this may be due to the functionless condition of P_2 . Similar variation is observed in Lama with respect to the non-occluding canine. The referred jaw, MCZ 4291, is not as deep as in the type or in MCZ 4086 by about 30 per cent. This kind of variation is also seen in Lama, although not to the same extent. MCZ 4291 also differs in the position of the posterior extent of the symphysis which is almost directly under P_1 rather than about 14 mm behind this tooth as in the type. McKenna (1966) notes two species of Floridatragulus, but does not discuss the reasons for this decision. The differences noted above possibly indicate a second species, but until additional material is available for study it is preferable to refer this specimen (MCZ 4291), at least tentatively, to F. dolichanthereus.

The camelid affinities of this species are inferred from such typical characters as the hooked angle of the jaw, auditory bullae filled with spongy bone and divided by a tympanohyal pit and groove, relatively simple premolars, and the similarity of the dentition as a whole to those of such early camels as *Poebrotherium* and *Paratylopus*.³

The upper dentition of F. dolichanthereus is more nearly like that of Paratylopus primaevus than like the Miocene Oxydactyluslike camels. The open orbit, squared molars, retention of prominent mesostyles, presence of median internal pillars, and graded increase in size from M¹ to M³ indicate an origin close to P. primaevus. In the elongated snout and deep jaws this form resembles Miotylopus bathygnathus, but this similarity is probably no more than a parallel development of habitus characters. Other characters which Miotylopus shares with Floridatragulus, such as median pillars, reduced upper canine, and (probably) an open

³G. M. Allen, in a personal communication to T. Barbour, expressed this view more than 20 years ago (correspondence in the Harvard Archives).

orbit, more likely indicate retention and development of the primitive characters of a *Paratylopus*-like ancestor than any close phylogenetic relationship.

The many distinctive characters which separate this genus from other late Tertiary Camelidae have justifiably confused past workers. The greatly elongated snout is a peculiar habitus character, which is only distantly approached in such specialized forms as *O. longirostris* and "*P*." cameloides, and the large caniniform incisors decreasing in size from I¹ to I³ are peculiar to this genus. In the mandible the long symphysis and exceptionally narrow jaw strongly divergent in the region of the cheek teeth are not seen in other camels. Also, the very simplified premolars and divided hypoconulid of M₃ tend to set this form off from other Miocene camels.

A number of astragali, calcanea, and proximal phalanges are referred to this species. The tarsal bones are similar to those of other Miocene camels and show no distinctive characters. As is common in other camels with an elongated snout, the phalanges are long and slender.

Two distinct morphological groups of phalanges are present; these are differentiated by the symmetry and dorsal extent of the distal articular facet. Differences of this type are present between the manus and pes of the Recent species of *Dorcatherium*, *Moschus*, and *Lama* and probably represent manus-pes differences in the present species also.

The referred metapodial fragments show that the metatarsals are closely appressed, with some fusion near the proximal end; the plantar processes are completely coossified. Metatarsal II is fused with metatarsal III, whereas metatarsal V is entirely separate from metatarsal IV and articulates with it by a small facet. Metacarpals III and IV are separate.

Because of the very peculiar characters of this genus and because of its distant relationship to contemporary camelids, it is proposed that a new subfamily, the Floridatragulinae, be established to receive it, with the subfamilial diagnostic characters being those of the genus until such time as additional members of this group are found.

DIAGNOSIS OF THE SUBFAMILY FLORIDATRAGULINAE

Differing from Miocene Alticamelinae in retention of many primitive characters such as complete brachyodont dentition, open orbits, and nearly square upper molars with median pillars; upper

incisors caniniform, lateral in position, separated from each other by diastemata, unlike those of Camelinae; premolars tending toward reduction and simplification, but less so than in Stenomylinae; lower molars simple with pillars, hypoconulid of M_3 divided.

TABLE 1

Comparative measurements of *Floridatragulus* dolichanthereus in mm

	Floridatragulus dolichanthereus		Paratylopus primaevus
	MCZ 3711	MCZ 3642	AMNH 9806
Skull length to condyles	^a 385	_	^a 200
Width of palate at P ¹	45	-	21
Width of palate at M ²	^a 76	_	52
Ratio: snout (Pmx to orbit) to skull length	*0.70	_	0.51
Tip of Pmx to I ¹	23		
I ¹ length	9	-	- \
I ¹ width	7	-	-
I ² length	7	-	-
I ² width	4.5	-	-
I ¹ to I ² diastema	37.5	_	
I ³ to canine	9	-	3
Canine to P1 diastema	9	_	4
P ¹ to P ² diastema	28		7.5
P ¹ length	11.5		
P ¹ width	4	_	
P ³ length	_	10	_
P ³ width	—	5	_
P ⁴ length	9	9	8
P ⁴ width	8.5	8.5	^a 8
M ¹ length	ь12	13.5	^a 10
M ¹ width	^b 15	15	ª12
M ² length	16	17	ª13
M ² width	17	17	ª13
M ³ length	18.5		16
M ³ width	18.5		14.5

	MCZ 3635	MCZ 4086	MCZ 4291
Jaw length	_	^a 300	_
Length of symphysis behind P ₁	13	14	3
Width of jaw at P ₁	18.7	19.5	_
Width at M ₃		*70	_
Depth of jaw under P ₁	21.5	21	14
Depth under P ₄	ª32	32	23
Depth under M ₃	*38	37	*32?
Canine to P ₁ diastema	_	28.5	_
P ₁ to P ₂ diastema	33	37	24
P ₂ length		10.5	_
P ₂ width		3.7	_
P ₂ to P ₃ diastema	21	10.5	19.5
P ₃ length		10.5	^a 10.5
P ₃ width	_	4.5	^a 4.5
P ₄ length	-	10	^a 10
P ₄ width	_	6	6
M ₁ length	ª13	10	10.5
M ₁ width	^a 9	9	8.5
M ₂ length	15.5	15	15.5
M ₂ width	11	11	11
M ₃ length	25.5	13	13
M3 width	12.5	13	13

Floridatragulus dolichanthereus

^a estimate based on incomplete specimen. ^b worn.

ALTICAMELINAE

NOTHOKEMAS FLORIDANUS (Simpson) 1932

Oxydactylus floridanus Simpson, 1932, pp. 35-37, figs. 20, 21. Paratylopus grandis White, 1940, p. 33, pl. V.

Nothokemas grandis White, 1947, pp. 508-515, figs. 5, 6.

Hypodigm: FSGS V-5247, type, incomplete right maxilla with P^2 to M^3 ; FSGS V-5238, paratype, right lower jaw with P_3 to M_3 ; MCZ 3636 (type of *N. grandis*), incomplete right mandible with P_3 to M_3 and alveolus for P_2 ; MCZ 4322, right maxilla with P_2 to M_3 ; MCZ 4323, left mandible with P_4 to M_2 and anterior crescent pair of M_3 ; MCZ 4324, partial left mandible with P_2 to

 P_4 ; MCZ 4325, left mandible with M_1 to M_3 and alveoli for P_2 to P_4 ; MCZ 4326, left mandible with dP_3 to M_2 ; MCZ 4329, crushed skull with poorly preserved P^2 to M^3 , rostrum anterior to P^{1} - P^{2} diastema missing; MCZ 4541, crushed skull with dP^{2} to M^3 , anterior snout missing; MCZ 7297, left mandible with dP_4 to M_3 ; MCZ 7592, incomplete left mandible with M_2 to M_3 ; AMNH 22672, left mandible with P_2 to M_3 ; MCZ 7767, 22 astragali; MCZ 7768, 10 calcanea; MCZ 7769, 17 cuboids; MCZ 7770, 3 naviculars; MCZ 7771, 15 proximal phalanges; MCZ 7772, 23 second phalanges; MCZ 7773, 8 ungual phalanges.

Horizon and locality: Middle Miocene, Hawthorne Formation, Thomas Farm, Gilchrist County, Florida.

Redescription: The present description is based on Simpson's account (1932, pp. 35-37) and on the referred material in the Museum of Comparative Zoology and American Museum of Natural History collections.

This species is about the size of Oxydactylus brachyodontus Peterson 1904 in measurements of the dentition, but the maximum skull length was doubtless considerably greater due to the elongation of certain of the diastemata. The rostrum is deep and very narrow. A prominent, quadrangular lacrimal vacuity lies in the maxillary bone and is as large as the orbit. The latter is completely closed behind by a wide process from the frontal bone. The last molar is somewhat anterior to the orbit, but less so than in *Floridatragulus*.

The incisors and canine are unknown; the anterior portion of the snout is missing on both referred skulls. A small depression is present in some broken bone on the anterior edge of MCZ 4329 which may be the socket for P¹. If this is correct this tooth was single rooted as in *O. brachyodontus*, but was very much smaller, being only a tiny and almost certainly functionless vestige. Behind P¹ is a long diastema approximately equal to the combined lengths of P⁴, M¹ and M².

 P^2 is a long, narrow, trenchant tooth essentially unreduced. Proportionately, it is narrower than in *O. longipes*, being more similar in this respect to *O. longirostris*. A complete internal basal cingulum originates anteriorly at the base of a style. A similar anterior style is present on the external face. The external and internal surfaces are somewhat folded and expanded into a convex longitudinal ridge in the region of the median cusp. The posterior cusp is strongly skewed externally in MCZ 4329, but less so in 4322. P^3 is larger than P^2 , considerably wider, and has a much stronger internal cingulum. A strong parastyle forms a wide convex fold and is continuous around the front of the tooth with a very narrow anterointernal style.

 P^4 has the internal crescent fully expanded and somewhat skewed anteriorly, as in "Paratylopus" cameloides. It is nearly as wide as it is long, resembling in this respect "P." cameloides and O. longirostris rather than O. longipes. A well developed cingulum extends along the posterior base of the internal crescent and a weaker one is present on the anterior side. The external surface is ribbed by a prominent anterior style, which widens toward the base, and a variable posterior style, which is moderately developed on MCZ 4329, but nearly absent on MCZ 4322.

The upper molars are brachyodont, with M^2 the widest of the series, as in *O. longipes*. They are proportionately longer and wider than in "*P.*" cameloides and resemble *O. longipes* more than any other species in this respect. A prominent internal pillar, V-shaped in cross-section, is present on all the molars, but decreases in size from M^1 to M^3 . In this character Nothokemas resembles "*P.*" cameloides and contrasts with the pillarless molars of Oxydactylus.

 M^1 has a moderate parastyle and strong mesostyle, the latter directed somewhat anteriorly. The metastyle is very weak to absent and the median ridges of the external faces are prominent, especially on the metacone. A strong basal cingulum extends around the base of the protocone becoming weak to nearly absent on the most lingual part of the crescent. A similar crescent is present along the posterior edge of the hypocone. The internal crescents remain separated from the outer ones until an advanced stage of wear is reached.

 M^2 is similar to M^1 , but is longer and has more prominent styles and ridges. The basal cingula are generally weaker and less extensive around the lingual curves. M^3 is proportionately more elongated than M^2 , the styles more prominent, and the cingula nearly absent. In contrast to *O. longipes* the parastyle is weak as in "*P*." cameloides. Also as in cameloides the protocone is somewhat narrower anteroposteriorly than the hypocone.

The mandible is long and relatively shallow as compared with that of *O. longipes*. The anterior portion of the symphysis, from I_1 to P_1 , is unknown. MCZ 4325 has a broken symphyseal area which contains what may be the socket for P_1 . If it is, this tooth was only slightly larger than P^1 and situated well in front of the posterior border of the symphysis. The long diastema between P_1 and P_2 is comparable to that in the upper dentition, being at least 43 mm in length in MCZ 4325.

The premolars are large and unreduced, and increase in size from front to back. P_2 is expanded medially with its internal face strongly convex. A small anterior cusp is connected with a high and pointed median cusp by a blade-like anterior crest. The posterior crest is strongly deflected laterally before turning posterad so that the posterior cusp lies external to the straight line through the anterior and median cusps. A strong posterior intermediate crest extends back from the central cusp for about one-half the distance to the posterior margin of the tooth, forming a shallow open valley between itself and the posterior crest.

 P_3 has the anterior cusp very strongly inflected internally, more so than P_4 . The posterior intermediate crest is somewhat more developed than in P_2 , enclosing with the posterior crest a deeper but still medially open valley. P_4 is similar to P_3 , but with the posterior intermediate crest long and completely enclosing a deep valley, which is confined to the posterior one-third of the tooth. A well defined cusp is present on the crest near its posterior margin, and a slightly oblique longitudinal ridge extends along the length of the crown on the lingual surface.

The lower molars are long and narrow, as in *O. brachyodontus* and less so than in *O. longipes*. A strong median pillar, variable in size, rises primarily from the protoconid, at least on M_2 . The metaconid remains isolated to the base and somewhat overlaps the entoconid, whereas the latter fuses with the protoconid early in wear. The entoconid overlaps the hypoconulid for about one-fourth of the latter's length and remains separated from it nearly to the base of the crown. A very weak parastylid is present on M_2 .

The tarsal bones and phalanges that may be referred to *Nothokemas* on the basis of size and relative abundance are very *Oxydactylus*-like, and the cuboid and navicular are separated, unlike those of hypertragulids. It is surprising that the limb material does not show the stilt-like character that might be expected to be associated with the elongated snout. These elements are somewhat more slender than those of *O. longipes*, but not nearly as stilt-like as in *O. longirostris*.

Discussion: Nothokemas floridanus differs from the hypertragulids, to which it was first referred (White, 1947), principally in the structure of the premolars, but also in that of the molars. In Hypertragulus, P_3 is a simple, single-rooted tooth with a very weak posterointernal fold, while the comparable tooth in Nothokemas is three cusped and much more complex in its folds and

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TABLE 2

Comparative measurements of Nothokemas floridanus in mm

			C	Dxydactylus	"Paratylopus"
	Nothokemas floridanus			longipes	cameloides
	MCZ 4329	MCZ 4322	MCZ 4541	CM 918	YPM 10917
Skull length	°340	-		340	^b 278
P ¹ -P ² diastema	^a 53	_	-	18	_
P ² length	13	12.5	-	11	
P ² width	6	5.2	-	6	
P ³ length	^a 13.3	13.4	-	14	
P ³ width	8.5	7.5		8	_
P ⁴ length	^a 13	13	_	14	11
P ⁴ width	11	12	_	10	10
M ¹ length		18.6	19.7	19	13
M ¹ width		18.5	18.5	16	—
M ² length		^a 22	22	23	17.3
M ² width		21.5	20.5	20	16.5
M ³ length	23	23	23	25	17.4
M ³ width	19	19.5	18.8	20	17.3

Nothokemas floridanus

Oxydactylus "Paratylopus" longipes cameloides

MCZ 3636 MCZ 4325 MCZ 4324 CM 918 AMNH 8197

P ₁ -P ₂ diastema		45.5		17	21
P ₂ length		-	10.8	10	10
P2 width		-	4.5	5	_
P ₃ length	13.8		12.8	12	12.5
P3 width	6.4	-	5.5	5	4.3
P ₄ length	15		14.5	12	13
P ₄ width	7.5	-	7.3	7	5.9
M ₁ length	^a 18	19.2	-	18	14
M1 width	10.7	10.7	-	10	14
M ₂ length	21.5	23.6	_	23	17.5
M ₂ width	14	13.2	-	14	11
M ₃ length	35	33	_	31	25
M ₃ width	16.5	14.1	-	13	12

^a estimated from incomplete specimen.

^b estimated from figure, Dougherty, 1940.

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crests. P_4 is marked by a very strongly inflected parastylid in *Hypisodus* and *Hypertragulus*, more prominent than in *Nothokemas* and extending farther towards the base of the crown. A strong stylid extends along the internal surface of the median cusp in the above mentioned hypertragulids so that the depression formed in front and behind this is very much deeper in the Florida species.

The lower molars of *Hypertragulus* are complicated by very strong cingula and strong pillars rising primarily from the protoconid. In hypertragulids generally, the hypoconulid is strongly divided, a condition not seen in *Nothokemas*. The upper dentition is also quite different, and generally more complex in the Hypertragulidae.

There can be no question that the dentition as described above is indicative of camelid affinities, a conclusion supported by the referred postcranial elements. Although highly specialized, Nothokemas floridanus presents no characters which could not easily be derived from an early Oxydactylus-like form, from which "P." cameloides may also have arisen. In many of its characters Nothokemas stands somewhere intermediate between typical Oxydactylus (as represented by longipes and brachyodontus), on the one hand, and "P." cameloides, on the other, and it is likely that both N. floridanus and "P." cameloides represent early specialized offshoots from the basal Oxydactylus line that possibly arose in earliest Arikareean time.

CAMELIDAE GEN. ET SP. INDET.

Several isolated teeth and bones suggest the presence of a third camelid in the Thomas Farm fauna. Three upper molars, MCZ 7811, are generally comparable to those of *Oxydactylus* from the Marsland deposits of western Nebraska and eastern Wyoming, but are higher crowned (Beryl Taylor, personal communication). P³ is represented by two specimens, MCZ 7812, which are very similar to P³ of *Alticamelus* in structure, but are considerably narrower. Four proximal phalanges, MCZ 7813, are long and slender with ungrooved distal articular facets and a very shallow proximal surface.

All of these specimens suggest the presence of a camel of a somewhat more advanced type than *Floridatragulus* or *Nothokemas*, but only additional material will reveal its relationships.

PROTOCERATIDAE

SYNTHETOCERAS (PROSYNTHETOCERAS) RILEYI AUSTRALIS (White), 1941 new rank as subspecies

Syndyoceras australis White, 1941 (in part), p. 97, pl. XV, figs. 2, 2a. Synthetoceras (Prosynthetoceras) douglasi White, 1947, pp. 504-505, fig. 3a.

Hypodigm: MCZ 3654, type, right mandible with P_1 , P_4 to M_3 , and alveoli for P_2 and P_3 , coronoid process and symphysis anterior to P_1 missing; MCZ 3708, right mandible with P_3 to M_3 and alveoli for I_1 to P_2 ; MCZ 3655, right mandible with P_1 to M_3 and partial alveoli for I_2 to the canine; MCZ 3656, right mandible with P_1 to M_3 and partial alveoli for I_2 to the canine; MCZ 3666, partial right mandible with P_3 to M_3 ; MCZ 4065 (type of *Synthetoceras douglasi*), palate with right and left P^3 to M^3 ; MCZ 7635, right mandible with P_4 to M_3 and alveoli for I_2 to P_3 ; MCZ 7636, incomplete left mandible with P_4 to M_3 ; MCZ 7637, left mandible with P_3 to M_3 and alveoli for P_1 and P_2 ; MCZ 7774, 13 astragali; MCZ 7775, 3 cuboids; MCZ 7776, 4 naviculars; MCZ 7777, 22 proximal phalanges; MCZ 7778, 19 second phalanges; MCZ 7779, 5 ungual phalanges.

Horizon and locality: Middle Miocene, Hawthorne Formation, Thomas Farm, 8 miles north of the town of Bell, Gilchrist County, Florida.

Diagnosis: Equal in size to *Synthetoceras rileyi rileyi*⁴ Frick, but P_3 is 13 per cent smaller, and median cusp of P_4 somewhat narrower, so that internal depression is flatter and deeper.

Description: The mandible is long and slender, remaining rather shallow beneath the molars. The angle of the jaw is a smooth, continuous curve, as in *Protoceras*. Anterior to P_2 , the jaw begins to flare outward so that P_1 is inclined at about 35 degrees from the vertical.

The alveoli for the incisors indicate that they were small, closely spaced, and quite procumbent. That for the canine is larger and also procumbent and close behind I_3 , suggesting that it was a functional member of the incisor series, as in *Protoceras*. P₁ follows after a short diastema equal to M₁ in length. In the

⁴ Frick's collection data is not precise, but the type specimen appears to have been collected in the Catahoula sandstone in Walker County, Texas. Although the age of this formation is still not settled, Fisk (1940) considers it of Miocene age, and Gidley (see Renick, 1936) of Middle Miocene age.

type and MCZ 3656 and 7637, P_1 is a large, single-rooted, recurved, caniniform tooth laterally compressed and with bladelike anterior and posterior edges. In MCZ 3708, 7635, and 3655 the alveolus for the first premolar indicates a very tiny vestigial tooth which could not have been functional to any great extent in the living animal. In size and dental morphology these two groups are identical. Since dimorphs of this kind are known among artiodactyls, and with no evidence to the contrary, it is preferable to consider these as sexual morphs rather than two distinct taxa, the latter group being the females.

A long diastema separates P_1 and P_2 . The latter is a two-rooted, simple, robust tooth equal to P_3 in length (Fig. 2). P_3 is proportionately smaller than the corresponding tooth in *S. rileyi rileyi*, but similar to it in structure. The anterior edge is somewhat recurved onto the internal face forming a moderate stylid. The high median cusp is connected with the anterior and posterior cusps by narrow crests. A posterior intermediate crest extends backward nearly to the edge of the tooth, but fails to fuse with the posterior crest, resulting in a partially closed lake which is open posteromedially.

 P_4 is similar to P_3 with a stronger parastylid and a lake which is completely closed near the base of the crown. It differs from *S. rileyi rileyi* in having a narrower median cusp.

The molars are indistinguishable from those of S. r. rileyi. M_1 and M_2 have narrow crescents, strong parastylids, and weak metastylids. The median ridges are well developed, especially on M_2 . M_3 is similar but with the posterior edge of the metaconid slightly overlapping the entoconid. The hypoconulid is C-shaped forming two functional grinding surfaces, and is quite variable in size.



Figure 2. Synthetoceras (Prosynthetoceras) rileyi australis, composite crown view of right lower cheek teeth, X1.

In the upper dentition, the referred palate most closely resembles that of *Synthetoceras francisi* Frick. M_3 is longer than broad with the posterior pair of crescents narrower than the anterior pair. The metastyle is weak and the mesostyle prominent, but less so

than in *S. francisi*. The parastyle is as strong as the mesostyle. The internal crescents fuse early and extend as a narrow process between the external crescents, which they do not fuse with until late in wear. A median pillar, check-shaped in cross section, is present between the internal crescents, with the longer arm along the protocone. A prominent elongate pillar rises from the cingulum along the anterior side of the protocone.

 M^2 is smaller than M^3 and shorter anteroposteriorly than in *Synthetoceras tricornatus;* the styles are as prominent as in that species and the median ridges are low and indistinct. M^1 is the smallest of the molar series and, although worn, appears to be similar to M^2 in character.

 P^4 is triangular, as in *S. francisi*, with a very strong anteriorly curved metastyle. Unlike conditions in the corresponding tooth of that species, however, the parastyle is nearly absent. P^3 resembles that of *S. francisi*, but has a stronger metastyle and a strong and complete internal cingulum. A small wear facet on the anterior edge of P^3 indicates that P^2 was present, as in *S. francisi*.

On the basis of relative size, a number of foot bones are referred to this species. The phalanges are short and heavy as in *Protoceras*.

Discussion: As can be seen from Table 3 the range of variability of *S. australis* is sufficient to include the type of *S. rileyi*. In the character of the molars there are no differences which could not be attributed to intraspecific variation. The premolars, except for the differences already noted, are nearly identical in the two forms.

The subspecific rank of *S. rileyi australis* is proposed in view of the premolar differences, and the distance between Walker County, Texas, and Gilchrist County, Florida (nearly 800 miles), and because of the possibility of a slight difference in horizon between these localities. Since both forms are so poorly known at present it is advisable to retain a subspecific distinction, at least until the extent of variation in each is better known.

Frick (1937) was apparently uncertain as to the subgeneric reference of *S. rileyi*, questionably placing it in the subgenus *Synthetoceras*. The subgeneric distinction between *S.* (*Synthetoceras*) tricornatus and *S.* (*Prosynthetoceras*) francisi is based on the smaller size of the latter, its shorter crowned teeth, the retention of P^2 , and the prominence of the upper canine alveolus.

S. rileyi is referred to the subgenus Prosynthetoceras because of its small size and lower crowned teeth as compared with S. tricornatus, and because of the retention of P^2 in the referred palate, MCZ 4065.

TABLE 3

Comparative measurements of Synthetoceras (Prosynthetoceras) rileyi australis in mm

Synthetoceras (P.) rileyi australis MCZ 4065

64.5
64.8
9.0
6.1
9.0
9.0
13.6
14.8
17.2
15.9
17.0
16.8

Synthetoceras (P.)	Synthetoceras (P.)
rileyi australis	rileyi rileyi

				AMNH 34181,
	MCZ 3654	MCZ 3708	MCZ 7635	type
Depth of jaw				
under P ₂	21.2	22.7	22.5	19.3
Depth under P ₄	23.6		23.0	20.5
Depth under M ₃	29.1	27.5	28.4	-
P ₂ to M ₃ length	85.4	76.6	76.7	77.4
P ₁ to P ₂ diastema	42.0	46.0	46.1	-
P ₂ length ^a	_	_		8.2
P ₂ width ^a	_	_		3.1
P ₃ length	_	8.5	_	9.7
P ₃ width	_	4.0		4.3
P ₄ length	10.5	10.5	10.1	10.4
P ₄ width	6.5	6.3	5.7	6.4
M ₁ length	13.0	12.2	14.4	12.4
M ₁ width	10.0	9.2	9.4	9.4
M ₂ length	18.0	16.1	15.4	16.7
M ₂ width	11.0	10.5	21.6	22.4
M ₃ length	25.5	25.0	21.6	22.4
M ₃ width	11.4	11.1	10.5	10.1

^a Known only from MCZ 3656; length, 8.2 mm, width, 4.0 mm.

MERYCOIDODONTIDAE MERYCHYINAE cf. Merychyus sp.

An oreodont is represented in the Thomas Farm fauna by a single left upper molar, MCZ 7765, and an incomplete tarsus, MCZ 7766. In structure and size the molar (Fig. 3) most closely resembles *Merychyus minimus*, but is also quite similar to *M. elegans* of a later age. The external faces of the outer crescents are transversely concave and longitudinally convex, so that their apices overhang the internal crescents in typical oreodont fashion. The posterior crescents are narrower than the anterior pair and are relatively longer anteroposteriorly, as in M^3 of *M. elegans*. A strong cingulum is present on the anterior side of the protocone and a weaker one on the posterior side of the hypocone.



Figure 3. Oreodont upper left molar; cf. *Merychyus*. External view (left), and crown view (right), $X1\frac{1}{2}$.

There can be little doubt of the oreodont affinities of the tarsal elements, which probably belong to a single individual. The calcaneum is relatively short, strong, and laterally compressed with a strongly truncated proximal end which bears a deep groove for the tendon of the gastrocnemius. The sustentaculum is very small and only slightly projecting beyond the medial surface of the tuber. The astragalar facet on the sustentaculum is relatively long and narrow.

The astragalus is wide, low, and quite asymmetrical. The proximal trochlear is inclined at an angle to the distal one, and is placed more lateral in position as is typical of oreodonts. The sustentacular facet is narrow, occupying little more than half of the plantar surface. These fragments are tentatively referred to the genus *Merychyus* because of the similarities to *M. minimus* in both size and morphology. However, a more certain reference must await more complete material.

The discovery of oreodont remains in Florida is a significant, although not a completely unexpected find. The apparent rarity of these animals in this region may not reflect their actual abundance. Schlaikjer (1935, p. 173) suggested that a gregarious habit combined with localized distribution and/or species habitat requirements of oreodonts could account for their great abundance in some areas, and relative rarity in others of the same age. As suggested by Thorpe (1937, p. 9) and Patterson (1949, p. 270), the absence of sediments deposited under appropriate conditions or their subsequent removal by erosion could be responsible for a meager oreodont fauna in certain areas. The idea, as proposed by Romer (1947, p. 10), that Florida was ecologically unfavorable for these animals is less attractive since the environment of the Florida Miocene was inferred partially by the absence of oreodonts. The rarity of this group from Florida beds is probably due to a combination of the first two factors: localized distribution and scarcity of sediments.

CERVIDAE

BLASTOMERYN (PARABLASTOMERYN) FLORIDANUS White, 1940

Hypodigr.: MCZ 3626, type, partial left mandible with P_4 , M_1 , the anterior external crescent of M_2 , and the alevoli for P_2 and P_3 ; MCZ 3627, paratype, upper left molar; MCZ 3706, right mandible with dP_2 to M_3 ; MCZ 3707, left mandible with dP_3 to M_3 ; MCZ 3912, left mandible with dP_4 to M_3 ; MCZ 4220, left mandible with P_1 , dP_3 to M_3 ; MCZ 4221, right mandible with P_3 to M_3 ; MCZ 4222, right mandible with P_2 , M_1 to M_3 ; MCZ 7795, 23 astragali; MCZ 7796, 24 calcanea; MCZ 7797, 17 cubonaviculars; MCZ 7798, 103 proximal phalanges; MCZ 7799, 53 second phalanges; MCZ 7800, 24 ungual phalanges; MCZ 7801, 6 metapodials; MCZ 7802, left tibia; MCZ 7803, right radius.

Horizon and locality: Middle Miocene, Hawthorne Formation, Thomas Farm, Gilchrist County, Florida.

Diagnosis: White (1940, p. 34) diagnosed this species as follows: "A large *Parablastomeryx*, paraconid of P_4 with very small stylid, metaconid large and placed about the mid-length of the tooth, entoconid projecting at nearly right angles to the axis of the tooth, crest of hypoconulid extending along posterior border of the tooth nearly to the inner border."

Discussion: Since White's diagnosis, many new specimens have been collected. These demonstrate a remarkable degree of variation in the premolars and reveal the character of the lower molars and milk dentition, which were not available to him. The molars (Fig. 4) tend to confirm White's observation that *B. floridanus* is similar to *B. primus*.



Figure 4. *Blastomeryx floridanus. a*, Composite crown view of left lower cheek teeth, X1¹/₂. *b*, MCZ 3706, right dP₄, X3.

The hypoconulid of M_3 has a prominent anterointernal cusp, and a strong palaeomeryx fold is present on the protoconid. The internal stylid of P_4 which White described as being "very small" on the type varies from strong on MCZ 7763 to absent on MCZ 4221. In P_3 of most of the specimens the entoconid is joined to the hypoconid by a semicircular crest around the posterior margin of the tooth, forming an enclosed lake. However, in MCZ 4349 the lake remains open posteriorly and is divided from the entoconid by a strong median ridge, which extends posteriorly to the end of the tooth and, after turning medially, ends in a minute capsule. These and other variants must be considered to be within the range of variation of this species since intermediate types link every extreme.

The lower milk teeth, dP_2 to dP_4 are known from two specimens, MCZ 3706 and 3707. DP_4 (Fig. 4b) is five cusped with an elongated pillar between the anterior inner cusps and a conical pillar between the posterior inner cusps. DP_3 is very similar to P_3 in structure and length, but is much narrower. There is little difference between dP_2 and P_2 .

Because of the palaeomeryx folds, hypoconulid cusp, and relatively large premolars, this species is referred to the subgenus *Parablastomeryx*.

Referred postcranial material includes numerous tarsal bones, phalanges, a tibia, a radius, and several cannon bones. The tarsus is typically cervid. The tuber of the calcaneum is light and laterally compressed; the cuboid and navicular are solidly fused. The proximal phalanx is lightly built and considerably more slender dorsoventrally than in Recent cervids.

The metatarsals are fused along their entire length and there is a deep longitudinal groove on the dorsal side between metatarsal III and metatarsal IV. The distal facets are completely keeled, and together are considerably wider than the shaft. The metacarpals are fused and somewhat shorter than the metatarsals. The dorsal groove is shallow and indistinct. The tibia is long and slender, but less curved laterally than in Recent forms.

TABLE 4

Comparative measurements of *Blastomeryx* (P.) floridanus in mm

	MCZ	MCZ	MCZ	MCZ
	7763	4221	4349	3626
Jaw and lower der	ntition:			
Jaw length		*132	-	_
P ₂ to M ₃	_	60.8	66.9	-
P ₂ length	5.6	_	_	_
P2 width	2.6		-	-
P ₃ length	7.3	8.0	8.2	_
P ₃ width	4.3	4.3	4.6	_
P ₄ length	8.9	8.4	8.7	8.2
P ₄ width	5.4	5.0	5.0	4.9
M ₁ length		10.1	10.3	9.0
M ₁ width		7.3	7.0	6.3
M ₂ length		11.8	11.7	_
M ₂ width		8.2	7.9	_
M ₃ length	_	16.2	17.3	_
M ₃ width	_	8.2	7.7	-

* estimated from incomplete specimen.

MACHAEROMERYX GILCHRISTENSIS White, 1941

Hypodigm: MCZ 3651, type, partial right mandible with P_4 to M_2 and alveoli for P_2 , P_3 and M_3 ; MCZ 3652, right mandibular fragment with M_1 , and a left upper molar; MCZ 3709, partial right mandible with P_3 to M_2 and part of M_3 ; MCZ 3710, partial right palate with M^1 and M^2 ; MCZ 7804, 37 astragali; MCZ 7805, 1 calcaneum; MCZ 7806, 3 cubo-naviculars; MCZ 7807, 24 proximal phalanges; MCZ 7808, 5 second phalanges; MCZ 7809, 2 ungual phalanges; MCZ 7810, 1 metacarpal.

Horizon and locality: Middle Miocene, Hawthorne Formation, Thomas Farm, Gilchrist County, Florida.

Diagnosis: Premolar series relatively longer than in M. tragulus, M_2 shorter, upper molars less square with outer crescents considerably wider than inner ones, median pillars of upper molars only vaguely suggested in contrast to M. tragulus.

Discussion: No new information can be added to the diagnosis since this species remains so poorly represented. Aside from the differences in proportion, the teeth are very similar to *M. tragulus*.

The few tarsal remains and a referred metcarpal are essentially like those of *Blastomeryx*, but much smaller.

CONCLUSION

The fossil selenodont artiodactyls from Thomas Farm, Gilchrist County, Florida, indicate faunal communication with other parts of the North American continent during the Lower Miocene. Synthetoceras r. australis is at most subspecifically distinct from the western S. r. rileyi, and Blastomeryx floridanus and Machaeromeryx gilchristensis are close to western species. The specialized camelids, Floridatragulus and Nothokemas, are so far unknown in the West, but they or closely related forms have been recorded from the Oakville of the Texas coastal plain (Wilson, 1962). This contradicts White's contention that north-central Florida was an island until the end of Oak Grove time. Continuity, even if intermittent, between Florida and the mainland certainly seems to have occurred during the earlier Miocene. On geological grounds, Cook (1945) suggests that a narrow peninsula persisted through much of this period, and Bader (1956), on the basis of his comparisons of the Thomas Farm equids with those of Texas, states that isolation was, at best, very ephemeral. The opportunity for faunal movement between these areas, then, must have been considerably greater than suggested by White (1942).

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Errata

Page 6, Fig. 1*a*, for X4/5 read X2/5.

- Page 10, Table 1, for P¹ length and width read P².
- Page 11, Table 1. M₃ length, MCZ 4086, for 13 read 25; MCZ 4291, for 13 read 24.
- Page 11, Nothokemas, line 8 (MCZ 4322) for P_2 to M_3 read P^2 to M^3 .
- Page 15, Table 2, M₁ width, AMNH 8197, for 14 read 9.5.
- Page 17, lines 9, 10. MCZ 3655, for P_1 to M_3 and partial alveoli for I_2 to canine, read M_1 - M_3 and alveoli for P_1 - P_4 .
- Page 17, line 11, for MCZ 3666 read 3660.
- Page 20, Table 3. M₂ width, MCZ 7635, for 21.6 read 10.3; AMNH 34181, for 22.4 read 10.4.
- Page 22, *Blastomeryx*, Hypodigm. Add MCZ 7763, partial left jaw with P_2 - P_4 , and MCZ 4349, left jaw with P_3 - M_3 .

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