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DONALD R. PROTHERO
Graduate Student, Department of Geological Sciences
Columbia University

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ABSTRACT

A joint American Museum of Natural History-Yale University expedition reopened Quarry Nine at Como Bluff, Wyoming, in 1968–1970. This locality had produced all but six of about 250 Jurassic mammal specimens known from North America prior to 1968. During the renewed collecting, four additional prospects were found in the vicinity, and 25 fossil mammal jaws and numerous teeth were collected.

A new genus and species of dryolestid, *Comotherium richi*, is described. The dryolestid genera *Melanodon* and *Herpetairus* are reviewed and rediagnosed. The anterior dentition of *Melanodon goodrichi* and better material of *Herpetairus humilis* are described. The crown and labial views of *Kepolestes*, previously obscured in matrix, are described. No dryolestid jaw in this collection shows any trace of a coronoid or splenial, contrary to the condition reported in Kimmeridgian Portuguese dryolestids.

The systematics of primitive Theria are reviewed, and an hypothesis of relationships for the non-tribosphenic Theria is proposed. This hypothesis corroborates the hypothesis of McKenna (1975). It is concluded that the symmetrodonts are a monophyletic group, and that *Amphitherium* is most closely related to the dryolestoids. A cladistic classification of the non-tribosphenic Theria is proposed. Six new taxa are named: sublegions Amphidontoidea and Spalacotherioidea, and infraclasses Tinodontida, Spalacotheriida, Amphitheriida, and Dryolestida. It is strongly urged that the term "pantothere" be abandoned, because it has misleading phylogenetic connotations and because it obscures non-tribosphenic therian diversity.

INTRODUCTION

The history of the Mammalia during the Jurassic Period has always been one of the most interesting, yet poorly documented phases of mammalian evolution. Mammals first appeared in the Rhaeto-Lias (late Triassic-early Jurassic, about 190 Ma), but are known from only three medial Jurassic localities and four late Jurassic localities. With the exception of one skeleton (Henkel and Krebs, 1977), no Jurassic therian mammal is known from more than fragmentary teeth and jaws.

In North America, Jurassic mammals are recorded only from the Morrison Formation, which is Tithonian (latest Jurassic), about 145 Ma. All but six of more than 250 mammal specimens collected prior to 1968 have come from Quarry Nine at Como Bluff, Wyoming. In the late 1870s and 1880s, the crews of Othniel C. Marsh discovered these specimens in Quarry Nine. They were redescribed by Simpson (1927, 1929). Except for the paurodont *Araeodon* (Simpson, 1937), no North American Jurassic mammals have been reported or described since 1929.

For this reason, at the suggestion of Malcolm C. McKenna, the American Museum of Natural History and Yale University sponsored an expedition that reopened Quarry Nine in the summers of 1968 to 1970. This expedition was led by Thomas H. Rich (then of the American Museum) and Charles R. Schaff (then of Yale University). The result of this expedition was a large collection of fragmentary vertebrates and invertebrates, including 25 mammal jaws and numerous teeth. This collection has been expertly prepared and given preliminary identification by Mr. Schaff, but has remained undescribed until I took up the task at the suggestion of Dr. Malcolm C. McKenna. Dr. Eugene S. Gaffney has described the turtles in the collection (Gaffney, 1979). Dr. A. W. Crompton discusses aspects of dental occlusion elsewhere. In the present paper I discuss the therian mammals in the new collection, including a new genus and species of dryolestid.

While my study of the new form described herein was in progress, it became necessary to review the systematics of the rest of the dryolestoids. New developments in phylogenetic analysis, known as "cladistics" or "phylogenetic systematics" (Hennig, 1965, 1966) are employed for reasons discussed below. The interrelationships of the numer-

ous taxa of "pantotheres" have been neglected since Simpson's monographs (1928, 1929). Simpson himself never attempted to analyze the relationships of the individual taxa. A cladistic framework not only makes this possible but demands it.

In the analysis of primitive versus derived character states and morphocline polarities in dryolestoids, the analysis naturally expanded into all the primitive Theria and therian sister groups. The cladogram (a branching diagram of relationships using only shared derived character states) was arbitrarily restricted to the non-tribosphenic Theria. Eventually it will be possible to include the rest of the Mammalia in a much larger cladogram currently in progress (McKenna, 1975).

Kimmeridgian (late Jurassic) dryolestoids from Guimarota, Portugal, have recently been described (Kühne, 1961, 1968; Krebs, 1969, 1971; Henkel and Krebs, 1977). However, none of the taxa except *Crusafontia*, from the Lower Cretaceous of Uña, Spain (Henkel and Krebs, 1969), has been diagnosed or figured adequately in the literature, and so could not be incorporated into this study. A number of tantalizing figures of named, but still undescribed forms appeared in a paper by Kühne (1968), but without descriptions or diagnoses.[1] I have examined all the North American material, and have studied excellent sterophotographs of the British material, courtesy of Dr. A. W. Crompton.

Most workers who have studied Mesozoic mammals have avoided explicit phylogenetic hypotheses, or have made them too vague to be tested. Admittedly, the fossil record of Mesozoic mammals is poor, and there is much we need to know. There is, however, a good deal of morphology in these animals that we do know, and some sort of phylogenetic hypothesis is warranted. The cladogram I present represents a preliminary hypothesis, based on all data available as of 1978. The publication of the Guimarota material will serve as an immediate test of this hypothesis. I hope that this preliminary hypothesis of relationships stimulates other workers to attempt to falsify it and to produce a more parsimonious explanation of the distribution of characters.

[1] Since these names and figures are published without descriptions, diagnoses, or designation of type specimens, they are *nomina nuda* under Article 13 of the International Code of Zoological Nomenclature.

ABBREVIATIONS

AMNH, Department of Vertebrate Paleontology, American Museum of Natural History.

USNM, Division of Vertebrate Paleontology, National Museum of Natural History, Smithsonian Institution

YPM, Peabody Museum of Natural History, Yale University

ACKNOWLEDGMENTS

Special thanks are due to three people who made the project possible. Dr. Thomas H. Rich initiated the project as the potential subject for a Ph.D. thesis. He spent many months in the field and laboratory working on it, but did not see it to its completion. Mr. Charles R. Schaff put in many months in the field and with his customary expertise prepared the specimens. Dr. Malcolm C. McKenna first suggested the project to both Dr. Rich and to me, and has guided the present manuscript through several revisions.

The field crew at Como Bluff was large and changed from year to year, but included (in alphabetical order): B. Abel, M. Albert, W. Barone, T. Buckley, J. Furst, P. Gooris, W. Graustein, J. Kadish, S. Koehle Bell, P. LaFollette, J. McCarthy, D. McKenna, S. Mendlinger, R. Ratkevich, A. Sigler, J. Thomson, P. Whybrow, and G. Winters; Drs. M. Chalifoux Coombs, C. Gawne, and P. V. Rich. I also thank Drs. A. W. Crompton and F. A. Jenkins, Jr. (Harvard University), R. J. Emry (Smithsonian Institution), and J. H. Ostrom (Yale University) for allowing me to examine specimens in their care. Drs. E. Gaffney (American Museum of Natural History), C. Patterson (British Museum of Natural History), and P. Galton (University of Bridgeport) have aided in the identification of the turtles, fish, and dinosaurs, respectively. Mr. C. Schaff (Harvard

University) did most of the preliminary identification of the mammals, and Mr. E. Manning (American Museum of Natural History) made preliminary identifications of the lower vertebrates and curated the collection. Drs. M. C. McKenna, P. M. Butler, E. S. Gaffney, T. H. Rich, and Messrs. E. Manning and C. Schaff have read all or parts of the manuscript and made helpful suggestions. Mr. Clifford R. Prothero contributed his talents to the illustrations. Mr. Chester Tarka has given me useful advice on the illustrations. I have gratefully received support from a Columbia University Faculty Fellowship and an NSF Graduate Fellowship during this project.

STRATIGRAPHY AND LOCALITIES

In July 1879 William H. Reed, one of the collectors for O. C. Marsh, discovered Quarry Nine at Como Bluff (Ostrom and McIntosh, 1966, p. 24). Marsh's collectors worked almost continuously in Quarry Nine for the next 10 years, and sent numerous cans and jars of small bones to New Haven. Finally, in June 1889 Marsh's operations at Como Bluff ceased when Quarry Nine appeared to have been exhausted. Quarry Nine yielded almost 250 mammal specimens during those 10 years. In 1897 the American Museum of Natural History worked Quarry Nine, but collected only one mammal jaw. This specimen remained hidden in matrix until it was discovered and described by Simpson in 1937. In the summers of 1968, 1969, and 1970 a joint American Museum-Yale University expedition reopened Quarry Nine intending to find the site of the original work and extending the excavations. During this time, four additional mammal localities were also discovered in the vicinity[2] (fig. 1).

The first phase of renewed operations concentrated on locating the layer from which all but three of the original Quarry Nine mammals came. It was known to underlie a bed of resistant sandstone according to correspondence between Marsh and his men. Test pits and trenches were dug, and the limits of both Marsh's excavation and the 1897 American Museum excavation were found. This confirmed statements by Marsh's workers that the richest part of the quarry was on the west side, and explained the lack of success of the 1897 expedition. From photographs in the American Museum archives, one can conclude that the efforts of 1897 were directed at the barren east side of the quarry.

In addition to trenches and test pits, the area immediately behind the west face of the quarry was bulldozed to expose about 150 square feet of the producing layer. The results of the work in the producing layer are listed in table 1.

Another deposit was found in the east wall of the quarry face, to the northeast of the 1897 American Museum excavation. These fossils came from a gray mudstone that immediately overlies the resistant sandstone bed. The greatest concentration was found in Pit A (see table 1), which yielded the most numerous and best preserved mammals in the collection. For this reason, the work in 1969 and 1970 was concentrated more on the eastern part of the quarry, and on Pit A. The specimens recovered from the layer above the resistant sandstone are listed in table 1. Both localities in Quarry Nine occur approximately 80 feet below the Morrison-Cloverly contact. The local generalized section for Quarry Nine is shown in table 2.

Four additional prospects that produced mammals were also found. In 1968 Dr. Malcolm C. McKenna found a locality about a mile west of Quarry Nine, near the crest of Como Bluff. Since it seems to lie near the Morrison-Cloverly contact, it was designated "Delta T" to indicate its unknown but

[2] The following discussion is abstracted from the field notebooks of Thomas H. Rich. These are stored in the Archives of the Department of Vertebrate Paleontology, American Museum of Natural History, and may be consulted for further details.

TABLE 1
Faunal List for the AMNH-Yale University Expedition to Como Bluff
(x denotes presence of taxon; six-digit numbers are AMNH catalogue numbers of specimens.)

	Quarry Nine				
	Producing layer	Pit A	Chuck's Prospect	Dead Rabbit Hill	Delta T
Class Gastropoda	x	—	—	x	—
Class Bivalvia	x	x	—	—	—
Class Osteichthyes					
Order Amiiformes	—	—	—	—	—
Ophiopsis sp.[a]	x	x	x	—	—
Order Dipnoi					
Ceratodus sp.	x	—	—	x	x
Class Amphibia					
Order Anura	—	x	—	—	—
Class Reptilia	—	—	—	—	—
Order Chelonia[b]	—	—	—	—	—
Family Baenidae	—	—	—	—	—
Glyptops plicatulus	x	x	x	x	—
Dinochelys whitei	x	—	—	—	x
Order Rhynchocephalia	—	—	—	—	—
Family Sphenodontidae	—	—	—	—	—
Opisthias rarus	x	x	—	—	—
Order Squamata					
Infraorder Eolacertilia					
Cteniogenys antiquus	x	x	x	—	—
Infraorder Lacertilia					
Paramacellodus sp.	x	x	—	—	—
Dorsetisaurus sp.	x	x	—	—	—
Order Crocodilia					
Family Goniopholidae					
Goniopholis sp.	x	x	x	—	x
Order Saurischia					
carnosaur fragments	x	x	—	—	—
Order Ornithischia[c]					
Family Stegosauridae	x	—	—	—	—
Family Fabrosauridae	x	—	—	—	—
Class Mammalia					
Order Triconodonta					
Family Triconodontidae	—	101145	—	—	—
Order Docodonta					
Docodon victor	104798	104796	—	104799	—
	104801	104797	—	—	—
	—	104800	—	—	—
	—	104828	—	—	—
Order Multituberculata					
Family Plagiaulacidae	104795	104794	104793	—	101146
	—	104802	—	—	—
	—	104803	—	—	—

TABLE 1—(*Continued*)

	Quarry Nine				
	Producing layer	Pit A	Chuck's Prospect	Dead Rabbit Hill	Delta T
Legion Cladotheria					
Family Dryolestidae					
Laolestes eminens	104827	101121	—	—	—
	—	101122	—	—	—
	—	101123	—	—	—
	—	101125	—	—	—
	—	101126	—	—	—
	—	101127	—	—	—
	—	101138	—	—	—
Dryolestes priscus	—	101136	101140	—	—
	—	101137	—	—	—
	—	101139	—	—	—
	—	101141	—	—	—
Amblotherium gracilis	101134				
Amblotherium debilis	—	101133	—	—	—
Amblotherium sp.	—	101143	101135	—	—
Herpetairus humilis	—	101128	—	—	—
	—	101129	—	—	—
Melanodon goodrichi	—	101131	—	—	—
Comotherium richi	104826	101132	—	—	—
Dryolestoid indeterminate	—	101142	104927	—	—
	—	101144	—	—	—
Therian petrosal			104830	—	—
Mammalia indeterminate	104926	104928	—	—	—

[a] Identification of *Ophiopsis* courtesy of Dr. Colin Patterson. This is the first notice of the occurrence of the genus in North America.

[b] Identification of the turtles courtesy of Dr. Eugene Gaffney.

[c] Identification of ornithischian dinosaurs courtesy of Dr. Peter Galton.

clearly younger age. "Delta T" produced a multituberculate premolar, another mammalian premolar, a badly fractured docodont tooth, and much fragmentary lower vertebrate material.

Another locality was discovered by Dr. Patricia V. Rich about a mile west of Quarry Nine. Designated "Dead Rabbit Hill" because a dead rabbit crowned it, the site was about 150 feet below the Morrison-Cloverly contact. The deposit was screenwashed and produced some *Ceratodus* teeth, turtle material, and a lower molar of *Docodon*.

In 1969 while prospecting in Bone Cabin Draw (see fig. 1), another locality was found by Charles R. Schaff. Called "Chuck's Prospect" it seems to be equivalent to "*Stegosaurus* Quarry 1899" shown in Loomis (1901, plate XXVI, fig. 2). If so, it occurs in Loomis's "No. 28 gray sandstone," approximately 40 feet from the top of the Morrison formation. "Chuck's Prospect" yielded a number of mammalian jaws before the deposit was apparently exhausted. A list of the specimens from this locality is shown in table 1.

A fourth locality was found by M. Albert in July 1969. It was designated "M area" and was 390 feet due east of Quarry Nine at the base of Como Bluff. The exact stratigraphic

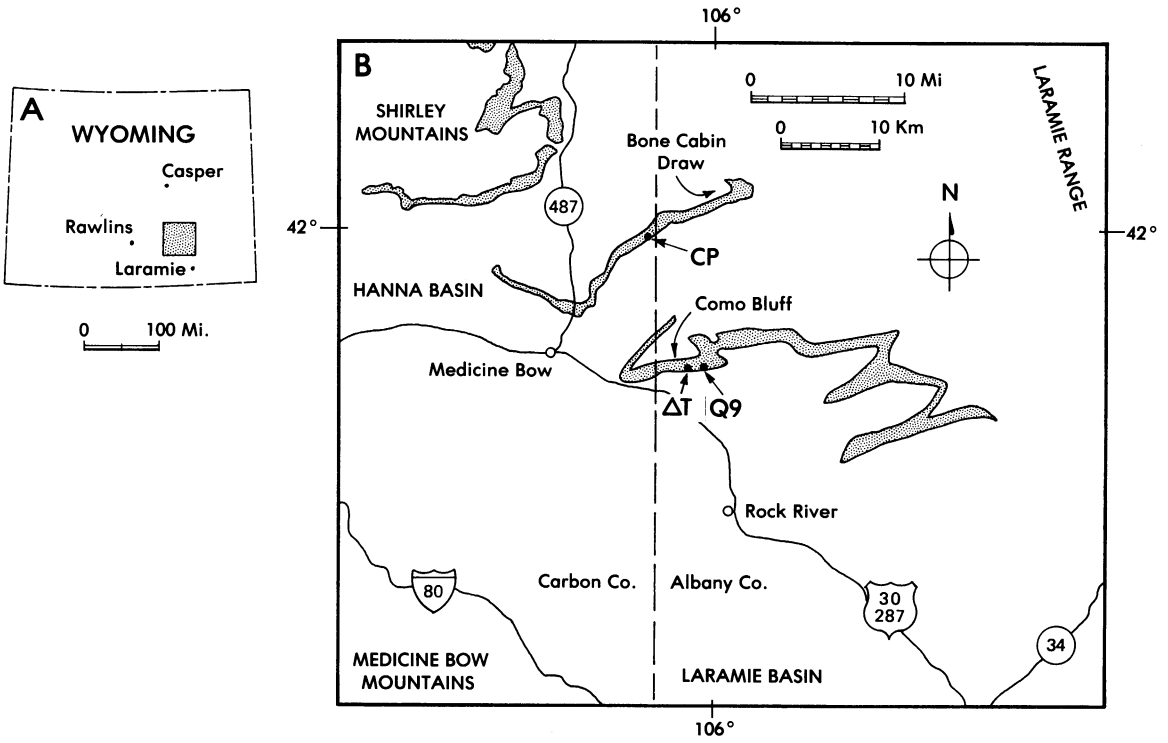


FIG. 1. A. Index map of Wyoming; stippled area is enlarged in B. B. Map of localities described in text. Stippled area indicates outcrops of Morrison Formation. Q9 = Quarry Nine, Dead Rabbit Hill and "M" area; T = Delta T; CP = Chuck's Prospect

position of this locality has not been determined. "M area" produced a fragmentary triconodont jaw, a gastropod, and some lacertilian material. The triconodont teeth are about 15 percent larger than any so far known from Como Bluff.

The work of 1970 produced no new mammals or localities.

SYSTEMATIC DESCRIPTIONS

CLASS MAMMALIA LINNAEUS, 1758
INFRACLASS THERIA PARKER AND HASWELL, 1897
LEGION CLADOTHERIA McKENNA, 1975
SUBLEGION DRYOLESTOIDEA BUTLER, 1939
FAMILY DRYOLESTIDAE MARSH, 1879

TAXA KNOWN FROM UPPER JAWS

COMOTHERIUM, NEW GENUS
Figures 2, 3A–C

TYPE SPECIES: *Comotherium richi*, new species.

KNOWN DISTRIBUTION: Latest Jurassic (Tithonian), Quarry Nine, Como Bluff, Albany County, Wyoming.

ETYMOLOGY: Como, from the type locality, Como Bluff, Wyoming; therium, Latinized form of the Greek θηριον, "beast."

DIAGNOSIS: Dryolestid upper jaws with stylocone placed at anterolabial end of paracrista. Heart-shaped labial border with large, raised, two-cusped metastyle contacting shelflike, enlarged parastyle anterolingually. No ridges or cusps in basin of trigon.

TABLE 2
Local section at Quarry Nine

Lithology	Thickness in meters
Variegated gray claystones and sandstones, with occasional chert lenses. Locally fossiliferous (see table 1, Pit A).	2–4
White sandstone with minor feldspar, orange staining and iron concretionary lenses near top. Unfossiliferous.	0.3–2
Green siltstone and sandstone. Locally fossiliferous (see table 1, producing layer).	0–0.35

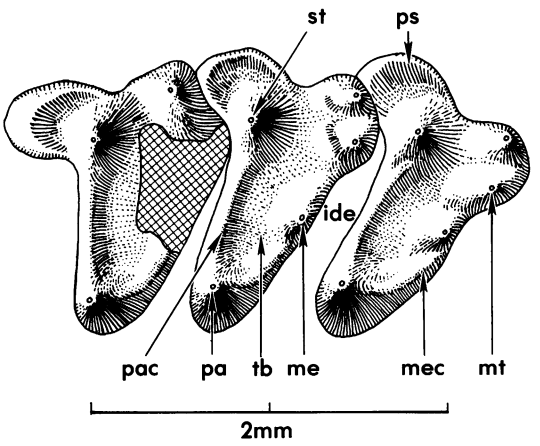


FIG. 2. *Comotherium richi*, AMNH 101132, genoholotype. Cross-hatched area is damaged. Symbols are as follows: ide = interdental embrasure, me = metacone, mec = metacrista, mt = metastyle, pa = paracone, pac = paracrista, ps = parastyle, st = stylocone, tb = trigon basin.

Interdental embrasure between trigons narrower than in any other dryolestid.

Comotherium richi, new species

TYPE SPECIMEN: AMNH 101132, a left maxillary fragment with three molars.

REFERRED SPECIMEN: AMNH 104826, an isolated right upper molar.

HORIZON AND LOCALITY: Same as for genus.

ETYMOLOGY: In honor of Dr. Thomas H. Rich, who led the 1968–1970 American Museum-Yale expedition to Como Bluff, and who discovered the first specimen of *Comotherium*.

SPECIFIC DIAGNOSIS: Same as for genus.

DESCRIPTION: AMNH 101132 consists of a left maxillary fragment with three molars. The anterior molar has been rotated posterolingually, so that the interdental embrasure is extremely narrow. This is partly due to crushing and partly natural. The embrasure between the second and third molars is also much narrower than in any other dryolestid, but the roots are firmly in place, and the axes of the second and third molars are still in line.

Except for the broken metacrista of the first tooth, the teeth are unworn and undamaged. The molars have high prominent paracones with two ridges: a paracrista and a metacrista that descend labially to form the anterior and posterior margins of a central trigon basin. No cusps or ridges are found in the basin, unlike those of most other dryolestoids. A small, conical stylocone occurs on the labial end of the paracrista. This extremely anterior position of the stylocone is unusual for dryolestids. The stylocone is set anterolingual to the medial external border, unlike the situation in most other dryolestids. The metacone is a small swelling midway along the metacrista. It is clearly seen only on the middle molar.

The stylar region of this specimen is much larger than in other dryolestids, forming a heart-shaped outer margin of the tooth. The metastyle of one tooth is closely appressed anterolingually to the parastyle of the posterior tooth, so that they appear to be fused in the case of the first and second teeth. The parastyles curve anteriorly from the stylocone, and in the first tooth form a right angle with the line of the paracrista. The parastyles also seem to show a small ridge running along their anterolabial margins. The enlarged metastyle is separated from the rest of the tooth by a distinct valley running diagonally across the tooth. Where the preservation is good, the metastyles show two

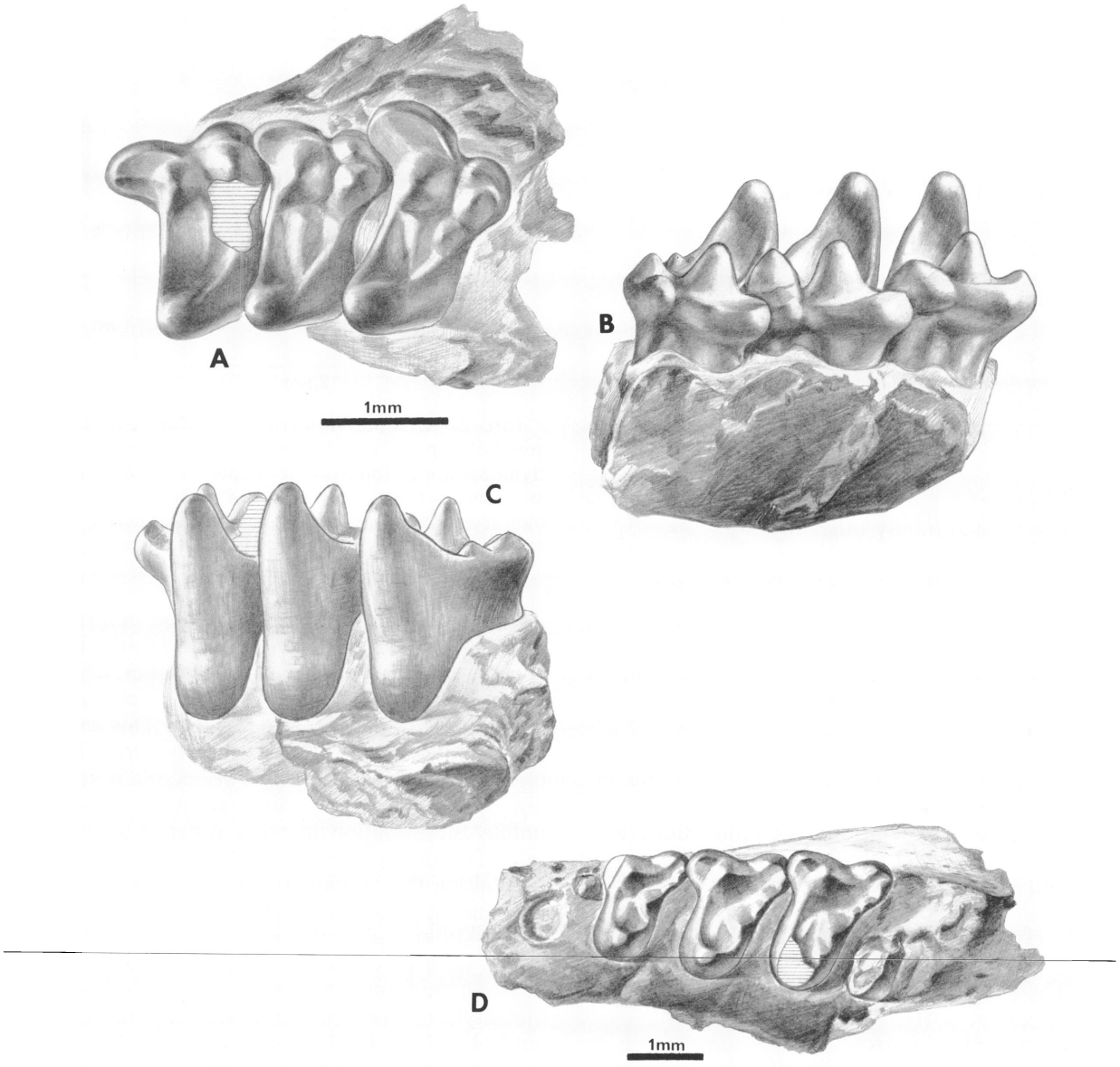


FIG. 3. *Comotherium richi*, AMNH 101132, genoholotype. A. Crown view. B. Labial view. C. Lingual view. D. *Herpetairus humilis*, AMNH 101130. Crown view.

cuspules, one at the labial end of the metacrista, the other on the anterolingual margin of the metastyle. The posterior metastyle cusp is approximately equal in height to the stylocone and metacone. All three cusps are much lower than the paracone, but higher than the anterior metastyle cusp. The parastyle is quite low, flat, and shelflike in labial view.

Alveoli for the tooth posterior to those described indicate that the molars are three rooted. The largest root is for the paracone;

a second large root, anterolingual to it, supports the stylocone and parastyle, and a broad, anteroposteriorly compressed root supports the metastyle. It is posterolingual to the parastyle-stylocone root, and posterolabial to the paracone root.

The extreme anterobasal part of the zygomatic arch is preserved on this specimen; it begins at the level of the last preserved molars. If the position of the zygomatic arch with respect to the molars is comparable in *Melanodon* and *Comotherium*, then the molars preserved would be M^{3-5}.

AMNH 104826, an isolated right upper molar from Quarry Nine (see table 1), is also referred to *Comotherium richi*. It shows all the characters of the type specimen, including the strong paracrista and metacrista, the high paracone, and the same shape and placement of the stylocone. It differs only in that the stylocone is not so strong as in the type, and the parastyle is not so strongly hooked. These differences, however, frequently occur on more anterior molars of other dryolestids. Since the type seems to consist of M^{3-5}, it is probable that AMNH 104826 is an M^1 or M^2.

MEASUREMENTS (IN MM.): M^3 length 1.01, width 1.75; M^4 length 0.96, width 1.69; M^5 length 0.84, width 1.63.

DISCUSSION: *Comotherium* was tentatively referred to *Euthlastus cordiformis* by the original workers, since both forms have strongly hooked parastyles, resulting in a heart-shaped labial margin. This character is much more strongly pronounced in *Comotherium*, whose parastyle and metastyle are much more closely appressed than in *Euthlastus*. Direct comparison of the two reveals some striking differences:

1. The teeth of *Comotherium* are about twice the size of *Euthlastus*.

2. *Comotherium* has a higher paracone, stronger paracrista and metacrista, and a more acute trigon angle than does *Euthlastus*.

3. The stylocone in *Comotherium* is distinct and conical, and lingual to the parastyle. In *Euthlastus*, the stylocone is a swelling on the posterolabial part of the parastyle.

4. In *Comotherium*, the metastyle is raised and separated from the trigon by a valley; this does not occur in *Euthlastus*.

5. *Euthlastus* has a single discrete parastyle cusp equal in size to the stylocone; *Comotherium* has no parastyle cusp.

Thus, AMNH 101132 and 104826 could not be referred to any genus of dryolestid upper teeth yet known, and are given a new genus. Interpretation of primitive and derived character states, and of the systematic position of *Comotherium* is given below.

MELANODON AND *HERPETAIRUS*

In 1927 and 1929 Simpson erected the genera *Melanodon* and *Herpetairus*, each with two species. Both forms are very similar in basic morphology, and are the most common upper-teeth taxa at Como Bluff. Butler (1939, p. 338) suggested that the distinction between the genera was insignificant. He figured a specimen (*Melanodon goodrichi*, YPM 13750) that has a median transverse ridge on one molar (a *Melanodon* character) and lacks this ridge on the molar anterior to it (a *Herpetairus* character). According to Butler, this was the primary character used by Simpson (1929, p. 75, not p. 85, as listed in Butler, 1939, p. 338) to distinguish the two genera, and therefore the distinction was doubtful.

I have examined the entire Marsh collection carefully, and disagree with this suggestion. The specimen in question does show a median transverse ridge on the anterior molar. There is a small break or gap in the center of the ridge, but its trace can be clearly seen on the labial face of the paracone. I could find no evidence of a stylocone-metacone ridge (diagnostic of *Herpetairus arcuatus*) shown in Butler's text-figure 5. In all other characters, particularly stylocone size and position, this specimen is typical of *Melanodon goodrichi*.

In examining the Marsh collection, I found that all four of Simpson's *Melanodon-Herpetairus* species could be distinguished easily and unambiguously. All the new specimens from Quarry Nine could be referred to one or another of these four species without difficulty. Because there are four diagnos-

TABLE 3
Comparison of *Herpetairus* and *Melanodon*

Character	*H. arcuatus*	*H. humilis*	*M. goodrichi*	*M. oweni*
Stylocone size	moderate	moderate	large	very large
Stylocone position on middle molars	marginal	marginal	marginal	central
Stylocone position on paracrista	posterior	slightly posterior	posterior	posterior
Median transverse ridge	absent	faint-moderate	moderate	strong
Metacone-stylocone ridge	present	absent	absent	absent
Paracrista cusp	small	small	small	large
Labial margin of middle molars	straight	straight	straight	concave
Stylocone shape	transversely compressed	transversely compressed	pyramidal	conical
P^{last} internal cingulum	present	?	?	absent
P^{last} external cingulum cusps	one, posterior	?	?	three

able clusters of morphology present, I continue to recognize Simpson's four species. Revised diagnoses are given below and in table 3 to make the distinctions more clear. For interpretation of primitive and derived character states, see Discussion.

MELANODON SIMPSON, 1927

Malthacolestes Simpson, 1927

TYPE SPECIES: *Melanodon oweni.*

REVISED DIAGNOSIS: Dryolestid upper jaws with large stylocone, placed posterior to paracrista. Strong parastyle, and two-cusped metastyle. Distinct transverse median crest on trigon. Last premolar without internal cingulum; external cingulum with three cusps: anterior, central, and posterior.

Melanodon oweni Simpson, 1927

TYPE SPECIMEN: YPM 10663, a right maxilla with P^4 and M^{1-5}.

REFERRED SPECIMENS: YPM 13752 (referred to *Melanodon goodrichi* by Simpson, 1929); YPM 13751, (type of *Malthacolestes osborni* Simpson, 1927).

REVISED SPECIFIC DIAGNOSIS: Stylocone very large, completely conical, labial to line of parastyle and metastyle. Labial margin of middle molars concave. Stronger median transverse ridge than *Herpetairus* or *Melanodon goodrichi.*

DISCUSSION: Several writers (Butler, 1939, p. 337; Kühne, 1968, among others) have suggested that *Malthacolestes osborni* is a dP^4 and M^1 of *Melanodon.* Unfortunately, M^1 of the type of *Melanodon oweni* is poorly preserved. One specimen (YPM 13752) in the Marsh collection appears to be M^{1-2} of *Melanodon oweni,* based on size and position of the stylocone, and by comparison with M^2 in the type. M^1 of YPM 13752 is practically identical with the second tooth of *Malthacolestes osborni.* Therefore, *Malthacolestes* is here synonymized with *Melanodon oweni.*

Melanodon goodrichi Simpson, 1927

TYPE SPECIMEN: YPM 13738, right maxilla with M^{3-5}.

REFERRED SPECIMENS: YPM 13750, 13749; AMNH 101131.

REVISED SPECIFIC DIAGNOSIS: Stylocone large, pyramidal in shape, placed on straight labial margin. Moderate median transverse ridge compared to *M. oweni.*

DESCRIPTION: AMNH 101131 (fig. 4A) consists of a left maxilla with M^{1-4} and the base of M^5. The preservation of Simpson's hypodigm is very poor in these teeth, so this specimen deserves detailed description.

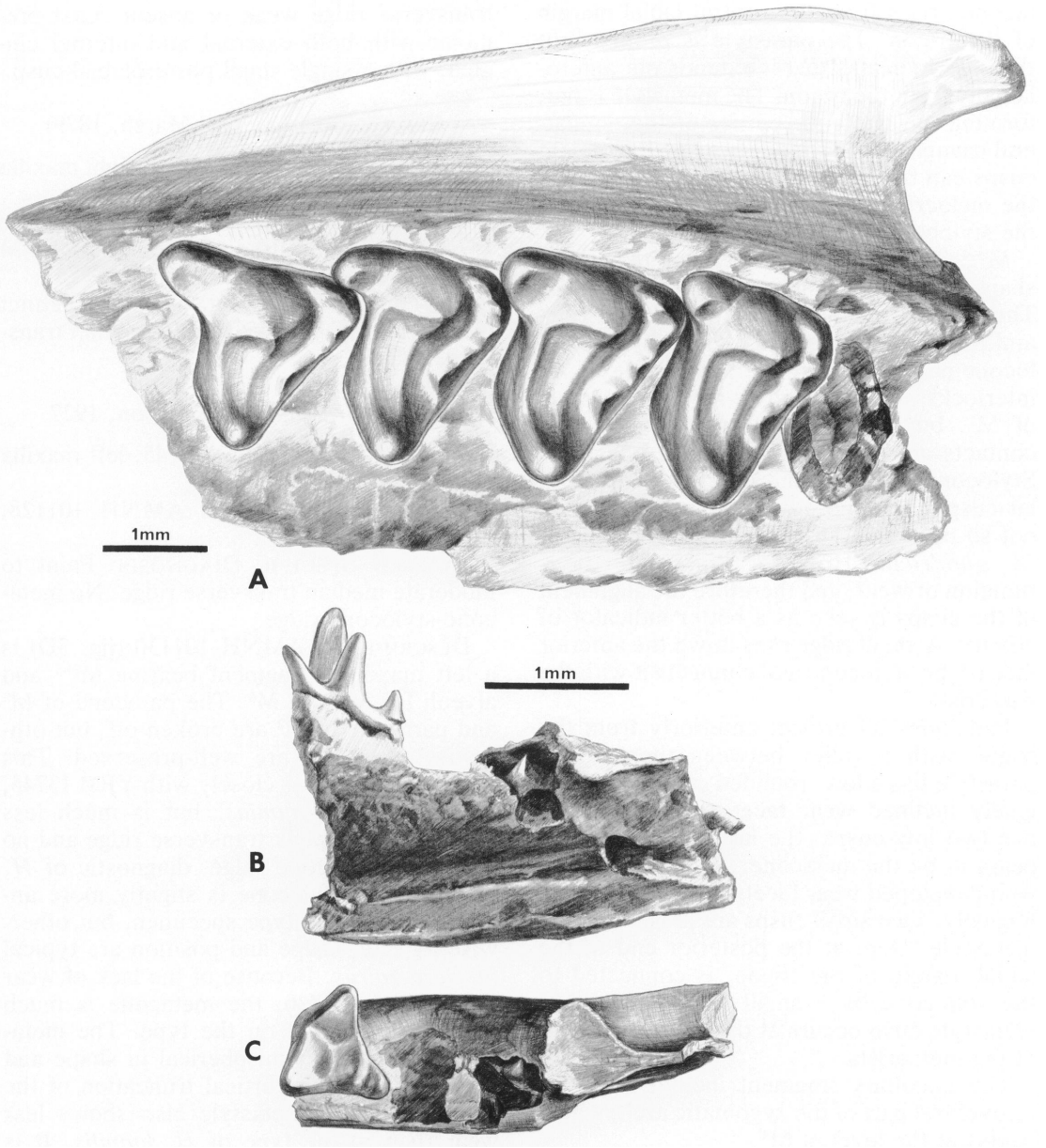


FIG. 4. A. *Melanodon goodrichi*, AMNH 101131, crown view. B. *Amblotherium debilis*, AMNH 101133. Posterior ramal fragment in lingual view. C. Oblique crown view of same specimen, showing M_8 erupting in crypt.

M^1 is narrower labiolingually than the other molars and has a simple, slightly basined crown, shaped like an equilateral triangle. A partly broken paracone rises from the lingual apex. The stylocone is larger than on the other molars, and is roughly conical with a distinct lingual and posterior facet. It is not so pyramidal as on the other molars. The sty-

locone arises from the central labial margin of the trigon. The parastyle is broken, but the base indicates that it extends out anterolabially from the trigon. The metastyle is flat, forming the posterior corner of the equilateral triangle of the trigon; two small incipient cusps can be seen. No metacone appears on the metacrista. A very weak ridge connects the stylocone and paracone.

M^{2-4} become progressively more wedge-shaped and anteroposteriorly compressed. The paracrista and metacrista are distinct and form valleys that are divided by the stylocone-paracone ridge. The parastyle of M^2 interlocks posterolabially with the metastyle of M^1, but succeeding parastyle-metastyle contacts are less labial and more posterior. Stylocones are high and in line with the stylar cusps (as opposed to *M. oweni*) but are not so pyramidal in shape as on the type of *M. goodrichi*. However, this could be a function of wear, and therefore the alignment of the cusps is seen as a better indicator of affinity. A small ridge runs down the anterior face of the stylocone and connects it with the paracrista.

Parastyles all project anteriorly from the trigon with a valley between them. Each parastyle has a low, rounded cusp with a lingually inclined wear facet. The metacrista has two low cusps, the larger of which appears to be the metacone. Both cusps show well-developed wear facets inclined posterolingually. Two small cusps are present on the metastyle. One, at the posterior end of the labial margin of the trigon, is connected to the stylocone by a small ridge. The other metastyle cusp occurs at the most labial end of the metacrista.

The maxillary fragment includes the anteroventral part of the zygomatic arch, which begins at the level of M^4.

HERPETAIRUS SIMPSON, 1927

TYPE SPECIES: *Herpetairus arcuatus*.

REVISED DIAGNOSIS: Dryolestid upper jaws with moderate, transversely compressed stylocone, placed posterior to paracrista. Parastyle and metastyle approximately equal to stylocone in size. Median transverse ridge weak or absent. Last premolar with both external and internal cingula, with a single small posterolabial cusp.

Herpetairus arcuatus (Marsh, 1879)

TYPE SPECIMEN: YPM 11822, right maxilla with M^{2-7}.

REFERRED SPECIMENS: YPM 13741, 13742, 13743, 13744, 13746, 13747, 13740; USNM 2724, 2762, 2800, 2818, 2845.

REVISED SPECIFIC DIAGNOSIS: Distinct metacone-stylocone ridge. No median transverse ridge.

Herpetairus humilis Simpson, 1927

TYPE SPECIMEN: YPM 13745, left maxilla with M^{3-6}.

REFERRED SPECIMENS: AMNH 101128, 101129, 101130.

REVISED SPECIFIC DIAGNOSIS: Faint to moderate median transverse ridge. No metacone-stylocone ridge.

DESCRIPTION: AMNH 101130 (fig. 3D) is a left maxillary fragment bearing M^{3-5} and alveoli for M^2 and M^6. The paracone of M^5 and parastyle of M^3 are broken off, but otherwise the teeth are well-preserved. This specimen compares closely with YPM 13745, the type of *H. humilis*, but is much less worn. It has a weak transverse ridge and no stylocone-metacone ridge, diagnostic of *H. humilis*. The stylocone is slightly more anterior than in the type specimen, but otherwise its size, shape and position are typical of *Herpetairus*. Because of the lack of wear on AMNH 101130, the metacone is much more distinct than on the type. The metacone is roughly hemispherical in shape and cut in half by the vertical truncation of the metacrista. The metastyle also shows less wear than in the type of *H. humilis*. It is narrower and more extended posteriorly. There is a distinct trough between the metacrista edge and the stylocone-metastyle ridge. The latter ridge terminates with a distinct metastyle cusp.

AMNH 101130 came from Quarry Nine, but its exact stratigraphic position is unknown, because the field number on the specimen proved to be in error.

AMNH 101129 is a right maxillary fragment with (?) M^{4-5} and an alveolus for (?) M^3. The teeth are very heavily worn, so that the metacone is gone and the trigon has a saddle-shaped appearance. The size and position of the stylocone, and a faint median transverse ridge, are in agreement with *H. humilis*.

AMNH 101128 is a right maxillary fragment with one molar (?M^4), followed by two three-rooted alveoli and part of a third alveolus. The tooth is moderately worn, with a broken parastyle, but the metacone has not yet been worn off. The stylocone proportions and faint median transverse ridge agree with *H. humilis*.

TAXA KNOWN FROM LOWER JAWS

AMBLOTHERIUM OWEN, 1871

Amblotherium debilis Simpson, 1927

TYPE SPECIMEN: YPM 11821.

REFERRED SPECIMENS: AMNH 101133; YPM 13728, 13730, 13734; USNM 2726.

DESCRIPTION: AMNH 101133 (fig. 4B-C) consists of two right ramal fragments: one segment has three molars (which three is hard to determine), and the other segment consists of M_6, alveoli for M_{7-8}, and the rear portion of the jaw. The last "alveolus" is of particular interest in that it has a molar still inside it and just about to erupt. The small size of this tooth (relative to the fully erupted M_6) and the partly formed trigonid suggest that this "alveolus" is a crypt for an M_8 that had not yet erupted at death. M_7 alveolus gives every indication that M_7 has been fully erupted. Apparently the eruption of M_8 took place much later than the rest of the teeth.

AMNH 101133 compares closely with *A. debilis* in that it is 20 to 25 percent smaller than *A. gracilis*, has a faint labial cingulum on the molars, and in that the paraconid is lower than the metaconid on M_6. One character not noted by Simpson is the fact that the paraconid overlaps the preceding talonid. The specimen has a marked inner groove ending at the dental foramen on the inside of the jaw, but there is no sign of splenial grooves found in Kimmeridgian dryolestids from Guimarota, Portugal (Krebs, 1971). Nor does the specimen show any trace of a coronoid sutural surface that is found in Portuguese forms. The pterygoid fossa is very deep on the internal surface of the jaw. The coronoid process is fragmentary but quite high; the condylar process is broken. The jaw apparently had a weak angular process.

Amblotherium gracilis Simpson, 1927

TYPE SPECIMEN: YPM 11883.

REFERRED SPECIMENS: AMNH 101134; YPM 13732, 13731, 13733; USNM 2142, 2693.

DESCRIPTION: AMNH 101134 is a left ramal fragment with one molar and three alveoli anterior to it. The molar is badly worn with a broken metaconid and talonid. However, the size (25 percent larger than *A. debilis*) and presence of a strong labial cingulum compares closely with *A. gracilis*.

Amblotherium sp.

REFERRED SPECIMENS: AMNH 101135, 101143.

DESCRIPTION: AMNH 101135 is a mandible fragment with four worn premolars. It is doubtfully referred to *Amblotherium* on the basis of size.

AMNH 101143, an isolated left lower molar, is most similar in morphology to *A. debilis*, but is the size of *A. gracilis*. Unlike all other specimens of *Amblotherium* except YPM 13732 (referred to *A. gracilis*), the paraconid is completely erect, and the talonid is cusplike, rather than forming a ledge. If this unique morphology occurred in more than just two isolated teeth, a new species might be justified. For the moment, this specimen is referred to *Amblotherium* sp.

DRYOLESTES MARSH, 1878

Dryolestes priscus Marsh, 1878

TYPE SPECIMEN: YPM 11820.

REFERRED SPECIMENS: AMNH 101140, 101139, 101136?, 101137?, 101141; YPM 11884, 10646; USNM 2722

DESCRIPTION: AMNH 101140 is a right jaw fragment with M_{4-6} preserved and

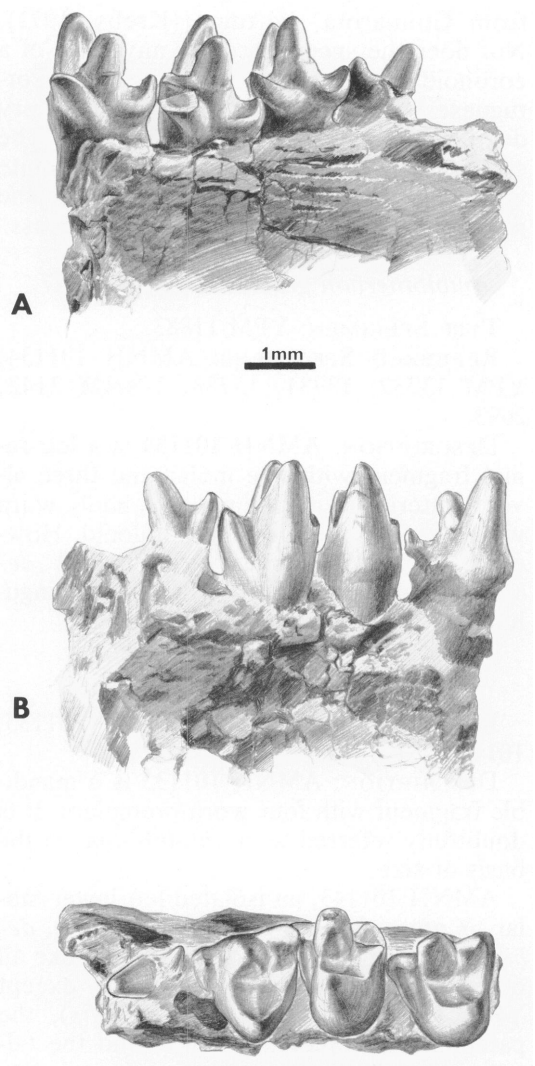


FIG. 5. *Dryolestes priscus,* AMNH 101140. A. Lingual view. B. Labial view. C. Crown view.

alveoli for M_{7-8}. Most of the back of the jaw is preserved, except for the angle, coronoid process, and condyle. The deep pterygoid fossa has a fairly large dental foramen in the anterior part. Around the internal groove there are no traces of insertion grooves for a splenial bone. Because the coronoid process is damaged on the lingual side, it is difficult to determine if there was any trace of a coronoid bone.

The teeth are more worn than in other specimens of *Dryolestes* and consequently the trigonids are very narrow anteroposteriorly. The bifid metaconid of *Laolestes* is absent in this specimen; this can often be due to wear, however. This specimen is distinct from *Amblotherium* in its lack of labial cingulum on the molars and presence of strongly procumbent paraconids. M_6 in this specimen has an apparent lingual "cingulum" that seems to be caused by a break through the crown of the tooth. The talonids are relatively broad and shelflike, with a small ridge on the lingual side that runs anteroposteriorly.

AMNH 101139 (fig. 5) is a right mandible fragment with five molars, possibly M_{3-7}. The last two are broken and only the lingual portions of the crowns remain. The crowns of the other three molars are excellently preserved and show the least amount of wear of any specimen in the collection. As a result, the conids are much more rounded, the notches between them deeper, and distinct wear facets are poorly developed. The metaconid is not bifid nor out of the paraconid-talonid line, distinguishing this specimen from *Laolestes*. Unlike *Amblotherium,* the paraconid is strongly procumbent and there is no labial cingulum.

The talonid on these teeth is relatively unworn and consequently has a strong anteroposterior ridge in its center. This gives the talonid a peaked, convex shape that disappears as the ridge wears down and is reduced to a remnant on the lingual corner, as in AMNH 101140. The paraconid of the most anterior tooth seems to have a cusp on it, whereas the paraconids of the two teeth behind it are flat, triangular shelves. Finally, the enamel on these teeth is markedly lighter in color than any other specimen in the collection.

AMNH 101137 is a left mandible fragment with P_4–M_3. The teeth are well worn, and the molars have trigonids shaped more like a U than a V. The talonids are shelflike but have a distinct cusp on the posterolingual corner with a ridge running anterior to it. The procumbent paraconids, lack of labial cingulum, and alignment of the lingual cusps seem to

assign this specimen to *Dryolestes*. However, P_4 has no anterior accessory cusp and the lingual cingulum is continuous, which contradicts Simpson's (1929, p. 57) diagnosis for *Dryolestes*.

AMNH 101136 is a right ramal fragment with three molars of uncertain designation. The procumbent paraconids, lack of labial cingulum, and non-bifid metaconids suggest *Dryolestes*. However, the metaconids are more labial to the paraconid-talonid line than other *Dryolestes*, and like most *Laolestes*. The paraconid shelf overlaps the preceding trigonid to a greater extent than in any other specimen. Consequently, the relatively unworn talonids have a strong ridge on them, oriented anteroposteriorly.

AMNH 101141 is a right ramal fragment with M_{7-8} and the back of the jaw poorly preserved. M_8 is about one-third smaller than the broken M_7. Both teeth have talonids that are much smaller than in other specimens and are strongly convex. The metaconid is about equal to the protoconid in height, but otherwise the characters of the teeth suggest *Dryolestes*.

LAOLESTES SIMPSON, 1927

Laolestes eminens Simpson, 1927

TYPE SPECIMEN: YPM 13719.

REFERRED SPECIMENS: AMNH 101121, 101138, 101124, 101126, 101125; YPM 10662, 10658, 10660, 10661, 13720, 13721, 13723, 13724, 13728, 13726; USNM 2727, 2729, 2731, 2732.

DESCRIPTION: AMNH 101121 (fig. 6A–B) is the most complete jaw in the collection, a left ramus with M_{2-7} and the alveoli for M_1 and M_8. Except for the coronoid process, the back of the jaw is complete. The inside of the jaw, however, is too badly fractured to discern any internal groove or splenial grooves, and even the pterygoid fossa is badly broken. No trace of a coronoid bone or a sutural surface for one is present. The condyle is well preserved, and is much higher and more vertical than in Simpson's (1929) figure 25. The chief articular surface is mostly dorsal (rather than posterodorsal, as it has been illustrated) and it is supported by a column developed on the posteroexternal surface of the jaw. The angle is also preserved, making the length of the mandible from M_{1-8} nearly equal to the jaw segment posterior to the tooth row. Simpson's figure 25 shows the molar part about one-third longer than the posterior part of the jaw. A single mental foramen appears below the alveoli for P_{3-4}.

The teeth, unfortunately, are extremely worn and blunt. The only diagnostic characters that are preserved are the presence of a labial cingulum on the molars and the procumbent paraconids, which together suggest *Laolestes*. However, AMNH 101121 is about 25 percent smaller than the holotype of *L. eminens*, and smaller than any other *Laolestes* in the collection. The talonids are broken on M_{2-3}, and M_1 is so worn as to be reduced to a knob.

AMNH 101138 is a left ramal fragment with M_{2-4} and alveoli for P_{3-4} and M_1. The bifid metaconids labial to the paraconid-talonid line, as well as the labial cingulum, clearly indicate *Laolestes*. The talonids are narrower than in other specimens, but do show a distinct posterolingual cusp with a ridge running anteriorly to the metaconid. The trigonids are much broader than the holotype of *L. eminens*. There is no mental foramen beneath the P_{3-4} alveoli.

AMNH 101124 is a left jaw fragment with slightly worn M_{2-6} and alveoli for M_{7-8}. It clearly shows the bifid, relatively labial metaconids and labial cingula characteristic of *Laolestes*. The paraconids tend to have anteriorly directed wear facets that become progressively more worn anteriorly. The talonids become progressively narrower posteriorly, but all have a distinct posterolingual cusp and an anteriorly-directed ridge.

AMNH 101125 is a right ramus with P_4–M_5 and alveoli for I_4, C, and P_{1-3}. The bifid molar metaconids become progressively more labial relative to the paraconid-talonid line in more posterior molars. The labial cingulum is also present, corroborating the identification of this specimen as a member of the genus *Laolestes*. The talonids preserved on M_{1-2} are narrow but have the characteristic posterolingual cusp and ridge. P_4, which is missing on the holotype, is much

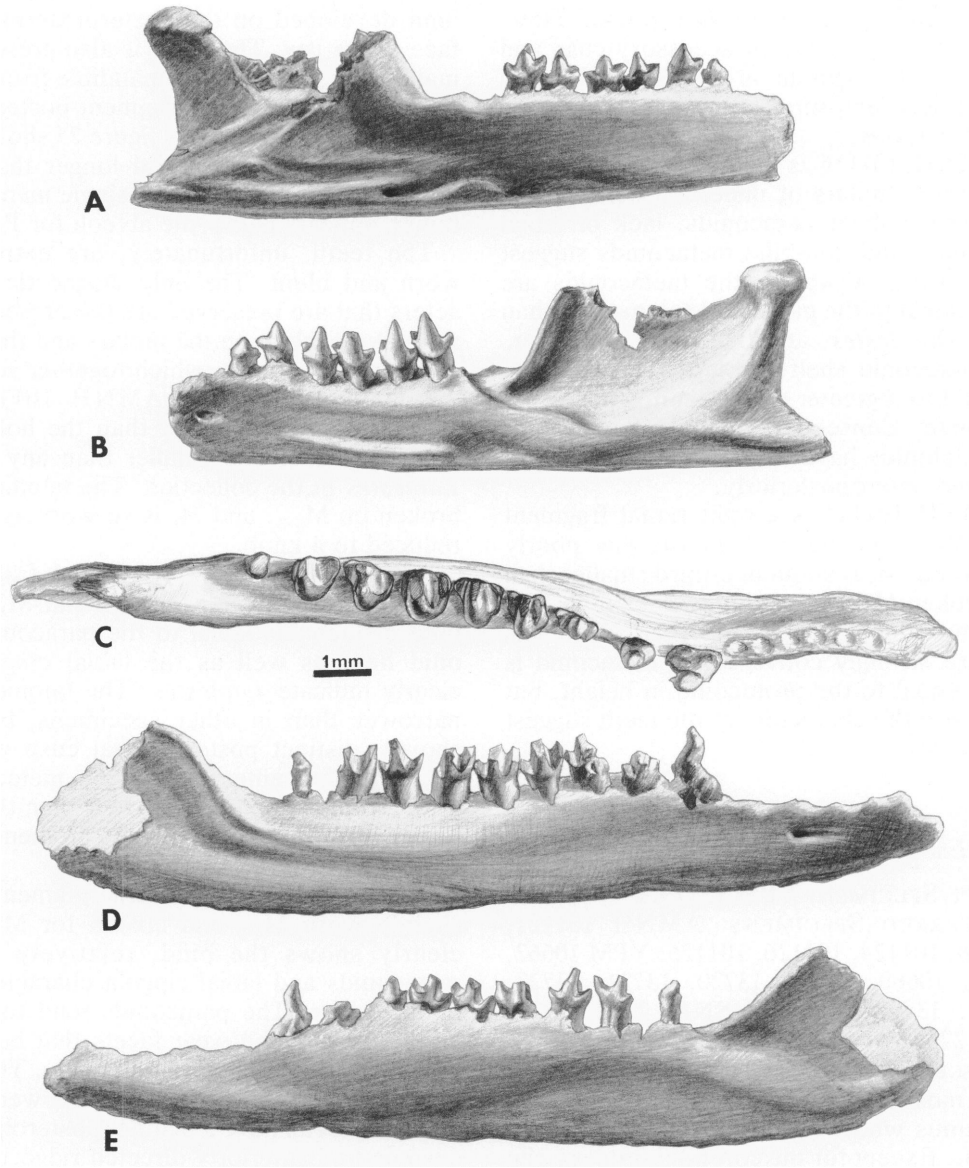


FIG. 6. *Laolestes eminens*, AMNH 101121. A. Lingual view. B. Labial view. C. *Kepolestes coloradensis*, USNM 2723. Crown view. D. Labial view. E. Lingual view.

larger than P_{1-3} or M_1, and has a faint lingual cingulum and a strong labial cingulum. There is no anterior accessory cusp.

AMNH 101126 is a left mandible with M_{3-5} and alveoli for M_{1-2} and M_{6-8}. The back of the jaw is not preserved. The molars have a strong labial cingulum and apparently bifid metaconids, suggesting *Laolestes*. The talonids are quite narrow and heavily worn, so that the posterolingual talonid cusp is also quite worn. This wear is greatest on M_3 and least on M_5.

KEPOLESTES SIMPSON, 1927
Figure 6C–E

Kepolestes coloradensis Simpson, 1927

TYPE AND ONLY SPECIMEN: USNM 2723.

REVISED DESCRIPTION: *Kepolestes coloradensis* is the only known Morrison therian that did not come from Como Bluff. It was found in Marsh's dinosaur quarries at Garden Park, Colorado. Simpson named (1927) and described it (1929, p. 67) on the basis of the lingual view of the jaw. The other side of the jaw remained unprepared and undescribed. When this specimen (USNM 2723) was graciously lent to me for study by Dr. R. J. Emry, it was decided that the preparation should be completed. Mr. Otto Simonis masterfully executed this delicate task.

Kepolestes coloradensis consists of a right lower jaw with P_4 and M_{1-8}. Alveoli for a canine and P_{1-3} are present. There may be indications of at least one incisor alveolus on the broken anterior end of the jaw. The jaw is very slender and tapers upward at its anterior end. An internal groove runs parallel to the ventral border and immediately above it. The back of the jaw lacks an angular process and condyle, but is otherwise complete. The coronoid process is heavy, slanting upward at a 30-degree angle to the tooth row. Its anterior border has a broad surface that is directed anterolabially. The pterygoid fossa is very shallow and poorly developed. The masseteric fossa, however, is quite deep and extends forward as a trough that terminates below M_6. A mental foramen appears below the alveolus for P_2.

The teeth are highly worn, so that M_{1-2} are reduced to featureless nubbins. P_4 is high and recurved, with no trace of anterior cusps or any cingula. However, its preservation is very poor, so these features cannot be too heavily relied upon.

M_{3-7} show the typical dryolestid molar pattern. The amount of wear has reduced the protoconid and metaconid to a low, saddle-shaped ridge, and consequently there is a narrowing of the trigonid. The wear has also reduced the paraconids to blades or wings, with deeply worn, U-shaped grooves separating them from the metaconids. Two distinctive derived characters clearly indicate the phylogenetic affinities of *Kepolestes*:

1. A labial cingulum, previously obscured in matrix, is visible on M_{3-6}. It is not so strongly developed as in *Laolestes,* but is nevertheless distinct. This is shared with *Laolestes, Crusafontia,* and *Amblotherium* (see fig. 8).

2. The metaconids are not so heavily worn on M_3 and M_7, and further preparation reveals that they are slightly bifid, contrary to Simpson's (1929, p. 70) statement. This character is found elsewhere only in *Laolestes* and thus unites *Kepolestes* and *Laolestes* as sister taxa (see fig. 8).

Kepolestes presents an additional bizarre feature revealed by further preparation. M_8 is reduced to a cylindrical peg, approximately the same height as M_7. This odd tooth morphology does not seem to be due to breakage or excessive wear, as the surfaces are smooth and the alveolus is the same diameter as the crown. The basal cross section is roughly ovoid and only one-third of the diameter of M_7. A small, triangular, anterolabially-facing wear facet is present, but otherwise the tooth is featureless. This tooth is difficult to interpret, and its morphology is apparently unique among primitive Theria. It may be due to abnormal development in this particular individual, or to other possible causes which must remain speculative. If another specimen of *Kepolestes* were found that showed this unique morphology, the form of M_8 would be considered an autapomorphy for the genus.

DISCUSSION

The study of the phyogeny of the non-tribosphenic Theria has been hampered by some special problems with which most mammalian paleontologists have not had to contend:

(1) Nearly all the known taxa occur in the

late Jurassic of North America and Europe. Thus, stratigraphic superposition cannot be used to reconstruct phylogeny.

(2) The taxa are known almost exclusively from fragmentary jaws and teeth, whose associations are unknown or doubtful in most cases. The skeleton of one Kimmeridgian dryolestid has been reported (Henkel and Krebs, 1977), but this does not resolve the taxonomy of the rest of the forms, which are primarily "upper jaw animals" and/or "lower jaw animals."

(3) The samples are exceedingly small, and come primarily from two localities: Quarry Nine, Como Bluff, Wyoming, and the Purbeck Beds of England (with new forms from Guimarota, Portugal, yet to be published adequately). Fourteen of the 29 taxa in figures 8 and 9 are known from single specimens. Also, most of the forms are quite distinctive and too specialized to represent ancestral morphotypes.

As a result, most workers have avoided discussing the relationships of the various taxa, limiting their work to morphological transitions between *Amphitherium, Peramus,* and some "typical" dryolestoid or "typical" symmetrodont. The unfortunate consequence of this practice is that the diversity of forms available has been widely ignored, simply because they were "too specialized to be the ancestor of later forms."

In view of these conditions, a cladistic approach to therian phylogeny is especially appropriate. Readers unfamiliar with the practice and terminology of cladistic systematics are referred to papers by Hennig (1965, 1966), Brundin (1966, 1968) Cracraft (1972), Griffiths (1972), Schaeffer et al. (1972), Eldredge and Tattersall (1975), and Wiley (1976, pp. 7–13). Cladistic systematics has the following additional advantages over competing systems of phylogeny reconstruction for the primitive Theria:

(1) Cladistic systematics does not rely on stratigraphic data to reconstruct phylogeny (Schaeffer et al., 1972).

(2) Cladistics presents a technique of analyzing diverse morphologic data and constructing a parsimonious phylogeny from it.

(3) Cladistics changes the emphasis from primitive, ancestral morphotypes to the acquisition of shared derived characters. Cladistic systematics, in the strictest sense, does not recognize ancestors (Schaeffer et al., 1972; Englemann and Wiley, 1977), since ancestors are unessential to the analysis. But even non-cladistic authors (e.g., Clemens, 1970, p. 369; Clemens and Mills, 1971, pp. 110–111; Fox, 1977) have been forced to admit that the generalized forms have specializations (or "autapomorphies" in cladistic terminology) which exclude them from ancestry of more derived taxa. If one is interested in the ancestral morphology, it can be extrapolated from the nodes of a cladogram, without making untestable assertions about a particular specimen "giving rise" to later animals.

The lack of association between most upper and lower dentitions made it necessary for Simpson (1928, 1929) to assign different generic names for each, except in the few cases where the association was proved. This proliferation of names gives a false impression of diversity, but no evidence is presently available to resolve the dilemma. Unfortunately, the diagnostic characters of the "lower jaw taxa" such as *Laolestes* and *Dryolestes* occur primarily on the lingual side of the teeth. Thus, these features would not appear on the upper teeth as wear facets, since the lingual side of the lower teeth is not in direct occlusion. Similarly, most of the distinguishing characters of taxa based on upper teeth, such as those of *Herpetairus* or *Melanodon,* occur on the labial margin or in the center of the trigon. Again, identification of diagnostic wear facets to determine the synonymy of these names would be very difficult, and is not attempted here.

Clemens and Lees (1971) have described an isolated upper tooth and lower tooth they call *Melanodon hodsoni,* from the early Cretaceous (Wealden) of England. The upper tooth appears to be indistinguishable from *Melanodon goodrichi,* except by size. The lower tooth, as far as it is preserved, shows a bifurcated metaconid, which is shared with *Laolestes.* However, it lacks the labial deflection of the metaconid that is usually found in *Laolestes.* The most consistent di-

agnostic feature of *Laolestes*, a labial cingulum, is not preserved, since the protoconid is broken off. Clemens and Lees were reluctant to synonymize *Melanodon* and *Laolestes* on this evidence, and I concur with this decision.

In addition, there are four distinct species of "upper jaw animals" (*Melanodon* and *Herpetairus*) that are the right size to be associated with three species of "lower jaw animals" (*Laolestes* and *Dryolestes*). Which belongs to which? We have gotten no further on this problem than Simpson did. Lower jaws of two species of *Amblotherium* are known from Como Bluff, but no uppers have been found so far. There are now four Como Bluff genera of "upper jaw animals" (*Pelicopsis, Miccylotyrans, Euthlastus,* and *Comotherium*) that seem to have no likely candidate for lower jaws. *Pelicopsis* has been suggested as the upper teeth of a paurodont (Simpson, 1929, p. 83), but there are five species of paurodont lower jaws known.

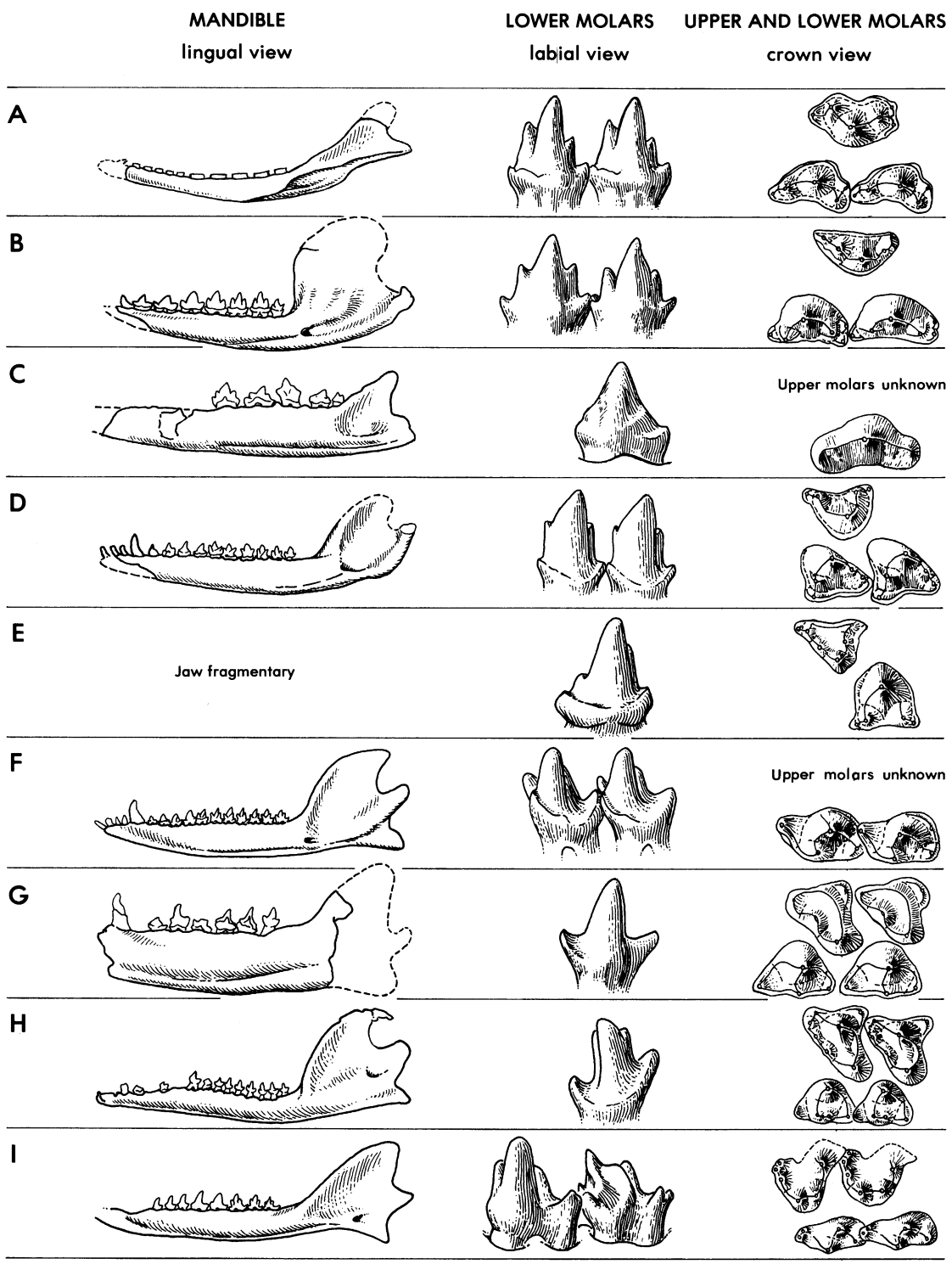
In view of this lack of correspondence between "upper jaw" and "lower jaw" taxa, it was necessary to analyze them separately and generate a cladogram for each. These are then combined into a cladogram of both upper and lower jaws, using only the taxa that have both, or whose associations are reasonably well demonstrated.

GENERAL TOOTH CHARACTERS

Occlusal Relations: The "reversed triangle" dental pattern of the posterior teeth, resulting from the labial shift of the protoconid, has been widely recognized as a shared derived character (or "synapomorphy" in cladistic terminology) uniting the Theria (Osborn, 1907; Patterson, 1956; Mills, 1964; Kermack et al., 1968; Crompton and Jenkins, 1968; Crompton, 1971, 1974; McKenna, 1975). This arrangement of cusps is derived with respect to the in-line cusps of morganucodonts and other triconodonts, and is not found in any other group of primitive mammals. Crompton (1971) also pointed out that the development of broad wear facets joining the cusps, rather than the primitive intercusp wear facets of triconodonts, is unique to the Theria. In all Theria, the molars are slightly "skewed"; that is, the protocristid-paracrista shear is more vertical and transverse, whereas the paracristid-metacrista shear is more oblique and diagonal (Crompton, 1971, p. 80). These characters are partly correlated with the reversed triangle arrangement, but did not develop simultaneously. In *Kuehneotherium, Amphidon,* and *Tinodon* (Crompton, 1971, p. 82), a single wear facet is developed on the anterior face of the trigon and posterior face of the trigonid (paracrista-protocristid), but there are still multiple wear facets (A and B, Crompton, 1971, fig. 8A) on the posterior trigon-anterior trigonid (paracristid-metacrista). The elimination of these metacrista wear facets and the development of a single metacrista-paracristid wear facet is apparently the derived condition. It occurs in spalacotherioid symmetrodonts, dryolestoids, *Peramus,* and the Tribosphenida. *Amphitherium,* however, still retains facet B and part of A on the paraconids of its anterior molars; the upper teeth are unknown (Crompton, 1971, fig. 8B).

Butler (1972, fig. 3) has shown that the inclination of shear movement in *Eozostrodon* (?=*Morganucodon*), and *Kuehneotherium* ranges from 30 to 40 degrees. This is also true of *Peramus* and spalacotherioid symmetrodonts and occurs in the primitive Tribosphenida. *Amphitherium* and the dryolestoids develop a shear inclination of 40 to 50 degrees, which indicates highly transverse mandibular movement (Butler, 1972, p. 478). Shear movement inclination of less than 40 degrees appears to be primitive for the Mammalia; an inclination of 40 to 50 degrees is therefore a derived character for the Dryolestoidea, including *Amphitherium.*

Dental Formula: Recently, there has been renewed debate about the number and homologies of postcanine teeth in the Theria (McKenna, 1975). If one accepts *Kuehneotherium* as the sister group of all remaining Theria (Trechnotheria), the primitive therian dental formula is still open to question. Kermack and others (1968) stated that *Kuehneotherium* could have had nine to 11 postcanine teeth, with five or six lower premolars


MANDIBLE
lingual view
LOWER MOLARS
labial view
UPPER AND LOWER MOLARS
crown view
A
B
C
Upper molars unknown
D
E
Jaw fragmentary
F
Upper molars unknown
G
H
I

and three to six lower molars. They did not figure any specimen, however, that shows molar alveoli, so it is not clear how they determined the number of molars. Their figure 8 indicates alveoli for six premolars, although the last two premolars have double roots and could also be molars. If six premolars is the primitive number for the Theria, then reduction to five would be derived for the Trechnotheria (McKenna, 1975). Reduction to three premolars is found in spalacotherioid symmetrodonts and is therefore considered a synapomorphy for the group. Dryolestids have reduced the number of premolars to four, and in North American paurodonts, it is further reduced to two. Kühne (1968) reported paurodonts with three, four, and five premolars, however.

Amphitherium was originally described with four premolars, but Clemens (personal commun.) has reexamined the specimens and now agrees with McKenna (1975) that it had five premolars.

McKenna thinks *Peramus* had five premolars, and reductions of this formula occurred variously in the Tribosphenida. Certainly the teeth called M_1^1 by Clemens and Mills (1971) and P_5^5 by McKenna (1975) look more like premolars than molars. If, however, this hypothesis is falsified, then a reduction to four premolars would be a synapomorphy for the cladotheres (excluding *Amphitherium*; see fig. 11). The position of *Peramus* as the sister group of the Tribosphenida is supported by several other characters (see fig. 12) and does not stand or fall on the premolar-molar count.

The number of molars in *Kuehneotherium* was given by Kermack and others (1968) as three to five, depending upon whether there are nine, 10 or 11 postcanine teeth. *Amphidon* and *Tinodon* have four molars, and *Peramus* has either three (McKenna, 1975) or four (Clemens and Mills, 1971). Spalacotheriids and dryolestoids (including *Amphitherium*) have increased the number of molars to at least seven, with eighth and ninth molars appearing variably in some dryolestids. The late eruption of the eight and ninth molars (see p. 293) may explain this variation. North American paurodonts have only four molars, but Kühne (1968) reported paurodonts with five or six molars. Perhaps this discrepancy is also due to late eruption, and to the poor condition of the few known North American paurodonts. In any case, the distinctive feature of the molar count is the increase from the primitive three to five, to at least six or seven that occurs in spalacotheriids, *Amphitherium*, dryolestids, and possibly some paurodonts.

LOWER JAW CHARACTERS

MANDIBLE CHARACTERS: The primitive therian jaw morphotype can be seen in *Kuehneotherium* and is closely comparable to *Morganucodon* (?=*Eozostrodon*) and some cynodonts (Kermack et al., 1973). *Kuehneotherium* has no angular process, but possesses a large dentary trough for the accessory jaw bones (which are not preserved), a facet for the rudimentary coronoid bone, a medial flange passing from the tooth row to the condyle, and a coronoid process at a very low angle to the tooth row. The condyle is on, or slightly below, the level of the tooth row. All of these characters appear in *Morganucodon* (?=*Eozostrodon*) and thus, by outgroup comparison, are plesiomorphic in *Kuehneotherium*. *Kuehneotherium* is more derived than *Morganucodon* (?=*Eozostrodon*) in that the medial flange is continuous, without an interruption of the abductor fossa.

Using *Kuehneotherium* as the sister group

←

FIG. 7. Comparison of representative taxa mentioned in text. A. *Kuehneotherium*. B. *Tinodon* (upper teeth of *Eurylambda*). C. *Amphidon*. D. *Spalaçotherium* (upper teeth of *Peralestes*). E. *Spalacotheroides*. F. *Amphitherium*. G. *Paurodon* (upper teeth of *Pelicopsis*). H. *Laolestes* (upper teeth of *Melanodon*). I. *Peramus*.

TABLE 4

Distribution of Characters in Genera Known from Lower Teeth

(Unless otherwise noted: − character reduced or absent; + character present; +/− both conditions; ? character unknown. For interpretations of primitive and derived conditions, see text.)

	Kuehneotherium	*Amphidon*	*Manchurodon*	*Tinodon*	*Spalacotheroides*	*Symmetrodontoides*	*Spalacotherium*	*Amphitherium*	*Paurodon*	*Archaeotrigon*	*Tathiodon*	*Araeodon*	*Peraspalax*	*Dryolestes*	*Kepolestes*	*Phascolestes*	*Laolestes*	*Crusafontia*	*Amblotherium*	*Palaeoxonodon*	Porto Pinheiro tooth	*Peramus*	Tribosphenida
1. Angle of coronoid to tooth row	15°	?	?	90°	?	?	70°	45°	?	?	45°	?	?	?	?	60°	70°	90°	45°	?	?	30°	45°
2. Angular process on dentary	−	?	?	−	?	?	−	+	?	+	+	?	+	+	?	+	+	+	+	?	?	+	+
3. Strong internal pterygoid ridge	−	+	?	+	?	?	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
4. Number of premolars	6?	4	?	3	?	?	3	4	2	2	2	3?	?	4	4?	4	4	4	4	?	?	5	3–5
5. Number of molars	3–5	4	?	4	?	6+	7	7	4	3–4	?	4?	7	8	8	8	8	7	7–9	?	?	3	3
6. P^{last} lingual cingulum	−	−	?	−	?	?	+	+	+	+	?	+	+	+	−?	+	+	−	+	?	?	−	+/−
7. P^{last} anterior cusp or cingulum	+	+	?	+	?	?	+	−	−	−	?	−	+	+	−?	?	−	−	−	?	?	−	+/−
8. Posterior molar root smaller	−	−	−	−	−	−	−	+	+/−	+	+/−	+/−	++	++	++	++	++	++	++	−	−	−	−
9. Alveolar border lower lingually	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+	?	?	−	−
10. Anterior molar trigonid angle	180°	140°	?	180°	?	180°	55°	45°	?	?	60°	?	40°	40°	30°	35°	40°	35°	50°	?	?	60°	10–90°
11. Posterior molar trigonid angle	100°	?	?	99°	70°	30°	45°	55°	60°	70°	60°	?	40°	40°	30°	35°	40°	35°	50°	?	70°	60°	10–90°
12. Trigonid compressed	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+	−	−	−	+/−
13. Metaconid lower than paraconid	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
14. Metaconid lateral to paraconid (i.e., transverse metacristid)	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+	−	−	−	+/−

TABLE 4—(*Continued*)

	Kuehneotherium	*Amphidon*	*Manchurodon*	*Tinodon*	*Spalacotheroides*	*Symmetrodontoides*	*Spalacotherium*	*Amphitherium*	*Paurodon*	*Archaeotrigon*	*Tathiodon*	*Araeodon*	*Peraspalax*	*Dryolestes*	*Kepolestes*	*Phascolestes*	*Laolestes*	*Crusafontia*	*Amblotherium*	*Palaeoxonodon*	Porto Pinheiro tooth	*Peramus*	Tribosphenida
15. Procumbent paraconid	−	−	−	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+	−	−	−	−
16. Metaconid lingual to paraconid-talonid line	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−
17. Talonid: expanded +, very expanded ++, reduced −, very reduced or absent —.	−	—	—	—	—	—	—	++	+	+	+	+	+	+	+	+	+	+	+	++	++	++	++
18. Develop hypoconulid and entoconid	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	++	++	++
19. Lose lower molar interlock	−	+	+	+/−	+	+	+	+/−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
20. Anterobasal cusp on molar	+	?	?	+	+	+	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	+/−
21. Labial cingulum on molar	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	+	+	+	−	−	−	−
22. Hypoconid shear facet from metacone	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+

of the remaining therians, all Trechnotheria share the loss of the medial flange extending from the tooth row to the condyle, and show an increase in the angle of the coronoid process. This angle ranges from about 45 degrees in *Peramus* to 90 degrees in *Tinodon,* but the distribution of this characters shows no consistent pattern within the Trechnotheria. Trechnotheres share a condyle that is above the level of the tooth row.

The condyles of *Morganucodon* (?= *Eozostrodon*) (Kermack et al., 1973) and *Kuehneotherium* (Kermack et al., 1968) are directed posteriorly and are dorsoventrally flattened. The condyle of *Kuehneotherium* is partly broken (Kermack et al., 1968, fig. 10), but it has been reconstructed so that it closely resembles *Morganucodon* (?= *Eozostrodon*) (Kermack et al., 1968, fig. 11). Where the condyle is preserved in higher therian jaws, it has a distinct trochlea that is usually dorsally or posterodorsally directed. This can be seen in *Tinodon* (Simpson, 1929, figs. 15 and 16), *Spalacotherium* (Osborn, 1907, fig. 11), *Laolestes* (Simpson, 1929, fig. 25), *Amblotherium* (Simpson, 1929, fig. 26), *Phascolestes, Peramus,* and *Amphitherium* (Simpson, 1928, fig. 35), and *Dryolestes* (Osborn, 1907, fig. 32).

A trochlear condyle can also be seen in non-therians such as *Docodon* (Osborn, 1907, figs. 20 and 21), but not in *Triconodon* or *Phascolotherium* (Osborn, 1907, figs. 11a and 6). The distribution of this character suggests that the lack of a distinct trochlea on the condyle is primitive for the Mammalia. The condition in *Docodon* and in the Trechnotheria would then be derived in parallel, if the other character distributions are correct in indicating that these taxa are not closely related. For purposes of this discussion, a distinct, posterodorsally, directed trochlear condyle is considered a shared derived character for the Trechnotheria (see fig. 12).

Morganucodon (?=*Eozostrodon*) has a feature labeled the angular process (Kermack et al., 1973), but Patterson (1956, p. 76) has given reasons for doubting its homology with the angular process of the Cladotheria. This process is certainly much farther anterior, and in shape dissimilar to the angular process of any cladothere. Indeed, the long, slender, somewhat dorsally deflected angular process seen in the Dryolestidae seems to be unique to that group; the angular process is unknown in paurodonts. The angular process of *Amphitherium, Peramus,* and the Tribosphenida is stout, triangular in profile, and ventrally deflected, unlike that of dryolestids, but much farther posterior than the process in *Morganucodon, Docodon,* or any other non-therian. Thus, the presence of a true angular process is considered a synapomorphy for the Cladotheria. The morphology of the dryolestid angle would then be a derived form of the primitive cladothere angle.

Symmetrodonts, lacking an angular process of any kind, have a modification in that area that seems synapomorphous for the group. *Tinodon, Amphidon,* and *Spalacotherium* (the only symmetrodonts with the back of the jaw known) show a distinct pterygoid crest that passes from the ventral border of the jaw continuously into the condylar process. This feature is unique within the Theria, although *Phascolotherium,* an amphilestid triconodont, shows something like it. However, because the Theria are a monophyletic group based on other character distributions, this feature would have to be derived in parallel from the primtiive *Kuehneotherium-Morganucodon* morphology. An adaptive-functional explanation might be suggested for this parallelism in jaws lacking angles, but will not be considered here.

Krebs (1969, 1971) has shown the existence of a rudimentary coronoid and splenial in dryolestids from Guimarota mine. These are primitively present in *Kuehneotherium,* but absent in all Trechnotheria not from Portugal. I have examined all the North American material with this problem in mind. No specimen that is adequately preserved shows any trace of a coronoid or splenial. Because other characters establish that dryolestids are trechnotheres, and derived ones at that, two explanations are possible: (1) These primitive bones were lost or fused independently in symmetrodonts, all dryolestoids except the Guimarota forms, and the Za-

theria; (2) the coronoid and splenial are neotenic retentions of the primitive condition in the Guimarota specimens. Unfortunately, none of the Guimarota dryolestoids has been described adequately or named, so it was impossible to include them in the cladogram. Therefore, the distribution of this character has been left out of the cladogram pending the publication of full descriptions of the Guimarota taxa.

In most primitive Theria the mandible is long and slender, with a long symphysis. Three genera of paurodonts (*Araeodon, Paurodon,* and *Archaeotrigon*) develop a jaw that is much shorter and stouter, with a short symphysis. This character is unique to the group, and is interpreted here as a synapomorphy for them. The fourth genus of paurodont, *Tathiodon,* appears to retain the primitive slender condition of the mandible. In other characters (see fig. 8 and table 4), *Tathiodon* is a good paurodont. It is therefore the primitive sister group of the remaining three genera.

LOWER TOOTH CHARACTERS

ROOTS: The Dryolestidae have long been recognized (Simpson, 1929, fig. 24D) by their unequal roots in the lower molars, the smaller of which is posterointernal and supports the reduced talonid. This feature is unique to the Dryolestidae, excluding the paurodonts. According to Butler (1939, p. 334), *Amphitherium* has slightly unequal roots. Yet Simpson (1928, p. 117) stated that *Amphitherium* has subequal roots, "although in posterior molars the posterior root does not extend quite so far externally as does the anterior one." Butler also reported that two paurodonts (YPM 13775, 13778) have "slightly unequal roots." Unfortunately, YPM 13775 has apparently been lost and YPM 13778 is broken so that the roots are no longer present. Most of the specimens of paurodonts examined by the writer have equal roots, but YPM 13776 has a slightly larger anterior root. If Butler's observations are correct, then slightly unequal roots would unite *Amphitherium* and some paurodonts as sister groups of the Dryolestidae. However, the extreme inequality of dryolestid roots is an unambiguous synapomorphy for the dryolestids.

Another character found in all the Dryolestidae is the unequal height of the alveolar border on each side of the molar. It is markedly deeper on the labial side (Simpson, 1929, fig. 24C), and at one time gave the impression that the lingual and labial views of *Amblotherium* molars were of different animals. This character is not found in paurodonts or *Amphitherium*, so it seems to be a shared derived character for the Dryolestidae.

TALONID DEVELOPMENT: *Kuehneotherium* has a distinctly expanded posterior cingulum which is larger than the anterior cingulum and seems homologous with the talonid. It has a single cusp which Kermack and others called the hypoconulid, but which Freeman (1976) considered the hypoconid. The talonid is not basined, and slopes away from the hypoconid crest. A posterior cingulum of some sort is primitive for the mammalian lower molar, and the enlargement seen in *Kuehneotherium* seems to be derived for the Theria.

With this polarity established, the symmetrodonts all share a reduction of the talonid until it is equal to the anterior cingulum in size, or lacking. Indeed, talonid reduction in this manner gives their molars the symmetrical appearance that is responsible for the name. The talonid of *Tinodon* is only slightly smaller than that of *Kuehneotherium* (Crompton and Jenkins, 1967, 1968), but the talonid is highly reduced in the Spalacotheriidae, and absent in the Amphidontidae.

In paurodonts, the talonid is larger than in *Kuehneotherium,* but it becomes broad and shelflike. The cusp on the talonid is present, but becomes progressively reduced in size, and is lost in *Paurodon. Paurodon* and *Archaeotrigon* are united by having a talonid that is semicircular in crown view. A triangular outline is the primitive condition because it is found in *Amphitherium,* dryolestids, and the paurodonts *Tathiodon* and *Araeodon.*

In the dryolestids, the talonid is slightly larger than in *Kuehneotherium,* but it be-

comes anteroposteriorly compressed along with the rest of the tooth. In most dryolestids it is a low shelf on the posterior side of the trigonid, triangular in crown view, with the hypoconid at the posterolabial apex. There is usually a ridge (possibly homologous to the cristid obliqua) from the base of the trigonid terminating at the hypoconid. Development of this characteristic talonid is hypothesized to be derived for the Dryolestidae.

Amphitherium presents a problem. Its talonids are more expanded than those of the dryolestids, and in this regard it seems to be more closely related to the Zatheria. The development of a cristid obliqua is also much stronger than in the dryolestids. This may be in conflict with other characters that unite *Amphitherium* with the Dryolestida (new rank; see Position of *Amphitherium*). If a broad talonid is hypothesized to be primitive for the Cladotheria, then the shelflike paurodont condition and the secondary reduction in dryolestids would be modifications of the *Amphitherium* condition. *Amphitherium* also shows a unique character in the extension of its talonid over the base of the trigonid of the succeeding molar (Mills, 1964; Clemens and Mills, 1971, p. 106). This character is not seen in any other therian, and is therefore an autapomorphy which excludes *Amphitherium* from ancestry of any other form (Clemens and Mills, 1971, p. 108).

Palaeoxonodon (Freeman, 1976) shows further development of the talonid. It is shallowly basined and has an incipient hypoconulid and entoconid. *Peramus* has a fully basined talonid with all three talonid cusps. These characters unite *Peramus* with higher Theria and are synapomorphous for the Zatheria. Krusat (1969) has described, but not named, a tooth from Porto Pinheiro, Portugal, that has three distinct talonid cusps but is not basined. Thus, it would seem to be intermediate on the morphocline between *Palaeoxonodon* and *Peramus*.

MOLAR CINGULA: *Kuehneotherium* has a strong anterior and lingual cingulum on its lower molars, but no labial cingulum. This is primitive for the Mammalia, as seen in *Eozostrodon* (?=*Morganucodon*) and *Thrinaxodon* (Crompton and Jenkins, 1968, fig. 9). The anterior cingulum persists in all symmetrodonts, in *Peramus* (as a cusp), and in many Tribosphenida. However, *Palaeoxonodon* and the Porto Pinheiro mammal have apparently lost it, insofar as can be determined from single, isolated teeth. It is also lost in all dryolestoids except *Crusafontia* (Henkel and Krebs, 1969). The lower molar lingual cingulum is lost in amphidontids (see Position of Amphidontids, below) and in all the Cladotheria. The loss of lower molar lingual cingula seems to be a good synapomorphy for the Cladotheria.

Primitive non-therians such as *Eozostrodon* (?=*Morganucodon*) and *Thrinaxodon* (Crompton and Jenkins, 1968) have several cuspules on the lower molar lingual cingulum. The largest of these, cusp "g" of Crompton and Jenkins (called the "Kühnecone" by Parrington, 1967) is lost in British (but not French—see Sigogneau-Russell, 1978) specimens of *Kuehneotherium* and all higher Theria. The loss of the "Kühnecone" therefore unites British *Kuehneotherium* and the trechnotheres.

Primitively, there is no labial cingulum on the lower molars. It develops in the symmetrodonts *Spalacotherium* and *Symmetrodontoides*, and in the dryolestids *Amblotherium*, *Crusafontia*, *Laolestes*, and *Kepolestes*.

MOLAR INTERLOCK: The lower molars of *Kuehneotherium* show an indentation on the posterior rim of the cingulum, which receives the main cusp of the talonid. This "tongue-in-groove" molar interlock is seen in the type specimen of *Tinodon bellus* (YPM 11843) and, to a lesser extent, in the lower teeth of *Eozostrodon* (?=*Morganucodon*) and *Thrinaxodon* (Crompton and Jenkins, 1968, fig. 9), *Megazostrodon*, and *Trioracodon* (Crompton, 1974). The distribution of this character suggests that it is primitive for the Mammalia, although it is lost in the rest of the non-Theria. In the Theria, it is lost in all symmetrodonts except one specimen of *Tinodon* and in all cladotheres except *Amphitherium* and *Crusafontia* (Krebs, 1971). However, this character is variably developed in the taxa named above, and succeeding teeth in the same jaw may

differ with respect to interlock. In view of this fact, multiple loss of this character seems a more parsimonious explanation of its distribution within the Theria (see fig. 8).

TRIGONID CHARACTERS: *Kuehneotherium* has a moderately high trigonid, with a metaconid-protoconid-paraconid angle of about 110 degrees. The metaconid is much lower than the paraconid, whereas it is as high or higher than the paraconid in all other Theria, and in outgroups such as *Morganucodon* (?=*Eozostrodon*). Therefore, this high paraconid is autapomorphic for *Kuehneotherium* and excludes it from the ancestry of the rest of the Theria. In all other characters, however, *Kuehneotherium* seems to be primitive for the Theria, and is used as the outgroup for comparison.

The distribution of trigonid angles is shown in table 5. In symmetrodonts that have complete tooth rows, the trigonid angle becomes progressively more acute posteriorly. *Tinodon* and *Symmetrodontoides* have an M_1 with cusps nearly in line. M_3 of *Tinodon* is shown to have an angle of about 99 degrees (Crompton and Jenkins, 1967), and in *Symmetrodontoides*, M_6 has an angle of about 30 degrees (Fox, 1976). Patterson (1956, fig. 13A) shows angles ranging from 55 degrees in M_1 to 45 degrees in M_6 of *Spalacotherium*, so this trend is present, but not so pronounced. Unfortunately, *Kuehneotherium* has no jaws with teeth in them, so the polarity of this character is difficult to establish. Parrington (1971, 1978) showed a number of teeth of *Kuehneotherium* which have angles ranging from 180 degrees to almost 100 degrees. Presumably, the in-line cusps of the anterior molars are the retained primitive condition, and the acute angle in the posterior molars is derived. In this case, all therians share a posterior trigonid angle of 100 degrees or less (except the amphidontids; see Position of Amphidontids).

Dryolestids show an extreme anteroposterior compression of the trigonids and narrowing of the angle, corresponding to the general shortening of the tooth. This seems to be a synapomorphy for the Dryolestidae, since it does not occur in paurodonts, *Peramus*, or *Amphitherium*. It is most strongly developed in *Amblotherium*, *Crusafontia*, *Laolestes*, and *Phascolestes*.

A character unique to the spalacotheriid symmetrodonts (but still primitive in *Amphidon* and *Tinodon*) is an extremely high crown, with long pointed cusps. This seems to be a synapomorphy for symmetrodonts minus *Amphidon* and *Tinodon*.

A characteristic feature of the dryolestoids is the strongly procumbent paraconid. The primitive condition is seen in *Kuehneotherium*, symmetrodonts, and *Peramus*, with the paraconid pointing dorsally or slightly anterodorsally. In paurodonts and dryolestids, it points very strongly anteriorly, at about a 70 degree angle to the vertical, metaconid axis. The condition in *Amphitherium* is difficult to interpret. It appears to be more procumbent than the primitive condition (Simpson, 1928, fig. 38; Mills, 1964, fig. 3; Crompton and Jenkins, 1968, fig. 11), but this is difficult to determine from sketches and stereophotographs that differ greatly. For purposes of this discussion, it is considered "moderately procumbent" and any sort of procumbent paraconid is a synapomorphy for the Dryolestoidea, including *Amphitherium*.

Paurodonts have further modified the paraconid so that it becomes shelflike, with a reduced cusp. In the most derived form (*Paurodon*) the paraconid is completely flat without a cusp. Paurodonts are also characterized by a reduction of the metaconid height relative to the protoconid. *Tathiodon* shows the beginnings of this condition. It is most pronounced in *Araeodon*, *Archaeotrigon*, and *Paurodon*.

Amblotherium and *Crusafontia* show a character that is apparently unique to them. The paraconid and metaconid in these animals are much more slender and rodlike, rather than shelflike or conical as in the rest of the Theria. I have never seen the actual specimens of *Crusafontia*, but figure 1 in Henkel and Krebs (1969) shows this character.

LOWER PREMOLAR CHARACTERS: Kermack et al. (1968) showed some isolated premolariform teeth that are referred to *Kuehneotherium*. None of these teeth show either

TABLE 5

Distribution of Characters in Genera Known from Upper Teeth

(Symbols as in table 4. For interpretation of primitive and derived character states, see text.)

	Kuehneotherium	*Eurylambda*	*Peralestes*	*Spalacotheroides*	*Pelicopsis*	*Euthlastus*	*Amblotherium*	*"Amblotherium" nanum*	*Kurtodon*	*Miccylotyrans*	*Comotherium*	*Herpetairus humilis*	*Herpetairus arcuatus*	*Melanodon oweni*	*Melanodon goodrichi*	*Peramus*	Tribosphenida
1. Number of premolars	?	?	?	?	?	?	4	4	4	?	?	?	4?	4?	4?	5	3–4
2. Number of molars	?	?	6+	6+	?	?	?	8	7	?	?	?	7	7	?	3	3
3. P^{last} with lingual cingulum	?	?	?	?	?	?	+?	–	+?	?	?	?	+	–	?	–	+
4. P^{last} with posterior cingulum	?	?	+	?	?	?	+	–	+	?	?	+	+	+	?	++	+/–
5. Number of molar roots	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3
6. Anterior trigon angle	115°	87°	180°	?	45°	?	50°	50°	40°	?	?	35°	35°	40°	40°	90°	10–100°
7. Posterior trigon angle	110°	?	60°	70°	40°	40°	40°	40°	40°	30°	25°	50°	50°	60°	60°	–	10–100°
8. Parastyle interlock	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
9. Straight labial margin	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	–	–
10. Lingual cingulum on molars	+	+	?	–	–	–	–	–	–	–	–	–	–	–	–	+	+
11. Ridge in trigon basin	–	–	–	–	–	–	–	+	+	+	–	+	–	+	+	–	–
12. Metastyle with two cusps	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	+	+/–
13. Stylocone marginal	+	+	+	+	+	+	+	+	+	+	–	+	+	–	+	?	+/–
14. Stylocone on parastyle	+	+	+	+	+	+	+	+	+	+	+	–	–	–	–	?	+/–
15. Hooked parastyle	–	–	–	–	+/–	+	+	+	+	+/–	+	?	–	+	+/–	+	+/–
16. Protocone	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
17. Lose metacrista facets A and B	–	–	+	+?	+	+	+	+	+	+	+	+	+	+	+	+	+
18. Trigon basined	–	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
19. Molars increase crown height	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–
20. Molars expand transversely	–	–	–	–	+	+	+	+	+	+	+	+	+	+	+	–	+
21. Transverse paracrista shear	–	–	–	–	+	+	+	+	+	+	+	+	+	+	+	–	–
22. Metacone with facet from hypoconid	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
23. Metacrista shear extends to paracone	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–

a labial or a lingual cingulum, except for a tooth shown in figure 6. It is not clear whether the cingulum on the tooth in figure 6 is labial or lingual. All of the figured premolariform teeth have an anterior cingulum or cusp of some sort.

There is no lingual cingulum on the last lower premolar of *Amphidon* or *Tinodon*. A lingual cingulum occurs (where known) on the last lower premolars of spalacotheriids, *Amphitherium*, and dryolestids except *Crusafontia*. It is absent from *Peramus* and primitive Tribosphenida. An interpretation of the distribution of this character is shown in figures 8 and 10.

The anterior cingulum or cusp on the last lower premolar is lost in all Cladotheria except *Peraspalax* and *Dryolestes*. This loss is interpreted as a derived character for the cladotheres, and the condition in *Peraspalax* and *Dryolestes* would therefore be secondarily regained.

UPPER TOOTH CHARACTERS

Kuehneotherium (Kermack, Kermack and Mussett, 1968) is also known from isolated upper teeth; in all respects these upper teeth show the primitive morphology for the Theria. *Kuehneotherium* still retains a complete cingulum around the tooth, a high central paracone, a large metastyle cusp and a parastyle tab that interlocks with a groove between the metastyle and metacone. These are primitive for the Mammalia, as demonstrated by outgroup comparison with *Eozostrodon* (?=*Morganucodon*) and other forms (Crompton and Jenkins, 1968, fig. 2). Other primitive characters include presence of only two molar roots, retention of wear facets A and B (Crompton, 1971) on the metacrista, paracrista and metacrista poorly developed (i.e., cusps still high and pointed), and lack of any trigon basin. *Kuehneotherium* shows the reversed triangle dentition and consequent labial deflection of the stylocone and metacone, which is a shared derived character for the Theria.

Kuehneon ("Duchy 33" of Kühne, 1950; named by Kretzoi, 1960) is a poorly preserved tooth that Kermack et al. (1968) considered to be a left upper molar. Simpson (1971, p. 188) considered it a probable synonym of *Kuehneotherium*. Considering the preservation and the isolated nature of all the Rhaetic fissure-fill teeth, it is placed with *Kuehneotherium* in the cladogram. Its distinguishing characters, if they are valid, appear to be autapomorphous.

Eurylambda is based on an upper tooth referred to *Tinodon* by Simpson (1929). This is corroborated by the work of Crompton and Jenkins (1967). It lacks a trigon basin and has a trigon angle of about 160 degrees (Crompton and Jenkins, 1967, fig. 1E). The metastyle cusp, although damaged, appears to be similar in size to that of *Kuehneotherium*. *Eurylambda* retains the primitive multiple wear facets on the metacrista (Crompton, 1971). It has one character, however, that is derived and shared with the rest of the Theria. In *Eurylambda*, there is no sign of a parastyle-metastyle interlock, although the lower teeth (*Tinodon*) still retain an interlock.

Most of the remaining symmetrodonts and cladotheres are known from more than isolated upper teeth. *Peralestes*, considered by Simpson (1929) to be the upper teeth of *Spalacotherium*, shows progressively more acute trigon angles on the more posterior molars (see Patterson, 1956, fig. 13A). Upper tooth rows are unknown from the other symmetrodont taxa. Judged from the lower teeth, however, the retention of the obtuse angle in the anterior molars is primitive, and the acute angle of the posterior molars is derived for all therians except *Eurylambda* and *Kuehneotherium*. According to Crompton and Jenkins (1967), *Eurylambda* is probably based on an M^1, so that its posterior molars could have been more acute (as suggested by the lower molars in *Tinodon*). This condition may even occur in *Kuehneotherium*. Kermack et al. (1968, fig. 2) show an upper molariform tooth with a more acute angle than the type upper molar. Acute posterior trigon angles, then, may be a shared derived character for the Theria as a whole, but in the absence of better evidence, this character can only be used to unite *Peralestes* with the Cladotheria.

The presence of a trigon basin, and the corresponding development of a paracrista and metacrista, appears in *Peralestes, Spalacotheroides,* and the cladotheres, but not in *Eurylambda* or *Kuehneotherium.* If *Eurylambda* is based on an M^1, this character would not be very pronounced, and might have existed in more posterior molars. For the purposes of the cladogram, this character can only be used to unite the symmetrodonts (excluding *Eurylambda*) and cladotheres.

METACRISTA CHARACTERS: "CUSP C" VS. METACONE: Crompton (1971) has analyzed the wear facets of the primitive Theria and concluded that *Kuehneotherium, Eurylambda,* and *Amphitherium* retain facets A and B on the metacrista. The upper molars of *Amphitherium* are unknown, however, so this is inferred from the corresponding wear on lower molars. Presumably, the loss of these facets is derived for all Theria except these three taxa.

Crompton (1971) has recently cast doubt on the homologies of the main metacrista cusp. According to his argument, in primitive Theria this cusp is not the metacone of all higher Theria, but what he has labeled "cusp c" in *Kuehneotherium.* Cusp c shears down a notch between the paraconid and protoconid of *Kuehneotherium,* giving rise to facets "2" and "A" (Crompton, 1971, fig. 7C). The paraconid shears up the notch between cusp c and the paracone, producing facets "A" and "B" in figure 7C.

In *Peramus,* the condition is quite different. The paraconid has retreated posterolingually, so that only part of the crista between the metacone and the metastyle shears against it. On the penultimate molar ($?M^3$, or M^2 according to McKenna, 1975) of the sole specimen of *Peramus* upper teeth (BM[NH] M21887), there is a minute cusp between the metacone and metastyle. Crompton called this cusp c and homologized it with the large metacrista cusp of *Kuehneotherium,* since its occlusal relations are similar. Due to the expansion of the talonid, the true metacone in *Peramus* does not shear the paraconid, but its anterolingual side shears against the posterolabial edge of the talonid (Facet 4, Crompton, 1971, fig. 5). However, this condition is only true of the penultimate molar ($?M^3$ or M^2). The molar anterior to it (M^2 or $?M^1$) has a metacone shearing the groove between the paraconid and the hypoconid, producing facets on each (Crompton, 1971, fig. 8C). This is distinct from the condition in *Kuehneotherium,* in which cusp c sheared the notch between the paraconid and protoconid and the talonid had not yet expanded posteriorly to meet it (Crompton, 1971, fig. 8A).

The source of controversy lies in the reconstruction of the unknown upper teeth of *Amphitherium.* The lower teeth have facets that show the *Kuehneotherium* condition on anterior teeth and the *Peramus* condition on posterior teeth (Crompton, 1971, fig. 6C). Crompton (personal commun.) considers it unlikely that a metacone could shift occlusal relations in the same jaw, i.e., shear the paraconid in the anterior part of the jaw and the hypoconid in the posterior part. Therefore he postulated (1971, fig. 6) a metacone arising *de novo* in front of cusp c on the upper teeth of *Amphitherium.* In his scenario, the metacone would enlarge and cusp c would reduce until it is barely visible on a single tooth of *Peramus,* and absent elsewhere.

An alternative hypothesis might also be suggested. The posterior expansion of the talonid and posterolingual retreat of the paraconid in posterior molars of *Amphitherium* would naturally cause a change in occlusal relations. The posterior metacrista cusp that shears down between the protoconid and paraconid would be "captured" as the paraconid retreats and the hypoconid rises in its place. This scenario is more parsimonious than one involving *de novo* addition of the metacone, and has been suggested by Butler (1972).

Crompton (personal commun.) objects to the latter hypothesis for the following reasons:

(1) It involves a shift in occlusal relation for the main metacrista cusp.

(2) Cusp c still remains on *Peramus.*

(1) The degree of change in the molars of *Amphitherium* is quite striking, so that a shift in occlusal relations seems quite plau-

sible. Such shifts do occur; Crompton himself documented an example (*Peramus*) in the same paper. Indeed, if one postulates both a metacone and cusp c on the metacrista of *Amphitherium*, then the metacone must change its occlusal relations (i.e., gradually come in contact with the hypoconid on more posterior teeth). Thus, the problem has not been eliminated, but instead becomes more complex.

(2) "Cusp c" in *Peramus* is so insignificant as to have been ignored by Clemens and Mills (1971, fig. 2 and text) in their analysis. Equating this small metacrista swelling on a single tooth of a single specimen of *Peramus* with the well-defined cusp c on all teeth of *Kuehneotherium* does not seem warranted. Crompton (personal commun.) claims that *Pappotherium*, *Prokennalestes* and *Cimolestes* also show cusp c. If the figures of these taxa are accurate, the metacrista cusps are barely worth mentioning, let alone being dignified with the "cusp c" homology.

It is impossible to settle this dispute until the upper teeth of *Amphitherium* are found. For the purposes of this paper, I shall utilize Occam's razor and consider "cusp c" homologous with the metacone. If Crompton's hypothesis is correct, then the metacone occurs only in *Amphitherium*, *Peramus*, and the Tribosphenida. It would then be a synapomorphy for these animals (as in fig. 11C, this paper). Other characters (see fig. 11B) make this hypothesis less parsimonious than the one adopted here.

If cusp c is equivalent to the metacone, *Peramus* and the dryolestoids all retain the primitive metacrista shear facet between the metacone and metastyle, seen in *Kuehneotherium*. The derived condition is seen in spalacotherioid symmetrodonts, which extend this facet to the paracone (Crompton, 1971, p. 85).

The metacone undergoes reduction and is sometimes lost due to wear in all the dryolestoids except *Pelicopsis*. Because *Pelicopsis* is considered to be based on the upper teeth of a paurodont (Simpson, 1929), the reduction of the metacone would then be a shared derived character for the Dryolestidae.

STYLAR REGION: All primitive Theria except *Kuehneotherium* and *Eurylambda* show a noticeable enlargement of the stylar region as the trigon angle becomes narrower. In most of these forms, the stylar regions of adjacent teeth contact each other. The parastyle projects anterolabially and usually contacts the posterolabial part of the metastyle. In a few forms the parastyle becomes extremely hooked and closely interlocked with the preceding metastyle. Related to the condition is the slightly indented stylar margin, which seems to be primitive for all Theria except *Kuehneotherium* and *Eurylambda*. In *Herpetairus* and *Melanodon goodrichi* the outer margin is straight. In *Euthlastus* and *Comotherium*, on the other hand, the labial margin is so indented as to give the crown a heartlike shape. Both of these conditions are interpreted here to be independently derived, since they conflict with all the remaining character distributions of these taxa (see fig. 9).

Clemens and Mills (1971, p. 111) have pointed out that the stylar region, stylocone, and posterior cingulum of the upper molars of *Peramus* are far more reduced than in higher Theria, such as *Pappotherium* and *Holoclemensia*. These characters are apparently autapomorphous and exclude *Peramus* from the ancestry of the Tribosphenida.

Primitively, the metastyle is large with a large single cusp, as in *Kuehneotherium* and *Eurylambda*. The advanced forms show a considerable reduction of the metastyle and especially its apex. In *Miccylotyrans*, *Comotherium*, *Herpetairus*, and *Melanodon* the metastyle is divided by a valley running anterolingually-posterolabially. Distinct cusps are present on each side of the metastyle valley in *Comotherium*, *Herpetairus*, and *Melandon*. These conditions are interpreted here as derived conditions uniting these taxa.

TRIGON CHARACTERS: As Crompton and Jenkins (1968, p. 455) have pointed out, symmetrodonts (excluding *Eurylambda*) are derived in that their trigons are expanded vertically and increase the paracone height. Dryolestoids, on the other hand, expand their molars transversely (or compress them anteroposteriorly, in other words). Both of

these conditions appear to be derived independently from the primitive condition, and neither is exhibited by *Peramus*. The Tribosphenida make their upper molars transversely wider by addition of the protocone, which is different from the mechanism employed by the dryolestoids.

The trigon of all the dryolestoids except *Euthlastus* and *Pelicopsis* has a high, distinct paracrista and metacrista that gives it a basined appearance. This seems to be a shared derived character for the remaining dryolestoid taxa.

In a number of dryolestoids, there is a transverse ridge on the trigon, which is not found in any other group. It appears faintly on M^5 of *Amblotherium nanum* (Simpson, 1928, p. 137) and is distinct on most molars of *Kurtodon, Miccylotyrans,* and *Herpetairus humilis*. It is very pronounced on all species of *Melanodon,* and this degree of development is diagnostic for the genus. However, it is absent in *Pelicopsis, Euthlastus, Amblotherium pusillum, Comotherium,* and *Herpetairus arcuatus*. In view of this and other character distributions (see fig. 9 and table 5), it seems most parsimonious to interpret this ridge as a synapomorphy for *Amblotherium nanum, Kurtodon, Miccylotyrans, Herpetairus,* and *Melandon,* with secondary loss in *Comotherium* and *Herpetairus arcuatus*. In keeping with this character distribution, *Amblotherium nanum, Kurtodon, Miccylotyrans, Comotherium, Herpetairus,* and *Melanodon* show a much narrower trigon not seen in *Pelicopsis, Euthlastus,* or *Amblotherium pusillum*. This implies that *Amblotherium nanum* is more closely related to the more derived dryolestids than it is to *A. pusillum*. Therefore, *Amblotherium* (as presently constructed) is a paraphyletic genus. Owen (1971) originally named it *Achyrodon nanus* and this was synonymized with *Amblotherium* by Simpson (1928, p. 120). Since *A. pusillum* is the type species of the genus, "*Amblotherium*" *nanum* requires a different generic name if taxonomists revising the British material corroborate this cladogram.

STYLOCONE CHARACTERS: In primitive therians, the stylocone is a wedge-shaped cusp, about equal in size to the metacone and located on the paracrista. This is modified in several ways in the dryolestids:

(1) Primitive dryolestids have this stylocone morphology, with some reduction in height, along with the reduction of the metacone. In *Comotherium, Herpetairus,* and *Melandon,* however, the stylocone is distinct and conical, projecting high above the labial margin of the tooth, and much higher than the metacone.

(2) In *Herpetairus* and *Melanodon,* the stylocone shifts posteriorly, so it is placed in the middle of the tooth and no longer on the paracrista.

(3) In *Comotherium* and *Melanodon oweni,* the stylocone shifts lingually to the stylar margin. This character is fairly equivocal, though, since it is a function of the size of the parastyle and can be less pronounced in more anterior molars.

(4) All species of *Melanodon* have a very large stylocone which dominates the trigon. This character is diagnostic for the genus.

The most parsimonious distribution of stylocone characters is shown in figure 9. This requires parallelism in the lingual stylocone shift (character 3 above), but, as noted, this character is often ambiguous.

CINGULUM CHARACTERS: A labial cingulum is present on the upper molars of *Kuehneotherium* and primitive non-therians but lost in all more derived therians. A lingual cingulum is primitive for therians, since it occurs in *Eozostrodon, Kuehneotherium, Peramus,* and the Tribosphenida (where it eventually develops a protocone). However, both dryolestoids and symmetrodonts (except *Eurylambda*) have lost the lingual cingulum. The loss of the upper molar lingual, cingulum might be used to unite these groups, but this character is in conflict with a number of others (see Symmetrodont Monophyly and below).

CLADOGRAM DISCUSSION

The cladograms in figures 8 and 9 are not strictly congruent. This is because fewer taxa are known from upper teeth than from lower teeth, and only a few taxa are known from both (*Kuehneotherium, Amblotherium,*

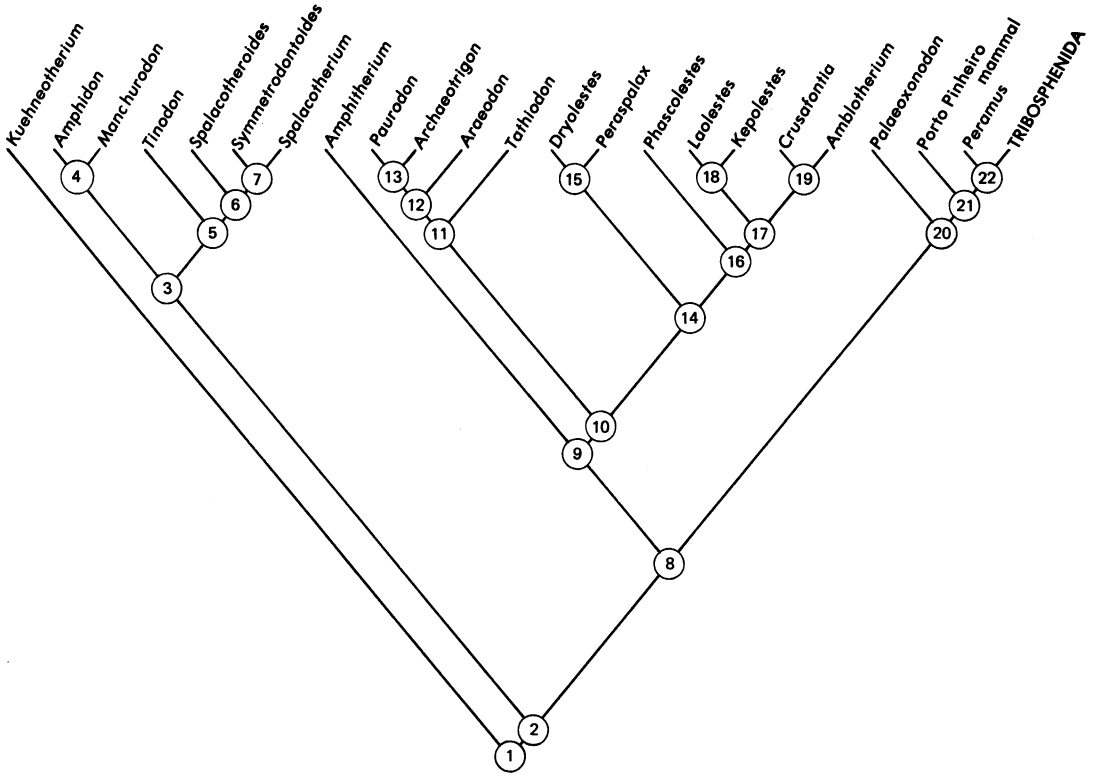


FIG. 8. Cladogram of taxa known from lower teeth and jaws. See table 6 for explanation.

Peramus, and the Tribosphenida[3]). *Eurylambda* and *Peralestes* are believed to belong to *Tinodon* and *Spalacotherium* respectively, and this is assumed in the composite cladogram (fig. 12). Patterson (1956, p. 10) referred an upper molar to his lower molar genus *Spalacotheroides* (Patterson, 1955). The suggestion that *Melanodon* and *Laolestes* might be synonymous (Clemens and Lees, 1971) is not followed here for reasons given above. In particular, the critical genus *Amphitherium* has no known upper teeth. This makes the composite cladogram more difficult to construct (see Position of *Amphitherium*, below). When the two cladograms are compared, one major difference can be seen: there are no synapomorphies in the upper teeth that unite the symmetrodonts (*Tinodon-Eurylambda, Spalacotheroides* and *Spalacotherium-Peralestes*). However, this may be due to the fact that *Eurylambda* is based on an isolated M^1 and no posterior molars are known.

SYMMETRODONT MONOPHYLY

Because symmetrodonts are not just isolated upper teeth, but animals with both upper and lower dentitions, characters of both must be combined in evaluating their possible monophyly. Four possible hypotheses of relationships are suggested:

(1) *Tinodon* plus *Amphidon* are the sister group of the spalacotherioids plus cladotheres (fig. 10A).

[3] Freeman (1976) referred an isolated upper tooth to *Palaeoxonodon*, but published figures and descriptions are inadequate to make any meaningful comparisons or to list it in table 5.

TABLE 6
Explanation of characters in Figures 8 and 9
(* indicates parallelism)

FIGURE 4: LOWER TOOTH CHARACTERS

1. Reversed triangle molar pattern, single wear facet on anterior trigon-posterior trigonid, broad wear surfaces join cusps, lose Kühnecone
2. Coronoid angle increases, lose medial condylar flange, reduce to five premolars, angle of posterior molar trigonids less than 100°, condyle above level of tooth row, trochlear condyle develops
3. Greatly reduced talonid, strong internal pterygoid ridge, reduce to four premolars*
4. Reduce metaconid and paraconid to crenulations on cristids, angle of trigonids about 140°
5. Reduce to three premolars
6. High slender trigonids, lose paraconid facets A and B (single paraconid wear facet)*
7. Increase to seven molars*, molars acquire labial cingulum*, continuous lingual cingulum on last premolar*
8. Lose lingual cingulum on molars, lose anterior cusp on last premolar, anterior molar trigonid angle reduces to less than 100°, develop true angular process, expand talonid, hypoconid wear facet for metacone
9. Slightly unequal molar roots, continuous lingual cingulum on last premolar*, more than six molars*, lose anterior cingulum on molars*, slightly procumbent paraconid
10. Transverse metacristid shear, strongly procumbent paraconid, reduce to four premolars*
11. Reduce to two premolars, broad shelflike paraconid and talonid, reduced paraconid and talonid cusps, metaconid slightly shorter than protoconid
12. Metaconid much shorter than protoconid, jaw short and stout with short symphysis, last lower premolar loses anterior cingulum
13. Talonid semicircular in crown view
14. Anterior molar root much larger than posterior root, trigonid and talonid anteroposteriorly compressed, lingual alveolar border lower than labial border, angular process slender and dorsally deflected
15. Anterior cusp on last premolar*
16. Narrower trigonids
17. Labial cingulum on molars*
18. Bifid metaconid
19. Slender metaconids and paraconids, three mental foramina (Henkel and Krebs, 1969, p. 460)
20. Incipient hypoconulid and entoconid
21. Strong hypoconulid and entoconid
22. Basined talonid, reduce to three molars

FIGURE 5: UPPER TOOTH CHARACTERS

1. Reversed triangle cusp pattern, single wear facet on anterior trigon, broad wear surfaces joining cusps
2. Lose parastyle tab interlock
3. Lose metacrista facets A and B, posterior trigon angle acute, trigon basin formed, reduce metastyle
4. Metacrista shear facet extends to paracone, molars increase crown height, lose lingual cingulum on molars*
5. Stylar regions enlarge and interlock, molars expand transversely, angle of anterior molar trigons less than 100°, metacone with facet from hypoconid shear, three roots on molars
6. Reduce to three molars, reduce stylocone
7. Reduce to four premolars, lose lingual cingulum on molars*, paracrista shear becomes transverse
8. Reduce metacone
9. Distinct paracrista and metacrista, higher paracone
10. Narrower trigon, weak transverse ridge on M^5
11. Distinct transverse ridge on most molars
12. Bifurcated metastyle with incipient cusps
13. Conical stylocone higher than metacone, metastyle with two cusps
14. Straight labial margin, stylocone shifts posteriorly

(2) *Amphidon, Tinodon,* and the spalacotherioids are a monophyletic sister group of the cladotheres (fig. 10B).

(3) *Spalacotherium, Spalacotheroides, Symmetrodontoides,* and *Amphidon* plus *Tinodon* are progressively more primitive sister groups of the Cladotheria (fig. 10C).

(4) *Spalacotherium* plus dryolestids are a monophyletic group, and the sister group to the Zatheria (fig. 10D).

Figure 10 and table 7 summarize the situation with respect to character conflicts in the symmetrodonts. Characters 5 and 6 must be parallelisms under Hypotheses 1, 2, and 3, because uniting dryolestoids and *Spalacotherium* (Hypothesis 4) generates the greatest number of conflicts. Characters 2 and 3 argue for symmetrodont monophly (Hypothesis 2), and 7, 8, and 9 against it (Hypotheses 1 and 3). But Hypothesis 3 has almost as many conflicts as Hypothesis 4. Hypotheses 1 and 2 each have five instances

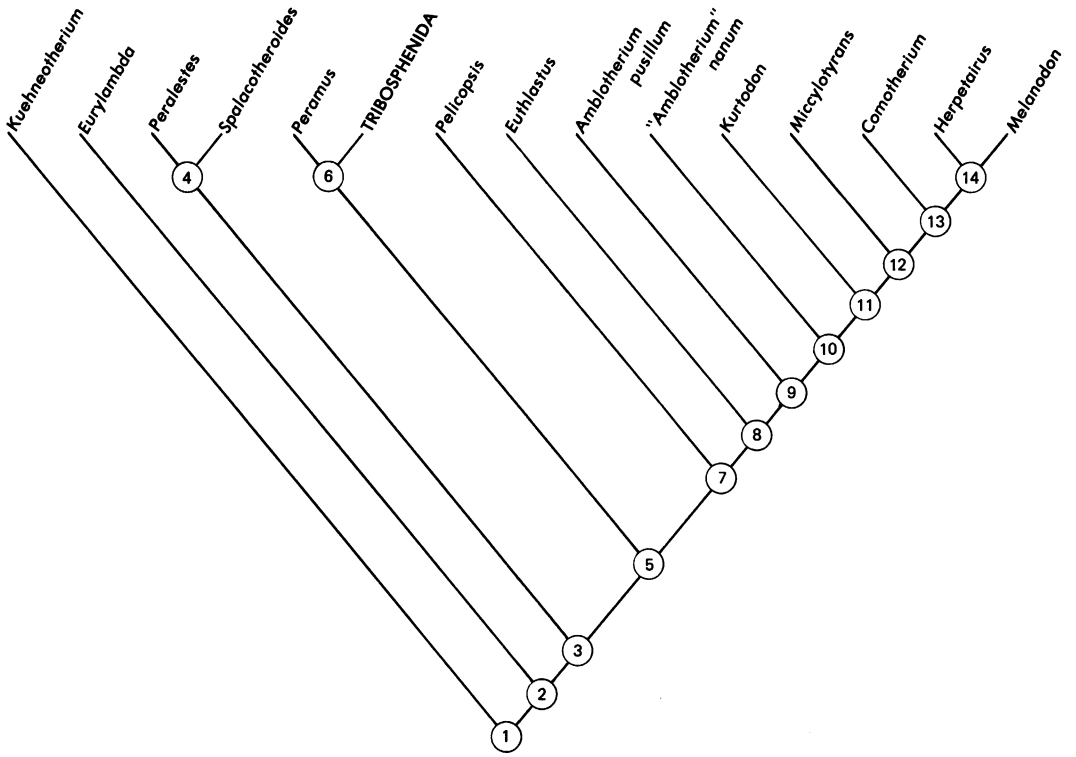


FIG. 9. Cladogram of taxa known from upper teeth. See table 6 for explanation.

of parallelism, and are therefore equally parsimonious. The distribution of character 15 (loss of upper molar lingual cingulum) conflicts with all the hypotheses above. This apparent parallelism was left off figure 10 to reduce clutter.

Since Hypotheses 1 and 2 are equally parsimonious, they should be expressed as an unresolved trichotomy, to be tested by further characters or by new specimens. For the present, I consider Hypothesis 2 (symmetrodont monophyly) to be the most parsimonious for the following reasons:

(1) Character 2 (strong internal pterygoid ridge) is very distinctive and is unique within the Theria.

(2) Character 3 (highly reduced talonid) is the diagnostic derived character that gives the group the symmetry responsible for the name. It is not found in any other primitive Theria.

(3) Character 7 (loss of metacrista-paraconid facets A and B occurs in spalacotherioid symmetrodonts as a result of the metacrista shear extending to the paracone (Crompton, 1971, p. 85). In cladotheres, these facets are lost, but the metacrista shear never goes beyond the metacone. *Amphitherium,* a good cladothere by other characters, has lost these facets on it its posterior teeth, but retains them on anterior teeth. Therefore, this character seems to develop in different ways and may not be homologous.

A case for splitting up the Symmetrodonta is not convincing. I therefore take the conservative course and recognize the Symmetrodonta as a monophyletic group (including

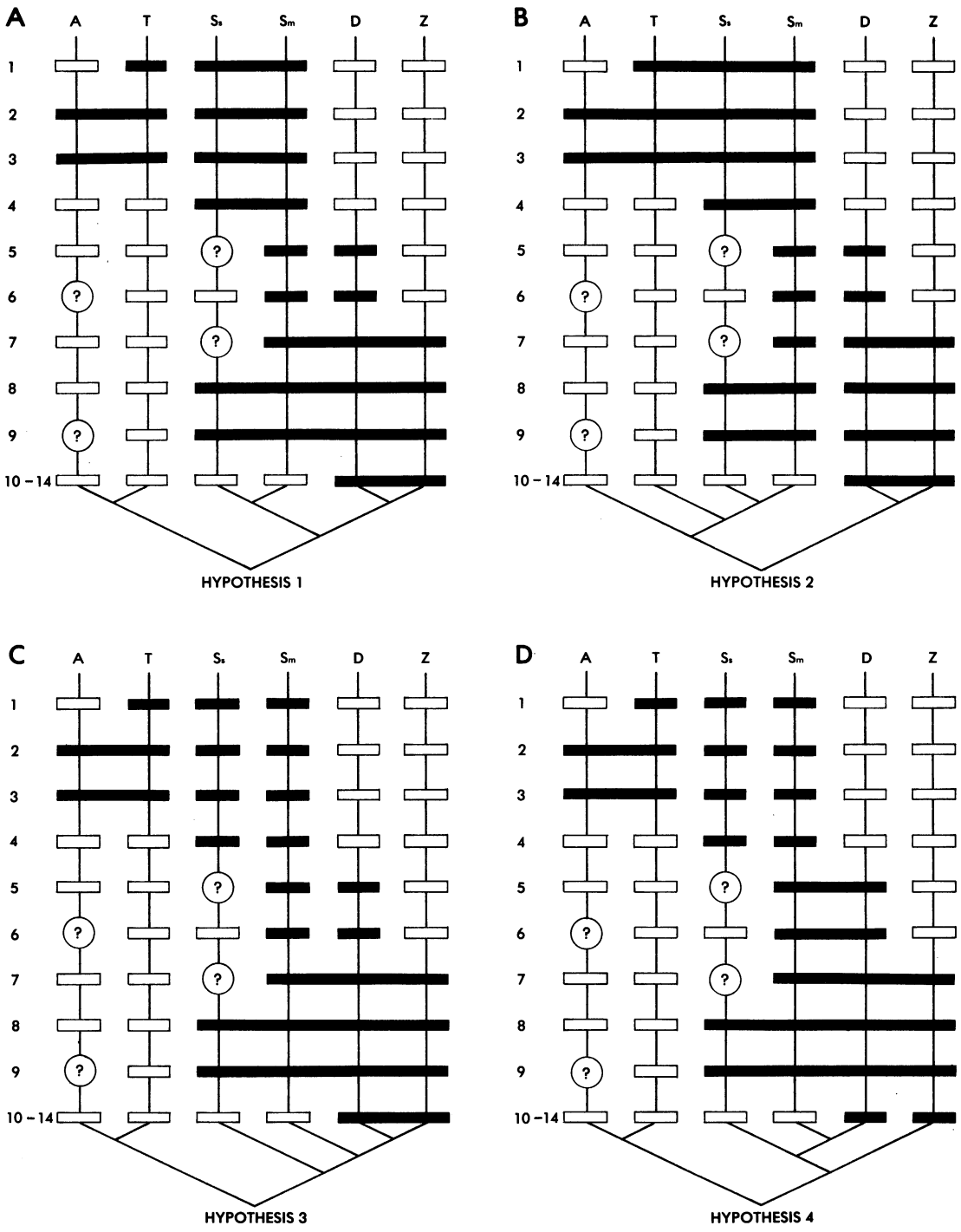


FIG. 10. Four hypotheses of symmetrodont relationships. See p. 313. Taxa are symbolized as follows: A = *Amphidon;* T = *Tinodon;* Ss = *Spalacotheroides;* Sm = *Spalacotherium;* D = dryolestoids; Z = Zatheria. Numbers correspond to character states in table 7. Primitive character states are shown by open bar; derived states by solid bar. Question mark indicates condition is unknown.

TABLE 7
Character Distribution in Symmetrodonts
(see figure 10)

Character	*Amphi-don*	*Tino-don*	*Spala-cothe-roides*	*Spala-cothe-rium*	Clado-theria	Notes
1. Reduce to three premolars	–	+	?	+	–	(two in some paurodonts)
2. Strong internal pterygoid ridge on mandible	+	+	?	+	–	
3. Highly reduced talonid	+	+	+	+	–	
4. Trigons very high, pointed	–	–	+	+	–	
5. Increase to seven molars	–	–	?	+	+/–	(in some dryolestoids)
6. P_{last} with continuous lingual cingulum	–	–	–	+	+/–	(in some dryolestoids
7. Lose metacrista-paraconid facets A and B	–	–	?	+	+	(except *Amphitherium*)
8. Anterior trigon-trigonids more acute, with basin formed in trigons	–	–	+	+	+	(except *Symmetro-dontoides*)
9. Reduced metastyle cusp	?	–	+	+	+	
10. True angular process	–	–	?	–	+	
11. Upper molars expand transversely	–	–	–	–	+	
12. Stylar region enlarges and interlocks	–	–	–	–	+	
13. Hypoconid shears metacone	–	–	–	–	+	
14. Lose anterior cusp on last lower premolar	–	–	?	–	+	
15. Lose upper molar lingual cingulum	?	+	–	?	+/–	(lost in dryolestids)

the amphidontids; see below). This decision is by no means final, but simply a challenge for other workers to test it further.

POSITION OF AMPHIDONTIDS

Amphidon superstes is known from a single specimen (YPM 13638), a right ramus with alveoli for three premolars, and crowns of the fourth premolar and four molars. Its systematic position has been controversial, because it has been used in the dispute between the "cusp rotation hypotheses" and the "*in situ* hypothesis" of the origin of the tritubercular molar pattern (Crompton and Jenkins, 1968, p. 447). Simpson (1925a, 1929) assigned *Amphidon* to the Symmetrodonta on the basis of its general morphology. It does share two unique derived characters with other symmetrodonts: greatly reduced talonids and a strong pterygoid ridge on the mandible.

The dental formula ($P_{1-4}M_{1-4}$) may be primitive, although five premolars seems more likely as the primitive trechnothere condition (see p. 299). If so, then reduction to four or less premolars is a synapomorphy for symmetrodonts, and reduction to three premolars unites the non-amphidontid symmetrodonts (see fig. 8).

The most puzzling character of *Amphidon* is that the molar "cusps" are no more than swellings or crenulations on the cristids. This makes the teeth functionally unicuspid. Small anterior and posterior cingula are present, but there is no lingual or labial cingulum. Simpson (1925a) interpreted this condition as evidence of incipient cusp formation on the cristids. Crompton and Jenkins (1968, p. 448) have pointed out that the specimen is heavily

worn, and the cusps may have been reduced by wear. Outgroup comparison with *Kuehneotherium* and triconodonts indicates that this condition is due to secondary reduction. Thus, its condition would be derived with respect to the remaining Theria, rather than a retention of a primitive unicuspid reptilian tooth.

In addition to its cusp reduction, *Amphidon* is highly modified in other features. It has lost the lingual cingulum on the lower molars and the molar interlock. The fourth molar is highly reduced in both size and morphology. In view of the amount of wear and preservation of the single specimen of *Amphidon,* these characters would appear to be autapomorphies.

The angle of the trigonid has led to some difficulties in determining the systematic position of *Amphidon. Amphidon* has a trigonid angle on M_1 of about 140 degrees. M_{2-3} seem to become only slightly more acute-angled, and M_4 is so reduced that there is no angle. Thus, it does not show the primitive therian character of a posterior trigonid angle of 100 degrees or less. This would place *Amphidon* on the morphocline between the Theria and outgroups with in-line cusps on posterior molars. However, in-line cusps on anterior molars are primitive for the Theria; in this respect *Amphidon* is more derived than *Kuehneotherium, Tinodon,* and *Symmetrodontoides*. In the face of these contradictions and other character distributions (see fig. 8 and table 4), both of these conditions are interpreted here as autapomorphic for *Amphidon.*

Manchurodon (Yabe and Shikama, 1938) is a poorly preserved jaw from the Husin coal field of Manchuria. Yabe and Shikama considered it to be late Jurassic in age, but Patterson (1956, p. 29) believed it to be early Cretaceous. The description and figures are so poor that it is impossible to say much about the specimen, except that it shares the molar morphology of *Amphidon.* Yabe and Shikama gave a dental formula of $P_{1-3}M_{1-5}$, but Patterson (1956, p. 29, note 2) gave reasons for interpreting the formula as $P_{1-4}M_{1-4}$. The latter formula would agree with that of *Amphidon.* For purposes of this discussion, *Manchurodon* is considered the sister

TABLE 8
Character Distribution in Cladotheres
(see figure 11)

Character	*Amphitherium*	Dryolestoids	Zatheria	Notes
1. Lose lower molar interlock	−	+	+	(also in symmetrodonts, some non-therians)
2. Lose metacrista-paracristid facets A and B	+/−	+	+	(also in symmetrodonts)
3. Broad talonid	+	−	+	
4. Posteroventrally deflected angular process	+	−	+	
5. Last lower premolar with continuous lingual cingulum	+	+	−	(also in *Spalacotherium*)
6. Six or more molars	+	+	−	(also in *Spalacotherium*; not in paurodonts)
7. Molar roots unequal	+	+	−	
8. Lose anterior cingulum on molars	+	+	−	(also in *Palaeoxonodon,* Porto Pinheiro tooth)
9. Procumbent paraconids	+	+	−	
10. Shear inclination greater than 40°	+	+	−	(secondarily in later therians)

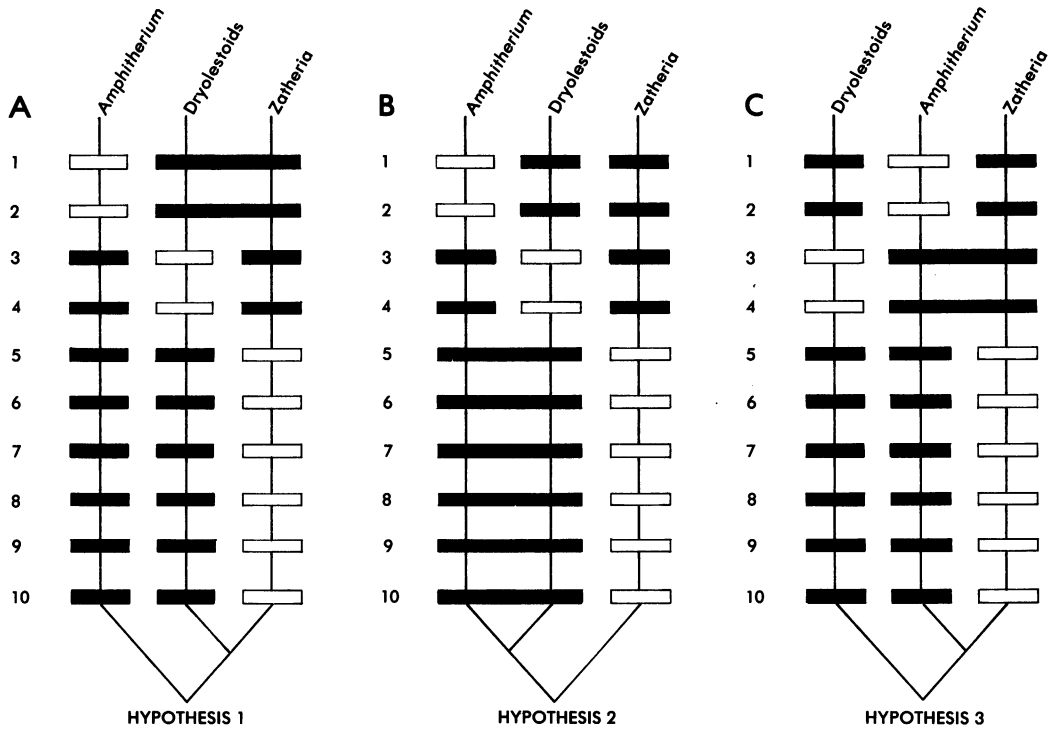


FIG. 11. Three hypotheses of cladothere relationships. Numbers correspond to character states in table 8. Primitive character states shown by open bar; derived states by solid bar.

group of *Amphidon*, until reexamination of the specimen reveals more diagnostic information.

POSITION OF *AMPHITHERIUM*

Amphitherium is known from lower jaws only. There has been a considerable diversity of opinion about its systematic position, although it is most commonly considered "on the main line of therian evolution" (Mills, 1964). This and other similarly vague assertions can be stated more precisely as follows:

(1) *Amphitherium* is the sister group of dryolestoids (Dryolestidae plus Paurodontidae) plus Zatheria (Fig. 11A). This hypothesis corresponds to a cladistic interpretation of Parrington's (1971, fig. 15) phylogeny.

(2) *Amphitherium* is more closely related to dryolestoids than it is to zatherians (fig. 11B). This hypothesis has been suggested by McKenna (1975).

(3) *Amphitherium* is more closely related to zatherians than it is to dryolestoids (fig. 11C). This point of view has been expressed by Hopson and Crompton (1969, fig. 12), Crompton and Jenkins (1968, fig. 11), and Crompton (1971).

The character distributions are shown in table 8 and the results are apparent from figure 11. *Amphitherium* is the sister group of the dryolestoids (Hypothesis 2), since it shares at least six good characters with them, and this requires less parallelism than either Hypothesis 1 or Hypothesis 3. Character conflicts 1 and 2 are discussed above. As in the case of symmetrodonts, they seem to be most parsimoniously explained as parallelism. Character 3 (expanded talonid) is the only good character that contradicts Hypothesis 2. However, it seems most parsi-

FIG. 12. Hypothesis of relationships of the non-tribosphenic Theria, using shared derived characters of taxa known from both upper and lower teeth. For explanation of characters, see table 9.

monious to call this a parallelism in the face of the other character distributions. It is also possible that the expanded talonid is a synapomorphy for the Cladotheria. Then the anteroposteriorly compressed talonids (but broader than the primitive condition) of dryolestoids would be a modification of the broad cladothere talonid. In view of the evidence, this interpretation is adopted here.

Likewise, character 4 (posteroventral deflection of the angular process) would seem to be the primitive condition for the cladothere angular process. The dryolestoid angular process is therefore a derived variant of this condition.

CLASSIFICATION

Combing the cladograms of upper- and lower-tooth taxa, and neglecting the taxa not known from both, gives the cladogram shown in figure 12. An exception is made for *Amphidon* and *Amphitherium* (see discussion above) because they are sufficiently well known from lower jaws to be considered. The cladogram can then be converted into a dichotomous classification as follows:

CLASS MAMMALIA LINNAEUS, 1758
Subclass Theria Parker and Haswell, 1897
Superlegion Kuehneotheria McKenna, 1975
Kuehneotherium
Superlegion Trechnotheria McKenna, 1975
Legion Symmetrodonta Simpson, 1925
Sublegion Amphidontoidea, new rank
Amphidon
Manchurodon
Sublegion Spalacotherioidea, new rank
Infraclass Tinodontida, new rank
Tinodon =*Eurylambda*

TABLE 9
Explanation of Characters Used in Figure 12
(* indicates parallelism)

1. THERIA: reversed triangle occlusal pattern, broad single wear surfaces joining cusps, lose "Kühne-cone"
2. *Kuehneotherium*: metaconid lower than paraconid
3. TRECHNOTHERIA: coronoid angle increases, lose medial condylar flange, reduce to five premolars, angle of posterior molar trigons-trogonids less than 100°, trochlear condyle above level of tooth row*
4. SYMMETRODONTA: reduce to four premolars*, greatly reduced talonids, strong internal pterygoid ridge
5. AMPHIDONTOIDEA: trigonid angles about 140°, reduce paraconid and metaconid to crenulations, lose lower molar lingual cingulum*
6. SPALACOTHERIOIDEA: reduce to three premolars, lose upper molar lingual cingulum*
7. *Tinodon* (=*Eurylambda*): coronoid process rises at right angle to tooth row
8. SPALACOTHERIIDA: high trigonids, wear facet on metacrista reaches paracone, lose facets A and B on metacrista-paraconid*, trigon basined*
9. *Spalacotheroides*: paracristid parallel to protocristid
10. *Spalacotherium* (=*Peralestes*): labial cingulum continuous on lower molars*
11. CLADOTHERIA: lose lower molar lingual cingulum*, expand talonid, lose anterior cusp on last lower premolar, lose metacrista-paraconid facets A and B (but shear does not reach paracone), develop true angular process, expand upper molars transversely, stylar region enlarges and interlocks, trigon basined*, hypoconid shears metacone, angle of anterior molar trigon-trigonids less than 100°, three upper molar roots
12. DRYOLESTOIDEA: increase to six or more molars, procumbent paraconids, posterior lower molar root smaller than anterior root, continuous lingual cingulum on last lower premolar*, lose anterior cingulum on lower molars*
13. *Amphitherium*: paraconid overlaps preceding talonid
14. DRYOLESTIDA: completely transverse paracrista-metacristid shear, strongly procumbent paraconids, reduce to four premolars*
15. PAURODONTIDAE: broad shelflike paraconid and talonid with reduced cusps, molars broaden anteroposteriorly, lose anterior cusp on last lower premolar*
16. DRYOLESTIDAE: reduce metacone, lower molar roots markedly unequal, slender angular process dorsally deflected, molars anteroposteriorly compressed, talonid becomes narrow shelf, lose upper molar lingual cingulum*
17. ZATHERIA: reduce to three molars, basined talonid, add hypoconulid and entoconid, reduce stylocone, lose anterior cingulum on lower molars*
18. *Peramus*: reduction of last molar, reduce stylar region, reduce stylocone, reduce posterior cingulum on molars
19. TRIBOSPHENIDA: add protocone, paracone anterior to metacone

Infraclass Spalacotheriida, new rank
Spalacotheroides
Symmetrodontoides
Spalacotherium =*Peralestes*
Legion Cladotheria McKenna, 1975
Sublegion Dryolestoidea Butler, 1939
Infraclass Amphitheriida, new rank
Amphitherium
Infraclass Dryolestida, new rank
Family Paurodontidae Marsh, 1887
Tathiodon *Pelicopsis*
Araeodon
Archaeotrigon
Paurodon
Family Dryolestidae Marsh, 1979
Dryolestes *Euthlastus*
Peraspalax *Amblotherium*
Phascolestes
"*Amblotherium*" *nanum*
Laolestes *Kurtodon*
Kepolestes *Miccylotyrans*
Crusafontia
Comotherium, new genus
Amblotherium *Herpetairus*
Melanodon
(=*Malthacolestes*)
Sublegion Zatheria McKenna, 1975
Infraclass Peramura McKenna, 1975
Peramus
Infraclass Tribosphenida McKenna, 1975
All remaining therians
Cladotheria, *incertae sedis*
Brancatherulum
Palaeoxonodon

The genera within infraclass Dryolestida have been placed in sequential rank according to the cladogram, and separated into columns for genera known from upper teeth

(right column) and lower teeth (left column). When the associations and synonymies are better known for these taxa, it will be possible to finish the dichotomous classification to the specific level. Until that time, I believe that it is prudent to leave the classification in the form given above.

Once the classification has separated out individual genera, no further monotypic taxa (e.g., "Legion Kuehneotheriida," "Sublegion Kuehneotherioidea," "Family Kuehneotheriidae," etc.) are used, since these names are redundant and clutter the classification (Farris, 1976).

The Use of the Term Pantothere

The order Pantotheria was proposed by Marsh in 1880 to include all non-multituberculate Mesozoic mammals (which at that time included triconodonts, docodonts, symmetrodonts, and dryolestids). The Greek roots also imply that the Pantotheria (πάντος, "all"; θήρ, "beast") included everything but the Allotheria (ἄλλος, "other"; θήρ, "beast"). The classification underwent numerous changes (documented by Simpson, 1929, pp. 45–47) until Simpson (1929, p. 47) restricted the term to *Amphitherium, Peramus,* paurodonts, and dryolestids. He excluded the symmetrodonts and triconodonts in this restricted usage. In his 1945 classification, Simpson created an additional infraclass Pantotheria and included the symmetrodonts within it. Kermack and Mussett (1958) then renamed "Order Pantotheria" the order Eupantotheria to distinguish it from infraclass Pantotheria.

The discovery and description of *Kuehneotherium* and further work on *Amphitherium* and *Peramus* (Mills, 1964; Clemens and Mills, 1971) led to considerable debate about the classification. In 1968, Kermack et al. listed three suborders within the Eupantotheria: Dryolestoidea (dryolestids), Symmetrodonta, and Amphitheria (*Kuehneotherium, Amphitherium, Peramus,* and paurodonts). Crompton and Jenkins (1968) returned the symmetrodonts to ordinal status, separate from Pantotheria, and placed *Kuehneotherium* in the Symmetrodonta. In 1971, Simpson erected infraclass Patriotheria to include the orders Pantotheria and Symmetrodonta. *Kuehneotherium* was placed in the latter order, and the rest of the "Amphitheria" were relegated to the Pantotheria.

The capricious and arbitrary nature of such taxonomic practice is readily apparent from the vicissitudes of the names under various workers. None of these classifications was supported by shared derived characters, and "Pantotheria" from its inception has been a horizontal, "wastebasket" taxon, roughly equivalent to "primitive therians." It has never been a monophyletic group in the sense of Hennig (1966). McKenna (1975) pointed out that "Pantotheria" were not a natural group, and so abandoned the term in his classification. However, the most recently published work on Mesozoic mammals (Lillegraven, Kielan-Jaworowska, and Clemens, 1979) persists in using this term.

My paper has corroborated McKenna's hypothesis of 1975 (with the original intent of falsifying it), and supported his cladogram with many more characters. Therefore, unless this cladogram is effectively falsified, there should be no doubt that the "pantotheres" are not a natural group, and should therefore have no formal status in taxonomy. All the taxonomic names proposed here are based on clearly formulated cladistic principles, and are supported by a parsimonious arrangement of shared derived characters. As a cladistic classification, it carries the maximum phylogenetic information content and is thus non-arbitary and maximally heuristic. This hypothesis is not based on authoritarian fiat, or arbitary, capricious, "Gestalt"-type phenetic lumping, and can (and should) be tested by anyone.

Some workers, however, will surely persist in using "pantothere" as a general term for "non-tribosphenic therian." This argument has been forwarded in favor of other paraphyletic and polyphyletic groups, on the grounds that they reflect "morphologic distance" or "genetic affinity" (Mayr, 1974). If the non-tribosphenic Theria were a group with uniformly primitive morphology, whose affinities were highly ambiguous, this argument might have some weight. However,

this is definitely not the case with the non-tribosphenic Theria. As a whole, the groups are highly derived and quite distinctive to anyone who has examined them more than superficially. The use of a wastebasket term like "pantothere" is pernicious, not only because it obscures relationships, but also because it gives a false impression that the whole group can be lumped together without further thought or discussion. This is particularly true of comparative studies between "typical pantotheres" and some other form. There is no such thing as a "typical pantothere."

As a didactic tool, the cladogram presented here does far more to explain therian evolution than widespread, vague assertions about "pantotheres" giving rise to higher mammals. Therefore, I strongly urge that the term "pantothere" be abandoned. If one wishes to refer to "pantotheres," the term "non-tribosphenic Theria," although less concise, does not carry misleading phylogenetic implications. In fact, this term carries more information content than "pantothere" and focuses attention on an important change in mammalian evolution, namely the acquisition of the protocone to form the tribosphenic tooth.

LITERATURE CITED

Brundin, Lars
1966. Transatlantic relationships and their significance as evidenced by chironomid midges. I. Principles of phylogenetic systematics and phylogenetic reasoning. Stockholm Kungl. Svenska Vetensk. Holl., vol. 11, pp. 1–472.
1968. Application of phylogenetic principles in systematics and evolutionary theory. *In* Ørvig, Tor (ed.), Current problems of lower vertebrate phylogeny. Nobel Symposium 4, New York, Interscience Publishers, John Wiley and Sons, pp. 473–495.
1972. Evolution, causal biology, and classification. Zool. Scripta, vol. 1, pp. 107–120.

Butler, Percy M.
1939. The teeth of Jurassic mammals. Proc. Zool. Soc. London (ser. B), vol. 109, pp. 329–356.
1972. Some functional aspects of molar evolution. Evolution, vol. 26, pp. 474–483.

Clemens, William A., Jr.
1970. Mesozoic mammalian evolution. Ann. Rev. Ecol. Syst., vol. 1, pp. 357–390.

Clemens, William A., Jr., and Patricia M. Lees
1971. A review of English early Cretaceous mammals. *In* Kermack, Doris M., and K. A. Kermack (eds.), Early Mammals, Supp. 1, Jour. Linn. Soc. (Zool.), vol. 50, pp. 117–130.

Clemens, William A., Jr., and J. R. E. Mills
1971. Review of *Peramus tenuirostris* (Mammalia, Eupantotheria). Bull. Brit. Mus. (Nat. Hist.), (Geol.), vol. 20, pp. 89–113.

Cracraft, Joel
1972. The relationships of the higher taxa of birds; problems in phylogenetic reasoning. The Condor, vol. 74, pp. 379–392.
1974. Phylogenetic models and classification. Syst. Zool., vol. 23, pp. 71–90.

Crompton, A. W.
1971. The origin of the tribosphenic molar. *In* Kermack, Doris M., and K. A. Kermack (eds.), Early mammals, Supp. 1, Jour. Linn. Soc. (Zool.), vol. 50, pp. 65–88.
1974. The dentitions and relationships of the southern African Triassic mammals *Erythrotherium parringtoni* and *Megazostrodon rudnerae*. Bull. Brit. Mus. (Nat. Hist.), vol. 24, pp. 397–437.

Crompton, A. W., and Farish A. Jenkins, Jr.
1967. American Jurassic symmetrodonts and Rhaetic 'pantotheres.' Science, vol. 155, pp. 1006–1009.
1968. Molar occlusion in late Triassic mammals. Biol. Reviews, vol. 43, pp. 427–458.

Eldredge, Niles, and Ian Tattersall
1975. Evolutionary models, phylogenetic reconstruction, and another look at hominid phylogeny. *In* Szalay, F. S., (ed.), Approaches to primate paleobiology, Contributions to primatology, vol. 5. Basel, S. Karger, pp. 218–242.

Englemann, George F., and Edward O. Wiley

1977. The place of ancestor-descendant relationships in phylogeny reconstruction. Syst. Zool., vol. 26, pp. 1–11.

Farris, James S.
1976. Phylogenetic classification of fossils with recent species. Syst. Zool., vol. 25, pp. 271–282.

Fox, Richard C.
1976. Additions to the mammalian local fauna from the Upper Milk River Formation (Upper Cretaceous), Alberta. Can. Jour. Earth Sci., vol. 13, pp. 1105–1118.
1977. Notes on the dentition and relationships of the late Cretaceous insectivore *Gypsonictops* Simpson. Can. Jour. Earth Sci., vol. 14, pp. 1823–1831.

Freeman, Eric F.
1976. Mammal teeth from the Forest Marble (Middle Jurassic) of Oxfordshire, England. Science, vol. 194, pp. 1053–1055.

Gaffney, Eugene S.
1979. The Jurassic turtles of North America. Bull. Amer. Mus. Nat. Hist., vol. 162, pp. 95–135.

Griffiths, Graham, C. D.
1972. The phylogenetic classification of the Diptera Cyclorrhapha, with special reference to the male postabdomen. 2. Principles and procedures of classification. The Hague, W. Junk, pp. 5–28.

Henkel, Siegfried, and Bernard Krebs
1969. Zwei Säugetier-Unterkiefer aus der Unteren Kreide von Uña (Prov. Cuenca, Spanien). Neues Jahrb. Geol. Paläont. Mh. 8, pp. 449–463.
1977. Die erste fund eines Säugetier-Skelettes aus der Jura-Zeit. Umschau 77, Heft 7, pp. 217–218.

Hennig, Willi
1965. Phylogenetic systematics. Ann. Rev. Ent., vol. 10, pp. 97–116.
1966. Phylogenetic systematics. Urbana, Chicago, London, Univ. Illinois Press.

Hopson, James A., and A. W. Crompton
1969. Origin of mammals. *In* Dobzhansky, T., M. K. Hecht, and W. C. Steere (eds.), Evolutionary biology, vol. 3, New York, Appleton-Century-Crofts, pp. 15–72.

Kermack, Doris M., Kenneth A. Kermack, and Frances Mussett
1968. The Welsh pantothere *Kuehneotherium praecursoris*. Jour. Linn. Soc. (Zool.), vol. 47, pp. 407–423.

Kermack, Kenneth A., and Frances Mussett
1958. The jaw articulation of the Docodonta and the classification of the Mesozoic mammals. Proc. Royal Soc. (ser. B), vol. 48, pp. 204–215.

Kermack, Kenneth A., Frances Mussett, and H. W. Rigney
1973. The lower jaw of *Morganucodon*. Journ. Linn. Soc. (Zool.), vol. 53, pp. 87–175.

Krebs, Bernard
1969. Nachweis eines rudimentären Coronoids im Unterkiefer der Pantotheria (Mammalia). Paläont. Zeitschr., vol. 43, pp. 57–63.
1971. Evolution of the mandible and lower dentition in dryolestoids (Pantotheria, Mammalia). *In* Kermack, Doris M., and K. A. Kermack (eds.), Early mammals, Supp. 1, Jour. Linn. Soc. (Zool.), vol. 50, pp. 89–102.

Kretzoi, M.
1960. Zur Benennung des ältesten Symmetrodonten. Vertebr. Hung., vol. 2, pp. 307–309.

Krusat, G.
1969. Ein Pantotheria-Molar mit dreispitzigem Talonid aus dem Kimmeridge von Portugal. Paläont. Zeitschr., vol. 43, pp. 52–56.

Kühne, Walter G.
1950. A symmetrodont tooth from the Rhaeto-Lias. Nature, vol. 166, pp. 696–697.
1961. Une faune de mammiferes lusitaniens (raport provisoire). Comunicacoes dos Servicos Geologicas de Portugal, vol. 45, pp. 211–221.
1968. Kimeridge [sic] mammals and their bearing on the phylogeny of the Mammalia. *In* Drake, E. J. (ed.), Evolution and environment, New Haven, Yale Univ. Press, pp. 109–123.

Lillegraven, J. A., Z. Kielan-Jaworowska, and W. A. Clemens (eds.).
1979. Mesozoic mammals: The first two-thirds of mammalian history. Berkeley, Univ. Calif. Press, pp. 1–311.

McKenna, Malcolm C.
1975. Toward a phylogenetic classification of the Mammalia. *In* Luckett, W. P., and F. S. Szalay (eds.), Phylogeny of the primates. New York, Plenum, pp. 21–46.

Marsh, Othniel C.
1887. American Jurassic mammals. Amer. Jour. Sci., vol. 33, pp. 328–348.

Mayr, Ernst
1974. Cladistic analysis or cladistic classification? Zeitschr. Zool. Syst. Evolutionforsch., vol. 12, pp. 98–128.
Mills, J. R. E.
1964. The dentitions of *Peramus* and *Amphitherium*. Proc. Linn. Soc. London, vol. 175, pp. 117–133.
Nelson, Gareth J.
1973. Classification as an expression of phylogenetic relationships. Syst. Zool., vol. 22, pp. 344–359.
Osborn, Henry Fairfield
1907. Evolution of mammalian molar teeth to and from the triangular type. New York, Macmillan, pp. 1–250.
Ostrom, John H., and John S. McIntosh
1966. Marsh's Dinosaurs: The collections from Como Bluff. New Haven, Yale Univ. Press, pp. 1–388.
Parrington, Francis Rex
1967. The origins of mammals. Advancement of science, London. vol. 24, pp. 165–173.
1971. On the Upper Triassic mammals. Phil. Trans. Royal Soc., Ser. B, vol. 261, pp. 231–272.
1978. A further account of the Triassic mammals. *Ibid.*, vol. 282, pp. 177–204.
Patterson, Bryan
1955. A symmetrodont from the Early Cretaceous of northern Texas. Fieldiana, Zool., vol. 37, pp. 689–693.
1956. Early Cretaceous mammals and the evolution of mammalian molar teeth. Fieldiana, Geol., vol. 13, pp. 1–105.
Schaeffer, Bobb, Max K. Hecht, and Niles Eldredge
1972. Phylogeny and paleontology. *In* Dobzhansky, T. M. K. Hecht, and W. C. Steere (eds.), Evolutionary biology, vol. 6. New York, Appleton-Century-Crofts, pp. 31–46.
Sigogneau-Russell, Denise
1978. Decourverte de mammiferes rhetiens (Trias superieur) dans l'est de la France. C. R. Acad. Sc. Paris, vol. 287, pp. 991–993.
Simpson, George Gaylord
1925a. Mesozoic Mammalia. II. *Tinodon* and its allies. Amer. Jour. Sci., vol. 10, pp. 452–470.
1925b. Mesozoic Mammalia. III. Preliminary comparison of Jurassic mammals. *Ibid.*, vol. 10, pp. 559–569.
1927. Mesozoic Mammalia. VI. Genera of Morrison pantotheres. *Ibid.*, vol. 13, pp. 407–416.
1928. A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum (Natural History). London, Brit. Mus. (Nat. Hist.), pp. 1–215.
1929. American Mesozoic Mammalia. Mem. Peabody Mus., Yale, vol. 3, pp. 1–235.
1937. A new Jurassic mammal. Amer. Mus. Novitates, no. 943 pp. 1–6.
1945. The principles of classification and a classification of the mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. 1–350.
1971. Concluding remarks: Mesozoic mammals revisited. *In* Kermack, Doris M. and K. A. Kermack (eds.), Early mammals, Supp. 1, Jour. Linn. Soc. (Zool.), vol. 50, pp. 181–198.
Wiley, Edward O.
1976. The phylogeny and biogeography of fossil and Recent gars (Actinopterygii: Lepisosteidae). Misc. Publ. Univ. Kansas, no. 64, pp. 1–111.
Yabe, H., and T. Shikama
1938. A new Jurassic mammal from South Manchuria. Proc. Imp. Acad. Tokyo, vol. 14, pp. 353–359.