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LOWER VERTEBRATES FROM SWAIN QUARRY,
"FORT UNION FORMATION," MIDDLE PALEOCENE (TORREJONIAN),
CARBON COUNTY, WYOMING

presented by

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ABSTRACT

LOWER VERTEBRATES FROM SWAIN QUARRY "FORT UNION FORMATION", MIDDLE PALEOCENE (TORREJONIAN), CARBON COUNTY, WYOMING

By

Robert M. Sullivan

The Swain Quarry local fauna (middle Paleocene: Torrejonian) of Carbon County, Wyoming, has yielded the largest Paleocene lower vertebrate microfauna described to date.

Fish are sparsely represented by an indeterminate teleost and by *Amia fragosa*. The amphibians are represented by the urodeles *Scapherpeton*, cf. *Opisthotriton* and *Habrosaurus*. A fragment of a dentary is referred to the Crocodilia.

The lizards comprise sixty-seven percent of the entire lower vertebrate microfauna based on minimum number of individuals, and thus form the most important component. Lizard genera noted from Swain Quarry include cf. *Contogenys*, *Paleoxantusia*, *Exostinus*, *Odaxosaurus* and cf. *Provaranosaurus*. A number of indeterminate specimens are referred to the subfamily Glyptosaurinae. A new lizard, *Swainiguanoides milleri* n. gen., n. sp., represents the oldest known North American iguanid. The subfamily Odaxosaurinae, new subfamily, is established for the primitive anguid *Odaxosaurus*. *Machaerosaurus torrejonensis* is identified for the first time by material other than the holotype.

Helagras prisciformis, a Torrejonian snake, is present in the Swain Quarry local fauna.

Despite the relatively large size of the lower vertebrate fauna from Swain Quarry, the sample size is too small to allow detailed ecological interpretation. General comparisons of the fauna with other Paleocene faunas, as well as the late Cretaceous faunas, show that the aquatic habitat is relatively unchanged across the Cretaceous-Tertiary boundary which is in agreement with analysis of previously studied Paleocene herpetofaunas. Diversification of anguid lizards may have occurred in response to the apparent Paleocene decrease in the diversity of other lizard families as documented by earlier studies.

In loving dedication to

my parents

Robert F. and Marian E. Sullivan

ACKNOWLEDGEMENTS

I am indebted to Eugene Gaffney and Charlotte Holton (American Museum of Natural History) for the loan of the Swain Quarry Lower vertebrate microfauna. I thank Michael Greenwald and J. Howard Hutchinson (University of California-Berkeley) for the loan of the *Odaxosaurus piger* specimens. J. Kieth Rigby Jr. (Bureau of Land Management, Albuquerque) was helpful in furnishing me with additional information regarding the fauna, collecting techniques and geology of Swain Quarry. Richard Estes (San Diego State University) critically reviewed the manuscript and conferred with me on the material and I am very grateful for his time and suggestions.

I thank my doctoral committee members Robert L. Anstey, Chilton E. Prouty and Richard Seltin for their guidance and interest throughout the course of my program at Michigan State University. Special thanks are extended to my adviser J. Alan Holman, whose guidance and support made this study possible.

The illustrations of the specimens were made by Merald Clark and I thank him for his time and meticulous care in making these drawings.

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INTRODUCTION

Paleocene vertebrate faunas are rare. In North America only two large Paleocene lower vertebrate microfaunas have been studied (Estes, 1975, 1976) but they are not nearly as large or as diverse as the late Cretaceous lower vertebrate assemblages reported by Estes (1964) and Estes et al. (1969). Most records of Paleocene lower vertebrates are from isolated accounts in Gilmore (1928, 1938 and 1942), Matthew (1937) and additions by Estes (1965b). Since the Paleocene is so poorly documented, the Swain Quarry lower vertebrate microfauna is an extremely important supplement to these previous studies of this major gap in the geologic record of the evolution of many vertebrate groups.

Swain Quarry, a major middle Paleocene (Torrejonian) site, was recently studied by J. Keith Rigby Jr. The mammalian fossils and geology of this quarry form the basis of his doctoral dissertation at Columbia University in 1977. Swain Quarry lies in the south-central part of Wyoming and has been known since the late 1950s as a potentially productive site for Paleocene microvertebrates. Rigby (1977) reviewed the historical aspects of Swain Quarry, along with its geology and geography and has studied the diverse micromammalian fauna.

The lower vertebrate microfauna was obtained with the mammalian fossils by screening projects conducted by Frederick Szalay in 1964, followed by more intensive screening efforts of J. Keith Rigby Jr. in 1972 and 1973. All fossils recovered from this quarry are in the collections of the American Museum of Natural History, New York (AMNH). Preliminary identification of some of the lower vertebrates from Swain Quarry were made by Richard Estes and Eugene Gaffney, but no thorough study of these lower vertebrates has occurred and a number of the preliminary identifications need to be reviewed.

This study supplements Rigby's (1977) work on the geology and the fossil mammals from Swain Quarry. The present study is not only important because of the rarity of Paleocene lower vertebrates in general, but is significant in that this small lower vertebrate microfauna occurs with a very large mammalian one whose time-stratigraphic position is well documented.

GEOLOGIC SETTING

Swain Quarry is located in south-central Wyoming, 37 kilometers northwest of Baggs, in the SE¼, NE¼, Sec. 3, T15N, R92W, Doty Mountain quadrangle (Figure 1). The quarry is situated 377 meters above the base of the "Fort Union Formation." Rigby (1977) thoroughly described the local geology, topography and historical aspects of Swain Quarry which are only briefly summarized here.

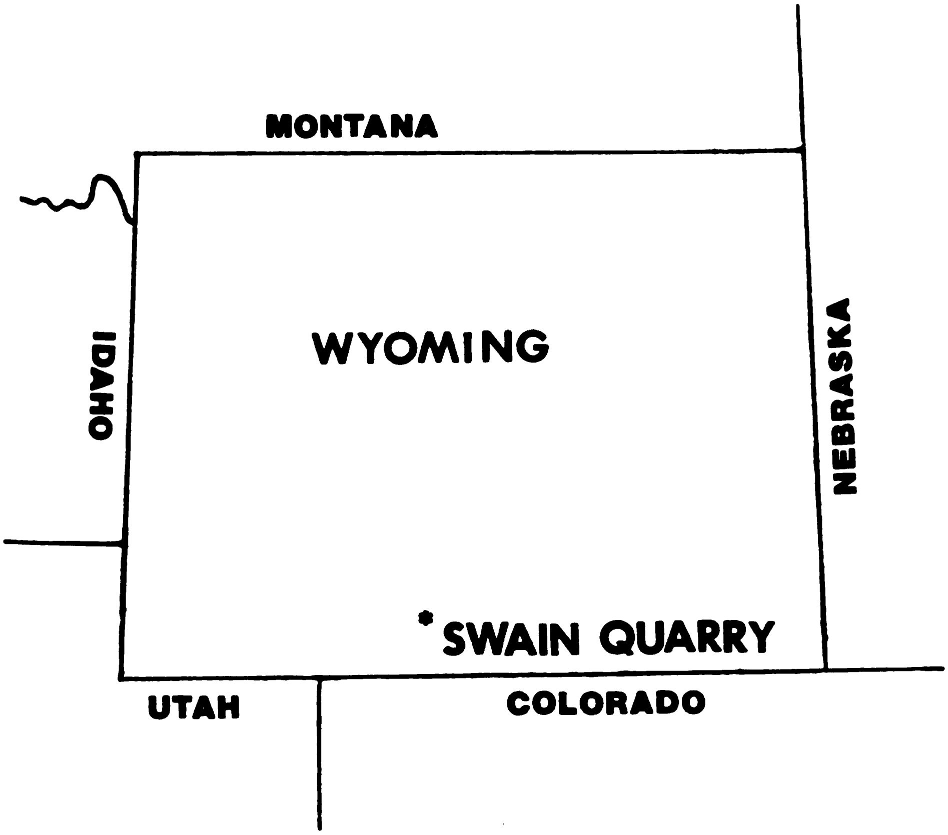

Figure 1. Location of Swain Quarry.

The local stratigraphy of the Swain Quarry region finds the late Cretaceous Lance Formation, overlain by the "Fort Union Formation" (Paleocene), which in turn is overlain by the Wasatch Formation (Hiawatha member). Swain Quarry occurs in the lower part of the "Fort Union Formation"[1] and is one of eight localities from that unit which has yielded fossil vertebrates. The quarry is part of a "block" consisting of massive cross-bedded sandstones that grade laterally into carbonaceous shales, mudstones and siltstones (Rigby, 1977). Swain (1957) presented evidence for local upper and lower lithologic units in this part of the "Fort Union Formation" but Rigby (1977) believes that the terms "lower" and "upper" should be applied locally in a relative sense.

The Swain Quarry local fauna was assigned a Torrejonian age based on fossil mammals by Rigby (1977), who compared the mammalian taxa of Swain Quarry to those of Gidley and Rock Bench quarries and to those of several sites in the Nacimiento Formation of the San Juan Basin, New Mexico. He concluded that the fauna from Swain Quarry was phylogenetically more derived than that of Gidley

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[1] Reference to the rocks at the Swain Quarry site as belonging to the "Fort Union Formation" is questionable owing to the poorly understood local stratigraphy (Rigby, 1977). The formation lacks stratigraphic continuity with the type section that occurs at Fort Union, Montana. The rocks at Swain Quarry have been referred to this formation solely on the basis of gross lithology and similar fauna and flora content.

Quarry, but was contemporaneous with those of the other Paleocene sites. Recently, in an unpublished correlation chart, Sloan (1979) placed Swain Quarry slightly above Gidley Quarry and slightly below Rock Bench Quarry, with all three quarries being equivalent in age (late most Torrejonian).

SYSTEMATIC PALEONTOLOGY

Class Osteichthyes

Order Amiiformes

Family Amiidae

Genus *Amia*

Amia fragosa (Jordon, 1927)

Referred material: AMNH 14303 and 14308 (Figure 2), oral teeth.

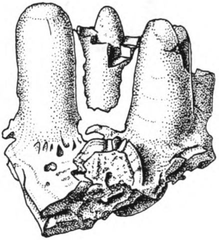

Figure 2. *Amia fragosa* (AMNH 14308), oral teeth. X 8.

Remarks: AMNH 14303 and 14308 consist of a relatively large cluster of bulbous teeth with faintly wrinkled crowns. These teeth are characteristic of the type found in the oral cavity of *Amia fragosa* and are here referred to that species.

Estes et al. (1969) have noted that amiids are common in the late Cretaceous and Paleocene of both North America and Europe.

cf. _Amia fragosa_

Referred material: AMNH 14301 (Figure 3), tooth.

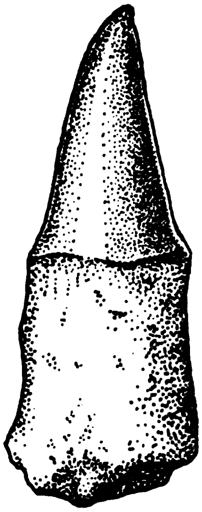

Figure 3. cf. _Amia fragosa_ (AMNH 14301), tooth. X 20.

Remarks: This specimen is typical of the marginal teeth of the maxilla, premaxilla and dentary of _Amia fragosa_ and is here provisionally referred to this species. The tooth measures approximately 3 mm in total length and is divided into two nearly equal parts. The enameloid part of the tooth is cone-shaped and slightly recurved at the tip (Figure 3).

Infraclass Teleostei

Teleostei *Incertae Sedis*

Referred material: AMNH 14302, anterior part of right dentary.

Remarks: The length of this incomplete specimen is approximately 3 mm. Based on the presence of clustered tooth bases, enough of it is preserved to indicate that it represents an anterior part of the right dentary of a small teleost. It is not possible to refer this specimen to any particular taxon.

Class Amphibia

Order Caudata

Suborder Ambystomatoidea

Family Scapherpetontidae

Genus *Scapherpeton*

Scapherpeton tectum Cope, 1876

Referred material: AMNH 12015 through 12022 (Figure 4), atlantes and AMNH 12024, trunk vertebra.

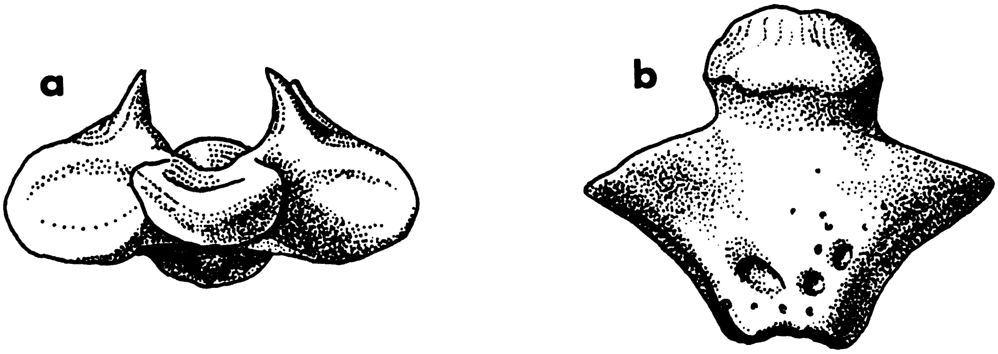

Figure 4. *Scapherpeton tectum* (AMNH 12017), atlas. a. axial view; b. ventral view. X 10

Remarks: The fragmentary *Scapherpeton tectum* material in Swain Quarry adds little to our knowledge to the osteology of this urodele. This species is mainly represented mostly by its distinctive atlantes which can be distinguished from those of the scapherpetontid *Lisserpeton* (Estes, 1965a) on the basis of the absence of an excavated ventral pit posterior to the condyle. The presence of eight atlantes representing a minimum of eight individuals of *Scapherpeton tectum* points to either the probability of a "pickers bias" in sorting concentrate or selective transport. In both cases the distinctive morphology may be the reason for the recovery. The possibility of "picker's bias" in sorting raises a question as to the degree the entire lower vertebrate fauna from Swain Quarry was selectively sorted, a question that will be addressed later.

Estes (1964, 1969a, 1975 and 1976) and Estes et al. (1969) reported that *Scapherpeton tectum* occurs from the late Cretaceous through the Paleocene of North America.

cf. *Scapherpeton tectum*

Referred material: AMNH 12009 (Figure 5), medial part of left dentary and 12010, medial part of left dentary.

Remarks: Both of these specimens lack teeth and are provisionally referred to *Scapherpeton tectum* based on the shallow breadth of the dentary.

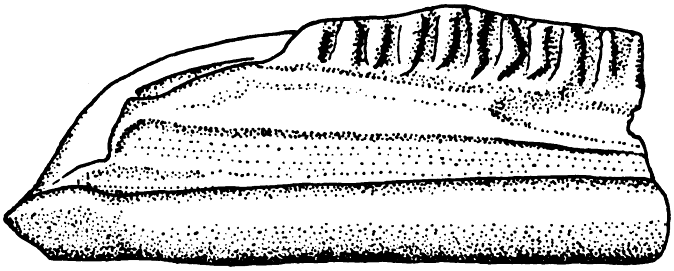

Figure 5. cf. Scapherpeton tectum (AMNH 12009), medial part of left dentary (lingual view). X 15.

Suborder Proteida

Family Batrachosauroididae

cf. Opisthotriton kayi Auffenberg, 1961

Referred materials: AMNH 12061, anterior part of right dentary; AMNH 12204, anterior part of left dentary; AMNH 12206, anterior part of right dentary; AMNH 12207, medial part of right dentary; and AMNH 14305 (Figure 6), atlas.

Remarks: The fragmentary dentaries are referred to this species on the basis of the spacing of the basal tooth attachment and the breadth of the dentaries. Some of this material may be referrable to Scapherpeton but owing to the incomplete nature of these specimens, precise taxonomic assignment is uncertain. The atlas (AMNH 14305, Figure 6) is missing the longitudinally-elongate neural crest that distinguishes it from Prodesmodon (Naylor, 1979), but the cotyles appear to be more circular than the ovoid cotyles

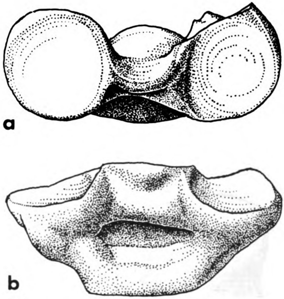

Figure 6. cf. Opisthotriton kayi (AMNH 14305), atlas.
a. axial view; b. ventral view. X 25.

of Prodesmodon and thus this specimen is provisionally referred to Opsithotriton.

Family Sirenidae

Genus Habrosaurus

Habrosaurus dilatus Gilmore 1928

Referred material: AMNH 12011, anterior part of left dentary; AMNH 12012, medial part of right dentary; AMNH 12013, medial part of right dentary; AMNH 12023 (Figure 7), atlas; AMNH 12205 (Figure 8), nearly complete left dentary; AMNH 12208, medial part of left dentary; and AMNH 14304, medial part of left dentary.

Remarks: The atlas (AMNH 12023, Figure 7) is referred to Habrosaurus dilatus based on the broad flattened ventral

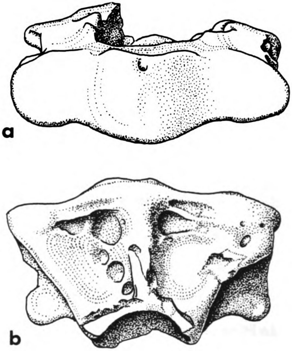

Figure 7. *Habrosaurus dilatus* (AMNH 12023), atlas. a. axial view; b. ventral view. X 7.

surface, presence of a deep lateral fossa behind the condyles and a circular cotyle. The teeth of all preserved dentaries are broken. Reference to *Habrosaurus dilatus* is based primarily on the wide tooth spacing and the wider breadth of the individual dentaries. These two features

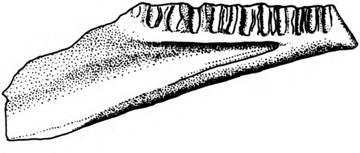

Figure 8. *Habrosaurus dilatus* (AMNH 12205), left dentary (lingual view). X 10.

allow separation from the other urodeles *Opisthotriton*, *Scapherpeton* and *Lisserpeton* (Estes, 1964, 1965a).

Estes (1964) extensively reviewed *Habrosaurus dilatus* Gilmore, 1928 and referred it to the family Sirenidae. *Habrosaurus dilatus* is known from the late Cretaceous (Estes, 1964) through the middle Paleocene (Estes, 1976).

Class Reptilia
Order Crocodilia
Suborder Eusuchia
Family Crocodylidae
Genus and species Indeterminate

Referred material: AMNH 12067, two fragments of right dentary.

Remarks: The larger fragment of this specimen measures 12 mm in length and is referred to the Crocodylidae based upon the pitted labial surface of the dentary. This specimen may represent *Allognathosuchus* sp. which occurs in the early Paleocene deposits of North America, but this taxonomic assignment cannot be made without the teeth.

Order Lacertilia
Suborder Iguania
Family Iguanidae
Swainiguanoides milleri n. gen., n. sp.

Holotype: AMNH 12082 (Figure 9), medial part of right dentary.

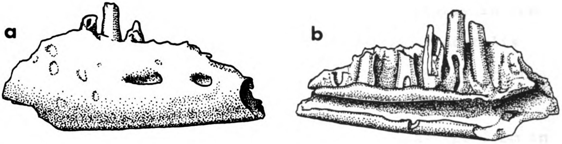

Figure 9. Swainiguanoides milleri n. gen., n. sp. (AMNH 12082, type), medial part of right dentary. a. labial view; b. lingual view. X 10.

Paratype: AMNH 12081, medial part of right dentary.

Type locality: Swain Quarry, Fort Union Formation, Carbon County, Wyoming.

Age: Middle Paleocene (Torrejonian).

Etymology: The generic name is established, in part, for the Swain Quarry from which the specimen came; iguanoides from the greek for small inguana-like. The specific name is established in honor of Alan V. Miller.

Diagnosis: Differs from living and fossil iguanines by the following combination of characters: teeth, non-striated, anterior-posteriorly compressed and compact with their bases expanded lingually. Teeth in cross section are ovoid and extend a little less than half their height beyond the parapet of the jaw. Tooth crowns are compressed linguolabially with four tiny cusps. The two inner cusps form a plateau in the middle that equally divides the tooth crown region into three separate parts. Two lateral cusps on either side are located below the medial cusps and form a slope of about 45°. Meckelian groove deep; both the dental shelf and ventral dentary border are nearly in the same vertical plane with a well defined sulcus dentalis. Intramandibular septum fused with a V-shaped notch at the posterior border.

Description: AMNH 12082 (Figure 9), measures 7 mm in length and represents a large part of the medial and posterior part of the dentary. One complete tooth and parts of four others are preserved. Spaces for three additional teeth are evident. The labial side of the dentary is relatively smooth, with two mental foramina located in the middle and anterior parts of the preserved dentary.

The paratype (AMNH 12081) measures 6 mm and is also a fragment of a right dentary. The tooth crowns are not preserved in this specimen, but it agrees in every other way with the holotype. Basal parts of five teeth are preserved and spaces for two are present. The labial side of the dentary is relatively smooth with one mental foramen present in the middle.

Both specimens display a deep Meckelian groove with well developed dorsal and ventral borders formed by the sulcus dentalis and the ventral lingual edge of the dentary, respectively, thus indicating that the splenial was restricted.

Discussion: Swainiguanoides milleri is assigned to the lizard family Iguanidae based on the Meckelian groove and tooth morphology which closely approaches the morphology of several species of the iguanid lizard *Sceloporus*. Although similar in some respects, there are significant differences that serve to distinguish the two genera. The Meckelian groove, although restricted in *Swainiguanoides*, is open and not partially enclosed or in contact as in Recent species of *Sceloporus*. The intramandibular septum of *Swainiguanoides* is more pronounced than that of *Sceloporus*, and the V-shaped notch of the intramandibular septum is more developed in the latter genus. The tooth crowns are nearly identical in morphology to those in large individuals of *Sceloporus poinsetti*, but the teeth are taller and thinner.

Etheridge (1964) noted that the teeth of Recent *Sceloporus* species are quite variable and offer few diagnostic characters. In the dentaries of all sceloporine lizards the borders of the Meckelian groove are always in contact although never fused. An open Meckelian groove is probably a primitive character state in iguanines. The morphology of the teeth of *Swainiguanoides milleri* is remarkably similar to that of Recent *Sceloporus*, and in combination with other characters displayed in the dentary, suggests that *Swainiguanoides milleri* is related to the sceloporine group.

Swainiguanoides milleri is significant in that it represents the oldest North American iguanid. The oldest

New World iguanid Pristiguana, reported by Estes and Price (1973) from the late Cretaceous of Brazil.

cf. Swainiguanoides milleri

Referred material: AMNH 12048 (Figure 10), medial part of left maxilla.

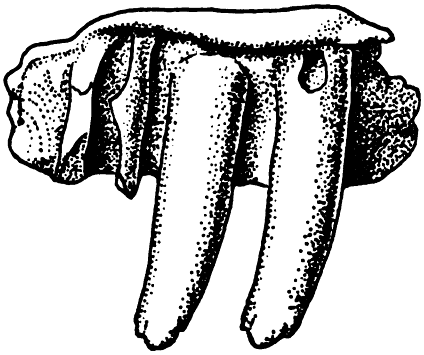

Figure 10. cf. Swainiguanoides milleri (AMNH 12048), medial part of left maxilla (lingual view). X 20.

Remarks: This fragmentary specimen (Figure 10) is provisionally referred to Swainiguanoides milleri on the basis of tooth morphology.

Suborder Scincomorpha

Family Scincidae

Genus Contogenys

cf. Contogenys sloani Estes, 1969b

Referred material: AMNH 12069 (Figure 11), posterior part of right maxilla bearing three teeth.

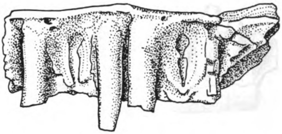

Figure 11. cf. Contogenys sloani (AMNH 12069), posterior part of right maxilla. X 15.

Remarks: This specimen is referred to Contogenys sloani based on the evidence of an expansion of the maxilla posteriorlaterally that indicates the probable presence of a triangular wedge reported by Estes (1969b) as well as the presence of strongly pleurodont teeth with squared-off tooth crowns.

Family Xantusiidae

Genus Paleoxantusia

Paleoxantusia fera Hecht, 1956

Referred material: AMNH 12028, posterior part of right maxilla; AMNH 12036, posterior part of left dentary; AMNH 12038, posterior half of left dentary; AMNH 12039, anterior part of right maxilla; AMNH 12040, left dentary; AMNH 12041, posterior part of right dentary; AMNH 12049, medial part of left dentary; AMNH 12064 (Figure 12), nearly complete left dentary; AMNH 12071, anterior part of right dentary; AMNH 12072, anterior part of right dentary; AMNH 12073, posterior part of right dentary; AMNH 12074,

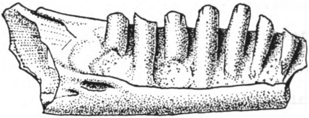

Figure 12. Paleoxantusia fera (AMNH 12064), left dentary (lingual view). X 15.

posterior part of right dentary; AMNH 12075, left dentary; AMNH 12076, nearly complete right dentary; AMNH 12077, posterior part of right dentary; AMNH 12078, posterior part of right dentary; AMNH 12079, anterior part of right dentary; AMNH 12080, posterior part of right dentary; AMNH 12083 (Figure 13), posterior part of left maxilla; AMNH 14312, 4 teeth; AMNH 14313, medial part of right dentary; and AMNH 14314, posterior part of right maxilla.

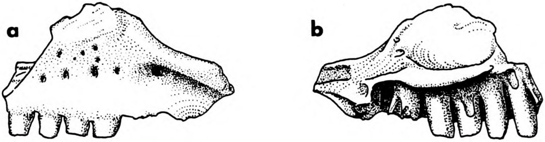

Figure 13. Paleoxantusia fera (AMNH 12083), posterior part of left maxilla. a. labial view; b. lingual view. X 12.

Remarks: Although Paleoxantusia fera is represented by a number of specimens from Swain Quarry, little can be said about variation in this species, owing largely to the fragmentary nature of most of the specimens. Most of the dentary material in which the teeth are not preserved are assigned to this species on the basis of the closed and fused Meckelian groove, lingual coronoid insertion surface and the anterior inferior alveolar foramen.

Estes (1976) noted the common occurrence of _Paleoxantusia_ _fera_ in the Tongue River Formation and extended the range of this species from the middle Eocene (Hecht, 1956) down to the middle Paleocene (Torrejonian). The numerous specimens of this species from Swain Quarry indicate that _Paleoxantusia_ _fera_ was either a relatively common lizard during the middle Paleocene or that the ecologic and/or sedimentological conditions were such that _P_. _fera_ was selectively preserved. In addition, Estes (1976) noted previously unreported faint lateral crests on the tooth crowns of _Paleoxantusia_ _fera_ (Hecht, 1956, 1959). These crests are well developed on a number of the Swain Quarry specimens where the tooth crowns are preserved.

cf. _Paleoxantusia_ _fera_

Referred material: AMNH 12043, medial part of right dentary; and AMNH 12059, medial part of right dentary.

Remarks: The fragmentary nature of these two specimens makes it impossible to refer them to _Paleoxantusia_ _fera_ with certainty, but are generally similar to the dentaries of Paleoxantusia fera and are provisionally referred to this species.

Family Xenosauridae

Genus Exostinus

Exostinus cf. E. lancensis Gilmore, 1928

Referred material: AMNH 14315 (Figure 14), medial part of right dentary; AMNH 14316, medial part of left dentary; AMNH 14317, medial part of left dentary; and AMNH 14318, anterior part of left dentary.

Figure 14. Exostinus cf. E. lancensis (AMNH 14315), medial part of right dentary. X 10.

Remarks: Based on characters used by Estes (1965, 1975 and 1976), these fragmentary specimens have a combination of diagnostic characters that allow assignment to Exostinus lancensis rather than to E. rugosus or E. serratus. The labial side of the specimen is slightly roughened. The teeth curve lingually, taper to a point, possess a faint groove labially and are slightly recurved. A non-continuous pigmented traverse band is present at the base of the crowns and at the top of the tooth shaft both lingually and labially.

Estes (1964) reported on a number of specimens referable to this species from the late Cretaceous of Wyoming and in a later paper (Estes, 1976), extended the range of this species upward through time, reporting *E. lancensis* from the middle Paleocene.

Suborder Anguimorpha

Family Anguidae

Subfamily Odaxosaurinae, New Subfamily

Type: *Odaxosaurus* Gilmore, 1928.

Known distribution: Late Cretaceous through (?) late Paleocene of North America.

Diagnosis: Differs from the Glyptosaurinae in the possession of non-tuberculate dermal armor. Differs from the other anguid subfamilies (Anguinae, Diploglossinae and Gerrhonotinae) in the possession of teeth with bulbous, expanded shafts and striated, blunt tooth crowns.

Discussion: This subfamily is established for the genus *Odaxosaurus* which was previously designated subfamily *incertae sedis* by me (Sullivan, 1979). *Odaxosaurus* was originally included within the subfamily Anguinae by Meszoely (1970) in the belief that this genus was closely related to the Recent anguines and diploglossines. However, I have shown (Sullivan, 1979) that *Odaxosaurus* shares more characters with the glyptosaurines than with the anguines, thus necessitating the transfer of this genus to another subfamily. By excluding *Odaxosaurus* from both the Anguinae and the Glyptosaurinae, both of these subfamilies retain their respective homogeneity. Many problems concerning anguid origins may be resolved by a revision of the fossil and Recent anguines.

The Odaxosaurinae as herein defined, is established solely for the species *Odaxosaurus piger*. The late Paleocene species "*Odaxosaurus*" *jepseni* has been discussed by me (Sullivan, 1979:58) and is being transferred to a new genus by Jacques Gauthier of the University of California-Berkeley (personal commun., 1980). "*Odaxosaurus*" *jepseni* may represent a transitional morphotype as it displays glyptosaurine tubercles on the dermal armor. The transitional dermal armor morphology seen in this species may not represent the inferred ancestral route from the Odaxsaurinae to the Glyptosaurinae via *Xestops*. I have stated (Sullivan, 1979, and in press) that there is evidence that the glyptosaurines were already established by the middle Paleocene, before the appearance of "*Odaxosaurus*" *jepseni*. Furthermore, the teeth of "*Odaxosaurus*" *jepseni* are different from *Odaxosaurus piger* and all other glyptosaurine lizards of both the Eocene and Oligocene. The teeth ". . . are pleurodont, stout, shafts compressed fore and aft with flattened sides, and closely spaced in the jaw" (Gilmore, 1942:162) are markedly different and thus probably represent a derived condition. This derived tooth morphology is distinctive and cannot be considered ancestral for the subfamily Glyptosaurinae. "Odaxosaurus" jepseni is here included within the Glyptosaurinae, but I consider this species as an early side branch of glyptosaurine evolution.

Genus Odaxosaurus

Odaxosaurus piger (Gilmore, 1928)

Peltosaurus ? piger Gilmore, 1928, p. 136.
Odaxosaurus obliquus Gilmore, 1928, p. 158.
Pancelosaurus piger Meszoely, 1970, p. 105.

Referred material: AMNH 12030, posterior part of right dentary; AMNH 12032, right dentary; AMNH 12033, medial part of right dentary; AMNH 12035, posterior part of right dentary; AMNH 12060, medial part of left dentary; AMNH 12084, medial part of left dentary; AMNH 12085 (Figure 15), posterior part of left dentary; and AMNH 12086, posterior part of left maxilla; AMNH 14310 (Figure 16), medial part of left dentary.

Remarks: These fragmentary specimens range in size from 6 mm (AMNH 12033) to 13 mm (AMNH 12085) and are quite variable as reported by Estes (1964). The apparent plasticity in tooth morphology in Odaxosaurus piger ranges from the stout, squared off, blunt-crushing tooth type with

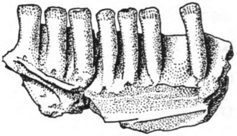

Figure 15. *Odaxosaurus piger* (AMNH 12085), posterior part of left dentary. X 5.

striated crowns as seen in AMNH 12085 (Figure 15) to that of a more gracile type with obliquely arranged teeth and less defined striations on the crowns as in AMNH 14310 (Figure 16). The variation in tooth morphology is due possibly in part to either: (1) representation of various ontogenetic stages of development or (2) the presence of more than one species. Meszoely et al. (1978) indicated the former when

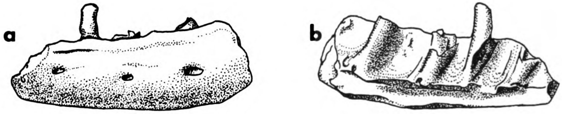

Figure 16. *Odaxosaurus piger* (AMNH 14310), medial part of left dentary. a. labial view; b. lingual view. X 10.

they synonymized *Odaxosaurus obliquus* (Gilmore, 1928:158) with *Pancelosaurus* (=*Peltosaurus* ?) *piger* (Gilmore, 1928: 136). Based on the Lance Creek specimens of the University of California-Berkeley I have seen, morphotypes of

Odaxosaurus piger can be consistently distinguished independent of size and/or topographic location on the dentary or maxilla. Osteological and statistical reevaluation of Odaxosaurus piger may be in order to test the validity of the synonymy of Odaxosaurus obliquus with Odaxosaurus piger.

These specimens are referred to Odaxosaurus piger based on size and morphology similar to specimens from the late Cretaceous Lance Formation. There appear to be no characters present that suggest a different species for these middle Paleocene specimens. Based on the non-abutting teeth, none of the specimens can be referred to "Odaxosaurus" jepseni.

Odaxosaurus piger has been to date known from the late Cretaceous deposits through late Paleocene (Tiffanian) of North America (Estes, 1964, 1975 and 1976).

Subfamily Glyptosaurinae

Glyptosaurinae Indeterminate

Referred material: AMNH 12031, posterior part of right maxilla; AMNH 12042, medial part of left dentary; AMNH 12044 (Figure 17), premaxilla; AMNH 12045, anterior part of left dentary; AMNH 12065, medial part of right dentary; AMNH 12070, anterior part of right maxilla; AMNH

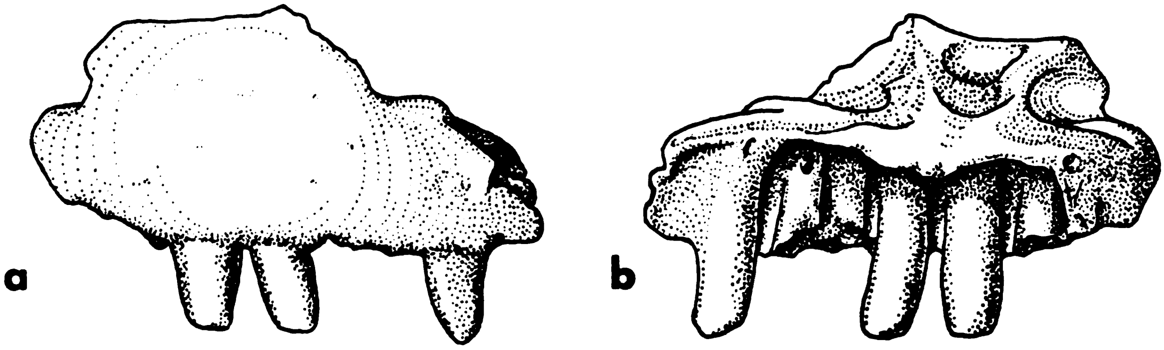

Figure 17. Glyptosaurinae Indeterminate (AMNH 12044), premaxilla. a. labial view; b. lingual view. X 10.

12088 (Figure 18), booth bearing region of right pterygoid; and AMNH 12091, medial part of (?) right maxilla.

Remarks: These fragmentary specimens (Figures 17 and 18) are referred to the anguid subfamily Glyptosaurinae on the basis of their large size and tooth morphology. A few

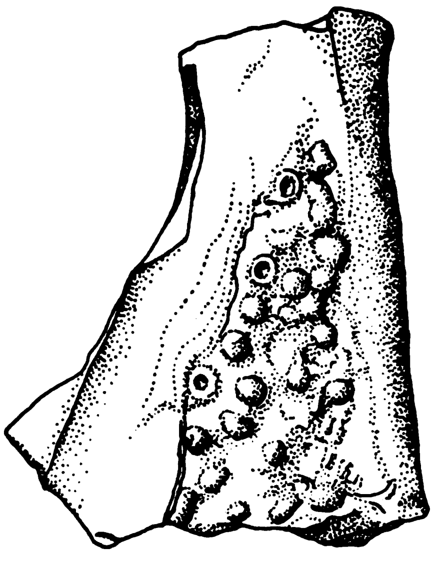

Figure 18. Glyptosaurinae Indeterminate (AMNH 12088), right pterygoid (palatal view). X 10.

of these specimens (AMNH Nos. 12042, 12045 and 12091) may be referable to the Odaxosaurinae due to their smaller size, but these specimens are quite fragmentary. I have noted (Sullivan, 1979) that distinguishing genera and species based on tooth and osteoderm morphology is impossible within the subfamily Glyptosaurinae and that the tooth morphology is very similar to that of the Odaxosaurinae.

Subfamily Glyptosaurinae and/or Odaxosaurinae Indeterminate

Referred material: AMNH 12089, 21 body osteoderms.

Remarks: Three morphotypes of osteoderms are represented in the material from Swain Quarry: (1) tubercular; (2) pit and ridge; and (3) combination pit and ridge/tubercular. The osteoderms of the subfamily Glyptosaurinae are characterized by the presence of tubercles whereas those of the Odaxosaurinae retain the primitive pit and ridge morphology that is seen in other anguid lizards. A few of the osteoderms from Swain Quarry, as well as some from the older Puercan age deposits from the San Juan Basin, New Mexico (Sullivan, in press) show a combined pit and ridge/tubercular morphology similar, if not identical, to that as reported for "*Odaxosaurus*" *jepseni*.

Subfamily Anguinae

Genus Machaerosaurus

Machaerosaurus torrejonensis Gilmore, 1928

Referred material: AMNH 12047, medial part of left dentary; AMNH 12063 (Figure 19), posterior part of right maxilla; AMNH 12066, medial part of right dentary; AMNH 12068 (Figure 20), anterior part of right maxilla; AMNH 12087 (Figure 22), left frontal; AMNH 12094, medial part of left dentary; AMNH 12095, posterior part of right maxilla; AMNH 12097, anterior part of left maxilla; and AMNH 12099 (Figure 21), nearly complete right dentary.

Remarks: Gilmore (1928) named Machaerosaurus torrejonensis based on an incomplete skull (AMNH 5184) from the Arroyo Torrejon, Nacimiento Formation (Torrejonian), San Juan Basis, New Mexico. No other species have been referred to this species prior to this study. Comparison

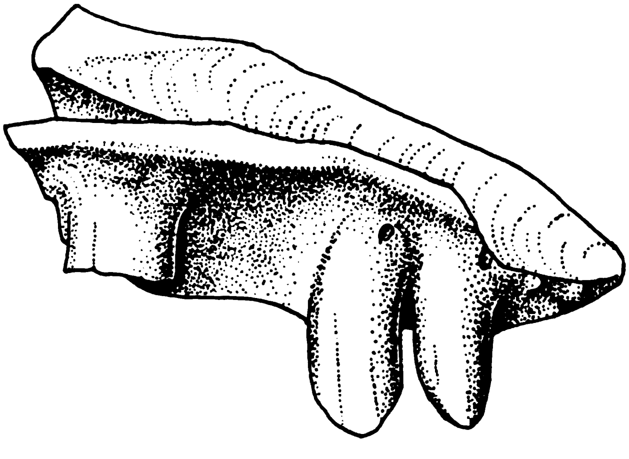

Figure 19. Machaerosaurus torrejonensis (AMNH 12063), posterior part of the right maxilla (lingual view). X 15.

of the Swain Quarry specimens with the holotype indicate that this taxonomic assignment is unquestionable. The Swain Quarry lizards referable to *Machaerosaurus torrejonensis* comprise a significant percentage of the lizard fauna. The disarticulated dentaries and maxillae offer for the first time a lingual view of the teeth of *Machaerosaurus torrejonensis*. The teeth extend a little less than half their height above and below the parapet of the dentary and maxilla. The labial surfaces of the teeth are non-striated but the lingual surfaces are grooved. Two grooves appear on the posterior maxillary teeth, with the anterior groove being more pronounced than the posterior one (Figure 19) and with both grooves extending to the tooth base. The teeth in the anterior portion of the maxilla (Figure 20) as well as the teeth of the dentary (Figure 21) have only the anterior groove. This groove ends approximately half way down the tooth shaft. All

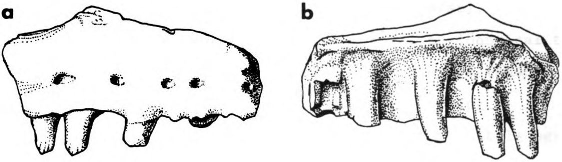

Figure 20. *Machaerosaurus torrejonensis* (AMNH 12068), anterior part of right maxilla. a. labial view; b. lingual view. X 10.

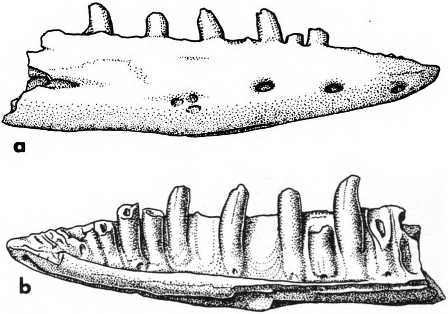

Figure 21. *Machaerosaurus torrejonensis* (AMNH 12099), right dentary. a. labial view; b. lingual view. X 8.

teeth are laterally compressed and slightly recurved in both the dentary and maxilla as seen in the holotype (AMNH 5184) recently redescribed by Sullivan (in press).

A left frontal, AMNH 12087 (Figure 22) is identical to the preserved edge of the frontal of the holotype (AMNH 5184), in size, shape and dermal armor sculpturing. Furthermore, this specimen indicates that the frontals were paired rather than fused. The frontal is significantly different from *Odaxosaurus piger* and other genera belong to the Anguinae, but compares closely to frontal material, shown to me by Richard Estes that has been tentatively referred to "*Odaxosaurus*" *jepseni*.

Figure 22. Machaerosaurus torrejonensis (AMNH 12087), left frontal (anterior direction is up). X 10.

Recently, Meszoely et al. (1978) reported the anguine lizard "Pancelosaurus" (=Odaxosaurus) pawneensis of the early and middle Oligocene of North America should be transferred to the genus Machaerosaurus. I suggested (Sullivan, in press) that the "pawneensis" form represents an undescribed genus that appears to be related to North American Ophisaurus; thus, Machaerosaurus is represented by only one species, M. torrejonesis. Machaerosaurus torrejonensis is still known only from middle Paleocene (Torrejonian) deposits of North America.

cf. Machaerosaurus torrejonensis

Referred material: AMNH 12034, posterior part of left maxilla; AMNH 12050, greater part of left dentary; AMNH 12051, posterior part of right dentary; AMNH 12055, medial part of left dentary; and AMNH 12092 (Figure 23), posterior part of right dentary.

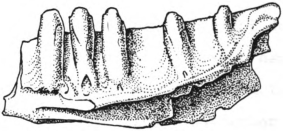

Figure 23. cf. Machaerosaurus torrejonensis (AMNH 12092), posterior part of right dentary (lingual view). X 10.

Remarks: The above specimens are designated cf. Machaerosaurus torrejonensis based primarily on size and shape of the dentaries or maxilla and in the case of AMNH 12055, an anterior groove that appears on the upper most part of the posterior most tooth. All of these specimens are missing the diagnostic tooth crowns from breakage or from wear as seen in AMNH 12092 (Figure 23).

Family Anguidae Indeterminate

Referred material: AMNH 12008 (Figure 24), proximal end of left ramus; AMNH 12029, posterior part of left

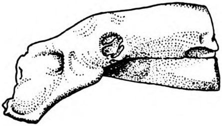

Figure 24. Anguidae Indeterminate (AMNH 12008), articular end of left ramus (lingual view). X 8.

maxilla; AMNH 12037 (Figure 25), medial part of right dentary; AMNH 12054, medial part of right dentary; AMNH 12062 (Figure 26), greater part of right dentary; AMNH 12090, medial part of right dentary; AMNH 12096, medial part of left dentary; AMNH 12098, posterior part of right dentary; AMNH 14319, anterior part of right dentary; AMNH 14320, medial part of right dentary; and AMNH 14321, greater part of left dentary.

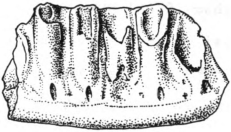

Figure 25. Anguidae Indeterminate (AMNH 12037), medial part of right dentary (lingual view). X 12.

Remarks: The fragmentary nature of the above specimens and those below questionably identified as indeterminate anguids make them impossible to place with certainty

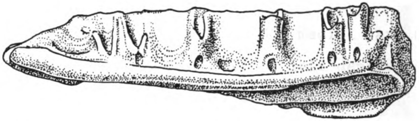

Figure 26. Anguidae Indeterminate (AMNH 12062), right dentary (lingual view). X 12.

in any anguid genus or subfamily. However, I believe that much of this material considered here may represent the subfamily Anguinae and the genus Machaerosaurus. Most of this material is assigned to the family Anguidae on the basis of an open, free intramandibulur septa, gracile morphology and boat-shaped dentaries.

cf. Anguidae

Referred material: AMNH 12052, medial part of left dentary; AMNH 12053, anterior part of left dentary; AMNH 12056, medial part of left dentary; AMNH 12057, anterior part of right dentary; AMNH 12058, medial part of left dentary; and AMNH 12093, anterior part of right dentary.

Remarks: These specimens are so fragmentary that familial assignment is uncertain, but are provisionally referred to the Anguidae based on size and shape.

Family Parasaniwidae

cf. Provaranosaurus sp.

Referred material: AMNH 14306, medial part of left dentary; AMNH 14307, medial part of left dentary; and AMNH 12309 (Figure 27), medial part of right dentary.

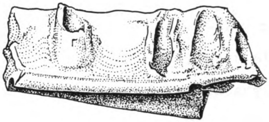

Figure 27. cf. Provaranosaurus sp. (AMNH 14309), medial part of right dentary (lingual view). X 10.

Remarks: The fragmentary nature of these specimens makes it difficult to establish their taxonomic position. All three specimens lack the diagnostic teeth, but the basal outlines of the teeth show that they are suboval in cross-section. The intramandibular septum is smoothly fused, and thus, with the tooth outlines, these specimens are provisionally referred to Provaranosaurus sp.

Estes (1975) noted that Provaranosaurus acutus was known to occur only in the Princeton Quarry local fauna (late Paleocene-Tiffanian). Material designated cf. Provaranosaurus sp. is known from the earlier middle Paleocene (Torrejonian) Medicine Rock local fauna (Estes, 1976). The Swain Quarry local fauna occurrence of cf.

Provaranosaurus sp. further establishes this lizard as a middle Paleocene form.

Indeterminate Lacertilia

Referred material: AMNH 12041, ventral part of basicranium; AMNH 12046, posterior part of left dentary; AMNH 14322, anterior part of left dentary; AMNH 14323, fragment of (?) right dentary; AMNH 14324, medial fragment of right dentary; AMNH 14325, medial part of right dentary; and AMNH 14326, medial part of left dentary.

Remarks: The fragmentary nature of the above specimens makes reliable familial and general assignment impossible.

Order Serpentes

Family Boidae

Subfamily Erycinae

Genus Helagras

Helagras prisciformis Cope, 1883

Referred material: AMNH 12025, trunk vertebra; AMNH 12026, trunk vertebra; and AMNH 12027 (Figure 28), trunk vertebra.

Remarks: Cope (1883) named Helagras prisciformis based on two articulated trunk vertebrae from the Puercan (early Paleocene) horizon of the Nacimiento Formation of the San Juan Basin, New Mexico. Gilmore (1938) redescribed

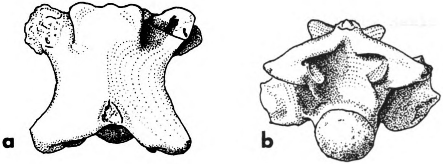

Figure 28. Helagras prisciformis (AMNH 12027), trunk vertebra. a. dorsal view; b. axial view. X 6.

the type specimen as well as referred material of H. prisciformis, and noted the boiid affinites, but hesitantly included this species within his "Serpentes of unknown family reference." Hoffstetter and Rage (1972:111) included Helagras within the Boidae, and furthermore within the subfamily Erycinae. Holman (1979), in his review of North American Tertiary snakes, suggested that the subfamilial designation of the North American species be considered tentative, pending a revision of the New World fossil snakes.

The three snake vertebrae from Swain Quarry are referred to Helagras prisciformis on the basis of the presence and/or evidence of a "short, thickened, tuberous-like neural spine" as described by Gilmore (1938:83).

Helagras princiformis is the only Paleocene North American snake known and has only been found in Puercan and Torrejonian (early and middle Paleocene) deposits. Its occurrence in Swain Quarry extends its paleogeographic range from its type locality in northwest New Mexico to southcentral Wyoming.

COMPARISON OF LATE CRETACEOUS AND PALEOCENE LOWER VERTEBRATE FAUNAS OF THE ROCKY MOUNTAIN REGION, NORTH AMERICA

Of the three major North American Paleocene lower vertebrate assemblages known (Princeton Quarry local fauna of Estes, 1975; Medicine Rocks Local fauna of Estes, 1976; and Swain Quarry local fauna, this paper), the Swain Quarry local fauna is the largest in terms of numbers of specimens, although its taxonomic diversity is comparable to the above faunas reported by Estes. In this section the Swain Quarry lower vertebrate local fauna is compared to previously reported local faunas of similar age and location in order to provide information on depositional-paleoenvironmental controls, evolutionary trends, endemic species and general paleobiogeographical patterns of particular taxonomic groups.

The Swain Quarry lower vertebrate microfauna is dominated by reptiles, primarily lizards, and by amphibians (urodeles). Percentages based on minimum number of individuals (MNI) show that the fish comprise 4.8% of the entire microfauna, amphibians, 24%, and reptiles 71% (Table 1). Among the reptiles the lizards comprise 67%, crocodilians 1.5%, and the snakes 1.5%. The anguid lizards

TABLE 1

LIST OF MINIMUM NUMBERS OF INDIVIDUALS (MNI) AND PERCENTAGES OF HIGHER TAXA FROM SWAIN QUARRY

Taxa	Number of Specimens	MNI		% of Higher Taxa Based on MNI
Amia fragosa	3	2		Fish = 4.8%
Toleostei *Insertae Sedis*	1	1		
Scapherpeton tectum	11	8		Amphibians = 24% (Urodeles)
cf. *Opisthotriton kayi*	5	3		
Habrosaurus dilatus	7	4		
Crocodilia Indeterminate	1	1	Reptiles = 71%	Crocodilians = 1.5%
Swainiguanoides milleri	3	2		Lizards = 67%
cf. *Contogenys sloani*	1	1		
Paleoxantusia fera	23	12		
Exostinus cf. *E. lancensis*	4	3		
Odaxosaurus piger	9	4		
Glyptosaurinae Indeterminate	8	3		
Machaerosaurus torrejonensis	14	4		
Anguidae Indeterminate	17	9		
cf. *Provaranosaurus* sp.	3	2		
Lacertilia Indeterminate	7	3		
Helagras prisciformis	3	1		Snakes = 1.5%
Total	120	63		

comprise 47% of the lizard fauna and 32% of the entire sample of the Swain Quarry lower vertebrate microfauna.

The above percentages represent an indication of the relative abundance of the lower vertebrates from this quarry which Estes reports (personal commun., 1980) is consistent with other lower vertebrate Paleocene microfaunas from quarries that yield a large number of mammalian fossils. The apparent rarity of the lower vertebrates from Swain Quarry is probably due to depositional factors as the meticulous sampling efforts of the AMNH field parties should have eliminated any bias in the recovery of these specimens (Rigby, personal commun., 1979).

Comparison of the Swain Quarry lower vertebrate microfauna to other North American faunas of the late Cretaceous and early Paleocene can be made with only a few others. Only two main late Cretaceous lower vertebrate faunas from the general region of Swain Quarry have been described by Estes (1964), Estes et al. (1969), and Estes and Berberian (1970). Only two major studies on North American lower vertebrate microfaunas from the Paleocene age have been made (Estes, 1975, 1976) and the taxa of these two studies are compared with that of Swain Quarry (Table 2). Most of our knowledge concerning the faunae of this time period comes from these studies and from some isolated descriptions by Gilmore (1928, 1942). Contributions concerning specific taxonomic groups of lizards

TABLE 2

OCCURRENCES OF LOWER VERTEBRATE TAXA FROM THE THREE MAJOR PALEOCENE LOWER VERTEBRATE LOCALITIES OF NORTH AMERICA

	Estes 1975	Estes 1976	This Paper	
TAXA	Fort Union Formation Big Horn Basin	Tongue River Formation S.E. Montana	Fort Union Formation Swain Quarry	Comments on the Occurrence of Taxa in Swain Quarry
Dasyatidae indeterminate		X		fish sparsely represented
cf. *Acipenser* sp.		X		
cf. *Palaeopsephurus* sp.		X		
Amia fragosa	X	X	X	
Amia uintaensis		X		
Lepisosteus occidentalis		X		
cf. *Palaeolabrus montanensis*		X		
Teleostei *incertae sedis*		X		
Scapherpeton tectum	X	X	X	urodeles moderately represented
Opisthotriton kayi	X	X	X	
Lisserpeton bairdi		X		
Habrosaurus dilatus		X	X	
Amphiuma jepseni	X			
Eorhinophrynus sp.	X			frogs absent
cf. *Scotiophryne* sp.		X		
Discoglossidae, undescribed gen. & sp.	X	X		
Anura *incertae sedis* indeterminate	X	X		
Platobaena bairdi		X		turtles not studied
Compsemys victa		X		
Indeterminate Baenidae		X		
cf. *Plastomenus* sp.		X		
Ptychogaster sp.	X			
Champsosaurus sp.				eosuchians absent
Leidyosuchus sp.		X		crocodilians largely not studied
Allognathosuchus sp.	X			
Crocodylidae indeterminate			X	
Alligatorinae, unidentified gen. & sp.		X		
Swainiguanoides milleri			X	lizards relatively abundant
Contogenys sloani		X	X	
Paleoxantusia fera		X	X	
Exostinus lancensis		X		
Exostinus cf. *lancensis*			X	
Exostinus rugosus	X			
Odaxosaurus piger	X	X	X	
cf. *Gerrhonotus* sp. (?=*Machaerosaurus*)		X		
Glyptosaurinae indeterminate			X	
Machaerosaurus torrejonensis			X	
Provaranosaurus acutus	X			
cf. *Provaranosaurus* sp.		X	X	
Oligodontosaurus wyomingensis	X			amphisbaenids absent
cf. *Oligodontosaurus* sp.		X		
Rhineuridae, unidentified gen. & sp.	X			
Coniophis sp.		X		snakes moderately represented
cf. *Dunnophis* sp.		X		
Helagras prisciformis			X	

from the early Tertiary are found in more comprehensive works by Meszoely (1970) and Sullivan (1979). Table 3 summarizes the time-stratigraphic occurrences of the Swain Quarry lower vertebrates based on the above papers.

A brief discussion of the compared faunas is presented below. Because of the incomplete sample size, paleoecological analyses proposed by Shotwell (1955) and used by Estes and Berberian (1970) for lower vertebrates cannot be used for the study of the Swain Quarry lower vertebrate microfauna. Any interpretation of the general paleoecology must rely heavily on the mammalian fossils, but may sometimes be augmented by the lower vertebrates.

Fish

Amia fragosa is indicative of a fresh water habitat, usually stagnant and/or lakes, ponds, or sluggish streams (Estes, 1964). The presence of this fish in the Swain Quarry suggests a drainage situation similar to the present day Gulf Coast of the Mississippi delta.

Amphibians

The urodeles *Habrosaurus dilatus*, *Scapherpeton tectum* and cf. *Opisthotriton kayi* also suggest a freshwater environment. Trends in their relative abundance from sites from the mid-Campanian through the late Paleocene were reviewed by Estes (1976). No frog remains are known from

TABLE 3

TIME-STRATIGRAPHIC DISTRIBUTION OF THE SWAIN QUARRY LOWER VERTEBRATES

SWAIN QUARRY LOWER VERTEBRATES	LATE CRETACEOUS	PALEOCENE				EOCENE
		Puercan	Torrejonian	Tiffanian	Clarkforkian	Wasatchian
	Estes, 1964	Gilmore, 1938 Sullivan (in press)	Estes, 1976 Gilmore, 1928 This Study	Gilmore, 1942 Estes, 1975	None	Meszoely, 1970 Sullivan, 1979
Amia fragosa	X	X	X	X	X	X
Scapherpeton tectum	X	X	X	X		
cf. Opisthotriton kayi	X	X	X	X		
Habrosaurus dilatus	X	X	X			
Crocodylidae Indeterminate	X	X	X	X	X	X
Swainiguanoides milleri n. gen., n. sp.			X			
cf. Contogenys sloani	X	X	X			
Paleoxantusia fera			X	X	X	X
Exostinus cf. lancensis	X	X	X			
Odaxosaurus piger	X	X	X			
Machaerosaurus torrejonensis			X			
Glyptosaurinae Indeterminate		X	X	X	X	X
cf. Provaranosaurus sp.	X	X	X			
Helagras prisciformis		X	X			

Swain Quarry and probably reflects a preservation factor owing to transport or diagenesis rather than reflecting an absence due to ecological factors. There are anuran remains from the two other Paleocene localities (Estes, 1975, 1976) although they are rare in early Tertiary deposits (Estes, 1970).

Crocodilians

Crocodilian remains from Swain Quarry and vicinity have been noted by Rigby (1977) and have been largely unstudied. A small dentary referrable to a crocodilian is the only specimen in the Swain Quarry microfauna that is representative of these reptiles.

Lizards

The lizards are the most important component of this lower vertebrate microfauna comprising a little over two-thirds of the lower vertebrates known from Swain Quarry based on minimum number of individuals.

Of the lizard families represented that are known from the late Cretaceous (Varanidae, Anguidae, Scincidae, Teiidae, Parasaniwidae and Xenosauridae), all but two (Varanidae and Teiidae) are represented in the Paleocene deposits of North America. The introduction of the lizard families Xantusiidae and Iguanidae occurs by middle Paleocene (Torrejonian) times. Genera that were relatively abundant in the late Cretaceous (i.e., Contogenys, Exostinus and Odaxosaurus) are relatively rare in Swain Quarry. Genera that were once known from the early Eocene such as Paleoxantusia and forms referable to the Glyptosaurinae appear to be well established by middle Paleocene times.

Two lizards from Swain Quarry appear to be either endemic species or forms that are known exclusively from Torrejonian age deposits; these include the new iguanid Swainiguanoides milleri and the anguid Machaerosaurus torrejonensis. The anguids form the largest number of lizard species, but are known from material that is difficult to assign to a subfamily.

Since the lizards from Swain Quarry are known from only fragmentary material, definitive paleoecological interpretation cannot be made concerning their life habits. Suggestions concerning dietary habits can be made based on tooth morphology according to guidelines presented by Hotton (1955), but extreme caution is necessary where particular morphologies lack living representatives. For example, it might be suggested that the species Machaerosaurus torrejonensis, which is restricted to the Torrejonian, had a diet consisting of primarily insects based upon the sharp, latterly compressed, slightly recurved tooth morphology. Beyond that inference, little else could be added concerning this lizard's life habits. Estes (1964) summarized the suggested ecologies for many of the species included in this study, using familial relationships in order to extrapolate the ecology of *Exostinus lancensis* and *Odaxosaurus piger*. In a later study, Estes and Berberian (1970:16 and 30) suggested that *Odaxosaurus piger* was probably aquatic based solely on percentages of occurrence but the dentition of *Odaxosaurus piger*, like that of the glyptosaurine lizards, suggests a diet of land molluscs and insects. Furthermore, the trend toward increasing thickness of dermal armor in these early anguids suggests fully terrestrial adaptations.

While Estes (1970) reports that the number of lizard families represented in North America drops significantly across the Cretaceous-Paleocene boundary, it is now apparent that some families, particularly the Anguidae, diversified in the wake of these changes. It is also clear that the apparent "explosive radiation" of the glyptosaurine lizards (Sullivan, 1979:6) at the outset of the early Eocene had its beginnings in the early Paleocene with a number of glyptosaurine lizards already present by Torrejonian times. The problem in determining the precise time of diversification of these lizards has been the result of unstudied and poorly known Paleocene herpetofaunas. The preservation of the Paleocene glyptosaurines, as yet, does not rival the excellently preserved material from the North American Eocene and Oligocene localities, and only indicates the inception of later diversity.

Snakes

The boiid _Helagras_ _prisciformis_ is exclusively known from trunk vertebrae from the Puercan and Torrejonian age deposits of North America. Holman (personal commun., 1979) reports that the vertebral morphology of _H_. _prisciformis_ is that of a fossorial snake which had a body length of only about one meter. Its occurrence in the Swain Quarry assemblage provides no additional information regarding the paleoecology of this snake.

General Faunal Comparisons

The Swain Quarry herpetofauna agrees with others from the Lance, Hell Creek, Tongue River and Fort Union formation (Estes, 1964, 1975, 1976 and Estes et al., 1969) that show that aquatic forms remain similar across the Cretaceous-Tertiary boundary while the terrestrial component shows a reduction in diversity of higher taxa in the Paleocene. This reduction may be a result of the poor sample of lower vertebrate microfaunas from the Paleocene as there seems to be evidence that suggest while there is a reduction of lizard families in the early Paleocene from the Cretaceous, by middle Paleocene times, diversification of particular groups, such as the anguids, occupy the "niches" formerly held by other forms.

Since the lizards make up the major portion of the Swain Quarry lower vertebrate microfauna, a riparian site of deposition, where this terrestrial component became incorporated without undergoing excessive post-mortem transport is suggested. This essentially agrees with Rigby's (1977) interpretation of Swain Quarry being representative of a deltaic fluvial system. Estes (1976:517) has pointed out that most of the known pertinent or comparable lower vertebrate microfauna localities of late Cretaceous and Paleocene age reflect similar lithologies and depositional environments. A number of taxa are common to these faunas, indicating that these sites, and Swain Quarry, are indicative of a freshwater, warm temperate coastal plain.

The great abundance of the lizards compared to that of the snakes seems to reflect a relatively true ecologic relationship. The larger reptilian components, including turtles and champsosaurs are not of concern here primarily due to size factors, which also affect the occurrence of crocodilians. Turtles have been noted to occur in the field area near Swain Quarry along with crocodilians (Rigby, 1977).

A warm climatic regime during the late Cretaceous and Paleocene of the Rocky Mountain region has been described by numerous studies based on paleobotanical and paleozoological evidence. The lower vertebrates from Swain Quarry provide no additional insight with regard to the climatic interpretation of North America during the middle Paleocene. Estes (1976) provided an excellent interpretation of the middle Paleocene warm temperate climate for the lower vertebrates and that is maintained here.

SUMMARY

1. The lower vertebrate microfauna from Swain Quarry, Carbon County, Wyoming, is the largest Paleocene lower vertebrate assemblage described to date and is relatively diverse despite the small minimum number of individuals present.

2. Fish are represented by *Amia fragosa* and an indeterminate teleost.

3. The amphibians are represented by the urodeles *Scapherpeton tectum*, *Habrosaurus dilatus* and cf. *Opisthotriton kayi*.

4. A fragmentary dentary is referred to the Crocodilia.

5. *Swainiguanoides milleri* n. gen., n. sp. is the oldest North American iguanid and is similar to Recent sceloporine lizards.

6. The lizards cf. *Contogenys sloani*, *Paleoxantusia fera*, *Exostinus* cf. *lancensis* and *Odaxosaurus piger* are noted from Swain Quarry.

7. Odaxosaurinae, new subfamily, is established for the primitive anguid lizard *Odaxosaurus piger*.

8. *Machaerosaurus torrejonensis* is noted for the first time by material other than the holotype and a complete left frontal indicates that this bone was paired.

9. Fragmentary specimens belonging to cf. *Provaranosaurus* sp. are noted.

10. *Helagras* prisciformis is the only snake in the Swain Quarry local fauna.

11. The sample size of Swain Quarry lower vertebrates is extremely small compared to the mammalian sample in other known Paleocene lower vertebrate faunas.

12. The Swain Quarry lower vertebrate microfaunal assemblage agrees with other comparable Paleocene herpetofaunas that show the aquatic habitat relatively stable across the Cretaceous-Tertiary boundary.

13. Anguid diversification probably occurred in response to the apparent decrease in lizard families represented in the North American Paleocene.

LITERATURE CITED

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Cope, E. D. 1883. First addition to the fauna of the Puerco Eocene. Proc. American Philos. Soc. 20: 545-546.

Estes, R. 1964. Fossil vertebrates from the late Cretaceous Lance Formation eastern Wyoming. Univ. Cal. Pub. Geol. Sci. 49:1-187.

________. 1965a. A new fossil salamander from Montana and Wyoming. Copeia 1965(1):90-95.

________. 1965b. Notes on some Paleocene lizards. Copeia 1965(1):104-106.

________. 1969a. The Batrachosauroididae and Scapherpetontidae, late Cretaceous and early Cenozoic salamanders. Copeia 1969(2):224-234.

________. 1969b. A scincoid lizard from the Cretaceous and Paleocene of Montana. Breviora 331:1-9.

________. 1975. Lower vertebrates from the Fort Union Formation, Late Paleocene, Big Horn Basin, Wyoming. Herpetologica 31(4):365-385.

________. 1976. Middle Paleocene lower vertebrates from the Tongue River Formation, southeastern Montana. Jour. Paleontol. 50:500-520.

Estes, R., and P. Berberian. 1970. Paleoecology of a late Cretaceous vertebrate community from Montana. Mus. Compar. Zool., Harvard Univ. Breviora 343:1-35.

Estes, R.; P. Berberian; and C. A. M. Meszoely. 1969. Lower vertebrates from the late Cretaceous Hell Creek Formation, McCone County, Montana. Mus. Compar. Zool., Harvard Univ. Breviora 337:1-33.

Estes, R., and L. I. Price. 1973. Iguanid lizard from the Upper Cretaceous of Brazil. Science 180:748-751.

Etheridge, R. 1964. The skeletal morphology and systematic relationships of sceloporine lizards. Copeia 1964(4):610-631.

Gilmore, C. W. 1928. Fossil lizards of North America. Mem. Nat. Acad. Sci. ix + 201 pp.

________. 1938. Fossil snakes of North America. Geol. Soc. Amer. Special Papers 9:v-96 pp.

________. 1942. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming. Proc. American Philosophical Soc. 85(2):159-167.

Hecht, M. 1956. A new xantusiid lizard from the Eocene of Wyoming. Amer. Mus. Nat. Hist. Novitates, No. 1774:1-8.

________. 1959. Reptiles and amphibians. *In* P. McGrew, The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. Bull. Amer. Mus. Nat. Hist. 117:121-176.

Hoffstetter, R., and J. C. Rage. 1972. Les Erycinae fossiles de France (Serpentes, Boidae) compréhension et histoire de la sous-famille. Extrait des Annales de Paléogie, vertébrés. LVIII:81-124.

Holman, J. A. 1979. A review of North American Tertiary snakes. Publ. Mus. Michigan St. Univ. Paleo Ser. 1(6):203-260.

Hotton, N. III. 1955. A survey of adaptive relationships of dentition to diet in North American Iguanidae. Amer. Midl. Nat. 53(1):88-114.

Meszoely, C. A. M. 1970. North American fossil anguid lizards. Bull. Mus. Compar. Zool., Harvard Univ. 139(2):87-149.

Meszoely, C. A. M.; R. Estes; and H. Haubold. 1978. Eocene anguid lizards from Europe and a revision of the genus *Xestops*. Herpetologica 34(2):156-166.

Naylor, B. G. 1979. The Cretaceous salamander *Prodesmodon* (Amphibia: Caudata). Herpetologica 35(1):11-20.

Rigby, J. K. Jr. 1977. Swain Quarry of the Fort Union Formation, middle Paleocene (Torrejonian), Carbon County, Wyoming: Geologic setting and mammalian fauna. Unpublished Ph.D. dissertation, Columbia University.

Shotwell, J. 1955. An approach to the paleoecology of mammals. Ecology 36:327-337.

Sloan, R. 1979. North American Paleocene land mammal ages and zone (abstr. and chart). Unpublished.

Sullivan, R. M. 1979. Revision of the Paleogene genus *Glyptosaurus* (Reptilia, Anguidae). *Bull. Amer. Mus. Nat. Hist.* 163:1-72.

________. (in press). Fossil lizards from the San Juan Basin, New Mexico. *In* B. Kues, S. Lucas, and J. K. Rigby Jr., eds., Advances in San Juan Basin Paleontology. Univ. New Mexico Press.

Swain, B. 1957. Fort Union Formation, west flank of the Sierra Madre, Carbon County, Wyoming. Unpublished Masters thesis, University of Wyoming, Laramie, Wyoming.