

# B R E V I O R A

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## PALEOECOLOGY OF A LATE CRETACEOUS VERTEBRATE COMMUNITY FROM MONTANA<sup>1</sup>

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**ABSTRACT.** At least 78 species representing five classes of vertebrates occur at the Bug Creek Anthills locality, in the Hell Creek Formation, McCone County, Montana. The fauna closely resembles that from the Lance Formation of Wyoming, also of late Cretaceous age.

Quantitative paleoecological techniques originally devised for late Cenozoic mammals required only slight modification to prove useful when applied to the late Cretaceous sample. The resulting analysis shows that at Bug Creek Anthills, fishes, aquatic salamanders, and mammals are more abundant than the amphibious or terrestrial turtles, dinosaurs, and (especially) lizards, when compared with these groups in the Lance Formation fauna. While the latter was probably deposited within the general environment of a swamp forest with relatively small watercourses, the Bug Creek Anthills fauna seems to have been laid down in the relatively deeper waters of major rivers issuing from those lowland swamps. Gar and bowfin fish, and elongated salamanders, are dominant species in the aquatic community nearest to the site of deposition; some of the mammals seem to have been part of a nearby riverbank community.

Excluding birds, 73 genera occur in the Cretaceous sample while 128 genera occur in its closest modern analogue, the Recent fauna of southern Louisiana. If this comparison is valid, the fossil sample may represent about two-thirds of the generic diversity present on the subtropical Cretaceous floodplain.

### INTRODUCTION

Recent work by Dr. Robert Sloan and his associates has resulted in recovery of a large collection of vertebrate fossils from a series of late Cretaceous localities in the upper one-third of the Hell Creek Formation, McCone County, Montana (Sloan and Van

<sup>1</sup> Fossil vertebrates from the late Cretaceous Hell Creek Formation, Montana: Contribution No. 9.



Valen, 1965). The lower vertebrates from this part of the section have been described in a series of papers listed by Estes, Berberian, and Meszoely (1969). The fossil sample is from a quarry, and the specimens were carefully concentrated by the use of washing and screening techniques (McKenna, 1962). All fossil material was removed and an attempt was made to identify each specimen; it is thus possible to make comparison with the similarly-collected sample from the Lance Formation of Wyoming (Estes, 1964), and to apply techniques of paleoecological analysis developed by Shotwell (1955). A substantial faunal similarity between the two samples indicates a similar environment and inferred climate; essential contemporaneity of the two localities further enhances the paleoecological significance of such a comparison.

Bug Creek Anthills (BCA) is the richest of the Hell Creek localities on and near Bug Creek that were discovered by Sloan. A collection from this locality made by a field party of the Museum of Comparative Zoology with the aid of Sloan and his field crew was used for the numerical analysis discussed below. The total faunal list was determined by examination of collections made by a number of institutions (Estes, et al., 1969). BCA is a quarry site that occurs in a cross-bedded stream channel within the upper one-third of the Hell Creek Formation, about 80 feet below the coal bed used locally as the arbitrary mapping boundary between the Cretaceous and Tertiary (Sloan and Van Valen, 1965).

#### FAUNAL LIST

This list includes only species from BCA and other localities in the section on Bug Creek; those not present in BCA are followed by locality data in brackets. The list of mammals has been provided by Sloan, with additions by W. A. Clemens, Jr. (1969, pers. comm.). With the further addition of the unidentifiable ornithomimid material cited by Osborn (1916), the ankylosaurid *Ankylosaurus magniventris* (Brown, 1908), and the panoplosaurid teeth noted by Brown (1907: 842) this becomes the most complete list of valid Hell Creek Formation vertebrates available. *Lamna* sp. was also cited as present by Brown (1907: 842) but the single specimen mentioned is no longer available to substantiate the identification.



VERTEBRATES FROM THE BUG CREEK LOCAL FAUNAS,  
HELL CREEK FORMATION

CLASS CHONDRICHTHYES

ORDER SELACHII

Family Hybodontidae

*Lonchidion selachos* Estes

ORDER BATOIDEA

Family Pristidae

*Ischyrhiza avoncola* Estes [Harbicht Hill]

Family Dasyatidae

*Myledaphus bipartitus* Cope

CLASS OSTEICHTHYES

INFRACLASS CHONDROSTEI

ORDER ACIPENSERIFORMES

Family Acipenseridae

*Acipenser eruciferus* Cope

*Protoscaphirhynchus squamosus* Wilimovsky [Rock  
Creek, SE $\frac{1}{4}$  Sect. 36, T23N, R43E]

Family Polyodontidae

*Paleopsephurus wilsoni* MacAlpin

INFRACLASS HOLOSTEI

ORDER ASPIDORHYNCHIFORMES

Family Aspidorhynchidae

*Belonostomus longirostris* (Lambe)

ORDER AMIIFORMES

Family Amiidae

*Amia fragosa* (Jordan)

*Amia* (= *Protamia*) sp.

ORDER AMIIFORMES?

Family Palaeolabridae

*Palaeolabrus montanensis* Estes

ORDER LEPISOSTEIFORMES

Family Lepisosteidae

*Lepisosteus occidentalis* Leidy

INFRACLASS TELEOSTEI

ORDER ELOPIIFORMES

Family Elopidae

unidentified genus and species

Family Phyllodontidae  
*cf. Paralbula casei* Estes

Family Albulidae  
*Coriops amnicolus* Estes

ORDER PERCIFORMES

Family Sciaenidae  
*Platacodon nanus* Marsh

TELEOSTEI *incertae sedis*

CLASS AMPHIBIA

ORDER CAUDATA

SUBORDER AMBYSTOMATOIDEA

Family Scapherpetontidae  
*Scapherpeton tectum* Cope  
*Lisserpeton bairdi* Estes

Family Prosirenidae  
*Prodesmodon copei* Estes

Family Batrachosauroididae  
*Opisthotriton kayi* Auffenberg

SUBORDER SALAMANDROIDEA?

Family Amphiumidae  
*Proamphiuma cretacica* Estes

SUBORDER MEANTES

Family Sirenidae  
*Habrosaurus dilatus* Gilmore

ORDER SALIENTIA

Family Discoglossidae  
*Scotiophryne pustulosa* Estes  
*cf. Barbourula* sp.  
undescribed genus and species  
Family Pelobatidae?  
*Eopelobates?* sp.

CLASS REPTILIA

ORDER EOSUCHIA

Family Champsosauridae  
*Champsosaurus* sp.



## ORDER TESTUDINATA

## Family Baenidae

*Eubaena cephalica* Hay

undescribed genus and species 1

undescribed genus and species 2

## Family Dermatemydidae

*Compsemys victa* Leidy*Adocus* sp.

## Family Testudinidae

## Subfamily Emydinae?

unidentified genus and species

## Family Trionychidae

*Trionyx* sp.

## ORDER SAURIA

## SUBORDER SCINCOMORPHA

## Family Teiidae

*Chamops segnis* Marsh*Leptochamops denticulatus* (Gilmore)*Haptosphenus placodon* Estes*Peneteius aquilonius* Estes

## Family Scincidae?

*Contogenys sloani* Estes

## SUBORDER ANGUIMORPHA

## Infraorder Diploglossa

## Family Xenosauridae

*Exostinus lancensis* Gilmore

## Family Anguidae

*Pancelosaurus piger* (Gilmore)

## Family Parasaniwidae

*Parasaniwa wyomingensis* Gilmore*Paraderma bogerti* EstesDiploglossa *incertae sedis**Colpodontosaurus cracens* Estes

## Infraorder Platynota

## Family Varanidae

*Palaeosaniwa*, cf. *P. canadensis* GilmoreSauria? *incertae sedis*Family *incertae sedis**Cuttysarkus mcnellyi* Estes



## ORDER SERPENTES

## Superfamily Booidea

## Family Aniliidae

*Coniophis precedens* Marsh

## Family Boidae

unidentified genus and species

## ORDER CROCODILIA

## SUBORDER EUSUCHIA

## Family Crocodilidae

## Subfamily Crocodilinae

*Leidyosuchus sternbergi* Gilmore*Thoracosaurus neocesariensis* (DeKay) [SW $\frac{1}{4}$   
Sect. 28, T24N, R44E]

## Subfamily Alligatorinae

*Brachychampsia montana* Gilmore

## ORDER SAURISCHIA

## SUBORDER THEROPODA

## INFRAORDER COELUROSAURIA

## Family Coeluridae?

unidentified genus and species

*Paronychodon lacustris* CopeTHEROPODA? *incertae sedis*

undescribed genus and species

## INFRAORDER DEINONYCHOSAURIA

## Family Dromaeosauridae?

unidentified genus and species

## INFRAORDER CARNOSAURIA

## Family Tyrannosauridae

*Gorgosaurus lancensis* Gilmore? [Bug Creek West;  
Harbicht Hill]*Tyrannosaurus rex* Osborn [NE $\frac{1}{4}$  Sect. 7, T22N,  
R43E]

## ORDER ORNITHISCHIA

## SUBORDER ORNITHOPODA

## Family Hypsilophodontidae

*Thescelosaurus neglectus* Gilmore

## Family Pachycephalosauridae?

unidentified genus and species

## Family Hadrosauridae

*Anatosaurus copei* Lull and Wright



SUBORDER CERATOPSIA

Family Ceratopsidae

*Triceratops prorsus* Marsh

CLASS AVES

ORDER CHARADRIIFORMES

Family Cimolopterygidae

*Cimolopteryx* sp.

CLASS MAMMALIA

SUBCLASS ALLOTHERIA

ORDER MULTITUBERCULATA

Superfamily Ptilodontoidea

Family Ectypodidae

*Cimexomys minor* Sloan and Van Valen

*Mesodma formosa* (Marsh)

*Mesodma thompsoni* Clemens

Family Ptilodontidae

*Cimolodon nitidus* Marsh

*Essonodon browni* Simpson

Superfamily Taeniolabidoidea

Family Cimolomyidae

*Cimolomys gracilis* Marsh

*Meniscoessus borealis* Simpson

Eucosmodontidae

*Stygimys kuszmauli* Sloan and Van Valen

Family Taeniolabididae

*Catopsalis joyneri* Sloan and Van Valen

SUBCLASS METATHERIA

ORDER MARSUPIALIA

Family Didelphidae

*Didelphodon vorax* Marsh

*Alphadon marshi* Simpson

*A. wilsoni* Lillegraven

*Pediomys elegans* Marsh

*P. krejci* Clemens

*P. hatcheri* (Osborn)

*P. cooki* Clemens

*P. florencae* Clemens

*Glasbius intricatus* Clemens



## SUBCLASS THERIA

## INFRAClass EUTHERIA

## ORDER DELTATHERIDIA

## Family Palaeoryctidae

*Cimolestes incisus* Marsh*C. magnus* Clemens and Russell*Procerberus formicarum* Sloan and Van Valen

## ORDER INSECTIVORA

## Family Leptictidae

*Gypsonictops hypoconus* Simpson*G. illuminatus* Lillegraven?

## ORDER PRIMATES

## Family Paromomyidae

*Purgatorius ceratops* Van Valen and Sloan [Harbicht Hill]

## ORDER CONDYLRARTHRA

## Family Arctocyoniidae

*Protungulatum donnae* Sloan and Van Valen*P. spp.* [Bug Creek West; Harbicht Hill]



## INTERPRETATION OF THE FAUNA

*Introduction*

The Bug Creek Anthills local fauna from the Hell Creek Formation differs only in detail from that of the Lance Formation (Estes, 1964).<sup>1</sup> There are few Lance species that do not also occur in the BCA sample, but the latter includes some additional forms of special interest as well as some significant differences in relative abundance (Table 1) from Lance forms (see also Estes et al., 1969: table 1).

Because time of deposition of the upper parts of both the Lance Formation and the Hell Creek Formation was essentially synchronous, because their lithologies are similar and indicate similar coastal floodplain environments of deposition, because both local faunas bear a similar relationship to late Cretaceous mid-continental seaways, because their vertebrate faunas are very similar, and because the two samples were carefully collected using the same techniques, an unusual opportunity is provided for comparing these samples.

The Bug Creek sample was carefully collected by the use of washing and screening techniques, all fossil material was retained, and an attempt was made to identify each fossil fragment; it was therefore possible to apply the community analysis method devised by Shotwell (1955, 1958). Since only a few aspects of Shotwell's method were applied to the Lance Formation sample by Estes (1964), we have used American Museum of Natural History Lance Formation samples from V5620 and V5711 to make some additional comparisons for this study.

The time spent in sorting and identifying the thousands of specimens used in this study (including collections from all institutions) has been the major factor delaying completion of this series of papers. However, we agree with Shotwell (1963: 9, in reply to Wilson, 1960: 9) that careful sorting, however time-consuming, is a procedure necessary to any quantitative study and that the time involved in this activity is not a valid objection to his method. Shotwell developed his method for analysis of late Cenozoic mammalian faunules; it is our intent to test its utility when applied to late Cretaceous lower vertebrate samples. Voorhies (1969) has offered some cogent criticisms of Shotwell's method. Some of these

<sup>1</sup> Comparisons with the Lance Formation refer only to the two major localities V5620 and V5711 (Clemens, 1963).



TABLE 1

Abundance and completeness of vertebrate remains from Bug Creek Anthills, Hell Creek Formation, Montana, with some comparative figures for V5620, Lance Formation, Wyoming.

	Bug Creek Anthills, Hell Creek Formation <sup>4</sup>				Lance Formation <sup>3</sup>			
	MNI	RA	NS	ENE	CNS	RC	MNI	RA
Lonchidion (C)	1	.2	3	130	2.3	2.3	3	.4
Myledaphus	1	.2	86	400	21.5	7.2	1	.1
Squatirhina	—	—	—	—	—	—	1	.1
Ischyrhiza	—	—	—	—	—	—	1	.1
Acipenser	7	1.0	66	80	82.5	11.8	1	.1
Paleopsephurus (A)	3	.4	8	56	14.3	4.8	1 <sup>2</sup>	.1
“Protamia” (D)	1	.2	1	170	.6	.6	1	.1
Amia	94	13.1	2024	170	1190.6	12.7	103	15.2
Belonostomus (D)	1	.2	1	200	.5	.5	3	.4
Lepisosteus	25	3.5	1790	200	895.0	35.8	7	1.0
Coriops (D)	3	.4	4	200	2.0	.7	22	3.2
cf. Paralbula (D)	1	.2	1	170	.6	.6	—	—
Palaeolabrus	7	1.0	72	200	36.0	5.1	—	—
Elopidae	1	.2	1	170	.6	.6	1	.1
Platacodon (C)	2	.3	8	200	4.0	2.0	42	7.0
Habrosaurus	9	1.3	100	90	111.1	12.4	71	10.5
Opisthotriton	107	14.9	980	90	866.7	8.1	41	6.0
Scapherpeton	61	8.6	744	70	1062.9	17.4	22	3.2

Lisserpeton	72	10.1	275	70	392.9	5.5	1 <sup>2</sup>	.1
Prodesmodon	2	.3	10	75	13.3	6.7	11	1.6
Proamphiuma	2	.3	15	100	15.0	7.5	—	—
Scotiophryne	6	.9	32	60	53.3	8.9	1 <sup>2</sup>	.1
cf. Barbourula	1	.2	1	60	1.7	1.7	1	.1
other frogs (B)	3	.6	8	60	6.6	<7 <sup>1</sup>	12	1.7
Adocus (C)	1	.2	5	190	2.6	2.6	—	—
Basilemys	—	—	—	—	—	—	1	.1
Compsemys (A)	1	.2	17	190	8.9	4.5	1	.1
Trionyx (A)	1	.2	10	190	5.3	5.3	1	.1
Eubaena	3	.4	85	190	44.7	14.9	1	.1
other baenids (E)	4	.6	85	190	44.7	<12 <sup>1</sup>	1	.1
Emydinae (D)	3	.3	5	190	2.6	1.3	1	.1
Brachychampsia (D)	1	.2	150	200	1.4	1.4	1	.1
Leidyosuchus (D)	1	.2	150	200	1.4	1.4	1	.1
Champsosaurus (A)	2	.3	11	130	8.5	4.2	1	.1
dinosaurs (A-D)	7	.2	131	var.	19.3	<4 <sup>1</sup>	8	1.2
Peneteius (D)	1	.2	1	120	.8	.8	—	—
Chamops (C)	3	.4	10	120	8.3	2.8	15	2.2
Meniscognathus	—	—	—	—	—	—	15	2.2
Leptochamops (D)	1	.2	2	120	1.7	1.7	15	2.2
Haptosphenus (D)	1	.2	1	120	.8	.8	2	.3
Contogenys (D)	4	.6	9	130	6.9	1.7	—	—
Sauriscus	—	—	—	—	—	—	4	.6
Exostinus (C)	3	.4	8	130	6.2	2.1	4	.6
cf. Gerrhonotus	—	—	—	—	—	—	2	.3



Bug Creek Anthills, Hell Creek Formation<sup>4</sup>Lance Formation<sup>3</sup>

	MNI	RA	NS	ENE	CNS	RC	MNI	RA
Pancelosaurus	15	2.1	95	130	73.1	4.9	20	2.9
Parasaniwa (C)	1	.2	3	130	2.3	2.3	36	5.2
Paraderma (D)	1	.2	2	130	1.5	1.5	2	.3
Palaeosaniwa (D)	1	.2	2	130	1.5	1.5	1	.1
Colpodontosaurus (D)	3	.4	4	130	3.1	1.0	2	.3
Litakis	—	—	—	—	—	—	1	.1
Cuttysarkus (D)	2	.3	2	130	1.5	.8	13	1.9
Coniophis (B)	1	.2	8	250	3.2	3.2	1	.1
Boidae (D)	1	.2	1	250	.4	.4	—	—
?Pterosauria	—	—	—	—	—	—	1	.1
birds (D)	1	.2	1	150	.7	.7	7	1.0
Mesodma	148	20.4	993	84	1182.1	8.0	55	8.0
Cimexomys (B)	10	1.8	50	84	6.0	1.4	—	—
Cimolodon	P	P	P	P	P	P	23	3.4
Essonodon	P	P	P	P	P	P	—	—
Glasbius	P	P	P	P	P	P	.2	.3
Cimolomys	P	P	P	P	P	P	8	1.2
Meniscoessus (C)	2	.3	4	78	5.1	2.6	11	1.6
Stygimys	28	4.0	224	84	266.7	9.5	—	—
Catopsalis	8	1.1	53	78	68.0	8.5	—	—
Didelphodon (D)	1	.2	2	108	1.9	1.9	6	.9
Alphadon (C)	3	.2	7	108	6.5	2.2	5	.7
Pedionomys	2	.3	16	108	14.8	7.4	51	7.5

Gypsonictops (D)									
Cimolestes	5	.7	7	104	6.7	1.3	14	2.0	
Batodon	P	P	P	P	P	P	5	.5	
Telacodon	—	—	—	—	—	—	1	.1	
Procerberus	—	—	—	—	—	—	1	.1	
Protungulatum	11	1.6	111	104	106.7	9.7	—	—	
Totals	16	2.3	198	104	190.4	11.9	—	—	
	709	100.0	8693				687	100.0	

<sup>1</sup> mean RC per taxon within lumped groups  
<sup>2</sup> additions since Estes (1964: table 5)  
<sup>3</sup> MNI and RA figures were available only for V5620; modified from Estes (1964).  
<sup>4</sup> Only the MCZ sample was used in this calculation

Abbreviations:  
MNI=minimum number of individuals  
RA=relative abundance (% of total MNI)  
NS=number of identified specimens of taxon  
ENE=estimated number of contributing elements possible for each taxon  
CNS=corrected number of specimens  
RC=relative completeness of representation of skeletal elements of each taxon  
—=taxon absent at locality  
P=taxon present at locality but not recovered in sample used  
(A)-(E)=taxa included in groups A-E in Figure 3



are noted below (pp. 21-22) with a discussion of their relevance to our study. Shotwell's terminology is used throughout this paper, and the terms are defined below (pp. 19-20).

### *General Comparisons*

#### Fishes

Excepting *Squatirhina americana*, all Lance Formation sharks are present in the Bug Creek localities, although they are much rarer there. *Ischyrrhiza avonicola* is represented only by a single tooth (from the Harbicht Hill locality), and *Lonchidion selachos* is represented only at Bug Creek Anthills (BCA) and by very few specimens. The best represented elasmobranch present is the ray *Myledaphus bipartitus*; this is perhaps a parallel for the fact that rays and skates are more common today in fresh waters than are other chondrichthyans. The low overall abundance of these forms at Bug Creek Anthills probably indicates a restriction of marine access relative to that of the major Lance Formation localities (Estes, et al., 1969: 28).

Bony fishes are represented by a more complete series of elements at Bug Creek Anthills than in the Lance sample; also, the state of preservation of the bone is generally better and there is less rolled and waterworn material. As a percentage of total *minimum number of individuals*, including mammals (Shotwell, 1955, etc.), bony fishes are less abundant than in the V5620 Lance sample (BCA 20%, Lance 27%). All Lance fishes also occur in the Bug Creek local faunas, and *Protoscaphirhynchus*, *Palaeolabrus* and cf. *Paralbula* are additional bony fish present at Bug Creek. The cf. *Paralbula* specimens do not necessarily indicate proximity of the nearshore marine environments in which this fish is usually found; more probably these few, poorly preserved specimens were transported into the Bug Creek area by some other contemporaneous animal.

In combination, the bony fishes (at least the primitive ones) indicate resemblance to the primitive fish fauna of the Mississippi River drainage today, especially in its lower reaches near the Gulf Coast (Estes, 1964: 166). *Acipenser*, *Polyodon*, *Lepisosteus*, and *Amia* all occur now in that area (See Table p. 23), as well as in the Wyoming and Montana fossil samples.

#### Amphibians

As for the bony fishes, the BCA salamanders show greater diversity than those of the Lance local fauna; all species found in



the latter are present and *Proamphiuma* occurs as well. Skull elements are somewhat better represented than in the Lance sample and most of the salamander bones give less indication of transportation wear. On the other hand, few limb elements of salamanders are found in the Bug Creek localities, in contrast to their relative frequency in the Lance sample. By analogy with Recent salamanders, the neotenic skull elements and vertebral form of the fossil salamanders indicate that all genera were fully aquatic (Estes, 1964), possibly excepting *Prodesmodon*.

In comparing *relative abundance* of Bug Creek species with that from the Lance Formation (Tables 1, 2; Figs. 1, 2), a significant increase for *Lisserpeton* and *Opisthotriton* is apparent, as is an equally significant and much reduced frequency of *Habrosaurus*. Although rarity of *Prodesmodon* makes comparison less meaningful, there seems to be a significant decrease in abundance. *Scapherpeton* shows an increase of a less striking magnitude. The total *relative abundance* (Table 1) of salamanders at Bug Creek Anthills (35.5%) is significantly greater than at V5620 in the Lance Formation (21.4%). The two quarries indicate great similarity in the manner of their deposition and this difference probably has ecological significance, as suggested below.

Sirenid and amphiumid salamanders resembling the fossil forms still live in the southeast United States today, while the Cretaceous frogs indicate relationships to now extinct or relict groups: discoglossids are now Palearctic and Oriental, and the Bug Creek forms show relationship to genera from both of these areas. With the possible exception of the *Alytes*-like form, all Bug Creek

TABLE 2

Comparison of *minimum number of individuals* and *relative abundance* of salamanders in two late Cretaceous localities.

	V-5620, Lance Formation		Bug Creek Anthills, Hell Creek Formation	
	MNI	RA	MNI	RA
Habrosaurus	71	49	9	4
Scapherpeton	22	15	61	24
Lisserpeton	1	1	72	28
Opisthotriton	41	28	107	42
Prodesmodon	11	7	2	1
Proamphiuma	0	0	2	1
	146	100%	253	100%



frogs appear to have been aquatic or semiaquatic, judging from their modern counterparts. The frogs are similar to those from the Lance Formation in being primarily discoglossid and in having genera in common (cf. *Barbourula*, *Scotiophryne*, *Eopelobates?* sp.).

### Turtles

All Lance turtles identified by Estes (1964) are represented at Bug Creek, except that *Adocus* seems to have replaced its close relative *Basilemys*, and undescribed baenid 2 does not occur in the Lance local fauna.

The baenids are the most abundant of the turtles; unfortunately they have no modern relatives and their ecological requirements are unknown. Both the baenids and the emydine-like testudinid were probably amphibious-aquatic types.

The other turtles are fragmentary and poorly represented. The trionychid material indicates permanent waters, either large rivers or streams, or large quiet bodies of water with soft mud or sandy bottoms.

### Champsosaurs

Champsosaurs were aquatic, fish-eating reptiles that perhaps filled niches analogous to those of the Recent garpike or the gavial.

### Lizards

Diversity of the lizard fauna from the Bug Creek Anthills locality is about the same as in the Lance Formation. The Lance forms *Meniscognathus*, *Litakis*, cf. *Gerrhonotus*, and *Sauriscus* do not occur, but these genera are very rare in the Lance Formation localities. In comparison with the latter, *relative abundance* of lizards at Bug Creek is strikingly reduced and the material is poorly preserved. *Contogenys* replaces *Sauriscus* as the scincoid in the fauna, and the highly specialized teiid *Peneteius* makes its first appearance. Only the anguid *Pancelosaurus* (Meszoely, 1970) is as abundant as it was in the Lance sample (approximately 2-3% of total individuals represented in the sample), suggesting that it may have been amphibious or aquatic.

### Snakes

The oldest known North American snake, *Coniophis* (Lance Formation, Wyoming), occurs in a number of other North American Upper Cretaceous, Paleocene, and Eocene deposits. With



the exception of *Helagras* from the Puerco and Torrejon Formations, no other fossil snake has been known to occur in North America until the Eocene.

The presence of a boid snake at Bug Creek Anthills is indicated by a single vertebra. This snake may have been related to the burrowing (or cryptic) Oligocene to Recent subfamily Erycinae.

### Crocodylians

Presence of both crocodiles and alligators in the Bug Creek local fauna recalls the situation in subtropical Florida today, in which both *Alligator* and *Crocodylus* are represented. Jepsen (1963: 680) has suggested that crocodylians occupied ecological niches in the past that are filled today by large terrestrial mammalian carnivores. Analysis of stomach contents of Recent crocodylians (Kellogg, 1929) reveals that only about 6% of their food is mammalian. If Kellogg's study can be used as a criterion, it is likely that, as today, mammals did not form a significant part of the diet of crocodylians in the past. Since the primary food of large mammalian carnivores today is other mammals, the niche relationships of crocodylians and large terrestrial mammalian carnivores are not necessarily comparable. Assuming the food habits of crocodylians to be conservative, it would be more logical to assume that large mammalian carnivores (themselves preying on mammals) evolved with their prey. This assumption can be correlated with, and receives support from, the late Cretaceous and early Cenozoic appearance of the significant predators of mammals: snakes, large varanid lizards, some birds, and of course, the carnivorous mammals themselves.

### Dinosaurs

Although similar in diversity to those from the Lance Formation, the dinosaurs at BCA are represented by a lower *relative weight* of specimens (see below, and Table 4). *Tyrannosaurus* is not present at BCA, and has not been found in the upper 100 feet of the Hell Creek Formation. We have used the name *Gorgosaurus* rather than *Dryptosaurus* here (*cf.* Estes, 1964) although firm generic identification cannot be made on the basis of isolated teeth. Sloan (1969, pers. comm.) states that all Hell Creek Formation ceratopsians are referable to *Triceratops prorsus*, and all hadrosaurians to *Anatosaurus copei*.



*Methods of Analysis*

Paleoecological analysis of any large sample of a diverse fossil vertebrate assemblage may yield useful information about past inter- and intra-community relationships, and contribute to an understanding of community development through geologic time. Such analysis must take into consideration factors that elucidate taphonomic changes (Olson, 1966) between the original community structure (life assemblage) and the death assemblage that the fossil sample represents. Some death assemblages preserved in or near their natural habitats (e.g., those of pond deposits), may differ little from their counterparts in life. Most fossil vertebrate deposits, however, result from deposition by moving water and thus may have their original composition modified by a variety of sedimentary, biological, and ecological factors. The weight differences between compact and spongy bone tissues, the size of bony elements, the amount of preservable tissue available in an individual, and the relative fragility of the skeletal tissues may interact with current speed to modify the original composition of the life assemblage. Sedimentary sorting may thus produce a sample radically different from the original life composition. Proximity of the life zone of the animals to the eventual area of deposition of the fossils is also a factor modifying the assemblage, and, as Olson points out, deposits formed by moving water may "tap a variety of life zone along the course of the stream and its tributaries."

Shotwell (1955, 1958, 1963) devised a quantitative method by which environmental reconstruction of some late Cenozoic mammal communities could be made. Many late Cenozoic vertebrate fossil samples are predominantly mammalian. This is the result of collecting bias in some samples, but other factors may apply. For instance, deossification has progressed through time in many lower vertebrates, resulting in fewer, more delicate bony elements in their descendants. Also, the relatively coarse sediments in which many late Cenozoic vertebrate samples occur imply rapid currents of deposition and a high rate of erosion of delicate elements.<sup>1</sup> Another factor is ecological; temperature and humidity have decreased in North America and Europe since the middle

<sup>1</sup> Bulk collecting methods may produce a large lower vertebrate fauna; thus Wilson (1968) collected a Pliocene fauna with 39 lower vertebrate and 34 mammalian species. Also, Shotwell (1969, *in litt.*) indicates that his recently collected samples "are primarily lower vertebrates, at least those occurring in fine-grained sediments [emphasis supplied]."



Cenozoic, and areas that were once humid, subtropical, and tropical are now temperate and more arid. Many lower vertebrates have retreated south in response to these changes, remaining with their temperature optima and evolving quite slowly or becoming extinct; many temperate niches thus became available for capture by the rapidly evolving mammals.

The community analysis method devised by Shotwell (1955) is summarized in his 1958 article. We will not recapitulate his method or findings here, but the major precepts of his analysis will, we hope, emerge in context below.

The first parameter obtained from a community analysis utilizing the Shotwell method is the *minimum number of individuals* (hereafter referred to as MNI). The MNI itself, reflecting the fewest number of individuals required to produce the fossil elements, is a rough indication of abundance, but it is more useful as a percent of the total MNI of the sample: this is the *relative abundance* (RA). The relative abundance alone is a ready means of comparison of samples, and one that is not difficult to calculate; Estes (1964) used it to show the constancy of vertebrate abundance in numerous Lance Formation localities. Wilson (1960: 9) suggested that a percentage "derived from numbers of specimens, with perhaps some subjective adjustment for other considerations" could be as useful as Shotwell's method. To us, percentages calculated from the actual numbers of individuals present have a clear biological advantage over those derived merely from numbers of specimens, especially for lower vertebrates. Bones of the latter are often common, particularly if an extensive dermal skeleton is present. Sedimentary or erosional factors, such as those operating postdepositionally in "blowout" accumulations, may selectively act on bones, and the number of elements, especially resistant ones, is thus much less likely to reflect actual abundance. Nevertheless, "accuracy" of the Shotwell or the Wilson method is not demonstrable for a fossil sample. Confidence in either method can only be *suggested* by the use of theoretical models or collection of material from modern sediments and comparison with existing abundance; these data are, in general, difficult to obtain and not yet available (Van Valen, 1964: 109).

As Shotwell has pointed out (1955: 331) different mammal groups vary widely in the number of elements that can be contributed by one individual. This difficulty is magnified when lower vertebrates are considered. Some species are wholly or in part cartilaginous or show strong ontogenetic variation in ossification. Others may enrich the sample (and perhaps give a false impression of abundance) by contributing mainly shed teeth from



an essentially continuous replacement process. In addition, because of the great antiquity of the fauna, some animals may contribute more bones than their Recent relatives because of decrease of ossification in, and loss of elements by, the modern forms. Therefore Shotwell's *corrected number of specimens* (CNS) (see below), a correction necessary because of group variation, is almost certainly a more variable factor as we have used it than it is for late Cenozoic mammals. We have given the *estimated number of contributing elements* (ENE) for the various taxa, basing it on the number of preservable, identifiable bones in modern relatives or in known complete fossil material. These estimates are necessarily approximations but are probably correct within the context used here. When Shotwell (1958: 273) made corrections in his 1955 figures, he noted that "the results are little different from those presented earlier," and we have made calculations with similar results. The estimates vary from animal to animal for reasons noted at the beginning of this section. Thus for the ray *Myledaphus* we include a figure only for teeth and precaudal vertebral column as the only recognizable, preservable structures, yet even this figure approaches five hundred, whereas for mammals, in which most bones are identifiable, the total figure is only about one hundred and ninety.

The total number of specimens for the species (NS) and the estimated number of elements (ENE) yields a *corrected number of specimens* (CNS) when formed as a ratio:

$$\text{CNS} = \frac{\text{number of specimens} \times 100}{\text{estimated number of elements}}$$

(Shotwell, 1958: 272-273). The *relative completeness* (RC) for each species is then determined according to Shotwell (1955: 332). This is the corrected number of elements for *each individual*:

$$\text{RC} = \frac{\text{CNS}}{\text{MNI}}$$

The RC is the parameter that is used to determine the closeness of an animal to the site of deposition and thus can be used as a measure of whether the animal belongs to a "proximal" or "distal" community (Shotwell, 1955: 330). In a wind-deflation locality ("blowout") the RC is less valid because erosion causes delicate elements to become unrecognizable in a short period of time. In such blowouts, the RC may become a measure of animals possessing the most numerous durable elements (Estes, 1964: 151-152). This is not the case with Bug Creek Anthills, however, which is a quarry.



Table 1 gives MNI, RA, NS, ENE, CNS, and RC for each species identified in the MCZ sample from Bug Creek Anthills; MNI and RA from Lance locality V5620 are included for comparison. A few rare taxa are not included since they were not recovered in the MCZ sample (*cf.* pp. 3-8).

Finally, it is necessary to discuss the criticisms of Shotwell's method offered by Voorhies (1969), in order to justify our use of it here. Voorhies discussed taphonomic processes that produced an accumulation of Pliocene vertebrate fossils in Nebraska, and emphasized the lack of sedimentary data used by Shotwell in his analysis. Shotwell assumed that attritional mortality produced the quarry accumulations in Oregon on which he developed his method; he could thereby interpret the minimum numbers of individuals as being representative of actual abundance in the Pliocene. Voorhies, on the other hand, suggested (1969: 54) that stream sorting of bones caused many of the differences between quarries that Shotwell ascribed to community differences. The fact that the Pliocene quarry accumulation in Nebraska was the result of mass mortality (probably winterkill) seems to have generated many of Voorhies' criticisms of Shotwell's method.

In spite of this and other objections raised by Voorhies, we feel that the minimum number of individuals recovered at Bug Creek Anthills and at the Lance Formation localities is, in general, representative of former life abundance. Our reasons for this belief are listed below but are specific to the localities studied here; each fossil accumulation must be judged separately. Techniques such as those proposed by Shotwell must be applied to a variety of fossil accumulations of diverse ages before the overall utility of the method for environmental reconstruction can be determined.

1. Estes (1964: 151-158) demonstrated the essentially uniform relative abundance of individuals in Lance Formation localities, and Estes et al. (1969; this paper, pp. 10-13) have shown that Lance relative abundance is similar to that at Bug Creek Anthills. In addition, the large BCA collections in various museums do not differ materially in relative abundance *inter se*.
2. The Lance and Hell Creek samples are composed of relatively small animals, in contrast to those studied by Voorhies and Shotwell. The common animals in the Cretaceous samples are represented by almost all of the principal skeletal elements. Although sedimentary sorting has modified relative numbers of some bones, their varied shapes and



sizes seem to indicate that sedimentary factors have not been the only influence on accumulation. With rare exceptions, selective preservation of uniform, durable elements (Estes, 1964: 157) does not appear to have modified relative abundance significantly either at V5620 or at BCA.

3. Abrasion of bony elements of members of the aquatic "proximal community" is significantly less than that for members of the various "distal communities." As in Voorhies' sample (1969: 57), a range of fresh and abraded examples of each bone can be demonstrated at BCA, reflecting, probably, contemporaneous reworking of channel deposits as noted by Estes (1964: 159) for the Lance Formation sample.
4. Bones of larger animals such as crocodilians, large turtles, and dinosaurs are reduced in numbers by sedimentary phenomena at BCA; the slow current speeds failed to transport the large bones. Except for baenid turtles, however, all BCA material of these groups is more abraded and fragmented than that from Lance Creek, where a similar paucity of large elements also occurred. This is one factor leading us to suggest that BCA was deposited farther from a riparian habitat than was V5620.
5. While larvae or young are poorly represented at both Lance and Bug Creek localities, a wide range of body size does occur. The greater number of small rather than of large individuals of many common species seems to indicate a natural proportion rather than a sedimentary reworking, since element size of small individuals is well below the median specimen size.
6. The large size of both Lance and Hell Creek samples reinforces the above conclusions.

Admittedly the above factors are subjective or hard to quantify. Nevertheless, they seem to suggest that attritional rather than mass mortality was operating to produce the Lance and Hell Creek samples, and that the relative abundance of fossils can be assumed to bear a reasonably close relationship to actual life abundance.

#### *Completeness of the Sample*

Shotwell (1955: 329) compared diversity of his Pliocene mammal faunas with that of the Recent fauna of the United States as a whole as well as with average figures for some Recent local faunas.



His comparison indicated a reasonable similarity in diversity and he used this as an indication that his quarry methods had sampled the Pliocene fauna rather well (about 85%, if the comparison is justified), although a better comparison might have been made with a fauna ecologically and climatically more similar to his fossil fauna, perhaps from an area in Africa. Ecological interpretation of the vertebrate fauna from the Lance Formation (Estes, 1964) applies equally well to that from the Hell Creek Formation, with some differences in detail discussed elsewhere in this paper. From both faunal and climatic standpoints, the closest modern analogue of the two fossil faunas can be found in the lower Mississippi River drainage and in similar areas on the Gulf Coast of the United States. Since the Mississippi drainage is related to the former path of some of the major epicontinental seaways in North America during the Cretaceous, the similarity of the fossil and Recent faunas is not surprising.

TABLE 3

## Generic Diversity of Cretaceous and Recent Faunas\*

	Lance genera	Bug Creek genera	Recent genera
chondrichthyans	4	3	3
chondrosteans	2	3	3
holosteans	4	5	2
teleosteans	3	4	34
(total fishes)	(13)	(15)	(42)
amphibians			
salamanders	5	6	10
frogs	4	4	5
(total amphibians)	(9)	(10)	(15)
reptiles			
turtles	6	7	11
eosuchians	1	1	0
lizards	14	12	5
snakes	1	2	18
crocodilians	2	2	1
dinosaurs	10	8	0
(total reptiles)	(34)	(32)	(35)
birds	5	1	149
mammals	14	16	36
total genera	75	74	277
total genera removing birds	70	73	128

\*The Recent fauna is that of southeastern Louisiana, the delta region of the Mississippi River (Blair, et al., 1968; Lowery, 1960; Bishop, 1947).



Table 3 compares the number of vertebrate genera for the two Cretaceous localities with that for the Recent Mississippi drainage area in southeastern Louisiana. Birds are included, although they must be removed in the final analysis (Shotwell, 1955: 328) in order to make the results more comparable. Table 3 shows several obvious major differences from the modern fauna: (1) relative absence of teleosts, snakes, and birds, (2) presence of dinosaurs, and (3) primitive nature of the mammals. Teleosts present in the modern fauna are mainly Clupeiformes, Cypriniformes, and Perciformes. The former group is not represented at Bug Creek but was common in contemporaneous seas. They would be difficult to recognize on the basis of disarticulated remains and may occasionally have penetrated into the freshwaters of the Cretaceous as they do today. Cypriniformes are not known before the Eocene. Perciformes first occur in the Cretaceous (Estes, 1964; Estes, et al., 1969) but they are not common until the Eocene. Relative lack of diversity of these two orders in the Cretaceous samples is thus probably in part an evolutionary rather than a sampling phenomenon.

The dinosaurs contribute notably to the Cretaceous fauna but are of course absent from the Recent fauna, where their niches as large herbivores and carnivores have been filled primarily by Artiodactyla and Carnivora.

The relative absence of snakes from the Cretaceous fauna is probably of evolutionary origin; most Recent and Cenozoic snake diversity occurs within the Colubridae, a family not yet known before the Miocene.

Only one bird is known from the Bug Creek Anthills site; Brodkorb (1963) has noted the presence of five genera in the very similar Lance local fauna. Even so, the presence of approximately 150 genera of birds in the Recent fauna of southeastern Louisiana forms the greatest contrast of fossil and Recent faunas. The habits of birds and the delicacy of their bones are probably partial reasons for the relatively small number of known late Cretaceous birds. However, as Brodkorb points out (1963: 70), the known Cretaceous forms (while well-distinguished) indicate that the characters of the modern orders are merging, and again much of this discrepancy between modern and fossil fauna must be an evolutionary one.

The difference in mammalian fauna seems also to be of evolutionary origin, since the Cretaceous fauna belongs to six primitive orders. The overall discrepancies between Recent and fossil groups



are easily seen, and when the difference in evolutionary development in fishes, snakes and birds is taken into account, the fossil sample may represent as much as two-thirds of the vertebrate species that might have lived on the Cretaceous mid-continental floodplain. As Fox (1968) has noted, the diversity known in the fossil habitat does not necessarily reflect the total diversity that was actually present in a group during the late Cretaceous; other habitats not represented in the fossil record undoubtedly included related forms.

### *Relative Weight*

Shotwell (1955, 1958, 1963) did not discuss the possibility of using figures based on weight of fossil specimens. It is clear that the vagaries of preservation and mineralization preclude using weight of fossils as an indication of biomass, however useful this item of information might be. Nevertheless, we have obtained some useful results from carefully qualified use of the relative weight (RW) of specimens for major groups of lower vertebrates and some other fossil material from both Lance and Bug Creek localities (Table 4). Specific gravity of the material and relative size of the animals from both V5620 and BCA are essentially identical; use of weight therefore seems justified.

The information on relative weight that is of particular interest is based on material that cannot be used to express the minimum number of individuals easily (if at all). For instance, floral materials are not common in washed and screened material. Seeds may occur, however, often as durable casts of the inside of the seed coat. In the Lance Formation locality V5620, such seed casts are common and may indicate closeness of that locality to stream-bank or riverbank, a conclusion also supported by the high relative weight of turtle material. Twice as much unidentifiable material occurs at V5711 than at V5620, emphasizing the extent of erosion in a blowout locality. The slightly higher RW of coprolites at V5711 is probably also caused by resistance to erosion of these hard pebblelike objects. At BCA, coprolites are rare, and invertebrates (except for a few traces) absent; this is probably because of deposition of the fossils farther away from the shore.

The abundance of bony fish material at BCA is clearly shown by the weight data. Although the relative abundance of Bug Creek bony fishes is slightly less overall than at Lance localities, the large amount of identifiable, unworn material at BCA makes it clear that this locality was quite close to the natural habitat of



(especially) *Lepisosteus* and *Amia*. Estimated body size of these two common fishes was similar in the two localities, so that this factor does not influence the weight data.

The difference in amount of dinosaur material is quantified by the weight data. Although tooth size of some BCA dinosaurs is slightly smaller than in the Lance localities, the difference is not enough to affect the relative weight significantly. In part, the reduction in RW of dinosaur material at Bug Creek, when compared to that of the Lance localities, may represent reduced frequency of dinosaurs in the presumed deeper, more open channels represented in this area of Hell Creek deposition. Nevertheless, the reduction in numbers of dinosaur individuals in the late Cretaceous that accompanied their eventual extinction probably was the most important factor in reduction of the relative weight of dinosaur fossils.

TABLE 4

Comparison of Relative Abundance by Weight of Major Groups in Lance Formation (Wyoming: UC Localities V5711 and V5620, AM Coll.) and Hell Creek Formation (Montana; Bug Creek Anthills, MCZ Collection)

	<i>V5711</i>	<i>V5620</i>	<i>Bug Creek</i> <i>Anthills</i>
	<i>Relative</i>	<i>Relative</i>	<i>Relative</i>
	<i>Abundance</i>	<i>Abundance</i>	<i>Abundance</i>
	<i>by weight (%)</i>	<i>by weight (%)</i>	<i>by weight (%)</i>
sharks	0.25%	0.64%	0.13%
bony fishes	4.10	6.33	39.35
salamanders	1.22	1.58	3.80
frogs	0.01	0.04	0.07
turtles	8.23	35.56	8.12
crocodiles	3.53	6.79	3.32
dinosaurs	10.90	14.56	0.70
snakes	0.01	0.00	0.01
lizards	0.18	0.04	0.46
other groups	0.05	0.90	5.58
unidentifiable material	69.61	30.24	38.60
invertebrates	0.38	0.90	0.00
coprolites	1.16	0.94	0.23
seeds	0.00	1.51	0.01
	<hr/>	<hr/>	<hr/>
	99.02%	100.03%	100.68%

Note: Calculations do not include mammals or gar scales because no weight figures were available for the Lance material.



Community Analysis  
Relative Abundance

Figures 1 and 2 and Table 5 express the relative abundance (RA) of dominant genera and major groups at BCA and Lance locality V5620.

The faunal analysis diagrams (Figs. 1, 2) also include mammals, and indicate that the increased diversity of the latter at BCA in comparison with that at V5620 is accompanied by an increased relative abundance as well: RA at V5620 = 26% ; RA at BCA = 33% . Lower vertebrates show greater abundance of some species at BCA than at V5620 (Fig. 1). *Amia*, *Scapherpeton*, *Opisthotriton*, *Lisserpeton*, and *Pancelosaurus* together account for about 50% of the MNI at BCA; the same taxa form only 27% at V5620. In the major groups (Fig. 2), bony fishes and salamanders account for about 50% of the MNI in both localities with mammals and lizards comprising about 45% of the remainder. At BCA, the relative proportions of these four groups are different from those at V5620: salamanders and mammals (rather than fishes and lizards) are the dominant groups, totaling about 65% of the MNI. There is a substantial complementary reduction in lizards, and (to lesser degree) fishes, from V5620 to BCA.

TABLE 5

Relative Abundance of Major Groups of Lower Vertebrates in Three Late Cretaceous Localities

	<i>Lance Formation</i>		<i>Hell Creek Formation</i>
	<i>V5620</i>	<i>V5711</i>	<i>Bug Creek Anthills</i>
sharks	2	1	1
bony fishes	38	25	30
salamanders	30	49	52
frogs	3	1	2
turtles	1	1	3
lizards	23	21	8
dinosaurs	2	1	2
other	1	1	2
	100%	100%	100%

These overall differences have some ecological significance, we believe. As Estes et al. (1969) note, the Bug Creek Anthills fossils indicate deposition in more open waterways, more lowland



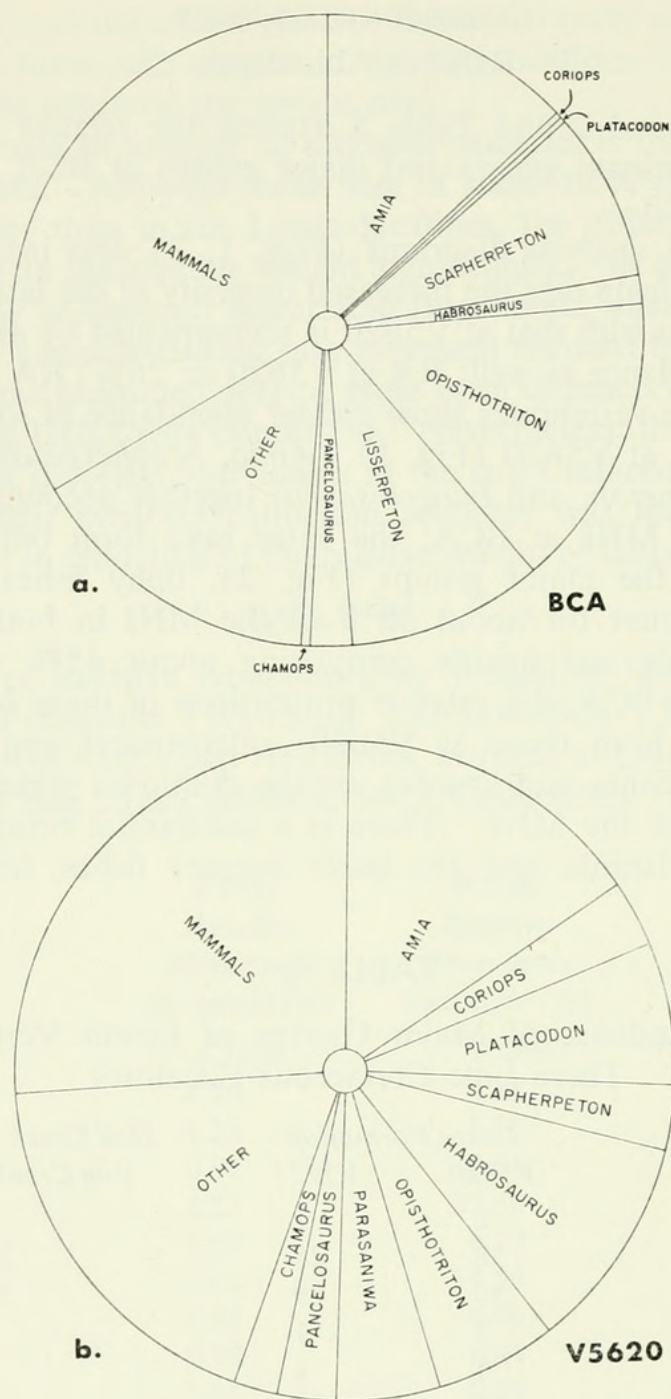


Figure 1. Relative abundance of dominant lower vertebrate genera in two late Cretaceous localities: *a*, Bug Creek Anthills; *b*, Lance locality V5620.



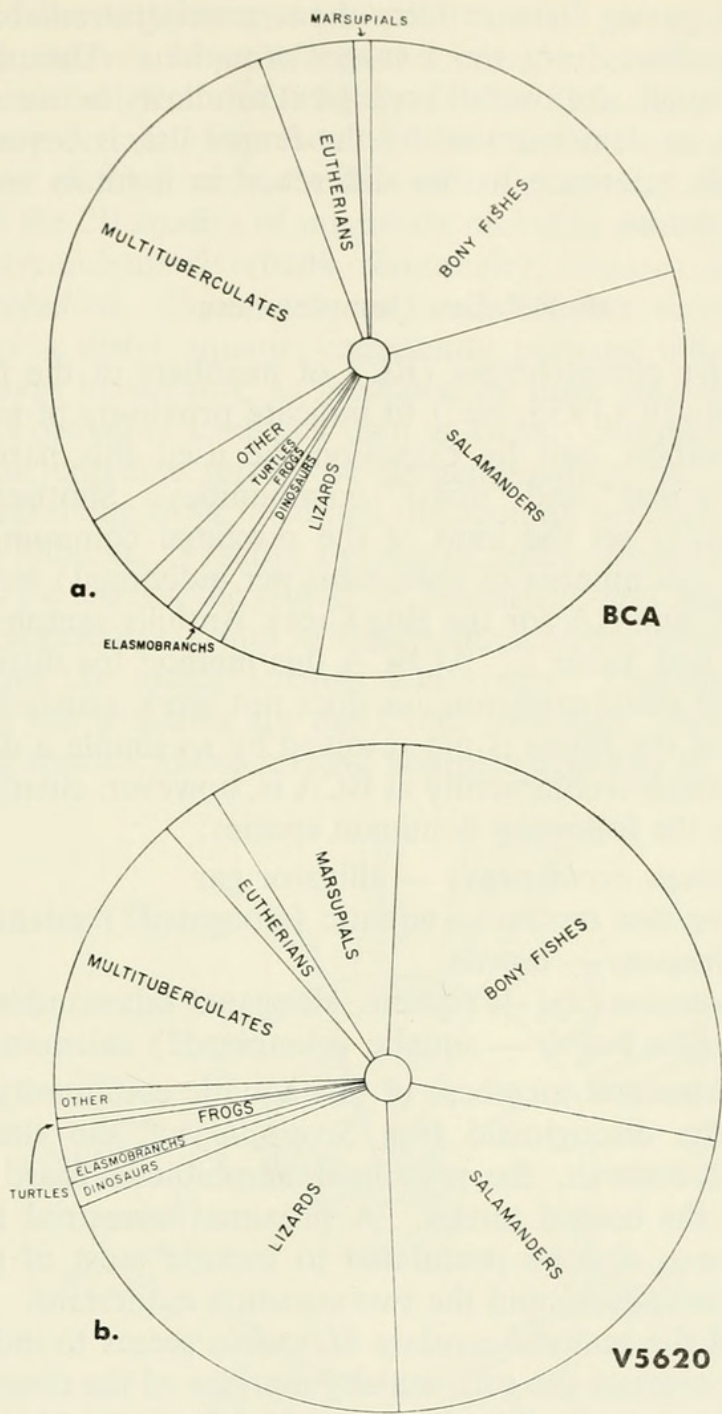


Figure 2. Relative abundance of major groups of vertebrates in two late Cretaceous localities: a, Bug Creek Anthills; b, Lance locality V5620.



habitat, and greater distance from the terrestrial, streambank habitat than do those from the Lance Formation. This difference, however, is small; the overall ecological similarity between the two local faunas, as demonstrated by the faunal list, is beyond doubt. More specific reference to the difference in habitats represented will appear below.

### Relative Completeness

The relative completeness (RC) of members of the fauna was used by Shotwell (1955, etc.) to indicate proximity of taxa to the site of deposition, and by extension, he used this parameter to delimit "proximal" and "distal" communities. Shotwell (1955: 332) arbitrarily set the limit of the proximal community at the average RC (= number of specimens per individual) for the total sample. RC and RA for the Bug Creek Anthills sample is shown in Figure 3 and Table 1. At BCA this method for distinguishing proximal and distal communities does not work satisfactorily; the complexity of the fauna is not resolved by so simple a distinction. The most proximal community at BCA is, however, clearly aquatic, and includes the following dominant species:

*Lepisosteus occidentalis* — alligator gar

*Scapherpeton tectum* — aquatic (elongated?) salamander

*Amia fragosa* — bowfin

*Opisthotriton kayi* — aquatic, elongated salamander

*Lisserpeton bairdi* — aquatic (elongated?) salamander

Other, less common members of this aquatic community included sturgeons, the discoglossid frog *Scotiophryne*, the sirenid salamander *Habrosaurus*, the presumed amphibious lizard *Pancalosaurus*, and the baenid turtles. A proximal terrestrial (riparian) community can also be postulated to include most of the multituberculate mammals, and the two common eutherians. The high frequency of the multituberculate *Mesodma* seems to indicate that it may have overrun the soft, marshy margins of the rivers as small rodents and some other small mammals do today. *Mesodma* and the other multituberculates seem, from their dentition, to have been seed or seed-coat eaters. The primitive ungulate *Protungulatum* was probably also herbivorous, adapted for browsing on marshy vegetation. Some of the mammals may have been amphibious, as occurs today in marshy habitats in various parts of the world.

Of the total of approximately 78 species, 42 belong to the "distal community" as delimited by Shotwell's method. Considerable



taxonomic diversity occurs among the “distal” group; sharks, bony fishes, salamanders, frogs, lizards, dinosaurs, crocodilians, birds and mammals are all included. Many (rather than one) distal communities are certainly represented, some aquatic and some terrestrial. Most of the lizards, the dinosaurs (excepting *Anatosaurus*), and 13 of the 20 species of mammals probably were part of a terrestrial, streambank-riverbank community; *Coriops* and *Platacodon*, *Lonchidion*, *Champsosaurus*, and *Trionyx* seem to be the nucleus of a distal aquatic community perhaps inhabiting local ponded areas in streams, as indicated by their greater abundance in Lance Formation localities than at BCA. Amphibious species such as the emydine turtle, the dermatemydids, the crocodilians, and the remaining frogs inhabited the ecotone between aquatic and terrestrial habitats. Finally, a group of fishes of essentially marine affinities (the sharks, the elopid, cf. *Paralbula*, and *Belonostomus*) seem to represent a group of diadromous forms occasionally migrating into the major streams and rivers. Unfortunately, RC figures are not available for the Lance localities. Nevertheless, a few Lance species whose relative completeness can be subjectively

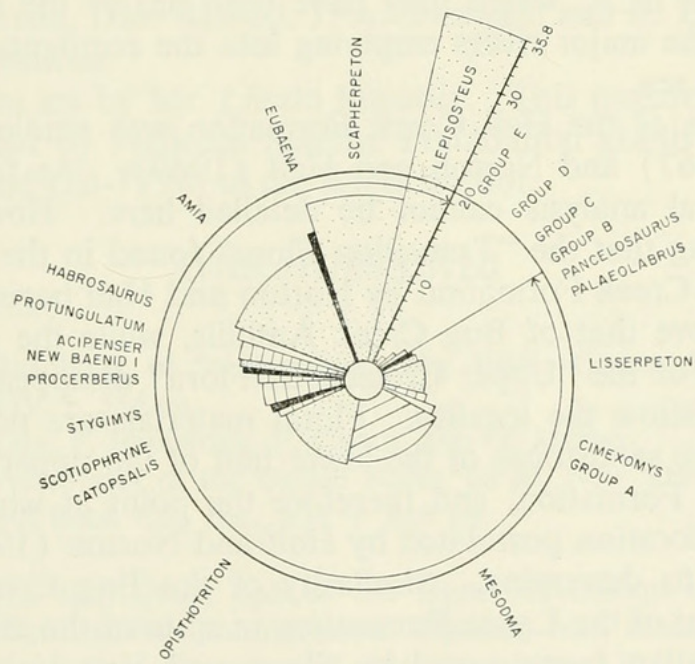


Figure 3. Relative completeness and relative abundance of vertebrates from Bug Creek Anthills. RC is given along the radius; RA in degrees of arc. The “proximal community” as indicated by the average RC ( $= 4.9$ ) is delimited by the arrowed circumferential line. Members of groups A - E are indicated by letters in parentheses following the name of taxa in Table 1.



estimated reinforce some of the above conclusions. These include *Coriops*, *Platacodon*, and *Habrosaurus*; their apparently greater RC at V5620 than at BCA tends to confirm our suggestion (based essentially on relative abundance) that they were stream-dwellers rather than river-dwellers.

Some substantiation for the postulated habitat differences between BCA and V5620 comes from the nature of the sediments themselves. While we cannot treat this subject in detail here, the relatively greater amount of clay-sized material in the sandstone at BCA indicates more sluggish waters and deposition nearer the open areas of the waterways than was the case at V5620, where sandy streambanks appear to have been the site of deposition of the fossils.

Among recent ecological situations, Lance locality V5620 probably represents a wooded swamp habitat, with small to medium-sized watercourses and some ponding. The equivalent for Bug Creek Anthills, however, seems to be a major waterway issuing from such a wooded swamp: similar habitats were available in or near both localities, but terrestrial and riparian habitats were restricted at BCA, which may have been nearer the delta region of one of the major rivers emptying into the remnants of the late Cretaceous sea.

The flora of the Hell Creek Formation was studied by Shoemaker (1967) and Norton and Hall (1969). As for the sediments, floral analysis cannot be detailed here. However, it is worth noting that the "Transition Flora" found in the upper part of the Hell Creek Formation by Norton and Hall begins at a level slightly above that of Bug Creek Anthills, while the majority of the species of the "Upper Cretaceous Flora" disappear at a level somewhat below the locality. Floral materials are poorly represented in the sandstones of the lower half of the upper part of the Hell Creek Formation, and therefore the point at which the climatic deterioration postulated by Hall and Norton (1969) begins is difficult to determine. Similarity of the Bug Creek Anthills fauna to that of the Lance Formation, in spite of the differences in the mammalian fauna noted by Sloan and Van Valen (1965), seems to indicate that a subtropical climate (as for the Lance Formation) still prevailed in this area of Montana in Bug Creek Anthills time.



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