ANALYSIS OF FOSSIL SALAMANDERS FROM CHEEK BEND CAVE, MAURY COUNTY, TENNESSEE

A Thesis

by

MACK DAVIS MILLER, JR.

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ABSTRACT

ANALYSIS OF FOSSIL SALAMANDERS FROM CHEEK BEND CAVE, MAURY COUNTY, TENNESSEE

(December 1992)

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In 1978 archaeological field parties from the University of Tennessee at Knoxville discovered a concentration of late Pleistocene-Holocene fossils in Cheek Bend Cave, central Tennessee. The earliest stratum was deposited approximately 16,000 YBP. Subsequent strata span the Pleistocene-Holocene transition. The matrix in the twilight area of the cave contained tens of thousands of faunal remains, consisting mostly of bats and insectivores (Klippel and Parmalee, 1982a). Nearly 2,000 salamander fossils comprised part of the herpetological component.

The salamander remains were sent to Appalachian State University where, after a few preliminary identifications made by Dr. R. W. Van Devender in 1979, detailed analysis was initiated by this author in 1988. Identification was achieved by comparing fossils to reference skeletons housed at Appalachian State University. Identified fossil species include: Ambystoma maculatum, Ambystoma tigrinum, Cryptobranchus alleganiensis, Eurycea cf. bislineata, Eurycea longicauda, Eurycea lucifuga, Necturus cf. maculosus, Notophthalmus viridescens, Plethodon dorsalis, and Plethodon glutinosus. All of these species are extant in central Tennessee.

With 1,749 identified skeletal elements, this collection represents the largest reported quantity of non-contemporaneous salamander fossils from any geologic period. Eurycea cf. bislineata and possibly Eurycea lucifuga were reported as fossils for the first time in both late Pleistocene and Holocene strata. Two morphological variations of Eurycea lucifuga vertebrae were noted in fossils and reference vertebrae. Large Ambystoma tigrinum vertebrae and leg bones that rival the largest living specimens (approximately 150mm SVL) were identified from early Holocene strata. Two fully aquatic species, Cryptobranchus alleganiensis and Necturus cf. maculosus, were interpreted as possible prey items. All other salamanders were probably resident.

ACKNOWLEDGEMENTS

Many thanks to the Department of Anthropology at the University of Tennessee at Knoxville for the loan of the Cheek Bend Cave salamander fossils and to Wayne Van Devender for allowing me to take on this project. I am also indebted to Ruth Dewel for many helpful suggestions and for patient assistance in producing my scanning electron micrographs. All other photographs were expertly taken by Wayne Van Devender. Credit for the artful modification of Figure 3 goes to Patrick Cook and his Macintosh computer. Thanks also to Ken McKinney, Richard Henson, Jeff Butts, Judy Williamsen, Debbie Macey, and Ruth Cook for calm patience, resourcefulness, and witty humor.

Computer time was provided by the Appalachian State University Department of Biology. Text and plates were printed by the Medical Center Print Shop at Wake Forest University. Financial support was provided by Appalachian State University.

DEDICATION

This work is dedicated to my parents, Mack and Barbara Miller, and to my grandparents Buren and Edith Ledford, and Rochelle Miller. Your love and support made this possible.

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INTRODUCTION

In 1978 archaeologists from the University of Tennesse at Knoxville discovered a late Pleistocene-Holocene [approximately 16,000 YBP (Years Before Present) to Modern] fossil bearing deposit in Cheek Bend Cave (CBC), Maury County, Tennessee. This deposit yielded some aboriginal artifacts and thousands of vertebrate remains, which were mostly small mammals, birds, fishes, reptiles and amphibians. Insectivores (18,000 bones) and bats (50,000 bones) comprised most of the collection (Klippel and Parmalee, 1982a). Preliminary sorting identified nearly 2,000 fossils as salamanders. This collection apparently represented one of the largest non-contemporaneous salamander paleofaunas to date. The purpose of this thesis was to describe, analyze, and interpret the fossils.

Salamanders are poorly represented in the fossil record [see summaries in Tihen (1968), Estes (1965), and especially Estes (1981)]. Of thirteen recognized caudate families, four are extinct, six are unknown before the Cenozoic, and one has no fossil record (Table 1). Half of the 56 salamander fossil genera are referable to living

TABLE 1. Known geological ranges of the salamander families (Estes, 1981).
--> = extant, X = extinct, Jura = Jurassic (190 to 136 Million Years Ago), Cret = Cretaceous (136 to 65 MYA), Pal = Paleocene (65 to 54 MYA), Eocene (54 to 37.5 MYA), Olig = Oligocene (37.5 to 26 MYA), Mio = Miocene (26 to 5 MYA), Plio = Pliocene (5 to 1.8 MYA), Pleist = Pleistocene (1.8 MYA to 12,000 YA).

```
                                                Time Period
   Family              Jura   Cret   Pal   Eocene   Olig   Mioc   Plio   Pleist   Hol
Ambystomatidae                                      --------------------------------->
Amphiumidae                    ---------------------------------------------------->
Batrachosauroididae            ------------------------------------X
Cryptobranchidae                      ---------------------------------------------->
Dicamptodontidae                      ---------------------------------------------->
Hynobiidae
Karauridae              --X
Plethodontidae                                             ------------------------->
Prosirenidae            ------------------------------------X
Proteidae                             ---------------------------------------------->
Salamandridae                         ---------------------------------------------->
Scapherpetontidae              -----------------------------------X
Sirenidae                             ---------------------------------------------->
```

living genera, but only a small percentage of living species are known as fossils (Estes, 1981). Furthermore, most fossil species are from Quaternary deposits. Not surprisingly, the salamander fossil record gives very little direct evidence concerning the evolution of this group (Tihen, 1968).

Salamander bones are often small and fragile, with low preservation and recovery potentials. Such small bones are easily crushed, scattered, and dissolved in acidic situations. Paleontologists and zooarchaeologists may tend to overlook and/or undersample salamander bones if they use mesh sizes larger than 1/8 inch when sifting through matrix for fossils.

The relative simplicity of salamander bones can make identification of fragmented fossils a frustrating task. Accurate identification is possible only after careful comparison with an extensive collection of salamander skeletons. Even under the best of circumstances, it is sometimes difficult to discover reliable characters differentiating some species. No keys are available for identification of salamander fossils, but several useful works include a comprehensive treatment of skeletal anatomy of a European salamander (Francis, 1934) and a more modern comprehensive account by Duellman and Trueb (1986). Excellent drawings accompany text in both works. Although lacking illustrations, Wake's (1966) comparative analysis of plethodontid osteology is an excellent source of detailed characters for differentiating genera of this large family. Wake (1963) provides a more thorough account of comparative osteology in three closely related genera: Aneides, Plethodon, and Ensatina. Tihen (1958) reports that several vertebral ratios (ie. centrum length divided by anterior centrum width) are helpful in identifying ambystomatid vertebrae to subfamily levels (ie. Ambystoma maculatum group). However, Davis (1973) suggests that these ratios should be re-examined and probably revised. Spinal nerve exiting patterns can sometimes be useful for identification of vertebrae at the family level and are summarized by Edwards (1976).

Although paleoherpetofaunal analyses usually include descriptions of fossil elements, most descriptions are vague, inadequately illustrated, and lack the criteria necessary for systematic identification. Estes (1981) provides a comprehensive compilation of salamander fossils reported through 1980. This work has numerous helpful illustrations, but it is of limited value for fossil identification below genus level. Most salamander paleofaunas seemingly lack diversity, bone quantity, and/or temporal expanse. Most fossil finds include fewer than 50 salamander bones (Estes, 1981) deposited under normal circumstances, such as cave sedimentation over a long period of time. Alternatively, large numbers of individuals may be deposited simultaneously in a drying pond (Tihen, 1942).

The fossils from CBC provide a unique opportunity to add to the quantity and temporal extent of the paleontological record for salamanders in eastern U.S. The primary objectives of this thesis are therefore: 1) to identify CBC salamander fossils by comparing them with skeletons of modern species, 2) to determine temporal distributions for each species and, 3) to relate CBC salamander fossils to other salamander paleofaunas from southeastern North American Quaternary deposits.

MATERIALS AND METHODS

Location

CBC was the largest of three caves situated on a bluff 30-40m above and away from the Duck River in the Nashville Basin, 13km ESE of Columbia, Maury County, Tennessee (Figure 1). The cave had an easily accessable lateral entrance on the bluff facing the river and a smaller vertical sink entrance. The main chambers were connected to a small underground stream via a vertical shaft (Figure 2)(Klippel and Parmalee, 1982b).

Excavation of 40MU261

Field parties from the University of Tennessee at Knoxville dug three 1mx2m excavation units (40MU261) to a depth of 4.5m in the twilight area of the bluff entrance. Matrix from each unit was removed in arbitrary 10cm increments within natural strata and washed through a series of nested screens ranging from 12.5mm at the top to 1.5mm at the bottom. Fossils and other material (flora, artifacts, and unmodified rock) were removed from screens, bagged, and transported to an archaeological field camp near Columbia, Tennessee to be dried and sorted (Klippel

FIGURE 1. Contour map with inset showing location of Cheek Bend Caves (square and arrow).

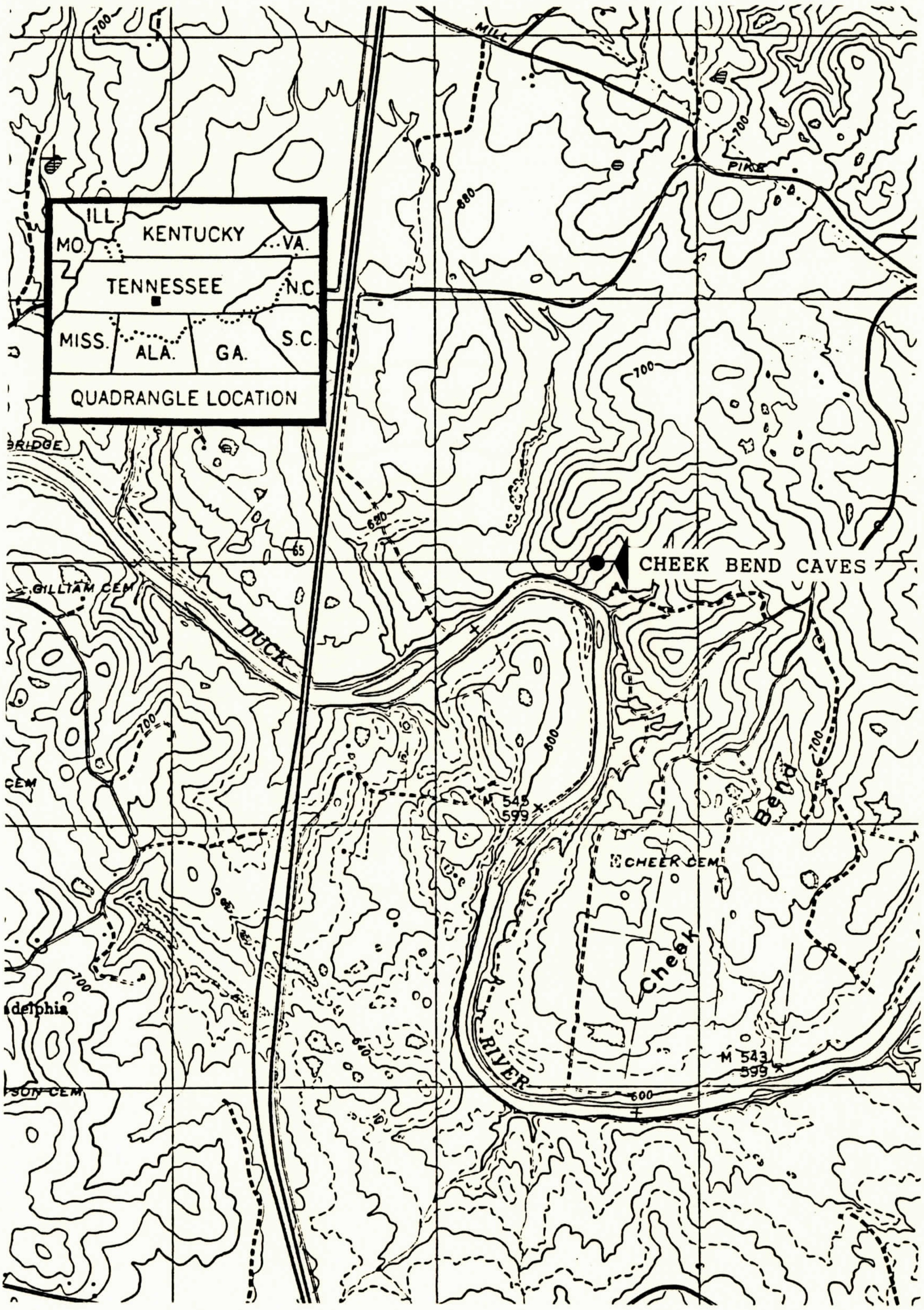
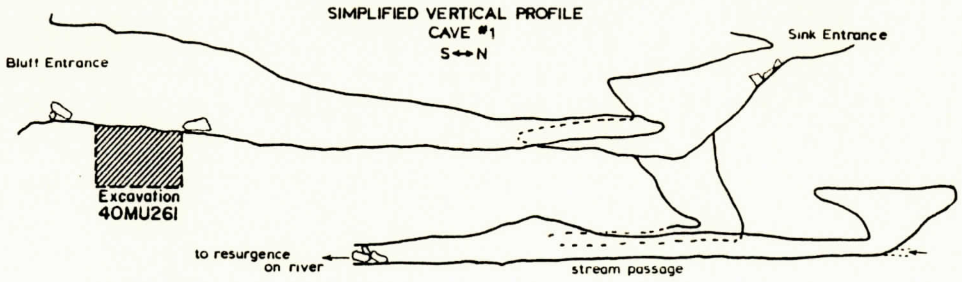
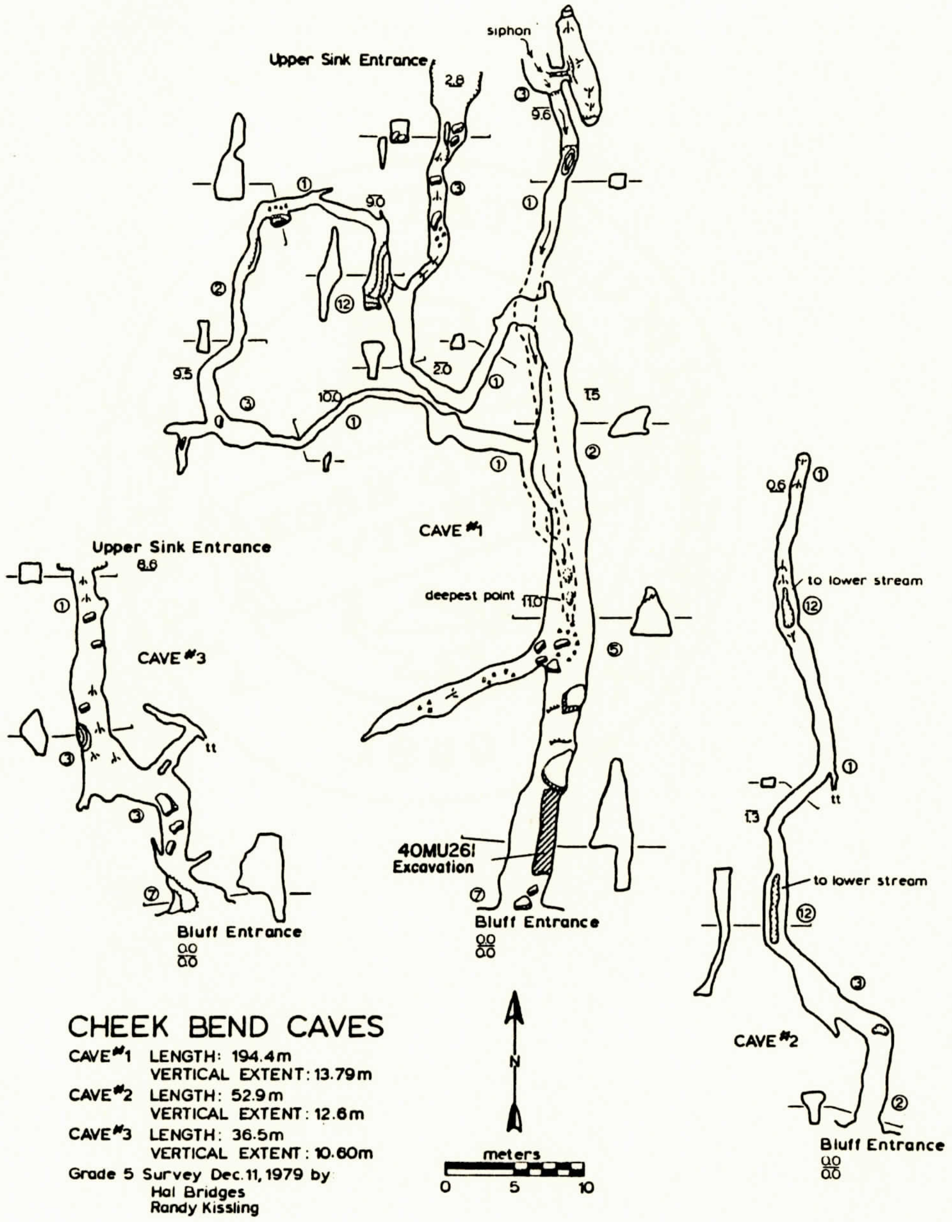

ILL.
MO.
KENTUCKY
VA.
TENNESSEE
N.C.
MISS.
ALA.
GA.
S.C.
QUADRANGLE LOCATION
CHEEK BEND CAVES
MILL
PIKE
BRIDGE
GILLIAM CEM
CEM
adelphia
SON CEM
DUCK
RIVER
Cheek
Bend
CHEEK CEM
65
700
880
620
600
M 545
599
M 543
599

FIGURE 2. Vertical and horizontal profiles of Cheek Bend Caves showing excavation 40MU261 (shaded). From Klippel and Parmalee, 1982b.



SIMPLIFIED VERTICAL PROFILE
CAVE #1
S↔N



CHEEK BEND CAVES

CAVE #1 LENGTH: 194.4m
VERTICAL EXTENT: 13.79m
CAVE #2 LENGTH: 52.9m
VERTICAL EXTENT: 12.6m
CAVE #3 LENGTH: 36.5m
VERTICAL EXTENT: 10.60m
Grade 5 Survey Dec. 11, 1979 by
Hal Bridges
Randy Kissling

and Parmalee, 1982b). Salamander remains were sent to the Department of Biology at Appalachian State University to be identified.

Dating of Strata

Strata were delineated based on stratigraphic horizon continuity and preliminary faunal identification. Dating of Holocene strata was done by carbon-14 assay of charcoal samples where possible. Earlier (lower) strata were dated by comparing insectivore assemblages from the cave with changes in full-, late-, and post-glacial vegetation in the mid-south. Carbon-14 dating of bone and shell was not utilized because this technique has proven unreliable with these materials (Klippel and Parmalee, 1982b).

Fossil Identification

After a few preliminary identifications by Dr. R.W. Van Devender in 1979, thorough identification of salamander fossils by this author began in 1988 by comparing them with specimens in the skeleton collection housed at Appalachian State University. This collection of more than 2000 specimens contains most North American salamander species, including all of those presently found in central Tennessee.

Fossil identification required extensive study of phylogenetic and ontogenetic variation in each skeletal element. Bones analyzed included the larger bones most likely to be preserved and recovered as fossils: vertebrae, larger leg bones (femur, humerus, etc.), tooth bearing bones (dentary, maxilla, etc.), and pectoral and pelvic girdles (Figure 3). Special attention was given to vertebral anatomy (Figures 4 & 5) since vertebrae are the most numerous skeletal element and are common fossils. Comparative skeletons included cleared and stained, articulated, and disarticulated specimens. Species identifications for those specimens were made by Dr. Van Devender before skeletonization and were usually represented by additional preserved material in the A.S.U. collection.

The first step in identifying each fossil was to determine the genus by searching for a set of generic characters ascertained through study of the comparative skeletons and published descriptions. Species determination and snout-vent length (SVL) estimation was done by direct comparison to modern skeletons of various sizes.

Data Analysis

Estimates of relative abundance of fossil salamanders were the number of identified elements (NIE) and minimum number of individuals (MNI). MNI was a conservative estimate of the minimum number of individual animals

FIGURE 3. A generalized terrestrial salamander skeleton. Adapted from Romer and Parsons, 1986.

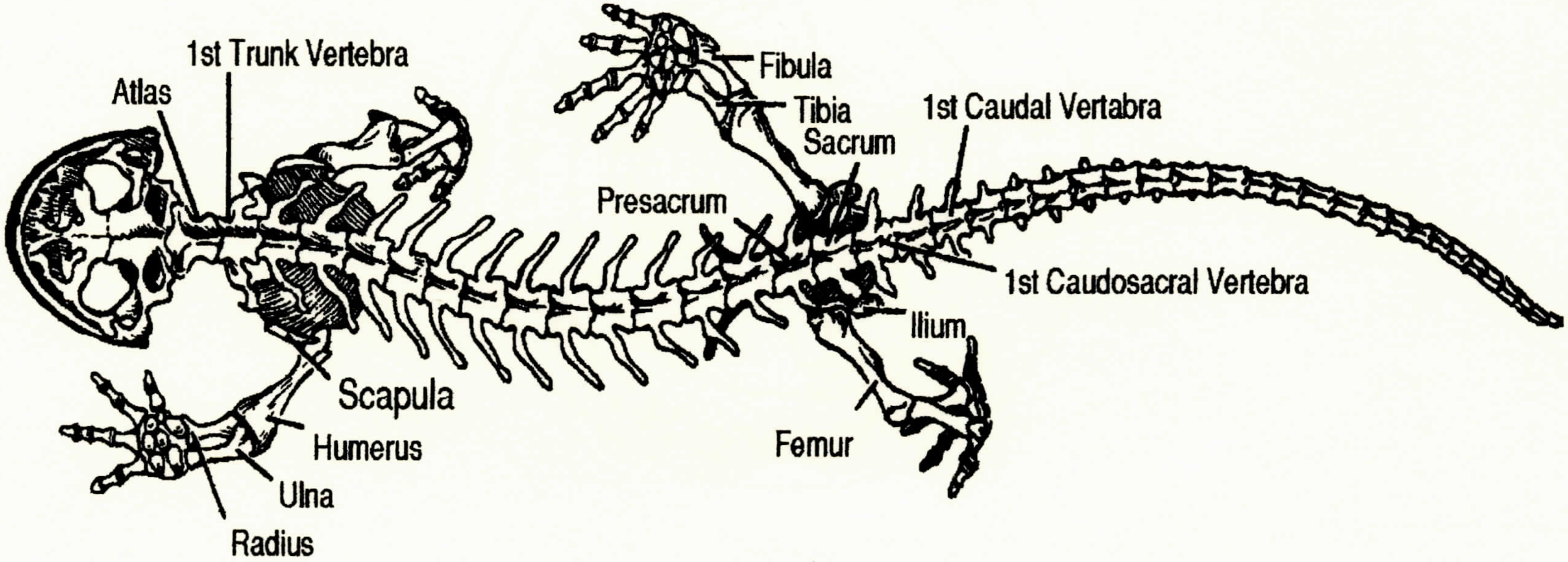

Atlas
1st Trunk Vertebra
Scapula
Humerus
Ulna
Radius
Presacrum
Fibula
Tibia
Sacrum
1st Caudal Vertabra
1st Caudosacral Vertebra
Ilium
Femur

FIGURE 4. Scanning electron micrograph (SEM) showing dorsal aspect of reference <u>Desmognathus ochrophaeus</u> midtrunk vertebra (T_m). AP alar process, CN centrum, HE hyperapophyses, NR neural ridge, PO postzygapophysis, PR prezygapophysis, PT pterygapophysis. Magnification = 130x.

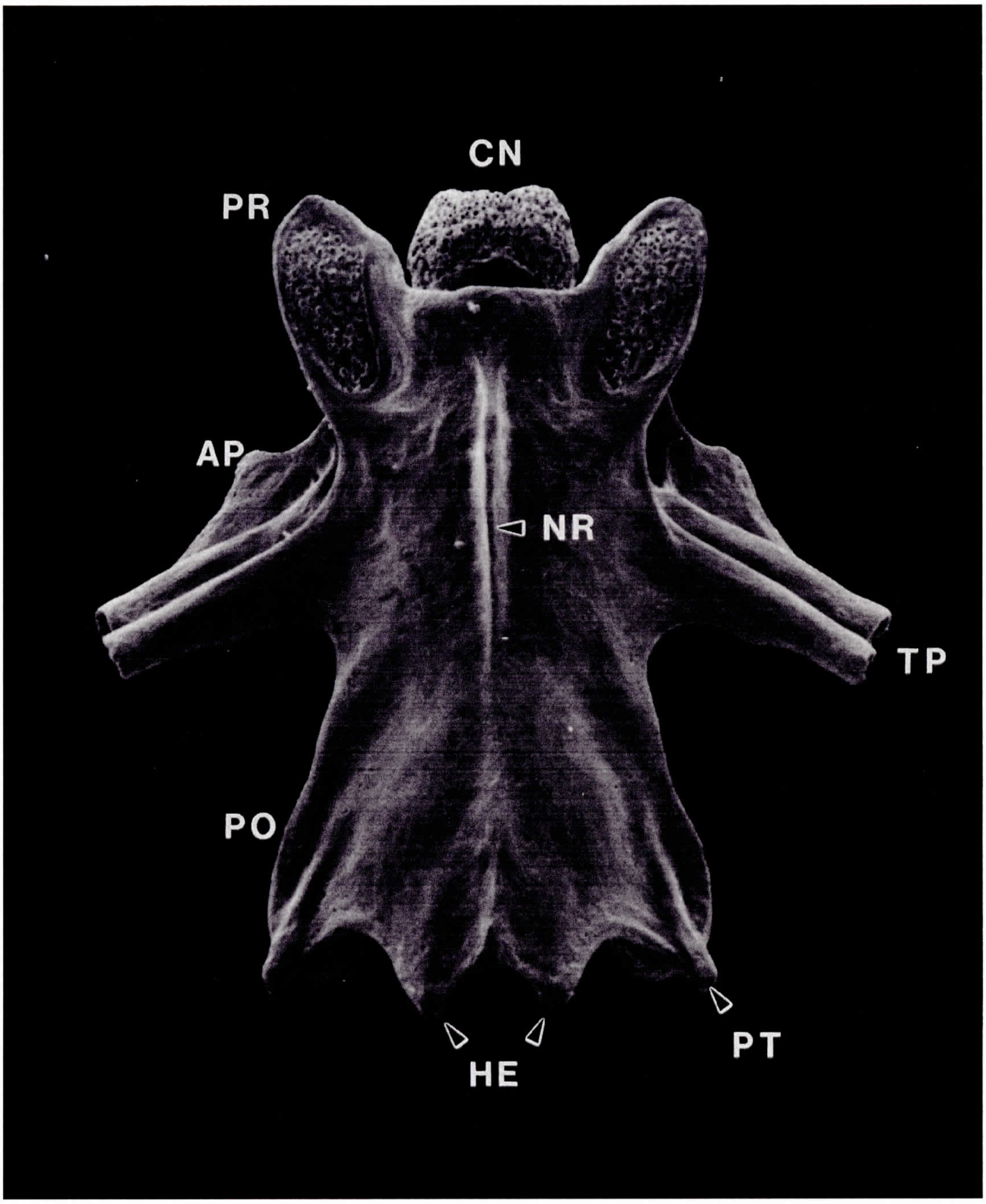
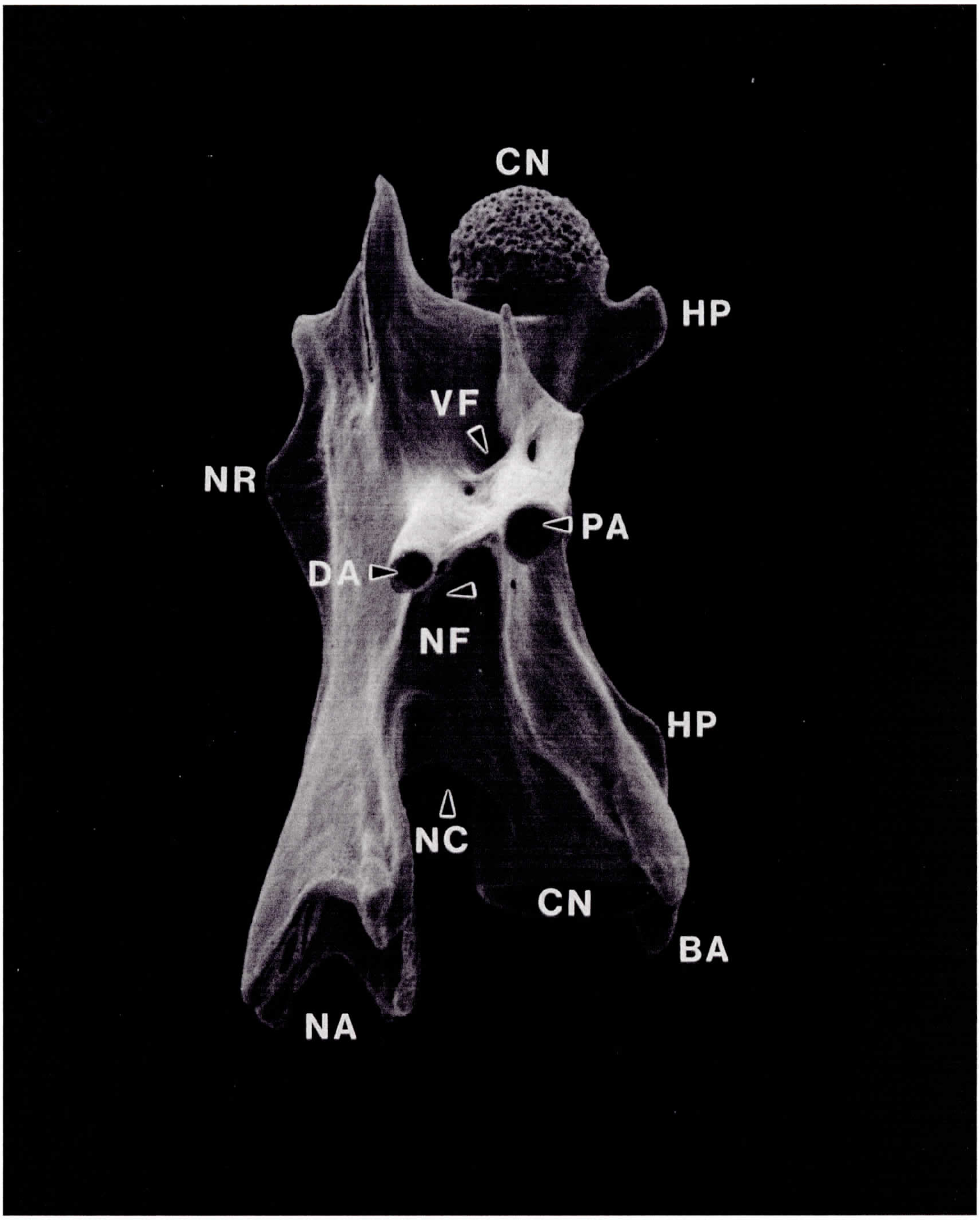

CN
PR
AP
NR
TP
PO
PT
HE

FIGURE 5. SEM showing lateral aspect of reference *Desmognathus ochrophaeus* T_m. BA basapophysis, CN centrum, DA diapophysis, HP hypophysis, NA neural arch, NC neural canal, NF (spinal) nerve foramen, NR neural ridge, PA parapophysis, VF vascular foramen. Magnification = 130x.


CN
HP
VF
NR
PA
DA
NF
HP
NC
CN
BA
NA

neccessary to account for the numbers of bones for each species in a stratum. For example, if one atlas and two sacral vertebrae (salamanders only have one of each) of a species were from the same stratum, MNI would be 2 for that species if the SVL estimated for the atlas agreed with that for one of the sacral vertebrae. Body size, expressed as estimated snout-vent length ranges (e.g. SVL = 50-55mm) of individuals, also affected MNI. If each of the vertebrae in the above example had different SVL ranges then MNI would be three.

Data recorded for identified fossils included family, genus, species, bone, estimated SVL, level, date of excavation, 40MU261 catalog number, and container number. To reconstruct stratigraphic/temporal sequence, data records were entered into a PC-File database and sorted according to stratigraphic level, family, genus, species, SVL, and bone. Number of identified elements (NIE) and MNI were tallied for each species and stratum. Anatomical terminology (see Glossary) largely followed that of Wake (1966), Duellman and Trueb (1986), and Auffenburg (1963) with some modification as mentioned in the text. Classification used was that of Duellman and Trueb (1986).

RESULTS

Site Description

Based on stratigraphic evidence and faunal content of the CBC excavation (40MU261), two major episodes of fill were delineated which could be subdivided into eight distinct strata (Figure 6)(Klippel and Parmalee, 1982b). The first fill episode, containing strata I-III, was deposited during the late Pleistocene (approximately 16,000 YBP to 12,000 YBP) and contained extant "temperate" species contemporaneous with many "boreal" species having present ranges which exclude central Tennessee. Strata IV-VIII comprise the second fill episode and were deposited during the Holocene (approximately 12,000 YBP to present). These strata contained only extant local species (Klippel and Parmalee, 1982b).

Systematic Accounts

A total of 1,749 bones represents at least 10 salamander species identified (Table 2). The following list of salamander fossil identifications includes descriptions of characters of each element at the family, subfamily, genus, and species levels where warranted. As

FIGURE 6. Vertical section of excavation 40MU261. Wisconsinan = late Pleistocene. Arabic numbers in strata represent carbon-14 dates. Stippled regions are boulders. From Klippel and Parmalee, 1982b.

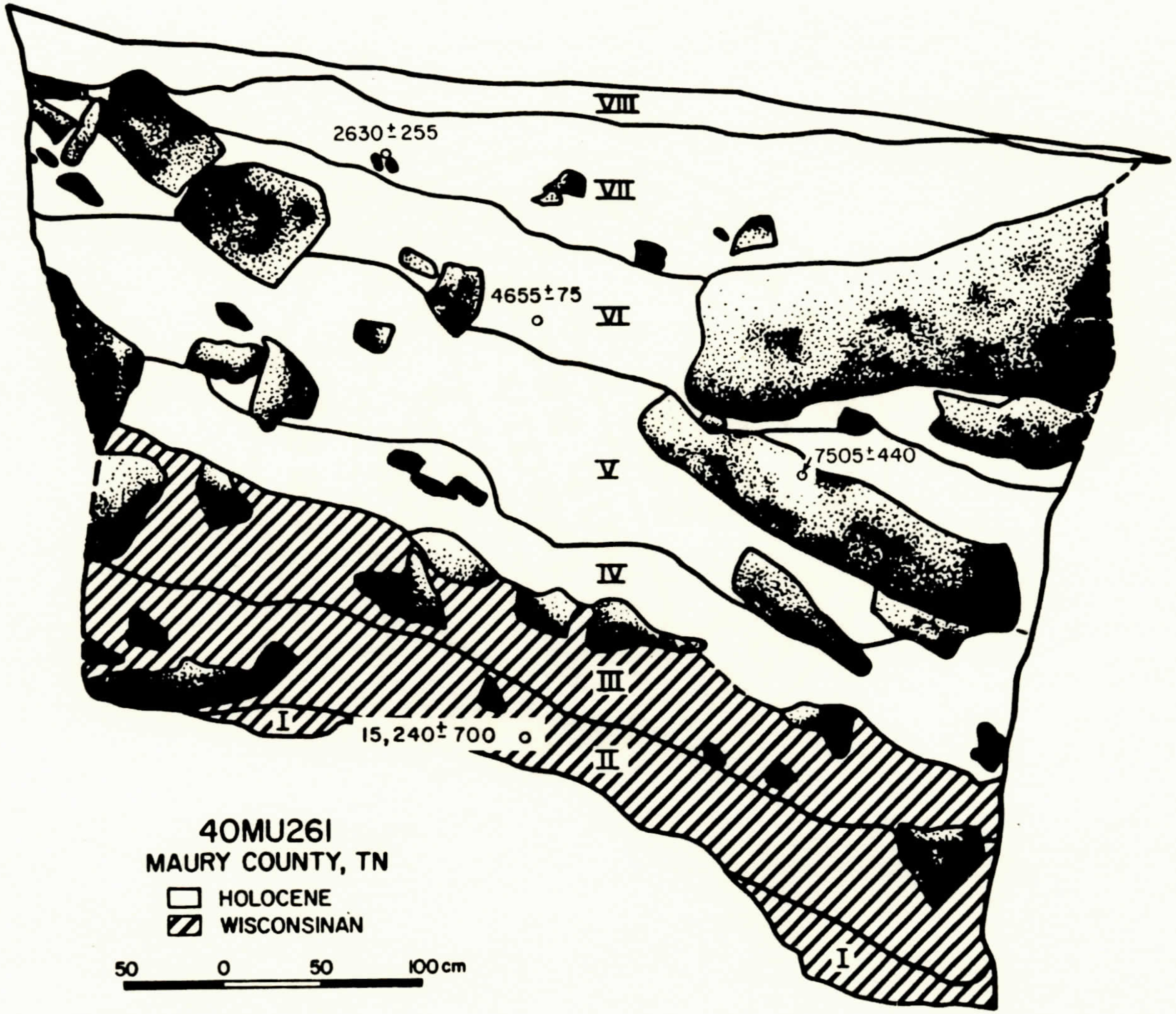

VIII
2630±255
VII
4655±75
VI
7505±440
V
IV
III
15,240±700
II
I
I
40MU261
MAURY COUNTY, TN
☐ HOLOCENE
▨ WISCONSINAN
50
0
50
100cm

TABLE 2. Stratigraphic distributions of fossil salamanders from Cheek Bend Cave. Numbers in parentheses are minimum numbers of individuals and all others are quantity of bones. Minimum numbers of individuals were estimated only for identifications at species level. Strata I, V/VI, and VI/VII had no salamander fossils and were omitted from the table. Strata I/II through III were deposited during the late Pleistocene with remaining strata deposited during Holocene times.

TAXON	STRATA												
	I/II	II	II/III	III	III/IV	IV	IV/V	V	VI	VII	VII/VIII	VIII	TOTAL
Ambystoma													
maculatum				1(1)		6(5)	4(3)	9(6)					20(15)
tigrinum		4(3)	1(1)	12(6)		5(7)	14(8)	12(11)			1(1)		49(37)
Ambystoma sp.				3		1	5	4					13
Cryptobranchus													
alleganiensis	9(1)	22(16)	2(2)	4(4)		1(1)	3(1)	11(10)	1(1)			1(1)	54(37)
Eurycea													
cf. bislineata		1(1)					59(6)	59(18)	6(4)				125(29)
longicauda								6(3)	3(1)				9(4)
lucifuga				11(5)	1(1)	76(30)	93(15)	451(67)	16(8)	3(3)		2(1)	653(130)
Eurycea sp.				3		51	119	357	35	7		1	573
Necturus													
cf. maculosus						3(1)		2(2)					5(3)
Notophthalmus													
viridescens						8(2)		13(4)					21(6)
Plethodon													
glutinosus						1(1)	9(3)	74(14)	15(5)				99(23)
dorsalis								20(9)	31(12)	21(2)	1(1)	1(1)	74(25)
Plethodontidae				1			3	16	10	3		1	34
Unidentified caudate	1	5		3			2	8	1				20
TOTAL	10	32	3	38	1	152	311	1042	118	34	2	6	1749

with most other assemblages of salamander fossils, vertebrae are the most abundant element from this deposit. Therefore, vertebral identification methods are emphasized here. Each species account for salamanders in CBC includes a listing of numbers of each fossil element type, number of identified elements (NIE), minimum number of individuals (MNI), temporal distribution (with number of elements for each stratum in parentheses), and remarks on distinguishing characteristics of each element type. MNI is estimated only for the species level. Temporal distributions, NIE, and MNI are summarized in Table 2.

Order Caudata Oppel, 1811
Suborder Cryptobranchoidea Dunn, 1922
Family Cryptobranchidae Cope, 1889
Genus *Cryptobranchus* Leukart, 1821
Cryptobranchus alleganiensis (Daudin, 1802)
hellbender

Fossil elements: 3 left dentaries, 3 right dentaries, 1 premaxilla?, 4 left maxillae, 3 right maxillae, 2 left vomers, 2 palatines, 5 unknown skull bones, 7 mid-trunk vertebrae, 1 caudosacrum, 5 caudals, 5 unknown vertebrae, 5 ribs, 4 humeri, 1 ulna?, 1 left femur, and 2 femora? NIE = 54 and MNI = 37.

Temporal distribution: Strata I/II (9), II (22), II/III (2), III (4), IV (1), IV/V (3), V (11), VI (1), and VIII (1).

Remarks: Most of these fossils were identified by Dr. R. W. Van Devender in 1979. Vertebrae are large, strongly amphicoelous, and lack spinal nerve foramena. Transverse processes are completely fused on T_1, and are united along entire lengths on subsequent trunk vertebrae. As a result of this union, the articular facets on post-T_1 transverse processes form a "figure 8" outline (Figure 7B). All transverse processes exceed zygapophyseal lateral margins Figure 7A). Hyperapophyses are united and terminate well short of the postzygapophyses on precaudal vertebrae. Hyperapophyses become elongate on anterior caudal vertebrae and are equal in length to the haemal spine on posterior caudals. Neural ridge is well-developed on T_1 through T_4 and absent or weakly-developed on subsequent vertebrae. The centrum bottom is a ridge similar to <u>Necturus</u> (Figure 19D), especially on anterior trunk vertebrae, and is bifurcated on the caudosacrum to form two ridges. Leg bones have non-calcified epiphyses and often lack, or have ill-defined, processes (e.g. crista dorsalis, Figure 7C). Cryptobranchid skull and leg bones can usually be separated from other salamanders by larger size alone.

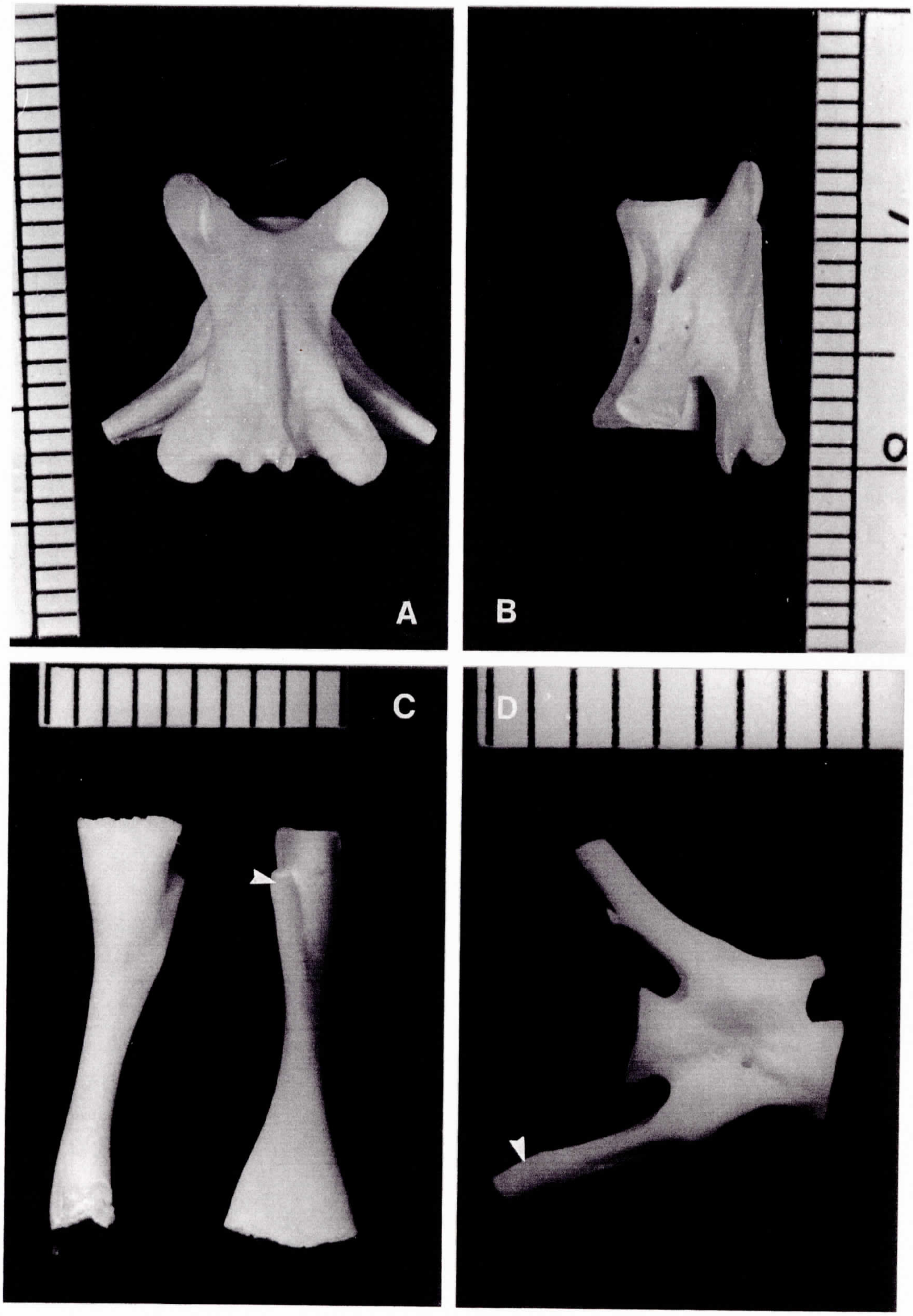
FIGURE 7. _Cryptobranchus_ _alleganiensis_ reference specimens. Scale = millimeters.

A. Dorsal aspect of T_m.

B. Lateral aspect of T_m.

C. Left and right humeri showing crista dorsalis.

D. Lateral aspect of a caudal vertebra showing hemapophysis.


A
B
1
0
C
D

Family Ambystomatidae Hallowell, 1856

Genus Ambystoma Tschudi, 1838

Ambystoma vertebrae are amphicoelous (Figure 8A) and have spinal nerve foramina exiting behind transverse processes (Figure 8B). The first trunk vertebra, T_1 has no spinal nerve foramina and has widely separated and heavy transverse processes (Figure 8C). Transverse processes of other trunk vertebrae are less robust and fused for 1/2 to 3/4 the lengths of the diapophyses and parapophyses (Figures 8A & 8C). Anterior trunk vertebrae (T_1- T_3) are shorter axially, and have a steeper neural arch with a larger neural canal (compare Figures 8B-8D). The presacrum is similar to the two caudosacral vertebrae (Figure 8B) in having completely fused transverse processes, but differs in having dorsally directed transverse processes rather than ventrally as in the caudosacrals. Other authors have not previously recognized the presacrum as distinct from trunk vertebrae. Sacral transverse processes are heavy like those of T_1, but are fused along most of length (Figure 8C). Hyperapophyses may be separate (Figure 9D) on all vertebrae as two terminal rugosities or may be united as a single pit (Figure 9C). Adult Ambystoma have well-ossified epiphyses on limb elements.

FIGURE 8. SEM's of <u>Ambystoma</u> <u>opacum</u> reference vertebrae. Scale = 0.5mm.

A. Anterior aspect of T_m showing amphicoelous centrum and anterior basapophyses.

B. Lateral aspect of caudosacrum (CS) showing accuminate transverse processes.

C. Lateral aspect of first trunk vertebra (T_1).

D. Lateral aspect of sacrum.

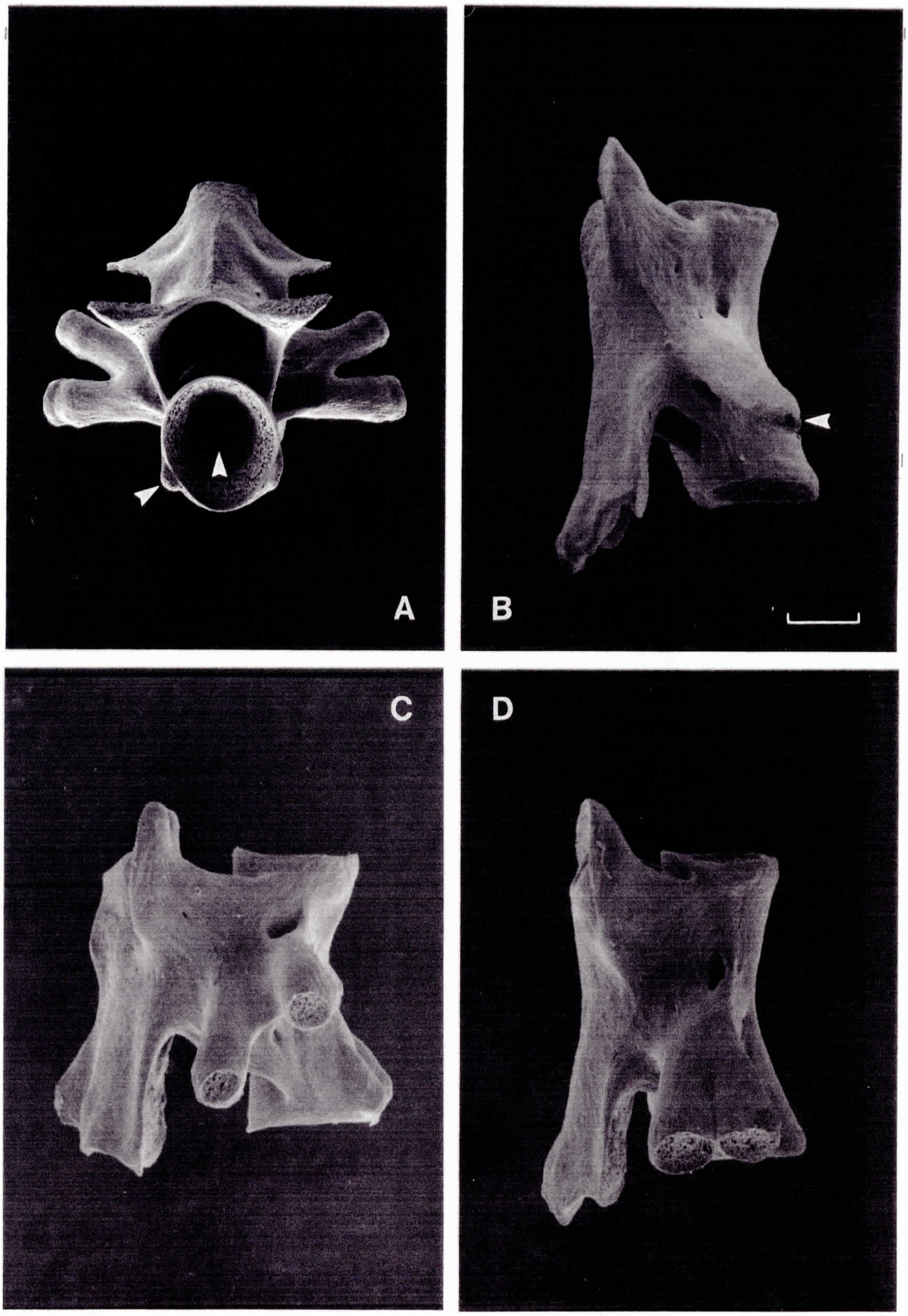

A
B
C
D

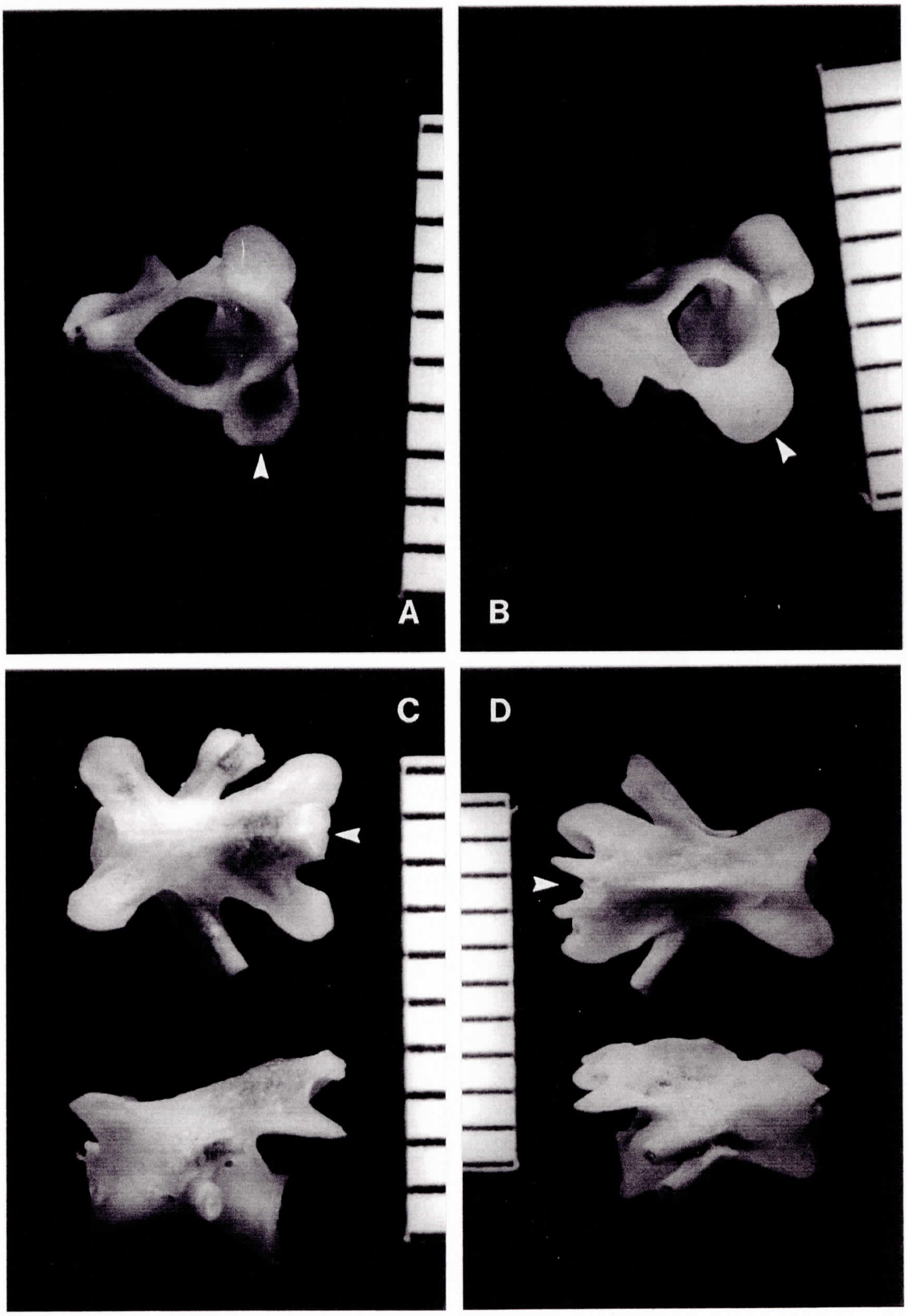
FIGURE 9. *Ambystoma* reference vertebrae. Scale = millimeters.

A. Anterior aspect of *Ambystoma tigrinum* atlas.

B. Anterior aspect of *Ambystoma maculatum* atlas.

C. Dorsal (top bone) and lateral (lower) aspects of *Ambystoma tigrinum* T_m.

D. Dorsal (top bone) and lateral (lower) aspects of *Ambystoma maculatum* T_m.


A
B
C
D

Ambystoma maculatum (Shaw, 1802)

spotted salamander

Fossil elements: 1 atlas, 13 mid-trunk vertebrae, 1 caudal, 2 vertebrae of unknown position, 2 left or right humeri, 1 right humerus. NIE = 20 and MNI = 15.

Temporal distribution: Strata III (1), IV (6), IV/V (4) and V (9).

Remarks: The atlas of *Ambystoma maculatum* is easily confused with that of *A. tigrinum*. The occipital cotyles of *A. maculatum* (Figure 9B), when viewed anteriorly, are more ventrally oriented than those of *A. tigrinum* (Figure 9A). A less obvious distinguishing characteristic of the *A. maculatum* atlas is the more pronounced, gently sloping dorso-lateral ridge located on the anterior portion of the neural arch. The spinal nerve foramina are often situated near the lateral mid-line of the occipital cotyle. One caudal vertebra and two fragmented vertebrae of unknown axial position were identified as *A. maculatum* on the basis of large size and flat neural arch profiles. Humeri were assigned to *A. maculatum* due to large size, a round radial condyle, and a gradual distal taper (compare Figures 11A and 11B).

Ambystoma tigrinum Green, 1825

tiger salamander

Fossil elements: 1 left dentary, 5 right dentaries, 1 right premaxilla, 12 mid-trunk vertebrae, 4 vertebrae of unknown position, 1 sacrum, 1 caudosacrum, 2 caudals, 2 right ilia, 3 left ilia, 6 right humeri, 11 left humeri, 2 left radii, 2 left femora, 4 right femora, 1 left fibula, 1 right tibia. NIE = 49 and MNI = 36.

Temporal distribution: Strata II (4), II/III (1), III (12), IV (5), IV/V (14), V (12), and VII/VIII (1).

Remarks: Tiger salamander bones are usually larger than those of spotted salamanders (A. maculatum). Dentaries have a long and spinous posterior mental process that usually has an associated lateral flange in mature specimens (Figure 10C). A species with a similar dentary is A. maculatum, which lacks the lateral flange (Figure 10D). Other ambystomatids have flattened posterior mental processes rather than spinous ones. The pars palatina of the A. tigrinum premaxilla has a strong supportive ridge just inside the distal margin of the pars nasalis, present only as a spine in A. maculatum. Fossil vertebrae were assigned to A. tigrinum on the basis of a high neural arch lateral profile of approximately 45 degrees, extending well beyond the end of the centrum as reported by Holman (1969) (Figure 9C).

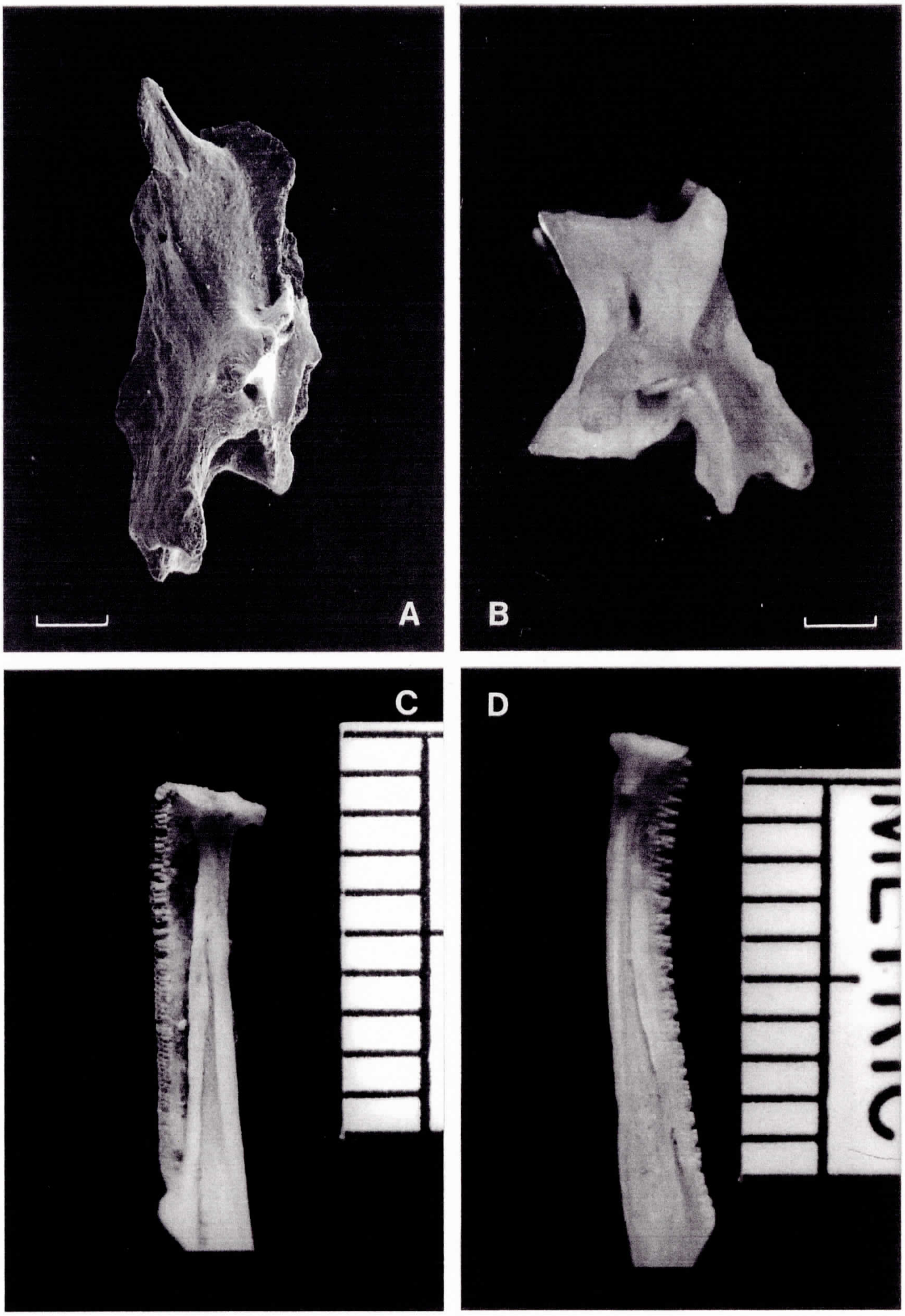
FIGURE 10. *Ambystoma* bones. Scale = millimeters.

A. Lateral aspect of *Ambystoma* *maculatum* T_m fossil.

B. Lateral aspect of *Ambystoma* *tigrinum* T_m fossil.

C. Lingual aspect of a reference *Ambystoma tigrinum* dentary.

D. Lingual aspect of a reference *Ambystoma maculatum* dentary.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METRIC

Tiger salamander humeri have a columnar diaphysis with an abrupt distal taper and an angular radial condyle (Figure 11B). The femoral trochanter of _A. tigrinum_ is flat (Figure 11D), while that of the similar _A. maculatum_ fibula is more rounded (Figure 11C). The tibial spur of _A. tigrinum_ (Figure 12A) lacks the extended ridge characteristic of _A. maculatum_ (Figure 12B). Radial diaphyses are straight in tiger salamanders (Figure 12C) and curved in spotted salamanders (Figure 12D). Strata IV and V of the early Quaternary contained at least three quite large tiger salamanders with SVL's estimated to be about 150mm.

Ambystoma sp.

Fossil material: 5 mid-trunk vertebrae, 4 caudal, 1 vertebra of unknown position, 1 ilium (?), 1 right (?) femur, 1 right humerus. NIE = 13.

Temporal distribution: Strata III (3), IV (1), IV/V (5), and V (4).

Remarks: These fossils display ambystomatid characteristics as previously discussed, but are too fragmentary for positive specific identification.

Family Plethodontidae Gray, 1850

Subfamily Plethodontinae Gray, 1850

Plethodontids are unique in having spinal nerve foramen anterior to transverse processes on T_1 (Figure

FIGURE 11. *Ambystoma* reference leg bones.
Scale = millimeters.

A. Left and right *Ambystoma maculatum* humeri.

B. Left and right *Ambystoma tigrinum* humeri.

C. Left and right *Ambystoma maculatum* femora.

D. Left and right *Ambystoma tigrinum* femora.


A
B
C
D

FIGURE 12. _Ambystoma_ reference leg bones. Scale = millimeters.

A. _Ambystoma_ _tigrinum_ ilia (top), tibia (bottom left), and fibula (bottom right).

B. _Ambystoma_ _maculatum_ tibiae (top) and ilia (bottom).

C. _Ambystoma_ _tigrinum_ radii (top), and ulnae (bottom).

D. _Ambystoma_ _maculatum_ radius (top left), ulna (top right), and fibulae (bottom).


A
B
C
D

13B) and two spinal nerve foramina simultaneously exiting anterior and posterior to transverse processes on T_2 (Figure 13D). All subsequent vertebrae have posterior spinal nerve foramina (Figure 14D). T_1, T_2, and T_3 have transverse processes directed more posteriorly (Figures 13A, 13C, and 14A), have larger neural canals (1.5-2 x centrum width), and are shorter axially than are other vertebrae. Vertebrae between T_3 and the presacrum are usually very similar and are refered to as mid-trunk vertebrae (Figures 14C and 14D). The presacrum has a reduced diapophysis which is accuminate and has either two spinal nerve foramina or a single large foramen (Figures 15A and 15B). The sacrum has heavy transverse processes united for most of their length (Figure 15C). Diapophyses and parapophyses on caudosacrals (CS) are fused into a single accuminate process and often have an alar process (Figure 15D). CS_1 has no haemal keel, and often has larger alar processes than CS_2. Plethodontids usually have leg bones with unossified epiphyses (unlike ambystomatids) and are difficult or impossible to identify at the species level.

Genus Eurycea Rafinesque, 1822

Eurycea vertebrae have widely separated transverse processes not greatly exceeding lateral margins of zygapophyses (Figures 14A). Also, parapophyses are well

FIGURE 13. SEM's of reference *Eurycea longicauda* vertebrae. Scale = 0.5mm.

A. Dorsal aspect of T_1.

B. Lateral aspect of T_1.

C. Dorsal aspect of T_2.

D. Lateral aspect of T_2.

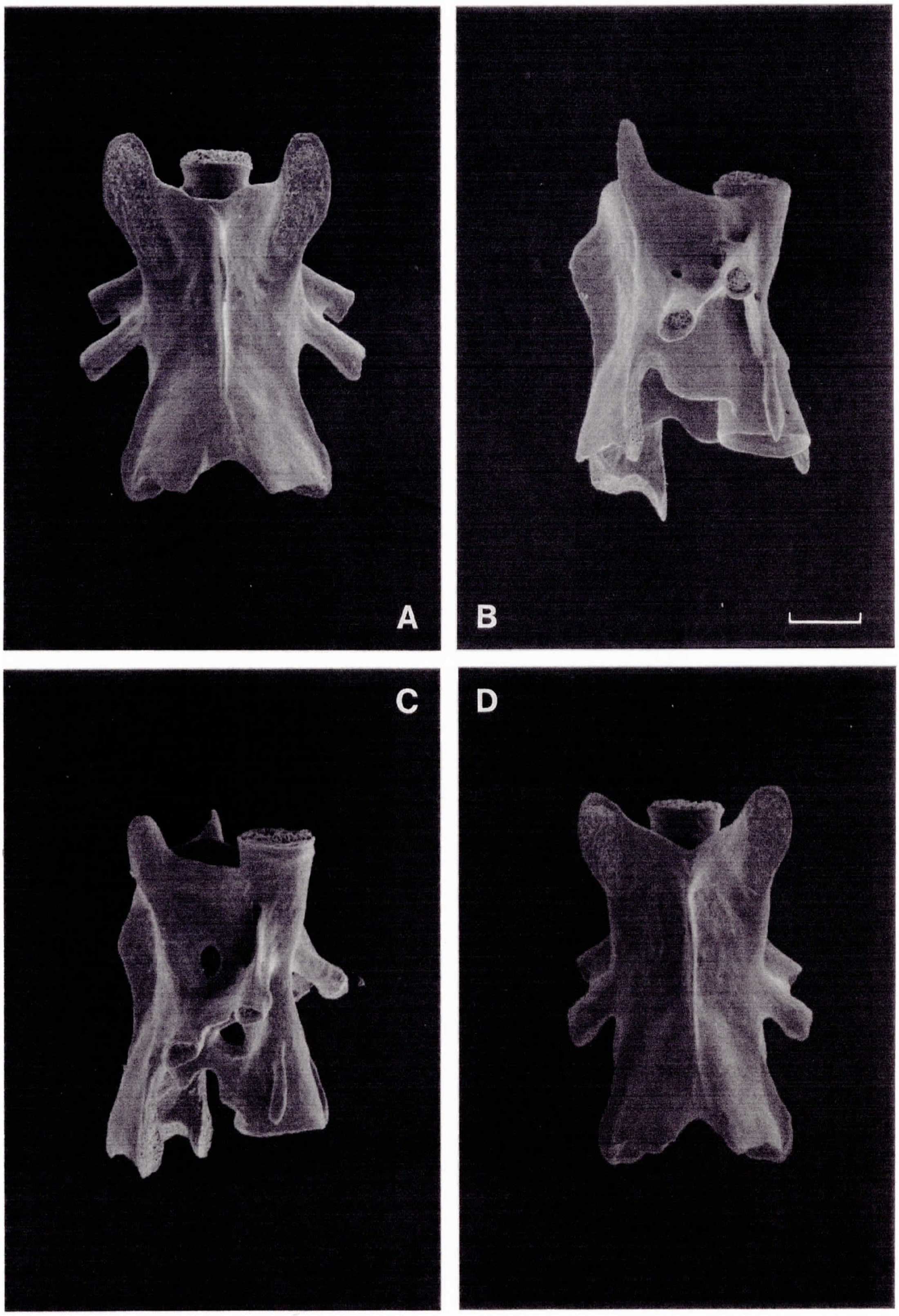
A
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FIGURE 14. SEM's of reference _Eurycea_ _longicauda_ vertebrae. Scale = 0.5mm.

A. Dorsal aspect of T_3.

B. Lateral aspect of T_3.

C. Dorsal aspect of fossil T_m.

D. Lateral aspect of T_m.

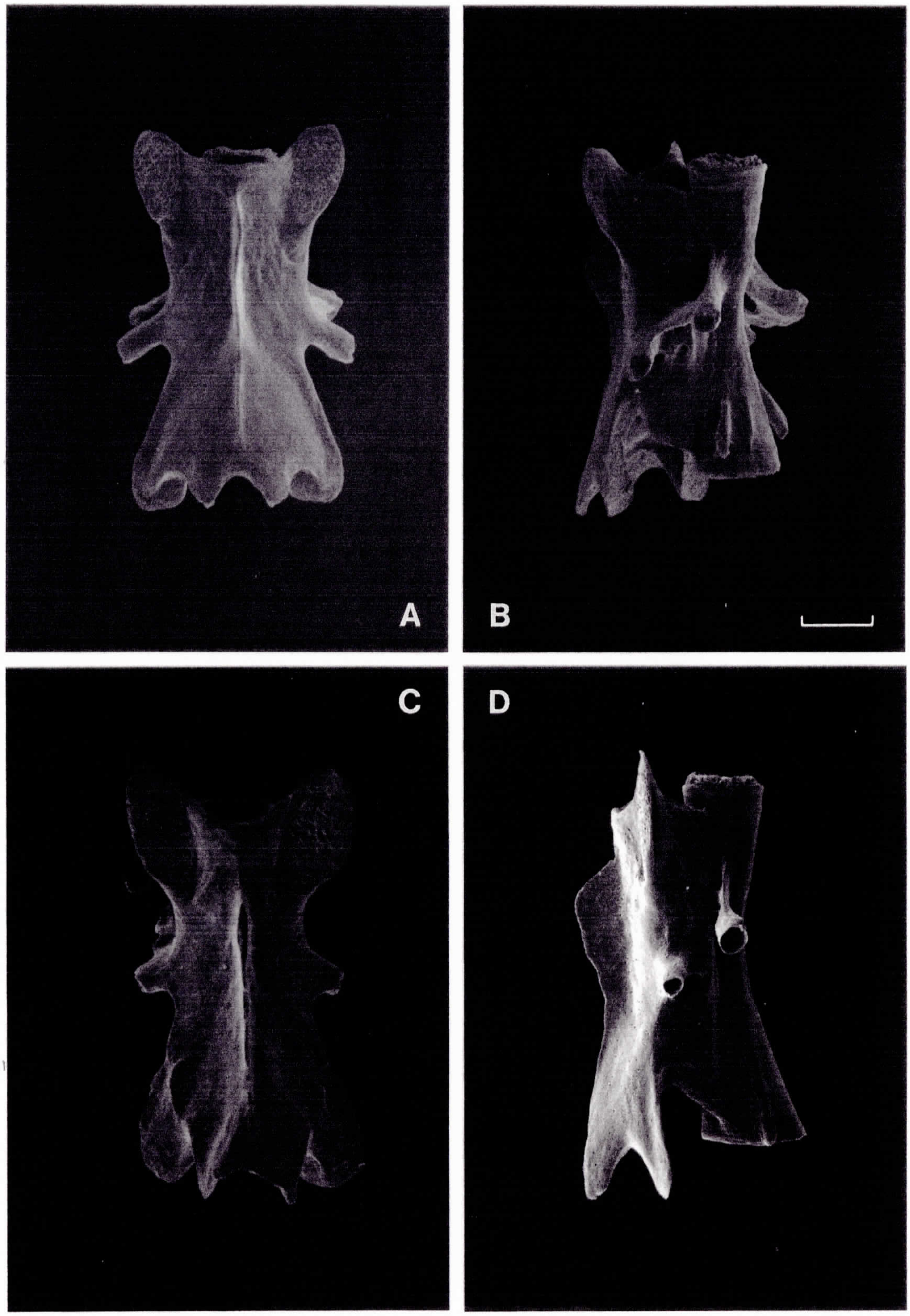
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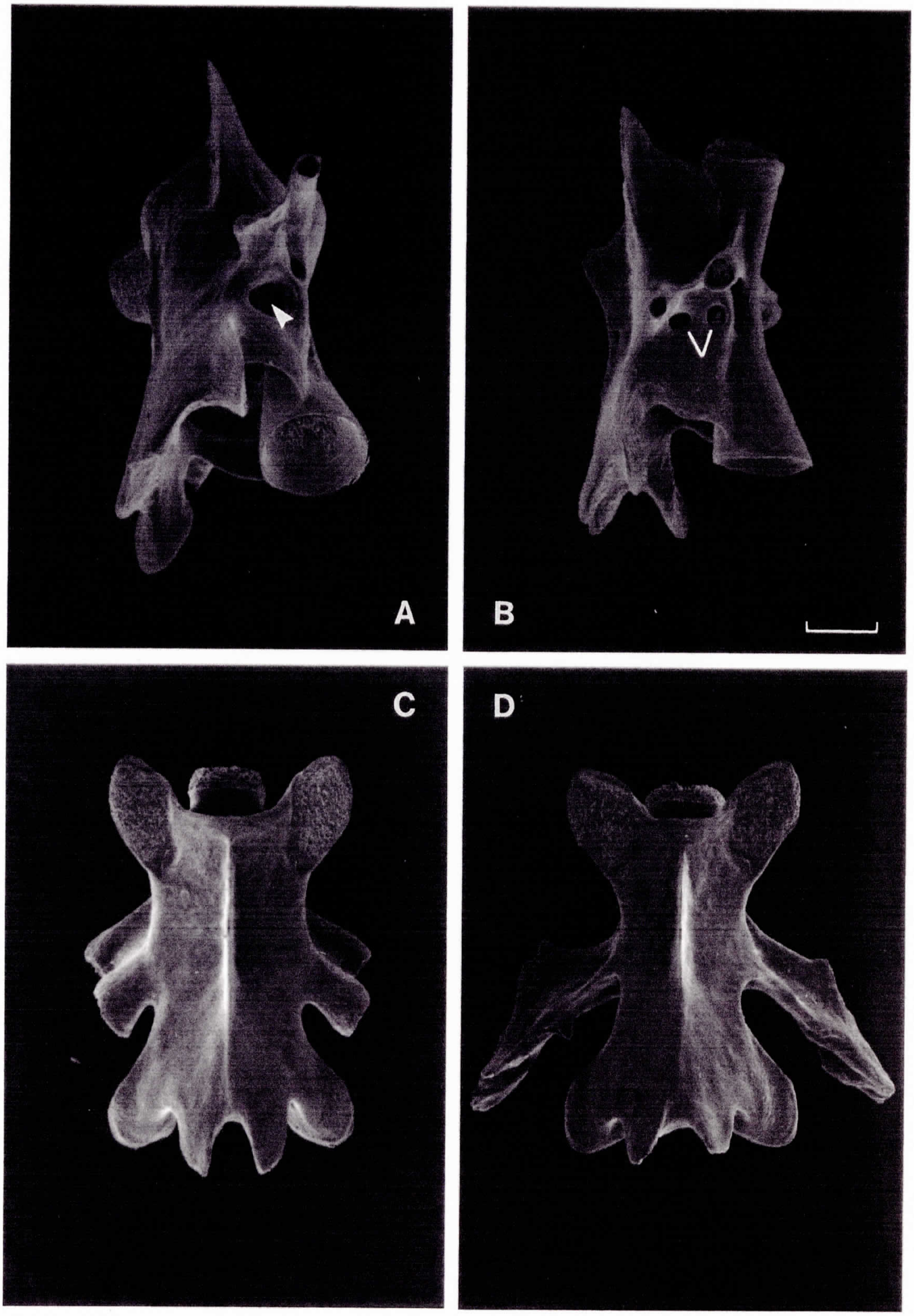
FIGURE 15. SEM's of reference Plethodon and Eurycea longicauda vertebrae. Scale = 0.5mm.

A. Dorsolateral aspect of Plethodon glutinosus presacrum. Note very large nerve foramen and accuminate diapophysis.

B. Lateral aspect of Eurycea longicauda presacrum. Note double nerve foramen and reduced diapophysis.

C. Dorsal aspect of Eurycea longicauda sacrum.

D. Dorsal aspect of Eurycea longicauda caudosacrum.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anterior to diapophyses. Neural ridges are weak-to well-developed. Hyperapophyses are separate and hypapophyses are absent. Posteriorly placed basapophyses are well-developed, especially on anterior vertebrae (Figure 16A). Vertebrae of most Eurycea species are at least slightly opisthocoelous due to a ring of calcified cartilage on the anterior end of the centrum.

Eurycea cf. bislineata (Green, 1818),
two-lined salamander

Fossil elements: 1 T_1, 4 T_2, 3 T_3, 62 mid-trunk vertebrae, 6 sacra, 11 caudosacra, 38 caudals. NIE = 125 and MNI = 29.

Temporal distribution: Strata II (1), IV/V (59), V (59), and VI (6).

Remarks: Adult vertebrae are small (prezygapophyseal to postzygapohyseal length approx. 1.5 - 2.5 mm) and are distinct in being pseudopisthocoelous (Figure 16A). The neural ridge is often weakly developed on posterior trunk vertebrae. Basapophyses are well-developed, especially on anterior trunk vertebrae. Eurycea quadridigitata (Holbrook, 1842) has vertebrae that are virtually indistinguishable from those of E. bislineata. These fossils are probably Eurycea bislineata since the modern distribution of this species includes central Tennessee, whereas E. quadridigitata is found on the Atlantic and

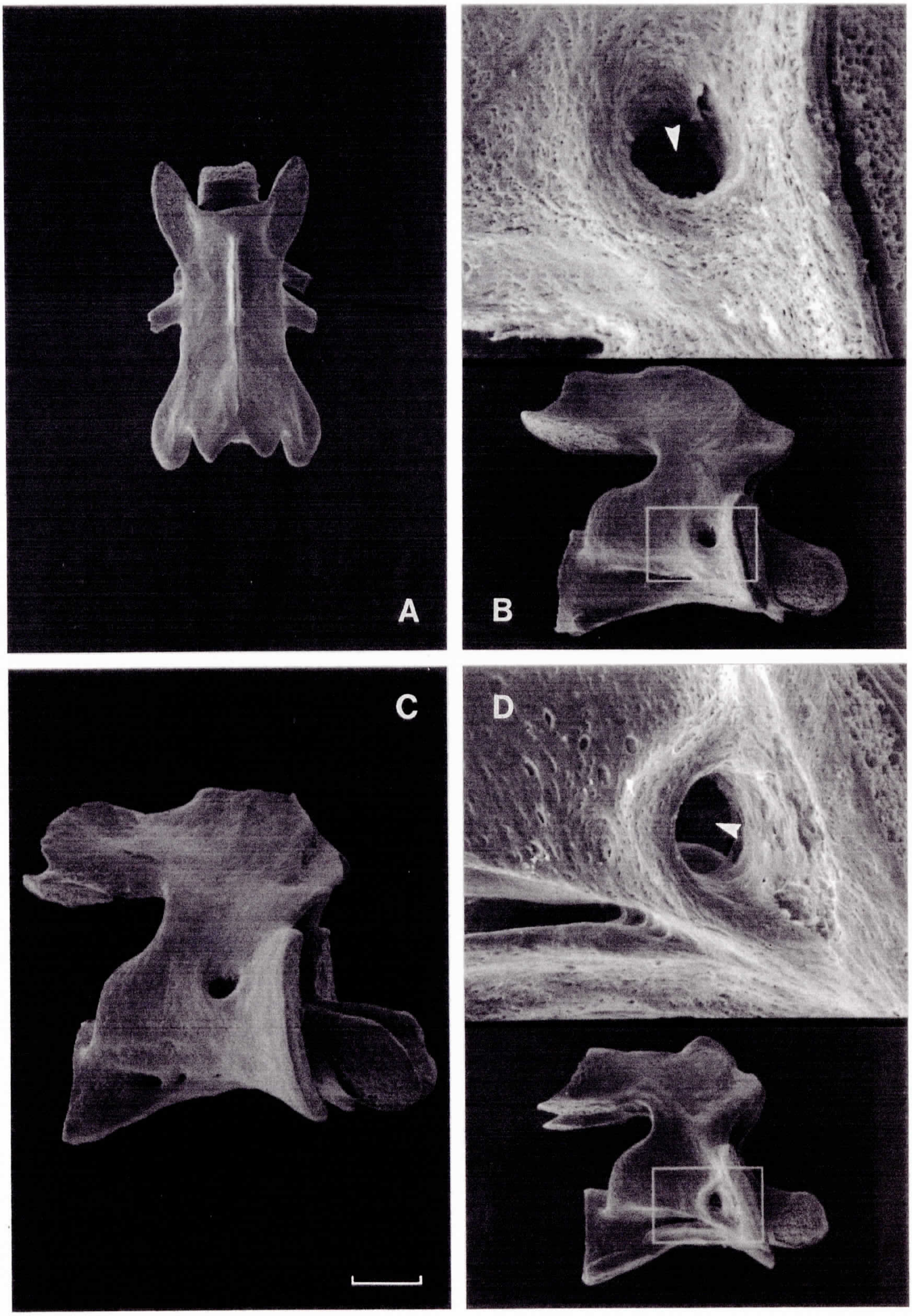
FIGURE 16. SEM's of Plethodontid vertebrae. Scale = 0.5mm.

A. Dorsal aspect of *Eurycea* cf. *bislineata* fossil T_m.

B. Lateral aspect of reference *Eurycea lucifuga* atlas. Note exit angle of nerve foramen. Close-up magnification = 5x.

C. Lateral aspect of fossil *Plethodon glutinosus* atlas. Note exit angle of nerve foramen.

D. Lateral aspect of reference *Eurycea longicauda* atlas. Note exit angle of nerve foramen. Close-up magnification = 5x.


A
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C
D

Gulf coastal plains or lower piedmont well outside of Tennessee.

Eurycea longicauda (Green, 1818)

long-tailed salamander

Fossil elements: 9 mid-trunk vertebrae. NIE = 9 and MNI = 4.

Temporal distribution: Stratum V (9).

Remarks: Vertebrae are larger than those of *Eurycea bislineata*. *E. longicauda* mid-trunk vertebrae are narrower and have more rounded zygapophyses, thus appearing more gracile than do those of *E. lucifuga* (see below; compare Figures 14C and 17A).

Eurycea lucifuga Rafinesque, 1822

cave salamander

Fossil elements: 15 atlantes, 6 T_1, 7 T_2, 8 T_3, 322 mid-trunk vertebrae, 2 presacra, 24 sacra, 62 caudosacra, 206 caudals. NIE = 653 and MNI = 130.

Temporal distribution: III (11), III/IV (1), IV (76), IV/V (93), V (451), VI (16), VII (3), and VIII (2).

Remarks: In the *Eurycea* atlas (Figures 16B and 16D), the angle of the spinal nerve foramina is less obtuse, and the sides of the odontoid processes are lower than in *Plethodon* (Figure 16C). Davis (1973) stated that the centrum of the *Plethodon* atlas "projects posteriorly to

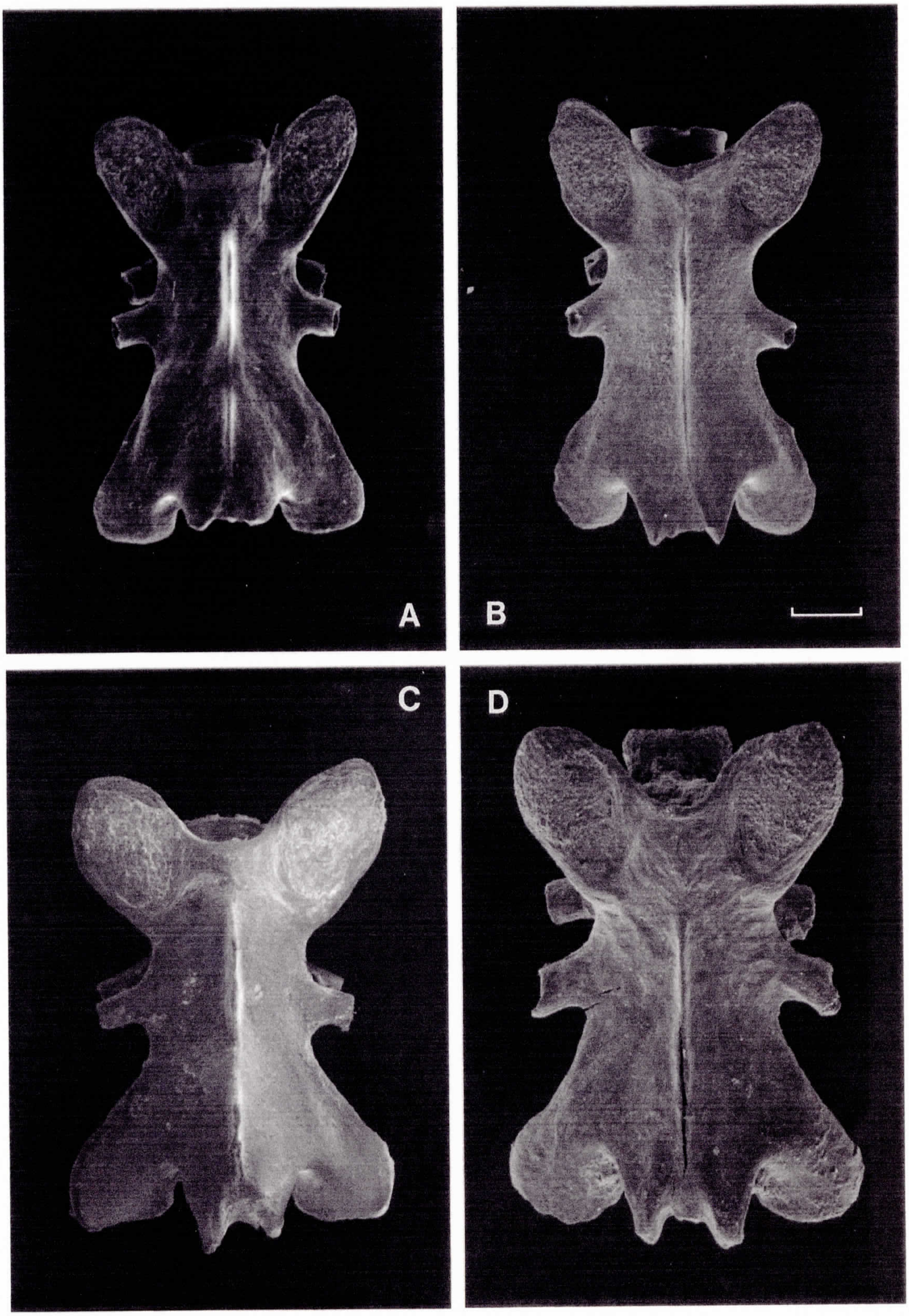
FIGURE 17. SEM's of *Eurycea lucifuga* vertebrae. Scale = 0.5mm.

A. Dorsal aspect of *Eurycea lucifuga* "normal" T_m.

B. Dorsal aspect of *Eurycea lucifuga* "normal" fossil T_m.

C. Dorsal aspect of *Eurycea lucifuga* "robust" T_m.

D. Dorsal aspect of *Eurycea lucifuga* "robust" fossil T_m.


A
B
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the neural arch proportionally less than in *Eurycea*." *E. lucifuga* (Figure 16B) can be distinguished from *E. longicauda* (Figure 16D) by atlas size and condition of its neural arch. In *E. longicauda*, the dorsal ridge of the neural arch becomes well-ossified at a smaller size, and has an anteriorly raised crest. This ridge is relatively straight in *E. lucifuga*. All adult *E. lucifuga* vertebrae are at least twice the size of *E. bislineata* vertebrae.

The remaining vertebral regions of CBC *Eurycea lucifuga* fossils seem to consist of two morphological populations: 114 "robust" vertebrae and 539 "normal" vertebrae (Figures 17A-D). At first mistaken for a different species of *Eurycea*, the "robust" bones are always large, well-ossified, and broader than the "normal" vertebrae. Only one comparative specimen (ASU 5302, SVL = 62 mm, male, locality unknown) was found to be identical to the "robust" population (Figure 17C). Other comparative skeletons of males show the "normal" form. Whether the condition is sexual dimorphism or age-related is unknown due to inadequate comparative material for *E. lucifuga*.

Eurycea sp.

Fossil elements: 1 atlas, 28 T_1, 18 T_2, 3 T_3, 96 mid-trunk, 2 prescra, 15 sacra, 25 caudosacra, 385 caudals. NIE = 573.

Temporal distribution: Strata III (3), IV (51), IV/V (119), V (357), VI (35), VII (7), and VIII (1).

Remarks: These fossils showed Eurycea characteristics but are either difficult-to-identify caudal vertebrae, too fragmented, or are too immature for specific identification. Bones of juvenile E. lucifuga and E. longicauda are difficult to differentiate. Due to the great abundance of E. lucifuga in the deposit, most of these Eurycea sp. fossils are probably remains of E. lucifuga.

Genus Plethodon Tschudi, 1838

Except for obvious differences in adult size, skeletal elements of most Plethodon species are very similar. Transverse processes of trunk vertebrae exceed zygapophyseal margins and arise united but are distally separate (Figures 18A and 18C). Parapophyses are slightly in advance of diapophyses on T_1 through T_3, and are completely in advance on following trunk vertebrae. Hyperapophyses are separate on all vertebrae. Basapophyses are absent or, if slightly indicated, placed at the equator of the centrum. Neural ridge of precaudal

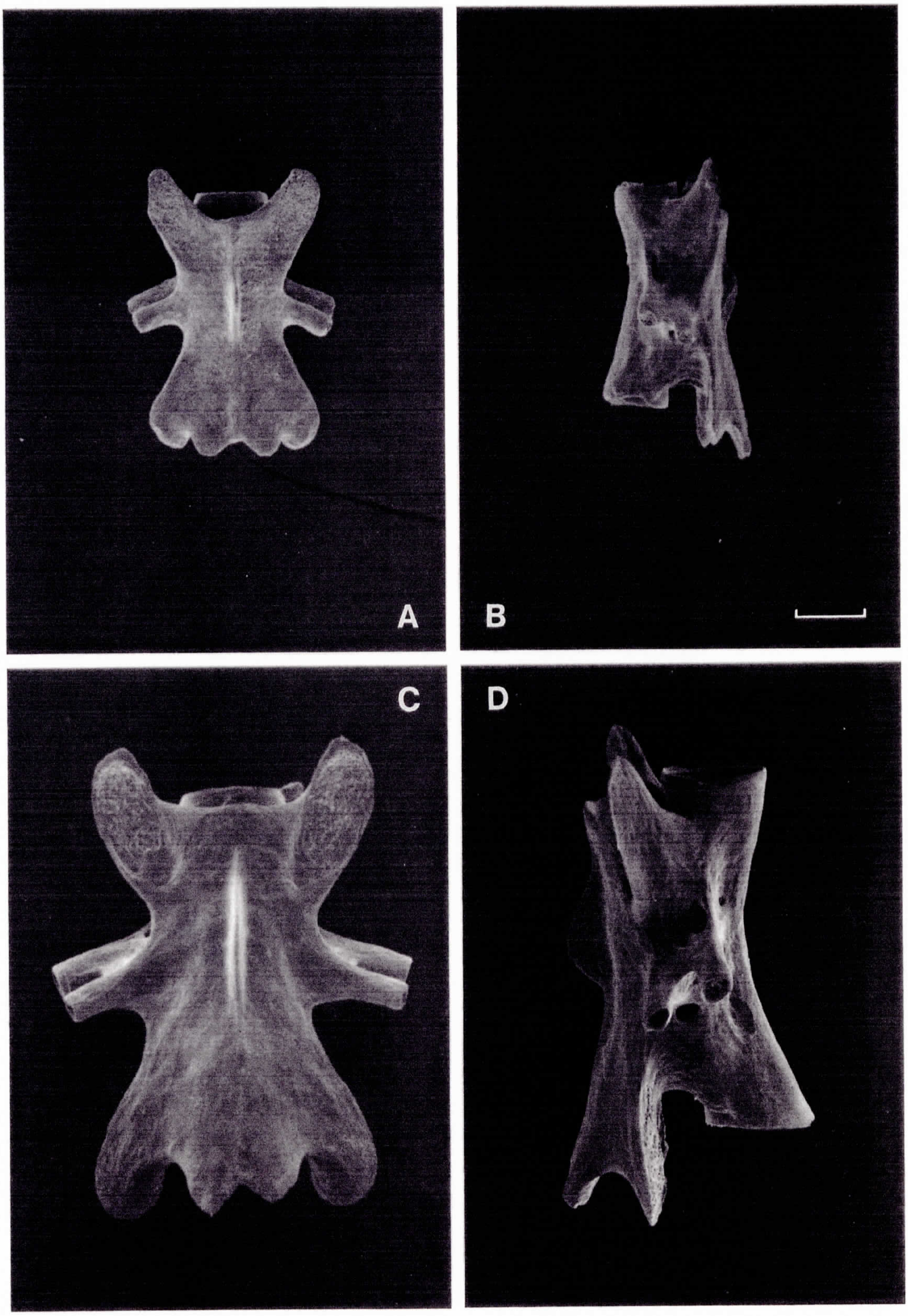
FIGURE 18. SEM's of *Plethodon* vertebrae. Scale = 0.5mm.

A. Dorsal aspect of *Plethodon dorsalis* fossil T_m.

B. Lateral aspect of *Plethodon dorsalis* fossil T_m.

C. Dorsal aspect of reference *Plethodon glutinosus* T_m.

D. Lateral aspect of reference *Plethodon glutinosus* T_m.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vertebrae weakly to moderately developed. Caudal neural ridges display gentle curvature in contrast to linear-type ridges of some _Eurycea_ species (compare Figures 19A-B). Posterior edge of postzygapophyses are rounded in most species.

Plethodon dorsalis Cope, 1889

zigzag salamander

Fossil elements: 1 atlas, 1 T_1, 1 T_2, 1 T_3, 64 mid-trunk vertebrae, 3 sacra, 19 caudosacra, 9 caudal. NIE = 99 and MNI = 23.

Temporal distribution: Strata IV (1), IV/V (9), V (51), and VI (15).

Remarks: Vertebrae of adult _P_. _dorsalis_ are small with prezygapophyseal to postzygapophyseal lengths of 2 to 2.5 mm on mid-trunk vertebrae (Figures 18A-B). A similar species, _P_. _cinereus_, has vertebrae in the same size range. All _P_. _dorsalis_ vertebrae have slightly less inclined neural arches than do _P_. _cinereus_ vertebrae. The atlas, T_1, and T_2 of the two species are extremely difficult to differentiate. Specific determination of the atlas fossil listed above was based on the absence of any other identifiable _P_. _cinereus_ fossils. Transverse processes of T_1 and T_2 are more widely spaced (approx. 1 transverse process width apart) than in _P_. _cinereus_. Neural ridges are weakly developed in mid-trunk vertebrae.

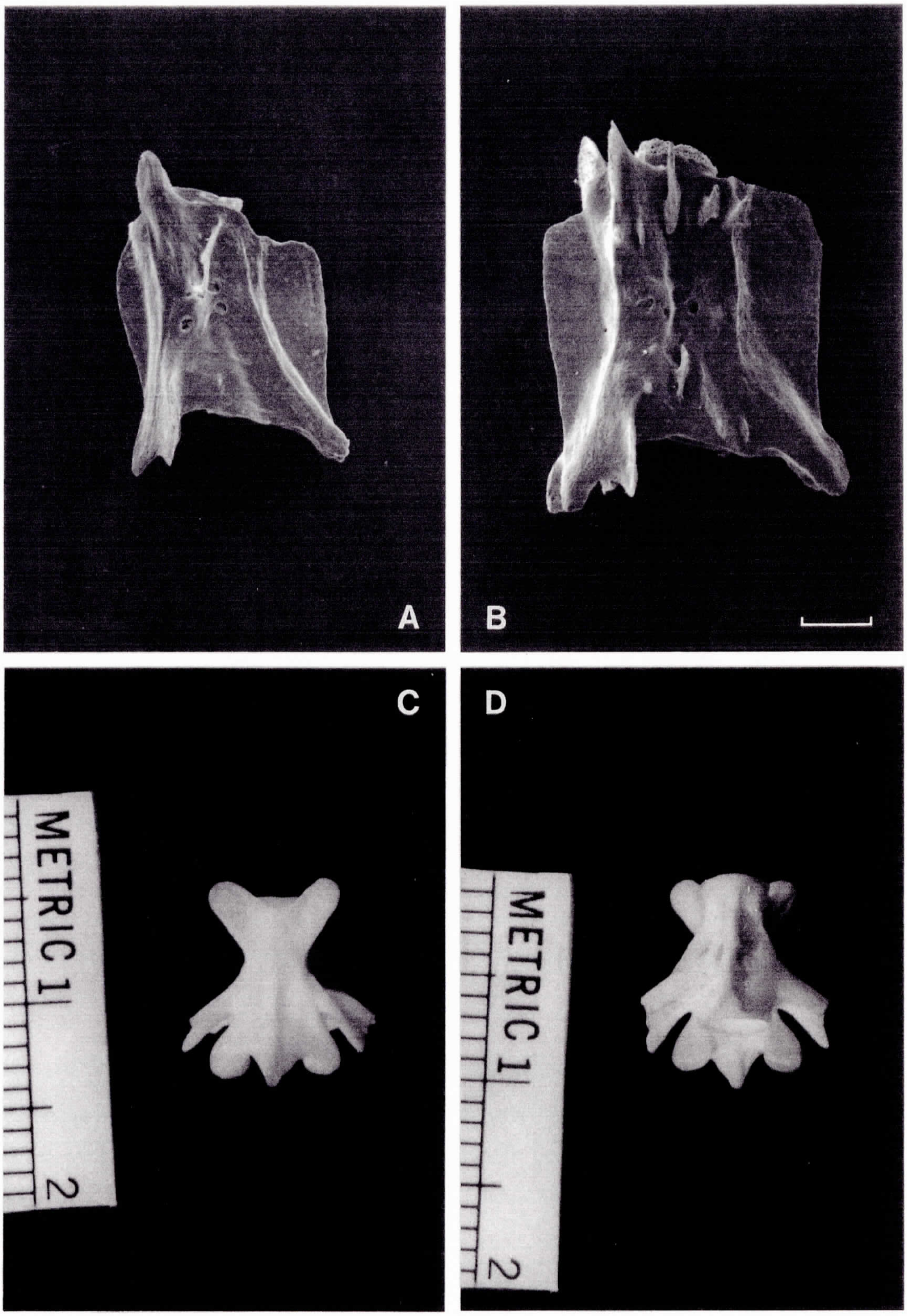
FIGURE 19. Plethodontid (SEM scale = 0.5mm) and proteid (scale = millimeters) vertebrae.

A. Lateral aspect of reference *Plethodon glutinosus* caudal vertebra.

B. Lateral aspect of reference *Eurycea* sp. caudal vertebra.

C. Dorsal aspect of reference *Necturus maculosus* T_m.

D. Ventral aspect of reference *Necturus maculosus* T_m.


A
B
C
D
METRIC 1
2
METRIC 1
2

Plethodon glutinosus (Green, 1818)

slimy salamander

Fossil elements: 1 atlas, 2 T_3, 22 mid-trunk vertebrae, 4 sacra, 7 caudosacra, 38 caudal. NIE = 74 and MNI = 25.

Temporal distribution: Strata V (20), VI (31), VII (21), VII/VIII (1), and VIII (1).

Remarks: In adult P. glutinosus, vertebrae (Figures 18C and 18D) are at least twice the size of P. dorsalis vertebrae and have a steeper neural arch (compare Figures 18A and 18B). Slimy salamander basapophyses, usually only slightly indicated, are situated on the equator of the centrum. The basapophyses of most other plethodontids are ventro-laterally placed.

Plethodontinae

Fossil elements: 34 vertebrae.

Temporal distribution: Strata III(1), IV/V(3), V(16), VI(10), VII(3), and VIII(1).

Remarks: These fragmented plethodontine vertebrae have no discernable genus level characters.

Family Proteidae Gray, 1825

Genus Necturus Rafinesque, 1818

Vertebrae are amphicoelous and, except for the atlas, have no spinal nerve foramina. The Necturus atlas is unique in having a reduced odontoid process and spinal nerves exiting above the occipital condyles. Other vertebrae have completely united hyperapophyses which terminate as a pit well beyond the postzygapophyses (Figure 19C). Trunk vertebrae possess a ventro-laterally pinched centrum and reduced diapophyses joined to the parapophyses by a boney web (Figure 19D). Parapophyses are also associated with the anterior and posterior ends of the centrum by a web of bone. As in other aquatic salamanders, the hyperapophysis of caudal vertebrae is elongated as is the haemal spine. Epiphyses of adult long bones are cartilaginous, resulting in an amphicoelous-type diaphysis in postmortem very similar to Cryptobranchus.

Necturus cf. maculosus (Rafinesque, 1818)

mudpuppy

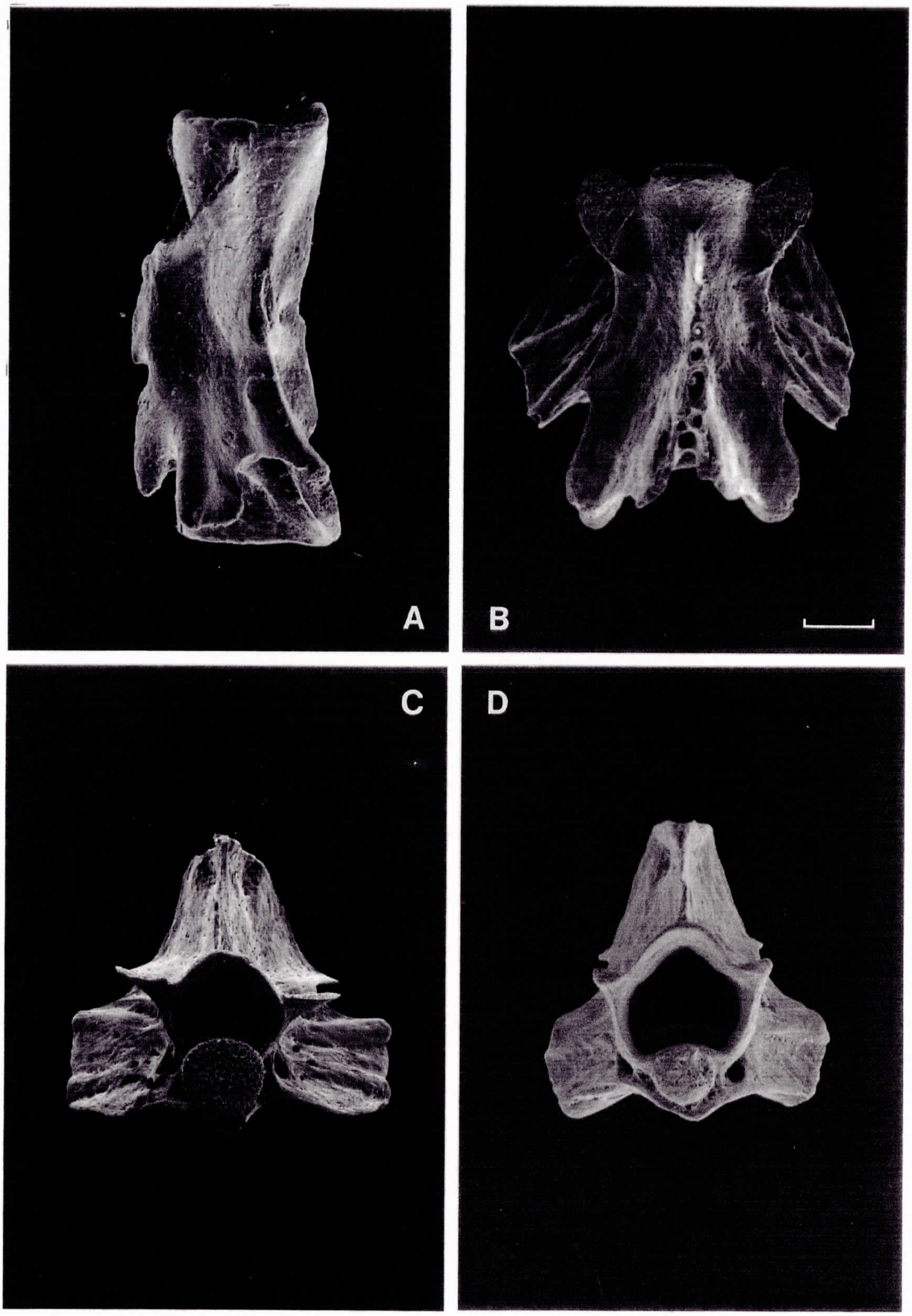
Fossil elements: 1 mid-trunk vertebra, 1 caudosacrum, 1 caudal, 1 left humerus, 1 right humerus. NIE = 5 and MNI = 3.

Temporal distribution: Strata IV (3) and V (2).

Remarks: The trunk vertebra (Figure 20A) was assigned to this species due to a reduced diapophysis with bone webbing connecting it to a broken parapophysis, and a ridge-like centrum bottom. Caudosacral vertebrae differ in having a flat centrum bottom and well defined lateral edges of the neural arch. Caudal vertebrae of Necturus

FIGURE 20. SEM's of *Necturus* and *Notophthalmus* vertebrae. Scale = 0.5mm.

- A. Lateral aspect of *Necturus maculosus* fossil trunk vertebra.
- B. Dorsal aspect of reference *Notophthalmus viridescens* T_m.
- C. Anterior aspect of reference *Notophthalmus viridescens* T_m.
- D. Anterior aspect of *Notophthalmus viridescens* fossil anterior trunk vertebra.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D

and Cryptobranchus are similar. However, the walls of the neural and haemal arches of Cryptobranchus (Figure 7D) are farther recessed from the posterior end of the centrum, and the neural arch is less upswept in Necturus.

Family Salamandridae Gray, 1825

Salamandrid vertebrae are opisthocoelous (Figure 20C) and all have spinal nerve foramina exiting behind transverse processes. The neural ridge is often well-developed on all vertebrae. Hyperapophyses are united or separate. Basapophyses and hypapophyses are absent. Diapophyses are joined (not fused) with parapophyses along entire length and exceed zygapophyses. Haemal keel is elongate and linear. North America's only living salamandrid genera are Taricha, the western newt, and Notophthalmus, the eastern newt.

Genus Notophthalmus Rafinesque, 1820

This genus contains three species: Notophthalmus meridionalis, N. perstriatus, and N. viridescens. The neural ridge on all vertebrae is extremely tall and is capped with a plataeu of pitted bone. N. perstriatus is a small salamander and has adult vertebrae about half the size of other species. N. meridionalis has shorter neural ridges and longer centra than does N. viridescens. These proportions are reflected by Tihen's (1974) centrum length/total height ratios of 0.95-1.38 and 0.69-0.92 for *N. meridionalis* and *N. viridescens* (Florida), respectively. A unique feature of *N. viridescens* is a highly concave inter-prezygapophyseal neural arch margin, whereas in other *Notophthalmus* species the margin is essentially linear. In contrast, the neural arch margin is convex in *Taricha* species. Alar processes are well-developed on all *Notophthalmus* species, especially in *N. viridescens* (Figure 20B).

Notophthalmus viridescens (Rafinesque, 1820)

red-spotted newt

Fossil elements: 19 vertebrae (position indeterminate), 1 humerus (?), 1 right femur. NIE = 21 and MNI = 6.

Temporal distribution: Strata IV (8) and V (13).

Remarks: Vertebrae were assigned to this species due to a very high and dorsally pitted neural ridge, a relatively short centrum, large alar processes, and being strongly opisthocoelous (Figure 20D). Femora of *Notophthalmus viridescens* are distinct in having a sharp lateral ridge expanding distally to give the bone a flattened appearence.

Unidentified caudates

Fossil material: 20 bone fragments.

Temporal distribution: I/II(1), II(5), III(3), IV/V(2), V(8), and VI(1).

Remarks: These salamander bone fragments are not assignable beyond the ordinal level.

DISCUSSION

Four important and necessary considerations for reconstructing and understanding the historical significance of paleofaunas are: habitat utilization, taphonomy, temporal analysis, and comparison to other sites. Living analogs of fossils provide essential information on habitat choice, behavior, and natural history. Taphonomy, the investigation of processes that affect the accumulation and preservation of fossils, assesses how well the preserved fauna represents the actual salamanders of the cave through the late Pleistocene and Holocene. Temporal distributions of salamander species provide minimal estimates of species living in and around the cave. Finally, data from CBC must be analyzed and interpreted in the context of faunal and chronological similarities or differences with other southeastern late Pleistocene-Holcene cave sites. Each of these considerations is addressed for CBC in the following paragraphs.

Habitat Utilization

Salamanders utilize a diversity of habitats, dictated primarily by reproductive mode. The main dichotomy of salamander reproduction is external versus internal fertilization. Cryptobranchids, hynobiids, and presumably sirenids use external fertilization of eggs laid in water. In the U.S. families of this group, offspring will hatch into aquatic larvae that develop into aquatic adults. Ambystomatids, amphiumids, plethodontids, proteiids, and salamandrids use internal fertilization via spermatophore. Most species have aquatic eggs and larvae. Species may exhibit such variations as terrestrial eggs and aquatic larvae, terrestrial eggs and terrestrial larvae, terrestrial eggs and direct developement (no larval stage), and ovoviviparity or viviparity (Duellman and Trueb, 1986). Most salamander larvae metamorphose into adults by losing larval characteristics like external gills, and may or may not become terrestrial. Paedomorphic salamanders retain some larval features and remain in water as adults. Some species complete their entire life cycle in water, either as neotenes or as transformed adults, and will hereafter be refered to as "aquatic" species. Semi-aquatic species spend at least part of their lives on land.

The only fully aquatic fossil salamanders from CBC are the neotenic species Cryptobranchus alleganiensis and

Necturus cf. *maculosus*. *Cryptobranchus alleganiensis* lives in larger streams or rivers where it is often found nestled under large flat rocks. *Necturus* also occurs in similar habitats. Neither species is known to leave the water to travel far overland. *Notophthalmus viridescens* larvae usually metamorphose into an "eft" stage and spend one to five years as a terrestrial adult. The eft usually returns to water to become the aquatic adult "newt" (Conant and Collins, 1991).

All other CBC fossil salamander species are essentially terrestrial as adults, but each has various microhabitat preferences. Ambystomatids, represented in CBC by *Ambystoma maculatum* and *A. tigrinum*, are fossorial for most of their lives, hence the common name "mole" salamanders. Both species are rarely found for most of the year. Most *Ambystoma* species congregate in temporary pools or ponds in large numbers during spring breeding season (Conant and Collins, 1991).

Eurycea longicauda and *E. lucifuga* are frequent cave dwellers. *Eurycea lucifuga* especially prefers the twilight area of cave entrances where light levels are low and generally occur in cave wall crevaces or shelves (Hutchison, 1956). *Eurycea bislineata* is essentially a brookside salamander, but can also be found in saturated areas near springs or seeps (Conant and Collins, 1991).

Plethodon dorsalis often occurs near cave mouths or in woodlands near springs (Conant and Collins, 1991). Plethodon "glutinosus" is a species complex usually encountered along moist woodland ravines, hillsides, or under rocks and logs and can often be found in caves (Conant and Collins, 1991). The complex is comprised of at least 16 species and semispecies, but P. glutinosus proper is the only species in central Tennessee today (Highton et al., 1989).

Taphonomy

Methods of faunal accumulation in caves may be by death of residents (attrition) or animals trapped in the cave, importation due to predator activity, or physical transport as summarized by Andrews (1990). Resident attrition is generally the result of non-predatory mortality of animals living in the caves. Cave pitfalls are known to accumulate a variety of animals. Accumulation of prey remains is common in caves suitable as lairs for predatory mammals such as canids, felids, and mustelids or as roosts for raptors like owls. These predators may lose prey remains or deposit scats or regurgitate pellets, respectively, that contain undigested bones. Assemblages from predation are biased by predator preferences and could result in importation of extralimital species. Transport of remains may occur by various means such as water movement or woodrat activity.

Most CBC terrestrial salamander fossils probably resulted from attrition. This seems especially true for the cave frequenting salamanders (Eurycea lucifuga, E. longicauda, E. cf. bislineata, Plethodon dorsalis, and P. glutinosus) which comprise 89% of the CBC salamander paleofauna. More puzzling is the presence of two aquatic species, Cryptobranchus alleganiensis and Necturus cf. maculosus. The main entrance of CBC is 30-40m above and away from the Duck River, which probably supports both species today. The presence of the wood turtle, Clemmys insculpta, in CBC Pleistocene strata seems to suggest a more saturated floodplain of the Duck River than presently exists (Parmalee and Klippel, 1981). Sporadic flooding of the cave during the Holocene is unlikely given its elevation (30-40m) above river level. A more plausible mode of accumulation would be by predator transport.

Ambystoma tigrinum fossils are common North American Pleistocene fossils (Holman, 1969). This abundance may be the result of predator activity. Holman (1976) reports finding A. tigrinum bones in a pellet from under the perch of a Great Horned Owl (Bubo virginianus), and this author has identified ambystomatid caudal vertebrae in racoon scats (unpublished data).

One might argue that large ambystomas are common fossils due to having relatively large and dense bones that are more likely to be fossilized and recovered. This hypothesis is very plausible but is not entirely supported by CBC fossils because larger salamander species (Ambystoma spp. and Cryptobranchus), though predominant (74%) in strata I/II through V of CBC (Table 2), are virtually absent in later strata while smaller species are abundant.

It is possible that some Ambystoma fossils are intrusive (anachronistic). According to Holman (1985) intrusive bones are almost always fossorial species such as ambystomatid salamanders or burrowing anurans. However, Holman further states that intrusive bones usually have a different color, texture, and density than the true fossils and are usually articulated. All CBC Ambystoma fossils are stained brown, fragmented, disarticulated, and seem to be more dense than comparative bones of the same species.

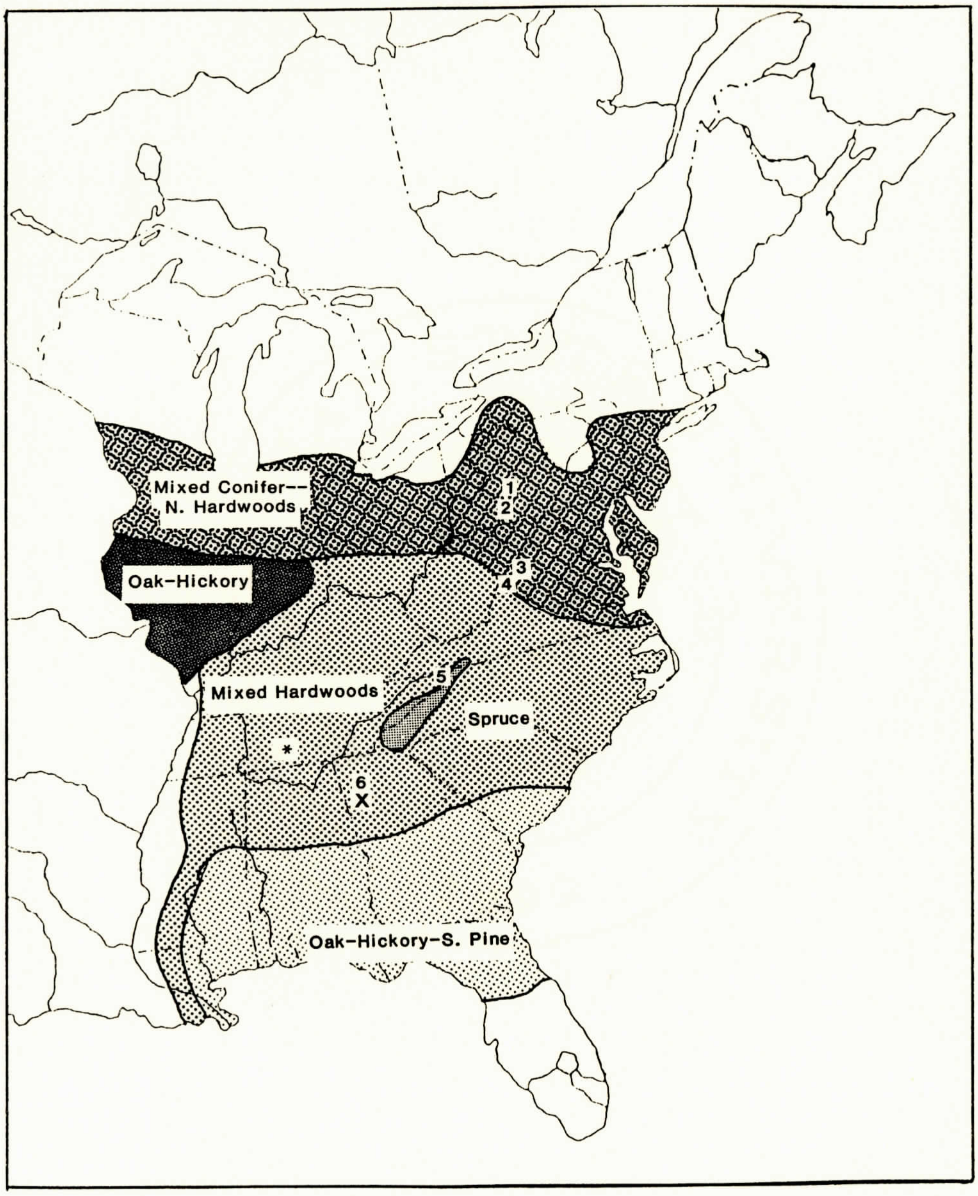
Temporal Analysis

Temporal distributions as seen in Table 2 show that 58% of salamander fossils occur in stratum V while strata I and VIII have 0% and 0.004%, respectively. Relative abundance of fossils roughly corresponds with the amount of matrix in each stratum: stratum V has the greatest volume and strata I and VIII have the least volume. Other fossil taxa show similar temporal quantities. The most numerous fossils are bats, 44% of which are in stratum V with 0.0001% and 0.002% of fossils occuring in strata VIII and I, respectively (Klippel and Parmalee, 1982b). Salamander temporal distributions yield no apparent indication of changes in local habitat, but probably reflect differences in taphonomic episodes and stratum volume.

Similar Sites

A re-evaluation and summary of six late Pleistocene-Holocene Appalachian herpetofaunas is provided by Fay (1988). The summary includes some of the most notable late Pleistocene paleoherpetofaunas of eastern North America: Frankstown Cave, Blair Co., Pennsylvania; New Paris Sinkhole No. 4, Bedford Co., Pennsylvania; Natural Chimneys, Augusta Co., Virginia; Baker Bluff Cave, Sullivan Co., Tennessee; Clark's Cave, Bath Co., Virginia; Kingston Saltpeter Cave, Bartow Co., Georgia (Figure 21). Another significant site, but not covered by Fay (1988), is Ladds Quarry, northwestern Georgia (Holman, 1985). The earliest unit of each deposit dates ca. Wisconsinan Age (no absolute date available), 11,000 YBP, 10,000 YBP (minimum biochronologic assesment), 19,000 YBP, 11,000 YBP, 10,000 YBP, and 17,500 YBP respectively.

FIGURE 21. Location of 8 Pleistocene-Holocene cave faunas and associated late Pleistocene vegetation. 1 = Frankstown Cave, 2 = New Paris Sinkhole No. 4, 3 = Natural Chimneys, 4 = Clark's Cave, 5 = Baker Bluff Cave, 6 = Kingston Saltpeter Cave, * = Cheek Bend Cave, x = Ladds Quarry. Adapted from Fay (1988).


Mixed Conifer--
N. Hardwoods
1
2
3
4
Oak-Hickory
5
Mixed Hardwoods
Spruce
*
6
X
Oak-Hickory-S. Pine

The modes of accumulation are: cave (raptor roost?) for Kingston Saltpeter (and CBC); fissure fill for Frankstown, New Paris, and Ladds Quarry; and raptor roosts for the remaining. The main faunal component for each site is mammal. Raptor activity is not neccessarily the accumulation agent for the associated herpetofaunas. Since most of the above sites are strictly Appalachian, CBC provides a needed westward and lower relief sampling of the eastern North American late Pleistocene herpetofauna.

As seen in Table 3, CBC and Kingston Saltpeter Cave have the second largest sum of salamander "taxa" listed for the Appalachian sites. The diversity of salamander taxa from the Appalachian sites is probably underestimated due to the conservative nature of Fay's taxonomic grouping: *Desmognathus* species, of which four modern species have ranges inclusive of all six sites, are listed simply as "Desmognathinae"; "*Plethodon*-type" is an informal grouping of the genera *Aniedes*, *Hemidactylium*, and *Plethodon*; *Eurycea* species are listed as "*Eurycea* sp." Also, Fay uses Tihen's (1958) subfamily classification of *Ambystoma* species: "*Ambystoma maculatum* group" consists of *A. laterale*, *A. jeffersonianum*, and *A. maculatum* while "*Ambystoma opacum* group" includes *A. talpoideum* and *A. opacum*, all of which have modern ranges in the Appalachian area. Fay's cautious approach towards identification of

TABLE 3. Checklist of salamanders from six late Pleistocene-early Holocene Appalachian local faunas (adapted from Fay, 1988), Cheek Bend Cave, and the Ladds Quarry paleofauna. Abbreviations: BB = Baker Bluff Cave, CC = Clark's Cave, FC = Frankstown Cave, KSC = Kingston Saltpeter Cave, NC = Natural Chimneys Cave, LQ = Ladds Quarry. "X" indicates taxon present.

	Locality							
Taxon	FC	NP4	NC	CC	BB	KSC	CBC	LQ
Cryptobranchus alleganiensis					X		X	
Necturus maculosus					X		X	
Notophthalmus viridescens	X	X	X	X		X	X	
Ambystoma maculatum-group		X	X	X	X	X	X	
Ambystoma opacum-group			X	X	X	X		
Ambystoma tigrinum			X			X	X	X
Ambystoma sp.	X	X		X	X		X	
Desmognathinae		X	X	X	X	X		X
Gyrinophilus porphyriticus			X	X				X
Pseudotriton ruber						X		X
Pseudotriton sp.		X	X	X				
Eurycea sp.		X	X	X		X	X	
Plethodon-type		X	X	X		X	X	
Number of Salamander "Taxa"	2	7	9	9	6	8	8	4
Number of Salamander Bones	10	432	468	675	253	506	1759	?

Desmognathus species is reasonable due to the extreme difficulty in distinguishing these species by single skeletal elements. However, vertebrae of *Aniedes*, *Hemidactylium*, *Plethodon*, some species of *Eurycea*, and some species within Tihen's *Ambystoma* groups are somtimes quite distinct. *Ambystoma*, *Plethodon*, and *Eurycea* fossils from CBC were identified to species level. Fay's taxonomic grouping diminishes the diversity of fossil salamanders from CBC.

Gyrinophilus porphyriticus and *Pseudotriton ruber* are present in the Appalachian sites but not in CBC presumably because modern ranges of those species have excluded central Tennessee. As seen in Table 3, desmognathine salamander remains are frequently recovered in Appalachian Pleistocene cave deposits. Athough the modern distribution of *Desmognathus fuscus* includes central Tennessee, the species is probably excluded as a fossil from CBC due to microclimate variations as discussed below. CBC represents the first known report of *Eurycea* cf. *bislineata* as a possible fossil and the first positive identification of *Eurycea lucifuga* and *Eurycea longicauda* as fossils. Davis (1973) reports fossils of *Eurycea* as being *E. lucifuga* or *E. longicauda*. All other fossil salamanders from CBC have been previously reported from other sites.

Most vertebrate paleontologists working with cave faunas seem to invest relatively little time in identifying salamander fossils. This is likely due to unfamiliarity with salamander bones, finding few salamander fossils, and/or having the additional burden of identifying anurans, lizards, snakes, turtles, and perhaps other taxa from the same site. The CBC salamanders merit close scrutiny because 69% of CBC herpetological skeletal elements belong to salamanders.

Quaternary Herpetofauna Stability

The late Pleistocene was characterized by global warming and corresponding glacial retreats, microclimatic fluctuations, and biota changes. Extinctions and range adjustments of North American late Pleistocene mammals and birds are well documented (Holman, 1991). Eight families, 46 genera, 197 species of mammals and two families and 19 genera of birds (number of species indeterminate) became extinct between the Pleistocene-Holocene boundary (Holman, 1991). Range adjustments are commonly noted, such as those indicated by the fauna of Fay's (1988) Appalachian sites and CBC (Klippel and Parmalee, 1982b). In contrast, late Pleistocene herpetofaunas have shown only a few species extinctions (land tortoises) and range adjustments (Holman, 1991). Extralimital fossil reptiles and amphibians from CBC include a few anurans, one snake, and, most significantly, a turtle (Clemmys insculpta) with a modern range removed 700km from this site (Klippel and Parmalee, 1981).

A common denominator of most North American late Pleistocene faunas (including CBC) is contemporaneous existence of "boreal" and "temperate" species. Some authors (e.g. Holman, 1978) have postulated that such "ecologically incompatible" species coexisted due to climatic equability. Presumably, cooler summers and milder winters would allow southerly distributed taxa to expand northward and vice versa. Rhodes (1984) argues that it is unnecessry to invoke climatic equability because microclimatic altitude ranges may have overlapped between boreal (higher altitude) and temperate animals. Rhodes' argument may be valid with most cave sites because they are most often found in high-relief Blue Ridge physiographic provience. However, CBC data refute this due to occuring in a low-relief area more than 300 km from extreme altitude gradients (Klippel and Parmalee, 1982a). In other words, raptors in the Nashville Basin (CBC area) do not have such a variable altitude/temperature gradient for feeding ranges as raptors in the Blue Ridge Province.

Fay (1988) lists possible alternative explanations for contemporaneous temperate reptiles and amphibians with "boreal" birds and mammals:

> "(1) There are fewer eastern North American boreal herptiles than mammals that could be displaced by

> glaciation + temperate association. (2) ...many species...go unrecognized because of osteological similarity to widespread taxa. (3) Herptiles did not repond as strongly to glacial-interglacial climatic changes as did other vertebrates. Herptiles have a marked capacity for acclimatization to seasonal climatic change that may also provide the ability to adapt to progressive, long term change by alterations in physiology or behavior rather than distribution. (4) Much of the herpetofauna of the central and southern Appalacians has its center of distribution here, reflecting probable center of origin and/or restricted microhabitat requirements for many of the species."

Holman (1991) suggests that some paleoherpetologists have "the ingrained idea that all Pleistocene herpetological material (other than certain large tortoise fossils) must belong to modern species" because "one who names an extinct Pleistocene species immediately becomes the object of intense scrutiny; but one who identifies a modern species on the basis of fragmentary material is seldom taken to task." Holman (1991) also points out that earlier Pleistocene extinctions could have been missed. In contrast to numerous late Pleistocene sites, early and middle Pleistocene sites are rare and have fewer species (Holman, 1991; Estes, 1981).

As with most Pleistocene herpetofaunas, the species of CBC fossil salamanders have modern ranges inclusive of the study site. However, distributions within ranges are usually not uniform and only certain species are expected to occur in a given microhabitat. CBC is centered in a cedar and hardwood glade characterized by dry and open conditions. A survey of reptiles and amphibians in the cedar glades of Lebanon State Forest in the Nashville Basin (central Tennessee) indicates that certain species common to mesophytic areas are uncommon in glades and vice versa (Jordan et al., 1968). Salamanders collected in the glades include *Ambystoma opacum*, *A. maculatum*, *Notophthalmus viridescens*, *Plethodon dorsalis*, and *Eurycea lucifuga*. The scarcity of brooks or seepages in glades presumably accounts for the absence of *Desmognathus fuscus* (as well as water snakes and most aquatic turtles) which is otherwise common in much of central Tennessee (Jordan et al., 1968). The same edaphic features of the CBC glade may also explain the absence of *D. fuscus* as a CBC fossil. *Ambystoma opacum* has a modern distribution which includes central Tennessee, but is absent from CBC as fossils for unknown reasons.

Suggestions for Future Studies

The initiation of salamander fossil identification in this study was difficult due to inadequate precedent descriptive work. Most paleoherpetological analyses are illustrated by an insufficient number of drawings or not at all. Verbal descriptions alone are usually difficult to interpret and are consequently of little use. This paleoherpetological study is unique in terms of graphic quality and reported detail.

Large and diverse reference collections are required in order to accurately assess variabilty that may affect the identification of a salamander fossil. Specific identifications of the CBC salamanders would have been impossible without such a collection. However, as Holman (1991) states: "...considering the intense conservation ethics that are embraced by most of us today, procuring a comparative skeleton collection that is adequate for variational studies often becomes a legal or ethical problem." Therefore, photographic surveys and keys to herpetological skeletons would constitute valuable references to paleoherpetologists.

Summary

The major points emphasized in this study are:

1) Ten fossil salamander species are identified from CBC: *Ambystoma maculatum*, *Ambystoma tigrinum*, *Cryptobranchus alleganiensis*, *Eurycea* cf. *bislineata*, *Eurycea longicauda*, *Eurycea lucifuga*, *Necturus* cf. *maculosus*, *Notophthalmus viridescens*, *Plethodon dorsalis*, and *Plethodon glutinosus*.
2) CBC represents the largest reported quantity (1,759 bones) of non-contemporaneus salamander fossils for any geologic time period.
3) *Eurycea* cf. *bislineata* and possibly *Eurycea lucifuga* are reported here as fossils for the first time.

4) Two seemingly distinct morphological variations of *Eurycea lucifuga* vertebrae are noted in fossils and reference material.

5) Exceptionally large vertebrae and leg bones of *Ambystoma tigrinum* from strata IV and V rival the largest of living tiger salamanders.

6) Although a few extralimital fossil reptiles and amphibians have been tenuously reported from CBC (Klippel and Parmalee, 1982b), all CBC salamander fossils represent species living in the region today. The absence of *Desmognathus* fossils may be due to dry edaphic conditions surrounding the cave. The cause for the absence of *Ambystoma opacum* fossils is unknown.

7) The presence of two aquatic species, *Cryptobranchus alleganiensis* and *Necturus maculosus*, in CBC are probably the result of predator activity. All other fossil salamanders were probably residents.

8) Variations in temporal distributions of salamanders probably reflect differences in taphonomic episodes and not microclimatic changes.

9) Ample illustrations in future paleoherpetological studies will enhance the ability of paleontologists to identify fossils, especially those of salamanders.

GLOSSARY

Acetabulum: A facet or socket in the ilium that recieves the head of the femur.

Alar process: A flat or wing-like process, usually extending downward and forward from the antero-ventral portion of the basal part of the parapophysis.

Amphicoelous: The condition in which the vertebral centrum is hollow at each end.

Appendicular skeleton: The pectoral girdle, pelvic girdle, and limb bones.

Articular facet: A depression in a bone permitting articulation with another bone.

Atlantal cotyle: One of a pair of anterior facets on the atlas which articulates with the occipital condyle.

Atlas: The first or most anterior vertebra of the vertebral column.

Axial skeleton: The vertebral column and ribs.

Basapophysis: One of a pair of ventro-lateral processes positioned on the anterior or posterior portion of the centrum.

Caudal vertebra: A tail vertebra.

Caudosacral vertebra: One of up to two vertebrae occuring posterior to the sacrum and anterior to the first caudal vertebra.

Centrum: The actual body of the vertebrae below the neural canal.

Crista dorsalis: Small knob-like dorsal projection on the proximal portion of the salamander humerus.

Crista ventralis: A flange-shaped ventral projection on the proximal portion of the salamander humerus.

Dentary: Most anterior tooth-bearing bone of the mandible.

Diaphysis: The shaft of a long bone.

Diapophysis: The upper member of paired rib articulations found on each side of a vertebra.

Epiphysis: Either end of a long bone, which articulates with another bone.

Femur: The thigh bone.

Fibula: One of two bones forming the leg segment distal to femur and knee.

Fossa: A depression for muscle attachment on a bone.

Haemal arch: Boney arch formed by the union of the haemal spines below the caudal artery on caudal vertebrae.

Haemal keel: See Hypophysis.

Humerus: The upper foreleg bone between the elbow and shoulder.

Hypophysis: A median ventral process of the centrum which can be either spine-like or ridge-like.

Hyperapophysis: Posterior projection(s) of the neural arch between the postzygapophyses.

Ilium: The largest of three bones that make up each half of the pelvic girdle. The ilium bears a flattened wing of bone that is attached by ligaments to the sacrum.

Ischium: The most posterior of the three bones that make up the pelvic girdle.

Foramen magnum: A large hole at the posterior base of the skull through which the spinal cord exits the skull.

Mandibular symphysis: The medial articulation between the right and left dentaries.

Maxilla: A paired lateral tooth-bearing bone posterior to the premaxilla in the upper jaw.

Meckelian groove: The slot on the posterior-medial side of the dentary where the articular bone inserts.

Mid-trunk vertebra: Any vertebra occuring between the third vertebra and the presacrum.

Neural arch: The two plates arising from the top of the centrum, surrounding the neural canal, and meeting at the midline.

Neural canal: The canal for the spinal cord, which passes under the neural arch and above the centrum of each vertebra.

Neural ridge: A dorsal, ridge-like process arising at the midline of the neural arch.

Notocord: A rod-like cartilaginous structure for axial support in larval amphibians, that is replaced by the vertebral column in adults.

Pars palatina: A ridge running above and parallel to the teeth on the salamander premaxilla.

Pars nasalis: A long, medial process projecting dorsally from the dorsal surface of the salamander premaxilla.

Posterior mental process: A spine-like, medio-ventral projection on the salamander dentary.

Premaxilla: The most medial paired tooth-bearing bone of the upper jaw.

Opisthocoelous: Condition in which the anterior portion of the vertebral centrum is filled with compact bone while the posterior portion is hollow.

Occipital condyle: One of a pair of bulb-like processes projecting from rear of the amphibian skull, articulating skull and atlas.

Odontoid process: A cup- or knob-shaped anterior projection of the atlas which articulates with the ventro-medial surface of the magnum foramen.

Parapophysis: The lower transverse process.

Pectoral girdle: The structure which supports a forelimb by articulating with the proximal end of the humerus and vertebral column.

Pelvic girdle: The structure which supports a hindlimb by articulating with the proximal end of the femur and vertebral column.

Postzygapophysis: One of a pair of posterior processes bearing ventral articular facets that articulate with a prezygapophysis of the following vertebra.

Premaxilla: The anteriormost paired (or not) tooth-bearing bone (or not) of the upper jaw.

Presacrum: The vertebra occuring immediately anterior to the sacrum.

Prezygapophysis: One of a pair of anterior processes bearing dorsal articular facets that articulate with a postzygapophysis of the preceding vertebra.

Pterygapophysis: A non-articulating process that arises from the dorsal surface of a postzygapophysis and extends postero-laterally.

Radius: One of the two largest long bones in the distal portion of the forelimb.

Sacrum: The vertebra which supports the pelvic girdle.

Scapula: The largest and most proximal of the bones that make up each half of the pectoral girdle.

Snout-vent length (SVL): The distance between the tip of the snout and the posterior end of the cloacal slit of a salamander.

Spinal nerve foramen: An opening in a neural arch through which a spinal nerve exits the neural canal.

Tibia: One of two long bones forming the second segment of the hindlimb.

Trochanter: The knob-like projection on the proximal portion of the salamander femur.

Trunk vertebra: Any vertebra occuring after the atlas and before the presacrum.

Tuberculum interglenoideum: See Odontoid process.

Transverse processes: The diapophyses and parapophyses. These structures articulate with rib heads.

Ulna: One of the two long bones forming the second segment of the forelimb.

Vascular foramen: A hole in a bone through which a blood vessel passes.

ABBREVIATIONS

CBC	Cheek Bend Cave
CS	Caudosacrum
MNI	Minimum Number of Individuals
MYA	Million Years Ago
NIE	Number of Identified Elements
PS	Presacrum
T_1	1st Trunk Vertebra
T_2	2nd Trunk Vertebra
T_3	3rd Trunk Vertebra
Tm	Mid-Trunk Vertebra
SVL	Snout-Vent Length
YBP	Years Before Present (1950)

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