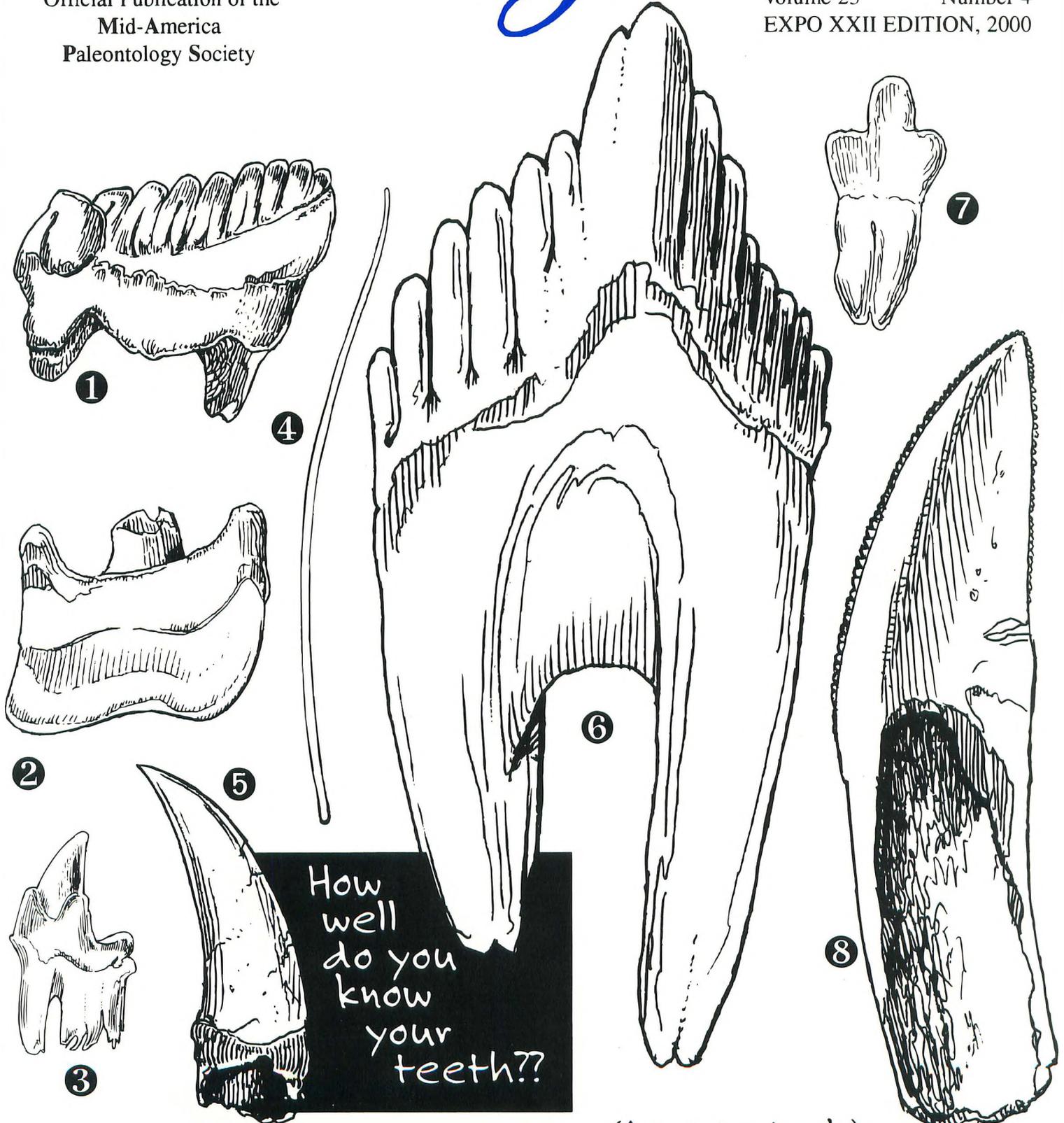


# M.A.P.S *Digest*

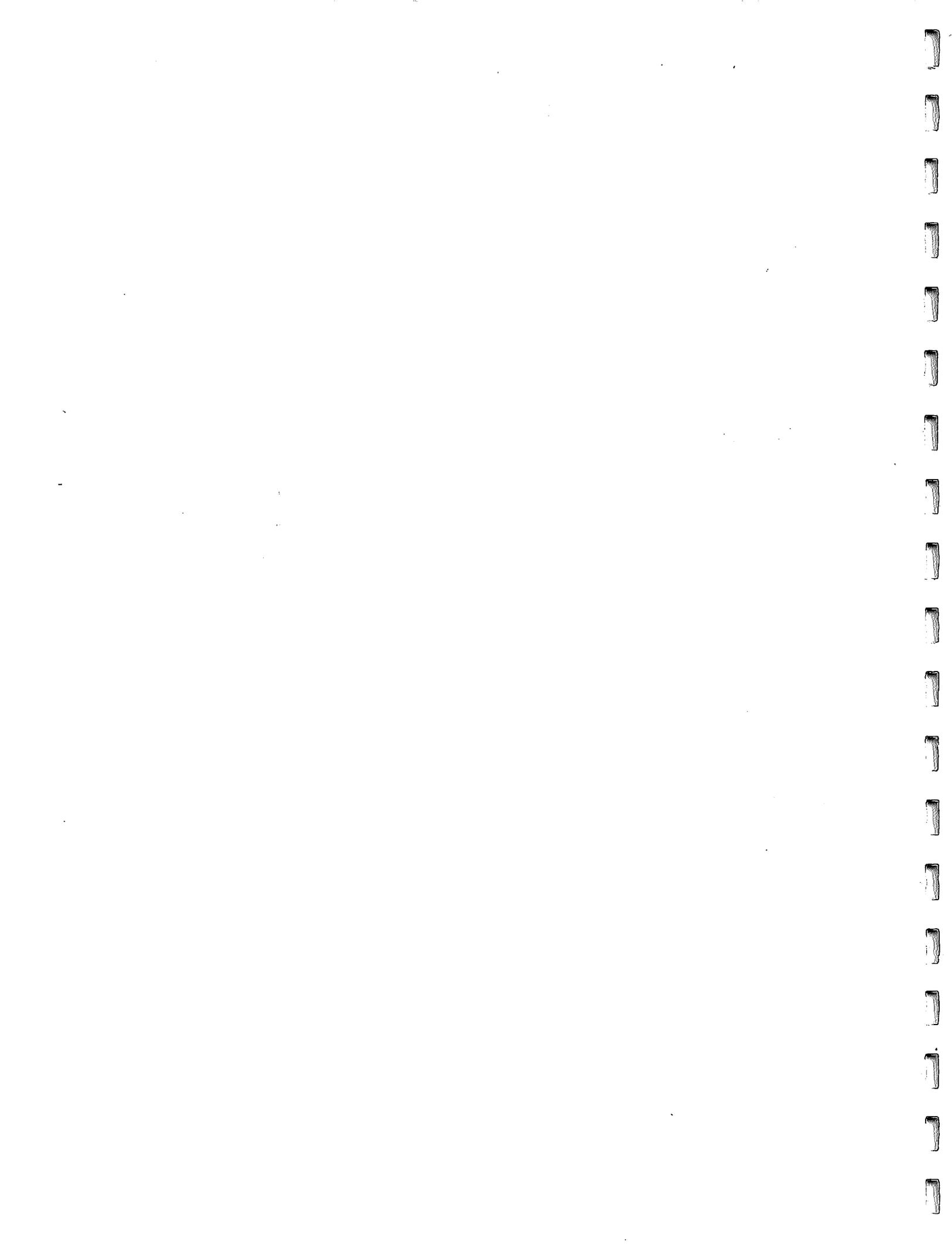
Official Publication of the  
Mid-America  
Paleontology Society

Volume 23      Number 4  
EXPO XXII EDITION, 2000



How well do you know your teeth??

(Answers on back.)



# TEETH

## M.A.P.S. DIGEST

### EXPO XX II EDITION

MID-AMERICA PALEONTOLOGY SOCIETY

A LOVE OF FOSSILS BRINGS US TOGETHER

Western Illinois University  
Union Ballroom  
Macomb, Illinois 61465  
April - 2000

1951

1951

1951

1951

1951

## ACKNOWLEDGEMENT

### TEETH

To recognize the **Authors & Artists** of this edition of the EXPO Digest -- "**TEETH**" is a privilege for me, as editor it always helps to know a little something about the Theme subject. On this one, you could write a book on all I don't know about TEETH (as the saying goes) except my own, and that doesn't count.

I am barely able to tell a shark's tooth from a dinosaur tooth. So, I do appreciate those who took the time to contribute to this issue.

I especially want to thank the Paleontology Society, and the authors there of for permission to use their articles.

Again we have some first time contributors: John Fagan, Carl Frailey, Leslie Heinzl, Betty Lemkau, Ralph Molnar, Dale Sparling, Ed Swiatova, Jessica Theodor, and David Thompson, and, of course our stand-bys, David Jones, Jim Konecny, Randy Patrick, Jim Brace-Thompson Also thanks to Frank Holmes our member in Australia who sent Molnar's article, and a big, big THANK YOU To David Peters for the art work. And how about the drawings of Serena Heinzl !! Shows much talent.

The Mid - America Paleontology Society was formed to promote popular interest in the subject of paleontology, to encourage the proper collecting, study, preparation and display of fossil material; and to assist other individuals, groups and institutions interested in the various aspects of paleontology. It is a non-profit society incorporated under the laws of the State of Iowa.

Karl A. Stuekerjuergen  
President, M.A.P.S.  
1503 265th Avenue  
West Point IA 52656-9029

Dale Stout  
1st Vice President  
2237 Meadowbrook Dr  
Cedar Rapids IA 52403

Marvin Houg  
2nd Vice President  
3330 44th St. N.E.  
Cedar Rapids IA 52402

Alberta Cray  
Secretary  
1125 J Avenue N  
Cedar Rapids, IA 52405

Sharon Sonnleitner  
Treasurer  
4800 Sunset Dr., SW  
Cedar Rapids, IA 52404

Dale Stout  
Membership  
2237 Meadowbrook Dr.SW.  
Cedar Rapids, IA 52403

Sharon Sonnleitner  
MAPS DIGEST EDITOR  
4800 Sunset Dr., SW  
Cedar Rapids, IA 52404

Allyn Adams  
Show Chairman  
612 W. 51st Street  
Davenport, IA 52806

Directors: Blane Phillips (00), Doug DeRosear (01), Tom Walsh (02)

Margaret E. Kahrs, Editor  
EXPO XXI EDITION MAPS DIGEST  
9145 W U.S. Hwy. 50 East  
Seymour, IN 47274 - 9104

COVER STORY  
By: David Peters

Identification of cover illustrations

1. Ektopodon - poorly known marsupial
  2. Thylacoleo - marsupial
  3. Kielantherium - early mammal
  4. Pterodaustro - pterosaur
  5. Spinosaurus - dinosaur
  6. Zygorhiza - whale
  7. Probainognayhus - cynodont
  8. Giganotosaurus - dinosaur
- \* Helicoprion - a shark, shown back cover

Table of Contents

MAPS EXPO XXII EDITION - TEETH

COVERSTORY/.....iv  
\* David Peters, St. Louis, Missouri

PROTOREODON WALSHI, A NEW SPECIES OF AGRIOCHOERID (OREODONTA,  
ARTIODACTYLA, MAMMALIA).....1  
Jessica M. Theodor, Providence, Rhode Island

SHARK TOOTH TALES: FOSSIL TEETH TELL THE STORY OF TWO  
ENVIRONMENTS.....13  
\* Jim Brace-Thompson, Ventura, California

ADVENTURES WITH DENTURES AT MAZON CREEK.....23  
\* Jim Konecny, Prescott, Arizona

RODENT TEETH AND CONVERGENCE.....28  
Carl D. Frailey, Overland Park, Kansas

CONODONTS FROM THE PROUT DOLOMITE OF NORTH CENTRAL OHIO AND  
GIVETIAN (UPPER MIDDLE DEVONIAN) CORRELATION PROBLEMS.....42  
Dale R. Sparling, Marshall, Minnesota

RECOGNISING FOSSIL MAMMAL TEETH.....58  
Ralph Molnar, Queensland, Australia

CHONDRICHTHYES FROM THE GLEN DEAN LIMESTONE FM. MIDDLE  
CHESTERIAN MISSISSIPPIAN, OF SOUTHERN INDIANA.....83  
\* Randy R. Patrick, Roachdale, Indiana, and Anne M. Shaw, Franklin Indiana

TEETH.....92  
\*David L. Thompson, Ann Arbor, Michigan

HOW DO YOU CHEW.....98  
\*David Jones, Worthington, Minnesota

SHARK BYTES.....103  
Ed Swiatova, Sherman, Texas

FOSSIL TEETH AND THE INTERNET.....109  
\* John J. Fagan, Chicago, Illinois

COLLECTING FOSSIL SHARK TEETH IN THE LEE CREEK MINE,  
AURORA, N.C. .... 110

\* Les Heinzl, Thurmont, Maryland

THE UNIQUE AND CURIOUS DESMOSTYLUS ..... 118

\* Betty L. Lemkau, Castro Valley, California

\* denotes M. A. P. S. members

---

THE UNIVERSITY OF CHICAGO  
DEPARTMENT OF CHEMISTRY  
5800 S. UNIVERSITY AVENUE  
CHICAGO, ILLINOIS 60637

RECEIVED  
MAY 15 1964

1964

# PROTOREODON WALSHI, A NEW SPECIES OF AGRIOCHOERID (OREODONTA, ARTIODACTYLA, MAMMALIA) FROM THE LATE UINTAN OF SAN DIEGO COUNTY, CALIFORNIA

Jessica M. Theodor

Department of Ecology & Evolutionary Biology, Brown University, Providence, RI 02912

**ABSTRACT**—A new agriochoerid, *Protoreodon walshi* new species, from the middle Eocene Santiago Formation, San Diego County, California, is described from the Jeff's Discovery and Rancho del Oro local faunas, considered to be late Uintan in age. It differs from most other species of *Protoreodon* in having an undivided P<sup>1</sup> para-metacone and a P<sup>1</sup> protocone connected to the paracone by a buccolingual crest. Associated postcranial material is abundant and well preserved. The postcranial skeleton shows several features which probably represent the primitive oreodont condition, including closely appressed metapodials, hooved ungual phalanges, the lunar in broad contact with both the magnum and the unciform in anterior view, and having the magnum larger than the trapezoid.

Two specimens of a larger morph, *Protoreodon* cf. *walshi*, show a different P<sup>1</sup> morphology and might represent another new species. Diversity of agriochoerid oreodonts in California is at least as high as has been reported for the Vieja Group of Texas, although not as high as in the Uinta Basin of Utah, where the genus *Diplobunops* is also present.

## INTRODUCTION

*PROTOREODON* IS a genus of small to medium-sized agriochoerids, known from the middle Eocene of North America. *Protoreodon* is widespread, is a characteristic component of Uintan age faunas, and also occurs in the early Chadronian. Fossils belonging to this genus are found in the Uinta Basin of Utah (Gazin, 1955; Scott, 1899), Badwater Creek, Wyoming (Black, 1978), Swift Current Creek, Saskatchewan (Storer, 1984), Trans-Pecos, Texas (Wilson, 1971), and Ventura and San Diego counties in southern California (Golz and Lillegraven, 1977; Walsh, 1991).

Walsh (1991, 1996) reported *Protoreodon* from a number of localities, recovered during salvage excavations for new housing developments and highway construction in San Diego County. *Protoreodon* is found in the Poway and Cloud 9 faunas and the Eastview, Jeff's Discovery, Rancho del Oro, Laguna Riviera, Mission del Oro, and Camp San Onofre local faunas. The material from Laguna Riviera has been referred to *P. pumilus* or *P. annectens*, that from Camp San Onofre and Mission del Oro to *Protoreodon* sp., and the rest to *Protoreodon* cf. *parvus* (Golz, 1976; Golz and Lillegraven, 1977; Kelly, 1990; Walsh, 1991) or *Protoreodon* new sp. 1 and *Protoreodon* new sp. 2 (Walsh, 1996). The material from the Jeff's Discovery and Rancho del Oro local faunas previously referred to *P. cf. parvus* (Walsh, 1991) and *Protoreodon* new sp. 1 (Walsh, 1996) represents at least one new species, intermediate in size for the genus, with relatively primitive molar and P<sup>1</sup> morphology, and an unusual P<sup>1</sup> morphology.

Little associated postcranial material of *Protoreodon* has been described. The San Diego collection allows an opportunity to describe the postcranial skeleton of *P. walshi* n. sp., as both articulated and disarticulated material is preserved.

## GEOLOGIC SETTING

Material described here was collected from localities in the upper part of the Santiago Formation in northwestern San Diego County near Oceanside, California. Near Carlsbad, the Santiago Formation unconformably overlies Cretaceous rocks, and consists of interbedded marine and nonmarine sediments (Golz, 1976). A recently reported marine section of the upper Santiago

Formation at Aviara, near Carlsbad, yielded a coccolith assemblage that is correlated with the calcareous nannoplankton zone CP14a. The age of zone CP14a is estimated to be 44–41 Ma and is considered to be late middle Eocene in age (Golz and Lillegraven, 1977; Walsh, 1991, 1996).

Most of the specimens reported here were recovered from two areas, Jeff's Discovery and Rancho del Oro (Fig. 1). Kelly et al. (1991) considered the material from the Jeff's Discovery and Rancho del Oro local faunas to be early Uintan in age based on the stage of evolution of the *Protoreodon* material in relation to species from Laguna Riviera and the Uinta Basin. However, the mammalian faunas from these sites include *Sespedectes*, *Protetrixoides*, *Dyseolemur*, *Griphomys* and *Simimys*, all of which Walsh (1991, 1996) recommended as indicators of a late Uintan age in southern California. None of the taxa which went extinct or emigrated from southern California at the local early-late Uintan boundary are found in either the Jeff's Discovery or Rancho del Oro local faunas. The late Uintan in southern California cannot be regarded as exactly correlating with late Uintan rocks within the Uinta Basin, as few characteristic late Uintan taxa are shared between California and the western interior (Walsh, 1991, 1996). Thus it seems most reasonable to accept a late Uintan age for these local faunas within southern California, although slightly older than the Laguna Riviera local fauna, and reserve judgment on the correlations with the faunas from the Uinta Basin.

The Jeff's Discovery fauna is the most diverse mammalian fauna of this age in the San Diego area. Walsh (1996) also reports *Protoreodon* new sp. 1 (*P. walshi*) from the Cloud 9 and Eastview local faunas. *Protoreodon* has also been recovered from the early Uintan Poway fauna of the Friars Formation, La Jolla Group, referred to *Protoreodon* new sp. 2.

## SYSTEMATIC PALEONTOLOGY

All measurements were made using Mitutoyo Digimatic calipers, and are given to the nearest 0.1 mm. Dental measurements are summarized in Tables 1–2, 4. Postcranial measurements are summarized in Table 3. Detailed locality data are on file at the San Diego Museum of Natural History. Dental terminology follows Golz (1976) and Gentry and Hooker (1988).

**Abbreviations.**—AP, anteroposterior; d, deciduous; L, length; Mc, metacarpal; Mt, metatarsal; T, transverse; W, width. LACM, Natural History Museum of Los Angeles County; YPM-PU, Princeton University Collection, Yale Peabody Museum;

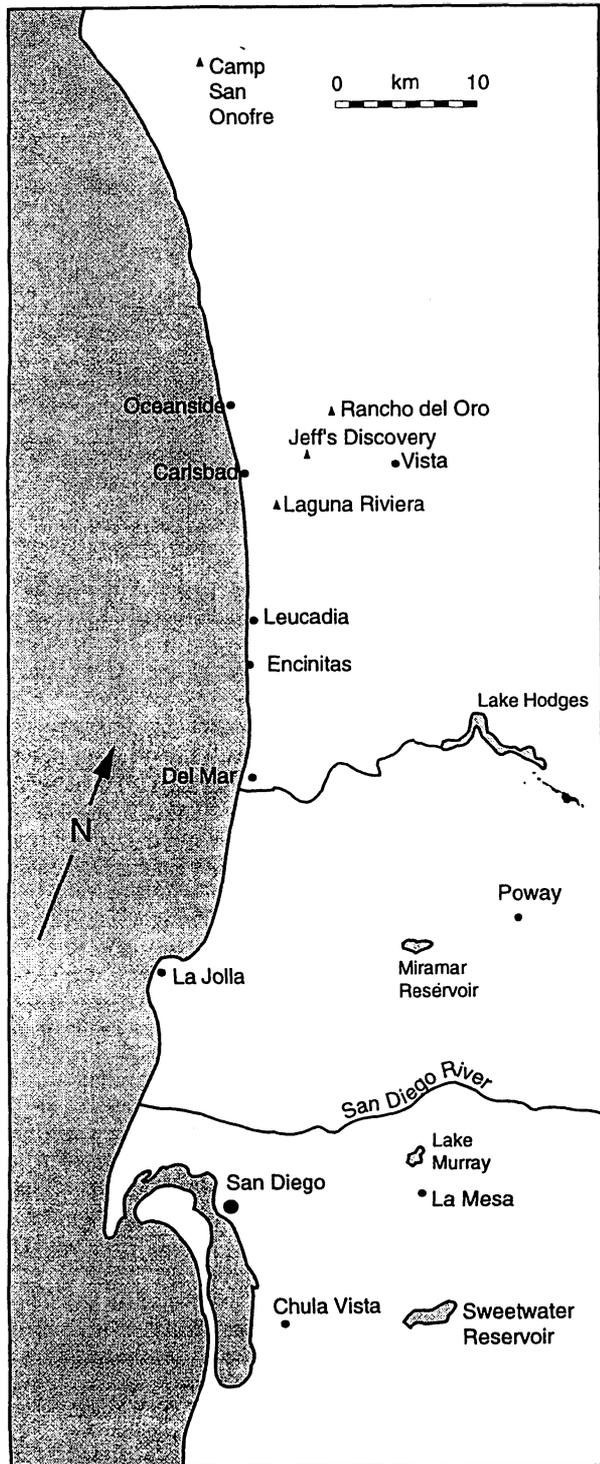


FIGURE 1—Selected localities of Eocene age in western San Diego County, California. After Walsh, 1991.

SDSNH, San Diego Museum of Natural History; UCMP, University of California Museum of Paleontology. Ma, Megannum; NALMA, North American Land Mammal Age.

Family AGRIOCHOERIDAE

Discussion.—Agriochoeridae is a small family of early orodonts, consisting of three genera, *Protoreodon*, *Diplobunops*,

and *Agriochoerus*. Agriochoerids have long been considered as ancestral to the Merycoidodontidae, with most authors deriving merycoidodonts from one of several lineages of *Protoreodon* (Gazin, 1955; Schultz and Falkenbach, 1968; Golz, 1976; Lander, 1978). Wilson (1971) thought that *Agriochoerus* and Merycoidodontidae were polyphyletic, with lineages evolving separately from different species of *Protoreodon*. Any phylogenetic analysis of agriochoerids must include merycoidodontids in order to examine the possibility that Agriochoeridae is paraphyletic, and test the monophyly of Merycoidodontidae. Unfortunately, the merycoidodontids have been subject to extreme taxonomic over-splitting by Schultz and Falkenbach (1940, 1947, 1950a, 1950b, 1954), who established eleven subfamilies and numerous genera and subgenera, often based on specimens showing post-mortem deformation (Lander, 1978; Stevens and Stevens, 1996; CoBabe, 1996). Subsequent work revising these taxa has been slow, and to date only three of those subfamilies have been carefully revised based on statistical analyses of variation (Merycoidodontinae and Minochoerinae in Stevens and Stevens, 1996; Leptaucheniinae in CoBabe, 1996). Lander (1998) presented an extensive taxonomic revision of the Merycoidodontidae, but did not provide any descriptive or statistical justification for his conclusions, making it difficult to evaluate the validity of the proposed taxa. This confusion in the literature makes it extraordinarily difficult to assess the character states for different species or genera for use in a cladistic analysis, and because any phylogeny of Agriochoeridae that excluded Merycoidodontidae would be invalid, I have not attempted to include a phylogenetic analysis here.

The postcranial skeleton of the new species does show a number of features which are shared with merycoidodontids, such as closely appressed metapodials in the fore and hindfeet, hoofed ungual phalanges, and some characters in the carpus. I do not think that these are shared derived characters for *Protoreodon walshi* n. sp. and merycoidodontids. The condition of the carpus differs in the genus *Agriochoerus*, but these differences are probably changes associated with the foot specializations of *Agriochoerus*, and I suspect that *Protoreodon* and merycoidodontids retain the primitive condition. *P. walshi* n. sp. shares an unusual P<sup>3</sup> morphology with *P. petersoni*, but *P. petersoni* shares a subdivided para-metacone with a number of other species of *Protoreodon*, while *P. walshi* n. sp. has an undivided para-metacone. The polarity of these characters is difficult to assess at present, and a more thorough review of the agriochoerid genera *Diplobunops* and *Agriochoerus* and the remaining merycoidodontid taxa is necessary to establish a reasonable character matrix for phylogenetic analysis.

The new species is referred to Agriochoeridae on the basis of several dental features. *Protoreodon walshi* n. sp. shows strong labial ribs on the molars and bulbous, more open molar mesostyles than those of merycoidodontids, more similar to agriochoerids. The P<sup>3</sup> of *P. walshi* n. sp. lacks the accessory crests found among merycoidodontids; and the molar postprotocrista terminates at and is perpendicular to the premetaconule crista like other agriochoerids, rather than extending towards the mesostyle as in merycoidodontids (Lander, 1998).

Given these considerations, I have chosen to continue to use the family name Agriochoeridae for the present, recognizing that this is probably a paraphyletic taxon, and that the taxonomy will likely require revision in light of a phylogenetic analysis.

Genus PROTOREODON Scott and Osborn, 1887

Type species.—*Protoreodon parvus* Scott and Osborn, 1887.

Other species.—*Protoreodon parvus*, *P. pumilus*, *P. paradoxicus*, *P. minor*, *P. petersoni*, *P. pacificus*, *P. transmontanus*, *P. minimus*, *P. walshi* new species.

**Discussion.**—Most of the taxonomic history of the genus *Protoreodon* was summarized in the synonymy provided by Golz (1976). Subsequently, Black (1978) synonymized *Protoreodon pearcei* with *Diplobunops matthewi*, reasoning that the material represented a single sexually dimorphic species.

Wilson (1971) used the presence of upper molar paraconules to diagnose *Protoreodon*, and used tooth dimensions to segregate species within the genus. He noted that this left both large and small species of *Protoreodon* containing specimens with split and undivided P<sup>4</sup> para-metacones. Golz (1976) revised the diagnosis of *P. pumilus*, using the split P<sup>4</sup> para-metacone as one of several diagnostic criteria. The material discussed here shows no variability in splitting of the para-metacone of P<sup>4</sup>. Wilson (1971, p. 14) pooled Uinta Basin material from several localities into approximate stratigraphic levels to assess the dental variability of *Protoreodon*, and given current problems in assessing Uinta Basin biostratigraphy (Walsh, 1996), it is possible that the variability found in this trait is in part a result of lumping specimens from different levels.

Lander (in Kelly, 1990), excludes the Texas and California material from *P. pumilus*, referring the former to *P. annectens* and the latter to a subspecies of *P. annectens*. Lander has proposed extensive changes in the taxonomy of *Protoreodon*: he removed *P. minimus*, *P. transmontanus*, and *P. petersoni* to separate new unnamed genera, synonymized *P. minor* with *P. parvus*, transferred *P. pumilus* and *P. pearcei* to *Agriochoerus*, and resurrected *P. annectens*, referring *P. medius*, *P. tardus* (both of which Gazin synonymized with *P. pumilus*) and *P. pacificus* to subspecies of *P. annectens*. However, Lander did not provide a diagnosis for any new taxa, nor any justification for these changes, and since they seem to be in conflict with the traditional conception of *Protoreodon*, the diagnoses provided by Gazin (1955) and Golz (1976) will be followed here.

The new species is assigned to *Protoreodon* based on dental traits such as the retention of molar paraconules and a less molarized P<sup>4</sup> than in *Agriochoerus*, and it shows none of the expansion of the rostrum nor the enlarged P<sup>1</sup> diastema typical of *Diplobunops*. However, several of the morphological characteristics used to diagnose *Protoreodon* are primitive for oreodonts, and it should be noted that the genus is probably paraphyletic.

The material from the Jeff's Discovery and Rancho del Oro local faunas previously referred to *P. cf. parvus*, *Protoreodon* new sp. 1 (Walsh, 1996), and *Protoreodon* new species Type A (Theodor, 1996) is here assigned to *Protoreodon walshi*.

PROTOREODON WALSHI new species  
Figures 2, 3.1–3.6, Tables 1–3

*Protoreodon* cf. *parvus*, p. 169, 171–173

*Protoreodon* new sp. 1 WALSH, 1996, p. 82

*Protoreodon* new species Type A THEODOR, 1996, p. 65 figs. 4.4–4.14

**Diagnosis.**—*Protoreodon*, P<sup>3</sup> with a small protocone, nearly 3 mm in diameter at the base, forming a large swelling at the base of the para-metacone. P<sup>3</sup> with a weakly crescentic anteroposterior crest with anterior portion angled labially, and with a buccolingual crest extending from the para-metacone down the lingual surface of the tooth to the protocone, turning posteriorly over the protocone to meet the postcingulum. P<sup>4</sup> with weak postprotocrista, undivided para-metacone. M<sup>1-2</sup> with narrow postcingulae and well-developed ribs on the buccal surface of the metaconule, lacking metastyles. Premetaconule cristae not reaching the base of the paracone. M<sup>3</sup> with well-developed metastyle, and premetaconule crista recurved towards the metacone.

Similar in size to *P. pacificus* and *P. parvus*, smaller than *P. pumilus* and *P. transmontanus*, larger than *P. paradoxicus*, *P.*

*minor*, *P. minimus* and *P. petersoni*. Differs from all other species of *Protoreodon* in more crescentic para-metacone of P<sup>3</sup>, with anterolabial orientation of parastyle.

Differs from *P. pacificus* in undivided para-metacone of both P<sup>3</sup> and P<sup>4</sup>.

Differs from *P. parvus*, *P. minimus*, *P. transmontanus* and *P. pumilus* by lack of subdivision of para-metacone of P<sup>4</sup>.

Differs from *P. paradoxicus* by presence of protocone on P<sup>3</sup>. Differs from *P. minor* by presence of buccolingual crest on P<sup>3</sup> protocone, with more pronounced cingulae and large molar endocingulae.

**Description.**—The skull preserved in the SDSNH 40806 skeleton is intact but partly obscured by matrix. Most of the cranial material has been dorsoventrally crushed but in general resembles Scott's description. The orbit is open posteriorly, and the supraoccipital crests are strong, curving back to meet the sagittal crest. The snout is short, and relatively narrow, tapering anteriorly. The zygomatic arch bears a short, pointed postorbital process. The dentition of SDSNH 40806 is exposed ventrally, but is more heavily worn than in several other specimens.

The upper dentition is complete and the molars are bunodont. Incisors are preserved in SDSNH 35226. The incisors increase in size, such that the crown of the third incisor is almost twice as wide as the first. I<sup>3</sup> (preserved in SDSNH 40809, Fig. 2.1) is lenticular in cross-section, and the crown is triangular in anterior view. The canine is slightly recurved, triangular in cross-section, with the apex directed lingually and a flattened distal face.

P<sup>1</sup> is separated from the canine by a wide diastema, and a shorter diastema separates it from P<sup>2</sup>. P<sup>1</sup> is two-rooted, and bears a single large cusp, with strong anteroposterior crests ending in very weak styles. The crown is transversely expanded at the distal end. The anterior crest is directed anteriorly, the posterior part is directed posterolabially. The anterolingual part of the crown bears a narrow cingulum. On the lingual face of the tooth, a crest runs from the apex of the cusp to the base, curving posteriorly towards the base of the crown. The area between this crest and the posterior crest is weakly basined. P<sup>2</sup> is similar in morphology, slightly larger, with stronger styles, and a wider cingulum. The posterior crest of P<sup>2</sup> curves buccally towards the posterior style.

P<sup>3</sup> is triangular in outline, longer and wider than P<sup>2</sup>. There is a single large buccal cusp, with a crest that runs anteriorly towards the anterior style, where it joins a wide anterolingual cingulum. The posterior crest curves posterolabially to meet the strong posterior style. The anterior and posterior crests together form a more crescentic para-metacone than in other species of *Protoreodon*, which have a relatively straight anteroposterior crest. A buccolingual crest runs from the apex of the crown to a weak protocone, turning posteriorly at the base to join a posterior cingulum. The protocone is a large swelling at the base of the para-metacone. The crown surface between the lingual and posterior crests is deeply basined in unworn specimens.

The P<sup>4</sup> has an undivided para-metacone, unlike most other species of *Protoreodon*. The para-metacone is crescentic, with well-developed styles. The protocone is more conical than the para-metacone, with slightly crescentic cristae. The postprotocrista is short, terminating bluntly near the base of the para-metacone, close to, or at, the postcingulum. The preprotocrista is longer, and tapers towards the parastyle. Most of the specimens have a strong postcingulum, which terminates on the lingual side of the protocone, and a very weak to absent precingulum. In SDSNH 43759, the cingulum is continuous and wide around the base of the protocone.

The molars are quadricusate, roughly rectangular, slightly wider transversely at the anterior end, and longer on the buccal

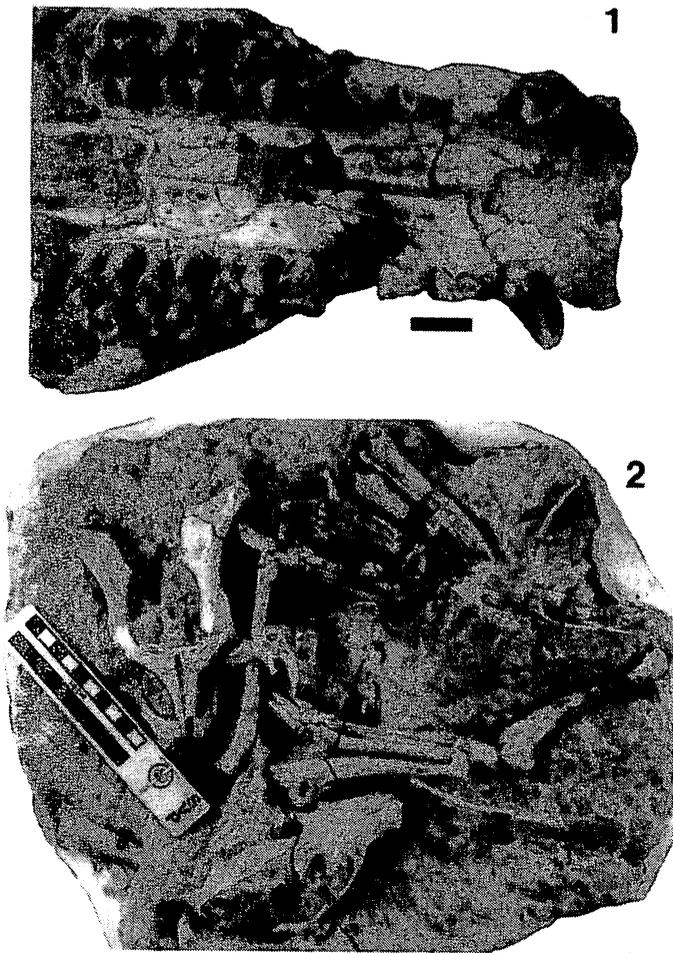


FIGURE 2—*Protoreodon walshi* n. sp. 1, SDSNH 40809, holotype, right and left C<sup>1</sup>–M<sup>3</sup>, occlusal view. Scale bar equals 1 cm; 2, SDSNH 40806, partially articulated skeleton.

side (Figs. 2.1, 3.5–3.6). As in all other species of *Protoreodon*, *P. walshi* retains molar paraconules. The molars increase in size from M<sup>1</sup> to M<sup>3</sup>. M<sup>1</sup> is considerably smaller than M<sup>2</sup>, while M<sup>2</sup> and M<sup>3</sup> are closer in size. The paracones and metacones of the molars are strongly crescentic, with well-developed parastyles and mesostyles. The metastyle is not strongly developed on M<sup>1–2</sup>, but is somewhat stronger on M<sup>3</sup>. Labial ribs are strongly developed on the paracone and metacone of the upper molars. The precingulum and postcingulum are wide. There is a wide endocingulum between the bases of the protocone and the metaconule. On SDSNH 32200 and SDSNH 43759, the endocingulum is continuous with the postcingulum, forming a ledge around the base of the protocone. A strong buccal rib is present on the protocone, and on some specimens a similar rib is developed on the buccal face of the metaconule. The preprotocrista is short, as the paraconule is very close to the cusp of the protocone. Anteriorly, a longer preparaconule crista meets the parastyle. The postprotocrista is short and angled perpendicular to the longer premetaconule crista, which extends anterolabially into the valley between the paracone and metacone, curving towards the metacone near its end. The premetaconule crista terminates at the base of the paracone, unlike *P. paradoxicus*, in which the premetaconule crista reaches the mesostyle.

The dentary is deep at the posterior end, with a wide rounded posterior edge. The horizontal ramus is narrower, with a heavy,

anteriorly tilted symphysis. Externally, a deep masseteric fossa is defined anterior to the condyle, below and behind the short coronoid process (Fig. 3.1). The bone of this fossa is very thin. The condyle is transversely cylindrical, relatively wide, and positioned slightly higher than the tooth row. The posterior end of the jaw bears a raised scar along the edge of the bone, approximately 5–6 mm from the edge. Internally, the posterior end of the jaw forms a round pterygoid fossa, with two to three high raised ridges, curving upwards from the posterior edge. There is a small foramen about 1 cm below P<sub>1</sub> on the external face of the jaw.

The lower incisors are small and spatulate. I<sub>2–3</sub> bear a small protuberance at the base of the distal side of the crown. The lower canine is incisiform, and is closely appressed to I<sub>3</sub>. It is slightly larger and wider than I<sub>3</sub>, but otherwise resembles the incisor. There is a short diastema between C<sub>1</sub> and P<sub>1</sub>. P<sub>1</sub> is caniniform, elliptical in cross-section, with a strong protoconid. The protoconid has prominent anterior and posterior crests. The paraconid is not quite cuspsate. The posterior crest bears a tiny cuspid at the base of the crown. The crown bears a strong lingual rib, and is lightly concave anterior and posterior to the rib.

P<sub>2</sub> bears a small posterolabial metaconid cusp. The metaconid is not joined to the protoconid by a crest. The crown is weakly basined posterior to the metaconid. There is a narrow posterolabial cingulid which ends at the metaconid. The posterior crest of the protoconid bears a thickening posterior to the apex, possibly representing a hypoconid. P<sub>3</sub> is slightly longer and wider than P<sub>2</sub>, with a well-developed metaconid and a cuspsate paraconid. The metaconid is joined to the protoconid by the protocristid. The lingual surface of P<sub>3</sub> is basined between the protocristid and the preprotocristid, the basin divided by a lingual rib on the protoconid. The talonid is deeply basined, opening posterolingually. There is a narrow posterolabial cingulid.

P<sub>4</sub> is broader transversely than P<sub>3</sub>, especially posteriorly. Morphologically, the third and fourth premolars are similar, but the P<sub>4</sub> metaconid is higher and more strongly developed. The anterior basin of the P<sub>4</sub> is undivided, deeper than that of P<sub>3</sub>. The posterolabial cingulid of P<sub>3</sub> is longer than in P<sub>4</sub>.

The lower molars show less crescentic selenes than the uppers. The protoconid and hypoconid are crescentic, the metaconid and entoconid more conical with anteroposteriorly oriented crests. The paraconid is poorly developed. Parastylids and entoconulids are weak or absent, and metastylids are small. The lingual ribs on the metaconid and entoconid are weakly developed. The protocristid meets the cristid obliqua at a 60 degree angle, and does not meet the metastylid. There is no hypolophid on any of the molars. M<sub>1–2</sub> lack hypoconulids, and the buccal and lingual postcristids do not quite meet posteriorly. M<sub>3</sub> bears a small hypoconulid, but the buccal postcristid does not meet it. There is a very small, short cingulid between the bases of the protoconid and hypoconid. The postmetacristid does not meet the entostylid. The heel of the M<sub>3</sub> is narrow and pinched mesially. In the less worn M<sub>3</sub>, the paracristid does not meet the parastylid, and the entoconulid is not connected to the metastylid.

The deciduous upper dentition is preserved in SDSNH 32175, SDSNH 40810, and SDSNH 43738 (Fig. 3.2). dC is short and slender, with slight anterior and posterior carinae. The crown is lentil-shaped in cross section and slightly posteriorly recurved. dP<sub>1</sub> has a single large paracone, and lacks a lingual protocone. A lingual crest travels posteriorly from the middle of the paracone, curving down the tooth to meet the postcingulum. The crown is basined behind this crest. A weak precingulum curves back from the preparacrista towards the postcingulum but terminates just short of the lingual crest. The posterior style is buccally recurved, and projects more buccally than the parastyle. In SDSNH 40810 and SDSNH 43738, there is a small pit by

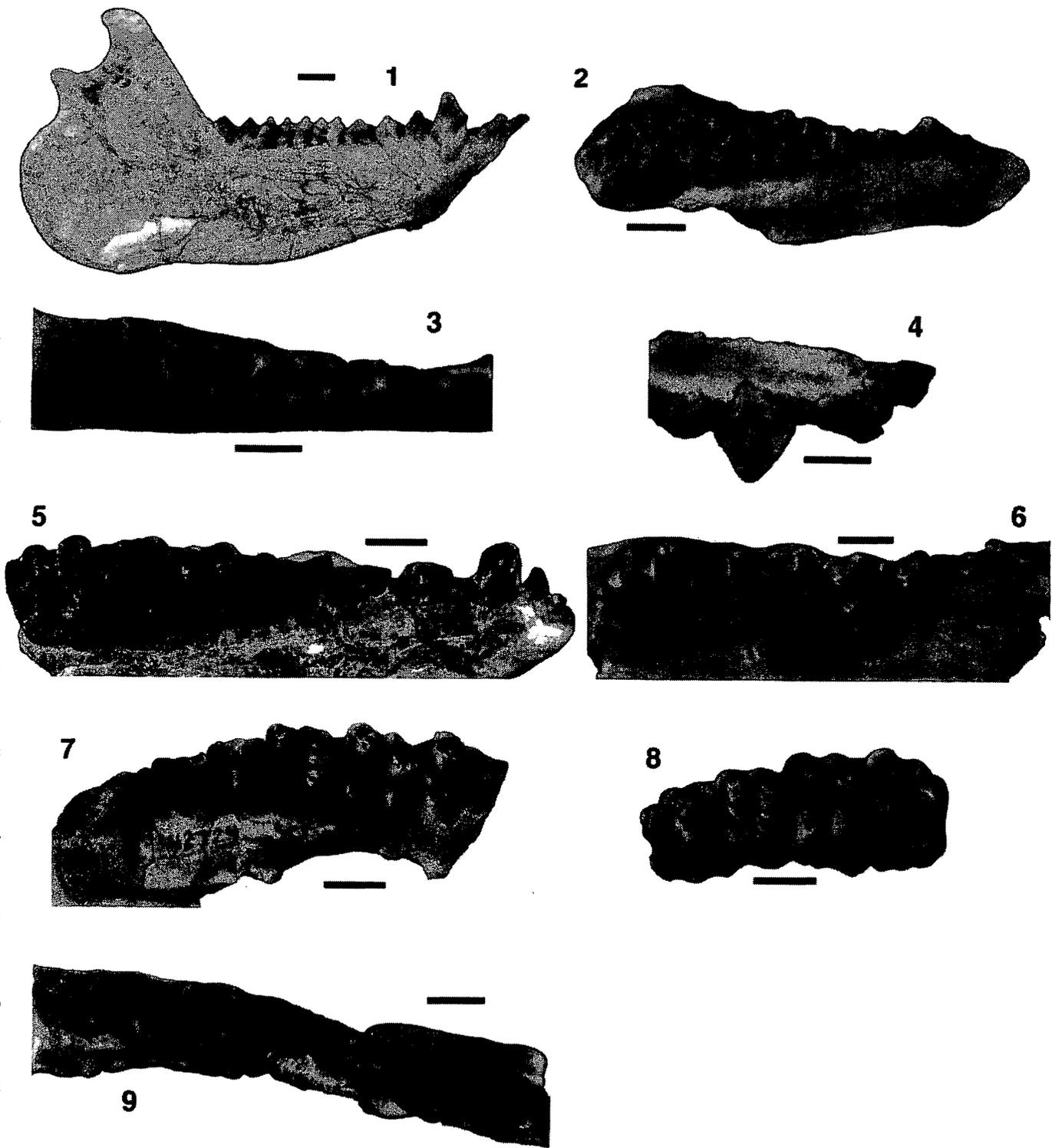


FIGURE 3—Dentitions of *Protoreodon* from San Diego County. 1–6, *P. walshi* n. sp. 1, SDSNH 40803, right dentary, lateral view; 2, SDSNH 43738, partial right maxilla with  $dP^1-M^3$ , occlusal view; 3, SDSNH 40803, right dentary,  $P_3-M_3$ , occlusal view; 4, SDSNH 40803, right dentary,  $I^1-P_2$ , occlusal view; 5 SDSNH 43754, partial right maxilla with  $I^1-M^3$ , occlusal view; 6, SDSNH 42725, partial right maxilla with  $P^1-M^3$ , occlusal view; 7–9, *P. cf. walshi*. 7, SDSNH 42724, partial left maxilla with  $P^1-M^3$ , occlusal view; 8, SDSNH 42618, partial left maxilla with  $P^2-M^3$ , occlusal view; 9, SDSNH 42724, partial right dentary with  $P_2-M_3$ , occlusal view. Scale bars equal 1 cm.

TABLE 1—Dental measurements for adult specimens of *Protoreodon walshi* new species. All measurements in mm, rounded to nearest 0.1 mm. Estimates marked by an \*.

Uppers	SDSNH	SDSNH	SDSNH	SDSNH 32200		SDSNH 40809		SDSNH 43759	
	42725 Right	42726 Left	43754 Left	Right	Left	Right	Left	Right	Left
F <sup>1</sup> AP	—	—	3.2	—	—	—	—	—	—
T	—	—	2.2	—	—	—	—	—	—
C <sup>1</sup> AP	—	—	6.4	—	—	5.9	7.2	—	—
T	—	—	5.7	—	—	5.6	6.6	—	—
P <sup>1</sup> AP	8.4*	—	—	6.9	6.7	7.6	7.7	7.1	7.0
T	5.4*	—	—	4.0	4.0	4.8	4.7	4.4	4.5
P <sup>2</sup> AP	7.8	—	7.7	—	—	7.5	7.8	7.6	7.4
T	5.8	—	4.9	—	—	5.7	5.8	5.5	5.2
P <sup>3</sup> AP	8.3	—	7.5	6.7	6.8	7.9	—	7.9	7.6
T	7.8	—	7.6	7.5	7.1	8.0	—	7.5	7.3
P <sup>4</sup> AP	7.4	6.4	6.2	6.1	6.3	7.9	7.8	7.2	7.0
T	10.4	9.1	8.9	9.4	9.4	10.2	10.3	9.8	9.4
M <sup>1</sup> AP	9.4	8.5	9.4	—	8.8	9.7	9.8	9.1	9.1
T	11.7	10.6	11.8	—	10.5	11.6	11.8	11.1	11.0
M <sup>2</sup> AP	10.4	9.7	10.7	10.0	9.7	11.2	11.2	10.6	10.5
T	13.7	12.9	13.8	12.8	12.5	14.1	14.0	13.2	13.1
M <sup>3</sup> AP	11.0	9.8	12.4	10.1	9.8	11.3	11.6	10.3	11.0
T	—	13.2	15.2	13.1	13.0	14.4	14.3	13.2	14.0
P <sup>1</sup> -P <sup>4</sup>	31.9	—	—	23.3	27.8	32.2	31.5	40.0	30.3
M <sup>1</sup> -M <sup>3</sup>	30.1	28.3	31.4	30.2	28.1	31.9	32.1	30.0	30.0
P <sup>1</sup> -M <sup>3</sup>	62.3	—	—	57.1	57.1	63.5	63.1	61.6	59.4
C <sup>1</sup> -P <sup>1</sup> diastema	—	—	—	—	—	4.8	4.7	—	3.9
P <sup>1</sup> -P <sup>2</sup> diastema	1.2	—	—	—	—	2.0	0.8	1.6	1.3
	SDSNH	SDSNH	SDSNH						
Lowers	40803 Right	42610 Right	42610 Left						
I <sub>1</sub> AP	2.2	—	—						
T	2.3	—	—						
I <sub>2</sub> AP	2.8	—	—						
T	2.3	—	—						
I <sub>3</sub> AP	—	—	2.6						
T	—	—	2.1						
C <sub>1</sub> AP	3.7	—	3.1						
T	3.7	—	3.2						
P <sub>1</sub> AP	9.4	6.3	7.0						
T	6.5	4.0	4.7						
P <sub>2</sub> AP	7.7	6.4	6.7						
T	4.2	3.8*	3.7						
P <sub>3</sub> AP	8.0	7.5	8.0						
T	4.7	4.3	4.5						
P <sub>4</sub> AP	8.6	7.7	7.8						
T	5.8	5.7	5.7						
M <sub>1</sub> AP	8.0	8.0	8.8						
T	7.1	6.7	6.7						
M <sub>2</sub> AP	9.1	9.2	9.2						
T	8.1	8.0	7.9						
M <sub>3</sub> AP	16.2	15.5*	15.5						
T	8.9	7.8	8.0						
P <sub>1</sub> -P <sub>4</sub>	31.9	29.7	30.4						
M <sub>1</sub> -M <sub>3</sub>	34.6	33.0	33.2						
P <sub>1</sub> -M <sub>3</sub>	65.5	62.4	63.5						
C <sub>1</sub> -P <sub>1</sub> diastema	3.7	—	2.4						
P <sub>2</sub> -P <sub>3</sub> diastema	2.0	1.7	1.1						

the parastyle anterior to the precingulum, which is not found in SDSNH 32175.

dP<sup>2</sup> is similar to dP<sup>1</sup> in general morphology, slightly shorter and transversely narrower. The postcingulum is stronger than on dP<sup>1</sup>, and the crown is more deeply basined posterior to the lingual crest. The posterior style of the paracone is not strongly mesially directed.

dP<sup>3</sup> is a complex tricusate tooth. The cusps are crescentic, forming one anterior selene, the paracone, and two posterior selenes, the metacone buccally and protocone lingually. The metacone is more V-shaped than the paracone. Although SDSNH 40810 and SDSNH 43738 are too worn to determine whether a paraconule is present, SDSNH 32175 lacks a paraconule and all three lack the precingulum.

dP<sup>4</sup> is quadricusate, generally similar to the adult molar morphology. The selenes are more triangular than in the adult molars. The precingulum is well developed, in contrast to the weak postcingulum, which extends to the lingual end of the metaconule. The lingual cingulum is narrow. The paraconule is present on the preprotocrista, and the parastyle is wider and more open than in the adult.

SDSNH 32167 preserves the deciduous P<sub>2-4</sub>. All three of the deciduous premolars preserved are two-rooted. dP<sub>2</sub> and dP<sub>3</sub> are strongly crested, lack a cusate hypoconid, and generally resemble the adult P<sub>2-3</sub>. dP<sub>2</sub> has a cusate paraconid, metaconid and protoconid. There is no cingulid posterolingually, unlike the adult P<sub>2</sub>. The protocristid is not well-developed.

The talonid of dP<sub>3</sub> is deeply basined, but the area which might

TABLE 2—Dental measurements for juvenile specimens of *Protoreodon walshi* new species. All measurements in mm, rounded to nearest 0.1 mm. Estimates marked by an \*.

Uppers	SDSNH	SDNH	SDSNH 40810	
	43738	32175	Right	Left
dC AP	—	2.7	—	—
T	—	2.5	1.8	—
dP <sup>1</sup> AP	7.1	7.8	6.5	6.7
T	4.1	4.8	4.8	4.7
dP <sup>2</sup> AP	6.9	6.9	5.8	5.6
T	3.8	4.5	4.1	3.9
dP <sup>3</sup> AP	8.4	9.6	7.9	8.0
T	6.8	7.2	7.3	7.3
dP <sup>4</sup> AP	7.9	9.9	8.1	8.1
T	9.2	10.25	9.0	9.5
M <sup>1</sup> AP	9.5	—	9.6	9.9
T	11.5	—	10.9	11.0
M <sup>2</sup> AP	11.1	—	10.5*	10.6
T	13.8	—	—	—
dC-dP <sup>1</sup> diastema	—	2.5	2.0	—
dP <sup>1</sup> -dP <sup>2</sup> diastema	1.1	1.9*	1.4	—
	SDSNH			
	32167			
Loweres	Left			
dP <sub>2</sub> AP	6.1			
T	3.9			
dP <sub>3</sub> AP	7.3			
T	4.6			
dP <sub>4</sub> AP	10.7			
T	6.8			

have borne a cingulid is broken. There is no anterior cingulid. The paraconid is cusped and close in size to the metaconid.

dP<sub>4</sub> bears six cuspids, arranged in paired selenes, similar in shape to the selenes in the adult molars. The anterior pair of cuspids is somewhat separated from the posterior two pairs. The cuspids increase in size posteriorly. All of the cuspids are strongly conical, with very weak stylids. Stylids are absent in the anterior pair of cuspids.

Scott (1899) described some postcranial material of *Protoreodon*, but the description is somewhat cursory, and no subsequent author has described postcranial material. The only description of postcranial material of *Diplobunops* is also relatively short (Peterson, 1931). Most of the postcranial descriptions of *Agriochœrus* (Scott, 1894, 1940) have focused on its unusual feet, which bear clawed unguals (Coombs, 1983), and have caused a great deal of taxonomic confusion in the earlier literature.

The scapula is preserved in SDSNH 40806, but the blade is largely obscured by the right tibia, and the glenoid abuts the skull and is obscured by matrix (Fig. 2.2). The coracoid process, visible in ventral view, is very short, knobby in shape and slightly recurved. The coracoid process of *Diplobunops* is much larger than in SDSNH 40806 or in *Agriochœrus* (Peterson, 1931, fig. 1; Scott, 1940, pl. 78, fig. 1).

Both humeri are preserved in SDSNH 40806. They generally resemble merycoidodontid humeri, but the olecranon fossa is obscured by matrix on one side and is in articulation with the radius and ulna. The humeri in this specimen are similar in size to that of *Oreonetes* (UCMP 31048), more lightly built than those of *Diplobunops*. The greater tuberosity is shorter than in *Oreonetes*, not greatly enlarged above the humeral head. The lesser tuberosity is slightly broader and blunter than in *Oreonetes*, and neither of the tuberosities overhangs the bicipital groove. The deltoid crest in *Agriochœrus* and *Protoreodon* is much shorter than in *Diplobunops*. The medial epicondyle is relatively small in the San Diego material, unlike that of

*Agriochœrus* or *Diplobunops*, where it is very prominent and rugose (Peterson, 1931; Scott, 1940).

The ulna resembles a typical merycoidodontid ulna, approximately the size of the ulna of *Oreonetes*. The shaft of the ulna is smaller than or equal to the diameter of the radial shaft for most of its length, as in *Agriochœrus*, while in *Diplobunops* the ulna is larger than the radius. The cuneiform facet on the distal end is triangular, slightly wider and flatter than in *Oreonetes* or *Prodesmatochoerus* (UCMP 34525), with a smaller expansion onto the posterior surface. Proximally, the groove on the end of the olecranon is shallower and wider in *Protoreodon* and *Agriochœrus* than in merycoidodontids, and the olecranon is slightly concave on the medial face of the bone.

The radius is also generally similar to merycoidodontids, but with shallower lunar and scaphoid facets on the distal end. The scaphoid facet is roughly trapezoidal, the anterior portion concave, the posterior part anteroposteriorly convex. The lunar facet is almost oval, concave, and sloping slightly laterally, with a triangular expansion onto the lateral face of the shaft, anterior to the distal ulnar articulation.

The entire manus is preserved in articulation in SDSNH 40806, and most of the carpals are disarticulated in SDSNH 35226 and 40807, which form much of the basis of this description. The carpus of *Diplobunops* is poorly preserved, and cannot be used for comparisons (Peterson, 1931).

The scaphoid bears a large concavo-convex facet for the radius on its proximal surface, and two facets on the distal surface. The medial trapezoid facet has an anterior portion which is lightly concave, and a posterior part which is a much deeper pit that articulates with a short projection on the trapezoid. The magnum facet is lateral to the anterior part of the trapezoid facet, and is higher and flatter in distal view. In contrast to merycoidodonts, the posterior face of the scaphoid lacks facets. The scaphoid of *Agriochœrus* was missing from the specimen described by Scott (1894), and I have found no other description.

The lunar is trapezoidal in anterior view. The proximal facet is divided by a slight ridge into a roughly rectangular medial radial facet and an anterolaterally directed triangle, the ulnar facet, which slants distally toward the anterior surface. The distal face bears an elongated, narrow, lateral unciform facet. The magnum contact is very narrow and does not seem to form a facet on the lunar. The lateral side of the lunar bears a small, proximal triangular cuneiform facet near its anterior end. The rest of this side of the bone is concave posteriorly. The scaphoid facet on the medial face of the lunar is poorly defined. The lunar rests approximately equally on the magnum and unciform in anterior view, the primitive condition (Fig. 2.2). Merycoidodontids show the derived condition, in which the lunar is shifted laterally, resting mostly on the unciform, with little or no magnum contact. *Agriochœrus* has an unusual derived condition, in which the lunar is shifted medially to rest primarily on the magnum, which is not known in other artiodactyls.

The cuneiform is a wedge shaped bone, wide in the medio-lateral direction, and short proximodistally. It is comma shaped in proximal view, with two triangular facets. The ulnar facet is anterior and anteroposteriorly concave. The posterior edge of the ulnar facet forms a raised ridge which separates it from the posterior, distolaterally slanted, concave pisiform facet. The pisiform facet slants over onto the palmar face of the cuneiform, but not as strongly as in *Agriochœrus* or *Prodesmatochoerus*. The distal face bears large, oval concave unciform facet. The lunar facet, on the medial side of the cuneiform, is flat, higher posteriorly than anteriorly, with a straight proximal edge. The pisiform is not visible in SDSNH 40806 and is not preserved in SDSNH 35226.

The trapezoid is a small triangular bone, with a trapezoidal

anterior face. The proximal scaphoid facet is slightly concave towards the posterolateral corner, ending in a short raised projection at the apex of the triangle. The distal Mc II facet is very slightly concave, triangular in shape. The lateral and medial facets are poorly delimited. The trapezoid is considerably smaller than the magnum, as in merycoidodontids, whereas in *Agriochœrus* the opposite is true (Scott, 1894, 1940). The trapezium is a small nodule, articulating laterally with Mc II.

The magnum is large, wedge shaped proximally, with a long stout posterior distally pointing projection. The proximal end bears two large facets that meet at a 60 degree angle near the midline. The medial scaphoid facet is oval, wider anteriorly, lightly anteroposteriorly concave, and slopes anteromedially, unlike *Agriochœrus* in which the scaphoid facet is small and restricted to the front of the magnum. The lunar facet is roughly pentagonal, with the apex anterior, and slopes posterolaterally, more steeply than the scaphoid facet. The distal Mc III facet is heart shaped and anteroposteriorly concave. The Mc II contact is very small, and as in *Agriochœrus* there is no facet for Mc II on the magnum (Scott, 1894).

The unciform is also complex, much larger than any other carpal in the wrist, and resembles the unciform of merycoidodontids. It bears a large, stout posterior projection, and is roughly rectangular in anterior view. Distally, it bears three facets. The Mc II facet visible on the medial side of the bone is flat, rectangular, and slopes medially. It forms the medial border of the large, flat, roughly rectangular Mc III facet. The Mc III facet forms the medial edge of the Mc IV facet, which is narrower mediolaterally, wider anteroposteriorly, and slants proximally and posteriorly. On the proximal end is a large, triangular convex cuneiform facet, which bears a slight ridge in the center. The portion lateral to the ridge is simply convex and articulates with the cuneiform. The medial portion articulates with the lunar, and is anteriorly concave and posteriorly convex. This differs from *Agriochœrus*, in which the head of the unciform is almost entirely covered by the cuneiform facet. The medial side of the bone bears a small anterior facet, distal to the Mc II facet described above, which also appears to articulate with Mc II, and an elongate facet on the projection whose articulation is unclear.

The metacarpals are closely appressed, arranged in an arch, with Mc II and Mc III approximately equal in diameter, and the lateral metacarpals thinner and somewhat shorter. This is in contrast to the splayed condition described for *Agriochœrus*. Mc I is not exposed on SDSNH 40806. However, Scott (1899) reported a pollex in *Protoreodon*, and is present in other agriochœrids and some merycoidodontids, thus it is reasonable to assume that one is present in the new species. The distal end of the metacarpals are similar to those in merycoidodontids, not as hemispherical as in *Agriochœrus* (Scott, 1899). The proximal and middle phalanges are typical for oreodonts. The ungual phalanges are slightly hoofed as in merycoidodonts, showing no resemblance to the clawlike condition seen in *Agriochœrus* or *Diplobunops* (Peterson, 1931). It is reasonable to assume that the differences in carpal morphology between *Protoreodon* and *Agriochœrus* are specializations of the feet in *Agriochœrus*, and are correlated with the evolution of claws.

The pelvis of SDSNH 35226 is crushed, but it preserves the sacrum. As in *Agriochœrus*, there are three fused sacral vertebrae, the first of which articulates with the ilium. Merycoidodontids have four or five fused sacral vertebrae. The pelvis is well preserved in ventral view in SDSNH 40806, and it resembles the pelvis of merycoidodontids and *Diplobunops* (the pelvis of *Agriochœrus* is not described). The tooth wear on the upper molars of this skeleton and state of fusion of other epiphyses indicate that it belonged to a mature animal, yet the anterior iliac epiphyseal lines are still strongly marked.

The femora in SDSNH 35226 are poorly preserved but resemble those of *Agriochœrus* in shape. The tibiae are well preserved and are similar to those of merycoidodontids and *Agriochœrus*, with a well-developed medial flange on the distal end, which fits into a deep median pit on the anterior face of the astragalus. The fibula is complete, with a thin and expanded distal end. The distal end bears a flat, elliptical, anteroposteriorly elongate cuboid facet. The medial side of the distal end bears a diagonal astragalus facet. The shaft of the fibula is more slender than those of merycoidodontids and other agriochœrids.

The astragalus, calcaneum, navicular and cuboid resemble Scott's description. The ectocuneiform and mesocuneiform are fused into a short, flat, oval bone, with a proximal navicular facet and distal Mt II and Mt III facets. The medial Mt II facet is slightly higher than the Mt III facet. The Mt II facet is small and semi-circular. The Mt III facet is kidney-shaped and at least three times wider than the Mt II facet. This bone fits the description of the meso-ectocuneiform of *Agriochœrus* given by Scott (1940, p. 724), except that he erroneously describes the distal metatarsal facets as belonging to Mt IV and Mt V, which articulate with the cuboid.

The short, stout entocuneiform is preserved in SDSNH 40806. It lacks an obvious facet for Mt I, and there is no other evidence for a hallux. The lateral metatarsals are only slightly shorter and smaller in diameter than the median ones. SDSNH 40806 preserves paired sesamoids over each metatarsophalangeal joint.

*Etymology.*—Named for S. L. Walsh, in recognition of his contributions to our knowledge of the geology and paleontology of San Diego County.

*Types.*—SDSNH 40809, dorsoventrally crushed skull with right I<sup>3</sup>-P<sup>2</sup>, P<sup>4</sup>-M<sup>3</sup>, left I<sup>3</sup>-M<sup>3</sup>.

*Other material examined.*—SDSNH 32167—left dentary P<sub>1</sub> and M<sub>1</sub> partially erupted, dP<sub>2-4</sub>; SDSNH 32175—juvenile right maxilla with dC, dP<sup>1-4</sup>, fragment of left maxilla bearing dP<sub>1</sub>; SDSNH 32178—right calcaneum, astragalus and cuboid; SDSNH 32200—skull with right and left P<sub>1</sub>, P<sup>3</sup>-M<sup>3</sup>; SDSNH 35226—skull with I<sup>1</sup>-M<sup>3</sup>, lower jaws and associated postcrania: left lunar, right magnum, right scaphoid, right trapezoid, right cuneiform, left and right partial unciforms, right fused ecto-mesocuneiform, left and right naviculars, partial right cuboid, right astragalus and partial right calcaneum (articulated), right and left partial femora, partial left tibia, pelvis; SDSNH 40802—mandible, right unciform, left magnum, right proximal radius, partial humerus; SDSNH 40803—right dentary I<sub>1</sub>-M<sub>3</sub>, worn; SDSNH 40805—articulated left radius and ulna; SDSNH 40806—skeleton, largely complete, slightly disarticulated; SDSNH 40807—Left astragalus, right astragalus, right calcaneum, left navicular, right ecto-mesocuneiform, a complete, articulated, right distal fibula; SDSNH 40810—juvenile skull with right and left dC, dP<sup>1-4</sup>, M<sup>1</sup>, M<sup>2</sup> partially erupted; SDSNH 42598—right articulated pes; SDSNH 42610—left dentary with I<sub>3</sub>-M<sub>3</sub>; SDSNH 42725—partial right maxilla with P<sup>1</sup>-M<sup>3</sup>; SDSNH 42726—partial left maxilla with P<sup>4</sup>-M<sup>3</sup>; SDSNH 43738—juvenile, right maxilla with dP<sup>1-4</sup>, M<sup>1-2</sup>; SDSNH 43748—left ulna; SDSNH 43754—partial right maxilla with P<sup>3</sup>-M<sup>3</sup>; SDSNH 43759—skull with right and left C-M<sup>3</sup>; SDSNH 60060, crushed articulated skeleton.

*Occurrence.*—Late Uintan NALMA, middle Eocene. Known from the following SDSNH localities in San Diego County, southern California, all collected from the Santiago Formation Member C (Fig. 1): 3378—College Ave.; 3276, 3560-3562, Jeff's Discovery; 3433, 3436, 3445, Rancho del Oro.

*Discussion.*—The species of *Protoreodon* do not show large taxonomic differences in tooth size, with the exception of *P. petersoni*, which is considerably smaller than the other species.

TABLE 3—Postcranial measurements of *Protoreodon walshi* new species. All measurements in mm, rounded to nearest 0.1 mm. Estimates marked by an \*.

Dimension	SDSNH 40806		SDSNH 40807	SDSNH 40805	SDSNH 43748	SDSNH 35226	SDSNH 40802
	Right	Left					
<b>Humerus</b>							
L from head to distal end	111*	114*	—	—	—	—	—
<b>Radius</b>							
Max. L	88.3*	—	—	82.4	110.5	—	—
<b>Ulna</b>							
Articular L	86.0*	—	—	—	—	—	—
Max. L	113.5*	—	—	106.8*	110.5*	—	—
Olecranon L	19.3*	—	—	19.6*	19.9	—	—
<b>Scaphoid</b>							
PD	4.9	—	—	—	—	5.7	—
ML	3.8	—	—	—	—	9.7	—
AP	—	—	—	—	—	6.6	—
<b>Lunar</b>							
PD	5.2	—	—	—	—	6.1	—
ML	5.7	—	—	—	—	9.6	—
AP	—	—	—	—	—	5.9	—
<b>Cuneiform</b>							
PD	5.0	—	—	—	—	5.1	—
ML	9.3	—	—	—	—	9.8	—
AP	—	—	—	—	—	6.1	—
<b>Trapezoid</b>							
PD	3.7	—	—	—	—	4.1	—
ML	—	—	—	—	—	5.1	—
AP	—	—	—	—	—	6.4	—
<b>Magnum</b>							
PD anterior	4.6	—	—	—	—	4.3	—
ML anterior	6.0	—	—	—	—	6.2	—
AP (not including hook)	—	—	—	—	—	12.5	—
<b>Unciform</b>							
PD	5.6	—	—	—	—	—	—
ML	8.6	—	—	—	—	—	—
<b>Metacarpals</b>							
Mc II L	—	—	—	—	—	—	32.0
Mc III L	—	—	—	—	—	—	42.2
<b>Tibia</b>							
L from medial eminence to medial malleolus	132.8	—	—	—	—	—	—
<b>Fibula</b>							
Calcaneal facet L	—	—	8.5	—	—	8.6	9.2
Calcaneal facet W	—	—	4.3	—	—	3.7	3.8
Astragalar facet L	—	—	8.6	—	—	8.7	9.2
Astragalar facet W	—	—	4.7	—	—	4.1	3.8
<b>Astragalus</b>							
PD lateral	—	—	23.8	—	—	21.7	—
PD medial	—	—	20.8	—	—	19.3*	—
Proximal W	—	—	12.1	—	—	11.6	—
Distal W	—	—	14.1	—	—	13.1	—
<b>Calcaneum</b>							
Max. L	—	40.0	46.1	—	—	—	—
Length of tuber posterior to facets	—	—	26.2	—	—	—	—
Fibular facet L	—	—	10.7	—	—	9.1	—
<b>Navicular</b>							
AP	13.0	—	—	—	—	—	—
PD	5.1	—	—	—	—	11.5	—
<b>Entocuneiform</b>							
AP	6.0	—	—	—	—	—	—
PD	8.5	—	—	—	—	—	—
<b>Ecto-mesocuneiform</b>							
PD	3.6	—	5.9	—	—	4.6	—
ML	10.7	—	11.0	—	—	9.0	—
AP	—	—	—	—	—	6.9	—
<b>Metatarsals</b>							
Mt II L	—	44.2*	—	—	—	—	—
Mt III L	55.1	54.6*	—	—	—	—	—
Mt IV L	53.7	54.5*	—	—	—	—	—
Mt V L	43.5	42.3*	—	—	—	—	—

The San Diego material represents a primitive dental morphology in the relatively unmolarized P<sup>3</sup>, well-developed styles and strong paraconules. It has an unusual P<sup>3</sup> morphology, with a crest joining the protocone to the crescentic para-metacone, while in other species the protocone is either absent or isolated from the para-metacone. The only species with a similar P<sup>3</sup> morphology is *P. petersoni*, which has a split P<sup>4</sup> para-metacone and is much smaller than the San Diego material. Specimens referred to *P. cf. parvus* (Golz, 1976) may belong to *P. walshi*. The descriptions are similar, and LACM 26342 and 17121, both juvenile specimens, cannot be distinguished from juvenile specimens of *P. walshi*. Unfortunately, I have not been able to examine the adult material to determine whether this material should be referred to *P. walshi*, and the figures of LACM 17117, 17119, and 26342 are insufficient to allow identification to the new species.

The P<sup>3</sup> protocone in *P. walshi* is comparable in size and degree of isolation from the para-metacone with those of *P. petersoni* and *P. minor* from the Myton Member of the Uinta Formation (=Uinta C), but is smaller and less separated from the para-metacone than *P. pumilus*. Among the Uinta B forms from the Wagonhound Member of the Uinta Formation, *P. paradoxicus* lacks the P<sup>3</sup> protocone entirely, and the protocone of *P. parvus* is smaller and less separated from the para-metacone than in *P. walshi*. The P<sup>3</sup> protocone of *P. pumilus* from Member C of the Santiago Formation at Laguna Riviera in San Diego County, and the Tapo Canyon and Brea Canyon local faunas of the Sespe Formation in Ventura County, is much larger than in *P. walshi*, and is more clearly separated from the para-metacone. *P. pacificus* from Pearson Ranch, Sespe Formation, also has a larger and more isolated P<sup>3</sup> protocone than in *P. walshi*.

The para-metacone of P<sup>4</sup> of *P. walshi* is completely unsplit, similar to the condition found in *P. paradoxicus* and *P. minor*. All of the other species from the Uinta Basin and other localities in California show some degree of separation of the paracone and metacone, from a groove on the P<sup>4</sup> para-metacone (*P. petersoni*, *P. parvus*), a twinned paracone and metacone (*P. pumilus* from both California and the Uinta Basin), or a full separate paracone and metacone (*P. pacificus*).

The molar parastyles and mesostyles are inflated, similar to those in *P. petersoni* and *P. minor*, while *P. pumilus* has a less inflated parastyle and more bulbous mesostyle. *P. parvus* and *P. minor* have smaller, less inflated parastyles and mesostyles, while *P. pacificus* has protuberant parastyles but smaller, less inflated mesostyles. The mesostyles in agriochoerids are invaded by the transverse valley of the molar, giving a less pinched, more open appearance than in merycoidodontids. The mesostyles of *P. walshi* are only moderately pinched, with considerable invasion by the transverse valley, similar to *P. minor* and *P. petersoni*, but more pinched than in *P. pumilus* and *P. pacificus*, and more open than *P. paradoxicus* or *P. parvus*.

In the lower molars of *P. walshi*, the cristid obliqua joins the hypoconid up to the posterolingual face of the metaconid, closing off the transverse valley, as in *P. pumilus* and unlike the more open condition in *P. parvus*, where the cristid obliqua does not meet the metaconid. The condition of this character cannot be assessed for several of the other species because the lower molars are too worn.

Because the stage of evolution of these characters is not uniformly similar to forms from Uinta B, the argument proposed by Kelly et al. (1991) that the *Protoreodon walshi* material is early Uintan in age is not supported, and the other elements of the fauna indicate at least a local late Uintan age (Walsh, 1996).

With the recognition of a new species from the Jeff's Discovery local fauna and the Rancho del Oro local fauna, the diversity of agriochoerids in California is increased. While there is only

one species that can be clearly determined in each of these faunas, they are close in age to the Tapo Canyon and Brea Canyon local faunas (Sespe Formation), which include *Protoreodon pumilus* (Golz, 1976). It had previously been noted (Golz, 1976; Black, 1978) that agriochoerid diversity in Western Interior faunas was much higher than that of California faunas, although within each basin diversity is similar. Agriochoerid diversity in the Uintan of California is at least as high as that reported from the Vieja Group in Texas and the Badwater Creek of Wyoming, although it does not reach the diversity seen in contemporaneous faunas in the Uinta Basin (Wilson, 1971; Golz, 1976; Black, 1978), in part because *Diplobunops* has not been found in California.

#### PROTOREODON cf. WALSHI new species

Figure 3.7–3.9, Table 4

*Protoreodon* new species Type B THEODOR, 1996 p. 81, figs. 4.15–4.16

**Description.**—The upper canine is long, recurved, with a triangular cross section. P<sup>1</sup> is two-rooted, triangular, lacking the posterior basin seen in the specimens referred to *Protoreodon walshi*. P<sup>3</sup> is crescentic, bears a weak protocone which is isolated from the para-metacone and lacks a buccolingual crest (Fig. 3.7). P<sup>4</sup> shows a strong postcingulum, a weak precingulum, and has well-developed styles and slight ribs on the external face which are weak on buccal face of the metaconule. The molar cingulae are reduced. The parastyles are enlarged, especially on M<sup>2-3</sup>, and the M<sup>3</sup> metastyles are larger than in *P. walshi*. The premetaconule crista of the M<sup>3</sup> meets the base of the paracone. The M<sup>3</sup> postprotocrista is absent, and the protocone is more conical than in M<sup>1-2</sup>. The buccal ribs on the protocone and metaconule are reduced.

P<sub>2</sub> resembles the P<sub>2</sub> of *P. walshi* (Fig. 3.4, 3.9). P<sub>3</sub> is deeply basined posteriorly, is closed posterolingually and is not basined anteriorly. P<sub>4</sub> is deeply basined, with a complete, well-developed talonid. The talonid basin does not open posterolingually. The paraconid, protoconid, metaconid and protocristid are weak. The hypoconid is present as a small crest or cuspid, lingually branching from the talonid. A small entoconid also appears to be present in this specimen.

The lower molars have very weakly developed parastylids, and the metastylids are smaller than in *P. walshi*. The molars lack entoconulids and hypolophids. The metaconid and entoconid are very stout and conical and entirely lacking crests, while the protoconid and hypoconid are more V-shaped and weakly crested. The protocristid does not meet the metastylid.

The specimens referred to *Protoreodon cf. walshi* differ from those referred to *P. cf. parvus* by Golz (1976) in the lower molar stylids, which are more prominent in *P. cf. parvus* (see Golz, 1976, fig. 9), and the closed talonid basin on P<sub>3</sub>, which is posterolingually open in *P. cf. parvus*. The P<sup>3</sup> protocone of *P. cf. parvus* is connected to the para-metacone by a crest (Golz, 1976) as in *P. walshi*, unlike the isolated P<sup>3</sup> protocone of SDSNH 27424.

**Material examined.**—SDSNH 42618—left maxilla with P<sup>4</sup>–M<sup>3</sup> preserved; SDSNH 42724—left maxilla with P<sup>3</sup>–M<sup>3</sup> preserved, P<sup>2</sup> broken, fragment with C–P<sup>1</sup>, partial right dentary, slightly deformed, with P<sub>2</sub>–M<sub>3</sub>.

**Occurrence.**—SDSNH localities 3561 and 3276, Jeff's Discovery Site, San Diego County, southern California.

**Discussion.**—These two specimens differ from the material referred to *P. walshi* and may belong to another new species. It is possible that *P. walshi* is sexually dimorphic (Black, 1978), although if that is the case there is a bias towards smaller individuals. The larger morph represented by SDSNH 42724 and SDSNH 42618 is only known from Jeff's Discovery Site. It

TABLE 4.—Dental measurements for adult specimens of *Protoreodon cf. walshi*. All measurements in mm, rounded to nearest 0.1 mm. Estimates marked by an \*.

Uppers	SDSNH 42724	SDSNH 42618
	Left	Left
P <sup>2</sup> AP	8.5*	—
T	5.4	—
P <sup>3</sup> AP	8.9	—
T	8.4	—
P <sup>4</sup> AP	7.8	8.7
T	10.5	10.5
M <sup>1</sup> AP	10.0	9.9
T	12.3	12.3
M <sup>2</sup> AP	11.7	11.6
T	14.5	14.5
M <sup>3</sup> AP	12.1	12.6
T	15.9	16.1
M <sup>1</sup> -M <sup>3</sup>	34.0	33.3

Lowers	SDSNH 42724
	Right
P <sub>2</sub> AP	8.2
T	4.5
P <sub>3</sub> AP	9.3*
T	4.9
P <sub>4</sub> AP	9.0
T	5.9
M <sub>1</sub> AP	10.2
T	7.8
M <sub>2</sub> AP	11.3*
T	8.7
M <sub>3</sub> AP	16.2
T	9.1
M <sub>1</sub> -M <sub>3</sub>	37.7

seems unlikely that all of the examples of one morph of a sexually dimorphic species would be found in one locality, and absent from others. Because there are only two specimens with this morphology, I have assigned them to *Protoreodon cf. walshi* rather than erect a new taxon.

#### ACKNOWLEDGMENTS

For access to specimens in their care, I thank T. A. Deméré (SDSNH), M. C. McKenna and J. P. Alexander (American Museum of Natural History), M. R. Dawson and A. Tabrum (Carnegie Museum of Natural History), R. Purdy (U.S. National Museum, Smithsonian Institution), M. A. Turner (Yale Peabody Museum) and S. McLeod (Los Angeles County Museum). W. A. Clemens, A. D. Barnosky and J. L. Patton provided useful comments on earlier versions of the manuscript. A. Kern, S. Gerson and J. Kane provided helpful comments on the figures, and K. D. Earls provided photo editing facilities. This work benefited greatly from discussions with T. A. Deméré, S. L. Walsh, J. H. Hutchison, P. A. Holroyd, D. Rasmussen and A. Weil. Especial thanks to J. Dahlgren, who discovered the Jeff's Site locality, and to R. Cerrutti, M. Roeder, and B. Riney, who collected much of the material. This work was supported in part by an NSF Graduate Fellowship and by the Annie Alexander Fellowship of the University of California Museum of Paleontology. Parts of this work appeared in Theodor (1996).

#### REFERENCES

- Black, C. C. 1978. Paleontology and geology of the Badwater Creek area, central Wyoming, Pt. 14, The artiodactyls. *Annals of the Carnegie Museum*, 47(10):223-258.
- COBAHE, E. A. 1996. Leptaucheniinae, p. 574-580. *In* D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene-Oligocene Transition in North America*. Cambridge University Press, Cambridge and New York.
- COOMBS, M. C. 1983. Large mammalian clawed herbivores: a comparative study. *Proceedings of the American Philosophical Society*, 73, 96 p.
- GAZIN, C. L. 1955. A review of the Upper Eocene Artiodactyla of North America. *Smithsonian Miscellaneous Collections*, 128(8):1-96.
- GENTRY, A. W., AND J. J. HOOKER. 1988. The phylogeny of the Artiodactyla, p. 235-72. *In* M. J. Benton (ed.), *The Phylogeny And Classification of the Tetrapods, Volume 2, Mammals*. Clarendon Press, Oxford.
- GOLZ, D. J. 1976. Eocene Artiodactyla of Southern California. *Natural History Museum of Los Angeles County, Science Bulletin*, 26:1-85.
- , AND J. A. LILLEGRAVEN. 1977. Summary of known occurrences of terrestrial vertebrates from Eocene strata of southern California. *University of Wyoming Contributions to Geology*, 15(1):43-65.
- KELLY, T. S. 1990. Biostratigraphy of Uintan and Duchesnean land mammal assemblages from the middle member of the Sespe Formation, Simi Valley, California. *Contributions in Science, Natural History Museum of Los Angeles County*, (419):1-42.
- KELLY, T. S., E. B. LANDER, D. P. WHISTLER, M. A. ROEDER, AND R. E. REYNOLDS. 1991. Preliminary report on a paleontologic investigation of the lower and middle members, Sespe Formation, Simi Valley Landfill, Ventura County, California. *PaleoBios* 13(50): 13 p.
- LANDER, E. B. 1978. A review of the Oreodonta (Mammalia, Artiodactyla), Pts. I, II and III. Unpublished Ph.D. dissertation, University of California, Berkeley, 474 p.
- , 1998. Oreodontoidea, p. 402-425. *In* C. M. Janis, K. M. Scott and L. L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America. Volume 1. Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*. Cambridge University Press, Cambridge.
- LEIDY, J. 1869. The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. *Journal of the Academy of Natural Sciences of Philadelphia*, 2:1-472.
- PETERSON, O. A. 1931. Two new species of agriocherids. *Annals of the Carnegie Museum*, 20:341-354.
- SCHULTZ, C. B., AND C. H. FALKENBACH. 1940. Merycochoerinae, a new subfamily of oreodonts. *Bulletin of the American Museum of Natural History*, 77:213-306.
- , AND —. 1947. Merychyinae. *Bulletin of the American Museum of Natural History*, 88:165-285.
- , AND —. 1950a. Phenacocoelinae. *Bulletin of the American Museum of Natural History*, 95:95-149.
- , AND —. 1950b. Promerycochoerinae. *Bulletin of the American Museum of Natural History*, 93:79-197.
- , AND —. 1954. Desmatochoerinae. *Bulletin of the American Museum of Natural History*, 105:153-256.
- , AND —. 1968. The phylogeny of the oreodonts. *Bulletin of the American Museum of Natural History* 139:1-498.
- SCOTT, W. B. 1890. Beiträge zur Kenntniss der Oreodontidae. *Morphologisches Jahrbuch*, XVI:319-395.
- , 1894. Osteology of *Agriocherus* Leidy [*Artionyx* O. & W.]. *Proceedings of the American Philosophical Society*, 23:243-251.
- , 1899. The selenodont artiodactyls of the Uinta Eocene. *Transactions of the Wagner Free Institute of Science, Philadelphia*, 6:9-121.
- , 1940. The mammalian fauna of the White River Oligocene, Pt. IV, Artiodactyla. *Transactions of the American Philosophical Society*, 28(4):363-746.
- , AND H. F. OSBORN. 1887. Preliminary report on the vertebrate fossils of the Uinta Formation, collected by the Princeton Expedition of 1886. *Proceedings of the American Philosophical Society*, 24:255-264.
- STEVENS, M. S., AND J. B. STEVENS. 1996. Merycooidodontinae and Minochoerinae, p. 498-573. *In* D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene-Oligocene Transition in North America*. Cambridge University Press, Cambridge and New York.
- STORER, J. E. 1984. Mammals of the Swift Current Creek Local Fauna (Eocene: Uintan), Saskatchewan. *Natural History Contributions, Saskatchewan Museum of Natural History*, 7, 158 p.

- THEODOR, J. M. 1996. Phylogeny, locomotor evolution and diversity patterns in Eocene Artiodactyla. Unpublished Ph.D. dissertation, University of California, Berkeley, 177 p.
- THORPE, M. R. 1937. The Merycoidodontidae: an extinct group of ruminant mammals. *Memoirs of the Peabody Museum of Natural History*, 3(4):1-428.
- WALSH, S. L. 1991. Eocene mammal faunas of San Diego County. *In* P. L. Abbot and J. A. May (eds.), *Eocene Geologic History, San Diego Region*. Pacific Section, Society of Economic Paleontologists and Mineralogists, 68:161-178.
- . 1996. Middle Eocene mammal faunas of San Diego County, California, p. 75-119. *In* D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene-Oligocene Transition in North America*. Cambridge University Press, Cambridge and New York.
- WILSON, J. A. 1971. Early Tertiary vertebrate faunas, Vieja Group Trans-Pecos Texas: Agriocheridae and Merycoidodontidae. *Bulletin of the Texas Memorial Museum*, (18):1-83.

ACCEPTED 7 JUNE 1999

Permission granted: to reprint this article, from Timothy Hazen, Associate Editor, Paleontology Society, and the Author, Jessica M. Theodor

## SHARK TOOTH TALES: FOSSIL TEETH TELL THE STORY OF TWO ENVIRONMENTS

**JIM BRACE-THOMPSON**

7319 Eisenhower Street, Ventura, California 93003, (805) 659-3577, Nbraceth@aol.com

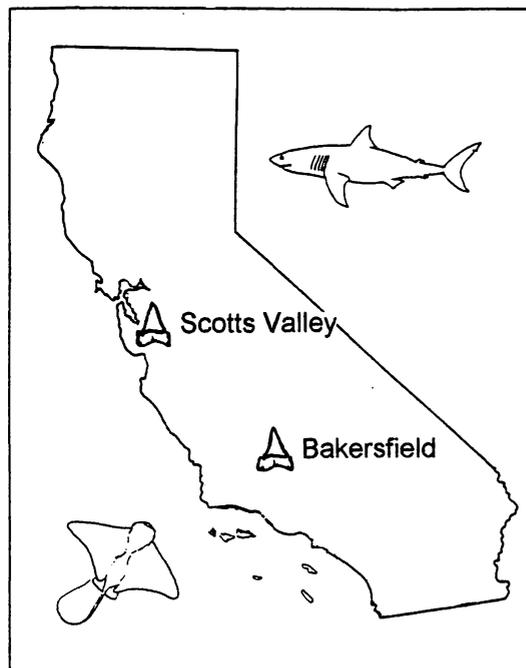
***ABSTRACT**—Fossil shark teeth from the Santa Margarita Formation of Scotts Valley and the Temblor Formation near Bakersfield assist in deducing two Miocene marine environments in California. Teeth were examined in relation to four criteria: the sediment encasing them, condition of preservation, relative abundance, and diversity. Loosely consolidated sandy conglomerate encases the Scotts Valley teeth, which are worn, relatively scarce, and lacking in diversity (most are from three open-ocean species). Silty sandstone encases the Bakersfield teeth, which are fairly pristine, abundant, and highly diverse, with notable numbers of shallow-water and bottom-dwelling species. Taken in context, the Scotts Valley teeth tell of a high-energy environment with a connection to the open ocean, whereas the Bakersfield teeth tell of a relatively calm, protected inland sea or bay.*

### INTRODUCTION

**W**hen looking at a relief map of California, you're immediately struck by the huge depression of the Great Valley cupped between the Sierra Nevada to the east and the Coast Ranges to the west. Just a modest rise in sea level, and you can easily imagine the Pacific Ocean rushing through San Francisco Bay, sweeping away the Golden Gate Bridge and the Pyramid Building to fill a great inland sea. Indeed, if not quite so dramatically, this has happened in the geological past. Seas, inlets, and bays have left shark teeth, sand dollars, reefs of giant oysters, and banks of barnacles and pecten scattered across California's interior.

An inland sea is a protected environment and thus relatively calm. However, any connection between that sea and the open ocean beyond is a turbulent place, as evidenced by the strong currents at San Francisco Bay that proved so effective at keeping inmates on Alcatraz island. Two California locales from the Miocene Epoch have assemblages of fossil shark teeth that tell the tale of two such very different environments. Sediments in the Sharktooth Hill area around Bakersfield tell of a calm, protected inland sea covering what is now the San Joaquin Valley (Dupras, 1985). Some 250 miles to the northwest, geologists believe the Scotts Valley area records the deposits of a near-shore environment, possibly connecting such an inland sea with the open Pacific beyond (Perry, 1994). Such a narrow seaway would

have been subjected to intense wave action and strong tidal currents as a result of the constant agitation of an inland sea meeting the open ocean. We'll visit both sites (Fig. 1) and then turn to the teeth to see how they supplied scientists with the evidence of two such distinct environments.



**FIGURE 1** – Locations of the Scotts Valley and Bakersfield, California, fossil shark tooth sites.

### The Sites

**Scotts Valley.** I first learned of the Scotts Valley site from a friend in a construction family, Jay House, of the Carmel Valley Gem & Mineral Society. Jay used to notice shark teeth in their gravel. It turned out that prime local sources of sand and gravel were ancient marine deposits still being quarried today in the Felton/Scotts Valley area near the central California coast. These deposits are part of the late or Upper Miocene Santa Margarita Formation (Perry, 1977).

Although deposits of the Santa Margarita Formation crop out all around this area, the site where I concentrated my collecting was in a small, inactive quarry at the edge of Scotts Valley. To reach the site, exit from Highway 1 in Santa Cruz onto State Highway 17 north toward San Jose. Travel just over three miles to the Felton/Mt. Hermon Road exit. Another 1.3 miles northwest on Mt. Herman Road (heading toward Felton) brings you to Lockhart Gulch Road. Turn right (north) onto this road, and you'll almost immediately see the abandoned sand quarry dug into the hillside to your right (Fig. 2).



FIGURE 2 – Abandoned sand quarry along Lockhart Gulch Road in Scotts Valley, California.

That is, you *used* to be able to see such a quarry! Unfortunately, if you wish to check out this particular site yourself, you can't. In the never-ending name of progress and Manifest Destiny here in California, everything that can be blacktopped will be. Thus, the site is now a self-storage lot despite the efforts of locals to protect this spot, where kids had dug fossils since the 1950s, as a local paleontology park. The

only concession developers made to public opinion was to allow the Santa Cruz City Museum to salvage what they could before the bulldozers moved in. Fossil sites within the same formation are scattered about this area, and should you be interested in collecting here, you may want to inquire with local organizations such as the Santa Cruz Gem & Mineral Society or the Santa Cruz City Museum.

**Bakersfield.** Whereas Scotts Valley is a relatively lush area near the north-central California coast, with foggy redwood forests nearby, the Sharktooth Hill area of Bakersfield has harsher, semi-desert conditions, with barren hills topped only by patchy grasslands. Debbie Bunn, of the Fossils for Fun Society in Sacramento, introduced me to this site, and I've made several trips since. In fact, it's been something of a Mecca for California fossil collectors for over 100 years. First described by U.S. Topological Corps geologist William Blake in 1853, Sharktooth Hill provided the first fossil shark teeth found west of the Rockies and was included in the United States Landmark Registry in 1976 as one of the most significant Miocene marine vertebrate localities in the world (Dupras, 1985). While Sharktooth Hill itself is off-limits to unauthorized collectors, the formation crops out in an area of about 10 square miles, and one site popular among amateur collectors is located across the Kern River, just west of the Lake Ming park and campground and the California Living Museum.

To reach this site, exit north off of State Route 178 (not far from its intersection with State Route 184) onto Alfred Harrell Highway and proceed just under two miles to its intersection with Lake Ming Road. Continue on the highway for 1.3 miles and turn left onto a dirt road. Follow the road to the right and drive parallel to the highway for about 0.1-0.2 mile down into a wash. Turn left and follow the wash to a wide, flat area immediately in front of you to park. (Alternatively, drive 1.5 miles from Lake Ming Road before turning left off the highway. Continue down a bit under 0.1 mile to a dirt access road, make a quick hairpin turn, and proceed down into the wash. Turn right and follow the wash up to the parking area.) Step out and face the highway. The hill to your left is your destination; simply follow the steep, well-traveled footpath upwards. You're likely to be puffing by the time you reach a flat spot midway up the hill, where you'll have a sweeping view of the highway and the Kern River valley to the east, with soccer fields inbetween. Turn around, and you'll see your goal: a line scratched into the hillside by the collectors who have come before you. The exposure forms a fringe midway up the bowl of an amphitheater-like gorge (Fig. 3).



FIGURE 3 – The Bakersfield fossil shark tooth locality is in a small gorge behind the flat-topped hill in the foreground. Simply follow the well-trod footpaths upward.

Access to this site is about to either improve or be lost forever. During my most recent visit over the Thanksgiving 1999 weekend, I overheard two bikers talking about a water treatment plant to be installed somewhere in the valley here. That conversation, along with a frenzy of new home construction in this general area, does not give me hope for the long-term prospects of access to this site. If construction workers don't get to it first, dirt bikers—who have torn the surrounding hills to shreds with increasing abandon—surely will.

In the meantime, though, you'll find fossils concentrated in a narrow horizon of pale gray sandstone, sandwiched between a layer of pale brown sandy siltstone below and sandy siltstone above. Most people apparently come and dig directly into the hillside itself, using picks, trowels, or screwdrivers to loosen clumps of sand to screen for shark teeth and bone. However, it also proves fruitful to scour the hillside beneath the exposure, where a variety of tiny shark teeth, vertebrae, and ray and skate toothplates and rare tail spines may be found on

the surface. While they say that this site lacks the abundance of Sharktooth Hill proper, my family still found 65 individual teeth during one two-hour stay, and 255 on our most recent visit. Although most were quite small, the variety more than compensated for the size.

The Sharktooth Hill beds belong to the Round Mountain Silt member of the Middle Miocene Temblor Formation (Dupras, 1985). It's a bit older than the Santa Margarita Formation. Depending upon the source you consult, the Temblor Formation—and the Temblor Sea that deposited it—has been dated at anywhere from 14 to 20 million years (Seiple, 1992; Dupras, 1985). In comparison, the Santa Margarita Formation has been dated at 10-12 million years (Perry, 1977).

### EXPLORING THE EVIDENCE

Although they're of slightly different ages, the Scotts Valley and Bakersfield sites provide extremely similar suites of fossil shark teeth, with identical species of various types of mako sharks, tiger sharks, and others. Certain differences, however, tell the tale of the very different environments in which these similar species lived, and I'll examine four such differences: the sediments surrounding the teeth, the condition of the teeth, their relative abundance, and finally, the diversity of species represented by tooth remains at each site.

#### Evidence from the Sediment

The pale gray Round Mountain Silt member of the Temblor Formation is composed of well-graded, medium-to-coarse grained fossiliferous marine sandstone and silt. Few fossils are found in over- and underlying units, but the fossil bed is exceedingly fossiliferous, with up to 100 individual bones and teeth contained in a single cubic foot of sediment at prime localities. Because of the presence of silt and sand and the absence of extensive clay beds, scientists suspect that the sea in this area was shallow and possibly near shore. Although shallow, it would not appear to have been turbulent nor to reflect heavy wave or current action, but to have been a relatively calm area of deposition (Dupras, 1985).

The younger Santa Margarita Formation at Scotts Valley is another story altogether. In technical terms, this formation is composed of loosely consolidated sandstones and conglomerates (Perry, 1977), or in plain English, coarse-grained sand and gravel (Fig. 4). Interleaving layers of sand and gravel indicate a turbulent, high-energy environment with constantly agitated water that could move and round large particles of sediment.

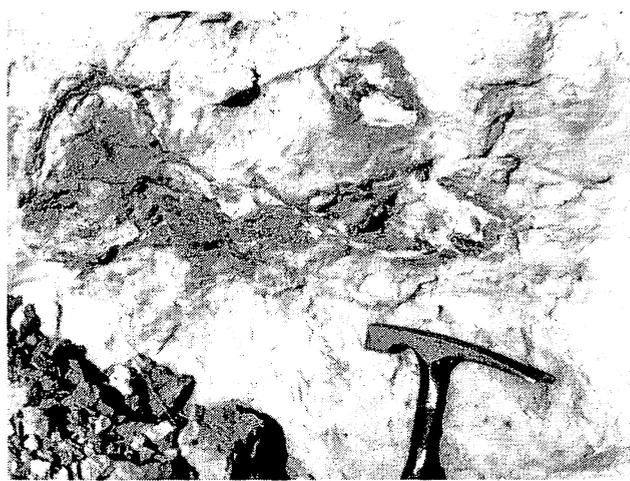
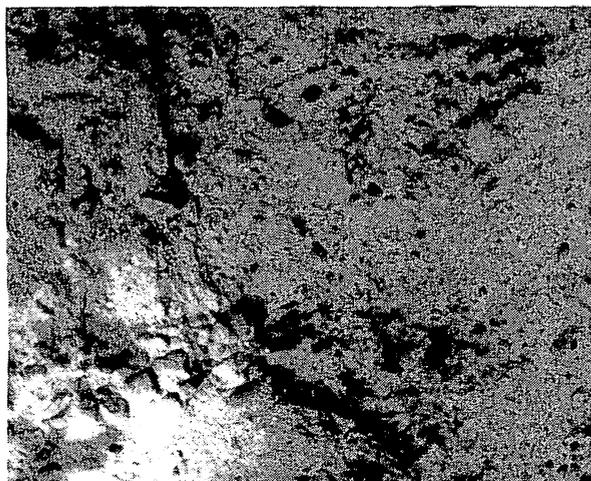


FIGURE 4 – The Round Mountain Silt member of the Temblor Formation at Bakersfield (left) and the coarse sands and conglomerate of the Santa Margarita Formation at Scotts Valley (right).

**Evidence from the Condition of the Fossils**

Taphonomy, according to *The Concise Oxford Dictionary of Earth Sciences*, is the study of the transition of an organism from the biosphere into the lithosphere (Allaby & Allaby, 1991). What happens from the time a shark is a living, swimming creature in the sea to when it's a pile of disarticulated teeth sandwiched between layers of silt, sand, and gravel? A taphonomic study of these two fossil assemblages shows dramatic differences (Fig. 5).

It's clear that the animals of Scotts Valley did not go gently into the deep but that their remains were transported and moved around quite a bit. The fossil teeth are water worn—abraded, rounded, and often fragmentary—as if they've spent a considerable amount of time in a giant tumbler. There's no single, clear layer of fossils; instead, shark teeth and bones are peppered throughout the sand and gravel and rather poorly preserved. Many are waterlogged upon being uncovered, turning chalky and brittle upon drying. Scientists speculate that the worn condition of the fossils is due to repeated winnowing of the sediments by tidal currents prior to final burial (Perry, 1994).

This is in stark contrast to the relatively pristine condition of the teeth and bones of the Bakersfield area. It's believed that these bones and teeth were also transported by currents—and thus the reason for an unusually high concentration of fossils in specific horizons (Dupras, 1985)—but if they have been moved, they've clearly not traveled as far nor as roughly as those we find in Scotts Valley. They're not rounded and abraded as they would be if exposed to prolonged and repeated movement. Teeth here retain sharp points and fine serrations, and—were it

not for the attractive orange hue from iron staining—you could easily imagine that they dropped from a shark's jaw just yesterday. Not so with the rounded tips and edges and worn roots of Scotts Valley teeth.

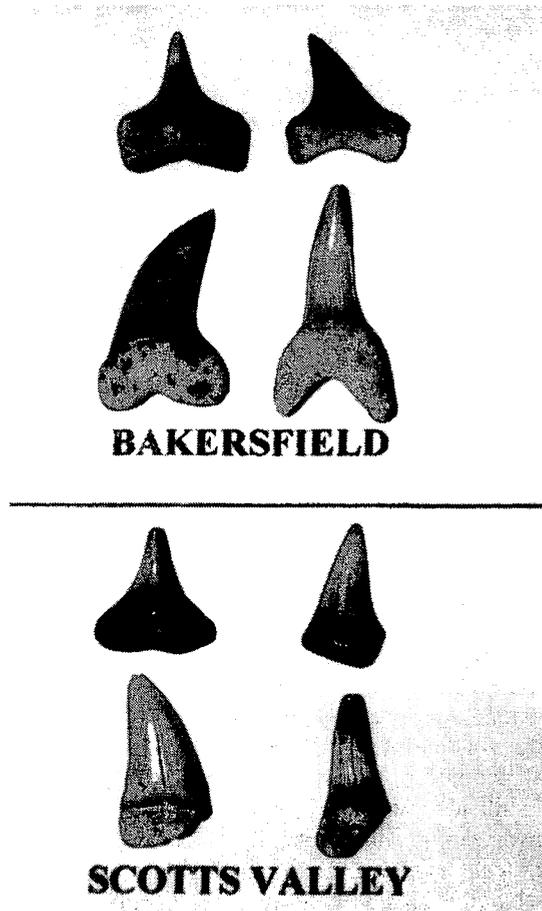


FIGURE 5 – Fairly pristine teeth of Bakersfield compared with abraded teeth from Scotts Valley.

Fossil bones back up evidence provided by the teeth. Bone is extremely common at the Bakersfield site and not as common at Scotts Valley. Although a locally famous skeleton of the sea cow *Metaxytherium jordani* (a cast of which hangs from the ceiling of the Santa Cruz City Museum) has been unearthed from a Scotts Valley sand quarry, most bony remains are small, water-worn fragments as soft as chalk, in keeping with the water-worn condition of the shark teeth.

This contrasts starkly with the quality and quantity of bony remains found in the Bakerfield area, which at places is a jumbled mass of extremely well preserved bones. Although most bones are in a disarticulated jumble, enough articulated skeletons of various marine mammals (including an almost perfect skeleton of an extinct sea lion, *Allodesmus*) have been found to indicate that the deposition of the sediments and fossils did not occur in a turbulent surf zone (Dupras, 1985).

**An aside.** Three questions about the taphonomy of the Sharktooth Hill bonebeds vex scientists: Why are the fossil teeth and bones so concentrated in a narrow band, with no traces of fossils in sediments above and below? Where are the invertebrates? (A typical shallow marine Tertiary fossil bed should include clams, snails, sand dollars, and other invertebrates, such as are found in Miocene beds of Calvert Cliffs in Maryland.) And why are bones and teeth densely packed in a mostly dissociated mix?

It's been observed that Sharktooth Hill fossils occur in "pockets" aligned parallel to one another, suggesting that currents may have been responsible for the origin of the fossil bed. But very delicate bones have been found and while some bones are abraded, they aren't abraded to the degree you would expect if mixed on the bottom by ocean currents. Were the tightly packed bone beds the result of a sudden mass extinction from a volcanic eruption, or from a red tide? If so, wouldn't invertebrates have died along with the vertebrates? One intriguing theory postulates that a relatively sudden change in topography resulted in currents dropping carcasses into submarine canyons, along with the well-graded sands and silts. Fortunately for future paleontology students in search of a dissertation topic, no explanation has yet proved fully adequate (Dupras, 1985).

#### **Evidence from the Relative Abundance of Teeth**

The relative abundance of teeth at each site also provides clues about the differing environments. At Bakersfield, teeth litter the ground. If you've never collected a single fossil tooth, within just a couple

hours you can come away with a respectable collection, in both number and variety of specimens. At Bakersfield, my family has collected 554 fossil teeth from four trips, or about 138 per trip. Such abundance suggests a protected, calm environment that provided an "Eden" supporting relatively large populations of animals.

In contrast, you could spend a day screening at Scotts Valley and come away with only a dozen or so fairly decent teeth, with many more tooth fragments. For instance, we've collected 222 fossil shark teeth from approximately a dozen trips, or about 20 teeth per trip. This relative lack of abundance suggests an environment that was somewhat less inviting and therefore inhabited by fewer animals.

#### **Evidence from Diversity of Species Represented**

Our final bit of evidence for differing environments is provided by the diversity of species represented at each site and comparison of those species to the lifestyles and preferred environments of modern-day representatives. In approaching this exercise, it should be noted how difficult it is for even a professional to definitively identify individual shark teeth because of "heterodonty." Just as our own teeth differ in size and shape (incisors versus canines versus molars), shark teeth often differ depending upon whether they're from the upper or lower jaw, the front of the mouth or the back (Perry, 1994). Thus teeth that look very different may well come from the very same individual. By the same token, teeth that look very similar sometimes come from different species (for instance, the various species of the *Carcharhinus* genus, which includes the gray shark, dusky shark, black-tipped shark, etc.). I'm definitely no professional, so in adding up the number of species in my own collection, I'm only going by what I can more-or-less confidently identify and thus leaving out a number of fossils or remaining at the genus level in many instances.

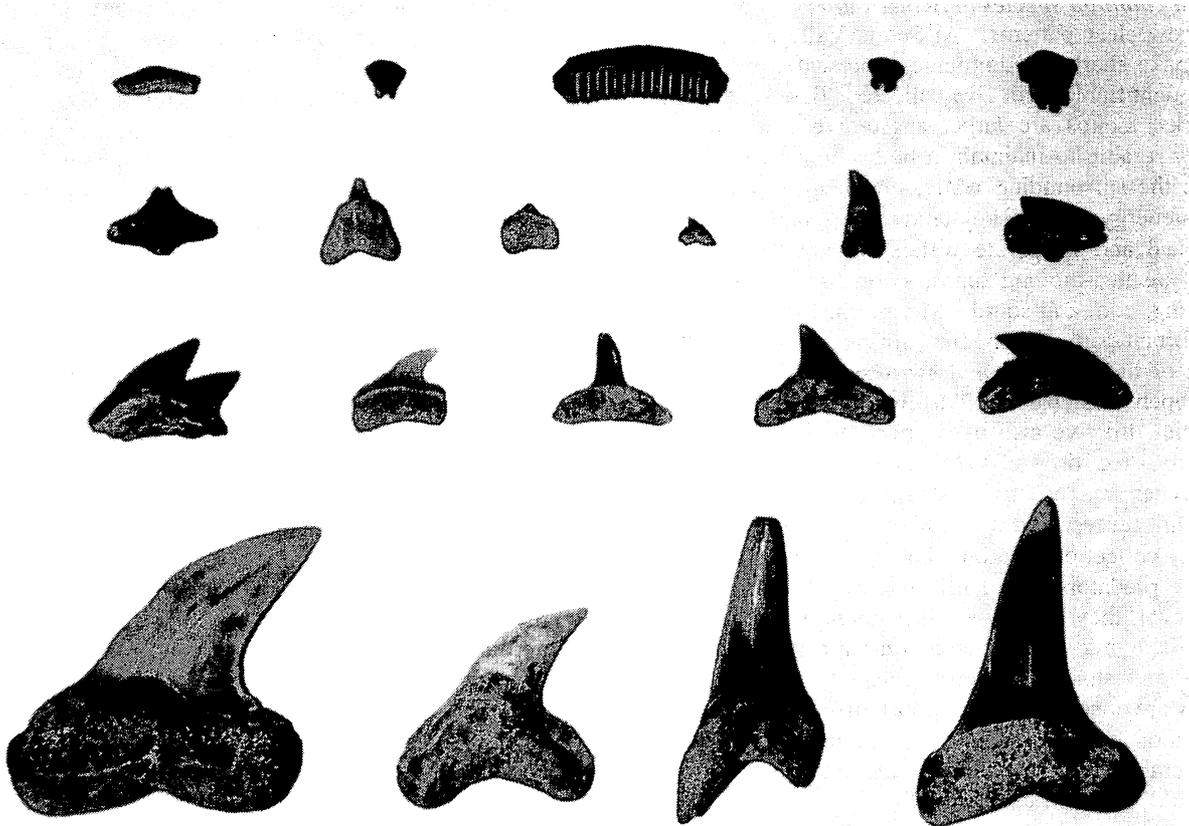
Up to 19 species of sharks and rays have been identified at Scotts Valley (Perry, 1994). Table 1 shows those in my collection. By comparison, at least 27 species of sharks and rays have been identified from the Bakersfield area, providing one of the world's largest Miocene shark tooth assemblages, with Sharktooth Hill being the type locality for a great many of them (Dupras, 1985). This is a large number, matched in California today by areas that are semi-enclosed and protected, such as the Monterey Bay, home to some 33 species of sharks and rays (Ferguson & Cailliet, 1990). Table 2 provides a listing of the Bakersfield species in my collection. Figure 6 shows representative species from both Scotts Valley and Bakersfield.

TABLE 1 – Shark and Ray Teeth Collected at Scotts Valley Locality

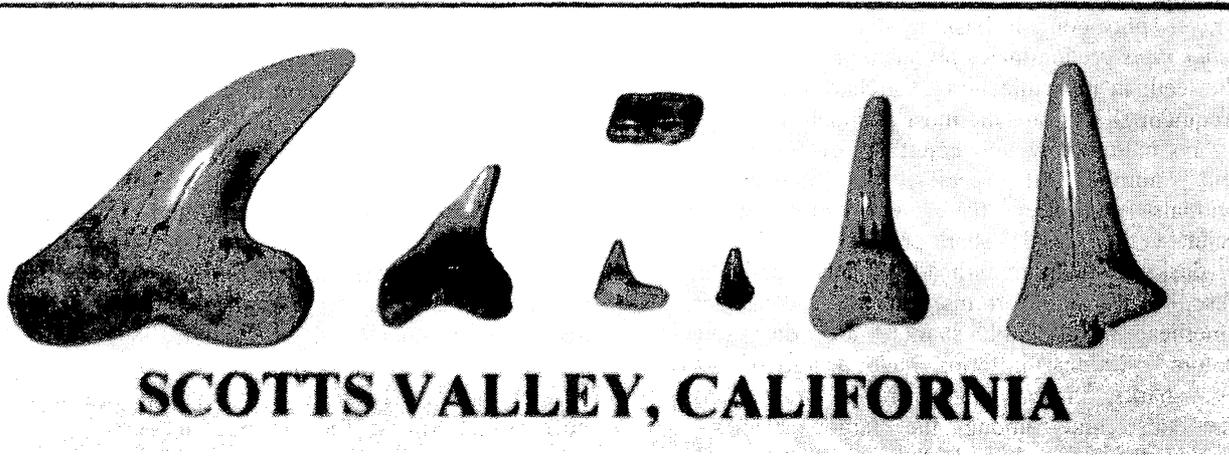
Scientific Name	Common Name	Number Found
<i>Isurus hastalis</i>	Big-Tooth Mako	46
<i>Isurus planus</i>	Hook-Tooth Mako	39
<i>Isurus oxyrinchus</i>	Shortfin Mako	28
<i>Galeocerdo</i> sp.	Tiger Shark	14
<i>Carcharhinus</i> sp.	Gray Shark	4
<i>Myliobatis</i> sp.	Bat Ray	1
Unidentified		90

TABLE 2 – Shark and Ray Teeth Collected at Bakersfield Locality

Scientific Name	Common Name	Number Found
<i>Carcharhinus</i> sp.	Gray, Dusky, etc.	202
<i>Squatina lerichei</i>	Angel Shark	67
<i>Myliobatis merriami</i>	Bat Stingray	51
<i>Squalus occidentalis</i>	Spiny Dogfish	49
<i>Dasyatis</i> sp.	Diamond Stingray	34
<i>Isurus hastalis</i>	Big-Tooth Mako	32
<i>Galeocerdo aduncas</i>	Tiger Shark	21
<i>Sphyrna</i> sp.	Hammerhead Shark	21
<i>Isurus planus</i>	Hook-Tooth Mako	17
<i>Cetorhinus</i> sp.	Basking Shark	15
<i>Mobula</i> sp.	Manta Ray	9
<i>Heterodontus</i> sp.	Horn Shark	7
<i>Galeocerdo productus</i>	Tiger Shark	6
<i>Raja</i> sp.	Skate	5
<i>Mustelus</i> sp.	Smooth Hound Shark	5
<i>Isurus oxyrinchus</i>	Shortfin Mako	4
<i>Hexanchus andersoni</i>	Six-Gilled (Cow) Shark	4
<i>Hemipristis serra</i>	Indian Ocean Shark	2
<i>Scyliorhinus</i> sp.	Cat Shark	1
<i>Galeorhinus</i> sp.	Soup-Fin Shark	1
<i>Alopias vulpinus</i>	Common Thresher	1



**BAKERSFIELD, CALIFORNIA**



**SCOTTS VALLEY, CALIFORNIA**

FIGURE 6 – The much greater variety of fossil shark teeth from Bakersfield as compared to Scotts Valley. Those from Scotts Valley include: Hook-Tooth Mako, Tiger Shark, two Gray Sharks, Shortfin Mako, Big-Tooth Mako, and (small bar-shaped object) a tooth plate of a Bat Ray. Bakersfield teeth include: (bottom row) Hook-Tooth Mako, Tiger Shark (*G. productus*), Shortfin Mako, Big-Tooth Mako; (second row) Six-Gilled or Cow Shark, Hammerhead, two Gray Sharks, Tiger Shark (*G. aduncus*); (third row) Angel Shark, Common Thresher, Horn Shark anterior tooth, Soup-Fin Shark, Basking Shark, Spiny Dogfish; (top row) Horn Shark lateral tooth, Diamond Stingray, Bat Ray, Skate (*Raja*), and Smooth Hound Shark.

**Most common species at Scotts Valley.** Tables 1 and 2 show clear patterns. At Scotts Valley, large teeth of mako sharks predominate, represented by 85% of the identifiable teeth I've collected. The fastest of all sharks, makos are large, aggressive, and graceful. They're able to maintain a body temperature higher than the surrounding water, which gives them their high energy level. They tend to be found offshore in tropical and temperate waters worldwide, and they feed on fast-moving tunas, swordfish, other sharks, herring, cod, and squid. Marine mammals aren't an important part of their diet (Springer & Gold, 1989). One of the strongest and swiftest sharks, they roam the open seas (Allen, 1996), but although an oceanic species, they've also been encountered in kelp beds and near reef drop-offs (Michael, 1993).

After makos, tiger sharks come in a distant second, represented by 11% of the identifiable teeth in my collection. Like makos, tiger sharks are large, fierce predators found in tropical and warm waters; however, they occupy a wider range of habitats than makos, living in the open ocean but also moving into bays and shallow inshore waters to feed at night. They are unselective and opportunistic, eating prey of all kind: bony fish and marine mammals, sea turtles and crabs, squid and other sharks and rays (Springer & Gold, 1989; Michael, 1993).

**Most common species at Bakersfield.** A much greater diversity exists at Bakersfield, with large numbers of teeth not only from makos and tiger sharks, but also requiem sharks, angel sharks, skates and rays, spiny dogfish, basking sharks, and others. *Carcharhinus* predominates by far, representing 45% of the teeth in my collection. Carcharhiniforms, or the requiem sharks, are the most abundant of sharks today no matter how you count it—by number of genera, number of species, or number of individuals—and they have what most would associate as the "classic" shark profile. They include gray, dusky, tiger, hammerhead, bull, cat, and blue sharks. The larger forms, such as the tiger, hammerhead, and bull sharks, are dangerous predators. Carcharhiniforms have a varied diet: other sharks, rays, bony fish, crustaceans, cephalopods, and—among the larger species—marine turtles and seals and other marine mammals (Springer & Gold, 1989). In short, they fed on many of the types of creatures found in the Bakersfield bone beds. They tend to inhabit warm, shallow, coastal areas and some, such as the gray shark, form loose groups or schools of up to 100 individuals, often entering shallow lagoons at night to feed on a variety of prey (Michael, 1993). Some forms are migratory, seeking out warm waters and shallow lagoons and bearing their young in protected waters

rather than the open oceans (Allen, 1996). Could the Temblor Sea of Bakersfield have been a shark "grocery" and "nursery" for carcharhinidae?

The next most common forms I've found at Bakersfield are the skates and rays, representing 18% of the specimens in my collection. (In contrast, I've found only one skate tooth plate at Scotts Valley.) Skates and rays are members of the shark family that have developed modifications for living on the sea floor: a round, flattened body and enlarged, wing-like fins. They're found in tropical and temperate waters around the world and today are abundant in California waters. They tend to be ground fish, often lying half-buried in the sand or mud of shallows and feeding on crabs, lobsters, clams, and other small invertebrates (Allen, 1996). They prefer calm waters and have been described as "peaceful bottom-dwellers," grubbing along the ocean floor for their meals (Ferguson & Cailliet, 1990).

Angel sharks represent 12% of the specimens in my collection. These have long, flat bodies that appear halfway between sharks and rays. They are slow-swimming, sluggish creatures common today in southern California (Ferguson & Cailliet, 1990). Bottom dwellers like rays, they live in shallow coastal areas of temperate and tropical seas and spend most of their time in repose, burying themselves in soft substrates to ambush prey with their broad mouths and needlelike teeth (Springer & Gold, 1989).

Spiny dogfish represent 9% of my specimens. Although small (2-3 feet long), these sharks are abundant and travel in great schools just above the seafloor, devouring everything in their path (Allen, 1996). Aggressive, they feed in packs, like dogs, and hence their name. Common in a variety of habitats, they range from near-shore shallows to the depths of submarine canyons (Ferguson & Cailliet, 1990). Second only to carcharhiniforms in abundance and in number of species, today they are found in temperate waters and conduct seasonal mass migrations correlated with water temperatures: inshore with warming of waters; back to deeper waters when inshore waters cool (Springer & Gold, 1989).

Nearly 3% of my collection is represented by basking sharks. These huge fish appear seasonally near coastal areas; for instance, modern basking sharks range California coastal waters from Monterey to San Simeon between November and February (Allen, 1996). At 30-50 feet, they are the second-largest fish in the world, yet their teeth are tiny and hook-like because they're plankton feeders, cruising near the surface and screening food in bristle-like gill rakers. Highly migratory, they inhabit both the open ocean and inshore environments (Michael, 1993).

Horn sharks—a small proportion of my collection at 1%—have lifestyles similar to skates and angel

sharks. Poor swimmers, they're small nocturnal bottom-dwellers and prefer calm, shallow waters, where they hide in shadows and crevices (Ferguson & Cailliet, 1990). They've been described as "living fossils" due to crushing teeth similar to those found in some ancient sharks. Their pig-like faces certainly give them a distinctly eerie and ancient appearance. They use their tooth batteries to crack the shells of mollusks, crustaceans, and sea urchins. Today, they inhabit warm, shallow waters of the Pacific and Indian oceans (Springer & Gold, 1989).

Makos, though much less common at Bakersfield than at Scotts Valley, still make up a significant 10% of my collection. Makos are migratory and are found seasonally today in relatively protected areas like the Monterey Bay (Ferguson & Cailliet, 1990). As noted earlier, although preferring the open ocean, they are occasionally found in shallower waters.

### RESULTS

Comparing the Miocene marine fossil beds at Scotts Valley with beds containing similar shark teeth at Bakersfield along four vectors, we see that:

1. Sediments encasing fossils at Scotts Valley are coarse sandstones and conglomerates compared with finer-grained sandstones and siltstones at Bakersfield. Further, the teeth tend to be scattered throughout the many layers of sand and gravel at Scotts Valley, whereas they are in a single, well-defined horizon at Bakersfield.
2. The fossil teeth at Scotts Valley tend to be rounded and worn, as compared to more-or-less pristine teeth at Bakersfield.
3. Teeth are much more abundant at Bakersfield than at Scotts Valley.
4. Bakersfield sediments hold a much greater variety of species than Scotts Valley. The Scotts Valley fossil teeth are dominated by open-ocean forms of large sharks (mako and tiger) whereas the Bakersfield teeth represent species that tended to be placid bottom dweller (skates and rays, angel and horn sharks), as well as sharks that tend to prefer shallow-water environments to the open ocean (the carcharhiniforms).

### Some Caveats

Before drawing conclusions from the relative abundance and diversity of teeth found at these two sites, I need to voice some caveats regarding both my own collecting style and the sorts of environments we're examining that could skew my conclusions.

The fossil assemblages used as evidence here represent the efforts of my personal collecting

activity and observations from specimens in my own collection. Because I'm not a professional, I tend to take a "lite" approach toward disturbing fossil beds. Much of my collecting is concentrated on screening through aprons of sediments that have weathered away from main deposits as opposed to digging directly into deposits. It therefore doesn't necessarily reflect the diversity that a professional paleontologist might find with a more meticulous excavation of the beds themselves at both sites. (For instance, the Santa Cruz City Museum has a much greater variety of Scotts Valley teeth on display.) However, I believe that my collection does provide at least an accurate "snapshot" of general trends and thus is sufficient to provide a relative idea of the differences in diversity between the two sites.

My conclusions might also be confounded because what's left today in the fossil record may not fully reflect the animals living at the time in Scotts Valley. In particular, we find many tiny teeth at Bakersfield, and it could be that such tiny teeth were shed at Scotts Valley but were subsequently worn away by the high-energy environment, leaving no evidence in the fossil record. Fossils in a high-energy environment often provide a less reliable snapshot of the living ecosystem because so many potential fossils were likely to have been scattered, washed away, or ground into dust (Perry, 1994).

### CONCLUSIONS

By itself, a single shark tooth might be considered an artifact of "fossilized behavior," a term frequently used in ichnology, or the study of fossil footprints and trackways. A collection of fossil footprints may hint at herding behavior, at various species that lived together, and at speeds at which an animal traveled. A tooth hints at how and what an animal ate, with differences in tooth shape indicating differences in feeding habits. Teeth with strongly serrated edges like those of the tiger shark indicate slicing and shredding; teeth that are long and needlelike, as with the shortfin mako, indicate a feeding strategy of impaling prey; and the flat, plate-like teeth of rays are perfect for crushing the hard shells of crustaceans and clams. Thus, an individual shark tooth can give an indication of "fossilized behavior."

But teeth also tell us a whole lot more if we move beyond individual specimens to examine a whole context. Although such an examination may seem to raise as many questions as answers (What are the depositional circumstances behind the concentration of the Bakersfield bone beds? Just how reliable is the fossil record of a high-energy environment?), the evidence provided by the teeth, in context, does tell certain tales.

The most common species by far at Scotts Valley are large, aggressive sharks that frequent the open seas, making forays into shallower waters primarily to feed. The predominance of makos suggests waters with a direct link to the offshore ocean (Perry, 1994). Such an environment tends to be turbulent, which we see in the rough-grained sand and gravel of Scotts Valley and the battered nature of the preserved teeth.

We can speculate that Bakersfield and its Temblor Sea was seasonally visited by open-ocean species, like makos and basking sharks, but in general was a shallow, protected area, calm and quiet. Many of the shark and ray species at Bakersfield seem to be nocturnal animals, resting on or under the substrate during the day, and hence a need for a calm environment. Paleontologist Clifford C. Church suggested the region was a coastal bay similar to Todos Santos Bay off Baja California, where whales and other marine mammals migrate to winter. Church notes nearly all the non-extinct marine mammal types from Sharktooth Hill are found today at Todos Santos Bay (Dupras, 1985). Such a shallow inland sea or bay would have been warmer and more hospitable than waters on the outer coast, which would have been cooled and scoured by ocean currents and upwellings (Perry, 1994).

From evidence gathered over the course of 150 years since William Blake offered his first report on Shark Tooth Hill, geologists see an ancient marine basin in the San Joaquin Valley, a large interior embayment that merged with the Pacific Ocean north of present-day Monterey via a relatively narrow channel (Harden, 1998). That basin—the Temblor Sea—covered the southern San Joaquin Valley until the end of the late mid-Miocene when a pronounced orogeny elevated the Sharktooth Hill region (Dupras, 1985). It's speculated that this orogeny also created the source for the Santa Margarita quartz sand and gravel deposits from Sierran granitic rocks to the east (Norris & Webb, 1990).

Although Scotts Valley and Bakersfield are widely separated today, during the Miocene they were almost neighborly. Scotts Valley was about 150 miles south of its present location and has been moved northward to its present, ever-shifting position by the San Andreas fault (Perry, 1994). Uplift of the Coast Ranges and Sierra Nevada and movement of the San Andreas fault eventually distorted and constricted the strait or narrow inlet through the rising Coast ranges that connected the inland sea with the open ocean until the strait eventually disappeared (Harden, 1998).

However, California's coastline continues to be geologically active, just as its interior persists as a lowland basin. Given enough global warming, watch for more inland seas and turbulent straits to supply

paleontologists of the long-distant future with shark teeth resting atop the blacktop and nestled in the sediment-choked rooms of buildings now covering fossil sites of old. These will be teeth with even stranger tales to tell!

#### ACKNOWLEDGMENTS

I am grateful to Jay House (Carmel Valley Gem and Mineral Society) and Debbie Bunn (Fossils For Fun Society) for introducing me to the Scotts Valley and Bakersfield localities, to Frank Perry (Monterey Bay Paleontological Society) for his fine publications and assistance in identifying the shark teeth of the Scotts Valley area and for guiding me to additional Scotts Valley sites, and finally, to Nancy, Hannah and Alex for putting up with the wanderings of an inveterate fossil collector!

#### REFERENCES

- Allaby, A., & Allaby, M. (1991). *The concise Oxford dictionary of the earth sciences*. Oxford & New York: Oxford University Press.
- Allen, T.B. (1996). *Shadows in the sea: The sharks, skates, and rays*. New York: Lyons & Burford.
- Buena Vista Museum of Natural History (1995). *Sharktooth Hill fossil finder's guide*. Bakersfield, CA: Buena Vista Museum of Natural History.
- Dupras, D.L. (1985). Sharktooth Hill: Life beneath the Temblor Sea, Kern County, California. *California Geology*, 38-7: 147-154.
- Ferguson, A., & Cailleit, G. (1990). *Sharks and rays of the Pacific coast*. Monterey, CA: Monterey Bay Aquarium.
- Harden, D. R. (1998). *California geology*. Upper Saddle River, NJ: Prentice Hall.
- Michael, S. W. (1993). *Reef sharks and rays of the world: A guide to their identification, behavior, and ecology*. Monterey, CA: Sea Challengers.
- Norris, R. N., & Webb, R. W. (1990). *Geology of California* (2nd ed.). New York: John Wiley & Sons, Inc.
- Perry, F. A. (1994). *Fossil sharks and rays of the southern Santa Cruz Mountains, California*. Natural History Guide No. 2. Santa Cruz, CA: Santa Cruz Museum Association.
- Perry, F. A. (1977). *Fossils of Santa Cruz County*. Santa Cruz, CA: Santa Cruz City Museum.
- Seiple, E. (1992). Amphitheatre for sharks. *Rock & Gem*, 22-8: 28 ff.
- Springer, V. G., & Gold, J. P. (1989). *Sharks in question: The Smithsonian answer book*. Washington, DC: Smithsonian Institution Press.
- Torrey, M. (1969). The sharks of Sharktooth Hill. *Gems & Minerals*, 378: 24-25.

## ADVENTURES WITH DENTURES AT MAZON CREEK

Jim Konecny

In spite of the fantastic diversity of both plant and animal life found in the Mazon Creek nodules the presence of teeth is quite scarce. For those unfamiliar with the Mazon Creek Area, it is middle Pennsylvanian Age, Carbondale Fm.-Francis Creek Shale Mem.. The fossils are preserved in Siderite (ironstone) concretions (nodules). The vertebrates (the animals

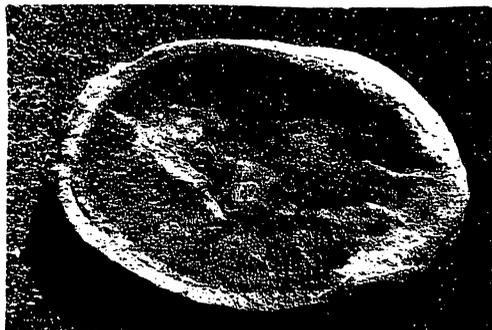


Fig.1. Typical size fish found in Mazon Creek nodules, X 1.

expected to possess teeth) that are found encased in the nodules consist mainly of fish and a few amphibians plus (as of now) one reptile. These critters are generally small - not over 3 inches in length (fig. 1). There may be a few that are a little larger, however I am aware of only one, a legless amphibian, that is considerably longer - 7½ inches (fig. 2). Langford (1963) when referring

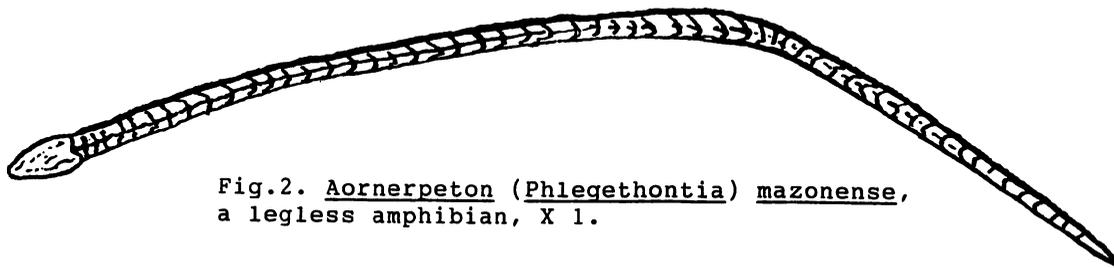


Fig.2. Aornerpeton (Phlegethontia) mazonense, a legless amphibian, X 1.

to fishes states "the largest that I am aware of is not over 9 inches long". In a personal communication with him he confessed not to have seen any over 3½ inches long - he was only informed of the larger ones by an amateur collector. A microscope or at least a 10X hand lens is needed to view the teeth in these small individuals (fig. 3). When looking at the enlarged drawings in figs. 3A and 3B one can imagine just how tiny the teeth are in the actual specimens. The jaws of the fish have the typical saw (mmmm) appearance.

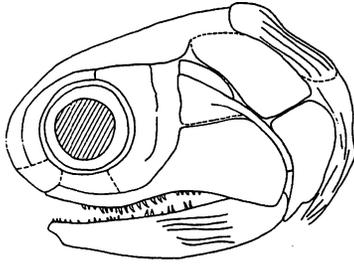


Fig.3A. Skull of one of the many species of fish, X 5.

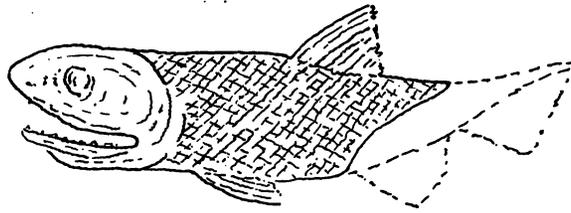


Fig.3B. Drawing of an almost complete specimen, X 1.5.

There have been four species of Agnathans (jawless fish)

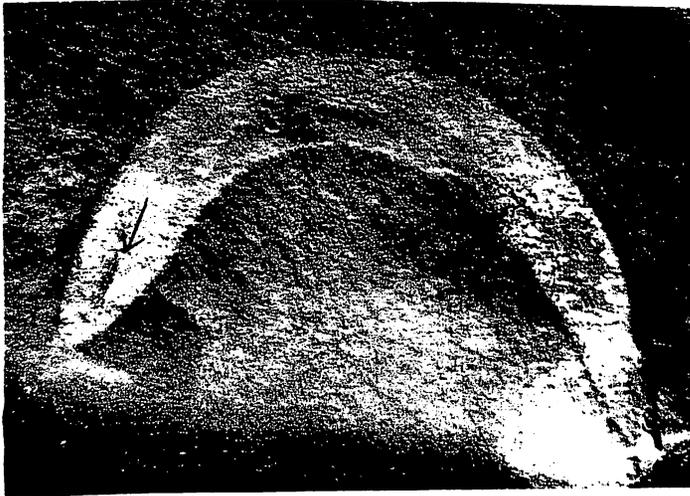


Fig.4A. Gilpichthys greenei, one of the Agnathans - the most commonly found, X 1.

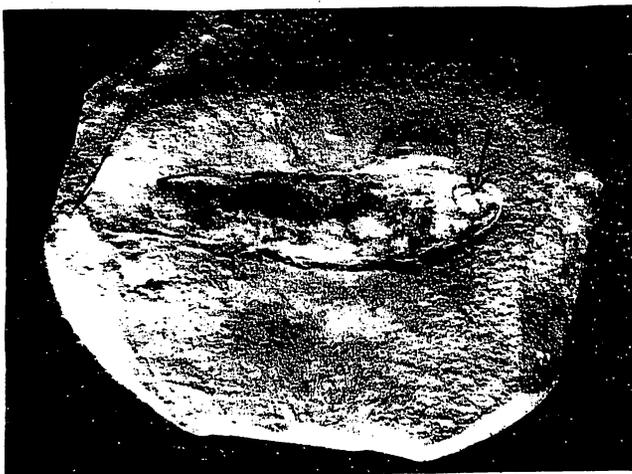


Fig.4B. Pipiscius zangerli, another Agnathan, X 1.

(fig. 4) identified from the Mazon Creek Area and they all have some form of feeding structures in or around the mouth, indicated by arrows in figs. 4A and 4B, that could in the broad sense be considered as a form of dentition (fig. 5).

These Agnathans are forerunners of present day lampreys and hagfish. It is very possible that the oral structures of the fossil Agnathans were used in the same manner as those of their present day cousins. As one can see these structures must also be viewed with high power magnifiers.

There are three amphibian specimens in the Konecny collection, all are preserved dorso -

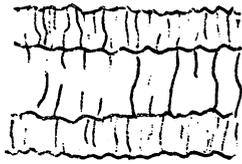


Fig. 5A. Drawing of oral structure of specimen in Fig. 4A, not to scale.



Fig. 5B. Oral structure of specimen in Fig. 4B, X 9.

ventrally. None of them has the teeth preserved, but one of them (fig. 6) does show tooth sockets where the teeth had been before falling out - no doubt after death. The specimen in Fig. 6 is the largest one of the three.

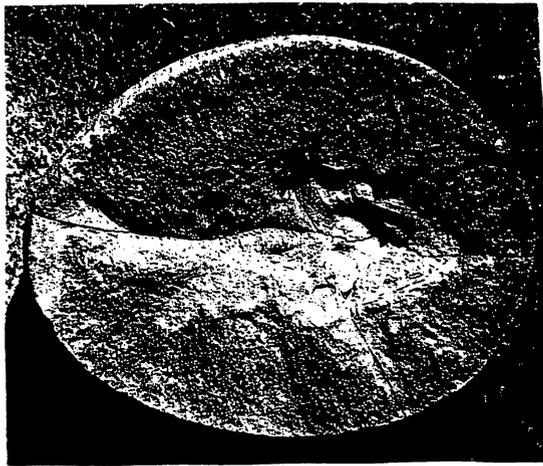


Fig. 6. An unidentified amphibian, X 1.

There is an anomaly that exists in the 'fish department'. Some large fish scales, as much as 2½ inches across, have been found. In fact it could be said that they are almost common. Some coprolites, bone fragments, head plates, spines, etc. belonging to these large fish have also been found. But, where are the teeth? With the fair abundance of large fish parts one would expect to find a fair amount of teeth from these individuals. However, this is not the case.

In our collection we have only three teeth. Two of these belong to the freshwater shark Xenacanthus sp. (fig. 7). The remains of these ubiquitous sharks are fairly common in Permian-Carboniferous deposits world wide. The third tooth in our



Fig. 7A. One of the Xenacanth teeth, X 1.

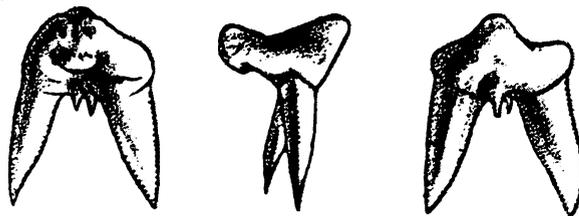


Fig. 7B. Drawing of typical Xenacanth teeth, X 1.5.

collection is a Petalodont (fig. 8). This shell crushing tooth has not been identified as to genus and species. According to the late Dr. Eugene S. Richardson, it is extremely rare in the Mazon Creek deposits. Unless additional specimens have been found in recent years, it is the only Petalodont tooth from the Mazon Creek Area.

Although this report is based on specimens in our collection, I find that the numbers seem quite consistent with the numbers in collections of other Mazon Creek Area collectors that I have spoken with.

This report produced an interesting question. Why are all of the Mazon Creek vertebrate animals

so small? Remains of large fish and large amphibians have been found in Pennsylvanian deposits world wide. Yet the remains of large vertebrates at Mazon Creek are meager. To answer this question a thorough investigation into the paleoenvironment of this region is in order.

Note: Figs. 2 & 3B are taken from Langford 1963.

Fig. 3A is taken from Bardack 1979.

Fig. 5A is taken from Bardack & Richardson 1977.

Fig. 7B is taken from Case 1982.

Fig. 8 photo taken by Dr. Eugene S. Richardson.

#### References:

- Bardack, D. 1979. Fishes of the Mazon Creek Fauna, in Mazon Creek Fossils, M.H. Nitecki Ed.
- Bardack, D. & E.S. Richardson, Jr. 1977. New Agnathus Fishes from the Pennsylvanian of Illinois. *Fieldiana Geology*, Vol. 33, No. 26.

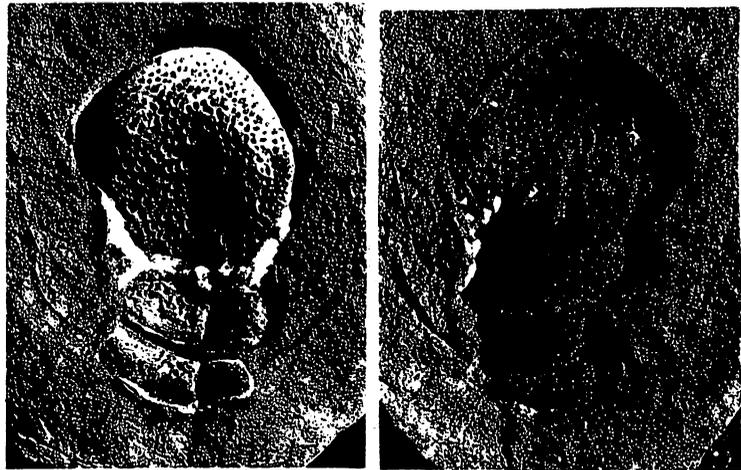


Fig.8. Petalodont tooth, part & counterpart, X 3.2.

Case, G.R. 1982. A Pictorial Guide to Fossils.

Langford, G. 1963. The Wilmington Coal Fauna and Additions to the Wilmington Coal Flora from a Pennsylvanian Deposit in Will County, Illinois.

Shabica, C.W. & A.A. Hay. 1997. Richardson's Guide to the Fossil Fauna of Mazon Creek.



Two collecting sites in the Mazon Creek Area.

## Rodent Teeth and Convergence

Carl D. Frailey  
12345 College Blvd.  
Overland Park, KS 66210-1299

Those who study mammals, and particularly those who study fossil mammals, are accused of giving inordinate attention to teeth. With a whole animal to study, why do researchers devote so much time to the crenulated surfaces of teeth, and particularly the cheek teeth (premolars and molars)? The answer is that scientists must use what is available to them and teeth are durable. They are covered with enamel (except in armadillos and sloths, the "edentates") and they lack projections that might get broken off and lost. Secondly, teeth in mammals are the first major manipulators of food and as such they are vital to the survival of an individual and are shaped to process a particular food type. Teeth are the most likely parts of a mammal to be preserved as fossils and they tell us a lot about the food the creature was eating. Because the shape of the tooth is an inherited characteristic, dental patterns have changed as environmental conditions (food) have changed and serve as a link to earlier and later populations. So there you have it. By following the changing patterns that show up on the crown of the tooth, one can follow the evolution of a group.

The simplest teeth among vertebrates are the single-cusped conical teeth of most fish, amphibians and reptiles. During the Mesozoic, the early mammals added additional cusps in various arrangements in a fascinating period of experimentation. Nearly all those patterns failed the ultimate test, survival (or were linked with other characteristics that proved ill-adapted) and those lineages ended in extinction. The pattern that won out is called the tritubercular or tribosphenic (three-cusped) pattern. It consists of what may be the primary single cusp of lower vertebrates (now called the protocone) as the tip of a

triangle of cusps. The other two cusps have been named the paracone and metacone (together, the three comprise the trigon, Fig. 1). That is, these are the names given to cusps on upper teeth. The nomenclature for lower teeth is protoconid, paraconid, and metaconid (the trigonid). On the upper teeth, the protocone (tip of the triangle) faces lingually (medially, towards the tongue or midline) and in the lower teeth the protoconid faces the opposite direction (labially or laterally, towards the lip or side). In the least modified arrangement, these triangles did not overlap but alternated with each other (Fig. 2). When the teeth were clenched, each tooth had two shearing surfaces. Today, marsupials and insectivores have dental patterns that are much like this. Notice, there is no crushing function in this simple system of triangles. To create crushing, there must be some overlap and a cusp must be aligned to meet a depression on the opposing tooth. For those animals that required crushing teeth, the teeth squared up with the additions of two more cusps. The hypocone developed from the enlarged gum-line crest just behind the protocone and another cusp, the entocone, developed on the edge of the basin opposite to the hypocone (the same is true for the lower teeth, but to simplify writing, only the upper dentition will be described). To get the full story, restate every sentence and add “-id” to each term). The new part of the tooth is called the talon. Carnivorous mammals emphasized the trigon in their evolution; omnivores have both trigon and talon well developed; and herbivores have reduced the trigon and enlarged the talon. This progression in complexity can be followed in the teeth of late Mesozoic and early Cenozoic mammals and is a wonderful expression of evolutionary change. The evolution of mammals during the Cenozoic can be described by the changes in this basic pattern that developed to serve the diverging lineages.

In rodents, the shearing function was eliminated in the cheek teeth. The high cusped, piercing teeth found in early mammals are replaced by flat-surfaced grinding tooth suitable to repeated passes of lower teeth against stationary upper teeth. Of the original three cusps, the paracone nearly disappeared. In its place is a crest on the anterior of the tooth. Looking at the occlusal surface of the tooth, the fundamental rodent dental pattern is quadrangular (four-sided) with a major cusp at each corner (quadritubercular) and a depression in the middle (Figs. 3,4). The squirrels still have this dental pattern and they are rightfully placed among the most primitive of rodents (or should we say, they specialized in simplicity?). They early found their place in the world and have been happily scampering about for some 40 million years searching out the seeds and nuts that require broad, shallow-basined teeth to process.

The biggest changes that occurred in the dental evolution of rodents were the elongation of the crown (hypsodonty) and infolding of the enamel. These came about in rodents (as in many other mammals) in response to food types that required intense grinding and which severely wore down the teeth as a result. To us, soft-food eating primates that we are, a break in the enamel surface of a tooth is cause for a trip to the dentist. To most mammals, this creates a thin edge of enamel buttressed by the underlying dentine. Two such edges on flat surfaces dragged by each other (one on an upper tooth, one on a lower) creates the equivalent of closing scissors and effectively slices durable food like grass (note that the original vertical slicing effect of the trigon has been recreated on the horizontal occlusal surface of these teeth). The thin edge of enamel on each tooth, as it folds in and out around the cusps, creates the enamel pattern

that is characteristic of each species and which has been used by paleomammalogists to follow the evolution of most mammals, including rodents.

To visualize how enamel patterns are made, think of the cusps of the tooth's crown as having been elongated upwards (Fig. 5). The valleys between the cusps are filled with another dental tissue called cement. When the elongated cusp is worn, a thin ring of enamel is produced. The enamel is hard and brittle but does not break because it is supported on one side by dentine (the interior side of the cusp) and on the other side by cement. If the valleys are shallow, the dental pattern will soon be obliterated. The teeth of one group of rodents, the now extinct cylindrodonts, had such a pattern. With just a little wear, their teeth consisted of a single outer ring of enamel. For most hypsodont rodents, some of the valleys are deep and others are shallow. In fact, valleys between labial and lingual cusps are often so shallow that with only slight wear, the cusps unite (put differently, the cusps may be connected by crests and with slight wear the enamel of the two cusps is worn into an irregular ring around both cusps and the exposed dentine of the two cusps is confluent, Fig. 5B). In most hypsodont teeth, advanced wear must be reached before the enamel pattern is worn away and only a single outer ring of enamel remains (Fig. 5C). At this wear stage, it is unlikely that the species can be identified from only a single tooth. When describing the cheek teeth of rodents, or any hypsodont mammal, the stage of wear (early, moderate, or late) must be considered because the enamel pattern will change as the tooth is worn away. On more than one occasion, in fossil rodents as well as in other mammals, several named species have been found to be nothing more than different wear stages in the cheek teeth of a single species.

Dental patterns such as enamel folding are important characteristics of mammals, but there are other features affect the place a species takes in nature, that is to say, its niche. One such other characteristic is size. Most rodents are small. They are the major group of herbivores among what is called the microfauna. The macrofauna is what we normally see when out and about. Macrofaunal mammals are deer, bear, coyotes, antelope, and all the great variety of carnivores and herbivores that one might see in a biotic community. Important but frequently overlooked elements of the community are the microfauna. Macro- and microfaunae interrelate in a community, a fox will eat a mouse for example, but they also create two separate worlds in what is a single habitat. In the small world, some rodents are omnivorous, but most are herbivorous. Curiously, the dental patterns of many mega- and microfaunal herbivores are similar. Part of this is due to common ancestry, but apparently there are certain alignments of cusps, crests and folds that are most efficient and these show up in the teeth of large and small herbivore alike. The following series of sketches are matched by the pattern of enamel seen in a moderately worn upper right tooth. A similar set of drawings could be made for the lower teeth.. The rodent tooth in each case would sit comfortably on the head of a pin but the drawings were enlarged for comparison.

In some teeth of both rodents and megafauna, the individual cusps are recognizable. In others the anterior cusps unite to form one crest and the posterior cusps form another. In some teeth the labial cusps form a crest; in a few, the lingual but not the labial cusps unite. The enamel walls of the cusps become crenulated in some forms. This increases the complexity of the enamel pattern as the teeth wear. This creates more enamel on the grinding surface of the tooth. Still, in all the examples the fundamental arrangement of a

quadritubercular, quadrangular cheek tooth is still visible although dietary choice and natural selection have taken this basic pattern in many directions. Rodents are the most diverse order of mammals with more than 1700 living species and about 50 families known in the Cenozoic. The adaptability of their dentition must surely have played a role in their success.

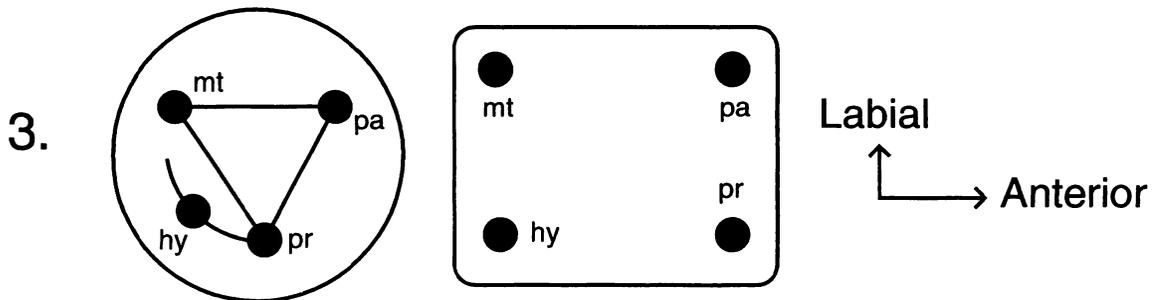
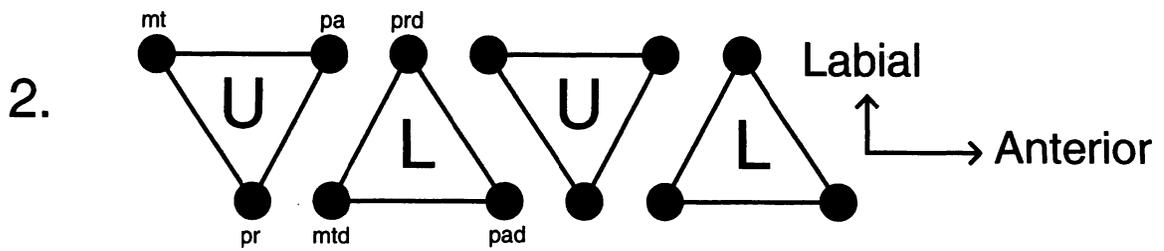
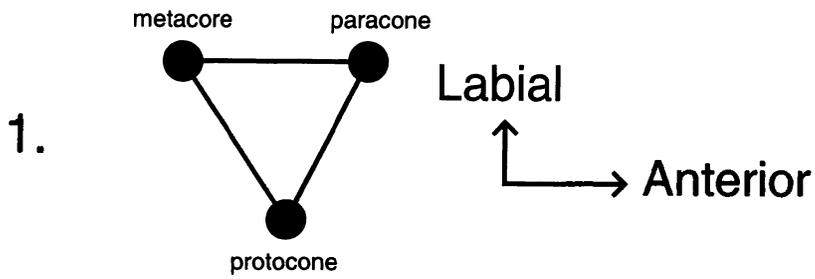
Might this convergence in dental patterns have other significance in the future? Species that have become specialized in some way have a competitive advantage over less specialized species but are more at risk of extinction during times of environmental stress. Large size is a specialization. Does it mean that if the megafauna were to become depleted, similarly adapted species of the microfauna could slip into the vacant niches merely by an increase in size? Perhaps so. In South America, continental isolation during most of the Cenozoic and the whims of evolution produced an odd (to us) assortment of megafaunal mammals. Prominent among the large herbivores were some rodents that were as large as cows. These dinomyids ("terrible mice") are poorly known as fossils but they seem to have been scaled-up versions of long-legged guinea pigs. Their skeletal and dental anatomy is typically rodent. A species is created not only by its genetic package but also by environmental parameters that include predators, prey or just impinging species that share the habitat. The sudden removal of several large species from a community would open many doors for the diverse microfaunal herbivores. Perhaps we should be more optimistic about faunal diversity in the coming centuries. Certainly the world's megafauna is stressed and extinctions in the wild of many favorite species will continue but dental pre-adaptation is in place that would rapidly replace the herds of buffalo, wildebeest, and antelopes with rodents.

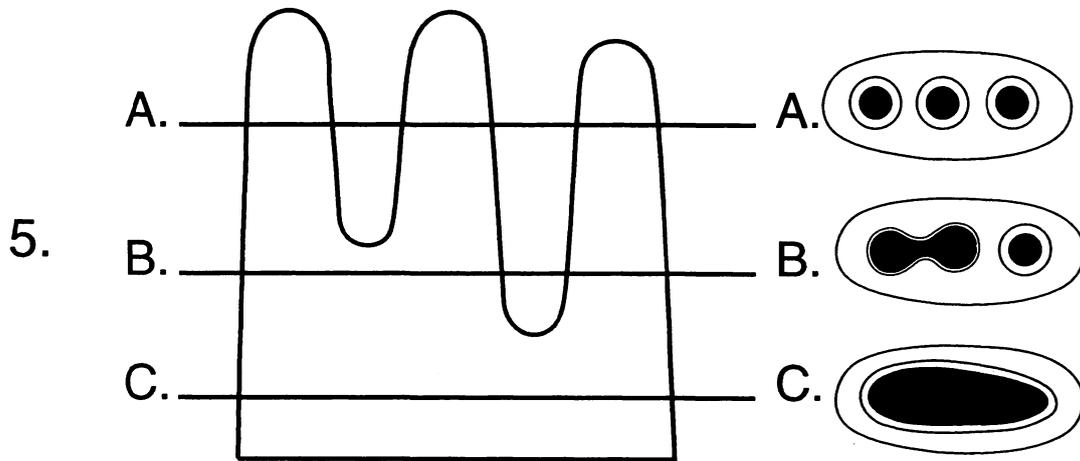
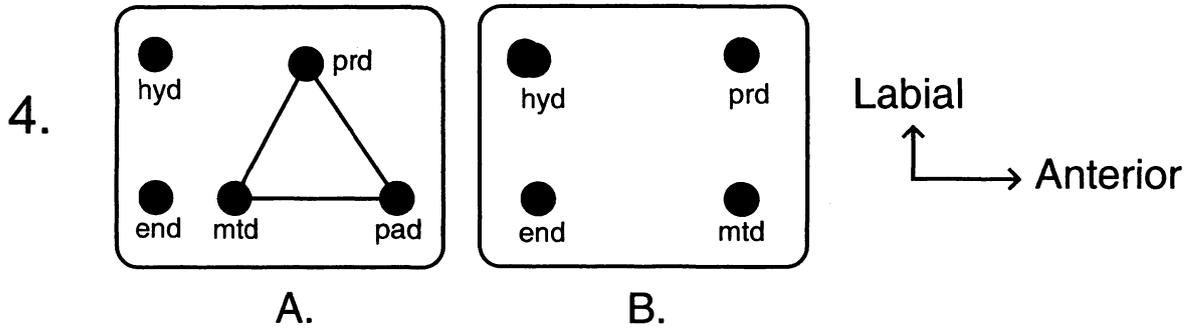
## Figure Captions

- Figure 1. Tritubercular cusp pattern of the upper right cheek tooth of a primitive mammal. The labial arrow indicates the position of the cheek. This is an occlusal view, *i.e.*, what one would see when holding the skull and looking at the chewing surface of the tooth.
- Fig. 2. Intersecting triangles of upper (U) and lower (L) cheek teeth of a primitive, tritubercular mammal. Following convention for designation of cusps on lower teeth, prd means protoconid, pad is paraconid, and mtd is metaconid. This is from the left side of the mouth and viewed from the top with the teeth in occlusion.
- Fig. 3. Drawing A shows the modification of the primitive, tritubercular pattern of an upper molar with the addition of a hypocone (hy). Drawing B is the basic rodent arrangement of four cusps placed at the margins of a four-sided (quadrangular) tooth.
- Fig. 4. Lower teeth, occlusal view. Drawing A is an early mammalian pattern with a talonid and two additional cusps, the hypoconid (hyd) and an entoconid (end). Drawing B is the basic rodent arrangement in which the paraconid (pad) is lost and a quadritubercular lower tooth is created. Note that the four cusps on the lower tooth are not the same four found on an upper tooth.

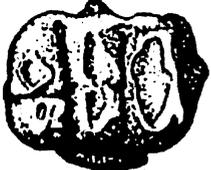
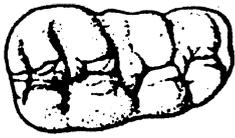
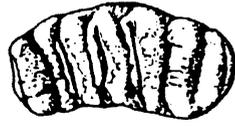
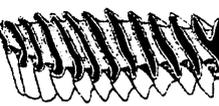
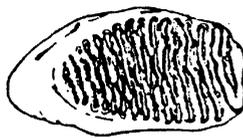
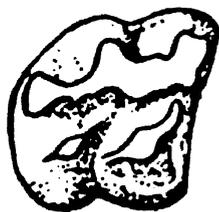
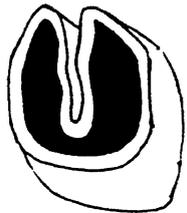
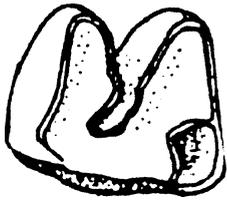
Fig. 5. Drawing to illustrate how crests form from cusps and how a dental pattern changes with wear. This simple tooth has three cusps in a row separated by two valleys of different depths. In cross-section A, all three cusps are separate. The black represents the dentine which has become exposed as wear created an enamel ring in the position of each cusp. In cross-section 2, two cusps have joined to create a crest. In cross-section 3, representing late wear that would be reached near the end of the animal's life, all the cusps have united into a single crest and only a ring of enamel is present on the occlusal surface.

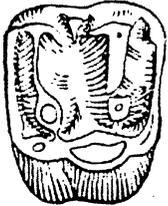
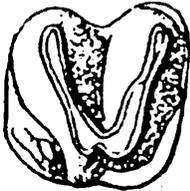
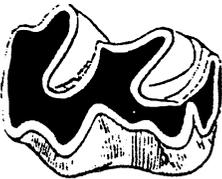
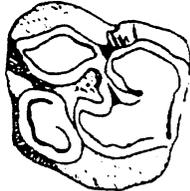
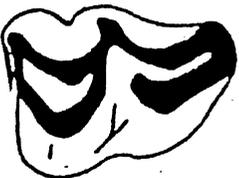
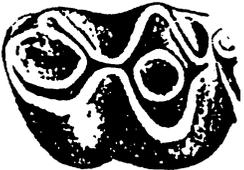
Fig. 6. Comparisons between upper right teeth of some rodents and an assortment of large mammals. Anterior is to the right in each case. Rodent teeth drawings are from "Die Trigonodontie der Simplicidentaten Nager" by H. G. Stehlin and S. Schaub, 1951, Schweizerischen Palaontologischen Abhandlungen. Rodent drawings are reversed from the originals to match the adjacent teeth. Drawings of large mammal teeth are from Vertebrate Paleontology by A. S. Romer, 1966, University of Chicago Press.





6. Upper molars of rodents, on left,  
and other mammals.

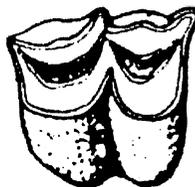
- |    |   |  |  |  |
|----|---|--|--|--|
| 1. |    | Brachytarsomys<br>Pleistocene<br>malagary<br>mouse |    | Mammut<br>Pleistocene<br>mastodon      |
| 2. |    | Mystromys<br>Recent<br>white-tailed rat            |    | Tetralophodon<br>Miocene<br>mastodon   |
| 3. |   | Echimys<br>Recent<br>spiny rat                     |   | Stegodon<br>Pliocene<br>mastodon       |
| 4. |  | Hydrochoerus<br>Pleistocene<br>capybara            |  | Mammuthus<br>Pleistocene<br>elephant   |
| 5. |  | Eumys<br>Oligocene<br>murid                        |  | Saghatherium<br>Eocene<br>hyrax        |
| 6. |  | Heteromys<br>Recent pocket<br>mouse                |  | Arsinotherium<br>Eocene<br>embrithopod |

- |     |   |   |  |   |
|-----|---|---|--|---|
| 7.  |    | <p><b>Paramys</b><br/>Eocene<br/>paramyid</p>                                 |    | <p><b>Miosiren</b><br/>Pliocene<br/>dugong</p>        |
| 8.  |    | <p><b>Prosciurus</b><br/>Eocene<br/>squirrel-like<br/>rodent<br/>allomyid</p> |    | <p><b>Hyopsodus</b><br/>Eocene<br/>ungulate</p>       |
| 9.  |    | <p><b>Gliravus</b><br/>Miocene<br/>dormouse</p>                               |    | <p><b>Uintatherium</b><br/>Eocene<br/>ungulate</p>    |
| 10. |  | <p><b>Euchoreutes</b><br/>Recent<br/>jerboa</p>                               |  | <p><b>Arctodus</b><br/>Pleistocene<br/>bear</p>       |
| 11. |  | <p><b>Selenomys</b><br/>Oligocene<br/>murid</p>                               |  | <p><b>Alticamelus</b><br/>Pliocene<br/>camel</p>      |
| 12. |  | <p><b>Mesocricetus</b><br/>Pleistocene<br/>hamster</p>                        |  | <p><b>Tetrameryx</b><br/>Pliocene<br/>antilopacid</p> |



13.

Plotomodon  
Miocene  
murid

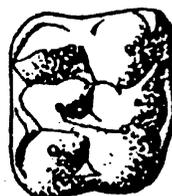


Tragocerus  
Pliocene bovid

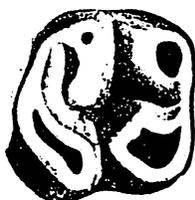


14.

Heliscomys  
Oligocene  
gopher



Dichobune  
Eocene hippo



15.

Xerus  
Pliocene  
sciurid

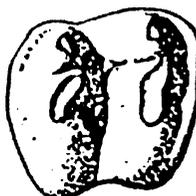


Hippopotamus  
Pleistocene hippo



16.

Florentiamys  
Oligocene  
gopher



Platygonus  
Pleistocene  
peccary



17.

Scottimus  
Pliocene  
murid

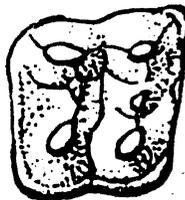


Sus  
Pliocene pig



18.

Perognathus  
Recent  
pocket  
mouse



Hyracotherium  
Eocene horse



19.

Sciurodon  
Miocene  
aplodontoid



Miocene horse  
Pliohippus

20.		Allomys Miocene aplodontoid		Equus Pleistocene horse
21.		Cavia Recent guinea pig		Subhyracodon Oligocene rhino
22.		Schistomys Miocene caviid		Protapirus Miocene tapir
23.		Perimys Miocene chinchillid		Homogalax Eocene tapir
24.		Protadelomys Eocene theridomyid		Pronycticebus Eocene primate
25		Adelomys Eocene theridomyid		Homo Pleistocene primate

## CONODONTS FROM THE PROUT DOLOMITE OF NORTH-CENTRAL OHIO AND GIVETIAN (UPPER MIDDLE DEVONIAN) CORRELATION PROBLEMS

DALE R. SPARLING

Earth Science Program, Southwest State University, Marshall, MN 56258

**ABSTRACT**—The Prout Dolomite of north-central Ohio lies disconformably above the lowest Givetian (upper Middle Devonian) Plum Brook Shale and below the lowest Famennian (upper Upper Devonian) Ohio Shale. A sample from its base yielded over 4,000 diverse conodont specimens. Included is *Polygnathus ansatus* Ziegler and Klapper, 1976, the index species for the Middle *varcus* Subzone, which is not reported from strata of this age in Ontario and Indiana, a fact that long caused their miscorrelation with the Lower *varcus* Subzone. Also present is *P. rhenanus* Klapper, Philip, and Jackson, 1970, considered to be also indicative of the Middle *varcus* Subzone in North America, and *P. ovatinodosus* Ziegler and Klapper, 1976. Lowest occurrences of the latter are in the middle part of this subzone; its presence indicates correlation with the lower Tully Limestone of New York, the basal unit of the Taghanic Series. The Prout and equivalent strata in the region therefore represent a long unrecognized continuous time-rock unit created by Johnson's (1970) Taghanic onlap. The collection includes a new species of *Ancyrolepis*, *A. huntleyi*; a new species of *Polygnathus* is left in open nomenclature, as are nine specimens assigned to *Tortodus* but of otherwise uncertain taxonomic status.

Givetian conodont correlation between North America and the Global Stratotype Section and Point established by the Subcommittee on Devonian Stratigraphy (SDS) in Morocco is extremely problematical because of relatively erratic distribution (probably owing to limited ecologic adaptability) of *P. ansatus* and *P. hemiansatus* Bultynck, considered herein to be an early morphotype of *P. ansatus*. The base of the Givetian Stage has been defined by the SDS as coinciding with the lowest occurrence of *P. hemiansatus*. The only possible evidence for the SDS's *hemiansatus* Zone in North America involves reported occurrence of that morphotype in the uppermost Arkona Shale of Ontario, a position above the top of the Plum Brook Shale, which has been considered to be of Givetian age for decades. Also it appears that the interval between the Eifelian (lower Middle Devonian) *kockelianus* Zone and the *hemiansatus* Zone at the SDS's global-stratotype section in Morocco is of questionable age and probably too thin to represent continuous sedimentation. Adoption of a widely recognized faunal break at the base of strata deposited during the If T-R cycle of North America and Europe as the base of the Givetian could provide a sound alternative.

### INTRODUCTION

**A** GENERAL paper on the Middle Devonian of north-central Ohio (Sparling, 1988) included preliminary results of a prolonged study of diverse and abundant conodonts from the Givetian Stage (upper Middle Devonian). Details of the collection from the Plum Brook Shale (lower Givetian) were described in a subsequent paper (Sparling, 1995), and a main purpose of this report is to provide details of the material from the disconformably overlying Prout Dolomite. An additional purpose is to present a more comprehensive discussion of correlation of both units, regionally and on a global scale, especially in light of recent developments with which the writer takes issue. An important aspect of this involves the index species that was most important in determining the biostratigraphic position of the Prout and its equivalents in the region, *Polygnathus ansatus* Ziegler and Klapper (*in* Ziegler, Klapper, and Johnson, 1976), which has become problematic over the past two decades.

As reported earlier (Sparling, 1988, 1992), the writer's initial sampling of the Prout northeast of Bloomingville, Erie County, yielded only a few non-diagnostic conodonts. However, a single sample taken at its base less than 1 km farther northeast (see Fig. 1), as directed by Frank Huntley, a geologist in the Toledo area, yielded over 4000 diverse specimens. (Many diverse microvertebrate specimens also extracted from this sample are the subject of a separate study in which Susan Turner is the principal investigator.) Other samples reported on herein include some from the basal black shale above the Prout (see Fig. 1) and one taken in a quarry at Delphi, Carroll County, Indiana from the base of the Little Rock Creek Formation, which provides a contrasting low-diversity conodont fauna that characterizes much of the chronostratigraphic unit to which the Prout belongs over much of the eastern North American craton. That low diversity in turn contributed to an understandable problem with regards to regional biostratigraphic correlation, and the following section

deals with the contribution the Prout fauna has made in solving this problem.

### PROUT DOLOMITE AND ITS BIOSTRATIGRAPHY

The Prout Dolomite is commonly less than 1 m thick but locally thickens to over 3 m in coralline topographic highs interpreted to be primary biostromal or reef structures (F. Huntley, personal commun., 1985; Krywany, 1982). According to Huntley (personal commun., 1985), the sample from which the diverse Prout conodont fauna was extracted was taken from the basal 15 cm near the northwestern edge of one of these buildups. It consisted of pure limestone, and Krywany (1982) interpreted such occurrences to be the product of dedolomitization. Since the sample lies above a disconformity, some conodonts could be derived from older strata although not a single obviously derived specimen was noted. The material appears to have been sorted to some extent by current action since very fine specimens (e.g., *Icriodus* cones) are notably scarce.

Early workers tended to treat the Prout as being associated with the Plum Brook Shale (e.g., in the "Prout series" of Grabau, 1917). Stumm (1942) studied the macrofaunas of both and determined that of the Prout to consist largely of corals and brachiopods, with fewer species of bryozoans, crinoids, and mollusks. Although only eight of 95 invertebrate species found by Stumm in the Prout were listed from the Plum Brook, no disconformable contact was indicated in his paper or in the contemporaneous publication by Cooper et al. (1942), which also showed a conformable relationship between the Arkona Shale and the Hungry Hollow Formation of southwestern Ontario. The Hungry Hollow had (as the Encrinal and coral zone units) been correlated with the Prout by Stauffer (1916, p. 485), and Stumm (1942, p. 562) considered his study to have confirmed that correlation. Stumm also cited faunal evidence for correlation of the Plum Brook with the Levanna Shale (=Skaneateles Formation of Fig. 2) of western New York. He further stated that "faunal

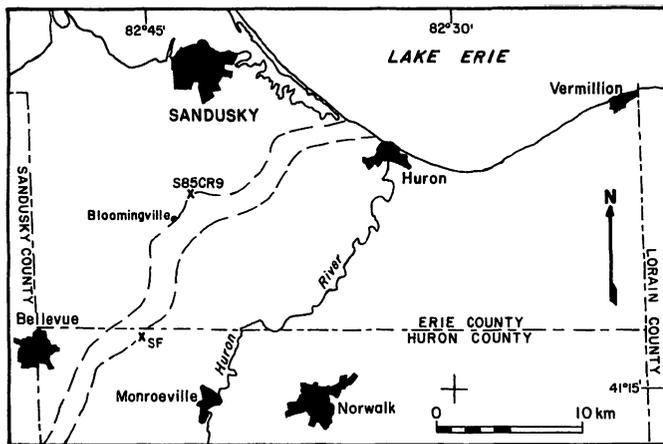


FIGURE 1—Approximate outcrop belt of the Prout Dolomite and locations of sample S85CR9, at its base, and samples taken by Sparling in 1987 and D. J. Over in 1998 from just above its top in the basal Huron Shale on the John Schaeffer farm (SF).

relationships indicate that the Prout limestone is the westward equivalent of the Centerfield limestone” of that region, shown to overlie the Levanna conformably in Cooper et al. (1942); no specific faunal evidence for that conclusion was given by Stumm, although Krywany (1982, p. 33) cited coral and brachiopod species common to both units. Stumm also correlated the Prout with the basal part of the Ten Mile Creek Dolomite of northwestern Ohio.

The earliest published conodont information on strata of comparable age in the region was provided by Orr (1971), who placed the upper Traverse Group in cores from northeastern Indiana (e.g., units 5–7 of his Section 9, p. 94) in the *varcus* Zone, which had been established by Bischoff and Ziegler (1957, p. 30–31). This assignment was based on specimens identified as *P. varcus* (Orr, 1971, pl. 5, figs. 4–8) that are in fact very similar to a specimen given that assignment by Bischoff and Ziegler (1957, pl. 18, fig. 34). Orr was no doubt unaware that *P. varcus sensu stricto* had recently been split into three species by Klapper et al. (1970). Orr’s material probably included both of the new species, *P. rhenanus* and *P. timorensis*, but the figured specimens are clearly not *P. varcus*. In another significant paper that year, Johnson (1970) called attention to a remarkable transgression that extended from the eastern margin of the North American craton onto the flank of the continental backbone and across its southern end. The timing of this event coincided with that of the Taghanic Stage (Cooper et al., 1942, p. 1733), and this “Taghanic onlap”, as Johnson called it, was extensive enough to end brachiopod provinciality and was later correlated with maximum conodont cosmopolitanism (Klapper and Johnson, 1980). The Appalachian, Michigan, and Illinois basins and intervening arches were shown by Johnson (1970, figs. 2, 4) to have been regions where the transgression extended across earlier Givetian strata, and the lower Taghanic was shown to correspond to the *varcus* Zone.

The *varcus* Zone was subsequently subdivided by Ziegler, Klapper, and Johnson (1976), and the Lower *varcus* Subzone was defined as the interval between the lowest occurrences of *P. timorensis* and a new species, *P. ansatus* Ziegler and Klapper, 1976. The Centerfield of New York and the Beechwood Limestone of central Indiana were known to contain the former species and were assigned to that subzone (Ziegler, Klapper, and Johnson, 1976, p. 113), but the upper Traverse of northern Indiana was not mentioned, even though Orr’s *P. varcus* was

placed in synonymy with *P. timorensis* in the systematic section. The Middle *varcus* Subzone was defined as the interval between the lowest occurrences of *P. ansatus* and *P. latifossatus*. The base of this zone in New York was placed well below the top of the Moscow Formation, and the base of the overlying Tully Limestone, which by definition is the base of the Taghanic Stage, was determined to correspond roughly to the middle of this subzone.

Uyeno (in Uyeno et al., 1982) identified immature and fragmented specimens from the uppermost Arkona Shale and overlying Hungry Hollow as belonging to the *Polygnathus varcus* Group of Klapper et al. (1970, p. 651), which included that species plus *P. xylus*, *P. rhenanus*, and *P. timorensis*, and found abundant specimens identified as the last of these in the overlying Widder and Ipperwash formations. The entire interval was assigned to the Lower *varcus* Subzone. A single large specimen of *P. timorensis* was later identified from the basal Hungry Hollow by Landing and Brett (1987, p. 211), who also assigned the formation to the Lower *varcus* Subzone and provided clear evidence for a disconformity at the top of the underlying Arkona Shale that they considered to be “temporally most significant.”

Sparling (1985, fig. 1) suggested the possibility of a disconformity between the Plum Brook and the Prout but placed the Prout and equivalents in the Lower *varcus* Subzone, as did all correlations current at that time. Perhaps the most prominent publication to incorporate that usage was the work of Johnson et al. (1985, fig. 8), in which the only unit between the Tully of New York and the lower Cedar Valley of Iowa to be assigned to the Middle *varcus* Subzone was the Lower Olentangy Shale of central Ohio, an assignment consistent with conodonts studied by Ramsey (1969) and by Ziegler and Klapper (in Ziegler, Klapper, and Johnson, 1976, p. 117). The only other unit that had ever been even tentatively correlated with the Tully across that expanse was the rather insignificant Little Rock Creek Limestone of Cooper (1941, p. 181) in the Kankakee Arch region of Indiana. Evidence of the Taghanic onlap between New York and Iowa was therefore conspicuously absent, and this was especially anomalous in the tectonically negative setting of the Chatham Sag between the Michigan and Appalachian basins in southwestern Ontario.

In reality, a rock record of the Taghanic onlap extends continuously across the region but went unrecognized owing to low-diversity conodont faunas in which the key index species, *P. ansatus*, was excluded. The tabulation for the Little Rock Creek sample in Table 1 is typical. Most of the species assigned herein to the *P. pseudofoliatus* Group (Sparling, 1995) occur widely, and the absence of all in the Taghanic strata of Ontario except for *P. timorensis* and the very closely related *P. rhenanus* (as defined herein) appears to reflect ecologic conditions to which only those species could adapt. The only other member of the group reported from Indiana rocks of this age is *P. pseudofoliatus* itself, which occurs in the Beechwood of southern Indiana (Klug, 1983).

The tabulation of Prout conodonts reveals a diversity that probably reflects ideal normal-marine conditions on the margin of the Appalachian Basin. In addition to *P. ansatus*, the index species for the Middle *varcus* Subzone, the fauna includes *P. rhenanus*, which (as a “late form of *P. timorensis*”) was also designated as diagnostic for this subzone in North America by Klapper (in Johnson, Klapper, and Trojan, 1980, p. 93), and *P. ovatinodosus* Ziegler and Klapper, 1976, a species apparently derived from *P. ansatus* whose lowest occurrences are in the middle part of the Middle *varcus* Subzone (Klapper and Ziegler, 1979, text-fig. 5). This combination therefore indicates a rather precise correlation with the lower Tully Limestone of New York, which as stated above defines the base of the Taghanic onlap.

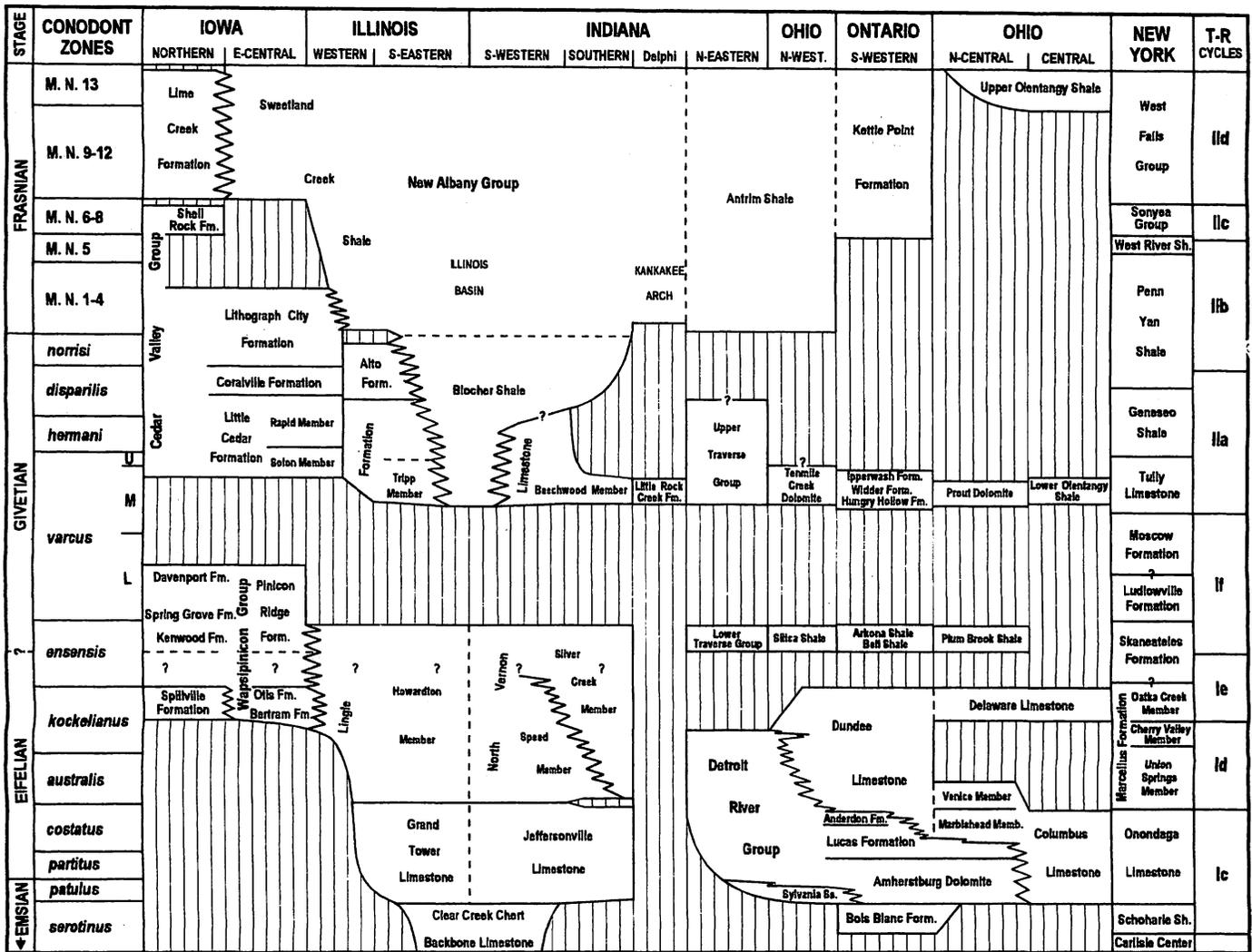


FIGURE 2—Regional correlation of upper Emsian through Frasnian stages. The transgressive-regressive (T-R) cycles and conodont zonation are those used by Johnson and Klapper (1992), including the Frasnian Montagne Noire zones of Klapper (1989). Other sources include Witzke et al. (1989, Iowa), North (1969, Illinois stratigraphy), Klug (1983, southern Indiana), and Johnson, Klapper, and Sandberg (1985, New York). Question marks at the level of the uppermost Eifelian are intended to suggest a possible undetected unconformity beneath the If cyclothem, as discussed in the text. The Centerfield Limestone mentioned in the text is the basal member of the Ludlowville Formation.

Macrofaunal correlations of the Prout with units of the same age allow extrapolation of the proper conodont zonation to other units across the craton (Sparling, 1988, 1992) as indicated in Fig. 2.

REGIONAL GIVETIAN CORRELATION

The proposed assignment of the Prout and equivalents to the upper Middle *varcus* Subzone (Sparling, 1988) was adopted by Johnson and Klapper (1992, fig. 1, p. 130–131). Figure 2 incorporates some of their correlations and shows the writer's interpretation for the uppermost Lower Devonian (Emsian Stage) through the lower Upper Devonian (Frasnian Stage) in the region discussed above, subject to uncertainty in some areas. The T-R cycles are those of Johnson et al. (1985). It should be pointed out that the validity of the Givetian conodont zonation up through the Middle *varcus* Subzone is not without question; this matter was alluded to by Johnson and Klapper (1992, p. 131) and is discussed below in the section on the *P. ansatus* problem.

In the important work of Cooper et al. (1942), the Plum Brook Shale was shown to be of Givetian age with the exception of

the basal part, which however had not been studied. Fifty years later it was assigned to the early If T-R cycle by Johnson and Klapper (1992, fig. 1) and placed just above an Eifelian/Givetian boundary marked by a question mark and positioned in the middle of the *ensensis* Zone, as is the case in Fig. 2. Assignment in 1995 to the upper *ensensis* Zone (Sparling, 1995, p. 1124) was based largely on the phylogenetic development of the *P. xylus* lineage, characterized by "phylogenetically late forms" of *P. xylus ensensis* as defined by Ziegler and Klapper (in Ziegler, Klapper, and Johnson, 1976) and an early form of *P. xylus xylus*. That same year the base of the Givetian was moved by the Subcommittee on Devonian Stratigraphy to a higher position based on assumptions with which the writer disagrees, as indicated below.

The Plum Brook conodont fauna represents a dramatic adaptive radiation within the genus *Icriodus* following the demise of all species thereof found in the underlying Delaware Limestone. Delaware sedimentation clearly ended with a regressive phase (Sparling, 1984), and the faunal break is reasonably attributable to an extensive regression affecting all of the eastern craton prior to the T-R cycle If transgression (Sparling, 1995, p. 1124, 1126).

TABLE 1.—Distribution of conodonts from the basal Prout Dolomite northeast of Bloomington (sample S85CR9) and from the Little Rock Creek Limestone near Delphi, Indiana (sample S8911).

Formation Sample Weight in kg Centimeters above base	Prout S85CR9 5.575 0-15	Little Rock Creek S8911 2.097 0-17
<b>Pa elements</b>		
<i>Ancyrolepis huntleyi</i> n. sp.	2	
<i>Icriodus expansus</i> Group		
<i>I. arkonensis</i>	142	
<i>I. brevis</i>	11	
<i>I. difficilis</i>	20	
<i>I. expansus</i>	124	
<i>I. sp. indet.</i>	196	
<i>I. regularicrescens</i> Group		
<i>I. eriensis</i>	9	
<i>I. janeae</i>	11	
<i>I. obliquimarginatus</i>	12	7
<i>I. sp. indet.</i>	3	
<i>I. excavatus</i>	17	
<i>Latericriodus l. latericrescens</i>	225	29
<i>Polygnathus linguiformis</i>		
<i>P. l. linguiformis</i>	1,836	102
<i>P. linguiformis klapperi</i>	45	4
<i>P. linguiformis</i> subspp. juv.	3	
<i>P. pseudofoliatus</i> Group		
<i>P. ansatus</i>	162	
<i>P. ovatinosus</i>	21	
<i>P. pseudofoliatus</i>	93	
<i>P. rhenanus</i>	46	10
<i>P. timorensis</i>	178	22
<i>P. xylus ensensis</i>	22	
<i>P. x. xylus</i>	31	
<i>P. sp. C</i>	1	
<i>P. sp. indet.</i>	224	
<i>Polygnathus sp.</i>	3	1
<i>Prioniodina</i> spp.	4	
<i>Prioniodina?</i> sp.	8	
<i>Tortodus</i> spp.	24	
<b>Pb elements</b>		
<i>Polygnathus sp.</i>	231	21
<i>Prioniodina sp.</i>	4	
<i>Prioniodina?</i> sp.	3	1
<b>M elements</b>		
<i>Polygnathus sp.</i>	136	11
<i>Prioniodina sp.</i>	20	1
<b>Sa elements</b>		
<i>Polygnathus sp.</i>	36	1
<i>Prioniodina sp.</i>	4	
<b>Sb elements</b>		
<i>Polygnathus sp.</i>	42	21
<i>Prioniodina sp.</i>	10	
<b>Sc elements</b>		
<i>Polygnathus sp.</i>	99	32
<i>Prioniodina sp.</i>	18	2
<b>Sd elements</b>		
<i>Polygnathus sp.</i>	52	10
<i>Prioniodina sp.</i>	23	1
<b>Simple cones</b>		
<i>Belodella</i>		3
<i>Dvorakia</i>	16	
<i>Icriodus</i>	17	2

The disconformable bases of If units in Ontario, northwestern Ohio and northern Indiana appear to be well defined, but this is not true for regions marginal to the Illinois Basin. Orr (1971, p. 17) placed the upper part of the Silver Creek Member in his *Latericriodus l. latericrescens* Zone, which he considered to be

lowest Givetian, and Klug (1983, fig. 6) listed *I. brevis* (common in the Plum Brook) from the same level. Yet the Silver Creek is underlain in southern Indiana by the Speed Member, which contains Eifelian species of *Icriodus* and was correlated with the *australis* and *kockelianus* zones by Klapper (in Klapper and Ziegler, 1979, text-fig. 4). The lower Silver Creek also contains Eifelian species of *Icriodus* (Klug, 1983, fig. 6). The entire lower North Vernon Limestone therefore ranges in age from *australis* Zone to upper *ensensis* Zone as shown in Fig. 2, but the question marks in the upper Eifelian interval for southern Indiana to Iowa are intended to suggest the possibility of an undetected discontinuity at the base of If-cycle strata in that region.

The Taghanic onlap is well represented in southwestern Ontario by the Hungry Hollow, Widder, and Ipperwash formations, which have a composite thickness of nearly 30 m (Uyeno et al., 1982). On the margin of the Michigan Basin in northeastern Indiana (Orr, 1971, p. 96, units 6-7; p. 98-99, units 2-7) the Upper Traverse is about 11-13 m thick. At Delphi, Indiana, the Little Rock Creek is a bit under 3 m thick, and the low-diversity fauna includes ubiquitous species *P. timorensis*, *P. rhenanus*, *Latericriodus l. latericrescens* and *P. l. linguiformis*, but also *P. linguiformis klapperi* (Table 1). The comparably thin Beechwood Member of the North Vernon Limestone in southern Indiana also contains *P. linguiformis klapperi* (Klug, 1983), and the writer is unaware of any occurrences of that subspecies in North America below the Middle *varcus* Subzone. Klug also found *P. pseudofoliatus* in the Beechwood in addition to an abundance of *P. timorensis*.

In north-central Ohio the Prout has been considered to be overlain by the Huron Shale, dated on the basis of conodonts studied by Hass (1947) as post-*triangularis* Zone Famennian (e.g., Johnson et al., 1985, p. 580, fig. 8). However, Hass collected along the Huron River from Monroeville downstream without starting at the base of the black shale (see Fig. 1). A sample taken in 1987 just above the Prout on the John Schaeffer farm (site SF, Fig. 1), about 6.6 km northwest of the Huron River in Monroeville, yielded a perfectly preserved specimen easily identified as *Palmatolepis linguiformis*, which defines and is limited to the uppermost Frasnian conodont zone and occurs in the uppermost Upper Olentangy Shale of central Ohio. That unit is well defined on gamma-ray logs by virtue of being distinctly less radioactive than the overlying Huron Shale and is about 11 m thick in a well in southeastern Erie County, roughly 30 km east of the Schaeffer farm (Rickard, 1984, fig. 4). In a detailed subsurface-geological study of that region, Schwietering (1979, figs. 4, 9) showed an overlapping wedge formed by the upper part of the Upper Olentangy extending into western Erie County (as in Fig. 2), with the zero isopach positioned near the Schaeffer farm. The writer assumed that a thin slice of Upper Olentangy existed at the Schaeffer site and discussed this interpretation at the 1998 Pander Society Meeting with D. J. Over, who had been working on Upper Devonian shales in the region and was skeptical. Fortunately he was later able to sample the Schaeffer site and found the basal shale to contain *Pa. triangularis* and *Pa. superlobata*; these were accompanied by *Pa. delicatula delicatula* in the interval 0.1 to 0.2 meters above the Prout. It is thus Huron Shale assignable to the Lower-Middle *triangularis* Zone of the lower Famennian (Over, personal commun., 1998), and the excellent specimen of *Pa. linguiformis* from that level is thus clearly derived. Over's findings correct the erroneous basal-Huron zonation derived from Hass's (1947) study.

#### THE *POLYGNATHUS ANSATUS* PROBLEM AND GLOBAL CORRELATION

*Polygnathus ansatus* Ziegler and Klapper, 1976, began its existence as a promising index species, but problems subsequently developed regarding its taxonomic status and its suitability for

worldwide correlation. It was established and designated as the index species for the Middle *varcus* Subzone in Europe and North America in the same publication (Ziegler, Klapper, and Johnson, 1976). Bultynck (in Bultynck and Hollard, 1980) subsequently reported specimens like the holotype of *P. ansatus* in the Givetian at Bou Tchrafine, Morocco, above *P. timorensis*, in an interval comparable to the Middle *varcus* Subzone of Europe and North America. But he also found that specimens like the narrower paratypes of *P. ansatus* extended downward to a point 1.85 m above the highest occurrence of *Tortodus kockelianus kockelianus* and below the lowest occurrence of *P. timorensis*; these were designated *P. aff. P. ansatus* (Bultynck and Hollard, 1980, p. 42). Klapper (in Klapper and Johnson, 1980, p. 452) placed Bultynck's *P. aff. P. ansatus* in synonymy with *P. ansatus*, as did García-López (1987, p. 87; personal commun., 1988). The writer agrees with these previous assessments on the basis of complete intergradation of the forms involved, which include the three specimens illustrated herein (Fig. 3.30–3.32).

In a later study Bultynck (1985, p. 269, pl. 6, figs. 19, 20) designated his *P. aff. P. ansatus* to be an early morphotype of *P. ansatus*, "characterized by an elongated, narrow platform." But still later he formalized his initial belief in its distinct nature by naming it *P. hemiansatus* (Bultynck, 1987, p. 161–162) in a paper in which its lowest occurrence in Morocco was proposed as the basis for defining the "Upper *ensensis* Subzone." The lowest occurrence of *P. timorensis* was equated with the base of the Lower *varcus* Subzone of Ziegler, Klapper, and Johnson (1976); the lowest occurrence of *P. rhenanus*, accompanied by *P. varcus*, was stated to define the base of a zone within their Lower *varcus* Subzone; and the occurrence of *P. ansatus* (as restricted therein) was equated with the Middle *varcus* Subzone (Bultynck, 1987, p. 155).

Subsequently the International Union of Geological Sciences (IUGS) Subcommittee on Devonian Stratigraphy (SDS) agreed to consider a proposal to make the lowest occurrence of *P. hemiansatus* the biostratigraphic marker for the Eifelian/Givetian boundary. The Bou Tchrafine section was rejected as a suitable candidate for a global-stratotype section for said boundary, and so an alternative section was studied and proposed, the Ou Dris east (ODE) section of southern Ma'ader, Morocco (Bultynck, 1989, p. 95). The final choice for the Eifelian/Givetian Global Stratotype Section and Point was yet another section in Morocco, at Jebel Mech Irdane in the Tafilalt region, and the boundary is at the lowest occurrence of the form known officially as *P. hemiansatus* (Walliser et al., 1995) and considered herein to be an early form of *P. ansatus*.

The writer believes that these developments have created a very questionable biostratigraphic classification. The lowest occurrences of the new index taxon for the base of the Givetian are underlain at all Moroccan sections by thin intervals considered by SDS members to represent the lower *ensensis* Zone, but illustrated specimens of "*P. ensensis*" include "phylogenetically late forms" of *P. xylus ensensis* as defined by Ziegler and Klapper (in Ziegler, Klapper, and Johnson, 1976). Even more significant are specimens very close to, or the same as, an early form of *P. xylus xylus* that occurs in the Plum Brook Shale, in the Givet Limestone well below *P. timorensis*, and in the upper *ensensis* Zone in Spain (Sparling, 1995, p. 1124); examples include specimens from the ODE section (Bultynck, 1989, pl. 2, figs. 15, 21) and from the global-stratotype section (Walliser, 1991, pl. 2, fig. 16; pl. 3, figs. 1, 10). In other words, the figured specimens of *P. ensensis* from the *ensensis* Zone in Morocco appear to represent a level of phylogenetic development similar to that of the same lineage in the Plum Brook Shale and thus similar in age to the upper *ensensis* Zone of current North American usage (e.g., Johnson and Klapper, 1992, fig. 1; Sparling, 1995 and

herein; Uyeno, 1998, fig. 17), which is considered to be lowest Givetian. Relative to this matter is the goniatite genus *Maenioceras*; long considered to be of lowest Givetian age, it occurs with *P. xylus* subspecies below the designated Eifelian/Givetian boundary at Jebel Mech Irdane, but this fact was considered an acceptable "small divergence" by the SDS (Walliser et al., 1995, p. 111).

The highest occurrence of clearly Eifelian taxa at the official stratotype section lies less than 0.25 m below the abbreviated *ensensis* Zone discussed above, where *P. angustipennatus*, *P. robusticostatus*, *P. trigonicus*, and *Tortodus kockelianus* occur within 10 cm of the top of a limestone, a horizon most easily explained if assumed to be a disconformity atop strata representing the Ie T-R cycle. Above that lies a black shale interpreted by the SDS to represent an "event" level that has been widely established (for numerous references see Walliser et al., 1995, p. 112). In an evaluation of important Devonian boundaries, Chlupáč (1995, p. 48–50) described this interval as being "marked by sudden or stepwise onset of anoxic conditions, faunal and palaeogeographic changes." He referred to the Kačák Event (one of several terms for this phenomenon) as an "easily determinable Eifelian-Givetian boundary" that was not accepted as such owing to the emphasis on conodont biostratigraphy and the fact that the "event level is not markedly reflected in conodonts . . ." although this is not true; the conodont faunal break at the global-stratotype section is as striking as the one in north-central Ohio. The shale, which lacks conodonts, likely represents the early If T-R cycle and could be close to the basal Plum Brook in age.

The writer therefore believes that the lowest occurrence of the early morphotype of *P. ansatus* occurs too high in the *ensensis* Zone to serve as an index species for the base of the Givetian. Furthermore, the section at Jebel Mech Irdane includes less than 0.5 m of strata that could conceivably belong to the Lower *ensensis* Subzone, even if the SDS definition is used; it is difficult to believe that this interval could represent the continuous sedimentation that should characterize a global-stratotype section. Chlupáč's suggested use of the Kačák Event to establish the base of the Givetian provides a practical alternative approach that could be used anywhere. The main criterion could be the occurrence of any taxa that did not exist before the onset of that phenomenon. In the Plum Brook, for example, the evidence would include all of the many species and subspecies of *Icriodus*. At Jebel Mech Irdane the occurrence of *Maenioceras* would suffice.

The overall value of *P. ansatus* as an index fossil appears to be questionable. The early form widely accepted as *P. hemiansatus* enjoys "world-wide geographic distribution" according to the SDS (Walliser et al., 1995, p. 113), but there are no published occurrences at an appropriate level for definition of the *hemiansatus* Zone anywhere in North America. In the Pine Point Formation south of Great Slave Lake, Northwest Territories, Uyeno (1998, table 1), using Bultynck's taxonomy, found the lowest level for *P. hemiansatus* to concur with that of *P. ansatus* about 2 m above the lowest occurrence of *P. timorensis*. One unpublished report of the early form involves small and fragmented specimens among those discussed above as being classified as *P. varcus* Group by Uyeno, from the uppermost Arkona Shale (in Uyeno et al., 1982, table 6). Bultynck examined this material in 1987 and concluded that his *P. hemiansatus* was present (Uyeno, personal commun., 1987, 1997), and Uyeno (personal commun., 1998) confirms the presence of a specimen with the characteristic "spoon-like structure" that is unknown in earlier taxa. The uppermost Arkona, which in this case lies on the margin of the Chatham Sag and is interpreted to be higher in the *ensensis* Zone than the eroded top of the Plum Brook on the

flank of the Findlay Arch, may be the same age as the *hemiansatus* Zone in Morocco. However, the Plum Brook, lower Arkona, and underlying Bell Shale all represent the If T-R cycle, and assigning them entirely to the Eifelian would be an unrealistic departure from past practice in North America.

Regarding the later morphotype of *P. ansatus*, its lowest occurrences in Europe and North America appear to be reasonably contemporaneous and by definition mark the base of the Middle *varcus* Subzone, yet its absence from so much of eastern North America created the correlation problems discussed above. Bultynck's (1987, p. 155) assumption that its lowest occurrence in Morocco is synchronous with the base of the Middle *varcus* Subzone of Europe and North America is also problematical. In the Bou Tchrafine section, the lowest occurrence of *P. ansatus* is over 5.5 m above the lowest occurrences of *P. rhenanus* and *P. linguiformis transversus* (Bultynck, 1987, fig. 4). As discussed above, *P. rhenanus* is limited in North America to the Middle *varcus* Subzone according to Klapper (*in* Johnson, Klapper, and Trojan, 1980, p. 93), and *P. linguiformis transversus* (= *P. l. linguiformis* eta morphotype) is limited to that subzone in Europe according to Klapper (*in* Ziegler, 1977; Klapper and Johnson, 1980) and in the Pine Point Formation of western Canada according to Uyeno (1998, table 1). If these taxa were used as Middle *varcus* indices in Morocco, the lowest occurrence there of the form that everyone agrees to call *P. ansatus* would be fairly high in that subzone rather than at its base.

A recent study sheds some light on this matter. It involves establishment of a quantitative biostratigraphy of the Eifelian and lower Givetian of southern Morocco, using Bultynck's extensive conodont studies as the data base (Belka, Kaufmann, and Bultynck, 1997), and includes a proposed alternative conodont zonation. The upper part of the *ensensis* Zone is referred to as the *hemiansatus* Zone in both the standard and alternative zonations, the Lower *varcus* Subzone is divided into the *timorensis* and *rhenanus* Zones, and the Middle *varcus* is designated as the *ansatus* Zone. *Polygnathus linguiformis transversus* is shown as being restricted to the *rhenanus* Zone (Belka et al., 1997, fig. 3). As part of that study, the diachroneity of lowest occurrences was determined for a number of conodont species. It was found to be very low for both *P. timorensis* and *P. rhenanus*. As indicated above, the ubiquity of those species on the eastern North American craton to the exclusion of other members of their lineage suggests a superior ecologic adaptability; an accordingly superior level of synchronicity *should* therefore characterize their lowest occurrences. The diachroneity of lowest occurrences for *P. ansatus* (i.e., the later morphotype) is not included in said study, but a significant qualitative indicator involves the fact that it was found in only one of three regions from which Givetian data had been provided, the Bou Tchrafine section. It is absent from the Middle *varcus* Subzone in the region of the Akka Bou Khedach and Taboumakhloûf sections (Bultynck, 1987, fig. 7), and the highest occurrences there of the early form (i.e., *P. hemiansatus*) are in the lower part of the *rhenanus* Zone. It thus seems that the adaptability of *P. ansatus* was less than one might wish for in an important index species and that the base of the Middle *varcus* Subzone in Morocco, as defined by its later form, may not correspond well to that level in Europe and North America.

#### RECOMMENDATIONS

In light of the problems discussed above, it is clear that any attempts to adopt the SDS definition of the basal Givetian to North American biostratigraphic classification at this time could only create more problems. Continued use of the upper *ensensis* Zone as the base is recommended, even though it may be hard to define in some cases. It is also recommended that the IUGS

consider Chlupáč's proposal to designate the widely recognized event horizon discussed above, and the faunal break that occurs at that level, as the basis for defining the lower Givetian boundary. Finally, it is recommended that a new search begin for a global-stratotype section in a tectonic setting that can guarantee a record of continuous sedimentation from the upper *kockelianus* Zone into the Lower *varcus* Subzone.

#### REPOSITORY

All specimens are in the collection at Ohio State University. Specimen numbers beginning with S85CR9 are from the basal Prout. Those beginning with S89I are from the basal Little Rock Creek of Delhi, Indiana.

#### SYSTEMATIC PALEONTOLOGY

This section includes a new species of *Ancyrolepis*, other new taxa treated informally, and selected species important to problems discussed above or of other significance. Synonymies of additional illustrated species can be found in Appendix II.

Family ICRIODONTIDAE Müller and Müller, 1957  
Genus ICRIODUS Branson and Mehl, 1938

*Type species*.—*Icriodus expansus* BRANSON AND MEHL, 1938.

#### ICRIODUS EXPANSUS Group

*Discussion*.—The term *Icriodus expansus* Group was used (Sparling, 1995) for material from the Plum Brook Shale including that species plus form species, *I. arkonensis* Stauffer and *I. brevis* Stauffer, which intergrade with it and were interpreted to be conspecific ecotypic variants at that biostratigraphic level. Such intergradation does not occur in the Prout, where speciation is considered to be complete for those three species and for a fourth member of the group, *I. difficilis* Ziegler and Klapper, which may have evolved from forms intermediate between *I. expansus* and *I. arkonensis*.

#### ICRIODUS REGULARICRESCENS Group

*Discussion*.—A subspecies of *I. regularicrescens* and six other species considered to have shared a common ancestry with it were placed in the *I. regularicrescens* Group by Sparling (1995). Of these, only *I. eriensis*, *I. janeae*, and *I. obliquimarginatus* are found in the Prout.

ICRIODUS ERIENSIS Sparling, 1995  
Figure 3.10, 3.13, 3.14

*Icriodus eriensis* SPARLING, 1995, p. 1131, fig. 6.16–6.21.

*Discussion*.—This species and *I. janeae* were both considered to be endemic to the region (Sparling, 1995, p. 1131) and thought to be restricted to the lower Givetian at the time of their publication. However, their survival into the time of the Taghnic onlap suggests that they might eventually be found outside of the region.

Family POLYGNATHIDAE Bassler, 1925  
Genus ANCYROLEPIS Ziegler, 1959

*Type species*.—*Ancyrolepis cruciformis* Ziegler, 1959.

ANCYROLEPIS HUNTLEYI new species  
Figure 3.1–3.3

*Diagnosis*.—Pa element narrow and gently curved, with carina formed of discrete, well formed denticles. Inner lateral lobe is small and trigonal, outer lobe somewhat larger. Basal cavity extends beneath lateral lobes but gives way near pit to well defined keels extending to anterior and posterior ends.

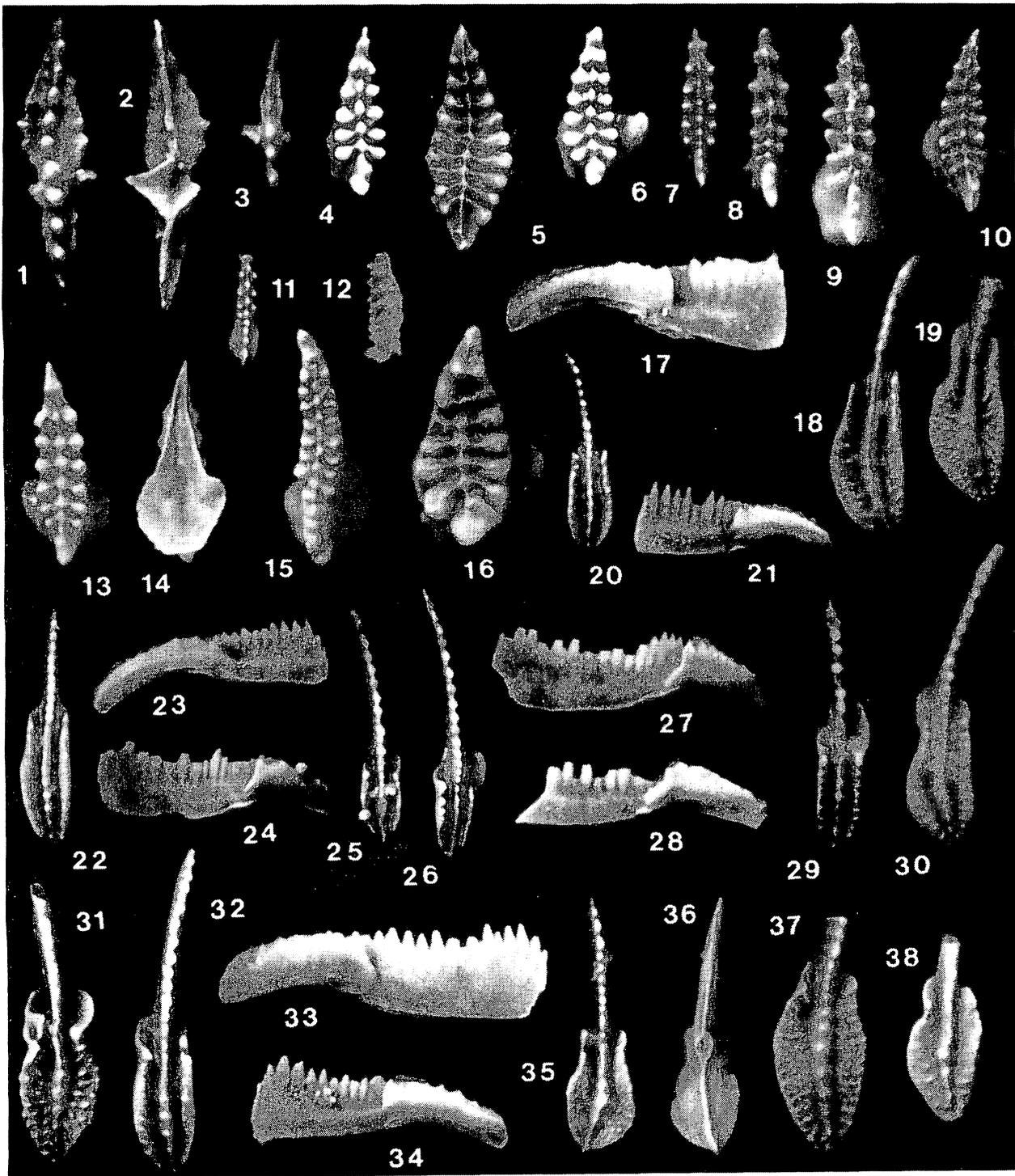


FIGURE 3.—Pa elements from samples S85CR9 and S8911 (specimens shown in 4, 5, 6, 7, 11, 18, 20, 22, 25, 26, 32, and 37 were previously illustrated in Sparling, 1988). 1-3 are  $\times 60$ , all others  $\times 40$ . 1-3, *Ancyrolepis huntleyi* new species: 1, 2, upper and lower views of holotype S85CR9s; 3, upper view of juvenile paratype, S85CR9t. 4, *Icriodus expansus* Branson and Mehl, upper view of S85CR9p. 5, *I. arkonensis* Stauffer, upper view of S85CR9k. 6, *I. difficilis* Ziegler and Klapper, upper view of S85CR9o. 7, *I. brevis* Stauffer, upper view of S85CR9x. 8, 9, *I. jancae* Sparling; 8, upper view of S85CR9qq; 9, upper view of S85CR9qq. 10, 13, 14, *I. eriensis* Sparling; 10, upper view of S85CR9ss; 13, 14, upper and lower views of S85CR9kk. 11, 12, 15, *I. obliquimarginatus* Bischoff and Ziegler; 11, 12, upper and lateral views of S85CR9w; 15, upper view of S8911a. 16, *I. excavatus* Weddige, upper view of S85CR9ll. 17-19, *Polygnathus pseudofoliatus* Wittekindt; 17, 18, inner lateral and upper views of S85CR9c; 19, upper view of S85CR9v. 20, 21, *P. xylus ensensis* Ziegler and Klapper, upper and inner lateral views of S85CR9h. 22, 23, *P. xylus xylus* Stauffer, upper and inner lateral views of S85CR9a. 24, 25, *P. timorensis* Klapper, Philip, and Jackson, inner lateral and upper views of immature specimen S85CR9g. 26-29, *P. rhenanus* Klapper, Philip, and Jackson; 26, 27, upper and inner lateral views of S85CR9q; 28, 29, inner lateral and upper views of S85CR9r. 30-33, *P. ansatus* Ziegler and Klapper; 30, upper view of S85CR9u; 31, upper view of S85CR9f; 32, 33, upper and inner lateral views of S85CR9d. 34-36, *P. sp. C*, inner lateral, upper, and lower views of S85CR9i. 37, 38, *P. ovatinodosus* Ziegler and Klapper; 37, upper view of S85CR9z; 38, upper view of S85CR9y.

*Description.*—On holotype (S85CR9s), two smooth oval-shaped denticles lie above the pit on opposite sides of the transverse axis thereof; evenly spaced denticles extend to both ends. Similarly spaced sharp nodes occur on margins of widest part of platform, anterior of pit, separated from carina by shallow adcarinal grooves. Sharp crest trends laterally on inner "lobe" without rising above nearest marginal node. Outer lobe is missing, but remnant of its posterior margin trends away from pit at an angle similar to that of inner lobe. Platform tapers to width of denticles at both ends. Keels extending from restricted basal cavity to both ends are narrow but not sharp edged and bear a faint median suture.

On juvenile paratype (S85CR9t), outer lobe is intact, larger than inner lobe, which appears to be mostly present but lacks any upward projection. Posterior portion of platform is missing, and lateral platform development occurs only anterior of pit.

*Etymology.*—The species is named for Frank D. Huntley, who was directly responsible for its discovery.

*Types.*—The larger illustrated specimen (S85CR9s) is designated as holotype, the smaller (S85CR9t) as paratype.

*Material examined.*—Only the two figured specimens were found.

*Occurrence.*—Prout Dolomite of north-central Ohio, the age of which is the middle part of the Middle *varcus* Subzone.

*Discussion.*—This genus is generally placed in the Polygnathidae, questionably so by Sweet (1988), and its derivation is certainly not revealed by examination of the fossil record to date. This species is distinctive from the slightly older Givetian species, *A. walliseri*, which has a prominent outer lobe with a secondary keel and a carina formed of fused denticles. The pit and main keel are similar, however, and *A. walliseri* was probably ancestral to *A. huntleyi*. The known range of the former is the uppermost Lower *varcus* Subzone into the lowermost part of the Middle *varcus* Subzone (Ziegler, Klapper, and Johnson, 1976, p. 113). *Ancyrolepis cixerriensis* Olivieri (1985, p. 286, 288, pl. 1, figs. 1a–6b) is clearly related. It bears a very similar carina formed of discrete denticles. Also the inner lateral lobe, while larger and generally rounded, is "angular in rare cases." The primary difference lies in the size and shape of the basal cavity in *A. cixerriensis*; it is very large and extends as a wedge onto the posterior lobe and as a narrow interruption of the keel anteriorly. Its occurrence in Sardinia is restricted to the uppermost sample of a section assigned to the Middle *varcus* Subzone (in thrust-fault contact with Frasnian strata) on the basis of presence of the delta morphotype of *P. linguiformis linguiformis* in all samples (Olivieri, 1985, p. 277–278). The overlying strata were found to contain the index species for the Upper *varcus* Subzone, *P. latifossatus*, and so occurrence of *A. cixerriensis* is apparently very high in the Middle *varcus* Subzone. It thus appears that *A. huntleyi* is intermediate between that species and *A. walliseri* in both morphology and biostratigraphic level.

#### Genus POLYGNATHUS Hinde, 1879

*Type species*—*Polygnathus dubius* Hinde, 1879.

#### POLYGNATHUS PSEUDOFOLIATUS Group

##### POLYGNATHUS ANSATUS Ziegler and Klapper, 1976 Figure 3.30–3.33

*Polygnathus ansatus* ZIEGLER AND KLAPPER, in Ziegler, Klapper, and Johnson, 1976, p. 119–120, pl. 2, figs. 11–26; BULTYNCK in Bultynck and Hollard, 1980, p. 41, pl. 8, fig. 13a–c, pl. 9, figs. 1–3; UYENO in Norris et al., 1982, p. 73, pl. 36, figs. 1–12; RACKI, 1985, p. 270, pl. 3, figs. 2, 7; GARCÍA-LÓPEZ, 1987, p. 86–88, pl. 11, fig. 23, pl. 12, figs. 1–13; BULTYNCK, 1987, p. 161, pl. 8, figs. 10–14; MAWSON AND TALENT, 1990, pl. 3, figs. 19–21; UYENO, 1991, pl. 3, fig. 2; UYENO, 1998, p. 161, pl. 12, fig. 28, pl. 15, figs. 7, 8.

*Polygnathus* aff. *P. ansatus* Ziegler and Klapper of BULTYNCK in Bultynck and Hollard, 1980, p. 42, pl. 5, fig. 18a–c, pl. 6, figs. 2, 3?, 4.

*Polygnathus ansatus* Ziegler and Klapper, early morphotype. BULTYNCK, 1985, pl. 6, figs. 19–20.

*Polygnathus hemiansatus* BULTYNCK, 1987, p. 161–162, pl. 7, figs. 16–27, pl. 8, figs. 1–7; BULTYNCK, 1989, p. 99, pl. 2, figs. 6, 7, 10, 11; MAWSON AND TALENT, 1990, pl. 3, figs. 14–18, 22, 23; UYENO, 1998, p. 161, pl. 12, figs. 29, 30.

*Discussion.*—The specimen illustrated in Figure 3.30 is typical (curvature of the free blade is affected by a healed fracture near the platform). Figure 3.31 shows an unusual specimen having the nodose ornamentation of *P. ovatinodosus* but not the shape; a specimen illustrated by Racki (1985, pl. 3, fig. 2) is similar. Figure 3.32 shows the form distinguished by Bultynck in the evolving usage shown in the synonymy. As indicated above, *P. hemiansatus* is considered herein to be an early morphotype of *P. ansatus* derived from *P. pseudofoliatus*, as documented by Bultynck (1989, p. 99), in early, but not earliest, Givetian time. The diagnosis for that early form emphasizes a nearly straight inner platform margin and the lack of an outward bowing of the inner anterior margin, although some early specimens do seem to be bowed slightly (e.g., Bultynck and Hollard, 1980, pl. 6, fig. 3). Many of the 162 specimens of *P. ansatus* from the Prout fit the diagnosis for *P. hemiansatus*, but a complete gradation to broader forms with anterior bowing on both sides exists; the inclusion of all morphotypes among the paratypes of *P. ansatus* by Ziegler and Klapper is considered justified on that basis.

##### POLYGNATHUS OVATINODOSUS Ziegler and Klapper, 1976 Figure 3.37, 3.38

*Polygnathus ovatinodosus* ZIEGLER AND KLAPPER, in Ziegler, Klapper, and Johnson, 1976, p. 124–125, pl. 2, figs. 1–9 [see for extensive synonymy]; BULTYNCK in Bultynck and Hollard, 1980, p. 44, pl. 8, figs. 10, 11; UYENO in Norris et al., 1982, p. 75, pl. 33, figs. 39–41; GARCÍA-LÓPEZ, 1987, p. 95–96, pl. 12, figs. 14–25.

*Discussion.*—The specimen shown in Figure 3.38 appears to be an intermediate form consistent with the proposal by Ziegler and Klapper that this species was derived from *P. ansatus*.

##### POLYGNATHUS PSEUDOFOLIATUS Wittekindt, 1966 Figure 3.17–3.19

*Polygnathus pseudofoliata* n. sp. WITTEKINDT, 1966, p. 637–638, pl. 2, figs. 20–23 [non fig. 19].

*Polygnathus pseudofoliatus* Wittekindt. UYENO, 1991, pl. 2, fig. 24; SPARLING, 1995, p. 1136–1137, fig. 2.1–2.8. 2.11–2.19, fig. 3.1–3.22 [see for further synonymy].

*Discussion.*—The specimen shown in Figure 3.19 is a morphotype in which the rostral area involves a constricted outer margin and a very thin rostral ridge on the inner side of the platform, which is otherwise ornamented by fine nodes. This form does not occur in underlying strata.

##### POLYGNATHUS RHENANUS Klapper, Philip, and Jackson, 1970 Figure 3.26–3.29

*Polygnathus rhenanus* sp. nov. KLAPPER, PHILIP & JACKSON, 1970, p. 654–655, pl. 2, figs. 13–15, 19–22, text-fig. 1 a–c; KLAPPER in Ziegler, 1973, p. 377–378, *Polygnathus*-pl. 2, fig. 1; BULTYNCK in Bultynck and Hollard, 1980, p. 45, pl. 6, figs. 15–17; GARCÍA-LÓPEZ, 1987, p. 98, pl. 11, figs. 3–12; BULTYNCK, 1987, p. 162, pl. 7, figs. 13–15.

*Polygnathus varcus* Stauffer. ORR, 1971, p. 53–54, pl. 5, figs. 4–8.

*Polygnathus timorensis* Klapper, Philip, and Jackson. KLAPPER in Johnson et al., 1980, pl. 3, fig. 38; UYENO in Uyeno et al., 1982 [partim], p. 30, pl. 2, figs. 13–15; MAWSON AND TALENT, 1990 [partim], pl. 4, figs. 9, 11, 12.

*Discussion.*—This species seems clearly to be derived from *P. timorensis* but is normally more asymmetric owing to lateral expansion and greater overall size of the outer platform margin anterior of the geniculation point. Ziegler and Klapper (*in* Ziegler, Klapper, and Johnson, 1976, p. 125) regarded *P. rhenanus* to be a junior synonym for *P. timorensis* on the basis that it “seems to have been based on juvenile specimens of” the latter. The holotype of the former is slightly longer than the immature specimen of *P. timorensis* illustrated herein (Fig. 3.24, 3.25) and could be considered of adequate size; also *P. rhenanus* does have page precedence over *P. timorensis*. In any case, both Bultynck (*in* Bultynck and Hollard, 1980, p. 45) and García-López (1987, p. 98) have specifically rejected the synonymy. The original diagnosis of *P. rhenanus* calls for a smooth platform, but Bultynck (1987, p. 162) does not regard that property to be of diagnostic importance and emphasizes the fact that the outer geniculation point lies from one-third to one-half of the distance between the anterior and posterior ends of the outer platform margin. That criterion is in fact very useful in distinguishing the two species from the type specimens of *P. timorensis* and from the illustrations of that species in Ziegler, Klapper, and Johnson (1976).

The synonymy in which Ziegler and Klapper (*in* Ziegler, Klapper, and Johnson, 1976, p. 125) equated *P. rhenanus* with *P. timorensis* also included the figured specimens identified as *P. varcus* by Orr (1971). These are considered to be *P. rhenanus* by García-López (1987) and herein. Also 1 of 4 Pa elements figured by Uyeno (*in* Uyeno et al., 1982) identified as *P. timorensis* fits the diagnosis used herein. It appears likely that both forms occur together throughout the region, including the Upper Traverse, Little Rock Creek, and Beechwood of Indiana.

POLYGNATHUS TIMORENSIS Klapper, Philip, and Jackson, 1970  
Figure 3.24, 3.25

*Polygnathus decorosus* STAUFFER, 1938 [partim], p. 438, pl. 53, fig. 11.  
*Polygnathus varca* Stauffer. BISCHOFF AND ZIEGLER, 1957 [partim], p. 98–99, pl. 18, fig. 34.

*Polygnathus timorensis* KLAPPER, PHILIP, AND JACKSON, 1970, p. 655–656, pl. 1, figs. 1–3, 7–10; KLAPPER *in* Ziegler, 1973, p. 385–386. *Polygnathus*-pl. 2, fig. 3; BULTYNCK, *in* Bultynck and Hollard, 1980, p. 45, pl. 6, figs. 8–14; UYENO *in* Uyeno et al., 1982, p. 30, pl. 2, figs. 7–12, 16–19 [non figs. 13–15=*P. rhenanus*]; KLUG, 1983, p. 108, fig. 11 I–K; WEDDIGE, 1984, pl. 2, figs. 28–32; GARCÍA-LÓPEZ, 1987, p. 98–99, pl. 10, figs. 20–29; BULTYNCK, 1987, p. 162, pl. 7, figs. 9, 10; MAWSON AND TALENT, 1990 [partim], pl. 4, figs. 7, 8, 10; UYENO, 1991, pl. 3, fig. 3; UYENO, 1998, p. 165, pl. 12, figs. 18, 19, pl. 15, figs. 3–6.

*Discussion.*—The derivation of this species from *P. xylus ensensis* appears to be well established; intermediate forms are reported from the upper *ensensis* Zone in Germany (Ziegler, Klapper, and Johnson, 1976, p. 125) and in Morocco (Bultynck, 1987, fig. 4, p. 161, pl. 7, figs. 7, 8). As stated above, the apparent adaptability of this species to ecologic conditions hostile to many other species in its lineage may have provided an ease of migration that would make it a superior index species in regard to the isochronism of its lowest occurrences around the world.

POLYGNATHUS XYLUS ENSENSIS Ziegler and Klapper, 1976  
Figure 3.20, 3.21

*Polygnathus xyla* Stauffer. SEDDON, 1970, p. 62–63, pl. 6, figs. 10–12.  
*Polygnathus xylus* Stauffer. KLAPPER, PHILIP, AND JACKSON, 1970 [partim], pl. 2, figs. 10–12.

*Polygnathus xylus ensensis* n. subsp. ZIEGLER AND KLAPPER *in* Ziegler, Klapper, and Johnson, 1976, pl. 3, figs. 4–9; SPARLING, 1995, p. 1137, figs. 2.20–2.24, 8.5, 8.6 [see for further synonymy]; UYENO, 1998, p. 165, pl. 12, figs. 4, 16, pl. 14, figs. 23–31, pl. 15, figs. 1, 2.

*Polygnathus ensensis* Ziegler and Klapper. BULTYNCK, 1987, p. 161, pl. 7, figs. 1–6; BULTYNCK, 1989 [partim], p. 97, 99, pl. 2, figs. 12–14, 16–20 [non 15, 21=*P. xylus xylus*?].

*Discussion.*—The posterior part of the platform of this subspecies normally arches downward quite strongly. Most Pa elements from the Prout do so, but not the figured specimen, which nonetheless has the shape and vertical anterior platform margins that characterize this taxon. This subspecies is considered herein to have given rise to *P. xylus xylus* in very early Givetian time and later to *P. timorensis*, yet Uyeno (1998, pl. 14, figs. 29–31, pl. 15, figs. 1, 2) illustrates specimens considered to be transitional to both of these from the Middle *varcus* Subzone of the Pine Point Formation, well above their lowest occurrences. Such forms are conceivably hybrids at that level.

POLYGNATHUS XYLUS XYLUS Stauffer, 1940  
Figure 3.22, 3.23

*Polygnathus xylus* STAUFFER, 1940 [partim], p. 430–431, pl. 60, figs. 54, 66, 72–74.

*Polygnathus xylus xylus* Stauffer. ZIEGLER AND KLAPPER *in* Ziegler, Klapper, and Johnson, 1976, p. 125, pl. 3, fig. 1; BULTYNCK, 1987, pl. 8, figs. 22, 27, pl. 9, fig. 12; SPARLING, 1995, p. 1137–1138, fig. 2.25–2.27 [see for further synonymy].

?*Polygnathus ensensis* Ziegler and Klapper. BULTYNCK, 1989 [partim], pl. 2, figs. 15, 21.

*Discussion.*—Early forms of this subspecies from the Plum Brook Shale (Sparling, 1995, p. 1137–1138, fig. 2.25–2.27) and the lower type Givetian well below the lowest occurrence of *P. timorensis* (Bultynck, 1987, pl. 9, fig. 12) have limited serration of anterior platform margins and an outer trough margin that slopes more gently than in *P. xylus ensensis*. Two specimens assigned by Bultynck (1989, pl. 2, figs. 15, 21) to *P. ensensis* appear to differ from that taxon in a very similar way.

POLYGNATHUS sp. C  
Fig. 3.34–3.36

*Description.*—Single Pa element. Anterior platform margins inclined steeply downward, posterior of which anterior inner margin bears a single notch and outer anterior margin is slightly constricted. Inner platform expands to maximum width near its midpoint, outer platform posterior thereof. Adcarinal grooves, deep anteriorly, extend approximately to position of large denticle at flexure point on carina, posterior of which denticles become very small. Platform posterior of rostral area is fairly broad and flat, ornamented only by small nodes. Free blade is slightly over half of specimen length. Pit lies near anterior end of platform.

*Discussion.*—This species bears some similarity to *P. strongi* Stauffer in regard to free-blade length, nodose ornamentation, and flat posterior platform. The platform outline in upper view is different from other members of the *P. pseudofoliatus* Group, although a specimen of *P. ansatus* illustrated by Bultynck (*in* Bultynck and Hollard, 1980, pl. 9, fig. 2) is actually quite close in shape, even to the point of having a platform posterior that is quite flat for that species. The slight constriction on the outer anterior platform margin of *Polygnathus* sp. C is also similar although the steep slope of the anterior margins contrasts with the gentler slope in *P. ansatus*.

POLYGNATHUS sp.  
Figure 4.3, 4.4

*Description.*—Single large Pa specimen, broken at pit, characterized by platform posterior therefrom that is flat, with discrete to fused denticles, a few of which are tied to lateral ridges. Ornamentation by narrow ridges and scattered nodes is notably irregular.

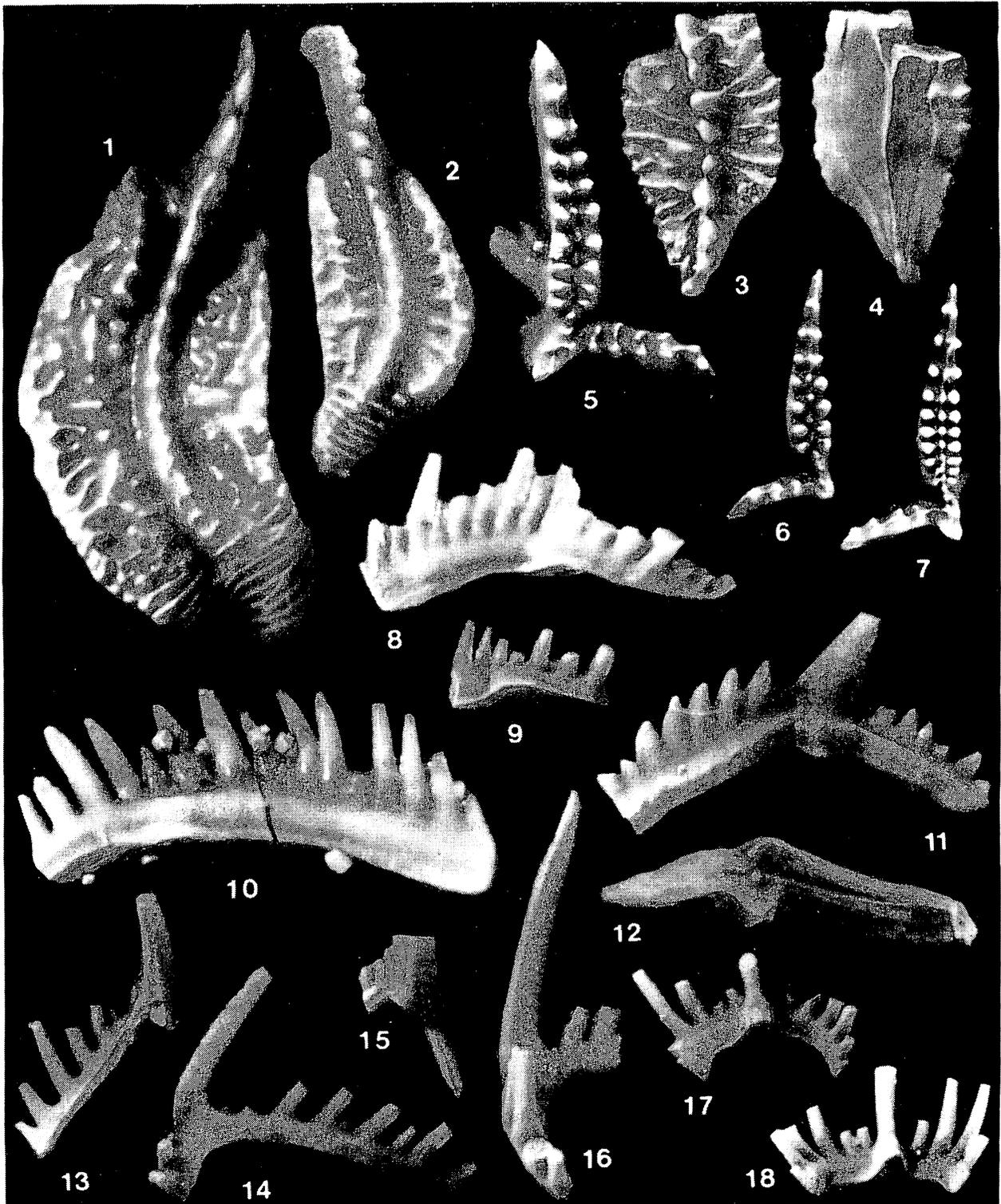


FIGURE 4—Specimens from samples S85CR9 and S8911. All are  $\times 40$  except as indicated. 1, 2. *Polygnathus linguiformis klapperi* Clausen, Leuteritz, and Ziegler: 1, upper view of very large Pa element S85CR9c; 2, upper view of Pa element S8911b. 3, 4. *P.* sp., upper and lower views of the posterior part of Pa element S85CR9uu. 5–7. *Laterieriodus latericrescens latericrescens* (Branson and Mehl): 5, upper view of Pa element S85CR9j; 6, upper view of Pa element S85CR9n; 7, upper view of Pa element S85CR9m. 8, 10–12. *Prioniodina?* spp.: 8, lateral view of Pa element S85CR9oo; 10, lateral view of Pa element with posterior end missing, S85CR9tt; 11, 12, lateral and lower views of Pb element with anterior end missing, S85CR9ww. 9, 13–18. *Prioniodina* spp.: 9, lateral view of Pa element broken at both ends, S85CR9xx; 13, posterior view of Sa element missing posterior process and one lateral process, S85CR9yy; 14, lateral view of Sb element S85CR9zz; 15, fragment of large ( $\times 16$ ) M element S85CR9bbb; 16, lateral view of Sc element S85CR9aaa; 17, lateral view of Sd element S85CR9vv; 18, lateral view of Sd element S85CR9jj.

## Family PRIONIODINIDAE Bassler, 1925

## Genus PRIONIODINA Bassler, 1925

*Type species.*—*Prioniodina subcurvata* Bassler, 1925.

*Discussion.*—This genus is considered to include 7 types of elements that were designated as prioniodellan, prioniodinan, neoprioniodontan, ligonodinan, longidensiform, lonchodinan and hibbardellan (Sparling, 1981); these correspond to the Pa, Pb, M, Sc, Sb, Sd, and Sa, respectively, of current usage. The Sd element is homologous with an one in *Polygnathus x. xylus* so designated by Nicoll (1985); in both cases the main cusp is inclined toward the inner side. *Prioniodina* probably evolved from the *Oulodus* lineage during the Early Devonian (Sparling, 1981, p. 308); it differs from that genus primarily in that the symmetrical Sa element bears a posterior process, which is lacking in *Oulodus*. *Prioniodina* species in the underlying Eifelian Columbus and Delaware limestones are characterized by round, discrete denticles with white matter restricted to the upper parts thereof. Recognition of all elements belonging to a single species is difficult unless all are segregated, which is not the case with the material studied herein. Also some large, mostly fragmental specimens tabulated as belonging to this genus could actually belong to *Tortodus*, which is represented by numerous large Pa elements.

## PRIONIODINA spp.

Figure 4.9, 4.13–4.18

*Oulodus* sp. UYENO in Norris et al., 1982, p. 79–80, pl. 35, figs. 1–12, 16, 17.

*Oulodus* sp. UYENO in Uyeno et al., 1982, p. 33, pl. 5, figures 36–39.

*Discussion.*—Uyeno (in Norris et al., 1982) figured 13 specimens assigned to *Oulodus* from the Dawson Bay Formation of southwestern Manitoba, including a typical *Prioniodina* hibbardellan (Sa) element (Norris et al., 1982, pl. 35, figs. 16, 17). Figure 4.13 herein is a similar specimen with the posterior process and one of the lateral processes broken off. Figure 4.17 is an Sd element very similar to one figured in Norris et al. (1982, pl. 35, fig. 6). The Pa element in Figure 4.9 is missing anterior and posterior parts, but the specimen could be the same species as a Pa from Manitoba (Norris et al., 1982, pl. 35, fig. 4).

Two specimens from the Widder Formation of Ontario assigned by Uyeno (in Uyeno et al., 1982, pl. 5, figs. 37, 39) to *Oulodus* sp. are probably the same species as those shown in Figure 4.18 (Sd) and 4.14 (Sb), respectively. The M element shown in Figure 4.15 (very large but shown at only X16) could belong to either of the species discussed above.

## PRIONIODINA? spp.

Figure 4.8, 4.10–4.12

*Discussion.*—Many specimens, especially large fragments, are assigned to this genus with uncertainty, in part owing to the fact that they may belong to the genus *Tortodus*. Figure 4.8 and 4.10 are Pa elements lacking a main cusp and may belong to *Prioniodina*. The first has uncharacteristically fused denticles and twisted posterior suggesting that it could belong to *Tortodus*, although the specimens assigned to that genus in this collection have laterally expanded platforms. The posterior end of the second is missing and could also be twisted and assignable to *Tortodus*. The specimen shown in Fig. 4.11, 4.12, is a Pb with the

anterior end broken off. The fused denticles and sharp ridge below them are normally not seen in *Prioniodina*.

## Family SPATHOGNATHODONTIDAE Hass, 1959

## Genus TORTODUS Weddige, 1977

*Type species.*—*Polygnathus kockelianus* BISCHOFF AND ZIEGLER, 1957.

*Discussion.*—Nine Pa specimens assigned herein to this genus are treated informally and as separate taxa owing to the fact that no two are clearly the same. Other specimens assigned to this genus in Table 1 are too small or fragmental to be linked with certainty to any of the nine forms. The most closely related taxa appear to be *Tortodus variabilis* (Bischoff and Ziegler, 1957), *Polygnathus beckmani* Bischoff and Ziegler, 1957, and *P. aff. P. beckmanni* of Bultynck (in Bultynck and Hollard, 1980), considered by him to be intermediate between the first two. Although all nine specimens are conceivably separate species, *T. variabilis* is in fact characterized by a variability that may be shared by these related forms. For the sake of simplicity they are assigned to 2 species and designated as separate morphotypes that may be better sorted out by future workers.

## TORTODUS sp. A

*Description.*—Species of *Tortodus* in which posterior of otherwise continuously curved Pa element is bent toward outer side, as in the type species.

## Alpha morphotype

Figure 5.1–5.3

*Description.*—Pa element found in two pieces, broken just anterior of pit but aligned quite closely for each figure. Platform gently arched, with flat upper surface, margins rounded except on outer side anterior of break and ornamented by small nodes and narrow ridges. Carina is gently inclined toward the outer side anterior of pit, erect posteriorly, and is flexed more sharply than platform. Pit, of moderate size, lies slightly posterior of specimen mid-length and inverts to fairly sharp keel in both directions.

## Beta morphotype

Figure 5.4–5.6

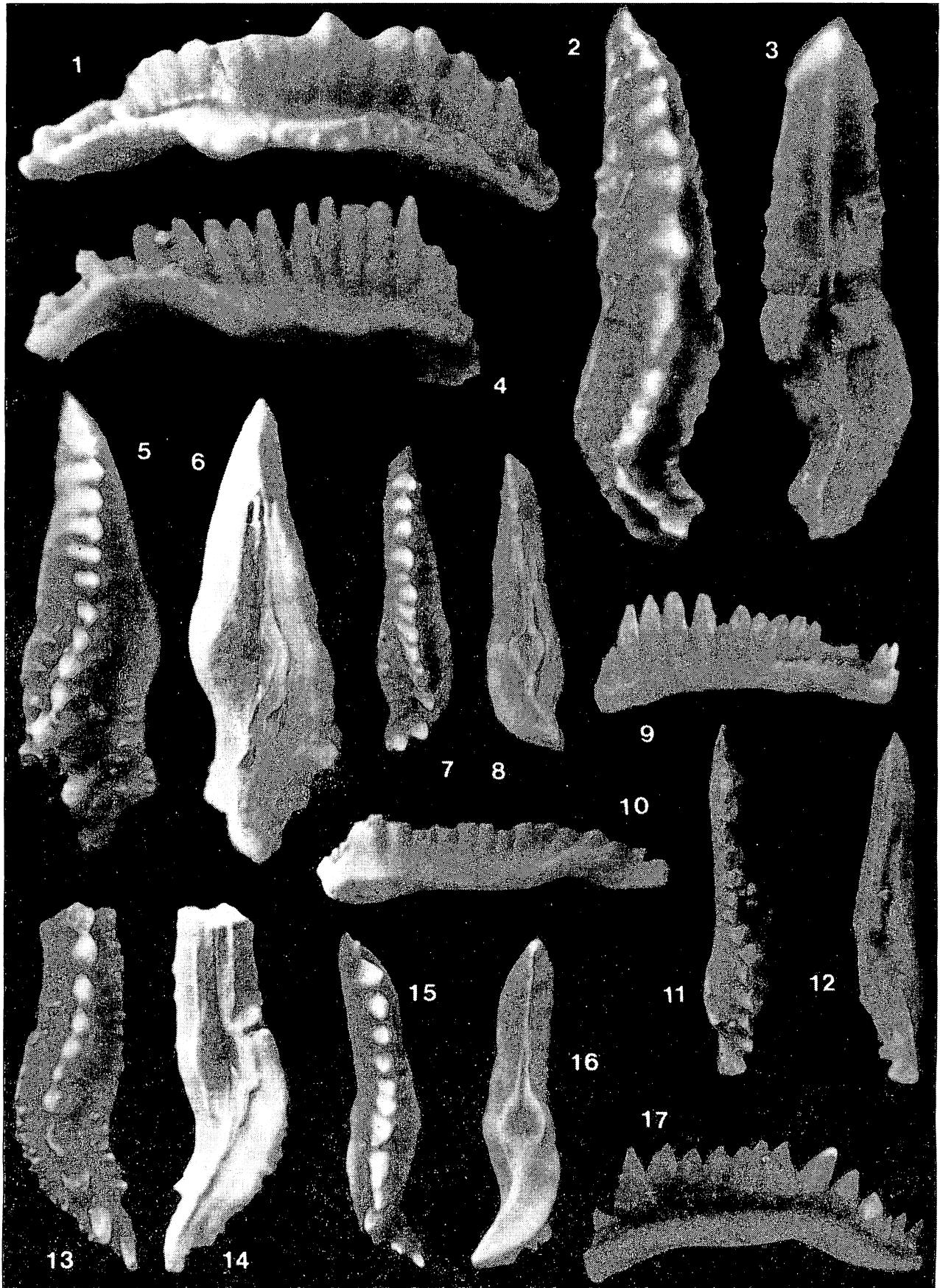
*Description.*—Specimen is notably asymmetrical and twisted about long axis so that inclination of carinal denticles reverses from end to end. Inner platform margin is high, narrow, smooth anteriorly, ornamented by a few nodes posterior of pit, and terminates just posterior of point of flexure of carina; outer platform margin is wider, slopes steeply downward anteriorly, rises and is ornamented by small nodes posteriorly, and is truncated adjacent to a point at which carina flexes again, toward the posterior. Pit is fairly large, extends anteriorly a considerable distance as a groove but inverts to a keel posteriorly. Narrow posterior inclines notably downward.

## Gamma morphotype

Figure 5.7–5.9

*Description.*—Platform expansion is ornamented by small nodes and extends from anterior end to point of flexure on inner

FIGURE 5—Pa elements of *Tortodus* from sample S85CR9. All are  $\times 40$ . 1–3, outer lateral, upper, and lower views of *T. sp. A*, alpha morphotype, S85CR9ee. 4–6, outer lateral, upper, and lower views of *T. sp. A*, beta morphotype, S85CR9hh. 7–9, upper, lower, and outer lateral views of *T. sp. A*, gamma morphotype, S85CR9dd. 10–12, outer lateral, upper, and lower views of *T. sp. B*, alpha morphotype, S85CR9ccc. 13, 14, upper and lower views of partial specimen of *T. sp. A*, delta morphotype, S85CR9pp. 15–17, upper, lower, and inner lateral views of *T. sp. A*, epsilon morphotype, S85CR9cc.



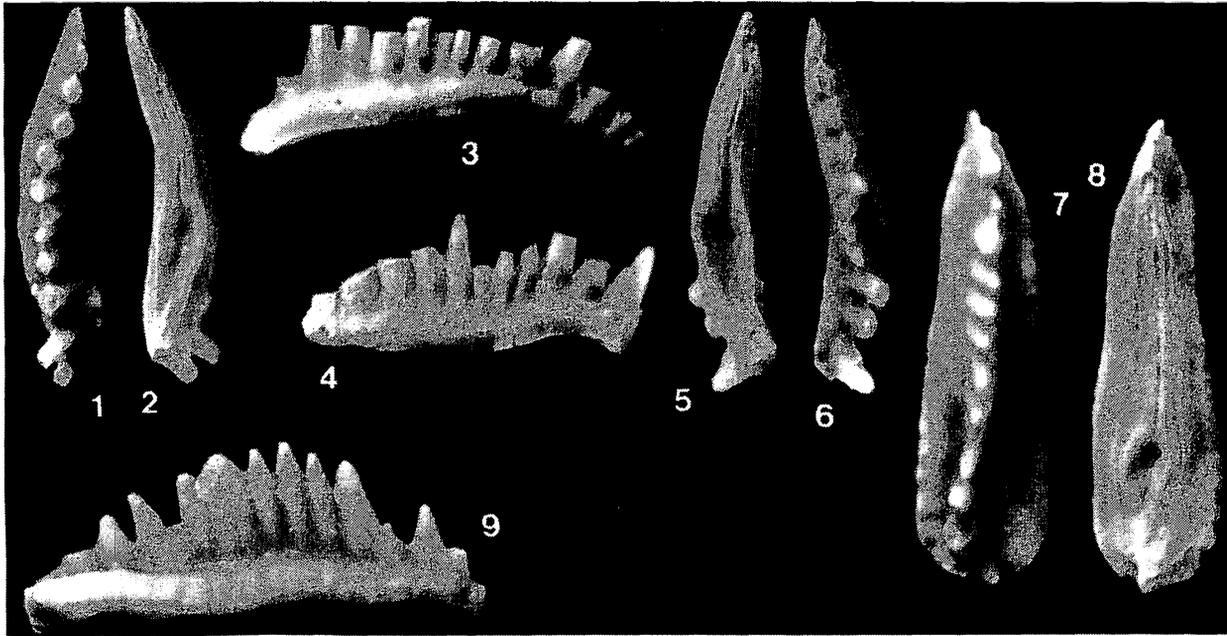


FIGURE 6—Pa elements from sample S85CR9. All are  $\times 40$ . 1–3, upper, lower, and inner lateral views (1, 2, with posterior tip missing) of *Tortodus* sp. B, beta morphotype, S85CR9nn. 4–6, outer lateral, lower, and upper views (posterior tip missing) of *T.* sp. B, gamma morphotype, S85CR9ddd. 7–9, upper, lower, and outer lateral views of *T.* sp. A, zeta morphotype, S85CR9mm.

side and on outer side is limited to posterior two-fifths of specimen. Denticles of carina are fused at base anterior of the point of flexure, more discrete posterior thereof. Pit lies less than 40 percent of the specimen length from posterior end, tapers gradually to curved keel posteriorly and anteriorly changes abruptly to thin, shallow groove that converts to a keel.

**Discussion.**—This morphotype bears considerable resemblance to Bultynck's *P.* aff. *P. beckmanni* (in Bultynck and Holard, 1980, p. 42, pl. 8, fig. 1), especially in regard to the platform, which is however more strongly ornamented with nodes. Also the flexure is more gradual and the pit much larger in the latter.

#### Delta morphotype Figure 5.13, 5.14

**Description.**—Upper surface of this broken platform is quite flat. Edge of inner side near break is smooth and rounded and becomes ornamented by small marginal nodes posteriorly. On outer side, short ridges anteriorly give way to marginal nodes posteriorly. Carina denticles are erect and fused at the base anteriorly and become inclined, round and discrete posteriorly. Fairly large pit is bordered by ridges continuing anteriorly to the break and converging posteriorly on a keel that begins within pit.

#### Epsilon morphotype Figure 5.15–5.17

**Description.**—Relatively narrow Pa element has rounded margins and a carina formed of laterally compressed denticles, erect and fused anterior of pit, inclined backward and discrete posteriorly. Posterior flexure of carina is abrupt. Pit tapers to posterior keel and is connected with anterior keel by a narrow groove. Complete lack of ornamentation is distinctive.

#### Zeta morphotype Figure 6.7–6.9

**Description.**—Sharp anterior end of Pa element widens to become fairly broad from a point anterior of pit to semicircular

posterior end. Carina reaches considerable height at midpoint, gradually migrates toward inner side, and ends at a round denticle (broken) at posterior margin. Flexure toward outer side is marked not by another denticle but by a single subdued node atop a vertical ridge, comparable to one on anterior margin, separated from rounded continuation of platform margin by a distinct notch. Platform ornamentation is limited to faint broad ridges and narrow grooves from near anterior end to pit on outer side and posterior of pit on inner side. Only very slight arching is seen in lateral view. Pit is positioned less than a third of specimen length from posterior end, tapers posteriorly and changes abruptly anteriorly to a very narrow groove extending a considerable distance anteriorly. No sharply defined keel exists at either end.

#### TORTODUS sp. B

**Description.**—Species of *Tortodus* in which anterior end of Pa element is gently curved but recurves over most of specimen length and then flexes to opposite direction near posterior end.

**Discussion.**—Three specimens assigned to this species (Fig. 5.10–5.12, Fig. 6.1–6.3, Fig. 6.4–6.6) are fairly similar to each other and differ from *T.* sp. A in that the posterior is quite straight or deflected slightly toward what appears to be the inner side rather than the outer. However, if the curvature of the anterior quarter of the platform is used to determine the outer versus inner sides, the normal *Tortodus* pattern is intact.

#### Alpha morphotype Figure 5.10–5.12

**Description.**—Anterior end of specimen is fairly narrow and gently curved, becoming recurved well ahead of pit. Carina lies along outer anterior margin (as defined by curvature of anterior end) as far as pit, where it migrates toward inner side and continues along slightly expanded platform to narrow posterior diverted very slightly toward outer side. Posterior expansion of platform on outer side rises posteriorly and bears two marginal

denticles. Pit is centered slightly posterior of midpoint and continues anteriorly as a narrow groove before inverting to a keel; posteriorly a very thin groove becomes a sharp keel.

**Beta morphotype**  
Figure 6.1–6.3

*Description.*—Platform is quite narrow with rounded margins, becoming slightly wider posterior of pit on outer side (as defined by curvature of anterior end) where only two very subdued nodes supply ornamentation. Carina formed of rounded denticles, fused at base anterior of pit and more discrete posterior thereof. Pit is deepest very slightly posterior of midpoint and tapers to keel continuing along narrowing posterior (broken in handling and shown only in Fig. 6.3), which is gently flexed outward. Anterior end of pit becomes short narrow slot. Anterior keel bearing faint narrow groove extends along inner side, beginning adjacent to pit (to right of it as seen in Fig. 6.2).

**Gamma morphotype**  
Figure 6.4–6.6

*Description.*—Platform is narrow, virtually absent on outer side (once again as defined by anterior end) anterior of pit, at which point carina migrates toward the center and then bends toward outer side, presumably to end, which is missing. Ornamentation is limited to a few very small nodes. Denticles of carina are laterally compressed, fused basally anteriorly and more discrete posteriorly. Pit is large, probably positioned close to specimen midpoint, tapers and shallows gradually toward posterior, becoming a sharp keel near break; anteriorly it forms a thin groove bordered by ridges, the inner of which dominates as a keel.

*Discussion.*—This form and the Beta morphotype are similar except for pit size.

ACKNOWLEDGMENTS

I am clearly indebted primarily to F. Huntley, without whose involvement this study would never have occurred. Much of the material was examined by T. T. Uyeno, G. Klapper, and M. J. Orchard, all of whom made helpful suggestions. During the writing phase, Uyeno and Klapper both provided information and opinions that were extremely important. Uyeno subsequently called attention to still further information and, together with F. Rogers, supplied a very helpful review. D. J. Over provided the first accurate zonation of the black shale above the Prout as well as a review. Additional useful suggestions were provided by J. E. Barrick.

REFERENCES

- BASSLER, R. S. 1925. Classification and stratigraphic use of the conodonts. *Geological Society of America Bulletin*, 36:218–220.
- BELKA, Z., B. KAUFMANN, AND P. BULTYNCK. 1997. Conodont-based quantitative biostratigraphy for the Eifelian of the eastern Anti-Atlas, Morocco. *Geological Society of America Bulletin*, 109:643–651.
- BISCHOFF, G., AND W. ZIEGLER. 1957. Die Conodontenchronologie des Mitteldevons und des tiefsten Oberdevons. *Abhandlungen des Hessischen Landesamtes für Bodenforschung*, 22, 136 p.
- BRANSON, E. B., AND M. G. MEHL. 1938. The conodont genus *Icriodus* and its stratigraphic distribution. *Journal of Paleontology*, 12:156–166.
- BULTYNCK, P. 1985. Lower Devonian (Emsian)—Middle Devonian (Eifelian and lowermost Givetian) conodont successions from the Ma'der and the Tafilalt, southern Morocco. *Courier Forschungsinstitut Senckenberg*, 75:261–286.
- . 1987. Pelagic and neritic conodont successions from the Givetian of pre-Sahara Morocco and the Ardennes. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 57:149–181.
- . 1989. Conodonts from a potential Eifelian/Givetian Global Boundary Stratotype at Jbel Ou Driss, southern Ma'der, Morocco. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 59:95–103.
- , AND H. HOLLARD. 1980. Distribution comparée de Conodontes et Goniatites dévoniens des plaines du Dra, du Ma'der et du Tafilalt (Moroc). *Aardkundige Mededelingen 1, Leuven University Press*, 73 p.
- CHLUPÁČ, I. 1995. Evaluation of some Devonian standard boundaries. *Nova Acta Leopoldina NF 71, Nr. 291*, p. 41–52.
- CLAUSEN, C.-D., K. LEUTERITZ, AND W. ZIEGLER. 1979. Biostratigraphie und Lithofazies am Südrand der Elser Mulde (hohes Mittel- und tiefes Oberdevon: Sauerland, Rheinisches Schiefergebirge). *Geologische Jahrbuch*, 51:3–37.
- COOPER, G. A. 1941. New Devonian stratigraphic units. *Journal of the Washington Academy of Sciences*, 31:179–181.
- , C. BUTTS, K. E. CASTER, G. H. CHADWICK, W. GOLDRING, E. M. KINDLE, E. KIRK, C. W. MERRIAM, F. M. SWARTZ, P. S. WARREN, A. S. WARTHIN, AND B. WILLARD. 1942. Correlation of the Devonian sedimentary formations of North America. *Geological Society of America Bulletin*, 53:1729–1793.
- GARCÍA-LÓPEZ, S. 1987. Los conodontos y su aplicación al estudio de las divisiones cronostratigráficas mayores del Devónico Asturleonés (España). *Publicaciones especiales del boletín geológico y minero*, 112 p.
- GRABAU, W. A. 1917. Age and stratigraphic relations of the Olentangy Shale of central Ohio, with remarks on the Prout limestone and so-called Olentangy shales of northern Ohio. *Journal of Geology*, 25:337–343.
- HASS, W. H. 1947. Conodont zones in Upper Devonian and Lower Mississippian formations of Ohio. *Journal of Paleontology*, 21:131–141.
- . 1959. Conodonts from the Chappel Limestone of Texas. *U. S. Geological Survey Professional Paper 294J*, p. 365–400.
- HINDE, G. J. 1879. On conodonts from the Chazy and Cincinnati group of the Cambro-Silurian, and from the Hamilton and Genesee-Shale divisions of the Devonian in Canada and the United States. *Quarterly Journal, Geological Society of London*, 35:351–369.
- JOHNSON, J. G. 1970. Taghanic onlap and the end of North American Devonian provinciality. *Geological Society of America Bulletin*, 81:2077–2105.
- , AND G. KLAPPER. 1992. North American Midcontinent Devonian T-R Cycles. *Oklahoma Geological Survey Bulletin*, 145:127–135.
- , —, AND C. A. SANDBERG. 1985. Devonian eustatic fluctuations in Euramerica. *Geological Society of America Bulletin*, 96:567–587.
- , —, AND W. TROJAN. 1980. Brachiopod and conodont successions in the Devonian of the northern Antelope Range, central Nevada. *Geologica et Palaeontologica*, 14:77–115.
- KLAPPER, G. 1989. The Montagne Noire Frasnian (Upper Devonian) conodont succession. *In* N. J. McMillan, A. F. Embry, and D. J. Glass (eds.), *Devonian of the world: Canadian Society of Petroleum Geologists Memoir 14*, v. 3, p. 449–468.
- , AND J. G. JOHNSON. 1980. Endemism and dispersal of Devonian conodonts. *Journal of Paleontology*, 54:400–455.
- , AND W. ZIEGLER. 1967. Evolutionary development of the *Icriodus latericrescens* group (Conodonta) in the Devonian of Europe and North America. *Palaeontographica, Abteilung A*, 127:68–83.
- , AND —. 1979. Devonian conodont biostratigraphy. *Palaeontological Association of London Special Papers*, no. 23, p. 199–224.
- , G. M. PHILIP, AND J. H. JACKSON. 1970. Revision of the *Polygnathus varcus* Group (Conodonta, Middle Devonian). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 1970, 11:650–667.
- KLUG, C. R. 1983. Conodonts and biostratigraphy of the Muscatatuck Group (Middle Devonian), south-central Indiana and north-central Kentucky. *Wisconsin Academy of Sciences, Arts and Letters 71*, part 1:79–112.
- KRYWANY, J. M. 1982. A biostratigraphic study of the Prout Limestone of north-central Ohio. Unpublished M.S. Thesis, University of Toledo, Toledo, Ohio, 150 p.
- LANDING, E., AND C. E. BRETT. 1987. Trace fossils and regional significance of a Middle Devonian (Givetian) disconformity in south-western Ontario. *Journal of Paleontology*, 61:205–230.
- MAWSON, R., AND J. A. TALENT. 1990. Late Emsian-Givetian stratigraphy and conodont biofacies—carbonate slope and offshore shoal to

- sheltered lagoon and nearshore carbonate ramp—Broken River, north Queensland, Australia. Courier Forschungsinstitut Senckenberg, 117: 205–259 [imprint 1989].
- MÜLLER, K. J. 1962. Zur systematischen Einteilung der Conodontophorida. *Paläontologische Zeitschrift*, 36:109–117.
- , AND E. M. MÜLLER. 1957. Early Upper Devonian (Independence) conodonts from Iowa, Part 1. *Journal of Paleontology*, 31:1069–1108.
- NICOLL, R. S. 1985. Multielement composition of the conodont species *Polygnathus xylus xylus* Stauffer, 1940 and *Ozarkodina brevis* (Bischoff and Ziegler, 1957) from the Upper Devonian of the Canning Basin, Western Australia. *BMR Journal of Australian Geology and Geophysics*, 9:133–147.
- NORRIS, A. W., T. T. UYENO, AND H. R. MCCABE. 1982. Devonian rocks of the Lake Winnipegosis-Lake Manitoba outcrop belt, Manitoba. *Geological Survey of Canada Memoir* 392, 280 p.
- NORTH, W. G. 1969. The Middle Devonian strata of southern Illinois. *Illinois State Geological Survey Circular* 441, 45 p.
- OLIVIERI, R. 1985. Middle and Late Devonian conodonts from Southwestern Sardinia. *Bollettino della Società Paleontologica Italiana*, 23: 269–310.
- ORCHARD, M. J. 1978. The conodont biostratigraphy of the Devonian Plymouth Limestone, south Devon. *Palaeontology*, 21:907–955.
- ORR, R. W. 1971. Conodonts from Middle Devonian strata of the Michigan Basin. *Indiana Geological Survey Bulletin*, 45, 110 p.
- RACKI, G. 1985. Conodont biostratigraphy of the Givetian/Frasnian boundary beds at Kostomloty in the Holy Cross Mts. *Acta Geologica Polonica*, 35:265–275.
- RAMSEY, N. J. 1969. Upper Emsian-Upper Givetian conodonts from the Columbus and Delaware Limestones and Lower Olentangy Shale of central Ohio. Unpublished M.S. thesis, The Ohio State University, Columbus, 79 p.
- RICKARD, L. V. 1984. Correlation of the subsurface Lower and Middle Devonian of the Lake Erie region. *Geological Society of America Bulletin*, 95:814–828.
- ROGERS, F. S. 1998. Conodont biostratigraphy of the Little Cedar and lower Coralville formations of the Cedar Valley Group (Middle Devonian) of Iowa and significance of a new species of *Polygnathus*. *Journal of Paleontology*, 72:726–737.
- SCHWIETERING, J. F. 1979. Devonian shales of Ohio and their eastern and southern equivalents. U.S. Department of Energy, METC/CR-79/2, 68 p.
- SEDDON, G. 1970. Pre-Chappel conodonts of the Llano region, Texas. *Texas Bureau of Economic Geology, Report of Investigations*, 68, 130 p.
- SPARLING, D. R. 1981. Middle Devonian conodont apparatuses with seven types of elements. *Journal of Paleontology*, 55:295–316.
- . 1984. Paleoecologic and paleogeographic factors in the distribution of lower Middle Devonian conodonts from north-central Ohio. In D. L. Clark (ed.), *Conodont biofacies and provincialism*. Geological Society of America Special Paper 196, p. 113–125.
- . 1985. Correlation of the subsurface Lower and Middle Devonian of the Lake Erie region: alternative interpretation. *Geological Society of America Bulletin*, 96:1213–1218.
- . 1988. Middle Devonian stratigraphy and conodont biostratigraphy, north-central Ohio. *Ohio Journal of Science*, 88:2–18.
- . 1992. On the age of the Hungry Hollow Formation. *Journal of Paleontology*, 66:339.
- . 1995. Conodonts from the Middle Devonian Plum Brook Shale of north-central Ohio. *Journal of Paleontology*, 69:1123–1139.
- STAUFFER, C. R. 1916. Relationships of the Olentangy shale and associated Devonian deposits of northern Ohio. *Journal of Geology*, 24: 476–487.
- . 1938. Conodonts of the Olentangy Shale. *Journal of Paleontology*, 12:411–443.
- . 1940. Conodonts from the Devonian and associated clays of Minnesota. *Journal of Paleontology*, 14:417–435, 441.
- STUMM, E. C. 1942. Fauna and stratigraphic relations of the Prout Limestone and Plum Brook Shale of northern Ohio. *Journal of Paleontology*, 16:549–563.
- SWEET, W. C. 1988. The Conodonta. *Oxford Monographs on Geology and Geophysics* No. 10, 212 p.
- UYENO, T. T. 1991. Pre-Famennian Devonian conodont biostratigraphy of selected intervals in the eastern Canadian Cordillera. *Geological Survey of Canada, Bulletin* 417, p. 129–161.
- . 1998. Conodont faunas. In *Middle Devonian brachiopods, conodonts, stratigraphy, and transgressive-regressive cycles*, Pine Point area, south of Great Slave Lake, District of Mackenzie, Northwest Territories. *Geological Survey of Canada, Bulletin* 522, Part II: 146–191.
- , P. G. TELFORD, AND B. V. SANFORD. 1982. Devonian conodonts and stratigraphy of southwestern Ontario. *Geological Survey of Canada Bulletin* 332, 55 p.
- WALLISER, O. H. 1991. Section Jebel Mech Irdane. In O. H. Walliser (ed.), *Morocco Field Meeting of the Subcommittee on Devonian Stratigraphy*, IUGS, 28 Nov.–4 Dec., 1991 Guidebook, p. 25–47.
- , P. BULTYNCK, K. WEDDIGE, R. T. BECKER, AND M. R. HOUSE. 1995. Definition of the Eifelian-Givetian Stage boundary. *Episodes*, 18:107–115.
- WEDDIGE, K. 1977. Die Conodonten der Eifel-Stufe im Typusgebiet und in benachbarten Faziesgebieten. *Senckenbergiana Lethaea*, 58:271–419.
- . 1984. Zur Stratigraphie und Paläogeographie des Devons und Karbons von NE-Iran. *Senckenbergiana Lethaea*, 65:179–223.
- WITTEKINDT, H. 1966. Zur Conodontenchronologie des Mitteldevons. *Fortschritte in der Geologie von Rheinland und Westfalen*, 9:621–651 [imprint 1965].
- WITZKE, B. J., B. J. BUNKER, AND F. S. ROGERS. 1989. Eifelian through Lower Frasnian stratigraphy and deposition in the Iowa area, central Midcontinent, U.S.A. In N. J. McMillan, A. F. Embry, and D. J. Glass (eds.), *Devonian of the world: Canadian Society of Petroleum Geologists Memoir* 14, v. 1, p. 221–250.
- ZIEGLER, W. 1959. *Ancyrolepis* n. gen. (Conodonta) aus dem höchsten Teil der Manticoceras-Stufe. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 108:75–80.
- . (ed.). 1973. *Catalogue of Conodonts, I. E. Schweitzerbart'sche Verlagsbuchhandlung, Stuttgart*, 504 p.
- . (ed.). 1977. *Catalogue of Conodonts, III. E. Schweitzerbart'sche Verlagsbuchhandlung, Stuttgart*, 574 p.
- , G. KLAPPER, AND J. G. JOHNSON. 1976. Redefinition and subdivision of the *varcus*-Zone (Conodonts, Middle-?Upper Devonian) in Europe and North America. *Geologica et Palaeontologica*, 10:109–140.

ACCEPTED 13 APRIL 1999

## APPENDIX I (LOCALITIES)

Material for this study was taken from the localities listed below.

(1) Sample S85CR9 (see Fig. 1) was taken during the summer of 1985 from the lowest 15 cm of the Prout Dolomite along a tributary of Pipe Creek, about 150 m west of the intersection of Campbell and Patrol roads, or about 2,390 m east of the west line and 510 m north of the south line of T6N, R32W, Erie County, Ohio (Kimball Quadrangle).

(2) Sample S87S1 (site SF on Fig. 1) was taken in the summer of 1987 from the basal 8 cm of the Huron Shale, just above the Prout Dolomite, in a drainage ditch on the John Schaeffer farm, 2.5 km due east of the intersection of state routes 4 and 113 in Strongs Ridge, Huron County, Ohio (Belleview quadrangle). Jeff Over collected the following Huron Shale samples from the same site in the summer of 1998: SF23VII98-01 and 02a, 0–0.05 m above base; SF23VII98-02b, 0.05–0.1 m; SF23VII98-03, 0.1–0.2 m; SF23VII98-04, 0.2–0.3 m; SF23VII98-05, 0.3–0.4 m.

(3) Sample S89I1 was taken during a Pander Society field trip in April of 1989 from the basal 17 cm of the Little Rock Creek Limestone (highly dolomitic here and called Traverse in current usage) as directed by R. W. Orr in the Delphi Limestone Co. north quarry, NE¼, SW¼, Section 19, T25N, R2W, northwest of Delphi, Carroll County, Indiana (Delphi Quadrangle).

## APPENDIX II (TAXONOMY)

This appendix employs an informal taxonomic approach, without regard for history of nomenclature, after the fashion of Klapper and Johnson (1980) and of Rogers (1998). It includes all illustrated species not found in the formal systematic section above; all synonymies and discussions are followed by figure designations.

*I. (=Icriodus)*

*I. excavatus* Weddige, 1984, p. 208, pl. 1, figs. 9–22 [see for further synonymy]; Bultynck, 1987, p. 158–159, pl. 6, figs. 21–25; Sparling, 1995, figs. 4.6–4.37. Figure 3.16.

*(I. expansus Group)*

*I. arkonensis* Stauffer, 1938, p. 429, pl. 52, figs. 10, 15; Sparling, 1995, p. 1129, fig. 5.1–5.7 [see for further synonymy]; Uyeno, 1998, p. 157, pl. 16, figs. 16–19. Figure 3.5.

*I. brevis* Stauffer, 1940, p. 424, pl. 60, figs. 36, 43, 44, 52; Stauffer, 1938, p. 430, pl. 52, figs. 11, 13; Sparling, 1995, p. 1129, fig. 5.38–5.46 [see for further synonymy]; Uyeno, 1998, p. 157, pl. 12, fig. 21, pl. 16, figs. 29–31. Figure 3.7.

*I. difficilis* Ziegler and Klapper in Ziegler, Klapper, and Johnson, 1976, p. 117–118, pl. 1, figs. 1–7, 17 [see for further synonymy]; Weddige, 1977, p. 292, pl. 2, fig. 36; Uyeno in Uyeno et al., 1982, p. 32, pl. 5 figs. 5–9, 18–20; Bultynck, 1987, pl. 9, figs. 25, 26; Uyeno, 1991, pl. 5, fig. 4; Uyeno, 1998, p. 157–158, pl. 16, figs. 1–15, 20, 21. Figure 3.6.

*I. expansus* Branson and Mehl, 1938, p. 160–161, pl. 26, figs. 18, 19; Sparling, 1995, p. 1131, fig. 5.26–5.37 [see for further synonymy]. Figure 3.4.

*(I. regularicrescens Group)*

*Icriodus janeae* Sparling, 1995, p. 1131, fig. 6.3–6.11. Figure 3.8, 3.9.  
*Icriodus obliquimarginatus* Bischoff and Ziegler, 1957, p. 62–63, pl. 6,

fig. 14; Sparling, 1995, p. 1133–1134, fig. 6.24–6.27 [see for further synonymy]. *Discussion*.—Finding this species in the basal Little Rock Creek as the only representative of its genus is unusual. Figure 3.11, 3.12, 3.15.

*L. (=Latericriodus Müller, 1962)*

*L. latericrescens latericrescens* (Branson and Mehl), 1938, p. 164, pl. 26, figs. 30–32, 34, 35; Klapper and Ziegler, 1967, pl. 10, figs. 4–9, pl. 11, figs. 1–5 [see for synonymy to 1965]; Seddon, 1970, p. 53, pl. 4, figs. 4–7; Orr, 1971, p. 36–37, pl. 2, figs. 10–13, 18, 19; Orchard, 1978, pl. 109, figs. 6, 11; Bultynck, in Bultynck and Hollard, 1980, p. 40, pl. 6, fig. 18; Uyeno in Uyeno et al., 1982, p. 32, pl. 4, figs. 27–30; García-López, 1987, p. 83–84, pl. 4, figs. 10–16; Bultynck, 1987, pl. 9, fig. 24. Figure 4.5–4.7.

*P. (=Polygnathus)*

*P. linguiformis klapperi* Clausen, Leuteritz, and Ziegler, 1979, p. 32, pl. 1, figs. 7, 8; Ziegler and Klapper in Ziegler, Klapper and Johnson, 1976, p. 123–124, pl. 4, figs. 3, 12, 14, 24; Klapper in Ziegler, 1977, p. 465, *Polygnathus*-pl. 10, figs. 5, 9, 10 [see for extensive synonymy]; Bultynck in Bultynck and Hollard, 1980, p. 44, pl. 7, figs. 2–7, 9; Uyeno in Norris et al., 1982, p. 74–75, pl. 34, figs. 20–22, pl. 35, figs. 13–15; Klug, 1983, p. 90, fig. 11 R–T; García-López, 1987, p. 92–93, pl. 13, figs. 11, 12; Uyeno, 1998, p. 162–163, pl. 13, figs. 22–27, pl. 14, figs. 1–11 [see for discussion of variability and related taxa]. *Discussion*.—Mature specimens of this subspecies range much larger than those of *P. l. linguiformis*. Figure 4.1, 4.2.

Permission granted : to reprint this article, from Timothy Hazen,  
Associate Editor, Paleontology Society; and Dale Sparling, Author

## RECOGNISING FOSSIL MAMMAL TEETH

Ralph Molnar. Queensland Museum, P.O. Box 3300 South Brisbane, Qld. 4101

Base drawings: Chris Glen, P.O. Box 399 Noosa, Qld. 4567

### INTRODUCTION

Most vertebrate fossils found in Australia are mammals, so its no surprise that most of those found by amateurs are mammals. The teeth are often the most resilient parts, and hence the most likely to be found, however, teeth are among the more difficult fossils for amateurs - not to mention some professionals - to identify. Although mammal teeth are the most widely used way of identifying fossil mammals, because the variety of tooth forms makes them diagnostic, the variety of different forms also makes learning which teeth belong to whom difficult. Furthermore, there is (almost) no information on identifying fossil mammal from bones (other than jaws with teeth), so we'll concentrate on recognising the different forms from their teeth. It is worth mentioning the one book available on identifying fossil mammal from bones, Merrilees & Porter, covers fossil mammal from Western Australia, but it is useful for the rest of the country as well. This article aims to introduce the fossil teeth of mammals, so that they can be recognised and identified, we shall show how to recognise the different kinds of teeth in the different kinds of Australian mammals. Only representative species are included, so that hopefully the reader will be able to recognise a bandicoot tooth, but not necessarily identify it as from a Northern Brown Bandicoot. Fishes and tetapods, other than mammals, will be mentioned but not discussed.

The forms of the teeth, especially the molers, of placetal mammals are unique to each species. Historically, teeth have played a large role in identifying and studing fossil mammals, as a result, teeth have received prolonged and detailed study, and a large and very complicated terminology for the features of the teeth have been developed. Not only are many of these terms incomprehensible to most amateurs, they are incomprehensible to about 95% of professionals (those who don't work with fossil mammals) as well. Luckily, one dosen't need to know all the term to be able to recognise the teeth.

### THE EVOLUTIONARY BACKGROUND OF MAMMAL TEETH

The earliest vertebrate teeth, those of fishes, are basically simple cones, we shouldn't be misled, however, into thinking that because these are the earliest and simplest of tooth forms, that all fishes have such teeth. Modern fishes have had just as long an evolutionary history as modern mammals, and just as much time to have developed complicated teeth, and some did. Some dark teeth are flattened and triangular, serrated like knives, and other fish have flat cushion, or button-like teeth used to break mollusc shells, and there are also the crested, almost comb-like teeth of lungfish.

Originally, fish teeth were much the same in form regardless of where they were placed in the mouth and this is still the case in many fishes. Others have evolved different tooth form in different parts of the mouth, so that some fish jaws can be (and have been!) mistaken by the general public for those of cats, or even humans. The lineage that led to mammals evolved more complex teeth very early on. Initially they were of different sizes in different parts of the jaw, but then they became different in forms as

well (Fig.1). As recently as the 1960's (some) paleontologist thought that all other lines of land dwelling vertebrates either lost their teeth (as did tortoises and birds) or retained simple, conical teeth of much the same form and size throughout the jaw. This belief was shattered by the discovery, in South Africa, of a dinosaur (*Heterodontosaurus*) with almost as many different forms of teeth as modern mammals, and similarly arranged in the jaws. It then turned out that some lizards and crocodilians also had teeth of different forms in different parts of their jaws - this had been known for some time (since the late 19th century), but only by the specialist studying those particular lizards or crocodilians. Some of these teeth were so similar to mammal teeth that there is an instance of Cretaceous crocodilian teeth (*Candidodon*) having been mistaken for mammal teeth. This greatly amused paleontologist studying fossil crocodilians, but those who work on fossil mammals weren't equally amused.

Fish and reptiles continually replace their teeth, which is why where fossil crocodilian teeth are found at all, they tend to be common, somewhere during the evolution of the differentiation of their teeth, mammals gave up this ability (and hence paved the way for the dental profession). Mammals replace most of their teeth only once, the first set are known as deciduous or milk teeth, and the second as permanent teeth, molars are the exception, they are not replaced. It has been thought that this loss of "throw away teeth" was the result of the evolution of the patterns on the crowns, and the corresponding precision in which upper and lower teeth must meet (occlude) in order to feed efficiently. This, in turn, is related to the evolution of a relatively high metabolic rate and constant body temperature.

Another feature of mammalian teeth which evolved early in their ancestry and may well have contributed to their evolution of a 'precision bite' and the complex patterns of the molar crowns, was the tooth socket. In fish and lizards the teeth often simply attach to the bone of the jaw, in mammals (and dinosaurs, crocodilians and even some fish) the teeth have roots that are set in distinct and often deep sockets. The teeth are held by connective tissue, which may allow some very slight movement of the crowns when the teeth come together, so contributing to the precise meeting of the teeth.

So, although mammals generally have developed the differentiation of their teeth to a fine degree, other vertebrates also have different forms of teeth in different parts of the jaws. However, most of these other vertebrates did not inhabit Australia, or at least have not yet been discovered, so fossil mammalian teeth found in Australia are readily recognised as being from mammals.

#### WHERE DOES THE TOOTH COME FROM: DIFFERENT KINDS OF TEETH IN THE JAW

In most mammals there are four different kinds of teeth (Fig.1) those at the front are simple, often bluntly blade-like in form, these teeth, the incisors, usually cut the food for eating. Just behind these are the canines, also called eyeteeth or fangs, these are often sharp, slightly curved cones in form, the canines may be used for killing prey, in carnivores and insectivores, and are often used in social displays. Canines may be lost in herbivorous animals.

Behind the canines are the cheek teeth, these take two forms, premolars and molars, the premolars are located between the canines and molars. Cheek teeth are more complex in form than incisors and canines as they have two or more low projections, or

peaks, that arise from the biting surface, these projections are called cusps. Molars are the teeth most widely used in identifying fossil mammals, so we will look mostly at these and return to the others only where the molars are not sufficient, or where there is some particular interest to the other teeth.

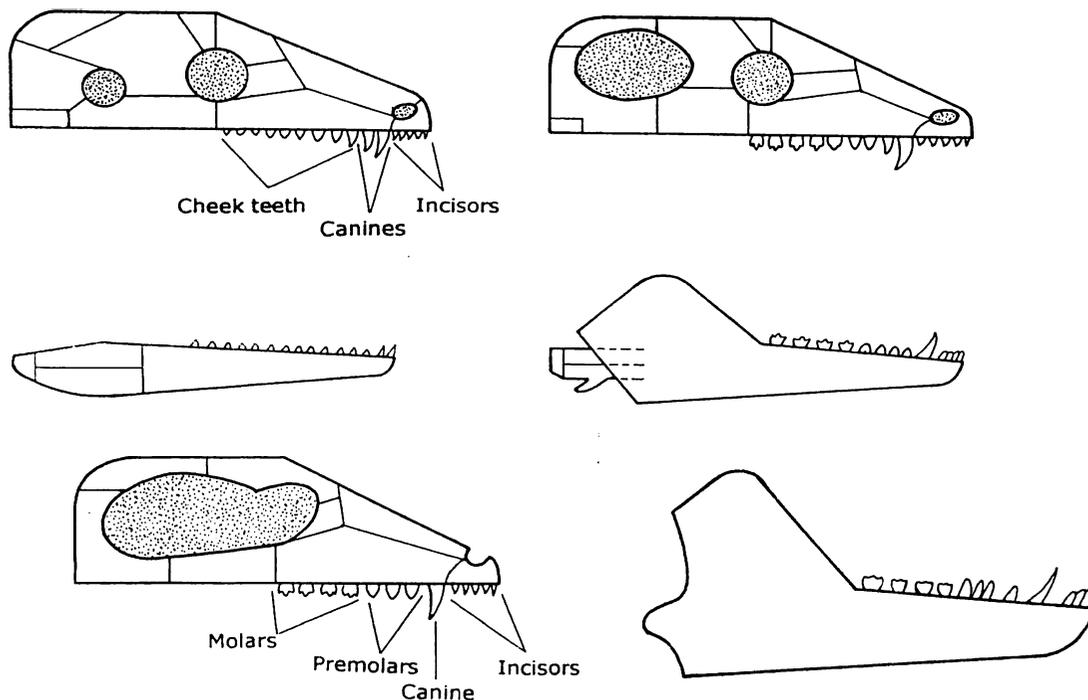


Figure 1. Schematic drawings showing the evolution of the teeth in mammals. In primitive mammal-like reptiles (pelycosaur), at top left, the teeth differed mostly in size, their form being pretty much alike throughout the tooth rows, but there were the beginnings of the development of incisors and canines, the remaining teeth are called cheek teeth. In later, more derived mammal-like reptiles (therapsids) at top right, the teeth developed four forms, those of the incisors (at the front), canines, premolars and molars (at back). This arrangement was maintained in the mammals themselves, bottom. Figure not to scale

### MAMMALIAN TOOTH (MOLAR) FORM

Paleontologists have long sought to make out the history of the evolution of mammalian teeth. Early in the twentieth century, they believed that the teeth of primitive therians (placentals + marsupials) provided a key to understanding the variety of forms of mammalian molars. Although the actual evolution appears to have differed somewhat from what was thought at the time, this scheme is still useful in learning to recognise and interpret molars.

Looking at the upper molars, of an early therian mammal, from its biting (occlusal) surface - its business end so to speak - we can see its triangular form. It bore three cusps, one at each angle, these are the paracone, metacone and protocone (Fig.2). This is the simple, basic form to which all other mammalian upper molars are related. Lower molars are a bit more complicated, they have a triangle with a 'trailer' behind, the talonid (Fig.2), the triangular portion, the trigonid, bears three cusps just like the upper molar, but to distinguish them from the upper cusps they are called the paraconid, metaconid and protoconid respectively. The two cusps of the talonid, which have no counterparts on the upper molar, are the hypoconid and entoconid (Fig. 2). The forms of the upper and lower molars of 'recent' (Cenozoic) mammals can

be related to these, by the enlargement or reduction, or the addition (Fig.2) of subtraction, of cusos. Of course, the actual forms of the teeth are much more complex, with additional smaller cusps, 'valleys', ridges, etc., but a knowledge of the basic cusps goes a long way toward learning to identify and recognise mammal teeth.

In placental mammals and the carnivorous marsupials, the upper and lower molars differ in form. In most advanced (i.e., Plio-Pleistocene & Recent) marsupials the difference between upper and lower molars (and even premolars) is reduced, so that the tooth forms are basically similar, but some differences can be seen.

In identifying fossil mammal teeth, it should be remembered that:

1. tooth form varies:
  - . from species to species
  - . also from tooth to tooth in the jaw, and
  - . sometimes between the deciduous and permanent teeth.

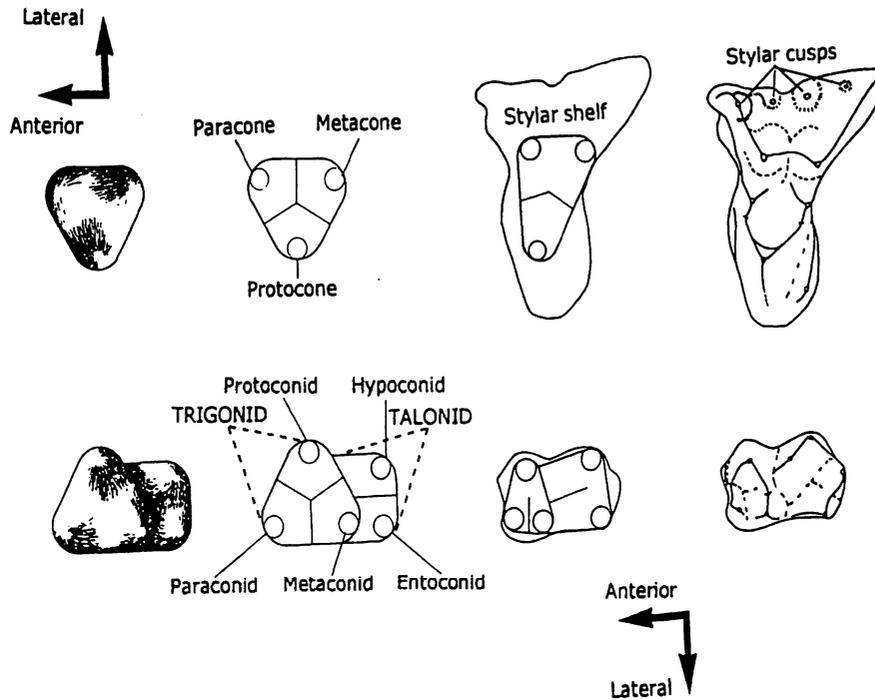


Figure 2. the scheme for identifying features of the crowns of primitive mammalian molar teeth. The molars are seen from the biting or occlusal surface, upper molars on top row, lower molars on bottom row. At left are the schematic forms showing the triangular, tricuspid form of the upper and the trigonid and talonid of the lowers with five cusps, three on the trigonid and two on the talonid. To the right of these are diagrams of these schematic forms with the cusps represented by small open circles and labeled and the 'valleys' between them represented by thin lines. For comparison, far right, are some actual Cretaceous mammal teeth, from *Gypsonictops*, a placental from North America. The images to the left of these show how the schematic pattern is applied to actual teeth. Although you can make out the pattern seen at left, you can also see that the occlusal surface can be a lot more complex. Some of the complicating features - additional cusps along the outer edge of the tooth (the styler cusps) and the shelf (styler shelf) that holds them - are labeled. Figure not to scal

2. that tooth form is not always adequate for identifying some marsupial species. In other words, there are marsupials - the Mountain possum (*Trichosurus caninus*) and the Brushtail (*Trichosurus vulpecula*), for example - whose teeth don't differ.
3. Although the front teeth, the incisors, are sometimes useful for identification (especially for kangaroos), it is the cutting teeth (premolars) and especially the grinders (molars) that are most useful.

Two marsupial groups, marsupicarnivores and bandicoots, have teeth that don't differ greatly from the basic pattern.

### MARSUPICARNIVORES

The molars of carnivorous marsupials (the marsupicarnivores) are basically similar to this basic mammalian pattern. Marsupicarnivores include the quolls (*Dasyurus*, *Dasyuroides*), thylacines (*Thylacinus*) Tasamanian devils (*Sarcophilus*) and so-called marsupial mice, like *Antechinus* and *Planigale*. All of these, except thylacines, are included in the dasyurids. The small 'mousy' forms show the basic pattern most clearly, but even thylacines and devils have the same fundamental forms, this form is probably close to that of the teeth of the ancestral marsupials.

*Antechinus* is a small animal, and hence has small teeth, they are so small, only a few millimetres across, that they would usually only be recovered by sieving. Here we will use *Antechinus* as the example of a dasyurid, or basic marsupicarnivor molar. The upper molars are triangular in shape (Fig.3, top), like the basic toothform described previously, however, the match is not perfect, dasyurids have a shelf along the outside of the tooth crown with low cusps on it. So it is the inner portion of the crown that corresponds to the basic molar tooth form. The protocone is reduced to a small cusp, about the size of those on the 'outside' (styler) shelf (called styler cusps). The final, back molar has this basic form, but much modified, with a smaller styler shelf and a smaller metacone (Fig. 3, top, at left). the lower molars are closer to the basic form (Fig. 3 bottom). The three cusps of the trigonid are the paraconid, protoconid and metaconid, and those of the talonid are the entoconid and hypoconid.

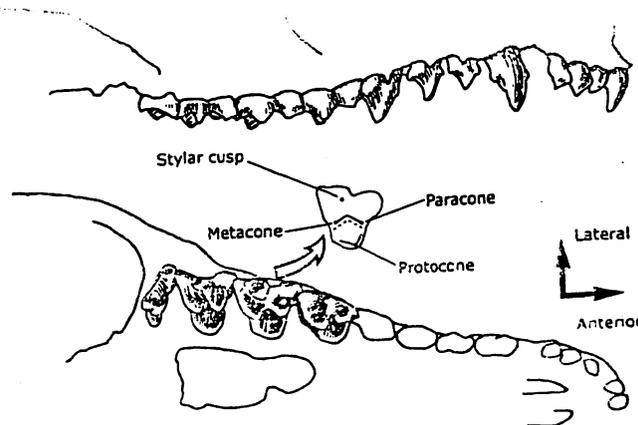


Figure 3. The teeth of a living Atherton, *Antechinus godmani*, based on an actual specimen. The uppers are shown at left in both lateral and occlusal view, and lowers at right in the same views, one molar from both upper and lower jaws is diagrammed to point out the prominent features. Major cusps are indicated by dots, major ridges by solid lines and major 'valleys' by dashed lines. The upper molars have the basic triangular, tricuspid form medially, with a styler shelf and one prominent and several smaller styler cusps, except for the last (at left). The lower molars have a prominent talonid, only slightly lower than the trigonid. The paraconid is reduced (and hence not indicated on the diagram) and the protoconid is the largest cusp. Figure not to scale.

In two kinds of dasyurids, the teeth somewhat deviate in form from those described previously.

The Tasmanian devil, *Sarcophilus*, has developed a powerful bite and accordingly modified its teeth. In the uppers, the outside styler shelf is very reduced giving a form closer to the basic form (Fig. 4 top). In the lowers, the talonid has also been reduced and the three basic cusps re-aligned to form an (almost) straight line Fig. 4, bottom). Its teeth are generally more robust than the smaller, more graceful teeth of the other dasyurids.

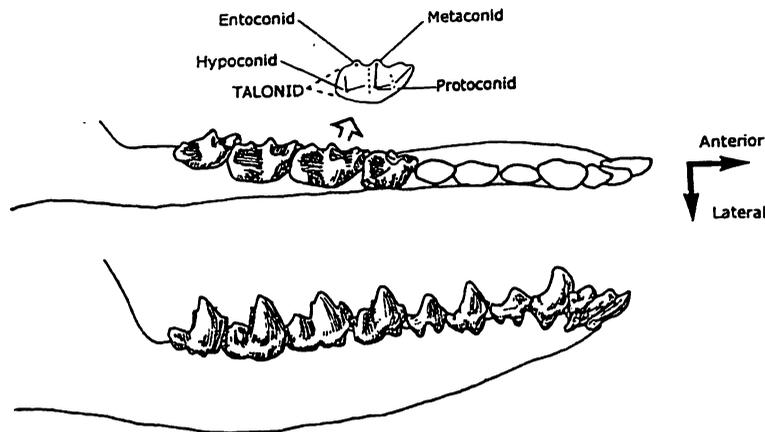


Figure 4. The teeth of a fossil devil, *Sarcophilus lanarius* this may be the same as the living *Sarcophilus harrisii*. Again this is based on actual specimens in the Queensland Museum ( The upper at left, from Rockhampton and the lowers, at right , from the eastern Darling Downs) to show what actual fossil teeth may look like. The uppers especially are somewhat worn and broken with the tips of some cusps of the lowers broken as well. The styler shelf is reduced on the upper molars and the metacone is the most prominent cusp. In the lower molars the talonid is much reduced and the protoconid the most prominent cusp. Not to scale

Thylacine teeth are not common, but they do turn up from time to time, in fact, they probably aren't much less common than devil or dasyurid teeth. The upper molars of *Thylacinus* resemble dasyurid teeth, but with a smaller styler shelf and smaller protocone, and the protocone and metacone are relatively closer together than in other dasyurids. Again, the last molar is modified like those in other dasyurids. In the lowers, the protoconid is quite strongly developed compared to the other cusps and dominates the tooth, so the teeth appear rather different from those of smaller dasyurids.

## BANDICOOTS

The molar teeth of the primitive (plesiomorphic) bandicoots, Such as *Peroryctes*, don't differ much from the basic pattern with the upper looking much like those of typical dasyurids. Viewed face-on, the upper molars are roughly triangular, most of them with the inner (lingual) angle truncated - only the last is really triangular. These carry the usual set of three cusps, but some have a fourth, the hypocone, adjacent to the protocone, they also have a Styler shelf, however these forms inhabit New Guinea, not Australia.

The Australian bandicoots, have teeth that differ from this basic pattern, here we show *Isodon*, the Short-Nosed Bandicoot (Fig. 5). In occlusal view the upper molar looks like

not one but two triangles joined together, this pattern arises from the development of prominent cusps along the outside margin of the crown, which rival the paracone and metacone in size. The protocone is very small and is part of a low shelf along the inner face of the crown, this gives the molars a squarish or quadrangular form. (In *Macrotis*, the Bilby, the shelf is not developed, but the protocone is still small, an inside adjacent to the paracone).

The lower molars of bandicoots, viewed face-on, also look like two triangles joined at one angle (Fig. 5). Near each angle of the joined triangle arises a sharp cusp. The lower molars of bandicoots looks like the basic tooth pattern for therian lower molars, however, the paraconid is small, and the cusps of the talonid, the entoconid and hypoconid, are as large as the metaconid and protoconid.

We will look at kangaroo, diprotodont, wombat, possum and koala teeth in the future parts of this article. Finally, remember that teeth get worn, so that the patterns described here may become obscure, or even if the animal had a long life - obliterated. In that case it becomes very difficult to identify the teeth.

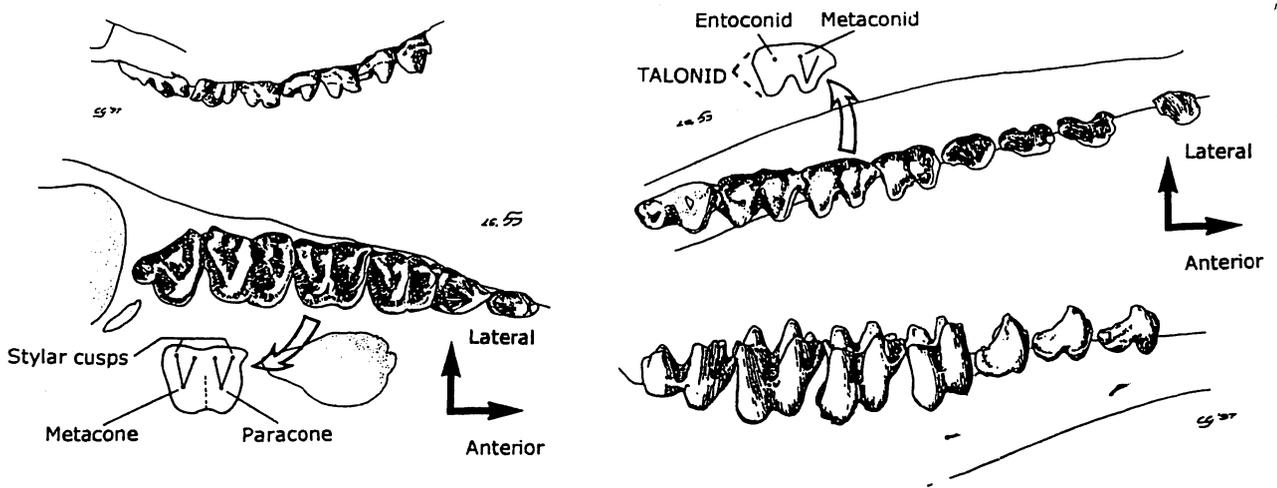


Figure 5. The teeth of a Northern Brown Bandicoot, (*Isodon macrourus*), from a specimen that lived near Cairns. Australian bandicoots show a more derived tooth from that of marsupicarnivores. The uppers (left) have a reduced protocone and a marked 'valley' that disguises the basic triangular pattern, in addition there is a set of prominent stylar cusps, of about the same height as the paracone and metacone. Thus the cusps and ridges of the upper molars form almost a W-like pattern. The lower molars (right) are closer to the basic scheme, the talonid is well developed and the entoconid and metaconid are about as high. Not to scale.

### DIPROTODONTANS

Diprotodontans were the largest of the marsupials, so it is no surprise that their teeth were large. The molars are also easy to recognise, at least if they are more or less complete and not broken. Upper and lower molars are also pretty much the same in form, both have two large transverse crests, known as lophs (technically speaking), those on the lower molars are lophids. The combination of large size and two lophs mark out diprotodont molars, and makes them easy to recognise, those of *Diprotodon* are specifically characterised by the largest.

This form of molar, with two lophs, was known in Europe as being characteristic of an extinct group of elephants, the deinotheres. Deinotheres were unusual as elephants in that the lower, rather than upper, incisors were developed into tusks. When the first teeth of *Diprotodon* went to England, in the 1840's, they they were taken to be the teeth of an Australian elephant, a deinotheres.

Figure 1 shows the molars of *Diprotodon* where the lophs are not worn. When chewing, the teeth are moved past each other in a fore-to-aft fashion (and back again), so the lophs cut up the plant material as they moved across each other. In old individuals, however, and in those that fed on gritty or abrasive

vegetation, the molars became worn, and in some cases very worn. The amount of wear can reveal both the age of the individual and whether fresh fodder was available or just dry plant material picked up from the ground, including sand and grit. Worn molars usually still retain the bases of the lophs and so can be recognised (Figure 1).

The premolars are rather smaller than the molars, and roughly triangular in occlusal view, the different species (probably) can be distinguished by the form of their premolars. These are actually the third premolars, but the anterior two have been lost. We will look at some of the premolars, just to show what diprotodont premolars look like, but premolars are found much less often than the molars.

There were several different kinds of diprotodontans during the Pliocene and Pleistocene, of which the Pleistocene *Diprotodon*, at about 1-2 tonnes, is the largest. But because the taxonomic relationship of the diprotodontans remain unstudied (or, anyway, unpublished) and because the consensus is that many of the current names are incorrect, we shan't - indeed, can't - go into how the diprotodontids differ from one another. Suffice to say that although *Diprotodon* is the largest diprotodontid, there are also small species of *Diprotodon*. However, the upper premolars of *Diprotodon* has a U-shape pattern of crests, when unworn, this is distinctive, so can be used to recognise *Diprotodon*, large or small.

Finally, since the origin of the lophs remain unknown, they may have originated in at least two ways (given in Archer, 1984). The identification of the cusps given here (Fig.2) shouldn't be taken too seriously.

There is another kind of diprotodontan that has not been mentioned, these are the palorchestids, and these are found less often than forms like *Diprotodon*. For reasons that will become apparent, we will discuss these after the Kangaroos.

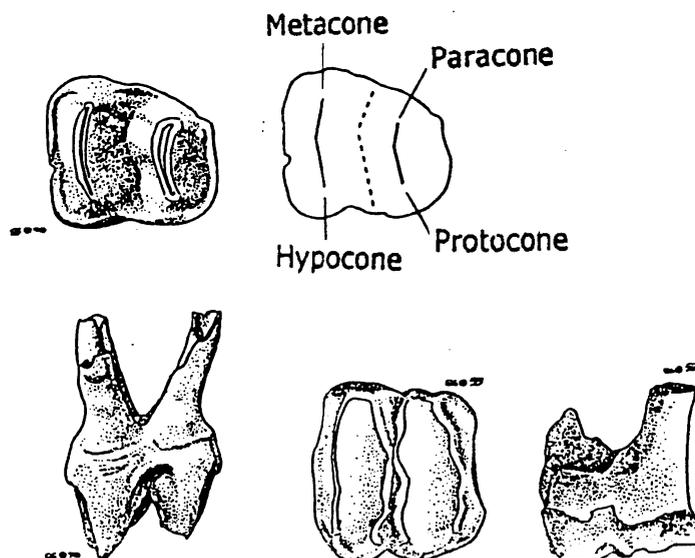


Figure 1. Two molars of diprotodontans. The unworn molar at left top and bottom is that of *Euryzygoma dunense*, and the worn molar at bottom middle and right is that of *Diprotodon optatum*. Both are based on Queensland Museum specimens, but unfortunately the museum did not have a sufficiently well preserved tooth in either a skull or jaw to draw. The characteristic and easily recognisable double lophs can be easily seen in the *Euryzygoma* tooth, this tooth may be the last (fourth) upper. Even when worn, as in the *Diprotodon* tooth, they are pretty obvious. The upper and lower molars of diprotodontans are very similar, and - since these are isolated teeth - it isn't clear whether they were uppers or lowers. Incidentally, diprotodontan teeth seem often to be more worn than fossil kangaroo teeth, suggesting that the diprotodontans lived to older ages and suffered less risk of dying young, than kangaroos. Not to scale

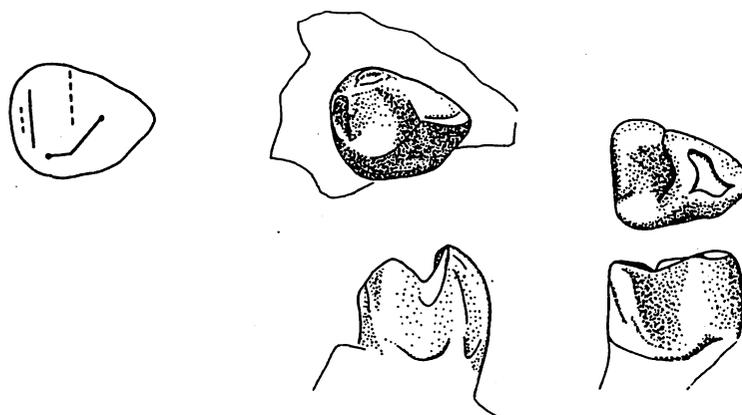


Figure 2. Diprotodontan premolars; a complete premolar of *Diprotodon*, center top and bottom, and a worn premolar of *Zygomaturus*, right top and bottom, both are based on Queensland Museum specimens. The diagram shows the ridges and cusps, but the identification will be discussed later. These premolars are quite different from those of Kangaroos, as shown in fig. 3 & 4.

### KANGAROOS

Kangaroo (macropodid) molars look roughly like those of diprotodonts, but are smaller. The Pliocene and Pleistocene forms show a similar [attern of two transverse lophs, but tht lophs are joined by a lower ridge, known as the crosslink or midlonk (Fig.3). The teeth of other marsupials do not have crosslinks, although in diprotodonts a ridge projects from the hypoconid diagonally toward the metaconid, which it dosen't reach (this ridge is technically termed the crista obliqua, the oblique crest). In the specimens of *Protemnodon anak* used for Figures 3 and 4, The teeth at the back of the tooth rows in each are unworn whilst those at the front have been worn. This is because the molars at the front erup before these ar the back, that just behind the premolars first, then that adjacent to it, etc., until the rear one erupts last. so the front molars have been exposed to wear for a longer period. In the lower jaw, the last molar, in fact had not yet erupted when the animal died, thus one can tell that both the animal from which the upper teeth are derived was probably a young adult and that from which the lower jaw was found had not reached maturity. Teeth can tell us about mammals than simply which they are.

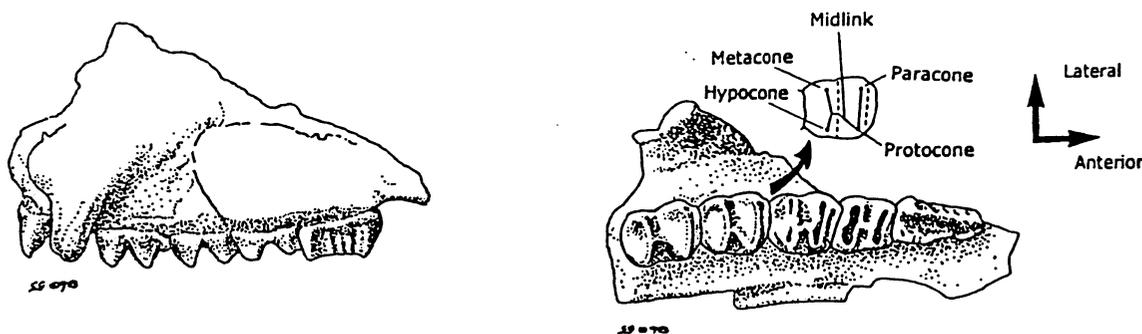


Figure 3. At left, teeth of a fossil macropodine kangaroo, *Protemnodon anak*, based on a specimen in the Queensland Museum. one of the unworn molars (the third) is diagrammed to show the prominent features. Positions of the major cusps are marked by dots, major ridges (lophs) by thick lines, minor ridges by thin lines and 'valleys' by dashed lines. As as in part 1, the toothrow is shown in both lateral (left) and occlusal (right) views. Both upper and lower molars are characterised by having two parallel, transverse ridges, these ridges are joined by the (roughly) transverse midlink (or crosslink). The upper molars resemble those of diprotodontans, in having two molars of any Plio-Pleistocene diprotodontan. Note the premolar at the right.. Not to scale

Kangaroo (macropod) species, like diprotodont species, are often distinguished on their premolars, not their molars. The teeth of more primitive macropods - betong and protoroos among others - are more similar in form to those of possums and koalas( to be discussed later. The molars of early kangaroos, such as those from Riversleigh, haven't (yet) developed a crosslink, and look mush like very small diprotodont teeth.

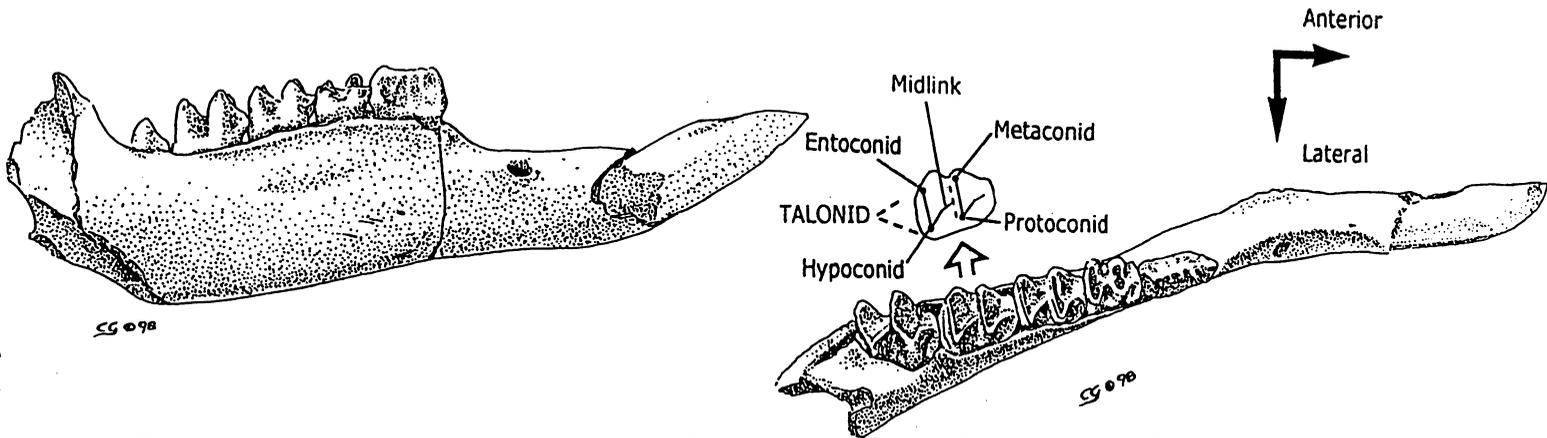


Figure 4. The lower teeth of the macropodine kangaroo, *Protetnodon anak*, based on another specimen in the Queensland Museum. The layout of the drawing and features diagrammed are as in Fig.3. the lowers differ from the uppers (and those of diprotodontans) in having a distinct cingulum in front of the anterior loph. (this is clearly shown in the figure but not labeled: it is labeled in figure 6) The basic form of the crown, two lophes joined by the midlink, is shown in the diagram of the third molar. Note the premolar at the right of the toothrow, and the incisor at the front of the jaw. Not to scale

The Plio-Pleistocene macropods come in two groups, The macropodines (grazing kangaroos) and the Sthenurines (browsing kangaroos). *Protetnodon anak* is a macropodine as are all modern kangaroos, the sthenurines have all but become extinct (well maybe, Tim Flannery thinks that *Lagostrophus*, the Banded Rat Kangaroo, is a surviving relative of the sthenurines). Sthenurines, the later ones at any rate, tended to have deep snouts and some had quite short skulls, almost as deep as they were long, they also developed only a single toe in the hind feet. The sthenurines were the biggest kangaroos, *Procoptodon* reached a height of three meters.

In terms of teeth, those of sthenurines were like th teeth of macropodines, but with 'frills' added (Figures 5&6, there were the same two parallel, transverse lophes, and crosslink, but in addition there were ridges on the lophes, mostly on the backs. These look like a bad case of wrinkles on the unworn molars and formed little loops and bands on worn teeth.

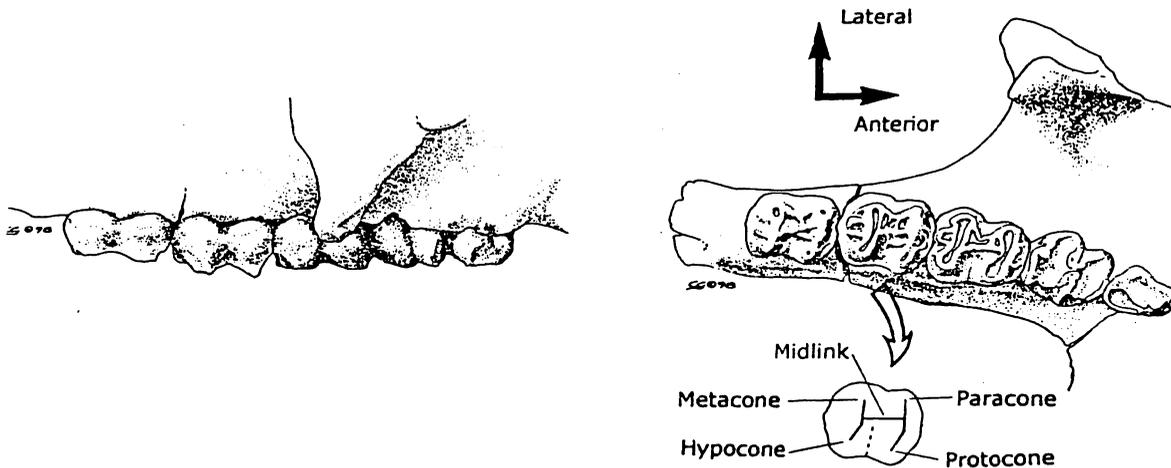


Figure 5. The cheek teeth of the sthenurine kangaroos were different from those of macropodine kangaroos such as *Protetnodon*. The teeth in this figure of the upper teeth of the sthenurine *Procoptodon pusio* (based on a Queensland Museum specimen). At right the much more ornamented form of the molars is clearly seen here, especially lateral to the midlink. The teeth appear more bulbous than those of macropodines and the lophes are less obvious in lateral view, the last molar (left) is almost entirely unworn, with only a little wear at the cusps. The teeth become more worn towards the front (right), with considerable wear on the first molar and premolar. Not to scale.

In basic form, sthenurine molars are like those of macropodines, but they have these extra structures giving them a more ornate form, also, their molars have a more bulbous, rounded appearance. When the lophes of sthenurines are worn, the worn surface has a slightly figure '8' shape, unlike those of macropodines.

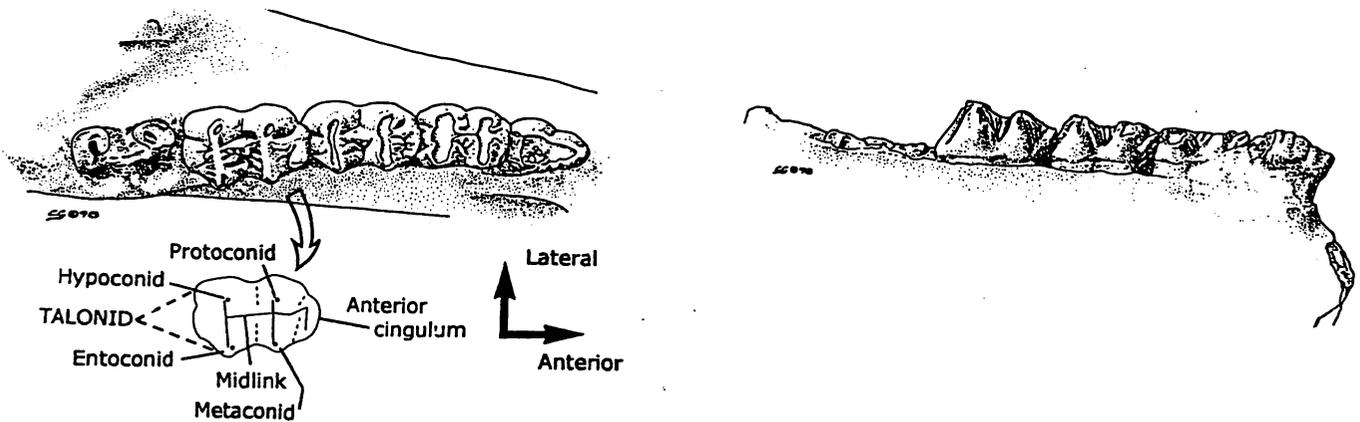


Figure 6. The lower cheek teeth of a related sthenurine, *Procoptodon rapha* (based on a QM specimen). Here, too, the bulbous and more intricate form of the molar is clear, the last molar (left) is broken, with the crown lost entirely, only the broken surface of the roots is seen, the next molar is almost unworn. As in Fig. 5, The teeth become more worn towards the front (right). Not to scale

### PALORCHESTIDS

There is only a single palorchestid in the Pliocene and Pleistocene of Australia, *Palorchestes* itself, although there were several earlier genera. The teeth of *Palorchestes* have double lophs, like those of diprotodontans, but also midlinks (Figure 7) like those of kangaroos, thus it is no surprise that when they were discovered they were taken to be the teeth of giant kangaroos. This was reflected in their name *Palorchestes*, 'the leaping one of ancient times', this might seem inappropriate, but since a name is a name, a label, any name (that's polite) is equally appropriate: just as long as it doesn't apply to two different organisms. It wasn't until the discovery of post-cranial remains that it was realised *Palorchestes* was a quadruped and not a kangaroo. Palorchestids were unusual animals, with large claws and a snout that suggests they may have had a short trunk, like that of a tapir.

Palorchestid teeth are basically like those of (other) diprotodontans, but with a midlink, they lack the ornament of sthenurine molars and are larger than macropodine molars.

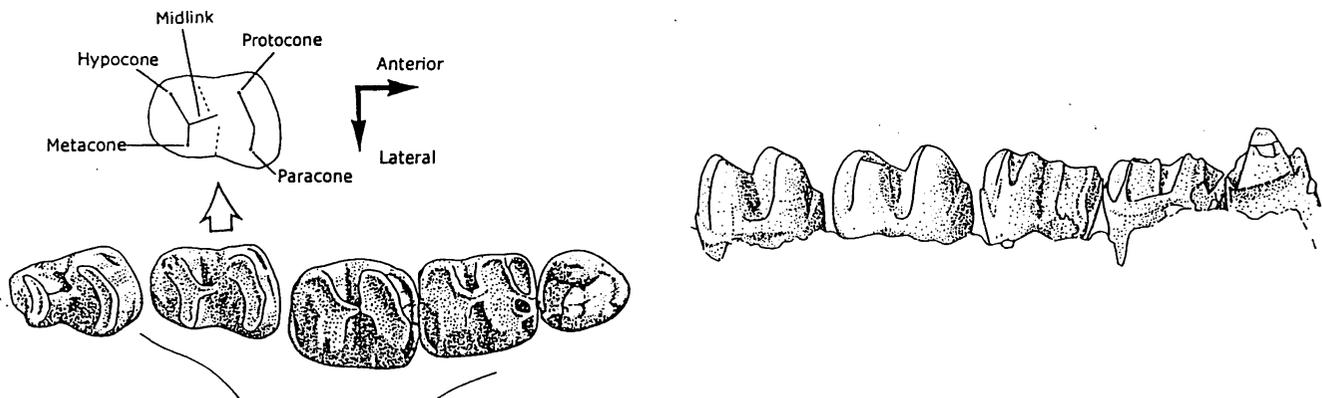


Figure 7. The right (cheek) teeth of *Palorchestes azael* from a Q M specimen (here) drawn from a cast. The reason why these teeth were first thought to be from a giant kangaroo can be seen. Like those of kangaroos, they have the two prominent lophs joined by a crosslink, note that the premolar (at the right end of the toothrow), however, is quite different from that of *Protemnodon anak* (in Fig.3). The teeth at the back of the toothrow (left) have little wear, but they are increasingly worn toward the front (right), and the first two molars are broken laterally. This specimen - the bone not the teeth - is slightly crushed, so that the toothrow is offset between the second and third molars. Not to scale

Next we will look at wombat, possum, and koala teeth, These can all be found in most Pliocene and Pleistocene fossil deposits, but their smaller size makes them more rare than diprotodontan and macropod teeth.

## INTRODUCTION

Diprotodontans and macropodids were the only large marsupials, and of these, some diprotodontans were much larger than any kangaroos. Some extinct representatives of the other marsupials, however, were larger than their relatives living today, there were giant possums, giant koalas and especially, giant wombats. Of these, the giant wombats were the largest: If they dug burrows, these burrows would have been about 35-40 cms in diameter.

The giant ringtail possum, *Pseudokoala*, was estimated to weigh 9-10 kg, and the giant koala, *Cundokoala*, had molars approximately 150- 175% as long as those of Modern koalas. Whether the whole animal was that much larger than present koalas, or whether it had unusually large teeth, We don't know. In these two cases, the larger forms were not very closely related to their modern relatives. For kangaroos, the the larger forms were more closely related : some paleontologists think that the Pleistocene *Macropus titan* was simply a larger race of the Eastern Grey Kangaroo, *Macropus giganteus*. Why these larger forms - whether races, species or genera - disappeared is still a major problem of paleontology. Larger mammals have a lower metabolic rate than smaller ones, so that one horse requires less food to keep going than one horseweight of cats. Larger mammals are also better suited for cold climates, in that they lose heat less rapidly, on the other hand, if food is scarce, then there might not be enough to support growth to the size of a horse, or a *M. titan*. The only thing we can say is that their disappearance had something to do with environmental change.

The fossil teeth of animals we are looking at in this part are not ascommonly found as those of diprotodontans or kangaroos. This is partly because they are smaller, and so less obvious, but also in some areas, such as the easternDarling Downs (Queensland), fossils of koalas and possums are absent - for reasons we do not yet understand. This is especially puzzling , as fossils of koalas have been found at Gore, just west of Darling Downs. Fossil wombat teeth, on the other hand, are more frequently found.

Carnivorous animals are always less abundant than their prey, so it is no surprise that their fossils are also less commonly found. There are however some exceptions to this rule, the famous La Brea Tar Pits in Los Angeles (U.S.A.), and the Cleveland-Lloyd dinosaur quarry in Utah (U.S.A.) are deposits in which the fossils of carnivorous animals - sabrecats and dire wolves at La Brea and *Allosaurus* at Cleveland Lloyd - are more abundant than those of the herbivores on which they (presumably) preyed. But such localities are uncommon, and no instances at any sites yielding land dwelling vertebrates in Australia. Thus the teeth of carnivorous marsupials aren't frequently found , but they do turn up. Most of these were discussed earlier in this article, the one that we haven't yet discussed is *Thylacoleo*, the so called 'marsupial lion'.

We'll turn first to the most likely of these fossil teeth to be found, those of wombats.

## WOMBATS

Identifying the molars of fossil wombats is - if you'll will pardon the pun - dead easy. Imagine two cylinders pressed together and then slightly curved, the result is a wombat molar, they have the cross section like the figure '8' (Figure 1), on other Australian animals - and very few anywhere else - have teeth of this shape. The upper and lower are basically the same, but curve in different directions, curved concave outwards in the scull and concave inwards in the lower jaw. However, if you have an isolated tooth, it would be difficult to tell if it was an upper or lower.

In addition, there are few other distinctive characteristics of wombat teeth. First, they grow continually like the teeth of rodents, thus they have an open root, in other words, the root is simply a hollow double cylinder. Again, no other Australian animal do this, other than rodents, but their teeth are also quite distinctive and can't be confused with those of wombats. Since wombat teeth are continuously worn down, so a figure on the cusp pattern of wombat teeth has not been included as it is worn away very early in life. If the reader is curious, Archer (1984) shows the pattern in Figure 69. Now that you know what

wombat molars look like, you can go on to something that is more difficult to learn.

On the other hand, if you find wombats interesting, there are a few more things to say. The living wombats are much of a muchness, having seen one wombat you can easily recognise them all, even the giant wombats (*Phascolonus*) probably look like living wombats, but were 50% larger (in linear dimensions). The teeth of *Phascolonus* look like those of other wombats too, but are larger. However, at least in Victoria and South Australia, there was a different kind of wombat during the Pleistocene. This is *Warenja wakefieldi*. Which seems to have been a nonburrowing, forest dwelling wombat, presumably, in this it was much like the ancestral wombats. Its molars are typical wombat in form, but less strongly curved than those of other wombats

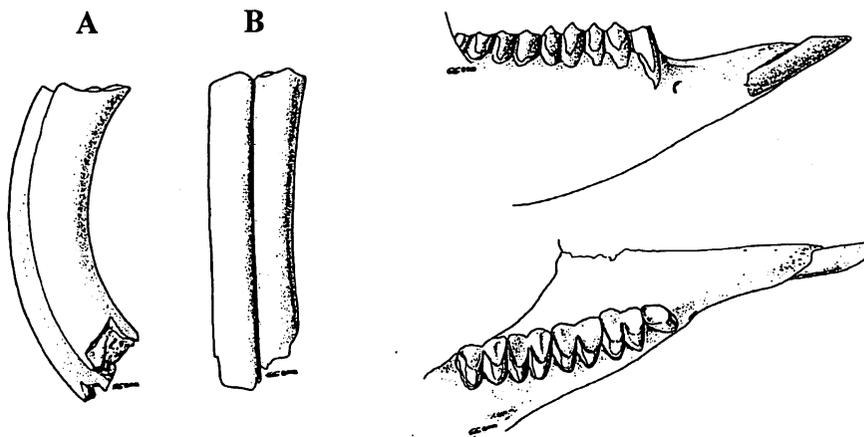


Figure 1. On the left is an isolated molar of the extinct giant wombat *Phascolonus gigas*. The tooth is seen in anterior (A) and lateral (B) views. On the right is the jaw of an extinct wombat *Phascolomys mitchelli* similar in size to those still living. This and the giant wombat molar are drawn to the same scale, so the large size of the giant is obvious. The jaw is seen in lateral view, above, and occlusal view, below the roughly 'figure 8' form of the four lower molars is readily seen in the occlusal view: the round cheek at the front (right) is the premolar. Both specimens are in the Queensland Museum (Q M).

### THYLACOLIONS

*Thylacoleo* is the so called 'marsupial lion', of course it was no more a lion than the 'koala bear' is a bear. It has often been described as being the size of a lion, but it must have been a very young lion, for it is in fact barely as big as a leopard, or even a large dog, its skeleton was well under a meter long (about 0.7 meters), from shoulder to hip. Noneless, its teeth are impressive. *Thylacoleo* was originally thought to have been a meat eater, hence the name derived from the Latin words indicating 'lion with a pouch'. Although this interpretation was generally accepted overseas, a sceptical response from Australian paleontologists led them to suggest that, far from being a predator, *Thylacoleo* was a mild mannered fruit eater, well, maybe not any more mild mannered than any other fruit eater, but still not a predator. The question was really only resolved in 1982, when scanning electron micrographs of the blade like teeth showed that they had cut through meat and skin, rather than slicing up juicy melons or such. Furthermore, fossil bones have been found that seem to have been scored by the teeth of *Thylacoleo*.

The molars of *Thylacoleo* are small and somewhat nondescript, and very rarely found on their own. The first two premolars are also small, but the third premolar was developed into a large, almost hatchet like cutting blade, this is the tooth that is usually found. It is easily recognised from its blade like form and size (Figure 2), no other teeth found in Australia, mammalian or not, look like this. Placental carnivores also have shearing teeth, the carnassials (premolars), but in none of them are the shearing blades developed to the extent (to as great a proportion of the length of the toothrow) as in *Thylacoleo*.

The lower molars are basically similar in form to the upper (Figure 3), or at least close enough that if you know one, you will recognise the other.

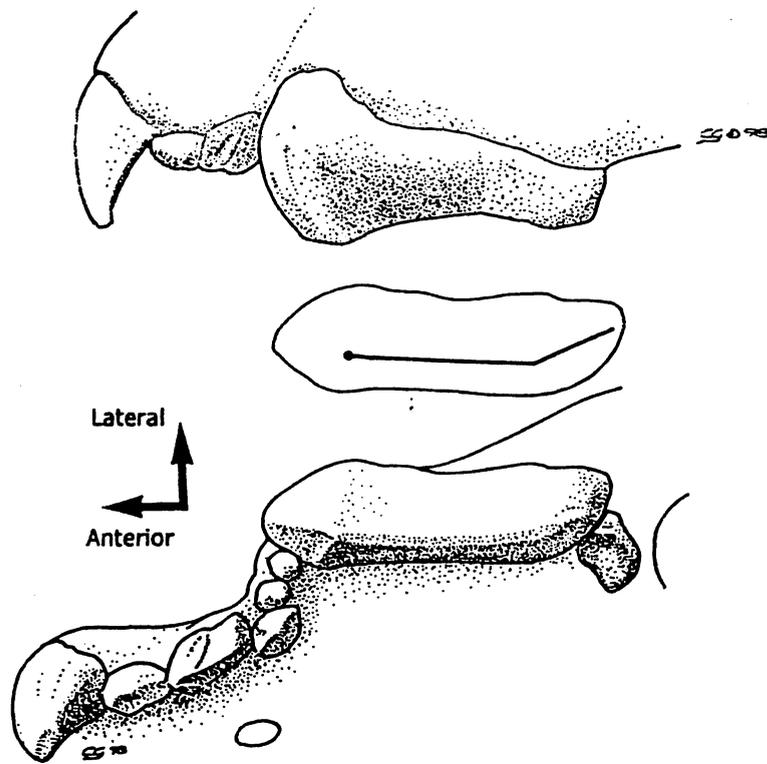


Figure 2. The upper teeth of *Thylacoleo carnifex* based on a specimen in the QM, they are seen lateral view above and occlusal view below. The most easily recognised of the teeth is the prominent, blade like last (third) premolar: the first molar is the small tooth just behind it in occlusal view. The cusps are not labelled in the diagram because their identification seems to be uncertain, this in turn, is due to the greatly evolved form of this tooth. Notice that, in lateral view, the shearing edge of the tooth is broadly concave, this is thought to have functioned to hold bones that were being cracked.

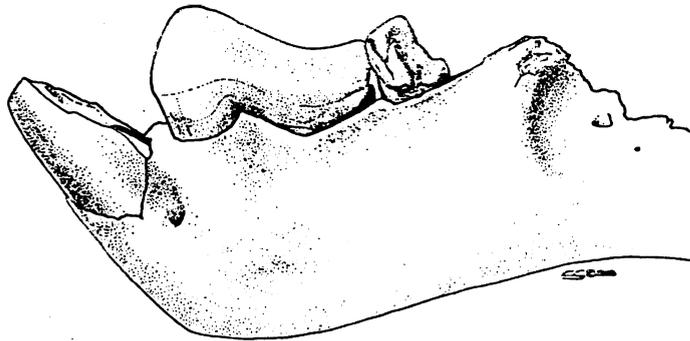


Figure 3. The lower jaw of *Thylacoleo carnifex*, in lateral view based on a QM specimen), the shearing premolar is clearly seen, the small tooth behind it is a molar, anterior is to the left, and the back of the jaw, at right, is badly broken. Note the corresponding curve of the edge of the tooth to hold bones being cracked. The white band along the cutting edge of the tooth is due to wear of the tooth against its opposite in the upper jaw. The upper tooth thus shows wear, but on the internal face

## KOALAS

Wombat and *Thylacoleo* teeth are easily recognised, but those of koalas and possums are basically similar. This doesn't indicate any particularly close relationship, in fact koalas are thought to be closely related to wombats, not possums, although fossil teeth from koalas have been confused for possum teeth by professional paleontologist. Koala teeth are not often found, but they do appear from time to time.

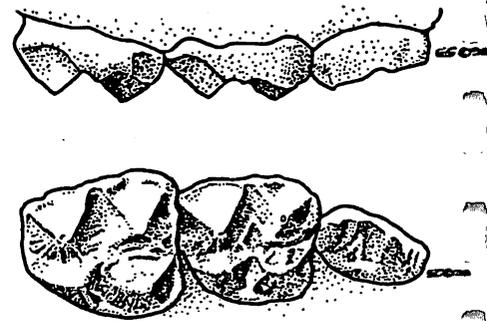
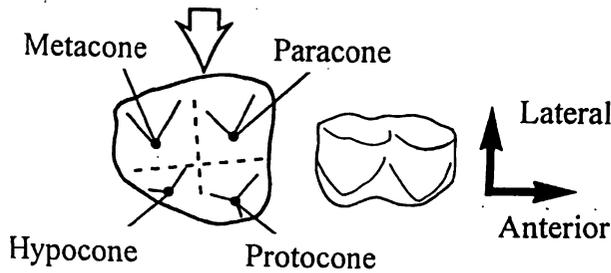


Figure 4. The upper cheek teeth - all those that are preserved - of the giant koala, *Phascolarctos stirtoni* (QM) specimen. They appear in lateral view at left (top) and occlusal view at bottom: the first tooth (at right) is the premolar. All four cusps are prominent on the molars and shaped roughly like small pyramids. Each cusp is separated from all others by a deep 'valley' (diagram at right) which is usually more prominent than in possums. Remember that cusps are indicated by dots, ridges by solid lines and 'valleys' by broken lines. The 'wrinkles' mentioned in the text can be seen around the base of the metacone in the second (diagrammed) molar. A lower molar (third right) of the living koala, *Phascolarctos cinereus*, is shown in outline between the arrows for orientation and the cusp diagram.

Koala molars have four cusps, one at each corner (Figure 4). Viewed 'face on' these cusps are roughly triangular in form, especially along the outer (libial) edge, these cusps are actually crescentic, with two sharp ridges extending anterolaterally and posterolaterally from each cusp. Koala molars have a wrinkled surface of thickened enamel around the bases of the cusps, particularly on the upper molars (Figure 4, second molar), but on some lower as well, these wrinkles are found in *Phacolarctos*, and may occur in older koalas. But in the older forms the fossil teeth are often worn so it is clear - at least to me - when these wrinkles first appeared, these wrinkles are not found on possums' teeth. Koala teeth are quite rare as fossils from Plio-Pleistocene beds, and there are only a few specimens in the Q M.

POSSUMS

Like those of koalas, possum molars also have four cusps, one at each corner, but these are arranged into two transverse pairs, separated by a marked 'valley' (Figure 5).

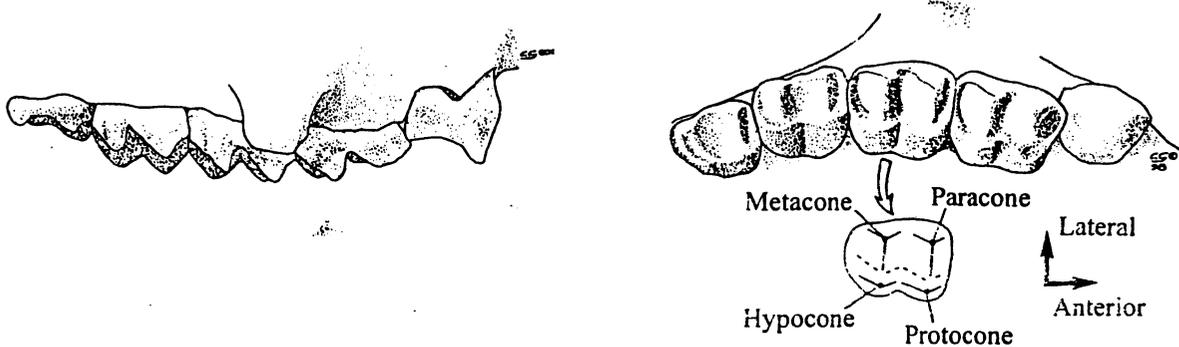


Figure 5. The upper cheek teeth of the common Brushtail Possum, *Trichosurus vulpecula*, based on a modern specimen in the Q M, the view is given at left and the occlusal view at right. The four cusps shown are prominent and almost joined in pairs by well developed transverse ridges, as indicated in the diagram. (the premolars of this specimen, both uppers and lowers, have a very unusual wear pattern, these are not normal brushtail premolars at all).

In this they are different from koala teeth, in which the cusps are not linked in transverse pairs (Figure 4). Here we will look at the teeth of phalangerids (brushtails and cuscuses). Phalangerid molars are slightly less square than those of koalas, and more elongate anteroposterly (Figure 5 and 6).

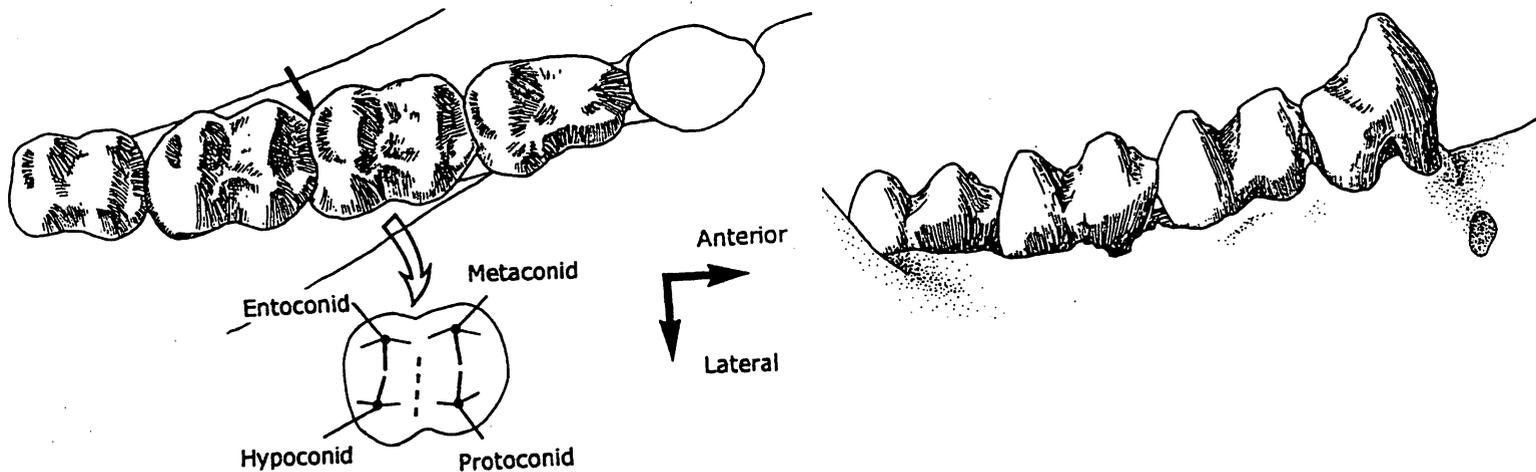


Figure 6. The lower cheek teeth of the Common Brushtail, the same specimen as in Figure 5, the occlusal view is at left and the lateral view is at right. As in the uppers, the four cusps are prominent and joined in the pairs indicated by well developed transverse ridges. A low cingulum (arrow) extends transversely across the back of the talonid (not indicated, but the back portion carrying the entoconid and hypoconid). Possum teeth are small, the one diagrammed (second molar is 5.5 mm long).

The molars of ringtails (pseudocheirids) are similar to those of koalas, but more complex. Viewed 'face on' these cusps are roughly triangular in form, especially these along the outer (labial) edge. In addition, there is another set of V-shaped, or crescent, ridges between the main cusps (Figure 7).

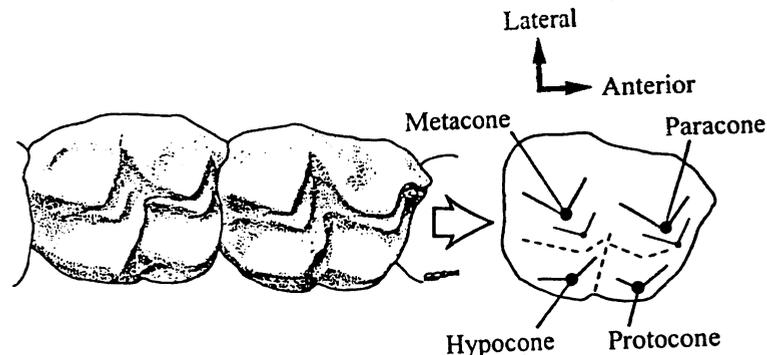


Figure 7. Two upper molars, number 3 and 4, of the Common Ringtail, *Pseudocheirus peregrinus*, drawn from a modern specimen in the Q.M. These are included simply to show that not all possum teeth look like those of the brushtail, some - these - are much more complex. The large dots and thick lines indicate major cusps, the small dots and thin lines, minor cusps. The minor cusps are the protoconule (anteriorly) and the metaconule (posteriorly).

The teeth of other possums, gliders, pygmy possums and cuscuses, are similar enough in form to be recognised as possum teeth from comparison with those of the common Brushtail and Ringtail. But this is not the case for older (Oligo-Miocene) possums and possum like marsupials. Fossil possum teeth are about as rare as koala teeth.

Next we will look at how to identify commonly found fossil mammal teeth other than molars and recognising the teeth of the fossil placentals of Australia: rodents and bats.

Now we shall turn to mammals other than marsupials, and teeth other than molars. Australia is known as the homeland of marsupials, although marsupials also survived in North and South America. They once, in the early Tertiary, had a much wider distribution including Europe and Asia. Marsupials seem to have been with Australia from the beginning, when it split from Antarctica in the Eocene. Placental mammals, however, seem to have been immigrants. The slow northward drift of Australia brought it within migrating

distance of Asia at approximately the beginning of the Pliocene, about 5 million years ago. And at about this time, the oldest rodent fossils turn up in the Australian fossil record.

Bats (chiropterans), with the ability to fly, arrived well before this time. The oldest Australian bat, *Australonycteris* from Murgon in southeastern Queensland, dates from the Eocene and so is almost as old as the oldest known bat fossils from overseas. Apparently, being able to fly, bats became broadly distributed across the world soon after they evolved.

Before continental drift was widely accepted by geologists and zoogeographers, it was generally thought that marsupials were prominent in Australia because of its isolated position. Marsupials were taken to be more primitive (i.e., older) than placentals, and this was often assumed (although rarely by those who thought seriously about it) to indicate that they were less 'advanced' or 'sophisticated' than placental mammals. Likewise, they were also thought to be more 'robust', better survivors. Thus they could better make the long island-hopping migration from Asia to really out-of-the-way places, like Australia. The presence of the only surviving monotremes also in Australia reinforced this idea, as monotremes were egg-layers. Clearly an older reproductive strategy than either marsupials or placentals use. An impediment to this view was the absence of Asian marsupials: it was thought that fossil marsupials should be found in Asia, perhaps in the Cretaceous, and these might represent the ancestors of the lineages that made it to Australia. Ironically, since continental drift did occur, such Cretaceous marsupials have been found in Mongolia.

This reopened the question of why the only native Australian placentals are those that clearly emigrated from Asia (and bats, some of which came from elsewhere). There is no obvious reason, since marsupials and placentals are about equally ancient (equally primitive) why the one made it to Australia and not the other. The obvious notion, that may be the 'other' did make it but became extinct, occurred to several paleontologists. And so there have been reports of fossils of placentals from the Eocene and the Cretaceous of Australia in the past decade. whilst the discoverers are enthusiastic about such finds, other paleontologists remain unconvinced. Had the Cretaceous Mongolian marsupials been recognised early in this century, they would have been taken as sure evidence that the Australian marsupials came ultimately from Asia, and used as more evidence against the notion of continental drift. Both conclusions we now know to be wrong, but logical. So although there is nothing inherently implausible about the claims of fossils of Australian placental mammals, they are based on fragmentary specimens and some scepticism is in order. Things are often not as we think, and one is entitled to wonder why, if other placentals did exist in Australia and then became extinct, both rats and bats later arrived and thrived.

Such consideration aside, rodents and bats were here during the Pliocene and Pleistocene, and so you might well find their fossils. both are relatively small forms compared to at least some of the marsupials.

## RODENTS

Rodent molars are also easy to recognise, at least to recognise as being from rodent, but working out just which rodent may be a different matter. In Australia we are looking at murids, the family that includes rats and mice and their relatives. Their molars have two or more low, sometimes curved transverse lophs (Figs 1 & 2). Shallow basins are left between the lophs, giving the impression, for some teeth, of modular construction. In murids, the first molar has three lophs, and the second and third two. As the molars wear, each loph wears into two low, blunt ridges, as explained in the caption to Fig. 1. This low ridged structure is characteristic of rodent molars. The curved incisors of rodents are also characteristic (Figs. 1, 2 & 14).

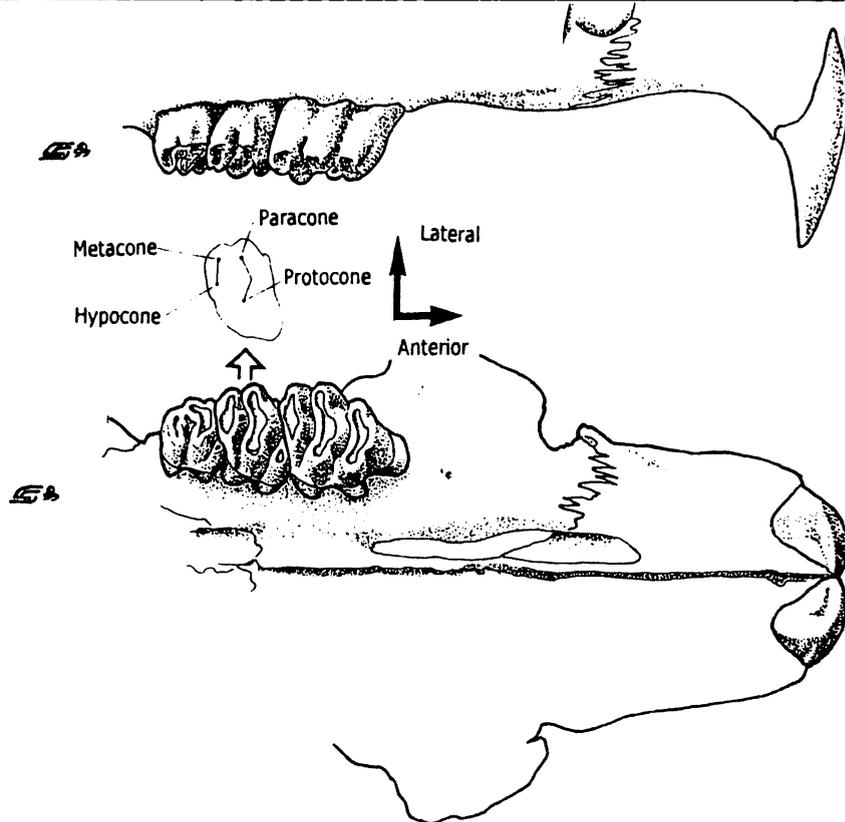


Figure 1. The upper teeth of a fossil murid, probably a mouse, from Elephant Hole (cave) in Queensland, seen in lateral view above, and occlusal view below. The characteristic forms of the molars and incisors (at right) may be seen. The molars have transverse lophs that wear to leave a set of low ridges and grooves on the occlusal face of the crowns: each loph wears in to two ridges, one ridge formed by the enamel of the anterior face of the loph, and one from that on the back face. Note that the second and third (at left) molars have two ridges, but the first has three.

Rodent teeth are always small, at least in Australia. Here the largest rodents are rats, although overseas, in South America for example, rodents get a lot larger, capybaras weigh up to 50 kilos, and some extinct forms were larger. Closer to home, the New Guinea giant rat *Hyomys*, reaches a head-body length of 36 cm. Just larger than that of the largest Australian water rat. *Hydromys chrysogaster*, at 37 cm. But the giant tree rats of New Guinea, *Mallomys*, and Indonesia, *Papaomys*, are larger, reaching 42 to 45 cm in head-body length respectively. The molars of the water rat are less than 3x4 mm in diameter, with incisors to 19 mm long (measured across the curve, not along it). Anything longer than this in Australia is not from a rodent - or else is a very interesting discovery.

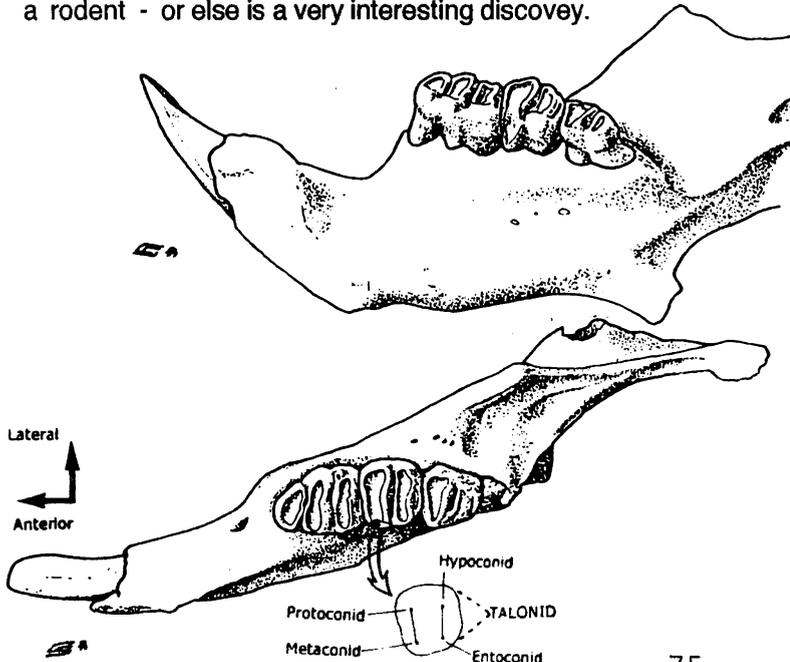


Figure 2. (left) The jaw of a fossil murid from elephant Hole in Queensland in lateral view (above) and occlusal view (below). Again the characteristic forms of the molars and incisors (at the left) may be seen: notice that the lower incisor is less strongly curved than the upper. The lower molars, like the uppers, have transverse lophs that wear to leave low ridges and grooves on the occlusal faces. These teeth have evolved to match the uppers, so that the talonid, although present, is hardly recognisable.

## BATS

Like the teeth of rodents and of marsupicarnivores (like *Antechinus*), bat teeth are small. Although Australian bats may get as large as 30 cm in head-body length, most of the bats are between 4 and 6 cm. as small as mice in other words. There are two groups of bats, microchiropterans and megachiropterans, sometimes called microbats and megabats. The former include the small insect eating bats, "most of the bats" mentioned above, and the latter are the large flying foxes. These are generally accepted as being closely related, although Prof. Jack Pettigrew, of the University of Queensland, has found good evidence that flying foxes are more closely related to primates (and hence people) than to microbats.

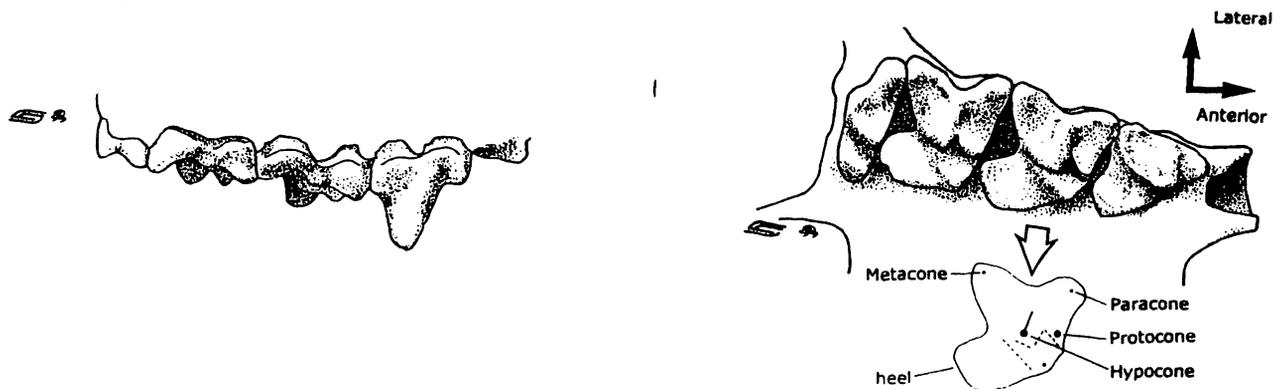


Figure 3. The upper teeth of the Ghost Bat (*Macroderma gigas*). showing the premolar (at right) and three molars, seen in lateral view (left) and occlusal view (right). The canine is missing, hence the empty alveolus seen at the right. These teeth retain a more primitive form than those of rodents. The protocone and hypocone are strongly developed and slightly higher than the paracone and metacone, the medial cusps (shown but not labelled) is lower, and the broad posteromedial heel even lower. The last (third) molar is much smaller than the others, and quite different in form. This specimen is from Dodgey's Cave (Queensland).

Bats' teeth are diverse in form, but the upper molars are usually more or less squarish in outline in occlusal view (Fig.3). The protocone is the largest cusp, the metacone second largest and the paracone is usually smallest. The hypocone is even smaller when it is present at all, but it is often lost. A series of cusps (or styles) is found on the labial edge of the upper molars. The paracone and metacone are each joined to these cusps by two ridges, or crests, extending anterolaterally and posterolaterally from each. Thus each cusp is at the apex of a V-shaped set of ridges, and both together give a W-shape to the ridges of the crown (Fig.3). Different species of living bats are distinguished by differences in the forms of the 'W' - by which crests are longer or shorter. In the upper molars a cingulum may be developed medially. I have shown here the teeth of the carnivorous Ghost Bat, *Macroderma gigas*, not because they are typical of microbat teeth, but if you can recognise *Macroderma* teeth, you will also be able to recognise other microbat teeth.

The lower molars are roughly rectangular in occlusal view, longer anteroposteriorly than wide (Fig. 4). They have five major cusps, and the three of the trigonid are higher than those of the talonid (particularly in carnivorous or primitive forms). On the lower there is usually a complete cingulum on the labial side. Megachiropteran (flying fox) teeth are quite different in form (Fig.5).

## PREMOLARS

There are other teeth in the mouths of mammals than molars, even if molars are often the most useful in identifying fossil (and live) mammals. In kangaroos, the premolars are more useful than the molars, although identifying macropod species from the premolars may be safely left to the expert, as they often

differ in subtle features. Living macropods, and related fossil forms like *Protemnodon*, have narrow, bladelike premolar with low verticle ridges (Fig.6) that may be worn off with age, producing a very bladelike crown. The premolars are basically similar in both upper and lower jaws: if you can recognise the one, you can often recognise the other. This is not to say that they are indistinguishable, and the lower is usually narrower than the upper, which has a slight medial shelf (Fig.6).

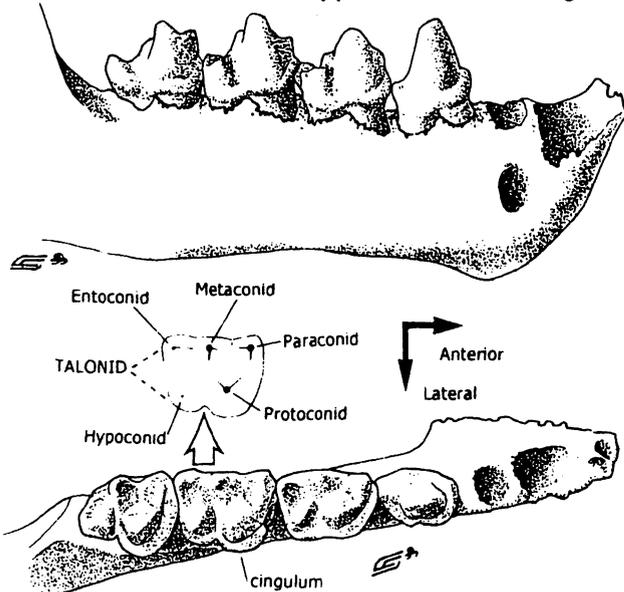


Figure 5. (right) upper and lower teeth of the Greyheaded Flying Fox, *Pteropus poliocephalus*, based on a recent specimen in the Q M collection. Both upper and lower molars are much more derived than those of microbats. These are shown for comparison with microbat teeth: so far, no fossils of flying foxes have been found in Australia.

Figure 4. (left) . The lower teeth of the Ghost Bat, *Macroderma gigas*, showing the premolars (at right) and three molars, seen in lateral view (above) and occlusal view (below). The canine and incisors are missing, leaving the aleveoli at the front (right) empty. The basic trigonid- talonid structure can still be seen here, and the trigonid is more prominent than the talonid. the molars have a low cingulum (labelled on the drawing, rather than diagram) laterally. this specimen is from Dodgey's Cave (Queensland).

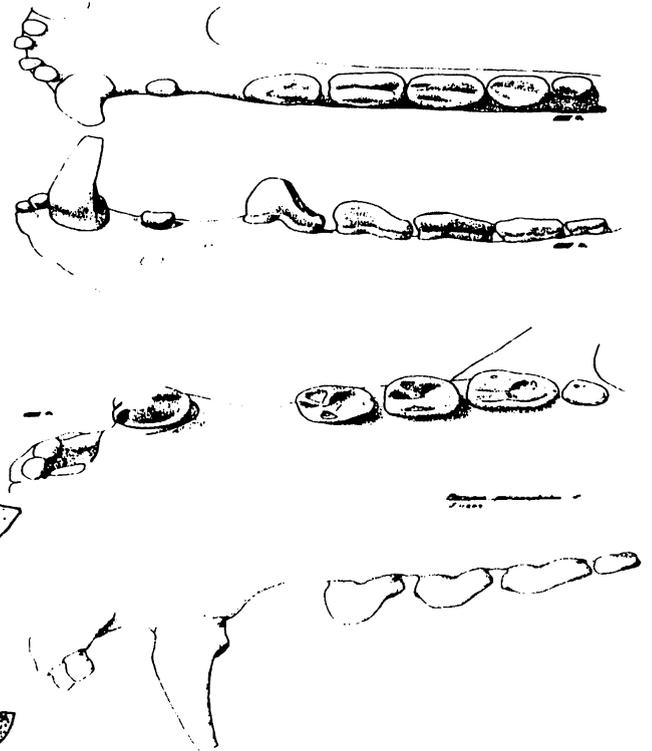


Figure 6. The premolars of *Protemnodon anak* an extinct macropodine kangaroo, upper at the left, lower at the right both seen from the side (above) and in occlusal view (below). (For both, the front is to the right.) this form of premolar, with a long ridged blade, is characteristic of most macropodines. The right upper premolar (at left) differs from the lower (right) in having a slight medial shelf that bears a series of small stylar cusps, which may become worn to a smooth surface (as in this specimen). The lower premolar is basically similar to the upper, but is narrower and lacks the medial shelf at the back.

But among the fossil forms, as is often the case, there was a greater variety. The sthenurines, or browsing kangaroos - discussed earlier - had premolars with two 'blades' - one along the medial and one on the lateral edge of the tooth (Fig. 7). The lateral 'blade' is the higher, but even so the unworn premolars have a distinctive appearance, reminding one of an old fashion bath tub, on a small scale. These teeth can easily and immediately be distinguished from those of macropodine kangaroos. But when they are worn, they often lose their characteristic 'two-bladed' form and wear down to a nondescript nubbin.

*Propleopus* had a large premolar, that is almost semicircular in outline, reinforced by a series of vertical ridges (Fig.8). Its slightly reminiscent of the blade of a buzz-saw, and unlike those other macropods. The lateral view tends to make one think the tooth is thin (like a saw-blade), but in fact it is fairly thick. especially at the neck, as may be seen in occlusal view. Mike Archer has convincingly argued that *Propleopus* was a carnivorous kangaroo. These three different forms, macropodine, sthenurine and propleopine, are the kind of kangaroo premolars that occur in Pliocene and Pleistocene sediments, but propleopine premolars - in keeping with their presumed carnivorous habita - are much rarer than the others.

Diprotodontan premolars are columnar (Fig.9), are quite different from the blade-like or 'double-bladed' form of macropod premolars. Unfortunately - like many in the Q M collection - they are often poorly preserved. A palorchestid (upper) premolar is shown in Fig.7, p11

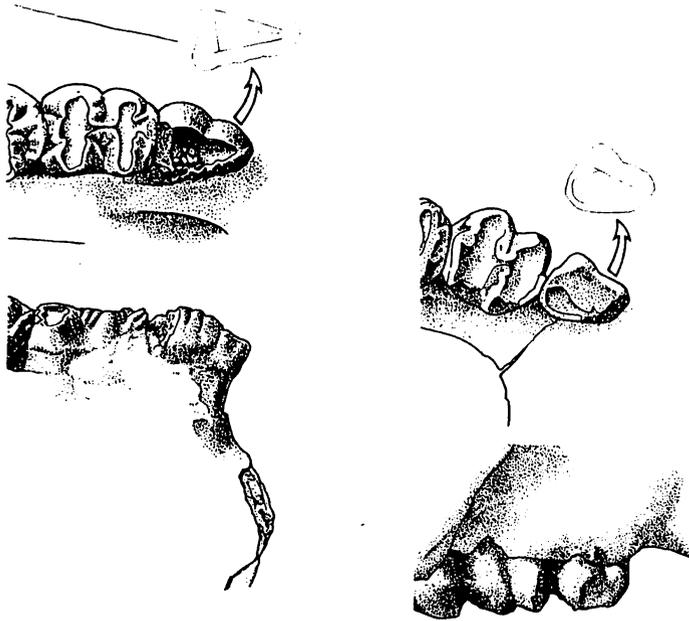
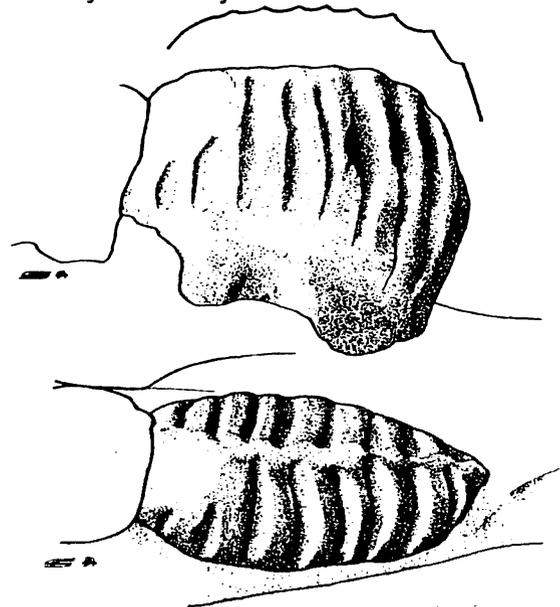


Figure 7. (left). The premolars of the sthenurine kangaroo *Procoptodon*, at right is *Procoptodon pusio*, at left *P. rapha* both seen from the side (above) and in occlusal view (below). (For both, the front is to the right) . This form of premolar, with a doubly ridged blade, is characteristic of most sthenurines. The right upper premolar (at right) is considerably more worn than the lower (left). and the diagrammed lateral ridge is almost entirely worn away.

Figure 8. (right). The lower premolar of a propleopine macropodine *Propleopus oscillans*, from Wellington Cave, N. S. W. (cast) in lateral (above) and occlusal (below) views. Propleopine lower premolars are almost semicircular in form when seen from the side (and unworn). this is a slightly worn tooth, the outline above the lateral view shows what the edge looks like when unworn.



INCISORS

Molars and premolars are multicusped teeth, incisors and canines are not, and so are much simpler in form. In fact, canines are so simple in form that they are more or less useless for identification. the crowns of incisors may be split rarely - but are usually long, simple, structures. In macropods they are sometimes blade-like, but in diprotodontans, wombats, etc. (including rodents) they are more rodlike, and usually curved.

Kangaroo upper incisors may be flattened or peg-like in form: the posterior (third) incisors, especially, are flattened (Fig. 10). these incisors are distinctly curved, and the third incisor may be split or slotted (Fig. 10) the lower incisors are thick, flattened teeth with convex surfaces (Fig. 7). having when unworn somewhat of the shape of a spearhead. Macropod lower incisors are easily recognised.

Diprotodontan, wombat and thylacoleon incisors are columnar, or rod-like, in form. Like those of macropods they are distinctly curved: those of the upper jaw often more sharply curved than those of the lower. Wombat incisors (Fig. 11). are quite rod-like, and those of thylacoleons are pointed (conical) (Fig.12). Those of some diprotodontans (such as *Euowenia* of the Pliocene) are also conical, but usually diprotodontan incisors are not. The prominent first uppers of diprotodontans (especially *Diprotodon*) are flatter in cross-section than the lowers (Fig. 13), although the smaller second and third upper incisors are less flattened, and more rod-like.

Isolated diprotodontan and kangaroo incisors are not uncommon, but those of thylacoleons and wombats are rarely found, Rodent incisors are often found: they are curved - more strongly in the uppers than the lowers - and quite small (Fig. 14).

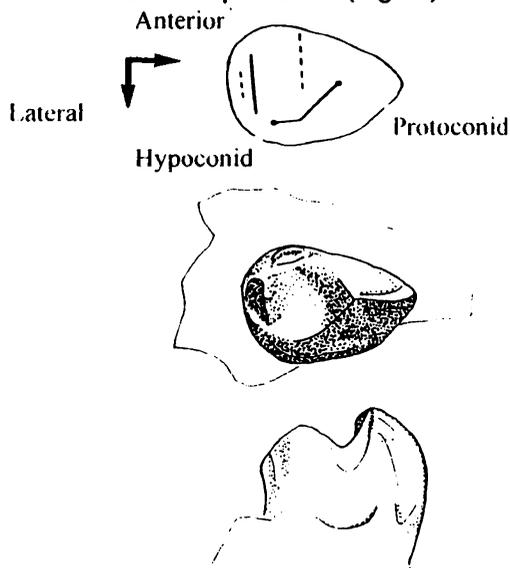
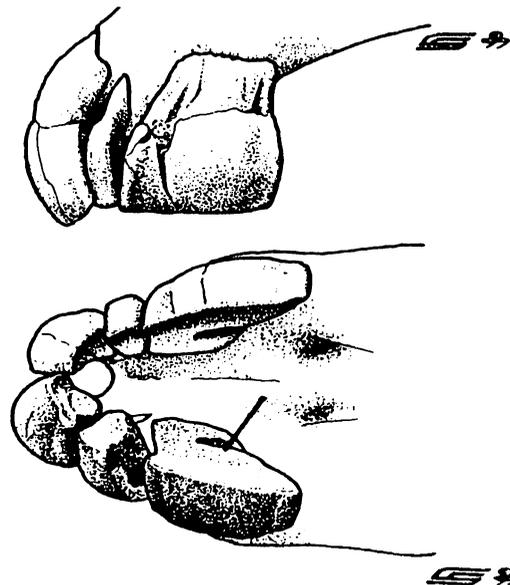


Figure 9. (left) an unworn diprotodontan premolar from Mammoth Cave, Western Australia (cast). Diprotodontan premolars may be relatively large, although not quite as large as the molars, but have a more complex pattern of cusps and 'valleys'. There was some difficulty in identifying this tooth, in part because diprotodontans have been studied recently, and it was identified as *Diprotodon* earlier in this text.(Fig. 2). but that is incorrect and it is a lower premolar of *Zygomaturus trilobus*.

Figure 10. (right) The upper incisors of *Sthenurus* sp. from Lake Callabonna, South Australia (cast), in lateral view (above) and occlusal view (below). the crowns are curved and rod-like to flatten in cross-sections. Note the slot in the medial face of the third incisor (marked by a bar) in occlusal view. The upper incisors of macropodine kangaroos are basically similar in form (but we don't have any really good ones in the collection). A macropod lower incisor is shown in Fig. 7., at the extreme right.



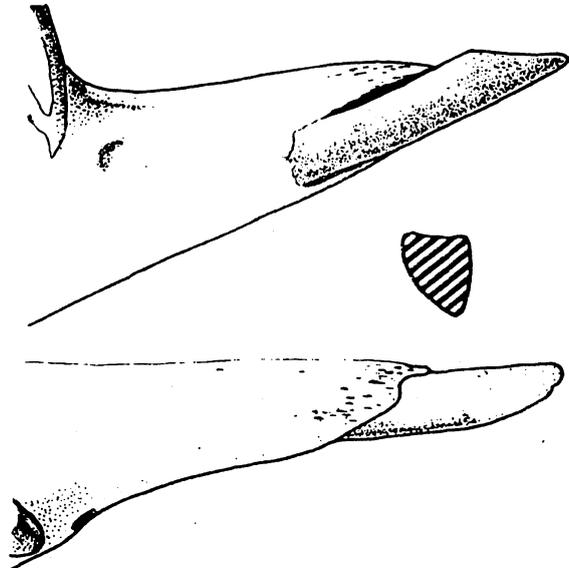


Figure 11. (left) incisors are rod-like teeth with a bevelled wear surface at the end. this is the right lower incisor of *Phacalomys mitchellii* Shown in lateral view(above) and occlusal view (below) In cross-section (hatched) the upper and medial faces are flattened, giving the tooth a cross-section like the quadrant of a circle. Both upper and lower incisors of most wombats look like this, but in the giant wombat, *Phascolonus*, the uppers are quite flattened and almost platelike

Figure 12. (right) Lower (at left) and upper at right incisors of a thylacoleon. The lower incisor had a cross-section like the quadrant of a circle (like wombat lower incisors). and the upper incisor in more rodlike, but flattened at the base (neck). the lower incisor shown here is broken on the upper surface, but if found at all these teeth are usually found intact

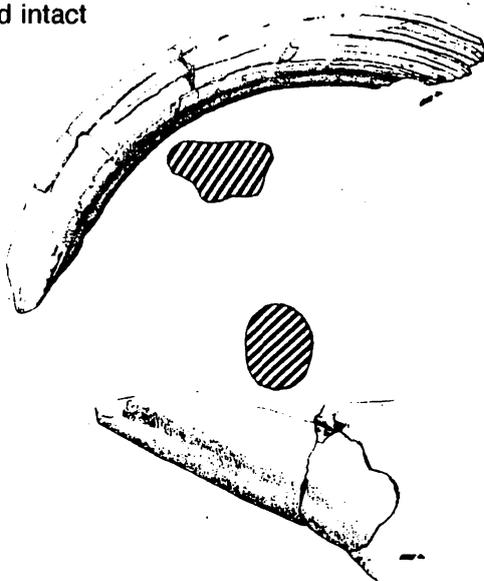


Figure 14. (right) The upper incisor of a rodent (murid) in side (left) and back (right) views. Although these may remind you of the upper incisor of a diprotodontan, they are much smaller, usually less than 1 cm long (the *Diprotodon* upper incisor in Fig. 13 measures 25 cm. across the curve), and flattened from side to side. This is an isolated incisor from a cave at Mt. Etna (Queensland). Murid lower incisors are similar in form, but less strongly curved. (Fig.2).

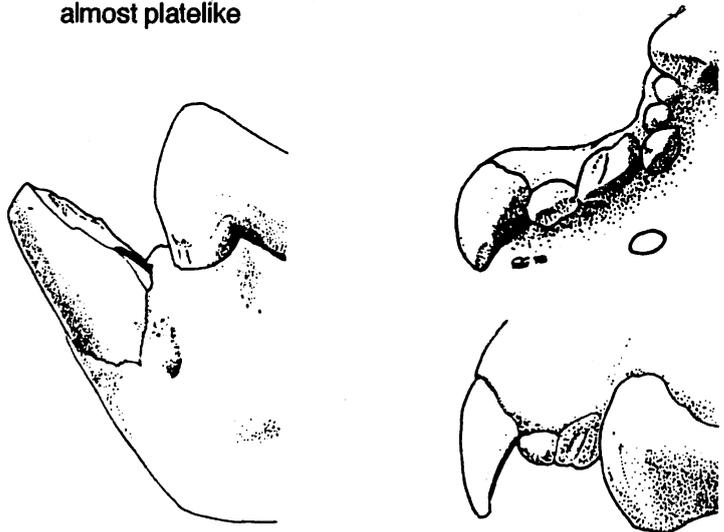
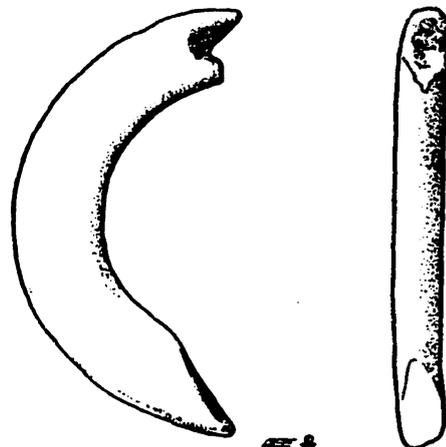


Figure 13. (left). Upper (above) and lower (below) Diprotodontan incisors of the large *Diprotodon* from the Darling Downs, Queensland. the upper is an isolated tooth, the root is to the right, and the bevelled 'cutting' (or grinding) edge at left. The cross-section, at approximately mid-tooth, is flattened and grooved. The lower incisor is still in place in the front of the jaw. It also has a bevelled 'cutting' edge, but is oval in cross-section. The two teeth are arranged approximately as they would occur in the live animal with its mouth slightly opened.



## DENTAL FORMULAE

One other item that will be useful in recognising fossil mammals should be introduced, this is dental formulae. As mentioned in the first part of this text, mammals usually have four kinds of teeth in each jaw: incisors, canines, premolars and molars. Although most mammals have only a single canine per jaw (per side), the numbers of the other teeth vary. Thus different groups of mammals can be recognised from their dental formulae. An example of a dental formulae is:

$$\begin{array}{c} \underline{2\ 1\ 2\ 3} \\ 2\ 1\ 2\ 3 \end{array}$$

This means there are 2 incisors, 1 canine, 2 premolars, and 3 molars in the upper jaw (above the line, reading from left to right), and 2 incisors, 1 canine, 2 premolars and 3 molars in the lower jaw (below the line). This is the dental formulae for humans.

The general form of the dental formulae is:

$$\begin{array}{c} \underline{(\text{number of}) \text{ incisors, canines, premolars, molars (in each upper jaw)}} \\ (\text{number of}) \text{ incisors, canines, premolars, molars (in each lower jaw)} \end{array}$$

but omitting the commas. if none of a kind of tooth are present, then a zero is used in the formula.

The earliest mammals had a formula of:

$$\begin{array}{c} \underline{3\ 1\ 4\ 3} \\ 3\ 1\ 4\ 3 \end{array}$$

and domestic dogs, for example, have:

$$\begin{array}{c} \underline{3\ 1\ 4\ 2} \\ 3\ 1\ 4\ 2 \end{array}$$

Primitive marsupials are thought to have been:

$$\begin{array}{c} \underline{5\ 1\ 4\ 4} \\ 3\ 1\ 4\ 4 \end{array}$$

and kangroos (macropodoids) have:

$$\begin{array}{c} \underline{3\ 1\ 3\ 4} \\ 2\ 0\ 3\ 4 \end{array}$$

Dental formulae are given in the technical literature and textbooks such as that by Archer and Clayton, when the specimens are complete enough that the formula can be worked out.

## FINAL COMMENTS

Remember that teeth get worn, so the pattern given here may be obscured, or obliterated. Isolated teeth may occur in any stage of wear. Those still in the toothrow will be worn more at the front, because in many herbivorous marsupials the molars erupt sequentially from front to back. Thus the front ones are older, and more heavily worn.

In references given at the end one can find pictures of worn teeth. In this text the teeth have been drawn from actual specimens, all worn to a greater or lesser extent. After all, one almost never finds fossil teeth in the field that are unworn, so these should give an idea of what teeth, in the field look like.

This text is intended to enable you to recognise the more common fossil mammal teeth, but you will doubtless find others. During February 1999, in an amateur's collection, I saw a tooth unlike any I had seen before. It was from Chinchilla (and so Pliocene) and was quite small, mildly sigmoid in form, and pointed at both ends. I later found that it was probably the last (posteriormost) incisor of a bandicoot or

small macropod. The crown of the tooth curves around that of the larger preceding incisor and its root, also, is curved to accommodate the root of that tooth. And, if you have difficulty in identifying a tooth, there are reptilian and fish teeth to consider as well.

### References

**Archer, M., & Clayton, G., eds., 1984.** Vertebrate Zoogeography & Evolution in Australia (Hesperian Press: Carlise), 1203 pp. The chapters on mammals, especially 6,7 give valuable information on mammal teeth.

**Rich, T.H., 1991.** Montotremes, placentals and marsupials: their record in Australia and its biases. In, P. Vickers-Rich, J.M. Monaghan, R.F. Baird, T.H. Rich, E.M. Thompson & C. Williams, eds. Vertebrate Paleontology of Australia. (Monash University Publications Committee: Clayton), pp 893-1004. Good pictures of the teeth of many fossil mammals, and also some information on the teeth of introduced mammals.

**Young, W.G., Jupp, R., Kruger, B.J., 1989** Evolution of the skull, Jaws and teeth in Vertebrates. (Dept. of oral Biology and Surgery, Univ. of Queensland: St. Lucia), 274pp. Covers the structure, different forms, functions and evolution of teeth: gives an introduction for what teeth are all about.

**Merrilees, D., & Porter, J.K., 1979.** Guide to the identification of teeth and some Bones of Native Land Mammals Occuring in the Extreme South West of Western Australia. (Western Australian Museum: Perth), 152 pp. The only guide available on identifying fossil bones (of any kind!).

**Peyer, B., 1968.** Comparative Odontology (University of Chicago Press: Chicago). 347 pp. A general introduction to tooth form and histology, very well illustrated.

There is also a series of articles done by the people in Mike Archer's lab (including Archer, himself at the Univ. of N.S.W. These were printed in Riversleigh Notes', the publication of the Riversleigh Society. Entitled 'Sinking one's teeth into odontology', covered dasyurids, wombats, thylacines, bandicoots, marsupials moles, koalas, some unusual extinct marsupials (yalkaparidontians and yingabalanarids), diprotodontids, thylacoleonids, bats, crocodilians and a basic introduction to teeth in general and mammalian teeth in particular.

Article contributed by: Frank Holmes

With permission to reprint from the author, Ralph Molner  
and Paul Tierney, Editor of the 'FOSSIL COLLECTOR'

THE FOSSIL COLLECTORS ASSOCIATION OF AUSTRALASIA

## Chondrichthyes from the Glen Dean Limestone Formation, Middle Chesterian, Mississippian, of Southern Indiana

Randy R. Patrick\*<sup>1</sup> and Anne M. Shaw<sup>2</sup>

Indiana State Museum, 204 South Alabama St., Indianapolis, Indiana 46204

\*Address Correspondence to: rpatrick@indy.tds.net

Current Address

1 Science Department, Southmont High School, 6425 US 231 So., Crawfordsville, IN 47933

2 Elsey Hall, Rm 221, Franklin College, Franklin, IN 46131

### Introduction

Mid-Paleozoic Chondrichthyan remains are rare but are being recovered by the thousands from the Megenity Peccary Cave because of a special secondary depositional environment. Isolated Chondrichthyan teeth, dermal denticles, and dorsal fin spines are widespread throughout the rocks of Mississippian through Permian Age. While being found as isolated individual specimens in most cases, they are comparatively abundant in some horizons. Teeth, dermal denticles, and dorsal fin spines are found in stratigraphic settings ranging from reef limestones to anoxic black shales. Complete dentitions are rare, with many genera and species being named from single isolated specimens, Hansen, 1985; Zangerl, 1963, 1981.

The Megenity Peccary Cave formed in the Glen Dean Limestone of southern Indiana, H.H.Gray, Personal Communication, 1995. The cave has produced not only thousands of Pleistocene vertebrate fossils, but also a concentration of Chondrichthyan vertebrate fossils that is unique. These materials along with hundreds of thousands of Pleistocene fossils are part of an ongoing study of the Indiana State Museum. The location of the cave on private property remains confidential. The authors will give a general overview of the Chondrichthyan specimens collected from the Megenity Peccary Cave Expeditions that will be useful as a field guide to the identification

of isolated Chondrichthyan denticles.

### Locality and Stratigraphy

The Glen Dean Limestone Formation of southern Indiana, Figures 1 and 2, was named by Butts, 1917, for exposures near Glen Dean, Beckenridge County, Kentucky. This skeletal and oolitic to biomicritic limestone ranges from nine to thirty-one feet thick in south central Indiana, Figure 3. It

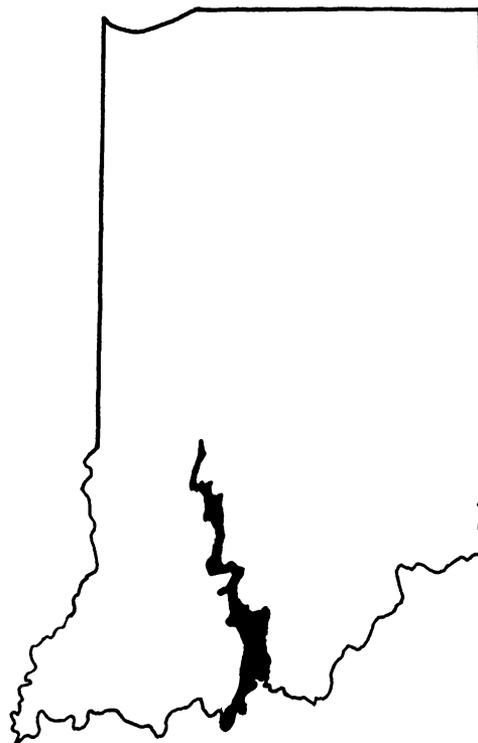


Figure 1. Indiana showing the Mid-Chesterian area of the Glen Dean Limestone.

Mississippian	Chesterian Series	Buffalo Wallow Group	Tar Springs Formation
			Stephensport Group
		Glen Dean LS	
		Hardinsburg Formation	

Figure 2. Stratigraphy of the Mid-Chesterian, Mississippian, of southern, Indiana.

typically contains brachiopods, blastoids of the genus *Pentremites*, and bryozoans including *Archimedes*. It is overlain conformably by the Tar Springs Formation, Buffalo Wallow Group, Mississippian, which is primarily shale containing scattered thin beds of limestone and massive local lenses of sandstone. The Tar Springs Formation is about sixty-five feet thick. The beds of limestone are interspersed in the shale in scattered thin beds with the sandstone being local massive lenses. The Hardinsburg Formation is overlain

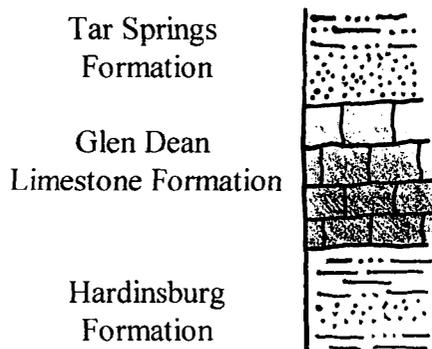


Figure 3. Mid-Chesterian formations of the Megenity Peccary Cave area, southern Indiana.

conformably by the Glen Dean Limestone Formation. It consists of a gray, soft carbonaceous shale and very fine-grained, ripple-bedded sandstone that is cliff forming and ranges from twenty to sixty-two feet thick, Shaver, 1986; Gray 1978.

The Chondrichthyan material collected from Megenity Peccary Cave is thought to be derived almost exclusively from the Glen Dean Limestone Formation. However, the Tar Springs Formation is exposed in the roof of the cave passageways and may contribute material to the wall rock solution concentrate in the cave deposits.

### Material and Methodology

The Megenity Peccary Cave represents a special depositional environment that has concentrated both Pleistocene vertebrate fossils and Mississippian wall rock fossils. The Pleistocene vertebrates were concentrated in several passageways within the cave system. The primary focus of the Megenity Peccary Cave Expeditions in the last thirteen years has been the systematic recovery of thousands of late Pleistocene vertebrate remains, Richards, 1988A, 1988B. The Chondrichthyan fossils were recovered along with the Pleistocene materials during the washing of cave sediments through one millimeter hardware cloth.

Approximately fifty-seven cubic meters of residual material has been removed from the cave. The resulting concentrate is dried in the laboratory and sorted under the binocular microscope for the recovery of co-mingled Pleistocene and Paleozoic fossils. Thousands of cubic meters of Glen Dean Limestone has been dissolved during cave formation leaving about six hundred cubic centimeters (.0006 cubic meter) of total Chondrichthyan vertebrate material sorted to date. More than eleven hundred hours of field recovery and screening in addition to several thousand hours

of sorting using binocular microscopes was needed to recover these specimens, R. Richards, personal communication, 2000.

Indiana Law prohibits the non-scientific collection of materials from any cave. In addition, the sheer amount of time and material required to collect a single tooth makes the prospect of collecting specimens within the cave environment generally non-productive. However, the authors suggest that weathered soils at Glen Dean Limestone outcrops of southern Indiana can be generally productive for Chondrichthyan remains by both surface examination and by bulk wet-screened methods.

### Morphology

Shark dentitions vary in tooth form as the age, sex, or position of the teeth change. Many of the isolated Paleozoic teeth have been given separate genus and species names. Few complete dentitions have been collected. Most teeth have been described from single isolated specimens. It is easier to list the number of tooth forms rather than attempt a species separation. In the past, isolated teeth were given species designation when individual Chondrichthyan species dentitions contained various tooth forms. Many, if not most, of the tooth forms would occur in the same species. The morphological figure, Figure 4, and definitions will be useful in the field identification of the various Chondrichthyan tooth forms, Kent, 1994; Welton and Farish, 1993.

### Definitions

Labial - Side of the tooth facing the lips.

Lingual - Side of the tooth facing the tongue.

Symphysis - The midline of each jaw where the left and right jaw cartilage meet.

Mesial - The side of the tooth toward the front of the jaw.

Distal - The side of the tooth toward the hinge

of the jaw.

Apical - The tip of the cusp or the top of the tooth.

Basal - Bottom or the base of the tooth. Also can be the root of the tooth.

Cusp - Usually prominent principle crown.

Cusplet - One or more often paired miniature cusps.

Crown - Pointed or rounded, enameloid-covered upper portion of the tooth.

Root - Lower portion of tooth attached to the dental membrane that supports the crown.

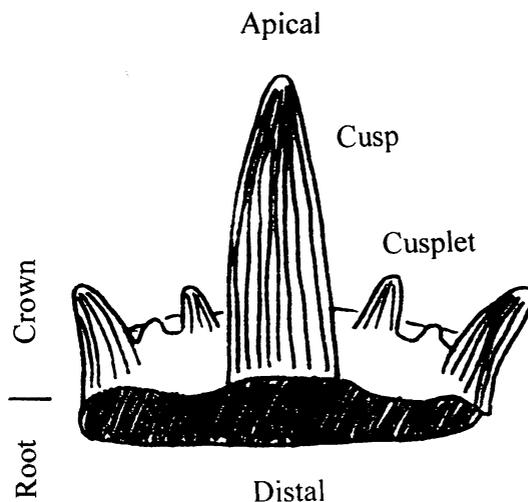


Figure 4. General morphology of the Chondrichthyan tooth form. This is a labial view of a *Cladodus* tooth.

### Systematic Paleontology

#### Classification of Paleozoic Chondrichthyes

Class Chondrichthyes

Subclass Elasmobranchii

Order Cladeselachida - U. Dev.

Family Cladeselachidae

Order Coronodontia - U. Dev.

Order Symmoriida - U. Dev. - Penn.

Family Symmoriide  
 Family Stethacanthidae  
 Order Eugeneodontida - Miss.- Tri.  
 Superfamily Caseodontoidea  
 Family Caseodontidae  
 Family Eugeneodontidae  
 Family Caseodontoidea  
 Superfamily Edestoidea  
 Family Agassizodontidae  
 Family Edestidae  
 Order Orodontida - L. Dev. - Miss.  
 Family Orodontidae  
 Order Squatinactida - Miss.  
 Superorder Euselachii  
 Order Ctenacanthiformes - M. Dev.-  
 Cret.  
 Superfamily Ctenacanthoidea  
 Family Ctenacanthoidae  
 Family Bandringidae  
 Family Phoebodontidae  
 Superfamily Hybodontoidea  
 Family Hybodontidae  
 Superfamily Protacrodontoidea  
 Family Tamiobatidae  
 Order Xenacanthida - U. Dev.- Perm.  
 Family Diplodoselachidae  
 Family Xenacanthidae

#### Subclass Holocephali

Order Chondrenchelyiformes-Miss.-  
 Penn.  
 Family Chondrenchelyidae  
 Order Copodontiformes - U. Dev.-  
 Miss.  
 Family Copodontidae  
 Order Psammodontiformes - U.  
 Dev.- Penn.  
 Family Psammodontidae  
 Order Incertae Sedis  
 Suborder Cochliodontoidei - Miss. -  
 Perm.  
 Family Cochliodontidae  
 Suborder Helodontoidei - U. Dev.-  
 Perm.  
 Family Helodontidae

Suborder Menaspoidei - Miss.-Perm.  
 Family Menaspidae  
 Order Chimaeriformes - U. Miss.-  
 Tert.  
 Suborder Echinochimaeroidei  
 Family Echinochimaeridae  
 Subclass Incertae Sedis  
 Order Iniopterygiformis - Penn.  
 Family Iniopterygidae  
 Family Sibyrhynchidae  
 Order Petalodontida - U. Dev.-Perm.  
 Family Pristodontidae  
 Adapted from Carroll, 1988.

#### *Cladodus*

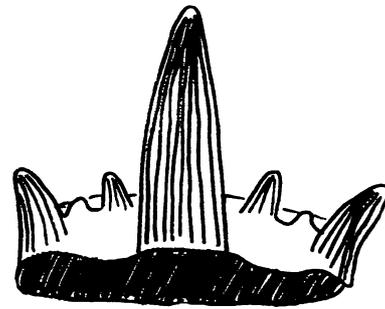


Figure Five -A

The Cladodont tooth form is a catchall for any tooth with a large, central cusp and an anaulacorhizous disc-like root. *Cladodus* tooth forms are grasping teeth. The crown has a large, median cusp that is curved lingually with cusplets; one to six in number, mesial and distal to the median cusp. The outermost cusplet is larger than the inner cusplets. Longitudinal ridges occur on the cusp and cusplets reaching from apical to basal crown surface. A dental band is present on well-preserved specimens. *Cladodus* is the most common tooth form from Meggenity Peccary Cave, having three obvious forms varying by cusplet number and root size.

	Small	Large
Length	.8 cm	4.0 cm
Width	.4 cm	1.7 cm
Height	.7 cm	1.6 cm Broken

*Venustodus*

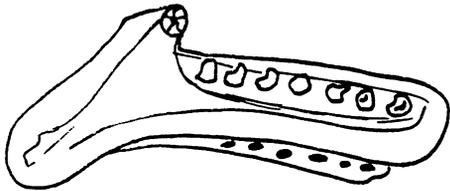


Figure Five - B

*Venustodus* is a low-crowned, laterally elongate tooth form with a robust, rounded medial cusp and smaller mesial and distal rounded cusplets. The crown is bordered basally by imbricated ridges covering the entire basal crown margin. The tooth base is short and simple. Medial symphyseal teeth are strongly arched into a V-shape. Teeth that are more distal show a great variation in form. Five tooth forms are presently described for this crushing tooth.

Length	1.1 cm
Width	.3 cm
Height	.7 cm

*Orodus*

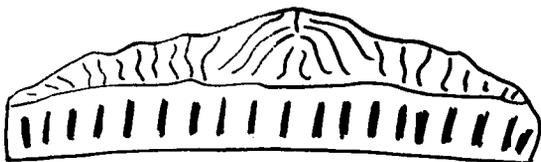


Figure 5 - C

*Orodus* tooth forms are laterally

elongated with the median cusp being a rounded cone. Mesial and distal cusplets are cone-shaped, rounded, and smaller than the central cusp. Ridges radiate medially out of the apical portion of these cusps and cusplets with oblique secondary ridges visible in well preserved specimens. The root is a simple anualacorhizous type with the crown being somewhat arched and may narrow laterally. *Orodus* tooth forms are considered to be crushing teeth.

Length	.9 cm
Width	.2 cm
Height	.3 cm

*Helodus*

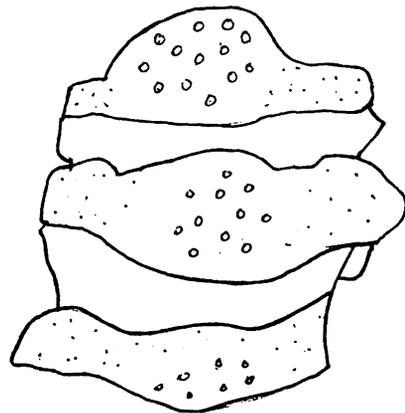


Figure 5 - D

*Helodus* is a polished, pitted, crushing tooth that is sub-conical and can have a central dome with sub-median tubercles on either side. *Helodus* teeth occur in a variety of forms and are usually found as broken tooth plates or partial tooth whorls. The Chondrichthyes of this type were probably a bottom feeding fish that had Arthropoda as the primary food source.

**Partial Tooth Whorl**

Length 1.1 cm  
 Width 1.0 cm  
 Height .5 cm

***Deltodus?***

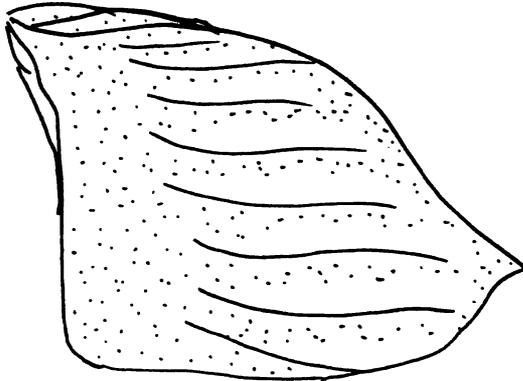


Figure 5 - E

*Deltodus* is a pavement tooth that is moderately arched longitudinally and rather strongly enrolled. Its outline is somewhat rectangular and can be broadly arched around the base. Low crown ridges are prominent on well-preserved specimens being most prominent near the mid-portion of the crown. The surface may show fine pits when weathered. Most specimens are collected as fragments of large teeth.

Length 2.2 cm Broken  
 Width 2.3 cm Broken  
 Height .5 cm

***Fissodus***

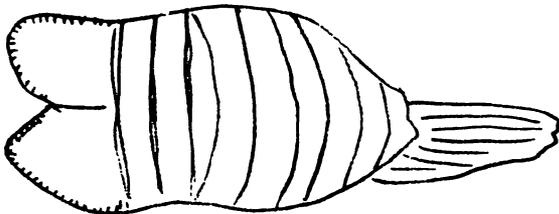


Figure Five - F

*Fissodus* is sigmoid in sagittal section with an anaulacorhizous root. The crown margin is divided into one or two triangular cusps with the lingual portion of the crown forming an elongated, flattened, transversely ridged heel, oriented nearly ninety degrees to the vertical portion of the crown. The tooth base is simple, short, and flaring, attached to the ventral surface of the lingual heel forming nearly a ninety degree angle with the heel. Five *Fissodus* tooth forms are present, all are characterized by their sigmoid sagittal section with the division of the crown margin into one or two triangular cusps. Lateral teeth are strongly asymmetrical. *Fissodus* is a nipping and crushing tooth form.

Length 2.3 cm  
 Width .9 cm  
 Height .4 cm

***Petalodus***

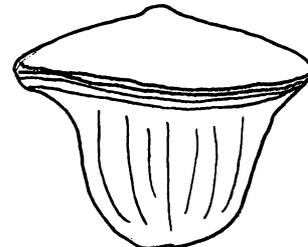


Figure 5 - G

The crown of *Petalodus* is labiolingually compressed and convexo-concave with a scooped out area on the basolingual portion of the crown. The tooth is medially acuminate with the crown margin forming a sharp cutting edge. The crown is bordered basally by a band of imbricated ridges that are more prominent lingually. The tooth base is long and tumid with the overall tooth being sigmoid in shape. Massed *Petalodus* teeth form a tooth pavement that was probably used for crushing and grinding food. The *Petalodus* teeth collected at the Megeniy Peccary Cave are usually broken

with very few complete specimens.  
 Length .7 cm Broken  
 Width .3 cm  
 Height .9 cm Broken

**Dermal Denticles**

*Petrodus*

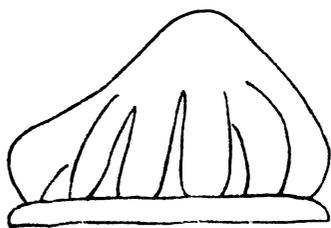


Figure 5 - H

*Petrodus patelliformis* is a small, rounded dermal denticle that is common in the Mississippian and Pennsylvanian rocks of Indiana, although it is not associated with any specific Chondrichthyan species. The root is flat, round, and attached to the crown by a short neck. The crown has a hemispheric shape in cross-section with radial ridges from apical to basal position. The most common form has a single, hemispheric cusp but can have as many as four hemispheric cusps. These enlarged placoid scales have different shapes depending on body position. Like teeth, dermal denticles are shed and replaced through life. Four *Petrodus* forms are common within the Glen Dean Limestone.

	Single	Double	Triple & Quad.
Length	.5 cm	1.1 cm	.7 cm
Width	.5 cm	.7 cm	.6 cm
Height	.5 cm	.4 cm	.3 cm

**Dorsal Fin Spines**

*Ctenacantus*



Figure 5 - I

Paleozoic Chondrichthyes have a bony, enameloid covered spine located just anterior to the dorsal fin. These spines grow throughout life and can be quite large. The spine fits over cartilage of the fin skeleton with the exposed enameloid covered portion projecting out of the body, while the spine trunk is attached deeply within the body. The spines are ornamented on their anterior surface. The ornamentation can be longitudinal ridges that in some cases have prominent costae. Fin spines are found as fragments, usually arch or wedge-shaped in cross-section.

The measurements of the Chondrichthyes in this paper are for representative specimens from each named form. The above form descriptions are from Hansen, 1985; Feldman, 1996; McKenzie and Bamber, 1978; St. John and Worthen, 1883; Zangerl, 1963, 1981.

**References**

Butts, C. 1917. Descriptions and Correlations of the Mississippian Formations of Western Kentucky. Kentucky Geologic Survey. 119 p.

Carroll, R. L. 1988. Vertebrate Paleontology and Evolution. Freeman. New York.

698 p.

Feldman, R. M. 1996. Fossils of Ohio. Bulletin 70, Ohio Department of Natural Resources, Division of Geological Survey. 577 p.

Gray, H. H. 1978. Buffalo Wallow Group Upper Chesterian (Mississippian) of Southern Indiana. Indiana Geological Survey Occasional Paper 25. 27 p.

Hanson, M. C. 1985. Systematic Relationships of Petalodontiform Chondrichthyans. Neuvie Congres International De Stratigraphie Et De Geologie Du Carbonifere. Compte Rendir, Vol. 5, p. 523-541.

Kent, B. W. 1994. Fossil Sharks of the Chesapeake Bay Region. Egan Rees & Boyer, Inc. 146 p.

McKenzie, M. A. and E. W. Bamber. 1979. An Occurrence of Lower Carboniferous Fish Remains from Alberta, Canada. Canadian Journal of Earth Science. Vol. 16, p. 1628-1631.

Richards, R. L. 1988 A. *Microtus xanthognathus* and *Synaptomys borealis* in the Late Pleistocene of Southern Indiana. Proceedings of the Indiana Academy of Science. Vol. 98, p. 561-570.

Richards, R. L. 1988 B. Quaternary Occurrence of the Fisher, *Martes Pennanti*, in Indiana. Proceedings of the Indiana Academy of Science. Vol. 98, p. 571-580.

Shaver, R. H., et al. 1986. Compendium of Paleozoic Rock-Unit Stratigraphy. Indiana Geologic Survey, Bulletin 59.

203 p.

St. John, O. and Worthen, A.H. 1883. Descriptions of Fossil Fishes. Geologic Survey of Illinois, Vol. VII, Geology and Paleontology.

Welton, B. J. and R. F. Farish. 1993. The Collector's Guide to Fossil Sharks and Rays from the Cretaceous of Texas. Before Time. 204 p.

Zangrel, R. 1981. Handbook of Paleoichthyology. Vol. 3A, Chondrichthyes I, Paleozoic Elasmobranchii. Gustav Fischer Verlag. 114p.

Zangrel, R. and E. S. Richardson, Jr. 1963. The Paleocological History of Two Pennsylvanian Black Shales. Fieldiana: Geology Memoirs Vol. 4.

### Acknowledgments

The authors wish to give a special thanks to Vern Swanson for the many thousands of hours of binocular sorting that he has completed on the Megenity Peccary Cave materials. We also wish to thank Ron Richards and the twelve dedicated Indiana State Museum staff members along with numerous volunteers, who, over many years, have removed and washed the Megenity materials. Special thanks go to Vic Porter, Dallas Evans, and Fred Lewis for all of their personal time dedicated to the Megenity Peccary Cave Project. We also wish to thank Linda Patrick for her critical reading of the final paper.

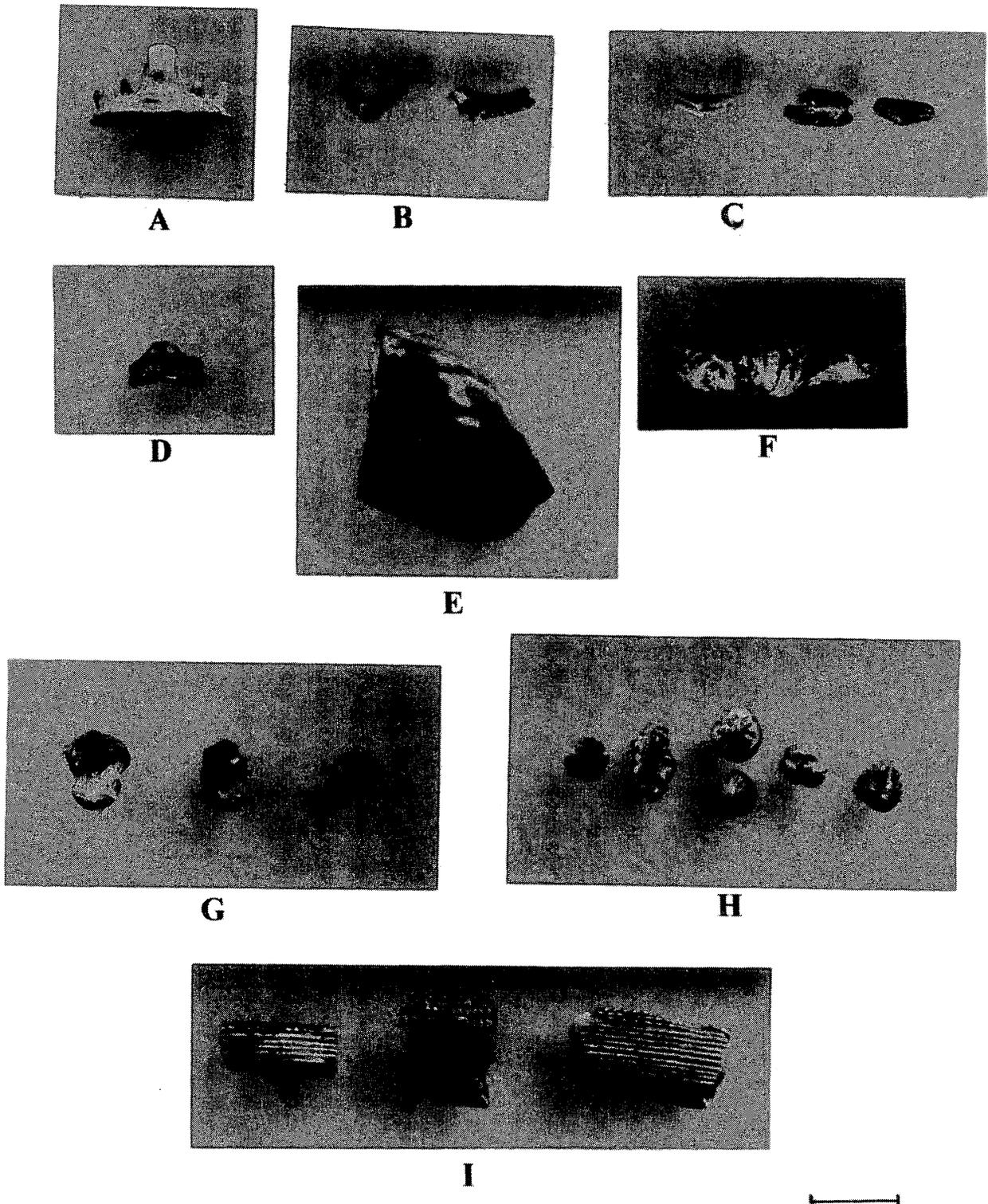


Figure 5. A. *Cladodus*. B. *Venustodus*. C. *Orodus*. D. *Helodus*.  
 E. *Deltodus*. F. *Fissodus*. G. *Petalodus*. H. *Petrodus*.  
 I. *Ctenacantus*. The scale bar equals one centimeter.

*David L. Thompson, 3389 Braeburn Circle, Ann Arbor, MI 48108-2617*

As a MAPS member I have had the opportunity to meet many helpful collectors through the years who share our hobby/passion for fossil collecting. I was glad to see "teeth" as a topic for our annual Expo because I feel this is a popular area for the amateur collector of all ages. Although Teeth, especially sharks teeth, are common and abundant fossils, common does not mean less complex! For instance there are thousands of types of sharks teeth alone and this one area is a fertile ground for hundreds of collectors with all levels of experience. As children become aware of fossils, dinosaurs are the first fossils that get attention, but the first actual fossil many of them got was a shark's tooth or a small Trilobite. Like other collectors I have given away thousands of sharks teeth to children at many fossil shows or programs and it never fails to be an exciting thing for them.

There are many types of teeth that range from simple water-worn sharks teeth on a beach to the rare, exotic one of a kind tooth to the magnificently preserved, large Great White teeth from phosphate pits around the world. They illuminate what that animal ate, evolutionary trends and speak of the type of animals they are descended from. This combined with other species found identify predator-prey communities and ecologies. Teeth are often very well preserved due to their hard mineral nature to start with and, as with the shark, may be one of the few parts fossilized.

My area of the country, Michigan, does not boast a lot of teeth for the collector although we do have Devonian fish teeth and jaw plates. These can be rather small and not easily found. We have Mastodon and other ice age mammal teeth, but these are generally from sites that are researched by professional paleontologists. I have had the chance to work at and to find some of these teeth at supervised digs. At some of these sites I have found wood with the tooth marks of both giant and common beavers clearly visible and have preserved this wood in alcohol. Still to collect teeth I have traveled with my collecting friends to other parts of the country most notably the Carolinas and the plains states.

I have had the opportunity to hunt at the Lee Creek site in Aurora, North Carolina several times and watched Becky and Frank Hyne as they

collected. No, I did not get a big Carcharodon (Carcharocles?) megalodon tooth myself but I saw some wonderful teeth others got. I did learn about the incredible variety of teeth at this and nearby sites and I am indebted to the many collectors who took their time to educate me in how and what to look for. It was here I learned about looking in road gravel "reject" to find some of the rare small teeth such as Squatina and Rhincodon; the Angel and Whale sharks respectively. I still look for the rare Cookie cutter shark's tooth (Isistius) and the Bramble shark (Echinorhinus) but I have been fortunate with both the Six-gill and Seven-gill cow sharks; Notorhynchus and Hexanchus and I have some wonderful examples of lower teeth of both types. I still look for the very differently shaped middle teeth, the symphyseals.

Moving back in time to the Cretaceous from the Eocene, I was introduced to the wonderful Genus Ptychodus with its many species. These pavement toothed sharks or fish are distinctive with rows of crushing teeth linked together. I have quite a few of the various species with mortoni and whipplei being some of my favorites. Again we witness the adaptation of teeth to the type of food available. These are clearly teeth designed to crush shellfish as opposed to the long, slim, barbed tooth for catching slippery fish or the big, sharp triangular teeth for taking chunks of flesh from large prey like seals or whales.

The appearance of variously shaped teeth define when many Mammal Families and Genus start in the fossil record such as the appearance of shearing teeth known as the carnassials which define the Orders Carnivore and Creodonta. Further development leads to such families as the Canids, the early dogs such as Hesperocyon that developed in the Americas and migrated with the Horse and Camels to Asia and Europe during the Oligocene through Miocene. When cleaning a small skull of a Hesperocyon, I have been fascinated by the dentation of this early dog. In addition I have cleaned the tiny skull of the early rabbit-like animal, Palaeolagus and been struck by the second set of incisors in the roof of the mouth behind the first set. These are quite tiny animals that have become larger as they move up in the fossil record and some of the primitive features of evolution have disappeared.

There are invertebrate "teeth" that are linked with mysteries of

paleoecology such as when did the radula, a rasp-like tongue, develop in early snails that are sometimes attached to Crinoids and Blastoids and what effects did this have on the development of Pelecypods and Brachiopods shell structure? Conodont teeth and jaws has only recently begun to resolve as more fossils of these worm like animals are found intact yet these "teeth" have been used as index fossils from the Ordovician to the Triassic and are extremely useful in this regard. The mandibles of the Devonian subclass *Phyllocarida* were thought to be fish teeth and labelled *Pseudodontichthys* meaning "false fish teeth". This interesting subclass of large shrimp-like creatures is still poorly known and difficult to collect, but beautiful examples of their teeth can be found.

Both the Scientific American and Natural History magazines in the past few months have articles on the teeth of dinosaurs with speculations on the purpose of serrations and tooth loss while feeding. The dinosaurs may have shed teeth while eating as sharks do and researchers are looking carefully for teeth of predators/scavengers at excavations. Serrations on teeth may not have acted in the traditional steak-knife cutting but as sites for toxic bacteria to breed and be introduced causing sepsis in the prey. This latter idea, introducing sepsis, is challenged in a later "Letters to the Editor" that question if this happens in cold blooded reptiles as it may in warm blooded mammals or this may give an additional boost to the belief in the warm blooded dinosaurs camp. There is still a lot to be learned about teeth and how they functioned in the past.

I look forward to reading other articles in the Digest on this topic this year!

Dave Thompson  
Ann Arbor, MI

References:

Alber, William L. "The Teeth of the *Tyrannosaurs*", Scientific American, September 1999: 50-51.

Erickson, Gregory M. "Breathing Life into *Tyrannosaurus rex*", Scientific American, September 1999: 44-49

Huchzermeyer, Fritz. "T. Rex Tactics" in "Letters to the Editors", Scientific American, January 2000: 6

Maxwell, Desmond. "Days of the Deinos", Natural History 12/99 - 1/00, pages 60-65.

McKenna, Malcolm C. "Early Relatives of Flopsy, Mopsy, and Cottontail", Natural History, April 1994:56-58

Bibliography of the many excellent books I could list, I especially enjoy,

Burns, Jasper. Fossil Collecting in the Mid-Atlantic States, The John Hopkins University Press, Baltimore, Maryland 1991 Softcover.

Carroll, Robert L. Vertebrate Paleontology and Evolution, W.H. Freeman and Company, New York 1988, Hardcover.

Carter, J. G., et al. Fossil Collecting in North Carolina, Bulletin 89, Dept. of Natural Resources and Community Development, Geological Survey Section, Raleigh, N.C. 1988 Softcover.

Case, Gerald R. A Pictorial Guide to Fossils, Krieger Publishing Company, Malabar, Florida. 1992 Hard and Softcover versions.

Chandler, Richard (text) and John Timmerman (Illustrations). Neogene Fossils of North Carolina. A Field Guide, The North Carolina Fossil Club, Inc, P.O.Box 2777, Durham, N.C. 27705, 1994 Softcover.

Chandler, Richard and John Timmerman. Cretaceous and Paleogene Fossils of North Carolina. A Field Guide, The North Carolina Fossil Club, Inc. 1995 Softcover. These two booklets by Chandler and Timmerman are

some of the best in identifying Sharks teeth and other fossils from the Carolinas

Garcia, Frank and Donald Miller. Jasper Burns (Illustrations), Discovering Fossils, Stockpole Books, 5067 Ritter Rd., Mechanicsburg, PA. 17055 1998 Softcover. Comprehensive book with clear illustrations by Burns. Section 1A, pgs. 95 to 129 is devoted to "Jaws and Teeth".

Kemp, David, Liz Kemp and David Ward. An Illustrated Guide to the British Middle Eocene Vertebrates, published by David Ward, London, 1990 Softcover Excellent drawings but Latin names identification only.

Kent, Bretton W. Fossil Sharks of the Chesapeake Bay Region, Egan Rees and Boyer, Inc., Columbia, Maryland 1994 Softcover Excellent drawings of teeth and especially of full mouth dentation in Appendix B.

Kocsis Jr., Frank A. Vertebrate Fossils: A Neophytes Guide, IBIS Graphics, Palm Harbor, Florida 1997 Softcover Excellent photos of sharks teeth as well as teeth and bones from all types of vertebrates.

Lauginiger, Edward M. and Eugene F. Hartstein. A Guide to Fossil Sharks, Skates and Rays from the Chesapeake and Delaware Canal Area, Delaware, Open File Report No.21, State of Delaware, University of Delaware, Delaware Geological Survey, Newark, Delaware May 1983 Softcover. Can be downloaded or requested in softcover for better photos.

Matsen, Brad and Ray Troll. Planet Ocean, Ten Speed Press, Berkeley, CA. 1994. Hardcover. Whimsical but accurate illustrations and text.

Moore, Raymond, Cecil Lalicker, Alfred Fischer. Invertebrate Fossils, McGraw-Hill Book Co., New York, 1952 Hardcover. Especially Chapter 23 (Lalicker) Conodonts.

Olsen, Stanley J. Origins of the Domestic Dog. The Fossil Record, The University of Arizona Press, Tucson, AZ. 1985 Hardcover.

Thomas, M.C. Fossil Vertebrates-Beach and Bank Collecting for Amateurs Revised Edition 1992, Copyright 1968 by M.C. Thomas, Softcover Photos of all kinds of teeth including sharks.

Welton, Bruce J. Ph.D. and Roger Farish. The Collectors Guide to Fossil Sharks and Rays from the Cretaceous of Texas, Before Time, #5 Remington Dr., Lewisville, TX. 75067 1993 Softcover. Superb book with photographs of teeth and coverage of the Genus Ptychodus.

Kesling, Robert V. and Ruth B. Chilman. Strata and Megafossils of the Middle Devonian Silica Formation, Published by Friends of The University of Michigan Museum of Paleontology, Inc., Papers on Paleontology, No.8 1975. Data on Phyllocarids also see Plates 93 (page 331) and 100 (pg. 343).

#### Web sites

[http:// www.elasmo.com/home.html](http://www.elasmo.com/home.html) Jim Bourdon has maintained this site for quite awhile and it is the best to start looking for Sharks and Ray teeth. Link with Jim Bourdon and Merle Graffam for Ptychodids at the same site.

## HOW DO YOU CHEW

### Tooth Structure, Diet and Survival

David Jones  
East Acres Park  
Worthington, Minnesota 56187

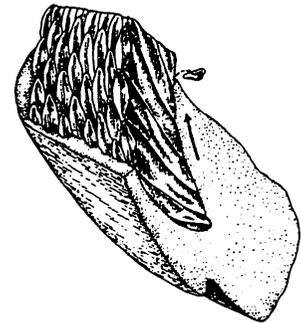
Most dinosaur teeth were simple in form and function. The giant sauropods, for example, had heads that were small in proportion to body size and dietary requirements. A dental battery of 35 or 40 spade-shaped teeth was efficient at stripping leaves from trees, but not much use in grinding the 1,000 or 1,500 pounds of leaves the average sauropod consumed each day.



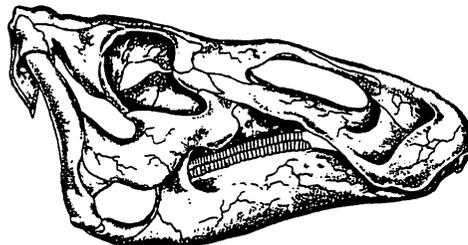
*Camarasaurus*, from the late Jurassic Morrison.

Digestion was effected by grinding stones in a muscular gizzard, and by 60 feet or more of small intestine.

The duckbill dinosaurs had the most efficient teeth: hundreds of small teeth, packed rigidly in overlapping rows, constituted the best equipment for grinding to pulp all kinds of vegetable matter.



Skull of *Edmontosaurus*,  
about 42 inches long



Section through a duckbill's  
jaw showing how teeth moved  
upward with use

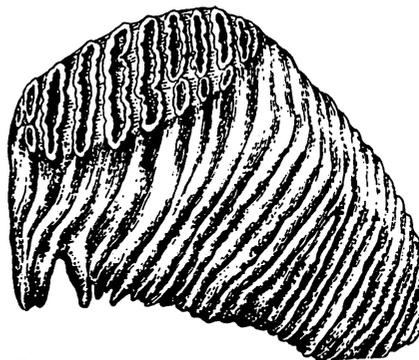
However, the mammals are the class of vertebrates that has the greatest variety of tooth shapes, sizes and structures. The most significant changes in tooth structure of mammal herbivores came in response to the spread of grasslands in the second half of the Tertiary. As the climate of the midwest and the Plains States became cooler and drier, wooded areas shrank and grassy open country expanded. Grass is a herbaceous perennial plant which is tolerant of extremes of heat, cold drought and floods. It will even resume growth after it has been burned by wildfire. So grass is prolific in growth in environments where other plants grow poorly, if at all. It has the added virtue of growing all season, even as mammal herbivores are chewing on it.

One difficulty about grass as food, is that it is mostly cellulose, which is not easily digestible. Large herbivores, especially the cloven - hoof *artiodactyls*, were successful in developing specialized digestive systems to get all the nutrition possible from the cellulose in grass. The other bad news about grass is that every molecule of its cellulose contains a few molecules of silica. The mineral hardness of silica is about 6 on the mohs scale, and the hardness of tooth enamel (calcium fluoro- apatite) is about 4. What to do to compensate for the rapid wearing of teeth that chewed on silica-laden grass? The large mammal herbivores developed a variety of solutions to the problem.

An interesting contrast in evolution of tooth structure is shown by the distantly related mastodon and mammoth. Mastodon tooth crowns bore three, four or five transverse crests, and the crown height was about 25% or 30% of the length of the roots. Mastodon tooth crowns were covered with a thin layer of enamel. When the enamel was chipped and worn away, the tooth crown soon wore down to a smooth stub, which no longer function for chewing. The animal's life became a misery of toothaches and indigestion.



*American mastodon.*



*woolly mammoth*

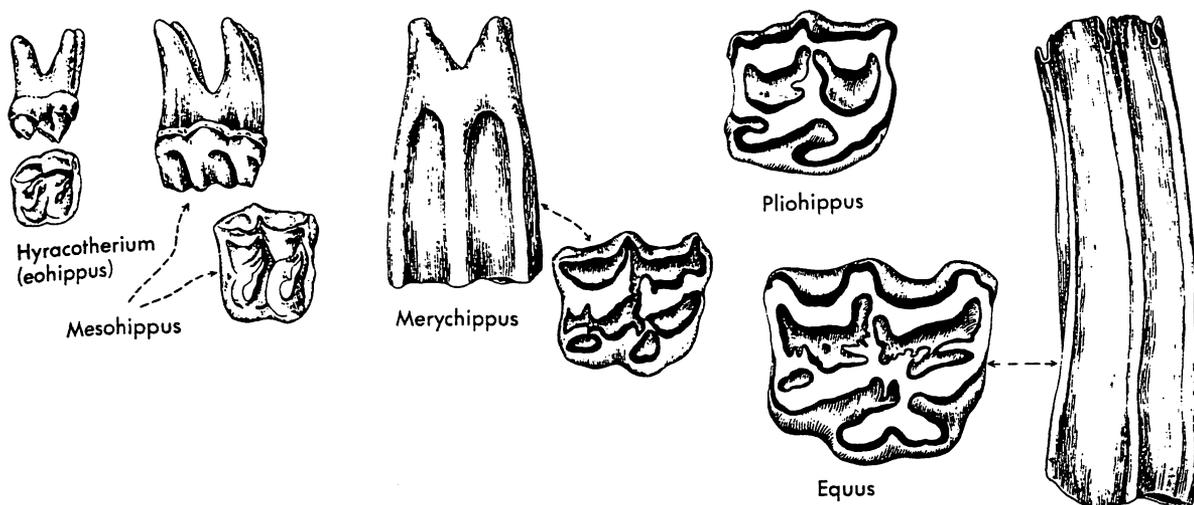
Mammoths, and their close relatives the elephants, mutated or developed from a specialized genus of Mastodon, *Stegodon*. Tooth structure of these animals developed in four ways: (1) Increased in number of transverse tooth crests from 6 to 12 or 15, and eventually up to (2) 26 or 28 Deepening of the troughs between the crests until the enamel was "inflolded" through the entire height of the crown; (3) increase in the height of the crown until it was four or five times the length of the root; (4) Increase in the size of the molar teeth until there was room for only one at a time in each maxilla (upper jaw) and one on

each side of the mandible. This last development required that, as the mammoth and elephant molars wore down to stubs, pressure of the next molar erupting pushed the worn tooth out of the jaw.

All of these structural changes in mammoth and elephant teeth likely brought longer life, and better digestion throughout life, and the ability to use a greater variety of food sources.

Development of horses, and their teeth, has been fully studied by vertebrate Zoologists for 150 years. They have used the great wealth of fossil horse specimens found in the Plains States. The earliest clearly recognizable relatives of horses have been found in sediments over 45 million years old, in southwestern Wyoming and adjoining parts of Colorado. They were small animals the size of a terrier. Cheek-teeth were low-crowned, with a thin cap of enamel. The row of upper cheek-teeth was about 2 1/2 inches long. This *Eohippus* or *Wyacotherium* of early Eocene time developed into the *Mesohippus* and *Miohippus* during the oligocene epoch, and to the *Anchitherium* and *Megahippus* by mid Miocene. There was not much change in body form to tooth structure over a time of about 20 million years, except a gradual increase in size. These animals' diet was limited to low-growing bushes and flowering plants in the woods.

The great revolution in the development of the grass-eating mammals was led by the horse genus *Merychippus*. Those horses with a tendency to grow high-crowned cheek teeth, with a deepening of the enamel in the troughs between the tooth crests, were the animals that made the best use of the expanding grasslands in the Plains States.



*As horses evolved, their molars, or grinding teeth, grew larger and the enamel (shown in black) was folded into more and more complex patterns.*

The deeply infolded enamel of the cheek teeth was exposed on the flat tooth crown in a raised pattern which varied by genus and species. The enamel was firmly fixed in dentine and "cement." The adult cheek teeth of grass-eating horses grow continuously through most of the animals' lives.

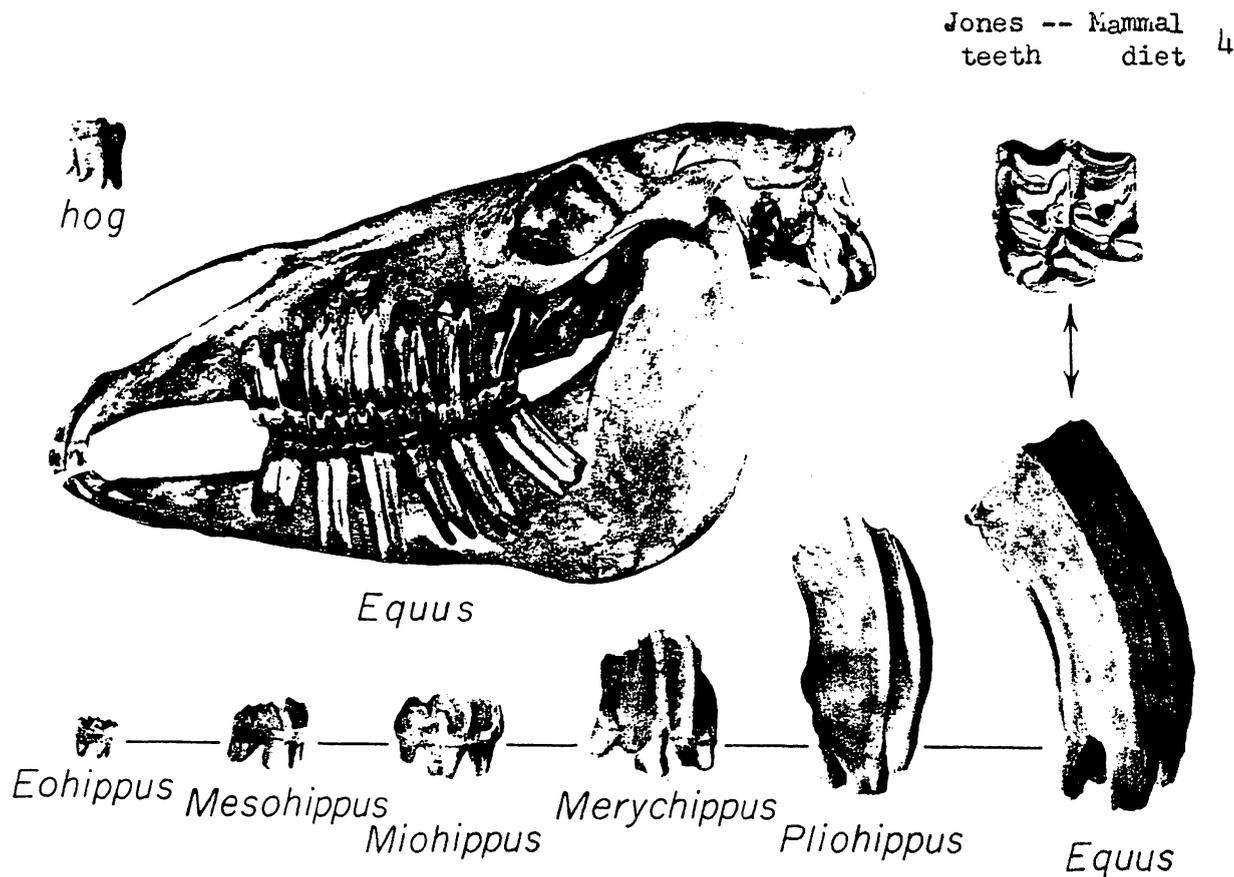


Figure 345. Low-crowned and high-crowned cheek teeth. Top left, molar tooth of a hog in which the crown is shorter than the roots; right, corresponding tooth of a modern horse, *Equus*, in which the crown is about 5 times as long as the roots. Center, skull of the horse ( $\times \frac{1}{6}$ ) dissected to show the high-crowned cheek teeth in place. Lower row, corresponding upper left molars of fossil horses from *Eohippus* to *Equus*, all at a uniform scale (about  $\frac{1}{2}$  natural size). The crown is low in *Eohippus*, *Mesohippus*, and *Miohippus*, then increases rapidly in height from *Merychippus* to *Equus*. The crown view of the worn tooth shows the ridges formed of the enfolded enamel. The skull was dissected by S. H. Chubb. (Yale

Meanwhile, we humans, who are members of the mammal order of primates, must struggle along with the low - crowned teeth which have a thin cap of enamel. Our fragile dental battery is sybject to a variety of accidents and afflictions. So, we frequently face hours of agony in the dentist's chair, and may face the final indignity of fake choppers which we park in a glass of water in the bathroom when we go to bed.

Sources and Credits:

Carl Dunbar, Historical Geology, second edition. John Wiley & Sons, New York, 1964

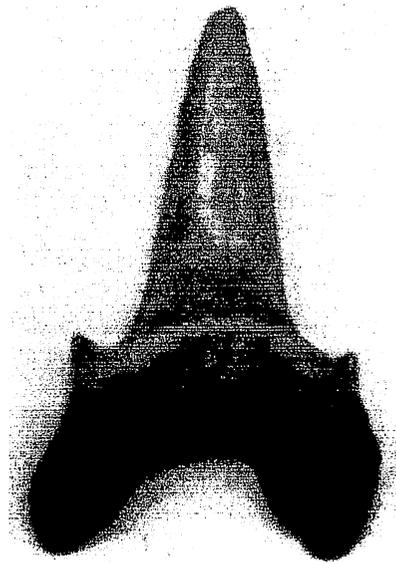
Carroll Fenton and Mildred Fenton, The Fossil Book. Doubleday & Co., Garden City, N Y, 1958

John Reader, The Rise of Life. Alfred A. Knopf, New York, 1986

## SHARK BYTES

Ed Swiatovy

469 Tee Taw Circle, Sherman, TX 75092



This is the first in what is intended to be an on-going series on fossil sharks. The focus, at least initially, will be on Cretaceous sharks of Texas. I will attempt to devote one article per month covering a specific shark species or a specific family of sharks. I also intend to have a question and answer section in each article wherein I will try to give reasonably coherent answers to any questions our readers may have concerning fossil sharks.

With the able assistance of Chris Vencevich and the magic of cyberspace, we intend to accompany the descriptions of sharks with photographs and illustrations of teeth and other fossil material.

The history of sharks is a long one. They first appeared around 400 million years ago as fresh water species. Although many other families of terrestrial and marine animals have long since ceased to exist, the family of sharks seems destined to continue indefinitely provided mankind does not succeed in its' destruction.

Although considered by some to be a primitive life form, sharks are probably more highly evolved than most bony fish and many terrestrial creatures. They have sensory organs for locating prey that far exceed anything mammals, birds or reptiles are endowed with. They can not only detect the presence of 1 or 2 parts per million of blood in water, some are capable of sensing the electrical impulses given off by the beat of the intended victim's heart and muscular contractions. Couple these abilities with tremendous speed and power, and you have a creature at, or near the top of the food chain.

Although fossil sharks have been the subject of research for well over a century, many species still wait to be discovered and/or recognized. Many of the known genera and species had been renamed and reclassified time and time again. In a field of study in which the subjects' quantifiable remains are usually little more than single teeth, partial dentitions or fragments of fossilized cartilage, a constant update of information is a must. As a result of this updating, it is often found that early assessments were inaccurate based on lack of material available for study.

The main problem faced by the avocational paleontologist is the scarcity, or absence, of reference material available for identification of fossil shark teeth or other hard parts that he, or she, has found. Compounding the problem is the fact that the nomenclature for many genera and species continues (as previously mentioned) to change and few publications are available to keep the non-professional abreast of the latest changes. A later article will address this problem of nomenclature and will include a list of invalid genera.

Individual fossil shark species will be discussed, one at a time, and will include the latest reference material available. This is intended to assist those unable to procure copies of the excellent publication co-authored by Bruce Welton and Roger Farish and those by other authors.

## SHARK BYTES PART 2 by Ed Swiatovy

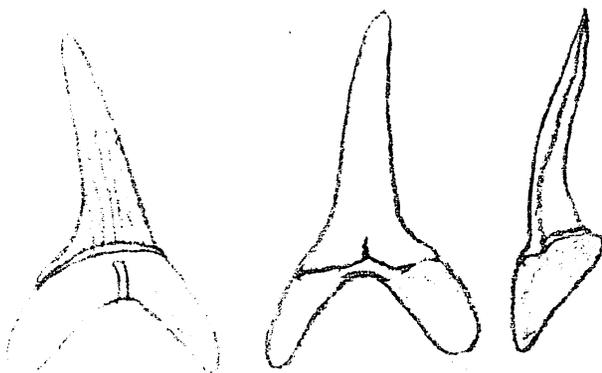
SCAPANORHYNCHUS, in addition to being a genus endowed with one of the most difficult names to pronounce, is one of the most sought-after Texas shark fossils. As the end of the Cretaceous approached, Scapanorhynchus emerged as the largest surviving member of the genera of Cretaceous sharks. Throughout the years, there has been some confusion regarding the genus to which Scapanorhynchus belongs. This is due to the fact that Scapanorhynchus bears more than a passing resemblance to sharks of the Odontaspis and Carcharias families. Scapanorhynchus was originally known as Lamna (Odontaspis). Agassiz made this assignment in the 1830's. The assignment to the genera *Scapanorhynchus* occurred over 100 years later.

Excavations of articulated Scapanorhynchus remains in Lebanon show the genera to be extremely close in physical appearance to the extant genera *Mitsukurina*. *Mitsukurina* (Goblin shark) is a fairly large shark living in the offshore waters of Japan at depths of as much as 1600 feet. It is characterized by its' long thin snout, protruding jaws and very long tail.

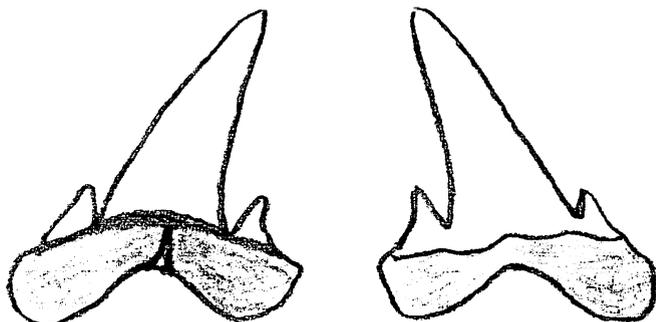
There are 2 main species of Scapanorhynchus present in the Cretaceous of Texas. The earlier, and smaller of the 2 is Scapanorhynchus aff. *raphiodon*. In this case, the terminology *aff. raphiodon* indicates that this particular species exhibits an affinity for the previously named species (*raphiodon*) but is not definitely assigned to it. Scapanorhynchus aff. *raphiodon* is generally accepted as being represented in Texas in strata dating from the Turonian through the Coniacian.

Scapanorhynchus aff. *raphiodon* is described as having anterior teeth with long cusps, usually lacking side cusplets, and a cutting edge that extends along the entire margin of the cusp. Cusplets, when present, will be limited to one diminutive pair. The cusp is sigmoidal in profile and will usually contain striations on the lingual crown face. The lingual crown face is strongly convex, while the labial face is nearly flat and is usually devoid of striations. The striations and cutting edges are useful in identifying Scapanorhynchus aff. *raphiodon* and in preventing confusing it with members of the Odontaspid or carcharias genera. While the striations are present in the afore-mentioned genera, those found on the anteriors of *S. aff. raphiodon* are unique in the fact that they diverge from the center of the tooth crown as they approach their termination near the point of the cusp.

The roots of the anterior teeth exhibit a prominent central protuberance, bisected by a deep nutrient groove, on the lingual surface. The root lobes are long and slightly flattened in the upper anteriors. The lobes are highly compressed, as well as more divergent in the lower anteriors. A prominent dental band separates the root from the cusp.

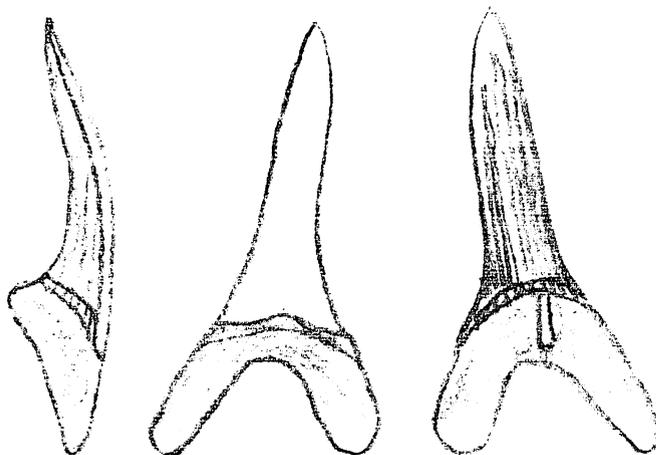


Lateral teeth exhibit cusps that are highly compressed in the labio-lingual aspect and are broader with striations that are greatly reduced or entirely missing. Inclination of the cusps towards the rear increases as the position of the tooth in the dentition approaches the posterior aspect of the jaw. Cutting edges cover the entire margin of the cusp. A pair of triangular cusplets is present on all laterals. The root retains as strong nutrient groove, but exhibits a reduced lingual protuberance when compared to the laterals. The root lobes are highly compressed labio-lingually and are strongly divergent with broadly rounded ends.

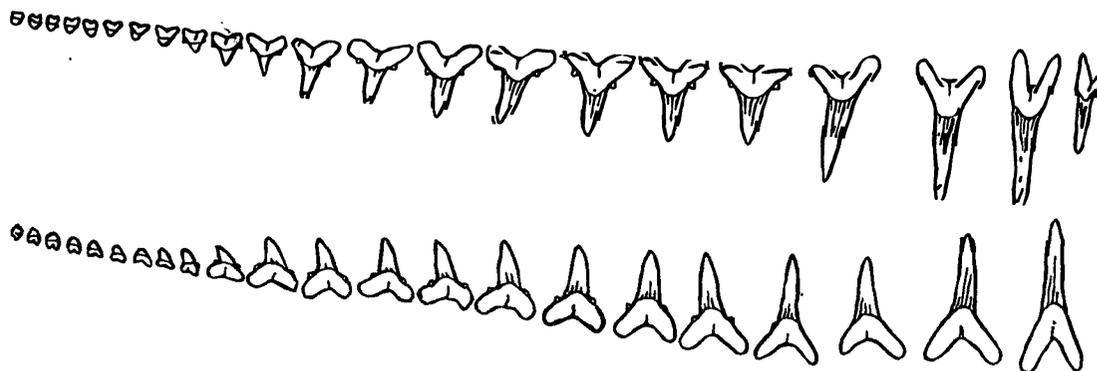


The second of the 2 main Scapanorhynchus species found in Texas is *Scapanorhynchus texanus*. *Texanus* is the big daddy of the genus with teeth approaching 2 inches in length. Teeth of *Scapanorhynchus texanus* are easily distinguished from *Odontaspis* and *Carcharias* by its' much greater size and by the complete cutting edges (as described above for *S. raphiodon*).

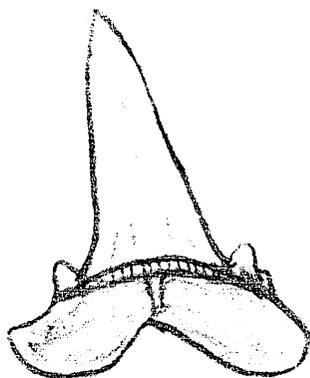
The cusps of the anteriors are strongly striated for most of their length, but the striations do not diverge as in *S. aff. raphiodon*. The lower 1/3 of the cusp is narrower than the area closer to the point. Cusplets, if present will be diminutive. The roots are as described for *S. aff. raphiodon*.



It is interesting to note the striations on the cusp extend completely across the dental band and onto the root of *S. texanus*. This also occurs in teeth from *S. aff. raphiodon* found in strata younger than Lower Coniacian. This characteristic is used, by some, to assign all teeth exhibiting these striations to *S. texanus*.



The lateral teeth of *S. texanus* are as described, above, for *S. raphitodon* except that the lateral or *S. texanus* are considerably greater in size and may exhibit a second set of triangular cusplets. The striations extending across the dental band, as described above as occurring in the anterior, are present in the lateral teeth of *S. texanus*.



Posterior teeth of both species are small and rather nondescript. Both are easily confused with posteriors from other species.

## SHARK BYTES part 3 by Ed Swiatovy

A genus of fossil shark that is quite common in Texas is **CRETOLAMNA**. A number of *Cretolamna* species occur throughout Texas Cretaceous strata dating from the Albian thru the Maastrichtian.

*Cretolamna appendiculata*, the species most familiar to Texas hunters, became extinct as recently as the Upper Eocene and had worldwide distribution. It is the archetypal species of *Cretolamna*.

*Cretolamna appendiculata* (fig. 1 and fig. 2) is characterized by its' moderately large size of up to 3 cm in length. The narrowly triangular primary cusp is convex on the lingual face and nearly flat on the labial face. Both faces are smooth. Cutting edges extend from the tip of the cusp to the base. A single pair of triangular cusplets flanks the cusp. The roots are bilobate with a u – shaped notch between the lobes of the anterior teeth and a notch more reminiscent of a shallow "V" separating the lobes of the lateral tooth lobes. The lingual aspect of the root shows a weak central protuberance with no nutrient groove, although a small foramen may be present. The dental band is narrow on all tooth positions.

The cusps of the lateral teeth are labio-lingually compressed with both faces being weakly convex. The cusps of the lateral and posterior teeth are distally inclined, with the inclination of the posteriors greater than that of the laterals. The lower edges of the lobes of the lateral and posterior teeth tend to be flattened to the extent that some appear almost square.

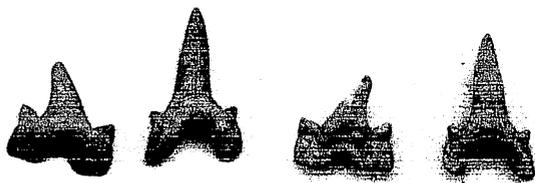


Fig. 1

Fig. 2

As is the case with many fossil shark genera, there is some controversy regarding the validity of the species *Cretolamna woodwardi* that is found in Turonian deposits. Since it is not the intent of the writer to take sides in this argument, I'll simply list the differences between *Cretolamna appendiculata* and *Cretolamna woodwardi*.

*Cretolamna woodwardi* differs from *appendiculata* in having more robust cusps with broadly convex cutting edges. One pair of peg-like divergent cusplets flanks the cusps. The roots are similar in shape to those of *appendiculata*, but more massive. The lingual dental band is well developed. The size of teeth from fully-grown individuals is similar in size to those of adult *appendiculata*. Tooth characteristics of juvenile and young adult individuals are unknown for this species.

A controversial sub-specie is *Cretolamna appendiculata lata*. It is considered by some to be a separate species and by others to be a simple ontogenetic variation within the *appendiculata* species. The features distinguishing this species from *appendiculata* are more broadly triangular cusplets, a broader cusp (retaining the same general outline as *appendiculata*) and a more robust root with shorter lobes. The range for the species is early to late Campanian.

The final species known from Texas is the Maastrichtian species *Cretolamna biauriculata maroccana* (fig. 3). This species has been, and still frequently is, confused with *Serratalamna serrata* to which the anterolateral teeth bear a strong resemblance.



Fig. 3

A broad triangular cusp, 2 pairs of triangular cusplets and a strongly obtuse lower root margin characterize *Cretolamna biauriculata maroccana*. The cusp is wide but rather flat. Normally, the nutrient groove is absent with weakly developed foramen serving that function. The cusplets nearest the primary cusp tend to diverge slightly, but to an equal degree. The secondary cusplets are quite small. The size of *maroccana* teeth compares favorably to *Cretolamna appendiculata*.

## SHARK BYTES PART 4 by Ed Swiatovy

The most sought-after genus of fossil shark from the state of Texas is *Cretodus*. The size and menacing appearance of teeth from the species of *Cretodus* occurring in Cenomanian through Coniacian deposits makes them irresistible to collectors of shark fossils.

*Cretodus* belongs to the *Cretoxyrhinid* family that also includes *Cretolamna* and *Cretoxyrhina*. The oldest member of the genus in Texas is *Cretodus semiplicatus*, (Figs. 1 & 2) which is found in the Pepper, Woodbine and lower Eagle Ford (Cenomanian) formations throughout Texas. The species is characterised by the following features:

A fairly large overall size (up to 40+ mm).

A high, narrow cusp exhibiting a weakly convex labial face and a strongly convex lingual face with strong folds in the enamel at the base of the crown and cusplets. The folds are more robust on the labial face of the cusp than on the lingual face. The cusp is weakly sigmoidal in profile.

One pair of strongly divergent cusplets, continuous with the primary cusp.

A large root containing a prominent lingual protuberance with no nutrient groove and having elongate lobes separated by a deep u-shaped notch.



Fig. 1



Fig. 2

The grand prize for collectors of fossil sharks teeth in Texas is *Cretodus crassidens* (Figs. 3 & 4) from Turonian through Coniacian deposits of the Arcadia Park, Eagle Ford and Atco formations of the Austin Group. *C. crassidens* is distinguished from *C. semiplicatus* by the following characteristics:

A much larger (65+ mm.) and more massive adult size.

Weaker folds in the enamel at the base of the cusp.

Relatively broader lingual protuberance almost completely spanning the upper part of the root, and forming a very strong shelf at the base of the cusp.

A broad, vertical dimple in the root protuberance.

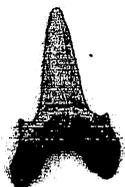


Fig. 3



Fig. 4

## Fossil Teeth and the Internet

John J. Fagan  
9757 Seeley Ave.  
Chicago, IL 60643

Any study of fossil shark and ray teeth would not be complete without the mention of a great source to identify these teeth. The source found on the Internet is **elasmocom**. The site was begun a few years ago by Jim Bourdon to provide collectors at the quarries of Auroa, NC. a forum to share information and keep abreast of news of the locality.

From these beginnings as an attempt to provide a brief overview of the *Leek Creek Fauna* at the site, its stratigraphy, it has grown to give a broad overview of the selachian material of the Atlantic Coastal Plain.

It started with the pictures and descriptions of the shark and ray teeth of the Lee Creek (Aurora) fauna that Jim collected over the years. In time it has grown to include over 150 linked pages. If you are looking for information about a fossil shark or ray genera from the Cretaceous to the Neogene this website will give you an excellent starting point, including bibliographical references.

It has expanded to include tooth identification from various sites including:

Cretaceous - Peedee Fm, Lake Waccamau, NC; Black Creek Fm, NC; Smoke Hill Fm  
of Kansas and Cretaceous of Utah.

Early Eocene of Virginia

Miocene Sharktooth Hill of California

The website also includes many links to other interesting fossil faunas and floras.

The serious or the casual collector could spend many profitable hours (days) on this website and surfing the many links that it contains

COLLECTING FOSSIL SHARK TEETH IN THE LEE CREEK MINE, AURORA, N.C.

Les Heinzl  
13 Windward Court  
Thurmont, Maryland 21788

The Lee Creek Mine at Aurora, North Carolina has yielded many thousands of fossil shark teeth of various sizes over the past decade. Currently, PCS Phosphate Inc. is mining the phosphate ore at this site and previously, Texasgulf Inc. performed mining operations for many years at Lee Creek. Numerous fossil clubs have these corporations to thank for allowing collecting by organized groups for most of the last 15 years. Although fossil collecting is not permitted at the present time, it is hoped the mine will be re-opened to collecting within a year or two. This article briefly discusses my experiences in collecting the more common shark teeth in the mine from the years 1988-98.

There are three major formations exposed in the mine and all three are from different geologic epochs. The oldest layer is the Pungo River Formation (14 million years in age, Miocene Epoch). This formation consists of gray, dolomitic sandy limestone and dark-greenish brown to dark gray sands. The dark phosphatic sands of this layer make up the rich phosphate ore, which justify the mining operations. The Yorktown Formation (4.5 million years in age, Pliocene Epoch) consists of blue gray, silty fine sand, which overlies the Pungo River Formation. The Yorktown sand is dark gray when wet. Above the Yorktown is the Plio-Pleistocene layer, generally named the Croatan Formation, which is estimated to be 2.1 to 1.8 million years in age. This formation has been sub-divided into the Chowan River Formation (Pliocene) and James City Formation (Pleistocene) by some authorities; however, for the purposes of this article, these beds have been grouped together as Croatan. The Croatan Formation is a blue-gray to greenish-gray sand with abundant white shell and coral. From a distance, exposed piles of this formation appear white because of its rich fossil content.

Becoming familiar with the geology of the mine is very helpful in collecting the fossils, and in particular, the shark teeth. Although marine fossils are very abundant in all three formations, shark teeth are only common in the Pungo River Formation and the Yorktown Formation. The Croatan Formation is very rich in fossil mollusks and coral; however, shark teeth are seldom found. Fossil teeth from the great white shark, *Carcharodon carcharias*, are occasionally found in the Croatan, especially since the black enamel of

this fossil tooth stands out well against the abundant white shell material of this layer. Unless the shark tooth collector is specifically looking for this species, he/she may want to move on to areas exposing the Yorktown or Pungo River Formation. Most fossil collectors that visit the Lee Creek Mine are interested in finding a large shark tooth or at least a smaller tooth from a rare species of shark. This is still an attainable goal, although over-collecting in a smaller, restricted area has diminished your chances in recent years. Still abundant in the Pungo River and Yorktown Formations are the more common shark teeth, as well as the remains of other fossil vertebrates, such as rays, bony fish, porpoises and whales.

Upon arriving on the company bus at the collecting area of the open-pit mine, one is impressed by the size of the mining operation, and the numerous mine tailing hills, ridges and flats. In the late 1980's and early 1990's this area was even larger and seemed to resemble some Badlands in the western U.S. Later mining methods involve filling in the pits more rapidly. Unfortunately, this resulted in a smaller, more restricted fossil collecting area.

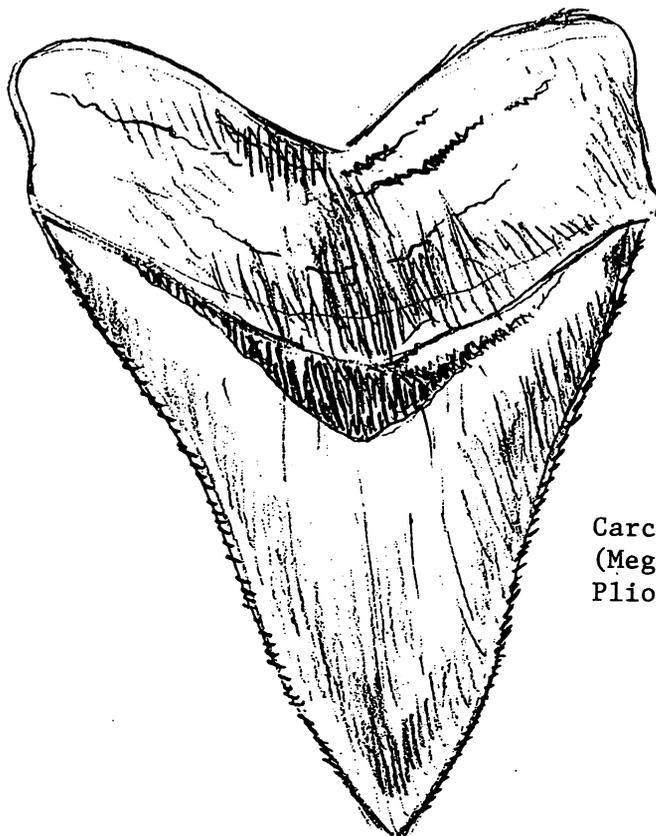
After unloading from the bus, the collecting party rapidly disperses into the pit. The experienced collector will choose the most promising hills or flats to head for. From a distance, the darker brown hills are usually Pungo River Formation exposures. As one gets closer, limestone boulders will also be present. The Yorktown Formation hills and flats will be lighter and blue gray in color. Finally, the Croatan exposures will appear white from the rich shell fossils. As with all mining operations, there is always some mixing of formation material. One side of a hill can be Yorktown while the other side can be Pungo River Formation.

The largest shark teeth are found in the Yorktown Formation, those of the giant extinct shark, *Carcharocles megalodon*. Teeth with a slant length of 6 $\frac{3}{4}$ " have been found in this layer. This shark species is also recognized as *Carcharodon megalodon* by some authorities and the older literature. Currently, many shark experts will argue that the extant great white shark, *Carcharodon carcharias*, is the only species with the valid genus *Carcharodon*.

The largest shark teeth in the Pungo River Formation are those of *Carcharoles chubutensis* which generally do not have slant length greater than 4". Some of the teeth of this species have lateral cusplets, while other specimens look very similar to *C. megalodon*. Again it is argued by some authorities that these sharks represent only a slight variation from *C. megalodon* and are not a separate species.



Carcharodon carcharias  
(Great White Shark)  
Pleistocene Age- Croatan Formation



Carcharocles megalodon  
(Mega-toothed Shark)  
Pliocene Age- Yorktown Fm.



Carcharocles chubutensis  
(Mega-toothed Shark)  
Miocene Age- Pungo River Fm.

Serena Heinzl  
Feb 2000

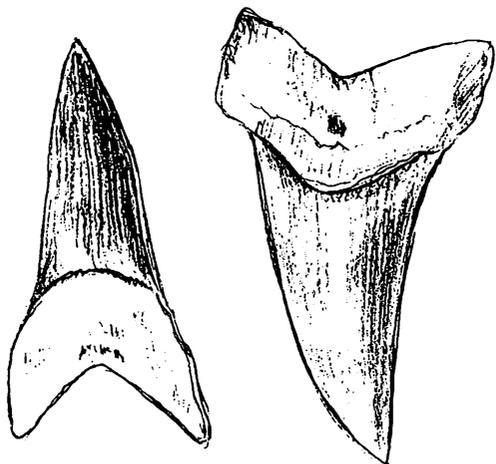
Often found in association with the larger shark teeth in both formations are the bones of porpoises and whales. This relationship makes sense since it is known that these marine mammals were the prey for the large shark predators. In fact, numerous porpoise and whale bones in the mine have been found with bite marks from the shark teeth. During a shark attack, the sharks would often lose some isolated teeth.

If the fossil collector is looking for large numbers of teeth versus size, the Pungo River Formation yields the greatest number of teeth. The medium-sized and smaller shark teeth often are often well preserved, and the fossilization process has resulted in beautiful coloration. Very common in the Pungo River Formation are the gray sharks, *Carcharhinus*, the extinct tiger sharks, *Galeocerdo contortus* and *G. aduncus*, and the sand tiger sharks, *Carcharias*. Also found are the larger teeth of the extinct mako shark, *Isurus hastalis*, and the snaggletooth shark, *Hemipristis serra*. The more rare teeth found of this layer are from the sevengill shark, *Notorynchus*, the bramble shark *Echinorhinus*, and the angel shark, *Squatina*. Finally, careful screening of the Pungo River material will yield hundreds of very small teeth and micro-teeth.

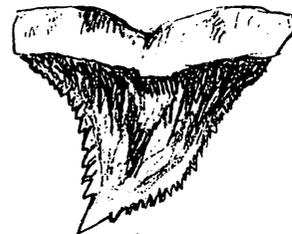
Experienced fossil collectors search in the Yorktown Formation, not only for the very large *C. megalodon* teeth, but also for some of the other large teeth that can be found in this stratum. Teeth of the extinct mako shark, *Isurus xiphodon* (some authorities recognize as *Isurus hastalis*), have been found up to almost 3" slant length. Teeth from the snaggletooth shark, *Hemipristis serra*, and the tiger shark, *Galeocerdo cuvier*, are also larger in the Yorktown Formation than their relatives in the Pungo River stratum. Probably the most common medium-sized teeth found in the Yorktown exposures are from the dusky shark, *Carcharhinus obscurus*. Although not common, the sevengill shark, *Notorynchus primigenius*, is more abundant in this formation than in the Pungo River Formation. The rare teeth to search for in the Yorktown stratum are from the false mako shark, *Parotodus benedeni*, the sixgilled shark, *Hexanchus gigas*, and the very rare megamouth shark, *Megachasma cf. pelagios*.

The problem in identifying different species of fossil sharks is that other than the teeth and occasional vertebral centra, most shark remains are not preserved. The teeth in a sharks jaw vary in size and shape, depending upon their position in the mouth. The teeth in the upper jaw are often quite different from those in the lower jaw. A shark will

SHARK TEETH OF THE PUNGO RIVER FORMATION (MIOCENE AGE)



*Isurus hastalis*  
(Mako Shark -extinct)



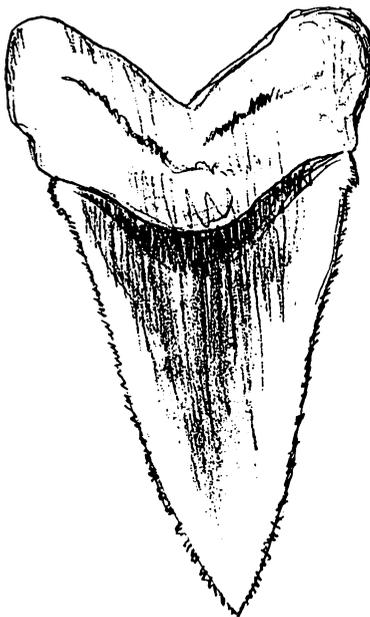
*Hemipristis serra*  
(Snaggletooth Shark)



*Galeocerdo contortus*  
(Tiger Shark -extinct)



*Sphyrna lewini*  
(Hammerhead Shark)



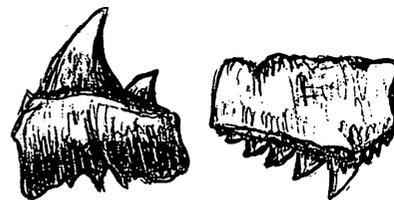
*Carcharocles chubutensis*  
(Mega-toothed Shark)



*Galeocerdo aduncus*  
(Tiger Shark -extinct)



*Negaprion eurybathrodon*  
(Lemon Shark)



*Notorynchus primigenius*  
(Sevengill Shark)



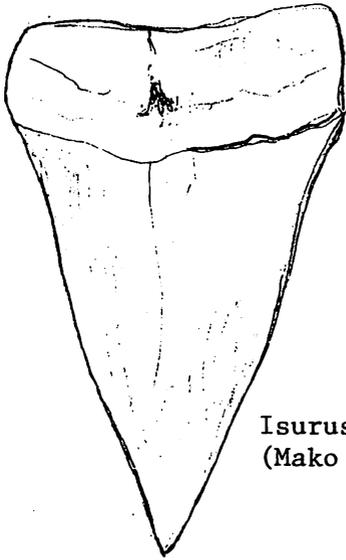
*Carcharias cuspidata*  
(Sand Tiger Shark -extinct)



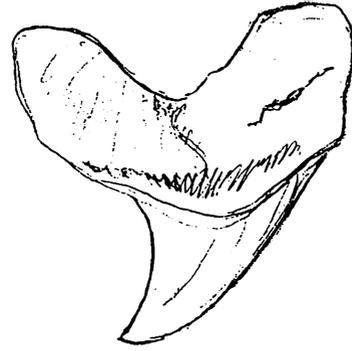
*Carcharhinus egertoni*  
(Gray Shark -extinct)

*Serena Heinzl*  
Feb 2000

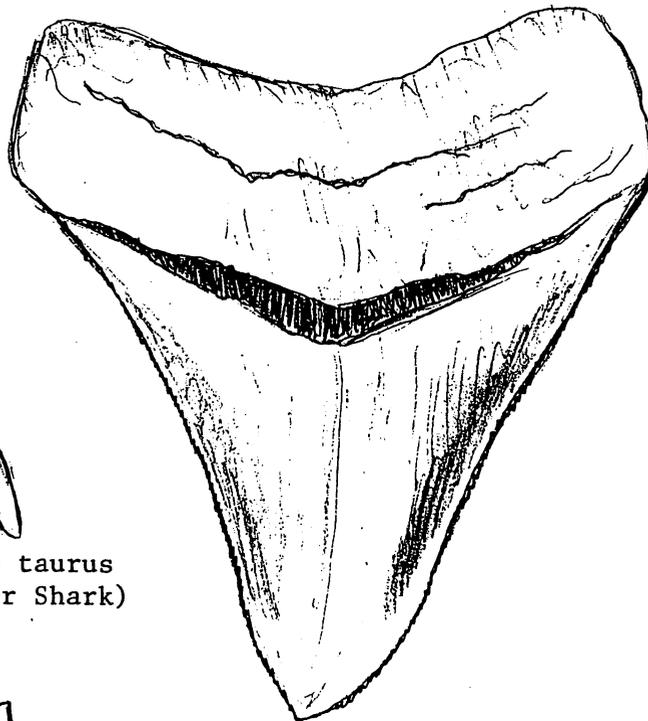
SHARK TEETH OF THE YORKTOWN FORMATION (PLIOCENE AGE)



*Isurus xiphodon*  
(Mako Shark -extinct)



*Paratodus benedeni*  
(False Mako Shark-extinct)



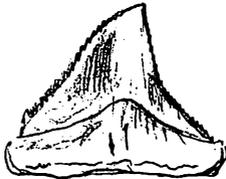
*Carcharocles megalodon*  
(Mega-toothed Shark -extinct)



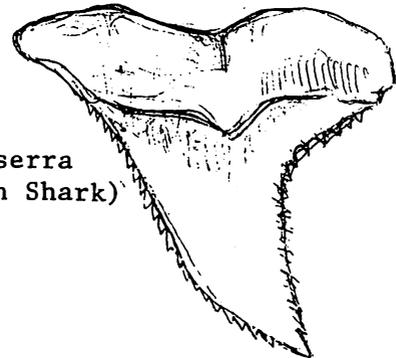
*Carcharias taurus*  
(Sand Tiger Shark)



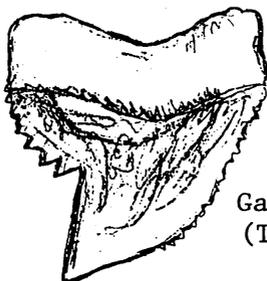
*Notorynchus primigenius*  
(Sevengill Shark)



*Carcharhinus obscurus*  
(Dusky Shark)



*Hemipristis serra*  
(Snaggletooth Shark)



*Galeocerdo cuvier*  
(Tiger Shark)

regularly lose and replace its teeth throughout its life. As a result, isolated shark teeth are common fossils in many sedimentary strata. Fortunately, fossil collectors have made rare finds of shark remains where the shark died and was rapidly buried. In these cases, the teeth from the same shark can be collected and an associated dentition can be reconstructed. A very rare associated dentition of the false mako shark, *Parotodus benedeni*, was collected at the Lee Creek Mine in 1992-1993 by George W. Powell Jr. Found at this site were 113 teeth and an associated dentition was reconstructed by Dr. Bretton Kent of the University of Maryland. In addition, a few associated dentitions of the giant extinct shark, *C. megalodon* have also been found at the Lee Creek Mine over the last 20 years.

Over the past ten years, ideal shark teeth collecting conditions has dwindled at the mine for a variety of reasons. The collecting has been restricted to a smaller area, which has led to over-collecting. There are times when you are simply walking in the footsteps of 60 people from the previous collecting trip. In addition, mining operations have moved away from the Pamlico River and Sound. The thickness of the fossiliferous strata seems to have been adversely affected by this trend. Future mining operations should reverse this trend. Hopefully, fossil collecting will again be permitted in the near future.

As for me, I have greatly enjoyed collecting at this mine over the past decade. Even when the collecting of shark teeth has been scarce, my interest in fossil mollusks and other invertebrates has resulted in me having a field day at Lee Creek. In the end, no matter what one was hunting for, all fossil collectors have the mine officials to thank for their Lee Creek memories.

#### Acknowledgements:

I would like to especially thank my daughter, Serena, for her artistic drawings of my shark teeth.

I would also like to express my sincere appreciation to the following people who have either provided information to me in the past concerning shark tooth identification, or information on the stratigraphy of the mine: Jim Bourdon, George Fonger, Tex Gilmore, Bill Heim, Becky Hyne, Scott McPhilliamy, Dr. Bretton Kent, Mark Palatas, George Powell Jr., and Dr. Robert Purdy. I would also like to express my gratitude to the authors of the following references:

References:

- Ray, C.E. 1987. Geology and Paleontology of the Lee Creek Mine, North Carolina II. Smithsonian Contributions to Paleobiology Bul.#61, Washington, D.C., 283 pages.
- Kent, B.W. 1994. Fossil Sharks of the Chesapeake Bay Region. Egan Rees & Boyer, Inc., Columbia, Maryland, 145 pages.
- Chandler R. and J. Timmerman 1994. Neogene Fossils of North Carolina, A Field Guide. North Carolina Fossil Club, Durham, N.C., 42 pages.
- Ashby W.L. 1986. Fossils Of Calvert Cliffs. Calvert Marine Museum, Solomons, Maryland, 19 pages.
- Case G.R. 1982. A Pictorial Guide to Fossils. Van Nostrand Reinhold Company, New York, 496 pages.
- Case G.R. 1973. Fossil Sharks: A Pictorial Review. Pioneer Litho Co., New York, New York, 64 pages.
- Maryland Geologic Survey 1904. Miocene Plates, The John Hopkins Press, Baltimore, Maryland, 127 pages.
- Purdy, R.W. 1990. A Key To The Common Genera Of Neogene Shark Teeth. Smithsonian Institute, Washington, D.C. 24 pp.

Web Site Reference:

- Bourdon J. and B. Heim 1996, [elasmo.com](http://elasmo.com), Lee Creek aka Aurora - A Neogene Fauna From North Carolina, Extinct Sharks and their Teeth, Shark Species I & II.

## THE UNIQUE AND CURIOUS DESMOSTYLUS

*Betty I. Lemkau*  
*22019 Young Ave.*  
*Castro Valley, CA 94546*

Professor O. C. Marsh obtained his first specimen of "teeth of an undescribed animal, unique and curious (Miocene) " from a Doctor Lorenzo Gordin Yates, a dentist and amateur collector of natural history objects. The teeth were collected in 1876 and listed in the Doctor's private catalogue in 1886. This was the first mention of an animal that later was described and named in 1888 by Professor Marsh. His formal description of *Desmostylus hesperus*, gen. et sp.nov., follows:

"The remains known of the present species indicate an animal of about 15 feet in length., and of robust proportions. The most characteristic parts preserved are the molar teeth, which are composed of a number of vertical columns, closely pressed together, and in adult animals, firmly united at their bases. These columns are thickly invested with enamel, which is rugose externally. Inside the enamel, is a body of dentine, in which there is a central cavity.

In immature teeth, the columns are nearly round, and loosely united, but as they increase in size they press together, and become more or less polygonal in cross section. Before being worn, they have their summits smooth and convex, but after some use, the center of each column presents a rounded elevation.... This is due to harder material forming the walls of the central cavity. As this apex is removed by further wear, the cavity is reached, and this central opening increases in size as the tooth is shortened by attrition.

The number of columns in a single tooth is uncertain, but there are indications of at least twelve or fifteen, and perhaps more. There were both upper and lower molar teeth of similar structure, but the rest of the dentition is unknown.... The known remains of this animal are from Alameda County, California, and are preserved in the "Museum of Yale College...."

Over the following years many more specimens were found in more than 25 locations in the Briones Formation and Temblor Formation of California. A skull, and not too many years ago a skeleton was found in Oregon, as well as in Japan, first written about in 1902.

There were many changes in Professor Marsh's interpretation necessitated by later work by other investigators, and not all of them could agree.

When I agreed to write an article about the teeth of *Desmostylus hesperus* for M.A.P.S. I didn't remember that in 1988 Larry L. Oliveri, a MAPS member had already written an excellent article for the Digest, and anything else I could write would be redundant except for some of the early history of the discoveries and descriptions by Prof. Marsh. My reference is "A study of the Miocene Sirenian *Desmostylus*", by V. L. Vanderhoof, University of California Press, Berkeley, California, 1937.

## HUNTING THE PECULAR DESMOSTYLUS

by Larry L. Oliveria Copied from MAPS Digest Feb. 1988

Subungulates, when considered as a whole, appear to be an unrelated group. Mammals like the tiny hyraces, dugongs, elephants and mastodons, and the strange amphibious desmostylians make up this group....

Both shores of the Pacific boast the presence of remains from *D. hesperus* and the closely related *Paleoparadoxia tabatai* (Tokunaga). The teeth are unusual. The large teeth.... consist of up to eight large cusps which are closely packed and thickly enameled cylinders.... as in other members of this group, teeth migrated forward in the jaw throughout life. Canines and incisors made up several tusks, and the lower anterior teeth resemble the shovel-tusked lower jaw of some mastodons.

The figured skull (Fig. 1) shows the typically low long, and broad skull of *D. hesperus*. Since all known remains of *D. hesperus* are found in marine deposits, many investigators confuse them with sirenians (sea cows). Reinhart correctly placed *D. hesperus* in its own order - *Desmostylia*. *D. hesperus* skeletons possess large well-developed limbs. Since their bodies are very hippo-like, it is as assumed that they lived in and about shallow coastal waters. The ancestry of *D. hesperus* is unknown but they appear to share descent with sirenians and proboscideans....

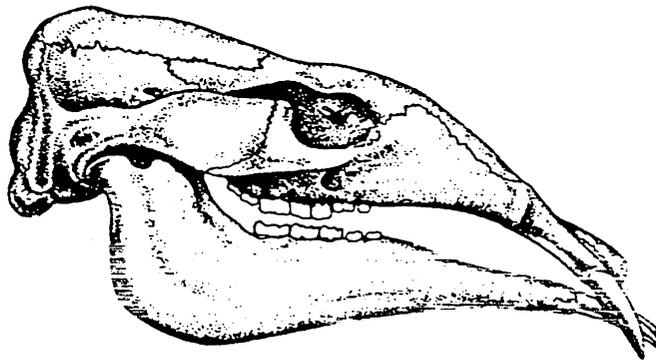


Fig.1. From Romer, (1966) *Desmostylus* 32 in. in length

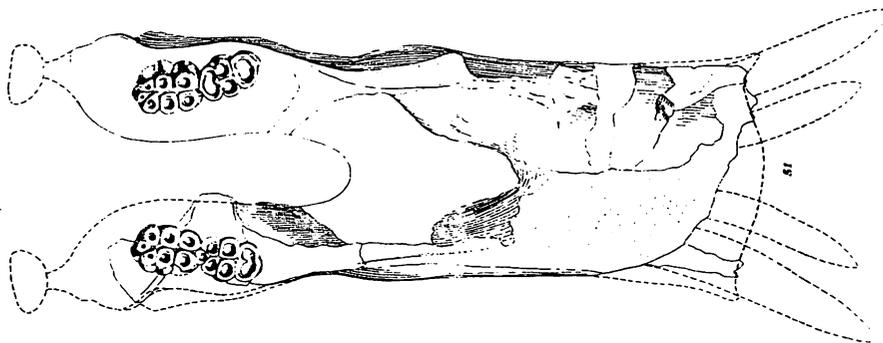
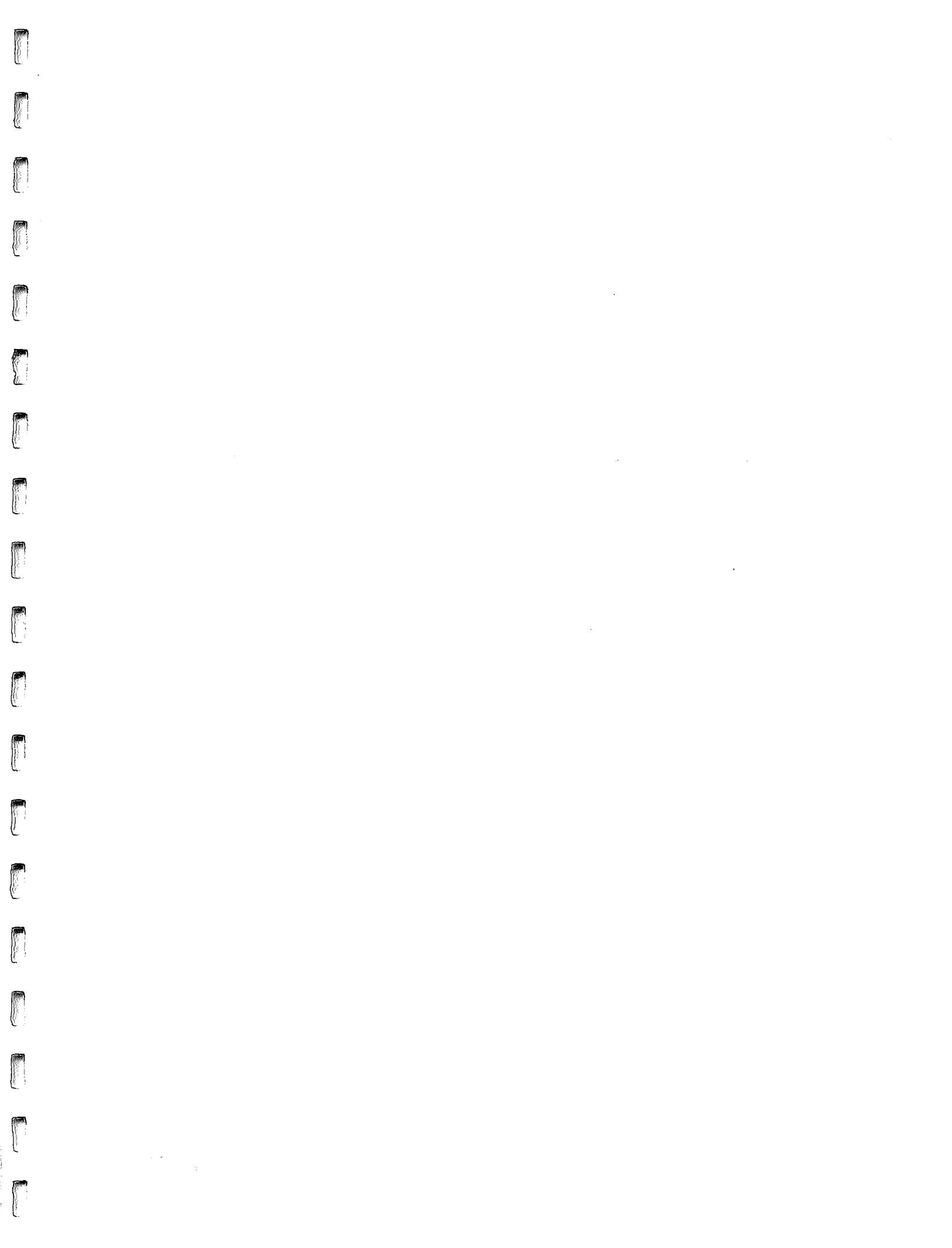


Fig. 2. From Vanderhoof, (1937) occlusal view of lower jaw. Tusk outlines restored, as are condyles. x.25





Identification of cover illustrations

# M.A.P.S *Digest*

1. Ektopodon - poorly known marsupial
  2. Thylacoleo - marsupial lion
  3. Kielantherium - early mammal
  4. Pterodaustro - pterosaur
  5. Spinosaurus - dinosaur
  6. Zygorhiza - whale
  7. Probainognathus - cynodont
  8. Giganotosaurus - dinosaur
- \* Helicoprion - a shark - shown here.

