UNIVERSITY OF ALBERTA

A SURVEY OF TOOTH ATTACHMENT HISTOLOGY IN SQUAMATA: THE EVALUATION OF TOOTH ATTACHMENT CLASSIFICATIONS AND CHARACTERS

by

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ABSTRACT

Various classifications of tooth attachment were reviewed and their historic usage evaluated. The traditional terminologies were determined to be useful for descriptive purposes. The utility of using traditional terms as character states in published phylogenetic analyses was tested empirically using new squamate dental histology data. I surveyed the dental attachment histology of 35 species of squamates. Acellular and cellular cement attached squamate tooth roots to the tooth attachment sites made of alveolar bone. Tooth attachment type was invalidated as an informative character in squamate phylogenetic analyses. Other published characters were valid with some modification. Attachment site vascularization, and the presence of acellular cement covering the tooth crown were introduced as characters worthy of investigation for use in phylogenetic analyses of squamates. It was concluded that discussions on the evolution of vertebrate tooth attachment are impeded with the retention of the traditional terminology and the examination of only gross morphology.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

4-20: (a)-(e) *Delphinapterus leucas*

CHAPTER 1

GENERAL INTRODUCTION

INTRODUCTION

Characters related to tooth attachment were used in recent cladistic analyses of squamates (the clade of lizards, snakes, their relatives, and most recent common ancestor) (Estes, de Queiroz & Gauthier, 1988; Caldwell, 1999; Lee & Caldwell, 2000; Rieppel *et al.*, 2002). The character "tooth attachment" usually had traditional categories (i.e., acrodonty, pleurodonty, thecodonty, *etc.*) as character states. Conventionally, chamaeleonids and agamids were considered acrodont, and all other squamates were considered pleurodont. There was an apparent problem with the coding of published characters; the characters were coded with the examination of gross morphology as opposed to histology, despite the inclusion of histologic criteria in the character states.

Thecodont tooth attachment was recently identified in the mosasaur (an extinct large marine lizard) *Platecarpus* (Caldwell *et al.*, 2003). Prior to this discovery, thecodonty had only been described in mammals, ichthyosaurs (extinct dolphin-like aquatic diapsids), plesiosaurs (extinct large aquatic diapsids) and archosaurs (Peyer, 1968). Caldwell *et al.* (2003) suggested that a survey of tooth attachment histology in squamates was necessary to understand how thecodonty evolved in mosasaurs.

OBJECTIVES

The primary objectives of this thesis were to examine the dental attachment histology of squamates and to use this new data to test the usage of traditional categories as character states in squamate phylogenetic analyses.

ORGANIZATION

The first body chapter (Chapter 2) of my thesis reviews a variety of tooth attachment classifications and examines their usage over the past 28 years. This study is significant because it critically compares and reviews the classifications and suggests appropriate ways to use the terminologies. This chapter suggests that the traditional tooth attachment terminology may not be useful as phylogenetic character states due to the broad definition of most categories, i.e., the terms assume a great diversity of morphologies down to usually four categories. Some of the terms discussed in this chapter were character states in squamate phylogenetic analyses (Caldwell & Lee, 2000; Rieppel *et al.*, 2002). The validity of these terms as character states in phylogenetic analyses of squamates is further evaluated, using squamate dental histology data, in Chapter 4.

The second body chapter (Chapter 3) presents the results of the study of the tooth socket histology of the Late Cretaceous extinct snake *Dinilysia* *patagonica*. *D. patagonica* is becoming better known due to recent discoveries of new fossils in Argentina (Caldwell & Albino, 2001; Caldwell & Albino, 2002). This fossil material was examined prior to the beginning of the main study of squamate dental histology (Chapter 4). The discovery of alveolar bone (an attachment tissue thought to be highly derived) in Dinilysia along with the discovery of alveolar boned in its more distant relative *Platecarpus* (Caldwell et al., 2003), hinted to me that we may have misidentified tooth attachment types in other squamates. This squamate dental histology is presented separate from the main study (Chapter 4) because it includes histologic data of a poorly known, yet significant fossil taxon relevant to discussions of the interrelationships of snakes and other squamate taxa. A review of amniote tooth attachment tissues is also included in Chapter 3.

The final body chapter (Chapter 4) presents the first survey of comparative dental histology of squamates. The traditional tooth attachment categories introduced and evaluated unempirically in Chapter 2 were tested empirically with the new squamate dental histology data in Chapter 4. The results of the evaluation of characters related to tooth attachment used in recent phylogenetic analyses of squamates (Lee & Caldwell, 2000; Rieppel *et al.*, 2003) is included in Chapter 4.

The general discussion, conclusions and implications of this thesis are presented in Chapter 5. Not only does this thesis indicate that we have misidentified squamate tooth attachment tissues and types, it also suggests that tooth attachment in other vertebrates requires reanalysis. This thesis is also significant because it shows how a reliance on ancient anatomic terminology, can hamper discussions of the evolution of a biologic system.

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CHAPTER 2

REVIEW AND EVALUATION OF TOOTH ATTACHMENT CLASSIFICATIONS AND THEIR USAGE

(To be submitted as "Budney, L.A. Review and evaluation of tooth attachment classifications and their usage" to Critical Reviews in Oral Biology and Medicine)

CONTEXT

Researchers often use modified versions of 19th century tooth attachment classification terminologies (acrodonty/pleurodonty/thecodonty) in descriptive studies and phylogenetic analyses. It is difficult to discuss tooth attachment evolution because of the differences in definition of the same terms. The purpose of this chapter is to introduce some of the used terminologies and the hazards of their use. The review and criticism of the historic usage of the classifications suggests that the traditional classification terminologies be used solely for descriptive purposes. The usage of tooth attachment terminology will be further examined in Chapter 4 with the evaluation of characters related to tooth attachment in published phylogenetic analyses of squamates.

INTRODUCTION

Tooth attachment classifications have been used for more than 150 years to classify the diversity of vertebrate tooth attachment histologies and morphologies. Tooth attachment classifications were developed to provide a common terminology for specific morphologies thereby facilitating the diagnosis and comparison of dental attachments. The morphologies/histologies named in the classifications were designated as stages in an evolutionary progression. Tooth attachment classification terminology is used today in taxonomic (Mackness & Hutchinson, 2000), phylogenetic (Johnson, 1986; Lee & Caldwell, 2000; Rieppel *et al.*, 2002) and comparative morphologic (Patchell & Shine, 1986) studies.

Although classifications have identical terminology with different definitions (Romer, 1956: Peyer, 1968; Edmund, 1969; Motani, 1997), attachment terminology is rarely cited. The problem with this is that readers do not know which definitions apply. It is important that tooth attachment terminology be properly defined and referenced because the terminology has been used to create categories defining taxonomic groups (e.g., Acrodonta Cope, 1865), as terms indicative of feeding behaviour (Tomes, 1898; Savitzky, 1988) and more recently as character states in cladistic analyses (Johnson, 1986; Casciotta & Arratia, 1993;Lee & Caldwell 2000).

The objective of this study is to examine how papers containing tooth attachment classifications have been used historically in other studies. It would be impossible to know how papers containing classifications were used were they not cited, although many studies use attachment classification terminology without citation (e.g., Hotton III, 1955; Cooper, Poole & Lawson, 1970; Olson, *et al.*, 1986; Olson *et al.*, 1987).

After determining the usage patterns, the validity of using the referenced tooth attachment classifications for different purposes is discussed based on a comparison of the classifications and their criticisms. Because authors do not justify their usage of a tooth attachment classification, I do not expect to see any trends in the use of the classifications.

MATERIALS AND METHODS

ISI Web of Science ® cited reference searches were conducted for selected references containing tooth attachment classifications (Tomes [1876-1923]; Romer [1956]; Peyer [1968]; Edmund [1969]; Fink [1981]; Shellis [1982]; Motani [1997]). Web of Science is a database of citations of science journal articles (including their references cited lists) published since 1975. I chose the above particular studies because they have been cited frequently since publication, they have been generally well received by the scientific community in that few criticisms have been leveled against them, and because they all had the intent to educate readers on the types of tooth attachment (this criterion was met if authors devoted a significant amount of the paper or a specific section of the paper to tooth attachment). Other papers (Owen, 1840-1845; Mummery, 1924; Gaengler & Metzler 1992; Gaengler, 2000) presenting tooth attachment classifications were not added to this study because they were referenced infrequently regarding tooth attachment

With the exception of Tomes (1876-1923) and Romer (1956), the chosen references were searched by author's last name and year of publication. The appropriate publication was then selected and Web of Science was searched for papers citing the chosen publication. Because Tomes (1876-1923) is in eight editions, it was searched by the author's last name, the appropriate book selected, and then Web of Science was searched again to discover the papers citing any edition of the book. Romer (1956) was searched by author's last name, publication year and topic "tooth or teeth" (i.e., combined general search and cited reference search). Then the source was selected and searched only if the page numbers were from the dentition chapter. This search procedure limited the number of non-tooth-related references. It was important to limit the citations because Romer (1956) is part of a larger publication on reptilian osteology.

Publications on the resultant lists of papers citing any of the chosen references were searched visually or electronically for the cited paper. Once found, the author's usage of that paper was documented; multiple uses of a paper were acceptable and documented. Several usage trends were noted; in order to compare the usage across the cited papers I limited my usage categories to "direct" for the attachment classification, "histology", "morphology", "ontogeny", “replacement”, “general”, “other”, and “not found”. To facilitate comparison, the number of references in a category was converted to a percentage of all citations relating to one classification (this normalized the data). The usage of the cited papers was then compared amongst the papers and between the different types of classifications (types were noticed when comparing the cited papers) to see if papers were used differently.

Review of usage categories

Assignment into the “direct” usage category required the author to have referenced an attachment term or classification directly. A statement such as “see Author (Year) for a review of dental anatomy features” was not sufficient to warrant classification in the “direct” category because it was too vague a statement to elucidate if it included attachment anatomy.

A paper fit into the “histology” category if it referred to a histologic description in a certain paper. For example, “the teeth of X were attached by cement (Author, Year)” included that paper in the “histology” usage category.

The “morphology” category was assigned to papers that cited a reference for general gross anatomy features. Examples of statements with morphologic categorization include, “teeth are large, round and pointy (Author Year)”, “tooth orientation terms e.g., distal, mesial, *etc.*, are from Author (Year)”. Tooth counts were not included in this category.

Papers citing a reference for describing dental ontogeny were placed in the "ontogeny" category. A statement such as "cement is deposited after the breakdown of Hertwig's epithelial root sheath (Author Year)" included the paper in the dental "ontogeny" category.

A paper that cited a reference for its information regarding tooth replacement was placed accordingly in the "replacement" category. "Tooth development is intraosseus (Author Year)", "a resorption pit formed prior to tooth loss (Author Year)" or "Zahnreihen theory (Author Year)"are examples of statements indicating the inclusion of a paper in the "replacement" category

The "general" category was reserved for papers that cited a reference because it contained general information and included references to a paper "containing information on tooth attachment (Author Year)."

Papers that cited references for reasons such as tooth counts, functional morphology, tooth homologies and statements such as "X, Y and Z have molars and A does not (Author Year)" were accommodated in the "other" category.

The "not found" category was reserved for papers in which I could not find the citation. Papers were relegated to this category after three visual reviews.

Review of studies used as cited references in this study

The classifications are reviewed in the order in which they were published to provide the reader with an historical context. Because the terminology for dental tissues is as plastic as that of tooth attachment, any named tissues are defined in Ten Cate (1998) and Caldwell *et al.* (2003). Table 2-1 summarizes the terminologies from the studied papers.

Tomes (1876-1923)

Tomes (1876-1923) consisted of 8 editions of a still often cited reference on human and comparative dental anatomy. Tomes (1876-1923) synthesized 20 more years of dental histology and morphology data than Owen (1840-1845), one of the earliest and most well respected comparative dental anatomy texts. Tomes (1876-1923) was aided greatly by the invention of microscopes with greater resolution and the development of better sectioning techniques previously unavailable to earlier researchers. Being a dentist, Tomes was intimately familiar with human dental ontogeny and recognized the commonalities of all vertebrate dental ontogenies. His section on comparative dental morphology is succinct and is an amalgamation of knowledge he gained by directly studying dentitions and reviewing primary literature.

Tomes's (1876-1923) tooth attachment classification was based on histology and used to classify the dentitions of fishes and all tetrapods. Tomes (1898: 222) noted it was difficult to create tooth attachment categories because "... the various methods by which teeth are fixed in their position upon the bones which carry them pass by gradational forms into one another, so that a simple and

Table 2-1: Comparison of the terminologies and attachment tissues from the studied cited references

General classifications based on morphology, and morphology and histology

Reference	Acrodonty	Pleurodonty	Subthecodonty/ protothecodonty	Thecodonty	Ankylosed thecodonty	Aulacodonty
Romer (1956)	NE	F, C	S- C	F, C	▨	▨
Peyer (1968)	BOA	BOA	P- BOA	NE	▨	▨
Edmund (1969)	C	C	P,S- C	F	▨	▨
Motani (1997)	B	B	S- NE(BOA)	F	B	U

General classifications based on histology

	Fibrous membrane	Hinge	Ankyolsis	Implantation in bony sockets
Tomes (1876 1923)	F	H	BOA	BS, PDL
	Fibrous	**Ankylosis**	**Socketed/ Thecodont**	
Shellis (1982)	D, I/PE	A, PL, P- BOA	BS, PDL	

Group specific classifications

	1	2	3	4
Fink (1981)	T>BOA>JB	T>BOA>L>JB	HA	HP
	Subthecodont	**Ankylosed thecodont**	**Aulacodont**	**Ichthyosaur thecodont**
Motani (1997)	NE(B)	B	U	NE(B)

LEGEND

A	acrodonty
B	bone
()	inferred
BOA	bone of attachment
BS	bony socket
C	cement
D	direct
F	fibrous
H	hinge
HA	hinged anteriorly
HP	hinged posteriorly
I/PE	indirect/pedicellate
JB	jaw bone
L	ligamentous
NE	not explicit
P	protothecodonty
S	subthecodonty
T	tooth
U	unknown
-	separates preferred name and tissue
>	sequentially
▨	not applicable

at the same time absolutely correct classification is impossible...". The four types of tooth attachment were fibrous membrane, hinge, ankylosis and implantation in bony sockets.

A fibrous membrane attachment was identified where a tooth was not attached directly to the jawbone, but to a band of fibrous tissue or annular ligament. Sharks, rays and sea breams (*Sargus*) were examples of animals having a fibrous membrane tooth attachment histology (Tomes, 1898). He asserted that fibrous membrane attachments had been misclassified as ankylosed attachments in the past due to researchers not detecting the very short ligament, (e.g., *Sargus* [Tomes, 1898]).

The fibrous membrane attachment type graded into the elastic hinge attachment type (Tomes, 1898). A tooth attached by an elastic hinge was recognized initially by the flexibility of the attachment site; a hinged tooth could be manipulated in place. Various morphologies and histologies were discovered upon examination of the hinged attachment site in different fish families. Some animals exhibited ankylosed and elastic hinged teeth in close proximity, (e.g., hake [Tomes, 1898]). Animals exhibiting the elastic hinged tooth attachment type included anglers, pike and cod. Tomes (1898) considered it worthy to note that teeth attached by an elastic hinge were found in a number of distantly related families.

A tooth attached by ankylosis was distinct from all other attachment types because it was not attached by fibrous tissue (Tomes, 1898). Instead, the tooth was mineralized to the attachment site on the jawbone; a distinct line where the tooth ended and the bone began was often indistinguishable. Teeth varied in their degree of ankylosis, some broke easily from their attachment sites while others broke off with bone attached to the base of the tooth. Tomes (1875) named the bony tissue attaching the teeth to the jawbone, bone of attachment. During the loss and replacement of the tooth, the bone of attachment would be lost and replaced as well. The other types of attachment were also facilitated by bone of attachment. Most reptiles and some fish had teeth attached to the jawbone by ankylosis.

Tooth attachment by implantation in a socket was recognized if a tooth was attached to a socket made of a bony tissue that was replaced when the tooth was replaced. Spanning the distance between tooth and socket was the alveolo-dental periosteum known today as the periodontal ligament. Tomes (1898) did not identify the bony tissue attaching the teeth in the sockets. Although he was aware that the bone making the sockets was associated directly with the teeth, he did not give it a distinct name. He did use "alveolar bone" (Tomes, 1898: 219) but this term was not used throughout the document. Some fish, reptiles and all mammals exemplified tooth attachment by implantation in a socket.

Romer (1956)

Romer's (1956) "Chapter 10: Dentition " began with a description of tooth histology, ontogeny, morphology and attachment and ended with a survey of reptilian dental anatomy.

His section on tooth attachment contains brief definitions of terminology based on histology and gross morphology as well as a survey of the tooth attachment types of many reptile groups. Romer's classification was not original; his terms, thecodont, pleurodont, acrodont and subthecodont, were acknowledged to be from unreferenced sources on "early studies of modern reptiles" (Romer, 1956: 442). Romer (1956) contained the most extensive survey of tooth attachment types in reptiles and acknowledged that classifying dentitions into single categories was difficult.

Histologic sections were not examined because most of the materials discussed were rare fossils and not likely to have been sacrificed for sectioning (Romer, 1956). Although Romer did not indicate exactly how he collected his data, it is likely that most of it was based on the examination of gross tooth attachment morphology. Examining gross morphology to determine tooth attachment type has been common practice but has resulted in the mistaken identification of tooth attachment types (e.g., Zaher & Rieppel, [1999]) because tissues appear different after drying or fossilization. Tooth attachment characteristics are best examined in histologic thinsections.

Thecodont tooth attachment was identified when teeth with long cylindrical roots were housed in sockets in the bone. The tooth could be attached to the jawbone by fibrous connective tissue or cement (spongy, bone-like tissue). Sauropterygians, placodonts, ichthyosaurs and archosaurs were some examples of animals with thecodont tooth attachment.

Pleurodont tooth attachment was identified when there was no socket and teeth were attached within a groove with a high labial wall and a relatively lower lingual wall. The majority of the attachment site was on the labial wall. As in thecodont attachment, teeth with a pleurodont attachment could be attached to the jawbone by fibrous connective tissue or cement. Snakes and some lizards exhibited pleurodont tooth attachment.

Acrodont tooth attachment was identified when teeth were fused directly to the top of the jawbone. Rhyncocephalians were acrodont, and amphisbaenids, teiids and some diploglossans had a condition approaching acrodont tooth attachment. Like Tomes (1876-1923), Romer asserted that the attachment types represented an evolutionary sequence of morphology.

Subthecodont tooth attachment was said to be “ill-defined” but similar to pleurodonty in that teeth are attached in a groove with a low lingual and higher labial wall. Subthecodont attachment was identified when teeth were attached in shallow sockets separated by transverse bony septa connecting the labial and lingual walls. Teeth were attached to the bone of the sockets and may have been cemented to the labial wall. Some cotylosaurs, champsosaurs and pelycosaurs had a subthecodont dentition. Subthecodonty was thought primitive for tetrapods; the other attachment types could be derived from subthecodonty with an increase in lingual wall height and socket depth producing thecodonty, a reduction in socket development and cement producing pleurodont attachment, and a further reduction in these two conditions producing acrodont attachment.

Peyer (1968)

Peyer (1968) was translated from German to English by R. Zangerl subsequent to Dr. Peyer's death in 1963. Zangerl acknowledged that translating Peyer's book was difficult owing to its technical nature. Peyer (1968) presented the largest review of comparative dental anatomy since Owen (1840-1845). His observations were more accurate than those in other publications because he observed many dental thinsections from a wide variety of dentitions. The last section of his book remains the largest collection of images of thinsections and whole dentitions.

Peyer (1968) presented a tooth attachment classification, based on gross morphologic characters, applicable to all vertebrates. It is worthwhile to note that he rarely used the terms from his classification in his overview of different vertebrate dentitions; instead, most attachments were described histologically. Peyer (1968), like Romer (1956), derived his terms from earlier literature citing Wiedersheim (see Peyer, 1937). The tooth attachment classification categories in Peyer (1968) (acrodont, pleurodont, thecodont and protothecodont) were similar in most respects to Romer (1956) and Edmund (1969).

Acrodont attachment was identified when teeth were fused to the "edges" of the jaws (Peyer 1968). Chamaeleons and agamid lizards exemplified acrodont attachment.

Pleurodont attachment was observed when teeth were attached by bone of attachment to the lingual face of the jaw. Varanid and lacertid lizards exhibited pleurodont attachment.

Thecodont attachments were diagnosed with the observation of teeth attached in deep pits that did not narrow towards their base. Peyer (1968), and Romer (1956), did not qualify thecodont attachment as requiring a ligamentous attachment; a ligamentous attachment characterized thecodonty in more recent publications (Edmund, 1969; Motani, 1997; Zaher & Rieppel, 1999).

Protothecodont attachment was identified when teeth were attached in a shallow pit. Protothecodont attachment and subthecodont attachment were synonomized by Edmund (1969).

Edmund (1969)

Edmund (1969) is a chapter in the "Morphology A" volume of the "Biology of the Reptilia" that reviewed the different aspects of dental anatomy, similar to Romer (1956), and then presented a survey of reptilian dentitions. Edmund (1969) seemed more aware of tooth development than either Romer (1956) or Peyer (1968) as he referenced more dental development literature. Edmund (1969) is based on observations of histologic sections, used for a review of tooth replacement (Edmund 1960), and whole specimens. Edmund (1969) presented a tooth attachment classification based on gross morphologic and histologic characters. Like Tomes (1876-1923), Romer (1956) and Peyer (1968), he viewed tooth attachment categories as being part of a spectrum of histologies and morphologies with each category being derived from another.

Acrodont tooth attachment was identified when teeth were ankylosed, by cement, to the apex of the jawbone. Teeth with acrodont attachment were replaced rarely. Agamid lizards, chamaeleons, and rhyncosaurs are examples of animals with acrodont attachment. All animals with teeth in multiple rows, (e.g., *Captorhinus* and rhyncosaurs), were thought acrodont even if all of the teeth were not on the crest of the jawbone.

Pleurodont attachment was identified when teeth were ankylosed, by cement, to the inner face of the labial wall of the jawbone. Pleurodont attachments varied in how much of the attachment site was on the labial and lingual walls; this varied amongst and within species and even along a single jawbone. Most lizards and snakes exemplified pleurodonty.

Thecodont tooth attachment was recognized when teeth with long cylindrical bases were set in deep bony sockets to which they were usually attached by uncalcified tissues (a periodontal membrane). Unlike Peyer (1968), Romer (1956) and Tomes (1876-1923), Edmund (1969) required the presence of a periodontal ligament to diagnose thecodonty. Mammals, archosaurs and a few reptiles were considered truly thecodont. Reptiles with teeth ankylosed to sockets could be considered to exhibit ankylosed thecodonty; Edmund (1969) did not give an example of ankylosed thecodonty but his description of *Diadectes* (Edmund, 1969: 150) fits his definition of ankylosed thecodonty. Edmund did not like the term ankylosed thecodont because it was similar to protothecodont attachment.

Protothecodont/subthecodont attachment was diagnosed when teeth were attached in relatively deep sockets by cement. Edmund did not single out a term and used both throughout his section on tooth attachment. He noted that cement was identical histologically and developmentally to bone of attachment and alveolar bone (1969: 126). The sockets were in the dental groove formed where the lingual and labial walls of the jawbone grade into each other with the labial wall usually being higher than the lingual wall. Protothecodonty was exhibited by pelycosaurs, eosuchians and most cotylosaurs. Protothecodonty was considered the primitive attachment type for reptiles and was not found in any living reptile.

Fink (1981)

Fink (1981) created a tooth attachment classification based on histology for actinopterygian fishes; his underlying premise was that paedomorphosis generated the tooth attachment diversity in actinopterygians. Because the classification is based on histologic data, readers can be reasonably confident that attachment tissues were identified consistently, if not correctly. Fink's categories did not resemble any of the aforementioned terminology. Instead he designated tooth attachment types numerically.

Type 1 tooth attachment was identified when teeth were ankylosed to the bone of attachment, which was attached to the jawbone. Type1 tooth attachment represented the primitive actinopterygian condition, (e.g., pike). Types 2, 3, and 4 were derived sequentially from type 1 attachment.

Type 2 attachment was characterized by an annular ligament (credited to Tomes, 1923 [final edition of Tomes, 1876-1923]) intervening between the tooth and the bone of attachment. Type 2 attachment was observed in elopomorphs, clupeomorphs and other more derived fishes. A reduction in ossification during the tooth attachment process was thought to result in an annular ligament remaining between the tooth and the attachment bone.

Type 3 attachment was a hinged attachment with an anterior axis of rotation; Stomiatiformes had a type 3 attachment. The anterior portion of the tooth was more completely mineralized to the attachment bone than the posterior portion; the posterior portion of the tooth was attached to a ligamentous hinge. Tooth manipulation resulted in the depression of the posterior hinge and a relatively stationary anterior end of the tooth. This attachment type was thought to have evolved due to the cessation of mineral deposition prior to the tooth being completely mineralized to the attachment site.

Type 4 attachment was a more extreme form of hinged attachment than type 3. The tooth being attached to the attachment bone by a posterior ligamentous hinge characterized type 4 attachment; the tooth had a posterior axis of rotation. The anterior portion of the tooth was not mineralized to the attachment bone. When depressed, the contents of the pulp cavity were exposed.

Eurypterygians, some stomiatiforms and *Esox* were examples of actinopterygians with a type 4 attachment. Type 4 tooth attachment evolved perhaps when dentine mineralization ceased prior to tooth attachment and collagen production ceased prior to its deposition on the more anterior end of the tooth. Fink did not think that type 4 tooth attachment developed the same way in all of the groups with this attachment type.

Shellis (1982)

Shellis (1982) was a review of vertebrate tooth attachment from a dental text focused on the periodontal ligament. Shellis used a literature review and some direct observations (mostly fish) in his survey of tooth attachments in vertebrates. His focus was on the relationships between the tissues and the functional morphology of the attachments.

Shellis (1982) presented a tooth attachment classification based on histologic data and recognized that collagenous tissue(s) of variable mineralization attached teeth to jaws in all vertebrates. Like Tomes (1876-1923) and Romer (1956), he acknowledged that discrete categories were impossibilities. There were three basic types of tooth attachment, ankylosis, fibrous attachment and socketed/thecodont attachment. Each category had sub-categories making nine attachment categories in total.

Tooth attachment by ankylosis was recognized when there was a complete mineralized attachment between tooth and jawbone. Teeth with ankylosed attachments were found in fishes and most extant reptiles. Bone of attachment, accredited to Tomes, attached tooth to jawbone in ankylosed dentitions.

There were three subcategories of ankylosis: acrodont ankylosis, pleurodont ankylosis and protothecodont ankylosis. Acrodont ankylosis was observed in reptiles where the teeth were mineralized to the apex of the jawbone. Pleurodont ankylosis was identified when teeth were mineralized to the lingual wall of the labial portion of the jawbone. Protothecodonty was identified when teeth attached to the inner walls of a groove in the jawbone formed by the labial and lingual walls of the jaw. This definition of protothecodont was markedly different from that of Romer (1956), Peyer (1968) and Edmund (1969). Diadectids and other early extinct reptiles exemplified protothecodonty.

Fibrous tooth attachment was identified when partly mineralized collagen fibres attached the tooth to the jawbone; the tooth had limited mobility on the jaw at the attachment site. There were two types of fibrous attachment, direct fibrous attachment and indirect/pedicellate fibrous attachment. Direct fibrous attachment was characterized by unmineralized collagen fibres running from the base of the tooth into the jawbone or the connective tissue covering the jaw cartilage. Direct fibrous attachment was found in elasmobranchs and some teleosts.

Indirect/pedicellate attachment was identified when unmineralized collagen fibres exited the tooth base and attached to a mineralized structure, called the pedicel, which was attached to the jawbone. Most teleosts and all extant amphibians were thought to have indirect/pedicellate attachments.

Socketed/thecodont attachment was identified when teeth, with roots, were attached to the walls of sockets or a groove in the jawbone by a periodontal ligament. Shellis did not like the term thecodont for mammalian socketed attachment because he considered mammalian socketed attachment different enough to warrant its own term, "gomphosis"; mammals had constricted root ends, molars with multiple roots and sockets that were regenerated when teeth were replaced. Crocodilians and some extinct reptilian groups had thecodont tooth attachment.

Shellis, though not convinced as he thought more data were needed, entertained the idea that the different tooth attachments morphologies evolved due to changes in the developmental processes of the tooth. He also suggested functional morphologic reasons for the evolution of the attachments. For example, thecodonty could have evolved because a ligamentous attachment was modified or resorbed easier than an ankylosed attachment.

Motani (1997)

Motani (1997) reviewed tooth attachment types in ichthyosaurs based on gross dental morphology. His study contained the largest review of published named tooth attachment types, thirteen in total. He considered most of the terms synonomous with, or variations of, one of five terms. Motani followed Romer (1956) and Edmund (1969) and used acrodonty, pleurodonty, thecodonty, subthecodonty and ankylosed thecodonty as terms in his classification. He also used the term aulacodonty (Mazin, 1983) and introduced ichthyosaur thecodonty. He discussed tooth attachment terminology twice in his document: first in the section introducing vertebrate tooth attachments, and second in the section presenting his classification of ichthyosaurian tooth attachments. Although identical terms were used in both sections of the paper, the definitions of the terms differed from section to section. To facilitate comparisons, I review both sets of terms; for the sake of brevity, I present only the terms lacking synonymies.

Vertebrate tooth attachment types

Acrodonty was identified when teeth were ankylosed to the margin of the jaw. Motani cited Miles and Poole (1967) in his definition. *Sphenodon* and some lizards exemplified acrodonty.

Ankylosed thecodonty was identified when teeth were attached to sockets, as deep as crown height, in the jawbone (cited Edmund [1969]). Motani noted that Edmund (1969) had difficulty with ankylosed thecodonty because it was similar to subthecodonty. Motani considered the terms different because subthecodont attachments were in a dental groove but ankylosed thecodont attachments were not in a dental groove. The maxillary teeth of the Triassic ichthyosaur *Mixosaurus cornalianus* exhibited ankylosed thecodonty.

Aulacodonty was identified when the teeth were attached within a dental groove lacking sockets. This definition was modified from Mazin (1983); Motani did not want the definition to include the idea that aulacodonty was evolved from thecodonty. Motani noted Mazin (1983) did not provide evidence of how the tooth was attached and concluded that if teeth were ankylosed to a shallow socket then it would be synonomous with subthecodonty. Aulacodonty was found in post-Triassic ichthyosaurs.

Pleurodonty was identified when teeth were ankylosed to the jawbone within a groove with a high labial wall and a lower lingual wall. Teeth were attached to the lingual surface of the labial wall and sometimes to the base of the groove. Motani preferred Romer's (1956) characterization of the jawbone walls being subequal rather than Edmund's (1969) assertion that the lingual wall is lost. Iguanid lizards and varanid lizards exemplified pleurodont attachment.

Subthecodonty, to which he synonomized protothecodonty as defined by Peyer (1968) and Edmund (1969), was characterized by a tooth attached in a shallow socket in a dental groove with a high labial wall and a lower lingual wall (Romer, 1956). Most early amniotes were considered to have subthecodont tooth attachments.

Thecodonty was identified when teeth with cylindrical roots were attached to deep sockets by fibrous connective tissue. Sockets could be deeper than the crown height. Archosaurs and mammals exemplified thecodonty.

Ichthyosaurian tooth attachment types

Subthecodont attachment was identified when teeth were attached in shallow sockets attached to the bottom of a dental groove. The tooth root walls were folded and the root widened basally resulting in a broad pulp cavity. The Triassic ichthyosaurs, *Utatsusaurus*, *Grippia* and *Pessosaurus,* exhibited subthecodont attachment.

Ankylosed thecodont attachment was identified when teeth were attached to sockets within a dental groove that decreased in depth from anterior to posterior. Sockets as deep as the crown height were found at the posterior end of the jaws. Tooth roots were relatively straight and the tooth attachment was bony. The Triassic ichthyosaurs, *Mixosaurus* and *Phalarodon*, had ankylosed thecodont attachment.

Aulacodont attachment was identified when teeth were attached, close together or more distant, in a dental groove. The straight tooth roots were not separated by bone but may have been attached to the jawbone by bone. *Merriamia*, *Shastosaurus*, post-Triassic ichthyosaurs, and perhaps *Himilayasaurus*, exemplified aulacodont attachment.

Ichthyosaurian thecodont attachment was identified when teeth were attached in sockets deeper than crown height. The teeth had straight roots and were perhaps ankylosed to the bottom of the socket; a space existed between the wall of much of the socket and the tooth. This implantation was not considered truly thecodont because teeth were ankylosed to the jawbone rather than attached with connective tissue to the jawbone. *Cymbospondylus* and *Shoniasaurus* were considered to exhibit ichthyosaurian thecodont attachment.

Ichthyosaurian tooth attachment diversity resulted from modifications of the attachment type primitive to ichthyosaurs, (i.e., subthecodont attachment). Motani (1997) also evaluated the attachment types in terms of functional morphology.

RESULTS

Types of tooth attachment classifications

Tooth attachment classifications can be grouped into different types based upon the size of the animal grouping they are applicable to and the type of data used to define the categories in the classification (Fig. 2-1). There are basically two types of tooth attachment classifications, general vertebrate tooth attachment classifications and group specific tooth attachment classifications. General vertebrate tooth attachment classifications represent the diversity of vertebrate tooth attachments whereas group specific classifications present terminology useful for a certain group of animals. Below that level, tooth attachment classifications can be categorized as being based solely on histology, (e.g., Tomes [1876-1923], Fink [1981] and Shellis [1982], based on both histology and gross morphology, (e.g., Romer [1956], Edmund [1969], Gaengler and Metzler [1992])

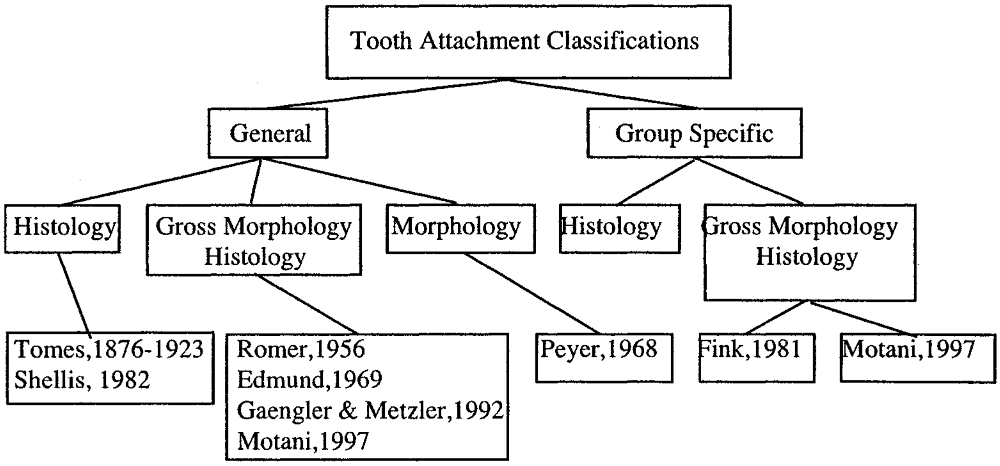

Figure 2-1: Concept map of the different types of tooth attachment classifications including examples.

and Gaengler [2000]), or based on gross morphology (e.g., Peyer [1968]). I did not consider Peyer to present a classification of categories based on histology and gross morphology because although he mentioned tissues in his category definitions, they were not given parallel importance across the categories. For example, acrodont teeth were fused to the jawbone by an unmentioned tissue and pleurodont teeth were attached by bone of attachment.

Although all are currently in use, each of the types of tooth attachment classification has merits and demerits. Group specific classifications are capable of classifying dental anatomy at a finer level than general classifications, but they are useless to comparative dental anatomists wishing to examine many different groups of vertebrates. Conversely, general classifications are criticized for not acknowledging a greater diversity of tooth attachments (Caldwell *et al.*, 2003; Gaengler & Metzler, 1992; Gaengler, 2000).

Perhaps more interesting are the disparities in usefulness between histology, histology and gross morphology, and gross morphology based classifications. General histologic classifications reduce complex tooth attachment interactions down to simple terms. Terminology from general histologic classification are not very useful for phylogenetic analyses because most groups of animals share uninformative histologic similarities due to commonalities in their dental developmental processes. Contrarily, group specific histologic classifications can bring to light informative phylogenetic patterns because they classify smaller numbers of dentitions from closely related animals

(Motani, 1997; Fink, 1981). Although classifications based on histology and gross morphology are the most often cited classifications, they are also the most often criticized and revised classifications.

Classifications based on histology and gross morphology are commonly taught in introductory biology classes because they are easy to visualize and easy to use. Unfortunately, classifications based on histology and gross morphology do not acknowledge as much diversity as classifications based on histology. This is because of the conflation of two independent developmental systems: the tooth bearing bone and the tooth. Gross morphology based classifications do not consider the actual tooth attachment tissues and instead focus on the relationship between the attached tooth and the geometry of the attachment site.

Although previous paragraphs suggest that tooth attachment classifications are complex and differ in their capabilities, the question is: Do researchers tend to treat them that way?

Usage of tooth attachment classifications

The results of the Web of Science search for the chosen references are summarized in Appendices 2-1, 2-2, 2-3. The studied references had different percentages of use amongst the categories (Fig. 2-2). Direct usage of the references for the tooth attachment classification ranged from 57.14% of references to Motani (1997) down to 2.69% of references to Peyer (1968). Direct

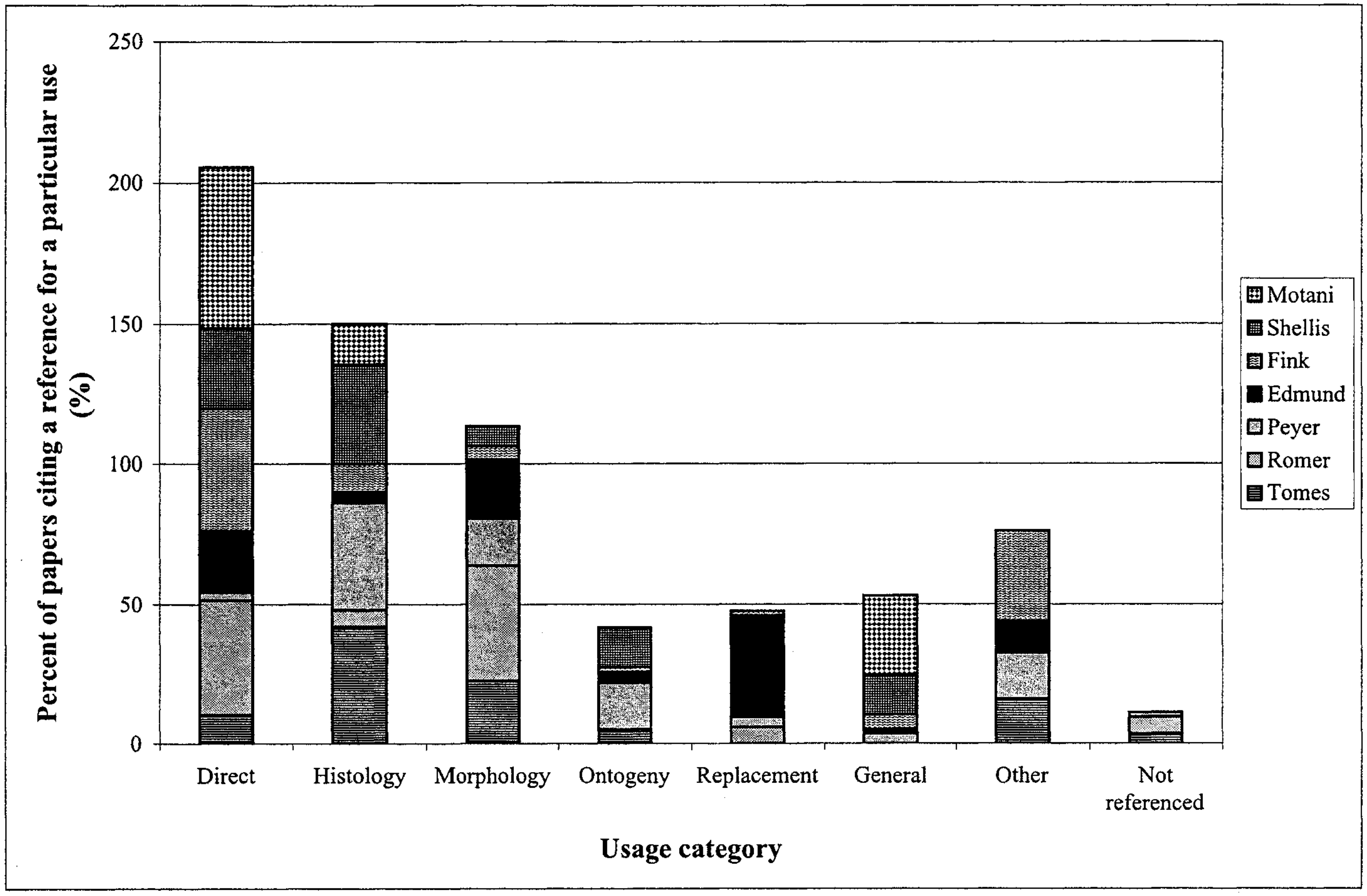

Figure 2-2: Comparison of the usage of the cited references by author. Percentages are stacked, not additive, to ease comparison.

usage was the most common usage of Motani (1997) and Romer (1956). Romer (1956) was used as much for morphologic data as for attachment terminology. Fink (1981), Romer (1956), Shellis (1982), Edmund (1969) and Tomes (1876-1923) followed Motani (1997) respectively in the percent of direct usage. Usage for histologic information ranged from 42.11% for Tomes (1876-1923) down to 3.88% for Edmund (1969). Peyer (1968), Shellis (1982), Motani (1997), Fink (1981) and Romer (1956), in order from greatest to least percent of use for histologic information, fill the gap between Tomes (1876-1923) and Edmund (1969). The most common usage of Peyer (1968) was for histologic information. Romer (1956) was referenced more often for morphology than any other studied reference with 41.18 % of citations. Tomes (1876-1923), with 22.81%, and Edmund (1969), with 20.93% of citations relating to morphology, are the next most often cited studied references for morphologic information. Peyer (1968), Shellis (1982), Fink (1981) and Motani (with no citations relating to morphology), are the next most frequently cited references for morphologic data. Overall, the papers were cited least often for ontogenetic data. Peyer (1968) with 16.67% and Shellis (1982) with 14.29% of citations for developmental data are the most often studied papers referenced for ontogenetic data. Tomes (1876-1923), Edmund (1969) and Fink (1981) respectively are the next most frequently cited papers for ontogenetic data. Motani (1997) and Romer (1956) were not cited for ontogenetic information. Edmund (1969) was most frequently cited for tooth replacement information with 36.43% of citations being for this purpose.

Shellis (1982) and Tomes (1876-1923) were not cited for tooth replacement data. Few of the cited papers were referenced for general information, with the exception of Motani (1997) that was cited for general purposes in 28.57% of papers. Fink (1981) was cited in 32.20% of papers for other reasons. Not evidenced in the charts is the fact that 13.56% of the papers citing Fink (1981) used it as a reference to paedomorphosis. Paedomorphosis had to be accommodated in the "other " category because the other studied papers were not cited for information on paedomorphosis.

Comparison of the usage of different types of tooth attachment classifications

I discovered patterns in the usage of different classification types contrary to my prediction of a random distribution of the data. The graph (Fig. 2-3) comparing the uses of the general classifications based on gross morphology and histology shows that these cited papers were used more variably than the papers from the other types of classifications (Figs. 2-4, 2-5, 2-6). The percentage of papers citing general classifications based on histology and gross morphology varied by almost 20% in the direct, morphology and replacement categories. No other tooth attachment classification type varied that much in percent of usage within a category. The group specific classifications and the general attachment classifications based on histology both showed similar usage percentages within a category. It is interesting to note that Peyer (1968) tended to cluster well with

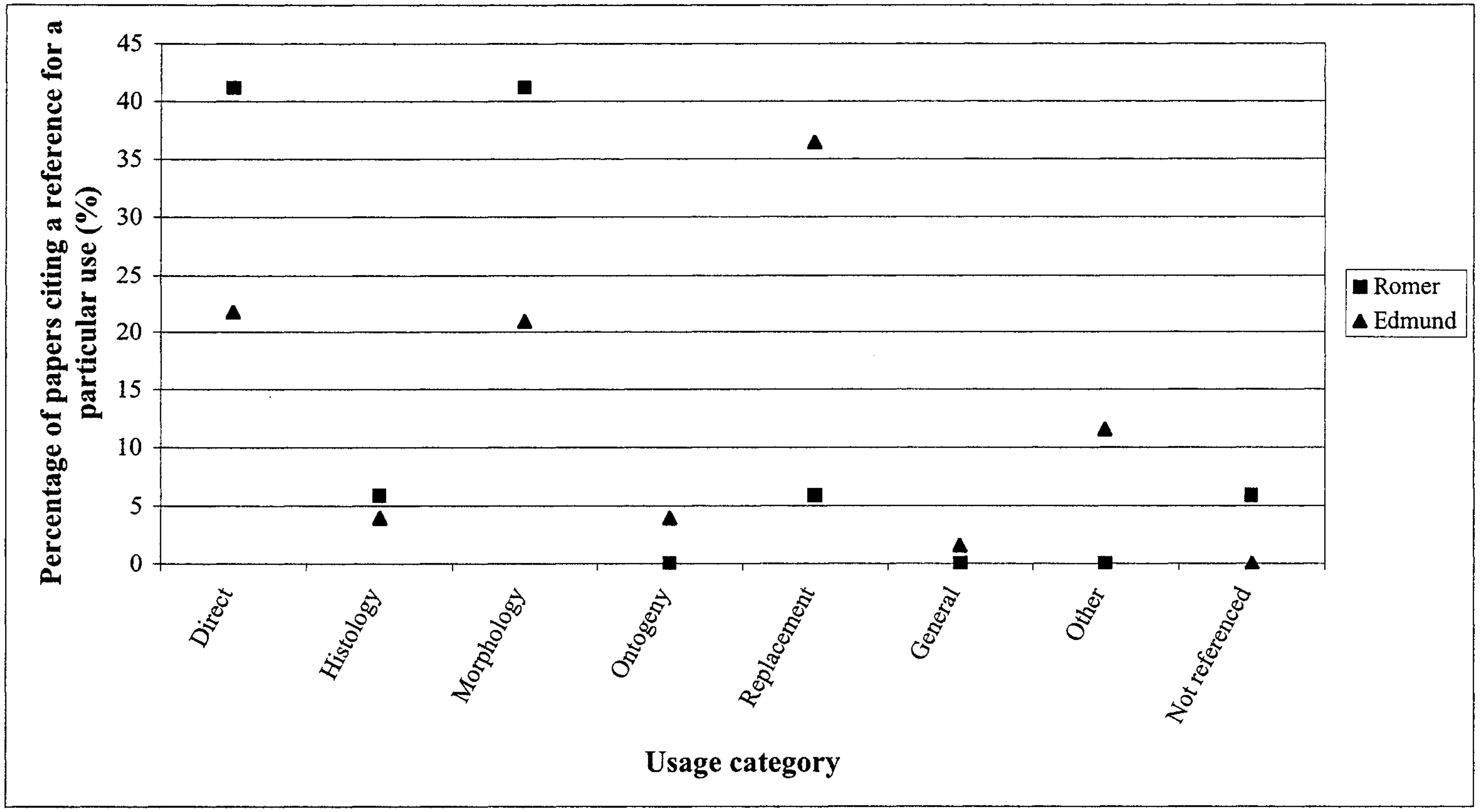

Figure 2-3: Comparison of the usage of the cited references containing general attachment classifications based on gross morphology and histology

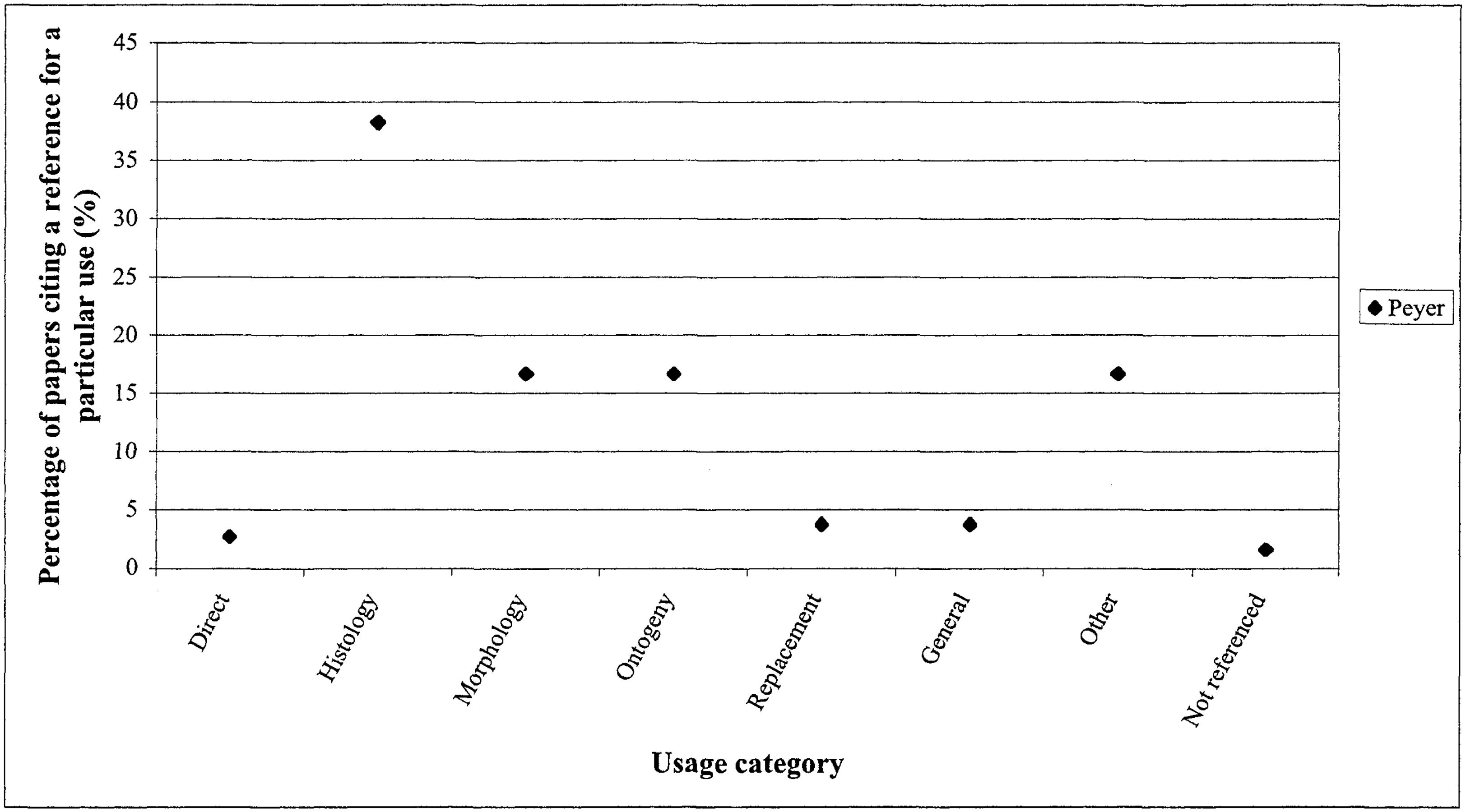

Figure 2-4: The usage of a general classification based on gross morphology

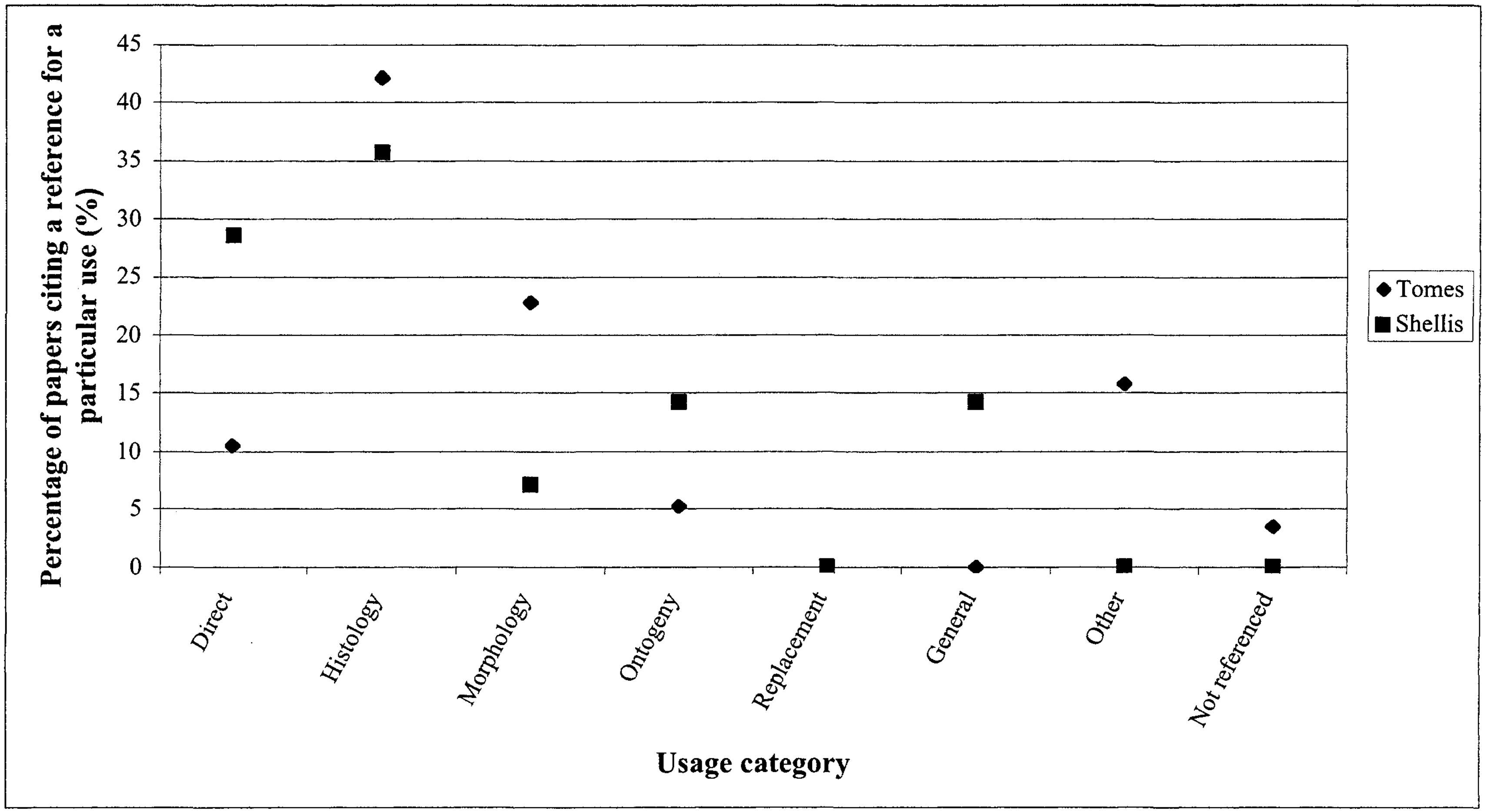

Figure 2-5: Comparison of the usage of the cited references containing classifications based on histology

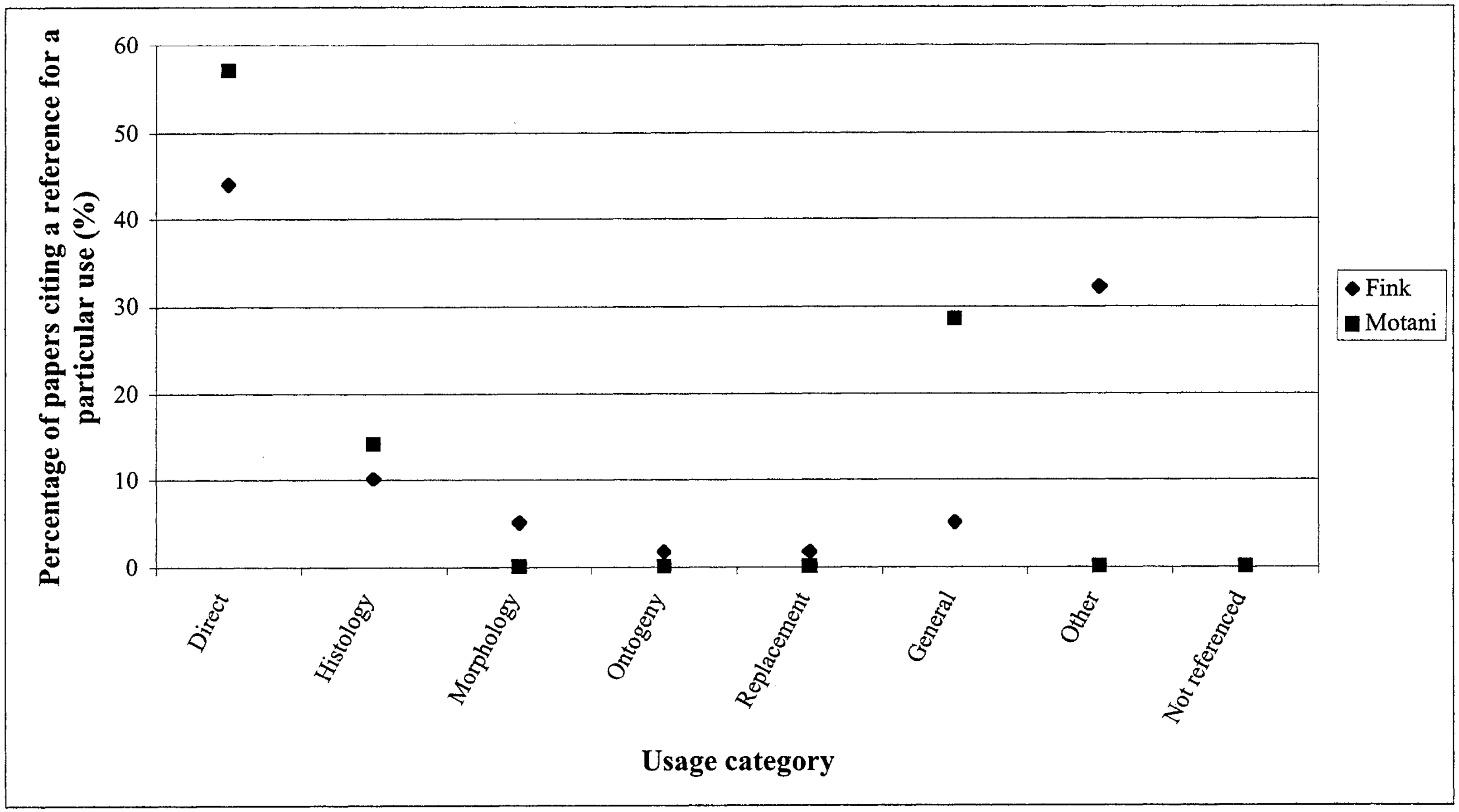

Figure 2-6: Comparison of the usage of the cited references containing group specific classifications

the data from the general tooth attachment classifications based on histology (Figs. 2-4, 2-5).

DISCUSSION

General comments

The usage data show that there were 3 dominant uses of papers containing tooth attachment classifications: direct, histology and morphology. Direct usage was the dominant use of Fink (1981) and Motani (1997), while Romer (1956) was used equally for direct and morphologic data. The studied papers were frequently cited directly for the classifications because a goal of every cited paper was to act as a guide for tooth attachment terminology. Most papers, specifically Tomes (1876-1923) and Shellis (1982), were cited more frequently for histologic data than other papers because they are based primarily on histologic data whereas the others relied more on morphologic data. Peyer (1968) was also often cited for histologic data, despite containing a classification based on morphologic data, because it contained a very large amount of histologic data. Because all of the studied classifications are based on morphologic and/or histologic data, it was not unexpected to find out that most of the papers were cited frequently for morphologic data.

Only rarely did a single studied paper dominate a usage category; Edmund (1969) and Romer (1956) dominated the replacement and morphology categories respectively. The high percentage of use of Edmund (1969) for replacement data is not surprising considering that Edmund wrote most of his publications with the goal of promoting the relatively new Zahnreihen theory of tooth replacement. Romer (1956) dominated the morphology category because it contained a large volume of gross dental morphology data compared to the other studied papers.

Comments on the usage of the different types of attachment classifications

It was surprising to note that the different types of classifications were generally used for different things. Authors rarely, if ever, justified why they used a tooth attachment classification. Therefore, I did not expect to see any data clusters and instead expected a random distribution.

The general tooth attachment classifications based on gross morphologic and histologic data did not cluster as much together as the other papers within their types, perhaps because each of the papers, Romer (1956) and Edmund (1969), presented different amounts and types of data (Figs.2-3, 2-4, 2-5, 2-6). Romer (1956) presented a large amount of gross morphology data because most of the specimens were fossilized, whereas Edmund (1969) presented morphologies related not only to tooth attachment, but also to tooth replacement. Contrarily, the papers presenting general classifications based on histology, and the papers presenting group specific classifications, were fairly consistent in the type of information presented, histology and limited amounts of gross morphology. It is therefore no surprise that the percentages of use across the categories for Peyer (1968) were similar to those of papers presenting general classifications based on histology as Peyer presented a large amount of histologic data. It is interesting to note that the papers containing group specific classifications were cited more often directly for the attachment classification within than the papers presenting other types of classifications; this is likely because the papers containing the group specific classifications were focused on presenting tooth attachment classifications and contained very little unrelated data.

The apparent correlation between the type of tooth attachment classification and its usage should inspire authors to consider why they are using a particular tooth attachment classification and how they are using it. For example, considering Motani (1997) presented his classification terminology to classify ichthyosaur dentitions, it would be incorrect for someone to use the term aulacodonty or even acrodonty (as defined in Motani, 1997) for a non-ichthyosaurian dentition. Although acrodonty, pleurodonty and thecodonty, may be commonly used terms, because they are discrete anatomic terms tied to definitions, authors should be careful when modifying classifications to suit their purposes. That said, what follows are criticisms of the studied tooth attachment classifications.

Criticisms of tooth attachment classification development and modification

Mayr and Bock (2002) defined classification as an ordering system where entities are grouped based on shared similarities amongst the entities in one group. Goals of classifications included sorting, information storage and retrieval, identification of an unknown entity, inferences about not yet studied properties, and to be the basis for comparative studies (Mayr & Bock, 2002). When constructing classifications, it is important to know what is being compared and contrasted to determine what categories to construct (Eberle, 1990).

All authors of the cited papers intended to present a classification useful to the scientific community. All of the classifications meet Mayr and Bock's (2002) goals for classifications; the diverse usage of the different classifications indicates this. If the classifications only met one goal you would expect not to see a diversity of uses of a classification. The acceptance and usage of a classification by the scientific community does not make the classification a good classification. If all of the classifications meet goals and are widely used, how do we know which classification to use when and how do we know when a classification is well constructed? This question is best answered by examining the construction and goals of each classification separately.

Tomes (1876-1923)

The details of Tomes's (1876-1923) classification and the other classifications are found above and will not be revisited here. Tomes (1876-1923) provided a very general classification of tooth attachment based solely on the type of tissue(s) attaching the teeth to the jawbone. The classification scheme in Tomes (1876-19323) was constructed "....for the purposes of description...." (Tomes 1898: 221 [8th edition of Tomes, 1876-1923]). The detailed descriptions of the attachment types give readers a good idea of what types of attachments fit in the different categories. Because the categories often accommodate tooth attachments for which homologies have not been proposed, the terminology should not be used to discuss evolutionary patterns.

Peyer (1968) and Edmund (1969)

Although the textual definitions of acrodonty, pleurodonty and protothecodonty differ little between Peyer (1968) and Edmund (1969), the figured acrodont and pleurodont attachments are different (Fig. 2-7). Peyer (1968: Fig. 9) did not diagram bone of attachment. It is inferred that tooth and jawbone are fused directly in acrodont and pleurodont dentitions. Edmund (1969: Fig. 8) diagrammed what is inferred to be cement (though not labeled but mentioned the text) attaching the teeth in acrodont, protothecodont and pleurodont

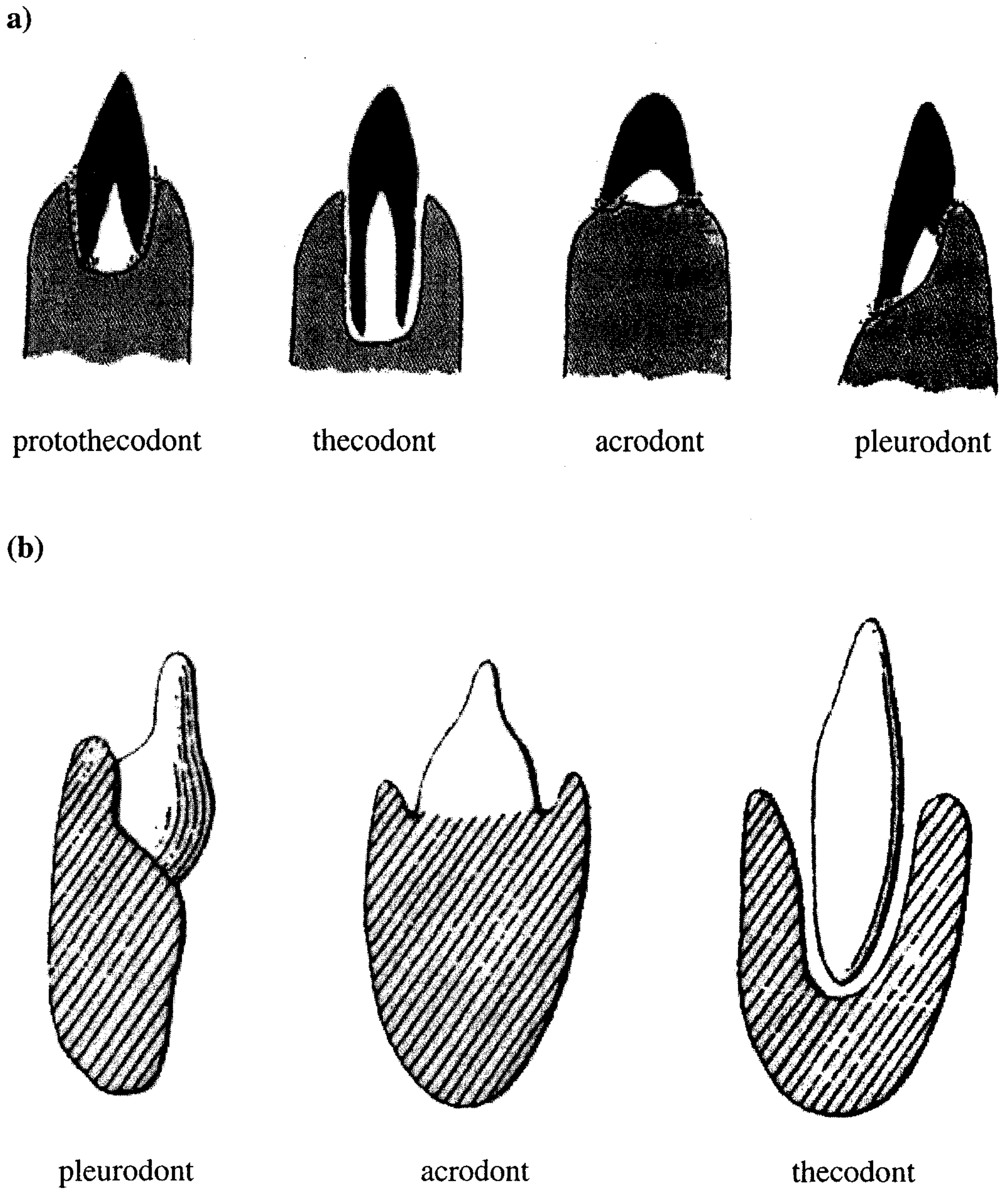

Figure 2-7: A comparison of the figured attachment types in Edmund (1969) and Peyer (1968). (a) Edmund 1969; (b) Peyer 1968. (a) and (b) were modified from Edmund (1969: Fig. 8) and Peyer (1968: Fig. 9) respectively.

dentitions. Another difference between the acrodont figures is that in Peyer (1968), the tooth is attached within a very shallow groove, not apparent in the textual definition, and in Edmund the tooth is attached to the apex of the jawbone as per the textual definition. Both Peyer (1968) and Edmund (1969) figured a gap between the tooth and the socket walls in thecodont attachment signifying an attachment tissue different than bone of attachment or cement; Edmund accounted for the periodontal ligament in his diagram but Peyer did not signify what this tissue was and did not acknowledge a different attachment tissue in his text either. This disparity in correlation between the diagram and text in Peyer (1968) and Edmund (1969) is confusing.

Romer (1956), Peyer (1968) and Edmund (1969)

The categories in Romer (1956), Peyer (1968) and Edmund (1969) are delimited by the tissue attaching the tooth (except Peyer, 1968) which is based only on morphology) and the morphology of the tooth attachment site. Romer refers to the difficulty of showing the distribution of tooth attachment types across the reptiles because so much information was lacking. These three authors's terminologies are quite difficult to use because they are based on two separately evolving data sets, the morphology of the tooth-bearing bone, and the histology of the attachment. Because the morphologies and histologies grade into each other, some dentitions do not classify easily into any category, (i.e., hinged attachments and ankylosed thecodonty). As mentioned above in the introductory review of Edmund (1969), the retention of the same terms with modified definitions and inconsistent diagrams has led to confusion of exactly what the terms mean.

Fink (1981)

Fink (1981) was the most unique studied classification because types were designated numerically, and it has been criticized more than any of the other reviewed classifications. Fink (1981) was based on the hypothesis that paedomorphosis was the dominant process in producing tooth attachment variety in actinopterygians. Because the attachment types are designated numerically and imply a sequence, the morphology and developmental process are more easily visualized than the terminological types of Romer (1956), Peyer (1968) and Edmund (1969) that also use heterochronic shifts to hypothesize the evolution of tooth attachment. Fink (1981) was criticized by Parenti (1986) for not considering acellular bone distribution when creating the classification. Trapani (2001) disagreed directly with Parenti (1986) and used Fink's terminology in his survey of tooth replacement in fishes. Most authors have adopted Fink's terminology. Few authors have not been able to classify observed dentitions using Fink (1981) (e.g., [Huysseune and Sire, 1997]), and some have suggested more data is necessary to refine the classification (Mullaney & Gale, 1996).

Fink's (1981) intention was to show that the diversity of tooth attachment in actinopterygians resulted from paedomorphism. He also wanted to show that tooth attachment was phylogenetically significant in cladistic analyses of Actinopterygia. Creating perfect categories for grades of morphology is difficult and likely impossible. Fink's categories were well constructed in that the criteria for inclusion in a category were unequivocal and simple. The categories were discrete making their usage for descriptive purposes easy. If used as characters for phylogenetic analyses the categories should be used and scrutinized in light of the fact that they represent a grade of morphologies. Unlike Tomes (1876-1923), Romer (1956), Peyer (1968), Edmund (1969), Shellis (1982) and Motani (1997), Fink (1981) actually presented an evolutionary sequence tied to a hypothesis of phylogeny. Fink (1981) interpreted that tooth attachment types in actinopterygians had a phylogenetic pattern due to paedomorphosis. Because Fink (1981) is a well-made classification based on a large data set and is usable for descriptive and phylogenetic purposes, it is a more effective tooth attachment classification than most.

Shellis (1982)

Shellis (1982) is similar to Romer (1956), Peyer (1968) and Edmund (1969) in that the classification presented is useful primarily for descriptive purposes. Unlike the aforementioned papers, it is more difficult to use because the three general categories, ankylosis, fibrous attachment and socketed attachment lack the definitions for terms integral to their definition. What is a periodontal ligament and how is it different from a fibrous attachment? How is a pedicel different from a socket or groove? The definitions of these terms are important, and lacking, to distinguish a fibrous attachment from a socketed attachment. Shellis (1982) did not discuss the evolutionary patterns and processes of the different attachments and chose to discuss them in terms of functional morphology, making it improper to use the terms for phylogenetic analyses.

Motani (1997)

Motani (1997) reviewed both a general and a group specific classification. This is a significant paper as it synonomizes several redundant tooth attachment terms. A problem is that the definition of certain terms, (e.g., ankylosed thecodonty), are presented twice, once in the introduction regarding vertebrate attachment and secondly specific to the ichthyosaur case. The changed definition may exclude certain species that have always been considered to have, for example, ankylosed thecodont tooth attachment. Like most of the other cited papers, Motani (1997) spoke of developmental transitions from one type of attachment to another. Unlike the other authors, he noted that until a good phylogenetic analysis of Ichthyosauria was completed, the evolution of tooth attachment in ichthyosaurs would remain unstudied.

Conclusions from criticism of the studied papers

A classification should be modifiable in light of new data. A classification should not be modified without considering the context of the classification. Is redefining categories necessary when a unique subtype of attachment is observed, (i.e., is it necessary to erect different terms for the different types of hinged attachments)? For simplicity's sake the answer would be 'no' as the morphologies share similarities that allow them to be classified as hinged (e.g., Tomes [1876-1923] and Shellis [1982]). Errors in redefinition of categories, (e.g., Motani [1997] mentioned above, and Zaher and Rieppel [1999] where the definition of thecodonty excluded mammals), show the danger in modifying well-used classifications. Realistically, a study such as Fink (1981) shows us that classifications can be made to better fit the data by creating new categories based on smaller group specific data sets. Group specific tooth attachment classifications are more useful than the other classification types when examining evolutionary questions because the categories of group specific classifications are likely to represent more diversity than those of general classifications.

On the danger of using classification categories as character states in phylogenetic analyses

Tooth attachment classification terminology must be used with caution in phylogenetic analyses because the terms may not acknowledge the anatomic diversity within the study group. This is reason enough to be cautious in using published tooth attachment categories in phylogenetic analyses. Additionally, most classifications of tooth attachment are not created with the intention of being used in phylogenetic studies and the categories may not represent structures proposed to be homologous. Fink (1981), Gaengler and Metzler (1992) and Gaengler (2000) acknowledged that tooth attachment diversity is greater than what is presented in most classifications. Fink (1981) acknowledged the diversity by creating a new classification specific to actinopterygians, and Gaengler and Metzler (1992), reprised in Gaengler (2000), addressed the issue by creating a new classification for vertebrates with recycled terminology, as well as all new terms, presented in an evolutionary sequence.

Tooth attachment should be examined within each studied group to ensure that the tooth attachment character states reflect the attachment diversity of the study group. Tomes (1876-1923) indicated that some attachments, (e.g., hinged attachment), are found in distantly related groups of fishes. To use hinged attachment (Tomes 1876-1923) as a state in a phylogenetic analysis of fishes may cause problems because several different morphologies, that have not been homologized, are accommodated in one category.

Our knowledge of dental development and anatomy is growing exponentially. As such, we should expect to modify centuries old terminology to better fit these new data. This must be a conscious and cautious exercise so as not to cause a confusion of terms. That said, and having recognized that classifications become modified over time, authors should not use a classification terminology without citing the source. The taxonomic authorship of a classification is just as important as that of a species.

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Appendix 2-1: Results of Web of Science cited reference searches

Reference	**Date of Search**	**Original number of papers**	**Number of papers considered in analysis**
Tomes (1876-1923)	July 3, 2003	57	57
Romer (1956)	July 3, 2003	36	17
Peyer (1968)	July 3, 2003	169	169
Edmund (1969)	July 17, 2003	114	114
Fink (1981)	May 26, 2003	57	57
Shellis (1982)	July 3, 2003	12	12
Motani (1997)	July 3, 2003	7	7

Appendix 2-2: Frequency of useage of the cited references

(a)

Reference	Direct	Histology	Morphology	Ontogeny	Replacement	General	Other	Not referenced	Total
Tomes (1876-1923)	6	24	13	3	0	0	9	2	57
Romer (1956)	7	1	7	0	1	0	0	1	17
Peyer (1968)	5	71	30	31	7	7	31	3	185
Edmund (1969)	28	5	26	5	47	2	15	0	128
Fink (1981)	26	6	3	1	1	3	17	0	57
Shellis (1982)	4	5	1	2	0	2	0	0	14
Motani (1997)	4	1	0	0	0	2	0	0	7

(b)

Reference	Paedomorphosis	NR	NF
Tomes (1876-1923)	0	0	0
Romer (1956)	0	19	1
Peyer (1968)	0	0	2
Edmund (1969)	0	0	1
Fink (1981)	8	0	1
Shellis (1982)	0	0	0
Motani (1997)	0	0	0

(a) Table showing raw data used in the production of bar graph and scatterplots.

(b) Table showing additional data. Only Fink (1981) was cited numerous times in relation to paedomorphosis. NR= not applicable, NF= references I was unable to view.

Appendix 2-3: Results of cited reference search coded with usages

Abbreviations:

D: direct for classification **H**: histology **M**: morphology
R: replacement **O**: ontogeny **Ot**: other
Otp: paedomorphosis (adds to Ot count) **G**: general
N: not tooth related **NF**: not found physically/visually

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CHAPTER 3

UNEXPECTED TOOTH SOCKET HISTOLOGY IN THE CRETACEOUS SNAKE *DINILYSIA*, WITH A REVIEW OF AMNIOTE DENTAL ATTACHMENT TISSUES

(To be submitted in a modified form as "Budney, L.A. & Caldwell, M.W. Unexpected tooth socket histology in the Cretaceous snake Dinilysia, with a review of amniote dental attachment tissues" to The Journal of Morphology)

CONTEXT

This study began prior to my Master's program and was completed during my Master's program. It is included in my thesis because it adds to our knowledge of a rare, fossil snake significant in discussions of the evolution of snakes. The finding of an unexpected dental tissue in *Dinilysia* (this chapter) and *Platecarpus* (Caldwell *et al.*, 2003) encouraged me to choose my thesis topic as the conclusions suggested strongly that tooth attachment histology in squamates had been misinterpreted through the examination of an incorrect data set: gross morphology versus histology, and classified using inappropriate terminology (reviewed in Chapter 2).

INTRODUCTION

Dinilysia patagonica was a terrestrial snake that lived during the Upper Cretaceous. New specimens of *D. patagonica* found near Neuquén, Argentina are contributing greatly to the knowledge of the anatomy and the paleobiology of this species (Caldwell & Albino, 2001; Caldwell &Albino, 2002). Prior to the discovery of the Neuquén specimens, *D. patagonica* was only known from the holotype specimen, a preserved skull and some associated vertebrae from Boca del Sapo (north of Neuquén) (Smith-Woodward, 1901; Estes, Frazzetta & Williams, 1970; Frazzetta, 1970; Hecht, 1982; Rage & Albino, 1989; Albino, 1996).

Descriptions of tooth attachment morphology and histology for *Dinilysia* are lacking in published literature. Likewise, the tooth attachment morphology of most extant snakes is not well known. Studies of extant snake tooth attachment have been restricted to discussions of the hinged tooth attachment novel to snakes that eat hard and/or large prey (Savitzky, 1981; Patchell & Shine, 1986). The histologic study of tooth attachment morphology is important because attachment morphology limits the hardness and size of prey that is ingestible by a species (Patchell & Shine, 1986) and because tooth attachment characters, usually non-histological, are used in phylogenetic analyses of Squamata (the clade containing lizards and snakes) (Estes *et al.*, 1988; Caldwell, 1999; Lee & Caldwell, 2000; Rieppel *et al.*, 2002).

We begin with a review of the basics of tooth ontogeny and histology that are well understood in medical-dental fields, but are not well understood by systematists and comparative anatomists. The terms reviewed below are those applied to the description of the dental histology of *D. patagonica.* A description of the tooth socket histology of *D. patagonica* follows the terminology review. We conclude our study with a comparison of the socket histology of *D. patagonica* with that of other available squamates and a discussion of the usage of tooth attachment characters in phylogenetic analyses of Squamata.

Dental ontogeny and histology: a review

Before describing the tooth attachment histology of *D. patagonica*, we review a number of poorly understood aspects of bone and tooth histology and ontogeny. Although enamel and dentine are important tooth tissues they will not be discussed in detail because they are not directly involved in tooth attachment. We restrict this discussion to amniote tissues because the ontogeny and histology of non-amniote tooth attachment tissues is poorly known and rarely studied.

Bone

Tooth-bearing bones, such as the maxilla and dentary are composed of an outer layer of periosteal bone and an inner layer of endosteal bone. Cells derived from the periosteum (i.e. the outer “skin” of a bone) and the endosteum (i.e. the inner “skin” of a bone) form periosteal bone and endosteal bone respectively. Periosteal bone and endosteal bone accumulate and change structure over time through accretion (bone tissue added to the bone surface) and remodeling processes (the conversion of primary bone to secondary bone). Remodeled periosteal and endosteal bone may feature well-developed secondary osteons (Haversian systems). Bone fabrics common to the tooth-bearing bones include compact bone tissues (lamellar and parallel-fibered bone), cancellous bone tissues and woven-fibred bone tissues.

Compact bone is a dense, slow-growing bone tissue with little to no vascularization. It usually forms on the outer surface of growing bones and can either form as a primary bone tissue or replace a primary bone tissue. Compact bone may show zonations representing differing rates of bone growth. There are two types of compact bone: lamellar bone and parallel-fibred bone. Most authors use the term “lamellar bone” incorrectly when discussing either lamellar or parallel-fibred bone. The use of a petrographic microscope is necessary to differentiate true lamellar bone and parallel-fibred bone (see details in Reid [1996: 29]). Lamellar bone proper is bone formed of fine collagen fibre bundles arranged in single bundle layers; the bundles in successive layers run in different, generally criss-crossing, directions (Reid, 1996). This is a highly organized, dense bone tissue found usually on the exterior surface of bones. Parallel-fibred bone is more organized than lamellar bone in that all collagen fibre bundles run in a single direction.

Cancellous bone is a highly vascularized bone tissue that forms as a primary or secondary tissue in the innermost region of a bone. The fibres forming cancellous bone may be well organized as in bone with parallel osteons or disorganized as in woven-fibred bone. Cancellous bone may show growth lines.

Contrary to the aforementioned tissues, woven-fibred bone is highly unorganized with a variable vascularization pattern. Collagen fibres of the bone matrix are interwoven in no discernible pattern. Woven-fibred bone is a fast growing tissue that may subsequently be replaced by compact bone tissues. It may be zonal and is commonly found in regions of fast tissue growth, near the central regions of bones and at tooth attachment sites.

Dental attachment tissues

Alveolar bone

Alveolar bone is a woven-fibred tissue externally adjacent to the periosteal bone of the tooth-bearing element. Alveolar bone almost surrounds completely the base of the tooth root and may fill the mesial-distal region between teeth, and between teeth and the tooth-bearing bone. Developmentally, alveolar bone is derived from osteoblasts differentiated from the basal cell layer of the dental follicle (layers of ectomesynchymal cells surrounding the base of the dental papilla) (Ten Cate &Mills, 1972); prior to this discovery, alveolar bone was thought to be produced by the periosteum of the tooth-bearing bone. During the tooth replacement process the alveolar bone of the shedding tooth is partially or completely resorbed. New alveolar bone tissue is deposited on top of any remaining alveolar bone by cells from the dental follicle of the newly forming replacement tooth. The bone filled mesial-distal region between teeth has been referred to as the interdental plate or transverse septum (e.g., Romer, 1956; Zaher & Rieppel, 1999). Some have suggested that the interdental plate is a portion of the tooth-bearing bone that grows between teeth (Zaher & Rieppel, 1999). In the case of mammals (Ten Cate, 1998), archosaurs (Berkovitz & Sloan, 1979), mosasaurs (Caldwell *et al.*, 2003) and sauropterygians (*pers. obs.*), histologic sections show that the interdental plates are formed of alveolar bone and are an artifact of tooth replacement and growth of the tooth-bearing bone.

Descriptions of alveolar bone are not found, or are fallible, in classic dental literature. Tomes (1898) did not observe alveolar bone per se, he saw "bone of attachment" ankylosing the teeth of vertebrate species to the tooth-bearing bone.

"... *it seldom, perhaps never, happens that a tooth is attached directly to a plane surface of the jaw which has been formed previously; but the union takes place through the medium of a portion of bone (which may be large or small in amount) which is specially developed to give attachment to that one particular tooth, and after the fall of that tooth is itself removed.*

For this bone I have proposed the name " bone of attachment"..." Tomes (1898: 229)

Other authors (e.g., Mummery, 1924; Orban, 1929) acknowledged alveolar bone as being a distinct tissue lining the tooth sockets but did not discuss its ontogeny.

Bone of attachment

"Bone of attachment" is a poorly defined term used traditionally to describe the tissue attaching the teeth of all non-mammalian, non-thecodont amniotes to the jawbone. It is defined as a bone-like tissue attaching the tooth to the tooth-bearing bone. Edmund (1969) suggested that "bone of attachment" and cement were synonymous. Osborn (1984) argued convincingly that "bone of attachment" is likely homologous to alveolar bone (described below), a tissue not identified by Tomes (1898). Osborn (1984) did not differentiate definitively between alveolar bone and "bone of attachment". As there is no definitive histologic character distinguishing "bone of attachment" and alveolar bone (Edmund, 1969; Osborn 1984, Caldwell *et al.*, 2003) we consider "bone of attachment" and alveolar bone synonymous and prefer the latter term.

Periodontal ligament

A periodontal ligament extends between the cement and alveolar bone. The periodontal ligament is a region of organized collagen fibre bundles; collagen fibre bundle organization is species specific and can vary within a species or an individual (Osborn, 1981). There are few cell types in this region, mainly fibroblasts (most abundant), undifferentiated mesenchymal cells that may be involved in collagen turnover, and epithelial cells (remnants of Hertwig's Epithelial Root Sheath; Hertwig's Epithelial Root Sheath disintegrates prior to the formation of cement [Ten Cate, 1998]). Blood vessels and nerves may also be found in the periodontal ligament.

Osborn (1984) suggested the periodontal ligament represents a non-calcified zone of the collagen matrix upon which cement and alveolar bone are deposited. A heterochronic shift in the amount of time for either or both of these tissues to develop would leave a region of uncalcified collagen fibres between the two tissues. Osborn (1984) suggested this hypothesis of homology with caution because little was known about the development of the dental follicle at that time. It is now well understood that the cells of the dental follicle differentiate into cementoblasts and osteoblasts prior to the formation of cement and alveolar bone (Ten Cate, 1998). No distinctive cell group has been identified producing periodontal ligament collagen specifically (Diekwisch, 2002). The continual lack of evidence of a distinct ontogeny for the periodontal ligament lends support to Osborn's (1984) hypothesis. We too believe that the periodontal ligament represents a region of a collagen fibre matrix not calcified by either osteoblast or cementoblast products; the periodontal ligament is viewed as a zone of potential biomineralization.

Cement

Cement resembles compact bone and attaches directly to the dentine of the tooth root. It may be cellular or acellular; it is common to see both types on any given tooth. Acellular cement is usually immediately adjacent to the tooth root and cellular cement is usually more distal to the tooth root. Cement is deposited by cementocytes that are differentiated from the dental follicle. Cementocytes trapped during the calcification process give cellular cement its name. Cement accretes throughout the life of the tooth and may show zones representing periods of differential growth; this knowledge is applied in aging mammals such as bears and cetaceans (e.g., Perrin &Myrick, 1978).

Cement has been observed rarely in small nonmammalian amniotes but is often observed in large nonmammalian amniotes (e.g., sauropterygians [Peyer, 1968], mosasaurs [Caldwell *et al.*, 2003]). The apparent lack of cement in small amniotes may be a problem of scale. Very thin layers of cement are unidentifiable using optic properties or light microscopy. Immunohistochemical techniques are the best method for observing thin cement layers but cannot be performed on fossil material.

Edmund (1969) suggested that cement attached the teeth of reptiles to the tooth-bearing bone. He also noted that cement, using his definition, in reptiles was identical to "bone of attachment" as defined by Tomes (1898); he preferred the term cement and only used "alveolar bone" in reference to archosaurian and mammalian dentitions. We suggest that Edmund's (1969) cement is actually alveolar bone, not cement.

Osborn (1984) identified a "protocement" tissue covering the tooth root of all nonmammalian, nonarchosaurian amniotes. He did not indicate how this tissue differed from cement observed in mammals and archosaurs. We suggest that "cement" and "protocement" are synonymous because there are no histologic features distinguishing either term from the other.

MATERIALS AND METHODS

Methods

The tooth socket morphology and histology of *Dinilysia patagonica* Woodward, 1901, was observed in a thinsection made from a broken left maxilla lacking teeth (UALVP unnumbered specimen). MPCA-PV 527, a portion of a right dentary bearing 3 teeth and MACN 1013, a portion of a right dentary bearing 1 tooth, were examined for gross dental morphology. HistoBest, Inc., Edmonton, Alberta, Canada made thinsections of extant snake material. The primary author stained these sections in the Department of Biological Science Microscopy Unit, University of Alberta. Images were taken using a Nikon Coolpix 990 digital camera mounted on a Nikon SMZ 1500 dissecting microscope or a Nikon Eclipse E600 POL microscope. Drawings were produced by digitally tracing images.

The colours in the figured digital images were inverted to highlight the different textures of alveolar bone and compact bone. We interpreted the tissue types using the terminology in Reid (1996), Caldwell *et al.*, (2003) and this paper.

Comparative material

Comparative material included vertical and horizontal thinsections from a partial dentary of *Platecarpus* sp. (NMC 40956), a dried specimen of *Cylindrophis rufus* (USNM 297456), a dried specimen of *Xenopeltis unicolor* (USNM 287277), a partial dentary of *Mosasaurus mokoroa* (CM ZFR1), vertical sections of the right dentary of *Thamnophis sirtalis* (UAMZ unnumbered) stained with Masson's trichrome or haemotxylin and eosin and vertical sections of the right dentary of *Sauromalus obesus* (CMNAR 25719) stained with Gomori's trichrome. The extant species were chosen because they either shared gross morphology similarities with *D. patagonica*, i.e. *C. rufus* and *X. unicolor*, or were squamates distantly related to *D. patagonica*, i.e. *Thamnophis* and *S. obesus*, readily available for thinsectioning.

Abbreviations

CM ZFR- Canterbury Museum, Christchurch, New Zealand; MACN- Museo Argenino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; NMC- Canadian Museum of Nature, Ottawa, Canada: CMNAR- Canadian Museum of Nature, Ottawa, Canada; MPCA-PV- Museo de la Ciudad de Cipoletti, Cipoletti, Río Negro Province, Argentina; UALVP- University of Alberta Laboratory for Paleontology; UAMZ- University of Alberta Museum of Zoology, Edmonton, Canada; USNM- Smithsonian Institution, United States National Museum, Washington, D.C., U.S.A.

RESULTS

Morphology and histology of *Dinilysia patagonica*

Gross morphology

The maxillae, dentaries, palatines and pterygoids are the tooth-bearing bones of *D. patagonica.* Based on socket sizes and teeth preserved on the holotype (Estes, Frazzetta & Williams, 1970) and the new material described by Caldwell & Albino (2002) of *D. patagonica*, pterygoid teeth and palatine teeth are extremely small and dentary teeth and maxillary teeth are larger and more robust. The number of tooth positions on a tooth-bearing bone is determined by counting the number of sockets in the tooth-bearing bone. Estes, Frazzetta & Williams, (1970) suggested that *D. patagonica* had 5 or 6 teeth on each palatine and pterygoid and 10 or 11 teeth per dentary. The number of teeth present on the holotype maxillae is unknown as both bones are incomplete. Caldwell and Albino's (2002) description of the new Neuquén material shows that each maxilla was capable of supporting at least 14 teeth.

Complete and *in situ D. patagonica* teeth are rare in the fossil record. The teeth of *D. patagonica* are hollow, conical, smooth and moderately recurved like the teeth of most primitive snakes. The hollowness of the teeth of *D. patagonica* was confirmed by examining a tooth broken during fossil preparation. The pulp cavity is broad and open and is similar to the pulp cavities of most squamates. The attachment site for the teeth is the alveolar crest (the socket aperture) (Fig. 3-1). It is noted that the basal circumferences of the teeth greatly underfit the socket apertures. The aperture shape of the sockets may be roughly circular, square or rectangular (longest side labial-lingual) and the base of the socket is concave. The size and shape of the sockets varies. The dimensions of the 3 sockets in the maxilla, anterior to posterior, is 3.5 mm x 4 mm, 3.5 mm x 5 mm and 4.5 mm x 5 mm (mesial-distal length x labial-lingual length). Socket depths are approximately equal; the sockets are 2 mm-3 mm deep and shallow gradually along the maxilla from the anterior socket to the posterior socket.

Histology

The thinsection examined for histological information was made through the mesial-distal region (interdental plate) between tooth positions on the left maxilla.

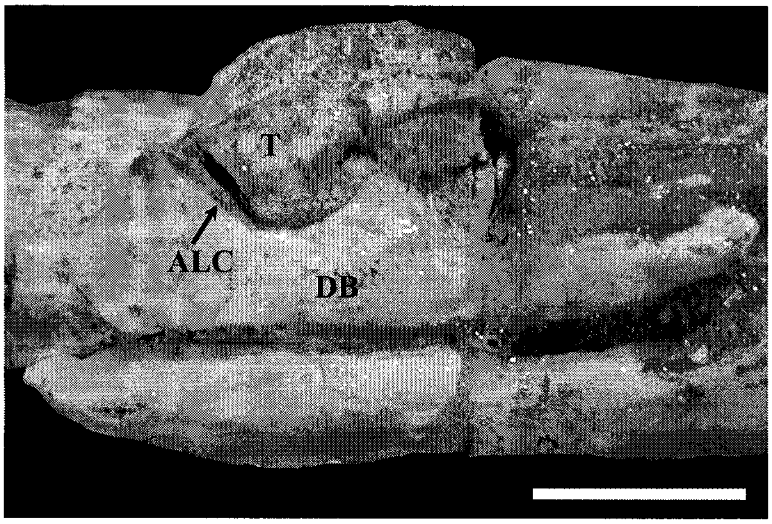

Figure 3-1: Lingual view of the right dentary of *Dinilysia patagonica* (MACN 1013) showing a robust recurved tooth preserved above the alveolar crest of an underlying socket. The tooth is not ankylosed to the underlying bony tissue. ALC, alveolar crest; DB, dentary; T, tooth. Scale bar= 5mm.

We observe three distinct bone tissues, compact zonal bone, cancellous bone, and woven-fibered bone (Fig. 3-2).

The compact zonal bone extends from the labial portion of the alveolar crest to the lingual portion of the alveolar crest effectively supporting the socket proper. The topology and morphology of the compact zonal bone is the same as that of bones derived dermally. We identify compact zonal bone as the tissue forming the external portion of the maxilla in *D. patagonica.*

Cancellous bone is observed underlying the socket and is bound by the compact bone tissue and the woven-fibred bone tissue. Most bones are made of an outer layer of compact bone and an inner layer of cancellous bone. Therefore, the observed cancellous bone tissue likely forms the central part of the maxilla.

We observe a woven-fibred bone tissue bounded labially and lingually by compact zonal bone and below by cancellous bone. The woven-fibred bone tissue is likely alveolar bone, based on its topologic and histologic similarity to alveolar bone. We note that it forms the tooth socket walls and fills the mesial-distal region between teeth in *D. patagonica.* The basal region of alveolar bone is a woven-fibred bone tissue with secondary osteons representing alveolar bone formed earlier in ontogeny that has not been resorbed during subsequent tooth replacement events.

Snakes are polyphyodont, meaning the teeth are replaced many times throughout an individual's life. Prior to the shedding of the functional tooth, some of the attachment tissues are resorbed to facilitate tooth loss. During the

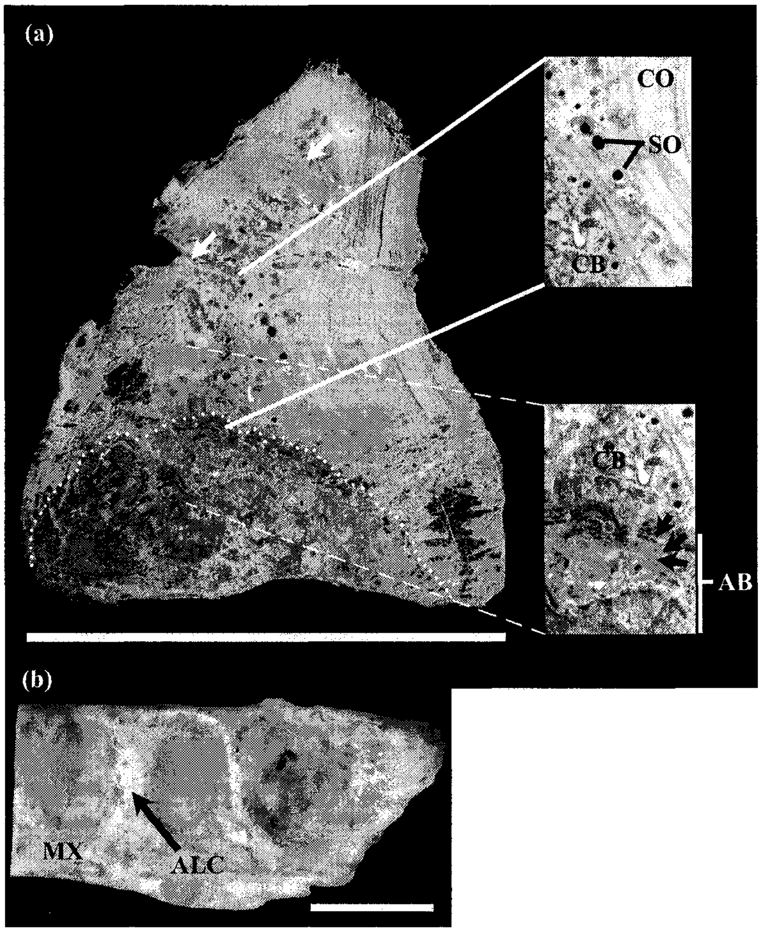

Figure 3-2: (a) Vertical thin section through the bony tissue filled mesial-distal space between tooth positions on the left maxilla of *Dinilysia patagonica* (UALVP unnumbered). Labial is to the left. The alveolar bone-filled mesial distal region between teeth is conspicuous as are several prior generations of alveolar bone. The ontogeny of the maxilla is evident in the changing lineations of the compact bone and the multiple zones of cancellous bone; (b) The left maxilla of *D. patagonica* (UALVP unnumbered) showing three empty tooth sockets. Mesial is to the left. Note the mesial part of the alveolar crest is more robust than the rest of the crest. The thinsection pictured above was sliced from the left end of this portion of the maxilla; hence the sharp, linear edge of the anterior end of the maxilla. AB, alveolar bone; ALC, alveolar crest; CO, compact bone; CB, cancellous bone; MX, maxilla; ⇨, former apical end of maxilla; ➡, prior generation of alveolar bone; o o o o, margin of alveolus. Scale bar = (a) 5 mm; (b) 4.5 mm.

development of the replacement tooth, new alveolar bone forms and attaches to the tooth attachment site. Remnants of previously deposited alveolar bone may be incorporated into the replacement tooth attachment apparatus. Over time, previous generations of alveolar bone remodel and exhibit secondary osteons like the ones seen in *D. patagonica.*

DISCUSSION

Inferred tooth attachment mode

A ligamentous hinge likely anchored the tooth of *D. patagonica* to the alveolar bone of the alveolar crest (the top of the socket). If a bony tissue directly attached the teeth of *D. patagonica* to the maxilla, we would expect to see more *Dinilysia* teeth preserved in the fossil record. We would also expect to see a bone tissue at the base of preserved teeth. Known specimens of *D. patagonica* meet neither of our expectations, e.g., MACN 1013 only shows one tooth in place (Fig. 3-1) (finding 3 teeth in position, as in MPCA-PV 527 is rare [Fig. 3-4: a]); note that no bony tissues support the teeth. We cannot determine the size or exact position of the hinged attachment in *D. patagonica.* The hinge in other snakes with hinged tooth attachments is attached to the postero-lingual side of the corona of the socket. A parapet of bony tissue wrapping around the mesial side of the socket corona is usually associated with hinged attachments (Fig. 3-4: b). We see a similar, though less dramatic, feature in Dinilysia (Fig. 3-2: a). Our reconstructed hinged tooth attachment morphology for *D. patagonica* is shown in Figure 3-3.

Comparative dental anatomy

The tooth attachment histology of *D. patagonica* shares similarities with that of some squamates with a hinged tooth attachment where the tooth is attached by a large ligament to one portion of the attachment site (e.g., *Xenopeltis unicolor* (Fig. 3-4: b) and some pygopodids [Savitzky, 1986]). The extant hinged toothed squamates and *D. patagonica* may share the presence of a zone of uncalcified tissue attaching the tooth to the tooth attachment site. Ahinged or ligamentous tooth attachment in squamates is usually correlated with a durophagous (hard food) diet (Patchell & Shine, 1986). A hinged attachment is a ligamentous attachment confined to a certain region of the attachment site; the tooth folds at the hinge in response to pressure. Hinged and ligamentous (the tooth is attached by a ligament surrounding the tooth root) attachments vary in the amount of ligamentous tissue present and the location of the ligamentous attachment to the alveolar bone.

The examined squamates with a hinged or ligamentous attachment share similar socket morphologies with *D. patagonica* (Fig. 3-2, 3-4). When comparing socket morphology in reptiles it is necessary to try and compare the dentitions on each tooth-bearing bone separately as tooth morphology and attachment can vary from one tooth-bearing bone to another. With the exception of *Sauromalus*

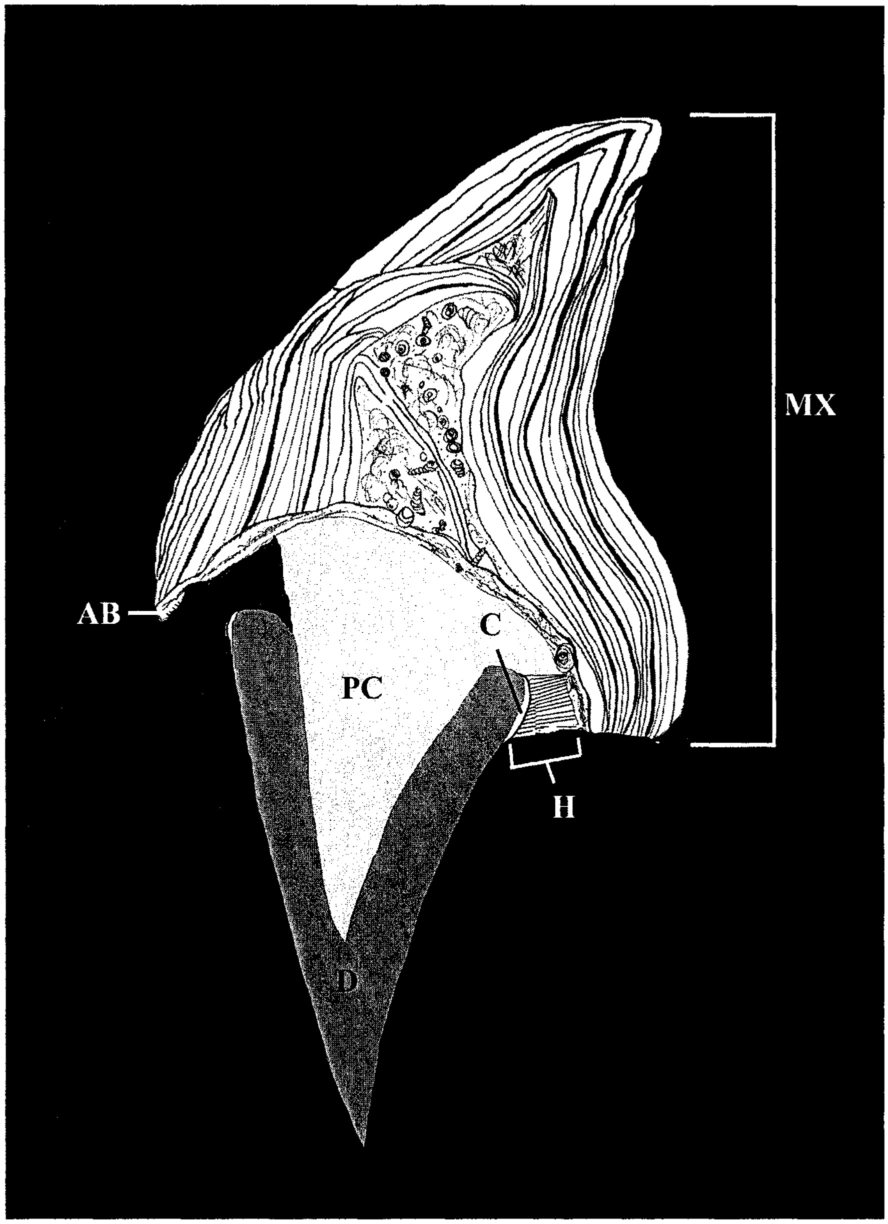

Figure 3-3: Inferred hinged tooth attachment of *Dinilysia patagonica*. The extent of development of the hinge and its attachment site on the alveolus is unknown. The presence of cement adjacent to the tooth root can not be confirmed. Cement is probably present as teeth usually attach to additional attachment tissues (e.g., alveolar bone, periodontal ligament) through cement. AB, alveolar bone; C, cement; D, dentine; H, hinge; MX, maxilla; PC, pulp cavity.

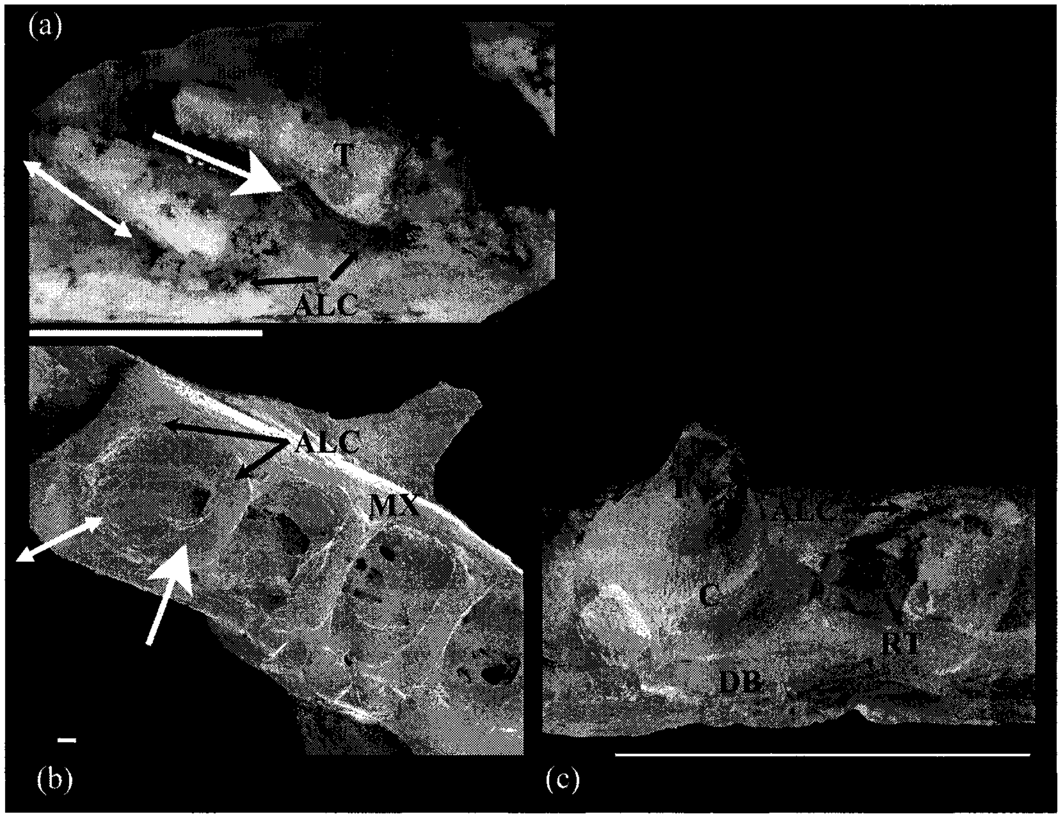

Figure 3-4: A comparison of the tooth socket morphologies of (a) *Dinilysia patagonica* (UALVP unnumbered); (b) *Xenopeltis unicolor* (left palatine); (c) *Platecarpus* sp. (right dentary- flipped horizontally). Note the presence of a mesial parapet of bony tissue typical of hinged attachment sites in (a) and (b) (Savitzky, 1981). Mesial is to the right in all images. ALC, alveolar crest; C, cement; DB, dentary; MX, maxilla; RT, replacement tooth; T, functional tooth, white arrows, mesial parapet of bony tissue; double headed white arrows, trajectory of rotatation. The hinge would attach to the tooth bearing bone on the postero-lingual side of the socket. Scale bar= (a) 5 mm; (b) 3 mm; (c) 40 mm.

obesus and *Platecarpus* sp., whose examined attachment sites are on the dentary, and *Xenopeltis*, whose attachment sites were observed on the palatine, all attachment site comparisons are made from attachment sites on maxillae and dentaries. The attachment sites of *Platecarpus* sp. do not differ significantly from one tooth-bearing bone to the next, therefore, we are comfortable with our comparison of this dentary dentition with that of the maxillary dentition in *D. patagonica*.

Compared to *X. unicolor*, the sockets of *D. patagonica* are very similar in that the sockets are mesial-distally compressed and have a large amount of bony tissue, likely alveolar bone, forming a region of the alveolar crest that is distinctly thicker than any other region of the crest. This pad of bony tissue likely supports the free anterior portion of the tooth; the part of the tooth not supported by the periodontal ligament in *X. unicolor*. A similar condition is seen in a nonamniote, the hake that is the classic example of a hinged tooth attachment (Tomes, 1898).

The mosasaur, *Platecarpus* sp., also has a ligamentous attachment. Unlike the hinged ligamentous attachment described above, *Platecarpus* sp. has a very short ligament attached to a very thick zone of cellular cement and a thin layer of alveolar bone (both cements cover the root) (Caldwell *et al.*, 2003). We have not observed cement in any of the other squamates examined and do not have appropriate material of *D. patagonica* to discern if this species has cement. The commonality between the tooth attachment of *Platecarpus* sp. and *D. patagonica* is the extent of development of the tooth socket within the tooth-bearing bone and the presence of alveolar bone forming the sockets.

The teeth of the other squamates examined, *Thamnophis sirtalis* and *Sauromalus obesus*, are ankylosed to the attachment site. Tomes (1898: 230 Fig. 107) diagramed the dental attachment of an unidentified snake tooth. The tooth is attached by "bone of attachment" within a shallow groove in the jawbone. Several generations of "bone of attachment" are observed under the tooth. The several generations of "bone of attachment" are likely the stratification of alveolar bone of previous generations of teeth. Our observations of the tooth attachment histology of *Thamnophis* and *S. obesus* are identical to those of Tomes (1898). *D. patagonica* and these squamate species are similar in having a dental attachment site made of successive generations of alveolar bone. They differ in that teeth of the other species are attached to the alveolar bone by an unidentified biomineralized tissue and a ligament likely attaches the teeth of *D. patagonica* to the alveolar bone.

Snake dental evolution

There are several general trends in dental character changes throughout snake evolution. There has been a reduction in the number of teeth overall (Edmund, 1969) and an increase in the complexity of the tooth surface over time (Young & Kardong, 1996). The maxillae, dentaries, pterygoids and palatines are the possible tooth-bearing bones in Ophidia. Only some booids (more primitive snakes) have teeth on the premaxillae; more advanced snakes have a greatly reduced premaxilla and no premaxillary teeth. Frazzetta (1970) inferred that *D. patagonica* should have premaxillary teeth based on this species supposed primitive position in snake phylogeny. The more primitive snakes, i.e. booids and aniliids tend to have isodont dentitions with all tooth-bearing bones bearing many similarly shaped teeth along the entire length of the tooth-bearing bones whereas more advanced snakes (e.g., elapids and colubrids), tend to be heterodont having a reduced number of teeth along any given tooth-bearing bone (Edmund, 1969). Studies of the evolution of snake dental attachment characters are hampered by a lack of snake dental histology data and the fact that snake phylogeny is highly unstable. The discovery of alveolar bone and a possible ligamentous attachment in *D. patagonica* indicates there are important and potentially phylogenetically significant dental attachment characters to be explored with a survey of snake dental histology.

Squamate phylogenies and tooth attachment characters

The phylogenetic relationship of *D. patagonica* to other snake taxa has been difficult to examine because a large number of morphologic features of *D. patagonica* are unknown due to the fragmental and incomplete nature of the specimens. Another problem is that it is difficult to determine the character polarity for characters in snake phylogenetic analyses because the positions of other important snake taxa, i.e. scolecophidian snakes, *Pachyrachis* and *Haasiophis* (Cretaceous marine snakes), and Madtsoiidae (early terrestrial snakes) are not agreed upon (Caldwell & Lee, 1997; Rage & Escuillié, 2000; Scanlon & Lee, 2000; Tchernov *et al.*, 2000). The relationship between snakes and other squamates (the clade comprised of lizards and snakes) is also not agreed upon. The two general hypotheses of relationship are 1) snakes are closely related to a clade composed of dibamids and amphisbaenids or 2) snakes are closely related to extinct marine lizards (mosasauroids) that may be nested with anguimorph lizards.

Tooth attachment type is a character that has proved convenient in separating Squamata into two general groups. Acrodonta Cope, 1864 (Agamidae and Chamaeleonidae today) has teeth attached in the acrodont fashion where the tooth is attached by alveolar bone to the jaw apex. Other, non-snake, non-amphisbaenid squamates were grouped into Pleurodonta Cope, 1864; pleurodonty (tooth attached by alveolar bone to the lingual pleura of the jaw) is the attachment type for the members of this group. Recent research by Lee (1997) and Caldwell *et al.* (2003) concluded that mosasaurs and snakes are thecodont (tooth attached by a ligament to the walls of a socket made of alveolar bone) and not pleurodont as suggested by another recent study (Zaher & Rieppel, 1999).

Caldwell *et al.*, (2003) attributed the misclassification of mosasaur tooth attachment by Zaher and Rieppel (1999) to several problems associated with their usage and redefinition of the conventional vertebrate tooth attachment classification scheme (acrodonty-pleurodonty-protothecodonty-thecodonty). Zaher and Rieppel (1999) did not use the accepted definitions of acrodonty, pleurodonty and thecodonty outlined in classic dental literature (e.g., Owen, 1840-1845; Tomes, 1898; Mummery, 1924; Edmund, 1969; Osborn, 1984). Instead they presented their own definitions. Their definition of thecodonty included only polyphyodont (animals that replace their teeth throughout life) animals; this definition excluded mammals, the classic example of thecodonty. Zaher and Rieppel (1999) used archaic, dental anatomy terms, labial pleurodonty and full pleurodonty, in their classification as well. These sub-categories were introduced by Lessmann (1952) and are based on the presence or absence of a basal plate and the presence or absence of a fluted tooth base. Both of these features have not been diagnosed histologically and cannot be seen in the gross morphology of attached teeth. Zaher and Rieppel (1999) did not use dental histology to classify mosasaur and snake tooth attachment type. Their conclusion that mosasaurs exhibit an attachment condition "... secondarily derived from a fully pleurodont dentition ..." is not a classification of mosasaur tooth attachment type, but a statement on the origin of the attachment type seen in mosasaurs. These authors tried to classify tooth attachment in mosasaurs within a phylogenetic context regardless of morphology. Within the confines of the traditional attachment classification scheme, based solely on morphology and not phylogeny, it is more correctly concluded that mosasaurs are subthecodont as in Lee (1997) or thecodont as in Caldwell *et al.*, (2003).

The problems with the traditional vertebrate tooth attachment scheme are that tooth attachment type is diagnosed primarily by examining gross morphology. The traditional categories describe two distinct characters and the traditional tooth attachment terms are constantly added to and redefined (Caldwell *et al.*, 2003). Caldwell *et al.*, (2003) suggested that tooth attachment type be determined by examining histologic data and not gross morphologic data because tissues can only be identified conclusively using histology. They also point out that the vertebrate tooth attachment classification scheme of acrodonty-pleurodonty-protothecodonty-thecodonty is not a classification of one character but two characters, where the tooth is attached and how it is attached. The conflation of the two characters into one has led authors to create many extra categories to accommodate tooth attachment diversity in nature (e.g., Motani, 1997) who listed 13 different attachment categories used to classify tooth attachments of ichthyosaurs, a group of extinct marine tetrapods.

While the usage of acrodonty-pleurodonty-protothecodonty-thecodonty may be useful to describe different general attachment morphologies it is clear that the simple classification terminology is not sufficient for phylogenetic studies nor to describe attachment in detail in the different groups of squamates. We suggest using dental histology characters in place of the traditional attachment categories when conducting phylogenetic analyses of Squamata.

CONCLUSION

We describe the histology of the alveolus and the maxilla of *D. patagonica* and compare it to the dental attachment features in some extant snakes, the fossil marine lizard (mosasaur) *Platecarpus* sp., and other non-snake squamates. The teeth of *D. patagonica* were likely attached by a ligament to the crest of an alveolus formed of alveolar bone. The maxilla of *D. patagonica* is formed from compact zonal bone and cancellous bone and the current socket is made of alveolar bone. Alveoli of previous tooth generations are preserved as alveolar bone with secondary osteons. The tooth attachment apparatus of *D. patagonica* is similar to that of all other squamates in that a zone of alveolar bone ultimately attaches the tooth to the tooth-bearing bone. The tooth sockets of *D. patagonica* are set deep within a groove in the maxilla, similar to the condition in the aniliids *X. unicolor*, *C. rufus* and the mosasaur *Platecarpus* sp. (Caldwell *et al.*, 2003). The sockets of *D. patagonica* are most similar to those of *X. unicolor*. Our study shows how important histology is when determining tooth attachment morphologies. We question the usage of the traditional tooth attachment categories (acrodonty-pleurodonty-protothecodonty-thecodonty) in phylogenetic analyses of Squamata and suggest that dental histology characters be experimented with in future cladistic analyses of Squamata.

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CHAPTER 4

SURVEY OF SQUAMATE TOOTH ATTACHMENT HISTOLOGIES: THE INVALIDATION OF TRADITIONAL CATEGORIES AS CHARACTER STATES

(To be submitted as "Budney, L.A. Survey of squamate tooth attachment histologies: the invalidation of traditional categories as character states" to The Journal of Herpetology)

CONTEXT

Problems with tooth attachment terminology and their application to squamate dental attachments were introduced in Chapters 2 and 3 respectively. The usage of tooth attachment terminology as character states in squamate phylogenetic analyses (Lee & Caldwell, 2000; Rieppel *et. al.*, 2002) will be tested empirically in this chapter. Chapter 4 contains the most comprehensive survey of squamate tooth attachment histology to date. There is enough histologic data presented to conclude that traditional tooth attachment terminology (introduced in Chapter 2) does not represent actual tooth attachments in squamates. Therefore, the traditional categories as character states (as defined in published literature) will be deemed phylogenetically insignificant. Other characters worthy of investigation as phylogenetically significant characters will be introduced based on the results of the comparative histology survey. The discovery of so-called derived attachment tissues (cement, periodontal ligament, alveolar bone) in a large group of early vertebrates, squamates, suggests these tissues evolved early in vertebrate history. The invalidation of the traditional tooth attachment categories in Chapters 2 and 4 as discrete anatomic entities combined with the discovery of derived attachment tissues in many early vertebrates suggests we have misunderstood not only squamate tooth attachment evolution, but vertebrate tooth attachment evolution as well.

INTRODUCTION

Squamata (clade consisting of lizards, snakes, their relatives and their common ancestor) contains more than 6000 species of animals organized into approximately 30 “families” (Fig. 4-1). Squamates may have teeth on the premaxilla, maxilla, vomer, palatine, pterygoid and dentary. Many studies of the gross dental morphology of squamates indicated that external tooth morphology was variable (Bogert, 1943; Hotton III, 1955; Savitzky, 1983, 1981; Patchell & Shine, 1986a, b; Vorobyeva &Chugunova, 1991; Coleman *et. al*, 1993; Young & Kardong, 1996). We are limited in our knowledge of squamate dental histology. Patchell and Shine (1986a/b), Caldwell *et al.* (2003), and Zaher and Rieppel (1999) are the only studies focused exclusively on comparative tooth attachment in squamates. Other accounts of squamate dental histology were found in reviews of vertebrate dentitions (Tomes, 1898; Romer, 1956; Peyer, 1968; Edmund 1969) or studies of the dentition of single squamate species (Cooper, 1966; Cooper & Poole, 1973; Throckmorton, 1979).

Squamate dental attachment histologies have not been studied because it was assumed that squamate dental attachment histology was invariant; squamate teeth were attached by bone of attachment (coined by Tomes, 1875), a cement-like bony tissue, to the tooth-bearing element (Tomes, 1898; Romer, 1956; Peyer, 1968). The hinged teeth of pygopodid lizards and some snakes were the acknowledged exceptions (Savitzky, 1981; Patchell and Shine, 1986a/b). The

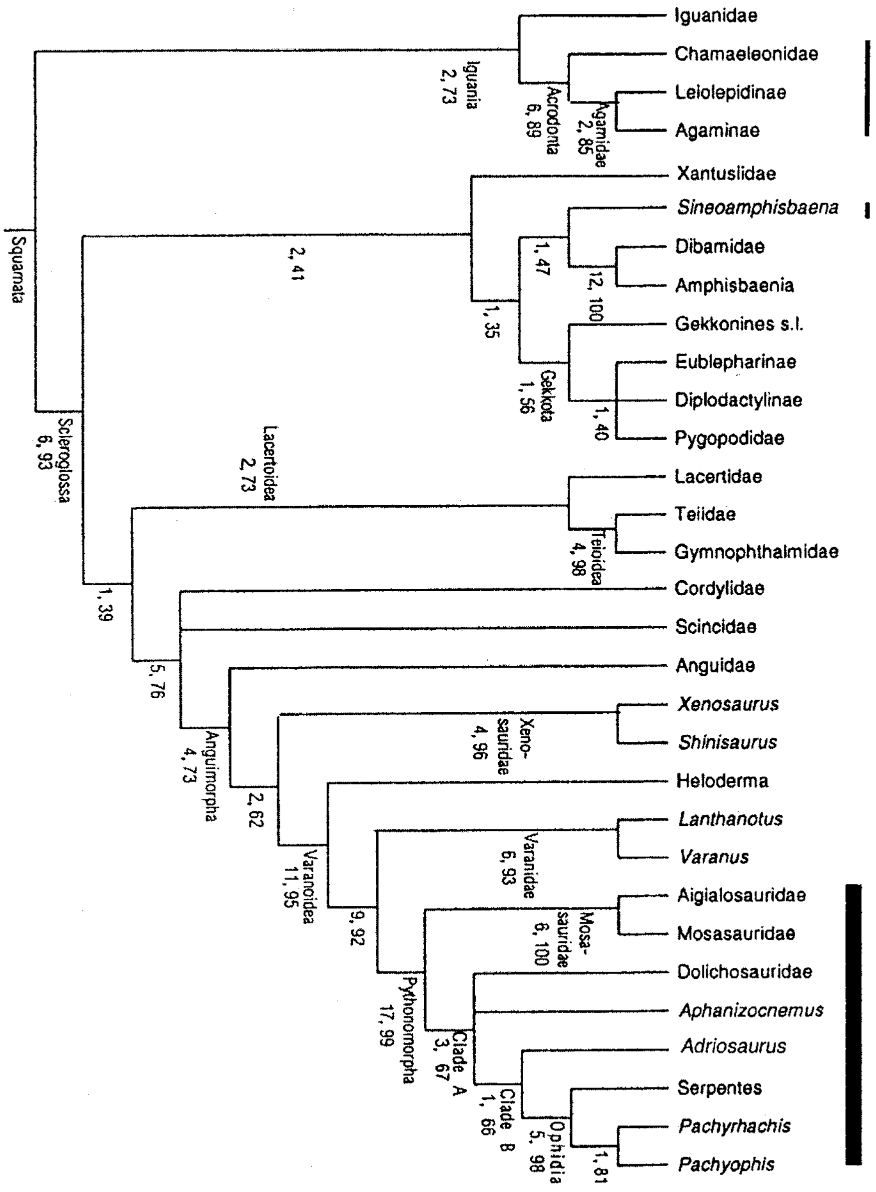

Figure 4-1: Cladogram of the interrelationships of squamates (Lee & Caldwell, 2000: 925). The thin black line indicates those squamate taxa exhibiting acrodonty. The thick black line indicates squamate taxa thought to exhibit thecodonty. All other squamates were coded pleurodont. These are Lee and Caldwell's (2000) codings. Other authors restricted thecodonty to Mosasauridae (Bell, 1997; Lee, 1997) and some others think that thecodonty is not present in squamates (Zaher & Rieppel, 1999).

location of the tooth attachment site on the tooth-bearing element was variable and was what differentiated the types of tooth attachment seen in squamates.

Until recently, two traditional types of tooth attachment had been observed in Squamata: acrodonty and pleurodonty (Fig. 4-1). Acrodonty was identified when the tooth was attached to the apex of the jawbone by bone of attachment, (e.g., in agamid and chamaeleonid lizards). Pleurodonty was identified when the tooth was attached to the lingual wall of the jawbone by bone of attachment, (e.g., all other squamates). These traditional categories have been redefined many times in the past century but the changes have not affected the classification of tooth attachment in squamates (Romer, 1956; Peyer 1968; Edmund, 1969; Augé, 1997; Zaher & Rieppel, 1999; Gaengler, 2000; see Chapter 2 for a review).

Recently, a third type of vertebrate tooth attachment, thecodonty, was observed in the extinct large aquatic mosasaur *Platecarpus* sp. (Caldwell *et al.*, 2003), putting to rest a debate on the type of tooth attachment exemplified by mosasaurs (Zaher & Rieppel, 1999; Lee, 1997); thecodonty was also identified in an early snake *Dinilysia patagonica* in this thesis (see chapter 3). Thecodonty was identified when the tooth was attached to the walls of a socket made of alveolar bone in the jawbone by cement and periodontal ligament. Because most squamate teeth are small and only the tooth attachment gross morphology is examined, it is possible that thecodont attachment has been overlooked in other studies of squamate dental attachment.

The use of traditional categories of tooth attachment in phylogenetic analyses of Squamata implied that those categories are phylogenetically significant in squamates (Estes, de Queiroz & Gauthier, 1988; Lee & Caldwell, 2000; Rieppel *et al.*, 2002). The phylogenetic studies of squamates vary in their definitions and codings of characters relating to tooth attachment. This variability in character construction would be unexpected of a well-known morphology or histology.

Tooth attachment character states have been assigned by examining gross dental morphology, not histology. This is problematic because short ligaments, and the different bony attachment tissues, cannot be identified gross morphologically. Recent debates on the tooth attachment type in mosasaurs (Lee, 1997; Zaher & Rieppel, 1999; Caldwell *et al.*, 2003) showed us that some squamate dental attachments had been misclassified. These studies noted that a survey of squamate tooth attachment histologies would provide data to better understand the evolution of tooth attachment in Squamata.

This study presents the first survey of comparative dental attachment histology in squamates. The results of an evaluation of the validity of some characters related to dental attachment used in cladistic analyses of squamates (Lee & Caldwell, 2000: Rieppel *et al.*, 2002) are also presented. This study concludes with suggestions of better characters related to tooth attachment worthy of investigation in future studies of squamate dentitions.

MATERIALS AND METHODS

Histology

The 35 squamate specimens in the study were obtained from the herpetology collections of the Canadian Museum of Nature (CMNAR, NMC), University of Alberta Museum of Zoology (UAMZ), University of Alberta Laboratory for Vertebrate Paleontology (UALVP), and Manitoba Museum (MM) [Table 4-1]. Six additional squamate specimens were not included in this survey because no teeth were observed in the produced thinsections. Two fish species, one caiman and one beluga whale were the comparative species representing better-known modes of tooth attachment (Table 4-1). Specimens were chosen based on their availability for thinsectioning. Portions (5 mm) of the posterior end of the tooth-bearing right dentary were excised, using scalpels and forceps, from the alcohol preserved specimens. Sampling was conducted in this fashion to minimize the visibility of the excision. Only portions of the right dentary were taken to standardize the tooth attachment data as tooth attachment can vary between the tooth-bearing bones (Fink, 1981).

Because the specimens were preserved in 70% ethanol (most had been preserved in formaldehyde prior to ethanol), they were very difficult to process for thinsectioning. Initial sections were made by myself in the University of Alberta's Department of Biology Microscopy Unit (BMU). Most sections were made by HistoBest, Inc., Edmonton, Alberta, Canada. All specimens were placed

SQUAMATA

CATALOGUE #	*FAMILY*	*SPECIES*	*SPECIMEN #*	*SECTIONS*
CMNAR 25026	ACROCHORDIDAE	*Acrochordus javanicus*	811	Y
CMNAR 32458-6	AGAMIDAE	*Agama agama*	829	Y
MM 1-3-145	AGAMIDAE	*Amphibolurus barbatus*	841	Y
CMNAR 30922-4	AGAMIDAE	*Calotes versicolor*	828	Y
CMNAR 29514-1	ANGUIDAE	*Celestes warreni*	NA	Y
CMNAR 1602	ANGUIDAE	*Elgaria coerulea principis*	NA	N
UAMZ unnumbered	ANGUIDAE	*Gerrhonotus principus*	815	Y
CMNAR 35067	ANILIIDAE	*Cylindrophis rufus*	827	Y
CMNAR 35170	BOIIDAE	*Epicrates cenchria*	835	Y
CMNAR 27262	BOIIDAE	*Lichanura trivirgata roseofusca*	821	Y
CMNAR 12588-2	CHAMAELEONIDAE	*Chamaeleo johnstoni*	813	Y
CMNAR 9116	COLUBRINAE	*Coluber constrictor priapus*	830	Y
UAMZ unnumbered	COLUBRINAE	*Pituophis melanoleucas*	810	Y
CMNAR 15418	CORDYLIDAE	*Cordylus cordylus cordylus*	822	Y
CMNAR 29492	CORDYLIDAE	*Cordylus warreni depressus*	NA	Y
CMNAR 30956	ELAPIDAE	*Dendroaspis anguticeps*	836	N
CMNAR 17921	ELAPIDAE	*Kolophis*	823	Y
CMNAR 29516-1	GEKKONIDAE	*Gekko gecko*	832	Y
CMNAR 29478-1	GEKKONIDAE	*Phelsuma guentheri*	833	Y
CMNAR 13907	IGUANIDAE	*Anolis sagrei ordinatus*	837	Y
UAMZ unnumbered	IGUANIDAE	*Dipsosaurus dorsalis*	825	N
CMNAR 25702	IGUANIDAE	*Holbrookia maculata*	816	Y
CMNAR 25719	IGUANIDAE	*Sauromalus obesus*	NA	Y
CMNAR 1353	LACERTIDAE	*Lacerta agilis*	826	N
CMNAR 4372	LACERTIDAE	*Lacerta vivipara*	831	Y
UALVP unnumbered	MATSOIIDAE	*Dinilysia patagonica*	NA	Y
NMC 40957	MOSASAURIDAE	*Platecarpus sp.*	NA	Y
CMNAR 29887-4	SCINCIDAE	*Eumesces fasciatus*	NA	Y
CMNAR 29529-2	SCINCIDAE	*Scincus scincus*	824	Y
CMNAR 25687-1	TEIIDAE	*Cnemidophorus exsanguis*	NA	Y
CMNAR 16295	TEIIDAE	*Cnemidophorus tigris*	NA	Y
MM 1-3-142	TEIIDAE	*Tubinambus teguixin*	843	N
CMNAR 30958	TROPIDOPHIIDAE	*Ungaliophis continentalis*	809	Y
CMNAR 35196	TYPHLOPIDAE	*Typhlops*	812	N
CMNAR 13884	VARANIDAE	*Varanus*	817	Y
MM 1-3-149	VARANIDAE	*Varanus niloticus*	842	Y
CMNAR 27386	VIPERIDAE	*Sistrurus catenatus*	820	N
CMNAR 10831-2	VIPERIDAE	*Vipera berus*	834	N
CMNAR 29482-1	XANTUSIIDAE	*Lepidophyma*	818	Y
CMNAR 29583	XENODONTINAE	*Heterodon playtrhinos*	814	Y
CMNAR 29530-3	XENOSAURIDAE	*Shinasaurus crocodylurus*	819	Y

COMPARATIVE SPECIES

CATALOGUE #	*FAMILY*	*SPECIES*	*SPECIMEN #*	*SECTIONS*
UAMZ unnumbered	ESOCIDAE	*Esox luscius*	838	Y
NMC 80-0401	LEPISOSTEIDAE	*Lepisosteus osseus*	839	Y
NMC 70-0336	LEPISOSTEIDAE	*Lepisosteus osseus*	840	Y
CMNAR 25747-4	CROCODYLIDAE	*Caiman sclerops*	NA	Y
DFO unnumbered	MONODONTIDAE	*Delphinapterus leucas*	NA	Y

Table 4-1: Specimens available for thinsectioning. Specimen #'s were given to specimens thinsectioned by HistoBest, Inc. Sections, refers to the success of the sectioning process. Y, yes; N, no.

initially in RDO, a commercial decalcification agent. Because the specimens did not decalcify well in RDO, some were decalcified, with limited success, using an endpoint decalcification protocol (Gabe, 1976). The specimens sectioned at BMU were processed and embedded in paraffin using an automatic histologic processor. Specimens sectioned by HistoBest, Inc. were processed and embedded by hand in a beeswax paraffin combination. Specimens were oriented so that sections would be cut perpendicular to the length of the tooth-bearing element. Serial sections were cut 5 um thick by hand using table-top microtomes. Sectioning was limited to 10 full slides of sections, with approximately 15 sections per slide. When mounted on slides, most sections were stained with Gabe's (1976) modified Gomori's trichrome by myself, with the exception of 10 sample slides stained by HistoBest, Inc. Some sections were stained in haemotoxylin and eosin or Masson's trichrome prior to the choosing of Gabe's (1976) modified Gomori's trichrome as a common staining agent. I chose this stain based upon discussions with HistoBest, Inc. It stains preferentially for collagen (the matrix of all tooth attachment tissues) and produces translucent colors good for black and white photography. When stained with Gomori's Trichrome, nuclei are black, cytoplasm is red, and collagen is green. The squamate biomineralized tissues stained unevenly but the squamate soft tissues stained appropriately. Despite unevenness in colour the structure and components of the biomineralized tissues were observable. The slides were coverslipped after staining.

The slides were examined using a transmitted light microscope (Nikon

SMZ 1500) or a polarizing/transmitted light microscope (Nikon Eclipse E600 POL). Images were taken with a Nikon DXM 1200F digital camera. A CD of all of the figures and plates in this chapter can be found in a pocket at the rear of this thesis (Appendix 4-2). The images on CD show more detail than printer resolution allows. Tissue identifications were made based on the tissue definitions in Caldwell *et al.* (2003), Ten Cate (1998) and Reid (1996). It was not possible to collect quantitative data (e.g. tissue thickness), as the specimens were oriented variably within the wax.

Testing of phylogenetic characters of tooth attachment

The phylogenetic characters relating to tooth attachment used by Rieppel *et al.* (2002) and Lee and Caldwell (2000) were evaluated based on data from the squamate dental histology survey. The characters within these published cladistic analyses would be supported if the squamate dental histologies agreed with the characters and character states. The published tooth attachment characters would be invalidated if the histologies disagreed with the character state definitions or if the diversity of histologies found is greater than that described by the character states. Tooth attachment would be considered insignificant phylogenetically in Squamata if there were no good characters related to tooth attachment to be used in cladistic analyses of Squamata.

RESULTS

General similarities- gross tooth structure

There were several similarities shared by all of the studied squamate dental attachments (Fig. 4-2). All images of squamate dental histology are included in Appendix 4-1 and Appendix 4-2. Orthodentine formed the tooth crown and root in all studied squamates. Because the specimens were decalcified, the presence and extent of the enamel could not be determined, although, it was observed being deposited by ameloblasts in specimens with poorly decalcified tooth germs. A tooth root (the dentine portion of the tooth not covered by enamel) covered by attachment tissues was observed in contrast to Peyer (1968) who suggested squamate teeth were rootless. Peyer (1968: 14-15) diagnosed a root as the cement covered dentine portion of the tooth below the crown. A root was identified only if the pulp cavity narrowed towards the attachment site. Peyer (1968) did not consider most reptiles to have a tooth root because the pulp cavity did not narrow towards the base of the tooth. The length of the tooth root varied based on the size and shape of the tooth attachment site (the portion of the dentary covered with tooth attachment tissues to which the tooth is attached). With the exception of the tooth roots in varanids, which had convoluted tooth roots, other squamate tooth roots were open and varied in length. Differences in the length of the tooth root seemed correlated with the tooth attachment site size, (i.e., the larger the tooth attachment site, the longer the tooth root) and the slope of the dentary. The

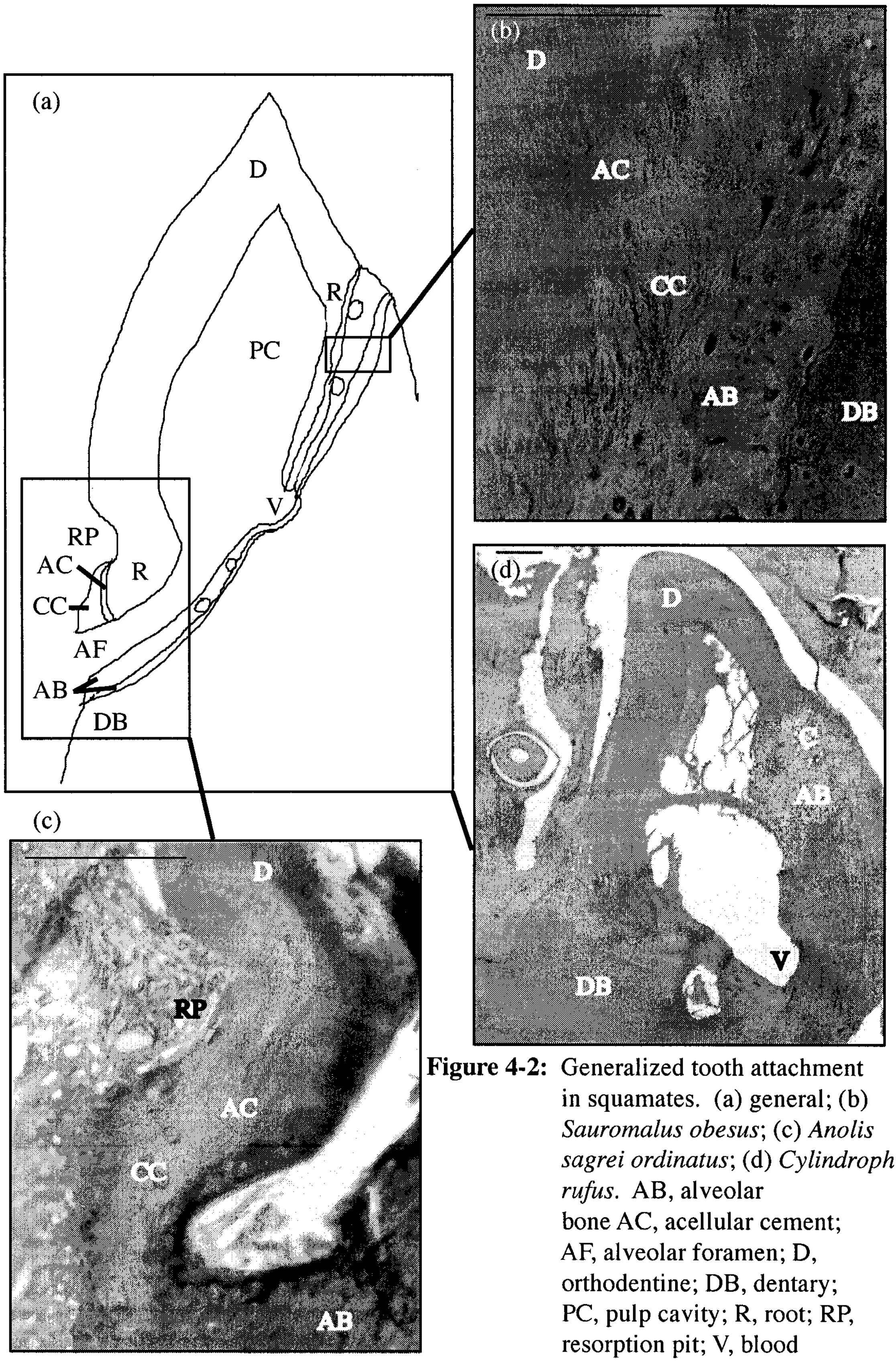

Figure 4-2: Generalized tooth attachment in squamates. (a) general; (b) *Sauromalus obesus*; (c) *Anolis sagrei ordinatus*; (d) *Cylindrophis rufus*. AB, alveolar bone AC, acellular cement; AF, alveolar foramen; D, orthodentine; DB, dentary; PC, pulp cavity; R, root; RP, resorption pit; V, blood vessel. All scale bars= 100 um.

slope of the dentary also controlled the amount of surface area for tooth attachment. Species with lesser-sloped dentaries had lesser amounts of tooth attachment tissues.

Dental vascularization was facilitated by a capillary bed underlying the tooth and vessels entering the tooth from the lingual side. There was one larger vessel underlying the pulp cavity and continuing along the entire length of the dentary of all species, including the comparative species. Most species had sections showing the presence of an alveolar foramen entering the pulp cavity from the lingual side of the tooth. Only agamids and chamaeleonids are thought not to have alveolar foramina (Zaher & Rieppel, 1999). I could neither confirm nor deny this observation as I usually only had a portion of a single tooth present in my sections.

General similarities- tooth replacement and development

Tooth replacement and development are not a primary objective of this study. Descriptions of dental development and replacement in squamates are presented here because they are lacking in published literature. This study provided a rare opportunity to compare dental development across Squamata.

The functional tooth was resorbed to a great extent prior to the loss of the tooth; Howship's lacunae, places where the large multinucleated absorbing cells (osteoclasts or odontoclasts) contacted the hard tissues, were observed in most sections. Several species showed evidence of the resorption of the entire tooth crown (Plate 4-12: e). Tooth resorption in squamates progressed from several fronts, the contact between the dental lamina (responsible for forming tooth germs) and the tooth, and the vascular network of the whole tooth attachment site. Odontoclasts and osteoclasts, the cells responsible for resorbing dentine and bone respectively, are differentiated in the blood (Ten Cate, 1998; Fuenzalida *et al.*, 1999). This explained why the vasculature of the tooth attachment site was associated with the tooth resorption fronts.

Resorption pits (entrances into the pulp cavity due to resorption) appeared to begin growing above the alveolar foramen (Fig. 4-2) (Cooper, 1966). Most species showed resorption into the pulp cavity. Some snakes, *Heterodon platyrhinos* (a colubrid) (Plate 4-18: a) and *Epicrates cenchria* (a boiid) (Fig. 4-3: d) showed conventional resorption pits with replacement teeth growing within the pits. This was an unexpected observation as it had been thought that anguinomorph squamates did not have resorption pits (Rieppel, 1978).

Many species across Squamata showed replacement teeth in many stages of development. The tooth germs were differentiated at the free end of the dental lamina (Plate 4-7: d). It was not unusual to see a few tooth germs forming at the same time in one section (Plate 4-11: a). Squamate tooth germs are similar structurally to those of other animals (Tomes, 1898; Howes, 1979; Osborn, 1984).

Structures responsible for the development of the tooth germ were observed facilitating the development of the tooth attachment, and the movement of the tooth into its functional position. The stellate reticulum of squamate tooth

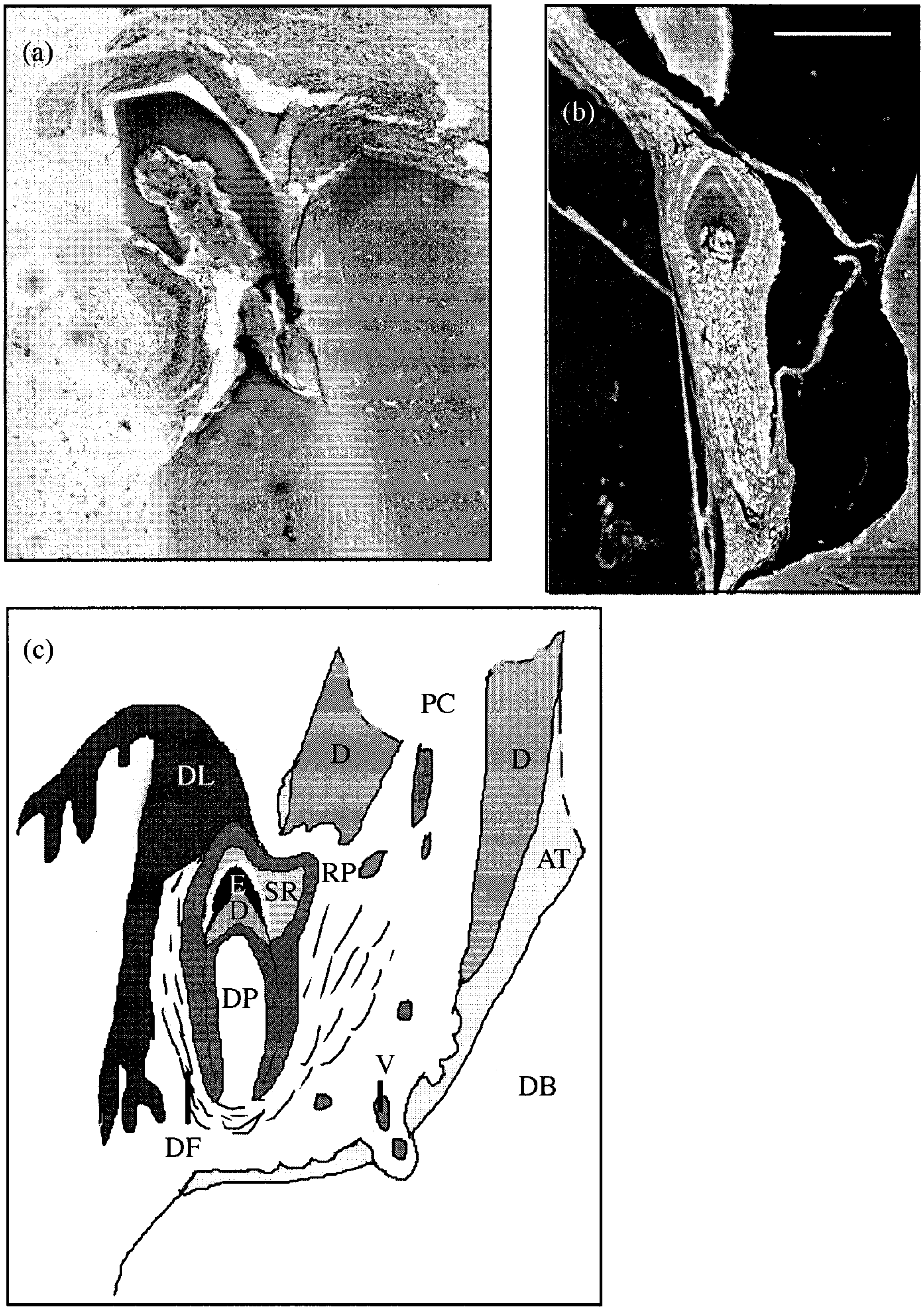

Figure 4-3: Generalized replacement tooth development. (a) Replacement tooth entering resorption pit; (b) Vertical section through a developing tooth germ entering the pulp cavity of the functional tooth; (c) Styalized diagram of tooth germ development. AT, attachment tissues; D, dentine; DB, dentary; DF, dental follicle; DP, dental papilla; E, enamel; PC, pulp cavity; RP, resorption pit; V, blood vessel.

germs appeared responsible for determining tooth crown shape and the "pulling" of tooth germs into the resorption pit (Fig. 4-3; Plate 4-8: a). When teeth were almost functional size, collagen fibres were observed filling the distance between the developing tooth and the tooth attachment site (Plate 4-4: e). The collagen fibre bundles anchored outside of the dentine were perpendicular to the tooth surface and the collagen fibre bundles being incorporated into the new alveolar bone were parallel to the surface of the tooth attachment site. A zone of mixed orientation collagen fibre bundles was in between the two developing biomineralized tissues. The fibres on the labial side of the tooth also draped over the labial edge of the dentary bone; this was also observed in *Caiman sclerops* (compare plates 4-4: e and 4-18: e). The collagen fibres were likely the matrix of the biomineralized attachment tissues. Cells differentiated by the dental follicle probably produced the fibres as they are only found outside of the tooth, the location of the dental follicle.

General similarities- tooth attachment

The squamate tooth attachment site was very vascular and a capillary bed could be seen infusing all layers of the tooth attachment tissues and the pulp cavity. The layers were considered as the attachment site because they constrain the size and nature of the new attachment. The tooth attachment site would grow thicker and larger as the individual grew unless the tooth attachment site was resorbed completely during every tooth replacement event. The tooth attachment site was a plane of weakness during sectioning and most species showed sections with a fracture between the oldest layer of alveolar bone and the bone of the dentary (Plate 4-10: e). Adjacent tooth attachment sites were bridged with remnants of former generations of attachment tissues. This structure had been referred to as the interdental plate and thought to be formed of bone of the tooth-bearing element (Lessmann, 1952; Zaher & Rieppel, 1999). I suggest the term interdental plate be modified to refer to the zone of tooth attachment tissues bridging adjacent tooth positions (the interdental region). An interdental plate would be absent if no attachment tissues were observed bridging the gap between adjacent tooth positions. I do not suggest abandoning the term, as in Caldwell *et al.* (2003), because characters of the interdental plate would be useful in discussions of tooth spacing and tooth replacement.

Details of the tooth attachment site were often difficult to observe because of the small size of the tooth attachment site. The amount of attachment tissues present varied with tooth size, (i.e., small teeth had less attachment tissues than large teeth). Most species had small amounts of tooth attachment tissues extending up the labial and lingual surfaces of the tooth root. The zone of tooth attachment tissues covering the lingual portion of the tooth had been called a theca (Lessmann, 1952; Zaher and Rieppel, 1999). I suggest abandoning the term theca (as the zone of attachment tissues covering the lingual wall of the tooth) as it is not a distinct anatomic entity and simply represents the lingual portion of the attachment site. Lessmann (1952) erected the name basal plate for the layers of dentary bone supporting the lingual base of the tooth root. I did not observe a basal plate. The buildup of unresorbed attachment tissues of the attachment site at the base of the tooth root (Plate 4-8, e, f, g) is likely what Lessmann (1952) called the basal plate. Therefore, I suggest abandoning the term basal plate.

Because the tooth attachment tissues were present in such a small amount, they were difficult to identify. Alveolar bone, cellular cement and acellular cement were the tooth attachment tissues present in the sections. Although most other studies have considered bone of attachment to be the sole tissue attaching teeth to the tooth bearing element in squamates (Tomes, 1898; Romer, 1956; Peyer, 1968), the tissues observed in this study were identified as better known tissues (cement, alveolar bone, periodontal ligament). The acellular cement, cement and alveolar bone present in squamates were similar in topologic position and histologic description to the known tissues. There was no significant dissimilarity between the known tooth attachment tissues and the squamate tooth attachment tissues indicating that the squamate tissues deserved special terminology. A periodontal ligament was not observed definitively in any squamate other than *Platecarpus* but most squamates showed the likely presence of a periodontal ligament biomineralized as extrinsic fibre cement (Ten Cate, 1998) (Fig. 4-2). All of the studied tooth attachments were immobile, with the exception perhaps of *D.* patagonica that may have had a hinged attachment (see Chapter 3). Soft tissue attachments were described in previous studies of pygopodid and dasypeltid squamates (Patchell & Shine, 1986a, b; Savitzky, 1981); I did not have access to specimens from these groups.

Alveolar bone

Alveolar bone was observed as the most basal tissues binding the tooth to the dentary in all squamates except the studied agamids that showed extensive remodeling of the original attachment tissues. Alveolar bone is a woven-fibred bone tissue produced by cells from the outer layer of the dental follicle during tooth development (Figs. 4-2, 4-3). It may be remodeled over time. Several generations of remnant alveolar bone were usually present making up the majority of the tooth attachment site. The retention of previous generations of alveolar bone is due likely to the growth of the individual. As the dentary grew, so did the size of the tooth attachment site. The process of tooth replacement continued but the sphere of influence of the tooth germ did not; therefore, less of the former attachment was resorbed. To ensure the vascularization of the tooth, the attachment site capillary bed migrated up to the surface of the alveolar bone leaving the former generations of alveolar bone beyond the influence of the resorbing cells formed in the vasculature.

Cement

Cement is a bone-like tissue formed by cells of the innermost layer of the dental follicle during tooth development. Cement functions primarily as an anchor for the periodontal ligament on the exterior surface of the dentinous tooth root. Unlike alveolar bone, cement is not known to remodel (Ten Cate, 1998).

A tissue made of parallel bundles of collagen fibres spanned the distance between alveolar bone and dentine in oblique sections of the attached tooth root (Fig. 4-2). The collagen fibre bundles were generally not as apparent in sections through the pulp cavity. The complete biomineralization of the mammalian or archosaurian periodontal ligament would look like the biomineralized collagen fibre bundles observed in squamates. This tissue is likely extrinsic fibred cement because the parallel nature of the fibre bundles is preserved.

Some specimens had an amorphous zone between the dentine and the collagen fibres reminiscent of acellular cement (Ten Cate, 1998) (Fig. 4-2). The location of the amorphous material on the surface of the dentine, next to other cement or alveolar bone, supported the identification of acellular cement.

Systematic review of tooth attachment histology in Squamata

The following is a systematic review of the observed squamate tooth attachments. Descriptions of the tooth attachment for each species follow comments on tooth attachment for the "family" group. Line drawings of the attachments are included to ease species comparisons. Some are reconstructions, but most are labeled tracings of the unlabeled images adjacent to them. All of the figures and plates in this chapter are contained on a CD (Appendix 4-2, in pocket at back of thesis). Due to limitations in print resolutions, it is beneficial to observe the plates on-screen.

Agamidae

The agamid tooth attachment sites were remodeled making it impossible to identify their original tooth attachment tissues and attachment site geometry. Agamid lizards do not replace their teeth, and over time the tooth is worn away and remodeled so that only a cutting edge on the tooth-bearing bone remains (Cooper & Poole, 1973). Throckmorton (1979) noted that teeth of the agamid *Uromastix aegyptius* developed a bony core. I did not observe a similar structure in the agamids I studied. A large vascular channel was observed near the base of the remodeling zone in the central zone of the dentary of all species. All of the studied agamid teeth were covered by what was likely several layers of acellular cement (Plate 4-1: c; 4-2:g; 4-3:c; Appendix 4-2). The hard, thin, layered tissue extended from the base of the remodeling zone on the lingual side of the tooth to below the remodeling zone on the labial side of the dentary. A few thin layers of a cellular bone-like tissue underlay the lingual and labial extents of the acellular, layered tissue. These cement tissues likely reduced and repaired the wear of the permanent dentition. Harrison (1901) made a similar discovery in *Sphenodon*, the sistertaxon to Squamata, but considered the layers covering the teeth to be a hard lamellar bone tissue. I identified these tissues as acellular and cellular cement because of their similarities to reparative cements in humans (see Ten Cate, 1998: Fig. 14-29, C).

Amphibolurus barbatus- Plate 4-1: a, b, c, d

The tooth sectioned in *Amphibolurus barbatus* had been worn down almost to the level of the dentary (Plate 4-1: a, b, d). The dentine still present was being remodeled and replaced by cellular bone in the form of Haversian systems and no pulp cavity was present (Plate 4-1: c). *A. barbatus* exhibited the largest zone of remodeling of all studied squamates.

Agama agama- Plate 4-1: e, f, g, h

The tooth appeared to attach to the apical region of the dentary (Plate 4-1: e, f); the extent of remodeling made it difficult to conclude the geometric relationship between the tooth attachment and the dentary. Although the sectioned tooth of *Agama agama* was not as worn as that of *A. barbatus*, the tooth showed evidence of basal remodeling with the replacement of dentine by Haversian bone (Plate 4-1: h). The pulp cavity opened basally into the vascular canal in some sections (not figured). An acellular cement layer covered the crown in *A. agama* (Plate 4-1: g).

Calotes versicolor- Plate 4-2: a, b, c

Like the other agamids, the tooth attachment site of *Calotes versicolor*, had undergone remodeling (Plate 4-2: a, b, c). Although comments on the robustness of the tooth attachment site in the different specimens must be made with caution because there was no way to standardize from what exact part of the dentary sections were made, the attachment site of *C. versicolor* was less robust than the other agamids. The dentary bone of *C. versicolor* was quite porous compared to the denser bone of the dentary of the other agamids. Pleurodont attachment site geometry was suggested by the great slope of the junction of the remodeled zone and the dentinous root. The remodeling zone was more vascular in *C. versicolor* than in the other agamids.

Chamaeleonidae- Plate4- 2: d, e, f

Chamaeleo johnstoni- Plate 4-2: d, e, f

Like the agamids, *Chamaeleo johnstoni* exhibited a basal region of remodeling (Plate 4-2: d, e, f). Because the remodeling was less extensive, cement and alveolar bone were identifiable as the attachment tissues of *C. johnstoni*. The alveolar bone was remodeled as was the dentary below. Due to the state of remodeling, I was unable to determine the extent of the original deposition of alveolar bone. Labial and lingual vessels facilitated the main vascularization of the pulp cavity.

Iguanidae- Plates 4-3 and 4-4

The studied iguanid tooth attachment sites had a pleurodont geometry. All of the observed teeth were undergoing resorption. Different stages of dental development were observed across the studied species. The polarity of the resorption fronts within the pulp cavity seemed associated with the location of vascular canals. The number and size of the vascular canals differed amongst the species but there were generally two larger canals, one lingual and one labial. A thin layer of alveolar bone was identified ultimately attaching the teeth to the dentary. Unlike some of the other squamates, the iguanids did not exhibit many layers of alveolar bone (the layers represent older generations of alveolar bone that were not resorbed completely during previous tooth replacement events).

Holbrookia maculata- Plate 4-3: a, b, c

The majority of the tooth crown of the figured specimen was lost during histologic processing. What remained was the basal part of the tooth root (Plate 4-3: a, b, c). Because the tooth was undergoing resorption, and most of the tooth crown was missing, I could not determine the apical extent of the attachment tissues. The curved tooth attachment site was lined with at least two generations of alveolar bone. A replacement tooth was forming on the lingual side of the tooth attachment zone (Plate 4-3: b [the colors of this image were inverted to enhance the image]). The resorption pit was formed at the contact of the developing tooth germ and the tooth attachment site (Plate 4-3: a, b, c).

Sauromalus obesus- Plate 4-3: d, e, f, g

Sauromalus obesus had a long tooth root covered in attachment tissues (Plate 4-3: e, f). The presence of acellular cement was indicated with the observation of an amorphous halo between dentine and alveolar bone (Plate 4-3: f). Several generations of remodeled alveolar bone were present overlying the more lamellar parallel-fibred bone of the dentary (Plate 4-3: f). An oblique section through the wall of the tooth root showed that a zone of parallel collagen fibre bundles extended between the dentine and the alveolar bone facilitated tooth attachment (Plate 4-3: g [this section is from another slide and the colour has been inverted to sharpen the image]). The tooth attachment site was very vascular with many openings into the pulp cavity (Plate 4-3: d).

Anolis sagrei ordinatus- Plate 4-4: a, b, c, d, e

Tooth attachment in *Anolis sagrei ordinates* (Plate 4-4: a, b, d) was very similar to that of *H. maculata*. The tooth was attached to the dentary bone by a thin layer of cellular cement to the alveolar bone overlying the dentary bone (Plate 4-4: d). *A. sagrei ordinatus* was one of two squamate species that showed a replacement tooth in the process of tooth attachment (Plate 4-4: c, e [colours were inverted]).

Dipsosaurus dorsalis- Plate 4-4: f, g, h, i

Tooth attachment in *Dipsosaurus dorsalis* (Plate 4-4: f, g, i) was similar to that of the other iguanids. Several remnants of previous generations of alveolar bone were preserved (Plate 4: i). A replacement tooth germ, early in its development, was observed entering the pulp cavity of a functional tooth (Plate 4-4: h). This was the best example of the early development of a tooth germ in a lizard.

Xantusiidae- Plate 4-5: a, b, c

Lepidophyma- Plate 4-5: a, b, c

The examined tooth was undergoing extensive resorption of the attachment site and the resorption pit opened into the pulp cavity although no tooth germ was preserved in the section (Plate 4-5: a, b). Resorption was not as extensive on the labial portion of the root and tooth attachment was observed to be similar to that of the iguanids and most other squamates. Several layers of remnants of the alveolar bone of previous tooth generations were visible and contrasted greatly with the parallel fibred lamellar bone of the dentary (Plate 4-5: c).

Gekkonidae- Plate 4-5: d, e, f; Plate 4-6: a, b, c

Both gekkonids examined were undergoing extensive resorption. The gekkonid tooth attachment sites examined were thin, showing few to no generations of remnants of prior generations of alveolar bone, even though the teeth were some of the largest examined in this study.

Phelsuma guentheri- Plate 4-5: d, e, f

Phelsuma guentheri had a very long tooth root (Plate 4-5: e); the zone of resorbing dentine demarcated the length of the root (Plate 4-5: f). The root length was long, relative to other squamates, in sections taken through all parts of the tooth. Nothing was interesting about the tooth attachment. A small tooth germ, in an early stage of development, was stimulating resorption at the base of the tooth attachment (Plate 4-5: d).

Gekko gekko- Plate 4-6: a, b, c

Tooth attachment in *Gekko gekko* was similar to that of most squamates. The figured tooth is in an advanced state of resorption with most of the crown and root surfaces being attacked by osteoclasts and odontoclasts (Plate 4-6: a). The tooth attachment site was very thin with only a thin region of alveolar bone present overlying the dentary bone (Plate 4-6: b [section is from a different slide but from a similar region as Plate 4-6: a]). It was unexpected to see this much resorption of a functional tooth associated with a replacement tooth in such early stages of development.

The developing tooth germ showed the formation of the two ridges characterizing the *G. gekko* tooth crown (not figured). A larger, more well developed, tooth germ was seen developing in an adjacent tooth attachment site (not figured). Besides the large tooth germ, at least one other replacement tooth was in the process of development in that section.

Lacertidae- Plate 4-6: d, e, f, g; Plate 4-7: a, b, c

The studied lacertids had shorter more robust teeth than most other squamates and were similar in stature to the studied cordylid, or teiid teeth. Similar to the gekkonids, the tooth attachment site showed no layers of remnant alveolar bone. The tooth attachment site was very vascular like most other non-serpentine squamates examined (Plate 4-6: g; Plate 4-7:a, c).

Lacerta vivipera- Plate 4-6: d, e, f, g

There was little unique about the tooth attachment site of *Lacerta vivipera.* The tooth attachment site was well vascularized (Plate 4-6: d, e, g) and quite thin (no remnants of alveolar bone were present [Plate 4-6: f). A replacement tooth was observed developing in an empty attachment site (Plate 4-6: g). Note how all of the vascular canals of the attachment site were enlarged and open. Some of these became closed over with attachment tissues (compare Plate 4-6: d, g).

Lacerta agilis- Plate 4-7: a, b, c

There was nothing unique about tooth attachment in *Lacerta agilis*. The figured tooth showed the early development of a large resorption pit (Plate 4-7: a, b). The junction between the dentine and alveolar bone did not exhibit the parallel collagen fibres noted in most other squamates (Plate 4-7: c), indicating this collagen fibre zone does not exist in this species or is very thin.

Teiidae- Plate 4-7: d, e, f, g, h; Plate 4-8: a, b, c, d

The teiids examined were from one genus, *Cnemidophorus*. The examined teeth were robust like those of the studied lacertids and cordylids. The tooth attachment tissues covering the root were noticeably thicker than in other squamates (Plate 4-7: g). Lessmann (1952) noted that teiids had thicker layers of tooth attachment tissues than most squamates. The spaces between adjacent teeth were filled with remnants of former generations of tooth attachment tissues (Plate 4-7: h). The studied gekkonids show replacement tooth germs in a similar stage of development being dragged into the pulp cavity by the stellate reticulum (Plate 4-8: d).

Cnemidophorus tigris- Plate 4-7: d, e, f, g, h

The tooth attachment tissues of *Cnemidophorus tigris* were deposited quite high on the lingual portion of the tooth root (Plate 4-7: d, e, g [this section is from another slide distal to (d) but is from a similar position as indicated in (d)]). The structure of the tooth attachment was similar to the other squamates in that a zone of parallel collagen fibre bundles extended perpendicular from the tooth root to meet and blend with the woven fibred collagen matrix of the alveolar bone (Plate 4-7: g). Alveolar bone formed the interdental plates between teeth (Plate 4-7: h). A developing tooth germ was observed just beginning to enter the pulp cavity (Plate 4-7: f)

Cnemidophorus exsanaguis- Plate 4-8: a, b, c, d

Tooth attachment and development in *Cnemidophorus exsanguis* was identical to that of *Cnemidophorus tigris*. Teeth were attached to the dentary by thin layers of cement and alveolar bone (Plate 4-8: c). A functional tooth was observed undergoing the early stages of tooth replacement (Plate 4-8: a, b, d). Note the stellate reticulum enters the pulp cavity of the functional tooth prior to the rest of the tooth germ in both of the examined teiids (Plate 4-8: a, d; Plate 4-7: d, f).

Scincidae- Plate 4-8: e, f, g, h; Plate 4-9: a, b, c

The examined skink dentitions had tooth attachments similar to other squamates. The teeth were attached by cement and alveolar bone. The only difference was the apparent condensation of the vascularity in the central region and labial region of the attachment site (Plate 4-8: e; Plate 4-9: a, c). Both species showed a larger than average deposit of remnant attachment tissues on the lingual portion of the attachment site (Plate 4-8: e, f, g).

Scincus scincus- Plate 4-8: e, f, g, h

Tooth attachment in *Scincus scincus* was similar to that of most other squamates. The only difference was the high number of layers of unremodeled remnants of attachment tissues making up the attachment site (Plate 4-8: e, f, g); this was also seen in other higher squamates (Plate 4-11: b; 4-15: c, e,). Attachment tissues deposited during prior tooth attachment events was usually remodeled within or between the layers if it was not resorbed completely during subsequent replacement events (compare Plate 4-3: f and Plate 4-8: g). Only the central and more labial region of the tooth attachment site exhibited the resorption and remodeling of previous generations of attachment tissues (Plate 4-8: h). The retention of several layers of unremodeled attachment tissues was likely due to the lack of vascularity in the lingual region of the tooth attachment site.

Eumeces fasciatus- Plate 4-9: a, b, c

The dentary of *Eumeces fasciatus* sectioned poorly. Sections obtained showed active resorption of two functional teeth, one in a late stage of resorption (Plate 4-9: b), and one just beginning to be resorbed (Plate 4-9: a [inverted colours], c). Like *Scincus scincus*, the lingual portion of the tooth attachment was very robust and tooth attachment tissues thick. A replacement tooth was forming and encouraging the growth of a resorption pit near the junction of the tooth attachment tissues and the dentine of the tooth root (Plate 4-9: a).

Cordylidae- Plate 4-9: d, e, f, g; Plate 4-10: a, b, c, d, e

The cordylids examined had teeth with thickened dentine walls covered with attachment tissues further to the crown apex than most of the examined squamates. Both species examined showed parallel collagen fibre bundles extended between the dentine and alveolar bone thereby indicating the presence of a periodontal ligament biomineralized as cement (not figured). Tooth replacement in these species was similar to that of the other squamates. A single vessel dominated tooth vascularity.

Cordylus cordylus cordylus- Plate 4-9: d, e, f, g

The robust tooth root of *Cordylus cordylus cordylus* was attached by cellular cement to the alveolar bone lining the tooth attachment site (Plate 4-9: f, g). The apical extent to which the attachment tissues covered the dentine root in this species was similar to that seen in *Platecarpus* (Plate 4-13: a). The layers of previous generations of unresorbed attachment tissues were not remodeled heavily and also lined the attachment site (Plate 4-9: f). The vasculature was centrally located with most of the tooth attachment site not showing evidence of many vascular canals (Plate 4-9: d, e).

Cordylus warreni depressus- Plate 4-10: a, b, c, d, e

The tooth attachment of *Cordylus warreni depressus* was similar to most other squamates but the attachment tissues extended higher-up on the crown than most studied species (Plate 4-10: a, b). The attachment site was well vascularized (Plate 4-10: a, b) and contrasted starkly with the poorly vascularized attachment site of *Cordylus cordylus cordylus* (Plate 4-9: a, b). The tooth attachment site had not been remodeled and a portion of the dentine of a former tooth was observed sandwiched between layers of attachment tissue remnants (Plate 4-10: d, e).

Tooth resorption had extended so far as to extend anterolabially from the resorption pit to attack the labial portion of the root of one tooth. Another tooth showed the retention of a small portion of the resorbing crown (present as resorbing dentine), under which a replacement tooth was developing (Plate 10, c).

Anguidae- Plate 4-10: f, g, h; Plate 4-11: a, b, c, d, e

There was nothing unique about the tooth attachments of the anguids. Both species showed a more robust region of attachment on the lingual side of the tooth similar to the cordylids.

Celestes warreni- Plate 4-10: f, g, h

The tooth attachment site was similar to that of most squamates. The lingual portion of the tooth attachment site was broader than in most other squamates (Plate 4-10: f, g). Note how the tooth attachment was broken at the junction of the alveolar bone and the dentary bone (Plate 4-10: h). This was a common fracturing point for most dentitions. Most of the squamate teeth examined were undergoing resorption to some extent. *C. warreni* shows features typical of the initial stages of the development of the resorption pit (Plate 4-10: f, g, h); the dentine exhibits a scalloped lingual margin (Howship's lacunae present- indicates presence of odontoclasts) and the adjacent dentine appears lamellated due to the alteration of the tissues by the action of the odontoclasts (Plate 4-10: h).

Gerrhonotus principus- Plate 4-11: a, b, c, d, e

The tooth attachment tissues of *G. principus* extended further up the tooth crown on the labial side of the tooth compared to most other squamates (Plate 4-11: c, d, e). Although the attachment site was well vascularized, there was a large parapet of unremodeled alveolar bone on the lingual side of the attachment site (Plate 4-11: a, b). This was similar to the condition observed in *Scincus* scincus (Plate 4-8: e, f, g).

There was a portion of an almost completely resorbed tooth crown found on the labial side of a resorbing functional tooth (Plate 4-11: d, e). This may have been a pathology because although it was not unusual to see crown tops resorbing just above the attachment site or within the vacuity created by the almost complete resorption of the tooth (e.g., Plate 4-11: g), no other species showed displacement of a resorbing crown in the labial direction. It is also possible the tooth had been displaced during histologic processing; note that that the epithelium covering the labial portion of the tooth is discontinuous (Plate 4-11: d, e)

Xenosauridae- Plate 4- 11: f, g

Shinasaurus crocodylurus- Plate 4-11: f, g

Only one histologic section of *Shinasaurus crocodylurus* was produced due to the hardness of the specimen. A curved attachment site was observed and most of the tooth attachment tissues were resorbed away (Plate 4-11: f). A replacement tooth was developing in close proximity to the almost completely resorbed crown of the former functional tooth (Plate 4-11: f). Soft tissues of the tooth germ were guiding the tooth further into the resorption pit (Plate 4-11: f, g).

Varanidae- Plate 4-12

Varanus- Plate 4-12: a, b, c; Varanus niloticus Plate 4-12: d, e

A very thin layer of alveolar bone attached the plicidentinous tooth root to the dentary (Plate 4-12: c, e). Cement was likely present as a thin layer of cellular cement on the outer surfaces of the dentine convolutions. A pulp cavity was still present as plicidentine is simply orthodentine deposited in a convoluted pattern as the base of the tooth root (Plate 4-12: a, b). It was interesting to observe that the dentine grooves ended basally in the vasculature (Plate 4-12: a, b, c, d, e). A few very thin layers of former generations of attachment tissues were preserved in the attachment site. Although this tooth attachment was very different than that of the other studied squamates, the tooth attachment site was very vascular and there was one larger central vascular channel.

Tooth replacement occurred differently in the varanids than most of the other squamates. A resorption pit formed prior to the replacement of the tooth (Plate 4-12: a), but the majority of the crown was lost prior to the movement of the developing tooth crown into the attachment zone (Plate 4-12: d). This was the first recognition of a resorption pit, defined as an entrance into the pulp cavity due to resorption, in varanids. It had been thought that the entire tooth root was resorbed simultaneously and the tooth shed prior to the movement of the replacement into its future position (Rieppel, 1978). Considering the high slope of the tooth attachment site and the height of the tooth crown in varanids (taller than most squamates, relatively speaking, varanid teeth are very large for their attachment site size), it was likely that the replacement tooth grew along side the functional tooth for a longer length of time than the other species to give the functional tooth a longer life and the opportunity for the replacement tooth to reach almost completion prior to being in a functional position. Were the replacement tooth to grow inside the pulp cavity, the functional tooth would probably have to be shed earlier because the pulp cavity is greatly reduced in size due to the presence plicidentine.

Mosasauridae- Plate 4-13: a, b, c, d

Platecarpus- Plate 4-13: a, b, c, d

This was the largest species examined in this study. *Platecarpus* was a large marine lizard that lived during the Cretaceous. The tooth attachment tissues in *Platecarpus* were similar to those seen in the other squamates, there was just larger amounts to observe. The dentary of *Platecarpus* was deeply grooved, unlike any other studied squamate. The tooth attachment tissues extend up the conical dentine root above the level of the dentary (Plate 4-13: a, b). The dentinous root is attached to the dentary by acellular cement (Plate 4-13: c), osteocement (an osteonic cellular cement), periodontal ligament (presence inferred from layers of Sharpey's fibres between and incorporated into both alveolar bone and cellular cement [Plate 4-13: d note the cellular cement in this image had been disturbed by calcite]) and alveolar bone respectively (Caldwell *et al.*, 2003). The alveolar bone completely surrounded the tooth and filled the space between adjacent teeth so that the teeth were set in bony sockets. The osteocement was most abundant and had been called the bony base, a bony root or pedestal in the past (Plate 4-13: a, b). This large amount of osteocement exaggerated the tooth attachment of *Platecarpus*. Its development was likely a response to the deepening of the groove in the dentary as the other tooth attachment tissues were deposited in thin layers, in similar proportions, to most other squamates.

Tooth replacement in *Platecarpus* was similar to that of the other squamates. A resorption pit began near the junction of the attachment tissues and the dentine and progressed as the developing tooth germ entered the pulp cavity (Caldwell *et al.*, 2003). Once the majority of the attachment site was resorbed, new attachment tissues were deposited. Just like in the other squamates, layers of former attachment tissues were preserved underneath the current attachment tissues.

Dinilysia patagonica- Plate 4-13: e, f, g, h

Dinilysia patagonica was a late Cretaceous terrestrial snake with an unknown phylogenetic affinity; it was likely a basal or derived snake (Caldwell & Albino, 2002). A portion of a left maxilla was sectioned for histologic analysis. This was not a section of the dentary, and therefore, it would be inappropriate to substitute the tooth attachment of the maxilla. This was an important species to include because it does show the presence of alveolar bone as the tissue forming the interdental plates (Plate 4-13: e, f, g, h) and may be the first fossil squamate to exhibit a hinged tooth attachment morphology. The alveolar bone, being a heavily woven-fibred bone tissue looked significantly different than the better-organized lamellar and cancellous bone of the maxilla (Plate 4-13: e, f, g, h). The interdental plate histology and tooth attachment type in *Dinilysia* was described in detail in Chapter 3.

Anilioidea- Plate 4-14: a, b, c, d

Cylindrophis rufus- Plate 4-14: a, b, c, d

The tooth attachment site in *Cylindrophis rufus* was more socket-like than that of the aforementioned squamates, with the exception of *Dinilysia* and *Platecarpus*. Thick deposits of former generations of unremodeled attachment tissues were observed making up the current attachment site and spanning the distance between teeth (Plate 4-14: c, d [image from another section through the interdental plate but in a similar location to that outlined in Plate 4-14: a]). The presence of thick layers of parallel Sharpey's fibres (biomineralized collagen fibres) indicated that cement was one the tooth attachment tissues (Plate 4-14: d); Sharpey's fibres in alveolar bone tend to be distorted due to the woven fibred nature of the alveolar bone (alveolar bone with a bundle bone fabric is the exception [Ten Cate, 1998]). Two large blood vessels were observed in the central and basal region of the relatively deep attachment site (Plate 4-14: a, b).

Boiidae- Plate 4-14: e, f, g; Plate 4-15: a, b, c

The tooth attachment site was curved and the tooth attachment tissues extended part way up the sides of the tooth. The layers of former generation of attachment tissues were thicker than that of most studied squamates. These thickened tissue layers were common in the studied snakes. Another commonality of most snakes was the presence of one large vascular canal running through the basal central region of the attachment site along the length of the dentary. Resorption fronts arose from this singular vascular canal and the contact between the replacement tooth germ and the junction of the attachment site and the dentine. Sections showed a replacement tooth entering a conventional resorption pit (Fig. 4-3: a). The observation of a resorption pit in a snake was unexpected because snakes were thought to shed their teeth without the formation of a resorption pit (Rieppel, 1978).

Epicrates cenchria- Plate 4-14: e, f, g

There was nothing unique about tooth attachment in *Epicrates cenchria.* The teeth were shorter than most squamates and were attached to a gently curving lingual slope of the dentary. Like the other nonvaranid-varanoids, the tooth was attached to the walls of a distinct socket of alveolar bone (Plate 4-14: g [image through an interdental plate]) and the vasculature was largely confined to a larger central vessel (Plate 4-14: e, f). Note that several generations of new replacement teeth were observed forming in some sections (Plate 4-14: g). These teeth would not replace the current tooth position as most snake teeth are greatly recurved and grow from crown tip to root in a posterolingual position relative to the tooth attachment site. I also observed a tooth forming within a large resorption pit (Fig. 4-3: a).

Lichanura trivigata roseofuca- Plate 4-15: a, b, c

There was nothing unique about tooth attachment in *Lichanura trivigata roseofuca* (not figured- very similar to *E. cenchria*). Tooth attachment tissues were observed forming on the outside of the root and on top of layers of former tooth attachment site (Plate 4-15: a, b, c). Note that remnants of several generations of previous attachment tissues are preserved on the lingual part of the attachment site (Plate 4-15: b). Vasculature is primarily constricted to a single vessel at the centre of the attachment site (Plate 4-15: a).

Tropidophiidae- Plate 4-15: d, e, f, g

Ungaliophis continentalis- Plate 4-15: d, e, f, g

Tooth attachment in *Ungaliophis continentalis* was quite similar to that of other snakes (Plate 4-15: f). The tooth attachment site was based on one large vascular canal (Plate 4-15: d, e, g), like most other snakes. This specimen showed that the vascular canals are Haversian systems and that they remodel over time (Plate 4-15: g). The interdental plate was a relatively thick deposit of alveolar bone (Plate 4-15: g) and was similar to the interdental plates of most snakes, except fewer generations of attachment tissues were present. This could be due to the age of the individual (young individuals have not undergone as many replacement cycles as older animals). It could also be due to the location of the section, the central region of the interdental plate seemed to be more remodeled as it represented the oldest layers of tooth attachment tissues that were likely beyond the influence of the resorptive processes.

Acrochordidae- Plate 4-16: a, b, c, d, e

Acrochordus javanicus- Plate 4-16: a, b, c, d, e

Tooth attachment in *Acrochordus javanicus* was similar to that of most other squamates (Plate 4-16: a). Tooth attachment was facilitated by cement and alveolar bone (Plate 4-16: d). Active resorption made it difficult to identify the tissues on the lingual wall of the root (Plate 4-16: c). The tooth attachment site was gently curved as in most snakes (Plate 4-16: a, b). The alveolar foramen appeared to act as the resorption pit (Plate 4-16: e).

Elapidae- Plate 4-16: f, g, h, i

Kolphophis- Plate 4-16: f, g, h, i

Tooth attachment, geometry and tissues, in *Kolphophis* were similar to that of the other snakes (Plate 4-16: f, g, h). The figured tooth was undergoing very mild external lingual, external labial and internal resorption (Plate 4-16: f). Several replacement tooth germs, portions of three, were observed lingual to the functioning tooth (Plate 4-16: f). The interdental plate histology was similar to that of other snakes (Plate 4-16: i [image from another section in a similar location indicated on Plate 4-16 f]). As in the other snakes, tooth vascularity was confined to a central vessel (Plate 4-16: f, h, i).

Colubrinae- Plate 4-17

The examined colubrines had similar tooth attachments. The only thing that differed was the shape of the tooth attachment site on the dentary. Both species had only one main vascular canal.

Pituophis melanoleucas- Plate 4-17: a, b, c, d

The tooth of *Pituophis melanoleucas* was attached to a relatively flat dentary surface compared to most other snakes (Plate 4-17: a, b, c). The tooth attachment tissues were similar to those of other squamates (Plate 4-17: d). Teeth were observed in various states of resorption. Developing tooth germs were observed in practically all sections (Plate 4-17: a, c). A developing tooth germ was observed above an empty tooth position (Plate 4-17: c) with the former attachment site having been almost completely resorbed.

Coluber constrictor priapus- Plate 4-17: e, f, g, h, i

Tooth attachment in *Coluber constrictor priapus* was similar to that of the other examined snakes (Plate 4-17: e, f, g). Several generations of alveolar bone were not lining the entire current tooth attachment site, but instead, were stepped up to the labial wall of the dentary (Plate 4-17: e, f). This likely was an artifact of the changing width of the tooth attachment site as the animal grew. This species showed the development of the snake tooth crown the best (Plate 4-17: h, i).

Xenodontinae- Plate 4-18: a, b, c, d

Heterodon platyrhinos- Plate 4-18: a, b, c, d

Tooth attachment tissues in *Heterodon platyrhinos* werer similar to those of the other snakes (Plate 4-18: d [colours inverted]). *H. platyrhinos* showed a tooth entering the pulp cavity through a resorption pit (Plate 4-18: c). There was a tall pinnacle of dentine and attachment tissues that had yet to be resorbed preserved underneath the developing tooth germ. This was unexpected to see because traditionally snakes were thought to shed their teeth prior to the replacement tooth germ assuming the position of the functional tooth (Rieppel, 1978). A tooth entering the pulp cavity through a resorption pit was also observed in another snake, *E. cenchria* (Fig. 4-3: a)

Comparative specimens

Lepisosteus osseus- Plate4- 18: e, f, g, h

Lepisosteus osseus (a gar) is a derived actinopterygian fish. Despite its very distant relationship with varanids, they shared similarities in their tooth attachments (Plate 4-12; Plate 4-18: e-h). *L. osseus* and the varanids studied had tooth roots made of plicidentine anchored to the dentary by a thin layer of bone, likely alveolar bone (Plate 4-18: h). Cement may be present as a thin layer of acellular cement on the outer surfaces of the dentine convolutions. Just like the studied varanids and most other squamates, a single large vascular channel, associated with a system of smaller vascular channels, bottomed the tooth attachment site (Plate 4-18: e, f).

Esox lucius- Plate4- 19: a, b, c, d

Esox lucius is another actinopterygian, less further up, in the phylogeny of actinopterygians than *Lepisosteus osseus.* Although the tooth attachments of *L. osseus*, *E. lucius* and varanids shared similarities in that the tooth root dentine was convoluted in all three species, *E. lucius* was different in that the whole pulp cavity had been infilled with trabecular dentine (Plate 4-19: a, b, c). Trabecular dentine is a dentine that forms around blood vessels that are present in the dental papilla during dental development (Osborn, 1981). Trabecular dentine can be osteonic and indeed this specimen showed evidence of the trabecular dentine being influenced by osteoblastic activity (not figured). The tooth attachment site was well vascularized and one canal dominated the base of the tooth attachment site (Plate 4-19: a, b, c). Collagen fibres joined adjacent dentine trabeculae (Plate 4-19: d).

Caiman sclerops- Plate 4-19- e, f, g, h

Caiman sclerops represented a diapsid with a thecodont tooth attachment. The teeth are set in sockets made of alveolar bone within a dental groove (e, f). Cement and a periodontal ligament to the alveolar bone attach the teeth (Plate 4-19: e, f, g, h). The periodontal ligament was the tooth attachment tissue present in the greatest amount. The cement extended quite high up the tooth crown; *C. sclerops* had a very long tooth root. A very thin layer of alveolar bone lined the socket in the very slight dentary (Plate 4-19: h). There was no evidence of former layers of attachment tissues. Resorption pits began forming relatively lower than in the squamates studied; resorption pits formed about half way down the root (Plate 4-19: g).

***Delphinapterus leucas*- Plate 4-20: a, b, c, d**

Delphinapterus leucas (beluga whale) represented thecodonty in mammals. The tooth root of *D. leucas* was added to periodically throughout the life of the tooth (Brodie, Gerarci & St. Aubin, 1990). The cement was very cellular, more so than that seen in *Caiman sclerops* and the examined squamates (Plate 4-20: d). The periodontal ligament extended from the cement to the alveolar bone (Plate 4-20: a, b). The alveolar bone blended with the bone of the dentary making it very difficult to distinguish the two tissues; the inability to distinguish between alveolar bone and dentary bone in mammals is a common problem and is an artifact of developmental processes (Osborn, 1981). Both the alveolar bone and dentary had been remodeled. The dentine exhibited remodeling in the form of osteodentine (Plate 4-20: c). Like the other dentitions studied, a large vessel was found at the base of the tooth attachment site (Plate 4-20: e [image from another section in a similar positon to that indicated in Plate 4-20: a).

DISCUSSION

Phylogenetic significance of tooth attachment histology in squamates

Owen (1840-1845) used acrodonty and pleurodonty as types of vertebrate tooth attachment in his studies on comparative dental anatomy. Tooth attachment was first used by Cope in 1864 to classify Squamata into two groups, Acrodonta (agamids, chamaeleonids and relatives) and Pleurodonta (all other squamates). Acrodonta is still used as a clade name (Scanlon & Lee, 2002) but Pleurodonta has fallen out of use as it was recognized that Acrodonta nested within Pleurodonta.

The terms acrodonty, pleurodonty, thecodonty, subthecodonty and their variations have subsequently been used as character states for tooth attachment characters in cladistic analyses of squamates (Estes *et al.*, 1988; Caldwell, 1999; Lee & Caldwell, 2000; Rieppel *et al.*, 2002). Lee and Caldwell (2000) and Estes, de Queiroz and Gauthier (1988) discussed problems in the definition of these terms and problems in assigning the terms to certain dentitions. Problems with the instability of dental attachment terminology and its usage were reviewed in Chapter 2 and will only be discussed here in the context of squamates.

Are characters related to tooth attachment phylogenetically significant in Squamata?

Regardless of what method is chosen to analyze the character data to create a phylogeny, i.e., parsimony, maximum likelihood, phenetics, *etc.*, characters and character states must be constructed with some criteria in mind. Good morphologic character states should be expressible in all taxa (inheritable), variable, and represent potentially homologous states of the character. Characters for phylogenetic analyses must not only describe morphology, they must represent an evolving morphology. Although characters are constructed prior to the phylogenetic analysis, poor characters are usually only noted after the analysis and materialize as multiple homoplasies (non-ancestral character distributions). Also, character states must be assigned after examining the appropriate data set (e.g., character states relating to tissues should be assigned by examining histology, not gross morphology). Authors of squamate phylogenetic analyses that used tooth attachment site geometry and histology to define their character states did not examine histology when assigning character states to taxa (Lee & Caldwell, 2000; Rieppel et al., 2002). My histologic data will be used to test the phylogenetic characters related to tooth attachment in Rieppel, Kluge and Zaher (2002), and Lee and Caldwell (2000).

Rieppel et al. (2002)

Rieppel *et al.* (2002) reexamined the relationships of Wonambi (an extinct snake) within Varanoidea. Two characters used in their cladistic analysis are related to tooth attachment.

> *Character 1. Tooth implantation pleurodont (0) (non-snake squamates and scolecophidian snakes), or (1) alethinophidian (as defined by Zaher and Rieppel, (1999) (all other snakes). Mosasauroids are coded pleurodont rather than thecodont (Zaher & Rieppel, 1999).* (Rieppel *et al.*, 2002: 827, 828)

Pleurodonty was defined as tooth attachment where the tooth was ankylosed to the sloping wall of the lingual pleura of the tooth-bearing element; the plane of the pleura was variable (Zaher & Rieppel, 1999). Labial pleurodonty (Lessmann, 1952) was said to better describe the pleurodonty observed in most non-varanoid squamates. Labial pleurodonty was identified when a basal plate (made of bone of the jaw) was observed supporting the basal lingual region of the tooth. An interdental ridge of bone of the jaw may separate teeth attached in the labial pleurodont fashion. If the interdental ridge fused with the basal plate, teeth would have seemed to be set in sockets, but these were not true sockets. Full pleurodonty, seen in most non-mosasauroid varanoids, was when the tooth attachment lacked a basal plate, and poorly-to-no-developed interdental ridges. Subpleurodonty was identified when a theca (made of bone of attachment) was observed covering the lingual side of the tooth base; usually the basal plate was lacking.

Alethinophidian tooth attachment was indirectly defined later in the document (Zaher & Rieppel, 1999). On page 13 they indicate that alethinophidian teeth were attached to non-thecodont sockets formed of the extensions of the interdental ridges, made of the bone of the tooth-bearing element, to surround most of the basal lingual region of the tooth.

Mosasaur teeth were thought to have an autapomorphic tooth attachment in that the tooth had an extended bony base made of bone of attachment ankylosed to the pleura of the jaw. A basal plate was thought to be absent and the dentary showed that the lingual pleura, along with the labial pleura, formed a dental groove in the tooth-bearing element. The lingual pleura did not support the lingual base of the tooth. Zaher and Rieppel (1999) classed mosasaurs as exhibiting a modified pleurodont condition. They said that authors that considered mosasaurs as exhibiting thecodonty or ankylosed thecodonty had incorrectly associated the dental groove and the enlarged replacement pits with thecodont sockets.

Caldwell *et al.* (2003) showed that tooth attachment in mosasaurs approached the thecodont condition, not the pleurodont condition (Zaher & Rieppel, 1999) as cement and evidence of a periodontal ligament (calcified

Sharpey's fibres) were observed attaching the teeth to sockets made of alveolar bone in a dental groove in the jawbone. All thecodont animals had teeth attached in this fashion (Osborn, 1984).

Based on my histologic analysis, Rieppel *et al.* (2002) used character states not applicable to tooth attachment in squamates. Bone of attachment, basal plates, theca and intedental ridges made of tooth-bearing element bone were not observed in any studied squamate thereby invalidating their pleurodonty and alethinophidian character states.

Character 2. Plicidentine absent (0), or present (1) (present only in Lanthanotus and Varanus). (Rieppel *et al.*, 2002: 827, 828).

The presence of plicidentine can only be confirmed by looking at the internal surface of the tooth root. Although the presence of plicidentine in *Varanus* has been confirmed in this study and other histologic studies, we do not know if the other squamates showed plicidentine because they have not been examined. It is possible that only the enamel may be wrinkled in species having grooves at the base of the tooth crown or that the tooth root morphology is hidden in the case of specimens with tooth attachment covering a large amount of the tooth root dentine. The coding of this character, not the character itself, in Rieppel, Kluge and Zaher (2002) is invalidated because the original coding was based on gross morphology, an inappropriate data set. The phylogenetic significance of the presence of plicidentine was discussed by Scanlon and Lee (2002)

Lee and Caldwell (2000)

Lee and Caldwell (2000) assessed the interrelationships of mosasaurs, snakes and dolichosaurs and other squamates. It is the most recent published phylogenetic analysis based on morphology, and including extinct taxa. Four characters included in their cladistic analyses can be evaluated based on the histologic survey in this study.

> *Character 161. Marginal teeth. Pleurodont, teeth set in a continuous groove (0) (non-pythonomorph, non-acrodont squamates); acrodont, teeth ankylosed to jaw margin (1) (Acrodonta); thecodont, teeth ankylosed in discrete alveoli and separated by well-developed interdental plates (2) (Pythonomorpha [non-helodermatid, non-varanid, non-lanthanotid varanoids]). Unordered. The teeth are thecodont in dolichosaurids (pers. obs); there is a deep groove and complete but thin interdental plates separating adjacent teeth. A similar situation also appears to be the case in the aigialosaur Opetiosaurus (pers. obs.). It has long been recognized that among squamates, only mosasauroids and snakes have teeth set in discrete alveoli, a condition often described as "thecodonty," "modified thecodonty," "subthecodonty," or "ankylosed thecodonty" (e.g., Edmund,*

> *1969; Bell, 1997; Lee, 1997). Recently, however, Zaher and Rieppel (1999) have argued that this is not the case. They redefine thecodonty very narrowly to refer only to taxa where the teeth are attached to the jaw by ligaments (rather than by bone of attachment) and continually replaced: presence of discrete alveoli is not sufficient (thus, even mammals are not thecodont under their definition). They then state that mosasauroids and snakes do not share their character state "thecodonty." However, the presence of discrete alveoli remains a synapomorphy of mosasauroids and snakes, whether one chooses to label it thecodonty or not. Among squamates, only mosasauroids and snakes have extensive interdental plates dividing the alveolar groove into discrete sockets; arguments that such complete plates and discrete sockets are lacking in scolecophidians, but present in some lizards such as Tiliqua are addressed elsewhere (Scanlon and Lee, in press). (Lee & Caldwell, 2000: 932).*

Character 161 is flawed in that Lee and Caldwell's (2000) criteria for differentiating the characters states were inconsistent. The definition of pleurodonty was very basic and did not mention the tissue responsible for tooth attachment whereas the definitions of acrodonty and thecodonty alluded to the tooth attachment tissue present in the usage of the term ankylosis (implying a bony attachment); they did not identify the ankylosing tissue. Although they mention the presence of interdental plates, they do not indicate what tissue makes up the interdental plates.

My observation that all squamate teeth were attached to a dental groove invalidated the shape of the attachment site as the defining characteristic of Lee and Caldwell's (2000) pleurodonty. All studied squamates, with the exception of the chamaeleonids (shape of the dentary near the attachment site was remodeled), had teeth set within a groove in the dentary. This was noted by Augé as well (1997). The groove varied in shape from being a steep slope as in varanids, to being a gentle groove as in most squamates, to being a subequal deep groove as in mosasaurs. The shape of this groove would also differ along the length of the dentary. This is probably why pleurodonty and acrodonty have been diagnosed on a single tooth-bearing element in agamids (Cooper and Poole, 1966).

Because the studied "acrodont" species either had teeth attached to the lingual pleura of the tooth bearing element (*Calotes versicolor*) or had remodeled attachment sites making it difficult to interpret the tooth attachment, Lee and Caldwell's (2000) assignment of acrodonty to agamids is erroneous or not applicable. Acrodonty as a discrete attachment type is likely nonexistent and instead represents the narrowing of the tooth attachment site or the shortening of the labial wall of the tooth-bearing bone, it only appears that teeth are perched on the apex of bone.

Lee and Caldwell's (2000) definition of thecodonty is also invalidated by dental histology. Interdental plates representing portions of the tooth-bearing element separating teeth and surrounding them partially, although not defined by Lee and Caldwell (2000), were not observed in any pythonomorph. Only alveolar bone is observed filling the distance between the teeth.

> *Character 163. Bases of marginal teeth. Smooth, dentine not infolded (0) (most non-varanoid squamates and dolichosaurs); dentine infolded ("plicidentine"), resulting in longitudinal grooves (1) (non-dolichosaur varanoids). While most snakes lack plicidentine, it is present in some basal forms such as madtsoiids (Scanlon and Lee, in press). Zaher and Rieppel (1999: 6 state that "mosasaurs lack plicidentine." However, the bases of the tooth crowns in mosasauroids typically have either true infoldings of the enamel (e.g., see photographs in Lingham-Soliar, 1994) or at least distinct ridges on the external surface (e.g., Russell, 1967).* (Lee & Caldwell, 2000: 932).

The presence of plicidentine in *Varanus* is confirmed by my histologic study. Scanlon and Lee (2002) presented a convincing argument that basal snakes exhibited plicidentine as well. It was interesting to note that *Dinilysia patagonica*, a snake with uncertain phylogenetic affinities, had teeth with a hollow base and did not seem to be plicidentinous (see Chapter 3). The only problem with this character was the comment that infoldings of the enamel was enough to diagnose the presence of plicidentine. It is possible that the enamel could exhibit structuring not assumed by the dentine. The presence of plicidentine must be diagnosed by examining the internal surface of the tooth. This character was not invalidated by my histologic survey but would require recoding based on a histologic data set.

> *Character 165. Marginal teeth. Without high pedestals (0) (non-aigialosaur, non-mosasaurian squamates); with high pedestals (1) (aigialosaurs and mosasaurs).* (Lee & Caldwell, 2000: 932).

The term pedestal was in reference to the large "tooth bases" of mosasaurs. Caldwell *et al.* (2003) showed that the tooth bases were just large amounts of osteocement. In order to evaluate if this tissue was present in aigialosaurs, as coded by Lee and Caldwell (2000), a broken tooth or histologic section would have to be observed to see what tissues are involved in the "pedestal". Presence of large amounts of cement forming a "tooth base" would be a better character descriptor than presence of pedestal because pedestal is a vague term that could easily be confused with the pedicel of earlier vertebrates (Howe, 1979 discussed the development of the pedicel in frogs) and see character 167 (Lee & Caldwell, 2000 evaluated below).

> *Character 167. Resorption pits associated with replacement teeth. At base of teeth (0) (non-varanoid squamates); on bony tooth pedicel (1)*

(mosasaurids); absent (2) (non-mosasaurid varanoids). (Lee & Caldwell 2000: 932).

This character had separated anguinomorphs from all other squamates (Rieppel, 1979). Character 167 stands but the character states need revising based on my histologic analysis. State 0 is a valid character state and is supported by my research. Resorption pits do form at the base of the teeth near the junction of the dentine root and the tooth attachment tissues. State 1 is invalid as mosasaur teeth do not have a tooth pedicel, and the resorption pit does start to develop near the base of the teeth as in state 1. Although the resorption pit appears absent in most non-mosasaurid varanoids, my research showed that a small portion of the basal lingual region of the tooth was resorbed in an external to internal polarity prior to the shedding of the tooth. The colubrid *Heterodon platyrhinos* (Plate 18: c) and boiid *Epicrates cenchria* showed replacement teeth developing in conventional resorption pits.

The extended presence of a large resorption pit (0) or the lack of an extended presence of a large resorption pit would be a better character rather than the location of the resorption pit. Mosasaurs would need to be recoded to (0) and serpentes could be considered polymorphic (0, 1). More snake dentitions need to be analysed in order to determine the distribution of the presence of large resorption pits.

Tooth attachment itself is not phylogenetically significant in Squamata

I have shown that the traditional categories of tooth attachment, i.e., acrodonty, pleurodonty, thecodonty, etc., can not be used as character states (as they are currently defined) in phylogenetic analyses of Squamata. Based upon my histologic data, there are several traditional characters related to tooth attachment for squamates that are not appropriate to include in phylogenetic analyses. The geometry of the dentary is too plastic to consider the slope of the dentary as a character. The tooth attachment tissues themselves are similar across most squamates and therefore plesiomorphic. Tooth attachment tissues may be different in the dolichosaurs and aigialosaurs, warranting a tooth attachment tissue character, but these have not been examined yet. Although lacertoids and higher squamates show the retention of a large amount of former generations attachment tissues on the lingual side of the tooth indicating this may be a synapomorphy shared between the groups in this clade, it can not currently be considered as such because this character is dependent upon the number of replacement events that have occurred. Perhaps other squamates show this character as well and my sample did not acknowledge this as the species examined had undergone fewer tooth replacement events.

Characters that may be phylogenetically significant in Squamata

Despite the plasticity of some characteristics related to tooth attachment and development of squamate teeth, the study of other characters related to tooth attachment and development that may be phylogenetically significant in Squamata is warranted.

Lee and Caldwell (2000) suggested a character, presence of discrete alveoli for tooth attachment, in their definition of Character 161. This would probably be a good character as some squamates, snakes specifically, do show more extensive developments of alveolar bone, the socket forming bone, and do show a deeper dental groove, than other squamates.

I noted that the vascularity of the attachment changed in the number of canals present, and the location of the major canals. Anguinomorphan squamates had more localized vasculature than other squamates. More research would have to be done to see if these vascular characteristics varied along the length of the dentary, or changed during the life of the tooth, prior to the creation of characters related to attachment site vascularity.

Although not directly related to tooth attachment, the presence or absence of a acellular cement layer covering teeth is worthy of study as a potential character. My studied showed that it was only present in agamids. It is possible that it could be a feature in other closely related groups; more research would be necessary to determine this.

As mentioned above in the character evaluations of Zaher, Rieppel and Kluge (2002) and Lee and Caldwell (2000), the presence of plicidentine, the location of the resorption pit, the persistence of the resorption pit and the presence of large amounts of cellular cement forming a large tooth base are also worthy of study as characters related to tooth attachment and development in squamates.

The evolution of tooth attachment in Vertebrata

Thecodonty has been considered the most derived tooth attachment type in Vertebrata (Peyer, 1968; Edmund, 1969). It evolved convergently in both mammals and crocodilians (Berkovitz & Sloan, 1979; Osborn, 1984). Most researchers consider thecodonty to be a unique attachment type without a homologous precursor. The discovery of thecodont tooth attachment tissues in squamates suggests that thecodonty evolved early in vertebrate history and has been modified over time. Osborn (1984) suggested that thecodonty (the presence a periodontal ligament) evolved from the cessation of mineral deposition prior to the meeting of the alveolar bone and cement biomineralization fronts. The soft collagen matrix of cement and alveolar bone would remain unmineralized as the periodontal ligament. Osborn's (1984) theory explains how thecodonty could evolve in mosasaurs (Caldwell et al., 2003) and why cement and alveolar bone (traditionally considered thecodont tissues) are found in squamates. Future research into earlier vertebrate dental histology would be necessary to examine when and how these tissues evolved.

It is likely that our understanding of the evolution of vertebrate tooth attachment has been hampered by our reliance on inappropriate terminology (i.e., acrodonty, pleurodonty, thecodonty, *etc.*) rather than an appropriate data set (histology). The terms should be abandoned in favour of basic tissue terminology in discussions of tooth attachment evolution, as it is the tissues and their relationships to one another that evolve, not the terminology.

CONCLUSION

A survey of the tooth attachment histologies of 35 squamates showed that there were few significant differences in tooth attachment across the squamate groups. This study contained the first recognition of an acellular cement layer covering the tooth in agamid lizards. The traditional tooth attachment types were invalidated as character states useful in phylogenetic analyses of Squamata in light of the survey of the tooth attachment histology. The modification of other characters related to tooth attachment, characters of the resorption pit, presence of pedestal, presence of alveoli, and presence of plicidentine, were suggested. The vascularity of the tooth attachment site was introduced as new potential characters worthy of investigation. Tooth attachment in squamates was suggested to be a more primitive condition of the tooth attachment type considered most derived, thecodonty. This study suggested the need for more research into dental attachment in Squamata and other vertebrates as many characteristics of tooth attachment have the potential to provide new information on the interrelationships of Squamata and the evolution of vertebrate dental attachments.

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Appendix 4-1: Index to images of thinsections

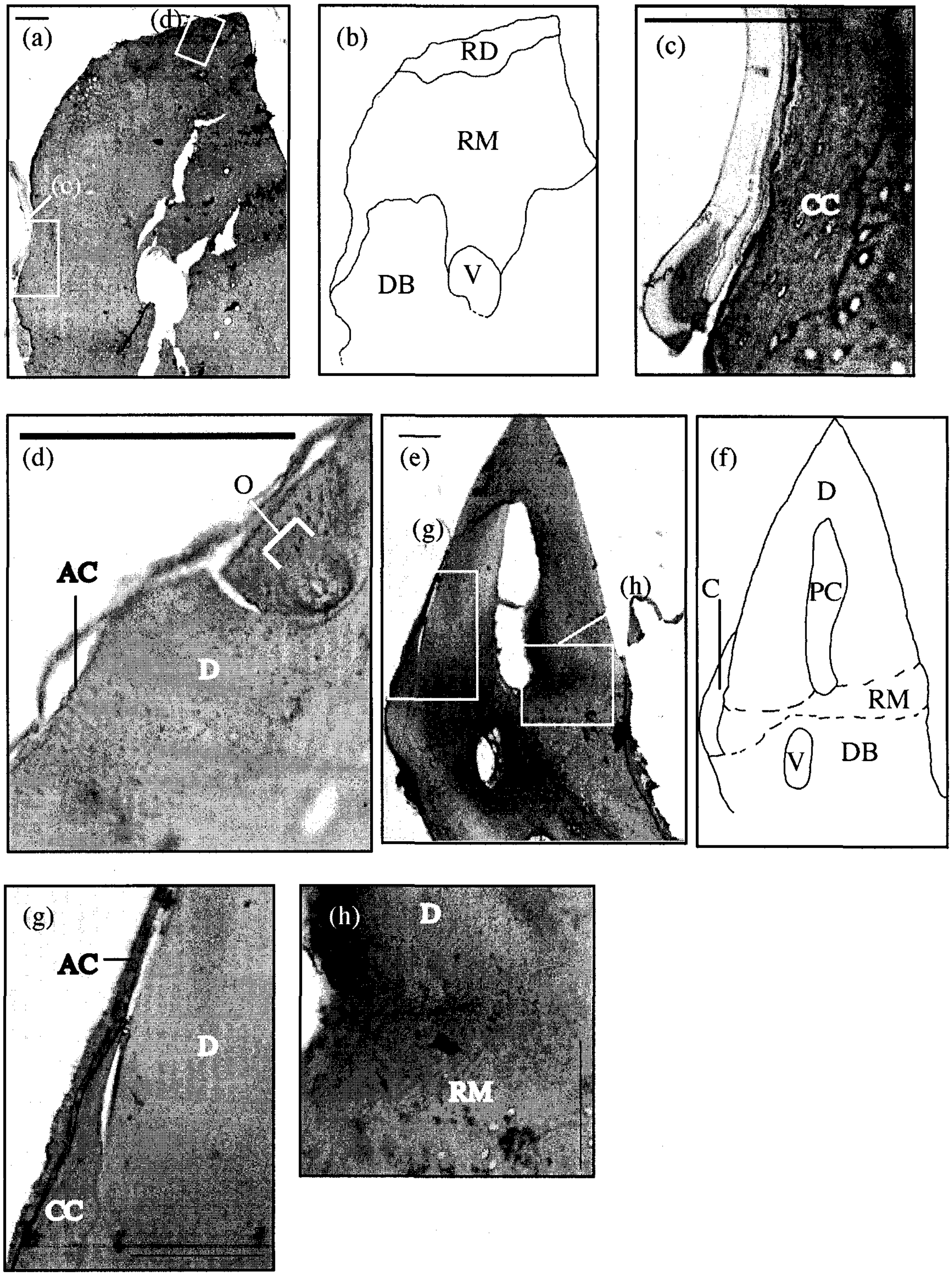
Appendix 4-1: Abbreviations

AB	alveolar bone
AC	cellular cement
AF	alveolar foramen
C	cement
CC	cellular cement
CF	collagen fibres
D	orthodentine
DB	dentary bone
DF	dental follicle
DL	dental lamina
HL	Howship's lacuna
O	osteon
OD	osteodentine
PC	pulp cavity
PD	plicidentine
R	remodeling
RAB	resorbing AB
RD	resorbing dentine
RM	remodeling zone
SF	Sharpey's fibres
SR	stellate reticulum
TD	trabecular dentine
TG	tooth germ
V	blood vessel

All scale bars = 100 um except Plate 4-13 (a, e) and Plate 4-20 (a) where scale bars= 5 mm

There are several images of each species. All of the images of each species are of a single thinsection unless stated otherwise in the text. Image sets for different species show similar aspects of tooth attachment and development to facilitate comparison between species.

Plate 4-1



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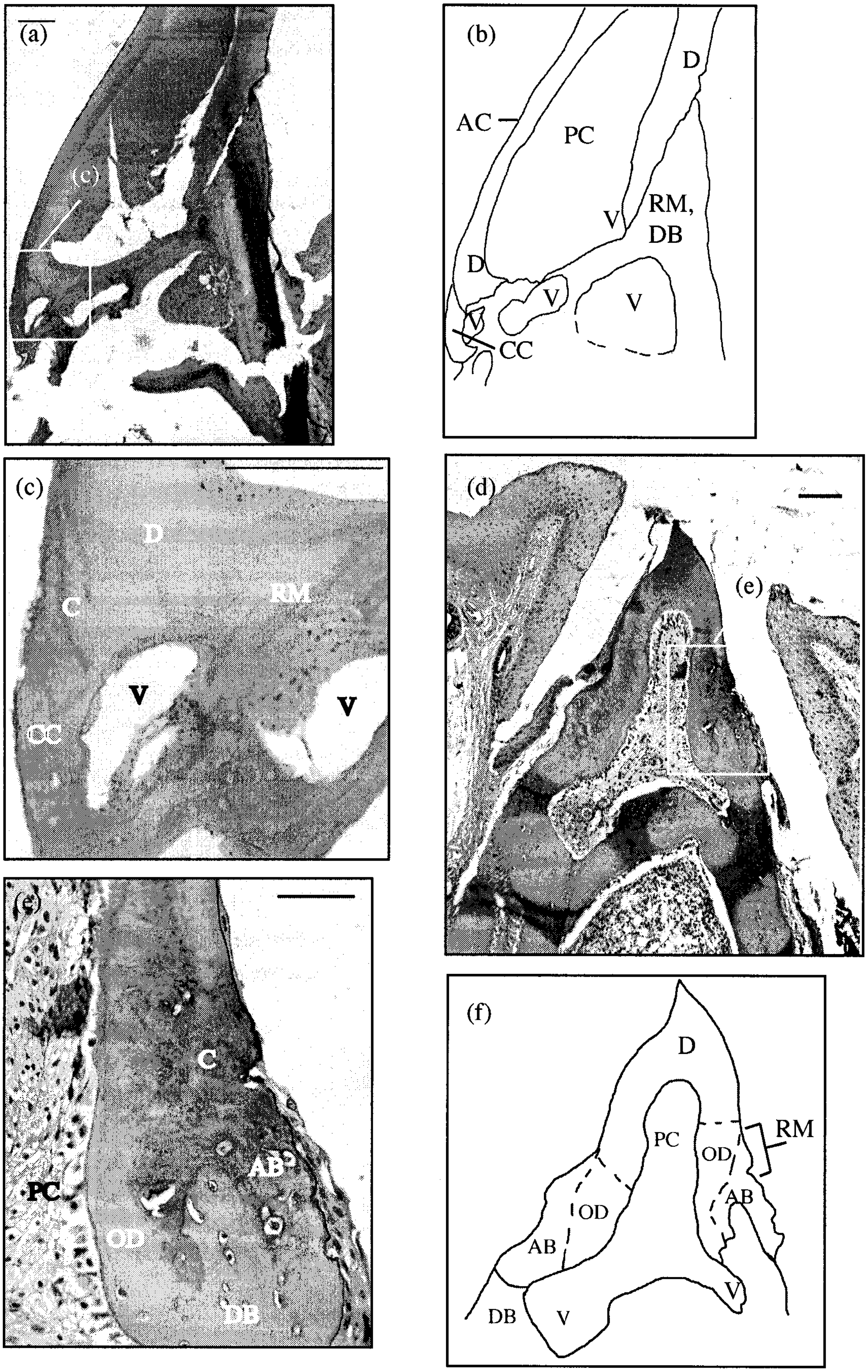
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Plate 4-3

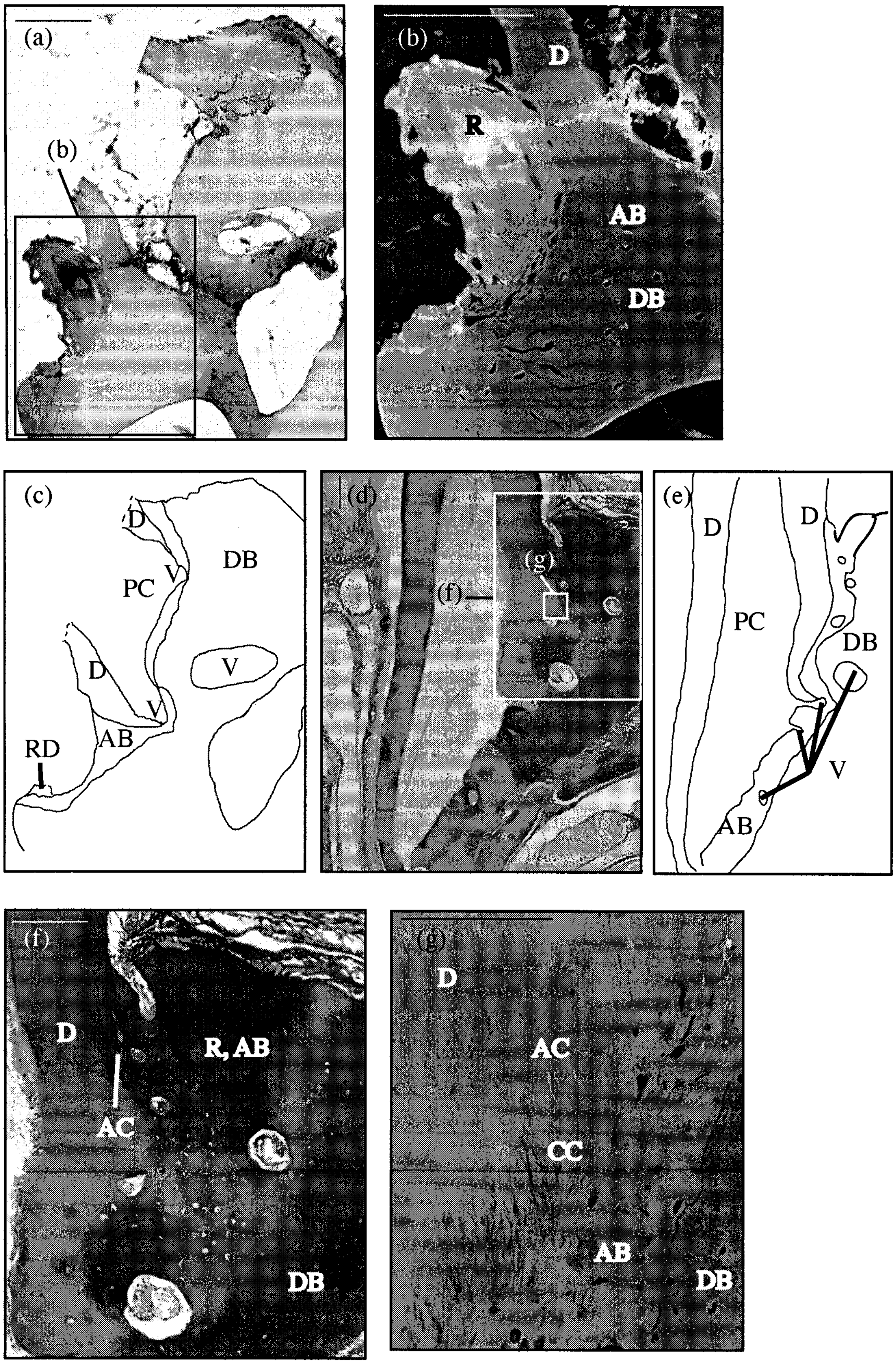
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Plate 4-4

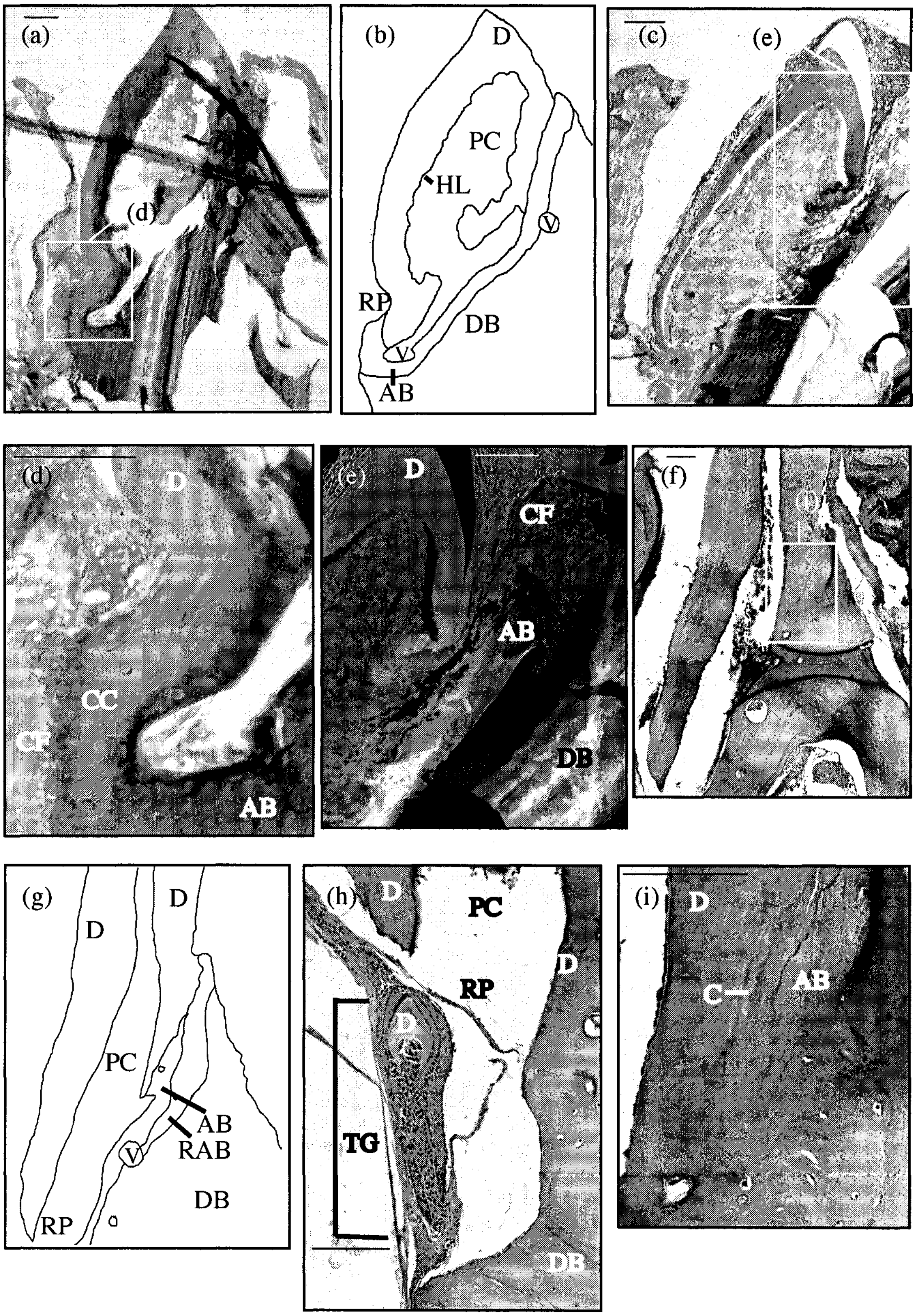
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Plate 4-5

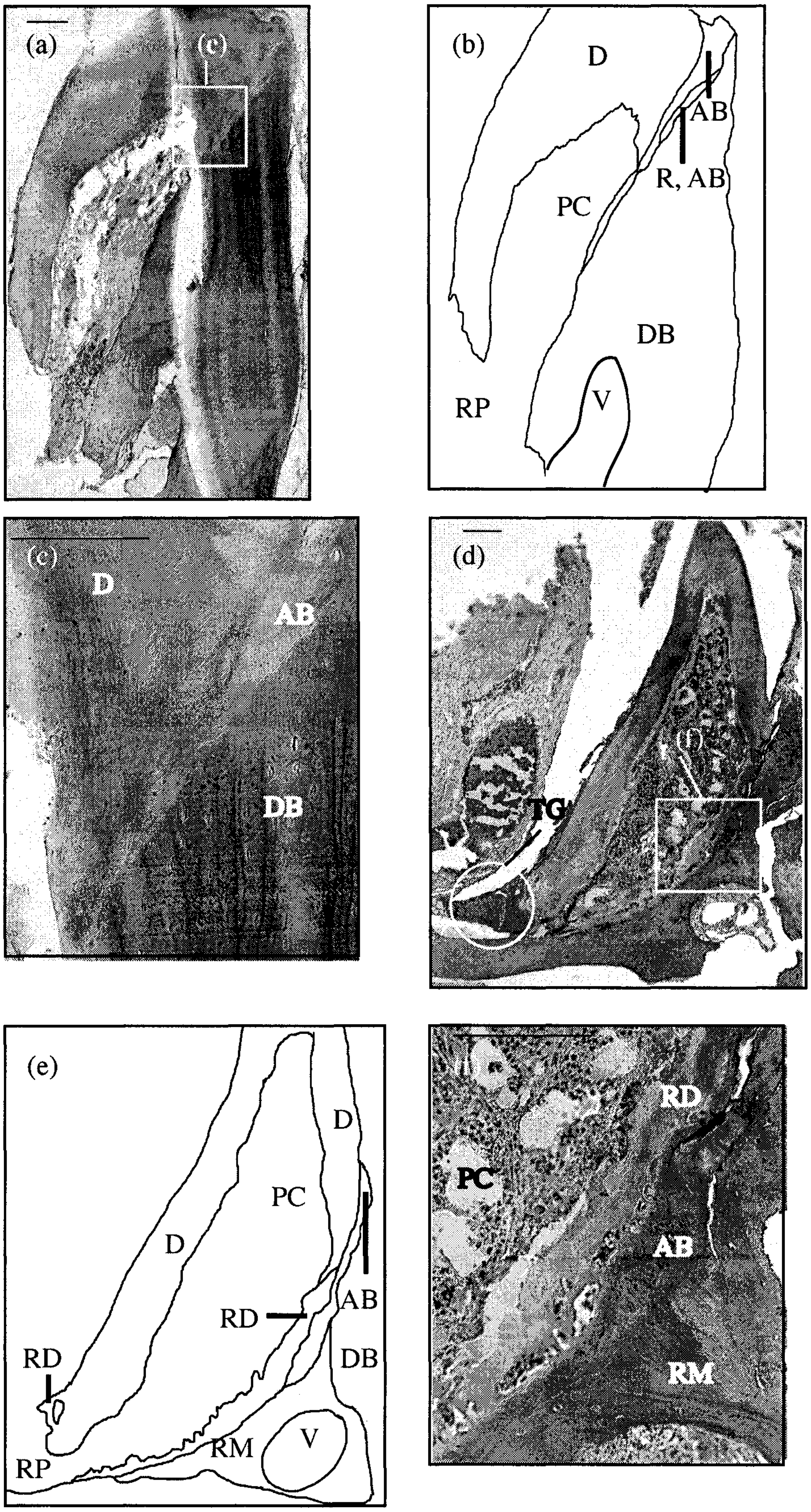
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Plate 4-6

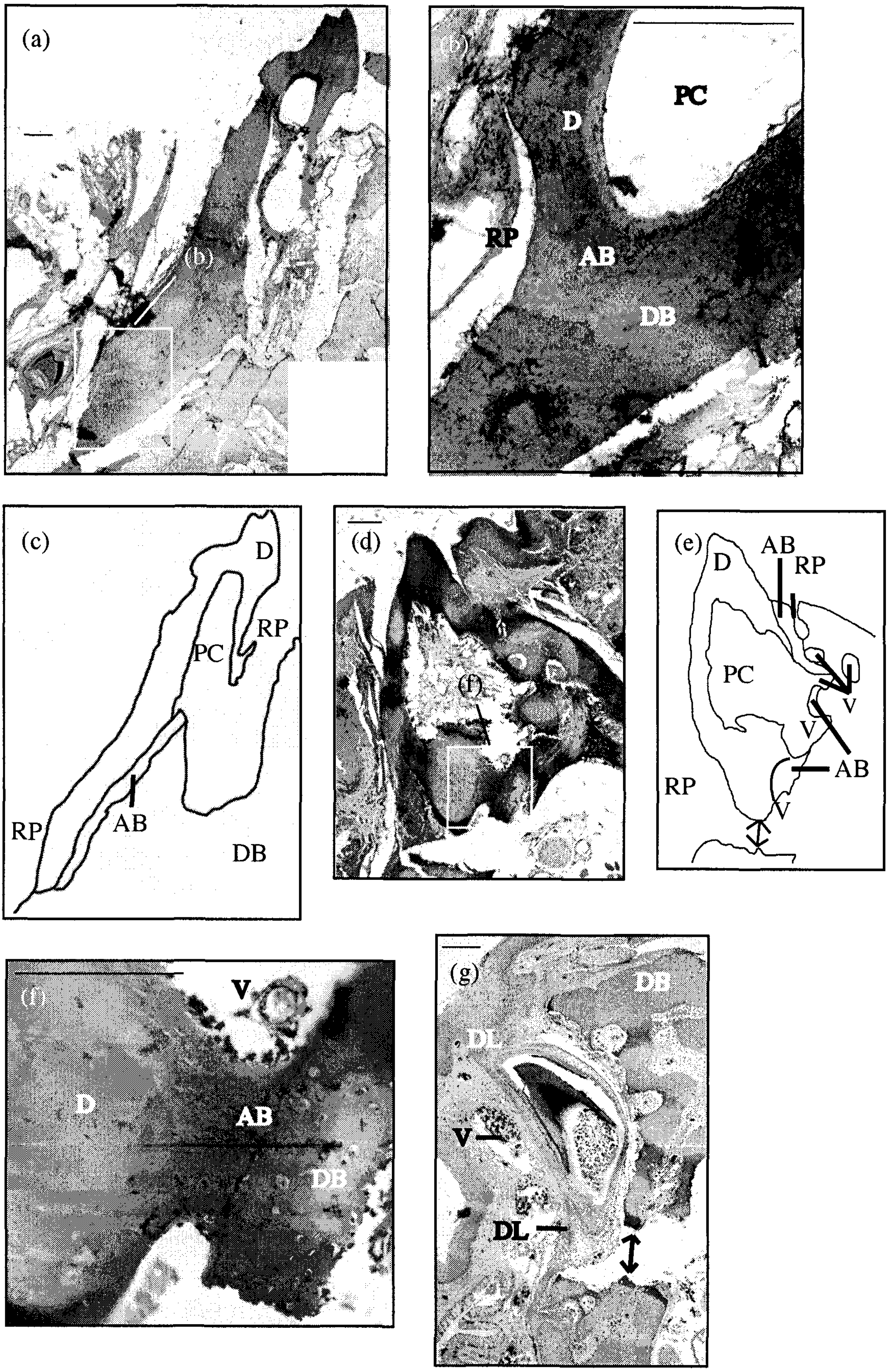
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Plate 4-7

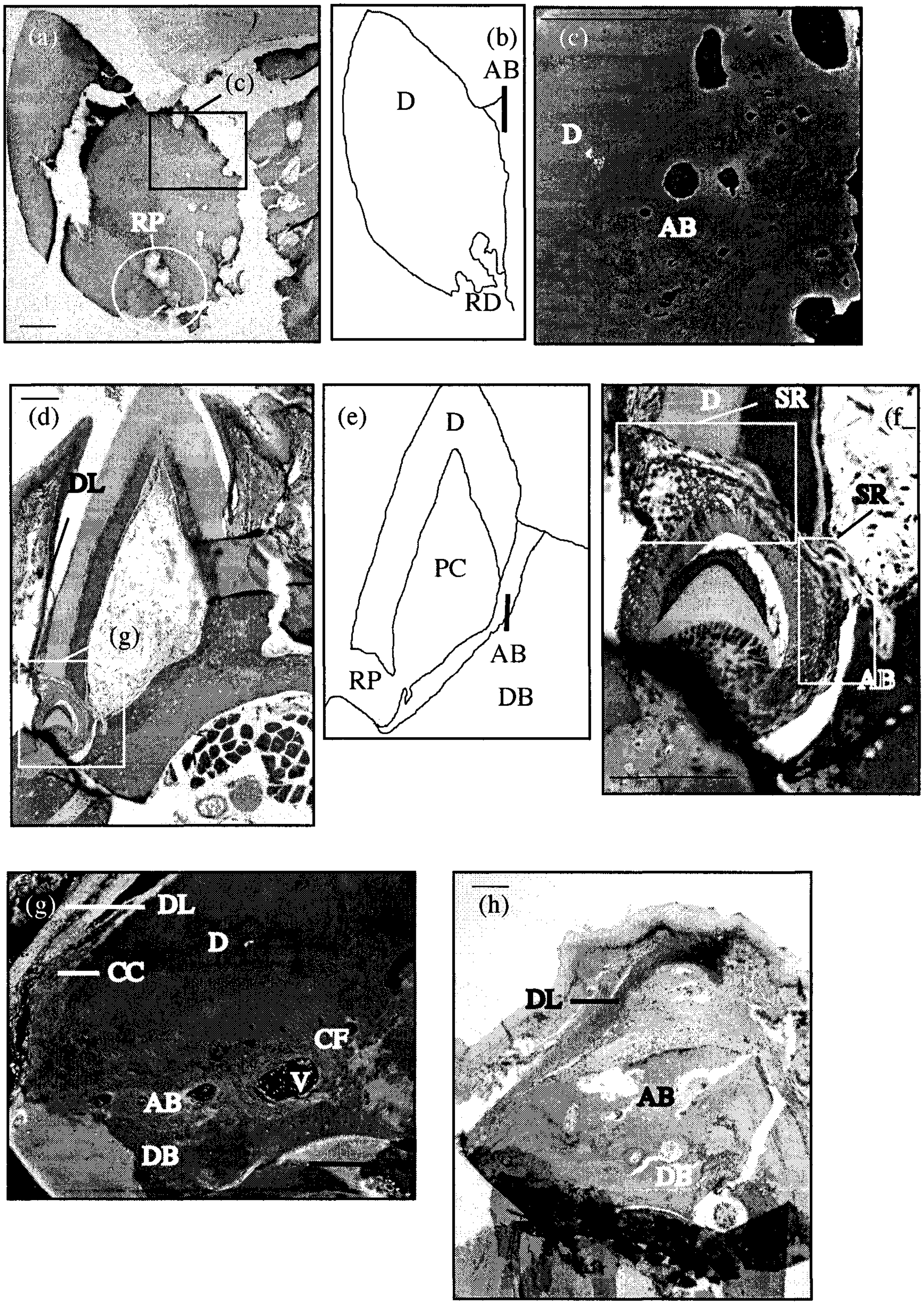
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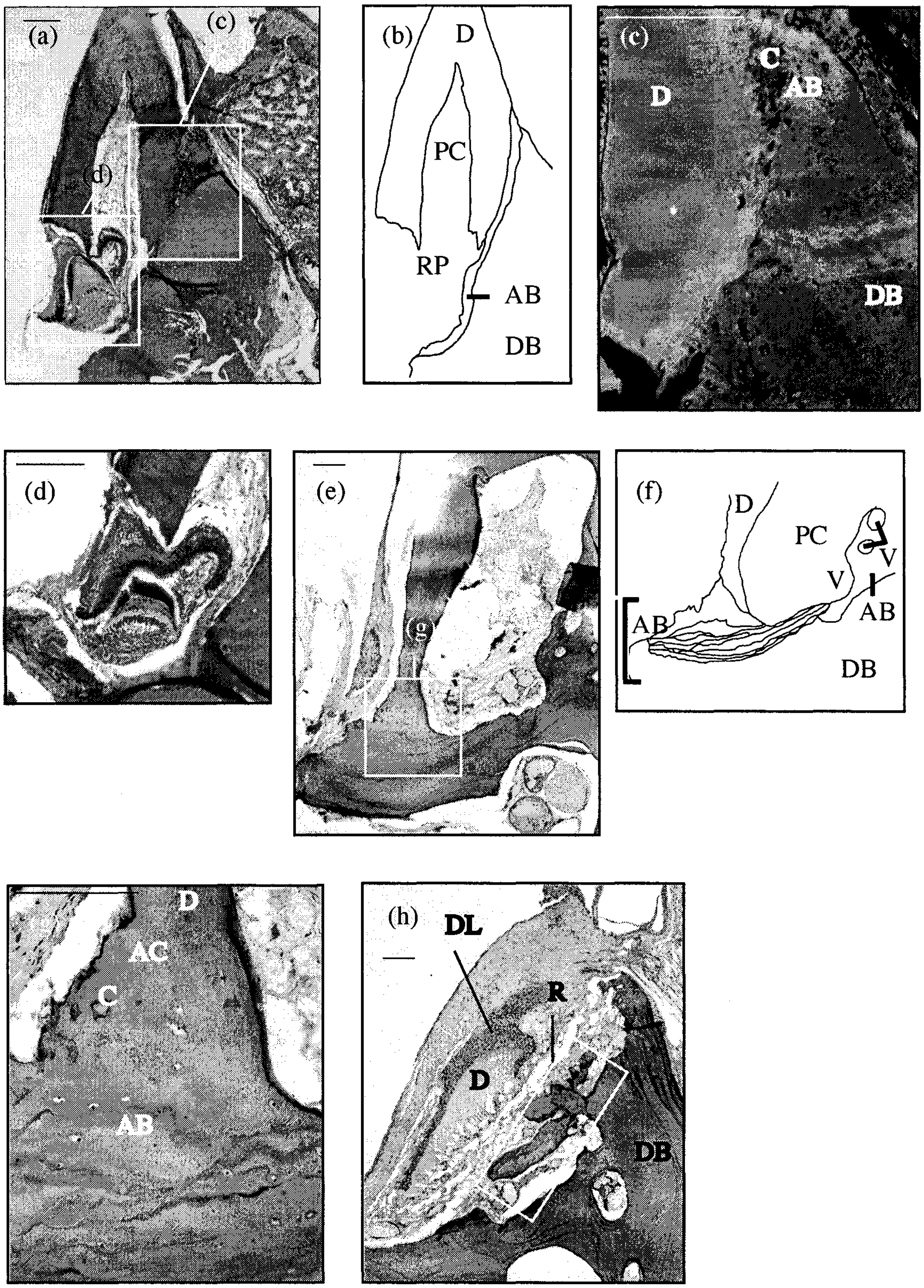
Plate 4-8



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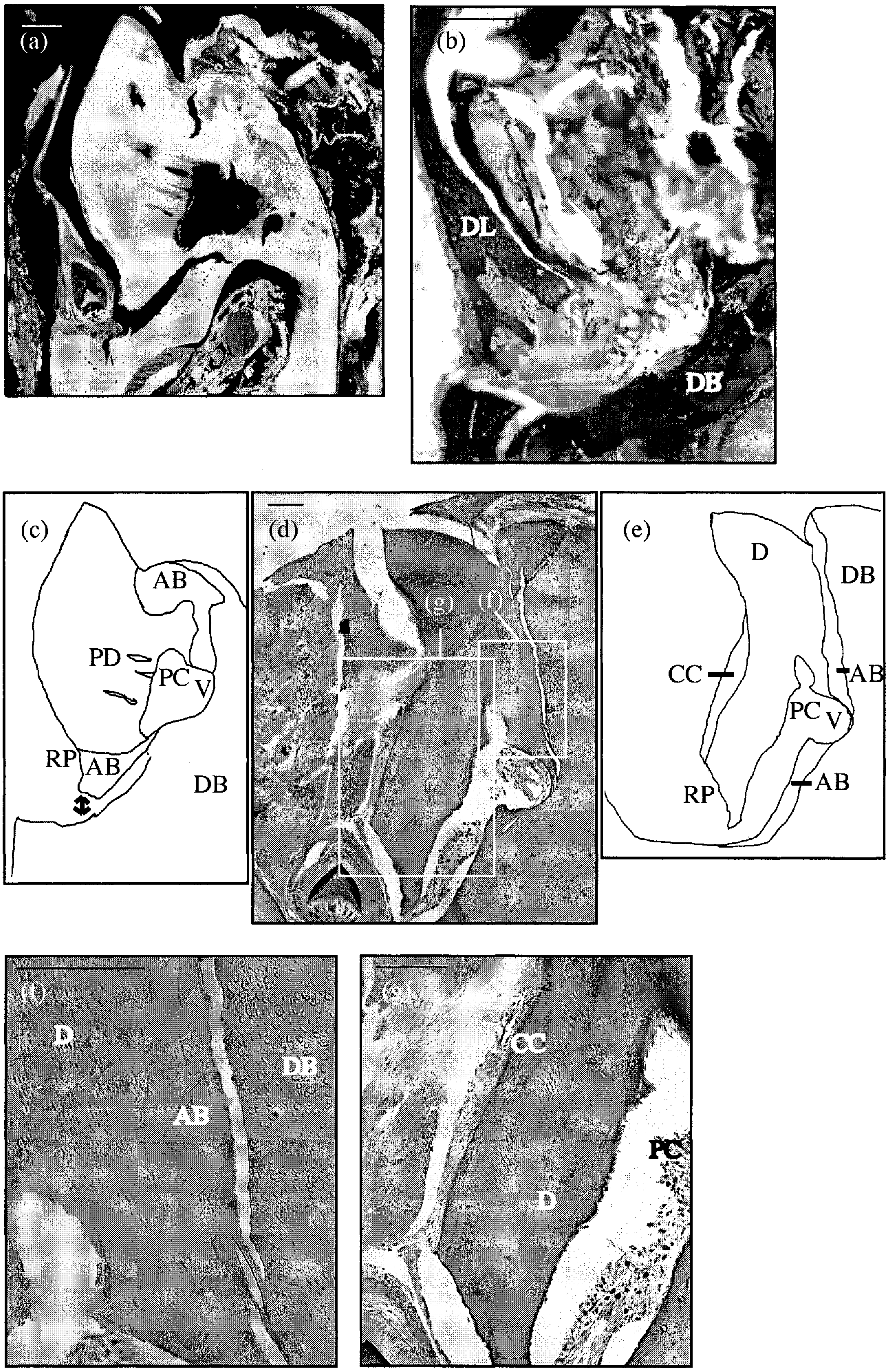
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Plate 4-10

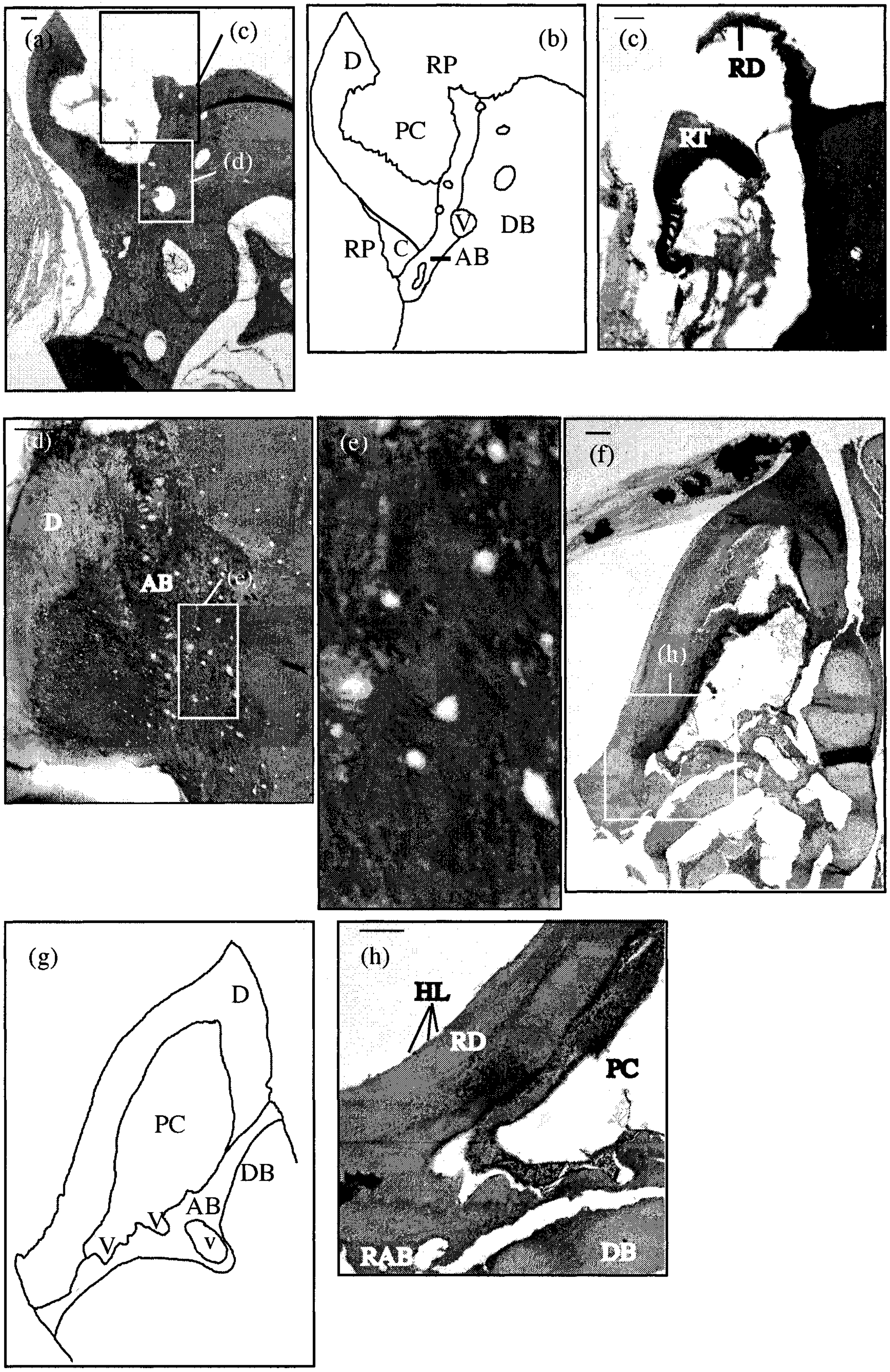
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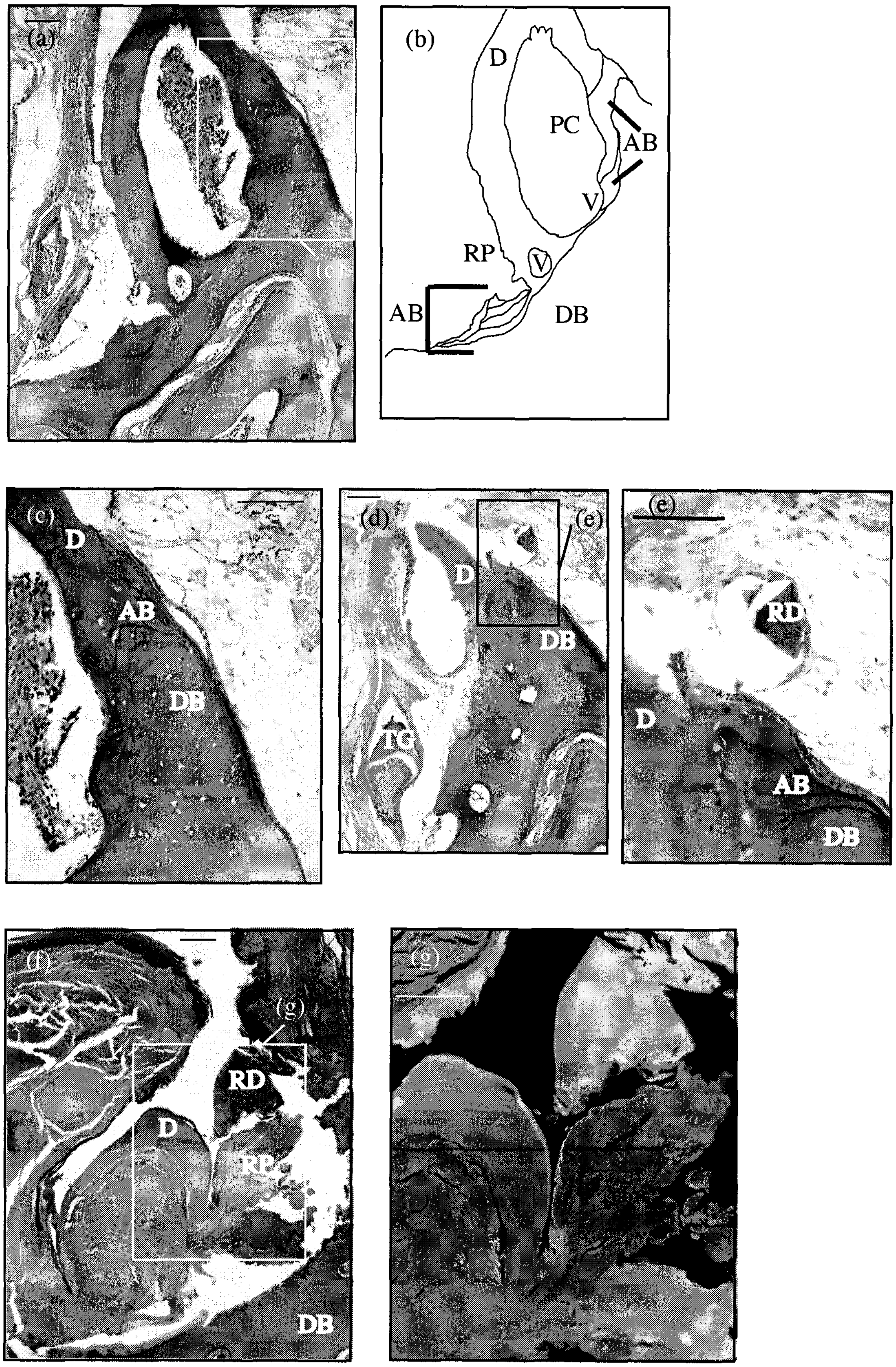
Plate 4-11



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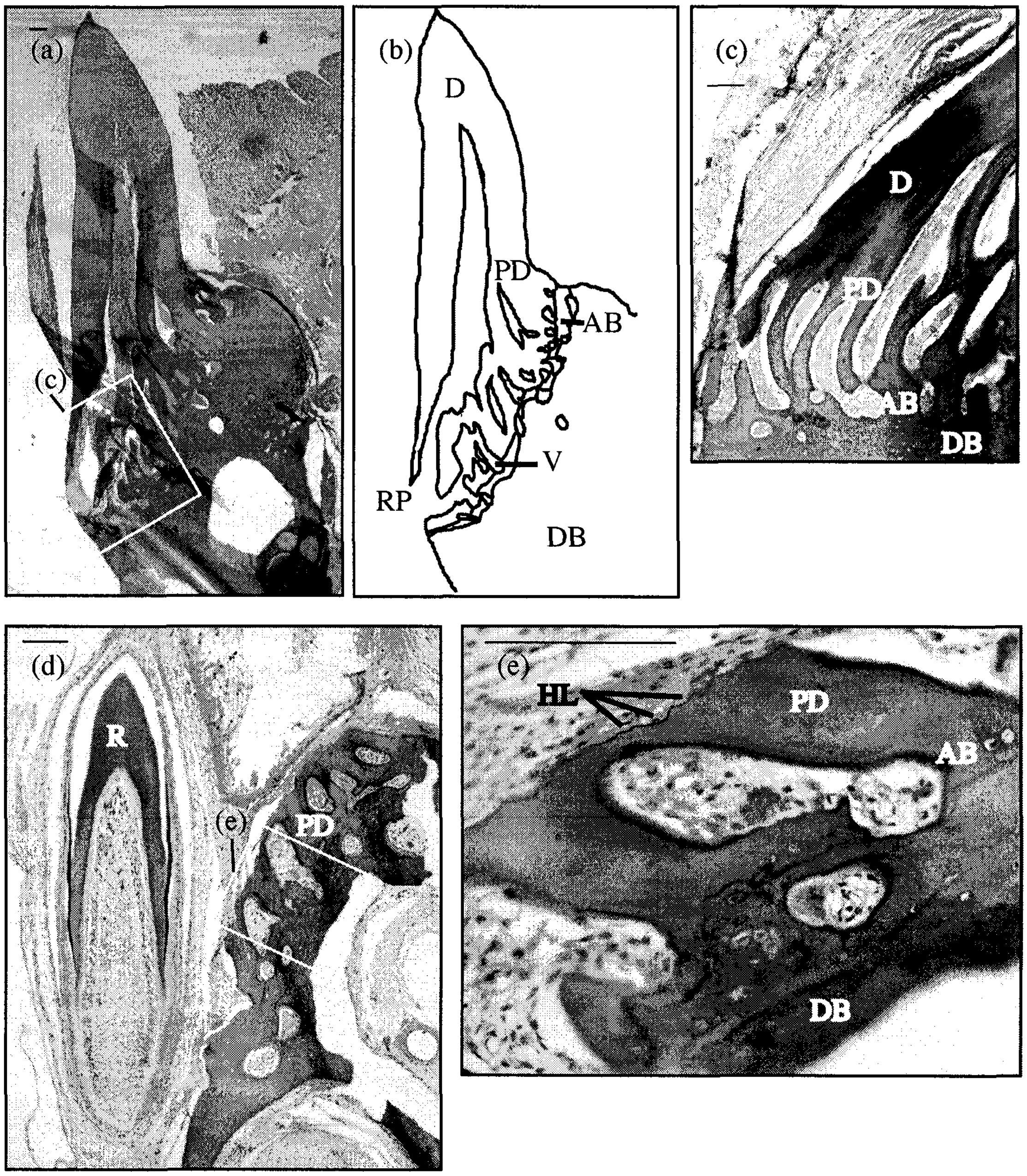

Plate 4-13

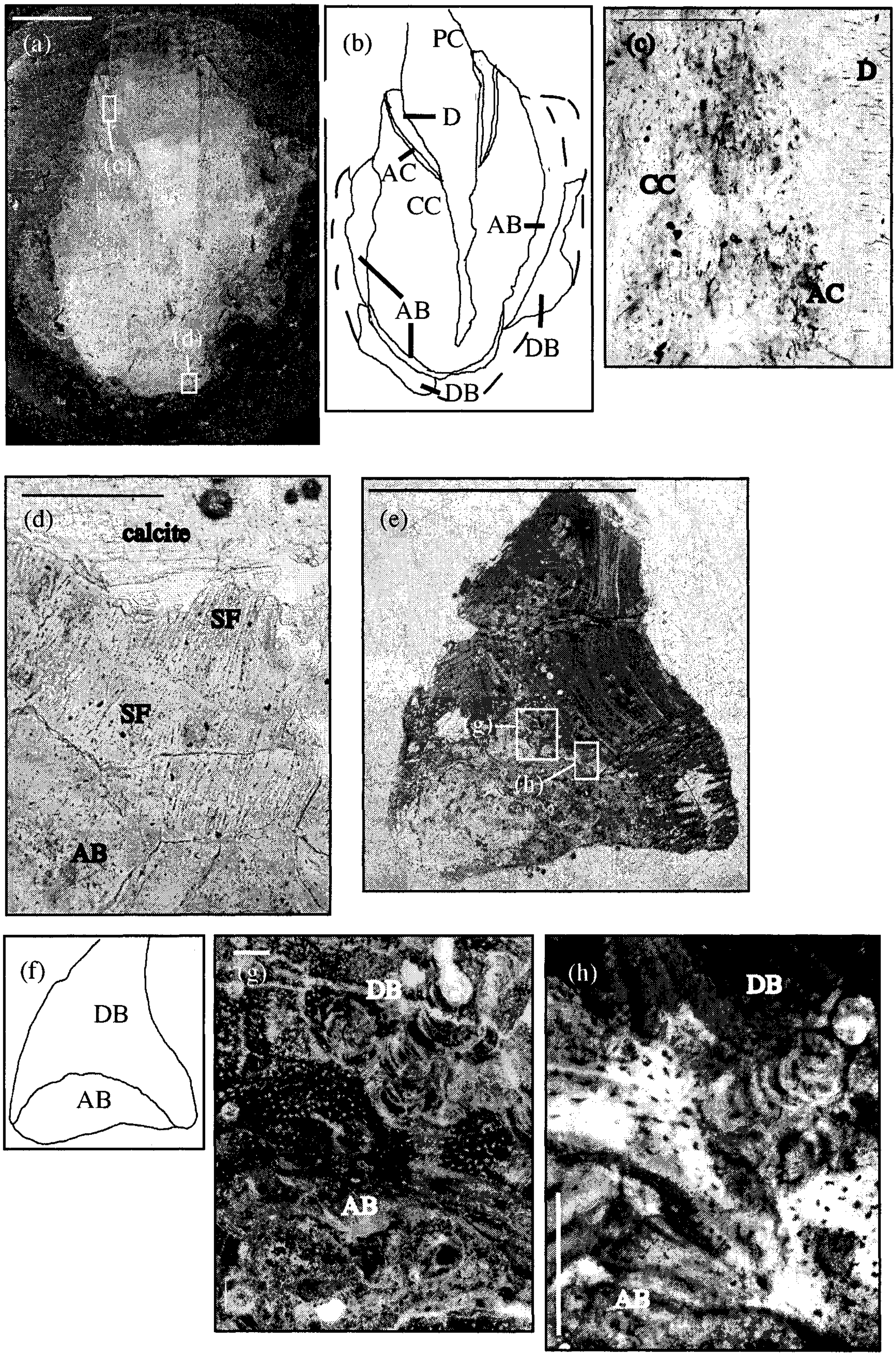
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Plate 4-14

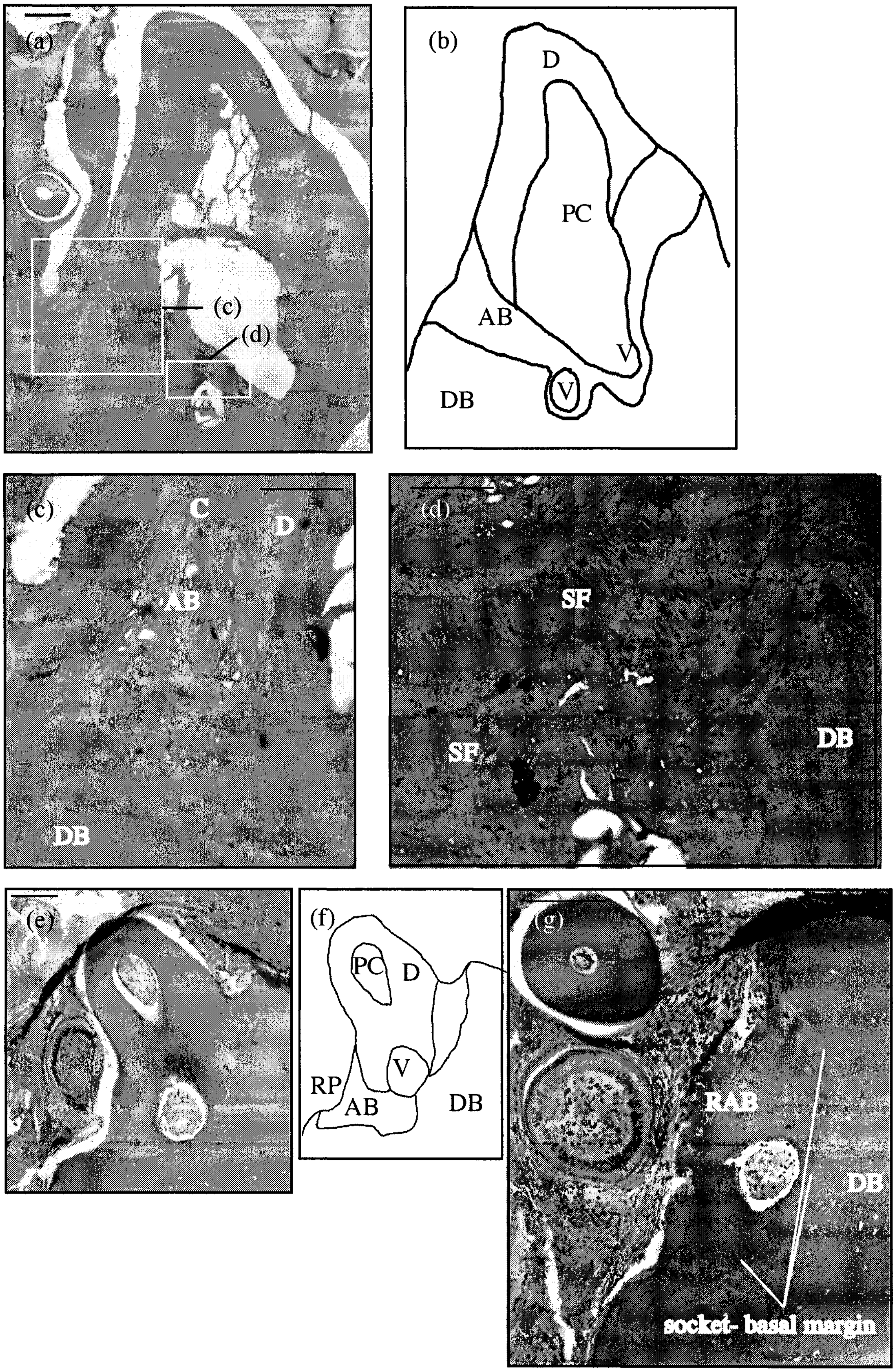
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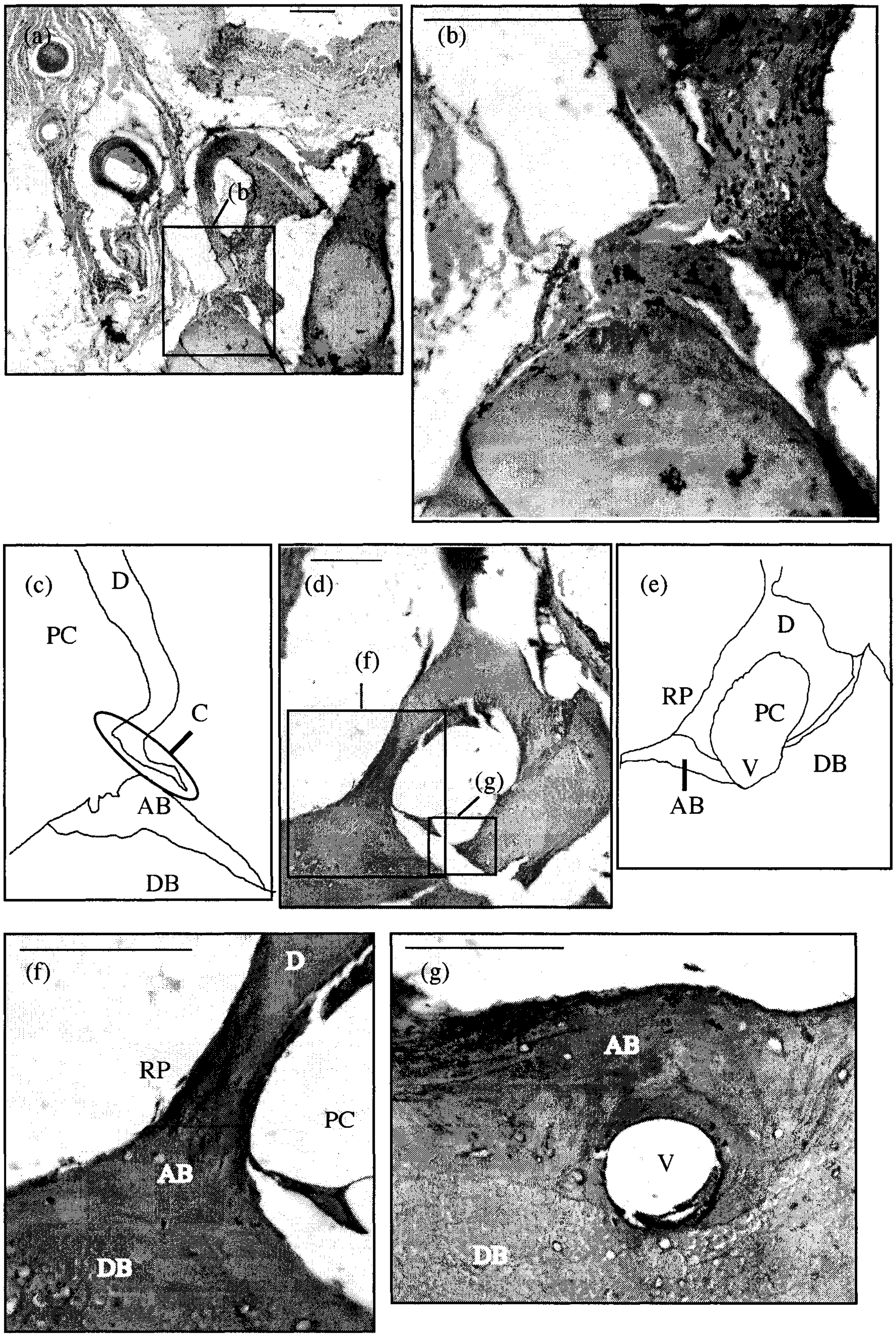
Plate 4-15



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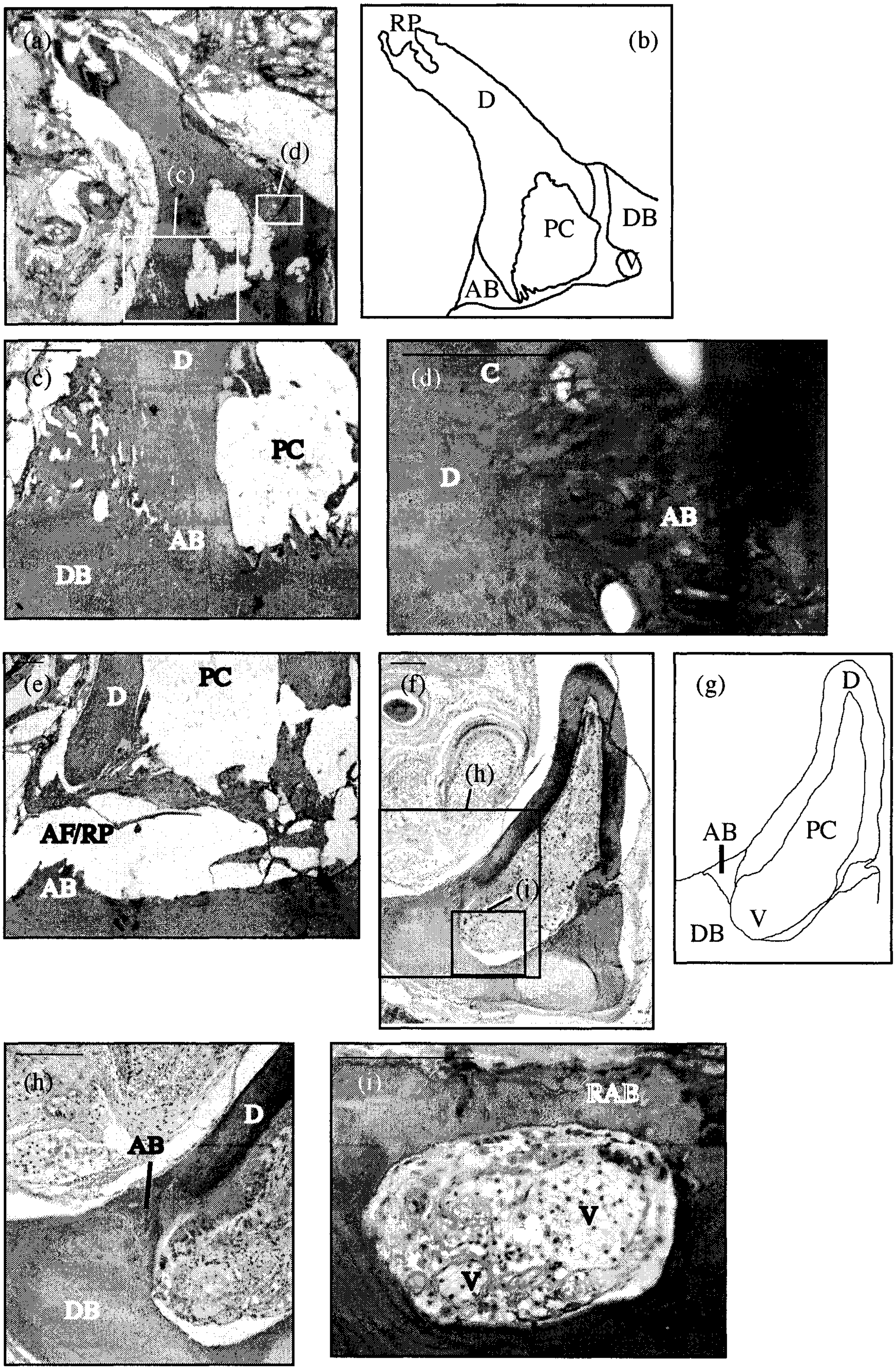
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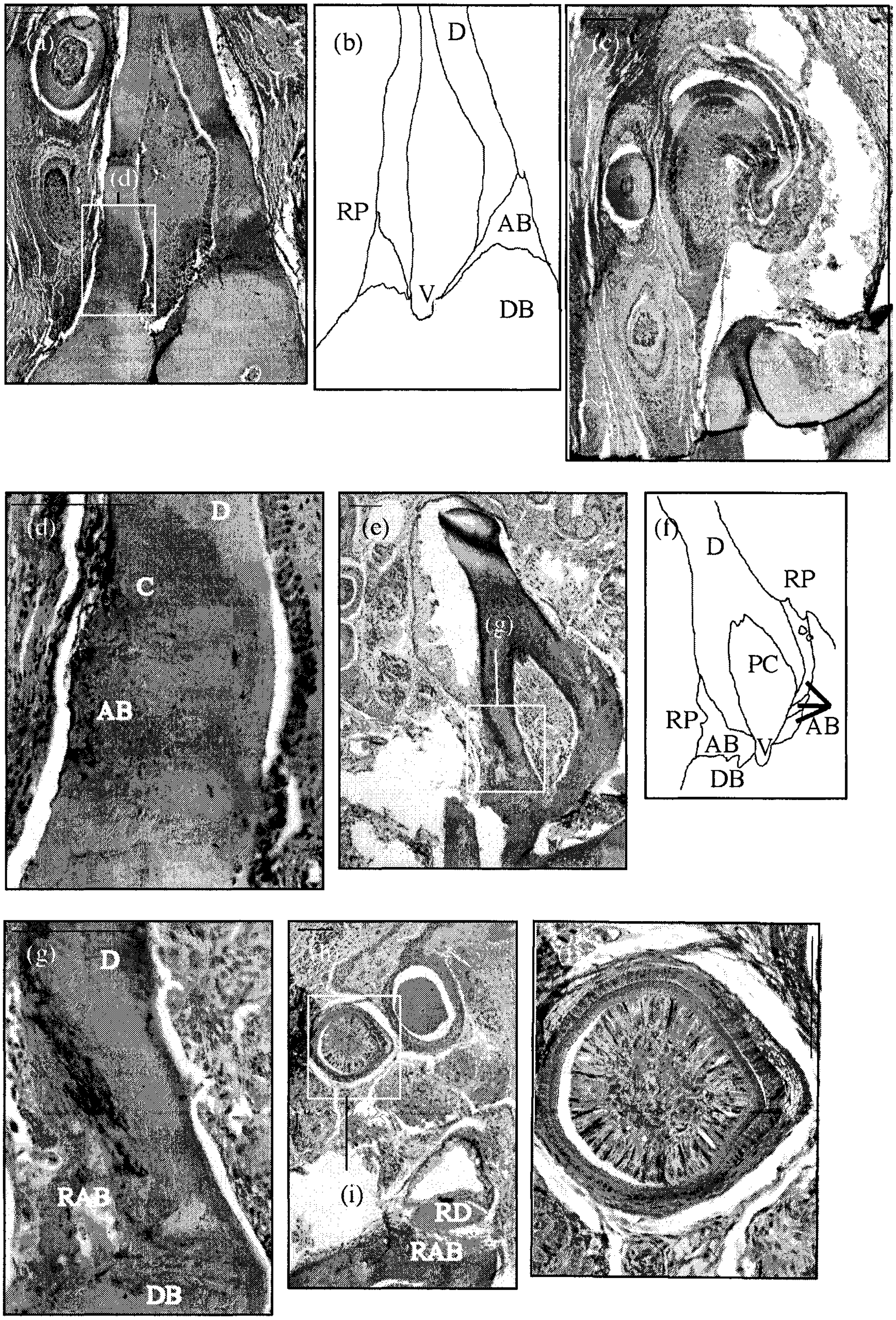
Plate 4-17



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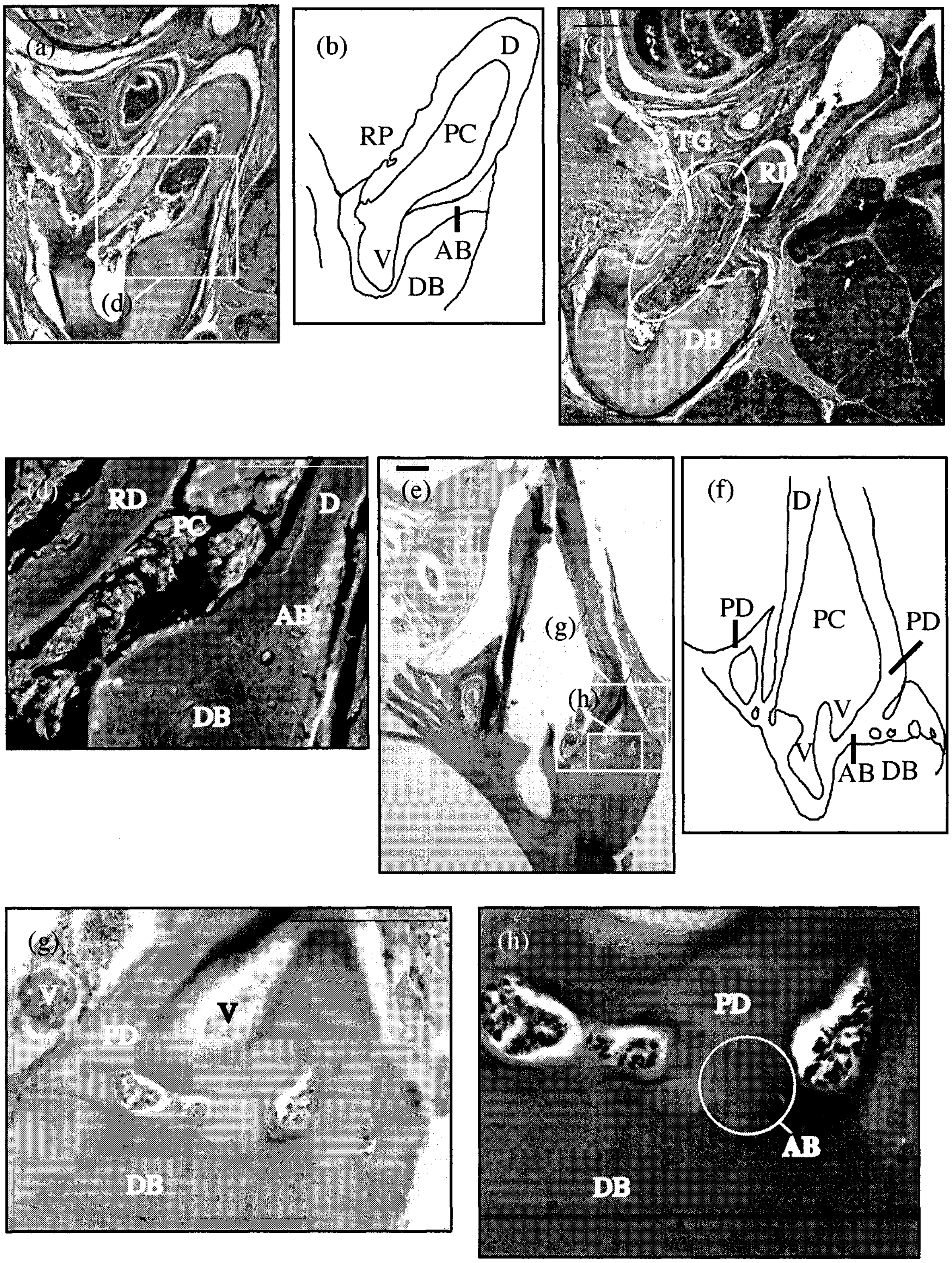
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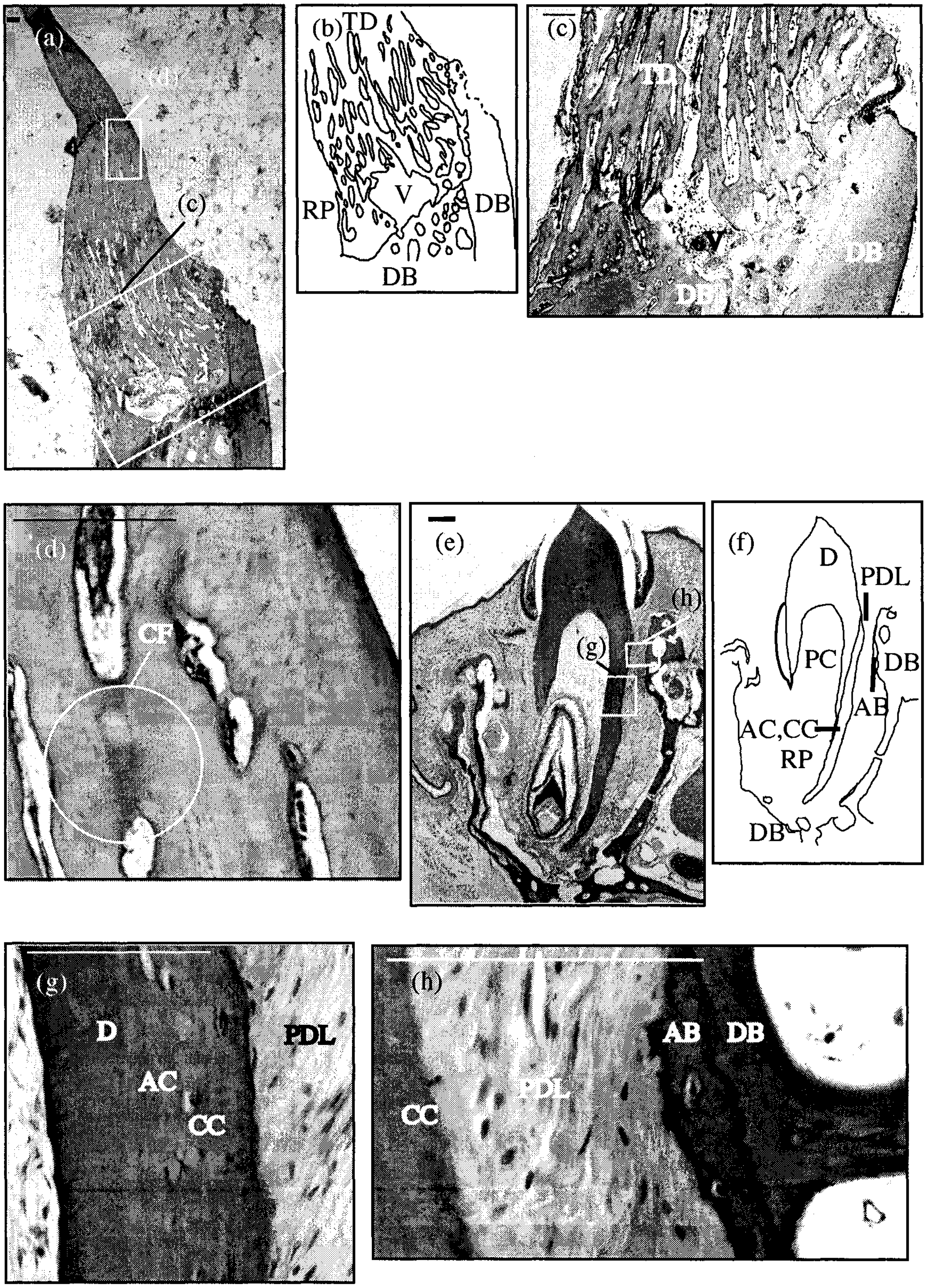
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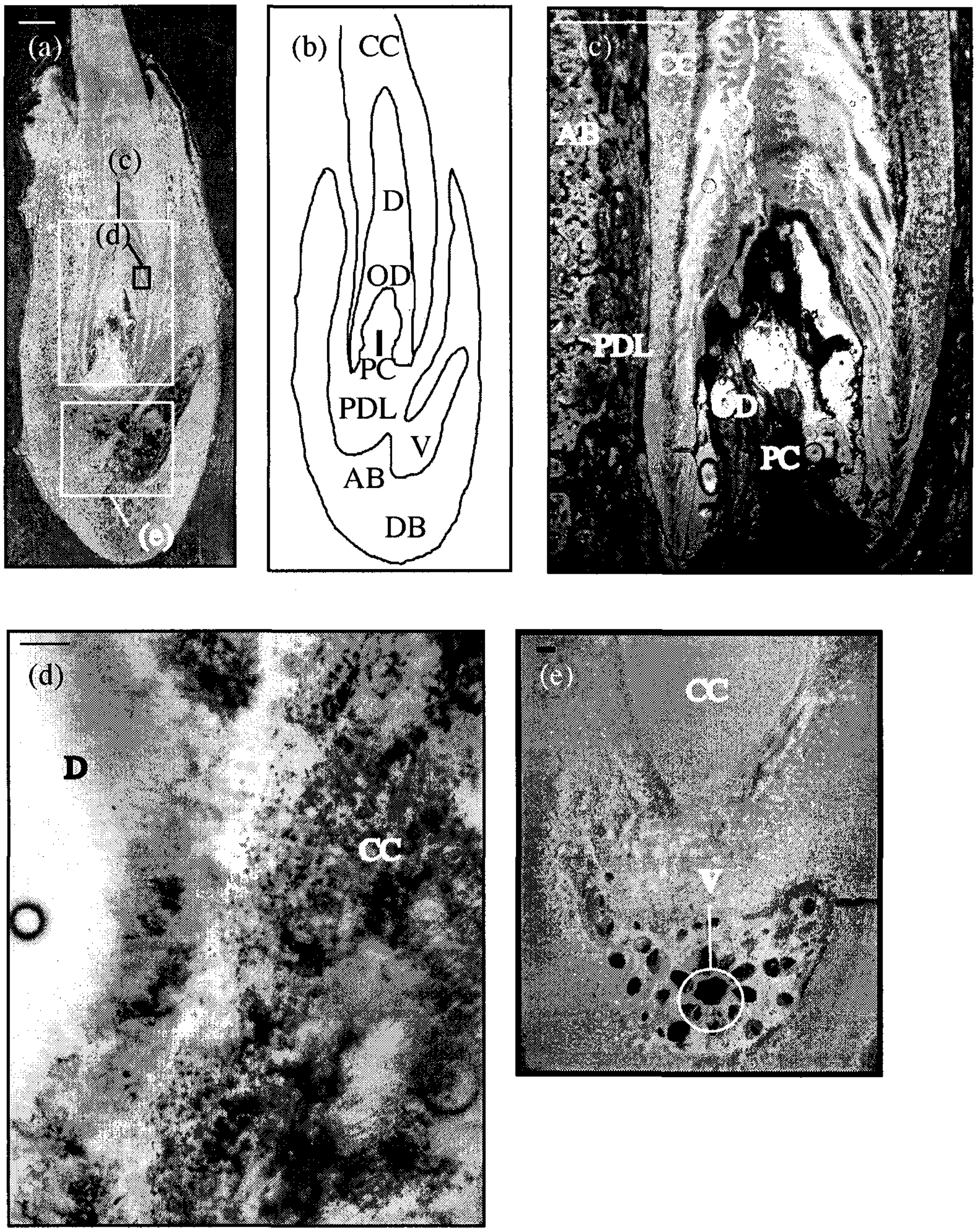
Plate 4-20



CHAPTER 5

GENERAL DISCUSSION AND CONCLUSIONS

This thesis examined traditional tooth attachment categories and their applicability as character states in phylogenetic analyses of squamates. It progressed from the introduction of traditional tooth attachment categories, to the recognition of an unexpected tooth attachment tissue (alveolar bone) and type (hinged) in the fossil snake *Dinilysia* and concluded with the evaluation of the traditional tooth attachment categories as character states in squamate phylogenetic analyses.

A review of various tooth attachment classifications and their usage was presented in Chapter 2. An extensive literature survey showed that tooth attachment classifications were cited primarily for the dominant type of information presented in the paper, rather than the classification terminology. The variability in the definitions of terms was suggested to be impeding discussions of the evolution of vertebrate tooth attachments. The traditional categories, i.e., acrodonty, pleurodonty, thecodonty, *etc.*, as defined in published literature, were suggested to be inappropriate as phylogenetic character states as the terms accommodate morphologies that have not been examined regarding their homology.

The tooth socket histology from a thinsection through the interdental plate from a maxilla of *Dinilysia* was described in Chapter 3. A review of the different amniote attachment tissues was also presented in this chapter. Alveolar bone was identified as the tissue making up the socket walls. Tooth attachment in Dinilysia was interpreted to be facilitated by a hinge. The presence of alveolar bone in the fossil snake *Dinilysia* combined with the discovery of thecodont attachment tissues in the mosasaur *Platecarpus* indicated that squamate tooth attachment may be misunderstood and worthy of investigation. The necessity of a survey of squamate dental histology was asserted in this chapter.

A survey of the dental histology of 35 squamate species and the evaluation of traditional tooth attachment categories as character states was presented in Chapter 4. Cement and alveolar bone attached the squamate teeth to the dentary bone. A periodontal ligament was interpreted to be biomineralized as cement. These histologies were then used to empirically test the conclusion in Chapter 2 that traditional tooth attachment categories are inappropriate to use as phylogenetic character states. The traditional tooth attachment types were not found in squamates, thereby invalidating them as good character states. The prior mischaracterization of squamate tooth attachment was suggested to be due to the lack in knowledge of squamate dental histology. The presence of plicidentine and the presence of a resorption pit were characters related to tooth attachment requiring reanalysis based on a more appropriate data set. Other aspects of tooth attachment, i.e., presence of a covering of acellular cement over the tooth crown, the nature and placement of the resorption pit, and the vascularization of the tooth attachment site were all suggestions for potentially viable phylogenetic characters.

This thesis presented evidence indicating that tooth attachment in Squamata has been largely misunderstood and misinterpreted. The chapters of this thesis presented cumulative evidence of the problems with our adherence to traditional ideas and data sets in studies of tooth attachment culminating in the suggestion that we are using inappropriate terminology in our discussions of the evolution of vertebrate tooth attachments. It was suggested that more early vertebrate dental histologies need to be examined and compared using simple tissue terminology to better understand the evolution of vertebrate tooth attachments. This thesis should encourage the careful evaluation of ancient anatomic terminologies created prior to the introduction of the theory of evolution. We should be suspicious of the application of general, plastic terminology to anatomies in specific groups of animals and endeavor to use terminology that reflects the diversity of anatomies within our study groups.