Primate Dentition

An Introduction to the Teeth of Non-human Primates

DARIS R. SWINDLER
Professor Emeritus
Department of Anthropology
University of Washington, USA

ILLUSTRATED BY

ROBERT M. GEORGE
Department of Biology
Florida International University, USA

CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK
40 West 20th Street, New York, NY 10011-4211, USA
477 Williamstown Road, Port Melbourne, VIC 3207, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain
Dock House, The Waterfront, Cape Town 8001, South Africa

http://www.cambridge.org

First published 2002

Printed in the United Kingdom at the University Press, Cambridge

Typeface Times Roman 10/12.5pt *System* Poltype® [VN]

A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication data

Swindler, Daris Ray
Primate dentition: an introduction to the teeth of nonhuman primates /
Daris R. Swindler; illustrated by Robert M. George.
p. cm. – (Cambridge studies in biological and evolutionary
anthropology; 32)
Includes bibliographical references (p.).
ISBN 0 521 65289 8 (hb)
1. Primates – Anatomy. 2. Dentition. 3. Teeth. I. Title. II. Series.
QL737.P9 S823 2002
573.3′56198 – dc21 2001037356

ISBN 0 521 65289 8 hardback

Contents

1 *Introduction*

Order Primates

Primates are a diverse group of mammals that have evolved from a group of insectivorous mammals some 60 million years ago. Indeed, it is difficult to define primates since they lack a single feature that separates them from other mammalian groups. At the same time, primates have remained plesiomorphic, retaining many ancestral features, rather than becoming highly apomorphic as did many groups of mammals, for example, the horse with a single digit in each foot.

Today, there are nearly 300 primate species grouped into about 80 genera (depending on the source), most of which live in tropical or subtropical regions of the world. The majority of living primate taxa are monkeys, and are present in both the New and Old Worlds, while prosimians are found in Madagascar, Africa, and Asia, the great apes inhabit Africa, Borneo, and Sumatra, and the lesser apes live in many regions of Southeast Asia. The remaining primate species, *Homo sapiens*, is the only living hominid and is found in most regions of the world. The primate classification presented here is often referred to as the traditional one since it is based on the level or grade of organization of the different primate groups. Table 1.1 presents a classification of living primates. This list includes only the primates examined in this book, and therefore does not represent a complete list of all extant genera. Classifications and scientific names often change through time; I have therefore attempted to include the changes that have occurred since the original version of this book appeared in 1976.

Dental cast collection

The basic data presented in this book were taken from plaster casts made from alginate impressions. The impressions and casts were made of the permanent and deciduous teeth of primate skulls housed in the following museums: American Museum of Natural History, National Museum of

Table 1.1. *Classification of living primates studied in this book*

ORDER PRIMATES

- Suborder: Prosimii
  - Infraorder: Lemuriformes
    - Superfamily: Lemuroidea
      - Family: Lemuridae
        - *Lemur catta*
        - *Eulemur macaco*
        - *E. rubiventer*
        - *E. mongoz*
        - *Varecia variegata*
        - *Hapalemur griseus*
      - Family: Lepilemuridae
        - *Lepilemur mustelinus*
      - Family: Cheirogaleidae
        - *Microcebus murinus*
        - *Cheirogaleus major*
        - *Phaner furcifer*
      - Family: Indriidae
        - *Indri indri*
        - *Propithecus verreauxi*
        - *Avahi laniger*
      - Family: Daubentoniidae
        - *Daubentonia madagascariensis*
    - Superfamily: Lorisoidea
      - Family: Lorisidae
        - *Loris tardigradus*
        - *Nycticebus coucang*
        - *Perodicticus potto*
        - *Arctocebus calabarensis*
      - Family: Galagidae
        - *Otolemur crassicaudatus*
        - *Galago senegalensis*
  - Infraorder: Tarsiiformes
    - Superfamily: Tarsioidea
      - Family: Tarsiidae
        - *Tarsius spectrum*
        - *T. bancanus*
        - *T. syrichta*
- Suborder: Anthropoidea
  - Infraorder: Platyrrhini
    - Superfamily: Ceboidea
      - Family: Cebidae
        - Subfamily: Callitrichinae
          - *Saguinus geoffroyi*
          - *Leontopithecus rosalia*
          - *Callithrix penicillata*
          - *Cebuella pygmaea*
          - *Callimico goeldii*
        - Subfamily: Cebinae
          - *Cebus apella*
          - *Saimiri sciureus*
          - *S. oerstedii*
        - Subfamily: Aotinae
          - *Aotus trivirgatus*
      - Family: Atelidae
        - Subfamily: Callicebinae
          - *Callicebus moloch*
        - Subfamily: Atelinae
          - *Ateles geoffroyi*
          - *A. belzebuth*
          - *A. paniscus*
          - *A. fusciceps*
          - *Lagothrix lagotricha*
          - *Alouatta palliata*
          - *A. seniculus*
          - *A. belzebul*
          - *Brachyteles arachnoides*
        - Subfamily: Pitheciinae
          - *Cacajo calvus*
          - *Chiropotes satanas*
          - *Pithecia pithecia*
  - Infraorder: Catarrhini
    - Superfamily: Cercopithecoidea
      - Family: Cercopithecidae
        - Subfamily: Cercopithecinae
          - *Macaca nemestrina*
          - *M. mulatta*
          - *M. fascicularis*
          - *M. nigra*
          - *Lophocebus albigena*
          - *L. aterrimus*
          - *Cercocebus torquatus*
          - *C. galeritus*
          - *Papio cynocephalus*
          - *Theropithecus gelada*
          - *Mandrillus sphinx*
          - *Cercopithecus nictitans*
          - *C. cephus*
          - *C. mona*
          - *C. mitis*
          - *C. lhoesti*
          - *C. neglectus*
          - *C. ascanius*
          - *Chlorocebus aethiops*
          - *Erythrocebus patas*
          - *Miopithecus talapoin*

Table 1.1 (*cont.*)

ORDER PRIMATES (*cont.*)

- Subfamily: Colobinae
  - *Piliocolobus badius*
  - *Colobus polykomos*
  - *Presbytis comata*
  - *Trachypithecus pileatus*
  - *T. cristata*
  - *T. phyrei*
  - *Pygathrix nemaeus*
  - *Simias concolor*
  - *Nasalis larvatus*
  - *Rhinopithecus roxellanae*
  - *Kasi johnii*
- Superfamily: Hominoidea
  - Family: Hylobatidae
    - *Hylobates klossi*
    - *H. moloch*
    - *H. lar*
    - *H. syndactylus*
  - Family: Pongidae
    - *Pongo pygmaeus*
    - *Gorilla gorilla*
    - *Pan troglodytes*
    - *P. paniscus*

Sources: Martin (1990), Swindler (1998), Fleagle (1999).

Natural History (Smithsonian Institution), Chicago Field Museum, and The Cleveland Museum of Natural History. Casts were also made of specimens in the collections of Dr Neil C. Tappen and Henry C. McGill.

The casting technique is relatively simple and provides permanent material for detailed study in the laboratory. All casts were poured within five to ten minutes after the impressions were made; this minimizes the possibility of dimensional change (Skinner, 1954). In addition, a study has shown that measurements taken on dental casts are directly comparable to measurements of the original teeth (Swindler, Gavan and Turner, 1963). The observed differences are more likely due to instrumentation than to dimensional change resulting from the dental materials. All casts were made by my assistants and myself.

The original specimens were collected for the respective museums and come from many different geographic areas of the world. In the majority of cases, species are represented from a wide range within their normal geographic range, although in certain groups, e.g. *Papio cynocephalus,* the animals were collected from a more limited area and may well approximate an interbreeding population. *Macaca mulatta* specimens from Cayo Santiago, Puerto Rico were used as well as *M. nemestrina* from the Regional Primate Research Center at the University of Washington. Unfortunately, several species were represented by only a few specimens, or in one or two cases, by a single specimen. This usually meant that these species were rare in museum collections and because of constraints of money and time, it was impossible to increase the sample. Also, the manner in which specimens were collected in the field influenced the randomness of a sample and anyone who has used museum collections is quick to realize this fact. There are obviously other biases in such a collection of specimens (ca. 2000) as studied in this book. However, since the principal objective of this work is to describe the normal dentition and present a statement of the range and magnitude of dental variability within the major genera and species of extant primates, the influences of these unavoidable biases should be mitigated.

The sex of the animals was determined in the field at the time of collection and any specimen of doubtful sex was excluded from the study. In the analytical descriptions in each section of the book the sexes are pooled unless otherwise stated.

The illustrations of the upper and lower teeth of all of the species in the book, unless otherwise stated, were drawn by Dr Robert M. George, Department of Biology, Florida International University, Miami, Florida. The number in millimeters (mm) that appears in the caption of each illustration represents the length of the maxillary arch of the original specimen measured from the mesial surface of the upper central incisors to a line perpendicular to the distal surfaces of the maxillary third molars or, in the callitrichids, the second molars.

Odontometry

All tooth measurements were taken with a Helios caliper. The arms were ground to fine points for greater accuracy. Mesiodistal and buccolingual dimensions of maxillary and mandibular teeth were taken. In all odontometric calculations, the sample size (n) refers to the number of animals measured. This procedure is more realistic than presenting the number of teeth measured since it is well known that there are very few significant differences between the dimensions of right and left teeth. The right side is presented here; however, if a tooth was badly worn or absent its antimere was used. Also, teeth exhibiting noticeable wear were excluded. It should also be mentioned that in many cases the n presented in Appendix 1 differs from the number of animals studied in the morphological section for a given species. This is due to the fact that in many cases the teeth could be examined for a particular morphological trait, yet were too worn to measure, or vice versa.

Repeated measurements taken on the same teeth revealed an average difference between measurements of 0.2 mm. The teeth were measured by

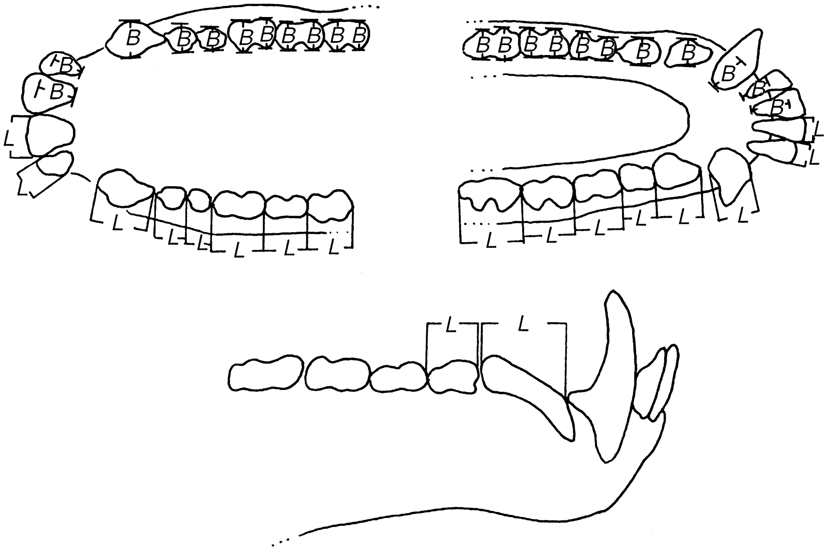


Fig. 1.1. Odontometric landmarks. B, breadth; L, length. Reprinted from Swindler, D. R. (1976) *Dentition of Living Primates*, with the permission of Academic Press Inc. (London) Ltd.

the author and research assistants, each of whom was trained by the author. The measurements are shown in Fig. 1.1 and are defined as follows.

Incisors

LENGTH. Mesiodistal diameter taken at the incisal edge of the upper and lower incisors.

BREADTH. Buccolingual diameter taken at the cementoenamel junction at a right angle to the mesiodistal diameter.

Canines

LENGTH. Upper canine: diameter from the mesial surface to the distolingual border. Lower canine: mesiodistal diameter measured at the level of the mesial alveolar margin.

BREADTH. Buccolingual diameter taken at the cementoenamel junction at a right angle to the mesiodistal diameter.

Premolars

LENGTH. Maximum mesiodistal diameter taken between the contact points. If the mesial contact is lacking on P^3 or P_3 owing to a diastema between it and the canine, the maximum horizontal distance is measured from the distal contact point to the most mesial point on the surface of the premolar. The same method is used on primates with three premolars, for example, P^2 or P_2 are measured as described above for P^3 and P_3.

BREADTH. Maximum buccolingual diameter taken at a right angle to the mesiodistal diameter.

Molars

LENGTH. Maximum mesiodistal diameter taken on the occlusal surface between the mesial and distal contact points.

BREADTH. Maximum buccolingual diameter measured at a right angle to the mesiodistal dimension. The breadths of both the trigon (trigonid) and the talon (talonid) were taken in this manner.

Statistical calculations for means and standard deviations (s.d.) were performed for the dental measurements of each species by sex. Hypotheses of equality of means between sexes of each species, where the samples were large enough, were tested by using the appropriate small sample *t*-test statistic (Sokal and Rohlf, 1969). The results of the *t*-tests for sexual dimorphism are presented for each species in the odontometric tables in Appendix 1.

Dental terminology

The incisors and canines are known as the anterior teeth; premolars and molars are the posterior teeth (Fig. 1.2). The tooth surfaces facing toward the cheek are called the buccal surfaces (odontologists often distinguish between the buccal and labial surfaces, labial being limited to the incisor and canine surfaces facing the lips, i.e. labia). All surfaces facing the tongue are referred to as lingual. The mesial (anterior) surface of a tooth faces toward the front of the oral cavity; those more distant are called the distal (posterior) surfaces. A cusp is defined as having structural or functional occlusal areal components delimited by developmental grooves and having independent apexes. The principal cusps, conules and styles, as well

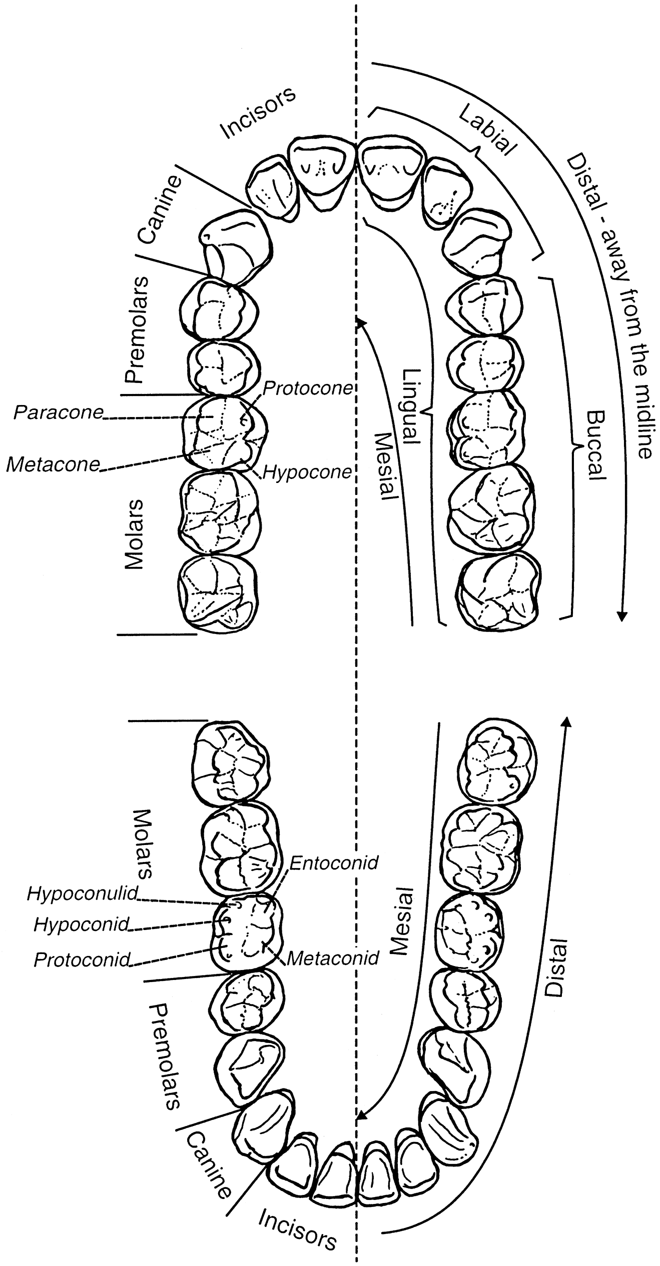


Fig. 1.2. The permanent upper and lower dental arches of the gorilla, with cusp terminology and terms of position within the oral cavity. Drawn by Linda E. Curtis.

as the functionally important crests connecting them in various ways on the occlusal surfaces, have had different names through the years. Since there is still frequent confusion regarding dental terminology in the literature, the terms used in this book as well as some of the more common synonymies are presented in Table 1.2.

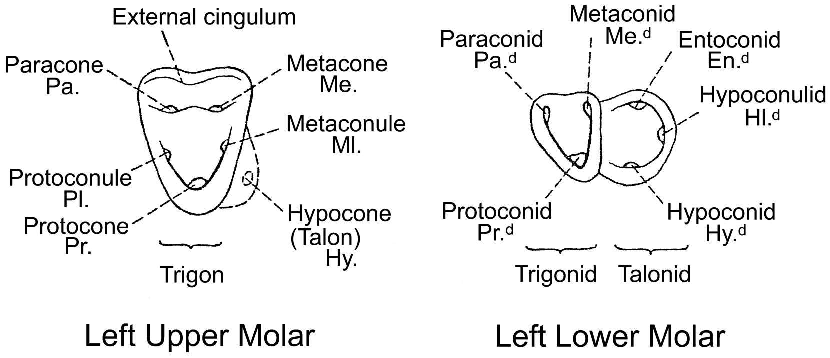
Many of the terms presented in Table 1.2 were suggested in the late nineteenth century for the cusp names of mammalian molar teeth by E. D. Cope (1888) and H. F. Osborn (1888). This terminology was based on their interpretation of the origin of the tritubercular upper and lower mammalian molar patterns that became known as the Tritubercular Theory. As mentioned, other terms have been proposed for the major cusps through the years, but the original names are so well entrenched, and their weaknesses and strengths so well recognized and understood by odontologists, that I have used them in this book. This is often referred to as the Cope–Osborn nomenclature for the principal cusps of mammalian molars (Fig. 1.2). For other views on the fascinating subject of the evolution of mammalian molars and the naming of the principal cusps, one should read the contributions of Vandebroek (1961) and Hershkovitz (1971).

Today it is known that the reptilian single cusp of the upper jaw is the paracone, not the protocone as thought by Cope. After the evolution of the protocone the molars evolved into a triangular pattern which Simpson (1936) termed tribosphenic (from the Greek *tribein,* to rub; *sphen,* a wedge), which better describes the grinding functions of the protocone and talonid basin along with the alternating and shearing action of the trigon and trigonid (Fig. 1.3). The upper molar is a three-cusped triangle, formed by the paracone, metacone, and protocone, known as the trigon (Fig. 1.3). The hypocone appears later and is added to the distolingual surface of upper molars forming the talon (Fig. 1.3). The lower molar has a trigonid (*-id* is the suffix added to the terms of all lower teeth) consisting of the paraconid, metaconid and protoconid (note, protoconid is the correct designation for the original cusp of the reptilian lower molars). In the majority of extant primates, with the exception of *Tarsius,* the paraconid is absent. The talonid develops on the distal aspect of the trigonid and often bears three cusps, hypoconid, entoconid, and hypoconulid (Fig. 1.3). A cingulum (cingulid) girdled the tribosphenic molar and portions of it may be present on the teeth of extant primates. When present, these structures are known as styles (stylids) and are named for their related cusp, e.g., paracone (parastyle). The molars of all extant primates are derived from the tribosphenic pattern; indeed, all living mammals, with the exception of monotremes, are descended from Cretaceous ancestors with tribosphenic molars (Butler, 1990). This has been the accepted theory of mammalian

Table 1.2. *Tooth nomenclature*

This book	Synonymy
Upper teeth	
Paracone (O)	Eocone (Vb)
Protocone (O)	Epicone (Vb)
Metacone (O)	Distocone (Vb)
Hypocone (O)	Endocone (Vb)
Metaconule (O)	Plagioconule (Vb)
Protoconule (O)	Paraconule (Vb)
Distoconulus (R)	Postentoconule (H)
Parastyle (O)	Mesiostyle (Vb)
Mesostyle (O)	Ectostyle-1 (H)
Metastyle (O)	Distostyle (Vb)
Distostyle (K)	—
Carabelli cusp	Protostyle (O)
Postprotostyle (K)	Interconule (R)
Preprotocrista (VV)	Protoloph (O)
Crista obliqua (R)	Postprotocrista (VV)
Entocrista (H)	—
Premetacrista (S)	—
Postmetacrista (S)	—
Trigon basin (S)	Protofossa (VV)
Lower teeth	
Paraconid (O)	Mesioconid (Vb)
Protoconid (O)	Eoconid (Vb)
Metaconid (O)	Epiconid (Vb)
Entoconid (O)	Endoconid (Vb)
Hypoconid (O)	Teloconid (Vb)
Hypoconulid (O)	Distostylid (Vb)
Mesiostylid (Vb)	—
Ectostylid (K)	—
Protostylid (K)	Postmetaconulid (H)
Tuberculum intermedium (R)	Postentoconulid (H)
Tuberculum sextum (R)	Protolophid (VV)
Protocristid (S)	Premetacristid (H)
Cristid obliqua (S)	—
Postentocristid (H)	Paralophid (VV)
Paracristid (S)	—
Postmetacristid (S)	—
Trigonid basin (S)	Prefossid (VV)
Talonid basin (S)	Postfossid (VV)

Sources: H, Hershkovitz (1971); K, Kinzey (1973); O, Osborn (1907); R, Remane (1960); S, Szalay (1969); Vb, Vandebroek (1961); VV, Van Valen (1966). Reprinted from Swindler, D. R. (1976) *Dentition of Living Primates*, with permission of Acadmic Press Inc. (London) Ltd.



Left Upper Molar

Left Lower Molar

Fig. 1.3. The generalized upper and lower mammalian molar pattern. Reprinted from Simpson, G. G. (1937). The beginning of the age of mammals, *Biological Reviews of the Cambridge Philosophical Society* **12**, 1–47, Fig. 11, p. 28. Reprinted with the permission of Cambridge University Press.

molar evolution until recently. The discovery of new pre-Cretaceous fossils with fully developed tribosphenic molars challenges the current idea concerning the timing of divergence of the main extant mammalian groups. It now appears that there may have been a dual origin of the tribosphenic molar (Luo, Cifelli and Kielan-Jawarowska, 2001). According to their hypothesis, a lineage with a tribosphenic molar radiated in southern Gondwanaland, giving rise to monotremes. The other lineage with a tribosphenic molar, evolved in the northern landmass of Laurasia, into the marsupials and placental mammals of today. This new paradigm will certainly engender controversy until it is either accepted or rejected. The evolutionary significance of the tribosphenic molar was clearly stated by Simpson (1936, p. 810) when he wrote ‘This is the most important and potent type of molar structure that has ever been evolved.’

One of the most comprehensive studies of the evolution of primate teeth still remains *The Origin and Evolution of the Human Dentition* (1922) by William King Gregory. Of course, this book is dated; however, it still contains much of interest to all students of primate dental evolution.

The original permanent mammalian dental formula was:

$$I^3\text{-}C^1\text{-}P^4\text{-}M^3 / I_3\text{-}C_1\text{-}P_4\text{-}M_3 \times 2 = 44$$

The majority of early primates had lost one incisor, and by the Eocene, premolar reduction had begun. The first (central) incisor is usually considered the missing member of the group and premolar reduction occurs from mesial to distal as explained below.

Primates have two sets of teeth, deciduous (also known as milk or primary) and permanent. The deciduous teeth, incisors, canines, and premolars emerge into the oral cavity before the permanent incisors, canines, and premolars that replace them, while the permanent molars emerge distally to the deciduous teeth (Chapter 3). The number and class of teeth in each quadrant of the jaw can be written for both deciduous and permanent teeth as a dental formula:

$$\mathrm{di}^2\text{-}\mathrm{dc}^1\text{-}\mathrm{dp}^2 \,/\, \mathrm{di}_2\text{-}\mathrm{dc}_1\text{-}\mathrm{dp}_2 \times 2 = 20$$

$$\mathrm{I}^2\text{-}\mathrm{C}^1\text{-}\mathrm{P}^2\text{-}\mathrm{M}^3 \,/\, \mathrm{I}_2\text{-}\mathrm{C}_1\text{-}\mathrm{P}_2\text{-}\mathrm{M}_3 \times 2 = 32$$

In this example, the formulas represent the deciduous and permanent dentitions of all catarrhine primates. A question arises regarding the designation of the deciduous cheek teeth. Since these teeth are actually the deciduous third and fourth premolars of other mammals and are replaced by the permanent third and fourth premolars, they should be called deciduous premolars (Delson, 1973; Hillson, 1996). However, the terms of human dentistry have not included mammalian dental evolutionary theory and have generally prevailed through the years. A similar issue exists regarding the permanent premolars: as noted above, there were originally four premolars in each quadrant of ancient mammalian jaws, but in all living primates, at least the first premolar has been lost. Hence, most prosimians and all platyrrhines have three premolars. Some genera have also lost more than one. A second premolar has been lost in all catarrhines. The remaining permanent premolars then are properly identified as P2, P3 and P4 or P3 and P4; however, traditional dentistry refers to them as P1 and P2. The zoological terminology is used in this book.

2 *Dental anatomy*

Anatomy

A typical mammalian tooth (Fig. 2.1) consists of a crown formed of enamel that covers the exposed, oral portion of the tooth. The principal mass of a tooth is composed of dentine, which is covered by the protective enamel crown; cementum surrounds the dentine of the tooth root. The central portion of the tooth is the pulp made up of soft tissues containing blood vessels and nerves which enter the tooth through the apical foramen. The mammalian tooth has a crown, cervix (neck), and root; this structure results from the way the tooth attaches to the jaw (Peyer, 1968). In most mammals, and all primates, the tooth root is anchored in a bony alveolus by a suspensory ligament, the periodontal ligament, which forms a fibrous joint known as a gomphosis. The bony alveolus covers the root up to the region of the cementoenamel junction, that is, the neck or cervical portion of the tooth. According to Peyer (1968), the neck is present only if its diameter is smaller than the crown. This definition eliminates the teeth of non-mammals and some mammals, but includes the teeth of all primates.

We have seen that primate teeth can be separated on the basis of form, position, and function into incisors, canines, premolars, and molars. This is a heterodont dentition and can be contrasted with a homodont dentition where the teeth consist of a single cusp that is similar in shape from incisors to molars, as for example, those found in many sea mammals. In primates, the upper incisors are generally chisel-shaped cutting and nibbling teeth; the lower incisors in most prosimians form a dental comb consisting of procumbent (extending forward from the lower jaw) incisors and canines, if present. Primate upper and lower canines are cone-shaped piercing teeth except in those prosimian genera where the lower canines join the incisors to form the dental comb. Premolars are transitional teeth situated between the anterior cutters and piercers and the posterior grinders and may have one to multiple cusps. In some species, there is a tendency for the most anterior premolar to become caniniform, and the most posterior premolar may be molariform. The molars possess anywhere from three to five major cusps. The premolars and molars, often called cheek teeth, form the main

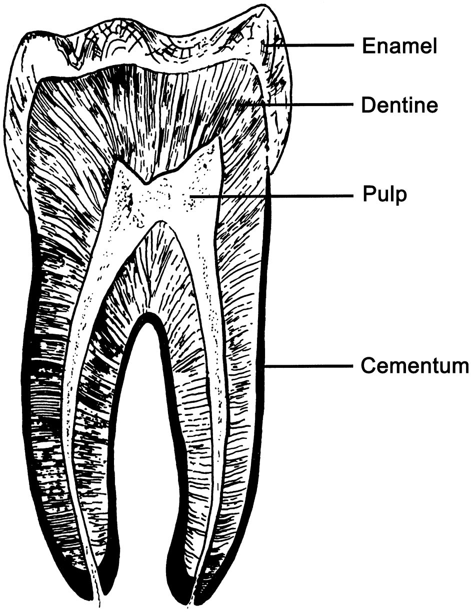


Fig. 2.1. The components of a mammalian tooth. Reprinted from Swindler, D. R. (1998) *Introduction to the Primates*, with permission of the University of Washington Press.

crushing and grinding teeth. There is recent evidence, however, suggesting that these terms do not describe what teeth do and that 'Such terms are members of a large family of words that simply denote fracture and, by masquerading as explanation, have stunted the understanding of how teeth work' (Lucas and Teaford, 1994, p. 183; see below and Chapter 4).

Mammalian molars display a variety of shapes and forms adapted for mastication. Although primate molars never express some of the extreme conditions seen in other mammals, the following terms are useful in describing their morphology. Molar crowns that tend to be wide and low are brachydont, whereas a hypsodont molar possesses a relatively high crown. When molars have separate, low, and moderately rounded cusps they are termed bunodont. If the cusps are aligned in linear ridges either transverse or oblique to the long axis of the occlusal surface the tooth is said to be lophodont. A final cusp arrangement, not found in primates, results when the cusps expand into crescents forming a selenodont molar, as found in deer, goats, and sheep.

A useful method enabling odontologists, particularly paleoanthropologists, to identify isolated teeth is to proceed in the following order. First, establish whether the tooth is deciduous or permanent (*set* trait); second, decide whether it is an incisor, canine, premolar, or molar (*class* trait); third, establish whether it is a maxillary or mandibular tooth (*arch* trait); and fourth, determine its position, e.g. first, second or third permanent molar (*type* trait). Because this book is concerned primarily with the teeth of non-human primates, there are also differences among families, genera, and species that will be discussed in later chapters.

Enamel

The tooth crown is covered with a normally smooth layer of enamel that is semi-translucent, varying in color from a light yellow to a grayish white. Enamel is the hardest biological structure in an animal's body, varying from 5 to 8 on the Mohs scale of hardness of minerals, where talc is 1 and diamond is 10. Enamel attains its full thickness before the teeth emerge into the oral cavity. Enamel is thicker over the cusps of unworn permanent premolars and molars, thinner around the cervical region. Deciduous teeth have thinner enamel than permanent teeth and may be slightly whiter.

Mature enamel is mostly inorganic calcium phosphate, about 96%, and belongs to the hydroxyapatite mineral group, which is found only in mammalian tissues (Hillson, 1996). Enamel formation is initiated along the dentinoenamel junction (Fig. 2.2) between the ameloblasts (enamel-forming cells) and odontoblasts (dentine-forming cells) when the latter commence to secrete predentine, which, in turn, almost immediately stimulates the ameloblasts to secrete the enamel matrix. It is interesting to note that enamel will not form in the absence of odontoblasts. Transplanted ameloblasts fail to form enamel unless accompanied by odontoblasts. The process begins at the incisal or cusp tips and proceeds down along the sides of the tooth. Soon after enamel matrix formation begins, inorganic calcified crystals appear, indicating the beginning of calcification. Thus, enamel formation involves matrix secretion followed by maturation. Enamel forms incrementally, reflecting the speeding up and slowing down of enamel secretion, and the closer the enamel layer is to the surface of the crown the more mineralized (denser) it becomes.

The basic histological structure of mammalian enamel is calcified rods or prisms that extend from the dentinoenamel junction to the external surface of the tooth. Enamel prisms have received a great deal of attention through the years because they appear in three patterns that may differ among primates and thus have proved useful for taxonomic allocations

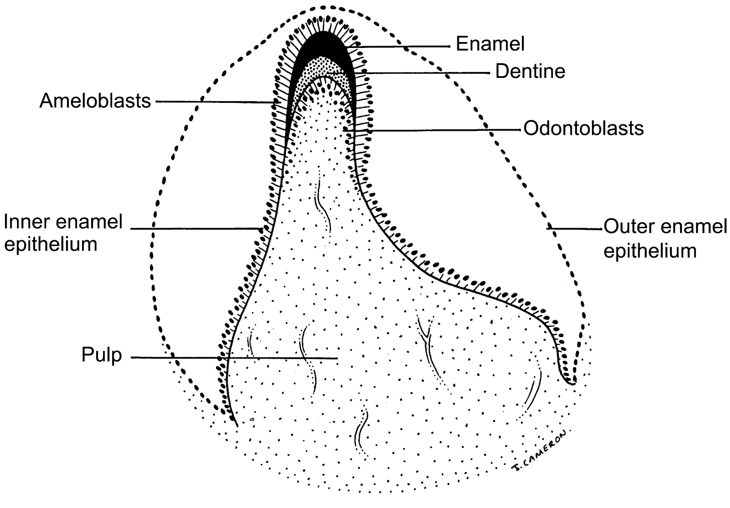


Fig. 2.2. Tooth germ showing formation of enamel and dentine. Reprinted from Aiello, L. and Dean, C. (1990) *An Introduction to Human Evolutionary Anatomy*. Reprinted with the permission of Academic Press.

(Boyde, 1976; Boyde and Martin, 1984; Gantt, 1982, 1986; Martin, 1985; Hillson, 1996). The three major shapes or patterns of prism cross-sections have been identified by Boyde (1969, 1976). These are: pattern 1, round closed circular enamel prisms formed by medium-sized ameloblasts; pattern 2, prisms arranged in alternate rows with an open surface and formed by small ameloblasts; pattern 3, prisms keyhole-shaped and formed by the largest ameloblasts (Fig. 2.3). The three patterns have been found in all primates; however, patterns 1 and 3 are more common in hominoids, and pattern 2 seems to be more frequent in Old World monkeys (Aiello and Dean, 1990).

Other important structures in enamel are the striae of Retzius and incremental lines. The striae of Retzius are lines of light brown to near black when seen in transmitted light microscopy, which cross the prism boundaries in arc-like layers beginning at the dentinoenamel junction and terminating at the enamel surface. The regular striae of Retzius are formed incrementally and are associated with surface perikymata. They vary in periodicity among primates during odontogenesis from 3 days in *Victoriapithecus* to 9 or 10 days in humans and great apes (personal communication, C. Dean). There are also other 'accentuated markings' that look like striae of Retzius but these result from various disturbances that occur during odontogenesis, however, they are 'crucial to histological studies of

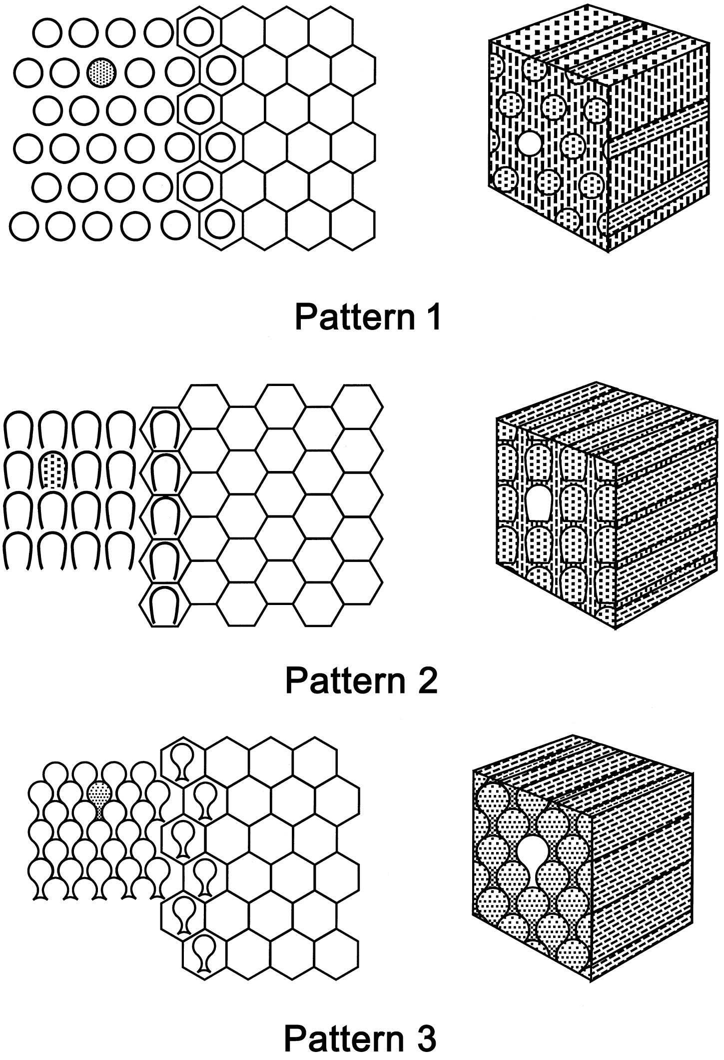


Fig. 2.3. Schematic illustration of prismatic enamel. Courtesy of David G.Gantt.

tooth growth since they mark both the internal structure and the surfaces of enamel (*perikymata*) and dentine forming at one time period' (Dean, 2000, p. 120, italics mine). Other lines, the incremental lines (known as short period lines or daily cross-striations) are visible between the long-period striae of Retzius when viewed with polarized light and other forms of microscopy (Dean, 1989, 2000). Cross-striations or varicosities represent the circadian rhythmic nature of the secretory cell cycle during enamel formation and appear as dark lines crossing the prisms. Although there is some debate regarding the nature of the cellular mechanisms controlling these circadian cycles 'these short-period incremental lines allow estimates of the linear daily secretion rate of enamel' (Schwartz and Dean, 2000, p. 214). Indeed, Dean (2000, p. 129) is hopeful that incremental lines, also found in dentine and cementum, along with 'New discoveries in developmental biology and evolutionary biology will eventually mean that we can ask more focused questions about the nature of the relationship between ontogeny and phylogeny.'

As we shall see in later chapters, enamel thickness varies a great deal among extant and extinct primates. Much evolutionary and taxonomic importance has been attached to the plethora of studies that have appeared during the past several decades (Martin, 1985; Shellis *et al.*, 1998). Because teeth are the primary organs responsible for reducing a wide variety of foods with different physical properties to digestible particles during mastication, it is understandable that there have been so many studies of primate enamel thickness. There is no doubt that primate taxa feeding on hard objects have relatively thicker enamel than taxa feeding on softer substances, but what is important to remember taxonomically is that these taxa may none the less be closely related (Dumont, 1995). What is becoming ever more clear to students studying the causal relation between tooth form and function is clearly stated by Strait (1997, p. 199): 'The physical properties of the foods that teeth encounter during mastication may be the primary factor affecting changes in dental morphology.' Indeed, this was appreciated by Lucas and Teaford (1994, p. 183) when they wrote 'The first step toward understanding dental-dietary adaptations is to consider the fracture properties of foods, because it is to these that teeth are ultimately adapted.' In addition, as we study primate teeth it will be well to remember that the endurance of a tooth can be extended by having thicker enamel or increasing the size of the tooth (Lucas, Corlett and Luke, 1986a). Variations in enamel thickness among primates will be considered further in the chapters on the different primate taxa.

There are several types of enamel defect present in primate teeth (Brook, 1998). One important defect is enamel hypoplasia, a deficiency of enamel thickness, which occurs during the secretory phase of amelogenesis (Goodman and Rose, 1990; this is also an excellent review of enamel hypoplasias in humans, as is the recent contribution of Guatelli-Steinberg and Lukacs (1999) for non-human primates). Enamel hypoplasias may be expressed in several ways, e.g. pits, single sharp horizontal lines, single grooves or furrows in the crown surface (Hillson, 1996; Hillson and Bond, 1997; Guatelli-Steinberg, 2000). Reid and Dean (2000) have also presented new methods for estimating the timing of linear enamel hypoplasia (LEH) in the anterior teeth of humans. Although used for years as an indicator of non-specific systemic stresses during crown development in humans, studies of enamel hypoplasia have a rather checkered history among non-human primates (Guatelli-Steinberg and Lukacs, 1999; Guatelli-Steinberg, 2000). The term linear enamel hypoplasia (LEH) is generally used to designate faint or deeper lines or grooves on the surface of a tooth crown (Goodman and Rose, 1990; Guatelli-Steinberg, 2000) and this is the definition accepted here. The defect forms due to a physiological stress, e.g. disease or poor nutrition, that disturbs enamel matrix formation, resulting in a deficiency of enamel thickness. In contrast to bone, enamel does not remodel, and once formed, the defect is permanently implanted in the enamel.

The most comprehensive studies and reviews of the prevalence and incidence of LEH in non-human primates are those of Guatelli-Steinberg (1998; Guatelli-Steinberg and Lukacs, 1999; Guatelli-Steinberg and Skinner, 2000). More details relating to the occurrence and frequency of LEH among different primate taxa will be considered in the general dental information sections of later chapters.

Dentine

Dentine (ivory) is not as mineralized as enamel, therefore it is softer than enamel but harder than bone. Dentine makes up the bulk of a tooth and its root. It is composed of collagen and hydroxyapatite and is more compressible and elastic than enamel. It is covered by the enamel crown. Cementum surrounds the root (Fig. 2.1). As with enamel, dentine formation occurs in two stages, organic matrix secretion and mineralization. Dentine tubules containing odontoblasts transverse the dentine from the dentinoenamel junction and dentinocemental junction to the pulp chamber.

It is also well known that during dentine formation the various systemic rhythms that affect the development of enamel result in incremental lines in dentine (Dean, 2000). In contrast to ameloblasts, odontoblasts remain capable of being productive throughout their lives. After the completion of tooth growth they produce secondary dentine. As enamel wears down during attrition, the production of secondary dentine increases, recognizable as small areas of dark tissue on the occlusal surface. Eventually, it may form the entire occlusal surface of the tooth. The presence of secondary dentine protects the pulp chamber from exposure as enamel is worn away.

Another physiological product of the odontoblasts is a hypermineralized form of dentine containing few, if any, collagen fibers, known as peritubular dentine. More than fifty years ago Gustafson (1950) and later Miles (1963) noted that, in ground sections of teeth, the roots tend to become more translucent in older teeth, which can be useful in estimating the approximate age of an individual. This transparency or sclerosis is due to the peritubular dentine matrix that continues to form as teeth get older. It is interesting to note that Drusini, Calliari and Volpe (1991), using an image analyzer, did not find any difference between this method and that of measuring the transparent area directly on tooth sections.

We have mentioned a few of the many investigations of the microstructure of enamel in the last several decades that have aided in sorting out some of the knotty problems in primate systematics of both extinct and extant primates, and considered their usefulness in establishing criteria for better understanding their growth, development, and maturation. For one reason or another, investigation of the microanatomy of dentine has not kept pace with that of enamel, although the importance of dentine for daily incremental studies has been known since Schour and Hoffman (1939) (reported in Dean (1993)) as has the probable taxonomic significance of dentine organization (Hildebolt *et al.*, 1986). In the study by Dean (1993 p. 199) he found that the daily rates of dentine formation on macaque tooth roots were consistently between 3 and 4 μm per day, suggesting 'a consistent rate of dentine formation in permanent macaque teeth.' Hildebolt *et al.* (1986, p. 45) studied dentine tubule density and patterning among *Canis, Papio* and *Homo*; allowing for the small sample sizes, the authors concluded that 'dentine does have important taxon-specific structural characteristics that are of use in phylogenetic and taxonomic studies.'

Cementum

Cementum develops over the root dentine and generally extends around the enamel at the cervix. Cementum is produced by cementoblasts that form two types of cementum, cellular and acellular. Cellular cementum is less hard than enamel or dentine, being more similar to bone except that it does not resorb and reform, rather, it grows by apposition, layer by layer. Remodeling can occur, however. When cementum is destroyed by odontoclasts, cementoblasts can repair the damaged areas (Hillson, 1996). Since cementum surrounds the tooth root, fibers of the periodontal ligament pass from the alveolar bone to attach to the cementum in helping to support the tooth in its alveolus. Cementum adds to the size and strength of a tooth as well as protecting the underlying dentine.

Cementum lines or annuli have proven useful as a means of estimating chronological age in primates (Wada, Ohtaishi and Hachiya, 1978; Yoneda, 1982; Kay *et al.*, 1984). As noted by Kay *et al.* (1984) there are still several questions regarding the interpretation of cementum annuli for age estimations. These and related problems are considered more thoroughly by Hillson (1996) and Dean (2000).

Tooth roots

Primate teeth usually have one, two, or three roots, although there may be extra or reduced root formation in most classes of teeth. In general, root reduction is more common than root increase, although both variations of root numbers have been reported for most classes of primate teeth (Bennejeant, 1936; Remane, 1960; James, 1960; Alexandersen, 1963; Miles and Grigson, 1990). An unusually high incidence (40%) of two-rooted maxillary canines in female *Macaca fuscata* was described by Yoshikawa and Deguchi (1992). All males had single roots. Two-rooted maxillary and mandibular canines have been reported in primates (De Terra, 1905; Alexandersen, 1963), but evidently it is quite rare (Swindler, 1995).

Roots begin to develop after enamel and dentine have reached the future cementoenamel junction. At this time the epithelial root sheath is formed, which, in turn, initiates root formation. The root consists of the pulp cavity surrounded by dentine and cementum. On occasion, cells of the epithelial root sheath may form ameloblasts and produce droplets of enamel between or on the surface of the roots. These are known as 'enamel pearls'.

Dental pulp

Dental pulp occupies the pulp cavity and is surrounded by dentine (see Fig. 2.1). Pulp consists of a variety of tissues among which are arteries and veins, nerves, and lymphatic vessels that become more fibrous and less vascular with age. These structures enter and leave the tooth through the apical foramen situated at the tip of the root. The pulp projects toward the cusps of multicusped teeth and is known as pulp horns. When pulp is exposed, whatever the cause, the result is severe pain.