

15 'Schultz's Rule' and the evolution of tooth emergence and replacement patterns in primates and ungulates

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15.1. Introduction

Paleontologists often reconstruct the sequence of eruption of teeth of fossil mammals (e.g., Stehlin, 1912; Gregory, 1920; Kellogg, 1936; Lamberton, 1938; Tattersall and Schwartz, 1974; Wallace, 1977; Kay and Simons, 1983; Gingerich, 1984; Lucas and Schoch, 1990; Smith, 1994; Martin, 1997). Evolutionary studies, however, have contradictory traditions about the meaning of such sequences. One tradition is that sequence of tooth eruption is a good phylogenetic character, capable of showing genetic relatedness among species (e.g., Tattersall and Schwartz, 1974; Schwartz, 1974; Byrd, 1981), and thus presumably non-adaptive or conservatively adaptive. A second school of thought is that sequence of eruption is an adaptive characteristic: either reflecting dental morphology (e.g., Slaughter *et al.*, 1974), facial architecture (Simpson *et al.*, 1990), or life history (Schultz, 1935, 1956). Indeed Schultz saw the eruption sequence of teeth as highly adapted to rate of post-natal growth. The obvious question is, does sequence of tooth eruption inform us of species taxonomic affiliation, dental function, facial form, or life history? One approach to the question is to re-examine Schultz's hypothesis on the adaptive nature of tooth eruption sequence. Here, Schultz's ideas are tested against newly gathered data on primates and ungulates, with a few additional data on small insectivorous mammals.

15.2. The dentition in a life-history context

Reptiles tend to grow throughout life, changing prey, and prey size slowly over time (Dodson, 1975). To keep

pace with growth and changing diet, reptiles erupt multiple waves of simple, ever-larger teeth (see Chapter 13). Mammals, however, share a system of tooth emergence and replacement that accommodates rapid growth to a fixed body size (see Pond, 1977; MacDonald, 1984). Fixed body size probably allowed mammals to evolve a lasting adult dentition with heterodont teeth that occlude in a complex manner (see Zeigler, 1971; Osborn and Crompton, 1973). The small mammalian neonate, however, still must eat through a considerable size transition. To do this, eutherians (placental mammals) form small 'primary' or 'deciduous' teeth in utero, teeth which erupt around the time of birth in precocial mammals or after birth in altricial mammals (Smith *et al.*, 1994). Most eutherians learn to eat with these teeth while still supplemented with mother's milk. Larger, sturdier 'secondary' or 'permanent' teeth appear later, including molars that fill in the back of the jaws and replacements that erupt underneath deciduous teeth. Metatherians (marsupial mammals) probably once shared this strategy, but subsequently reduced tooth replacement to a single tooth in each quadrant (Luckett, 1993; Cifelli *et al.*, 1996; Martin, 1997), coping with early growth stages by intense lactation (Pond, 1977). For marsupial or placental, however, development and appearance of teeth must be coordinated with growth. Mammals must have teeth to be weaned and the permanent teeth that erupt must be able to acquire, prepare, and chew adult food for a lifetime.

The order of emergence of mammalian teeth is highly patterned and a tiny fraction of theoretically possible variants appear in life. In eutherians, the entire deciduous set is typically erupted, sometimes with the exception of the first premolar (see below), before permanent teeth appear. First molars are very commonly the first

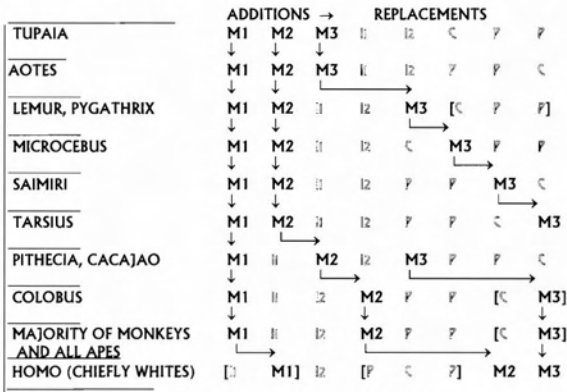


Figure 15.1. Diagrammatic representation of the sequence of eruption of the permanent teeth in primates, redrawn from Schultz (1956, Figure 20). Replacement teeth are shown in light outline font to emphasize molar progression. Parentheses indicate that the particular teeth enclosed vary in position. Arrows follow progress of molars to later positions in sequence across the primate *scala naturae*.

permanent tooth to emerge. Molars emerge from front-to-back and no mammal species, where tooth identification is clear, is known to alter this order. Other teeth also tend to a front to back appearance, although there are exceptions (see Ziegler, 1971; Osborn and Crompton, 1973). Eruption order is similar in the maxilla and mandible, but not identical, often with the mandibular tooth emerging slightly ahead of its maxillary isomere. Beyond these similarities, however, there is real variation to explain. In extant mammals, incisors tend to emerge together and premolars tend to emerge together, but this seems not to be the case in early mammals (see Martin, 1997). And although the permanent dentition most often begins with the first molar, it may end with any tooth, an incisor, canine, premolar, or molar, varying even among closely related species.

It is worth keeping in mind that the fundamental mammalian plan of tooth number, kind, and replacement evolved in some particular species which possessed some particular life history strategy and dento-facial morphology. Early eutherians were small, presumably rapidly growing, and had long dentaries with 11 tooth positions per quadrant (three incisors, one canine, four premolars, and three molars). Many lineages subsequently evolved larger body size, slower growth, shorter faces, and reduced tooth number. Mammals at extremes of body size or environment, notably the shrews, some bats, rodents, elephants, and sea mammals, greatly altered teeth and tooth replacement. Many lineages, however, including primates, ungulates, carnivores and larger insectivores continued to maintain fairly generalized eruption and replacement of teeth. Paradoxically, the breadth of mammals retaining a primitive system of

eruption and replacement testifies both to the flexibility and conservatism of the system.

15.2.1. Schultz's hypotheses

Adolph Schultz (1935) and others (Krogman, 1930; Bennejeant, 1936) clarified the basic outline of tooth eruption in primates and left us with a much simplified arena for testing hypotheses. Schultz (1956, 1960) went furthest to find meaning in sequence of eruption, proposing a very limited pattern that varied in a regular way across primates.

To understand eruption sequence (Figure 15.1), Schultz contrasted molars (M1–M3), which are 'additions' to the deciduous dental arch, with 'replacement' teeth, the permanent incisors, canines and premolars that replace deciduous predecessors. When permanent teeth are so divided, primates showed a striking pattern across the *scala naturae* (Figure 15.1): at top, *Tupaia*, the tree shrew (then classified with primates) erupts all three molar teeth before replacing any deciduous teeth. Moving to slower-growing, longer-lived primates, molars scatter to later and later positions, but little else changes in the progression. Humans, particularly 'white' populations, are shown with a particularly extreme sequence in which M1 is no longer the first permanent tooth to erupt and the two other molars are very last to emerge.

• Schultz himself was convinced of the underlying cause of the trend: 'There can be little doubt that these ontogenetic specializations represent necessary adaptation to the gradual prolongation of the period of post-natal growth' (Schultz, 1960:13). On one point, however, his illustration overpowered the text. The dashed-in molar progression strongly suggests that primates are characterized by late molar appearance. The accompanying text, however, proposes that long life places an extra load on deciduous teeth and that species adapt by replacing them relatively early. Thus, Schultz's adaptive model might dash in, not the backward drift of molars, but a forward march of replacement teeth.

What I will call 'Schultz's Rule' is the tendency for replacing teeth to come in relatively early in slow-growing, longer-lived species. My first task is to try to replicate Schultz's observations on primates, and the second, to test his explanation against other mammals. If 'Schultz's Rule' is a powerful one, it should apply to more than just primates.

15.2.2. An adaptive model

Figure 15.2 presents a simple model of tooth eruption sequence by contrasting rapidly and slowly growing mammals. In Figure 15.2A, the springbok *Antidorcas* erupts teeth in three sets: set 1 (deciduous), set 2 (molars), and set 3 (replacing teeth). In contrast, *Homo sapiens*

A. Rapidly growing mammal (*Antidorcas*):

-- set 1-- ----- set 2 ----- ----- set 3 -----
 iicppp M1 M2 M3 I I C P P

B. Slowly growing mammal (*Homo*):

← ----- set 3 -----
 -- set 1-- ----- set 2 -----
 iicpp I M1 I C M2 PP M3

Figure 15.2. Model of 'Schultz's Rule,' the adaptation of tooth eruption sequence to fast and slow growth. Very rapidly growing species (case A) erupts the three sets of teeth sequentially: deciduous teeth, molars, replacement teeth. As growth and development slows (case B), deciduous teeth wear out before growth is completed. Set 3 shifts to replace deciduous teeth relatively early and sets 2 and 3 become simultaneous. Little else changes.

(Figure 15.2B), replaces deciduous teeth before completing molar eruption. Although the *Homo* sequence appears to be quite different from that of *Antidorcas*, we can account for it by a simple shift of replacement teeth. Whereas *Antidorcas* erupts sets 2 and 3 sequentially, *Homo* erupts them simultaneously.

As Schultz suggested, the shift of replacement teeth may be related to growth rate and life span. *Antidorcas* is a small (34 kg) bovid that grows to adult size in about 2 years (Rautenbach, 1971; Nowak and Paradiso, 1983). In *Homo sapiens*, the slowest-growing mammal, however, some 20 years pass before the face can accommodate third molars. If humans followed the springbok pattern, deciduous teeth would have to function for some 20 years before replacement—far longer than their size and structure allow. One solution to the problem of slow growth would be to evolve larger deciduous teeth, but these teeth are formed in utero, presumably under some size constraint. A less costly solution is to shift the replacing set to a relatively early position.

The model in Figure 15.2 suggests that complexity of the human sequence (which switches back and forth between eruption of molars and replacement teeth) is superficial. The human sequence can be understood as a crossing over of sets of teeth adapting to different factors. In this view, the development of deciduous teeth and molars is primarily timed to match growth of the face, a relatively invariant adaptive problem. Development of replacement teeth, however, is on a sliding scale, adapting to demands on deciduous teeth.

Because early mammals were small and rapidly growing, Figure 15.2A or something close to it, is likely to be more 'primitive' in an evolutionary sense and Figure 15.2B is likely to be relatively 'advanced.' If tooth eruption is a functional system adapted to life history, we might expect to find a scattering of both 'primitive' and 'advanced' sequences through mammalian orders. Further, since the timing of events in life (e.g., age of maturation, life span) and the size of organisms (body weight, brain weight) are correlated (see Harvey and

Clutton-Brock, 1985), 'primitive' sequences might characterize small mammals and 'advanced' sequences characterize larger ones. Thus, if the simple model presented is a good one, extant species with identical eruption sequences may be only distant relatives.

15.3. Materials and methods

Sequences of eruption of mandibular permanent teeth are described in the Appendix for a series of extant mammals with fairly generalized dentitions.

15.3.1. Definitions

Defining eruption sequence is not easy, since sequences of calcification, initial movement, emergence through alveolus or gingiva, and completed eruption are not necessarily in agreement (Garn and Lewis, 1963; Schwartz, 1974). In dentistry and many primate studies, the marker of tooth eruption preferred for clarity and replicability is *appearance of any part of the cusp or crown through the gingiva*, usually called 'tooth emergence.' The sequences reported here are 'emergence sequences' as much as possible. This criterion is easily met for primates, although not so easily met for other orders. For ungulates, several stages of eruption were often described in original studies (e.g., tooth just above bone, mid-eruption, fully erupted). Since alveolar emergence can long precede gingival emergence for molariform teeth (Garn and Lewis, 1963), 'just above bone' was not taken as erupted. It was most helpful when studies noted whether teeth were faceted and in wear (e.g., Wallace, 1977; Kay and Simons, 1983).

15.3.2. Taxa

Emergence sequences of members of the orders Primates (12 species), Scandentia (1), and Soricomorpha (2) are contrasted with those of members of Artiodactyla (17), Perissodactyla (2), and Hyracoidea (1). The first group has

adaptive similarity but not taxonomic coherence, since Primates and Scandentia (grouped in the grandorder Archonta) may be only distant relatives of soricomorph insectivores. Group one is referred to here in an informal sense as 'primates/insectivores.' Group two consists of herbivorous hoofed mammals, all members of the grandorder Ungulata. Within orders, species chosen have complete data for all permanent mandibular teeth and span, as much as possible, the largest available range of body size within wild taxa. Domestic mammals are excluded because artificial selection is presumed to have altered life history. Only the mandible is studied because ruminant artiodactyls lack maxillary incisors.

Complete data and sources appear in the Appendix. Higher level taxonomy follows Eisenberg (1981); genus and species names follow Wilson and Reeder (1993) for ungulates and Smith *et al.*, (1994) for primates.

Within Primates, six of 11 families are known by complete data for gingival emergence sequence, but Calitrichidae are omitted here because members lack M3, an important tooth in patterns under investigation. For anthropoids, sequences are based on very substantial samples and fine-grained studies except for the leaf-eating monkey *Alouatta*, which is based on a single individual. Lemurids have been studied on a fine scale, but sample size is also small. Unfortunately, data for the smallest primates (e.g., *Microcebus*, *Tarsius*) are preferentially missing. Because comparable complete data could not be found for any tiny insectivorous primate, *Urotrichus* (the Japanese shrew mole, order Soricomorpha) and *Tupaia* (the tree shrew, order Scandentia) are substituted to give some representation to very quickly growing generalized mammals.

Within Artiodactyla, data were located for seven of eight families. No data were located for Tragulidae (chevrotains), the smallest living members of the order. The Camelidae is omitted here because extant members are domestic (camel, llama), have reduced tooth number (guanaco), or ever-growing incisors (vicuna). Within Perissodactyla, two of three families are represented, Equidae and Rhinocerotidae. The latter contains the slowest-growing ungulates besides the elephant, but is of limited diagnostic value because the family has eliminated all incisors, both deciduous and permanent. Data located for the Tapiridae (the tapir) were incomplete.

For ungulates, exceptional studies with excellent data include those of *Sus* (wild pig), *Tayassu* (peccary), and *Odocoileus* (white-tail deer), which are detailed, fine-scaled, and backed up by large numbers of subjects; studies of *Antilocapra* (pronghorn), *Bison*, and *Hemitragus* (tahr) are also very good. For other ungulates, data are of lower quality overall; data were sometimes sketchy, and some sequences had to be based on combinations of

observations of gingival emergence, radiographs of living individuals, and skeletonized individuals.

15.3.3. Methods

All data were taken from the literature, constructing sequences from original publications. The goal was to construct a gingival sequence of emergence, building a sequence of the order of teeth appearing through the gingiva and in wear. Sequences were compiled from (1) actual reports of sequences observed within individuals, and (2) mean ages of tooth emergence. The two methods (the most common sequence within individuals and sequences of means) are equivalent when samples are substantial and well spread out over juveniles (Smith and Garn, 1987). For three primate species, *Macaca nemestrina*, *Pan troglodytes*, and *Homo sapiens*, actual compilations of most likely sequences were available (Smith, 1994). Two sequences are given for *Homo sapiens*, from Australian Aborigine males and American white males, to represent the range of findings for human populations. When sexes differ (as in humans), male sequences were used.

15.3.4. Appendix

In the Appendix, special notation gives some extra information on variation, first premolars, and special dental adaptations: Whenever variants in sequence are known to be substantial, square brackets [] surround the tooth pair, following Schultz (1935). Parentheses () mark cases in which the actual order has not been determined, i.e., the teeth are 'tied.'

Only five extant taxa studied here possess a mandibular first premolar: *Sus*, *Hippopotamus*, *Equus*, *Ceratotherium*, and *Procavia*. These mammals, along with most others that retain a first premolar, typically erupt only a single tooth in this position, and it is unclear to which series the tooth belongs, deciduous or permanent. Kindahl (1967), Zeigler (1971, 1972), and Luckett (1993), all of whom considered the question over a range of mammals, allocate it to the deciduous dentition. Luckett (1993) regards *Tapirus* as the only unequivocal case in which a first premolar (upper jaw only) has two tooth generations. Extinct archaeocetes are thought to have a replacing permanent P1 in the mandible (Kellogg, 1936; Uhen, 1996), although the evidence is not unequivocal. In the Appendix, emergence of p1 appears if timing is known (it tends to appear between the deciduous and permanent dentitions or with M₁), but the tooth is dropped from further analysis.

Lemuroidea modified mandibular incisors and canine into a procumbent 'tooth comb,' which erupts as a unit (Eaglen, 1985). Here the tooth comb is represented as a unit labeled 'tc' since it is unlikely individual teeth could erupt separately.

Also in the Appendix, two life history variables appear alongside emergence sequences: age of emergence of the mandibular first molar (from Smith *et al.*, 1994) and life span (from Harvey and Clutton Brock, 1985 and Nowak and Paradiso, 1983). Age of M_1 emergence serves as an objective estimate of rate of postnatal growth: a low age of M_1 emergence indicates fast growth and a high age indicates slow growth. In primates, age at which M_1 erupts is highly associated with other measures of life history (Smith, 1989). In mammals studied here, emergence of M_1 ranges from about 1 month to over 6 years. Life span ranges from 11 to 100 years, although that of the little known *Urotrichus* may be much shorter.

For three genera with unknown age of M_1 emergence (the insectivore *Urotrichus*, the primate *Alouatta*, and the ungulate *Okapia*), post-natal growth rate was approximated by comparing other aspects of life history among species (Nowak and Paradiso, 1983). In one case (*Tupaia*), an unknown age of emergence of M_1 was estimated with some confidence. It is known that the entire permanent dentition erupts between about 1 and 3 months of age in *Tupaia* (Shigehara, 1980; Tsang and Collins, 1985; Hertenstein *et al.*, 1987). Further, it is likely that M_1 appears after completion of the deciduous dentition (day 27) and before males begin puberty (day 40–50). Data on 24 primate species (Smith *et al.*, 1994) were used to calculate an equation predicting age of M_1 emergence from age of completion of the deciduous dentition. The resulting equation predicts emergence of M_1 at day 31 in *Tupaia*, an estimate that fits well with other life history data for the genus.

15.3.5. Analysis

A glance at the appendix will show that complete sequences of tooth emergence are hard to evaluate. The first 'analysis' of data is simply to diagram sequences in a manner that brings out patterns in the data. Diagrams (see Figures 15.4–15.7) focus on seven non-canine teeth shared by almost all taxa (I1–2, P3–4, M1–3). Canines are discarded because they have heterogeneous special functions, sometimes featured in male–male competition and sometimes serving only as an extra incisor. The I₃ and P₂, teeth that disappeared in the evolution of many mammalian taxa, are shown, but are collapsed with the tooth emerging nearest in time. Further, numbers are stripped from incisors because I₁ and I₂ always emerge in that order in present data. Numbers are stripped from premolars to simplify comparison and premolar order is discussed separately. This notation amounts to a special language of reporting tooth eruption sequence, but it is a language that makes patterns clearer.

The second analysis quantifies aspects of sequence and looks for associations with age of M_1 emergence, life

| | | | | | | | |
|--------------------------|-----|-----|----|-----|-------|-----|----|
| <i>Urotrichus</i> | M1 | M2 | M3 | PP | P | I | |
| | ↓ | ↓ | ↓ | | | | |
| <i>Tupaia</i> 0.09? | M1 | M2 | M3 | PIP | I | P | I |
| | ↓ | ↓ | ↓ | | | | |
| <i>Lemur</i> 0.34 | M1 | M2 | | tc | P | PP | M3 |
| | ↓ | ↓ | | | | | |
| <i>Aotus</i> 0.36 | M1 | M2 | I | M3 | I | P | PP |
| | ↓ | ↓ | | | | | |
| <i>Saimiri</i> 0.37 | M1 | M2 | I | I | P | PP | M3 |
| | ↓ | ↓ | | | | | |
| <i>Eulemur</i> 0.42 | M1 | | tc | M2 | PM3 | P | P |
| | ↓ | | | ↓ | | | |
| <i>Varecia</i> 0.48 | M1 | | tc | M2 | PP | M3 | P |
| | ↓ | | | ↓ | | | |
| <i>Alouatta</i> | M1 | I | (I | M2) | PP | P | M3 |
| | ↓ | | | ↓ | | | |
| <i>Cercopithecus</i> 0.8 | M1 | I | I | M2 | P | P | M3 |
| | ↓ | | | ↓ | | | |
| <i>Cebus</i> sp. 1.1 | M1 | I | I | M2 | P | P | M3 |
| | ↓ | | | ↓ | | | |
| <i>Macaca</i> 1.4 | M1 | I | I | M2 | P | P | M3 |
| | ↓ | | | ↓ | | | |
| <i>Papio</i> 1.6 | M1 | I | I | M2 | (P | P) | M3 |
| | ↓ | | | ↓ | | | |
| <i>Pan</i> 3.2 | M1 | I | I | [M2 | P = | P] | M3 |
| | ↓ | | | ↓ | | | |
| <i>Homo</i> Austr. <6.0? | [M1 | I] | I | P | [M2 = | P] | M3 |
| | ↓ | | | ↓ | | | |
| <i>Homo</i> Wh.Am. 6.3 | [I | M1] | I | [P | [P] | M2] | M3 |

Figure 15.3. New (post-1960) data on sequences of gingival emergence of mandibular teeth in primates plus two small insectivorous mammals (members of Soricomorpha and Scandentia). When ranked by the age at which M_1 emerges (at left), molars scatter to later positions, M_3 greatly, M_2 partly, and M_1 in only the slowest growing mammal. The trend is imperfect at M_3 , as Schultz also found.

span, brain weight, and body weight, all aspects of 'life history.'

Brain and body weights for primates (not shown here) are taken from Harvey and Clutton-Brock (1985) and for other mammals from Gingerich (n.d.), a compendium which will be described elsewhere. With the exception of the predicted M_1 emergence in *Tupaia*, all data analyses count time from birth. Repeating analyses with time counted post-conception did not change conclusions about emergence sequence, probably because most of the mammals studied here (excepting *Tupaia* and *Urotrichus*) are precocial (born well developed after a long gestation), and share many characteristics of the timing of events in development. Broad comparisons of altricial and precocial mammals, however, might need to count time from conception.

15.4. Results

15.4.1. Can Schultz's findings be replicated?

Patterns in eruption sequence emerged when Schultz (1956) ranked species by the *scala naturae* (see Figure 15.1). New data allow species to be ranked more objectively, here by the age at which a developmental marker is crossed. In Figure 15.3, species are listed by increasing

| | | | | | | | | | | | |
|---------------------------|-------------|------------|----|-----------|-------------|------------|---|-----------|-----|---|-----|
| <i>Urotrichus</i> | M1 | | | M2 | | | | M3 | PP | P | I |
| <i>Tupaia</i> 0.09? | M1 | | | M2 | | | | M3 | PIP | I | P I |
| <i>Lemur</i> 0.34 | M1 | | | M2 | tc | P | P | M3 | | | |
| <i>Aotus</i> 0.36 | M1 | | | M2 | | | I | M3 | I | P | PP |
| <i>Saimiri</i> 0.37 | M1 | | | M2 | I | I | P | M3 | | | |
| <i>Eulemur</i> 0.42 | M1 | | tc | M2 | | | | M3 | P | P | |
| <i>Varecia</i> 0.48 | M1 | | tc | M2 | | | | M3 | P | | |
| <i>Alouatta</i> | M1 | I | (I | M2 | PP | P | | M3 | | | |
| <i>Cercopithecus</i> 0.83 | M1 | I | I | M2 | P | P | | M3 | | | |
| <i>Cebus</i> sp. 1.1 | M1 | I | I | M2 | P | P | | M3 | | | |
| <i>Macaca</i> 1.4 | M1 | I | I | M2 | P | P | | M3 | | | |
| <i>Papio</i> 1.6 | M1 | I | I | M2 | P | P | | M3 | | | |
| <i>Pan</i> 3.2 | M1 | I | I | M2 | P | [P] | | M3 | | | |
| <i>Homo</i> <6.0? | [M1 | I] | I | P | [M2 | P] | | M3 | | | |
| <i>Homo</i> 6.3 | [I | M1] | I | [P | [P] | M2] | | M3 | | | |

Figure 15.4. Diagram of mandibular tooth emergence in primate/insectivores. Molars (boldface) are represented as stable and replacement teeth (outline font) as mobile. Extra conventions: all replacement teeth and teeth within a field (premolars, incisors) are kept together if possible and left shifts of replacement teeth are conservative; I3 and P2 are doubled with tooth nearest in time. When ordered by increasing age of M1 emergence (at left), replacement teeth sweep across molars to earlier positions.

age of M₁ emergence, and emergence sequences are based on data published after Schultz's 1956 diagram.

For anthropoids, Schultz's sequences were primarily based on skeletal samples with jaw unspecified. Although new data are limited to mandibular gingival emergence, new and old data (Figures 15.1, 15.3) are in fair agreement. As Schultz showed, little variation has been described between catarrhine species (see Smith, 1994). Few new data have appeared since Schultz for colobine monkeys, but those available suggest colobines are more rapidly growing and have more primitive sequences than cercopithecines (Wolf, 1984). Large studies of living humans have substantiated Schultz on human sequence: the first incisor erupts before the first molar in many individuals, and may characterize some populations. In a study of 6000 American children, Smith and Garn (1987) found that I₁ M₁ characterizes just over half of males and about a third to half of females.

For prosimians and the tree shrew, Schultz's sequences were taken from Bennejeant (1936), and these data differ most from newer sources. More recently, Shigehara (1980) found premolars before incisors in *Tupaia*, a reversal of Schultz's diagram. *Urotrichus* also shows premolars before incisors (Usuki, 1967), as do some fast-growing ungulates, evidence that this is a real phenomenon. These two non-primate species, both small and rapidly growing, show eruption of all three molars before any tooth replacement. No living primate appears to maintain this primitive sequence as the dominant one (see also Schwartz, 1974), although it may appear as a variant. Lemurids all show some form of advancement, whether in early appearance of the incisor-canine tooth comb or M₃ (Eaglen, 1985).

In Figure 15.3, molars drift to late positions in step with life history evolution, as represented here by M₁ emergence. Starting at the top and going down the chart, all species retain M₁ as the first tooth until *Homo sapiens*. The second molar shows a perfect trend, drifting from position 2 to 4, 5, and 6 as M₁ emergence increases from

0.4 to 6.3 years. Exceptions from the trend appear only with M₃, which appears later than expected in *Lemur* and *Saimiri*. Rankings here are tentative, however, because *Lemur*, *Aotus*, and *Saimiri* erupt M₁ at very nearly the same time (0.34, 0.36, and 0.37 years) and a new study of any of these species might reorder them, improving the trend. But in any case, no rearrangement of taxa produces a perfect trend in M₃ appearance.

For a new perspective on Schultz's rule, Figure 15.4 diagrams sequence in a manner that emphasizes replacement teeth. In it, molars are kept in rigid alignment as if they are stable, attuned to facial growth; replacement teeth are shown as if mobile. Although more cumbersome, this diagram shows the sweep of the changes across taxa in a striking fashion. In Figure 15.4, replacement teeth appear to march forward across columns of molars. Incisors traverse the greatest distance, crossing from the very last teeth to the very first teeth. Premolars have a more modest range, from just after M₃ to just before M₂. With its resemblance to a scatter graph with a cloud of points, Figure 15.4 de-emphasizes imperfections and emphasizes an overall association between life history and position of replacement teeth in sequence. The answer to the question posed is clear: Schultz's primate pattern can be replicated, although lemurids show some specializations regarding the tooth comb.

15.4.2. Do ungulates follow 'Schultz's Rule'?

Ungulates (Figure 15.5) span a very similar range in age of M₁ emergence and length of life as do the primates/insectivores above (Figure 15.4). Discounting humans, M₁ emergence ranges from 0.09 to 3.2 years in the primate/insectivore group and from 0.08 to 2.75 years in ungulates; life span is known to range from about 11 to 50+ years in each. Primates certainly contain many more slowly growing species, however. A glut of bovids and cervids emerge M₁ at about 0.2 year, whereas many anthropoid primates do so at one year or more. Thus, if

UNGULATES

| | | | | | | | | | | | | |
|---------------------------|----|---|---|-----|------|----|----|-----|-----|-----|----|-----|
| <i>Antidorcas</i> 0.08 | M1 | | | M2 | | | | M3 | I | II | P | P |
| <i>Antilocapra</i> 0.17 | M1 | | | M2 | | | | M3 | I | P | P | IPI |
| <i>Rangifer</i> 0.17 | M1 | | I | M2 | | | II | M3 | PP | P | | |
| <i>Odocoileus</i> 0.18 | M1 | | I | M2 | | | II | M3 | P | PP | | |
| <i>Muntiacus</i> 0.2? | M1 | | | M2 | | | I | M3 | I | PP | PI | |
| <i>Hemitragus</i> 0.21 | M1 | | | M2 | | | I | [M3 | I] | P | PP | PI |
| <i>Sylvicapra</i> 0.23 | M1 | | | M2 | | | | M3 | PP | P | I | II |
| <i>Aepyceros</i> 0.33 | M1 | | | M2 | | | I | M3 | I | PP | IP | |
| <i>Okapia</i> | M1 | | | M2 | | | I | (M3 | I) | PI | PP | |
| <i>Cervus</i> 0.33? | M1 | | | M2 | | I | I | M3 | IPP | P | | |
| <i>Tayassu</i> 0.40 | M1 | I | | M2 | I | I | P | PP | M3 | | | |
| <i>Connochaetes</i> 0.46 | M1 | | | M2 | | | | I | M3 | I | P | PI |
| <i>Sus</i> 0.47 | M1 | | | M2 | I | P | PP | I | M3 | | | |
| <i>Taurotragus</i> 0.53 | M1 | | | M2 | | | | I | M3 | II | PP | P |
| <i>Bison</i> 0.54 | M1 | | | M2 | | | | IP | M3 | P | I | IP |
| <i>Procavia</i> 0.54 | M1 | I | I | (M2 | PP | P) | | M3 | | | | |
| <i>Giraffa</i> 0.66 | M1 | | | M2 | | | [I | M3] | [P | PP] | II | |
| <i>Equus</i> 0.88 | M1 | | | M2 | | I | PP | M3 | I | PI | | |
| <i>Hippopotamus</i> ~2 | M1 | I | I | M2 | (PP) | P | | M3 | | | | |
| <i>Ceratotherium</i> 2.75 | M1 | P | | [M2 | P | P] | | M3 | | | | |

Figure 15.5. Diagram of mandibular tooth emergence in ungulates. Molars are represented as stable and replacement teeth as mobile. Conventions as in Figure 15.4. Replacement teeth in ungulates tend to shift to early positions with slower growth and development, but major exceptions appear in large bovinds and the giraffe.

the two charts were combined, anthropoid primates would fit in near the bottom.

The most striking finding is that ungulate tooth succession is much like that of the primates/insectivores. Overall, replacement teeth range over similar positions in the two charts (Figures 15.4, 15.5). In each group, the first molar begins the sequence, but any tooth may end it. While incisors tend to emerge together and premolars tend to emerge together, incisors tend also to precede premolars except in very rapidly growing species. Like primates (Figure 15.4), ungulates (Figure 15.5) also replace teeth in a pattern relative to life history. Eruption of all three molars before any teeth are replaced is found in rapidly growing members *Antidorcas*, *Antilocapra*, and *Sylvicapra*. Moving down the chart towards large-bodied, slow-growing taxa, replacement teeth begin to cross over molars. Most taxa show some incisor emergence before M₃, and several even erupt premolars before M₃, including *Tayassu*, *Sus*, *Procavia*, *Hippopotamus*, and *Ceratotherium*, a finding also common in higher primates. The rhinoceros is especially interesting because its premolars emerge relatively early, as one would expect with slow growth, even though all incisors have been lost.

Despite similarities to primates/insectivores, ungulates follow Schultz's Rule more intermittently. Figure 15.5 (ungulates) is much less tidy than Figure 15.4 (primates/insectivores) and substantial exceptions appear. Two deer (*Odocoileus* and *Rangifer*) show very early emergence of I₁, more extreme even than the lemur tooth comb. The larger bovinds *Connochaetes*, *Taurotragus*, and *Bison* delay M₁ until about one-half year, but fail to adapt emergence sequence significantly. A striking exception to the rule is found in the giraffe. Sources (sometimes tables and text within a source) disagree on the giraffe sequence;

it may match that of its relative the okapi (M₁ M₂ I₁ M₃ I₂ ...) or it may have an even more primitive sequence (M₁ M₂ M₃ I₁ I₂ ...). At 500 kg or more, the giraffe makes a spectacular exception to any idea that body size alone predicts eruption sequence. At 2 kg, the hyrax *Procavia* has a sequence far more 'advanced.' Overall, a tendency toward Schultz's rule can be seen in ungulates, but considerable unexplained variation remains.

On closer examination, Figure 15.5 gives the distinct impression that ungulates are heterogeneous in response of eruption sequence to life history. In particular, the 'generalized' and 'specialized' herbivores are difficult to force into the same box. The specialized group might be thought of as ruminant artiodactyls (antilocaprids, cervids, bovinds, giraffids) and perissodactyls. The former evolved selenodont cheek teeth to consume a low quality diet and the latter evolved lophodont cheek teeth to consume an extremely low quality diet (see MacDonald, 1984). If these specialized herbivores are separated from more generalized ones, two relatively homogeneous groups emerge. Taxa with more generalized adaptations, including artiodactyls of suborder Suina (suids, tayasuids, hippos) and the order Hyracoidea, interleave perfectly with Soricomorpha, Scandentia, and Primates (Figure 15.6). While Suina and Hyracoidea show a fluid adaptation of sequence to life history, specialized ungulates (Figure 15.7) seem comparatively inert. Specialized ungulates do step up along with Schultz's Rule, but they take only one or two steps towards earlier tooth replacement, rather than the several expected from their life histories.

15.4.3. Quantitative measures

Ordering raw data as in Figures 15.3-15.7 is a first step, but, quantitative expressions of sequence patterns are

GENERALIZED MAMMALS

| | | | | | | | | | | | | | | | | |
|---------------------------|-----|-----|---|----|-----|----|-----|------|----|----|--|-----|-----|---|----|---|
| <i>Urotrichus</i> | M1 | | | | | | M2 | | | | | M3 | PP | P | I | |
| <i>Tupaia</i> 0.09 | M1 | | | | | | M2 | | | | | M3 | PIP | I | P | I |
| <i>Lemur</i> 0.34 | M1 | | | | | | M2 | tc | P | P | | PM3 | | | | |
| <i>Aotus</i> 0.36 | M1 | | | | | | M2 | | | I | | M3 | I | P | PP | |
| <i>Saimiri</i> 0.37 | M1 | | | | | | M2 | I | I | P | | M3 | | | | |
| <i>Tayassu</i> 0.40 | M1 | I | | | | | M2 | I | I | P | | M3 | | | | |
| <i>Eulemur</i> 0.42 | M1 | | | | | tc | M2 | | | | | PM3 | P | P | | |
| <i>Sus</i> 0.47 | M1 | | | | | | M2 | I | P | PP | | M3 | | | | |
| <i>Varecia</i> 0.48 | M1 | | | | | tc | M2 | | | | | M3 | P | | | |
| <i>Procavia</i> 0.54 | M1 | I | I | | | | (M2 | PP | P) | | | M3 | | | | |
| <i>Alouatta</i> | M1 | I | I | | | | (I | M2) | PP | P) | | M3 | | | | |
| <i>Cercopithecus</i> 0.83 | M1 | I | I | | | | M2 | P | P | | | M3 | | | | |
| <i>Cebus</i> sp. 1.1 | M1 | I | I | | | | M2 | P | P | | | M3 | | | | |
| <i>Macaca</i> 1.4 | M1 | I | I | | | | M2 | P | P | | | M3 | | | | |
| <i>Papio</i> 1.6 | M1 | I | I | | | | M2 | P | P | | | M3 | | | | |
| <i>Hippopotamus</i> ~2 | M1 | I | I | | | | M2 | (PP) | P | | | M3 | | | | |
| <i>Pan</i> 3.2 | M1 | I | I | | | | [M2 | P | P] | | | M3 | | | | |
| <i>Homo</i> <6.0? | [M1 | I] | I | P | | | [M2 | P] | | | | M3 | | | | |
| <i>Homo</i> 6.3 | [I | M1] | I | [P | [P] | | M2] | | | | | M3 | | | | |

Figure 15.6. Diagram of mandibular tooth emergence in generalized mammals (Soricomorpha, Scandentia, Primates, suine artiodactyls, Hyracoidea). Molars are represented as stable and replacement teeth as mobile. Conventions as in Figure 15.4. Generalized herbivores and primate/insectivores share a fluid adaptation of sequence to slow growth.

SPECIALIZED UNGULATES

| | | | | | | | | | | | | | | | | |
|---------------------------|-----|--|---|--|--|--|-----|---|----|----|----|------|-----|-----|-----|-----|
| <i>Antidorcas</i> 0.08 | M1 | | | | | | M2 | | | | | M3 | I | II | P | P |
| <i>Antilocapra</i> 0.17 | M1 | | | | | | M2 | | | | | M3 | I | P | P | IPI |
| <i>Rangifer</i> 0.17 | M1 | | I | | | | M2 | | | | II | M3 | PP | P | | |
| <i>Odocoileus</i> 0.18 | M1 | | I | | | | M2 | | | | II | M3 | P | PP | | |
| <i>Muntiacus</i> 0.2? | M1 | | | | | | M2 | | | | I | M3 | I | PP | PI | |
| <i>Hemitragus</i> 0.21 | M1 | | | | | | M2 | | | | I | [M3 | I] | P | PPI | |
| <i>Sylvicapra</i> 0.23 | M1 | | | | | | M2 | | | | | M3 | PP | P | I | II |
| <i>Aepyceros</i> 0.33 | M1 | | | | | | M2 | | | | I | M3 | I | PP | IP | |
| <i>Okapia</i> | M1 | | | | | | M2 | | | | I | (M3 | I) | PI | PP | |
| <i>Cervus</i> 0.33? | M1 | | | | | | M2 | | I | | I | M3 | IPP | P | | |
| <i>Connochaetes</i> 0.46 | M1 | | | | | | M2 | | | | I | M3 | I | P | PI | |
| <i>Taurotragus</i> 0.53 | M1 | | | | | | M2 | | | | I | M3 | II | PP | P | |
| <i>Bison</i> 0.54 | M1 | | | | | | M2 | | | | IP | M3 | P | I | IP | |
| <i>Giraffa</i> 0.66 | M1 | | | | | | M2 | | | | I | [M3] | [P | PP] | II | |
| <i>Equus</i> 0.88 | M1 | | | | | | M2 | | I | PP | | M3 | I | PI | | |
| <i>Ceratotherium</i> 2.75 | M1P | | | | | | [M2 | P | P] | | | M3 | | | | |

Figure 15.7. Diagram of mandibular tooth emergence in specialized ungulates (ruminant artiodactyls, Perissodactyla). Molars are represented as stable and replacement teeth as mobile. Conventions as in Figure 15.4. Premolars adapt much as expected in Schultz's Rule, but slowly growing specialized herbivores resist shifting incisors forward in sequence. Except for *Equus*, all lack upper incisors or all incisors (*Ceratotherium*) and may take over incisor function with soft tissues.

needed to allow statistical analysis. Several quantitative schemes might be tried, but since incisor position is crucial to Schultz's Rule, emergence of the first incisor was ranked relative to molars as 0.5 (I₁ emerges before M₁), 1.5 (I₁ emerges after M₁), 2.5 (after M₂), or 3.5 (after M₃). In this scheme the two human populations have advanced I₁ to ranks 0.5 and 1.5; ranks 2.5–3.5 characterize the other mammals. Advancement of P₃ relative to molars ('P₃ position') was quantified in the same manner, ranking P₃ as 1.5 in humans (P₃ emerging after M₁), and 2.5–3.5 (after M₂ or M₃) in other mammals. Given rank order, correlation can readily demonstrate trend and direction, although it is a weak statistical approach given the restricted number of assigned ranks.

For numerical analyses, lack of life history data for the little known *Urotrichus* restricts study to Archonta (primates plus the tree shrew) and Ungulata. Table 15.1 shows Spearman's correlation between rank of replacement tooth position (0.5–3.5) and rank of a series of life history variables (1–N). Schultz's Rule predicts negative correlations for Table 1 since replacement teeth are pre-

dicted to drop rank as timing and size measures increase. As shown, 22 of 24 correlations computed over all taxa or within grandorders were negative and 14 were significantly so at P<0.05. Results for I₁ and P₃ tell a similar story: for all taxa combined, advance of replacing teeth is associated with a slowing of life history, as measured by increasing age of M₁ eruption and life span (rho = -0.56 to -0.75). Thus, as mammals grow up more slowly and live longer, their first incisors and third premolars appear earlier in sequence. Both incisors and premolars tend to shift, shown by a positive correlation of I₁ and P₃ position (rho = 0.60). When dissected into grandorders, however, the strength of the trend lies within archontans (rho = -0.77 to -0.87). Although in the proper direction, correlation is weaker for ungulates (rho = -0.26 to -0.63). Combining taxa, correlations of tooth position with size (body weight, brain weight) were uneven in direction (rho = -0.16 to 0.11), a sign of underlying heterogeneity.

To try to resolve heterogeneity in the data, Table 15.1 also groups species by adaptive categories 'generalist'

Table 15.1. Spearman's rank order correlation between eruption sequence (appearance of I_1 or P_3 relative to mandibular molars¹) and life history variables for extant taxa

| Taxon/group | Spearman's rho | | | | | | | |
|--|-------------------|------|-----------|------|-------------|------|--------------|------|
| | Age M_1 emerges | (N) | Life span | (N) | Body weight | (N) | Brain weight | (N) |
| Appearance of I_1 relative to molars | | | | | | | | |
| All taxa | -0.66* | (30) | -0.56* | (30) | 0.03 | (32) | -0.16 | (29) |
| Archontans | -0.87* | (12) | -0.85* | (11) | -0.84* | (13) | -0.84* | (13) |
| Ungulates | -0.32 | (18) | -0.26 | (19) | -0.21 | (19) | -0.08 | (16) |
| Generalists | -0.87 | (16) | -0.67 | (15) | -0.49 | (17) | -0.59 | (17) |
| Specialists | -0.13 | (14) | -0.46 | (15) | -0.31 | (15) | -0.23 | (12) |
| Appearance of P_3 relative to molars | | | | | | | | |
| All taxa | -0.75* | (31) | -0.60* | (31) | 0.11 | (33) | -0.20 | (30) |
| Archontans | -0.77* | (12) | -0.77* | (11) | -0.80* | (13) | -0.83* | (13) |
| Ungulates | -0.63* | (19) | -0.40* | (20) | -0.09 | (20) | -0.13 | (17) |
| Generalists | -0.71 | (16) | -0.61 | (15) | -0.67 | (17) | -0.76 | (17) |
| Specialists | -0.59 | (15) | -0.49 | (16) | -0.41 | (16) | -0.51 | (13) |

Note: ¹Appearance of I_1 coded as: 0.5, before M_1 ; 1.5, after M_1 ; 2.5, after M_2 ; 3.5, after M_3 ; appearance of P_3 coded as: 1.5, after M_1 ; 2.5, after M_2 ; 3.5, after M_3 .
*Significantly different from zero at $P < 0.01$ in one-tailed test (negative associations predicted). No tests performed for 'generalists' and 'specialists' (ruminant artiodactyls, perissodactyls) because division was made *post hoc*, in an attempt to resolve heterogeneity in the data.

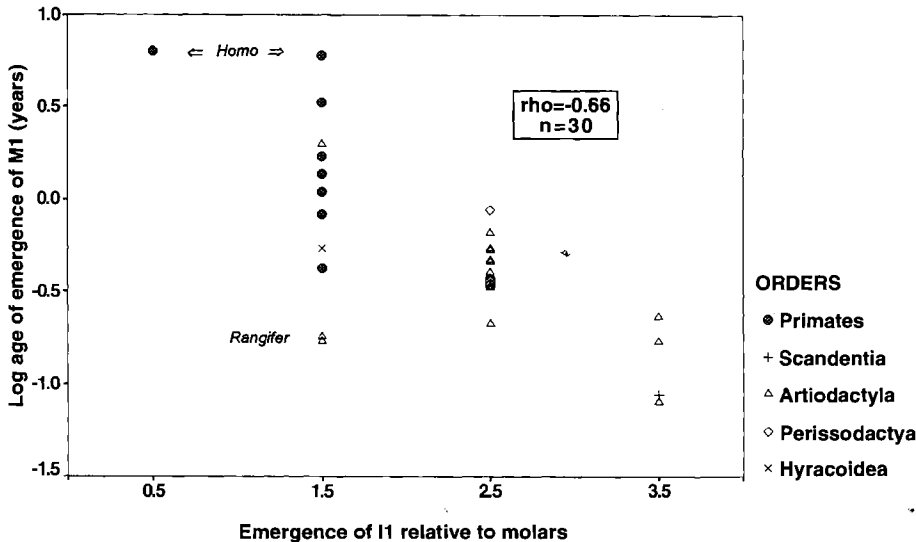


Figure 15.8. Log (base 10) of the age of emergence of mandibular first molar for species different I_1 positions: 0.5, before M_1 ; 1.5, after M_1 ; 2.5, after M_2 , and 3.5, after M_3 . Two deer (*Rangifer* and *Odocoileus*) appear as outliers for sequence 1.5. Despite considerable overlap in timing, age at first molar emergence steps up as incisors shift to early positions.

and specialist' (the same division as in Figures 15.6 versus Figure 15.7). Tests were not performed because the division was made *post hoc*, but comparisons are still instructive. Dividing species into adaptive categories reduces heterogeneity, resulting in two groups with correlations of coherent direction and similar strength. Moreover, results suggest that any and all life history variables - M_1 emergence, life span, body weight, and brain weight - are associated with emergence sequence. Thus, within adaptive categories, species that have larger bodies, larger brains, grow up more slowly, and live longer, tend to shift replacement teeth forward in sequence of emergence. Premolar progression is very similar in the two adaptive categories, but incisor progression is not. 'Generalists' advance incisors strongly with life history

evolution ($\rho = -0.87$), whereas specialists either eliminate incisors (the rhinoceros) or advance them little ($\rho = -0.13$).

A stronger statistical approach to the influence of life history on tooth eruption is to sort taxa by sequence and compare life histories. In Figure 15.8 (supporting data in Table 15.2), the logarithm of age of M_1 emergence is graphed for each position of I_1 in the emergence sequence. Variance of age of M_1 emergence is particularly high for taxa with sequence 1.5 ($M_1 I_1 M_2 M_3$) where the distribution is expanded by a human population at the high end and by two deer (*Odocoileus* and *Rangifer*) at the low end. The 'primitive' sequence, $M_1 M_2 M_3 I_1$ (shortened to MMMI in Table 15.2) is associated with a median age of M_1 emergence of 0.13 years. With each shift forward in I_1 ,

Table 15.2. Timing of life events (M_1 emergence and life span) in mammals with different emergence sequences

| Mandibular sequence code and string ^a | Age of emergence of M_1 (years) | | | Life span (years) | | |
|--|-----------------------------------|-----------|----------------------------------|----------------------|--------|----------------------------------|
| | Median ^b | Range | <i>N</i> species ^c | Median ^b | Range | <i>N</i> species ^c |
| Incisor position | | | | | | |
| 0.5 I1 M M M | 6.30 | – | 1 | 100 | – | 1 |
| 1.5 M I1 M M | 1.10 | 0.17–6.00 | 11 | 31 (11) ^d | 20–100 | 10 |
| 2.5 M M I1 M ^e | 0.39 | 0.21–0.88 | 14 | 24 | 13–36 | 15 |
| 3.5 M M M I1 | 0.13 | 0.08–0.23 | 4 | 13 | 11–17 | 4 |
| Premolar position | | | | | | |
| 1.5 M P3 M M | 6.17 | 6.0–6.3 | 2 | 100 | – | 2 |
| 2.5 M M P3 M | 0.88 | 0.34–3.33 | 13 | 29 (11) ^d | 21–45 | 12 |
| 3.5 M M M P3 | 0.28 | 0.08–2.00 | 16 | 20 | 11–54 | 17 |

^aDisregarding other teeth. Molars always erupt as M1 M2 M3.

^bKruskal–Wallis test finds medians significantly different at $P < 0.01$.

^cEach population of *Homo sapiens* entered separately.

^dHyrax life span (11 years) is an outlier, much shorter than expected given its protracted dental development.

^eWithout specialized ungulates, values are, respectively: 0.37, 0.34–0.47, 5, 25, 13–27, 5.

the pace of life events slows and M_1 is delayed, with median ages of emergence of 0.39, 1.10, and finally 6.3 years. Since variances are significantly different for sequence codes 1.5–3.5, non-parametric comparisons are in order. By the Kruskal–Wallis test, median age of M_1 emergence differs in the three sequence groups with $N > 1$ ($P < 0.01$) as shown in Table 15.2. Also shown in Table 15.2, as I_1 shifts forward, life span increases from 13 to 24, 31, and 100 years. Repeating the exercise for P_3 position produced a very similar result, showing systematic increase in age of M_1 emergence and life span as P_3 advances relative to molars (Table 15.2).

Comparisons in Figure 15.8 beg one further question, whether the age of M_1 emergence associated with a particular sequence is the same regardless of taxon or adaptive group. To be brief, a series of two-way analyses of variance (ANOVAs) (with factors grandorder versus I_1 position, adaptive group versus I_1 position, grandorder versus P_3 position, adaptive group versus P_3 position) demonstrated no strong evidence for taxonomic or adaptive effects across the board – thus no real evidence of different ‘set points’ for M_1 timing. Until stronger evidence emerges, it appears that a given sequence is associated with a particular age of M_1 emergence whatever the grandorder. An exception can be made for specialized ungulates, where a significant interaction points to unusual values for one particular category. Specialized ungulates drift into moderately slow growth while maintaining the sequence MMIM, rather than the expected MIMM.

Given these analyses, it can be proposed that ungulates tend to follow Schultz’s Rule in tooth replacement patterns, but that slowly growing specialized ungulates resist shifting incisor position.

15.4.4. Early replacement teeth or late molars?

Patterned changes in tooth eruption sequence observed here could be brought about by relatively early replacement teeth or relatively late molars or both; sequence data alone cannot determine which. The ultimate resolution of which teeth are late and which early must come from numerical data on ages of emergence of teeth. While some such data support early replacing teeth as a major contributor to sequence variation in primates (Smith, 1992), ungulate adaptations may be more varied. At least one genus, *Procavia*, the hyrax, shows several oddities in emergence timing. Its molars continue to erupt slowly over several years, completing eruption as late as 5 years of age (Steyn and Hanks, 1983), a value almost half its life span (Nowak and Paradiso, 1983). This is sufficiently out of proportion to other mammals to suggest that *Procavia* has initiated an elephant-like or kangaroo-like late progression of molars.

15.4.5. Does emergence sequence reflect facial architecture?

If Schultz’s Rule holds good, life history should be a better predictor of eruption sequence than facial architecture or simply membership in a taxonomic group. In mammals collected here, primates/insectivores have a closed tooth row with either long or short faces, whereas ungulates tend to a more stereotyped long face, often with a large diastema between anterior and cheek teeth. Thus, if facial architecture is crucial, we might expect to see changes that correspond to face shape in the former and relatively fixed sequences of emergence within the latter. On the other hand, sequences that step up in pace with life history, no matter the taxonomic grouping, argue for a life history explanation.

A few comparisons cast doubt on the determinative

Table 15.3. Primate/insectivores paired with their best match in mandibular emergence sequence among ungulates (showing seven tooth positions shared by all taxa, with I3 and P2 collapsed with tooth nearest in time)

| Taxon pairs, age M ₁ emerges | Emergence sequence | | | | | | |
|--|--------------------|----|----|-----|----|-----|-----|
| <i>Urotrichus</i> (early?) | M1 | M2 | M3 | PP | P | I | |
| <i>Sylvicapra</i> 0.23 | M1 | M2 | M3 | PP | P | I | II |
| <i>Tupaia</i> ca. 0.09 | M1 | M2 | M3 | PIP | I | P | I |
| <i>Antilocapra</i> 0.17 | M1 | M2 | M3 | I | P | P | IPI |
| <i>Aotus</i> 0.36 | M1 | M2 | I | M3 | I | P | PP |
| <i>Aepyceros</i> 0.33 | M1 | M2 | I | M3 | I | PP | IP |
| <i>Lemur</i> 0.34 | M1 | M2 | tc | | P | P | PM3 |
| <i>Tayassu</i> 0.40 | M1I | M2 | I | I | P | PP | M3 |
| <i>Eulemur</i> 0.42 | M1 | tc | M2 | | | PM3 | P |
| <i>Rangifer</i> 0.17 | M1 | I | M2 | II | M3 | PP | P |
| <i>Saimiri</i> 0.37 | M1 | M2 | I | I | P | PP | M3 |
| <i>Tayassu</i> 0.40 | M1I | M2 | I | I | P | PP | M3 |
| <i>Cebus</i> ^a 1.1 | M1 | I | I | M2 | P | P | M3 |
| <i>Procavia</i> 0.54 | M1 | I | I | M2 | PP | P | M3 |
| <i>Pan</i> 3.2 | M1 | I | I | M2 | P | P | M3 |
| <i>Hippopotamus</i> ~2 | M1 | I | I | M2 | PP | P | M3 |
| <i>Homo</i> 6.3 (elephants?) | I1 | M1 | I | P | P | M2 | M3 |

No adequate match was found for *Alouatta* or *Homo*, but all other primates could be matched approximately choosing from 20 ungulates.

^a Cercopithecine monkeys all match *Cebus* or *Pan*.

tc, tooth comb.

effect of gross facial form on emergence sequence. First, within primates there is little similarity among emergence sequences of *Saimiri*, *Cebus*, and *Homo*, although all have short faces. *Lemur* and *Papio*, the more dog-faced species, are equally mismatched in sequence (Figure 15.3). While it is true that mid-size ruminants seem relatively inert, ungulate emergence sequences step up through a considerable range despite comparatively stereotyped facial form (Figure 15.5).

In Table 15.3, primates/insectivores are paired with a best match in emergence sequence in ungulates. Close resemblance pairs the Japanese shrew mole with the duiker, the tree shrew with the pronghorn, the night monkey with the impala, the true lemur with the caribou, the squirrel monkey with the peccary, the cebus monkey with the hyrax, and the chimpanzee with the hippopotamus. It is difficult to imagine a hypothesis about facial morphology that could explain pairings such as these. Matched pairs, however, share aspects of life history, as shown by the correlation between their ages of M₁ emergence of $r = 0.65-0.98$ (depending on how matches are allocated in *Cebus*, *Pan*, *Procavia*, and *Hippopotamus*, which all share the same sequence). Humans have no match in ungulates, perhaps because elephants, the only ungulate to grow up as slowly as humans, have greatly modified tooth succession.

Although gross facial morphology has no simple and obvious explanatory power for emergence sequence, more precise hypotheses about dental function remain promising. The specialized herbivores, including ruminant artiodactyls and perissodactyls, for example, appear to slow growth without much advancement of incisors. These mammals make extensive use of the tongue and soft tissues in acquiring food (MacDonald, 1984) and incisors may be comparatively under used. Indeed, most of the Ruminantia have no upper incisors and the rhinoceros has no incisors whatsoever. Both dental function and dental morphology remain likely contributors to emergence sequences.

15.4.6. Can we predict life histories from sequences of tooth emergence?

If life history is a fundamental determinant of tooth eruption sequence, simple sequence strings preserved in teeth of fossil mammals might inform us whether a species lived and died on a fast time scale, like a small bovid, for example, or a slow one, like a monkey.

Table 15.4 contains test cases of eruption/emergence sequences for extinct mammals reconstructed from original illustrations or raw data in listed sources (although some uncertainty remains over the definitions of eruption). Life histories of extant taxa which share the same sequence characteristics are tabulated for comparison.

One extra caution is needed before proceeding. Life histories may have been distributed uniquely in long extinct mammal faunas. For example, long life and slow growth were probably rare or absent in very early mammals (Lillegraven *et al.*, 1987). If underlying life history distributions differ between the present and the past, it is safer to compare fossils with the total range known in extant mammals rather than apply specific means from the present to the past. Mean values would be highly dependent on the particular distribution of mammals living today and sampled in the present study.

In Table 15.4 each case is of interest because it is not clear how to choose a living model for life history. *Coryphodon* is a primitive ungulate-like mammal of large body size known from the Paleocene and Eocene of the northern hemisphere, only distantly related to extant mammals. Authors of an ontogenetic study compared *Coryphodon* to hippos based on body size and habitat (Lucas and Schoch, 1990). Judging from the hippo, we might expect that *Coryphodon* grew up very slowly, with M₁ emergence about 2 years of age and long life, perhaps 40-50 years. However, I₁ and P₃ positions like that of *Coryphodon* are found today in mammals emerging M₁ between 0.34-0.88 years, with life spans on the order of 21-35 years. If we limit comparison to generalized

Table 15.4. Reconstructed sequences of tooth eruption/emergence for extinct species and ranges of life events in similar extant taxa.^a

| Order Genus/species | Sequence/source ^b | Range in extant species matched for sequence code | | |
|--|---|---|---|-------------------------|
| | | Sequence code (I ₁ position, P ₃ position) ^c | Age of emergence of M ₁ (years) ^d | Life span (years) |
| Pantodonta | | | | |
| <i>Coryphodon</i> sp. | (M1 I3) p1 M2 P4 P3 (P2 I1) C (M3 I2) Lucas and Schoch, 1990 | 2.5, 2.5 | 0.34–0.88 0.34–0.47 | 21–35 21–27 |
| Archaeoceti | | | | |
| Dorudontinae | (M1 p1) M2 M3 P4 P3 P2 (P1? I3 C) | 3.57, 3.5 | 0.08–0.66 | 11–36 |
| <i>Zygorhiza kochii</i> plus <i>Dorudon atrox</i> | I1 erupts sometime after M2 and probably after M3; I2 is after P4 Kellogg, 1936; Uhen, 1996 | | 0.09–0.42 | 12–31 |
| Primates | | | | |
| <i>Adapis parisiensis</i> | (M1 p1) M2 (I1 I2 M3) [P4 C] P3 P2 Stehlin, 1912; Gingerich, unpublished data | –, 3.5 | 0.08–0.66 0.09–0.42 | 11–36 12–31 |
| <i>Notharctus tenebrosus</i> | M1 M2 M3 (P4 P3 P2) Gregory, 1920 | –, 3.5 | 0.08–0.66 0.09–0.42 | 11–36 12–31 |
| <i>Archaeolemur majori</i> | M1 M2 I1 I2 M3 P4 P3 P2 Lamberton, 1938 | 2.5, 3.5 | 0.21–0.66 0.36 | 13–36 13 |
| <i>Apidium phiomense</i> | M1 M2 P2 P4 (P3 M3) C Kay and Simons, | –, 2.57 | 0.34–3.33 | (11) ^e 21–55 |
| <i>Australopithecus africanus</i> | M1 I1 I2 M2 P3 P4 C? M3 Smith, 1994 | 1.5, 2.5 | 0.54–3.33 | (11) ^e 26–55 |

^a Living archontans and ungulates with same I1 and P3 position in sequence.

^b Sequence uncertain (); sequence varies, []; teeth omitted if no basis for assigning order.

^c As in Table 15.3.

^d First line, all taxa; second line, generalized mammals only (removing specialized herbivores).

^e *Procavia* has an unusually short lifespan (11 years); other species with comparable sequences have lifespans >20 years.

mammals, the estimate becomes more restricted (M₁ at 0.34–0.47 years and a 21–27 year life span), pointing to a life history considerably faster than a hippo, something more like a large deer or pig.

For several other cases in Table 15.4 more could be said if incisors could be placed relative to molars in sequence. *Zygorhiza* and *Dorudon* are both dorudontine archaeocetes (primitive whales) with body length something on the order of a mid-sized odontocete (toothed whale). Modern whales grow up fairly slowly, but are so transformed in adaptation from land mammal ancestors that they are questionable models for archaeocete life history. Since archaeocetes preserved primitive tooth replacement, however, their emergence sequence makes a place to start. As shown, the late appearance of premolars in archaeocetes tends to rule out the longest lived models. If comparison is limited to generalized mammals, life history of dorudontine archaeocetes is predicted to have run a fast to moderate pace (M₁ at 0.09–0.42 years, life span of 12–31 years).

The cases of two adapid primates *Adapis parisiensis* and *Notharctus tenebrosus* are instructive, although incisors have not been placed relative to M₃. Even in these Eocene primates, no hard data support a truly primitive emergence sequence, with all molars before replacement teeth. Based on incisor alveoli, one specimen of *Adapis parisiensis* observed by Gingerich (unpublished data) sug-

gests mandibular incisors were in place before M₃. If so, *Adapis parisiensis* had the sequence shown for *Archaeolemur*, a subfossil indriid from Madagascar (also in Table 15.4). The *Archaeolemur* sequence suggests a life history on pace with a large lemur or small anthropoid.

Apidium phiomense is an anthropoid known from the Oligocene of Egypt. Kay and Simons (1983) were able to demonstrate that P₄ and probably P₃ erupt in an advanced position, which in turn suggests a life history somewhat slowed, at least not on the fastest pace.

A last prediction can be made for *Australopithecus africanus*, the extinct early hominid. Its growth rate was originally compared to *Homo sapiens* (Mann, 1975); its dental development and emergence sequence, however, place it with great apes and monkeys (Smith, 1994). From Table 15.4, the *Australopithecus* emergence sequence suggests M₁ erupted from 0.54 to 3.33 years with life span ranging up to 55 years – in other words, matching a chimpanzee perhaps, but not a human.

Predicted life histories are just that until they are supported by other data. Fortunately, study of incremental lines in teeth promises to be able to establish the age of tooth eruption in many extinct species. One such study put M₁ emergence at about 3 years in *Australopithecus africanus* (Bromage and Dean, 1985). Until such detailed and time-consuming work is done on a large scale however, emergence sequences can provide some basis

for choosing a living model for life history of an extinct mammal.

• Other aspects of sequence than those studied here may prove productive in predicting life histories. For example, the tendency for some fossil mammals to erupt premolars before incisors is intriguing, but too few living mammals with this pattern have been sampled here to understand its meaning. Predictions should also improve as the data base for living mammals expands.

15.4.7. Unexplained variation

Schultz's Rule has some power of explanation in present data, but it cannot explain all variance in emergence sequence. Such unexplained variance may give information about dental function or simply phylogenetic history. One unexplained feature is the characteristic 'backwards' emergence of premolars, the order $P_4 P_3$, in primates (Schwartz, 1974; Tattersall and Schwartz, 1974), tree shrews (Shigehara, 1980), many insectivores, some carnivore families (Slaughter *et al.*, 1974), and some other fossil mammals (Table 15.4). Most regard the distant ancestral order to be $P_3 P_4$, with the 'backwards' $P_4 P_3$ sequence the phylogenetic novelty (Slaughter *et al.*, 1974, Tattersall and Schwartz, 1974). In primates, premolar order does revert to $P_3 P_4$ in apes and humans, a change which has been interpreted as a retardation of distal teeth in presence of slow growth (Smith, 1994). Looking at other mammals, however, no patterns emerge with respect to length of post-natal life. The ungulates erupt premolars in the 'front-to-back' order $P_3 P_4$ across the board (see Appendix), regardless of the pace of growth.

Whereas the $P_3 P_4$ sequence tends to characterize groups of related mammals, P_2 appearance is much more variable. Kay and Simons (1983) cautioned that P_2 is very variable in primates. Although it tends to appear together with other premolars, P_2 can jump position even in closely related species (see Appendix). In a study of insectivores and carnivores, Slaughter *et al.* (1974) simply concluded that the tooth had so little functional importance that it was more free to vary than other teeth.

Real exceptions to Schultz's Rule can be found in lemuriforms (lemurs and lorises) with tooth combs. Living lorises (not included here because complete gingival sequences are unavailable) are said to replace some anterior teeth very early, even before emergence of M_1 (Schwartz, 1974). Clearly this cannot be because lorises grow up slowly; quite the opposite is true. Perhaps deciduous tooth combs are discarded early for functional reasons, as may also be true in *Eulemur* and *Varecia*. To generalize this finding, specialized dental functions should warn that Schultz's Rule might not apply.

Finally, patterns of emergence in other mammalian

orders, notably the Carnivora and Chiroptera (the latter also included in Archonta), remain to be explained. Preliminary investigation finds very 'advanced' sequences in these orders. Such major differences between higher taxa may make eruption sequences useful in mammalian systematics. Even such major taxonomic differences, however, are likely to have adaptive explanations.

15.5. Conclusions

To understand Schultz's Rule, one can imagine that replacement teeth (I1–P4) are on a sliding scale, adapting to demands on deciduous teeth. In slowly growing species, replacement teeth 'slide' to earlier positions to compensate for increased loads on deciduous teeth. The dampened response observed in specialized herbivores however, suggests that either their deciduous incisors manage to carry the load imposed by slow growth or that soft tissues have taken over some of the work of incisors.

Resemblance in tooth emergence sequence cross-cuts taxonomic group and facial form to a surprising degree. Sequences trend from (presumed) primitive (M M M P P I I) to (presumed) advanced (M I I M P P M) within two grandorders, Archonta (primates + tree shrew) and Ungulata. The large range of sequences in each grandorder is strong evidence that tooth eruption is a highly functional adaptive system. Thus, emergence sequence must be used with care in phylogenetic analysis.

Evidence suggests that sequence of eruption of teeth is a signature of life history, but this is not to say that phylogenetic history and dento-facial morphology leave no trace. Primates and the tree shrew share a characteristic 'backwards' emergence of the premolars P_4 and P_3 (Schwartz, 1974), a sequence of unknown significance for life history. It may be taxonomically useful, as may minor sequences involving teeth not studied here (deciduous teeth and permanent C, I₃, P₂). In addition, work in progress on Carnivora and Chiroptera finds more 'advanced' sequences than those described here, sequences that might reflect morphology and phylogeny. The hypothesis that face shape is correlated in a simple manner with emergence sequence, however, can be rejected. Despite considerable differences in facial architecture of archontans and ungulates, tooth eruption sequences are pages taken from the same book. Near matches in sequence characterize the tree shrew and the pronghorn, the peccary and the squirrel monkey, and the chimpanzee and the hippopotamus, pairs that share few characteristics of facial architecture. Similarity of the overall pace of life, however, can account for such matches.

Finally, emergence sequences must be seen as limited data. While they can show an orderly response to life history, they cannot discern how change is brought about – which teeth are early and which late. Allochronic analyses of actual ages teeth erupt could answer many more questions (Smith, 1992). Complete data of that type, however, are still relatively scarce, although basic sequences allow some predictions about life histories of extinct mammals. For such predictions, the most important datum appears to be position of incisors relative to molars, and secondly, position of premolars to molars. New approaches in histological study (Bromage and Dean, 1985; Dean, 1989; Swindler and Beynon, 1993) promise we will soon be able to test such hypotheses by reconstructing actual times of events in life history for extinct species. When such data are available, we will have a powerful tool for making inference about the evolution of life history in mammals.

Summary

Adolph Schultz's empiric search for a pattern in tooth emergence resulted in a general rule that is more widely applicable than he knew. 'Schultz's rule,' the tendency for replacing teeth to appear relatively early in slow-growing, long-lived species, applies to a broad range of mammals. The rule successfully orders new data from the orders Primates, Scandentia, and Soricomorpha, and the more generalized members of the grandorder Ungulata (Hyracoidea and suine Artiodactyla). The rule applies in a more limited way to the specialized Ungulata (Perissodactyla and ruminant Artiodactyla). As growth rate slows (M_1 emerges late) and life lengthens, generalized herbivores and omnivores fluidly adapt sequence of tooth emergence, whereas specialized herbivores adapt stiffly.

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- Appendix: complete mandibular emergence sequence (age of emergence of M₁ and life span (both in years) follow species name)**
- Note: parentheses () surround teeth when actual sequence has not been resolved, i.e., teeth are 'tied'; square parentheses [] surround teeth known to vary in sequence at >15%; = indicates variation is > 40%. Premolars omit numbers when there is no basis for assigning order. tc* tooth comb (I₁, I₂, C₁) emerges all at once.
- I. GRANDORDER INSECTIVORA**
- ORDER SORICOMORPHA**
- TALPIDAE
- Urotrichus talpoides* M1 M2 M3 P2 P3 P4 I1 C
- Urotrichus pillirostris* M1 M2 M3 (P2 P3 P4) I1 C p1
- II. GRANDORDER ARCHONTA**
- ORDER SCANDENTIA**
- TUPAIDAE
- Tupaia glis* c. 0.097, 12.4 M1 M2 M3 P2 I3 P4 (I1 C) P3 I2
- ORDER PRIMATES**
- LEMURIDAE
- Lemur catta* 0.34, 27.1 M1 M2 tc* P4 P3 P2 M3
- Eulemur fulvus* 0.42, 30.8 M1 tc* M2 P2 M3 P4 P3
- Varecia variegata* 0.48, – M1 tc* M2 P2 P4 M3 P3
- CEBIDAE
- Aotus trivirgatus* 0.36, 12.6 M1 M2 I1 M3 I2 P4 P3 P2 C
- Saimiri sciureus* 0.37, 21 M1 M2 I1 I2 P4 P3 P2 M3 C
- Alouatta caraya* M1 I1 (I2 M2) P P P4 M3
- Cebus sp.* 1.1, 40 (no data P2) M1 I1 I2 M2 P4 P3 M3 C?
- CERCOPITHECIDAE
- Cercopithecus aethiops* 0.8, 31 M1 I1 I2 M2 P4 P3 C M3
- Macaca nemestrina* (male) 1.4, 26.3 M1 I1 I2 M2 P4 P3 M3 C
- Papio anubis* (male) 1.6, – M1 I1 I2 M2 C (P4 P3) M3
- PONGIDAE
- Pan troglodytes* 3.2, 44.5 M1 I1 I2 [M2 P3=P4] M3 C
- HOMINIDAE
- Homo sapiens*
- Australian Aborig. <6.0?, 100 (male) [M1 I1] I2 C P3 [M2=P4] M3
- White American 6.3, 100 (male) [I1 M1] I2 [C P3 [P4] M2] M3
- III. GRANDORDER UNGULATA**
- ORDER ARTIODACTYLA**
- SUBORDER RUMINANTIA**
- ANTILOCAPRIDAE
- Antilocapra americana* 0.17, 11.2 M1 M2 M3 I1 P3 P4 I2 P2 I3 C
- BOVIDAE
- Antidorcas marsupialis* 0.08, 17.1 M1 M2 M3 I1 (I2 I3 C) P3 P4
- Hemitragus jemlahicus* 0.21, 21.8 M1 M2 I1 [M3 I2] P3 [P2 P4] I3
- Sylvicapra grimmia* 0.23, 14.3 M1 M2 M3 (P P P) I1 [I2 I3] C
- Aepyceros melampus* 0.33, 17.5 M1 M2 I1 M3 I2 (P2 P3) I3 C P4
- Connochaetes taurinus* 0.46, 21.4 M1 M2 I1 M3 I2 (P3 P4) I3 C
- Taurotragus oryx* 0.53, 23.5 M1 M2 I1 M3 I2 I3 C (P2 P3) P4
- Bison bonasus* 0.54, 20 M1 M2 I1 P2 (M3 P3) I2 I3 P4 C
- CERVIDAE
- Rangifer tarandus* 0.17, 20.2 M1 I1 M2 I2 I3 M3 (P3 P2) P4
- Odocoileus virginianus* 0.18, 20 M1 I1 M2 (I2 I3 C) M3 P2 (P3 P4)
- Muntiacus reevesi* 0.27, 17.6 M1 M2 I1 M3 I2 (P3 P2) P4 (I3 C)
- Cervus elaphus* 0.33, 26.7 M1 M2 I1 I2 M3 (I3 C) [P2 P3] P4
- GIRRAFFIDAE
- Okapia johnstoni* –, 33 M1 M2 I1 (M3 I2) (P3 I3) P4 P2 C
- Giraffa camelopardalis* 0.66, 36.2 M1 M2 [I1 M3] I2 [P4 P3 P2] I2 I3 C
- SUBORDER SUINA**
- TASSUIDAE
- Tayassu tajacu* 0.40, 24.6 M1 C I3 M2 I1 I2 P P P M3
- SUIDAE
- Sus scrofa* 0.47, 27 M1 p1 I3 C M2 I1 P3 P4 P2 I2 M3
- HIPPOPOTAMIDAE
- Hippopotamus amphibius* –2, 54.3 p1 M1 (I1 I2 C) M2 (P2 P3) P4 M3
- ORDER PERISSODACTYLA**
- EQUIDAE
- Equus burchelli* 0.88, 35 (male) p1 M1 M2 I1 (P2 P3) M3 I2 (C P4) I3
- RHINOCEROTIDAE
- Ceratotherium simum* 2.75, 36 p1 M1 P2 (M2 P3 P4) M3
- Order Hyracoidea**
- PROCAVIIDAE
- Procavia capensis* 0.54, 11 M1 (I1 I2) (M2 P P P) M3

Sources: I: Usuki (1967) II: Shigehara (1980); original primate literature cited in Smith & Garn (1987), Smith (1994) and Smith *et al.* (1994). III: Hoover *et al.* (1959); Rautenbach (1971); Caughley (1965); Wilson *et al.* (1984); Roettcher and Hofmann (1970); Attwell (1980); Jeffery and Hanks (1980) and Kerr and Roth (1970); Wegrzyn and Serwatka (1984); Miller (1972); Severinghaus (1949); Chapman *et al.* (1985); Quimby and Gaab (1957); Jaspers and DeVree (1978); Hall-Martin (1976) and Singer and Boné (1960); Kirkpatrick and SOWLS (1962); Matschke (1967); Laws (1968); Smuts (1974); Hillman-Smith *et al.* (1986); Steyn and Hanks (1983) and Roche (1978).