Homologies of the Anterior Teeth in Indriidae and a Functional Basis for Dental Reduction in Primates

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ABSTRACT In a recent paper Schwartz ('74) proposes revised homologies of the deciduous and permanent teeth in living lemuriform primates of the family Indriidae. However, new evidence provided by the deciduous dentition of Avahi suggests that the traditional interpretations are correct, specifically: (1) the lateral teeth in the dental scraper of Indriidae are homologous with the incisors of Lemuridae and Lorisidae, not the canines; (2) the dental formula for the lower deciduous teeth of indriids is 2.1.3; (3) the dental formula for the lower permanent teeth of indriids is 2.0.2.3; and (4) decrease in number of incisors during primate evolution was usually in the sequence 13, then 12, then 11. It appears that dental reduction during primate evolution occurred at the ends of integrated incisor and cheek tooth units to minimize disruption of their functional integrity.

Anterior dental reduction in the primate family Indriidae illustrates a more general problem of direction of tooth loss in primate evolution. All living lemuroid and lorisoid primates (except the highly specialized Daubentonida) share a distinctive procumbent, comb-like configuration of the anterior lower dentition — the dental scraper or "toothcomb" used in ingesting resin, prying bark, and in grooming. This dental scraper is composed of six teeth in Lemuridae and Lorisidae, generally considered to be four incisors bordered by two canines (Swindler, '76). The dental scraper of Indriidae consists of only four teeth. It is agreed that these teeth are homologous with four of the six teeth in the scraper of lemurids and lorisids, but the question remains whether the two teeth lost in going from the generalized lemurid condition to the more specialized indriid condition were incisors or canines. The four teeth remaining in the dental scraper of Indriidae are usually considered to be incisors (i.e., the canines were lost; see Vallois, '55; Le Gros Clark, '71; Martin, '72; among others), but they have also been interpreted as an incisor pair bordered by left and right lower canine teeth (i.e., an incisor pair was lost: e.g., Gregory, '20: p. 214).

Schwartz ('74) recently reviewed the problem of tooth homologies in the dental scraper of Indriidae and concluded that no real evidence has ever been presented to support the interpretation that indriids possess four lower incisors and no canines. He then gave several reasons in support of the contrary interpretation that two incisors and two canines make up the indriid scraper.

In the course of a study of dental variation in Indriidae, a specimen of Avahi retaining deciduous teeth was found that supports the traditional interpretation of homologies of the permanent and deciduous dentition of Indriidae. This new evidence is presented to help clarify anterior dental reduction in Indriidae. The whole problem is especially important as it has a direct bearing on our understanding of the general problem of dental reduction in primate evolution.

MATERIALS AND RESULTS

Dried skulls of adult animals of virtually all genera of Lemuridae, Lorisidae, and Indriidae were examined in the collections of the Cleveland Museum of Natural History, the British Museum (Natural History) in London, the Rijksmuseum van Natuurlijke Historie in Leiden, and the Laboratoire d'Anatomie Com-
Lemuridae, Lorisidae, and Indriidae have the same number of deciduous teeth (six) in each mandible. These teeth in Lorisidae and Lemuridae (figs. 3, 4) have basically the same morphology, and the deciduous formula is agreed to be 2.1.3, with the first three teeth forming a deciduous dental scraper. In the Indriidae, both Indri and Propithecus (fig. 1) have a rather different configuration, with only two procumbent anterior teeth in each mandible contributing to the deciduous dental scraper. In Indri and Propithecus these are followed by a small tooth, a relatively large tooth, a small tooth, and another relatively large tooth. By comparison with Lemuridae, the deciduous dental formula of Indriidae is usually given as 2.1.3 in spite of the morphological differences of the teeth from those in Lemuridae. However, Schwartz ('74) has recently interpreted this deciduous formula as 1.1.4 (as did Gregory, '20).

The smallest indriid species, Avahi laniger, significantly has an anterior deciduous dentition more similar to that of Lemuridae than to Indri and Propithecus (fig. 2). Of particular importance is the third tooth in the deciduous series, a tooth Schwartz ('74) called tooth “A.” Tooth “A” in Indri and Propithecus (fig. 1) is a very small tooth usually separated from the dental scraper by a small diastema. However, in Avahi this tooth “A” has an elongated, procumbent crown that forms a functional unit with the other teeth of the deciduous dental scraper. The crown of tooth “A” in Avahi is relatively much larger than tooth “A” in Indri and Propithecus. It does not show the wear found in Schwartz’s Age Group II Indriidae and its position cannot be attributed to mesial drift associated with wear. Because of its similarity in position and morphology to the lower deciduous canine of Lemuridae, tooth “A” in Avahi is almost certainly a deciduous canine. The lower deciduous formula of the Indriidae is thus probably 2.1.3 as it is in Lemuridae and Lorisidae, which also matches the upper deciduous formula in these three families.

As shown in figures 3 and 4, the incisors and canines of the deciduous dental scraper in Lemuridae are all replaced by incisors and canines of the permanent scraper, whereas in Propithecus, Indri, and Avahi (fig. 2), the deciduous canine “A” is not replaced by a permanent tooth. Thus it appears that the permanent lower dental formula of Indriidae is properly interpreted as 2.0.2.3, which matches the permanent upper formula of 2.1.2.3 except for loss of the canine.

DISCUSSION OF HOMOLOGIES IN INDRIIDAE

Schwartz ('74) based his conclusion that the lower deciduous dental formula of Indriidae is 1.1.4 and the lower permanent formula 1.1.2.3 on three lines of evidence: (1) the morphology of the lateral tooth in the indriid dental scraper (both deciduous and permanent) is most similar to that of the canine in lemurs and lorisids; (2) tooth “A” in indriids sometimes occludes behind the upper canine and thus by definition tooth “A” must be a deciduous premolar and not a canine; and (3) ontogenetic studies on the mammalian dentition have shown that incisor teeth develop from the dental lamina in an anteroposterior direction. Each of these lines of evidence is discussed in turn.

Dental morphology is correlated with tooth function, and morphological similarity is not always a reliable indicator of homology. The left and right lateral teeth in the indriid dental scraper are most similar morphologically to the canines in the lemurid or lorisid dental scraper. The main feature that makes them similar is a raised crest running along the lateral margin from the tip to the base of the crown. However, a very similar raised lateral crest (a “margocristid”: Gingerich, '76) is also present on the enlarged procumbent central incisors of early Tertiary plesiadapid, microsypid, and omomyid primates. Furthermore, a 6-tooth dental scraper or comb virtually identical to that of a lemur, including the raised margocristids on the lateral teeth, is known in the early Eocene condylarth Thryptacodon (Princeton University no. 20853), which also retains large projecting canine teeth — the lemur-like lateral teeth of
the scraper are thus incisors and not canines as in *Lemur*. The presence of raised margo-
cristids on the lateral teeth in the dental
scraper of indriids is probably closely corre-
lated with tooth position and dental function
and not a reliable indicator of their homology
with the lower canines of lemurids.

The fact that tooth “A” sometimes occludes
behind the deciduous upper canine (in very
young individuals of Schwartz’s Age Group I)
does not necessarily define its homology, as
Schwartz (’74: p. 112) suggests. The conven-
tional identifications of teeth widely used in
mammalogy refer primarily to tooth positions
and occlusal relationships in primitive and
generalized mammals — to prove that a given
tooth in a specialized mammal is homologous
with the canine tooth in a generalized mam-
mall requires that the tooth be traced phy-
letically back to the canine in a generalized
mammal. Unfortunately, the fossil record of
Indriidae is insufficient to permit one to trace
the deciduous tooth “A” back to its homologue
in a generalized mammal — it can only be
compared with similar teeth occupying the
same position in the closely related Lemuri-
idae and Lorisidae. As discussed above, when
the deciduous dentition of *Avahi* is compared
with that of the Lemuridae, it is seen that
tooth “A” in Indriidae is almost certainly ho-
logous with the tooth identified in Lemuri-
daes as a deciduous lower canine and not a pre-
molar.

Phylogenetic sequences are not necessarily
recapitulated in ontogenetic sequences, and
ontogenetic development cannot be used in
any deterministic way to rediscover phyloge-
netic history. Functional adaptation and the
selective value of all stages of development
prevent a direct reading of phylogenetic his-
tory from ontogenetic sequences. Thus one
must view cautiously Schwartz’s (’74) sugges-
tion that incisors will be lost phylogenetically
from the front to the back of the jaws because
they develop ontogenetically from the front
to the back. Schwartz’s discussion (’74: pp. 112-
113) is based on the questionable assumption
that the development of the incisor series
plays an essential role in development of the
canine. According to Schwartz, inhibition of
the posterior end of the incisor sequence
would effect an inhibition on the canine. To
prevent this inhibition of canine development,
Schwartz reasons that incisor inhibition
would occur at the front and not at the back of
the incisor series. However, the reference
Schwartz cites on dental development in
mammals, Osborn (’73: p. 554) states that in-
cisor, canine, and molar determinants are
usually present in the earliest embryos in
which tooth formation is evident. In other
words, the canine determinant is present
whether the incisor developmental sequence
approaches it or not. Thus it is unlikely that
Schwartz is correct in assuming that inhibi-
tion of the posterior incisor series would ef-
flect an inhibition of the canine. Following
Osborn (’73), the fact that deciduous incisors
develop from front to back would make it ap-
pear that the easiest way to reduce the num-
ber of incisors in a dental series would be to
suppress those that develop last, i.e., reduce
the sequence by losing I₃ first, then I₂, and fin-
ally I₁.

FUNCTIONAL BASIS FOR DENTAL REDUCTION
IN PRIMATES

Another reason to expect incisors to be lost
from back to front has to do with the func-
tional adaptation interface between develop-
ment and phylogeny alluded to above. The
mammalian dentition can be divided into sev-
eral functional units: an incisor unit related
to food acquisition; a canine unit related to
food acquisition, display, etc.; and a cheek
tooth unit related to the mastication of food.
These functional units obviously correspond
to Butler’s (’39) morphogenetic fields in the
mammalian dentition. If any unit is reduced
in functional importance it may be reduced in
size, and perhaps ultimately lost. This gradual
reduction can be expected to proceed in a defi-
nite way, however, to preserve the functional
integrity of the unit as a whole. If projecting
and interlocking canine teeth are not required
they can be reduced and altered into in-
cisiform or premolariform teeth to contribute
to food acquisition or mastication. In some
mammals the canines are lost entirely.

Since the cheek tooth series usually func-
tions as a unit in each jaw, loss of teeth from
the front or back of the series would be ex-
pected rather than loss of teeth from the mid-
dle of the series. An exception may occur
when the most anterior lower premolar par-
ticipates in the canine functional unit (as
happens in Indriidae, where P₃ appears
to have been lost, while P₂ was retained as part
of the canine unit; see fig. 1 and Godfrey, ’76).
Loss of M₁ in New World Callitrichidae illus-
trates molar loss from the back of the cheek
tooth series.
Given that left and right incisors function as a single unit crossing the midline of the skull, one would expect, for functional reasons, that loss of incisors would occur from the sides of the unit and not from the middle of it. This is perhaps the most compelling reason why one would expect that incisors would be lost in the sequence I₂, then I₁, and finally I₁. In lemuriform primates where the lower canines are functionally the lateral members of the incisor series, one would expect the canines to be lost before the more centrally placed incisors are, and this sequence appears to be documented by partial reduction of the lower deciduous canines in *Avahi*, their more complete reduction in *Propithecus* and *Indri*, and complete loss of lower canines in the permanent dentition of all three extant genera of Indriidae.

In some of the best documented phyletic series of fossil primates, incisors were clearly lost from back to front (Plesiadapidae: Gingerich, '76), and premolars of the cheek tooth series were reduced from front to back (Plesiadapidae, Carpolestidae: Rose, '75; Adapidae: Gingerich, '77).

For reasons primarily related to the functional integrity of the incisor and cheek tooth units, it is concluded that incisors are usually lost phylogenetically from back to front in primates (i.e. in the sequence I₂, then I₁, then I₁), premolars are usually lost from front to back, and molars are usually lost from back to front. This general conclusion makes sense developmentally in that it is easily effected by suppression of the latest forming tooth buds, and it is supported by the available paleontological evidence.

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**LITERATURE CITED**


PLATE
PLATE 1

EXPLANATION OF FIGURES

1 Propithecus verreauxi in oblique lateral view, showing the deciduous dentition. Permanent first and second molars in course of eruption are visible in the upper dentition. Tooth "A" is here regarded as the deciduous lower canine by analogy with tooth "A" in Avahi (fig. 2) and the deciduous lower canine of Hapalemur (C in fig. 3) and Lemur (C in fig. 4). Scale approximately twice natural size. Specimen is in Leiden, Propithecus verr. coquereli "f."

2 Avahi laniger in occlusal view stereophotograph, showing the lower deciduous dentition. Deciduous P, has been replaced by the erupting permanent Pc, and M, is fully erupted. Tooth "A" is followed by dP, and a small dP3 on the left side, as in Propithecus (fig. 1). On the right side dP3 has fallen out. Note the forwardly inclined, styliform tooth A, which is slightly reduced in size but otherwise similar to the deciduous canine (C) in Hapalemur (fig. 3) and Lemur (fig. 4). The central four teeth are permanent replacement teeth, but tooth "A" lacks a permanent replacement. Scale four times natural size. Specimen is in Leiden, no. 23118.

3 Hapalemur griseus in occlusal view stereophotograph showing the lower deciduous dentition and the lower first permanent molar. Tooth "C," the lateral tooth in the deciduous dental scraper is replaced by the permanent canine, which also forms the lateral tooth in the permanent dental scraper. Scale is twice natural size. Specimen is in Leiden, Hapalemur griseus "p."

4 Lemur macaco in occlusal view stereophotograph showing the lower deciduous dentition and the lower first permanent molar. As in Hapalemur (fig. 3), tooth "C" is the deciduous lower canine. Note six teeth of the permanent dental scraper visible behind the teeth forming the deciduous scraper. Scale is twice natural size. Specimen is in Leiden, Lemur macaco "w."

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