**Folia Primatologica**
Editor: J. BIEGERT, Zurich
Publishers: S. KARGER, Basel
SEPARATUM (Printed in Switzerland)
Folia primatol. *28:* 144–153 (1977)

# Dental Variation in Early Eocene *Teilhardina belgica*, with Notes on the Anterior Dentition of Some Early Tarsiiformes

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*Key Words.* Dental variation · *Teilhardina* · Omomyidae · Eocene primates

*Abstract.* Statistical analysis of dental variation in specimens currently placed in *Teilhardina belgica* from the Belgian locality of Dormaal suggests that these specimens probably represent no more than a single biological species. Within this species sample, most specimens have an alveolus for '$P_1$' (or the anterior root of $P_2$), but one specimen clearly lacks this alveolus. In the type specimen of *Teilhardina belgica*, the alveolus for the lower central incisor was only slightly larger than that for $I_2$, a similarity to some other omomyids. The similarities shared by *Teilhardina* and Eocene Adapidae all appear to be retentions of primitive primate morphology, and thus they do not necessarily indicate any close relationship of early Omomyidae and Adapidae.

## *Introduction*

TEILHARD DE CHARDIN [1927] first described the most common small primate from the Belgian locality of Dormaal as a new species of *Omomys*. Subsequently, SIMPSON [1940] placed TEILHARD'S species in a new genus *Teilhardina*. This species, *Teilhardina belgica*, has been figured and discussed by many authors subsequently. Most recently BOWN [1976] and SZALAY [1976] have published somewhat contradictory interpretations of the Belgian *Teilhardina*. The purpose of this paper is to describe the variation in tooth measurements and dental formulae seen in the Dormaal material, with particular reference to the question of whether more than a single biological species may be represented. In addition, the alveolar conformation of the anterior dentition of *Teilhardina* is described and compared with that of some other omomyids, and certain implications for the phylogenetic relationships of *Teilhardina* are discussed.

### *Tooth Size*

The entire sample of *T. belgica* in the Institut Royal des Sciences Naturelles, Brussels, and two additional mandibles in the private collection of Dr. P. GIGASE in Antwerp, were studied to quantify variation in tooth size and in dental formulae. Teeth in 17 mandibles were measured. Unfortunately, the only maxilla known [SZALAY, 1976, fig. 2] is now badly damaged, and it was possible to measure only the length of each tooth from that specimen. The remainder of the dental measurements were made on isolated teeth. Each of the lower teeth is sufficiently distinctive to permit its true homology to be determined by inspection, but in the upper dentition isolated $M^1$ and $M^2$ cannot be distinguished reliably and thus the measurements of these two teeth had to be combined for analysis.

The available data on variation in tooth size in *Teilhardina* are presented in table I. The coefficients of variation of these dental measurements are all well within the range typical of a single population of a fossil or modern biological species [GINGERICH, 1974].

The histogram of *Teilhardina* plotted in figure 1 indicates that variation in $M_1$ size is approximately normally distributed, and that this variation is comparable to that of other Omomyidae (s.l.) from the early and middle Eocene of Europe. In each of the three examples given in figure 1, the total range of variation is about 0.15 on the log scale used. The range and distribution of variation in *T. belgica* is comparable to that of other biological species, and the most reasonable conclusion, given the very close morphological similarity of all specimens, is that a single biological species is represented at Dormaal. There is no evidence from dental morphology or size variation to suggest that more than a single species is represented.

### *Dental Formula*

The dental formula of *T. belgica* has been much discussed in the primate literature. Most recently, BOWN [1976] has stated that *T. belgica* definitely lacked a $P_1$, and that those specimens, if any, retaining a $P_1$ must belong to a different genus. On the other hand, SZALAY [1976] states that *T. belgica* definitely does retain $P_1$. In an attempt to determine the true dental formula of this species, all specimens were carefully examined under a binocular microscope to determine the presence or absence of the alveolus labeled 'a' in figure 2. The results of this examination are given in table II.

*Table I.* Summary of dental measurements of *T. belgica* from Dormaal

| | | n | Range | x | s | V |
|---|---|---|---|---|---|---|
| $P_3$ | L | 10 | 1.2–1.3 | 1.22 | 0.042 | 3.5 |
| | W | 10 | 0.8–1.0 | 0.91 | 0.057 | 6.2 |
| $P_4$ | L | 18 | 1.2–1.5 | 1.41 | 0.080 | 5.7 |
| | W | 18 | 1.0–1.3 | 1.14 | 0.078 | 6.8 |
| $M_1$ | L | 17 | 1.7–1.9 | 1.78 | 0.075 | 4.2 |
| | W | 16 | 1.2–1.5 | 1.39 | 0.072 | 5.2 |
| $M_2$ | L | 12 | 1.7–1.8 | 1.73 | 0.045 | 2.6 |
| | W | 13 | 1.4–1.6 | 1.49 | 0.049 | 3.3 |
| $M_3$ | L | 9 | 1.6–2.1 | 1.88 | 0.156 | 8.3 |
| | W | 9 | 1.1–1.3 | 1.22 | 0.067 | 5.5 |
| M. depth | | 7 | 2.8–3.2 | 3.03 | 0.125 | 4.1 |
| $P^4$ | L | 8 | 1.4–1.6 | 1.49 | 0.083 | 5.6 |
| | W | 7 | 2.0–2.3 | 2.11 | 0.121 | 5.7 |
| $M^{1+2}$ | L | 16 | 1.5–1.8 | 1.62 | 0.075 | 4.6 |
| | W | 13 | 2.3–2.9 | 2.65 | 0.185 | 7.0 |
| $M^3$ | L | 2 | 1.1 | – | – | – |
| | W | 2 | 1.9–2.0 | 1.95 | – | – |

All specimens in the Institut Royal des Sciences Naturelles, Brussels. L = length; W = width; M. depth = mandibular depth below $M_1$. Isolated upper $M^1$ and $M^2$ cannot be distinguished reliably, and measurements on these teeth have been combined for statistical analysis. n = Sample size; range = range of variation; x = sample mean; s = standard deviation; V = coefficient of variation. Measurements in mm.

Only one specimen of *T. belgica* lacks any trace of alveolus 'a'. The type specimen, Ct.M. 64 (fig. 2), definitely preserves a small laterally placed alveolus 'a' [contrary to BOWN, 1976, p. 65], as did four other specimens. Five specimens preserve a relatively large and more medially placed alveolus 'a'. Thus there is variation in the number, size, and placement of premolar alveoli in *Teilhardina*. Variation of this degree is sometimes seen in other populations of a single species [*Plesiadapis fodinatus* for example, GINGERICH, 1976], and I cannot agree with BOWN [1976] that forms having alveolus 'a' are distinct at the generic level from those that lack it. The morphological variation seen in *T. belgica* is continuous, and within the range characteristic of other biological species, and thus it is probable that a single species is present at Dormaal.

All that can be said at present about the dental formula of *Teilhardina belgica* is that some specimens definitely had two incisors, a canine, only three

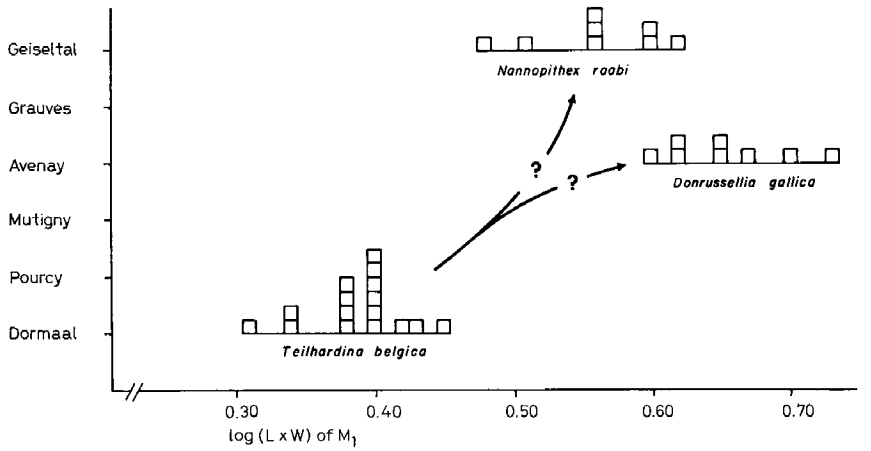


*Fig. 1.* Histograms of $M_1$ size for samples of the European Omomyidae (s.l.) *T. belgica* from Dormaal (Belgium), *Donrussellia gallica* from Avenay (France), and *Nannopithex raabi* from Geiseltal (FRG). Measurements for *Donrussellia* (= *'Teilhardina?'*) are from RUSSELL *et al.* [1967, p. 8]. Dormaal and Avenay are early Eocene localities, and Geiseltal is middle Eocene in age – the total amount of time represented from Dormaal to Geiseltal is about 5–6 million years. The sequence of biostratigraphic reference levels listed at left is discussed in HARTENBERGER [1973]. Phyletic relationships of the three genera shown are as yet unproven.

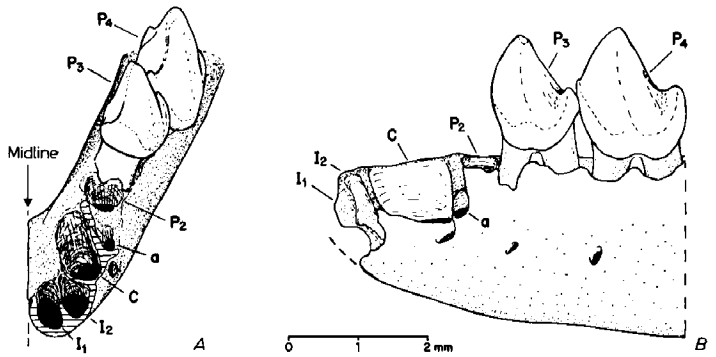


*Fig. 2.* Camera lucida drawings of the type specimen of *T. belgica* (Ct. M. 64), a left mandible from Dormaal. *A* Oblique anterior view looking directly down the incisor alveoli. Horizontal cross-hatching indicates broken bone. Note that the alveolus for $I_1$ is slightly larger than that for $I_2$ – even though it is broken slightly below the level at which $I_2$ is broken. Note also the small size of alveolus 'a', and its lateral position relative to the following alveoli. *B* Same specimen in lateral view showing the position of alveolus 'a'.

premolars (with a single-rooted $P_2$), and three molars, whereas the majority of specimens either retained a $P_1$ or had a double-rooted $P_2$. Uncertainty as to the exact number of premolars will remain until specimens are found preserving the crown of $P_2$ and/or $P_1$ intact.

### *Incisor Conformation*

Two of the most diagnostic differences between Eocene Adapidae and Omomyidae are the relative size and shape of the lower incisors (fig. 3). All adapids for which the lower incisors are known had incisors with spatulate crowns, and central incisors smaller than the lateral ones – like primitive anthropoid primates. All omomyids for which the lower incisors are known had incisors with pointed crowns, and central incisors the same size or larger than the lateral ones – like Paleocene Plesiadapiformes and the living *Tarsius* (in which the lateral pair of incisors has been lost). The incisor morphology of *T. belgica*, one of the earliest omomyid primates known, is of particular importance to understanding the evolution of the incisors in tarsiiform primates. Unfortunately, no mandibles of *Teilhardina* preserve the incisors in place, and no isolated incisors are known that can be referred to this genus. In one specimen of *Teilhardina* it is possible, however, to determine the relative size of the lower central and lateral incisors from their preserved alveoli.

The type specimen of *T. belgica* (Ct. M. 64) preserves enough of the incisor alveoli to permit a reasonably accurate comparison of the size of the two lower incisors. For this purpose a camera lucida drawing was prepared looking directly down the incisor alveoli from the front (fig. 2A). This drawing clearly shows, in agreement with the reconstruction published by SZALAY [1976, fig. 3] that the central incisor alveolus was slightly larger than the lateral one. *Teilhardina* is thus like most other omomyids in having central incisors relatively larger than the lateral ones, and it is unlike adapids and anthropoid primates in this characteristic.

Specimens of two omomyid genera, *Anaptomorphus* and *Washakius*, having small lower central incisors are illustrated in figure 4. These are the only specimens of omomyids having small lower central incisors for which the anterior alveoli are preserved intact. *Teilhardina* had a relatively small lower central incisor (fig. 2), and judging from SZALAY's [1976] monograph, *Chlororhysis*, *Chumashius*, *Loveina*, and *Shoshonius* (the latter, at least, possibly being ancestral to *Washakius*) also had small lower central incisor alveoli. The lower incisors and/or alveoli are known in many of the remaining twenty

*Table II.* Relative development of alveolus 'a' (fig. 2) in *T. belgica*

| Development | Specimen numbers | Total |
|---|---|---|
| No alveolus 'a' | Gigase-1 | 1 |
| Small alveolus 'a', laterally placed | Ct. M.-64 (type), 65, 1165, No number Gigase-2 | 5 |
| Relatively large alveolus 'a', only slightly to lateral side of mandible | Ct. M.-1262, 1263, 4296, 4297, No number | 5 |

Ct. M.-4287 was on loan, and thus not seen. Specimens preceeded by Ct. M. are in the Institut Royal des Sciences Naturelles in Brussels, those preceeded by Gigase are in the private collection of P. GIGASE in Antwerp.

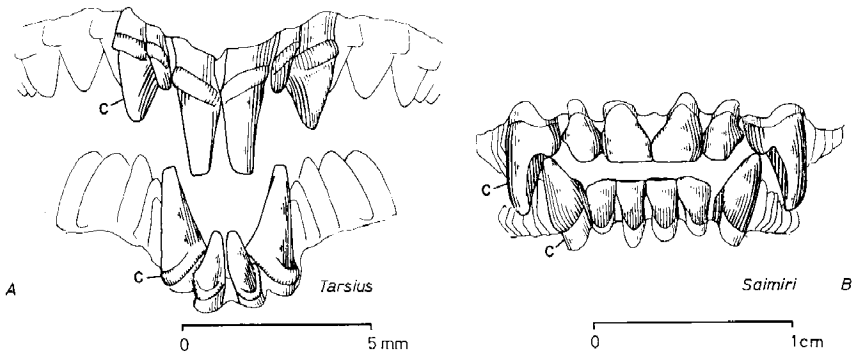


*Fig. 3.* Comparison of the anterior dentition of a living *Tarsius* having procumbent pointed lower incisors (A) with that of a living anthropoid *Saimiri* having vertical spatulate lower incisors (B). *Tarsius*, like all Omomyidae, has an unfused mandibular symphysis, whereas *Saimiri*, like advanced Adapidae and other anthropoid primates, has a fused mandibular symphysis.

or so omomyid genera, and in these the central incisor was clearly larger than the lateral one, as it is in plesiadapiform primates.

The only omomyid with a small lower central incisor in which any part of the crown is known is *Washakius insignis* (fig. 4c, d). Only a small portion of the medial side of the crown is preserved, but it appears to conform more closely to the morphology of incisors having a pointed crown, like that of *Tarsius* (fig. 4E), than to the morphology characteristic of adapids and primitive anthropoids, which have flaring spatulate incisor crowns. Thus, even in

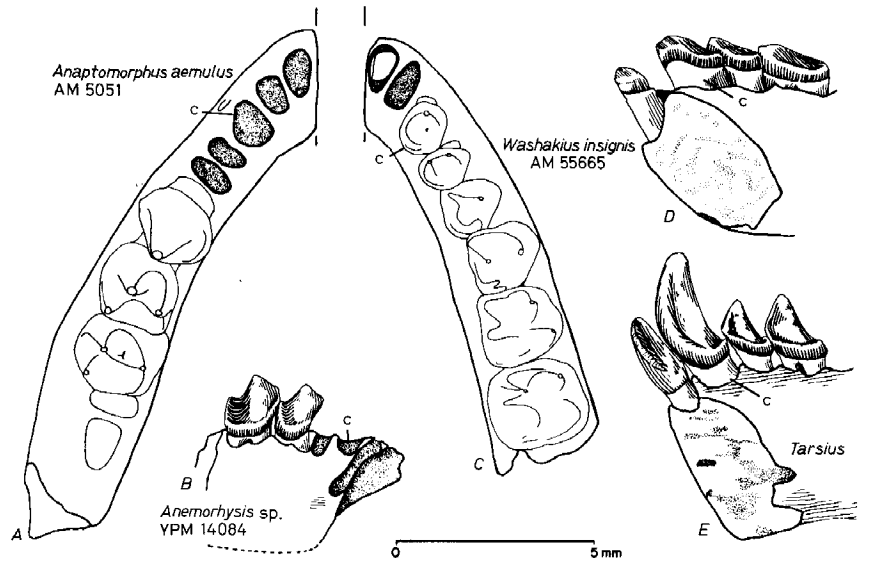


*Fig. 4.* Anterior dentitions of some Eocene North American Omomyidae compared to that of a living *Tarsius*. Letter 'c' indicates position of lower canine in each specimen. Note that *Anaptomorphus* and *Washakius* have small central incisor alveoli approximately the same size as the lateral incisor alveoli, whereas in *Anemorhysis*, as in most Omomyidae, the central incisor was much larger than the lateral one. The central incisor of *Tarsius* is procumbent and pointed as in known tarsiiform fossil primates, but the lateral incisor has been lost completely. Note faint ridge of enamel on medial side of preserved portion of the crown of $I_1$ in *Washakius*, suggesting that this incisor had a pointed rather than flared spatulate crown. *A* Left mandible of *Anaptomorphus aemulus* (type) in oblique occlusal view. *B* Right mandible of *Anemorhysis* sp. in lateral view. *C* Right mandible of *Washakius insignis* in oblique occlusal view. *D* Same specimen as C in medial view. *E* Anterior dentition of *Tarsius* in medial view.

the few omomyids with small lower central incisors, these central incisors were as large or larger than the lateral ones and they probably had pointed crowns.

## *Phylogenetic Relationships*

SIMONS [1972] referred to the Eocene omomyids and adapids as 'primates of modern aspect' contrasting them in grade with earlier and more primitive

*Table III.* Morphological characteristics shared by *Teilhardina* and primitive plesiadapiform primates (left column), and characteristics shared by *Teilhardina* and primitive adapid primates (right column)

| *Teilhardina* – Plesiadapiformes | *Teilhardina* – *Pelycodus* |
|---|---|
| Dental formula $\overline{2} \cdot \overline{1} \cdot \overline{3} \cdot \overline{3}$ (possibly all *Teilhardina*) | Dental formula $\overline{2} \cdot \overline{1} \cdot \overline{4} \cdot \overline{3}$ (possibly some *Teilhardina*) |
| Relatively large, projecting canines | Relatively large, projecting canines |
| Postprotocingulum on upper molars | Postprotocingulum on upper molars |
| Slightly molarized premolars | Slightly molarized premolars |
| Arrangement of trigonid cusps | Arrangement of trigonid cusps |
| Relatively small size | |
| $I_1$ as large or larger than $I_2$ | |

Characters from BOWN [1976, p. 63] and other sources.

plesiadapiform primates. I have previously suggested that the close similarity of the molars of *Pelycodus*, *Teilhardina*, and *'Tetonoides' (Anemorhysis)* indicated that the Omomyidae and Adapidae were closely related [GINGERICH, 1973]. BOWN [1976] writes of the early Eocene Lemuroidea and Tarsioidea as a single adaptive radiation, and SZALAY [1976, fig. 138] has suggested that tarsiiform Omomyidae may have originated from an as yet unknown Paleocene member of the lemuriform Adapidae. As one of the earliest known omomyids, *Teilhardina* might be considered to have special importance in determining whether the Omomyidae and Adapidae are parts of a single adaptive radiation or represent two separate parallel radiations. Stated somewhat differently, and more specifically, the question is whether *Teilhardina* is more closely related to the contemporary early Eocene adapid *Pelycodus* or to plesiadapiform primates characteristic of the Paleocene.

*Teilhardina* is compared with *Pelycodus* and with primitive Plesiadapiformes in table III. As might be expected in comparing very early, primitive primates, all of the character states shared by *Teilhardina* and plesiadapiform primates are thought to be primitive. Significantly, all of the similarities shared by *Teilhardina* and *Pelycodus* that have been previously cited in the literature are also primitive characteristics by comparison with *Purgatorius* and middle Paleocene primates – these similarities are fewer in number and appear to be of less importance than the similarities between *Teilhardina* and

plesiadapiform primates. Thus *Teilhardina* furnishes no evidence to contradict the hypothesis that the Omomyidae represent a radiation derived from Paleocene Plesiadapiformes, and the Adapidae represent a separate parallel radiation in the Eocene [GINGERICH, 1976, fig. 42]. The only primate known that could possibly represent the last common ancestor of the Omomyidae and Adapidae is *Purgatorius* [CLEMENS, 1974] from the early Paleocene of North America.

## *Acknowledgments*

I thank Dr. P. BULTYNCK, Institut National des Sciences Naturelles, Brussels, and Dr. P. GIGASE, Antwerp, for access to specimens of *T. belgica*. Professor H. MATTHES, Halle, permitted study of specimens of *Nannopithex* in his care. In addition, I am indebted to Professors E. L. SIMONS (Yale Peabody Museum; YPM), and M. C. MCKENNA, American Museum of Natural History (AM) for the loan of specimens figured here. This research was conducted during tenure of a NATO Postdoctoral Fellowship in the Laboratoire de Paléontologie, Université de Montpellier, and I thank Professor L. THALER for laboratory facilities. At the University of Michigan, Ms. KRYSTYNA SWIRYDCZUK drew figures 3 and 4, and Mrs. GLADYS NEWTON typed the manuscript. I also thank KENNETH D. ROSE for his comments improving the manuscript.

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