Darwinius is an adapoid primate from the Eocene of Germany, and its only known specimen represents the most complete fossil primate ever found. Its describers hypothesized a close relationship to Anthropoidea, and using a Saimiri model estimated its age at death. This study reconstructs the ancestral permanent dental eruption sequences for basal Euprimates, Haplorhini, Anthropoidea, and stem and crown Strepsirrhini. The results show that the ancestral sequences for the basal euprimate, haplorhine and stem strepsirrhine are identical, and similar to that of Darwinius. However, Darwinius differs from anthropoids by exhibiting early development of the lower third molars relative to the lower third and fourth premolars. The eruption of the lower second premolar marks the point of interruption of the sequence in Darwinius. The anthropoid Saimiri as a model is therefore problematic because it exhibits a delayed eruption of P2. Here, an alternative strepsirrhine model based on Eulemur and Varecia is presented. Our proposed model shows an older age at death than previously suggested (1.05–1.14 years), while the range for adult weight is entirely below the range proposed previously. This alternative model is more consistent with hypotheses supporting a stronger relationship between adapoids and strepsirrhines.

1. Background

Adapoids were medium-sized, arboreal euprimates, widespread throughout portions of Europe, Asia, Africa and North America from the Early Eocene to the Late Miocene. Adapoids were a very diverse group, comprising six families and more than 100 species [1–3]. Despite receiving considerable attention in the literature, the evolutionary relationships of adapoids to modern strepsirrhines or haplorhines remain unclear. Currently, two opposing hypotheses predominate: (i) the Adapoid–Anthropoid hypothesis [4–17] and (ii) the Adapoid–Strepsirrhine hypothesis [18–25].
The Adapoid–Strepsirrhine hypothesis has been more broadly accepted for the past two decades, based on the fact that it is recovered in all broadly sampled, recent phylogenetic analyses [22,26–29]. However, the debate surrounding the phylogenetic position of adapoids was thrust back into prominence with the description of the most complete fossil primate skeleton, the caenopithecid adapoid *Darwinius masillae*. Franzen et al. [17] proposed a stronger relationship between *Darwinius* and haplorhines, and Gingerich et al. [30] later united it specifically with anthropoids. Since then, the biology and the evolutionary relationships of *Darwinius* and adapoids to modern primates have been discussed extensively in the literature (e.g. [23,24,31–36]). An area that has received much less treatment than the question of *Darwinius*’ phylogenetic position is the age model used [17] to reconstruct its body mass and age at death. This paper considers the appropriateness of anthropoids generally, and *Saimiri* specifically, with respect to choosing an appropriate model for *Darwinius*’ development, and also assesses the relevance of growth data to the phylogenetic debates.

1.1. Relevance of dental eruption sequences in primate life history

Life-history analysis assesses the chronology of development and reproduction throughout a species’ lifetime, from conception to death. The pattern and timing of tooth emergence known for extant primates can be used to broadly infer the life history of fossil groups [37–39]. This is particularly useful for fossil taxa, in which the dentition is the primary and most reliable gauge of ontogeny [39]. The relevance of the dentition as a source of information to explain life history relies on the fact that it is not strongly influenced by environment [40]. There is also a relationship between the sequence of dental eruption and the overall pace of growth, maturation and other aspects of primate life history [41]. For example, *M*₁ is the first permanent tooth to erupt in primates, and the timing of its emergence is highly correlated with adult brain weight, body weight and probably reflects infant precociality [40,42]. In order to use data from dental eruption sequences in modern taxa to form inferences about a fossil, it is necessary to define the point of interruption of the sequence. Defining this point allows for modern growth trajectory data to be used to determine not only age at death but also other variables such as projected adult weight (e.g. [17]).

1.2. Dental eruption and life history of *Darwinius*

The *Darwinius* specimen is split into two parts: PMO 214.214 and its counterpart WDC-MG-210 [17]. The specimens, altogether nicknamed ‘Ida’, come from the site of Messel (near Darmstadt, Germany; 47.5 Ma [43]). The individual was a weaned and independently feeding juvenile, with an erupted *M*₁ [17]. Based on the absence of a baculum, the specimen has been interpreted as female [17], although it is possible that this element was lost (e.g. along with the left lower limb below the knee) or had not fully developed at the time of the animal’s death.

The preserved dentition (figure 1) allows for several inferences about the permanent dental eruption sequence. We follow Gingerich & Smith’s [44] inference that *P*₂ is an adult tooth, and Franzen et al. [17] in considering it to be the last tooth to have emerged before death. It is known that variability in the premolar eruption sequence is common in some New World monkeys, such as in *Callithrix, Alouatta, Saimiri, Callithrix, Mico, Saguinus* and *Cebus* [45–47]. However, there is no intraspecific variability reported in the presence of *P*₂ in adapoids [48,49], and no reported variation in eruption sequences [44]. Therefore, *a priori*, there is no empirical basis for believing the eruption of *P*₂ in *Darwinius* is variable, or that *P*₂ erupted unusually early or late in ‘Ida’. We are additionally assuming that d*P*₂ is replaced by *P*₂ in ‘Ida’, as it is in modern primates that retain this tooth. It is possible that this is an incorrect assumption, and that *P*₂ emerged without having a deciduous precursor, in a manner similar to *P*₁ in many living mammals [50]. However, loss of *P*₁ replacement is inferred to be a very ancient feature in mammalian evolution, based on its absence in even some non-eutherians (e.g. *Didelphis* [51]), whereas in all adapoids for which there are adequate data, *P*₂ is known to be replaced [18,44]. As such, arguing for a lack of a deciduous precursor for *P*₂ would require the assumption that this particular lineage developed a peculiar homoplasy, not observed in living primates. Although this is of course possible, in the absence of any data it seems more parsimonious to assume that *Darwinius* was a typical adapoid and replaced its *P*₂. It is worth noting that in applying a *Saimiri* model, or indeed a model based on any living primate (e.g. [17,44]), this same assumption is being made.

¹PMO: Geological Museum, Natural History Museum, University of Oslo; WDC-MG: Wyoming Dinosaur Center, Messel Grube collection.
Following from this inference, the teeth of *Darwinius* can be divided in two sets: \((M_1\ M_2\ I_1\ P_2)\), which are adult and erupted, and \((I_2\ M_3\ C\ P_4\ P_3)\), which are in various stages of development and have yet to erupt, with the point of interruption in the sequence occurring after the eruption of \(P_2\) [17]. Using the dental eruption sequence of the New World anthropoid *Saimiri* as a model, Franzen et al. [17] estimated an age at death between 9 and 10 months based on the interruption of the dental eruption sequence, and a projected adult weight between 650 and 900 g. For the unerupted teeth, it is also possible to make certain inferences about their likely place in the sequence based on their degree of development. For example, the crown of \(M_3\) is completely formed and the tooth is in process of erupting. It was probably only covered by soft tissue, although it still lacks mineralized roots [17]. Therefore, this would place the timing of eruption of \(M_3\) early in the sequence.

The goals of the present study are to reassess the age estimate for *Darwinius* by using ancestral reconstruction of dental eruption sequences, and to further explore the life history of *Darwinius*. Specifically, we assess the validity of using the anthropoid (*Saimiri*) model for inferring the age and life history of *Darwinius*.

2. Material and methods

Ancestral state reconstruction has been embraced by both systematists and evolutionary biologists for many years [52] as a way of making inferences about the pattern of evolution of particular traits or character complexes. Indeed its implementation can be traced back almost 30 years to the work of Felsenstein [53]. Since then, this method has been applied extensively by many authors in the field of palaeontology (e.g. [54–64]). For the ancestral state reconstruction analysis in this study, dental eruption sequences for 97 fossil and extant taxa were used, including Primates, Scandentia and Soricomorpha (table 1). A matrix of 14 characters related to eruption sequences was created (table 2). The 14 characters used in our matrix constitute the minimum number of informative characters needed to allow the reconstruction of eruption sequences. These characters code for presence or absence of certain teeth, and relative timing of eruption of teeth in different positions. By reconstructing the ancestral states for every character, it is possible, from the information they provide, to infer the order of dental eruption at any particular node on the tree. Although not all of the characters are independent, because of the way they are defined, it is impossible for them to generate conflicting reconstructions. For example, in electronic supplementary material, table S2, the ancestral reconstruction for the euprimate node for character 6 ‘Eruption of \(I_1\) relative to the earliest premolar’ recovers both states (i.e. \(I_1\) erupting before or after the earliest premolar), instead of one ancestral state. However, because all incisors erupt unequivocally before \(M_2\) (character 8, state 3) and all premolars erupt unequivocally after \(M_2\) (character 12, state 0), the ancestral state for character 6 resolves as \(I_1\) erupting before the earliest premolar.
Table 1. List of lower permanent dental eruption sequences for 97 taxa. Taxa marked with an asterisk (*) had published information on only upper dentition. The time of eruption between lower and upper dentition differs, but the sequence of eruption is usually the same for both dentitions. Parentheses () group teeth that in a fossil are either all emerged or all have not emerged yet. Square brackets [ ] surround teeth when actual sequence has not yet been resolved. Simultaneous eruptions are indicated with teeth united by hyphens, i.e. toothcombs.

| taxon                        | permanent dental eruption sequence                  |
|------------------------------|------------------------------------------------------|
| *Darwinius masillae* [17]    | (M₃, M₂, I₁, P₂) (I₂, C M₃, P₄, P₃)³a               |
| Dymedon pilirostris [65]      | M₃ M₂ M₁ P₄ P₃ I₁ C P₃                              |
| Tupaiya glis [65]             | M₃ M₂ P₄ I₁ P₃ (I₂, C) I₂ P₃                      |
| Acidomomys hebeticus [66]     | M₃ M₂ P₄ (I₁ M₃ I₂ P₃)                             |
| Plesiadapidae [67]            | [M₃, M₂, P₃], [M₃, P₄]                             |
| Microcebus murinus [68]       | M₃ M₂ I₁-I₂-C P₂ M₃ P₄ P₃                         |
| Mira caquereli [68]           | M₃ I₁-I₂-C M₂ P₂ M₃ P₄ P₃                         |
| Cheirogaleus major [68]       | [M₁, I₁-I₂-C M₃], P₄ M₃ P₄ P₃                      |
| Cheirogaleus medius [68]      | [M₁, I₁-I₂-C M₂], P₂ M₃ P₄ P₃                      |
| Allocebus trichotis [68]      | [M₁, I₁-I₂-C M₃], P₂ M₃ P₄ P₃                      |
| Megaladapis edwardsi [69]     | M₃ I₁-I₂-C M₂, P₄ M₃ PP                            |
| Lepilemur mustelinus [68]     | M₃ M₂ I₁-I₂-C P₂ M₃ P₄ P₃                         |
| Archaeolemur majori [68,69]   | M₃ M₂ I₁-I₂ M₄ P₄ P₃                               |
| Archaeolemur edwardsi [69]    | M₃ M₂ PP M₃ IIP                                    |
| Hadropithecus stenognathus [68,69] | M₃ M₂ I₁-I₂ M₄ P₄ P₃                              |
| Ailanthus [68,69]             | M₃ M₂ I₁-I₂ P₂ M₄ P₃                              |
| Propithecus verreauxi [68,69] | M₃ M₂ I₁-I₂ P₃ M₄ P₃                              |
| Propithecus diadema [68,69]   | M₃ I₁-I₂ M₄ P₄ P₃                                 |
| Hapalemur griseus [68]        | M₃ I₁-I₂-C M₂ P₄ M₃ P₄ P₃                         |
| Lemur catta [42,70]           | M₃ M₂ I₁-I₂-C P₂ M₄ P₃ P₃                         |
| Eulemur mongoz [71]           | M₃ I₁-I₂-C M₂ P₄ M₃ P₄ P₃                         |
| Eulemur rufus [42,70]         | M₃ I₁-I₂-C M₂ P₄ M₃ P₄ P₃                         |
| Eulemur macaco [71,72]        | M₃ I₁-I₂-C M₂ P₄ M₃ P₄ P₃                         |
| Varecia sp. [42,73]           | M₃ I₁-I₂-C M₂ P₄ M₃ P₄ P₃                         |
| Otolemur crassicaudatus [74]   | M₃ I₁-I₂-C M₂ P₄ M₃ P₄ P₃                         |
| Sciurocheirus alleni [74]     | M₃ I₁-I₂-C M₂ P₄ M₃ P₄ P₃                         |
| Galago senegalensis [74]      | M₃ I₁-I₂-C M₂ P₄ M₃ P₄ P₃                         |
| Galago gallarum [74]          | M₃ I₁-I₂-C M₂ P₄ M₃ P₄ P₃                         |
| Galago moholi [74]            | M₃ I₁-I₂-C M₂ P₄ M₃ P₄ P₃                         |
| Galagoideus demidovii [74]    | M₃ M₂ I₁-I₂-C M₂ P₄ P₃ P₄ P₃                      |
| Loris tardigradus [74]        | I₁-I₂-C M₂ M₃ M₂ M₃ P₄ P₃                         |
| Nycithecus javanicus [74]      | I₁-I₂-C M₂ M₃ M₂ M₃ P₄ P₃                         |
| Nycticebus couang [74]        | I₁-I₂-C M₂ M₃ M₂ M₃ P₄ P₃                         |
| Perhideticus potto [74]       | I₁-I₂-C M₂ M₃ M₂ M₃ P₄ P₃                         |
| Notharctus tenebrosus [18,44] | M₃ P₄ M₃ M₂ P₄ P₃                                 |
| Adapis parisiensis [2,44,75]  | M₃ P₄ M₂ P₄ P₃                                     |
| Sivaladapis nagri [1]         | M₃ I₁ P₂ (C P₃) P₃                                 |
| Tarsidae [76]                | [M₃, P₃], I₁ M₂ M₃-C P₄ P₃                        |
| Homunculus patagonicus* [77]  | [M₁, I₁], M₂ P₄ P₃ P₃ M₃ C                         |

(Continued.)
| taxon                                      | permanent dental eruption sequence |
|-------------------------------------------|-----------------------------------|
| *Saguinus fuscicollis* [78]               | M₁ I₁ I₂ M₂ P₂ P₃ P₄ C            |
| *Saguinus oedipus* [46]                   | M₁ I₁ [I₂ M₂] (P₂ P₄) P₃ C       |
| *Saguinus midas* [46]                     | M₁ I₁ I₂ M₂ P₂ P₃ C              |
| *Saguinus mystax* [46]                    | M₁ I₁ I₂ M₂ (P₄ P₃) P₃           |
| *Saguinus bicolor* [46]                   | M₁ I₁ [I₂ M₂] P₄ P₂ P₃            |
| *Leontopithecus sp.* [79]                 | M₁ I₁ I₂ M₂ P₄ P₂ P₃ C           |
| *Callimico goeldii* [79]                  | M₁ [M₂ I₁] [P₄ P₂ P₃ M₃] C       |
| *Cebuella pygmaea* [79]                   | M₁ [M₂ I₁] [P₄ P₂ P₃] C          |
| *Callithrix jacchus* [80, 81]              | M₁ M₂ I₁ [P₄] P₃ [C M₃]          |
| *Mico argentatus* [46, 81]                | M₁ [M₂ I₁] [P₄ P₃] P₃ C          |
| *Mico humeralifer* [46, 81]               | M₁ M₂ [I₁ I₂] P₂ P₄ P₃ C         |
| *Aotus trivirgatus* [65]                  | M₁ M₂ I₁ M₂ I₃ P₄ P₂ P₃ C        |
| *Cebus capucinus* [79]                    | M₁ I₁ I₂ M₂ P₂ P₃ [P₄ M₃] C      |
| *Cebus albifrons* [79]                    | M₁ I₁ I₂ M₂ P₂ P₃ [C M₃]         |
| *Sapajus apella* [79]                     | M₁ I₁ I₂ M₂ P₂ P₃ C M₃           |
| *Saimiri sciureus* [70]                   | M₁ M₂ I₁ M₂ P₃ P₂ P₃ C           |
| *Alouatta sp.* [79]                       | M₁ I₁ I₂ M₂ P₂ [P₃ M₃] C         |
| *Stirtonia victoriae* [47]                | (M₁ I₁ P₂) P₄ P₃ M₃ C           |
| *Lagotricha sp.* [79]                     | M₁ I₁ I₂ M₂ P₂ P₃ P₄ P₃ M₃ C     |
| *Ateles sp.* [79]                         | M₁ I₁ I₂ M₂ P₂ P₃ P₄ C M₃        |
| *Brachyteles sp.* [79]                    | M₁ I₁ I₂ M₂ P₂ P₃ P₄ C M₃        |
| *Chiropotes sp.* [79]                     | M₁ I₁ I₂ M₂ P₂ P₃ P₄ C M₃        |
| *Cacajao sp.* [79]                        | M₁ I₁ I₂ M₃ P₂ P₃ P₄ C M₃        |
| *Pithecia sp.* [79]                       | M₁ I₁ I₂ M₃ P₂ P₃ C M₃           |
| *Galago* [79]                             | M₁ I₁ I₂ M₃ P₂ P₃ C M₃           |
| *Apidium phiomense* [66]                  | M₁ M₂ P₂ P₄ (P₃ M₃) C           |
| *Parapithecus grangeri* [72]              | M₁ M₂ P₂ P₄ (P₃ M₃) C           |
| *Chlorocebus pygerythrus* [65]             | M₁ I₁ I₂ M₂ P₂ P₃ C M₃           |
| *Cercopithecus ascanius* [82]              | M₁ I₁ I₂ M₃ P₂ P₃ C M₃           |
| *Macaca nemestrina* [83]                  | M₁ I₁ I₂ M₃ P₂ P₃ C M₃           |
| *Macaca mulatta* [83]                     | M₁ I₁ I₂ M₃ P₃ C M₃              |
| *Macaca fascicularis* [84]                | M₁ I₂ M₃ P₃ C M₃                 |
| *Paradolichopithecus arvemensis* [74]     | M₁ I₁ I₂ M₃ P₂ P₃ C M₃           |
| *Papio anubis* [83]                       | M₁ I₁ I₂ M₃ [P₂ P₄] M₃           |
| *Papio cynocephalus* [83]                 | M₁ I₁ I₂ M₃ P₂ P₃ C M₃           |
| *Papio hamadryas hamadryas* [85]          | M₁ M₂ I₃ P₂ P₃ C M₃              |
| *Theropithecus gelada* [86]               | M₁ I₁ I₂ M₃ P₂ P₃ C M₃           |
| *Lophocebus albigenu* [82]                | M₁ I₁ I₂ [P₂ P₃] M₃ C M₃         |
| *Mandrillus sphinx* [83]                  | M₁ I₁ I₂ M₃ P₂ P₃ C M₃           |
| *Kaseracoelobus aramisi* [87]             | M₁ I₁ I₂ M₂ M₃                   |
| *Mesopithecus pentelicus* [87]            | M₁ I₂ M₂ I₂ PP C M₃              |

(Continued.)
| Table 1. (Continued.) |permanent dental eruption sequence |
|------------------------|----------------------------------|
| Pliocolobus badius [87] | $M_1 \{ I_1 \ I_2 \ M_2 \} \ [P_4 \ P_3 \] \ [C \ M_3]$ |
| Procolobus verus [87]   | $M_1 \ I_1 \ M_2 \ I_2 \ P_3 \ P_4 \ C \ M_3$ |
| Colobus angolensis [83] | $M_1 \ M_2 \ I_1 \ I_2 \ P_4 \ P_3 \ M_3 \ C$ |
| Colobus guereza [83]    | $M_1 \ I_1 \ I_2 \ P_3 \ P_4 \ P_5 \ M_3 \ C$ |
| Presbytis sp. [83]      | $M_1 \ M_2 \ I_1 \ M_3 \ P_4 \ P_3 \ C$ |
| Semnopithecus priam [85]| $M_1 \ I_1 \ I_2 \ P_3 \ C \ P_3 \ M_3 \ C_3$ |
| Trachypithecus sp. [88] | $M_1 \ I_1 \ \{ I_2 \ M_2 \} \ P_4 \ P_3 \ [C \ M_3]$ |
| Nasalis larvatus [87,89]| $M_1 \ I_1 \ I_2 \ M_3 \ \{ PP \ C \}$ |
| Pygathrix sp. [88,89]   | $M_1 \ M_2 \ \{ I_1 \ I_2 \} \ M_3 \ P_4 \ P_3$ |
| Victoriopithecus macinnesi [87,90] | $M_1 \ M_3 \ PP$ |
| Homosapiens             | $M_1 \ I_1 \ M_2 \ P_3 \ P_4 \ M_3 \ C$ |
| Hylabates lar [85]      | $M_1 \ I_1 \ I_2 \ M_3 \ P_4 \ P_3 \ M_3 \ C$ |
| Symphalangus syndactylus [85]| $M_1 \ I_2 \ I_1 \ M_2 \ P_3 \ P_4 \ C \ M_3$ |
| Pongo sp. [41]          | $M_1 \ I_1 \ I_2 \ M_3 \ P_4 \ P_3 \ C \ M_3$ |
| Gorilla sp. [41]        | $M_1 \ I_1 \ I_2 \ M_2 \ P_4 \ P_3 \ C \ M_3$ |
| Pan troglodytes [65]    | $M_1 \ I_1 \ I_2 \ M_3 \ \{ P_3 \ P_4 \} \ M_3 \ C$ |
| Australopithecus africanus [91]| $M_1 \ I_1 \ I_2 \ M_2 \ P_4 \ P_3 \ C \ M_3$ |
| Homo sapiens (Australian aboriginal) [65]| $[M_1 \ I_1 \ I_2 \ C \ P_3 \ \{ M_3 \ P_4 \}] \ M_3$ |
| Homo sapiens (White American) [65]| $[I_1 \ M_1 \ I_2 \ \{ C \ P_3 \ P_4 \ M_3 \}] \ M_3$ |

* $I_2$ to $P_3$ are not erupted.

| Table 2. Description of the characters used in the ancestral state reconstruction analysis. Characters are treated as unweighted and unordered. |
|---------------------------------|----------------------------------|
| no.    | character                        | states                      |
| 1      | eruption of replacement teeth    | 0: after molar eruption; 1: first erupted replacement tooth erupts before the last erupted molar |
| 2      | premolar eruption sequence       | 0: 2-3-4; 1: 2-4-3; 2: 4-2-3; 3: 4-3-2; 4: absence of $P_2$ |
| 3      | premolar eruption sequence (if no $P_2$) | 0: 3-4; 0: 4-3 |
| 4      | eruption of $P_3$ relative to $M_3$ | 0: $P_3$ erupts after $M_3$; 1: $P_3$ erupts before $M_3$ |
| 5      | eruption of $P_3$ relative to $M_3$ | 0: $P_3$ erupts after $M_3$; 1: $P_3$ erupts before $M_3$ |
| 6      | eruption of $I_1$ relative to the earliest premolar | 0: $I_1$ erupts after the earliest premolar; 1: $I_1$ erupts before the earliest premolar |
| 7      | simultaneous eruption of $I_1$, $I_2$, and $C$ (or $I_1$ and $I_2$ only) | 0: not simultaneous; 1: simultaneous |
| 8      | number of incisors erupting after $M_2$ | 0: 3; 1: 2; 2: 1; 3: 0 |
| 9      | number of premolars erupting after $M_3$ | 0: 3; 1: 2; 2: 1; 3: 0 |
| 10     | eruption of the incisors relative to $M_3$ | 0: all incisors erupt after $M_3$; 1: $M_3$ erupts between two incisors; 2: all incisors erupt before $M_3$ |
| 11     | eruption of the incisors relative to the premolars | 0: the earliest incisor erupts after the latest premolar; 1: intermediate situation; 2: the latest incisor erupts before the earliest premolar |
| 12     | eruption of the premolars relative to $M_2$* | 0: all premolars erupt after $M_3$; 1: at least one premolar erupts before $M_3$. (*) Coded as inapplicable if $P_1$ is present |
| 13     | eruption of $M_1$ | 0: first tooth to erupt; 1: not the first tooth to erupt |
| 14     | eruption of $P_3$ relative to $M_3$ | 0: $P_3$ erupts after $M_3$; 1: $P_3$ erupts before $M_3$ |
Figure 2. Phylogenetic relationships of the 97 fossil and extant taxa used in this analysis. The ancestral nodes for Euprimates, stem Strepsirrhini, crown Strepsirrhini, Haplorhini and Anthropoidea are indicated. Combined cladogram from Marivaux et al. [92], Gunnell [93], Arnold et al. [94], Silcox et al. [95], Steiper & Seiffert [27], Kay [96], Kistler et al. [97] and Seiffert et al. [29].

The cladogram (figure 2) used in this analysis is a supertree based on Marivaux et al. (used for placing Sivaladapis [92]), Gunnell (for Notharctus [93]), Arnold et al. (for all living primates [94; v. 3], Silcox et al. (for plesiadapiforms and Tupaia [95]), Steiper & Seiffert (for Victoriaiipithecus [27]), Kay (for
for living taxa was taken from Arnold et al. eruption sequence to further constrain the basal euprimate node. Temporal branch length information on plesiadapiforms is considered stem primates (following [103–114]). A representative of Scandentia, archaic mammals widespread during the Palaeocene and the Eocene throughout North America, Europe and Asia. Representatives of plesiadapiforms in our tree include plesiadapids and paromomyids. Here, plesiadapiforms are considered stem primates (following [103–114]). A representative of Scandentia, Tupaia glis, as outgroup for Primates (including plesiadapiformes) has been used. Although ideally we would have also included a dermopteran taxon, no permanent dental eruption sequences for dermopterans have been published. Although the lack of dermopterans in the cladogram would have been problematic if the ancestral primate node was reconstructed, the lowest node reconstructed is the ancestral euprimate node. Because plesiadapiforms are inferred to be closer to Euprimates than any other groups (following Silcox et al. [95]), under the Outgroup Algorithm [115] they have the greatest impact on polarizing the euprimate node, so it is very unlikely for dermopterans to produce a new unequivocal resolution at that node. Also, the most comprehensive relevant study supports Sundatheria (the combined clade of Scandentia and Dermoptera) as the living sister group of Primates [51], rather than Dermoptera alone [116] or Scandentia alone [117]. This makes Dermoptera no more relevant than the included scandentian in reconstructing the basal euprimate node. The dental eruption sequence of Dyneecodon pilirostris (Soricomorpha) has been added as a primitive representation of a mammal dental eruption sequence to further constrain the basal euprimate node. Temporal branch length information for living taxa was taken from Arnold et al. [94]. The branch lengths for fossil taxa originate from many sources and the choices of dates of appearance of lineages are reported and explained in electronic supplementary material, table S4, and electronic supplementary material, figure S2.

Ancestral state reconstructions were executed in the MESQUITE v. 3.01 software package [118], using parsimony. The generalized parsimony algorithm can be applied to optimization of a character of unknown polarity onto a rooted tree, and no additional algorithmic complications are presented by trees containing polytomy [55]. MESQUITE also allows missing data when using the parsimony algorithm, but cannot do likelihood calculations with gaps or soft polytomies. Because the data include a significant proportion of relevant fossil taxa, which sometimes produce partially complete eruption sequences, it is important to apply software and an algorithm that can accommodate these limitations, making parsimony the best option. Ancestral permanent dental eruption sequences were reconstructed for five hypothetical ancestors: (i) Euprimates, (ii) stem Strepsirrhini, (iii) crown Strepsirrhini, (iv) Haplorhini, and (v) Anthropoidea. For the ancestral state reconstruction, only lower permanent dental eruption sequences were used, because they are more often reported in the literature, thus increasing the number of taxa available for analysis. Canines were not included in the reconstruction because their time of eruption appears to be influenced by sexual dimorphism [42,82]. Although some primitive primates retain P1, eruption data on first premolars are not included in this analysis because the loss of this tooth early in primate evolution renders this character ambiguous at several nodes. To generate the ancestral eruption sequences, all hypothetical ancestors were assumed to have a P2. The ambiguities in ancestral state reconstructions for the characters ‘Eruption of P2 relative to M3’, ‘Eruption of I1 relative to the earliest premolar’ and ‘Eruption of incisors relative to premolars’ are resolved with restrictions implied by other characters. For the five nodes studied here, the ancestral state reconstructions result in one permanent dental eruption sequence for each hypothetical ancestor. The ancestral reconstruction analysis was also run without including fossil data (see electronic supplementary material, figure S1 and text S2), to evaluate the effect of fossils on the reconstruction.

As discussed in detail below, several lemurids that were similar to Darwinius in body mass and life-history variables were chosen as sources of comparative data. Age-specific body mass data for Eulemur macaco, Eulemur rufus and Varecia variegata (V. v. variegata) were taken from the Duke Lemur Center (DLC) database [119]. Although ‘Ida’ has been inferred to be female [17], because this inference is based on negative evidence (see above), we have followed the conservative course of including both male and female data in our analysis. None of the living species are known to be sexually dimorphic, and use of
just the female data led to extremely similar results (not shown). The percentage of adult body mass achieved at 'Ida’s’ age at death was determined using the age-specific mass estimated from the Lowess regressions from the three lemurid species, and adult mean body mass estimates from each regression. Lowess regressions were obtained using PAST [120]. Dental eruption times for the three lemurids are taken from Smith et al. [42].

It is important to note that some of the specimens from which the data were collected in Eaglen [73], and subsequently reported in Smith et al. [42] are currently assigned to other taxa. What Eaglen [73] classifies as Eulemur fulvus is currently ascribed to *E. rufus* according to the DLC, and consequently will be referred to as *E. rufus* in this paper. Also, the *V. variegata* sample in Eaglen [73] is composed of a mixture of individuals of *V. variegata* and hybrids of *V. variegata* and *V. rubra* [119]. Therefore, in this paper we are assigning the dental eruption sequence for these specimens to the genus *Varceia* in general.

The dental eruption sequence that we use for *Saimiri* (M1 M2 I1 I2 M3 P4 P2 P3) is the same one as that used by Franzen et al. [17], as the purpose of this paper is to reassess the viability of the original anthropoid model. However, another eruption sequence is known for *Saimiri* [79], which differs in the relative time of eruption of the third molar (M1 M2 I1 I2 P4 P2 P3 M3). While we use Franzen et al.’s [16] eruption sequence throughout the paper, we discuss in the conclusion how Henderson’s [79] eruption sequence would influence conclusions about the *Saimiri* model.

### 3. Results and discussion

#### 3.1. Ancestral reconstruction of permanent dental eruption sequences

Ancestral dental eruption sequences were reconstructed for five nodes (euprimates, stem strepsirrhines, crown strepsirrhines, haplorhines and anthropoids; table 3), based on the ancestral state reconstruction for the 14 characters (see electronic supplementary material, table S2).

The earliest members of Adapoidea and Omomyoidea are very similar in dental morphology [49], so unsurprisingly there is little variation in eruption sequence inferred for the ancestral nodes. Our ancestral reconstruction suggests two clear trends in the evolution of eruption sequences. The strepsirrhine line is characterized by a primitive dental eruption sequence at the base of stem Strepsirrhini that matches the one inferred for the basal euprimate. Subsequently, this primitive sequence is modified in crown strepsirrhines by the simultaneous eruption of the incisors, along with the canine, in association with the evolution of the toothcomb. The haplorhine line is similarly marked by a primitive basal eruption sequence that resembles the basal euprimate sequence, and then it is characterized by a late eruption of M3 at the base of anthropoids. There are several genera of anthropoids in which M3 erupts comparatively early (*Saimiri, Aotus, Pithecia, Pygathrix* and *Presbytis* [65,70,79,83,88,89]), but based on the distribution of this trait on this tree this is inferred here to represent evolutionary events occurring in the context of Anthropoidea, like the loss of M3 in callitrichines. In contrast to the inferred primitive state for anthropoids, *Darwinium* exhibits early eruption of M3 suggesting that it was more strepsirrhine-like. These results therefore make it difficult to determine the relationship of adapoids to either stem strepsirrhines or basal haplorhines, because they both present the same dental eruption sequence. However, these results are less consistent with the Adapoid–Anthropoid hypothesis because adapoids appear to lack the delay of M3 eruption, a synapomorphic characteristic of primitive anthropoids.

### Table 3. Reconstructed ancestral permanent dental eruption sequences for five primate nodes (see electronic supplementary material, table S2 for the nodal reconstructions on which these sequences were based). Parentheses () group teeth that in a fossil are either all emerged or all have not emerged yet.

| ancestral node     | ancestral permanent dental eruption sequence |
|--------------------|-----------------------------------------------|
| Euprimates         | M1 I1 I2 M2 P4 P3                             |
| stem Strepsirrhini | M1 I1 I2 M2 P4 P3                             |
| crown Strepsirhini | M1 I1 I2 CM2 P4 P3                            |
| Haplorhini         | M1 I1 I2 M2 P4 P3                             |
| Anthropoidea       | M1 I1 I2 M2 P4 P3                             |
| *Darwinius masillae* | (M1 I1 I2 P2) (I2 CM3 P4 P3)                  |

*I* to *P* are not erupted.
The crown strepsirrhines show another distinctive feature: the presence of a toothcomb. The eruption of a toothcomb results in the almost simultaneous emergence of the incisors and the canine. The eruption of the toothcomb is generally early for crown strepsirrhines [42,68,69,71,73,74], with the exception of Archaeolemur edwardsi [69]. However, the pattern of eruption for the toothcomb does not differ markedly from the eruption pattern of incisors for euprimates, stem strepsirrhines or Darwinius, all of which share an early and contiguous eruption of incisors.

The ancestral reconstruction analysis not including fossil taxa provides similar results (electronic supplementary material, table S3), but there is a substantial difference in the final reconstruction. In the analysis that excludes fossils it is not possible to unequivocally reconstruct the primitive premolar eruption sequence for Anthropoidea, with four different states being inferred to be equally parsimonious. This is particularly problematic because the time of eruption of P2 is crucial for the study of life history of Darwinius specifically. Therefore, the inclusion of fossil data in the analysis is required to resolve relevant ancestral state reconstructions.

3.2. Reassessment of the Saimiri model

Based on the contrasts between anthropoids and Darwinius in the ancestral state reconstruction of dental eruption patterns, Saimiri may not be a good model for the growth of Darwinius, as previously proposed by Franzen et al. [17]. But, contrary to the general anthropoid trend, Saimiri is a fast-growing platyrrhine that, like Darwinius, exhibits an early eruption of M3 [70]. The ancestral state reconstruction analysis, however, indicates that this early eruption of the third molar appears secondarily in Saimiri. Because the hypothesized relationships of Darwinius are to stem anthropoids [30], not Platyrrhini generally, or Saimiri specifically, this similarity would necessarily be a case of homoplasy. Also, cebids generally show a late eruption of P2 [70,79], with the exception of Cebus albifrons [79], in which it appears to be quite variable [72]. Saimiri especially stands out among the Cebidae for having one of the latest eruptions of the second premolar. Therefore, this pattern contrasts markedly with that observed in Darwinius, in which this tooth is already erupted, with five teeth still remaining unerupted. This has profound implications for calculating the age at death, because it is after the eruption of P2 when the sequence is interrupted by death in Darwinius [17,44]. It is worth noting that Henderson [79] provides another dental eruption sequence for Saimiri in which the relative time of eruption of the M3 is markedly later. One of the most convincing arguments in favour of the Saimiri model is that squirrel monkeys have, according to the sequence used in Franzen et al. [17], one of the most strepsirrhine-like dental eruption sequences among anthropoids, precisely because of an earlier relative eruption of M3. In the light of this fact, if Henderson’s [79] sequence is correct, Saimiri would make an even less appropriate model.

By contrast, both stem strepsirrhines and basal haplorhines would make good models for the growth of Darwinius, because of their primitive-looking dental sequences. The only non-anthropoid haplorhine taxa in our sample are tarsiids, which exhibit a dental eruption sequence (table 1) which differs from that inferred for the basal haplorrhine (i.e. extremely early eruption of P2, lack of I2, and simultaneous eruption of M3 and C), making tarsiers a poor choice as model taxa. On the other hand, stem strepsirrhines and Darwinius also share early eruption of M3 and P2. Given that stem strepsirrhines are known only from extinct taxa, without direct information available about their age-specific growth and development, a new growth model based on living strepsirrhines is needed for Darwinius.

Three families of strepsirrhines primitively share a dental eruption sequence similar to that of Darwinius: Lemuridae, Galagidae and Cheirogaleidae [42,68,71,73,74]. Galagidae and Cheirogaleidae are significantly smaller than caenopithecids [3]. Generally, in mammals, most life-history variables are correlated to body mass [121], making these very small primates inappropriate models for Darwinius. On the other hand, lemurids exhibit similar body masses to caenopithecids [3], which makes them a more reasonable model. Dental eruption sequences are known from six lemurids: Lemur catta, Hapalemur griseus, E. rufus, E. macaco, E. mongoz and Varecia sp. [73]. However, L. catta and H. griseus would make poor models for the growth of Darwinius because the eruption of P2 in these two species occurs much later in the sequence, and, as discussed above, this tooth is of critical importance in determining the age at death of this particular specimen. Lemur catta and H. griseus also possess a premolar eruption sequence of 4-3-2, which is derived in the context of Lemuridae, instead of the primitive 2-4-3 pattern found in the rest of lemurids and stem strepsirrhines. Among the three Eulemur species, E. mongoz differs the most from Darwinius in having a late eruption of P2. It would be preferable to apply a model based on species with earlier P2 eruptions. Like E. rufus and E. macaco, Varecia has a 2-4-3 premolar eruption pattern and an early P2 eruption. Additionally, these fast-growing primates are fairly well studied, making them the best living models available for the growth of Darwinius.
Figure 3. Lowess regressions illustrating patterns of ontogeny for individuals of three lemurid species from birth to the age of 8 years. Smoothing factor of 0.1 for all regressions. (a) *Eulemur macaco*; (b) *Eulemur rufus*; and (c) *Varecia variegata*. Vertical lines indicate the supposed interruptions of the sequence in *Darwinius*. 
The age of eruption of P2 in *E. rufus* is 1.14 years, 1.05 years in *E. macaco* and 1.06 years in *Varecia*. Therefore, the age at death of *Darwinius* based on this model would have been between 1.05 and 1.14 years, older than previously suggested (9–10 months = 0.75–0.83 years [17]).

For estimating body mass at death, we used ages at death of 1.05 years for *E. macaco*, 1.14 years for *E. rufus* and 1.06 years for *Varecia*. Individuals of *E. macaco* that aged similarly to *Darwinius* weigh 75.6% of the adult body mass (approx. 1876 g/2481 g; figure 3a), whereas individuals of *E. rufus* weigh 78% of the adult body mass (approx. 1699 g/2177 g; figure 3b). Finally, *V. variegata* achieves 77.7% of the adult body mass at the relevant age (approx. 2763 g/3556 g; figure 3c). Therefore, our lemurid model suggests that ‘Ida’ would have been between the narrow range of 75.6% and 78% of her adult body mass when she died. Franzen et al. [17] suggested an estimated body weight at death of 485 g. According to the new lemurid model, the projected adult body mass would be between 622 and 642 g. This is consistent with the adult body mass estimations for other caenopithecids (between 500 and 3500 g [3]), and falls entirely below the estimated adult mass by Franzen et al. [17] (650 and 900 g).

4. Conclusion

Our ancestral state reconstruction infers the same dental eruption sequences for basal Euprimates, stem Strepsirrhini and basal Haplorhini. These hypothesized primitive sequences resemble that of *Darwinius* in the early eruption of M3 and the non-simultaneous eruption of I1-I2-C in contrast to anthropoids and crown strepsirrhines, respectively. The late eruption of M3 in anthropoids and the fact that M3 seems to be the next tooth to erupt in *Darwinius* at the moment of her death suggests that anthropoids likely do not provide the most appropriate model for estimating growth in adapoids, including *Darwinius*. The eruption of P2 is important for defining the interruption of the sequence in this particular specimen, and the late eruption of P2 in *Saimiri* suggests that this genus in particular does not represent a good model for *Darwinius*.

Our results also suggest that eruption sequences carry useful phylogenetic information. Although variable to some extent, higher level primate taxa (e.g. crown Strepsirrhini, Anthropoidea) can be grouped based on different trends in eruption sequences. Therefore, the study of eruption sequences can contribute to our understanding of primate phylogenetic relationships, in a way that allows for the incorporation of fossil material. In this case, the contrast between the inferred late eruption of M3 in the common ancestor of Anthropoidea, and the advanced stage of development of this tooth in *Darwinius*, could be interpreted as conflicting with the Adapoid–Anthropoid hypothesis.

The lemurid model for the development of *Darwinius* proposed in this study does not categorically invalidate the *Saimiri* model. However, it is an alternative in closer agreement with the more similar dental eruption sequences found in strepsirrhines. Also, it agrees with the currently most widely supported hypothesis for adapoid relationships: the Adapoid–Strepsirrhine hypothesis. This model suggests an older age at death (1.05–1.14 years, depending on the model used) than previously proposed (0.75–0.83 years [17]). Our model also suggests a narrower range for the projected adult weight (622–642 g) and entirely below the previously proposed (650–900 g [16]), consistent with caenopithecidean range of body masses. Although the current data on lemurid growth are sufficient for certain species of lemurids, better documentation of data on growth, and development, and eruption sequences for more lemurid species would certainly improve the quality of potential new models.

Data accessibility. All supporting data are available as the electronic supplementary material.

Authors’ contributions. S.L.T. collected the data and drafted the manuscript. All authors conceived of the study, participated in the design of the study, participated in data analysis, interpreted the data, revised the content of the article and gave final approval for publication.

Competing interests. The authors declare that they have no competing interests.

Funding. This work was supported by an NSERC Discovery grant to M.T.S.

Acknowledgements. We are grateful to S. R. Leigh and J. G. Fleagle for providing access to unpublished data. We thank K. D. Rose, M. A. O’Leary and M. Godinot for their insight on adapoid P2 variability. We thank C. L. Makowski for observations relevant to the assessment of the sex of *Darwinius*. Thanks to K. Padian and anonymous reviewers for comments that substantially improved this paper.

References

1. Gingerich PD, Sahni A. 1984 Dentition of *Sivalodapis nagri* (Adapidae) from the late Miocene of India. *Int. J. Primatol.* 5, 63–79. (doi:10.1007/BF02375148)

2. Gebo DL. 2004 Adapiformes: phylogeny and adaptation. In *The primate fossil record* (ed. WC Hartwig), pp. 21–43. Cambridge, UK: Cambridge University Press.

3. Fleagle JG. 2013 *Primate adaptation and evolution*, 3rd edn. San Diego, CA: Academic Press.

4. Wortman JL. 1903–1904 Studies of Eocene Mammalia in the Marsh collection, Peabody
Rasmussen DT. 1990. The phylogenetic position of the Oligocene anthropoid Apidium and the origin of Anthropoidea. Folia Primatol. 19, 329–337. (doi:10.1159/000551549)

Gingerich PD. 1984. Primates evolution: evidence from the fossil record, comparative morphology, and molecular biology. Warh. Phys. Anthropol. 27, 57–72. (doi:10.1002/ajpa.1330270504)

Rasmussen PD. 1990. Primates in the Eocene. In The world at the time of Messel: puzzles in palaeoenvironment, and the history of early primates (eds T Lehman, SFR Schaal), pp. 67–68. Frankfurt am Main, Germany: Senckenberg Gesellschaft für Naturforschung.

Rasmussen PD, Schoeneiger M. 1977. The fossil record and primate phylogeny. J. Hum. Evol. 6, 483–505. (doi:10.1016/0048-124X(77)90059-6)

Rasmussen DT, Simons EL. 1994. A whole new world of ancestors: Eocene anthropoids from the Fayum, Egypt. Folia Primatol. 51, 182–208. (doi:10.1159/000156272)

Rasmussen DT, Simons EL. 1992. Paleobiology of oligopitheciens, the earliest known anthropoid primates. Int. J. Primatol. 13, 477–508. (doi:10.1007/BF02611070)

Simons EL. 1989. Description of two genera and species of late Eocene Anthropoidea of Egypt. Proc. Natl Acad. Sci. USA 86, 9596–9590. (doi:10.1073/pnas.86.24.9596)

Simons EL, Rasmussen DT. 1989. Cranial morphology of Aggytopithecus and Tarsius and the question of the tarsier-anthropoid clade. Am. J. Phys. Anthropol. 79, 1–23. (doi:10.1002/ajpa.1330790103)

Rasmussen EL, Simons DT. 1994 A whole new world of ancestors: Anthropoidea from Africa. Evol. Anthropol. 3, 128–139. (doi:10.1002/evan.600030407)

Rasmussen DT. 1990. The phylogenetic position of Mahgarita stevensi: proconsulanthropoid or lemuroid? Int. J. Primatol. 11, 439–469. (doi:10.1007/BF02696131)

Rasmussen DT. 1994. The different meanings of a tarsio-anthropoid clade and a new model of anthropoid origin. In Anthropoid origins (eds JG Fleagle, RF Kay), pp. 335–360. New York, NY: Plenum.

Boyer DM, Seiffert ER, Simons EL. 2010. Astragalar phylogeny and its implications for the tarsier-anthropoid clade and an alternative hypothesis of simian origins. Int. J. Primatol. 31, 23–33, (doi:10.1007/s12549-013-0022-z)

Seiffert ER, Jepsen PL, Brandt KL. 2010. Astragalus and early primate evolution: a comprehensive analysis of living primate ecology, biology, and behaviour. Paleobiologist. Paleosimulium. 92, 573–583. (doi:10.1007/s12549-012-0089-1)

Beard KC, Dagosto M, Gebo DL, Godinot M. 1988. Interrelationships among primate higher taxa. Nature 331, 712–714. (doi:10.1038/331712a0)

Dagosto M. 1988. Implications of postcranial evidence for the origin of eurypithecines. J. Hum. Evol. 17, 35–56. (doi:10.1006/jhevol.2004.2484-88(90)0048-6)

Kay RF, Ross CF, Williams BA. 1997 Anthropoid origins. Science 275, 797–804. (doi:10.1126/science.275.5300.797)

Williams BA, Kay RF, Kirk EC, Ross CF. 2010. Darwinius masillae is a strepsirhine—a reply to Franzen et al. (2009). J. Hum. Evol. 59, 567–573. (doi:10.1016/j.jhevol.2010.01.003)

Gilbert CC, Maiolino SA. 2015. Comment to ‘Primates in the Eocene’ by Gingerich (2012). PaleoBio. Paleontium. 95, 237–241. (doi:10.1159/000350412-1)

Marignó J, Minwer-Barakat R, Moyà-Solà S. 2011. New Anchomomys (Adapoidae, Primates) from the Robanico (Middle Miocene) of northeastern Spain. Taxonomic and evolutionary implications. J. Hum. Evol. 60, 665–672. (doi:10.1016/j.jhevol.2010.12.006)

Steiper ME, Seiffert ER. 2012. Evidence for a convergent slowdown in primate molecular rates and its implications for the timing of early primate evolution. Proc. Natl Acad. Sci. USA 109, 6095–6091. (doi:10.1073/pnas.1119506109)

Ni X, Gebo DL, Dagosto M, Meng J, Tafforeau P, Flynn JF, Beard KC. 2013. The oldest known primate skeleton and early halephaline evolution. Nature 498, 60–64. (doi:10.1038/nature12200)

Seiffert ER, Gostev L, Boyer DM. 2015. Primate tarsal bones from Egerkingen, Switzerland, attributable to the middle Eocene adapiform Coepithecus lemuroides. PeerJ 3, e1036. (doi:10.7717/peerj.1036)

Gingerich PD, Cranley JJ, Brandt KL. 1994 Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. Yearb. Phys. Anthropol. 37, 177–211. (doi:10.1002/ajpa.1330370504)

Franzen JL. 2005. The implications of the numerical dating of the Messel fossil deposit (Eocene, Germany) for mammalian biochronology. Ann. Paléontol. 91, 329–335. (doi:10.1007/s12549-013-0122-z)

Simons EL, Rasmussen DT. 1997. Palaeopathology and fate of Ida Darwinius masillae. Primates, 38, 383–385. (doi:10.1073/pnas.1119506109)

Gingerich PD, Smith BH. 2010. Premolar eruption of early Eocene adapoids Cantius rathbuni and Cantius abdita (Mammalia, Primates). Contrib. Mus. Paleontol. Univ. Mich. 32, 41–47.

Byrd KE. 1997. 1997 Sequences and asymmetries of dental development and eruption in the Ceboida. PhD dissertation, University of Washington, USA.

Byrd KE. 1981. Sequences of dental ontogeny and callitrichid taxonomy. Primates 22, 103–118. (doi:10.1007/BF02382561)

Kay RF, Madden RH, Plucan CM, Cifelli RL. 1987. Striatonervorum, a new species of Miocene Colombian primate. J. Hum. Evol. 16, 173–196. (doi:10.1006/jhevol.2004.2484-87(97)00075-3)

Bown TM. 1976. Affinities of Teilhardina (Primates, Omomyidae) with description of a new species from North America. Folia Primatol. 25, 62–72. (doi:10.1159/000153570)

Rose KD, Bown TM. 1991. Additional fossil evidence on the differentiation of the earliest eurypithecids. Proc. Natl Acad. Sci. USA 88, 98–101. (doi:10.1073/pnas.88.1.98)

Lockett WF. 1993. An ontogenetic assessment of dental homologies in thiraean mammals. In Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes (eds FS Szalay, MJ Novacek, MC Molenaar), pp. 182–204. New York, NY: Springer.
