Complete Primate Skeleton from the Middle Eocene of Messel in Germany: Morphology and Paleobiology

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Abstract

Background: The best European locality for complete Eocene mammal skeletons is Grube Messel, near Darmstadt, Germany. Although the site was surrounded by a para-tropical rain forest in the Eocene, primates are remarkably rare there, and only eight fragmentary specimens were known until now. Messel has now yielded a full primate skeleton. The specimen has an unusual history: it was privately collected and sold in two parts, with only the lesser part previously known. The second part, which has just come to light, shows the skeleton to be the most complete primate known in the fossil record.

Methodology/Principal Findings: We describe the morphology and investigate the paleobiology of the skeleton. The specimen is described as Darwinius masillae n.gen. n.sp. belonging to the Cercamoniinae. Because the skeleton is lightly crushed and bones cannot be handled individually, imaging studies are of particular importance. Skull radiography shows a host of teeth developing within the juvenile face. Investigation of growth and proportion suggest that the individual was a weaned and independent-feeding female that died in her first year of life, and might have attained a body weight of 650–900 g had she lived to adulthood. She was an agile, nail-bearing, generalized arboreal quadruped living above the floor of the Messel rain forest.

Conclusions/Significance: Darwinius masillae represents the most complete fossil primate ever found, including both skeleton, soft body outline and contents of the digestive tract. Study of all these features allows a fairly complete reconstruction of life history, locomotion, and diet. Any future study of Eocene-Oligocene primates should benefit from information preserved in the Darwinius holotype. Of particular importance to phylogenetic studies, the absence of a toilet claw and a toothcomb demonstrates that Darwinius masillae is not simply a fossil lemur, but part of a larger group of primates, Adapoidea, representative of the early haplorhine diversification.

Introduction

A set of extraordinary circumstances produced one of the most complete skeletons of a fossil primate ever recovered, here described as a new genus and species Darwinius masillae. The holotype is a juvenile that died at the margin of a volcanic lake in a para-tropical rain forest and was preserved in Middle Eocene sediments of Messel, Germany (Grube Messel or ‘Messel pit,’ herein simply Messel). The fossil was apparently unearthed in 1983 by private collectors who split and eventually sold two parts of the skeleton on separate plates: the lesser part (herein plate B) was restored and in the process partly fabricated to make it look more complete. This was eventually purchased for a private museum in Wyoming, and then described by one of us who recognized the fabrication [1]. The more complete part (plate A; Figs. 1–2) has just come to light, and it now belongs to the Natural History Museum of the University of Oslo (Norway). When made available for study, plate A was immediately recognizable as the complete complementary and unaltered counterpart of plate B.

The new specimen, like some other Messel finds, is complete even to distal phalanges and terminal tail vertebrae. Moreover, it was exceptionally preserved during fossilization, retaining soft tissue outlines and contents of the digestive tract. Like other Messel fossils, however, the skeleton is lightly crushed and must be examined in place. Individual bones and teeth cannot be physically removed to examine individually, a difficulty we have partially overcome with innovative CT imagery.

The specimen is a juvenile, but erupting teeth indicate the developmental age and enable prediction of further growth of the body and limbs. The completeness of the fossil allows us to reconstruct aspects of life history, diet, and locomotion that are difficult to study in fossils. In addition, the skeleton enables identification of characteristics routinely used to distinguish strepsirrhine and haplorhine primates. Our focus here is on
morphology and paleobiology, but the skeleton has interest for primate phylogeny as well. The skeleton’s features clarify morphologies that have been given critical weight in primate phylogeny, and call into question accepted wisdom about the origin of higher primates.

Eocene primates

The first primates of modern aspect appeared at the beginning of the Eocene epoch, about 55 m.y. before present. Two superfamilies can be recognized from the beginning: (1) Tarsioidae, including Eocene Omomyidae and Microchoeridae and living Tarsius; and (2) Adapoidea, including Eocene Notarchitidae and Adapidae, with later representatives but no living primates. Tarsioidae are generally smaller, with estimated body weights less than 500 g; Adapoidea are generally larger, with estimated body weights greater than 500 g [2–4]. Within Notarchitidae, the subfamily Cercamoniinae (sometimes considered a family Cercamoniidae) has special interest because of its shortened, robust dentaries, reduced antemolar dentition, and interlocking canines with monkey-like honing premolars [5], all features that may foreshadow anthropoids. Cercamoniinae include primates as widely dispersed as Protoadapis and Cercamomius from France,

Figure 1. *Darwinius masillae*, new genus and species, from Messel in Germany. (A)— Plate A (PMO 214.214) showing holotype skeleton in right lateral view. (B)— Plate B (WDC-MG-210) left side of holotype (reversed for comparison with plate A). Plates show part and counterpart of the same skeleton. Plates have different museum numbers because they are in different museum collections. Note the exceptional completeness of the articulated skeleton in plate A, with left and right hands and the right foot complete, including distal phalanges, and the tail complete to the tip. Stained matrix shows the soft-tissue body outline. Abdomen contains organic remains of food in the digestive tract. All of plate A and parts 1 and 2 on plate B (enclosed in dashed lines) are genuine; remainder of plate B was fabricated during preparation.

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Europolemur from Germany, Caenopithecus from Switzerland, Maharita from Texas, and Aframomus from Egypt.

Messel

Messel is a maar lake deposit. The basin in which the deposit accumulated formed during a volcanic explosion. It filled with water, which seemingly, one way or another, accumulated gases that poisoned animals individually, episodically, or periodically [6–8]. The result is a diverse fauna of exceptionally preserved insects, fishes, amphibians, reptiles, birds, and mammals [9–12].

The Messel locality is inferred to represent a paratropical Eocene rain forest. Primates are rare faunal elements at Messel, in spite of the rainforest habitat, and only eight primate specimens are known, all previous finds fragments of partial skeletons (Table 1) [13–19].

In all, three primate species are known from Messel: Europolemur koenigswaldi, Europolemur kelleri, and a species formerly identified as Godinotia neglecta (see below). All belong to Notharctidae and subfamily Cercamoniinae. No tarsioid primates have been found at Messel, but they are common in contemporary deposits elsewhere in Europe and should be present. The Messel fauna belongs to the early middle Eocene or earliest Geiseltalian, MP11 [20] with a calculated radiometric age of ca. 47 Ma based on a basalt fragment coming from an underlying volcanic chimney [21].

History of the specimen

In order to comprehend how part and counterpart of the same individual fossil can have such different histories, it is essential to understand how fossils at Messel are collected and preserved. Here
Table 1. Systematic synopsis of the primate remains from Messel, with museum collection numbers, Messel primate number, Messel grid coordinates (for map see Fig. S1).

| Present designation | Preserved Parts | Collection | Number and locality | Description |
|---------------------|----------------|------------|---------------------|-------------|
| Darwinius masillae  | Complete skeleton, same individual as No. 6b | Natural History Museum Oslo PMO 214.214 (found by private collectors in 1982) | No. 6 A [77H, 72, 8H] | Plate A |
|                     |                |            |                     | (holotype) Complete skeleton, same individual as No. 6b - Darwinius masillae |
|                     |                |            |                     | No. 6 B [76H, 67, 8H] | |
|                     |                |            |                     | SMF-ME 1228 (found in 1982) | No. 1 [9M–13M] |
|                     |                |            |                     | SMNK-Me1125 (found in 1990) | No. 3 [9D] |
|                     |                |            |                     | SMF-ME-3379 (found by private collectors in 1990) | No. 2 [7G] |
|                     |                |            |                     | HLMD-Me 7430 (found in 1975) | No. 4 [10L] |
|                     |                |            |                     | SMF-ME 2966 (found in 1997) | No. 7 [9E] |
|                     |                |            |                     | SMF-ME 1683 (found in 1987) | No. 8 [17] |
|                     |                |            |                     | SMNK III 1641 (found in 1984) | No. 5 [9D] |
| Europolemur koenigswaldi | Two fragments of a skeleton, same individual as No. 6A | No. 6 [9G] | [13] |
|                     |                |            |                     | fragmentary mandible with cheek-teeth | No. 2 [9G] |
|                     |                |            |                     | SMF-ME 2966 (found in 1997) | No. 1 [10L] |
|                     |                |            |                     | SMFK-ME 1125 (found in 1990) | No. 1 [10L] |
|                     |                |            |                     | SMFK-ME-3379 (found by private collectors in 1990) | No. 3 [9D] |
|                     |                |            |                     | HLMD-Me 7430 (found in 1975) | No. 4 [10L] |
|                     |                |            |                     | SMNK III 1641 (found in 1984) | No. 5 [9D] |
| Europolemur kelleri | Complete, but dorso-ventrally compressed skull | SMF-ME-3379 (found by private collectors in 1990) | No. 8 [17] |
|                     |                |            |                     | SMF-ME 1683 (found in 1987) | No. 4 [10L] |
|                     |                |            |                     | SMNK III 1641 (found in 1984) | No. 5 [9D] |
| Europolemur sp.     | Pelvis, baculum, and both hindlimbs | SMF-ME-3379 (found by private collectors in 1990) | No. 8 [17] |
|                     |                |            |                     | SMF-ME 1683 (found in 1987) | No. 4 [10L] |
|                     |                |            |                     | SMNK III 1641 (found in 1984) | No. 5 [9D] |
|                     |                |            |                     | SMF-ME 2966 (found in 1997) | No. 1 [10L] |
|                     |                |            |                     | SMFK-ME 1125 (found in 1990) | No. 1 [10L] |
|                     |                |            |                     | SMFK-ME-3379 (found by private collectors in 1990) | No. 3 [9D] |
|                     |                |            |                     | HLMD-Me 7430 (found in 1975) | No. 4 [10L] |
|                     |                |            |                     | SMNK III 1641 (found in 1984) | No. 5 [9D] |
|                     |                |            |                     | SMF-ME 2966 (found in 1997) | No. 1 [10L] |
|                     |                |            |                     | SMFK-ME 1125 (found in 1990) | No. 1 [10L] |
|                     |                |            |                     | SMFK-ME-3379 (found by private collectors in 1990) | No. 3 [9D] |
|                     |                |            |                     | HLMD-Me 7430 (found in 1975) | No. 4 [10L] |
|                     |                |            |                     | SMNK III 1641 (found in 1984) | No. 5 [9D] |

Complete fossil mammal skeletons are well preserved, along with those of fish, amphibians, reptiles and birds. These almost always lie on bedding planes of the laminated sediment. During the early years of excavation for fossils, between 1971 and 1985, mining for oil shale had extensively exposed sediments. Once mining was finished, plans arose to use the open pit as a garbage dump. With this in mind, early excavations for fossils were necessarily rushed, and less attention was paid to careful bed by bed collecting of fossils. Large blocks of the oil shale were removed and split along bedding planes using long knives. The presence of fossils enhances the splitting.

Before starting preparation of a plate for study, the surface damaged by splitting must be embedded in epoxy or polyester resin. Then the as yet unexposed lateral surface of the plate is prepared to expose the lateral side of the little-damaged fossil. This procedure is necessary as dehydration of the oil shale destroys a fossil. The ideal situation is when part and counterpart are mirror images, and both right and left sides of the animal can be prepared equally well. Alternatively, the split can be such that most bones remain on one plate, leaving their natural cast on the counterpart plate.

From what we know of the present fossil, it was privately collected at Messel in 1983, at the foot of what is known as the Schilkrottenhügel [Turtle Hill] see Fig. S1, although the exact horizon is unknown [personal communication from previous owner of plate A, Thomas Perner, Bad Homburg].

Plate B (Figs. 1,2), originally described by Franzen [18] as the sixth Messel primate (Table 1), had a curious history. It was purchased in 1991 by Dr. Burghard Pohl for the Wyoming Dinosaur Center at Thermopolis, Wyoming. This plate holds a partial skeleton viewed from the left side, embedded in a plate of polyester. Franzen [18] showed that some of the specimen is real, while substantial parts were faked to give an illusion of greater completeness. Working from what was available, Franzen attributed the specimen to the species “Protrycocephalus neglectus” (Thalmann, Haubold & Martin, 1989) described from Geiseltal [22]. He first placed the species in Canohipithecus, and then assigned it to a new genus Godinotia [1].

Plate A (Figs. 1,2) described here, became available for sale and was purchased in 2007 by the Natural History Museum of the University of Oslo (Norway). This plate, showing a skeleton from the right side, proves to be the hitherto unknown and much more complete counterpart of the Wyoming Plate B. Careful study and comparison of the new and more complete plate indicates that the specimen cannot belong to Godinotia neglectus (see below).

The Oslo specimen, plate A, clarifies exactly which parts of plate B were faked, including notably, hands and feet (where some proportions of constructions may have been based on reversed photos of A) and the tail vertebral column. Traces on the surrounding polyester resin background suggest that a cast of the tail of another mammal was inserted into plate B. Additional parts such as the vertebrae between sections 1 and 2 as well the nasal part of the skull on plate B were simply fabricated.

The almost complete skeleton on plate A has been well prepared, and it also lies on a polyester resin background. Preservation is unique. The cranium is compressed, but a combination of plates A and B shows virtually the entire dentition. Plate A also shows almost the entire right side of the body and several parts of the left side of the body that are missing on plate B. Only the distal part of the left leg is missing on both plates. Thus the skeleton of Darwinius masillae is much more complete than any known for Notharctus Gregory 1920 [23], and in addition it is unique in exhibiting the entire soft body outline as well as contents of the digestive system [24].
Methods

Study of the compressed skeleton was facilitated by X-radiography and microcomputerized tomography (CT):

1. Contact microradiographs were made with conventional X-ray sources (Faxitron 43804 X-ray cabinet, and Faxitron 43856A X-ray cabinet, Hewlett Packard, USA) on a 25 micron storage screen (SR-HD-IP, Fuji, Japan), combined with a laser scanning digitizer (HD-CR 35 NDT, Duerr-NDT, Germany).

2. Microradiographs were enlarged by direct projection of the specimen using a microfocus X-ray tube with 10-micron resolution (FTX 100.52, Feinfocus/Yxlon, Germany) on a real-time digital sensor (C7942 CK12, version modified for small bones, Hamamatsu, Japan). Moderately enlarged microradiographs (1.9×) of comparative primate specimens (Fig. 3) were made with a conventional clinical digital mammography system (Mammomat Novation with enlargement set, Siemens, Germany).

3. CT images were obtained using an industrial Micro CT System (RayScan 200 XE, RayScan Technologies, Germany). The microfocus X-ray tube makes it possible, in principle, to achieve resolutions below 10 microns when small probes a few cm in size are used. However, the principal Darwinius plate is large (plate A), and it cannot be separated into smaller parts for CT analysis. For the whole plate, the maximum resolution was 430 microns, even using micro CT. This problem was overcome using a special algorithm (‘region of interest’ micro CT) on the RayScan apparatus, which increased the resolution to 68 microns. Artefacts of this algorithm are progressive fusion and loss of contrast of bones and teeth in the images, due to averaging of originally different densities. However, complications can be found that are still acceptable at this resolution. Image processing of CT-data was undertaken with VGStudio MAX 2.0.1 (Volume Graphics, Germany).

Mapping of developing teeth was done using ArcGIS. First a high-resolution digital photograph of the dentition visible on the surface of plate A was mapped, tooth by tooth, using good light and a binocular microscope. The high-resolution digital X-ray was geo-referenced using landmarks visible in the photograph and X-ray. This permitted identification of some teeth that were not visible on the surface. Next in sequence a shaded CT image of the same region (Fig. 4A), a reversed shaded CT image of the same region viewed from the back side of plate A (Fig. 4B), a reversed photograph of the surface of plate B [1: fig. 4] and a reversed X-ray image of plate B were geo-referenced. Each tooth could be viewed, mapped, and checked by toggling between these superimposed images. In this way virtually all teeth and developing teeth in both plates and from all jaw quadrants were identified unambiguously.

Measurements of the holotype of Darwinius masillae n.gen. n.sp. were made using calipers, with the aid of a binocular microscope or hand lens. Comparisons with other specimens from Messel were made in the Senckenberg Museum, Frankfurt am Main, while comparisons with specimens from Geiseltal were made at the Geiseltal Museum in Halle.

William Jungers (Stony Brook, New York) provided an extensive set of comparative measurements for multivariate analysis of skeletal proportions. Comparisons with the postcranial skeletons of modern primates were made using skeletons in the Senckenberg Museum Darmstadt, Messel-Collection; PMO: Geological Museum, University of Oslo, Norway, SMF-ME: Senckenberg Museum Frankfurt, Messel Collection; SMNK-M: Staatliches Museum für Naturkunde Karlsruhe, Messel Collection; UMMZ: University of Michigan Museum of Paleontology vertebrate collection; UMMZ: University of Michigan Museum of Zoology mammal collection; WDC-MG: Wyoming Dinosaur Center, Messel Grube collection.

Results

Systematic Paleontology
Order Primates Linnaeus, 1758
Suborder Euprimates Hofstetter, 1977
Family Notharctidae Trouessart, 1879
Subfamily Cercamoniinae Gingerich, 1975
Darwinius new genus
Type species. Darwinius masillae n.gen., n.sp.
Derivatio nominis. Honoring Charles Darwin on the occasion of his 200th birthday.
Darwinius species new species
Holotype. By monotypy plate A, (PMO 214.214) with counterpart (plate B WDC-MG-210).
Derivatio nominis. Masilla=Messel in the Codex of the Lorsch monastery, 800 AD.
Type locality. Messel, near Darmstadt (South Hessen, Germany); geographic coordinates are: 49°55′7″ North, 8°45′22″ East.
Type horizon and age. Messel Formation (middle part of section), early Middle Eocene or early Geiseltalian [MP 11], ca. 47 Ma [20–21].
Diagnosis. M1 and M2 display a well developed hypocone but no mesostyle. A metaconule is lacking. The M1 and M2 show a small trigonid and a very broad talonid. In the permanent dentition, P3/P4 have been lost whereas P4/P3 are unicuspid and uniradical, especially reduced in the maxilla. The lower segments of the anterior and posterior limbs are conspicuously short and robust. The phalanges are elongated. A toilet or grooming claw is not present. Molars of Darwinius masillae are distinct in morphology and intermediate in size between those of contemporary species of Periconodon and Europlemar.

Different diagnoses. Darwinius masillae differs from species of Europlemar Weigelt, 1933 (Geischtal-obere Mittelkohle and
Messel) in having a very small, single-rooted P2/P2, whereas P1/P1 are completely reduced (lost).

Differs from *Caenopithecus lemuroides* Ru¨timeyer, 1862 (Egerkin-gen [26]) in being smaller and having upper molars that lack a mesostyle (postcrania skeleton of *Caenopithecus* is unknown except for an isolated talus; see below).

Differs from *Cercamonius brachyrhynchus* (Stehlin, 1912), from Prajous (Quercy Phosphorite deposits) in having a mandibular...
Figure 4. Micro-CT of the skull of *Darwinius masillae*, new genus and species. (A)—CT image of the skull in plate A, viewed from the right side. (B)—CT image of the skull in plate A, viewed from the left side. Note the presence of a postorbital bar, parts of the auditory bulla below the acoustic opening, and possible hyoid bones. Tooth homologies are mapped in greater detail in Figure 6 and sutures in S2.

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Table 2. Measurements of the skull and postcranial skeleton of the holotype of *Darwinius masillae*, n. gen., n. sp.

| Skeletal element | Measurement (mm) | Remarks |
|------------------|------------------|---------|
| **Cranium**      |                  |         |
| Cranial length   | 52.0             | Total skull length |
| Orbital diameters | 11.5 x 16.5     | Width and height |
| M1 crown         | 3.80 x 4.65      | Length and width; measured on CT reconstruction |
| M2 crown         | 4.05 x 2.90 x 3.30 | Length, trigonid width, talonid width; measured on CT reconstruction |
| M3 crown         | 3.90 x 3.20 x 3.75 | Length, trigonid width, talonid width; measured on CT reconstruction |
| **Postcranial**  |                  |         |
| Thorax           | 61.0             | Sum of thoracic centrum lengths as articulated |
| Lumbus           | 60.0             | Sum of lumbar centrum lengths as articulated |
| Scapula          | 24.7             | Maximum length |
| Humerus          | 46.7             | Maximum length |
| Radius           | 36.5             | Maximum length |
| Hand             | 46.0             | Measured from base of wrist to most distal phalanx |
| Femur            | 65.5             | Maximum length |
| Tibia            | 65.2             | Maximum length |
| Foot             | 67.0             | Length measured from end of calcaneum to most distal phalanx |
| **Skeleton as a whole** |          |         |
| Vertebral column | ca. 53 cm        | Proximal atlas to end of tail |
| Total length with skull | ca. 58 cm | Skull plus vertebral column |
| Head and body length | ca. 24 cm | Without tail |

Based on Micro-CT reconstructions of teeth and x-radiographs of the skeleton. doi:10.1371/journal.pone.0005723.t002

Discussion. When Franzen described the counterpart specimen (plate B) and assigned it to *Godinotia neglecta* from Geiseltal [1], the permanent dentition of the Messel specimen was only represented by a fragmentary left M1 and an incomplete forelimb and lower leg without hands and feet. He therefore did not recognize the difference of limb proportions, basing his determination mainly on the similar degree of reduction of the antemolar dentition. In 1994 similarities of the dentition led him to assign Geiseltal and Messel specimens to the genus *Caenopithecus* described by Rutimeyer in 1862 from Egerkingen γ [18,27]. Now that the completely preserved right side of the Messel specimen (plate A) is known and described herein, it is clear that *Darwinius masillae* n.gen., n.sp. differs considerably from the type specimen of *Godinotia neglecta* in the postcranial skeleton and in particular, the limb proportions. Moreover, its dentition is clearly different from that of *Europolemur koenigswaldi* as well as *E. kelleri* from Messel and it differs from that of *Caenopithecus lemarnoides* from Egerkingen in lacking a mesostyle on the upper molars.

The limb proportions of *Europolemur kelleri* Franzen, 2000a, *E. koenigswaldi* Franzen, 1988, and the North American *Natharctus osborni* Gregory, 1920, are similar, whereas the limbs of *E. klatti* Weigelt, 1933, from Geiseltal are unknown. The dentition of *E. kelleri*, *E. koenigswaldi* and *E. klatti* (type species) correspond so well, that there is no doubt that they belong to the same genus. Radiographs demonstrate that all species of *Europolemur* match each other in possessing unicuspid but two-rooted P2/P2, while that of *Godinotia neglecta* and that of *Darwinius masillae* are small, straight and one-rooted, almost remnants in the maxilla (Fig. 5). The type specimen of *G. neglecta* from Geiseltal clearly differs from *E. kelleri*, *E. koenigswaldi*, and *D. masillae* in having very gracile limb bones (Figs. 1–3). The postcranial skeleton of *E. klatti* is little known save for an isolated astragalus, calcaneum, and atlas, the species determination of which is uncertain [22: 50, 62–65, fig. 2.20].

**Description**

**Cranium.** (Figs. 4, S2). The cranium in plate A is seen from the right side, while that in plate B is seen from the left [1: 290–293]). Bones and teeth are well preserved in both, but plate A is more complete. The profile of the face shows that the rostrum was relatively short, the face steep and the orbit large (see below). Measurements are listed in Table 2, and Appendix S1.

**Rostrum and orbit.** Nasal: The anterior parts of the nasals are not preserved. The ventral suture with the premaxilla is about one-third of the length of the suture with the maxilla and lachrymal (or median process of maxilla, see below). Following the impressions, the right nasal extends mesially to above I2 whereas the left ends above the border between I1 and I2. The right nasal contains three similar sized slit-like nasal foramina. The most caudal one is situated above the anterior rim of the orbit. The most mesial one occurs above the tip of the deciduous upper canine.

Premaxilla: The suture between the two premaxillae is recognizable between the central incisors. The right premaxilla contains two permanent incisors (Figs. 4–5). The bone is almost triangular and has a long caudal suture with the maxilla, as well as...
a straight, upwardly-directed suture with the premaxilla of the left side. Above there is also a dorsomesial suture with the right nasal. The bone reaches distally to above upper dC1.

Maxilla: The bone forms a large part of the face. It contains the canine, two deciduous premolars, P2 and three molars (Fig. 4). The maxilla is very flattened and damaged and hard to distinguish from the other bones. The anterior border is located above the precanine diastema. Its suture with the premaxilla is steep and curving caudally into the suture with the nasal. There might be a median process of the maxilla dorsal to the lachrymal as seen in Lemur, but this cannot be decided from the X-ray photographs or CT scans. In the intraorbital part of the maxilla, there is a large infraorbital foramen. The mesial opening of the infraorbital channel is very small and situated above the metacone of dP4.

Lachrymal: The lachrymal bone is crushed. There seems to be a substantial facial part, but most of the bone lies within the orbit. The lachrymal foramen is not visible.

Frontal: The frontal bone forms the medial and upper half of the posterior border of the orbit. Mesially, it has a suture with the nasal and lachrymal. There is a well-defined ethmoidal foramen. The processus jugalis is robust and meets the processus frontalis of the jugal halfway. Together the two bones form the postorbital bar.

Jugal: The mesiodorsal beginning of the zygomatic arch as well as the ventral border of the orbit is situated above the metacone of dP4. The zygomatic arch is mesially low and slender. The jugal size increases considerably distally until the divergence of the processus frontalis. Behind this the jugal narrows to about half of its former height. This is also the width of the postorbital bar.

Squamosum: The bone forms the posterior half of the zygomatic arch and ends caudally in the fossa gnoioidalis.

Auditory region. Squamosum: Caudally of the rather massive processus postglenoidalis there is a deep porous acusticus, which is not surrounded by an external meatus. The squamosum forms the dorsal roof of the meatus.

Petrosum: The bulla tympanica has completely collapsed. However, the posterior and dorsal part is visible. The bulla of the left side is preserved on plate B, where the dorsal half of the annulus tympanicus is clearly seen on the X-ray photograph [1: fig. 5].

Braincase. Part of the left parietal and frontal is visible above the well exposed sutura sagittalis. Because of compaction, the skull appears higher than it was originally. A crista sagittalis was not developed. The rather voluminous braincase ends distally at the crista nuchalis. Caudoventrally, the in situ planum nuchale is turned up and crushed.
The following bones form the dorsal and lateral parts of the braincase:

Frontal: As usual, the bone forms the mesial part of the braincase.

Parietal: The bone makes up most of the lateral side of the braincase. It is both deep and wide. Mesially, the parietal meets the frontal bone and caudally it has a long suture with the dorsal part of the occipital. It ends posterolaterally at the nuchal crest.

Occipital: The dorsal extension of the occipital bone (protoberbantia occipitales externa) is wedged between the parietals as a triangular plate.

On the caudal end of the skull, the dorsal rim of the foramen magnum is visible. The atlas is visible to the right of the foramen magnum, pressed against the occipital plane.

Lower jaw. The right ramus mandibularis is exposed laterally, with the teeth visible in buccal view. In contrast to adapid skulls [23], its height increases mesially, but not as much as it seems on its left counterpart [1: 293, fig. 4]. In addition, the mesial outline of the mandible is not as steep as it is on the left side (plate B). Both may result from damage during preparation. The micro-CT shows that the symphysis was fused ventrally but still open dorsally, due to the juvenile age of the individual (see below).

The angular area increases caudally, where it extends into a well developed, caudally-protruding processus angularis. Some flat bony fragments located ventral and caudal to the processus angularis seem to belong to the hyoids. The processus articularis is still articulated with the fossa goenoidalis, which is situated about 6 mm above the occlusal surface of the mandibular cheek teeth. The coronoid process appears dorsal to the arcus zygmaticus, but it is not fully exposed making description impossible. There is only one foramen mentale appearing below P2 in the middle of the corpus.

Dentition. The dentition of *Darwinius masillae* shows the holotype to be a juvenile, and imaging reveals a host of developing teeth within the face and jaw (Fig. 5). Much of the face preserves natural occlusion of upper and lower teeth. Studies of higher primates show that teeth generally begin eruption sometime after roots begin to mineralize, emerging through bone and gum before roots are complete [28]. In this light, images of *Darwinius* crown and root development reveal a coherent, readable pattern, in which we see: (1) fainter, less dense deciduous crowns with long roots; (2) developing permanent molars with densely mineralized crowns and incomplete roots; and (3) mineralizing crowns of the replacing permanent teeth (*I*-1/P*-P*-P*-P*), largely, but not entirely, buried within the face. Basically, the entire permanent dentition was mineralizing while the deciduous dentition had only begun to be shed.

Deciduous teeth: In the mandible, it appears that the central deciduous incisors (dl1) have been shed and replaced. Much smaller second deciduous incisors (dl2) remain in the mandible, on right and left sides. We cannot positively identify any upper deciduous incisors, which may have been shed. Clearly, upper and lower deciduous canines are in place. All four deciduous third and fourth premolars are erupted and in occlusion. All the deciduous teeth have long roots, consistent with circumnatal emergence. At the second premolar position we see only a single tooth generation in the mandible and maxilla, and, after more extensive comparison, conclude that dp2 was probably shed at an early age.

Permanent molars: All three permanent molars can be seen in the dentary. The first permanent molar in the dentary, M1, is fully erupted, occluding in normal position with M1. The long, but open roots of M1 suggest that it was probably erupted for some time (weeks or possibly months). The mandibular second molar, M2, is just erupting, and its roots are less developed. The upper second molar, M2, is displaced but lacks sufficient root development for eruption. Third molars, M2/M3, had no roots mineralized, and these crowns were probably still covered by soft tissues.

Replacement teeth: The first permanent incisor is the most advanced of the replacement teeth; this tooth is fully erupted with root length mineralized perhaps ⅓ or ⅔ of final adult length. The tooth labeled I1 is permanent because it is much larger than dl2 and it has a denser crown. Development of I2 is well underway, but it is significantly behind dl2.

In the premaxilla, we can see four incisor teeth. The right side is clearest: here, the I1 (with its labial edge slightly broken) is erupted, with a long root (⅔ or more mineralized). The more caniniform right I2 shows root development of about ⅓. Radiographs also show a well developed incisor from the left side that is more difficult to identify (it may be I1 or possibly I2; one of these teeth is missing in either case). Maxillary permanent incisors were at or near emergence.

The developing lower canine crown, C1, is substantial, but probably no more than half its eventual size. The massive upper permanent canine crown is probably caught at its maximum width, as mineralization was just outlining flanges at the base of the crown, indicating that a wide but not extremely tall crown was forming. The second premolar is represented by a tiny maxillary tooth, P5, on plate B, and a small mandibular tooth, P2, on both plates A and B. The mandibular tooth has a more densely mineralized crown, casting a denser shadow on radiographs and alloying it with other permanent teeth. Root development is long and clearly advanced over that of the remaining permanent premolars. The crown of P1 is less than ⅓ formed, but noticeably advanced over that of P3; crowns of P4 and P5 can be identified in radiographs, with P5 again much advanced over P4.

Molar morphology. Little can be seen of the crowns of the molars in either plate A (Fig. 5) or plate B. However, we have succeeded in extracting three molars using micro-CT and graphic reconstruction (Fig. 6).

The crown of M1 is subrectangular in occlusal outline, with a prominent protocone, paracone, and metacone well spaced on the crown. There is a well-developed hypocone developed on a broad lingual cingulum, but a pericone, if present, was weakly developed (Fig. 6A–B). This tooth has the classic simplicity of cercamoniine upper molars. Roots are relatively well developed, which is consistent with its early eruption. Measurements are listed in Table 2.

The crown of M2 is relatively long and narrow (Fig. 6C–D). There is no distinct paracristid, but a looping paracristid encloses a basined trigonid. The protoconid and metaconid are well developed on the trigonid, followed by a distinct hypoconid and entoconid on the talonid. There is no hypoconulid, but a well developed metastylid distally from the metaconid. The talonid of M1 is distinctly broader than the trigonid, but less broad than the talonid on M2. The cristid oblique or prehypocristid runs mesiolingually toward the notch in the protostylid of the protoconid and metaconid are well developed on the talonid, and again they are followed by a distinct hypoconulid and entoconid on the talonid. There is neither a hypoconulid nor a metastylid. The
Figure 6. Micro-CT reconstructions of molar teeth of *Darwinius masillae*, new genus and species. Tooth crowns shown here were extracted digitally to show the entire crown for teeth that are only partially exposed in Plate A (see Fig. 5). (A–B)— right M₁, in buccal and occlusal view. (C–D)— right M₂, in buccal and occlusal view. (E–F)— right M₂, in buccal and occlusal view. Note the absence of a mesostyle on M₁, and the presence of a hypocone on the broad lingual cingulum of this tooth. Note too the absence of a distinct paraconid and hypoconulid on M₁ and M₂, and the very broad talonid on M₂. Molars of *Darwinius masillae* are distinct in morphology and intermediate in size between those of contemporary species of *Periconodon* and *Europolemur.*

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lingual cingulid is more pronounced than that on M₈; so nM₁, there is a distinct cristid oblique that ends near the base of the protoconid. Measurements are listed in Table 2 and Appendix S1.

Vertebral column. (Figs. 1–2, 7, S3, and measurements in Appendix S1). The vertebral column is complete, although laterally compressed and, in part, crushed. Altogether it comprises 7 cervical, 11 thoracic, 7 lumbar, 3 sacral, and 31 caudal vertebrae. The whole vertebral column, from the proximal end of the atlas to the end of the last caudal vertebra, measures ca. 53 cm (Table 2). Together with a basal length of the skull of about 5 cm, this results in a total skeleton length of ca. 58 cm, whereas the head and body length is ca. 24 cm without the tail.

The atlas is broken and incomplete. It is attached to the planum nuchale of the cranium. The left wing of the atlas is crushed, whereas the right wing is seen in dorsal view, with a well-developed foramen vertebrale laterale. The lateral surface of the axis is visible in plate A, however the prominent processus spinalis is crushed. C3–C5 are visible in lateral view. Their processus spinales are only partially exposed, whereas their processus transversi are clearly visible. Caudally in the cervical series, the processus transversi become more and more expanded. C6 is crushed, whereas the right scapula covers C7.

By including the first and second thoracic vertebrae, which are hidden below the right scapula, 11 thoracic vertebrae are present although their exact number is difficult to determine and therefore somewhat ambiguous. Whereas T3–T5 are laterally exposed, T6–T8 have rotated around their long axis so that they are seen in dorsal aspect, while T9–T11 are visible laterally. There is no diaphragmatic vertebra, because even the processus spinalis of T11 is slightly but clearly dipping caudally. The ribs are not well preserved. Most of their cartilaginous parts exist only as natural casts. The right humerus mostly covers the sternum.

Caudal to the thoracics are 7 lumbar vertebrae. They are comparatively massive and display cranially oriented transverse processes, which become more and more expanded caudally. No spinal processes are evident on L1–L3, but L4 carries a rather small process slightly dipping caudally. The spinal process of the lumbar vertebrae becomes somewhat larger caudally and dips more in this direction. The os sacrum comprises 3 vertebrae, S1–S3, the most proximal one of which is damaged.

Altogether, there are 31 caudal vertebrae but the last one ends fragmented at a fault. So there may have been one or two more. The 3 most proximal are comparatively short and display strong transverse processes that become weaker more distally in the series. The last transverse process is developed on Ca₄, which is already considerably longer and shows only a small processus transversus at its caudal end. All following vertebrae have no processus transversi.

In D. masillae the dorsal vertebral column shown on plate A is gently curved (that of plate B is fake) and the tail is only slightly curved. The length profile of the proximal half of caudal vertebrae is close to that of living Callithrix jacchus, while more distally D. masillae is more curved.
**masillae** has much longer vertebrae. Altogether, the tail is much longer than that referred to *Europolemur koenigswaldi* (Fig. 7). In *D. masillae*, the length profile of Ca8–Ca20 differs from that of the living *Avahi laniger*, even more so from *Eulemur mongoz*, and considerably from *Ateles geoffroyi*. Clearly, *Darwinius* did not have a prehensile tail. The tail was presumably used primarily for balance, and possibly for steering while leaping. Its soft body contours are incomplete. Therefore, it is impossible to decide whether it was bushy or not.

**Shoulder girdle and forelimb.** (Figs. 8–9, S4, and measurements in Appendix S1). The right scapula represents most of the shoulder girdle (Fig. 8). Its dorsal part is heavily crushed. The crista scapulae passes proximocranially into a rather expansive processus hamatus for articulation with the clavicle. The left scapula appears dorsal to the vertebral column and its dorsal part can be viewed medially. The processus hamatus is curved in a craniodorsal direction, more so than in *Notharctus osborni*, while the caudal extension of the margo costalis dorsal to the collum is not as expressed. In *Eulemur mongoz*, *Varecia variegata*, *Avahi laniger*, and *Loris* sp., such a caudal extension of the margo costalis is totally missing, and the same holds for *Callithrix jacchus* and *Cercopithecus neglectus*. Dorsally, the crista scapulae reaches the margo vertebralis of the

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Figure 8. Shoulder girdle and forelimb of *Darwinius masillae*, new genus and species. Photograph (A) and X-ray image (B) show the specimen preserved on plate A (Fig. 1). Note excrescence at the distal end of the right forearm, and a fracture of the basal phalanx of the left pollex (details are shown in Fig. 9).

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scapular blade. The facies supra spinam is evidently much smaller than the facies infra spinam. A fragment of the clavicle can be seen dorsal to the processus hamatus of the right scapula, but no details are observable.

The right humerus is well exposed in lateral view. Only the distal part of the left humerus can be seen, in medial view. Both are articulated with their respective forelimbs. Proximally, the epiphyseal suture is still present, although nothing can be said about the proximal epiphysis because it is completely obscured by siderite. Here, as elsewhere on the skeleton, siderite formed as a concretion around decomposing cartilage. The crista deltoidea of the humerus is well developed and runs up to the middle of the distal diaphysis. A crista brachiolateralis (crista epicondyli lateralis) is visible distally, and this expands as is seen typically in prosimians. It is not as broad as that of Notharctus osborni, and it is more like that seen in Eulemur mongoz, Varecia variegata, and Avahi laniger. Mediocaudally, where the left humerus is close to the trochlea, a foramen entepicondyloideum is well developed as common to many mammals as well as primitive anthropoids such as platyrhine primates.

The trochleae of both humeri are in articulation so no details are visible.

The ulna and radius are completely separated, as is typical for primates. The forearm is unusually short, being about the same

Figure 9. Hands and wrist of *Darwinius masillae*, new genus and species. Photograph (A) and X-ray image (B) show the specimen preserved on plate A (Fig. 1). (C)— explanatory drawing, where I–V represent digits one to five. (D)— Inset interpretive drawing of the left wrist (box in C). doi:10.1371/journal.pone.0005723.g009
length as the humerus. This is the case in *Varecia variegata, Callithrix jacchus* and *Cercopithecus neglectus*, whereas the forearm becomes proportionally longer in the series *Eulemur mongoz, Notharctus osborni, Avoahi laniger*, and especially *Gedinnia neglecta* from Geiseltal. The right forearm of *Darwinius* is preserved in pronation, so that the radius is exposed from the lateral side and the ulna is viewed medially. The left forearm, however, is preserved in supination, so that the radius and ulna are both seen from the medial side. The ulna is more robust proximally, while the radius is more robust distally. Proximally the caudal outline of the ulna curves cranially, while distally the radius curves in a caudal direction. The processus olecrani is short but high when compared with *Lemur*.

The left ulna has a well developed processus anconaeus, and the incisura semilunaris is deep. The distal end of the left forearm is still articulated with the carpus, whereas that of the right forearm lies on top of the carpus. In both cases, articular facets are not discernible. Of special interest is a substantial ex crescence that inflates the distal ends of the right ulna and radius, causing them to be secondarily fused (Figs. 8–9). The excrescence is of bone and differs in both color and structure from the bright yellow siderite below and between bone fragments. Clearly, on the right arm the callus covered and fused the carpus. Evidently the animal suffered a fracture at the distal end of the right forearm. The latter covers the carpus, so that only the hamate and its articular facets for metacarpals V and a small part of the capitate are visible. In an X-ray the proximal articulation of the right metacarpal I with the trapezium is not clearly visible. However, the mediolateral extension of the proximal epiphysis of metacarpal I suggests that this was a saddle-shaped rather than a ball and socket articulation. This is confirmed by the left carpus.

The left carpus is proximally exposed from its palmar side. Left metacarpal I is proximally disarticulated, exposing part of the articular facet for articulation with the trapezium. This articulation is clearly saddle-shaped, indicating beyond doubt that the thumb was opposable. The proximal carpals include a transversally oriented pisiform that articulated originally with the ulna proximally and the hamate distally. The rather small lunate articulates proximally with the radius and with the ulna, medially with the scaphoid, and distally with the centrale (Fig. 9). In *Darwinius* the arrangement of the carpals corresponds to that known for *Eurotopolm* and *Notharctus* [17,30]. It differs from the arrangement in *Adapis*, where the lunate is excluded from any contact with the centrale [27,31]. Metacarpal II lies across the distal metacarpals, exposing its dorsal side. Proximally it is disarticulated, so that the face of its saddle-shaped articulation with the trapezoid is exposed. The distal end of metacarpal I is covered by silderite, and this is more or less hidden below the pisiform and the hamate (Fig. 9). Metacarpals III–V are all seen in palmar view, but their proximal articulations are mostly hidden by metacarpal II. Metacarpal V, displays much of a saddle-shaped articulation with the hamate. With the exception of the pollex, all of the basal phalanges are very long: the longest being digit III, followed by digits IV and V. Digit II is a little shorter than digit V, and the shortest digit is that of the thumb.

The articulated basal and terminal phalanges of the pollex lie across the distal ends of the radius and ulna. The distal end of the basal phalanx appears to be somewhat deformed, being bent lateropalmarily. It is exposed in lateral aspect. An X-ray (Fig. 9) shows a transverse fracture of the midshaft of the basal phalanx. The terminal phalanx of the pollex, on the lateral side of the ulna, is scutiform in dorsal view. The basal phalanx of the second digit is completely exposed from its medial side, and its distal half covers most of the distal ends of metacarpal II–V. The complete basal phalanx of digit III is seen in medial view. It articulates proximally with metacarpal III, as do metacarpals IV–V with digits IV and V, respectively. Whereas the basal phalanx of digit IV is exposed palmarly, that of digit V is exposed laterally. In a distal direction, the basal phalanges of digits III and V come so closely together that the distal end of the basal phalanx of digit IV is almost completely covered by them. The intermediate phalanges of digits III–V are all exposed in medial view, and digit IV is seen crossing over the diaphysis of the intermediate phalanx of digit V. The terminal phalanx of digit I is exposed from the dorsal side, whereas those of digits II–IV, are seen in palmarolateral view. The terminal phalanx of digit V is exposed between the intermediate phalanges of digits III and IV. All are scutiform, and hence were nail-bearing.

On the right hand, all metacarpals and most phalanges are exposed in dorsal view. Only the phalanges of digit V are turned progressively so that the terminal phalanx is completely exposed in palmar view. The lengths of the basal and middle phalanges of digits II–V are remarkable and resemble those of the modern *Lemur*, whereas the metacarpals are much shorter. The latter, as well as the basal and middle phalanges, especially the latter distally, are slightly bent palmarly. In contrast to the hallux, the pollex is rather small and short. All terminal phalanges of the right hand clearly bore nails.

All in all, the hand of *Darwinius* is similar to that of *Eurotopolm* and *Notharctus*, as well as the metacarpals are much shorter. The latter, as *Gedinnia* and *Eulemur*, but not *Adapis*, have a hand similar to those of living galagos. The function of the hand is evidently not correlated particularly well with locomotor type [32: 273], although it must constrain the size of branches the hand could grip. The functional significance of mesaxony in primate hands and feet, which *Darwinius* shares with *Eurotopolm* and living anthropoids, is not clear.

**Pelvis and posterior limb**. (Figs. 10–11, S5, and measurements in Appendix S1). The right side of the pelvis is visible in lateral view, with the ilium, pubis and ischium still not fused (Fig. 10). The os sacrum and vertebral column cover most of the left side. The articular surfaces of the acetabulum and the caput femoris cannot be seen, but the latter is surrounded by the ilium craniodorsally and the pubis cranioventrally, and by the ischium posteriorly. Consequently, the foramen obturatum is completely hidden. The iliac blade is narrow and extends cranioventrally as in prosimian primates, although such morphology also occurs in *Callithrix jacchus*. It is as narrow as in *Loris*, and clearly narrower than in *Cercopithecus neglectus*. The tuber sacrale is situated dorsomedially near the middle of the ilium. The crista iliaca is short and cranially convex. Details of the pubis are restricted to the cranially directed pecten. Compared with *Lemur*, the tuber ischiadicum is rather weak.

The proximal part of the left femur is mostly covered by that belonging to the right side, which is laterally exposed. Compared with the caput, the neck of the femur is very short and the trochanter major is very low as in *Notharctus osborni*. The trochanter major is higher in *Eulemur mongoz, Varecia variegata, Avoahi laniger*, and particularly *Cercopithecus neglectus*. All growth sutures are still open and unfused. The right patella is exposed laterally. The distal end of the left femur is more robust than in *Notharctus osborni*, the trochanter major is higher in *Eulemur mongoz, Varecia variegata, Avoahi laniger*, and particularly *Cercopithecus neglectus*. All growth sutures are still open and unfused. The right patella is exposed laterally. The distal end of the left femur is more robust than in *Notharctus osborni*, whereas the metacarpals are much shorter. The latter, as *Gedinnia* and *Eulemur*, but not *Adapis*, have a hand similar to those of living galagos. The function of the hand is evidently not correlated particularly well with locomotor type [32: 273], although it must constrain the size of branches the hand could grip. The functional significance of mesaxony in primate hands and feet, which *Darwinius* shares with *Eurotopolm* and living anthropoids, is not clear.
Figure 10. Pelvis and hind limb of *Darwinius masillae*, new genus and species. Photograph (A) and X-ray image (B) show the specimen preserved on plate A (Fig. 1). Note the large opposable hallux. Hind limb proportions are compared to those of other primates in see also Figure S5, and an explanatory drawing is provided in Figure 11.

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marks on the adjacent bones. The lower leg and foot of the right limb are completely preserved. The tibia is seen in lateral view and the fibula is exposed mainly from its cranial side. Both lie parallel to each other and are not fused. Proximally as well as distally, growth sutures are still visible. The crista tibiae is not well defined, and the proximal end of the tibia is slightly bent caudally as in *Lemur*, but not to the extent as that of *Godinotia neglecta* from Geiseltal [22: 58–60, fig. 2.18].

The tarsus is exposed in laterocranial view (Fig. 10), with the processus coracoideus situated dorsally from behind the middle of the calcaneum as in *Lemur* and *Europolemur kelleri* [13: 70–71]. This differs considerably from omomyids and even more so from *Tarsius*, in which the part of the calcaneum distal to the processus coracoideus is extremely elongated, while it is much shorter in anthropoids. Hence it appears plesiomorphic for prosimians. Except for its smaller size, the tarsus of *Darwinius*, seen in lateral view, resembles that of *Adapis parisienus* figured by Decker & Szalay [33: fig. 3]. The talofibular facet is steep and the peroneal tubercle is rather small and sharply angled [33] which is unlike that seen in adapids, *Lemur*, *Hapalemur*, and other lemuriforms, and is more like that in haplorhines (see [34,35] for discussion). Unfortunately, the groove for the flexor fibularis cannot be seen while only a small part of the talotibial facet is exposed. These two characters, together with the shape of the talofibular facet, form the talar morphology shared by known Eocene adapiforms with lemuriforms and lorisiforms [33,35]. The steep fibular facet on the talus alone is not a synapomorphy for anthropoids because it also occurs in outgroups such as Scandentia, Dermoptera and

**Figure 11. Right foot of *Darwinius masillae*, new genus and species.** Photograph (A) and X-ray image (B) show the specimen preserved on plate A (Fig. 1). (C)— explanatory drawing. (D)— drawing of foot of *Eulemur mongoz* for comparison. Note the large opposable hallux, and absence of a grooming claw on digit II in *Darwinius*. doi:10.1371/journal.pone.0005723.g011
Plesiadapiformes. Among primates it is, however, a haplorhine apomorphy [33,37], and its presence in Darwinius supports taxonomic and phylogenetic classification with haplorhines rather than strepsirrhines (Table 3).

The cuboid, which is situated between the calcaneum proximally and metatarsals IV–V distally, articulates proximomedially with a remarkable high navicular bone. On the lateral side a sesamoid is visible. Seen from the lateral aspect only, it is not possible to decide whether it has a pivot joint with the calcaneum like most primates. The navicular is situated between the talus proximally and the ecto- and mesocuneiform distally. It is a long bone compared to that in lorises, indris and anthropoids [34], and it is more like that of Hapalemur and Eulemur, although it is not as wide. The naviculocuboid articulation is broad and contiguous with both the ectocuneiform and mesocuneiform facets shaped like those of living lemuriforms and all known notharcines [36]. Proximolaterally, the navicular articulates with the calcaneum. As is the case with Eulemur, the entocuneiform is rather deep. Proximally, it articulates with the navicular bone.

By far the strongest of all metatarsals is metatarsal I, as is the entire hallux. Metatarsal I is about twice as thick as metatarsals II–V. As preserved, metatarsal I extends medially almost at right angles to the other metatarsals when viewed dorsally. Proximomedially, part of the articular facet for the entocuneiform can be seen (Fig. 11). Although partially crushed, and covered laterally by the entocuneiform, metatarsal I appears to be saddle-shaped, indicating that the hallux was opposable. The prehensibility of the hallux corresponds with that of the pollex. Little can be said about metatarsals II–V except for their proportions, which are not as slender as in Lemur. Metatarsal II articulates proximally mainly with the mesocuneiform, and only laterally also with the ectocuneiform. Proximally, metatarsal III is supported by the entocuneiform medially and the cuboid laterally.

All phalanges are exposed mainly from their dorsal side, and all are slightly bent plantarily. Morphologically, the basal and intermediate phalanges do not differ very much from those of the manus, although they are somewhat more robust. This difference in robustness is particularly true for digits I and II of the pes, which are much more robust than their counterparts in the manus. Terminal phalanges IV–V are seen from their dorsal aspects, while III and II are seen progressively but slightly dorsomedially. All terminal phalanges are definitely scutiform, and were therefore nail-bearing, although those of digit II and III appear to be rather narrow. The toilet or grooming claw reported were therefore nail-bearing, although those of digit II and III tend to erupt incisors and even premolars before third or even second molars. In Darwinius we can distinguish a first set of teeth that emerged before a second set, (M1 M2 M3 I1 P2)( I2 M2 C P1 P3), an order of tooth eruption that characterizes “medium fast” growing primates. This pattern is associated with more rapid growth and aging in primates and in some other mammals [41].

Schultz [42] first noted a regular pattern shift between molars and replacement teeth in primates: the slower-growing primates tend to erupt incisors and even premolars before third or even second molars. In Darwinius we can distinguish a first set of teeth that emerged before a second set, (M1 M2 M3 I1 P2)( I2 M2 C P1 P3), an order of tooth eruption that characterizes “medium fast” growing primates with a maximum life span of about 12–20 years.

Outside of living primates, some very rapidly growing mammals erupted all three molars before replacing any deciduous teeth. The tree shrew for example has the sequence M1 M2 M3 P3 I1 P1 (I1, C) P3 I2 [43]. Fast-living ungulates have similar sequences [40], and the association of eruption sequence and growth rate continues to hold up in primates as more are studied.

**Sex of the Darwinius holotype**

Male primates commonly preserve a baculum or penis bone [40]. Four specimens of cercamomine primates are known from Messel that preserve hind limbs. Two of these have a large baculum preserved in association with the hind limbs. Both are Europolemur kelleri (HLD ME 7430 and LNK ME 604), and both are clearly male [13,14]. Two specimens with hind limbs have no baculum. One is Europolemur koenigswaldi (SMNK ME 1125a,b), of unknown sex, and the other is the type of Darwinius masillae described here. The specimen of Darwinius on plate A is so complete and well preserved, and the known bacula of cercamomines are so large, that a baculum, if present, should be evident either as a preserved bone or as an impression. Lacking evidence of a baculum, we interpret the holotype of Darwinius masillae as female.

**Tooth emergence sequence and the pace of life and aging**

Sequence of tooth eruption can inform us about other aspects of primate life history. A broad look at tooth formation of Darwinius shows that the third molar crowns are well developed, while the deciduous dentition has only begun to shed—a degree of simultaneous tooth development that does not appear in slow growing primates. This pattern is associated with more rapid growth and aging in primates and in some other mammals [41].

Schultz [42] first noted a regular pattern shift between molars and replacement teeth in primates: the slower-growing primates tend to erupt incisors and even premolars before third or even second molars. In Darwinius we can distinguish a first set of teeth that emerged before a second set, (M1 M2 M3 I1 P2)( I2 M2 C P1 P3), an order of tooth eruption that characterizes “medium fast” growing primates with a maximum life span of about 12–20 years.

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**Life stage of Darwinius**

Eruption of the first permanent molar marks an important transition for primates, that from infant to juvenile [42]. Primates tend to be weaned about this time, especially species with higher-
Table 3. Interpretation of morphology of *Darwinius masillae* in comparison to characteristics distinguishing extant strepsirrhine and haplorhine primates.

| Anatomical/morphological characteristic | Lem | Lor | Tar | Ceb | Cer | Hom | ref | Primitive or derived | *Darwinius masillae* | Interpretation |
|----------------------------------------|-----|-----|-----|-----|-----|-----|-----|----------------------|---------------------|-----------------|
| **Strepsirhini**                        |     |     |     |     |     |     |     |                      |                     |                 |
| 1 Moist nose with median cleft in upper lip | X   | X   |   |     |     |     | 74: p.24 | Primitive | N/A                | —                  |
| 2 Jacobson’s vomeronasal organ          | X   | X   | X   |     |     |     | 74: p.24 | Primitive | N/A                | —                  |
| 3 Sphenoidal recess in nasal cavity     | X   |     |     |     |     |     | 74: p.23 | Primitive | N/A                | —                  |
| 4 Reflecting tapetum lucidum in eye    | X   | X   |     |     |     |     | 74: p.82 | Derived? | N/A                | —                  |
| 5 Small brain and braincase            | X   |     | X   |     |     |     | 74: p.82 | Primitive | Present            | —                  |
| 6 Brain with relatively large olfactory bulbs | X   | X   |     |     |     |     | 74: p.20 | Primitive | N/A                | —                  |
| 7 Stapedial/pharyngeal blood supply to brain | X   | X   |     |     |     |     | 74: p.22 | Derived? | N/A                | —                  |
| 8 Cranium with long rostrum            | X   |     |     |     |     |     | 74: p.15 | Primitive | Absent            | —                  |
| 9 Shallow mandibular ramus             | X   |     |     |     |     |     | 74: p.15 | Primitive | Absent            | —                  |
| 10 Open metopic suture between frontal bones | X   | X   | X   |     |     |     | 74: p.15 | Primitive | Present            | —                  |
| 11 Postorbital bar without postorbital closure | X   | X   |     |     |     |     | 74: p.82 | Primitive | Present            | —                  |
| 12 Ectotympanic free or in lateral wall | X   | X   | X   |     |     |     | 74: p.28 | Primitive | Present            | —                  |
| 13 Open mandibular symphysis           | X   | X   |     |     |     |     | 74: p.13 | Primitive | Partial            | —                  |
| 14 Procumbent to vertical pointed incisors | X   | X   |     |     |     |     | 74: p.15 | Primitive | Absent            | —                  |
| 15 Tooth comb of lower incisors-canines | X   | X   |     |     |     |     | 74: p.82 | Derived | Absent            | —                  |
| 16 Non-dimorphic canine teeth          | X   | X   |     |     |     |     | 87    | Primitive | N/A                | —                  |
| 17 Upper molar quadrates with hypocone cusp | X   | X   | X   | X   |     |     | 75: p.53 | Derived | Present | Indet.          |
| 18 Premolar $P_4$ molarized            | X   | X   |     |     |     |     | 75: p.53 | Derived? | N/A                | —                  |
| 19 Lower molars quadrate w. reduced paraconid | X   | X   | X   | X   |     |     | 75: p.53 | Derived | Present | Indet.          |
| 20 Capitate (os magnum) laterally compressed | X   | X   |     |     |     |     | 75: p.51 | Derived | N/A                | —                  |
| 21 Sloping fibular facet on astragalus or talus | X   | X   |     |     |     |     | 74: p.82 | Primitive? | Absent            | —                  |
| 22 ‘Tarsi-fulcrumating’ pes with long tarsals | X   | X   |     |     |     |     | 75: p.40 | Derived | Absent            | —                  |
| 23 Mediolaterally-compressed mesocuneiform | X   | X   |     |     |     |     | 75: p.52 | Derived | Absent            | —                  |
| 24 Pes with fourth toe longest         | X   | X   |     |     |     |     | 75: p.40 | Derived | Absent            | —                  |
| 25 Grooming claw on pedal digit II     | X   | X   |     |     |     |     | 74: p.82 | Primitive | Absent            | —                  |
| 26 Two or more pairs of mammary glands | X   | X   |     |     |     |     | 74: p.82 | Primitive | N/A                | —                  |
| 27 Bicorneate uterus                  | X   | X   |     |     |     |     | 74: p.83 | Derived | N/A                | —                  |
| 28 Epitheliochorial placenta           | X   | X   |     |     |     |     | 74: p.83 | Primitive | N/A                | —                  |
| 29 More precocial (more teeth at birth) | X   | X   | X   |     |     |     | 50, 88 | Primitive | N/A                | —                  |
| 30 Lack of SINE human Alu transpositions | X   | X   |     |     |     |     | 89    | Primitive | N/A                | —                  |
| **Haplorhini**                        |     |     |     |     |     |     |     |                      |                     |                 |
| 1 Dry nose and continuous upper lip   | X   | X   | X   | X   |     |     | 74: p.24 | Derived | N/A                | —                  |
| 2 Loss of Jacobson’s vomeronasal organ | X   | X   |     |     |     |     | 74: p.24 | Derived | N/A                | —                  |
| 3 Sphenoidal recess greatly reduced   | X   | X   | X   |     |     |     | 74: p.23 | Derived | N/A                | —                  |
| 4 Retinal fovea in eye                | X   | X   | X   |     |     |     | 74: p.82 | Derived? | N/A                | —                  |
| 5 Larger brain and braincase         | X   | X   | X   |     |     |     | 74: p.82 | Derived | Absent            | —                  |
| 6 Brain with relatively small olfactory bulbs | X   | X   | X   |     |     |     | 74: p.20 | Derived | N/A                | —                  |
| 7 Promontory arterial blood supply to brain | X   | X   | X   | X   |     |     | 74: p.22 | Derived? | N/A                | —                  |
| 8 Cranium with short rostrum         | X   | X   | X   |     |     |     | 74: p.15 | Derived | Present | Synap.          |
| 9 Deep mandibular ramus              | X   | X   | X   |     |     |     | 74: p.15 | Derived | Present | Synap.          |
| 10 Fused metopic suture uniting frontals | X   | X   | X   |     |     |     | 74: p.15 | Derived | Absent            | —                  |
| 11 Partial to complete postorbital closure | X   | X   | X   |     |     |     | 74: p.82 | Derived | Absent            | —                  |
| 12 Ectotympanic in lateral wall or tubular | X   | X   | X   |     |     |     | 74: p.28 | Derived | Absent            | —                  |
| 13 Fused mandibular symphysis         | X   | X   | X   |     |     |     | 74: p.13 | Derived | Partial | Synap.          |
| 14 Vertical spatulate incisors        | X   | X   | X   |     |     |     | 74: p.82 | Derived | Present | Synap.          |
| 15 Interlocking canine teeth          | X   | X   | X   |     |     |     | 74: p.15 | Primitive | Present            | —                  |
| 16 Sexually dimorphic canine teeth    | X   | X   | X   |     |     |     | 87    | Derived | N/A                | —                  |
### Table 3. cont.

| Anatomical/morphological characteristic | Lem | Lor | Tar | Ceb | Cer | Hom | ref |Primitive or derived | Darwinius masillae | Interpretation |
|----------------------------------------|-----|-----|-----|-----|-----|-----|-----|---------------------|-------------------|----------------|
| 17 Upper molars quadrate with hypocone cusp | X   | X   | X   | X   | X   | 77: p.16 | Derived | Present | Indet. |
| 18 Premolar P₄, simple w. transverse pad-mgd crest | X   | X   | X   | X   | 76: p.16 | Derived | N/A | — |
| 19 Lower molars quadrate w. reduced paraconid | X   | X   | X   | X   | X   | 76: p.16 | Derived | Present | Indet. |
| 20 Capitate (os magnum) uncompressed | X   | X   | X   | X   | 76: p.16 | Primitive | N/A | — |
| 21 Relatively small, steep fibular facet on astragalus | X   | X   | X   | X   | 74: p.82 | Derived | Present | Synap. |
| 22 'Metatarsi-fulcrumating' pes w. long metatarsals | X   | X   | X   | 76: p.15 | Primitive | Present | — |
| 23 Non-compressed mesocuneiform | X   | X   | X   | 76: p.15 | Primitive | Present | — |
| 24 Pes with third toe longest | X   | X   | X   | 76: p.15 | Primitive | Present | — |
| 25 Loss of all grooming claws | X   | X   | X   | 74: p.82 | Derived | Present | Synap. |
| 26 Single pair of mammary glands | X   | X   | X   | 74: p.82 | Derived | N/A | — |
| 27 Simplex uterus | X   | X   | X   | 74: p.83 | Derived | N/A | — |
| 28 Hemochorial placenta | X   | X   | X   | 74: p.83 | Derived | N/A | — |
| 29 Less precocial (fewer teeth at birth) | X   | X   | 50 | Derived | N/A | — |
| 30 SINE human Alu transpositions C7, C9, C12 | X   | X   | X   | 89 | Derived | N/A | — |

**Abbreviations:** Lem, Lemuroidea; Lor, Lorisoidea; Tar, Tarsioida; Ceb, Ceboidea; Cer, Cercopithecoida; Hom, Hominoida; N/A, not applicable; Synap, synapomorphy.

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quality diets [44,45]. The *Darwinius* holotype, with both first and second lower molars erupted, lived past infancy, was weaned, and had started to feed independently before dying.

To evaluate *Darwinius* maturation further, we must choose a model from living primates. The best predictor of growth rate in primates is adult brain size; body weight is a distant second [46]. The best we can do in present circumstances is to choose a model of similar body size and tooth eruption sequence. Among small to medium-sized living primates, the lemurs (e.g., *Lemur*, *Eulemur*, and *Varecia*) develop and age on a time scale closely similar to that of the New World monkey *Saimiri*. Living lorisoids (*Loris*, *Galago*) and the single living tarsioid (*Tarsius*) grow and age on a faster time scale, but fewer data are available for detailed comparisons. *Saimiri* is relatively well studied, allowing the best comparison with *Darwinius* ontogeny. Whether this time scale applies, or one that is step faster, we can begin to integrate the growth and development of different organ systems.

Figure 12 shows the developmental position of the *Darwinius* holotype in the middle of the period of permanent tooth eruption. As expected from comparison to a range of living primates, major epiphyses remain open.

If *Darwinius* grew on a *Saimiri* time scale, the holotype individual died at ca. 9–10 months of age. We expect that she would have begun to mature sexually as she neared her third year; with incremental growth possible until about 3 years of age. *Saimiri* females begin to reproduce as early as 30 months, but since they are strictly seasonal breeders in the wild [47], a first birth at 36 months seems likely. It is reasonable to expect that a primate the size and likely growth rate of *Darwinius* lived a maximum of about 20 years.

### Projected growth remaining to adulthood

Organ systems in *Saimiri* (and by analogy *Darwinius*) mature at different rates: the brain reaches more than 90% of its volume in the first two months, for example, while body weight is added more slowly. Measures of body length are intermediate in growth rate. If we place *Darwinius*, like a *Saimiri*, between the emergence of permanent I₁ and I₂, we can expect that she had achieved about 85% of adult head and body length, with growth in foot length slightly ahead of growth in femur length. We have less information about how growth would change the intermembral index, but Young [48] notes that 8–10 month old *Saimiri boliviensis* achieved an intermembral index of 79.9, close to the reported adult value for *Saimiri* of 79.1, so this is unlikely to change substantially.

For a check on these projections, we can compare *Darwinius* to longitudinal growth in *Galago senegalensis*, a more rapidly growing primate. *Galago* mothers carry or park infants for about 7 weeks; weaning is said to be in the range of 70–100 days, with first birth at about a year of age and maximum life span of 16 years [47,49]. Less is known of tooth emergence, but we can broadly estimate that a juvenile comparable to *Darwinius* in tooth emergence is somewhere near 100 days old [50]. In the captive *Galago* colony studied by Schaefer and Nash [49], an intermembral index of about 60 at birth declined to 57 at 100 days, reaching 55 at full growth. For *Galago*, it appears that relative growth added more to the hindlimb and trunk than to the forelimb. There is however, no universal direction of intermembral index ontogeny; Schaefer and Nash point out that the trend is away from evenness, but that forelimb dominated species like the apes will increase the intermembral index late in life.

Thus, with either *Galago* or *Saimiri* as a living model, we arrive at similar relative place in life history: *Darwinius* was a weaned, independently feeding juvenile with a fraction of growth remaining that might have altered its intermembral index by a percent or two. Further, we would expect that brain and orbit size were near adult values, although some growth remained in face length.

### Locomotion

There are several ways to try to understand locomotion in primates, and these often involve ratios or indices of pairs of measurements. A favorite is the intermembral index (ratio of humerus + radius length divided by femur + tibia length) [51: fig. 10.5, 22; fig. 3.13]. Such indices simplify comparison of proportions to a simple linear scale that is always as dependent...
on the denominator as it is on the numerator, and simply cannot identify the effects of overall size let alone remove them.

Here we have taken a different approach, compiling measurements of 11 skull, trunk, and limb lengths for 45 species of extant primates, subjecting these to a multivariate principle components analysis (PCA; following [52]). This provides loadings and contrasts that enable functional interpretation of axes, and scores that enable insertion of *Darwinius* masillae to see how it compares.

Measurements included are cranial length plus the 10 postcranial measurements listed in Table 2. Species analyzed included Cheirogaleidae (6 species), Lemuridae (9), Lepilemuridae (4), Indriidae (4), Daubentoniidae (1), Galagidae (8), Lorisidae (5), Tarsiidae (1), Callitrichidae (3), and Cebidae (4).

*Darwinius* was analyzed both at the size it was when it died (Table 2), and at the size it is expected to have become when it was full grown. The latter required projection using the expected change in proportions of individual body segments. The only source of such information is the compilation by Sirianni and Swindler [53] for *Macaca* (this is not an ideal primate model, but the requisite growth information for primates is rare). Measurements for *Darwinius* masillae are listed in Table 2, and the PCA results are illustrated in Figure 13.

Figure 13A is a bivariate plot of PC-I and PC-II, with both axes drawn to the same scale. All loadings for PC-I are similar and positive, indicating that PC-I represents body size. Loadings for PC-II contrast thorax length and foot length, with climbers having a longer thorax and shorter foot, and leapers having a longer foot and shorter thorax. Figure 13B is a bivariate plot of PC-III and PC-II, again with both axes drawn to the same scale (the latter plot is an enlarged projection of scores looking down the PC-I axis of Fig. 13A). Loadings for PC-III contrast lumbus length and scapula length, with climbers having a longer lumbus and shorter scapula, and leapers having a longer scapula and shorter lumbus. Thus both PC-II and PC-III distinguish leaping from climbing primates.

When *Darwinius* is projected into this PCA, as the juvenile it is (filled red circle) or as the adult it is projected to have become (open red circle), the result is virtually the same. *Darwinius* falls in the middle of both plots, near Callitrichidae in size, and overlapping Lemuridae and Cebidae in trunk and limb proportions. Thus *Darwinius* is interpreted as an arboreal quadruped specialized neither for slow climbing nor for leaping. *Notharctus osbornianus* (filled blue circle) is a larger North American contemporary of *Darwinius masillae*, but it occupies a similarly central position in the PCA.

**Body weight and diet**

Body weight is an important parameter of life history and functional morphology [54]. For mammals it is often said that calculations based on cranial and postcranial measurements yield lower and more reasonable body weights than those derived from dental measurements [16: 168, 55, 22: 72]. The advantage with the complete skeleton of *Darwinius masillae* is that it is possible to compare its body size with that of living primates in several different ways. The maximum skull length of *Darwinius masillae*,...
Figure 13. Principle components analysis (PCA) of trunk and limb proportions in extant Lemuroidea, Lorisoidea, Tarsioidea, and Ceboidea. (A)—Bivariate plot of PC-I and PC-II, with both axes drawn to the same scale. All loadings for PC-I are similar and positive, indicating that PC-I represents body size (small primates are at left and larger primates are at right; the coefficient of determination ($R^2$) for PC-I and body weight is greater than 0.8). Loadings for PC-II contrast thorax length and foot length, with climbers having a longer thorax and shorter foot, and leapers having a longer foot and shorter thorax. (B)—Bivariate plot of PC-III and PC-II, with both axes drawn to the same scale. Interpretation of PC-II is the same as in A, but here the scale is expanded. Loadings for PC-III contrast lumbus length and scapula length, with climbers having a longer lumbus and shorter
Darwinius can be projected into this PCA in two ways: as the juvenile it is (filled red circle) or the adult it is projected to become (open red circle); projection computed by augmenting each body segment by the amount it is expected to grow to reach adulthood, using growth curves of [53]. Position of Notharctus is shown for comparison, based on measurements in [23]. Family abbreviations: Lemuroidea—Che, Chirogaleidae; Dau, Daubentoniidae; Indi, Indriidae; Lep, Lepilemuridae. Lorisioidea—Gal, Galagidae; Lor, Lorini; Tarsioidae—Tar, Tarsiidae. Ceboidoidea—Cal, Callitrichidae; Ceb, Cebidae. Note that Darwinius falls in the middle of both plots, near Callitrichidae in size, and overlapping Lemuridae and Cebidae in trunk and limb proportions. Darwinius is interpreted as an arboreal quadruped specialized neither for slow climbing nor for leaping.

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Phylogenetic Relations

Living primates have long been divided into Strepsirrhini, with a moist nose and median cleft in the upper lip, and Haplorhini, with a dry nose and continuous upper lip. Strepsirrhini was named by Étienne Geoffroy Saint-Hilaire in 1812 [62], who included here six genera: Indri, Lemur, Loris, Nycticebus, Galago, and Tarsius, all sharing ‘sinuous’ noses (strep-si-rhini, Gr., bent, twisted noses). Haplorhini (haplo-rhini, Gr., simple noses) was named much later by Pocock [63], who separated Tarsius from lemurs and lorises and grouped it with higher primates. Pocock classified Lemuroidea (including lorises) and Chiromyoidae as suborders within Strepsirrhini, and he classified Tarsioida and ‘Pithecoidea’ (Anthropoidea) as suborders within Haplorhini.

Fossils came into the picture in several ways. Hubrecht [64] featured Cope’s Eocene Anaptomorpha homunculus as showing that the evolutionary lineage leading to Tarsius and apes was of great antiquity. Gregory [65] classified Primates in two suborders, Lemuroidea and Anthropoidea, with the former including Lemuriformes (including the ‘primitive’ Eocene Adapidae), Loriformes, and Tarsiiformes (including Eocene ‘Anaptomorphidae’). Finally, Elliott Smith [Smith 1919] emphasized the primitive tarsiod traits retained in the Oligocene anthropoid Parapithecus to “establish the truth of the Tarsioid ancestry of the Apes.” The primitive tarsiod traits to which he referred (lower dental formula of 1.1.3.3 and V-shaped mandible) have both proven to be artifacts of breakage [Simons 1972, p. 190].

Fossil tarsioid primates including Eocene Omomyidae and Microchoeridae were elevated to haplorhine status from the beginning for the simple reason that Tarsius was included in Haplorhini. Eocene notharctines and adapines have never been considered haplorhines. This is due in part to definitions of Strepsirrhini and Haplorhini that are based on characteristics of the rhinarium that do not preserve in fossils [68,69,70], and it is also due to Gregory’s [63] inclusion of notharctines and adapines in strepsirhine Lemuroidea. Any paleontologist who works in early Eocene deposits, however, knows how easy it is to confuse the dentitions of primitive tarsioid and adapoid primates because of their similarity [71,72,73].
The complete skeleton of *Darwinius masillae* described here provides an opportunity for a broad comparison to Strepsirrhini and Haplorhini. Table 3 lists 30 anatomical and morphological characteristics commonly used to distinguish extant strepsirrhine and haplorhine primates. These were taken from the standard primate textbook by Fleagle [74], from the classic W. C. Osman Hill monographs on Strepsirrhine and Haplorhini [75,76], and from additional references listed in Table 3. The distributions of characteristics across the strepsirrhine superfamilies Lemuroidea and Lorisoidea and across the haplorhine superfamilies Tarsioidae, Ceboidea, Cercopithecoidea, and Hominoidea are tabulated by X's (unusually specialized taxa excepted). Standard interpretations of each character as primitive or derived within Strepsirrhini or Haplorhini are listed. Characters that are preserved in *Darwinius masillae* are recorded as present or absent depending on whether they are consistent with the corresponding state in the character list. The final column at the right in Table 3 shows which character states can reasonably be considered synapomorphies of *Darwinius* and either Strepsirrhini or Haplorhini (requiring that states be both derived and present). Some characters may be noted as indeterminate for *Darwinius* because of evidence of convergence, for example, presence of tributicular molars in extant and early Eocene representatives of Tarsioidae means quadrate molars evolved independently and convergently in Strepsirrhini and most later Haplorhini.

All of the determinate synapomorphies in Table 3 link *Darwinius masillae*, and by implication other Adapoidea, to Haplorhini rather than Strepsirrhini (see also Fig. S7). This is a surprising result, but on reflection the grouping of adapoids like *Notharctus* and *Adapis* with Strepsirrhini [63] was based on retention of primitive characteristics like the free ring-like ectotympanic within the auditory bulla. Consideration of adapoids to be Haplorhini, as tarsioids are, helps to explain why the earliest representatives of both groups are so similar and sometimes confused. Note that *Darwinius masillae*, and adapoids contemporary with early tarsioids, could represent a stem group from which later anthropoid primates evolved, but we are not advocating this here, nor do we consider either *Darwinius* or adapoids to be anthropoids.

As currently conceived, the history of Anthropoidea is traced through the Eocene in somewhat speculatively identified lineages of isolated teeth [e.g., 77,78]. *Darwinius masillae* shows that it is possible to recover much more complete and informative primate fossils. Most primates in the Eocene, certainly most known from cranial remains, are not anthropoids. Continued recovery of complete skeletal remains, like those of *Darwinius masillae* described here, will help to clarify the systematic position of additional primates relative to the strepsirrhine-haplorhine dichotomy within the order, focus attention on specimens complete enough for phylogenetic interpretation, and define the threshold required for inclusion in Anthropoidea.

**Conclusions**

We can now document the history of an extraordinary fossil, here named *Darwinius masillae*. Its two parts, although split by private collectors and dispersed to two continents, are virtually reunited here 26 years after discovery. The fossil, including an entire soft body outline (preserved in the Oslo specimen) as well as contents of the digestive tract (investigated in the Wyoming specimen), documents paleobiology and morphology of an extinct early primate from the Eocene of Germany.

After comparative study, we conclude that the *Darwinius* holotype was a juvenile female, weaned and feeding independently on fruit and...
leaves in the middle floor of early Middle Eocene rain forest of Messel. She may have been nocturnal. She moved as an agile, nail bearing arboreal quadruped and, although perhaps only 60 percent of adult weight at death (Fig. 12), would have grown to be the size of an adult female Hapalopithecus, in the range of 650–900 g. Her pattern of tooth development shows that her species grew up fairly quickly and suggests that she died before one year of age.

Darwinius masillae is now the third primate species from the Messel locality that belongs to the cercamoniine adapiforms, in addition to Europolemur koenigswaldi and E. kelleri. Darwinius masillae is unrelated to Godinotia neglecta from Geiseltal, which was much more slenderly built. Darwinius and Godinotia neglecta are similar, however, in the degree of reduction with their antemolar dentition. Morphological characteristics preserved in Darwinius masillae enable a rigorous comparison with the two principal subdivisions of living primates: strepsirrhines and haplorhines. We do not interpret Darwinius as anthropoid, but the adapoid primates it represents deserve more careful comparison with higher primates than they have received in the past.

Darwinius masillae is important in being exceptionally well preserved and providing a much more complete understanding of the paleobiology of an Eocene primate than was available in the past.

Supporting Information

Figure S1 Maps showing the provenance of Darwinius masillae, new genus and species, from Messel in Germany. Inset map shows the location of the town and fossil locality of Messel near Frankfurt in the southwestern part of Germany. Larger map shows the locations of Messel primates 1–7 (Table 1) within the Messel oil shale excavation. Messel primate 6 near turtle hill is the type of Darwinius masillae. It is not known where in the site Messel primate 0, type specimen of Europolemur kelleri, was found.

Found at: doi:10.1371/journal.pone.0005723.s001 (0.44 MB TIF)

Figure S2 Skull of Darwinius masillae, new genus and species. (A)- Detailed photo. (B)- drawing of sutures observed on the skull. (C)- Micro-CT of the skull in plate A, viewed from the right side. Rectangle showing area enlarged in D. (D)- Enlarged view of ear region. Dark grey: petrosal. Abbreviations: bocc-basoccipital, cn-crista nuchalits, fr-frONTAL, j-jugal, l-lachrymal, m-mandible, mx-maxilla, n-nasale, occ-occipital, p-petrosal, pa-parietal, pmx-premaxilla, sq-squamosal. A-C at same scale.

Found at: doi:10.1371/journal.pone.0005723.s002 (9.32 MB TIF)

Figure S3 Skeletal drawing of Darwinius masillae, new genus and species, showing the identification of vertebrae. Drawing represents the skeleton visible in plate A (Fig. 1.2). Abbreviations: C-cervical vertebra; T-thoracic vertebra; L-lumbar vertebra; S-sacral vertebra; and Ca-caudal vertebra.

Found at: doi:10.1371/journal.pone.0005723.s003 (0.10 MB TIF)

Figure S4 Right forelimb of Darwinius masillae, new genus and species, compared to those of other Eocene primates. (A)- Notharctus osborni (after [23]). (B)- Godinotia neglecta, holotype (HMID-Me 7430). (C)- Europolemur koenigswaldi (SMNK-ME 1125). All are scaled to the same femur length for comparison. The upper and lower leg of Darwinius are projected to grow an additional 12%, which would not alter the proportions shown here.

Found at: doi:10.1371/journal.pone.0005723.s005 (0.18 MB TIF)

Figure S5 Right hind limb of Darwinius masillae, new genus and species, compared to those of other Eocene primates. (A)- Darwinius masillae, holotype (plate A; PMO 214:214). (B)- Europolemur kelleri (HLMD-Me 7430). (C)- Europolemur koenigswaldi (SMNK-ME 1125). All are scaled to the same femur length for comparison. The upper and lower leg of Darwinius are projected to grow an additional 12%, which would not alter the proportions shown here.

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Figure S6 Life restorations of Darwinius masillae. n. gen., n. sp. Sketches are by Bogdan Bocianowski.

Found at: doi:10.1371/journal.pone.0005723.s007 (4.73 MB TIF)

Appendix S1 Measurements of individual bones of Darwinius masillae. Tables 4–23.

Found at: doi:10.1371/journal.pone.0005723.s008 (0.24 MB DOC)

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Author Contributions

Conceived and designed the experiments: JH. Performed the experiments: JH. Analyzed the data: JLF, PDG, JH, JHH, WvK, BHS. Wrote the paper: JH. Conceived and designed the experiments: JH. Performed the experiments: JH. Analyzed the data: JLF, PDG, JH, JHH, WvK, BHS. Wrote the paper: JH. Analyzed the data: JLF, PDG, JH, JHH, WvK, BHS. JH. Analyzed the data: JLF, PDG, JH, JHH, WvK, BHS.

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