

Anthropoid versus strepsirhine status of the African Eocene primates *Algeripithecus* and *Azibius*: craniodental evidence

Rodolphe Tabuce^{1,*}, Laurent Marivaux¹, Renaud Lebrun²,
Mohammed Adaci^{1,3}, Mustapha Bensalah³, Pierre-Henri Fabre¹,
Emmanuel Fara⁴, Helder Gomes Rodrigues¹, Lionel Hautier¹,
Jean-Jacques Jaeger⁵, Vincent Lazzari⁶, Fateh Mebrouk^{7,8},
Stéphane Peigné⁹, Jean Sudre¹, Paul Tafforeau¹⁰, Xavier Valentin⁵
and Mahammed Mahboubi⁸

¹Institut des Sciences de l'Evolution UMR5554, cc064, Université Montpellier II, place Eugène Bataillon, 34095 Montpellier cedex 05, France

²Anthropologisches Institute, Universität Zürich-Irchel, Winterthurerstrasse 190, 8057 Zürich, Switzerland

³Laboratoire de recherche n°25, Département des Sciences de la Terre, Université Abou Bekr Belkaïd, B.P. 119 Tlemcen 13000, Algeria

⁴Biogéosciences UMR5561, Université de Bourgogne, 6 Boulevard Gabriel, 21000 Dijon, France

⁵Institut International de Paléoprimateologie, Paléontologie Humaine: Evolution et Paléoenvironnements UMR6046, Faculté des Sciences Fondamentales et Appliquées, Université de Poitiers, 40 avenue du Recteur Pineau, 86022 Poitiers cedex, France

⁶Steinmann-Institut, Paläontologie, Universität Bonn, Nussallee 8, 53115 Bonn, Germany

⁷Département des Sciences de la Terre, Faculté des Sciences, Université de Fijel, B.P. 98 Ouled Aïssa, 18000 Fijel, Algeria

⁸Laboratoire de Paléontologie stratigraphique et Paléoenvironnement, Université d'Oran, B.P. 1524 El M'naouer, Oran 31000, Algeria

⁹Centre de Recherches sur la Paléobiodiversité et les Paléoenvironnements UMR 7207, Département Histoire de la Terre, Muséum national d'Histoire naturelle, 8 rue Buffon, 75005 Paris, France

¹⁰European Synchrotron Radiation Facility, 6 rue J. Horowitz, BP 220, 38043 Grenoble Cedex, France

Recent fossil discoveries have demonstrated that Africa and Asia were epicentres for the origin and/or early diversification of the major living primate lineages, including both anthropoids (monkeys, apes and humans) and crown strepsirhine primates (lemurs, lorises and galagos). Competing hypotheses favouring either an African or Asian origin for anthropoids rank among the most hotly contested issues in paleoprimateology. The Afrocentric model for anthropoid origins rests heavily on the >45 Myr old fossil *Algeripithecus minutus* from Algeria, which is widely acknowledged to be one of the oldest known anthropoids. However, the phylogenetic position of *Algeripithecus* with respect to other primates has been tenuous because of the highly fragmentary fossils that have documented this primate until now. Recently recovered and more nearly complete fossils of *Algeripithecus* and contemporaneous relatives reveal that they are not anthropoids. New data support the idea that *Algeripithecus* and its sister genus *Azibius* are the earliest offshoots of an Afro–Arabian strepsirhine clade that embraces extant toothcombed primates and their fossil relatives. *Azibius* exhibits anatomical evidence for nocturnality. *Algeripithecus* has a long, thin and forwardly inclined lower canine alveolus, a feature that is entirely compatible with the long and procumbent lower canine included in the toothcomb of crown strepsirhines. These results strengthen an ancient African origin for crown strepsirhines and, in turn, strongly challenge the role of Africa as the ancestral homeland for anthropoids.

Keywords: Algeria; primate evolution; toothcombed primates; activity pattern

1. INTRODUCTION

Among the few early Paleogene continental sites from Afro–Arabia that have yielded a diverse mammalian fauna, the Glib Zegdou and Gour Lazib localities in

Hammada du Dra, southwestern Algeria, are famous for their fossil primates dating from the early or early middle Eocene (between approx. 52 and 46 Ma). These primates document an important but poorly known phase of the early Paleogene primate radiation in Africa. *Azibius* and *Draolestes* were tentatively thought to be related to the 'plesiadapiforms' (= 'archaic' primates) (Sudre 1975; Tabuce *et al.* 2004) and *Algeripithecus* plus *Tabelia* (Godinot & Mahboubi 1992, 1994; Godinot 1994)

* Author for correspondence (Rodolphe.Tabuce@univ-montp2.fr).

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were considered as basal anthropoids, closely related to the much later Eocene–Oligocene forms documented from the Fayum in Egypt (Simons 1992, 1995, 1997a; Seiffert *et al.* 2005a; Seiffert *et al.* in press); a fossil record that has engendered the hypothesis that Africa is the homeland of the Anthropoidea clade (Simons & Rasmussen 1994b). Simultaneously, discoveries of basal anthropoids in the Eocene of southern and eastern Asia have demonstrated that Asia has also played a critical role in the origin and early radiation of anthropoid primates (Beard *et al.* 1994, 1996, 2004; Kay *et al.* 1997; Jaeger & Marivaux 2005; Bajpai *et al.* 2008). The various geographical scenarios for our basal history thus depend on the putative anthropoid status of *Algeripithecus* and *Tabelia*, these critical issues being linked to the fragmentary nature of their fossil remains.

In the framework of our paleontological project in the early Tertiary of North Africa, since 2003, we have focused our yearly field researches on the vast outcrops situated in the Gour Lazib area, including the Glib Zegdou outlier. Intensive survey of the red to yellow siltstones and sandstones of fluvial origin of the continental Glib Zegdou Formation has allowed the discovery of well-preserved craniodental remains of at least 30 eutherian species documenting several primates, hyraxes, rodents, elephant-shrews, insectivoran-grade mammals, chiropterans, creodonts and ‘condylarths’ (Adaci *et al.* 2007; Tabuce *et al.* 2007). The mammalian fauna from the Glib Zegdou Formation is currently the most diverse from the entire Afro–Arabian Eocene. The new fossil primates demonstrate that *Azibius* is a senior synonym of *Tabelia* and that *Draolestes* is invalid because its hypodigm includes specimens of both *Azibius* and *Algeripithecus*. Our study reveals a close relationship between *Azibius* and *Algeripithecus*, which are now the only known valid genera within the Azibiidae. The phylogenetic study of azibiids highlights their strepsirrhine affinities and rejects the anthropoid status of *Algeripithecus* as a result.

2. SYSTEMATIC PALEONTOLOGY

Order Primates, Linnaeus, 1758

Suborder Strepsirhini, Geoffroy, 1812

Family Azibiidae, Gingerich, 1976

(a) *Included genera*

Azibius Sudre, 1975 and *Algeripithecus* Godinot & Mahboubi, 1992.

(b) *Emended diagnosis*

Azibiids (figures 1 and 2) differ from all other primates in having high, mesio-distally aligned P_{3-4} cusps, forming a blade-like structure; P_{3-4} also present a degree of overlapping and a mesial crown elevation associated with an inclination of the lingual cingulid. On M_{1-2} , azibiid traits are the distally offset metaconid, the absence of hypoconulid, and the narrow sub-circular talonid basin, which is open lingually by a deep notch in front of the entoconid. The P^{3-4} have a peak-shaped lateral profile resulting from the labially inclined protocone and the very high and vertical sharp edge aspect of the ectoloph. The bunodont M^{1-2} have a large hypocone, a thick lingual cingulum, and lack a distinct metaconule.

(c) *Remarks*

Algeripithecus is smaller than *Azibius* (table S2 in the electronic supplementary material). Based on the various available equations, deriving from the regressions of M_1 area against body mass of living primates (e.g. Conroy 1987; Bajpai *et al.* 2008), the estimated body mass of *Algeripithecus* ranges from 65 to 85 g and *Azibius* from 115 to 160 g. *Algeripithecus* differs also from *Azibius* by rather less bunodont teeth, a higher metaconid (or possibly protostylid) on P_{3-4} , a longer trigonid and shorter talonid on M_1 , a smaller third lobe on M_3 , the lack of both paraconule and parastyle on P^4 , and by a more reduced M^3 . Azibiids are only known from the late early or early middle Eocene (Mahboubi 1995; Mebrouk & Feist 1999; Adaci *et al.* 2007) of the Glib Zegdou Formation, Gour Lazib area, Algeria. However, another taxon, close to *Algeripithecus*, could also be present in the contemporaneous site of Chambi, Tunisia (Seiffert *et al.* in press).

3. RESULTS AND DISCUSSION

(a) *The euprimate affinities of Azibiidae*

Sudre (1975) described *Azibius* as a possible ‘paromomyiform’ (=‘Plesiadapiformes’). Later, Gingerich (1976) suggested *Azibius* is a euprimate (primates of modern aspect), and erected the Azibiinae, a new subfamily of Adapidae. He thereby rejected the assumption proposed by Szalay (1975) according to which *Azibius* was a hypodontid-like condylarth. More recently, Holroyd & Simons (1991) have reinforced the adapid status of *Azibius*, while Hartenberger *et al.* (1997) have suggested a macroselidid affinity. Finally, after the discovery of *Draolestes*, which was considered to be the sister taxon of *Azibius*, Tabuce *et al.* (2004) suggested that azibiids are related to carpolestid plesiadapiforms, reviving Sudre’s initial attribution. This hypothesis was criticized by Godinot (2006) and Silcox (2008), who favoured euprimate affinities for azibiids. The abundant new material reveals that *Draolestes* is invalid because its hypodigm contains specimens of both *Azibius* and *Algeripithecus* (table S1 in the electronic supplementary material). The supposed carpolestid affinities of *Azibius* relied on the morphology of the P_4 , which are enlarged in both taxa compared to the molars, exodaenodont (a lobe of enamel overhangs the labial side of the roots), and show apical cusps aligned anteroposteriorly in a blade-like structure. However, from a detailed comparison, Silcox (2008) suggested that this blade-like morphology is non-homologous between *Azibius* and carpolestids. We agree with her opinion because the P_3 of azibiids, previously unknown, are also enlarged, exodaenodont, high-crowned and have a similar shearing morphology as the P_4 , while the P_3 of carpolestids is reduced and lacks the blade-like morphology. Most importantly, the new material reveals that the upper tooth originally thought to be the M^2 of ‘*Draolestes*’ (GZC-41, holotype) is in fact a P^4 of *Azibius*. This new dental allocation clearly precludes any carpolestid affinities for azibiids. The bona fide upper and lower molars of *Azibius* show, as do those of *Algeripithecus*, a euprimate morphology.

(b) *Testing the anthropoid status of Algeripithecus and Azibius*

Algeripithecus was successively considered as a propithecoid, a proteopithecoid or a parapathecoid anthropoid



Figure 1. *Algeripithecus minutus*. (a) Composite of isolated P^2 (HGL50/297, reversed), P^3 (HGL50/298, reversed), P^4 (HGL50/299, reversed), M^1 (GZC7), M^2 (GZC1) and M^3 (HGL50-321) in occlusal views. (b) M^2 (GZC1). (c) P^4 (HGL50/299) in mesial and distal views, respectively. (d–f) Mandible with P_3 – M_3 and alveoli for C– P_2 (denoted by red and yellow arrows, respectively) (HGL50/397) (d) in occlusal, (e) mesial and (f) labial views. (g) P_{3-4} (HGL50/397) in lingual view. Scale bar, 1 mm.

(Godinot & Mahboubi 1992; Godinot 1994; Seiffert *et al.* 2005a, in press). Its upper molars strongly resemble those of *Biretia*, a primitive parapithecoid from the late middle Eocene of Algeria and the early late Eocene of Egypt (de Bonis *et al.* 1988; Seiffert *et al.* 2005a). Common traits include a similar degree of bunodonty, the same occlusal outline, the robustness and the postero-lingual position of the hypocone, and the important development of the lingual cingulum (figure 1a). Upper molars of *Biretia* differ in having an uninterrupted lingual cingulum and enlarged conules. Further differences that are evident on premolars and molars clearly distinguish parapithecoids from azibiids: P^2 of *Biretia* is three-rooted, P^4 is less molariform due to the absence of the metacone, the roots of P_{3-4} are oblique in orientation, their crown is low, their metaconid is offset lingually and the entoconid is present on P_4 ; the paraconid occurs on M_1 , the metaconid is transverse to the protoconid on M_{2-3} , the cristid obliqua reaches the trigonid wall at a more labial point, the hypoconulid is enlarged and central on the postcristid of M_{1-2} , and M_3 is reduced. Azibiids also lack some dental features of later parapithecoids (*Abuqatrania*, *Apidium* and *Parapithecus*; Seiffert *et al.* in press) such as the bulbous conules on upper molars and the absence of lower molar protoconids. Other basal anthropoid families such as proteopithecids and eosimiids are also distinct from azibiids, and all dental resemblances represent only primitive

retentions or convergences (see text 2 in the electronic supplementary material). Azibiids also differ from most omomyiforms by their large hypocone and the loss of the paraconid. Some superficial similarities on lower premolars with microchoerines and anaptomorphines are the anterior elevation of the thick basal cingulid and the pronounced overlapping of P_{3-4} (Godinot 2006). However, the buccolingually enlarged and molariform P_4 of omomyiforms are clearly distinct from the mesiolingually elongated and blade-like P_4 of azibiids.

In addition to this purely dental evidence, the newly recovered fossils of *Algeripithecus* and *Azibius* include dentary and maxilla, which are decisive in reconstructing the affinities of azibiids. The maxilla of *Azibius* lacks P^1 and shows above P^{2-3} a very anterior position of the infraorbital foramina (IOF) (figure 2a–c). In occlusal view, the lateral maxillary broadening starts at the level of the P^2 . By comparisons with extant and extinct primates, these characters indicate that *Azibius* possesses a short rostrum. The pronounced curve and the thickening of the mandible under P_4 in *Algeripithecus* are also indicative of a short jaw (figure 1d). Besides, *Azibius* presents a reduced suborbital depth of the maxilla above P^4 . This feature is also observed in the omomyid *Necrolemur*, in the platyrrhine *Aotus*, as well as in most small and medium-sized modern strepsirhines (e.g. *Loris*, *Galago*, *Microcebus*). *Tarsius* and *Biretia megalopsis* show an extreme compression of the suborbital region in having a complete

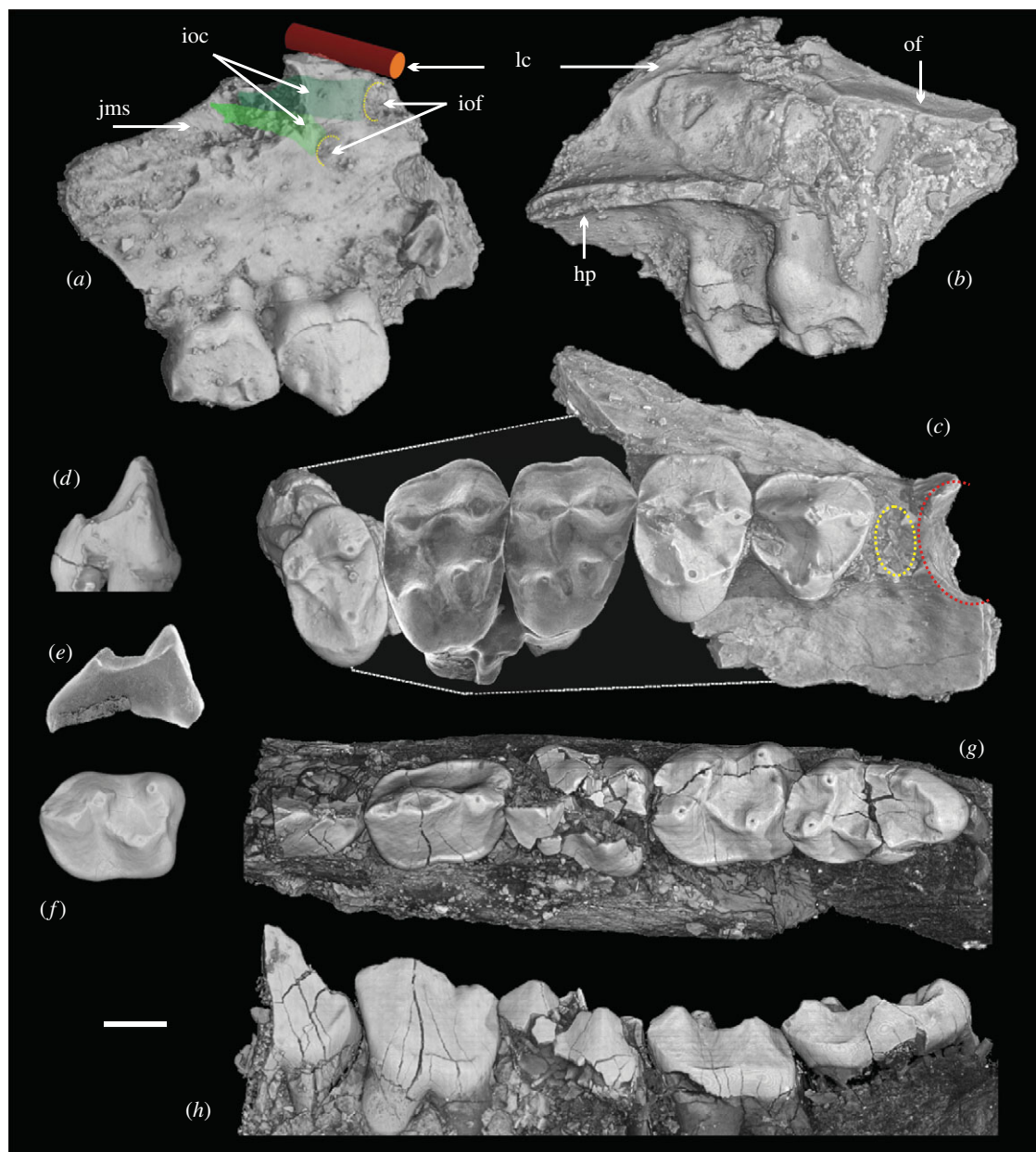


Figure 2. *Azibius trerki*. (a,b) Maxilla with P³⁻⁴ (HGL51/46) in labial (a) and disto-lingual (b) views. (c) Composite of maxilla with M¹⁻² (HGL50/396, reversed), P³⁻⁴ and M³ with alveoli for C–P² (denoted by red and yellow circles, respectively) (HGL51/46) in occlusal view. (d) P³ (HGL51/46) and (e) P⁴ (GZC41) in distal view. (f) M₁ (HGL50/248, reversed) in occlusal view. (g,h) Mandible with P₃–M₃ (HGL50/256) in occlusal (g) and labial (h) views. Abbreviations: hard palate, hp; infra-orbital canals, ioc; infra-orbital foramina, iof; jugo-maxillary suture, jms; lacrimal canal, lc; orbital floor, of. Scale bar, 1 mm.

orbitopalatal fusion and an exposure of the lingual roots of molars in the orbit floor (Seiffert *et al.* 2005a). The reduced suborbital depth of the maxilla and the orbitopalatal fusion are observed in primates having large orbits and a nocturnal activity pattern. Comparative scans performed using conventional and synchrotron microtomography (see text 3 in the electronic supplementary material) of the maxilla through the lingual P⁴ root of some of these primates (see figure S1 in the electronic supplementary material) show that *Azibius* is comparable to *Aotus* and intermediate in condition between *Tarsius* and *Loris*, thereby suggesting very large orbits in *Azibius* probably associated with a nocturnal activity pattern. The cumulative area (0.74 mm²) of the two IOFs in *Azibius* is greater than it is in *Tarsius*, most small anthropoids and living strepsirhines of equivalent weight (e.g.

Galago senegalensis, *Loris tardigradus*; Muchlinsky 2008; Rossie *et al.* 2006). Several omomyiforms (e.g. *Shoshonius*, *Necrolemur*) have a large IOF, like *Azibius*. In mammals, the IOF transmits the infraorbital nerve and a small artery to the maxillary region; a large IOF is correlated with an increase in vibrissa number, which is characteristic of nocturnal species (Muchlinsky 2008). The large IOF in *Azibius* thus indicates a fine sensory acuity of the face, and strengthens the hypothesis of a nocturnal activity pattern. Comparative three-dimensional microtomographic reconstructions show that the course of the lacrimal canals in *Azibius* is oblique rostroventrally (figure 2a–b) as in all living strepsirhines, adapiforms (e.g. *Adapis*) and omomyiforms (e.g. *Microchoerus*; figure 3). In contrast, *Tarsius* and all anthropoids (Rossie *et al.* 2006), including taxa with long snouts such

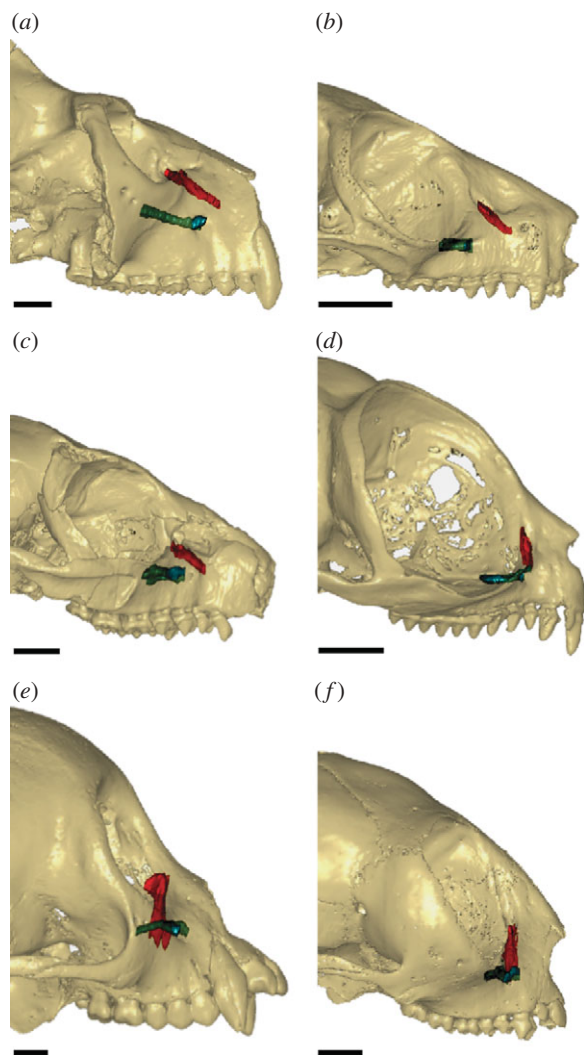


Figure 3. Variability in the configuration of the lacrimal and infraorbital canal in extant and extinct primates (virtual three-dimensional surfaces derived from μ CT image data; see text 3 and table S3 in the electronic supplementary material). (a) *Adapis* sp., (b) *Microcebus murinus*, (c) *Microchoerus erinaceus*, (d) *Tarsius syricta*, (e) *Cebus apella* and (f) *Aotus trivirgatus*. Note how these canals tend to be perpendicular in anthropoids and *Tarsius*, but form a narrower angle in *Azibius trerki* (figure 2), crown and stem strepsirhines and *Microchoerus*, an extinct omomyiform primate. Scale bar, 5 mm.

as *Theropithecus*, show a lacrimal canal that is vertical and oriented perpendicular to the infraorbital canal (figure 3). The maxilla of *Azibius*, although partially preserved, thus reveals distinctive cranial traits that allow us to exclude anthropoid affinities for azibiids.

Consequently, the first unquestionable occurrence of anthropoids in Afro–Arabia is the parapithecoid *Biretia* from the late middle to early late Eocene of Algeria (Bir El Ater) and Egypt (Birket Qarun Locality 2) (de Bonis *et al.* 1988; Seiffert *et al.* 2005a). This result, along with the recent discovery of a putative early Eocene eosimiid in India (Bajpai *et al.* 2008; see also Rose *et al.* 2009) and the well-supported basal position of this primate family within the anthropoids (Kay *et al.* 1997; Jaeger & Marivaux 2005; Bajpai *et al.* 2008), seems to support a South Asian origin for anthropoids (Beard 2004, 2006) and a subsequent dispersal into Africa during the

middle Eocene. Such a mammalian dispersal event between Africa and South Asia has also been proposed for several groups including anthracotheriid artiodactyls, and anomaluroid and hystricognathous rodents (Tabuce & Marivaux 2005; Gheerbrant & Rage 2006).

However, this paleobiogeographical issue for the early evolution of anthropoids is complicated by (i) the morphological gap between African parapithecoids and Asian eosimiids and (ii) the poorly documented omomyiform *Altiatlasius* from the late Paleocene of Morocco (Sigé *et al.* 1990), which was recently reconsidered either as a stem primate (Tabuce *et al.* 2004; Marivaux 2006; Silcox 2008) or a possible eosimiid-like anthropoid (Beard 2004, 2006; Seiffert *et al.* 2005a; Marivaux 2006; Bajpai *et al.* 2008; our phylogenetic results, see figure S2 in the electronic supplementary material). As such, *Altiatlasius* could be the earliest anthropoid, a record that equivocally supports an African origin of anthropoids during the late Paleocene, or their early dispersal into Africa from Asia, at least during the Paleocene (Beard 2006). This would extend the root of the Anthropoidea clade back to the Paleocene. In the absence of any undisputed *Altiatlasius* descendant in Africa during the early to middle Eocene (with the exception of two half-teeth, putatively related to *Altiatlasius*, from the Lutetian of Morocco (Tabuce *et al.* 2005), a Paleocene African origin of anthropoids would imply a big gap of about 20 Myr in the anthropoid fossil record in Africa, pre-dating the first appearance of the earliest parapithecoids. The existence of such a long ghost lineage seems speculative given the debate surrounding the phylogenetic affinities of *Altiatlasius*. Indeed, the extremely fragmentary nature of *Altiatlasius* cautions against over-interpreting its affinities, especially in light of the example of *Algeripithecus*.

(c) Higher-level affinities of the Azibiidae

Phylogenetic analyses of primates based on craniodental and postcranial characters show that azibiids are nested within the Strepsirhini clade, setting *Algeripithecus* clearly apart from the Anthropoidea clade. The analysis reveals two major groups within Strepsirhini (figure 4): (i) the paraphyletic adapiforms mainly known from the Eocene of Europe, North America and Asia (Godinot 1998; Marivaux *et al.* 2006); and (ii) an Eocene–Oligocene Afro–Arabian clade that gave rise to living crown strepsirhines (lemurs, lorises, galagos) (Seiffert *et al.* 2003, 2005b; Godinot 2006). Within this Afro–Arabian clade, azibiids are successive sister taxa of djebelemurines (*Djebelemur*, Hartenberger & Marandat 1992; ‘*Anchomomys*’ *mulleri*, Simons 1997b) and a group that embraces *Plesiopithecus* (Simons 1992; Simons & Rasmussen 1994a) and crown strepsirhines, including their late Eocene–Oligocene fossil representatives from the Fayum, that is, *Wadilemur*, *Saharagalago* and *Karamisia* (Seiffert *et al.* 2003, 2005b; figure 4), and possibly *Omanodon* and *Shizarodon* from the Oligocene of Oman (Gheerbrant *et al.* 1993; Godinot 2006). Also, noteworthy is the putative lemuriform *Bugtilemur* from the Asian Oligocene, which is now regarded as a peculiar adapiform without direct affinities with crown strepsirhines (Marivaux *et al.* 2006). Within the paraphyletic adapiforms, the European cercamoniine *Anchomomys* appears to be the sister taxa of the Afro–Arabian strepsirhine clade.

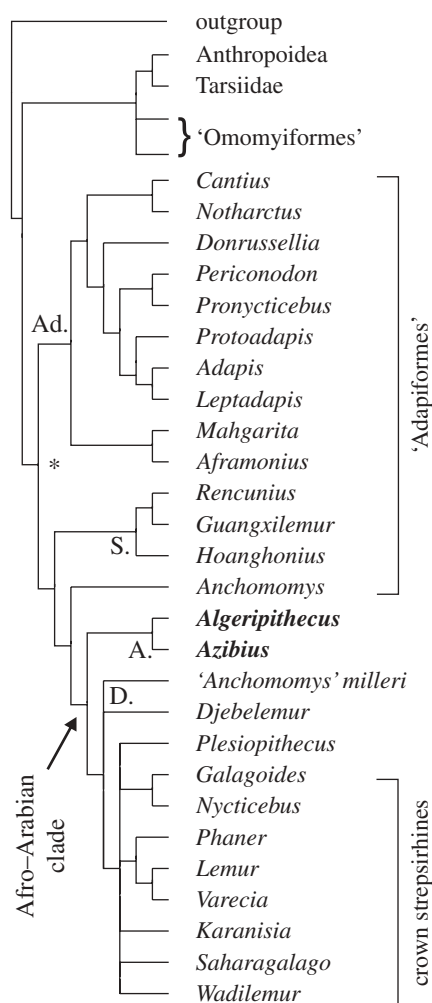


Figure 4. Phylogenetic position of the azibiids *Algeripithecus* and *Azibius* (in bold) within the Strepsirhini clade (denoted by the asterisk). This topology results from an analysis, including 83 primate taxa and 341 dental, cranial and postcranial characters, having generated 369 equally most parsimonious trees of 2851 steps each (consistency index, CI = 0.1887; retention index, RI = 0.5335) (see text 2 and figure S2 in the electronic supplementary material). Abbreviations: Azibiidae, A.; Adapidae, Ad.; Djebelemurinae, D.; Sivaladapidae, S.

Anchomomys does not present, however, the derived characters of the Paleogene Afro–Arabian taxa, notably the overlapping and the anterior coronal elevation of lower premolars. The tree topology could be explained by some convergences on molars between *Anchomomys* species and '*Anchomomys*' *milleri*, hence the initial name given to this Fayum primate (see also Seiffert *et al.* 2005b). Considering the middle Eocene age of the oldest *Anchomomys* and the much earlier age of both azibiids and *Djebelemur*, it is difficult to conceive that a European 'anchomomyine' lineage, having developed a hypocone, gave rise to the Afro–Arabian strepsirhine clade.

Within this group, the djebelemurines and crown strepsirhines have more derived lower molars than the azibiids by the development of a mesial fovea built by the connection of the long curved paracristid with the premetacristid. Except on the M_3 of *Azibius*, where this mesial fovea occurs, azibiids show instead a short premetacristid on M_{2-3} (generally absent on M_1), which is usually isolated from the paracristid. Lower molars of *Omanodon*

and *Plesiopithecus* also display this incomplete mesial fovea. Furthermore, azibiids along with *Djebelemur*, *Plesiopithecus* and *Wadilemur* differ from *Karanisia*, *Saharagalago* and '*Anchomomys*' *milleri* by the absence of the posterolingually protruding entoconid lobe on lower molars; in *Azibius* the entoconid is moderately expanded posteriorly on the M_1 . On upper molars, azibiids are more primitive than crown strepsirhines by the association of a larger paraconule, a symmetrical crown without waisting of the distal border, and by the absence of the connection between the mesiolingually directed hypometaconulecrista and the postprotocrista (except on some M^1 of *Algeripithecus*). *Azibius* and *Plesiopithecus* differ in numerous premolar and molar traits but they share bunodont molars and, more importantly, a cranium with a short rostrum and very large orbits indicative of a nocturnal activity pattern. As many adapiforms are diurnal according to their rather small orbit sizes, they appear much more distant from crown strepsirhines than azibiids. This is critical regarding the ancestry of crown strepsirhines as this group was indeed considered as emerging from a nocturnal lineage (e.g. Godinot 2006). However, recent results based on opsin genes have shown that ancestral strepsirhines were diurnal or cathemeral, and that nocturnality has evolved several times within crown strepsirhines and haplorhines as well (Tan *et al.* 2005; Ankel-Simons & Rasmussen 2008). Despite the apparent lability of nocturnality, it is worth pointing out that some stem strepsirhines, such as *Azibius*, have already achieved this trait early in the Tertiary.

(d) *The early diversity of 'pre-toothcombed' primates in Africa*

The lower toothrow of crown strepsirhines is characterized by an unusual incisor–canine toothcomb, in which the incisiform canine is reduced and strongly procumbent (Rosenberger & Strasser 1985). *Wadilemur* and *Karanisia* provide the earliest fossil evidence for such a lower dental structure (Seiffert *et al.* 2003, 2005b). Djebelemurines are considered to be stem strepsirhines because they do not develop the toothcomb, their canine being only moderately reduced. The anterior dentition of azibiids is unknown, but the alveoli in front of P_3 in the mandible of *Algeripithecus* show that the canine alveolus is long, thin and forwardly inclined, suggesting that this tooth would be incisiform and procumbent (figure 1d–f). Such a canine may indicate that azibiids were toothcombed primates. The broadening of the maxilla at the level of the large canine in *Azibius* is also characteristic of the dental arcade morphology of some extant strepsirhines. However, as azibiids seem to diverge cladistically before djebelemurines (figure 4), a group without the toothcomb, this implies either the absence of a 'true' toothcomb in azibiids or its secondary loss in djebelemurines, a hypothesis that appears unlikely. Even if further evidence is required to ascertain the presence of a 'true' toothcomb in azibiids, it appears that *Algeripithecus* is unique among early Paleogene African primates documented to date in having a long and procumbent lower canine. This morphology seems compatible with the incisor–canine functional unit that pre-dates the toothcomb of crown strepsirhines. The toothcomb of crown strepsirhines is coupled with a P_2 , which is often

caniniform and commonly higher and/or larger than the other premolars. These derived traits, observed in Miocene and Recent strepsirrhines (Fleagle 1999), are achieved as early as the late Eocene in *Wadilemur* (Seiffert *et al.* 2005b). The tall and sub-caniniform P₂, along with the loss of P₁ and the reduced and procumbent canine, were proposed as synapomorphies of crown strepsirrhines (Rasmussen & Nekaris 1998). Therefore, even if *Algeripithecus* possesses the two latter traits, its reduced P₂ seems to preclude direct relationships between azibiids and crown strepsirrhines. However, this character is not as definite as *Karanisia* (a crown strepsirrhine or even a stem lorisiform based on molar characters) and seems also to present a reduced P₂, thereby suggesting that the toothcomb could pre-date the specialization of the P₂ within Paleogene Afro–Arabian strepsirrhines.

Thus, the question of whether azibiids are stem or crown strepsirrhines is unresolved based on the known morphology of their front dentition. However, the phylogenetic analysis assessed on the global morphological evidence suggests that azibiids are the earliest offshoot of stem strepsirrhines to the exclusion of adapiforms. Azibiids are furthermore characterized by numerous autapomorphic features such as a pronounced bunodonty of molars, a large hypocone, a loss of paraconid and high-crowned posterior premolars forming a blade-like structure. As *Plesiopithecus* does by its very large procumbent lower canine, azibiids exemplify, therefore, an aberrant group of stem strepsirrhines, reinforcing the diversity, unsuspected for a long time, of Afro–Arabian Paleogene strepsirrhines. The apparent high degree of specialization of the azibiid family, associated with its late early or early middle Eocene age reveals the antiquity of this Afro–Arabian clade. As a result, we cannot exclude the possibility that this clade is rooted in a primitive, yet unknown, African lineage older than the earliest Eocene. This working hypothesis is tantalizing, especially in view of the age of *Altiatlasius*, testifying to the presence of primates as early as the late Paleocene in Africa. The divergence time of crown strepsirrhines, estimated by recent molecular analysis as between 67 and 84 Ma (Horvath *et al.* 2008), and the possibility that *Algeripithecus* displays a true toothcomb are two interesting arguments in favour of the great antiquity of ‘pre-toothcombed’ primates in Africa.

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REFERENCES

- Adaci, M. *et al.* 2007 Nouveaux sites à vertébrés paléogènes dans la région des Gour Lazib (Sahara Nord-occidental, Algérie). *C. R. Palevol.* **6**, 535–544. (doi:10.1016/j.crpv.2007.09.001)
- Ankel-Simons, F. & Rasmussen, D. T. 2008 Diurnality, nocturnality and the evolution of primate visual systems. *Yearbook Phys. Anthro.* **137**, 100–117. (doi:10.1002/ajpa.20957)
- Bajpai, S., Kay, R. F., Williams, B. A., Das, D. P., Kapur, V. V. & Tiwari, B. N. 2008 The oldest Asian record of Anthropoidea. *Proc. Natl Acad. Sci. USA* **105**, 11093–11098. (doi:10.1073/pnas.0804159105)
- Beard, K. C. 2004 *The hunt for the dawn monkey: unearthing the origins of monkeys, apes and humans*. Berkeley, CA: University of California Press.
- Beard, K. C. 2006 Mammalian biogeography and anthropoid origin. In *Primate biogeography* (eds S. M. Lehman & J. G. Fleagle), pp. 439–467. New York, NY: Springer.
- Beard, K. C., Qi, T., Dawson, M. R., Wang, B. & Li, C. 1994 A diverse new primate fauna from middle Eocene fissure-fillings in southeastern China. *Nature* **368**, 604–609. (doi:10.1038/368604a0)
- Beard, K. C., Tong, Y., Dawson, M. R., Wang, J. & Huang, X. 1996 Earliest complete dentition of an anthropoid primate from the Late–Middle Eocene of Shanxi province, China. *Science* **272**, 82–85. (doi:10.1126/science.272.5258.82)
- Bonis, L. de, Jaeger, J.-J., Coiffait, B. & Coiffait, P.-E. 1988 Découverte du plus ancien primate catarrhinien connu dans l’Eocène supérieur d’Afrique du Nord. *C. R. Acad. Sci. Paris* **306**, 929–934.
- Conroy, G. C. 1987 Problems of body-weight estimation in fossil primates. *Int. J. Primatol.* **8**, 115–137. (doi:10.1007/BF02735160)
- Fleagle, J. G. 1999 *Primate adaptation and evolution*, 2nd edition. San Diego, CA: Academic Press.
- Gheerbrant, E. & Rage, J.-C. 2006 Paleobiogeography of Africa: How distinct from Gondwana and Laurasia? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **241**, 224–246.
- Gheerbrant, E., Thomas, H., Roger, J., Sen, S. & Al-Sulaimani, Z. 1993 Deux nouveaux primates dans l’Oligocène inférieur de Taqah (Sultanat d’Oman): premiers Adapiformes (?Anchomomyini) de la péninsule arabe? *Palaeovertebrata* **22**, 141–201.
- Gingerich, P. D. 1976 Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *Pap. Paleont.* **15**, 1–141.
- Godinot, M. 1994 Early North African primates and their significance for the origin of simiiformes (=Anthropoidea). In *Anthropoid origins* (eds J. G. Fleagle & R. F. Kay), pp. 235–295. New York, NY: Plenum Press.
- Godinot, M. 1998 A summary of Adapiform systematics and phylogeny. *Folia Primatol.* **69**, 218–249. (doi:10.1159/000052715)
- Godinot, M. 2006 Lemuriform origins as viewed from the fossil record. *Folia Primatol.* **77**, 446–464. (doi:10.1159/000095391)
- Godinot, M. & Mahboubi, M. 1992 Earliest known simian primate found in Algeria. *Nature* **357**, 324–326. (doi:10.1038/357324a0)
- Godinot, M. & Mahboubi, M. 1994 Les petits primates simiiformes de Glib Zegdou (Eocène inférieur à moyen d’Algérie). *C. R. Acad. Sci. Paris* **319**, 357–364.
- Hartenberger, J.-L. & Marandat, B. 1992 A new genus and species of an early Eocene primate from North Africa. *J. Hum. Evol.* **7**, 9–16.
- Hartenberger, J.-L., Crochet, J.-Y., Martinez, C., Feist, M., Godinot, M., Mannai Tayech, B., Marandat, B. & Sigé, B. 1997 Le gisement de mammifères de Chambi (Eocène, Tunisie centrale) dans son contexte géologique. Apport à la connaissance de l’évolution des mammifères en Afrique. In *Actes du congrès BiochroM’97* (eds J.-P. Aguilar, S. Legendre & J. Michaux), pp. 263–274. Montpellier, France: Mém. Trav. EPHE, Inst. Montpellier.

- Holroyd, P. A. & Simons, E. L. 1991 The phyletic relationships of *Azibius*. *Am. J. Phy. Anthro.* **12**, 94.
- Horvath, J. E., Weisrock, D. W., Embry, S. L., Fiorentino, I., Balhoff, J. P., Kappeler, P., Wray, G. A., Willard, H. F. & Yoder, A. D. 2008 Development and application of a phylogenomic toolkit: resolving the evolutionary history of Madagascar's lemurs. *Genome Res.* **18**, 489–499. (doi:10.1101/gr.7265208)
- Jaeger, J.-J. & Marivaux, L. 2005 Shaking the earliest branches of anthropoid primate evolution. *Science* **310**, 244–245. (doi:10.1126/science.1118124)
- Kay, R. F., Ross, C. F. & Williams, B. A. 1997 Anthropoids origins. *Science* **275**, 797–804. (doi:10.1126/science.275.5301.797)
- Mahboubi, M. 1995 Etude géologique et paléontologique des formations continentales paléocènes et éocènes d'Algérie. Oran: Université d'Oran, Institut des Sciences de la Terre.
- Marivaux, L. 2006 The eosimiid and amphipithecoid primates (Anthropoidea) from the Oligocene of the Bugti Hills (Balochistan, Pakistan): new insight into early higher primate evolution in South Asia. *Paleovertebrata* **34**, 29–109.
- Marivaux, L., Chaimanee, Y., Tafforeau, P. & Jaeger, J.-J. 2006 A new strepsirrhine primate from the late Eocene of peninsular Thailand (Krabi). *Am. J. Phy. Anthro.* **130**, 425–434. (doi:10.1002/ajpa.20376)
- Mebrouk, F. & Feist, M. 1999 Nouvelles charophytes de l'Eocène continental de l'Algérie. *Géol. Méditerranéenne* **26**, 29–45.
- Muchlinsky, M. N. 2008 The relationship between the infra-orbital foramen, infraorbital nerve and maxillary mechanoreception: implications for interpreting the paleoecology of fossil mammals based on infraorbital foramen size. *Anat. Record* **291**, 1221–1226.
- Rasmussen, D. T. & Nekaris, K. A. 1998 Evolutionary history of loriform primates. *Folia Primatol.* **69**, 250–285.
- Rose, K. D., Rana, R. S., Sahni, A., Kumar, K., Missiaen, P., Singh, L. & Smith, T. 2009 Early Eocene primates from Gujarat, India. *J. Hum. Evol.* **56**, 366–404. (doi:10.1016/j.jhevol.2009.01.008)
- Rosenberger, A. L. & Strasser, E. 1985 Toothcomb origins: support for the grooming hypothesis. *Primates* **26**, 73–84. (doi:10.1007/BF02389048)
- Rossie, J. B., Ni, X. & Beard, K. C. 2006 Cranial remains of an Eocene tarsier. *Proc. Natl Acad. Sci. USA* **103**, 4381–4385. (doi:10.1073/pnas.0509424103)
- Seiffert, E. R., Simons, E. L. & Attia, Y. 2003 Fossil evidence for an ancient divergence of lorises and galagos. *Nature* **422**, 421–424. (doi:10.1038/nature01489)
- Seiffert, E. R., Simons, E. L., Clyde, W. C., Rossie, J. B., Attia, Y., Brown, T. M., Chatrath, P. S. & Mathison, M. E. 2005a Basal anthropoids from Egypt and the antiquity of Africa's higher primate radiation. *Science* **310**, 300–304. (doi:10.1126/science.1116569)
- Seiffert, E. R., Simons, E. L., Ryan, A. S. & Attia, Y. 2005b Additional remains of *Wadilemur elegans*, a primitive stem galagid from the late Eocene of Egypt. *Proc. Natl Acad. Sci. USA* **102**, 11396–11401. (doi:10.1073/pnas.0505310102)
- Seiffert, E. R., Simons, E. L., Fleagle, J. G. & Godinot, M. In press. Paleogene anthropoids. In *Cenozoic mammals of Africa* (eds W. J. Sanders & L. Werdelin). Berkeley, CA: University of California Press.
- Sigé, B., Jaeger, J.-J., Sudre, J. & Vianey-Liaud, M. 1990 *Altiatlasius koulchii* n. gen. et sp., primate omomyidé du Paléocène supérieur du Maroc, et les origines des euprimates. *Palaeontographica* **214**, 31–56.
- Silcox, M. T. 2008 The biogeographic origins of primates and euprimates: east, west, north or south of Eden? In *Mammalian evolutionary morphology: a tribute to Fredrick S. Szalay* (eds E. J. Sargis & M. Dagosto), pp. 199–231. Dordrecht, The Netherlands: Springer.
- Simons, E. L. 1992 Diversity in the early Tertiary anthropoid radiation in Africa. *Proc. Natl Acad. Sci. USA* **89**, 10743–10747. (doi:10.1073/pnas.89.22.10743)
- Simons, E. L. 1995 Skulls and anterior teeth of *Catopithecus* (Primates, Anthropoidea) from the Eocene and Anthropoid origins. *Science* **268**, 1885–1888. (doi:10.1126/science.7604261)
- Simons, E. L. 1997a Preliminary description of the cranium of *Proteopithecus sylviae*, an Egyptian Late Eocene anthropoid primate. *Proc. Natl Acad. Sci. USA* **94**, 14970–14975. (doi:10.1073/pnas.94.26.14970)
- Simons, E. L. 1997b Discovery of the smallest Fayum Egyptian primates (Anchomomyini, Adapidae). *Proc. Natl Acad. Sci. USA* **94**, 180–184. (doi:10.1073/pnas.94.1.180)
- Simons, E. L. & Rasmussen, D. T. 1994a A remarkable cranium of *Plesiopithecus teras* (Primates, Prosimii) from late Eocene of Egypt. *Proc. Natl Acad. Sci. USA* **91**, 9946–9950. (doi:10.1073/pnas.91.21.9946)
- Simons, E. L. & Rasmussen, D. T. 1994b A whole new world of ancestors: Eocene anthropoids from Africa. *Evol. Anthro.* **3**, 128–139. (doi:10.1002/evan.1360030407)
- Sudre, J. 1975 Un prosimien du Paléogène ancien du Sahara nord-occidental: *Azibius trerki* n. g. n. sp. *C. R. Acad. Sci. Paris* **280**, 1539–1542.
- Szalay, F. S. 1975 Phylogeny, adaptations and dispersal of the tarsiform primates. In *A phylogeny of the primates. A multidisciplinary approach* (eds W. P. Luckett & F. S. Szalay), pp. 357–404. New York, NY: Plenum Press.
- Tabuce, R., Adnet, S., Cappetta, H., Noubhani, A. & Quillevéré, F. 2005 Aznag (bassin d'Ouarzazate, Maroc), nouvelle localité à sélaciens et mammifères de l'Eocène d'Afrique. *Bull. Soc. Géol. France* **176**, 381–400. (doi:10.2113/176.4.381)
- Tabuce, R., Mahboubi, M., Tafforeau, P. & Sudre, J. 2004 Discovery of a highly specialized Plesiadapiformes (Mammalia, Primates) in the Eocene of Africa. *J. Hum. Evol.* **47**, 305–321. (doi:10.1016/j.jhevol.2004.08.005)
- Tabuce, R. & Marivaux, L. 2005 Mammalian interchanges between Africa and Eurasia: an analysis of temporal constraints for the plausible Paleogene anthropoid dispersions. *Anthropol. Sci.* **112**, 27–32.
- Tabuce, R., Marivaux, L., Adaci, M., Bensalah, M., Hartenberger, J.-L., Mahboubi, M., Mebrouk, F., Tafforeau, P. & Jaeger, J.-J. 2007 Early Tertiary mammals from North Africa reinforce the molecular Afrotheria clade. *Proc. R. Soc. B* **274**, 1159–1166. (doi:10.1098/rsob.2006.0229)
- Tan, Y., Yoder, A. D., Yamashita, N. & Li, W.-H. 2005 Evidence from opsin genes rejects nocturnality in ancestral primates. *Proc. Natl Acad. Sci. USA* **102**, 14712–14716. (doi:10.1073/pnas.0507042102)