broadening the "lifting cloud base hypothesis" for biotic changes in Central American mountains, by providing an alternative mechanism—upwind deforestation of lowlands—that may increase convective and orographic cloud bases even more than changes in sea surface temperature do. Cloud forests will differ in their sensitivity to upwind deforestation and sea surface temperature changes. On the one hand, inland cloud forests like those of southern Mexico may be profoundly influenced by regional deforestation. On the other hand, coastal forests like those of some Caribbean islands (e.g., the Luquillo forest of Puerto Rico) may have too little upwind lowland to experience deforestation impacts such as those we discuss. Nonetheless, these results suggest that current trends in tropical land use will force cloud forests upward, and they will thus decrease in area and become increasingly fragmented—and in many low mountains may disappear altogether.

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A Fossil Lemur from the Oligocene of Pakistan

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In the absence of a comprehensive fossil record, the origin and early evolution of Malagasy lemurs have been subject to much uncertainty. We report here the discovery of a strepsirrhine fossil with strong cheirogaleid lemur affinities, *Bugtilemur mathesoni* gen. et sp. nov., from early Oligocene deposits of the Bugti Hills (Balochistan, Pakistan). *Bugtilemur* represents the earliest record of Lemuriformes, which hence appear to have already diversified outside of Madagascar at least 30 million years ago. This fossil clearly enhances the critical role of the Indian subcontinent in the early diversification of lemurs and constrains paleobiogeographic models of strepsirrhine lemur evolution.

The endemic Malagasy lemurs (Lemuriformes) and the Afro-Asian lorises (Lorisiformes) make up the living Strepsirrhini (*1*), the tooth-combed primates. Although these groups are widely diversified (*2*), their evolutionary history is still poorly documented. Lorisiforms have a limited fossil record extending back to the Miocene in Africa and Asia (*3*, *4*), whereas lemuriforms have so far remained unknown, with the exception of Malagasy subfossils.

Recent field expeditions in the Bugti Hills (Balochistan, Pakistan) (Fig. 1) have led to the discovery of a fossiliferous lens of fluvio-deltaic sands at the Paali Nala locality in the lowermost levels of the Oligocene continental sequence (*5*). Screen washings have yielded a diverse assemblage of marine, deltaic, and aquatic invertebrates and vertebrates, together with terrestrial mammals (such as rodents, bats, insectivores, primates, carnivores, creodonts, artiodactyls, and perissodactyls). Primate fossils represent the second most diversified mammalian group after rodents. From several dozen isolated teeth, five new primate forms have been identified, including anthropoids (amphipithecids and oligopithecids), adapiforms (sivaladapids), and the new lemuriform described here.

The new lemuriform is classified as follows: Order Primates Linnaeus, 1758; Suborder Strepsirrhini Geoffroy Saint-Hilaire, 1812; Infraorder Lemuriformes Gregory, 1915; Family Cheirogaleidae Gray, 1872; *Bugtilemur mathesoni* gen. et sp. nov.

Holotype: DBC 2146 (Dera Bugti level C), isolated right M^2 [temporarily at the Paleontology Department, University of Montpellier, France (Fig. 2L).

Referred material: one right P^2 DBC 2164 (Fig. 2H)]; one right P^3 [DBC 2150 (Fig. 2I)]; two right P^4 [DBC 2147 (Fig. 2J) and 2155]; one right M^1 (DBC 2145); two left M^1 [DBC 2156 and 2151 (Fig. 2K)]; two right M^2 [DBC 2152 (Fig. 2M) and 2153]; one left M^2 (DBC 2154); one right C_1 [DBC 2138 (Fig. 2C)]; one left P_3 [DBC 2139 (Fig. 2D)]; two right P_4 (DBC 2140 and 2159); one left P_4 [DBC 2143 (Fig. 2E)]; one left M_1 [DBC 2141 (Fig. 2F)]; one right M_2 (DBC 2142); and two left M_2 [DBC 2160 and 2161 (Fig. 2G)].

Horizon and type locality: Chitarwata Formation, Bugti Member (Fig. 1), early Oligocene, Paali Nala C2 (DBC 2).

Etymology: The genus name refers to the Bugti Hills and the species name is in honor of Sylvia A. Matheson for her contribution to the understanding of the traditions of the Bugti tribes.

Diagnosis: Small strepsirrhine primate of the size of the living dwarf lemur *Allocebus*. Differs from Adapiformes (adapids, sivaladapids, and notharctids), Lemuriformes (living Malagasy indrids and lepilemurids), Lorisiformes [living African galagonids and Afro-Asian lorids, and the Miocene Pakistani *Nycticeboides* (*3*)], and extant Tarsiiformes in having the following combination of characters: M^{1-2} without hypocone and conule, with strong, short, and distolingually directed postprotocrista, greater development of buccal shearing crests, and distally open trigon; P4 molarized with strong metaconid and enlarged talonid; M_{1-2} with mesiodistally narrow trigonids bearing cuspidate lingual paraconid, mesiolingual protocristid-protoconid connection, short and lateral cristid obliqua, and continuous hypocristid. Differs from living cheirogaleid lemurs such as *Allocebus*, *Mirza*, *Microcebus*, and *Phaner* (except *Cheirogaleus*) in showing waisted triangular upper molars without hypocone, a continuous anterocingulum reaching the parastyle, and a low and oblique protocone with a short and lateral postprotocrista, and in having a reduced entoconid, a hypoconulid, a strong postprotoconid ridge, an elevated paracristid, a lateral cristid obliqua on lower molars, and a molarized P_4. Differs from *Cheirogaleus* and living lemurid lemurs (*Varecia*, *Lemur*, and *Eulemur*) in having a tiny, low, and oblique metacrista and a shorter postprotocrista on upper molars, small but distinct hypoconulid and entoconid, a paraconid, and a lingual talonid wall deeply notched on lower molars, and differs only from lemurids in lacking a pericone on the upper molars.

Description: M^1 is similar to M^2, except that M^1 is slightly lingually wider and has a less protruding parastyle. Both teeth have a waisted triangular outline, lack conules and hypocone, and have a continuous lingual cingulum that extends buccally to the metastyle and parastyle. The protocone is oblique and develops a short and distolingually oriented postprotocrista. Such a derived arrangement is unusual and resembles that in lemurids and the cheirogaleid *Cheirogaleus* (Fig. 2O) but contrasts with the condition in other lemuriforms, lorisiforms, or adapiforms [among which is the Oligocene Omani adapiform *Omanodon*, previously closely compared (*6*) with cheirogaleids], in which the postprotocrista is buccally oriented to the metaconule or the metacone. The trigon is open distally, bearing a tiny and oblique metacrista, but it is bounded mesially by the preprotocrista, which is connected mesiolingually to the paracone. The postparacrista and premetacrista are elevated, which is a derived shearing condition shared with *Cheirogaleus* (Fig. 2O).

The P^4 is triangular and waisted and shows a well-developed metacone and a protruding protocone, as in *Cheirogaleus*. Although smaller, this tooth has a molariform morphology. It differs from the molars in lacking the metacrista and the postprotocrista. P^3 and P^2 are high-crowned and single-cusped (paracone) and exhibit a triangular occlusal outline.

The bilaterally flattened and slightly procumbent tooth attributed to *Bugtilemur* (DBC 2138, Fig. 2C), shows a scoop-shaped dorsal surface, which is similar to the lower canine (C_1) included in the tooth comb of living strepsirrhines. However, this tooth is not as long-crowned, and the angle between the root and the crown is not as pronounced as in lemuriforms and lorisiforms.

Although M_2 is much larger than M_1, the dental organization of both teeth is similar. The lower molars are characterized by an enlarged talonid and by a mesiodistally pinched trigonid that is slightly higher than the talonid. A weak paraconid occurs mesial and well inferior to the metaconid. Despite the primitive retention of a paraconid, the lower molar trigonid shares derived characters with lemuriforms that are not found among lorisiforms and Eocene adapiforms. In *Bugtilemur*, the protoconid is widely spaced from the metaconid, and the protocristid is connected mesiolingually to the protoconid, which is typical for lemuriforms. The protoconid and the metaconid have a well-marked postprotoconid ridge and postmetacristid respectively, as in *Cheirogaleus* (Fig. 2B) and lemurids. The paracristid is straight and transverse, but it presents a short buccal por-

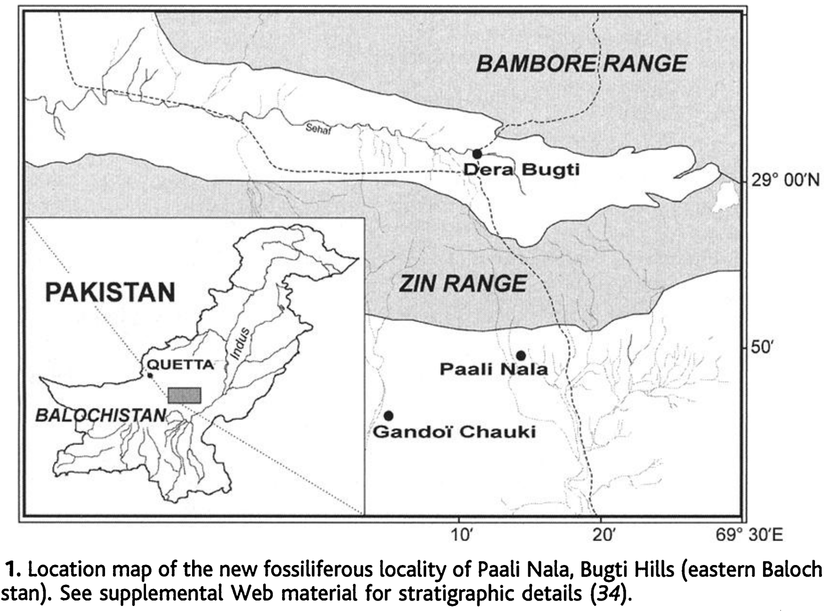

Fig. 1. Location map of the new fossiliferous locality of Paali Nala, Bugti Hills (eastern Balochistan, Pakistan). See supplemental Web material for stratigraphic details (*34*).

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tion that is mesially oriented, as observed in *Cheirogaleus* (Fig. 2B). The talonid is unusual in having a straight, short, and lateral cristid obliqua that runs to the base of the trigonid wall at a point distal to the postprotoconid ridge on M_1 and M_2. The lateral position of the cristid obliqua is characteristic of both *Cheirogaleus* and lemurids. Such a derived condition contrasts with that in adapiforms, omomyiforms, and lorisiforms, in which the cristid obliqua reaches the trigonid wall distolingually to the protoconid or distally to the metaconid (usually on M_1 in adapiforms). The hypoconid of M_1 and M_2 is mesiodistally enlarged and marginally located due to the lack of a buccal cingulid. The talonid is distally enclosed by a well-marked continuous postcristid, which includes a prominent and median hypoconulid. The entoconid is situated mesial to the hypoconid and is separated from the postmetacristid by a deep and narrow notch.

The P_4 displays a molariform structure in having a strong development of the metaconid and hypoconid and a small entoconid. It differs from molars in showing a trigonid that is buccolingually narrower and higher than the talonid, a greater development of the postmetacristid and postprotoconid ridge, and a lack of the hypoconulid and paraconid. The presence of a broad talonid and strong postprotoconid and postmetaconid crests are derived conditions shared with *Cheirogaleus*. Such a molariform structure contrasts with that in other living cheirogaleids, in which the P_4 is simple, single-cusped, and without an enlarged talonid. However, the tendency of a molarized P_4 is also observed in some lemuriforms (*Hapalemur*), lorisiforms (*Galago*), and adapiforms (for example, *Leptadapis*, *Adapis*, and Miocene sivaladapids). The P_3 is reduced and single-cusped (protoconid) and develops a high and lateral paracristid and a low cristid obliqua originating from a minute hypoconid.

Phylogeny: The evolutionary history and subsequent diversification of living strepsirrhines are prominent questions in primate evolution. Strepsirrhine fossil affinities have long been questioned, pointing out the peculiar relationships exhibited between lemuriforms (circumscribed to Madagascar) and the extinct Paleogene adapiforms ("lemur-like"). Indeed, several possibilities for close phylogenetic relationships (based on dental and postcranial comparisons) have been mooted, interpreting adapiforms as the sister group of lemuriforms (*7*), as nested clades originating within lemuriforms (*8*), or as direct ancestors of lemuriforms (*9*, *10*). It is now widely accepted [as supported by our phylogenetic results (Fig. 3A)] that lemuriforms and lorisiforms are more closely related to each other than either is to adapiforms (*4*, *11*). Nonetheless, the phylogenetic position of the Malagasy Cheirogaleidae (the "dwarf and mouse lemurs") among living Strepsirrhini has long been subject to diverse interpretations, and it remains ambiguous in term of systematic and biogeographic implications. Cheirogaleids may be relatively close to the ancestral strepsirrhine condition with respect to their global morphology, behavior, and ecology (*12*). Several morpho-anatomical studies (*13–15*) (mainly shared cranial and vascular characters) indicate the existence of a cheirogaleid-loris clade, whereas molecular approaches (*1*, *16*) and total evidence (*11*, *17*) consistently support a cheirogaleid-lemur clade, thus corroborating the monophyly of Malagasy primates, in accordance with the traditional classification (*18*).

The strepsirrhine phylogeny we propose here is based on dental evidence (Fig. 3A) and a combined analysis of dental and morpho-anatomical characters [DMAc's (Fig. 3B)]. It provides further support for placing Cheirogaleidae within Lemuriformes rather than within Lorisiformes (*19*). From dental characters, Adapiformes [sampled with some European adapids and notharctids, Asian sivaladapids, and the Afro-Arabian taxa *Omanodon* (*6*) and *Wadilemur* (*20*) (previously compared with cheirogaleids)] represent the sister group of the Lemuriformes-Lorisiformes clade (Fig. 3A). The new genus *Bugtilemur* exhibits a combination of dental characters that are unusual among Paleogene primates. The derived features we have described set *Bugtilemur* apart from Adapiformes, Tarsiiformes, and Lorisiformes, but consistently point toward strepsirrhine lemuriform affinities. In both dental and DMAc analyses (Fig. 3, A and B), *Bugtilemur* and the cheirogaleid *Cheirogaleus* form a clade nested within Lemuriformes. There is no support for the monophyly of Cheirogaleidae from the dental data set (Fig. 3A): *Bugtilemur* and *Cheirogaleus* appear more closely related to lemurids (*Eulemur*, *Varecia*, and *Lemur*) than to other cheirogaleids (including two subclades, *Microcebus-Mirza* and *Phaner-Allocebus*). This result is not unexpected given that the general dental organization of *Cheirogaleus* (and *Bugtilemur*) contrasts with that of other cheirogaleids (see diagnosis). However, from the combined DMAc analysis, Cheirogaleidae are depicted as a monophyletic taxon within Lemuriformes [with the same subclades as above (Fig. 3B)], in which *Cheirogaleus* (*21*) and *Bugtilemur* represent the earliest offshoots of the family. In that phylogenetic context, some of the dental features shared by *Cheirogaleus*, *Bugtilemur*, and Lemuridae might have evolved convergently within Lemuriformes.

Discussion: *Bugtilemur* comprises the

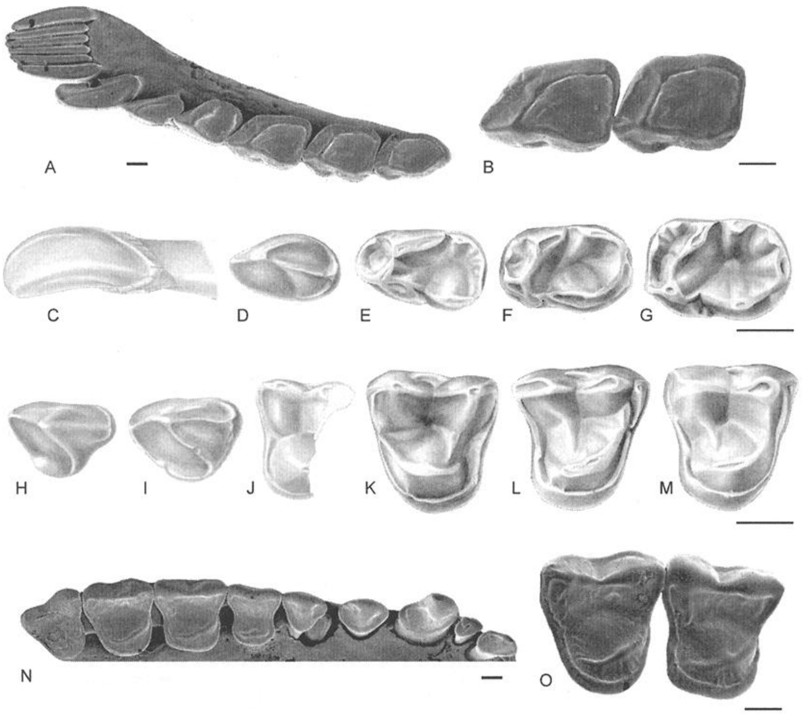

Fig. 2. Extant and Oligocene Lemuriformes. (**A** and **B**) and (**N** and **O**) Modern Malagasy Lemuriformes Cheirogaleidae (SEM micrographs of casts): *Cheirogaleus major* [MNHN 1653; (B) (left $M_{1\text{-}2}$) and (O) (right $M^{2\text{-}1}$) show details of (A) and (N), respectively]. (**C** to **G**) and (**H** to **M**) *Bugtilemur mathesoni* gen. et sp. nov.: DBC 2138 [(C) occlusal view] right C_1 [length (mm) by width (mm), 2.82 by 1.3]; DBC 2139 (D) left P_3 (2.08 by 1.18); DBC 2143 (E) left P_4 (2.45 by 1.5); DBC 2141 (F) left M_1 (2.25 by 1.53); DBC 2161 (G) left M_2 (2.50 by 1.78); DBC 2164 (H) right P^2 (1.74 by 1.35); DBC 2150 (I) right P^3 (1.9 by 1.53); DBC 2147 (J) right broken P^4 (– by 2.09); DBC 2151 (K) left M^1 (2.33 by 2.66); DBC 2146 (L) right M^2, holotype (2.34 by 2.5); DBC 2152 (M) right M^2 (2.27 by 2.44). Scale bar, 1 mm. [Drawings from L. Meslin].

only unequivocal evidence for lemuriforms outside the remote island of Madagascar at least since the early Oligocene. One of the most enigmatic questions in primate evolution is when and how strepsirrhine lemurs first arrived in Madagascar, and their unexpected presence on the Indian subcontinent provides a greater puzzle. The breakup of Madagascar and Greater India occurred about 88 million years ago (*22*) (in the middle Late Cretaceous). Even if recent molecular studies (*1*) infer an initial loris-lemur split at ≥62 million years ago (Ma) and a lemur radiation at ≥54 Ma, and more precisely a Middle Eocene age (37.9 to 46.5 Ma) for the lepilemurid, cheirogaleid, indrid, and lemurid clade (*11*), the water barrier separating both land masses was already important at that time. An earlier time of divergence between the Indian and Malagasy cheirogaleids might be compatible with a possible vicariance hypothesis. Some recent molecular phylogenies (*23*) assume that primates originated far earlier [around 90 Ma for the origin of primates and 87 Ma for the origin of strepsirrhines (*24*)] than the fossil record indicates so far (around 55 Ma). In that context, Indian and Malagasy lemurs could be interpreted as derived residues of an ancestral common stock distributed on the Cretaceous Indo-Malagasy block. However, the important number of synapomorphies uniting *Bugtilemur* and the extant *Cheirogaleus* is not consistent with such an early divergence, and a more recent time of divergence seems alternatively more relevant. In this way, a migration of lemurs should be expected, implying that a dispersal route between Madagascar and the drifting Greater India may have taken place after the breakup. Although the geological evidence would tend to negate such a derivation, it has been proposed that terrestrial Malagasy gastropods were able to colonize India during the Tertiary (*25*). The Eocene Mascarene and Indian (Chagos-Laccadive) paleoridge systems might have been involved in potential filter or sweepstakes dispersal routes for lemurs. A pertinent question then arises about the direction of that migration, which depends on the geographic location considered wherein strepsirrhine were likely to have originated. Taking into consideration phylogenies (*1*, *11*, *12*, *17*), biogeography (*11*), and the limited strepsirrhine fossil evidence (*4*), an early Paleogene origin for the lemur-loris common ancestor in Africa has been hypothesized. In that frame, two intercontinental migrations of lemurs are required: an initial eastward migration of the African ancestral lemuriform to Madagascar (*26*, *27*) and a subsequent northward migration of an ancestral Malagasy cheirogaleid to India. However, the fact that pre–Late Pleistocene continental deposits are virtually nonexistent on Madagascar makes uncertain an old occurrence of lemurs on the island. The same is true for India, where the limited Paleogene fossiliferous localities have so far failed to recover any lemur or loris evidence. *Bugtilemur* represents the first, notably early, record of lemurs. Although the possibility that India may have been the source of primate colonizers of Madagascar (*28–30*) has until recently seemed unlikely (*1*, *11*, *31*), the alternative hypothesis involving an Asian or-

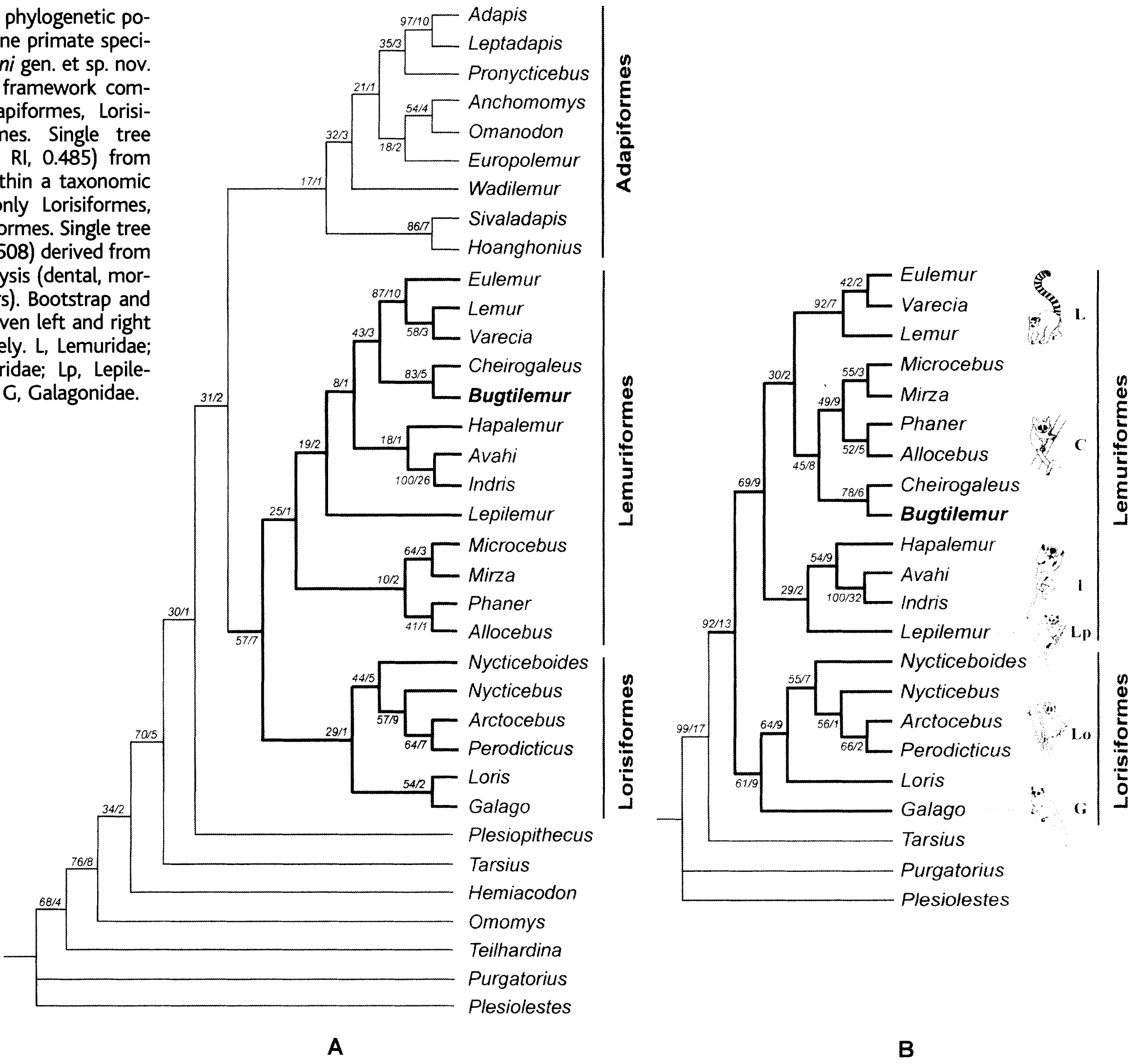

Fig. 3. Assessment of the phylogenetic position of the new Oligocene primate specimen, *Bugtilemur mathesoni* gen. et sp. nov. (**A**) Within a taxonomic framework comprising Tarsiiformes, Adapiformes, Lorisiformes, and Lemuriformes. Single tree (length, 1138; CI, 0.276; RI, 0.485) from dental characters. (**B**) Within a taxonomic framework comprising only Lorisiformes, Lemuriformes, and Tarsiiformes. Single tree (length, 953; CI, 0.4; RI, 0.508) derived from the combined DMAc analysis (dental, morpho-anatomical characters). Bootstrap and Decay Index values are given left and right from the slash, respectively. L, Lemuridae; C, Cheirogaleidae; I, Indridae; Lp, Lepilemuridae; Lo, Loridae; and G, Galagonidae.

igin for the loris-lemur clade cannot be ruled out (*24*) in the light of this new discovery. A similar scenario (adapted from molecular data) has been suggested for endemic Malagasy rodents (*32*).

The possibility that lemuriforms and lorisiforms originated in Asia rather than in Africa cannot be rejected without further paleontological evidence from both continents and from Madagascar. It must, however, be emphasized that their origin is undoubtedly as ancient as that of adapiforms (Fig. 3A). The discovery of a cheirogaleid-like lemur in Oligocene deposits of Pakistan suggests that whatever the timing and direction of faunal dispersions, South Asia was, as for anthropoids (*33*), an important theater of early strepsirrhine evolution, reflecting the complex role played by the drifting Greater India in the evolutionary history of Malagasy lemurs.

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Caenorhabditis elegans p53: Role in Apoptosis, Meiosis, and Stress Resistance

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We have identified a homolog of the mammalian p53 tumor suppressor protein in the nematode *Caenorhabditis elegans* that is expressed ubiquitously in embryos. The gene encoding this protein, *cep-1*, promotes DNA damage–induced apoptosis and is required for normal meiotic chromosome segregation in the germ line. Moreover, although somatic apoptosis is unaffected, *cep-1* mutants show hypersensitivity to hypoxia-induced lethality and decreased longevity in response to starvation-induced stress. Overexpression of CEP-1 promotes widespread caspase-independent cell death, demonstrating the critical importance of regulating p53 function at appropriate levels. These findings show that *C. elegans* p53 mediates multiple stress responses in the soma, and mediates apoptosis and meiotic chromosome segregation in the germ line.

The *p53* tumor suppressor is among the most frequently mutated genes in human cancer and plays a critical role in maintaining genomic stability by regulating cell cycle progression and apoptosis in response to DNA damage (*1, 2*). Analysis of the mechanisms through which p53 integrates the cellular response to stress and damage in vivo has been limited by the absence of a genetic system. Recently, a p53 homolog was shown to participate in apoptosis induced by genotoxic stress in *Drosophila* (*3–5*) on the basis of forced expression of dominant negative forms; however, the organism-wide role of the gene could not be assessed in these experiments.

Standard searches of the genomic sequence suggested that *C. elegans* does not have a *p53*-like gene (*6*). However, using additional algorithms, we identified a *C. elegans* gene encoding a protein with signature sequences common to the p53 family, including the residues most frequently mutated in human cancers (*7*). The cDNA sequence of this gene, *cep-1* (denoting *C. elegans* p53-like–1), predicts a 429–amino acid protein that is similar to the human protein in the NH_2-terminal transactivation domain and the highly conserved DNA binding domains (Fig. 1). CEP-1 appears to be the only p53 family member encoded in the *C. elegans* genome, which suggests that p53 paralogs (including p63 and p73) may have evolved from a single ancestor related to CEP-1.

To assess the in vivo function of *cep-1*, we isolated a chromosomal rearrangement, *cep-1(w40)* (*8*). This mutant strain contains an intact copy of *cep-1* at its normal genomic location; the *cep-1(w40)* mutant gene, which encodes a truncated protein lacking the DNA binding domain, is translocated elsewhere in the genome. Although they exhibit impenetrant ($\sim$2%) embryonic lethality, *cep-1(w40)* mutants are generally viable and fertile. Moreover, depleting *cep-1* function by RNA interference (RNAi) (*9*) similarly leads to impenetrant embryonic lethality (Table 1). It is likely that RNAi results in a strong loss-of-function phenotype, as it eliminates detectable expression of a CEP-1::GFP

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