

accurately predicting particle size distributions than on predicting detailed chemical composition. Although particle chemistry is important to model aerosol growth and transformation processes, the complex effects of particle chemical composition on CCN activation could be parameterized by cutoff diameters depending on location and/or aerosol type without introducing large errors. Assuming a “typical” size distribution (such as for a generalized “continental” aerosol) will lead to much larger errors than assuming a “typical” composition. Our findings also provide a basis for the estimation of CCN abundances over larger time and space scales by remote sensing, because aerosol size distributions are inherently more accessible by remote sensing than particle compositions. Because current sensors are limited, however, in their ability to detect particles in the CCN-relevant size range of 50 to 150 nm, this requires the development of appropriate sensors.

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Supporting Online Material

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Materials and Methods

Figs. S1 to S5

References

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A New Genus of African Monkey, *Rungwecebus*: Morphology, Ecology, and Molecular Phylogenetics

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A new species of African monkey, *Lophocebus kipunji*, was described in 2005 based on observations from two sites in Tanzania. We have since obtained a specimen killed by a farmer on Mount Rungwe, the type locality. Detailed molecular phylogenetic analyses of this specimen demonstrate that the genus *Lophocebus* is diphyletic. We provide a description of a new genus of African monkey and of the only preserved specimen of this primate. We also present information on the animal's ecology and conservation.

A previously unknown monkey from southern Tanzania was recently discovered and described as the new species *Lophocebus kipunji*, depicting the holotype and paratype with photographs (1). On 3 August 2005, a subadult male monkey matching the species description of *L. kipunji* (1) was found dead in a trap set by a resident farmer in a

maize field adjacent to the forest on Mount Rungwe in southwestern Tanzania. The specimen was preserved and deposited at the Field Museum of Natural History (FMNH) in Chicago, USA, as a study skin, skull, and partial skeleton (bones from the right fore- and hindlimbs). Muscle tissue was collected for molecular analyses, and the remaining cadaver was preserved in fluid. Although a subadult, the specimen exhibits features differentiating it from any other known primate species (1).

The specimen matches the original description of *L. kipunji* (1) in having black eyelids that do not contrast with the color of the face (fig. S1), a crown with a broad erect crest of hair (figs. S1 and S2), long cheek whiskers (fig. S2), and an off-white distal half of the tail [fig. S2 and supporting online material (SOM) text].

The individual was a subadult on the basis of the presence of deciduous canines and premolars, eruption of only the first molars (SOM text), and the lack of a fused suture between the basioccipital and basisphenoid bones (Fig. 1). Although not fully grown, the skull does exhibit some of the features characteristic of *Lophocebus* compared with *Cercocebus* (2), such as a relatively narrow zygomatic breadth, zygoma that turn smoothly toward the skull at their posterior ends, and upper and lower margins of the mandible divergent anteriorly (Fig. 1). In the postcranium, the long-bone epiphyses are fused to the diaphyses, but many features are not yet fully developed, including those distinguishing the *Lophocebus-Theropithecus-Papio* clade from the *Cercocebus-Mandrillus* clade (3). One postcranial feature, the ratio of scapular width to length, appears to distinguish *L. kipunji* from *Papio*, which has a relatively long and narrow scapula (3).

Mangabeys were once considered to be monophyletic based on their phenotypic similarities (4), and all species were included in *Cercocebus*. After immunological studies (5) and because of cranial differences and a resemblance between *Lophocebus* and *Papio* in some of those features, they were divided into *Cercocebus* and *Lophocebus* (2). Characters that have historically been used to unite mangabeys were discounted as being erroneous observations or convergent similarities (2). It was stated that *Lophocebus*, unlike *Cercocebus*, has dark eyelids that are not lighter than the facial skin, and the deep suborbital fossae of mangabeys may have evolved independently in relation to facial shortening (2). This generic

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division was corroborated by analyses of both mitochondrial and nuclear data (6–9), suggesting that *Cercocebus* is the sister taxon to *Mandrillus*, whereas *Lophocebus* is more closely related to *Papio* and *Theropithecus*, and the deep suborbital fossae represent a homoplastic character that evolved more than once in Papionini, the cercopithecine tribe that includes macaques, mangabeys, baboons, geladas, mandrills, and drills. Recently, several putatively derived postcranial features and one dental character that unite the *Lophocebus-Papio-Theropithecus* clade, as well as one apomorphic postcranial feature shared by *Cercocebus* and *Mandrillus*, were identified (3). Hence, both morphological and molecular evidence indicates that the phenetic similarities shared by *Cercocebus* and *Lophocebus* are not indicative of a close phylogenetic relationship.

To determine the phylogenetic affinities of *L. kipunji*, we conducted maximum likelihood and Bayesian analyses (SOM text) (10) of DNA sequence data obtained from the specimen from Mount Rungwe, including 390 base pairs (bp) of the mitochondrial (mtDNA) 12S ribosomal RNA (rRNA) gene (12S), 686 bp of the mtDNA cytochrome *c* oxidase subunit I gene (COI), 684 bp of the mtDNA cytochrome *c* oxidase subunit II gene (COII), 573 bp of the *y*-linked testis-specific protein gene (TSPY), and 486 bp of the autosomal alpha-1,3-galactosyltransferase pseudogene (α 1,3-GT). Phylogenetic analysis of each individual gene with a diverse sample of homologous cercopithecoid sequences available on GenBank either strongly supported [all three mtDNA genes (e.g., Fig. 2)], weakly supported (α 1,3-GT), or failed to contradict (TSPY) a clade uniting *L. kipunji* with *Papio* (figs. S3 to S8). All single-gene maximum likelihood analyses in which two or more species of *Papio* were included recovered a monophyletic *Papio* as either the sister-taxon to *L. kipunji* (COI and COII) or part of an unresolved trichotomy with *L. kipunji* and *Theropithecus* (12S) (SOM text). No single-gene analysis recovered a monophyletic *Lophocebus*, yet all data sets in which *L. kipunji*, *L. aterrimus*, and *L. albigena* were included (COII, TSPY, and α 1,3-GT) strongly supported a sister taxon relationship between the latter two species (SOM text). We therefore concatenated the 12S sequence for *L. aterrimus* with the remaining sequences for *L. albigena* and performed analyses on two combined data sets, one including all three mtDNA genes (17 taxa, 1732 included positions) and the other including all mtDNA genes and both nuclear genes (9 taxa, 2959 included positions). As with the individual gene analyses, *L. kipunji* was strongly supported as the sister taxon to *Papio* (Figs. 3 and 4).

Despite the compelling molecular evidence that *L. kipunji* is more closely related to *Papio* than it is to its putative congeners, it lacks the diagnostic morphological features required to place it in that genus, such as the long rostrum

or deep mandibular fossae characteristic of *Papio* (as well as *Theropithecus* and *Mandrillus*). Furthermore, although *L. kipunji* possesses deep suborbital fossae on the maxillae, like those of *Lophocebus* and *Cercocebus*, these can easily be distinguished from the deep maxillary fossae present on the rostrum of *Papio* (as well as *Theropithecus* and *Mandrillus*) (Fig. 1). In summary, molecular evidence precludes the inclusion of *L. kipunji* in *Lophocebus* and morphological evidence prohibits its placement in *Papio*, thereby making it necessary to name a new genus.

Rungwecebus Davenport, Stanley, Sargis, De Luca, Mpunga, Machaga, and Olson genus nov.

Lophocebus Palmer, 1903; type species *Presbytis albigena* Gray, 1850.

Lophocebus kipunji Ehardt, Butynski, Jones, and Davenport, 2005.

Holotype. Adult male in photograph taken in the type locality at 9°07'S 33°44'E (1).

Paratype. Adult in photograph taken in Ndundulu Forest Reserve at 07°48'45"S 36°31'05"E, Udzungwa Mountains, Tanzania (1).

Specimen examined. FMNH 187122. Subadult male collected on the southwestern slopes of Mount Rungwe, Rungwe District, Mbeya Region, Tanzania, 09°09'50"S 33°37'55"E, 1769 m above sea level (asl).

Type locality. Rungwe-Livingstone (09°07' to 09°11'S and 33°36' to 33°55'E), Southern Highlands, Tanzania.

Diagnosis. Pelage of dorsum light to medium gray-brown, center of ventrum and distal half of tail off-white (fig. S2). Crown with very long, broad, erect crest of hair (fig. S1). Eyelids black, not contrasting with color of face (fig. S1). Tail longer than body, mainly curled up and backward at rest and during locomotion (fig. S2). Adults emit a distinctive, loud, low-pitched “honk-bark” (1). Predominantly arboreal. Found only at high altitudes (1300 up to 2450 m asl) and low-temperature tolerant.

Measurements. Head-body length of adult males in the Rungwe-Livingstone population estimated at 85 to 90 cm. Adult male body weight estimated at 10 to 16 kg (1). Measurements of preserved subadult male (taken before preservation) include total length, 894 mm; head and body length, 370 mm; tail length, 499 mm; hindfoot length (nail included), 128 mm; ear length, 35 mm; and mass, approximately 4000 g.

Etymology. The genus name acknowledges Mount Rungwe, where this monkey was first observed and the first voucher specimen was obtained and which is home to the largest known population of the genus. Because of the demonstrated polyphyly of “mangabeys” and the ambiguity that common name now carries, we suggest the common name of members of this genus to be “kipunji.”

Distribution. Known to occur in about 70 km² of Rungwe-Livingstone in the Southern

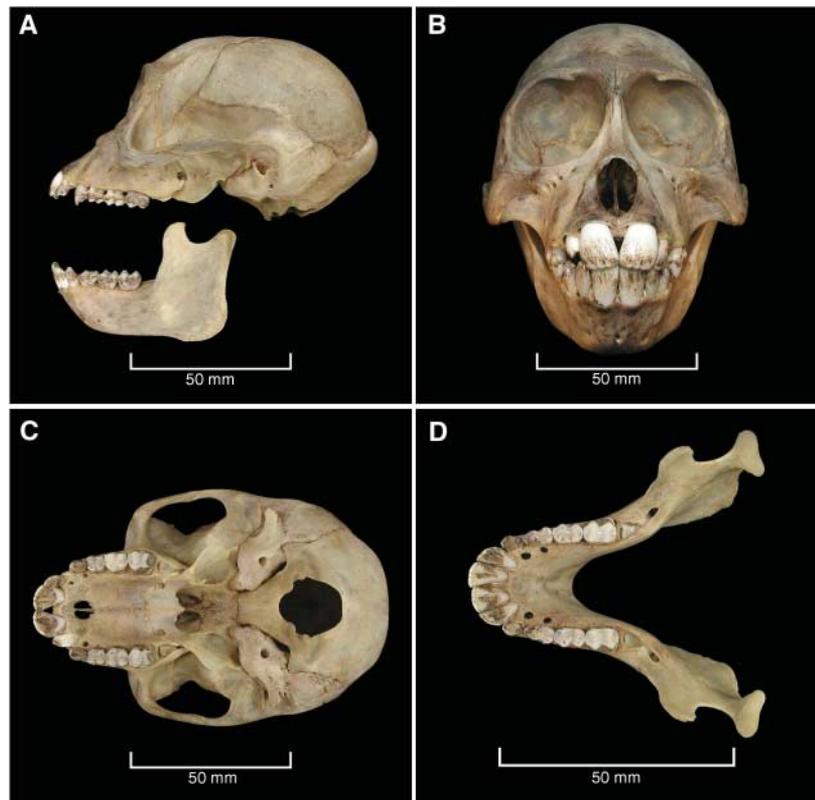


Fig. 1. Skull of *Rungwecebus kipunji* (FMNH 187122). Photographs show lateral (A) and anterior (B) views of the cranium and mandible and occlusal views of the cranium (C) and mandible (D).

Highlands, Tanzania, from 1750 up to 2450 m asl and from about 3 km² of Ndundulu Forest Reserve, Tanzania, from 1300 to 1750 m asl.

Habitat. From pristine submontane forest in Ndundulu to degraded montane and upper montane forest in Rungwe-Livingstone.

Rungwecebus differs from mangabeys, baboons, and geladas (11) as follows: (i) *Rungwecebus* is more closely related to *Papio* than to *Lophocebus*, *Theropithecus*, *Cercocebus*, or *Mandrillus* based on molecular evidence. (ii) *Rungwecebus* differs from the semiterrestrial *Cercocebus* (2) in being predominantly arboreal and having noncontrasting eyelids (fig. S1). (iii) *Rungwecebus* differs from *Lophocebus* (12, 13) in having a light to medium gray-brown pelage, an off-white center of ventrum and distal half of tail, and crown with very long, broad, erect crest of hair (fig. S1). *Rungwecebus* usually holds its tail curled up and backward (fig. S2), but very rarely vertical

or arched forward. *Rungwecebus* gives a distinctive “honk-bark” when conspecific groups meet (1) and when threatened. The “honk-bark” bears some structural similarity with the *Papio* “roar-grunt” (14), but *Rungwecebus* does not emit the “whoop-gobble” loud-call characteristic of *Lophocebus* and *Cercocebus torquatus atys* (15, 16). (iv) *Rungwecebus* differs from *Papio* and *Theropithecus* in that it lacks the long rostrum and deep mandibular fossae characteristic of these genera (and *Mandrillus*). *Rungwecebus* possesses deep suborbital fossae on the maxillae similar to those of *Lophocebus* and *Cercocebus*, but these are distinct from the deep maxillary fossae present on the rostrum of *Papio* and *Theropithecus* (and *Mandrillus*). *Rungwecebus* is smaller in body size and more arboreal than *Papio* and *Theropithecus*.

Rungwecebus kipunji is endemic to Tanzania and known only from the Rungwe-Livingstone

forest in the Southern Highlands and the Ndundulu Forest in the Udzungwa Mountains. The remote and unexplored nature of these forests and the cryptic nature of the animal may explain why the kipunji has remained undetected for so long. Recent discoveries in Ndundulu have revealed other vertebrates that show ancient and geographically distant affinities with taxa in western Africa or Asia (17, 18). Furthermore, *Rungwecebus* demonstrates the critical biogeographical importance of Tanzania’s Southern Highlands relative to the Eastern Arc Mountains.

Social groups comprise several adult males and females. In three focal groups studied (SOM text), there was a maximum of two infants per group, but there is no evidence that solitary animals occur. Group size estimates are from 30 to 36 individuals with a mean of 32.33 (SE 1.86; $n = 3$), larger than usually found in *Lophocebus* (13). Home range estimates were from 0.24 to 0.99 km² with a mean of 0.54 km² (SE 0.132; $n = 5$). To date, we have recorded at least 16 groups across Rungwe-Livingstone. In Ndundulu, only three groups are known (1).

R. kipunji is primarily arboreal but has been observed coming to the ground in both Ndundulu and Rungwe-Livingstone to avoid intragroup conflict and predation, as well as to

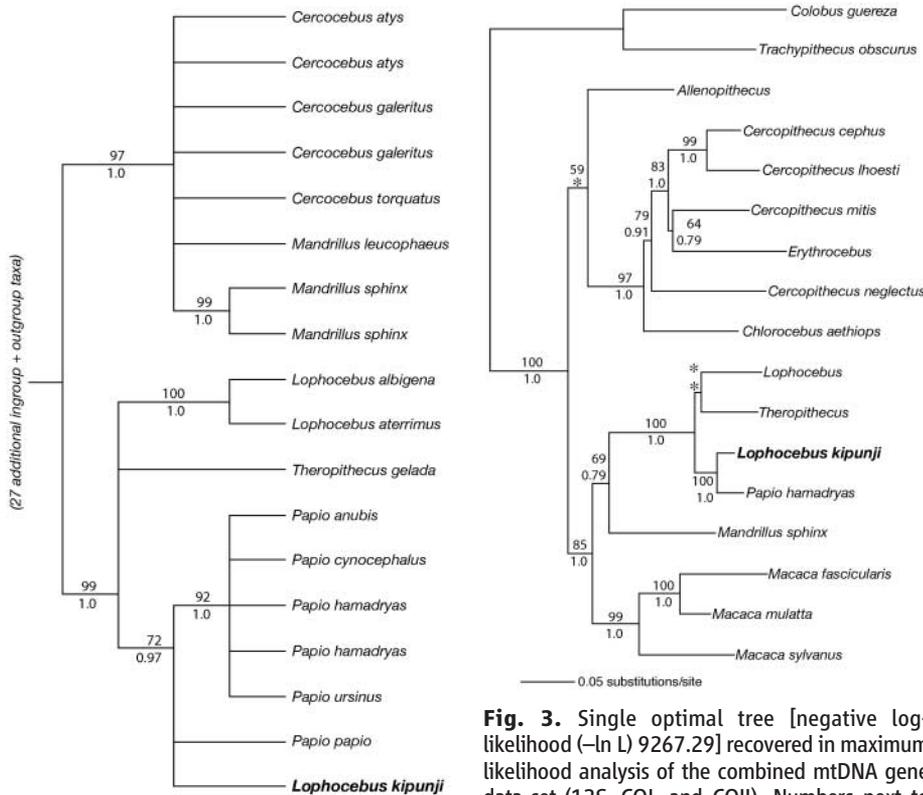


Fig. 2. Phylogenetic relationships among *Cercocebus*, *Mandrillus*, *Theropithecus*, *Papio*, and *Lophocebus* (sensu lato) as recovered in maximum likelihood analysis of the mtDNA COII gene. Numbers next to select nodes represent likelihood bootstrap proportions (top) and Bayesian posterior probabilities (bottom). Nodes receiving <70% bootstrap support and posterior probabilities <0.95 have been collapsed. An additional 31 sequences representing 27 species-level taxa were included in the analysis but have been trimmed from this figure. Entire tree and additional information are available in the SOM text.

Fig. 3. Single optimal tree [negative log-likelihood (–ln L) 9267.29] recovered in maximum likelihood analysis of the combined mtDNA gene data set (12S, COI, and COII). Numbers next to each node as in Fig. 2. Asterisks indicate nodes not recovered in ≥50% of the bootstrap replicates or with posterior probabilities of ≤0.5. Based on evidence from single-gene analyses that *L. aterrimus* and *L. albigena* are each other’s closest relative, the 12S sequence from the former was concatenated with the remaining sequences available for the latter. Tree was rooted with the two colobine sequences shown. Tree resulting from ML search constrained to recover a monophyletic *Lophocebus* (sensu lato) was a significantly poorer fit to the data ($P = 0.02$, Shimodaira-Hasegawa test). Additional information is available in the SOM text.

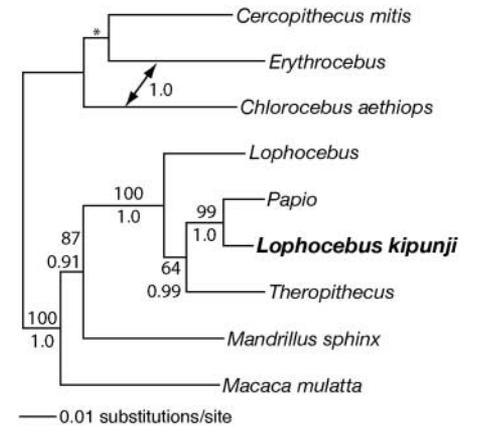


Fig. 4. Single optimal tree (–ln L 8427.57) recovered in maximum likelihood analysis of the combined mtDNA plus nuclear DNA data set (12S, COI, COII, α 1,3-GT, and TSPY). Numbers and asterisk as in Fig. 2. Sequences from *Lophocebus albigena* and *L. aterrimus* were concatenated as in Fig. 3, and the mtDNA sequences available for *Papio hamadryas* were concatenated with the nuclear sequences published for *P. anubis*. Arrow indicates the grouping of *Erythrocebus* with *Chlorocebus aethiops* strongly supported in Bayesian analysis of this data set, which may represent a rooting artifact. Tree was rooted with the three Cercopithecini figured and cannot be rerooted to recover a monophyletic *Lophocebus* (sensu lato). Tree resulting from maximum likelihood search constrained to recover a monophyletic *Lophocebus* (sensu lato) was a significantly poorer fit to the data ($P = 0.002$, Shimodaira-Hasegawa test). Additional information is available in the SOM text.

feed. In Rungwe-Livingstone, they also descend to cross degraded forest patches. The referred specimen was caught in a trap on the ground set by a farmer for crop-raiding primates and had corn in its mouth. *Lophocebus* species, however, are almost entirely arboreal, rarely descending to the ground or raiding crops (2). The main predators of *R. kipunji* are crowned eagles, *Stephanoaetus coronatus*, and possibly leopards, *Panthera pardus* (19). The kipunji is also widely hunted by humans on Mount Rungwe (19) as retribution for and prevention against the raiding of maize, beans, and sweet potato crops. It is also taken as a bycatch when hunting Sykes' monkeys (*Cercopithecus mitis*), and kipunji meat is sometimes eaten by the residents of Rungwe District.

The kipunji's omnivorous diet includes young and mature leaves, shoots, flowers, bark, ripe and unripe fruits, lichen, moss, and invertebrates. In Rungwe-Livingstone, groups form polyspecific associations with *Angola colobus*, *Colobus angolensis*, and *C. mitis*, especially in early mornings and late afternoons, when the three species often sleep in neighboring trees.

Formal assessment for the IUCN Red List of Threatened Animals is ongoing; *R. kipunji* will probably be designated as "critically endangered." In Rungwe-Livingstone, logging, charcoal-making, poaching, and unmanaged resource extraction are common (1, 19, 20). Although Ndundulu Forest Reserve is largely undisturbed, *R. kipunji* is present in very low numbers and the reasons for this remain unclear (20). The target for the genus must be the con-

servation and management of Mount Rungwe and the Bujingijila Forest Corridor that connects Mount Rungwe to Livingstone (19, 20). Without intervention, both forests will be further fragmented. Any hunting of the kipunji or loss of its vulnerable habitat, with the latter probably increasing the frequency of the former, will further threaten this new genus.

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D.W.D. located, observed, and collected all behavioral and ecological data; T.R.B.D., W.T.S., E.J.S., and L.E.O. wrote the paper with editorial input from D.W.D., N.E.M., and S.J.M. W.T.S. and E.J.S. conducted the morphological analysis; L.E.O. conducted all molecular analyses. M. Snapp, R. Banasiak, and M. Schulenberg provided assistance with analysis, specimen preparation, and figures. T. Roberts and M. Alfaro advised us on phylogenetic methodology. K. Hildebrandt assisted with lab work, which was funded by the University of Alaska Museum. DNA sequencing was conducted in the University of Alaska Fairbanks Institute of Arctic Biology (UAF-IAB) Core Facility for Nucleic Acid Analysis with support from NSF Experimental Program to Stimulate Competitive Research grant EPS-0346770. Analyses were conducted on the UAF-IAB Bioinformatics Cluster supported by NIH grant RR-16466-01, NSF grant EPS-0092040, the Alaska IDeA Networks for Biomedical Research Excellence program, and the University of Alaska Foundation. R. Phillips, M. Fungo, W. Mwalwengele, O. Mwaipungu, M. Haruna, A. Mwaambo, S. Kimiti, and G. Picton Phillips provided logistical, field, and Geographic Information Systems support. J. Fooden, A. Gardner, and T. Jones offered valuable advice. Fieldwork was funded by the Wildlife Conservation Society. We are grateful to Tanzania National Parks, Tanzania Wildlife Research Institute, and the Rungwe District Council, and we thank the anonymous reviewers for their helpful comments on earlier versions of this manuscript.

Supporting Online Material

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Checkpoint Proteins Control Survival of the Postmitotic Cells in *Caenorhabditis elegans*

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Checkpoints are evolutionarily conserved signaling mechanisms that arrest cell division and alter cellular stress resistance in response to DNA damage or stalled replication forks. To study the consequences of loss of checkpoint functions in whole animals, checkpoint genes were inactivated in the nematode *C. elegans*. We show that checkpoint proteins are not only essential for normal development but also determine adult somatic maintenance. Checkpoint proteins play a role in the survival of postmitotic adult cells.

Many DNA damage checkpoint and repair proteins are essential for development. We identified a checkpoint gene in a genetic screen for whole-organism stress resistance. The predicted

protein, CID-1, has homology to poly(A)⁺ polymerase (PAP) domain proteins (fig. S1), including the fission yeast *Schizosaccharomyces pombe* S-M checkpoint protein caffeine-induced death (Cid) protein-1 (I-3). In *C. elegans*, we observed that worms carrying the *cid-1(rf34::Tc4)* mutation or worms with reduced expression of *cid-1* by RNA interference (RNAi) were highly thermotolerant (Fig. 1, A and B, and table S1).

It was not obvious why checkpoint proteins would affect organismal stress resistance in *C. elegans* where the soma is composed of nondividing cells. Consequently, we further investigated the extent to which *cid-1* determined cell survival in worms and whether it was related to checkpoint functions.

The ribonucleotide reductase inhibitor hydroxyurea (HU) causes stalled replication forks. Wild-type worms had arrested development in the presence of HU, but *cid-1(rf34::Tc4)* mutants and *cid-1(RNAi)* worms developed into adults (Fig. 1C). This is consistent with *C. elegans* CID-1 having a checkpoint function. It is also required for normal development, as *cid-1* mutants had shorter, thicker gonads with fewer proliferating and developing germ cells. The worms contained disorganized embryos, produced fewer offspring, and took 24 hours longer to develop into reproductive adults compared with wild-type worms (fig. S2 and table S2). Of *cid-1(rf34::Tc4)* adult worms examined, 20 to 40% developed a protruding vulval defect that blocked egg laying and resulted in premature death.

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