

# Ensembles of human myosin-19 bound to calmodulin and regulatory light chain RLC12B drive multimicron transport

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Myosin-19 (Myo19) controls the size, morphology, and distribution of mitochondria, but the underlying role of Myo19 motor activity is unknown. Complicating mechanistic *in vitro* studies, the identity of the light chains (LCs) of Myo19 remains unsettled. Here, we show by coimmunoprecipitation, reconstitution, and proteomics that the three IQ motifs of human Myo19 expressed in Epi293 human cells bind regulatory light chain (RLC12B) and calmodulin (CaM). We demonstrate that overexpression of Myo19 in HeLa cells enhances the recruitment of both Myo19 and RLC12B to mitochondria, suggesting cellular association of RLC12B with the motor. Further experiments revealed that RLC12B binds IQ2 and is flanked by two CaM molecules. *In vitro*, we observed that the maximal speed (~350 nm/s) occurs when Myo19 is supplemented with CaM, but not RLC12B, suggesting maximal motility requires binding of CaM to IQ-1 and IQ-3. The addition of calcium slowed actin gliding (~200 nm/s) without an apparent effect on CaM affinity. Furthermore, we show that small ensembles of Myo19 motors attached to quantum dots can undergo processive runs over several microns, and that calcium reduces the attachment frequency and run length of Myo19. Together, our data are consistent with a model where a few single-headed Myo19 molecules attached to a mitochondrion can sustain prolonged motile associations with actin in a CaM- and calcium-dependent manner. Based on these properties, we propose that Myo19 can function in mitochondria transport along actin filaments, tension generation on multiple randomly oriented filaments, and/or pushing against branched actin networks assembled near the membrane surface.

Mitochondrial dynamics are paramount for cell survival and are perturbed in neurodegenerative diseases, hearing loss, and cancer (1–3). Mitochondrial health requires fusion and fission events that ensure an even inheritance of undamaged proteins and mitochondrial DNA. In addition, mitochondria need to be

redistributed appropriately before cell division. Myosin-19 (Myo19) has critical roles in mitochondrial partitioning (4, 5), regulating the balance of fission and fusion (6), and has recently been implicated in cristae organization (7). Myo19 dysregulation is associated with glioma, breast cancer, and hearing impairment (8–10). How Myo19 participates in these functions at the molecular level remains an open question.

Myo19 belongs to its own class-19 subgroup of the myosin superfamily that shares a conserved, plus end-directed motor domain (MD), a lever arm containing three light chain (LC)-binding IQ motifs, and a unique tail region termed the Myosin Mitochondrial Outer Membrane-Associated (MyMOMA) domain that directs Myo19 to mitochondria (Fig. 1A) (11–14). The MyMOMA domain contains a putative monotopic membrane insertion segment and a segment that interacts with the mitochondrial Rho GTPases, Miro1 and Miro2 (15–17). Myo19 was recently found to associate with the SAM-MICOOS complex that bridges the outer and inner mitochondrial membranes and may thus act as a mechanical tether for cristae formation and regulation (7).

A gap in our knowledge regarding the molecular mechanism of Myo19 is the identity of the LCs that bind to its lever arm. Most biochemical studies have been performed assuming calmodulin (CaM) binds the three IQs of Myo19 (12, 14, 18). However, one study identified RLC9 (MYL9/MRLC1) and RLC12B (MYL12B/MRLC2), but not CaM, as the endogenous LCs of Myo19 using proteomics and reconstitution experiments (13). In the proteomic screen, recombinant Myo19 was exposed to a kidney extract to identify novel tissue-level binding partners. It is possible, however, that there are tissue-specific differences in the LC composition of Myo19 or that the IQs were not fully occupied. RLC12B is ubiquitously expressed, whereas RLC9 is a more specialized LC isoform expressed in many but not all tissues. Since Myo19 is also ubiquitously expressed (11), it is possible that RLC9 is not always bound. The primary sequences of the putative IQ motifs of Myo19 deviate to varying degrees from the consensus IQ sequence and provide no obvious indication as to the

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