SHORT REPORT
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A Unified Taxonomy for Ciliary Dyneins

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The formation and function of eukaryotic cilia/flagella require the action of a large array of dynein microtubule motor complexes. Due to genetic, biochemical, and microscopic tractability, *Chlamydomonas reinhardtii* has become the premier model system in which to dissect the role of dyneins in flagellar assembly, motility, and signaling. Currently, 54 proteins have been described as components of various *Chlamydomonas* flagellar dyneins or as factors required for their assembly in the cytoplasm and/or transport into the flagellum; orthologs of nearly all these components are present in other ciliated organisms including humans. For historical reasons, the nomenclature of these diverse dynein components and their corresponding genes, mutant alleles, and orthologs has become extraordinarily confusing. Here, we unify *Chlamydomonas* dynein gene nomenclature and establish a systematic classification scheme based on structural properties of the encoded proteins. Furthermore, we provide detailed tabulations of the various mutant alleles and protein aliases that have been used and explicitly define the correspondence with orthologous components in other model organisms and humans.

Key Words: *Chlamydomonas*, cilia, dynein, flagella, microtubule

Introduction

The assembly and motility of eukaryotic cilia and flagella require the action of a large array of dynein microtubule motor complexes. These enzymes display distinct motile properties [Kagami and Kamiya, 1992; Moss et al., 1992a, 1992b; Sakakibara and Nakayama, 1998] and contain one or more heavy chain(s) (HCs; ~500 kDa) that exhibit ATPase and microtubule motor activity. In addition, the dynein HCs are associated with a complex array of smaller polypeptides that are necessary for motor assembly, regulation, and attachment to the appropriate cargo [reviewed in King and Kamiya, 2009]. Due to the ease of genetic and biochemical analyses, a cell architecture that allows clear observation of flagellar movement, and a sequenced genome [Merchant et al., 2007], the biflagellate green alga *Chlamydomonas reinhardtii* has become the premier model system in which to dissect the role of dyneins in axoneme-based motility and in the assembly of cilia/flagella.

Chlamydomonas expresses 16 dynein HCs that form a series of motor complexes with different functions. The outer

Additional Supporting Information may be found in the online version of this article.

Abbreviations used: DC, docking complex; HC, heavy chain; IC, intermediate chain; IFT, intraflagellar transport; LC, light chain; LIC, light intermediate chain; LRR, leucine-rich repeat; NDK, nucleoside diphosphate kinase.

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dynein arm, containing three distinct HCs, is required for high power output by the flagellum [Piperno and Luck, 1979; Pfister et al., 1982; Brokaw, 1999]. Two different general types of inner dynein arms, one containing a HC heterodimer and a second consisting of monomeric HC species, are needed to define the waveform [Brokaw and Kamiya, 1987; Kamiya et al., 1991] and/or for beating under high viscous load [Yagi et al., 2005]. Finally, a homodimeric dynein (here, termed the intraflagellar transport [IFT] dynein) powers retrograde IFT and is thus necessary for assembly and maintenance of the organelle [Pazour et al., 1999; Porter et al., 1999]. Although *C. reinhardtii* contains a large complement of flagellar dyneins, its genome does not encode most of the components comprising the conventional *cytoplasmic* dynein 1/dynactin system that in other organisms (such as mammals) is required for a wide array of microtubule-based intracellular transport activities [Pfister et al., 2006; Merchant et al., 2007; Wickstead and Gull, 2007]; the exceptions are certain light chains (LCs) employed by both conventional cytoplasmic dynein and other dynein subtypes [King et al., 1996; Harrison et al., 1998; Bowman et al., 1999].

To date, a total of fifty-four gene products have been identified in *C. reinhardtii* as integral components of these dynein motors or as factors required for their assembly in the cytoplasm, transport into the flagellum, and/or localization within the axonemal superstructure [see Cole, 2009; King and Kamiya, 2009 for reviews]. These proteins have been identified by numerous laboratories over many years utilizing a variety of methods including genetic analysis of mutants with defective flagella, direct protein biochemistry, and, more recently, comparative genomic approaches. As a result, the genes, their encoded proteins and mutant strains have been given a wide variety of names derived from various nomenclature schemes. The resulting plethora of terms and aliases has become unwieldy and complicated. Moreover, the nomenclature of the orthologous dynein components in other species is often quite distinct from that used in *C. reinhardtii*, and this continues to engender considerable confusion in the literature, and in some cases has led to the misidentification of gene products.

Historically, this general problem derives, at least in part, from the fact that many *C. reinhardtii*, sea urchin[1] and *Tetrahymena thermophila* dynein proteins were given alphanumeric assignments based on the order of their migration in SDS and/or urea polyacrylamide gels many years before any of the sequences were known. Thus, differences in migration patterns due to minor variations in size, sequence and/or charge resulted in orthologous proteins being given completely different designations. Unfortunately, the issue was compounded during annotation of the mouse and human genomes when certain dynein genes were named after their *C. reinhardtii* counterparts whereas others followed the sea urchin protein nomenclature. For example, mammalian DNAL4 was named after the LC4 component of the sea urchin outer arm dynein which is orthologous to *C. reinhardtii* LC10; confusingly, in *C. reinhardtii* LC4 denotes a calmodulin homolog and thus a member of a completely unrelated protein family. Conversely, mammalian DNAL1 was named after the *C. reinhardtii* outer arm dynein leucine-rich repeat protein LC1 (the sea urchin ortholog of which is termed LC2 in one nomenclature scheme), whereas sea urchin LC1 is a member of the Tctex1/Tctex2 protein family. This level of confusion also extends to the HCs where, for example, the gene for the 1α HC of inner arm dynein I1/f is *DHC1* in *C. reinhardtii*, *DNAH10* in sea urchins and mammals and *DYH6* in *T. thermophila*, while the 1β HC of that same dynein is termed *DHC10* (*C. reinhardtii*), *DNAH2* (sea urchins and mammals), and *DYH7* (*T. thermophila*).

Given the long history of these names in dynein research combined with the complexity of the gene families and the large variety of organisms involved, there seems to be no way of synthesizing a gene nomenclature/numbering scheme that is completely consistent across a broad phylogenetic spectrum and incorporates all the major model organisms while still maintaining continuity with the older literature. Consequently, as part of a reannotation effort for the *C. reinhardtii* genome, we describe in this report a new consensus nomenclature for dynein genes in *C. reinhardtii*. Furthermore, we provide a series of tables that indicate (i) the various gene aliases, and mutant and protein names that have been used in *C. reinhardtii* and (ii) the identity of the orthologous components in a variety of other model organisms where that correspondence can be unambiguously defined.

The Nomenclature

Here, we propose new names for the *C. reinhardtii* dynein genes. The formal standard for gene names in *C. reinhardtii* is a three-letter root (all capitals) followed by a number [Dutcher and Harris, 1998]. As the dynein genes encode a wide range of protein structural and functional types, we have employed these features, as far as possible, to form the basis of the new nomenclature. A list of the proposed dynein gene roots and their derivation is provided in Table I. The assignment of new gene names, the older gene indicator(s) used in previous annotations of the *C. reinhardtii* genome, the accession number and the encoded protein products are tabulated in Table II. Whenever possible, the proposed gene names are based on previous names; e.g., *DHC1–DHC11* are unchanged. The nomenclature scheme also provides a rational basis for the

[1]Multiple species of sea urchin have been used for biochemical studies by different laboratories depending on geographic and seasonal variables. The most commonly employed include: *Anthocidaris crassispina, Arbacia punctulata, Hemicentrotus pulcherrimus, Lytechinus pictus, Pseudocentrotus depressus, Strongylocentrotus droebachiensis, Strongylocentrotus purpuratus*, and *Tripneustes gratilla*.

Table I. Proposed Roots for *C. reinhardtii* Dynein Genes

Gene family root	Root derivation	Characteristics of protein family
DHC	*D*ynein *H*eavy *C*hain	ATPases/motors
DIC	*D*ynein *I*ntermediate *C*hain	WD-repeat proteins
DLI	*D*ynein *L*ight *I*ntermediate chain	Originally named based on migration between ICs and LCs. Class found only in "cytoplasmic" dyneins, including IFT dynein
DLU	*D*ynein components with *LeU*cine-rich repeats	Contain ββα barrels derived from leucine-rich repeats
DLX	*D*ynein *L*ight chain thioredo*X*in	Redox-sensitive thioredoxins with vicinal dithiols
DLT	*D*ynein *L*ight chain *T*ctex1-like	Tctex1/Tctex2 family proteins; some are also found in conventional cytoplasmic dynein
DLR	*D*ynein *L*ight chain *R*oadblock-like	Related to the roadblock light chains found in conventional cytoplasmic dynein
DLL	*D*ynein *L*ight chain in *LC*8 family	Very highly conserved family of dimeric light chains found in many enzyme systems
DLE	*D*ynein *L*ight chain in *E*F-hand family	Ca^{2+}-binding components containing EF-hand motif(s)
DCC	*D*ynein *C*oiled *C*oil	Contain extensive regions of coiled-coil structure
DOI	*D*ynein *O*uter arm-*I*nteracting	Associate with outer arm dynein but do not fall into other categories
DII	*D*ynein *I*nner arm-*I*nteracting	Associate with inner arm dyneins but do not fall into other categories
DAP	*D*ynein *A*ssembly *P*IH domain	Required for dynein assembly and contain PIH domains
DAW	*D*ynein *A*ssembly *W*D repeat	Required for dynein assembly and contain WD-repeat motifs
DAU	*D*ynein *A*ssembly le*U*cine-rich repeat	Required for dynein assembly and contain leucine-rich repeat motifs
DAB	*D*ynein *A*ssembly *B*locked	Required for dynein assembly but do not fall into other categories

naming of new genes encoding dynein subunits as these are identified; we propose these be numbered sequentially.

It is important to note that although we propose altering the gene names to yield an internally consistent scheme, we suggest that current mutant and protein names be retained so as to maintain continuity in the literature. Thus, we recommend that when describing a gene product in a publication, the corresponding gene name be used at first mention so that the gene product is unambiguously identified, and that the common protein and/or mutant names be employed thereafter. This could be readily achieved by inclusion of a brief statement such as "DHC1b (encoded at *DHC16*) is the dynein motor subunit responsible for retrograde IFT."

Mutants, Protein Aliases, and Orthologs

Mutants defective in dynein genes have been identified through a variety of genetic screens following UV or insertional mutagenesis. These strains exhibit a range of phenotypes including various degrees of flagellar dysfunction, slow swimming, and impaired flagellar assembly depending on the mutant allele and the particular component that is altered. For example, strains unable to assemble outer dynein arms exhibit a characteristic slow, jerky swimming phenotype [Kamiya and Okamoto, 1985; Mitchell and Rosenbaum, 1985], whereas those with defective inner arms have defects in forming bends of appropriate amplitude [Kamiya et al., 1991]. The mutant alleles that have been isolated for each component and the various aliases used for the encoded proteins are listed in Table III.

As detailed above, much confusion has built up in the literature about which dynein components are orthologous due to the long history of dynein research and the multiple naming schemes used in various organisms. Consequently, Table IV provides a listing of the current *C. reinhardtii* gene and protein names along with their orthologs (where those can be unambiguously determined) in the ciliate *T. thermophila*, the sea urchins *Anthocidaris crassispina* and *Strongylocentrotus purpuratus*, the primitive chordate *Ciona intestinalis*, the fish *Danio rerio*, and the mammal *Homo sapiens*. A more comprehensive tabulation is provided in the supplemental table available online.

In conclusion, we describe here a new consensus nomenclature for the flagellar dynein genes of *C. reinhardtii* and provide a comprehensive tabulation of the gene products and various aliases, the mutant alleles isolated for each gene, and the designations of orthologous components in other model organisms. Axonemal dyneins provide the basis for ciliary motion in all organisms with motile cilia, and IFT dynein is necessary for the assembly and maintenance of cilia in most ciliated organisms. Because of its utility for biochemical and genetic analyses, *C. reinhardtii* has been a favorite model for understanding

Table II. *C. reinhardtii* Dynein Gene Nomenclature[a]

New gene name	Original gene name	Accession number	Description of encoded protein
Heavy chains			
DHC1	*DHC1 (IDA1, PF9)*	Q9SMH3	1α heavy chain of inner arm I1/f
DHC2	*DHC2*	XP_001694660	Inner arm dynein species d heavy chain
DHC3	*DHC3*	XP_001696272	Inner arm dynein heavy chain (minor species)[b]
DHC4	*DHC4*	EDP07657	Inner arm dynein heavy chain (minor species)[b]
DHC5	*DHC5*	XP_001699742	Inner arm dynein species b heavy chain
DHC6	*DHC6*	XP_001700741	Inner arm dynein species a heavy chain
DHC7	*DHC7*	XP_001692695	Inner arm dynein species g heavy chain
DHC8	*DHC8*	XP_001692092	Inner arm dynein species e heavy chain
DHC9	*DHC9 (IDA9)*	BAE19786	Inner arm dynein species c heavy chain
DHC10	*DHC10 (IDA2)*	Q9MBF8	1β heavy chain of inner arm I1/f
DHC11	*DHC11*	XP_001694047	Inner arm dynein heavy chain (minor species)[b]
DHC12	*DHC1a (PCR4)*	EDP05194	Inner arm dynein heavy chain[c]
DHC13	*ODA11*	Q39610	α outer arm heavy chain
DHC14	*ODA4*	Q39565	β outer arm heavy chain
DHC15	*ODA2*	Q39575	γ outer arm heavy chain
DHC16	*DHC1b*	Q9SMH5	Dynein heavy chain that mediates retrograde IFT
WD-repeat intermediate chains			
DIC1	*ODA9*	Q39578	IC1 from outer arm dynein
DIC2	*ODA6*	P27766	IC2 from outer arm dynein
DIC3	*IDA7*	AAD45352	IC140 from inner arm I1/f dynein
DIC4	*BOP5*	AAU93505	IC138 from inner arm I1/f dynein
DIC5	*FAP133*	XM_001699649	IFT dynein intermediate chain
Light intermediate chains			
DLI1	*D1bLIC*	AAT37069	Light intermediate chain of IFT dynein
Leucine-rich repeat proteins			
DLU1	*LC1 (DLC1)*	AAD41040	Outer arm dynein γ heavy chain-associated
DLU2	*ODA8 (MOT37)*	EPD09919	ODA8 protein required for outer arm assembly
Thioredoxin-like light chains			
DLX1	*LC3 (DLC3)*	Q39592	LC3 thioredoxin associated with outer arm β heavy chain
DLX2	*LC5 (DLC5)*	Q39591	LC5 thioredoxin associated with outer arm α heavy chain
Tctex1-like light chains			
DLT1	*LC9*[d]	AAZ95589	LC9 present in outer arm dynein
DLT2	*ODA12*	AAB58383	LC2 present in outer arm dynein
DLT3	*TCTEX1*	AAC18035	Tctex1 present in inner arm I1/f
DLT4	*TCTEX2b*	DAA05278	Tctex2b present in inner arm I1/f
Roadblock-like light chains			
DLR1	*ODA15 (DLC7a)*	AAD45881	LC7a present in outer arm and inner arm I1/f dyneins
DLR2	*LC7b (DLC7b)*	EDP03034	LC7b present in outer arm and inner arm I1/f dyneins
DYNLL/LC8 family light chains			
DLL1	*FLA14*	Q39580	LC8 present in outer arm, inner arm I1/f and IFT dyneins. Also a component of the radial spokes
DLL2	*ODA13*	Q39579	Outer arm dynein LC6
DLL3	*LC10 (MOT24)*	EDP00562	Outer arm dynein LC10

(Continued)

Table II. (Continued)

New gene name	Original gene name	Accession number	Description of encoded protein
Calmodulin (EF-hand) homologs			
DLE1	*LC4 (DLC4)*	Q39584	LC4 present in outer arm dynein. Binds Ca^{2+}
DLE2	*VFL2*	P05434	Centrin present in monomeric inner arm dyneins b, e, and g. This gene is also termed CNT1 (named for CeNTrin). Binds Ca^{2+}
DLE3	*ODA14*	AAP49435	DC3 component of outer arm docking complex. Binds Ca^{2+}
Coiled-coil proteins			
DCC1	*ODA3*	AAC49732	DC1 of the outer arm docking complex
DCC2	*ODA1*	AAK72125	DC2 of the outer arm docking complex
DCC3	*ODA5*[d]	AAS10183	ODA5 protein that associates with an adenylate kinase
Outer arm dynein interacting proteins			
DOI1	*LIS1*[d,e]	ABG33844	LIS1 protein associates with α heavy chain of outer arm
Inner arm dynein interacting proteins			
DII1	*IDA4*	Q39604	p28 light chain present in inner arm species a, c, and d
DII2	*FAP146*	BAG07147	p38 associates with inner arm species d
DII3	[d]	BAF98914	p44 associates with inner arm species d
DII4	*IDA5*	P53498	Actin, present in inner arm dynein species a, b, c, d, e, g, and some minor species. This gene is also known as ACT1 (named for ACTin)
DII5	*NAP1*	AAC49834	NAP, novel actin-related protein that can substitute for actin in inner arm dyneins b and g. This gene is also known as ARP12 (named for Actin Related Protein).
DII6	*FAP94*	EDP03678	IC97 present in inner arm I1/f dynein
DII7	*FAP120*	EDP07339	Ankyrin-repeat protein that interacts with IC138(DIC4) from inner arm I1/f
Dynein assembly proteins containing a PIH domain			
DAP1	*PF13 (MOT45)*	BAG69288	PF13 protein required for inner/outer arm assembly in cytoplasm
DAP2	*IDA10 (MOT48)*	BAI83444	MOT48 protein required for inner arm assembly in cytoplasm[f]
Dynein assembly proteins containing WD repeats			
DAW1	*ODA16*	AAZ77789	ODA16 protein acts as an IFT adaptor for outer arm dynein
Dynein assembly proteins containing leucine-rich repeats			
DAU1	*ODA7*	Q09JZ4	ODA7 is a LRR protein required for outer arm assembly in cytoplasm
Dynein assembly blocked			
DAB1	*PF22*[g]	AEC04845	PF22 is required for assembly of outer arms

[a]Alternative gene names are indicated in parentheses in the second column.
[b]Yagi et al. [2009].
[c]Yagi (unpublished results).
[d]These genes were missing and/or not named in the *C. reinhardtii* version 3 genome catalog.
[e]Not to be confused with the *LIS1* (light-influenced suppressor) locus of Dutcher et al. [1988].
[f]Yamamoto et al. [2010].
[g]This gene is missing from the *C. reinhardtii* version 4 genome assembly.

the composition and function of these flagellar dyneins. As research on dynein advances in *C. reinhardtii* and other model organisms with their own advantages, the nomenclature proposed here will provide a logical basis for the naming of newly identified dynein genes and mutant alleles and facilitate comparisons between *C. reinhardtii* and the other organisms. Finally, defects in subunits of both IFT dynein and axonemal dyneins are known to result in

Table III. Nomenclature of *C. reinhardtii* Dynein Proteins and Representative Mutant Alleles

Gene name	Mutant alleles	Protein aliases[a]
DHC1	*ida1-1 → ida1-6, pf9-1 → pf9-4, pf30*	**1α HC**
DHC2	–	**DHC2**
DHC3	–	**DHC3**
DHC4	–	**DHC4**
DHC5	–	**DHC5**
DHC6	–	**DHC6**
DHC7	–	**DHC7**
DHC8	–	**DHC8**
DHC9	*ida9*	**DHC9**
DHC10	*ida2-1 → ida2-6*	**1β HC**
DHC11	–	**DHC11**
DHC12	–	**DHC12**
DHC13	*oda11*	**α HC**
DHC14	*oda4-1 → oda4-4, oda4-s7, sup_{pf}1-1, sup_{pf}1-2*	**β HC**
DHC15	*oda2, oda2-t, pf28, sup_{pf}2*	**γ HC**
DHC16	*dhc1b-1, stf1-1, stf1-2, dhc1b-2(dhc1b^{ts})*	**DHC1b**
DIC1	*oda9-1, oda9-2(V5), oda9-3(V8), oda9-4(V24), oda9-5(V27)*	**IC1**, IC78, IC80, M_r78,000
DIC2	*oda6-1, oda6-2, oda6-r75, oda6-r88*	**IC2**, IC69, IC70, M_r 69,000
DIC3	*ida7*	**IC140**, M_r 140,000
DIC4	*bop5-1, bop5-2*	**IC138**, M_r 138,000
DIC5	–	**D1bIC**, FAP133
DLI1	*d1blic, d1blic::D1bLIC(K53S), d1blic::D1bLIC(K53I, S54A)*	**D1bLIC**, LIC
DLU1	–	**LC1**, M_r 22,000
DLU2	*oda8-1 → oda8-3*	**ODA8**
DLX1	–	**LC3**, M_r 16,000
DLX2	–	**LC5**, M_r 14,000
DLT1	–	**LC9**
DLT2	*oda12-1,[b] oda12-2*	**LC2**, M_r 19,000
DLT3	–	**Tctex1**
DLT4	*pf16(D2)*[c]	**Tctex2b**
DLR1	*oda15*	**LC7a**, LC7
DLR2	–	**LC7b**
DLL1	*fla14-1, fla14-2*	**LC8**, M_r 8,000, 8 kDa
DLL2	*oda13*	**LC6**, M_r 11,000
DLL3	*oda12-1*[b]	**LC10**, MOT24
DLE1	–	**LC4**, M_r 18,000
DLE2 (CNT1)	*vfl2-1, vfl2-R1, vfl2-R5, vfl2-R8, vfl2-R10, vfl2-R11, vfl2-R13*	**Centrin**
DLE3	*oda14-1(V06), oda14-2(V16), oda14-3(F28),*[d] *oda14-1::ODA14 (E74Q, E152Q)*	**DC3**
DCC1	*oda3-1, oda3-2, oda3-4, oda3-5*	**DC1**
DCC2	*oda1-1 → oda1-3*	**DC2**
DCC3	*oda5-1, oda5-2*	**ODA5**
DOI1	–	**LIS1**
DII1	*ida4-1 → ida4-3*	**p28**
DII2	–	**p38**
DII3	–	**p44**
DII4 (ACT1)	*ida5*	**Actin**
DII5 (ARP12)	–	**NAP**
DII6	–	**IC97**, IC110
DII7	–	**FAP120**
DAP1	*pf13-1, pf13-2(pf13A), pf13-3*	**PF13**
DAP2	*ida10, mot48*	**MOT48**
DAW1	*oda16*	**ODA16**
DAU1	*oda7*	**ODA7**
DAB1[e]	*pf22-1, pf22-2(pf22A)*	**PF22**

[a]The current preferred protein name is indicated first in bold type.
[b]The *DLT2* and *DLL3* genes are adjacent; both are completely deleted in *oda12-1*.
[c]*pf16(D2)* lacks both the *DLT4* and *PF16* genes; the latter encodes a component of the central pair microtubule complex.
[d]The *oda14-3(F28)* allele also lacks the *RSP14* gene which encodes a component of the radial spokes.
[e]The *DAB1* gene is currently missing from the version 4 genome assembly.

human disease [Dagoneau et al., 2009; Escudier et al., 2009; Leigh et al., 2009; Merrill et al., 2009], and the homologous relationships between *C. reinhardtii* and *H. sapiens* genes clarified here should expedite identification and analysis of candidate disease genes in human patients.

Methods

The *Chlamydomonas* dynein genes identified here are the result of a *C. reinhardtii* genome reannotation initiative

Table IV. Nomenclature of Orthologous Ciliary/Flagellar Dynein Components[a,b]

	C. reinhardtii		*T. thermophila*	*A. crassispina and S. purpuratus*[c]	*Ci. intestinalis*	*D. rerio*	*H. sapiens*
	Gene	Protein	Gene (Protein)	Protein	Protein	Gene	Gene
Heavy chains							
Inner arm I1/f	*DHC1*	1α HC	*DYH6*	DNAH10			*DNAH10*
	DHC10	1β HC	*DYH7*	DNAH2			*DNAH2*
Outer arm	*DHC13*	α HC	*DYH5* (γ HC)	–	–		–
	DHC14	β HC	*DYH4* (β HC)	β HC (Sp-DNAH9)	α HC		*DNAH9*
							DNAH11
							DNAH17
	DHC15	γ HC	*DYH3* (α HC)	α HC (Sp-DNAH5, Sp-DNAH8, Sp-DNAH15)	β HC		*DNAH5* *DNAH8*
IFT dynein[d]	*DHC16*	DHC1b	*DYH2*	Sp-DYNC2H1		*Dync2h1*	*DYNC2H1*
Inner arm group 3	*DHC4*	DHC4	{*DYH8*	{DNAH3		{*DNAH7*	{*DNAH3*
	DHC5	DHC5	*DYH10*	DNAH4		*DNAH12*}	*DNAH7*
	DHC6	DHC6	*DYH12*	DNAH7			*DNAH12*
	DHC8	DHC8	*DYH13*	DNAH12}			*DNAH14*}
	DHC9	DHC9	*DYH14*				
	DHC11	DHC11	*DYH17*				
			DYH18				
			DYH25}				
Inner arm group 4	*DHC2*	DHC2	{*DYH9*	DNAH1			{*DNAH1*
			DYH11				*DNAH6*}
			DYH16				
			DYH19				
			DYH20}				
Inner arm group 5	*DHC3*	DHC3	{*DYH15*	–			
	DHC7	DHC7	*DYH22*	DNAH6			
			DYH23				
			DYH24}				
Unassigned	*DHC12*	DHC12					

(Continued)

Table IV. (Continued)

	C. reinhardtii		*T. thermophila*	*A. crassispina and S. purpuratus*[c]	*Ci. intestinalis*	*D. rerio*	*H. sapiens*
	Gene	Protein	Gene (Protein)	Protein	Protein	Gene	Gene
Intermediate chains							
Outer arm	–	–	–	IC1[e]	IC3[e]		*TXNDC3*[e] (*Sptrx2*)
	DIC1	IC1	*IC2*	IC2 (Sp-DNAI1)	IC2	*zgc:158666*	*DNAI1*
	DIC2	IC2	*IC3*	IC3 (Sp-DNAI2)	IC1	*LOC100004620*	*DNAI2*
Inner arm	*DIC3*	IC140	*IC5*				*WDR63*
	DIC4	IC138	*IC6*			*Wdr78*	*WDR78*
IFT dynein	*DIC5*	D1bIC	*D2IC*			*Dync2i1*	*WDR34*
Light intermediate chain[d]							
	DLI1	D1bLIC	*D2LIC*	D2LIC (Sp-DYNC2LI1)		*Dync2li1*	*DYNC2LI1*
Light chains							
Leucine-rich repeats	*DLU1*	LC1	*LC1*	LC2 (Sp-DNAL1)	LC1	*zgc:92542*	*DNAL1*
	DLU2	ODA8		LRRC56			*LRRC56*
Thioredoxine-like	*DLX1*	LC3	*LC3A* (LC3-like A)	–		–	–
			LC3B (LC3-like B)				
	DLX2	LC5		–	–	–	–
Tctex1-like	*DLT1*	LC9	{*TCT1A* (Tctex1A)	LC3 (Sp-DYNLT1)	LC3		{*DYNLT1*[f] (*Tctex1*)
	DLT3	Tctex1	*TCT1B* (Tctex1B)}				*DYNLT3 (rp3)*}
	DLT2	LC2	{*LC2A*	LC1 (Sp-DYNLT2)	LC2	{*Tctex1d1*	{*TCTE3*
	DLT4	Tctex2b	*LC2B*			*Tctex1d2*}	*TCTEX1D2 (Tctex2)*}
Roadblock-like	*DLR1*	LC7a	*LC7A*	RBPH (Sp-DYNLRB1) LC7L1 (Sp-DYNLRB2)	LC5	*Dynlrb1*	{*DYNLRB1*[f]
	DLR2	LC7b	*LC7B*}				*DYNLRB2*}
LC8 family	*DLL1*	LC8	*LC8*[g]	LC6 (Sp-DYNLL1)	LC6	{*Dynll1*	*DYNLL1*
						Dynll2}	*DYNLL2*
	DLL2	LC6	*LC8x* (LC8-like)[g]	–			–
	DLL3	LC10	*LC10*	LC4 (Sp-DNAL4)	LC4	*zgc:100999*	*DNAL4*
EF-hand	*DLE1*	LC4	*LC4A*	–			–
			LC4B				
	DLE2 (*CNT1*)	Centrin	*CEN1* (Centrin)				*CETN1, CETN2, CETN3*
	DLE3	DC3					

(Continued)

Table IV. (Continued)

	C. reinhardtii		*T. thermophila*	*A. crassispina and S. purpuratus*[c]	*Ci. intestinalis*	*D. rerio*	*H. sapiens*
	Gene	Protein	Gene (Protein)	Protein	Protein	Gene	Gene
Other components							
Coiled-coil	*DCC1*	DC1			IC4		
	DCC2	DC2			IC5, Axp66.0		*CCDC114*
	DCC3	ODA5					*CCDC63*
Outer arm-interacting	*DOI1*	LIS1				{*Wdr5* *Poc1b*}	
Inner arm-interacting	*DII1*	p28	*p28A* *p28B* *p28C*	p33 (Sp-DNALI1)		*Dnali1*	*DNALI1*
	DII2	p38		ZMYND12			ZMYND12
	DII3	p44		TTC29			*TTC28*
	DII4 (ACT1)	Actin	*ACT1* (Actin)	Actin	Actin	*Actin*	*Actin*[h]
	DII5 (ARP1)	NAP					
	DII6	FAP94		CASC1			*CASC1*
	DII7	FAP120					
Assembly factors							
PIH domain	*DAP1*	PF13				*Kintoun*[i]	*DNAAF2*
	DAP2	MOT48		PIH1D1		*Pih1d1*	*PIH1D1*
WD repeats	*DAW1*	ODA16		WDR69		*Wdr69*	*WDR69*
Leucine-rich repeats	*DAU1*	ODA7		LRRC50		*Lrrc50*	*DNAAF1 (LRRC50)*
Blocked assembly	*DAB1*	PF22					

[a]Initial biochemical identification of proteins comprising the axonemal dyneins of various model organisms was reported by multiple groups including: for *C. reinhardtii*, Pfister et al. [1982], Piperno and Luck [1979]; for the sea urchin *Tripneustes gratilla*, Bell et al. [1979]; for *T. thermophila*, Porter and Johnson [1983]; and for *Ci. intestinalis*, Hozumi et al. [2006].

[b]This table illustrates the names of orthologous components where that can be unambiguously determined. In some cases, multiple proteins in one organism are more closely related to each other than they are to any proteins present in another organism, as indicated by brackets, {. . .} across row entries. Thus, for the monomeric inner arm HCs (and some other components), phylogenetic analysis does not provide for a clear correspondence at the level of individual proteins. However, subgroupings are more clear [see also Wickstead and Gull, 2007; Wilkes et al., 2008] and are indicated here, although it is important to note that some ambiguity still remains.

[c]There are at least two nomenclatures for sea urchin axonemal dynein components currently in use. One derives from the original protein biochemistry and early sequence analysis of outer arm dynein components performed by a number of laboratories most notably those of Ian Gibbons [e.g., Bell et al., 1979] and Kazuo Ogawa [e.g., Ogawa et al., 1996, and light chain sequences published only in the database]. More recent annotation of the *S. purpuratus* genome identified additional components of sea urchin dyneins and provided alternate names for some components based mainly on the scheme used in mammals [Morris et al., 2006].

[d]The IFT dynein subunits in the nematode *Caenorhabditis elegans* are known as CHE3 (heavy chain), XBX-1 (light intermediate chain), and XBX-2 (a Tctex1/Tctex2 family light chain). A dynein IC involved in IFT has not yet been unambiguously identified in *Ca. elegans*. *Ca. elegans* lacks axonemal dyneins.

[e]These ICs are modular proteins consisting of an N-terminal thioredoxin domain followed by several catalytic nucleoside diphosphate kinase (NDK) modules. The N-terminal domain is closely related to *C. reinhardtii* LC3 (DLX1) and LC5 (DLX2). However, subunits of the *C. reinhardtii* outer arm do not contain the NDK modules.

[f]Mammals express two canonical Tctex1 proteins (DYNLT1 and DYNLT3) and two DYNLRB proteins. It remains uncertain which members of these groups are orthologous to the *C. reinhardtii* flagellar dynein components. Thus, both members of each group are listed.

[g]The analysis of Wilkes et al. [2007] recognized LC8 and five LC8-like sequences (ABF38951–ABF38955) in *T. thermophila*; LC8D (LC8-likeD) (ABF38954) appeared most closely related to *C. reinhardtii* LC6 (DLL2), although our analysis suggest this assignment is ambiguous with respect to other LC8-like sequences, notably LC8C (ABF38953). Furthermore, none of these *T. thermophila* LC8-like sequences contain the loop region insert that characterizes *C. reinhardtii* LC6. The most recent *T. thermophila* genome release includes only canonical LC8 and LC8E (LC8-likeE) genes. As amino acid differences occur throughout the LC8-likeA to LC8-likeE sequences, these sequences are unlikely to be generated by alternative splicing. It is possible that the current genome assembly has erroneously combined these genes into a common locus/scaffold.

¶For organisms which express multiple actin isoforms, it has not yet been determined which isoform(s) are present in cilia/flagella.

#The kintoun (Ktu) mutant was originally identified in medaka [*Oryzias latipes*; Omran et al., 2008].

[Hom et al., in preparation], based on models generated using the gene-calling program AUGUSTUS [Stanke et al., 2008]. Proteome datasets (sources given in Supplementary Information, Table SI) for *T. thermophila* C3, *Trypanosoma brucei* TREU 927, *S. purpuratus* (sea urchin), *Ci. intestinalis* (sea squirt), *Drosophila melanogaster* (fruit fly), *D. rerio* (zebra fish), and *H. sapiens* (human) were pairwise aligned to the set of *C. reinhardtii* dyneins by context-specific BLAST [Biegert and Soeding, 2009]. Hits with bit scores within 2% of the best hit were collected and orthologs were assigned by manual inspection, mindful of the analyses by Wickstead and Gull [2007] and Wilkes et al. [2008]. Hits to multiple *C. reinhardtii* dynein genes were treated conservatively: when one-to-one ortholog associations were uncertain, homologous proteins were grouped into subclasses.

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