

Table 2

Major characteristics of some of the currently known PMLOs

Name (abbreviation) (Content of disordered residues (CDR), % ± Std.Err.)	Function	Cellular location	Number per cell	Size/shape	Fluidity	Composition	
						Protein ^a (MobiDB consensus disorder content, %, [61**])	Nucleic acids or RNPs
Sam68 nuclear bodies (SNBs) 58.0 ± 6.4 ⁴	mRNAs trafficking through the nucleus	Nucleus	10–30	300–1000 nm	Fluid (?)	hnRNPG (87.0), YTS21 (74.1), Sam68 (66.1), SLM1 (63.6), SLM2 (54.3), hnRNPD (44.5), hnRNPL (39.9), hnRNPK (34.1), Saf-B (89.6), TonEBP (85.9), 9G8 (64.7), SF2/ASF (48.8), SRp30 (45.2), HSF1 (41.6), HSF2 (36.9)	Long non-coding RNA
Nuclear stress bodies (nSBs) or perichromatin granules (PGs) 56.1 ± 7.0 Insulator bodies (OPT domains) 40.6 (human) 50.1 ± 5.7 (<i>Drosophila</i>)	Response to heat shock and other forms of stress	Nucleus	4–6	2000–2500 nm	Fluid (?)		pre-mRNA, SatIII DNA, SatIII ncRNAs, chromatin
Response to osmotic stress	Nucleus, periphery-associated	10–30	200–2000 nm	Fluid		In human: CTCF (40.6); In <i>Drosophila</i> : CP190 (70.4), GAF (59.9), Su(Hw) (39.9), Mod(mdg4)67.2 (64.2), CTCF (46.1), Zwi5 (28.3), BEAF-32 (25.1) MDC1 (77.7), BP1 (74.7), PTF6 (58.74), PTFα (57.7), TBP (46.3), Oct1 (42.7), PTFγ (39.7), γH2AX (33.6), PTFβ (13.9)	No DNA or RNA
Oct1/PTF/transcription domains (OPT domains) 49.4 ± 6.7 Chromatin 46.1 ± 2.9	Response to the replication stress	Nucleus	One or few	1000–3000 nm; spherical	Fluid		Nascent mRNAs
	Genomic DNA compaction and packaging; DNA reinforcement; prevention of the DNA damage; control of DNA replication and gene expression	Nucleus	Equivalent to the number of chromosomes	Elongated, coiled, thread-like	Non-fluid		DNA
						HIST1H1D (91.0), HIST1H1B (89.4), HIST1H1E (87.7), HIST1H1A (87.0), HIST1H1 C (86.4), H1FOO (85.8), H1FNT (82.0), H1F0 (78.4), H1FX (74.2), HIST1H1 T (69.6), HIST1H2BA (46.5), H2BFS (46.0), HIST1H2BL (44.4), HIST1H2BN (44.4), HIST1H2BD (44.4), HIST1H2BM (43.7), HIST1H2BB (43.7), HIST1H2BC (43.7), HIST1H2BH (43.7), HIST1H2BO (43.7), HIST2H2BE (43.7), H2AFZ (41.4), HIST1H2BK (41.3), HIST3H3 (39.7), HIST2H3A/C/D (39.0), HIST1H3A/B/C/D/E/FG/I/J (39.0), H2AFV (38.3), H2AFB1 (37.4), HIST1H2AA (36.6), H2AFB2 (35.7), H2BFM (36.8), H2BFWT (34.9), H2AFX (33.6), HIST2H2AA3 (32.3), HIST2H2AC (31.8), HIST1H2AC (31.5), HIST1H4A/B/C/D/E/F/H/I/J/K/L (31.1), HIST2H4A/B (31.1), HIST4H4 (31.1), HIST1H2AB (30.8), H2AFJ (30.2), HIST1H2AD (30.0), HIST1H2AG (30.0), HIST1H2AH (29.7), HIST1H2AJ (28.9), H2AFY (26.3), H2AFY2 (25.0), HIST1H4G (21.4)	
Histone locus bodies (HLBs) 42.9 ± 6.6	Processing of the histone pre-mRNAs	Nucleus	1–16	1000 nm	Fluid	SLBP (70.4), NELFE (67.9), LSm11 (66.1), Coilin (56.6), NPAT (53.9), FLASH (53.9), NELFA (52.5), ZPR1 (32.5), HINF-P (24.8), LSm10 (17.9), NELFB (10.7), NELFC/D (7.8)	Histone DNA, U7 snRNA, U85 scaRNA
Neuronal RNA granules 41.1 ± 4.1	Protein synthesis in response to exogenous stimuli	Cytoplasm of neurons	10–50	Heterogeneous, ranges from 150 to 1000 nm; spherical	Fluid (droplet-like)	Sam68 (66.1), RNG105 (63.6), SMN (57.8), G3BP (56.0), hnRNPA2 (49.9), Stauf1 (47.5), Stauf2 (42.3), Purα (41.9), FMR1 (38.9), SYNCRIP (37.4), CPEB (27.4), eIF2 (23.4), HuD (22.9), eIF4E (21.2), ZBP1 (19.6)	Silenced mRNAs, ribosomes
Stress granules (SGs) 41.0 ± 4.8	Response to stresses that strongly repress translation	Cytoplasm	10–100	100–200 nm; spherical	Fluid (droplet-like)	eIF4B (91.3), YB-1 (80.3), TTP (72.7), eIF4G (58.1), SMN (57.8), G3BP (56.0), eIF3 (49.1), Stauf1 (47.5), FAST (47.2), BRP1 (46.5), Smaug (43.5), FMR1 (38.9), TDP43 (37.0), CPEB (27.4), eIF2 (23.4), TIA-1 (22.5), XRN1 (22.5), eIF4E (21.2), PABP-1 (20.6), TIAR (19.5), HuR (11.4), eIF4A (8.5)	Non-translating mRNA, 40S ribosomal subunits
Subnuclear organelles containing polycomb group proteins (PoG bodies) 40.5 ± 5.7 Cleavage bodies 40.5 ± 9.3	Contribute to the regulation of gene expression	Nucleus	6–14	200–1500 nm; spherical	Fluid (?)	HPH2 (52.0), RING1 (50.0), CTCF (40.6), BMI1 (40.1), HPC2 (19.9)	DNA, RNA
	Associated with RNA metabolism; potentially serves as storage/assembly sites for proteins involved in transcription, splicing, 3'-end processing of pre-mRNAs, and RNA degradation	Nucleus	1–4	300–1000 nm; spherical	Fluid	TFIIFα (69.6), CstF-64 (61.4), TFIIEα (43.7), TFIIEβ (38.1), CPSF-100 (17.1), TFIIFβ (13.2)	No RNA or DNA
Nucleolus 39.9 ± 7.5	Ribosome synthesis and assembly	Nucleus	1	1000–10,000 nm, depending on cell size; spherical	Fluid	NOPP140/NOLC1 (91.0), Nucleolin (64.9), GAR1 (59.5), Nucleophosmin (53.7), NOP10 (39.1), Fibrillarin (33.6), NOP56 (26.3), NOP58 (24.8), Dyskerin (24.3), NHP2 (15.7), NHP2L1 (6.3) CBP (66.0), CREB-2 (61.8), c-Jun (45.0), SUMO-1 (41.6), γCREB-1 (40.5), USP11 (15.5), Ubc9 (7.0)	snoRNAs, 40S ribosome, 60S ribosome
SUMO-1 nuclear bodies (CNBs) 39.6 ± 8.3	Response to DNA damage response, site of protein SUMOylation	Nucleus	1–3	1000–3000 nm	Fluid (?)		Probably, no DNA or RNA

Table 2 (Continued)

Name (abbreviation) (Content of disordered residues (CDR), % ± Std.Err.)	Function	Cellular location	Number per cell	Size/shape	Fluidity	Composition	
						Protein ^a (MobiDB consensus disorder content, %, [61 ^{**}])	Nucleic acids or RNPs
Nuclear speckles or interchromatin granule clusters 38.9 ± 5.3	Related to the pre- mRNA splicing	Nucleus	25–50	500–1000 nm, size varies, irregular shape	Fluid (droplet-like)	SRSF4 (74.1), CPSF6 (72.1), SRSF2 (70.1), SRSF6 (65.4), SRSF7 (64.7), CSTF2 (61.4), SRSF3 (56.7), SRSF5 (52.9), SRSF1 (48.8), PRP3 (42.9), NIPP1 (42.2), SF3b1 (29.8), CLK (28.9), CPSF4 (27.5), PRP6 (24.4), CPSF2 (17.1), CPSF1 (14.8), SNU114 (8.2), U5-200KD (6.6), PRP8 (4.8), CPSF3 (3.7)	Non-coding RNAs, snRNPs, spliceosome subunits, MALAT1 RNA, Poly(A)+ RNA
Promyelocytic leukemia (PML) nucleic bodies or PML oncogenic domains (PODs) or nuclear dots 38.5 ± 3.1	Control of cellular senescence and stem cell self- renewal; involved in oncogenesis and viral infection	Nucleus	5–30	250–500 nm; spherical	Fluid	CBP (66.0), DAXX (63.5), Sp100 (61.0), ATRX (59.1), HP1 (58.1), BRCA1 (54.1), SUMO-1 (41.6), NBS1 (41.2), H3F3A (39.7), HIST2H3A/C/D (39.0), HIST1H3A/B/C/D/E/FG/I/J (39.0), HIST1H2AA (36.6), γH2AX (33.6), BLM (33.3), HIST1H2AC (31.5), HIST1H4A/B/C/D/E/F/H/I/ J/K/L (31.1), HIST1H2AB (30.8), HIST1H2AD (30.0), HIST1H2AG (30.0), HIST1H2AH (29.7), HIST1H2AJ (28.9), PML (27.0), RAD51 (9.4), Int-6 (8.8)	Nascent RNA at the periphery
Cajal bodies (CBs) 37.7 ± 6.5	snRNP biogenesis	Nucleus	1–5	100–2000 nm, spherical	Fluid	NOLC1 (91.0), GAR1 (59.5), SMN1 (57.8), Coilin (56.6), NOP10 (39.1), TCAB1 (37.0), Fibrillarin (33.6), NOP56 (26.3), NOP58 (24.8), Dyskerin (24.3), TERT (16.4), NHP2 (15.7), NHP2L1 (6.3)	Sca RNAs, snRNAs, TERC RNA, snoRNAs
Paraspeckles 37.6 ± 5.7	Regulation of the expression of certain genes in differentiated cells by nuclear retention of RNA	Nucleus	5–20	500–1000 nm in diameter; sausage-like	Fluid	SOX9 (77.6), PSF (74.5), WTX (73.6), CFIm68 (72.1), PSP2 (57.4), P54NRB (56.1), BCL11A (53.3), PSPC1 (52.2), WT1 (44.8), RPB1 (30.0), RPABC2 (29.9), RPB4 (28.2), RPABC4 (25.9), RPB3 (23.6), RPB9 (16.0), RPABC3 (11.3), RPB11-a (9.4), RPB2 (7.3), RPABC5 (5.6), RPB7 (4.1)	Long non- coding RNA, mRNAs with extended 3'UTR, mRNAs with Alu sequences
Processing bodies (P-bodies or PBs) 34.4 ± 4.3	Response to stress	Cytoplasm	2–20, proportional to the flux of mRNAs undergoing decapping	100–300 nm; spherical	Fluid (droplet-like)	GW182 (79.9), TTP (72.7), DCP1a (50.5), PATL1 (48.2), FAST (47.2), BRF1 (46.5), Lsm4 (41.0), hEDLS (38.5), DCP2 (31.4), LAF-1 (42.5), EDC3 (27.0), XRN1 (22.5), eIF4E (21.2), RCK (20.7), Lsm7 (19.4), Lsm5 (18.7), Lsm3 (17.7), Lsm6 (17.5), Lsm1 (15.8), Lsm2 (9.5)	Non-translating mRNA
DDX1 bodies 33 ± 28	Related to the pre- mRNA processing	Nucleus	0–15	500 nm	Fluid	CstF-64 (61.4), DDX1 (4.9)	
Perinuclear compartment (PNC) 31.1 ± 6.2	Involved in polymerase III RNA metabolism	Nucleus, periphery of nucleolus, unique to tumor cells	1	250–4000 nm; irregularly shaped, mesh composed of multiple strands		KSRP (67.8), Raver1 (45.4), HNRPK (34.1), Raver2 (25.0), CELFL-1 (20.6), Rod1 (19.0), PTBP1 (18.6), PTBP2 (18.5)	Newly synthesized RNAs of RNA polymerase III, DNA
Germline P-granules, or germ cell granules, or nuages 30.8 ± 4.1	Regulation of germ cell development and function	Cytoplasm of embryonic cells	10–200, changes during germ cell development	Continually growing and shrinking; spherical	Fluid (droplet-like)	RDE-12 (56.3), GLH-4 (53.8), GLH-2 (51.8), DCP1a (50.5), Ddx4 (39.8), GLH-1 (39.5), PGL-3 (30.2), GLH-3 (25.3), PP2A (23.4), PGL-1 (29.9), eIF4E (21.2), eIF5A (25.5), CSR-1 (19.3), WAGO-1 (11.5), PRG-1 (8.1), CGH-1 (6.1)	Maternal mRNA
Gemini of Cajal bodies, or Gemini of coiled bodies, or Nuclear gems 26.8 ± 5.7 ^c	Unknown, may be related to further maturation, storage or recycling of splicing factors	Nucleus	1–5	100–2000 nm, spherical	Fluid (?)	SMN1 (57.8), GEMIN8 (38.4), GEMIN7 (36.6), ZPR1 (32.5), GEMIN3 (30.7), GEMIN2 (18.2), GEMIN5 (16.6), GEMIN6 (7.8), GEMIN4 (2.8)	Do not contain snRNPs
Centrosome 24.5 ± 3.2	Microtubule organizing center	Cytoplasm of metazoan cells	2	Droplet-like structure around two centrioles, which are hollow cylinders of 400– 1400 nm in the length and 500– 1000 nm in the diameter	Fluid	Cep131 (58.6), Centrin-1 (41.3), PIK4 (36.2), Centrin-2 (34.9), CDK5RAP2 (31.0), Pericentrin (35.4), Cenexin (33.2), Cep63 (30.0), Cep192 (25.7), Cep152 (24.3), Ninein (23.7), Tektin-4 (20.7), Centrin-3 (17.4), Cep290 (15.3), Tektin-3 (11.2), Tektin-1 (10.8), Tektin-2 (10.2), Tektin-5 (4.1), γ-tubulin (1.6)	Centrosomal RNA (cnRNA)
Chloroplast RNA granules or chloroplast stress granules (cpSGs) 18.0 ± 4.0	Response to specific stress stimuli	Chloroplasts	2–5	300 nm; spherical	Fluid (?) (droplet-like)	L2 (29.5), cPABP (29.1), Hsp70B (15.9), S21 (15.2), L12 (14.2), Rubisco (4.2)	Chloroplast- specific mRNAs
Mitochondrial RNA granules 11.9 ± 1.6	Posttranscriptional RNA processing and biogenesis of mitochondrial ribosomes	Mitochondria	Number varies in line with the cellular metabolic state	100–1000 nm; spherical	Fluid (?) (droplet-like)	MRM1 (21.3), MTPAP (19.9), SUPV3L1 (17.4), RNMTL1 (17.3), GRSF1 (16.3), DDX28 (16.1), DHX30 (12.1), TRMT10 C (9.2), FASTKD5 (9.0), KIAA0391 (7.6), HSD17B10 (6.5), PNPase (5.0), FTSJ2 (4.9), FASTKD2 (4.4)	Mitochondrial mRNAs, mitochondrial ribosomes

^a Information on the protein content of various nuclear bodies is retrieved from Table 1 in [62^{**}].

^b According to the accepted classification [63], PMLOs with content of disordered residues (CDR) ≥30% are considered as highly disordered, and their CDR values are shown in red.

^c PMLOs with 10 ≤ CDR < 30% are considered as moderately disordered [63], and their CDF values are shown in pink.

61. Potenza E, Di Domenico T, Walsh I, Tosatto SC: **MobiDB 2.0: an improved database of intrinsically disordered and mobile proteins.** *Nucleic Acids Res* 2015, **43**:D315–D320.

This study represents new developments in the MobiDB database of intrinsically disordered and mobile proteins. MobiDB provides detailed description of experimentally validated and predicted intrinsic disorder status of the UniProt proteins.

62. Morimoto M, Boerkoel CF: **The role of nuclear bodies in gene expression and disease.** *Biology (Basel)* 2013, **2**:976–1033.

Various aspects related to the roles of nuclear bodies in gene expression and disease are discussed.

63. Rajagopalan K, Mooney SM, Parekh N, Getzenberg RH, Kulkarni P: **A majority of the cancer/testis antigens are intrinsically disordered proteins.** *J Cell Biochem* 2011, **112**:3256–3267.