eLIFE
elifesciences.org

SHORT REPORT

Swimming eukaryotic microorganisms exhibit a universal speed distribution

Maciej Lisicki[1,2†*], Marcos F Velho Rodrigues[1†], Raymond E Goldstein[1], Eric Lauga[1*]

[1]Department of Applied Mathematics and Theoretical Physics, University of Cambridge, Cambridge, United Kingdom; [2]Institute of Theoretical Physics, Faculty of Physics, University of Warsaw, Warsaw, Poland

Abstract One approach to quantifying biological diversity consists of characterizing the statistical distribution of specific properties of a taxonomic group or habitat. Microorganisms living in fluid environments, and for whom motility is key, exploit propulsion resulting from a rich variety of shapes, forms, and swimming strategies. Here, we explore the variability of swimming speed for unicellular eukaryotes based on published data. The data naturally partitions into that from flagellates (with a small number of flagella) and from ciliates (with tens or more). Despite the morphological and size differences between these groups, each of the two probability distributions of swimming speed are accurately represented by log-normal distributions, with good agreement holding even to fourth moments. Scaling of the distributions by a characteristic speed for each data set leads to a collapse onto an apparently universal distribution. These results suggest a universal way for ecological niches to be populated by abundant microorganisms.
DOI: https://doi.org/10.7554/eLife.44907.001

***For correspondence:** maciej.lisicki@fuw.edu.pl (ML); e.lauga@damtp.cam.ac.uk (EL)

†These authors contributed equally to this work

Competing interest: See page 8

Funding: See page 8

Received: 05 January 2019
Accepted: 29 June 2019
Published: 16 July 2019

Reviewing editor: Arup K Chakraborty, Massachusetts Institute of Technology, United States

Introduction

Unicellular eukaryotes comprise a vast, diverse group of organisms that covers virtually all environments and habitats, displaying a menagerie of shapes and forms. Hundreds of species of the ciliate genus *Paramecium* (***Wichterman, 1986***) or flagellated *Euglena* (***Buetow, 2011***) are found in marine, brackish, and freshwater reservoirs; the green algae *Chlamydomonas* is distributed in soil and fresh water world-wide (***Harris et al., 2009***); parasites from the genus *Giardia* colonize intestines of several vertebrates (***Adam, 2001***). One of the shared features of these organisms is their motility, crucial for nutrient acquisition and avoidance of danger (***Bray, 2001***). In the process of evolution, single-celled organisms have developed in a variety of directions, and thus their rich morphology results in a large spectrum of swimming modes (***Cappuccinelli, 1980***).

Many swimming eukaryotes actuate tail-like appendages called flagella or cilia in order to generate the required thrust (***Sleigh, 1975***). This is achieved by actively generating deformations along the flagellum, giving rise to a complex waveform. The flagellar axoneme itself is a bundle of nine pairs of microtubule doublets surrounding two central microtubules, termed the '9 + 2' structure (***Nicastro et al., 2005***), and cross-linking dynein motors, powered by ATP hydrolysis, perform mechanical work by promoting the relative sliding of filaments, resulting in bending deformations.

Although eukaryotic flagella exhibit a diversity of forms and functions (***Moran et al., 2014***), two large families, 'flagellates' and 'ciliates', can be distinguished by the shape and beating pattern of their flagella. Flagellates typically have a small number of long flagella distributed along the bodies, and they actuate them to generate thrust. The set of observed movement sequences includes planar undulatory waves and traveling helical waves, either from the base to the tip, or in the opposite direction (***Jahn and Votta, 1972***; ***Brennen and Winet, 1977***). Flagella attached to the same body might follow different beating patterns, leading to a complex locomotion strategy that often relies also on the resistance the cell body poses to the fluid. In contrast, propulsion of ciliates derives from the motion of a layer of densely-packed and collectively-moving cilia, which are short hair-like flagella covering their bodies. The seminal review paper of ***Brennen and Winet (1977)*** lists a few examples from both groups, highlighting their shape, beat form, geometric characteristics and swimming properties. Cilia may also be used for transport of the surrounding fluid, and their cooperativity can lead to directed flow generation. In higher organisms this can be crucial for internal transport processes, as in cytoplasmic streaming within plant cells (***Allen and Allen, 1978***), or the transport of ova from the ovary to the uterus in female mammals (***Lyons et al., 2006***).

Here, we turn our attention to these two morphologically different groups of swimmers to explore the variability of their propulsion dynamics within broad taxonomic groups. To this end, we have collected swimming speed data from literature for flagellated eukaryotes and ciliates and analyze them separately (we do not include spermatozoa since they lack (ironically) the capability to reproduce and are thus not living organisms; their swimming characteristics have been studied by ***Tam and Hosoi, 2011***). A careful examination of the statistical properties of the speed distributions for flagellates and ciliates shows that they are not only both captured by log-normal distributions but that, upon rescaling the data by a characteristic swimming speed for each data set, the speed distributions in both types of organisms are essentially identical.

Results and discussion

We have collected swimming data on 189 unicellular eukaryotic microorganisms ($N_{fl} = 112$ flagellates and $N_{cil} = 77$ ciliates) (see Appendix 1 and ***Source data 1***). ***Figure 1*** shows a tree encompassing the phyla of organisms studied and sketches of a representative organism from each phylum. A large morphological variation is clearly visible. In addition, we delineate the branches involving aquatic organisms and parasitic species living within hosts. Both groups include ciliates and flagellates.

Due to the morphological and size differences between ciliates and flagellates, we investigate separately the statistical properties of each. ***Figure 2*** shows the two swimming speed histograms superimposed, based on the raw distributions shown in ***Figure 2—figure supplement 1***, where bin widths have been adjusted to their respective samples using the Freedman-Diaconis rule (see Materials and methods). Ciliates span a much larger range of speeds, up to 7 mm/s, whereas generally smaller flagellates remain in the sub-mm/s range. The inset shows that the number of flagella in both groups leads to a clear division. To compare the two groups further, we have also collected information on the characteristic sizes of swimmers from the available literature, which we list in Appendix 1. The average cell size differs fourfold between the populations (31 μm for flagellates and 132 μm for ciliates) and the distributions, plotted in ***Figure 2—figure supplement 2***, are biased towards the low-size end but they are quantitatively different. In order to explore the physical conditions, we used the data on sizes and speeds to compute the Reynolds number $\mathrm{Re} = UL/\nu$ for each organism, where $\nu = \eta/\rho$ is the kinematic viscosity of water, with η the viscosity and ρ the density. Since almost no data was available for the viscosity of the fluid in swimming speed measurements, we assumed the standard value $\nu = 10^{-6} m^2/s$ for water for all organisms. The distribution of Reynolds numbers (***Figure 2—figure supplement 3***), shows that ciliates and flagellates operate in different ranges of Re, although for both groups $\mathrm{Re}<1$, imposing on them the same limitations of inertia-less Stokes flow (***Purcell, 1977***; ***Lauga and Powers, 2009***).

Furthermore, studies of green algae (***Short et al., 2006***; ***Goldstein, 2015***) show that an important distinction between the smaller, flagellated species and the largest multicellular ones involves the relative importance of advection and diffusion, as captured by the Péclet number $Pe = UL/D$, where L is a typical organism size and D is the diffusion constant of a relevant molecular species. Using the average size L of the cell body in each group of the present study ($L_{fl} = 31\ \mu m$, $L_{cil} = 132\mu m$) and the median swimming speeds ($U_{fl} = 127\mathrm{m/s}$, $U_{\mathrm{cil}} = 784\mathrm{m/s}$), and taking $D = 10^3(\mu\mathrm{m})^2/\mathrm{s}$, we find $Pe_{\mathrm{fl}} \sim 3.9$ and $Pe_{\mathrm{cil}} \sim 103$, which further justifies analyzing the groups separately; they live in different physical regimes.

Examination of the mean, variance, kurtosis, and higher moments of the data sets suggest that the probabilities $P(U)$ of the swimming speed are well-described by log-normal distributions,

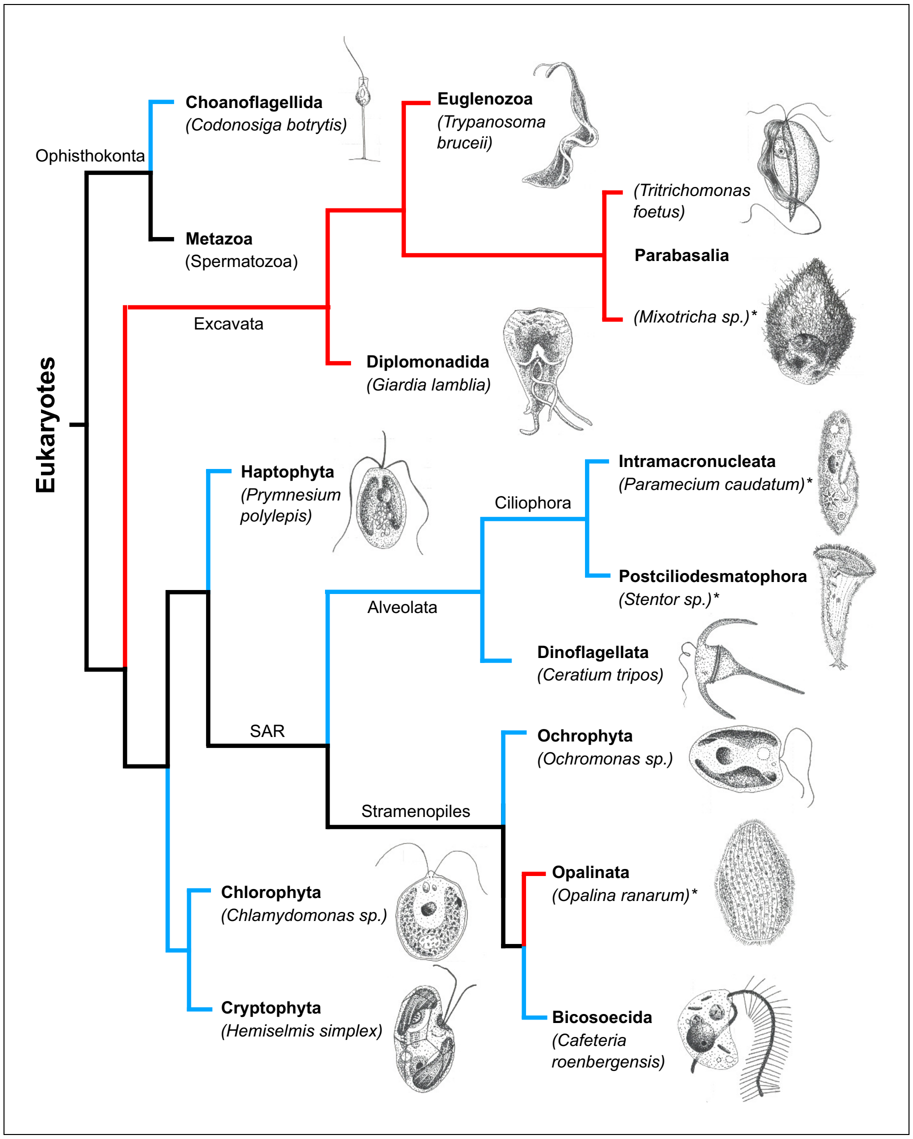

Figure 1. The tree of life (cladogram) for unicellular eukaryotes encompassing the phyla of organisms analyzed in the present study. Aquatic organisms (living in marine, brackish, or freshwater environments) have their branches drawn in blue while parasitic organisms have their branches drawn in red. Ciliates are indicated by an asterisk after their names. For each phylum marked in bold font, a representative organism has been sketched next to its name. Phylogenetic data from ***Hinchliff et al. (2015)***.

DOI: https://doi.org/10.7554/eLife.44907.002

$$P(U) = \frac{1}{U\sigma\sqrt{2\pi}} \exp\left(-\frac{(\ln U - \mu)^2}{2\sigma^2}\right), \tag{1}$$

normalized as $\int_0^\infty dUP(U) = 1$, where μ and σ are the mean and the standard deviation of $\ln U$. The median M of the distribution is e^μ, with units of speed. Log-normal distributions are widely observed across nature in areas such as ecology, physiology, geology and climate science, serving as an empirical model for complex processes shaping a system with many potentially interacting elements (***Limpert et al., 2001***), particularly when the underlying processes involve proportionate fluctuations or multiplicative noise (***Koch, 1966***).

The results of fitting (see Materials and methods) are plotted in ***Figure 3***, where the best fits are presented as solid curves, with the shaded areas representing 95% confidence intervals. For

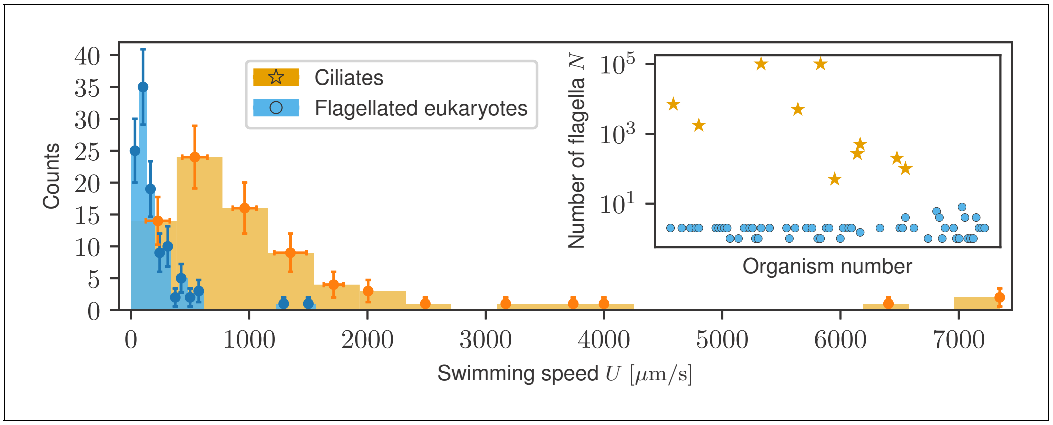

Figure 2. Histograms of swimming speed for ciliates and flagellates demonstrate a similar character but different scales of velocities. Data points represent the mean and standard deviation of the data in each bin; horizontal error bars represent variability within each bin, vertical error bars show the standard deviation of the count. Inset: number of flagella displayed, where available, for each organism exhibits a clear morphological division between ciliates and flagellates.

DOI: https://doi.org/10.7554/eLife.44907.003

The following figure supplements are available for figure 2:

Figure supplement 1. Linear distribution of swimming speed data.

DOI: https://doi.org/10.7554/eLife.44907.004

Figure supplement 2. Distribution of organism sizes in analyzed groups.

DOI: https://doi.org/10.7554/eLife.44907.005

Figure supplement 3. Distribution of Reynolds numbers for organisms in analyzed groups.

DOI: https://doi.org/10.7554/eLife.44907.006

flagellates, we find the $M_{fl} = 127\mathrm{m/s}$ and $\sigma_{fl} = 0.978$ while for ciliates, we obtain $M_{cil} = 784\mathrm{m/s}$ and $\sigma_{cil} = 0.936$. Log-normal distributions are known to emerge from an (imperfect) analogy to the Gaussian central limit theorem (see Materials and methods). Since the data are accurately described by this distribution, we conclude that the published literature includes a sufficiently large amount of unbiased data to be able to see the whole distribution.

We next compare the statistical variability within groups by examining rescaled distributions (***Goldstein, 2018***). As each has a characteristic speed M, we align the peaks by plotting the distributions versus the variable U/M for each group. Since P has units of 1/speed, we are thus led to the form $P(U,M) = M^{-1}F(U/M)$ for some function F. For the log-normal distribution, with M the median, we find

$$F(\xi) = \frac{1}{\xi\sigma\sqrt{2\pi}}\exp\left(-\frac{\ln^2\xi}{2\sigma^2}\right), \tag{2}$$

which now depends on the single parameter σ and has a median of unity by construction. To study the similarity of the two distributions we plot the functions $F = MP(U/M)$ for each. As seen in ***Figure 4***, the rescaled distributions are essentially indistinguishable, and this can be traced back to the near identical values of the variances σ, which are within 5% of each other. The fitting uncertainties shown shaded in ***Figure 4*** suggest a very similar range of variability of the fitted distributions. Furthermore, both the integrated absolute difference between the distributions (0.028) and the Kullback-Leibler divergence (0.0016) are very small (see Materials and methods), demonstrating the close similarity of the two distributions. This similarity is robust to the choice of characteristic speed, as shown in ***Figure 4—figure supplement 1***, where the arithmetic mean U^* is used in place of the median.

In living cells, the sources for intrinsic variability within organisms are well characterized on the molecular and cellular level (***Kirkwood et al., 2005***) but less is known about variability within taxonomic groups. By dividing unicellular eukaryotes into two major groups on the basis of their difference in morphology, size and swimming strategy, we were able to capture in this paper the log-

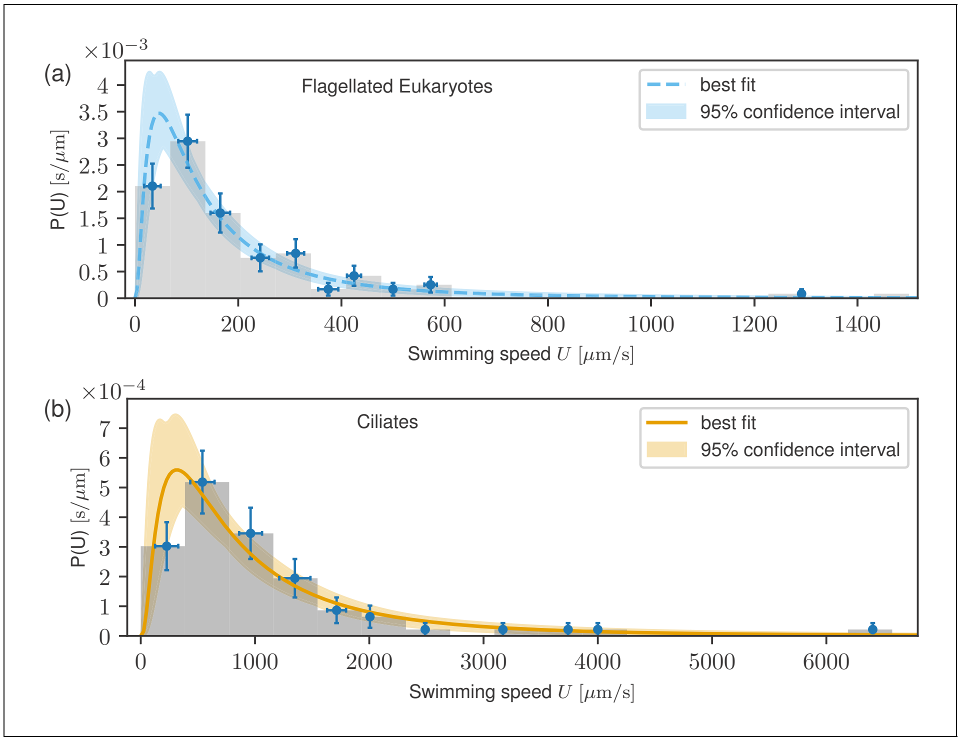

Figure 3. Probability distribution functions of swimming speeds for flagellates (**a**) and ciliates (**b**) with the fitted log-normal distributions. Data points represent uncertainties as in ***Figure 2***. Despite the markedly different scales of the distributions, they have similar shapes.

DOI: https://doi.org/10.7554/eLife.44907.007

The following figure supplement is available for figure 3:

Figure supplement 1. Higher moments of the swimming speed distributions obtained from the data compared with those calculated from the fitted log-normal distribution.

DOI: https://doi.org/10.7554/eLife.44907.008

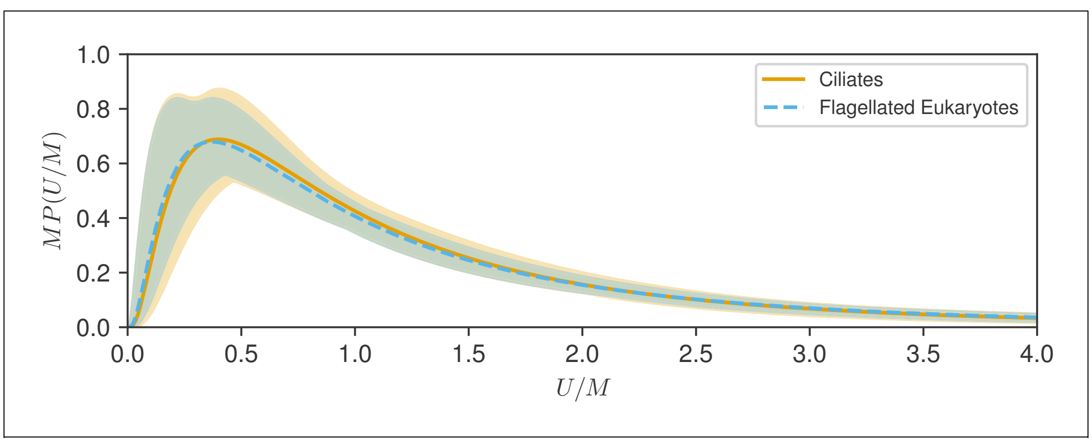

Figure 4. Test of rescaling hypothesis. Shown are the two fitted log-normal curves for flagellates and ciliates, each multiplied by the distribution median M, plotted versus speed normalized by M. The distributions for show remarkable similarity and uncertainty of estimation.

DOI: https://doi.org/10.7554/eLife.44907.009

The following figure supplement is available for figure 4:

Figure supplement 1. Data collapse as in the main figure, but using the mean speeds U^{*} instead of the median M.

DOI: https://doi.org/10.7554/eLife.44907.010

normal variability within each subset. Using a statistical analysis of the distributions as functions of the median swimming speed for each population we further found an almost identical distribution of swimming speeds for both types of organisms. Our results suggest that the observed log-normal randomness captures a universal way for ecological niches to be populated by abundant microorganisms with similar propulsion characteristics. We note, however, that the distributions of swimming speeds among species do not necessarily reflect the distributions of swimming speeds among individuals, for which we have no available data.

Materials and methods

Data collection

Data for ciliates were sourced from 26 research articles, while that for flagellates were extracted from 48 papers (see Appendix 1). Notably, swimming speeds reported in the various studies have been measured under different physiological and environmental conditions, including temperature, viscosity, salinity, oxygenation, pH and light. Therefore we consider the data *not* as representative of a uniform environment, but instead as arising from a random sampling of a wide range of environmental conditions. In cases where no explicit figure was given for U in a paper, estimates were made using other available data where possible. Size of swimmers has also been included as a characteristic length for each organism. This, however, does not reflect the spread and diversity of sizes within populations of individual but is rather an indication of a typical size, as in the considered studies these data were not available. Information on anisotropy (different width/length) is also not included.

No explicit criteria were imposed for the inclusion in the analyses, apart from the biological classification (i.e. whether the organisms were unicellular eukaryotic ciliates/flagellates). We have used all the data found in literature for these organisms over the course of an extensive search. Since no selection was made, we believe that the observed statistical properties are representative for these groups.

Data processing and fitting the log-normal distribution

Bin widths in histograms in ***Figure 2*** and ***Figure 3*** have been chosen separately for ciliates and flagellated eukaryotes according to the Freedman-Diaconis rule (***Freedman and Diaconis, 1981***) taking into account the respective sample sizes and the spread of distributions. The bin width b is then given by the number of observations N and the interquartile range of the data IQR as

$$b = 2\frac{\mathrm{IQR}}{N^{1/3}}. \tag{3}$$

Within each bin in ***Figure 3***, we calculate the mean and the standard deviation for the binned data, which constitute the horizontal error bars. The vertical error bars reflect the uncertainty in the number of counts N_j in bin j. This is estimated to be Poissonian, and thus the absolute error amounts to $\sqrt{N_j}$. Notably, the relative error decays with the number of counts as $1/\sqrt{N_j}$.

In fitting the data, we employ the log-normal distribution ***Equation (1)***. In general, from from data comprising N measurements, labelled x_i $(i = 1, \ldots, N)$, the n-th arithmetic moment $\mathcal{M}_n$ is the expectation $\mathbb{E}(X^n)$, or

$$\mathcal{M}_n = \frac{1}{N}\sum_{i=1}^{N} x_i^n \tag{4}$$

Medians of the data were found by sorting the list of values and picking the middlemost value. For a log-normal distribution, the arithmetic moments are given solely by μ and σ of the associated normal distribution as

$$\mathcal{M}_n = M^n \Sigma^{n^2}, \tag{5}$$

where we have defined $M = \exp(\mu)$ and $\Sigma = \exp(\sigma^2/2)$, and note that M is the median of the distribution. Thus, the mean is $M\Sigma$ and the variance is $M^2\Sigma^2(\Sigma^2-1)$. From the first and second moments, we estimate

$$\mu = \ln\left(\frac{\mathcal{M}_1^2}{\sqrt{\mathcal{M}_2}}\right) \quad \text{and} \quad \sigma^2 = \ln\left(\frac{\mathcal{M}_2}{\mathcal{M}_1^2}\right). \tag{6}$$

Having estimated μ and σ, we can compute the higher order moments from ***Equation (5)*** and compare to those calculated directly from the data, as shown in ***Figure 3—figure supplement 1***.

To fit the data, we have used both the MATLAB fitting routines and the Python scipy.stats module. From these fits we estimated the shape and scale parameters and the 95% confidence intervals in ***Figure 3*** and ***Figure 4***. We emphasize that the fitting procedures use the raw data via the maximum likelihood estimation method, and not the processed histograms, hence the estimated parameters are insensitive to the binning procedure.

For rescaled distributions, the average velocity for each group of organisms was calculated as $U^\star = \frac{1}{N_i}\sum_{i=1}^{N_i} U_i$, with $i \in \{cil, fl\}$. Then, data in each subset have been rescaled by the area under the fitted curve to ensure that the resulting probability density functions p_i are normalized as

$$\int_0^\infty p_i(x)\mathrm{d}x = 1. \tag{7}$$

In characterizations of biological or ecological diversity, it is often assumed that the examined variables are Gaussian, and thus the distribution of many uncorrelated variables attains the normal distribution by virtue of the Central Limit Theorem (CLT). In the case when random variables in question are positive and have a log-normal distribution, no analogous explicit analytic result is available. Despite that, there is general agreement that a sum of independent log-normal random variables can be well approximated by another log-normal random variable. It has been proven by ***Szyszkowicz and Yanikome (2009)*** that the sum of identically distributed equally and positively correlated joint log-normal distributions converges to a log-normal distribution of known characteristics but for uncorrelated variables only estimations are available (***Beaulieu et al., 1995***). We use these results to conclude that our distributions contain enough data to be unbiased and seen in full.

Comparisons of distributions

In order to quantify the differences between the fitted distributions, we define the integrated absolute difference Δ between two probability distributions $p(x)$ and $q(x)$ (x>0) as

$$\Delta = \int_0^\infty |p(x) - q(x)|\mathrm{d}x. \tag{8}$$

As the probability distributions are normalized, this is a measure of their relative 'distance'. As a second measure, we use the Kullback-Leibler divergence (***Kullback and Leibler, 1951***),

$$D(p,q) = \int_0^\infty p(x)\ln\left(\frac{p(x)}{q(x)}\right)\mathrm{d}x. \tag{9}$$

Note that $D(p,q) \neq D(q,p)$ and therefore D is not a distance metric in the space of probability distributions.

Acknowledgements

This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement 682754 to EL), and from Established Career Fellowship EP/M017982/1 from the Engineering and Physical Sciences Research Council and Grant 7523 from the Gordon and Betty Moore Foundation (REG).

Additional information

Competing interests
Raymond E Goldstein: Reviewing editor, *eLife*. The other authors declare that no competing interests exist.

Funding

Funder	Grant reference number	Author
H2020 European Research Council	682754	Eric Lauga
Engineering and Physical Sciences Research Council	EP/M017982/	Raymond E Goldstein
Gordon and Betty Moore Foundation	7523	Raymond E Goldstein

The funders had no role in study design, data collection and interpretation, or the decision to submit the work for publication.

Author contributions
Maciej Lisicki, Conceptualization, Data curation, Software, Formal analysis, Validation, Investigation, Methodology, Writing—original draft, Writing—review and editing; Marcos F Velho Rodrigues, Data curation, Software, Formal analysis, Investigation, Visualization, Methodology, Writing—original draft, Writing—review and editing; Raymond E Goldstein, Investigation, Methodology, Writing—review and editing; Eric Lauga, Conceptualization, Formal analysis, Supervision, Funding acquisition, Validation, Investigation, Methodology, Writing—original draft, Project administration, Writing—review and editing

Author ORCIDs
Maciej Lisicki https://orcid.org/0000-0002-6976-0281
Marcos F Velho Rodrigues https://orcid.org/0000-0002-8744-6966
Raymond E Goldstein https://orcid.org/0000-0003-2645-0598
Eric Lauga https://orcid.org/0000-0002-8916-2545

Decision letter and Author response
Decision letter https://doi.org/10.7554/eLife.44907.016
Author response https://doi.org/10.7554/eLife.44907.017

Additional files

Supplementary files
- Source data 1. Spreadsheet data for swimming eukaryotes listed in Appendix 1 and Appendix 2.
DOI: https://doi.org/10.7554/eLife.44907.011
- Transparent reporting form
DOI: https://doi.org/10.7554/eLife.44907.012

Data availability
All data generated or analysed during this study are included in the manuscript.

References
Adam RD. 2001. Biology of giardia lamblia. *Clinical Microbiology Reviews* **14**:447–475. DOI: https://doi.org/10.1128/CMR.14.3.447-475.2001, PMID: 11432808

Allen NS, Allen RD. 1978. Cytoplasmic streaming in green plants. *Annual Review of Biophysics and Bioengineering* **7**:497–526. DOI: https://doi.org/10.1146/annurev.bb.07.060178.002433, PMID: 352247

Bargul JL, Jung J, McOdimba FA, Omogo CO, Adung'a VO, Krüger T, Masiga DK, Engstler M. 2016. Species-Specific adaptations of trypanosome morphology and motility to the mammalian host. *PLOS Pathogens* **12**: e1005448. DOI: https://doi.org/10.1371/journal.ppat.1005448, PMID: 26871910

Barsanti L, Coltelli P, Evangelista V, Frassanito AM, Gualtieri P. 2016. Swimming patterns of the quadriflagellate *Tetraflagellochloris mauritanica* (Chlamydomonadales, chlorophyceae). *Journal of Phycology* **52**:209–218. DOI: https://doi.org/10.1111/jpy.12384, PMID: 27037586

Bauerfeind E, Elbrächter M, Steiner R, Throndsen J. 1986. Application of laser Doppler spectroscopy (LDS) in determining swimming velocities of motile phytoplankton. *Marine Biology* **93**:323–327. DOI: https://doi.org/10.1007/BF00401099

Beaulieu NC, Abu-Dayya AA, McLane PJ. 1995. Estimating the distribution of a sum of independent lognormal random variables. *IEEE Transactions on Communications* **43**:2869. DOI: https://doi.org/10.1109/26.477480

Beveridge OS, Petchey OL, Humphries S. 2010. Mechanisms of temperature-dependent swimming: the importance of physics, physiology and body size in determining protist swimming speed. *Journal of Experimental Biology* **213**:4223–4231. DOI: https://doi.org/10.1242/jeb.045435, PMID: 21113003

Blake JR. 1975. Hydromechanical aspects of ciliary propulsion. In: Wu T, Brokaw C. J, Brennen C (Eds). *Swimming and Flying in Nature*. New York: Plenum. p. 185–209.

Boakes DE, Codling EA, Thorn GJ, Steinke M. 2011. Analysis and modelling of swimming behaviour in *Oxyrrhis marina*. *Journal of Plankton Research* **33**:641–649. DOI: https://doi.org/10.1093/plankt/fbq136

Bray D. 2001. *Cell Movements*. New York: Garland Science.

Brennen C, Winet H. 1977. Fluid mechanics of propulsion by cilia and flagella. *Annual Review of Fluid Mechanics* **9**:339–398. DOI: https://doi.org/10.1146/annurev.fl.09.010177.002011

Buetow DE. 2011. *Euglena*. American Cancer Society. DOI: https://doi.org/10.1002/9780470015902.a0001964.pub3

Bullington WE. 1925. A study of spiral movement in the ciliate infusoria. *Archiv für Protistenkunde* **50**:219–274.

Bullington WE. 1930. A further study of spiraling in the ciliate *Paramecium*, with a note on morphology and taxonomy. *Journal of Experimental Zoology* **56**:423–449. DOI: https://doi.org/10.1002/jez.1400560404

Buskey EJ, Coulter C, Strom S. 1993. Locomotory patterns of microzooplankton: potential effects on food selectivity of larval fish. *Bulletin of Marine Science* **53**:29–43.

Campanati L, Holloschi A, Troster H, Spring H, de Souza W, Monteiro-Leal LH. 2002. Video-microscopy observations of fast dynamic processes in the protozoon *Giardia lamblia*. *Cell Motility and the Cytoskeleton* **51**: 213–224. DOI: https://doi.org/10.1002/cm.10026, PMID: 11977095

Cappuccinelli P. 1980. *The Movement of Eukaryotic Cells*. Netherlands, Dordrecht: Springer. DOI: https://doi.org/10.1007/978-94-009-5812-8_4

Chen J, Lenaghan SC, Zhang M. 2012. Analysis of dynamics and planar motion strategies of a swimming microorganism - *Giardia lamblia*. IEEE International Conference on Robotics and Automation 4204–4209. DOI: https://doi.org/10.1109/ICRA.2012.6225014

Christensen-Dalsgaard KK, Fenchel T. 2004. Complex flagellar motions and swimming patterns of the flagellates *Paraphysomonas vestita* and *Pteridomonas danica*. *Protist* **155**:79–87. DOI: https://doi.org/10.1078/1434461000166, PMID: 15144060

Crawford DW, Lindholm T. 1997. Some observations on vertical distribution and migration of the phototrophic ciliate *Mesodinium rubrum* (= *Myrionecta rubra*) in a stratified brackish inlet. *Aquatic Microbial Ecology* **13**:267–274. DOI: https://doi.org/10.3354/ame013267

Dölger J, Nielsen LT, Kiørboe T, Andersen A. 2017. Swimming and feeding of mixotrophic biflagellates. *Scientific Reports* **7**:39892. DOI: https://doi.org/10.1038/srep39892, PMID: 28054596

Fenchel T. 2001. How dinoflagellates swim. *Protist* **152**:329–338. DOI: https://doi.org/10.1078/1434-4610-00071, PMID: 11822661

Fenchel T, Blackburn N. 1999. Motile chemosensory behaviour of phagotrophic protists: mechanisms for and efficiency in congregating at food patches. *Protist* **150**:325–336. DOI: https://doi.org/10.1016/S1434-4610(99)70033-7, PMID: 10575704

Fenchel T, Jonsson PR. 1988. The functional biology of *Strombidium sulcatum*, a marine oligotrich ciliate (Ciliophora, oligotrichina). *Marine Ecology Progress Series* **48**:1–15. DOI: https://doi.org/10.3354/meps048001

Freedman D, Diaconis P. 1981. On the histogram as a density estimator: L_2 theory. In: *Zeitschrift Fü Wahrscheinlichkeitstheorie Und Verwandte Gebiete*. **57** Springer. p. 453–476.

Funfak A, Fisch C, Abdel Motaal HT, Diener J, Combettes L, Baroud CN, Dupuis-Williams P. 2015. *Paramecium* swimming and ciliary beating patterns: a study on four RNA interference mutations. *Integrative Biology* **7**:90–100. DOI: https://doi.org/10.1039/c4ib00181h, PMID: 25383612

Gadelha C, Wickstead B, Gull K. 2007. Flagellar and ciliary beating in trypanosome motility. *Cell Motility and the Cytoskeleton* **64**:629–643. DOI: https://doi.org/10.1002/cm.20210, PMID: 17549738

Gilbert JJ. 1994. Jumping behavior in the oligotrich ciliates *Strobilidium velox* and *Halteria grandinella*, and its significance as a defense against rotifer predators. *Microbial Ecology* **27**:189–200. DOI: https://doi.org/10.1007/BF00165817, PMID: 24190275

Gittleson SM, Hotchkiss SK, Valencia FG. 1974. Locomotion in the marine dinoflagellate *Amphidinium carterae* (Hulburt). *Transactions of the American Microscopical Society* **93**:101–105. DOI: https://doi.org/10.2307/3225224

Gittleson SM, Jahn TL. 1968. Flagellar activity of *Polytomella agilis*. *Transactions of the American Microscopical Society* **87**:464–471. DOI: https://doi.org/10.2307/3224220

Gittleson SM, Noble RM. 1973. Locomotion in *Polytomella agilis* and *Polytoma uvella*. *Transactions of the American Microscopical Society* **93**:101–105. DOI: https://doi.org/10.2307/3225176

Goldstein RE. 2015. Green algae as model organisms for biological fluid dynamics. *Annual Review of Fluid Mechanics* **47**:343–375. DOI: https://doi.org/10.1146/annurev-fluid-010313-141426, PMID: 26594068

Goldstein RE. 2018. Are theoretical results 'Results'? *eLife* **7**:e40018. DOI: https://doi.org/10.7554/eLife.40018, PMID: 30033910

Guasto JS, Johnson KA, Gollub JP. 2010. Oscillatory flows induced by microorganisms swimming in two dimensions. *Physical Review Letters* **105**:168102. DOI: https://doi.org/10.1103/PhysRevLett.105.168102, PMID: 21231018

Hand WG, Collard PA, Davenport D. 1965. The effects of temperature and salinity change on swimming rate in the dinoflagellates, Gonyaulax and Gyrodinium. *The Biological Bulletin* **128**:90–101. DOI: https://doi.org/10.2307/1539392

Hand WG, Schmidt JA. 1975. Phototactic orientation by the marine dinoflagellate *Gyrodinium dorsum* kofoid. ii. flagellar activity and overall response mechanism. *The Journal of Protozoology* **22**:494–498. DOI: https://doi.org/10.1111/j.1550-7408.1975.tb05217.x

Harris EH, Stern DB, Witman GB. 2009. *The Chlamydomonas Sourcebook*. 2nd edition. London: Academic Press.

Hinchliff CE, Smith SA, Allman JF, Burleigh JG, Chaudhary R, Coghill LM, Crandall KA, Deng J, Drew BT, Gazis R, Gude K, Hibbett DS, Katz LA, Laughinghouse HD, McTavish EJ, Midford PE, Owen CL, Ree RH, Rees JA, Soltis DE, et al. 2015. Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *PNAS* **112**:12764–12769. DOI: https://doi.org/10.1073/pnas.1423041112, PMID: 26385966

Holwill MEJ. 1974. Hydrodynamic aspects of ciliary and flagellar movement. In: Sleigh M. A (Ed). *Cilia and Flagella*. London: Academic Press. p. 143–176.

Holwill MEJ. 1975. The role of body oscillation in the propulsion of microorganisms. In: Wu T, Brokaw C. J, Brennen C (Eds). *Swimming and Flying in Nature*. New York: Plenum. p. 133–141.

Holwill ME, Peters PD. 1974. Dynamics of the hispid flagellum of *Ochromonas danica*. The role of mastigonemes. *The Journal of Cell Biology* **62**:322–328. DOI: https://doi.org/10.1083/jcb.62.2.322, PMID: 4426910

Horstmann U. 1980. Observations on the peculiar diurnal migration of a red tide dinophyceae in tropical shallow waters. *Journal of Phycology* **16**:481–485. DOI: https://doi.org/10.1111/j.1529-8817.1980.tb03064.x

Jahn TL, Bovee EC. 1967. Motile behavior of protozoa. In: Chen T. T (Ed). *Research in Protozoology*. New York: Pergamon. p. 41–200. DOI: https://doi.org/10.1016/B978-0-08-011846-8.50005-0

Jahn TL, Fonseca JR. 1963. Mechanisms of locomotion of flagellates: v: *Trypanosoma lewisi* and *T. cruzi*. *The Journal of Protozoology* **11**.

Jahn TL, Hendrix EM. 1969. Locomotion of the telotrich ciliate *Opisthonecta henneguyi*. *Revista De La Sociedad Mexicana De Historia Natural* **30**:103–131.

Jahn TL, Votta JJ. 1972. Locomotion of protozoa. *Annual Review of Fluid Mechanics* **4**:93–116. DOI: https://doi.org/10.1146/annurev.fl.04.010172.000521

Jakobsen HH, Everett LM, Strom SL. 2006. Hydromechanical signaling between the ciliate *Mesodinium pulex* and motile protist prey. *Aquatic Microbial Ecology* **44**:197–206. DOI: https://doi.org/10.3354/ame044197

Jonsson PP, Tiselius P. 1990. Feeding behaviour, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. *Marine Ecology Progress Series* **60**:35–44. DOI: https://doi.org/10.3354/meps060035

Jung I, Powers TR, Valles JM. 2014. Evidence for two extremes of ciliary motor response in a single swimming microorganism. *Biophysical Journal* **106**:106–113. DOI: https://doi.org/10.1016/j.bpj.2013.11.3703, PMID: 24411242

Kamykowski D, Reed RE, Kirkpatrick GJ. 1992. Comparison of sinking velocity, swimming velocity, rotation and path characteristics among six marine dinoflagellate species. *Marine Biology* **113**:319–328.

Kamykowski D, Zentara S-J. 1977. The diurnal vertical migration of motile phytoplankton through temperature gradients1. *Limnology and Oceanography* **22**:148–151. DOI: https://doi.org/10.4319/lo.1977.22.1.0148

Kirkwood TB, Feder M, Finch CE, Franceschi C, Globerson A, Klingenberg CP, LaMarco K, Omholt S, Westendorp RG. 2005. What accounts for the wide variation in life span of genetically identical organisms reared in a constant environment? *Mechanisms of Ageing and Development* **126**:439–443. DOI: https://doi.org/10.1016/j.mad.2004.09.008, PMID: 15664632

Koch AL. 1966. The logarithm in biology. 1. Mechanisms generating the log-normal distribution exactly. *Journal of Theoretical Biology* **12**:276–290. DOI: https://doi.org/10.1016/0022-5193(66)90119-6, PMID: 5972197

Kullback S, Leibler RA. 1951. On information and sufficiency. *The Annals of Mathematical Statistics* **22**:79–86. DOI: https://doi.org/10.1214/aoms/1177729694

Lauga E, Powers TR. 2009. The hydrodynamics of swimming microorganisms. *Reports on Progress in Physics* **72**:096601. DOI: https://doi.org/10.1088/0034-4885/72/9/096601

Lee JW. 1954. The effect of pH on forward swimming in *Euglena* and *Chilomonas*. *Transactions of the American Microscopical Society* **84**:395–406.

Lenaghan SC, Davis CA, Henson WR, Zhang Z, Zhang M. 2011. High-speed microscopic imaging of flagella motility and swimming in *Giardia lamblia* trophozoites. *PNAS* **108**:E550–E558. DOI: https://doi.org/10.1073/pnas.1106904108, PMID: 21808023

Leonildi A, Erra F, Banchetti R, Ricci N. 1998. The ethograms of *Uronychia transfuga* and *Uronychia setigera* (ciliata, hypotrichida): a comparative approach for new insights into the behaviour of protozoa. *European Journal of Protistology* **34**:426–435. DOI: https://doi.org/10.1016/S0932-4739(98)80011-4

Levandowsky M, Kaneta PJ. 1987. Behaviour in dinoflagellates. In: Taylor F. J. R (Ed). *The Biology of Dinoflagellates (Botanical Monographs)*. **21** Blackwell Scientific. 360–397.

Lewis NI, Xu W, Jericho SK, Kreuzer HJ, Jericho MH, Cembella AD. 2006. Swimming speed of three species of *Alexandrium* (Dinophyceae) as determined by digital in-line holography . *Phycologia* **45**:61–70. DOI: https://doi.org/10.2216/04-59.1

Limpert E, Stahel WA, Abbt M. 2001. Log-normal distributions across the sciences: keys and clues. *BioScience* **51**:341–352. DOI: https://doi.org/10.1641/0006-3568(2001)051[0341:LNDATS]2.0.CO;2

Lowndes AG. 1941. On flagellar movement in unicellular organisms. *Proceedings of the Zoological Society of London* **A111**:111–134. DOI: https://doi.org/10.1111/j.1469-7998.1941.tb08476.x

Lowndes AG. 1944. The swimming of *Monas stigmatica pringsheim* and peranema *Trichophorum (Ehrbg.) Stein.* and *Volvox* sp. Additional experiments on the working of a flagellum. *Proceedings of the Zoological Society of London* **114**:325–338. DOI: https://doi.org/10.1111/j.1096-3642.1944.tb00228.x

Lyons RA, Saridogan E, Djahanbakhch O. 2006. The reproductive significance of human fallopian tube cilia. *Human Reproduction Update* **12**:363–372. DOI: https://doi.org/10.1093/humupd/dml012, PMID: 16565155

Machemer H. 1974. Ciliary activity and metachronism in protozoa. In: Sleigh M. A (Ed). *Cilia and Flagella*. London: Academic Press. p. 199–287.

Marangoni R, Batistini A, Puntoni S, Colombetti G. 1995. Temperature effects on motion parameters and the phototactic reaction of the marine ciliate *Fabrea salina*. *Journal of Photochemistry and Photobiology B: Biology* **30**:123–127. DOI: https://doi.org/10.1016/1011-1344(95)07160-4

Metzner P. 1929. Bewegungsstudien an Peridineen. *Z.Bot* **22**:225–265.

Meunier CL, Schulz K, Boersma M, Malzahn AM. 2013. Impact of swimming behaviour and nutrient limitation on predator–prey interactions in pelagic microbial food webs. *Journal of Experimental Marine Biology and Ecology* **446**:29–35. DOI: https://doi.org/10.1016/j.jembe.2013.04.015

Miyasaka I, Nanba K, Furuya K, Nimura Y. 1998. High-speed video observation of swimming behavior and flagellar motility of *Prorocentrum minimum* (Dinophyceae). *Protoplasma* **204**:38–46. DOI: https://doi.org/10.1007/BF01282292

Moran J, McKean PG, Ginger ML. 2014. Eukaryotic flagella: variations in form, function, and composition during evolution. *BioScience* **64**:1103–1114. DOI: https://doi.org/10.1093/biosci/biu175

Nicastro D, McIntosh JR, Baumeister W. 2005. 3D structure of eukaryotic flagella in a quiescent state revealed by cryo-electron tomography. *PNAS* **102**:15889–15894. DOI: https://doi.org/10.1073/pnas.0508274102, PMID: 16246999

Peters N. 1929. Über Orts- und Geisselbewegung bei marinen Dinoflagellaten. *Archiv für Protistenkunde* **67**:291–321.

Petroff AP, Pasulka AL, Soplop N, Wu XL, Libchaber A. 2015. Biophysical basis for convergent evolution of two veil-forming microbes. *Royal Society Open Science* **2**:150437. DOI: https://doi.org/10.1098/rsos.150437, PMID: 26716000

Purcell EM. 1977. Life at low Reynolds number. *American Journal of Physics* **45**:3–11. DOI: https://doi.org/10.1119/1.10903

Ricci N, Luverà G, Cacciatori M, Banchetti R, Lueken W. 1997. The effects of 2 µm Hg++ on the ethogram of *Euplotes vannus* (Ciliata, Hypotrichida). *European Journal of Protistology* **33**:63–71. DOI: https://doi.org/10.1016/S0932-4739(97)80021-1

Riisgård HU, Larsen PS. 2009. Ciliary-propelling mechanism, effect of temperature and viscosity on swimming speed, and adaptive significance of 'jumping' in the ciliate *Mesodinium rubrum* . *Marine Biology Research* **5**:585–595. DOI: https://doi.org/10.1080/17451000902729704

Roberts AM. 1981. Hydrodynamics of protozoan swimming. In: Levandowski M, Hunter S (Eds). *Biochemistry and Physiology of Protozoa*. Academic Press. p. 5–66.

Rodríguez JA, Lopez MA, Thayer MC, Zhao Y, Oberholzer M, Chang DD, Kisalu NK, Penichet ML, Helguera G, Bruinsma R, Hill KL, Miao J. 2009. Propulsion of african trypanosomes is driven by bihelical waves with alternating chirality separated by kinks. *PNAS* **106**:19322–19327. DOI: https://doi.org/10.1073/pnas.0907001106, PMID: 19880745

Short MB, Solari CA, Ganguly S, Powers TR, Kessler JO, Goldstein RE. 2006. Flows driven by flagella of multicellular organisms enhance long-range molecular transport. *PNAS* **103**:8315–8319. DOI: https://doi.org/10.1073/pnas.0600566103, PMID: 16707579

Sibley TH, Herrgesell PL, Knight AW. 1974. Density dependent vertical migration in the freshwater dinoflagellate *Peridinium penardii* (lemm.) lemm. fo. *Californicum* javorn. *Journal of Phycology* **10**:475–476. DOI: https://doi.org/10.1111/j.1529-8817.1974.tb02743.x

Sleigh MA. 1968. Patterns of ciliary beating. *Symposia of the Society for Experimental Biology* **22**:131–150. PMID: 4972207

Sleigh MA. 1975. *Cilia and Flagella*. London: Academic Press.

Sleigh MA, Aiello E. 1972. The movement of water by cilia. *Archiv für Protistenkunde* **50**:219–274.

Sleigh MA, Blake JR. 1977. Methods of ciliary propulsion and their size limitations. In: Pedley T. J (Ed). *Scale Effects in Animal Locomotion*. Academic Press. p. 243–256.

Sournia A. 1982. Form and function in marine phytoplankton. *Biological Reviews* **57**:347–394. DOI: https://doi.org/10.1111/j.1469-185X.1982.tb00702.x

Szyszkowicz S, Yanikome H. 2009. Limit theorem on the sum of identically distributed equally and positively correlated joint lognormals. *IEEE Transactions on Communications* **57**:3538–3542. DOI: https://doi.org/10.1109/TCOMM.2009.12.070539

Tam D, Hosoi AE. 2011. Optimal kinematics and morphologies for spermatozoa. *Physical Review E* **83**. DOI: https://doi.org/10.1103/PhysRevE.83.045303

Throndsen J. 1973. Motility in some marine nanoplankton flagellates. *Norwegian Journal of Zoology* **21**:193–200.

Togashi T, Motomura T, Ichimura T. 1997. Production of anisogametes and gamete motility dimorphism in *Monostroma angicava*. *Sexual Plant Reproduction* **10**:261–268. DOI: https://doi.org/10.1007/s004970050096

Visser AW, Kiørboe T. 2006. Plankton motility patterns and encounter rates. *Oecologia* **148**:538–546. DOI: https://doi.org/10.1007/s00442-006-0385-4

Votta JJ, Jahn TL, Griffith DL, Fonseca JR. 1971. Nature of the flagellar beat in *Trachelomonas volvocina*, *Rhabdomonas spiralis*, *Menoidium cultellus*, and *Chilomonas paramecium*. *Transactions of the American Microscopical Society* **90**:404–412. DOI: https://doi.org/10.2307/3225455, PMID: 5112382

Wang W, Shor LM, LeBoeuf EJ, Wikswo JP, Taghon GL, Kosson DS. 2008. Protozoan migration in bent microfluidic channels. *Applied and Environmental Microbiology* **74**:1945–1949. DOI: https://doi.org/10.1128/AEM.01044-07, PMID: 18165365

Wheeler B. 1966. Phototactic vertical migration in *Exuviaella baltica*. *Botanica Marina* **9**:15–17. DOI: https://doi.org/10.1515/botm.1966.9.1-2.15

Wichterman R. 1986. *The Biology of Paramecium*. Springer.

Wood CR, Hard R, Hennessey TM. 2007. Targeted gene disruption of dynein heavy chain 7 of *Tetrahymena thermophila* results in altered ciliary waveform and reduced swim speed. *Journal of Cell Science* **120**:3075–3085. DOI: https://doi.org/10.1242/jcs.007369, PMID: 17684060

Appendix 1

DOI: https://doi.org/10.7554/eLife.44907.013

The Appendix contains the data which form the basis of our study. The tables contain data on the sizes and swimming speed of ciliates organisms and flagellated eukaryotes from the existing literature. Data for ciliates were sourced from 26 research articles, while data for the flagellates were extracted from 48 papers. In the cases where two or more sources reported contrasting figures for the swimming speed, the average value is reported in our tables. The data itself is available in ***Source data 1***.

Data for swimming flagellates

Abbreviations: dflg. – dinoflagellata; dph – dinophyceae; chlph. – chlorophyta; ochph. (het.) – ochrophyta (heterokont); srcm. – sarcomastigophora, pyr. – pyramimonadophyceae; prym. – prymnesiophyceae; dict. – dictyochophyceae; crypt. – cryptophyceae; chrys. – chrysophyceae

Species	Phylum	Class	$L[\mu\mathrm{m}]$	$U[\mu\mathrm{m}/s]$	References
Alexandrium minutum	dflg.	dph.	21.7	222.5	(***Lewis et al., 2006***)
Alexandrium ostenfeldii	dflg.	dph.	41.1	110.5	(***Lewis et al., 2006***)
Alexandrium tamarense	dflg.	dph.	26.7	200	(***Lewis et al., 2006***)
Amphidinium britannicum	dflg.	dph.	51.2	68.7	(***Bauerfeind et al., 1986***)
Amphidinium carterae	dflg.	dph.	16	81.55	(***Gittleson et al., 1974***; ***Bauerfeind et al., 1986***)
Amphidinium klebsi	dflg.	dph.	35	73.9	(***Gittleson et al., 1974***)
Apedinella spinifera	ochph. (het.)	dict.	8.25	132.5	(***Throndsen, 1973***)
Bodo designis	euglenozoa	kinetoplastea	5.5	39	(***Visser and Kiørboe, 2006***)
Brachiomonas submarina	chlph.	chlorophyceae	27.5	96	(***Bauerfeind et al., 1986***)
Cachonina (Heterocapsa) niei	dflg.	dph.	21.4	302.8	(***Levandowsky and Kaneta, 1987***; ***Kamykowski and Zentara, 1977***)
Cafeteria roenbergensis	bygira (heterokont)	bicosoecida	2	94.9	(***Fenchel and Blackburn, 1999***)
Ceratium cornutum	dflg.	dph.	122.3	177.75	(***Levandowsky and Kaneta, 1987***; ***Metzner, 1929***)
Ceratium furca	dflg.	dph.	122.5	194	(***Peters, 1929***)
Ceratium fusus	dflg.	dph.	307.5	156.25	(***Peters, 1929***)
Ceratium hirundinella	dflg.	dph.	397.5	236.1	(***Levandowsky and Kaneta, 1987***)
Ceratium horridum	dflg.	dph.	225	20.8	(***Peters, 1929***)
Ceratium lineatus	dflg.	dph.	82.1	36	(***Fenchel, 2001***)
Ceratium longipes	dflg.	dph.	210	166	(***Peters, 1929***)
Ceratium macroceros	dflg.	dph.	50	15.4	(***Peters, 1929***)
Ceratium tripos	dflg.	dph.	152.3	121.7	(***Peters, 1929***; ***Bauerfeind et al., 1986***)

continued on next page

continued

Species	Phylum	Class	$L[\mu\text{m}]$	$U[\mu\text{m/s}]$	References
Chilomonas paramecium	cryptophyta	crypt.	30	111.25	(**Lee, 1954**; **Jahn and Bovee, 1967**; **Gittleson et al., 1974**)
Chlamydomonas reinhardtii	chlph.	chlorophyceae	10	130	(**Gittleson et al., 1974**; **Roberts, 1981**; **Guasto et al., 2010**)
Chlamydomonas moewusii	chlph.	chlorophyceae	12.5	128	(**Gittleson et al., 1974**)
Chlamydomonas sp.	chlph.	chlorophyceae	13	63.2	(**Lowndes, 1944**; **Lowndes, 1941**; **Bauerfeind et al., 1986**)
Crithidia deanei	euglenozoa	kinetoplastea	7.4	45.6	(**Gadelha et al., 2007**)
Crithidia fasciculata	euglenozoa	kinetoplastea	11.1	54.3	(**Gadelha et al., 2007**)
Crithidia (Strigomonas) oncopelti	euglenozoa	kinetoplastea	8 .1	18.5	(**Roberts, 1981**; **Gittleson et al., 1974**)
Crypthecodinium cohnii	dflg.	dph.	n/a	122.8	(**Fenchel, 2001**)
Dinophysis acuta	dflg.	dph.	65	500	(**Peters, 1929**)
Dinophysis ovum	dflg.	dph.	45	160	(**Buskey et al., 1993**)
Dunaliella sp.	chlph.	chlorophyceae	10.8	173.5	(**Gittleson et al., 1974**; **Bauerfeind et al., 1986**)
Euglena gracilis	euglenozoa	euglenida (eugl.)	47.5	111.25	(**Lee, 1954**; **Jahn and Bovee, 1967**; **Gittleson et al., 1974**)
Euglena viridis	euglenozoa	euglenida (eugl.)	58	80	(**Holwill, 1975**; **Roberts, 1981**; **Lowndes, 1941**)
Eutreptiella gymnastica	euglenozoa	euglenida (aphagea)	23.5	237.5	(**Throndsen, 1973**)
Eutreptiella sp. R	euglenozoa	euglenida	50	135	(**Throndsen, 1973**)
Exuviaella baltica (Prorocentrum balticum)	dflg.	dph.	15.5	138.9	(**Wheeler, 1966**)
Giardia lamblia	srcm.	zoomastigophora	11.25	26	(**Lenaghan et al., 2011**; **Campanati et al., 2002**; **Chen et al., 2012**)
Gonyaulax polyedra	dflg.	dph.	39.2	254.05	(**Hand et al., 1965**; **Gittleson et al., 1974**; **Kamykowski et al., 1992**)
Gonyaulax polygramma	dflg.	dph.	46.2	500	(**Levandowsky and Kaneta, 1987**)
Gymnodinium aureolum	dflg.	dph.	n/a	394	(**Meunier et al., 2013**)
Gymnodinium sanguineum (splendens)	dflg.	dph.	47.6	220.5	(**Kamykowski et al., 1992**; **Levandowsky and Kaneta, 1987**)
Gymnodinium simplex	dflg.	dph.	10.6	559	(**Jakobsen et al., 2006**)
Gyrodinium aureolum	dflg.	dph.	30.5	139	(**Bauerfeind et al., 1986**; **Throndsen, 1973**)

continued on next page

continued

Species	Phylum	Class	$L[\mu m]$	$U[\mu m/s]$	References
Gyrodinium dorsum (bi-flagellated)	dflg.	dph.	37.5	324	(**Hand et al., 1965**; **Gittleson et al., 1974**; **Kamykowski et al., 1992**; **Levandowsky and Kaneta, 1987**; **Brennen and Winet, 1977**)
Gyrodinium dorsum (uni-flagellated)	dflg.	dph.	34.5	148.35	(**Hand and Schmidt, 1975**)
Hemidinium nasutum	dflg.	dph.	27.2	105.6	(**Levandowsky and Kaneta, 1987**; **Metzner, 1929**)
Hemiselmis simplex	cryptophyta	crypt.	5.25	325	(**Throndsen, 1973**)
Heterocapsa pygmea	dflg.	dph.	13.5	102.35	(**Bauerfeind et al., 1986**)
Heterocapsa rotundata	dflg.	dph.	12.5	323	(**Jakobsen et al., 2006**)
Heterocapsa triquetra	dflg.	dph.	17	97	(**Visser and Kiørboe, 2006**)
Heteromastix pyriformis	chlph.	nephrophyseae	6	87.5	(**Throndsen, 1973**)
Hymenomonas carterae	haptophyta	prym.	12.5	87	(**Bauerfeind et al., 1986**)
Katodinium rotundatum (Heterocapsa rotundata)	dflg.	dph.	10.8	425	(**Levandowsky and Kaneta, 1987**; **Throndsen, 1973**)
Leishmania major	euglenozoa	kinetoplastea	12.5	36.4	(**Gadelha et al., 2007**)
Menoidium cultellus	euglenozoa	euglenida (eugl.)	45	136.75	(**Holwill, 1975**; **Votta et al., 1971**)
Menoidium incurvum	euglenozoa	euglenida (eugl.)	25	50	(**Lowndes, 1941**; **Gittleson et al., 1974**)
Micromonas pusilla	chlph.	mamiellophyceae	2	58.5	(**Bauerfeind et al., 1986**; **Throndsen, 1973**)
Monas stigmata	ochph. (het.)	chrys.	6	269	(**Gittleson et al., 1974**)
Monostroma angicava	chlph.	ulvophyceae	6.7	170.55	(**Togashi et al., 1997**)
Nephroselmis pyriformis	chlph.	nephrophyseae	4.8	163.5	(**Bauerfeind et al., 1986**)
Oblea rotunda	dflg.	dph.	20	420	(**Buskey et al., 1993**)
Ochromonas danica	ochph. (het.)	chrys.	8.7	77	(**Holwill and Peters, 1974**)
Ochromonas malhamensis	ochph. (het.)	chrys.	3	57.5	(**Holwill, 1974**)
Ochromonas minima	ochph. (het.)	chrys.	5	75	(**Throndsen, 1973**)
Olisthodiscus luteus	ochph. (het.)	raphidophyceae	22.5	90	(**Bauerfeind et al., 1986**; **Throndsen, 1973**)
Oxyrrhis marina	dflg.	oxyrrhea	39.5	300	(**Boakes et al., 2011**; **Fenchel, 2001**)
Paragymnodinium shiwhaense	dflg.	dph.	10.9	571	(**Meunier et al., 2013**)
Paraphysomonas vestita	ochph. (het.)	chrys.	14.7	116.85	(**Christensen-Dalsgaard and Fenchel, 2004**)

continued on next page

continued

Species	Phylum	Class	$L[\mu\mathrm{m}]$	$U[\mu\mathrm{m}/s]$	References
Pavlova lutheri	haptophyta	pavlovophyceae	6.5	126	(**Bauerfeind et al., 1986**)
Peranema trichophorum	euglenozoa	euglenida (heteronematales)	45	20	(**Lowndes, 1941**; **Gittleson et al., 1974**; **Brennen and Winet, 1977**)
Peridinium bipes	dflg.	dph.	42.9	291	(**Fenchel, 2001**)
Peridinium cf. quinquecorne	dflg.	dph.	19	1500	(**Bauerfeind et al., 1986**; **Levandowsky and Kaneta, 1987**; **Horstmann, 1980**)
Peridinium cinctum	dflg.	dph.	47.5	120	(**Bauerfeind et al., 1986**; **Levandowsky and Kaneta, 1987**; **Metzner, 1929**)
Peridinium (Protoperidinium) claudicans	dflg.	dph.	77.5	229	(**Peters, 1929**)
Peridinium (Protoperidinium) crassipes	dflg.	dph.	102	100	(**Peters, 1929**)
Peridinium foliaceum	dflg.	dph.	30.6	185.2	(**Kamykowski et al., 1992**)
Peridinium (Bysmatrum) gregarium	dflg.	dph.	32.5	1291.7	(**Levandowsky and Kaneta, 1987**)
Peridinium (Protoperidinium) ovatum	dflg.	dph.	61	187.5	(**Peters, 1929**)
Peridinium (Peridiniopsis) penardii	dflg.	dph.	28.8	417	(**Sibley et al., 1974**)
Peridinium (Protoperidinium) pentagonum	dflg.	dph.	92.5	266.5	(**Peters, 1929**)
Peridinium (Protoperidinium) subinerme	dflg.	dph.	50	285	(**Peters, 1929**)
Peridinium trochoideum	dflg.	dph.	25	53	(**Levandowsky and Kaneta, 1987**)
Peridinium umbonatum	dflg.	dph.	30	250	(**Levandowsky and Kaneta, 1987**; **Metzner, 1929**)
Phaeocystis pouchetii	haptophyta	prym.	6.3	88	(**Bauerfeind et al., 1986**)
Polytoma uvella	chlph.	chlorophyceae	22.5	100.9	(**Lowndes, 1944**; **Gittleson et al., 1974**; **Lowndes, 1941**)
Polytomella agilis	chlph.	chlorophyceae	12.4	150	(**Gittleson and Jahn, 1968**; **Gittleson and Noble, 1973**; **Gittleson et al., 1974**; **Roberts, 1981**)
Prorocentrum mariae-lebouriae	dflg.	dph.	14.8	141.05	(**Kamykowski et al., 1992**; **Bauerfeind et al., 1986**; **Miyasaka et al., 1998**)
Prorocentrum micans	dflg.	dph.	45	329.1	(**Bauerfeind et al., 1986**; **Levandowsky and Kaneta, 1987**)
Prorocentrum minimum	dflg.	dph.	15.1	107.7	(**Bauerfeind et al., 1986**; **Miyasaka et al., 1998**)
Prorocentrum redfieldii Bursa (P. triestinum)	dflg.	dph.	33.2	333.3	(**Sournia, 1982**)

continued on next page

continued

Species	Phylum	Class	$L[\mu m]$	$U[\mu m/s]$	References
Protoperidinium depressum	dflg.	dph.	132	450	(**Buskey et al., 1993**)
Protoperidinium granii (Ostf.) Balech	dflg.	dph.	57.5	86.1	(**Sournia, 1982**)
Protoperidinium pacificum	dflg.	dph.	54	410	(**Buskey et al., 1993**)
Prymnesium polylepis	haptophyta	prym.	9.1	45	(**Dölger et al., 2017**)
Prymnesium parvum	haptophyta	prym.	7.2	30	(**Dölger et al., 2017**)
Pseudopedinella pyriformis	ochph. (het.)	dict.	6.5	100	(**Throndsen, 1973**)
Pseudoscourfieldia marina	chlph.	pyr.	4.1	42	(**Bauerfeind et al., 1986**)
Pteridomonas danica	ochph. (het.)	dict.	5.5	179.45	(**Christensen-Dalsgaard and Fenchel, 2004**)
Pyramimonas amylifera	chlph.	pyr.	24.5	22.5	(**Bauerfeind et al., 1986**)
Pyramimonas cf. disomata	chlph.	pyr.	9	355	(**Throndsen, 1973**)
Rhabdomonas spiralis	euglenozoa	euglenida (aphagea)	27	120	(**Holwill, 1975**)
Rhodomonas salina	cryptophyta	crypt.	14.5	588.5	(**Jakobsen et al., 2006**; **Meunier et al., 2013**)
Scrippsiella trochoidea	dflg.	dph.	25.3	87.6	(**Kamykowski et al., 1992**; **Bauerfeind et al., 1986**; **Sournia, 1982**)
Spumella sp.	ochph. (het.)	chrys.	10	25	(**Visser and Kiørboe, 2006**)
Teleaulax sp.	cryptophyta	crypt.	13.5	98	(**Meunier et al., 2013**)
Trypanosoma brucei	euglenozoa	kinetoplastea	18.8	20.5	(**Rodríguez et al., 2009**)
Trypanosoma cruzi	euglenozoa	kinetoplastea	20	172	(**Jahn and Fonseca, 1963**; **Brennen and Winet, 1977**)
Trypanosoma vivax	euglenozoa	kinetoplastea	23.5	29.5	(**Bargul et al., 2016**)
Trypanosoma evansi	euglenozoa	kinetoplastea	21.5	16.1	(**Bargul et al., 2016**)
Trypanosoma congolense	euglenozoa	kinetoplastea	18	9.7	(**Bargul et al., 2016**)
Tetraflagellochloris mauritanica	chlph.	chlorophyceae	4	300	(**Barsanti et al., 2016**)

Appendix 2

DOI: https://doi.org/10.7554/eLife.44907.013

Data for swimming ciliates

Abbreviations: imnc. = intramacronucleata; pcdph. = postciliodesmatophora; olig. – oligohymenophorea; spir. – spirotrichea; hettr. – heterotrichea; lit. – litostomatea; eugl. – euglenophyceae

Species	Phylum	Class	$L[\mu m]$	$U[\mu m/s]$	References
Amphileptus gigas	imnc.	lit.	808	608	(**Bullington, 1925**)
Amphorides quadrilineata	imnc.	spir.	138	490	(**Buskey et al., 1993**)
Balanion comatum	imnc.	prostomatea	16	220	(**Visser and Kiørboe, 2006**)
Blepharisma	pcdph.	hettr.	350	600	(**Sleigh and Blake, 1977**; **Roberts, 1981**)
Coleps hirtus	imnc.	prostomatea	94.5	686	(**Bullington, 1925**)
Coleps sp.	imnc.	prostomatea	78	523	(**Bullington, 1925**)
Colpidium striatum	imnc.	olig.	77	570	(**Beveridge et al., 2010**)
Condylostoma patens	pcdph.	hettr.	371	1061	(**Bullington, 1925**; **Machemer, 1974**)
Didinium nasutum	imnc.	lit.	140	1732	(**Bullington, 1925**; **Machemer, 1974**; **Roberts, 1981**; **Sleigh and Blake, 1977**)
Euplotes charon	imnc.	spir.	66	1053	(**Bullington, 1925**)
Euplotes patella	imnc.	spir.	202	1250	(**Bullington, 1925**)
Euplotes vannus	imnc.	spir.	82	446	(**Wang et al., 2008**; **Ricci et al., 1997**)
Eutintinnus cf. pinguis	imnc.	spir.	147	410	(**Buskey et al., 1993**)
Fabrea salina	pcdph.	hettr.	184.1	216	(**Marangoni et al., 1995**)
Favella panamensis	imnc.	spir.	238	600	(**Buskey et al., 1993**)
Favella sp.	imnc.	spir.	150	1080	(**Buskey et al., 1993**)
Frontonia sp.	imnc.	olig.	378.5	1632	(**Bullington, 1925**)
Halteria grandinella	imnc.	spir.	50	533	(**Bullington, 1925**; **Gilbert, 1994**)
Kerona polyporum	imnc.	spir.	107	476.5	(**Bullington, 1925**)
Laboea strobila	imnc.	spir.	100	810	(**Buskey et al., 1993**)
Lacrymaria lagenula	imnc.	lit.	45	909	(**Bullington, 1925**)
Lembadion bullinum	imnc.	olig.	43	415	(**Bullington, 1925**)
Lembus velifer	imnc.	olig.	87	200	(**Bullington, 1925**)
Mesodinium rubrum	imnc.	lit.	38	7350	(**Jonsson and Tiselius, 1990**; **Riisgård and Larsen, 2009**; **Crawford and Lindholm, 1997**)
Metopides contorta	imnc.	armophorea	115	359	(**Bullington, 1925**)
Nassula ambigua	imnc.	nassophorea	143	2004	(**Bullington, 1925**)
Nassula ornata	imnc.	nassophorea	282	750	(**Bullington, 1925**)

continued on next page

continued

Species	Phylum	Class	$L[\mu m]$	$U[\mu m/s]$	References
Opalina ranarum	placidozoa (heterokont)	opalinea	350	50	(**Blake, 1975**; **Sleigh and Blake, 1977**)
Ophryoglena sp.	imnc.	olig.	325	4000	(**Machemer, 1974**)
Opisthonecta henneg	imnc.	olig.	126	1197	(**Machemer, 1974**; **Jahn and Hendrix, 1969**)
Oxytricha bifara	imnc.	spir.	282	1210	(**Bullington, 1925**)
Oxytricha ferruginea	imnc.	spir.	150	400	(**Bullington, 1925**)
Oxytricha platystoma	imnc.	spir.	130	520	(**Bullington, 1925**)
Paramecium aurelia	imnc.	olig.	244	1650	(**Bullington, 1925**; **Bullington, 1930**)
Paramecium bursaria	imnc.	olig.	130	1541.5	(**Bullington, 1925**; **Bullington, 1930**)
Paramecium calkinsii	imnc.	olig.	124	1392	(**Bullington, 1930**; **Bullington, 1925**)
Paramecium caudatum	imnc.	olig.	225.5	2489.35	(**Bullington, 1930**; **Jung et al., 2014**)
Paramecium marinum	imnc.	olig.	115	930	(**Bullington, 1925**)
Paramecium multimicronucleatum	imnc.	olig.	251	3169.5	(**Bullington, 1930**)
Paramecium polycaryum	imnc.	olig.	91	1500	(**Bullington, 1930**)
Paramecium spp.	imnc.	olig.	200	975	(**Jahn and Bovee, 1967**; **Sleigh and Blake, 1977**; **Roberts, 1981**)
Paramecium tetraurelia	imnc.	olig.	124	784	(**Funfak et al., 2015**)
Paramecium woodruffi	imnc.	olig.	160	2013.5	(**Bullington, 1930**)
Porpostoma notatum	imnc.	olig.	107.7	1842.2	(**Fenchel and Blackburn, 1999**)
Prorodon teres	imnc.	prostomatea	175	1066	(**Bullington, 1925**)
Spathidium spathula	imnc.	lit.	204.5	526	(**Bullington, 1925**)
Spirostomum ambiguum	pcdph.	hettr.	1045	810	(**Bullington, 1925**)
Spirostomum sp.	pcdph.	hettr.	1000	1000	(**Sleigh and Blake, 1977**)
Spirostomum teres	pcdph.	hettr.	450	640	(**Bullington, 1925**)
Stenosemella steinii	imnc.	spir.	83	190	(**Buskey et al., 1993**)
Stentor caeruleus	pcdph.	hettr.	528.5	1500	(**Bullington, 1925**)
Stentor polymorphus	pcdph.	hettr.	208	887	(**Bullington, 1925**; **Sleigh and Aiello, 1972**; **Sleigh, 1968**)
Strobilidium spiralis	imnc.	spir.	60	330	(**Buskey et al., 1993**)
Strobilidium velox	imnc.	spir.	43	150	(**Gilbert, 1994**)
Strombidinopsis acuminatum	imnc.	spir.	80	390	(**Buskey et al., 1993**)
Strombidium claparedi	imnc.	spir.	69.5	3740	(**Bullington, 1925**)
Strombidium conicum	imnc.	spir.	75	570	(**Buskey et al., 1993**)
Strombidium sp.	imnc.	spir.	33	360	(**Buskey et al., 1993**)

continued on next page

continued

Species	Phylum	Class	$L[\mu\text{m}]$	$U[\mu\text{m}/s]$	References
Strombidium sulcatum	imnc.	spir.	32.5	995	(***Fenchel and Jonsson, 1988***; ***Fenchel and Blackburn, 1999*** ***Fenchel and Blackburn, 1999***)
Stylonichia sp.	imnc.	spir.	167	737.5	(***Bullington, 1925***; ***Machemer, 1974***)
Tetrahymena pyriformis	imnc.	olig.	72.8	475.6	(***Sleigh and Blake, 1977***; ***Roberts, 1981***; ***Brennen and Winet, 1977***)
Tetrahymena thermophila	imnc.	olig.	46.7	204.5	(***Wood et al., 2007***)
Tillina magna	imnc.	colpodea	162.5	2000	(***Bullington, 1925***)
Tintinnopsis kofoidi	imnc.	spir.	100	400	(***Buskey et al., 1993***)
Tintinnopsis minuta	imnc.	spir.	40	60	(***Buskey et al., 1993***)
Tintinnopsis tubulosa	imnc.	spir.	95	160	(***Buskey et al., 1993***)
Tintinnopsis vasculum	imnc.	spir.	82	250	(***Buskey et al., 1993***)
Trachelocerca olor	pcdph.	karyorelictea	267.5	900	(***Bullington, 1925***)
Trachelocerca tenuicollis	pcdph.	karyorelictea	432	1111	(***Bullington, 1925***)
Uroleptus piscis	imnc.	spir.	203	487	(***Bullington, 1925***)
Uroleptus rattulus	imnc.	spir.	400	385	(***Bullington, 1925***)
Urocentrum turbo	imnc.	olig.	90	700	(***Bullington, 1925***)
Uronema filificum	imnc.	olig.	25.7	1372.7	(***Fenchel and Blackburn, 1999***)
Uronema marinum	imnc.	olig.	56.9	1010	(***Fenchel and Blackburn, 1999***)
Uronema sp.	imnc.	olig.	25	1175	(***Sleigh and Blake, 1977***; ***Roberts, 1981***)
Uronychia transfuga	imnc.	spir.	118	6406	(***Leonildi et al., 1998***)
Uronychia setigera	imnc.	spir.	64	7347	(***Leonildi et al., 1998***)
Uronemella spp.	imnc.	olig.	28	250	(***Petroff et al., 2015***)