

# Teofil Nakov - CV

## Aquatic Evolutionary Biologist

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## Education

Year	Degree
2014	Ph.D. Plant Biology, Section of Integrative Biology, The University of Texas at Austin, Austin, Texas
2005	B.S., Biochemistry, Institute of Biology, Ss Cyril and Methodius University, Skopje, Macedonia

## Employment

Period	Position
2020-	Bioinformatics Consultant   R/Python Developer   Genomics • Transcriptomics • Data Science
2014-2020	Postdoctoral Research Fellow, University of Arkansas, Fayetteville
2013-2014	Continuing Doctoral Fellow, University of Texas at Austin
2007-2013	Graduate Teaching/Research Assistant, University of Texas at Austin
2004-2007	Teaching/Research Assistant, Institute of Biology, Ss Cyril and Methodius University, Skopje, Macedonia

## Publications

\* equal contribution, § undergraduate coauthor  
Brief summary for selected papers is in bold below the reference

### 2025

- Alverson AJ, Roberts WR, Ruck EC, **Nakov T**, Ashworth MP, Brylka K, Downey KM, Kociolek JP, Parks M, Pinseel E. Phylogenomics reveals the slow-burning fuse of diatom evolution. *Proceedings of the National Academy of Sciences* 122(22): e2500153122, 2025.
- Pinseel E, Ruck EC, **Nakov T**, Jonsson PR, Kourtchenko O, Kremp A, Pinder MIM, Roberts WR, Sjöqvist C, Töpel M. Genome-Wide Adaptation to a Complex Environmental Gradient in a Keystone Phytoplankton Species. *Molecular Ecology*, e17817, 2025.

### 2023

- Pinseel E, Ruck EC, **Nakov T**, Jonsson PR, Kourtchenko O, Kremp A, et. al Local adaptation of a marine diatom is governed by genome-wide changes in diverse metabolic processes. *bioRxiv*, 2023.09. 22.559080

### 2022

- Pinseel E, **Nakov T**, Van den Berge K, Downey KM, Judy KJ, Kourtchenko O, Kremp A, Ruck EC, Sjöqvist C, Töpel M et al. Strain-specific transcriptional responses overshadow salinity effects in a marine diatom sampled along the Baltic Sea salinity cline. *The ISME Journal* 16: 1776-1787

## 2021

- Alverson AJ, Chafin TK, Jones KA, Manoylov KM, Johnson H, Julius ML, **Nakov T**, Ruck EC, Therior EC, et al. Microbial biogeography through the lens of exotic species: the recent introduction and spread of the freshwater diatom *Discostella asterocostata* in the United States. *Biological Invasions*, 23: 2191-2204
- Hamlin JAP, **Nakov T**, Williams-Newkirk A. `tinseLR` –an R Shiny Application for Annotating Phylogenetic Trees. *Microbiology Resource Announcements* 10, e00227-21

## 2020

- **Nakov T**, Judy KJ, Downey KM, Ruck EC and Alverson AJ. Transcriptional response of osmolyte synthetic pathways and membrane transporters in a euryhaline diatom during long-term acclimation to a salinity gradient. *Journal of Phycology* 56: 1712-1728
- Ozersky T, **Nakov T**, Hampton S, Rodenhouse NL, Shchapov K, Woo KH, ... and Timofeev MA. Hot and sick: Impacts of warming and oomycete parasite infection on endemic dominant zooplankton of Lake Baikal. *Limnology and Oceanography* 65: 2772-2786

## 2019

- **Nakov T**, Beaulieu JM, and Alverson, AJ. Diatoms diversify and turn over faster in freshwater than marine environments. *Evolution*, 73: 2497-2511.

**Many clades that span the marine-freshwater divide are disproportionately more diverse in the younger and short-lived freshwater environments than they are in the marine realm, which covers most of the biosphere. How these patterns have been shaped is an open question. Using a novel set of diversification models that control for the effects of interacting factors and unobserved variables, we show that freshwater diatoms both speciate and go extinct faster than marine clades. We also found that colonizations of alternate environments have had different probabilities across the tree leading to communities (e.g., marine vs. freshwater plankton) with vastly different phylogenetic and functional diversities.**

- Onyshchenko A, Ruck EC, **Nakov T**, and Alverson AJ. A single loss of photosynthesis in diatoms. *American Journal of Botany*, 106: 560– 572.

## 2018

- **Nakov T**, Beaulieu JM and Alverson AJ. Insights into global planktonic diatom diversity: The importance of comparisons between phylogenetically equivalent units that account for time. *International Society of Microbial Ecology Journal (ISME-J)*, 2018 Jul 16:1

**Metabarcoding offers unprecedented insights into microbial diversity, however, most analyses assume that taxonomic ranks are biologically meaningful and that identically ranked groups are comparable. In this study, using a Tara Oceans diatom metabarcode dataset, we illustrate the limits of this approach and the advantages of using a phylogenetic framework to make inferences about microbial ecology, diversity, and biogeography.**

- Guillori WX, Onyschenko A, Ruck EC, Parks M, **Nakov T**, Wickett N and Alverson AJ. Recurrent loss, horizontal transfer, and the obscure origins of mitochondrial introns in diatoms (Bacillariophyta). *Genome Biology and Evolution*, 10: 1504-1515
- Parks M, **Nakov T**, Ruck EC, Wickett NJ and Alverson AJ. Phylogenomics reveals an extensive history of genome duplication in diatoms (Bacillariophyta). *American Journal of Botany*, 105: 330-347

**The first phylogenomic study to assess polyploidy in diatoms. Our results, based on an array of methods for detecting whole genome duplications (WGD), suggest that WGD has played a major role in the evolution of diatom genomes. We outline challenges in reconstructing paleopolyploid events in diatoms that, together with these results, offer a framework for understanding the impact of genome duplication in a group that harbors substantial genomic diversity.**

- **Nakov T**, Beaulieu JM and Alverson AJ. Accelerated diversification is related to life history and locomotion in a hyperdiverse lineage of microbial eukaryotes (Diatoms, Bacillariophyta). *New Phytologist*, 219: 462–473

**We constructed and time-calibrated the largest-to-date diatom phylogeny and used it to estimate, for the first time, diversification rates across lineages and through time. We found that a clade with vegetative cells capable of active movement diversified much faster than other diatoms. We proposed that the evolution of motility facilitated outcrossing and improved utilization of habitat complexity, ultimately leading to enhanced opportunity for adaptive divergence and accelerated diversification.**

- Mejdandžić M, Bosak S, **Nakov T**, Ruck EC, Orlić S, Gligora Udovič M, Peharec Štefanić P, Špoljarić I, Mršić G and Z Ljubešić. Phylogenetic and taxonomic diversity of the canal-raphe diatom genus *Entomoneis* (Bacillariophyta) in marine plankton: six new species from the Adriatic Sea. *Journal of Phycology*, 54: 275–298

## 2017

- **Nakov T**, Boyko JD, Alverson AJ and Beaulieu JM. Models with unequal transition rates favor marine origins for cyanobacteria and photosynthetic eukaryotes. *Proceedings of the National Academy of Sciences USA*, 114: 13055–13056.
- Ruck EC, Linard SR, **Nakov T**, Theriot EC and Alverson AJ. Hoarding and horizontal transfer led to an expanded gene and intron repertoire in the plastid genome of the diatom *Toxarium undulatum* (Bacillariophyta). *Current Genetics* 63: 499–507.
- Chust G, Vogt M, Benedetti F, **Nakov T**, Villéger S, Aubert A, Vallina SM, Righetti D, Not F, Biard T, Bittner L, ..., Ayata S-D. Mare incognitum: A glimpse into future plankton diversity and ecology research. *Frontiers in Marine Science* 4 (122).

## 2016

- Ruck EC and **Nakov T**. Nomenclatural transfers associated with the phylogenetic reclassification of the Surirellales and Rhopalodiales. *Notulae algarum* 1–4.
- Ruck EC, **Nakov T**, Alverson AJ and Theriot EC. Phylogeny, ecology, morphological evolution, and reclassification of the diatom orders Surirellales and Rhopalodiales. *Molecular Phylogenetics and Evolution* 103: 155–171.

## 2015

- **Nakov T**, Guillory WX, Julius ML, Theriot EC and Alverson AJ. Towards a phylogenetic classification of species belonging to the diatom genus *Cyclotella* (Bacillariophyceae): Transfer of species formerly placed in *Puncticulata*, *Handmannia*, *Pliocaenicus* and *Cyclotella* to the genus *Lindavia*. *Phytotaxa* 217: 249–264.
- Theriot EC, Ashworth MP, **Nakov T**, Ruck EC and Jansen RK. Dissecting signal and noise in diatom chloroplast protein encoding genes with phylogenetic information profiling. *Molecular Phylogenetics and Evolution* 89: 28–36.

## 2014

- **Nakov T**, Ashworth MP and Theriot EC. Comparative analysis of the interaction between habitat and growth form in diatoms. *International Society of Microbial Ecology Journal (ISME-J)* 9: 246–255.
- **Nakov T**, Ruck EC, Galachyants Y, Spaulding SA and Theriot EC. Molecular phylogeny of the Cymbellales (Bacillariophyceae) with a comparison of models for accommodating rate-variation across sites. *Phycologia* 53: 359–373.
- Ruck EC, **Nakov T**, Jansen RK, Theriot EC and Alverson AJ. Serial gene losses and foreign DNA underlie size and sequence variation in the plastid genomes of diatoms. *Genome Biology and Evolution* 6: 644–654.
- Jovanovska E, Buczkó K, **Nakov T** and Levkov Z. *Diploneis transylvanica* (Bacillariophyceae), a new diatom species from a Neogene fossil deposit in Romania. *Nova Hedwigia* 98: 3–4.

## 2013

- **Nakov T**, Theriot EC and Alverson AJ. Using phylogeny to model the evolution of cell size in marine and freshwater diatoms. *Limnology and Oceanography* 59: 79–86.

**Virtually any ecological and physiological feature of phytoplankton is related to cell size, so the evolution of cell size is central to phytoplankton biology. Here, for the first time, we**

**investigated phytoplankton cell size evolution in a phylogenetic framework revealing an adaptive divergence between marine and freshwater lineages related to differences in nutrient regimes and sinking rates between habitats with different salinities.**

- Ashworth MP, **Nakov T** and Theriot EC. Revisiting Ross and Sims (1971): Towards a molecular phylogeny of the Biddulphiaceae and Eupodiscaceae (Bacillariophyceae). *Journal of Phycology* 6: 1207–1222.
- Jovanovska EŠ, Buczkó K, Ognjanova-Rumenova N, **Nakov T** and Levkov Z. Identity and typification of *Diploneis ostracodarum*, *Diploneis budayana*, and *Diploneis praeclara* (Bacillariophyta). *Phytotaxa* 137: 15–26.
- Jovanovska EŠ, **Nakov T** and Levkov Z. Observations of the genus *Diploneis* (Ehrenberg) Cleve from Lake Ohrid, Macedonia. *Diatom Research* 28: 237–262.

## 2010

- Theriot EC, Ashworth MP, Ruck EC, **Nakov T** and Jansen RK. A preliminary multigene phylogeny of the diatoms (Bacillariophyta): challenges for future research. *Plant Ecology and Evolution* 143: 278–296.

## 2009

- Pavlov AŠ, **Nakov T**, Levkov Z, Furey P, Lowe R and Ector L. *Luticola grupcei* (Bacillariophyceae)—a new freshwater diatom from Mountain Baba (Macedonia) and Great Smoky Mountains National Park (USA): comparison with the type material of *L. goeppertiana* (Bleisch) D.G. Mann. *Nova Hedwigia* 89: 147–164.

## 2008

- Levkov Z and **Nakov T**. *Rhoicosphenia tenuis*, a new diatom species from Lake Ohrid. *Diatom Research* 23: 377–388.
- Levkov Z, Edlund MB and **Nakov T**. Identity and typification of *Navicula hasta* (Bacillariophyceae). *Phycological Research* 56: 46–57.

## 2007

- Levkov Z, Blanco S, Krstic S, **Nakov T** and Ector L. Ecology of benthic diatoms from Lake Macro Prespa (Macedonia). *Algological Studies* 124: 71–83.

## 2006

- Edlund MB, Brant LA, Levkov Z, and **Nakov T**. An emended description of *Decussata* (Patrick) Lange-Bertalot and Metzeltin that includes protoplast organization and detailed valve and cingulum ultrastructure. *Diatom Research* 21: 269–280.

## 2005

- Levkov Z, Krstic S, **Nakov T** and Melovski L. Diatom assemblages on Shara and Nidze mountains, Macedonia. *Nova Hedwigia* 81: 501–538.

## Books, Book Chapters, and Conference Papers

## 2011

- Theriot EC, Ruck E, Ashworth MP, **Nakov T** and Jansen RK. Status of the Pursuit of the Diatom Phylogeny: Are Traditional Views and New Molecular Paradigms Really That Different? In: *The Diatom World. Cellular Origin, Life in Extreme Habitats and Astrobiology*. Ed: J. Seckbach and P. Kociolek, pp. 119–142. Springer, Netherlands.

## 2007

- Levkov Z, Krstic S, Metzeltin D and **Nakov T**. Diatoms of Lakes Prespa and Ohrid. About 500 taxa from ancient lake system. *Iconographia Diatomologica* 16, ARG Gantner Verlag, Germany. pp. 1–613.

**Ancient lakes—basins of tectonic origin up to several million years old—are hotspots of biodiversity for many organisms. In this book, that I helped prepare as an undergraduate student, we characterized the diatom diversity in ancient Lake Ohrid (Macedonia) describing dozens of species as new to science and identifying several groups with properties of “species flocks”. This book has since become one of the primary references for diatoms from ancient lakes.**

## 2006

- Edlund MB, Levkov Z, Soninkhishig N, Krstic S and **Nakov T**. Diatom species flocks in large ancient lakes: the *Navicula reinhardtii* complex from Lakes Hövsgöl (Mongolia) and Prespa (Macedonia). In: *Proceedings of the 18th International Diatom Symposium*. Ed: Witkowski, A, pp. 61–74.
- Krstic S, Levkov Z and **Nakov T**. Diatom diversity in Republic of Macedonia-our present knowledge. In: *Proceedings of the 18th International Diatom Symposium*. Ed: Witkowski, A, pp. 209–220.
- Levkov Z, Krstic S and **Nakov T**. A new *Gyrosigma* species from lakes Prespa and Ohrid. In: *Advances in phycological studies: Festschrift in honor of Dobrina Temniskova-Topalova*. Ed: Ognyanova-Rumenova, N. and Manoylov, K. pp. 155–165.

## Conference Presentations

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### 2018

- **Nakov T**, Beaulieu JM and Alverson AJ. Freshwater diatom lineages diversify faster than marine in both planktonic and benthic habitats. Joint meeting of the Phycological Society of America and International Society of Protistologists; Vancouver, BC, Canada.
- **Nakov T**, Beaulieu JM and Alverson AJ. Diatom diversification through the lens of large sequence, fossil, trait, and diversity databases: Examining the roles of life history strategies and environmental gradients. International Diatom Symposium; Berlin, Germany.

### 2016

- **Nakov T**, Ruck EC, and Alverson AJ. Diatom evolution across the plankton-benthos and marine-freshwater divides. Joint conference of the American Society of Naturalists, the Society for the Study of Evolution and the Society of Systematic Biologists; Austin, TX, USA.
- **Nakov T**, Ruck EC, and Alverson AJ. Opportunities and constraints in diatom evolution. PlankDiv: EuroMarine foresight workshop on the “Impact of climate change on the distribution of plankton functional and phylogenetic diversity”; Villefranche-sur-mer, France.

### 2014

- **Nakov T**, Ashworth MP, and Theriot EC. Comparative analysis of the interaction between habitat and growth form in diatoms. Joint Aquatic Sciences Meeting (PSA, ASLO, SFS, SWS); Portland, OR, USA.

### 2013

- **Nakov T**, Ruck EC, Galachyants Y, Likhoshway E, Spaulding SA and Theriot EC. Phylogenetic Signal, Noise and the Phylogeny of Cymbellales (Bacillariophyceae). Phycological Society of America Meeting; Orlando, FL, USA.

### 2012

- Ruck EC, **Nakov T**, and Theriot EC. Phylogenetic insight into the origins of endemic diatom diversity: The Robustoid Surirellaceae from Lake Ohrid. Speciation in Ancient Lakes 6, Bogor, Indonesia.

### 2011

- **Nakov T**, Alverson AJ, and Theriot EC. Using a phylogenetic framework to study the evolution of cell size in the diatom order Thalassiosirales. International Diatom Symposium, St.Paul, MN, USA.

### 2010

- **Nakov T** and Theriot EC. The phylogenetic position of *Didymosphenia geminata* and evaluating molecular markers for distinguishing populations. ASLO/NABS meeting, Santa Fe, NM, USA.

### 2009

- **Nakov T** and Theriot EC. Preliminary molecular phylogeny of the Cymbellales. Phycological Society of America; North American Diatom Symposium, Iowa Lakeside Lab, IA, USA.

### 2008

- **Nakov T**, Spaulding SA and Theriot EC. A preliminary phylogeny of the cymbelloid diatoms using molecular data with emphasis on the genera *Didymosphenia* M. Schmidt and *Navicymbula* Krammer. Phycological

Society of America Meeting, New Orleans, LA, USA.

## Teaching

Period	Role
2016, 2018	Guest lecturer, Programming for Biologists, University of Arkansas, Fayetteville
2016	Guest lecturer, Evolutionary Biology, University of Arkansas, Fayetteville
2008-2013	Teaching assistant, Genetics, The University of Texas at Austin
2011	Teaching assistant, and Natural History of Protists, The University of Texas at Austin
2005	Teaching assistant, Ecology and Systematics of Diatoms, Iowa Lake Side Laboratory
2004-2007	Teaching assistant, Limnology and Phycology, Institute of Biology, Ss Cyril and Methodius University, Skopje, Macedonia

## Mentoring (*undergraduate students*)

### University of Arkansas, Fayetteville

Wilson Guillory (2014-2017); Yufei Li (2014-2017); Kameila Nedd (2014-2016); Jake Harris (2015-2017); Annie Dickens (2015-2016); Rachel Ungar (2016-2018)

### The University of Texas at Austin

Ellice Tran (2008-2009); Patricia Park (2008-2009); Sloane Kaminski-Ditzel (2012); Ryan Hadfield (2013); Hector Gutierrez (2013)

### Institute of Biology, Skopje

Aleksandar Pavlov (2004-2007); Elena Jovanovska (2004-2007)

## Awards

Year	Award
2013-2014	Continuing Doctoral Fellow, The University of Texas at Austin (\$21,200)
2013, 2009	Ruth Hoshaw Award, Phycological Society of America
2012, 2011	Student Research Award, Plant Biology Graduate Program, The University of Texas at Austin
2005	John C. Kingston Diatom Fellowship, Friends of Iowa Lakeside Laboratory

## Professional Affiliations and Service

### Associate Editor

- Diatom Research, 2018-2020
- Annals of Botany Plants, 2018-2019

## Peer Reviewer

Diatom Research, Phycologia, Phytotaxa, PLoS One, Marine and Freshwater Research, Ecological applications, Diatoms of the United States, Ecological Indicators, Protist, Science of the Total Environment

## Member

- Association for the Sciences of Limnology and Oceanography
- Society for the Study of Evolution
- Phycological Society of America
- International Society for Diatom Research

## Certifications

Year	Certification
2024	AWS Certified Cloud Practitioner, AWS Amazon Web Services Training and Certification
2025	Post Graduate Program in Artificial Intelligence and Machine Learning, Texas McCombs School of Business

## Web Applications & Software Packages

### Developed in R + Shiny

**VisualRoutines:** <https://visualroutine.org> (<https://visualroutine.org>)

A web application to create and manage visual routines to support executive functioning.

**r2lambda:** <https://github.com/teofiln/r2lambda> (<https://github.com/teofiln/r2lambda>)

An R package to get started and become productive with AWS lambda from R. It provides a simple interface to deploy R functions as AWS Lambda functions, and to invoke them from R or other AWS services.

### Phynotate

**GitHub:** <https://github.com/teofiln/phynotate> (<https://github.com/teofiln/phynotate>)  
Shiny modules for interactive annotation of phylogenies

### PRioritize\_Dx

**App:** [https://idinsight.shinyapps.io/PRioritize\\_Dx/](https://idinsight.shinyapps.io/PRioritize_Dx/) ([https://idinsight.shinyapps.io/PRioritize\\_Dx/](https://idinsight.shinyapps.io/PRioritize_Dx/))

A Shiny application in a Golem R package for optimized use of Covid-19 testing resources in low and middle income countries

### NewscatcherR

**GitHub:** <https://github.com/discindo/newscatcherR> (<https://github.com/discindo/newscatcherR>)  
Programmatically collect normalized news from (almost) any website using R

### HiSSE -web

**App:** <https://diatom.shinyapps.io/hisse-web/> (<https://diatom.shinyapps.io/hisse-web/>)

Website for summarising and plotting results from the R package `HiSSE`

### gghisse

**GitHub:** <https://github.com/teofiln/utilhisse> (<https://github.com/teofiln/utilhisse>)

R package for summarising and plotting results from the R package `HiSSE`

### Skeletonema local adaptation

**App:** <https://diatom.shinyapps.io/Skeletonema-marinoi-salinity-reaction-norms/> (<https://diatom.shinyapps.io/Skeletonema-marinoi-salinity-reaction-norms/>)

marinoid-salinity-reaction-norms/)

Interactive visualization and management of large scale common garden experiments with microalgae.

### **Baltic Sea gradient data**

**App:** <https://diatom.shinyapps.io/baltic-sea-gradient-maps/> (<https://diatom.shinyapps.io/baltic-sea-gradient-maps/>)

Interactive visualization of physico-chemical data for the Baltic Sea salinity gradient.

### **Diatom transcriptomes**

**App:** <https://diatom.shinyapps.io/TranscribedDiatoms/> (<https://diatom.shinyapps.io/TranscribedDiatoms/>)

Interactive visualization of diatom transcriptome data. [in development]

### **Interactive diatom phylogeny**

**App:** <https://diatom.shinyapps.io/InteractiveDiatomPhylogeny/> (<https://diatom.shinyapps.io/InteractiveDiatomPhylogeny/>)

An interactive browser for the diatom phylogeny.

## **References**

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### **Andrew J. Alverson**

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### **Edward C. Theriot**

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