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PEET: Lower Worms Of The Meiofauna - Models for Early Metazoan Evolution

Seth Tyler

Principal Investigator; University of Maine, Orono, styler@maine.edu

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Final Report for Period: 09/2007 - 02/2008**Submitted on:** 06/12/2008**Principal Investigator:** Tyler, Seth .**Award ID:** 0118804**Organization:** University of Maine**Submitted By:****Title:**

PEET: Lower Worms Of The Meiofauna - Models for Early Metazoan Evolution

Project Participants**Senior Personnel****Name:** Tyler, Seth**Worked for more than 160 Hours:** Yes**Contribution to Project:****Name:** Sterrer, Wolfgang**Worked for more than 160 Hours:** Yes**Contribution to Project:**

Senior collaborator on subcontract through the Bermuda Zoological Society. Dr. Sterrer trains students particularly on techniques of collection and identification and is handling the database on Gnathostomulida. He is otherwise supported as Senior Curator with the Bermuda Aquarium, Museum, and Zoo.

Post-doc**Name:** Hooge, Matthew**Worked for more than 160 Hours:** Yes**Contribution to Project:**

Postdoctoral fellow. Matthew Hooge started in this project as a graduate student and assumed his appointment as post-doctoral fellow in June, 2002. He plays the major role in revision of the taxonomy of the Acoela and helps train graduate students in techniques of confocal microscopy, reconstruction from serial sections, and molecular phylogenetics.

Name: Todt, Christiane**Worked for more than 160 Hours:** Yes**Contribution to Project:**

Dr. Todt is investigating comparative morphology of the pharynges of acoels by electron microscopy. These acoels appear to be among the more primitive groups, and thus the pharynx may be a plesiomorphic character for the Acoela as a whole. Understanding the evolution of pharynges through will help us decipher relationships of major groups. Dr. Todt is working in our laboratory on an 18-month Schrödinger Stipendium from FWF Austria.

Graduate Student**Name:** Ogunlana, Maxina**Worked for more than 160 Hours:** Yes**Contribution to Project:**

Research Assistantship and tuition funded by the grant. Ms. Ogunlana is starting her work on the project June, 2003.

Name: Petrov, Anatoly**Worked for more than 160 Hours:** Yes**Contribution to Project:**

Research assistantship and tuition funded by the grant. Mr. Petrov is researching ultrastructure of Acoela and preparing a monograph on the Otocelididae.

Name: Hrouda, Martina**Worked for more than 160 Hours:** No

Contribution to Project:

is conducting EST (Expressed Sequence Tag) genome project on animals we are providing (*Convolvula pulchra*), specifically for genes expressed during embryonic development; she worked for 2 weeks in our lab spring 2004 and is continuing work on this study at the University of Innsbruck (her home institution). Project provided some travel support and laboratory supplies.

Name: Zhang, Rui

Worked for more than 160 Hours: Yes

Contribution to Project:

Rui Zhang is a graduate student in the Department of Spatial Engineering, UMaine. We hired him to develop the programs that draw maps of distribution from our georeference data.

Name: Barneah, Orit

Worked for more than 160 Hours: No

Contribution to Project:

Orit is a student at Tel Aviv University, Israel, and collaborates with us in the study of coral-associated acoels. She provided specimens of a new species we described and collaborates with our team in publications on the physiology and ecology of these species.

Name: Tekle, Yonas

Worked for more than 160 Hours: No

Contribution to Project:

Jonas is a graduate student in the Department of Systematic Zoology, Evolutionary Biology Centre, Uppsala University, Sweden. We collaborate with him in a project on the molecular phylogeny of Proporidae and Haploposthiidae with. We sent him material on 22 described and undescribed species in these acoel families and collaborate with him on analysis of COI and 18S rDNA sequences of these and other acoels.

Name: Achatz, Johannes

Worked for more than 160 Hours: Yes

Contribution to Project:

Graduate work jointly at UMaine and the University of Innsbruck, Austria. Funded October, 2005, through August, 2007, on research assistantship from this grant

Name: Wahlberg, Andreas

Worked for more than 160 Hours: No

Contribution to Project:

Collaborated in molecular systematics of Hofstenia, an acoel from the Caribbean. Currently a student at Uppsala University, Sweden

Undergraduate Student

Name: Lacey, Elizabeth

Worked for more than 160 Hours: No

Contribution to Project:

Senior capstone project participant. Elizabeth Lacey conducted research on the biogeography of acoels in the family Convolvutidae, gathering data on distribution from the literature and entering that into databases that could be linked to GIS software to show distribution of species. This is the first of the biogeographic data that will be employed on our Web site. (Display of such georeference material in maps is still under development, expected to be online by the end of August, 2002.)

Name: Crowley, Ian

Worked for more than 160 Hours: No

Contribution to Project:

senior capstone research project describing a new species of Acoela

Technician, Programmer

Name: Maloy, Aaron

Worked for more than 160 Hours: No

Contribution to Project:

Aaron is a technician in the Dept. Biochemistry, Microbiology, and Molecular Biology, UMaine. He collaborates with us on molecular phylogenetics of the Acoela; he isolates DNA from specimens we provide and prepares sequences of them.

Other Participant

Name: Stephen, Schilling

Worked for more than 160 Hours: No

Contribution to Project:

Volunteer assistant with database. Steve Schilling is assisting us with entry of data from card files into our SQL database, and he occasionally works with observations of living animals. He has worked before with the staff at the Smithsonian Institution in database development and volunteered to help our own development with that experience.

Name: Gschwentner, Robert

Worked for more than 160 Hours: No

Contribution to Project:

Collaborator on scientific papers dealing with the Acoela. We are working with Dr. Gschwentner on papers dealing with musculature of acoels as revealed in confocal microscopy. Most recently, we completed a manuscript on musculature of *Convolutriloba longifissura* for which Dr. Gschwentner had images that we helped him interpret.

Name: Rieger, Reinhard

Worked for more than 160 Hours: No

Contribution to Project:

Collaborator on scientific papers and consultant on systematics of Catenulida. Dr. Rieger participated in manuscripts on confocal microscopy we are publishing and helps us in dealing with one of the three groups of lower worms we are preparing a monograph on: the Catenulida, for which he described the first known marine representatives.

Name: Sorensen, Martin

Worked for more than 160 Hours: No

Contribution to Project:

collaborator in research on Gnathostomulida, including fluorescence microscopy of musculature and scanning electron microscopy of jaws, and phylogenetics of the group.

Name: Smith, Julian

Worked for more than 160 Hours: No

Contribution to Project:

collaborator in collecting and describing new species of Acoela

Name: Hochberg, Richard

Worked for more than 160 Hours: No

Contribution to Project:

Dr. Hochberg collaborates in collecting Acoela in Australia (while he served as Postdoctoral Fellow at the Queensland Museum, Brisbane, NSW) and Florida (while a Postdoctoral Fellow at the Harbor Branch Institute, Ft. Pierce), as well as other sites he visits.

Name: Ladurner, Peter

Worked for more than 160 Hours: No

Contribution to Project:

is conducting EST (Expressed Sequence Tag) genome project on animals we are providing (*Isodiametra pulchra*), specifically for genes expressed by stem cells; he worked for 3 weeks in our lab spring 2004 and is continuing work on this study at the University of Innsbruck (his home institution), at the laboratory of Dr. K. Agata in Japan (summer 2004), and with a research team at Konstanz Univ., Germany (2004-2005). Our project provides some travel support and laboratory supplies.

Name: Litvaitis, Marianne

Worked for more than 160 Hours: No

Contribution to Project:

Dr. Litvaitis is on the faculty at the Univ. of New Hampshire. We collaborate with her on molecular phylogenetics of flatworms, and she advises us on procedures and techniques of analysis. We provide material for her own projects on polyclad flatworms, assist her in identifying flatworms, and train her students in confocal microscopy and techniques for handling meiofauna.

Name: Owen, Michael

Worked for more than 160 Hours: No

Contribution to Project:

Dr. Owen is Associate Dean at University of Western, Ontario. He spent 6 weeks working in our lab learning techniques of handling meiofauna while on sabattical leave.

Name: Jondelius, Ulf

Worked for more than 160 Hours: No

Contribution to Project:

Collaborates on molecular systematics of Acoelomorpha. We share specimens and DNA samples and collaborate on publications

Name: Hartenstein, Volker

Worked for more than 160 Hours: No

Contribution to Project:

Collaborates on culturing of platyhelminths and trained graduate student Johannes Achatz in his laboratory at University of California, Los Angeles, on techniques of immunocytochemistry of neurotransmitters and other components of nervous systems and on three-dimensional reconstruction techniques used for nervous systems.

Research Experience for Undergraduates

Name: Apse, Kathryn

Worked for more than 160 Hours: Yes

Contribution to Project:

artist rendering images for taxonomic key, glossary, and K-12 outreach material

Years of schooling completed: Junior

Home Institution: Same as Research Site

Home Institution if Other:

Home Institution Highest Degree Granted(in fields supported by NSF): Bachelor's Degree

Fiscal year(s) REU Participant supported: 2003

REU Funding: REU supplement

Name: Eppinger, Neil

Worked for more than 160 Hours: No

Contribution to Project:

conducted senior capstone research project with the project, describing a new species of acoel from California. Project provided tuition support.

Organizational Partners

Bermuda Zoological Society

Dr. Sterrer's participation in this project is through a subcontract awarded through the Bermuda Zoological Society, which funds the institution at which Dr. Sterrer is Senior Curator, the Bermuda Aquarium, Museum, and Zoo.

Winthrop University

Julian P.S. Smith, III, at Winthrop U. provided facilities (microscopes, lab space) during a collecting trip to the N. Carolina coast and collaborated in descriptions of species collected then.

University of Innsbruck

Reinhard Rieger and Robert Gschwentner collaborate with us in fluorescence microscopy of musculature in turbellarians and in research on the nature of stem cells in these animals. Dr. Gschwentner visited our lab in June, 2003, and worked with us for one week in collecting animals and doing immunocytochemistry. Peter Ladurner, Martina Hrouda, and Johannes Aschatz collaborate with us in an EST project on a species from Maine; they visited our lab in spring 2004 for 3 weeks and summer 2005 for 2 weeks.

Queensland Museum

Rick Hochberg provided facilities (microscopes, cameras, lab space) at Queensland Museum during a collecting trip to Australia.

University of Copenhagen

Martin V. Sorensen of the Zoological Museum at U. Copenhagen uses our confocal microscopy facilities and collects with us for our collaboration on Gnathostomulida and other Gnathifera. We plan a visit, as well, to his institution.

University of Aarhus

Dr. Peter Funch of this University collaborates with us on confocal microscopy of Gnathifera. He has used our microscope in publications we are publishing jointly.

University of Sao Paulo

The University of Sao Paulo provided travel funds and facilities at its marine laboratory in exchange for help with its project 'Benthic Marine Biodiversity of the State of Sao Paulo, Brazil' (Carlos Rocha, PI, Foundation of Support to the research of the State of Sao Paulo [FASESP]). Postdoc Matthew Hooge visited the facility and contributed an identification manual on Turbellaria for this project. Material he collected there also is key to our PEET project, and material on groups other than Acoela has been sent to other collaborating laboratories. Hooge is describing new acoel species from Brazil and extending distribution records of known species.

Tel Aviv University

Dr. Yehuda Benayahu and his student Orit Barneah have sent us acoels infesting corals in the Red Sea for identification, and we used this material for one of our student's (Maxina Ogunlana) research. It forms the basis of our examination of acoels living in this relatively unusual habitat. We also met with these researchers when we both did field work in Tanzania, looking for coral-associated acoels. We have published 3 papers with these workers.

University of California-San Diego Scripps Inst of Oceanography

Dr. Nick Holland at Scripps provided laboratory facilities to Dr. Sterrer and Dr. Hooge for a field trip to the San Diego area where they collected gnathostomulids and acoels.

University of California-Los Angeles

Dr. Volker Hartenstein and his staff and students trained graduate student Johannes Achatz in techniques of immunocytochemistry and involved him, as well, in their three-dimensional-reconstruction project on the brains of acoelomorph turbellarians.

Swedish Museum of Natural History

We collaborate with the laboratory of Ulf Jondelius at this Museum, providing animals for his and his students' research in molecular systematics and obtaining assistance in sequencing DNA from animals we study. Through funding from the European Union in the form of a

SYNTHESYS grant, graduate student Johannes Achatz was able to visit and work in this laboratory in early 2008, preparing material for the final chapter of his monograph on the Convolutidae.

Other Collaborators or Contacts

Dr. Irv Kornfield of the University of Maine's School of Marine Science provides assistance and facilities for molecular systematics for our students. We provide supplies and facilities for research we have in common on systematics.

Dr. Gonzalo Giribet of Harvard University received from us collections and collaborated on molecular phylogeny of Gnathostomulida.

Dr. Martin Sørensen of the University of Copenhagen collaborated on the the ultrastructure of gnathostomulid mouthparts.

Dr. Monika Müller of the University of Osnabrück collaborated on the musculature and nervous system of Gnathostomulida.

Dr. Katrine Worsaae of the University of Copenhagen collaborated on the description of Annelida-Polychaeta.

Activities and Findings

Research and Education Activities:

We are investigating the phylogenetic relationships of three groups of the phylum Platyhelminthes--the Acoela, Nemertodermatida, and Catenulida--and of the whole of the small phylum Gnathostomulida. The major thrust of the project is the training of students in the techniques for dealing with these invertebrate groups, including techniques for finding and examining specimens, processing them for electron and fluorescence microscopy, describing species, reconstructing phylogenies, deciphering biogeographical relationships, and applying bioinformatics to the study of these groups.

To obtain specimens for this research, we collect at a variety of sites world-wide, trying to correct the bias that has dominated systematics of these groups, namely that they are known largely from the relatively narrow geographic range at which former taxonomists happened to be concentrated, mostly in Europe. Our home territory in the Atlantic coast of North America provides rich collecting of little-known and undescribed species, and we are expanding the geographic base with collecting as well in the Pacific Northwest, the Caribbean, South America, Australia, SE Asia, Japan and the Indian Ocean coast of Africa.

Two long-distance collecting trips were conducted by the postdoctoral associate in 2002, one to the mid-Atlantic US coast (North Carolina) and one to Queensland, Australia. Other collecting in the Gulf of Maine included deep-water dredging and involved collaboration by visiting scientists from the University of Innsbruck and the University of Vienna.

During 2003-2004, we collected in Brazil, the Galapagos, Baja California, Belize, Honduras, Panama, and British Columbia. Postdoc Hooge led the trips to the Caribbean (accompanied there by PI S. Tyler) and Brazil. Co-PI Sterrer collected in the Galapagos, and

both he and S. Tyler collected in British Columbia.

Major collecting trips in 2004-2005 were to Bermuda, British Columbia, New Brunswick (Canada), and Tanzania. Post-doc Matthew Hooge conducted all but the British Columbia trip and took student Maxina Ogunlana on the trip to Tanzania and new postdoc Christiane Todt on the trip to Bermuda. S. Tyler took student Anatoly Petrov on the trip to British Columbia and accompanied post-doc Hooge on trips to the Caribbean sites. Co-PI Sterrer participated on the trips to Belize, Baja California, and British Columbia with other team members, as well as taking one trip on his own to Denmark to work with collaborator Martin Sørensen at the zoological museum in Copenhagen.

In 2006-2007, we expanded collecting to sites in South Africa and islands in the Indian Ocean (November-December, 2006), to Hong Kong, Borneo, and Japan (16 July - 20 August 2007) and to Sweden (September 2007) with trips by Sterrer, especially for Gnathostomulida. Graduate student Johannes Achatz also collected Gnathostomulida in Bermuda for a comparative study of spermatogenesis being done in collaboration with the University of Innsbruck, and he collected convolutids and other acoels for his thesis work in Thailand and sites in the Andaman Sea (March-April, 2007).

We study this material with electron and confocal microscopy for comparative morphology (of musculature, spermatozoa, parts of the female reproductive system, and pharynx) and sequencing of 18S and COI genes for molecular phylogenetics. Student J. Achatz began applying immunocytochemical techniques in 2007 with markers for nervous-system components to better characterize the central nervous system of acoel turbellarians, which display considerable diversity in the degree of development of brain and major nerve cords, presumably as a reflection of their basal condition among bilaterians. Characters here should be especially relevant to his revision of the Convolutidae. We continue to expand our database of molecular characters (of 18S rDNA as well as COI and now 28S rDNA) with new sequence analyses of representatives of the lower families of acoels and of species representative of the revised families we have established to test the predictability of our phylogenetic trees. Molecular systematics of the Gnathostomulida continues to be carried out through collaboration with the laboratories of Gonzalo Giribet (Harvard) and M. Sørensen (Denmark).

Some molecular work is being done through collaboration with other laboratories, including U. Innsbruck (Drs. P. Ladurner and R. Rieger in an EST project on *Isodiametra pulchra*), The Natural History Museum, London (Dr. D.T.J. Littlewood, a genome project), Ashworth Laboratories Edinburgh (Drs. A Aboobaker and Blaxter, a genome project), and the Department of Systematic Zoology, Uppsala (Yonas I. Tekle), to all of whom we are supplying specimens and exchanging sequence data. Student J. Achatz will be finishing his research on the Convolutidae in 2008 with molecular-sequencing projects in the laboratories at the Swedish Museum of Natural History (with Ulf Jondelius).

In 2005, we were asked by the National Human Genome Research

Institute to provide genomic DNA of a representative acoel, which we are doing, for them to assess whether it would be appropriate to sequence as a model potentially representing the most primitive extant bilaterian taxon. We continue with this collaboration in 2007 and 2008 with procurement of more high-molecular-weight DNA extracts for sequencing by this lab. This work is being balanced with the EST sequencing project in collaboration with the University of Innsbruck, so its timing has been delayed somewhat as we wait to see how the EST data is to be applied.

Our database on turbellarian Platyhelminthes grows in content and content-display mechanisms. Several systematists, including some we had not even known were working on turbellarians, have told us the Web site displaying this database is useful to them. In 2002-2003 we completed the transcription of an index-card collection of the late Dr. Louise Bush into the section on Acoelomorpha and Catenulida, and in 2004-2005 we added the entirety of her index-card database by scanning all cards not transcribed and providing appropriate links to all turbellarian groups, even those outside the groups that are the focus of our project. Data in the Acoelomorpha was also converted to a form for export to the ITIS database and submitted to them in the fall of 2002. The taxonomic database has been expanded to include georeference data and appropriate references were entered in 2003-2004 with support of a small contract from OBIS (Ocean Biogeographic Information System) to a volunteer who assists with all data entry (Steve Schilling); the bulk of this data comes from our surveying the literature (using a large, inherited reprint collection with papers dating back to the 1700's), but we also record yet-unpublished data from our own collections. That biogeographic data is linked through DiGIR to OBIS and other georeference providers (work in progress 2008). A similar database on Gnathostomulida was converted to a Web-accessible form June, 2003, and is being edited and added to with information like that for the turbellarian database. As of early 2008, that database is up-to-date with new collection records and recent revisions in the taxonomy of Gnathostomulida that co-PI Sterrer has accomplished.

We conducted a workshop on taxonomic databases at the Tenth International Symposium on Flatworm Biology, Innsbruck, Austria, 2006, and found agreement among all taxonomists present that our database would be the central repository. It was gratifying to see how widely used our database is. Expanding the database, including better facilitation of contributions by colleagues worldwide through password-protected editing access, will be the major focus of our research over the next year after expiration of the grant.

We devoted considerable effort to programming for database management and Web display in 2004-2005. One project was in graphics, delivering maps of species distribution from data entered this year. The programs were initially developed by graduate student Anatoly Petrov in C+ and adapted for Web display and linkage with our taxonomic database by graduate student Rui Zhang in Java using Tomcat to interface with our server. A second major programming effort was in developing resources for registering character matrices and for using those matrices to produce interactive keys. Mapping is now (as of changes made in 2006-2007) conducted through an API from Google Maps, which provides the considerable advantage that it allows better interactive use of the maps.

Educational activities in this project center on the training of five graduate students (three PhD-level and two Masters-level), and two postdoctoral fellows. One of those graduate-student positions was funded in the first year of the project as well as was part of a postdoctoral fellowship. Two graduate positions and the postdoctoral position were funded in the second through fourth years, and a fifth Ph-D level student added in fall 2005. The MS students graduated in 2005, and remaining funds were used to support the fifth graduate student during a no-cost extension. The salary of the second postdoc was funded through the Austrian Schroedinger Stipendium while we supported her research and travel costs with NSF grant funds. We also supported a sixth graduate student (MS-level) from the UMaine Department of Spatial Information in 2004-2005 by hiring him to program for spatial data (that is, mapping) and providing him training on the biology and ecology of the organisms. By collaborating with graduate students in other laboratories (namely at Uppsala, Sweden, and Tel Aviv, Israel), supporting their research in part, we have advanced understanding of several families of acoels (Haploposthiidae, Actinoposthiidae, Childiidae, Convolutidae) and have contributed to these students' training in systematics; we have published several papers with those students as co-authors.

Presentation of results from this project were made at three meetings in 2001-2002: the Eleventh International Meiobenthologists Conference in Boston, the annual meeting of the Society for Integrative and Comparative Biology and the American Microscopical Society in Anaheim, and the meeting of PEET IV in Berkeley. Presentations were also made in forums at the University Maine, including one graduate symposium and a campus-wide seminar. We also participated in K-12 training by providing specimens for display and training of participants in a K-12 training grant.

In 2002, a poster presentation at the Fifth Annual Graduate Exposition (U. Maine) by the graduate trainee who started in the fall semester, Anatoly Petrov, won the award for First Place in Biological Sciences.

Presentations of our findings at scientific meetings in 2003-2004 included three papers at the annual meeting of the Society for Integrative and Comparative Biology, New Orleans, LA. Postdoc Hooge also present invited seminars to the public at the University of Sao Paulo and at the Centro de Biologia Marinha Universidade de Sao Paulo (Brazil) in 2004. We also participated in a workshop on Invertebrates of Bocas del Toro, Panama, demonstrating acoels and meiofauna to other participants in the workshop (organized by Rachel S. Collins, STRI, Panama), and in a workshop on marine meiofauna at Tjörn÷ Marine Biological Station, Sweden (organized by Ulf Jondelius, University of Göteborg).

In 2004-2005, presentations at scientific meetings in both oral and poster formats included two at the Twelfth International Meiofauna Conference, Ravenna, Italy; two at the annual meeting of the Society for Integrative and Comparative Biology, San Diego, CA; and three at PEET V (Partnerships for Enhancing Expertise in Taxonomy), University of Illinois, Urbana-Champaign. We also delivered invited seminars to more general audiences at the University of the Virgin

Islands and the Bamfield Marine Science Centre, British Columbia. Postdoc Hooze contributed to the Gulf of Mexico project (GoMex) with a paper surveying turbellarians of the Gulf and consulted with Donna Turgeon of NOAA on an effort to produce a complete list of known platyhelminths for North America, Hawaii, and the Gulf of Mexico.

Presentations in 2005-2006 included several by the two postdocs at the annual meeting of the Society for Systematic Biology, a prize-winning poster by graduate student J. Achatz at the Graduate Research Exposition, Univ. Maine, and four by postdoc C. Todt, graduate student J. Achatz, and PI S. Tyler at the Tenth International Symposium on the Biology of Flatworms at Innsbruck, Austria. Presentations for more general audiences included an invited seminar at the University of Maine by the PI.

In 2007-2008, the last graduate student on the project, Johannes Achatz, has been wrapping up his studies of the Convolutidae in preparation for a monograph on the group. In February-March 2008, Achatz worked at the Swedish Museum of Natural History (Naturhistoriska riksmuseet, Stockholm) through an EU-funded SYNTHESYS grant and collaborated there with Ulf Jondelius's laboratory, sequencing three genes in convolutids. These data and their analyses will form a major section in his doctoral dissertation which he expects to complete by the end of 2008.

The publication of a major paper on the position of the Acoela and Platyhelminthes in the tree of life that we have been working on in collaboration with colleagues at the University of Innsbruck and the University of Konstanz has been delayed by the death of the senior author, R. Rieger. In late 2007 and early 2008, new data on stem cells in platyhelminths and outgroup phyla procured by one of his students has been added and we expect to submit the revised manuscript in mid-2008.

Educational activities to benefit the general public are delivered also through our Web site, where we publish accounts of the groups of animals we study in language understandable by the general public and provide interactive keys.

Findings:

Our first major accomplishment in the first year of the project was the establishment of a database on taxonomy of turbellarian Platyhelminthes. In the following year we established a similar database on the Gnathostomulida, and both databases have been updated and expanded through all succeeding years of the project. They are available for public use on the World Wide Web (<http://turbellaria.umaine.edu/> and <http://devbio.umesci.maine.edu/styler/gnathostomulida/>). These databases detail the taxonomic hierarchy of the groups and provide data on synonymies, type species, diagnoses, taxonomic as well as other research literature, and georeferences (geographical distribution).

We also completed the first study of molecular systematics of the Acoela, in the first year, using sequence data in the 18S rDNA gene. Quite importantly, the gene tree that emerged from this analysis fits well with morphological characters that we discerned in feasibility studies we did in preparation for this project. Specifically, it is concordant with trees based on characters in patterns of body-wall musculature discerned through confocal

microscopy. It is also concordant with ultrastructural features of spermatozoa, characters which until now have appeared to fall almost randomly across the current taxonomic system for the Acoela because of the polyphyletic nature of four of the families of acoels. The remarkable association between our gene tree and the morphological characters of body-wall musculature and sperm suggest that we have made a significant breakthrough in identifying characters that can be used to reorganize the systematics of the Acoela into natural groupings.

In 2002-2003, our molecular phylogenetic hypothesis was further tested by graduate student Anatoly Petrov through a broadly comparative study of ultrastructure of spermatozoa in representatives of the major monophyletic groups detected there. His work corroborates the monophyly of a group of large-bodied convolutid acoels as well as the polyphyly of the family Otocelidae. This work is a springboard for Petrov's monograph on otocelidids (Otocelidae plus related species now assigned to other families).

Collecting in 2002-2003 in North Carolina and Australia provided many new species of Acoela, including some that must be assigned to two new families and three new genera. This new material also further corroborates our hypotheses of relationships among members of the Convolutidae, and a monograph on this large family has been completed (see below).

From collecting trips in 2003-2004 to Brazil, Baja California, and the Caribbean, we added considerable new material, including new species and new distribution records. Among the descriptions of these we have published (2004-2005) are several attributable to student trainees. Undergraduate Neil Eppinger published a description of a new species from Baja California, and MS student Maxina Ogulana established identity of coral-associated acoels (sent to us from the Red Sea and Palau); this work was part of her thesis and was published.

Material for a comparative ultrastructural study of spermatogenesis in the Gnathostomulida and Catenuilida, specifically looking for homologues among the strange types of sperm that characterize the higher taxonomic groupings of gnathostomulids was also collected in 2003-2004.

Field work on Gnathostomulida in 2004-2005 revealed a new genus from the North American West Coast (California, British Columbia; published in 2006) as well as new distribution records for another dozen species. And an analysis of material collected earlier in New Zealand, also published in 2006, revealed 10 species of Gnathostomulida, three new.

Collaboration with Harvard University resulted in the first phylogeny of Gnathostomulida based on molecular loci (18S rRNA, 28S rRNA, histone H3 and cytochrome c oxidase subunit I) and morphology. The results clearly support monophyly as well as the basal split into Filospermoidea and Bursovaginoidea but did not support a sister-group relationship between Gnathostomulidae and Austrognathiidae, placing the latter basally within the Bursovaginoidea instead. A more comprehensive analysis using the same four loci, and exploring the relationships of Micrognathozoa with Gnathostomulida and Rotifera, failed to provide support for a gnathiferan clade.

We published a monograph on the largest family of the Acoela, the Convolutidae, in 2005. New characters discerned through confocal and electron microscopy have corroborated molecular-sequence data showing that this family is polyphyletic and provided a means to separate off a new family, which we call the Isodiametridae. We provide means for distinguishing members of these two families through techniques conventionally used in acoel taxonomy rather than forcing future systematists to have to rely solely on the tools of confocal and electron microscopy.

New and fuller molecular sequences of the 18s rDNA gene are helping us resolve especially family groupings of Acoela. Combined with COI sequence data, which yet proves problematic, we hope to use such data for a final resolution of relationships at both the family and generic levels. Particularly significant findings emerging from this sequence data are such things as the close relationship between Hofstenia and Paratomella, thus establishing the intriguing Hofstenia at the base of the Acoela. The molecular work also shows that all Hofstenia species described in the Caribbean are synonymous, and we expect to establish synonymy also with the first-described species from Japan. Also significant in the molecular phylogenies are positions of some needle-bearing otocelidids (Philocelis, etc.) with members of the Actinosthiidae which we established, and of other otocelidids now clearly seen to be closely related to another family we established, the Isodiametridae, and others yet to Haploposthiidae. Establishing the relationships of the core species remaining in the Otocelididae remains the next major problem being addressed by graduate student Petrov.

A new comparative study of the ultrastructure of the bursal nozzle, a distinctive sclerotic structure in the female reproductive system having a curiously disjunct distribution among acoels, was conducted by graduate student Anatoly Petrov in 2004-2005 (published 2006). He found a consistent ground pattern to the structure of these nozzles in all acoels, unlike that in similar sclerotic structures in other animal groups, showing that all such structures are probably homologous in the Acoela. New characters he discovered by electron microscopy may prove useful in further work he is doing on systematics of the Otocelididae and Mecynostomidae.

Graduate student Johannes Achatz has continued our revision of the Convolutidae through studies of species from the Red Sea, Tanzania, Belize, Panama, and Thailand. Besides describing new species from these areas, he is preparing a monograph on the family as it was revised from our 2005 study which separated from it those species now ranked in the family Isodiametridae. Achatz's findings on arrangement of musculature and sclerotized parts of the copulatory organs as revealed through confocal microscopy, on structure of the central nervous system as revealed through immunocytochemistry, and on molecular sequences, show the family to be a well-defined taxon with sister-group relationship to the Sagittiferidae, two new members of which he has also described.

Through collaborative work with the University of Innsbruck and University of Konstanz, we have produced the first phylogeny of the lower Bilateria based on EST genome data, namely 40 genes compared

across representatives of the Platyhelminthes, Acoelomorpha, Cnidaria, Deuterostomia, and other Protostomia. Statistical analysis of this phylogeny shows the Acoelomorpha and Platyhelminthes together at the base of the Protostomia when Bayesian methods are applied but at the base of the Bilateria when Maximum Likelihood is applied. We are preparing a manuscript on this phylogeny using morphological characters to demonstrate the likelihood of either possibility.

As hoped, our study of the Acoelomorpha has provided data for a better placement of the phylum and its relationship to the remaining platyhelminths and to the major phyla of invertebrates. In our final analysis, the more detailed, information-rich molecular-sequence data from the EST genome study has provided corroboration of the basal position of the phylum among the Bilateria and of its distance from the major group of platyhelminths, the Rhabditophora. At the same time, morphological data on stem cells of platyhelminths, as revealed by our collaborators at Innsbruck, show that the acoelomorphan and rhabditophoran platyhelminths share a major apomorphy that cannot be denied. The special stem cells, known as neoblasts, are unique in platyhelminths in that they reside only in the mesoderm and are competent to replace any and all cell types of the body, including germ cells. In contrast all other bilaterians have stem cells in the epidermis as well as in the mesoderm, and these appear to be more specialized to tissue types and independent of the germ line. The Platyhelminthes, then, can be seen as a paraphyletic phylum, all its members occupying a basal position in the Bilateria but its descendants include other phyla. Acoelomorpha is basalmost, as the molecular-sequence data show, and the other two platyhelminth groups, the Catenulida and Rhabditophora, are descendants of it. Other phyla branch from an ancestor that would be classified as a rhabditophoran, evidenced particularly through characters of embryonic development.

Training and Development:

Students working on this project are being trained in microscopical techniques (electron microscopy, laser confocal scanning microscopy, microtechniques), and techniques of comparative morphology, cladistics, biogeography, molecular systematics, bioinformatics, and museum curation. They also participate in collecting trips at a variety of locations around the world. The research team will apply the data gathered to revise the classification of these worms, to publish new classification systems that better reflect evolutionary relationships. Training in preparation of monographs comes as the students prepare specific monographs as part of their theses.

Because the funding period for this grant started at the beginning of an academic year, there was a necessary lag in recruitment of new graduate students into the project. We trained one graduate student over this first year (Matthew Hooge), and two others started in the second year, namely Anatoly Petrov, who started in the fall of 2002, and Mrs. Maxina Ogunlana, a native of Tanzania, who started in summer 2003. Mrs. Ogunlana completed a Masters degree in 2005 with a thesis on coral-associated acoels. We have sufficient funds remaining to start the training of a fourth graduate student on a

no-cost extension, beginning in fall 2005. We expect that student to be Johnny Aschatz who has expressed an interest in preparing a monograph on the comparatively large *Convoluta* and relatives.

The one graduate student funded in the first year, Matthew Hooge, completed his doctorate and assumed the position of postdoctoral fellow in the grant in June, 2002. A second postdoc, Christiane Todt, whose salary is funded by the Austrian Schroedinger Stipendium, started a project on comparative ultrastructure of pharynges in Acoelomorpha in fall, 2004, with all research and travel support provided by this NSF grant.

We are recruiting undergraduate students for the project as well and had one or two such students in each year of the grant (during the academic year) as well as a student in an REU-funded position in the summer of 2003.

We expose undergraduates to animals of the meiofauna also through our teaching of courses in invertebrate biology. Lab sections in these courses (BIO 353, BIO 454) provide training in extracting and observing meiofauna. We also train students in techniques of microscopy, both electron and fluorescence microscopy, in other courses centering on microscopical techniques (among them BIO 441, BIO 542). Our laboratories in the electron microscopy and fluorescence microscopy course involve meiofaunal specimens, so the students learn how to handle such animals and to appreciate their phylogenetic position.

Four undergraduate students---Elizabeth Lacey, Ian Crowley, Kathryn Apse, and Neil Eppinger---worked with the project to produce senior capstone theses. Lacey used our databases to assemble information on the distribution of species in a major family of the Acoela, the Convolutidae, and plotted this data using GIS software. This study formed the nucleus of a more comprehensive database of geographical distribution for all of the species in the groups we study. Ian Crowley and Neil Eppinger learned histological and reconstruction techniques to describe new species of Acoela. Eppinger's work will be published in 2004 as part of a paper describing species from California. Kat Apse prepared artwork for our Web site, including a generalized scheme of acoel anatomy to better orient the public on what acoels are, and images used in a key to the Acoelomorpha; with this work, Kat not only learned how to apply computer graphics to scientific illustration but also how taxonomic characters are identified, illustrated, and applied in taxonomic descriptions and keys.

One of our graduate students, Anatoly Petrov, has been trained through courses in the Spatial Information Department in handling of databases and GIS data. He plans to apply this to our research on biogeography of Gnathostomulida and Acoela.

Graduate student Johannes Achatz completed training in confocal microscopy, histological techniques, computer graphics, and database management under tutelage especially of postdoc M. Hooge. He also received training in culturing of acoels from R. Anderson of Bigelow Laboratories and S. Tyler, and he developed his own special techniques for this culturing. In 2007 he was

trained in immunocytochemistry of nervous-system elements through a visit to Volker Hartenstein's laboratory at UCLA, and trained in techniques for handling Gnathostomulida for comparative work on their spermatozoa through a visit to the Bermuda lab of co-PI W. Sterrer. He completed further training in molecular systematics at Ulf Jondelius's laboratory at the Swedish Museum of Natural History in 2008.

Outreach Activities:

The major link we have with the public is through our Web site detailing the taxonomy of turbellarians and gnathostomulids. An REU student prepared artwork during summer 2003 and spring 2004 in support of general-language and graphic pages suitable for K-12 students to learn about lower worms of the meiofauna.

Our Web site also serves as a central repository of taxonomic information on turbellarian platyhelminths. Other systematists consult it to see our compilation of the current taxonomic system, to contribute data on species they have newly described or revised, and to participate in clarification of a searchable, illustrated glossary we are constructing as a hyperlinked page. We conducted a workshop on the database for the 10th International Symposium on Flatworms, 2006. We have also participated in other invertebrate workshops, notably at the Marine Laboratory in Bocas del Toro, Panama, and the Tjörn÷ Marine Biological Laboratory in Sweden.

(As described under previous sections of this report, we also participate in demonstrations of animals and microscopic techniques to K-12 students and other members of the general public. Part of this training comes under the auspices of an NSF Training Grant for GK-12 whose fellows use our material.)

Journal Publications

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Web/Internet Site

URL(s):

<http://devbio.umesci.maine.edu/styler/globalworming/>

Description:

This site is the Web page introducing our PEET project, with hyperlinks of information comprehensible to the general public as well as links to the more technical products of our research. The most important hyperlink is to a database on the taxonomy of turbellarian platyhelminths in general, including the clades that are the subject of this grant, the Acoelomorpha and Catenulida, and the Rhabdocoela (which comprises the rest of the platyhelminths). The bulk of our effort in developing this site, however, is devoted to the Acoelomorpha and Catenulida. A link to taxonomy of the Gnathostomulida, the other major group we research, is also set here.

Other Specific Products

Product Type:

Data or databases

Product Description:

Database on the taxonomy of the Gnathostomulida, including taxonomic hierarchy, diagnoses, references, and geographical distribution.

Sharing Information:

Accessible via the World Wide Web at URL <http://devbio.umesci.maine.edu/styler/gnathostomulida/>

It is also being developed in the format used by the Biodiversity Center of the Expert Center for Taxonomic Identification (planned for distribution on CD).

Product Type:

Teaching aids

Product Description:

Tyler, S. (2004) Platyhelminthes--the nature of a controversial phylum. [A WWW article in answer to many misrepresentations of the

phylum in textbooks and non-specialist articles as well as to inquiries I have had concerning the significance of recent papers from molecular systematists that separate the Acoela from the Platyhelminthes as a phylum on its own.]

Sharing Information:

The article is posted on the Web at URL <http://devbio.umesci.maine.edu/styler/globalworming/platyhelm.htm> and is hyperlinked from our home pages and from our database on taxonomy of the Platyhelminthes.

Product Type:

Teaching aids

Product Description:

Tyler, S., M.D. Hooge, T. Artois, and E. Schockaert (2003) How many species of turbellarian platyhelminths in the meiofauna? [A WWW article in answer to Frequently Asked Questions by E-mail]

Sharing Information:

URL <http://www.umesci.maine.edu/biology/labs/howmany.htm> as a Web page hyperlinked from our home page and other pages on turbellarians.

Product Type:

Data or databases

Product Description:

Turbellarian taxonomy --- a database displaying the taxonomic hierarchy of the Platyhelminthes exclusive of the Neodermata, with synonymies, literature, notes on references to species of Acoelomorpha and Catenuvida in the literature, and georeference data for all turbellarians.

Sharing Information:

Posted on the WWW at URL <http://turbellaria.umaine.edu> (public site) and at <http://devbio.umesci.maine.edu/styler/turbellaria/> (where we and outside contributors log in to update the site).

Updates and corrections provided by colleagues world-wide working on turbellarian systematics.

Product Type:

Teaching aids

Product Description:

Tyler, S., M.D. Hooge, and K. Apse: An on-line key to the Acoelomorpha

Sharing Information:

This key is available at <http://devbio.umesci.maine.edu/turbellaria/key.php>. It is in development.

Product Type:

Workshop

Product Description:

Workshop: "On-line databases" at the Tenth International Symposium on Flatworm Biology. Innsbruck, Austria. July, 2006.

Sharing Information:

On-line poster at <http://turbellaria.umaine.edu/poster/> (digital poster presented to introduce the workshop)

Product Type:

Poster**Product Description:**

Poster: Achatz J., M.D. Hooge, and S. Tyler (2006)
 Describing Acoela in the new millenium.
 Assoc. Grad. Stud. Graduate Research Exposition, Univ. Maine.
 Proceedings of the Student Research and Creative Achievement Week, April, 2006.
 Abstract in Program, p. 5
 (Awarded 3rd prize in category of posters for grad. student J. Achatz.)

Sharing Information:

displayed at the exposition as well as in Murray Hall, UMaine, indefinitely

Product Type:**Invited presentation****Product Description:**

Invited seminar: "The Acoelomorpha: an ancient worm returns to the spotlight."
 Bamfield Marine Sciences Centre, Bamfield, British Columbia.
 July, 2005.

Sharing Information:

public seminar

Product Type:**Invited presentation****Product Description:**

Invited seminar: "The Acoelomorpha: an ancient worm reveals secretes of early animal evolution."
 Dept. Biological Sciences, UMaine. November, 2006.

Sharing Information:

public seminar

Contributions**Contributions within Discipline:**

Our studies are clarifying the evolutionary relationships of the Acoela in particular, a group that has gained prominence recently because of proposals from several molecular systematists that it is the most basal of all bilaterian groups, forming, it seems, a taxon separate from the phylum Platyhelminthes. Such studies have used perforce only single representatives from the group because most acoels have what appears to be extremely rapidly diverging sequences (in the 18S rDNA gene). Ours is the first study to find characters relevant to deciphering relationships of taxa within the Acoela; before this, subtaxa (families) have simply been pigeon-holed in fairly readily recognizable groupings without regard to phylogeny. We are the first to have a firm basis, in both morphological and molecular characters, for revising the taxonomy of the Acoela.

Our database, accessible via the World Wide Web, provides the latest taxonomic information on the turbellarian platyhelminths, and we have received thanks from platyhleminth specialists as well as other biologists for providing this service.

We expect that our world-wide sampling regimen will provide the first comprehensive collection of lower turbellarians yet assembled.

Contributions to Other Disciplines:**Contributions to Human Resource Development:**

Because a primary goal of this project is the training of a new generation of taxonomists, development of human resources is a major concern. Four graduate students have been trained through the grant, two at the PhD level (Hooge, Achatz) and two at the MS level (Ogunlana, Petrov) both of which have gone on for the PhD (completed by Petrov at the Zoological Institute, Moscow). Two postdoctoral collaborators have worked with the project, Hooge and Todt. Hooge is now employed in Portland, Oregon, and Todt now has a longer-term postdoctoral appointment in Denmark. We also exposed undergraduate students to the rewards of studying living representatives of evolutionarily significant groups.

Contributions to Resources for Research and Education:

The software we have developed for displaying taxonomic data is, we think, more intuitive and easy to use than that running other taxonomic Web sites. We know of others interested in using this software or adopting the model we have for displaying such data and are in the process of establishing it as Open Source software for access by download.

Contributions Beyond Science and Engineering:**Categories for which nothing is reported:**

Contributions: To Any Other Disciplines

Contributions: To Any Beyond Science and Engineering