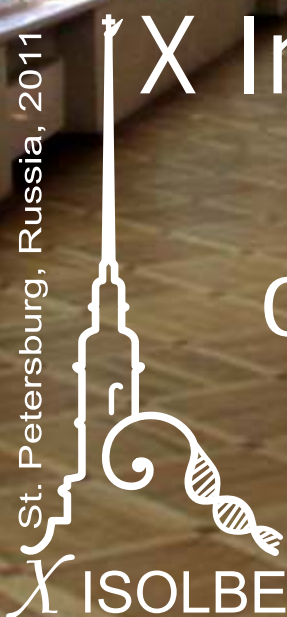


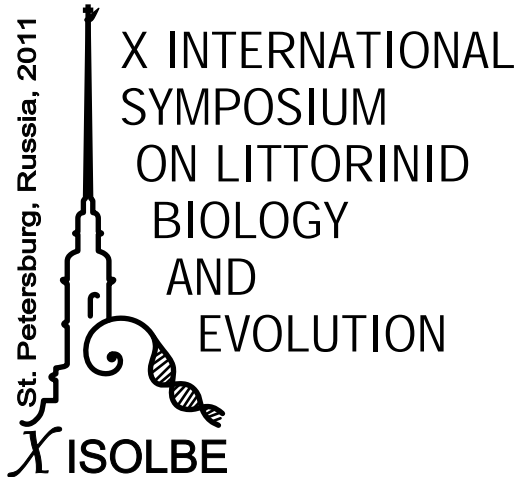
Saint-Petersburg  
State University, Russia  
July 24-29 2011

St. Petersburg, Russia, 2011



X International  
Symposium  
on Littorinid  
Biology and  
Evolution

X ISOLBE



Saint-Petersburg  
State University

Russia

July 24-29  
2011

**X INTERNATIONAL  
SYMPOSIUM  
ON LITTORINID  
BIOLOGY  
AND  
EVOLUTION**

## **Organizing Committee:**

Co-Heads of the Symposium Committee:

**Andrey I. Granovitch** - *St. Petersburg State University*

**Natalia A. Mikhailova** - *Institute of Cytology RAS*

Secretary: **Anna G. Gonchar** - *St. Petersburg State University*

Other members of the Symposium Committee:

**Oleg N. Pugachev** - *Director of the Zoological Institute RAS*

**Vladimir N. Parfenov** - *Director of the Institute of Cytology RAS*

**Alexey A. Sukhotin** - *Zoological Institute RAS*

**Larisa D. Barabanova** - *Genetics Department, SPbSU*

Undergraduate and PhD students (Invertebrate Zoology Department):

**Zinaida Starunova**, *PhD student*

**Alexey Maximovitch**, *PhD student*

**Darya Krupenko**, *PhD student*

**Vladimir Krapivin**, *PhD student*

**Anastasiya Eremina**, *undergraduate student*

**Vladislav Grabovoy**, *undergraduate student*

**Innokentii Danilov**, *undergraduate student*

**Julia Gracheva**, *PhD*

**Antonina Chernetskaya**, *graduate SPbSU*

## **Financial Support:**

St. Petersburg State University

Grant 1.41.1164.2011

The Malacological Society of London

Russian Foundation of Basic Research (RFBR)

Grant 11-04-06047-?

Russian Academy of Sciences

*“Littorinids are one of the very few molluscan families with a sufficient following among researchers that they merit their very own symposia”*

David Reid

**1986 – First International Symposium on Littorinid Biology, Natural History Museum, London, UK (26 November 1986)**

**1988 – Second International Symposium on Littorinid Biology, Tjarno Marine Biological Laboratory, Sweden (4-8 July 1988)**

**1990 – Third International Symposium on Littorinid Biology, Dale Fort Field Centre, Wales UK (5-12 September 1990)**

**1993 – Fourth International Symposium on Littorinid Biology, Roscoff Biological Station, France (19-25 September 1993)**

**1996 – Fifth International Symposium on Littorinid Biology, University College, Cork, Ireland (7-13 September 1996)**

**1999 – Sixth International Symposium on Littorinid Biology, Hofstra University Marine Laboratory, Priory, Jamaica (21–31 July 1999)**

**2002 – Seventh International Symposium on Littorinid Biology, Shoals Marine Laboratory, Appledore Island, Isles of Shoals, Maine, USA (23-28 August 2002)**

**2005 – Eighth International Symposium on Littorinid Biology, Slapton Ley Field Centre, Devon, UK (30 August – 4 September 2005)**

**2008 – Ninth International Symposium on Littorinid Biology and Evolution, Talaso Atlántico Hotel in Baiona, Vigo, Spain (2-7 September 2008)**

**2011 – Tenth International Symposium on Littorinid Biology and Evolution, Saint-Petersburg State University, Saint-Petersburg, Russia (24-28 July 2011)**

# International littorinid research during the past 25 years (1986 - 2011)

**Kerstin Johannesson**

*University of Gothenburg, Sweden*

Periwinkles (fam Littorinidae) are familiar to all visitors of rocky shores, worldwide. In addition, they are found in mangrove forests, salt marches and on shallow soft bottoms. Littorinids have for a long time been attractive as study objects in undergraduate courses in marine ecology as well as for master projects and research training. Indeed, some very successful carriers took off from littorinid research (eg. Dave Raffaelli, Jane Lubchenco).

Early littorinid research largely aimed to unravel the taxonomy of species, some of which turned out to be unusually complicated with highly variable phenotypes. At this time different morphs, including different colour-morphs, were classified and given species, subspecies or variety names, resulting in an almost endless list of names for species such as *L. obtusata* and *L. saxatilis* (thoroughly reviewed in Reid 1996).

By the early 1980ies the situation was rather confused, as researchers at that time had started to realize that taxonomy based on colour and shell phenotype alone were likely erroneous. The situation became even more frustrating when suddenly two new species popped up on the scene, *Littorina arcana* and *Littorina fabalis*. These species having been overlooked by most established littorinid researchers for decades despite rather obvious morphological differences in reproductive structures, and it was somewhat embarassing that one of the species (*L. arcana*) was introduced by a PhD student (Celia Hannaford-Ellis).

During the past 25 years, that is from the time of the first ISOLBE meeting in London 1986 and until now, research has evolved substantially not least due to new approaches to study genetic relationships (allozymes, RAPD, mtDNA sequencing, microsatellites). Notably, the research focus is still linked to issues relating to taxonomy and systematics, but the focus is now also on what mechanisms of evolution give rise to the observed patterns. When it is now time to celebrate the 10th ISOLBE meeting, littorinid research is on its way to embark on the genomic research vehicle. Most likely a necessary step to advance our understanding of, for example, ecotype and species formation, as well as, gene function and how genes evolve by drift and selection. A main challenge is now to sequence the complete genome of the first littorinid species, and from here develop this group of mollusc into a powerful model for studies of evolutionary biology and address issues such as evolution of biodiversity and mechanisms of speciation.

This review is an attempt to summarize the main advances and milestones in littorinid research since the first ISOLBE meeting arranged by David Reid at the Natural History Museum in London 1986, that is 25 years ago. Although, not all important littorinid research has been presented at ISOLBE meetings over the years, I will stress that these meetings have played an important role in advancing science in this topic and many of the meetings were also of the kind that issues were raised that led to further research initiatives in a dynamic process. One such issue were the discussion on the taxonomy of *Littorina neglecta*, initiated at the Tjarno meeting in 1988, and I will use this example as an illustration of how science may evolve driven by fruitful disagreements.

The availability of new genetic tools became an important lever to advance knowledge in littorinid biology. The early use of allozymes, introduced by Bob Ward, and later on expanded into sequencing of mitochondrial DNA, RAPD and similar used by the groups of David Reid, Thierry Backeljau, Natalia Mikhailova and others. A most successful initiative by Craig Wilding, Roger Butlin and John Grahame, to use the powerful AFLP approach to fingerprint large number of "genes" became a break-through that not only made *Littorina* genetics famous but also introduced approaches that were widely useful (outlier analysis to identify potentially selected loci).

While ten-fifteen years ago eager attempts were made to find truly neutral markers, some other studies indicated unusually strong selection on individual alleles of some allozyme systems (e.g. Johannesson et al. 1995). A growing interest for the importance of natural selection in evolution of ecotypes made search for candidate loci again in focus.

With various genetic markers at hand it seemed as if the taxonomy would be heavily revised, using these powerful tools. However, the comprehensive taxonomic revision undertaken by David Reid on basis of morphological traits of soft parts and shells (Reid 1996) has hitherto remained unchallenged by the studies of genetic relationships. However, the overall phylogeny of the genus *Littorina* was established using mtDNA sequencing (Reid, Rumbak & Thomas 1996). Quite much later have detailed phylogeographic studies of individual species been undertaken. This year, for example, came two phylogeographic studies of *L. saxatilis* both showing interesting and new results of a strongly subdivided species (Panova et al. 2011; Doellman et al 2011).

Over these 25 years it has become more and more apparent that some of the species (in particular the species of the direct developing complexes; *L. saxatilis*, *L. obtusata*, *L. subrotundata* and *Bembicium vittatum*) offer interesting but challenging cases for studies of evolutionary processes and mechanisms, and indeed the potential to explore these systems further to understand mechanisms of ecological and sympatric speciation, genotype-environment interactions and similar is extremely good. Today we have a BAC library, a few EST libraries, microarrays and proteomics to study gene expression, and the hope is for the sequence of the complete genome in a few years from now. This means that we are still in the match, and littorinids seem as promising as ever to develop further into invertebrate models for research on hotly debated topics such as speciation, gene-environment interactions and how genetic variation is maintained under natural selection.

1<sup>st</sup> International Symposium on Littorinid Biology,  
Natural History Museum, London, UK (26 November 1986)



2<sup>nd</sup> International Symposium on Littorinid Biology,  
Tjarno Marine Biological Laboratory, Sweden (4-8 July 1988)



3<sup>rd</sup> International Symposium on Littorinid Biology,  
Dale Fort Fiel Centre, Wales UK (5-12 September 1990)



4<sup>th</sup> International Symposium on Littorinid Biology,  
Roscoff Biological Station, France (19-25 September 1993)



5<sup>th</sup> International Symposium on Littorinid Biology,  
University College, Cork, Ireland (7-13 September 1996)



6<sup>th</sup> International Symposium on Littorinid Biology,  
Hofstra University, Marine Laboratory, Priory, Jamaica (21-31 July 1999)







7<sup>th</sup> International Symposium  
on Littorinid Biology,  
Shoals Marine Laboratory,  
Appledore Island,  
Isles of Shoals,  
Maine, USA  
(23-28 August 2002)

8<sup>th</sup> International Symposium  
on Littorinid Biology,  
Slapton Ley Field Centre,  
Devon, UK  
(30 August – 4 September 2005)



9<sup>th</sup> International Symposium on Littorinid Biology and Evolution,  
Talaso Atlántico Hotel Baiona, Vigo, Spain (2-7 September, 2008)



**“GOODBYE *NEGLECTA* MY OLD FRIEND”**  
Lyrics Williams & Lewis;© Littorina Songs

To the tune “Sound of Silence”, with apologies to P. Simon,  
and with the kind permission of J. Grahame

Goodbye *neglecta* my old friend,  
We won't be seeing you again.  
In the shadows softly creeping,  
I smelt your slime and I was weeping.  
And your shape,  
Was a vision of John Grahame's eye,

Eye, eye, eye  
They should be all, *saxatilis*.

And in the naked light I saw,  
Ten thousand snails upon the shore.  
They were mating un-assortatively,  
They had the same penis morphology,  
And they all looked the same to you and I

I, I, I  
They should be all, *saxatilis*.

Then it came as in a dream,  
Shapes of snails I'd never seen.  
Image captured and then digitized,  
Statistic Tables that hurt our eyes.  
But the result was plain for all to see,

Hee, hee, hee  
They're all, still *saxatilis*.



*Singers (from left to right):*  
*Mak Yiu Ming, Mark Davies, Rupert Lewis & Gray Williams,*

*The FIRST-FIRST place winner*  
*at 5th Littorinid Symposium, Cork, 7-13 September 1996*

St. Petersburg, Russia, 2011

X INTERNATIONAL  
SYMPOSIUM  
ON LITTORINID  
BIOLOGY  
AND  
EVOLUTION

X ISOLBE

# PROGRAM

**PROGRAM  
X INTERNATIONAL SYMPOSIUM  
ON LITTORINID BIOLOGY AND EVOLUTION (X ISOLBE)**

25th July (Monday)

9:00-10:00 – Registration

10:00– Petrovsky Hall, St. Petersburg State University  
Anniversary Session

10:00-10:15 –  
Andrey Granovitch (St. Petersburg State University, Russia)  
Welcome to the meeting

10:15-11:00 –  
Kerstin Johannesson (University of Gothenburg, Tjörn, Sweden)  
International littorinid research during the past 25 years (1986-2011)

11:00-12:00 – coffee break

11:30 – Auditorium 140 Biological Faculty SPbSU  
Session 1  
Chairman - Peter Marko (*Clemson University, South Carolina, USA*)

12:00-12:30 -  
**Cynthia Yee-Man Wong, Shirley S.L. Lim** (*Nanyang Technological University, Singapore*)  
Shell morphology and microstructure of two Singapore's littorinids, *Echinolittorina malaccana* and *E. vidua*

12:30-13:00 –  
**Eugene Kozminsky** (*Zoological Institute RAS, St. Petersburg, Russia*)  
Inheritance of bands and spots on the shell of *Littorina obtusata* (Gastropoda: Prosobranchia)

13:00 –14:30 – Lunch at “Emperor” restaurant

14:30 – Auditorium 140 Biological Faculty SPbSU  
Session 2

Chairman – Mark Davies (*University of Sunderland, UK*)

14:30 –15:00 –  
**Terence Pun Tung Ng** (*The Swire Institute of Marine Science, Hong Kong, China*)  
Reproductive behaviour of mangrove littorinid snails: how do males successfully mate with females?

15:00 – 15:30 –

**Sara Hintz Saltin, Eva-Lotta Blom, Kerstin Johannesson** (*University of Gothenburg, Tjörnö, Sweden*)

Reproductive barriers between sister-species (*Littorina fabalis* and *Littorina obtusata*)

15:30 – 16:00 –

**Elizabeth Boulding** (*University of Guelph, Canada*)

Effect of developmental mode on the responses of four northeastern Pacific *Littorina* populations to ENSO events

16:00-16:30 – coffee break

16:30 – Auditorium 140 Biological Faculty SPbSU

Session 3

Chairman – Kerstin Johannesson (*University of Gothenburg, Sweden*)

16:30-17:00 –

**Sharon Degnan, Sue Hull** (*Centre for Environmental and Marine Sciences, University of Hull, UK*)

Effect of reciprocal transplants on survivorship and growth of two *Littorina saxatilis* (Olivi) morphs

17:00-17:30 –

**Maria Saura, Mónica Martínez-Frenández, Humberto Quesada, Emilio Rolán-Álvarez** (*University of Vigo, Spain*)

Parallel ecological divergence in the marine snail *Littorina saxatilis*

17:30-18:00 –

**Richard Stafford<sup>1</sup>, Gray A. Williams<sup>2</sup>, Mark Davies<sup>3</sup>** (*University of Bedfordshire, Luton, UK, <sup>2</sup>The Swire Institute of Marine Science and School of Biological Sciences, The University of Hong Kong, <sup>3</sup>University of Sunderland, UK*)

What is the value in modeling the behaviour of populations of snails?

18:00-19:00 – Dinner at “Academy” Restaurant

19:00 – Photo (Vasilievsky Island, Old Stock Exchange building)

19:15 – 21:00 City bus tour (final destination – Oktyabrskaya Hotel)

26th July (Tuesday)

09:00 – Auditorium 140 Biological Faculty SPbSU

Session 4

Chairman – Alexander Gorbushin (*Institute of Evolutionary Biochemistry and Physiology RAS, St. Petersburg, Russia*)

09:00-09:30 –

**Alexey Maximovich, Andrey Granovitch** (*Saint-Petersburg State University, Russia*)  
Long-term population dynamics of *Littorina obtusata* and *L. saxatilis* in the White Sea

09:30 – 10:00 -

**Kathy H. T. Li** (*The Swire Institute of Marine Science and School of Biological Sciences, The University of Hong Kong*)

Thermal tolerance of *Echinolittorina* spp. in Hong Kong: implications for their vertical distribution?

10:00 – 10:30 -

**Gray A. Williams<sup>1</sup>, Kathy H.T. Li<sup>1</sup>, C.D. McQuaid<sup>2</sup>, Given Matumba<sup>2</sup>, Monthon Ganmanee<sup>3</sup>, Cynthia Y.M. Wong<sup>4</sup>, Abdul Adzis, Kee-Alfian<sup>5</sup>, Nur-Leena W.S. Wong<sup>6</sup>, Lizhe Cai<sup>7</sup>, B.K.K. Chan<sup>8</sup>, Yunwei Dong<sup>7</sup> and D.J. Marshall<sup>9</sup>**

(<sup>1</sup>*The Swire Institute of Marine Science and School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong*; <sup>2</sup>*Rhodes University, South Africa*; <sup>3</sup>*King Mongkut's Institute of Technology Ladkrabang, Bangkok, Thailand*; <sup>4</sup>*National Institute of Education, Nanyang Technological University, Singapore*; <sup>5</sup>*Marine Ecosystem Research Centre (EKOMAR), National University of Malaysia, Malaysia*; <sup>6</sup>*Institute of Bioscience, University Putra Malaysia*; <sup>7</sup>*Xiamen University, China*; <sup>8</sup>*Biodiversity Research Center, Academia Sinica, Taipei, Taiwan*; <sup>9</sup>*University Brunei Darussalam, Brunei*)

Thermal tolerance of *Echinolittorina* snails in the Indo-West Pacific: are we measuring the right variables?

10:30 – 11:00 –

**Christopher McQuaid<sup>1</sup>, Tshifhiwa Matumba<sup>1</sup>, David Marshall<sup>2</sup>** (<sup>1</sup>*Rhodes University, South Africa*; <sup>2</sup>*University Brunei Darussalam, Brunei Darussalam*)

Thermal tolerance and heart function of littorinid snails: a comparison of tropical, subtropical and temperate species

11:00-11:30 – coffee break

11:30 – Auditorium 140 Biological Faculty SPbSU

Session 5

Chairman – Emilio Rolán-Alvarez (*University of Vigo, Spain*)

11:30-12:00 -

**Alexander Gorbushin, Nadya Iakovleva** (*Institute of Evolutionary Biochemistry and Physiology RAS, St. Petersburg, Russia*)  
*Littorina littorea* immunobiology

12:00-12:30 –

**Elena Borisova<sup>1</sup>, Nadya Iakovleva<sup>2</sup>, Alexander Gorbushin<sup>2</sup>** (<sup>1</sup>*St. Petersburg State University*; <sup>2</sup>*Institute of Evolutionary Physiology and Biochemistry, RAS, St. Petersburg, Russia*)

The new C-type lectin from *Littorina littorea*

12:30-13:00 –

**Carl Andre, Marina Panova, Kerstin Johannesson** (*University of Gothenburg, Tjörnö, Sweden*)

Ecotype transcriptomics in *Littorina saxatilis*

13:00 –14:30 – Lunch at “Emperor” restaurant

14:30 - Auditorium 140 Biological Faculty SPbSU

Session 6

Chairman – David Reid (*Natural History Museum, London, UK*)

14:30 –15:00 –

**Anastasiya Eremina, Andrey Granovitch** (*St. Petersburg State University, Russia*)

Analysis of abnormal shell shape variability of *Littorina obtusata*

15:00 –15:30 -

**Peter B. Marko<sup>1</sup>, Lisa Nicole Cox<sup>1</sup>, Nadezhda Zaslavskaya<sup>2</sup>** (<sup>1</sup>*Clemson University, South Carolina, USA*; <sup>2</sup>*Institute of Marine Biology RAS, Far Eastern Federal University, Vladivostok, Russia*)

Phylogeography of the Amphi-Pacific Gastropods *Littorina sitkana* and *Nucella lima*

15:30 –16:00 –

**Natalia Mikhailova** (*Institute of Cytology RAS, St.Petersburg, Russia*)

Microspatial distribution of *Littorina saxatilis* and *L.arcana* sibling species: arguments for interspecific hybridization

16:00-16:30 – coffee break

16:30 –

Visiting enclosed court of St.Petersburg State University  
(including backyard of the Philological Faculty SPbSU)

Pedestrian crosswalk towards to the pier for passenger ships

18:00-21:00 – Banquet dinner onboard the ship

(Pier for passenger ships on the English Embankment  
in front of the Senate and Synod building)

Bus shuttle to Oktyabrskaya Hotel is available at 21:00

27th July (Wednesday)

09:00 – Auditorium 140 Biological Faculty SPbSU

Session 7

Chairman – Elizabeth Boulding (*University of Guelph, Canada*)

09:00-09:30 –

**Rui Faria**<sup>1,2</sup>, **Petri Kemppainen**<sup>3</sup> (<sup>1</sup>*University of Porto, Portugal*; <sup>2</sup>*University Pompeu Fabra, Spain*; <sup>3</sup>*University of Manchester, UK*)

The paths of parallel evolution and their genetic crossroads: lessons from *Littorina fabalis* (a starting project)

09:30 – 10:00 -

**Grégory Charrier** (*University of Gothenburg, Tjärnö, Sweden*)

Evolutionary history of local ecotypes in *Littorina saxatilis*: insights from nuclear genes

10:00 – 10:30 -

**Max E. Maliska**<sup>1</sup>, **David G. Reid**<sup>2</sup>, **Billie J. Swalla**<sup>1</sup> (<sup>1</sup>*University of Washington, USA*; <sup>2</sup>*Natural History Museum, London, UK*)

Evolutionary history and speciation in *Littorina* using a molecular phylogenetic approach

10:30 – 11:00 –

**David G. Reid**<sup>1</sup>, **Johan Hollander**<sup>2</sup>, **Carole Smadja**<sup>3</sup>, **Roger K. Butlin**<sup>4</sup>, **Suzanne T. Williams**<sup>1</sup> (<sup>1</sup>*Natural History Museum, London, UK*; <sup>2</sup>*Lund University, Sweden*; <sup>3</sup>*Montpellier University, France*; <sup>4</sup>*Sheffield University, UK*)

A periwinkle supertree and its use to test hypotheses of reinforcement and life-history evolution

11:00-11:30 – coffee break

11:30 – Auditorium 140 Biological Faculty SPbSU

Session 8

Chairman – Christopher D. McQuaid (*Rhodes University, South Africa*)

11:30-12:00 -

**Susan Hull** (*Centre for Environmental and Marine Sciences, University of Hull, UK*)

Embryo abnormalities in H and M *Littorina saxatilis* on eight shores in North East England

12:00-12:30 –

**Sophie Webster**, **John W. Grahame**, **Roger K. Butlin** (*University of Sheffield, UK*)

Ecological measures of selection and migration in H and M ecotypes of *Littorina saxatilis*

12:30-13:00 –

**María José Rivas Quelle**, **Antonio Carvajal-Rodríguez** (*University of Vigo, Spain*)

Detection of divergent selection at genomic level in *Littorina saxatilis*

13:00 –14:30 – Lunch at “Emperor” restaurant



14:30 – Auditorium 140 Biological Faculty SPbSU

Session 9

Chairman – Gray Williams (*The University of Hong Kong, Hong Kong, China*)

14:30 – 15:00 –

**Marina Panova<sup>1</sup>, Carl André<sup>1</sup>, Björn Canbäck<sup>2</sup>, Kerstin Johannesson<sup>1</sup>, Tomas Johansson<sup>2</sup>, Anders Tunlid<sup>2</sup>** (<sup>1</sup>*University of Gothenburg, Tjörnö*, <sup>2</sup>*Lund University, Sweden*)

Inter-specific and intra-specific divergence in *Littorina* by microarray-based genomic hybridization

15:00 – 15:30 –

**Emilio Rolán-Alvarez<sup>1</sup>, María Saura<sup>1</sup>, Juan Galindo<sup>1</sup>, Mónica Martínez-Fernández<sup>1</sup>, Carmen López<sup>2</sup>, Jaime Gosálvez<sup>2</sup>, Zita Ferreiro<sup>3</sup>, Xana Pinto<sup>3</sup>, María Jose Rivas<sup>1</sup>, Armando Caballero<sup>1</sup>** (*University of Vigo, University of Madrid, Spain; University of Porto, Portugal*)

About the meaning of the term hybrid in the Galician *Littorina saxatilis* hybrid zone: is exogenous or endogenous selection maintaining ecotype cohesion?

15:30 – 16:00 –

**Roger Butlin, Juan Galindo, Ben Lackson** (*University of Sheffield, UK*)

Using Approximate Bayesian approaches to uncover the history of ecotypes in *Littorina saxatilis*

16:00-16:30 – coffee break

16:30 – Auditorium 140 Biological Faculty SPbSU

Session 10

Chairman – Marina Panova (*University of Gothenburg, Tjörnö, Sweden*)

16:30-17:00 –

**Zinaida Starunova<sup>1</sup>, Natalia Mikhailova<sup>1,2</sup>, Andrey Granovitch<sup>1</sup>** (*St. Petersburg State University, <sup>2</sup>Institute of Cytology RAS, St. Petersburg, Russia*)

The detection of shell shape differences in “*saxatilis*” species complex by geometric morphometric methods

17:00-17:30 –

**Vladislav Grabovoi<sup>1</sup>, Andrey Granovitch<sup>1</sup>, Natalia Mikhailova<sup>1,2</sup>** (*<sup>1</sup>St. Petersburg State University, <sup>2</sup>Institute of Cytology RAS, St. Petersburg, Russia*)

Zonal patterns of five *Littorina* species distribution in habitats with different salinity (the Barents Sea, Russia)

17:30-18:00 –

**Andrey Granovitch** (*St. Petersburg State University, Russia*)

Is the time coming to change an evolutionary paradigm? Tyhogenesis versus orthogenesis.

18:00 – Dinner Dinner at “Academy” Restaurant

Free time

28th July (Thursday)

09:00 – Bus from Oktyabrskaya Hotel  
to the pier on the English Embankment

10:00 – 14:00 – Peterhof Park

14:00 – 15:00 – Lunch at “Emperor” restaurant

15:00–16-00

INVITED LECTURE

Jerry COYNE (*Department of Ecology and Evolution, University of  
Chicago, USA*)

The genetical biogeography of speciation

16:00-16:30 – coffee break

16:30 – 18:00

ISOLBE Committee summit

Poster session

Time for collaboration

18:00 – Dinner at “Emperor” restaurant

Closing Ceremony

St. Petersburg, Russia, 2011

X INTERNATIONAL  
SYMPOSIUM  
ON LITTORINID  
BIOLOGY  
AND  
EVOLUTION

X ISOLBE

# ABSTRACTS

# Ecotype transcriptomics in *Littorina saxatilis*

Carl André, Marina Panova, Kerstin Johannesson

*Göteborg University, Sweden*

*Littorina saxatilis* form distinct ecotypes in different habitats on European shores. Snails living in wave- exposed areas are smaller and have a thinner shell, whereas snails in sheltered areas with high densities of predatory crabs typically are larger and more thick-shelled. Breeding experiments show that these ecotype differences are to some extent inherited, but the genes involved are not described. We used analyses of gene expression to search for genes involved in the ecotype formation. Field-collected snails representing the exposed (E) ecotype and the sheltered “Crab” (S) ecotype from different localities were acclimatized to similar conditions in the lab, and then exposed to either crab smell or used as control. RNA was extracted, converted to cDNA and hybridized against a Nimblegen 12-plex microarray with 26 000 putative genes in *L. saxatilis*. The genes used can be find in the database LSD at <http://mbio- serv2.mbioekol.lu.se/Littorina/>. Preliminary analyses show that a high number of genes were differentially expressed in the two ecotypes, but also that many genes are differentially expressed in snails from different localities.

# The new C-type lectin from *Littorina littorea*

Elena A. Borisova<sup>1</sup>, Nadya V. Iakovleva<sup>2</sup>, Alexander M. Gorbushin<sup>2</sup>

<sup>1</sup>*Saint-Petersburg State University, Russia*

<sup>2</sup>*Sechenov Institute of Evolutionary Physiology and Biochemistry, Russia*

Study of features in innate immunity of molluscs provides a more precise understanding of the mechanisms involved in Protostomata defense against viruses and bacteria. In the present work aimed on characterization of *Littorina littorea* immune molecules we report on the new pattern recognition receptor. We have documented the novel gene encoding the protein (named LiCTL) with one carbohydrate-recognition domain. This lectin consists of 199 amino acids and its predicted molecular mass is about 24 kDa. LiCTL showed high similarity to other members of C-type lectin superfamily which play crucial role in the innate immunity of both the invertebrate and the vertebrate defenses. The functions of LiCTL were investigated using the recombinant LiCTL (rLiCTL). Expression of the cDNA fragment encoding the mature peptide was established in yeast *Pichia pastoris*. The rLiCTL agglutinates human, mouse and rabbit red blood cells in Ca<sup>2+</sup>-dependent manner and regulates hemocyte adhesion to a glass surface. The lectin shows opsonization activity and significantly increases the phagocytic index of hemocytes. Using the polyclonal antibodies against rLiCTL we have found the lectin is secreted by hemocytes into a culture medium in the experiments in vitro, binds to the cell wall of yeast and *Escherichia coli* bacterium. Immunohistochemical staining of circulating cells revealed that hemocyte population is heterogeneous in the degree of the lectin expression. The staining of littorina's tissue sections has shown that LiCTL is expressed at the high level in mucous cells of surface epithelium, cells of hypobranchial gland and the inner side of the mantle. The lectin LiCTL acts as a part of the integumentary mucous immune barrier and a humoral pattern-recognition receptor defending the common periwinkles against pathogen invasions.

The study is supported by RFBR grants 09-04-01255, 11-04-0156. Access to the animals and lab space during field studies are granted by WSBS “Kartesh”.

# Effect of developmental mode on the responses of four northeastern Pacific *Littorina* populations to ENSO events

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Developmental mode has been hypothesized to strongly affect the responses of marine animal populations to climate change but datasets with sufficient temporal replication to test this are rare. I monitored the population dynamics of four northeastern Pacific littorinid gastropod species - two with and two without a planktotrophic larval phase - over an 18 year period on the west coast of Vancouver Island, Canada. Twice each year I counted and measured all *Littorina* species inside 65 square 10 cm permanent quadrats at two intertidal sites near Bamfield Marine Science Centre. The abundances of the four species were then compared with environmental variables such as sea surface temperature, wind speed, wave height, air temperature, rainfall and the ENSO index using multivariate general linear models. I found that these environmental variables were often highly correlated with one another making it difficult to identify the proximate factors causing population fluctuations. Average sea surface temperature (SST) at the La Perouse Bank weather buoy was observed to be highly correlated with air temperature at Tofino airport ( $r=0.937$ ,  $p<0.001$ ) but inversely correlated ( $r = -0.521$ ,  $p<0.001$ ) to total rainfall. Nevertheless it was clear that the direct developing species sometimes responded to different factors than the planktotrophic species. For example, the summer juvenile abundance of the most common direct-developing species, *L. subrotundata*, was highly correlated with the rainfall during the previous January but those of the two planktotrophic species were not. This strong environmental response by the former is in contrast to our previous hypothesis that the higher early survivorship by direct-developing littorinid species may bring about their higher effective population sizes relative to planktotrophic littorinid species.

# Using Approximate Bayesian approaches to uncover the history of ecotypes in *Littorina saxatilis*

Roger Butlin, Juan Galindo, Ben Jackson

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Approximate Bayesian Computation offers many advantages for testing alternative models of population history using genetic data, and estimating the parameters of preferred models. Here we discuss the application of this method to data from crab and wave exposed ecotypes of *Littorina saxatilis* from the UK, Sweden and Spain generated in a collaborative project with the Vigo and Tjarno groups. Specifically, we aimed to compare hypotheses about the parallel evolution of ecotypes at different levels: within country, between the UK and Sweden and between northern and southern Europe.

# The genetical biogeography of speciation

Jerry Coyne

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Perhaps the most contentious area of speciation is its biogeography: do new species usually originate in allopatry, parapatry, or sympatry? The question of biogeography is, however, closely connected with that of gene flow, and the biogeographic and genetic views of speciation often do not coincide. In this talk I discuss the differences in these views of speciation, concentrating on sympatric speciation. It turns out that many cases considered "sympatric" in the biogeographic sense are not "sympatric" in the genetic sense, since they involve biological features that from the outset reduce the antagonism between selection and recombination.



# **Evolutionary history of local ecotypes in *Littorina saxatilis*: insights from nuclear genes**

Gregory Charrier

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The seashore periwinkle *Littorina saxatilis* is characterized by the existence of a number of distinct ecotypes specific to shore microhabitats. The two contrasting ecotypes named "crab" and "wave" and described in Sweden, Spain and UK are the best investigated ones, but their origin remains still unknown: does each ecotype emanate from a single or multiple parallel differentiation process(es)?

Thus, we have conducted a collaborative project with researchers from Sheffield University, UK, and Vigo University, Spain, with the aim of determining the evolutionary history of both "crab" and "wave" ecotypes. Both ecotypes were sampled in two localities, 100-200 km apart, in Sweden, Spain and UK, and 16 individuals were analysed by population sample. The neutral genetic differentiation between ecotypes, localities and countries was surveyed by cloning and sequencing three nuclear introns: calreticulin, elongation factor and thioredoxin peroxidase.

Respectively 27, 41 and 17 alleles were identified over all populations. All three loci displayed contrasted patterns of genetic variability and population structure. Overall, most of the genetic differentiation appeared to be driven by the geographical distribution of population samples, and a lack of genetic structure was observed between ecotypes. Thus these results seem to support the hypothesis that both "crab" and "wave" ecotypes might have emerged from multiple parallel evolutionary events.

# Effect of reciprocal transplants on survivorship and growth of two *Littorina saxatilis* (Olivi) morphs

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Predation and heavy wave action are considered to be major causes of mortality in littorinids, with these pressures resulting in divergent morphological characteristics depending on the habitat occupied. On the Yorkshire coast, UK two distinct morphs of *Littorina saxatilis* (Olivi) occur. These show differences in shell characteristics, reproductive strategy and occupy different microhabitats: the H morph is found in cliff crevices and on large boulders in the upper shore in more exposed areas, whereas the M morph occurs on boulders and rock platforms in the mid shore. At Thornwick Bay, East Yorkshire, a semi-exposed shore where winter densities of the predator *Carcinus maenas* (L.) are very low, these habitats are contiguous and the two morphs are found in close proximity. During winter 2009, reciprocal transplants using tethered snails were undertaken in two areas of the shore to examine whether the two morphs exhibited differential survival and growth between native and transplanted habitats in the absence of predation. All surviving snails showed evidence of growth and although differences between the four experimental populations were not significant, growth in H morphs was greater than that of M morphs in both habitats. Survival curves generated using the Kaplan-Meier procedure were significantly different for both H and M morphs, with the H morph showing higher survivorship than the M morph irrespective of habitat, indicating a possible selective advantage for the H morph in wave-exposed areas. Snails tethered on the cliffs had significantly lower survival than those tethered on boulders, irrespective of morph. There was no visible evidence of crab predation during the study, with the results suggesting that the H morph may be able to survive in the M morph habitat in the absence of *Carcinus*. However predation may be an important factor limiting its survival in the mid shore during summer months and this is currently under investigation.

# **Analysis of abnormal shell shape variability of *Littorina obtusata***

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Extremely high shell shape variation was found in *Littorina obtusata* population of Oskar's Bay (Dalniye Zelentsy, Barents Sea). Several types of the shell “anomalies” representing a continuous “row of morphs” were described. Frequency of the abnormal mollusks is as high as 23% in this population compared to 0-4% in other Barents and White Sea populations. It is not dependent on trematode infestation or pollution by heavy metals (Cu, Cd, Pb). Males and females were characterized by the same frequency of abnormal shells. Relatively more abnormal shells were found in adult *L. obtusata* compared to juveniles. Geometric morphometry is a good tool for complex analysis of shell shape variability in Oskar's Bay population as well as other *L. obtusata* populations of Barents and White Seas. It is important to emphasize that general components of variation are the same in all investigated populations. The “abnormal forms” are extreme variants of shell shape distribution. The variability of *L. obtusata* in Oskar's Bay population was much more than interpopulation variability among other populations under consideration.

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# The paths of parallel evolution and their genetic crossroads: lessons from *Littorina fabalis* (a starting project)

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The study of repeated evolution of adaptation in natural populations is fundamental for understanding the mechanisms involved in adaptive evolution and ecological speciation. Among several well studied model systems, marine intertidal snails of the genus *Littorina* have been shown to be well suited for studying evolution of local adaptation and of reproductive barriers on small scales (in the range of meters) in their natural habitats. Here we will outline a new research project recently funded by the Portuguese Science Foundation (FCT) to study the nature of the genetic variation responsible for parallel ecotypification in *L. fabalis*.

Two locally adapted ecotypes, 'Large ecotype in Moderately exposed habitats' (LM) and 'Small-Sheltered ecotype' (SS), can be found for *L. fabalis* throughout Northern Europe, while three other ecotypes exist in Iberia, associated with different host algae genera located in different parts of the intertidal zone (*Fucus vesiculosus*, *Zostera marina* and *Mastocarpus stellatus*). While the first is relatively common, the two others are much less abundant, in agreement with their host algae scarcity. This allows us to focus on some unique questions for which the three ecotypes of *L. fabalis* are particularly well suited, such as: how is adaptation possible in marginal ecological niches with potentially small effective population sizes? is there any co-adaptation between the ecotypes and their respective host plants?

With this international collaborative project we aim to understand the main biotic and abiotic factors behind the local adaptations, and most importantly, to use the latest molecular genetic techniques to identify loci under selection and understand their evolutionary history in a phylogeographic context. We hope that this project can complement existing studies on other *Littorina* species and shed more light on the complexity of the genetic mechanisms behind adaptive evolution and speciation.

# Zonal patterns of five *Littorina* species distribution in habitats with different salinity (the Barents Sea, Russia)

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Spatial distribution of five *Littorina* species was investigated by quantitative method of “zonal transects” with sampling of mollusks in three habitats of East Murman (Barents Sea, Russia). Collected snails were identified using morphological criteria. Sampling sites are differing in salinity.

All studied populations are characterized by the strong ecological zonality and subsequent patterns of *Littorina* spp. distribution. The species distribution in the population with “normal” salinity (about 30-34 ppm) represents the following features. 1. *L. fabalis* population is restricted to upper sublittoral zone. 2. *L. obtusata* and *L. compressa* fully overlap within the zone of macrophytes. 3. *L. arcana* occupies mostly microhabitats from the macrophytes belt up to the splash zone with the maximum density on the upper border of macrophyte distribution. 4. *L. saxatilis* population is widespread along all littoral zones. At the shore with lower salinity littorinid population is characterized by absence of *L. fabalis* and very low density of *L. arcana* species. Finally, only two species, *L. saxatilis* and *L. obtusata*, were found in estuarine location. *L. arcana*, *L. compressa* and *L. fabalis* are most sensitive to the impact of the fresh water.

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# Is the time to change an evolutionary paradigm? Tyhogenesis versus orthogenesis

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A paradigm is an epistemological notion that can be defined as a philosophical and theoretical framework of a scientific school or discipline within which theories, laws, generalizations are formulated and supporting experiments are carried out.

Currently “statistical” paradigm dominates in biology. The evolutionary hypothesis named tihogenesis (the term was proposed by Osborn, 1929) is the reflection of this paradigm. It is also called selectogenesis emphasizing the assumed major role of the natural selection.

However, there are many other hypotheses (models of evolution) which are characterized by different parameters: main driving forces of evolution; role of accident or law; meaning of the directionality, or trends, in the evolution; meaning of polymorphism, and so on.

Several of these models, though differ in details, share an assumption of direct evolutionary development of life. All together they are called orthogenetic evolutionary hypothesis, or orthogenesis (the term was proposed by Haacke, 1893). This idea of evolution represents another complex of biological notions, another paradigm. This is a so-called “systemic” paradigm which will soon replace the old statistical paradigm in biology. New data and conceptions in biology indicate that.

1. There are huge new paleontological data files which are impossible to explain in accordance with tihogenesis. 2. Acceptance and wide distribution of the punctuated equilibrium hypothesis (Eldredge, Gould, 1972). 3. Rapid expansion of EVO-DEVO branch of the developmental biology. Within this framework ontogenetic changes are represented as obviously determined and made up of blocks. 4. The notion of living systems as dissipative structures, which are characterized by self-assembly and self-maintenance (Prigogine, Stengers, 1986). 5. Wide discussion of “parallel evolution” problems. This is considered both at the “small scale” (parallel formation of the large taxonomic groups) and at the “large scale” (direct restricted variability in speciation and ecological race formation). The latter is demonstrated especially brightly using the complexes of ecological races and sibling species of *Littorina*.

In general, it seems that obvious background to change evolutionary tihogenetic notions to evolutionary orthogenetic ones, and “statistical” paradigm to “systemic” one, is well prepared. Subsequently, the main objectives, goals and methodology of routine evolutionary investigation will change. But it is natural for the science. As Thomas Kuhn wrote in his book “The Structure of Scientific Revolutions” (1962): “Successive transition from one paradigm to another via revolution is the usual developmental pattern of mature science”.

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# ***Littorina littorea* immunobiology**

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The common periwinkle, *Littorina littorea*, is the only representative of taxonomic clade Caenogastropoda established as an important immunobiological model. Presumably, natural die-offs resulting from exposure periwinkles to viruses or bacteria are very likely to go unnoticed, so the pathogen burden borne by littorinids may be much higher than presently appreciated. The main immune effectors in processes of an invader killing and elimination in mollusc are hemocytes. Only agranular cells were observed in the hemolymph of *L. littorea*: juvenile round cells, intermediate cells and large mature hemocytes with well appreciated defensive roles in phagocytosis, cytotoxic and encapsulation reactions. Key to understanding hemocyte effector functions are the intracellular signal transduction pathways likely to be activated by exposure of hemocytes to immune stimuli. We have characterized littorina STAT-protein, c-Jun N-terminal kinase, ERK and p38 MAPK-activated protein kinase and their transient activation in response to several immune inducers. Rel-like NF-kB transcription factor is also sequenced and identified, so Toll-like pathway homologs with their functional relevance are waiting for discovering. As compared to some other molluscs, the study of periwinkle hemocyte membrane-associated receptors is in its infancy. Just the integrin and LUSTR-like receptor present on the surface of *L. littorea* hemocytes have been documented till now. Humoral immune factors are important mechanisms in the architecture of periwinkle defense system. We have found and characterized three novel *L. littorea* lectins: C-type lectin, fibrinogen-bearing lectins and fucolectin with unique and previously unknown domain architecture. Antimicrobial peptides are presumably to be present in periwinkles although their descriptions are as yet absent.

The study is supported by RFBR grants 09-04-01255, 11-04-0156. Access to the animals and lab space during field studies are granted by WSBS "Kartesh".

# **Reproductive barriers between sister-species (*Littorina fabalis* and *Littorina obtusata*)**

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Mate choice is central to fitness of organisms and hence a key trait in the evolution of most species. Females are usually the most choosy sex as egg production is more costly than sperm production. However in species where males have extensive costs of mating, male mate choice is expected. For Littorinid snails, mate search is time- and energy consuming for the males and great benefits can be obtained from being choosy early in this process, for example when choosing a mucus trail to follow. We study male mate choice in *Littorina fabalis* using video recordings and live observations of pre-copula and copulation behaviours. Upon encounter, males preferred to mate large and more fecund females over small females. When offered a choice of different sized females they most frequently tracked mucus trails of the largest females, regardless if these were of the larger sister-species *Littorina obtusata*. However, copulations between the two species were rare and considerably shorter than intraspecific copulations, suggesting species-recognition mechanisms that prevent interspecific copulations. Hence, our study shows evidence of a trade-off for males that tend to choose female traits from large females over those of small females. Although fecundity increases by female size, there is also an increased risk to spend time and energy on tracing a female of another species.



# Embryo abnormalities in H and M *Littorina saxatilis* on eight shores in North East England

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At various sites across Europe, recent studies have shown that *Littorina saxatilis* is undergoing differentiation. One feature of the H and M populations on the North East coast of the UK is the presence of rare intermediates that contain a high proportion of abnormal embryos within the brood pouch suggesting a partial reproductive barrier. The current study aimed to determine if the proportion of embryo abnormalities was the result of extremes distribution or habitat type, high population densities, the incidence of parasitism within populations or occurred primarily in regions of population overlap between morphs. Using transects down the shore, animals were sampled across their entire distributional range of both H and M morphs on eight shores. Shores were chosen according to the relative overlap in distribution or presence absence of the two morphs; two shores contain either H or M only, two where H and M had little overlap and two where morphs are found along an environmental continuum and overlap in their distribution. Preliminary findings indicate that the proportion of abnormal embryos within the broods of the H and M morphs is not related to the incidence of parasitism, extremes in their distribution or habitat type, but appears to be related to the amount of overlap in the distribution of the two morphs.

# **Inheritance of bands and spots on the shell of *Littorina obtusata* (Gnastropoda: Prosobranchia)**

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Morphology and inheritance of brown, orange, white bands and pattern of white spots on the shell in the snail *Littorina obtusata* have been studied.

Two brown bands are located above and below the periphery of the whorl. These bands are formed as interlayers of brown pigment in the external part of ostracum. The maximum number of white bands is three. They are located at the suture, on the periphery of the whorl and in the columellar region. In some individuals, some of these bands may be absent. White bands are also formed as interlayers of pigment in the external part of ostracum. Orange band is always single; it is located on the periphery of the whorl. Such bands appear as interlayers of orange pigment in the internal part of ostracum, spread through the whole ostracum and disappear in the 4-5 year life, moving in to hypostracum. Bands of different colours may appear simultaneously on one specimen. White lenticular regions in the external part of ostracum correspond to a mottling. The arrangement and the degree of correlation between the elements of the spots pattern vary even within a single individual, even though all the elements are formed in a similar way.

Inheritance of bands and spots was studied by using the method of “mother-progeny”: the progeny of females caught in the wild was obtained and segregation in  $F_1$  was analysed. Half-sib families were divided into full-sibs by microsatellite DNA analysis. As the obtained results showed, five loci appeared to be involved in inheritance of bands and pattern of white spots. Brown and white bands are controlled by two separate biallelic genes. Presence of these bands is dominant to their absence. Separate gene is responsible for presence of an orange band, but presence of orange bands is recessive to their absence. The gene responsible for brown bands appears to be linked to that responsible for shell background coloration. Two separate complementary genes are responsible for presence of white spots. The presence of at least one dominant allele at both loci is necessary for manifestation of the trait. High variability of spots pattern indicates that it is controlled by much more genes than are found now.

# Thermal tolerance of *Echinolittorina* spp. in Hong Kong: implications for their vertical distribution?

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Temperature plays an important role in determining species' vertical distributions on intertidal rocky shores by affecting their fitness. Many studies have demonstrated that thermal tolerance of species is positively correlated with the shore height they occupy, and have investigated possible physiological and molecular mechanisms that drive variation between species. However, most work has been conducted in the temperate eastern Pacific and the Atlantic, and little is known about species in the tropical western Pacific. *Echinolittorina malaccana*, *E. radiata* and *E. vidua* are highly abundant, and show a distinct and consistent vertical distribution over tropical shores in the western Pacific, and as such are excellent models to investigate the relationship between thermal tolerance and vertical distribution. Field surveys and laboratory experiments reveals that in Hong Kong, thermal tolerance of *E. malaccana*, which dominates the highest shore level, is the greatest, followed by *E. radiata*, and finally the lower shore species *E. vidua*. As with studies in temperate regions, thermal tolerance increases with increasing shore height. These findings inform further investigations into the physiological and molecular mechanisms underlying a species' thermal tolerance, such as heart rate and enzymatic activities, in order to help explain the differential thermal tolerance of *Echinolittorina* spp.

# Evolutionary history and speciation in *Littorina* using a molecular phylogenetic approach

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*Littorina* gastropods have come to inhabit nearly every temperate rocky shore of the Northern Hemisphere. This group has been extensively studied taxonomically and ecologically, however their evolutionary history is still not entirely understood. Using collections of multiple individuals of all 18 described species, most throughout their ranges, we aim to examine the evolutionary history of this group. Eight species are known to be planktotrophic while nine have evolved encapsulated lecithotrophy and one viviparity. Previous studies have shown that migration rates and effective population sizes are significantly smaller in the species with non-planktonic larvae. Basic population genetic theory then predicts that selection should more quickly overcome the swamping effects of migration and local adaptation, so that speciation (and extinction) should occur more readily in these species. We aim to test this theory using a molecular coalescent phylogenetic approach, which will allow us to assess ancestral population sizes throughout the genus and differentiate the coalescent process of gene trees and the true species tree. Preliminary data suggest a species topology very similar to that derived from morphological characters, however more data are still needed to assess deeper relationships within the genus.

# Phylogeography of two Amphi-Pacific Gastropods, *Nucella lima* and *Littorina sitkana*

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Fluctuating climate over the last 2 million years (MY) has repeatedly caused latitudinal shifts in species distributions. But, did the glacial-interglacial dynamics of the Pleistocene drive regional genetic differentiation and potentially speciation? For species whose distributions spanned the entire north Pacific, regional extinction of northern populations during cooler glacial periods may have resulted in isolation of eastern and western populations, potentially leading to trans-Pacific differentiation and speciation. To characterize patterns of east-west differentiation in rocky-shore species whose current (i.e., interglacial) distributions span the entire north Pacific, we have gathered genetic data from two intertidal gastropods, *Nucella lima* and *Littorina sitkana*. MtDNA sequences from *N. lima* are reciprocally monophyletic with respect to eastern and western populations, suggesting an extended period of geographic isolation. In contrast, *L. sitkana* is continuously distributed across the entire North Pacific and lacks any obvious east-west mtDNA phylogeographic structure. To determine if differences in mtDNA genealogies actually reflect different population histories (rather than stochastic variation in gene tree coalescences), we have now gathered data from several nuclear genes, which will presumably allow us to jointly estimate divergence times, gene flow, and effective population sizes between eastern and western populations with greater precision than mtDNA alone.

# Thermal tolerance and heart function of littorinid snails: a comparison of tropical, subtropical and temperate species

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The temperature relationships of heart function of aestivating temperate, subtropical and tropical littorinid snails were investigated using impedance plethysmography, and related to their thermal tolerances, estimated as  $LT_{50}$ . There were clear differences in heart rate regulation between tropical and subtropical or temperate species. Tropical *Echinolittorina* species (*E. malacana* and *E. vidua*) showed good regulation of heart rate rendering it independent of temperature across a range of approximately 20-23°C. This falls within the range experienced under natural conditions. In contrast, subtropical *E. natalensis*, and subtropical and temperate *Afrolittorina* species showed mixed responses that included regulatory, semi-regulatory and non-regulatory responses to heat stress. Overall, subtropical *E. natalensis* showed semi-regulation, while *Afrolittorina* spp. (*A. africana* and *A. knysnaensis*) showed high individual variability, some animals exhibiting regulation while others did not. These effects appear to be largely phylogenetically determined as there were no differences in the responses of subtropical and warm temperate *A. africana* or between warm and cool temperate *A. knysnaensis*. Thermal tolerances conformed to expectations, with clear trends from high tolerance of tropical species to lower tolerances of temperate species. Thus,  $LT_{50}$  seems to reflect biogeography, while heart rate function is largely phylogenetically determined.

# Long-term population dynamics of *Littorina obtusata* and *L. saxatilis* in the White Sea

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*Littorina saxatilis* and *L. obtusata* were collected annually in two distinct locations of the White Sea during 16-years period (1982-1997). Sampling methods remained the same throughout the study. Population density, age, sex structure and prevalence with trematodes were assessed separately in different types of microhabitats, taking into account their zonal pattern. Linear regression model was used to describe the connection between population density and variable of interest estimated last year or year before the last one (age-specific population density, prevalence of trematodes, type of microhabitat, wet weight of macrophytes etc.). Our data indicate that *L. saxatilis* subpopulations from various microhabitats (stones, gravel, macrophytes) are different functional parts of a population as a whole. Mollusks of younger age seem to be associated with gravel and then, while growing, migrate to nearby fucoids or stones. Population dynamics of *L. obtusata* are in accordance with model of core population (with high level of self-sustenance) inhabiting lower intertidal zone, middle and upper littoral zones being “peripheral”. Population density in “peripheral” parts of the population is only dependent on core part, and shows no tendency for self-sustainment. Our data also show strong negative correlations between prevalence of trematode invasion (overall and for most abundant species) and population density of both littorinid species in the following year. This can be viewed as the first documented evidence of trematode invasion impact on littorinid population size.

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# Microspatial distribution of *Littorina saxatilis* and *L. arcana* sibling species: arguments for interspecific hybridization

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The two sibling species *Littorina saxatilis* (Olivi 1792) and *L. arcana* (Hannaford Ellis 1978) frequently occur in sympatry in the Barents and Norwegian Seas. Only mature females can be unambiguously distinguished on the base of the pallial gland complex structure. No clear-cut diagnostic features have been found to discriminate between males or juveniles of the two species. Nuclear DNA fragment A2.8 (Mikhailova et al., 2010) mostly characterized of *L. arcana* females and have never been discovered in the genomic DNA of *L. saxatilis* females and males from allopatric populations.

We discriminated between females using a combination of morphological criteria (the structure of the pallial gland complex) and molecular criteria (amplification of A2.8 fragment) and between males (molecular criteria). In some individuals molecular and morpho-anatomical criteria suggested conflicting species' affiliation. We hypothesized that interspecific hybridization were able to explain these observations and we used logistic regression models to examine the correspondence between hybrid frequencies and the distribution of parental species frequencies. Our data on microdistribution of unambiguous *L. saxatilis* and *L. arcana* individuals were in two sites studied able to explain the presence of about 20% interspecific hybrids. Moreover, hybridization seemed to be asymmetrical with *L. arcana* and *L. saxatilis* as partners.

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# Reproductive behaviour of mangrove littorinid snails: how do males successfully mate with females?

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Diverse reproductive behaviours in animals are developed to increase individual fitness. Some behavioural traits are selected to overcome environmental constraints, whereas others are evolved through sexual selection to maximize reproductive success. Most littorinid snails in the genus *Littoraria* inhabit mangrove trees in the Indo-Pacific region. Searching for mates within the complex 3-dimensional habitat of tree leaves, branches and trunks would appear a difficult task for these snails. Field studies of two co-occurring species in Hong Kong, *Littoraria ardouiniana* and *L. melanostoma*, however, showed that these species can successfully locate mates as over 90% of mating pairs were 'true' pairs (a male mating with a conspecific female). This success is achieved through males of both species following mucus trails to locate conspecific females during the mating season. In both species, males were also capable of detecting the direction (polarity) of the trails of conspecific females. "Fighting" behaviour, which involves two males aggressively pushing each other when they encounter a female, was also observed in *L. ardouiniana* but not in *L. melanostoma*. Such aggressive behaviour during mate acquisition can be attributed to the male-biased sex ratio in natural populations of *L. ardouiniana*, which may drive competition for mates amongst males.

# Inter-specific and intra-specific divergence in *Littorina* by microarray-based genomic hybridization

Marina Panova<sup>1</sup>, Carl André<sup>1</sup>, Björn Canbäck<sup>2</sup>, Kerstin Johannesson<sup>1</sup>,  
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Sequence divergence is used to estimate phylogenetic relationships between species and isolated population within species. However, gene trees may vary within a given species trees, and it has been a subject for a vivid debate how many and which genes should be used to reliably reconstruct the species history. When a suitable microarray platform is available, microarray-based comparative genomic hybridization may be an alternative way to reconstruct phylogenies, using hybridization success as approximation for sequence divergence between a test species and the species, represented on the array. We used high-density oligoarrays representing 25 000 partial gene transcripts and some genomic regions of *Littorina saxatilis* to reconstruct phylogeny of several North Atlantic *Littorina* species (*L. fabalis*, *L. compressa*, *L. arcana* and *L. saxatilis*) as well as to compare several geographic regions within *L. saxatilis* (Spain, UK and Sweden) and, finally, ecotypes found within these regions. Relative divergences between the studied species (estimated as number of probes with significantly different hybridization level) and their phylogenetic relationships (analyzed by PCA on hybridization signals) were surprisingly similar to the *Littorina* phylogeny, produced earlier by sequencing only few “traditional” genes (Reid et al. 1996). Moreover, clustering of geographic populations of *L. saxatilis*? close relationships between UK and Sweden and higher divergence of Spain? corresponded well to phylogeographic history of the species, reconstructed earlier from variation in the mitochondrial cytochrome b gene (Panova et al. 2011). Finally, we did not find any genes with significant divergence between *L. saxatilis* ecotypes in UK or Sweden, but 27 genes showed significant divergence between the Spanish ecotypes.

# A periwinkle supertree and its use to test hypotheses of reinforcement and life-history evolution

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A combination of molecular phylogenetics, anatomical and biogeographic study suggests that there are 152 biological species of true periwinkles (Littorinidae: subfamily Littorininae). For 147 (97%) of these, DNA sequences are now available from one nuclear (28S) and two mitochondrial genes (12S, COI) and these have been used to reconstruct a 'supertree' for the subfamily. This confirms the existing generic classification, but adds new information about relationships among deeper lineages.

Phylogenies are used to test evolutionary hypotheses. From the littorinine tree 40 sister-species pairs were identified as a test of the reinforcement hypothesis. This predicts that where sister species exist in sympatry selection will act to enhance morphological differences in male genitalia, so that penes of sympatric pairs should display significantly greater differences than those that are allopatric.

The new tree includes a more well-resolved phylogeny of the 18 species of *Littorina* than has been available previously, and permits a test of the hypothesis that direct development has arisen only once (in the subgenus *Neritrema*).

# Detection of divergent selection at genomic level in *Littorina saxatilis*

María José Rivas, Antonio Carvajal-Rodríguez

*University of Vigo, Spain*

On exposed intertidal rocky shores from Galicia (Northwestern Spain) there are two ecotypes of *Littorina saxatilis* adapted to different shore levels and microhabitats. These ecotypes hybridize at low frequency in the mid shore. Phenotypic and genetic differences have evolved between the two sympatric ecotypes causing a sharp ecological gradient. The ridged, banded and bigger form (RB) is usually found on the upper shore dominated by barnacles, while the smooth, unbanded and smaller one (SU) is found on the lower shore dominated by blue mussels. The thicker shells and smaller apertures of the RB snails are assumed to be an adaptation to intense predation by crabs, heat desiccation, and a lack of wave action. The SU snails, living in a high wave-action environment during the whole range of tides, tend to have more flattened thinner shells and have wider apertures to accommodate a larger foot, which provides a better grip on the substrate and allows for hiding in cracks and crevices. Thus, the two ecotypes of *L. saxatilis* living at different shore levels are being exposed to intense divergent selection.

In the present work we will modify a selection detection statistic to suit to the specific case of divergent selection in non-model species as is the case with *L. saxatilis*. In doing so, we will use empirical estimates of demographic parameters (migration, population size) from RB and SU to simulate the genomes of two populations undergoing divergent selection. The ultimate goal of our work is to develop a tool for detection of divergent selection at genomic level in non-model species.

# **About the meaning of the term hybrid in the Galician *Littorina saxatilis* hybrid zone: is exogenous or endogenous selection maintaining ecotype cohesión?**

Emilio Rolán-Alvarez<sup>1</sup>, María Saura<sup>1</sup>, Juan Galindo<sup>1</sup>,  
Mónica Martínez-Fernández<sup>1</sup>, Carmen López<sup>2</sup>, Jaime Gosálvez<sup>2</sup>, Zita Ferreiro<sup>3</sup>,  
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Hybrid zones represent key evolutionary processes for our understanding of ecological mechanisms of speciation. Two ecotypes of the intertidal marine gastropod *Littorina saxatilis* meet and mate in sympatry in a well-known ecological hybrid zone, showing a strong but incomplete pre-mating reproductive isolation. A recent review claims that even ecological hybrid zones should be preferentially maintained by endogenous rather than exogenous selection against hybrids (Bierne et al., 2011). We present here a number of experimental studies from our group that verifies the actual mechanism of maintenance of this hybrid zone. These include a number of laboratory crosses comparing F1 and parental progeny, a morphological (8 shell measurements) and genetic (1996 AFLP markers) study of hybrid specimens in the wild, and the application of a novel technique to infer the degree of sperm fragmentation in individual specimens in nature. The results point to a mechanism of extrinsic postzygotic isolation acting locally and differentially in each site, causing that hybrid unfit may vary across traits and localities, which could explain the absence of reinforcement in this system.

# **Parallel ecological divergence in the marine snail *Littorina saxatilis***

María Saura, Mónica Martínez-Frenández,  
Humberto Quesada, Emilio Rolán-Álvarez

*University of Vigo, Spain*

Ecotype formation in the marine snail *Littorina saxatilis* provides an excellent model system for the study of adaptation driven by ecological factors. In different geographic areas from Europe, morphologically different ecotypes coexist in sympatry, each one associated to different microhabitats from the intertidal zone. These ecotypes show partial reproductive isolation, producing narrow hybrid zones in the overlapping zone. Two major evolutionary processes have been proposed for the origin of these ecotypes: 1) divergence in allopatry followed by secondary contact, and 2) non-allopatric divergence by parallel or repeated evolution. Both scenarios allow performing different predictions on the phylogeographic distribution of haplotypes in both neutral and adaptive loci. In this study, we have tested these predictions through the analysis of morphological and phylogeographic variation of mitochondrial DNA in the three geographical areas where these ecotypes are better characterized (Sweden, UK and Spain). Our results support the hypothesis that non-allopatric and parallel evolution have played a key role in the ecological adaptation of these ecotypes, at least in the Galician shore.

# What is the value in modelling the behaviour of populations of snails?

Richard Stafford<sup>1</sup>, Gray A. Williams<sup>2</sup>, Mark S. Davies<sup>3</sup>

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<sup>3</sup>*University of Sunderland, UK*

High shore littorinid snails lend themselves to attempts to model their behaviour using simple theoretical rules because they often live in more-or-less two dimensional habitats and have few predators. In general we have found the outputs of such computer models closely match observed distribution patterns on the shore. These findings raise the obvious questions of 'what use are these models' and 'what can they tell us that is not obvious from traditional observations or experiments?'

At low tide we see complex distribution patterns of inactive snails, often involving aggregations in crevices, that may be regarded as emergent properties or self-organisation. Computational techniques allow us to investigate how such self-organisation can arise and be maintained.

The self-organisation appears to be relatively insensitive to changes at the individual agent (organism) level and so is largely self-perpetuating. Since information-processing of self-organised groups may not need to be as great as for agents performing tasks alone, it is possible that self-organisation allows organisms to bypass the development of complex sensory systems yet still behave optimally in relation to environmental conditions.

Such agent-based computer simulations allow manipulations that are not physically possible. For example, we can programme simple behavioural rules and determine how the outcomes match reality to try to understand decision-making process in animals with relatively rudimentary nervous systems. We can then vary or even remove these rules individually and examine the resultant virtual distribution patterns. Our studies show that a few simple rules can generate complex spatial patterns and, using an evolutionary algorithm, the models can explain how co-operative behaviour might evolve.

From this finding arises the question, 'is the behaviour we have described purely co-operative or are there 'cheats' in the system'? By manipulating virtually the proportion of cheats we show co-operation in a two-species system to be relatively robust to the presence of cheats, implying that the selective pressures acting on the two species are different.

Models, therefore, can move us beyond what we know from palpable study. The question is, if we can't test the results against reality, how can we be sure?

# The detection of shell shape differences in “*saxatilis*” species complex by geometric morphometric methods

Zinaida Starunova<sup>1</sup>, Andrey Granovitch<sup>1</sup>, Natalia Mikhailova<sup>1,2</sup>

<sup>1</sup>St.Petersburg State University, <sup>2</sup>Institute of Cytology RAS, Russia

Geometric morphometric methods were used to study of shell shape differences in three rough periwinkles of “*saxatilis*” species complex. Due to the difficulties with males identification only shell of females *L. saxatilis*, *L. arcana* and *L. compressa* were analyzed. Material was collected from populations of the Barents Sea (Russia), where populations of the sister species coexist in sympatry. It was shown that *L. arcana* population is tightly linked to the upper gravel intertidal zone; *L. compressa* is common in the low part of *Fucus vesiculosus* belt whereas *L. saxatilis* is widely-distributed and habitats all intertidal levels from the upper gravel zone till the low tide level. Results obtained with the help of geometric morphometric methods shown that shall shape of *L. saxatilis* from the upper and lower intertidal zones are strongly differs. There are significant differences between shell shape of *L. arcana* and *L. saxatilis* as well as between of *L. saxatilis* and *L. compressa* from sympatric populations in the same intertidal zone. Intraspecific differences associated with various microbiotops. Intraspecific and interspecific variability of shell shape is visualized with the help of geometric morphometric methods. We assume that intraspecific plasticity of shell shape can overlay interspecific in “*saxatilis*” species complex.

This study was supported by Russian Foundation for Basic Research (grants 09-04-01728-a, 10-04-10039-k, 11-04-10040-k) and St.Petersburg State University (expedition grant 1.42.527.2011).



# Thermal tolerance of *Echinolittorina* snails in the Indo-West Pacific: are we measuring the right variables?

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It is generally accepted that predicted climate change scenarios will result in dramatic changes to species' ranges. Littorinid snails are excellent candidates to study the potential impact of predicted climate change on intertidal organisms as they are widely distributed around the world, often inhabiting the physically-stressful eulittoral zone where they are assumed to be already living close to their thermal limits. The wide distribution and well studied phylogeny of the monophyletic genus *Echinolittorina*, in the Indo-West Pacific, makes this genus well suited to the investigation of potential species range shifts. In June 2009, a workshop attended by 20 researchers from 8 countries covering 31° latitude from Qingdao in northern China to Singapore, was held to devise experiments to determine variation in temperature tolerance of *Echinolittorina*. Participants collaborated to quality-assure appropriate experimental protocols to measure the Lethal Temperature (LT<sub>50</sub>) of *Echinolittorina* at their own home locations. LT<sub>50</sub> values indicated a slight latitudinal trend, and ranged between 55-59°C, which is well above predicted, climatically derived estimates of global warming. Predictions of climate change, however, are traditionally derived from modeled changes in air or seawater temperatures. In the case of high shore littorinids, this may be misleading because they derive much of their heat from solar radiation and conduction from the substratum, confounding our predictions of the impact of climate change.

# Shell morphology and microstructure of two Singapore littorinids, *Echinolittorina malaccana* and *E. vidua*

Cynthia Yee-Man Wong, Shirley S.L. Lim

*Nanyang Technological University, Singapore*

Littorinids *Echinolittorina malaccana* and *E. vidua* in Singapore orient 'in-line' to sun's direction and 'stand' respectively during low tide. Inter-specific differences in the shell morphology and microstructure of the littorinids were studied. Morphological parameters such as shell length, shell width, shell weight, inner and outer aperture length and width were measured and were used to determine the following morphological characteristics: aperture area, apical angle, shell thickness, shell spire and shell volume of the two species. Principal component analysis showed that the shell length and shell width accounted for the highest variances among the observed variables in *E. malaccana* whereas shell width and outer aperture width accounted for the highest variances in *E. vidua*. These results provide quantitative evidence to support visual observations that *E. malaccana* is elongated whereas *E. vidua* is globose. Scanning electron microscopy revealed that both *Echinolittorina* species have aragonitic shells consisting of cross-lamellar layers, which are the structural characteristics of shells found in tropical regions. The thermal conductivity of the outer shell surface (estimated using a gem tester) of *E. malaccana* is higher than that of *E. vidua*, suggesting that heat is more readily gained in *E. malaccana* than in *E. vidua*. The light-grey, rough and nodulous outer shell surface of *E. malaccana*, however, maximizes the effect of convection to allow cooling. The outer shell surface of *E. vidua*, despite being lower in thermal conductance, is smooth and dark-brown in colour which encourages effective heat gain. The inter-specific differences in the shell morphology, thus, suggests that the two *Echinolittorina* species adopt different behavioural responses to overcome thermal stress: elongated *E. malaccana* minimises heat gain by aligning its major axis parallel to sun's direction whereas globose *Echinolittorina vidua* 'stands' to minimise heat gain from rock surface.

# A cryptic species of *Littorina sitkana* from Western Pacific: new data findings on the basis of a mitochondrial DNA analysis

Nadezhda I. Zaslavskaya<sup>1</sup>, L. Nicole Cox<sup>2</sup>, Peter B. Marko<sup>2</sup>

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In 2004, a genetically distinct species of *Littorina* was found through allozyme electromorph comparisons of snails from rocky shores of the northwestern Pacific at Kasatka Bay (Pacific coast of Iturup Island). The new species (*L. sp.*) was sympatric with *L. sitkana*. The extent of genetic differentiation between these species ( $D=0.622$ ) corresponded with the mean level of differentiation for congeneric species estimated by Thorpe (1982) for various taxonomic levels. *L. sp.* inhabits the middle littoral zone but absent from the upper littoral zone where *L. sitkana* was abundant. Structural similarities in the reproductive systems of *L. sp.* and *L. sitkana* suggested they are sister-species.

We assessed species status by sequencing 671 base pairs of the mitochondrial cytochrome *b* (*cyt b*) gene in *L. sitkana* and its putative sister species, *L. sp.*, from the eastern and western Pacific. Comparisons of DNA-sequences support the hypothesis that *L. sp.* is a distinct species. The new species was found on Sakhalin Island, the Kamchatka Peninsula and Iturup Island together with *L. sitkana*. The specimens of this species form a distinct group (100% bootstrap support) from *L. sitkana*.

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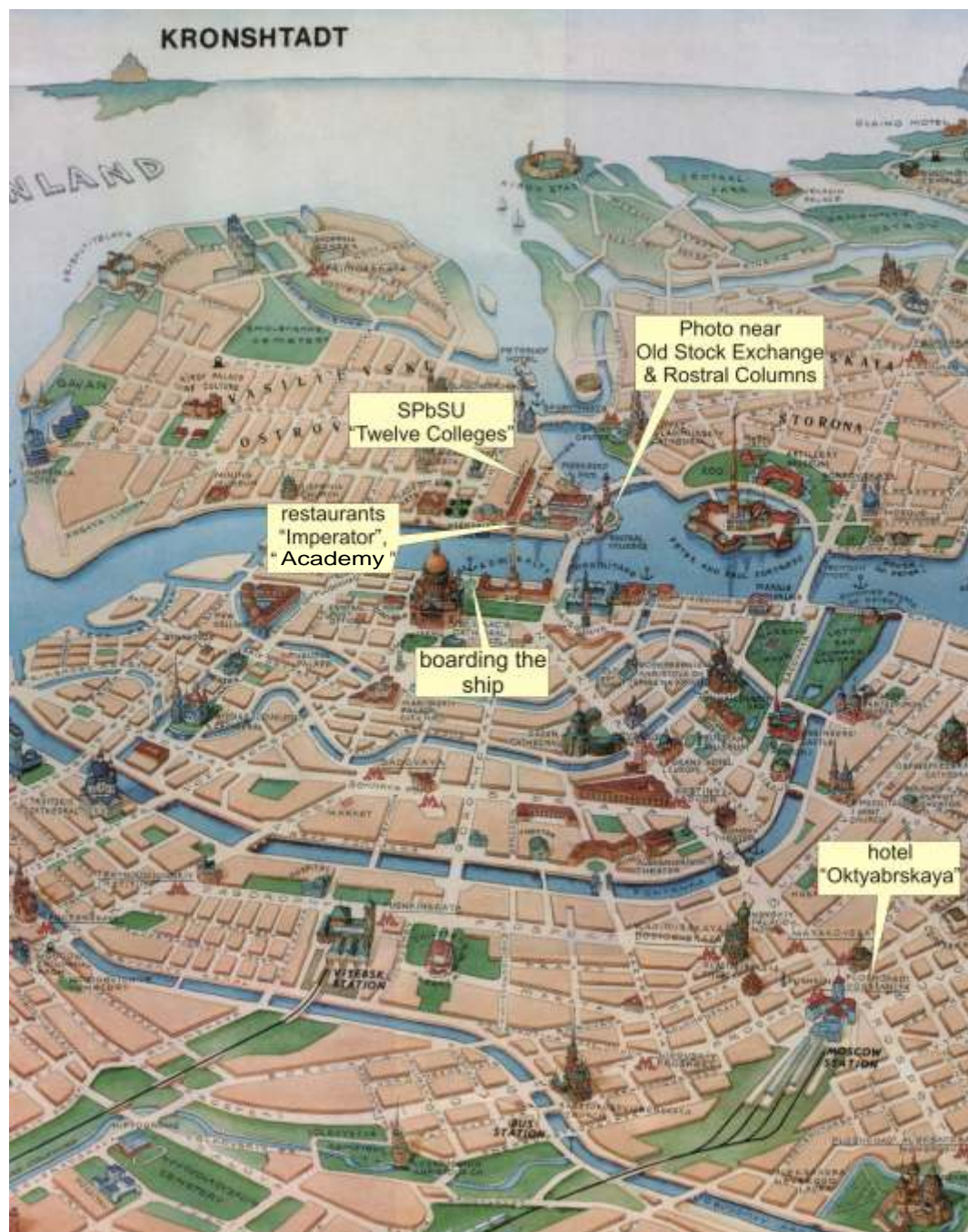
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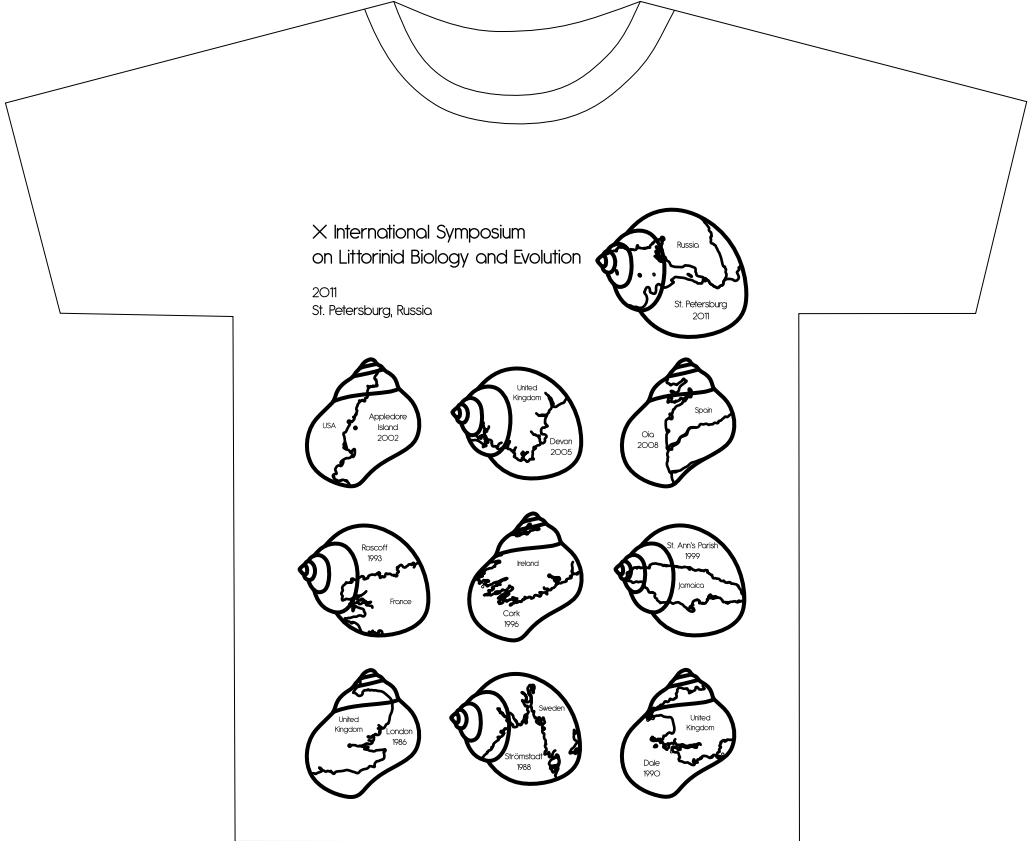
# APPENDIX

# Symposium Schedule

Time	Monday 25.07	Tuesday 26.07	Wednesday 27.07	Thursday 28.07
8.00	Breakfast	Breakfast	Breakfast	Breakfast
9.00	Registration			Peterhof park
10.00	Opening session at Petrovsky Hall	Oral 10-13	Oral 22-25	
11.00	coffee break	coffee break	coffee break	
12.00	Oral 1-3	Oral 14-16	Oral 26-28	
13.00	Lunch	Lunch	Lunch	
14.00				Lunch
15.00	Oral 4-6	Oral 17-19	Oral 29-31	Invited lecture
16.00	coffee break	coffee break	coffee break	coffee break
17.00	Oral 7-9	Oral 20-21	Oral 32-34	ISOLBE Committee summit Poster session
18.00	Dinner	Banquet dinner onboard the ship	Dinner	Dinner
19.00	Photo		Free time	
20.00	City bus tour			







Design by Daria Krupenko



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Front cover photo:

*"Hallway in the Twelve Collegia building"* by Zinaida Starunova

Back cover photo (from up to bottom):

*"The Barents sea, near the Marine Station at Dalnie Zeletsy"*

by Andrei Granovitch

*"Are they all saxatilis?"* by Ylia Gracheva

*"The White sea"* by Gita Paskerova

Map of St.Petersburg from

<http://mappery.com/map-of/St-Petersburg-Tourist-Map-2>

Symposium symbol by Andrei Granovitch

Design of T-shirt by Daria Krupenko

Layout by Zinaida Starunova & Natalia Mikhailova

