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Report

**Artedi Lectures in Systematic
Ichthyology**

23 April 2013

Beijer Hall, the Royal Swedish Academy of Sciences, Stockholm



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About the Artedi Lecture series

The Artedi Lectures are given in commemoration of Sweden's famous ichthyologist Petrus Artedi (1705-1735). Chosen to be lecturers are ichthyologists of considerable scientific excellence and recognition, who have made a contribution to ichthyology by a broad approach combining discovery, description, analysis and synthesis in a way that has significantly enthused new generations of ichthyologists.

The first Artedi Lectures were organised by FishBase Sweden, the Swedish Museum of Natural History and the Royal Academy of Sciences in 2005, at the tercentennial of Artedi's birth. Lecturers were five renowned fish researchers, drs G. David Johnson, Maurice Kottelat, Richard L. Mayden, Lynne R. Parenti and Mutsumi Nishida. The 2008 Lectures were given by Drs Joseph Nelson, Gloria Arratia and Meemann Chang.

This year, lectures attracted the largest audience ever. Attendants got the opportunity to listen to three highly interesting presentations on the origin of fishes, by drs Min Zhu from Chinese Academy of Sciences in Beijing, Philippe Janvier from Muséum national d'Histoire naturelle in Paris and Per Ahlberg from University of Uppsala.

By organising the Artedi Lectures, we hope to inspire more systematic research and highlight the importance of the contemporary systematics to the study of the biological diversity of the Earth as well as the early Swedish contribution to the field by Artedi, Linnaeus and the Royal Academy of Sciences, of which the Swedish Museum of Natural History was then a part.

Petrus Artedi

Petrus Artedi was born to the parish of Anundsjö in northern Sweden, and grew up in Anundsjö and the nearby town of Nordmaling. In 1724 he matriculated at Uppsala University where he made a lasting acquaintance with Carl Linnaeus. Artedi and Linnaeus both specialized in the study of natural history and pioneered biological systematics as now known. Artedi designed the system of naming organisms by a generic name and a specific epithet, and from that Linnaeus created the binominal nomenclature and hierarchical classification that is still in use for all organisms.

Artedi's life was short. In 1735 he drowned in a canal in Amsterdam, leaving in the aftermath only fragments of knowledge about his person - just a few manuscripts, a single letter, Linnaeus' brief summary of his life and career, no portrait, no diary, and not even any scientific correspondence. Linnaeus, however, published his major manuscript, in 1738 as *Ichthyologia sive Opera omnia de piscibus*. It became the starting point for modern descriptive systematics and created a standard for fish taxonomy that is still followed today. Artedi's interaction with Linnaeus was apparently also influential for the development of Linnaeus' achievements in organismal systematics.

Petrus Artedi – Father of Modern Ichthyology

Artedi Lecture on Systematic Ichthyology

23 April 2013, 9:00 – 13:30

Beijer Hall, The Royal Swedish Academy of Sciences, Stockholm

Programme

Moderator Professor Else Marie Friis, Swedish Museum of Natural History

- 9:00 – 9:20** Registration, coffee
- 9:20 – 9:25** Professor Else Marie Friis
Welcome address
- 9:25 – 9:30** Professor Staffan Normark, Permanent secretary, Royal Swedish Academy of Sciences
Opening address
- 9:30 – 10:20** Philippe Janvier, Muséum national d'Histoire naturelle, Paris, France
The history of jawless fishes: cyclostomes and stem gnathostomes
- 10:20 – 11:10** Professor Min Zhu, Chinese Academy of Sciences, Beijing, P.R. China
Chinese fossil fishes from deep time shed critical light on the origin and early evolution of jawed vertebrates
- 11:10 – 11:30** Coffee break
- 11:30 – 12:20** Professor Per Ahlberg, University of Uppsala, Sweden
Evolution, development and the origin of the jawed vertebrate face: evidence from the earliest fossil fishes
- 12:20 – 12:30** Professor Staffan Normark
Presentation of Artedi Lecturer diploma
- 12:30 – 12:35** Close of the symposium

12:35 – 13:30 Lunch

At Klubbvillan, to the left outside main building

Artedi lectureships 2013

Introduction

The Artedi 2013 lectures focused on early vertebrate evolution, and the relationship of the jawless cyclostomes (lampreys and hagfishes) to the jawed gnathostomes (all other vertebrates). This is a field which has deep roots at the Swedish Museum of Natural History, through the pioneering work of professor Erik Stensiö, but which has also seen great recent advances. New technologies such as x-ray microtomography scanning, and the recent discoveries of exceptionally well-preserved fossils are revolutionizing our view of early vertebrate evolution and the origin of jawed vertebrates.

After a welcome greeting by the moderator, professor Else-Marie Friis of the Swedish Museum of Natural History, the Permanent secretary of the Royal Swedish Academy of Sciences Staffan Normark gave the opening address. The moderator then introduced the first speaker.

Dr. Philippe Janvier of the Centre National de la Recherche Scientifique and the Muséum National d'Histoire Naturelle, Paris, talked about the “ostracoderms” and the two competing theories that hagfishes and lampreys either form a monophyletic group, or are independent offshoots of the branch leading to the gnathostomes. Professor Zhu Min, of the Chinese Academy of Sciences, Beijing, showed us remarkable fossils from the Silurian Xiaoxiang fauna. *Guiyu*, the “ghost fish”, is the earliest near-complete fossil of a jawed fish, and the discovery is pushing back the origin of the gnathostomes to well before the Devonian, while other three-dimensionally preserved fossils show characters of both jawless and jawed fish. Professor Per Ahlberg of the University of Uppsala, talked about how the evolution of skull morphology was related to the migration of neural crest cells during early embryonic development, and introduced the methodology of x-ray synchrotron microtomography scanning as a revolutionary method for visualizing three-dimensional fine detail of fossils.



Artedi Lectures 2013. From left: Dr. Sven O. Kullander; Professor Else Marie Friis; Professor Staffan Normark, Permanent Secretary of the Royal Swedish Academy of Sciences; Professor Per Ahlberg, Dr. Philippe Janvier and Professor Zhu Min.

Speaker presentations

Dr. Philippe Janvier is currently Director of Research at the Centre National de la Recherche Scientifique (CNRS) and head of the Research Centre for Palaeobiodiversity and Palaeoenvironments at the Muséum National d'Histoire Naturelle, Paris. He did his PhD at the University of Paris under the supervision of Prof. J.P. Lehman, and later worked (1972-1974) at the Palaeozoology section of the Naturhistoriska Riksmuseet, Stockholm, under the direction of professors Erik Jarvik and Tor Ørving. He later returned to France, where he became (1975) a CNRS researcher at the Muséum National d'Histoire Naturelle, where he has remained since. Philippe Janvier is a specialist of Palaeozoic fishes and early vertebrate phylogeny, hence his numerous field expeditions on the Palaeozoic vertebrate sites, notably in Spitzbergen, South America and Southeast Asia, in search for fossil fishes. His book *Early Vertebrates* (1996) sums up the current data on the subject. He was awarded the Del Duca Prize of the French Academy of Science in 2008 for his contribution to the knowledge of vertebrate phylogeny and evolution.



Staffan Normark, Philippe Janvier



Min Zhu

Professor Zhu Min is one of the world's best known paleoichthyologists. Born in China, he received his Ph.D from the Chinese Academy of Sciences in 1990 on Devonian placoderms (~400 million-year-old armoured fishes), and conducted post-doctoral research at the National Museum of Natural History in Paris and at the Museum of Natural Science in Berlin. As the director of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) in Beijing from December 1999 to February 2008, Professor Zhu developed the Institute into one of the world's leading centers of paleontology and evolutionary biology in the 21st century. A feature story in the January 12, 2001 issue of *Science* praised him for applying "youthful vigor" to promote paleontological research and institutional reform in China. Through some 90 scientific papers and books, Professor Zhu has made outstanding contributions to the studies on the morphology, histology, phylogeny, biogeography and evolutionary history of many early fish groups.

Professor Zhu is recognized for revitalizing the quest for the origin of osteichthyans (bony fishes and tetrapods) from non-osteichthyan gnathostome groups, backed by his field work to unveil many early fossils with exceptional character complement, and for making unique contributions to the research on the fish-tetrapod transition and the origin of the jaw as well.

Professor Per Erik Ahlberg. Born in Stockholm in 1963, I moved with my parents to London in 1977 and ended up spending the next 26 years in Britain. I studied Natural Sciences at University of Cambridge, gaining a BA in Zoology in 1985, and stayed on to do a PhD on porolepiform fishes (a group of extinct lobe-fins from the Devonian period) under the supervision of Dr Jennifer A. Clack. This was followed by five years as a Departmental Lecturer in Zoology at University of Oxford before I took up a research position in Palaeontology at the Natural History Museum, London, in 1994. In 2003 I returned to Sweden to become Professor of Evolutionary Organismal Biology at Uppsala University. In 2012 I was elected a member of the Royal Swedish Academy of Sciences.

The palaeontological research of my group focuses mainly on the early evolution of vertebrates, with special emphasis on the origin of jawed vertebrates and the transition from fish to land animals. Most of the fossils we study come from the Silurian (443-419 million years ago) and Devonian (419-359 million years ago) periods. Noteworthy discoveries include the Devonian tetrapods *Elginerpeton* and *Ventastega*, as well as the earliest known tetrapod footprints in the world, from a Middle Devonian locality in Poland. At present we are working on a number of projects including a study of the origin of the jawed vertebrate face, based around the Early Devonian placoderm (primitive armoured fish) *Romundina*. Most of this research utilizes very high resolution tomographic scans made at the European Synchrotron Radiation Facility (ESRF) in Grenoble. We are also interested in the interaction between evolution and development, and have created a zebrafish facility (which forms part of the Comparative Genetics Platform of the national infrastructure initiative SciLifeLab) to study the molecular regulatory basis for certain aspects of vertebrate development.



Staffan Normark, Per Ahlberg

The history of jawless fishes: cyclostomes and stem gnathostomes

Philippe Janvier

Muséum National d'Histoire Naturelle, UMR7207 du CNRS, 8 rue Buffon, 75231 Paris Cédex 05, France; janvier@mnhn.fr

Living jawless fishes, or cyclostomes, are a minor vertebrate group of only ca 107 species belonging to two clades, hagfishes (Hyperotreti or Myxiniiformes) and lampreys (Hyperoartia or Petromyzontiformes). They have been first considered as a monophyletic group, and an early offshoot of the vertebrate tree, but it was later suggested that they could be paraphyletic, thus possibly providing information about the stepwise assembly of the vertebrate body plan and the evolutionary transition towards the jawed vertebrates, or gnathostomes. Now, extensive molecular data strongly support cyclostome monophyly, but recent studies on various micro-RNA expression profiles during development also suggest that some of the supposedly primitive features of the cyclostomes are in fact the result of character losses, a discovery that supports old conceptions about the “degeneracy” of these jawless fishes. Living cyclostomes differ from living gnathostomes by a considerable phenotypic (morphological and physiological) gap, and thus tell us little about the origin of the gnathostome characters. Nevertheless, this gap is “filled” by a number of strongly ossified, Early Palaeozoic jawless fishes (“ostracoderms”), and we owe the Swedish palaeontologist Erik A. Stensiö the elucidation of the anatomy of these extinct fishes, which he first regarded as ancestral to the cyclostomes but are now interpreted as jawless stem gnathostomes. Here we trace back the reasoning of Stensiö and some of his disciples who, although defending the monophyly of jawless vertebrates as a whole, paradoxically paved the way to the current views on the evolutionary transition from jawless to jawed vertebrates. Since Stensiö’s early works on “ostracoderms”, new major jawless fish clades have turned up, such as the arandaspids, galeaspids or pituriaspids, and new imaging techniques now allow reconstructing their anatomy in detail. However, the question of the origin of jaws still rests essentially on developmental data, and “ostracoderms” only provide information on certain cranial structures that are prerequisites to the rise of jaws.

The stem of the gnathostome tree is partly elucidated thanks to the fossil “ostracoderms”, but that of the cyclostome tree still remains obscure because of the lack of a mineralized skeleton, even in the earliest presumed cyclostome relatives. However, exceptional cases of soft tissue preservation or occasional cartilage calcifications in certain, Early Palaeozoic cyclostome-like fossils throw some light on this early divergence in vertebrate history.

Chinese fossil fishes from deep time shed critical light on the origin and early evolution of jawed vertebrates

Min ZHU

Key Laboratory of Vertebrate Evolution and Human Origin of CAS, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (CAS), Beijing 100044, China; zhumin@ivpp.ac.cn

The past two decades have seen inspiring discoveries of primitive fishes from the Silurian and Early Devonian of China. These findings have yielded unprecedented character complements for inferring the sequence of character transformation at the root of osteichthyans (bony fishes plus tetrapods), and at the root of modern jawed vertebrates in general, and have shed significant light on other key issues bearing on the origin and early evolution of jawed vertebrates.

A recent study on the cranial anatomy of galeaspids, a 435–370-million-year-old jawless group from China and northern Vietnam, has provided the earliest fossil evidence for the disassociation of the nasohypophyseal complex in vertebrate phylogeny, a condition that current developmental models regard as prerequisites for the development of jaws. The anatomical details of the fossil intersect with predictions of developmental biology-based hypotheses, adding a rare dimension to both paleontological and developmental studies on the origin of vertebrate jaws.

The gnathostome or jawed fish findings from the Silurian Xiaoxiang Fauna of China have pushed the early radiation of jawed vertebrates well before the advent of the Devonian period or the 'Age of Fishes'. As the first significant finding of the Xiaoxiang Fauna, *Guiyu* ('ghost fish') - the oldest near-complete gnathostome - provides critical fossil record to calibrate the molecular clock regarding the divergence time between two major osteichthyan lineages (i.e., actinopterygians and sarcopterygians). Coupled with seven other early sarcopterygians from the Silurian and earliest Devonian strata of southern China, *Guiyu* establishes the paleobiogeographic importance of ancient South China region as a center of origin and diversification for sarcopterygians. Most recent discoveries of the Xiaoxiang Fauna include a three-dimensionally preserved armoured fish that displays typical placoderm features yet also has features previously restricted to osteichthyans such as the presence of premaxilla, maxilla and dentary, thus offering a new model for studying the origin of modern gnathostome morphology. The research on the Xiaoxiang Fauna promises to improve our understanding of early diversification of jawed vertebrates, especially when the range of morphological features found in acanthodians and the various primitive placoderms can be fully deciphered and analyzed in light of the new paradigm regarding the origin of osteichthyans from non-osteichthyan groups.

Evolution, development and the origin of the jawed vertebrate face: evidence from the earliest fossil fishes

Per Erik Ahlberg

Department of Organismal Biology, Uppsala University, Norbyvägen 18A, 752 36 Uppsala;
per.ahlberg@ebc.uu.se

The most fundamental phylogenetic and anatomical divide among living vertebrates is that between the jawless cyclostomes (lampreys and hagfishes) and the jawed gnathostomes (all other vertebrates), two lineages that appear to have separated from each other at least 500 million years ago. Differences between them can be seen in most parts of the anatomy, but nowhere more so than in the contrasting architecture of the face. Cyclostomes have a single median nasohypophysial duct, an anterior hypophysis and a short forebrain, while gnathostomes have a pair of nasal sacs opening externally, a more posterior separate hypophysis opening in the palate and a longer forebrain. These differences have their basis in the development of the face. In cyclostomes, infraorbital premandibular crest cells migrate forwards either side of the nasohypophysial placode to form the upper lip; in gnathostomes they migrate between the hypophysial and nasal placodes to form the trabecular-ethmoid region. Supraoptic neural crest remains posterior to the nasohypophysial duct in cyclostomes, whereas it moves forward to create the nasal capsules in gnathostomes.

The gnathostome stem group, i.e. the assemblage of fossil vertebrates that falls outside the clade of extant gnathostomes but is more closely related to it than to cyclostomes, includes both jawless and jawed forms. A jawless, cyclostome-like anatomy is thus primitive for vertebrates as a whole and ancestral to gnathostome anatomy. Some fossil forms illustrate a sequenced transition between these two patterns. The Silurian galeaspid (jawless stem gnathostome) *Shuyu* has a nasohypophysial duct, a short telencephalon, and an anteriorly oriented hypophysis, but the paired nasal sacs and hypophysis are separated by a rudimentary trabecula. A synchrotron-scanned skull of the primitive Early Devonian placoderm (jawed stem gnathostome) *Romundina* shows a cranial cavity reminiscent of that of *Shuyu* (anteriorly directed hypophysis, very short telencephalon). The trabecular-ethmoid region is long and wide, extending anterior to the small nasal capsule which is located just in front of the orbits. We interpret these features as uniquely primitive among gnathostomes. In size and position the trabecular-ethmoid region of *Romundina* resembles the upper lip of cyclostomes and *Shuyu*, suggesting a cyclostome-like pattern of proliferation coupled with a gnathostome-like migration path for the premandibular crest. The position of the nasal capsule suggests that the supraoptic crest had not migrated forwards. A new phylogenetic analysis suggests that the evolutionary sequence for the creation of the extant gnathostome face from a cyclostome ancestral pattern involved 1) separation of the nasal and hypophysial placodes (galeaspids: *Shuyu*), 2) loss of the nasohypophysial duct (basal placoderms: antiarchs, *Brindabellaspis*, *Romundina*), 3) shortening and narrowing of the trabecular-ethmoid region, the nasal capsule becoming anterior (derived placoderms such as arthrodires); 4) lengthening of the telencephalon (crown gnathostomes). Galeaspid facial anatomy appears closer to gnathostomes than that of osteostracans, but it is unclear whether osteostracans are primitive or autapomorphic in this respect.

List of participants, Artedi Lectures 2013

Artedi Lecturers

Philippe Janvier, Muséum National d'Histoire Naturelle , France

Min Zhu, Chinese Academy of Sciences, China

Per Ahlberg, Uppsala University, Sweden

Opening address

Staffan Normark, Royal Swedish Academy of Sciences, Sweden

Moderator

Else Marie Friis, Swedish Museum of Natural History, Sweden

Participants

Yvonne Arremo, Swedish Museum of Natural History, Sweden

Hans Ackefors, Stockholm University, Sweden

Gunnar Aneer, Sweden

Germund Beliaev, Sweden

Stefan Bengtson, Swedish Museum of Natural History, Sweden

David Bernvi, Stockholm University, Sweden

Maria Bíró, Hungary

Péter Bíró, Balaton Limnological Institute, Hungary

Henning Blom, Uppsala University, Sweden

Bertil Borg, Stockholm University, Sweden

Ulf Borgen, Sweden

Oskar Bremer, Uppsala University, Sweden

Donglei Chen, Uppsala University, Sweden

Daniel Ocampo Daza, Uppsala University, Sweden

Bo Delling, Swedish Museum of Natural History, Sweden

Vincent Dupret, Uppsala University, Sweden

Bo Fernholm, Swedish Museum of Natural History, Sweden

Christina Franzén, Swedish Museum of Natural History, Sweden

Gun Frostling, Sweden

Harald Frostling, Sweden

Mikael Himberg, Åbo Akademi University, Finland

Philip Jacobsson, Sweden

Linus Jaenson, Stockholm University, Sweden

Anna Jerve, Uppsala University, Sweden

Torbjörn Järvi, Sweden

Leif Jonsson, Göteborg Natural History Museum, Sweden

Bodil Kajrup, Swedish Museum of Natural History, Sweden

Daniela Kalthoff, Swedish Museum of Natural History, Sweden

List of participants, continued

Kamlesh Khullar, Swedish Museum of Natural History, Sweden
Sven Kullander, Swedish Museum of Natural History, Sweden
David Lagman, Uppsala University, Sweden
Dan Larhammar, Uppsala University, Sweden
Anna Lindström, Swedish Museum of Natural History, Sweden
Tyrone Lundström, Stjerberg trading, Sweden
Thomas Mörs, Swedish Museum of Natural History, Sweden
Grzegorz Niedzwiedzki, Uppsala University, Sweden
Åsa Nilsson, Stockholm University, Sweden
Michael Norén, Swedish Museum of Natural History, Sweden
Lennart Nyman, Man & Water, Sweden
Susanne Nyquist, Swedish Museum of Natural History, Sweden
Lilianna Olimpia Pap, Stockholm University, Sweden
Carl Pleijel, Guest researcher PZ-NRM, Sweden
Onésime Prud'homme, Swedish Museum of Natural History, Sweden
Chrysoula Roufidou, Stockholm University, Sweden
Piotr Rowiński, Stockholm University, Sweden
Mark Sabaj Pérez, Drexel University, USA
Sophie Sanchez, Uppsala University, Sweden
Daniel Snitting, Uppsala University, Sweden
Anders Stark, National Food Agency, Sweden
Viktor Thunell, Stockholm University, Sweden
Anna Wall, Stockholm University, Sweden
Hoshuai Wang, Stockholm University, Sweden
Lars Werdelin, Swedish Museum of Natural History, Sweden
Ulf Wiel-Berggren, Sweden
Lovisa Wretman, Uppsala University, Sweden
Rickard Yngwe, Stockholm University, Sweden
Rihab Yousif, Swedish Museum of Natural History, Sweden
Erik Åhlander, Swedish Museum of Natural History, Sweden

