

The
LINNEAN
SOCIETY
of London



**A CONTRIBUTION TO THE ORIGIN AND EARLY
EVOLUTION OF SNAKES**



© Gabriela Bittencourt Silva

Monday 24 June 2019 09:30–19:00
*The Linnean Society of London,
Burlington House,
Piccadilly, London, W1J 0BF*

Snakes are a major clade of vertebrates, comprising > 3,700 extant species found on all major continents except Antarctica. They exhibit a wide range of body-form and ecological diversity including fully fossorial, arboreal and marine forms, and species feeding on social insects to large mammals using macrostomy, constriction and envenomation. Although unarguably squamates, snakes are phenotypically strikingly different from their extant lizard relatives, and thus their origins and early diversification have long enthused and challenged evolutionary biologists. The origin and early evolution of snakes is a broadly interdisciplinary topic for which experts in palaeontology, ecology, physiology, phylogenetics and molecular developmental biology have made important contributions. Within the last 20 years there has been a surge of interest, partly as a result of new fossil material and new techniques in molecular and systematic biology, and this has attracted new researchers to the field. Despite this, several major controversies remain. The aim of this meeting is to summarise and discuss knowledge, approaches, data and debates.

PROGRAMME

- 9.30–9.50 Registration
9.50–10.00 Welcome and announcements

Session 1

- 10.00–10.20 Susan Evans and Roger Benson: **The early history and diversification of squamates**
10.20–10.40 Jason Head: **Snakes and stratigraphy**
10.40–11.00 Krister Smith: **A complete skeleton of the earliest known erycine boid and its implications for booid biogeography**

11.00–11.30 Tea/Coffee in Reading room (and viewing of posters)

Session 2

- 11.35–11.55 Hussam Zaher: **Mesozoic marine pachyophiids and their bearing on the origin of snakes**
11.55–12.15 Martin Ivanov: **Late Palaeogene/early Neogene Eurasian snake communities**
12.15–12.35 Michael Polcyn: **What, if anything, is a pythonomorph?**
12.35–12.55 Bruno Augusta and Louis Jacobs: **New data on basal mosasaurians highlights their varanoid, not snake, affinities**

12.55–14.15 Lunch in Reading room (and viewing of posters)

Session 3

- 14.15–14.35 Sara Ruane & Jeff Streicher: **Conflicting histories—assessing phylogenetic signal across the genomes of snakes**
14.35–14.55 Kartik Sunagar: **Differential diversification and degeneration of the venom system in toxicoferan reptiles**
14.55–15.15 Giovanna Montingelli: **Diversity and evolution of hemipenes in the major lineages of extant snakes**
15.15–15.35 Leonardo Oliveira: An overview of the morphology of oral glands in snakes

15.35–16.05 Tea/Coffee in Reading room (and viewing of posters)

Session 4

- 16.10–16.30 Selma de Almeida-Santos: **Reproductive strategies and the evolution of sperm storage**
16.30–16.50 Hongyu Yi: **Revealing ecological traits of ancestral snakes using inner ear morphometrics**
16.50–17.10 David Cundall and Frances Irish: **Perspectives on macrostomy and snake phylogeny**
17.10–17.30 David Gower: **Eyes, vision, and snake origins**
17.30–17.40 Closing Remarks

17.45–19.00 Wine reception in Reading room

Organisers: David Gower (NHM, London) & Hussam Zaher (USP, São Paulo, Brazil)

ABSTRACTS

THE EARLY HISTORY AND DIVERSIFICATION OF SQUAMATES

Susan Evans (UCL, London, UK) and Roger Benson (University of Oxford, UK)

This talk will present the palaeontological context of the debate about snake origins by summarizing and synthesizing what is known about the early history of squamates in the Jurassic and Cretaceous.

SNAKES AND STRATIGRAPHY

Jason Head (University of Cambridge, UK)

This talk will provide the geological context of the snake fossil record. It will especially address the extent to how alternative scenarios of snake origins and early evolution match with the temporal distribution of relevant squamate taxa in the rock record.

A COMPLETE SKELETON OF THE EARLIEST KNOWN ERYCINE BOID AND ITS IMPLICATIONS FOR BOID BIOGEOGRAPHY

Krister Smith (Senckenberg Research Institute, Frankfurt am Main, Germany)

This talk will present new findings on a fossil erycine snake from the Middle Eocene Messel Formation. This is the oldest known record of an erycine snake. Phylogenetic and biogeographical implications of the new morphological evidence will be discussed.

MESOZOIC MARINE PACHYOPHIID SNAKES AND THEIR BEARING ON THE ORIGIN OF SNAKES

Hussam Zaher (Universidade de São Paulo, Brazil)

This talk will review the controversial anatomy of the key Cenomanian marine snake radiation, and addressing their phylogenetic affinities based on new high-resolution CT-scanning data. In the last decade, these fossils have fueled much of the debate on the origin of snakes. However, their detailed morphology has not been addressed thoroughly and some important aspects of their cranial anatomy remain controversial. Clarifying these issues will provide a refreshing new start in the debate of snake origins.

LATE PALEOGENE/EARLY NEOGENE EVOLUTION OF EURASIAN SNAKE COMMUNITIES

Martin Ivanov (Masaryk University, Brno, Czech Republic)

This talk will review the Eurasian snake fauna following the late Eocene cooling that strongly affected biota adapted to tropical climates. The relatively cool Oligocene climate enabled the survival of aniliids and small-sized boids in western Europe. However, palaeogeographical changes as well as increased temperature and humidity at the beginning of the Neogene enabled extensive penetration of advanced snake families of mostly Asiatic origin into Europe. Recent research on the early Miocene localities from central Europe indicates that this important change in composition of European snake fauna preceded warmest stages of the Miocene Climatic Optimum. Although Neogene snakes are still poorly known from areas east of Europe, fossil snake fauna recently reported from several early and middle Miocene localities in east Europe and Asia elucidate debate concerning differences in composition of snake communities throughout the Eurasia as well as origin of modern snake fauna of Europe.

WHAT, IF ANYTHING, IS A PYTHONOMORPH

Michael Polcyn (Southern Methodist University, Dallas, Texas, U.S.A)

The 19th century clade name Pythonomorpha was coined by E.D. Cope to include two family-rank clades of mosasaurs, as the sister taxon of his Ophidia. This concept was largely rejected by his contemporaries, and for much of the 20th century, mosasaurs were generally accepted as varanoid lizards and not particularly closely related to snakes. In recent decades, some workers revived Pythonomorpha to include snakes and mosasaurians, inspiring a research cycle elucidating much of the morphology underlying the purported synapomorphies; however, recent large-scale phylogenetic analyses have failed to resolve the position of mosasaurs within Squamata, largely due to taxon selection and missing data issues. This talk will provide a synthesis of past work and present new data from well preserved primitive mosasaurs in an effort to clarify the phylogenetic position of mosasaurs within Squamata and address purported synapomorphies uniting snakes and mosasaurs.

NEW DATA ON BASAL MOSASAURIANS HIGHLIGHTS THEIR VARANOID, NOT SNAKE, AFFINITIES

**Bruno Augusta (Universidade de São Paulo, Brazil) and
Louis Jacobs (Southern Methodist University, Dallas, U.S.A.)**

The Pythonomorpha hypothesis claims that mosasaurian lizards are the closest relatives of snakes, especially based on dental, mandibular and postcranial features supposedly shared by both groups. In this talk, new anatomical data on the basalmost radiation of mosasaurians, the dolichosaurs, are provided in the light of new coniasaur remains from Texas and reinterpretation of key features from European dolichosaurs. New phylogenetic analyses strongly support the hypothesis of varanoid, not snake, affinities for Mosasauria.

CONFLICTING HISTORIES: ASSESSING PHYLOGENETIC SIGNAL ACROSS THE GENOMES OF SNAKES

**Sara Ruane (Rutgers University, Newark, U.S.A.) and
Jeff Streicher (Natural History Museum, London, UK)**

The first molecular phylogenetic analyses of the relationships among snakes and extant lizards presented a major challenge to some hypotheses erected on the basis of morphology. Since then, techniques of molecular genetic data generation and analysis have progressed rapidly. This talk will summarize progress and limitations as snake phylogenetics has entered the phylogenomic era, focusing on conflicting signals, and advancing suggestions for how the field might advance in the coming years.

DIFFERENTIAL DIVERSIFICATION AND DEGENERATION OF THE VENOM SYSTEM IN TOXICOFERAN REPTILES

Kartik Sunagar (Indian Institute of Science, Bangalore, India)

Complex venoms and complex venom delivery systems are major features of many extant snakes, and a profound difference between snakes and non-snake squamates (lizards). Thus, venom systems play an important role in studies of the origin and early diversification of snakes. Molecular genetics has contributed substantially to the debate, most notably in the Toxicofera concept – a clade of snakes and of those lizards that have potentially toxic saliva with genes encoding for bioactive compounds potentially homologous to those found in snakes. Since 2003, there has been a debate about the extent to which some extant lizards (and ‘basal’ extant snakes) exhibit plesiomorphic precursors to more elaborate venom systems evolved by ‘higher’ snakes, possibly derived reductions of more sophisticated systems present in extinct squamates, and/or systems that are partially convergent with those found in ‘higher’ snakes. This talk will review the debate based on the latest research.

DIVERSITY AND EVOLUTION OF HEMIPENES IN THE MAJOR LINEAGES OF EXTANT SNAKES

Giovanna Montingelli (Universidade de São Paulo, Brazil)

The hemipenes of extant snakes are highly diverse and distinctive, and they are frequently used as a source of important systematic characters – particularly within ‘higher’ snakes. However, little attention has been paid to the early diversity and diversification of snake hemipenes. This talk will summarize the similarities and differences between lizard and snake hemipenes, and summarize the main axes of morphological variation among and within major lineages of living snakes.

ORAL GLANDS: AN OVERVIEW OF MORPHOLOGY AND EVOLUTION IN SNAKES

Leonardo Oliveira (Universidade de São Paulo, Brazil and NHM, London, UK)

Oral glands underwent a substantial modification during the origin and diversification of snakes, most notably in relation to the diversification of feeding ecologies and the evolution of venom production and delivery systems. Oral glands have provided a rich source of data for snake systematics, and for informing evolutionary scenarios about the adaptive radiation of the snake feeding apparatus. This presentation will summarize the main axes of variation in the morphology of oral glands of the major lineages of extant snakes, with special reference to the potential to infer ancestral states.

REPRODUCTIVE STRATEGIES OF SNAKES AND THE EVOLUTION OF SPERM STORAGE

Selma de Almeida-Santos (Instituto Butantan, São Paulo, Brazil)

Snakes exhibit diverse and distinctive reproductive strategies, such as autumnal mating, dissociated reproductive cycles, and sperm storage. This talk will provide an overview of aspects of snake reproductive biology. It will especially focus on characteristics of sperm storage in snakes, making novel associations with reproductive seasonality.

REVEALING ECOLOGICAL TRAITS OF ANCESTRAL SNAKES USING INNER EAR MORPHOMETRICS

Hongyu Yi (Chinese Academy of Sciences, Beijing, China)

A key contribution to debates about the origin and early evolution of snakes comes from attempts to infer ecology and/or behaviour from the anatomy of extinct taxa. This enterprise relies heavily on being able to identify osteological correlates of ecology and behaviour, something which has benefitted from the recent expansion of the use of new microCT and quantitative shape analysis techniques. This talk will review recent developments and identify the potential and pitfalls in this approach.

PERSPECTIVES ON MACROSTOMY AND SNAKE PHYLOGENY

**David Cundall (Lehigh University, Bethlehem, USA) and
Frances Irish (Moravian College, USA)**

Snakes are unusual among terrestrial vertebrates for the mobility of their jaw apparatus relative to the rest of the skull. The clade includes some species capable of increasing the area of the mouth opening to several times the area achieved by simply depressing the mandibles to their maximum extent. On the other hand, many species retain the essential skeletal features of macrostomy without ever expressing the extreme functions seen in more spectacular members. Because the performance potential of many species is difficult to determine, those structural features easily measured have been assumed to confer similar capabilities. Following a review of snake apomorphies, Müller's Macrostromata was resurrected to define a clade whose monophyly is not supported by some analyses of molecular sequence data. Here we re-examine the structures underlying macrostomy and reconsider the evolution of both the structures and functions of the jaws of snakes in light of current molecular hypotheses of the phylogeny of snakes, and of hypotheses incorporating fossil evidence. We conclude that the major behavioral and ecological attributes of highly macrostomous snakes are a result of complex soft tissue modifications that remain poorly understood both structurally and functionally and correlate only loosely to skeletal features. Assumptions about the relationships of skeletal features or sequence data to macrostomy are largely unsupported by behavioral observations of extant species. Hence, some critical aspects of the evolution of snakes continue to defy simple resolution and await further innovation and analysis.

EYES, VISION AND SNAKE ORIGINS

David Gower (Natural History Museum, London, UK)

The eye has played a prominent role in debates about the ecological origins of snakes – in terms of attempts to infer the ecomorphology of the most recent common ancestor of all living snakes. Historically, debates about snake origins including the visual system were based on the disparate anatomy of snake eyes, especially those of the least deeply phylogenetically nested extant lineages. More recently, molecular genetic data about the visual system have contributed to the debate. This talk will take a look at some historical and recent developments.



