PHILOSOPHICAL TRANSACTIONS B

royalsocietypublishing.org/journal/rstb

Preface



Cite this article: Kratochvíl L, Stöck M. 2021 Preface. *Phil. Trans. R. Soc. B* **376**: 20200088. https://doi.org/10.1098/rstb.2020.0088

Accepted: 17 May 2021

One contribution of 12 to a theme issue 'Challenging the paradigm in sex chromosome evolution: empirical and theoretical insights with a focus on vertebrates (Part I)'.

Subject Areas:

evolution, genetics, genomics

Keywords:

evolution, sex chromosomes, vertebrates

Authors for correspondence:

Lukáš Kratochvíl e-mail: lukas.kratochvil@natur.cuni.cz Matthias Stöck e-mail: matthias.stoeck@igb-berlin.de

THE ROYAL SOCIETY PUBLISHING

Preface

Lukáš Kratochvíl¹ and Matthias Stöck^{2,3}

¹Department of Ecology, Faculty of Science, Charles University, Viničná 7, Prague, Czech Republic ²Leibniz-Institute of Freshwater Ecology and Inland Fisheries—IGB (Forschungsverbund Berlin), Müggelseedamm 301, 12587 Berlin, Germany

³Amphibian Research Center, Hiroshima University, Higashi-Hiroshima 739-8526, Japan

(D) LK, 0000-0002-3515-729X; MS, 0000-0003-4888-8371

This preface introduces the two parts of a theme issue on vertebrate sex chromosome evolution (title below). We invited and edited 22 articles concerning the following main topics (Part 1): sex determination without sex chromosomes and/or governed by epigenetics; origin of sex-determining genes; reasons for differentiation of sex chromosomes and differences in their rates of differentiation as well as (Part 2): co-option of the same linkage groups into sex chromosomes; is differentiation of sex chromosomes a unidirectional pathway?; consequences of differentiated sex chromosomes; differences in differentiation of sex chromosomes under male versus female heterogamety; evolution of sex chromosomes under hybridization and polyploidy.

This article is part of the theme issue 'Challenging the paradigm in sex chromosome evolution: empirical and theoretical insights with a focus on vertebrates (Part I)'.

Sitting on a hill not far from Tonglu, a Chinese town unexpectedly hosting the World Congress of Herpetology in 2016 (due to 'security reasons' for the planned G20 summit, the whole congress was moved away from Hangzhou by the Chinese government, just a few hours before the meeting's start), we discussed what we know and do not know about sex chromosome evolution. We agreed that a large revision, based mostly on empirical results in a group of animals with a large diversity in sex determination systems and sex chromosomes, would be great to illuminate the research field, and to see where it has moved during the more than 100 years since the pioneering steps of the paradigm on sex chromosome evolution [1]. You may guess that we were and still are convinced that vertebrates are the most suitable group (we say so with great respect for other organisms) to address these questions. This choice reflected our own research interests and the fact that vertebrates are popular for empirical research, allowing us to dive much deeper into several aspects-such as gene ontology and molecular pathways-than in less well-examined groups. Of course, this also considers our own taxonomic classification, and naturally, we are interested in the evolution of our phylogenetic past, although-at the same time-such an anthropocentric view results in some obvious scientific limitations.

Our initial idea started to 'materialize' during a first meeting on sex chromosome evolution in vertebrates, organized by us and hosted by the Faculty of Science of the Charles University in Prague in 2018, when a group of vertebrate sex-determination enthusiasts discussed sex chromosome evolution and identified the most controversial and vivid topics, not only for discussion in the classroom, but also amongst ourselves during the observation of voracious feeding of Komodo dragons and giant salamanders in the Prague Zoo. Equally fruitful was the second meeting in 2019, hosted by IGB in Berlin [2], to which thanks to support from the German Science Foundation (DFG)—we were able to invite more experts from even further afield, and outlined the topics for the current Theme issues in detail. This time, we were inspired not only by dinosaur skeletons in the Berlin Natural History Museum, but also by the delicate beauty of plants and flowers in the Botanical Garden in Berlin-Dahlem. From here, it was a straightforward next step to work on the application for this Theme issue.

We would like to thank the editorial board of *Philosophical Transactions B* for giving us the opportunity to publish the results of this project. In particular, Helen Eaton, Senior Commissioning Editor provided great help at every step of the work. We are grateful for her very professional and at the same time amiable help.

Of course, these issues present a collective work, and we are most grateful to the authors; it was a great pleasure to work with all of them, with their particular contributions forming a mosaic of the concepts to elaborate the general paradigm. The friendly, but fierce and thus jokingly named 'religious wars' over definitions of some key terms and concepts (mainly concerning the Glossary in [3]) were demanding, but provoked deeper thinking about the meaning of words, and as it appeared, our understanding and use of scientific terms may sometimes differ to a large extent. The issues are founded on a taxonomic overview of sex determination/sex chromosomes in vertebrates with a pledge for 'sexomics' [3], then frame a mosaic of topics and case studies, demonstrate and discuss specific aspects, and lead to a concluding paper, intended to show how all the contributions together make up a complex, up-to-date overview of many questions of vertebrate sex chromosome evolution [4].

In Part 1, we gather articles around the following major topics:

- Sex determination without sex chromosomes and/or governed by epigenetics [5,6];
- Origin of sex-determining genes [7–9];
- Reasons for differentiation of sex chromosomes and differences in their rates of differentiation [10–14].

- In Part 2, we assemble papers on these main topics:
- Co-option of the same linkage groups into sex chromosomes [15,16];
- Is differentiation of sex chromosomes a unidirectional pathway? [17,18];
- Consequences of differentiated sex chromosomes [19];
- Differences in differentiation of sex chromosomes under male versus female heterogamety [20,21];
- Evolution of sex chromosomes under hybridization and polyploidy [23–24].

We are grateful to all reviewers; their comments were absolutely essential. We would also like to thank Jörg Wachtel (Brachwitz, Germany), who kindly prepared the cover images. We bothered him by our obsession for some anatomical details of the depicted organisms and branching based on up-to-date phylogenies, potentially important for biologists, but less for the artist—we are glad that thanks to Jörg's patience and skilfulness, we did not harm the graphical appeal of the figures too much.

Last but not least, we are grateful that we can work with such beautiful organisms and on such an interesting and intellectually challenging topic as sex chromosome/determination evolution. We are impatiently awaiting progress in the field. As evolutionary biologists, we are convinced that evolution can only be predicted to some degree...thus, we are sure that amazing empirical surprises are still lying ahead, and that curiosity drives us.

Data accessibility. This article has no additional data. Authors' contributions. Equal contribution. Competing interests. We declare we have no competing interests. Funding. We received no funding for this study.



Guest editors' biographic sketches

Lukáš Kratochvíl is a full professor of Ecology at the Charles University, Prague. He has been studying aspects of the evolution of sexual dimorphism, sex determination and sex chromosomes, especially in vertebrates, with reptiles as his most favourite organisms. He currently focuses on the question of unequally distributed variability in sex determination across vertebrates and evolutionary causes of stability versus turnovers in sex determination.



Matthias Stöck is a scientist at the Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB) in Berlin, and holds a licence to teach Zoology at the Humboldt University Berlin; in 2021/2022, he is honoured by a Visiting Professorship at the Amphibian Research Center, Hiroshima University, Japan. His research includes a spectrum of topics on animal evolution including sex, speciation and polyploidy that he mostly addresses empirically in amphibians and fish. He dedicates his work to the memory of his father, Dr Horst Stöck (1938–2021), physicist.

References

- Muller HJ. 1918 Genetic variability, twin hybrids and constant hybrids, in a case of balanced lethal factors. *Genetics* 3, 422–499.
- Stöck M, Kratochvíl L. (eds.) 2019 Paradigm shift in sex chromosome evolution: Abstracts of the workshop held in Berlin, 19–22 September 2019. Berlin and Prague: Institute of Freshwater Ecology and Inland Fisheries (IGB). (doi:10.4126/FRL01-006417884)
- Stöck M *et al.* 2021 A brief review of vertebrate sex evolution with a pledge for integrative research: towards 'sexomics'. *Phil. Trans. R. Soc. B* 376, 20200426. (doi:10.1098/rstb.2020.0426)
- Kratochvíl L *et al.* 2021 Expanding the classical paradigm: what we have learnt from vertebrates about sex chromosome evolution. *Phil. Trans. R. Soc.* B 376, 20200097. (doi:10.1098/rstb.2020.0097)
- Weber C, Capel B. 2021 Sex determination without sex chromosomes. *Phil. Trans. R. Soc. B* 376, 20200109. (doi:10.1098/rstb.2020.0109)
- Piferrer F. 2021 Epigenetic mechanisms in sex determination and in the evolutionary transitions between sexual systems. *Phil. Trans. R. Soc. B* 376, 20200110. (doi:10.1098/rstb.2020.0110)
- Adolfi MC, Herpin A, Schartl M. 2021 The replaceable master of sex determination: bottom-up hypothesis revisited. *Phil. Trans. R. Soc. B* 376, 20200090. (doi:10.1098/rstb.2020.0090)
- Pan Q, Kay T, Depincé A, Adolfi M, Schartl M, Guiguen Y, Herpin A. 2021 Evolution of master sex determiners: TGF-β signalling pathways at regulatory crossroads. *Phil. Trans. R. Soc. B* 376, 20200091. (doi:10.1098/rstb.2020.0091)
- Bertho S, Herpin A, Schartl M, Guiguen Y. 2021 Lessons from an unusual vertebrate sex-determining gene. *Phil. Trans. R. Soc. B* 376, 20200092. (doi:10. 1098/rstb.2020.0092)
- 10. Perrin N. 2021 Sex-chromosome evolution in frogs: what role for sex-antagonistic genes? *Phil.*

Trans. R. Soc. B **376**, 20200094. (doi:10.1098/rstb. 2020.0094)

- Song X-Y, Furman BLS, Premachandra T, Knytl M, Cauret CMS, Wasonga DV, Measey J, Dworkin I, Evans BJ. 2021 Sex chromosome degeneration, turnover, and sex-biased expression of sex-linked transcripts in African clawed frogs (*Xenopus*). *Phil. Trans. R. Soc. B* **376**, 20200095. (doi:10.1098/rstb. 2020.0095)
- Jeffries DL, Gerchen JF, Scharmann M, Pannell JR.
 2021 A neutral model for the loss of recombination on sex chromosomes. *Phil. Trans. R. Soc. B* 376, 20200096. (doi:10.1098/rstb.2020.0096)
- Charlesworth D. 2021 The timing of genetic degeneration of sex chromosomes. *Phil. Trans. R. Soc. B* 376, 20200093. (doi:10.1098/rstb. 2020.0093)
- Kuhl H et al. 2021 A 180 Myr-old female-specific genome region in sturgeon reveals the oldest known vertebrate sex determining system with undifferentiated sex chromosomes. *Phil. Trans. R. Soc.* B **376**, 20200089. (doi:10.1098/rstb.2020.0089)
- Lichilín N, Taher AE, Böhne A. 2021 Sex-biased gene expression and recent sex chromosome turnover. *Phil. Trans. R. Soc. B* 376, 20200107. (doi:10.1098/ rstb.2020.0107)
- Kratochvíl L, Gamble T, Rovatsos M. 2021 Sex chromosome evolution among amniotes: is the origin of sex chromosomes non-random? *Phil. Trans. R. Soc. B* **376**, 20200108. (doi:10.1098/rstb. 2020.0108)
- Sember A, Nguyen P, Perez MF, Altmanová M, Ráb P, Cioffi M de B. 2021 Multiple sex chromosomes in teleost fishes from a cytogenetic perspective: state of the art and future challenges. *Phil. Trans. R. Soc.* B 376, 20200098. (doi:10.1098/rstb.2020.0098)
- Lisachov AP, Tishakova KV, Romanenko SA, Molodtseva AS, Prokopov DY, Pereira JC, Ferguson-Smith MA, Borodin PM, Trifonov VA. 2021

Whole-chromosome fusions in the karyotype evolution of *Sceloporus* (Iguania, Reptilia) are more frequent in sex chromosomes than autosomes. *Phil. Trans. R. Soc. B* **376**, 20200099. (doi:10.1098/rstb. 2020.0099)

- Peona V et al. 2021 The avian W chromosome is a refugium for endogenous retroviruses with likely effects on female-biased mutational load and genetic incompatibilities. *Phil. Trans. R. Soc. B* 376, 20200186. (doi:10.1098/rstb. 2020.0186)
- Bista B, Wu Z, Literman R, Valenzuela N. 2021 Thermosensitive sex chromosome dosage compensation in ZZ/ZW softshell turtles, *Apalone spinifera*. *Phil. Trans. R. Soc. B* **376**, 20200101. (doi:10.1098/rstb.2020.0101)
- Rovatsos M, Gamble T, Nielsen SV, Georges A, Ezaz T, Kratochvil L. 2021 Do male and female heterogamety really differ in expression regulation? Lack of global dosage balance in pygopodid geckos. *Phil. Trans. R. Soc. B* **376**, 20200102. (doi:10.1098/ rstb.2020.0102)
- Ogata M, Suzuki K, Yuasa Y, Miura I. 2021 Sex-chromosome evolution from a heteromorphic to a homomorphic system by inter-population hybridization in a frog. *Phil. Trans. R. Soc. B* 376, 20200105. (doi:10.1098/rstb. 2020.0105)
- Roco ÁS, Ruiz-García A, Bullejos M. 2021 Interaction between sex-determining genes from two species: clues from *Xenopus* hybrids. *Phil. Trans. R. Soc. B* 376, 20200104. (doi:10.1098/rstb. 2020.0104)
- Stöck M, Dedukh D, Reifová R, Lamatsch DK, Starostová Z, Janko K. 2021 Sex chromosomes in meiotic, hemiclonal, clonal and polyploid hybrid vertebrates: along the 'extended speciation continuum'. *Phil. Trans. R. Soc. B* **376**, 20200103. (doi:10.1098/rstb.2020.0103)

3