Preface

This special issue of *Sexual Development* entitled 'Evolution of External Genital Development' continues and complements the story begun in the recent two themed issues 'Control of Gonadal Development' and 'Sexual Differentiation of Vertebrate Reproductive Organs'. This issue focusses on the very important questions of the origin and development of the amniote phallus. In all amniotes examined to date, the external genitalia emerge as a pair of genital swellings on either side of the cloaca. However, until recently, there was little information on the morphogenesis of the external genitalia in birds and reptiles and even relatively little in mammals. This issue fills that gap and provides five excellent review articles focusing on birds and reptiles.

In a previous special issue, Gredler et al. [2014] suggested that the intromittent phallus may be a shared, derived character in amniotes. In the present issue, Leal and Cohn, and Gredler, Sanger and Cohn show that the squamate sulcus (the homologue of the urethra) develops from the surface ectoderm and does not express Sonic hedgehog (Shh), in contrast to the sulcus of turtles and the urethra of mammals which characteristically express Shh. Although some patterns of gene expression are shared between the squamate hemipenes and penis development in non-squamate amniotes, these fundamental differences in the development of the external genitalia suggest that these structures may not be homologous.

There is a commonly held belief that the phallus evolved separately in each amniote group. However, in the turtle, Larkins and Cohn show that the development of the genital tubercle is remarkably similar to that of mammals. In the red-eared slider turtle, they show that the expression patterns of BMP signalling and apoptic genes are correlated with the development of the open urethral groove and closely resemble that of mice, suggesting they are homologous structures.

Avian genitalia are highly variable, but the majority of birds do not have an intromittent penis. The exceptions are ducks that have the longest penis relative to body size of any birds. Herrera, Brennan and Cohn suggest that the genital difference seen in three species of ducks occurs after hatching, and that there is a parallel between the atrophy of the clitoris in the female duck and the process of apoptosis that occurs in the tip of the penis in birds that have a non-intromittent penis. They suggest that the mechanisms that control penis loss in birds may therefore be a result of adopting the pre-existing mechanisms of feminization.

In the final review, Gredler, Seifert and Cohn show that septation of the cloacal endoderm by the urorectal septum mesenchyme in alligators is similar to the process that occurs in mammals, but it arrests midway through genital development to form the shared urinary and ano-rectal chamber, the cloaca. It appears that reciprocal *Fgf10-FgfR2* signalling during maturation of the sulcal epithelium in alligators may be conserved with that seen in the urethral epithelium of mammals, but modifications of an ancestral programme of urogenital development has contributed to the diverse external genitalia of modern amniotes.

This is indeed a tour de force from the Cohn group and adds immensely to our knowledge and understanding of the evolution and development of this important, but relatively little studied organ, the amniote phallus.

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Reference

Gredler ML, Larkins CE, Leal F, Lewis AK, Herrera AM, et al: Evolution of external genitalia: insights from reptilian development. *Sex Dev* 8:311–326 (2014).