Origins of copulation - ancient Scottish fishes did it sideways, square-dance style.

Author



John Long

Strategic Professor in Palaeontology at Flinders University

Disclosure Statement

John Long receives funding from The Australian Research Council and Flinders University.

The Conversation is funded by CSIRO, Melbourne, Monash, RMIT, UTS, UWA, ACU, ANU, ASB, Baker IDI, Canberra, CDU, Curtin, Deakin, Flinders, Griffith, the Harry Perkins Institute, JCU, La Trobe, Massey, Murdoch, Newcastle, UQ, QUT, SAHMRI, Swinburne, Sydney, UNDA, UNE, UniSA, USC, USQ, UTAS, UWS, VU and Wollongong.

A new discovery published today in the journal <u>Nature</u> reveals that the intimate act of copulation first evolved in ancient armoured <u>placoderm fishes</u> called <u>antiarchs</u>. Fossils of the antiarch <u>Microbrachius dicki</u> show males with large bony L-shaped claspers for transferring sperm, whereas females bore small paired bones to help dock the male organs into position. These discoveries represent the first appearance of sex involving copulation in <u>vertebrates</u> (back-boned animals). It's also the first time in vertebrate evolution that males and females appear with distinct differences in their physical appearance.

Little arms, big genitals

Microbrachius means "little arms" from its small paired pectoral limbs. It inhabited ancient rivers and lakes about 385 million years ago. Its species name '*dicki*' honours <u>Mr Robert</u> <u>Dick</u>, an avid fossil collector in Scotland in the late 19th century who first found its fossils in the north of Scotland.



The 385 million year old placoderm fish Microbrachius dicki from Scotland shows the first evidence for mating by copulation in our evolutionary lineage. The males bore large L-shaped bony claspers for inseminating the females. Left, female fossil; centre, male fossil; right, mating position. J.Long, Flinders University

The new discoveries began late last year when I was working at the <u>University of Technology</u> <u>in Tallinn</u>, Estonia, with my colleague <u>Dr Elga Mark-Kurik</u>. She handed me a box of isolated *Microbrachius* bones from Estonia to examine. I found a tiny plate, less than 2cm long, which had a tube of bone attached to it and I couldn't identify it. Eventually I realised it was a primitive vertebrate sexual organ, a <u>clasper</u>. Claspers are found in male sharks and rays and used for copulation. It was one of those sublime eureka moments as the discovery was profound: it basically meant a complete rethinking of the evolution of sexual strategies in jawed vertebrates.



This small single fossil bone in the collections of the University of Technology, Tallinn, was the first clue as to the how antiarch placoderms like Microbrachius mated. The bony clasper is the organ used to transfer sperm into the female.

Antiarchs had never before shown any evidence for reproduction. We had long assumed they simply <u>spawned</u> in water, like many living fishes. The new discovery meant they had the ability to copulate, so internally fertilised their eggs. As antiarchs are the most primitive jawed vertebrates (gnathostomes) it meant that highly complex sexual reproduction first appeared at more or less the same time as jaws and paired hind limbs appeared.

We began searching other museum collections in Europe, Australia and the USA for more evidence. Eventually some amazing complete specimens of *Microbrachius* held in private collections by UK and Dutch collectors were revealed to us, showing distinct male and female features. These were then donated to the <u>Natural History Museum</u>, <u>London</u>, so we could complete our study.

First vertebrates copulated 'square-dance' style

It's bizarre that these tiny fishes mated from a sideways position, the male and female resting alongside each other. They likely intertwined their bony jointed pectoral appendages (arms) using the rows of hooks on their inside edge. The outside arms could have helped them manoeuvre their large claspers into the mating position. With their hooked 'arms' interlocked, the act of copulation in these fishes somewhat resembled square dancing the dosi-

The female's paired genital plates bore a roughened surface like a cheese grater for the male claspers to latch on to. Once the male's clasper was in the mating position only the tip could be inserted inside the cloaca of the female to deposit sperm.

Despite their awkward looks, *Microbrachius* were highly successful little fishes whose species are found in UK, China and Estonia. The antiarchs could have all mated in this way as other forms like *Bothriolepis* show similar genital structures preserved. *Bothriolepis* was the most ubiquitous vertebrate known in the Devonian period, with over 150 species found. It lived on every continent, including Antarctica. Such antiarchs were probably the world's first truly widespread vertebrates. We now think it likely that their movable bony arms which facilitated copulation were the key to their migratory success.



A 3D preserved Bothriolepis from the Gogo site in Western Australia shows its jointed bony arms. Such arms might have been the key to the success of this little fish whose remains are found on every continent. J.Long, Flinders University.

Placoderm sex and live birth

The new discovery follows on the heels of a string of recent finds elucidating how the oldest backboned animals mated. In 2008 we discovered the oldest evidence for <u>live birth</u> (viviparity) in a placoderm fish fossil from <u>Gogo</u>, Western Australia. It showed a 3D embryo fossil attached by a mineralised umbilicial cord. We named it <u>Materpiscis attenboroughi</u>, meaning "Attenborough's mother fish". This discovery was followed in 2009 by another equally unexpected find, more placoderm embryos inside another group of placoderms, the <u>'arthrodires</u>'.

The arthrodires were the most diverse clade of placoderms. Yet despite thousands of specimens in museum collections, none had shown any evidence for how they reproduced. Our discovery proved they used internal fertilisation and that males had bony claspers for mating. Earlier this year we added to this by showing that <u>placoderm claspers</u> did not develop in the same way as shark claspers, as part of the pelvic fin, but evolved more or less like an extra pair of limbs.

Placoderm claspers were at first fixed rigidly to their body plates as in *Microbrachius* so the fish had to move its entire body around to mate. More advanced placoderms such as the

arthrodire *Incisoscutum* evolved flexible bony claspers capable of rotating forwards and becoming erect for mating.

The rise and fall and rise again of male intromittent organs

Our new research implies something that was thought impossible in biology - that fishes went from using copulation (internal fertilisation) to reverting back to external fertilisation (spawning in water), the default primitive condition seen in jawless fishes like lampreys. This must have occurred when bony fishes (Osteichthyes) first evolved from placoderms as none of the primitive fossil or living species (like *Polypterus*) show any evidence for internal fertilisation.



An evolutionary summary of how male intromittent sexual organs evolved, from extinct placoderm fishes through to humans.

we know that <u>coelacanths</u> mate using internal fertilisation even though they lack copulatory structures. Some families of advanced bony fishes, the <u>teleosts</u>, evolved different kinds of internal fertilisation. <u>Guppies</u>, for example, use a modified anal fin spine to transfer sperm (a <u>gonopodium</u>), although none of these teleosts ever developed paired claspers similar to those in placoderms or sharks.

Our study concludes that the most primitive jawed vertebrates originally evolved copulation as the main way of mating, then lost it early on in their evolution. Later it reappeared again and again in many different animal groups. Snakes and some lizards have <u>hemipenes</u> (paired penises), but crocodiles, tortoises, mammals and some birds all have a single penis. The

<u>Argentine Lake Duck</u> has the longest penis relative to body size for any living vertebrate (43cm for an average sized duck). The penis was secondarily lost in many lineages of flying birds. We humans thus mate in a way that first evolved in crocodiles and tortoises back in the age of dinosaurs. We can thank our distant ancestors, the placoderms, for first evolving this unique method of reproduction.