the WINNOWER

A Transgender Brazilian Cave Insect

Yoshizawa, K., R. L. Ferreira, Y. Kamimura, and C. Lienhard. 2014. "Female penis, male vagina, and their correlated evolution in a cave insect." Curr. Biol. 24: 1006-1010. doi: 10.1016/j.cub.2014.03.022.

KAZUNORI YOSHIZAWA [1], RODRIGO L FERREIRA [2], YOSHITAKA KAMIMURA [3], CHARLES LIENHARD [4]

1. Hokkaido University, School of Agriculture, Systematic Entomology, Sapporo 060-8589, Japan
2. Federal University of Lavras, Biology Department, Lavras, MG 37200-000, Brazil
3. Keio University, Department of Biology, Yokohama 223-8521, Japan
4. Natural History Museum of the City of Geneva, CP 6434, 1211 Geneva 6, Switzerland

CORRESPONDENCE:
psocid@res.agr.hokudai.ac.jp

DATE RECEIVED:
September 03, 2014

DOI:
10.15200/winn.140978.89418

KEYWORDS:
female penis, male vagina, gynosome, cave insect

The penis is, by definition, the male copulatory organ (e.g., *New Oxford American Dictionary*). Sex-specific features are not restricted to copulatory organs, and many examples of sex-specific elaborations are known, such as the horns of antlers or the decorative feather of peacocks. Evolution and exaggeration of sex-specific elaborations have attracted the attention of many biologists, including Darwin (Darwin 1871). It is now widely accepted that sexual selection promotes the evolution of elaborate sex-specific features (Trivers 1972). Because sexual selection usually acts on the male, sex-specific elaborations are frequent in male, and the male penis is highly diversified morphologically and functionally whereas female genitalia are usually simple (Eberhard 1985).

Recently, we reported the most masculine females ever discovered (Yoshizawa et al. 2014). In the Brazilian cave insect genus *Neotrogla* (Insecta: Psocodea: 'Psocoptera': Prionoglarididae), females have a highly elaborate penis-like organ, termed a gynosome, whereas the males have a simple vagina-like genital chamber. Furthermore, the female penis has species-specific elaborations such as numerous spines, by which a female anchors to a male during a long copulation (30-70 hours!) to receive a nutritious seminal gift. The male vagina possesses species-specific pouches that accept the spines on the female penis. This is the first definite discovery of a female intromittent organ in the animal kingdom and also the first detection of reversed genital coevolution.

As briefly discussed below, discovery of the female penis potentially has great impacts for the studies of sexual selection and origins of novel traits. However, the project was originally launched as a pure descriptive taxonomic study. It should also be noted that *Neotrogla* belongs to Psocoptera, one of the most neglected insect taxa with only a handful active taxonomists in the world (Psocoptera were formerly treated as an independent order but are now regarded as a paraphyletic assemblage of free living members of Psocodea, an order which also includes parasitic lice: Yoshizawa & Johnson 2006). In 1998, Ferreira, a specialist of cave ecosystems, collected specimens of this insect by chance for the first time. Later, these specimens together with other species collected subsequently were sent to Lienhard, a taxonomist of this group of insects, for identification. These were completely unknown insects and were described as new species representing a new genus (Lienhard, Do Carmo and Ferreira 2010). In this study, the very impressive penis-like organ of the female was first described and illustrated; it was denoted by the new term gynosome and its potential function as an intromittent organ

was discussed. In Yoshizawa et al. (2014), it was shown, for the first time, that the gynosome actually functions as an intromittent organ to uptake sperm from the males.

Therefore, discovery of the female penis itself is not truly a novel discovery for the study. The novel discovery presented in Yoshizawa et al. (2014) is that the female *Neotrogla* can coercively grasp and copulate with a male for a long time by using the penis. In animals, coercive mating is generally an exclusive feature of males (Arnqvist & Rowe 2005), and it means that there is less chance to perform pre-copulatory female choice. Instead, females sometimes discard sperm from low-quality males or seek re-mating with a superior male (post-copulatory or cryptic female choice: Eberhard 1996). However, these options are not available for male *Neotrogla* because males do not receive gametes from females. How do males respond to coercive mating by females? This is a unique question about sexual selection, to which only *Neotrogla* can answer. It is also important to unveil why, among many sex-role reversed animals (i.e., the animals in which males invest more for offspring than females via nuptial gift or paternal care: Gwynne 2008), only *Neotrogla* evolved the elaborated female penis. To understand this, we have to study the behavioral (such as mating posture), physiological (such as the characteristics of the spermatophore: the capsule containing semen and nutrition), and developmental (such as the developmental origin of the gynosome) backgrounds (or pre-adaptations) that enabled *Neotrogla* to originate the female penis.

In order to observe *Neotrogla* copulation, new techniques were developed. However, all of them are very simple and cheap. For example, liquid nitrogen is generally used to fix insects in copula (e.g., Briceno *et al.* 2007). However, it was unavailable in the caves, several hundred kilometers away from the lab. The very simple solution was use of hot water by which insects in copula can be killed instantaneously without modification, before later transferring them into 80% ethanol for permanent fixation. To observe the inside of the coupled genitalia after fixation, internal soft tissues such as muscles must be dissolved. However, connection between the male and female genitalia is maintained by muscles so that their dissolution causes detaching of the coupling pairs. The solution to this dilemma was to embed them into agarose before dissolving. In future studies on the origin of the female penis, establishing healthy cultures of *Neotrogla* would be quite useful but also a big challenge because *Neotrogla* species live in very specialized environment and feed on very restricted foods. In order to examine the sexual selection working on the insects, we need to develop experiments that control the relative quality of males and females by modulating the quality and/or availability of their food. Therefore, we hope to find controllable foods available for future studies on *Neotrogla* (e.g., flour, yeast and skim milk are used to rear domestic psocopterans: Wearing-Wilde 1996).

The paper has been actively featured or discussed in huge numbers of newspapers, TV stations, online news sites, blogs, and Twitter because discovery of a "female penis" itself has great impact for the public. The *Neotrogla* female penis is also ranked as the third strangest genital organ ever discovered (Braun 2014). As mentioned above, the penis is, by definition, the male copulatory organ and is widely believed to define males. Therefore, many lay audiences were confused about the definition of *Neotrogla* sexes, although sexes are actually defined by their gamete size, not by external genital features. Extremely long duration of copulation controlled by female *Neotrogla* seems to be of interest for many people. Our findings completely reverse our general ideas about the roles of sexes and thus it attracted a lot of public interest. Of course the discovery attracted attention from the scientific point of view as well because these insects give us new possibilities to test some theories of sexual selection, one of the most active fields of evolutionary biology.

In addition, there were active debates on the usage of the term "penis" for a female intromittent organ (Newitz 2014; Yong 2014). Of course, the female penis is not homologous to the male one, and it may be natural to use a different term (gynosome) for a different structure. However, the male penises evolved many times independently and thus are also not homologous between different groups of animals (e.g., the human penis is not homologous with that of turtles: Kelly 2004). Non-homologous structures have long been termed as penis without any doubt because they share some key features in common: they are exclusively owned by males, inserted into females, and are used for sperm transfer.

Although owned by the opposite sex, the "female penis" shows a lot of analogous features with the male one, e.g., it is an erectile intromittent organ used for sperm transfer, and has spines to anchor to the opposite sex. Therefore, we consider that adopting the term "penis" also to the female structure can be justified. It may even be possible to extend the definition of penis as "an intromittent organ used for sperm transfer", without considering the sex of possessor.

REFERENCES

Arnqvist, G. and Rowe, L. 2005. *Sexual conflict*. Princeton, NJ: Princeton Univ. Press.

Braun, B. *Evolutie tussen de benen*. 2014. Available from http://www.mareonline.nl/archive/2014/05/08/evolutie-tussen-de-benen

Briceno RD, Eberhard W. G. and Robinson A. 2007. Copulation behavior of *Glossina pallidipes* (Diptera: Muscidae) outside and inside the female, and genitalic evolution. Bulltin of Entomological Research 97:1-18.

Darwin, C. R. 1871. *The Decent of Man and Selection in Relation to Sex*. London: John Murray.Eberhard, W. G. 1985. *Sexual Selection and Animal Genitalia*. Cambridge: Harvard University Press.

Eberhard, W. G. 1996. *Female control: sexual selection by cryptic female choice.* Princeton, NJ: Princeton Univ. Press.

Gwynne, Darryl T. 2008. "Sexual conflict over nuptial gifts in insects." *Annual Review of Entomology* no. 53: 83-101. doi: 10.1146/annurev.ento.53.103106.093423.

Kelly, D. A. 2004. Turtle and mammal penis designs are anatomically convergent. Proceedings of the Royal Society of London B (Suppl.). 271: S293-S295.

Lienhard, C., Do Carmo, T.O., and Ferreira, R.L. 2014. "A new genus of Sensitibillini from Brazilian caves (Psocodea: 'Psocoptera': Prionoglarididae)." *Revue suisse de Zoologie* no. 117 (4): 611-635.

Newitz, A. *Your penis is getting in the way of my science*. 2014. Available from http://io9.com/your-penis-is-getting-in-the-way-of-my-science-1564473352

Trivers, R. L. 1972. "Parental investment and sexual selection." In *Sexual Selection and the Descent of Man, 1871-1971*, edited by B G Campbell, 136-179. Chicago: Aldine Publishing Co.

Wearing-Wilde, Judy. 1996. "Mate choice and competition in the barklouse *Lepinotus patruelis* (Psocoptera: Trogiidae): The effect of diet quality and sex ratio" *Journal of Insect Behavior* no. 9 (4): 599-612. doi: 10.1007/BF02213883.

Yong, E. *In this insect, females have penises and males have vaginas* 2014. Available from http://phenomena.nationalgeographic.com/2014/04/17/in-this-insect-females-have-penise s-and-males-have-vaginas

Yoshizawa, K., and Johnson, K.P. 2006. "Morphology of male genitalia in lice and their relatives and phylogenetic implications." *Systematic Entomology* no. 31 (2): 350-361. doi: 10.1111/j.1365-3113.2005.00323.x.

Yoshizawa, Kazunori, Rodrigo L. Ferreira, Kamimura Yoshitaka, and Charles Lienhard. 2014. "Female penis, male vagina, and their correlated evolution in a cave insect." *Current Biology* no. 24 (9): 1006-1010. doi: 10.1016/j.cub.2014.03.022.