In worm-bacteria symbioses some microbes remain faithful to their hosts, others to their location

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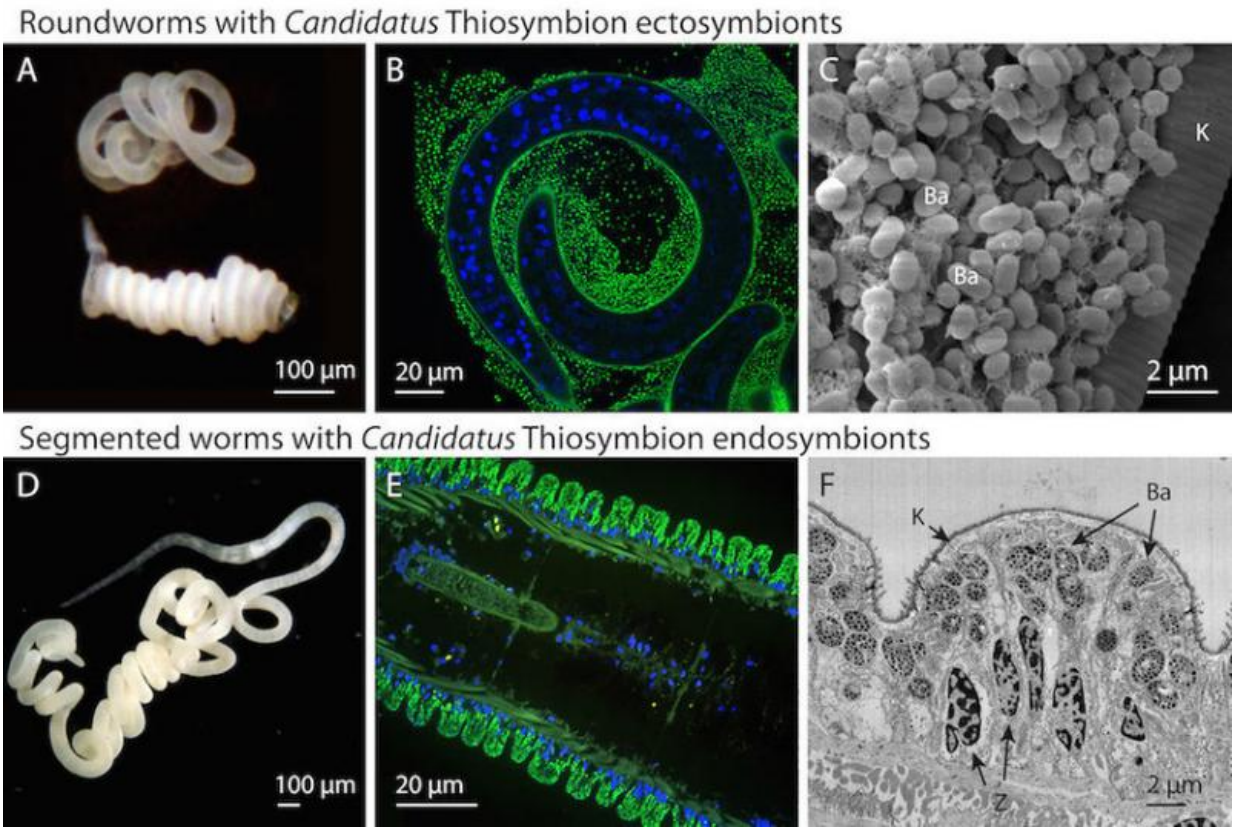

Roundworms and segmented worms and their bacterial symbionts, called Candidatus Thiosymbion. In the middle image, bacterial cells are colored green and host nuclei are stained blue. In the images on the right, symbionts are labelled “Ba”. Credit: MPI for Marine Microbiology

If your favourite pub moves – would you move too or look for another pub? For bacteria living in symbiosis with marine worms it all depends on whether they sit outside or inside the pub. Scientifically speaking: bacteria living on the body surface of their hosts are loyal to those, while bacteria living inside their hosts prefer to stay local, as scientists from the Max-Planck-Institute for Marine Microbiology from Bremen now revealed.

Nematodes and annelids. These are roundworms and segmented worms. They are just worms, one might think. "In fact, these two animal phyla are about as different as men and turtles", says Judith Zimmermann from the Max Planck Institute for Marine Microbiology in Bremen, Germany. "And yet they live in symbiosis with very closely related bacteria."

The symbiotic tenants of roundworms and segmented worms belong to a group of closely related bacteria named Candidatus Thiosymbion. These bacteria supply their hosts with nutrition. In the roundworms – in a subfamily called Stilbonematinae -, they live on the body surface. "The bacteria cover the worm like a sleeping bag, only the head and the tip of the tail peek out", Zimmermann explains. In contrast, in segmented worms – in the gutless oligochaetes –, the bacteria live underneath the worms' skin and feed their host so well that they have lost their mouth and gut.

"Our results show that these symbiotic bacteria appear to have switched multiple times between roundworms and segmented worms and accordingly between ecto- and endosymbiotic lifestyles during the course of their evolution", Zimmermann explains. "This flexibility is remarkable, because bacteria are generally adapted to one type of lifestyle and one group of hosts", adds Cecilia Wentrup who also participated in the study. "It was the large amount of data we analysed during this study that allowed us to reconstruct the closely interwoven

evolution of these symbionts and their marine hosts."

Outside and loyal or inside but fickle

Despite their remarkable flexibility, however, the symbionts are very loyal to their hosts in some concerns. Once again, Zimmermann and her colleagues were in for a surprise. Contrary to the expectations of Zimmermann and her colleagues, the external tenants seem to show more long-term loyalty to their hosts than the internal cohabitants. "Long-term means over millions of years", Zimmermann clarifies. "The host-symbiont-relationship is very stable for the roundworms and their bacteria. Apparently, they have co-evolved with each other without changing their partner." Closely related roundworms were always associated with closely related symbionts. This high fidelity was seen in hosts from around the world, whether Zimmermann and her colleagues looked at roundworm-bacteria associations from Sylt, the Caribbean, the Mediterranean or Australia.

The picture is different in the symbiosis between segmented worms and their bacteria. "Relationships were much less stable in these associations", Wentrup explains. "In the segmented worms, not only the host species plays a role." Rather, the location is also important. The researchers often found that distantly-related host species from the same geographic region had very similar symbionts. And vice-versa, closely related hosts from different geographic regions often had only distantly-related symbionts. "Closely related segmented worms from Australia and the Caribbean, for example, do not always have closely related symbionts", Wentrup adds. "This suggests that in the segmented worms, the original bacterial symbionts were often replaced by local bacteria".

The results of this study clearly show how flexible and full of surprises marine symbioses are. "Next we plan to investigate what determines the lifestyles of these symbionts", says Nicole Dubilier, Director of the

Department of Symbiosis at the Max Planck Institute for Marine Microbiology. Which factors decide whether the Candidatus Thiosymbion-bacteria remain external and attached to the surfaces of their hosts or become internal and live under the worms' skin? How do host and symbionts recognize each other? And do ectosymbionts become endosymbionts, or the other way round? This is what the Max Planck researchers want to find out in further studies.

More information: Judith Zimmermann et al. Closely coupled evolutionary history of ecto- and endosymbionts from two distantly-related animal phyla, *Molecular Ecology* (2016). DOI: 10.1111/mec.13554

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