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Quick guide

Triturus newts

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***What is* Triturus?** *Triturus* is a genus of salamanders distributed across most of Europe and adjacent Asia, known as the 'crested' (seven species) and 'marbled' newts (two species). Crested newts are generally dark and drab, except for their fiery-orange belly, which warns potential predators of a powerful neurotoxin secreted through the skin. Marbled newts have a marbled green-black pattern and instead of a brightly colored belly sport a blazing dorsal stripe to signal they are not to be snacked upon. *Triturus* newts are mostly terrestrial, but return to the water each year to breed. When they do, males develop spectacular breeding costumes (Figure 1). While crested newts grow a strongly denticulated crest, marbled newts keep it smooth.

What is special about* Triturus *newts? *Triturus* males perform ritualized courtship at underwater leks to wow the females. The slenderer a species is, the longer it stays in the breeding pond. Hence, a causal relationship between body build evolution and ecological specialization is assumed. The different *Triturus* species have a parapatric distribution, meaning they exclude each other geographically. Where the different species meet, they hybridize (Figure 1). Cases are known where one species displaces another and their hybrid zone moves as a consequence. *Triturus* newts represent the most famous example of a balanced lethal system, in which exactly 50% of embryos suffer from a genetically determined lethality. How such a wasteful system could evolve remains an evolutionary mystery.

What does mating by* Triturus *involve? Male *Triturus* newts congregate and perform elaborate dances, meanwhile wafting pheromones toward females to further entice them (Figure 1). When a female is taken in by a particular male's display, he creeps away and she follows him. Once she signals her interest by touching his tail, the male deposits a spermatophore (a package of sperm) and guides the female over it. Finally, the female takes up the spermatophore with her cloaca. Eggs are fertilized internally and as the female lays her clutch in the aquatic vegetation, she gently wraps each individual egg in a leaf. The larvae hatch after several weeks to become the apex predators in their ponds. A few months later they metamorphose into land-dwelling juveniles.

How did the variation of body build in* Triturus *evolve? The amphibious lifestyle of *Triturus* requires them to annually alternate between a terrestrial and aquatic lifestyle. However, being adapted to life on land and in the pond poses contrasting demands on body build. More aquatic and elongated *Triturus* species possess a higher number of trunk vertebrae (Figure 1). The variation in trunk vertebrae shown by *Triturus* is unparalleled in newts, suggesting an important role for trunk vertebrae during *Triturus* evolution. When tracing the number of trunk vertebrae along the phylogenetic tree, the minimal amount of potential vertebra additions during *Triturus* evolution has to be inferred. So, the ecological expansion within the genus was accomplished by a stepwise elongation and resulted in adaptive radiation because all intermediate body builds survive until this day.

How do we know that* Triturus *hybrid zones move? Early on during speciation, nascent species can typically still exchange genes, a process known as introgression. The hybrid zones that such young species establish where and when they meet facilitate introgression in nature. If a hybrid zone were to move, a key prediction is that the receding species leaves behind a trail of selectively neutral alleles, within the expanding one. Empirical examples are rare and it is not clear how prevalent historical hybrid zone movement is. Yet, a genomic footprint of hybrid zone movement in the guise of strongly asymmetrical and geographically extensive introgression has been found in several *Triturus* hybrid zones. Furthermore, independent evidence of hybrid zone movement is provided by

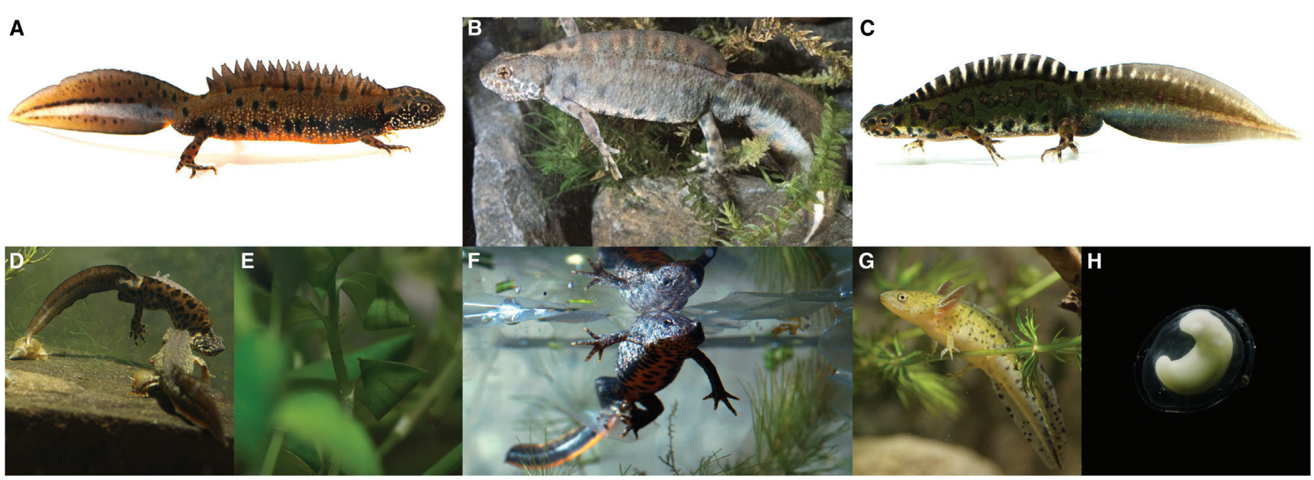

Figure 1. *Triturus* newts and their behavior.
(A) Male Danube crested newt (*Triturus dobrogicus*), a relatively aquatic species; (B) F1 hybrid between a marbled (*Triturus marmoratus*) and crested (*Triturus cristatus*) newt species; (C) Male pygmy marbled newt (*Triturus pygmaeus*), a relatively terrestrial species; (D) *Triturus* male courting a female; (E) Folded leaves containing *Triturus* eggs; (F) *Triturus* female using her hind legs to deposit eggs; (G) *Triturus* larva; (H) *Triturus* embryo at late tail-bud stage. (Photos: Michael Fahrbach (A,C–H), Paolo Mazzei (B).)

enclaves of the receding species, holding on locally as the expanding species moves around and past them.

How come 50% of* Triturus *embryos never hatch? In a balanced lethal system, two chromosome forms carry distinct lethal alleles that are reciprocally compensated for by functional genes on the alternative chromosome form. Therefore, both chromosome forms, and in effect their linked lethal alleles, are required for survival. All adult *Triturus* newts invariably possess two forms of chromosome 1 that can be distinguished under the microscope, known as 1A and 1B. Yet, according to the rules of Mendelian inheritance, half of the offspring produced are homozygous (possessing two copies of either 1A or 1B). These homozygotes die at the late tail-bud stage, approximately halfway through embryological development (Figure 1). Which genes cause this lethality is still unknown.

Are* Triturus *newts endangered? All species studied have shown population declines in response to land use change, affecting both their aquatic and terrestrial habitats. Habitat fragmentation, changes in water use, pollution and exotic species (such as fish and crayfish, but also invasive *Triturus* species) pose conservation concerns. *Triturus* newts are susceptible to the chytrid fungus *Batrachochytrium salamandrivorans*, and its spread into Europe via the pet trade is a worry to *Triturus* newt conservation.

Where can I find out more?

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Q & A

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Jenny Read is Professor of Vision Science at Newcastle University's Institute of Neuroscience. She has a degree in Physics (1994), a doctorate in Theoretical Physics (1997) and a Masters in Neuroscience (1999), all from Oxford University. From 1997 to 2001 she was a Wellcome Training Fellow in Mathematical Biology at Oxford University and then from 2001 to 2005 she was a postdoctoral fellow at the US National Eye Institute. She returned to the UK in 2005 with a University Research Fellowship from the Royal Society, Britain's national science academy. Her lab works on many aspects of visual perception, especially stereoscopic or '3D' vision.

What led you to move from physics to neuroscience? A mixture of 'push' and 'pull'. Like many a student before me, I was feeling rather fed up with my doctoral research. It was about why disk galaxies have their beautiful spiral arms, and while this is a fascinating question the day-to-day work just involved writing a lot of Fortran code to solve a set of differential equations, and it seemed rather remote from anything that anyone would care about. So I diverted myself by attending lectures on neuroscience. I had not studied biology beyond the age of 16, so it was a revelation to me. I remember one lecture that showed the orientation tuning curves from Miller *et al.*'s paper on the cricket cercal sensory system (J. Neurophysiol. (1991) *66*, 1680–1689) — four neurons with peaks at 45°, 135°, 225° and 315°. At that point, I had no idea that it was even possible to record activity in individual neurons let alone that a biological system could act in such a lawful way. I was and remain in complete awe of Hodgkin and Huxley's work on the action potential. So I became very excited about the possibility of moving into biology and applying mathematics to living systems.

Was it easy to make the transition? To address my woeful ignorance of biology, I took two excellent courses with the Open University: 'Biology: brain and behaviour' (SD206) and 'Human biology and health' (SK220). I wasn't at all sure how to move into biology, but I had a breakthrough when I went to see Julian Jack at Oxford University's Laboratory of Physiology. He was incredibly encouraging and supportive, and he helped me to apply for a Training Fellowship in Mathematical Biology: a scheme that the Wellcome Trust was running at that time specifically to help people with maths skills to move into biology (or biologists to acquire maths skills). This funded me for four years, during which time I obtained Oxford's then-new MSc degree in Neuroscience. By the end of that time, I was starting to feel like a proper neuroscientist.

How did you come to study stereoscopic vision? I was first exposed to stereo vision when I went to talk with Andrew Parker during my Wellcome Fellowship. I remember him drawing a Keplerian array and explaining the stereo correspondence problem to me. For my MSc in Neuroscience, I had to choose two research projects: I ended up choosing a psychophysics project with Richard Eagle and a computational one with Andrew Parker and Bruce Cumming. As both projects were on stereopsis, I thought that they would go well together — they did and I never looked back! Tragically, Richard died suddenly during my time in his lab. I really regret not having had a chance to get to know him better; I am sure we