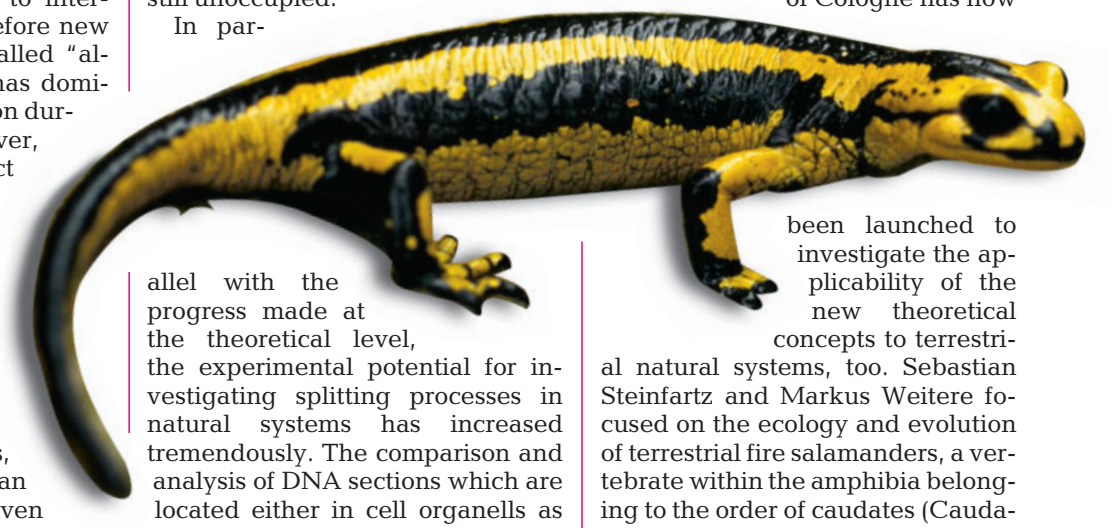
The Fire Salamander: Source for New Species

What you should know about the colourful fire salamanders: how a new species arises through adaptation to its environment is of general interest

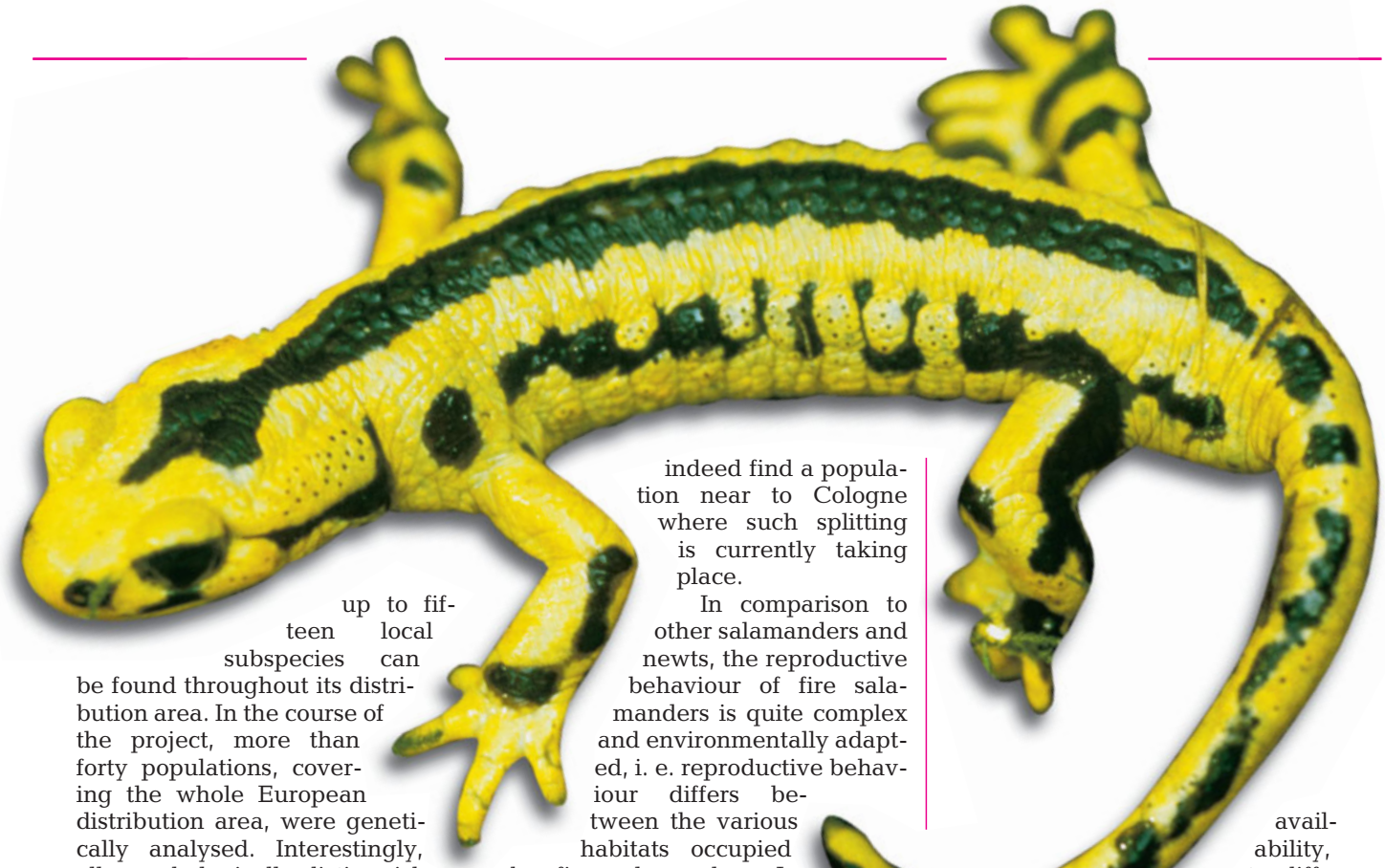
One of the central and most debated topics in evolutionary biology is the question how new species arise and how they are able to stay separated from each other. Until very recently it has been the common view that new species arise through geographical isolation, e. g. through isolation by watersheds, mountain massifs or in environmental refugia during ice ages. Such a geographic isolation prevents gene flow between the separated populations and finally (normally after million of years) both populations are not able to interbreed and represent therefore new species. This process is called "allopatric speciation" and has dominated the species discussion during the last century. However, alternative concepts predict that speciation can happen under natural conditions even without geographical separation – i. e. speciation can take place under "sympatric conditions". In contrast to "allopatric speciation", which can be seen as a purely passive process, "sympatric speciation" is an active process, mainly driven by adaptation.

New theoretical models suggest that intraspecific competition under sympatric conditions is the starting point for speciation, which then leads to the formation of differently adapted subpopulations. These subpopulations can only split into different species if intermixing is prevented by "assortative mating". In this context "assortative mating" assumes that partners of the same adaptation type prefer mating with their own type, and avoid mating with other adapted types. Considering these two factors, i. e. adaptation in combination with assortative mating, new species can form very rapidly (within less than 100 generations) without the long time postulated for geographic isolation mechanisms. The process of adaptive speciation can be expected to occur in newly colonized habitats, where appropriate ecological niches are still unoccupied.



In parallel with the progress made at the theoretical level, the experimental potential for investigating splitting processes in natural systems has increased tremendously. The comparison and analysis of DNA sections which are located either in cell organells as the mitochondrium or in the nucleus can be used to trace differentiation and speciation. To investigate very recent splitting events, highly variable DNA markers are required. Tandemly repeated DNA stretches which are located in the nucleus are known as "microsatellites". Microsatellites can be used for „fingerprinting" individuals, thus making it possible to test whether subpopulations under investigation still have genetic exchange or have already separated from each other.

Some of the best documented examples of sympatric speciation have been provided for cichlid species found in crater lakes in Cameroon. A former Ph. D. student in the laboratory in Munich, Ulrich Schliewen, showed that in one of these lakes, the Barombi Mbo, several new species had formed under sympatric conditions from a single founder species. A project at the University of Cologne has now been launched to investigate the applicability of the new theoretical concepts to terrestrial natural systems, too. Sebastian Steinfartz and Markus Weitere focused on the ecology and evolution of terrestrial fire salamanders, a vertebrate within the amphibia belonging to the order of caudates (Caudata). Fire salamanders represent the most variable terrestrial vertebrates and have adapted to various different niches, and are thus an ideal model system for studying adaptive speciation. Its conspicious appearance has always attracted the interest of naturalists and collectors. At least five distinct species of fire salamanders can be distinguished, and



up to fifteen local subspecies can be found throughout its distribution area. In the course of the project, more than forty populations, covering the whole European distribution area, were genetically analysed. Interestingly, all morphologically distinguishable subspecies were also genetically different, suggesting that differentiation goes beyond the subspecific level. Even within the lineage which currently colonizes Middle Europe, interesting local adaptations can be detected. This reflects the pattern that is expected from the theoretical models of adaptive speciation, which assume that after the recolonization of open niches (as is the case after an ice age) conditions are ideal for new species to form under sympatric conditions. By carrying out an area-wide investigation of Germany analysing more than 50 populations of fire salamanders, the research team under Professor Tautz tried to identify a candidate population in which the splitting of differently adapted ecotypes could be studied under natural conditions. They did indeed find a population near to Cologne where such splitting is currently taking place.

In comparison to other salamanders and newts, the reproductive behaviour of fire salamanders is quite complex and environmentally adapted, i. e. reproductive behaviour differs between the various habitats occupied by fire salamanders. In Central Europe and Germany fire salamanders are a character species of old broadleaf forests on low mountain ranges such as the Harz Mountains and the Black Forest. Normally the females deposit living larvae in oxygen-rich streams. Until metamorphosis – the transition from the aquatic to the terrestrial habitat – the larvae are strictly confined to water. After their metamorphosis, the fire salamanders are strictly terrestrial and need up to five years to become mature. Accordingly, mating is performed on land. In some areas of Germany fire salamanders can be also found in "atypical" flatland habitats in which streams are rare. In such habitats the fire salamanders have started to use stagnant waters such as ponds and slopes for reproduction. However, the ecological conditions with respect to oxygen content, temperature, food availability, etc. differ sharply between ponds and streams. Low food availability, especially when taken in combination with a high desiccation risk in ponds, creates unfavourable conditions for amphibian larvae in general. As a consequence, the fire salamanders have to adapt to these conditions. The degree of differential adaptation to stream versus pond habitats was analysed under both laboratory and natural conditions. Representative stream-breeding populations were therefore studied in the Bergisches Land and the Eifel and compared to pond-breeding populations in the Ville near Cologne and Bonn. The results confirmed that the occupation of stream and pond habitats

Impressive variety: The fire salamander, a member of the Caudata, embraces numerous species and sub-species, augmented by regional and local variants. Left: A fire salamander from North-west Spain. Above: An example from the Pyrenees. Right: An animal conspicuous by its striking colouration.

In our latitudes, the fire salamander is a classical inhabitant of wooded hill-country. It deposits its larvae in oxygen-rich streams. Only the adult animals live permanently on land. In many regions the fire salamander may, notwithstanding, be found in flat areas with standing water.

has already led to genetically fixed adaptations.

To test whether the adaptation to stream- and pond-breeding also leads to a splitting of these ecotypes under sympatric conditions (as predicted from the theoretical model discussed above) an area had to be found in which both reproductive types occur in sympatry. The Kottenforst, near Bonn, is such an area. Ponds and streams are irregularly distributed across the Kottenforst and are inhabited by fire salamander larvae. The current genetic and ecological analyses suggest that pond- and stream-breeding fire salamanders are indeed in the process of speciation.

To interpret genetic patterns in terms of speciation it is necessary to know as much as possible about the behaviour of the organism under investigation. Therefore, factual knowledge regarding its movements, expansion and reproductive behaviour are crucial. Under captive breeding conditions, the male sperm of fire salamanders can be stored for several years by the females and still be used for successful fertilisation of the eggs at a later point in time. However, the extent to which such sperm storage and multiple paternities occur also under natural conditions is an open question. Long-time sperm storage and multiple paternities do not only have an impact on the population structure, but the analysis of multiple paternities will also permit conclusions to be drawn regarding assortative mating, which is the key factor for keeping differently adapted types apart. To study the migratory behaviour of individuals, so-called "transponders" were planted under the skin of more than one hundred individuals from a selected fire salamander population. These transponders comprise a small magnetic coil, and enable individuals collected at later times to be unequivocally re-identified. It was thus possible to track the individuals and to determine their movements over a period of more than three years. In parallel with this, it was possible to test the offspring of several individuals by microsatellite fingerprinting and to show that sperm storage and multiple paternities are indeed common in fire salamanders, even under natural conditions.

The Salamander Project is still in its initial phase. Further research effort will focus on the genetic analysis of recently diverged stream- and pond-types to obtain detailed data for testing a speciation scenario under sympatric conditions. Once the preliminary data have been verified, detailed behavioural studies and crossing experiments between both ecological types will be used to determine the genetic principles of sympatric speciation. This study suggests a shift in focus: speciation has not necessarily to be studied in tropical regions – new species arise in front of our doorstep.

Dr. Sebastian Steinfartz
Prof. Diethard Tautz
Universität zu Köln