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Hybridization Increases Species Diversity in Evolution

By

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The term “hybridization” should be applied to all evolutionary processes in which barriers against the exchange and the recombination of genetic material between individuals from distinct phylogenetic units (clades, taxa) are overcome and hybrid progeny originates. Thorough multidisciplinary and DNA-analytical phylogenetic studies on many seed plant clades have shown that hybridization processes often lead to an increase in genetic variation and result in the formation of new species. This is demonstrated by selected examples from seed plants and other organisms. Evidence is accumulating that cycles of differentiation and hybridization in general are key phenomena of evolution.

The model genus *Achillea* (*Asteraceae-Anthemideae*) is particularly suited to demonstrate, how the evolutionary processes of differentiation and hybridization are linked with each other (GUO & al. 2004, 2005, 2006, EHRENDORFER & GUO 2006). Hybrid swarms between two very different species have originated in man-disturbed habitats of Bulgaria, the diploid (2x) *A. clypeolata* and the tetraploid (4x) *A. collina*. Their ploidy barrier has been circumvented by the occasional production of unreduced egg cells by the 2x-partner, the formation of 4x-F₁ and subsequent crosses and backcrosses on the 4x-level. DNA fingerprinting (AFLP) shows that the specific markers of the parent species reappear variously recombined in the morphologically well recognizable hybrids, but that no new post-hybridization markers have appeared yet. This contrasts with another, but geologically evidently much older 4x-hybrid bridge (called *A. alpina* agg.-4x) which has been formed in China between two 2x-taxa from different *Achillea* sections, *A. acuminata*-2x and *A. asiatica*-2x. A corresponding AFLP analysis of this 2x/4x-clade documents in addition to the parental

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markers the appearance of new 4x-markers, missing on the 2x-level. Furthermore, parallel eco-geographical differentiation of the 4x-aggregate has resulted in the formation of new taxa, expanding over E-Asia and into northern N-America.

Even more complex evolutionary processes evidently have led to the origin of the polyploid complex of *Achillea millefolium* agg. It includes, in addition to *A. asiatica*-2x and *A. collina*-4x about 20 other taxa on the 2x-, 4x-, 6x- and 8x-level which extend from western Eurasia over the whole N-Hemisphere, and world-wide as neophytes. By crossing experiments between the hygrophilous Pannonian *A. asplenifolia*-2x and the xerophilous Pontic *A. setacea*-2x it was possible to create synthetic *A. collina*-4x, suggesting how this taxon, wide-spread throughout continental Europe, could have originated. Further multidisciplinary studies have shown that the 2x-basis of *A. millefolium* agg. also includes *A. ceretanica*-2x (E-Pyrenees), *A. cuspidata* (W-Himalaya), *A. bucharica*-2x (mountains of C-Asia) and *A. asiatica*-2x (Altai to N-China). AFLP marker, mainly localized in the nucleus, and plastid markers, only transmitted on the maternal side, demonstrate, how the genetic material of these 2x-taxa was handed on to the 4x-level of the complex, mostly by reticulate and hybrid processes, and how it was also exchanged extensively in a "horizontal" way among different 4x-taxa. From *A. ceretanica*-4x in France to *A. asiatica*-4x in E-Asia and further to *A. borealis*-4x (= *A. lanulosa*-4x) in N-America these 4x-taxa have differentiated in a highly polymorphic and nearly continuous fashion. Many new AFLP and plastid markers have originated during this new differentiation phase. Comparable processes have been repeated in the parallel and polyphyletic development of the 6x-level (i.a. *A. millefolium* s.str.-6x, *A. distans*-6x, *A. borealis*-6x) and finally the 8x-level (i.a. *A. monticola*-8x, *A. pannonica*-8x) of the complex.

How fast and successful ecological radiation and adaptation can occur under a hybridization regime has been clearly shown by a crossing experiment between two extremely different ecotypes of the N-American *Achillea borealis*-6x, the subarctic pygmy subsp. *borealis* (Alaska, Aleutes) and the subtropical giant subsp. *gigantea* (salt pans of C-California) (HIESEY & NOBS 1970). Numerous F₂ individuals from that cross were cloned and cultivated in experimental gardens at 30m, 1400m and 3050m in California. During several years natural selection favoured numerous recombinant types which grew well at elevations, where none of the parental ecotypes could survive.

Only brief comments are possible here for the following examples of hybrid speciation, grouped according to main cytogenetic mechanisms involved. In the two first cases there is no polyploidization, one speaks of homoploid hybridization. In the summergreen oaks of the N-Hemisphere (*Quercus* subg. *Quercus*, *Fagaceae*) species are based on well adap-

ted and coherent 2x gene pools. Even when sympatric, oak species hardly mix completely, in spite of very weak genetic isolation and strong potentials for hybridization. Still, in their glacial refugia and during postglacial re-migration, European species must have experienced considerable genetic reconstruction and changes. Evidence for this comes from the distribution of their plastid types which does not conform to species but is reticulate and follows regional patterns (PETIT & al. 2004). The hybrid origin of a number of annual species of *Helianthus* (*Asteraceae-Heliantheae*) in western N-America can be demonstrated by a detailed analysis of their genomes: They are composed of chromosomes and chromosome segments from their postulated parental taxa in a mosaic-like fashion (RIESEBERG 1997).

In the following groups of examples, the processes of hybridization and polyploidization are coupled: allopolyploidy. Geologically younger polyploid complexes, where the parental 2x-taxa have at least partly survived to the present, are called neopolyploid. In contrast, those consisting exclusively of polyploids are palaeopolyploid.

Neopolyploid complexes, as those described for *Achillea* before, are often true centres for the origin of new species diversity. The genus *Tragopogon* (*Asteraceae-Cichorieae*) has not produced allopolyploid taxa in the Old World. But in N-America three introduced 2x-species have formed sterile 2x-hybrids. From these, two very successful and aggressive new allo-4x species have originated (SOLTIS & al. 2004). The genus *Nicotiana* (*Solanaceae*; $x = 12$) is centred in the New World and includes both, relatively recent single 4x-taxa (e.g., *N. tabacum* or *N. rustica*, both with $n = 24$) and older, species-rich 4x-clades, as the *N. sect. Suaveolentes*, predominantly in Australia. A comparison of their DNA-sequences shows that they are most closely related in their plastid DNA with 2x-precursors from *N. sect. Noctiflorae*, whereas their nuclear DNA corresponds with 2x-members of *N. sect. Alatae*. These two sections are limited to S-America and it is likely that the 4x-precursors of *N. sect. Suaveolentes* with $n = 24$ also have originated there. Possibly via S-Africa (only with *N. africana*) *N. sect. Suaveolentes* must have reached Australia by long distance dispersal. There, they have differentiated into numerous species with descending dysploidy ($n = 24, 23, 22, 20, 19, 18$ and 16), whereas their ancestors in S-America have become extinct. Comparable phylogeographic events have led to the settlement of Australia and New Zealand by allopolyploid members of *Lepidium* (*Brassicaceae*). They evidently have originated from long-distance dispersed African diploids with corresponding nuclear genome and from Californian ones with which they share their plastid genome (MUMMENHOFF & al. 2004).

In addition to sexually reproducing polyploids there are plant (and animal) groups which have formed agamic polyploid complexes. Their members have partly switched to $\pm$ complete asexual, apomictic re-

production which allows the propagation of hybrid, $\pm$ sterile, sometimes 3x or 5x, but otherwise well adapted and competitive genotypes. This has often led to most polymorphic clades, as in the Angiosperm genera *Rubus*, *Taraxacum*, *Hieracium* or *Poa*.

Numerous examples for palaeopolyploid clades are found among pteridophytes and among ancient Angiosperm groups. In the *Laurales* fossils and DNA-analyses help to date shifts from 2x- to 4x- and 8x-levels back to the Lower Cretaceous and thus to the final phases of the break down of Gondwana (RENNER 2004). In the light of such findings it is surprising that even the well known and short-lived experimental *Arabidopsis thaliana* with the low chromosome number $n = 5$ is a palaeopolyploid (HENRY & al. 2006). The complete DNA-sequences available for *Arabidopsis* has revealed numerous duplications which can only be explained by an ancient polyploidization of $n = 4 + 4 \rightarrow 8$ about 15 mya bp and a dysploid reduction from $n = 8 \rightarrow 5$ about 5 mya bp. A comparable, obviously also quite old case of allopolyploidy has been demonstrated for a fungus, the yeast *Saccharomyces cerevisiae* (KELLIS & al. 2004).

Finally, one should consider the evolutionary situation in early pro- and eukaryotes as well as in animals. For various animal groups examples of homoploid and also polyploid hybrid speciation are reported in increasing numbers (e.g., ARNOLD & MEYER 2006). For many of the prokaryotic *Archaea* and *Bacteria* parasexual processes and horizontal gene transfer has been demonstrated (RIVERA & LAKE 2004). Furthermore, the decisive primary endocytobiotic processes between different prokaryotes which have led to the origin of the eukaryotes and the following secondary endocytobioses among eukaryotes have to be understood as hybridization phenomena *sensu lato*. This is justified because these processes are also accompanied by a lot of genetic transfers and recombinations.

In retrospect one can say that the importance of hybridization, often coupled with polyploidization, in the evolution of all organisms, has been underestimated. It is particularly relevant that these processes strongly stimulate speciation and innovation, and thus lead to continuous cycles of differentiation and hybridization.

References

- ARNOLD M. L. & MEYER A. 2006. Natural hybridization in primates: one evolutionary mechanism. – *Zoology* 109: 261–276.
- CHASE M. W, KNAPP S., COX A. V., CLARKSON J. J., BUTSKO Y., JOSEPH J., SAVOLAINEN V. & PAROKONNY A. S. 2003. Molecular systematics, GISH and the origin of hybrid taxa in *Nicotiana* (*Solanaceae*). – *Ann. Bot.* 92: 107–127.
- EHRENDORFER F. & GUO Y.-P. 2006. Multidisciplinary studies on *Achillea sensu lato* (*Compositae-Anthemideae*): new data on systematics and phylogeography. – *Willdenowia* 36: 69–87.

- GUO Y.-P., EHRENDORFER F. & SAMUEL R. 2004. Phylogeny and systematics of *Achillea* (*Asteraceae-Anthemideae*) inferred from nrITS and plastid trnL-F DNA sequences. – *Taxon* 53: 657–672.
- , SAUKEL J., MITTERMAYER R. & EHRENDORFER F. 2005. AFLP analyses demonstrate genetic divergence, hybridization, and multiple polyploidization in the evolution of *Achillea* (*Asteraceae-Athemideae*). – *New Phytologist* 166: 273–289.
- , VOGL C., VAN LOO M. & EHRENDORFER F. 2006. Hybrid origin and differentiation of two tetraploid *Achillea* species in East Asia: molecular, morphological and eco-geographical evidence. – *Mol. Ecology* 15: 133–144.
- HENRY Y., BEDHOMME M. & BLANC G. 2006. History, protohistory and prehistory of the *Arabidopsis thaliana* chromosome complement. – *Trends Plant Sc.* 11: 267–273.
- HIESEY W. M. & NOBS M. A. 1970. Genetic and transplant studies on contrasting species and ecological races of the *Achillea millefolium* complex. – *Bot. Gaz.* 131: 245–259.
- KELLIS M., BIRREN B. W. & LANDER E. S. 2004. Proof and evolutionary analysis of ancient genome duplication in the yeast *Saccharomyces cerevisiae*. – *Nature* 428: 617–624.
- MUMMENHOFF K., LINDER P., FRIESEN N., BOWMAN J. K., LEE J.-Y. & FRANZKE A. 2004. Molecular evidence for bicontinental hybridogenous genomic constitution in *Lepidium sensu stricto* (*Brassicaceae*) species from Australia and New Zealand. – *Amer. J. Bot.* 91: 254–261.
- PETTIT R. J., BODENES C., DUCOUSO C., ROUSSEL G. & KREMER A. 2004. Hybridization as a mechanism of invasion in oaks. – *New Phytologist* 161: 151–164.
- RENNER S. S. 2004. Variation in diversity among *Laurales*, early Cretaceous to present. – *Biol. Skr.* 55: 441–458.
- RIESEBERG L. H. 1997. Hybrid origins of plant species. – *Annu. Rev. Ecol. Syst.* 28: 359–389.
- RIVERA M. C. & LAKE J. A. 2004. The ring of life provides evidence for a genome fusion origin of eukaryotes. – *Nature* 431: 152–155.
- SOLTIS D. E., SOLTIS P. S., PIRES J. C., KOVARIK A., TATE J. A. & MAVRODIEV E. 2004. Recent and recurrent polyploidy in *Tragopogon* (*Asteraceae*): cytogenetic, genomic and genetic comparisons. – *Biol. J. linn. Soc.* 82: 485–501.

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