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INVESTIGATIONS

- 1787–1796 **Gene Expression in the Skin of Dogs Sensitized to the House Dust Mite *Dermatophagoides farinae***
Paz Schamber, Rachel Schwab-Richards, Stefan Bauersachs, and Ralf S. Mueller
- Atopic dermatitis is a multifactorial disease in humans and dogs with genetic predispositions. The authors analyzed gene expression in allergen-exposed and control skin of normal Beagles and Beagles sensitized to dust mites. After 24 hours 361 genes were detected with higher and 226 with lower mRNA concentration in allergen treated skin of sensitized dogs compared to control specimens. Genes with augmented expression were involved in inflammation; downregulated genes were associated with barrier function of the skin. This confirmed similarities between human and canine atopic dermatitis and identified genes not previously known to be involved in canine atopic dermatitis.
- 1797–1812 **SNPs in Genes Functional in Starch-Sugar Interconversion Associate with Natural Variation of Tuber Starch and Sugar Content of Potato (*Solanum tuberosum* L.)**
Lena Schreiber, Anna Camila Nader-Nieto, Elske Maria Schönhals, Birgit Walkemeier, and Christiane Gebhardt
- The quality of potato tubers for consumption, processing, and industrial uses is critically influenced by the content of starch and sugars, complex traits that are controlled by multiple genetic and environmental factors. Using association genetics, the authors identified natural DNA variants in genes functional in starch-sugar interconversion that are diagnostic for superior or inferior tuber starch and sugar content. These variants and their effects on tuber quality provide insight into the genetic architecture of potato complex traits and constitute a molecular toolkit that can be used for optimizing the process of breeding improved varieties.
- 1813–1824 **Widespread Genomic Incompatibilities in *Caenorhabditis elegans***
L. Basten Snoek, Helen E. Orbidans, Jana J. Stastna, Aafke Aartse, Miriam Rodriguez, Joost A.G. Riksen, Jan E. Kammenga, and Simon C. Harvey
- Genetic incompatibility is a key barrier contributing to species isolation caused by genetic interactions. The Bateson-Dobzhansky-Muller (BDM) model explains speciation based on incompatibilities which emerge from the deleterious interactions of alleles. As yet however, evidence is scant showing genome-wide interactions underlying these incompatibilities. Using QTL analyses in two different recombinant inbred populations, the authors report multiple BDM incompatibilities between the genomes of *C. elegans* wild types CB4856 and N2. For two QTL regions identified, results are inconsistent with a model of pairwise interaction between two loci, suggesting that the incompatibilities are a consequence of complex interactions between multiple loci.

- 1825–1836 **Sensory Rewiring in an Echolocator: Genome-Wide Modification of Retinogenic and Auditory Genes in the Bat *Myotis davidii***
Nicholas J. Hudson, Michelle L. Baker, Nathan S. Hart, James W. Wynne, Quan Gu, Zhiyong Huang, Guojie Zhang, Aaron B. Ingham, Linfa Wang, and Antonio Reverter
- Bats are iconic mammals, whose capacity for echolocation is a product of specialization in both vocalization and hearing. However, the genetic basis of these sensory changes has not been fully elucidated. Here we find evidence for modification in visual and auditory system genes in the echolocator *Myotis davidii*. They are consistent with a small eye, dim-light adapted vision and hearing specialization. One line of evidence is the presence of disabling mutations in redundant visual genes, the second is extreme bias in codon usage in a set of vision and hearing genes. Together, they provide mechanistic insight into sensory rewiring.
- 1837–1848 **An X-Linked Sex Ratio Distorter in *Drosophila simulans* That Kills or Incapacitates Both Noncarrier Sperm and Sons**
William R. Rice
- A wide diversity of forms of genomic conflict have been discovered over the last century. Are there any major forms that have escaped detection? A new form of genomic conflict was recently predicted by theory: sexually antagonistic zygotic drive of the sex chromosomes (SA-ZD). It occurs when genes on one sex chromosome in an XY father kill the sex of offspring that does not carry it. Here, the author develops a new assay to unambiguously distinguish SA-ZD from other sex ratio distorting mechanisms and uses it to demonstrate the operation of SA-ZD in a model organism (*Drosophila simulans*).
- 1849–1858 **Regulation of Centromere Localization of the *Drosophila* Shugoshin MEI-S332 and Sister-Chromatid Cohesion in Meiosis**
Cristina Nogueira, Helena Kashevsky, Belinda Pinto, Astrid Clarke, and Terry L. Orr-Weaver
- Shugoshin (Sgo) proteins play an essential role in accurate chromosome segregation in mitosis and meiosis, by protecting the cohesin complex at the centromere. Here, the authors investigate the centromere localization and function of the founding member of the Sgo family, *Drosophila* MEI-S332, in meiosis. Several important conclusions result from this study. The results show that MEI-S332 can be inactivated in meiosis to release centromere cohesion without itself delocalizing from the centromere. The authors find that MEI-S332 is not required on meiotic chromosomes after anaphase I for accurate meiotic chromosome segregation and thus is not crucial for spindle assembly or microtubule-kinetochore interactions.
- 1859–1870 **Complex Cooperative Functions of Heparan Sulfate Proteoglycans Shape Nervous System Development in *Caenorhabditis elegans***
Carlos A. Díaz-Balzac, María I. Lázaro-Peña, Eillen Teclé, Nathali Gomez, and Hannes E. Bülow
- Development of the nervous system is a complex process requiring the integration of countless cues in the extracellular space. For example, KAL-1/anosmin-1, a molecule mutant in Kallmann Syndrome requires heparan sulfate, extracellular sugars, to function *in vivo*. Here, the authors use the small nematode *Caenorhabditis elegans* to identify and genetically dissect the role of heparan sulfates for KAL-1. They find heparan sulfate core proteins from different tissues and with distinct heparan sulfate sugars attached to act redundantly. Based on previous studies, the genes identified could be candidate genes to be mutant in patients with Kallmann Syndrome.
- 1871–1880 **Fine Mapping and Evolution of the Major Sex Determining Region in Turbot (*Scophthalmus maximus*)**
Xoana Taboada, Miguel Hermida, Belén G. Pardo, Manuel Vera, Francesc Piferrer, Ana Viñas, Carmen Bouza, and Paulino Martínez
- Sex determination (SD) displays a high evolutionary rate in fish. Turbot (*Scophthalmus maximus*) is a flatfish with a major SD QTL. Refined mapping failed to identify the master SD gene (SDg) but confirmed a ZW system and suggested a narrower mapping position for SDg. Neither genetic differentiation nor recombination frequency differences were detected along the main SD group between sexes, supporting a recent origin of the SD region. Sex association analysis with markers in the main sex-related linkage groups provided evidence for a transition from an ancient XY system in brill to a novel ZW mechanism in turbot.

- 1881–1892 **Endogenous Retrovirus Insertion in the *KIT* Oncogene Determines *White* and *White spotting* in Domestic Cats**
Victor A. David, Marilyn Menotti-Raymond, Andrea Coots Wallace, Melody Roelke, James Kehler, Robert Leighty, Eduardo Eizirik, Steven S. Hannah, George Nelson, Alejandro A. Schäffer, Catherine J. Connelly, Stephen J. O'Brien, and David K. Ryugo
 The domestic cat *Dominant White* locus (*W*) has been of interest to geneticists due to the co-occurrence of multiple phenotypes (white coat, deafness, blue eyes). The authors identify *KIT*, as the feline *W* locus, where a remarkable retrotransposition and evolution of an endogenous retrovirus, interrupting a previously described regulatory site, is characterized as generating multiple phenotypes, *White* and *white spotting*. Deafness is linked and associated with the *KIT W* allele. A large population-genetic survey supports the authors' findings and demonstrates statistical significance of the long terminal repeat and full-length element with *Dominant White* ($p < 0.0001$) and *white spotting* ($p < 0.0001$), respectively.
- 1893–1906 **Transcriptome and Complexity-Reduced, DNA-Based Identification of Intraspecies Single-Nucleotide Polymorphisms in the Polyploid *Gossypium hirsutum* L.**
Qian-Hao Zhu, Andrew Spriggs, Jennifer M. Taylor, Danny Llewellyn, and Iain Wilson
 Only varietal single nucleotide polymorphisms (SNPs) but not sub-genome specific SNPs are useful in breeding of polyploid crops; however, varietal SNPs are still very limited in cotton. The authors identified ~38K varietal SNPs among 18 *G. hirsutum* varieties using a novel algorithm based on the rationale that varietal SNPs can be more confidently called when flanked by sub-genome-specific SNPs. Approximately 86% of the SNPs were verified using different genotyping platforms and ~17K of them have been used in the first 70K infinium cotton SNP chip. These SNPs provide the cotton community a valuable marker resource applicable to genetic analyses and breeding programs.
- 1907–1918 **Evidence of Hermaphroditism and Sex Ratio Distortion in the Fungal Feeding Nematode *Bursaphelenchus okinawaensis***
Ryoji Shinya, Koichi Hasegawa, Anthony Chen, Natsumi Kanzaki, and Paul W. Sternberg
 Nematodes have a great diversity of life histories, which includes considerable variation in sexual reproductive strategies and ecological niches ranging from parasitic to free-living. The authors demonstrate that the fungal feeding nematode *Bursaphelenchus okinawaensis* has two sexes: a self-fertilizing hermaphrodite and a male. By isolating and characterizing visible mutations, the authors show that this close relative of *B. xylophilus*, the scourge of pine trees, is amenable to genetic analysis and has unique sexual characteristics. *B. okinawaensis* will be therefore an attractive model for evolutionary studies, with *Caenorhabditis elegans* and *Pristionchus pacificus* as excellent references.
- 1919–1930 **Genome-Wide Linkage Disequilibrium in Nine-Spined Stickleback Populations**
Ji Yang, Takahito Shikano, Meng-Hua Li, and Juha Merilä
 This article provides the first investigation of genome-wide LD patterns in the nine-spined stickleback. It is also one of the most extensive studies exploring patterns of habitat variation in LD in wild vertebrates. In general, the findings shed new light on the patterns and extent of inter-habitat variation in LD as well as the evolutionary factors driving them. The levels of LD uncovered here also have some important implications for future gene mapping studies in nine-spined sticklebacks.
- 1931–1942 **Crossability of *Triticum urartu* and *Triticum monococcum* Wheats, Homoeologous Recombination, and Description of a Panel of Interspecific Introgression Lines**
Agostino Fracano, Andrea Brandolini, Laura Rossini, Pierre Sourdille, Joerg Wunder, Sigi Effgen, Alyssa Hidalgo, Daniela Erba, Pietro Piffanelli, and Francesco Salamini
 AFLP fingerprinting of 496 *T. monococcum* and *T. urartu* accessions revealed rare *T. urartu* lines showing gene flow between the two taxa. The authors produced rare fertile hybrids between the two species and developed interspecific introgression lines. These findings are new because the two species are considered reproductively isolated. The obtainability of fertile introgression lines opens new perspectives for genetic studies and breeding purposes (including practical applications, e.g. search of superior alleles and their use in breeding). Furthermore, the availability of *T. urartu* DNA fragments in promising *T. monococcum* lines is an important addition to wheat stocks.

- 1943–1954** **QTug.sau-3B Is a Major Quantitative Trait Locus for Wheat Hexaploidization**
Ming Hao, Jiangtao Luo, Deying Zeng, Li Zhang, Shunzong Ning, Zhongwei Yuan, Zehong Yan, Huaigang Zhang, Youliang Zheng, Catherine Feuillet, Frédéric Choulet, Yang Yen, Lianquan Zhang, and Dengcai Liu
- Allopolyploid plants are common in natural ecosystems and among important crop species. They are produced by processes that duplicate chromosome sets from interspecific hybrids. Meiotic non-reduction resulting in unreduced gametes is thought to be the predominant mechanism for chromosome doubling. However, its genetic base was largely unknown. The authors address this using wheat and found a major locus responsible for unreduced gamete formation, which promotes the spontaneous chromosome doubling in wheat triploid hybrids. A collinear homolog of *CYCA1;2/TAM* which results in the formation of unreduced gametes in *Arabidopsis thaliana* was found to be closely located to this QTL in wheat.
- 1955–1962** **Performance of the Cas9 Nickase System in *Drosophila melanogaster***
Xingjie Ren, Zhihao Yang, Decai Mao, Zai Chang, Huan-Huan Qiao, Xia Wang, Jin Sun, Qun Hu, Yan Cui, Lu-Ping Liu, Jun-Yuan Ji, Jiang Xu, and Jian-Quan Ni
- Off-target effect with the Cas9/sgRNA system is a major concern when analyzing mutant phenotypes. These authors demonstrate here that Cas9 nickase transgenes efficiently generate heritable mutants with paired sgRNAs in *Drosophila*, without any significant off-target effects. A novel *piwi* mutant is generated through this system through homology-directed repair, which demonstrates how to reliably make a precisely defined allele of a germline-essential gene. The transgenic flies and DNA vectors in this study will be of interest to the fly community.
- 1963–1970** **Resolution of Genetic Map Expansion Caused by Excess Heterozygosity in Plant Recombinant Inbred Populations**
Sandra K. Truong, Ryan F. McCormick, Daryl T. Morishige, and John E. Mullet
- Recombinant inbred populations of many plant species exhibit more heterozygosity than expected under the Mendelian model of segregation. This segregation distortion causes the overestimation of recombination frequencies and consequent genetic map expansion. Here the authors build upon existing genetic models of differential zygotic viability to model a heterozygote fitness term and calculate expected genotypic proportions in recombinant inbred populations propagated by selfing. Accounting for excess heterozygosity resolves map expansion and allows for more accurate estimates of linkage, benefiting linkage-based analyses used in the identification and utilization of causal genetic variation.
- 1971–1980** **A Saturated Genetic Linkage Map of Autotetraploid Alfalfa (*Medicago sativa* L.) Developed Using Genotyping-by-Sequencing Is Highly Syntenous with the *Medicago truncatula* Genome**
Xuehui Li, Yanling Wei, Ananta Acharya, Qingzhen Jiang, Junmei Kang, and E. Charles Brummer
- The authors developed a saturated genetic linkage map for alfalfa using genotyping-by-sequencing. This method enabled them to cost-effectively generate a map much faster in this autotetraploid species than other methods. Comparison of marker order on the genetic linkage maps with the physical whole genome sequence of *Medicago truncatula* showed that the genomes are highly syntenous. A formerly known translocation between chromosomes 4 and 8 in *M. truncatula* was identified relative to alfalfa as was another inversion on chromosome 1. The map will make molecular breeding applications more straightforward in this important crop.
- 1981–1990** **Small RNA Expression from the Human Macrosatellite DXZ4**
Michael Pohlars, J. Mauro Calabrese, and Terry Magnuson
- Small non-coding RNAs play several roles in regulating gene expression. In the nucleus, small RNA-Argonaute complexes recruit epigenetic modifying activities to genomic sites. The authors describe in human somatic cells a potential link between the expression of small RNAs from the macrosatellite DXZ4 and Argonaute-dependent DNA methylation. DXZ4 was found to express a wide range of small RNAs potentially representing several classes of small RNAs. A subpopulation of these RNAs are bound by Argonaute. Moreover, the authors show AGO association with DXZ4 and that the Argonaute proteins AGO-1 and PIWIL4 are required for DNA methylation of DXZ4.

- 1991–2002 **Bayesian Genomic-Enabled Prediction as an Inverse Problem**
Jaime Cuevas, Sergio Pérez-Elizalde, Victor Soberanis, Paulino Pérez-Rodríguez, Daniel Gianola, and José Crossa
- Genomic prediction models address the collinearity that arises when the number of molecular markers is larger than the sample size. Penalized regression methods address the collinearity problem by attempting to suppress the effect of the collinearity. In this study the authors propose four Bayesian approaches with prior variances as a way of potentially increasing the prediction accuracy. To evaluate these methods, maize and wheat data were employed for measuring prediction accuracy using the proposed models. Results indicate that these Bayesian models yielded prediction accuracy up to 3% higher than that of standard Bayesian regression models, with less computational effort.
- 2003–2012 **Genomic Characterization of the LEED..PEEDs, a Gene Family Unique to the *Medicago* Lineage**
Diana I. Trujillo, Kevin A. T. Silverstein, and Nevin D. Young
- Legume plants have the ability to establish symbiotic relationships with nitrogen-fixing soil bacteria in dedicated root organs called nodules. The successful establishment of this relationship is regulated in part through the exchange of signaling molecules between the plant host and bacterial partners. This research article describes LEED..PEED (LP) genes, a family of 13 putatively secreted peptides with nodule-specific expression. The LP gene family has expanded recently in *Medicago* species, with copy number variation among accessions, and is absent in close legume relatives, suggesting an important novel function in nodulation.
- 2013–2022 **The Alternative Oxidase AOX Does Not Rescue the Phenotype of *tko*^{25t} Mutant Flies**
Kia K. Kemppainen, Esko Kemppainen, and Howard T. Jacobs
- The *Drosophila* mutant *tko*^{25t} is a model for diseases caused by lack of mitochondrial protein synthesis. Although unable to support ATP synthesis, the alternative oxidase (AOX) from the tunicate *Ciona intestinalis* can correct phenotypic defects of flies in which mitochondrial respiration is inhibited by toxins or genetic ablation of cytochrome oxidase, a major product of mitochondrial protein synthesis. Here the authors found that AOX could not alleviate the developmental retardation and sensitivity to mechanical stress-induced seizures characteristic of *tko*^{25t}. They infer that the *tko*^{25t} mutant phenotype is due to a complex metabolic defect, rather than simply to impaired mitochondrial respiration.
- 2023–2034 **Complete Plastome Sequences from *Glycine syndetika* and Six Additional Perennial Wild Relatives of Soybean**
Sue Sherman-Broyles, Aureliano Bombarely, Jane Grimwood, Jeremy Schmutz, and Jeff Doyle
- Seven complete chloroplast genome sequences from the genus *Glycine* are compared to the previously published soybean sequence (*G. max*). The number of repetitive sequences reported for soybean was very high; this investigation reduced that number by considering location and number of times a repeat was found in the plastome sequence. Rearrangement of gene order in plastome sequences has been reported in other legume species. However, all of the plastome sequences described here are highly similar. High levels of sequence similarity between divergent species are likely due to an introgression event that occurred approximately 1.6 million years ago.
- 2035–2048 ***De Novo* Assembly and Annotation of the Transcriptome of the Agricultural Weed *Ipomoea purpurea* Uncovers Gene Expression Changes Associated with Herbicide Resistance**
Trent Leslie and Regina S. Baucom
- The agricultural weed *Ipomoea purpurea* is a model in ecological genetics investigations. This species is also evolving resistance to the widely used herbicide RoundUp. Here the authors provide an annotated transcriptome for the *Ipomoea* community and use this genomics resource to investigate gene expression differences of resistant and susceptible *Ipomoea* lines following herbicide application. This work uncovers candidate loci involved in the resistance response for future investigations and greatly increases genomics resources for this important weedy plant species.

2049 **CORRIGENDUM**