

# Characterisation of the Context-Dependence of the Gene Concept in Research Articles

## Possible Consequences for Teaching Concepts with Multiple Meanings

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**Abstract** The purpose of this study is to interpret and qualitatively characterise the content in some research articles and evaluate cases of possible difference in meanings of the gene concept used. Using a reformulation of Hirst’s criteria of forms of knowledge, articles from five different sub-disciplines in biology (transmission genetic, molecular biology, genomics, developmental biology and population genetics) were characterised according to knowledge project, methods used and conceptual contexts. Depending on knowledge project, the gene may be used as a location of recombination, a target of regulatory proteins, a carrier of regulatory sequences, a cause in organ formation or a basis for a genetic map. Methods used range from catching wild birds and dissecting beetle larvae to growing yeast cells in 94 small wells as well as mapping of recombinants, doing statistical calculations, immunoblotting analysis of protein levels, analysis of gene expression with PCR, immunostaining of embryos and automated constructions of multi-locus linkage maps. The succeeding conceptual contexts focused around concepts as meiosis and chromosome, DNA and regulation, cell fitness and production, development and organ formation, conservation and evolution. These contextual differences lead to certain content leaps in relation to different conceptual schemes. The analysis of the various uses of the gene concept shows how differences in methodologies and questions entail a concept that escapes single definitions and “drift around” in meanings. These findings make it important to ask how science might use concepts as tools of specific inquiries and to discuss possible consequences for biology education.

## 1 Introduction

In this article, I consider how the gene concept is used in different fields of biological research, as exemplified in genetics research articles. I first review some complications regarding the

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gene concept from a biological and philosophical perspective followed by consequences for science education, and then turn to research related to the contextual understandings of concepts. The article concludes with a discussion about what the findings of the context-dependence of the gene concept could mean for the conceptual content of biology curricula and also science education more generally.

## 1.1 The Gene Concept

Knowledge of the gene as a biological entity since the beginning of the twentieth century has undergone immense development regarding details and complexity (Hausmann 2002; Portin 2002). The chromosome, often illustrated as a straight line, is quite a dynamic and flexible place, with overlapping genes, alternative splicing, parasitic and mobile genes, epigenic modifications, etc. (Gerstein et al., 2007). Relations between DNA, phenotypic expressions and development are also found to be increasingly intricate networks. Different sub-disciplinary fields have developed; molecular biologists study intricacies in how genes are regulated; researchers in genomics study many genes and many gene products on a large scale; developmental biologists study, for example, homeotic genes, which if mutated can lead to the loss of an entire body segment. In parallel, there have been developments in population genetics and studies about the genetic basis of natural selection.

The gene has thus been an interesting and complex concept to analyse from a philosophical perspective—Kitcher's *Genes* (1982) being a somewhat early example. Here, the gene concept was discussed in relation to scientific development, conceptual change and reductionism, as molecular developments seemed to offer a causal explanation of how the genes with almost "magical power" exerted "control" (as Demerec wrote about the gene in 1939). Since then, suggestions of what to include in the gene concept have developed, with examples such as a claim that we should focus on the molecular level (Fogle 1990), a definition of the gene as a linear sequence in a product at some stage of genetic expression (Waters 1994), an argumentation for a differentiation between the molecular gene and the evolutionary gene (Griffiths and Neumann-Held 1999), a distinction of a "gene-P" as determinant for phenotypic differences and "gene-D" as responsible for development (Moss 2001). Keller (2000) even argued that the "century" of the gene concept is over due to the introduction of new concepts and other ways of thinking about the organisation of living systems. Indeed, the almost "magical power" of control that Demerec attributed the gene in the early 1900s (1939), one finds currently beyond the gene. El-Hani (2007) discussed the risk of having the gene concept deleted from the genetic vocabulary and saw the idea of the gene as a single unit as the main difficulty, challenged by the evolving complexity and diversity of genomic organisation. A solution suggested was to accept that a variety of gene concepts can have an explanatory and heuristic power. A concluding example is Waters (2014), who stated that a philosophical agreement over what a gene is among philosophers seems hopeless (p.124).

With this biological and philosophical background, it is no wonder that science education sees that the gene concept is coupled to documented learning problems in schools. The genetic content is identified as a difficult school subject (Johnstone and Mahmoud 1980; Bahar et al. 1999), and problems in learning could be a problem of misconceptions (Pashley 1994; Venville and Treagust 1998; Marbach-Ad 2001) or even unidentifiable alternative conceptions (Lewis and Kattmann 2004). Studies also show that it can be difficult to relate concepts from different biological hierarchical levels of

explanation (Marbach-Ad and Stavy 2000; Wood-Robinson et al. 2000; Venville et al. 2005). This is also shown in Duncan and Reiser (2007) where interviews and written assessments of 10th grade students show a lack of understanding of the centrality of proteins in genetic phenomena. Gericke and Smith (2014) concluded that in genetics education research, knowledge of learning problems is so well known that the problem now lies with transforming this knowledge into educational practice.

Furthermore, different studies describe a diversity not only regarding learning and understanding, but also in educational materials for schools (Gericke and Hagberg 2010; dos Santos et al. 2012) and in textbooks at college level (Albuquerque et al. 2008; Flodin 2009). Studies of textbooks show that the gene concept (Flodin 2009) and genetic models (Gericke and Hagberg 2010) are often presented and explained in a variety of scientific contexts. At the same time, this plurality is seldom addressed in science textbooks either for school (Gericke et al. 2014) or college (Albuquerque et al. 2008; Flodin 2009). This plurality includes, for example, historical developments of explanatory models of gene function: the Mendelian model, the classical model, the biochemical-classical model, the neoclassical model and the modern model (Gericke and Hagberg 2007). Another example is different categories of gene concepts (Flodin 2009): the gene as a trait, an information-structure, an actor, a regulator and a marker. These categories are coupled to sub-disciplinary discourses: transmission genetics, molecular biology, genomics, developmental biology and population genetics. Within the field of science studies, a strong connection has thus become evident between the concepts used by scientists, their enquiries and ways of making their phenomena evident and possible to describe (Carlsen 2007; Kelly 2008).

## 1.2 Concepts as Contextually Understood

Concepts as contextually understood imply a more complex understanding of a concept, including different circumstances where the concept is used. Andrew Pickering (1995) used, for example, historical documents to show how physicists “mangle” their concepts and artefacts to better suit their undertakings and make their phenomena conceptually tangible. This so-called “mangle” means that concepts in these activities change their meanings to better suit their purposes. Pickering (1995, pp. 145–146) argued that “...the specific contents of scientific knowledge are always immediately tied to specific and very precisely formed fields of machines and disciplines”, where disciplines are specific patterns of human agency, routinized ways of connecting marks and symbols in a conceptual practice. An empirical study by Stotz et al. (2004) used questionnaires given to active researchers from different fields in biology, asking them to apply the gene concept to specific cases. The answers showed that differences in the experimental practises used by certain scientists were reflected in differences in how they seemed to explicitly conceptualise genes. Waters (2014) argued for a practice-centred epistemology and a turn towards focusing on scientific contexts. When we do that, we see for example that: “Genes are used as a lever to manipulate and investigate a wide variety of biological processes” (Waters 2008, p. 258). The reductionist view of the gene as a causal explanation of what happens in an organism has turned to a view of the gene as a methodological tool.

Therefore, these different studies suggest that specific inquiries of each field seem to be more important for understanding the meaning of the concept, rather than one accepting an overarching archetype gene concept. Thus, the question of how the concepts are contextualised in subject teaching must be asked. van Oers (1998) argued that the view of knowledge in

education as decontextualised and generalised is in fact a question of continuous recontextualisations. This is in line with Bosch and Gascón (2006) who highlighted the notion of didactical transpositions, i.e. to deconstruct and rebuild knowledge (for example, to choose, restructure and recontextualise content). However, in school for example, the content knowledge is often not recontextualised in a meaningful way (Osborne and Dillon 2008). Therefore, it is important to study from what recontextualisations take place, used as one way to create meaningful knowledge contents in teaching and to exert conscious didactical transpositions. Inspired by Hirst's way of analysing knowledge contexts in terms of forms of knowledge, this is a contribution to how such an investigation could be made on scientific articles within biology.

### 1.3 Theoretical Background

For many years, the focus within science education studies has been on problems of learning. Following theorists like Hirst, I would like to shift the focus to content and what we choose to teach. Hirst characterised forms of knowledge as the following (1974, p. 44):

- They each involve certain central concepts that are peculiar in character to the form (for example, “acceleration” and “photosynthesis” in science, “God” and “sin” in religion, and “good” and “wrong” in moral knowledge).
- In a given form of knowledge, these and other concepts that denote certain aspects of experience form a network of possible relationships in which experience can be understood. As a result, the form has a distinctive logical structure.
- The form has expressions or statements that in some way or another are testable in relation to experience, in accordance with particular criteria that are peculiar to the form.
- The forms have developed particular techniques and skills for exploring experience and testing their distinctive expressions, for instance the techniques of science and those of the various literary arts.

Hirst formulated his forms of knowledge in relation to the notion of liberal education: what do we want our students to acquire according to mankind's historically developed ways to understand and explain the world?<sup>1</sup> Hirst (1993) described his earlier work (1974) as being founded on a rational context of justification, seeking a systematic coherent framework for the formation of educational aims. He later saw knowledge not to be primarily propositionally based, but: “... such knowledge must also be seen as the product of practices that seek a particular form of satisfaction” (1993, p. 192). Authors like Wartofsky (1979) argued that perceptions have mainly been studied and conceived as an almost ahistorical biological feature “within” a person's head. Although processes like perception certainly have cognitive aspects, Wartofsky argued (1979, p. 194) that modes of perception vary in relation to historical changes in the forms or modes of human action (or praxis). As mankind's actions and practises change (based on needs) and are manifested in the different artefacts we

<sup>1</sup> The different forms of knowledge that Hirst claimed humanity had developed so far were the following: mathematics, physical sciences, human sciences, history, religion, literature and the fine arts, and philosophy (1974, p. 46).

use, we are also changing our perceptions of the world (ibid.). Thus, it is possible to re-interpret and reformulate Hirst's (1974) knowledge forms with Hirst's (1993) view of knowledge as historically developed ways of solving needs, which in turn means using concepts, tools, methods, and a way of judging and so on. Concepts could, in these perspectives, be a cultural-historical codified synthesis of dealing with certain kinds of problems (Radford 2013).

#### 1.4 Aim, Purpose and Questions

Several studies have shown that in school or college textbooks the gene concept is used in a variety of ways, depending on the model (Gericke and Hagberg 2010; dos Santos et al. 2012) or the disciplinary context (Albuquerque et al. 2008; Flodin 2009). One educational question is: how to develop a productive progression in understanding, according to different models or disciplinary usage of the gene? Another question is the opposite: how to develop productive recontextualisations and didactical transpositions of the research content into teaching?

The aim of this study is to contribute to a general discussion about how the meaning of a concept is dependent on its scientific context. According to a contextual view of scientific knowledge, it is not only the results, facts, concepts, principles and logical relationships that are important. It is also the science internship, working methods, type of judgments and values about what is right and true, as well as the ways to communicate, write and distribute knowledge. This study focuses on how science is communicated via the formalised, propositional presentation of which scientific articles are an example, in relation to previous studies done on formalised textbooks. Therefore, the purpose of this study is to turn to research texts to interpret and qualitatively characterise the variation of the content in these specific scientific contexts and evaluate cases of possible difference in meanings of the gene. The following research questions will be asked:

- 1) What kinds of differences in scientific contexts, or knowledge forms, are found in genetics research articles?
- 2) When comparing these forms, what differences in the use of the gene concept can be discerned?

I will use and reformulate Hirst's way of structuring knowledge content as an analytical tool in order to examine and describe the scientific context, as expressed in written form in scientific articles. In this study, five research texts from one journal *Genetics* are examined. The article concludes with a discussion about the findings and their meanings for education when the gene concept becomes an object of teaching in biology.

## 2 Material and Method

The purpose of this study is to interpret and qualitatively characterise instances of variation of the knowledge content in scientific research texts. Accordingly, articles in the journal *Genetics* are studied. By using and developing Hirst's categorisation of conceptual and methodological knowledge, the articles are characterised structurally, experimentally and discursively.

Moreover, studying variation in a more restricted context, such as one journal, provides a conservative estimate of the significance of context for conceptual meaning, where the selected articles constitute five examples.

## 2.1 Selection of Journal

The journal *Genetics* was founded in 1916 and is published by The Genetics Society of America. It "...publishes high quality, original research presenting novel findings on a range of topics bearing on heredity and variation".<sup>2</sup> It is a journal with a scope broad enough to enable a variation of concept use. The journal publishes empirical studies of organisms, ranging from microbes to mice, to humans, as well as theoretical works. Therefore, the journal provides a sound basis for studying variation within one frame of context.

## 2.2 Selection of Issue

Inheritance is a basic biological phenomenon, which can be studied from a variety of perspectives and with different sub-disciplinary approaches. The study has as its starting point previous studies of gene concept use in different sub-disciplines in biology. The year is selected in approximate relation to these previous studies in textbooks, for example, a biology textbook from 2006 in Flodin (2009). Since the emphasis of this study is to describe different context parameters that influence gene concept variation and not specific definitions or meanings, any research texts could in fact be used. Regarding the selected issue of *Genetics*, from September 2006, the articles are categorised under different headings by the journal, which suggests their main focus: genome integrity and transmission, gene expression, developmental and behavioural genetics, population and evolutionary genetics, genetics of complex traits and genome and systems biology.<sup>3</sup> This categorisation, made in the journal, correlates approximately to sub-disciplinary fields in biology.

## 2.3 Selection of Articles

Articles were selected from the various sections of the journal. The purpose of taking samples from different sections was that, to some extent, they correspond to the different sub-disciplines (Table 1) identifiable in an educational context. In Flodin (2009), the sub-disciplines were as follows: transmission genetics, molecular biology, genomics, developmental biology and population genetics. The sections in the journal can be said to correspond to the genetic parts of these sub-disciplines.

The sections in the journal contained several articles (except "genetics of complex traits" that contained only one). In order to adequately study gene concept use, the content of the articles needed to be about genes (in one way or another). Further, the articles are not selected on a basis of statistical sampling, since the purpose of this study is to interpret and qualitatively characterise instances of variation in scientific

<sup>2</sup> The citation is made from the editorial board page in the July 2015 issue.

<sup>3</sup> In the following issue, October 2006, the editors found it necessary to introduce an additional hierarchical level, the cell, under the heading "Cellular genetics".

contexts. It will not be possible to include discussion of the “population of scientific contexts” in general; however, it will be possible to mention how differences in scientific contexts may be characterised and how the gene concept may vary with that context. That, in turn, will be a sample of how the gene concept may be used and conceived in science and what consequences there could be for teaching and learning. Thus, the selected articles are examples of different biological scientific contexts, but still close enough in content to be comparable according to their use of the gene concept. At the same time, they are not too similar in research focus to address the same kind of problem.

Therefore, the articles were selected on the basis of the following:

- Each section corresponding to a sub-disciplinary field should be represented.
- They use the term *gene* in one way or another.
- The contents dealt with are issues typical of the sub-discipline, in an attempt to cover as large a variation as possible between articles.

Five articles were selected according to these criteria from the first issue of volume 174 (2006). The order in which they are analysed (numbering also according to Tables 1, 2, 3 and 4) is as follows:

1. a study of recombination
2. a study of regulation of levels of molecules
3. a study of large expression outputs of RNA and proteins
4. a study of control of development
5. a study of gene order in a chromosome

**Table 1** The articles chosen from the journal *Genetics* (Volume 174, Issue 1, 2006) are ordered according to the sections of the issue and their sub-disciplinary fields

Article title	Authors	Section in journal	Sub-disciplinary field
(1) Effects of trans-acting genetic modifiers on meiotic recombination across the a1-sh2 interval of maize	Yandeau-Nelson, et al.	Genome integrity and transmission	Transmission genetics
(2) A role for sterol levels in oxygen sensing in <i>Saccharomyces cerevisiae</i>	Davies and Rine	Gene expression	Molecular biology
(3) Introns regulate RNA and protein abundance in yeast	Juneau et al.	Genome and systems biology	Genomics
(4) The <i>Tribolium castaneum</i> ortholog of sex combs reduced controls dorsal ridge development	Shippy et al.	Developmental and behavioural genetics	Developmental biology
(5) Genetic mapping in a natural population of collared flycatchers ( <i>Ficedula albicollis</i> ): conserved synteny but gene order rearrangements on the avian Z chromosome	Backström et al.	Population and evolutionary genetics	Population genetics

The abstracts of each article with all authors are listed in [Appendix](#).

## 2.4 Analysis

The analysis starts with a characterisation of the research context and content using a development of Hirst's (1974) way of structuring science as knowledge forms. Therefore, the research contexts are characterised from pre-made categories, according to the following:

- a) Knowledge project, i.e. ways to organise the problem
- b) Methods, i.e. ways to practically solve the problem
- c) Central concept use, i.e. ways of communicating the problem (specifically in terms related to the *gene* concept)

The meanings of these categories are developed below.

The analysis continues with a comparison of the gene concept use in the texts, in relation to the knowledge project, the function of the gene as a biological entity and the different methods used. Finally, the analysis is concluded by describing also the various conceptual contexts.

A problem with presenting a study of research articles in biology is that the articles are formulated with a variety of technical terms. This means it is not an easy content to read if you are not already familiar with the projects, methods or concepts. The descriptions of the content in terms of the categories "knowledge project" and "methods" are therefore made with as few terms as possible, which require a certain processing of the material. Examples of the gene concept use, however, are not rewritten and appear verbatim.

### 2.4.1 Characterisation of Scientific Context in Research Texts

Below are Hirst's categories of forms of knowledge developed:

- a) *Knowledge project: ways to organise the problem*

Hirst (1974) starts by characterising concepts, but here I turn the criteria around and start with the *knowledge project*, within which logical relationships and methods are formed. The questions asked about the data are: What are the problems or questions that seek answers? What are the purposes of the testable claims and methods? What kind of model organism is used? Therefore, the Hirst criteria of forms of knowledge will be extended to also include practice, which is in line with his later views of seeing the satisfactions of the practice as primary. This category is presented as a simplification and summary of the main content. The simplifications have been checked by a biological researcher and were corrected. Although no specific research question is in fact formulated in any of the articles, a specific research question is deduced from the title and introduction of the article, and added to the category.

- b) *Methods: ways to practically solve the problem*

There are huge differences regarding technologies and methods between the forms of knowledge that Hirst characterised (physics, mathematics, religion and so on). However, within one form of knowledge, and within a part of a form such as a sub-discipline of biology, the methods and techniques are more or less similar, despite some differences. The question asked about the data is: What specific methods are used to solve the problem? Working with a



particular organism has impact on the options available. There is a difference between working with yeast or maize, or birds that lives in the wild. Furthermore, the methodology is superficially described. All parts in the huge complex of methods are not addressed, but those which specifically distinguish the articles. The method description has been checked by a biological researcher. One comment was that from a biological perspective they were somewhat too minimalistic described to understand what was actually done. However, for the purpose of this article, which is not to illustrate details in the processes of solving *specific* problems but to highlight *differences* between problem-solving practises, it is considered as adequate to make a case. This method section is also supplemented with figures from the articles, taken as illustrations of what are described in the texts and lastly concluded with some of the results (figures are reprinted with permission).

c) *Gene concept use: ways of communicating the problem*

Hirst (1974) emphasises the central concepts of the form of knowledge and their different logical relationships. Here, this criterion is rephrased to be about the gene concept (a central concept), its use and conceptual context. The questions asked about the data are: What kind of gene concept use can be found? In what kind of conceptual context? As with the description of the methods above, focus is on differences. The descriptions of gene concept use are centred on how the term “gene” is used to describe a biological entity or phenomenon, and its conceptual context. The differences found in the articles are highlighted, but there is no intention to provide a thorough description of every kind of gene concept use. In consequence, commonalities or similar expressions are excluded in the study. In this way, it is easier to gain a conception of what characterises a specific context when these overlaps are excluded. The observed concept relations are printed in bold in the excerpts from the texts in order to facilitate judgement on how the concept relations were read. These differences are not interpreted from a biological perspective that is, what the researcher actually *means* or what scientists actually *know*. Instead, they are considered as specific ways of expressing ideas about genes that are found in specific research contexts, where contents and meanings are taken for granted.

#### 2.4.2 Comparison of Gene Concept Use in Relation to Knowledge Forms

The different categories of forms of knowledge involves: how the gene is used as a biological entity, what kinds of methods are used, and the term “gene” and its use as a concept and conceptual context. In the second part, after the presentation of each article, the gene concepts used in the articles are compared according to the differences regarding: (1) gene function in the project of knowledge, (2) methodological conditions and (3) the conceptual contexts. These comparisons result in a limited estimate of the relation between the scientific context as knowledge forms and difference in gene concept meaning.

### 3 Results

The results are first presented article by article. They are analysed in the order of: (1) transmission genetics, (2) molecular biology, (3) genomics, (4) developmental biology and (5) population genetics. Each article is described and characterised according to the contextual categories: (a) the knowledge projects, (b) the methods and what they entail and (c) gene concept use. The results for each article are then compared to each other, and the section ends with a conclusion.

### 3.1 Article 1: Transmission Genetics

Title: “Effects of *trans*-acting genetic modifiers on meiotic recombination across the *a1-sh2* interval of maize.”

#### a) *Knowledge project: ways to organise the problem*

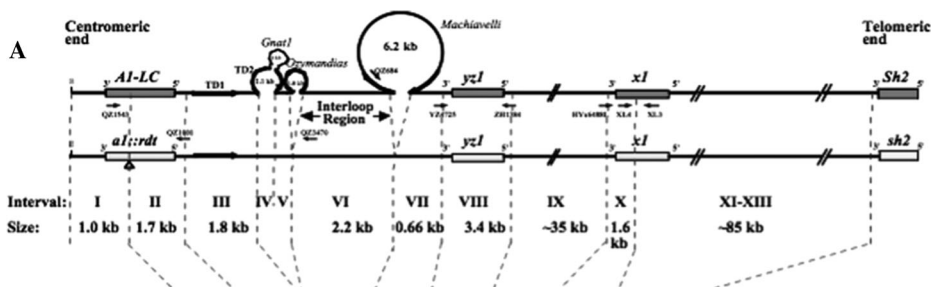
The recombination of alleles during meiosis does not happen randomly. They occur at specific sites (hot spots) rather than others (cold spots). In many organisms, hot spots are rich in genes, but there are also hot spots that do not contain genes and cold spots that contain genes. For a recombination to occur, several proteins are needed so that chromatin can be restructured. The gene is used as a physical interval to monitor whether the recombination of DNA has occurred.

Model organism: maize

Specific question: How are recombination frequencies in maize affected by the existence of a *trans*-acting “factor” or genetic modifier?

#### b) *Methods: ways to practically solve the problem*

The study concerns whole organisms and the effects of recombination at the molecular level after having crossed and selected different plants. However, it is time-consuming to find the right strains because the maize must be crossed and selected for generations. In order to keep the surrounding effects as constant as possible, researchers have worked, for example, in the same field for an entire summer. Some problems were, for example, that the seeds did not germinate in the soil. Instead, they let them germinate on sterilised germination paper. They chose the strains that they were interested in, based on the shape and colour of the maize kernel seeds. Recombinants were easily detected based on the colour and shape of seeds. Then, they prepared DNA from nuclei and recombinant breakpoints were found with physical mapping. Genetic map distance was calculated to acquire the recombination frequencies, and visualisation of the gene recombination regions is shown as a figure in the text, which identifies how the article represents genes as boxes on a line (see Fig. 1).



**Fig. 1** Adapted (figure is cut) from Yandeu-Nelson et al. (2006). Part of figure text: “Distributions of recombination breakpoints across the *a1-sh2* interval in the A632/LC, Oh43/LC, and W64A/LC genetic backgrounds. (A) A schematic of the *A1-LC Sh2* and *a1:rdtsh2* haplotypes in which boxes represent genes.” (bold emphases added, reprinted with permission)

The study shows that one of the protein factors affects both recombination frequencies and where the recombination takes place.

c) *Gene concept use: ways of communicating the problem*

The recombination of alleles occurs during meiosis and the gene is something that has a place, a locus and that corresponds to a trait. The article pictures the gene as a small “box” on a line. The gene has a clear position on the chromosome, exemplified with the sentence: “The *shrunk-2* (*sh2*) **gene is located on chromosome 3...**”, (bold emphases added), and it is quite a straightforward part of the chromosome.

The article uses the gene concept in characteristic ways. The gene is a distinct place for recombination, but is not in itself active in the recombination process:

A high-resolution recombination mapping study across the -140-kb multigenic maize *al-sh2* interval supports **that genes *per se* are preferred recombination hot spots** and intergenic regions are cold spots; even so, nongenic hot spots and genic cold spots do exist... (bold emphases added).

Other expressions are coupled to recombination rates:

...recombination rates are negatively correlated with **gene density**... recombination rates are higher in **gene-rich** than in **gene-poor regions** of the genome... To analyze the effects of **genetic background** on recombination across the *al-sh2* interval, each of the *trans* stocks was crossed to the inbred line C (cross1). ... For each physical interval examined, **genetic distances** (in centimorgans) were compared among **genetic backgrounds** using  $\chi^2$  homogeneity tests. ... **Trans-acting** modifiers involved in **chromatin organization** or remodeling might be responsible for the transformation of the **nongenic** subinterval... (bold emphases added).

The gene is expressed as a physical interval, measured in distance and provides background on which recombination occurs.

### 3.2 Article 2: Molecular Biology

Title: “A role for sterol levels in oxygen sensing in *Saccharomyces cerevisiae*”

a) *Knowledge Project: ways to organise the problem*

Ergosterol (ERG) is a molecule that is included in the cell membranes of fungi. The antifungal agents used nowadays are mainly interfering with a fungal formation of ergosterol. Therefore, there is a practical need to understand how the fungus synthesises the substance. The corresponding reaction pathway in mammalian cells is cholesterol synthesis, but the regulation is different. There are several regulatory proteins (transcription factors) involved in the regulation of the *ERG* gene expression. Some of these proteins also bind to genes associated with the yeast cell wall change when it grows in low oxygen. Oxygen affects the synthesis of ergosterol in yeast cells among other things. At low oxygen levels, the fungus starts to take up sterols from the environment rather than synthesise these itself. The gene is here used to study the mechanism by which transcription factors Upc2p and Ecm22p regulate *ERG* gene expression.

Model organism: yeast.

Specific question: How are the genes for ergosterol biosynthesis regulated under different oxygen conditions in yeast?

b) *Methods: ways to practically solve the problem*

The study was performed on the molecular level of the single-cell organism. Yeast cells were grown in synthetic media, i.e. a substance with well-defined content. For oxygen-poor growth, cells were grown in tightly closed bottles without shaking. Different strains were created with the genetic material accurately modified, which was accomplished with the help of a PCR-based gene disruption method. Cell extracts were then analysed in terms of protein content (via immunoblotting) and RNA content. RNA expression was measured using quantitative RT-PCR. The “gene” may be studied indirectly based on formed proteins and RNA. The text shows, for example, bands of proteins on a gel electrophoresis so that genes and their products may thus be represented via the presence or non-presence of different protein spots (see Fig. 2).

The study shows how various factors (Upc2p and Ecm22p transcription factors) interact in the regulation of the genes for ergosterol biosynthesis (*ERG* genes) under different conditions. The transcription factors Upc2p and Exm22p may in turn be dependent on another transcription factor Hap1.

a) *Gene concept use: ways of communicating the problem*

The gene is clearly something that is expressed. The dominant forms of statements are that genes are encoding: the gene is expressed, the gene is activated, induced or suppressed or regulated. Examples are seen as:

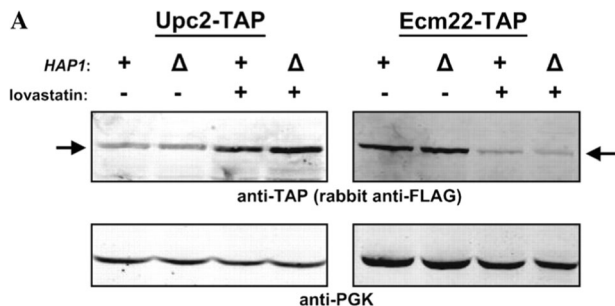
**Genes encoding** enzymes of ergosterol biosynthesis **are** transcriptionally **regulated** in response to the need for ergosterol... Hypoxia also **induced** these three **genes**...Upc2p and Ecm22p **regulate the expression** of many of the ergosterol biosynthesis (*ERG*) **genes**...The **activation of target genes** by Upc2p occurred in response to low sterols...Hap1p might **modulate *ERG* gene expression** indirectly... Hap1p might act more directly to influence either the binding of Upc2p and Ecm22p at *ERG* **promoters**...**genes** that are **induced** by sterol depletion...If the differences in *ERG2* expression were the result of a single Mendelian locus, high and low *ERG2* expression levels would be expected to segregate 2:2 when these two strains were crossed and sporulated (bold emphases added).

The gene concept is combined with concepts about regulation and transcription factors of different cellular synthetic pathways.

### 3.3 Article 3: Genomics

Title: “Introns regulate RNA and protein abundance in yeast”

**Fig. 2** Adapted (figure is cut) from Davies and Rine (2006). Part of figure text: “(A) Levels of Upc2p and Ecm22p [transcription factors] were unaffected by deletion of *HAP1*.” (i.e. gene for transcription factor Hap1(*bold emphasis* added). Protein levels were analysed by immunoblotting (reprinted with permission)



a) *Knowledge Project: ways to organise the problem*

Genes in eukaryotic organisms often contain introns. These are non-coding DNA sequences, which do not correspond to any amino acid sequence in the final protein. The purpose of this study is to evaluate the effect of introns in the cells when it comes to cellular fitness. These introns often contain regulatory sequences for the transcription and processing of the pre-mRNA molecule that is formed during protein synthesis. Genes are here used as carriers of introns and regulatory sequences.

Model organism: yeast

Specific question: What is the functional relevance of introns in yeast genes?

b) *Methods: ways to practically solve the problem*

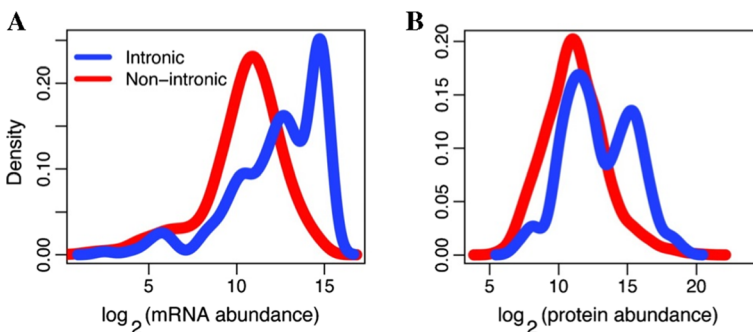
Yeast cells were cultured in small wells that allow mechanical readings of growth. The study is based on the whole genome with examples from various key genes. Intron-deficient yeast strains were constructed with, for example, PCR-based gene replacement. Strains (different mating types) were crossed and intron-deficient diploid strains were selected. The RNA was then extracted from different growing yeast cells strains, and then reverse transcribed into cDNA and analysed with quantitative PCR. That is, the “genes” can be studied indirectly through the amount of RNA produced, and the gene copies can be measured corresponding to density (see Fig. 3).

The study shows that introns improve translational “output” of the genes they “live in”.

c) *Gene concept use: ways of communicating the problem*

The gene is something that is expressed and regulated, but also something that produces and manufactures proteins. It is in a context of a cell and it is the effects of these genes on cellular growth, or fitness, which are of interest: “...deletion of introns from three essential genes decreased cellular RNA levels and caused measurable growth defects”. Examples are also the following:

...and these intron-containing ribosomal genes produce ~24% of cellular RNA... Intron-containing **genes** in *S. cerevisiae* **produce** more RNA and more protein than intronless genes. ... We found that duplicated



**Fig. 3** From Juneau et al. (2006). Part of figure text from article: “Intronic genes are highly expressed. (A) RNA abundance; (B) protein abundance. The abundance ( $\log_2$ ) of intronic genes (blue) and nonintronic genes (red) is shown. **The Density (y-axis) corresponds to the relative number of genes at a given abundance....**” (bold emphases added, reprinted with permission)

**genes ... produce**, on average ...ribosomal **i-genes**, which **manufacture** large amounts of RNA... (bold emphases added).

Other typical expressions were as follows:

We conclude that introns improve the **translational output of the genes** they occupy and thus i-genes are significantly more sensitive to both heterozygous and homozygous deletion. ... Here we show that **when intron-containing genes are challenged** they appear to **buffer** against deleterious effects **by improving** protein production. ... To investigate the role that introns may play in cellular fitness we studied their **genetic contribution to the fitness** of *Saccharomyces cerevisiae* (bold emphases added).

Here, the gene concept is in a somewhat manufacturing context of “production”, “output” and “buffering”.

### 3.4 Article 4: Developmental Biology

Title: “The *Tribolium castaneum* ortholog of *sex combs reduced* controls dorsal ridge development”

#### a) *Knowledge Project: ways to organise the problem*

The body of an insect is clearly divided into three regions: head, thorax and abdomen. Between the head and thorax, in most insects, is a small dorsal ridge. The development of the red flour beetle dorsal ridge follows a typical insect pattern. Hence, it is an attractive system to study how the dorsal ridge is formed. Different gene mutants are used to study consequences on dorsal ridge development.

Model organism: red flour beetle (*Tribolium castaneum*)

Specific question: How is the formation of the dorsal ridge of the red flour beetle (*Tribolium castaneum*) controlled?

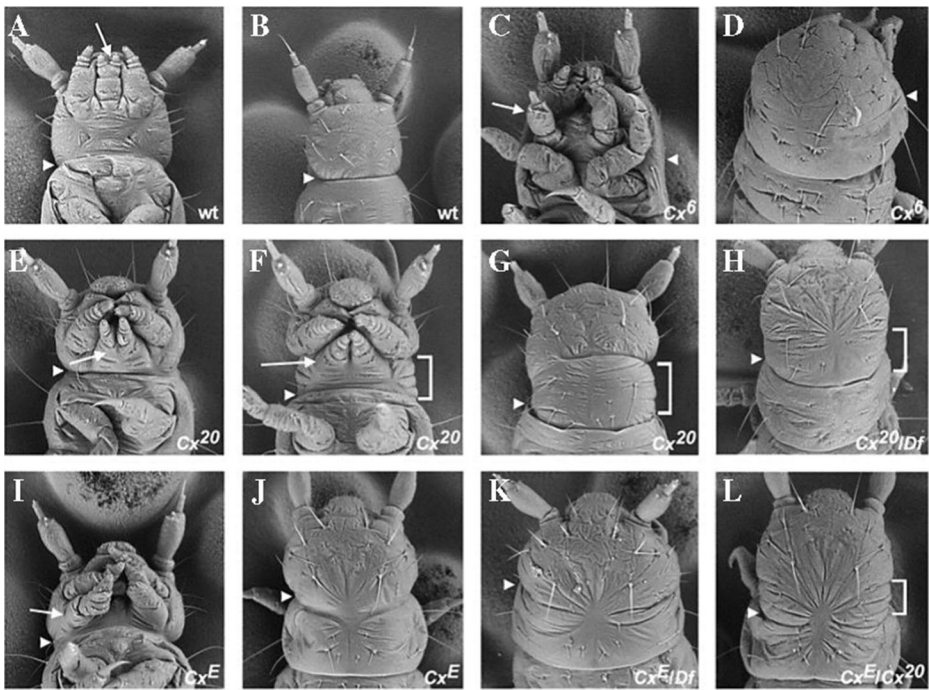
#### b) *Methods: ways to practically solve the problem*

The study follows the ontogenesis of a multicellular organism. The red flour beetle was grown on yeast and a mixture of rye and wheat flour. They were allowed to mate and eggs were collected every 2 days and allowed to develop at 30 °C. Scanning electron micrographs were obtained. To study gene expression, embryos were coloured with immune staining and separated from the yolk. Other larvae were in turn homogenised and the DNA was amplified using PCR. Then, the gene mutations were located and studied to identify the effect they had on the production of the protein. That is, the “gene” was studied both directly via its DNA sequence and indirectly via its phenotypic effects, which are shown by scanning electron micrographs of morphological changes in the beetle (see Fig. 4).

The study shows that the gene *Cephalothorax* (*Cx*) promotes the fusion in the dorsal ridge formation, and specific regions of its protein, Cephalothorax (*Cx*), are required at different stages.

#### c) *Gene concept use: ways of communicating the problem*

Here, the gene is clearly connected to a phenotype (morphological appearance). The *Cx* allele is *causing the fusion* of certain segments and transformation of the larva’s appendages and the *Cx*-gene is also regulated in different ways. The gene has a nucleotide sequence that is printed in the article. The article mentions a certain gene-phenotype (the *Cx*<sup>20</sup>-phenotype),



**Fig. 4** From Shippey et al. (2006). Part of text from figure in article: “Scanning electron micrographs of wild-type and *Cx* mutant *Tribolium* larvae. The boundary between head and thorax (approximated in cephalized mutants) is denoted by an arrowhead in A–L, and the labial appendages are indicated by an arrow in all ventral views. ... (E) *Cx*<sup>20</sup> homozygote, ventral view. **The phenotype of *Cx*<sup>20</sup> homozygotes** is variable. In this mildly affected individual, the labial appendages are more posteriorly located than in wild type and only the most proximal segment of each appendage is fused. The extra dorsal segment between the head and T1 is not visible from the ventral side.” (Bold emphases added, reprinted with permission)

which is how the genes are identified: their effect on the formation of the labial addendum and dorsal ridge. Hence:

These results suggest that the *Cx*<sup>20</sup> phenotype is due to loss-of-function effects. ... described a class of *Cx* alleles that cause fusion of the first thoracic segment (T1) with the head (cephalization) as well as transformation of the larval labial appendages to antennae (bold emphases added)

The gene is expressed in a specific location (specific cells) in the organism:

In *Cx*<sup>E</sup> homozygotes, posterior maxillary expression is limited to cells near the ventral midline... (bold emphases added)

A special character of the article is the repeated alternation between gene (*Cx*, i.e. in italics) and its protein (*Cx*, not in italics):

Examination of *Cx* expression in *Cx*<sup>E</sup>/*Cx*<sup>E</sup> embryos reveals an abnormal expression pattern that is first evident during germband elongation (bold emphases added)

Throughout the text, the gene *Cx*, or its mutants, are closely connected to a visual phenotype.

### 3.5 Article 5: Population Genetics

Title: “Genetic mapping in a natural population of collared flycatchers (*Ficedula albicollis*): Conserved synteny but gene order rearrangements on the avian Z chromosome”

a) *Knowledge Project: ways to organise the problem*

Genetic mapping approaches usually require some form of prior knowledge about the genetics of the species, which is not usually the case when it comes to species of natural populations. An increasing number of linkage maps for different organisms exist, but these genetic maps primarily concerns species that are easy to breed in captivity or that have large litters of offspring, which is not the case with most species of birds. Here, they use a recent developed draft sequence of the chicken genome as prior knowledge. This study aims to develop the genetic map of the collared flycatcher—a well-studied species in evolutionary research—and use it to address how the gene content has been preserved during evolution on one of the sex chromosomes.

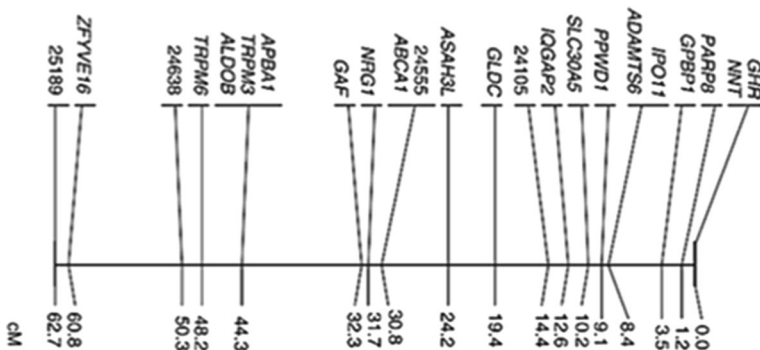
Model organism: the collared flycatcher

Specific question: What is the genetic order in the collared flycatcher sex chromosome?

b) *Methods: ways to practically solve the problem*

Blood samples were taken over 13 years from birds breeding in nest boxes on the islands of Öland and Gotland. The blood was stored and the DNA was extracted from the blood cells. One problem was “illegitimate offspring”, whose DNA samples had to be removed. The genes were found using SNP (single nucleotide polymorphism) genotyping. Gene sequences were determined and largely automated constructions of multi-locus linkage maps were created.

That is, the genes were studied structurally as variants, and in what order they were in relation to each other on a chromosome. In most cases, the functions of the genes were of no interest. Results are presented as best-order linkage maps in the article. Genes are positioned as



**Fig. 5** From Backström et al. (2006). Text from figure in article: “A best-order linkage map of the collared flycatcher chromosome based on all gene markers genotyped in the pedigree. Positions are given as the **cumulative genetic position of gene markers in the linkage map.**” (*bold emphases added, reprinted with permission*)



markers and some genes are only marked as numbers, with no (yet) known function (see Fig. 5) and are named in the text as “hypothetical protein”.

c) *Gene concept use: ways of communicating the problem*

Here, the gene is primarily a variant. The differences in gene sequences, positions on the chromosome and order are used as markers to trace for evolution. Typical expressions that occur in the text are as follows:

Throughout the article we use the term **synteny** to refer to **conserved gene content** of orthologous chromosomes, irrespective of gene order...Two-point analysis revealed that all **gene markers** were significantly ... **linked** to at least one other **locus**...This syntenic segment **has a genetic length** of 63 and 135 cM in collared flycatcher and chicken, respectively, ...how local adaptation relates to genotypic variation and how **genetic variation** can be maintained for fitness-related traits by, for instance, genotype–environment interaction ...We have generated a pedigree of >350 birds with parentage confirmed by **genetic profiling**... (bold emphases added).

The gene contributes to a genetic profile or gene content that varies or is conserved according to adaptations and genotype-environment interactions.

### 3.6 Comparison of Articles

The uses of gene concepts across the articles are compared according to: (1) gene function in the project of knowledge, (2) methodological conditions, and (3) the conceptual contexts.

#### 3.6.1 Gene Function in Project of Knowledge

When comparing the different projects of knowledge, exemplified by the articles and the uses of the gene concept therein, there is a difference. The gene, the biological entity, is used for a different purpose. The genes are used to study the mechanisms of chromosome recombination, the regulation of coding information and the regulation of expression, as well as evolutionary processes. Therefore, the gene functions as a place where recombination occurs, a target of regulatory proteins, a carrier of regulatory sequences (introns) and a cause in organ formation, as well as an instrument for developing a genetic chart (see Table 2). Focus here is on differences in function. Even though, for example, a gene as a target of regulatory sequences also implies that it has a location, there is a difference in primary use of the gene.

**Table 2** Comparison of purpose, question and use of the gene as a biological entity

Knowledge project: purpose of study in article (nr)	Specific question (shortened)	Primary use of the gene
(1) Meiotic recombination in maize	How are recombination frequencies affected?	Location of recombination
(2) Sterol synthesis in yeast	How are genes in ergosterol biosynthesis regulated?	Target of regulatory proteins
(3) Purpose of introns in yeast	What is the functional relevance of introns in genes?	Carrier of regulatory sequences
(4) Organ development in red flour beetle	How is the formation of the dorsal ridge controlled?	Cause in organ formation
(5) Gene content conservation in the collared fly catcher	What is the gene order in a sex chromosome?	Basis for a genetic map

The gene as a biological entity is involved in various problems, but it is not the gene itself that is in focus here. Rather, it is its function as a mediator or as a lever in solving diverse problems where it has a role.

### 3.6.2 Methodological Conditions

The articles exhibit differences in practises. It is not one kind of method that is used, but a whole complex set of different methods. Regarding the model organisms, for example, the methods range from catching birds and dissecting beetle larvae to growing yeast cells in 94 small wells. The problems with acquiring the genetic material to study are therefore also different. The awareness of what it takes to solve a scientific question becomes more complex when closely studying what is actually occurring. This despite the fact that in a scientific article many procedural activities are usually excluded. Therefore, there is partially different procedural knowledge linked to the laboratory practice. That is to say, a specific type of question entails certain methods, which in turn entails certain concept usage. The concept is linked to the different experimental conditions (Table 3). What is possible to say is coupled with what is experimentally possible to do, yet methods are developing. Examples from the articles are as follows:

- When studying recombination to identify genetic intervals, genes are physically mapped, specific regions on chromosomes are identified and genes are visualised on the drawn maps. Genes have a specific locus.
- When studying sterol levels, protein levels are analysed with immunoblotting on gels. The result of gene activity is clearly visible, and gene expression is measured as protein expression (immunoblotting) or RNA expression (quantitative RT-PCR, fluorescent sample measurements). Then, genes are activated or induced (presence or no presence of RNA/protein product).
- When studying the relevance of introns in genes, cultures are cultivated in 96-well plates, and large-scale studies on gene activity have been conducted. Therefore, genes are seen as producers: they produce large (or less large) quantities or amounts of RNA or protein products.
- When studying dorsal ridge development, gene expression is studied as phenotypic differences in the insect or as fluorescent spots in insect tissues, as the genes have visual phenotypic effects.
- When studying the conservation of gene order and creating a genetic map, largely automated constructions of multi-locus linkage maps were used.

### 3.6.3 The Conceptual Context

The project of knowledge and methodological complex entails a particular conceptual context. The conceptual context does not merely consist of the properties associated with the gene per se, i.e. what one expresses about the gene specifically. The context also means the concepts used in addition to the gene concept or the concepts that the gene concept is embedded in. This conceptual context contains *content leaps*. The articles are, conceptually speaking, in various discourses. In the “meiosis-discourse” (article one), how alleles are swapped in cell division is important, not how gene expression is regulated. In “gene order-discourse” (article five), it is not the exact protein product that

**Table 3** Overview of the relations between research questions, and type of methods and gene concept use

The main question in article (nr)	Answered by (for example)	Gene concept use typical of text
(1) How are recombination frequencies affected in maize?	-Creation of genetic strains -Cultivation of maize -Isolation of genetic recombinants -Mapping of recombinants -Statistical calculations	“...[gene] <i>yz1</i> the most recombinationally active region...” “For each physical interval examined, genetic distances (in centimorgans) were compared among genetic backgrounds using $\chi^2$ homogeneity tests.” “...that genes per se are preferred recombination hot spots...”
(2) How are genes in ergosterol biosynthesis regulated in yeast?	-Creation and cultivation of yeast strains under different conditions -Immunoblotting analysis of protein levels on gels -Analysis of gene expression with PCR	“Hypoxia also induced these three genes...” “...“The activation of target genes by <i>Upc2p</i> occurred in response to low sterols...”, genes that are induced by sterol depletion...”, “...to influence either the binding of <i>Upc2p</i> and <i>Ecm22p</i> at ERG promoters...”
(3) What is the functional relevance of introns in genes in yeast?	-Construction and cultivation of yeast cells and selection of strains -Extraction of RNA -Analysis of RNA levels with PCR	“...we studied their genetic contribution to the fitness ...”, “...We found that duplicated genes ... produce, on average ...” “...deletion of introns from three essential genes decreased cellular RNA levels and caused measurable growth defects.”
(4) How is the formation of the dorsal ridge controlled in red flour beetle?	-Grow insect strains -Isolated genomic DNA to find the right DNA sequence (southern) -Expression studies: immunostaining of embryos	“...described a class of <i>Cx</i> alleles that cause fusion of the first thoracic segment...” “These observations suggest that <i>Cx</i> is responsible for the migration and fusion of the wild-type labial appendages.”, “In <i>CxE</i> homozygotes, posterior maxillary expression is limited to cells near the ventral midline...”
(5) What is the gene order in a sex chromosome in collared flycatcher?	-Collecting blood samples from wild birds -Clean up DNA to identify and remove “illegitimate offspring” -Find genetic variants to create a genetic map	“This syntenic segment has a genetic length of 63 and 135 cm in collared flycatcher and chicken, respectively...” “Two-point analysis revealed that all gene markers were significantly ... linked to at least one other locus...”

is important, but how the product, whatever it is, varies between populations. In “biosynthetic regulatory-discourse” (article two), what the protein looks like and the precise molecular interactions is of importance, and it is not primarily an evolutionary focus. In “organ formation-discourse” (article four), what effect a gene product has on morphological structures is important, not how mRNAs are processed. In “gene expression-discourse” (article three), how the total genetic production varies in the cell is important, not how a gene recombines or where it has its place (locus).

Therefore, it can be said that one makes different types of content leaps when studying the genes. The leap can be a gene-organ, or gene-protein product, or nearly have no leap at all, say when studying the specific RNA product. Leaps entail different conceptual contexts, which include different content leaps are further related to the different journal sections in which the articles were sorted (see Table 4). These sections can in turn be seen to approximate of biological sub-disciplines (see also Table 1).

**Table 4** Gene function in relation to knowledge project, conceptual context and section in journal

Knowledge project and model organism in article (nr)	Gene function in study	Conceptual context in article	Section in the journal
(1) Meiotic recombination in maize	Location of recombination	Meios, chromosome, genetic distance chromatin, alleles, <i>cis</i> , <i>trans</i>	Transmission genetics
(2) Sterol synthesis in yeast	Target of regulatory proteins	Encoding, gene expression, enzymes, promotor, regulation, biosynthesis	Molecular biology
(3) Purpose of introns in yeast	Carrier of regulatory sequences	Growth, gene subsets, fitness, RNA levels, production, translational output	Genomics
(4) Organ development in the red flour beetle	Cause in organ formation	Larvae, embryo, organ formation, body patterns, body parts, phenotypes	Developmental biology
(5) Gene content conservation in the collared flycatcher	Basis for a genetic map	Gene order, synteny, chromosomes, variation, selection, adaptation, evolution	Population genetics

### 3.7 Conclusions

When comparing the five research articles, certain types of questions, model organisms and functions of the gene as entity (Table 2) led to certain types of methods that in turn entail certain types of gene concept use (Table 3) in a certain type of conceptual context (Table 4). Therefore, the uses of the gene concepts are suggested as a consequence of different epistemic contexts consisting of various knowledge projects and methodological uses of the term in specific conceptual schemes. This, in turn, leads to differences in gene conceptual meanings and certain content leaps. There is a shift in meaning and in connotation of the gene concept depending on the questions and methods used.

## 4 Discussion

The discussion starts with a summary and description of the scientific contexts for the gene concept(s) and the differences of meaning. These results are then compared and used to discuss gene concept use in research and in teaching, and possible consequences for biology education. Although this study is limited to five research articles, the findings indicate why it is important to ask how we use concepts as part of specific knowledge forms.

### 4.1 Summary

The aim of this study is to contribute to a general discussion on how the meaning of a concept is dependent on its scientific context. This in turn may affect the ways we teach and enable learning and the recontextualisations we need to do. The focus is on research context and the gene concept is chosen as an example. The purpose of this study is to

interpret and qualitatively characterise the variation of the knowledge content in these specific scientific contexts and evaluate cases of possible difference in the meanings of the “gene”. The scientific contexts were described and interpreted with Hirst’s criteria on forms of knowledge.

#### *4.1.1 What kind of Differences in Scientific Contexts, or Knowledge Forms, are Found in Genetics Research Articles?*

In the five examined articles, the gene as a biological entity was used in different knowledge projects: the gene was used to study the mechanisms of chromosome recombination, the regulation of coding information, the regulation of global gene expression, the phenotypic changes and the evolutionary processes. Model organisms ranged from maize and yeast cells to a beetle and a wild bird and a plethora of different methods were used. There were differences in exerted procedural knowledge, which were linked to the different model organism and laboratory practises. Examples from the articles are as follows: Studying recombination hot spots (i.e. an “area” or “place”) entails the view of genes as a physical distance; studying protein content in the form of more or less visible “blots” on a gel entailed the view of genes as induced or not induced; studying densities of expressed gene products entailed the view of different genes as measurable and studying morphology in electron micrographs entailed the view of genes as responsible for different phenotypic changes.

#### *4.1.2 When Comparing These Forms, What Differences in the Expressed Use of the Gene Concept can be Discerned?*

Examples from the different articles are:

- The gene is a physical interval, measured in distance, and provides background on which recombination occurs; a recombination active region, a preferred recombination hot spot (Article 1).
- The gene is regulated by transcription factors of different cellular synthetic pathways; genes are induced, activated and expressed (Article 2).
- The gene is in a manufacturing context of production; introns in genes improve translational “output”, improve fitness (Article 3).
- The gene is closely connected to a visual phenotype; cause fusion of a thoracic segment, responsible for migration and fusion of appendages (Article 4).
- The gene contributes to a genetic profile or gene content that varies or is conserved through adaptation (Article 5).

In the five research articles, the project of knowledge and methodological complex entails a particular conceptual context. Certain types of questions, model organisms and use of the gene as entity (Table 2) led to certain types of methods which in turn entail certain types of gene concept use (Table 3) in a certain type of conceptual context (Table 4). Therefore, the uses of the gene concepts are suggested as a consequence of different epistemic contexts consisting of various knowledge projects and methodological uses of the term in specific conceptual schemes. Hence, it is possible to understand the different meanings of the gene concept as different ways of knowing about biological phenomena. The gene concept is furthermore used

in these contexts without being particularly well defined and conceptual schemes are not static but contain different *content leaps*.

## 4.2 Genes and Experimental Practice

Due to scientific developments, what the gene actually denotes, as well as the limitations of the concept, have changed. However, I would argue that this shift in the content and the leaps regarding what is important or not in different contexts, especially from a teaching point of view, is not especially well researched. One example is Mendelian genetics and its place in education. What was the question Mendel asked in his studies? Rosen (1994) described it as:

Mendel was thereby proposing a new kind of causal framework for these characters; a new way to answer a question of the form “why this phenotypic character?” with an answer of the form “because this hereditary factor”. Lying rather deeper is the tacit idea that the pea plant itself is only an aggregate or sum of its individual phenotypic characters (p. 348).

Is that kind of question really related to questions about gene function or how genes are regulated, and if so how? One may ask how this slippage from Mendel’s questions and mathematical calculations of visible, phenotypic traits to genes and molecular mechanisms is managed in education and in what sense a model about gene function (Gericke and Hagberg 2007) is considered to be Mendelian. However, do experimental conditions and methodologies disappear during the scientific developments? Here are three examples from the studied *Genetics* articles.

In the transmission genetics article, researchers are cultivating maize, selecting the mutants after the form and colour of the seeds, and crossing them in a controlled manner no different from Mendel’s pea crop. They have the same problems as Mendel, with respect to seeds that do not germinate (Mendel 1866, translated in *Scientific American* 1981): how the plants are pollinated, the importance of growing them in the greenhouse, and that cultivation takes time, and how one selects the seeds based on how they look.

Mendel’s crossing procedures also exist in the molecular biology article where they express differences in *ERG2* expression as a result of a single Mendelian locus. High and low *ERG2* expression levels are expected to segregate 2:2 when these two strains were crossed and sporulated. Here, the researchers switch perspectives to the Mendelian locus, not primarily because of mixing explanatory models but because they are actually *doing* Mendelian crosses in yeast and studying genetic inheritance. It is as if the different fields have stuck to certain historically contingent aspects of the gene concept (for example, Mendelian genetics) due to historically developed epistemological reasons.

In the population genetics article, the genetic linkage map they created in the article resembles that of Sturtevant and Plunkett’s (1926). It is a similar illustration of a chromosome as a straight line with genes as crossing lines, and a corresponding way of using gene maps experimentally; although the methods in producing the maps differ. Here, they are talking about genes as specific orders because they are actually *constructing* a genetic map.

An inclusive rendering of history would be that over time science accumulates conceptual uses and associated methods to allow scientists to deal with an increasing number of problems, and that through the process science may allow for various uses. Therefore, scientists do not deal exclusively with producing propositional explanations of the world. They build machines, develop methods and mangle concepts that will help

them solve diverse scientific problems and perceive the world in different ways (Pickering 1995; Wartofsky 1979).

This contextual understanding implies that the use of the same term within a discipline can be explained through shared history, or shared methods, not because the word intends to portray exactly the same phenomenon. Thus, older uses of a term may live alongside newer ones, simply because they are both needed to help scientists deal with the different kinds of problems occurring over the years. The results of this study also imply that using different model organisms is not primarily a question of different hierarchical organising levels in biology, but a question of what is possible to do and know. For historical reasons, it is not possible to do and know the same things on a genetic level regarding a wild bird compared to yeast, for example, or even to know the relation between genes, proteins and phenotypes formed.

### 4.3 Drifting Concepts, Content Leaps and Consequences for Teaching

The different aspects of the gene, as shown in various contexts, depend on what one knows about the gene in question and what the research focus is. Many methods are still used, not as the end points as such, but as transformed parts of the contemporary methodology. This mixture of methods and questions leads to a genetic concept that slides around in meanings. It “drifts” through different epistemic contexts and in explaining different questions or problems. It is not only synthenous from a semantic perspective (designating different meanings), but also part of various knowledge forms where certain content leaps are made.

This should have consequences for the teaching of concepts. Hirst (1974) wrote that learning a new concept is about using it, not about learning true conceptual relationships: “Learning a concept is like learning to play tennis, not like learning to state the rules and principles that govern play” (p. 125). This strengthens the argument for inquiry-based learning, not because it will necessarily produce better written test outcomes, but because it considers the empirical fact that concepts gain and change meaning through use, which is also true for science students (Lemke 1990; Kelly et al. 1998; Wickman and Östman 2002a). An example from higher education is how Kelly et al. (2000) showed how college students in an oceanography class productively learned epistemology and conceptual subject matter through practice alongside scientists, rather than through stipulated definitions. Another is how the meaning of concepts in a university entomology class, need to be mangled with real pinned insects (with a zoologist) to make sense about, for example, the form of an insect wing (Wickman and Östman 2002a, b). Further example is Gelbart et al. (2009) that developed a simulation of genetic research for students in high school in a way that differs from typical school problems. The students applied the concepts and processes from genetics while carrying out the practice of linkage analysis and using the bioinformatics tools. Together, these studies suggest that in order to situate student inquiries in scientifically relevant ways, we need to examine the meanings made of scientific concepts as part of the different scientific knowledge projects and not merely as propositionally defined.

The knowledge forms used in this study can be compared with the model view of gene function, which is used as a tool for analysis in several studies (for example, Gericke and Hagberg 2010; Gericke et al. 2013). Since the models are created in relation to scientific historical development (Gericke and Hagberg 2007), they increase in complexity regarding DNA structure, gene regulation and gene expression, and so can serve as a useful way of depicting developments in understanding. The models are said to be about the same biological

phenomenon, i.e. gene function. The meaning of the gene concept varies accordingly in relation to different historically developed and *constructed models of understanding* gene function. As an addition, this study suggests that the variation in gene concept meaning is in relation to *what is carried out*. When are the different models of understanding gene function applicable? For example, when working with wild animals where the genetics is very little known, a so-called Mendelian model might be useful. What kinds of aspects about gene function are of interest in different models? When we conduct a close-up study of how science is practised, the meanings of concepts are dependent on how the use of the concepts is of help in solving certain problems through the methods used. Science is not merely about explaining, but also about using conceptual schemes, activities and artefacts to understand the world (Pickering 1995; Wartofsky 1979).

The results of this study can also be seen as a development of the discursive basis for gene concept meaning, described in Flodin (2009). The gene that was there categorised as a trait, an information-structure, an actor, a regulator and a marker in the different sub-disciplines (transmission genetics, molecular biology, genomics, developmental biology and population genetics) could in this study be coupled to specific ways of knowing as different knowledge forms: different knowledge projects, complex of methods and as a consequence, different gene concept use. The model organisms used relate to certain possible questions to answer due to practical solutions. The gene as a biological entity is here used in various ways in order to answer different kinds of questions and the term is therefore used, as a concept, in different ways and in conceptual relations that include certain content leaps. The content leaps may also be considered as differences in specificity. According to Waters (2014, p. 125): “A careful analysis of how contemporary geneticists reason when they use the term ‘gene’ reveals that they use a multiplicity of concepts”. Waters also adds that their preciseness varies, i.e. when working in a specific scientific context, the different vagaries and specificities are implicitly known. These findings make it important to ask how science might use concepts as tools of particular inquiries and what consequences that has regarding concept meaning and teaching concepts.

#### 4.4 Teaching Scientific Concepts as Contextually Understood

Rheinberger’s (1997) historical study of *epistemic things* in scientific research developed the idea of the gene as an “epistemic object” during the development of molecular biology—i.e. an entity whose name is introduced as a target of research. The understandings are then set by the experimental practises. The entity and its naming is thus more of a tool in problem solving than a description of something stipulated. That is also what Demerec meant in the early twentieth century: “Any concept of the gene has to be temporary, and designed primarily not for the purpose of explaining the data now available but for use in planning experiments to test the validity of various assumptions” (1933, p. 375). What might this mean when the concept becomes a “teaching object” in biology?

The image of the gene concept (or other concepts with multiple meanings) that stands out can be set in contrast to the focus of teaching students to learn the concepts as well defined. A basic idea of what it means to learn biology is also that it means to learn key concepts and principles (Anderson and Hounsell 2007). But, it is one thing to consider how research is being conducted and how knowledge is developed, and another thing what we choose to teach, as is how we may didactically transpose and recontextualise the content to be useful for students.



In order to develop student reasoning and ability to evaluate scientific data, Hoskins et al. (2007) developed a method based on research articles from one laboratory, which described a single line of research as it developed over a period of years. The students were first engaged in understanding methods and interpretation of data, followed by a comparison of their own formulated hypothesis and conclusions with the real articles. Scientific concepts were applied within this kind of investigative process. But, in order to help students to understand that concepts may have multiple meanings depending on context, it is also possible to focus on how to understand these inconsistencies based on *diverse* conceptual contexts. Colucci-Gray et al. (2013) used concept maps with such a focus. In an interdisciplinary course on sustainable development, concept maps were a basis of showing how the terms are used in different ways and in different disciplines, not as an essence of right or wrong relationships. Via the construction of concept maps related to, for example, key concepts in biology such as *gene*, they are used as "...tools designed to aid conceptual restructuring as an ongoing process of establishing links between ideas and creating new meanings and ideas" (ibid., p. 161).

Research in science education argues for encouraging students of all levels to become more involved in the process of conducting scientific research. Also, nature of science and scientific literacy are key aspects of how science education can enable relevant learning conditions. Educational activities should be designed to help students engage in more authentic science experiences grounded in the scientific reasoning (Chinn and Malhotra 2002) or tools, techniques, attitudes and processes of scientific inquiry (Houseal et al. 2014). If that educational situation is the case, what follows is a more contextual use of scientific concepts, but not necessarily an understanding of the different epistemic functions that concepts have across disciplinary boundaries. Wierdsma, Knippels, van Oers and Boersma's (2015) study about teachings in cell respiration from a cultural-historical activity theory (CHAT) perspective. "Since activities, goals, and the objects that subjects interact with differ in different social practices, the same knowledge may have different meanings in activities from different practices" (ibid., p. 2). It is possible to discuss if knowledge is "the same", or a consequence of an activity, but this is an additional example of a concept that is used with different meanings in different activities and a possible way to solve it practically in the classroom. They developed a strategy of introducing biological contexts where different aspects of respiration were central, from lungs to cellular processes, and students were engaged in varied practical situations that sought answers.

To conclude, the traditional image of scientific concepts with constant meanings is problematic. This study is a contribution to the view that meanings are based on different contexts depending on what is of interest, the question being asked and methods available. When, for example, Johannsen once coined the terms *gene*, *genotype* and *phenotype* in the beginning of the twentieth century, it was against a preformationist view of the transmission of traits (Johannsen 1911). He argued that, instead of looking at inheritance as transmissions of characters, the inheritance phenomenon consisted of "unit-factors" in the gametes. Concepts can thus be seen as formed in an activity and in relation to a specific conception of reality. Instead of looking at science as a knowledge hierarchical structure, as Kinchin (2011) advocates, I would like to return to Paul Hirst and look at science as knowledge forms and ways of knowing. Instead of focusing on concept maps, ask what kind of phenomenon is of interest, what methods are available and what functions the concepts have in this explanation. The gene concept is not one concept, in this perspective, but rather several concepts in relation

to what kind of question is being asked and what methods are being used. This, in turn, determines what is possible to say.

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#### **Compliance with Ethical Standards**

**Conflict of Interest** The author declares no conflict of interest.

## **Appendix**

Article 1: Yandea-Nelson, M. D., Nikolau, B. J., & Schnable, P. S. (2006). Effects of trans-acting genetic modifiers on meiotic recombination across the *a1-sh2* interval of maize. *Genetics*, 174(1), 101–112.

Abstract: Meiotic recombination rates are potentially affected by *cis*- and *trans*-acting factors, i.e., genotype-specific modifiers that do or do not reside in the recombining interval, respectively. Effects of *trans* modifiers on recombination across the 140-kb maize *a1-sh2* interval of chromosome 3 L were studied in the absence of polymorphic *cis* factors in three genetically diverse backgrounds into which a sequence-identical *a1-sh2* interval had been introgressed. Genetic distances across *a1-sh2* varied twofold among genetic backgrounds. Although the existence of regions exhibiting high and low rates of recombination (hot and cold spots, respectively) was conserved across backgrounds, the absolute rates of recombination in these sequence-identical regions differed significantly among backgrounds. In addition, an intergenic hot spot had a higher rate of recombination as compared to the genome average rate of recombination in one background and not in another. Recombination rates across two genetic intervals on chromosome 1 did not exhibit the same relationships among backgrounds as was observed in *a1-sh2*. This suggests that at least some detected *trans*-acting factors do not equally affect recombination across the genome. This study establishes that *trans* modifier(s) polymorphic among genetic backgrounds can increase and decrease recombination in both genic and intergenic regions over relatively small genetic and physical intervals.

Article 2: Davies, B. S., & Rine, J. (2006). A role for sterol levels in oxygen sensing in *Saccharomyces cerevisiae*. *Genetics*, 174(1), 191–201.

Abstract: Upc2p and Ecm22p are a pair of transcription factors responsible for the basal and induced expression of genes encoding enzymes of ergosterol biosynthesis in yeast (*ERG* genes). Upc2p plays a second role as a regulator of hypoxically expressed genes. Both sterols and heme depend upon molecular oxygen for their synthesis, and thus the levels of both have the potential to act as indicators of the oxygen environment of cells. Hap1p is a heme-dependent transcription factor that both Upc2 and Ecm22p depend upon for basal level expression of *ERG* genes. However, induction of both *ERG* genes and the hypoxically expressed *DAN/TIR* genes by Upc2p and Ecm22p occurred in response to sterol depletion rather than to heme depletion. Indeed, upon sterol depletion, Upc2p no longer required Hap1p to activate *ERG* genes. Mot3p,

a broadly acting repressor/activator protein, was previously shown to repress *ERG* gene expression, but the mechanism was unclear. We established that Mot3p bound directly to Ecm22p and repressed Ecm22p- but not Upc2p-mediated gene induction.

Article 3: Juneau, K., Miranda, M., Hillenmeyer, M. E., Nislow, C., & Davis, R. W. (2006). Introns regulate RNA and protein abundance in yeast. *Genetics*, *174*(1), 511–518.

Abstract: The purpose of introns in the architecturally simple genome of *Saccharomyces cerevisiae* is not well understood. To assay the functional relevance of introns, a series of computational analyses and several detailed deletion studies were completed on the intronic genes of *S. cerevisiae*. Mining existing data from genomewide studies on yeast revealed that intron-containing genes produce more RNA and more protein and are more likely to be haplo-insufficient than nonintronic genes. These observations for all intronic genes held true for distinct subsets of genes including ribosomal, nonribosomal, duplicated, and nonduplicated. Corroborating the result of computational analyses, deletion of introns from three essential genes decreased cellular RNA levels and caused measurable growth defects. These data provide evidence that introns improve transcriptional and translational yield and are required for competitive growth of yeast.

Article 4: Shippy, T. D., Rogers, C. D., Beeman, R. W., Brown, S. J., & Denell, R. E. (2006). The *Tribolium castaneum* ortholog of *Sex combs reduced* controls dorsal ridge development. *Genetics*, *174*(1), 297–307.

Abstract: In insects, the boundary between the embryonic head and thorax is formed by the dorsal ridge, a fused structure composed of portions of the maxillary and labial segments. However, the mechanisms that promote development of this unusual structure remain a mystery. In *Drosophila*, mutations in the *Hox* genes *Sex combs reduced* and *Deformed* have been reported to cause abnormal dorsal ridge formation, but the significance of these abnormalities is not clear. We have identified three mutant allele classes of *Cephalothorax*, the *Tribolium castaneum* (red flour beetle) ortholog of *Sex combs reduced*, each of which has a different effect on dorsal ridge development. By using Engrailed expression to monitor dorsal ridge development in these mutants, we demonstrate that *Cephalothorax* promotes the fusion and subsequent dorsolateral extension of the maxillary and labial Engrailed stripes (posterior compartments) during dorsal ridge formation. Molecular and genetic analysis of these alleles indicates that the N terminus of Cephalothorax is important for the fusion step, but is dispensable for Engrailed stripe extension. Thus, we find that specific regions of Cephalothorax are required for discrete steps in dorsal ridge formation.

Article 5: Backström, N., Brandström, M., Gustafsson, L., Qvarnström, A., Cheng, H., & Ellegren, H. (2006). Genetic mapping in a natural population of collared flycatchers (*Ficedula albicollis*): conserved synteny but gene order rearrangements on the avian Z chromosome. *Genetics*, *174*(1), 377–386.

Abstract: Data from completely sequenced genomes are likely to open the way for novel studies of the genetics of nonmodel organisms, in particular when it comes to the identification and analysis of genes responsible for traits that are under selection in natural populations. Here we use the draft sequence of the chicken genome as a starting point for linkage mapping in a wild bird species, the collared flycatcher—one of the most well-studied avian species in ecological and evolutionary research. A pedigree of 365 flycatchers was established and genotyped for single nucleotide polymorphisms in 23 genes selected from (and spread over most of) the chicken Z chromosome. All genes were also found to be located on the Z chromosome in the collared flycatcher, confirming conserved synteny at the level of gene content across distantly related avian lineages. This high degree of conservation mimics the

situation seen for the mammalian X chromosome and may thus be a general feature in sex chromosome evolution, irrespective of whether there is male or female heterogamety. Alternatively, such unprecedented chromosomal conservation may be characteristic of most chromosomes in avian genome evolution. However, several internal rearrangements were observed, meaning that the transfer of map information from chicken to nonmodel bird species cannot always assume conserved gene orders. Interestingly, the rate of recombination on the Z chromosome of collared flycatchers was only 50% that of chicken, challenging the widely held view that birds generally have high recombination rates.

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