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Chapter 17: Organisms in Experimental Research

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Abstract

Research on non-human organisms has been a major focus in the scholarship of historians of biology, especially over the past 25 years. This chapter identifies four overarching trends concerning historical scholarship on the use of non-human organisms for experimental purposes, paying attention both to its style and epistemic goals, and to the species and research locations that have been studied and documented. The first trend (1970s-1980s) focused on organisms as one of the many other components of epistemic cultures, the second (1990s) on organisms themselves as units of historical study, the third (late 1990s-2000s) on the organisms in relation to their experimental and institutional context, and the fourth (ongoing) on the diversification of methods and types of research under examination, including multispecies work and the study of practices in a wider range of biological subfields and across geographic locations.

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Introduction

Non-human organisms are central to much of biological practice and play crucial roles in informing researchers' theorizing and intellectual trajectories. Biologists' perceptions of what defines life develop hand in hand with the observational and interventionist strategies used to study the characteristics, life cycles, and behavior of organisms, particularly when organisms are brought into controlled experimental environments. Thus unsurprisingly, non-human organisms have been a main focus in the scholarship of historians of biology, especially over the past 25 years. This chapter explores the existing literature and outlines overarching trends concerning historical scholarship on the use of non-human organisms for experimental purposes.

A temptation in approaching a review of this scholarship is to focus solely on well-known historical examples, particularly since several famous biologists have come to be strongly associated with the particular organisms on which they worked. Thomas Hunt Morgan has become synonymous with the fruit-fly *Drosophila melanogaster*, for instance, while Barbara McClintock has come to exemplify research on maize, Max Delbruck on phage, Sydney Brenner on the nematode *Caenorhabditis elegans*, Eric Kandel on *Aplysia*, and so on. However, far from being associated solely with one research group, some of these organisms have become so popular so as to function as anchors for entire scientific communities, with journals, infrastructures, funding streams, and discussion venues dedicated explicitly to them, and thousands of researchers around the world adopting them as their main materials for experimental work. Particularly since the advent of the large-scale genomic

sequencing projects associated with the Human Genome projects, these widely used, highly tractable organisms have been ubiquitously referred to in biological discourse as 'model organisms,' that is, non-human species that are easy to breed and maintain in large numbers under laboratory conditions, and which are extensively studied in order to understand a range of biological phenomena, with the hope that data and theories generated through use of the model will be applicable to other organisms (Ankeny and Leonelli 2011). The most widely acknowledged inventory of these organisms includes those that have been officially recognized by the U.S. National Institutes of Health as model organisms for biomedical research, such as mouse, rat, zebrafish, fruitfly, nematode worm, and thale cress. The merits of other organisms as potential model organisms are under regular debate (Behringer, Johnson, and Krumlauf 2009).

Given its defining role for 20th century biological science, it is of course important for historians to study the emergence and development of model organism research. This approach to inquiry aligns with other 'big science' initiatives emerging in the same period in other disciplines (Agar 2012), and constitutes an excellent platform to examine the role of scale and infrastructures in knowledge production, as well as the importance of translational discourse and attempts to apply biological results to questions relating to human health and disease, as well as food security concerns (Leonelli and Ankeny 2012; Leonelli 2016). At the same time, model organisms constitute a tiny fraction of the enormous variety of species used by life scientists to conduct research (Dietrich, Ankeny, and Chen 2014), and are quite distinct in various senses from the highly diverse set of experimental organisms with

which researchers have investigated and interacted over the course of the last three centuries. As Adele Clarke and Joan Fujimura (1992) aptly put it, the choice of an organism for research often amounts to determining what is the 'right tool for the job,' and there is a staggering diversity of jobs for which experimental organisms have been used within biological research, that historians have labored to document at least to some extent. In what follows, we provide a taxonomy of this historiographical work, paying attention both to its style and epistemic goals, and to the species and research locations that have been studied and documented. As is the case with all broad taxonomies, this one acknowledges the presence of exceptions and outliers, yet we believe it is broadly correct and will be useful for others in the field, particularly when attempting to uncover themes, areas, periods, and organisms that are yet unexplored.

The first trend that we identify, running from the 1970s until the end of the 1980s, is the treatment of non-human organisms as one among many components within local research cultures, with no specific prominence attributed to them within the narrative, and few questions asked around their status, epistemic roles, or practical significance. We have identified at least two reasons for this tendency. The first is associated with the particular historic episodes that have been considered: the specific cases of experimental work under examination often utilized more than one type of organism, and hence within these histories there was not a focus on particular species, which in turn influenced the overall intellectual approach used by historians in this period. This scholarship typically hybridized the methods and traditions of intellectual, biographical, and/or institutional history with more detailed attention to

scientific research, and thus placed more emphasis on other aspects of the research process rather than on the materials and technologies which it involves, including organisms.

The second trend, which became particularly notable in the early 1990s, was a turn to using organisms themselves as units of historical study. Hence rather than focusing on theories, problems, researchers, institutions, or disciplines, organisms (and usually individual species) became the main characters in these narratives. Together with this change came increased attention to scientific work and practices and greater emphasis on the provenance, characteristics, and behaviors of individual species. Many of these histories stressed the agency and specificity of biological materials used in experimental research, and the link between attributes that organisms have and the type of research approach and focus being pursued.

The third trend can be viewed as a hybrid of the first two outlined above, and came to prominence in the late 1990s. This type of historical scholarship tends to combine the analysis of institutions, scientists, and fields within biology with close attention to the organisms themselves within the context of the experimental work being performed. There is particular attention to the research practices, methods, and technologies adopted in biological laboratories, to the tensions and opportunities created when importing and using organisms in those environments, and to Rheinberger's idea of using biological materials of various types as 'things to know with' (e.g., his book *Toward a History of Epistemic Things* (Rheinberger 1997)). This literature focuses on a range of themes, including the ways how certain organisms came to be foci, particularly those that are considered 'model organisms'; how they

are integrated into specific projects and bring together disciplines or fields; and the details of particular set-ups within experimental settings and their implications particularly for theoretical and conceptual work.

Finally, the fourth trend that we investigate is currently underway and we wish to encourage the continued expansion of the field in these directions. It involves use of more diverse methods for studying the history of experimental organisms as well as attention to a wider range of subfields in biology and related research areas. In terms of methods, there have been some attempts to pursue more quantitative findings to supplement the almost exclusively qualitative scholarship that documented above that has dominated the field to date. An additional part of this trend is to utilize methods, literature, and concepts not only from the history of biology, but also from philosophy, sociology, and anthropology, including continental approaches. As the majority of literature on the history of experimental organisms has focused on their uses in genetics and molecular biology, other biological subdisciplines have begun to be mined for insights into similarities and differences in these scientific practices. Finally, there has been greater emphasis on multispecies research and on groups of organisms as units of analysis, as well as on non-Anglo-American settings which have been largely neglected in the Anglophone literature.

It is significant to note that these historiographic trends developed in parallel with, and arguably in reaction to, trends within 20th century biology itself. In the first half of the century, biologists predominantly worked on problem-driven research using a variety of organisms, an approach that was reflected in the outlook and choice of case studies by historians. As biological research became increasingly focused on

genetic and then molecular approaches, some individual species, and especially the model organisms discussed above, commanded overwhelming attention, and historians also came to pay greatly increased attention to research on particular species in the latter half of the century. The turn of the millennium brought a renewed interest in integrative and comparative research across species, biological fields, and geographical locations, with an increasingly global research culture emerging in parallel to the Open Science movement and the internationalization of networks and funding sources. At the same time, historians also enlarged their vision beyond the local, to embrace more complex comparative and international narratives, sometimes through the adoption of new historical methods.

In what follows, we devote a section to each of the trends that we have identified, with a concluding section outlining the reasons why investigating organisms constitutes a useful lens for historians of biology, though of course by no means the only useful one. Before delving into the material, we should note that our analysis will focus on organisms as conventionally defined, so we do not examine other types of experimental systems which arguably come to have the status or role that organisms do as research materials, such as cell cultures and probes (which are examined in detail by Landecker (2009), Creager and Landecker (2009), Landecker (this volume) and Crowe (this volume)). Furthermore, we consider solely non-human organisms, since an analysis of human experimental subjects would lead us beyond the life sciences, and into medicine; more generally we tend to focus on literature from history of science and do not explore the voluminous literature from the history of medicine on animal experimentation, rights, and vivisection. Hence we limit our

analysis to laboratory settings, since the growing literature on the use of organisms in other research contexts (such as observational fieldwork, zoos, museums, and clinics) is highly multidisciplinary and evidences a variety of different concepts and trends in comparison to that which focuses on experimental organisms. Finally, while drawing attention to some of the key contributions from continental Europe and elsewhere that are likely to be of interest to historians of science, we primarily analyze trends in Anglophone scholarship, and we focus largely on scholarship from the 1980s onwards, since many of the seminal works in the history of biology that appeared before this time tended to be large-scale narratives without any detailed explorations of experimental organisms (e.g., Coleman (1971); Allen (1978), to name just a few).

Tracing Organisms through Biographies, Research Fields, and National Trends

Although much contemporary literature in the history of biology has a strong emphasis on organisms as the organizing trope around which accounts of scientific practice are constructed, this focus is relatively new. Relevant literature in the 1970s and 1980s tended toward broader narratives examining particular scientists or institutions, or the emergence of certain research fields or national styles of doing biology. This type of historical work often explored research with non-human organisms as part of studies with much wider scope, for instance noting the different species chosen and handled by various researchers. Much of this literature generated detailed investigations of the findings, models, or theories that resulted from the use of organisms in the lab, and placed strong emphasis on how the adoption of specific

organisms shaped existing or emerging individual careers, biological fields, or institutions and related conceptual and organizational trends. Thus organisms were part of a larger story: this literature did not tend to probe or conceptualize the use of organisms as a main focus, nor to emphasize their materiality and its constraints as a key theme.

The biographical genre details the rise in prominence of particular biologists, and in so doing also devoted some attention to the organisms on which they worked. A key example here is Garland Allen's book (1979) on Thomas Hunt Morgan and his those with whom he collaborated, in which the focus is the group's scientific work, while Drosophila itself is discussed but remains a relatively small part of the story (note that Allen's (1975) article, discussed below, takes a different approach, as does Carlson's (1981) biography of H. J. Muller). Both Evelyn Fox Keller (1983) and later Nathaniel Comfort (2001) comment extensively on the significance of Barbara McClintock's handling of maize within their biographies of the scientist, although the organism itself retains a secondary role in their narratives. For instance, Keller emphasizes McClintock's 'feeling for the organism,' but more as a means of exploring McClintock's own intellectual and career development. A more journalistic take can be found in Horace Freeland Judson's (1979) *Eighth Day of Creation* which follows the trajectories of key scientists involved in the development of the field of molecular biology, with passing reference to some of the research organisms used, particularly in the later period; again here, the scientists are the main actors with the organisms presented merely as instrumental to the scientific practices examined.

A second theme within this literature can be found in the numerous discussions of emergent research traditions or fields in biology, which again touched on experimental organisms but did not explore their specific roles, characteristics, or epistemological status in any great detail. An early example of this approach is Nicholas Mullins's (1968) sociologically-focused, Kuhnian-influenced exploration of the origins of the field of molecular biology via research with bacteriophage by the 'Phage Group,' which draws considerably on the volume edited by John Cairns et al. (1966) tracing the origins and accomplishments of the Phage Group through milestones as seen by its participants; this study is a classic in the history of biological community formation but the organism is not central to this discussion. William Coleman's examination of Claude Bernard's views on the discipline of psychology (1985) does address the epistemological importance of experimenting on living organisms, and yet does not devote much attention to the type of organisms used by Bernard in his research. Bernardino Fantini's (1985) investigation of organismal choice in embryological and genetic studies in the early 20th century specifically compares work on sea urchins with work on fruit flies as a means of examining distinct research traditions which each of the organismal types are argued to 'symbolize.' Jan Sapp's (1987) history of cytoplasmic inheritance discusses the use of marine invertebrates and protozoa within this subfield of genetics without documenting and analyzing precisely how organisms were handled or the underlying conceptual or epistemological frameworks associated with choice and use of these organisms.

Finally, considerable scholarship has been done on the use of non-human organisms in the context of the development of biological research within a particular locale, or institutional or national context. This literature seamlessly blends analysis of macro trends at the national and international levels with investigations of practices within specific institutions and labs. A key example is Jonathan Harwood's (1987) work analyzing and comparing the rise and professionalization of genetics in post-war Germany and the US, which mentions the importance of work on *Drosophila* while also critiquing historians' tendency to focus exclusively on T. H. Morgan's work. Timothy Lenoir (1982) and Lynn Nyhart (1987; 1995) also focus on biological trends in 19th century Germany, and particularly the development and eventual decline of morphology as a prominent field of research. Richard Burian, Jean Gayon, and Doris Zallen (1988) reconstruct the distinct trajectory taken in France in terms of the reception of Mendelian genetics, including passing discussions of research with mice and *Drosophila.* Considerable attention also was devoted to documenting American trends in a variety of biological subdisciplines and periods. Among these works, Gerald Geison's (1987) edited collection on American physiology, which spanned the 1850s to the 1950s and featured chapters by Adele Clarke and Louise Marshall specifically on research materials including organisms is of particular note for our purposes, as it documents themes that come to be prominent in subsequent stages of the history of biology to be reviewed below. In addition, two volumes on 20th century American biology commissioned by the American Society of Zoologists and edited by Ronald Rainger, Keith Benson, and Jane Maienschein (1988; 1991), and Maienschein's (1991) own book on trends in American biology at the turn of the 20th century touch

on key themes relating to use of organisms within larger narratives about institutional and national styles, as well as providing close attention to prominent biologists and their practices.

In summary, the literature in the history of biology that was published in the 1970s and 1980s did explore the use of non-human organisms, sometimes in detail, but as one among many components, and typically as another form of instrument or technology along with others. Much of the science explored in this period utilized more than one type of organism (with some exceptions such as McClintock on maize), and hence it is not surprising that no one organism is central to any particular research program or the narratives about it. Perhaps most importantly, this scholarship typically hybridized the methods and traditions of intellectual, biographical, or institutional history with more detailed attention to scientific research, and to show less influence of philosophy of biology or science and technology studies. Hence there tended to be less emphasis on themes from these literatures such as the materiality of organisms and how this impacts on research practices, or on epistemological considerations, as compared to the subsequent stages of research on these topics.

Organisms as Units of Study

We contend that a turning point in the historiography of biology occurred in the early 1990s, and involved focusing on organisms—rather than scientists, theories, problems, institutions, or disciplines—as the unit of, and narrative thread for, historical study. This widespread change in perspective resulted in increased

attention to scientific work and practices together with focus on the contingencies, characteristics, and behaviors of individual species particularly those imposed by their materiality. Thus scholarship in this period also placed considerably more emphasis on the agency and specificity of biological materials used in experimental research, especially organisms. This turn in the field was due in part to the growth of interdisciplinary scholarship in studies of biology, but also to influences of themes from fields outside of history, notably science and technology studies, and particularly sociology and anthropology, and philosophy of biology. There are a few early precedents for this type of work, such as Allen's (1975) article which rejects the typical 'discovery' account of Morgan and *Drosophila* (on the historiography of discovery accounts, see Woolgar (1976) and Löwy (1990)), and outlines previous research work with the organism including the social and collective efforts as well as the qualities of the organism itself that led to *Drosophila*'s adoption.

Crucial to the emergence of this historiographical trend was the interdisciplinary volume edited by Adele Clarke and Joan Fujimura (1992) entitled *The Right Tools for the Job: At Work in the Twentieth-Century Life Sciences*, which grew out of an organized session at held at the biennial meeting of the International Society for the History, Philosophy and Social Studies of Biology (ISH) in 1989. As the title indicates, the collection's main focus is on identifying and discussing tools deployed in order to do specific types of work in the life sciences, and several of the contributions focus on particular organisms as 'tools.' Drawing on scholarship from science and technology studies and sociology, anthropology, and philosophy of science as well as history of science, the volume's approach is constructivist and

ecological, showing that the conditions of scientific practice are highly specific and situated, as outlined in the introduction (Clarke and Fujimura 1992). Among the articles focused on organisms, of note is Gregg Mitman and Anne Fausto-Sterling's (1992) exploration of the rise and fall of the flatworm *Planaria* particularly in C. M. Child's work, and how it became embedded with conceptual, social, and personal assumptions that contributed to explaining its lack of success as an experimental organism (except for pedagogical purposes). A chapter on R. A. Emerson's work with maize in agricultural genetics by Barbara Kimmelman (1992) illustrates how this organism was 'right' for not only scientific and technical reasons but also for various social reasons. In both cases, the authors explicitly use their cases to challenge to scientific and historical representations of *Drosophila* as an organism particularly well-suited for genetic research.

Another piece of scholarship that made key contributions to this trend was the special issue edited by Muriel Lederberg and Richard Burian (1993) in the *Journal for the History of Biology*. Their mandate was to explore organismal choice, particularly what characteristics make specific organisms suitable for particular kinds of research, and how do those qualities evolve and adapt to shift in techniques, questions, and research environments (Lederman and Burian 1993), and which again came out of a special symposium held at ISH in 1991. In this work, the relationship between the choice of a species and the kind of research produced was conceptualized in at least three different ways. In some cases, the 'job' to which an organism is assigned is primary, and the organism is secondary in the sense of being sought and even constructed to fill that particular role. This narrative underlies the

contributions by Bonnie Clause (1993) on rat, Robert Kohler (1993) on *Drosophila*, and Doris Zallen (1993) on the use of algae for photosynthesis research. In other cases, the 'job' is created partially or completely by the features and behavior displayed by the organism in the lab: part of Kohler's story also fits this picture, as does the contribution by Muriel Lederman and Sue Tolin (1993) on viruses. Still other contributions, notably F. Larry Holmes's (1993) article on the frog, reject the teleological analysis of organismal use implied by the use of the terminology of 'jobs' and 'rightness,' and instead focused on the ongoing processes characteristic of scientific work. He provides an overview of experimental uses of frogs, which enables him to highlight their ability to withstand pain as a major motivation for their adoption as biological materials in physiology.

A milestone in this genre was Kohler's (1994) book *Lords of the Fly: Drosophila genetics and the experimental life*, whose appearance is widely recognized to have marked an important moment in the evolution of scholarship on research organisms (his approach was foreshadowed in several articles including his 1991 and 1993 described above). Ironically enough, this book returned to the classic organism *Drosophila* but took an atypical approach, explicitly exploring the material culture and way of life of experimentalists who worked on the fruit fly, which he conceptualizes as their 'co-worker.' His simultaneous attention to the technological, biological, and moral aspects of both Drosophilists' work practices and of the organism itself set a precedent for much history of biology that was to follow particularly due to its ecological vision, and especially scholarship exploring experimental organisms. The book emphasizes the commensal relationship between

organisms and scientists who use them, including the idea that laboratory organisms undergo a form of 'domestication,' hence drawing on diverse historiographic trends in the more general literature on human-animal relationships (e.g., Serpell 1986; Ritvo 1987) as well as more ecological approaches to history (e.g., Cronon 1991; Worster 1990). Kohler also saw his work as a call for scholars to avoid the technicalities and specificities which he viewed as endemic within histories of special sciences at that time, including the biological sciences, thus providing a model for development of more 'general' histories of science through shared focus on experimental practices.

This literature grew in dialogue with the more general trend during this period toward attending in more detail to material cultures in scientific practice, and the dynamics of experimentation, particularly in history and philosophy of science (e.g. Hacking 1983; Shapin and Schaffer 1985; Gooding 1990). As noted in Andrew Mendelsohn's (2003) dialogical paper "Lives of the Cell", this scholarship raised a range of innovative questions, created creative tensions, and had an overall revolutionary effect on historical and philosophical discussions around the choice and use of organisms in research. Within scholarship specifically focused in the life sciences, this trend arguably culminated in Hans-Jörg Rheinberger's (2010) proposal to use whole experimental systems as units of analysis, particularly notable for our purposes because several of the systems he discusses in detail center around the choice and handling of specific organisms (such as *Ephestia, Pisum, Eudorina,* and tobacco mosaic virus).

Other important influences included the debates on the epistemic role of

standardization (usefully reviewed in Timmermans and Epstein (2010)) and expanded discussions and problematizing of organisms as "boundary objects" (Star and Griesemer (1989); for an application of this concept, see Keller (1996) on *Drosophila* embryos' transformation from transitional objects to boundary objects). It also is clear that many historians of biology integrated consideration of the Latourian emphasis on the active role of non-human actants within social networks (what Latour (1993) calls "heterogeneous engineering") into their accounts, as well as actively considering literature from the history and sociology of technology that encouraged viewing experimental organisms as technologies which undergo construction in a similar way to any form of scientific instrumentation (e.g., Bijker, Hughes, and Pinch 1987). Another relevant concept was Steven Shapin's (1988) application of E.P. Thompson's term 'moral economy' to scientific workplaces, which encouraged other historians to relate the use of research materials to the social, ethical, and institutional norms and conditions of laboratory work. An essay on research materials in the reproductive sciences by Clarke ((1995), revised from her contribution to Geison ed. (1987)) similarly stresses the need to develop a richer concept of 'ecology of knowledge' relating to the organization of research materials (including organisms) and the development of techniques to study them, hence forcing more attention to the social and material conditions associated with knowledge production in science.

While particularly influential within history of biology, the tendency to focus on organisms as a thread for historical narratives also came to be popular in cultural and intellectual approaches to history in this period. This extensive literature typically

forgoes in-depth discussions of the role of particular organisms in research, focusing instead on their importance in trade and food cultures (see for instance the many monographs devoted to the potato, none of which explore its use in scientific research, such as Salaman, Burton, and Hawkes (1985), Zuckerman (1999), Reader (2009), Smith (2011), and Gentilcore (2012)). A notable exception is the Reaktion series on 'biographies' of animals, which includes brief discussions on organisms as experimental subjects in the case of the rat (Burt 2006), chicken (Potts 2012), octopus (Schweid 2013), leech (Kirk and Pemberton 2013) and rabbit (Dickenson 2013). Jim Endersby's (2009) *A Guinea Pig's History of Biology* exemplifies the fruitfulness of combining approaches from history of science and cultural studies to create a narrative about organisms, as demonstrated by the wide appeal that the book generated well beyond traditional academic audiences.

The use of organisms as a main thread also was common among historically-oriented narratives by scientists themselves, sometimes in collaboration with historians (e.g., Gurdon and Hopwood (2000) on *Xenopus*; Laubichler and Davidson (2008)), although these accounts tend to be much more internalistic and focused on pragmatic issues within the lab. To name just a few, these include S.G. Ernst (1997) on sea urchins, Francois Jacob's (1998) more popular book on part of his work with mice and flies, and John T. Bonner (1999) on slime molds. Sommerville and Koornneef (2002) on *Arabidopsis* is an interesting exception, as they draw particular attention to social dynamics and community building on a global scale for *Arabidopsis*, reflecting the conscious effort done within the community to advertise and expand the range of research uses for the model plant.

In summary, a key stage in the historiography of biology for those studying non-human organisms was the turn to using organisms themselves as the central units of historical study. This trend was accompanied by increased attention to scientific work and practices and greater emphasis on the provenance, characteristics, and behaviors of individual species, and opened up conceptual spaces and new questions that have come to characterize scholarship in this area.

Organisms in and as Research Practices

Historical scholarship in the life sciences since the mid-1990s has tended to explore the diverse practices of scientists who work with various organisms with focus on a range of themes, including the ways in which these organisms are used as resources for longer-term collaborative projects, how they are integrated into specific projects, the details of particular set-ups within experimental settings and their implications, and the broader cultural and institutional contexts in which these organisms are employed. In a sense, this trend can be viewed as a hybrid of the first two outlined above, as the scholarship tends to be attentive to the research practices, methods, and technologies adopted in biological laboratories, and to the tensions and opportunities created when importing and using organisms in those environments. Rheinberger's (1997) idea of using biological materials of various types as 'things to know with' was particularly influential for scholars working on these topics. Thus this scholarship tends to combine the analysis of institutions, scientists, and fields within biology in some cases national trends with close attention to the organisms themselves within the context of the experimental work being performed.

In addition, the emergence of this trend can be argued to have run in parallel to developments in the life sciences themselves, particularly within molecular biology where the concentration of resources around few model species was increasingly overtaking research emphasizing variation and biodiversity (for historiographic work on this issue, see Churchill (1997), Laubichler (2000), Geison and Laubichler (2001), Ankeny (2010)). As outlined in the introduction to this paper, this period saw the rise of the term 'model organism' within the biological and biomedical sciences (particularly due to the Human Genome projects and their associated large-scale genomic sequencing efforts) to refer to species used as gateways to understanding fundamental processes in ways that can then be generalized to other organisms, and fostered numerous analyses and critiques of these concepts (Gest 1995; Bolker 1995; Ankeny 2000; Gilbert 2009; MacLeod and Nersessian 2013).

Key individual species were the primary focus of scholarship in this period, with a tendency to examine the rise and use of canonical model organisms within their institutional and community contexts. For example, Karen Rader (1998; 2004) traces how standardized mice came to have the prominence which they now have in contemporary biomedicine, including the methods for balancing their natural attributes with laboratory-induced features, with particular focus on the Jackson Laboratories; this work is particularly important due to its stress on processes of standardization and their effects. Soraya de Chadarevian (1998) and Rachel A. Ankeny (2001; 2000) explore the development and use of the nematode *Caenorhabditis elegans* as an experimental organism in genetics, developmental biology, and neurobiology in the context of the Cambridge Laboratory of Molecular

Biology, with special attention to various aspects of community formation (see also de Chadarevian (2002)), a theme that continues in Sabina Leonelli's (2007) investigation of the use of the mustard cress *Arabidopsis thaliana,* which traces how the material features of the organism in particular together with the growth in and efforts of the international community associated with this work together made *Arabidopsis* the most well-researched plant model organism. Marcel Weber (2004) examines the material characteristics and experimental culture (particularly the technique of chromosomal walking) that made *Drosophila* into the most successful model organism in the 1980s for positional cloning.

A second theme in this period is how organisms can be used in projects which utilize diverse disciplinary perspectives or bring together several fields. For example, Rheinberger (2000) examines Alfred Kühn and colleagues' work in Germany on the flour moth *Ephestia*, particularly his use of this organism in projects derived from a range of disciplinary perspectives or research traditions including embryology, physiology, genetics, and biochemistry, and the hybridization of these fields within their experimental system. Angela Creager (2002) examines Wendell Stanley's laboratory's use of tobacco mosaic virus and how the experimental techniques and instruments that they developed came to be used by others studying TMV and beyond in other fields of research. Christopher Lyons and Karen-Beth Scholtholf (2015) follow the evolution of the wild grass *Brachypodium distachyon* to its current status as a model organism, drawing together distinct trajectories which ground contemporary research on it, including studies of taxonomy, host-pathogen interaction, and biofuels.

Some scholarship stresses interactions between organismal use, experimental practices, and the resulting theories. For instance, Judy Johns Schloegel (1999) explores Tracy Sonneborn's research with the protozoan *Paramecium aurelia,* and how his detailed knowledge about this organism helped to shape his defense of it as a research organism as well as his advocacy of a more unifying definition of species. Schoegel and Henning Schmidgen (2002) examine the use of unicellular organisms in late 19th and early 20th century psychophysiological research, and how these organisms forced researchers to change their views on the ontological status of these organisms which in turn had major impacts on fundamental concepts in psychology. Scott Gilbert (2009) analyzes the demands that research with different species imposes on conceptualizations of evolutionary developmental biology and its relation to the rest of the life sciences, and V. Betty Smocovitis (2009) shows how the adoption of the weed genus *Crepis* as biological material at Berkeley in the 1920s and 1930s grounded a radical rethink of systematics in the context of the modern synthesis. John T. Bonner's work with the slime mold, *Dictyostelium discoideum,* and how it contributed to his views on developmental theory and practice, is explored in detail in Mary Sunderland (2011). Robert Meunier (2012) traces the use of zebrafish in developmental biology from the 1970s on and its use as a platform for mechanistic models.

In general, this literature emphasizes the practical, biological, and epistemic implications of importing organisms into a new ecosystem: the laboratory. The advantages, disadvantages, and peculiarities of these types of moves have been well-discussed in the scientific and philosophical literature, and in historical scholarship

with reference to specific case studies. Scholars have worried in particular about the extent to which organismal features and behavior adapt to experimental environments, which often results in radical changes in the characteristics of organisms, thus potentially compromising any attempts to draw easy inferences from the study of life in the laboratory to knowledge about life in the wild (e.g., Griesemer and Wade 1988; Griesemer and Gerson 2006). A related, though perhaps less prominent, focus is the extent to which specific features of organisms affect the construction and long-term development of laboratory facilities. This concern, which was already voiced in Bruno Latour's (1993) account of Louis Pasteur's isolation of germs, has been further developed by Edmund Ramsden and Robert Kirk, who have documented the sophisticated interplay between experimenter's objectives, organismal behaviors, and the design and modification of the space where animals are kept in the case of rats in behavioral psychology (Ramsden 2011a; 2011b; 2012), sheep in the investigation of the psychology and physiology of stress (Kirk and Ramsden forthcoming), and the production of standardized and germ-free animal strains (Kirk 2008; 2012; 2013).

The importance of organism choice in the context of discipline building continues to be subject of debate, but with special emphasis on the ways in which particular species fit (or not) and shape the demands and affect (or fail to affect) the intellectual and institutional directions of given communities and areas of research. Daniel P. Todes ((1997), see also his book (2001)) looks at the systems of production in Pavlov's laboratories, including the 'dog technologies,' and traces their effects on the resulting experimental practices, relations within the laboratory, physical

structures, and products. Cheryl Logan (2001; 2002) traces the use of rats in a variety of experimental settings related to psychology, with particular attention to the interplay between the practices associated with use of these organisms and the underlying conceptual and experimental assumptions that accompanied such research; a key theme in her work also are the trade-offs between the benefits of standardization and the potential limits on making claims that are more generalizable.

A growing trend particularly in the 2010s has been attention to other areas of human activities in which organisms are actively co-opted but which have relevance for experimental science. Aside from the abundant work on Darwin and his pigeons (e.g., Secord 2011), documentation of the intersections between animal fancying and experimental scientific research remains relatively limited, exceptions being Christian Reiss's (2012) work on axolotls where he investigates the relation between the popularity of aquaria and 19th century zoology in Europe, and Endersby's (2013) contribution on the public appeal of primroses, Hugo DeVries's organism of choice, in relation to the establishment of early 20th century mutation theory. Sheep breeding and its contributions to knowledge of heredity are examined in Roger Wood and Vítezslav Orel (2001), with particular focus on the activities of non-scientist sheep breeders. The increasing amount of research on dogs, which includes work by Kirk and Ramsden discussed above (as well as Kirk (2014)), is particularly interesting insofar as it documents the research implications of these animals' roles as companions as well as 'workers' engaged in the provision of specific services (such as assistance for the blind, in hunting, and as sniffer dogs for smelling dangerous or

illegal substances in law enforcement). Key early examples which fruitfully exploited the intersection of history of biology and institutional and agricultural history include Diane Paul and Barbara Kimmelman (1988) and Deborah Fitzgerald (1990). Harriet Ritvo's work (e.g., 2010) also is of note, as an example of broader historical explorations in the growing field of animal studies, in this case focused on the importance of non-human animals to human culture.

In short, organisms became an extremely popular focus of historical studies in the 1990s onward, in parallel with trends in the biological sciences that emphasized using individual species as cornerstones for research programs. Key themes included how and why certain organisms come to be utilized, particularly as model organisms, and the importance of processes of standardization and community building; how organisms can be used to bring together several disciplinary perspectives or fields; and how work with particular organisms helps to shape underlying concepts or theories in the life sciences.

Current Directions: Comparative, Quantitative and Integrative Work Beyond the Western Lab Environment

There are a number of ways in which historians are building on the existing sophisticated work carried out on individual species over recent decades. To begin, there has been a recent push toward broader methodological approaches, such as the integration of quantitative analysis and related large data collection with the almost exclusively qualitative scholarship based on in-depth interpretative study of predominantly textual sources that has dominated the field to date. Quantitative

methods can include citation and network analysis, as well as data-intensive forms of research such as text- and data-mining from digital archives and statistical records, which can be supported by computational analysis and typically require the commitment of larger research groups (including individuals with skills from other disciplines, such as statistics, computer science, and information systems). Examples focused on experimental organisms include early work by Churchill (1997) with regard to quantitative tracking of institutions and training trends; and Michael Dietrich and colleagues' (Dietrich, Ankeny, and Chen 2014; Crowe et al. 2015) use of extensive data mining to document long-term, broad trends in the choice and use of, and funding support for specific organisms within particular fields. Katherine McCain (1991) pioneered the use of citation analysis in correlation with detailed accounts of the origins and development of research within specific labs, an approach we feel could be usefully applied to other areas and periods, as well as application of more 'computational' approaches as recently advocated by historians of science (e.g., Laubichler, Maienschein, and Renn 2013).

Another approach to promoting methodological innovation with regard to historical studies of organisms and the research associated with them is to integrate insights from the history and philosophy of biology more explicitly with literature and concepts from cultural and intellectual history, sociology, and anthropology, including continental approaches (which, as we noted in our introduction, have largely proceeded without intersecting with scholarship in the history and philosophy of biology). A key early example which blended historical and sociological approaches, albeit using work with organisms largely in a non-experimental context,

was the paper by Susan Leigh Star and James Griesemer (1989) discussed above in which the terminology of 'boundary objects' was coined. More recent examples include Nick Hopwood's (2015) article on public views on amphioxus *(Branchiostoma);* Sarah Franklin's (2007) book on Dolly which contains useful historical material on the economic, social, and scientific significance of the creation of this clone, presented within a broader anthropological frame that seeks to contextualize the significance of this animal's creation; and Kirk's (2008)work on guinea pigs, which blends history of science with economic and social history to analyze how specific laboratory organisms were sourced, and what the resulting consequences were in terms of their experimental handling and the knowledge thus produced. More emphasis on the range of financial and economic situations in which organisms are selected, sourced, and disseminated for experimental work is also crucial to comparing the handling of specific species and identifying patterns attached to specific cases. This gap is particularly evident in the case of research on mouse, where the commercial value attached to transgenic mice over the last two decades has fundamentally altered the directions and dynamics of molecular biology, particularly in its medicine-facing incarnations, as documented for instance by Gail Davies (2013).

Aside from methodology, what has become evident of late is the need to diversify the historiographical foci employed in historical research on experimental organisms. For a start, the majority of literature to date has focused on genetics and molecular biology, thus leaving aside the numerous roles and uses of non-human organisms in other biological subdisciplines. It is particularly critical to pay more

detailed attention to the use of experimental organisms in fields such as immunology and psychology, as well as in emerging fields such as synthetic biology, which have so far mostly been analyzed by philosophers (see for instance Fagan's (2013)work on the use of organisms in stem cell research and Nersessian's on 'in silico model systems' [forthcoming]). Luis Campos' (2015) book on radium, for instance, mines a treasure trove of new material on hitherto unacknowledged contributions to plant development and evolutionary engineering by researchers working on various organisms.

Furthermore, some of the most philosophically-inspired approaches to experimentation on non-humans are starting to look beyond research on individual species, and thus increase the body of scholarship that compares the handling of different organisms in various types of experimental contexts, as well as work across species and on groups as units of analysis, including not only research on population science but also on entomology, microbiology, zoology, ecology, and other fields concerned with dynamics outside, rather than only within, individuals. Examples include Ankeny and Leonelli's (2011) comparison of the history and use of model species, Rasmus Winther et al. (2015) on modeling populations, Griesemer (2015) on the role of model taxa, and Maureen O'Malley (2013) and Alan Love and Michael Trevisano (2013) on microbial cultures. All of these topics are in need of more extensive and detailed historical research.

Such historical approaches can sometimes require conceptualizing research environments as going beyond the lab and as including fields, zoos, clinics, hospitals, museums, and other places of relevance to the study of non-human organisms for

scientific purposes. This type of focus is already well-established in environmental and agricultural history; a prominent example is Kathy Cooke's research on early 20th century breeding research on chicken and its intersections with farming practice (Cooke 1997). However, these approaches have yet to be fully exploited in historical studies of the role of experimental organisms in research. Some prominent scholars have started to make inroads into exploring the use of organisms in these environments, although for the most part their focus remains on broad cultural, scientific, and institutional trends rather than on the organisms themselves. For instance, Kohler (2002) mentions several organisms in his exploration of research at the border between lab and field, and yet does not specifically discuss their contributions to shaping these boundaries. Similarly, Harwood (2005; 2012), Berris Charnley (2011), Giuditta Parolini (2015), and Dominic Berry (2015), among others, have probed research cultures and practices at the intersections of farming techniques and knowledge, agricultural policy and governance, and biological research (particularly Mendelian genetics), yet this strand of research does not tend to place emphasis on the role that specific species of plants, and particularly wheat and barley, played in British and German agriculture-focused research. Looking instead at biomedicine, Ilana Löwy and Jean-Paul Gaudillière have documented the use of animal models in hospitals and clinics. Löwy (1992) in particular devotes considerable attention to the conditions under which specific organisms such as rabbits, guinea pigs, and bacterial strains were handled in order to yield experimental results that could inform theories and practices regarding vaccination on humans. In contrast, Gaudillière mentions experimental organisms in his discussion of different

types of biomedical research (e.g., Gaudillière (2008)), but does not explore more detailed questions concerning the role of non-human organisms in medical environments.

More historical work also is being carried out on the role played by zoos and botanical gardens in promoting experimental and observational research on non-human organisms. Research focused on contemporary history includes Carrie Friese (2013) on the cloning of endangered animals in zoos for conservation purposes, and Lene Koch and Metter Svendsen (2014) on capuchin monkeys initially used for psychiatric research and then brought into a private zoo, where they became subjects of an altogether different type of experiment concerning conditions of life in captivity. Finally, another area in need of expansion concerns the handling of organisms in natural history and other types of museums, a strand of research which is exemplified by Erika Milam (2009), Sunderland (2013), and of course Star and Griesemer (1989).

Finally and perhaps most importantly, Anglophone histories of experimental organisms are broadening beyond Europe and North America to include more research on scientific practices with experimental organisms in the former Soviet Union and Russia, Asia, South America, and Africa, as well as continuing work in other languages that document national episodes and trends (of course there has been some previous excellent scholarship on these locales, some of which has been discussed above). The globalization of historical outlook is becoming increasingly prominent across a range of subfields, and presents fascinating methodological questions concerning the meaning and possible methods for making cross-cultural comparisons, the difficulties of mastering the relevant languages and primary

sources, and the complex work of contextualization involved in investigating multinational research programs (see Chapter 17). Examples of relevant work focused on non-Western settings include explorations of plant genetics in Mexico (Barahona and Gaona 2001), emerging research on 19th and 20th century Russian biology, particularly botany and its relation to agriculture (Loskutova and Fedotova 2015), and Lisa Onaga's (2010) analysis of the use of silk worms in early 20th century Japan. Illustrating the power of cross-national comparisons, the recent volume *New Perspectives on the History of Life Sciences and Agriculture* (2015), edited by Denise Phillips and Sharon Kingsland, brings together contributions spanning over two centuries of research in Germany, France, Italy, Russia, the United States, Japan, Austria, Java, and China, and Michael Dietrich (2016) explores experimental systems used to study the genetics of sex reversal across four national contexts.

Conclusion

Our journey through the Anglophone historiography related to the experimental use of non-human organisms, though limited in scope and timescale, emphasizes the extensive interest paid by historians of biology to this topic, and the variety of approaches and styles used to pursue it. In closing, we would like to address a question that lies at the core of such work and its extension into the future: whether and how such literature is still relevant, and for what? In other words, what is the point of this work, and why is it still an active research area, given all the scholarship that has already been published which elucidates the roles and impacts of non-human organisms in biological experimentation?

We contend that documenting the history of biology while paying attention to the organisms used as experimental tools, and the reasons and circumstances for their use, is important for at least five reasons. First, it helps to unravel the material basis of theoretical developments, and the extent to which practical and concrete concerns shape and guide experimentation and its outputs. Second, it forces focus on questions concerning where, be it geographically, institutionally, culturally, and otherwise, research is being conducted, since the choice and use of non-human organisms varies dramatically depending on social norms and availability (e.g., whether researchers can source the organism in question locally, or need to procure it through trade or exchange). Third, it brings to the fore questions about the limits and opportunities related to standardization practices, attempts to enact experimental control, and the status of technology and instrumentation in scientific practice, all of which are at their most complex when dealing with living entities. Fourth (and related), it encourages a reflexive outlook on biological practices and the paradoxes of studying life by interfering with it and isolating individual organisms or groups from their wider environments.

Finally, normative questions about whether and in what sense research on a particular experimental organism is appropriate, and for which purposes, have clear social, political, and economic implications for how science is conducted and how knowledge is constructed. Historical work exploring the roots of organismal choice and its impact on research can inform the conduct of contemporary science and how we understand the underlying epistemic structures and scientific practices relating to this field of research. For example, many criticisms have been raised by scientists

as much as those who study science about the overly limited selection of reference species exemplified by the pursuit of model organisms for biological experimentation (Bolker 1995; J. A. Davies 2007). Historical research has corroborated these critiques, by showing how the model organism concept has been prominent in biological research agendas over the last three decades, making it more difficult to pursue biological research on organisms not considered to be model organisms, and thus potentially limiting research on questions that do not fit these particular models (but see Dietrich, Ankeny, and Chen 2014; Crowe et al. 2015). At the same time, attention to historical sources can help to counter some of the accusations of reductionism and intellectual myopia levelled to the founders of model organism communities, since it reveals that these scientists' willingness to temporarily sacrifice attention to biodiversity was in most cases a strategic choice to allow the building resources and knowledge toward a goal of a truly integrative biology, and was accompanied by the intention to expand the number of species under investigation as soon as practically possible.

In this respect, it is also important to note that a large body of work in philosophy and social studies of science has also addressed the role of organisms in biological research, focusing on questions such as how knowledge is created using non-human organisms, what such organisms represent, whether and in which sense they should be regarded as models, how processes of idealization and abstraction contribute to and warrant their use, when and why arguments about projectability of data and other results are well-founded, what the relationship is between such organisms and the experimental contexts within which they are utilized, and how the

epistemic structures and shared scientific practices within the communities of scientists focused on these organisms influence the ways in which the research is conducted and how these organisms are understood. As we noted in the previous section, some of this work has made a significant impact on historiography, pushing historians to pay more attention to the framing and objects of their scholarship. Accordingly, we encourage more productive dialogue between historians and philosophers of biology on this topic, as well as better awareness among historians in this field of related useful discussions in the social sciences. A recent debate in anthropology, for instance, concerns the idea of "multispecies ethnographies" focusing on hitherto undocumented encounters among "non-charismatic" species (Kirksey and Helmreich 2010), which are those types of organisms defined in opposition to the "charismatic" species such as whales and tigers that are used by environmental activists as flag bearers for conservation concerns. Beyond this single example, there is a vast scholarship on human-animal relations and intersections between species in anthropology and cultural studies which could be explored to see whether some of these ideas can be co-opted to expand the quantity and variety of species and research settings under investigation, and also the impacts of human-non-human organismal relations on biological research.

In turn, new historical work can provide critical starting points for conceptual discussions of interest to all students of the life sciences, whether they are philosophers, sociologists, geographers, or anthropologists. A case in point is the potential expansion of historical work on the use and handling of microbial communities within and beyond the laboratory, which was discussed in the previous

section. Such work could open up questions regarding what counts as an 'organism' in the first place, how organisms are grouped and standardized, and what impact these practices have on their representational power vis-à-vis other organisms or phenomena, and indeed how organisms are described, classified, counted, and conceptualized across periods, disciplines, and experimental cultures.

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