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# The analytic geometry of genetics: part I: the structure, function, and early evolution of Punnett squares

W. C. Wimsatt

**Abstract**    A square tabular array was introduced by R. C. Punnett in (1907) to visualize systematically and economically the combination of gametes to make genotypes according to Mendel's theory. This mode of representation evolved and rapidly became standardized as the canonical way of representing like problems in genetics. Its advantages over other contemporary methods are discussed, as are ways in which it evolved to increase its power and efficiency, and responded to changing theoretical perspectives. It provided a natural visual decomposition of a complex problem into a number of inter-related stages. This explains its computational and conceptual power, for one could simply "read off" answers to a wide variety of questions simply from the "right" visual representation of the problem, and represent multiple problems, and multiple layers of problems in the same diagram. I relate it to prior work on the evolution of Weismann diagrams by Griesemer and Wimsatt (What Philosophy of Biology Is, Martinus-Nijhoff, the Hague, 1989), and discuss a crucial change in how it was interpreted that midwifed its success.

## 1 Introduction

The Punnett square, first invented in 1906, rapidly became one of the most important conceptual tools of classical Mendelian genetics. It proved to be remarkably tolerant and adaptable to theoretical change. Used by theorists on different sides of major debates in between 1909 and 1926, it became a central tool as Mendelian genetics

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became Morganian genetics, and in principle[1] should be capable of surviving the molecular revolution. The popularity, success, and adaptive radiation of its various forms arise primarily from their special virtues as problem-solving tools. This, in turn, has to do with their combinatorial, nearly decomposable—and ultimately—with their spatial character. This study will address several questions and explore the connection of this history to ideas of cultural evolution and transmission.

I.   Jim Griesemer and I have sought to exploit the particular suitability of scientific visualizations as materials to study conceptual evolution. I review features of diagrams we noted in 1989, add others that have since emerged as important, and comment on relevant differences between the Weismann diagrams of that project and Punnett squares. These review the features of Punnett Squares as model organisms for studying cultural evolution, and are analogous to reflections on the "Methods" section of a scientific paper. Since both "organism" and "methods" are unfamiliar, I focus in detail on their "natural history," particularly features that are methodologically relevant for studying cultural evolution.

II.  Punnett squares are fundamentally tabular arrays. Why describe them as visualizations rather than as a specialized form of text? I explore logical features that make it appropriate to do so—features that they have simply as tabular arrays, and additional ones that they possess as special kinds of tabular arrays. These are crucial to their particular and highly innovative character as scientific inventions. Their representational power and adaptability derives from their use as visual devices that exploit our cognitive heuristics effectively to aid understanding of complex relationships in genetics. These features: how their "physiology" makes them powerful scaffolding or symbionts facilitating a set of inferences crucial to the use and development of classical and cytogenetics, and didactically important for population genetics, explains their high scientific "fitness," and rapid spread and evolution as classical genetic developed.

III. A closing discussion reviews some of the reasons why Punnett squares have proved to be such effective and widely adaptable tools.

## 2 Properties of diagrams as good units for studying conceptual evolution

In Griesemer and Wimsatt (1989), we argued that scientific diagrams in general, and Weismann diagrams in particular are ideal "study organisms" to track conceptual evolution.[2] Many features noted then also fit Punnett squares and new ones emerge.

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[1] The Punnett square was not invalidated by the revolution in molecular genetics. But hybridizations between whole organisms capable of producing an array of gametic types is not a central theoretical tool in the days of PCR. Thus the Punnett square has lost its centrality and methodological relevance, and may disappear entirely from molecular genetics texts. Such tools and analytical structures are still relevant for population genetics, so variants of the Punnett square are likely to survive there in any case.

[2] **Diagrams** are not the only plausible choices. In 1989, we suggested that **equations** also had many desirable properties to use as objects to track scientific evolution. **Physical artifacts** and possibly **experimental procedures** need to be added to this list, though both have their own special problems. (Basalla 1988 discusses the former, and Clark and Fujimura 1992 the latter). The concrete reality and relative ease of dating physical artifacts is misleading. If we cannot find out in substantial detail how they were used and

I take for granted issues discussed there: differences between biological and cultural evolution and heredity; whether the latter are Lamarckian or Weismannian and what that would mean[3]; the problem of how to characterize conceptual change on various scales; and whether to regard diagrams as analogous to organisms or to traits of organisms in their evolution. We have recently elaborated our views on these issues Wimsatt and Griesemer 2007. I will mark points in the present analysis affected by these discussions.

We have collected over 150 Weismann diagrams over a dozen years (we had 41 in 1989),[4] but Punnett squares are so easily found (for reasons I will explain below) that I collected more than 200 in about 3 months.

Weismann diagrams and Punnett squares are clearly in the same phylum as conceptual organisms, but they occupy not only different conceptual niches but also different *kinds* of niches. Major differences deriving from the use of Punnett squares as computational tools make features quite important for Weismann diagrams less so for Punnett squares, and conversely. I review six features discussed in 1989 (pp. 93–98), and comment on their sometimes different importance for Punnett squares. I add other features that have emerged since as important for both, or are particularly relevant to Punnett squares. The following properties of diagrams made them particularly good objects to study cultural evolution.

## 2.1 Features originally noted

**1. Locality** and **2. Well-boundedness** We tend to regard the organism–environment boundary as well-marked, and different in this from cultural elements. This is a

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Footnote 2 continued

manufactured, we are likely not to be able to understand many of their characteristics. Experimental procedures are promising for their successive refinement and proximity to the problems laboratory scientists face. Notebooks of laboratory procedures represent a mother lode of rich data. (Schank 1991 has a theoretical framework for dealing with these.) But the expertise for appreciating all their characteristics rarely extends far beyond the participants in the original research.

David Hull (in conversation) has suggested **explicit definitions**. These may work in some cases, but if these definitions turn on other key concepts, they would share many of the problems of locality discussed for concepts. For equations, you must be willing to track "non-fundamental" ones or else there will neither be enough instances nor enough changes in them to be useful. "Non-fundamental" equations in turn suggest **mathematical models**. These have some of the disadvantages of theories, but are usually both more localizable and more common, since most theories will have a cluster of associated models derived as tools for applying them in different areas. But a useful discussion of the evolution of models requires both knowledge of the detailed theoretical developments in an area—something which few historians or philosophers of science possess, and as well a large number of models with known genealogies and which differ in small respects so that they can be usefully compared. Despite all these difficulties, Jeff Schank has gotten lovely preliminary results in analyzing the 22 predator–prey models found in Hassell (1978) and the many (2–3 times more) other related models he found while doing so. See Schank and Koehnle (2007). Also see new theoretical perspectives on models that provide relevant dimensions of comparison, particularly Schank and Koehnle (2007), Wimsatt (1987) and Wimsatt and Schank (1993).

[3] See Chap. 9 of Callebaut (1993), especially the diagram of cultural inheritance (Figure 9-2, p. 428) and commentary on it (pp. 425–429). (That diagram, a descendant of Fig. 1 in Griesemer and Wimsatt, is a Weismann diagram for cultural inheritance!) See also Wimsatt and Griesemer (2007).

[4] I can provide a complete bibliography of the Weismann diagrams and Punnett squares identified so far for interested parties.

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potential problem for "populational" theories of cultural evolution.[5] Unlike ideas, concepts, theories, or even propositions, diagrams are paradigmatically well-bounded, "small," and local in character. Anyone can tell the boundaries between a picture, and its surrounding text, and in this they are better than most things we could talk about for analyses of scientific change. We have no problems with counting them, and usually with agreeing on the count. Diagrams are also well-bounded, and their niche reaches out to include figure labels and explications in the text necessary to interpret them— usually within the surrounding page or two. Even with references elsewhere in the text, the very modularity of the figure is an aid: *unlike ideas, figures and equations are usually numbered, and referred to by number.*[6]

Theories are "much larger" in terms of the work necessary to understand and analyze them than diagrams. Absent the confident formalism of logical positivism where theories just were a set of axioms and definitions, their boundaries have become less clear: theories shade off into applications, models, technologies, experimental exemplars, procedures, techniques, methods of data presentation and analysis, ad infinitum. Many of these they share with other theories, so these ambiguities make it difficult to tell where one theory leaves off and another begins, as well as where theory ends and other kinds of things begin. Moreover, I do not see interesting questions that such boundary disputes would answer. (Reasons for these boundary problems in cultural evolution are explored in Wimsatt and Griesemer 2007.)

Other theoretical candidates, representations of important ideas or concepts, are also problematic. They occur in various contexts and are used for different ends and applications in a text. Context is often crucial to understanding them: an apparently monolithic concept may have multi-dimensional and often conflicting meanings. Recovering these is a laborious process requiring extended textual analysis, often of other works of the author over an extended period of time, during which the stability of these meanings is itself in question. (Authors change their minds over the lifetime of an argument, usually without warning.) Not surprisingly, such studies have relatively low reliability—different students of the texts disagree about the meanings of key terms for the writer. Some studies surely require this kind of detail but their labor-intensive character is inconsistent with doing many of them, as would be required for a comparative evolutionary analysis. The locality of diagrams is by contrast clear and simple, and simplifies many of the problems discussed below.

**3. Easy scoring, evaluation, and comparison of characters** While one may need to reach into the text to interpret a diagram, most traits can be read off from the icon itself. At most, general knowledge of the intended significance of a diagram's properties are needed to score and interpret it. *By contrast, most of the characters of an idea, even where intrinsic, must be evaluated by looking at the relational properties of the*

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[5] Levins and Lewontin (1985) discuss the difficulty of separating characterizations of the organism and environment because many of the relevant properties are relational (including the "organismal" property of 'fitness' and the "environmental" concept of the 'niche').

[6] One must also add explicitly recognized assumptions, which can play a role like axioms or equations in derivations, and are often marked off in list or tabular form.

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*idea.*[7] (This explains the popularity of functional theories of meaning, e.g., Putnam 1975, though when conjoined with an apocalyptic holism, these go too far.) Analysis of Punnett squares has revealed at least 25 characters, most easily and reliably scored. It should be possible to use formal taxonomic methods to analyze their descent relationships,[8] probably unlike any of the entities normally studied by conceptual evolutionists. To our knowledge, no-one has even tried.

**4. Easy determination of ancestry** Determining ancestry for diagrams is easier than for ideas or (until recently) for biological organisms, for at least two reasons: (1) dating is relatively unambiguous, and not itself the subject of theory-mediated determinations—something true for published text as well as for diagrams. (2) Citations (indicating ancestry) are much more commonly given for the sources of diagrams than for ideas. Comparable data for organisms over evolutionary spans of time would require both a rich genetic database and substantial analysis.

Citations are common for diagrams, which are subject to copyright, and thus like quoted text. Authors also seem to have more invested in claiming originality for ideas than for diagrams. (So sanctions for pinching diagrams without attribution might be less, Hull 1988). But false claims for originality of diagrams should be easier to detect than for text, and far less contestable than claims over ideas. A person's reputation is too valuable a quantity to risk so cheaply.) Thus, lines of descent for diagrams are less likely to be hidden than those for ideas.

Punnett squares differ from Weismann diagrams in two important respects. As computational tools, they are treated more like ideas—not subject to copyright. (Punnett squares are often referred to as a "method" rather than as a kind of diagram.) For all their status as common currency, they are still commonly marked in ancestry by name, in interestingly different ways among different "dialect" groups, e.g., as the "chessboard" and "checkerboard" methods by English and American authors, respectively. If ideas were presented in figures that were literally (e.g., photographically) copied, copyrights would apply and explicit citations would remain common. Here the second difference enters: Punnett squares are basically tables. Absent special artwork (which they often contained) tables may be more easily (and cheaply) typeset than literally copied from the other source.[9] Punnett squares with artwork—especially attractive

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[7] I treat graphical marks that are parts of the figure are intrinsic properties of it, though their interpretations are mediated both by general conventions for reading diagrams (e.g., that time is represented from left to right in graphs), and by more specific conventions for reading diagrams of that type, (such as that the "starting point" for a cellular descent tree is interpreted as a zygote). Elements of the diagram may also refer—iconically or conventionally—to features of the external world. Symbol keys are special. It is clear by convention that the key is supposed to tell what the symbol means, and one also understands the key by seeing how the symbol is used. Perhaps symbol keys are more like explicit definitions. The relational character of concept meaning seems more analogous to representational features of the diagram that depend upon and become apparent only from the surrounding text.

[8] Cladistic methods assume monophyly, which is problematic given the multiple parentage and cross-lineage borrowing characteristic of scientific and more generally of cultural evolution on the time scales appropriate for our analysis. This seems a bigger problem for Punnett squares than for Weismann diagrams because of feature 11 below, though analysis should probably start using cladistic methods in a purely heuristic and exploratory fashion for the purely pragmatic reason that those tools exist.

[9] The cost is not just that of production, but also of seeking (and often paying for) permissions.

artwork—were more likely to be copied and cited. If just typeset as tables, they were more likely to be reset anew; if anything was cited, it would be the experimental work on which they were based.

**5. (Relative) context-independence** Greater ease in interpreting diagrams than ideas or concepts flows from their relatively well-delimited context-dependence. First, most character traits of diagrams are intrinsic properties, which can be read off from the icon without reference to context at all, or at most to the generic context of diagrams of that type. The conception of a diagram as a cellular descent tree is sufficient to read off the properties of most diagrams of Weismannism. This is contextual knowledge not specific to any one of the diagrams. Many features of Punnett squares follow because they are tabular arrays, and we have conventions for reading and interpreting tables or arrays. Second, relevant context for diagrams seems generally much smaller and more compact than the relevant context for ideas. This should break down only when the interpretation of a feature of a diagram is dependent on the interpretation of an idea or ideas about which there is some argument.

More than diagrams of Weismannism, Punnett Squares were neutral across different theoretical contexts,[10] and widely used by all sides in arguments over the nature of heredity and hereditary units. One need not read the arrays unaffected by which theory you believed. They were not absolutely neutral. Punnett's earliest interpretations best fit an abstract Mendelism of algebraic factors, while the emergence of their interpretation as a gametic cross-multiplication naturally suggested some sort of material embodiment. Accounts of underlying processes differed for Bateson and Punnett's embryologically inspired reduplication theory of linkage from the Morgan school, who invoked differential crossing-over and recombination rates among factors linearly arranged along a physically and theoretically characterized chromosome. One could hardly have imagined more different sorts of mechanisms to explain the same phenomena. This affected some of the associated iconography (Morgan's *Drosophila* group often represented relevant differences with icons of different chromosomes (Morgan et al. 1915); Bateson and Punnett never did). But these differences had no impact on how the diagram was constructed and used at the time they spread throughout genetics. There was no critical reason to tie Punnett squares to chromosomes until more than two decades later, when the chromosome theory was widely accepted and new theoretical developments allowed a new cytogenetic function for the diagrams

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[10] But even when theoretically neutral, diagrams may not be *pragmatically* neutral: if the activities they serve become less relevant to the research of an area, they may be relegated to a teaching role, or even die off through simple inattention to their problems. Punnett squares are essential to the presentation of classical genetics, and survive in texts even when they no longer satisfy problem-solving functions for researchers. Many more molecular texts go directly to how the molecular machinery works—usually without Punnett squares or discussion of classical breeding experiments. Population geneticists have more need, not only of their own special (locus-invariant) versions of Punnett squares but also the structure of their theory is more closely allied with the results of classical genetics and to classical (gamete-invariant) Punnett squares. This association might change through elaboration of the interest of evolutionists and evolutionary geneticists in development and developmental genetics. The latter is now pursued in quite a molecular fashion, but even if it were not, it is not clear that Punnett squares would have any other than a very peripheral role in presentation of results there.

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based directly on aspects of chromosome morphology and behavior. This will be discussed in the second paper.

The interpretation of diagrams may be relatively independent of context while their fitness to make the points in question changes significantly. The context—particularly the problem context—leads to introduction of the diagram, and determines its fitness. A diagram particularly useful in conveying an idea will be used if known and available. If existing diagrams are relevant but not quite right, context enters crucially in the explanation of changes made to accomplish the new purposes of the different context. *The diagram's context thus points to relevant features of their ecology to identify selection pressures affecting their evolutionary change. The desire to communicate should lead authors to mark these selective factors clearly. By contrast, identifying relevant selective factors in nature is often the most difficult and hotly contested part of an adaptationist analysis* (Gould and Lewontin 1979).

**6. Portability** Greater context-independence of diagrams makes them easier to study, but also easier to borrow. Similar reasoning applies for equations.[11] Less context-dependence makes them easier to understand, and more likely to be borrowed. *Diagrams and equations thus have a greater potential for migrating out of their original contexts.* With less context-dependence, there is also a greater chance that they will prove to be useful elsewhere, i.e., *they have a greater chance of being able to migrate into and successfully colonize new contexts.* In other words, their heritability of fitness is higher. This is a truly fundamental desideratum of evolving objects. *These consequences of context-independence naturally make diagrams good conceptual organisms, serving both to increase their reproductive rates and also to increase their probability of evolution through adaptive radiation into new contexts.*

Compare practices governing ideas imported through quotation. Quote marks stylistically isolate the quotation and indicate that the quoted material is not in its natural context. Quotation is frowned upon as a way of expressing one's own ideas, as opposed to accurately expressing the ideas of others—particularly relevant if they are about to be attacked. No similar onus attaches to borrowing diagrams. Publishers of profusely illustrated elementary textbooks—no doubt strongly influenced by images of large royalty costs and desires for a unity of style—are an exception. Such books are probably the biggest single source of redrawn illustrations, with journals having strong style requirements a likely close second. (See, e.g., the redrawn version of Wilson's Weismann diagram (1896, Fig. 5, p. 11) as Fig. 1, p. 243 of Gilbert (1985) textbook on Developmental Biology.)

## 2.2 New features

Features not in our original list will be marked with "g" or "p" postscripts (for "general" or "Punnett," respectively) to signify whether they seem to apply more generally or may be special to Punnett squares (or other sufficiently similar devices).

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[11] Equations are precisely localized, and though often not as readily understood as diagrams, are almost invariably items of high importance since they are both central reflections of the assumptions and structure of a theory or model, and also crucial tools for its application to new problems.

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**7g. Compactness** Diagrams are compact representations of complex relationships—the old saw that a picture is worth a thousand words—another reason for borrowing them. True for Weismann diagrams, it is even more so for Punnett squares. Equations are also paradigmatically compact. All could count as cultural "informational macromolecules." As concentrated carriers of information, more effective to some audiences, and generators of further perspectives and ideas, there are ample reasons for borrowing them, or for using diagrams rather than or to supplement words. Problems particularly suited for pictorial representation tend to have a multi-dimensional character (Wimsatt 1991). This contributes to the high information density of their representations, and makes them less suitable for presentation or analysis via a linear text stream.[12] This is true of Weismann diagrams and—even more clearly—of Punnett squares, as we will see below.

**8g. Number of cases** With just 41 Weismann diagrams found in 1989, it was already clear that there would be many more distinguishable variants of a successful diagram than of a successful theory or concept. With 150+ of each variety known and more to be discovered, it is now abundantly clear! The emphasis is on "distinguishable," and perhaps "recorded." Hull (1988) demonstrated large variations among scientists who claim to hold the "same" theory: variations in the finer details of exactly what they believe, differential weightings placed on scientific principles held in common, how they use and what they know about different applications of the theory, and the like.[13] As the "populational" view of theories replaces the older "typological" view, evolutionary models of scientific change become increasingly attractive and inevitable.

But how do we detect this variability? The finer discriminations required to individuate variants of a theory are not trivial, and seem to require more specialized knowledge and insight than philosophers, historians, sociologists of science, or any single scientist could muster, and enormous efforts to find, record, and analyze the differences. This diversity emerges from the scientific community: individual scientists often are not aware of these differences, or do not mark them as important.[14] Without the labor (and exceedingly rare opportunities) for studies like Hull's remarkable 20-year longitudinal "insider's" study of nearly 100 systematists as they worked their ways through a scientific revolution, no-one would ever bother to record in any detail what 20 or

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[12] This issue alone should raise questions about translatability theses which, during the hegemony of linguistic philosophy, regularly claimed that anything meaningful was translatable into language, which was taken to mean speech or text.

[13] I have developed a model of scientific change utilizing "generative entrenchment," or degree of use and dependence of individual scientists on various elements of the theory and the means of its application. Variability of response among scientists in how they deal with specific anomalies is predictable in terms of the differential generative entrenchment they have for the same principles because of the different applications they have been making of the theory in their diverse conceptual and experimental niches. See Wimsatt (1999, 2001), Wimsatt and Griesemer (2007), and also Douglas Allchin (1991) ecological model of theory competition and differentiation.

[14] Scientists are usually quite aware of differences between their views and those of their collaborators or competitors. (Whether they perceive—or remember—them accurately is another matter, as Hull shows.) But these locally perceived differences, taken individually, do not yield a broad overview. Secondly, differences within the community are usually papered over when individuals represent "the views of the community" to those outside. See Hull (1988).

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50 or 90% of the scientific community thought at different historical times. And for many problems that labor may be in search of answers to the wrong question.

Diagrams, tables, and other graphical devices are widely used in research and teaching, and widely recorded in research papers and textbooks.[15] Large numbers and relative ease of analysis provide opportunities for the study of conceptual evolution with higher resolution, broader scope, lower cost (primarily in time and necessary specialist's knowledge) than one could have thought possible. (Diagrams and tables are like *Drosophila*—the geneticist's ubiquitous fruit fly. By contrast, tracking theories is like trying to do genetics by breeding elephants). The questions about scientific evolution one is likely to address most effectively are bound to change with this different kind of resource. But it should also give workable purchase on new questions, which were not answerable before. And just as there are many more diagrams than theories, there are many more of some types of diagrams than others. As adaptable computational tools, there are many more Punnett squares than Weismann diagrams. There is usually only one Weismann diagram per book. For Punnett squares, 5–8 or more is common. Texts like Babcock and Clausen (1918) or Sturtevant and Beadle (1939) have 20 or more.

**9g. "One Shot" illustrations versus working tools** Virtually all Weismann diagrams we considered in 1989 were "one-shot" illustrations of a theoretical claim. The use of cellular descent trees in the comparative description of gametogenesis in the life history of diverse kinds of organisms applies very similar diagrams as descriptive tools for comparative morphology, and requires many such diagrams. These fill the third (1925) edition—a large fraction of the 500-plus illustrations—of E. B. Wilson's book. The most common diagram in that book is what Tufte (1983) calls the "small multiple"—a compound diagram or illustration with homologous (or analogous) instances of the same structure drawn over and over again for comparative purposes (in this case, in different organisms, with the individual figures often taken or redrawn from the works of different authors).

Punnett squares also serve taxonomic functions—to describe and classify the heredity of combinations of characters in the various organisms studied. This gives them

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[15] *This confident statement hides an important—even a critical—problem for students of scientific change.* Libraries know that they should keep old journals, but old textbooks—unless the authors are famous—are remaindered, offered in library sales, and increasingly in the last two decades, ignored by the growing used book market. Kuhn tells us that a science that fails to forget its history is lost, and old science textbooks are of little value to most people. Used science texts do not sell and bring so little that many book dealers no longer buy them. They are often simply discarded or shredded. The chance of finding all editions of an important textbook even in one of our leading university research libraries is small. These texts are complex ecosystems for hundreds of diagrams and tables of different sorts, and tracing their respective fates through successive editions is often a sensitive indicator of what is going on with the application and teaching of a scientific theory by and to those "in the trenches." We are losing the data necessary to study an unusually and multiply accessible case—that of scientific evolution—and at as great a rate as we lose biological variability with the juggernaut mass destruction of tropical rain forest. Steve Gould has reported (personal conversation) similar problems in pursuing some of his own research on illustrations of the evolution of man in scientific and semi-popular textbooks. We should deal with this. A few thousand volumes, well-chosen and collected editions of key textbooks would provide an enormous reserve wealth of data for future researchers, and if we could enlist the aid of amateur collectors, many a university library could very cheaply acquire such a resource. I have more detailed suggestions for how to accomplish this.
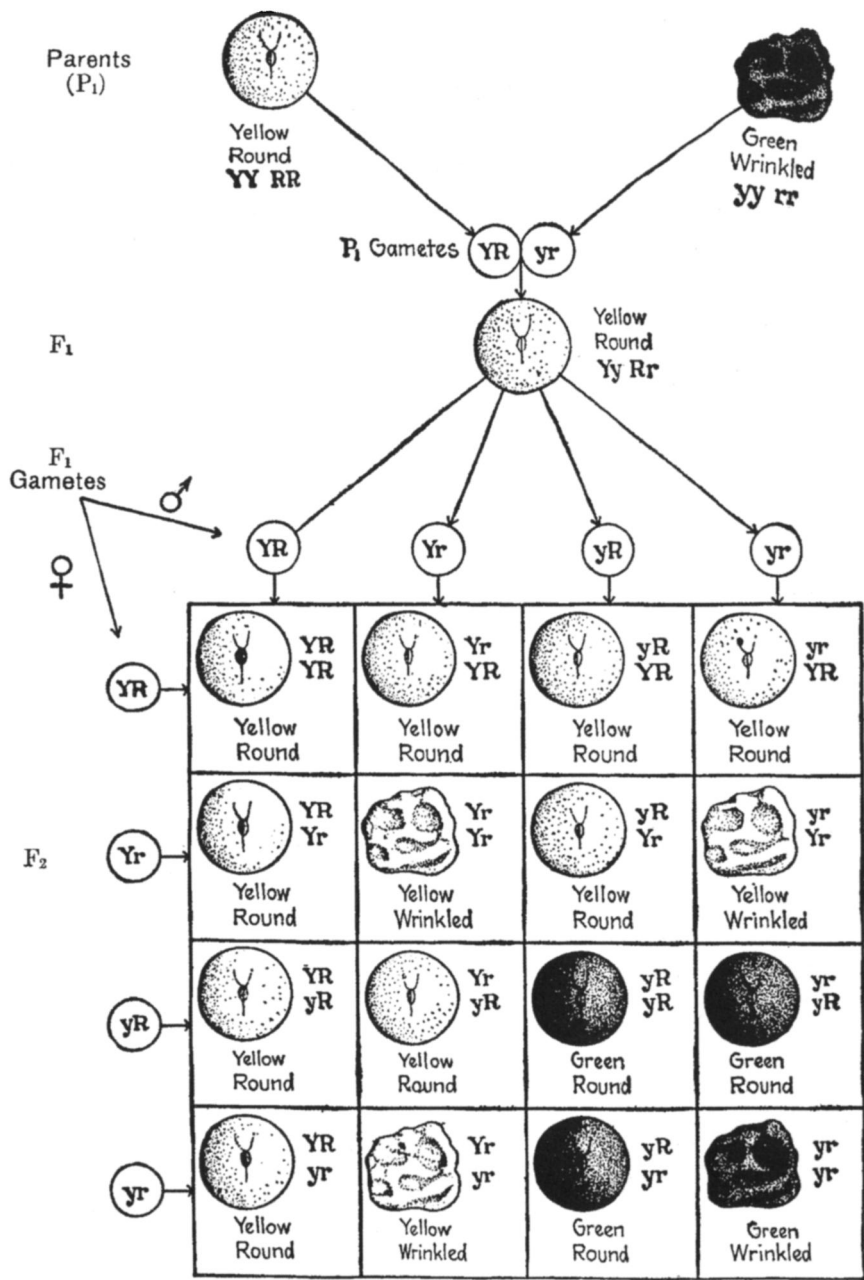
FIG. 27. Diagram showing the independent assortment in peas of two pairs of characters in which dominance is complete. In a cross between a plant homozygous for yellow and round seeds and a green, wrinkled-seeded one, the appearance, genotype, and gametes of parents and F₁ are shown. The results of random union between the four types of gametes formed by the F₁ heterozygote are presented in the F₂ checkerboard.

**Fig. 1** Sinnott et al. (1950), Fig. 27, p. 63

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another shared characteristic with "taxonomic" Weismann diagrams—*they have a specific identity rather than the broad schematic character appropriate to a general conceptual illustration.* Roughly a dozen classic experiments or series of experiments involving specific characters of specific organisms performed by specific scientists are cited and drawn upon, then redrawn again and again. The all-time winner among Punnett squares (the analogue to Wilson (1896) diagram of Weismannism in popularity) is the case of yellow versus green and round versus wrinkled peas. It takes two of Mendel's original characters—indeed the two which are easiest to diagram iconically. Figure 1 is descended from a diagram in Conklin (1915), with ancestors going back to Darbishire (1911) and Walter (1913). In its iconic form, it is probably the diagram most commonly reproduced and cited, rather than reset.

A diagnostic feature of working tools is also reflected in this case: they will be used more than once. Thus, *if a kind of diagram is a working tool, we should find multiple variants of it in the same book.* And conversely, there is no reason to have multiple conceptual illustrations of the same idea in one book, so multiple diagrams of a given type indicate its use as a representational tool for a class of related problems, objects, structures, or data structures. This is just what we find for Punnett squares. They are used more abstractly than Wilson's taxonomic diagrams: we almost never find books in which the same hereditary pattern (say a 9:7 ratio) is diagrammed more than once, even though additional cases are often listed to support the importance of that hereditary pattern with its representative diagram.[16] Instead, each diagram reports a paradigmatic experimental case reflecting a different kind of hereditary pattern. The exemplary case becomes a pattern-matching template that the reader is expected to learn to apply and recognize in their own research. Sinnott et al. through various editions (e.g., 4th ed., 1950) present a canonical collection of eight Punnett square templates for di-hybrid crosses. Seen all together, their use as pattern recognition tools becomes clear. Like the various figures of the syllogism that students of Aristotelian logic were expected to learn, they are perhaps even richer in the diverse types of information one could bring to them or get out of them.

Punnett squares were used as tools for computation, bookkeeping, and teaching a complex combinatorial theory. They are extremely compact data structures for storage and rapid recall of many different kinds of data. In some contexts, they seem little more than a useful and elegant way of teaching genetics. This impression would be misleading. Their structure elegantly reflects fundamental causal features of the theory.[17] Their 2-dimensional form represents the diploid and sexual nature of metazoan genomes. Not even limited to bisexual organisms, they were also used for mating

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[16] This is surely a context-dependent difference—one as it were in the eye of the beholder. To a comparative anatomist or morphologist, the different cases reported in Wilson's "small multiples" were not an exhaustive survey of taxa, but as broad and representative sample as he could find. Thus, the various "highly specific" diagrams in his figures could each themselves be taken as representative abstractions—a first guess at what the anatomist or develop-mental biologist could expect to find for species in that taxon, or phylogenetically closest to that species.

[17] This point is also nicely made by Lindley Darden in her exemplary book, *Theory Change in Science: strategies from Mendelian genetics* (Darden 1991). Her point was directed to hybrid-cross (tree) diagrams, probably even more commonly used (particularly by the Morgan school) than Punnett squares, but it also fits here. See her discussion of the use of diagrams pp. 192–196.

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systems with multiple sexes or mating types in protists and self-incompatibility systems in plants—see the many examples in Darlington (1937). Punnett squares were for decades fundamental tools to apply relevant theory, not merely popular dydactic devices, and were used essentially universally.[18]

**10p. and 11p. High selection intensities for crucial characters, and near-decomposability of phenotypes** Key innovations in Punnett squares spread with unusual rapidity—the use of a gamete-invariant format, explicit representations of gametes along the margins, and standardized orders for presentation of the gametes, notation for genotypes in the cells, and the common mapping of phenotypic characters into the cells. (Other features became universal for more specialized applications, such as the use of algebraic multipliers for relative frequencies of gametic types in population genetics). Once introduced, many of these characters became essentially universal within 2–5 years, close to the fastest response possible. They appeared in other work within a year or two, and it took much of that time to revise and print a book! Since most series of editions had separations of 5 years or more, there were unavoidable lags that masked the true rate of spread of the ideas, which was truly remarkable.

Some of these changes gave big improvements in problem-solving ability and spread rapidly to different authors in a manner worthy of special attention. Boyd and Richerson (1985) note that cultural evolution involves "horizontal transmission," like diseases—i.e., from author to author. But the spread here is multiply horizontal: When picked up by other authors, desirable features are not only inherited by all diagrams of that *specific* type but also adopted wholesale and applied to *all* Punnett squares—they are spread within the cultural objects. This kind of cross-lineage "horizontal infection" is second-order, and resembles more the (horizontal) plasmid-mediated spread of resistance to antibiotics between bacterial strains, each (horizontally) transmitted to hosts. Because the value of such features is relatively context-independent (if they work for one type of Punnett square, they are likely to work for most) and nearly decomposable (they can be changed without changing other features), the author *generalizes*

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[18] Failure to use them is rare. William Castle, a premier exception, appeared to prefer algebra. Though he called them "ingenious" (1916, p.104), his praise is patronizing: "A checkerboard ... will be found very clarifying ... for the beginner, particularly if he is not accustomed to thinking in algebraic terms, when he comes to deal with crosses involving simultaneously three or four independent characters." (p. 106). This is hubris on his part. A glance at Mendel's paper shows that a 2-factor Punnett Square is already significantly simpler than its algebraic expansion. Three is forbiddingly complex algebraically, though readily comprehensible in a Punnett because of the cognitive advantages of 2-dimensional tables I discuss in the next section. Mendel does not do four. More than 90% of Punnett Squares are 2-factor. Three are uncommon. I have never seen four. As Castle notes, these would involve 16 distinguishable phenotypes, 256 genotypes, and a $16 \times 16$ table. (How would you fit one in a text?) Baur (1914) presents a 5-factor case, but not in a Punnett square. He uses a confusing welter of trees in several illustrations and a dozen pages of text.

A deeper reason for the dominion of 2-factor crosses, as the Drosophilists demonstrated, is that even the most complicated interactions arising in linkage mapping (with constant breakdowns of Mendel's second law) require only data on crosses reporting 2 factors at a time—*even though some of these operations required constructed strains with markers or factors at as many as 7 loci to get the right data* (Wimsatt 1992). And as the Drosophilist's research program took hold, linkage became the primary target. This data reduction (for linkage mapping only, not gene interactions in general) anticipates and is isomorphic with von Neumann and Morgenstern (1944) famous argument (and their construction of a "lottery") that everything you wanted to know about preferences could be gotten from comparisons of a preference with at most two others.

them relatively painlessly. At the feature level, inheritance appears to be *hyper-horizontal*. This kind of *hyper-horizontal* transmission is common in cultural evolution because of the conceptual near-decomposability of many of our problems and the potential independent inheritance—through imitation—of many of the features of our solutions, a kind of modularity. Weismann diagrams tended to be borrowed whole—usually through reproduction of the whole illustration, type-face, and all. The more easily reset tabular forms of many Punnett squares facilitate this kind of piecemeal lateral borrowing. (Boyd and Richerson 1985; Wimsatt and Griesemer 2007 review and analyze many relevant complexities of cultural evolution.)

The greater decomposability or separable inheritance of traits for Punnett squares appears to yield less *heritable* variation of many small or neutral traits than for Weismann diagrams because their tabular character makes them easily reset. (Typological characteristics are likely to be changed if the tables are reset rather than copied.) So Punnett squares are more likely to be simply *reconstructed* than Weismann diagrams, and differences which do not make a difference are free to vary. This is a methodological disadvantage: features with high heritability that do not make a functional difference aid in tracking ancestry. This problem is more acute for Punnett squares: as common tools they are less commonly accompanied by explicit citations. Despite this, some descriptive terms in the text are quite diagnostic of different lineages—thus the (absolutely identical) "chessboard method" and "checkerboard method" found on English and American sides of the Atlantic—appellations apparently heritable from teacher to student.

## 3 On the visual nature of tabular forms in general (and Punnett squares in particular)

To illustrate the discussion of Punnett squares, consider Fig. 27, p. 63, of Sinnott et al. (1950). [It appears in the first edition of Sinnott and Dunn in 1925 (Fig. 27) and is preserved in later editions in 1932 (Fig. 33) and 1939 (Fig. 27)]. While richer than most earlier variants, it is nonetheless paradigmatic as the most widely visible diagram in a long lineage, and some features which vary widely earlier have become fixed in it—by design or by convention, through processes of generative entrenchment Wimsatt and Griesemer (2007).

(1)  This case is paradigmatic as a popular diagram from a very popular genetics text. It was reproduced or redrawn widely in other texts.

(2)  It depicts the inheritance of round versus wrinkled, and yellow versus green peas first described by Mendel in 1866. This case became emblematic with the obligatory description of Mendel's work in textbooks, and occurs more often than any other single Punnett square or empirical case. The earliest Punnett squares of this cross are found in Darbishire (1911), p. 207, Dendy (1912), p. 203 (clearly copied from Darbishire), and Walter (1913), Fig. 44. The first with iconic representations of characters are presented in mono-hybrid ($2 \times 2$), di-hybrid ($4 \times 4$), and tri-hybrid ($8 \times 8$) forms by Conklin in 1915 (Figures 52, 53, and 54, pp. 240, 241, and 245, respectively), and subsequently reproduced or redrawn in other books (including Morgan 1916, Fig. 22, p. 54) before Sinnott and Dunn.
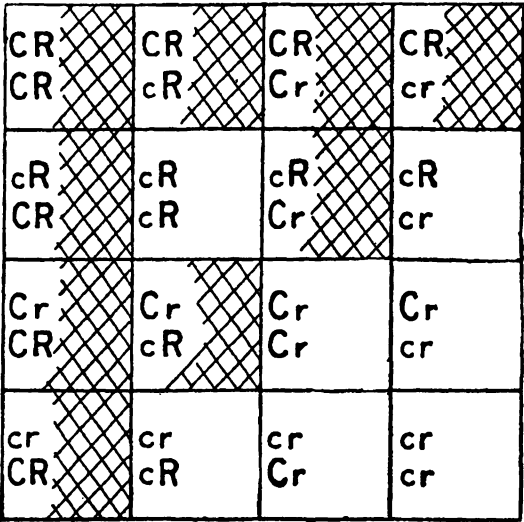
**Fig. 1.** Diagram showing the nature of the ratio 9 : 7 in $F_2$. The character, colour for example, appears only when $C$ and $R$ meet. Each square is a zygote, and the lettering shows its gametic composition. The hatched squares represent coloured plants; the plain are whites.

**Fig. 2**  Bateson et al. (1906), Fig. 1, p. 153 (2-factor cross)

(3)  It is a *gamete-invariant* array, in which the possible gametic types coming from males and females are arrayed along the top and (left) side margins (symbolized by letters), and repeated in the squares down and across, respectively. In it, whole genotypes are depicted in the matrix array as the intersection of corresponding gametic types (again symbolized by letters), their analytical composition deliberately mimicking the biological process of composition as sperm and egg fuse to form the zygote, and the array representing the possible offspring of that mating, how they arise, and their proportions. This is the dominant type of genetic array. It gives all the information of the algebraic expansion of a Mendelian cross, but in a much more tractable form for seeing its consequences.

(4)  The location of the gametes (male on top, female on left side) and their order (AB, Ab, aB, ab, from left to right and top to bottom) while initially different, and then variable, had before 1925 become fixed by convention, a fixity which serves higher-order pattern recognition.

(5)  It is a two allele at two locus or 4 × 4 table—not only the first type represented (see Fig. 2) but also far and away the most common. (The 2 × 2 single-factor cross came after the 4 × 4 and was invented as a teaching tool to convey the "logic" of construction of the 2- and 3-factor arrays).

(6)  It associates phenotypic states with each genotype in the various cells of the array. Indeed, it redundantly deploys *two* of the three most common devices for indicating this; using (a) words and (b) iconic representations of these phenotypic character states. Even though redundant, the latter facilitate higher-order pattern recognition. The third and probably most common device (c) is a pattern-

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ing scheme, like those found in Figs. 2, 3, and 5. This last feature is paradigmatic (in both figures in the original Bateson et al.'s paper of 1906), though it is not essential for a Punnett square. Devices containing only genotypic representations are common.[19]

Other features are not paradigmatic, but nonetheless quite common.

(7)  Although a particular case, it is presented as an instance of broader types. It both shows an example of a di-hybrid dominant–recessive pattern, and also illustrates the phenomenon of *independent assortment*, often called "Mendel's second law." The mode of presentation and assessment of the different experiments makes it clear that it is the type that counts. Thus texts tend to discuss each type known, but only one representative of each (usually the first discovered).

(8)  Subsidiary arrows indicate the origin of gametic types, imbedding the process of zygote formation in the rest of the mating cycle.

To consider this Punnett square as nothing more than a table, remove everything which is overtly iconic: imagine the pea icons erased, leaving only the gametic and genotypic letters preserved in the square array, with—as appropriate—the word descriptions of the character states added. Punnett squares are used for inferences getting from gametes to genotypes, or from genotypes to identify the ways in which they could have been composed by gametes, or from these associations to expected phenotypic patterns or ratios, or from observed phenotypic patterns or ratios to possible gametic or genotypic explanations of them. They are combinatorial computers which allow you to see, and to integrate or differentiate in different ways the information necessary to reason about hereditary patterns, and to do so effectively and efficiently, with minimal error.[20] Thus simplified, the diagram resembles Fig. 1 from the original 1906 paper of Bateson et al.

Why should Punnett squares (or tables generally) be regarded as diagrams or visualizations, rather than as a specialized form of text? They are both: this is not a necessary opposition. Tables are text. They can be and usually are read in the normal textual order—left to right and top to bottom (in English). But tabular arrays also have a visual form that functionally exploits their 2 (or higher)-dimensional character, and facilitates readings in different orders of different assemblages of information. For categorical data, the tabular array exploits topological features of a multi-dimensional structure. When data with ordinal or metrical properties is used, this dependence on the dimensional structure of the array becomes even stronger.

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[19]  This makes a decision about what to call a Punnett square. Since the "method" is more often referred to than the "square," arrays with and without associated phenotypic characters are both counted as employing the "chessboard" or "checkerboard" method, and it is the array form or representation that gives the leap in cognitive facility, I have decided to call both Punnett squares—in affect naming the array form as its crucial core. But as we will see, the interpretation of the array is also crucial, so crucial that it is tempting to ask in retrospect whether Punnett did indeed invent the Punnett square!

[20]  The most obvious omission in description of the genotype to modern eyes is the deliberate lack of distinction made between whether the gamete or gene comes from mother or father. This was a strongly held assumption from Mendel on, but fails to recognize the phenomenon of "genetic imprinting" (usually associated with DNA methylation) and some other modes of "maternal effect" in which the action of the gene differs when inherited from mother or father. Nonetheless, the gametic array remains perhaps the best way of representing the Mendelian consequences of this phenomenon.

Some of the strongest evidence for their multi-dimensional character should be *the pursuit of notational and other modifications that facilitate the perceptual exploitation of different significant lower dimensional slices or higher dimensional aggregations of the data*. This is characteristic both of the use and of the evolution of Punnett squares. The designed use of our powers of spatial pattern recognition in understanding, organizing, and getting information out of the table is a dead giveaway that we are dealing with a visual object. That does not mean that they are (must be) iconic pictures. These particular diagrams are abstract representations of processes (more like a flowchart or biochemical pathway than an architect's structural plan.) The evidence I provide for their being visual objects is evidence (1) for their multi-dimensional character, and (2) that we use them as such. It amounts first to saying that in their logical structure, they are spatial representations. And second, that they are arranged on the page so as to utilize our natural perceptual heuristics for perceiving and analyzing spatial objects to communicate modes of organization and relationships among the data.

The "spatial" features discussed fall into three groups:

A.  intrinsic properties of tables, features which follow from the nature of any tabular array (and thus features which confer a visual character on any table);

B.  additional intrinsic properties of Punnett squares that follow from their specific subject matter (largely the combinatorial properties of Mendelian genetics) and how it is represented; and

C.  further extrinsic or contextual properties (such as the additional of symbolic icons for the characters whose variations provide the data, or to locate the process of zygote formation addressed by the Punnett square in the larger context of the reproductive cycle.)

## 3.1 Intrinsic spatial properties of tables

- *Crossed invariant structure* It is natural to see a two-dimensional table with two or more rows and columns as having what I would call a "crossed invariant" structure. A property characteristic or component of each entry in the array is invariant down each column (but different across rows), and another property is invariant across rows (but different down columns). This can generalize for higher dimensional arrays. This structure is responsible for many of the properties that follow.

- *Multiple possible reading orders* Unlike normal textual material, tabular arrays not only allow but also actively encourage multiple ways of getting at, grouping, and using the information in the table. Considering just the planar structure of the table (its organization as a 2-dimensional data structure), the vertical and horizontal columns as whole, and the vertical and horizontal location of any entry in those columns will be significant. Any entry may be accessed as a datum by multiple paths, and may be grouped with different larger units which are only partially ordered by inclusion, fundamentally spatial properties of all tables. Thus, a cell will be a part of a row and of a column, neither of which includes the other, though both of which are included in the whole table.

- *Multiple possible groupings or decompositions of the data* With a 2 (or higher)-dimensional table, each entry has more neighbors. So one can group the entity with

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contiguous elements in more ways. When alternative groupings are each significant, the object can have a hierarchial (when the groupings or decompositions are nested) or multi-dimensional (or multi-perspectival) character (when the groupings or decompositions are cross-cutting). Multiple possible groupings or decompositions of a cross-cutting character indicates multiple possible reading orders and multiple sources of information. (Multiple reading frames will do even in a one-dimensional continuum, as genetic frame-shift mutations for reading messenger RNA demonstrate.)

## 3.2 Additional intrinsic spatial properties of Punnett squares

- Other properties arise from the *indexical, combinatorial, and other special properties of components* of the problems that Punnett Squares represent. In different contexts, the descending diagonal, ascending diagonal, and for array elements, its off-diagonal symmetry pair are all significant, making multiple possible inputs, outputs, and combinations of them relevant to the solution of different problems.
- A *third dimension* is produced by adding further information to the cells. Most common is information about the phenotypes associated with the genotypes—the color and the shape of the peas in Fig. 1. This is important because it allows construction of predicted Mendelian ratios among offspring. Other information allows adaptation of Punnett squares to other specialized tasks. (The first item under C below gives a very partial list.) This layers different kinds of data "vertically" (out of the plane of the paper) in different planes parallel to that of the table.[21] This makes mappings of individual array elements to these additional properties, and patterns of relationship in their distribution significant. In the simplest case (widely used for Punnett squares), when the properties form equivalence classes (as when multiple genotypes make the same phenotype), class membership of a cell or group of cells becomes significant (e.g., producing expected "Mendelian ratios") as does the "shape" or pattern these cells form on the underlying matrix.
- The combinatorial properties of the problem space give it *closure properties*—thus it is possible to talk about all possible gametes, genotypes, phenotypes, genotype–phenotype mappings, etc., relative to a given formulation which defined a problem-space.
- Some representations have additional *metrical features*: The height or width of rows and columns and the areas of cells may have explicit implied significance as expected probabilities or frequencies of different classes of events or types of objects. The properties thus measured are defined with the strongest possible metric—a *ratio* metric.
- In some other contexts, the order of gametes is not just categorical, but may be significant as defining at least a *partial ordering*, which, together with *rules for*

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[21] This is not metaphorical: in class I use as many as 7 overlays, each containing different information to construct and illustrate functions of multi-layered Punnett Squares arising from the juxtaposition of property distributions.

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*the combination of these partial orderings*, is important for formulation of some problems, e.g., in quantitative genetics.

- Punnett squares represent the production of genotypes which have physically significant syntactic properties (e.g., the distinction between allelelic and non-allelic variations). These are combinatorially coded in different ways significant to their representation.

- Other elements exploit a systematic "visual logic" as suggested in Griesemer (1994). Some examples: (1) the coadaptation of notation in cells to facilitate seeing the relation of components of the cell to others in the same row and column—the relevant invariances, as in Fig. 8. (2) devices used to mark phenotypic information off from genotypic information as in another plane. Thus the verbal coding of the character states in Fig. 1 gives the relevant information in a form appropriate to individual cells in the matrix, but seeing the broader patterns in the distribution of types in the 9:3:3:1 ratios is facilitated by adding the formally redundant iconic representations of the characters. Similarly, the relative numbers of larger circles in the different cells of Fig. 9 give a qualitative perceived density to the squares which models the intensity of the perceived shade of the wheat in the case discussed.

### 3.3 Extrinsic and contextual spatial properties of Punnett squares

- Punnett squares represent genotypes that produce phenotypes. Either may, in their physical realizations, have characteristic spatial properties that are iconically depicted because they are important. Thus peas may be represented as green or yellow (with color or black and white shading) and round or wrinkled (as in Fig. 1)—phenotypic properties. Genes may be represented as on the same or different chromosomes, with allelic states represented with symbolic or pattern coding, as in Fig. 16, (Sinnott and Dunn 1939, Fig. 68, p. 185). Different karyotypes produced in meiosis by hybrids of different chromosomal rearrangements of the same factors may be represented in diagrammatic form (Sturtevant and Beadle 1939, see Fig. 74, also Figures 70–76). (These "karyokinetic figures" strongly affect fitness since they may result in abnormal additions to or deletions from gametic genotypes, and this is predictable from analysis of their forms.) In these cases the added icons are extrinsic to the nature of Punnett squares, though their use in this form of constrained canonical representation facilitates new kinds of analysis, higher-order pattern-recognition, and may even be essential to the performance of their specialized functional role (as in the representation of the physical geometry of karyotypes).

- Locating the Punnett square in a causal sequence or flow chart diagram may code both the physical natures of the processes, and their causal order, using spatial location and conventions for depicting causal and temporal processes. This information is conveyed by placing a Punnett square in a larger context. This feature is at least partially intrinsic to the Punnett square if we take the nature of its inputs (gametes) as given. Thus, Fig. 66, p. 170 of Sinnott et al. (1950) depicts details of the process of gametogenesis as well as their combinatorial assortment (in this case, concretely, of chromosomes).

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## 4 The evolution and adaptive radiation of Punnett squares

It seems most likely that Punnett squares arose directly as an alternative representation of the combinatorial logic of Mendelian genetics. They have some logical similarities with Galton's bivariate normal statistical distributions and tables, and other similarities with 2 × 2 tables used for multiple purposes in statistics. But in the second paper of this series, I argue that neither of these are plausible ancestors, and that Bateson's commitment to and interpretation of Mendelism, internal evidence in the explanation of the tables and and the logic of their use all favor a direct Mendelian inspiration.

The early conception of Punnett squares is somewhat problematic, and will be dealt with more fully in another paper. Only the smaller (2-factor, 4 × 4) table from the 1906 paper of Bateson et al. is a Punnett square. The conception of the Punnett square as we know it (a gamete-array) emerged gradually over the next 7 years, with insightful modifications or supplements by Bateson (1909), Herbert (1910), Darbishire (1911), and probably most substantially, jumping the Atlantic, by Walter in 1913. Punnett's own diagrams and descriptions in 1907 and 1911 were problematic, and did not contribute to the modern interpretation. Analysis of the larger 3-factor 8 × 8 table from the same 1906 paper shows that it was constructed according to different (and possibly hybrid) principles, possibly at Galton's suggestion[22]. The result is confusing at best, is not a Punnett square, and cannot be seen as an ancestor to the 8 × 8 3-factor Punnett square first introduced by Walter in 1913 (Fig. 55, p. 189) in his elegant depiction (Fig. 9) of Nilsson–Ehle's quantitative coat-color inheritance in wheat.

More seriously, it raises the question whether any of them, and Punnett in particular, had grasped fully the principles behind the construction of Punnett squares. It would be as if Mendel had argued that different principles were required for 3-factor inheritance than for 2-factor (rather than just appropriately different algebra to cover the added factor). It was Mendel's clear understanding, given an $n$-factor case, that we know how using the same principles to construct an $n + 1$-factor case, which indicated the rich mathematical power and generality of the theory: that it could handle cases of arbitrary multi-factorial complexity. The same power was there for Punnett squares, but Punnett apparently did not see it: not in 1906 or 1907, and perhaps not later. Indeed, it makes sense to ask in retrospect whether Punnett did indeed invent the Punnett square!

Even with this understanding of how to construct larger Punnett squares to represent more segregating factors, there remained a crucial ambiguity in their interpretation. They were interpreted in one way by Punnett, and probably by Bateson, Saunders and their contemporaries in that period. But over the 6 years from 1907 until 1913, another interpretation emerged. It was only at this later point that the Punnett square and the "chessboard" (or "checkerboard") methodology spread rapidly and became universal and the new interpretation rapidly became entrenched. It is possible to track its emergence through modifications in how the arrays are presented, constructed, talked, (and of course thought) about. The change was like a "Gestalt switch" in total effect, but one achieved gradually and through definable intermediate stages. It was a Kuhnian

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[22] Robert Olby has shown me a letter from Galton to Bateson in 1905 discussing the form of the 8 × 8 table published in the 1906 paper.

revolution writ small, and provides hope for those who would seek Darwinian continuity in a world of conceptual saltation. This new interpretation, a different way of reading the Punnett array, was critical to its emergence as a powerful conceptual tool. One can thereby understand why the enormous expansion in its use owes a great deal to this change.

With this reinterpretation, Punnett squares became powerful and adaptable tools—much more so that their (few and partial) competitiors. This reconceptualization was extremely fertile, and did not change the logical design of the table, but only its interpretation. It was followed almost immediately by a rapid increase in their use, and further diverse changes—an adaptive radiation to occupy new kinds of conceptual niches, as discussed in the second paper in this series. In this two-stage process—a period of "relative quiescence" or "invisible change" followed by an enormous adaptive radiation, the evolution of Punnett squares is reminiscent of pre-Cambrian evolution (slower or at least invisible, because most of the evolution was in "soft parts" which were not preserved) followed by the "Cambrian explosion" in which there was a rapid (and visible) adaptive radiation of different and diverse organisms.[23] For Punnett squares all was preserved, but the less visible evolution proceeded largely in single less well-known texts replaced almost immediately by later stages in other less well-known texts, until with the adaptive radiation following 1913 they came to be represented essentially simultaneously in virtually all texts for which they were appropriate.

### 4.1 The first Punnett squares and their relatives

William Bateson—Mendel's most zealous missionary to the English speaking world—set out after the rediscovery of Mendel's work in 1900 to explore the application of Mendel's principles throughout the plant and animal kingdoms. The first "Punnett Square" (Fig. 2) appeared in a classic paper he co-authored with his students, R. C. Punnett and E. Saunders, describing patterns of inheritance in sweet peas (Bateson et al. 1906, Fig. 1, p. 153). Within a decade, the Punnett Square became the canonical way of representing and thinking about problems involving the outcomes of multifactorial crosses. It is hard to find a genetics text even today without one. They evolved rapidly, with changes in how they were read and interpreted, in format and notation, new ways of adding additional layers of information, and new uses for different purposes. They became one of the most ubiquitous tools for representing and conceptualizing problems in classical genetics, and related sub-disciplines like cytogenetics and population genetics. Only the *tree diagrams* used to describe the results of crosses and *linkage maps* have been of comparable use in the history of genetics. These three devices represented diverse kinds of information compactly and intuitively. Two of them particularly—the Punnett square and the linkage map—functioned to organize and process different specific kinds of complex data, serving as computational tools of impressive power in the days when the complexity of even relatively simple computations *really* mattered. (For more on linkage maps, see Wimsatt 1991, 1992, and Kohler 1994; for more on the mating-cross tree diagram, see Darden 1991.)

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[23] Comparison with the Cambrian explosion was suggested by Greg Mikkelson.

Five kinds of arrays differing fundamentally in their construction, organization, and many of their properties are called Punnett squares or resemble them. In consequence, they are applied to different kinds of problems. Two kinds are found in the 1906 paper, though no comment is made about their radically different logical forms. Their *first* (Fig. 2) is used on a problem in the inheritance of two independent factors—in modern terms, a "two locus" case. I call this form *gamete-invariant*, because constant gametic types are found in each cell of each given row, and, separately, in each cell of each given column.[24] (A cell in the table is analogous to a point located by its $x$- and $y$-coordinates, only the coordinates are gametic types. Each cell contains two gametes, and is defined by the intersection of the row and column for those gametes). The generality of this representation stems ultimately from the importance of sex and diploidy in genetics and in evolutionary biology. The use of a 2-factor (i.e., 2 locus) problem is less crucial, though, for various reasons, the 2-factor cross became the primary application for Punnett squares. They were applied broadly to diverse problems involving *individual* matings in classical and modern transmission genetics.

A *second* type, a modification of the first which appeared much later, is a *quantitative gamete-invariant* array. This was first introduced by Hogben in 1946, in a different discipline, population genetics.[25] It was applied primarily to one-locus cases, though sometimes with more than two alleles. It used the frequencies of gametes in *populations* to predict genotype frequencies under various different assumptions. I will discuss it more fully in the second paper in this series. Most authors who use them call both of these types **Punnett squares**, so I will also.

In a particularly interesting third type, the *locus-invariant array*, the genotypes possible at one locus (AA Aa, aA, aa) are arrayed along one margin and the genotypes possible at a second locus (BB, Bb, bB, bb) arrayed along the other. (The gamete-invariant array for this case would have gametes (AB, Ab, aB, and ab) arrayed along both margins.) Both compose genotypes but in different, indeed orthogonal, ways. The 2-locus genotypes in the cells of a locus-invariant array are the logical composition of the row and column contributions of single-locus genotypes. The whole array gives the whole range of possibilities (Fig. 3). For the special case of Mendelian dominance at both loci it localizes the four distinct phenotypes in compact regions, unlike Punnett's gamete-invariant array (Fig. 2). Surprisingly, it appears to occur in pure form in only one case (Wilson 1916, unnumbered table, p. 17). This type seems at first like a powerful and genuine alternative to gamete-invariant arrays. Understanding its limitations gives a deeper understanding of the strengths of the gamete-invariant array, so I discuss it at length.

For 2-loci the locus-invariant array seems to fit the logic of Mendel's paper well. But its advantages stop there, and there are severe disadvantages. First, the representation

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[24] A gamete has one copy of a gene from each locus. Since genes at the same locus are denoted by the same letter, and differentiated by using either capital and small letters (**A** and **a**, **B** and **b**, ...) where they represent dominant and recessive traits, or subscripts ($\mathbf{A}_1, \mathbf{A}_2, \mathbf{A}_3$, ...) at loci where more than two alternative alleles are found, gametes will be represented by strings of different letters of the alphabet (e.g., **aBc** or $\mathbf{A}_1\mathbf{B}_4\,\mathbf{C}_3$), whereas loci will be represented by pairs of the same letter (e.g., **Cc** or $\mathbf{C}_3\,\mathbf{C}_5$).

[25] This is not the only quantitative gametic variant array. The Morgan school used quantitative coefficients as multipliers in arrays for some linkage problems in the early 1920s. But this persisted, while that died out quickly.
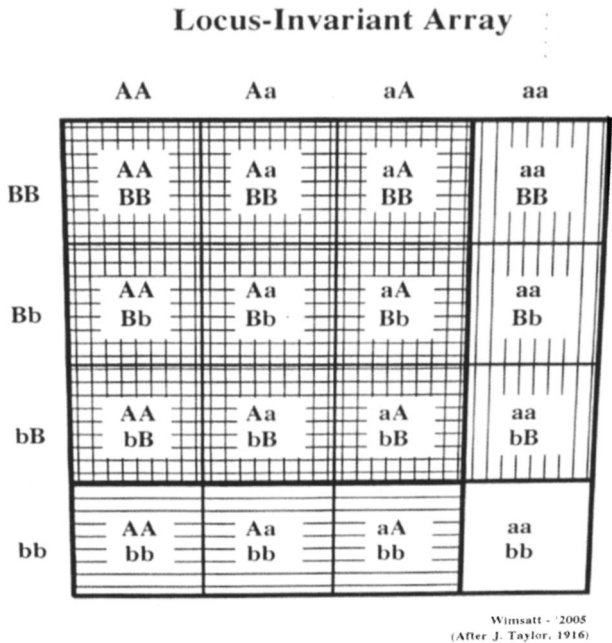
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## Locus-Invariant Array



|  | AA | Aa | aA | aa |
|---|---|---|---|---|
| **BB** | AA BB | Aa BB | aA BB | aa BB |
| **Bb** | AA Bb | Aa Bb | aA Bb | aa Bb |
| **bB** | AA bB | Aa bB | aA bB | aa bB |
| **bb** | AA bb | Aa bb | aA bb | aa bb |

Wimsatt · 2005
(After J. Taylor, 1916)

**Fig. 3** Locus-invariant array

fails to correspond to physically significant modules in the inheritance process. Entries along row and column each include an allele from both parents, together comprising the combinatorial possibilities at a locus. Combining them gives the possibilities at both loci simultaneously. This gives an algebraic unity but the contribution of a gamete is nowhere represented. As a result the locus-invariant representation is less adaptable when it matters to a process how the genes are packaged and transmitted. Recombination and linkage problems require treating chromosomes or gametes as units, and these emerge as crucial in classical genetics.[26]

Second, taking gametes from each parent as the basic elements to be combined rather than doing the logical assembly of a genotype locus by locus also allows one to parcel out the contributions of the two organisms to different sides of the array. This is often an advantage in conceptualizing problems in both genetics and evolutionary biology.

Third, the locus-invariant array works as a 2-dimensional square array only for 2 factors. The natural generalization of the locus- invariant schema requires going to higher dimensions—adding a dimension to the array for each segregating factor or locus considered. So 3 factors would require going to three dimensions. The only alternative is an awkward decompositions into four 4 × 4 arrays to stay in three dimensions. This last course was taken for the other figure in the 1906 paper of Bateson et al., producing for a 3-factor cross an 8×8 array organized according to a strange hybrid

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[26] Figure 12.3 of Wimsatt (2007, p. 290) is a gamete-invariant Punnett square designed specifically to show how recombination, gametic organization, bisexuality and diploidy place physical constraints that affect linkage disequilibrium.

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scheme that was nearly unintelligible.[27] (By contrast, the 8 × 8 gamete-invariant Punnett square for 3 factors is a natural and easily readable extension of the 4 × 4 array for 2 factors).

So the mathematical generality of Mendel's scheme as applied to 2, 3, 4, or $n$ factors, could not be reflected in a 2-dimensional representational scheme with the locus-invariant format. But it can with the gamete-invariant format because diploidy and sex mean that there will always be exactly 2 gametes! List all the gametes of each parent in a mating and you have the makings of a 2-dimensional gamete-invariant array. Any number of alleles and loci can be represented merely by listing the gametic combinations possible from the specific alleles at different loci present in the parents, and listing them at the head of the rows and columns in an array. This is done by an operation exactly analogous to producing a truth-table.

A natural extension of this procedure lists all gametic combinations one could assemble in a population by different choices of mates. This larger array has significance in population genetics. Thus the representational generality of the gamete-invariant Punnett square is equal to (indeed greater than) the possible crosses among multi-allele, multi-locus genotypes in any Mendelian (indeed in any Morganian) scheme.

A *fourth* and apparently very different variant is represented by the second figure in the 1906 paper (Fig. 2, p. 160). It is in fact what one would get if one constructed a 3-factor locus-invariant 4 × 4 × 4 cubic array, and then took the third dimension apart as four slices for the four possible values of the third-factor genotype, each slice a 2-factor 4 × 4 locus-invariant array for the first 2 factors, and laid out the four slice meta-array in a plane as a 2 × 2 of 4 × 4. Unfortunately, the net effect is no longer locus-invariant in 2-dimensions. This kind of array has no name, though it might be appropriate to call it a **Galton array**. I have (courtesy of Robert Olby) correspondence from Galton to Bateson dated October 1, 1905, in which Galton proposes what is (with minor notational changes) the same 3-factor table. I will discuss it more fully in the second paper in this series.

A *fifth* kind of array, representing the results of crossing whole genotypes without breaking them down to the gametic level appears from time to time in various forms. Most commonly, the purpose is to represent fertility or infertility in crosses between different mating types, species or self-incompatible plants, as in its apparent first use by Morgan to depict the distribution of fertility or infertility in matings in *Ciona* (1913, p. 218, Fig. 105). This kind of array makes sense only where the different gametic combinations from a genotype produce the same outcome for the question asked (e.g., for uniform effects at the level of a cross between different species), or where no information is available that can be used to generate alternatives at the gametic level which can be related to the outcome. I will not discuss it further here.

Punnett publishes the first edition of his book, *Mendelism*, in 1905, with no pictures. In 1907, a second edition includes several 2-factor arrays. These are particularly interesting because they are redrawn and differ from the 1906 array, and presumably

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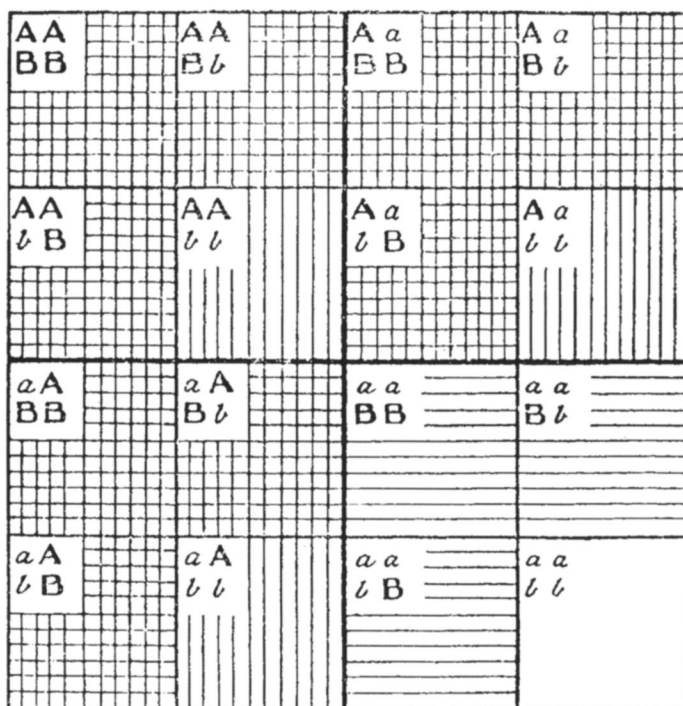[27] Their 8 × 8 array for the 3-factor cross will be analyzed in the second paper in this series.

**Fig. 4** Unnumbered figure, p. 45, of Punnett (1907)

best reflect his own understanding of them. The key last three sentences of this quote looks quite unusual to modern eyes:

> …we may briefly recapitulate in a generalized form the main features of the phenomenon, …with the help of the diagram opposite [Fig. 4]. *Aa* and *Bb* denote two pairs of unit-characters such that *A* is dominant to *a* and *B* is dominant to *b*. If we suppose one of the original parents to have been homozygous for *A* and *B*, and the other for *a* and *b*, we may represent them as *AABB* and *aabb*, respectively. The constitution of the F1 individual must therefore be *ABab*, and since it is heterozygous for the *Aa* pair, it will give in F2, *AA* + 2*Aa* + *aa*. This is denoted by the four large squares of the diagram. Again, since the F1 individual is heterozygous for the *Bb* pair, the F2 generation will be of the form, *BB* + 2*Bb* + *bb* for this pair of characters. This is represented in the diagram by dividing up each of the original squares into 4 again. … (Punnett 1907, pp. 44–46).

This description suggests that he saw the square as being in a hierarchial "Fractal-Recursive" form, in which each additional segregating factor generates a 2 × 2 division of each square of the preceding stage[28]. If so, it would have been more diffi-

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[28] That is, *if* he saw it as indefinitely extendable. There are no 3-factor squares by either Bateson or Punnett, save for the strange one in their 1906 paper.
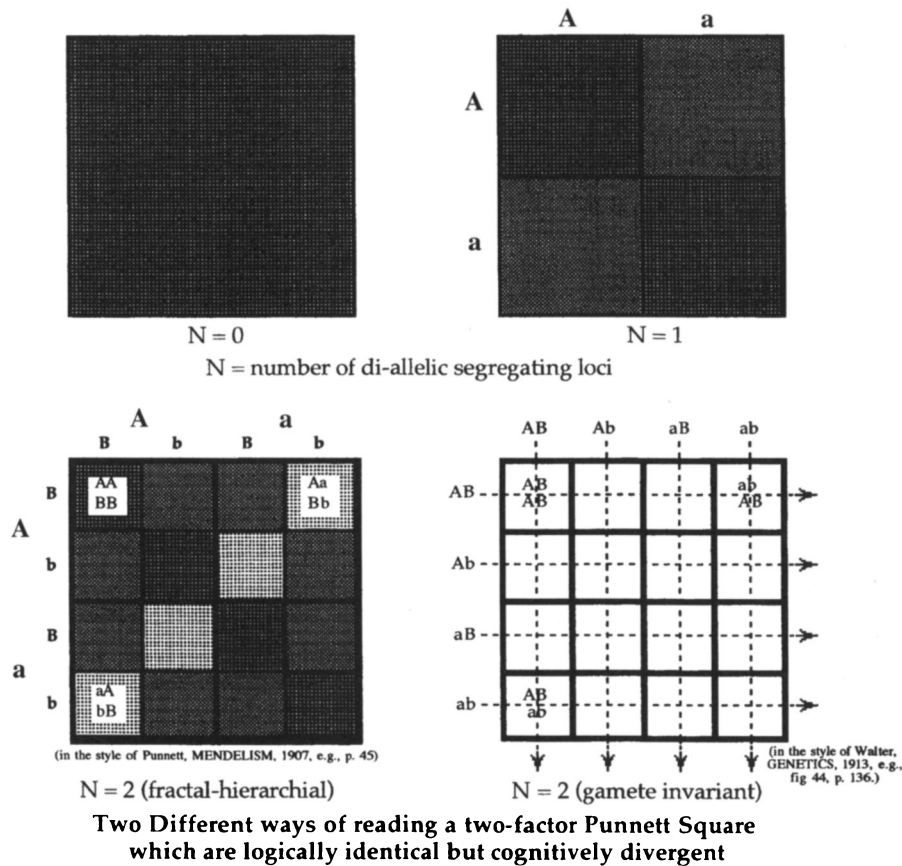
N = 0  N = 1

N = number of di-allelic segregating loci



(in the style of Punnett, MENDELISM, 1907, e.g., p. 45)

N = 2 (fractal-hierarchial)

(in the style of Walter, GENETICS, 1913, e.g., fig 44, p. 136.)

N = 2 (gamete invariant)

**Two Different ways of reading a two-factor Punnett Square which are logically identical but cognitively divergent**

**Fig. 5** Fractal versus cross-multiplying views of Punnett squares

cult to see it as a cross-multiplication of (or a cross-decomposition to) gametic types. These two representations of the Punnett square are extensionally equivalent: they can produce the same arrays in the same order. But they are cognitively divergent: the conception of how they are generated and structured is different, and seeing them as a cross-multiplication of gametic types is enormously more fruitful.

Punnett's diagram in 1907 is also anomalous in how he writes the genotypes. Although his figure is a gamete-invariant array (like Fig. 2), it begs to be misread as a locus-invariant array because of the natural reading order from left-to-right. We see the two A's together in the top row and reify them as a locus, and the B's below them as a second locus. (But then we are tricked, because this is not a locus-invariant array: the locus specifications change at both the A-locus and the B-locus as we go across rows or down columns. We can see the invariant gametes only by reading from top to bottom—an "unnatural act" in our culture, unless there is something else to guide the eye in that direction. (Sinnott et al. use vertical notation with vertical chromosomes in their Fig. 66 (1950 p. 170), but no such help is provided here.) Seeing the

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array as gamete-invariant requires moving the eye from top-to-bottom in a cell to pick up the alleles in a column, and then scanning for that chunked assemblage across rows or down columns of cells. Figure 5 directly compares the two interpretations with the corresponding correct notation:

Even by 1911, when he has reverted to the preferable notation of the 1906 array, Punnett did not appear to see his squares as a gametic cross-multiplication, but as a writing exercise:

> A convenient and simple method of demonstrating what happens under such circumstánces is the method sometimes termed the 'chessboard' method. For two series each consisting of four different types of gamete we require a square divided up into 16 parts. The four terms of the gametic series are first written horizontally across the four sets of four squares, so that the series is repeated four times. It is then written vertically four times, care being taken to keep to the same order. (Punnett 1911, p. 37.)

This description of Punnett's method (and its first baptism as the "chessboard method") is much closer to a cross-multiplication of gametic types, but he still does not conceptualize the alternatives individually. Rather he suggests copying the whole column of gametic possibilities from one parent across the different columns (each representing a given gametic type from the other parent) until one has covered all the columns, then following this by copying the row of gametic possibilities from the other parent down through all the rows of the individual gametic possibilities of the first. The emphasis is on the series, rather than on individual gamete types. It is like a vector multiplication of possibilities rather than a scalar multiplication of the effects of individual outcomes. And it plays more naturally as a symbolic operation than as a material physical combination—a view consonant with Bateson's resistance to genetic atomism at that time (see Coleman 1970). It does, however, resonate with the figures introduced by Bateson in 1909 and Herbert in 1910.

### 4.2 The evolution of the "gametic cross-multiplication" form of Punnett square

How do we get from this elegant but awkward hierarchial–fractal represèntation to the extensionally, combinatorially, and logically equivalent, but generatively or cognitively divergent conception of a Punnett square as a cross-multiplication of gametic types? Starting with Punnett's diagram in 1907 we can count four successive stages in which the eye is invited, ever more effectively, to *physically* trace the crossed trajectories of a gametic array, or to see the tracks as decomposed into units in ways appropriate to the second representation. This is achieved in the final stage. When it is achieved, the three earlier stages disappear from the literature[29], as the fourth stage and variants of it become effectively universal. Along with the crucial transitions mentioned a number of other changes, ranging from important to trivial in significance,

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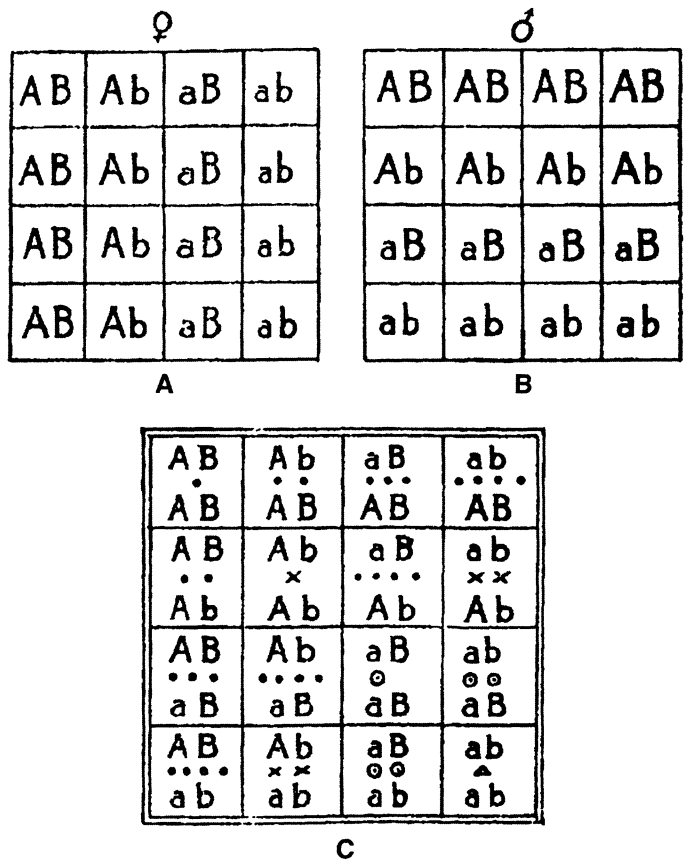[29] Punnett is an exception here. He retains the images from his 1911 book through two later editions, the last in 1927.

♀               ♂

| A B | Ab | aB | ab |
|-----|----|----|----|
| AB | Ab | aB | ab |
| AB | Ab | aB | ab |
| AB | Ab | aB | ab |

| AB | AB | AB | AB |
|----|----|----|----|
| Ab | Ab | Ab | Ab |
| aB | aB | aB | aB |
| ab | ab | ab | ab |

**A**               **B**

| AB · / AB | Ab · · / AB | aB · · · / AB | ab · · · · / AB |
|-----------|-------------|---------------|------------------|
| AB · · / Ab | Ab × / Ab | aB · · · · / Ab | ab × × / Ab |
| AB · · · / aB | Ab · · · · / aB | aB ⊙ / aB | ab ⊙ ⊙ / aB |
| AB · · · · / ab | Ab × × / ab | aB ⊙ ⊙ / ab | ab ▲ / ab |

**C**

Fig. 52.—PUNNETT'S SQUARE FOR DIHYBRIDS.

*A*, female gametes arranged vertically ; *B*, male gametes arranged horizontally ; *C*, male and female gametes superimposed.

**Fig. 6** Herbert's 1910 4 × 4, Fig. 52 p. 129

are occurring and becoming fixed and entrenched. The second paper in the series will describe and discuss them.

The first stage beyond Punnett's representation is found only as a transitional form in the books of Bateson (1909) and Herbert (1910). Both use the interesting expository device of decomposing a single-factor 2 × 2 square into horizontal and vertical components contributed by the respective gametes, and then recomposing the whole square out of the superposition of the two component squares, complete with male and female symbols marking where the gametes come from. Herbert also decomposes the 4 × 4 2-factor case (Fig. 6), which Bateson leaves to the imagination. He is the first to call it a Punnett square. Presentation of the squares for each sex makes clear the "reading directions" which show invariance for the two gametes in the composite diagram.

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**Fig. 7** Darbishire (1911/1913), unnumbered figure, p. 214

| | | ♂ gametes | | |
| --- | --- | --- | --- | --- |
| | **AB** | **Ab** | **aB** | **ab** |
| **AB** | AA.BB | AA.Bb | Aa.BB | Aa.Bb |
| **Ab** | AA.Bb | AA.bb | Aa.Bb | Aa.bb |
| **aB** | Aa.BB | Aa.Bb | aa.BB | aa.Bb |
| **ab** | Aa.Bb | Aa.bb | aa.Bb | aa.bb |

(♀ gametes, left axis)

When Herbert composes them below, the gametes are separated above and below, retaining their integrity, so they are readily visually tracked across and down. This kind of diagram showing the assembly of Punnett squares is found only rarely again, and then under special circumstances[30]. It is almost as if these partial diagrams were giving instructions for teachers as to how to compose them on the boards, (e.g., "Write down everything for one sex first!") Once that knowledge was disseminated, one could suppose, it was passed down in the classroom and did not need to be presented in the textbooks, where one saw only the already composed squares (Fig. 7).

The next stage is provided by Darbishire in 1911[31], who generates an uncommonly large collection of (unnamed) Punnett squares and a discussion of their use extending over several chapters. He experiments with a profusion of variants. The notation is in flux in this period, forced by discovery of new complexities of inheritance, each of which he illustrates in a Punnett square. After discussions of notations with different letter abbreviations of the (supposed two) alternative character states, and the D/R notation favored by Bateson for dominant and recessive unit-characters[32], and various special symbols, he settles on using the modern A/a, B/b, C/c, ...notations for dominant and recessive factors at loci A, B, C, .... His genotypic specifications

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[30] Thus, Crew (1925, pp. 18–19) uses it for a special case where the sexes *need* to be distinguished—a situation producing a 3:1 ratio of gametic types in one sex and a 1:1 ratio in the other.

[31] I have only seen the 1913 edition of his book, though remarks in the preface suggest that there are no significant changes from the first (1911) edition. Similarly, I use the 1913 edition of Bateson's book, which makes a similar claim relative to the 1909 edition. Should either edition have typographic changes in the relevant figures, I would have to change this assessment.

[32] Carlson 1967 (Chap. 4) discusses the confusions introduced by the idea of the "unit-character" and explanations of the notational changes throughout this period.

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causes the former to recede from view, these nine genotypes may be combined into four phenotypes as follows : —

| Phenotypes . . | $9\,SY$ | $3\,SG$ | $3\,WY$ | $1\,WG$ |
|---|---|---|---|---|
| Genotypes . . | $4\,S(G)(W)Y$ <br> $2\,S(G)SY$ <br> $2\,SY(W)Y$ <br> $SYSY$ | $SGSG$ <br> $2\,SG(W)G$ | $WYWY$ <br> $2\,WYW(G)$ | $WGWG$ |

From this analysis it may be said that the Mendelian ratio for a typical dihybrid is phenotypically $9 : 3 : 3 : 1$, while that for a monohybrid, as we have already seen,
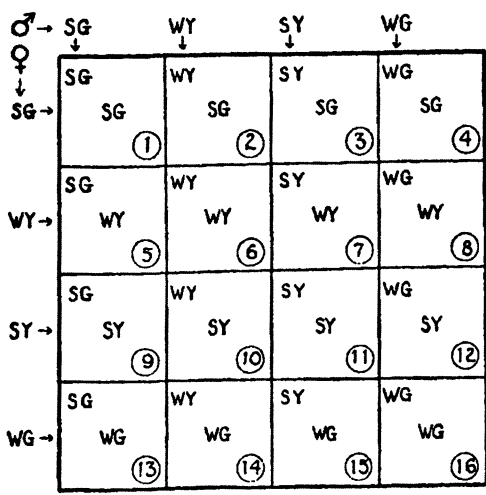


Fig. 44. — Diagram to illustrate the possible combinations arising in the second filial generation ($F_2$) following a cross between yellow-smooth YS and green-wrinkled GW peas.

**Fig. 8**    Walter (1913), Fig. 44, p. 136

in the cells, however, are of the confusing form, "**Aa.Bb**," which again suggests a locus-oriented rather than a gamete-oriented reading order—preserving the strongly locus-centered nature of Mendelian combinatorial thinking, where number of loci is the primary determinant of the kind of problem you are dealing with. This scheme buried the gametes as the symbols at positions 1 and 3 or 2 and 4 in the symbol string for the genotypes. However, he recognized the importance of keeping track of them
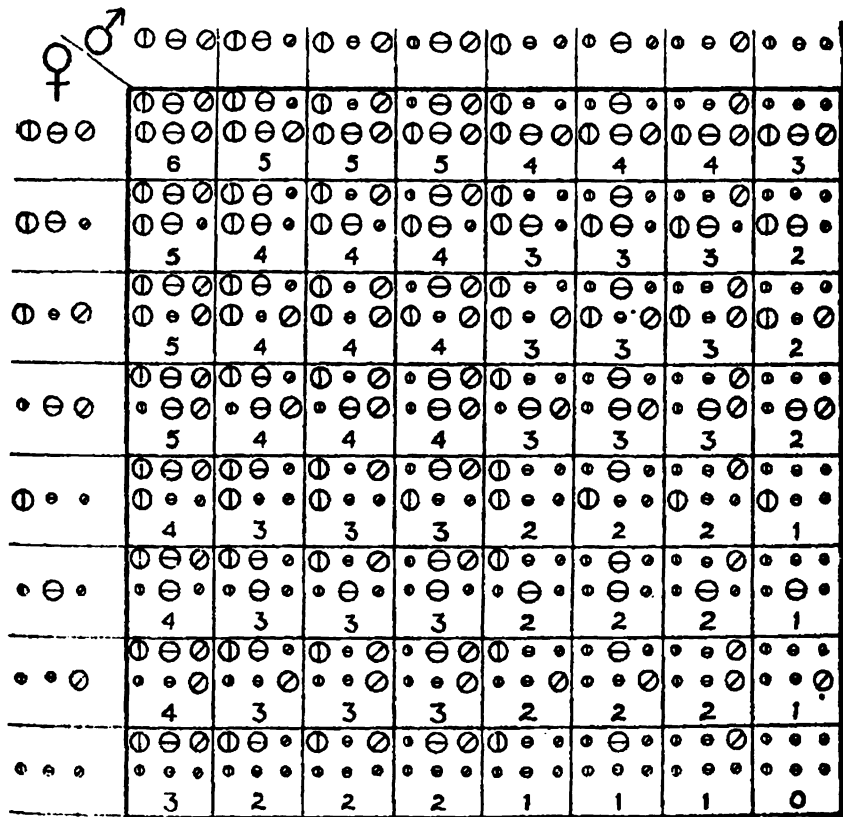
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FIG. 55.—Diagram to illustrate Nilsson-Ehle's case of trihybrid red wheat. The large screwheads each represent a single determiner for the red character. The small screwheads symbolize the absence of the red character, or white. The number in each square indicates how many doses of the "red" determiner is present. For further explanation see text.

**Fig. 9**  Walter (1913), Fig. 55, p. 189

because he wrote the gametic types at the head of the columns and the left of the rows. This action naturally contributes to and only makes sense in the context of a "gamete-invariant" mode of thinking. This was a critical notational change, for it supported a new way of thinking. Its importance is reflected in its near-immediate subsequent universality.

The final stage in this series is generated in 1913 by Herbert Walter, then assistant professor at Brown, in the first edition of his visually inventive textbook, where he experimented even more richly than Darbishire with the visual possibilities of the new devices. His key move was to combine the nicely separated gametes in the genotypic specification of Herbert or Bateson with their listing in the margins in the style of Darbishire (with arrows added) to produce a diagram in which the cross-multiplication of

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gametes was an almost unavoidable consequence of the visual tracking of the eye in reading the table. I offer two (of many) diagrams from Walter. The first, Fig. 8 (Walter's Fig. 44, p. 136) is his presentation of the 2-factor case. See how readily the eye picks out the relevant invariant gamete in scanning this figure across or down, facilitated here by lining up the gametic entries in the cells with their source gamete along the top or side margin—and, specifically, *not* with each other. The cells are numbered (from 1 to 16, for a 2-factor table), a practice which commonly pointed in earlier texts[33] to an accompanying "break-out" table (p.137) which listed genotype, count of cells and cell identifying numbers having that genotype, corresponding phenotype of that genotype, and count of cells and cell identifying numbers having that phenotype. But just as Punnett squares became truly common after Walter, the break-out table in the form of a linear list was increasingly dropped as the array form became more familiar and/or ways were found to incorporate its information (particularly the phenotypic data) into the Punnett square. The numbering of cells died with it, or even before as the expectations associated with Punnett squares became common conventions.

Some of Walter's inventiveness with visual illustrations and his mastery of the potential of the method is found in his symbolic representation of Nilsson–Ehle's tri-hybrid cross for seed color in red wheat (Fig. 9). Walter diagrammed two 3-factor crosses, and was the first to do so in a gamete-invariant form, making them the first 3-factor Punnett squares. Walter's other tri-hybrid diagram (Fig. 47, p. 141) used the modern notation ("A/a" form) for Castle's work on inheritance of coat characteristics in guinea pigs (using the letters "R/r," "S/s," and "P/p" for "rosetted," "short hair," and "pigmented" traits and their recessive counterparts, respectively. But Nilsson–Ehle's tri-hybrid represented a case of the so-called quantitative inheritance, in which alleles at each of three loci contributed (or not) equally to the intensity of the red seed color. Arguments between "Mendelians" and "Biometricians" (who argued that quantitative inheritance was different in kind from Mendelian inheritance) in the preceding decade generated special interest in such cases (Provine 1971). To indicate this symmetry of alleles at different loci in their mode of action, Walter denoted the genotypic states with large and small screw heads (the large ones contributed to the red tint, the small ones did not), with the different loci indicated by the differing angles of the screw slots.[34] He also indicated the phenotypic state in each cell by counting the number of large screw heads, (seven color states, from 0 to 6), but since the larger screw heads used more ink and physically filled the box more, the icons also gave a redundant qualitative representation of the color intensity of the wheat through filling and darkening of the box.

Walter's book was widely read if the spread of his diagrams and their conventions is any indication. Both his Punnett squares and his inventive Weismann diagrams (Griesemer and Wimsatt 1989) were widely borrowed. The next 15 years saw an explosion of books on genetics, heredity, and evolution, many going through several editions. Centrally important scientists such as Morgan, Castle, and Conklin wrote or

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[33] This form appears to originate in Darbishire (1911, see e.g., p. 211).

[34] While it was important to tell which was which in the conduct of breeding experiments, they were functionally inter-substitutable in affecting seed color, and this iconic device elegantly allowed one to step in to identify them when necessary while generally stepping back to better appreciate their net effect.

coauthored multiple books and monographs. I found no text after 1913 that discusses genetics in any depth without using Punnett squares. Virtually all use the mature form found in Walter's book—many of them, with their own added variations. In this period also we get the fixation of several conventional features that were still variable in Walter. These are things that could equally well be done in various ways, as long as everyone does it the same way—the classic problem of the coordination game. Thus with rare exceptions (inevitably made appropriate by other devices and contexts), we have the order of gametes fixed as 'AB, Ab, aB, ab'. With somewhat more variability, the male gametes are commonly arrayed across the top and the female gametes down the left side.[35]

### 4.3 Alternatives and competitors—advantages of the Punnett square

There are no alternatives to Punnett squares that accomplish the same purposes with the same elegance and comprehensibility. Algebraic expansions like those in Mendel's paper are in principle equivalent, but in practice difficult to comprehend. A partial alternative, the widely exploited mating-cross tree-diagram achieved a currency probably unmatched by any other form of representation (see Darden 1991), probably because it was the dominant form for representing single-factor crosses. Two-factor crosses were too complex for this form, as we can see in the last figure, discussed below.

The common "tree diagram" was phenotypic rather than genotypic in its representation, and could not serve exactly the same function as the Punnett square. In some cases (with matings of the right known genotypes), there was still a 1-1 mapping between distinguishable phenotypes and genotypes, and one could write down genotypes for the offspring of these tree diagrams, but this was only under special conditions. Nonetheless, it persisted as a common form (even more common than the Punnett square, though less interestingly variable) because of its natural correspondence with the physical process of mating two individuals of known phenotypes. It listing their offspring, classified by phenotype, underneath in a manner reflecting the long-standing form of genealogical or family trees. (Bateson 1909, pp. 214–241 has half a dozen examples of the latter, and it is reasonable to see the tree diagrams in part inspired by them.)

There is one diagram (Fig. 10) which is logically equivalent to the 2-factor $4 \times 4$ table of the gamete-invariant Punnett square, though, in its representation of the parents and F1 generations, it is also part tree diagram. Interestingly, it was as much a

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[35] There is a reason even for the difference between these two cases: the order of gametic types can make a difference in the pattern produced by a given mode of inheritance, and if there were not agreement on this order, it could hinder learning or recognizing this array pattern, so there is a definite advantage for agreement on standards here. But for characters commonly investigated in this period, the arrays were symmetric about the diagonal of homozygous elements because it made no difference whether one got a given allele from the male or from the female parent. This fact made it natural to go to Darlington and Mather's explicitly symmetric "diamond" array, a new competitor in superficial form, but logically and functionally identical: it simply rotates the array clockwise by 45 ° (1949, Fig. 15, p. 67.) which has seemed to be growing in popularity in these politically sensitive times. Ironically there are now growing reasons to revert to the classical form with the currently increasing interest in asymmetric cases of maternal inheritance and "genetic imprinting" motivated by developmental biology.
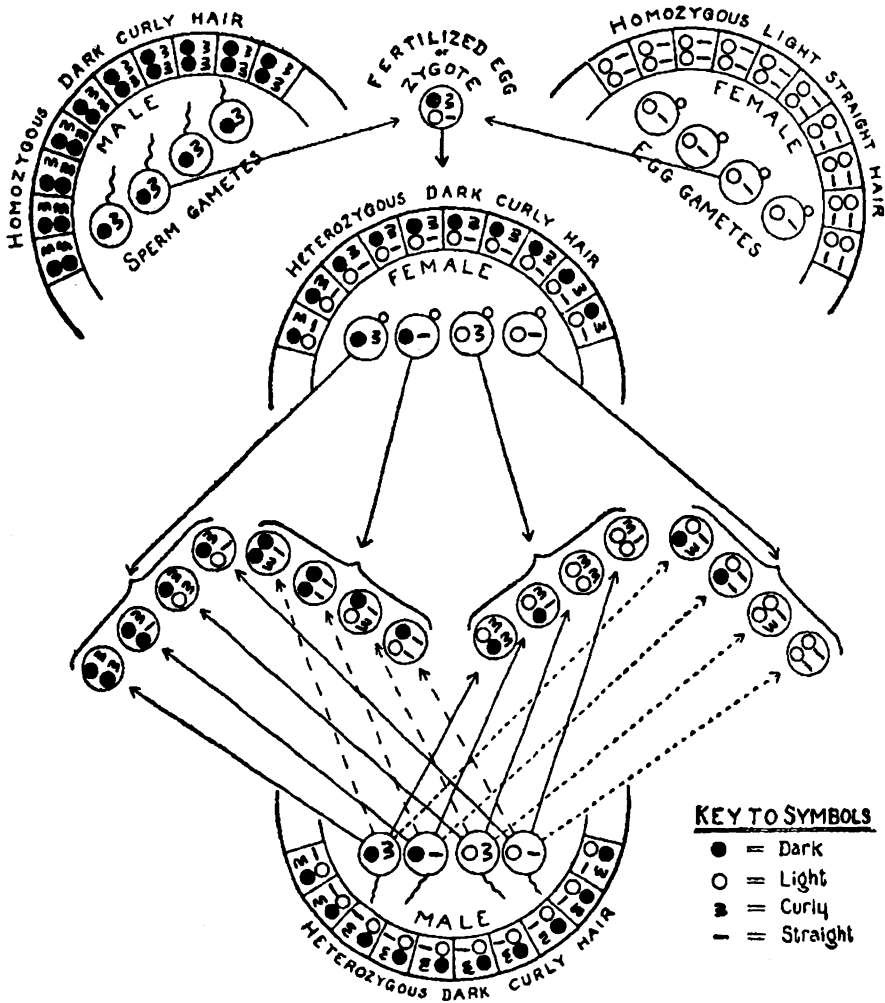
FIG. 45. — The heredity of human hair according to data by C. B. and G. C. Davenport. The arcs represent the somatoplasms of four individuals. Within the arcs are the gametes formed by these individuals. The dominant character is placed on the outside of the arc where it will be visible.

**Fig. 10** Walter (1913), Fig. 45, p. 138 "arc diagram"

failure as Walter's version of the Punnett squares were a success. This is Walter's "arc diagram" [my terminology]. Though logically equivalent as a representation to the Punnett square, it was hardly visually equivalent. It appears in just one place in his text, right after the introduction of 2- and 3-factor Punnett squares. He kept it there in subsequent editions, but never tried to expand its scope of application to replace them,

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and to my knowledge it was never copied by anyone else.[36] Whatever his intention, it is a standing testimonial for Punnett squares. The complexity with which it represented the gametic combinations, the necessity to track a network of multiple crossing arrows (a problem also of many tree diagrams[37]), and its lack of compactness made it enormously more visually complex, and much more difficult to see the systematic character of its relationships. One can see Walter's diagram as a kind of transformed or disassociated Punnett square—an atavism in which (to exploit a material analogy) the regular geometry of an integrated circuit chip regresses to the complex intersecting wiring harnesses stringing together the corresponding separate circuit boards and components of computers a generation before. Through it, one can really appreciate the remarkable visual economy of the Punnett square.

These advantages arise in even the simplest case. The mono-hybrid cross is intelligible without the 2 × 2 Punnett square, though even this simplest of crosses benefits from it. And, as commonly noted, seeing the 2 × 2 mono-hybrid cross gives you the logic for understanding the di- and tri-hybrid Punnett squares, and in principle, for constructing Punnett squares of any arbitrary size. Even the di-hybrid cross is almost too cumbersome to represent (and surely to think about) in any other way, and the idea of using a "tree diagram" (the only plausible alternative) to represent a tri-hybrid cross is almost too forbidding to think about.

It is clear why "Punnett squares" were adopted even without seeing Walter's "arc diagram," though the arc diagram helps to remind you what you're missing! Any reader of Mendel's paper who has struggled with how to see order in his linear lists of the 16 di-hybrid or 64 tri-hybrid types of offspring, or to verify which hybrid types came from which combination of gametes, sees its advantages immediately. The systematic, causal, and combinatorial order which comes from seeing these results as 4 × 4 and 8 × 8 tables, where rows and columns are gametic types from the two parents, and the squares are the genotypes resulting from their combination, is astounding. Another really significant advantage (which I did not appreciate until I did 8 × 8 tables for myself, though it helps already for 4 × 4) is how the whole table can be composed by simply copying invariant contributions down columns and across rows in a way that makes it automatic and virtually error free. The resulting freedom from having to think, "Now what do I write in this space?" when constructing the tables by writing down the genotypes in sequence (which I did at first!) speeds their construction enormously and probably significantly reduces errors.

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[36] Its use to diagram data collected by the Davenports in 1907 and 1908 raises the possibility that Walter invented this diagram before he had seen any Punnett squares, or at least Darbishire's productive modifications which he presumably built upon. For all its complexity, it has some nice features, e.g., in his proposal to "...place the dominant character on the outside of the arc where it will be visible." Like Punnett's exposition of 1911 quoted above, this diagram tends to chunk and to cross-multiply whole arrays of gametic possibilities rather than individual alternatives.

[37] In my experience, tree diagrams work well only for a single-factor cross, or (as with Morgan's depiction of linkage between sex-linked characters) of two-factor crosses where special conditions limit the number of phenotypes of the offspring in any given cross to no more than four. A full characterization of data for the sex-linkage case involved multiple (from 3 to 6) tree diagrams, which may also favor them, since they correspond naturally to a series of individual matings in an experimental design or narrative.

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## 5 Conclusions

I have not discussed here a whole other dimension of possible influence of the Punnett square. It provided a very successful paradigm which all biologists educated after about 1920 had to see because of its center stage position in a science which was itself becoming central to the rest of biology. Punnett squares were also explorations of the combinatorial potentials of a different kind of data structure—the tabular array. One wonders how many other problems in biology unrelated to the combinatorics of forming offspring found an organizing schema in this paradigm. An obvious case to start with (though I have not done the relevant history) is the 4 × 4(×4) table for the mapping from the base sequences of the triplet code to the amino acids they code for. (This table *is* found in all modern molecular genetics textbooks!) This is an extension to a different part of genetics—but still quite close to home. I suspect that there are many other examples further afield.)

Punnett squares have a variety of particular virtues both as instruments of conceptualization and of computation. Their widespread use on problems like those they were originally invented for is thus not surprising. But this does not explain their enormous adaptive radiation into a variety of new contexts where they have played a role in conceptualizing and solving a number of diverse problems. This radiation will be elaborated in the second paper of this series. Their special virtues arise through a representation of information involving actual and possible matings which makes transparent the natural fracture lines of a complex problem into independently solvable sub-problems. The result is like (it is almost iconic for) some kinds of integrated circuit chip, in which data can be read (or fed) in on a variety of alternative input lines, and almost immediately the answers can be read off (or out) in a variety of output modes. I have used as many as seven multiple overlays simultaneously for the representation and solution of complex problems involving the interaction of gametic states, frequencies, and phenotypic characters. Each overlay adds a particular kind of information to each cell, and its addition to the common matrix of information allows the representation and solution of a new kind of problem or problems. The overlays can be "mixed and matched" to represent and solve different kinds of problems. Viewed in this way, the evolution of this mode of representation is seen to increase the operating efficiency and range of this device, extending its computational virtues to new kinds of problems.

Some of their advantages are simply products of their powerful combinatorial structure, but this is not enough. (Why then are not locus-invariant forms more common? They should have the same combinatorial advantages.) Like a good metaphor, this representational device appears to work almost any way you look at it. Another reason beyond their modularity and computational efficiency explains their spread, and explains as well why this very modularity is possible. The reproductive cycle and bisexuality is so common to different life forms, and so important in understanding their adaptations that something which addresses its structure as centrally as the Punnett square will have a central role in organizing and solving a diversity of problems. Its role in genetics is in many ways like that of the conservation laws in physics: it can show how to set up a problem, and provides important constraints on its solution for many different kinds of problems. This explains why the gamete-invariant form rather

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than the locus-invariant form is the dominant representation in genetics. The number of loci is the number of differentiating characters, and was a central variable in the formulation of problems in Mendelian genetics. But since the gametes represent natural biological and physical objects, which are indeed separated at a stage of the life cycle and recombined at another—which loci are not—this use of a natural fracture point in natural objects made the gamete-invariant form a much more theoretically fruitful representation. *The gamete-invariant representation also factors the genotype and conjoint phenotypic results into the two genetic variables most readily manipulated in mating experiments—the genetic composition of the two gametes.* Indeed it is the only representation which can be given a straightforward causal account corresponding to the genetic processes of segregation and independent assortment as they occur in the gametes, and gametic fusion as it occurs in the zygote. Thus it is mechanically faithful to the biology, whereas the locus-invariant representation is misleading.

You can cut nature any way you choose, but you would be a fool to do so, both for positive and for negative reasons. On the positive side, if you cut nature at its joints, you find those divisions confirmed again and again as you approach them from the perspective of different problems, with different methods, and at different levels of organization. Gametes are real joints, in the only sense of "real" appropriate to science (Wimsatt 1981): they are detectable, derivable, and usable in a variety of ways. And then there is the negative side: because of this multiple consilience of problems and methods at these common boundaries, it is also less frequent that a decomposition along these boundaries will lead to a serious misrepresentation of a problem—a parsing which generates a legion of "functional localization fallacies." In science we want not only productive tools that produce lots of results, but also safe tools which yield a higher proportion of good results. There are no magic bullets, and no-one but perhaps a philosopher would look for them. But that does not mean that we cannot seek brands which misfire less frequently.

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