keeping a meticulous record of stratification, modern archeology has means by which to tell the date of plant material, and by specialization the botanist will, in the long run, learn to identify the battered remains of the plants. Thus, by joining hands, the two sciences establish a third, paleoethnobotany, which endeavors to help delineate man's victories and defeats in his battle against nature for survival and multiplication, and to unravel the complicated history of the plants upon which even modern civilization is ultimately dependent.

References and Notes

1. R. J. Braidwood, *Yearbook of the American Philosophical Society* (1955), p. 311.
2. J. Iversen, *Danmarks Geol. Undersøgelse II* (1941), p. 66.
3. Primary domestication involves specific and conscious attention to a wild plant in its natural habitat; secondary domestication is the segregation, for intentional cultivation, of a weed growing in cultivated soil which already unintentionally has been subjected to a process of selection through being reaped along with the intended crop. In the cases of rye and oats, this segregation occurred far from their centers of natural distribution; by comparison, barley is secondary only insofar as human intention is concerned, not in respect to habitat.
4. Barley might have been selected for domestication in any place from Central Asia to the Atlantic, but since we know of no ancient culture based upon barley alone, and since evidence of domesticated wheat distinguishes that portion of the wild-barley area in which incipient agriculture has been established archeologically, the conclusion is inevitable that wheat was the species that caused man to attempt plant domestication in the first place.
5. R. J. Braidwood, *Bull. Am. Schools Oriental Research* 124 (1951).
6. ———, *The Near East and the Foundations for Civilization* (Univ. of Oregon Press, Eugene, 1952).
7. ———, *Science* 127, 1419 (1958).
8. ———, *Antiquity* 31, 73 (1957), and K. M. Kenyon, *ibid.* 31 (1957); but see 7 and F. E. Zeuner, *Palestine Exploration Quart.* 55 (1958).
9. H. Helbaek, *Ann. Repts. Inst. Archaeol. Univ. London, Rept. No. 9* (1953), p. 44; ———, in R. J. Braidwood *et al.*, in preparation.
10. R. J. Braidwood *et al.*, *J. Near East Studies* 11, 1 (1952).
11. On behalf of the Oriental Institute of the University of Chicago and the Iraqi Government I undertook, in 1957–58, an investigation of traces of early plant husbandry in Iraq. Relevant pottery and carbonized material were examined in European museums and in the Iraq Museum in Baghdad, and field investigations were carried out in numerous sites of ancient cities in lower Iraq, from Aqer Quf, north of Baghdad, to Ur and Eridu in the south. Throughout this article reference is made to the main results of this project. See also T. Jacobsen and R. M. Adams, *Science* 128, 1251 (1958).
12. H. Helbaek, *Dansk. Biol. Med.* 21, 8 (1953).
13. ———, *Proc. Prehist. Soc.* 21, 93 (1956).
14. ———, *ibid.* 18, 194 (1952).
15. S. P. Tolstov, *Ann. Repts. Inst. Archaeol. Univ. London, Rept. No. 13* (1955–56).
16. O. Heer, *Die Pflanzen der Pfahlbauten* (Zürich, 1865).
17. E. S. McFadden and E. R. Sears, *J. Heredity* 37, 81 (1946).
18. W. U. Guyan, *Das jungsteinzeitliche Moordorf von Thayngen-Weier; Das Pfahlbauproblem* (Schaffhausen, 1954).
19. G. Caton-Thompson and E. W. Gardner, *The Desert Fayum* (London, 1934).
20. H. Helbaek, unpublished investigation.
21. ———, in O. Tufnell *et al.*, "The Bronze Age," *Lachish IV* (Oxford Univ. Press, London, 1958).
22. ———, *Arboger for Nordisk Oldkyndighed* (1954), p. 198.
23. See, for example, J. R. Harlan, *Sci. Monthly* 72, 87 (1951) and *Am. Naturalist* 85, 97 (1951), on the great diversity and rapid evolution of plants in Turkey.
24. E. Neuweiler, *Vierteljahresschr. naturforsch. Ges. Zürich Beih.* 100 (1956).
25. H. Helbaek, *Acta Archaeol.* 13, 97 (1952).
26. V. L. Täckholm and M. Drar, *Flora of Egypt* (Cairo, 1941), vol. 1.
27. I except here, of course, the concept of F. Koernicke that the wild *H. spontaneum* was the progenitor of all cultivated barley, a proposal which has been consistently rejected. See the brief survey of theories regarding the derivation of barley in E. Aberg, *Symbolae Botan. Upsaliensis* 4 (1940).
28. N. Nybom, *Acta Agr. Scand.* 4, 430 (1954).
29. Many reports on Egyptian grain postulate the occurrence of naked barley in prehistoric and dynastic deposits. No documentation has ever been published, and according to my experience, which includes examination of many grain finds, the postulate is unfounded.
30. I examined a sample of the barley from Mersin at Reading University and found it to be a small-grained hulled form of *H. hexastichum.* Its date, as pronounced by V. Gordon Childe, who brought the sample back from Mersin, was "well into the fourth millennium, probably earlier."
31. *H. hexastichum* has very often been reported for northern European prehistoric grain finds; most of these "reports" are manifestly unjustified.
32. F. Netolitzky, *Kaisl. Akad. Wiss. Wien* 123, 1 (1914).
33. Because of a protruding hilum and radicel point, the seeds of this species suffer rather more than most in the carbonized state and are therefore in many cases not recognizable in prehistoric material.
34. Arpachiyah, Halafian period.
35. Ur, Early Ubeidian period.
36. H. Helbaek, *Kuml* (Aarhus, 1959).
37. H. Helbaek, in preparation.
38. ———, appendix to P. J. Riis, "Hama, les cimetières à crémation," in *Nationalmuseets Skrifter* (Copenhagen, 1948), pp. 205–207.
39. V. L. Täckholm and M. Drar, *Flora of Egypt* (Cairo, 1950), vol. 2.
40. H. Helbaek, in *Acta Inst. Rom. Regn. Suec.* (1956), vol. 17, p. 155.

Age of Sex-Determining Mechanisms in Vertebrates

Distribution of differentiation patterns indicates the evolutionary path of genes and chromosomes.

Emil Witschi

In vertebrates hermaphrodism may occur as an exceptional condition. However, as a rule the production of eggs and sperm is separately managed by female and male individuals. In most species the basic sex ratio—that is, the proportion of males and females unaffected by differential mortality or selection—is close to equality. It has been shown that this balance is maintained by a self-perpetuating genetic mechanism. One of the sexes produces two types of germ cells—female-determining and male-determining ones; this is the digametic sex. The two types of gametes are produced in equal numbers because they result from a difference in genic content between partners of a single pair of chromosomes, the sex chromosomes or heterochromosomes. Geneticists designate the condition of somatic cells and of primary gonia that have uneven pairs of chromosomes or genes (hereditary factors) as heterozygoty. *Hence, the digametic sex is also heterozygous.* It produces two types of gametes in equal numbers, because the unequal chromosome pairs become mechanically segregated during a maturation division, each gamete receiving one or the other of the partners. The other sex produces only one type of gamete. It is unigametic, because the sex-chromosome pair of its gonia consists of even partners, which are the equal of one only of the heterochromosomes of the digametic sex.

To understand this article it is important to realize that this genetic and chromosomal mechanism of sex determination occurs in two patterns, depending on which sex is the heterozygous and digametic one. If, as in man (or the opossum) this is the male, then one designates the partners of the hetero-

The author is professor of zoology at the State University of Iowa, Iowa City.

chromosomal pair as X and Y, and it is understood that X stands for the chromosome type which appears as an even pair (XX) in the female. Hence, the total formula of this pattern is written as XX-XY, symbols for all the other chromosomes (autosomes) being omitted. On the other hand, in all species that have digametic females and unigametic males, the pattern formula is ZW-ZZ, the female being heterozygous (ZW) and the male homozygous (ZZ).

Table 1. Categories of genetic and physiologic types of sex determination in vertebrates.

Species or taxonomic group	Genetic pattern	Physiologic reaction patterns: 1. Hormonal sex reversal*	2. Inductive sex reversal*	3. Self-differentiation of secondary sex characters	4. Reaction of oviducts to testosterone
Oryzias (teleost)	XX-XY	F→M; M→F			
Rana	XX-XY	F→M; m→f	F→M		Neg.
Xenopus	ZW-ZZ	M→F	F→M		Pos.
Bufo	ZW-ZZ	m→f	M→F		
Pleurodeles	ZW-ZZ	M→F			
Ambystoma	ZW-ZZ	M→F	F→M; m→f	Ambisexual	Pos.
Reptiles	ZW-ZZ	m→f	F→M	Ambisexual	Pos.
Birds	ZW-ZZ	m→f	F→M	Ambisexual and male	Pos.
Opossum	XX-XY	m→f			Pos.
Eutheria, *Homo*	XX-XY	f→m	F→M	Female	Neg.

* M→F, complete reversal of genetic male into female; F→M, complete reversal of genetic female into male; m→f and f→m, incomplete reversals.

Genes and Chromosomes

The peculiar distribution, among vertebrates, of the genotypes XX-XY and ZW-ZZ raises the question whether initially mere chance or specific physiologic conditions decide the alternative of evolution toward male or female digamety. Some fishes (for example *Xiphophorus*) apparently have not yet established a genetic sex-determining mechanism (1). Inasmuch as microscopically identifiable sex chromosomes are unknown in the entire superclass, the Pisces represent, altogether, a primitive and ancient condition. Nevertheless, the existence of competent sex chromosomes is revealed by the sex-linked inheritance of color marks and of other somatic characteristics in several species. The Japanese rice fish *Ozyzias latipes,* bred after sex reversal, furnishes direct evidence of male heterozygoty in a sex-determining factor (*2*). It is significant that in some river systems of Mexico and Honduras, *Platypoecilus maculatus* is XX-XY type and in other river systems, of ZW-ZZ type. Apparently each pattern was acquired after the rivers had gained separate outlets to the sea, an estimated 300,000 years ago (*3*).

Genetic differentiation is also rather primitive in the Amphibia. Morphologically identifiable sex chromosomes are reported only for males of true frogs (*4*) and tree frogs (*5*). They are not distinctly dimorphic but show characteristic peculiarities of incomplete conjugation not observed in spermatocytes of sex-reversed females. Breeding experiments confirm that frog males are of -XY type. The other anurans (toads) and all the urodeles that were genetically tested follow the ZW-ZZ pattern of sex inheritance; sex chromosomes are not morphologically recognizable.

All genetically and cytologically analyzed mammals have proved to be of the XX-XY type. Visibly differentiated X and Y chromosomes have been reported for males of about 240 species. Conversely, reptiles (nine species) and birds (37 species) are uniformly of the ZW-ZZ type (*6*). It is usually assumed that in the course of evolution the W chromosomes have disappeared, so that sauropsid females actually would be of ZO constitution, but so far, the absence of the W chromosome has been demonstrated unequivocally only for the domestic chicken (*7*). The chromosomal and genetic uniformity in higher vertebrate classes indicates that all sauropsids are descended from a small stock of ancestors that had already assumed the ZW-ZZ type, and all mammals, from a corresponding group that had acquired the XX-XY type. Since fossils do not reveal anything about chromosomes and genetic mechanisms of sex determination, the state of evolution attained 250 million years ago by Devonian lungfishes, ancestors of all tetrapods, remains conjectural. Nevertheless, the universality of the -ZW type among sauropsids suggests that it originated very early, probably in amphibian or even piscine ancestors. The possibility presents itself that, genealogically, salamanders (ZW) thus may be rooted close to the sauropsids, and frogs (XY), near the mammalian evolutionary lines. This possibility is discussed below.

Physiologic Patterns

Not so sharply defined and less generally known are the physiologic types of sex determination in vertebrates. The balance of genic sex factors directs the embryonic differentiation of gonads and secondary sex characters by chain reactions, which, however, may be modified or entirely switched about by the interference of physiologic, chemical, and physical factors. It is possible to arrange some of them in four categories (Table 1). Remarkably often they parallel the genetic sex types (*8*).

1) Exposure of embryos to steroid sex hormones during, and sometimes also after, primary sex differentiation may lead to partial or complete gonadal sex reversal. In the genetic XX-XY type, particularly in frogs and Eutheria, masculinization of genetic females is often successful, while in the ZW-ZZ type, feminization of genetic males is the usual reaction. Feminization of *Pleurodeles* and *Xenopus* after estradiol treatment is so complete that functional females of male genotype can be produced at will and bred with nonreversed males. Two notable exceptions to the rule that steroid hormones reverse preferably the homozygous sex are presented by the opossum and the small teleost *Oryzias.* Both belong to the -XY type. In the opossum, Burns (*9*) obtained considerable cortical development in estrogen-treated males, and in *Oryzias,* Yamamoto induced complete transformation in both directions, using either estrogens or androgens (*2*). The case of *Oryzias,* though very interesting, is not discussed here because the embryologic process of gonadal differentiation in *Oryzias* is very different from that in higher vertebrates.

2) Inductive sex reversal has been obtained by natural or experimental parabiosis, and by teratologic or surgical reduction of the genetically epistatic gonadal element (medulla in the case of

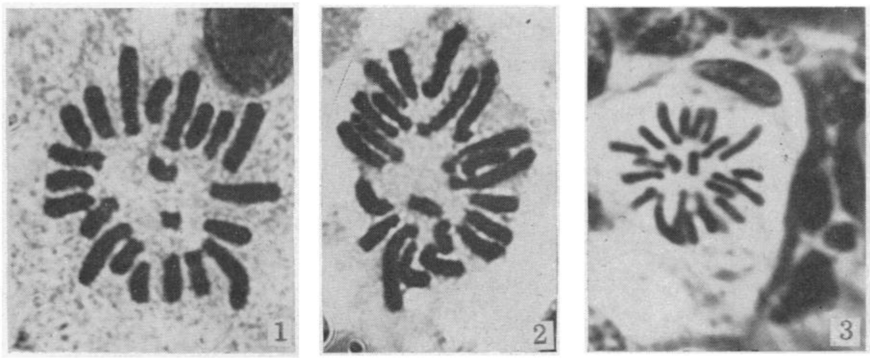

Fig. 1. Spermatogonial metaphase; X and Y chromosomes in the center. Fig. 2. Metaphase of dividing somatic cell of a female animal; two X chromosomes in lower central region. Fig. 3. Ovogonial metaphase with two X chromosomes in center. All figures show the total number of 22 chromosomes, characteristic for the opossum; Figs. 1 and 2 are from squash preparations; Fig. 3 is from a section of the ovary. [All × 1500.]

Bufo, cortex in the female bird). Some completely sex-reversed frogs, toads, hens, and human individuals (pseudomales, typically exhibiting the Klinefelter syndrome) produce mature germ cells—eggs or sperms—of the assumed sex. It will be noted that in ZW- types, the direction of this transformation usually is the reverse of that produced by hormone treatments.

3) Secondary sex characters arise from primordia that are identical in both sexes and in early castrates. The later development of a male or a female organization ordinarily corresponds to the presence of testes or of ovaries, respectively. However, in mammals the female type of gonaducts and external genitalia is also assumed in the absence of gonads, by self-differentiation, regardless of chromosomal constitution (*10*). In castrated amphibians (those most thoroughly investigated were newts), a neutral, ambisexual condition of the gonaducts is maintained (*11*), and in agonadic ducks, the phallic organ and the syrinx spontaneously acquire the male type during the later part of the incubation period. The gonaducts of all early castrates in birds and reptiles maintain an ambisexual condition, with persistence of paired oviducts and mesonephric ducts (*12*). In summary, if self-differentiation of secondary sex characters continues into the phase of sexual dimorphism, it follows the pattern of the homozygous genetic type.

4) Oviducts, in response to treatment with testosterone, become greatly enlarged in *Xenopus,* salamanders, reptiles, and birds, while in frogs (*13*) and Eutheria their growth is only slightly stimulated or is reversed. The refractoriness common to frogs and Eutheria, supports other evidence which suggests relatedness of these taxonomically distant groups. Exceptional among mammals is the opossum, whose oviducts show a strong positive reaction to testosterone treatments (*14*), resembling the response in reptiles (*15*).

The Case of the Opossum

Since there are striking similarities in hormonal reactions between the opossum and the sauropsids, it seemed desirable, in order to assert the reliability of the evidence in support of male heterozygoty for these vertebrates, to reinvestigate the chromosomal condition by modern methods. The study made with the assistance of K. Mikamo confirms the occurrence of a small XY pair of chromosomes in the male (*16*). In spermatogonial divisions, it is usually located in the center of the metaphase plate (Fig. 1). The same position is held by the XX pair in ovogonial and in female somatic mitoses (Figs. 2 and 3).

Discussion and Conclusions

Although it is quite singular and has still not been completely investigated, the case of the opossum proves that physiologic reaction patterns do not issue from, and are not determined by, the genic sex type. The existing correlations are more readily explained on a genealogic basis, according to which the peculiar reaction of the opossum appears to be an old inheritance from a premammalian epoch, when genic sex patterns had not yet evolved. The further inference that the XX-XY pattern originated after the Cretaceous mammals separated from primitive reptiles, but before they branched into marsupials and insectivores, is plausible even though not strictly compelling. (In separate groups the same genetic type may become initiated merely by chance.) In addition to the American opossum, about 30 Australian marsupials are known to have heterochromosomes in the male sex. In view of the early separation of the two faunas, this finding adds new support to the contention that the XX-XY pattern was already established at the inception of mammalian evolution.

The genetic and physiologic similarity of ranid amphibians and Eutheria poses a difficult problem. In some frogs the difference between the sex-determining values of the X and Y chromosomes is very small. This condition establishes a formal proximity to the origin of male digamety (*17*); however, it does not necessarily imply that genetic sex determination in such species is of recent date. For some obscure reason, in fishes and amphibians the sex genes have changed more slowly than in sauropsids and mammals. The same circumstances that kept the lower vertebrates morphologically at a Paleozoic level apparently have also retarded their sexual evolution. In some taxonomic groups protracted periods of arrest must have occurred. Evidence of slow changes in the Y chromosomes of frogs during the postglacial epoch (*18*) favors the view that mutational frequency and evolution depend on particular environmental influences.

For obvious reasons it is difficult to reconstruct the history of the types of physiologic reaction. The sauropsid and salamander type, characterizing also the lower mammals (opossum) and anurans (toads), with its low grade of specificity in hormonal reactions, seems to be the more primitive and hence the more ancient of the two. The eutherian and frog type, with its more discriminating reactions and restricted taxonomic distribution, probably evolved more recently.

In conclusion, the fact that the parallelism between genetic and physiologic patterns of sex determination is not without notable exceptions serves to disprove the supposition that causal relationships exist between genetic digamety and hormonal reaction types (*19*). On the other hand, the distribution of all patterns can be understood on the basis of genealogic relationships. The finding of an exceptional, mixed type in the opossum supports the assumption that the XX-XY type originated before the separation of marsupials and insectivores and before the evolution of the eutherian reaction pattern. The separation of the anuran amphibians into -XY frogs and ZW- toads makes it clear that here the genetic mechanisms of sex differentiation evolved after the anurans (Salientia) had made their appearance (Jurassic period) but before separation into the families of today. When the available evidence is pieced together, it appears that genic sex determination in tetrapod vertebrates originated during the Jurassic period, an estimated 150 million years ago. Since evolution proceeded more slowly in some groups than in others, continued studies in comparative cytogenetics can be expected to furnish a complete recapitulation of the successive steps in the evolution of sex-determining genes and of sex chromosomes (*20*).

Summary

Certain characteristic patterns of physiologic sex determination are not causally linked with types of genic and chromosomal constitution (XX-XY or ZW-ZZ). The observed widespread but not universal parallelism in the distribution of genetic and physiologic patterns among vertebrate groups expresses genealogic relationship. On the basis of this interpretation one may estimate the approximate evolutionary age of the mechanism of genetic sex determination. It is concluded that in all tetrapod vertebrates these mechanisms originated during the Jurassic period. Environmental conditions seem to affect the progress of this evolution.

References and Notes

1. B. Friedman and M. Gordon, *Am. Naturalist* 68, 446 (1934).
2. T. Yamamoto, *Genetics* 40, 406 (1955); *J. Exptl. Zool.* 137, 227 (1958).
3. M. Gordon, *Zoologica* 37, 91 (1952); *Animal Kingdom* 52, 118 (1949).
4. E. Witschi, *Z. Zellforsch. u. mikroskop. Anat.* 1, 523 (1924).
5. T. H. Yosida, *J. Fac. Sci. Sapporo Univ.* 13, 352 (1957).
6. S. Makino, *A Review of the Chromosome Numbers in Animals* (Tokyo, 1956).
7. R. A. Miller, *Anat. Record* 70, 155 (1938); E. Witschi, *Cytologia* (Tokyo) Suppl., 133 (1957).
8. ———, *J. Fac. Sci. Sapporo Univ.* 13, 428 (1957).
9. R. K. Burns, Jr., personal communication.
10. A. Jost, *Recent Progr. in Hormone Research* 8, 379 (1953).
11. J. deBeaumont, *Wilhelm Roux' Arch. Entwicklungsmech. Organ.* 129, 120 (1933).
12. E. Wolff, *Arch. anat. microscop. morphol. exptl.* 39, 426 (1950).
13. L. Gallien, *Bull. biol. France et Belg.* 78, 257 (1944).
14. R. K. Burns, Jr., *J. Morphol.* 65, 497 (1939).
15. P. L. Risley, *J. Exptl. Zool.* 87, 477 (1941); T. R. Forbes, *Anat. Record* 72, 87 (1938).
16. T. S. Painter, *J. Exptl. Zool.* 39, 197 (1924).
17. E. Witschi, *ibid.* 54, 157 (1929).
18. ———, *ibid.* 56, 149 (1930).
19. V. Dantchakoff, *Arch. anat. microscop. morphol. exptl.* 39, 368 (1950); C. Y. Chang, *Anat. Record* 123, 467 (1955).

20. This study was aided by grants from the Rockefeller Foundation, the National Science Foundation, and the National Institutes of Health.

News of Science

International Oceanographic Congress To Meet at United Nations Headquarters

The world's leading oceanographers, perhaps 600 strong, will meet in New York at the end of August for their first international congress. The scientists, representing more than 35 countries, will participate in a broad study of the oceans—of their histories, their inhabitants, their boundaries and basins, and their deep areas. The congress, which will be the first large scientific meeting ever held in the United Nations headquarters, will be in session from 31 August to 12 September. Seven oceanographic vessels, including the Soviet Union's new *Mikhail Lomonosov,* are expected to be on display at New York piers during the 13-day congress.

Three scientific organizations—the AAAS, UNESCO's International Advisory Committee on Marine Sciences, and the Special Committee, on Oceanic Research of the International Council of Scientific Unions—are sponsoring the meeting. Financial support is being provided by 21 governmental and private agencies.

A number of factors lie behind the decision to hold the oceanographic congress. The primary one was the success of the AAAS's 1955 Arid Lands Conference, held at Albuquerque, N.M. This meeting, which was attended by 525 people, showed the value of international gatherings of experts from scientific fields in which, because of the interdisciplinary nature of the field, congresses are seldom or never held. Reports indicated that conservation groups throughout the world found new support for their programs as a result of the arid lands meeting. Because no such congress had been held in oceanography, the officers of the AAAS and the other sponsoring organizations planned the forthcoming meetings.

There have been a number of recent indications of a growth of interest in oceanography. One was the publication early this year of a 12-part report by the committee on oceanography of the National Academy of Sciences–National Research Council. This report, which represented the work of the committee since its establishment in 1957, assessed the current state of oceanography in America and outlined a program for the future. The picture presented was not encouraging; less is known, the committee reported, about the ocean floor than is known about the near side of the moon.

Hearings in the U.S. Congress were held to study the 10-year program called for in the report. This resulted in an increase in interest on the part of the scientific community and the public. Recently *Time* devoted its cover story and six pages of photographs to oceanography and to Columbus Iselin, director of the Woods Hole Oceanographic Institution.

Papers and Events

During the morning sessions of the conference, some 30 papers will be offered by leading oceanographers. Papers to be read on the opening day are "Shape and structure of ocean basins," by Maurice Ewing of the Lamont Geological Observatory; "Forces and processes at work in ocean basins," by Sir Edward Bullard of Cambridge University; and "Stratigraphy of the deep sea," by Edwin Hamilton of the U.S. Navy Electronics Laboratory, San Diego, Calif.