The Present State of the Problem of the «Keimbahn» in the Vertebrates

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Introduction

In the last quarter of the 19th century WEISMANN[2] published his "Keimbahn" theory, a hypothesis, chiefly based on theoretical considerations. This theory, which appeared after DARWIN's theory of descent, opened a new field of research and gave rise to a large number of important investigations. So far the existence of a "Keimbahn" has not completely been proved in any group of the Vertebrates; on the contrary, very various opinions exist concerning its validity. I will try to give a short survey of the present state of the various aspects of this problem in order to stimulate further research in this important field of investigation.

The content of the "Keimbahn" theory of WEISMANN can be given in a few sentences. This general theory of heredity was based on the idea of the continuity of an immortal "Keimplasma" through successive generations. In every ontogeny a part of this plasm, localized in the nucleus, is reserved for the next generation. Originally mingled with the somatic plasm—the latter will form the mortal body of the animal—the "Keimplasma" is gradually segregated during embryonic development by successive cell-divisions, after which the germinal character of the cells containing it becomes more and more expressed. In other words, the germ cells are the carriers of the "Keimplasma".

From investigations on heredity we now know that every cell of an individual has the same genetic properties, the bearers of which are localized for the most part in the nucleus. For this reason WEISMANN's theory cannot be upheld in its original form. The distinction between germ cell and somatic cell must, therefore, be localized in the cytoplasm of the cell. In other words, an immortal "Keimplasma" can only be of cytoplasmatic character.

A modified theory was therefore proposed by NUSSBAUM[3] and others to the effect that there is a continuity of the germ cells themselves during the whole life of the animal. A second idea has, however, been added to this modification of WEISMANN's theory, viz. the necessity of an *early* segregation of the germ cells from the somatic part of the individual. This conception, however, certainly did not emanate from WEISMANN himself.

Further comparative-anatomical points of view concerning the origin of the germ cells in the various groups of the Vertebrates have confused the original general theory of WEISMANN.

In consequence of the fact that the young germ cells have almost the same appearance as the entodermal blastomeres yet another opinion has been introduced: that only an entodermal origin of the primordial germ cells would represent an origin from really omnipotent embryonic cells, whereas a mesodermal origin would mean that these cells have been derived from differentiated somatic cells, which have already lost their embryonic character.

All these views have confused the original problem. Unfortunately, the large number of descriptive investigations made on this problem have not been able to abolish the general confusion, as the methods used have been inadequate for absolute proof of any definite theory. The descriptive methods by which the germ cells are traced back to ever earlier stages of development meet the great difficulty that the differences between the various types of cells also decrease more and more when following the development in reversed direction.

In order to avoid further confusion I will define the modern content of a "Keimbahn" hypothesis as sharply as possible. In every ontogenesis a special cytoplasmic differentiation is already present in the unfertilized egg and probably also in the sperm. During cleavage this special cytoplasm is localized in special blastomeres, which will form the future germ cells of the adult animal. We can, therefore, speak of a continuity of a special "germinal cytoplasm" through successive generations.

In the last two decades a beginning has been made in attacking the problem with experimental methods, which, in my opinion, have really brought the problem nearer to its solution. Only crucial experiments can *prove* a certain theory by excluding other possibilities. This last remark must, however, not be misunderstood: Not an experimental analysis alone, but a combination of experimental and descriptive methods may give us the solution of a biological problem.

Considering the work done on this problem in the various groups of the Vertebrates, it is evident that the most important progress has been made in the Amphibians. The birds come second, whereas our know-

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[2] A. WEISMANN, *Die Continuität des Keimplasmas als Grundlage einer Theorie der Vererbung* (Jena 1885, in-8, 122 p.); *Das Keimplasma*. Eine Theorie der Vererbung (Jena 1892, in-8, XVIII, 626 p.).

[3] M. NUSSBAUM, Arch. mikr. Anat. Bonn *18*, 1 (1880).

ledge of this problem in fishes, reptiles and especially in mammals is still very limited. Therefore, it seems to me that it is best to begin with the present position of the problem in the Amphibians. We must, however, also distinguish between Urodeles and Anura, as will be shown in the following pages. Afterwards we can extend our discussion also to the other groups of Vertebrates.

Critical analysis of the investigations made to elucidate the origin of the germ cells in Vertebrates.

It seems to me highly impracticable to discuss the large number of investigations chronologically. It is, moreover, completely impossible to mention all of them. I will therefore give only the most important facts.

The first general problem I will discuss is *the place and time of origin of the primary primordial germ cells*[1] *in embryonic development.*

The large number of descriptive investigations cannot solve this question. Various opinions still differ very much. An early entodermal as well as an early mesodermal origin of the germ cells have been defended by several authors, and, moreover, the view that there is a pure transformation of differentiated somatic cells into germ cells (WALDEYER[2]) has found many adherents. Except for the thorough histological investigation of BOUNOURE[3], all authors failed to trace the primordial germ cells back to stages earlier than that of the young tail-bud, so that the question of the real origin of the germ cells could not possibly be solved. Here I will only mention the names of ALLEN[4] and WITSCHI[5] on *Rana*, KING[6] on *Bufo* and ABRAMOWICZ[7] and HUMPHREY[8] on *Triturus* and *Amblystoma* respectively.

In my opinion, the histological investigations of BOUNOURE may be of great importance for the final solution of the problem. He was able to follow the displacements and fate of a special "cytoplasme germinal" during the whole development from the fertilized egg up to the adult animal. In *Rana* it is situated at the vegetative pole in the fertilized egg, and is displaced during the first cleavages to the centre of the blastocœl bottom and afterwards during gastrulation and neurulation to the ventro-caudal entoderm. According to BOUNOURE, the separation between somatic and germinal plasmas takes place gradually before the early blastula stage. An internal displacement of this "cytoplasme germinal" from the periphery to the centre of the cell occurs shortly before the initial gastrulation. Afterwards the primordial germ cells characterized by this plasmatic differentiation, migrate through the dorsal entoderm to the definitive germ ridges.

An experimental proof of this conception remains, however, to be given. In my opinion, the few experiments done on the Anura are not convincing. BOUNOURE's irradiation experiments of the upper and lower poles of the uncleaved egg of *Rana*—the lower pole showed a much higher sensitivity to X-rays than the upper pole, while below a certain dose only irradiation of the lower pole gave rise to a strongly decreased number of germ cells—may, for instance, also be explained by assuming a different absorption (dispersion) of the X-rays by the high quantity of pigment present in the upper half of the egg. Also the possibility of a secondary degeneration of the germ cells by unfavourable internal conditions caused by the irradiation may give us an explanation of the phenomenon observed. Finally, an effect on an inductive centre, whereby the determination of the germ cells is interfered with, may be supposed to occur.

Unpublished experiments of my own on *Xenopus lævis*—a large quantity of entodermal blastomeres was removed from the bottom of the blastocœl at the early gastrula stage without influencing the number of primordial germ cells—caution me against the assumption of a general entodermal origin of the p. p. germ cells in the Anura, although the possibility exists that the situation in this species, which is a typical in other respects, may really be different from that in other Anura.

In my opinion also, the experiments of MONROY[1] on *Discoglossus* neurulæ—in contradistinction to the effect of extirpation of the dorsal entoderm, the removal of the ventral entoderm from caudal halves of embryos caused complete sterility—do not give an absolute proof of an entodermal origin of the germ cells in the Anura, as the assumption of a removal of an inductive centre can also explain the facts he obtained.

In the Urodeles the situation of our knowledge is nearly the converse of that in the Anura. Here there is only a small number of not very extensive histological investigations, whereas the experimental analysis has made more important progress.

Summarizing the results of the histological investigations we can say that a purely entodermal (BOUNOURE[2]) as well as a purely mesodermal origin of the p. p. germ cells (HUMPHREY[3]) have been defended for this group.

[1] Cf. P. D. NIEUWKOOP, Arch. Néerl. Zool., Leiden *8*, 58 Terminology (1947).

[2] W. WALDEYER, *Eierstock und Ei.* Ein Beitrag zur Anatomie und Entwicklungsgeschichte der Sexualorgane (Leipzig 1870, in-8, VIII, 174 p.).

[3] L. BOUNOURE, Ann. Sci. nat. Paris, 10e sér. *8*, 201 (1925); *L'origine des cellules reproductrices et le problème de la lignée germinale*, Collection des actualités biologiques, (Gauthiers-Villars, Paris 1939).

[4] B. M. ALLEN, Anat. Anz. Jena *31*, 339 (1907).

[5] E. WITSCHI, Arch. mikr. Anat. Bonn *85*, Abt. II, 9 (1914).

[6] H. D. KING, J. Morph., Philadelphia *19*, 369 (1908).

[7] H. ABRAMOWICZ, Morph. Jb., Leipzig *47*, 593 (1913).

[8] R. R. HUMPHREY, J. Morph., Philadelphia *41*, 1 (1925).

[1] A. MONROY, Arch. ital. Anat. Embriol., Firenze *41*, 368 (1939).

[2] L. BOUNOURE, Ann. Sci. nat. Paris, 10e sér. *8*, 201 (1925).

[3] R. R. HUMPHREY, J. Morph., Philadelphia *41*, 1 (1925).

From experiments HUMPHREY[1] found that in *Amblystoma* the germ cells are localized in the lateral mesoderm from the early tail-bud stage. The experiment of SEMBRAT[2]—removal of a large group of blastomeres from the bottom of the blastocœl in *Tr. alpestris* and *Amblystoma mexicanum* caused a considerable decrease in the number of germ cells—has been repeated by the author with a completely contrary result[3].

Two further experimental series prove that the germ cells have quite another origin in the Urodeles, namely from the lateral mesoderm. The heteroplastic transplantation of the whole entoderm between early neurulæ of *Tr. alpestris*, *Tr. cristatus* and *Amblystoma mexicanum* showed that all the germ cells present had originated from the ecto-mesodermal germ-layers[4]. The converse experiment, in which the ventro-lateral mesoderm (presumptive lateral plate and nephrogenic cord cell-material) was grafted heteroplastically between *Tr. alpestris* and *cristatus* at the yolk-plug stage, demonstrated that the germ cells had been quantitatively furnished by the lateral mesoderm and, moreover, that they could differentiate from lateral plate tissue alone[5]. This series finally showed that the presumptive germ cells had probably been regularly scattered among the whole presumptive lateral plate mesoderm[6,7]. New experiments are, however, needed to solve the last question definitively.

Summarizing we see from all these experiments that the primordial germ cells have a mesodermal origin in the Urodeles, whereas they derive probably from the central entoderm in the Anura.

Are the presumptive germ cells specific elements, or can they be formed from ordinary lateral plate cells?

In the Anura the presumptive primordial germ cells are characterized by the presence of a special "cytoplasme germinal" which fact pleads in favour of the first opinion.

The following arguments support the same opinion in the Urodeles. Here a removal of the presumptive lateral plate mesoderm at the early neurula stage caused absolute sterility, notwithstanding that the deficiency in the lateral mesoderm regulated for the greater part from adjacent dorsal mesoderm. Under the experimental conditions no formation of germ cells took place from this regulated lateral plate tissue[8]. A graft of presumptive *cranial* lateral plate mesoderm (outside the germinal region) of *Tr. cristatus* in the place of more caudal lateral plate mesoderm of *Tr. alpestris* formed no germ cells[1]. Finally, the number of germ cells in normal and also in experimental animals never surpasses a certain limit—removal or implantation of the notochord[2], the pronephros and Wolffian duct, the yolk entoderm, etc., did not influence the number of germ cells[3].

The above-mentioned arguments allow, however, only a preliminary answer to this important question, namely that the p. p. germ cells *probably* represent specific elements. An infallible proof still needs many more crucial experiments.

A specificity of the germ cells has still another consequence. Many authors defend a formation of germ cells from somatic cells (secondary primordial germ cells[4]), during various phases of development. This opinion is not compatible, however, with a specific character of the germ cells.

The exclusively histological arguments of the above-mentioned authors were critisized in 1914 by WITSCHI[5], who rejected all of them.

My own experiments point in the same direction. The absolute sterility of the larvæ (up to stage 42/43, GLAESNER[6]) after removal of the presumptive lateral plate mesoderm at the early neurula stage[7] argue against a secondary formation of germ cells from somatic (genital ridge) cells. The possible necessity of a preceding stimulus from the primary primordial germ cells can also be rejected, as in some animals of the series, in which a heteroplastic transplantation of the ventro-lateral mesoderm had been performed, a part of a genital ridge consisting of cell material of the "donor species", contained only germ cells of the "host species"[8].

These experiments prove that a secondary formation of germ cells (from somatic cells) does not take place during early development, anyhow not before stage 42/43 (GLAESNER).

The experiments on castration—made in adult animals by MORGAN and MACNAB[9] and by ADAMS and KIRKWOOD[10]—which caused sterility after complete

[1] R. R. HUMPHREY, J. Exp. Zool., Philadelphia *49*, 363 (1927); Anat. Rec. Philadelphia *35*, 40 (Abstract) (1927); Anat. Rec. Philadelphia *40*, 67 (1928); Anat. Rec., Philadelphia *42*, 301 (Abstr.) (1929).

[2] K. SEMBRAT, C. R. Soc. Biol., Paris *115*, 639 (1934).

[3] P. D. NIEUWKOOP, Arch. Néerl. Zool., Leiden *8*, 70 (1947).

[4] Id., ib. *8*, 122 (1947).

[5] Id., ib. *8*, 129 (1947).

[6] One qualification must be made. The germ cells originated only from a cranio-caudally restricted region of the lateral plate mesoderm, called by me the germinal region[9].

[7] P. D. NIEUWKOOP, Arch. Néerl. Zool., Leiden *8*, 144 (1947).

[8] Id., ib. *8*, 102 (1947).

[9] Id., ib. *8*, 58 (1947).

[1] P. D. NIEUWKOOP, Arch. Néerl. Zool., Leiden *8*, 144 (1947).

[2] The implantation of a supernumerary notochord prevented the differentiation of a part of the germ cells in some cases.

[3] P. D. NIEUWKOOP, Arch. Néerl. Zool., Leiden *8*, 70, 153, 160 (1947).

[4] Cf. id., ib. *8*, 58, Terminology (1947).

[5] E. WITSCHI, Arch. mikr. Anat. Bonn *85*, Abt. II, 9 (1914).

[6] L. GLAESNER, *Keibels Normentafel zur Entwicklungsgeschichte der Wirbeltiere*, Heft 14. *Normentafeln zur Entwicklungsgeschichte des gemeinen Wassermolchs (Molge vulgaris)* (Jena 1925).

[7] P. D. NIEUWKOOP, Arch. Néerl. Zool., Leiden *8*, 102 (1947).

[8] Id., ib. *8*, 144 and 146 (1947).

[9] A. H. MORGAN and A. MACNAB, Anat. Rec., Philadelphia *34*, 128 (Abstract) (1926).

[10] A. E. ADAMS and E. S. KIRKWOOD, Anat. Rec. Philadelphia *41*, 35 (Abstract) (1928–9).

removal of the gonads, indicate that a formation of germ cells from other elements than the primordial germ cells probably also does not exist in adult animals.

The missing links in the argument demand, however, further investigations in order to exclude the possibility which still exists of a formation of secondary germ cells at intermediate stages of development.

The next problem, also connected with the specificity of the germ cells, is *whether there is a complete self-differentiation or a dependent development of the presumptive germ cells.*

From two experimental series it has become evident that the presumptive germ cells present in the lateral mesoderm of the young Urodele gastrula need a more or less specific stimulus from the dorso-caudal entoderm for their final differentiation. Removal of a part of this entoderm caused a considerable decrease in the number of germ cells[1] and, moreover, their degree of cytological differentiation was lowered[2]. The removal of the complete entoderm at the early neurula stage provides the strongest argument for this opinion. In the entoderm-free larvæ germ cells have differentiated from the presumptive lateral plate mesoderm only in the *cranial* part of the germinal region. Only this part of the mesoderm has come into contact with the dorso-caudal entoderm. The *caudal* lateral plate mesoderm, which invaginated after the removal of the entoderm (by the post-gastrulation movements) showed no differentiation of germ cells[3].

A rather high specificity of this action of the dorso-caudal entoderm may be inferred from the fact that it cannot be replaced by other inductive stimuli, which normally occur in the same zone of the trunk, e. g. the inductive influence on the differentiation of the dorsal, lateral and ventral mesoderm, emanating from the notochord[4], and the influence of the Wolffian duct on the differentiation of the mesonephros rudiments[5]. Finally, a reversed implantation of the whole ecto-mesoderm into the ventral side of a second neurula, by which in respect to the grafted embryonic rudiment cranial entoderm took the place of the caudal entoderm, also prevented the differentiation of germ cells in the graft[6]. Further experiments are needed, however, to support this argument.

All these experiments point to the necessity of a rather specific influence of the dorso-caudal entoderm on the final differentiation of the germ cells in the Urodeles.

A final question I will discuss here is *the character of the presumptive germ cells before this action of the dorso-caudal entoderm.*

The results of heteroplastic transplantation of the ventro-lateral mesoderm at the early yolk-plug stage indicate that the presumptive germ cells already have a more or less specific character *before* the action of the dorso-caudal entoderm, which action does not take place earlier than the neurula stage. From the experiments in which the whole entoderm was removed at the early neurula stage it is, moreover, evident that a very short contact between the presumptive germ cells and the dorso-caudal entoderm suffices to ensure their final differentiation[1]. From these data we may conclude that the character of the presumptive primordial germ cells probably represents a kind of "predetermination".

One is very tempted to combine together the results obtained in the two groups of the Amphibians. I must, however, seriously warn against attaching too much weight to conclusions formed in this way, as we have already seen how important the differences may be between Urodeles and Anura. The reason I nevertheless attempt to combine the results is evident, when one realizes the important perspectives for further investigation which are opened by the co-ordination of these facts.

The mesodermal origin of the germ cells in the Urodeles and their probable entodermal origin in the Anura indicate that *place of origin* is not of primary importance, and may vary greatly even in related groups of Vertebrates. From the beginning the germ cells, which are already recognizable, or the presence of which is already experimentally demonstrable at early stages of development, probably represent more or less specific elements. This opinion was defended by HUMPHREY as early as 1925, who supposed that "the p. p. germ cells are specific elements, which do not belong to one of the germ layers".

The experimental analysis in the Urodeles has given some arguments in favour of a predetermined state of the presumptive germ cells before the action of the dorso-caudal entoderm. Their special cytoplasmic differentiation, found in the Anura, suggests that this predetermination may be based on the presence of a special "cytoplasme germinal" in these cells, which would mean a special chemo-differentiation of their cytoplasm. The segregation of the "cytoplasme germinal" of the uncleaved egg into particular cells during cleavage would give these cells a special "competence", which enables them to react to specific inductive stimuli by a final differentiation into real germ cells. Further, the topographical

[1] As the heteroplastic transplantation experiments prove, the germ cells originate quantitatively from the presumptive lateral plate mesoderm. A possible explanation by assuming a partial origin of the germ cells from the entoderm cannot, therefore, be upheld.

[2] P. D. NIEUWKOOP, Arch. Néerl. Zool., Leiden *8*, 80 (1947).

[3] Id., ib. *8*, 114 (1947).

[4] The notochord can even suppress the differentiation of the germ cells after a normal stimulation from the dorso-caudal entoderm.

[5] P. D. NIEUWKOOP, Arch. Néerl. Zool., Leiden *8*, 153 (1947); Exper. *4*, 391 (1948).

[6] Id., ib. *8*, 186 (1947).

[1] P. D. NIEUWKOOP, Arch. Néerl. Zool., Leiden *8*, 118, 150 (1947).

displacement of this "cytoplasme germinal" within the presumptive germ cell, described by BOUNOURE, in the Anura, cf. p. 309, may represent the first visible effect of the inductive action of the dorso-caudal entoderm on the presumptive germ cells, found in the Urodeles. However, the two phenomena do not completely coincide in time in the two groups, so that this suggestion certainly needs further investigation.

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The investigations on the other groups of the Vertebrates throw little new light upon the problem of origin and character of the germ cells. The results of purely histological investigations in fishes, reptiles, and mammals so strongly contradict one another that the sole suggestion in common which may be given, is the relatively early segregation of the p. p. germ cells from the other cells of the body in several fishes, reptiles, and even in some mammals. Contrary opinions are, however, also defended.

The experimental investigations of BENOIT[1], DANTSCHAKOFF[2], WILLIER[3], and GOLDSMITH[4] support the hypothesis of a "Keimbahn" in birds. The removal of the entodermal, extra-embryonic germinal crescent by ultraviolet radiation (BENOIT) or by cauterization (DANTSCHAKOFF) caused complete sterility, while grafts of the sterile gonad-forming area, transplanted to the chorio-allantoic membrane, only developed into sterile gonads (WILLIER, GOLDSMITH). In the converse experiment, in which the gonad-forming area, while still sterile, was removed, normal gonads were formed cranially to the original wound. These gonads were reared on the chorio-allantoic membrane for as long as 15 days, and showed the formation of completely differentiated gonads.

Although there are still many points of doubt and several new data have already modified and complicated the original theory of WEISMANN, we can say that the hypothesis of a "Keimbahn" has been strongly supported by facts in the Amphibians and partially also in birds, while the hypothesis may perhaps also have validity in the other groups of the Vertebrates. We may therefore pronounce the hope that this important hypothesis will be proved in the near future.

I will finish this short survey of our knowledge concerning this general biological problem with the hope and trust that a reading of this review may stimulate further histological and experimental work.

[1] J. BENOIT, C. R. Soc. Biol. Paris *104*, 1329 (1930); Proc. 2nd int. Congress for Sex Research, 162 (1930).

[2] W. DANTSCHAKOFF, Verh. anat. Ges. Jena *35* (1929); Z. Zellf. mikr. Anat., Berlin *13*, 448 (1931); *14*, 376 (1932); *15*, 581 (1932); C. R. Soc. Biol. Paris *109*, 845 (1932); Z. Zellf. mikr. Anat. Berlin *18*, 56 (1933); C. R. Soc. Biol., Paris *113*, 874 (1933). – W. DANTSCHAKOFF, W. DANTSCHAKOFF JR., and L. BERESKINA, Z. Zellf. mikr. Anat., Berlin *14*, 323 (1932).

[3] B. H. WILLIER, Anat. Rec., Philadelphia *34*, 158 (1926) (Abstract); Roux Arch., Berlin *130*, 616 (1933), Anat. Rec., Philadelphia *70*, 89 (1937).

[4] J. B. GOLDSMITH, J. Morph., Philadelphia *58*, 537 (1935).

Zusammenfassung

Die «Keimbahn»-Hypothese WEISMANNS muß entsprechend dem heutigen Stand der Vererbungslehre in verschiedener Hinsicht geändert werden.

Die deskriptiven Untersuchungen an den Anuren deuten auf einen entodermalen Ursprung der Urgeschlechtszellen hin. Die präsumtiven Urgeschlechtszellen sind durch den Besitz eines spezifischen Plasmas charakterisiert. Dieses Geschlechtsplasma verlagert sich während der Entwicklung von der Zelloberfläche zu einer mehr zentralen Stelle hin. Die experimentellen Befunde sind nicht sehr zahlreich; sie können diese Auffassung nur teilweise stützen.

Bei den Urodelen sind die deskriptiven Untersuchungen sehr widerspruchsvoll. Die experimentellen Daten weisen mit großer Wahrscheinlichkeit auf einen mesodermalen Ursprung der Urgeschlechtszellen aus dem Seitenplattenmaterial hin. Die Urgeschlechtszellen repräsentieren vermutlich spezifische Zellelemente, die schon vom Beginn der Entwicklung an eine bestimmte Fähigkeit zur Geschlechtszellentwicklung besitzen. Die endgültige Differenzierung wird durch einen mehr oder weniger spezifischen Einfluß des kaudalen Entoderms bewirkt. Die definitiven Geschlechtszellen entwickeln sich wahrscheinlich quantitativ aus diesen primären Urgeschlechtszellen.

Die Synthese der Befunde bei Anuren und Urodelen darf nur mit großem Vorbehalt als Arbeitshypothese gegeben werden: Die Ursprungsstellen der Geschlechtszellen dürften bei den einzelnen Gruppen der Wirbeltiere stark differieren. Die Bildung eines Geschlechtsplasmas, als erste Chemodifferenzierung, verursacht die Fähigkeit zur Geschlechtszelldifferenzierung. Die endgültige Determination durch das kaudale Entoderm stimmt mit einer Verlagerung des Geschlechtsplasmas in der Zelle überein.

Die Untersuchungen bei andern Wirbeltiergruppen deuten ebenfalls auf eine frühzeitige Sonderung der präsumtiven Urgeschlechtszellen hin. Die experimentellen Befunde unterstützen bei Vögeln die «Keimbahn»-Hypothese in ihrer neueren Form. Die Urgeschlechtszellen sollen hier von entodermalem Ursprung sein.