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Helene Zalpeter.

The Isopotency of Generally Homologous Parts of the Body. Investigations upon the Homeosis Phenomena in the Crayfish.

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By

Helene Zalpeter

With 16 figures in the text

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(From the Institute of Comparative Anatomy and Experimental Zoology of the Latvian University in Riga. Director: N. G. LEBEDINSKY.)

THE ISOPOTENCY OF GENERALLY HOMOLOGOUS PARTS OF THE BODY.

INVESTIGATIONS UPON THE HOMEOSIS PHENOMENA IN THE CRAYFISH.

By

HELENE ZALPETER.

With 16 figures in the text.

(Eingegangen am 7. Juni 1927.)

In his recent work N. G. LEBEDINSKY (30, 31, 32) claims that generally homologous parts of the body are developmentally isopotent. One of the basis of the theory of isopotency is homeosis (W. BATESON), particularly well expressed in crustaceans. Homeosis is the phenomenon in arthropodes, when often instead of a certain appendage or organ a structure developes with characteristics of an organ of another metamer.

The object of my work was to trace the phenomena of homeosis in animals of one species not only in one direction, but also in the reverse direction, i. e. to investigate the possibilities of homeotic heteromorphosis in caudal-cranial and cranial-caudal directions, and thus to prove complete isopotency of such general homologous organs as appendages of arthropodes. According to recorded data upon this question the ten-leged crayfishes seemed to be the most available material. As far as now homeosis in crustaceans has been studied principally upon specimens occasionally found in museums.

I began the investigations in the spring of 1924 at the suggestion of Prof. N. G. LEBEDINSKY and worked under his direction and supervision. At the very beginning I will acknowledge my indebtedness to Prof. N. G. LEBEDINSKY for his aid and suggestions.

I collected material during two summers — 1924 and 1926 at the crayfish-export-trade-firms in Riga „*Vežu Centrs*“ and „*Sabiedriba Vieniba*“, to whom I owe a great deal of thanks for their cordiality and welcome. The firms had collected the crayfishes in Latvia (Livlandia and Latgalia). The greatest quantity of the investigated crayfishes belong to the species *Potamobius astacus* L. that is widely spread in Latvia.

I did not make it a special object to determin whether in the material were specimens of the species *Potamobius leptodactylus* Eschz. found here comparatively rarely. My observations extended over more than 17 000 crayfishes. Among the 12 thousands I examined during the first summer I found two crayfishes with homeotically transformed appendages, and three with other abnormalities. And among the five thousands examined during the last summer there were three with homeotically

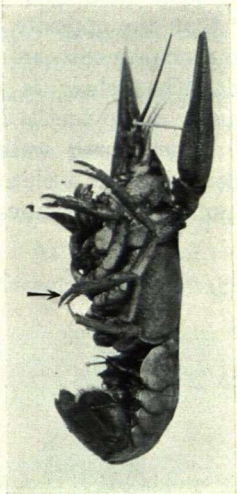

Fig. 1. Female No. 1, with the fourth, left walking leg homeotically transformed into a cheliped.

Fig. 2. The same individual as on fig. 1. The homeotically transformed leg magnified.

transformed appendages and eight with supernumerary or no genital pores. During the observations made in the first summer I paid no attention to the genital pores. The technical part of my work consisted in the dissection of crayfishes with abnormal genital pores, in order to investigate the structure of their internal genital organs.

I. Homeosis Phenomena.

1. Descriptive Part.

In the following description I distinguish upon Thorax, besides maxillipedes, five pairs of walking legs. As it is known, the very fore pair of walking legs is supplied with especially large and powerful chele, and the two following pairs have cheles of moderate size, whereas the hind pairs terminate in smaller clutches. In order to give an idea about the size of the examined animals I shall point out the measure of the largest of both fore cheles.

A. Homeosis Phenomena on Appendages.

No. 1. Female. Fig. 1 and 2. The right large chele measures 4 cm in length. The left, fourth walking leg has instead of a clutch a normally developed chele. The index of propodite is a little shorter than those of the two preceeding legs. The chele is covered with normally dense tactile hairs.

No. 2. Female. Fig. 3 and 4. The right large chele measures 4,2 cm in length. The left, fourth walking leg has a chele instead of a clutch. The index of its propodite is considerably shorter and thinner than that of the preceeding legs. This leg is smaller than the opposite leg. Its carpopodite and propodite are remarkably short. The chele is covered with normally dense tactile hairs.

No. 3. The fourth walking leg has a chele instead of a clutch.

Unfortunately, the removal of the

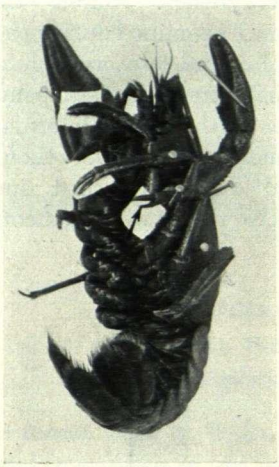

Fig. 3. Female No. 2, with the fourth, left walking leg homeotically transformed into a cheliped.

Fig. 4. The same individual as on fig. 3. The homeotically transformed leg magnified.

Institute to another building resulted in the loss of the crayfish and therefore further description concerning it cannot be given.

No. 4. Male. Fig. 5 and 6. The right, large chele measures 5,2 cm in length. The third, right walking leg does not terminate in a chele as it is usually the case, but in a clutch. The structure of this dactylopodite differs from the usual structure of dactylopodites of the third and the following appendages in that respect, that in transverse section

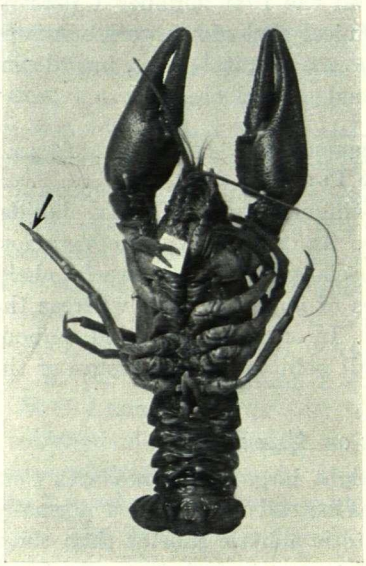

Fig. 5. Male No. 4, with the third, right cheliped homeotically transformed into a walking leg with a clutch.

Fig. 6. The same individual as on fig. 5. The homeotically transformed leg magnified. From below.

it is roundish and is not covered with hairs so densely as usual. The end is obtuse. The propodite has at both sides of its base two wee buds. Otherwise it is normally developed.

No. 5. Female. Fig. 7 and 8. The right chele is torn off. The only left chele measures 4 cm in length. The third left walking leg has a clutch instead of a chele. This dactylopodite is roundish, shorter than a normal right one and its surface is tubercular, with scanty hairs. The propodite is thinner and shorter than that of a normal leg, by half.

B. Homeosis Phenomena in the Base of Extremities.

No. 6. Female. Fig. 9. The right large chele measures 4,3 cm in length. At the base of the right, fourth walking leg (i. e. according to the characteristic arrangments on the third pair) there is a supernumerary genital pore, but smaller than a normal one nearly by half. The form of the pore is normally oval. But the third pair of walking legs is as usually supplied with oviducts, whereas the supernumerary genital pore of the fourth pair is wanting same.

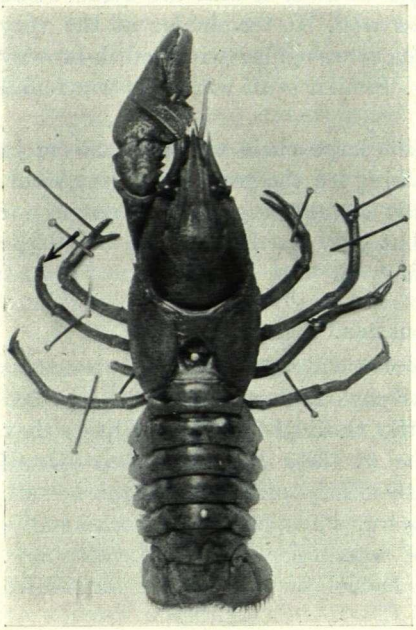

Fig. 7. Female No. 5 with the third, left cheliped homeotically transformed into a walking leg with a clutch.

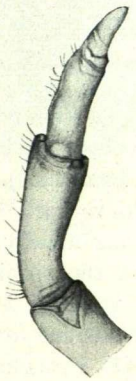

Fig. 8. The same individual as on fig. 7. The homeotically transformed leg magnified.

No. 7. Female. The right large chele measures 3,9 cm in length. Here we observe a supernumerary genital pore in the fourth walking leg. Its location is normal, i. e. such as of the third pair. But it is smaller than a normal pore by half. Shape — oval. Oviduct is absent. Structure of other parts of the body is normal.

No. 8, 9, 10, 11. Females. Besides the two females with supernumer-

ary genital pores described above, I found still four females with supernumerary genital pores in the fourth walking leg. The supernumerary pores were found equally often on one as well as on the other side. On dissection of the two specimens, it became apparent that here too the supernumerary pores were not supplied with oviducts. The other two specimens had not been conserved, therefore no statement concerning their anatomy can be given.

No. 12. Female. Fig. 10. The right, large chele measures 6 cm in length. At the base of the third, right walking leg the genital pore is absent. But a tubercle covered with a tuft of hair projects at the place where it should have been. There is also no common backing in on the coxopodite at the base of the leg, as it is the case with the first four pairs of legs.

On dissection of the animal it was to be seen that the oviduct had been developed on the right side as well. It terminates at the very base of the leg. Either of the oviducts was filled with redish-browny stuff containing eggs of same colour. Similar stuff with eggs was found here and there in the ovary.

No. 13. Male. Fig. 11. The right, large chele measures 4,5 cm in length. At the base of the fifth walking leg the genital pore is absent. In other respects the leg is normally developed. Vas deferens is not developed altogether on this side, but only on the left side where the peculiar genital pore is to be found.

2. Discussion.

As far as now much cases of homeotically transformed appendages have been observed in crabs *Cancer pagurus* L. (Th. Cornish, W. Bateson, H. Przibram). Instead of the third jaw-leg (maxilliped) they have well developed chelipeds. One of them had only three distall segments homeotically transformed, the other — five, and the third — all.

Crabs of the species *Cancer pagurus* have, although occasionally, a kind of walking legs instead of maxillipeds (H. Przibram [26]). Similar phenomena of regeneration have been observed in long-tailed crayfishes (H. Przibram [26]).

A particularly remarkable case of homeosis in *Carcinus maenas* has been described by A. Bethe (11) 1896. The individual has at the sixth segment of abdomen a normally developed right walking leg, which is usually not the case.

The ordinary regeneration of the left, and the repeated regeneration of the right, first cheliped in *Cambarus propinquus* resulted in a left cheliped, and a right swimmeret (I. D. Haseman [22]). Supernumerary genital pores as homeotic phenomena are often found in *Decapoda*. They may be observed relatively often in *Astacidae* too. There were genital

pores in *Nephrops norvegicus*, 1) in the fourth pair, 2) in the fourth pair, and third, right walking leg, 3) in the fourth pair and third, left walking leg. A case has been recorded where even in females of *Potamobius* and *Cambarus propinquus* the genital pore is developed in the fifth and fourth pair of walking legs, and not in the third one, and the genital pore of male *Nephrops* is situated in the second pair of walking legs.

A. HASE (28) describes a male *P. leptodactylus* with supernumerary genital pores in the fourth pair of walking legs and in one of the third pair. There are also cases of reduction of one of the genital pores, but they are comparatively rare. One of such cases is described by H. PRELL (29) in which a female *Astacus leptodactylus* has a developed genital pore only on the right side. Oviducts of this crayfish are developed on both sides equally.

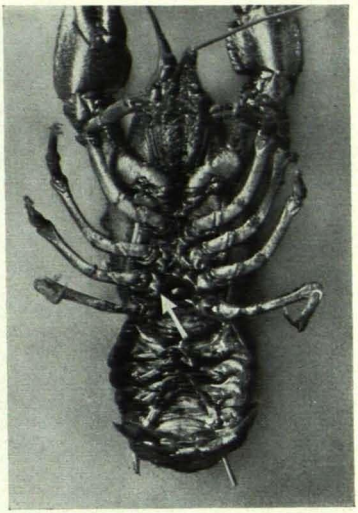

Fig. 9. Female No. 6 with a supernumerary genital pore in the fourth, right walking leg.

From the above-stated cases of homeosis, where on a certain segment one organ, characteristic for one of the neighbouring segments developes instead of another, it is evident that these organs are liable to develop characteristics of other homologous organs.

As it appears by above mentioned facts, a normally developed clutch is liable to develop into a chele, a cheliped is apt to produce a clutch, legs void of genital pores have the potency to reproduce such, and a leg possessing a genital pore may develop into a leg wanting same; consequently the fact of isopotency of appendages is asserted.

Further we observed that the abdomenal segment has the potency to develop a walking leg (*Carcinus*). Jaw-legs develop into chelipeds and occasionally even into walking legs (*Cancer*). At a repeated regeneration the first chele may turn into swimmerets, i. e. abdomenal appendage (*Cambarus*). Although no reverse cases of heteromorphosis are known yet, still this is enough to prove once more, though partly, the availableness of isopotency.

A view is maintained (26) that a highly differentiated organ cannot develop instead of a less differentiated one and that cases of homeosis occur in the posterior direction.

Thus it appears that a cheliped cannot develop instead of a clutch,

the former being of course the highly developed organ. And a walking leg cannot develop instead of a swimmeret and so on.

Yet the three specimens I found, with chelipeds instead of clutches serve as an example of a reverse phenomenon, i. e. they prove that a highly differentiated organ can develop instead of a less differentiated one. The last case being even more frequent than the first in the described specimens. Among the seventeen thousands of examined crayfishes I found three cases of a lower organisation having turned into a higher organisation and only two reverse cases. Besides a substitutive chele in the place of a clutch is developed normally, whereas a substitu-

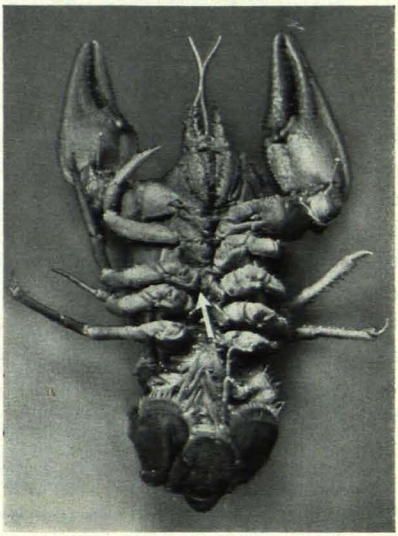

Fig. 10. Female No. 12, devoid of the genital pore in the third, right walking leg.

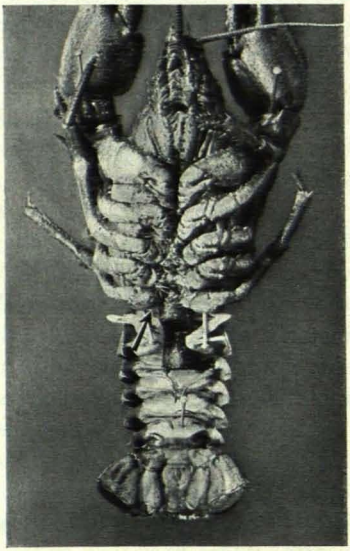

Fig. 11. Male No. 13, devoid of the genital pore in the fifth, right walking leg.

tive clutch instead of a chele is rather defficient in its structure. A case of a more differentiated organ in the place of a less differentiated one has been recorded already. That is *Carcinus maenas* with a walking leg in the abdomen. This phenomenon interpreted by A. BETHE (11) as homeosis has later been disputed and presumptively commented as a case of autotransplantation during embryonal development. The feebleness of the last view has been thouroughly discussed by N. G. LEBEDINSKY (33) and he too in compliance with the author who first described this phenomenon refers it to the cases of homeosis.

All these cases — four of them with a highly differentiated organ instead of a less differentiated one, and the relatively frequent cases of less differentiated organs instead of highly differentiated ones, prove

that these organs possess besides the power to develop typically a latent potency of developing structures of organs prior and posterior of them. This serves as the best illustration for the theory of isopotency of generally homologous organs.

II. Superregenerations and other Abnormalities.

Investigating the vast material I happened to come across abnormalities that are of no essential importance for the aim of my work, but which nevertheless I describe at the end of my article as phenomena of general scientific interest.

No. 14. Female. Fig. 12, 13. The right large chele measures 6,5 cm

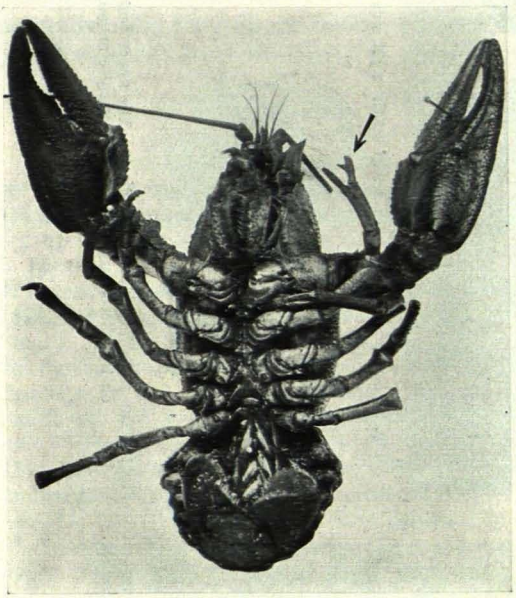

Fig. 12.

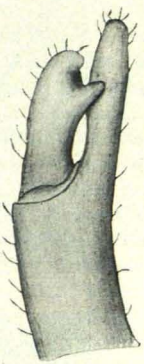

Fig. 13.

Fig. 12. Female No. 14 with a bud on the dactylopodite of the chele of the second left walking leg.
Fig. 13. The same individual as on fig. 12. The bud on the dactylopodite of the chele magnified.

in length. A bud projects from the middle of the dactylopodite of the left walking leg. The dactylopodite is rather thick and the more so towards the distal end. The side facing propodite is flat. The other side is shorter of its normal length. The projecting bud is small and pointed. As the bud is very small it is difficult to judge about its significance. The propodite is developed normally, like other parts of the leg.

No. 15. Male. Fig. 14. The right, large chele measures 4 cm in length. The chele of the left, second walking leg is bent in the medial direction. At the lateral side of the propodite is a knob, bearing two buds, which reminds at first sight an independent chele. But a careful examination shows that the buds on the knob are mobile. It is difficult to state whether both buds are to be regarded as dactylopodites, be-

cause their shape is not sufficiently typical. They differ from normal dactylopodites because of a roundish form at transverse section and being sparingly covered with hairs.

The inwardly bent chele is of a normal structure.

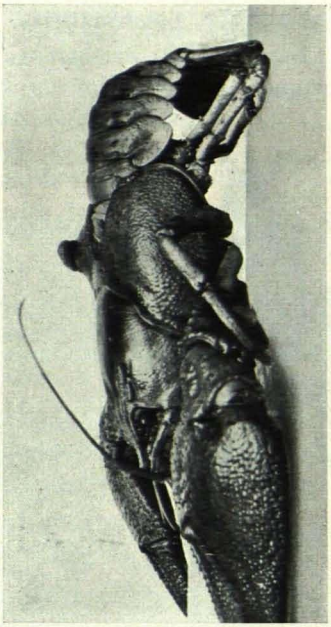

Fig. 15. Specimen No. 16 with a bud on the right side of thorax.

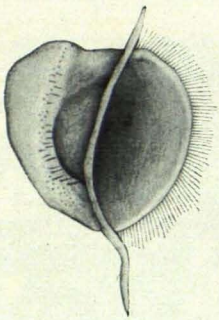

Fig. 16. The same individual as on fig. 15. The upper and the under bud on the sliced part of the branchiostegite magnified.

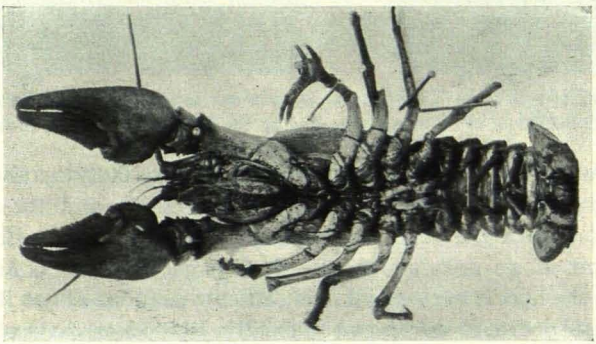

Fig. 14. Male No. 15. Double-structure of the chele of the second left walking leg.

No. 16. Fig. 15 and 16. This crayfish has, in the middle of the right side of thorax (branchiostegite) a tongue-like bud turned to the base, being about a centimetre in size. From above as well as from below it is completely covered with hairs, which are particularly thick on the rounded fringe of the bud.

On taking of the shell another similar bud is found on the inside just below the external bud. Yet the first differs from the latter in being thinner and having thick dark hairs only on the fringe. In order to investigate whether the layers of chitine in the buds are developed normally, I prepared celloidine sections of either of the buds and of the normal shell. For decalcination and in order to remove the stain I successfully applied „*Diaphanol*" of the firm LEITZ. The sections (20 μ thick) were dyed with iron haematoxylin and picric acid. Microscopical examinations showed that the layers of either of the buds are developed normally: the two upper layers are succeeded by a pigment layer. There was also great similarity in the structure of the hairs.

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