



TITLE:

Studies on the Double Monsters in the Newt, *Triturus pyrrhogaster*, with Special Reference to the Origin of Their Development

AUTHOR(S):

Ichikawa, Mamori

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Studies on the Double Monsters in the Newt,
Triturus pyrrhogaster, with Special
Reference to the Origin of Their
Development*

By

Mamori ICHIKAWA

(Konan High School, near Kobe)**

With 34 text-figures

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Introduction

In Amphibians double monsters are indeed not of rare occurrence in nature. The instances have occasionally been given by previous authors, such as BORN (1881), KLAUSSNER (1890), LOYEZ (1897), GROCHMALICKI (1909),

* This work was carried out in the Zoological Institute, Kyoto Imperial University, under the direction of Prof. Yô K. OKADA.

** Present address is again the Zool. Inst., Kyoto Imp. University.

JOSEPHY (1913), KAUFMAN (1913), LEBEDINSKY (1923), POLITZER (1926), OYAMA (1927-'29) etc. However, most of these reports concerned with the morphology of the monsters, and only a few of them presented an explanation of their origin, mostly based on the knowledge of rather old embryology. Since SPEMANN (1903) obtained experimentally a double or two embryos by the imperfect or perfect isolation of a *Triton* egg on the median plane, the mechanism of the double formation in Amphibians was much investigated by the same method of ligation [SPEMANN and FALKENBERG (1919), RUUD and SPEMANN (1922), RUUD (1925), SPEMANN (1928), SCHMIDT (1933) etc.], by fusion of two eggs [MANGOLD (1920), MANGOLD and SEIDEL (1927)] or of two gastrula-halves [SPEMANN (1918), WESSEL (1926), KOETHER (1927)] as well as by means of transplantation of the blastoporic lip, viz. the organiser [SPEMANN and H. MANGOLD (1924), his associates and others]. Since then, the term "organiser" here applied to the upper lip of the blastopore has come to be used by some embryologists in much wider sense, and it was extended to all inductors including the tissues and substances, organic and inorganic, that evocate the formation of an embryonic body on the host derm, under their influences. The development of some organs is further proved to be dependent on the presence of the so-called secondary or tertiary organiser. For example, the lens is induced by the optic cup [SPEMANN (1901) etc.], the nose by the forebrain [ZWILLING (1934), RAVEN (1935), KAWAKAMI (1938)], the ear by the medulla oblongata [STONE (1931), GUARESCHI (1935), ALBAUM and NESTLER (1937)], and the gill by the branchial endoderm [SEVERINGHAUS (1930), ICHIKAWA (1934-'38), etc.]. The ear is now said to be also induced by the underlying mesoderm [ZWILLING (1941)].

With such knowledge of the experimental embryology, the present author has intended to study the duplicity and other monstrosities found in a newt *Triturus pyrrhogaster*, hoping to throw light on their origin. For this purpose, he examined 34 specimens which were collected by himself and other members of the Zoological Institute of Kyoto Imperial University from 1932 to 1938.

Here the author wishes to express his hearty thanks to Prof. Yô K. OKADA for his kind encouragement and helpful criticisms, and thanks are also due to other members of the Institute for their kindness of always paying attention to such monsters and putting aside them from their experimental material at his disposal.

Material

Specimens are classified into 4 groups according to the degree and mode of duplicity. Naturally this classification is arbitrary for the convenience' sake, and there are transitional types from one to another group.

The first group contains 8 anadidymi, showing division of head upto the ocular level in the external appearance. In sections there occurs at most an extra (median) ear between two heads.

The second group contains 7 anadidymi, doubling extending beyond the cervical region to the branchial level, and both heads lie symmetrically side by side to the median plane which passes through the middle of the single posterior part of the body.

The third group contains 5 specimens in which doubling extends upto the tail end. Two heads are rather twisted from the original median plane so as to face each other on the ventral side, especially in the anterior part of the body. Some of them are anakatadidymous, doubling taking place both at the anterior and posterior ends of the body.

The fourth group contains 14 anadidymi, showing asymmetrical bifurcation, the degree of which varies according to different specimens, but they have such a common character that one member of a pair is more or less reduced in size so as to constitute the parasite to the other member.

These specimens are tabulated as follows :

Group	Degree and mode of doubling		Numbers of specimens	Notation of specimens
I	Union at eye-level	A) 3 eyes and 2 ears	1	No. 5
		B) 4 eyes and 2 ears	4	No. 8, No. 12, No. 3, No. 15
		C) 4 eyes and 3 ears	3	No. 24, No. 1, No. 22
II	Union near the forelimb	A) 4 ears and 2 forelimbs	5	No. 28, No. 21, No. 20, No. 23, No. D
		B) 4 ears and 3 forelimbs	2	No. 7, No. 19
III	Duplicity extending to the tail end		5	No. 2, No. 11, No. F, No. 16, No. 25
IV	Unequal duplicity, parasite and autosites	A) parasite excrescent	4	No. 4, No. 26, No. A, No. B
		B) parasite proportionate	5	No. 6, No. 18, No. 17, No. E, No. 27
		C) parasite defective	2	No. 9, No. 13
		D) parasite acephalous	3	No. 14, No. C, No. 10
Total			34	

Observation

1. *First group*

Double No. 5 (1933): When lived, the specimen was observed to be oedematous, almost normal in the dorsal view, but double in the ventral aspect with two mouths, two operculi and a median extra eye and balancer (fig. 1). There were 3 nostrils externally, but were detected 4 in the histological examination. Two hearts occurred first, but they were later reduced to a median organ. Whether this reduction was due to the union

of the two hearts or it was due to the degeneration of one of them, accompanying subsequent shifting of the dominant one to the present position, was not ascertained. In any case, from the features presented, the specimen belongs to the anadidymous type.

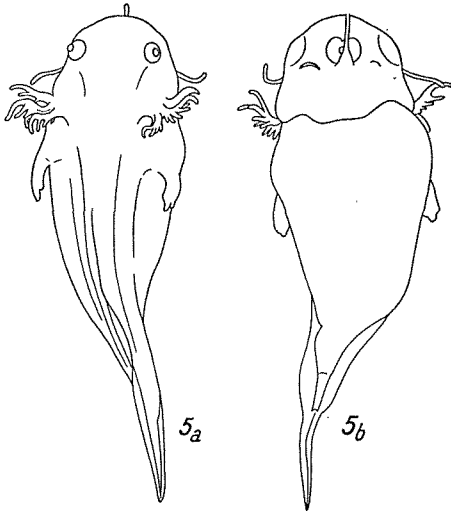


Fig. 1. Outline sketch of the specimen No. 5. *a*, Dorsal view. *b*, Ventral view.

The ventromedian eye was considerably larger than others, with shallow indentation on its anterior side. This structure suggested that the eye in question was the union of two eyes which separated themselves, when doubling was greater, to each side of the head. The eye enclosed proportionately a large lens, i. e., the eye constituted a synophthalmia unilenticata according to WERBER'S terminology. An extra balancer was abnormal with a thick basal portion. Mouths were first doubled, but at the time of fixation the left one was degenerated, only leaving its vestige. The other mouth was also abnormally small. Gills were undergrown on account of the ill-circulation of blood. While the posterior portion of the body was nearly normal and perfect, the head and the anterior part of the trunk was however slightly oedematous with fluidal accumulation under the skin and in the body cavity. The swelling was particularly great in the region of forelimbs.

The examination of sections discloses the median nose consisting of two nasal rudiments closely united as in the median synophthalmic eye; it is remarkably large and contains two nasal cavities. The median eye consists of two C-like eye-cups facing each other with a common lens on the inner side. The lens possesses two fibrous centres enclosed by a common epithelium (fig. 2 *b*).

As expected from the double nature of the sense organs such as eye and nose, the central nervous system is also doubled; doubling extends behind the infundibulum. But the indication of duplicity can still be traced back upto the anterior two-third of the trunk, where the neural canals of a coalesced spinal cord show first the normal shape by the confluence of the left cavity into the right one. The chorda is bifid accompanying on each side of the neural canal even behind the cross section of the canal becomes single and perfect. The alimentary tract is single and the vestigial mouth has no perforation at all.

Trabecular bars of the cranium are two pairs, but the other cranial and visceral cartilages are one pair as in the normal case, though they are quite irregular both in shape and arrangement. The circulatory system remains single but is conspicuously abnormal; even the heart is in degeneration, situs of which being indistinct. This condition of the heart is

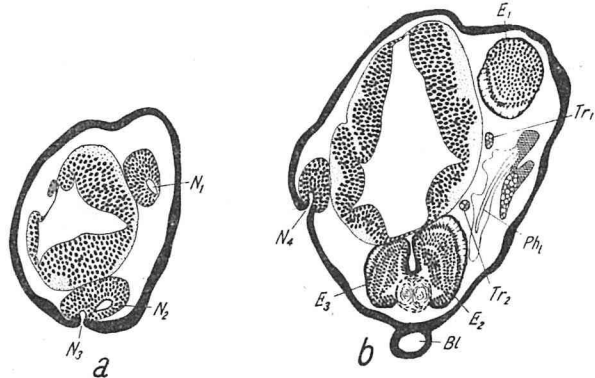


Fig. 2. Cross sections of the specimen No. 5. *a*, Through the level of a median nose. *b*, Through the level of a median eye; a common lens has two fibrous centres.

perhaps the reason why the specimen was oedematous in appearance.

Double No. 8 (1933): Doubling was slightly asymmetrical, the left partner being smaller and defective (fig. 3, 8). The head on this side possessed a pair of nearly perfect nostrils and a pair of eyes which were imperfect without lenses; the outer eye turned backwards and the inner eye directed toward the inner eye of the other head. The mouth was abnormally small, nothing but a pit-like perforation. Behind and ventral to the mouth there occurred a balancer which represented the left component, while the right was missing. On the median part of doubling there was another balancer, but this seemed from its position to represent the left balancer of the opposite head. This head was almost normal and perfect in size and in constitution, being provided with the normal number of organs. The operculum was single and common to both heads, and beneath it a heart was found. Gills were all normal. The bifid heads were bent towards right and ventral in the cervical region. The body behind this level was quite normal externally at least.

Examination in sections reveals that the inner eye of the left head directly contacts with the tapetum of the inner eye of the right head. In such condition of the eye the lens-induction from the tapetum is expected from the recent experimental data. But in reality no trace of lens-formation is detected in this case. Moreover, at the median side of this abnormal eye there is another fragmental eye, consisting of retina and tapetum, and facing toward the brain (fig. 4). It has also no lens within it.

A normal ear occurs behind the outer eye on each head. The mouth of the left head is provided with only a few teeth papillae; it is connected with the pharynx of the other head by a narrow slit-like space. Other alimentary organs are not yet well differentiated.

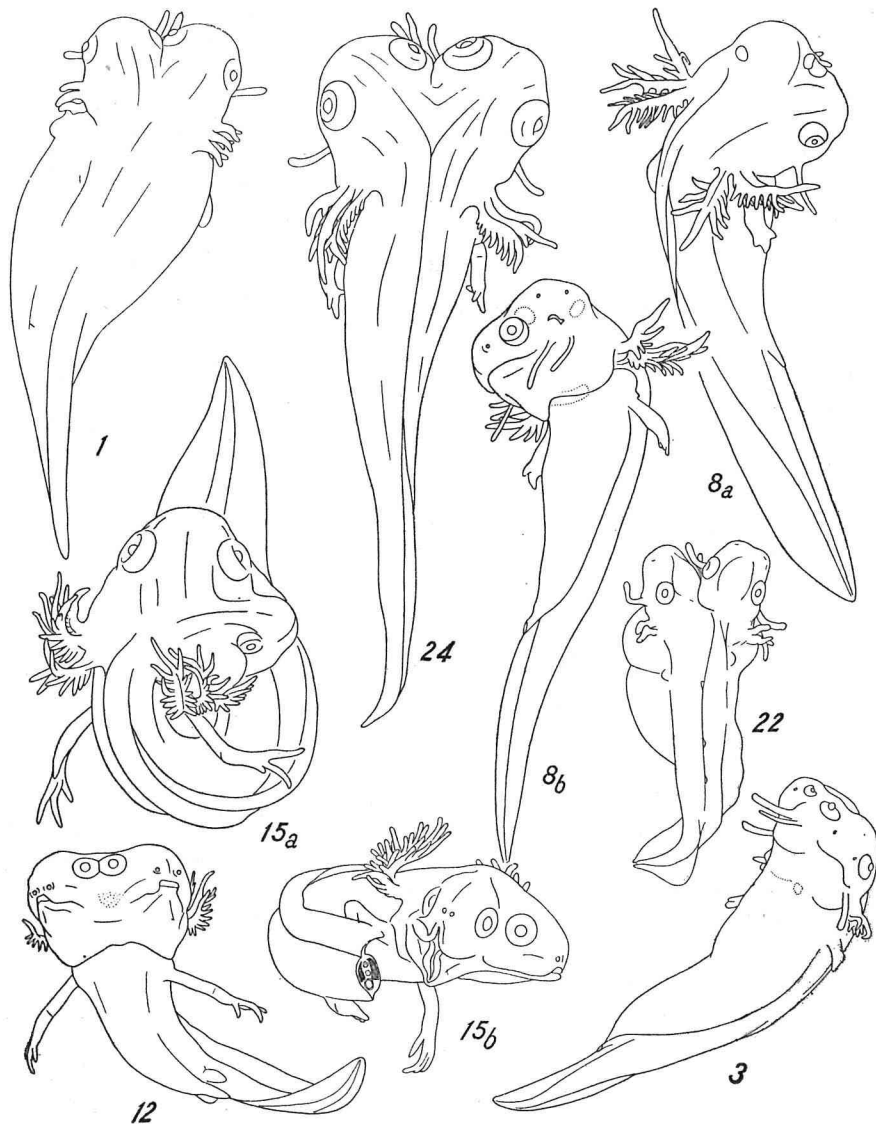


Fig. 3. Outline sketches of the anadidymous specimens belonging to the first group. Numerals represent the specimen numbers in the text.

Doubling of the cranial cartilages is only confined within the anterior-most region, i. e., the trabecular bars only are of two pairs. The development of the other visceral cartilages is normal, in spite of the position being more or less dislocated. The heart is subnormal, sinus being somewhat larger than normal. The chorda of each head gradually approaches

each other posteriorly and fuses finally at the level of anterior two-third of the trunk. In some sections before and after this level the chordal cells contain still some yolk granules. Between these chordæ the myotomes are irregularly arranged.

The central nervous system is naturally forked anteriorly; the branching point being found long before the attaching point of two chordæ. The latter is divided at the level of the 12th somite. There are two dorsal aortæ accompanying each to each chorda. They unite also immediately before the point where the neural canals become single. Of the three axial organs named, therefore, the dorsal aorta first, the neural canal secondly and the chorda finally present union. The pronephros and the Wolffian duct are one pair respectively.

Double No. 12 (1934): Bifurcation was symmetrical; two heads stood one another in the relation of mirror-image (fig. 3, 12). The body curved in an inverted C-shape. Each head was provided with a mouth, a pair of nostrils and a pair of eyes. The inner eye of the two pairs touched each other and became a synophthalmia bilentica. Gills were missing on the inner side, but the vestiges of balancers were indicated by pigmented spots at the usual place. Operculum was single and normal in development, and beneath it there was a heart. The posterior part of the body was entirely normal in appearance, except the C-shaped curvature above mentioned.

The specimen is examined in cross sections. All the eyes and noses are structurally normal as in the external appearance except the median eyes which are fused into a synophthalmic structure. Ears are only found on the outer side of each head. Two mouth-cavities unite immediately and connect with a common stomach. The alimentary tract is normal in situation with the stomach in the left and the liver in the right of the body cavity (fig. 5, C). Heart is also normal.

Bifurcation of the brain is complete in its anterior part, but both branches approach one another, first on their dorsal side, as if their roofs break through, at the level of the base of infundibulum (fig. 5, b). The infundibulum occurs corresponding to each brain. The double nature of the brain on the ventral side extends upto the spinal cord, which is conspicuously broad, with a ventral concavity, in the anterior portion. In the caudal portion this spinal cord becomes round gradually, nevertheless the nuclei arrange themselves around the neural canal according to its double nature, i. e., in the shape of two horns directed to each corresponding chorda (fig. 5, C). The chorda becomes single at the posterior part of the trunk in a few sections, but it is again separated before their final union taking place in the tail. Beneath chordæ are the dorsal aortæ, of which

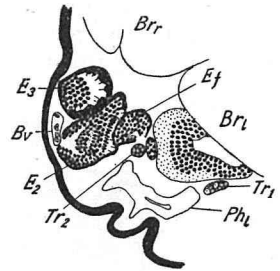


Fig. 4. Cross section of the inner eyes of the specimen No. 8, showing the abnormal (E_2) and the fragmental (E_f) eyes of the left member. In both there are no lenses.

the right one is slender and contains only a few blood corpuscles, while the left one is stout and seems to be functional. The former approaches gradually and fuses completely into the latter at the level of the forelimbs.

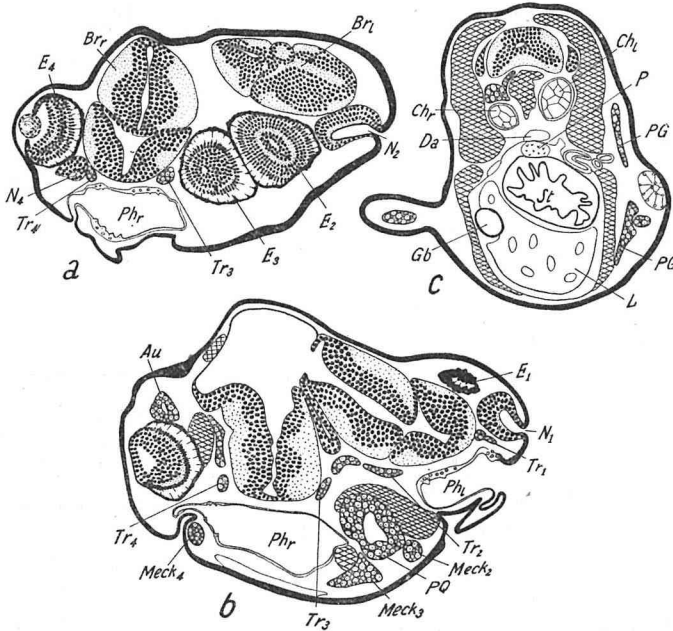


Fig. 5. Cross sections through the specimen No. 12. *a*, Showing the synophthalmic state of the median eyes. The brains are independent in this region. *b*, Section through the level where the ventricles of the brains break through each other; two sets of trabecular bars are well shown. The pharynges are separated. *c*, Duplicity in the anterior part of the trunk is indicated by the horny arrangement of the nuclei in the spinal cord as well as by the presence of two chordæ. The digestive system in this region is single and normal in structure as well as in situation.

The most remarkable abnormality is found in the cranial cartilaginous system. There occur two pairs of trabecular, MECKEL'S and palatoquadrate cartilages, of which those on the inner side fuse with the partner of the opposite side respectively. The process is especially conspicuous in the paratoquadrate, which become ring-like and are pushed aside dorsally to be located above and articulated with the junction of MECKEL'S cartilages (fig. 5, *b*).

Double No. 3 (1933): The specimen was anadidymous, the anterior division being slightly stronger than in the previous case (No. 12). Eyes on the inner sides were completely separate, one of which belonging to the right head was however smaller. One heart occurred but its contraction was abnormal. Accordingly, gills were undergrown and the body became more and more hydropsical, especially in the forelimb region. On the ventromedian part of the heads; there were two balancers, of which the one belonging to the left head was abnormal, looking like a spine (fig. 3, 3). Other parts of the body was single at least in the external appearance. The body was bent slightly towards the ventral side at the middle of the trunk.

This specimen was preserved in an early stage and cut in cross sections. Although we cannot say much about the alimentary tract, the pharyngeal cavity is separated by an undifferentiated endodermal mass. Whether this endodermal separation may or may not disappear, as the development goes on, is uncertain. There is a rudimentary stomach; the other organs are still nothing but a large yolk mass. Heart is abnormal and not well differentiated. Mesectodermal cartilages are also in the procartilaginous stage and the exact examination is therefore difficult. But supernumerary is noticed in this system. The developmental mode of the cartilages is supposed from the external appearance to be similar to the previous No. 12.

In this specimen an unusual space filled with blood corpuscles is found ventral to the median eyes and in front of the bases of balancers (fig. 6). Median eyes approach each other internally as shown in the figure. The anterior end of the forebrain is forked, and bears a pair of nose respectively. At the level of the outer noses the divided brains are united. This union takes place practically at the same level as in the specimen No. 12, despite the external doubling being slightly stronger in this specimen. The single spinal cord having internally two canals extends almost along the whole length of the trunk. There are two chordæ closely approached and touched each other at the anterior two-third of the trunk and soon separated so perfectly that the muscular tissue occurs between them. They become single finally, however, by the disappearance of the left member near the level of the anus (5 sections posterior to the junction

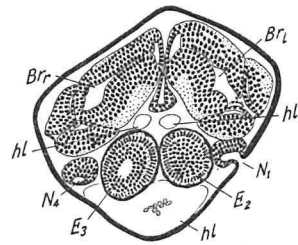


Fig. 6. Cross section through the head of the specimen No. 3. The inner eyes of both members touch each other. Hydropic lacunæ appear here and there, one of which contains the blood corpuscles.

of the neural canals). Each chorda is accompanied beneath it by a dorsal aorta, which likewise unites with that of the other side. The definite union of these aortæ takes place, after they touch and separate 3 times before.

Double No. 15 (1933): Division was subequal; the right head being slightly smaller and abnormal (fig. 3, 15). The mouth of this twin was laterally compressed, so that the upper and lower jaws were broken in the median, with the result of producing a vertical, instead of horizontal, opening (fig. 3, 15 b). Eyes were smaller, but proportionate to the head. Nostrils were in close approximation. The left head was almost normal. There were 3 pairs of gills as usual. From this region backwards the body was single, but curving and twisting in such a way that the tail comes under the heads horizontally, with its ventral fin on the left and the dorsal fin on the right with respect to the larger head. Heart and limbs were all normal. Sections were cut horizontally with respect to the main head, but they were more or less oblique.

At any rate, examination of them reveals that the eyes of the right

head are united internally by an interlocated neural tissue, and the pigment layers of both eyes are continuous (fig. 7). This union of eyes may be resulted from the fact that the expansion of the eye-forming areas is checked because of lack of space. There are only a pair of ears to both heads on

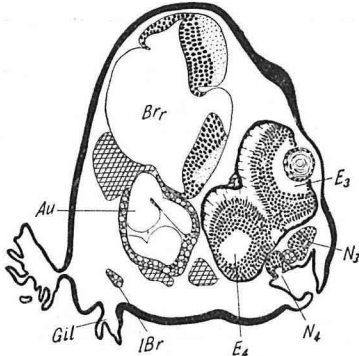


Fig. 7. Cross section through the right head of the specimen No. 15, showing the fused eyes and approximated noses.

visceral cartilages are normal in number and in articulation, but some of them are more or less dislocated.

Double No. 24 (1937): The anterior portion of the specimen was divided equally and the two heads were placed symmetrically with respect to the median plane of the body (fig. 3, 24). Each head was provided with a perfect mouth and each pair of nostrils, balancers and eyes. And a median gill was found at the junction of both heads. In reality, the gill was found to belong to the right head. Two pairs of opercular folds existed, of which those on the inner sides united with one another and projected cephalad and ventrad as tongue-like processes, while the operculum was built up by the union of the folds on the outer sides. The heart, which was seen through the skin, was more or less larger than that of the normal size. As a whole, duplicity of this specimen was slightly stronger than that of the specimen No. 12.

Horizontal sectioning was applied to this specimen. The most conspicuous feature which distinguishes this monster from those so far as described is an occurrence of the median ear. This ear is smaller and less differentiated than those situated outside the brain, and which head it belongs to is not certain. It is quite probable that it originates through the induction to meet the common influences issued from both medullæ, though its composite nature is unrecognizable. In all 4 eyes the retina is so thick that

the outer sides; the right one is attached to the outer eye of the right head, while the left one is situated in the normal position with respect to the left head. Chorda is bifid at the pronephric level. Visceral organs, especially the stomach and the liver are all in normal situations.

As to the cranial cartilages, all the derivatives of the mandibular mesectoderm seem to be doubled, at least the anterior trabecular bars, palatoquadrates and MECKEL'S cartilages are found in two pairs. Of these cartilages the inner palatoquadrate of the right head is attached to the same cartilage of the other head as is shown diagrammatically in fig. 8. Other

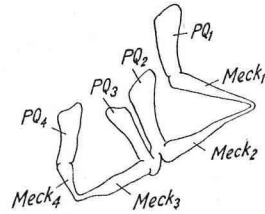


Fig. 8. Reconstruction of MECKEL'S and palatoquadrate cartilages (No. 15).

there remains almost no posterior chamber. Two chordæ unite at the level of the 18th somite, and the dorsal aortæ come also together at the same level, while the spinal cords unite slightly before. Between two spinal cords there occur some myotomes. The stomach and the liver are both single and normal in their position. Pronephros is one pair, and the heart is also single.

Out of the visceral cartilages, palatoquadrate and MECKEL'S cartilages, i. e., derivatives of the mandibular mesectoderm, are 2 sets in number and rather normally located with respect to each head. But the branchial basket of the single part of body is established by the union of the outer primordia of each head, as indicated by the opercular formation. Hyoid cartilage of the inner side extends caudally to touch the same cartilage of the opposite side of the same head, and the branchial cartilages in this region fuse into 2 pieces, one is enormously large and the other, small. This state of cartilages is semidiagrammatically shown in fig. 9.

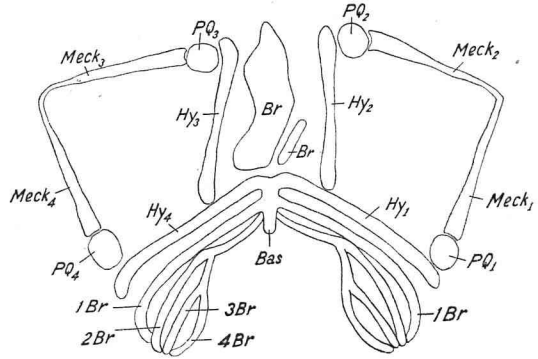


Fig. 9. Semidiagrammatic representation of the visceral cartilages of the specimen No. 24.

Double No. 1 (1933): Anterior division of this specimen was slightly less than that of the previous No. 24, and between two heads there occurred no gills (fig. 3, I). Balancers, noses, eyes and mouths were all doubled, while the heart was single.

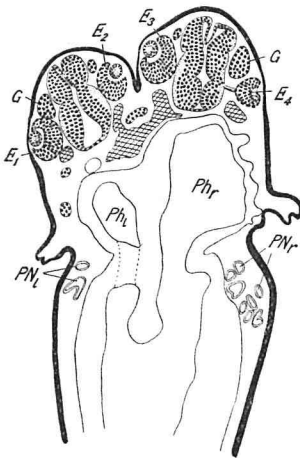


Fig. 10. Frontal section through the specimen No. 1, showing independence of both pharynges, and also no appearance of the median pronephros.

Internally there are 3 ears, of which the median is smaller and less differentiated than the other two found outside. Two pharyngeal cavities are separated by the endodermal folding (fig. 10). Oesophagus and stomach are not yet differentiated; it is uncertain whether these organs remain single or become double. Perhaps the former is the case, judging from the previous case, in which they are all single. Heart is observed to be somewhat laterally expanded. There occur two chordæ, arranged parallel so long as the sections are traced back until the 12th somite (posterior part is missing in preparation). Between the lower chordæ and the upper spinal cords there occur well-differentiated myotomes. The spinal cords unite

each other in the cervical region, but their canals remain separately through the whole length so far as the examination of sections is concerned. Pronephros is one pair, normal in structure and only situated outside of the body.

Double No. 22 (1936): This specimen was observed from the late stage of neurulation. Duplicity was found to take place symmetrically upto the medulla region, the heads diverging in about 120 degrees. They possessed respectively a mouth, nostrils, eyes and balancers in normal way. Gills failed to develop on the inner side, but on the outer side of both heads there occurred 2 gills (fig. 3, 22). Both outer eyes were abnormal. The inner eye of the left head sank deep into the mesenchyme, while that of the right head turned upwards; they were all provide with a lens respectively. At first there occurred two hearts, but they were gradually reduced to one median organ. The development of the dorsal fin was peculiar; it was divided into 3 spine-like processes in the trunk region. Limbs were undergrown. Later the left head turned in such a way that its dorsal side directed to the left eye of the opposite head. The body became hydropsical gradually and oedematous swellings appeared between two eyes on both heads. After died, the specimen was preserved and sectioned. Accordingly, the minute structures were unable to examine in sections. Nevertheless, one median ear is detected besides two outer ears, of which the left one is slightly smaller. The chorda is furcated at the level of the 12th somite, and the spinal cord at the level of the 9th somite. The divided portion of the spinal cord diverge so widely that the myotomes come to appear between them, but they are fused again unusually in the region of the hindbrain. Such a double union of the nervous system is peculiar and entirely unique to this specimen.

2. *Second group*

Double No. 28 (1938): In this specimen the bifurcation took place symmetrically with respect to the median plane of the body, and it was confined to the cephalic region. Both heads, turned slightly outwards, were provided with 3 pairs of gills as well as one pair of eyes, noses and balancers. The gills of the inner side of the right head were directed upwards, while those of the left head downwards. At its basal portion the tail curved remarkably to the ventral side (fig. 11, 28). Forelimb developed only on either side of the single body, and even a rudiment was not observed on the median part. The heart seemed to be single but abnormal. Cross sectioning was applied to the specimen.

Sectional study reveals that the above mentioned heart is peculiarly constituted: Bulbus arteriosus alone is doubled and each leaves the common ventricle from its either right or left side. Spinal cords meet together at the level of the 9th somite, but it is difficult to ascertain where the chordæ fuse with each other, on account of the posterior part of the body being bent ventrad. It is only said that the union of this axial organ

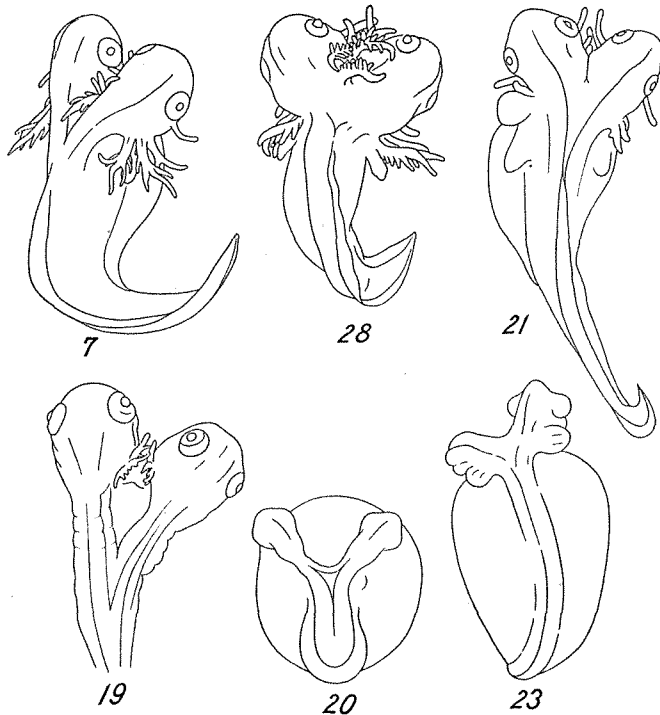


Fig. 11. Outline sketches of the anadidymi belonging to the second group. Numerals represent the specimen numbers.

takes place more posterior to that of the spinal cord. Between chordæ appear the myotomes even where the spinal cord recovers already its normal shape. Between the forked anterior portion of the median myotomes, occurs a bit of pronephric tissue, which is not accompanied by a Wolffian duct. The outside pronephri are nearly normal as in the cases of similar duplicity. The stomach is large and its cavities are now two in number, each corresponding to each member, but seems to become one, as the development goes on, because on one hand the cells between them are very scarce and not arranged regularly, and because on the other hand mesodermal membrane envelops them together.

Double No. 21 (1936): This specimen was observed from the middle of neurulation, when the neural folds of the left member were just closed, while those of the right member were only touched in the cervical region. The folds were still widely open in the posterior common part of the body. Both heads were nearly equal in size, though the left one was slightly larger. The posterior part of the body curved a little towards the right, and the tail end bent dorsally. The oedematous swelling appeared in the outer branchial region of the left partner, so that the development of the second and third gills were entirely suppressed (fig. 11, 21). But the inner

side of this head and both sides of the other were provided respectively with 3 gills. Forelimb was observed in the shape of bud on either side of the single body part. There occurred no median limb in this specimen. Hearts were doubled; the left one was shifted a little medianwards, and beat rather normally, while the right one rather weakly. The larva was fixed in a dying condition.

Histological examination shows the presence of a large vacuole to each head near the anterior extremity; it is arisen from hydropsy (fig. 12). Each

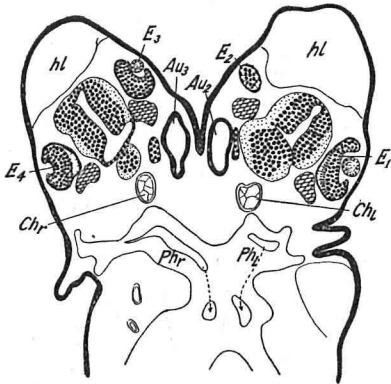


Fig. 12. Frontal section through the specimen No. 21, showing the inner ears being separated.

head is provided with a pair of ear rudiments. The cross section of the neural canal makes a crescent shape in the united anterior part, but recovers the normal shape at the level of the 13th somite, where the chordæ touch each other. The latter becomes single definitely still 3 somite posteriorly. Between the furcated parts of the chorda are count 12 somites, though the last one is considerably smaller. Oesophagi are doubled and open separately into a large yolk mass (see the figure). The stomach seems to be also doubled, though its differentiation is not yet distinct. As to the

liver, nothing can be said because of its still incomplete differentiation. There appears a pair of pronephri only on the outer sides, and their existence cannot be noticed in the median of the forked portion of the body. Both hearts are found to be in degenerating process and their situation is uncertain.

Double No. 7 (1933): Anterior division was equal, extending to the forelimb region (fig. 11, 7). Each head was furnished with 3 pairs of the well-developed gills; the inner gills of the left head directed downwards, while those of the right head upwards, so that the latters were alone seen in the dorsal view of the specimen, besides outer gills of each head. A heart developed in the normal position to either member of the pair; both seemed to be functional and contracted nearly at the same rate. Further the direction of blood circulation in the left heart was normal, whereas that in the right was opposite; i. e., in the mirror-image to the other. This way of circulation indicated the inversed orientation of the right heart. In the vicinity where the two members of the twin joined into a single body there occurred a conical prominence, pointing dorsad, which was taken for a rudiment of the forelimb, though its development was quite delayed as compared with outside limbs. The dorsal fin was single and bent towards the right side along the whole length.

Examination of sections cut transversely to the body axis reveals that the conical prominence just mentioned is clearly a rudimentary limb. While the pectoral girdle fails to develop, it contains a cartilaginous rod referable to the humerus. Immediately behind the median limb there occurs a rudimentary pronephros, tubules of which are counted at most 3 in one section. But it is not accompanied by the Wolffian duct. The outside pronephros of the right partner is normal and is attended by the well-differentiated Wolffian duct; that of the left partner is subnormal, and the Wolffian duct is more or less in arrested development, namely slender in calibre, the lumen being compressed dorsoventrally here and there. Moreover, it ends blindly into the intestinal wall. At the level of forelimbs, after the disappearance of the median pronephros, the myotomes of the inner sides unite perfectly, then the neural canals unite near the caudal end of the trunk at the level closely anterior to the hindlimb rudiments. Finally, the chordæ become single definitely at the level through the middle of the anal tube. As already clear in the external observation, two hearts stand in a distinct enantiomorphic relation, the structure of the right one being situs inversus (fig. 13, *a*). The dorsal aorta of the right twin is slightly slender than normal. There are two hepatic veins running forwards along the outer margins of the liver (fig. 13, *b*) and enter the heart of the corresponding side. Two stomachs occur in the common abdominal cavity, and at the level of the pectoral girdle each passes into the intestine, which seems to be also doubled at least in its anterior portion. Under the stomach is found a common liver, located symmetrically with respect to the median plane of the body. Gall-bladders are observed nowhere. A single pancreas is noticed dorsal to the stomachs as a continuous lobe of organ.

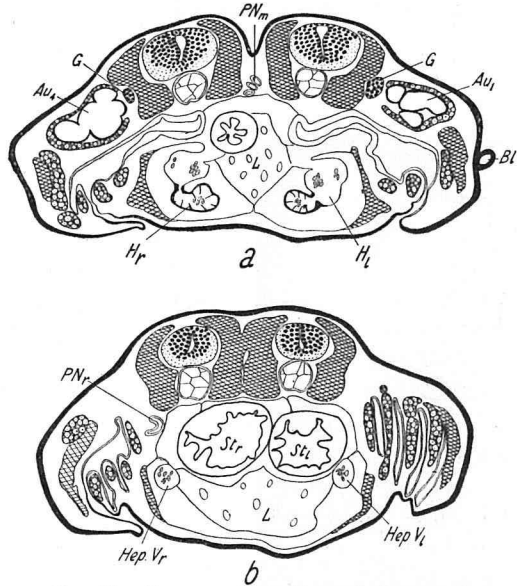


Fig. 13. Cross sections through the specimen No. 7. *a*, Showing the enantiomorphic relation in the internal structures, especially in the heart. *b*, Showing the independence of both stomachs. Hepatic vein is doubled.

As to the cranial cartilages nothing is worth to record here, as they are quite normal in either head.

Double No. 19 (?): The history of this specimen was unknown. It came to my hand through the kindness of Prof. OKADA, in a mounted condition on the slide glass. Two heads were equal in size, but the right one

bent slightly outside. On the inner side of either head were found 3 gills, while the out-sided gills were lost entirely, though they should be present when the specimen was alive. Balancers were also missing. A median forelimb rudiment was found slightly caudal to the inner gills as a small conical process. A similar limb rudiment was also noticed on the outer side of the right twin. Dorsal fins were doubled so far as the observation was possible on the specimen. It was prepared in cross section, but the poor state of preservation made a closer examination difficult.

The development of the axial organs of the anterior part are symmetrical to each twin. There are two spinal cords, chordæ and dorsal aortæ respectively. The stomachs are also doubled, but the liver is single and meets common to both stomachs as in the previous specimen No. 7. Hearts are damaged completely. The humerus of the median limb is articulated with a pectoral girdle. The inner pronephri of both twins come together posteriorly, whether it is then followed by the Wolffian duct is uncertain.

Double No. 20 (1936): The specimen was bifid equally (fig. 11, 20), but died in the stage when the neural folds were just closed. The internal structures were unable to examine.

Double No. 23 (1936): The medulla oblongata of the left partner of this specimen was broken 6 days after the closure of the neural folds, and the endoderm was protruded through this wound. It died before giving any farther differentiation and it was not examined in sections (fig. 11, 23).

Double No. D (1932): Precise record of this monster is missing, but from the accompanying photograph doubling is clear to be equal, and each head is formed perfectly. Two hearts are noticed by the presence of the dark pigments at their usual positions of development (fig. 14). Perhaps no median forelimb is formed.

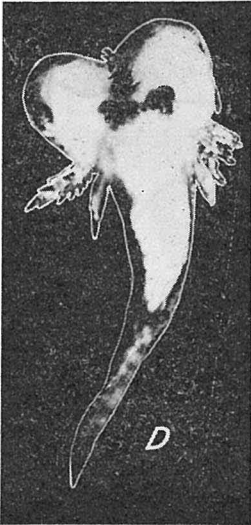


Fig. 14. Photograph of the specimen No. D.

3. Third group

Double No. 2 (1933): Doubling was equal and extended almost to the tail end; two dorsal fins did not unite anywhere. The ventral fin was lacking. Both partners turned about 45 degrees towards their respective outer side. The development of the anterior parts was entirely normal, resting on a common yolk mass. Anus was single. This specimen died a little later than fig. 15, 2 was drawn. Fixation was done after death. In sections each partner is observed to be provided with a pair of pronephri. The duct-parts are unfortunately much damaged on account of deformation of the tissue. For the same reason and also due to the embryo being too young, the status of the heart and the stomach is uncertain. Nevertheless, the chorda and the spinal

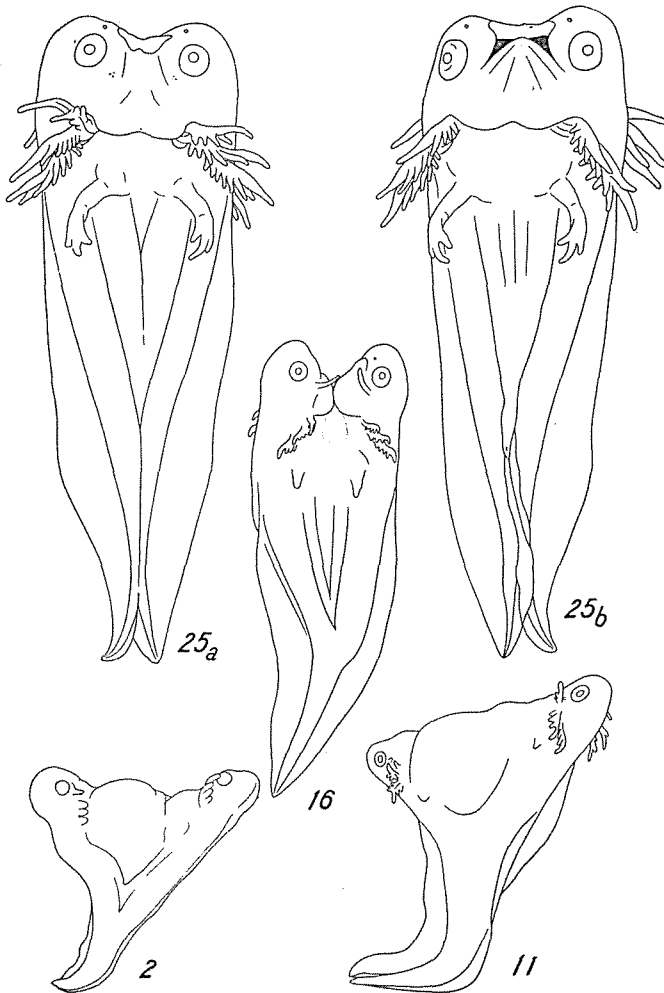


Fig. 15. Outline sketches of the double monsters in the third group. Numerals represent the specimen numbers.

cord are found certainly doubled to the tail end.

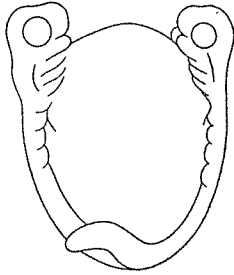
Double No. 11 (1934): The mode of duplicity of this specimen was much like the previous No. 2 (fig. 15, *11*). The right member was slightly larger than the left one. The tail end was separated into two, each of which was provided with the ventral and dorsal fins, but the main part of the tail was single, with two dorsal and one ventral fins. Anus was single. The development of gills were greatly suppressed, particularly in the left member. By far the most remarkable abnormality of this partner was found in the eye and nose. Eye was present only on the right side, and nostril only on the left side. The forelimb buds were present on both

sides. The right twin was almost normally organized, though the development of different organs was more or less arrested. Both hearts were found weakly beating and blood circulation was almost entirely hindered.

Examination on sections shows also as in the external observation that the right twin is approximately normal in structure, while the left one is deficient. The only eye of the latter is smaller and monophthalmia unilentic, but it is not cyclopean. The lens is also small in proportionate to the eye-cup. The structure of the head of this partner becomes symmetrical, arriving at the level just in front of the ear. Yet the right ear is smaller and the left ear is enormously larger. They are retained in vesicular forms with initial sign of septum-formation. Each partner of the twin is provided with a rudimentary tube-like heart. But considering from its mode of bending, the left heart is normal, while the right is inversed.

The development of the left pronephros is a little advanced in both partners. Alimentary tract is not yet differentiated, but seems to be doubled at least in the anterior part, because of the fore-gut being duplicated.

Double No. F (1932): Two partners of the twin were nearly equal in size, facing each other in situation and embracing a large yolk mass between them (fig. 16). They were organized normally, but for the tail which was common. This specimen died soon after the drawing was made; it was not preserved, because the skin was already degenerated when found.



F
Fig. 16. Outline sketch of the specimen No. F.

Double No. 16 (1935): Doubling occurred as far back as the tail end. Two partners were united belly to belly (fig. 15, 16). However, the distinction of the original dorsal and ventral sides of the twin could be easily determined by the presence of an anal depression and a still larger yolk mass on the ventral side. It is also easy to distinguish the right and the left of the two partners for the same reason. The ventral fin failed to develop. Operculum was formed on the ventral side by the union of the outer opercular fold of the right partner with that of the left partner, and on the dorsal side by the union of the inner fold of the right partner with that of the left partner. Two hearts occurred under these opercula. They should be produced by the union of different primordia belonging to different partners, instead of by the union of both primordia of the same partner as it is the case in the normal development. These hearts beat very weakly, and therefore the development of gills was conspicuously arrested as shown in the accompanying figure.

Visceral cartilages are observed in sections to be nearly normal so far as each head is considered as a unit. But as the first basibranchia of both members touch each other directly at their caudal ends, there is no room

for the second basibranchia and the hearts to be placed normally. As a consequence these structures are forced to develop rotated 90 degrees outside. Namely, the second basibranchia are located in the direction towards lateral, instead of caudal. This situation of the cartilages suggests that they are formed by the fusion of different anlagen located originally on the hypobranchial region of each partner, as referred above to the formation of heart and operculum. Hearts are very rudimentary and represent still the tubular forms, containing practically no blood corpuscles in them.

Each partner is provided with a pair of pronephri, the right one of which is always well developed, while the left one is undergrown. This developmental difference is especially marked in the left partner of the twin. The Wolffian ducts are also ill-developed on the outer sides; they are solid cords in the anterior part, and become tubular in the posterior part. These ducts belonging to the same partner first fuse each other into a common duct, and then unite with also a common duct of the other partner. However the composite duct thus produced terminates blindly beyond the anal region in the mesenchyme without any communication with the cloaca.

The alimentary tract is single and straight, situated in the middle between the two partners of the twin (fig. 17, *b*). The posterior section is not perforated through and terminates blindly. Livers are two in number; each seems to lie on the right-dorsal side of the alimentary tract. As it is, however, suspended by another mesentery from the cœlomic wall in the middle of the other member, the definite situation cannot say. It may be considered as normal and at

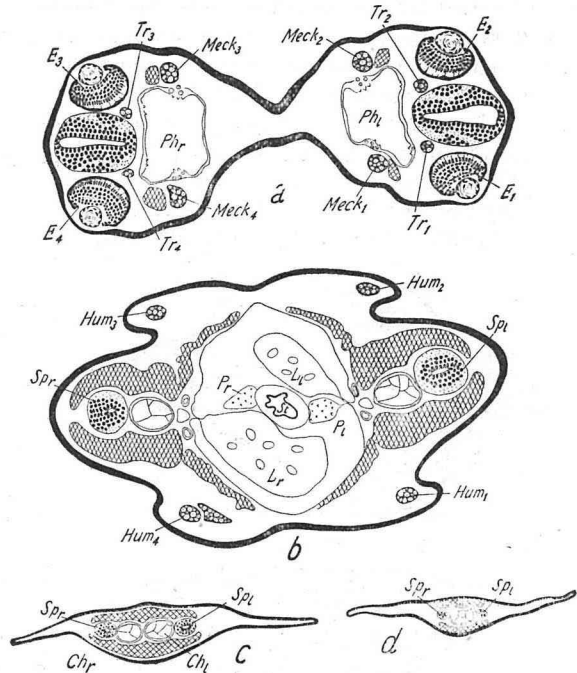


Fig. 17. Cross sections through the specimen No. 16. *a*, Through the head region. Structures of each head are normal, despite the connection with other member in the ventral portion. *b*, Through the forelimb level. Digestive systems are enclosed in a common body cavity, stomach being single, but liver and pancreas double. *c*, Through near the tail end, where the chordæ touch each other. *d*, More posterior to previous section, chorda being single and spinal cord, double.

the same time as reversed also. Pancreas is also doubled, and located on the dorsal side of the alimentary tract.

Two chordæ unite near the tail end, but the spinal cords are separated almost upto the terminal end (fig. 17. *c. d*). They are united in a few sections of the posterior extremity. Near the posterior end of the alimentary tract there occurs, on the original ventral side, a pair of rudimentary hindlimbs, of which the right one is considerably smaller. On the dorsal side no such primordia are detected.

Double No. 25 (1938): The formation of opercula and hearts of this specimen was quite similar in the previous No. 16. Namely, these organs were formed by the union of different rudiments of these sides of the different partners. In this specimen, what is more, the lower jaws were formed in the same way and situated also laterally with respect to the median plane of each partner (fig. 15, 25). Mouth opening was common and enormously larger. Two hearts were found both to be functional, though slightly sluggish as compared with the normal healthy ones. Nevertheless, gills were all well developed and fully expanded as in the normal larvæ. Each partner of the twin lay to meet exactly face to face at least in the anterior half, while in the posterior half, both turned slightly towards the

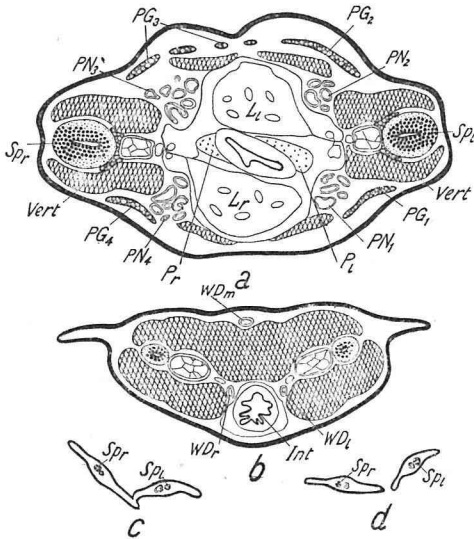


Fig. 18. Cross sections through the specimen No. 25. *a*, Showing two sets of internal organs, but for the stomach. Livers are normally located to the common stomach. *b*, Through the posterior part of the trunk. Myotomes of the inner sides of both members fuse with each other, outside of which, under the integument, lies the median Wolffian duct. *c*, Through the level where the tail is ready to be separated. *d*, Showing the separated portion of the tail.

original dorsal (inner) side to make an obtuse angle between them. Anus was single and open rather to the right side. The tail end was bifid and provided with the dorsal and ventral fins respectively. This specimen may better be mentioned as an example of the anakata-didymous monster. Anterior four-fifth of the ventral fin was however united. Two forelimbs were projected dorsad with respect to each partner, making a symmetrical pair respectively on either side with those of the other partner (fig. 15, 25). The hindlimb rudiments were not recognized from outside. Cross sectioning was applied to the specimen for the further study of internal structures.

Histological examination certifies the external observations as to the peculiar formation of the jaw, heart and operculum. The visceral ap-

paratus are formed by the union of two primordia lying on the same side of different members of a twin, instead of by the union of those of the opposite side of the same member. Alimentary tract is single and situated in the middle of the body cavity, while the liver and the pancreas are doubled (fig. 18, *a*). The liver of the left partner and that of the right partner are respectively on the original dorsal and ventral sides of the twin body. Therefore, if we consider these organs respectively, they are quite normally situated, namely the stomach on the left and the liver on the right. Each excretory system of the inner side is underdeveloped. Pronephri show degenerating appearance, and the Wolffian ducts are solid here and there without lumens. Furthermore, in some place they contain some vestiges of degenerating cells. The same state of things is also noticed in the outer Wolffian duct of the left partner. In spite of the deficient structure, the Wolffian ducts of the inner sides unite in the posterior part of the trunk, to shift laterally and to run tailwards between the myotomes and the integument (fig. 18, *b*). But this common duct ends blindly. On the same side and at the place slightly posterior to the union of the Wolffian ducts just mentioned, the myotomes of the different members approximate also each other and at length fuse themselves. The outer Wolffian ducts are open into cloaca respectively in the ordinary way. A compact mass of mesenchymal cells—possibly the hindlimb rudiment—is noticed on the original ventral side to each side of the alimentary tract; none of such structure is detected on the original dorsal side. Two chordæ run through independently, except in a few sections near the tail end where they touch, but soon become separated again. The nervous system is completely doubled throughout the whole length of the body. Out of two hearts, the one, originally ventral, viz. composed of the left component of the left partner and the right component of the right partner, is situated in normal orientation, when viewed from the side, originally ventral. Another heart which is also of composite nature of different components is rather less differentiated, but its situation is sufficiently estimated to be also normal, when the side, originally dorsal, is assumed as the ventral with respect to the heart in question. Two sets of visceral cartilages occur, but are dislocated laterally with respect to the other cranial cartilages. Each set is composed of, as the heart does, half of the elements of different partners that are located on the same side.

4. *Fourth group*

Double No. 4 (1933): On the dorsal side behind the right eye of this specimen there occurred an outgrowth of the brain, and on the ventral side of which 2 balancers developed one behind the other (fig. 19, 4). Other appearance was perfectly normal in the external view. Therefore, by the casual observation the duplicity of the specimen might be overlooked.

However, histological examination gives evidences that the specimen should be classified as the anadidymous monster. First of all, in the system of the visceral cartilages there occur two sets, one after the other, of hyoid, paratoquadrate and MECKEL'S cartilage on the right side (fig. 20). These cartilages of the first set appear a little anteriorly to the mates of the opposite normal side; the paratoquadrate is connected normally with

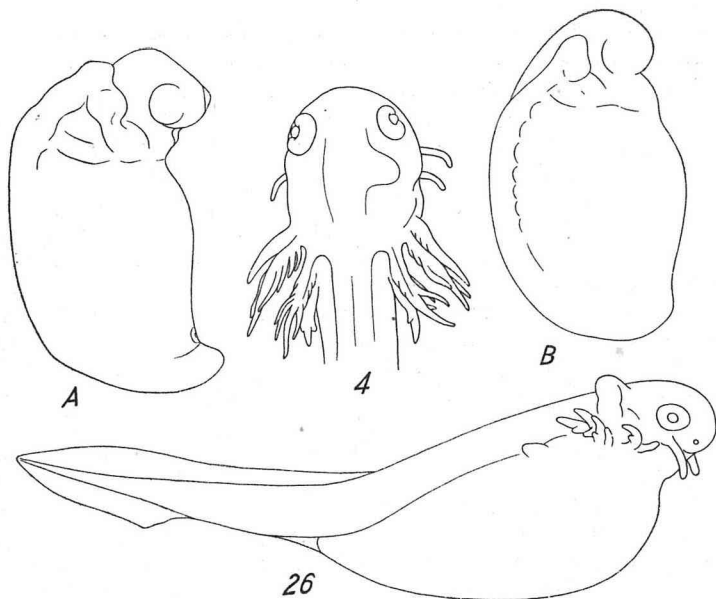


Fig. 19. Outline sketches of the specimens belonging to the division A of the fourth group. Numerals represent the specimen numbers.

MECKEL'S cartilage, to which MECKEL'S cartilage of the second set is attached from behind by its anterior slender tip. The posterior end of this second MECKEL'S cartilage is articulated with also the palatoquadrate of the second set as in the first set. By another tip the latter cartilage is connected with

the excess trabecular bar, which runs anteriorly in a short distance along the ventral side of the second brain, upto the palatoquadrate of the first set. Further, the double sets of hyoid cartilage are also observed, with the posterior end of the cartilage of the first set is connected with the same cartilage of the second set by its anterior tip. The branchial part is nor-

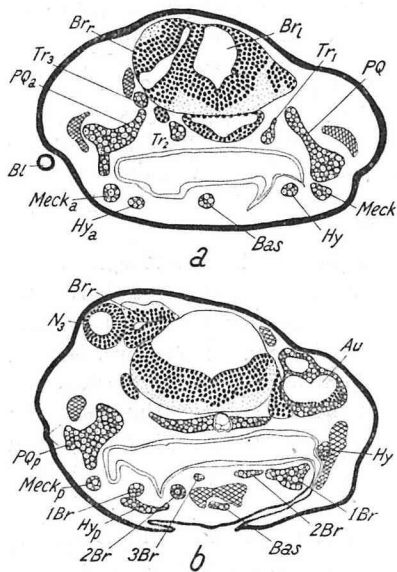


Fig. 20. Cross sections through the head of the specimen No. 4. *a*, Showing the composite nature of the brain and the first set of visceral cartilages derived from the autosome's mesectoderm. *b*, Section posterior to *a*, showing the second set of visceral cartilages derived from the parasitic mesectoderm. They are pushed behind considerably as compared with the same cartilages of the opposite side of the head. Subscribed small letters, *a* and *p*, show the origin of cartilages; *a*, derived from the autosome, and *p*, from the parasite.

mal; except only that the first branchial cartilage touches the hyoid. From these findings, the mesectodermal groups which produce the visceral cartilages may be supposed at first to be arranged as shown diagrammatically in fig. 21. The neural plate is bifid unequally near its anterior end and in the parasitic plate the mesectoderm develops only on the outer side, while the inner side is occupied by the mesectoderm of the autosite.

Another evidence to the anadidymous nature of this specimen is the structure of the brain. The outgrowth contains a brain directed rather posteriorly, and the latter induces an extra nose anterodorsal to the normal ear (fig. 20, *b*). This nose however does not open outside. (Such a condition of nose is frequently met with, according to KAWAKAMI (1938), in heterotopical induction of the same organ through the transplantation of a piece of brain.) No other cephalic organs such as eyes, ears etc. are detected anymore with respect to this brain.

Double No. 26 (1932): The parasite was represented as a wart in the right otic region of the host, accompanied with a supernumerary production of gills on this side (fig. 19, 26). These gills were arranged into two groups, two in the anterior and four in the posterior group. The first gill of the latter group was the most rudimentary. This specimen became œdematous and the abdomen distended out markedly. The ventral fin of the tail was present only in the distal half and lacking in the proximal half.

Examination of the horizontal sections of this specimen reveals that the right wall of the brain bulges in the region of the medulla oblongata to the dorsal of the ear and the fore-gut juts out also to the same direction. The ear of this side appears just below this neural evagination. In the parasitic wart there is no trace of the development of any sense organ. The most peculiar feature of this specimen, however, is found in the visceral pouches. The first three pouches are nearly normal, while the fourth (the third branchial) one is strongly abnormal; it is divided into two pouches, the anterior one is again divided into two and the new anterior one is once again subdivided into anterior and posterior endodermal cell masses. Thus, 3 extra arches are produced between the second and third branchial arches (fig. 22), each of them bearing respectively a gill outside. The gill is always proportionate to the size of the arch, the anterior being the smaller. According to this supernumerary of arches, the branchial cartilages are also increased, though the number of which is not definitely told, as they are still in the procartilaginous condition. In the most posterior extra arch is found distinctly the mesectodermal cell-cluster, which later gives rise to the branchial cartilage, while in the other anterior two excess arches such a cell-cluster is hardly detectable.

Double Nos. A and B (1932): These specimens were bifid unequally and the right member was nothing but a wart in the otic region like the

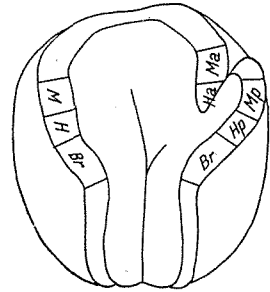


Fig. 21. Diagrammatic figure, showing the formation of duplicity in the specimen No. 4.

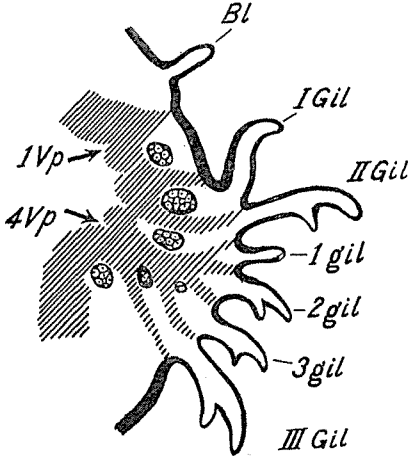


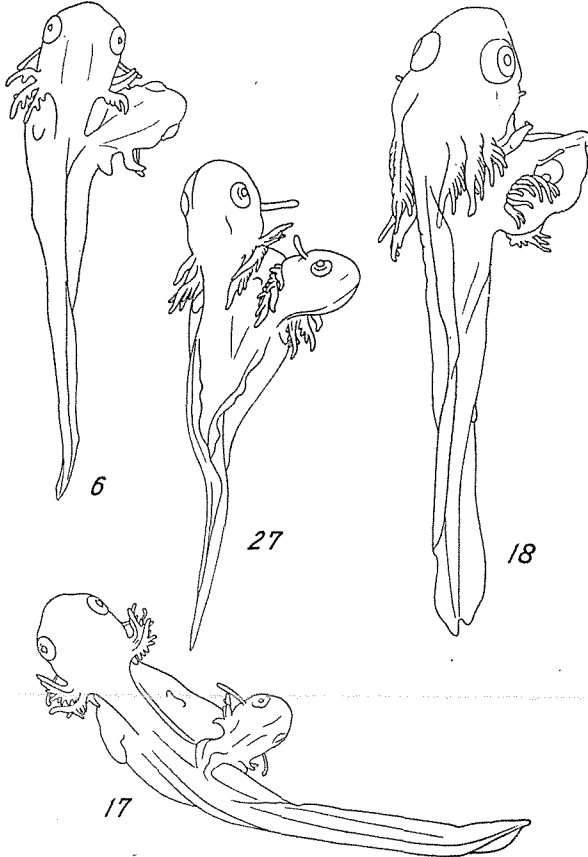
Fig. 22. Frontal section, semidiagrammatical, through the specimen No. 26, showing the formation of supernumerary gills.

Fig. 23. Outline sketches of the specimens belonging to the division B of the fourth group. Numerals represent the specimen numbers.

autosite (fig. 23, 6). Two hearts were present: the one belonging to the autosite pulsated normally, while the other, i. e., that of the parasite beat slow and weakly; the autosite's heart was once counted to contract 103 times per minute, and the parasite's heart 95 times per minute. Consequently, bloods entered less into the latter heart, and caused in-

case in the previous No. 26 (fig. 19, A, B). Their development was traced upto the early tail-bud stage, when they died. So far as the observation was made, there occurred no sense organs in the wart.

Double No. 6 (1933): The right member was parasitic and its developmental tempo was behind the left member through the whole larval life observed. At first both members were bent outwards symmetrically, but with the advancement of development the left member became gradually straight to give rise to an



ferior nutrition of the parasitic member, especially the development of the gills were suppressed. There were 3 rudimentary forelimbs, one on the out side of each member and the third on the median between them.

In the internal examination the cartilaginous system of the head is found to be normal in both members. Chorda of the parasite terminates in the 7th somite of the host without fusion with the latter's, while the spinal cord is united with that of the host at the same level. Axial somites of the parasite are 4 pairs, and the 4th somite of the inner side is united with the 6th of the autosite (fig. 24).

The right heart or that of the parasite is, as has been stated, inferior in development to that of the host and its situation is inverted in accordance with the general rule of the situs cordis of the right member. Stomachs are doubled; the host's one is well differentiated and connected with the definitive duodenum, while the parasite's one is less differentiated and attended by also less differentiated duodenal part of the intestine, the posterior part of which ends blindly in the yolk-mass. When the yolk would have been exhausted, it should be connected with the host's intestine. Liver is single and occupies the normal position with relation to the host, i. e., on the right side of the stomach, while on the ventral to the stomach of the parasite. There occur two pancreas; each finding its position behind the corresponding stomach. Pronephri are 3 in number; the left one is entirely normal with an attendance of a normal course of Wolffian duct, while the Wolffian duct of the right pronephros runs inside across the chorda of the parasite upto the 7th somite of the host to end posteriorly. The median pronephros is composed two kinds of tubules highly convoluted, one having large cells, and the other, numerous small cells. In the ventral part it is divided by the cœlomic cavity into two portions; each belonging to the corresponding member of the pair. A single Wolffian duct runs out from the portion of the pronephros belonging to the host to end blindly in the region just posterior to the host's stomach.

Double No. 18 (?): This specimen came to my hand from Prof. OKADA's collection mounted on a slide glass. The left partner was the autosite and the right one, the parasite. In the preparation the parasite was twisted outwards about 90 degrees so that its side only was allowed to be seen from the dorsal aspect of the specimen (fig. 23, 18). The autosite was also inclined slightly outside. The dorsal fin was bifid at the level slightly anterior to the rudimentary hindlimbs and extended headwards to its respective

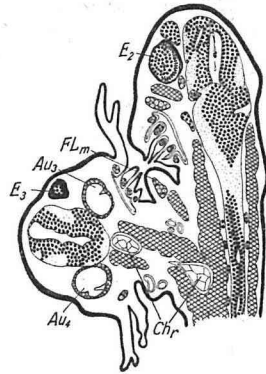


Fig. 24. Frontal section through the specimen No. 6. The chorda of the parasite terminates in the neighbouring myotomes without connection with that of the autosite.

partner. Therefore, while the fin of the autosite kept the ordinary course, that of the parasite passed gradually ventrad with respect to the autosite. The ventral fin was single. The outer side of the autosite seemed to be practically normal, but the inner side was abnormal; the forelimb was shifted to locate greatly forwards and downwards near to the level of the second gill. It was very defective and undergrown. Strictly speaking, however, it is quite problematical to regard the limb now in question as the right member of the host's forelimbs, since its position can be also occupied by the left member of the parasite's forelimbs. The right limb of the parasite was not seen from above. The hindlimbs were seen as rudimentary buds at the normal position of the single part of the body. The autosite as well as the parasite were provided with 3 pairs of gills and a pair of balancers. The development of gills of the parasite was considerably arrested, and the resorption of balancers was also retarded as compared with that of the autosite's. When alive, the developmental delay of the parasite might be general. The specimen was stripped from the slide and again prepared in cross sections with respect to the autosite.

Histological examination reveals that there are no remarkable anomalies upto the pronephric region of the autosite. The heart is normal both in structure and in orientation. The pronephros is also normal on the outer (left) side. It is followed by the well-differentiated Wolffian duct. On the inner (right) side the pronephros is composed of two kinds of tubes.

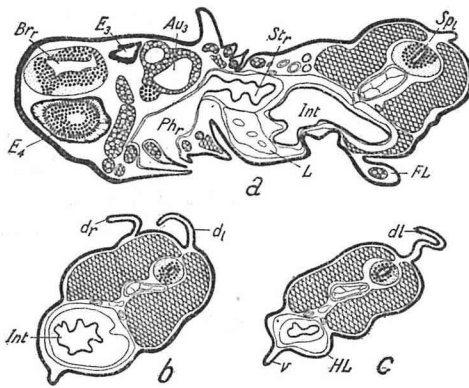


Fig. 25. Cross sections through the specimen No. 18. *a*, Showing the independent occurrence of the parasite's stomach. *b*, Through the posterior part of the trunk, showing disappearance of the parasite's spinal cord. The outer Wolffian duct of the parasite lies in the ordinary place as if it belongs to the autosite. *c*, Though the level of the hindlimb-rudiments. The dorsal fin of the parasite vanishes, so that the section becomes perfect in structure.

the other is made up of the cells twice or thrice as many as the former, in spite of nearly the same calibre. Such an abnormality of the pronephros is often met with on the inner side of other specimens of similar duplicity. In the present case the abnormal pronephros of the autosite is elongated posteriorly and united with the same organ of the parasite. But both of them are not followed by the Wolffian ducts. The outer pronephros of the parasite is normal; its duct is gradually shifted dorsad with respect to the autosite to find finally the place under the myotomes of the autosite, as if it belongs to the latter (fig. 25, *b*).

The central nervous system of the parasite does not connect with that of the autosite. It becomes gradually narrower as it goes posteriorly and finally disappears at the outside of the autosite's myotomes. Chorda is not found anywhere, but this fact is perhaps due to its secondary reduction. That the nervous systems of the autosite and the parasite remain separate should be also regarded as the secondary phenomenon. The abdominal cavity is common to both partners, and the position of the autosite's liver is occupied by the stomach of the parasite. Accordingly, the liver is dislocated to the ventral, instead of the right of the autosite's stomach. It is uncertain whether the liver is single or double, owing to the strong compression of the organ. On the right side of the autosite, myotomes are divided into dorsal and ventral portions in some distance near the posterior end of the parasite's spinal cord. The single part caudal to the rudimentary hindlimbs is wholly normal.

Double No. E (1932): Precise record on this anadidymus is missing, but it is clear from the photograph that it belongs to the fourth group (fig. 26). The right member, well-proportionate in itself, represents the parasite and it makes an angle of about 80 degrees to the autosite. Bifurcation occurs immediately behind the branchial region, so that the heart is shown to each head by the characteristic pigmentation. Gills are also seen on either side of each head, but their exact number cannot be said.

Double No. 27 (1938): Bifurcation occurred unequally at the posterior part of the body, as shown clearly by the dorsal fin. The right member was the parasite and the left member, the autosite (fig. 23, 27). Both members twisted outwards considerably; twisting of the parasite was so remarkable that its left side alone was seen from above. Both heads were provided with the sense organs, balancers and gills in the normal way. But the forelimb in the median was single and common, its development was considerably behind the other outside limbs. The anus was common and the ventral fin was single. The free margins of the dorsal fins separated near the tail end, though their bases became united at the root of the tail.

Histological examination shows that the spinal cord becomes completely normal at the level of the cloaca. Near this level (precisely a few sections anterior to) the dorsal fins are also coalesced by their bases as already stated in the surface view. At the level where the spinal cord

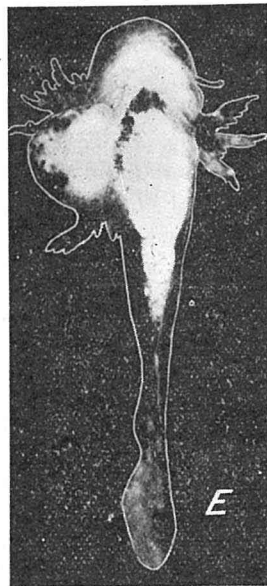


Fig. 26. Photograph of the Specimen NO. E.

becomes perfectly single, two chordæ lie still touching each other; the one which is small and belonging to the parasite, is located ventrolateral to the other of the autosite. They become single near about the middle of the tail. The dorsal aortæ of both members become confluent far before the union of the spinal cords. Therefore, in this specimen is held the general rule, that the aorta is the first, the spinal cord the second and the chorda the last in their union with each other. The left heart is normal in orientation, but the right one is reversed. As to the alimentary tract, only a little can be said, because the yolk granules are not yet exhausted. The oesophageal portion is clearly separated, but it is difficult to ascertain where two canals unite. The rudimentary livers occupy the normal position posterior to each heart, but they unite to make a common large lobe. Pronephri of the inner sides fuse into a median single organ. Its Wolffian duct is very short and terminates blindly. Outside pronephri run posteriorly in the normal course of the respective member, viz. under the outside myotomes, and open into the cloaca from its dorsolateral sides.

Double No. 17 (1935): In this specimen bifurcation occurred unequally at the posterior part of the trunk. Being however the trunk of the parasite still underdeveloped, the parasite appeared to attach by neck to the host's trunk (fig. 23, 17). The growth of the parasite was fairly arrested as a whole, but a small head was proportionate in its parts. As to the autosite abnormal structures were only found in the forelimb on the right side and the ventral fin of the tail. The right limb was nothing but two conical processes appeared one immediately behind the other, and their development was extremely retarded. Whether the processes give rise to one or two limbs is problematical. It was unknown however because of the specimen having died before showing any farther differentiation. The ventral fin was found only near the posterior end as in the case in No. 26. The larva was found dead and could not be available for sectional study due to maceration of the body.

Double No. 9 (1934): The dorsal fin of the parasite ran first obliquely dorsad and then caudad along the side of the autosite from the middle of the trunk near to the end of the tail. It was united finally with the ventral fin of the autosite, whose dorsal fin was quite normal (fig. 27). The anterior free part of the parasite projected from the autosite immediately behind the heart and soon turned backwards in a rather caudal direction. And in this free part, the most marked abnormality of the structure was noticed; two balancers stood side by side on the ventromedian surface. There developed 3 gills on the left side and only one on the right side (fig. 27, 9 a). The development of these gills was very retarded as compared with that of the autosite's. A structure like the mouth was first noticed, but became gradually indistinct and finally hard to detect from outside. There occurred later a cyclopean eye at the anterior extremity, but no sign of the nostril was recognized in its vicinity. Heart was produced at the

junction with the autosite and beat more quickly at first, but became gradually weaker than that of the autosite. Posteriorly the parasite was gradually flattened and blended into the tissue of the autosite; its extension was only detectable through the heavy pigmentation characteristic to the back of the body. A rather small but well proportionate forelimb was found developing on the left side, while the right limb was extremely small and only provided with 2 fingers, nevertheless its orientation seemed to be normal.

When it was alive, the appearance and behavior of the autosite was quite upright and normal, except that the parasite hung from the middle of the abdomen.

Cross section was applied with respect to the autosite. The head of the autosite is entirely normal upto the vicinity of the heart. It is extraordinary noteworthy that this heart shows the inversed structure. As the autosite was the left member, the heart inversion in this case was the only exception to the general rule in which situs inversus cordis takes

place on the right member of a pair. Not only the heart, but also visceral organs are inversed; stomach appears on the right and liver on the left of the abdominal cavity. Needless to say, the stomach is formed on the left and the liver on the right in the normal course of development. The liver of the autosite is united with the same organ of the parasite, which appears dextral and ventral to the stomach of the autosite. Livers are respectively provided with a gall-bladder.

The abnormality of the autosite is farther extended to the Wolffian duct. At the level of the left pronephros of the parasite, it sends out a branch which runs posteriorly outside the somites and terminates blindly. The pronephric tubules of the parasite, however, open into the main stem of this duct, but it does not extend tailwards anymore. Accordingly, the right side of the autosite is devoid of the Wolffian duct caudal to this level.

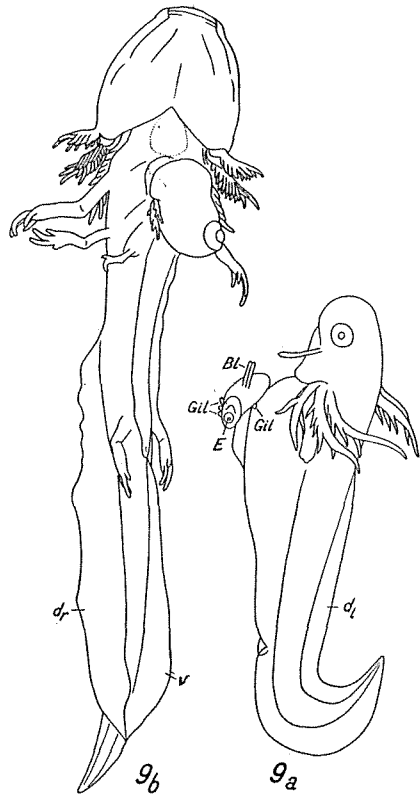


Fig. 27. Outline sketches of the specimen No. 9. *a*, Yonug larva, showing the developmental delay of the parasite. *b*, Its old stage.

In spite of the absence of the duct, the mesonephros develops in the proper position. In other words the development of this organ is shown to be independent to the presence of the Wolffian duct. The mesonephros in this case is, of course, not followed by any leading duct. The fact involves the suggestion that the mesonephros has no faculty to repair the duct when it is absent.

By far the most abnormality appears in the heart of the parasite. It is less differentiated, exceedingly abnormal and almost hard to say its situation being normal or inversed. As to the visceral cartilages, the branchials are reduced in number; there are only two on the left and one on the right. The cartilage which may be considered as the second basibranchium is not connected with the first basibranchium; it is located freely in front of the heart. Hyoid cartilages are quite normal and attaches by their ventral tips, to the first basibranchium like in the normal case. Between the dorsal portions of the hyoids there appears a large cartilage, which divides anteriorly into left and right halves, but fuses again in the more anterior region into the V-shape in cross sections. Which cartilage it is equivalent to, is uncertain.

As the sections proceed posteriorly, e. i., anteriorly with respect to the parasite, ears begin to appear. They are located respectively on the outside of the arms of the uncertain V-shaped cartilage just mentioned, but touch each other in the middle part. In this part the cartilaginous capsule is common, surrounding both ear vesicles. The arms of the above named cartilage become gradually shorter to take the oval shape and disappear finally. Then a cyclopean eye begins to appear in the place of the cartilage. It is nearly normal in structure and encloses a well-formed lens. However, one thing peculiar to this eye is that a small lentoid body is found buried in the retinal tissue near the iris (fig. 28). It may be produced from the iris-margin.

In front of the eye there occurs a nose (in sections posterior to the

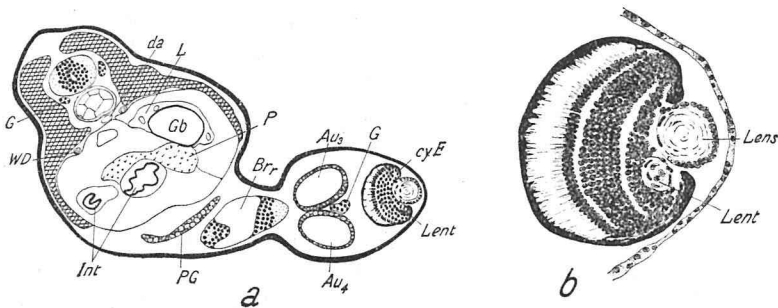


Fig. 23. Cross section through the specimen No. 9. *a*, Showing a cyclopean eye and a small lentoid. Auditory capsules are in contact with each other. *b*, Enlargement of the cyclopean eye.

eye), which has no nostril and contains only a vesicle, whose wall becomes gradually thinner towards the outer surface. Brain is highly defective, its ventricle being reduced into a small cavity. Spinal cord is also abnormal, and its canal is obliterated to become a solid cord near its posterior end, and ends bluntly in the abdominal mesenchyme of the autosite in the vicinity of the right limb of the parasite. Therefore, this spinal cord bears no direct relation to that of the autosite. The chorda fails to be found anywhere. The pronephros of the left side is described above, while the same organ is not formed on the right side, though what is the reason is unknown.

The oesophagus of the parasite is short and ends blindly. The stomach is not produced, but the liver is formed as already mentioned.

The posterior part of the autosite is nearly normal, except only the presence of the parasite's dorsal fin.

Double No. 13 (1935): This specimen was the exceptional case to the general tendency that the right partner becomes parasitic. Here the left partner was the parasite and the right one represented the autosite; the former having been shifted to the ventral side of the latter (fig. 29). The parasite was greatly defective and abnormal; the eye was single and the balancers were 4 in number, produced at the unexpected position posterodorsal to the eye. Resorption of these balancers was almost at the same time as those of the autosite. Mouth-like aperture was noticed on the ventral side. Gills appeared much posteriorly in agreement with the level of the autosite's gills. They were 3 on the left side, while 2 on the right side, the development of which was much delayed and retained in the rudimentary state, especially on the right side. Forelimbs occurred also at the level at which the autosite's limbs were produced. Accordingly, the distance between gills and limbs was disproportionately long to the body width of the parasite. These limbs were smaller but harmonious with the body of the parasite. Their developmental state was nearly comparable with that of the autosite's. What is more, another forelimb rudiment was produced later between the parasite's right limb and the autosite's left limb (fig. 29, 13*b*). Though it was retained in a finger-like process without digit-formation, the differentiation of the upper and lower arms was distinct. They were articulated parallel to the autosite's and therefore symmetrical to the parasite's. The origin of this extra limb was entirely unknown, but it is interesting that its differentiation is effected by the parasite's limb, instead of the autosite's.

There occurred 2 hearts, which were established on either side of the hypobranchial region of the autosite. They were quite normal in the external aspect and both functioned in a similar way with approximately the same pulsating frequency. This interesting larva died unexpectedly in a sultry night of June, and it was found next morning already unavailable for the internal anatomy in sections.

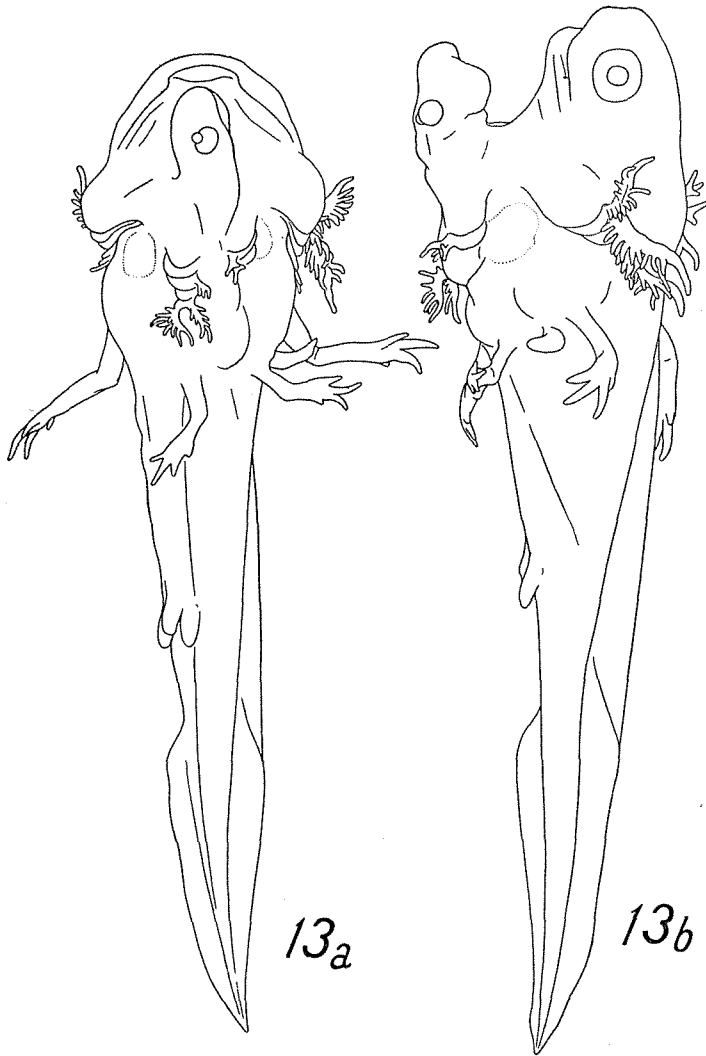


Fig. 29. Outline sketches of the specimen No. 13. *a*, Ventral view with respect to the autosite. *b*, Lateral view from the left side of the autosite.

Double No. 14 (1935): The right parasitic partner of this anadidymous monster lacked its anterior part upto and including the heart (fig. 30, 14). The specimen like this was very rare in nature. It was provided with a pair of forelimbs, which were situated harmoniously; the left (inner) limb was slightly larger than the right (outer) one. The trunk was gradually flattened with the developmental advance, though the dorsal fin was dis-

tinctly formed. The trunk of the host was approximately normal, save for the attachment of the parasite. The tail turned to the right considerably, but there appeared no abnormality in itself.

The last observation was done several hours passed after the specimen died, and the skin began already to macerate. Nevertheless, it was fixed and cut in cross sections.

The anterior part of the autosite is entirely normal. The first sign of abnormality comes out in a section cut through behind the forelimb region by the début of the left forelimb of the parasite, as is expected from the surface observation. The pectoral girdle belonging to this limb is curiously constructed, namely the ventral tip of the coracoid, which runs toward the midventral line in the normal

development, is prolonged in the opposite direction, i. e., in the direction like in the right forelimb of the host and also in the same direction of the

right forelimb of the parasite which appears more posteriorly (fig. 31). In these regions of the parasite there occurs neither spinal cord nor chorda, but it is uncertain whether these axial organs did not appear from the first or have been degenerated during development in these anterior parts of the parasite. From the occurrence of the forelimbs the second view seems to be more plausible. The parasite is an acardia.

As to the structure of the pronephros the remarkable abnormality is also observed. The right Wolffian duct of the host is connected with the left pronephros of the parasite behind the forelimb of the latter. Leaving this level, the duct is gradually shifted outside and passes across the median plane of the parasite towards its right side. Then it is related to the right mesonephros of the host which is also dislocated. In short, the right Wolffian duct of the host passes through the left



Fig. 30. Outline sketches of the specimens with acephalous parasite.

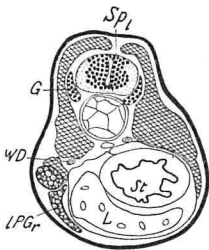


Fig. 31. Cross section through the trunk of the specimen No. 14, showing the left pectoral girdle of the parasite growing to an unexpected direction, viz. opposite.

convoluted pronephros of the parasite in the way to its own mesonephros. The right pronephros of the parasite fails to develop as in the specimen No. 9 due perhaps to the potential conflict between the host and the parasite.

The spinal cord and the chorda of the parasite appear first at the level through the mesonephros of the host; their anterior ends become gradually slender. The spinal cord is degenerating, so that the definitive outline of this organ is hardly taken. It is united with that of the host at the level through the middle of the anal tube. The chorda is separated far posteriorly; it is uncertain where it is united with the host's one on account of the deformation of the posterior portion of the specimen.

A small independent liver of the parasite appears in the common body cavity besides the larger host's one. It is not provided with a gall-bladder. The alimentary tract is nothing but a blind tube evaginated from the host's canal towards its dorsal side at the level behind the gall-bladder of the host.

There are one pair of the hindlimbs which belong without fail to the host, and no structures comparable to them are found in the parasite.

Double No. C (1932): On the ventral side of this embryo there was another prominence, extending from the middle of the yolk mass to the blastopore. This prominence seemed to be one of the neural fold which did not fuse completely with its mate of the opposite side, when viewed from the blastoporic side (fig. 30, C). To what monster the embryo grew up was unknown, but it would become perhaps an anadidymus, one member of which was devoid of the head like the specimen No. 14. It died in this stage and was not sectioned.

Double No. 10 (1934): This specimen was more or less slender in shape. On the ventral yolk mass there occurred another embryo-like structure, though it was devoid of head and limbs to the last (fig. 32). It was nothing but a prominence running along the ventromedian of the host; its anterior extremity passed insensibly to the general surface of the host at the midway of the abdomen. The posterior part of the parasite was shifted towards the left of the host and finally protruded as a tail-like process with the dorsal and ventral fins. The parasite was pigmented like the autosome. The sectional examination reveals, however, that it may be erroneous to call the parasitic structure the secondary embryo. It is devoid of the axial organs such as chorda and spinal cord. It consists of only muscular and nephric tissues (fig. 33, *a*). In the latter pronephric and mesonephric tissues may be distinguished; the more posterior level, the more mesonephric tissue being found.

On the left side of the host the Wolffian duct is ill-developed and in some parts it is entirely missing. On

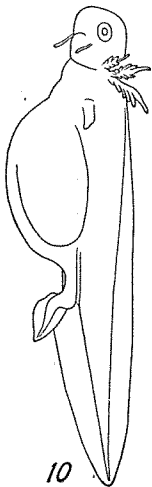


Fig. 32. Outline sketch of the specimen with a supernumerary tail-like appendix (No. 10).

the other hand the same duct is found on the left side of the parasite. The parasitic elements are finally unite with those of the left-side elements of the host. The left Wolffian duct opens into the right one, which in turn opens into the cloaca. The tail-like protrusion above mentioned is not a true tail. It is composed of only a mesenchymal tissue and devoid of axial structures (fig. 33, *b*).

The origin of this ventral prominence is problematical; either the degeneration of the axial organs or the splitting of the nephric tissue with the surrounding muscles may be considered in this case. If the latter is the case, strictly speaking, this specimen cannot be contained in the category of a double monsters, but is only a malformation.

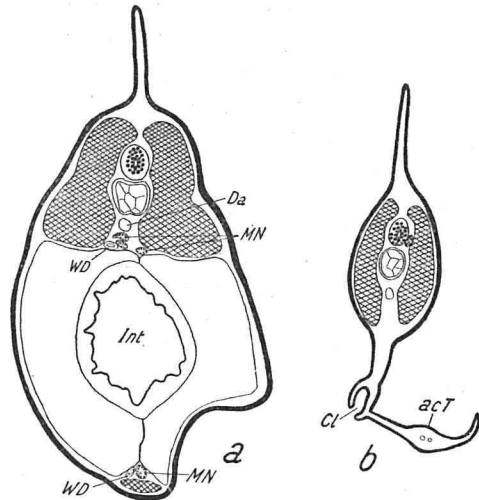


Fig. 33. Cross sections through the specimen No. 10. *a*, Showing the lack of axial organs in the parasitic prominence, and the presence of muscular and mesonephric tissues accompanied by the Wolffian duct. Just the same tissues and duct are missing on the left side of the host. *b*, Showing the lack of the axial structures in the tail-like appendix.

Considerations

1) *Formation of the double monsters*: After SPEMANN's findings (1903) that the double-headed embryos or partial twins are produced experimentally by means of constriction along the median plane of an Amphibian egg, KAUFMAN (1913) has ascribed the occurrence of such a monstrosity of *Salamandra maculosa* in nature to the same mechanical reason. Namely, as this animal is ovoviviparous, the egg, if constricted by the mouth of the uterus when the egg capsule is disproportionately larger and protruded from the uterus into the oviduct, would be expected to develop to the double-headed embryo. If such were the case, the monsters should be found, at least, near the end of the capsule. But in fact they are located in the middle of the capsule. KAUFMAN's assumption of uterin constriction may, therefore, be not plausible, as POLITZER (1926) has already pointed out. Especially, in the oviparous animals such as the present newt it is by no means hold.

In POLITZER's opinion the katadidymus is an embryo, posterior part of which is splitted as a result of the disturbed gastrulation, something like "spina bifida". It is likely that the disturbed gastrulation is the cause not only the katadidymous monstrosity, but also of the anadidymous mal-

formation, though the meaning of the term "disturbed gastrulation" is by far different from POLITZER's. He believes in the concrescence theory of gastrulation and therefore says, as to the genesis of the katadidymous anomaly, that "Der normale Verschluss des Urmundes unterblieb in einem von den kranialen Chordaenden bis zu den Schwanzwurzeln reichenden Bezirk" (l. c. p. 191). As to the formation of the anadidymous monster he seems to maintain the similar view as presented in fishes by ardent advocates of the concrescence theory. In fishes RAUBER (1877-'80) explained as thus: when the separate embryonic shields should appear on the same blastoderm, each embryo would use half of the portion of the germ between them as the inner half of the axial organs of the trunk, but after this intermediate portion being exhausted completely, the outer side of two embryos should be united into a single body. The degree of bifurcation is, therefore, dependent upon the distance between the two embryonic shields. STOCKARD (1921) believes, based on his extensive experimental works on the effect of changed conditions, that the twins or double embryos of a fish *Fundulus* are the result of secondary budding which occurs on another place of a germinal disc as a consequence of a developmental arrest of a primary bud or embryonic shield, something like in plants.

At the present state of our knowledge the gastrulation process is, however, not to be concrescent, but to be convergent, so that the mechanism of the double formation becomes to require another explanation. Thanks to the discovery of the organiser by SPEMANN and H. MANGOLD (1924) and also to the result of local staining of the germ surface by VOGT (1925), our knowledge of an Amphibian development becomes very advanced, especially the fact that the formation of the neural plate is dependent on the presence beneath it of the organising material is capitally important. According to BAUTZMANN (1926), such an organising material in *Triton* occupies the area immediately above the blastoporic lip of a young gastrula upto about 90 degrees and spreads out also halfway around the egg. Any part of this limited area, if either transplanted elsewhere or inserted into the blastocoel and happened to lie under the surface ectoderm, can induce the secondary neural plate in the overlying ectoderm. Even a piece far from the dorsal lip has the faculty to call forth the neural induction, so far as it is taken within the limit of the named organiser area (BAUTZMANN, 1926). Furthermore, it is known that the blastoporic lip of a later gastrula has specific inducing potency of somewhat different sort. Namely, when it is implanted, it induces the secondary embryo deprived of a head and composed only with a trunk and a tail so far as it lies in the flank of the host embryo. To this is applied the term "trunk-organiser" and the former dorsal lip of a young gastrula is designated as "head-organiser" (SPEMANN, 1927). The specificity of the head-organiser is to induce always a embryo with a head in any part of the host.

In the process of gastrulation, if one should assume that the dis-

turbance should occur for some reason only in its early stage in such a way that the organising material is divided physiologically or potentially and also if this disturbance should be taken away in its later stage so as to recover the normal course of event, it is obvious that the invaginated organising material would become Y-shaped in the inducing effect; a part of the head-organiser being forked, whereas that of the trunk-organiser remains single. As the result, the double-headed embryo would be induced. Thus, the doubling is assumed to be a phenomenon involving essentially a physiological isolation of the organising material. In fact, we can isolate the organising material into Y-shape to obtain the similar anadidymous embryo, by the mechanical constriction of an egg (SPEMANN, 1903) or by the union of two gastrula-halves, with dorsal lips turned at an angle away from each other (SPEMANN, 1918; KOETHER, 1927). If this assumption is right, the degree of bifurcation may logically be the function either to the time of disturbance or to the degree of angles made by the forked portions of the organising material or to both. In reality, it is clearly evidenced by the fact that the external bifurcating degree is well proportionate on one hand to the level where the chorda is separated, which is the direct transformation of the organising material, and on the other hand to the angle made by the divided portion of the chorda. For example, comparing the specimens No. 8 and No. 22, in spite of the chordæ being divided at the approximately same level of the 12th somite in both individuals, the apparent doubling of the former is less remarkable due to the fact that the bifurcating angle of chorda is smaller in it than in the latter. The same example is also found as comparing the specimens No. 24 and No. 7, in which the chordæ are separated at the level of the 17th somite. While, if comparison be made between the specimens No. 8 and No. 7, one cannot fail to find the correlation existing between the external doubling and the level where the chorda is divided; the duplicity of the latter is far remarkable.

If the division of the organising material should be unequal, the parasite and autosite would result, because the dimension of the neural plate, and accordingly the size of the embryo is proportionate to that of the inducing material (MARX, 1925). In the extreme case, the parasite should be represented only by a small excrescence appearing on the lateral side of the host's head and being hardly recognizable as an embryo (ref. Nos. 4 and 26). Indeed, in the constriction experiment, if the ligature is oblique so as to divide the organising material unequally, the same relation of autosite and parasite is established (SPEMANN, 1903). It is worth to record here that in all specimens, except No. 13, of anadidymus asymmetros described in the present paper the left member of a pair shows the greater tendency to give rise to the autosite. In POLITZER's specimen of his so-called *Dicephalus tetrabranchis dipus asymmetros* the same relation of autosite and parasite is shown, and in OYAMA's katadidymous specimen is also presented the domi-

nancy of the tail on the left side, the right tail being undergrown. To settle whether it is a mere chance occurrence or whether it shows the existence of such a tendency, the material is too scarce in my hand, and the experiment is also lacking.

The specimen No. 14 is perhaps produced as follows: After the normal invagination of the head-organiser, the disturbance takes place so as to split the trunk-organiser unequally. Thus, the induced embryo by the branch of trunk-organiser would be without head. Recently, MANGOLD (1936) obtained the similar acephalous secondary embryo by implanting into a blastocoel a piece of an archeenteron-roof, taken from a portion equivalent to the trunk-organiser, though in this specimen the parasitic embryo is not connected with the primary embryo by the axial organs. In this point MANGOLD's specimen bears a more resemblance to the specimen No. 10 in the external appearance. This specimen No. 10 is supposed, as its developmental process was not traced, to be produced probably by that in the middle of gastrulation the portion of the trunk-organiser is separated completely or by that another organising centre occurs independently in the lateral lip of the blastopore, like the case of the transplantation of the trunk-organiser into another embryo. However, the examination in sections of the specimen proves that this assumption may not be correct, because the secondary embryo is not provided with the axial organs such as a neural tube and a chorda. It is only composed of the muscles and the nephric structure with a duct. The tail-like process of this specimen is also nothing but a fin, containing the mesenchyme. Such a so-called secondary tail without the axial organs has been reported by RUUD and SPEMANN (1922), who consider it as a reduced form of one tail of the spina bifida. This assumption is, however, not plausible in the present specimen. It should be rather considered as the result of a mere translocation of a part of the tail mesoderm.

The formation of the katadidymous monsters not contained in the present material would be also explained by the furcation of the organising material. If a disturbance should occur in the course of invagination of the endoderm and of epibolic movement of the dorsal lip, the blastopore should remain without closing. In such a case the movement of the surface ectoderm as well as organising material is by no means normal; first the organising material, which should be gathered confluent into the dorso-median of the body, would be divided bilaterally by the existence of the protruded endoderm, and it would roll in *in situ* through the lateral lip. It should call forth the neural induction respectively on either side of the uninvaginated plug of the endoderm, and would result in the formation of the double-tailed anomaly. Therefore, the katadidymus is regarded as a double formation like the anadidymus, and naturally the forked portions are not half embryos, but whole embryos, though the structural defects are remarkable on the inner side of each. POLITZER's specimen of such

monsters shows the distinct defects of the inner side of each bifurcated portion, while in OYAMA's specimen the left partner is provided with the somites of nearly normal size (his Fig. 12) and the right partner also has the piece of somite at some parts on their inner sides (his Fig. 14). Comparing these two specimens, it is likely that the disturbance is stronger in the former than in the latter. The more extensively the organising material rolls in, the more perfect structures may result. Thus, the defects of the inner side are highly attributable to the deficiencies of the mesodermal material in consequence of its space being already occupied by the yolk-plug. This assumption is supported experimentally in another way by the result that the embryos induced by the transplanted organiser from the presumptive ventral side of the host embryos, where no presumptive somatic material exists, are often provided on both sides of them with the somites derived solely from the material *in situ* of the host. Therefore, the structural defects of the inner side are not a necessary reason for it being the half embryo as insisted by the supporters of the conrescence theory. That the approximately half size of the neural tube and chorda is not also a reason for their being half, may be indisputable in the light of MARX's findings quoted above in the consideration of the parasitic formation.

This explanation to the morphogenesis of katadidymi is easily applicable to the specimens of the so-called *spinæ bifidæ*, but rather difficult, not altogether unavailable, to the formation of *Duplicitas posterior* in the strict sense, namely to the specimens in which the two posterior parts of the body possess no defects and no endoderm left between them. Such a katadidymous specimen of Amphibians is not found hitherto in nature, so far as I am aware, although it is rather common in the meroblastic animals such as bird, reptile and fish. In these classes the organising centres may apparently occur at the two positions of the same blastoderm, and the gastrulation takes place in such a direction that the invaginated head-organisers come to fuse each other. In Amphibians these monsters are only known to be produced experimentally by the union of two gastrula-halves with dorsal lips turned at an angle towards each other (SPEMANN, 1918; WESSEL, 1926; KOETHER, 1927). To this type of monstrosities highly resembles OYAMA's specimen, of which the left partner is nearly normal in its axial constitution, but a small yolk-plug seems to remain in exposition. Therefore, it cannot represent *Duplicitas posterior* in the strict sense in the present definition.

The brief conclusion concerning the formation of the double monsters can here be reached from the above statement as follows: All specimens of anadidymi as well as katadidymi found in nature are brought into being by the physiological or potential bifurcation of the organising material in the course of gastrulation. As to the cause of this physiological bifurcation we may account for mainly the unfavourable environmental conditions, in which the eggs are subjected to develop during a critical period

of differentiation, as has been demonstrated with fishes by STOCKARD (1921) and by HINRICHS and GENTHER (1931). Since the susceptibility of the Amphibian egg to the deleterious effects of the unfavourable environmental conditions is greatest in the dorsal lip region (BELLAMY, 1919), this part may be the first to be affected to disintegrate or to lose its inductive effect upon the overlying ectoderm. Thus, the bifurcation of the organising material may result. HINRICHS and GENTHER's statement that "early exposures (to the ultra-violet radiation) produce only anterior dichotomy (anadidymy), while double-tailed forms or posterior dichotomy (katadidymy) appears only as a result of later exposures" (p. 481) seems to afford another evidence to the above assumption of physiological isolation of organiser, though the difference of head- and trunk-organisers has not yet postulated in fishes. In Amphibians, at any rate, the different susceptibility of gastrula may be the essential cause for the physiological isolation of the organiser, which in turn calls forth the formation of the double-embryo from the overlying ectoderm.

2) *Bifurcating degree of the axial organs:* That the bifurcation of the chorda is greater in degree of the caudal extension than that of the neural tube in every case of anadidymy, has been already pointed out by previous authors who worked on the same kind of Amphibian monstrosities. This rule is of course applicable to the present anadidyamous specimens. As the explanation for this fact, POLITZER (l. c.), based on the conrescence theory, says "Es hat . . . beim Rückenmark eine Verschmelzung der ursprünglich getrennten Anlage stattgefunden, während ein ähnlicher Vorgang im Bereich der Chorda nicht erfolgt" (p. 188). This phenomenon, I think, can easily be elucidated by the fact that the neural plate is invariably greater in width than the presumptive chorda by which it is induced. Namely, as diagrammatically shown in Fig. 34, if the chorda anlage is bifurcated into two branches at a point A and induces each a corresponding neural plate, the two plates must fuse each other at a distance A-B anterior to A. Thus, the bifurcating degree of the chorda becomes greater than that of the neural plate. This elucidation is also applicable to the case of one neural tube with two chordæ beneath it. In this case the chorda rudiments are parallel each other, and induced plates may fuse lengthwise in the median.

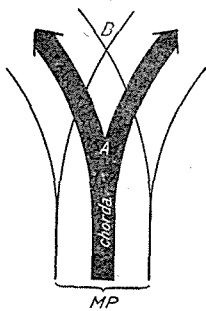


Fig. 34. Diagrammatic figure to show why union of the spinal cords takes place anterior to that of the chordæ. See explanation in the text.

The doubling of the dorsal aorta is nearly the same in extension as that of spinal cord. But the bifurcation of the viscera, especially the alimentary organs, is limited far anteriorly. In the specimen No. 24 the chorda is forked as posterior as the 18th somite, but no sign of duplicity is found in the alimentary system, but for the branchial cavity. The specimen No. 1 shows first the sign of doubling in the oesophageal

region by the elongation of the endodermal folding of the branchial cavity into this region, but the more posterior part of this system seems to be undivided. In the specimen No. 21 the gastric portion may be divided, but somewhat uncertain on account of its being fixed before the definitive organ differentiates. The bifurcation of the stomach is first clearly shown in the specimen No. 7, in which the chorda is separated up to the level of the anus. The bifurcation of the chorda is essentially proportionate in degree to that of the neural tube, but not strictly so to that of the alimentary canal in consequence of the various diverging angles made by the branches of the chorda. However, we can safely conclude that the bifurcation of the chorda is the greatest in degree and that of the neural tube comes next, whereas the duplicity of the alimentary canal stands always the last.

3) *Eye*: That the formation of eyes is much dependent on the conditions of the underlying substratum, especially to the status of the prechordal plate and prechordal (mandibular) mesoderm is now clear by the experiments injuring the whole or part of the substratum by means of mechanical or chemical treatments (ADELMANN, 1930-'37; MANGOLD, 1931-'36; ALDERMANN, 1935, '38; LEHMANN, 1926-'38; SHEN, 1937). According to the previous workers, the inducing effect of the prechordal substratum is at first a generalized stimulus for the formation of a harmonic equipotential eye-field or optico-ocular apparatus, and within this field the bilaterality is then effected by some influence exerted from the prechordal mesoderm. ADELMANN (1937) is inclined from his ingenious experiments to believe that the inducing stimulus is of chemical nature of substances, which are produced by the prechordal substratum, especially produced more actively by the two prechordal mesoderms situated laterally than by the median prechordal plate. This physiological difference serves essentially "to establish two lateral centres of higher eye-forming potencies" (p. 222). "The close union of the neural plate and prechordal plate possibly function in a mechanical way to facilitate the lateral movement of materials. The cyclopean eye and forebrain would arise from the generalized field induced when the proper physico-chemical interrelation between substratum and reacting materials is upset." (pp. 222-223). This assumption may be also applicable to the cyclopean eye of the parasite of the specimens Nos. 9 and 13 in the present material which would be likely formed from the disturbed relation between the substratum and the neural plate. But other cyclopean and synophthalmic eyes are interpreted to be induced otherwise. Namely, when the bifurcation of the head-organiser occurs, the material of the prechordal substratum is also divided anteriorly into two parts. Thus, each substratum has the capacity of determining the optico-ocular apparatus in the corresponding forebrain induced also by the same substratum. But in the formation of the prechordal mesoderm or in the so-called lateral "massing" of the neural plate, the tissue of the inner side may fuse each other. According to this degree of fusion the cyclopean or synophthalmic eye may be resulted. The median eye of some specimen of WESSEL's *Duplicitus cruciatus* (1926)

may represent such a cyclopean eye.

After WERBER's nomenclature (1916), the synophthalmic eyes are further classified into two groups by the degree of side by side fusion: Synophthalmia unilenticata encloses one lens and synophthalmia bilenticata encloses two lenses situated side by side. We find the former example in the specimen No. 5 and the latter examples in the specimens Nos. 8, 12 and 15 of the present material. The last specimen No. 15 seems externally to be provided with two sets of eyes, but sections reveal that the eyes of the inner sides fuse internally each other and form a synophthalmic eye. And it may be said to represent the passing state from synophthalmia to perfectly separate eyes. The median eye of the first specimen No. 5 much resembles to the cyclopean type, but it has shallow indentation revealing the synophthalmic nature. Furthermore, synophthalmic character of this eye is suggested by the arrangement of the lens-fibres. This lens is a perfect and normal ball in the external appearance. But there are two centres of fibrous arrangement enclosed by a common epithelium. Such a lens with two centres is produced in *Rana* experimentally by the union of two optic cups (PERRI, 1934). The morphogenesis of such structure of a lens may be explained in two ways: First, there appear two fibre-differentiating centres in one vesicle, effected by the stimuli exerted highly from the two parts of the united retina, each corresponding its own emerging centre when separated. Second, there appear two vesicles, and after commencing the fibrous differentiation they unite into a single ball. The first interpretation is supported by DRAGOMIROV's experiments (1929), in which two fibre-differentiating centres are established in one vesicle by the transplantation of the ear near to it. In this case the grafted ear is no doubt the factor responsible for the formation of the extra centre. The second explanation is supported by SATO's experiments (1930). He found the union of the two lenses into one composite lens in the implantation of a iris-piece into the eye chamber.

In the connection of this lens-formation, another abnormal eye remains to be considered. It is a cyclopean eye of the specimen No. 9. In this eye there is a lens with the normal structure and position. Besides it there occurs another lentoid buried partly within the retinal tissue. As it is traced close to the margin (iris) of the retina, this lentoid may be originated from this part of the eye. The similar figure is found by FISCHER (1902) in the case of the iris-transplantation into the eye, and he considered it as the transformation of the grafted piece accidentally placed in the retinal tissue.

4) *Nose*: ZWILLING (1934), using the intermediate neurulæ of *Rana pipiens*, succeeded to induce a nasal placode in the flank ectoderm by the transplantation of the part of the forebrain, median and slightly anterior to the optic vesicle. KAWAKAMI (1938) has attempted to ascertain ZWILLING's finding with the embryos of Urodelan *Triturus pyrrhogaster* and reached to the same conclusion. Therefore, in Urodeles as well as Anurans the deve-

lopment of the nasal placode is well proved to be related to the preexistence of the forebrain. The supernumerary nose of the specimen No. 4 is, therefore, understood to be induced by the parasitic branch of the brain, which, though now reduced in size and dislocated in position at a side posterior to the eye, may be equivalent to the anterior extremity of the autosome's forebrain, because of the double occurrence of the cranial cartilages derived from the mandibular group of mesectoderm.

A monorhinal appearance in the parasite of the specimen No. 9 is attributed to either the fact that the nose inducing centre is single or the fact that the reaction-system is too narrow spatially to produce a pair, though the inducing centre being doubled, or both of them. ADELMANN (1937) maintains the former view in the statement that "(we have found) a close correlation between the degree of bilateral massing of the materials of the forebrain and the extent to which single or double olfactory placodes or sacs are differentiated." (p. 223). Namely, when the supersession of the bilateral massing occurs, the single olfactory sac is formed from an harmonious equipotential olfactory field due to prevention of producing two centres of induction. It is also quite logical consequence that the cyclopean specimens are often monorhinal like in the specimen No. 9 and others in other literatures. Such a nose is often situated dorsad to the cyclopean eye due to the spacial narrowness.

5) *Ear*: The development of the ear is subservient to the inducing influence exerted from the lateral wall of medulla oblongata (STONE, 1931; GUARESCHI, 1935; ALBAUM and NESTLER, 1937). Therefore, it is quite natural that in the anadidymous embryos the development of the organ is much conditioned by the degree of bifurcation. Namely, when the bifurcation occurs behind the level of medulla oblongata, the heads are provided each with a pair of the ear, but when it occurs anterior to medulla oblongata, the composite heads are provided with a pair of the organ only on the outer side of each element. When the bifurcation takes place just at the level of medulla oblongata, there develop 3 ears; 2 on the outer side of each head and one in the median. This median ear is due to the inducing influence of both heads, but it develops as one, because the latter are too nearer each other to have the respective effect of induction to the reaction-system of the ectoderm. We find the examples of the first type in the second and third groups, those of the second type in the first group (A, B) and those of the third type in the first group (C). Furthermore, we can find theoretically the composite or united ear as a connection between the first and the third types, though not found in the present material. In the parasite of the specimen No. 9 we find the example of the composite type. However, in this case the inducing centres belong to the same system and have the separate effect; the composite nature being only secondarily aroused by the fusion of each other due to a particular condition that occurs on the ventromedian of the medulla oblongata. These composite vesicles are sur-

rounded by a common cartilaginous capsule. OYAMA's specimen (1927) represents the passing structure from this type of fusion to the separate one, showing a pair of capsules fused together along the inner sides of the posterior part.

6) *Pro- and mesonephri*: The inductor of the pronephros is not yet known, but it is certain that the other mesodermal tissue, if placed in this field before the critical stage of determination, can give rise to the pronephros (YAMADA, 1937). In the anadidymous monsters, we find this organ on the inner side only when the bifurcation occurs in this field, i. e., in the specimens belonging to the second group of the present materials. In the specimens Nos. 7 and 19 there is a single median pronephros common to both partners. The median pronephros of the latter specimen is forked anteriorly into Y-shape and represents a passing state to the separate organs of the more strongly bifurcated individuals.

It is also uncertain whether a correlation between the pronephros and Wolffian duct exists or not in their morphogenesis, but the experiments, in which the extirpation of the pronephric rudiment is followed always by no or at least rudimentary formation of the duct, seems to show its existence (YAMADA, 1937). But in the present materials the pronephros is not necessarily attended by the Wolffian duct. The duct of the median pronephros, if formed, terminates blindly, and in no case it reaches so far posteriorly as to the cloaca. In his transplantation experiments, MASCHKOWZEFF (1934) found the development of the duct on the body side, running dorso-caudad to fuse with the normal duct. In these cases, however, it is questionable whether the duct is dependent in its development on the presence of the pronephros or whether it is merely an extension of the latter as the duct. The latter view is maintained by LILLIE (1919) and WADDINGTON (1938) in chick, but in Amphibia it is not quite conclusive. To this question the present study gives no contribution.

As to the development of the mesonephros there are now two different opinions. One believes its subservient development to the presence of the Wolffian duct (MIURA, 1930, in *Rana* and *Bufo*), while the other neglects such correlation and maintains its independent- or self-differentiation (SHIMASAKI, 1930, in *Bufo*; MASCHKOWZEFF, 1934, in *Rana* and *Siredon*). Recently, GRÜNEWALD (1937), from his experiences in the chick embryos, says that "... das Vorhandensein des Wolffschen Ganges zum Differenzierung der Urnier notwendig ist, dieser Gang also einen induzierenden Einfluss auf das mesonephrogene Gewebe ausübt." (p. 796). WADDINGTON (1938) studied also this problem on the chick and the frog and came to the conclusion conformable to the findings of MIURA and GRÜNEWALD. He says "... in Anura also the pronephric duct plays a large part in the initial induction of mesonephros development." (p. 375). At the same time, however, he admits the existence of a feeble power of self-differentiation of the mesonephros as a double assurance in both classes.

Now, examination of the present materials supports conclusively, against the recent opinion, the view of independent formation. In the specimen No. 9, the mesonephros is produced in spite of the absence of the Wolffian duct and differentiated well with lumen. This mesonephros is of course not provided with any duct to function in future.

In brief, the correlation between the pronephros and the Wolffian duct is uncertain, but that between the duct and the mesonephros is certainly lacking in the initial formation of the latter organ, at least so far as the present Urodelan monsters are consulted.

7) *Heart and situs inversus cordis*: The primordia of heart are at first located separately in the hypobranchial regions of both sides of the head and then migrate ventromesad to unite with each other and differentiate into one organ. Accordingly, in the cases of the anadidymous monsters, in which the bifurcation occurs behind this region, it is quite natural that they should be furnished with two hearts, each corresponding to either head. It is also quite clear that there is one heart in the specimens in which the doubling is limited only in the anteriormost and not reaches to this region.

It is interesting here to say that when two hearts coexist, the left one is always normal in situation with only one exceptional case (specimen No. 9), while the right one is inverse more or less without exception. Thus, the two hearts are mirror-imaging to each other. This status of hearts is distinctly shown in the specimens Nos. 6, 7, 11 and others. POLITZER (1926) reported also one good example of situs inversus cordis of the right partner, but he failed to find any case of such inversion of the left partner among his materials. SPEMANN and FALKENBERG (1919) obtained the similar heart inversion of the right partner in 47 per cent (14 out of 30 individuals), whereas the left partner only in 4 per cent (one out of 25 individuals) among the twins experimentally produced by ligation. Aftarwards RUUD and SPEMANN (1922) repeated the same experiment and ascertained the above findings. The double hearts are also produced experimentally by interlocating the indifferent tissue in the median before the union of primordia takes place, as each half primordium gives rise to a heart. By this method, EKMAN (1925) in *Bombinator* and recently ICHIKAWA (1937) in *Triturus* obtained the enantiomorphic appearance of the hearts; the left member being always normal, while the right, inverse. From these examples produced experimentally as well as found in nature, it is highly probable to conclude that as a rule it is the right heart that takes the inverse orientation. However, how this general tendency is determined is a point of question. WILHELM (1921) proposed the situs-factor which would be located on the left side of the body and would control the orientation of the visceral organs, including, of course, the heart. According to his hypothesis, situs inversus is the result of this factor being destroyed, HUXLEY and DE BEER (1934) and recently KOMAI (1938) supposed the physiological gradient, decreasing

gradually from the left to the right side of the body and this gradient disturbance should be the cause of the situs inversus viscerum including the heart. SPEMANN, with FALKENBERG (1919) offered two hypothetical views based on their constriction experiments. His first hypothesis is that the fertilized egg is to be composed, from the first, of asymmetrical so-called "Intimstruktur". When the egg is constricted by the baby's hair, the inversion of this "Intimstruktur" in the right half would occur as the forerunner of situs inversus viscerum of the later embryo, as in the case of certain asymmetrical crystals after injury. The inversion of the "Intimstruktur" was, however, opposed later by MANGOLD (1921) from his repeated experiments. SPEMANN's second hypothesis of "Wundkrümmung" is that the weak building of the inner side of the body would be the essential factor which determines the situation of the visceral organs. Namely, the right (inner) side of the left partner of twin is weakly formed, as a direct effect of the injury, so that the body curves more or less towards this side according to the degree of deficiencies. This curving of the body is in the same direction as that of viscera, and there should occur no morphological conflict in their development. As the result the visceral situation of the left partner becomes normal. On the contrary, the right partner has a tendency to curve towards the left side due to the same reason just described. This body curving is in the opposite direction to the visceral curving, and thus the morphological conflict would take place between them. When the body curving would overcome the visceral curving, the situs inversus viscerum should be resulted, while, when vice versa, the normal situation might be yielded.

The writer is, however, of the opinion that the structure of the fertilized eggs of the higher animals such as Amphibians, would be already bilaterally symmetrical, with respect to the median plane at least in potency, which should decrease in gradient from left to right and from right to left respectively. When such eggs are forced to give rise to the anadidymous or twin embryos by ligation or by bifurcation of the organizing material, the inner sides of them would be repaired with the materials other than of normal prospective fates so as to recover the symmetrical relation in themselves. In this newly settled bilaterality the outer side with the normal prospective fate should be prepotent or superior in morphogenetical potencies to that of the inner side now newly destined so. Thus, the right (outer) side of the right partner would assimilate potentially its left side to produce the situs inversus viscerum. The writer's above assumption is applicable best of all to the explanation of the situs inversus cordis. Both primordia of heart are highly probable to have the potency to give rise to the symmetrical organs with respect to the median plane of the body, like the other paired organs such as limb, eye, ear and others. Namely, the left primordium should have the potency to bend into S-shape with the advance of development, while the right primordium should have the potency

to give rise to the inverted S-shaped tube. Both primordia should be only different in potential intensity i. e., the left one should be always dominant, and the right one, recessive. Even in the normal development, the heart would suffer always this potential conflict, and the left primordium would overcome the right one with the resultant production of the heart with the structure and situation similar to the organ produced out of only the left primordium by itself. However, when the union of both primordia is checked experimentally by interlocating the indifferent tissue between them, they give rise independently to the hearts with their own original twisting tendency. Thus, the enantiomorphic relation should be established, the left heart being normal, while the right one inverse, as in reality found in the experimental specimens of EKMAN (1925), COPENHAVER (1925-'26) and the writer (1937). GOERTTLER (1928) has already suggested from his experimentation experiment that the left primordium of the heart is potentially dominant as compared with the right one. The term "potency" in my opinion is essentially in agreement with LUDWIG's "Agens". Quite recently, ZWANZIG (1938) explains the situs inversus viscerum according to the "Agens"-hypothesis.

SPEMANN (1906), PRESSLER (1911) and MEYER (1913) have succeeded respectively in producing the specimens with the reversed orientation of visceral organs by means of rotating the medullary plate along with its substratum in 180 degrees around the dorsoventral axis of the egg. Afterwards SPEMANN (1918) repeated the same experiment with the medullary plate alone, and obtained no case of such visceral inversion. It is, therefore, assumed that the substratum would be the factor responsible for the determination of the visceral orientation. It may be also allowed to suppose that the rotation of the substratum may first call forth the situs inversus viscerum, especially of stomach and liver, and the latter in turn affect the heart so as to become inverted, because the heart rudiments are not effected directly by the operation. ZWANZIG (1938) explains this kind of situs inversus viscerum by assuming another factor that "L-Agens" implanted to the right side becomes inactive in the "R-Millieu", while "R-Agens" suffers little such a reduction of its effectiveness in the "L-Millieu". Whether this hypothesis is applicable to the explanation of situs inversus viscerum et cordis requires further experiments.

Summary

1. 34 specimens of double monsters of the Japanese newt, *Triturus pyrrhogaster*, was examined, with special reference to the origin of monstrosities.

2. The specimens are classified into 4 groups according to the degree and mode of duplicity. In the first group the bifurcation takes place most slightly; it being confined to the anterior half of the head upto the eye level. 8 specimens belong to this group. In the second group the doubling

extends upto the forelimb level, and in it are contained 7 specimens. In the third group the duplicity occurs along the whole length of the body, from head to the tail end, but they are fused belly to belly by the common abdomen. 5 specimens belong to this group. In the fourth group the duplicity takes place unequally, and one which is large develops to an autosite and the other which is small, a parasite. In this group are contained 14 monsters, out of which the parasite is represented as only a wart-like prominence in 4 specimens, it is defective in 2 specimens and acephalous in 3 specimens. In the remaining 5 specimens the parasite is proportionately formed.

3. The origin of such a double formation is referred to the physiological or potential isolation of the organiser. When it occurs only in the anteriormost, the degree of duplicity should be the slightest: the resultant embryo being provided with 3 eyes as in the specimen No. 5. The more the organising material is isolated, the more posteriorly the resultant embryo should be divided. However, it should be mentioned here that the external duplicity is also the function of diverging angle of the organiser. Namely, the greater the diversing angle of the organiser, the greater the external duplicity in the caudal extent. When the doubling of the organiser is unequal, the one induced by the larger part should become the autosite and the other induced by the smaller part, the parasite. Some specimens belonging to the fourth group seems to be produced as such. When the doubling takes place in the so-called trunk-organiser, the acephalous secondary embryo should be produced such as in the specimen No. 14.

4. Among the axial organs, the dorsal aorta is the first, the spinal cord next and chorda the last in their union with each other.

5. In the first group, the heart, when it is single, is produced by the union of the outside primordia of both members. The operculum and the branchial basket of visceral cartilages are also established in the like manner. These organs in the third group are also produced likewise, viz. by the union of outer or inner primordia of both members respectively.

6. Union of the eyes occurs in some specimens, but its degree varies with different individuals. When union is complete, synophthalmia unilentica is resulted, but when incomplete, synophthalmia bilentica is formed.

7. The median pronephros appears in the furcated region of some specimens, but its Wolffian duct terminates blindly as a rule.

8. The mesonephros is probably auto-differentiating organ and, indeed, it develops independently of the pronephros or its leading duct.

10. When two hearts appear in the same individual, that of the right member shows situs inversus cordis as a rule. The reason for this fact is given in the section of considerations.

Abbreviations in the text-figures

AcT, accessory tail	Int, intestine
Au, auditory capsule	L, liver
Bas, basibranchium	IPG, left pectoral girdle
Bl, balancer	Lent, lentoid
Br, brain	Meck, МЕССЕЛ'S cartilage
Bv, blood vessel	MN, mesonephros
Ch, chorda	MP, neural plate
Cl, cloacal opening	N, nose
Cy. E, cyclopean eye	P, pancreas
d, dorsal fin	PG, pectoral girdle
Da, dorsal aorta	Ph, pharynx
E, eye	PN, pronephros
Fl, forelimb	PQ, palatoquadrate
G, ganglion	Sp, spinal cord
Gb, gall-bladder	St, stomach
Gil (gil), gill	Tr, trabecular bar
H, heart	v, ventral fin
hl, hydropic lacuna	Vert, vertebra
Hl, hindlimb	Vp, visceral pouch
Hum, humerus	WD, Wolffian duct
Hy, hyoid cartilage	1Br-4Br, first to fourth branchial car- tilages

Subscribed small letters, r and l, represent the right and left members of a pair, and also the subscribed numerals, 1-4 refer to the order of the same structures observed from left to right.

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