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Problem of Situs Inversus Viscerum, as Studied on Single and Duplicate Salmon Embryos*

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With Plates I, II and 3 Text-figures

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Contents

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Introduction

Much has been published on the monstrosity of fishes. But, of all the problems concerning this matter, that on twinning and duplicate monstrosity are apparently the most interesting. As the material for this study, the embryos of salmon or trout are probably more preferable than any other, because the eggs of these fishes are comparatively large, and are raised in great quantities by artificial means.

Of the previous works on the duplicity of fishes, the more important ones are: KLAUSSNER (1890), WINDLE (1895), SCHMITT (1901), LEREBOULLET (1855), SCHWALBE (1907), GEMMILL (1912) and HANDA (1924), dealing with the general problem; OELLACHER (1873), KOPSCH (1899) and INUKAI (1925), specially on mesodidymi or katadidymi; SUZUKI (1926) on the central nervous system in double as well as single monstrosities; MORRILL (1919), SWETT (1921), NEWMAN (1923) and BOVET (1931), primarily on situs inversus viscerum. Of the researches by experimental methods, STOCKARD's work (1921, 1931) with low temperature or reduced oxygen supply is widely known. HINRICHS and GENTHER's experiment (1931) with ultra-violet radiation gave a result similar to STOCKARD's. More recently, GOETSCH and SCHLINDLER (1934) examined the effect of ligation on developing twin embryos of salmonids.

Of the duplicate monstrosities, many points found in fishes are in common with similar phenomena occurring in other vertebrates. But there are also facts peculiar to fishes, as, the rarity of duplication in the posterior region, and the comparatively high frequency of situs inversus viscerum.

This work deals primarily with the problem of situs inversus viscerum of duplicate monsters as well as of single embryos of the salmon *Oncorhynchus keta*. But other problems of duplication and deformations found in the same material are also dealt with.

The material was obtained from the quantities of salmon embryos artificially raised in the governmental Trout and Salmon Hatchery at Titosemura, Hokkaido from 1934 to 1936. Mr. S. OKADA kindly supervised the work of the Aino women, who were employed for collecting the material. It is my pleasure to express my thanks to Mr. OKADA and also to Mr. Y. HANDA, the director of the hatchery, for their help and cooperation which enabled me to get the rich material used in the present study. My thanks are also due to my private assistant, Mr. T. TERAMOTO, who helped my work of dissecting the material, as well as to Dr. K. NAKAMURA, who took all the photographs reproduced in this paper.

Observations

Types of Duplicity

In this collection, all the types of duplicity recorded in previous authors' works, namely, duplication of anterior (anadidymi), posterior (katadidymi), middle (mesodidymi) regions, of both anterior and posterior regions (ana katadidymi), besides many cases of independent duplications (omphalosites), are represented. There are also two examples of triple monstrosities (Pl. I, figs. 6, 7).

Of all the duplications, those of the posterior regions (katadidymi) are the rarest. There are 6 specimens in all, belonging to this type, in my collection (figs. 1, 2). In GEMMILL's opinion (1912), the katadidymi found in fishes are of a kind somewhat different from those occurring in other vertebrates—that is, they are formed as a result of longitudinal splitting of the posterior region of a single embryo, something like spina bifida. Both INUKAI (1925) and SUZUKI (1926), however, give some cases of genuine katadidymi which do not belong to the type mentioned by GEMMILL, since they have their posterior regions duplicated with both halves complete. In all of the specimens of this type in my collection, the duplicated posterior regions seem to be abnormally thin and incomplete. Dissection has shown that the heart, œsophagus and stomach are single, the intestine duplicated; the liver is single, but has an appearance of being a double structure (fig. 2). It is likely that this type of duplication is initiated in a relatively advanced stage; the power of regeneration of the defective parts, therefore, is smaller than in the case of anterior duplication.

Another specimen of similar appearance, shown in Pl. I, figs. 4 and 5, is a typical Janus with the component individuals well developed and perfect. Although SCHMIDT (1912, also cited in SPEMANN 1918) denies the occurrence of the Janus in teleostomi, this is a typical example of the kind. SPEMANN (1918) and WESSEL (1926) have obtained triton embryos highly similar to this embryo by uniting two gastrulae, after removing a small quantity of material from the animal pole, in such a way that the anterior ends of the dorsal lips come opposite to each other. It is almost a certainty that my Janus embryo did not result from two eggs fusing into one. It is likely that the embryo was originated from two embryonic rudiments, both on the same egg but with their axes exactly 180° apart from each other, which were brought subsequently into fusion with the anterior ends. If similarly placed rudiments fail to meet each other, double embryos such as in fig. 3 probably arise.

Deformities found in Duplicate Embryos

Certain rules concerning the duplicity in fish embryos have been set forth by STOCKARD in his well-known work (1921). He states, "In double individuals in which the two components are equal in size, the larger component is almost always normal in structure, and the smaller component is always deformed. The degree of deformity in smaller component varies directly with the extent of difference in size between the two components." (p. 259). Further, "The types of defects and the degree of deformity exhibited by the smaller component are exactly similar in kind and degree to the deformities found among single individuals—. The depressed state of one component is the result of an inhibiting influence exerted by the other." (p. 259). Practically the same argument is presented in his "Physical Basis of Personality" (1931).

In STOCKARD's opinion, both complete and partial duplicities have their cause in the arrested development of the embryo; and the twin embryos or twin structures of a single embryo are in a state of competition with each other during the course of development. The one which wins this struggle develops quite normally, whereas the loser, practically without exception, becomes abnormal. When the components are equal in size, both are normal in structure, but when they are unequal, the smaller member is always more or less defective. This deformity belongs to the same type as that found in the single embryos.

The validity of the above assertion was examined with regard to the present material. For this purpose, the following numbers of single and double specimens were used: 200 normal single embryos, 300 deformed single embryos, 502 sets of separate twin embryos, 287 sets of partially duplicate twin embryos. All through this paper, the embryo has been classified as 'underformed' when it has all its parts normal and in ordinary proportion, even if it is smaller in size than average embryos; it is designated as 'deformed' when it shows deformity in some part or other, or when the development of its parts is disproportionate; the embryos that are difficult to classify were excluded. The materials were selected at random, by a few Aino women, from a great number raised in the named hatchery. There was evidently no purposive selection for any particular type.

My findings on the material may be stated briefly as follows:

1. There is no distinction in the type and degree of deformities between the single and twin embryos, partial or separate.

2. If the twins are equal in size, both are normal in about 80% of the cases, while in the rest, one or both members are defective. This is equally true for either separate or partially-duplicate twins (Table 1).

Table 1. Frequency of deformities among equal-sized separate or partially-duplicate twin embryos.

	Separate equal-sized twins——129 sets	Partially duplicate equal-sized twins——161 sets
Both members undeformed	178 (81.3±2.6%)	131 (81.3±3.1%)
One member undeformed, the other deformed	34 (15.5±2.4%)	15 (9.3±2.3%)
Both members deformed	7 (3.2±1.2%)	15 (9.3±2.3%)

3. If the twins are unequal in size, both are normal merely in about 30% of the cases, whereas, the smaller twin only is defective in more than 60% of them, and both are defective in less than 10%. There are cases, although very rare, in which the larger twin only is defective. Of the 283 sets of unequal separate twins examined, there were 6 cases of this last kind, but in the 132 sets of unequal partially-duplicate twins, not one was found (Table 2).

Thus, even if the twins are unequal in size, both twins are normal in ca. 30% of the cases; and there are even cases in which the larger twin

Table 2. Frequency of deformities among unequal-sized separate or partially-duplicate twin embryos.

	Separate unequal-sized twins——283 sets	Partially-duplicate unequal-sized twins——132 sets
Both members undeformed	73 (25.8±2.6%)	41 (31.1±2.6%)
Only larger member deformed	6 (2.1±0.8%)	0
Only smaller member deformed	190 (67.1±2.8%)	80 (60.5±4.3%)
Both members deformed	14 (4.9±1.3%)	11 (8.3±2.4%)

only is defective. The above rules set forth by STOCKARD, therefore, hold only with certain limitations.

It may be pointed out concerning the problem of whether one twin's deformation is due to competition with the other twin, that there is scarcely any difference in the degree and frequency of deformity between the separate sets and partially-duplicate sets, in spite of the fact that such competition should be far more intense in the latter sets than in the former. So it seems unlikely that most of the deformities so commonly found in such embryos, are brought about by such competition.

Next, an examination was made to see whether there is any difference in the frequency of deformities occurring in duplicate embryos, between the member situated on the right side and that on the left side. Of all the 287 sets of partially-duplicate twins examined, 154 consisted of members of equal size; in 35 sets of these the right member was smaller and in 48 sets the left member was smaller. Of the 96 sets in which one member was defective, 57 had the defective member on the right side and 39 on the left. If both size and side are taken into consideration, we find the following relations (Table 3).

Table 3. The frequency of deformities in right or left members of partially-duplicate twin embryos——287 sets.

Relative size	Number of specimens examined	Right member deformed	Left member deformed
Equal size	154	9 (5.8±1.9%)	7 (4.5±1.7%)
Right member smaller	85	48 (56.5%)	0
Left member smaller	48	0	32 (66.7%)

Thus, as a general tendency, it may be recognized that the right member of the partial twins is more liable to underdevelopment and deformity than the left.

Findings on Situs Inversus Viscerum

It is widely known that in fish and urodele duplicate twins, situs inversus viscerum occurs fairly commonly. MORRILL (1919) examined some twin embryos of trout and found cases of complete or partial inversion of the viscera. He also found that such inversions appear always in the right member of the partially duplicate twins, and that there is no relation between the frequency of inversion and the degree of duplication. Further, when the twins are in the autosite and parasite state, inversion always occurs in the autosite; but there is no relation between the inversion and the deformity of structure. SWETT (1921) found, also in twin embryos of trout, that the situs viscerum can not be related to the degree of external doubling. The inversion of viscera is not, therefore, a necessary consequence of any duplicate condition. The inversion may occur in either twin (right or left) but it is commoner in the right twin than in the left. Parasites as well as autosites may show this abnormality. Furthermore, there is no relation between the deformity of structure and the inversion of the visceral situs.

More recently, BOVET (1931) found from his examination of 63 examples of duplicate trout embryos, that the frequency of situs inversus viscerum varies greatly according to the material. The inversion may appear in one of the twins or in both of them, whether of separate sets or of partially-duplicate sets. There is hardly any distinction in the frequency of such inversions between the right and left twin members.

In the well-known series of ligaturing experiments on triton eggs by SPEMANN and FALKENBERG (1919), it was revealed that situs inversus viscerum appears predominantly in the right member of the partial or separate twins. WILHELMI (1921) has obtained situs inversus, also in triton, by removing some material from the left side of the blastula.

For the factor which brings about the reversal of the visceral situs, some authors maintain the presence of some local cause. In SPEMANN and FALKENBERG's view, for instance, the situs inversus is caused by the deficiency of building material in the internal part of the right member of the partially-duplicate twins. WILHELMI postulates a local center which determines the orientation of the viscera. This center, he claims, is lacking in the right member; hence the reversal of orientation of the viscera. MORGAN (1927) also favors the view of the local cause. Certain other authors, on the other hand, advocate more general causes for this abnormality. According to NEWMAN (1923), the partially duplicate twins are equivalent to the bilateral halves of a normal individual, so that the mirror-imaging of the visceral situs is but a natural consequence of the partial separation and independence of such halves. BOVET (1931) maintains that situs inversus viscerum results from an aberration in the process of the settlement of the symmetry of the embryo. The earlier the stage in which the disturbance sets in, the higher the percentage of inversion. Certain authors, e. g. NEWMAN, HUXLEY and DE BEER (1934), recognize the existence of a kind of gradient, passing from the left to the right side in the body of an embryo, and if this gradient is reversed by some influence, the reversal of the visceral situs results.

The present study has been undertaken to contribute some knowledge toward the understanding of this interesting problem. For this purpose a fairly large amount of material was gathered and statistically treated.

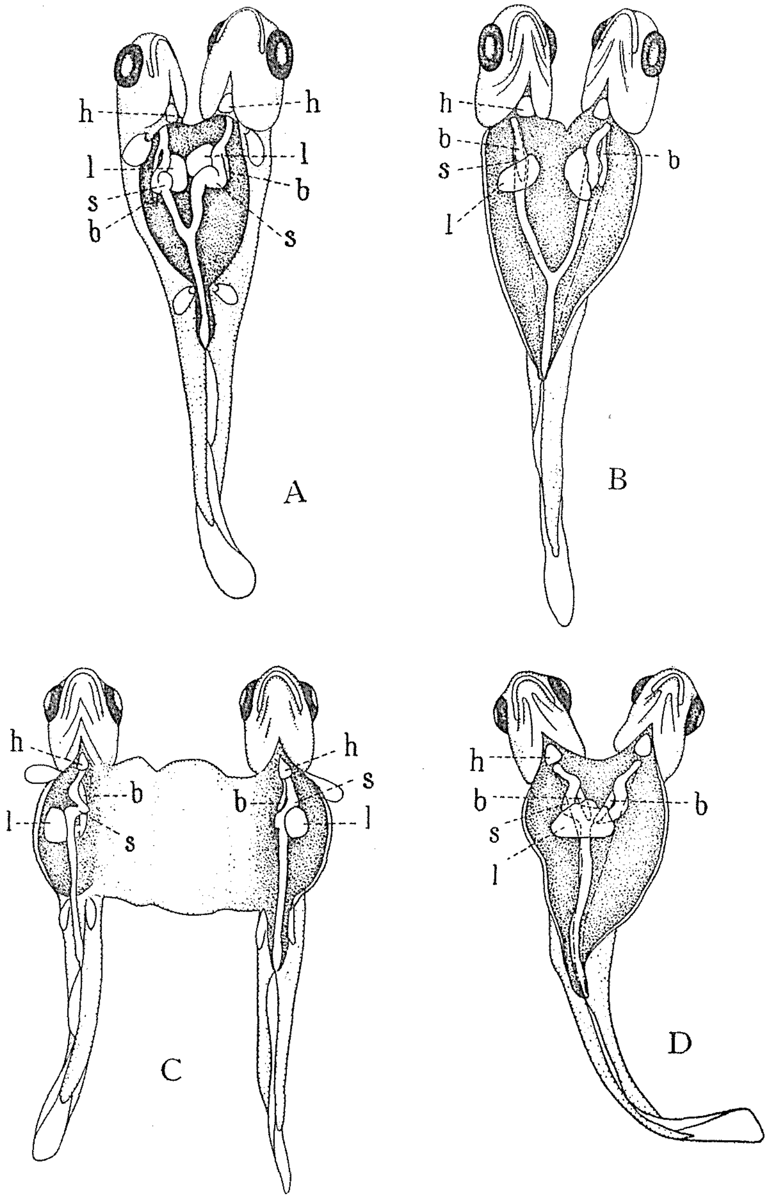

Fig. 1. Situs viscerum in various types of twin embryos. b—air-bladder, h—heart, l—liver, s—stomach. A.—Partially-duplicate embryo with the right member showing situs inversus viscerum perfectus. B.—partially-duplicate embryo with the right member showing situs inversus viscerum imperfectes. C.—A set of separate twin embryos of which one member (right in figure) shows situs inversus viscerum perfectus. D.—Partially-duplicate embryo with fused livers.

The normal configuration of the viscera (situs solitus) is as follows (Fig. 1 A, Pl. II, figs. 12, 14, left member): The œsophagus lies nearly on the median plane; the stomach (s) turns first to the left side (cardiac portion), then back to the right and somewhat forward (pyloric portion), and goes over into the intestine which lies on the median line. The airbladder (b) lies on the left, and also somewhat on the dorsal, side of the stomach, whereas the liver (l) is on the right, slightly on the ventral, side. In the case of a perfect situs inversus viscerum, the viscera appear in a mirror-image of the normal position (Fig. 1 A, Pl. II, figs. 12, 14, right member). There are also cases in which this reversal is incomplete (Fig. 1 B, Pl. II, figs. 13, 15, right member). In these, the winding of the stomach is less marked, and moreover, the displacement of the liver (l) is only to the extent of being situated in front of the digestive tract, overlying it. In the specimens of anterior duplication of but a small extent, the digestive tract is furcated only in its anterior portion. When the furcation occurs in front of the point of attachment of the liver, the liver is usually single but double-sized (Fig. 1 D, Pl. II, figs. 10, 11, 16).

1. *Situs Inversus Viscerum Found in Single Embryos*

a. Undeformed and deformed embryos compared

Situs inversus viscerum may occur in single embryos. Of these, the undeformed and deformed embryos are compared with regard to the frequency of the inversion (Table 4).

Table 4. Frequency of situs inversus viscerum among single embryos, deformed vs. undeformed

	Undeformed—200	Deformed—420
S. i. v. perf.	0	33 (7.9±1.3%)
S. i. v. imperf.	13 (6.5±1.7%)	55 (13.1±1.6%)

Thus s. i. v. is more frequent in deformed embryos than in undeformed.

b. Embryos twisted to the left side compared with other embryos

If s. i. v. is caused by the deficiency of material on the left side of the right member of partially-duplicate twins, we might expect in the single embryos, those which are twisted to the left side (Fig. 2, B), would be more liable to the reversal of visceral situs than those which are twisted to the right (A), or to the ventral side. Table 5 shows that such a tendency, if it occurs, is very slight.

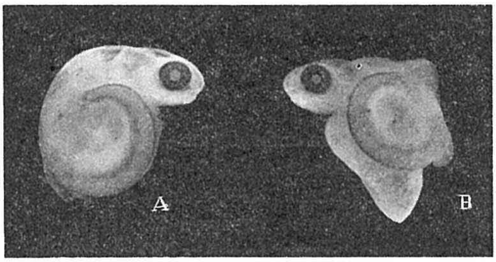

Fig. 2. Embryo twisted to the right (A), and embryo twisted to the left (B).

Table 5. Frequency of situs inversus viscerum among twisted single embryos

	Embryos twisted to the left side——114	Embroys twisted to the right side——103	Embryos twisted to the ventral side—164
S. i. v. p.	10 (6.8±2.4)	6 (5.8±2.8%)	8 (4.9±1.7%)
S. i. v. imp.	19 (16.7±3.3)	15 (13.2±3.3%)	18 (11.0±2.4%)

2. *Situs Inversus Viscerum Found in Separate Twin Embryos*

a. Larger and smaller members compared

Of the 251 sets of separate undeformed twins, 175 sets consist of equal-sized members and 76 of unequal-sized members. The frequency of s. i. v. is presented in Table 6.

Table 6. Frequency of situs inversus viscerum among separate twins of which both members are undeformed.

	Equal-sized ——175 sets	Unequal-sized——76 sets
S. i. v. p. in one member only	10 (5.7±1.8%)	(Smaller member) 4 (5.3±2.6%)
S. i. v. p. in both members	0	0
S. i. v. imp. in one member only	13 (7.4±2.0%)	(Smaller member) 9 (11.8±3.7%) (Larger member) 2 (2.6±1.8%)
S. i. v. imp. in both members	1 (0.6±0.6%)	

Thus, there is scarcely any tendency of s. i. v. being commoner in unequal-sized twins than in equal-sized twins. Among the unequal-sized pairs, however, it is more frequently found in smaller members than in larger members.

b. Undeformed and deformed members compared

The frequency of s. i. v. of the sets of separate twins, of which one member is undeformed and the other deformed, is shown in Table 7.

Table 7. Frequency of situs inversus viscerum among separate twins of which one member is deformed—226 sets

	Undeformed member only	Deformed member only	Both members
S. i. v. p.	4 (1.8±0.9%)	14 (6.2±1.6%)	0
S. i. v. imp.	8 (3.6±1.2%)	22 (9.7±2.0%)	1 (0.4±0.4)

In the 25 sets of separate twins of which both members are deformed, there are 7 (28.0%) cases of s. i. v. p., and 7 (28.0%) cases of s. i. v. imp.

The above 276 deformed embryos have been classified into two groups according to the degree of deformity, and the frequency of s. i. v. of each group obtained (Table 8).

Table 8. Frequency of situs inversus viscerum among deformed members of separate twins.

	Deformity less pronounced—227	Deformity more pronounced—49
S. i. v. p.	12 (5.3±1.5%)	7 (14.3±5.0%)
S. i. v. imp.	25 (11.0±2.0%)	4 (8.2±3.9%)

Thus, of separate twins, deformed members are more liable to show s. i. v. than undeformed members. This is in line with the fact found in single embryos. There is also a tendency that more severely deformed embryos show s. i. v. more commonly.

3. *Situs Inversus Viscerum Found in Partially-Duplicate Twin Embryos (Anadidymi and Ana-Katadidymi)*

a. Larger and smaller members compared

Of the 166 sets of partially-duplicate twins of which both are undeformed, 125 sets are equal-sized and 41 sets are unequal-sized. In the more extreme of the latter type, the larger member becomes the autosite, and the smaller member the parasite. The frequency of s. i. v. among the members of such twins is presented in Table 9.

Table 9. Frequency of situs inversus viscerum among partially-duplicate twins of which both are undeformed

	Equal-sized—125 sets	Unequal-sized—41 sets
S. i. v. p. in one member only	19 (15.2±3.2%)	Larger member 6 (14.6±5.5%) Smaller member 4 (9.8±4.6%)
S. i. v. imp. in one member only	26 (20.8±3.6%)	Larger member 7 (17.1±5.9%) Smaller member 7 (17.1±5.9%)
S. i. v. p. in both members	1 (0.8±0.8%)	0
S. i. v. p. in one member, s. i. v. imp. in the other	1 (0.8±0.8%)	S. i. v. p. in smaller member 1 (2.4±2.4%)
S. i. v. imp. in both members	9 (7.2±2.3%)	2 (4.9±3.4%)
Double liver	24 (19.2±3.5%)	2 (4.9±3.4%)

Thus, in partially-duplicate twins, s. i. v. is more frequent than in separate twins. Apparently there is scarcely any difference in the frequency of s. i. v. between larger and smaller members. Yet, in most of the cases where the larger members only show s. i. v., they are right members; and, as stated below, the right members are more apt to show s. i. v. So we need not draw from these data any conclusion which contradicts the rule obtained in the case of separate twins.

b. Undeformed and deformed members compared

Among the 94 sets of partially-duplicate twins each consisting of one undeformed and one deformed member, the frequency of s. i. v. is as shown in Table 10.

Table 10. Frequency of situs inversus viscerum among partially-duplicate twins of which one member is undeformed and the other deformed.

	Undeformed—94	Deformed—94
S. i. v. p.	7 (7.4±2.7%)	19 (20.2±4.1%)
S. i. v. imp.	17 (18.1±3.9%)	19 (20.2±4.1%)

Of 27 sets of partially-duplicate twins each consisting of two deformed members, there are 6 cases of s. i. v. p. (22.2%) and 7 cases of s. i. v. imp. (25.9%).

Thus, it is clear that in partially-duplicate twins too, s. i. v. is commoner in deformed members than in undeformed.

c. Right and left members compared

Among the 125 sets of equal-sized partially-duplicate undeformed twins examined, the frequency of s. i. v. is as shown in Table 11.

Table 11. Frequency of situs inversus viscerum among partially-duplicate twins of which both members are undeformed and equal in size—right and left members compared—125 sets.

	Right members	Left members
S. i. v. p.	19 (15.2±3.2%)	3 (2.4±1.4%)
S. i. v. imp.	29 (23.2±3.7%)	16 (12.8±3.0%)

Of 41 sets of unequal-sized partially-duplicate undeformed twins, 29 have smaller right and larger left members, and 12 have larger right and smaller left members. The frequency of s. i. v. is presented in Table 12.

Table 12. Frequency of situs inversus viscerum among partially-duplicate twins of which both members are undeformed but unequally developed—the right and left members compared.

	Smaller right m.——28	Larger left m. ——29	Larger right m.——12	Smaller left m. ——12
S. i. v. p.	4 (13.8±6.4%)	0	6 (50.0±14.4%)	1 (8.3± 7.1%)
S. i. v. imp.	4 (13.8±6.4%)	6 (20.7±7.5%)	4 (33.3±13.6%)	5 (41.7±14.2%)

The frequency of s. i. v. among the 80 sets of unequal-sized partially-duplicate twins, of which the larger members are undeformed and the smaller deformed, is as shown in Table 13.

Table 13. Frequency of situs inversus viscerum among partially-duplicate twins of which one member is undeformed and the other deformed—the right and left members compared.

	Right normal m.——33	Left deformed m.——33	Left normal m. ——47	Right deformed m.——47
S. i. v. p.	5 (15.2±6.2%)	6 (18.2±6.7%)	1 (2.1±2.0%)	10 (21.3±6.0%)
S. i. v. imp.	3 (9.1±4.7%)	3 (9.1±4.7%)	11 (23.4±6.2%)	9 (19.2±5.7%)

All the above Tables 11–13 show that s. i. v. is commoner in the right than in the left members of partially-duplicate twins. This is true even when the twins are equal-sized and both undeformed. When the right member is deformed and the left member undeformed, the preponderance of s. i. v. in the right member is especially marked.

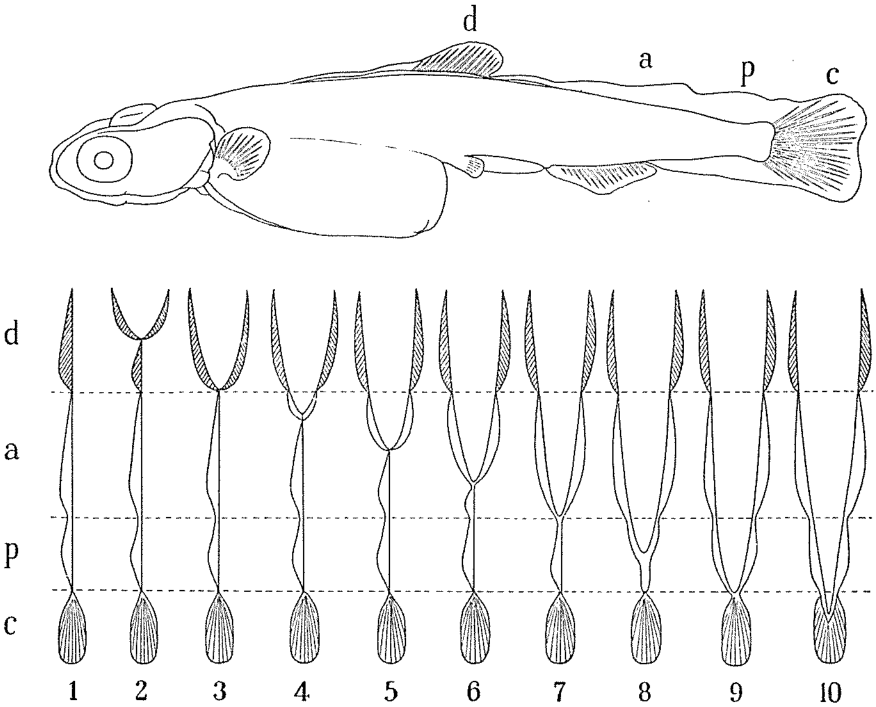

Fig. 3, illustrating the grade of duplication in anadidymi. a—adipose fin, c—caudal fin, d—dorsal fin, p—pre-caudal ridge.

1—single embryo, 2–10—anadidymi; the duplication includes respectively, half of dorsal fin (2), whole dorsal fin (3), anterior part of adipose fin (4), half of adipose fin (5), posterior part of adipose fin (6), whole adipose fin (7), part of pre-caudal ridge (8), whole caudal ridge (9), and part of caudal fin (10).

d. The frequency in relation to the degree of partial duplication

The partial duplication has been graded by the degree of duplication of the dorsal and adipose fins as in Text-fig. 3. The frequency of situs inversus viscerum among the different types is shown in Table 14.

Table 14. Frequency of situs inversus viscerum among different types of partially-duplicate twins classified according to the scheme shown in Fig. 3—287 sets, 574 heads

Grade	Total	S. i. v. p.	S. i. v. imp.	Double liver	Normal
1.	35 sets 70 heads	3 (4.3±2.4%)	5 (7.1±3.1%)	60	2
2.	17 ,, 34 ,,	2 (5.9±2.3%)	11 (32.4±2.5%)	16	5

Table 14. Continued

3.	40 ,,	80 ,,	6 (7.5±2.8%)	19 (23.7±4.7%)	14	41
4.	13 ,,	26 ,,	3 (11.5±6.2%)	5 (19.2±7.7%)	—	18
5.	12 ,,	24 ,,	3 (12.5±6.8%)	4 (16.7±7.6%)	—	17
6.	12 ,,	24 ,,	2 (8.3±5.7%)	8 (33.3±9.6%)	—	14
7.	30 ,,	60 ,,	15 (25.0±5.5%)	10 (16.7±4.8%)	—	35
8.	22 ,,	44 ,,	6 (13.6±5.2%)	7 (15.9±5.5%)	—	31
9.	64 ,,	128 ,,	19 (14.8±3.0%)	22 (17.2±3.3%)	—	87
10.	9 ,,	18 ,,	3 (16.7±8.8%)	2 (11.1±7.4%)	—	13

Thus there is scarcely any positive correlation between the grade of duplicity and the frequency of s. i. v.

Summary and Conclusion

1. Besides complete duplicities, all the types of conjoint duplicity recorded by previous authors, namely, ana-, kata-, anakata- and mesodidymi, have been observed. Also a typical example of Janus formation is recorded.

2. In either separate or partially-duplicate twins, when the members are equally developed, both are undeformed in about 80% of the cases, while in the rest one or both members are deformed.

3. In either separate or partially duplicate twins, when the members are different in size, both are undeformed in about 30% of the cases; the smaller members only are deformed in more than 60% of the cases; exceptionally the larger members only are deformed.

4. Of partially-duplicate twins, the right members are more frequently deformed than the left members.

5. Situs inversus viscerum may occur either in single or in twin embryo (partial or separate). But it is apparently commoner in partial twins than in separate twins or in single embryos.

6. Situs inversus viscerum is commoner in deformed (either single or twin) embryos than in undeformed embryos. More severely deformed embryos show s. i. v. more often.

7. Situs inversus viscerum is somewhat commoner in smaller members than in larger members of separate unequal twin-pairs.

8. Situs inversus viscerum is commoner in right members than in left members of partially-duplicate twins. This is true even in cases where the twins are equal-sized and undeformed.

9. There is scarcely any correlation between the degree of duplication and the frequency of s. i. v.

These facts seem to throw some light on the problem of the origin of situs inversus viscerum. Since s. i. v. tends to be associated with underdevelopment and deformation, it is apparently a result of a disturbance of the normal developmental process, much as the small size and deformation themselves*. Yet, s. i. v. is apparently more common in partially-duplicate

* This fact seems to be in harmony with the observation that the human cases of situs inversus viscerum are commonly associated with other structural abnormalities, such as hare-lip, hexadactylism, atresia of digestive tract and malformation of heart (LUDWIG, 1932).

twins than in single embryos or in independent twins. It is therefore certain that the partially duplicate state makes the appearance of s. i. v. easier. The influence of this particular state, however, does not seem to be very strong, inasmuch as there is no positive correlation between the degree of duplication and the frequency of s. i. v. This fact, furthermore, seems to disfavor the theory of a local cause accounting for the origin of s. i. v. The fact that s. i. v. is not particularly common in embryos twisted to the left side, also does not agree with this theory.

It is also remarkable that the right member of partially-duplicate twins are more liable to underdevelopment, deformation and s. i. v. This tendency can only be accounted for by assuming the presence of a kind of physiological gradient from left to right, as has been pointed out by some previous authors. Hence:

10. Situs inversus viscerum seems to be a phenomenon associated with the disturbance of the normal developmental process, and due to a general rather than a local cause.

11. There is apparently a kind of physiological gradient passing from the left to the right of the body of a fish embryo. The derangement of this gradient probably brings about the situs inversus viscerum.

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Explanation of Plates

Plate I.

(l=liver)

Fig. 1. A katadidymus.

Fig. 2. Another katadidymus dissected.

Fig. 3. A pair of separate twin embryos with polarities almost reverse of each other.

Fig. 4. The Janus embryo.

Fig. 5. The same embryo dissected and viewed from the other side.

Fig. 6. A case of triplicitas anterior.

Fig. 7. An anadidymus with an additional deformed embryo on the yolk sac.

Fig. 8. A pair of separate twin embryos, of which the left one in the figure shows situs inversus viscerum perfectus.

Fig. 9. A pair of separate twin embryos of which one is severely deformed.

Plate II.

Fig. 10. Duplication of head region only, with a severely deformed left member; the livers are coaresced and situated on the right side of the digestive tract.

Fig. 11. Duplication of head region only, with partially coaresced livers.

Fig. 12. Anterior duplication down to middle region, the right member showing s. i. v. perf.

Fig. 13. Anterior duplication down to a point slightly in front of middle region; the right member showing s. i. v. imperf.

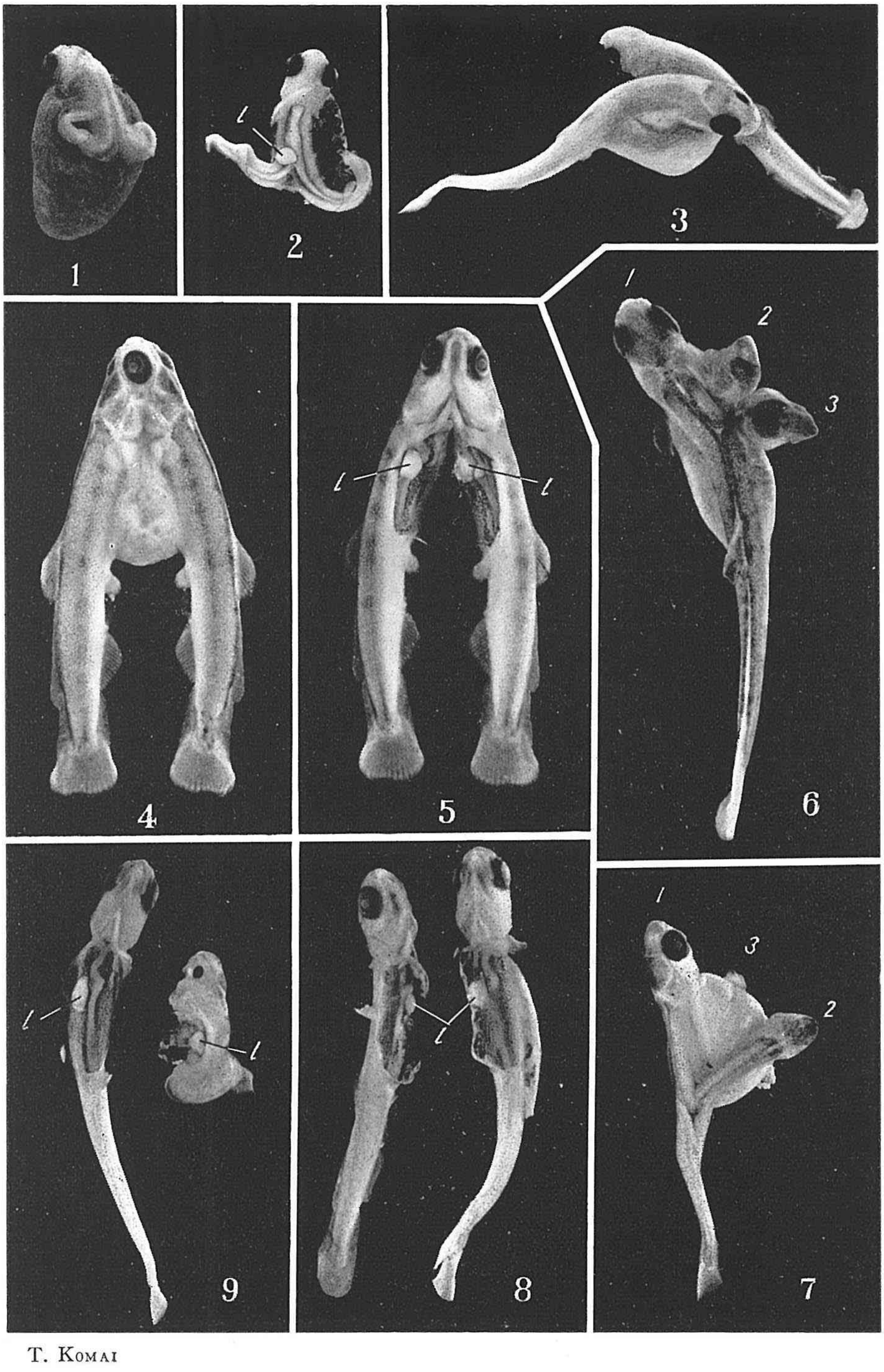
Fig. 14. Anterior duplication down to neck region, the right member showing s. i. v. perf.

Fig. 15. Anterior duplication almost down to anal region, the right member showing s. i. v. imperf.

Fig. 16. Anterior duplication of about the same type as in Fig. 14; the livers are coaresced and placed in front of digestive tract.

Fig. 17. Anterior duplication of about the same type as in Fig. 12, the right member showing s. i. v. perf.

Fig. 18. Ana-katadidymus of which the right member shows s. i. v. perf.



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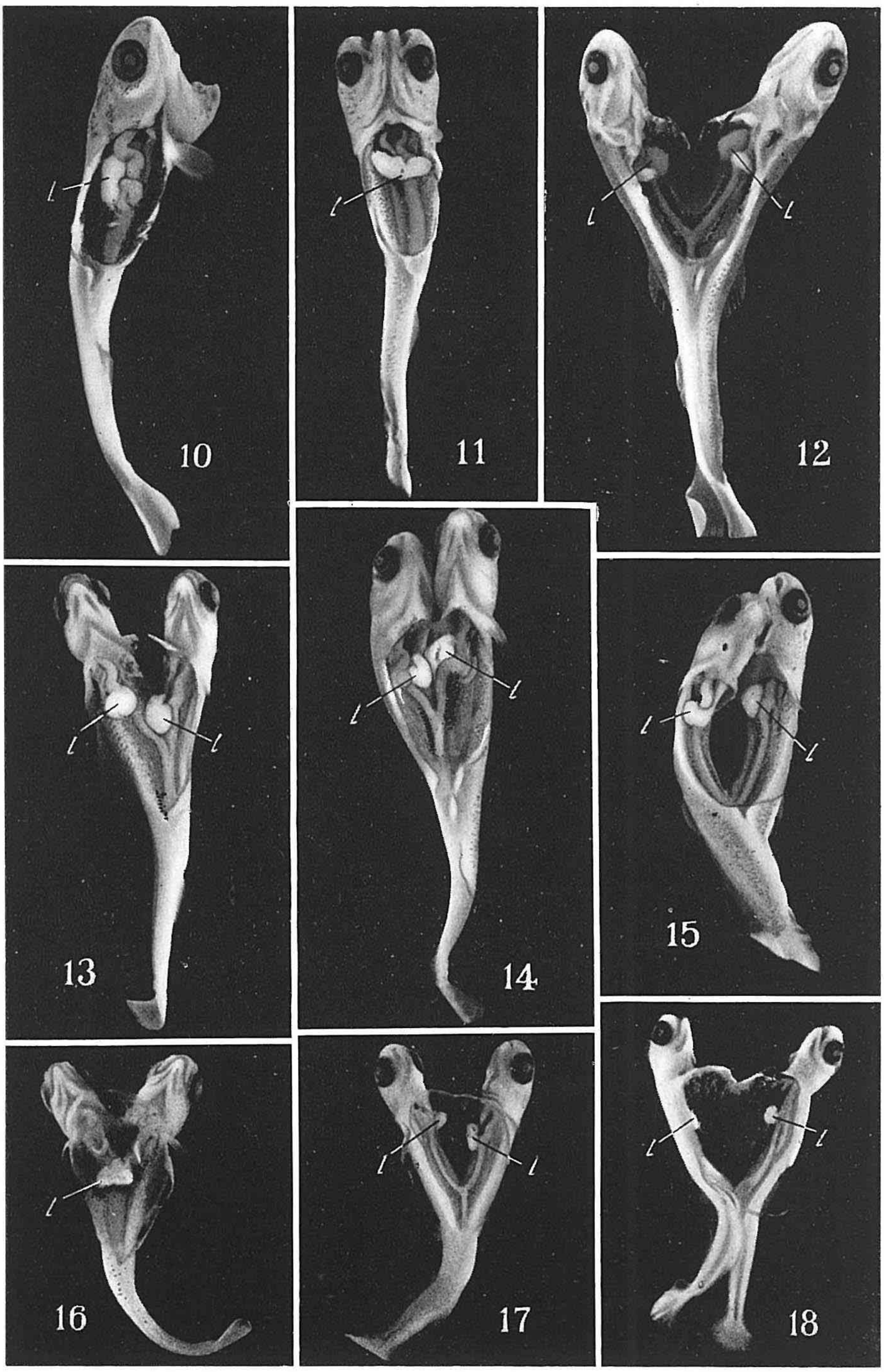

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