The Reversible Asymmetry in the Opercula of *Hydroides ezoensis*
I. Observations on the Intact Opercula[1)]

By

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(*With 3 Tables and 1 Textfigure*)

I

Hydroides ezoensis Okuda is a common Serpulid found on the coast of Hokkaido living attached to stones, molluscan shells and other hard materials. The branchial crown, which, when the worm is undisturbed, projects from the opening of its calcareous tube, consists of two semicircular rows of branchiae and bears two opercula. These branchial rows are located upon the anterior surface of the head end, one on each side of the mouth. The opercula are situated near the dorsal end of each branchial row, not on the line of the branchiae but dorsal to it.

Usually one operculum is larger than the other, *i. e.* the one on the left side may be larger than the other which is on the right side or *vice versa*. Namely the larger operculum is functional and serves to close up the opening of the tube when the worm retracts itself into it for protection. The functional operculum consists of a stout, naked stalk bearing at its distal end a funnel-shaped expansion. This terminal part has two sets of spinose circles, arranged so as to form a double cup, *viz.* an efficient plug for the open end of the tube. Near the base of the stalk is a distinct transverse suture or breaking joint. In certain circumstances, as we shall see later, the organ may break off from the body, separating at this joint. On the opposite side of the mid-dorsal line, there is a tiny rudimentary

1) Contributions from the Akkeshi Marine Biological Station, No. 37.

Jour. Fac. Sci., Hokkaido Imp. Univ., Series VI, Zoology, Vol. VIII, No. 1, 1942.

operculum. A slender stalk has a slight terminal enlargement, *i. e.* a rudimentary cup and near the base of the stalk is also found a transverse suture, a distinct line of demarcation between a basal region and the main part of its body.

According to a provisional observation made during summer and winter of 1939, in *Hydroides ezoensis*, the individuals whose opercula are of functional type on both sides were not so rare as was reported by Zeleny of *H. dianthus* (1905, p. 33). The two opercula of a set are more or less similar in structure but differ in size, the larger one being invariably less active than the smaller functional operculum on the opposite side with the result that the former can externally be observed to be somewhat curved with insufficient blood circulation considerable foreign material often clinging to the cup. The foregoing fact enables us to predict that the functional operculum of this Serpulid grows old and drops off quite naturally even where no injury is inflicted from outside and that it is finally replaced by a fresh operculum. On such an occasion, the rudimentary operculum on the opposite side may develop into a new functional operculum similar to the old one while in place of the old functional stalk a new rudimentary bud develops.

In Table I, the total of 9925 worms, most of them were collected on various spots on the beach near the Akkeshi Marine Biological Station, from May 9th to October 20th, 1940, the rest of them, which were 189 in number from the same locality being gathered on December 17th, are grouped into I) specimens with a functional operculum on the left side and a rudimentary operculum on the right side, II) specimens that show the reverse condition, having a functional operculum on the right and a rudimentary operculum on the left side and lastly III) specimens which have functional opercula on both right and left sides.

Our general conclusion regarding the distribution of the opercula of those with the well-developed functional and small rudimentary is that the right- and the left-handed forms are nearly equal in number, but that there is a slight advantage in favour of the right-handed ones. On the other hand, certain general trends in the increase and decrease of the both functional forms are discernible. A scarcity, reaching a minimum in June, continued until early August. The gradual increase was observed during August and this increase reached a peak in the middle portion of September, amount-

TABLE I. Relative positions of functional and rudimentary opercula in adult *Hydroides ezoensis*

Date	No. of individuals	F = left R = right	F = right R = left	Both functional opercula	
				No.	%
May 9—May 20	1006	498	480	28	2.8
May 21—June 5	848	384	456	8	0.9
June 6—June 20	1001	379	613	9	0.9
June 21—July 25	766	383	367	16	2.0
July 26—Aug. 4	1237	608	593	36	2.9
Aug. 5—Aug. 20	776	340	337	99	12.8
Aug. 21—Sept. 10	1154	540	501	113	9.8
Sept. 11—Sept. 15	426	150	152	124	29.1
Sept. 16—Sept. 30	378	146	148	84	22.2
Oct. 1—Oct. 7	1038	410	468	160	15.4
Oct. 8—Oct. 20	1106	530	514	62	5.6
December 17	189	92	93	4	2.1

F = Functional operculum.
R = Rudimentary operculum.

ing to as much as 29.1 per cent. In the early part of October the percentage decreased somewhat; later, as winter approached, the trend appeared to be one of decrease. An examination of 189 normal individuals which were gathered on December 17th, 1940 showed that only four, or 2.1 per cent, had the functional opercula on both right and left sides. This decreasing trend would result in a similar scarcity in the following summer.

In order to ascertain the actual reversal of opercula in a given individual, several groups of worms were kept under observation for a considerable length of time, *viz.* about two months. When the adult worms with a large functional on one side and a small rudimentary on the other, were taken out of their tubes but not otherwise injured and reared up in the laboratory, in a few of these, the position of the functional operculum was reversed after about two months (Table II, A). However, in the vast majority of cases of the specimens with opercula of functional type on both sides, there took place the replacement of the larger functional operculum by a fresh

TABLE II. Alternation of functional and rudimentary opercula in adult worms

Section A. Individuals which have one functional operculum on the left or the right sides

No. of individuals	Duration of observation	Cases of opercular reversal	Cases of no opercular reversal
11	May 8—Oct. 19	3	8
16*	May 10—Aug. 29	1	5

Section B. Individuals which have functional opercula on both sides

No. of individuals	Duration of observation	Larger functional is replaced by a rudimentary	No change in opercula
16**	July 9—Oct. 28	18	0
3	July 9—Oct. 28	3	0
14**	July 9—Oct. 28	11	0
9	Aug. 22—Oct. 28	8	1
7	Aug. 30—Oct. 28	6	1

* 10 died during observation.

** 3 died during observation in respective groups.

In no case was evidence of the opercular change noted. Such individuals are not included in the present table.

rudimentary one in about the same length of time (Table II, B). Thus the resultant opercula in these specimens consisted of a fairly typical functional and a fairly typical rudimentary opercula. Bearing in mind that the larger functional of a set was older than the smaller one as was evidenced by the fact that the former was invariably less active and its stalk was curved with insufficient blood circulation, we might expect that the resultant condition of opercula would be a reversal of the former condition before the both functional stage had been established. Accordingly it became known that the reversal of opercula occurs in the adult forms of *H. ezoensis*. Also it is to be noted that the specimens that have functional opercula on both sides are not a distinct form in respect of the arrange-

ment of the operculum, but that they are normal being at an intermediate stage of opercular reversal.

II

In this section we deal with correlation between the two opercula at their first appearance and up to the time when they assume the adult condition[2]. The youngest specimen observed is found to have four primitive branchiae on each side of the mouth with no trace of the opercular structure. At the stage represented in Fig. 1 the second branchia, the next to the most dorsal one, of the four branchiae on one side comes to lose its branchlets (pinnules) and has an enlargement at the distal end of the bare stalk, which soon assumes the shape of an inverted cone. This cone finally results in a single, basal (posterior) cup with a serrated edge. From a conical elevation in the centre of the posterior cup there projects a new spinose circle (anterior cup). We thus have a primary functional operculum. While the corresponding branchia on the other side drops off, the stalk breaks near its base where a new outgrowth of a bud starts. In this way we have a primary rudimentary operculum. It is to be noted that the primary functionary operculum is not restricted to the left side in this species although there is a considerable advantage in favour of the left-handed ones. The primary rudimentary operculum gradually develops making first an anterior cut and then a posterior one, till at length it comes to assume the shape of a functional operculum. Next, the primary functional operculum breaks off from the body, leaving only a small stump. After it has dropped a new bud appears on the distal end of the stump and

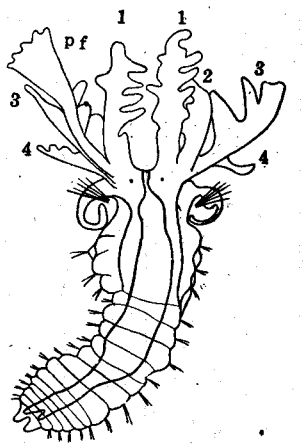

Fig. 1. Outline drawing of a larval *Hydroides ezoensis* taken out of its tube. On left side is primary functional operculum with naked stalk and basal or posterior cup. Dorsal view. pf, primary functional operculum; 1,2,3,4, branchiae. × ca 33.

2) A detail account of the early development of opercula is to be found in the work of Zeleny ('05) for *Hydroides dianthus*.

gradually develops until it attains the character of the former rudimentary operculum of the opposite side. This is a secondary rudimentary operculum. The primary rudimentary operculum that has

TABLE III. Relative positions of functional and rudimentary opercula in juvenile *Hydroides ezoensis*

Register number	Date of observation	Left functional	Right functional	Both functional	
				Left>Right	Right>Left
1	Sept. 20	15	1		
2	Sept. 20	8	3	2	
3	Sept. 20	5	1	3	
4	Sept. 20	7	6	4	
5	Oct. 4	25	3		
6	Oct. 4	50	11	5	1
7	Oct. 4	11	16	8	
8	Oct. 12	17	14	5	
9	Oct. 14	110	83	8	1
10	Oct. 14	33	24	2	2
11	Oct. 14	8	1		
12	Oct. 14	46	19		1
13	Oct. 14	37	27	3	
14	Oct. 16	3	4	3	
15	Oct. 16	8	5	1	
16	Oct. 16	24	6	1	
17	Oct. 16	35	18	5	
18	Oct. 16	26	12	4	
19	Oct. 20	13	20	9	
20	Oct. 20	5	10	8	
21	Oct. 20	5	7	1	
22	Oct. 20	6	5		
Total number		497	296	72	5

Sum-total = 870.

developed into a functional one is called a secondary functional operculum. Accordingly the resulting arrangement is the exact reciprocal of the former one. This is the first reversal of the opercula in the ontogeny of the worm.

In Table III, 870 juvenile forms of various stages which were collected from September 20th to October 20th of 1940 are grouped into the left-handed, the right-handed and the both functional types.

As shown in the above table, 497 specimens have the functional operculum on the left side and the rudimentary on the right, while 296 specimens have the opposite arrangement. Of these, a good many were found to have two primary opercula, but there were also some in which the first reversal of the opercula had been completed and whose opercula were secondary ones. The two opercula of a set in the specimens of the last group were not exact duplicates, the one of the other, but one operculum was larger than the other. The larger one was invariably a primary functional operculum and the smaller was a secondary functional operculum, *viz.* a former primary rudimentary developed. Among 77 specimens at the intermediate stage of the first reversal of opercula, a majority of 72 against 5 showed the primary functional operculum on the left side and the secondary one on the right, while the latter five had the opposite arrangement. Evidently the juvenile forms appear first as left-handed ones in most cases.

Summary and Conclusion

1. The examination of 9925 adult individuals gave 4722 individuals with a functional operculum on the right side and a rudimentary operculum on the left side, while 4460 showed the reverse arrangement, having a functional operculum on the left and a rudimentary one on the right. The remaining 743 had functional opercula on both right and left sides.

2. In nature certain general trends in the increase and decrease of the both functional forms are discernible. The noticeable increase takes place in September.

3. Worms which have functional opercula on both sides are normal being at an intermediate stage of opercular reversal.

4. The adult worms kept in dishes in the laboratory exhibit the opercular reversal.

5. The primary functional operculum appears on the left side in most cases, but some worms appear first as right-handed ones.

6. The first reversal of opercula in the ontogenetic development of the worm takes place in the autumn of the year.

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