A COMPARISON OF THE REACTIONS OF A SPECIES OF SURFACE ISOPOD WITH THOSE OF A SUBTER- RANEAN SPECIES

PART II

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This paper is the second of a comparative study of the reactions of the surface isopod *Asellus communis* Say and its widely distributed subterranean relative *Cæcidotea stygia* Packard. The study was undertaken to determine in what ways and to what extent these animals differed physiologically and to learn why the one animal is a cave inhabitant while the other, its near relative living in the same region, rarely occurs in caves.

¹ Part I, on the reactions to light, has already been published in the JOURNAL OF EXPERIMENTAL ZOÖLOGY, vol. 8, no. 3, p. 243.

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I. EXPERIMENTS WITH MECHANICAL STIMULATION

I. With Bristles

The first method of testing the sensitiveness of the two animals to mechanical stimulation was by touching various parts of their bodies with delicate bristles. Six bristles ranging from 0.3 mm. in diameter to the finest camel's hair were employed at first, but it was found unnecessary to use so many and finally three were selected for use, a coarse pig bristle 0.3 mm. in diameter, a human hair and a fine camel's hair. The bending strain of the three bristles was 1.7 grams, .0025 gram, and .001 gram respectively. These will be referred to in future as bristles 1, 2, and 3. They were firmly fixed to the ends of slender glass rods by means of small rubber bands. About one centimeter of the bristle extended beyond the end of the rod.

The animals to be experimented with were placed each in a separate glass dish containing water to a depth of about two centimeters. Dishes with either ground-glass or wax-covered bottoms were used, since a smooth glass surface afforded no foothold for the animals and they were unable to move with certainty upon it. Since *Cæcidotea* normally lives in water at a temperature near 11°C., the water was kept at about this temperature during the experiments. *Asellus*, being normally subjected to a considerable range of temperatures, would probably not be much influenced by slight changes of heat and cold, but for the sake of uniformity it was kept and experimented upon at the same temperature as *Cæcidotea*.

One specimen of each species was tested at a time. The dishes containing the two individuals to be used were placed in a larger dish of water so that the temperature of the two animals would remain the same. A thermometer was kept between the two small dishes. From time to time cold water or bits of ice were added to

the water in the larger dish to keep the temperature from rising. When necessary the excess of water was removed.

The animals were given fifteen minutes or longer to become somewhat settled in their new quarters. When they had apparently begun to act and move about normally, the test was begun. First the largest bristle was used and the *Asellus* and *Cæcidotea* gently touched on various portions of the body and the sensitiveness as indicated by the animals' movements noted. No record was made until after several trials unless the reaction was unmistakable at once. First, for example, the *Asellus* was tested with one of the bristles upon the flagella of the antennæ, then the *Cæcidotea* was tested for the corresponding part. In like manner similar tests were made for other parts of the body. No special sequence was followed in testing the various portions of the body. Sometimes one portion was tested first and sometimes another. But the corresponding parts of the two species were always tested one after the other.

The response to the various stimuli indicating corresponding grades of sensitiveness were designated by the following terms—extremely responsive, strongly responsive, fairly responsive, slightly responsive, and not responsive. An animal was considered *extremely* responsive if the movement was prompt and decidedly vigorous; *strongly* responsive if the response was slightly less prompt and vigorous than indicated for the extreme responses, but more vigorous than the normal movements of the animal; *fairly* responsive when the reaction resembled the normal movements of the animal in rapidity and vigor; *slightly* responsive when there was any observable response less active or pronounced than the normal movements; and *not* responsive if no movements were observed after several attempts at stimulation. The following table will serve to illustrate the tests made and the manner of recording them.

This record (Table 1) is typical of the differences in sensitiveness to mechanical stimulation between the two species. It will be noted that whereas to bristle No. 1 the *Asellus* was very responsive, to bristle No. 3 it was scarcely responsive at all. With *Cæcidotea* the extreme responsiveness was as marked with the

small bristle. No. 3, as with No. 1. There are noticeable individual differences in both species, but in these tests the most responsive *Asellus* was less so than the least responsive *Cæcidotea*. The two individuals whose reactions are recorded in Table I represent for the two species about the average conditions as far as reactivity to mechanical stimulation is concerned.

A series of ten pairs of individuals was tested and the results are summarized in Table II.

TABLE I

Reactions of Asellus communis, No. 2, ♂, length, 10.8 mm., and of *Cæcidotea stygia*, No. 2, ♂, length 10.2 mm., to stimulation by bristles.

OCTOBER 30, 1905. TEMPERATURE OF WATER, 11.4° C.

Bristle No. 1 (*A* pig bristle 0.3 mm. in diameter)

	ASELLUS COMMUNIS	CÆCIDOTEA STYGIA ²
1. Flagella of the antennæ	<i>Slightly</i> responsive; moved the stimulated part occasionally	<i>Strongly</i> responsive; usually moved very quickly
2. Basal segments of the antennæ	<i>Strongly</i> responsive; moved the stimulated part or crawled	<i>Extremely</i> responsive; moved backward very quickly
3. Antennules	<i>Strongly</i> responsive; reached for bristle with antennæ and gnathopods	<i>Strongly</i> responsive; moved backward quickly
4. Top of head	<i>Strongly</i> responsive; moved appendages or crawled	<i>Extremely</i> responsive; with quick and vigorous movements
5. First free body segments	<i>Strongly</i> responsive; less action than when head was touched	<i>Extremely</i> responsive; similar movements but less vigorous than produced when head was stimulated
6. Other body segments	<i>Strongly</i> responsive; less vigorous reaction than when head or first segment was stimulated, but similar in character	<i>Extremely</i> responsive; with movements like those made when head or first segment was stimulated, but less vigorous
7. Legs	<i>Fairly</i> responsive; animal often moved	<i>Strongly</i> responsive; slightly less than when uropods were stimulated
8. Uropods	<i>Strongly</i> responsive; animal crawled quickly	<i>Strongly</i> responsive; usually crawled quickly

²This animal had recently undergone ecdysis and consequently was perhaps more than usually sensitive.

TABLE I—Continued

OCTOBER 30, 1905. TEMPERATURE OF WATER, 10.8° C.

Bristle No. 2 (A human hair)

	ASELLUS COMMUNIS	CÆCIDOTEA STYGIA
1. Flagella of the antennæ	<i>Slightly</i> responsive; moved antennæ or gnathopods	<i>Extremely</i> responsive; waved antennæ and crawled
2. Basal segments of the antennæ	<i>Strongly</i> responsive; quickly moved antennæ and gnathopods	<i>Extremely</i> responsive; waved antennæ and sometimes crawled backwards
3. Antennules	<i>Strongly</i> responsive; quickly moved antennæ and gnathopods	<i>Strongly</i> responsive; quickly moved antennæ and gnathopods
4. Top of head	<i>Slightly</i> responsive; moved antennæ	<i>Extremely</i> responsive; excited extremely vigorous movements which did not soon cease
5. First free body segments	<i>Slightly</i> responsive; moved antennæ or gnathopods	<i>Strongly</i> responsive; usually crawled
6. Other body segments	<i>Slightly</i> responsive; moved antennæ and gnathopods and finally crawled	<i>Strongly</i> responsive; usually crawled
7. Legs	<i>Slightly</i> responsive; moved leg to avoid stimulation or crawled	<i>Extremely</i> responsive; crawled quickly
8. Uropods	<i>Slightly</i> responsive; crawled occasionally	<i>Strongly</i> responsive; usually crawled

OCTOBER 30, 1905. TEMPERATURE OF WATER 11.2° C.

Bristle No. 3 (A small camel's hair)

	ASELLUS COMMUNIS	CÆCIDOTEA STYGIA ³
1. Flagella of the antennæ	<i>Not</i> responsive; or only slightly so at times	<i>Extremely</i> responsive; moved violently at first touch
2. Basal segments of the antennæ	<i>Slightly</i> responsive; sometimes with movements of antennæ	<i>Extremely</i> responsive; moved violently at first touch
3. Antennules	<i>Slightly</i> responsive; moved antennæ or gnathopods often	<i>Extremely</i> responsive; crawled at once
4. Top of head	<i>Slightly</i> responsive; moved antennæ or gnathopods	<i>Extremely</i> responsive; crawled vigorously
5. First free body segment	<i>Slightly</i> responsive; moved antennæ or gnathopods	<i>Strongly</i> responsive; crawled, but less vigorously than when head was touched
6. Other body segments	<i>Not</i> responsive; or at best only very slightly so	<i>Strongly</i> responsive; crawled quickly
7. Legs	<i>Not</i> responsive	<i>Strongly</i> responsive; animal crawled
8. Uropods	<i>Slightly</i> responsive; moved after a time	<i>Extremely</i> responsive; crawled instantly and most vigorously

³ A touch, however slight, produced a vigorous movement in nearly every case.

TABLE II
ASELLUS COMMUNIS

DEGREE OF RESPONSE		EXTREME			STRONG			FAIR			SLIGHT			NO		
BRISTLE		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
1. Flagella of the antennæ.....					1	1		2			6	6	5	1	3	5
2. Basal segments of the antennæ.....	1				6	7	4	2	2	4	1	1	2			
3. Antennules.....					5	6	2	2	1	1	3	3	5			2
4. Top of head.....	2	1			8	2	3		4	3		3	4			
5. First free body segment.....	1	1			9	1	1		3	2		4	5		1	2
6. Other body segments.....					10	1			5	3		3	5		1	2
7. Legs.....	1				7			2	4	3		4	3		2	4
8. Uropods.....					6	2		4	1	1		5	4		2	5
Totals for each bristle.....		5	2	0	52	20	10	12	20	17	10	29	33	1	9	20
Totals for vigor of responses.....		7			82			49			72			30		

CÆCIDOTEA STYGIA

DEGREE OF RESPONSE		EXTREME			STRONG			FAIR			SLIGHT			NO		
BRISTLE		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
1. Flagella of the antennæ.....	3	3	4		5	2	3		3	1	2	2	2			
2. Basal segments of the antennæ.....	7	5	4		3	3	5		2	1						
3. Antennules.....	4	1	3		4	6	4	1	2	1	1	1	2			
4. Top of head.....	6	6	5		4	3	4		1				1			
5. First free body segment.....	3	2			7	6	6		1	2		1	1			1
6. Other body segments.....	2	2			8	6	4		1	3		1	2			1
7. Legs.....	5	5	4		4	3	5		2				1			
8. Uropods.....	5	4	5		5	4	4		2	1						
Totals for each bristle.....		35	28	25	40	33	35	2	14	9	3	5	9	0	0	2
Totals for vigor of responses.....		88			108			25			17			2		

Table II is a summary of the vigor of responses made by ten individuals each *Asellus* of *Cæcidotea*. The tests were made on various parts of the body by bristles numbered 1, 2, 3. No. 1 was a pig bristle 0.3 mm. in diameter, No. 2 a human hair, and No. 3 a fine camel's hair. In the first column to the left are designated the parts of the animals' body touched. In the successive triple columns to the right of the first column are indicated how many of the ten individuals experimented upon were *extremely* responsive when the various parts were stimulated by bristles 1, 2, 3, how many were *strongly* responsive, *fairly* responsive, *slightly* responsive and *not* responsive to stimulation upon the flagellum of the antenna by bristle No. 1, two were *fairly* responsive, six were *slightly* responsive, and one was *not* responsive at all. To stimulation upon the antennules five *Asellus* were *strongly* responsive to No. 1, six to No. 2 and two to No. 3, etc.

This summary indicates clearly that *Cæcidotea* is more sensitive to mechanical stimulation than *Asellus* is. Of the individual tests made upon the ten *Cæcidotea* 88 responses from the 240 trials indicated extreme sensitiveness and 108 indicated that the animal was strongly sensitive. The same test upon *Asellus* produced only 7 extreme responses indicating extreme sensitiveness and 82 strong responses. Of the whole number of tests with the three bristles, only 2 tests aroused no response in *Cæcidotea*, though 30 tests failed to produce reactions in *Asellus*. Bristle No. 1 produced 35 extreme responses with *Cæcidotea* and only 5 with *Asellus*. With bristle No. 3, 25 extreme responses were gotten from *Cæcidotea* and none from *Asellus*.

The responsiveness of *Cæcidotea* to the different bristles is very much the same, there being 35, 28 and 25 extreme responses to bristles Nos. 1, 2, and 3 respectively. With *Asellus* there is a very rapid falling off in responsiveness to the smaller bristles indicating a decided decrease in sensitiveness. The different bristles gave 5, 2 and to extreme responses and 52, 20 and 10 strong responses, respectively, indicating that with *Asellus* the predominating grade, of responsiveness to the coarsest bristle used is only of the grade, strongly sensitive, and that this responsiveness is much less pronounced with the finer bristles with which

only 20 and 10 such reactions were obtained. Hence it seems clear that *Asellus* is much the less responsive of the two species to this form of mechanical stimulation; that its responsiveness decreases rapidly with stimulation by the more delicate bristles; and that the threshold of stimulation is reached by the bristles used, whereas *Cæcidotea* is more responsive to such stimulation; in fact is nearly as responsive to stimulation by the smaller as by the larger bristles; and is extremely responsive beyond the threshold of stimulation for *Asellus*.

Asellus is more deliberate and less hasty in its reactions to mechanical stimulation than *Cæcidotea* is. This difference in the character of the reactions may influence one's judgment of the vigor of the reactions, so that the vigor of the response of *Asellus* is underestimated. Consequently a greater number of responses made by the *Asellus* possibly should be credited to the extreme column, than has been done. But if such an error should exist with reference to the extreme column for *Asellus*, it cannot affect the general result, as there can be no doubt of the diminution in number and vigor of the responses. Moreover, in many tests the actual lack of reaction in *Asellus* indicating lack of sensitiveness to more delicate stimulation is in strong contrast with the extreme sensitiveness of *Cæcidotea*.

The flagellum of the antennæ and the antennules are very delicate organs. Both are armed with many sensory hairs and might readily be thought highly sensitive to tactile stimulation. The flagella of the antennæ are relatively long and in both species, when the animals crawl, these organs extend in advance for a distance equal to more than half the length of the body. They appear to serve as important organs of touch. However, it appears that these organs in both species are relatively slightly sensitive to tactile stimulation of the sort employed. A remarkable difference exists between the sensitiveness of the flagella of the antennæ in the two; in *Cæcidotea* the flagella are only moderately sensitive, but in *Asellus* they are scarcely sensitive at all.

From the foregoing experiments the following conclusions may be drawn:

1. Asellus is decidedly less sensitive than Cæcidotea to mechanical stimulation by delicate bristles.
2. The responsiveness of Asellus decreases rapidly with stimulation by the more delicate bristles, while Cæcidotea was nearly as responsive to the finest as to the coarsest bristle used.
3. The threshold of stimulation for Asellus is much above that for Cæcidotea.
4. The antennules and flagella of the antennæ in both species are only slightly sensitive to mechanical stimulation.
5. The flagella of the antennæ are very much more sensitive in Cæcidotea than in Asellus, in which they are scarcely sensitive at all.

II. With Localized Currents of Water

A second kind of test for the sensitiveness of Asellus and Cæcidotea to mechanical stimulation was made by using localized currents of water. Fine glass tubes of various calibers were used through which delicate but constant currents of water were carefully directed upon the various parts of the animals. This afforded an easily controllable means of testing sensitiveness to mechanical stimulation.

The animals, as before, were placed in small wax-bottomed glass dishes containing water to a depth of 2 cm. These small dishes were put into a larger dish of water in which was a thermometer. The water was kept as near 11° as possible. A gallon bottle nearly filled with water was placed upon a support on the table so that the water level within the bottle was about 40 cm. above the level of the top of the table. Water was siphoned from this bottle through a rubber tube, into the free end of which was inserted a short glass tube drawn out to a fine point. The siphon flowed with a constant current and the rubber tube permitted the short glass end to be freely moved about, making it possible to direct the current wherever desired. A thermometer was kept suspended in the supply bottle. Water of the proper temperature

to keep the whole contents of the bottle near 11°C. was added from time to time in such amounts as to maintain a nearly constant level in the bottle. Tubes of four sizes were used. The bore of the largest was 118 μ in diameter and allowed a flow of water at the rate of 73 cc. per hour. This will be referred to as current No. 1. The next in size had a diameter of 90 μ , and permitted a flow of 25 cc. per hour; its current will be designated as No. 2. The third was 38 μ in diameter and permitted a flow of 18 cc. per hour; its current will be called No. 3. The smallest was 26 μ in diameter and allowed a flow of 15 cc. per hour; its current is No. 4. In a few cases a fifth tube 12 μ in diameter and allowing a flow of about 4 cc. per hour was used; current No. 5. The diameters of the tubes were only approximately obtained but the rates of flow of water through the tubes were readily and accurately determined and these were made the basis of selecting the currents of various strengths.

The individuals to be experimented upon were given at least fifteen minutes to become settled in the dishes before experimentation began. The corresponding parts of an individual of each species were tested in succession by a given current, but no regular sequence was followed in testing the various parts. After all the tests upon a given pair were made with one strength of current, the experiments were repeated with the weaker currents till all four currents had been used. In making these tests, the end of the tube which directed the current was always held under water and at 4 to 5 mm. from the part stimulated. Care was exercised to have the current of water flow squarely upon the part undergoing the test and so directed that other parts of the animal were not affected by it.

Records were kept after the same plan as was used for the tests with bristles (see p. 441), except that in the experiments with currents no records were made other than those of the vigor of the responses, for, even in the experiments with bristles this feature was finally found to be the only significant one. The following record, Table III, in which current 5, as well as the four usual ones, was used, will illustrate the results obtained from stimulation of this sort.

Both the individuals whose reactions are recorded in Table III were active and vigorous animals and the records shown are typical of the two species. It will be noted that *Asellus* was less sensitive than *Cæcidotea* to all the currents and scarcely sensitive at all to current No. 4, while *Cæcidotea* was extremely sensitive to the four currents and was only slightly less sensitive to the

TABLE III

Reactions of Asellus communis, No. 7, ♂, length 9 mm. and *Cæcidotea stygia*, No. 7, ♂, length 8.8 mm. to mechanical stimulation by small, locally directed currents of water. The first column on the left indicates the parts stimulated. In the second to sixth columns are indicated the different currents used (Nos. 1 to 5) and the vigor of the reactions to these currents when directed upon the parts of the body indicated

ASELLUS COMMUNIS, NO. 7, ♂, 9 MM.

Temperature of Water, 12°C.

CURRENTS USED	No. 1 ⁴	No. 2	No. 3	No. 4	No. 5
1. Flagella of the antennæ.	Little	Little	Not	Not	Not
2. Basal segments of the antennæ.....	Extremely	Extremely	Strongly	Strongly	Not
3. Legs.....	Strongly	Strongly	Not	Not	Not
4. Top of head.....	Extremely	Extremely	Strongly	Strongly	Not
5. First free body segment	Strongly	Strongly	Fairly	Not	Not
6. Other body segments..	Strongly	Strongly	Strongly	Little	Not
7. Abdomen.....	Strongly	Strongly	Not	Not	Not
8. Uropods.....	Strongly	Strongly	Not	Not	Not

CÆCIDOTEA STYGIA, NO. 7, ♂, 8.8 MM.

Temperature of Water, 12°C.

CURRENTS USED	No. 1	No. 2	No. 3	No. 4	No. 5
1. Flagella of the antennæ	Not	Not	Not	Not	Not
2. Basal segments of the antennæ.....	Extremely	Extremely	Extremely	Extremely	Strongly
3. Legs.....	Extremely	Extremely	Extremely	Extremely	Not
4. Top of head.....	Extremely	Extremely	Extremely	Extremely	Strongly
5. First free body segment	Extremely	Extremely	Strongly	Strongly	Not
6. Other body segments...	Extremely	Extremely	Strongly	Strongly	Not
7. Abdomen.....	Extremely	Extremely	Extremely	Extremely	Not
8. Uropods.....	Extremely	Extremely	Strongly	Extremely	Not

⁴For a description of these currents, see page 448

weakest than to the strongest of them. With current No. 5, however, which was probably much below the threshold of stimulation for Asellus, Cæcidotea showed no sensitiveness except upon the head and the base of the antenna.

All the tests with currents 1 and 2 produced *extreme* responses Cæcidotea except those directed upon the flagellum of the antenna. The same tests with Asellus produced *extreme* responses only upon the head and base of the antenna. Current 4 produced five extreme responses in the eight tests upon Cæcidotea, while but three tests aroused any response at all from Asellus. Current 5 aroused no response whatever from Asellus while Cæcidotea showed sensitiveness to stimulation by it upon the head and bases of the antennæ.

Ten pairs of Asellus and Cæcidotea were similarly experimented upon. Records of these experiments are summarized in Table IV.

Thus to stimulation upon the head by current No. 1, 7 Asellus were *extremely* responsive, 3 *strongly* responsive and none *fairly*, *slightly* or *not* responsive. To currents 1, 2, 3, and 4 applied upon the head a total of 16 were *extremely* responsive, 14 *strongly* responsive, 6 *fairly* responsive, 1 *slightly*, and 3 *not* responsive, etc.

This table shows that to mechanical stimulation by localized currents of water, Cæcidotea is decidedly more responsive than Asellus. Out of a total of 320 individual tests made upon 10 animals of each of these species, Cæcidotea gave 168 *extreme* responses and 51 failures to respond, while Asellus gave 61 *extreme* responses and 90 failures to respond.

The flagella of the antennæ are strangely unresponsive to this sort of stimulation and will receive special consideration elsewhere. If for the present they be left out of account, the number of tests followed by no responses in Cæcidotea is reduced to 15, though in Asellus it remains at 73, nearly five times as many.

The difference in sensitiveness is equally marked when the results of tests by the different currents are compared. Cæcidotea gave 59, 53, 36, and 20 *extreme* responses to currents 1, 2, 3, and 4, respectively, while Asellus gave 32, 23, 6, and 0 *extreme* responses to corresponding tests. With the weakest current (No.

TABLE IV

Summary of the reactions of ten *Asellus* and of ten *Cæcidotea* to localized currents of water. In the first column to the left are indicated the parts of the body against which the currents were directed. In the succeeding columns, each divided into four minor columns, are given the numbers of individuals out of a total of 10. EXTREMELY, STRONGLY, FAIRLY, SLIGHTLY, and NOT responsive to stimulation upon the various parts by currents 1, 2, 3, and 4, respectively

ASELLUS COMMUNIS

DEGREE OF RESPONSE	EXTREME				STRONG				FAIR				SLIGHT				NO			
CURRENTS USED	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
1. Flagella of the antennæ..					1				3	2	1		4	6	5	2	2	2	4	8
2. Basal segments of the antennæ.....	7	6	3		3	2	5	3		1	1	3		1	1					4
3. Top of head	7	7	2		3	2	5	4		1	3	2				1				3
4. First, free body segment..	4	1			4	7	3		2	2	1				2	1			4	9
5. Other body segments..					8	7			1	1	3				2				5	10
6. Abdomen	4	1			3	5			1	3	3		2	1	2				5	10
7. Legs.....	5	3			4	4	2		1	3			2	3					2	10
8. Uropods	5	5	1		2	2	4		2	2	1		1	2	1	1			2	9
	32	23	6	0	18	29	19	7	9	13	16	5	8	13	17	5	3	2	22	63
	61				83				43				43				90			

CÆCIDOTEA STYGIA

DEGREE OF RESPONSE	EXTREME				STRONG				FAIR				SLIGHT				NO			
CURRENTS USED	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
1. Flagella of the antennæ									1				1	1	1		8	9	9	10
2. Basal segments of the antennæ.....	8	8	6	5	2		3	1		2		1		1	1					2
3. Top of head.....	10	9	9	5		1	1	3				2								
4. First free body segment	8	7	4	1	2	2	3	5		1	1	1		2						3
5. Other body segments..	8	6			2	3	6	5		1	1	1		3	2					2
6. Abdomen.....	9	8	4	1			4	4	1	1	1	2		1	1					3
7. Legs.....	9	7	7			2	3	4	1	1		1								2
8. Uropods.....	7	8	6	5	3	2	3	2			1									3
	59	53	36	20	9	10	23	14	3	6	4	8	1	2	8	3	8	9	9	25
	168				66				21				14				51			

4) 20 *extreme* responses were given by *Cæcidotea* and only 25 of the tests; 10 of which were upon the flagellum of the antenna, failed to produce any reaction at all. With *Asellus* the same tests produced no *extreme* responses, while there were 63 failures to respond out of a total of 80 tests. Hence it appears that *Cæcidotea* is quite responsive to the weakest current used while *Asellus* is only slightly so.

The same relative lack of sensitiveness noted in the flagella of the antennæ, when stimulated by the bristles, was again noted with the currents. To stimulation by localized currents the flagella in both species are rather insensitive. This is especially true with *Cæcidotea*, whose flagella seemed less sensitive to this sort of stimulation than those of *Asellus*. To stimulation by bristles the reverse was true for in those experiments the flagella of the antennæ were more sensitive in *Cæcidotea* than in *Asellus*. A possible explanation of this discrepancy is that bristles tend to produce vibrations more than currents do and that the flagella are probably quite sensitive to frequent vibrations. This will be taken up again when the discussion of the reactions to sound is reached. The portions of the body of *Asellus* most sensitive to stimulation by currents are the head and the bases of the antennæ. They were almost the only parts responsive to the weakest currents. In *Cæcidotea* the maximum sensitiveness is less confined to the head and flagella of the antennæ than in *Asellus*, since it is shared somewhat by the uropods and legs. This point was well brought out by using current 5 with a number of pairs of individuals. *Cæcidotea* was found to be somewhat sensitive to this current upon the head, base of the antennæ, uropods and legs, but *Asellus* was seldom sensitive to it at all and never except occasionally upon the head and bases of the antennæ.

From these experiments upon the effects of mechanical stimulation by localized currents of water the following conclusions are drawn:

1. *Cæcidotea* is much more sensitive to water currents than *Asellus*.
2. The sensitiveness of *Cæcidotea* is only a little less marked

with the weakest than with the strongest of the four currents used, while the sensitiveness of *Asellus* almost disappears within the same range of stimulation.

3. The threshold of stimulation for *Cæcidotea* is considerably below that for *Asellus*.

4. The flagella of the antennæ in both species are only slightly sensitive; contrary to what is usually true, to water currents this organ is more sensitive in *Asellus* than in *Cæcidotea*.

5. The most sensitive parts of the body in each species are the head and bases of the antennæ, but the uropods and legs of *Cæcidotea* are only slightly less sensitive than such other parts.

3. *With the Concussion Produced by a Falling Solid Body Striking upon a Surface of Wood*

A third method of testing the relative sensitiveness of *Asellus* and *Cæcidotea* to mechanical stimulation was by trying the effect of a mechanical vibration produced by the concussion of a falling solid body upon a surface of wood. A steel ball and a lead shot were used. The steel ball weighed 3.505 grams; the shot 0.542 grams. At first only the steel ball was used and it was dropped through a distance of from 50 cm. to 2 cm. Since the threshold of stimulation was not reached for either species by the concussion produced by the steel ball, the lead shot was used in an endeavor to get a weaker stimulus. The momenta of the two falling bodies were calculated,⁵ and the falling distances chosen so that the concussions produced by the two bodies would form a graded series.

The metal balls were dropped upon the flat, smooth surface of a pine board 30 cm. long, 19 cm. broad and 1.2 cm. thick. The balls were dropped from between the thumb and forefinger at various levels, as determined by a meter stick, and made to fall at a particular place on the board. The isopod to be experimented upon was put into a waxed-bottomed stender dish 6 cm. in diame-

⁵ The effect of the friction of the air and the difference in the hardness and density of the two bodies were not taken into account.

ter. The dish was placed near the center of the board and 8 cm. from the place where the ball struck the board. In order to observe slight movements of *Cæcidotea* during the tests, these animals, which are white, were placed in a dish the bottom of which was black. For a similar reason the rather dark *Asellus* was experimented upon in a dish having a whitish bottom. In every case the animals were allowed to remain from 15 minutes to an hour in the dish to become accustomed to the new surroundings before the experiments were begun and no animal was experimented with until it had apparently begun to act and move normally after its transference.

In these tests the following grades of stimuli were used. The steel ball was dropped from 50 cm., 20 cm., 10 cm., 5 cm., and 2 cm., and had the following momenta at the instant of striking the board: 1097, 694, 491, 347, and 219 C. G. S. units.⁶

In using the lead shot for the lower range of stimuli, it was deemed advisable as a check to test the reactions of the animal to vibrations produced by both the steel ball and the lead shot when they collided with the board with the same momentum. Hence the shot was dropped 83.6 cm. and the ball 2 cm., so that in each case the bodies struck the board with a momentum of 219 C. D. S. units. The shot was used also from 50, 30, 20, 10 and 5 cm., producing momenta of 169, 131, 107, 76 and 54 C. G. S. units. The whole series of momenta used then was (1) 1097, (2) 694, (3) 491, (4) 347, (5) 219 (steel ball), (6) 219 (shot), (7) 169, (8) 131, (9) 107, (10) 76 and (11) 54 C. G. S. units. These will be referred to in future as momenta of grades 1 to 11 respectively. In testing an animal the greatest momentum was first used for 20 trials. After each individual trial the result was recorded and the animal allowed to come to rest again, if it had responded to the stimulus. If the animal seemed erratic in any way, subsequent sets of 20 tests were made till constant results were obtained. After com-

⁶ momentum = $m v$

$v = 1' 28g$

∴ momentum = $m 1' 28g$

m = mass, s = distance through which the body falls, v = velocity, and g = gravity.

pleting the tests with one momentum for an *Asellus*, the dish containing the animal was gently removed from the table so as to be beyond the influence of the vibrations, and the experiments were repeated on a *Cæcidotea*. This method of procedure was followed for each pair of animals through all the eleven momenta used.

The kinds of reactions were designed by numbers as follows:

0, no reaction.

1, slight movements of antennæ or other appendages.

2, more extended movements of antennæ or other appendages.

3, movements of appendages and bending anterior end of body.

4, same as "2" or "3" followed by the animal's crawling.

5, crawling at once.

For each test the number corresponding to the reaction was recorded. Table V shows one of these records complete.

Table V indicates that the responsiveness of this *Asellus* was most pronounced to the vibrations produced by the falling bodies striking the wood with 1097 and 694 C. G. S. units of momentum, and that there was a rapid decrease as the lower momenta were reached. With *Cæcidotea* the reactions were most pronounced to the higher momenta used and a rapid decrease in responsiveness occurred with momenta below grade 4, but the responsiveness is not entirely lost even with momenta of grade 11, only 54 C. G. S. units. *Cæcidotea* responded not only more often but with a greater vigor of reactions to all the grades of stimuli. These two individuals are typical of the reaction of the two species as Table VI will show.

From Table VI *Asellus* is shown to be less reactive than *Cæcidotea* to this sort of stimulation. This difference appears not only in the number of the responses, but in the vigor of the responses, and in the range of responsiveness, for *Asellus* is not sensitive at all to such stimulation when the momentum is less than 169 units, while *Cæcidotea* appears somewhat responsive to as low a momentum as 54 units. *Asellus* gave the following aver-

TABLE V

ASELLUS COMMUNIS NO. 1, ♀, 9 MM. LONG

BODY USED	STEEL BALL						LEAD SHOT				
	50	20	10	5	2	83.6	50	30	20	10	5
Distance of fall in cm.....	1097	694	491	347	219	219	169	131	107	76	54
Momenta in C. G. S. units.....											
Grades of momenta.....	1	2	3	4	5	6	7	8	9	10	11
	0	1	0	0	0	0	0				
	1	2	0	0	0	0	0				
	3	5	1	0	0	0	0				
	2	4	0	0	0	0	0				
	0	2	0	0	0	0	0				
	0	0	0	0	0	0	0				
	3	0	0	0	0	0	0				
	0	0	0	0	0	0	0				
	0	0	1	0	0	0	0				
Reactions.....	1	0	1	0	0	0	0				
	2	2	0	0	2	0	0				
	3	3	0	0	0	1	0				
	4	4	0	2	0	0	0				
	2	0	0	1	0	0	0				
	2	1	1	0	0	0	0				
	1	1	0	0	0	0	0				
	3	4	0	0	0	0	0				
	5	3	0	0	0	0	0				
	1	0	0	1	0	0	2				
	0	4	0	4	0	0	0				
Number of responses in 20 trials.....	14	13	4	4	1	1	1				
Sum of responses.....	33	36	4	8	2	1	2				
Average vigor of responses.....	24	28	1	2	2	1	2				

TABLE V

CÆCIDOTEA STYGIA, NO. 1, ♂, 10 MM. LONG

BODY USED	STEEL BALL						LEAD SHOT					
Distance of fall in cm.....	50	50	10	5	2	83.6	50	30	20	10	5	
Momenta in C. G. S. units.....	1097	694	491	347	219	219	169	131	107	76	54	
Grades of momenta	1	2	3	4	5	6	7	8	9	10	11	
Reactions.....	5	2	5	5	0	0	1	5	3	0	0	
	5	5	4	4	0	0	0	0	3	0	0	
	4	5	5	4	5	1	0	0	0	0	0	
	5	1	1	2	0	4	4	0	0	0	0	
	4	5	3	5	5	0	1	0	0	0	0	
	2	1	2	4	0	0	0	0	0	0	0	
	3	5	2	0	0	0	0	0	0	1	0	
	5	5	5	4	0	0	0	0	0	0	0	
	5	3	5	3	0	4	0	0	1	0	4	
	3	3	4	5	1	2	0	5	1	1	0	
	2	5	5	0	0	2	0	3	0	0	0	
	4	4	2	3	0	4	0	0	1	1	0	
	2	5	1	5	0	1	0	0	0	0	0	
	0	2	5	4	1	0	4	0	0	0	0	
	5	5	5	2	0	0	0	0	1	0	0	
	5	4	5	5	2	1	1	0	0	0	0	
	5	5	2	0	1	0	0	0	0	0	0	
	1	1	2	4	1	0	0	3	0	0	0	
	0	5	3	0	0	0	0	4	0	0	0	
	4	1	1	4	4	1	0	4	0	1	0	
Number of responses in 20 trials.....	11	19	20	17	8	8	5	5	7	4	1	
Sum of responses.....	71	67	69	66	20	19	11	20	14	4	4	
Average vigor of responses	4.3	3.53	3.45	3.88	2.5	2.37	2.2	4	2	1	4	

TABLE VI

Summary of the reactions of six *Asellus communis* and six *Carcidotea stygia* to mechanical vibrations produced by the concussions of bodies falling with various momenta. The body used in producing the concussion, the distance of its fall, its momentum at the time of producing the concussion, and the grade of its momentum, are indicated in successive horizontal columns at the top of the table. For each individual tested are given in italics the total number of reactions obtained out of 20 trials for each momentum used, and the sum of these reactions on the basis of their vigor. Following the summaries for the six pairs of individuals are given in the last four horizontal columns the total number of responses, the average number of reactions out of 20 trials, the average sum of the reactions for each 20 trials, and the average vigor of the reactions for each momentum used. For example, *Asellus* No. 1 gave 14, 13, 4, 4, 1, 1, 0, 0, 0, and 0 reactions to the different momenta used, and the sums of the vigor of these reactions were 33, 36, 4, 8, 2, 1, 2, 0, 0, and 0

ASELLUS

BODY USED		STEEL BALL						SHOT				
Distance of fall in cm.....	50	20	10	5	2	83.6	50	30	30	10	5	
Momenta, in C. G. S. units.....	1097	694	471	347	219	219	169	131	107	76	54	
Grades of momenta.....	1	2	3	4	5	6	7	8	9	10	11	
No. 1, ♀, 9	No. of responses.....	14	13	4	4	1	1	1				
mm. long												
No. 2, ♀, 8.5	No. of responses.....	16	16	11	4	1	2	0				
mm. long												
No. 3, ♀, 9.4	No. of responses.....	9	5	6	3	0	0	0				
mm. long												
No. 4, ♀, 9	No. of responses.....	5	4	6	3	1	1	0	No reaction s			
mm. long												
No. 5, ♀, 6	No. of responses.....	5	4	4	4	2	1	0				
mm. long												
No. 6, ♀, 10	No. of responses.....	18	10	7	0	0	2	0				
mm. long												
Total number of responses.....	67	52	38	18	5	7	1					
Average number of responses to 20 trials.....	11½	8½	6½	3	¾	1½	1½					
Average sum of the responses to 20 trials.....	18	17½	11	5½	1½	1½	½					
Average vigor of responses.....	1.61	2	1.74	1.88	2.2	1.57	2					

Average vigor of responses to whatever stimulus, 1.79.

TABLE VI—Continued

CÆCIDOTEA

BODY USED		STEEL BALL					SHOT				
Distance of fall in cm.....	50	20	10	5	2	83.6	50	30	20	10	5
Momenta, in C. G. S. units.....	1097	694	471	347	219	219	169	131	107	76	4
Grades of momenta.....	1	2	3	4	5	6	7	8	9	10	11
No. 1, ♂, 10 mm. long	} No. of responses.....	19	19	20	17	7	8	5	4	7	4
		75	67	69	66	20	29	11	16	14	4
No. 2, ♀, 7.4 mm. long	} No. of responses.....	20	20	20	19	5	6	2	2	3	2
		94	75	78	72	14	24	9	8	9	8
No. 3, ♀, 7 mm. long	} No. of responses.....	12	5	3	4	5	5	1	1	1	0
		41	11	6	18	23	16	3	1	1	0
No. 4, ♀, 7 mm. long	} No. of responses.....	18	14	12	10	4	2	1	1	2	3
		55	37	22	21	12	8	4	1	6	7
No. 5, ♀, 5 mm. long	} No. of responses.....	16	16	14	11	7	8	10	9	3	3
		63	67	47	42	17	22	23	20	6	7
No. 6, ♀, 7 mm. long	} No. of responses.....	18	15	11	10	6	5	4	2	3	1
		64	55	36	28	26	21	16	17	11	3
Total number of responses.....	103	89	80	71	34	34	23	19	19	13	7
Average number of responses to 20 trials.....	17½	14½	13½	11½	5½	5½	3½	3½	3½	2½	1½
Average sum of the responses to 20 trials.....	65½	52	43	41½	18½	19½	11	10½	7½	5	2½
Average vigor of responses.....	3.8	3.53	3.23	4.83	3.29	3.41	2.87	3.31	2.47	2.32	1.4

Average vigor of responses to whatever stimulus, 3.37

age number of responses out of 20 trials to stimulations of grades 1 to 7, $11\frac{1}{6}$, $8\frac{2}{3}$, $6\frac{1}{3}$, $3\frac{5}{6}$, $1\frac{1}{6}$, and $\frac{1}{6}$. To the same grades of stimuli Cæcidotea gave the following average number of reactions: $17\frac{1}{6}$, $14\frac{2}{3}$, $13\frac{1}{3}$, $11\frac{5}{6}$, $5\frac{2}{3}$, $5\frac{2}{3}$, and $3\frac{5}{6}$, while the reactivity continued to stimuli of grades 8, 9, 10, and 11 with the following average number of responses: 3, $\frac{1}{6}$, $2\frac{1}{6}$, $2\frac{1}{6}$, and $1\frac{1}{6}$. The averages for the vigor of the responses of Asellus for the grades of stimuli 1 to 7 were of the grades of response 1.61, 2, 1.74, 1.88, 2.2, 1.57, and 2. The corresponding averages for Cæcidotea were 3.8, 3.5, 3.23, 3.48, 3.29, 3.41, and 2.87, while to the lowest grades of stimulation to which Asellus did not respond the averages of Cæcidotea's responses were 3.31, 2.47, 2.3, and 2.14. The average on the basis of vigor of response for the whole number of reactions obtained from Asellus

is 1.79; the same average for *Cæcidotea* is 3.37. Asellus, out of 120 trials, 20 upon each of six animals gave but one reaction to stimulation by grade 7 (169 units of momentum) and no reactions were gotten from stimulation below this grade. *Cæcidotea* continued to respond to the lower grades and to some extent even to the lowest grade used (54 units of momentum). The close agreement of results obtained by grades 5 and 6, in which different bodies strike with the same momentum removes any reasonable doubt as to the justification of considering the effectiveness of the stimulation to be dependent upon the momentum.

As already noted it sometimes occurs that animals upon which tests were being made were moving at the time of the test. Under such circumstances the movements of the animals were often arrested. An arrest of movements due to a stimulus is of course as definite a reaction as the inciting to movement by a stimulus. Such arrests of movements were recorded with the other reactions.

One of the most delicate reactions was a twitching of the flagellum of the antenna or a stroking of the antenna by the gnathopod. This reaction suggested the possibility that the flagellum is particularly sensitive to such mechanical stimulation.

The results of the foregoing experiments may be summarized as follows:

1. Falling bodies having the same momenta produce virtually the same reactions. These become more numerous as well as more vigorous with increase of momentum.
2. Asellus responds much less often than *Cæcidotea* to such stimuli of whatever grade.
3. Asellus responds less vigorously than *Cæcidotea* to such stimuli; the average of the vigor of responses for the whole number of responses for Asellus was 1.79 and for *Cæcidotea* 3.37.
4. The threshold of stimulation for Asellus was found to be near that of grade 5 and 6 (219 units of momentum), while the threshold for *Cæcidotea* was approached only with the lowest stimulation used, grade 11 (54 units of momentum), a grade only $\frac{1}{4}$ as high.

4. With Vibrations, 100 per Second

A fourth method of testing the relative responsiveness of these two species to mechanical stimulation was by means of an electric tuning fork whose rate was 100 complete vibrations per second. The animals, as in previous experiments were placed in small stentor dishes, the *Asellus* over a light-colored bottom and the *Cæcidotea* over a black one. The stentor dish containing the animal was placed upon a heavy block of hard pine wood 41 cm. long, 22 cm. broad and 11 cm. thick, with planed surfaces. The dish was firmly fixed upon the block near one end by being clamped between three nails driven partly into the block. The block rested upon a pile of crumpled paper two inches thick placed upon a table whose legs rested upon crumpled paper. Close by the first table was a second one likewise supported on paper, and upon this table lay the fork, also on a thick pad of paper. The piles of paper prevented any perceptible transmission of the vibrations (other than when desired) from the fork to the stentor dish in which the animal was confined. The fork was driven by a Columbia No. 6 dry cell and a simple key was used to make and break the circuit as desired. Two cells were used alternately to avoid the effects of running down.

The manner of experimentation was as follows: The animal to be tested was allowed to remain in the stentor dish in position for a sufficient length of time to become thoroughly settled, after which the fork was set in vibration and slipped over its support of paper (upon which rested a smooth sheet of glass) until its base came into firm contact with the end of the block on which the stentor dish rested. After a momentary contact the fork was withdrawn and a record of the response of the animal, if any was made. The test was repeated after about ten seconds or more. Twenty of these tests were made upon each individual, first as *Asellus* then a *Cæcidotea*, until 15 pairs of individuals had been tested. The responses were ranked, as in the experiments on the effect of stimulation by the concussions of falling balls (see p. 453), though it was found expedient to add another class. Sometimes the animals moved just at the instant before

the stimulus was applied and in such cases often an arrest of movement occurred. This was indicated by an "A." Table VII shows the detailed records of the fifteen pairs of individuals tested in this manner.

An examination of Table VII discloses the fact that in every case where a pair of the two species were subjected to test, the *Cæcidotea* was the more responsive of the two. *Asellus* made on an average for the 15 individuals tested 6.8 responses in 20 trials, with an average vigor of 1.39, while the 15 *Cæcidotea* averaged 11.8 responses in the same number of trials, with an average vigor of 3.02. Hence the number of responses made by *Cæcidotes* was nearly twice as large as the number made by *Asellus* and at the same time they were on the average considerably more than twice as vigorous.

Very often, particularly with *Asellus*, the animal responded by trembling or quivering movements of the flagellum of the antenna or a quick stroking of the antenna with the gnathopod. Such reactions occurred often with this sort of stimulation as well as with the stimulation from the concussions of falling balls, but to stimulation by bristles or locally applied currents of water it was scarcely ever noted. These results suggest that the response to mechanical vibrations may be more or less localized in the flagellum of the antenna.

The following statements summarize these results:

1. *Asellus* is less sensitive to such vibrations than *Cæcidotea*.
2. *Asellus* responds to such stimulation scarcely more than half as often as *Cæcidotea*.
3. *Asellus* responds to such stimulation less than half as vigorously as *Cæcidotea*.
4. Arrest of movements is often caused by this form of stimulation.
5. The fact that the antennæ are so often whipped about and rubbed by the gnathopod during such stimulation suggests that they are more sensitive to this stimulus than other parts of the body although to pure tactile stimulation they are scarcely at all sensitive.

5. *General Summary of Experiments with Mechanical Stimulation*

To all kinds of mechanical stimulation, whether pure tactile stimulation or mechanical vibrations, *Cæcidotea* is decidedly more responsive than *Asellus*. This becomes evident both from examining the frequency of response and the vigor of response, *Cæcidotea* responding more often and more vigorously than *Asellus*. The difference in vigor of response is particularly noticeable toward the stimuli of lower intensity to which *Asellus* responds only very slightly, if at all; but *Cæcidotea*, as long as the stimulus produces any response at all, continues to respond vigorously.

The flagella of the antennæ of both species were surprisingly unresponsive to pure tactile stimulation by contact with bristles or localized currents of water, but they seemed to be extremely sensitive to vibrations such as those produced by the tuning fork or by the concussion of a falling body. While the latter was not actually demonstrated, it was strongly indicated by the different behavior of the animals under the two sorts of stimulation—pure tactile and mechanical vibrations. When the flagellum of the antenna did respond to tactile stimulation the response was usually accompanied, especially in *Asellus*, by a trembling or jerking motion and a withdrawal of the stimulated part or a stroking or rubbing of the whole antenna with the gnathopod. Such a response occurred very commonly to stimulation by concussion and by the tuning fork. With the concussions the stimulus was only momentary and the response was of short duration, but quite like the response to the vibrations of the fork, except that it was not carried so far. To the vibrations of the fork the response was quite often only the above-mentioned movements of the antennæ and gnathopods. If the stimulus was continued without break, however, these movements were usually followed by the animals' crawling. In short, the responses to stimulation of the animal as a whole by mechanical vibrations are the same as the responses to local stimulation of the flagella of the antennæ by pure tactile stimulations. In the latter case the stimulation was local, and

TABLE VII, PART I

Part I shows the reactions of the 15 *Asellus communis* to stimulation by vibrations at the rate of 100 per second produced by an electric tuning fork. Part 2 shows the same for the 15 *Cacidoalea stygia* under similar conditions. The responses of each individual are indicated in a separate column. The characteristics used in indicating the reactions refer to the various grades of responses (see p. 7).

Following the detailed responses as indicated for each individual, are given in successive horizontal columns, the number of responses gotten from each animal in 20 trials, the sum of the vigor of these responses, and the average vigor of the responses for each individual tested. In each part of the table at the lower right hand corners are given the average number of responses out of 20 trials for each of the species, the average sum of the vigor of the responses to 20 trials for each species and the average vigor of the response for each species.

ASELLUS COMMUNIS														
NO. 1	NO. 2	NO. 3	NO. 4	NO. 5	NO. 6	NO. 7	NO. 8	NO. 9	NO. 10	NO. 11	NO. 12	NO. 13	NO. 14	NO. 15
♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
6.6 MM.	11 MM.	9 MM.	9.4 MM.	7.2 MM.	7 MM.	9.5 MM.	7 MM.	6.5 MM.	10 MM.	8.5 MM.	8.5 MM.	6.5 MM.	6.3 MM.	7.5 MM.
Responses.....	6.6 MM.	11 MM.	9 MM.	9.4 MM.	7.2 MM.	7 MM.	9.5 MM.	7 MM.	6.5 MM.	10 MM.	8.5 MM.	8.5 MM.	6.5 MM.	6.3 MM.
3	0	0	0	0	0	3	2	0	1	0	0	0	0	1
0	1	0	0	0	0	5	0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
3	2	1	2	0	1	2	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
4	2	0	0	0	1	1	0	0	0	1	1	1	1	1
0	0	0	4	0	0	1	1	0	0	0	1	1	0	0
0	2	0	3	0	0	0	1	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0	0	0	1	1	1	1

TABLE VII, PART 2

CECIDOTEA STYGIA

NO. 1 ♀ 7 MM.	NO. 2 ♂ 7.5 MM., 7.5 MM.	NO. 3 ♂ 7.5 MM.	NO. 4 ♂ 7.5 MM.	NO. 5 ♀ 6.5 MM.	NO. 6 ♀ 7 MM.	NO. 7 ♂ 10 MM.	NO. 8 ♀ 6 MM.	NO. 9 ♂ 7 MM.	NO. 10 ♀ 8 MM.	NO. 11 ♂ 6 MM.	NO. 12 ♀ 5.7 MM.	NO. 13 ♀ 5 MM., 6.3 MM.	NO. 14 ♀ 6.3 MM.	NO. 15 ♀ 6 MM.	AVER- AGES
1	5	0	3	5	0	0	5	0	0	0	1	5	3	0	
2	0	0	0	0	1	0	5	0	0	5	0	5	5	A	
5	5	1	5	2	4	2	4	0	0	5	2	0	0	5	
0	0	3	0	2	0	0	1	5	5	5	0	2	0	1	
3	3	0	5	0	4	3	0	2	0	3	0	5	2	0	
0	3	0	0	1	1	1	5	1	2	1	0	5	2	1	
0	3	5	5	1	0	0	0	0	1	0	1	3	0	0	
5	3	5	5	2	0	0	0	3	5	0	2	5	0	3	
4	3	0	5	3	3	1	0	3	2	1	5	0	5	0	
0	3	0	5	0	4	1	2	0	0	5	0	5	A	3	
1	2	0	5	3	3	1	0	1	1	5	1	5	0	1	
2	0	5	0	0	3	5	0	0	3	3	3	3	0	0	
5	4	1	5	5	0	0	0	2	0	A	5	5	0	0	
0	0	0	0	1	2	0	0	1	3	5	5	5	0	1	
0	3	0	5	2	4	0	0	1	2	5	5	0	5	3	
0	1	0	2	1	0	2	0	5	0	0	C	A	5	0	
0	1	4	1	1	3	5	0	4	0	5	0	3	4	3	
5	3	0	2	2	0	0	0	0	0	5	1	5	3	0	
5	2	0	0	1	0	3	0	0	5	A	0	0	5	3	
1	3	1	0	1	2	0	0	5	5	2	0	0	0	0	
12	16	8	12	16	12	10	6	12	11	16	9	15	11	11	11.8
39	47	25	48	33	34	24	22	33	34	55	18	61	39	24	35.75
3.25	2.94	3.12	4	2.06	2.83	2.4	3.66	2.75	3.09	3.44	2	4.07	3.55	2.18	3.02

Responses

Total number of re-
sponses
Sum of vigor of re-
sponses
Average vigor of re-
sponses.....

the response was local; in the former the stimulation was general but the response was local. Hence it would seem that inasmuch as the first and most common response to a general stimulation of the animal by mechanical vibration is in movements of the antennæ, accompanied by movement of the gnathopod, which response is the same as that produced by local stimulation of the antennæ by pure tactile stimulation, that the antennæ are particularly sensitive to vibrations, and that we here have a case of specialization in which the antennæ, though only slightly sensitive to pure tactile stimulation, are decidedly sensitive, and, in fact, the parts most sensitive to mechanical vibrations.

It was noticed repeatedly that *Asellus* and *Cæcidotea* were very sensitive to any movement in the water. This sensitiveness was much the more marked in *Cæcidotea*. Even dipping a small camel's hair brush or the end of a pencil into the water would often rouse a *Cæcidotea* to sudden movement, notwithstanding that it might be 40 to 50 cm. away from the point where the disturbance started. A few times during experimentation with *Cæcidotea* when I accidentally breathed upon the surface of the water, the animals responded vigorously. This acute sensitiveness to a disturbance in the water was noted, to, in collecting *Cæcidotea* in the caves, where slight and unusual movements in the water at one side of a pool would arouse to active movements every *Cæcidotea* within a radius of 2 or 3 meters, the animals generally leaving the borders of the pools and moving toward the deeper water where they soon became concealed under the edges of stones or in small depressions in the bottom.

This greater sensitiveness of *Cæcidotea* to mechanical stimulation of whatever sort and its relatively slight response to light is a good illustration of the principle of compensation in special senses.

II. EXPERIMENTS WITH THE ANIMALS IN CURRENTS OF WATER

A special trough was constructed for experiments on the effects of currents of water on *Asellus* and *Cæcidotea*. Two thin strips of glass, 46 cm. long by 2 cm. wide, were cemented in vertical par-

allel planes, 2.3 cm. apart, upon a base of slate 46 cm. long by 6 cm. wide. The slate afforded a fairly good foothold for the animals which crawl, but do not swim. This base of sufficient width to prevent an easy overturning of the trough. The upper end of the trough, into which the water flowed, was closed by a piece of tin to within 4 mm. of the top; the lower end was closed also by a piece of tin which, however, rose only to within 1 cm. of the top. Closely fitting partitions of copper gauze 16 meshes to the centimeter were used to confine the animals within the more nearly central part of the trough, where the current was uniform. Across the tank over each of these partitions was laid a piece of glass to prevent the animals from crawling over the partition.

The trough when in use was supported upon a small stand. A glass jar 31 cm. high was placed close to the upper end of the tank and under a faucet. The jar was kept filled to overflowing with water during the experiments. Siphons of various sizes, depending upon the strength of current desired within the trough were used to conduct the water from the jar to the trough. The gauze partitions were placed at 10.5 cm. from the upper end and 3.5 cm. from the lower end, this making the functional part of the trough, within which the animals were confined, 32 cm. long.

The siphon used introduced the water near the extreme upper end of the trough and below the level of the water. There were considerable irregularities in the upper portion of the current. In order to break up these irregularities and reduce the current to uniformity, three partitions of wire netting, 5 meshes to the centimeter, were interposed at intervals of about 2 cm. between the place where the siphon discharged into the trough and the upper partition of copper gauze. This arrangement secured a practically uniform current throughout that portion of the trough in which the animals were placed.

During some of the experiments one end of the tank was darkened while the other end was illuminated by direct sunlight, diffuse day light or by a 6-glower Nernst lamp. The part of the trough darkened was covered with a closely fitted black cloth; when the upper end was covered the cloth was held about the siphon by a stout rubber band, and when the lower end was dark-

ened the cloth was formed into a rude hanging tube through which the water escaped. While this arrangement certainly did not make the darkened end light-proof, it at any rate cut off nearly all the light except that which entered from the light part of the trough. Doubtless a great deal did so enter, but under all circumstances there was a strong contrast between the illuminated part of the trough and the rest as judged by the eye.

Ten animals were found most satisfactory to experiment with at a time, but occasionally as few as five or as many as twenty were used. In general, currents of two strenghts were used: 435 centimeters per minute and 140 centimeters per minute. Currents stronger than 435 cm. per minute swept the animals, especially the *Asellus*, down the trough and currents weaker than 140 cm. seemed to produce no decided results.

1. Asellus

When, after having become quiet, *Asellus* was subjected to a current of water in the apparatus described, it usually responded very quickly by crawling against the current. Individuals which went down-stream soon turned back from the partition and crawled up-stream. Individuals which reached the upper end did not usually turn back. Hence the rheotaxis was very marked.

The animals, when first subjected to a current, crept rapidly for a time. In doing so they did not adhere well to the slate bottom of the trough, and many were swept off their feet and carried all or part way towards the lower end of the trough. Those swept down ordinarily persisted in crawling up-stream again, and after a time, when they had come to crawl less rapidly, fewer were carried back by the current, and they became collected at the upper end of the trough.

Asellus tends somewhat to remain on the copper gauze partitions at the ends of the trough. The great amount of moving back and forth in the trough especially during the early part of an experiment is sufficient warrant that this is not a very disturbing factor, however.

The maximum response as indicated by the number of indi-

viduals which collected at the upper end of the trough was attained in from five minutes to four and a half hours after the experiment began, but on the average it occurred in about 1.4 hours. The persistence of the response was extremely variable; in some cases the animals remained at the upper end of the trough for only about a quarter of an hour, while in one experiment (No. 16) they stayed continuously for two days, after which they gradually left the upper end of the trough. Commonly, however, the rheotactic response did not persist more than two or three hours, and in cases in which the experiment was run over night, the response usually became decidedly reduced before the next morning.

Table VIII shows the results of the characteristic experiments of this series.

2. *Cæcidotea*

Cæcidotea, when first subjected to a current of water, moved about usually with little reference to its direction, though it sometimes reacted almost at once, crawling towards the upper end of the trough. *Cæcidotea* crawls more slowly than *Asellus* and keeps more closely to the substratum, so that it is better able to adhere to a fairly smooth surface than *Asellus*. It was not often swept off its feet by a current of 435 cm. per minute, and it moved about in the current with greater ease than *Asellus*.

With *Asellus* the direction of the current could be readily determined at almost any time during the beginning of an experiment by examining the direction in which the animals within the trough were headed. This was not so with *Cæcidotea*, for often, so far as their positions were concerned, one would not suspect that there was a current. *Cæcidotea*, while remaining on the copper gauze partitions of the trough at times, did not do so as persistently as *Asellus* did.

After a time in most of the cases in which reactions did not appear promptly, *Cæcidotea* gradually collected toward the upper end of the trough. The maximum rheotactic response, *i.e.*, the collecting of the maximum number in the upper end of the trough, with one exception occurred within $\frac{3}{4}$ to 5 hours after the experiment began and averaged about 2.1 hours. This rheotactic

response persisted in most cases as long as the experiment lasted, and in one instance it lasted three days.

In some experiments the animals appeared altogether indifferent to the current and either moved about freely or tended to remain in the lower half of the trough. Two such results (experiments Nos. 2 and 6) may have been due to poor conditions of the animals, which had only 2 or 3 days before arrived from the caves of Indiana. Vigorous animals nearly always gave a definite and persistent response. A record of some of the experiments of this series is given in Table IX.

As compared with *Asellus*, *Cæcidotea* does not respond to the influence of a current so quickly; the maximum response with the former appears on an average in about 1.4 hours after the experiment starts, with the latter in about 2.1 hours. But the response of *Cæcidotea* continues longer than that of *Asellus* and usually lasts indefinitely.

In the experiments combining the effects of light and currents of water, where the upper end of the trough was darkened and the lower end subjected to strong illumination, both *Asellus* and *Cæcidotea* collected pretty generally in the upper darkened end. With *Asellus* this response reached its maximum in about three-quarters of an hour; with *Cæcidotea* in about an hour. After about an hour *Asellus* seemed to remain less generally in the dark end than before, while with *Cæcidotea* the reaction usually persisted without much diminution as long as the experiment was continued.

When the lower end of the trough was darkened and the upper strongly illuminated both *Asellus* and *Cæcidotea* showed tendencies to enter the upper end in spite of the light. With *Asellus* this tendency was very pronounced for a time, but the animals became so active on entering the light area that they were often carried off their feet and swept back into the lower end again. If *Asellus* was not swept back into the lower end it crawled back after a time and the rheotactic stimulus finally failed to bring it again into the upper end. *Cæcidotea* for a time entered and moved about in the upper light end to some extent. This persisted for various lengths of time so that on an average several

[illegible]

Average time until maximum response 1.4 hr.

Average time until response decreased 7 hr.

Experiment was continued over night and the following day, the record of which is given in the adjoining column.

The animals were driven to the lower end of the tank and further observations recorded in the adjoining column.

TABLE IX
This table gives the details of the experiments on *Cæcidotea* with currents of water. The plan of this table is like that of Table VIII already described.

NUMBER OF EXPERIMENT	1	2	3	4	5	6	7	8		9				
DATE	NOVEMBER 6, 1906	NOVEMBER 9, 1906	NOVEMBER 13, 1906	NOVEMBER 10, 1906	NOVEMBER 26, 1906	NOVEMBER 28, 1906	DECEMBER 18, 1906	DECEMBER 19, 1906	SECOND DAY, EXPERIMENT CONTINUED FROM PRECEDING DAY	THIRD DAY, EXPERIMENT CONTINUED FROM PRECEDING DAY	DECEMBER 20, 1906	EXPERIMENT CONTINUED FROM PRECEDING DAY	EXPERIMENT CONTINUED FROM PRECEDING DAY	
NUMBER OF ANIMALS USED	10	10	10	10	10	10	10	10			10			
STRENGTH OF CURRENT IN CM. PER MIN.	435	435	140	134	140	435	435	435			435			
Number in upper end at start.	7	1	5	6	6	6	7	2	6	4	5	6	6	
After 5 min.	7	1	4	6	7	7	6	—	—	—	—	—	—	
10 min.	7	1	5	—	5	7	6	—	—	—	—	—	—	
15 min.	7	1	5	—	5	7	6	—	—	4	—	—	—	
2 hr.	6	1	6	—	3	—	7	—	6	—	—	6	6	
3 hr.	8	2	6	—	2	—	—	—	—	—	—	—	—	
1 hr.	7	1	4	8	3	6	—	—	—	—	—	—	—	
1½ hr.	6	3	7	9	4	—	—	7	—	—	—	—	—	
1¾ hr.	5	2	—	9	—	—	—	—	—	4	—	—	—	

remained in the upper end for about three-quarters of an hour, after which time the animals that entered the light seldom remained long. *Cæcidotea* was not often swept back. It wandered about in the light upper end for a time and entered the dark end again apparently by accident. Often, too, it turned back into the dark as soon as it came to the light area.

Under the last conditions of experimentation *Asellus* seems more rheotactic at first than *Cæcidotea*, but this reaction persists for a shorter time than in *Cæcidotea*. Probably a better way of describing this state in *Asellus* is that at first its rheotaxis is stronger, as compared with its negative phototaxis, than *Cæcidotea*'s, but that its rheotaxis soon gives place to negative phototaxis; while *Cæcidotea* does not so soon cease to enter the light as *Asellus*, it never enters and collects in the light in large numbers. Its negative phototaxis is from the first stronger than its rheotaxis.

In regions of caves the cave streams, as I know them, ordinarily originate underground and flow out of the caves, although there are many exceptions to this rule. In Mayfield's Cave, near Bloomington, Indiana, which is the source of some of my material, there is no inflow into the cave from above ground except through sink holes in times of heavy rains or thaws. The stream is merely an outlet for underground drainage.

The experiments in which the upper end of the trough was darkened while the lower remained light, thus resembled in miniature the conditions met with in this cave. Judging from the results of these experiments *Asellus* and *Cæcidotæ* ought both to enter such a cave, but *Asellus* being less persistently rheotactic would be less inclined to follow up the stream and remain within the cave. *Cæcidotæ*, while less strongly rheotactic at the beginning, is persistently so, and hence would tend to creep persistently into the cave. The added fact that *Asellus*, after having been in darkness for some hours, is positively phototactic would induce the animals to leave a cave after once having become indifferent to the current, provided that they were carried by accident to within a glimmer of light.

The experiments in which the lower end of the trough was

darkened and the upper end illuminated afforded conditions somewhat resembling conditions in caves which are entered by streams from the outside. Under such conditions, judging from the results of the experiments, *Asellus*, when carried to the inlet, would tend to leave the cave because of its relatively stronger rheotaxis. In addition to this factor, however, the positive phototaxis of *Asellus* after having been in darkness would also aid. *Cæcidotea*, on the contrary, is always negatively phototactic, and while it shows a tendency under these circumstances to enter the light because of its rheotaxis, it is probable that this form of reactions is always subordinate to its negative phototaxis.

III. STUDY OF THE FOOD

Attempts were made to ascertain if a difference in the food of *Asellus* and *Cæcidotea* was possibly an important factor in determining the habitats of the two species. To this end specimens of *Cæcidotea* were taken direct from the caves in Indiana and preserved in formaline before they had an opportunity to feed upon other substances than those they might get in their normal surroundings and the same was done with *Asellus communis* obtained near Cambridge, Mass.¹⁰

The digestive tracts of each were then carefully examined to determine their contents.

Afterward several individuals of each species were kept in clean tap water without food for several days and then placed in separate jars with bits of decayed leaves and living *Ceratophyllum* and subsequently examined to determine what was taken for food when living and dead plant tissue were equally present.

With *Cæcidotea* the evidence pointed to the conclusion that the animal in the cave collects for food whatever decaying organic matter it happens upon. Naturally dead plant tissue forms

¹⁰*Mancasellus tenax dilata*, the common and extremely abundant *Asellid* from southern Indiana, was similarly treated and examined. It was found that the food of this species from the region about the cave in Indiana is practically the same as that of *Asellus communis* near Cambridge, Mass.

the main part of its food. The digestive tracts contained relatively small amounts of mineral matter. Those placed with living and decaying plant tissue ate relatively small amounts of green algæ, probably only that taken in with the decayed plant tissue.

From the evidence obtained from the series of examinations of *Asellus* it seemed probable that it takes its food either from surfaces of dead plant tissue or from living plants. In cases where material apparently quite recently taken as food was found in the digestive tract there was always more or less fresh plant tissue and those individuals which were deprived of food for a time and then placed with both the decaying leaves and the living *Ceratophyllum* seemed to have collected nearly all their food from the *Ceratophyllum*. There was, however, no evidence to prove that green plant tissue was a necessary portion of the food of *Asellus*. It probably could live upon decaying organic matter exclusively, as *Cæcidotea* does, but it partakes of both kinds of food and will use living plant tissue largely when both living and dead are present.

In every case the digestive tracts of those *Asellus* examined contained a large percentage of mineral matter, in most cases as much as 85 per cent of the contents being inorganic. It will be remembered that the digestive tracts of even those *Cæcidotea* which were taken directly from the caves contained very little mineral matter.

The difference between the amounts of mineral matter taken with the food in the two species is remarkable in caves where *Cæcidotea* obtains its food, organic matter is extremely scarce, while, where *Asellus* lives, the proportion of organic to mineral matter is very many times as great. This difference suggests that *Cæcidotea* possesses a superior discriminative power in selecting its food. Such ability would be of immense advantage to an animal in a cave. The lack of discrimination in selecting food clearly indicates, I believe, that *Asellus* is incapable of meeting the food conditions within caves.

IV. GENERAL DISCUSSION

The significance of the various separate results obtained in the different series of experiments has in several cases been pointed out in summarizing these results.

Cæcidotea stygia and *Asellus communis* have quite similar habits, except for the fact that the former lives almost exclusively in subterranean waters, whereas the latter, though occasionally found in cave water, is extremely rare there. Its occurrence in caves has been mentioned only a few times. When collecting in caves I have never seen either *Asellus communis* or *Mancasellus tenax dilata*, although both species occurred near caves in which I did much collecting, and the latter species was present in immense numbers immediately outside the caves. *Cæcidotea*, when found above ground, has occurred only in water near and immediately connected with underground waters.

These two animals, though differing in habitat, are much alike in many of their reactions to stimuli. Both are negatively phototactic to such intensities of light as they respond to at all; both respond in like manner to various tactile and mechanical stimuli, and the regions of the body most highly sensitive to these stimuli, are nearly the same in the two species; both are rheotactic, responding to currents of water in like manner. When subjected to the influence of a current of water, in a trough one end of which was strongly illuminated, both species, though for a time responding to the rheotactic stimulus alone, soon, in most cases, reacted to the light alone. Their food is nearly the same, both species feeding largely upon decaying plant tissue.

The following differences in the reactions of the two species were noted:

1. *Asellus* is decidedly more responsive to light stimuli and responds to much lower light intensities (2.5 C. M.) than *Cæcidotea* (80 C. M.); after retention in darkness *Asellus* is for a time positive to a considerable range of intensities (2.5 C. M. to 80 or more C. M.). *Cæcidotea* is never positive.

2. *Cæcidotea*, on the other hand, is decidedly the more respon-

sive to mechanical stimulation, this difference appearing in the number and vigor of its responses and in its having a decidedly lower threshold of stimulation than Asellus.

3. *Cæcidotea*, though at first less rheotactic than Asellus, is persistently rheotactic, whereas rheotaxis with Asellus is only temporary. When the stimulus of strong illumination in the lower part of the trough was added to the stimulus of a current, the *Cæcidotea* more persistently remained within the upper dark end.

Although there are considerable differences between the responses of the two species in minor details, these are, after all, not so much differences of kind as of degree. Physiologically considered, the two species are very much alike.

The relatively slight sensitiveness to light shown by *Cæcidotea*, as compared with Asellus, is what one might expect from the responses of eyeless animals in general, as compared with those which possess eyes. For example, Dubois ('89, pp. 358-359) found that *Proteus*, the blind salamander of the European caves, responded to light from a projection lantern. Semper ('89, p. 79) states that *Proteus* is sensitive even to daylight. Eigenmann ('00, pp. 113-116) found the blind fish, *Amblyopsis*, sensitive to strong light suddenly thrown upon it as well as to diffuse daylight, for these animals, when kept in a pool in the open air, where they remained concealed among rocks during the day, swam about freely in twilight and at night. It has been shown by Payne, ('07) that *Amblyopsis* reacts to light from a "100 c.p." acetylene lamp at 32 inches from the end of the aquarium; but with this intensity of illumination an average of only 54 per cent of the individuals were in the end farther from as against 46 per cent in the end nearer to the light. With considerably greater intensities he found the reactions were much more decided. Hence it seems that the lower intensity used by Payne ('07, p. 318) is near the threshold of stimulation for *Amblyopsis*.

There is no reason to suppose from any of these observations that such animals respond to low intensities of illumination.

The nicety with which even slight sensitiveness to light may regulate an animal's movements is well illustrated by the following case. Parker ('05, p. 418) found sensitiveness to strong light in the skin of the tail of *Ammocœtes*, and pointed out the significance of this in relation to the burrowing habit of the animal. Here again, the sensitiveness was to intense light only. The eyes of these animals probably subserve all light-receptive functions necessary for swimming about, but in burrowing the integumentary organs of the tail serve to distinguish intensities sufficiently to direct the animal to continue burrowing until completely covered. Here, as in the other cases cited, the organs are not highly discriminating light-receptive organs, but they suffice for the regulation of the animal's movements.

Among the higher animals those that possess degenerate, or poorly developed eyes are such as in general live in dark situations. Their light-perceiving organs are of advantage to them only in aiding them to remain within a suitable environment. Highly developed light-receptive organs are of no advantage in their dark habitat, and organs capable of perceiving only considerable changes in intensity of illumination are sufficient to serve as a check to keep them in their proper surroundings.

Cæcidotea nearly always lives in absolute darkness and ordinarily has little occasion to discriminate between intensities of illumination. If, however, in approaching the mouth of a cave it becomes subjected to increased illumination, its light-receptive organs ordinarily are discriminative enough to prevent its leaving its subterranean abode. Whether its light-perceptive organs were adapted to its cave habitat or whether its cave habitat was adopted because its organs suited it for such surroundings, does not here concern us. At any rate, *Cæcidotea*'s light-receptive organs are sufficiently discriminating to serve their part in regulating the movements of the organisms within caves.

We have no reason to suppose that a species lives where there is extremely little light because it is extremely responsive to light. On the contrary, we have every reason to suppose the opposite—that when an animal lives where there is little light and where it has little opportunity or occasion to be influenced by light, it will

be little responsive to this influence. It is a part of the adaptive economy of nature, a frugality long noted with reference to eye structures, but apparently less remarked with regard to light perception in general.

Such animals as the cockroach and *Oniscus* (cf. Cole, '07, pp. 373-380) remain in relatively closely circumscribed and restricted dark situations by day. While their habits are such that highly discriminative eyes would be of little use to them, slightly acute organs for discriminating differences in intensity serve them very well, aiding them in reaching and remaining concealed within their diurnal haunts. *Asellus* often lives in fairly exposed situations, but, like *Oniscus*, it tends to seek the darker of the available regions. It possesses better powers of discrimination than *Cæcidotea*, and this serves it well in aiding it to find quite small and restricted shaded areas, which *Cæcidotea* can not do.

The experiments discussed in this paper clearly show that the subterranean species, *Cæcidotea stygia*, has greater sensitiveness to mechanical stimulation (whether purely tactile or vibrations) than its near relative, *Asellus communis*, which lives above ground. *Cæcidotea* proved decidedly the more sensitive, both in having a lower threshold of stimulation and in responding more generally and more vigorously to such stimuli. Hence these isopods furnish an undoubted case in support of the common belief that cave animals have acquired greater sensitiveness to mechanical stimulation than their near relatives living in other situations.

Since *Cæcidotea* was shown to be much less sensitive to light than *Asellus*, its greater sensitiveness to mechanical stimulation is a good illustration of the principle of increase in sensitiveness to one sort of stimulation in compensation for the partial loss of sensitiveness to another, *i.e.*, the organism is so adapted to its environment that when one influence ceases to regulate its movements another acquires increased importance and in a measure replaces it.

There still remains one point to be considered—the bearing of these experiments on a possible explanation of the occurrence of the cave species within caves rather than outside of them and the

occurrence of non-caverniculous species outside of rather than within caves.

One needs to experiment with the two species for only a short time to be struck with the similarity of their responses to various influences. The minor differences in their reactions, however, are very significant in relation to the habitats of the animals. While *Cæcidotea* is responsive to only fairly high intensities of light (80 C.M. or greater), it is always negative to any intensity to which it responds at all. Hence, if outside a cave, its light reactions alone would tend to lead it into a cave if there were one near, while if it were in a cave and wandered into the light near an outlet, its negativity to light would prevent its leaving the cave and passing into waters above ground. If *Asellus* were near a cave, its response to light would at first tend to direct it into the cave. But, after having been in darkness within the cave for a time, it would again become positively phototactic, so that if it came in reach of light from the outside it would escape.

Again, *Cæcidotea*, while less strongly rheotactic than *Asellus*, when first subjected to a current, is more persistently rheotactic. In experiments combining the effects of a current of water with light stimulation under such conditions that when the animals moved against the current they passed into a darkened region, it was shown that *Cæcidotea* remained in the darkened region more persistently than *Asellus* did. This, as already stated, repeats in miniature the usual conditions found in cave streams, since they generally flow out of caves rather than into them. In such cases, even if *Cæcidotea* were not rheotactic, its greater tenacity in holding to the substratum would better enable it to make its way into caves and remain there; whereas, if the stream were swift, *Asellus* could not hold its own against the current. In the experiments with light combined with a current of water under such conditions that when the animals moving against the current passed out of a darkened region into a strongly illuminated one, the other cave stream condition (found in streams which enter caves from above ground) was in a way duplicated. In those experiments *Asellus* was more vigorously rheotactic at first, but *Cæcidotea* more persistently so, although under these condi-

tions neither persisted in entering the light for any great length of time. Asellus, however, after having been in a cave in darkness for a time, would become positively phototactic and would then have both its rheotactic and its positively phototactic impulses to direct it out of the cave.

The suggestion that cave conditions involve fewer mechanical disturbances in underground waters than are found in out-door streams and pools, and that the relative immunity from mechanical disturbance within caves is a factor in determining the distribution of the one species within caves and the other outside, seems hardly worth following up.

The difference in the food taken by the two species seems to be a factor in determining their habitats. *Cæcidotea* eats nearly exclusively dead plant tissue, even when provided with living and dead tissue in equal abundance. While *Asellus* takes much fresh plant tissue in addition to the dead plant tissue which it also feeds upon, it is not shown that living plant tissue forms a necessary part of its food, so that apparently it might feed upon dead plant tissue exclusively. There is an extremely small amount of organic matter and a great prevalence of sand, etc., in caves as compared with the amounts of organic matter and inorganic matter in the situations in which *Asellus* lives. In view of this fact the relatively very small amount of dirt and small particles of mineral matter within the digestive tract of *Cæcidotea* as compared with that of *Asellus* suggests that *Cæcidotea* exercises more discrimination than *Asellus* in taking its food.

The importance to an animal living in a cave of a superior ability in selecting its food could not be overestimated, since the organic matter there is so scanty. If *Cæcidotea* possesses such an advantage over *Asellus* that alone may be a very important factor in determining the suitability of *Cæcidotea* to a cave habitat and the unsuitability of *Asellus* for the same locality.

To recapitulate, we find some apparent importance in the factors of the animals' food and their different rheotactic responses in determining the habitats of the two species, but the one factor which seems of most importance, and which alone affords an explanation of *Cæcidotea*'s living in caves and *Asellus* not living

in caves, is the different responses to light,—*Cæcidotea* always responding negatively to such intensities as it responds to at all, and *Asellus*, after having been in darkness, being positively phototactic for a time.

Since *Asellus* is so closely related to *Cæcidotea* morphologically and physiologically, it would seem that if under stress of circumstances any epigeal animal could suddenly become a cave inhabitant, *Asellus* might be expected to be capable of undergoing such change in environment. *Asellus* is in many ways apparently nearly suited for cave habitation, and in time it may become further modified so that it will be capable of living in caves, but it is not fitted for cave life. Its physiological reactions are such that it is prevented from taking up cave life, and further its apparent lack of discriminative ability in selecting food renders most improbable the continued existence of a straggler of this species within a cave. This case fails to support Lankester's ('93, p. 389) theory of the sudden and accidental origin of cave animals, but rather lends support to the theory that cave animals must become closely adapted for cave life before they are capable of taking up such existence.

V. SUMMARY

Mechanical Stimulation

1. *Asellus* and *Cæcidotea* respond in much the same manner, and corresponding parts in the two species are the regions of greatest sensitiveness.
2. *Cæcidotea* is decidedly more responsive than *Asellus*, reacting more often, more vigorously, and to weaker stimuli.
3. The threshold for *Cæcidotea* is below that for *Asellus*.

Rheotaxis

1. *Asellus* and *Cæcidotea* are rheotactic and respond to currents in like manner.

2. *Cæcidotea*, though at first less rheotactic than *Asellus*, is persistently rheotactic, whereas the rheotactic response with *Asellus* is only temporary.

Photic and Rheotactic Stimulation

1. When subjected to the influence of a current of water in a trough the upper end of which is strongly illuminated, both species, though for a time apparently responding to the rheotactic stimulus alone, soon react principally to the light.

2. When the upper end of the trough is darkened, *Cæcidotea* more persistently remains within the darkened upper end.

Food

1. *Cæcidotea* and *Asellus* take about the same food, but *Asellus* eats much live plant tissue with the decaying plant tissue.

2. *Asellus* takes in vastly more debris and particles of mineral matter with its food than *Cæcidotea*.

General Habits

1. *Cæcidotea stygia* and *Asellus communis* are not only structurally similar, but their habits and reactions to various stimuli are very much alike although there are several minor differences in their reactions.

2. The cave species is decidedly less sensitive to light than its above-ground relative.

3. Cave animals do not have need for highly discriminating light-receptive organs. Their movements are well regulated by light-receptive organs which are capable of distinguishing only considerable intensities of illumination, so that when approaching the outlet of subterranean waters their negative response to light restrains them from passing beyond the limits of caves.

4. The subterranean *Cæcidotea* is clearly very much more sensitive to tactile stimulation than its epigeal relative.

5. Cæcidotea, being less sensitive to light stimulation than Asellus and more sensitive to mechanical stimulation, affords an illustration of compensative sensitiveness to one influence for a partial loss in sensitiveness to another influence.

Habitat

There are several possible factors which determine the habitat of one of these species to be within and the other outside of caves.

1. There is a remote possibility that the relative freedom from mechanical disturbance within cave waters is a factor in determining the existence of Cæcidotea in caves.

2. The difference in the reactions of Asellus and Cæcidotea to light affords an explanation of the occurrence of Cæcidotea in caves, and subterranean waters in general, and the virtual non-occurrence of Asellus in such situations; for the negative response of Cæcidotea to light would aid in directing it into caves and keeping it there; but Asellus after being in darkness becomes positive, and therefore would move toward the light, *i.e.*, out of a cave in case it had by chance made its way into one.

3. Cæcidotea, being more persistently rheotactic than Asellus, and being able in creeping to hold its own against a current better than Asellus, would not readily be swept away by a stream flowing out of a cave. Asellus, on entering a cave under such conditions, would soon lose its rheotactic response and further would become positively phototactic in a few hours. Hence, if it by chance came near the mouth, it would react to the light and escape.

4. The reactions to the influence of a current of water combined with the influence of light afford an additional factor in determining the distribution of the two animals.

5. An apparently superior discrimination on the part of Cæcidotea in selecting its food may make it possible for Cæcidotea, rather than Asellus to live in caves where organic matter is extremely scanty.

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