The Regeneration of Two »Crusher-Claws« following the amputation of the Normal Asymmetrical Chelæ of the Lobster (*Homarus americanus*).

By

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With Plate XV.

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Introduction.

It has been a matter of considerable doubt whether or not a lobster is ever found with a »crushing« claw on each of the two »great chelipeds«. The only case recorded is in a footnote to HERRICK's ('96) description of variations in the form of lobster chelæ; »I have heard of a single case reported by a fisherman, where similar crushing claws were developed on both sides of the body«. P. 143. This seemed to PRZIBRAM ('01), for theoretical reasons about to be mentioned, such an incredible phenomenon that he concluded that: »Der eine Fall von einer Häutung beiderseitigen »crushing-claw«, von dem HERRICK nur vom Hörensagen durch Fischer Kenntnis erhielt, wird wohl in das Reich der Fischermeythen zu verweisen sein.« P. 333. In the adult lobster the »great« claws are almost invariably asymmetrical with reference to each other — the claw on one side of the body being a »nipper«, the other a »crusher«. On the other hand, in the young lobster the two claws are alike and similar to the »nipping« type; and the fact that in the rare instances in which symmetrical claws have been found in adult lobsters, both were always of the »nipping« or embryonic type, has created a

strong presumption that a »crushing« claw would not be developed on each cheliped of this crustacean.

The specimen about to be described furnishes a well authenticated case of a lobster with two »crushing« claws.

I.

A. Data.

The present observations were made at the Experiment Station of the Rhode Island Commission of Inland Fisheries, during a series of studies on the phenomenon of regeneration in the lobster ('05, '06). The lobster which regenerated the two crushing claws, soon to be described, had been recently taken from the fishing-traps, and was kept in a floating car in as nearly a normal environment as possible. The original appendages of this specimen were all normally developed, and the animal was in a healthy condition throughout the experiment. The lobster was a female, and measured $8\frac{3}{16}$ inches in length.

On July 26th, 1905, both chelipeds and the second and third right walking legs were autotomously removed by pinching the tip of the limb with a forceps. On September 28th, sixty-four days after the amputation, the lobster molted and then measured $8\frac{1}{2}$ inches. It had meantime regenerated both chelipeds, and the second and third right thoracic legs.

The original chelipeds of this lobster were of the normal asymmetrical type. The left claw (Fig. I) was a completely developed »crusher«, characterized by the wide massive claws with an almost entire absence of tactile hairs, and by the presence of broad tubercle-like teeth. The right chela (Fig. II) was of a characteristic »nipping« type with a relatively slender claw, pointed cutting teeth, and a fringe of tactile hairs along the jaws. The right and left chelipeds respectively measured 146 and 140 mm. in length.

Soon after the amputation of these limbs another pair of chelipeds began to regenerate from the remaining stump or basipodite. On July 18th, twenty-three days after the amputation, the regenerating buds both measured 5 mm. in length. By the time the segments of the future limbs were well outlined, attention was drawn to the very similar appearance of the two regenerating structures. Usually, as the lobster approaches the culmination of the molting period, the

regenerating chelipeds become so clearly differentiated that a distinction between the »crusher« and »nipper« can often be readily detected. In the present case, however, no characteristic differences could be observed between the right and left regenerating buds, and moreover the general morphological appearance of each was such that it led to the prediction that both were developing into the »crushing« type of claws.

After the lobster had molted, the regenerated chelipeds assumed their normal shape and both measured 63 mm. in length. Each cheliped was very similar to the other in form and displayed the morphological characters of a true »crusher«. All the other appendages were in a normal condition except the regenerated second right leg, which had developed a double claw. After the molt the limbs were again autotomously removed and an attempt made to keep the lobster through the winter in order to see what type of chelæ would be reproduced by the next regeneration. Unfortunately, however, the unnatural conditions under which it was necessary to keep the animal during the winter resulted in the lobster's death on January 6th, 1906, before an answer was obtained for this interesting question.

B. Morphological Comparison of the Normal and Regenerated Chelæ.

a.

The morphological comparison of the normal and regenerated chelæ may be best presented by making first a detailed analysis of some of the characters not clearly shown in the photographs. For this purpose the drawings (Figures V, VI, VII and VIII) have been made of the index or propodite part of each claw to show the characteristic dentition and distribution of tactile hairs.

The original right »nipper« index (Fig. VI) is of a characteristic normal type. Tactile hairs (*h*) are distributed in a dense fringe on each side of the dented margin, and along the distal outer border of the jaw. The teeth are narrow and pointed. These »cutting« teeth are arranged in a linear series, and in a periodic sequence with a formula of 1:4:3:4:2:4:3:4 for a perfect period (*P*)¹. All the teeth of the propodite are included in this

¹) According to the schema of STAHR ('98) and HERRICK ('05).

single linear series except a stout displaced tooth (*d*) about midway in the dentate margin, which forms the »lock« to the claw (HERRICK, '05). Another characteristic feature in the arrangement of the teeth is that at the posterior part of the jaw the single series of teeth are shunted off toward the upper face of the propodite in the direction of the upper or outer side (*a*) of the joint (*j*) formed by the union of the two segments of the claw.

The original left claw (Fig. V) is a typical normal »crusher«. The index or propodite part of the claw, in marked contrast to the morphological characters just described for the »nipper«, is characterized by the almost entire absence of tactile hairs, only a few isolated tufts (*h*¹) remaining near the angle of the jaw. The »stout displaced tooth« of the nipper is absent. Instead of the »pointed cutting teeth«, the jaw is dentated with broad »crushing« tubercles (*t*) formed by the fusion of periodic teeth (according to HERRICK, '05). A normal feature in the dentition is the double-row of tubercle teeth (*t*²) at the posterior part of the index. An equally typical feature is that these two rows of teeth do not shunt off toward one side of the joint, as in the »nipper«, but are arranged along either side of the median line of the jaw.

In this lobster the propodite of the regenerated left claw (Fig. VII) closely resembled the original »crusher«. No tactile hairs are apparent, except a few tufts (*h*) near the angle of the jaw. The teeth (*t*) are broad and tubercle like in form; periodic sequence in arrangement is not evident, and at the posterior part of the jaw the characteristic »double-crushing« teeth have reappeared.

The regenerated right claw, on the other hand, is plainly unlike the original »nipper«. If we examine the propodite part of the claw (Fig. VIII) it is seen that only a few tufts of tactile hairs (*h*) have regenerated in place of the prominent fringe on the former claw (Fig. VI). The teeth are not like the pointed »cutters«, but are of the broad tubercle form. And finally, the wide departure of the regenerated structure from the original »nipping« type, and its identity as a »crusher« is completely established by the presence of the characteristic double toothed arrangement of the tubercles (*t*²) at the posterior part of the jaw.

b.

Extending this morphological analysis to the chelæ as a whole, the structural characters for both the original and the regenerated claws may be directly compared in the following tabulated data:

	Original left claw. Fig. I. (Normal.)	Original right claw. Fig. II. (Normal.)	Regenerated left claw. Fig. III.	Regenerated right claw. Fig. IV.
General form.	Relatively short and stubby; distinctly bent.	Relatively long and slender; nearly straight.	Relatively short and stubby; distinctly bent.	Relatively short and stubby; distinctly bent.
Dentition.	Broad tubercle-like »crushing« teeth; occasional indications of perisodontic sequence.	Pointed »cutting« teeth; arranged in periodic sequence with formula 1:4:3:4:2:4:3:4 ¹)	Broad tubercle-like »crushing« teeth; occasional indications of perisodontic sequence.	Broad tubercle-like »crushing« teeth; occasional indications of perisodontic sequence.
Tactile hairs.	No tactile hairs, except a few tufts near angle of jaw.	Dense fringe on either side of dentate margin.	No tactile hairs, except a few tufts near angle of jaw.	No tactile hairs, except a few tufts near angle of jaw.
Number of spines.	1, on outer border, near joint.	1, on outer border, near joint.	1, on outer border, near joint.	1, on outer border, near joint.
General form.	Broad and massive.	Comparatively slender and tapering toward apex.	Comparatively broad and massive.	Comparatively broad and massive.
Dentition.	Broad tubercle-like »crushing« teeth. Double posteriorly near angle of jaw.	Pointed »cutting« teeth, arranged in a single linear series, with a stout displaced tooth near the middle of the dentate margin.	Broad tubercle-like »crushing« teeth. Double posteriorly near angle of jaw.	Broad tubercle-like »crushing« teeth. Double posteriorly near angle of jaw.

Dactylopodite.

podite.

Pro-	Tactile hairs.		No tactile hairs, except a few tufts near angle of jaw.		Dense fringe on either side of dentate margin, and along the outer distal border of the under face.		No tactile hairs, except a few tufts near angle of jaw.		No tactile hairs, except a few tufts near angle of jaw	
	Number of spines.		1		1		1		1	
	Posterior outer border.									
	Near angle of jaw.		Upper face, 1 Lower face, 2		Upper face, 0 Lower face, 0		Upper face, 1 Lower face, 2		Upper face, 1 Lower face, 3	
	Inner border.		5 ²⁾		5 ²⁾		8 ³⁾		7 ⁴⁾	
	Ratio of length of dactylopodite to greatest width of propodite.		$\frac{43 \text{ mm.}}{40 \text{ mm.}} = 1.1$		$\frac{52 \text{ mm.}}{34 \text{ mm.}} = 1.6$		$\frac{31 \text{ mm.}}{25 \text{ mm.}} = 1.2$		$\frac{29 \text{ mm.}}{25 \text{ mm.}} = 1.2$	
	Ratio of length of dactylopodite to length of propodite.		$\frac{43 \text{ mm.}}{81 \text{ mm.}} = .54$		$\frac{52 \text{ mm.}}{90 \text{ mm.}} = .58$		$\frac{31 \text{ mm.}}{58 \text{ mm.}} = .53$		$\frac{29 \text{ mm.}}{55 \text{ mm.}} = .53$	
	Ratio of length of dactylopodite to the distance on the propodite from angle of jaw to the 2 nd joint.		$\frac{43 \text{ mm.}}{38 \text{ mm.}} = 1.1$		$\frac{52 \text{ mm.}}{38 \text{ mm.}} = 1.4$		$\frac{31 \text{ mm.}}{26 \text{ mm.}} = 1.2$		$\frac{29 \text{ mm.}}{26 \text{ mm.}} = 1.1$	
	Dominant characters in each claw.		»Crusher«.		»Nipper«.		»Crusher«.		»Crusher«.	

1) Compare schema of STÅHR ('98) and HERRICK ('05).

2) Third spine slightly below the direct line of the others.

3) Posterior spine is double, and the third is below the direct line of the others.

4) Posterior spine double; second one is below direct line.

C. Resume.

a) The normally asymmetrical chelipeds of an adult lobster were autotomously removed. The right claw was a »nipper«, and the left a »crusher«.

b) After amputation the chelipeds regenerated, but the regenerative processes did not reproduce the original asymmetrical types of chelæ. The regenerated left claw was a true »crusher« like the former claw; but the regenerated right claw had the general characters, not of the »nipper«, but of a typical »crusher«.

c) A close analysis of the structural features of the regenerated right claw demonstrated that, in all its morphological characters, it corresponded point for point with both the normal and the regenerated »crusher« of the left side, in respect to the general form, size, and proportions, in the shape and arrangement of the teeth, and even in the number and distribution of the tufts of tactile hairs.

The regenerated claws of this lobster are, therefore, symmetrical in form, and are both of the »crushing« type of chelæ.

II.

Discussion.

This regeneration of two »crushing« claws in the lobster presents several interesting aspects:

1) The full grown lobster is almost invariably asymmetrical in respect to the chelipeds, — one of the two claws being a »crusher«, and the other a »nipper«. The present case, therefore, furnishes a rare exception in that both claws are alike.

2) Moreover, this case is apparently unique, for in all other well authenticated cases of similar claws of which I am aware, the two claws were always of the »nipping« type. In examining over 2,400 lobsters, HERRICK ('96) found only 3 which had similar claws developed on each side of the body, and in these the claws were all of the »cutting« or »nipping« form (P. 143). During the summer of 1905, among the lobsters caught in the traps near the Experiment Station, I found another adult lobster with two similar »nipping« claws. It may be of value to add that after I had autotomously removed both chelæ, the regenerative processes directly reproduced two »nipping« claws, like those removed.

3) The fact that the double »crushing« claws here described are regeneration products, indicates that the symmetrical chelæ occasionally found in the adult lobster, are not necessarily congenital in nature, but may be the result of regenerative processes.

4) It is evident that this case of regeneration cannot be brought into the category of »reversal« phenomena, for no transposition of types from one side of the body to the other occurred. It is also apparently impossible to interpret such a regeneration as a case of »compensatory regulation« in ZELENY's ('05) sense, for the regenerated chelæ are almost identically similar both in size and in form. At present, therefore, this phenomenon must rather be described merely as the substitution by regeneration of a »crushing« claw in place of an original »nipping« claw.

5) This »substitution« of a »crushing« in place of a »nipping« claw is a striking deviation from the normal method of »direct regeneration« in *Homarus* (PRZIBRAM, and MORGAN), in that it consists in the regeneration of a phylogenetically younger type of claw (STAHR, '98, PRZIBRAM, '01) in place of the amputated more primitive form of chela.

PRZIBRAM ('02) has pointed out in the European lobster what MORGAN ('04) has observed in the American species, and what I have since found in several experiments ('06a), namely, that when the »crushing« claw has been autotomously removed, the regenerated »crusher« is not always at first distinguishable as such, but rather presents characters intermediate or transitional between the more primitive »nipping« and the more highly developed »crushing« type. If the crushing claw is phylogenetically the younger type, this might perhaps be expected, for then the variation in the regenerating structure might be regarded as a reversion to the phylogenetically older or nipping type of claw. But to this, the present case is a remarkable exception. On the left side there was, indeed, a »direct regeneration« of the original »crushing« claw, but on the right side, the regenerative process, instead of leading to the reproduction of the original »nipper« and thus to the restoration of the normal asymmetry, passed beyond all the transitional stages in one molt and produced on this side, also, a »crushing« claw, i. e., one of a phylogenetically younger type.

6) I have no suggestion to offer in explanation of this case of regeneration. Evidently the regenerative cells in the stump remaining after autotomy, may have the potentiality of either a »crushing« or

»nipping« claw. But what factors determined that a claw of the crushing type be produced, is another question. WILSON's ('03) suggestion for *Alpheus*, »that the initial factor (Auslösung) that sets in motion the complex process of differentiation of which either side is capable, is primarily only a difference in the amount of material on the two sides« (P. 210), can hardly apply here, for the chelæ were both removed autotomously and at the same time, consequently there seems no reason to believe that the »amount of material« was unequal on the two sides. As far as the present data go, the regeneration of similar »crushing« claws, like that of PRZIBRAM's ('05) similar toothed claws, »still remains unexplained«.

Theoretical speculations aside, the fact is that we have an authentic case of the regeneration of a perfectly typical »crushing« claw on each side of the body of the lobster¹⁾. The occurrence of two »crushing« claws in this crustacean is not, therefore, a phenomenon which must be »relegated to the realm of fishermen's myths«.

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Zusammenfassung.

a) Die normalerweise asymmetrischen Scherenfüße eines erwachsenen Hummers wurden durch Autotomie entfernt. Die rechte Klaue war eine Zwick-schere (»nipper«), die linke eine Quetschschere (»crusher«).

b) Nach der Amputation regenerierten sich die Scherenfüße, aber die Regenerationsprozesse brachten nicht die ursprünglichen asymmetrischen Scherentypen hervor. Die regenerierte linke Klaue war eine echte Kauschere (»crusher«), wie die vorher dagewesene; aber auch die regenerierte rechte Klaue hatte die allgemeinen Kennzeichen der typischen Kauschere, nicht die der Zwick-schere.

c) Eine genauere Analyse der Struktureigentümlichkeiten der regenerierten rechten Schere zeigte, daß sie in allen ihren morphologischen Kennzeichen Punkt für Punkt sowohl mit der normalen als der regenerierten Kauschere der linken Seite übereinstimmte, und zwar mit Bezug auf die allgemeine Gestalt, die Größe und Größenverhältnisse, in bezug auf Gestalt und Anordnung der Zähne, ja sogar in der Zahl und Verteilung der Tasthaarbüschel.

¹⁾ Since this article has gone to press a series of experiments were made in which I succeeded in obtaining another lobster with two crushing claws. The specimen was an 8 inch male lobster whose chela had the usual asymmetry; the right being a »crushing«, and the left, a »nipping« claw. Both chelæ and the second left by were autotomously removed on August 4th, 1906. By the middle of October the lobster had molted and regenerated two chelæ which were both typical »crushing claws«. I hope to give a more detailed description at a later time.

Die regenerierten Klauen dieses Hummers sind somit der Gestalt nach symmetrisch und gehören beide dem Typus der Kauschere (»crusher«) an.

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Explanation of Plate.

Plate XV.

Figs. I and II are photographs of the original normal chelipeds of the lobster used in the present experiment (about $\frac{1}{2}$ natural size). Fig. I, left normal »crushing« chela. Fig. II, right normal »nipping« chela.

Figs. III and IV; photographs of the left and right chelæ, respectively, which regenerated after the amputation of the original limbs (about $\frac{1}{2}$ natural size).

Figs. V and VI show the index or propodite part of the original claws represented in Figs. I and II ($\frac{4}{3}$ natural size). Fig. V, index of normal left »crusher«. (Drawn from the upper face.) Fig. VI, index of normal right »nipper«. (Drawn from the lower face.)

Figs. VII and VIII represent the index or propodite part of the regenerated claws shown in Figs. III and IV ($\frac{4}{3}$ natural size). Fig. VII, index of regenerated left »crusher«. (Drawn from upper face.) Fig. VIII, index of regenerated right claw. (Drawn from lower face.)

Reference letters.

<i>a</i>	Outer part of the joint formed by the union of the propodite and dactylopodite.	<i>p</i>	Group of teeth on »nipping« claw showing typical periodic sequence.
<i>h</i>	Tactile hairs.	<i>pr</i>	Index or propodite part of claw.
<i>j</i>	Socket into which the dactylopodite sets to form the joint of the claw.	<i>t</i>	Typical tubercle-like teeth on »crushing« claw.
		<i>t</i> ²	Characteristic double teeth on »crushing« chela.

Emmel.