THE PHYSIOLOGY OF THE DIGESTIVE TRACT
OF ELASMOBRANCHS.

By M. X. SULLIVAN.

[From the Laboratory of the U. S. Bureau of Fisheries, Woods Hole, Mass., and the
Laboratory of Comparative Anatomy, Brown University.]

SIXTEEN per cent of the dogfish taken at the laboratory of the
Bureau of Fisheries, Woods Hole, Mass., during the summer of
1904, were found to contain lobsters; 34.17 per cent rock crabs, and
20.1 per cent spider crabs. The carapace of these organisms consists
of salts and chitin, which is highly resistant to reagents. As the car-
apace was found in varying degrees of decomposition, and further
since the carapace of crabs and lobsters fed to the fish could not be
found in the stomach after four days of digestion, the question arose
as to whether the dogfish really did digest chitin. Accordingly,
during this summer I began a physiological study of the alimentary
canal of Mustelus canis, and extended the work to include the sand
shark (Carcharias littoralis) and the spiny dogfish (Squalus acan-thias).

The experiments of 1904 consisted in the study of the normal con-
tents of the stomach and the spiral valve; in the determination of the
digestive power of the juices contained in the stomach and spiral
valve; in the preparation for artificial digestion of extracts of buccal,
esophageal, gastric, and intestinal mucous membranes, and of the
extracts of the pancreas; and finally in determining whether or not
these fishes digested chitin.

During the summer of 1905 the work of the previous summer was
reviewed, amplified, and extended to include the torpedo (Tetronarce
occidentalis), the dusky shark (Carcharhinus obscurus), the skate
(Raja erinacea), and the mackerel shark (Lamna cornubica). More
attention was paid to the physiology of the pancreas, middle intestine,
and spleen; and histological preparations were made of the various
parts of the alimentary canal from the esophagus to the anus. The
résumé of the work is as follows:
Physiology of the Digestive Tract of Elasmobranchs. 43

(A) Buccal cavity. — These fish as a rule swallow their prey whole without mastication. Naturally, we should suppose that the buccal mucus has little digestive action. This probability is increased by the absence of glands. The buccal mucus consists of epithelium and connective tissue. There are several layers of epithelium. Next to the connective tissue are cylindrical cells. Above these cells are several layers of mucous cells. The superficial epithelium consists of oval or irregularly polygonal cells. Extracts of buccal mucus have no digestive action on starch, fibrin, or fat.

(B) Esophagus. — The reaction of the esophagus is often acid, probably due to regurgitation from the stomach. Extracts of esophageal mucus of the fasting fish have no digestive action. The mucus contains ciliated cylindrical cells and goblet cells.

(C) Stomach. — The stomach of elasmobranchs consists of a large cardiac sac and a narrow pyloric tube.

Cardiac sac. — An analysis of the contents of the sac of Mustelus canis, Carcharias littoralis, Squalus acanthias, Tetronarce occidentalis, Carcharhinus obscurus, Raja erinacea, Lamna cornubica, Galeocerdo tigrinus, showed as a rule syntonin, proteoses, and peptones. Occasionally in the stomach contents no peptones could be found. Using phenolphthalein, alizarin, and dimethyl-amido-azobenzol, as indicators, experiments were made to determine —

1. The total acidity of the stomach contents in terms of hydrochloric acid.
2. The physiologically active hydrochloric acid.
3. The free hydrochloric acid.

The results are given in the table on page 44.

The acidity of the stomach contents depends on the period of digestion, the fasting stomach being practically neutral, and upon the nature of the food, the greatest acidity being found when the stomach was full of partly digested lobsters and crabs.

Glycerin-hydrochloric acid extracts of the mucus of the cardiac sac digest fibrin at 20° C., but better at 38° C., with the formation of syntonin, proteoses, and peptones.

In the cardiac part of the stomach we can distinguish superficial epithelium, the lumen of the peptic glands, and the glandular epithelium in the crypts. The superficial epithelium consists of pyramidal cells. The peptic glands begin just behind the esophagus and extend to the pylorus, with the deepest glands in the centre. Each gland is a cylindrical tube. The epithelium of the neck of the glands consists
of cylindrical cells, while the cells of the body of the glands are regularly polygonal, highly granular, and closely packed together. Only this one kind of cell can be distinguished in the body of the gland.

Pyloric tube. — The pyloric tube has no digestive function. The superficial epithelium is like that of the stomach. The glands are short, and the polygonal peptic cells are absent.

(D) Middle intestine. — Extracts of the middle intestine or duodenum of Mustelus canis and Carcharias littoralis show no digestive action. The epithelium consists of cylindrical cells and goblet cells.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total acidity in percentage hydrochloric acid.</th>
<th>Physiologically active hydrochloric acid, average percentage.</th>
<th>Highest percentage free hydrochloric acid.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mustelus canis . . . . . .</td>
<td>0.04-1.00</td>
<td>0.538</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>Aver. 0.73</td>
<td>6 individuals</td>
<td></td>
</tr>
<tr>
<td></td>
<td>50 individuals</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carcharias littoralis . . .</td>
<td>0.1-1.2</td>
<td>0.614</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>Aver. 0.87</td>
<td>10 individuals</td>
<td></td>
</tr>
<tr>
<td></td>
<td>25 individuals</td>
<td>No tests</td>
<td></td>
</tr>
<tr>
<td>Squalus acanthias . . . .</td>
<td>Aver. 0.67</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>60 individuals</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carcharinus obscurus . .</td>
<td>Aver. 0.55</td>
<td>0.493</td>
<td>0.254</td>
</tr>
<tr>
<td></td>
<td>2 individuals</td>
<td>2 individuals</td>
<td></td>
</tr>
<tr>
<td>Lamna cornubica . . .</td>
<td>0.275</td>
<td>0.229</td>
<td>0.172</td>
</tr>
<tr>
<td></td>
<td>1 individual</td>
<td>1 individual</td>
<td></td>
</tr>
<tr>
<td>Galeocerdo tigrinus . .</td>
<td>0.93</td>
<td>0.812</td>
<td>None.</td>
</tr>
<tr>
<td></td>
<td>1 individual</td>
<td>1 individual</td>
<td></td>
</tr>
<tr>
<td>Tetronarce occidentalis .</td>
<td>0.51</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(E) Spiral valve. — The arrangement histologically is like that of the middle intestine. Extracts of the spiral valve show no digestive action.

(F) Pancreas. — Extracts of the pancreas vary in their action. Some have no digestive action whatever. Neither water extracts nor sodium carbonate extracts of the pancreas of the various elasmobranchs have any digestive action on hard-boiled egg or fibrin. Extracts of the middle intestines do not activate the pancreas. Bile activates the pancreatic extracts slightly. The spleen activates the pancreas most. A boric acid extract of the pancreas, plus a boric extract of the spleen of a fish in full digestion, gave the greatest digestion of fibrin. Pancreatic fistulas were of little value. Of six made, but one gave a juice having any digestive action on fibrin, and even this was slight.
Analysis of the contents of the spiral valve showed leucin and tyrosin, proving that the pancreas acts in these animals as in the higher animals. The fresh pancreas emulsifies olive oil. Glycerin-acetic extracts of Mustelus canis convert starch to sugar. None of the standard extracts of the pancreas of Carcharias littoralis and Raja erinacea showed the amylolytic ferment.

(G) Rectal gland.—The rectal gland is a compound tubular gland. Extracts of this gland do not show any digestive activity.

(II) Action of gastric juice on chitin.—The natural juice of the stomach of Mustelus canis digested fish and fibrin in vitro with the formation of syntonin, proteoses, and peptones, but did not digest the carapace of lobsters and crabs. The frequent change of the gastric juice and much trituration, however, softened the shells and broke them up into a fine mass such as may be found in the spiral valve of the fish. The chitin is not regurgitated. Pieces may be found intact in the spiral valve. These fishes do not derive nourishment from the carapace, but dissolve out the salts by means of the relatively strong acid which collects in the stomach, and triturate the chitinous mass into extremely fine particles. This finely divided mass is excreted.