ON THE STRUCTURE AND MECHANISM OF THE GASTRIC MILL IN DECAPODA.

II. A Comparative Account of the Gastric Mill in Brachyura.

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1. Introduction.

In my previous paper (1934) dealing with the structure and mechanism of the gastric mill in P. guerini, it was shown how the presence of the gastric mill and simple masticatory appendages is correlated with the nature of the food material, the digestive and absorptive mechanism and the habit and habitat of the crab. In the present communication it is proposed to give a comparative account of the gastric mills of a number of representative Brachyura. Incidentally an attempt is made to collect further data on correlation of these structures with the various factors mentioned above.

2. Material and Method.

The material consisted of specimens obtained from the Biological Supplies Stations at Ennur and Plymouth. The twelve types examined and described in this paper represent all the five tribes of the sub-order Brachyura and represent the following eleven families:—

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<tr>
<th>Tribe</th>
<th>Family</th>
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<tr>
<td>Dromiacea</td>
<td>Dromiidae</td>
<td><em>Dromia rumphi</em> (Fabr.)¹</td>
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<td>Oxystomata</td>
<td>Calappidæ</td>
<td><em>Matuta victor</em> (Fabr.)¹</td>
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<td>Leucosiidæ</td>
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<td>Cyclometopa</td>
<td>Corystidæ</td>
<td><em>Corystes cassivelanus</em>²</td>
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<td></td>
<td>Cancridæ</td>
<td><em>Cancer Pagurus</em>²</td>
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<td>Portunidæ</td>
<td><em>Neptunus sanguinolentus</em> (Herbst.)¹</td>
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<td>Xanthidæ</td>
<td><em>Pilumnus hirtellus</em>²</td>
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<td></td>
<td>Telphusidæ</td>
<td><em>Paraophusa guerini</em> (M. Edw.)³</td>
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¹ Obtained from Ennur.
² Obtained from Plymouth.
³ Collected locally.
The material in some cases was not very suitably preserved for the dissection of minute parts but the foregut with its chitinous lining was always intact. Three specimens of each type were dissected. The following description is confined to the general anatomy of the cardiac and the pyloric stomach and the principal ossicles of the gastric mill. A diagram of the main ossicles of the gastric mill, all viewed on the same plane, is provided with in each case.

3. **The Cardiac and the Pyloric Stomach.**

(A) **The Cardiac Stomach.**—The Brachyura have a dorsoventrally flattened body which, in the thoracic region, is always broader than long. Correlated with the flattening of the body, the cardiac stomach is a subspherical sac also slightly flattened dorsoventrally and possesses the following characteristic features which are common to all the types examined by me and have an important bearing on the alimentation of food:—

(a) **The ventral grooves.**—The floor of the cardiac stomach is limited on either side by a deep groove (Part I, Fig. 2; v.g.), which leads backwards along the sides of the cardiac pyloric valve and opens into the ventral chamber of the pyloric stomach. This groove is covered over by linear rows of elongated setae. These setæ drive backwards the food particles received in the groove. The ventral groove also acts as a channel, which, according to Yonge (1924), brings digestive juices from the midgut into the cardiac stomach.

(b) **The lateral accessory teeth.**—On the lateral wall of the cardiac stomach, anterior to the lateral tooth of the gastric mill, lie a group of chitinous spines known as the lateral accessory tooth (Part I, Fig. 2; l.a.t.). The number and shape of the spines which constitute the lateral accessory tooth are variable. The tooth consists of a single stout spine in *Philyra* (Fig. 11; l.a.t.), of three small spines in *Corystes, Macropodia* and *Cancer* (Figs. 4, 5 and 10; l.a.t.), while in *Pilumnus, Neptunus, Dromia, Graspus, Matuta* and *Cardisoma* (Figs. 1, 2, 3, 6, 7 and 8; l.a.t.) the spines are small.

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1 Obtained from Ennur.
2 Obtained from Plymouth.
Gastric Mill in Decapoda

rose-thorn-like and their number exceeds four. In Lambrus, the spines are of unequal size and are probably more than four in number (Fig. 9; l.a.t.). The function of the lateral accessory teeth is not known. Probably during the peristaltic movements of the cardiac stomach, they may tear and lacerate the food received in the cardiac stomach.

(c) The cardiac pyloric valve.—The cardiac pyloric valve (Part I, Fig. 2; c.p.v.) guards the cardiac pyloric opening (o.). It is usually a calcified triangular plate which may be flat or curved. The apex of the plate points backwards and may be either pointed as in Neptunus, Macropodia, Graspus, Matuta, Cardisoma and Cancer (Figs. 2, 5, 6, 7, 8 and 10; c.p.v.) or more or less truncated as in Pilumnus, Dromia, Corystes and Lambrus (Figs. 1, 3, 4 and 9; c.p.v.). It is generally covered over with elongated setae pointing backwards but in some forms, e.g., Cardisoma (Fig. 8) and Paratelphusa it is covered by a thick corrugated layer of deeply pigmented chitin which indicates that the cardiac pyloric valve gets rubbed over by the to and fro movements of the median tooth of the gastric mill.

(d) The gastric mill.—Typically there are ten ossicles in the gastric mill arranged as follows:—Three ossicles, a median mesocardiac and a pair of lateral pterocardiac ossicles, form an anterior arch which is convex anteriorly; five ossicles, a median pyloric and two pairs of lateral ossicles, the inner exopyloric and the outer zygocardiac ossicles bearing the lateral teeth, form the posterior arch which is convex posteriorly. The outer ends of the lateral ossicles of the two arches, i.e., of the pterocardiac and the zygocardiac ossicles of the same side, are connected to one another by a ligament. The mesocardiac and the pyloric ossicle are connected to one another by a median column of two ossicles, the anterior urocardiac bearing the median tooth and the posterior prepyloric ossicle. While these ten ossicles are typically present in all the Brachyura examined by me, they vary in different members of the group in shape, size and arrangement. A comparative account of each ossicle is detailed below.

(1) The Mesocardiac Ossicle.—The mesocardiac ossicle forms the keystone of the anterior arch of the gastric mill. In Pilumnus, Neptunus, Dromia, Macropodia and Lambrus (Figs. 1, 2, 3, 5 and 9; m.c.) it is a triangular plate, the apex of which points forwards and may be more or less truncated. The sides of the plate are usually curved. In Corystes, Matuta and Cancer (Figs. 4, 7 and 10; m.c.) the mesocardiac ossicle is an oblong plate with its long side along the transverse plane. The sides of the plate are either straight or curved. In Graspus, Cardisoma and Philyra (Figs. 6, 8 and 11; m.c.) it is a narrow elongated strip-like plate. In all cases it is laterally connected to the pterocardiac ossicle while at its base it is very
Gastric Mill in Decapoda

![Diagram of Gastric Mill in Decapoda](image)

Key:
- p.t.c. (posterior transverse crest)
- u.c. (upper curve)
- m.t. (middle tooth)
- p.r.p. (primary retractor process)
- e.x. p. (external process)
- z.c. (zygomatic crest)
- l.t. (left transverse)
- p. (primary process)
- c.p.v. (corpus ventriculus)

Measurements:
- 2.0 mm
- 5.5 mm
firmly ankylosed to the urocardiac ossicle. The large anterior gastric muscles are inserted on the mesocardiac ossicle or as in Paratelphusa (Part I, Fig. 8A; a.g.) partly on the mesocardiac and partly on the pterocardiac ossicle of its side.

(2) The Pterocardiac Ossicles.—The pterocardiac ossicles in all the Brachyura examined by me were more or less similar, i.e., flat, elongated and wedge-shaped plates (Figs. 1 to 11; pt.c.). In Astacus (Huxley, 1880) (and in many other Macrura examined by me and to be described in a subsequent paper), the pterocardiac ossicle is a much smaller ossicle than it is in Brachyura. This small size is invariably correlated with the large size of the mesocardiac ossicle. It is noteworthy of all Brachyura that the mesocardiac ossicle is a much smaller ossicle and the pterocardiac ossicles are comparatively larger.

(3) The Zygocardiac Ossicles.—These are the stoutest and the largest of all the ossicles of the gastric mill. Each zygocardiac ossicle is roughly a triangular plate projecting into the cavity of the cardiac stomach from each side (Part I, Fig. 2; z.c.). Laterally it is prolonged into a rod-shaped process which runs upwards and is connected to the pterocardiac ossicle of its side. Posteriorly it is connected to the exopyloric ossicle. Its median edge bears a number of denticles and ridges which constitute the lateral tooth. In all the Brachyura examined by me, the zygocardiac ossicle resembles the typical form just described. The number of the denticles and the ridges of the lateral tooth is variable in different forms. Thus in the small-sized forms, e.g., Pilumnus, Macrobdia, Graspus and Philyra (Figs. 1, 5, 6 and 11; t.t.) it is composed of two or three large denticles situated anteriorly. These are followed by a vertical row of thin ridges. In the remaining forms the number of denticles varies from two to four and the vertical ridges are numerous and thick. The ridges and the denticles do not lie in the same plane but form a curved row with the convexity pointing downwards. The denticle and ridges of the lateral tooth, as also of the median tooth, are invariably covered with a thick layer of cuticle which has a shining surface and which is impregnated with the brown or yellow pigment. This coloration is always associated with those parts of the hard structures which masticate food material. It is interesting to note that a similar colour is developed on the molar processes of the mandibles in prawns or in the thick chitinous lining of a bird’s gizzard.

(4) The Exopyloric Ossicles.—These are so called because they lie one on each side of the pyloric ossicle. Each exopyloric ossicle is typically a triangular plate with its apex facing downwards. It is wedged between the pyloric ossicle and the zygocardiac ossicle of its side. It always affords
insertion for the outer posterior gastric muscles (Part I, Fig. 8A; o.p.g.).
The shape of the ossicle varies a little in different Brachyura examined by
me, e.g., in Graspus (Fig. 6; ex.p.) it is very elongated and in Cardisoma
(Fig. 8; ex.p.) it is roughly four-sided.

(5) The Pyloric Ossicle.—The pyloric ossicle is the key-stone of the
posterior arch of the gastric mill. It is really composed of a pair of ossicles
which lie on either side along the median line and are connected to one
another by a membrane which may be more or less calcified. In Neptunus,
Dromia, Corystes, Macropodia, Matuta, Cancer and Philyra (Figs. 2, 3, 4, 5, 7,
10 and 11; p.) the paired appearance is obliterated, while in Pilumnus,
Graspus and Cardisoma (Figs. 1, 6 and 8; p.), it shows a paired appearance
as the connecting membrane is feebly calcified and thin. Anteriorly the
pyloric ossicle develops a more or less horn-like process on either side.
Between these processes it encloses the base of the prepyloric ossicle. The
pyloric ossicle gives attachment to the inner posterior gastric muscles (Part I,
Fig. 8A; i.p.g.).

(6) The Urocardiac Ossicle.—The urocardiac ossicle is an elongated
flattened plate running obliquely downwards along the middle of the roof of
the cardiac stomach (Part I, Fig. 2; u.c.). Anteriorly it is connected to the
base of the mesocardiac ossicle, while posteriorly it is joined to the lower
end of the prepyloric ossicle. It is more or less rectangular in shape as in
Pilumnus, Neptunus, Corystes, Macropodia, Lambrus and Cancer (Figs. 1, 2, 4, 5,
9 and 10; u.c.), but in other forms, e.g., Dromia, Graspus, Matuta and Cardi-
soma (Figs. 3, 6, 7 and 8; u.c.) its lateral edges are curved inwards so as to
give it an appearance of a flat wine bottle. On the posterior half of its
ventral surface it bears a number of denticles which together constitute the
median tooth. The latter shows interesting modificatious in the number,
size and configuration of the denticles. In Matuta, Lambrus and Cancer
(Figs. 7, 9 and 10; m.t.), the median tooth consists of a single large U-shaped
dentine and a pair of small lateral denticles. In Dromia and Philyra (Figs. 3
and 11; m.t.) the single median denticle is heart-shaped. In some forms, e.g.,
Pilumnus, Neptunus, Macropodia and Graspus (Figs. 1, 2, 5 and 6; m.t.) the
median tooth consists of two oval denticles placed one behind the other. In
Cardisoma and Paratelphusa (Fig. 8; m.t., and Part I, Fig. 5; m.t.),
the median tooth is very large and is composed of six or three large rhomboid
denticles of different sizes placed one behind the other along the median line.

(7) The Prepyloric Ossicle.—The prepyloric ossicle is usually a thick
triangular plate lying obliquely vertical with its apex pointing downwards.
Its apex is always bifid and is firmly fixed to the lower or posterior end of
the urocardiac ossicle. Its base is enclosed within the two horn-like
processes of the pyloric ossicle. The base and the sides of the prepyloric ossicle may be more or less straight as in *Nephtes* (Fig. 2; *pr. p.*) but more usually, e.g., *Pilumnus, Corythes, Macropodia* and *Lambrus* (Figs. 1, 4, 5 and 9; *pr. p.*), the three sides of the triangular plate are deeply curved towards the middle of the plate, giving it an appearance of a Y. The prepyloric ossicle is always densely calcified but in *Cardisoma* (Fig. 8; *pr. p.*) the middle portion is thin and membranous and the ossicle looks as if it is perforated in the middle.

(B) The Pyloric Stomach.—The pyloric stomach is always short, narrow and is constricted off from the expanded cardiac stomach. The structure of the pyloric stomach in *P. guerini*, described in my previous paper (1934) may be taken as typical of Brachyura. It is divided into an upper and a lower chamber by a pair of lateral folds. The ventral chamber is always modified into a characteristic filtering apparatus, while the upper chamber is comparatively simple. The opening between the cardiac and the pyloric portions of the stomach is guarded by the cardiac pyloric valve already described, and in *Nephtes* and *Paratelmphus* there is a pair of lateral valves near the dorsal portion of the opening.

The opening between the pyloric stomach and the midgut is typically guarded by four valves which are elongated and are lined with elongated setae along the margin. The four valves are typically arranged as follows: one from the roof, one from each side and one from the floor of the pyloric stomach. Such a typical arrangement is found in *Lambrus* and *Macropodia*. In *Cardisoma, Nephtes, Dronia, Pilumnus* and *Graspus* the dorsal valve is split into two. In *Cardisoma* and *Paratelmphus* the ventral valve is also similarly forked. The wall of the pyloric stomach also supports a number of variously shaped ossicles. The filtering apparatus, the chitinous framework and the elaborate valvular mechanism regulate the passage of food to the midgut and prevent its regurgitation into the foregut.

(C) The Midgut.—A word about the midgut and the hepatopancreas would not be out of place. In all the Brachyura examined by me, the midgut is extremely shortened, only a few millimetres in length. It is provided with three cææ. The connection of the pyloric stomach and the midgut is marked by a pair of lateral elongated cææ, while a third dorsal cæcum probably marks the commencement of the hindgut. The hepatopancreas is a massive, paired, lobulated structure lying on either side of the foregut. Essentially each lobe is a mass of short branching tubules which are connected together to form a single duct opening into the midgut. Each tubule is lined by a layer of variously modified epithelial cells having diverse functions. (For details of the structure and function of the hepatopancreas
see Yonge, 1924.) It has already been remarked in my previous paper that such a reduced midgut and the narrow hepatopancreatic tubules subserving the function of digestion and absorption require the food material coming to this part of the alimentary tract to be in a fine state of division, unmixed with non-digestible portion, to facilitate easy digestion and quick absorption. The gastric mill, the pyloric filter and the hepatopancreatic tubules are thus correlated adaptations for proper alimentation of food.

4. Feeding Mechanism of Brachyura.

The feeding mechanism of the crab, *Carcinus*, has been described in detail by Borradaile (1922). At the outset it would be interesting to note the remarkable similarity in structure of the most important masticatory appendages, the mandibles (Fig. 12). Typically, a mandible in Brachyura consists of an elongated Sympod (constituting the Precox and the Coxa), the distal end of which is modified into a flattened, sharply edged, chisel-shaped cutting plate, the incisor process, which may be constricted off from the rest of the Sympod. The incisor process is convex ventrally and on its superior surface it bears a prominence, the so-called "molar process". The rest of the limb is represented by a two-jointed palp borne on the anterior side of the Sympod. Of the two joints of the palp, the proximal one represents the basi-ischium. The distal joint lies on the dorsal or inner side of the cutting plate and is flattened and covered with stiff setae along the median edge. The incisor process may have a sharp and straight edge as in *Pilumnus, Neptunus* and *Maiuta* (Fig. 12, A, B and C) or may be finely serrated as in *Cardisoma* and *Philyra* (Fig. 12, H and K). The cutting plates are rarely used for slicing or cutting food. Their usual function is to hold or shovel morsels of food into the buccal cavity.

The process of feeding involves seizure of food material, its transference to oral aperture, tearing it into suitably sized morsels for swallowing, separation of non-digestible from digestible portions and reduction of the digestible into suitable forms for easy digestion and subsequent absorption. The food of the crabs consists of dead fishes, larval forms of Crustacea, insects or fishes, smaller Crustacea, water snails, tiny sea weeds, etc. Thus the food material is usually locked up into undigestible chitinous, calcareous or silicious envelopes. The food material is always caught and transferred to the oral aperture by the pincer claws. The mandibles hold it in front of the mouth opening, while the maxillipeds and even the chelae tear away morsels of it and push them towards the mouth. The lips and the palp assist the mandibles in shovelling the morsels of food into the buccal cavity, while the setose gnathobases of the oral appendages make it difficult for food to spurt out of the buccal cavity. Thus the oral appendages are involved in the
seizure of food, its tearing into morsels and shovelling the morsels into the buccal cavity for swallowing and incidentally in a partial separation of non-digestible from the digestible portions of food. The next operation is the mastication of food taken into the buccal cavity. In Decapoda there are three ways of mastication of food: (1) by the molar processes of the mandibles working into the buccal cavity; (2) by the gastric mill in the cardiac stomach and (3) partly by the mandibles and partly by the gastric mill. In all the Brachyura examined by me, it is the gastric mill which brings about mastication of food, the mandibles being ill-adapted for such function.
A definite masticatory mechanism, either in the form of powerfully toothed mandibles working in the buccal cavity or as a gastric mill in the cardiac stomach, is necessitated by the quality of the food material and the nature of the digestive and absorptive processes. Why is it that in Brachyura the masticatory mechanism is situated deep in the interior of the cardiac stomach and not in the buccal cavity as it is in the Caridoid Macrura?

While refuting Pütter's theory (1904) that marine animals obtain a considerable part of their total nourishment in the form of dissolved organic matter, Benjamin, Edie, Moore and Whitley (1914) have pointed out that "larger animals have either so distributed themselves along the pathways and situations of a richer supply of food, or actively followed an equable distribution of food so as to enable themselves to live upon richer zones of minute organisms, or captured other animals of greater size than minute plankton, which in turn fed upon microscopic plankton or upon vegetation along the shore or on the sea bottom." In following such pathways along which food material was to be found in abundance, Brachyura came to choose the habitat of rocky, sandy or muddy bottoms, and adapted by having flattened bodies, heavily armoured skeletons, long straddling legs capable of gripping flat stones and by having developed crawling and climbing habits. It should be noted that all Decapoda which have more or less developed such features and habits, e.g., lobsters, hermit-crabs and crabs, are characterised by the presence of the gastric mill. Indeed, it may be said that the presence of a gastric mill is a characteristic feature of the sub-order Reptantia (Boas, 1880 and Borradaile, 1907), which includes these groups of Crustacea.

The universal presence of the gastric mill in Brachyura can also be explained with reference to the phylogeny of the crabs. It is generally believed that lobsters are derived from prawn-like swimming ancestors which had lost some of their agility and had developed a heavy armour, retaining, however, the power of sudden and rapid motion in case of emergency. Crabs are derived from lobster-like ancestors which had totally lost even this power of rapid motion and had taken to slow locomotion by crawling and climbing (Calman, 1911). It may therefore be said that the gastric mill is a legacy from the lobster-like ancestors in which the gastric mill is usually well developed.

Apart from these considerations, the presence of the gastric mill in all Brachyura is well suited to their habits and habitats. Crabs are characterised by having resorted to various masking adaptations. Shore crabs, e.g., Carcinus and Cancer, lurk in crevices of rocks or hide themselves behind
Gastric Mill in Decapoda

These sponge crabs. *Dorippe* holds a bivalve shell or a leaf over its carapace by its modified hind legs and thus masks itself. *Dromia* puts on a coat of living sponges over its carapace. Spider crabs disguise themselves under a cover of sea weeds. A large number of crabs, e.g., *Matuta* and *Corystes*, burrow themselves in deep sand or, as in *Cardisoma* and *Paratelphusa*, in wet earth. These masking habits subserve a double function (1) of securing the prey, and (2) of adaptation to protect the crabs from their powerful enemies, e.g., marine forms of Octopus or predaceous Cods. Hypnosis, i.e., cessation of activity when the animal is disturbed, has been very often observed in crabs. Similarly, autotomy, the power of shedding a limb and the subsequent regeneration have reached their highest development in this group of animals. In the walking legs, there is a definite breaking plane and a valvular mechanism situated in the middle of basi-ischium. Regeneration begins immediately by the rapid growth of the epithelial cells grown over the exposed surface and the new limb lies folded upon itself. Following the next moult, it at once expands and grows very rapidly to its normal size (Paul, 1915). The purpose of self-amputation in crabs, as pointed out by Paul, is the prevention of haemorrhage produced by the crushing of limbs by the movements of stones.

The wide prevalence of masking adaptations, hypnosis and autotomy and regeneration indicate that in spite of their heavy armour and powerful pincers, crabs lead a very uneasy life, being in constant fear of their enemies or changes in the environment. Such wary and alert life must necessitate a hurried swallowing of food thrust into the buccal cavity, leaving its complete mastication to be carried out by the deeply-seated gastric mill.

I am grateful to the Nagpur University for having given me a research scholarship which alone has made this and my previous work possible.


In all the Brachyura examined, the gastric mill is universally present.

The gastric mill is essentially typical in all cases. A comparative account of the principal ossicles of the gastric mill together with a short account of other associated structures, concerned in the process of alimentation of food, is given.

The invariable presence of the gastric mill and of simple mandibles is explained with reference to

(a) the constant presence of similar structures in other groups of Decapoda Crustacea constituting the sub-order *Reptantia*,

(b) the belief that crabs are derived from lobster-like ancestors and, therefore, the gastric mill may be a legacy from such lobster-like ancestors,
(c) the various protective adaptations of crabs which indicate their wary and alert life necessitating hurried swallowing of food, leaving its mastication to the deeply-seated gastric mill.

REFERENCE LETTERS.

- **c.p.v.**.. Cardiac pyloric valve.
- **ex.p.**.. Exopyloric ossicle.
- **l.a.t.**.. Lateral accessory tooth.
- **l.t.**.. Lateral tooth.
- **m.a.**.. Mesocardiac ossicle.
- **m.t.**.. Median tooth.
- **p.**.. Pyloric ossicle.
- **p.r.p.**.. Prepyloric ossicle.
- **p.l.c.**.. Pterocardiac ossicle.
- **u.c.**.. Urocardiac ossicle.
- **z.c.**.. Zygoocardiac ossicle.

EXPLANATION OF FIGURES.

The ossicles of the gastric mill all viewed on the same plane. Inner view.

- **Fig. 1.** *Platymnus hirtellus*.
- **Fig. 2.** *Neptunus sanguinolentus*.
- **Fig. 3.** *Dromia rumphi*.
- **Fig. 4.** *Coryphes cassivelanus*.
- **Fig. 5.** *Macropraus longirostris*.
- **Fig. 6.** *Graspus strigosus*.
- **Fig. 7.** *Matuta victor*.
- **Fig. 8.** *Cardisoma carnifex*.
- **Fig. 9.** *Lambrus*.
- **Fig. 10.** *Cancer pagurus*.
- **Fig. 11.** *Philyra globosa*.
- **Fig. 12.** Inner view of the "head" of the mandible:
  - A. *P. hirtellus*.
  - B. *N. sanguinolentus*.
  - C. *D. rumphi*.
  - D. *C. cassivelanus*.
  - E. *M. longirostris*.
  - F. *G. strigosus*.
  - G. *M. victor*.
  - H. *C. carnifex*.
  - I. *Lambrus*.
  - J. *C. pagurus*.
  - K. *P. globosa*.

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*Gastric Mill in Decapoda*